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Sedimentation rates in a suspended mussel farm (Great-Entry Lagoon, Canada): biodeposit production and dispersion

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ABSTRACT: Experimental and field studies were carried out to characterise biodeposit dynamics in a suspended mussel *Mytilus edulis* L. farm in Great-Entry Lagoon, eastern Canada. We assessed: (1) the quantity and quality of biodeposits produced by different age classes of mussels, (2) the size-dependent sinking velocity of faeces and (3) the variation in sedimentation rates at different spatial and temporal scales. Individual 0+ mussels produced on average only 63 % of the mass of biodeposits (32.4 mg dry wt d^{-1} ind.$^{-1}$) that 1+ mussels did (51.5 mg dry wt d^{-1} ind.$^{-1}$). In contrast, the amount of biodeposits produced per unit body weight (dry weight of soft tissue) was greater for 0+ than for 1+ mussels. Faecal pellet sinking velocity ranged from 0.27 to 1.81 cm s^{-1} for mussels ranging in size from 3 to 7 cm, and was best correlated with faecal pellet width. Sedimentation rates were greater within the farm than at reference sites, supporting the hypothesis that mussel farming increases sedimentation rates. Variations in sedimentation were also observed at small spatial scales and through time. Prior to the harvesting of 1+ mussels, sedimentation rates directly under the 1+ mussel lines were about twice those 10 m distant, between the lines, and in other zones (reference sites and sites in the lease with 0+ mussels). These observations and sedimentation patterns along transects leading away from the mussel farm suggest that biodeposits from the farm are not dispersed broadly. The estimated initial dispersal of faecal pellets ranges from 0–7.4 m (1+ mussels) to 7–24.4 m (0+ mussels).

KEY WORDS: Faeces · *Mytilus edulis* · Aquaculture · Biodeposit production · Sinking velocity · Sedimentation rates · Dispersion · Spatial scale

INTRODUCTION

Aquaculture production of fish, shellfish and algae is increasing worldwide, with greater volumes and varieties of species being produced. Thus, there are increasing concerns about the ecological effects of this industry, especially in coastal areas where the bulk of the production is located. To date, most research on aquaculture–environment interactions has focused on finfish (see reviews by Black 2001, Hargrave 2005). The influence of this type of culture is often considerable because of the great biomass that is often grown in small areas, the addition of external feed and the use of antibiotics. The accumulation of organic wastes under fish cages may induce local organic enrichment, potentially leading to increased oxygen uptake, ammonium release and changes in benthic community structure (Hargrave 2005). In contrast to finfish aquaculture, research on bivalve aquaculture–environment interactions is relatively scarce (see review by Kaiser et

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al. 1998). This may be partly due to the general perception that bivalve aquaculture has less dramatic environmental effects than does finfish aquaculture, as bivalves are grown at comparatively low biomass per unit area and feed is not added to the environment. However, bivalve farms are typically much more extensive than fish farms, at times covering many square kilometres. In Canada, the most important bivalve in production, in terms of biomass (22 857 t in 2004), is the mussel *Mytilus* spp. (statistics of the Department of Fisheries and Oceans Canada retrieved January 2006 from www.dfo-mpo.gc.ca/communic/statistics/aqua/aqua04_e.htm). In order to ensure the sustainable development of the mussel industry, a better understanding of the relationship between mussel production and its influence on the benthic environment is needed.

Bivalves produce faeces and pseudofaeces, hereafter collectively referred to as biodeposits, which are large compacted aggregates of particles (0.5 to 3 mm) that sink more rapidly than their constituent particles (Haven & Morales-Alamo 1966), thereby increasing sedimentation rates within bivalve culture sites (Dahlbäck & Gunnarsson 1981, Hatcher et al. 1994). Although some studies have not detected biodeposit-related responses at bivalve culture sites (Crawford et al. 2003, Danovaro et al. 2004), others have shown that the accumulation of biodeposits may lead to enhanced sulphate reduction (Dahlbäck & Gunnarsson 1981), enhanced ammonium release (Hatcher et al. 1994) and structural changes in the resident microbial (Mirto et al. 2000), meiofaunal (Mirto et al. 2000) and/or macrofaunal (Mattsson & Lindén 1983, Kaspar et al. 1985, Hartstein & Rowden 2004) communities.

Although biodeposition may play an important role in pelagic–benthic coupling, few studies have paid attention to the dynamics of biodeposition. Little is known about biodeposit quality (Navarro & Thompson 1997), biodeposit production rates (Kautsky & Evans 1987), or their potential for dispersion (Miller et al. 2002, Giles & Pilditch 2004, Hartstein & Stevens 2005). Further, empirical relationships between biodeposit size and sinking velocity are poorly estimated by simple sinking velocity equations, such as Stoke's law, as has been shown by Chamberlain (2002) and Giles & Pilditch (2004). A better understanding of the relationship between these factors is necessary in order to make accurate predictions of benthic loading and subsequent effects on the local environment (Henderson et al. 2001).

In the present study, we evaluated various parameters relating to the production and dispersal of biodeposits by cultured mussels in Great-Entry Lagoon, Magdalen Islands, eastern Canada. The work was done throughout the summer, when biodeposit production is likely to be maximal (Hatcher et al. 1994). Specifically, we assessed: (1) the quantity and quality of biodeposits produced by different age classes of mussels, (2) the size-dependent sinking velocity of faeces and (3) the variation in sedimentation rates at 3 spatial scales: among different zones within the lagoon (large scale), within the mussel culture site (small scale), as well as around the site (spatial extent). This work is part of a larger collaborative study to determine the benthic carrying capacity of sites for mussel farming.

MATERIALS AND METHODS

Study site. This study was carried out from June to September 2003, in Great-Entry Lagoon (GEL) in the Magdalen Islands, eastern Canada (47° 37′ N, 61° 31′ W) (Fig. 1). The GEL has an approximate length of 25 km and a surface area of 58 km^2. The environmental conditions in GEL have been described in past studies (Auclair 1977, Mayzaud et al. 1992, Koutitonsky et al. 2002). The GEL is characterised by an average tidal range of 0.58 m at its entrance and is covered by ice during the winter (Koutitonsky et al. 2002). Temperature increases from 8°C in June to an average maximum of 20°C during the third week of August and then decreases to 9°C by October (Myrand 1991). Seasonal salinity within the lagoon ranges from 25 to 31.5‰ (Poirier & Myrand 1982). Mean currents in GEL are weak, with typical speeds of 5 cm s^{-1} and occasionally increasing to 10 cm s^{-1} during strong wind events, resulting in a well-mixed water column (Koutitonsky et al. 2002). An 8 m deep navigation channel separates the GEL into a shallow (1 to 3 m) sandy area to the west and a deeper (5 to 7 m) muddy basin to the east where the mussel farm is located (Fig. 1). Mussels *Mytilus edulis* L. are cultured on longlines in a 2 yr grow-out cycle at a density of approximately 575 mussels m^{-1} of mussel line. Longlines are separated by 20 m. The farm currently produces 180 t yr^{-1} and has been in operation since the 1980s. The mussel culture site covers a 2.5 km^2 area and is divided into 2 zones, one with 0+ and the other with 1+ mussels, the latter are replaced by juveniles each fall following harvest. Mussels in the region spawn between May and August, and spat recruitment starts at the end of June and lasts about 3 mo. During this study, 0+ and 1+ mussels were ca. 11 to 14 and 23 to 26 mo old, respectively.

Environmental conditions. Wind direction and speed were obtained from the Environment Canada meteorological station located at Grindstone, ca. 35 km southwest of GEL (Fig. 1). A 500 kHz SonTek acoustic Doppler current profiler was moored 500 m southwest of the mussel lease (Fig. 1) between June and October

2003. The upward-facing instrument was mounted on a frame set on the seabed and measured current speed and direction in pulse-coherent mode in 20 equally spaced cells of 0.25 m thickness from 0.6 to 5.6 m above the bottom. Measurements were averaged over 2 min at 20 min intervals. Temperature, salinity and chlorophyll *a* (chl *a*; fluorescence) were measured using a YSI-6600-EDS (yellow spring instruments) multi-parameter probe, moored within the mussel lease, i.e. a site within a farmer has exclusive rights to farm mussels (Fig. 1). Suspended particulate matter (SPM) concentration and quality (percent organic matter, %OM) were quantified within a collaborative study with Dr. Suzanne Roy (Université du Québec à Rimouski, Canada). Water samples were collected weekly at depths of 1 and 4 m at the YSI station (Fig. 1) and filtered through pre-burned and pre-weighed glassfibre filters (Whatman GF/F, 0.7 µm). Filters were then analysed as outlined in the 'Biodeposit production and quality' section.

Biodeposit production and quality. Biodeposition by the 0+ and 1+ mussel cohorts was measured *in situ* by placing a fixed number of mussels within cylindrical vexar cages fitted into the top of sediment traps for periods of 24 h. The sediment traps were constructed from PVC tubing (10.2 cm diameter, 76.2 cm height), with a funnel at the base leading to a 250 ml sampling bottle. The experimental design consisted of 5 treatments: 0+, 1+, $0+_{shell}$, $1+_{shell}$ and a control without mussels. Each treatment had 3 replicates on each trial date (14 to 15 August, 18 to 19 August, 21 to 22 August). Traps were deployed in an array 800 m from the mussel site at a depth of 7 m (Fig. 1). Live mussels were used in the 0+ and 1+ treatments, while the $0+_{shell}$ and $1+_{shell}$ treatments consisted of only mussel shells. The number of mussels used ensured that about 2/3 of the cage area was covered by a layer of mussels. Thus, for the 0+ cohort, each cage contained 6 mussels measuring 3.0 to 4.5 cm in length and, for the 1+ cohort, each cage contained 3 mussels measuring 5.5 to 7.0 cm. These size ranges were selected based on preliminary field measurements of mussels on mussel lines at that time. For the $0+_{shell}$ and $1+_{shell}$ treatments, mussels were boiled, the tissue removed and the valves glued together leaving an opening similar to a natural gape. The shell treatments were used because sedimentation rates may be altered by the mussel shells physically blocking a part of the trap area and modifying the hydrodynamics at the trap entrance. A further control, without mussels, was also used to measure background sedimentation rates.

After 24 h, sediment traps were retrieved and the contents filtered through pre-burned and pre-weighed

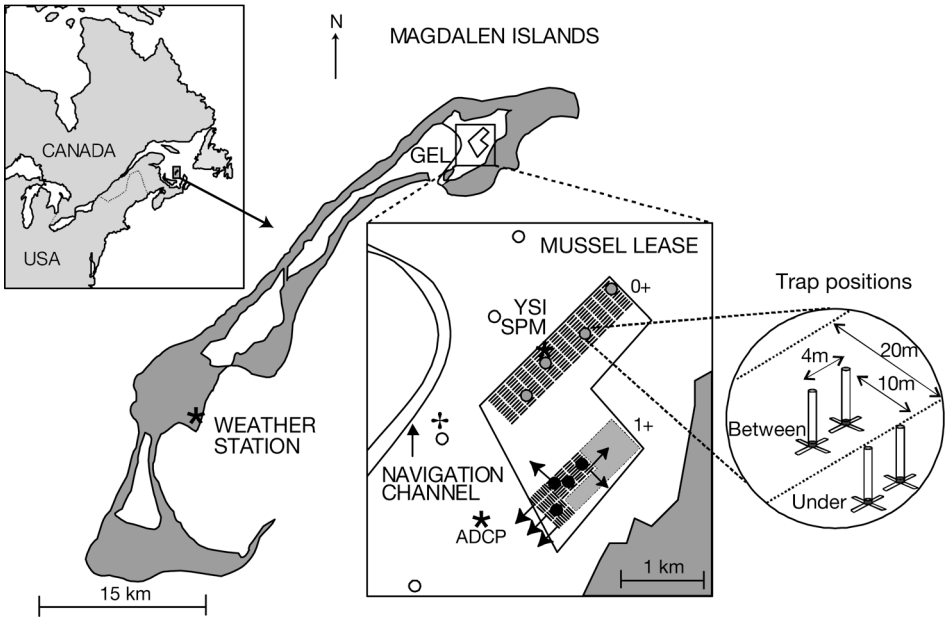

Fig. 1. Location of the mussel farm (polygon) studied in Great-Entry Lagoon (GEL) in the Magdalen Islands, Canada. The farm is divided into 2 zones based on age classes: 0+ and 1+. Mussel lines are indicated by hatched rows and the area of harvested mussel lines (1+ zone) is light grey. Inset shows position of sediment traps within a site. Dotted lines in inset represent mussel lines and traps are shown in positions directly 'under' and 'between' the lines. Sampling sites (4 sites per zone) are indicated for: 0+ (◎), 1+ (●) and reference sites (○). The sites indicated on the map represent an example of the sampling design for 1 sampling date; positions differed on each of the 6 sampling dates. Black arrows represent transects, which were placed perpendicular (except for the NE direction) to the last mussel line on each side of the 1+ zone. (*) Positions of the YSI (Yellow Springs Instruments) multi parameter probe, ADCP (acoustic Doppler current profiler), water sampling site suspended particulate matter determination (SPM) and weather stations; B: site for the biodeposit production experiments

glassfibre filters (Whatman GF/F, 0.7 µm). Swimmers seen by the naked eye were rinsed to remove any particles adhering to them and then discarded. Filters were rinsed with ammonium formate, dried at 65°C for 72 h to constant weight and weighed. The %OM in the sedimented material was calculated as the weight loss of dried material combusted at 450°C for 5 h (Byers et al. 1978). Sub-samples of sedimented material from control traps without mussels and faecal pellets from traps with mussels were transferred with a Pasteur pipette to glassfibre filters (Whatman GF/F, 0.7 µm) for CHN (carbon, hydrogen and nitrogen) analysis on a Perkin-Elmer 2400 elemental analyzer.

Biodeposition was calculated as the amount of material collected in sediment traps with mussels minus the average sedimentation obtained in the corresponding shell controls. Biodeposition was then divided by the number of individuals in each trap to obtain an average biodeposit production per individual. Biodeposit production was also expressed in relation to mussel weight. Mussels were weighed to measure the fresh wet weight (WW), dried at 65°C and weighed to obtain tissue and total mussel dry weights (DW).

Biodeposit sinking velocities. The sinking velocity of faecal pellets was measured to estimate the dispersal of mussel biodeposits in GEL. Faecal pellets were collected for 5 size classes of mussels (3, 4, 5, 6 and 7 cm shell length) using sediment traps deployed for 24 h, as described in the previous section (3 mussels $trap^{-1}$). The sinking speed of individual faecal pellets was measured in a cylindrical glass sinking column (45 cm height, 10.5 cm diameter) filled with filtered (0.7 µm) seawater (21 ± 1°C, 28 psu) collected the same day. The contents of each sampling bottle were carefully transferred to a Petri dish. Individual faecal pellets were randomly chosen, measured (length and width) and transferred to the sinking column using a Pasteur pipette. Faeces were gently introduced just below the water surface, and the sinking velocities were measured by timing the decent between 2 marks, 10 cm apart, the first of which was 7 cm below the water surface. Preliminary tests showed that constant speed was attained and that a distance of 13 cm from the bottom of the sinking column was sufficient to avoid any influence from the bottom of the column on sinking velocity. The dimensions and sinking speed of at least 25 randomly chosen faecal pellets were measured for each mussel size class.

No pseudofaeces were observed in the samples. However, as the SPM concentration at which pseudofaeces are first produced is approximately 4.5 to 5 mg l^{-1} (Widdows et al. 1979), it is possible that pseudofaeces were produced in low quantities and were perhaps present but undetected in the flocculated sedimented matter. For consistency with other studies, we use the term 'biodeposits' throughout the text, except when referring specifically to faecal pellets.

Sedimentation rates. Sedimentation rates were evaluated at 3 spatial scales: among zones within the lagoon (large scale), within the mussel farm (small scale) and around the farm (spatial extent). Sedimentation rates were evaluated using sediment traps, made from PVC tubing (50 cm height, 5 cm diameter) with clear PVC bases to allow for visual inspection. The 10:1 height:diameter ratio was chosen to limit the resuspension of particulate matter within the trap (Gust & Kozerski 2000). The traps fit into bases made of flat steel crosses, with a plastic pipe cap to allow for easy deployment and retrieval. Bases were installed on the bottom at least 24 h before deploying the sediment traps, to avoid contamination by resuspended matter. Sediment traps were deployed for 24 h, and no preservatives were used.

To evaluate large-scale effects, sediment traps were deployed at each of 4 sites within the 0+ and 1+ zones of the farm, as well as at 4 reference sites (R), located at least 500 m from the mussel farm (zone) on each sampling date. In all cases, sampling sites were randomly selected within each zone on each sampling date to ensure the independence of the data. Small-scale effects were evaluated by deploying pairs of sediment traps, separated by 4 m, directly under mussel lines with a further pair of traps 10 m NW of these, directly between mussel lines (position, Fig. 1). Thus, SE and NW positions at reference sites correspond to 'under' and 'between' positions in 0+ and 1+ zones. To evaluate if the patterns observed at the large scale were simply site-related differences and not related to aquaculture activities, we made use of a 'natural' experiment. Mussels in the 1+ zone were scheduled to be harvested in mid-August 2003; we divided our sampling effort to sampling before and after this time (Periods 1 and 2, respectively). Thus, sampling was done on 3 dates before and 3 dates after the scheduled 1+ harvest. It was predicted that sedimentation rates would change from 1+ > 0+ > R before the harvest to 0+ > 1+ = R after the harvest, thus showing the influence of aquaculture and discounting site effects. It was further predicted that $1+_{under} > 1+_{between}$ in Period 1 but that $1+_{under} = 1+_{between}$ in Period 2, following harvesting. However, some 1+ mussels were not harvested in August, but the planned sampling design was respected, and sediment traps were placed under lines without mussels, keeping in mind that 1+ mussels were still in this zone.

The spatial extent of biodeposition was evaluated using the sediment traps described above and set up along transects extending away from the mussel farm. Paired sediment traps, separated by 4 m, were positioned at distances of 0, 3, 6, 12, 15 and 30 m along transects placed perpendicular to the edge of the mussel farm and usually

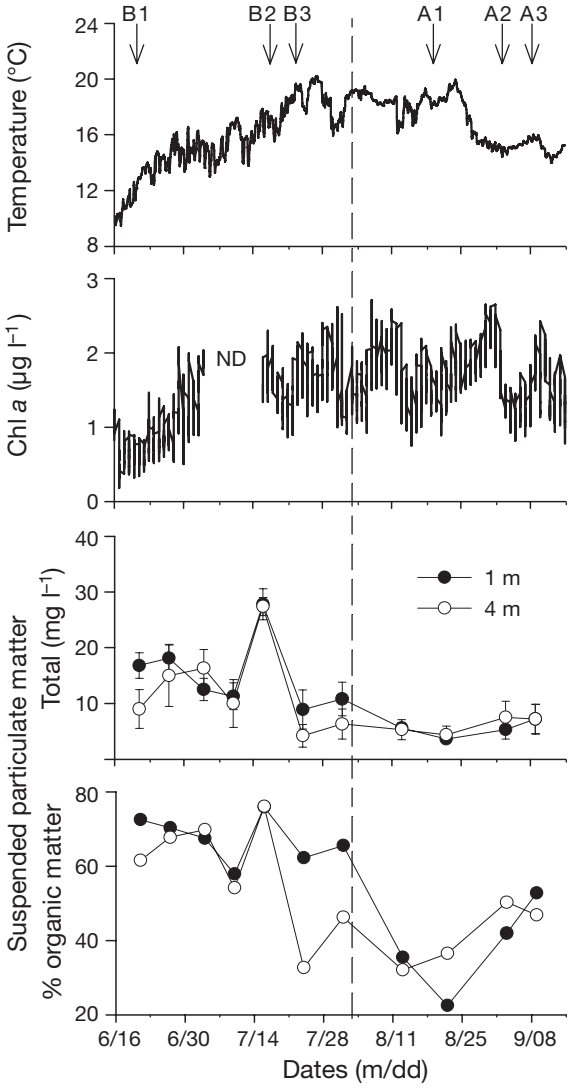

Fig. 2. Time series of environmental data on temperature, chlorophyll *a* and suspended particulate matter (total and % organic matter) in 2003. ● and ○: samples that were collected at a depth of 1 and 4 m, respectively; B1, 2, 3 and A1, 2, 3: sampling dates (B) before and (A) after the 1+ mussel harvest (dashed line); ND: no data

to the mussel lines themselves. To evaluate the spatial variation in along-transect sedimentation rates, we first measured sedimentation rates along 3 parallel transects separated by 100 m and all oriented in the direction of the dominant SW current on 2 to 3 August (Fig. 1). To evaluate the dispersion of biodeposits around the farm, sedimentation rates along transects leading from each of the 4 sides of the 1+ zone were measured on 13 to 14 August (Fig. 1). As differences were not observed among the 3 transects in the same direction (see 'Results'), transects were not replicated in the different directions. Following a 24 h deployment, sediment traps were retrieved and the contents analysed as outlined in the 'Biodeposit production and quality' section.

Statistical analyses. The relationship between: (1) mussel DW and WW, (2) mussel size and biodeposit production, (3) mussel size and faecal pellet size, and (4) faecal pellet size and sinking velocity were evaluated by linear regression using SYSTAT. Variations in biodeposit production between dates were evaluated by ANCOVA, with mean mussel mass as the covariate using SYSTAT on $\log_{10}$-transformed data. Variation in sedimentation rates was evaluated using ANOVA followed by Student–Newman–Keuls (SNK) multiple comparison tests (Underwood 1997). Data for sedimentation along transects in different directions was $\log_{10}$-transformed prior to analysis by ANOVA to satisfy the assumptions of the statistical model. Balanced ANOVA models were assessed using GMAV, unbalanced models, by using SYSTAT.

RESULTS

Environmental conditions

The temporal variations of temperature, chl *a*, and SPM concentration and quality are given in Fig. 2. During the sampling period, temperature varied from 10°C in early June to a maximum of 20°C at the end of July. Salinity varied only slightly, ranging from 30.4 to 30.8‰ (data not shown). Chl *a* concentration increased from 0.2 µg l^{-1} at the beginning of the study and ranged between 1.0 and 2.7 µg l^{-1} from July to September. SPM concentrations ranged between 9.0 and 27.4 mg l^{-1} from mid-June to mid-July, thereafter decreasing to <10.8 mg l^{-1}. The %OM in SPM was generally high from mid-June to mid-July (54 to 76%) and <53% between mid-August and September.

Biodeposit production and quality

Detailed results on the relationship between *Mytilus edulis* size and biodeposit production are given in Table 1. For brevity, results are expressed in relation to tissue dry weight (see Table 2a for conversions). Shell controls collected less sedimented material than did controls with no mussels (Table 1). We interpret this difference as being due to mussel shells in the $0+_{shell}$ and $1+_{shell}$ treatments having reduced the sedimentation rate by a proportion similar to the physical space they occupied and/or to the shells having altered the hydrodynamics at the trap entrance and thus its collection efficiency. These effects probably also occurred in the 0+ and 1+ treatments, and thus biodeposit production was estimated as the difference between the sedimented material recovered in the 0+ and 1+ treatments and that from the $0+_{shell}$ and $1+_{shell}$ treatments, respectively.

Table 1. *Mytilus edulis.* Biodeposit production measured *in situ* for 2 mussel cohorts (0+ and 1+) and 3 control treatments (cage without mussels, cages with $0+_{shell}$ and with $1+_{shell}$) in Great-Entry Lagoon during 3 sampling periods. Mean mussel length, tissue weight (DW), mass of sedimented material and percent organic matter (%OM, ±SE) are given. 0+ treatments: 6 mussels $cage^{-1}$ (n = 3); 1+ treatments: 3 mussels $cage^{-1}$ (n = 3)

Date/ treatment	Mean mussel length (cm)	Mean tissue weight (g)	Sedimented material (mg d^{-1})	%OM	Biodeposit production rate (mg $ind.^{-1}$ d^{-1})	(mg g^{-1} tissue d^{-1})
14 to 15 August						
Control	–	–	124.6 ± 38.9	12.7 ± 0.5	–	–
$0+_{shell}$	–	–	67.2 ± 23.8	13.7 ± 0.4	–	–
$1+_{shell}$	–	–	71.8 ± 23.3	12.5 ± 3.6	–	–
0+	4.0 ± 1.1	0.4 ± 0.3	241.4 ± 28.5	20.4 ± 0.4	29.1 ± 4.8	80.4 ± 13.7
1+	6.9 ± 0.2	1.4 ± 0.7	204.9 ± 31.6	21.7 ± 1.6	44.4 ± 10.5	31.1 ± 8.1
18 to 19 August						
Control	–	–	105.7 ± 30.3	14.8 ± 0.8	–	–
$0+_{shell}$	–	–	54.0 ± 13.9	17.8 ± 1.8	–	–
$1+_{shell}$	–	–	42.7 ± 14.5	17.8 ± 1.9	–	–
0+	4.5 ± 0.3	0.5 ± 0.1	360.6 ± 151.0	21.0 ± 0.7	51.1 ± 25.2	114.0 ± 65.2
1+	6.7 ± 0.2	1.6 ± 0.3	300.7 ± 103.0	21.9 ± 1.0	86.0 ± 34.3	54.7 ± 16.9
21 to 22 August						
Control	–	–	63.5 ± 33.1	19.8 ± 3.8	–	–
$0+_{shell}$	–	–	39.1 ± 27.2	23.7 ± 6.3	–	–
$1+_{shell}$	–	–	21.6 ± 20.1	28.4 ± 11.3	–	–
0+	5.2 ± 0.3	0.7 ± 0.4	140.9 ± 34.2	23.4 ± 2.0	17.0 ± 5.7	23.6 ± 8.5
1+	6.7 ± 0.3	1.4 ± 0.5	104.8 ± 23.5	24.7 ± 1.4	24.2 ± 7.8	18.3 ± 8.3

Table 2. *Mytilus edulis.* Results of the linear regression analysis of: (a) mussel dry weight (DW) as a function of mussel wet weight (WW), (b) biodeposit production DW as a function of mussel tissue DW on different sampling dates, (c) faecal pellet size as a function of mussel length for 3 to 6 cm mussels, and (d) sinking velocity as a function of faecal pellet size. For all analyses: $y = ax + b$

	Dependent (y)	Independent (x)	a	b	r^2	p	n
(a)	Mussel DW (including shell, g)	Mussel WW (including shell, g)	0.391	0.820	0.965	0.001	27
	Mussel tissue DW (g)	Mussel DW (including shell, g)	0.137	0.255	0.918	0.001	27
(b)	Biodeposit production (log_{10}, mg g^{-1} tissue d^{-1})	Mussel tissue DW (log_{10}, g)					
		14 to 15 August	–0.691	1.625	0.762	0.005	8
		18 to 19 August	–0.809	1.832	0.714	0.001	11
		21 to 22 August	–1.060	1.316	0.656	0.001	7
(c)	Faecal pellet size (mm)						
	Width	Mussel length (cm)	0.222	0.022	0.539	0.000	178
	Length	Mussel length (cm)	1.141	–1.523	0.162	0.000	178
	Area	Mussel length (cm)	2.152	–5.477	0.232	0.000	178
(d)	Sinking velocity (cm s^{-1})	Faecal pellet size (mm)					
		Width	0.589	0.328	0.426	0.000	235
		Length	0.037	0.761	0.128	0.000	235
		Area	0.029	0.783	0.193	0.000	235

The natural background sedimentation rates varied between the 3 sampling dates (Table 1). On the last sampling date, about half the quantity of sedimented material was collected as compared to that on the first 2 dates. Biodeposit production was also temporally variable, but, on average, individual 0+ mussels produced 63% the mass of biodeposits relative to that produced by 1+ mussels (32.4 vs. 51.5 mg DW d^{-1} $ind.^{-1}$, respectively; Table 1). In contrast, biodeposit production per unit mussel biomass was greater for 0+ than for 1+ mussels (72.7 vs. 34.7 mg d^{-1} g^{-1} tissue, respectively). There was a temporally variable but consistent negative linear relationship between mussel tissue DW and biodeposit production (mg DW g^{-1} tissue d^{-1}) (Fig. 3, Table 3).

The %OM collected in the sedimented material was significantly greater in treatments containing live mussels than in controls and shell treatments on the first date (SNK test, data not shown). Between Dates 1 and 3, the %OM increased in the controls, but this trend

was not apparent in the treatments with live mussels (Table 1). CHN analysis of the flocculated sedimented material and faecal pellets indicated that the percent organic carbon was slightly greater in faecal pellets than in naturally sedimented material: 2.4 ± 0.5 vs. 1.1 ± 0.2%, respectively (F = 13.40, p = 0.011). The percent organic nitrogen in faecal pellets and the SPM did not differ (F = 3.857, p = 0.097) and ranged between 0.2 and 0.4%. The average carbon to nitrogen ratio of faecal pellets (7.4) was greater than that of naturally sedimented material (6.1) (F = 8.137, p = 0.029).

Biodeposit characteristics and sinking velocity

Faecal pellets could be seen by the naked eye and were easily differentiated from the flocculated sedimented matter. The faecal pellets were shaped as long half cylinders cut lengthwise, had a grainy texture and were light to dark brown in colour. Mussels produced faecal pellets of varying sizes, ranging from 0.7 to 29.0 mm in length and from 0.3 to 1.8 mm in width. Of the 3 measures of faecal pellet size evaluated, mussel size best predicted pellet width (Table 2c). Overall, larger mussels produced larger faeces. However, 7 cm mussels were an exception to this trend (see Table 4) and were thus not included in the correlation between mussel size and faecal pellet size given in Table 2c. Variation in sinking velocity was best explained by faecal pellet width, although surface area and length also explained significant but lesser proportions of the variance in sinking velocity (Table 2d). The relationship between sinking velocity and faecal pellet width is given in Fig. 4. Minimum and maximum sinking velocities were 0.27 and 1.81 cm s^{-1}, respectively

Table 3. *Mytilus edulis.* ANCOVA examining the influence of sampling date and mussel size (dry weight of soft tissues) on the production of biodeposits. All data were log_{10}-transformed prior to analysis: (a) analysis to test the assumption of equal slopes (i.e. the interaction effect) and (b) analysis to test for main effects, with the variance associated with the interation effect pooled with the residual error. Bold: statistically significant values

Source of variation	df	MS	F	p
(a)				
Date	2	0.521	19.85	**0.000**
Mass	1	0.825	31.41	**0.000**
Date × Mass	2	0.010	0.37	0.693
Error	20	0.026		
(b)				
Date	2	0.547	22.09	**0.000**
Mass	1	1.295	52.23	**0.000**
Error	22	0.025		

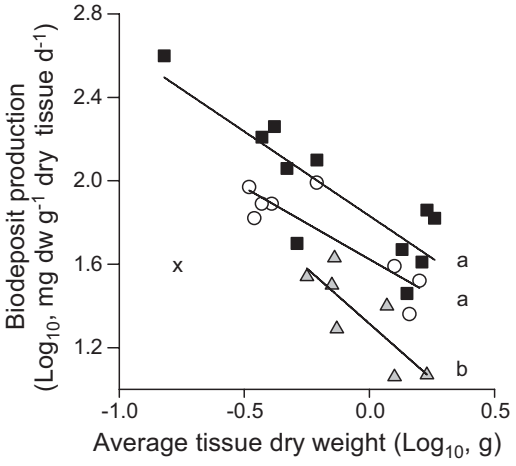

Fig. 3. *Mytilus edulis*. Relationship between biodeposit production and dry weight of mussels on 3 sampling dates: 14 to 15 August (○), 18 to 19 August (■) and 21 to 22 August (△). The 'x' symbol represents an outlier from the 14 to 15 August data. Solid lines represent linear regressions fitted to the log_{10}-transformed data. Regression statistics are given in Table 2b. Daily biodeposit production denoted by different letters are significantly different (pairwise comparison, p < 0.01). ANCOVA analysis is given in Table 3

Table 4. *Mytilus edulis.* Summary of mussel characteristics (mussel shell length and mussel tissue weight, means ± SD), faecal pellet width (mean ± SD) and associated sinking velocities of faecal pellets produced by mussels of different size classes (mean values are ±SD). Several long and folded faecal pellets (denoted by asterisks) were produced by mussels in the 6 cm size class. Parentheses: number of faecal pellets measured in each size class

Mussel size class (shell length, cm)	Mean tissue weight (DW, g)	Mean faecal pellet width (mm)	Sinking velocity (cm s^{-1}) Minimum	Maximum	Mean
3.1 ± 0.1	0.16 ± 0.04	0.62 ± 0.20 (56)	0.27	0.99	0.63 ± 0.17
4.1 ± 0.2	0.37 ± 0.06	0.99 ± 0.24 (67)	0.45	1.67	0.92 ± 0.24
4.9 ± 0.1	0.61 ± 0.07	1.19 ± 0.04 (25)	0.73	1.45	1.04 ± 0.17
6.3 ± 0.1	1.40 ± 0.33	1.16 ± 0.10 (21)	0.73	1.56	1.09 ± 0.21
		1.52 ± 0.19 (9)*	1.17	1.62	1.35 ± 0.16*
7.0 ± 0.1	1.53 ± 0.38	0.91 ± 0.25 (57)	0.50	1.81	0.86 ± 0.25

(Table 4). Long faecal pellets, folded in half, had the greatest sinking velocity.

Field measures of sedimentation rates

The variation in sedimentation rates and the quality of the sedimented material (%OM) throughout the sampling period at large and small spatial scales is given in Fig. 5. On the whole, the results support the hypothesis that sedimentation rates are greatest within

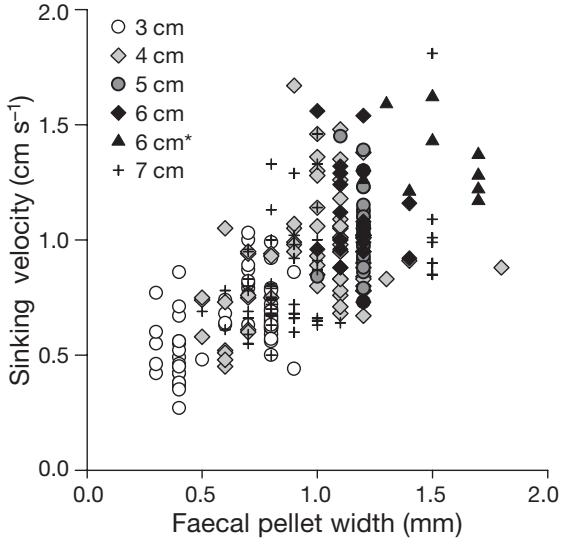

Fig. 4. *Mytilus edulis*. Relationship between the sinking velocity (cm s^{-1}) and faecal pellet width (mm) produced by 5 mussel size classes (6 cm*: faecal pellets from the 6 cm mussel size class that were observed to fold in half while settling). Regression statistics are given in Table 2d

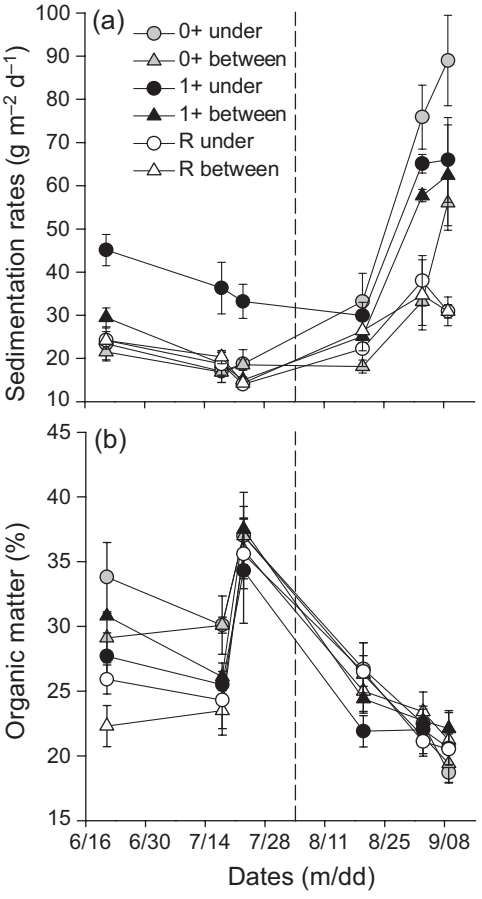

Fig. 5. *Mytilus edulis*. (a) Sedimentation rates (mean ± SE, n = 4 for each value) and (b) %OM of the sedimented material at 1+, 0+ and reference (R) sites, in 2003. Data are given for positions 'under' and 'between' mussel lines, corresponding to the SE and NW positions for reference sites, respectively. The dashed vertical line separates samples from prior to and after the harvesting of the 1+ mussels

Table 5. *Mytilus edulis*. ANOVA results for sedimentation rates and %OM observed within and outside a mussel farm in Great-Entry Lagoon in the summer 2003. Fixed factors were zone (Z), period (Pe) and position (Po). Random factors were site (S) and date (D). See 'Materials and methods' for details. Statistically significant values are indicated in **bold**

Source of variation	df	Sedimentation rates			% OM		
		MS	*F*	p	MS	*F*	p
Z	2	25705.38	5.90	**0.027**	124.59	2.87	0.115
Pe	1	143033.64	4.89	0.091	4354.90	5.67	0.076
D (Pe)	4	29225.78	23.81	**0.000**	768.26	21.16	**0.000**
Z × Pe	2	10772.33	2.47	0.146	172.82	3.98	0.063
Z × D (Pe)	8	4360.46	3.55	**0.002**	43.38	1.19	0.320
S (Z × D [Pe])	54	1227.50	4.90	**0.000**	36.32	3.37	**0.000**
Po	1	23912.96	23.13	**0.009**	2.80	0.20	0.675
Po × Pe	1	2812.63	2.72	0.174	11.97	0.87	0.403
Po × D (Pe)	4	1034.05	2.14	0.088	13.72	1.01	0.409
Po × Z	2	7139.84	16.78	**0.001**	55.58	4.70	**0.045**
Po × Z × Pe	2	11756.31	27.62	**0.000**	11.51	0.97	0.418
Po × Z × D (Pe)	8	425.60	0.88	0.539	11.82	0.87	0.545
Po × S (Z × D [Pe])	54	483.36	1.93	**0.001**	13.54	1.26	0.144
Error	144	250.33			10.77		

the culture area with 1+ mussels (significant position × zone × period interaction; Table 5). During the first period, sedimentation rates directly under the mussel lines in the 1+ zone were almost twice those observed in other zones and positions (Fig. 5a). In contrast, sedimentation rates for $1+_{under}$ and $1+_{between}$ did not differ after harvesting. An overall increase in sedimentation rates was observed at all positions and in all zones throughout the sampling period. The increase in sedimentation rates was, however, most pronounced in the 0+ zone (sedimentation rates during Period 2 were 3.5 times greater than those in Period 1). Moreover, differences between positions ($0+_{between}$ vs. $0+_{under}$) were significant only in the 0+ zone during Period 2.

The %OM of sedimented material varied among zones between the 2 periods (Fig. 5b) such that it was typically greatest in the 0+ and 1+ zones during Period 1, but did not differ among sites in Period 2. The %OM of sedimented material tended to decrease in Period 2, although this effect was not statistically significant (Table 5).

Dispersion

The 3 parallel transects deployed perpendicular to the last SW mussel line indicated that along-transect sedimentation rates did not differ significantly among transects (Table 6a). This shows that a single transect is representative of sedimentation patterns for a given direction. The single transects placed in each of 4 different directions (3 of which were used in the statistical analyses) around the mussel farm showed that the dispersion of biodeposits was fairly localised. Regardless of transect direction, sedimentation decreased rapidly along the transects leading away from the mussel farm and became indistinguishable from background levels by about 3 m in the NW direction, 6 m in the SE direction and 12 m in the SW direction (Fig. 6a, Table 6b). The dominant water current direction during the sampling period was towards the SW (Fig. 6b), and this likely explains the pattern of sedimentation at this time. The NE transect, which unlike all other transects continued in the same orientation as the mussel line, was not included in the statistical analyses.

Table 6. ANOVA examining along-transect variation in sedimentation rates among transects placed perpendicular to mussel lines: (a) 3 transects oriented in the SW direction and (b) single transects oriented in a SE, SW, or NW direction. The NE transect was not included in the analysis, since it was not perpendicular to the mussel lines. Data were $\log_{10}$-transformed to obtain homoscedasticity. Statistically significant values are highlighted in **bold**

Source of variation	df	MS	*F*	p
(a) Same direction				
Transect	2	44.881	2.42	0.113
Distance	6	84.792	4.57	**0.004**
Transect × Distance	12	14.802	0.80	0.649
Error	21	18.555		
(b) 3 directions				
Direction	2	0.089	13.27	**0.000**
Distance	6	0.103	15.32	**0.000**
Direction × Distance	12	0.018	2.63	**0.025**
Error	21	0.007		

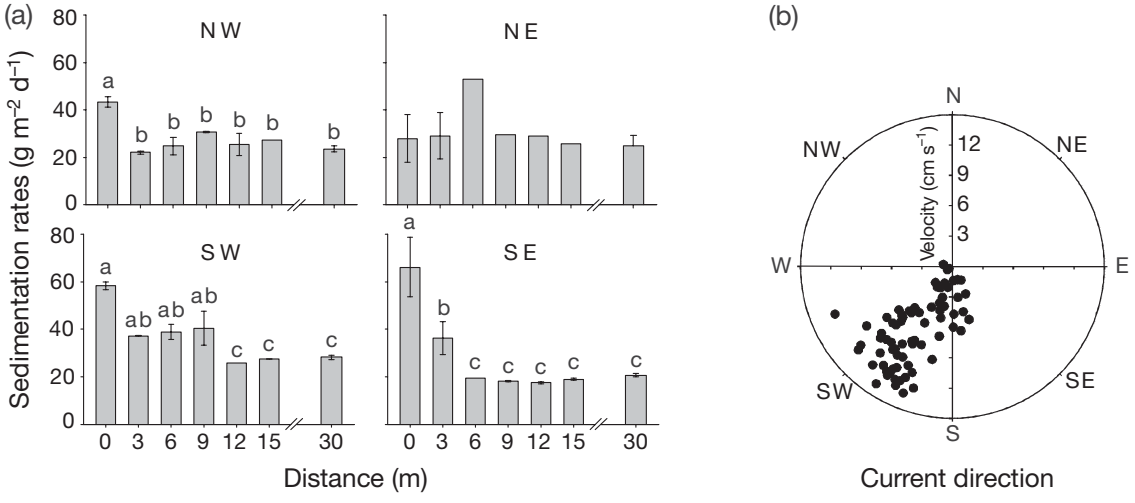

Fig. 6. *Mytilus edulis*. (a) Sedimentation rates (mean ± SE, g m^{-2} d^{-1}) recorded on 13 to 14 August along 3 transects, placed perpendicular to mussel lines and orientated towards the SE, SW, or NW. Results of the corresponding ANOVA are given in Table 6b. The NE transect ran along the same orientation as the mussel line and was therefore not included in the statistical analyses. Differences in sedimentation among distances within a direction are indicated by different letters. (b) Current direction and velocity (cm s^{-1}) 1 m above the bottom during the 24 h sampling period. Black dots: averaged measures recorded over 2 min at 20 min intervals

DISCUSSION

Biodeposit production

This study showed that biodeposit production was a function of *Mytilus edulis* size. The 2 mussel cohorts differed in terms of their biodeposit production, with 1+ mussels producing, on average, 1.6 times more biodeposits than the 0+ mussels. In contrast, the amount of biodeposits produced per unit body weight was greater for smaller mussels than for larger ones. Similar patterns have been reported for *M. edulis* by Tsuchiya (1980) and for other suspension-feeding bivalves, including the oyster *Crassostrea virginica* (Haven & Morales-Alamo 1966) and the lamellibranch *Laternula elliptica* (Ahn 1993). This has been explained by the higher clearance rates of younger mussels compared to older ones (Tsuchiya 1980). Physiological rates are an allometric function of body size and thus decline with the relative body surface area available for oxygen diffusion, which decreases with respect to body size as the organism grows (Hawkins & Bayne 1992).

Biodeposit production differed between sampling dates, and this may be related to changes in food quantity and quality, as has been observed in previous studies (Tenore & Dunstan 1973, Navarro & Thompson 1997). The quantity of naturally sedimented matter on the first 2 sampling dates was almost twice that on the third date. This could suggest a difference in seston concentration on these dates. Although seston concentration data were not available for these specific dates to support this hypothesis, there was a general decrease in SPM concentration between 13 and 22 August from 5.6 ± 1 to 3.6 ± 0.5 mg l^{-1} (1 m depth), which may explain the observed variations in biodeposit production. Some studies have shown a positive relationship between biodeposit production and temperature (Tsuchiya 1980, Kautsky & Evans 1987), and/or salinity (Widdows 1985). However, variation in temperature and salinity were probably not responsible for the observed differences in biodeposit production, as both were relatively stable throughout the sampling period. Although several studies have shown relationships between environmental conditions and mussel metabolism, a field study that measured daily seston availability and several environmental parameters showed that these factors explained only 28% of the variation in daily ingestion rates of mussels (Cranford & Hill 1999). Further, excretion has been shown to vary greatly over small periods of time (8 h) without any apparent relationship with exogenous influences (Hawkins & Bayne 1992). It is thus difficult to identify which factors best explain the observed temporal variation in biodeposit production in this study.

Faecal pellet sinking velocity

As noted by Giles & Pilditch (2004), sinking velocity was best correlated with faecal pellet width. Thus, measures of pellet width are more important for understanding sinking velocity than are other measures of pellet size. Faecal pellet width is related to mussel morphology, whereas pellet length is more a function of current speed (Giles & Pilditch 2004). Thus, mussel size may be used to predict sinking velocities under varying current regimes, allowing for valid estimates of dispersal in the field. In the present study, faecal pellet width was a function of mussel size for mussels in the size range of 3 to 6 cm. However, for unexplained reasons, 7 cm mussels produced smaller faecal pellets.

The average sinking velocity of 1.0 ± 0.3 cm s^{-1} for *Mytilus edulis* faecal pellets measured in this study was about twice that observed by Chamberlain (2002) for 4.2 cm *M. edulis* individuals. Our results were within the 0.2 to 4.5 cm s^{-1} range observed for the mussel *Perna canaliculus* measuring 2.7 to 11.4 cm (Giles & Pilditch 2004). De Jong (1994) reported that faecal pellets of *P. canaliculus* settled at a rate of 1.2 ± 0.1 cm s^{-1}, although the size of the mussels studied was not given and Hartstein & Stevens (2005) reported that faecal pellets from 6 cm individuals of the same species settled at 3.0 ± 0.4 cm s^{-1}. Miller et al. (2002) found sinking velocities for *Atrina zelandica* faecal pellets, ranging from 1.1 to 3.0 cm s^{-1}, but these were from considerably larger individuals (18.5 to 26 cm) than those used in the present study. Variations in sinking velocity are likely due in part to variations in faeces composition. Food quality has been shown to influence faecal pellet density. For example, faecal pellets from mussels fed on diets with a high silt content sank more rapidly than those from mussels fed on mostly algal diets (Chamberlain 2002, Miller et al. 2002, Giles & Pilditch 2004).

Field measurements of sedimentation rates

This study noted significant variations in sedimentation rates at all spatial and temporal scales considered. In general, sedimentation rates were greater within the farm than at reference sites, supporting the hypothesis that mussel farming increases sedimentation rates of SPM (Kautsky & Evans 1987). Our results are in accordance with other studies, which have shown that suspended mussel culture can increase sedimentation by a factor of 1.3 to 5.5 (Hatcher et al. 1994, Stenton-Dozey et al. 1999, Danovaro et al. 2004, Hartstein & Rowden 2004).

As predicted, sedimentation rates were initially greatest directly under the mussel lines in the zone

with 1+ mussels. Further, after these were harvested, sedimentation was greatest in the $0+_{under}$ position, and no differences were observed between $1+_{under}$ and $1+_{between}$ positions. These observations support the hypothesis that the enhanced sedimentation in the 1+ zone was due to the presence of mussels and not due to some other intrinsic feature of the zone. However, during the second period, sedimentation rates in the 1+ zone were still greater than those at reference sites. A combination of easily resuspendable faecal material (Walker et al. 2005) that had accumulated in the 1+ zone and an overall increase of wind strength during August and September may have resulted in sediment resuspension being greater at this time. Moreover, because not all of the 1+ mussel lines had been harvested by the second period, the presence of mussels and the handling of longlines by the mussel grower may have increased overall turbidity in the water column and thus sedimentation rates in the 1+ zone.

That higher sedimentation rates were observed within the 1+ zone than within the 0+ zone prior to harvesting may be explained by the greater biodeposit production (per individual) of 1+ mussels relative to 0+ mussels. Biodeposition from epibiota (such as polychaetes, starfish and hydrozoans), which were more abundant on 1+ than 0+ lines (authors' pers. obs.), may also have contributed to this observation. The increased sedimentation rates observed at the end of August and in September may have resulted from several factors. First, the increase in sedimentation rates, which was more pronounced within the 0+ zone than within the other zones, was probably partly due to the rapid growth of the 0+ mussels, from 2.5 cm in June to >4.5 cm in September (A. Trottet pers. comm.), which would lead to a greater overall production of biodeposits. Second, differences in food quantity and quality may have increased biodeposition rates. Although increased SPM concentrations were not observed in relation to the increase in sedimentation rates, the particulate organic matter decreased from Period 1 (ranging from 5.4 to 20.8 mg l^{-1}) to Period 2 (<3.8 mg l^{-1}). It is possible that mussels increased their filtration rates to compensate for the lower food quality (Bayne et al. 1993) and thus increased their biodeposit production. However, no data on seston composition were available to confirm a relationship between food quality and sedimentation rates.

In addition to large-scale variations, we observed that sedimentation rates were generally greater under than between mussel lines, providing further evidence that mussel biodeposit production increases sedimentation locally. That this effect became more pronounced through the summer for 0+ mussels may be explained by a number of factors. As the 0+ mussels grew, they became heavier, and the lines sank closer to the bottom due to insufficient flotation (authors' pers. obs.). Therefore, biodeposits had less time to sink and thus be dispersed before they were collected by the sediment traps. Further, as the mussels grew, their faeces would tend to get larger and thus have a greater sinking velocity, again enhancing sedimentation under the lines. The presence of more easily resuspended sediments in the mussel lease (Walker et al. 2005) may have increased this effect.

The sedimentation rates measured along the 4 transects around the 1+ zone also show that biodeposit dispersion is limited to about 12 m around the mussel farm. That the sedimentation rates measured between lines and at reference sites did not differ throughout the sampling period further supports the idea that biodeposition is localised. Most studies that have evaluated biodeposit dispersion based on biodeposit settling velocity, water depth and current velocity (Chamberlain 2002, Giles & Pilditch 2004, Hartstein & Stevens 2005) have suggested that dispersion is limited to within about 50 m of the farm site.

Estimated dispersion of mussel biodeposits

A small variation in biodeposit sinking velocity, current velocity, or water column depth may have a significant impact on the extent of biodeposit dispersion (Giles & Pilditch 2004). The potential dispersion of mussel biodeposits in GEL differed greatly between the 2 mussel cohorts. The average summer current speed in GEL was 5.5 cm s^{-1}. Given the average sinking velocity of 0.79 cm s^{-1} for 0+ mussel faecal pellets and the distance between the 0+ mussel lines and the bottom (1 to 3.5 m), the initial deposition may be estimated to be between 7 and 24.4 m. In contrast, faecal pellets from the 1+ mussels sank at an average velocity of 0.97 cm s^{-1}, the distance below 1+ mussel lines was between 0 and 1.3 m and, thus, the initial deposition is estimated to be between 0 and 7.4 m. However, during strong wind events, the current velocity can reach 18 cm s^{-1} and the estimated dispersion of biodeposits may be up to 79.7 and 24.1 m for faecal pellets from the 0+ and 1+ mussels, respectively.

Both the field studies reported here and the simple dispersal estimates suggest that initial deposition of biodeposits is localised to the vicinity of mussel lines. It is obvious that the choice of a site for mussel farming will determine the dispersal potential for the biodeposits produced there. In the Gulf of St. Lawrence region, mussel farms are usually established in relatively shallow coastal areas (e.g. 3 to 5 m; Grant et al. 2005) as compared to other areas (e.g. 8 to 42 m in New Zealand; Hartstein & Stevens 2005) and characterised by low current velocities. All things being equal, the accumu-

lation of biodeposits will be higher in these types of farms than in ones established in areas with deep waters and strong currents (Hartstein & Stevens 2005).

Ecological implications

Given the observed low initial dispersal of biodeposits and that the labile component of mussel biodeposits is degraded very quickly (Fabiano et al. 1994), the potential effects on benthic communities would also be expected to be quite localised. We estimated that during the first half of the summer the flux of OM under the 1+ mussel lines was twice that at reference sites. Several studies have shown that an increase in biodeposition associated with bivalve aquaculture may lead to changes in benthic sediment geochemistry and communities (Dahlbäck & Gunnarsson 1981, Mattsson & Lindén 1983). This also appears to be the case for GEL, as the sediment below mussel lines was organically enriched compared to that at reference sites, and benthic communities were dominated by opportunistic species (Callier et al. 2004).

Results from the present study are part of a larger programme to determine the benthic carrying capacity of mussel aquaculture sites. The spatial extent of aquaculture-related biodeposition and the benthic response to varying levels of biodeposition will be modelled by adapting the DEPOMOD model (Cromey et al. 2002), originally developed for marine cage fish farming, to bivalve aquaculture.

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Multi-scale spatial variations in benthic sediment geochemistry and macrofaunal communities under a suspended mussel culture

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ABSTRACT: The chemical and biological effects of biodeposition from a mussel culture were evaluated at multiple spatial scales during the summer of 2003 in Great-Entry Lagoon, eastern Canada. Sediment samples were collected directly under and between mussel lines (positions 10 m apart: 10 m scale) from multiple sites (located ca. 100 m apart: 100 m scale) in each of 3 zones: reference (R), 0+ and 1+ mussel cohort zones (located at least 500 m apart: km scale). In general, redox potential decreased and sulphide concentration increased with sediment depth but did not differ among zones or positions. A clear difference in macrofaunal community structure was observed among R, 0+ and 1+ zones, as well as between the positions directly under mussel lines in 1+ sites ($1+_{under}$) and those between 1+ mussel lines ($1+_{between}$). The benthic community at $1+_{under}$ positions was dominated by an opportunistic species (*Capitella capitata*) and had the lowest diversity and biomass. 0+ sites were characterised by the greatest number of species and biomass, suggesting that some species have benefited from a moderate organic loading from the 0+ mussels. Historical data indicate that the deeper part of the lagoon was a naturally enriched environment. The mussel farm probably contributes to local organic enrichment. Comparison of benthic communities from the present study (>20 yr after the initiation of mussel aquaculture) in the site to similar historical data from 3 periods (1975 and 1978, before mussel farming; 1982, at the start of farming activities; and 2004, after the 1+ mussel harvest) showed that community structure differed largely because of the greater abundance of deposit feeders in 2003. However, among these 3 periods the differences in benthic community structure were no greater than differences observed between years within the periods.

KEY WORDS: Aquaculture · Biodeposition · Organic enrichment · Redox potentials · Sulphide · Macrofaunal community structure · Spatial scale

INTRODUCTION

Aquaculture production is increasing worldwide, as are concerns about its influence on the environment (see Hargrave 2005). Suspension-feeding bivalves produce biodeposits (faeces and pseudofaeces) that have greater sinking velocities than their constituent particles (Haven & Morales-Alamo 1966). Consequently, bivalve biodeposition may increase sedimentation rates under culture sites (by a factor of 1.3 to 5.5; see Hatcher et al. 1994, Callier et al. 2006, Giles et al. 2006). The accumulation of biodeposits under suspended bivalve culture may lead to local organic enrichment and potentially increased oxygen uptake and ammonium release (Hatcher et al. 1994), sulphate reduction (Dahlbäck & Gunnarsson 1981) and changes in benthic community structure (Mattsson & Lindén 1983, Kaspar et al. 1985).

According to the general model of organic enrichment outlined by Pearson & Rosenberg (1978), macro-

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benthic communities subject to increased organic loading will exhibit decreased species richness, increased abundance because of the dominance of opportunistic species, a decrease of total biomass, and shifts in the dominance of trophic groups (Weston 1990). For example, subsurface deposit feeders are expected to become increasingly dominant with increasing organic enrichment (Pearson & Rosenberg 1978). However, studies on the influence of suspended bivalve culture on the benthic environment do not show consistent effects. While some studies have observed a lower total number of individuals, a lower species richness (Mattsson & Lindén 1983, Kaspar et al. 1985, Chamberlain et al. 2001), and a dominance of opportunistic species at mussel farms compared to reference sites (Chamberlain et al. 2001: Site 2), others have not detected significant differences (Chamberlain et al. 2001: Site 1, Miron et al. 2005). In some cases, 'non classical eutrophication responses,' such as greater Shannon-Wiener diversity index measures and biomass, have been observed at mussel farm sites (e.g. Grant et al. 1995) due to the presence of scavengers attracted by mussel drop-off. Differing effects may be explained in part by site (hydrodynamics, topography, background enrichment, sediment type) and culture (bivalve density, culture depth, mussel size) differences. Together, these factors may influence biodeposit production and dispersion (Giles & Pilditch 2004, Callier et al. 2006) and therefore their potential impact on the benthic environment.

In this study, we evaluated the influence of suspended mussel *Mytilus edulis* L. culture on the chemical and biological benthic environment of Great-Entry Lagoon (GEL), Magdalen Islands, eastern Canada. At this site, Callier et al. (2006) observed that sedimentation rates directly under lines with mussels at least 1 yr old (1+) were twice those in areas 10 m distant, between the lines, and in other zones studied, i.e. sites with mussels less than 1 yr old (0+) and reference sites outside the mussel farm (R). It was predicted that the benthic condition in GEL will vary in relation to observed differences in organic sedimentation. Although several studies have examined the influence of bivalve culture on benthic environments, few have evaluated smaller-scale variations in benthic characteristics within a culture site (1) under long lines vs. between long lines or (2) in areas with juvenile bivalves (i.e. at the beginning of the growth cycle) vs. bivalves of commercial size. Such variation should be taken into account when evaluating the influence of bivalve culture on the benthic environment and when determining the environmental carrying capacity of sites for bivalve aquaculture.

The objective of this study therefore was to determine the influence of the mussel farm in GEL on the benthic environment at several spatial scales: 10 m scale (samples were taken at positions directly under mussel lines and 10 m distant, directly between mussel lines), 100 m scale (among multiple sites separated by ca. 100 m within each of 3 zones), and 1 km scale (among 0+, 1+ and R zones, which are separated by > 500 m). Sites were sampled at the 100 m scale to ensure the generality of the findings in GEL. We assessed effects in terms of both chemical (redox potential, sulphide concentration and percent organic matter [%OM]) and biological (diversity, abundance, biomass, and community and trophic group structure) characteristics. The chemical indicators examined were chosen because these have been described as the most sensitive physicochemical indicators of organic enrichment (Hargrave et al. 1997). Further, we compared the benthic community data from the current study with similar historical data in the study area to evaluate the long-term temporal changes in benthic community structure to better understand the importance of bivalve culture in influencing benthic communities.

MATERIALS AND METHODS

Study site. The mussel farm studied is located in GEL in the Magdalen Islands, eastern Canada (47° 37′ N, 61° 31′ W) (Fig. 1). Detailed environmental conditions in the lagoon are provided in Callier et al. (2006). The farm covers a total surface area of ca. 2.5 km^2, has been in operation for about 23 yr and produces about 180 t of mussels annually. The 1+ mussels attain market size (5 to 6 cm) and are harvested and replaced by juveniles each fall. Thus the farm is divided into 2 zones which are stocked with either 0+ or 1+ mussel cohorts, the age classes in a zone alternating between years. Each zone contains ca. 200, 91 m longlines spaced 20 m apart. Water depth in the sampling area ranged from 5 to 7 m. During the sampling period, average surface temperature and salinity were, respectively, 18°C and 31 psu. The average water current velocity (at 4 m depth) during the summer of 2003 was 5 cm s^{-1} with a maximum of 18 cm s^{-1} (Callier et al. 2006).

Sampling design. The study was conducted in summer (August 2003), when biodeposit production is likely to be maximal (Hatcher et al. 1994). Variations in sediment characteristics and benthic communities were evaluated at 3 spatial scales. At the largest scale (zones separated by at least 500 m: km scale), samples were collected in each of the 2 farm zones (0+ and 1+) and R (Fig. 1). In order to account for natural variation in benthic characteristics, samples were taken in each of 4 randomly chosen sites separated by ca. 100 m within each zone (100 m scale). During the sampling period, we observed that one of the 4 R sites (the most northern

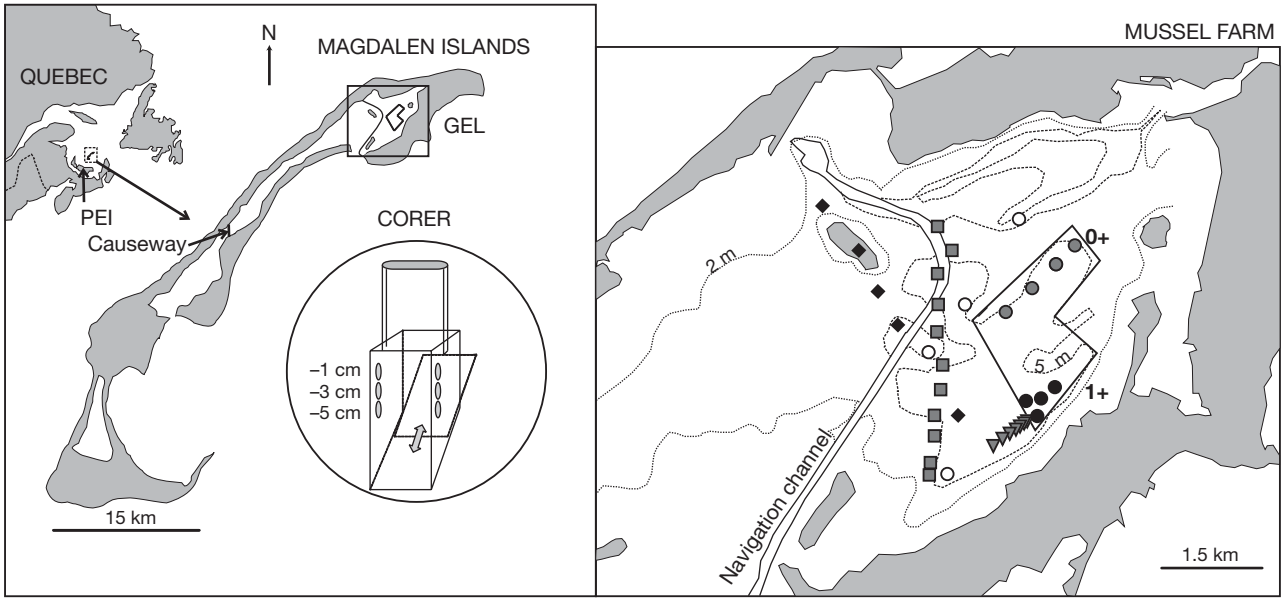

Fig. 1. Mussel farm (dotted polygon) in Great-Entry Lagoon (GEL) in the Magdalen Islands, Canada. The farm is divided into 2 zones based on the age classes of mussels within them: 0+ (less than 1 yr old, ●); 1+ (greater than 1 yr old, ●). ○: reference sites. At each site, 3 core replicates were taken both directly under and between the mussel lines. Sampling sites from historical studies: (◆), 1975; (■), 1978; and (▼), 2004. Sampling sites in 1982 were situated within the mussel farm but their exact positions are unknown. PEI: Prince Edward Island

site) was situated in a depositional zone for detritic seagrass *Zostera marina* and macroalgae. We thus decided to remove this site from subsequent analyses.

To evaluate the small-scale influence of the mussel farm, samples were taken directly under mussel lines (i.e. $0+_{under}$ and $1+_{under}$) and at positions 10 m NW of these, directly between the mussel lines (i.e. $0+_{between}$ and $1+_{between}$). The same sampling design was used at both mussel and R sites to allow for comparisons of small-scale spatial patterns in different zones. Thus, 'under' and 'between' positions in 0+ and 1+ zones correspond to SE and NW positions at reference sites, respectively (i.e. R_{under} and $R_{between}$ positions) . At each position, 3 replicates were sampled using a wedge corer (Fig. 1) with a vertical array of pre-drilled holes in the sides of the corer to take sediment sub-samples at –1, –3 and –5 cm sediment depths to determine chemical sediment characteristics. Samples were taken by SCUBA divers to ensure that the cores were returned to the surface as undisturbed as possible.

Sedimentation rates. Callier et al. (2006) evaluated sedimentation rates in GEL from June to September 2003. In sum, greater sedimentation was observed in the $1+_{under}$ position than in all other positions (which did not differ) in June. This trend changed as 0+ mussels grew and 1+ mussels were harvested to a situation where sedimentation was greatest in $0+_{under}$ positions in August and September.

Sediment geochemical characteristics. Redox potentials (Eh, mV, 2 replicates depth^{-1} core^{-1}) were measured in the field, directly from the sediment core, using a combined reference and platinum redox electrode. The redox probe was calibrated using Zobell's solution. Eh was expressed as mV at ambient temperature relative to a normal hydrogen electrode (Eh_{NHE}). A cut off, 5 ml plastic syringe was pushed through holes at each depth to obtain sediment sub-samples. Sediment sulphide concentration (µM, 2 replicates depth^{-1} core^{-1}) was determined using an Orion® silver/silver sulphide electrode with a combined calomel electrode as reference. A sulphide anti-oxidant buffer solution was added to each sediment sub-sample. The analysis was done in the field and when storage was required for a short period of time (<3 h), samples were placed on ice in the dark. Details of the methodology used are provided in Wildish et al. (1999). Sediment %OM was calculated as the weight loss of dried material combusted at 450°C for 5 h (Byers et al. 1978).

Macrofaunal community analysis. The corer sampled an area of 263 cm^2 to a depth of ca. 15 cm. Samples were gently sieved through a 500 µm mesh. The material retained on the sieve was preserved in a 5% formaldehyde-saline solution. Infaunal specimens were stored in 70% ethanol after sorting. Identifications were done to the lowest taxonomic level possible, usually to species. Sites were characterised in terms of total abundance, total biomass and diversity (number of species per site, S; Shannon-Wiener diversity index, H'; and equitability, J'). The biomass of each species was measured as blotted wet weight. All individuals of

a species in a core were grouped for biomass measurements. Animals were removed from tubes prior to biomass determination but the biomass of molluscs includes their shell weight (Weston 1990).

Statistical analysis. Variations in redox potential, sulphide, %OM and univariate indices of the benthic communities were evaluated using ANOVA followed by Tukey multiple comparison tests with SYSTAT. Data were transformed when necessary to satisfy the assumptions of the statistical model (see Results for details). Nonparametric multivariate analyses of community structure, including multi-dimensional scaling (MDS), and SIMPER analyses (to determine the contribution of each species to the total similarity among samples within a given zone) were performed using PRIMER. Analyses were done using individual cores as replicates. Variation in benthic community structure was evaluated using DISTLM (a distance-based nonparametric multivariate analogue of ANOVA) (Anderson & Ter Braak 2003). Multivariate pair-wise comparisons were done using ANOSIM. Data were √-transformed for all multivariate analyses. Species were classified into trophic groups according to the classification available in the literature (e.g. Word 1990).

Inter-annual comparison. The community structure based on abundance data observed in the present study (following > 20 yr of mussel aquaculture) was compared to similar data from 3 periods: (1) before the farm was established, in 1975 (Bourget 1976, Bourget & Messier 1982: 625 cm^2 grab samples sieved on a 500 µm screen) and 1978 (J. Munro unpubl. data: 560 cm^2 grab samples sieved on a 500 µm screen); (2) at the start of farming activities, in 1982 (Élouard et al. 1983: 625 and 1000 cm^2 grab samples sieved on a 1 mm screen); and (3) after the mussels in the 1+ zone were harvested, in 2004 (M. D. Callier et al. unpubl. data: 78.5 cm^2 core samples sieved on a 500 µm screen). In all but one case (Élouard et al. 1983), the raw georeferenced data was available and provided by the appropriate authors (see Fig. 1). In the case of Élouard et al. (1983), only means of 8 samples from the general area within the present culture site on each of 3 sampling dates (June, August and October) were available from the publication. In all other cases, sampling was done in August. Because of taxonomic inconsistencies among the different data sets, the combined data set was reduced such that each taxa was at the same level of taxonomic resolution. Thus, although most taxa were identified to the species level, some were grouped at higher taxonomic levels (e.g. Capitellidae). For 2003 and 2004, replicate samples within a position were pooled to obtain surface sampling areas that were similar to those sampled in 1975 and 1978 (i.e. 3×263 cm^2 replicates = 789 cm^2 for 2003 and 5×78.5 cm^2 replicates = 392.5 cm^2 for 2004). All data were then transformed to number of ind. m^{-2} prior to analysis. Because of inconsistencies among data sets, trends are only compared graphically (MDS analysis) and with respect to trophic groupings.

RESULTS

Sediment geochemical characteristics

Sediment redox potentials, sulphide concentrations and %OM did not differ among zones (0+, 1+ and R) or between positions (under vs. between), but all measurements varied significantly with depth (Table 1). The greatest sulphide concentrations and the lowest redox potentials were recorded at −3 and −5 cm (Fig. 2). %OM decreased significantly with increasing sediment depth (Table 1, Fig. 2). A uniform black colour was observed throughout all sediment cores.

Table 1. ANOVA results for sulphide concentration (µM), redox potential (Eh_{NHE}, mV) and percentage organic matter (log OM) measured within and outside the mussel farm in Great-Entry Lagoon in the summer 2003. Fixed factors were zone (Z), position (PO) and depth (DE). Random factor was site (SI). See 'Results' for details. Statistically significant values indicated in **bold**

Sources of variations	df	Sulphide (µM) MS	*F*	p	Redox potential (mV) MS	*F*	p	df	log OM MS	*F*	p
Z	2	3152809	1.419	0.304	8951	0.496	0.629	2	0.123	0.815	0.476
SI (Z)	7	2222241	5.386	**0.000**	18064	12.594	**0.000**	8	0.151	13.860	**0.000**
PO	1	870843	0.632	0.453	1088	0.232	0.645	1	0.003	0.500	0.500
DE	2	4575458	16.100	**0.000**	23324	21.072	**0.000**	2	0.064	4.267	**0.033**
Z × PO	2	4081792	2.960	0.117	8370	1.783	0.237	2	0.002	0.333	0.726
Z × DE	4	637374	2.243	0.117	1665	1.504	0.254	4	0.028	1.867	0.166
PO × SI (Z)	7	1378945	3.342	**0.002**	4693	3.272	**0.003**	8	0.006	0.534	0.827
DE × SI (Z)	14	284185	0.689	0.783	1107	0.772	0.699	16	0.015	1.352	0.195
PO × DE	2	184717	0.782	0.477	3485	1.886	0.188	2	0.025	1.667	0.220
Z × PO × DE	4	140119	0.593	0.673	1363	0.738	0.582	4	0.018	1.200	0.349
DE × PO × SI (Z)	14	236309	0.573	0.884	1848	1.288	0.219	16	0.015	1.404	0.168
Error	176	412599			1434			65	0.011		

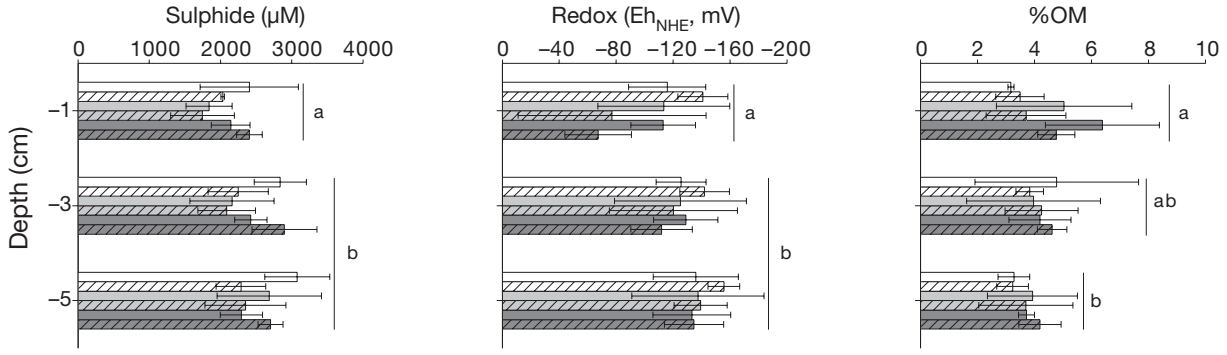

Fig. 2. Sediment depth-specific sulphide concentration (µM), redox potential (Eh_{NHE}, mV) and percentage organic matter (% OM) (average ± SD, n = 3–4). Zones = R (white), 0+ (light grey) and 1+ (dark grey) zones. Positions = under the line (solid colours), between the lines (hatched). Results from the corresponding ANOVAs are given in Table 1

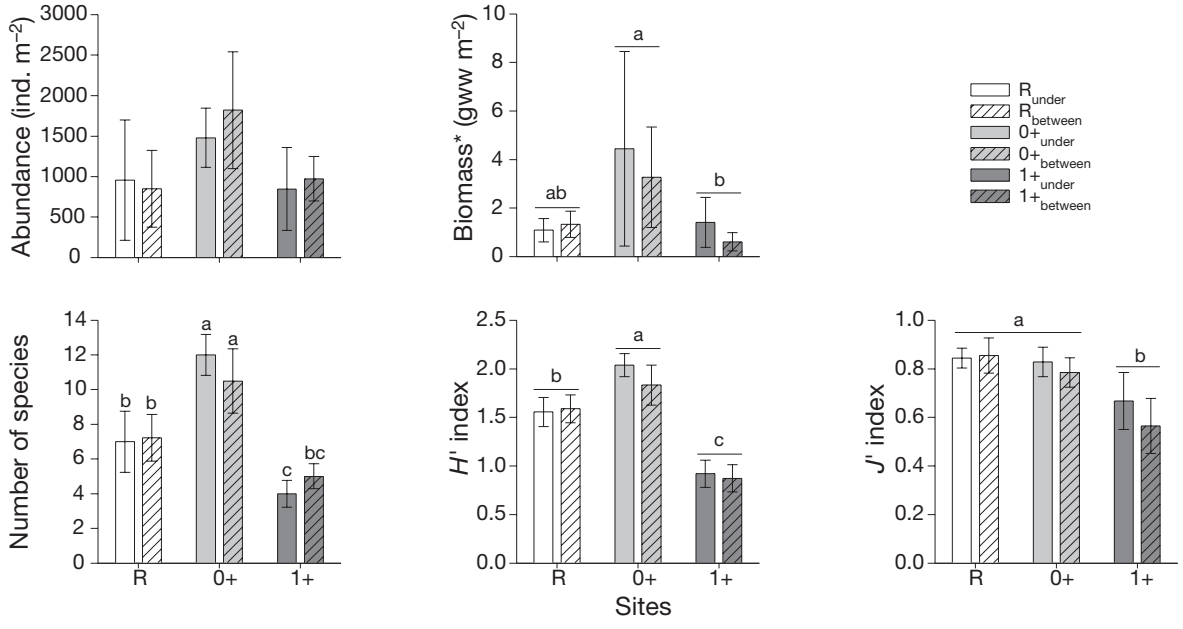

Fig. 3. Macrofaunal characteristics from 3 zones and 2 positions (average ± SD, n = 3–4). Note that Abundance and Biomass* are expressed as a function of m^{-2} and that Biomass* includes only those organisms <100 mg wet wt (see 'Results' for details). Results from the corresponding ANOVAs are given in Table 2. Significant differences among groups as identified by pair-wise contrasts are indicated by different letters. *H'* and *J'*: Shannon-Wiener diversity and equitability, respectively

Benthic community

Abundance and biomass

The mean abundance of organisms was 1177 ind. m^{-2}, ranging from 280 to 2560 ind. m^{-2}. Although a visual inspection of the data (Fig. 3) suggests that abundance was greatest in the 0+ zone, this effect was not statistically significant (Table 2). Biomass differed significantly among zones (Table 2) such that the greatest biomass was observed in the 0+ zone and the lowest in the 1+ zone. However, part of this pattern was driven by the presence of 6 large individuals (*Ensis directus*, *Nereis virens*, *Glycera dibranchiata* and 3 *Yoldia limatula* with body mass ranging from 100 to 10^4 mg wet wt) within separate replicates. As the sampling protocol was not designed to sample this size class of organism (see Andrew & Mapstone 1987), these organisms were removed from the data set and the analysis rerun (see biomass* in Table 2). The new analysis supported the original results (Fig. 3).

Species diversity

A total of 45 species was observed. The number of species observed was a function of the interaction

Table 2. ANOVA results for macrofauna characteristics: abundance, biomass, biomass* (without rare individuals weighing >100 mg), Number of species core^{-1}, Shannon-Wiener diversity H' and equitability J' indices observed at GEL during summer 2003. Fixed factors were zone (Z) (0+, 1+, R) and position (PO) (under and between the mussel lines). Site (SI) was a random factor (4 sites in 0+ and 1+ and 3 sites in reference: R). Abundance and biomass data were (log x + 1) transformed to satisfy the assumptions of the statistical model

Source of variation	df	MS	*F*	p	MS	*F*	p	MS	*F*	p
		Log abundance			Log biomass			Log biomass*		
Z	2	0.727	3.847	0.068	1.194	5.686	**0.029**	0.672	9.205	**0.008**
SI (Z)	8	0.189	3.259	**0.005**	0.210	0.955	0.483	0.073	0.890	0.533
PO	1	0.092	1.278	0.291	0.473	2.867	0.129	0.008	0.108	0.751
Z × PO	2	0.008	0.111	0.896	0.134	0.812	0.477	0.032	0.432	0.663
PO × SI (Z)	8	0.072	1.241	0.299	0.165	0.750	0.648	0.074	0.902	0.523
Error	43	0.058			0.220			0.082		
		Number of species *S*			Shannon H'			Equitability J'		
Z	2	277.243	35.412	**0.000**	6.617	79.723	**0.001**	0.336	18.667	**0.000**
SI (Z)	8	7.829	1.260	0.289	0.083	0.449	0.885	0.018	0.783	0.620
PO	1	0.194	0.092	0.770	0.086	1.564	0.246	0.031	1.240	0.298
Z × PO	2	9.643	4.559	**0.048**	0.075	1.364	0.309	0.016	0.640	0.552
PO × SI (Z)	8	2.115	0.340	0.945	0.055	0.297	0.963	0.025	1.087	0.390
Error	43	6.213			0.185			0.023		

between zone and position (Table 2), such that the greatest number of species was recorded in the 0+ zone and the lowest in the 1+ zone, with a trend for greater and lesser richness directly under lines in the 0+ and 1+ zones, respectively (Fig. 3). Both H' and J' differed significantly among zones (Table 2) such that H' was greatest in the 0+ zone and least in the 1+ zone and J' was least in the 1+ zone (Fig. 3).

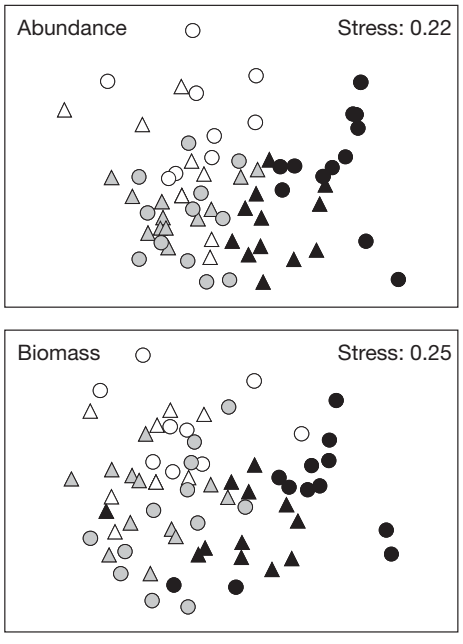

Fig. 4. Non-metric multi-dimensional scaling illustrating variation in community structure (√-transformed) among R (white), 0+ (grey) and 1+ (black) zones in both between (triangles) and under (circles) mussel line positions. Results from the corresponding DISTLM analysis are given in Table 3 and pair-wise comparisons (ANOSIM) in Table 4

Community structure

Analysis of community structure based on abundance and biomass data showed the same pattern. Samples from R, 0+, 1+$_{between}$ and 1+$_{under}$ sites formed clusters that were distinct (Fig. 4) and significantly different (Tables 3, 4) from one another. DISTLM analysis showed that, other than variation among replicates, differences among zones explained the greatest proportion of the variation in community structure (Table 3).

The average abundance and biomass of the dominant species as well as their contribution to the similarity among replicates within zones and positions are given in Table 5. In the R zone, *Pectinaria granulata*, juvenile *Macoma calcarea* and *Polydora ciliata* were the most abundant species, while *Heteromastus filiformis* and *P. ciliata* accounted for the greatest biomass. In the 0+ zone, juvenile *M. calcarea*, *Hydrobia minuta* and *P. granulata* were the most abundant species. The greatest biomass was represented by *P. granulata* and *Nassarius trivittatus* at 0+$_{between}$ positions, whereas juvenile *Nereis* sp. and *Nephtys caeca* accounted for most of the biomass at 0+$_{under}$ positions. At 1+$_{between}$ positions, juvenile *M. calcarea* and *Capitella capitata* were the most abundant species and

Table 3. DISTLM (distance-based multivariate analysis) results for the benthic community structure sampled in GEL in summer 2003. Fixed factors were zone (Z: 0+, 1+, R = reference) and position (PO, under and between the mussel lines). Site (SI) was a random factor. VE% indicates the percentage of variation explained by each factor. Analyses based on both total abundance and total biomass data of each species are given. All data were √-transformed prior to analysis

Source of variation	df	MS	Pseudo-*F*	p (perm)	VE%
Abundance					
Z	2	18212.42	6.056	0.000	25.2
SI (Z)	8	3007.39	2.137	0.000	16.6
PO	1	8050.30	6.713	0.000	5.6
Z × PO	2	4248.26	3.543	0.000	5.8
SI (Z) × PO	8	1199.21	0.852	0.823	6.6
Residual	54	1407.58			
Biomass					
Z	2	19216.78	5.054	0.000	18.1
SI (Z)	8	3802.46	1.513	0.001	14.3
PO	1	8281.34	3.871	0.000	3.9
Z × PO	2	4519.29	2.113	0.005	4.3
SI (Z) × PO	8	2139.14	0.851	0.889	8.0
Residual	54	2512.92			

represented the greatest biomass. The dominance of these 2 species switched in the $1+_{under}$ positions, where *C. capitata* represented 59% of the total biomass.

Trophic structure

Of the species observed, 18 were deposit feeders, 8 were suspension feeders (e.g. *Spio filicornis*, *Polycirrus* sp. *Mya arenaria*, *Ensis directus*, *Dyastylis polita*), and 8 were carnivores (e.g. *Retusa canaliculata*, *Nephtys caeca*, *Harmothoe imbricata*). All communities were dominated by deposit feeders (Table 6) which accounted for more than 70% of the total number of individuals in each zone. Suspension feeders accounted for ca. 10% of the abundance at reference and 0+ sites.

Table 4. Results of pair-wise comparisons of community structure between Zone and Position using ANOSIM. Upper right half of table compares abundance data, whereas lower half compares biomass data. See text for heading definitions. Statistically significant values are indicated in **bold**

	R_{under}	$R_{between}$	$0+_{under}$	$0+_{between}$	$1+_{under}$	$1+_{between}$
R_{under}	–	0.444	**0.009**	**0.027**	**0.001**	**0.001**
$R_{between}$	0.191	–	**0.001**	**0.001**	**0.001**	**0.001**
$0+_{under}$	**0.036**	**0.001**	–	0.131	**0.001**	**0.001**
$0+_{between}$	**0.006**	**0.001**	0.491	–	**0.001**	**0.001**
$1+_{under}$	**0.001**	**0.001**	**0.001**	**0.001**	–	**0.001**
$1+_{between}$	**0.001**	**0.001**	**0.001**	**0.001**	**0.001**	–

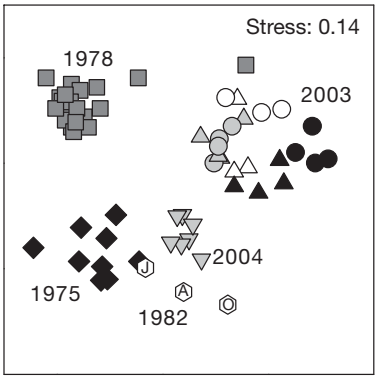

Fig. 5. Non-metric multi-dimensional scaling illustrating variation in historical community structure in GEL. Sample dates include the period prior to the dredging of a navigation channel and the start of mussel farming (1975, 1978), after the dredging and at the beginning of farming (1982), and following >20 yr of mussel aquaculture (2003—the current study—and 2004). Years indicated by symbols as in Fig. 1 except for 2003, shown in Fig. 4. Symbols for 1982 indicate the sample date (J: June, A: August, and O: October)

Inter-annual comparison

MDS analysis showed that benthic community structure differed among years (Fig. 5). However, samples taken from before (1975), at the start of (1982) and after >20 yr of mussel culture (2004) in the lagoon were relatively similar and different from samples taken in 1978 and 2003. In fact, comparing samples from 1975, 1982 and 2004 shows that differences in benthic community structure among these 3 periods are no greater than differences observed between years within periods, i.e. before (1975 and 1978) and after (2003 and 2004) the start of mussel culture. The similarity among samples from 1975, 1982 and 2004 can be explained largely by the dominance of the carnivorous gastropod *Retusa canaliculata* and the extent to which its presence contributes to the within-year similarity among replicates (30–50%, Table 7). The deposit feeder *Tellina agilis* was also common in each of those 3 yr. In 1975 and 1982, the benthic community was characterised by a *Retusa–Tellina–Spisula* association and in 2004 by a *Retusa–Nassarius–Hydrobia* association (Table 7). The 1978 community differed from those in 1975 and 1982 because of the very high abundance of *Mya arenaria* (33 696 ind. m^{-2}). Other than *M. arenaria*, the 1978 benthic community was also characterised by a *Retusa–Tellina–Polydora* association. The 2003 community was dissimilar to the others largely due to the absence of the suspension feeder *Spisula* spp. (also absent in 2004) and the

Table 5. Mean abundance (N: ind. m^{-2}) and biomass (B: g m^{-2}) of dominant species in R, 0+ and 1+ zones in both between and under positions. Results of SIMPER analyses identifying species that contribute most to the similarity among replicates within zones and positions are also given (%). Data were √-transformed. (juv): juvenile specimens; AS: average similarity; ns: species abundance or biomass does not contribute significantly to the similarity among replicates

Species	N	%	B	%	Species	N	%	B	%
$R_{between}$	AS = 42.7		AS = 39.8		R_{under}	AS = 37.2		AS = 27.1	
Pectinaria granulata	228	17	130	11	*Pectinaria granulata*	292	21	ns	ns
Macoma calcarea (juv)	203	21	58	10	*Polydora ciliata*	156	24	205	23
Polydora ciliata	97	27	134	27	*Macoma calcarea* (juv)	110	20	22	11
Heteromastus filiformis	89	20	489	41	*Heteromastus filiformis*	97	12	549	45
Mya arenaria (juv)	59	3	ns	ns	*Capitella capitata*	46	11	124	10
Nereis sp. (juv)	ns	ns	23	3					
$0+_{between}$	AS = 50.7		AS = 29.8		$0+_{under}$	AS = 44.8		AS = 26.3	
Macoma calcarea (juv)	463	27	190	19	*Macoma calcarea* (juv)	459	26	351	20
Hydrobia minuta	371	11	117	7	*Pectinaria granulata*	171	15	102	14
Pectinaria granulata	260	18	941	22	*Hydrobia minuta*	155	5	46	5
Heteromastus filiformis	158	12	247	11	*Mya arenaria* (juv)	89	11	18	8
Mya arenaria (juv)	98	4	ns	ns	*Hydrobia* sp.	70	5	48	5
Polydora ciliata	89	7	127	10	*Nereis* sp. (juv)	67	4	1475	8
Tellina sp. (juv)	54	5	12	3	*Polydora ciliata*	54	6	98	9
Retusa canaliculata	51	4	ns	ns	*Ensis* sp. (juv)	41	7	13	5
Nassarius trivittatus	ns	ns	717	5	*Heteromastus filiformis*	38	4	77	4
Nereis sp. (juv)	ns	ns	89	4	*Harmothoe imbricata*	35	4	ns	ns
Scoloplos armiger	ns	ns	113	3	*Nephtys caeca*	ns	ns	618	5
					Ampharete sp.	ns	ns	54	3
$1+_{between}$	AS = 52.7		AS = 35.2		$1+_{under}$	AS = 47.6		AS = 31.2	
Macoma calcarea (juv)	732	76	78	57	*Capitella capitata*	548	47	781	59
Capitella capitata	44	5	35	11	*Macoma calcarea* (juv)	200	46	23	30
Polydora ciliata	38	6	ns	ns					
Hydrobia sp.	ns	ns	36	12					
Retusa canaliculata	ns	ns	81	8					

Table 6. Composition of trophic groups (% ± SD) at the R, 0+ and 1+ zones in both between and under positions

Abundance (%)	$R_{between}$	R_{under}	$0+_{between}$	$0+_{under}$	$1+_{between}$	$1+_{under}$
Deposit feeders	79 ± 11	75 ± 2	82 ± 8	71 ± 8	84 ± 5	85 ± 4
Carnivores	7 ± 6	1 ± 2	4 ± 2	7 ± 2	5 ± 4	4 ± 1
Suspension feeders	9 ± 7	10 ± 10	10 ± 5	12 ± 4	6 ± 1	6 ± 3
Herbivores	1 ± 1	2 ± 3	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Omnivores	2 ± 2	3 ± 2	1 ± 1	4 ± 3	1 ± 0	1 ± 1
Not determined	2 ± 4	10 ± 8	3 ± 3	6 ± 8	3 ± 1	3 ± 1

dominance of deposit feeders (81% of all organisms, see Table 7).

DISCUSSION

We examined the influence of a 23 yr old mussel farm on the sediment and infaunal benthic community at multiple spatial scales. As a concomitant study (Callier et al. 2006) observed a greater flux of organic matter to the bottom in some zones and positions relative to others, we predicted that we would observe corresponding chemical and biological signatures.

Sediment geochemical characteristics

The flux of organic matter to the bottom in June and July ranged from 5 to 11 g OM m^{-2} d^{-1} at R and $1+_{under}$ positions, respectively (Callier et al. 2006). This flux represents approximately 1 to 3 g C m^{-2} d^{-1}, based on 30% carbon in organic matter (Holmer et al. 2005). Sedimentation rates of 1 to 5 g C m^{-2} d^{-1} may result in hypoxic sediments and increases in sulphate reduction around bivalve aquaculture sites (Dahlbäck & Gunnarsson 1981). Thus, it was predicted that increased organic loading resulting from the presence of mussel lines would increase the organic content of the sedi-

Table 7. Results of SIMPER analysis (√-transformed data) to show major differences in community structure among sample years. Average abundances (N, ind. m^{-2}) and the % contribution of the major taxa to within-year similarities (%) are shown. Data compared are from 1975 (Bourget 1976, Bourget & Messier 1982), 1978 (J. Munro et al. unpubl. data), 1982 (Élouard et al. 1983), 2003 (the present study) and 2004 (M. D. Callier at al. unpubl. data)

	1975		1978		1982		2003		2004	
	N	%	N	%	N	%	N	%	N	%
Carnivores										
Retusa canaliculata	924	(49)	1296	(10)	260	(30)	21		827	(50)
Suspension feeders										
Spisula spp.	105	(12)	123		2361	(27)				
Ensis directus	5		1123		1		25	(6)	4	
Mya arenaria			33 696	(58)			55	(3)		
Omnivores										
Nephtys sp.	46	(17)	33		14	(12)	4		29	
Nereis sp.			3		4		22	(3)		
Deposit feeders										
Tellina agilis	167	(8)	1897	(11)	164	(10)	19	(3)	49	(4)
Pectinaria granulata	110	(5)	153	(4)			151	(10)	5	
Nassarius trivittatus	18		9		14	(11)	11	(2)	147	(21)
Polydora sp.			1188	(10)	1		64	(9)	29	
Capitellidae			85		6	(3)	202	(23)	76	(10)
Hydrobia minuta			14		2		106	(4)	79	(8)
Macoma sp.			33				355	(30)	22	

ments and consequently lead to a localized reducing environment characterized by negative redox potentials and increased sulphide concentrations in the sediments. However, none of the sediment characteristics varied significantly among zones or positions.

It was predicted that the greatest %OM would be observed in $1+_{under}$ sediments, where the greatest sedimentation rates were recorded (Callier et al. 2006). Although the average %OM at the –1 cm depth tended to be greatest at $1+_{under}$ sites (see Fig. 2), this was not statistically significant. The analysis of the labile component of the OM in the 0 to 0.5 cm of the sediment surface, where the biodeposits accumulate, would have probably been a more appropriate method to detect difference between zones (Nickell et al. 2003). White mats, likely the sulphur bacteria *Beggiatoa* spp., were observed directly under the 1+ mussel lines (pers. obs.), as they have been in mussel culture sites elsewhere (Grant et al. 1995). The presence of *Beggiatoa* indicates that reducing conditions have reached the sediment-water interface at those sites (Holmer et al. 2005)

Sediment sulphide concentrations increased with depth at all sites and were typically >2000 µM, indicating hypoxic benthic conditions (Wildish et al. 1999). Redox potentials decreased slightly with depth, as is expected in muddy and silty habitats (Diaz & Rosenberg 1995). However, both parameters did not differ among zones. Sediment redox potential and sulphide levels can be used to detect the effects of high organic loading under fish cages (Hargrave et al. 1997, Anderson et al. 2005), but were probably not sensitive enough to detect the effect of mussel biodeposition. Other recent studies on bivalve aquaculture have reached the same conclusion (Anderson et al. 2005, Miron et al. 2005). Anderson et al. (2005) suggested that in depositional environments where the content of organic matter is naturally high, biodeposition from cultured bivalves does not significantly affect these parameters.

Relatively small increases in sedimentation, as measured in GEL by Callier et al. (2006), may have been obscured by background processes. Giles et al. (2006) suggested that rapid mineralization of mussel biodeposits in mussel farms may lead to a decoupling of sedimentation and sediment characteristics. Detritus from other sources within culture sites, such as plankton, seagrass or biodeposits from species associated with the cultured species (Stenton-Dozey et al. 2001), may further obscure the influence of mussel biodeposition. For example, Giles (2006) has estimated that only 14% of the increased biodeposition within a mussel culture site in New Zealand was due to mussel faeces biodeposition.

Benthic community

Subtle changes in environmental conditions may be reflected in altered biomass or species composition of macrofaunal communities before they are detectable in sediment chemical properties (Weston 1990, Edgar et al. 2005). This was observed in the current study

using both univariate and multivariate indices; the observed differences were likely due to differences in deposition rates among zones and positions.

Although not statistically significant, the abundance of benthic fauna tended to be greatest in the 0+ zone. Biomass was greatest in 0+ sites, largely due to the presence of *Nephtys caeca*, *Nassarius trivittatus*, *Pectinaria granulata*, and juvenile *Nereis* spp. that probably benefit from the moderate organic loading. Various responses have been observed in terms of biomass at mussel farms. Kaspar et al. (1985) did not detect a pattern with respect to biomass but other studies have observed either lower (Stenton-Dozey et al. 1999) or greater (de Jong 1994, Grant et al. 1995) biomass under mussel farms, the latter being due at times to the presence of scavengers attracted by mussel drop-off.

All measures of diversity evaluated (*S*, *H'* and *J'*) were reduced in the 1+ zone and *S* and *H'* were greatest in the 0+ zone. Other studies have reported decreases in *S* and *H'* (Mattsson & Lindén 1983, Kaspar et al. 1985, Stenton-Dozey et al. 1999, Chamberlain et al. 2001) of benthic macrofaunal communities under mussel cultures. Low *H'* in the 1+ zone resulted from the low number of species present. The dominance of the *Capitella capitata* at $1+_{under}$ positions and of juvenile *Macoma calcarea* at $1+_{between}$ positions further contributed to the low *H'* and accounted for the low *J'* values in the 1+ zone.

In the present study, the analysis of trophic structure was not useful for detecting differences between mussel farm and reference zones as the communities in all zones were dominated by deposit feeders, indicating a generally enriched environment. This is likely related to the high level of organic sedimentation in the lagoon (1 to 3 g C m^{-2} d^{-1}). Benthic communities in organically enriched areas are typically dominated by deposit feeders (Pearson & Rosenberg 1978) while suspension feeders often dominate less organically rich environments, as organic debris may have a smothering impact, preventing them from thriving (Kaspar et al. 1985). The results obtained from studies on trophic structure in mussel farms are inconsistent. Mattsson & Lindén (1983) observed higher abundances of deposit feeders at mussel culture sites compared to reference sites. In contrast, others have observed a dominance of predators and carnivores under mussel farms (de Jong 1994, Grant et al. 1995, Stenton-Dozey et al. 1999) that profit from mussel drop-off. Thus, care should be taken in using deposit feeders as indicators of organic enrichment at bivalve farms. This is particularly true in coastal areas where many such farms are located and which have naturally organically enriched sediments (Miron et al. 2005).

Although effects were not detected with trophic structure analysis, species-level effects were apparent in this study at both large and small spatial scales. *Macoma calcarea* was, overall, dominant in all sites in 2003. However, the initial spatfall and distribution of *Macoma* sp. has been shown to be largely a function of hydrodynamic processes (Armonies & Hellwig-Armonies 1992). The juveniles then undergo a secondary dispersal into low intertidal and infralittoral areas. Their importance in signalling organic inputs is therefore doubtful and they are not discussed further.

R and 0+ zones were dominated by *Polydora ciliata*, *Pectinaria granulata*, and *Heteromastus filiformis* with *Hydrobia minuta* also being dominant in the 0+ zone. Some species, such as *H. minuta*, may have benefited from the moderate organic loading in the 0+ zone. This was apparent by their great abundance there and near absence in other zones. Other abundant species, such as *P. granulata* and *P. ciliata*, are generally abundant in both the 0+ and reference zones and may reflect a general enrichment of the lagoon as they are characteristic of an intermediate stage of organic enrichment (Pearson & Rosenberg 1978). Communities differed at small spatial scales but only within the 1+ zone. $1+_{between}$ positions were dominated by *P. ciliata* and *Capitella capitata* while at $1+_{under}$ positions *P. ciliata* was absent and *C. capitata* increased in abundance by more than a factor of 12. This suggests a shift from an intermediately enriched environment between mussel lines to a greatly enriched stage directly under the $1+_{under}$ lines, only 10 m distant. Such a switch between *P. ciliata* and *C. capitata* has been described in the past (Pearson & Rosenberg 1978), with *P. ciliata* living at the edge of an enriched area dominated by *C. capitata*. *C. capitata* is a non-specialized surface deposit feeder and has some resistance to sulphide toxicity and hypoxia (Diaz & Rosenberg 1995).

A number of biological interactions may also explain the absence of other species at 1+ sites. The mussels may have had indirect effects on infaunal community structure by feeding on the larvae of infauna (Woodin 1976) and generally decreasing food resources (Peterson & Black 1987). In contrast, Commito & Boncavage (1989) have shown that mussels do not affect the abundance of infaunal species that do not disperse as planktonic larvae. *Capitella* sp. produces broods of 30 to 400 eggs which develop into lecithotrophic larvae that are competent to settle almost immediately after being released by female worms (Linton & Taghon 2000), possibly partly explaining the abundance of this species in $1+_{under}$ positions. Predation by large invertebrates attracted by the presence of fallen mussels (de Jong 1994, Grant et al. 1995) may also have an influence on the infauna. For example, lobsters were observed feeding on razor clams *Ensis directus* in the culture site during this study.

Since benthic effects as described above may be limited to the areas directly under the mussel lines, remote methods (i.e. ship-deployed) are likely to be less efficient for detecting such localized effects. Studies using direct sampling methods (i.e. SCUBA divers) have often observed accumulations of scavengers attracted by mussel drop-off (e.g. de Jong 1994, Grant et al. 1995) that have not been observed using remote methods. This may have an impact on our perception of the role of bivalve culture on the benthic environment and make comparisons between studies difficult.

Historical data

The present study showed localized effects of mussel culture. The comparison between $1+_{under}$ and $1+_{between}$ positions that were only 10 m apart showed that near-field benthic effects were likely due to the biodeposition of the mussels and not other intrinsic features within the zone. However, all zones showed some indications of organic enrichment and it is difficult to determine if the benthic communities at the 0+ and R zones were under a diffuse and broader influence of the mussel farm or if the mussel farm had no influence on those zones. Indeed, there are a number of factors that may explain such general organic enrichment in GEL. The lagoon is a very complex system as various modifications have occurred within it over the past half century. A causeway that separates GEL from the lagoon to the south (see Fig. 1) was constructed in 1947. A navigation channel was dredged in the 1980s for a port constructed in GEL. Islands were also constructed with the material dredged during this activity (e.g. the island next to the opening of the channel in Fig. 1). Commercial mussel farming was initiated in the early 1980s. Traditional ecological knowledge also suggests that *Zostera marina* beds have expanded considerably in recent years. Separating the importance of these different factors, which may modify currents and/or sedimentation rates and thus benthic community structure, is difficult.

To address this question, the benthic communities observed in the present study were compared to others conducted before the mussel farm was established (1975, 1978), at the start of farming activities (1982), and after the 1+ mussels were harvested (2004). Although the comparison was difficult because of differences in site locations (see Fig. 1) and sampling methods, some observations could be made. Benthic communities differed among years, but 1975, 1982, and 2004 were similar. *Retusa canaliculata* and *Tellina agilis* were very abundant in all years except 2003. This *Retusa–Tellina* association has been previously observed in neighbouring Prince Edward Island (see PEI, Fig. 1) by Hughes & Thomas (1971). They also mentioned the presence of a *Yoldia–Tellina* association with *R. canaliculata* and *Pectinaria granulata* for deeper sites. Miron et al (2005) also reported that the gastropods *R. obtusa* and *Nassarius trivittatus* and the bivalves *T. agilis* and *Yoldia limatula* were the dominant species at mussel farm sites in PEI (Fig. 1).

The 2003 community was dissimilar to the others largely due the absence of the suspension feeder *Spisula* spp., the lesser abundance of the carnivore *Retusa canaliculata* and the greater abundance of Capitellidae and *Macoma* sp. Weisberg et al. (1997) indicated that *Spisula* sp., *Retusa* sp. and *Macoma* sp. are pollution-sensitive taxa, while Capitellidae is a pollution-tolerant family. As discussed above, the great abundance of *Macoma calcarea* in 2003 was probably due to their recruitment to the deeper part of the lagoon, as *M. calcarea* is a typical intertidal species (Bourget 1976). The absence of *Spisula* spp., a large active suspension feeding bivalve, is possibly explained by greater organic input related to mussel farming. One yr after the mussel harvest (2004), *Capitella capitata* was almost absent, indicating that the organic enrichment decreased rapidly. However, the presence of the deposit feeders *Nassarius trivittatus*, *Heteromastus filiformis* and *Hydrobia minuta* in 2004 indicates that the sediment was still organically rich.

Bourget (1976) and Bourget & Messier (1982) suggested that the low benthic diversity and biomass in the middle of GEL was characteristic of an 'unstable community'. They also compared the biomass of the benthos in GEL to other regions and found that it was considerably lower than that observed elsewhere (e.g. PEI). In 1978, Munro et al. (unpubl. data) observed lower macrofaunal diversity and abundance in the deeper part as compared to other parts of the lagoon. They also found that the sites >4 m deep were characterized by a greater proportion of mud than other parts of the lagoon. Water currents are reduced in the deeper parts of the lagoon and water turnover in the area, where the mussel farm is located, is ca. 25–40 d (Koutitonsky & Tita 2006). This relatively low flushing rate likely contributes to the general hypoxic conditions of the sediment, especially when winds are weak and water temperatures high, as observed in August. Degradation of seagrass and algae detritus during the ice-covered winter months may further contribute to the general hypoxia of the deeper parts of the lagoon.

Irrespective of the source of variation among infaunal communities among sampling periods (before, at the start of and following >20 yr of mussel farming), several observations may be made. First, macrobenthic community samples taken from each of these 3 periods are, at times, quite similar. Second, differences in community structure between years within periods are at

least as large as differences among community structures among periods. Together, this suggests that any impacts associated with aquaculture, at decadal temporal scales, will be hidden by natural temporal variation in benthic macrofaunal community structure. The data from the current study showing a preponderance of deposit feeders in 2003, especially in the $1+_{under}$ position, suggest that mussel aquaculture does have local enrichment effects. However, any such effects seem to disappear within 1 yr, as indicated by the structure of benthic communities in 2004.

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Influence of suspended mussel lines on the biogeochemical fluxes in adjacent water in the Îles-de-la-Madeleine (Quebec, Canada)

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Abstract: Oxygen consumption and nutrient fluxes were measured in 80 L enclosures containing water, 1- or 2-year-old mussels, or 1- or 2-year-old line sections (mussels plus associated fauna – organic matter complex: AFOM) in August and September 2003 in the Îles-de-la-Madeleine. Mussel lines acted as nutrient sources and oxygen sinks in adjacent water. The magnitude of fluxes at the mussel line interface depended on the nutrient (NH_4 >> $Si(OH)_4$, PO_4 > NO_3 > NO_2). Mussel metabolism contributed greatly to O_2 consumption and NH_4 and PO_4 releases. Mussel influence was greater in stressful periods. The AFOM complex mainly contributed to NO_3, NO_2, and $Si(OH)_4$ fluxes. These fluxes could originate from organic matter decomposition rather than from associated faunal metabolism. The influence of AFOM depended on its composition and thus on line immersion time. Mussel lines by ammonia releases could be a factor of reduction of N limitation in the water column. Mussel line should be integrated as a new interface of biogeochemical exchanges in environmental carrying capacity studies.

Résumé : Des flux d'oxygène et de nutriments ont été mesurés dans des enceintes de 80 L contenant de l'eau, des moules de 1 ou 2 ans, ou des sections de filières de 1 ou 2 ans (moules plus complexe faune associée – matière organique : AFOM) en août et en septembre 2003 aux Îles-de-la-Madeleine. Les filières agissent comme une source de nutriments et comme un puit d'oxygène dans l'eau adjacente. L'importance des flux à l'interface de la filière dépend du nutriment (NH_4 >> $Si(OH)_4$, PO_4 > NO_3 > NO_2). Le métabolisme des moules contribue largement à la consommation d'O_2 et à la libération de NH_4 et de PO_4. L'influence des moules est plus importante en période de stress. Le complexe AFOM contribue principalement aux flux de NO_3, de NO_2 et de $Si(OH)_4$. Ces flux proviennent probablement davantage de la dégradation de la matière organique que du métabolisme de la faune associée. L'influence du complexe AFOM dépend de sa composition et donc du temps d'immersion des lignes. Grâce à leur production d'ammonium, les filières de moules pourraient être un facteur de réduction de la limitation en azote du milieu. Les filières de moules devraient être intégrées comme une nouvelle interface d'échanges biogéochimiques dans les études de capacité de charge.

Introduction

Natural, cultivated, or invasive bivalve populations can play a predominant role in nutrient turnover (Murphy and Kremer 1985; Dame and Libes 1993; Dankers and Zuidema 1995) and strongly modify the functioning of shallow coastal ecosystems (Cloern 2001; Chauvaud et al. 2003). In the case of suspended bivalve cultures, studies have focussed more on the influence of bivalve biodeposition on biogeochemical fluxes at the water–sediment interface (Baudinet et al. 1990; Hatcher et al. 1994; Christensen et al. 2003) than on the effect of the bivalve culture devices on biogeochemical fluxes in the water column (Mazouni et al. 1998; LeBlanc et al. 2003; Mazouni 2004). Nevertheless, in agreement with Mazouni et al. (1998, 2001), it is possible that suspended aquaculture structures can act as a new interface for solute exchanges by macrofaunal (bivalves + epibionts) metabolism and by the mineralization of organic matter trapped between shells. This new interface could play a central role in nutrient recycling. In addition to the influence of mussel lines on nutrient pools, various nutrient releases can change the nutrient ratios in water (Redfield et al. 1963) and enhance the probability of modifying phytoplankton species composition (Smayda 1990).

Blue mussels (*Mytilus edulis* Linneus) have been cultivated on suspended longlines since the 1980s in Grande-Entrée la-

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goon, Îles-de-la-Madeleine (Quebec, Canada; 47°37′N, 61°31′W). Commercial size is obtained after 18 months of culture. Thus, 2-year-old and 1-year-old mussel lines are deployed in the farm. The principal aim of this study was to test the influence of these two types of mussel lines on O_2 and nutrient (NH_4, PO_4, NO_3, NO_2, and $Si(OH)_4$) fluxes in surrounding waters and to evaluate the relative contributions of mussels and of the associated fauna – organic matter complex (hereafter AFOM) on biogeochemical fluxes during the summer (ice-free period), which is the productive season and is when suspended mussel line influence on biogeochemical fluxes is probably greater. Since the magnitude of the mussel line influence probably depends on various factors related to macrofaunal metabolism and organic matter mineralization, such as the water temperature, mussel condition, and AFOM composition, experiments were carried out during two contrasted periods: (*i*) in August, when water temperature is high and mass mussel mortality events are regularly observed in the Îles-de-la-Madeleine (Tremblay et al. 1998), and (*ii*) in September, when temperature is lower and mussel condition and the associated faunal biomass are probably greater.

More specifically, three hypotheses were tested: (*i*) mussel metabolism contributes to biogeochemical fluxes, and its influence depends on water temperature and mussel stress, (*ii*) the AFOM complex also contributes to biogeochemical fluxes, and its influence depends on its composition and thus on mussel line immersion time, and (*iii*) mussel lines have a significant influence on nutrient pools and ratios. The results of this study should help us to highlight the necessity to integrate the total influence of this new suspended interface on the biogeochemical cycle in benthic–pelagic coupling in future environmental carrying capacity studies.

Materials and methods

Experimental system

Tank experiments were performed using the facilities of the Ministère de l'Agriculture de la Pêche et de l'Alimentation du Québec, Îles-de-la-Madeleine. The tank (180 cm length × 110 cm width × 64 cm height) was filled with unfiltered seawater to avoid disturbance in organism metabolism and biogeochemical fluxes in the incubation chambers (e.g., metabolic stress due to starvation; Hatcher et al. 1997). Two benthic chambers (Boucher and Boucher-Rodoni 1988; Boucher and Clavier 1990; Thouzeau et al., in press[2]) were placed in the tank's circulating water to avoid water warming during the experiments. Water warming is known to modify biogeochemical fluxes (e.g., by increasing the O_2 consumption of benthic communities; Hargrave 1969; Grant et al. 1991; Nakamura 2003). The original opened-bottom benthic chambers were modified for this study and will be referred to hereafter as the "Aquamoule". The Aquamoule is a closed chamber made of opaque polyacrylate that is 50 cm in diameter and 80 L in volume. This large volume allowed us to evaluate the influence of large mussel biomasses (up to 500 g dry weight of mussels) on the biogeochemical fluxes in water without provoking confinement (see Incubation protocol), thus decreasing the small-scale flux variability within treatments. Opaque chambers were used to prevent photosynthesis activity. Thus, only the processes linked to respiration activity of the whole community were studied (Hargrave 1969; Boucher and Clavier 1990; Plante-Cuny et al. 1998).

Experimental design

In summer 2003, two sets of experiments were performed. The experiments were carried out (*i*) between 5 and 11 August (hereafter August) when temperature was high, mussels were in poor conditions (Tremblay et al. 1998), and dead and dying mussels were observed in situ in suspended mussel lines, and (*ii*) between 31 August and 2 September (hereafter September) when temperature was lower, mussels were probably in better condition, and mussel spat recruitment was observed.

Two types of suspended mussel lines were randomly collected by SCUBA divers in the mussel farm of the Grande-Entrée lagoon. The differences between both lines were (*i*) mussel age (1-year-old mussels were 13 and 14 months old in August and September, respectively, whereas 2-year-old mussels were 25 and 26 months old) and (*ii*) line deployment in the water column (1-year-old mussel lines were deployed vertically (traditional line), whereas 2-year-old mussel lines were deployed in loops (continuous sleeve) along a horizontal axis). Both structures were deployed on ~2 m height in the water column.

Mussel line handling was performed carefully to avoid the loss of the associated fauna and organic matter trapped between the mussel shells. Dying and dead mussels observed in August were not removed before the experiments to preserve the original composition of the lines. Lines were cut into 12 sections of 20–25 cm in length. Twelve sections of each type of line were randomly kept along mussel line to integrate the vertical variability of line composition (mussels, associated fauna, and organic matter amount) on the whole measures.

Six sections of 1- and 2-year-old mussel lines were cleaned of associated fauna and sediment to keep only mussels (referred to hereafter as M1 and M2, respectively). The six others sections were replicates of the original 1- (L1) or 2- (L2) year-old lines. These sections were not cleaned and corresponded to the whole assemblage of a mussel line (mussels + associated fauna + organic matter mats). The last treatment (control) consisted of water from the lagoon (referred to hereafter as W; six replicates). A total of 60 incubations were performed during this study.

Incubation protocol

The Aquamoules could contain W, M1, M2, L1, or L2. The treatment inside the chambers was chosen randomly each time to integrate variability due to changing experimental conditions (e.g., possible water temperature variations during a day) within each treatment to exclusively test the effect of treatment on biogeochemical fluxes. Two independent Aquamoules were used at the same time. The incubation

[2] Thouzeau, G., Grall, J., Clavier, J., Chauvaud, L., Jean, F., Leynaert, A., Longphuirt, S., Amice, E., and Amouroux, D. In press. Spatial and temporal variability in benthic biogeochemical fluxes in the Thau lagoon associated with macrophytic and macrofaunal distribution. Estuar. Coast. Shelf. Sci.

time was selected to be 1.5 h (T_{1h30}) after a pilot study was conducted to identify the ideal incubation time, allowing NH_4 fluxes to be measured and final O_2 concentrations no more than 20% below the initial O_2 concentrations. The aim was to prevent hypoxic conditions to develop, which could modify bivalve metabolism (Mazouni et al. 1998). The short incubation time also prevented mussel starvation, since the latter would occur 24 h later after the guts were completely empty (Khalil 1994). Moreover, starvation is known to modify bivalve metabolism only after several days (Bayne and Scullard 1977; Khalil 1994). During the experiments, no modification of mussel metabolic activity was thus presumed.

Physico-chemical measurements and sample collections

Each Aquamoule was linked to a submersible pump and YSI 6600 probe. Adjustable submersible pumps connected to waterproof batteries provided homogenization of the water inside the enclosures without noticeable particulate matter resuspension. Water flow in each enclosure was adjusted to 2 $L \cdot min^{-1}$, allowing stable measurements to be recorded by the probes (Thouzeau et al., in press[2]). The YSI probes recorded O_2 concentration ($mg \cdot L^{-1} \pm 0.01$), temperature (°C ± 0.01), and salinity (±0.01) in the chambers each minute. This monitoring allowed us to check if there was any change in the experimental conditions that could modify the biogeochemical processes in the enclosures (e.g., an increase in water temperature).

Water samples were collected using 60 mL syringes every 30 min (start, middle, and end of incubation) for nutrient (NH_4, $Si(OH)_4$, PO_4, NO_3, and NO_2) analyses. Three syringes were filled at each sampling time to minimize the variability of measured nutrient concentrations. At the end of each incubation, each Aquamoule was emptied. Water contained in Aquamoules was removed from the tank to avoid modifying the reference water for the next experiment. Mussels or line sections were frozen at –20 °C for biomass measurements in the laboratory. The faeces and pseudofaeces sedimented on bottom of the Aquamoules were collected and removed from the tank. Finally, for the subsequent experiments, the Aquamoules were refilled with reference water contained in the tank, which was from the adjacent lagoon.

Laboratory processing

Mussel and AFOM complex

Line sections were washed over a 0.5 mm sieve to separate mussels from the associated fauna. Mussels were counted and measured with a calliper (±0.01 mm) in each replicate. The associated fauna was sorted, counted, and identified to the genus level and separated into two groups (infauna and epifauna) and two subgroups (sedentary and errant) (Table 1). For counting purpose, epibionts ≤1 mm (e.g., mussel spat) were subsampled with a Folsom splitter (Van Guelpen et al. 1982). As mussel spat settled after the installation of the commercial mussel lines and was not harvested later on, its influence on biogeochemical fluxes was considered with the associated fauna and not with the commercial mussels.

The mussels and the associated fauna were dried separately at 60 °C for 48–72 h, weighed, and burned for 4 h at 450 °C to calculate the ash-free dry weight (AFDW) (Thouzeau et al., in press[2]). Mussel AFDW was measured to the nearest 0.1 g and the associated faunal AFDW to the nearest 0.01 mg with PG 5001-S and AG285 Mettler Toledo balances, repsectively.

Since the extraction of organic matter from washing water and byssus fragments was not possible, the organic matter biomass could not be measured. The hypothetic contribution of processes linked to organic matter on biogeochemical fluxes would be deduced by subtracting the associated faunal contribution to the total AFOM complex contribution.

Nutrient analyses

Ten millilitres per syringe were immediately sampled to measure NH_4 concentration according to the orthophtaldialdhehyde method (Holmes et al. 1999) with an Aquafluor handheld Turner Designs fluorimeter. The remaining water samples were stored in three cryovials and frozen (–80 °C) after filtering on 0.2 m cellulose acetate Target syringe filters. Analyses for dissolved NO_3, NO_2, PO_4, and $Si(OH)_4$ were performed on a II PAA II Brann and Luebbe Technicon auto-analyser according to Tréguer and Lecorre (1975).

Data standardization

Whereas the dry weight (with shells) of 2-year-old mussels of 20–25 cm length line sections was greater than that of 1-year-old mussels, analysis of variance (ANOVA), which tested the effect of treatment (M and L), age (1 and 2), and date (August and September) on AFDW mussel biomass, revealed that date was the only significant source of variation for mussel AFDW biomass ($p = 0.002$). Mussel biomass increased between August and September (49.43 ± 1.46 g AFDW in August vs. 56.99 ± 1.97 g AFDW in September). There was no significant ($p = 0.074$) difference in mussel biomass among treatments (M, L), allowing a good comparison of treatments for each age at each date. Gross data were reported to a standardized 50 g AFDW mussel biomass, since this biomass was nearly equivalent to the mean mussel biomass (± standard error, SE) of 20–25 cm length sections (53.21 ± 1.33 g AFDW). Standardization in biomass was preferred to standardization in length, since the influence of mussel lines is more easily associated with mussel biomass (production) for modelling purposes than with culture line length.

Flux and Redfield ratio calculations

O_2 and nutrient fluxes were determined from the slopes of the linear regressions established between concentration and incubation time. Fluxes were reported to the chamber volume and standardized to 50 g AFDW mussel biomass. NH_4, NO_3, and NO_2 concentrations were summed to calculate total nitrogen (N) concentrations for each treatment and date at the beginning (T_0) and at the end (T_{1h30}) of each incubation. Initial and final N/P, Si/N, and Si/P ratios were calculated in atomic equivalents.

Mussel metabolic rates and condition index

To compare mussel metabolism between age and date, use of individual metabolic rate was preferred to metabolic rate expressed by grams AFDW, since for a given biomass, mean density of M1 was almost three times greater than those of

Table 1. Macrofaunal community associated with 1- and 2-year-old mussel lines (L1 and L2) in August and September 2003.

	L1		L2	
	August	September	August	September
Sedentary infauna				
Total biomass (mg)	0	0.05±0.02	11.73±3.1[a]	13.67±3.15[a]
Abundance of each genus				
Polychaeta, *Amphitrite*	0	0	22.64[b]	24.06[b]
Amphipoda, *Corophium*	0.15	14.67	0.11	3.52
Total abundance	0.15±0.15	14.67±6.25	22.74±3.06	27.58±4.58
Total number of genera	0.17±0.17	1	1.17±0.17	2
Sedentary epifauna				
Total biomass (mg)	0.92±0.14[a]	55.71±16.41[a]	1.37±0.36	6.18±1.28
Abundance of each genus				
Anthozoa, *Metridium*	0.18	3.13	0.12	4.29
Gastropoda, *Crepidula*	8.42	12.98	1.39	3.86
Bivalva, *Anomia*	0.17	0.18	1.73	0.63
Bivalva, *Mytilus*	152.53[b]	11 259.24[b]	24.77[b]	418.57[b]
Cirripedia, *Balanus*	0.48	0	0.79	1.26
Amphipoda, *Caprella*	4.80	10.52	0.37	4.31
Total abundance	161.78±36.25	11 275.23±5 069.34	28.80±6.49	428.61±65.46
Total number of genera	3.5±0.22	4.17±0.17	3.5±0.43	4.67±0.33
Errant epifauna				
Total biomass (mg)	1.35±0.41	1.24±0.32	1.38±0.24	5.03±0.62
Abundance of each genus				
Polychaeta, *Harmathoe*	19.01[b]	20.14[b]	7.74[b]	20.49[b]
Gasteropoda, *Odostomia*	0	0.74	0	5.64
Gasteropoda, *Hydrobia*	0	0	0	2.12
Asteroida, *Asterias*	0.29	6.27	2.03	14.95
Total abundance	19.3±4.54	27.15±4.75	9.78±1.5	43.2±2.95
Total number of genera	1.17±0.17	2.67±0.21	2±0.26	3.83±0.17
Total biomass of associated fauna (mg)[c]	2.28±0.45	57.00±16.35	14.48±3.12	24.88±3.29
Total abundance of associated fauna[c]	235.17±39.69	11 379.19±5 076.31	128.16±9.44	557.98±67.93
Total number of associated fauna genera	4.83±0.48	7.83±0.31	6.67±0.42	10.50±0.43
Associated fauna biomass/total biomass (%)[d]	0.005±0.001	0.114±0.033	0.029±0.006	0.050±0.006

Note: Biomass is given in mg ash free dry weight (AFDW) ± standard error.
[a]Values correspond to the community's main components in terms of biomass for each treatment.
[b]Values represent the dominant genus in abundance in each faunal group.
[c]n = 6; values standardized to 50 g AFDW of mussels.
[d]n = 6.

M2. Individual mussel respiration and excretion (NH_4 and PO_4) rates of M1 and M2 were calculated from the ratios of O_2, NH_4, and PO_4 fluxes to mussel density of the corresponding replicate. Allometric relationships were ignored, since only one mussel cohort was present on each mussel line. The stressful condition index, O/N ratio (Schlüter and Josefsen 1994; Hatcher et al. 1997; Tremblay et al. 1998), was calculated for each mussel treatment (M1, M2) in atomic equivalents according to the formula: O/N = (mg $O_2 \cdot h^{-1}/16$)/(mg $NH_4 \cdot h^{-1}/14$) (Widdows and Johnson 1998).

Statistical analyses

The mussel lines used for this study originated from two different suspended culture techniques (traditional line vs. continuous sleeves). This change in mussel culture technique had one consequence on the data interpretation; to avoid adding confounding factors because of the techniques used and the mussel age, we made no comparisons of the absolute values between the two types of lines. The fact that data were standardized to a mussel biomass led us to separately analyze the two sets of data (August and September).

ANOVAs were performed to compare (*i*) O_2 consumption and nutrient fluxes among the three treatments (W, M, L) for each type of line (1 and 2) at each date (August and September) (Table 2); (*ii*) respiration, excretion (PO_4 and NH_4) rates, and O/N ratios among the two mussel treatments (M1 and M2) and the two dates (Table 3); and (*iii*) nutrient ratios (N/P, Si/N, and Si/P) among the five treatments (W, M1, M2, L1, and L2), two dates, and two incubation times (T_0 and T_{1h30}; Table 4). Cochran's test was used to verify homogeneity of the variances (Underwood 1997). When required, data were transformed to achieve homogeneity of variances (see Tables 2 and 4). As more than one ANOVA was done for the same hypothesis, the p values were adjusted with a Bonferroni correction for each of the three models (see Tables 2–4). When a source of variation was significant

Table 2. Results of the one-way analyses of variance (ANOVAs) testing the effect of treatment (TR) on the oxygen demand (O_2) and nutrient fluxes (ammonium, NH_4; phosphates, PO_4; nitrates, NO_3; nitrites, NO_2; silicates, $Si(OH)_4$) in August and in September 2003.

			W, M1, L1						W, M2, L2					
			August			September			August			September		
Flux	Source	df	MS	*F*	*p*	MS	*F*	*p*	MS	*F*	*p*	MS	*F*	*p*
O_2	TR	2	3 418.76	57.04	<0.0001	24.8843*	41.92	<0.0001	4.32†	58.09	<0.0001	6171.07	31.11	<0.0001
	Error	15	59.93			0.5936			0.07			198.36		
NH_4	TR	2	710 658.75	70.21	<0.0001	24 096.59	22.51	<0.0001	1 087 597.03	97.31	<0.0001	2.08‡	60.16	<0.0001
	Error	15	10 122.24			1 070.52			11 176.93			0.03		
PO_4	TR	2	1.68§	53.81	<0.0001	278.01	17.86	0.0001	1.35§	34.75	<0.0001	116.02	10.49	0.0014
	Error	15	0.03			15.57			0.04			11.06		
NO_3	TR	2	32.71	13.91	0.0004	9.77	23.05	<0.0001	1.43‖	19.07	0.0001	73.33	71.4	<0.0001
	Error	15	2.35			0.42			0.07			1.03		
NO_2	TR	2	1.57¶	42.59	<0.0001	0.13	4.86	0.0236	2.52¶	88.25	<0.0001	5.77	62.71	<0.0001
	Error	15	0.03			0.03			0.03			0.09		
$Si(OH)_4$	TR	2	52.79	4.40	0.0313	229.61	4.08	0.0385	130.57	5.29	0.0183	2594.67†	22.76	<0.0001
	Error	15	11.99			56.27			24.69			114.02		

Note: W, control; M1 and M2, 1- and 2-year-old mussel lines, respectively, that were cleaned of associated fauna and sediment to keep only mussels; L1 and L2, replicates of the original 1- or 2-year-old lines, respectively; df, degrees of freedom; MS, mean square. Adjusted *p* value is 0.0042.

*$(x + 1)^2$.
†ln (x).
‡ln $(x + 80)$.
§ln $(x + 10)$.
‖ln $(x + 3)$.
¶ln $(x + 1)$.

Table 3. Results of the analysis of variance (ANOVA) testing the effect of treatment (TR: M1, M2), date (Da: August, September), and their interaction on individual respiration rates, excretion (PO_4 and NH_4) rates, and O/N ratios.

Variable	Source of variation	df	MS	*F*	*p*
O_2 rate	TR	1	4.0381	46.77	<0.0001
	Da	1	0.0002	<0.01	0.9619
	TR × Da	1	0.1623	1.88	0.1855
	Error	20	0.0863		
PO_4 rate	TR	1	0.0532	7.86	0.0110
	Da	1	0.0044	0.65	0.4290
	TR × Da	1	0.0024	0.36	0.5544
	Error	20	0.0068		
NH_4 rate	TR	1	7.3297	161.24	<0.0001
	Da	1	10.2925	226.42	<0.0001
	TR × Da	1	0.4179	9.19	0.0066
	Error	20	0.0455		
O/N ratio	TR	1	32.2133	1.43	0.2456
	Da	1	2227.3	98.95	<0.0001
	TR × Da	1	6.7181	0.3	0.5909
	Error	20	22.5087		

Note: df, degrees of freedom; MS, mean square; M1 and M2, 1- and 2-year-old mussel lines, respectively, that were cleaned of associated fauna and sediment to keep only mussels. Adjusted *p* value is 0.0127.

($p < 0.05$), Student–Newman–Keuls (SNK) pairwise multiple comparison tests were carried out to identify the differences.

Results

Environmental conditions

According to the YSI measurements, the mean (± SE) salinity during the incubations was 30.5 ± 0.15 in August vs. 31.14 ± 0.1 in September. The mean water temperature in August (19.33 ± 0.83 °C) was significantly higher than water temperature in September (15.7 ± 0.48 °C). The mean O_2 saturation in water was 90.44% ± 1.56% in August; it was significantly higher in September (101.42% ± 3.42%).

Associated fauna with mussels

The biomass (AFDW) of the associated fauna with 50 g AFDW of 1-year-old mussels varied from 1.47 to 4.45 mg in August and from 22.71 to 135.24 mg in September (Table 1). In a standardized 2-year-old mussel sample of 50 g AFDW, there was 5.60–26.87 mg of epibionts in August and 14.21–36.63 mg in September. The epibiont biomass in L1 made up 0.005% of the total biomass of macrofaunal organisms (epibionts + mussels) fixed on the mussel lines in August. This proportion was significantly higher in September (0.114%; Table 1). Accordingly, the percent biomass of the epibionts in L2 was significantly higher in September (0.05%) than in August (0.029%). The total abundance of the associated fauna in L1 was 235 in August and 11 379 in September, while in L2 it was 128 in August and 558 in September (Table 1). The specific composition of the associated fauna is reported in Table 1; a total of 12 genera were identified on the lines, which included both infaunal and epifaunal taxa. The mean number (±SE) of genera observed in L1 was 4.83 ± 0.48 in August vs. 7.83 ± 0.31 in September. In L2, there were 6.67 ± 0.42 genera of epibionts in August vs. 10.50 ± 0.43 in September.

Infauna

Infaunal biomass was scarce in L1 in August (<0.01 mg per 50 g AFDW mussel) and September (0.07 mg per 50 g AFDW mussel), with the only organism being the amphipod *Corophium* sp. (Table 1). Infauna in L2 was almost exclusively (>99%) represented by a sedentary polychaete (*Amphitrite* sp.). Infauna accounted for 80.98% of the total associated faunal biomass in L2 in August vs. 54.94% in September (Fig. 1).

Epifauna

Epifauna (sedentary and errant forms) accounted for most genera (10 of 12) of the faunal community associated with mussels (Table 1). In L1, sedentary organisms represented 40.35% of the total epifaunal biomass in August, but 97.82% in September. In L2, the variations between dates were less marked (49.81% in August vs. 55.12% in September). The biomass of sedentary epifauna in L1 and L2 was composed mainly of mussel spat (L1: 76.32% in August vs. 95.96% in September; L2: 64.47% in August vs. 59.02% in September), with a mean spat abundance reaching 11 259 individuals on L1 in September. Mussel spat size ranged from 0.5 to 1 cm. The relative biomass of sedentary epifauna among the epibionts was much higher in L1 than in L2 (43.63%–97.73% vs. 9.48%–24.86% from August to September, respectively; Fig. 1). In both L1 and L2, the most abundant errant epifauna was a carnivorous scale worm (*Harmathoe* sp.) (Table 1). The errant epifauna found in L1 accounted for only 2.18% of the total biomass of the macrofauna associated with cultivated mussels in August vs. 59.37% in September (Fig. 1). In L2, the errant epifauna represented 9.53% and 20.20% of the total epibiont biomass in August and September, respectively.

Table 4. Results of the analyses of variance (ANOVAs) testing the effect of treatment (TR: W, M1, M2, L1, L2), date (Da: August, September), incubation time (*T*: T_0, beginnig; T_{1h30}, end), and their interactions on N/P, Si/N, and Si/P ratios.

Ratio	Source of variation	df	MS	*F*	*p*
N/P	TR	4	116.54	23.11	<0.0001
	Da	1	3523.94	698.69	<0.0001
	T	1	730.32	144.8	<0.0001
	TR × Da	4	67.96	13.47	<0.0001
	TR × *T*	4	73.01	14.48	<0.0001
	Da × *T*	1	320.13	63.47	<0.0001
	TR × Da × *T*	4	26.95	5.34	0.0006
	Error	100	5.04		
Si/N	TR	4	2.31*	36.68	<0.0001
	Da	1	41.74	663.23	<0.0001
	T	1	11.72	186.3	<0.0001
	TR × Da	4	0.14	2.26	0.0684
	TR × *T*	4	1.02	16.14	<0.0001
	Da × *T*	1	0.01	0.23	0.6332
	TR × Da × *T*	4	0.09	0.09	0.2165
	Error	100	0.06		
Si/P	TR	4	10.27	20.61	<0.0001
	Da	1	23.25	46.62	<0.0001
	T	1	28.24	56.63	<0.0001
	TR × Da	4	1.16	2.33	0.0612
	TR × *T*	4	2.34	4.69	0.0016
	Da × *T*	1	5.78	11.59	0.0010
	TR × Da × *T*	4	0.78	1.56	0.1914
	Error	100	0.5		

Note: df, degrees of freedom; MS, mean square; W, control; M1 and M2, 1- and 2-year-old mussel lines, respectively, that were cleaned of associated fauna and sediment to keep only mussels; L1 and L2, replicates of the original 1- or 2- year-old lines, respectively. Ajusted *p* value is 0.0169.
*ln (*x*).

O_2 consumption

According to the ANOVAs, treatment was a significant source of variation for O_2 demand in August and September (Table 2). Oxygen fluxes were always negative during this study, showing O_2 consumption in all cases (Fig. 2*a*). O_2 consumption rates were not significantly different in L and M treatments for either 1- or 2-year-old mussels in August (SNK a posteriori tests). O_2 consumptions measured in L and M were about four times higher than those measured in W (Fig. 2*a*). In September, (*i*) O_2 consumption in W (control) was significantly lower than O_2 consumption of M and L, and (*ii*) O_2 consumption in L1 and L2 was significantly higher than O_2 consumption in M1 and M2 (Fig. 2*a*). Mussel respiration accounted for 73.8% of the total O_2 demand for the 1-year-old lines vs. 55.4% for the 2-year-old lines.

Nutrient fluxes

The majority of the nutrient fluxes measured in the Aquamoules containing M1, M2, L1, or L2 were positive and corresponded to nutrient releases into the water (Figs. 2 and 3). Fluxes measured in the controls (W) were generally low and were positive or negative (uptake) depending on the particular nutrient and the date. The ANOVAs showed that treatment was a significant source of variation for the majority of nutrient fluxes in August and September (Table 2).

NH_4

NH_4 fluxes were the highest nutrient fluxes recorded in this study (Fig. 2*b*), reaching 837.49 mol $NH_4 \cdot L^{-1} \cdot h^{-1}$. NH_4 fluxes in water were always significantly lower than those measured in the mussel and line treatments for both age and date (Fig. 2*b*; multiple pairwise tests). Moreover, NH_4 fluxes in M were not significantly different from those in L for both ages and dates. NH_4 fluxes measured in M and L for a standardized 50 g AFDW mussel biomass in August were almost six times higher from those measured in September.

PO_4

PO_4 fluxes in the water were significantly smaller than the fluxes measured in all other treatments (Fig. 2*c*; SNK tests). In August, no significant difference was observed for PO_4 release between M1 and L1 and between M2 and L2. In September, no significant difference was observed for PO_4 release between M2 and L2, but the mean PO_4 flux in L1 was twice the mean flux in M1 (significant difference; Fig. 2*c*).

$Si(OH)_4$

$Si(OH)_4$ fluxes were either negative (uptake) or positive (release) depending on the treatment and date (Fig. 3*a*). The mean $Si(OH)_4$ flux in W was not significantly different from those measured in M1 and L1 in August and in September (Table 2, Fig. 3*a*). The same pattern was observed in August

for 2-year-old treatments (Table 2, Fig. 3*a*). In September, no difference was observed for $Si(OH)_4$ flux between W and M2 (uptakes), while L2 exhibited high $Si(OH)_4$ release (Fig. 3*a*).

NO_3

The mean NO_3 flux in W was close to nil for both experimental periods and was significantly lower than fluxes in all other treatments (SNK tests; Fig. 3*b*). NO_3 fluxes in L were significantly higher than fluxes in M for both experimental dates. The mean contribution of the AFOM complex to NO_3 release was estimated by subtracting the mussel contribution from the line contribution (L minus M); it reached 57.76% in August and 52.71% in September for the 1-year-old mussel lines and 71.83% in August and 82.59% in September for 2-year-old lines.

NO_2

NO_2 fluxes were the lowest nutrient fluxes recorded in this study and ranged from –0.18 to 3.70 mol $NO_2 \cdot L^{-1} \cdot h^{-1}$ (Fig. 3*c*). NO_2 fluxes exhibited the same patterns as NO_3 fluxes in August for both ages (L > M > W; Fig. 3*c*). By contrast, in September the mean NO_2 flux measured in W was not significantly different from those in M1 and L1 (Fig. 3*c*). Nevertheless, at the same date, the mean NO_2 flux measured at L2 was significantly greater than those measured in M2 and W (Fig. 3*c*). The contribution of the AFOM complex of the 1-year-old lines to NO_2 fluxes was 75.35% in August; the contribution of the AFOM complex of the 2-year-old lines was still higher (86.68% in August and 95.15% in September).

Mussel metabolic rates and condition index

Treatment was a source of variation for mussel respiration rate and PO_4 excretion (Table 3). O_2 consumption and PO_4 excretion rates of 2-year-old mussels (1.34 ± 0.13 mg $O_2 \cdot individual^{-1} \cdot h^{-1}$ and 0.2 ± 0.03 mol $PO_4 \cdot individual^{-1} \cdot h^{-1}$, respectively) were significantly greater than those of 1-year-old mussels (0.52 ± 0.03 mg $O_2 \cdot individual^{-1} \cdot h^{-1}$ and 0.1 ± 0.004 mol $PO_4 \cdot individual^{-1} \cdot h^{-1}$, respectively). The interaction of treatment and date was a source of variation for NH_4 excretion rates (Table 3); rates of M1 (4.15 ± 0.3 mol $NH_4 \cdot individual^{-1} \cdot h^{-1}$) and M2 (16.5 ± 1.7 mol $NH_4 \cdot individual^{-1} \cdot h^{-1}$) in August were significantly greater than those in September (M1: 1.46 ± 0.1 mol $NH_4 \cdot individual^{-1} \cdot h^{-1}$; M2: 3.4 ± 0.3 mol $NH_4 \cdot individual^{-1} \cdot h^{-1}$).

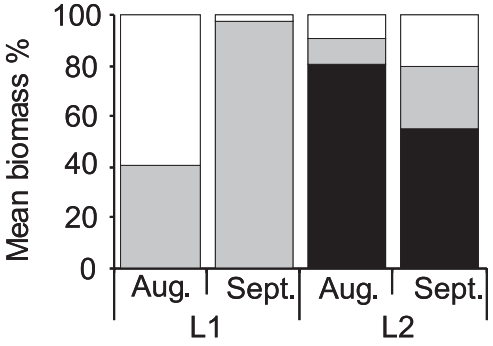
Mean O/N ratios (±SE) were 6.76 ± 0.48 and 5.51 ± 0.6 for M1 and M2, respectively, in August vs. respective values of 27.09 ± 2.66 and 23.71 ± 2.71 in September. M1 and M2 values were not significantly different between dates, allowing us to calculate mean condition indices of 1- and 2-year-old mussels in August and September (Fig. 4). According to the ANOVA results, date was a significant source of variation (Table 3) for mussel bioenergetic status. According to a posteriori tests, the mussel O/N ratio increased significantly from August to September (Fig. 4).

Variations of nutrient ratios

N/P ratio

According to the ANOVA results, the interaction of treatment, date, and time was significant for N/P ratios (Table 4).

Fig. 1. Mean biomass percentage of each faunal group of the macrofauna associated with mussels (sedentary epifauna, shaded bars; errant epifauna, open bars; sedentary infauna, solid bars) on 1- (L1) and 2- (L2) year-old lines in August and September 2003.



In August, N/P ratios measured in W were not significantly different at T_0 and T_{1h30} (SNK tests; Fig. 5), in contrast with M1, M2, L1, and L2 where the mean N/P ratio at T_{1h30} was always higher than the value at T_0: 1.75 times higher in M1, 1.5 times higher in L1, 2 times higher in M2, and more than 2 times higher in L2. In September, N/P ratios were significantly lower than those observed in August, whatever the incubation time and treatment (Fig. 5; SNK tests). The N/P ratios in W and L1 did not vary significantly during the incubations, whereas they increased significantly with incubation time in M1, M2, and L2 (Fig. 5). Increases in the N/P ratios in September were less marked than in August (1.5 times in M1, 1.8 times in M2, and 1.6 times in L2).

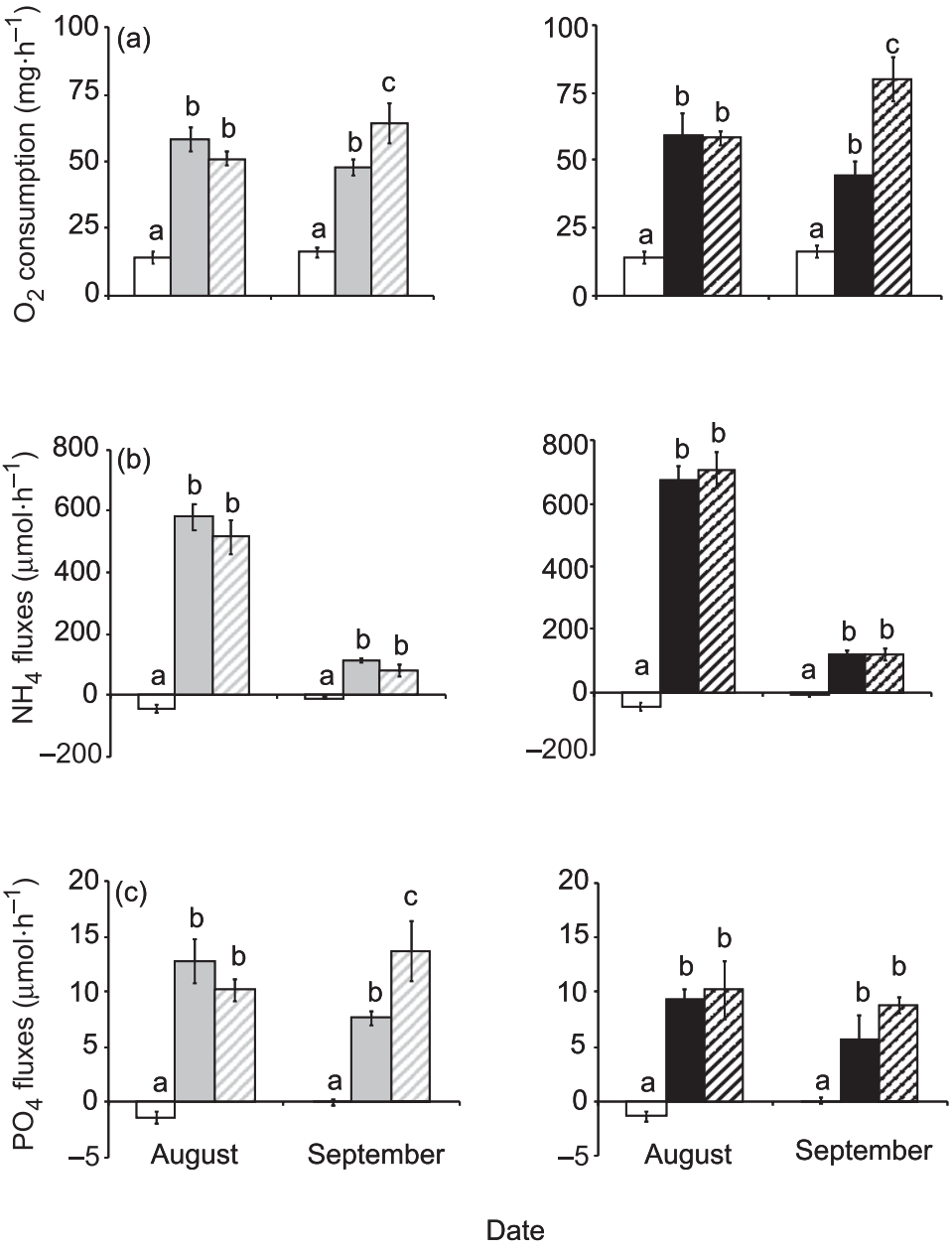
Si/N ratio

The interaction of treatment and time was a significant source of variation for Si/N ratios (Table 4). The Si/N ratios measured in W were not significantly different at T_0 and T_{1h30}, while significant decreases were observed with time in M1, M2, L1, and L2 (Fig. 6*a*; SNK tests). A mean decrease of 49% ± 3% was recorded in M1, vs. 39% ± 3% in M2, 48% ± 3% in L1, and 48% ± 5% in L2. Even though the evolution of the Si/N ratios with incubation time exhibited the same pattern in August and September, date was also a source of variation for Si/N ratios (Table 4); the August values (0.09–0.70) were significantly smaller than the values of September (0.36–1.61; SNK tests).

Si/P ratio

The interaction of date and time was significant for the Si/P ratios (Table 4). The September ratios were significantly greater than the August values at the beginning (5.64 ± 0.14 vs. 4.32 ± 0.1, respectively) and at the end (4.23 ± 0.26 vs. 3.79 ± 0.16, respectively) of the incubations. The interaction of treatment and time was also significant for Si/P ratios (Table 4). Ratios were not significantly different at T_0 and T_{1h30} in W in contrast with all other treatments (greater values at T_0 than at T_{1h30}; Fig. 6*b*, SNK tests), where we observed a mean decrease of 76% ± 3% in M1, 76% ± 5% in M2, and 64% ± 6% in L1 vs. 85% ± 4% in L2.

Fig. 2. Mean (± standard error) oxygen (*a*), ammonium (*b*), and phosphate (*c*) fluxes measured in the Aquamoule experiments for each treatment (control (water, W), open bars; 1-year-old mussels (M1), shaded bars; 1-year-old lines (L1), grey hatched bars; 2-year-old mussels (M2), solid bars; 2-year-old lines (L2), black hatched bars) in August and September 2003. Except for W, flux values were standardized to 50 g ash free dry weight (AFDW) mussel biomass. Different letters indicate a significant difference between treatments at a given date; Student–Newman–Keuls (SNK) tests, $p < 0.05$.



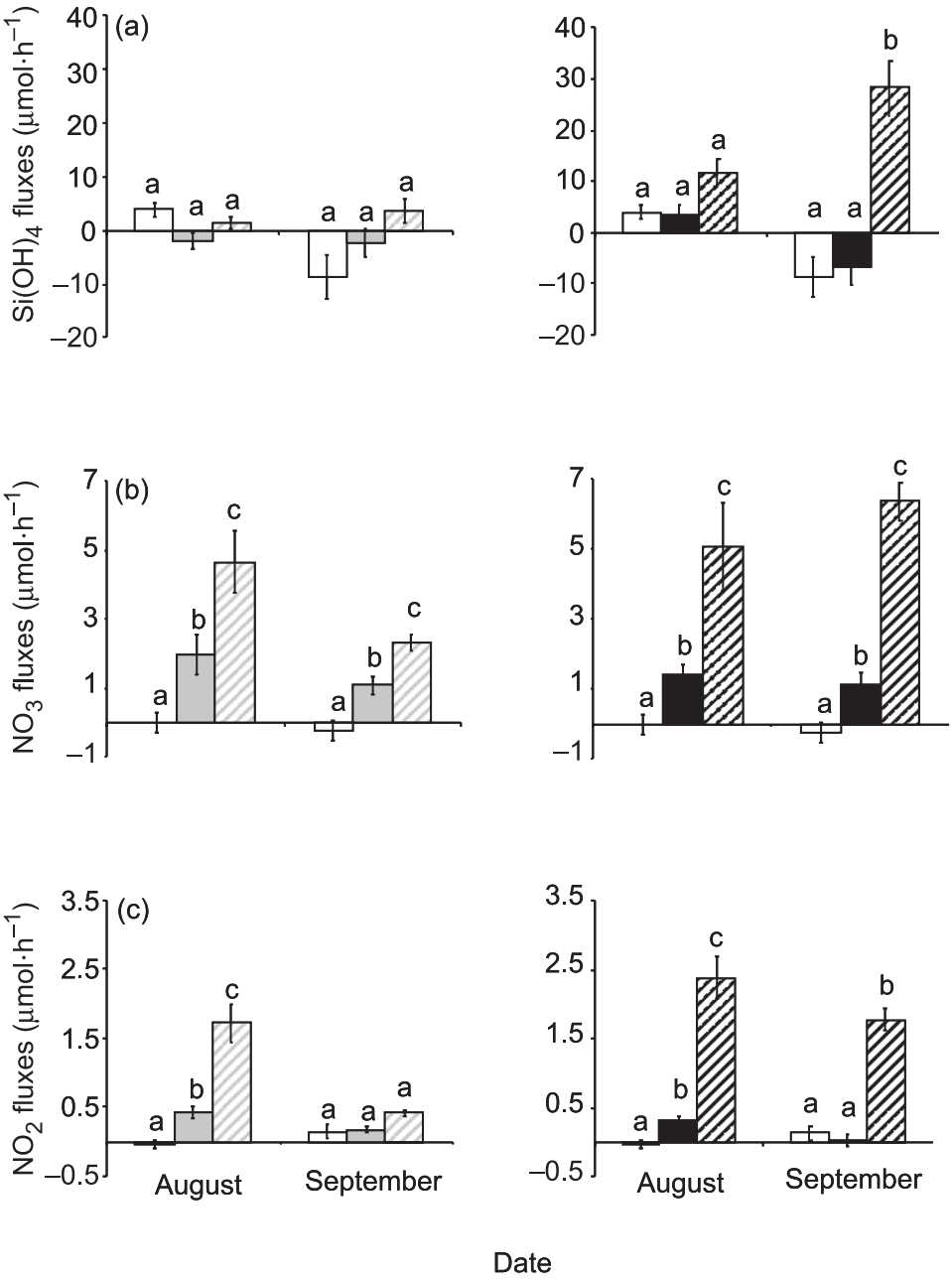
Discussion

This study clearly shows the influence of mussel lines on the biogeochemical fluxes in adjacent waters. Biogeochemical fluxes at the line interfaces (L treatments) were mainly superior to fluxes measured in water. Mussel lines act as oxygen sinks and nutrient sources (with $NH_4 >> Si(OH)_4$, $PO_4 > NO_3 > NO_2$). Biogeochemical fluxes at the water–line interfaces result from the metabolic activities of the macrofauna (mussels and associated fauna) and from organic matter degradation by bacteria. In this study, the relative influence of these processes varied according to type of flux and the date.

Influence of mussel metabolism on biogeochemical fluxes in water

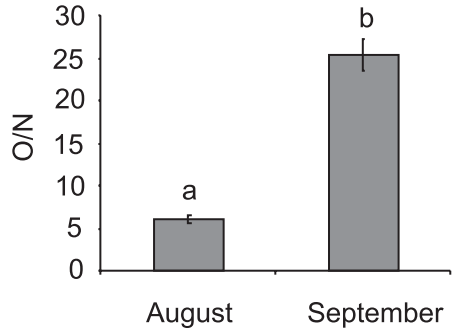
In this study, NH_4, PO_4, and NO_3 releases were greater in the mussel treatments (M1 and M2) than in controls (W). LeBlanc et al. (2003) also observed N and P productions by mussels. These fluxes were considered to be the result of mussel metabolic activities, since the inorganic products of

Fig. 3. Mean (± standard error) silicate (*a*), nitrate (*b*), and nitrite (*c*) fluxes measured in the Aquamoule experiments for each treatment (control (water, W), open bars; 1-year-old mussels (M1), shaded bars; 1-year-old lines (L1), grey hatched bars; 2-year-old mussels (M2), solid bars; 2-year-old lines (L2), black hatched bars) in August and September 2003. Except for W, flux values were standardized to 50 g ash free dry weight (AFDW) mussel biomass. Different letters indicate a significant difference between treatments at a given date; Student–Newman–Keuls (SNK) tests, $p < 0.05$.



bivalve excretion are mainly NH_4 (Dame et al. 1984; Boucher and Boucher-Rodoni 1988) and PO_4 (Dame and Libes 1993; Schlüter and Josefsen 1994; Asmus et al. 1995), while bivalve faeces and pseudofaeces are sources of P (Sornin et al. 1986; Grenz et al. 1992; Asmus et al. 1995) and N (Kautsky and Evans 1987; Smaal and Zurburg 1997). NO_3 excretion would be the result of enhanced natural nitrification processes by bacteria occurring in some parts of the bivalve digestive glands (Boucher and Boucher-Rodoni 1988). In addition, NH_4 release by the mussels would have stimulated the nitrification process, as has been observed in oysters (Gilbert et al. 1997). This would explain why NO_2, which is an intermediate product of the nitrification process, displayed significantly higher fluxes in August in the mussel treatments than in water. $Si(OH)_4$ fluxes measured in the mussel treatments were similar to Si fluxes measured in water. $Si(OH)_4$ uptakes could originate from the consumption of silicates by siliceous phytoplankton (diatoms). $Si(OH)_4$ release originates from the dissolution of siliceous phytoplankton tests (Balzer et al. 1983; Lerat et al. 1990). It

Fig. 4. Mean (± standard error) values of the mussel O/N ratios (M1 and M2 were combined) in August and September 2003. Different letters indicate a significant difference between dates; Student–Newman–Keuls (SNK) tests, $p < 0.05$.



is not surprising that mussels alone do not modify $Si(OH)_4$ release into the water. Indeed, during the experiment, mussels synthesized fresh biodeposits probably containing siliceous phytoplankton tests. A 1.5 h incubation time would be too short to observe biogenic silica dissolution in water, since Baudinet et al. (1990) considered that $Si(OH)_4$ regeneration taking place within 2 months was rapid.

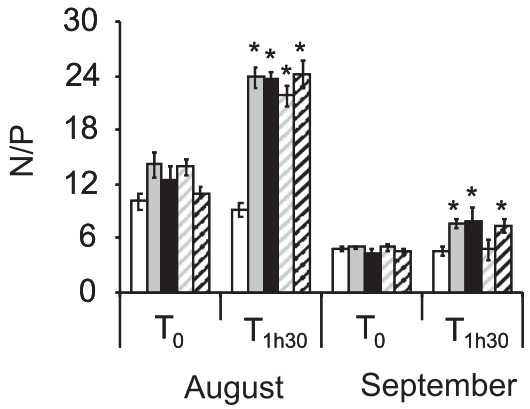
The influence of 50 g AFDW of 1-year-old mussels on O_2 consumption and NH_4 and PO_4 releases seemed to be equivalent to that of 50 g AFDW of 2-year-old mussels. Nevertheless, as Bayne and Scullard (1977) and Sukhotin et al. (2003) related, mussel size had a significant influence on individual metabolic rates, since individual respiration and excretion rates of 2-year-old mussels were greater than those of 1-year-old mussels.

Influence of mussel metabolism on biogeochemical fluxes varied between the two dates of experimentation; it is shown by the individual NH_4 excretion rates decreasing significantly from August to September. These results could be explained by the decrease in water temperature between August (19.33 ± 0.83 °C) and September (15.70 ± 0.48 °C), since temperature influences bivalve metabolic activities such as NH_4 excretion (Khalil 1994; Schlüter and Josefsen 1994; Mazouni et al. 2001). Nevertheless, the decrease of individual NH_4 excretion rate was important compared with the temperature decrease; the Q_{10} for NH_4 excretion in *Mytilus edulis* for the temperature interval 16–21 °C is known to be 1.3 (Bayne and Scullard 1977). Thus, temperature was not the only source of variation for NH_4 excretion.

By contrast, individual mussel respiration and PO_4 excretion rates did not decrease between dates. O_2 consumption (Kautsky and Wallentinus 1980; Murphy and Kremer 1985; Boucher and Boucher-Rodoni 1988) and PO_4 release (Schlüter and Josefen 1994) are known to be influenced by water temperature. Bayne and Scullard (1977) also found that bivalve O_2 consumption and NH_4 excretion do not always vary in the same direction, or to the same extent, in response to changes in the environment.

Variations in the individual O/N ratios integrate the changes in O_2 consumption and NH_4 excretion and give information on the physiological status of the organisms (Schlüter and Josefen 1994; Hatcher et al. 1997; Tremblay et al. 1998). An O/N ratio under 25–30 indicates that a high proportion of proteins is being catabolized (Widdows 1978). In this study, there was no significant difference between the

Fig. 5. Mean (± standard error) values of the N/P ratios measured at the beginning (T_0) and at the end (T_{1h30}) of the incubation experiments for each treatment (control (water, W), open bars; 1-year-old mussels (M1), shaded bars; 1-year-old lines (L1), grey hatched bars; 2-year-old mussels (M2), solid bars; 2-year-old lines (L2), black hatched bars) and each date (August and September 2003). N = total nitrogen. Asterisks indicate that N/P ratios were significantly different between T_0 and T_{1h30}; Student–Newman–Keuls (SNK) tests, $p < 0.05$.



O/N ratios of M1 and M2, on either date, implying a similar physiological condition for all mussels. The ratio values exhibited significant differences between the two dates of experimentation, from 5–7 August to 24–27 September. A maximum value of 30 was found for *Mytilus edulis* in Upper South Cove, Nova Scotia (Canada; Hatcher et al. 1997). In the Îles-de-la-Madeleine, Tremblay et al. (1998) also found low O/N ratios (14 ± 3) at the beginning of August and attributed these values to unfavourable environmental and mussel physiological conditions. Hatcher et al. (1997) stated that O_2 consumption and NH_4 excretion could be linked to mussel reproductive status. Similarly, Bayne and Scullard (1977) assumed that high NH_4 excretion rates could be due to the catabolism of short-term reserves used to support reproduction requirements. In the Îles-de-la-Madeleine, mussels spawn twice during summer: in late June (Myrand 1991) and late July (Myrand and Gaudreault 1995). Thus, mussels could be in a weak post-spawning state in early August. Tremblay et al. (1998) related the decrease in the O/N ratios in August to reproduction because the mantle undergoes autolysis, reorganization, and regeneration following spawning. This period also includes frequent but sporadic mass mortality events (Myrand and Gaudreault 1995; Tremblay et al. 1998). Summer mortality would be the result of a synergistic interaction involving high temperature, a possible post-spawning stress, and the genetic characteristics of the stock (Tremblay et al. 1998). The decomposition of dead organisms (Balzer et al. 1983), as dead and dying mussels observed in mussel lines in August, and protein catabolism by mussels in poor condition could explain the great NH_4 excretion and consequent low O/N ratios in August. Mussel condition probably improved rapidly between early August and late August – early September, since mean daily mussel shell growth rates in this period (220 $m \cdot day^{-1}$ for 1-year-olds and 83 $m \cdot day^{-1}$ for 2-year-olds; M. Richard, unpublished data) were among the highest ever recorded in the Îles-de-la-Madeleine. Indeed, mean daily mussel shell

growth rates in the range of 125–224 m·day^{-1} were recorded in pearl nets for 1-year-olds between late July and late August 1990 vs. 46–72 m·day^{-1} for 2-year-olds held in cages between June and November 1991 (Myrand and Gaudreault 1995). The variability of the influence of mussel metabolism on N fluxes in adjacent water between August and September could depend mainly on mussel physiological state.

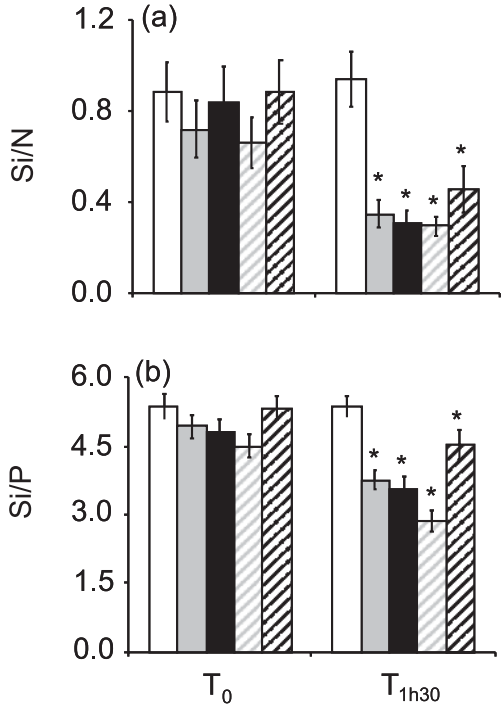
Influence of the AFOM complex on biogeochemical fluxes

Mussel lines provide a new substrate for the settlement of marine benthic invertebrates, thus leading to the creation of a new ecological niche (Lesser et al. 1992; Dalby and Young 1993; Claereboudt et al. 1994; this study). Indeed, 12 invertebrate genera were observed on mussel lines in our experiment. Most of these biofoulers have already been observed on mussel lines in Tracadie Bay, Prince Edward Island (PEI), Canada (LeBlanc et al. 2003). In our study, the total biomass of the associated macrofauna was very low (≤0.16%) compared with the mussel biomass of the standardized samples. In comparison, Mazouni (1995) found that the associated fauna could represent up to 80% of the total faunal biomass on oyster lines in the Thau lagoon (France) in summer. The biomass of the associated fauna in this study was also much lower than that found on mussel lines in PEI (681 mg for 10 g AFDW of mussels in September; LeBlanc et al. 2003).

The dominant species of associated fauna depended on line age. The faunal community of L1 was mainly composed of epifauna (mostly mussel spat), whereas that of L2 was dominated by infauna. This result would signify that the thickness of the organic matter biodeposit was sufficient to sustain an infaunal community at the 2-year-old mussel line interface. Indeed, biofouling organisms and cultivated bivalves are known to generate organic matter accumulation within aquaculture structures, leading to the creation of a new "soft-bottom" interface suspended in the water column (Arakawa 1990; Mazouni et al. 2001). The associated fauna of L2 was more diverse than that of L1, which agrees with Taylor et al. (1997), who observed that the number and composition of fouling species associated with the pearl oyster varied considerably with immersion time. Pearson and Rosenberg (1978) found that food availability was the most fundamental variable underlying the structure (diversity) of marine communities. The faeces and pseudofaeces trapped between mussel shells on lines could be a supplementary food source for the associated fauna and even the main food source for deposit-feeding species. Organic matter increase with immersion time could explain the greater abundance of deposit-feeding infauna (*Amphitrite* sp. and *Corophium* sp.) on L2 compared with L1. The increasing complexity with age of the line microhabitat would partly explain higher faunal diversity on L2 compared with L1.

The AFOM complex was a major contributor to NO_3 and NO_2 fluxes in this study (e.g., 52%–83% of total NO_3 fluxes and 75%–95% of total NO_2 fluxes, depending on the date and line age) and to $Si(OH)_4$ fluxes in the case of L2 in September. This contribution, which could not mainly originate from the metabolism of the low associated faunal biomass, was likely to result from biodeposit mineralization. Indeed,

Fig. 6. Mean (± standard error) values of the Si/N (*a*) and Si/P (*b*) ratios measured at the beginning (T_0) and at the end (T_{1h30}) of the incubation experiments for each treatment (control (water, W), open bars; 1-year-old mussels (M1), shaded bars; 1-year-old lines (L1), grey hatched bars; 2-year-old mussels (M2), solid bars; 2-year-old lines (L2), black hatched bars). Values were combined within dates according to analysis of variance results. N = total nitrogen. Asterisks indicate that the ratios were significantly different between T_0 and T_{1h30}; Student–Newman–Keuls (SNK) tests, $p < 0.05$.



the decomposition of biodeposits (faeces and pseudofaeces) trapped between bivalve shells is a great N source (Sornin et al. 1983; Boucher and Boucher-Rodoni 1988; Grenz et al. 1992), explaining the NO_2–NO_3 releases after nitrification processes (Henricksen and Kemp 1988; Gilbert et al. 1997; Christensen et al. 2003). In the same way, dissolution of siliceous phytoplankton tests contained in mussel biodeposits trapped between shells could explain the great $Si(OH)_4$ releases on L2. Greater contribution of the L2 AFOM complex to $Si(OH)_4$, NO_3, and NO_2 fluxes, compared with L1, could originate from the mineralization of a probably greater organic matter amount in L2.

By contrast, the contribution of the AFOM complex to NH_4 fluxes was not significant compared with mussel metabolism, which disagrees with previous studies on bivalve culture devices and beds (Boucher and Boucher-Rodoni 1988; Grenz et al. 1992; LeBlanc et al. 2003). Moreover, bioturbation activities by infaunal organisms (deposit feeding, sediment reworking and irrigation, construction of burrows and tubes; Rosenberg 2001), such as *Amphitrite* sp. and *Corophium* sp. in our study, are known to increase NH_4 releases (Lerat et al. 1985; Kristensen and Blackburn 1987; Biles et al. 2003). The nonsignificant contribution of the AFOM complex to NH_4 fluxes could probably originate from higher intra-treatment than inter-treatment variability

of NH_4 releases, but also from the low associated faunal biomass compared with mussel biomass.

Our study also emphasizes the variability of the AFOM complex's contribution to the biogeochemical fluxes between the two dates of experimentation. The O_2 and PO_4 fluxes at the L1 interface were significantly different from those measured at the M1 interface in September but not in August. The higher contribution of the AFOM complex to the O_2 and PO_4 fluxes in September (despite the temperature decrease) could be associated with higher epifaunal biomass (mainly mussel spat). The increase in the epifaunal biomass on L1 would be due to the growth of juvenile mussels recruited in August according to the duration of the mussel larval stage in the Îles-de-la-Madeleine (3–4 weeks; Poirier and Myrand 1982). The metabolic activities of growing mussel spat largely explained why the contribution of the L1 AFOM complex to O_2 and PO_4 fluxes increased with time. In contrast, the significant decreases in the NO_3 and NO_2 fluxes between August and September (in both the M1 and L1 treatments) could emphasize the decrease of mussel NH_4 excretion.

A different pattern was observed on the 2-year-old mussel lines; a probable increase, with immersion time, of the amount of mussel biodeposits trapped on the line sections could have stimulated microbial activity (Dahlbäck and Gunnarson 1981) and induced higher O_2 demand and nutrient (NO_3 and $Si(OH)_4$) fluxes in September compared with August. The increase of infaunal taxa between August and September would have promoted bioturbation activities within the biodeposit mat and thus increased the microbial activity, O_2 demand (Murphy and Kremer 1985; Kristensen and Blackburn 1987; Nickell et al. 2003), and nitrification process (Jenkins and Kemp 1984; Kristensen and Blackburn 1987; Aller 1988). Excretion products (NH_4 and fecal pellets) are transformed by nitrifying bacteria and induce NO_3–NO_2 fluxes at the interface. As well, bioturbation can also enhance $Si(OH)_4$ release (Baudinet et al. 1990; Caffrey et al. 1996).

Influence of mussel lines on nutrient pools and ratios

Mussel lines acted as nutrient sources to the adjacent water. In particular, large amounts of NH_4 and PO_4 releases, mainly by-products of mussel metabolism, were observed at the water–line interfaces, while small NH_4 uptakes occurred in water. Biodeposition and nutrient excretion by filter feeders can play a large role in controlling the amounts of nutrients regenerated in coastal ecosystems. High abundances of bivalves can enhance N (Dame et al. 1989; Smaal and Zurburg 1997; Smaal et al. 2001) and P (Dame et al. 1989; Asmus et al. 1995) turnover. The ecological importance of nutrient regeneration is the reduction of nutrient limitation for phytoplankton, which could result in increased primary production (Smaal 1991). Disequilibria in nutrient release kinetics can change the original nutrient ratios and the specific composition of phytoplankton communities (Baudinet et al. 1990; Chauvaud et al. 2000; Ragueneau et al. 2002). According to Redfield et al.'s theories (1963), normal nutrient ratios for phytoplankton growth are 16:16:1 for Si:N:P. Any variation of this ratio results in nutrient limitation (Ragueneau 1994).

In this study, the initial N/P ratios were <16, indicating potential N limitation (Howarth 1988; Dame and Libes 1993) in lagoon water, especially in September. Souchu et al. (1991) have mentioned that N could be limiting for phytoplankton production in the Îles-de-la-Madeleine. The higher N/P ratios observed at the M and L interfaces compared with the controls (W) at T_{1h30} suggest that mussel lines could reduce the probability or amplitude of N deficiency in adjacent water. A 1.6- to 2.2-fold increase in the N/P ratios was measured in the M and L treatments during the incubations in August vs. a 1.5- to 1.8-fold increase in September. The large decreases in the initial N/P ratios from August to September in the M and L treatments would mostly result from variability of NH_4 excretion by mussels between August and September and thus from mussel condition. Similar NH_4 releases in the M and L treatments at both dates demonstrate that NH_4 out-flux was totally driven by mussel excretion in this study. It is likely that NH_4 excretion by mussels among other NH_4 sources, as benthic interface or atmospheric inputs, could play an important role in N recycling in the Îles-de-la-Madeleine lagoon. This N source could favour the growth of small-sized phytoplankton (flagellates and dinoflagellates; Officer et al. 1982).

The N source at the line interfaces was greater than the $Si(OH)_4$ source. The Si/N ratios calculated in water were ~2 times greater than those calculated for mussels or lines at the end of the incubations, whatever the date. There was no apparent $Si(OH)_4$ limitation in water at T_0 (Si/N ~ 1) in contrast with the mussel or line treatments at T_{1h30} (Si/N ≤ 0.4). When considering the Redfield ratios, mussel metabolism (NH_4 excretion) could be a factor of $Si(OH)_4$ limitation that could favour the development of nonsiliceous microalgae (Smayda 1990). However, diatom growth may depend more on $Si(OH)_4$ concentration than on nutrient ratios. For example, Egge and Asknes (1992) observed in Norway that diatom dominance occurred when $Si(OH)_4$ concentration was >2 $mol \cdot L^{-1}$, while flagellates were dominant with lower Si concentrations. Kennington et al. (1999) also showed that the specific composition of phytoplankton blooms in the northeast Irish Sea varied according to nutrient concentrations and nutrient ratios. $Si(OH)_4$ concentrations were always >2 $mol \cdot L^{-1}$ in this study and increased with incubation time in the L treatments. The final $Si(OH)_4$ concentration was maximal in L2 (up to 3.96 $mol \cdot L^{-1}$). Since mussel lines increased $Si(OH)_4$ concentration in adjacent water but decreased the Si/N ratio, their potential effect on phytoplankton specific composition is not clear. Further studies in situ are required to investigate the possible effect on phytoplankton composition.

This study illustrates the influence of two types of suspended mussel lines on biogeochemical fluxes (oxygen and nutrients) in the surrounding water. Results showed that (*i*) mussel metabolism contributed mainly to O_2 demand, NH_4, and PO_4 fluxes. Mussel influence was greater in stressful conditions (high temperature and post-spawning state) that lead to high NH_4 releases. (*ii*) The associated fauna – organic matter complex could greatly contribute to NO_3, NO_2, and $Si(OH)_4$ fluxes. In regard to low associated faunal biomass, this contribution could originate from mineralization of organic matter trapped between shells rather than

from associated faunal metabolism. The magnitude of the contribution of the AFOM complex on these nutrient sources could depend on the AFOM complex composition and thus on line immersion time. (*iii*) The mussel lines could lead to an increase in nutrient availability, particularly for NH_4 in adjacent water. At the lagoon level, this supplied source among others, such as benthic and atmospheric sources, could be a factor of reduction of the N limitation in water column.

This experimental study shows that mussel lines act as a new "benthic-suspended" interface for biogeochemical exchanges in the water column. Introduction of this new interface in the cultivated ecosystem changes the biogeochemical cycles from a benthic–pelagic system to a benthic–pelagic–aquaculture structure system and should be considered in environmental carrying capacity models.

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Influence of suspended scallop cages and mussel lines on pelagic and benthic biogeochemical fluxes in Havre-aux-Maisons Lagoon, Îles-de-la-Madeleine (Quebec, Canada)

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Abstract: An in situ experiment was done in July 2004 to test and compare the influence of suspended bivalve cultures (1- and 2-year-old blue mussels (*Mytilus edulis*) and sea scallops (*Placopecten magellanicus*)) on biogeochemical fluxes in the water column and at the benthic interface in Havre-aux-Maisons Lagoon (Quebec, Canada). Aquaculture structures increased the pelagic macrofaunal biomass (PMB) and acted as an oxygen sink and nutrient source in the water column under dark conditions. Although PMB was lower in scallop culture, the influence of scallop cages on pelagic fluxes was similar to or greater (nitrate and nitrite) than that of mussel lines. Sediments were organically enriched, and benthic macrofaunal abundances were decreased in mussel culture zones relative to the control zone, but such an effect was not observed in the scallop zone. Nevertheless, benthic oxygen demand did not vary among culture types and control zones. Benthic nutrient fluxes were greatest beneath aquaculture structures. Both pelagic and benthic interfaces may modify oxygen and nutrient pools in culture zones in Havre-aux-Maisons Lagoon. The contribution of aquaculture structures to oxygen, ammonium, and phosphate pools may be a function of PMB and type. While aquaculture structures had an important role on nitrate and nitrite cycling, silicate turnover was mainly driven by benthic mineralization of biodeposits.

Résumé : Une série d'expériences in situ a été réalisée en juillet 2004 afin de tester et de comparer l'influence de cultures de bivalves en suspension (moules (*Mytilus edulis*) de 1 an et de 2 ans et pétoncles (*Placopecten magellanicus*)) sur les flux biogéochimiques dans la colonne d'eau et à l'interface eau-sédiment dans la lagune du Havre-aux-Maisons (Québec, Canada). Les structures aquacoles augmentent la biomasse de la macrofaune pélagique (PMB) et agissent comme un puits d'oxygène et une source de nutriments dans la colonne d'eau en condition d'obscurité. Bien que la PMB soit plus faible au niveau de la pectiniculture, l'influence des paniers de pétoncles sur les flux pélagiques est similaire, voire supérieure (nitrates et nitrites), à celle des filières de moules. Au contraire de la pectiniculture, les cultures de moules enrichissent le sédiment en matière organique et diminuent l'abondance des organismes benthiques par comparaison aux zones témoins. Cependant, la demande benthique en oxygène ne varie pas entre les différentes zones de culture et les zones témoins. Les flux benthiques de sels nutritifs atteignent un maximum sous les structures aquacoles. L'interface benthique et l'interface pélagique modifient potentiellement les stocks d'oxygène et de sels nutritifs dans les zones de cultures de la lagune du la lagune du Havre-aux-Maisons. La contribution des structures aquacoles aux stocks d'oxygène, d'ammonium et de phosphates pourrait dépendre de la PMB et du type des bivalves en culture. Alors que les structures aquacoles jouent un rôle important dans le cycle des nitrates et des nitrites, le cycle du silicium est régi principalement par la minéralisation benthique des biodépôts.

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Introduction

Structures used in suspended bivalve aquaculture, such as longlines or cages, provide substrates for both cultivated and biofouling organisms in the water column (Lesser et al. 1992; Claereboudt et al. 1994; McKindsey et al. 2006). Over time, organic matter accumulates within the structure, and the abundance and biomass of the associated organisms increase (Taylor et al. 1997; Mazouni et al. 2001; Richard et al. 2006). Only four studies have examined the influence of this novel suspended benthic interface on biogeochemical fluxes in the water column (i.e., Leblanc et al. 2003; Mazouni 2004; Nizzoli et al. 2006; Richard et al. 2006), although the metabolism of cultivated bivalves and their associated fauna as well as the degradation of associated organic matter have been shown to increase oxygen consumption and nutrient releases in the adjacent water (Richard et al. 2006).

Biodeposition by cultivated bivalves has been shown to organically enrich sediments (Grenz et al. 1990; Deslous-Paoli et al. 1998; Stenton-Dozey et al. 2001), which has been shown to increase oxygen consumption and nutrient fluxes at the water–sediment interface (Baudinet et al. 1990; Hatcher et al. 1994; Christensen et al. 2003). Organic enrichment and decreased oxygen concentrations may lead to less diverse benthic communities (Pearson and Rosenberg 1978; Nilsson and Rosenberg 2000; Gray et al. 2002). Since benthic community metabolism depends partly on macrofaunal biomass (Mazouni et al. 1996) and abundance (Nickell et al. 2003; Welsh 2003), any change in macrofaunal biomass or abundance may influence benthic biogeochemical fluxes.

Aquaculture structures contain a great biomass of macrofauna, whereas the benthic interface is largely dominated by the mass of sediments. Owing to their different compositions, biogeochemical processes may vary between interface types and lead to contrasting nutrient release ratios (e.g., Si/N/P). Disequilibria in nutrient release kinetics can alter the original nutrient ratios and thus the specific composition of phytoplankton communities (Baudinet et al. 1990). Thus, the two interfaces may have different influences on phytoplankton community composition. The contribution of the pelagic interface to these pools is likely to be a function of the density of aquaculture structures as well as their composition (bivalve size and species, associated organisms, detritus, etc.).

The aim of this study was to examine and compare the influence of suspended bivalve culture on oxygen and nutrient pools and nutrient ratios in a semi-enclosed lagoon. Specifically, we used in situ mensurative experiments (sensu Hulbert 1984) to evaluate oxygen and nutrient fluxes at both the pelagic (i.e., aquaculture structure) and benthic (sediment) interfaces associated with all types of aquaculture being practiced in the studied lagoon (i.e., sea scallops (*Placopecten magellanicus* Gmelin) in pearl nets and 1- and 2-year-old blue mussels (*Mytilus edulis* L.) on longlines). This study is the first to test the influence of suspended scallop culture and one of the few studies to compare benthic and pelagic influences of suspended bivalve cultures (Mazouni 2004; Nizzoli et al. 2006). For efficacy, we use the term flux when discussing either oxygen consumption (i.e., decreasing oxygen concentration) or nutrient generation (i.e., increasing nutrient concentration). Several factors associated with bivalve culture (organic matter, associated macrofaunal assemblages) were also evaluated to better understand the mechanisms involved.

More specifically, three hypotheses were evaluated in this study: (*i*) the introduction of suspended aquaculture structures increases biogeochemical fluxes in the water column; (*ii*) sediment organic matter content, macrofaunal abundance, and fluxes are greater at the benthic interface in culture zones than in a control zone, whereas the opposite is true with respect to macrofaunal biomass; and (*iii*) ratios of nutrient releases and the contribution to oxygen and nutrient pools differ between interfaces, such that pelagic interfaces consume more oxygen and produce more nitrogen and phosphate, whereas benthic interfaces produce more silicate. We further predict that both the benthic and pelagic influences of 2-year-old mussel lines would be greater than those of 1-year-old mussel lines and scallop cages, as their biomass was greatest.

Materials and methods

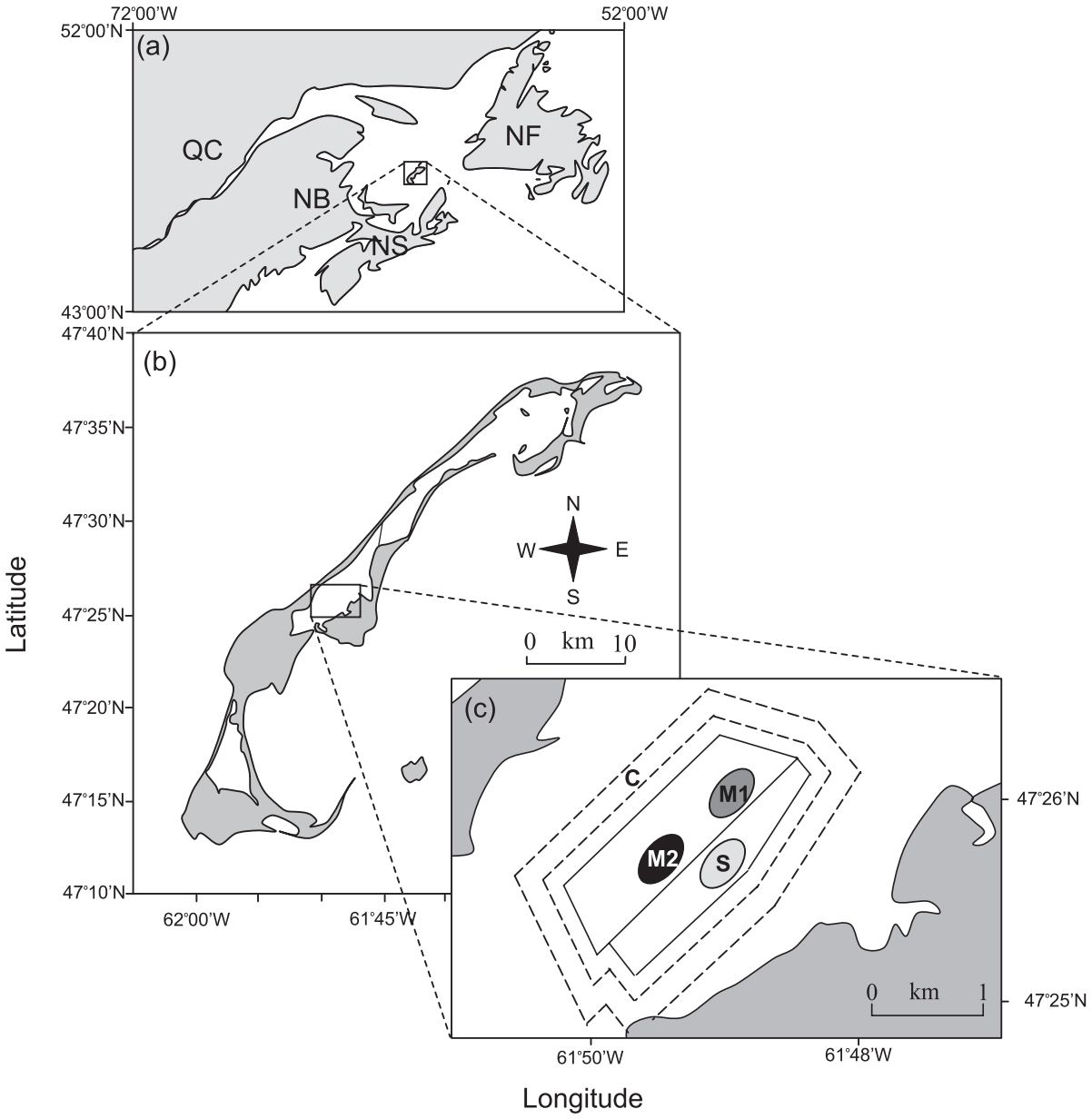
Study area

The study was done in the Îles-de-la-Madeleine archipelago located in the Gulf of St. Lawrence, eastern Canada (Fig. 1*a*). The study area was the Havre-aux-Maisons Lagoon (HAM) located in the central part of the archipelago (47°26′N, 61°50′W; Fig. 1*b*). The surface area of HAM is 30 km^2 (Comité ZIP des Îles 2003). HAM is linked to the Gulf of St. Lawrence in the southeast and to the Grande-Entrée Lagoon in the northeast (Fig. 1*b*). As in Grande-Entrée Lagoon, rainfall is the only source of fresh water to HAM because of the absence of rivers (Souchu and Mayzaud 1991). Tides are small (mean of 0.58 m; Koutitonsky et al. 2002). As observed in Grande-Entrée Lagoon (Souchu et al. 1991), shallow water (maximum depth of 6 m) and frequent winds up to 15 $m \cdot s^{-1}$ (Souchu et al. 1991) may lead to water column mixing. Over the course of the study in July 2004, the mean (± standard error, SE) salinity, temperature, and oxygen concentration were 30.83 ± 0.02 psu, 19.07 ± 0.14 °C, and 7.1 ± 0.13 $mg \cdot L^{-1}$, respectively. The mean chlorophyll *a* concentration (± standard deviation, SD) measured in the summer 2004 was 1.90 ± 1.09 $g \cdot L^{-1}$ (May to September; G. Tita, Centre de recherche sur les milieux insulaires et maritimes (CERMIM), 37 Chemin Central, Havre-aux-Maisons, Îles-de-la-Madeleine, QC G4T 5P4, Canada, guglielmo_tita@uqar.qc.ca, unpublished data).

Study shellfish cultures

HAM has been exploited for blue mussel culture since the 1980s. In 2004, mussel cultures were located in the central portion of the lagoon (Fig. 1*c*). In 2004, the annual production was 160 tonnes, and the farm surface area was 1.25 km^2 (A. Huet, Moules de culture des Iles, 721 chemin Gros-Cap, Étang du Nord, Îles-de-la-Madeleine, QC G4T 3M5, mciaqua@tlb.sympatico.ca, personal communication). The mussel grow-out cycle is approximately 2 years. For practical reasons, the 1-year-old (M1) and the 2-year-old (M2) mussel longlines were deployed in two distinct zones (Fig. 1*c*). Mussels were cultivated on 244 m long suspended mussel lines that are deployed in loops and attached to 76 m

Fig.1. Location of study area: (*a*) Gulf of St. Lawrence, Canada (QC, Quebec; NB, New Brunswick; NS, Nova Scotia; NF, Newfoundland); (*b*) Îles-de-la-Madeleine; (*c*) Havre-aux-Maisons Lagoon. Polygons with solid borders show the extent of scallop and mussel culture areas in July 2004. Ellipses correspond to scallop (S), 1 year-old mussel (M1), and 2-year-old mussel (M2) study zones. The control zone (C) is indicated by the peripheral polygon with broken borders.



long horizontal longlines anchored in the sediment at each end. These mussel longlines were separated from each other by 12 m (A. Huet, personal communication). In July 2004, there were 200 lines for M1 mussels and 40 lines for M2 mussels in the lease area, as most of the latter had already been harvested (A. Huet, personal communication). At that time, the density of mussel lines, expressed as the length of mussel sock per square metre of culture area (where mussel lines were still present, was 26 $cm \cdot m^{-2}$ in both mussel zones.

The sea scallop has also been cultivated on suspended longlines in HAM since the end of the 1990s to seed juveniles for scallop fishery areas located in the Gulf of St. Lawrence (Cliche and Guiguère 1998). The scallop culture zone (S) was located in the southeast portion of the lagoon (Fig. 1*c*). In fall 2003, juvenile scallops from collectors were transferred to pearl nets. Each of these pyramidal-shaped cages contained 100–150 scallops (shell size: 7–25 mm; D. Hébert, CultiMer, 55 route 199, Fatima, Iles-de-la-Madeleine, QC G4T 2H6, petoncle@tlb.sympatico.ca, personal communication). Cages were stacked in series of five and hung from the same type of longlines as used in mussel culture. One hundred and twenty-five of these stacks were installed on each longline in fall 2003 (S. Vigneau, CultiMer, 55 route 199, Fatima, Iles-de-la-Madeleine, QC G4T 2H6, petoncle@tlb.sympatico.ca, personal communication), 465 longlines supported scallop cages (≈29–44 million scallops). In July 2004, after the spring seeding of most of the scallops, only seven lines still had pearl nets (S.

Vigneau, personal communication). At that time, the density of scallop cages, expressed as the number of cages per square metre of culture area (in which scallop cages were still present), was $0.785 \cdot m^{-2}$ in S.

Experimental design

In situ experiments were performed in HAM during the summer when biogeochemical fluxes were known to be the greatest (Mazouni et al. 2001), such that they may lead to anoxia and eutrophication events in extreme cases (Deslous-Paoli et al. 1988; Gray et al. 2002). Experiments were thus carried out between 14 and 23 July 2004 in four zones: control (C, no bivalve culture), S, M1, and M2 (Fig. 1*c*). In contrast with many authors (e.g., Grenz et al. 1992; Grant et al. 1995; Mazouni et al. 1996), we designated a peripheral control zone rather than a single, local control site to distinguish the effect of aquaculture from the natural variability of the studied parameters (Fig. 1*c*). This design is more adequate to test the influence of given treatments (see Underwood 1997). It decreases confounding factors and the misinterpretation of results. Since the influence of bivalve biodeposition is typically considered to be restricted to a radius of 10–40 m around the farm (Dahlbäck and Gunnarson 1981; Mattsson and Lindén 1983; Callier et al. 2006), the control zone was located >100 m away from the bivalve farms to avoid or limit any potential impact of bivalve biodeposition on the benthic environment. The depth of each study zone was similar (5.6 ± 0.1 m).

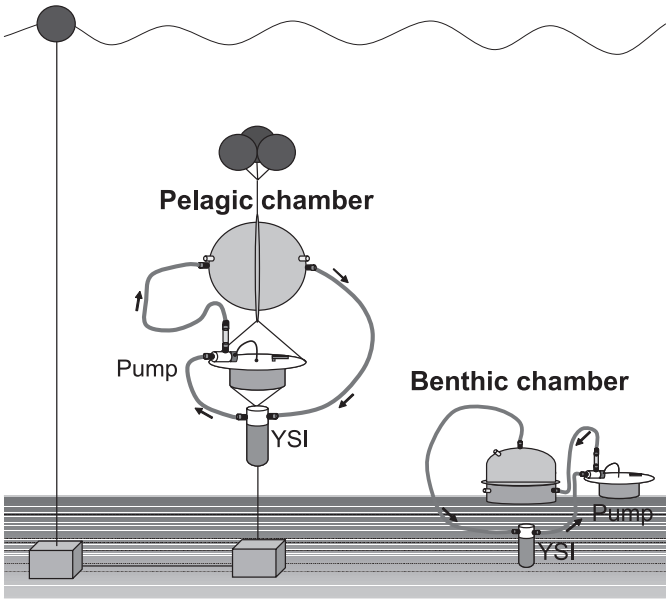
Pelagic chambers were deployed in each study zone by scuba divers at the mean depth of bivalve structures (3 m), whereas benthic chambers were placed at the water–sediment interface (Fig. 2). Pelagic chambers were maintained in the water column by anchoring them to the bottom with a cement block while keeping them buoyant with Styrofoam floats (Fig. 2). In the control zone, pelagic chambers were filled only with water, since there were no aquaculture structures in that zone. In contrast, they were filled with water and culture structures in culture zones (a scallop cage in S and a 15 cm mussel line section in M1 and M2). Care was taken to ensure that the pearl nets and mussel line sections were disturbed as little as possible during the experimental setup, as previous work in the area (Richard et al. 2006) has shown that organisms and sediments associated with such structures may have an important influence on fluxes. Experiments were done within each of six randomly chosen sites for each interface (pelagic vs. benthic) within each zone (C, S, M1, M2). Thus, a total of 48 in situ incubations were done.

Experimental chambers

Macrophytes were not observed on the sea floor or on aquaculture structures in the study zones. Dark chambers were used in preference to clear ones to prevent potential effects of microphyte photosynthesis (Lerat et al. 1990) on biogeochemical fluxes to isolate the effect of aquaculture on respiration and nutrient regeneration rates (Bartoli et al. 2001).

Pelagic chambers were composed of two removable acrylic hemispheres, whereas benthic chambers (Boucher and Clavier 1990; Richard et al. 2007; Thouzeau et al. 2007) were composed of an acrylic tube and a removable acrylic hemisphere (Fig. 2). The large volume of water in pelagic (82.5 L) and benthic (55.7–72.4 L, depending on the depth

Fig. 2. Schematic of in situ deployment of pelagic and benthic experimental systems. Both systems consisted of a dark chamber with a port to collect water samples, YSI 6600 probe, and submersible pump connected to waterproof batteries and three hoses. Pelagic chambers were deployed at the same depth as the bivalve structures (~3 m), whereas benthic chambers were placed at the water–sediment interface. The arrows indicate the direction of water circulation in the system.



to which the base was inserted into the sediment) chambers limited the increases of diffusive and metabolic fluxes caused by confinement or water warming. The large size of the benthic chambers (50 cm diameter, ~0.2 m^2 surface area) was also selected to limit disturbances of biogeochemical processes due to the insertion of the base into the sediment (Glud and Blackburn 2002) and to minimize the effects of spatial heterogeneity in the distribution of benthic fauna (Balzer et al. 1983).

Each chamber was linked to an adjustable, battery-fed submersible pump and YSI 6600 probe (Fig. 2). Water flow in each chamber was adjusted to 2 $L \cdot min^{-1}$ to mix the water inside the enclosures, eliminate noticeable particle resuspension, and allow stable measurements to be recorded by the YSI probes (Richard et al. 2006, 2007; Thouzeau et al. 2007).

Physico-chemical measurements and sample collections

Pelagic and benthic chambers were incubated for 1 and 2 h, respectively. These incubation times were selected to allow ammonium fluxes to be measured and to attain final oxygen concentrations that were not lower than 80% of initial concentrations (Richard et al. 2006, 2007). This was to prevent hypoxic conditions from developing that could modify macrofaunal metabolism (Mazouni et al. 1998). The YSI probe recorded oxygen concentration ($mg \cdot L^{-1}$ ± 0.01), temperature (°C ± 0.01), and salinity (psu ± 0.01) in the chamber at 1 min intervals throughout the incubation. This monitoring allowed us to verify if there was any change in the experimental conditions that could modify the biogeochemical processes in the chambers (e.g., an increase in water temperature).

Water samples (n = 3) were collected through ports in the chambers by scuba divers using 60 ml syringes at the start, middle (just for benthic chambers), and end of the incubations for nutrient (ammonium, silicate, phosphate, nitrate, and nitrite) analyses. At the end of pelagic incubations, scuba divers opened the chambers and collected the scallop cage or mussel line section to determine its composition (cultivated bivalves and associated macrofauna) in terms of biomass and abundance. At the end of benthic incubations, the hemispheres were gently pulled off the bases and scuba divers used 60 mL disposable syringes with the ends cut off to collect three sediment samples for analysis of the organic matter contained within the first 2 cm. A single larger sediment core (surface area = 262.5 cm^2; Wildish et al. 2003) was also collected by scuba divers for analysis of benthic macrofaunal biomass and abundance. We assume that the large core surface used to collect the benthic community samples was representative of the whole community in the benthic chamber.

Sample processing

Pelagic and benthic macrofauna

Aquaculture structure and benthic macrofaunal samples were sieved through a 0.5 mm screen. Cultivated bivalves and associated and benthic macrofauna were frozen separately at –18 °C until processed. Abundances of the cultured bivalves and associated and benthic macrofauna were determined. Cultured bivalves were thawed in aluminium trays in the laboratory to retain leached water, dried at 60 °C for 72 h, and weighed so as to not underestimate their dry weight (DW: dry weight with shells). The biomass of associated and benthic organisms was similarly obtained. Mussel and scallop biomasses were measured to the nearest 0.1 g with a PG 5001-S Mettler Toledo balance, whereas associated and benthic macrofaunal biomasses were measured to the nearest 10^{-5} g with an AG285 Mettler Toledo balance. Following the methods used by Mazouni et al. (1998) and Nizzoli et al. (2006), pelagic macrofaunal biomass and abundance (in-chamber biomass and abundance expressed per 15 cm mussel sock and per scallop cage) were standardized to the in situ density of aquaculture structures in culture zones (i.e., 26 cm of mussel lines and 0.785 cage·m^{-2} of lagoon bottom in mussel and scallop zones, respectively) to obtain in situ pelagic macrofaunal biomass and abundance (g DW·m^{-2} or individuals·m^{-2}). Benthic macrofaunal biomass and abundance were similarly standardized per square metre of lagoon bottom.

Sediment organic matter content

Sediment samples were dried at 60 °C for 72 h, weighed, and combusted for 4 h at 450 °C to calculate ash-free dry weight (AFDW; Byers et al. 1978). Sediment AFDW was measured to the nearest 10^{-5} g with an AG285 Mettler Toledo balance. Sediment organic matter (OM) content was expressed as percent total sediment weight.

Nutrient analyses

Subsamples (10 ml) were immediately taken from each 60 mL water sample in the field to measure ammonium concentration using the orthophtaldialdhehyde method outlined by Holmes et al. (1999) with an Aquafluor handheld Turner Designs fluorimeter. The remainder of each water sample was stored in cryovials and frozen (–80 °C) after filtering through 0.2 m cellulose acetate Target syringe filters. Analyses for dissolved nitrate, nitrite, phosphate, and silicate were done using a II PAA II Brann + Luebbe auto-analyser following Tréguer and Le Corre (1975).

Flux calculation and standardization

Correction for water influence

Pelagic and benthic biogeochemical fluxes were determined either from the slopes of the linear regressions between oxygen concentration and incubation time (values expressed as mg $O_2 \cdot L^{-1} \cdot h^{-1}$) or from changes in nutrient concentrations through incubation (mol nutrients·L^{-1}·h^{-1}) multiplied by chamber volume (values expressed as mg·h^{-1} or mol·h^{-1}). Water within the chambers contributes to biogeochemical fluxes through, for example, degradation of suspended matter and respiration of plankton. However, the aim was to isolate the portion of the biogeochemical flux measured in pelagic and benthic chambers that was due uniquely to the presence of the aquaculture structures and the benthic interface, respectively. To this end, we subtracted the influence of water (estimated as the mean fluxes measured in the dark pelagic chamber filled with water) from the gross fluxes measured within pelagic and benthic chambers. The mean oxygen consumption measured in water was 0.104 mg·L^{-1}·h^{-1}, whereas mean nutrient fluxes were 0.0679 (NH_4), –0.0004 (PO_4), –0.0035 ($Si(OH)_4$), 0.0098 (NO_3), and –0.016 (NO_2) mol·L^{-1}·h^{-1}.

Standardization

Fluxes were standardized to a common constant to compare between interfaces (pelagic vs. benthic) in culture zones. Gross pelagic fluxes (corrected for water influence) were standardized to in situ pelagic macrofaunal biomass (g DW·m^{-2}; Mazouni et al. 1998; Mazouni 2004; Nizzoli et al. 2006). Pelagic fluxes in culture zones were thus expressed as mg·m^{-2}·h^{-1} (O_2) or mol·m^{-2}·h^{-1} (nutrients) and were comparable with benthic fluxes (corrected for water effect) standardized to a 1 m^2 surface area of the bottom. To evaluate the effect of pelagic macrofaunal biomass (PMB) on the pelagic fluxes among types of aquaculture structure (S, M1, M2), pelagic fluxes were standardized to 1 kg PMB (Nizzoli et al. 2006). As several authors (e.g., Baudinet et al. 1990; Balzer et al. 1983; Dame et al. 1989) have done, molar ratios of silicate, nitrogen (ammonium + nitrate + nitrite), and phosphate releases (i.e., Si/N/P) were calculated for each experimental chamber deployed in culture zones to obtain mean ratios of nutrient releases per interface per zone.

Statistical analyses

A series of analyses of variance (ANOVAs) were performed for each study objective. The first series of ANOVAs was done to compare pelagic macrofaunal (bivalve, associated fauna, total fauna) biomass and abundance (Table 1) and pelagic fluxes (ammonium, silicate, phosphate, nitrate, and nitrite; Tables 2, 3) among culture zones (S, M1, M2). Zone C was not included in the latter model, as suspended aquaculture was not present in that zone. A second series of

Table 1. Results of analyses of variance testing the effect of culture zone (scallops, 1-year-old mussels, 2-year-old mussels) on the biomass and abundance of total suspended macrofauna (Total), cultivated bivalves (Bivalve), and associated fauna (Associated).

Variable	Source	df	MS	*F*	*p*
Biomass					
Total*	Zone	2	4.06	56.54	<0.0001
	Error	14	0.07		
Bivalve*	Zone	2	4.36	59.07	<0.0001
	Error	14	0.07		
Associated†	Zone	2	7.66	19.74	<0.0001
	Error	14	0.39		
Abundance					
Total*	Zone	2	3.68	32.13	<0.0001
	Error	14	0.11		
Bivalve*	Zone	2	0.54	10.14	0.0019
	Error	14	0.05		
Associated*	Zone	2	6.79	40.37	<0.0001
	Error	14	0.17		

*ln(x).
†%(x).

Table 2. Results of analyses of variance testing the effect of culture zone (scallops, 1-year-old mussels, 2-year-old mussels) on pelagic fluxes (O_2, NH_4, PO_4, $Si(OH)_4$, NO_3, NO_2).

Fluxes	Source	df	MS	*F*	*p*
O_2*	Zone	2	0.84	4.853	0.0251
	Error	14	0.17		
NH_4	Zone	2	12 876.20	1.013	0.3883
	Error	14	12 712.30		
PO_4*	Zone	2	0.16	0.835	0.4542
	Error	14	0.19		
$Si(OH)_4$*	Zone	2	0.89	2.117	0.1573
	Error	14	0.42		
NO_3	Zone	2	138.28	3.238	0.0699
	Error	14	42.71		
NO_2	Zone	2	48.45	35.26	< 0.0001
	Error	14	1.37		

*ln(x).

ANOVAs compared sediment organic matter content, benthic macrofaunal biomass and abundance (Table 4), and benthic fluxes (Table 5) among the four zones (C, S, M1, and M2). The interaction among culture zones (S, M1, and M2) and interface types (pelagic–benthic) on ratios of nutrient releases (Si/P, N/P; Table 6) and biogeochemical fluxes were also evaluated using ANOVA (Table 7). The assumptions of normality and homoscedasticity were evaluated using the Shapiro–Wilk (Shapiro and Wilk 1965) and Brown–Forsythe (Brown and Forsythe 1974) tests, respectively. When required, data were log- or square-root-transformed to satisfy both assumptions (details given where appropriate). A single replicate was excluded from each of the pelagic (M2 bivalve abundance) and benthic (C sediment organic content) databases, as their Cook's D influences were greater than $4/n$ (n = total number of replicates; Cook and Weisberg 1982). Tukey's HSD (honestly significant difference) pairwise multiple comparison tests adapted to unbalanced designs (Kramer 1956; Hayter 1984) were used to identify the differences when a source of variation was significant ($p < 0.05$). Although biogeochemical fluxes were analysed separately, they were represented in the same figure for brevity.

Results

Influence of mussel and scallop cultures on the pelagic environment

Pelagic macrofauna

In the culture zones, suspended pelagic macrofaunal biomass and abundance varied between 47.8 and 503.1 g DW·m^{-2} and 181.5 and 2408 individuals·m^{-2}, respectively. Pelagic macrofaunal biomass and abundance differed among culture zones (Table 1), such that M2 > M1 > S (total faunal and cultivated bivalve biomasses; Fig. 3*a*), M2 = S > M1 (associated faunal biomass; Fig. 3*b*), and S > M2 > M1 (total faunal and associated faunal abundances; Fig. 3*c*). The pelogic macrofaunal biomass (PMB) was mainly represented by cultivated bivalves (86.6%–99.9%; Fig. 3*a*), whereas the abundance of pelagic macrofauna was mainly represented by associated fauna (56%–94%; Fig. 3*c*).

Pelagic fluxes

Pelagic oxygen fluxes were negative, whereas nutrient fluxes were mostly positive, highlighting that oxygen consumption and nutrient releases in the water column originated from the aquaculture structures (Figs. 4*a*–4*f*). The greatest nutrient release by aquaculture structures was ammonium, followed by phosphate, silicate, nitrate, and then nitrite (Figs. 4*b*–4*f*). Pelagic oxygen consumption varied significantly among culture zones (Table 2) and was twice as great in M2 than in S (Fig. 4*a*). Pelagic ammonium, phosphate, silicate, and nitrate fluxes did not vary significantly among culture zones (Table 2; Figs. 4*b*–4*e*). Pelagic nitrite fluxes were more than five times greater in scallop zones than in mussel zones (Table 2; Figs. 4*g*–4*f*).

Standardized (to 1 kg PMB) pelagic fluxes measured at the interface of aquaculture structures varied among aquaculture structure types (Table 3). Biogeochemical fluxes were always significantly greater at the interface of scallop cages than at the interface of mussel lines (except for $Si(OH)_4$; Table 3).

Influence of mussel and scallop cultures on the benthic environment

Sediment OM

Sediment OM ranged from 3.4% to 36.2% and differed among zones (Table 4). The results of the a posteriori tests showed that the mean OM in the first 2 cm of sediment was more than twice as great in M1 and M2 than in C and S (Fig. 5*a*). OM tended to be greater in S than in C, but this trend was not significant (Fig. 5*a*).

Benthic macrofauna

Benthic macrofaunal biomass ranged from to 0.2 to 142 g DW·m^{-2}. Although the trend for biomass among zones was C, S > M1, M2 (Fig. 5*b*), mean macrofaunal bio-

Table 3. Mean fluxes (± standard error, SE) measured at the interface of aquaculture structures standardized to 1 kg dry weight (DW) of macrofauna (bivalve + associated fauna).

	O_2	NH_4	PO_4*	$Si(OH)_4$	NO_3	NO_2*
S	557.53±94.94	2008.89±234.98	175.05±29.50	78.12±19.83	119.61±16.50	76.61±8.57
M1	311.72±49.58	834.70±172.44	76.38±14.31	41.95±6.49	1.29±12.49	4.58±0.38
M2	223.84±36.61	566.18±88.09	44.57±8.30	31.70±8.97	12.27±6.02	4.54±1.69
ANOVA	0.0113	0.0002	0.0005	0.0738	<0.0001	<0.0001
HSD	S ≥ M1 ≥ M2	S > M1 = M2	S > M1 = M2	S = M1 = M2	S > M2 = M1	S > M2 = M1

Note: S, scallops; M1, 1-year-old mussels; M2, 2-year-old mussels. Fluxes are expressed as mg O_2 and mol nutrient·kg $DW^{-1}·h^{-1}$. Significance of analysis of variance (ANOVA) and honestly significant difference (HSD) tests comparing the influence of aquaculture structure type (S, M1, M2) on pelagic fluxes are also given.

*$\sqrt{(x)}$.

Table 4. Results of analyses of variance testing the effect of zone (control, scallops, 1-year-old mussels, 2-year-old mussels) on sediment organic matter content (OM, %) and macrofaunal biomass and abundance.

Variable	Source	df	MS	*F*	*p*
OM (%)*	Zone	3	1.42	8.03	0.0012
	Error	19	0.18		
Biomass†	Zone	3	2.91	2.77	0.0696
	Error	19	1.05		
Abundance‡	Zone	3	3065.10	13.55	<0.0001
	Error	19	226.10		

*$\ln(x)$.
†$\ln(x + 1)$.
‡$\sqrt{(x)}$.

Table 5. Results of analyses of variance testing the effect of zone (control, scallops, 1-year-old mussels, 2-year-old mussels) on benthic fluxes (O_2, $Si(OH)_4$, NH_4, PO_4, NO_3, NO_2).

Fluxes	Source	df	MS	*F*	*p*
O_2	Zone	3	2 471.59	1.63	0.2156
	Error	19	1 515.55		
NH_4	Zone	3	116 103	3.37	0.0401
	Error	19	34 457		
$Si(OH)_4$	Zone	3	133 846	12.61	<0.0001
	Error	19	10 613		
PO_4	Zone	3	2 259.01	7.84	0.0013
	Error	19	288.20		
NO_3	Zone	3	46.10	1.60	0.2220
	Error	19	28.77		
NO_2	Zone	3	17.21	7.14	0.0021
	Error	19	2.41		

mass did not vary significantly among zones (Table 4). Benthic macrofaunal abundance ranged from 76 to 10 857 individuals·m^{-2} and varied significantly among zones (Table 4), such that it was six times greater in C and S than in the M1 and M2 (Fig. 5*c*).

Benthic fluxes

As observed in the water column, oxygen fluxes were negative, indicating oxygen consumption at the benthic interface (Fig. 4*a*). Except for nitrate fluxes, which were negative in the M1 zone, mean fluxes of the other nutrients were positive, indicating nutrient releases from sediments (Figs. 4*b*–4*f*). Ammonium represented the greatest release at the benthic interface, followed by silicate, phosphate, nitrate, and nitrite releases (Fig. 4). In contrast with oxygen consumption and nitrate fluxes, ammonium, silicate, phosphate, and nitrite fluxes varied significantly among zones (Table 5; Fig. 4). Mean ammonium, silicate, and phosphate fluxes were 2.5–4.5 times greater in culture zones (S, M1, and M2) than in the control zone (C; Figs. 4*b*–4*d*). Benthic ammonium fluxes did not vary among culture zones (Fig. 4*b*). In contrast, mean silicate and phosphate fluxes were greater in M1 than in M2 (Figs. 4*c*, 4*d*). Mean nitrite fluxes were more than seven times greater at the water–sediment interface in S than in M1 and M2 (Fig. 4*f*).

Table 6. Results of analyses of variance testing the effects of culture zones (scallops, 1-year-old mussels, 2-year-old mussels), interface type (pelagic, benthic), and their interaction (Zone × Interface) on nutrient ratios (silicate/phosphate (Si/P) and nitrogen/phosphate (N/P)).

Ratio	Source	df	MS	*F*	*p*
Si/P*	Zone	2	0.02	0.12	0.8879
	Interface	1	38.55	276.79	< 0.0001
	Zone × Interface	2	0.18	1.31	0.2850
	Error	29	0.14		
N/P	Zone	2	130.62	3.28	0.0521
	Interface	1	0.38	0.01	0.9227
	Zone × Interface	2	37.84	0.95	0.3987
	Error	29	39.87		

*$\sqrt{(x)}$.

Pelagic vs. benthic interfaces

Ratio of nutrient releases

The mean release ratio of silicate to phosphate (Si/P) differed significantly between interfaces (Table 6) and was greater at the benthic interface than at the interface of aquaculture structures. In contrast, mean release ratios of nitrogen to phosphate (N/P) did not differ among culture zones and interfaces (Table 6). The mean release ratio among silicate, nitrogen, and phosphate (Si/N/P) was thus 0.62/13.11/1 at the pelagic interface and 8.34/13.11/1 at the benthic interface.

Table 7. Results of analyses of variance testing the effect of culture zone (scallops, 1-year-old mussels, 2-year-old mussels), interface type (pelagic, benthic), and their interaction (Zone × Interface) on biogeochemical fluxes (O_2, $Si(OH)_4$, NH_4, PO_4, NO_3, NO_2).

Fluxes	Source	df	MS	*F*	*p*
O_2	Zone	2	288.90	0.25	0.7836
	Interface	1	8 067.29	6.87	0.0138
	Zone × Interface	2	8 298.35	7.06	0.0032
	Error	29	1 174.58		
NH_4	Zone	2	14 690.10	0.52	0.5972
	Interface	1	518 194.10	18.51	0.0002
	Zone × Interface	2	17 969.89	0.64	0.5335
	Error	29	27 988.83		
$SiOH_4$*	Zone	2	0.70	2.67	0.0862
	Interface	1	111.77	427.16	<0.0001
	Zone × Interface	2	0.96	3.68	0.0377
	Error	29	0.26		
PO_4*	Zone	2	0.44	2.12	0.138
	Interface	1	5.60	26.99	<0.0001
	Zone × Interface	2	0.32	1.55	0.2302
	Error	29	0.21		
NO_3	Zone	2	126.26	4.68	0.0173
	Interface	1	163.39	6.06	0.0201
	Zone × Interface	2	67.21	2.49	0.1004
	Error	29	26.98		
NO_2	Zone	2	69.30	39.95	0.0010
	Interface	1	23.35	13.46	<0.0001
	Zone × Interface	2	4.49	2.59	0.0922
	Error	29	1.73		

*ln(*x*).

Contribution to oxygen and nutrient pools

Oxygen consumption was observed at both interfaces (pelagic and benthic) in culture zones (Fig. 4) and was a function of the interaction between zone (M1 vs. M2 vs. S) and interface (pelagic vs. benthic; Table 7). Oxygen consumption did not vary significantly between interfaces in M1 and M2, but was 2.8 times greater at the benthic interface than at the pelagic (i.e., pearl net) interface in S (Fig. 4*a*). Ammonium fluxes varied significantly between interfaces in culture zones (Table 7), such that they were twice as great at benthic interfaces than at aquaculture structure interfaces (Fig. 4*b*). Ammonium was the nutrient released in the greatest quantity in culture zones. Silicate fluxes were a function of the interaction between zone and interface (Table 7) and were, overall, about 33 times greater at benthic than at pelagic interfaces (Fig. 4*c*). Phosphate fluxes also varied between interfaces (Table 7), such that benthic fluxes were more than twice those at pelagic aquaculture structure interfaces (Fig. 4*d*). Nitrate fluxes varied between interfaces and zones (Table 7). Overall, they were almost five times greater at pelagic than at benthic interfaces (Fig. 4*e*). As an extreme example, the mean nitrate flux was about 22 times greater at the pearl net interface than at the benthic interface in S (Fig. 4*e*). Mean nitrate releases were greater in S and M2 than in M1. Nitrite fluxes varied significantly between zones and interfaces (Table 7). Overall, pelagic nitrite fluxes were twice those of benthic nitrite fluxes (Fig. 4*f*). Mean nitrite releases were about five times greater in S than in M1 and M2, which did not differ (Fig. 4*f*).

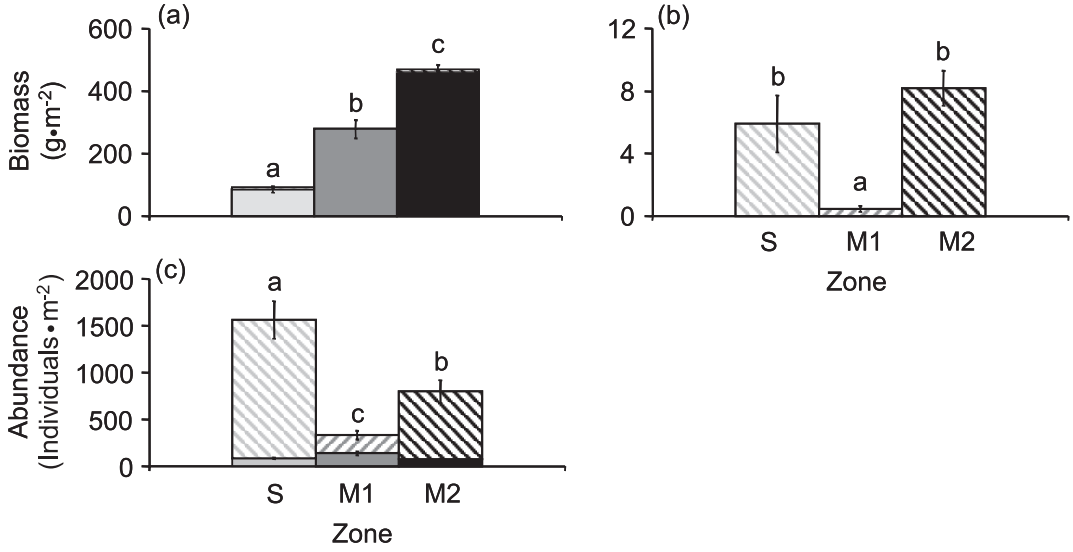
Discussion

Influence of mussel and scallop cultures on the pelagic environment

The introduction of aquaculture structures in HAM increased the abundance and biomass of sessile organisms in the water column. As suggested by others (e.g., Lesser et al. 1992; Ross et al. 2004; McKindsey et al. 2006), the aquaculture structures provided novel substrates for the settlement and growth of a variety of benthic invertebrates. The biomass and abundance of associated fauna were greater on scallop cages and M2 lines than on M1 lines. This may be explained by the comparatively larger surface area available for settlement and growth on scallop cages and the greater immersion time of M2 lines compared with M1 lines. However, the degree of biofouling on aquaculture structures observed in HAM was not great relative to observations in other shellfish culture areas around the world. Indeed, the associated fauna only represented between 0.01% (M1) and 2.5% (M2) of the total macrofaunal biomass associated with mussel lines in this study. In contrast, mussel socks from the Ria de Arosa in Spain supported >400 g DW of epifauna (34% of total biomass) for every metre of mussel sock (Tenore and González 1976). In the Thau Lagoon (France), the associated fauna (mainly ascidians) can represent up to 80% of total biomass on oyster ropes in July (Mazouni 1995). Likewise, the maximum DW of associated fauna per scallop cage was 12.5 g in HAM, whereas it was almost 200 g in August in Baie des Chaleurs, eastern Canada (Claereboudt et al. 1994).

Aquaculture structures, composed of the mooring system, the cultivated bivalves, and the associated fauna – organic matter complex, represent novel suspended benthic interfaces in the water column and may be new interfaces for biogeochemical exchanges (Mazouni et al. 2001; Mazouni 2004; Nizzoli et al. 2006). In HAM, mussel lines and scallop cages may be considered as suspended bivalve communities, with associated oxygen consumption as has been observed for benthic mussel beds by Dankers et al. (1989) and nitrogen and phosphate releases to the adjacent waters as has been observed in benthic systems by Dame et al. (1984, 1985, 1989) for oyster reefs and by Asmus et al. (1995) for mussel beds. Considering the low biomass of fauna associated with aquaculture structures in HAM, particularly in M1, respiration and excretion by cultivated bivalves were likely mainly responsible for the great observed pelagic fluxes, as was noted by Richard et al. (2006) at the interface of mussel line sections in laboratory experiments. However, cultivated bivalves and biofouling organisms can generate considerable amounts of organic matter (Callier et al. 2006), and this may accumulate within aquaculture structures (Arakawa 1990; Mazouni et al. 2001; Nizzoli et al. 2006). Thus, the observed oxygen consumption and ammonium and phosphate releases could also have originated from the degradation of biodeposits trapped within the aquaculture structures, as bivalve biodeposits are known to be an important source of nitrogen (Sornin et al. 1983; Grenz et al. 1990; Mazouni et al. 1996) and phosphorus (Sornin et al. 1986; Peterson and

Fig. 3. Mean (±standard error) pelagic macrofaunal (*a*, *b*) biomass and (*c*) abundance in scallop (S), 1-year-old mussel (M1), and 2-year-old mussel (M2) zones in Havre-aux-Maisons Lagoon. Solid bars represent the biomass or abundance of the cultivated bivalves, whereas hatched bars represent biomass and abundance of the associated fauna. Note that (*b*) focuses on the mean biomass of associated fauna among culture zones and that the scale of the *y* axis differs from that in (*a*). Different letters indicate significant ($p < 0.05$) differences among culture zones.



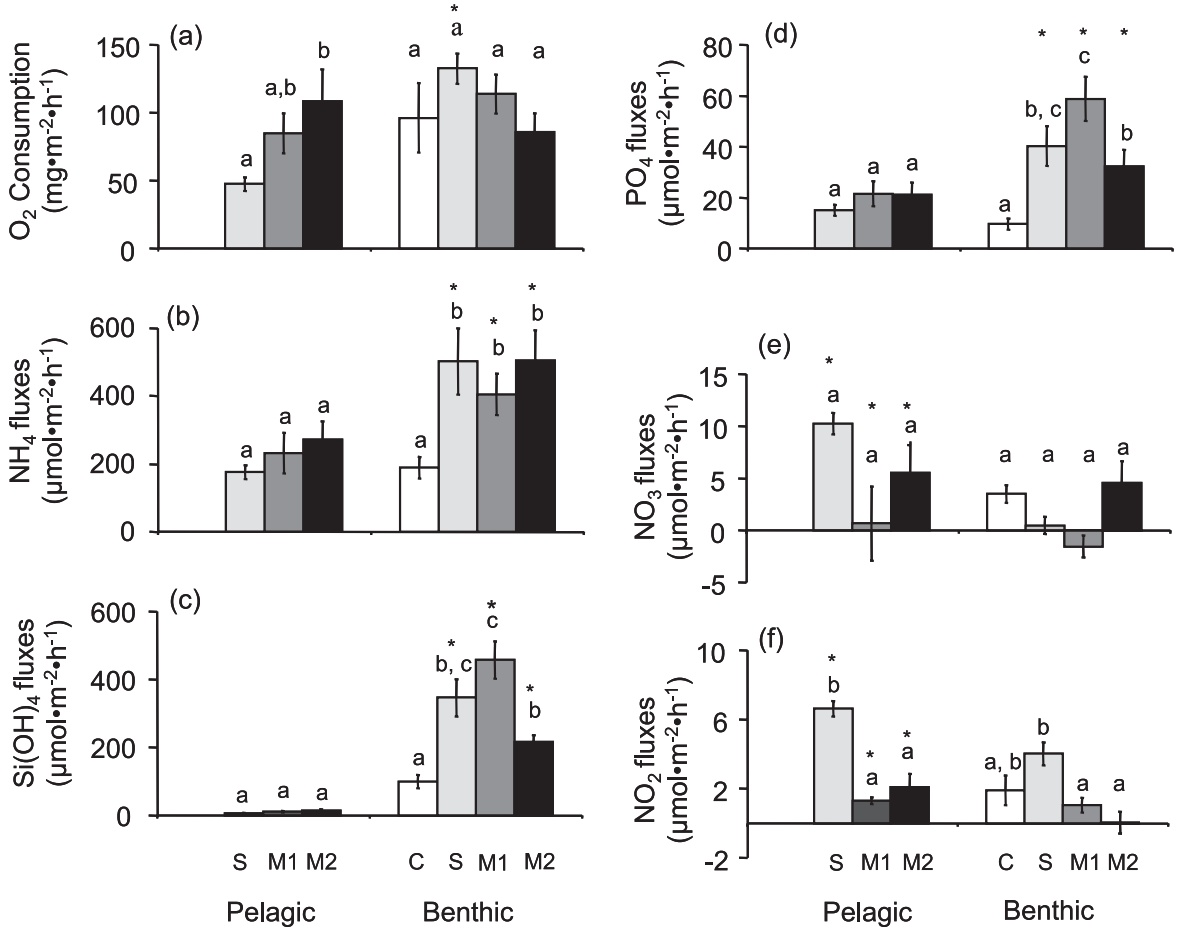
Heck 1999). The increased silicate release measured at the interface of each aquaculture structure in this study suggests degradation of biodeposits trapped within the structures. Diatom cell walls contain silica embedded within an organic matrix (Bidle and Azam 1999), and silicate releases at the pelagic interfaces likely originate from the dissolution of diatom frustules (Balzer et al. 1983; Lerat et al. 1990) trapped in biodeposits accumulated between mussel shells or in the net of scallop cages.

Although the pelagic macrofaunal biomass in the M2 zone was almost two (vs. M1) to five (vs. S) times greater than that in other culture zones, of all the fluxes measured, only pelagic oxygen consumption in M2 was greater than that observed in S. In contrast with what was expected based on biomass differences among zones, the M2 lines did not have a greater influence on pelagic nutrient fluxes than did the other cultures in HAM. Macrofaunal, biomass-standardized pelagic fluxes (to 1kg PMB) were greater at the interface of scallop cages than at the interface of mussel lines. The percentage of flesh DW/total DW (with shell) ranged from 14% to 17% between bivalve species in July 2004 (M. Richard, unpublished data), and thus size- and species-related differences in this variable cannot explain the 2–16 times greater fluxes recorded at the interface of scallop pens. Since bivalve physiology depends on species (Tenore et al. 1973; Qian et al. 2001) and individual age or size (Yukihira et al. 1998; Sukhotin and Pörtner 2000; Qian et al. 2001), 1-year-old scallops may have greater respiration and excretion rates per unit biomass than do 2-year-old mussels. Nevertheless, the metabolism of 1-year-old scallops alone can probably not entirely explain the greater nutrient releases measured at the scallop cage interface. We suggest that the contribution of the associated fauna – organic matter complex to pelagic fluxes would be greater at scallop pearl net interfaces than at mussel line interfaces because of the greater quantity of trapped organic matter and abundance of small-sized macrofaunal organisms (e.g., the burrowing amphipods (*Corophium* sp.)) that are associated with pearl nets. Differences among aquaculture structures may also explain the greater nitrate and nitrite releases at the interface of scallop cages. Indeed, in contrast with mussels that are attached on lines, scallops are held in cages. Nets of cages, as with internal and external surfaces of bivalves (Welsh and Castadelli 2004), may be colonised by nitrifying bacteria. The dissolved products excreted by scallops, such as ammonium, could diffuse through the net of the cages, stimulate the nitrification process, and be released as nitrite and nitrate forms to the adjacent water. In contrast, ammonium excreted by mussels was released directly into the adjacent water. Moreover, the water exchanges through the mesh of scallop cages, and the bioturbation activities (burrow construction and irrigation) by dense amphipod (*Corophium* sp.) populations may favour the oxygenation and degradation of the trapped organic matter (Pelegri and Blackburn 1994; Mermillond-Blondin et al. 2004; 2005), stimulate the nitrification process (Henricksen and Kemp 1988; Gilbert et al. 1997; Christensen et al. 2003), and enhance oxygen and nutrient fluxes (Mermillond-Blondin et al. 2004; 2005) at scallop cage interfaces.

Influence of mussel and scallop cultures on the benthic environment

Dense assemblages of filter-feeding bivalves remove suspended matter from the water column and transfer it as feces and pseudofeces to the bottom (Peterson and Heck 1999; Cranford et al. 2003). Indeed, shellfish farms are well known to enhance sedimentation rates due to bivalve biodeposition (Dahlbäck and Gunnarson 1981; Hatcher et al. 1994; Callier et al. 2006). In HAM, the organic matter content in the first 2 cm of sediment beneath suspended mussel lines was more than twice that observed in the control zone. This organic matter enrichment may originate from the accumulation of

Fig. 4. Mean (±standard error) pelagic and benthic fluxes measured in scallop (S), 1-year-old mussel (M1), 2-year-old mussel (M2), and control (C: only for benthic fluxes) zones in Havre-aux-Maisons Lagoon: (*a*) oxygen consumption (O_2) and (*b*) ammonium (NH_4), (*c*) silicate ($Si(OH)_4$), and (*d*) phosphate (PO_4) fluxes. Different letters indicate significant ($p < 0.05$) differences among culture zones for a given interface (i.e., benthic or pelagic). Asterisks (*) indicate a significant difference between interface types for a given culture zone (i.e., S, M1, or M2).

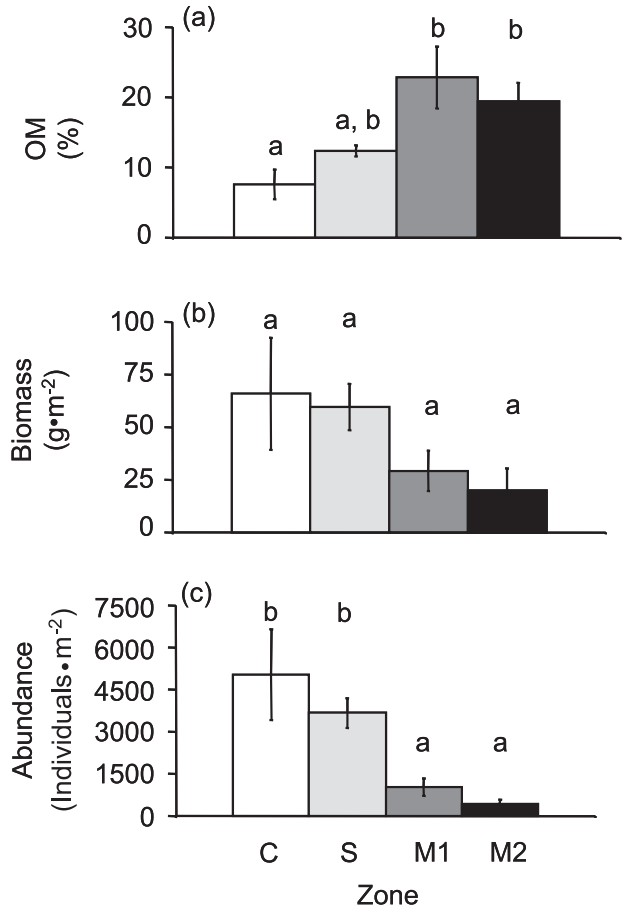


mussel feces and pseudofeces on the bottom, as observed by several authors (Dahlbäck and Gunnarsson 1981; Stenton-Dozey et al. 2001; Hartstein and Rowden 2004). In contrast, scallop cages did not induce significant organic enrichment in the first 2 cm of sediment. This may be explained by the low macrofaunal biomass (bivalves plus associated fauna) in scallop cages as compared with that associated with mussel lines. Mallet et al. (2006) found a similar result for oyster culture in New Brunswick (Canada). Alternatively, the great variability of sediment OM in the control zone could have masked the influence of scallop cages on sediment organic enrichment.

In contrast with other shellfish cultures (see Hatcher et al. 1994; Grant et al. 1995; Christensen et al. 2003), the suspended bivalve cultures in HAM did not substantially modify the benthic macrofaunal biomass in culture zones. However, great variability of benthic biomass in the control zone may have masked the effect of mussel culture. Indeed, benthic biomass tended to be lowest at mussel sites. Increasing the number of replicates to decrease uncertainty associated with treatment means would allow this hypothesis to be better evaluated. The benthic macrofaunal abundance was six times lower in mussel cultures than in the control zone. This change is likely due to the organic enrichment observed under mussel lines, as has been noted in several studies (e.g., Mattsson and Lindén 1983; Hartstein and Rowden 2004).

High sediment OM is known to stimulate microbial (Dahlbäck and Gunnarson 1981; La Rosa et al. 2001) and macrofaunal (Pearson and Rosenberg 1978) activity and consequently increase oxygen consumption (Mattsson and Lindén 1983; Christensen et al. 2003; Cranford et al. 2003). Indeed, oxygen consumption measured under aquaculture structures is often greater than that measured outside the farms (Hargrave et al. 1993; Mazouni et al. 1996; Christensen et al. 2003). In HAM, although sediment organic enrichment and decreased macrofaunal abundance was observed under suspended mussel lines, oxygen consumption did not differ between the control and culture zones. This was also observed by Stenton-Dozey et al. (2001) in South Africa, Grant et al. (1995) in Nova Scotia (eastern Canada), and Richard et al. (2007) in Grande-Entrée Lagoon. Benthic oxygen consumption is driven by the respiration of organisms and by the microbial-mediated oxidation of organic matter and reduced inorganic metabolites (Nickell et al. 2003). Since respiration of the macrofaunal community depends partly on biomass (Mazouni et al. 1996) and abundance (Nickell et al. 2003), the benthic oxygen demand ob-

Fig. 5. Mean (±standard error) sediment organic matter (OM, %) content (*a*), benthic macrofaunal biomass (*b*), and abundance (*c*) measured in control (C), scallop (S), 1-year-old mussel (M1), and 2-year-old mussel (M2) zones in Havre-aux-Maisons Lagoon. Different letters indicate significant differences among culture zones.



served in mussel cultures and control zones are likely driven by different processes. The measurement of CO_2 production and calculation of benthic respiratory quotient (CO_2/O_2) in dark conditions would have permitted to distinguish aerobic and anaerobic processes that drove oxygen demand in each experimental zone (Hargrave and Phillips 1981; Hatcher et al. 1994; Welsh 2003).

Benthic ammonium, phosphate, and silicate fluxes were two–five times greater in bivalve culture than in control zones. The large ammonium and phosphate releases measured at the benthic interface in culture zones could result from the degradation of bivalve feces and pseudofeces, as bivalve biodeposits are rich in nitrogen and phosphorus (Kautsky and Evans 1987). Similar to what may occur for the suspended interface, higher silicate fluxes under aquaculture structures could originate from the dissolution of diatom tests trapped in biodeposits accumulated at the benthic interface (Balzer et al. 1983). Drastic increases in nutrient fluxes are often correlated with biodeposit accumulation on the bottom under shellfish farms (Baudinet et al. 1990; Grenz et al. 1992; Christensen et al. 2003). Since scallop cages did not induce organic enrichment in the underlying sediments, great benthic nutrient fluxes in the zone could signify that scallop biodeposits reaching the water–sediment interface beneath the cages were completely remineralized and did not accumulate.

The influence of mussel lines on sediment organic content and macrofauna communities was greater than that of scallop cages. Nevertheless, in contrast with what was expected, nutrient fluxes were not significantly greater in M2 than in M1 and S zones. The quantity and quality of biodeposits underneath aquaculture structures could vary among culture zones, as biodeposition rate and biodeposit composition vary according to bivalve species (Shumway et al. 1985) and age (Callier et al. 2006). Great nitrite releases in S may result from nitrification processes enhanced by bioturbation by the dense subsurface deposit feeder population (*Pectinaria* sp.) observed in that zone. Nitrification is favoured (Jenkins and Kemp 1984; Kristensen and Blackburn 1987) by a deeper oxic layer and increased oxygen diffusion through finer sediments due to bioturbation (Pearson and Rosenberg 1978).

Pelagic vs. benthic interfaces: relative contributions and roles

Several authors (e.g., Kaspar et al. 1985; Baudinet et al. 1990; Mazouni et al. 1996) have suggested that nutrient regeneration in shallow waters is ensured by benthic remineralization, as sediments may regulate the production (fluxes) and standing stocks (concentrations) of nutrients in the water. This study showed that mussel lines and scallop cages acted as additional sinks for oxygen and sources of nutrients in the water column in HAM. Thus, both pelagic and benthic interfaces contribute to the production and standing stocks of nutrients and oxygen in the water column. This study highlighted that the contribution of aquaculture structures to oxygen and nutrient pools was considerable when compared with benthic interfaces. Indeed, the contribution of mussel lines (vs. benthic interface) to oxygen pools was approximately 50% of the total combined consumption in the mussel zones, whereas scallop cages accounted for approximately 25% of the total oxygen consumption in the scallop zone. The contributions of aquaculture structures to the total ammonium and phosphate releases by both interfaces were greater than 30%. Only two other studies have addressed this issue: one for oyster (Mazouni 2004) and the other for mussel (Nizzoli et al. 2006) culture. In contrast with the current study, the contribution of mussel ropes to the ammonium pool in Sacca di Goro Lagoon, Italy, was similar to that of the benthic interface (1200 $mol \cdot m^{-2} \cdot h^{-1}$; Nizzoli et al. 2006). In Thau Lagoon, the contribution of oyster ropes to the total ammonium produced by both interfaces was greater than 90% in July (3000 vs. 250 $mol \cdot m^{-2} \cdot h^{-1}$ for sediment; Mazouni 2004). The greater ammonium releases and contributions to ammonium standing stocks in Italy and France likely result from the greater cultivated bivalve biomasses in those locations relative to that cultured in HAM. Indeed, biomass of mussels in Sacca di Goro in July (3 kg wet weight$\cdot m^{-2}$; Nizzoli et al. 2006) was more than two times greater than the biomass of M2 in HAM (460.78 g DW$\cdot m^{-2}$ with shell = 1.25 kg wet weight$\cdot m^{-2}$ in this study), and the oyster biomass in Thau Lagoon (Mazouni 2004) was more than 15 times greater (1000 vs. 68.51 g AFDW$\cdot m^{-2}$). One possible effect of nutrient releases at aquaculture structure interfaces could be an enhancement of primary production through a feedback loop

(phytoplankton consumed by the bivalves would be rapidly remineralized), as suggested by Dame et al. (1985) and Dame and Libes (1993) for oyster reefs and by Kaspar et al. (1985) for mussel farms. This aspect is enhanced in closed system such as the Thau Lagoon, where the water residence time is 220 days (Bacher et al. 2005), relative to that in to more open systems such as HAM lagoon, where the water mass is renewed more rapidly (20–35 days; Koutitonsky and Tita 2006).

Biogeochemical processes differ between pelagic and benthic interfaces, as shown by the mean Si/N/P ratios (13-fold difference for silicates). In HAM, silicate releases at benthic interfaces were >30 times those at aquaculture structure interfaces. This result highlights the dominant role of benthic relative to pelagic interfaces for silicate cycling, with a turnover known to be faster because of bivalve biodeposition (Ragueneau et al. 2002; Thouzeau et al. 2007). Disequilibria in nutrient release kinetics can alter nutrient ratios and the specific composition of phytoplankton communities (Baudinet et al. 1990). The two interfaces could therefore have a different influence on phytoplankton production and composition. The great silicate supply by the benthic interface may favour siliceous phytoplankton production (Egge and Asknes 1992), whereas the great pelagic nitrogen releases may favour nonsiliceous phytoplankton (Officer et al. 1982; Smayda 1990). Pelagic nitrogen was mainly released as ammonium, which may favour the growth of small-sized phytoplankton (Officer et al. 1982). Aquaculture structures also play a role in nitrate and nitrite cycling in HAM, as they may enhance the standing stocks of these nutrients. The proportional contribution of pelagic releases to nitrate and nitrite pools varied between 65% and 95% (of the combined total released by benthic and pelagic interfaces). Nitrite–nitrate availability was greater in S than in M1 and M2, which may favour the production of large-sized phytoplankton (Officer et al. 1982).

This study had three main findings. (*i*) Mussel lines and scallop cages acted as suspended macrofaunal communities that increased oxygen consumption and nutrient releases (especially ammonium and phosphate) in the water column. (*ii*) Mussel culture induced organic matter enrichment in the sediment and decreased benthic macrofaunal abundance, in contrast with scallop culture, which did not. Nevertheless, great nutrient releases were observed at the water–sediment interface in all zones with suspended bivalve culture. This study is the first to show that the influence of suspended scallop cages on biogeochemical fluxes could be similar to the well-documented influence of suspended mussel culture. (*iii*) Pelagic interfaces also contribute to oxygen and nutrient fluxes. Their contribution in HAM is slight compared with two more productive European bivalve farms. Pelagic and benthic interfaces had different influences on nutrient cycles; benthic interfaces exhibited major silicate turnover, whereas aquaculture structures (especially scallop cages) mainly modified nitrate and nitrite pools. This study emphasized that the influence of suspended aquaculture structures on biogeochemical cycles should not be ignored, even if the density of cultivated bivalves is low as is the case in the Îles-de-la-Madeleine. A better understanding of the seasonal trends for these measures should be the next step to integrate carrying capacity models for the development of sustainable aquaculture. In contrast with what was expected, M2 lines did not have a greater influence on pelagic and benthic fluxes than did other culture types. Future manipulative experiments could test (*i*) the influence of the species being cultivated, of individual age–size and bivalve density–biomass, and of the associated fauna – organic matter complex on pelagic fluxes; and (*ii*) the influence of species-related biodeposition gradients on sediment organic matter enrichment, benthic nutrient fluxes, and benthic community changes.

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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

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 km^2 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

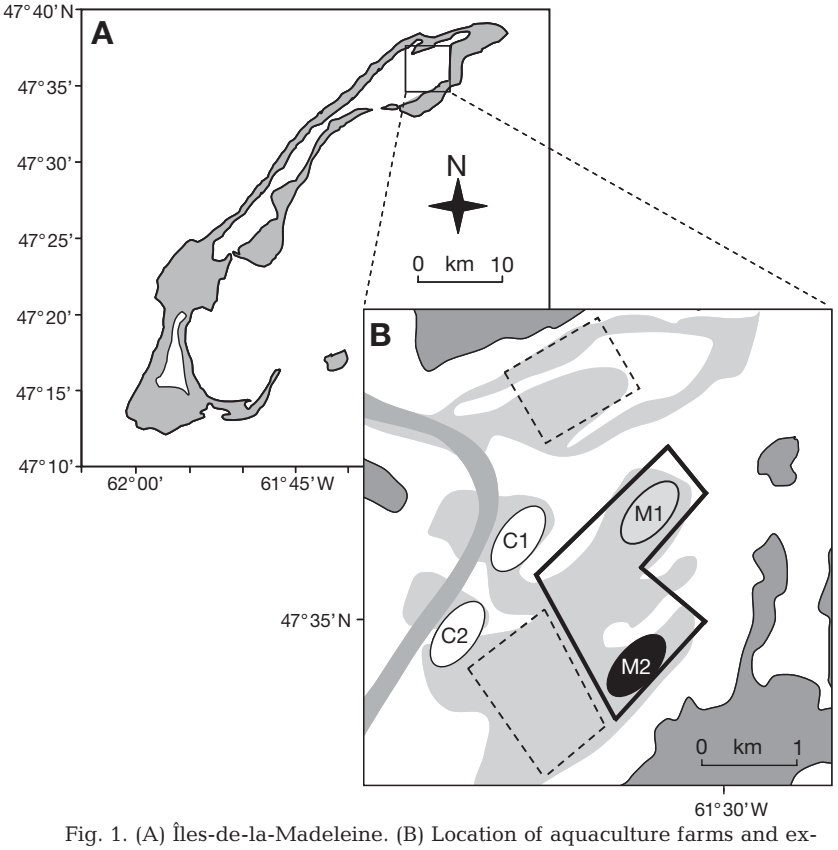

Fig. 1. (A) Îles-de-la-Madeleine. (B) Location of aquaculture farms and experimental sites in Grande-Entrée lagoon; black-contoured polygon: mussel farm location; dash-contoured quadrants: scallop farms (southern scallop farm was unproductive whereas northern farm was productive between 1999 and 2004); 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 µg 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; ±SE) m^{-1} line was 1293.08 ± 212.07 g DW m^{-1} for M1 vs. 1657.28 ± 373.87 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 (±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 (mg l^{-1} ±0.01), temperature (°C ±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 Aquafluor 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 µm 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 µmol m^{-2} 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 × 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 × 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 ($t_{3\,h}$) 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 $t_{3\,h}$) (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°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).

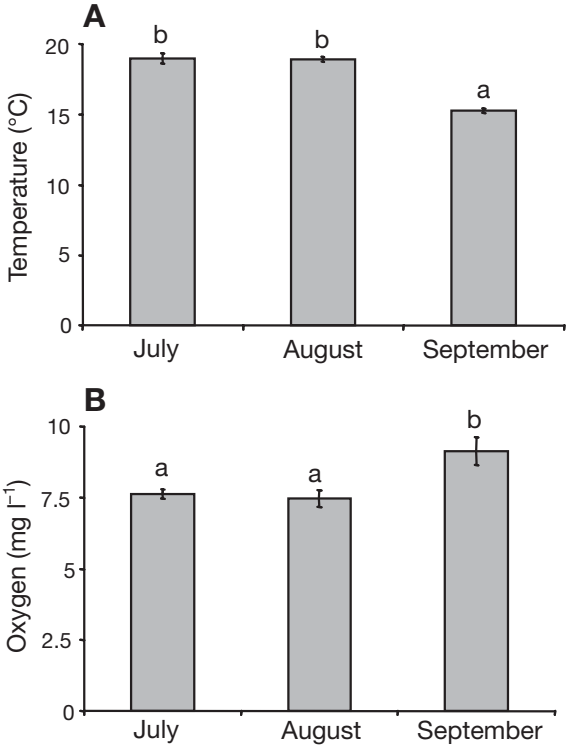

Fig. 2. (A) Bottom water temperature and (B) oxygen concentration at the 3 experimental sites. Different letters indicate statistically significant difference between dates. Data are means ± SE

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 µmol $(SiOH)_4$ m^{-2} h^{-1}. The interaction of treatment and date was a significant source of variation for silicate flux (ANOVA; Table 2). 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 µmol NH_4 m^{-2} 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-

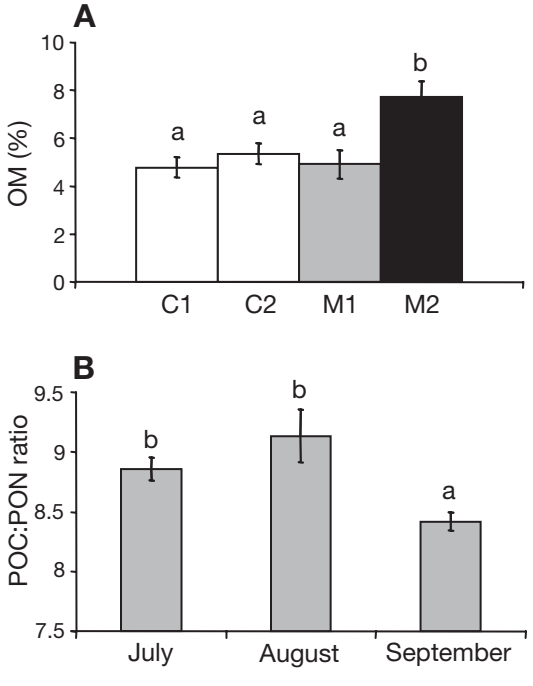

Fig. 3. (A) Organic matter content (OM) of sediment at the 4 sites; (B) POC:PON calculated for the 3 experimental dates: Different letters indicate statistically significant difference between treatments (A) or dates (B). Data are means ± SE; site abbreviations as in Fig. 1

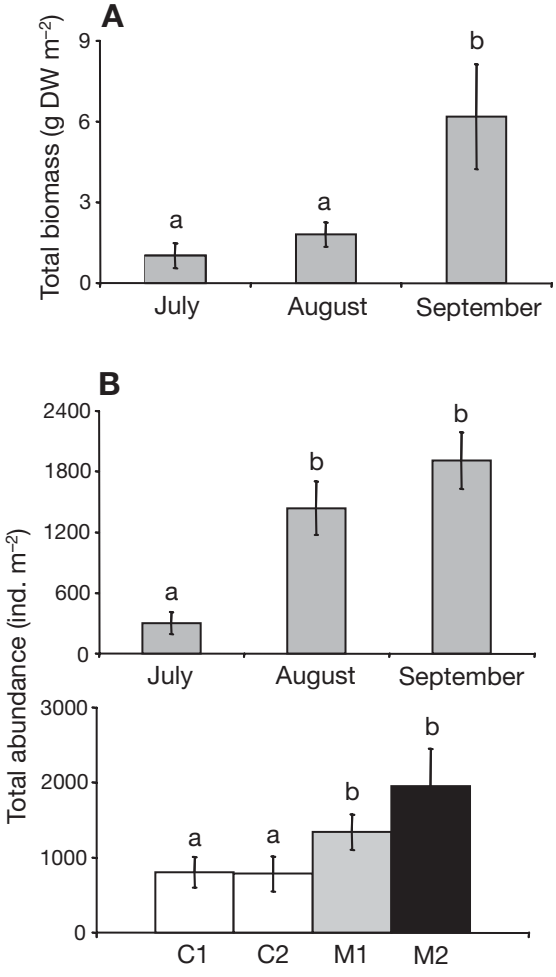

Fig. 4. (A) Total macrofauna biomass and (B) abundance on the 3 experimental dates and at the 4 sites. Different letters indicate statistically significant difference between dates (A and B) or treatments (B). Data are means ± SE; site abbreviations as in Fig. 1

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		

[a]ln(*x*+1)

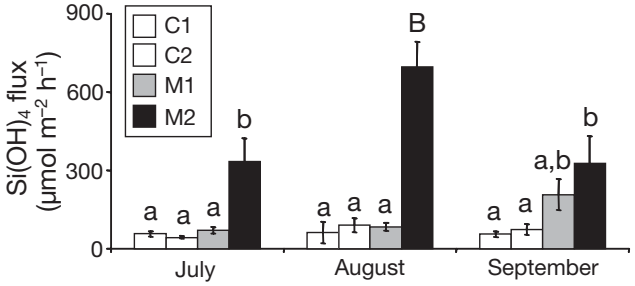

Fig. 6. Mean (±SE) silicate flux at the 4 sites on the 3 experimental dates. Different letters indicate statistically significant difference between treatments on a given date; capital letter indicates significant difference between dates for given treatment; site abbreviations as in Fig. 1

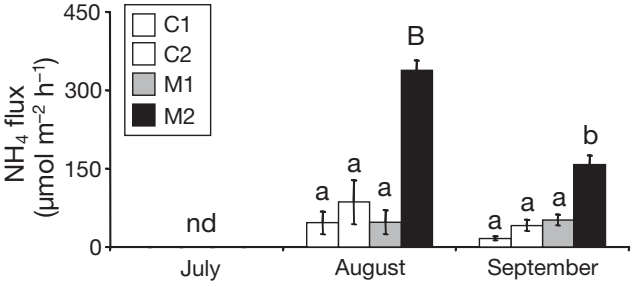

Fig. 7. Mean (±SE) ammonium flux at the 4 sites on the 3 experimental dates. Different letters indicate statistically significant difference between treatments on a given date; capital letter indicates significant difference between dates for given treatment; nd: no data; site abbreviations as in Fig.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

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 µmol PO_4 m^{-2} h^{-1}. Date was a significant source of variation (Table 2). The mean phosphate flux measured in July 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 µmol NO_3 m^{-2} 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 µmol NO_2 m^{-2} 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).

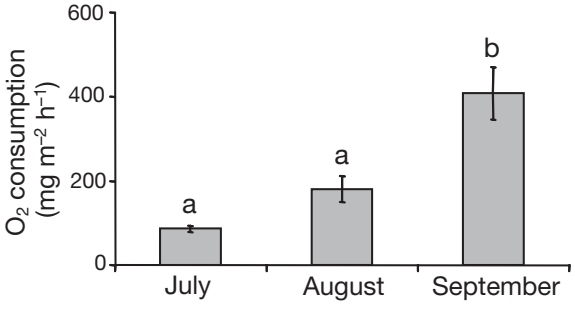

Fig. 5. Mean (±SE) oxygen consumption on the 3 experimental dates. Different letters indicate statistically significant difference between dates

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 ($t_{3\ h}$) measured at M2 was greater than that at C1, C2 and M1 (Fig. 10). The final

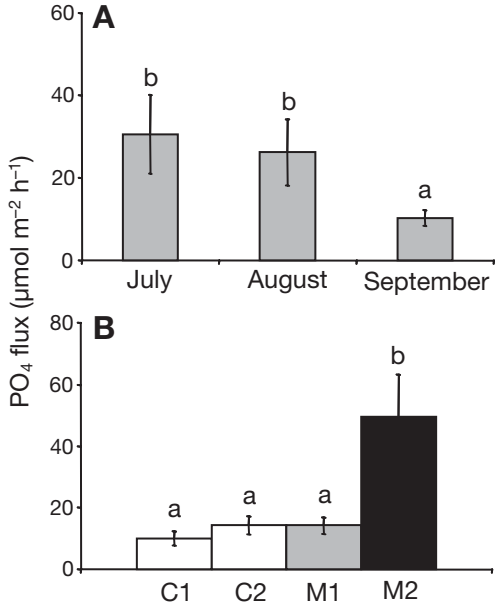

Fig. 8. Mean (±SE) phosphate flux at the 4 sites on the 3 experimental dates. Different letters indicate statistically significant difference between dates (A) or treatments (B); site abbreviations as in Fig. 1

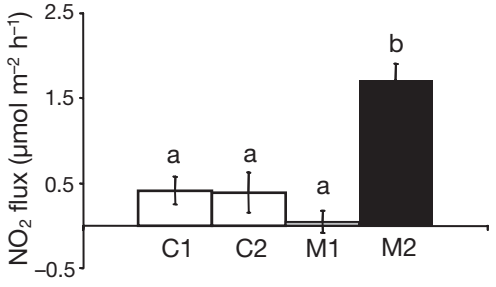

Fig. 9. Mean (±SE) nitrite flux at the 4 sites. Different letters indicate statistically significant difference between treatments; site abbreviations as in Fig. 1

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 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).

Table 3. Results of analyses of variance (ANOVAs) testing effect of treatment, date, incubation time, Ti (t_0, $t_{3\,h}$) 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]$(x + 1)^2$

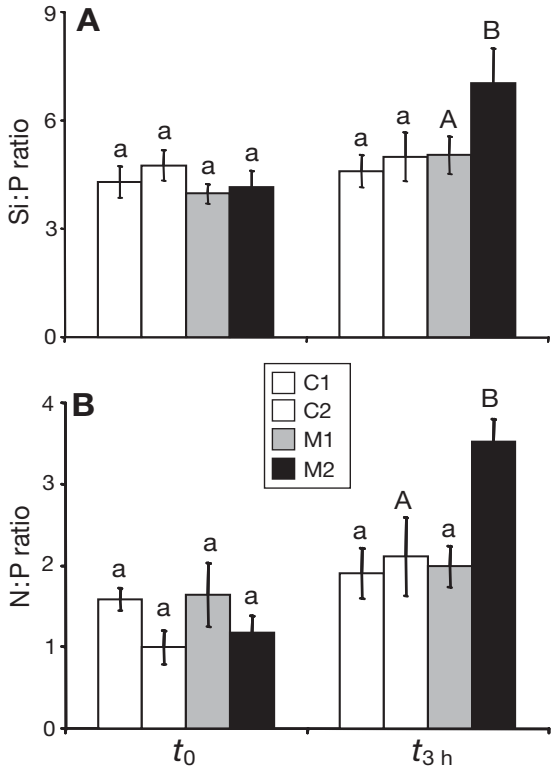

Fig. 10. Mean (±SE) of (A) Si:P and (B) N:P calculated for the 4 sites at beginning (t_0) and at end ($t_{3\,h}$) of incubation. Different letters indicate statistically significant difference between treatments; site abbreviations as in Fig. 1

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-

mum 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 O_2 m^{-2} h^{-1} in July and August to 408 mg O_2 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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