Benthic microphytic activity at two Mediterranean shellfish cultivation sites with reference to benthic fluxes

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ABSTRACT

Microphytobenthos activity in coastal waters has been studied at two shellfish farming sites: an oyster farm in Thau lagoon and a mussel farm in Carteau bay (NW Mediterranean coast). In both cases, shellfish are cultivated on ropes hanging from rigid structures (tables) in shallow waters (- 5 m). An "under table" station and an "outside table" (reference) station were chosen at each site. Oxygen and ammonia fluxes at the water-sediment interface were measured in dark and transparent benthic chambers.

Chlorophyll a concentrations were two- to threefold higher in "under table" sediments than outside (260 mg Chl a m^{-2} under the oyster table, 436 mg Chl a m^{-2} under the mussel table in winter). Net oxygen fluxes were negative at all stations, except at the Carteau reference station and under the oyster table at the beginning of the summer (+ 20 mg O$_2$ m^{-2} h^{-1}). Maximum negative fluxes (- 70 mg O$_2$ m^{-2} h^{-1} under a mussel table) were recorded during spring at all stations, when mollusc trophic activity was maximal as reflected in high phaeopigment content under the tables. Gross primary production was lowest in spring at the Thau stations as well as at the Carteau reference station. Under the mussel table, primary production increased steadily from autumn to summer, from 0 to 100 mg O$_2$ m^{-2} h^{-1}. Ammonia release was higher under shellfish farming structures (200 µmol N-NH$_4^+$ m^{-2} h^{-1}) than at the reference stations (70 µmol N-NH$_4^+$ m^{-2} h^{-1}). The discrepancy between O$_2$ production and microphytic biomass suggests that mechanisms other than photosynthesis prevail under shellfish structures. Mussel cultures were shown to have a stronger impact on benthic fluxes below the tables than oysters.

In localities with shellfish farms, oxygen produced by microphytobenthos activity cannot always meet the total oxygen demand of the sediment, increased by accumulation of mollusc biodeposits and, sometimes drastically in the lagoon, by macroalgae decay.

Oceanologica Acta, 1994. **17**, 2, 211-221.

RÉSUMÉ

Activité du microphytobenthos et flux benthiques dans deux sites conchylicoles en Méditerranée

L'activité du microphytobenthos a été étudiée dans deux sites conchylicoles : un élevage d'huîtres dans l'étang de Thau et un élevage de moules dans l'anse de Carteau (côte nord-ouest de la Méditerranée). Dans les deux cas, les mollusques sont cultivés sur des cordes suspendues à des structures rigides (« tables ») implantées en zone peu profonde (- 5 m). Dans chaque site, une station «sous table» et une station « hors table » (référence) ont été sélectionnées. Les flux d'oxygène et d'ammonium ont été estimés dans des enceintes benthiques claires et noires. Les concentrations en chlorophylle a sont deux à trois fois plus élevées

sous les tables que dans les stations de référence (260 mg Chl a m^{-2} sous les tables à huîtres, 436 mg Chl a m^{-2} sous les tables à moules en hiver). Les flux nets d'oxygène étaient négatifs à toutes les stations, sauf à la station de référence de Carteau et sous les tables à huîtres au début de l'été (+ 20 mg O_2 m^{-2} h^{-1}). Les flux les plus négatifs (- 70 mg O_2 m^{-2} h^{-1} sous une table à moules) ont été obtenus au printemps dans toutes les stations, lorsque l'activité trophique des mollusques était intense, ce qui se traduit par des concentrations en phéopigments très importantes sous les tables. La production primaire brute était minimale au printemps à Thau et à la station de référence à Carteau. Sous les tables à moules, la production primaire a augmenté régulièrement de l'automne à l'été, de 0 à 100 mg O_2 m^{-2} h^{-1}. Le relargage de NH_4^+ par le sédiment a été plus important sous les tables (200 μmol N-NH_4^+ m^{-2} h^{-1}) qu'aux stations de référence (70 μmol N-NH_4^+ m^{-2} h^{-1}). La production primaire et la biomasse microphytique ne sont pas corrélées positivement, ce qui suggère que des mécanismes autres que la photosynthèse interviennent sous les tables conchylicoles. L'impact des tables à moules sur les échanges à l'interface eau-sédiment est plus important que celui des tables à huîtres. Dans ce type d'environnement, la quantité d'oxygène produite par le microphytobenthos ne peut pas toujours compenser la consommation d'oxygène par le sédiment, du fait de l'importance de la biodéposition en particulier dans les sites de mytiliculture. La décomposition des macroalgues au voisinage des élevages d'huîtres pendant l'été accentue saisonnièrement de façon drastique les effets de la biodéposition.

INTRODUCTION

Benthic microphytes play a role in the regulation of nutrient fluxes at the water-sediment interface in marine coastal sediments (Hargrave et al., 1983; Shaffer and Onuf, 1983; Rizzo, 1990; Sundbäck et al., 1991; Rizzo et al., 1992; Wiltshire, 1992).

Their contribution to the oxygen production is not restricted to very shallow bottoms; several studies show that their oxygen production rates could attain those of phytoplankton (Cadée and Hegeman, 1974; Sundbäck and Jönsson, 1988; Herndl et al., 1989; Cahoon and Cooke, 1992), or even exceed phytoplankton production rates in depths of several metres in a wide range of environments (Varela and Penas, 1985; Plante-Cuny and Bodoy, 1987; Charpy-Roubaud, 1988).

Intensive culture of filter-feeding molluscs may alter the biological status of the original ecosystem. They consume oxygen from the water column and reduce phytoplankton stock, while increasing sedimentation rates and organic matter contents in the sediments (Kautsky and Evans, 1987; Dame and Dankers, 1988; Boucher and Boucher-Rodoni, 1988; Grenz, 1989; Smaal and Vonck, 1989; Baudinet et al., 1990; Grenz et al., 1992). Organic enrichments cause changes in physico-chemical conditions in the sediment, including oxygen depletion, changes in redox-potential and ammonia concentration (Admiraal and Peletier, 1979; Granéli and Sundbäck, 1985). An interesting question therefore is whether microphytobenthos activity contributes to the maintenance of oxic conditions in the superficial sediments of bivalve cultivation sites. Quantification of this contribution to the total oxygen balance can help to improve our understanding of the ecology of such sites.

The impact of bivalve cultivation on the environment may vary, depending on the mollusc species and the hydraulic conditions. Two sites were then chosen: a lagoon, half open to the sea, with an oyster culture; and a bay with a mussel culture. Both are located in the Mediterranean sea, with the same average depth; and at both the molluscs are cultivated on suspended ropes.

Oxygen and ammonia fluxes at the sediment-water interface may be used as indicators of metabolic processes in the sediments (Kelly and Nixon, 1984; Baudinet et al., 1990; Bolalek and Vershinin, 1991; Vidal et al., 1992). Measurements in light and dark conditions give an estimate of the total oxygen production by taking into account the respiration of the total benthic community. Previous studies in Thau lagoon (Grenz et al., 1992) and in Carteau bay (Baudinet et al., 1990) have shown that nitrate fluxes at the water-sediment interface to be very low in comparison with ammonia fluxes. Data from Picot et al. (1990) for Thau lagoon and from Folack (1986) for Carteau bay indicate that phosphorus is not likely to be a limiting factor for phytoplankton growth.

This study focuses on ammonia and oxygen fluxes at the water-sediment interface. Results obtained under the culture units were compared with those obtained in outside unit sediments at each site, in order to estimate the impact of shellfish culture, and the activity of microbenthic algae.

MATERIAL AND METHODS

Two sites were studied:

The Thau lagoon (Fig. 1) is located on the French Mediterranean coast. This lagoon has an average depth of 3.5 m and covers an area of 75 km^2. There are two sea-water inlets, and several inputs of fresh water from small streams and the Hérault river. It has been fully described by Amanieu et al. (1989). The second site, Carteau bay (Fig. 1) is
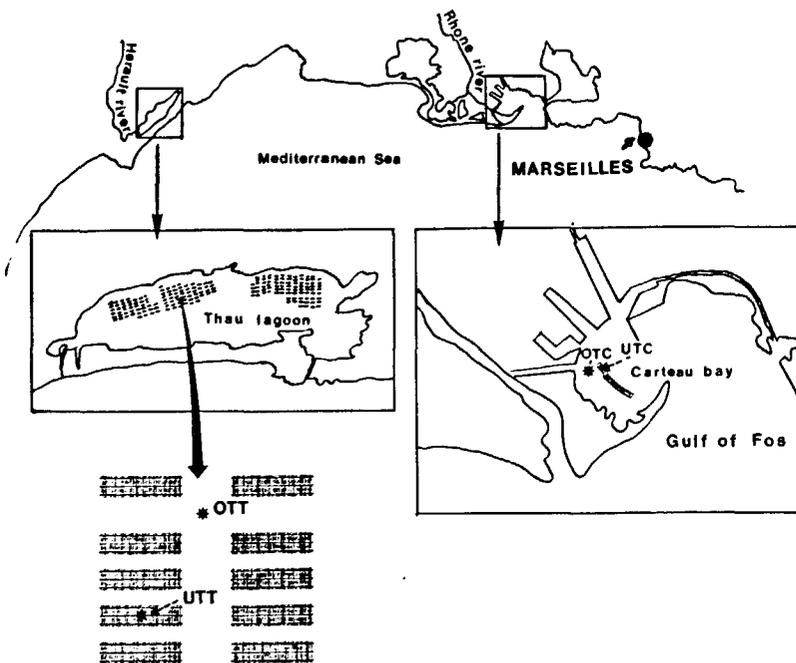
Figure 1

Location of the study sites in the Mediterranean Sea. Thau lagoon stations: UTT: Under oyster Table at Thau; OTT: Outside of Table at Thau. Carteau bay stations: UTC: Under mussel Table at Carteau; OTC: Outside of Table at Carteau.

Situation des sites d'étude en mer Méditerranée. Stations de l'étang de Thau : UTT : sous la table à huîtres à Thau ; OTT : hors de la table à Thau. Stations de la baie de Carteau : UTC : sous la table à moules à Carteau ; OTC : hors de la table à Carteau.

located near the Rhône river delta in the Gulf of Fos, and has a wide opening to the sea. The area of the bay is about 13 km², with an average depth of 4 m; freshwater inputs from the rivers Rhône and Durance sometimes cause salinity stratification. There are shellfish farms at both sites. Thau lagoon has been a site of oyster production (*Crassostrea gigas*) for nearly thirty years; farming structures cover about 20 % of the lagoon area. Since 1984, intensive mussel cultivation (*Mytilus galloprovincialis*) has been developed in Carteau bay, occupying about 0.4 % of the bay surface. Farming structures are similar in both sites: hanging ropes fixed to a rigid structure called a table.

Nutrient contents of the water column have been studied throughout the year by Picot *et al.* (1990) in Thau lagoon, and by Baudinet (1991) in Carteau bay.

Hydrodynamic conditions at both sites have been studied by Millet (1989). Average residence times of waters are approximately ninety days for Thau lagoon and twenty days for Carteau bay, where hydrodynamics are mainly controlled by the local wind regime (Millet *et al.*, 1994), producing strong exchanges with the open sea.

Sediments at both sites may be described as muddy sands. Diversity of the benthic plant populations is higher in the oyster breeding area in Thau lagoon than in Carteau bay. At Thau, in small channels between the tables, *Zostera marina* sea grass beds cover the lagoon bottom. In the larger channels between cultivation units, dense populations of macroalgae (*Gracilaria, Ectocarpus*) are present. At the intersection of the channels separating the blocks of tables, the sediments are bare. We chose these sediments as a reference station for comparison with the Carteau "outside table" station.

Two stations were studied at each site: under cultivation structures, UTT (Under Table Thau), UTC (Under Table Carteau); OTT (Outside of Table Thau), OTC [Outside of Table Carteau (Fig. 1)].

In situ measurements

Four seasonal surveys were carried out at each site.

Measurements in the bottom waters

Temperature and salinity were measured using a Valeport series 600MK II CTD. The photon flux of photosynthetically available radiation (PAR) was measured throughout the duration of the experiment at the surface of sediments with a cosinus Li-Cor[R]LI-192SB quantum sensor interfaced with a Licor LI 550. Data were integrated every ten minutes. Results are expressed in µmol m⁻² s⁻¹. Water samples for ammonia analysis were immediately filtered through 0.2 µm pore size filters. Ammonia measurements were performed according to Koroleff (1969). Dissolved oxygen concentrations were measured using an Orbisphere oxymeter model 2609 (polarographic cell 2120 and sensor 2112).

Flux measurements at the water-sediment interface

Oxygen and nutrient fluxes were measured by incubation in hemispherical bell jars, of 13.8 l volume covering a surface of 0.11 m², similar to those described by Grenz *et al.* (1991). Water was circulated inside these mesocosms by magnetic stirrers. Mesocosms were placed *in situ* and sampled by scuba divers. Three transparent and three darkened bell jars were incubated for periods of four to six hours around noon. Surface and bottom waters were incubated in 300 ml bottles (three transparent and three dark) at the same time in order to estimate oxygen and ammonia variations in the water column.

For NH₄ measurements, 100 ml samples were withdrawn from the bell jars using syringes at the beginning and the end of the experiment. Ammonia fluxes were calculated as the difference between final and initial concentrations in the bell jar and were expressed in µmol N-NH₄ m⁻² h⁻¹. Samples from similar bell jars were pooled. Ammonia was

then measured on three replicates of one sample. Values measured in transparent and dark bottles were subtracted from values obtained in bell jars, in order to eliminate the effects of pelagic processes.

Oxygen was measured at the beginning and end of incubation and at one intermediate time. One bell jar was connected to an oxygen recorder throughout the incubation.

Net oxygen fluxes in the transparent bell jars and benthic oxygen consumption in the dark jars were calculated by pooling the data from the three replicates, calculating the slope of the regression of $[O_2]$ against time, and then converting the results into mg O_2 m^{-2} h^{-1} (Grenz et al., 1991). Gross primary production was calculated by adding net oxygen fluxes measured in the transparent bell jars to respiration rates measured in the dark jars.

Sediment analyses

All cores were collected by scuba diving. Readings of redox potential were performed on freshly collected cores at a temperature close to that of the environment using a PVRTC Ponselle pH meter with a platinium electrode. We estimated the depth of the lower part of the redox potential discontinuity layer in millimetres, according to Plante et al. (1989). The porosity of the first centimetre of the sediment was calculated, according to Berner (1971) as:

Porosity = V water/(V water +V solids) where V = volume.

Water volume was estimated after freeze-drying slices containing the first centimetres from three cores.

Organic matter was then estimated from weight loss of calcined dried sediment after 12 hours at 500°C. Total carbon, organic carbon and total nitrogen were analyzed using a CHN Leco 800 CHN analyzer. All results were expressed as percentage of dry sediment (g/100 g dry weight).

Twelve 2.7 cm diameter cores were taken at each station and processed individually to estimate chlorophyll a and phaeopigment concentrations. The number of cores sampled was intended to give an error not larger than 10 % ($n = t^2$ x $CV^2/10^2$, for $p < 0.05$). The top layer of sediment (0-1 cm) was freeze-dried, Chl a and phaeopigments were extracted with 90 % acetone and concentrations estimated by spectrophotometry. OD was read at 665 nm before and after acidification of the extract with 30 µl of HCl 0.4N in a 4 ml cell (Riemann, 1978).

Pigment concentrations were calculated by the equations of Lorenzen (1967), related to dry weight of sediment and expressed as mg m^{-2} (Plante-Cuny, 1978). Chl a concentration was used as an index of plant biomass.

Statistical tests

Differences between ammonia fluxes were tested using paired unilateral t tests.

For oxygen fluxes, tests for the equalities of slopes were used to establish the differences in oxygen fluxes for the seasons. The confidence intervals for gross production were calculated with the variance of the difference of two variances.

The differences in Chl a contents between UT and OT stations were tested with an ANOVA ($p = 0.001$). A Hartley test showed that variances should be stabilized, so we transformed the data into $[(logx)^2$; Frontier, 1981] suitable for aggregative distributions. This transformation did not stabilize the variances completely, so we used a $p < 0.001$ for more accuracy. A multifactor ANOVA was performed with Chl a data to show the triple interaction between the factors: sites, seasons and stations.

The effects of environmental factors were examined by multiple linear regression treating flux data within the bell jars as variables dependent on temperature, PAR, respiration rates, net production rates, sediment chlorophyll a and organic matter contents.

RESULTS

Environmental conditions

During our experiments, water temperature ranged from 12.5° to 22.5 °C at Carteau, and from 5.3° to 22.8 °C at Thau. Salinity varied from 33 to 38.6 at Carteau, and 38 to 39 at Thau. Concentrations of NH_4 near the bottom generally decreased during the daytime, except under the tables in spring. Oxygen concentrations in near-bottom waters increased during the daytime. Maximum values of 10 mg O_2 l^{-1} were observed in winter (Tab. 1).

PAR at Carteau was maximal in summer (215 µmol m^{-2} s^{-1}) and minimal in spring [36 µmol m^{-2} s^{-1} at OTC (Tab. 1)]. At Thau, maximal values were recorded in spring at OTT (about 470 µmol m^{-2} s^{-1}); minimal values were found in winter at every station (24 and 25 µmol m^{-2} s^{-1}).

The porosity and water content of the top layer (1 cm) of sediment are higher at Thau than at Carteau. The lower part of the redox potential discontinuity layer depth fluctuated over the seasons. In Carteau bay, it varied from 1 to 5 mm below the surface and in the lagoon from 1 to 18 mm (Tab. 2).

The organic matter content in the upper layer of the sediments showed slight seasonal variations at both sites. UTC was richer in organic matter than OTC. All values for organic matter and organic C were higher at the Thau stations. C/N ratios were higher at Carteau than at Thau (Tab. 2).

Chl a concentrations in the sediments (Fig. 2 a) were generally higher at UT stations than at OT; both UT stations showed similar seasonal patterns with maximal Chl a values in winter: 436 mg Chl a m^{-2} at UTC and 260 mg Chl a m^{-2} at UTT. OTT concentrations varied between 52 mg Chl a m^{-2} in spring and 130 mg Chl a m^{-2} in winter; OTC showed minor seasonal variations. Multifactorial analysis of variance showed that season was a significant factor influencing Chl a concentrations ($p < 0.001$). The interaction between season and site (Carteau-Thau) was not significant, the chlorophyll concentrations demonstrating similar seasonal patterns at both sites.

Table 1

Parameters recorded in bottom waters at the four stations. Ammonia: μmol l⁻¹; oxygen: mg l⁻¹; PAR : μmol m⁻² s⁻¹.

Paramètres mesurés dans l'eau au niveau du fond aux quatre stations. Ammoniac : μmol l⁻¹ ; oxygène : mg l⁻¹ ; PAR : μmol m⁻² s⁻¹.

		UTT						OTT			
Season	T°	S‰	ammonia	oxygen	PAR	T°	S‰	ammonia	oxygen	PAR	
AUTUMN	16,9	38	3,2-2,5	6,5-7,3	125						
WINTER	5,3	38,7	0,7-0,5	10-10,1	25	5,7	38,4	0,7-1,3	9,5-9,7	24	
SPRING	13	39	2,2-7	8,1-8,1	166	13	39	0,9-1,0	7,8-9,3	470	
SUMMER	22,8	38	1,3-1,6	6,0-7,1	280	21,7	38,3	3,3-2,4	5-5,8	260	

		UTT						OTC			
Season	T°	S‰	ammonia	oxygen	PAR	T°	S‰	ammonia	oxygen	PAR	
AUTUMN	22,2	37	0,8-0,3	5,7-7,0	130	22,5	38	2,0-1,7	6,2-6,9	100	
WINTER	12,5	38,6	2,3-1,4	7,6-8,9	120	12,6	38,1	2,0-2,0	7,9-8,4	125	
SPRING	19,9	33	1,81-2,1	7,5-7,6	90	18,6	34	1,96-1,92	6,3-7,2	36	
SUMMER	21	35	0,8-0,7	7,7-8,3	150	20	35,5	2,39-2,42	5,8-7,1	215	

Table 2

Biogeochemical characteristics of superficial sediments in Thau lagoon and Carteau bay. UTT, OTT, UTC and OTC as defined in Figure 1.

Caractéristiques biogéochimiques des sédiments superficiels des zones d'élevage dans l'étang de Thau et la baie de Carteau.

	Thau		Carteau	
	UTT	OTT	UTC	OTC
Porosity	0.79	0.76	0.72	0.68
LRDP [1]	1-18 mm	2-15 mm	1-4 mm	2-5 mm
Org. Matt. [2]				
AUTUMN	22.7	22.9	17.5	15.2
WINTER	22.1	25.6	17.3	10.6
SPRING	24.4	23.8	15.8	10.9
SUMMER	29.4	24.2	15.9	11.7
Org. Carbon [3]				
AUTUMN	8.2	6.87	5.97	4.12
WINTER	5.91	7.08	4.57	2.85
SPRING	6.92	6.13	3.83	3.09
SUMMER	7.35	5.16	5.38	3.19
C/N [4]				
AUTUMN	12.9	10.8	19.5	27.7
WINTER	10.3	10.0	11.9	29.6
SPRING	10.5	10.5	13.9	22.5
SUMMER	9.3	10.7	12.4	18.6

[1] LRDP = depth within the sediment of the lower part of the redox potential discontinuity.
[2] Organic Matter: expressed in % sediment dry weight (0-1 cm).
[3] Organic Carbon: expressed in % sediment dry weight (0-1 cm).
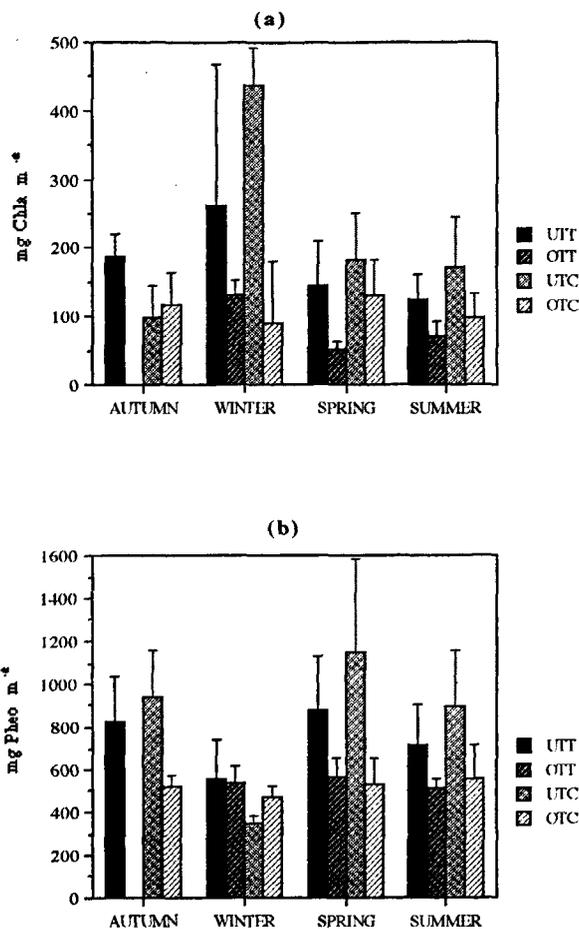[4] C/N = Organic Carbon/Nitrogen Ratio.

Figure 2

Seasonal variations of pigment contents in the upper layer (0-1 cm) of the sediments (mg m⁻²). Stations UTT, OTT at Thau lagoon and UTC, OTC at Carteau Bay. a) Chl a; b) phaeopigments.

Variations saisonnières des teneurs en pigments (mg m⁻²) dans les sédiments superficiels (0-1 cm). Les quatre stations UTT, OTT, UTC, OTC sont définies dans la figure 1. a) Chl *a* ; b) phéopigments.

Phaeopigment concentrations at OT stations remained stable and lower than at UT stations, except in winter. UT stations had their maximal concentrations in spring (1 146 mg Pheo m^{-2} at UTC and 882 mg Pheo m^{-2} at UTT), UTC being the richest station (Fig. 2 b).

Fluxes at the water-sediment interface

Ammonia

Production or uptake of ammonia in the water column near the bottom was negligible compared to NH_4 fluxes at the water-sediment interface; maximal negative flux in the bottles was recorded in spring, under tables (- 0.21 N-NH$_4$ µmol h^{-1} l^{-1} at Thau and - 0.07 at Carteau bay). Inside the chambers, ammonia was released from the sediment. At both sites, ammonia fluxes within the bell jars were higher under the shellfish cultivation units (Fig. 3 a) than outside (Fig 3 b). Maximal values were recorded in summer at both UTT and OTT (194 µmol N-NH$_4$ m^{-2} h^{-1} and 165 µmol N-NH$_4$ m^{-2} h^{-1} respectively). In Carteau bay, maximal

values were recorded in autumn (382 µmol N-NH$_4$ m^{-2} h^{-1} UTC) and minimal fluxes in summer (15 µmol N-NH$_4$ m^{-2} h^{-1} OTC). Average flux of ammonia was higher under table in Carteau bay than in the corresponding station in Thau lagoon (t test, p < 0.005) and than outside table in Carteau (p < 0.005). Ammonia release outside the table was higher in dark jars than in transparent jars (p < 0.1). The converse was recorded at UTC in autumn, winter and spring.

Oxygen

Most of the R^2 from the slopes of net oxygen fluxes were significant (26 from 30, p < 0,005). Net oxygen fluxes were not significant in four cases in transparent bell jars: OTC in spring (R^2 = 0.353; p = 0.0918), UTC in summer (R^2 = 0.304, p = 0.257) and UTT in autumn and winter (R^2 = 0.096, p = 0.417, and R^2 = 0.018, p = 0.63 respectively).

Net oxygen fluxes showed similar trends throughout the year at all stations (Fig. 4). All stations at both sites had their maximal negative fluxes in spring (i. e. UTC, 69 mg O$_2$ m^{-2} h^{-1}). At Carteau, fluxes were always negative under tables and positive outside, except in spring. In Thau lagoon, significant net positive fluxes were recorded under tables in summer (21 mg O$_2$ m^{-2} h^{-1}, R^2 = 0.577, p < 0.05). Respiration tended to increase from autumn to spring at all stations (Fig. 5); maximal values were recorded during spring at UTC (135 mg O$_2$ m^{-2} h^{-1}, R^2 = 0.963, p < 0.05). Respiration was lower under the table at Thau (UTT) than at Carteau (UTC), except in winter; the maximal at Thau is in summer 75 mg O$_2$ m^{-2} h^{-1} and at Carteau in spring (133 mg O$_2$ m^{-2} h^{-1}).

There were substantial seasonal differences in gross primary production at both study sites (Fig. 6). The pattern of primary production at the under table stations differed between the two sites. Although the pattern of change over the year was the same at OTT and OTC, OTC was consistently more productive. At Carteau UT station, production increased from autumn to summer (no primary production was
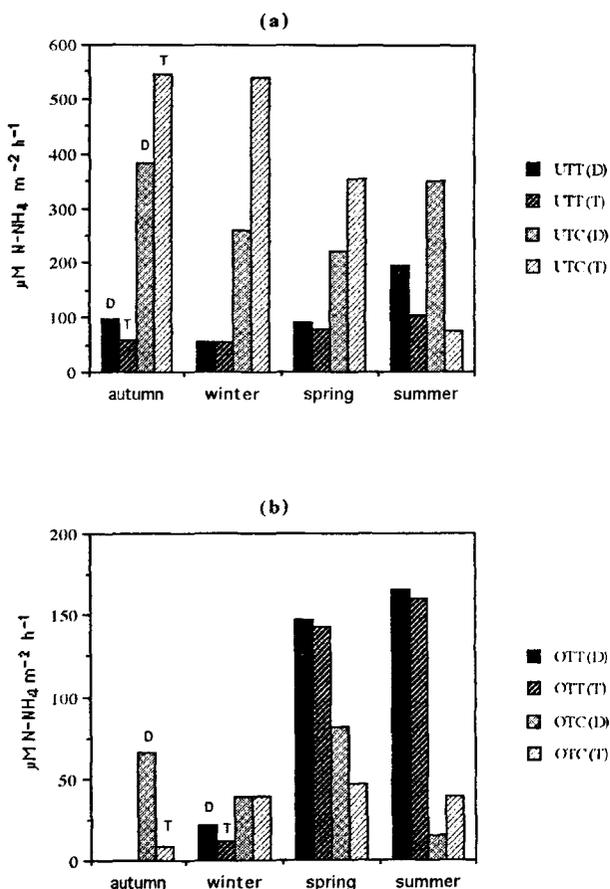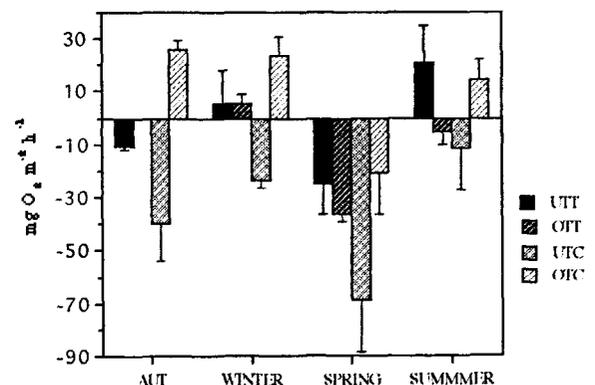

Figure 3

Seasonal variations of ammonia (µmol N-NH$_4$ m^{-2} h^{-1}) fluxes at the water-sediment interface in Thau lagoon (UTT and OTT) and in Carteau bay (UTC and OTC). a) ammonia release under shellfish table; b) ammonia release outside table. D: dark bell jars; T: transparent bell jars.

Variations saisonnières des flux d'ammoniac (µmol N-NH$_4$ m^{-2} h^{-1}) à l'interface eau-sédiment dans l'étang de Thau et dans la baie de Carteau. Les quatre stations UTT, OTT, UTC, OTC sont définies dans la figure 1. a) relargage de NH$_4$ sous les tables conchylicoles ; b) relargage hors des tables ; D: cloches noires ; T: cloches transparentes.

Figure 4

Net oxygen fluxes recorded in the transparent bell jars in hourly rates (mg O$_2$ m^{-2} h^{-1}) at each season. UTT, OTT, UTC and OTC as defined in Figure 1.

Flux nets d'oxygène mesurés dans les cloches transparentes aux différentes saisons, exprimés par heure (mg O$_2$ m^{-2} h^{-1}). Les quatre stations UTT, OTT, UTC, OTC sont définies dans la figure 1.
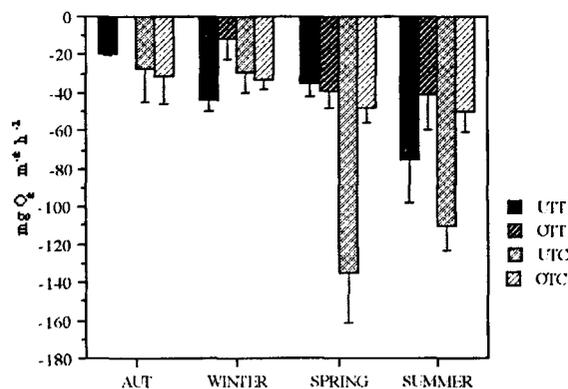
Figure 5

Respiration rates (biological respiration + chemical oxygen demand measured in dark bell jars) expressed in mg O_2 m^{-2} h^{-1} at each season.

Taux de respiration (demande biologique + demande chimique en oxygène du sédiment) mesurés dans les cloches noires, exprimés en mg O_2 m^{-2} h^{-1}. Les quatre stations UTT, OTT, UTC, OTC sont définies dans la figure 1.

Figure 6

Hourly rates of gross primary production (mg O_2 m^{-2} h^{-1}) calculated from data recorded in dark and transparent bell jars (net oxygen flux + respiration) in our survey stations.

Production primaire benthique brute par heure (mg O_2 m^{-2} h^{-1}), calculée d'après les données obtenues dans les cloches transparentes et les cloches noires (flux nets d'oxygène + respiration).

detected in autumn and 100 mg O_2 m^{-2} h^{-1} in summer). At Thau lagoon, oxygen production was consistently higher at the UT than at the OT station: in summer an oxygen flux of 96 mg m^{-2} h^{-1} was recorded at UTT as opposed to 36 mg m^{-2} h^{-1} at OTT. Subtraction of gross phytoplankton production from the total oxygen fluxes recorded in bell jars did not change the production pattern, phytoplankton production remaining consistently low in bottom waters compared with benthic production (by a factor of approximately ten, i. e. 0.03 mg l^{-1} h^{-1}, against 0.31 mg l^{-1} h^{-1}).

GP/B and GP/R ratios

Rates of gross primary production (GP) expressed as mg O_2 m^{-2} h^{-1} were converted into mg C m^{-2} h^{-1}, assuming a photosynthetic quotient of 1, i. e. 1 mg C = 0.375 mg O_2, (Hargrave *et al.*, 1983; Oviatt *et al.*, 1986). In terms of productivity, the highest gross production/biomass (GP/B) ratio: mg C (mg Chl a)$^{-1}$ h^{-1} was recorded at OTC in winter and summer, coinciding with the maximum of gross primary production (Tab. 3). UTC ratios increased from autumn to summer in the same way as gross primary production. At Thau, maximal GP/B values occurred in summer, and low values were recorded in spring [0.02 mg C (mg Chl $a)^{-1}$ h^{-1} for UTT and 0.01 for OTT]; the highest GP/B ratio was recorded at UTT (0.29). Daily ratios of sediment gross primary production to respiration (GP/R) showed different patterns, but were always < 1, indicating a heterotrophic dominance (Tab. 3). At UT stations GP/R was maximal in summer (0.55 and 0.80). For both OT stations it was minimal in spring, and for OTT the ratio was particularly low (0.05) at this time of the year.

DISCUSSION

– Shellfish farming areas are located in shallow waters, characterized by high plankton productivity. Prior to the
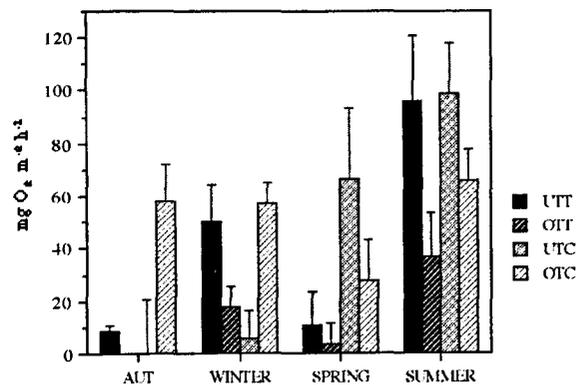
Table 3

Seasonal GP/R and GP/B ratios [gross production/respiration and gross production/biomass: mg C (mg Chl $a)^{-1}$ h^{-1}].

Variations saisonnières des rapports GP/R et GP/B [production brute/respiration et production brute/biomasse: mg C (mg Chl a)$^{-1}$ h^{-1}].

Season	UTT		OTT	
	GP: R	GP: B	GP: R	GP: B
AUTUMN	0,21	0,010		
WINTER	0,48	0,070	0,65	0,040
SPRING	0,17	0,020	0,05	0,010
SUMMER	0,80	0,290	0,55	0,190

Season	UTC		OTC	
	GP: R	GP: B	GP: R	GP: B
AUTUMN	0,22	0,000	0,96	0,180
WINTER	0,09	0,001	0,83	0,240
SPRING	0,29	0,110	0,34	0,070
SUMMER	0,55	0,210	0,80	0,240

analysis of differences between sites and impact of shellfish cultivation, the general features of our study sites should be examined and compared with other temperate shallow water environments.

The range of ammonia fluxes within the dark bell jars is similar to those measured in temperate shallow waters. We did not observe negative fluxes in our experiments. NH_4 release from sediment towards the water column was minimal in winter, whereas higher fluxes were observed in spring and summer (Aller and Benninger, 1981; Boucher and Boucher-Rodoni, 1988; Elderfield *et al.*, 1981; Rizzo, 1990; Ullman and Sandstrom, 1987).

As observed by Rizzo (1990), NH_4 fluxes were in general higher in dark than in transparent jars. The lower fluxes are generally explained by microphytobenthos ammonia uptake; the influence of microphytobenthos activity in nutrient exchange at the water-sediment interface has been pointed out previously (Henriksen et al., 1980; Granéli and Sundbäck, 1985; Nowicki and Nixon, 1985; Asmus, 1986; Simon, 1988, Jensen et al., 1990). Using atomic Redfield ratios (C:N = 106:16), assimilated carbon can be estimated from ammonia uptake: it ranges from 4 to 100 % of the fixated carbon as estimated from oxygen production. Bearing in mind that Redfield ratios were established for phytoplankton and that the photosynthetic quotient in the estuarine zone may vary during daytime from 0 to 5 (Oviatt et al., 1986), this suggests that ammonia is not the only source of nitrogen used by benthic microalgae.

Regression analysis showed that ammonia fluxes were significantly correlated with respiration, the latter being responsible for 41 % of the variation in released ammonia [ammonia flux = 1.5 (respiration) + 25.4; R 0.64; p < 0.01], a percentage close to the 50 % reported by Rizzo (1990) for estuarine shallow waters. At both sites, seasonal changes in respiration rates were those typical for organic matter-enriched environments, either sublittoral (Davis and McIntire, 1983; Hargrave et al., 1983; Sundbäck et al., 1991), or intertidal (van Es, 1982).

In spring, when phytoplankton biomass is high, enhancing sedimentation rates (Grenz, 1989), negative oxygen balances were observed at every station. Respiration rates

are higher than those found in other environments at similar depths in sediments less enriched with organic matter, whereas gross primary production is lower (Cahoon and Cooke, 1992; Rizzo et al., 1992). No significant correlation was found either between primary production and ammonia fluxes or primary production and Chl a contents in sediments; this is in agreement with findings of Hansen et al. (1987) and Cahoon and Cooke (1992). Other authors have found significative correlations between Chl a and gross primary production in sublittoral sediments (Davis and McIntire, 1983; Andersen and Kristensen, 1988; Sundbäck et al., 1991).

The microphytic bottom community was more productive in summer at all stations, when light irradiance was generally the highest. The rates of gross primary production measured for microphytobenthos are within the range of those measured by other authors in sublittoral sediments (Tab. 4), but they remain lower than the 100 g C m^{-2} year^{-1} recorded for intertidal sediments (Cadée and Hegeman, 1977; van Es, 1982; Colijn and de Jonge, 1984).

– Despite their common features, the two sites exhibited some differences. The main difference in magnitude of ammonia fluxes between Thau lagoon and Carteau bay was recorded in spring and summer. It should be noted that in our experiments, temperatures differed for the same season at the two sites. Within the same temperature range, ammonia release from OT sediments was higher at Thau than at Carteau. This might be related to the higher organic matter content of the sediments in the lagoon.

Table 4

Comparison between our data on microphytobenthic production and biomass in sublittoral sediments and data from the literature.

Comparaison des données de production microphytobenthique et de biomasse dans des sédiments sublittoraux avec les données de la littérature.

Author	Environment	Depth	PAR µmol/m²/s	g C/m²/year	mg C/m²/h	Chl a
Davis & McIntire (1983)	Netarts Bay Oregon	1,5	100-200	75-162	25-47	46-94 mg/m²
Nienhuis & de Bree (1984)	Lake Grevelingen The Netherlands	5,3	9-145	32-35		80 mg/m²
Bodin et al. (1985)	Bay of Douarnenez France	0-10	–	25		45 µg/g
Sundbäck (1986) Sundbäck & Jönsson (1988)	Lahom Bay Sweden	5-8	20-320	7-11		20 mg/m²
Cahoon & Cooke (1992)	Onslow Bay North Caroline	15-32	81-115	52	25	17-52 mg/m²
Daehnick et al. (1992)	Sand microflora in seagrass beds	1-1,5	81-900	340	77	mean-value = 44 mg/m²
Present work	Mediterranean Sea					
	Thau lagoon					
	under oysters	5	25-280	65	14	179 mg/m²
	outside oysters	5	24-470	28	6	84 mg/m²
	Carteau bay					
	under mussels	4,5	90-150	75	15	222 mg/m²
	outside mussels	4,5	36-215	82	19	108 mg/m²

Overall differences between sites would appear to be partly due to hydrodynamic factors and partly to the cultivation itself. Thau lagoon has been the site of extensive shellfish farming, covering about 15 km^2, for almost thirty years; it is, moreover, somewhat cut off from the open sea. Carteau bay has been a farming area for less than fifteen years, it is less extensive (about 0.053 km^2), and water circulation is more strongly influenced by fresh- and seawater inputs. These factors might explain the higher accumulation of organic matter in the lagoon and the lower oxygen release by OT sediments in comparison with Carteau bay. In Thau lagoon, dystrophic crises occur at the beginning of the summer: with high temperature, high salinity and windless weather, anoxia occurs in near bottom shallow water together with decreasing pH and H$_2$S production. High mortality of benthic fauna is then observed. As suggested by Asmus and Asmus (1991), shellfish produce a great amount of ammonia that can be used as nutrient for macroalgae. In Thau lagoon, where the waters are transparent, macroalgae (*Gracilaria, Ectocarpus*) cover the bottom between the tables; these macroalgae are the main oxygen suppliers in winter, but when the temperature rises and nutrients are depleted, they die and decay. Additional incubations confirmed this observation; at the beginning of July, oxygen depletion in bell jars located in macroalgal beds occurred after two hours (Barranguet and Alliot, unpublished). On the other hand, high gross primary production and high P/B ratios were recorded at UTT during the same period; microphytes under the tables are then responsible for oxygen production in the warm season, but they cannot offset the general oxygen demand and anoxia that periodically occurs.

– The impact of cultivation structures at the water-sediment interface was reflected in all our measurements. As expected, ammonia release was higher under shellfish cultivation units than outside at both sites (Boucher and Boucher-Rodoni, 1988; Baudinet *et al.*, 1990). Accumulation of organic matter under shellfish cultivation units has been shown to be about three times higher than control measurements in open water in the same area (Grenz, 1989). Organic matter of biodeposits seems to be rapidly recycled (Grenz *et al.*, 1991), enhancing nutrient release at the water-sediment interface. With regard to ammonia fluxes, our observations show higher ammonia release under mussels than under oysters. These differences might be explained by specific features of shellfish cultivation:
– higher biomass of mussels on mussel tables, producing more deposits;
– differences in biodeposit composition as shown by Grenz (1989) with higher organic content of mussel biodeposits;
– the difference in size of the shellfish farming areas, with an overall biomass of oysters in the lagoon about ten times greater than the mussel biomass in Carteau bay. As pointed out by Picot *et al.* (1990), ammonia concentration in the lagoon water may reach very high values compared to those observed in the bay, limiting the diffusion process from the sediment towards the water column. In Carteau bay, ammonia fluxes in transparent bell jars were higher than in dark jars except in summer. We could not find a clear explanation for this phenomenon.

Available light does not exclusively determine gross primary production: OTC was on average the most productive station, and the only station where PAR and primary production were significantly correlated (R = + 0.82). UTC behaved as an oxygen sink in every season; during our experiments, PAR seemed high enough to allow photosynthesis in all seasons (Shaffer and Onuf, 1983; Sundbäck, 1986; Blanchard and Montagna, 1992) whereas gross production undergoes major seasonal changes. At UTT station, even if high values were observed for both gross production and PAR in summer, there was no correlation between light and oxygen production.

With regard to microphytic biomass under the table, the Chl *a* content of UT sediments is probably enhanced by phytoplankton contained in faeces and pseudofaeces of filter-feeders, where a part of the Chl *a* has not been degraded (Hawkins *et al.*, 1986; Barranguet, 1990). This might explain why UTC, despite being the richest station in Chl *a*, is not the most productive with very low GP/B ratios (Tab. 3 and 4).

Phaeopigment concentrations can be an estimate of bivalve metabolism (Mann, 1977; Gelder and Robinson,1980; Hawkins *et al.*, 1986); these are coloured chlorophyll degradation products, mainly linked to the feeding activity of molluscs (faeces and pseudofaeces) in these farming areas. They are significantly higher at UT stations, and become particularly abundant in spring, when shellfish feeding metabolism is at its highest. OT concentrations would appear not to be influenced by the seasonal phytoplankton cycle.

With regard to percentages of organic matter in the sediment, the difference between UT and OT stations is clear at Carteau, UTC being richer in organic matter and carbon than OTC. In the lagoon, due to the age of the culture and the hydrodynamics, no difference between UT and OT sediments was observed. Comparisons with results obtained by Baudinet *et al.* (1990) under a table in Carteau bay four years earlier, suggest that cumulative effects of biodeposition induce higher respiration rates. The balance in favour of a heterotrophic metabolism (GP/R < 1) is not due to the increasing depth, as it is the case in an undisturbed system; just a few metres apart, and at the same depth, OTC station has a GP/R close to 1, which is similar to that reported by Rizzo (1990) for similar depths, the community not being affected by biodeposition.

Concerning the general pattern of changes induced by the type of cultivation, our findings suggest that mussel tables have a stronger impact than oyster cultivation units on benthic fluxes. While yearly balances of primary production rates are difficult to ascertain and remain very approximate, it should nonetheless be noted that despite the difference in net fluxes between under table stations, both UT stations produce comparable quantities of carbon per year (Table 4) and that mussels increase respiration in under table sediments more than oysters. In Carteau bay under the tables, with accumulation of phaeopigments indicating high sedimentation of organic matter, net negative oxygen balance is always observed at the water-sediment interface. Thus the contribution of the microphytobenthos is not strong enough to ensure a positive balance. Outside the tables in Carteau, the microphytobenthos plays an important role in oxygen balance, as has been observed for other sublittoral areas.

Acknowledgements

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