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Benthic-pelagic coupling under juvenile oyster influence in a French Mediterranean coastal lagoon (Thau Lagoon)

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Abstract

The aim of the present work was to test the influence of juvenile oyster culture on benthic-pelagic coupling in the French Mediterranean Thau Lagoon. Although the period of juvenile growth induces the introduction of millions of juvenile oysters in the lagoon over a short duration, the effects on the water-column and on the benthic ecosystem are poorly known. Using a multiple ecological approach, water column parameters, sedimentation rates, sediment characteristics and benthic fluxes were monitored on three occasions during the oyster pre-growth period, from October to December, at two sites inside the farming area and two sites outside the farming area that served as reference. In the water column, results showed a significant lower ratio between total phytoplankton biomass (chlorophyll-*a*) and degraded pigments (pheopigment), a significant increase in the contribution of phytoplankton containing chlorophyll-*b* (*ie* chlorophytes) to total phytoplankton biomass and a significant decrease in the contribution of phytoplankton containing chlorophyll-*c* (mainly diatoms) to the total phytoplankton biomass at farm sites, attributed to the grazing pressure caused by juvenile oysters on large particles, as described for adult oysters. No significant effect was observed at the benthic interface during this period, due to the dispersion of the small quantities of biodeposit produced by juveniles in the low water temperature conditions. A multivariate approach supported the effect of juvenile oysters on the water column and revealed a trend in benthic conditions with farm sites being distinct from the reference ones. The long farming history of the lagoon could have shaped sediment properties such that farming areas maintain different benthic conditions.

Keywords: Shellfish farming; phytoplankton; biodeposition; benthic fluxes; coastal lagoon

1. Introduction

Shellfish aquaculture relies on the introduction of high densities of organisms in an environment thereby creating a wide range of interactions. This may result in major changes in exploited ecosystems, for example (i) depletion of plankton through filter feeding (Gallardi, 2014; Pinkerton et al., 2018), (ii) increased nutrient turnover through direct excretion into the water column (Lacoste et al., 2014; Nizzoli et al., 2011; Richard et al., 2006) and/or the transfer and recycling of organic matter at the sediment-water interface (Gaertner-Mazouni et al., 2012; Richard et al., 2007b) and (iii) localized supplies of organic material (biodeposit and organisms fall-off) that may affect sediment properties and benthic communities (Callier et al., 2009, 2008; Lacoste et al., 2018). The influence of cultivated bivalves on ecosystems is usually studied by estimating their impact on the benthic-pelagic coupling (Lacoste and Gaertner-Mazouni, 2016; Nizzoli et al., 2006; Richard et al., 2007), which contributes substantially to primary production in shallow ecosystems (Ferrón et al., 2009; Grenz et al., 2019). Fewer studies have described the influence of bivalve culture on the composition of planktonic communities through grazing pressure (Hulot et al., 2020; Trottet et al., 2008). However, some authors showed that feeding of bivalves may impact the size-structure and composition of the plankton pool with cascading effect on the food-web (Karuza et al., 2016; Mostajir et al., 2015). Thau Lagoon is the main French Mediterranean area for shellfish production (*Crassostrea gigas* and *Mytilus galloprovincialis*), which covers about 1/4 of its total surface area (ca 1 700 ha). Annual oyster production (ca. 7 000 tons) represents 10% of the national production and 90% of shellfish production in the French Mediterranean region. Previous studies evidenced that shellfish farming modifies the dynamics of both the benthic (Gilbert et al., 1997; Metzger et al., 2007; Thouzeau et al., 2007) and pelagic (Mazouni, 2004) compartments in Thau Lagoon in all four seasons (Souchu et al., 2001). These studies also highlighted variability of benthic and pelagic processes due to differential habitat characteristics and wide fluctuations in environmental conditions driven by seasonal trends.

The ecological functioning of such a semi-enclosed costal lagoon is very fragile and disturbances can, for example, lead to hypoxia/anoxia events with significant economic impacts, as already observed in the past (Chapelle et al., 2000; Derolez et al., 2020a; Souchu et al., 1998). Since the late 2000s, mitigatory actions have been designed, targeting in particular sewerage networks in estuarine watersheds, and allowing a decrease in nutrient inputs. This has resulted in the ecological recovery of French Mediterranean lagoons, at varying speed and with different patterns, modifying therefore their ecological functioning (Collos et al., 2009; Derolez et al., 2019). This make it necessary to update our knowledge about shellfish culture and environment interactions in Thau lagoon. Moreover, while some studies analyzed interactions between larvae (Lagarde et al., 2019, 2017; Ubertini et al., 2017) or adult oysters (Mazouni, 2004; Thouzeau et al., 2007) and the environment, knowledge is lacking on the pre-growth phase (juvenile culture), despite the fact more than 530 million juveniles are introduced in this lagoon every year (Pete et al., 2020).

Thus, the aim of this study was to investigate interactions between oyster culture (*C. gigas*) and the benthic and pelagic systems following the massive introduction of juvenile oysters in the lagoon and before they were glued on ropes during winter for the growing phase. In the present study, we used an integrated ecological approach to simultaneously quantify nutrient concentration and phytoplankton biomass in the water column, sedimentation rates, sediment composition, the biomass of benthic organisms (macrophytes, macrofauna, meiofauna) and nutrient and oxygen benthic fluxes, at two sites under the devices systems (“tables”) and two reference sites outside the farming zone, as representative of natural conditions. In many studies, only one site per treatment (farm *vs* reference) is considered to highlight the impact of aquaculture on the benthic environment (Table S1). In contrast with these studies, we choose to use two farm sites and two references sites in order to oppose farm effect to natural variability, as recommended by Underwood (1997). Two farm sites with equivalent density and biomass of juvenile oysters were selected to theoretically obtain the same initial level of pressure by oysters activities (filtration, excretion and biodeposition) on the benthic-pelagic coupling. The two reference sites were blindly selected in the same area, located 200 m away from farms, and with the same depth, without information on benthic habitat characteristics. This approach allowed us to test the effect of juvenile oysters in their pre-growth phase, opposing it with the natural variability of benthic habitats, without any initial *a priori* on the benthic compartment.

2. Materials and Methods

2.1. Study area and sampling design

Thau Lagoon is an important shellfish farming area located on the French Mediterranean coast (Fig. 1). Shellfish farming structures cover 1/4 of the lagoon surface in three distinct cultivation zones (Fig. 1). Oysters are reared on metal structures (50 × 10m) called “tables” (Fig. 1). Juveniles are introduced in the lagoon where they grow in lanterns (Fig. 1) from summer until they are glued on suspended ropes during winter. In the farming areas, we sampled two sites directly below juvenile tables (FO and FE: Fig. 1). The two farm sites belong to the same company and were chosen for their equivalent lantern type, density of juveniles per table, initial oyster size and introduction period in the lagoon (between July 28 and August 13). Two other sites were blindly chosen at a distance of 200 m outside each farming area (RO and RE; Fig. 1) to serve as reference sites, assuming they were beyond the influence of biodeposition. The main characteristics of the four sites are listed in Table 1.

Water column parameters, sedimentation rates, sediment characteristics, the biomass of benthic organisms (macrophytes, macrofauna and meiofauna) and benthic fluxes were measured on three occasions in 2015 (Sept. 29–Oct. 2; October 28–Nov 4 and Dec 1–Dec 4, hereafter referred to as October; November and December) during the growing period of juveniles in lanterns, in order to obtain results that are representative of the whole period of juvenile production.

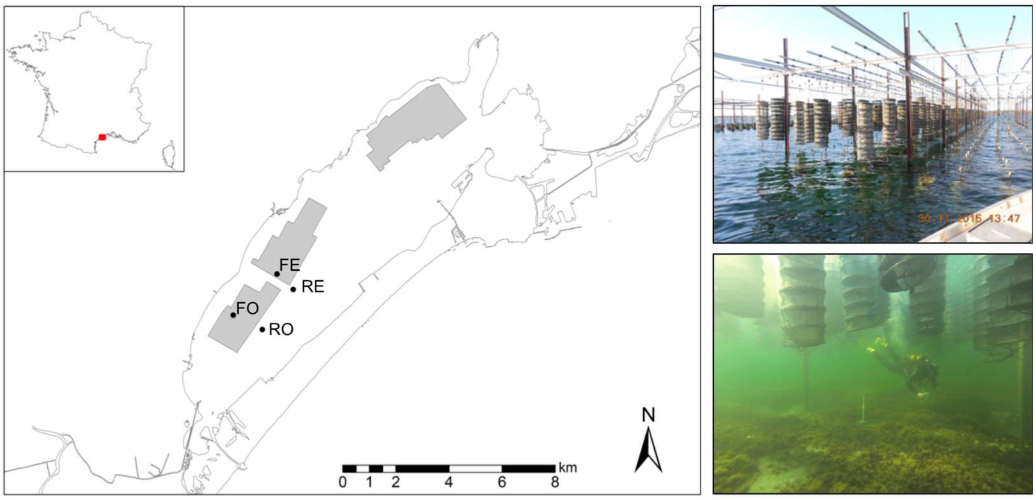
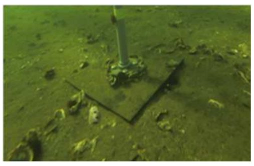
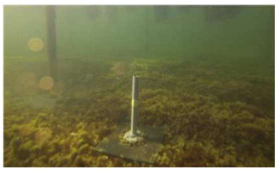
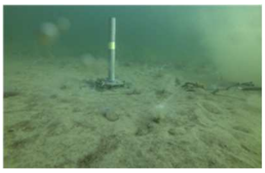
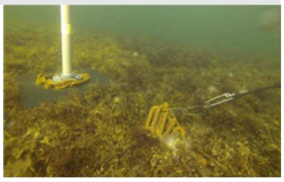


Figure 1. Location of the 4 study sites in the western shellfish zone of Thau Lagoon. Grey areas are exploited for shellfish farming. FO and FE sites were situated directly below juvenile tables. RO and RE are reference sites located in areas considered to be beyond farm influence. Photographs show lantern nets suspended on a "table". (Photo M. Richard & P. LeGall)

Table 1. Summary description of the 4 sample sites.

	Farm sites		Reference sites	
	FE	**FO**	**RE**	**RO**
Depth	4.2 m	3.6 m	4.2 m	3.7 m
Initial abundance/ density (per m^2) of juvenile	3 390 000 / 6 780	3 170 000 / 6 340	-	-
Initial biomass of juvenile (t per table*)	1.1	1.4	-	-
Bottom observations				
Macrophytes	-	++	+	+++

*At the beginning of the experiment, 30 individuals were randomly sampled in 3 different lanterns per site and weighed to estimate initial shellfish stock.

2.2. Water column parameters

During each survey at each site, the temperature of the surface water was recorded with a field sensor and water was sampled in plastic bottles by scuba divers for chlorophyll (n=3), microphytoplankton taxonomy (n=1), cytometry analysis (mid-column, n=3) and nutrient (bottom water, n=3). Back at the laboratory, 200 mL of water were filtered on Whatman GF/F to measure the pigments contained in total phytoplankton. Pigments were estimated from 90%

acetone extract and spectrofluorometry (Neveux and Lantoine, 1993). Chlorophyll *a*, *b* and *c* (hereafter chl-*a*, chl-*b* and chl-*c*) concentrations were used as proxies for total phytoplankton, small "green flagellates" (mainly chlorophytes) and diatoms plus dinoflagellates biomass respectively (Trottet et al., 2016), while the pheopigments (pheo) were used to assess the standing stock of pigment degradation products. Microphytoplankton were counted in a 2 L water sample taken at each site. Sampling procedure and identification respected the "REPHY" monitoring network methodology (Neaud-Masson, 2015). Organisms bigger than 20 µm, plus smaller species that form colonies or chain structures were identified and counted. For the enumeration of heterotrophic bacteria, cyanobacteria, pico- and nanophytoplankton, 1.5 mL water samples were fixed with glutaraldehyde, frozen (−20°C), and stored at −80°C until analysis. These microorganisms were quantified using a FACSCalibur flow cytometer (Becton Dickinson) as described by Pecqueur et al. (2011). Nutrient concentrations were measured using a Seal AA3 analytical autoanalyzer according to the method described by Aminot and Kérouel (2007) with colorimetric detection (from SEAL Analytical, Germany) for phosphate (PO_4), silicates ($Si(OH)_4$) and nitrites (NO_2) + nitrates (NO_3) (hereafter NO_X), and a fluorometric detection (from JASCO, FP-2020plus, France) for ammonium (NH_4).

2.3. Sedimentation rates, sediment characteristics and benthic community biomass

Sedimentation rates were assessed using sediment traps made of 50 cm long PVC pipes (internal diameter 45 mm) with one end closed by PVC and fixed to bases on the sediment. The height: diameter ratio was chosen to limit the resuspension of particulate matter inside the trap (Gust and Kozerski, 2000). At the beginning of each survey, three traps were deployed for 24 h at the farm sites (biodeposition + natural sedimentation), and at the reference sites to obtain the natural level of sedimentation. Back in the lab, the contents of the traps were filtered through pre-combusted and pre-weighed glass fiber filters (Whatman GF/F, 0.7 µm). Organic carbon, nitrogen and phosphorus (hereafter OC, N, P) contents were analyzed using a CHN autoanalyzer (Raimbault et al., 2008, 1999). Sedimentation rates of OC, N and P were calculated relative to the surface of the traps and the time of deposit, and are expressed in mg m^{-2} day^{-1}.

At each date (October, November, December), surficial sediment was collected by divers at all four sites. Three cores (4.5 cm diameter, 0.5 cm surface) were used to determine the carbon, nitrogen and phosphorus contents of the sediment (%OC, %N, %P respectively), using the same method as described above. Three supplementary cores (9 cm diameters, 0-10 cm) were sampled to describe the biological communities, including infauna and macrophytes (aquatic plants and macroalgae). The detailed protocol and description of infauna associated with the aquaculture system is available in Lacoste et al. (2020a). After collection and identification of all organisms, biomass of each sample was estimated. Macrofauna was dried for 48 h at 60°C to estimate total dry mass (DM). Ash free dry mass (AFDM) was estimated after burning for 5 h at 450°C. Following individual identification, biomass of meiofauna was calculated with the following equation: $V = 530\ L \times W^2$ (Warwick and Price, 1979), where V = volume in nanoliters and L and W are respectively, the measured length and maximum width of the specimens in mm. Wet mass (WM) was calculated by multiplying the volume by a specific gravity of 1.13 µg nL^{-1} (Wieser, 1960) and finally converted into dry mass (DM) using a DM:WM ratio of 0.25 (Vanaverbeke et al., 1997). Total macrophyte mass was estimated using dried samples.

2.4. Measurement of benthic fluxes

Benthic oxygen and nutrient fluxes were measured *in situ* using dark benthic chambers (mean volume of 38 L, surface area covered = 0.13 m^2). Dark chambers were used to evaluate benthic respiration and mineralization without accounting for primary production processes. During each period (October, November, December), one site per day was randomly sampled. At each site, three chambers were randomly positioned by divers, ensuring minimum sediment disturbance. A submersible pump connected to waterproof batteries was used to insure continuous gentle mixing of water in the chambers. Once hermetically sealed, nutrients were sampled at the beginning and end of the incubation period (between 2 and 4 hours). A dissolved oxygen probe (HOBO® U26-001) was attached to the inside wall of the benthic chambers, and the oxygen concentration measured continuously at one-minute intervals. Nutrient fluxes were calculated as the difference between initial and final nutrient concentrations, relative to the surface area of the chamber and the incubation period. Oxygen fluxes were estimated as the slope of linear regression versus incubation time.

2.5. Statistical analyses

The main objective of this study was to evaluate whether any differences in studied parameters could be detected between the Reference and the Farm treatments, irrespective of the sampling period and sites to obtain a global view of potential farm impacts on benthic-pelagic coupling in Thau lagoon. Thus, the effect of juvenile aquaculture on the response variables was explored using linear mixed effect model with Treatment (Farm *vs* Reference) as fixed effect and Site (nested in Treatment) and Date as random effects. Models were graphically validated (Quinn and Keough, 2002; Zuur et al., 2005) and where there was evidence for unequal variance in the residuals, we set up heterogeneous residual variance structure (Zuur et al., 2005). This was accommodated with the *nlme* R package (Pinheiro et al. 2018) and validated using AIC scores combined with residual plots for models developed using restricted maximum likelihood. The effect of Treatment was considered as significant when the null *vs* main effect models (using maximum likelihood estimation) differed significantly (ANOVA, $p < 0.05$).

To summarize the environmental conditions recorded at the four sites in the three periods and to illustrate potential differences between Farm and Reference treatments, a principal component analysis (PCA) was performed using representative benthic (sediment organic carbon, nitrogen and phosphorus contents, fauna and macrophyte biomasses) and water column (nutrient, chlorophyll, pheopigment concentrations and ratios) parameters. Selected parameter correlations were < 0.8. All analyses were performed using R 3.5.0 (2018).

3. Results

3.1. Water-column parameters

The water temperature was 18.8°C in October and 15.7°C in November, while at the end of autumn in December, there was a sharp drop in water temperature to below 10°C.

Although mean chl-*a* and chl-*c* concentrations tended to be lower at the farm sites than at the reference sites (Fig. 2a, c), the difference was not statistically significant (chl-*a*: L-ratio = 2.380, $p = 0.123$; chl-*c*: L-ratio = 3.042, $p = 0.08$), nor was the difference in chl-*b* (Fig. 2b, L-ratio = 0.011, $p = 0.916$). The highest concentration of pheo was observed at the farm sites but there was no significant difference compared with the reference sites (Fig. 2d, L-ratio = 3.323, $p = 0.068$). The contribution of phytoplankton containing chl-*c* to the total phytoplankton biomass (chl-*a*) (L-ratio = 6.564, $p < 0.005$) and the ratio between chl-*a* and pheopigment (L-ratio = 9.255, $p < 0.005$) were significantly lower at the farm sites such that more degraded products and a lower proportion of organisms containing chl-*c* (Fig. 2f, g) were found at farm sites. Conversely, a significant higher contribution of organisms containing chl-*b* to the total phytoplankton biomass was found at farms (Fig. 2e, L-ratio = 12.739, $p < 0.005$).

Treatment had no effect on cyanobacteria and picophytoplankton populations (Table 2). The nanophytoplankton, which almost only comprised particles < 6 µm, was also present in the same abundance at the farm and reference sites (Table 2). Although microphytoplankton concentrations tended to be higher at reference than at farm sites, no significant difference was detected (Table 2), mainly due to the low and highly variable concentrations over time (51.7 10^3 cell L^{-1} at the reference site in October *vs* 10.7 10^3 cell L^{-1} at the farm sites in November).

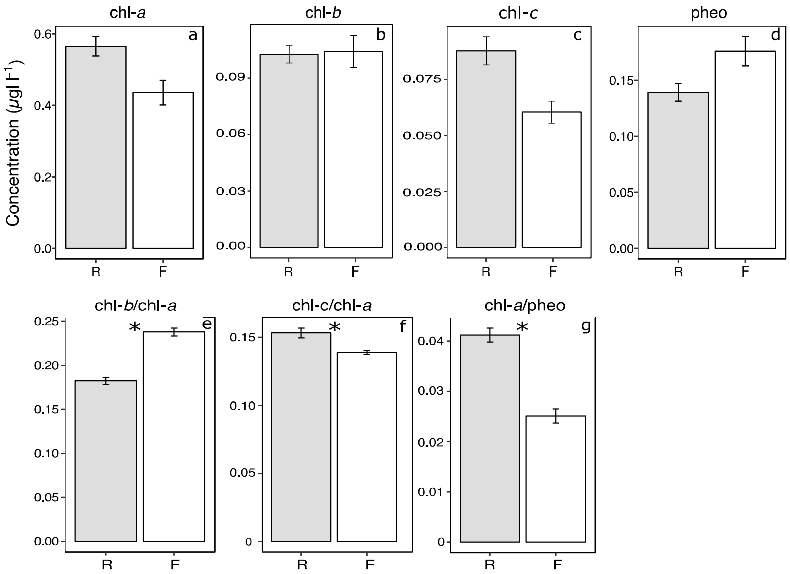


Figure 2. Mean (±SE) concentration of chlorophyll-*a* (chl-*a*), chlorophyll-*b* (chl-*b*), chlorophyll-*c* (chl-*c*) and pheopigments (Pheo), and different ratios at farm (F) and reference (R) treatments. Stars indicate statistical significance of Treatment.

Table 2. Mean (±SE) abundance of **Cyano**bacteria, **Pico**phytoplankton, **Nano**phytoplankton (10^6 cell L^{-1}) and **Micro**phytoplankton (10^3 cell L^{-1}) at the farm and reference treatments.

		Reference	Farm	L-ratio	*p-value*
Cyano		0.37 ± 0.03	0.35 ± 0.04	0.236	0.627
Pico	10^6 cell L^{-1}	27.06 ± 1.59	24.41 ± 1.32	2.371	0.124
Nano		15.42 ± 1.56	14.7 ± 0.94	0.119	0.730
Micro	10^3 cell L^{-1}	31.40 ± 13.1	14.33 ± 3.5	1.108	0.292

The phytoplankton pool both at the farm and reference sites was largely dominated by picophytoplankton (ca. 60%) followed by nanophytoplankton (Fig. 3). Microphytoplankton — that represent overall chl-*c* biomass — represented less than 1% of phytoplankton abundance. Among microphytoplankton, diatoms largely dominated over dinoflagellates and other microphytoplankton (>80%) with no apparent farm effect (Fig. 3). Among diatoms, the most abundant taxon was *Chaetoceros* sp. followed by *Pseudonitzschia* sp., mainly observed in

November. “Other” was mainly represented by the Euglenoidea *Eutreptiella* spp., that contribute to the chl-*b* biomass.

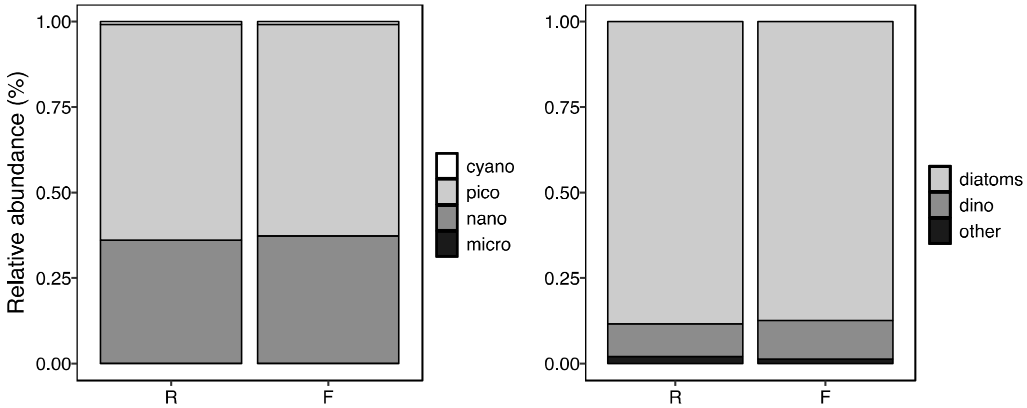


Figure 3. Relative abundance (%) of the 4 size classes of phytoplankton (left) and of microphytoplankton groups (right) at farm (F) and reference (R) treatments.

The concentration of NH_4 in the water column was more than twice higher at farm sites than at the reference sites, and the difference was significant (Table 3). Although values observed within farm sites tended to be higher than those observed at reference sites, PO_4 and NO_X concentrations and DIN:PO_4 ratio (DIN = NH_4 + NO_X) did not differ significantly (Table 3), nor did Si concentrations between the farm and reference sites (Table 3).

Table 3. Mean (±SE) dissolved nutrient concentration (μmol l^{-1}) and nitrogen/phosphorus ratio in the water column at the farm and reference treatments. NH_4 : ammonium, NO_X : nitrates + nitrites, PO_4 : phosphate, DIN : NH_4 + NO_X, Si : silicates. **Statistical significance of Treatment.*

	Reference	Farm	L-ratio	*p-value*
NH_4	0.22 ± 0.03	0.49 ± 0.06	9.068	*< 0.005**
NO_X	0.17 ± 0.01	0.20 ± 0.01	1.503	0.220
PO_4	0.09 ± 0.01	0.11 ± 0.01	1.642	0.202
DIN/PO_4	4.38 ± 0.38	6.31 ± 0.48	3.368	0.066
Si	11.53 ± 0.92	10.61 ± 1.15	1.538	0.215

3.2. Sedimentation rates, sediment characteristics and benthic community biomass

Neither mean sedimentation rates nor OC, N or P concentrations varied significantly between the farm and reference treatments, (Table 4). Although higher values were always observed at the farm treatment, no significant differences in sediment OC, N and P contents were recorded (Table 4). Sediment samples contained 6.5% of organic carbon, less than 1% of nitrogen and phosphorus content was almost negligible whatever the treatment (Table 4).

Macrophyte, macrofauna and meiofauna biomass tended to be higher at reference sites than at farm sites (Table 4). However, the effect of Treatment was only statistically significant for meiofauna biomass (Table 4). Macrophytes were mainly represented by the red macroalgae *Halopitys* sp. It should be noted that site FE was free of *Halopitys* sp.

Table 4. Mean (±SE) quantities of deposited material in mg m^{-2} d^{-1} (organic carbon: OC, nitrogen: N, phosphorus: P), element content (%) and biomass of organisms/macrophytes in sediment cores at farm and reference sites. Biomass values are expressed per square meter (m^2), as dry mass (DM, g) and ash free dry mass (AFDM, g) for macrofauna, as dry mass (mg) for meiofauna, and as dry mass for macrophyte (g). **Statistical significance of Treatment*

Compartment	Response variable	Reference	Farm	L-ratio	*p-value*
Deposition (traps)	OC	195.91± 35.44	201.84 ± 19.35	0.023	0.879
	N	20.48 ± 2.83	21.97 ± 1.95	0.198	0.656
	P	2.71 ± 0.39	3.25 ± 0.36	2.286	0.131
Sediment	%OC	5.95 ± 0.29	6.97 ± 0.44	2.051	0.152
	%N	0.62 ± 0.06	0.92 ± 0.05	2.354	0.125
	%P	0.04 ± 0.01	0.06 ± 0.01	2.386	0.066
	Macrofauna DM	25.9 ± 4.3	10.4 ± 2.5	2.695	0.100
	Macrofauna AFDM	5.7 ± 0.9	2.5 ± 0.5	2.908	0.088
	Meiofauna	4.2 ± 0.6	1.7 ± 0.2	4.915	*<0.05**
	Macrophytes	62.0 ± 6.0	27.1 ± 7.1	1.796	0.180

3.3. Benthic fluxes

Nitrogen fluxes did not differ between treatments, either for NH_4^+ (mean = 14.4 ± 4.4 µmol m^{-2} h^{-1}) or NO_X (mean = 2.1 ± 0.8 µmol m^{-2} h^{-1}) (Table 5). Negative values of NH_4^+fluxes (sediment uptake) were observed on three occasions at site FO (in 2 chambers in October and in one chamber in December) and in one chamber at RO in November. NO_X fluxes were mostly positive (70%) although some negative values were recorded (< -5 µmol m^{-2} h^{-1}). Minimum values of -61.4 µmol m^{-2} h^{-1} and -4.3 µmol m^{-2} h^{-1} and maximum values of 82.7 µmol m^{-2} h^{-1}

and 20.8 µmol m^{-2} h^{-1} were measured for NH_4^+ and NO_X respectively. Although some negative fluxes were recorded, fluxes were mostly positive, so overall, nitrogen (NH_4^+ + NO_X) was released from the sediment into the water column. Treatment had a significant effect on benthic PO_4 fluxes which were higher at the reference sites than at the farm sites (Table 5). Si and O_2 fluxes did not vary due to Treatment (Table 5). Si was released from the sediment into the water column at a mean rate of 41.7 ± 9.2 µmol m^{-2} h^{-1}. The negative values for O_2 indicated sediment oxygen consumption (mean of -105.0 ± 12.2 mg m^{-2} h^{-1}).

Table 5. Mean benthic fluxes (±SE) measured at the sediment-water interface at reference (R) and farm sites (F) and summary of the significant terms found in the linear mixed-effect model. Nutrient fluxes are expressed in µmol h^{-1} m^{-2} and O_2 fluxes in mg h^{-1} m^{-2}. **Statistical significance of Treatment*

	Reference	Farm	L-ratio	*p-value*
NH_4	19.0 ± 5.5	10.3 ± 6.7	0.418	0.518
NO_x	0.6 ± 0.8	3.4 ± 1.3	1.773	0.183
PO_4	3.3 ± 0.5	1.1 ± 0.4	1.773	*< 0.01**
Si	45.0 ± 14.5	38.7 ± 11.9	0.066	0.797
O_2	-122.0 ± 14.5	-88.6 ± 19.0	1.019	0.313

3.4. Multivariate characterization of the sites

A PCA of the environmental variables explained 54% of variation on the first two axes. The three variables that contributed most to the first axis were the ratio of chl-*b* to chl-*a* (chl-*b*/chl-*a*, -0.855) and the percentage of nitrogen (%N, -0.789) and phosphorus (%P, -0.720) in the sediment. The first axis (35.3%) clearly distinguished between farm and reference treatments (Fig. 4). Farm sites (FO and FE) were characterized by higher concentrations of nitrogen and phosphorus in the sediment and by a higher chl-*b*/chl-*a* ratio, due to lower concentrations of chl-*a*. In contrast, at the reference sites (RO and RE), the ratio of chl-*a* to pheo was higher (indicating less proportion of degraded phytoplankton), concentrations of nutrients in the water column were lower and macrophyte and infauna biomass was higher. This trend was mainly driven by the higher biomass of macrophyte at site RO which is distinct from site RE, whereas, according to the PCA, farm sites were more similar. The second axis (18.7%) mostly highlighted variations over time, mainly explained by differences in phytoplankton pigments (chl-*a*: -0.831, chl-*c*/chl-*a*: -0.654, pheo: -0.628).

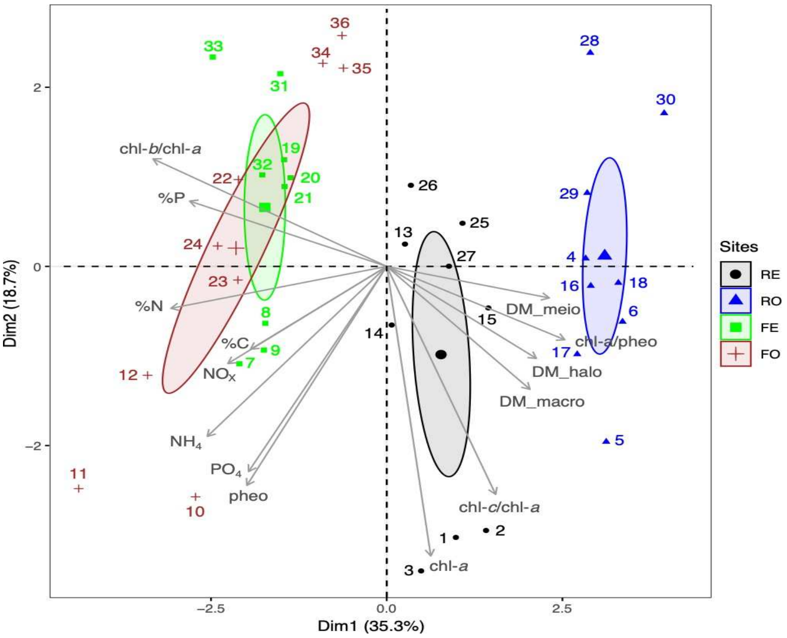


Figure 4. PCA biplot of studied parameters analysed at the 4 sites. Ellipses summarize the point dispersion (95% confidence) for each site. Code: chl-*a*, chl-*b*, chl-*c*, pheo: chlorophyll- and pheopigments; %P, %N, %OC: phosphorus, nitrogen and organic carbon content in the sediment; NO_X, NH_4, PO_4: dissolved nutrients in the water column; DM_meio, DM_halo, DM_macro: dry mass of meiofauna, macrophyte and macrofauna in sediment. Numbers 1 to 12: October, 13 to 24: November, 25 to 36: December.

4. Discussion

4.1. Influence of juvenile oysters on water column parameters

In shallow semi-enclosed ecosystems, where bivalve aquaculture often takes place, the biological production is usually considered to be mainly controlled by benthic-pelagic coupling (e.g. Gibbs et al., 2005; Ouisse et al., 2013), meaning that the influence of bivalves as an anthropogenic biological forcing on benthic systems has been widely studied (Lacoste et al., 2020b and references therein). However, bivalves may also have a significant effect on phytoplankton turnover and overall water column production thanks to nutrients released via direct excretion (bottom-up effect), and depletion of suspended particles through filtration (top-down effect) (Gallardi, 2014; Newell, 2004; Prins et al., 1998). Increased nutrient concentration and a shift in the phytoplankton community structure to the benefit of small eucaryotes are both frequently observed in shellfish exploited ecosystems (Jacobs et al., 2016; Naddafi et al., 2007). In Thau Lagoon, Mazouni (2004) showed the importance of cultivated oysters in the recycling of dissolved nitrogen in the water column compared with their contribution to benthic mineralization. The positive effect of oyster culture on nutrient concentration in the overlying water was also reported to be significant in a study by Souchu et al. (2001), with annual increases of 73%, 36% and 19% recorded for ammonium, phosphates and silicates respectively. Our findings are in accordance with these results since we observed higher concentrations (× 2) of ammonium in the water column at oyster farming sites compared with reference sites, although the excess of this nutrient was lower than that reported by Souchu et al. (2001). One possible explanation for this difference could be the bathymetry and the location of our study sites. Souchu et al. (2001) reported that nutrient excess in the shellfish farming area was lower in the western part than in the eastern part of the lagoon, because the shallower depth (4 m) allows light to reach the bottom which enables benthic macroflora to grow on nutrients of benthic origin. Although no measurement of juvenile metabolism has been done in this study, the difference with the study of Souchu et al. (2001) could also be explained by a lower NH_4^+ excretion by tables of juvenile oysters compared with adults. In terms of flesh biomass, a table of juvenile represents about 25 kg (3 millions individuals) whereas a standard table of adults (ca 150 000 individuals) weighs more than 300 kg (data from Ifremer). Given the same range of excretion values measured for juveniles (Richard et al., 2017) and adults (Buzin et al. 2015), nutrient renewal is reduced during the pre-growth phase, accentuated by the low temperatures observed during this period (10°C-18.8°C). Overall, it should be noted that nutrient concentrations were in the lower range of values reported for Thau lagoon (Collos et al., 2005) as being characteristic of early winter, such that the interactions between juvenile oysters and the environment were reduced, as already observed by Mazouni (2004).

Souchu et al. (2001) also reported a shift in phytoplankton composition due to the activity of filter feeders, with a higher abundance of picophytoplankton at farm sites favored by rapid use of regenerated nitrogen. In the present study, picophytoplankton dominated (60%) at both treatments, with no difference between farm and reference sites, and we did not observe an increase in small particles biomass at the farm sites, likely due to lower nutrient concentration and picophytoplankton production in winter. However, even though phytoplankton abundance and biomass were low in our study – which is typical of winter conditions (Fiandrino et al., 2019) – the results showed that oysters induce relative control over the community composition, as evidenced by two observations made at farm: (i) a lower ratio between total chlorophyll and degraded pigments (pheo), highlighting a grazing pressure of oysters on autotrophic organisms, (ii) a lower contribution of organisms containing chl-*c* – mainly diatoms > 20 µm – and a higher contribution of organisms containing chl-*b* – probably small chorophytes – to the total phytoplankton biomass (chl-*a*), emphasizing the higher grazing pressure of juveniles on larger particles, as is the case for adult oysters whose gills retain all > 5 µm flagellates, microphytoplankton, dinoflagellates, ciliates and zooplankton (Dupuy et al., 2000).

4.2. Low biodeposition of juvenile oyster culture

Bivalve aquaculture generally modifies sediment composition and benthic fluxes due to increased inputs of organic material (biodeposition) that stimulate benthic metabolism (Lacoste et al., 2020b and references therein). Historical data concerning sedimentation rates both inside and outside farming areas in Thau Lagoon are scarce. Biodeposition values were only found in De Casabianca (1977) and Grenz (1989). Their results indicate that shellfish biomass produces from 300 to 500 kg ha^{-1} year^{-1} of nitrogen and about 3 000 kg ha^{-1} year^{-1} of carbon as biodeposition, whereas values measured in the present study were five and four times lower for nitrogen and carbon, respectively, with no apparent effect of oyster culture. Thus, the absence of benthic footprint observed in our study may be due to these low sedimentation rates, which, in turn, are probably due to the lower rate of biodeposition by juvenile oysters compared with adults along with the low water temperature during our experiment, which slows down oyster metabolism and hence biodeposition (Mitchell, 2006). In Korea, Hyun et al. (2013) reported that the production of feces and pseudo-feces increased with an increase in the wet weight of oysters (*C. gigas*). Other authors (Callier et al., 2006; Giles and Pilditch, 2004) who studied suspended mussel culture, also observed that larger mussels produced bigger biodeposits in larger quantities, thereby increasing the transfer of organic matter to the benthic system. Thus, smaller biodeposits of juveniles with a lower settlement rate were likely decomposed and/or advected farther afield by prevailing currents, explaining why we observed reduced localized biodeposition under the tables and no immediate effect on the benthic compartment over our study period. Benthic impact in aquaculture systems results from a balance between sedimentation, resuspension, and decay of biodeposits. Because these mechanisms are site-specific and often vary over time, field measurements are the best way to obtain reliable information on the intrinsic complexity of such ecosystems. In Thau Lagoon, such information is rare and further studies are required to evaluate biodeposition on an annual basis, including different operating systems, along with measurement of potential subsequent benthic modifications.

4.3. Low benthic impact during the pre-growth period

Benthic fluxes in dark conditions give a snapshot of organic material mineralization and associated sediment oxygen consumption at a given site. The intensity of fluxes is increased with organic material input, such as biodeposition, and is further stimulated by high temperature. In accordance with that, Mazouni et al. (1996) and Thouzeau et al. (2007) observed increased oxygen demand and nutrient release at the sediment-water interface in shellfish farming areas, with maximum values in summer. In conjunction with the low levels of biodeposition and low temperature during the period of the study, we detected almost no difference between benthic fluxes under juvenile oysters and at the reference areas.

Although no immediate benthic effect of farming was observed in this study, the concentrations of organic carbon, nitrogen and phosphorus in the sediment were indicative of an enriched area (Baehr et al., 2013) with slightly, although not significant, higher levels at the farm sites, as illustrated by the PCA. This may be due to the history of the area, which has been used for shellfish farming for many years. In the past, several evaluations of the lagoon showed that nitrogen and phosphorus were more concentrated in sediment directly under and in the corridors between shellfish areas compared with in other parts of the lagoon (Anschutz et al., 2007; Deslous-Paoli et al., 1998; Pichot et al., 1994), which had an impact on the structure of the benthic communities (Duport et al., 2007; Thouzeau et al., 2007). The significant effect of juvenile oysters on macro- and meiofauna community composition and biomass (Lacoste et al., 2020a, this study) further supports this hypothesis and suggests that farming areas are distinct from other parts of the lagoon. This underlines the importance of developing integrated approaches looking at several ecosystem components to assess the overall effect of shellfish farming in coastal ecosystems, as already discussed in Lacoste et al. (2020a, 2020b). In the present study, the use of multivariate analysis in addition to the univariate approach provided additional information on the influence of oyster farming, highlighting that fact that long-term transfer of organic matter from the water column to the benthic system may have contributed to the stocking of organic carbon, nitrogen and phosphorus in the sediment and the decrease of infauna biomass.

With the reduction of nutrient inputs from the watershed since the 2000s, the phosphorus sediment stock has been shown to decrease while it is released to other compartments of the ecosystem (Derolez et al., 2020a; Deslous-Paoli et al., 1998). Derolez et al. (2020a) hypothesize that the benthic compartment began to recover its ecological functions and structure of the reference conditions after a period of hysteresis. The potential effect of shellfish farming on the progressive restauration of the lagoon remains however unknown since no other comparison exists between farming areas and other parts of the lagoon. In the current state of oligotrophication, phosphorus plays a key role in controlling both phytoplankton and oyster production in Thau lagoon (Pete et al. 2020). Thus it will be necessary to study in details the role of oysters in the P cycle and the influence of biodeposits and P sediment stock under shellfish farming devices on the structure of the phytoplankton community and on primary productivity in Thau lagoon, as exemplified by (Porter et al., 2020) in a mesocosm study. Moreover, it also appears necessary to determine the resilience of the benthic system to disturbances caused by shellfish farming on an annual basis, more specifically in a context of cumulative impacts on coastal ecosystems (eg increase in temperature, hypoxia).

4.5. Conclusions and future outlook

Understanding and predicting anthropogenic impacts on marine ecosystem is essential in a context where habitat and biodiversity are continuously altered. In Thau Lagoon where aquaculture occupies 1/4 of the area, the role aquaculture plays in ecosystem functioning needs to be identified to enable sustainable aquaculture. Using a multi-compartment approach, our findings suggest that juvenile oyster metabolism may have partially controlled the water nutrient pool and phytoplanktonic community composition during our study period. Conversely, the pre-growth stage in autumn/winter did not appear to have a significant impact on the benthic ecosystem, due to low sedimentation rates observed during this period and the potential dispersion and resuspension of biodeposits. However, the long farming history of the lagoon may have shaped sediment composition in farming areas compared with other parts of the lagoon by increasing sediment N and P contents and decreasing macro and meiofauna biomasses. As a typical transitional coastal area, Thau Lagoon offers a wide range of habitats and is subject to natural environmental variations making the effect of shellfish farming difficult to highlight. The use of two sites per Treatment (Farm *vs* Reference) in this study, instead of one, allowed to obtain a global view of farm effect regardless of natural variability.

To go further, more studies are needed to describe the nutrient and oxygen dynamics in Thau Lagoon, in relation with seasonal variability of oyster culture practices (juveniles in lanterns *vs* adults on ropes) and stock (biomass per table). Such information will contribute to improve the lagoon functioning model specifically developed for Thau (Pete et al. 2020) to predict the influence of several climate and exploitation scenarios its functioning. These topics must be urgently addressed for management purposes to reconcile the achievement of good ecological status and the sustainability of shellfish aquaculture in Thau Lagoon in a context of oligotrophication, climate change and increased risk of anoxia.

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