



**HAL**  
open science

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

Élise Lacoste, Beatrice Bec, Patrik Le Gall, Fehmi Boufahja, Patrick Raimbault, Grégory Messiaen, Vincent Ouisse, Emmanuelle Roque d'Orbcastel, Dominique Munaron, Annie Fiandrino, et al.

► **To cite this version:**

Élise Lacoste, Beatrice Bec, Patrik Le Gall, Fehmi Boufahja, Patrick Raimbault, et al.. Benthic-pelagic coupling under juvenile oyster influence in a French Mediterranean coastal lagoon (Thau Lagoon). *Estuarine, Coastal and Shelf Science*, 2022, 267, pp.107779. 10.1016/j.ecss.2022.107779 . hal-03622223

**HAL Id: hal-03622223**

<https://hal.umontpellier.fr/hal-03622223v1>

Submitted on 22 Jul 2024

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution - NonCommercial 4.0 International License

1 Running head: Benthic-pelagic coupling under juvenile oyster influence

2

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

5

6 Élise Lacoste<sup>1\*</sup>, Béatrice Bec<sup>3</sup>, Patrik Le Gall<sup>1</sup>, Fehmi Boufahja<sup>4</sup>, Patrick Raimbault<sup>5</sup>, Gregory  
7 Messiaen<sup>1</sup>, Vincent Ouisse<sup>1</sup>, Emmanuelle Roque d'Orbcastel<sup>1</sup>, Dominique Munaron<sup>1</sup>, Annie  
8 Fiandrino<sup>1</sup>, Franck Lagarde<sup>1</sup>, Sébastien Mas<sup>6</sup>, Myriam Callier<sup>7</sup>, Nabila Gaertner-Mazouni<sup>2</sup>,  
9 Marion Richard<sup>1</sup>

10

11 <sup>1</sup> MARBEC, Univ Montpellier, CNRS, Ifremer, IRD, Sète, France

12 <sup>2</sup> Univ. Polynésie française, IFREMER, ILM, IRD, EIO UMR 241, Tahiti, Polynésie française

13 <sup>3</sup> MARBEC, Univ Montpellier, CNRS, Ifremer, IRD, Montpellier, France

14 <sup>4</sup> Laboratory of Biomonitoring of the Environment, Coastal Ecology and Ecotoxicology Unit, Carthage University,  
15 Faculty of Sciences of Bizerte, Zarzouna 7021, Tunisia

16 <sup>5</sup> Aix Marseille Univ., Université de Toulon, CNRS, IRD, MIO, UM 110, 13288, Marseille, France

17 <sup>6</sup> MEDIMEER (Mediterranean Platform for Marine Ecosystems Experimental Research), OSU OREME, CNRS,  
18 Univ Montpellier, IRD, IRSTEA, Sète, France

19 <sup>7</sup> MARBEC, Univ Montpellier, CNRS, Ifremer, IRD, Palavas, France

20

21 \*Corresponding author. [eliz.lacoste@gmail.com](mailto:eliz.lacoste@gmail.com)

22

23

## 24 **Abstract**

25 The aim of the present work was to test the influence of juvenile oyster culture on benthic-  
26 pelagic coupling in the French Mediterranean Thau Lagoon. Although the period of juvenile  
27 growth induces the introduction of millions of juvenile oysters in the lagoon over a short  
28 duration, the effects on the water-column and on the benthic ecosystem are poorly known.  
29 Using a multiple ecological approach, water column parameters, sedimentation rates, sediment  
30 characteristics and benthic fluxes were monitored on three occasions during the oyster pre-  
31 growth period, from October to December, at two sites inside the farming area and two sites  
32 outside the farming area that served as reference. In the water column, results showed a

33 significant lower ratio between total phytoplankton biomass (chlorophyll-*a*) and degraded  
34 pigments (pheopigment), a significant increase in the contribution of phytoplankton containing  
35 chlorophyll-*b* (*ie* chlorophytes) to total phytoplankton biomass and a significant decrease in the  
36 contribution of phytoplankton containing chlorophyll-*c* (mainly diatoms) to the total  
37 phytoplankton biomass at farm sites, attributed to the grazing pressure caused by juvenile  
38 oysters on large particles, as described for adult oysters. No significant effect was observed at  
39 the benthic interface during this period, due to the dispersion of the small quantities of  
40 biodeposit produced by juveniles in the low water temperature conditions. A multivariate  
41 approach supported the effect of juvenile oysters on the water column and revealed a trend in  
42 benthic conditions with farm sites being distinct from the reference ones. The long farming  
43 history of the lagoon could have shaped sediment properties such that farming areas maintain  
44 different benthic conditions.

45

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

47

## 48 **1. Introduction**

49 Shellfish aquaculture relies on the introduction of high densities of organisms in an environment  
50 thereby creating a wide range of interactions. This may result in major changes in exploited  
51 ecosystems, for example (i) depletion of plankton through filter feeding (Gallardi, 2014;  
52 Pinkerton et al., 2018), (ii) increased nutrient turnover through direct excretion into the water  
53 column (Lacoste et al., 2014; Nizzoli et al., 2011; Richard et al., 2006) and/or the transfer and  
54 recycling of organic matter at the sediment-water interface (Gaertner-Mazouni et al., 2012;  
55 Richard et al., 2007b) and (iii) localized supplies of organic material (biodeposit and organisms  
56 fall-off) that may affect sediment properties and benthic communities (Callier et al., 2009,  
57 2008; Lacoste et al., 2018). The influence of cultivated bivalves on ecosystems is usually

58 studied by estimating their impact on the benthic-pelagic coupling (Lacoste and Gaertner-  
59 Mazouni, 2016; Nizzoli et al., 2006; Richard et al., 2007), which contributes substantially to  
60 primary production in shallow ecosystems (Ferrón et al., 2009; Grenz et al., 2019). Fewer  
61 studies have described the influence of bivalve culture on the composition of planktonic  
62 communities through grazing pressure (Hulot et al., 2020; Trottet et al., 2008). However, some  
63 authors showed that feeding of bivalves may impact the size-structure and composition of the  
64 plankton pool with cascading effect on the food-web (Karuza et al., 2016; Mostajir et al., 2015).  
65 Thau Lagoon is the main French Mediterranean area for shellfish production (*Crassostrea gigas*  
66 and *Mytilus galloprovincialis*), which covers about 1/4 of its total surface area (ca 1 700 ha).  
67 Annual oyster production (ca. 7 000 tons) represents 10% of the national production and 90%  
68 of shellfish production in the French Mediterranean region. Previous studies evidenced that  
69 shellfish farming modifies the dynamics of both the benthic (Gilbert et al., 1997; Metzger et  
70 al., 2007; Thouzeau et al., 2007) and pelagic (Mazouni, 2004) compartments in Thau Lagoon  
71 in all four seasons (Souchu et al., 2001). These studies also highlighted variability of benthic  
72 and pelagic processes due to differential habitat characteristics and wide fluctuations in  
73 environmental conditions driven by seasonal trends.

74 The ecological functioning of such a semi-enclosed costal lagoon is very fragile and  
75 disturbances can, for example, lead to hypoxia/anoxia events with significant economic  
76 impacts, as already observed in the past (Chapelle et al., 2000; Derolez et al., 2020a; Souchu et  
77 al., 1998). Since the late 2000s, mitigatory actions have been designed, targeting in particular  
78 sewerage networks in estuarine watersheds, and allowing a decrease in nutrient inputs. This has  
79 resulted in the ecological recovery of French Mediterranean lagoons, at varying speed and with  
80 different patterns, modifying therefore their ecological functioning (Collos et al., 2009; Derolez  
81 et al., 2019). This make it necessary to update our knowledge about shellfish culture and  
82 environment interactions in Thau lagoon. Moreover, while some studies analyzed interactions

83 between larvae (Lagarde et al., 2019, 2017; Ubertini et al., 2017) or adult oysters (Mazouni,  
84 2004; Thouzeau et al., 2007) and the environment, knowledge is lacking on the pre-growth  
85 phase (juvenile culture), despite the fact more than 530 million juveniles are introduced in this  
86 lagoon every year (Pete et al., 2020).

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

106

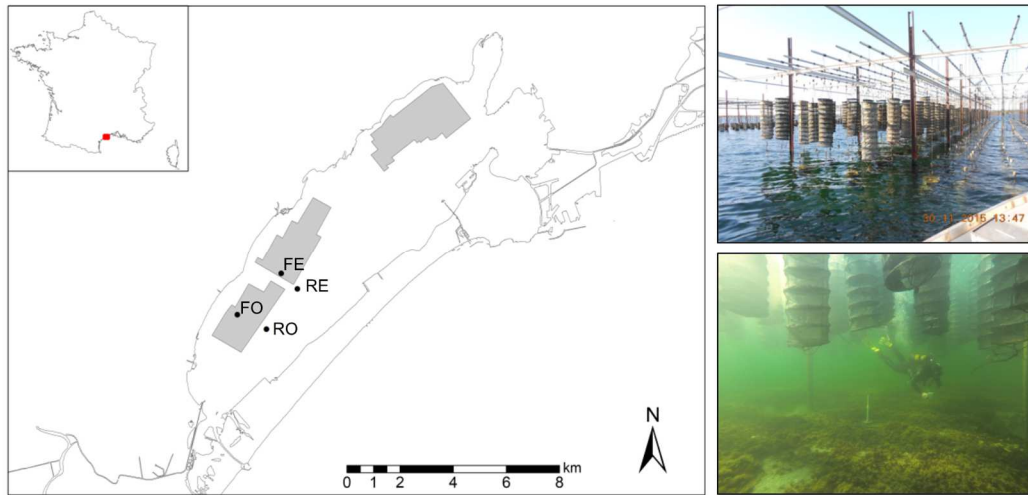
## 107 **2. Materials and Methods**

## 108 **2.1. Study area and sampling design**

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

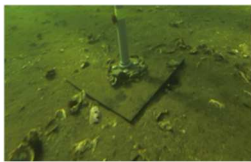
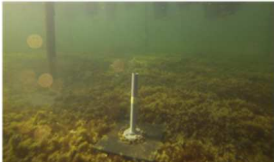
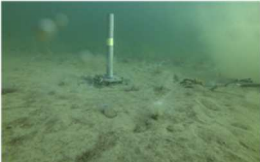

120 Water column parameters, sedimentation rates, sediment characteristics, the biomass of benthic  
121 organisms (macrophytes, macrofauna and meiofauna) and benthic fluxes were measured on  
122 three occasions in 2015 (Sept. 29–Oct. 2; October 28–Nov 4 and Dec 1–Dec 4, hereafter  
123 referred to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

126



127  
 128 **Figure 1.** Location of the 4 study sites in the western shellfish zone of Thau Lagoon. Grey areas are  
 129 exploited for shellfish farming. FO and FE sites were situated directly below juvenile tables. RO and  
 130 RE are reference sites located in areas considered to be beyond farm influence. Photographs show  
 131 lantern nets suspended on a “table”. (Photo M. Richard & P. LeGall)  
 132

133 **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 <sup>2</sup> ) 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	-	++	+	+++

134 \*At the beginning of the experiment, 30 individuals were randomly sampled in 3 different lanterns per site and  
 135 weighed to estimate initial shellfish stock.  
 136

## 137 2.2. Water column parameters

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

143 acetone extract and spectrofluorometry (Neveux and Lantoiné, 1993). Chlorophyll *a*, *b* and *c*  
144 (hereafter chl-*a*, chl-*b* and chl-*c*) concentrations were used as proxies for total phytoplankton,  
145 small “green flagellates” (mainly chlorophytes) and diatoms plus dinoflagellates biomass  
146 respectively (Trottet et al., 2016), while the pheopigments (pheo) were used to assess the  
147 standing stock of pigment degradation products. Microphytoplankton were counted in a 2 L  
148 water sample taken at each site. Sampling procedure and identification respected the “REPHY”  
149 monitoring network methodology (Neaud-Masson, 2015). Organisms bigger than 20 µm, plus  
150 smaller species that form colonies or chain structures were identified and counted. For the  
151 enumeration of heterotrophic bacteria, cyanobacteria, pico- and nanophytoplankton, 1.5 mL  
152 water samples were fixed with glutaraldehyde, frozen (−20°C), and stored at −80°C until  
153 analysis. These microorganisms were quantified using a FACSCalibur flow cytometer (Becton  
154 Dickinson) as described by Pecqueur et al. (2011). Nutrient concentrations were measured  
155 using a Seal AA3 analytical autoanalyzer according to the method described by Aminot and  
156 Kérouel (2007) with colorimetric detection (from SEAL Analytical, Germany) for phosphate  
157 (PO<sub>4</sub>), silicates (Si(OH)<sub>4</sub>) and nitrites (NO<sub>2</sub>) + nitrates (NO<sub>3</sub>) (hereafter NO<sub>x</sub>), and a  
158 fluorometric detection (from JASCO, FP-2020plus, France) for ammonium (NH<sub>4</sub>).

159

### 160 **2.3. Sedimentation rates, sediment characteristics and benthic community biomass**

161 Sedimentation rates were assessed using sediment traps made of 50 cm long PVC pipes  
162 (internal diameter 45 mm) with one end closed by PVC and fixed to bases on the sediment. The  
163 height: diameter ratio was chosen to limit the resuspension of particulate matter inside the trap  
164 (Gust and Kozerski, 2000). At the beginning of each survey, three traps were deployed for 24 h  
165 at the farm sites (biodeposition + natural sedimentation), and at the reference sites to obtain the  
166 natural level of sedimentation. Back in the lab, the contents of the traps were filtered through  
167 pre-combusted and pre-weighed glass fiber filters (Whatman GF/F, 0.7 µm). Organic carbon,



168 nitrogen and phosphorus (hereafter OC, N, P) contents were analyzed using a CHN  
169 autoanalyzer (Raimbault et al., 2008, 1999). Sedimentation rates of OC, N and P were  
170 calculated relative to the surface of the traps and the time of deposit, and are expressed in  $\text{mg m}^{-2}$   
171  $\text{day}^{-1}$ .

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

188

#### 189 **2.4. Measurement of benthic fluxes**

190 Benthic oxygen and nutrient fluxes were measured *in situ* using dark benthic chambers (mean  
191 volume of 38 L, surface area covered =  $0.13 \text{ m}^2$ ). Dark chambers were used to evaluate benthic  
192 respiration and mineralization without accounting for primary production processes. During

193 each period (October, November, December), one site per day was randomly sampled. At each  
194 site, three chambers were randomly positioned by divers, ensuring minimum sediment  
195 disturbance. A submersible pump connected to waterproof batteries was used to insure  
196 continuous gentle mixing of water in the chambers. Once hermetically sealed, nutrients were  
197 sampled at the beginning and end of the incubation period (between 2 and 4 hours). A dissolved  
198 oxygen probe (HOBO® U26-001) was attached to the inside wall of the benthic chambers, and  
199 the oxygen concentration measured continuously at one-minute intervals. Nutrient fluxes were  
200 calculated as the difference between initial and final nutrient concentrations, relative to the  
201 surface area of the chamber and the incubation period. Oxygen fluxes were estimated as the  
202 slope of linear regression versus incubation time.

203

## 204 **2.5. Statistical analyses**

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

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

223

### 224 **3. Results**

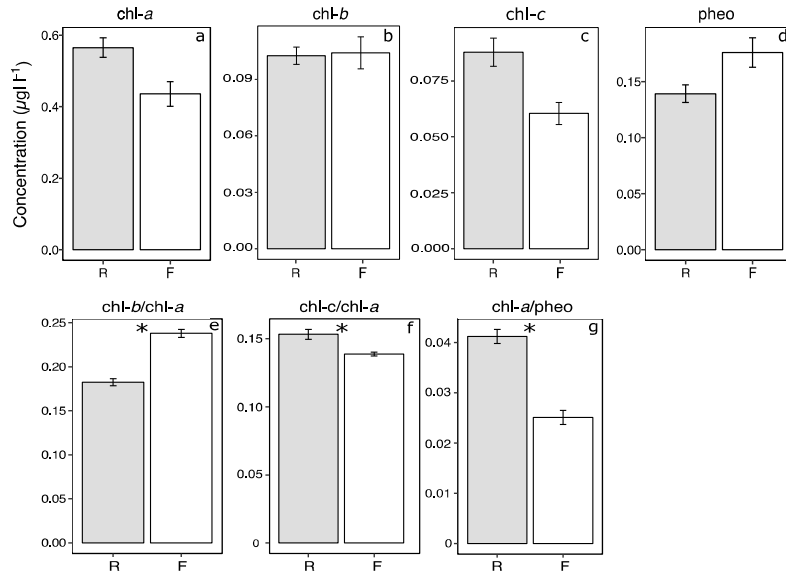
#### 225 **3.1. Water-column parameters**

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

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

239 Treatment had no effect on cyanobacteria and picophytoplankton populations (Table 2). The  
240 nanophytoplankton, which almost only comprised particles  $< 6 \mu\text{m}$ , was also present in the  
241 same abundance at the farm and reference sites (Table 2). Although microphytoplankton

242 concentrations tended to be higher at reference than at farm sites, no significant difference was  
 243 detected (Table 2), mainly due to the low and highly variable concentrations over time (51.7  
 244  $10^3 \text{ cell L}^{-1}$  at the reference site in October vs  $10.7 \cdot 10^3 \text{ cell L}^{-1}$  at the farm sites in November).



245  
 246 **Figure 2.** Mean ( $\pm$ SE) concentration of chlorophyll-*a* (chl-*a*), chlorophyll-*b* (chl-*b*), chlorophyll-*c* (chl-  
 247 *c*) and pheopigments (Pheo), and different ratios at farm (F) and reference (R) treatments. Stars indicate  
 248 statistical significance of Treatment.  
 249

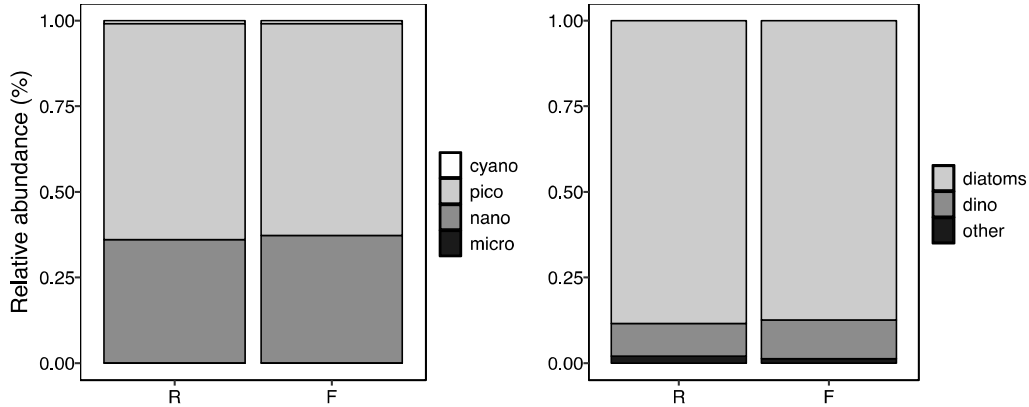
250 **Table 2.** Mean ( $\pm$ SE) abundance of **Cyanobacteria**, **Picophytoplankton**, **Nanophytoplankton** ( $10^6 \text{ cell}$   
 251  $\text{L}^{-1}$ ) and **Microphytoplankton** ( $10^3 \text{ cell L}^{-1}$ ) at the farm and reference treatments.

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

252  
 253 The phytoplankton pool both at the farm and reference sites was largely dominated by  
 254 picophytoplankton (ca. 60%) followed by nanophytoplankton (Fig. 3). Microphytoplankton —  
 255 that represent overall chl-*c* biomass — represented less than 1% of phytoplankton abundance.  
 256 Among microphytoplankton, diatoms largely dominated over dinoflagellates and other  
 257 microphytoplankton (>80%) with no apparent farm effect (Fig. 3). Among diatoms, the most  
 258 abundant taxon was *Chaetoceros* sp. followed by *Pseudonitzschia* sp., mainly observed in

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

261



262

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

265

266 The concentration of  $\text{NH}_4$  in the water column was more than twice higher at farm sites than at  
 267 the reference sites, and the difference was significant (Table 3). Although values observed  
 268 within farm sites tended to be higher than those observed at reference sites,  $\text{PO}_4$  and  $\text{NO}_x$   
 269 concentrations and DIN: $\text{PO}_4$  ratio (DIN =  $\text{NH}_4 + \text{NO}_x$ ) did not differ significantly (Table 3),  
 270 nor did Si concentrations between the farm and reference sites (Table 3).

271

272 **Table 3.** Mean ( $\pm$ SE) dissolved nutrient concentration ( $\mu\text{mol l}^{-1}$ ) and nitrogen/phosphorus ratio in the  
 273 water column at the farm and reference treatments.  $\text{NH}_4$  : ammonium,  $\text{NO}_x$  : nitrates + nitrites,  $\text{PO}_4$  :  
 274 phosphate, DIN :  $\text{NH}_4 + \text{NO}_x$ , Si : silicates. \*Statistical significance of Treatment.

	Reference	Farm	L-ratio	<i>p</i> -value
$\text{NH}_4$	$0.22 \pm 0.03$	$0.49 \pm 0.06$	9.068	$< 0.005^*$
$\text{NO}_x$	$0.17 \pm 0.01$	$0.20 \pm 0.01$	1.503	0.220
$\text{PO}_4$	$0.09 \pm 0.01$	$0.11 \pm 0.01$	1.642	0.202
DIN/ $\text{PO}_4$	$4.38 \pm 0.38$	$6.31 \pm 0.48$	3.368	0.066
Si	$11.53 \pm 0.92$	$10.61 \pm 1.15$	1.538	0.215

275

### 276 3.2. Sedimentation rates, sediment characteristics and benthic community biomass

277 Neither mean sedimentation rates nor OC, N or P concentrations varied significantly between  
 278 the farm and reference treatments, (Table 4). Although higher values were always observed at

279 the farm treatment, no significant differences in sediment OC, N and P contents were recorded  
 280 (Table 4). Sediment samples contained 6.5% of organic carbon, less than 1% of nitrogen and  
 281 phosphorus content was almost negligible whatever the treatment (Table 4).

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

286

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

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

292

293

### 294 3.3. Benthic fluxes

295 Nitrogen fluxes did not differ between treatments, either for  $\text{NH}_4^+$  (mean =  $14.4 \pm 4.4 \mu\text{mol m}^{-2}$   
 296  $\text{h}^{-1}$ ) or  $\text{NO}_x$  (mean =  $2.1 \pm 0.8 \mu\text{mol m}^{-2} \text{h}^{-1}$ ) (Table 5). Negative values of  $\text{NH}_4^+$  fluxes  
 297 (sediment uptake) were observed on three occasions at site FO (in 2 chambers in October and  
 298 in one chamber in December) and in one chamber at RO in November.  $\text{NO}_x$  fluxes were mostly  
 299 positive (70%) although some negative values were recorded ( $< -5 \mu\text{mol m}^{-2} \text{h}^{-1}$ ). Minimum  
 300 values of  $-61.4 \mu\text{mol m}^{-2} \text{h}^{-1}$  and  $-4.3 \mu\text{mol m}^{-2} \text{h}^{-1}$  and maximum values of  $82.7 \mu\text{mol m}^{-2} \text{h}^{-1}$

301 and 20.8  $\mu\text{mol m}^{-2} \text{h}^{-1}$  were measured for  $\text{NH}_4^+$  and  $\text{NO}_x$  respectively. Although some negative  
 302 fluxes were recorded, fluxes were mostly positive, so overall, nitrogen ( $\text{NH}_4^+ + \text{NO}_x$ ) was  
 303 released from the sediment into the water column. Treatment had a significant effect on benthic  
 304  $\text{PO}_4$  fluxes which were higher at the reference sites than at the farm sites (Table 5). Si and  $\text{O}_2$   
 305 fluxes did not vary due to Treatment (Table 5). Si was released from the sediment into the water  
 306 column at a mean rate of  $41.7 \pm 9.2 \mu\text{mol m}^{-2} \text{h}^{-1}$ . The negative values for  $\text{O}_2$  indicated sediment  
 307 oxygen consumption (mean of  $-105.0 \pm 12.2 \text{ mg m}^{-2} \text{h}^{-1}$ ).

308

309 **Table 5.** Mean benthic fluxes ( $\pm\text{SE}$ ) measured at the sediment-water interface at reference (R) and farm  
 310 sites (F) and summary of the significant terms found in the linear mixed-effect model. Nutrient fluxes  
 311 are expressed in  $\mu\text{mol h}^{-1} \text{m}^{-2}$  and  $\text{O}_2$  fluxes in  $\text{mg h}^{-1} \text{m}^{-2}$ . \*Statistical significance of Treatment

	Reference	Farm	L-ratio	<i>p</i> -value
$\text{NH}_4$	$19.0 \pm 5.5$	$10.3 \pm 6.7$	0.418	0.518
$\text{NO}_x$	$0.6 \pm 0.8$	$3.4 \pm 1.3$	1.773	0.183
$\text{PO}_4$	$3.3 \pm 0.5$	$1.1 \pm 0.4$	1.773	< 0.01*
Si	$45.0 \pm 14.5$	$38.7 \pm 11.9$	0.066	0.797
$\text{O}_2$	$-122.0 \pm 14.5$	$-88.6 \pm 19.0$	1.019	0.313

312

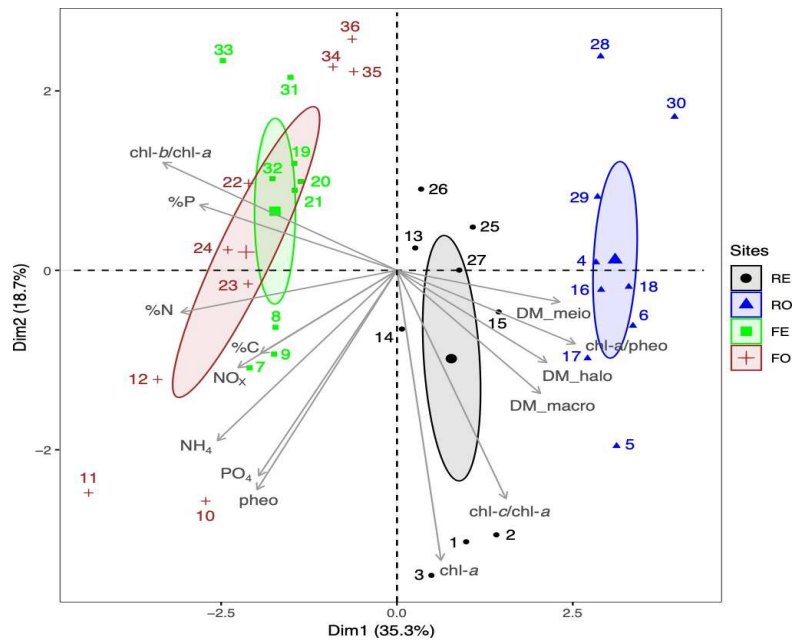
313

### 314 3.4. Multivariate characterization of the sites

315 A PCA of the environmental variables explained 54% of variation on the first two axes. The  
 316 three variables that contributed most to the first axis were the ratio of chl-*b* to chl-*a* (chl-*b*/chl-*a*,  
 317 *a*, -0.855) and the percentage of nitrogen (%N, -0.789) and phosphorus (%P, -0.720) in the  
 318 sediment. The first axis (35.3%) clearly distinguished between farm and reference treatments  
 319 (Fig. 4). Farm sites (FO and FE) were characterized by higher concentrations of nitrogen and  
 320 phosphorus in the sediment and by a higher chl-*b*/chl-*a* ratio, due to lower concentrations of  
 321 chl-*a*. In contrast, at the reference sites (RO and RE), the ratio of chl-*a* to pheo was higher  
 322 (indicating less proportion of degraded phytoplankton), concentrations of nutrients in the water  
 323 column were lower and macrophyte and infauna biomass was higher. This trend was mainly  
 324 driven by the higher biomass of macrophyte at site RO which is distinct from site RE, whereas,

325 according to the PCA, farm sites were more similar. The second axis (18.7%) mostly  
 326 highlighted variations over time, mainly explained by differences in phytoplankton pigments  
 327 (chl-*a*: -0.831, chl-*c*/chl-*a*: -0.654, pheo: -0.628).

328



329

330 **Figure 4.** PCA biplot of studied parameters analysed at the 4 sites. Ellipses summarize the point  
 331 dispersion (95% confidence) for each site. Code: chl-*a*, chl-*b*, chl-*c*, pheo: chlorophyll- and  
 332 pheopigments; %P, %N, %OC: phosphorus, nitrogen and organic carbon content in the sediment; NO<sub>x</sub>,  
 333 NH<sub>4</sub>, PO<sub>4</sub>: dissolved nutrients in the water column; DM\_meio, DM\_halo, DM\_macro: dry mass of  
 334 meiofauna, macrophyte and macrofauna in sediment. Numbers 1 to 12: October, 13 to 24: November,  
 335 25 to 36: December.

336

## 337 4. Discussion

### 338 4.1. Influence of juvenile oysters on water column parameters

339 In shallow semi-enclosed ecosystems, where bivalve aquaculture often takes place, the  
 340 biological production is usually considered to be mainly controlled by benthic-pelagic coupling  
 341 (e.g. Gibbs et al., 2005; Ouisse et al., 2013), meaning that the influence of bivalves as an  
 342 anthropogenic biological forcing on benthic systems has been widely studied (Lacoste et al.,  
 343 2020b and references therein). However, bivalves may also have a significant effect on  
 344 phytoplankton turnover and overall water column production thanks to nutrients released via



345 direct excretion (bottom-up effect), and depletion of suspended particles through filtration (top-  
346 down effect) (Gallardi, 2014; Newell, 2004; Prins et al., 1998). Increased nutrient concentration  
347 and a shift in the phytoplankton community structure to the benefit of small eucaryotes are both  
348 frequently observed in shellfish exploited ecosystems (Jacobs et al., 2016; Naddafi et al., 2007).  
349 In Thau Lagoon, Mazouni (2004) showed the importance of cultivated oysters in the recycling  
350 of dissolved nitrogen in the water column compared with their contribution to benthic  
351 mineralization. The positive effect of oyster culture on nutrient concentration in the overlying  
352 water was also reported to be significant in a study by Souchu et al. (2001), with annual  
353 increases of 73%, 36% and 19% recorded for ammonium, phosphates and silicates respectively.  
354 Our findings are in accordance with these results since we observed higher concentrations ( $\times 2$ )  
355 of ammonium in the water column at oyster farming sites compared with reference sites,  
356 although the excess of this nutrient was lower than that reported by Souchu et al. (2001). One  
357 possible explanation for this difference could be the bathymetry and the location of our study  
358 sites. Souchu et al. (2001) reported that nutrient excess in the shellfish farming area was lower  
359 in the western part than in the eastern part of the lagoon, because the shallower depth (4 m)  
360 allows light to reach the bottom which enables benthic macroflora to grow on nutrients of  
361 benthic origin. Although no measurement of juvenile metabolism has been done in this study,  
362 the difference with the study of Souchu et al. (2001) could also be explained by a lower  $\text{NH}_4^+$   
363 excretion by tables of juvenile oysters compared with adults. In terms of flesh biomass, a table  
364 of juvenile represents about 25 kg (3 millions individuals) whereas a standard table of adults  
365 (ca 150 000 individuals) weighs more than 300 kg (data from Ifremer). Given the same range  
366 of excretion values measured for juveniles (Richard et al., 2017) and adults (Buzin et al. 2015),  
367 nutrient renewal is reduced during the pre-growth phase, accentuated by the low temperatures  
368 observed during this period (10°C-18.8°C). Overall, it should be noted that nutrient  
369 concentrations were in the lower range of values reported for Thau lagoon (Collos et al., 2005)

370 as being characteristic of early winter, such that the interactions between juvenile oysters and  
371 the environment were reduced, as already observed by Mazouni (2004).  
372 Souchu et al. (2001) also reported a shift in phytoplankton composition due to the activity of  
373 filter feeders, with a higher abundance of picophytoplankton at farm sites favored by rapid use  
374 of regenerated nitrogen. In the present study, picophytoplankton dominated (60%) at both  
375 treatments, with no difference between farm and reference sites, and we did not observe an  
376 increase in small particles biomass at the farm sites, likely due to lower nutrient concentration  
377 and picophytoplankton production in winter. However, even though phytoplankton abundance  
378 and biomass were low in our study – which is typical of winter conditions (Fiandrino et al.,  
379 2019) – the results showed that oysters induce relative control over the community composition,  
380 as evidenced by two observations made at farm: (i) a lower ratio between total chlorophyll and  
381 degraded pigments (pheo), highlighting a grazing pressure of oysters on autotrophic organisms,  
382 (ii) a lower contribution of organisms containing chl-*c* – mainly diatoms > 20 µm – and a higher  
383 contribution of organisms containing chl-*b* – probably small chorophytes – to the total  
384 phytoplankton biomass (chl-*a*), emphasizing the higher grazing pressure of juveniles on larger  
385 particles, as is the case for adult oysters whose gills retain all > 5 µm flagellates,  
386 microphytoplankton, dinoflagellates, ciliates and zooplankton (Dupuy et al., 2000).

387

#### 388 **4.2. Low biodeposition of juvenile oyster culture**

389 Bivalve aquaculture generally modifies sediment composition and benthic fluxes due to  
390 increased inputs of organic material (biodeposition) that stimulate benthic metabolism (Lacoste  
391 et al., 2020b and references therein). Historical data concerning sedimentation rates both inside  
392 and outside farming areas in Thau Lagoon are scarce. Biodeposition values were only found in  
393 De Casabianca (1977) and Grenz (1989). Their results indicate that shellfish biomass produces  
394 from 300 to 500 kg ha<sup>-1</sup> year<sup>-1</sup> of nitrogen and about 3 000 kg ha<sup>-1</sup> year<sup>-1</sup> of carbon as

395 biodeposition, whereas values measured in the present study were five and four times lower for  
396 nitrogen and carbon, respectively, with no apparent effect of oyster culture. Thus, the absence  
397 of benthic footprint observed in our study may be due to these low sedimentation rates, which,  
398 in turn, are probably due to the lower rate of biodeposition by juvenile oysters compared with  
399 adults along with the low water temperature during our experiment, which slows down oyster  
400 metabolism and hence biodeposition (Mitchell, 2006). In Korea, Hyun et al. (2013) reported  
401 that the production of feces and pseudo-feces increased with an increase in the wet weight of  
402 oysters (*C. gigas*). Other authors (Callier et al., 2006; Giles and Pilditch, 2004) who studied  
403 suspended mussel culture, also observed that larger mussels produced bigger biodeposits in  
404 larger quantities, thereby increasing the transfer of organic matter to the benthic system. Thus,  
405 smaller biodeposits of juveniles with a lower settlement rate were likely decomposed and/or  
406 advected farther afield by prevailing currents, explaining why we observed reduced localized  
407 biodeposition under the tables and no immediate effect on the benthic compartment over our  
408 study period. Benthic impact in aquaculture systems results from a balance between  
409 sedimentation, resuspension, and decay of biodeposits. Because these mechanisms are site-  
410 specific and often vary over time, field measurements are the best way to obtain reliable  
411 information on the intrinsic complexity of such ecosystems. In Thau Lagoon, such information  
412 is rare and further studies are required to evaluate biodeposition on an annual basis, including  
413 different operating systems, along with measurement of potential subsequent benthic  
414 modifications.

415

### 416 **4.3. Low benthic impact during the pre-growth period**

417 Benthic fluxes in dark conditions give a snapshot of organic material mineralization and  
418 associated sediment oxygen consumption at a given site. The intensity of fluxes is increased  
419 with organic material input, such as biodeposition, and is further stimulated by high

420 temperature. In accordance with that, Mazouni et al. (1996) and Thouzeau et al. (2007)  
421 observed increased oxygen demand and nutrient release at the sediment-water interface in  
422 shellfish farming areas, with maximum values in summer. In conjunction with the low levels  
423 of biodeposition and low temperature during the period of the study, we detected almost no  
424 difference between benthic fluxes under juvenile oysters and at the reference areas.

425 Although no immediate benthic effect of farming was observed in this study, the concentrations  
426 of organic carbon, nitrogen and phosphorus in the sediment were indicative of an enriched area  
427 (Baehr et al., 2013) with slightly, although not significant, higher levels at the farm sites, as  
428 illustrated by the PCA. This may be due to the history of the area, which has been used for  
429 shellfish farming for many years. In the past, several evaluations of the lagoon showed that  
430 nitrogen and phosphorus were more concentrated in sediment directly under and in the corridors  
431 between shellfish areas compared with in other parts of the lagoon (Anschutz et al., 2007;  
432 Deslous-Paoli et al., 1998; Pichot et al., 1994), which had an impact on the structure of the  
433 benthic communities (Duport et al., 2007; Thouzeau et al., 2007). The significant effect of  
434 juvenile oysters on macro- and meiofauna community composition and biomass (Lacoste et al.,  
435 2020a, this study) further supports this hypothesis and suggests that farming areas are distinct  
436 from other parts of the lagoon. This underlines the importance of developing integrated  
437 approaches looking at several ecosystem components to assess the overall effect of shellfish  
438 farming in coastal ecosystems, as already discussed in Lacoste et al. (2020a, 2020b). In the  
439 present study, the use of multivariate analysis in addition to the univariate approach provided  
440 additional information on the influence of oyster farming, highlighting that fact that long-term  
441 transfer of organic matter from the water column to the benthic system may have contributed  
442 to the stocking of organic carbon, nitrogen and phosphorus in the sediment and the decrease of  
443 infauna biomass.

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

459

#### 460 **4.5. Conclusions and future outlook**

461 Understanding and predicting anthropogenic impacts on marine ecosystem is essential in a  
462 context where habitat and biodiversity are continuously altered. In Thau Lagoon where  
463 aquaculture occupies 1/4 of the area, the role aquaculture plays in ecosystem functioning needs  
464 to be identified to enable sustainable aquaculture. Using a multi-compartment approach, our  
465 findings suggest that juvenile oyster metabolism may have partially controlled the water  
466 nutrient pool and phytoplanktonic community composition during our study period.  
467 Conversely, the pre-growth stage in autumn/winter did not appear to have a significant impact  
468 on the benthic ecosystem, due to low sedimentation rates observed during this period and the

469 potential dispersion and resuspension of biodeposits. However, the long farming history of the  
470 lagoon may have shaped sediment composition in farming areas compared with other parts of  
471 the lagoon by increasing sediment N and P contents and decreasing macro and meiofauna  
472 biomasses. As a typical transitional coastal area, Thau Lagoon offers a wide range of habitats  
473 and is subject to natural environmental variations making the effect of shellfish farming difficult  
474 to highlight. The use of two sites per Treatment (Farm vs Reference) in this study, instead of  
475 one, allowed to obtain a global view of farm effect regardless of natural variability.  
476 To go further, more studies are needed to describe the nutrient and oxygen dynamics in Thau  
477 Lagoon, in relation with seasonal variability of oyster culture practices (juveniles in lanterns vs  
478 adults on ropes) and stock (biomass per table). Such information will contribute to improve the  
479 lagoon functioning model specifically developed for Thau (Pete et al. 2020) to predict the  
480 influence of several climate and exploitation scenarios its functioning. These topics must be  
481 urgently addressed for management purposes to reconcile the achievement of good ecological  
482 status and the sustainability of shellfish aquaculture in Thau Lagoon in a context of  
483 oligotrophication, climate change and increased risk of anoxia.

484

#### 485 **Acknowledgements**

486 This work is a contribution to the MORTAFLUX program, funded by Ifremer Scientific Direction and  
487 the EC2CO BIOHEFFECT action (Coordinator: M. Richard). The Postdoctoral fellowship of É. Lacoste  
488 was funded by Ifremer and the University of French Polynesia. Macrofauna analysis was funded by  
489 MARBEC UMR. Many thanks to F. Tarbouriech, head of the MEDITHAU farm for allowing us to take  
490 samples from his tables. Thanks also to his employees, L. Ritter, P. Avila and PE. Galavielle for  
491 providing information on table densities and for help during oyster sampling. We thank S. Poirier, E.  
492 Hatey and C. Hubert for lab analyses, N. Cimiterra for the map realization (Figure 1) and C. Pelaprat  
493 for macrofauna identification. The authors are very grateful to their retired colleagues: S. Mortreux, M.  
494 Fortune, C. Chiantella for their help in the field and lab. This article was written in memoriam of  
495 J. Oheix and T. Berteaux, who scuba-dived during this study.

496

497 **References**

- 498 Aminot, A., K erouel, R., 2007. Dosage automatique des nutriments dans les eaux marines : m ethodes  
499 en flux continu. Ed Quae. 188p.
- 500 Anschutz, P., Chaillou, G., Lecroart, P., 2007. Phosphorus diagenesis in sediment of the Thau Lagoon.  
501 Estuar. Coast. Shelf Sci. 72, 447–456. <https://doi.org/10.1016/j.ecss.2006.11.012>
- 502 Baehr, A., Derolez, V., Fiandrino, A., Le Fur, I., Malet, N., Messiaen, G., Munaron, D., Oheix, J.,  
503 Ouisse, V., Roque d’Orbcastel, E., Bec, B., 2013. Bilan m ethodologique de l’outil de diagnostic  
504 de l’eutrophisation du RSL. Quatorze ann ees de r esultats en R egion Languedoc-Roussillon.  
505 RST/LER/LR/13.08. <https://archimer.ifremer.fr/doc/00165/27662/>
- 506 Barton, K., 2020. Mu-MIn: Multi-model inference. R Package Version 1.43.17. [https://CRAN.R-](https://CRAN.R-project.org/package=MuMIn)  
507 [project.org/package=MuMIn](https://CRAN.R-project.org/package=MuMIn)
- 508 Buzin, F., Dupuy, B., Lefebvre, S., Barill e, L., Haure, J., 2015. Aquacultural Engineering Storage of  
509 Pacific oysters *Crassostrea gigas* in recirculating tank: ammonia excretion and potential  
510 nitrification rates. Aquac. Eng. 64, 8–14.
- 511 Callier, M.D., McKindsey, C.W., Desrosiers, G., 2008. Evaluation of indicators used to detect mussel  
512 farm influence on the benthos: Two case studies in the Magdalen Islands, Eastern Canada.  
513 Aquaculture 278, 77–88. <https://doi.org/10.1016/j.aquaculture.2008.03.026>
- 514 Callier, M.D., Richard, M., McKindsey, C.W., Archambault, P., Desrosiers, G., 2009. Responses of  
515 benthic macrofauna and biogeochemical fluxes to various levels of mussel biodeposition: An in  
516 situ “benthocosm” experiment. Mar. Pollut. Bull. 58, 1544–1553.  
517 <https://doi.org/10.1016/j.marpolbul.2009.05.010>
- 518 Callier, M.D., Weise, A.M., McKindsey, C.W., Desrosiers, G., 2006. Sedimentation rates in a  
519 suspended mussel farm (Great-Entry Lagoon, Canada): Biodeposit production and dispersion.  
520 Mar. Ecol. Prog. Ser. 322, 129–141. <https://doi.org/10.3354/meps322129>
- 521 Chapelle, A., M enesguen, A., Deslous-Paoli, J.M., Souchu, P., Mazouni, N., Vaquer, A., Millet, B.,  
522 2000. Modelling nitrogen, primary production and oxygen in a Mediterranean lagoon. Impact of  
523 oysters farming and inputs from the watershed. Ecol. Modell. 127, 161–181.  
524 [https://doi.org/10.1016/S0304-3800\(99\)00206-9](https://doi.org/10.1016/S0304-3800(99)00206-9)
- 525 Collos, Y., Bec, B., Jauzein, C., Abadie, E., Laugier, T., Lautier, J., Pastoureaud, A., Souchu, P.,  
526 Vaquer, A., 2009. Oligotrophication and emergence of picocyanobacteria and a toxic  
527 dinoflagellate in Thau lagoon, southern France. J. Sea Res. 61, 68–75.  
528 <https://doi.org/10.1016/j.seares.2008.05.008>
- 529 Collos, Y., Husseini-Ratrema, J., Bec, B., Vaquer, A., Thong, L.H., Rougier, C., Pons, V., Souchu, P.,  
530 2005. Pheopigment dynamics, zooplankton grazing rates and the autumnal ammonium peak in a  
531 Mediterranean lagoon. Hydrobiologia 550, 83–93. <https://doi.org/10.1007/s10750-005-4365-1>
- 532 Dame, R.F., Prins, T.C., 1998. Bivalve carrying capacity in coastal ecosystems. Aquat. Ecol. 31(4),  
533 409–421.

534 De Casabianca, M.L., 1977. Résultats préliminaires des expériences sur la biodéposition en milieu  
535 lagunaire. Rapport de la Commission Internationale pour l'Exploration Scientifique de la Mer  
536 méditerranée. 24. pp 91-92.

537 Dedieu, K., Rabouille, C., Thouzeau, G., Jean, F., Chauvaud, L., Clavier, J., Mesnage, V., Ogier, S.,  
538 2007. Benthic O<sub>2</sub> distribution and dynamics in a Mediterranean lagoon (Thau, France): An in situ  
539 microelectrode study. *Estuar. Coast. Shelf Sci.* 72, 393–405.  
540 <https://doi.org/10.1016/j.ecss.2006.11.010>

541 Derolez, V., Bec, B., Munaron, D., Fiandrino, A., Pete, R., Simier, M., Souchu, P., Laugier, T.,  
542 Aliaume, C., Malet, N., 2019. Recovery trajectories following the reduction of urban nutrient  
543 inputs along the eutrophication gradient in French Mediterranean lagoons. *Ocean Coast. Manag.*  
544 171, 1–10. <https://doi.org/10.1016/J.OCECOAMAN.2019.01.012>

545 Derolez, V., Malet, N., Fiandrino, A., Lagarde, F., Richard, M., Ouisse, V., Bec, B., Aliaume, C.,  
546 2020a. Fifty years of ecological changes: Regime shifts and drivers in a coastal Mediterranean  
547 lagoon during oligotrophication. *Sci. Total Environ.* 732, 139292  
548 <https://doi.org/10.1016/j.scitotenv.2020.139292>

549 Derolez, V., Soudant, D., Malet, N., Chiantella, C., Richard, M., Abadie, E., Aliaume, C., Bec, B.,  
550 2020b. Two decades of oligotrophication: evidence for a phytoplankton community shift in the  
551 coastal lagoon of Thau (Mediterranean Sea, France). *Estuar. Coast. Shelf Sci.* 241, 106810.  
552 <https://doi.org/10.1016/j.ecss.2020.106810>

553 Deslous-Paoli, J.M., Souchu, P., Mazouni, N., Juge, C., Dagault, F., 1998. Relations milieu-  
554 ressources: Impact de la conchyliculture sur un environnement lagunaire Méditerranéen (Thau).  
555 *Oceanol. Acta* 21, 831–843. [https://doi.org/10.1016/S0399-1784\(99\)80010-3](https://doi.org/10.1016/S0399-1784(99)80010-3)

556 Duport, E., Gilbert, F., Poggiale, J.C., Dedieu, K., Rabouille, C., Stora, G., 2007. Benthic macrofauna  
557 and sediment reworking quantification in contrasted environments in the Thau Lagoon. *Estuar.*  
558 *Coast. Shelf Sci.* 72, 522–533. <https://doi.org/10.1016/j.ecss.2006.11.018>

559 Dupuy, C., Vaquer, A., Lam-höai, T., Rougier, C., Mazouni, N., Lautier, J., Collos, Y., Gall, Solange  
560 Le, Le Gall, S., 2000. Feeding rate of the oyster *Crassostrea gigas* in a natural planktonic  
561 community of the Mediterranean Thau Lagoon. *Mar. Ecol. Prog. Ser.* 205, 171–184.  
562 <https://doi.org/10.3354/meps205171>

563 Ferrón, S., Alonso-Pérez, F., Anfuso, E., Murillo, F.J., Ortega, T., Castro, C.G., Forja, J.M., 2009.  
564 Benthic nutrient recycling on the northeastern shelf of the Gulf of Cádiz (SW Iberian Peninsula).  
565 *Mar. Ecol. Prog. Ser.* 390, 79–95. <https://doi.org/10.3354/meps08199>

566 Fiandrino, A., Ophelie, S., Dominique, M., Nicolas, C., Serge, M., Valerie, D., Eric, A., Anais, C.,  
567 Clarisse, H., 2019. Qualité du Milieu Marin Littoral Bulletin de la surveillance 2018  
568 Départements des Pyrénées Orientales, de l'Aude, de l'Hérault, du Gard.  
569 ODE/LITTORAL/LERLR/19.05. <https://archimer.ifremer.fr/doc/00507/61877/>

570 Gaertner-Mazouni, N., Lacoste, É., Bodoy, A., Peacock, L., Rodier, M., Langlade, M.J., Orempuller,



571 J., Charpy, L., 2012. Nutrient fluxes between water column and sediments: Potential influence of  
572 the pearl oyster culture. *Mar. Pollut. Bull.* 65, 500–505.  
573 <https://doi.org/10.1016/j.marpolbul.2012.02.013>

574 Gallardi, D., 2014. Effects of Bivalve Aquaculture on the Environment and Their Possible Mitigation :  
575 A Review. *Fish. Aquac. J.* 5, 8. <https://doi.org/10.4172/2150-3508.1000105>

576 Gibbs, M., Funnell, G., Pickmere, S., Norkko, A., Hewitt, J., 2005. Benthic nutrient fluxes along an  
577 estuarine gradient: Influence of the pinnid bivalve *Atrina zelandica* in summer. *Mar. Ecol. Prog.*  
578 *Ser.* 288, 151–164. <https://doi.org/10.3354/meps288151>

579 Gilbert, F., Souchu, P., Gilbertl, F., Souchu, P., 1997. Influence of shellfish farming activities on  
580 nitrification, nitrate reduction to ammonium and denitrification at the water-sediment interface of  
581 the Thau lagoon, France. *Mar. Ecol. Prog. Ser.* 151, 143–153.

582 Giles, H., Pilditch, C.A., 2004. Effects of diet on sinking rates and erosion thresholds of mussel *Perna*  
583 *canaliculus* biodeposits. *Mar. Ecol. Prog. Ser.* 282, 205–219.  
584 <https://doi.org/10.3354/meps282205>

585 Giles, H., Pilditch, C.A., Bell, D.G., 2006. Sedimentation from mussel (*Perna canaliculus*) culture in  
586 the Firth of Thames, New Zealand: Impacts on sediment oxygen and nutrient fluxes. *Aquaculture*  
587 261, 125–140. <https://doi.org/10.1016/j.aquaculture.2006.06.048>

588 Grenz, C., 1989. Quantification et destinée de la biodéposition en zones de production conchylicole  
589 intensive en Méditerranée. Thèse de doctorat. Université Aix-Marseille II. 313p.

590 Grenz, C., Moreno, M.O., Soetaert, K., Denis, L., Douillet, P., Fichez, R., 2019. Spatio-temporal  
591 variability in benthic exchanges at the sediment-water interface of a shallow tropical coastal  
592 lagoon (south coast of Gulf of Mexico). *Estuar. Coast. Shelf Sci.* 218, 368–380.  
593 <https://doi.org/10.1016/j.ecss.2019.01.012>

594 Gust, G., Kozerski, H.P., 2000. In situ sinking-particle flux from collection rates of cylindrical traps.  
595 *Mar. Ecol. Prog. Ser.* 208, 93–106. <https://doi.org/10.3354/meps208093>

596 Hayakawa, Y., Kobayashi, M., Izawa, M., 2001. Sedimentation flux from mariculture of oyster  
597 (*Crassostrea gigas*) in Ofunato estuary, Japan. *ICES J. Mar. Sci.* 58, 435–444.  
598 <https://doi.org/10.1006/jmsc.2000.1036>

599 Hulot, V., Saulnier, D., Lafabrie, C., Gaertner-Mazouni, N., 2018. Shellfish culture: a complex driver  
600 of planktonic communities. *Rev. Aquac.* 12(1), 33-46. <https://doi.org/10.1111/raq.12303>

601 Hyun, J.H., Kim, S.H., Mok, J.S., Lee, J.S., An, S.U., Lee, W.C., Jung, R.H., 2013. Impacts of long-  
602 line aquaculture of Pacific oysters (*Crassostrea gigas*) on sulfate reduction and diffusive nutrient  
603 flux in the coastal sediments of Jinhae-Tongyeong, Korea. *Mar. Pollut. Bull.* 74, 187–198.  
604 <https://doi.org/10.1016/j.marpolbul.2013.07.004>

605 Jacobs, P., Riegman, R., van der Meer, J., 2016. Impact of introduced juvenile mussel cultures on the  
606 pelagic ecosystem of the western Wadden Sea, The Netherlands. *Aquac. Environ. Interact.* 8,  
607 553–566. <https://doi.org/10.3354/AEI00196>

608 Jansen, H., Strand, Ø., Strohmeier, T., 2011. Seasonal variability in nutrient regeneration by mussel  
609 *Mytilus edulis* rope culture in oligotrophic systems. Mar. Ecol. Prog. Ser. 431, 137–149.

610 Lacoste, É., Boufahja, F., Pelaprat, C., Le Gall, P., Berteaux, T., Messiaen, G., Mortreux, S., Oheix, J.,  
611 Ouisse, V., Roque d’Orbcastel, E., Gaertner-Mazouni, N., Richard, M., 2020a. First  
612 simultaneous assessment of macro- and meiobenthic community response to juvenile shellfish  
613 culture in a Mediterranean coastal lagoon (Thau, France). Ecol. Indic. 115, 106462

614 Lacoste, É., Drouin, A., Weise, A.M., Archambault, P., McKindsey, C.W., 2018. Low benthic impact  
615 of an offshore mussel farm in Îles-de-la-Madeleine, eastern Canada. Aquac. Environ. Interact.  
616 10, 473–485. <https://doi.org/10.3354/aei00283>

617 Lacoste, É., Gaertner-Mazouni, N., 2016. Nutrient regeneration in the water column and at the  
618 sediment–water interface in pearl oyster culture (*Pinctada margaritifera*) in a deep atoll lagoon  
619 (Ahe, French Polynesia). Estuar. Coast. Shelf Sci. 182, 304–309.  
620 <https://doi.org/10.1016/j.ecss.2016.01.037>

621 Lacoste, É., Gueguen, Y., Le Moullac, G., Sham Koua, M., Gaertner-Mazouni, N., 2014. Influence of  
622 farmed pearl oysters and associated biofouling communities on nutrient regeneration in lagoons  
623 of French Polynesia. Aquac. Environ. Interact. 5, 209–219. <https://doi.org/10.3354/aei00107>

624 Lacoste, É., McKindsey, C.W., Archambault, P., 2020b. Biodiversity-Ecosystem Functioning (BEF)  
625 approach to further understanding aquaculture-environment interactions. Rev. Aquac. 12(4),  
626 2027-2041. <https://doi.org/10.1111/RAQ.12420>

627 Lagarde, F., Fiandrino, A., Ubertini, M., D’Orbcastel, E.R., Mortreux, S., Chiantella, C., Bec, B.,  
628 Bonnet, D., Roques, C., Bernard, I., Richard, M., Guyondet, T., Pouvreau, S., Lett, C., 2019.  
629 Duality of trophic supply and hydrodynamic connectivity drives spatial patterns of Pacific oyster  
630 recruitment. Mar. Ecol. Prog. Ser. 632, 80-100. <https://doi.org/10.3354/meps13151>

631 Lagarde, F., Roque D’orbcastel, E., Ubertini, M., Mortreux, S., Bernard, I., Fiandrino, A., Chiantella,  
632 C., Bec, B., Roques, C., Bonnet, D., Miron, G., Richard, M., Pouvreau, S., Lett, C., 2017.  
633 Recruitment of the Pacific oyster *Crassostrea gigas* in a shellfish-exploited Mediterranean  
634 lagoon: Discovery, driving factors and a favorable environmental window. Mar. Ecol. Prog. Ser.  
635 578, 1–17. <https://doi.org/10.3354/meps12265>

636 Le Fur, I., 2018. Rôle des macrophytes dans la restauration des milieux lagunaires : successions  
637 écologiques. Thèse de doctorat. Université de Montpellier. 209p.

638 Mazouni, N., 2004. Influence of suspended oyster cultures on nitrogen regeneration in a coastal  
639 lagoon (Thau, France). Mar. Ecol. Prog. Ser. 276, 103–113. <https://doi.org/10.3354/meps276103>

640 Mazouni, N., Deslous-Paoli, J.-M., Landrein, S., 1998. Influence d’un élevage ostréicole sur les flux  
641 de nutriments et d’oxygène dans un écosystème lagunaire. Oceanol. Acta 21, 845–858.  
642 [https://doi.org/10.1016/S0399-1784\(99\)80011-5](https://doi.org/10.1016/S0399-1784(99)80011-5)

643 Mazouni, N., Gaertner, J.C., Deslous-Paoli, J.M., Landrein, S., Geringer D’Oedenberg, M., 1996.  
644 Nutrient and oxygen exchanges at the water-sediment interface in a shellfish farming lagoon

645 (Thau, France). *J. Exp. Mar. Bio. Ecol.* 205, 91–113. <https://doi.org/10.1016/S0022->  
646 0981(96)02594-4

647 Menu, M., Vaz, S., Bajjouk, T., Derolez, V., Fiandrino, A., Giraud, A., Grillas, P., Ouisse, V., 2019.  
648 Rapport final du projet CHAMILA (Cartographie des habitats en milieu lagunaire  
649 méditerranéen). R.ODE/UL/LER/LR/19.34. <https://doi.org/10.13155/70545>

650 Metzger, E., Simonucci, C., Viollier, E., Sarazin, G., Prévot, F., Jézéquel, D., 2007. Benthic response  
651 to shellfish farming in Thau lagoon: Pore water signature. *Estuar. Coast. Shelf Sci.* 72, 406–419.  
652 <https://doi.org/10.1016/j.ecss.2006.11.011>

653 Mitchell, I.M., 2006. In situ biodeposition rates of Pacific oysters (*Crassostrea gigas*) on a marine  
654 farm in Southern Tasmania (Australia). *Aquaculture* 257, 194–203.  
655 <https://doi.org/10.1016/j.aquaculture.2005.02.061>

656 Naddafi, R., Pettersson, K., Eklöv, P., 2007. The effect of seasonal variation in selective feeding by  
657 zebra mussels (*Dreissena polymorpha*) on phytoplankton community composition. *Freshw. Biol.*  
658 52, 823–842. <https://doi.org/10.1111/j.1365-2427.2007.01732.x>

659 Neaud-Masson, N., 2015. Observation et dénombrement du phytoplancton marin par microscopie  
660 optique photonique - Spécifications techniques et méthodologiques appliquées au REPHY.  
661 R.INT.ODE/DYNECO/VIGIES/15-13. <https://archimer.ifremer.fr/doc/00292/40293/>

662 Neveux, J., Lantoiné, F., 1993. Spectrofluorometric assay of chlorophylls and phaeopigments using  
663 the least squares approximation technique. *Deep. Res. Part I* 40, 1747–1765.  
664 [https://doi.org/10.1016/0967-0637\(93\)90030-7](https://doi.org/10.1016/0967-0637(93)90030-7)

665 Newell, R.I.E., 2004. Ecosystem influences of natural and cultivated populations of suspension-  
666 feeding bivalve molluscs: A review. *J. Shellfish Res.* 23, 51–61.

667 Nizzoli, D., Welsh, D., Viaroli, P., 2011. Seasonal nitrogen and phosphorus dynamics during benthic  
668 clam and suspended mussel cultivation. *Mar. Pollut. Bull.* 62, 1276–87.  
669 <https://doi.org/10.1016/j.marpolbul.2011.03.009>

670 Nizzoli, D., Welsh, D.T., Bartoli, M., Viaroli, P., 2005. Impacts of mussel (*Mytilus galloprovincialis*)  
671 farming on oxygen consumption and nutrient recycling in a eutrophic coastal lagoon, in:  
672 *Hydrobiologia*. 550(1), 183–198. <https://doi.org/10.1007/s10750-005-4378-9>

673 Nizzoli, D., Welsh, D.T., Fano, E.A., Viaroli, P., 2006. Impact of clam and mussel farming on benthic  
674 metabolism and nitrogen cycling, with emphasis on nitrate reduction pathways. *Mar. Ecol. Prog.*  
675 *Ser.* 315, 151–165. <https://doi.org/10.3354/meps315151>

676 Ouisse, V., Fiandrino, A., de Wit, R., Malet, N., 2013. Restauration des écosystèmes lagunaires :  
677 évaluation du rôle du sédiment et des herbiers à phanérogames Rapport final du Contrat n° 2012  
678 1835. ST/LELR 13-09. <https://archimer.ifremer.fr/doc/00166/27774/>

679 Pecqueur, D., Vidussi, F., Fouilland, E., Le Floc'h, E., Mas, S., Roques, C., Salles, C., Tournoud,  
680 M.G., Mostajir, B., 2011. Dynamics of microbial planktonic food web components during a river  
681 flash flood in a Mediterranean coastal lagoon. *Hydrobiologia* 673, 13–27.

682 <https://doi.org/10.1007/s10750-011-0745-x>

683 Pete, R., Guyondet, T., Bec, B., Derolez, V., Cesmat, L., Lagarde, F., Pouvreau, S., Fiandrino, A.,  
684 Richard, M., 2020. A box-model of carrying capacity of the Thau lagoon in the context of  
685 ecological status regulations and sustainable shellfish cultures. *Ecol. Modell.* 426, 109049.  
686 <https://doi.org/10.1016/j.ecolmodel.2020.109049>

687 Pichot, P., Ximenes, M.C., Deslous-Paoli, J.M., Juge, C., 1994. Bilan de l'azote et du phosphore dans  
688 le système Lagune-Bassin versant de Thau. *R.INT.DEL/94.11/Sète*.  
689 <https://archimer.ifremer.fr/doc/00039/15017/>

690 Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., R Core Team (2018). nlme: Linear and Nonlinear  
691 Mixed Effects Models. R package version 3.1-137, URL:[https://CRAN.R-](https://CRAN.R-project.org/package=nlme)  
692 [project.org/package=nlme](https://CRAN.R-project.org/package=nlme)

693 Pinkerton, M., Gall, M., Wood, S., Zeldis, J., 2018. Measuring the effects of bivalve mariculture on  
694 water quality in northern New Zealand using 15 years of MODIS-Aqua satellite observations.  
695 *Aquac. Environ. Interact.* 10, 529–545. <https://doi.org/10.3354/AEI00288>

696 Plante-Cuny, M.R., Plante, R., Mazouni, N., Fontaine, M.F., Souchu, P., Deslous-Paoli, J.M., Grenz,  
697 C., 1998. Oxygen fluxes involving the benthic micro- and macrophytic components in the Thau  
698 Lagoon under pre-anoxic conditions. *Oceanol. Acta* 21, 819–829. [https://doi.org/10.1016/S0399-](https://doi.org/10.1016/S0399-1784(99)80009-7)  
699 [1784\(99\)80009-7](https://doi.org/10.1016/S0399-1784(99)80009-7)

700 Porter, E., Robins, E., Davis, S., Lacouture, R., Cornwell, J., 2020. Effects of resuspension of eastern  
701 oyster *Crassostrea virginica* biodeposits on phytoplankton community structure. *Mar. Ecol.*  
702 *Prog. Ser.* 640, 79–105. <https://doi.org/10.3354/meps13277>

703 Prins, T.C., Smaal, A.C., Dame, R.F., 1998. A review of the feedbacks between bivalve grazing and  
704 ecosystem processes. *Aquat. Ecol.* <https://doi.org/10.1023/A:1009924624259>

705 Quinn, G.P., Keough, M.J., 2002. *Experimental Design and Data Analysis for Biologists*, Cambridge,  
706 UK. ed. Cambridge University Press. 553p.

707 R Core Team (2018). R: A language and environment for statistical computing. R Foundation for  
708 Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.

709 Raimbault, P., Diaz, F., Pouvesle, W., Boudjellal, B., 1999. Simultaneous determination of particulate  
710 organic carbon, nitrogen and phosphorus collected on filters, using a semiautomatic wet-  
711 oxidation method. *Mar. Ecol. Prog. Ser.* 180, 289–295. <https://doi.org/10.3354/meps180289>

712 Raimbault, P., Garcia, N., Cerutti, F., 2008. Distribution of inorganic and organic nutrients in the  
713 South Pacific Ocean – evidence for long-term accumulation of organic matter in nitrogen-  
714 depleted waters. *Biogeosciences* 5, 281–298. <https://doi.org/10.5194/bg-5-281-2008>

715 Richard, M., Archambault, P., Thouzeau, G., Desrosiers, G., 2007a. Summer influence of 1 and 2 yr  
716 old mussel cultures on benthic fluxes in Grande-Entrée lagoon, Îles-de-la-Madeleine (Québec,  
717 Canada). *Mar. Ecol. Prog. Ser.* 338, 131–143. <https://doi.org/10.3354/meps338131>

718 Richard, M., Archambault, P., Thouzeau, G., Desrosiers, G., 2006. Influence of suspended mussel

719 lines on the biogeochemical fluxes in adjacent water in the Îles-de-la-Madeleine (Quebec ,  
720 Canada). *Can. J. Fish. Aquat. Sci.* 63, 1198–1213. <https://doi.org/10.1139/F06-030>

721 Richard, M., Archambault, P., Thouzeau, G., McKindsey, C.W., Desrosiers, G., 2007b. Influence of  
722 suspended scallop cages and mussel lines on pelagic and benthic biogeochemical fluxes in  
723 Havre-aux-Maisons Lagoon, Îles-de-la-Madeleine (Quebec, . *Can. J. Fish. Aquat. Sci.* 1505,  
724 1491–1505. <https://doi.org/10.1139/F07-116>

725 Souchu, P., Mazouni, N., Juge, C., Dagault, F., Deslouspaoli, J., 1998. Relations milieu-ressources:  
726 impact de la conchyliculture sur un environnement lagunaire méditerranéen (Thau). *Oceanol.*  
727 *Acta* 21, 831–843. [https://doi.org/10.1016/S0399-1784\(99\)80010-3](https://doi.org/10.1016/S0399-1784(99)80010-3)

728 Souchu, P., Vaquer, A., Collos, Y., Landrein, S., Deslous-Paoli, J., Bibent, B., 2001. Influence of  
729 shellfish farming activities on the biogeochemical composition of the water column in Thau  
730 lagoon. *Mar. Ecol. Prog. Ser.* 218, 141–152.

731 Thouzeau, G., Grall, J., Clavier, J., Chauvaud, L., Jean, F., Leynaert, A., ni Longphuiert, S., Amice, E.,  
732 Amouroux, D., 2007. Spatial and temporal variability of benthic biogeochemical fluxes  
733 associated with macrophytic and macrofaunal distributions in the Thau lagoon (France). *Estuar.*  
734 *Coast. Shelf Sci.* 72, 432–446. <https://doi.org/10.1016/j.ecss.2006.11.028>

735 Trottet, A., Leboulanger, C., Vidussi, F., Pete, R., Bouvy, M., Fouilland, E., 2016. Heterotrophic  
736 Bacteria Show Weak Competition for Nitrogen in Mediterranean Coastal Waters (Thau Lagoon)  
737 in Autumn. *Microb. Ecol.* 71, 304–314. <https://doi.org/10.1007/s00248-015-0658-8>

738 Ubertini, M., Lagarde, F., Mortreux, S., Le Gall, P., Chiantella, C., Fiandrino, A., Bernard, I.,  
739 Pouvreau, S., Roque d’Orbcastel, E., 2017. Gametogenesis, spawning behavior and larval  
740 abundance of the Pacific oyster *Crassostrea gigas* in the Thau lagoon: Evidence of an  
741 environment-dependent strategy. *Aquaculture* 473, 51-61  
742 <https://doi.org/10.1016/j.aquaculture.2017.01.025>

743 Underwood, A.J. 1997. Experiments in ecology: their logical design and interpretation using analysis  
744 of variance. Cambridge University Press, Cambridge, UK. 499p.

745 Vanaverbeke, J., Arbizu, P.M., Dahms, H.U., Schminke, H.K., 1997. The metazoan meiobenthos  
746 along a depth gradient in the Arctic Laptev Sea with special attention to nematode communities.  
747 *Polar Biol.* 18, 391–401. <https://doi.org/10.1007/s003000050205>

748 Warwick, R.M., Price, R., 1979. Ecological and metabolic studies on free-living nematodes from an  
749 estuarine mud-flat. *Estuar. Coast. Mar. Sci.* 9(3), 257-271. [https://doi.org/10.1016/0302-3524\(79\)90039-2](https://doi.org/10.1016/0302-3524(79)90039-2)

750

751 Wieser, W., 1960. Benthic studies in Buzzards Bay II. The meiofauna. *Limnol. Oceanogr.* 5, 121–137.  
752 <https://doi.org/10.4319/lo.1960.5.2.0121>

753 Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2005. Mixed Effects Models and  
754 Extensions in Ecology with R, Public Health. <https://doi.org/10.1016/B978-0-12-387667-6.00013-0>

755