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

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

5

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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

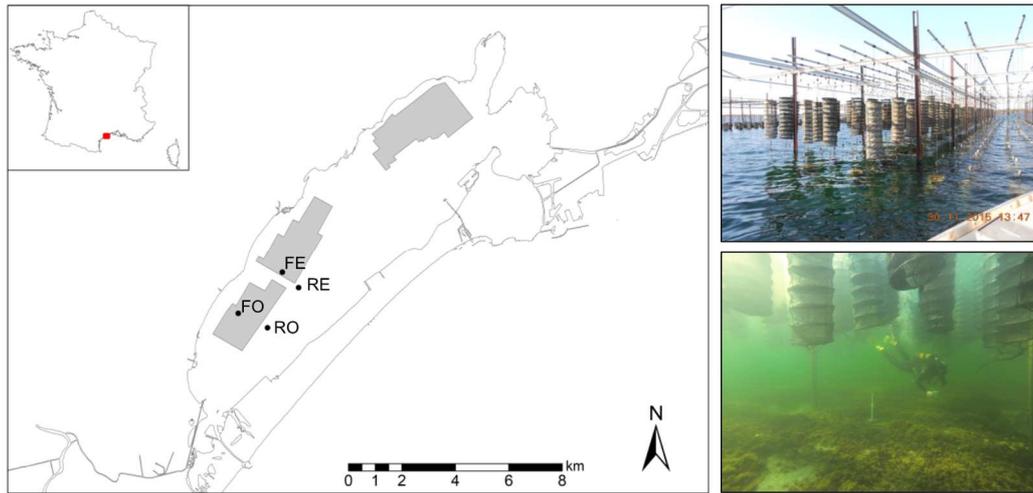
107 **2. Materials and Methods**

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.

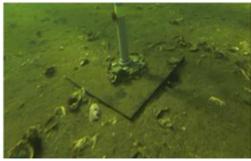
120 Water column parameters, sedimentation rates, sediment characteristics, the biomass of benthic
121 organisms (macrophytes, macrofauna and meiofauna) and benthic fluxes were measured on
122 three occasions in 2015 (Sept. 29–Oct. 2; October 28–Nov 4 and Dec 1–Dec 4, hereafter
123 referred to as October; 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 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	-	++	+	+++

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 (phea) 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 (PO₄), silicates (Si(OH)₄) and nitrites (NO₂) + nitrates (NO₃) (hereafter NO_x), and a
158 fluorometric detection (from JASCO, FP-2020plus, France) for ammonium (NH₄).

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 mg m^{-2}
171 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 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**

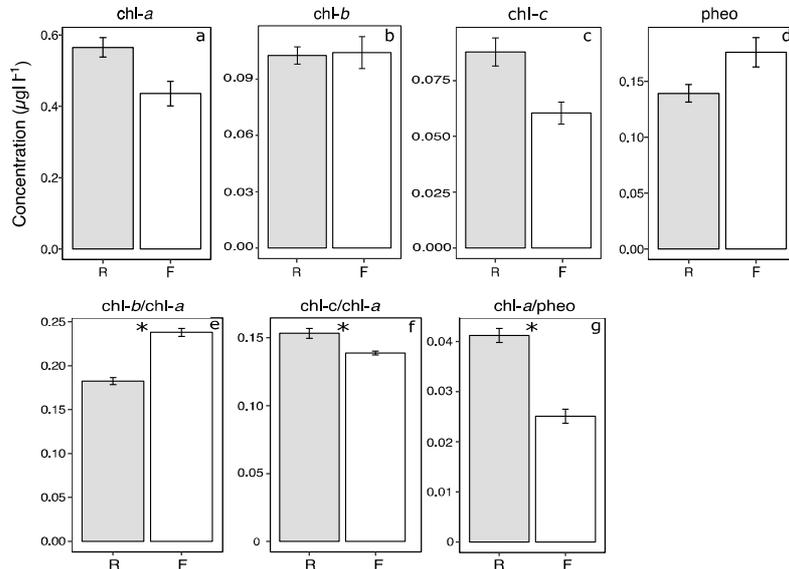
225 **3.1. Water-column parameters**

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 cell L^{-1} at the reference site in October vs $10.7 \cdot 10^3$ 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

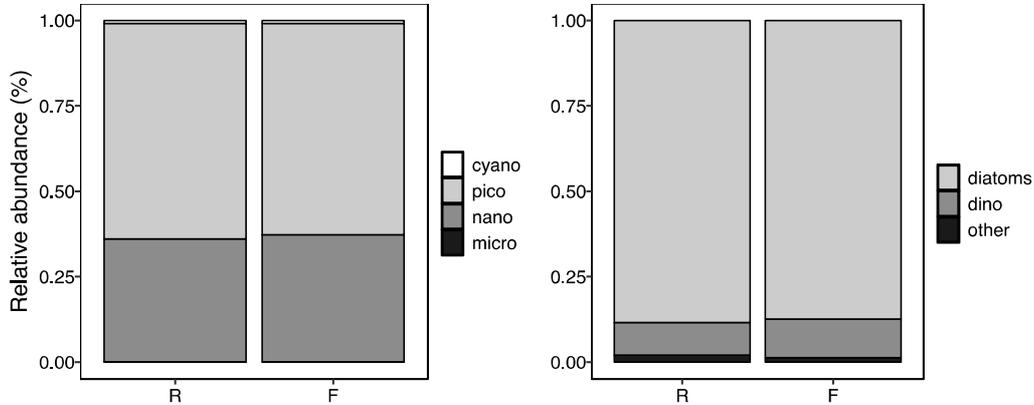
250 **Table 2.** Mean (\pm SE) abundance of **Cyanobacteria**, **Picophytoplankton**, **Nanophytoplankton** (10^6 cell
 251 L^{-1}) and **Microphytoplankton** (10^3 cell L^{-1}) at the farm and reference treatments.

		Reference	Farm	L-ratio	<i>p</i> -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

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 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, PO_4 and NO_x
 269 concentrations and DIN: 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. NH_4 : ammonium, NO_x : nitrates + nitrites, 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
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

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 (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 NH_4^+ (mean = $14.4 \pm 4.4 \mu\text{mol m}^{-2}$
 296 h^{-1}) or NO_x (mean = $2.1 \pm 0.8 \mu\text{mol m}^{-2} \text{h}^{-1}$) (Table 5). Negative values of 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. 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 NH_4^+ and 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 PO_4 fluxes which were higher at the reference sites than at the farm sites (Table 5). Si and 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 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 O_2 fluxes in $\text{mg h}^{-1} \text{m}^{-2}$. *Statistical significance of Treatment

	Reference	Farm	L-ratio	<i>p</i> -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

312

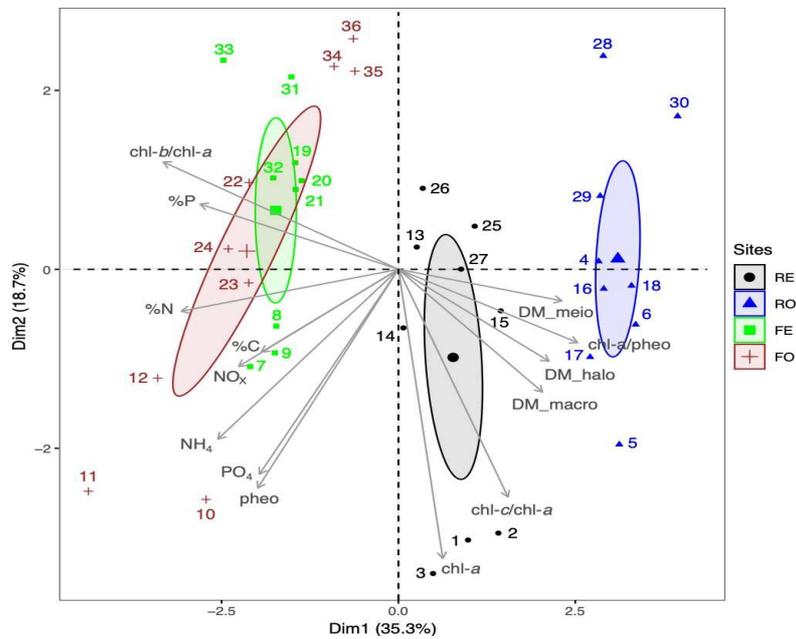
313

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_x,
 333 NH₄, PO₄: 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 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⁻¹ year⁻¹ of nitrogen and about 3 000 kg ha⁻¹ year⁻¹ 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

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496

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