First simultaneous assessment of macro- and meiobenthic community response to juvenile shellfish culture in a Mediterranean coastal lagoon (Thau, France)

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Abstract :

Shellfish aquaculture has the potential to alter benthic assemblage composition with subsequent modifications of ecosystem functioning. While the impacts of aquaculture on the taxonomic structure of macro- and — to a lesser extent — meiofauna, have been widely studied, the functional changes of these communities remain relatively unknown. The recent development of biological trait analysis (BTA) has made it possible to produce information about how ecosystem functioning could change across specific terrestrial or aquatic system. In the present study, we used a BTA in parallel with standard taxonomic analysis to evaluate how well the two approaches detected the potential influence of juvenile oyster culture on the benthic community in the French Mediterranean Thau Lagoon. Two sites were sampled under farm structures and compared with two reference sites beyond the influence of farming. This study is the first detailed parallel description of macro- and meiofauna (nematodes). A total of 118 and 41 taxa were determined for macrofauna and nematodes respectively. Some taxa were more abundant or exclusively observed under farm structures such as *Chaetozone gibber* and *Neanthes acuminata* for macrofauna and *Daptonema fallax* and *Anticoma eberthi* for nematodes.

Overall, our results indicate that biological traits and functional indices both detected the impact of shellfish culture on benthic assemblages, whereas macrofauna taxonomic indices revealed no difference. Our results thus suggest that trophic and ecological groups are particularly good indicators of the effects of shellfish culture. This study confirms the relevance of the functional approach, and more generally of multi-index approaches, to detect the influence of aquaculture on benthic communities. Further work is required to test multiple traits in different regions and under different systems, but this work paves the way for environmental impact assessment using a trait based approach.

Highlights

► Aquaculture influence on benthic functional diversity is described. ► Taxonomic approach was used in parallel with biological trait analysis. ► This is the first detailed description of macrofauna and nematodes in Thau lagoon. ► Trophic and ecological groups are good indicators of the effects of shellfish culture. ► Environmental impact assessment of aquaculture using a functional approach is proposed.

1. Introduction

Coastal ecosystems are facing drastic environmental changes due to many human pressures that threat the integrity of communities and may have major impacts on ecosystem functioning and its ability to sustain ecosystem services (Halpern et al. 2008, Cardinale et al. 2012). In shallow costal ecosystems, benthic communities play a central ecological role in benthic-pelagic coupling through their feeding and movements that promote nutrient and oxygen exchange throughout the sediment layer. Thus, any alteration of these communities may have implications for ecosystem structure and performance (Thrush et al. 2006, Kristensen et al. 2014) and understanding how they respond to disturbance is crucial to predict future changes and help maintain and improve the quality of marine ecosystems. To date, most studies have focused on the response of benthic macrofaunal communities to disturbances (Pratt et al. 2015,

57   Dimitriou et al. 2017, Ellis et al. 2017). Recently, interest has been growing in the study of

58   meiofauna, since it has been shown that these organisms may modulate biological interactions

59   in the sediment layer (Bonaglia et al. 2014, Lacoste et al. 2018a) and play a significant role in

60   benthic ecosystem processes and services (Schratzberger and Ingels 2017). Due to their

61   widespread distribution, short life and reproductive cycles, high abundance and diversity,

62   meiofauna are thus beginning to be used as biological indicators for the assessment and

63   monitoring of aquatic ecosystems (Semprucci et al. 2015, Zeppilli et al. 2015, Bianchelli et al.

64   2018).

65   Bivalve aquaculture has various environmental impacts (McKindsey et al. 2011, Brenner et al.

66   2014) including the accumulation of biodeposits on the bottom under culture sites that may

67   results in local organic enrichment. Such disturbance typically affect benthic communities

68   according to the Pearson and Rosenberg (1978) model of organic enrichment with a progressive

69   increase in the abundance of enrichment-tolerant species in the vicinity of farms, whereas

70   communities directly under the farming structures are dominated by a few opportunistic species

71   (Callier et al. 2007, 2009, McKindsey et al. 2011). Several studies have reported lower richness

72   and/or abundance of organisms, as well as differential community composition of macrofauna

73   (Christensen et al. 2003, Harstein and Rowden 2004, Lacoste et al. 2018b), or meiofauna (Mirto

74   et al. 2000, Mahmoudi et al. 2008, Netto and Valgas 2010) under farming structures compared

75   with reference sites. One notable feature of these studies is the focus on structural attributes of

76   the benthos (e.g. taxonomic composition, number of species) whereas functional changes are

77   disregarded. Only a few studies have used a functional approach to investigate the impact of

78   interactions between the environment and fish (Papageorgiou et al. 2009, Dimitriadis and

79   Koutsoubas 2011), or mussel (Lacoste et al. 2019) aquaculture.

80   Growing awareness that changes in biodiversity may modify ecosystem functioning (e.g.

81   Loreau et al. 2001, Naeem et al. 2009) has led to the recognition that impacts on the functional

82   diversity of benthic assemblages, as opposed to their structural features, should be better

83   quantified (e.g. Strong et al. 2015, Cernansky 2017). Due to functional redundancies in

84   communities, observed changes in species composition may be buffered (Walker 1992,

85   Snelgrove 1998) such that structural impacts on benthic assemblages are not always matched

86   by their functional counterparts (Bolam 2012). Otherwise, trophic pathways (indicator of

87   ecosystem functioning) may be impacted without apparent changes of the overall benthic

88   diversity (Dubois et al. 2007). Thus, functional-based approaches, including biological trait

89   analysis and the computation of functional diversity (FD) indices, provide useful proxies to

90   investigate the effect of human disturbances at the ecosystem-functioning level (Mouillot et al.

91   2006, 2013) and to anticipate the potential loss of ecosystem services associated with

92   biodiversity erosion (Cardinale et al. 2012). Moreover, this approach can be used to compare

93   communities that have no species in common but do share traits.

94   Thau Lagoon is a Mediterranean marine ecosystem of notable economic importance due to the

95   many ecosystem services it supports, in particular, the significant oyster farming activity (about

96   7 000 tons per year, near 10% of the national production). A few authors have described

97   changes in macrofaunal communities in relation to oyster culture (Mazouni et al. 1996, Duport

98   et al. 2007, Thouzeau et al. 2007), and one study showed spatial variation of meiofauna

99   abundance (Guelorget et al. 1994). But to date, no list has been published of meiofauna

100   assemblages in the lagoon, even though these communities may respond more rapidly to

101   biodeposition than macrofauna do and could be good indicators of lagoon ecological status.

102   Potential associated functional changes in macro- and meiofauna remain unknown. Thus, in a

103   global context of increasing intensity and frequency of climatic and anthropogenic

104   disturbances, there is a need to describe and predict changes in functional community structure

105   to anticipate potential losses of ecosystem services associated with biodiversity modifications

106   in coastal areas such as Thau Lagoon.

107   The aims of this study were therefore 1/ to document macrobenthic and meiobenthic (nematode)

108   communities in relation to oyster culture in Thau Lagoon and 2/ to compare the response of

109   some selected taxonomic and functional attributes to disturbances caused by shellfish culture

110   for macro- and meiofauna assemblages. To our knowledge, this is the first time the impact of

111   bivalve aquaculture on macro- and meiobenthic communities has been studied simultaneously

112   using a traditional taxonomic based approach coupled with a functional approach.

113

114   **2. Materials and Methods**

115   *2.1. Study area and sampling strategy*

116   Thau Lagoon is a French Mediterranean semi-enclosed shallow lagoon (mean depth 4 m)

117   covering an area of 68 km^2 (Fig. 1). It is the most important French Mediterranean shellfish

118   farming zone with an annual production of about 7 330 tons of oysters in 2016 (DDTM34 2017)

119   reared on spatially organized structures, called "tables". Each table is 50×12 m long and

120   supports between 800 and 1200 suspended nets or ropes holding juvenile or adult oysters.

121   Sixteen tables form a 'block' and the blocks are separated from each other by a distance of

122   150m. Annual variations in water temperature and salinity in the lagoon are large, varying from

123   3 °C to 30 °C and from 33 to 40 PSU respectively (Messiaen et al. 2019).

124   The study was conducted in a dedicated shellfish-farming zone in the western part of the lagoon

125   (Fig. 1). As a part of a research program (see Richard et al. 2017, 2019), the study focused on

126   juvenile production, whose impact on ecosystem has never previously been evaluated in Thau

127   Lagoon. Samples were collected at two sites in the farmed zone directly below juvenile tables

128   (TO and TE sites) and at two additional sites located at a distance of 200 m outside the farming

129   zone (CO and CE sites) (Fig. 1). Some characteristics of the four sites are given in Table 1, the

130   main difference being algal cover (*Halopytis* sp.) which was greater at TO and CO sites.

131   Sampling was done during three surveys in 2015 (September 29–October 2; October 28–

132   November 4 and December 1–December 4, hereafter referred to as October, November and

133   December) covering the whole juvenile production period. Each date, three replicate sediment

134   cores (9 cm diameter, 10 cm depth) were randomly collected by scuba divers at each site. The

135   samples were preserved in 10% buffered formalin and later transferred into 70% alcohol.
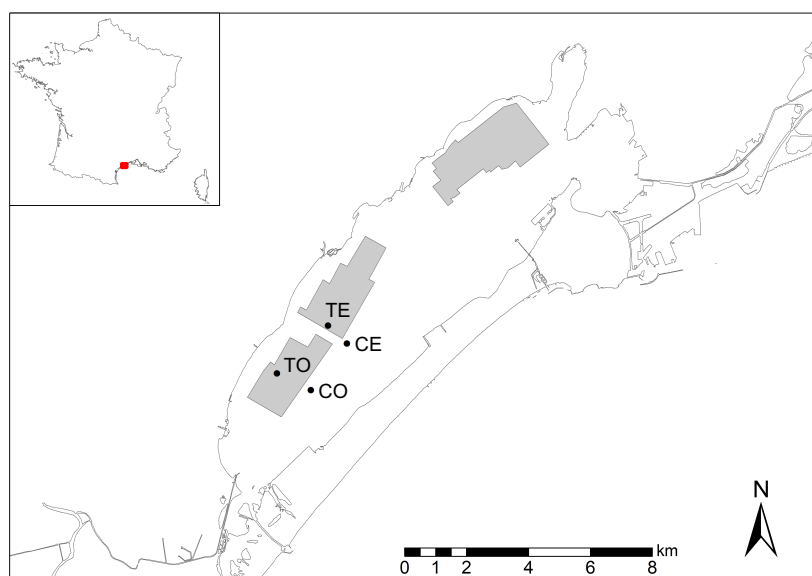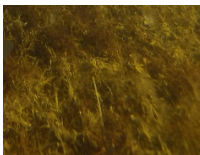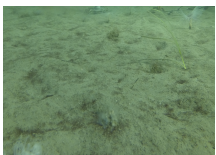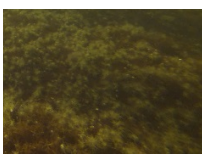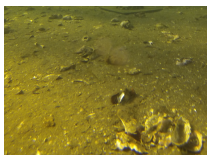

136
137   Figure 1. Location of the four sampling sites in Thau lagoon. The two T sites (TE & TO) were directly
138   under the tables and the two reference sites (CE & CO) were located at a distance of 200 m from the
139   shellfish farming area.
140

141
142   Table 1. Summary description of the 4 sampled sites

	Reference sites		Farm sites	
	CO	**CE**	**TO**	**TE**
Depth	3.7 m	4.2 m	3.6 m	4.2 m
Bottom observation				
Culture system	-	-	Juvenile oysters ca. 1.1 t per table*	Juvenile oysters ca. 1.4 t per table

143   *Calculation from initial measurements on a sub-sample

144

145   *2.2. Abundance and species richness*

146   Back to the laboratory, the content of each core sample was passed through a 1mm mesh sieve.

147   Macrofauna in the > 1mm fraction was sorted and identified to the lowest taxonomic resolution

148   possible, up to species in most cases. The < 1 mm fraction was decanted over a 40-μm sieve.

149   All nematodes were sorted under a stereo-microscope, transferred to glycerol through a series

150   of ethanol-glycerine solutions, mounted on glycerine slides (Somerfield et al. 1994) and

151   identified to the lowest taxonomic level possible using the generic keys of Platt and Warwick

152   (1983, 1988) and Warwick et al. (1998) and species descriptions in the literature.

153   Abundance (N) and species richness (S) of macrofauna and nematodes were characterized. The

154   Shannon-Wiener diversity index (H') and Pielou's eveness (J') were calculated for each site.

155   Taxa that were observed only once were removed from analyses (Clarke and Warwick 2001);

156   all results are expressed per core (63 cm^2).

157

158   *2.3. Functional analysis*

159   The common step in all functional ecology studies is to characterize the functional strategy of

160   each species of interest by identifying a relevant combination of functional traits (Violle et al.

161   2007). There is currently no consensus on the methodology for selecting the most appropriate

162   traits for a given study (Marchini et al. 2008). As the aim of the present study was to use traits

163   as a proxy for assemblage response to shellfish culture, we decided to focus on the biological

164   traits and ecological groups of macrofauna that have already been shown to be good indicators

165   of organic enrichment in this specific context (Borja et al. 2000, Lacoste et al. 2019). To our

166   knowledge, this is the first study to simultaneously evaluate the functional response of both

167   macrofauna and meiofauna (nematodes) to bivalve aquaculture. We thus selected nematodes

168   biological traits that have been shown to respond to organic enrichment (Alves et al. 2013,

169   Kandratavicius et al. 2018), with the assumption that they are comparable with those of

170   macrofauna. Thus, selected traits for both assemblages were related to trophic guilds, ecological

171   strategy, and interaction with sediments (Table 2). Each selected trait was subdivided into

172   several modalities (Table 2). Organisms identified up to species level were classified in

173 functional groups based on existing literature (e.g. Wieser 1953, Thistle et al. 1995, Queiros et

174 al. 2013, WoRMS Editorial Board 2020). When reliable information was not available, data

175 from the closest phylogenetic neighbor were used or the taxon was excluded from subsequent

176 analysis. All nematodes and 44 macrofaunal (accounting for 91% of all individuals identified)

177 taxa were thus retained for functional analysis. The subsequent 'trait per taxon' matrix was

178 combined with the 'taxa per sample' matrix (abundance) to create a 'trait per sample' matrix.

179 The relative abundance of the functional groups was then calculated by summing abundance

180 across all taxa allocated to each functional group at a given site per sampling date. Finally, the

181 two matrices were used to calculate functional indices (functional richness: FRic, functional

182 eveness: FEve and functional dispersion: FDis) as outlined by Villéger et al. (2008) and

183 Laliberté and Legendre (2015) for both macrofauna and nematodes. Using only categorical

184 traits, FRic was defined as the number of unique trait combinations (equivalent to singular

185 species).

186 Although its results are ambiguous (Semprucci et al. 2015), the Index of Trophic Diversity

187 (ITD, Heip et al. 1985) is popular and widely used for nematodes. We thus calculated ITD for

188 both nematodes and macrofauna, using their respective trophic guilds, with the aim of

189 evaluating its consistency in the case of disturbances caused by shellfish culture. The index was

190 calculated following Heip et al. (1985): $ITD = \sum \theta^2$, where θ is the percentage contribution of

191 each feeding type. Thus, a low ITD value corresponds to high trophic diversity (each group

192 accounting for the same percentage).

193

194

Table 2. List of biological traits and respective categories selected for macrofauna and nematodes.

	Category	Level	Code
Macrofauna	Feeding group	Filter/suspension-feeder	F
		Grazer/Detritivorous	Gr
		Deposit-feeder	D
		Subsurface deposit-feeder	SubD
		Carnivorous	C
	Ecological group	Very sensitive	I
		Tolerant	II
		Indifferent	III
		2^d-order opportunistic	IV
		1st-order opportunistic	V
	Mobility	Fixed in a tube	I
		Limited movement	II
		Slow movement	III
		Free movement (burrow system)	IV
	Reworking type	Epifauna	E
		Surficial modifier	S
		Biodiffusers	B
		Upward conveyors	UC
		Upward/downward conveyors	UDC
Nematodes	Feeding groups	Selective deposit-feeder	1A
		Non selective deposit-feeder	1B
		Epigrowth feeder	2A
		Predators/omnivores	2B
	Cp-score	Opportunistics	2
		to	3
			4
		Persisters	5
	Adult shape	Long/thin	Lt
		Slender	Sl
	Amphid shape	Circular	Cr
		Indistinct	Id
		Pocket-like	Pk
		Rounded or elongate loop	REL
		Spiral	Sp

2.4. Statistical analysis

The effect of Date × Condition (Farm vs Reference) on univariate measurements of benthic communities (taxonomic and functional indices) was tested using linear mixed effect models (lMEM; modelling normally distributed responses) with site as a random factor nested in

202 Condition. The effect of factors was considered as significant when the null vs main effect

203 models (using maximum likelihood estimation) differed significantly (ANOVA, $p < 0.05$).

204 Assumptions were assessed visually by examination of residual plots (Quinn and Keough 2002,

205 Bates et al. 2015). All mixed effect models were constructed in R using *lme4* (Bates et al. 2015)

206 and Tukey's HSD tests as implemented in library *emmeans* (Lenth 2019) were used as post hoc

207 tests to compare conditions at each date if lMEM showed a significant effect of the interaction.

208 Variation in multivariate assemblage structure (abundance data) was visualized using model-

209 based ordination (generalized linear latent variable model) with the R package *gllvm* (Niku et

210 al. 2019) and evaluated using multivariate linear modelling with the R package *mvabund* (Wang

211 et al. 2012), assuming a negative binomial distribution. Species that contributed significantly

212 to differences among conditions were identified using the *p.uni* argument that allows univariate

213 'species-by-species' comparisons in *mvabund*. Variation in assemblage functional composition

214 between dates and conditions ('traits by site' matrix) was also compared using the same

215 multivariate approach.

216

217 **3. Results**

218 *3.1. Taxonomic indices*

219 A total of 2 679 organisms belonging to 118 taxa were identified in the macrofaunal community

220 in this study. Annelida (36.7%) and Mollusca (35.5%) were the most widely represented group

221 followed Arthropoda (25.8%). The mollusk *Musculus subpictus* alone represented 24.2% of the

222 total sample, whereas we found a single individual of 42 taxa, which were subsequently

223 removed from analyses.

224 A total of 778 nematodes belonging to 41 taxa were identified. Two taxa, *Paracomesma dubium*

225 and *Spirina gerlachi*, represented 34% of the organisms recorded and 6 taxa were represented

226 by a single individual. As this is the first time the nematodes have been described for Thau

227 Lagoon, a complete list of taxa is provided in Table S1.

228 Table 3 lists the values of each index averaged per Condition (for all sampling dates). Statistical

229 results are those of the Condition effect (pairwise comparison), except in case of a significant

230 effect of Date × Condition interaction. Although there was a trend of more taxa and greater

231 abundance of macrofauna at reference sites, the Condition effect was not statistically significant

232 (Table 3). The effect of Condition on the diversity indices was neither significant (Table 3).

233 A similar pattern was observed for nematodes, with the greatest abundance and richness values

234 observed at reference sites (Table 3). lMEM revealed a significant effect of Date × Condition

235 on S, H' and J', with contrasts indicating higher values of S and H' in December at reference

236 sites (S = 11 ± 3 and H = 2.1 ± 0.1) compared to farm sites (S = 4 ± 1 and H = 1.3 ± 0.2).

237

238 Table 3. Macrofauna and nematodes characteristics (mean ± SE, n = 3) under juvenile oyster tables
239 (Farm sites) and beyond the farming zone (Reference sites). Abundance (number of individuals, N) and
240 richness (number of taxa, S), Shannon diversity (H') and Pielou's eveness (J'). Statistical effect of
241 factors (Fc) Condition (Cd: Farm *vs* Reference) or Date × Condition interaction (D × Cd). *Significant*
242 *difference at the 0.05 level.*

		Farm	Reference	Fc	df	L-ratio	*p*
Macrofauna	**N**	40±8	106±16	Cd	3	5.592	0.133
	S	13±1	21±2	Cd	3	2.941	0.401
	H'	2.1±0.1	2.3±0.1	Cd	3	2.740	0.480
	J'	0.8±0.1	0.8±0.1	Cd	3	5.791	0.122
Meiofauna	**N**	12±1	31±5	Cd	3	5.962	0.113
	S	6±1	10±1	D×Cd	5	12.356	*0.030**
	H'	1.5±0.1	1.9±0.1	D×Cd	5	20.704	*<0.001**
	J'	0.9±0.1	0.8±0.1	D×Cd	5	12.538	*0.028**

243

244 *3.2. Community structure*

245 The model-based projection of macrofauna community structure (Fig. 2A) showed a clear

246 distinction between conditions. The multivariate test confirmed the significant difference

247 between communities at the farm *vs* at the reference sites (Table 4). Univariate comparisons

248   were significant for five taxa; three of which were more abundant at the farm sites (*Chaetozone*

249   *gibber*, *Notomastus sp*. and *Neanthes acuminata*) and two that were observed only at reference

250   sites (*Phascolion strombus* and *Pusillina lineolata*).

251   The ordination based on nematodes abundance (Fig. 2B) also showed a distinction between

252   communities from the two conditions (Farm *vs* Reference), confirmed by the significance of

253   the multivariate test (Table 4). Differences between sites within conditions were less clear

254   relative to macrofauna as there was a major overlap of symbols representing samples from

255   different sites (especially TO and TE) in the ordination graph (Fig. 2B). Nematode assemblages

256   also varied among dates (Table 4). Pairwise comparisons indicated that assemblages differed

257   significantly between October and November (*p = 0.041*). Among species that best explained

258   variation among sites, *Paracomesoma dubium*, *Anticomopsis longicaudata* and *Spirina*

259   *gerlachi*, were more abundant at the two reference sites. Conversely, one taxon was more

260   abundant under farming structures than at the reference sites (*Daptonema fallax*) and three taxa

261   were present only at the two farm sites (*Anticoma eberthi*, *Eurystomina* sp. and

262   *Metalinhomoeus* sp.).

263
264   Table 4. Results of the GLM testing the effect of Date, Condition and their interaction on macrofauna
265   and nematode assemblages composition (abundance). *Significant difference at the 0.05 level*.

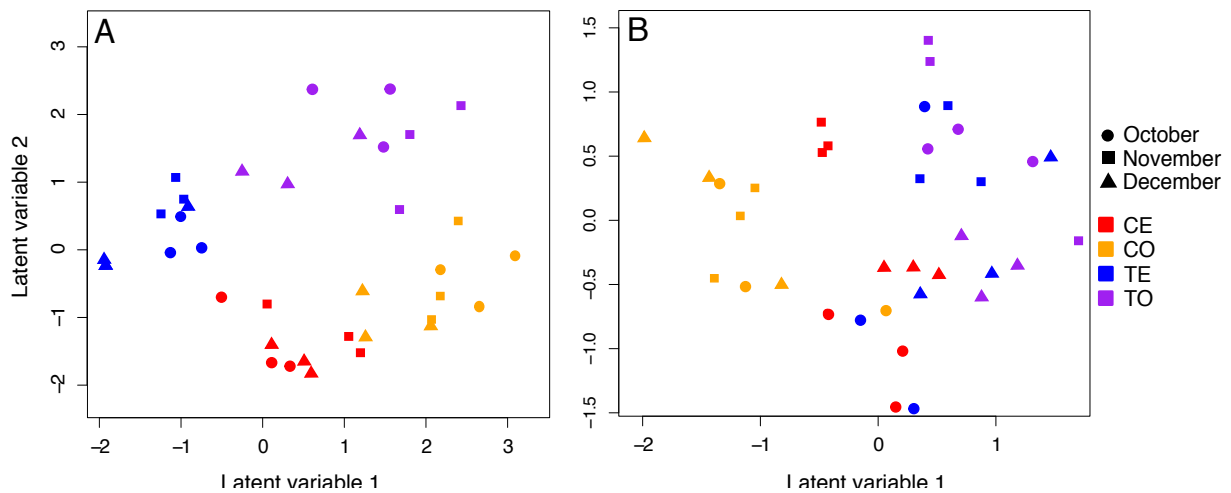|		df	Dev.	*p*
Macrofauna	Condition	1	341.3	*0.001**
	Date	2	214.7	0.109
	Condition × Date	2	121.2	0.089
Meiofauna	Condition	1	141.8	*0.001**
	Date	2	125.6	*0.019**
	Condition × Date	2	78.1	0.055

266
267
268

Figure 2. Model based biplot (unconstrained ordination) of abundance data for (A) macrofauna and (B) nematodes. Samples (cores) are shown in colors indexed by Site and Date (symbols).

3.3. Functional analysis

3.3.1 Macrofauna functional composition

Figure 3 shows the relative abundance of each biological trait. Although there was some variability within conditions and between dates, macrofauna at the reference sites was mainly characterized by filter-feeder organisms (ca 50%: Fig. 3), which are mostly sensitive to organic enrichment (ecological group I, Fig. 3). The proportion of filter-feeders was lower in the farming zone, whereas the proportion of deposit feeders and grazers increased (Fig. 3). These communities were dominated by animals that are mostly tolerant to organic enrichment or first-order opportunistic (ecological groups III and IV: Fig. 3). Mobility and reworking types did not allow us to clearly distinguish farming and reference sites (Fig. 3), except that upward-downward conveyors (UC and UDC: Fig. 3) appeared to be more abundant at the farm sites. The high abundance of surficial reworkers (S) at site TO (Fig. 3) was mainly due to the presence of many Arthropoda, also belonging to grazers (Gr) and ecological group I, and the the bivalve *Musculus subpictus*. These taxa were mainly found in association with the algae *Halopithys* sp. The GLM indicated a significant effect of Condition on the functional composition of

13

288   assemblage (df = 1, Dev. = 225.45, $p < 0.001$), with no significant effect of the interaction

289   (Date × Condition, df = 2, Dev. = 48.39, $p = 0.393$).
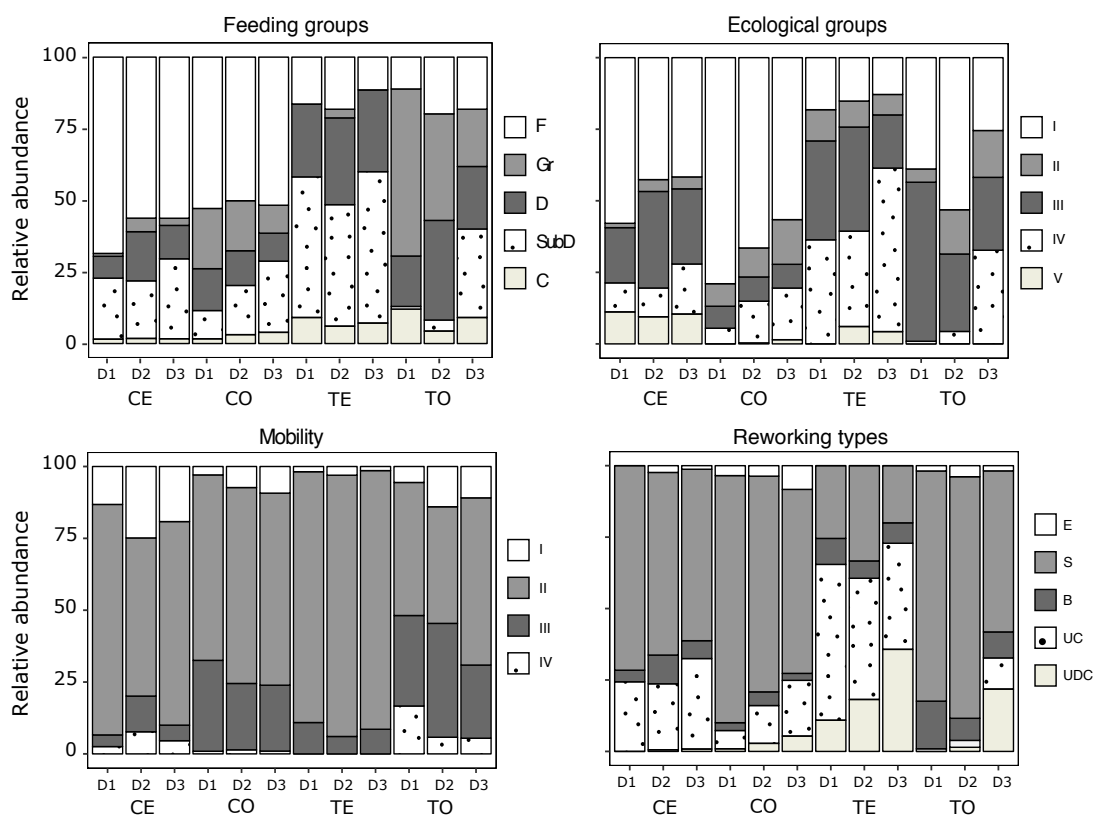

290

291   Figure 3. Relative abundance of the different macrofauna functional groups at the farm sites (TE, TO)
292   and at the reference sites (CE, CO) on the three sampling dates (D1: October, D2: November, D3:
293   December). Feeding groups: F: filter-feeder, Gr: grazer, D: deposit-feeder, SubD: subsurface deposit-
294   feeder, C: carnivorous; Ecological groups from very sensitive (I) to opportunistic (V) ; Mobility from
295   fixed (I) to burrower (IV) ; Reworking types: E: epifauna, S: surficial modifier, B: biodiffuser, UC:
296   upward conveyor, UDC: up-/downward conveyor.

297

298

299   *3.3.2. Nematode functional composition*

300   The most representative feeding group at reference sites was epigrowth feeders (2A) whereas

301   the percentage of detritivores (1B) was increased at the farm sites (Fig. 4). Overall, the

302   community at the two reference sites was dominated by taxa with a cp score of 3 (Fig. 4) and

303   amphids with a spiral shape (Sp: Fig. 4). At the two farm sites, the percentage of opportunistic

304   nematodes (cp score of 2: Fig. 4) with circular amphid (Cr) increased (Fig. 4). The adult shape

305   did not clearly differ betweenfarming zone sites and those outside the farming zone (Fig. 4).

306   The high percentage of long/thin adults (lt) at site TO in September was mainly due to the

307 presence of *Metalinhomoeus longiseta*. The GLM indicated a significant effect of Condition on

308 assemblage functional composition (df = 1, Dev. = 154.49, $p < 0.001$), with no significant

309 effect of the interaction (Date × Condition, df = 2, Dev. = 48.22, p = 0.212).
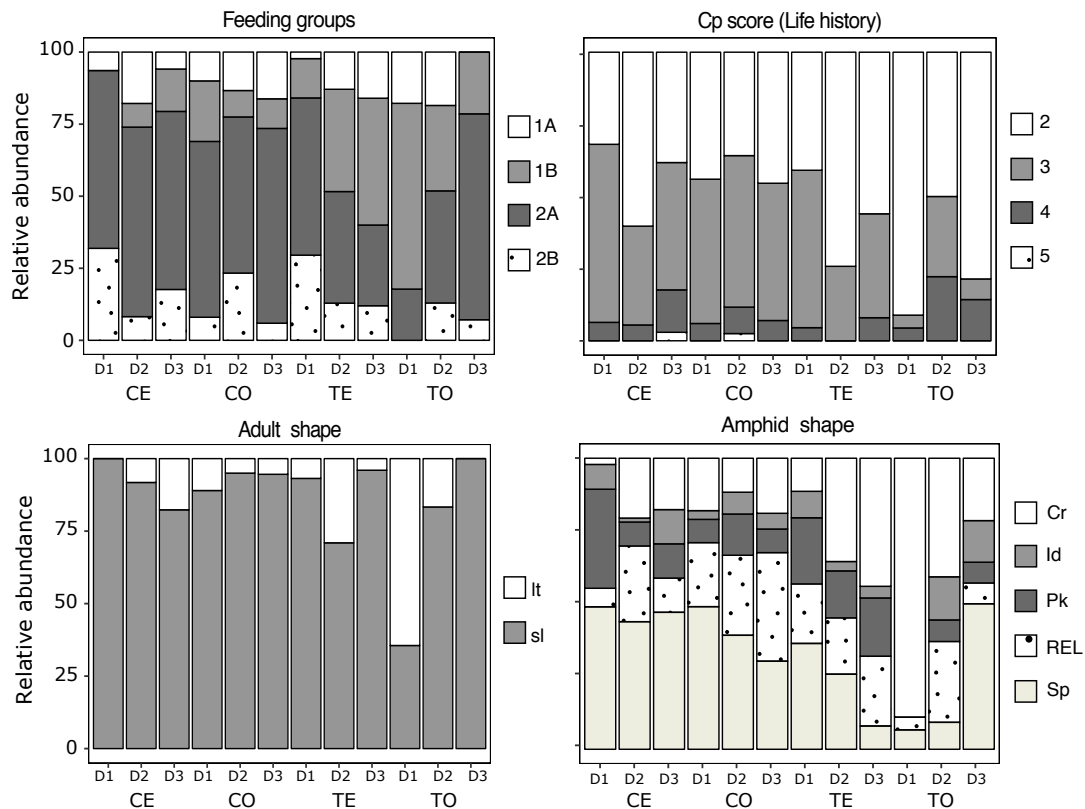
310

311
312 Figure 4. Relative abundance of the different nematode functional groups at the farm sites (TE, TO) and
313 at the reference sites (CE, CO) on the three sampling dates (D1: October, D2: November, D3:
314 December). Feeding groups: 1A: selective or 1B: non selective deposit-feeder, 2A: epigrowth feeder,
315 2B: predators; Life history: opportunistic (2) to persister (5); Adult shape: lt: long/thin, sl: slender ;
316 Amphid shape: Cr: circular, Id: indistinct, Pk: pocket-like, REL: rounded or elongate, Sp: spiral.
317

318 *3.3.2. Functional indices*

319 The lowest FRic values of both macrofauna and nematodes were recorded under the tables (TE

320 and TO) (Table 5). The Date × Condition interaction had a significant effect for nematodes,

321 with contrasts indicating significantly higher FRic values at reference sites in December

322 (9.2 ± 1.6) compared with the farm sites (4 ± 0.6). Macrofauna FEve was higher under the

323 tables in November (0.72 ± 0.06) and December (0.72 ± 0.04) than at the reference sites

324 (0.57 ± 0.04 and 0.56 ± 0.04 respectively in November and December) whereas no difference

15

325 was found for nematodes. The Date × Condition interaction had a significant effect on

326 nematodes FDis but with no difference between conditions each date.

327 The ITD for macrofauna was significantly lower at the farm sites (Table 5) indicating that these

328 sites presented a higher trophic diversity than did reference sites. For nematodes, the

329 Date × Condition interaction had a significant effect on ITD but no difference was found

330 between conditions at each date.

331

332 Table 5. Macrofauna and nematodes functional characteristics (mean ± SE, n = 3) at sites under the juvenile
333 oyster tables (Farm sites) and outside the farming zone (Reference sites). (FRic: functional richness, FEve:
334 functional evenness, FDis: functional dispersion, ITD: Index of Trophic Diversity). Statistical effect of factors
335 (Fc) Condition (Cd: Farm *vs* Reference) or Date × Condition interaction (D × Cd) *Significant difference at the*
336 *0.05 level*.

		Farm	Reference	Fc	df	L-ratio	*p*
Macrofauna	**FRic**	8±1	12±1	D×Cd	5	10.657	0.05
	FEve	0.7±0.1	0.5±0.1	D×Cd	5	11.805	*<0.05**
	FDis	0.4±0.1	0.4±0.1	Cd	3	1.520	0.677
	ITD	0.4±0.1	0.7±0.1	Cd	3	9.237	*<0.05**
Meiofauna	**FRic**	6±1	9±1	D×Cd	5	12.326	*<0.05**
	FEve	0.7±0.1	0.7±0.1	Cd	3	2.481	0.479
	FDis	0.3±0.1	0.4±0.1	D×Cd	5	13.69	*0.017**
	ITD	0.5±0.1	0.5±0.1	D×Cd	5	13.043	*<0.05**

337

338

339 **4. Discussion**

340 *4.1. First description of nematodes in Thau Lagoon*

341 With the exception of marine benthic ecosystems in Italy and Tunisia (Semprucci et al. 2008,

342 Boufahja et l. 2014), there is a serious gap in knowledge concerning the Mediterranean

343 meiofauna. This is particularly true for coastal lagoons, for which the spatial and temporal

344 distribution of meiofauna, including free-living nematodes, is not well documented or is

345 underestimated, despite they often greatly contribute to the biodiversity of coastal areas

346 (Balsamo et al. 2012). Nematodes can provide critical information on the functioning of

347 ecosystems and have already been proposed as potential indicators of anthropogenic

16

348   disturbance (Schratzberger et al. 2004, Danovaro et al. 2008, Moreno et al. 2011, Pusceddu et

349   al. 2011). Our study is the first to provide a complete list of nematode taxa observed in the

350   French Mediterranean Thau lagoon. Compared to the few studies that have documented other

351   Mediterranean coastal areas, the number of taxa reported here from Thau Lagoon is similar but

352   abundances were in the lower range (Mirto et al. 2000, Danovaro et al. 2004, Mahmoudi et al.

353   2008). The community structure showed many similarities with checklists of Italian and

354   Tunisian lagoons, published respectively by Semprucci et al. (2008) and Boufahja et al. (2014).

355   Ten of the common species found in Thau Lagoon have also been found in Italy (e.g. *Anticoma*

356   *eberthi*, *Longicyatholaimus longicaudatus)* and 18 species were recorded in both Thau Lagoon

357   and Tunisia (e.g. *Spirinia gerlachi*, *S. parasitifera*, *Thalassironus britannicus*, for details, see

358   Table S1). These shared records could be linked to common environmental parameters among

359   areas and to water exchanges between the two Mediterranean basins, which make large-scale

360   dispersal between Tunisia, Italy and France possible. The checklist of nematodes resulting from

361   this study could be the basis to further documenting meiobenthic diversity in Mediterranean

362   coastal areas, with the aim to advance our understanding of its spatio-temporal variability.

363

364   *4.2. Response of macrofaunal and nematode assemblages to shellfish culture*

365   Overall, community structure (taxonomic and functional) differed between conditions, with

366   lower abundance and richness (some significant, some not) at farm sites, as expected from

367   previous studies (Mirto et al. 2000, Christensen et al. 2003, Callier et al. 2008). The presence

368   of opportunistic species under the farm tables (e.g. *Neanthes acuminata*, *Prionospio fallax*,

369   *Daptonema* sp.) whose abundance is favored under organically enriched conditions, showed

370   that biodeposition by juvenile oysters impacts the benthic environment below farm structures

371   in the study area. However, the high and similar species evenness values (J) at the farm and

372   reference sites revealed the absence of strongly dominant species that would be expected in an

373　organically enriched environment (Pearson and Rosenberg 1978). The organic enrichment due

374　to the presence of juvenile oysters is likely low compared with that of adult oysters, but the

375　continuous exploitation of the area for farming may have modified community characteristics

376　compared with outside of the farming zone.

377　The results of the analysis of nematodes revealed differences in both univariate indices and

378　community structure at the farm and reference sites. Our results for nematodes are in agreement

379　with the study of Mirto et al. (2000) who reported decreased meiofauna richness and abundance

380　in aquaculture sites relative to reference areas (Mirto et al. 2000). Inversely, a study in Bizerta

381　Lagoon indicated increased nematode abundance at farm sites relative to control sites

382　(Mahmoudi et al. 2008). The latter authors suggested that increased abundance was due

383　to differential tolerance to organic matter, decreased competition, and a subsequent competitive

384　release of more resistant species due to sediment organic enrichment. However, other factors

385　(biotic and abiotic) could also explain the distribution of species since, for example,

386　*Paracomesma dubium* was more abundant at farm sites in the study by Mahmoudi et al. (2008),

387　whereas in our study, we observed a higher abundance at reference sites. Temperature

388　variations may have contributed to explain temporal changes since when significant, the effect

389　of Condition was mostly detected in December.

390　In this study, macrofaunal taxonomic indices failed to detect a significant effect of shellfish

391　culture whereas the multivariate approach did, as already reported in other studies (Grant et al.

392　2012, Lacoste et al. 2018a). Previous studies in Thau Lagoon produced conflicting results on

393　the impact of aquaculture on macrofauna, ranging from low (Mazouni et al. 1996, Duport et al.

394　2007) to severe with a completely defaunated site in a deep shellfish area (Thouzeau et al.

395　2007). These authors highlighted the concomitant role of depth, algal cover and aquaculture in

396　community composition. Our study also suggests that algal cover played an important role, at

397　least for the macrofauna community. Some arthropods, (e.g. *Gammarella* sp., *Cymodoce*

398   *truncata*) were found attached to the algae *Halopithys* sp., so the TO and CO sites had specific

399   assemblages structure due to these taxa.

400   The general trend thus supports the hypothesis that juvenile oysters slightly influenced both

401   macrobenthic and nematode communities, although the variability between sites within

402   conditions may have masked statistical differences in some indicators. Although this may

403   require a labor-intensive sampling effort, it is recommended to sample several farm and

404   reference sites to disentangle the influence of aquaculture on benthic communities, if such an

405   influence exists, from the natural variability. This is particularly important in transitional waters

406   as coastal lagoons where high natural variability may exist due to rapid environmental changes.

407

408   *4.3. Insights from the functional approach*

409   To date, the effect of aquaculture on benthic communities has usually been evaluated using

410   traditional taxonomic approaches (Lacoste et al. 2020). Here, we demonstrate that some species

411   traits can be used to predict the response of macro- and meiofauna to disturbances caused by

412   shellfish culture since the distribution of traits and functional indices performed well in

413   distinguishing between the farm and reference sites.

414   For both assemblages, trophic group and ecological group/life history were the traits that best

415   responded to the presence of oyster tables. As reported in other studies, the presence of

416   aquaculture facilities often decreases the abundance and diversity of filter-feeding organisms

417   (Forrest and Creese 2006, Dubois et al. 2007, Fabi et al. 2009) whereas increased organic supply

418   in farm zones favors the presence of non-selective deposit feeders. Following the classification

419   of Grall and Glemarec (1997) and Borja et al. (2000), farming zones favored the presence of

420   tolerant and opportunistic taxa whereas reference sites were dominated by sensitive organisms.

421   Among the meiofauna, epigrowth feeders were the most abundant organisms at reference sites

422   and were replaced by non-selective deposit feeders in the farming zone. The reduction in the

423   abundance of epigrowth feeders at the farm sites may be due to excluding competition with

424   other groups but we can also hypothesize a lower abundance of diatoms under oyster tables due

425   to a shading effect (McKindsey et al. 2011).

426   Amphids are complex sensorial organs of nematodes used in the search of food and partners,

427   and are useful for taxonomical identification. To date, there is no information linking amphids

428   to a particular type of marine environment, except Semprucci et al. (2018), who described a

429   potential link between inconspicuous amphids and rich food sources areas. Accordingly, our

430   results suggest that the more intense and regular food supply at farm sites may limit the

431   advantage of large amphids (REL, Sp) and hence that nematodes with smaller amphids (Cr) are

432   more abundant in farming zones. However, this preliminary result requires further investigation

433   to highlight potential links between morphological features of nematodes and their marine

434   habitat.

435   Functional diversity (FD) indices were computed for macrofauna and nematodes to evaluate

436   the relevance of these indices in the case of aquaculture-induced disturbances. Nematode FRic

437   was reduced at the farm sites and FD indices revealed the influence of aquaculture on

438   macrofauna assemblages that was not detected using taxonomic indices. This confirms the

439   usefulness of the functional approach, and more generally of multi-index approaches to detect

440   the influence of farming (Borja et al. 2009, Lacoste et al. 2019). Interestingly, macrofauna FD

441   indices indicated a higher trophic diversity and functional evenness at farm sites whereas no

442   changes were detected at the richness level. The actual level of disturbance may therefore have

443   shifted community composition that promoted a more even use of the trophic niche, which, in

444   turn, may have increased the productivity of the system (Mason et al. 2005). Compared with

445   the taxonomic approach, functional analysis not only offers the opportunity to study the

446   response of communities to the environment but also the subsequent impact of the changes on

447 ecosystem properties (Lavorel and Garnier 2002, Lacoste et al. 2020), which is essential to

448 evaluate the sustainable exploitation of aquaculture systems.

449

450 *4.4 Limitation and future outlook of the functional approach*

451 This work provides insights into the functional response of benthic communities to aquaculture-

452 induced disturbance. We proposed the use of four selected traits that may respond both for

453 macrofauna and nematode assemblages, that we assumed referred to similar behavior. The

454 choice of biological traits may strongly influence the calculation of functional indices (Petchey

455 and Gaston 2006). It was not our objective to test the most appropriate traits to use from a wide

456 selection of possible choices. Rather we wished to highlight the potential of functional analysis

457 to evaluate the impact of aquaculture using various kinds of benthic organisms (macrofauna

458 and nematodes) and traits that have already been shown to respond to organic enrichment (Borja

459 et al. 2000, Alves et al. 2013, Kandratavicius et al. 2018, Lacoste et al. 2019). Future

460 experiments that examine multiple traits in different regions and systems will be needed to

461 evaluate if functional analysis is a reliable tool to assess the benthic impacts of aquaculture.

462 The number of taxa and the completeness and accuracy of the species trait data play a significant

463 role in the estimation of functional trait metrics (Pakeman and Quested 2007, Pakeman 2014).

464 In this exploratory study, we chose to use the maximum number of taxa for which traits were

465 available. However, the inclusion of arthropods, for example, is questionable since it appears

466 that these organisms were mostly associated with *Halopithys* sp. algae and are very mobile, so

467 they could also have been classified as epifauna instead of infauna and disregarded. When we

468 excluded them from the functional analysis (data not shown), we obtained differences in the

469 representation of relative abundances based on traits, but no difference with respect to FD

470 indices.

471   Although further studies are needed to identify the traits that react most consistently in a given

472   manner or the taxonomic groups to considered, this work provides interesting information on

473   the potential of the trait based approach to detect disturbances caused by aquaculture. Along

474   with theoretical work, we think that further studies encompassing different kinds of disturbance

475   across ecosystems will enable the implementation of a framework intended to include the

476   functional approach in benthic monitoring programs.

477

478   **Conclusion and Perspectives**

479   This study documented the macrobenthic and the nematode communities in relation with

480   juvenile oyster culture in Thau Lagoon. The trait-based approach we propose in this work shows

481   the feasibility of detecting the impact of shellfish culture on the functional structure of both

482   macro- and meiofauna communities in coastal lagoons, although further studies are needed to

483   identify general patterns, within and across biogeographical regions and aquaculture systems.

484   Combining taxonomic and functional approaches may add relevant ecological information and

485   help obtain a clearer understanding of the functioning of benthic communities that are impacted

486   by anthropogenic activities. For aquaculture, as well as other human-induced disturbance, the

487   functional approach will undoubtedly enhance our ability to monitor activities and aid

488   compliance with conservation strategies such as the Water Framework Directive Strategy (EC

489   2000), which requires an understanding of both how function varies spatially and how it

490   responds to human disturbances. Several gaps that represent many research opportunities

491   should however be addressed to 'operationalize' such approach. As examples i) new tools such

492   as eDNA would allow to get rapid identification of organisms once taxonomic validation of

493   database will be improved, ii) further description of benthic organisms biological and ecological

494   traits should be completed to feed databases.

495

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Table S1. Complete list of nematodes recorded during the study with total occurrence (by core) and abundance. Species also observed in Italy and/or Tunisia are indicated.

Species	Occurence	Total Abundance	Italy	Tunisia
Paracomesoma dubium	30	136	X	X
Spirinia gerlachi	25	135		X
Longicyatholaimus longicaudatus	20	76	X	
Terschellingia longicaudata	17	42	X	X
Leptonemella vestari	15	39		
Viscosia glabra	15	38		X
Halichoanolaimus dolichurus	12	26		X
Anticomopsis sp	11	25		
Linhomoeus undulatus	11	24		X
Daptonema fallax	9	20		X
Desmodora granulata	9	19		
Paralinhomoeus tenuicaudatus	9	16		X
Viscosia elegans	9	15		
Eleutherolaimus stenosoma	8	15		X
Metalinhomoeus longiseta	7	13	X	
Ptycholaimellus pandispiculatus	7	13		
Chromadora brevipapillata	6	12		X
Paralongicyatholaimus mastigodes	6	12		
Prochromadorella longicaudata	6	11	X	X
Sabatieria pulchra	6	10	X	X
Spirinia parasitifera	6	10		X
Steineria sp.	6	10		
Terschellingia communis	6	8	X	X
Thalassironus britannicus	6	7		X
Odontophora wieseri	5	7	X	X
Ptycholaimellus ponticus	5	6	X	X
Monhystera sp.	4	4		
Anticoma eberthi	3	4	X	
Cobbia sp.	3	4		
Camacolaimus sp.	2	3		
Enoplus sp.	2	3		
Eurystomina sp.	2	3		
Metalinhomoeus sp.	2	2		
Molgolaimus sp.	2	2		
Synonchiella sp.	2	2		
Epsilonema sp.	1	1		
Oncholaimus brevicaudatus	1	1		X
Parachromadorita sp.	1	1		
Pomponema sp.	1	1		
Sphaerolaimus sp.	1	1		
Theristus sp.	1	1		