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# 1 Jellyfish degradation in a shallow coastal Mediterranean lagoon

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26 **Key words:** *Aurelia coerulea*, Macrobenthic community, Thau lagoon, Sediment, Seagrass

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29 **Abstract**

30 Recurrent jellyfish blooms in the coastal zone call for understanding the impacts of jelly-falls on the  
31 functioning of benthic communities, especially in shallow enclosed ecosystems where their biomass can  
32 affect local carbon cycling and productivity. Each year, blooms of the jellyfish *Aurelia coerulea* appear  
33 and collapse in a semi-enclosed coastal Mediterranean lagoon (the Thau lagoon, south of France).  
34 Although the lagoon is shallow, large accumulations of dead jellyfish are never observed on its bottom,  
35 so it was hypothesized that decaying jellyfish were rapidly consumed by local macrobenthic organisms.  
36 The current work aimed to test this hypothesis, by estimating the impact of the presence of dead *A.*  
37 *aurelia* medusae on local macrobenthic community composition and assessing their biomass loss rates  
38 under different scenarios of accessibility by the macrobenthos. Unexpectedly, our results revealed a  
39 limited role of macrobenthic scavengers in the disappearance of dead medusae, although this later was  
40 particularly fast (19 to 78h). Only one taxon (*Tritia* sp., Nassariidae family) showed a significant  
41 response to the presence of dead *A. coerulea* medusae on the seabed. Thus, our results suggest that the  
42 fast disappearance of dead jellyfish biomass in Thau results from its rapid degradation and consumption  
43 by local microorganisms, likely due to the combined effects of high local temperatures and the small  
44 size of *A. coerulea* medusae. Thus, the important biomass produced during *A. aurelia* blooms in Thau  
45 might essentially boost its microbial food web. The potential role of jellyfish blooms in controlling  
46 biogeochemical cycles and food web functioning in shallow lagoons is discussed, underlying the need  
47 to include this process in ecosystem-based models.

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## 50 1. Introduction

51 Jellyfish (in particular scyphozoans) are famous for their conspicuous blooms, which may locally  
52 generate biomasses exceeding 10 t wet weight  $100 \text{ m}^{-3}$  (Lilley et al. 2011). The population  
53 dynamics of jellyfish at the pelagic stage is frequently described as ‘bloom and bust’, since  
54 jellyfish blooms collapse rapidly, usually within a few weeks or months (Pitt et al. 2014). This  
55 might cause large accumulations of sinking dead jellyfish (referred to as *jelly-falls*) on the seafloor  
56 (Lebrato et al. 2012), which can be particularly impressive, especially in deep-sea habitats (Billett  
57 et al. 2006; Yamamoto et al. 2008; Lebrato and Jones 2009; Sweetman and Chapman 2011, 2015)  
58 where they can form localized layers of up to 70 cm in thickness ( $78 \text{ g C m}^{-2}$ ) on the seabed  
59 (Billett et al. 2006). These massive accumulations of jelly-falls are likely sporadic and considered  
60 as anomalies when compared with the mean annual jellyfish fluxes in those regions (Luo et al.  
61 2020). However, jellyfish are common worldwide and represent a global biomass of 290 Tg C  
62 (Luo et al. 2020) with very high sinking speeds (Lebrato et al. 2013) which calls for a better  
63 understanding of the impacts of jelly-falls on the functioning and productivity of benthic  
64 communities.

65 When jellyfish blooms collapse, this accumulated organic matter has several possible fates. First,  
66 it can be consumed or fragmented by pelagic predators and scavengers (Cardona et al. 2012; Bos  
67 et al. 2017; Hays et al. 2018; Marques et al. 2019). Otherwise, carcasses sink through the water  
68 column (Lebrato et al. 2012) where they can be degraded by pelagic microbial communities  
69 (Titelman et al. 2006; Blanchet et al. 2015; Tinta et al. 2016, 2020). The amount of jellyfish  
70 biomass that reaches the seafloor depends, thus, on their decay rate, the sinking speed of the  
71 carcasses, the depth at which the jellyfish die, and the depth of the water column itself (Lebrato  
72 et al. 2011, 2019). Decay rates for jellyfish depend on the temperature (Lebrato et al. 2011), while  
73 their sinking speed is a function of their size, diameter, bio-volume, geometry, density, and drag  
74 coefficients (Yamamoto et al. 2008; Lebrato et al. 2011, 2012, 2013). If not degraded in the water  
75 column (Titelman et al. 2006; Tinta et al. 2016, 2020), jelly-falls accumulate on the seabed, with  
76 potentially important impacts on both the biogeochemical cycling and the functioning of benthic  
77 ecosystems (Sweetman et al. 2016). Jellyfish biomass tend to be rapidly degraded because it is

78 characterized by protein-rich organic matter, low C:N ratio, and no hard exoskeleton, being  
79 described as highly bioavailable for some particular microbial organisms with very high growth  
80 efficiency (Tinta et al. 2012, 2020). This may lead to high consumption of dissolved oxygen and  
81 a drastic decrease of its concentrations in the vicinity of jellyfish carcasses (West et al. 2009;  
82 Sweetman et al. 2016; Chelsky et al. 2016; Guy-Haim et al. 2020), which might induce  
83 inhospitable conditions for the benthic macrofauna, decreasing its activity, causing local  
84 emigrations or even massive mortalities (Sweetman et al. 2016; Chelsky et al. 2016).  
85 Nevertheless, dead jellyfish can also potentially provide suitable food for many benthic species,  
86 including fishes, echinoderms, anthozoans, polychaetes, gastropods, and crustaceans (Lebrato et  
87 al. 2012; Sweetman et al. 2014; Chelsky et al. 2016; Ates 2017). These later can consume  
88 considerable amounts of jelly-falls biomass within few hours, which considerably boosts benthic  
89 productivity (Sweetman et al. 2014). This scavenging behaviour plays a key role in benthic  
90 ecosystem functioning as it determines the fate of the organic matter that reaches the seafloor, *i.e.*  
91 whether the organic material from jelly-falls contributes to the microbial loop or enters the  
92 macrofaunal food web (Sweetman et al. 2014, 2016).

93 So far, the microbial degradation of jelly-falls has been relatively well described (Titelman et al.  
94 2006; West et al. 2009; Tinta et al. 2010, 2012, 2020; Condon et al. 2011; Frost et al. 2012;  
95 Blanchet et al. 2015; Sweetman et al. 2016). However, studies investigating the impact of jelly-  
96 falls on benthic macrofaunal communities are still scarce (Sweetman et al. 2014; Chelsky et al.  
97 2016; Dunlop et al. 2017). Such studies are imperative for coastal habitats, where the highest  
98 jellyfish biomass values were reported (Luo et al. 2020) and the anthropogenic impacts are intense  
99 and pointed out as likely promoters of jellyfish blooms (Purcell 2012). This is particularly evident  
100 in coastal lagoons, where jellyfish blooms occur regularly (e.g. Fuentes et al., 2011; Marques et  
101 al., 2015a), with abundances that can overcome 530 tonnes km<sup>-2</sup> (Pitt and Kingsford 2003). These  
102 ecosystems are very productive enclosed systems, supporting important ecological processes and  
103 providing numerous ecosystem services (Newton et al. 2014; De Wit et al. 2017), but very little  
104 information is available regarding the fate of jelly-falls within these shallow environments  
105 (Chelsky et al. 2016). Despite the frequent occurrence of jellyfish blooms, to our knowledge,

106 massive accumulations of jelly-falls on coastal lagoons' floor were never reported. Although  
107 jellyfish can be rapidly degraded by pelagic microbial communities (Tinta et al. 2020), jelly-falls  
108 should still be observed on lagoons' seabed because, in such shallow habitats, sinking jellyfish  
109 are likely to reach the bottom even before they die (Lebrato et al. 2012). Therefore, the absence  
110 of dead jellyfish on the seabed in these environments suggest that jelly-falls are rapidly eaten by  
111 local benthic scavengers and/or decomposed by local microorganisms.

112 The current work aims to investigate this issue and evaluate the contribution of macrobenthic  
113 scavengers in the disappearance of jellyfish biomass in coastal lagoons. To this aim, we studied  
114 the fate of dead medusae of the jellyfish *Aurelia coreulea* when ending on the seafloor in a shallow  
115 lagoon located in the south of France: the Thau lagoon. *In situ* experiments were carried out by  
116 adding dead medusae on the seabed of the lagoon under different scenarios of accessibility by  
117 macrobenthic scavengers. The experiments were performed in two contrasting types of habitat,  
118 typical of this shallow ecosystem, assuming that the different macrobenthic community  
119 composition associated with each habitat would have a different impact on the biomass loss rate  
120 of the jelly-falls. In particular, we tested whether if the addition of dead jellyfish on the seabed  
121 altered the composition of macrobenthic communities by, for instance, attracting benthic  
122 scavengers (Chelsky et al. 2016).

123

## 124 **2. Material and Methods**

### 125 *2.1. Study site and jellyfish collection*

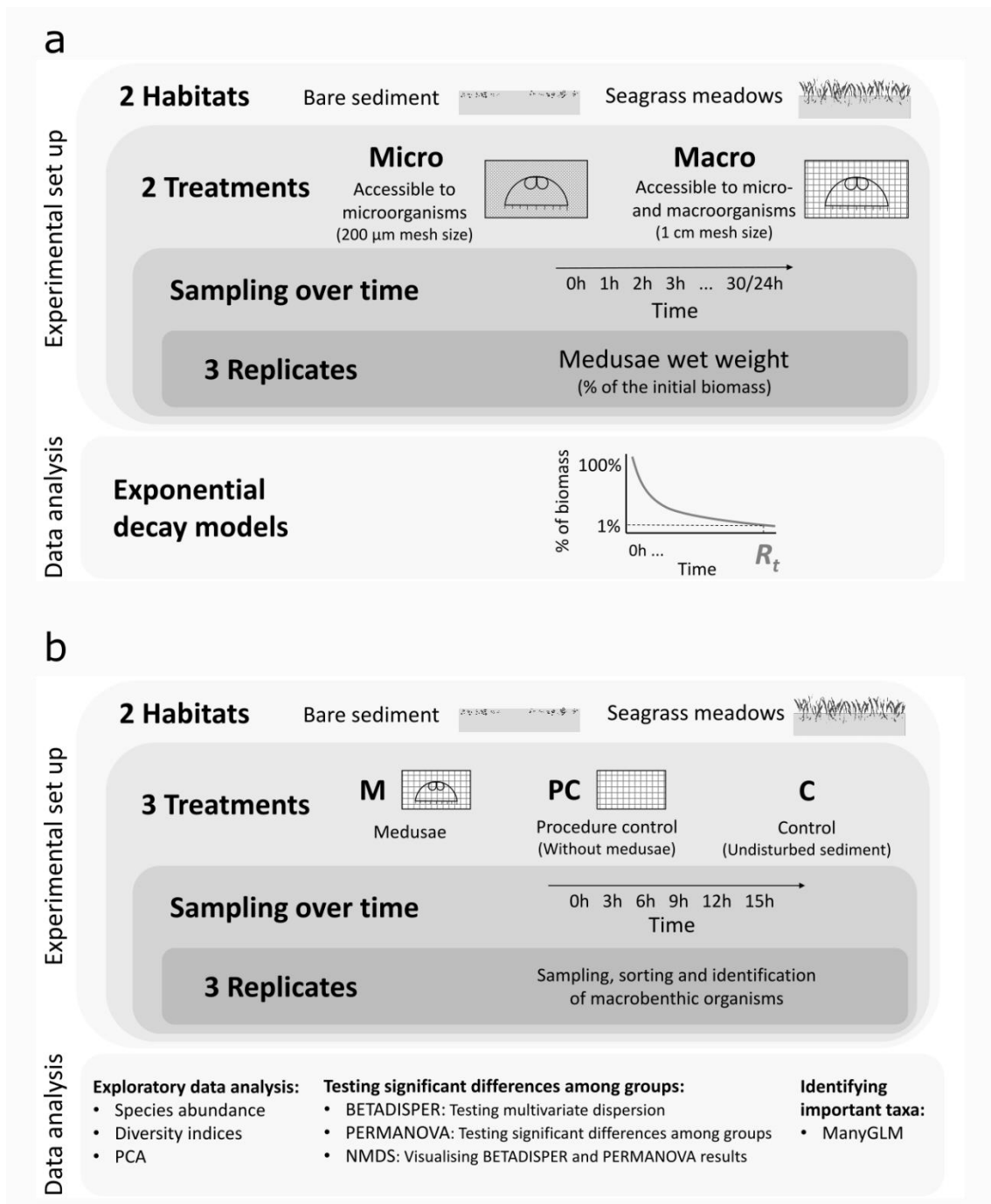
126 The Thau lagoon (43°25'31.1"N; 03°42'0.9"E) is a semi-enclosed coastal lagoon of 75 km<sup>2</sup>,  
127 connected to the Mediterranean Sea by three narrow channels. It is shallow, with a mean of 4 m  
128 depth, and is highly influenced by strong wind events (Fiandrino et al. 2012). The local tidal range  
129 is weak (< 1 m), which promotes a high water residence time (1 - 4 months, Fiandrino et al.,  
130 2012). With regards to jellyfish, the Thau lagoon has the particularity to harbour its own  
131 population of *Aurelia coerulea*, isolated from those in the Mediterranean Sea (Bonnet et al. 2012;  
132 Marques et al. 2015b) which offers a rare occasion to study the fate of the blooms of this species.  
133 In the lagoon, *A. coerulea* ephyrae first appear in the early winter (November – December), to

134 give rise to medusae at the beginning of spring (April – May), when temperature increases  
135 (Marques et al. 2015a). High abundances of medusae, associated with high growth rates generate  
136 the annual jellyfish bloom, which usually collapses in the early summer (June-July). Although  
137 sparse decaying medusae are regularly seen on the lagoon floor, either on bare sediment or  
138 entangled in seagrass leaves (R. Marques, personal observation), large accumulations of *A.*  
139 *coerulea* carcasses have never been observed so far.

140 To try to elucidate the local fate of *A. coerulea* jelly-falls, two different *in situ* experiments were  
141 performed: one (1) to assess medusae biomass loss rates under different scenarios of medusae  
142 accessibility for benthic scavengers, and one (2) to study the impact of jellyfish presence on the  
143 seafloor on the composition of local macro-benthic communities (Fig. 1). Both experiments were  
144 performed in a shallow area (< 1m depth), where dead jellyfish had already been observed on the  
145 seabed and repeated in the two most common habitats found in the lagoon (Plus et al. 2003): on  
146 bare sediments and in seagrass (*Zostera noltii*) meadows.

147 This study was conducted in 2018, during the collapse of the annual bloom of *A. coerulea*. Due  
148 to logistic constraints, the two experiments were performed on different days (on May 30<sup>th</sup> and  
149 June 07<sup>th</sup>, 2018). However, all the medusae used were collected alive on the same day (May 28<sup>th</sup>,  
150 2018). This was done using hand nets to avoid damaging the medusae and they were immediately  
151 transported to the laboratory in ambient seawater. All medusae were then kept alive for 2 to 10  
152 days, in 1 m<sup>3</sup> tanks (ca. 100 ind.m<sup>-3</sup>) with open seawater circulation system (i.e. seawater from  
153 the lagoon) to ensure similar rearing conditions as *in situ*. They were all fed once per day with  
154 newly hatched *Artemia* to ensure their survival. A few hours before each experiment, live, healthy  
155 and active medusae were selected from the husbandry tanks and equally distributed in 30 L cold  
156 boxes, filled with ambient seawater. Medusae were killed by sparging the water with nitrogen gas  
157 for ca. 3h following Chelsky et al. (2016). The medusae were then immediately transported (20  
158 min) to the experimental site and placed in the experimental bags.

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## 2.2. Jellyfish biomass loss rates

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### 2.2.1. Experimental set-up

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Jellyfish biomass loss rates were assessed both on the bare sediment and seagrass meadows

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habitats under two different scenarios of accessibility to dead medusae for the macrobenthic

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organisms of the lagoon (Fig.1a).



170 The first scenario (Micro) involved placing individual medusae in  $20 \times 15$  cm net bags with a  
171 mesh size of  $200 \mu\text{m}$  so they were accessible only to microorganisms (*e.g.* bacteria,  
172 microzooplankton, and small mesozooplankton species). In the second scenario (Macro),  
173 medusae were placed in  $20 \times 15$  cm net bags with a mesh size of 1 cm, which allowed both  
174 microorganisms and macroorganisms (*e.g.* gastropods, amphipods, crustaceans) to access them.  
175 In both scenarios, the net bags containing the dead medusae were protected with a  $1.50 \times 2.00 \times$   
176  $0.15$  m net cage with a coarse mesh size of 2.5 cm, to prevent medusae consumption by large  
177 organisms (*e.g.* large fish, echinoderms, crustaceans). However, the Macro scenario was also  
178 replicated without the protection net cage to assess if medusae consumption by large scavengers  
179 was significant. Since no significant effect of the cage could be evidenced (generalised nonlinear  
180 least square model,  $p$ -value = 0.17 and 0.62 for bare sediment and seagrass habitats, respectively),  
181 data from Macro scenarios with and without cage were pooled.

182 Before each experiment, dead medusae were partially dried on a paper towel to absorb the excess  
183 water and mucus from their surface, weighted (wet weight in g, to the nearest 0.1 g), measured  
184 (bell diameter in cm), and placed individually in a bag. In each scenario, 24 bags were fixed on  
185 the sediment using tent pegs, with a minimum distance of 1.5 m between them. For each of the  
186 two scenarios (Micro and Macro) and irrespective of the habitat (bare sediment or seagrass  
187 meadow), three replicates of individual medusa were collected at regular time intervals: every 1h  
188 at the beginning of the experiment (when medusae degradation is usually faster, Titelman et al.,  
189 2006), and every 2 to 5h afterwards, adjusted in each habitat type to ensure all the medusae  
190 biomass had disappeared from the net bags by the end of the experiment. The total experimental  
191 time was, therefore, different between habitats (24h and 30h for the seagrass meadows and the  
192 bare sediment habitats, respectively). At each sampling time, collected bags were immediately  
193 placed inside a hermetic plastic bag to avoid the loss of biological material. The remaining medusa  
194 biomass within each bag was partially dried on a paper towel to absorb the excess water (when  
195 possible) and weighed to the nearest 0.1 g (wet weight). *In situ* temperature was measured (EC  
196 300 VWR international/ WTW model 350i) right before the start and end of each experiment to  
197 detect differences in temperature between habitats.

198 2.2.2.Data analysis

199 For each habitat (bare sediment and seagrass meadow) and accessibility scenarios (Micro and  
200 Macro), jellyfish biomass loss rates were determined by fitting exponential decay models to the  
201 non-averaged wet weights of medusae (percentage of the initial biomass) as a function of time:

202 
$$M_t = M_0 e^{-\lambda t}$$

203 where  $M_t$  is the percentage of medusa biomass at time  $t$  (in hours),  $M_0$  and  $\lambda$  are the model  
204 coefficients representing the initial ( $t = 0$ ) medusa biomass (in percentage) and the loss rate,  
205 respectively. The biomass loss rates were then used to calculate the degradation time ( $D_t$  in hours),  
206 *i.e.* the time required to achieve a loss of 50% ( $t = 0.5$ ) and 99% ( $t = 0.01$ ) of the initial biomass  
207 of medusa, according to the following equation (Lebrato et al. 2011):

208 
$$D_t = \frac{-\ln(t)}{\lambda}$$

209 Differences, according to the accessibility scenarios and the habitats, were tested by fitting  
210 generalised nonlinear least square models (GNLS) using “nlme” package (Pinheiro et al. 2019),  
211 which allows fitting the model to zero values, using 100 and 0.01 as starting parameters, for  $M_0$   
212 and  $\lambda$ , respectively.

213 Significant differences in the initial medusae biomass and environmental conditions (temperature)  
214 between habitats and treatments were assessed by Kruskal-Wallis and T-tests, after verifying the  
215 normality assumptions.

216

217 2.3. Impact on macrobenthic community composition

218 2.3.1.Experimental set-up

219 To test the impact of dead jellyfish presence on benthic community composition, a second  
220 experiment was carried out on both habitats.

221 The experiments started ( $t_0$ ) at 16h30 and 15h40 on the seagrass meadows and the bare sediment,  
222 respectively, and samples were collected at five sampling times (every 3h) for 15h (Fig. 1b), based  
223 on the preliminary results of the jellyfish biomass loss rates experiments. In each habitat, three  
224 different treatments were performed. The *medusa* (M) treatment was a replication of the Macro

225 scenario from the previous experiment: one dead medusa was placed within a 1 cm mesh net bag,  
226 thereby being accessible to both micro- and macroorganisms. The *procedure control* (PC)  
227 treatment aimed to test the effect of the experimental setup and therefore the M treatment was  
228 reproduced without any medusa in the net bag. The last treatment was for *control* (C). In this case,  
229 the sampling was performed on undisturbed areas of each habitat. To assess differences in  
230 macrobenthic community composition between treatments, the substrate (sediment and seagrass)  
231 below each bag was collected, as well as the organisms present on its surface and top of the bags.  
232 This sampling was performed immediately upon medusae (in M) or empty bag (in PC) collection.  
233 Three replicates were collected per combination of habitat, treatment, and sampling time. In each  
234 case, the sediment was sampled using a shovel (0.03 m<sup>2</sup>, 4 cm deep) and placed inside a hermetic  
235 plastic bag, ensuring a minimum sample loss. Samples were stored in cold boxes and frozen  
236 within 6h, until later laboratory analysis. *In situ* temperature was measured (EC 300 VWR  
237 international/ WTW model 350i) before the start of the experiment and at each sampling time to  
238 detect differences in temperature between habitats.

239 Once in the laboratory, the volume of sediment in each sample was measured using a graduated  
240 beaker to standardize the abundance of organisms by sampling area (m<sup>2</sup>). The sediment was  
241 sieved (1 mm mesh size) and its macrofauna was sorted, counted, and identified under a dissecting  
242 microscope according to D'Angelo and Gargiullo (1978), Fauvel (1927), and Fauvel (1923). The  
243 organisms were identified to the lowest taxonomic level. However, since identification at the  
244 species level was not possible for all organisms, species of the same genus were grouped.  
245 Annelids and Decapods were identified down to the family level only.

246

### 247 2.3.2.Data analysis

248 Only taxa representing more than 1% of the total community biomass in each habitat were  
249 considered for data analysis, to reduce the influence of rare organisms. Diversity indices (Shannon  
250 and Pielou's evenness indices) were calculated using the "BiodiversityR" package (Kindt and  
251 Coe 2005), based on "vegan" package in R (Oksanen et al. 2019). The changes in total abundance  
252 (after logarithmic transformation) and diversity indices, among habitats, scenarios, and sampling

253 times were tested using linear models. For each variable (*i.e.* total abundance, Shannon, and  
254 Pielou's evenness indices) a full model was produced, with all main terms and respective  
255 interactions (index ~ habitat \* treatment \* sampling time). Model selection was then carried out  
256 using the Akaike information criterion (AIC), following Zuur et al. (2009). Visual inspection of  
257 residual plots did not reveal any obvious deviations from homoscedasticity or normality.  
258 Differences between each combination of treatment and sampling time within each habitat were  
259 tested using post hoc Tukey HSD tests for multiple comparisons.

260 Changes in community composition among habitats, treatment, and sampling time were analysed  
261 using three different complementary approaches. First, the community composition was  
262 represented through a principal component analysis (PCA) of the abundances ( $\log(x+1)$ ).  
263 Second, differences between community composition among habitats, treatments, and sampling  
264 times were assessed through a permutational multivariate analysis of variance (PERMANOVA,  
265 with 9999 permutations), using Bray-Curtis distance. Since homogeneity of dispersion between  
266 factors is an assumption of the PERMANOVA analysis, multivariate dispersion was first tested  
267 using BETADISPER. When significant differences were observed, a pairwise comparison was  
268 performed (PERMUTEST, with 9999 permutations). Nonmetric Multidimensional Scaling  
269 (NMDS) plots were used to visualize the results of BETADISPER and PERMANOVA, as  
270 recommended (Anderson 2017). These analyses were performed using the package "vegan"  
271 (Oksanen et al. 2019).

272 Third, to cope with the limitations reported for PERMANOVA, which does not take into  
273 consideration the influence of the mean-variance structure of each species (Warton et al. 2012),  
274 we also ran a model-based approach using a multi-taxa generalized linear model (ManyGLM,  
275 "manyglm" function, from package "mvabund"; Wang et al., 2012). A two fixed factor model  
276 structure (sampling time and treatment) was used, separately for each habitat, with a negative  
277 binomial distribution and a log-link function. The examination of residual plots of the model  
278 showed the absence of a clear pattern, validating the model. This analysis was also used to  
279 determine which species contributed most to the differences observed.

280

281 **3. Results**

282 *3.1. Jellyfish biomass loss rates*

283 The initial wet weights of the *A. coerulea* medusae used in the experiments (Table 1) were similar  
284 among scenarios within each habitat (Kruskal-Wallis,  $\chi^2 = 0.32$ ,  $df = 1$ ,  $p$ -value = 0.57 and  $\chi^2 =$   
285 0.61,  $df = 1$ ,  $p$ -value = 0.44 for bare sediment and seagrass, respectively), but differed between  
286 habitats (Kruskal-Wallis,  $\chi^2 = 81.33$ ,  $df = 1$ ,  $p$ -value < 0.001). Indeed, as the experiments started  
287 on different days for the two habitats and medusae were kept alive between the two experiments,  
288 differences in the time spent in captivity likely induced a bias on the initial weight of the medusae.  
289 The initial and final experimental temperatures were similar for the two habitats ( $23.5 \pm 0.7$  °C  
290 and  $23.4 \pm 0.5$  °C on the seagrass meadows and bare sediment, respectively; T-test,  $p$ -value =  
291 0.8), suggesting a limited effect of temperature on the results.

292 The disappearance of *A. coerulea* biomass was fast irrespective of the scenario or habitat (Fig. 2),  
293 with  $\lambda$  coefficient ranging from -0.24 to -0.06 per hour (*i.e.* -1.42 to -5.8 per day, Table 1). All  
294 model fits and correspondent coefficients were statistically significant (GNLS,  $p$ -value < 0.001,  
295 Table 2). On the bare sediment habitat, the jellyfish biomass loss rate was not affected by the  
296 accessibility scenarios (GNLS,  $p$ -value = 0.798), while on the seagrass meadow the biomass loss  
297 rate was significantly higher (GNLS,  $p$ -value < 0.001) in the Micro scenario than in the Macro  
298 one. Irrespective of the scenario, medusae degradation was significantly faster on the bare  
299 sediments (GNLS,  $p$ -value < 0.001), where 99% of the initial medusae biomass was lost in about  
300 19 hours in both accessibility scenarios (Table 1). Medusae biomass loss was slower on seagrass  
301 meadows: under the Macro scenario,  $R_t$  was estimated at 78 h, while microorganisms alone  
302 degraded 99% of the biomass in 32 h. However, medusae biomass loss was consistently faster  
303 during the first few hours of the experiments, with a 50% loss of the initial biomass in 3h on bare  
304 sediment (both scenarios), against 5 and 12h on seagrass meadows, for Micro and Macro  
305 scenarios, respectively.

306

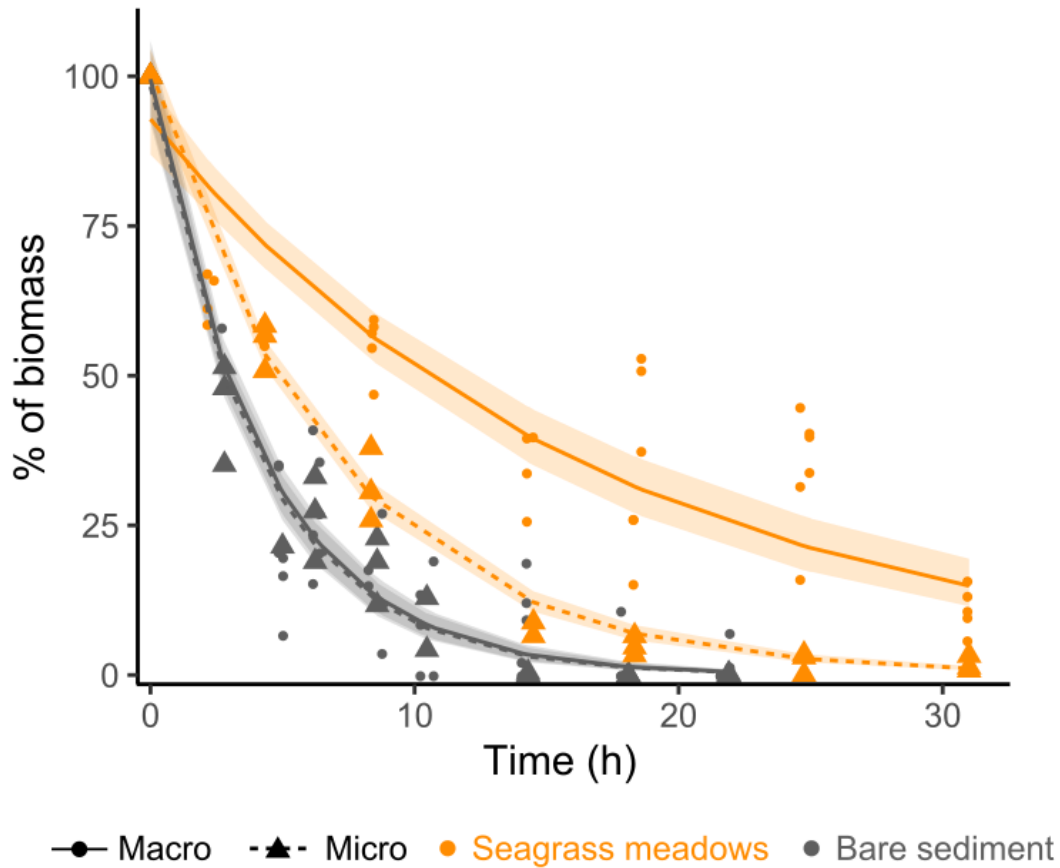
307 Table 1: Mean initial wet weights (W) and bell diameters (BD) of the dead *A. coerulea* medusae used in each experiment  
308 and resulting estimates of biomass loss rate ( $\lambda$  in hours) and degradation time ( $Dt$  in hours).

Scenario	Initial W (g $\pm$ SD)	Initial BD (cm $\pm$ SD)	$\lambda$ (h)	$Dt$ (h)
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	<b>Bare sediment</b>			
Macro	34.8 ± 12.4	8.0 ± 1.3	-0.24	19.51
Micro	32.8 ± 14.9	8.1 ± 1.5	-0.24	19.05
	<b>Seagrass meadows</b>			
Macro	107.5 ± 20.0	12.8 ± 0.9	-0.06	78.04
Micro	111.8 ± 19.0	13.2 ± 1.0	-0.15	31.56

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312 Fig. 2: Dynamic of *A. coerulea* medusae biomass loss in both habitats (bare sediment and seagrass meadows) under  
 313 both accessibility scenarios (Macro and Micro). Exponential decay models (lines) were fitted to the non-averaged data  
 314 of biomass (in % of the initial medusae biomass), with 95% confidence intervals (shadow areas).  
 315

316 Table 2: Estimation of the parameters ( $M_0$  and  $\lambda$ ) by the GNLS models used to assess differences between scenarios  
 317 within each habitat. Significant differences ( $p$ -value < 0.05) are indicated in bold.

	<b>Value</b>	<b>Std.Error</b>	<b>t-value</b>	<b>p-value</b>
<b>Bare sediment</b>				
<b><math>M_0</math></b>				
Macro (Intercept)	99.514	2.944	33.805	< 0.01
Micro	-1.228	5.025	-0.244	0.807
<b><math>\lambda</math></b>				
Macro (Intercept)	0.236	0.013	18.509	< 0.01
Micro	0.006	0.023	0.257	0.798
<b>Seagrass meadows</b>				
<b><math>M_0</math></b>				
Macro (Intercept)	92.834	2.511	36.974	< 0.01
Micro	8.045	6.095	1.320	0.192
<b><math>\lambda</math></b>				

Macro (Intercept)	0.059	0.004	14.525	< 0.01
Micro	0.087	0.017	5.142	< <b>0.01</b>

318

319

320 *3.2. Benthic community changes*

321 *3.2.1. General composition of macrobenthic communities*

322 A total of 9478 macrobenthic organisms, belonging to 34 different taxa, were identified during  
323 the study. The two types of habitats investigated differed in terms of species richness with a higher  
324 average number of taxa on seagrass meadows (29) than on bare sediments (20). However,  
325 macrobenthic communities on seagrass meadows were clearly dominated by nine taxa only (Fig.  
326 3). On this type of habitat, the gastropods *Bittium* sp. and the bivalves *Ruditapes* sp. represented  
327 together more than 80% of the total abundance recorded in all treatments: Medusae (M, 67.8 and  
328 17.4%, respectively), Procedure Control (PC, 58.5 and 25.4%, respectively) and Control (C, 41.6  
329 and 41.3%, respectively). On bare sediments, macrobenthic communities were more balanced: in  
330 the C treatment, 81.7% of the total abundance was represented by the annelid Glyceridae (28.2%),  
331 and the gastropods *Bittium* sp. (23.6%), *Tricolia* sp. (17.9%), and *Rissoa* sp. (12.1%); in the M  
332 treatment, the contribution of Glyceridae dropped to 12.5%, while taxa like *Ruditapes* sp. and  
333 *Tritia* sp. increased their importance representing 15.8% and 8.9% of total abundance,  
334 respectively; and in the PC treatment the most abundant taxa were *Bittium* sp. (24.4%), *Tricolia*  
335 sp. (16.5%), *Rissoa* sp. (15.4%) and Glyceridae (12.2%).





355 > 0.05), except at 12h in the seagrass habitat, when it was significantly lower than at  $t_0$  (Tukey  
 356 HSD, p-value = 0.02) (Fig. 4A and B).

357 The diversity of macrobenthic organisms (Shannon diversity index) appeared to vary differently  
 358 depending on the habitat (Fig. 4C and D, Table 3). In seagrass meadows, it increased significantly  
 359 at the end of the study period (9, 12, and 15h; Tukey HSD, p-value < 0.05; Fig. 4C), but did not  
 360 vary among treatments while, on bare sediments, differences were only observed among  
 361 treatments, with higher diversities in M and PC than in C at 3h (Tukey HSD, p-value = 0.01; Fig.  
 362 4D).

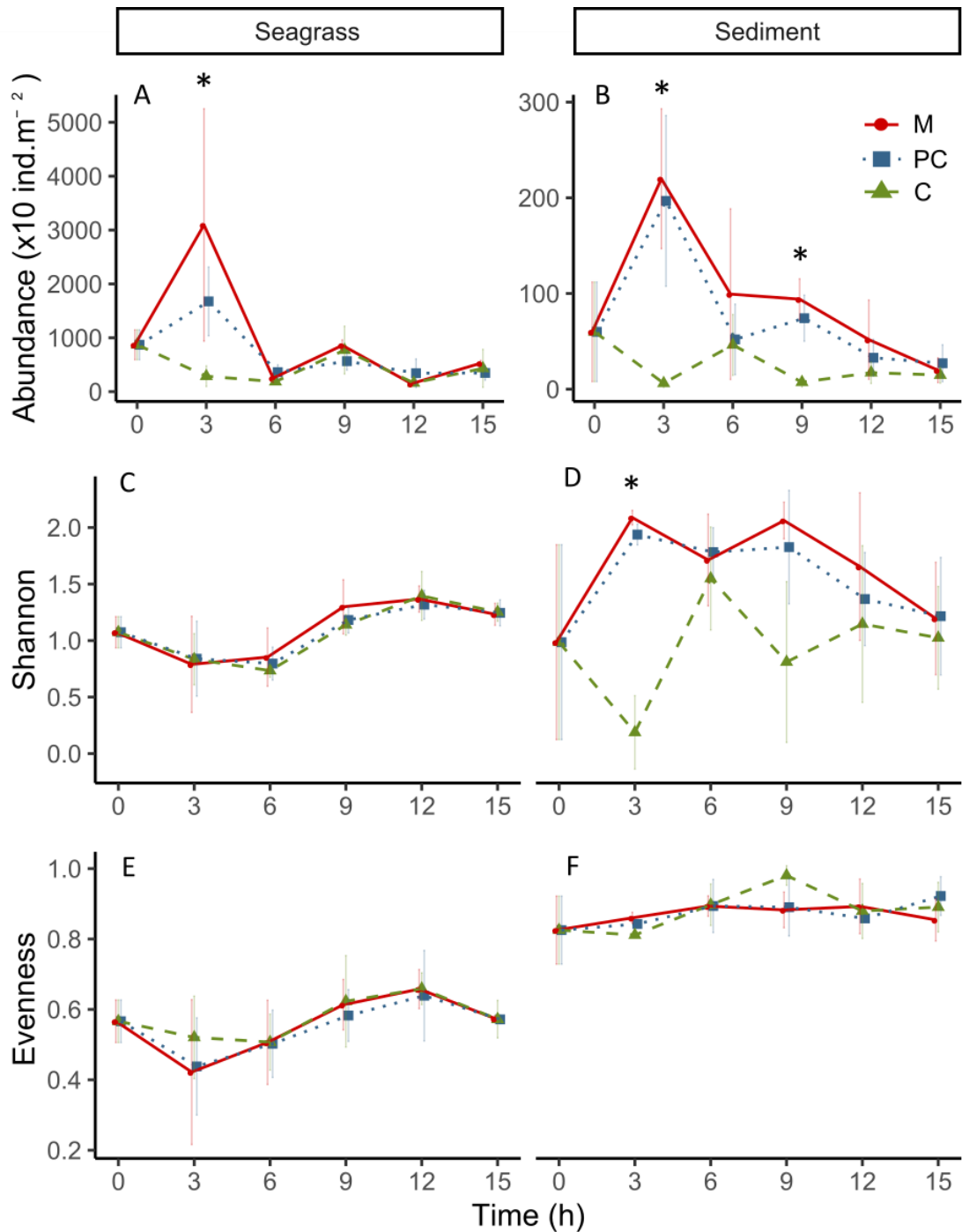
363 For Pielou's evenness index, only the sampling time and habitat factors were retained in the linear  
 364 model (Table 3), showing that the treatment did not affect community evenness. Differences in  
 365 the evenness were only observed on the seagrass meadows, where it was lower at 3h, suggesting  
 366 a possible disturbance of the community (Tukey HSD, p-value < 0.05; Fig. 4E and F).

367

368 Table 3: Results of the linear models and the effect of each factor (Habitat, Time, and Treatment), on each variable  
 369 (Abundance, Shannon, and Evenness diversity indices). Bold values indicate significant differences between at least  
 370 two groups, at  $\alpha = 0.05$ .

<b>Abundance</b>	<b>Df</b>	<b>Sum Sq</b>	<b>Mean Sq</b>	<b>F value</b>	<b>Pr(&gt;F)</b>
Time	5	18.294	3.659	8.687	<b>&lt;0.001</b>
Treatment	2	24.407	12.204	28.974	<b>&lt;0.001</b>
Habitat	1	156.490	156.490	371.541	<b>&lt;0.001</b>
Time:Treatment	8	19.163	2.395	5.687	<b>&lt;0.001</b>
Time:Habitat	5	8.792	1.758	4.175	<b>0.002</b>
Treatment:Habitat	2	4.745	2.372	5.633	<b>0.006</b>
Time:Treatment:Habitat	8	6.233	0.779	1.850	0.084
<b>Shannon</b>					
Time	5	1.304	0.261	1.853	0.115
Treatment	2	2.986	1.493	10.610	<b>&lt;0.001</b>
Habitat	1	2.528	2.528	17.962	<b>&lt;0.001</b>
Time:Treatment	8	2.195	0.274	1.949	0.068
Time:Habitat	5	3.180	0.636	4.519	<b>0.001</b>
Treatment:Habitat	2	2.612	1.306	9.281	<b>&lt;0.001</b>
Time:Treatment:Habitat	8	2.176	0.272	1.933	0.070
<b>Evenness</b>					
Time	5	0.201	0.040	6.956	<b>&lt;0.001</b>
Habitat	1	2.332	2.332	403.462	<b>&lt;0.001</b>
Time:Habitat	5	0.085	0.017	2.936	<b>0.017</b>

371



372

373 Fig. 4: Abundance of macrobenthic organisms (A and B, note the different scales for the two habitats), Shannon  
 374 diversity index (C and D), and Pielou's equitability index (Evenness) on the seagrass meadow (A, C, and E) and bare  
 375 sediment (B, D, and F) habitats. For each variable, dots represent average values and vertical bars standard deviations  
 376 for each treatment (M: medusae, PC: procedure control, C: control). Asterisks indicate significant differences between  
 377 treatments at  $\alpha = 0.05$ .  
 378

379

### 3.2.3. Differences in the community composition

380

In the principal component analysis (PCA), only the first two axes (PC1 and PC2, Fig. 5) were

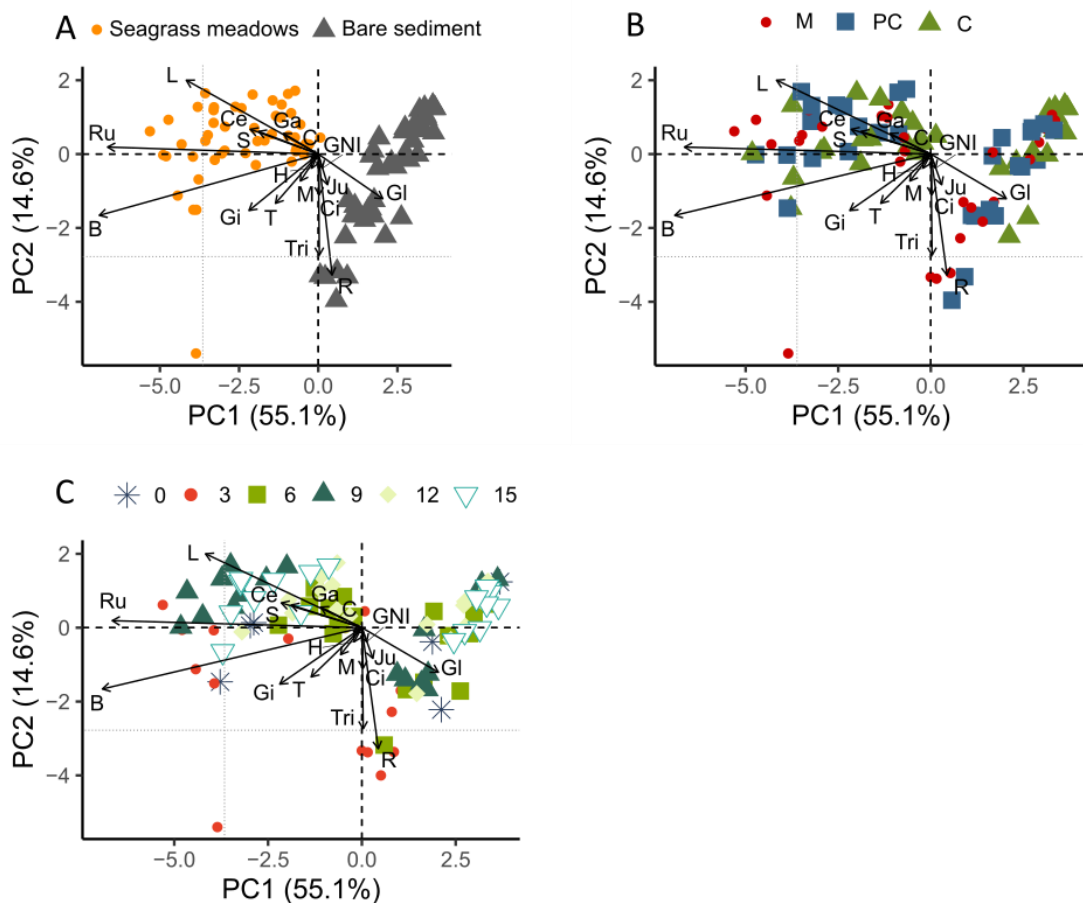
381

retained since they represent the majority of the variability of the data (69.7%). These axes

382

discriminated the samples from the two habitats (Fig. 5A), showing that habitat type is the main

383 driver of the variation in macrobenthic community composition observed between samples. In  
 384 seagrass meadows, the community was characterized by high abundances of *Bittium* sp. (B),  
 385 *Ruditapes* sp. (Ru), and *Loripes* sp. (L), whereas on the bare sediment Glyceridae (Gl), *Rissoa* sp.  
 386 (R), and *Tricolia* sp. (Tri) highly contributed to differentiate these groups. The effect of the  
 387 treatment or time on the community composition was not evident in the PCA (Fig. 5B and C).  
 388 However, 17 samples presented high Euclidean distance from the centre (outside the grey lines,  
 389 Fig. 5A, B, and C), suggesting that they had a different community composition. Most of these  
 390 samples (10) were collected at 3h (Fig. 5C) and only 3 were C samples (Fig. 5B).

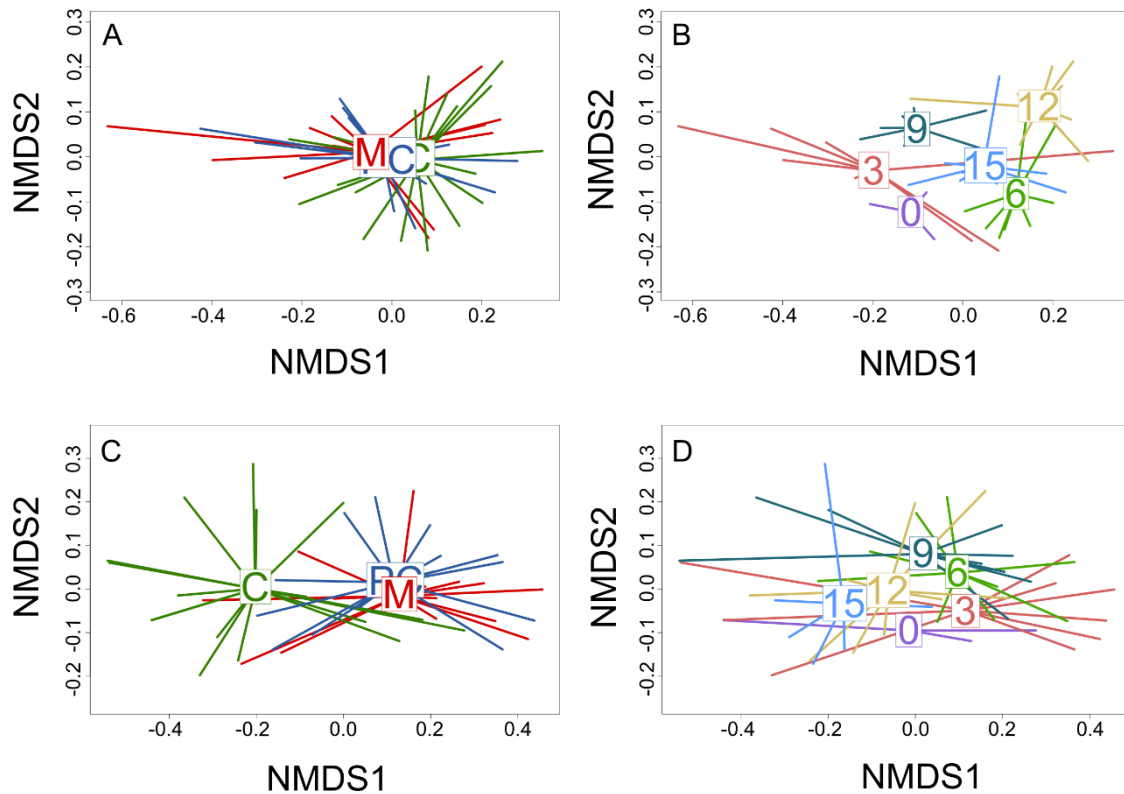


391  
 392 Fig. 5: Biplots of Principal Component Analysis (PCA). Samples (points) and taxa (arrows) are presented. In A, B,  
 393 and C, samples are identified according to habitat, treatment (M: medusae, PC: procedure control, C: control), and  
 394 sampling time (in h), respectively. Grey dotted lines are indicative thresholds to identify the samples with high  
 395 Euclidean distance from the centre. For the sake of simplicity, taxa names are abbreviated (see Fig. 3 with taxa codes).  
 396  
 397 The results from BETADISPER did not detect significant changes in community dispersion over  
 398 time ( $F=0.7$ ,  $p=0.6$ ) or among treatments ( $F=2.5$ ,  $p=0.08$ ). However, the community dispersion

399 was different between the two habitats ( $F= 13.2$ ,  $p\text{-value} < 0.001$ ), and, therefore, BETADISPER  
400 and PERMANOVA were performed for each habitat separately.

401 On the seagrass meadows, community dispersion was homogeneous among treatments ( $F = 0.5$ ,  
402  $p\text{-value} = 0.6$ , Fig. 6A), but not across sampling time ( $F = 2.5$ ,  $p\text{-value} = 0.045$ , Fig. 6B). Pairwise  
403 comparisons identified the samples collected at 3h as being different from those collected from 6  
404 to 15h ( $p\text{-value} < 0.05$ ). The analysis was, therefore, repeated without the samples collected at 3h,  
405 to ensure homogeneity of dispersion among samples ( $F = 0.3$ ,  $p\text{-value} = 0.9$ ). Accordingly, a  
406 PERMANOVA was performed to determine changes in the community for the seagrass meadow,  
407 between treatments, sampling times, and the respective interaction (full model), omitting the  
408 samples collected at 3h. The results indicate that the community composition did not vary between  
409 treatments ( $F = 0.6$ ,  $p\text{-value} = 0.8$ , Fig. 6A), but showed significant differences over time ( $F= 9.3$ ,  
410  $p\text{-value} < 0.01$ , Fig. 6B).

411 In the bare sediment habitat, community dispersion was homogeneous across sampling times and  
412 among treatments ( $F = 0.6$ ,  $p\text{-value} = 0.7$  and  $F = 0.4$ ,  $p\text{-value} = 0.7$ , respectively, Fig. 6C and D).  
413 Therefore, a full factorial model of PERMANOVA (*i.e.* treatment, sampling time, and interaction)  
414 was performed for this habitat. The results show that both factors significantly affected  
415 macrobenthic community composition ( $F = 2.8$ ,  $p\text{-value} < 0.01$  and  $F = 4.8$  and  $p\text{-value} < 0.01$ ,  
416 respectively), with PC and M presenting similar values, whereas treatment C was significantly  
417 different (Fig. 6C). However, the interaction between both factors was not significant ( $F = 1.4$   
418 and  $p\text{-value} = 0.09$ ) indicating that changes in community composition among treatments were  
419 not affected by sampling time.



421

422 Fig. 6: Results from the Nonmetric Multidimensional Scaling (NMDS) analysis on the seagrass meadows (A and B)  
 423 and the bare sediment habitats (C and D), showing the dispersion of the samples (lines) around the centroid of each  
 424 group, by treatment (A and C): M: medusae, PC: procedure control, C: control; and by sampling time in hours (B and  
 425 D).

426

427 The results of the two-factor multivariate linear model (mvabund), for each habitat, were  
 428 consistent with the results of the PERMANOVA (reported above). In the seagrass meadows, the  
 429 treatment alone did not affect the community composition, but it was significant when combined  
 430 with sampling time (significant interaction, Dev = 175.6, p-value = 0.007). On the bare sediment,  
 431 both the treatment and sampling time affected the community composition (p-value < 0.05).

432 This analysis allowed the identification of the taxa that contributed most to the observed  
 433 differences between treatments (Table 4): *Bittium* sp. in the seagrass meadows and *Tricolia* sp.,  
 434 *Hexaplex* sp., *Tritia* sp. and *Ruditapes* sp. on the bare sediment habitats (Fig. 7). These organisms  
 435 exhibited higher abundances in M and PC at 3h but no difference of abundances between M and  
 436 PC treatments were observed ( $P_{adj} > 0.05$ ). Indeed, differences between M and PC treatments  
 437 were only observed for *Tritia* sp. ( $P_{adj} = 0.04$ ), which showed higher abundances for M during the  
 438 first 9h of the study period (up to  $14.9 \pm 3.6 \times 10 \text{ ind.m}^{-2}$ , Fig. 7D). Therefore, although *Bittium*

439 sp. (in seagrass meadows), *Hexaplex* sp., *Tricolia* sp., and *Ruditapes* sp. (on the bare sediment)  
 440 appeared to have positively responded to the presence of jelly-falls, especially at 3h, only the  
 441 *Tritia* sp. (on the bare sediment) revealed statistical evidence of a positive response to the presence  
 442 of dead *A. coerulea* medusae on the bottom.

443

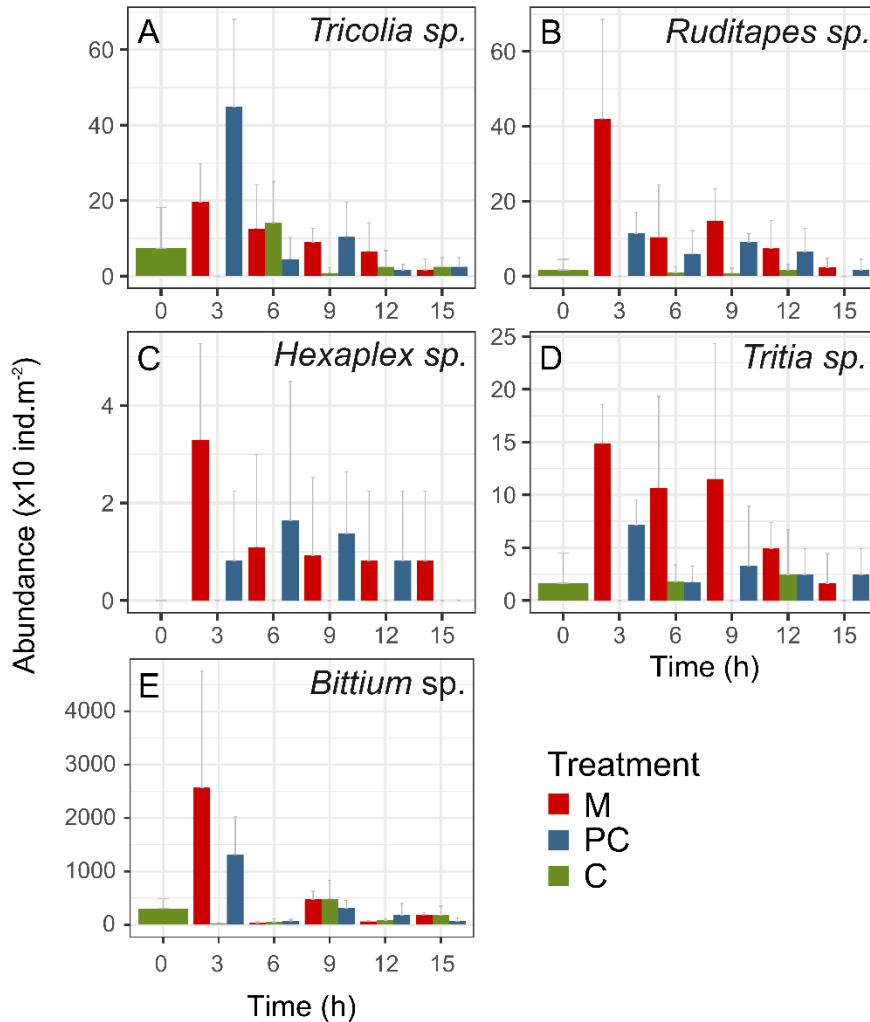
444 Table 4: Results of the ‘species-by-species’ two-factor multivariate linear model (ManyGLM), with the terms and the  
 445 significance of each term (adjusted p-values) in the model (treatment, sampling time, and interaction). Bold values  
 446 indicate significant differences at  $\alpha = 0.05$ .

Seagrass meadows	Treatment		Sampling time		Treatment: Sampling time	
	Dev	P <sub>adj</sub>	Dev	P <sub>adj</sub>	Dev	P <sub>adj</sub>
<i>Cerastoderma</i> sp.	0.433	0.982	26.982	<b>0.008</b>	5.557	0.945
<i>Gastrana</i> sp.	0.676	0.982	18.624	0.055	5.012	0.945
<i>Loripes</i> sp.	1.876	0.958	60.183	<b>0.001</b>	19.451	0.359
<i>Ruditapes</i> sp.	0.249	0.982	41.143	<b>0.001</b>	9.649	0.918
<i>Bittium</i> sp.	7.987	0.449	41.265	<b>0.001</b>	40.549	<b>0.001</b>
<i>Cerithium</i> sp.	2.013	0.958	7.663	0.768	4.902	0.945
<i>Gibbula</i> sp.	6.677	0.548	20.578	<b>0.030</b>	25.757	0.100
<i>Hexaplex</i> sp.	3.726	0.936	7.681	0.768	7.366	0.935
<i>Jujubinus</i> sp.	0.000	1.000	0.000	1.000	0.000	1.000
<i>Rissoa</i> sp.	3.409	0.941	9.682	0.555	8.813	0.918
<i>Tricolia</i> sp.	7.972	0.449	6.472	0.768	7.810	0.935
Gastropoda NI	0.000	1.000	0.000	1.000	0.000	1.000
<i>Sphaeroma</i> sp.	2.843	0.941	11.816	0.381	15.583	0.582
<i>Microdeutopus</i> sp.	3.262	0.941	4.412	0.850	8.919	0.918
Cirratulidae	2.402	0.941	3.750	0.850	0.001	0.945
Glyceridae	0.000	1.000	0.000	1.000	0.000	1.000
<i>Tritia</i> sp.	1.452	0.958	14.332	0.214	16.203	0.582
<b>Bare sediment</b>						
<i>Cerastoderma</i> sp.	0.391	0.843	7.686	0.661	9.641	0.794
<i>Gastrana</i> sp.	0.000	1.000	0.000	1.000	0.000	1.000
<i>Loripes</i> sp.	1.764	0.713	3.137	0.948	6.730	0.794
<i>Ruditapes</i> sp.	24.699	<b>0.001</b>	18.268	<b>0.036</b>	8.739	0.794
<i>Bittium</i> sp.	9.271	0.109	32.619	<b>0.001</b>	20.626	0.140
<i>Cerithium</i> sp.	6.039	0.395	2.509	0.948	4.872	0.794
<i>Gibbula</i> sp.	7.441	0.251	15.723	0.067	8.634	0.794
<i>Hexaplex</i> sp.	12.639	<b>0.024</b>	3.401	0.948	1.955	0.794
<i>Jujubinus</i> sp.	6.794	0.313	17.327	<b>0.048</b>	10.152	0.794
<i>Rissoa</i> sp.	8.154	0.177	22.319	<b>0.014</b>	19.967	0.145
<i>Tricolia</i> sp.	4.182	0.576	16.865	0.051	25.929	<b>0.046</b>
Gastropoda NI	4.280	0.576	15.542	0.067	2.883	0.794
<i>Sphaeroma</i> sp.	0.000	1.000	0.000	1.000	0.000	1.000
<i>Microdeutopus</i> sp.	4.852	0.567	5.147	0.892	0.000	0.830
Cirratulidae	4.720	0.567	24.968	<b>0.003</b>	8.259	0.794

Glyceridae	3.377	0.596	5.275	0.892	10.271	0.794
<i>Tritia</i> sp.	21.770	<b>0.001</b>	12.924	0.136	12.333	0.638

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#### 455 4. Discussion

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Fig. 7: Abundance of the macrobenthic organisms which showed significant contributions to the observed differences among treatments and sampling time (ManyGLM) on bare sediment (A to D) and seagrass meadows (E) habitats. Note the differences in scale between graphs.

##### 4.1. The contribution of macrobenthic consumption to the fast degradation of jellyfish in

##### *Thau*

Local scavengers might play a significant role in jelly-falls disappearance from the benthic

environments by consuming jellyfish biomass that sinks or accumulates on the seafloor

(Sweetman et al. 2014). In our study, though, irrespective of the habitat, macrobenthic

461 communities appear to have a limited impact on the biomass loss of dead *A. coerulea* medusae in  
462 the Thau lagoon. This is supported by the lack of significant differences in jellyfish biomass loss  
463 rates between the Micro and Macro scenarios and by the limited response of the benthic  
464 communities to the addition of jelly-falls to the seabed (except for one particular taxon, the *Tritia*  
465 sp.). Therefore, our results suggest that, in the Thau lagoon, jelly-falls are likely mainly degraded  
466 by microorganisms (e.g. bacteria, microzooplankton, and small mesozooplankton species) with a  
467 limited contribution of macrobenthic consumption in their disappearance.

468 The *in situ* degradation of *A. coerulea* medusae in the Thau lagoon was very fast, with biomass  
469 loss rates ranging from 0.06 to 0.24 h<sup>-1</sup> (1.42 to 5.8 d<sup>-1</sup>) and a 99% degradation of dead jellyfish  
470 biomass in about 19 hours on bare sediments and less than 3.5 days on seagrass meadows. High  
471 jellyfish biomass loss rates have been previously reported, with complete degradation of fresh  
472 dead jellyfish occurring within 5 to 14 days (Titelman et al. 2006; West et al. 2009; Qu et al.  
473 2015). These rapid degradations of dead jellyfish (mainly by microbial decomposition) were  
474 attributed to the biochemical composition of their tissues, with a high proportion of proteins, low  
475 C:N ratio, and lack of hard structures, providing high-quality substrate for specific bacteria  
476 (Titelman et al. 2006; Tinta et al. 2012, 2020). Indeed, simulated scenarios performed with  
477 *Aurelia aurita* showed that about half of its dead organic matter is instantly available as dissolved  
478 organic matter and rapidly consumed by microbes (within 1.5 days, Tinta et al., 2020). Decay  
479 rates are also known to vary with seawater temperature and jellyfish size (Titelman et al. 2006;  
480 Lebrato et al. 2011, 2012). Temperature is probably one of the most important factors driving  
481 differences in jellyfish decay rates (Lebrato et al. 2011). In the Thau lagoon, the collapse of the  
482 *A. coerulea* bloom coincides with the peak of summer temperatures (>20 °C; Marques et al.  
483 2015a). This might promote fast medusae degradation by the microbenthos, but also in the water  
484 column (Tinta et al. 2020), thereby reducing the amount of jellyfish biomass that reaches the sea  
485 bed. The biomass loss rates observed in Thau are in the range of those decay rates estimated for  
486 tropical shallow environments, where less than one day is required to decompose 99% of jellyfish  
487 organic matter (Lebrato et al. 2011). However, degradation rates also depend on the initial  
488 medusae biomass, with smaller individuals decaying faster than larger ones (Titelman et al. 2006).



489 The medusae of *A. coerulea* in Thau are usually smaller than those of other *Aurelia* species  
490 (Marques et al. 2015a) or scyphozoans (Pitt 2000; Fuentes et al. 2011; Prieto et al. 2013).  
491 Therefore, it is a combination of small-sized medusae and high local temperature which likely  
492 promotes fast biomass loss rates of jelly-falls in this shallow ecosystem, through the action of  
493 microorganisms.

494 We initially hypothesised that differences in macrobenthic community composition associated  
495 with different habitats would have a distinct impact on the biomass loss rate of the jelly-falls. The  
496 consumption of dead jellyfish by macroorganisms can be expected to be more important in  
497 habitats with lower food availability (Sweetman et al. 2014) since local organisms depend on less  
498 frequent inputs of new sources of organic matter (Holmer et al. 2004). Indeed, in the Thau lagoon  
499 and as expected (Thouzeau et al. 2007; Rueda et al. 2009), macrobenthic communities differed  
500 between the two tested habitats, and higher biomass loss rates were observed on bare sediments,  
501 where the amount of available organic matter is lower (Plus et al. 2003). Furthermore, it was on  
502 bare sediments that the only macrobenthic organism was significantly attracted by jelly-falls  
503 (gastropods from the *Tritia* genus). These results suggest a possible contribution of the  
504 macroorganisms consumption to the disappearance of *A. coerulea* jelly-falls in the lagoon.  
505 However, these results must be considered with caution since the effect of the habitat in our study  
506 was not completely independent from the initial biomass of *A. coerulea* used in each experiment  
507 (higher on the seagrass meadows than on the bare sediment), which has been shown to affect  
508 jellyfish decay rates (Titelman et al. 2006). The experiments were performed on different days  
509 and, although individuals were randomly selected, the captivity time between experiments might  
510 have induced a bias on the initial weight of the medusae. Furthermore, although this was not tested  
511 in the present work, this captivity time might have also affected the biochemical composition of  
512 jellyfish tissues, potentially affecting our results.

513 Within each habitat, our results suggest a limited consumption of jelly-falls by macrobenthic  
514 organisms. On the bare sediments, the results from the degradation experiment showed that  
515 jellyfish decay rates were not affected by the accessibility scenarios, while on the seagrass  
516 meadows, the biomass loss of dead medusae was even faster for the Micro than for the Macro

517 scenario, which was unexpected. This might partially be caused by our experimental setup.  
518 Indeed, the small mesh of the net bags (200  $\mu\text{m}$ ) used in this scenario, might have promoted the  
519 physical retention of microorganisms, protecting them against local currents, thereby avoiding  
520 their advection and dilution in the surrounding water. Moreover, by eliminating large organisms,  
521 the retention of microorganisms within the bag might have modified the trophic interactions, by  
522 simultaneously providing high concentrations of organic matter and decreasing the grazing  
523 pressure on microorganisms, boosting their proliferation. If this is true, it is possible that the decay  
524 rates obtained for the Micro scenario are greater than those actually occurring in the lagoon.

525 The results from our second experiment corroborate the limited contribution of macrobenthic  
526 organisms in the disappearance of jelly-falls in Thau. The lack of significant difference in  
527 community composition among the M and PC treatments indicates that the addition of jelly-falls  
528 to the seabed did not significantly disturb the community composition, either by attracting or  
529 repelling organisms. However, the species-specific analysis (i.e. ManyGLM), revealed potential  
530 positive responses of some particular taxa. Among those are the *Bittium* sp. in the seagrass  
531 meadows and the *Tritia* sp., *Hexaplex* sp., and *Ruditapes* sp. on the bare sediment. Indeed, peaks  
532 of their abundance were recorded, especially, for the M treatment at 3h, which co-occurred with  
533 the maximum in jellyfish biomass loss rates in our study. This might suggest a limited but still  
534 possible contribution of these macroorganisms consumption to the disappearance of dead  
535 medusae in the lagoon. Nevertheless, only the *Tritia* sp. (Nassariidae family; Galindo et al., 2016)  
536 revealed significant differences between the M and the PC treatments, indicating that, jelly-falls  
537 only significantly attracted this particular species, as also reported by Chelsky et al. (2016).

538 Nassariidae species are common on soft sediment habitats and reported as herbivorous,  
539 carnivorous, but mainly as scavengers, feeding opportunistically on the available dead organic  
540 matter (Morton 2011). These organisms rapidly detect carrions from long distances and move fast  
541 towards the carcasses, but they leave it once they are satiated to avoid potential predators (Morton  
542 2011). They appear to eat large amounts of organic matter (20 to 60% of their weight) in as fast  
543 as 8 minutes (Morton 2011; Lucena et al. 2012) and the amount of time they spend on feeding  
544 appears to be a function of their hunger, with individuals living in habitats with lower food supply,

545 eating a larger amount of food and spending more time feeding (Morton and Chan 1999). This  
546 might explain the peak of *Tritia* sp. abundance observed during the first hours of the experiment  
547 on the bare sediment habitat. Therefore, although our results suggest a limited consumption of *A.*  
548 *coerulea* carcasses by the macrobenthos after the annual blooms of the jellyfish in Thau, the  
549 scavenging activity of the gastropods from the *Tritia* genus might still contribute to the fast  
550 disappearance of its jelly-falls on the lagoon's bare sediment habitats.

551

#### 552 4.2. Potential ecological impacts of jellyfish degradation in Thau

553 Our results suggest that the rapid biomass loss of *A. coerulea* jelly-falls in the Thau lagoon is  
554 mostly caused by a fast degradation of its dead medusae by local microorganisms, with a possible  
555 contribution of some particular species of scavenger on the bare sediment habitat. This might  
556 have several ecological implications in Thau, but also in other shallow coastal habitats.

557 The increase of dissolved inorganic nutrients in the surroundings of decaying jellyfish might  
558 enhance the local phytoplankton and algal production through direct assimilation of dissolved  
559 inorganic compounds (Pitt et al. 2009; Blanchet et al. 2015). Likewise, bacterial production might  
560 be enhanced during the jellyfish degradation process (Tinta et al. 2010, 2012, 2020), which  
561 represents an important food source for microzooplankton (Rassoulzadegan and Sheldon 1986).  
562 This supports the hypothesis that the available energy of jelly-falls can be directly (if consumed  
563 by some scavengers) or indirectly (through microorganisms) transferred to higher trophic levels.

564 However, the ecological consequences of the rapid degradation of *A. coerulea* blooms by the  
565 bacterial community in Thau might also be negative. During the summer, anoxic crisis episodes,  
566 known as 'malaïgues', occasionally occur in the lagoon. They are caused by the bacterial  
567 degradation of high concentrations of organic matter as the combination of high water  
568 temperatures, weak winds, and important water residence times which promotes stratification of  
569 the water column and decreases oxygen exchanges at the surface or with the sea (Harzallah and  
570 Chapelle 2002). During jellyfish degradation, large amounts of highly bioavailable dissolved  
571 organic matter are released and quickly metabolized by the microbial community, decreasing the  
572 dissolved oxygen concentrations in the vicinity of jellyfish carcasses (West et al. 2009; Pitt et al.

573 2009; Sweetman et al. 2016; Chelsky et al. 2016; Guy-Haim et al. 2020). Therefore, the collapse  
574 of the *A. coerulea* bloom in the early summer might amplify the magnitude of summer anoxic  
575 crises, potentially leading to massive benthic community mortalities. Lastly, the summer collapse  
576 of the jellyfish bloom and its degradation by local bacteria might partially contribute to the  
577 summer mortalities of the cultivated oyster *Crassostrea gigas* that sporadically occur in Thau  
578 (Pernet et al. 2012). Indeed, the bacterial degradation of *A. coerulea* medusae has been shown to  
579 enhance abundances of *Vibrio* spp. in the surrounding water (Tinta et al. 2012; Blanchet et al.  
580 2015), and peaks of these microorganisms (from *Vibrionacea* family) have been associated with  
581 *C. gigas* mortalities (Pernet et al. 2012; Cantet et al. 2013). Although this scenario is very  
582 speculative, it needs to be investigated, because shellfish farming is the most important local  
583 economic activity in the lagoon, and shellfish mortality events have dramatic consequences on  
584 the local economy (Pernet et al. 2012).

585

586

## 587 **5. Conclusion**

588 Evaluating the ecological impacts of jellyfish blooms requires identifying the fate of their organic  
589 matter, *i.e.* whether they are scavenged by demersal or benthic predators, decomposed by  
590 microorganisms, or both. In Thau, the absence of large accumulations of dead medusae of *A.*  
591 *coerulea* on the seafloor probably partially results from their ingestion by several local fish  
592 species (Marques et al. 2019) and rapid degradation in the water column (Tinta et al. 2020).  
593 However, we show that, upon their arrival on the sea bed, their fast biomass loss is mainly caused  
594 by their rapid degradation by local microorganisms, favoured by the high local summer  
595 temperatures and the small size of the medusae. Ingestion by benthic scavengers is possible but  
596 limited. Therefore the collapse of the jellyfish blooms in the lagoon has a limited impact on its  
597 macrobenthic communities. Instead, they have the potential to significantly modify local  
598 biogeochemical cycles, reshape ecosystem functioning and, ultimately, affect ecosystem services  
599 with important implications on several economic activities. This supports the need for further

600 investigations on jellyfish degradation in coastal lagoons and calls for incorporating this process  
601 in ecosystem-based models.

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