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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.

48

49

1. Introduction

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

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

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

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

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 30th and

149　June 07th, 2018). However, all the medusae used were collected alive on the same day (May 28th,

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^3 tanks (ca. 100 ind.m^{-3}) 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.

159

Fig. 1: Schematic representation of the two *in situ* experiments performed in this study: a) assessing jellyfish biomass loss rates under different scenarios of medusae accessibility for benthic scavengers; b) assessing the impact of jellyfish degradation on the macrobenthic community composition.
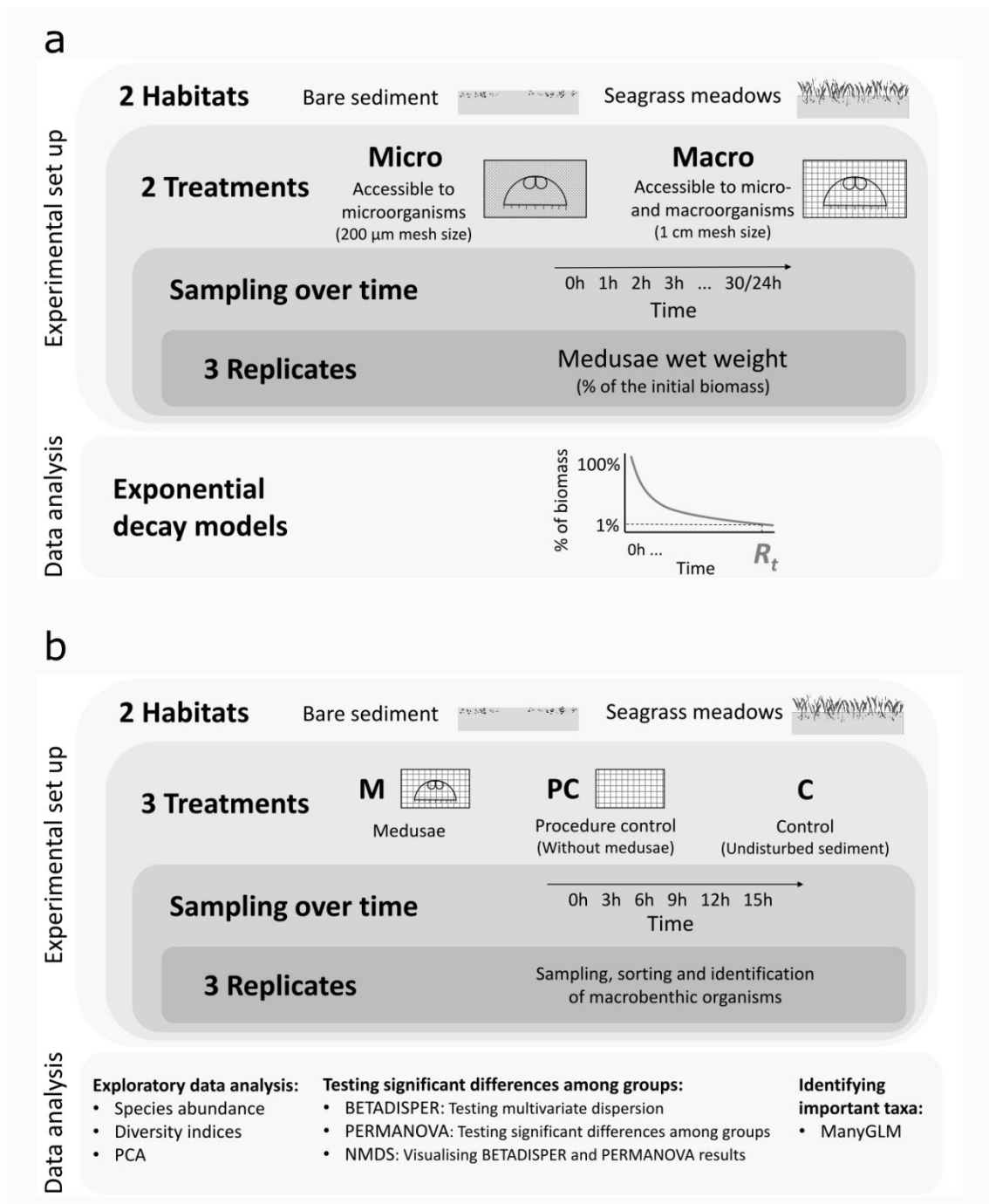
2.2. Jellyfish biomass loss rates

2.2.1. Experimental set-up

Jellyfish biomass loss rates were assessed both on the bare sediment and seagrass meadows habitats under two different scenarios of accessibility to dead medusae for the macrobenthic organisms of the lagoon (Fig.1a).

170   The first scenario (Micro) involved placing individual medusae in 20×15 cm net bags with a

171   mesh size of 200 µm 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 20×15 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 λ 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 λ, 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^2, 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^2). 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 ± 0.7 ℃

290 and 23.4 ± 0.5 ℃ 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 λ 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, *Rt* 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 (λ in hours) and degradation time (*Dt* in hours).

Scenario	Initial W (g ± SD)	Initial BD (cm ± SD)	λ (h)	*Dt* (h)

	Bare sediment			
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
	Seagrass meadows			
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

309

310
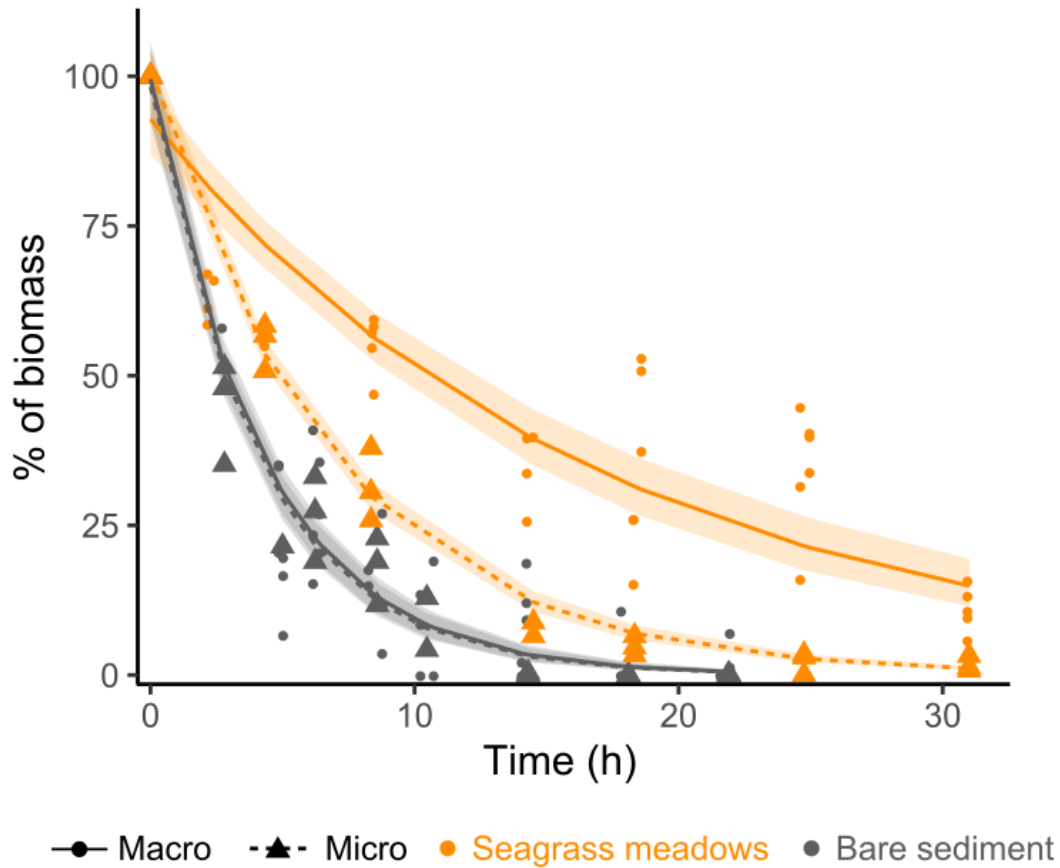
Fig. 2: Dynamic of *A. coerulea* medusae biomass loss in both habitats (bare sediment and seagrass meadows) under both accessibility scenarios (Macro and Micro). Exponential decay models (lines) were fitted to the non-averaged data of biomass (in % of the initial medusae biomass), with 95% confidence intervals (shadow areas).

315

Table 2: Estimation of the parameters (M0 and λ) by the GNLS models used to assess differences between scenarios within each habitat. Significant differences (p-value < 0.05) are indicated in bold.

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

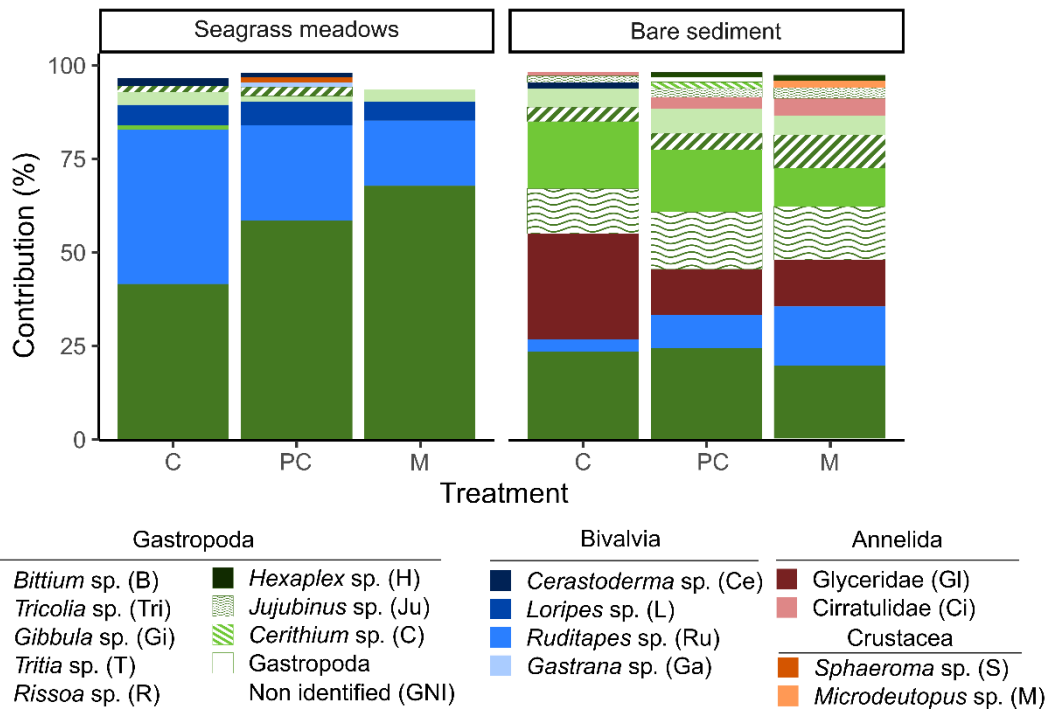|				
Macro (Intercept)	0.059	0.004	14.525	< 0.01
Micro	0.087	0.017	5.142	**< 0.01**

318

319

3.2. Benthic community changes

3.2.1. General composition of macrobenthic communities

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

Fig. 3: Contribution of the most important taxa to the total abundance of the community on the seagrass meadows and bare sediment, in each treatment (M: Medusae, C: Control, PC: Procedure control). Only species that contributed to more than 1% of the total abundance are presented.

3.2.2. Abundance and diversity indices

The abundance of macrobenthic organisms was, on average, 10 times higher (p-value < 0.001, Fig.4A and B, Table 3) on the seagrass meadows than on the bare sediments ($6\ 800 \pm 8830$ and 637 ± 717 ind.m^{-2}, respectively). It was significantly affected by all factors considered (habitat, sampling time, and treatment, Table 3), but the overall interaction among these factors was not significant, indicating that treatment and time similarly affected the abundance of organisms within each habitat. Differences in total macrobenthic abundance among treatments were only observed at 3h on the seagrass meadows, and 3 and 9h on the bare sediments (Tukey HSD, p-value < 0.05; Fig. 4A and B). This was particularly evident at 3h, when a peak of macrobenthos abundance was detected for both M and PC (both over 1500 ind.m^{-2} and 190 ind.m^{-2}, on seagrass meadows and bare sediment, respectively), with significantly higher values than in C (Tukey HSD, p-value < 0.05). However, no differences in abundance were observed between M and PC (Tukey HSD, p-value > 0.05) over the whole experiment time. In both habitats, the abundance of macrobenthic organisms in the controls did not vary significantly over time (Tukey HSD, p-value

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 α = 0.05.

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

371
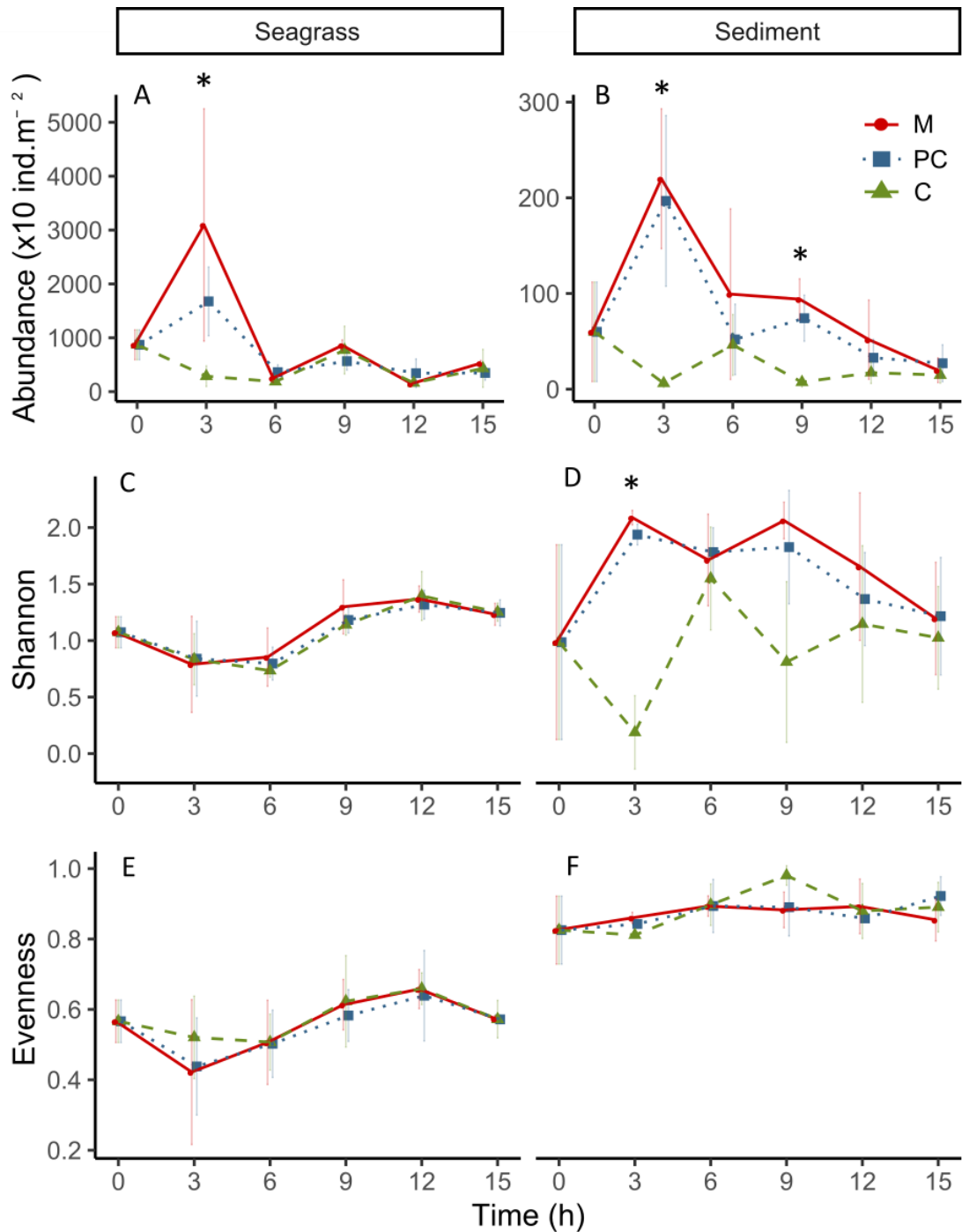
Fig. 4: Abundance of macrobenthic organisms (A and B, note the different scales for the two habitats), Shannon diversity index (C and D), and Pielou's equitability index (Evenness) on the seagrass meadow (A, C, and E) and bare sediment (B, D, and F) habitats. For each variable, dots represent average values and vertical bars standard deviations for each treatment (M: medusae, PC: procedure control, C: control). Asterisks indicate significant differences between treatments at $\alpha = 0.05$.

3.2.3. Differences in the community composition

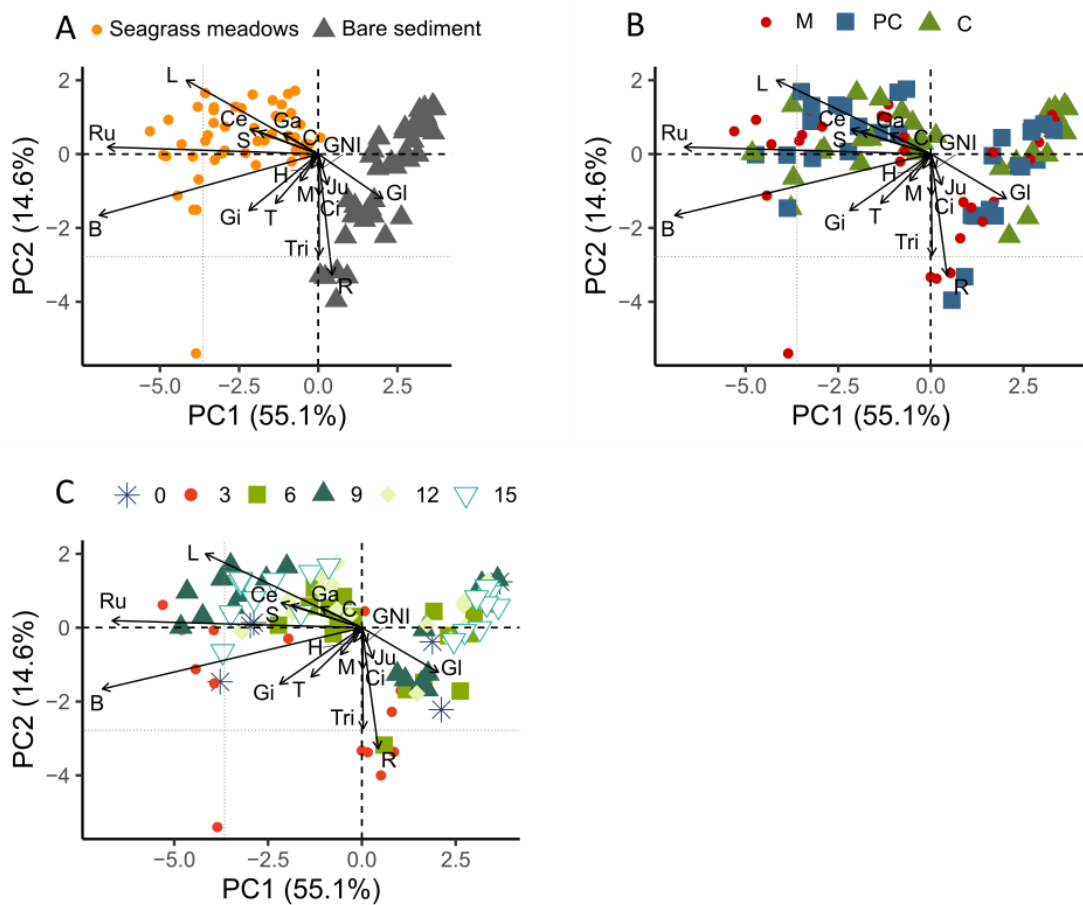In the principal component analysis (PCA), only the first two axes (PC1 and PC2, Fig. 5) were retained since they represent the majority of the variability of the data (69.7%). These axes discriminated the samples from the two habitats (Fig. 5A), showing that habitat type is the main

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-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-value = 0.6, Fig. 6A), but not across sampling time (F = 2.5, p-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-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-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-value = 0.8, Fig. 6A), but showed significant differences over time (F= 9.3,

410   p-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-value = 0.7 and F = 0.4, p-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-value < 0.01 and F = 4.8 and p-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-value = 0.09) indicating that changes in community composition among treatments were

419   not affected by sampling time.

420
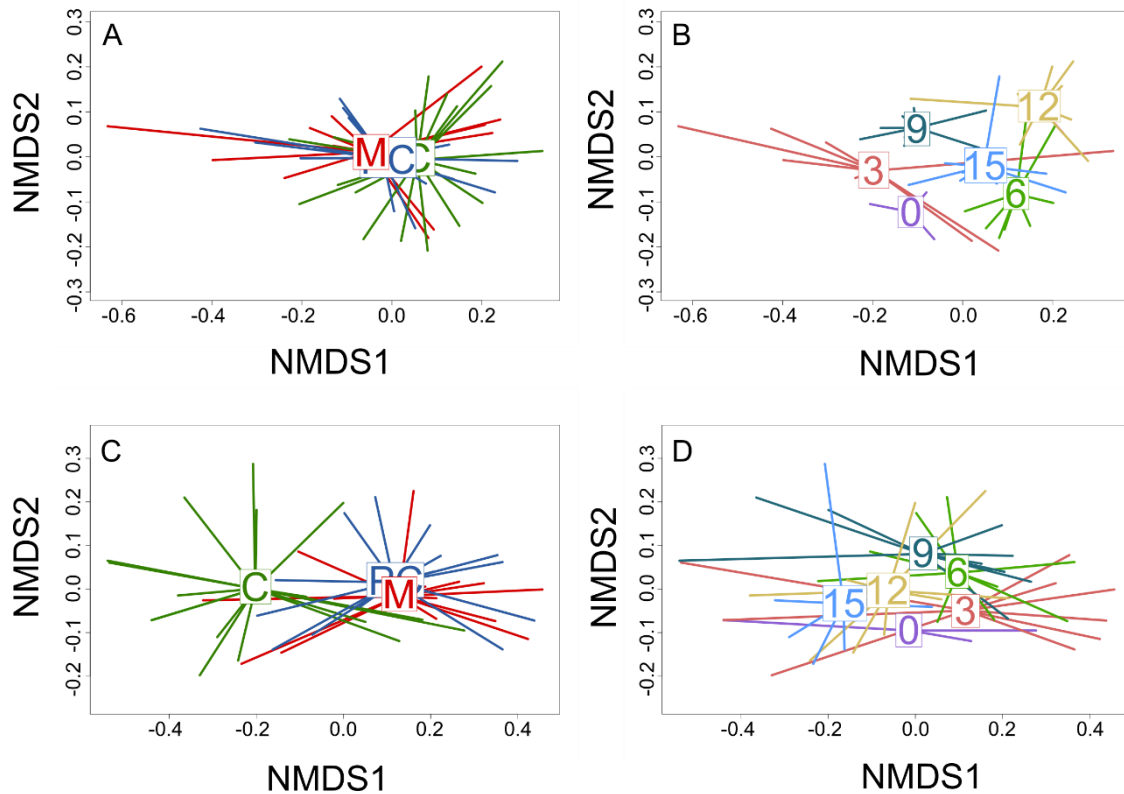
Fig. 6: Results from the Nonmetric Multidimensional Scaling (NMDS) analysis on the seagrass meadows (A and B) and the bare sediment habitats (C and D), showing the dispersion of the samples (lines) around the centroid of each group, by treatment (A and C): M: medusae, PC: procedure control, C: control; and by sampling time in hours (B and D).

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

This analysis allowed the identification of the taxa that contributed most to the observed differences between treatments (Table 4): *Bittium* sp. in the seagrass meadows and *Tricolia* sp., *Hexaplex* sp., *Tritia* sp. and *Ruditapes* sp. on the bare sediment habitats (Fig. 7). These organisms exhibited higher abundances in M and PC at 3h but no difference of abundances between M and PC treatments were observed ($P_{adj} > 0.05$). Indeed, differences between M and PC treatments were only observed for *Tritia* sp. ($P_{adj} = 0.04$), which showed higher abundances for M during the first 9h of the study period (up to 14.9 ± 3.6 x 10 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

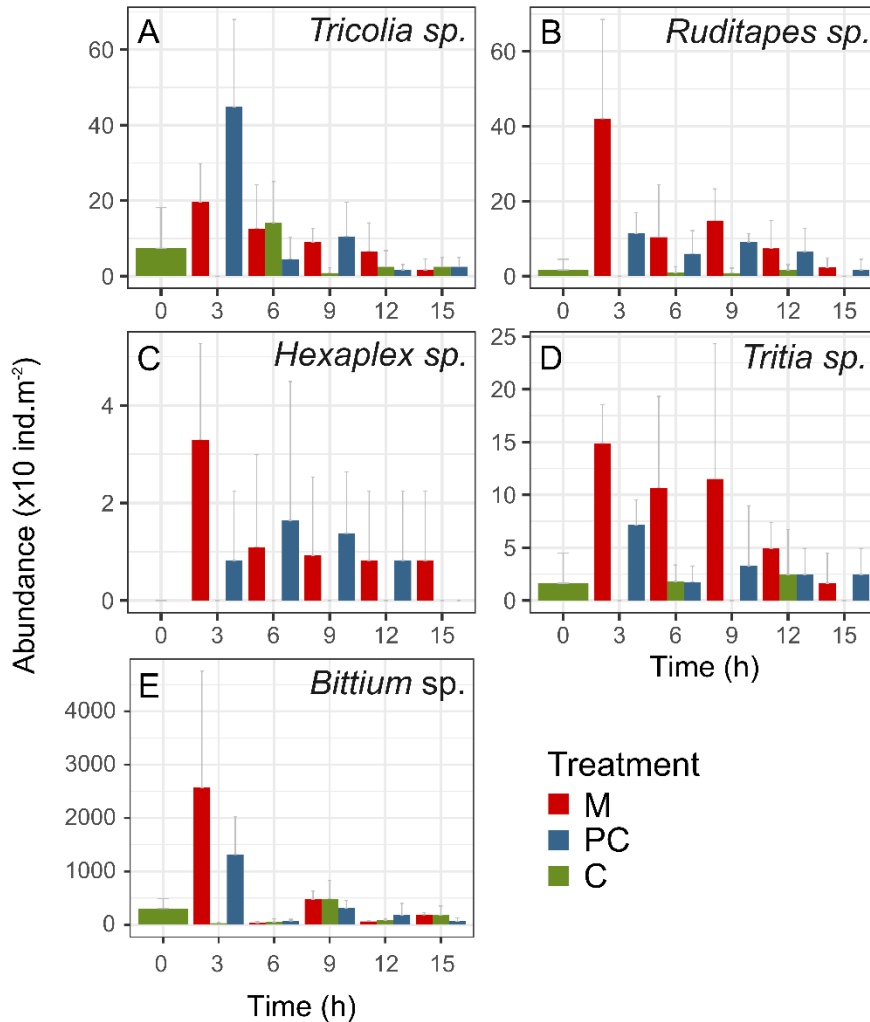442   of dead *A. coerulea* medusae on the bottom.

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

Glyceridae	3.377	0.596	5.275	0.892	10.271	0.794
Tritia sp.	21.770	**0.001**	12.924	0.136	12.333	0.638

447

448

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.

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455   **4.   Discussion**

456   *4.1. The contribution of macrobenthic consumption to the fast degradation of jellyfish in*

457   *Thau*

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

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

460   (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^{-1} (1.42 to 5.8 d^{-1}) 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 ºC; 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 µm) 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 *coreulea* 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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