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Abstract

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

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

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^{-2} (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^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

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

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

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

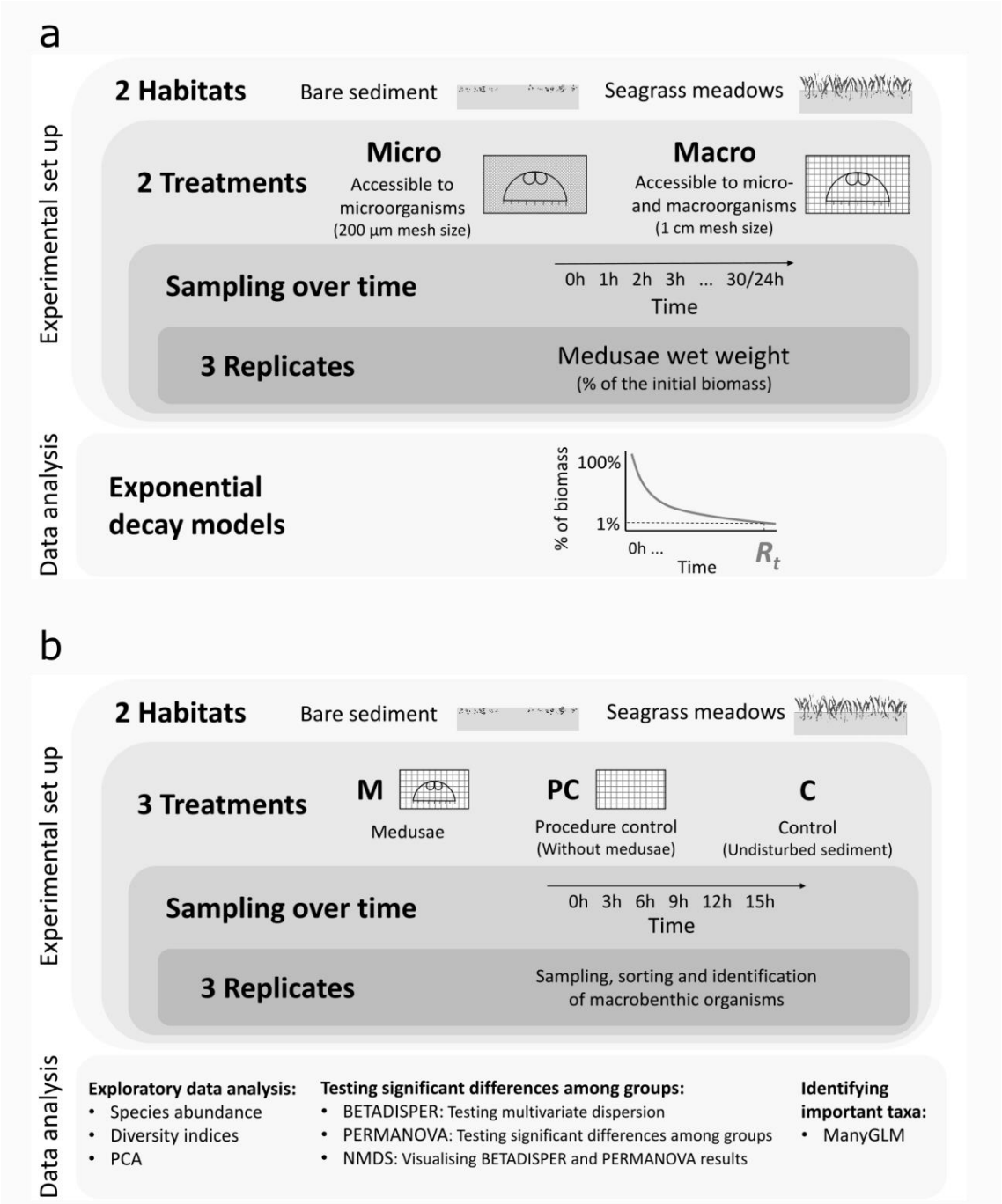

Fig. 1: Schematic representation of the two *in situ* experiments performed in this study: a) assessing jellyfish biomass loss rates under different scenarios of medusae accessibility for benthic scavengers; b) assessing the impact of jellyfish degradation on the macrobenthic community composition.

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).

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

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

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

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

2.3.2. Data analysis

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

3. Results

3.1. Jellyfish biomass loss rates

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

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

Table 1: Mean initial wet weights (W) and bell diameters (BD) of the dead *A. coerulea* medusae used in each experiment 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

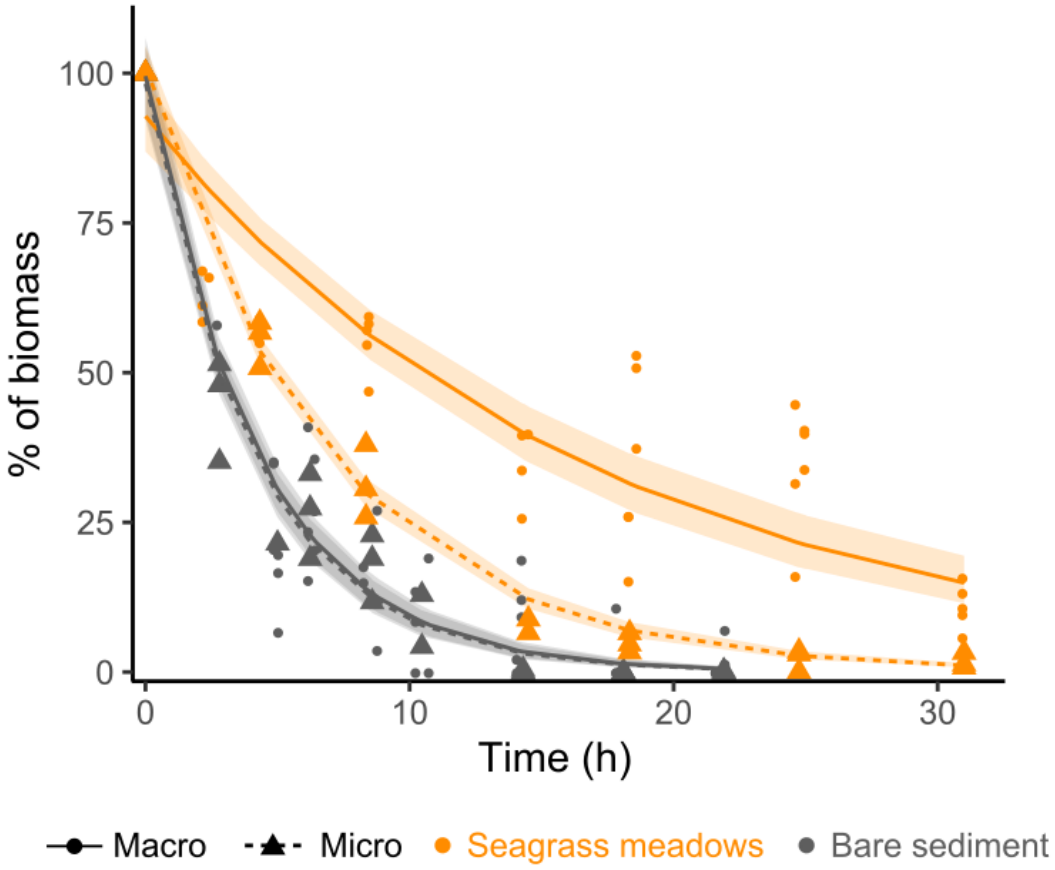

Fig. 2: Dynamic of *A. coerulea* medusae biomass loss in both habitats (bare sediment and seagrass meadows) under both accessibility scenarios (Macro and Micro). Exponential decay models (lines) were fitted to the non-averaged data of biomass (in % of the initial medusae biomass), with 95% confidence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

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

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%).

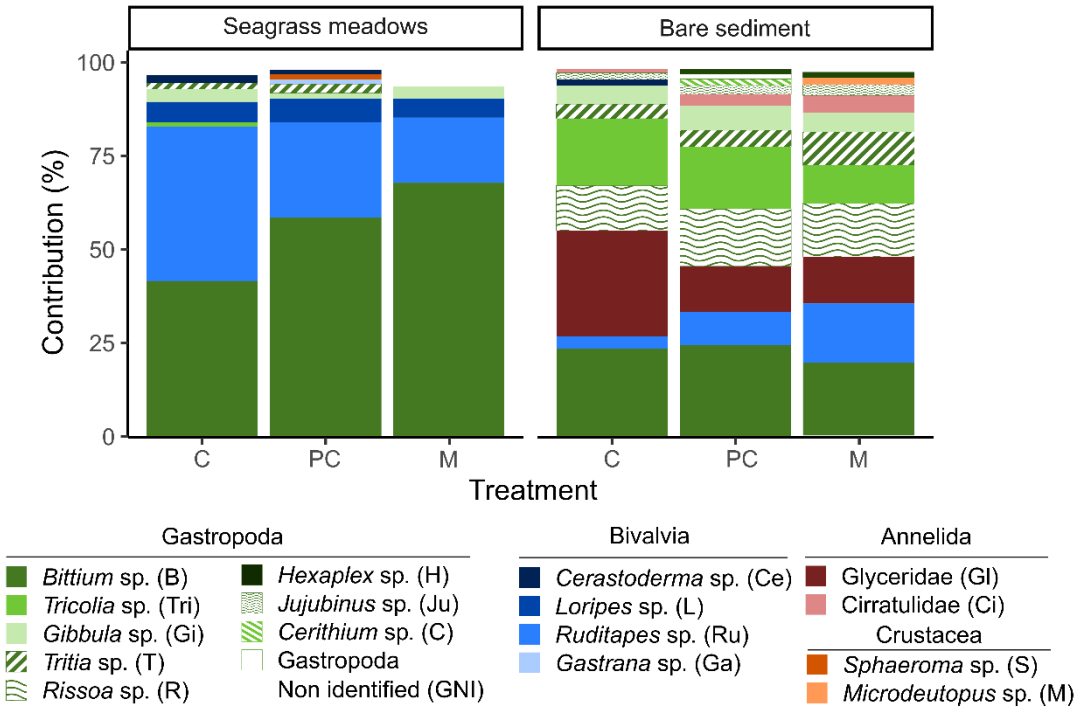

Fig. 3: Contribution of the most important taxa to the total abundance of the community on the seagrass meadows and bare sediment, in each treatment (M: Medusae, C: Control, PC: Procedure control). Only species that contributed to more than 1% of the total abundance are presented.

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 ± 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 $\alpha = 0.05$.

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

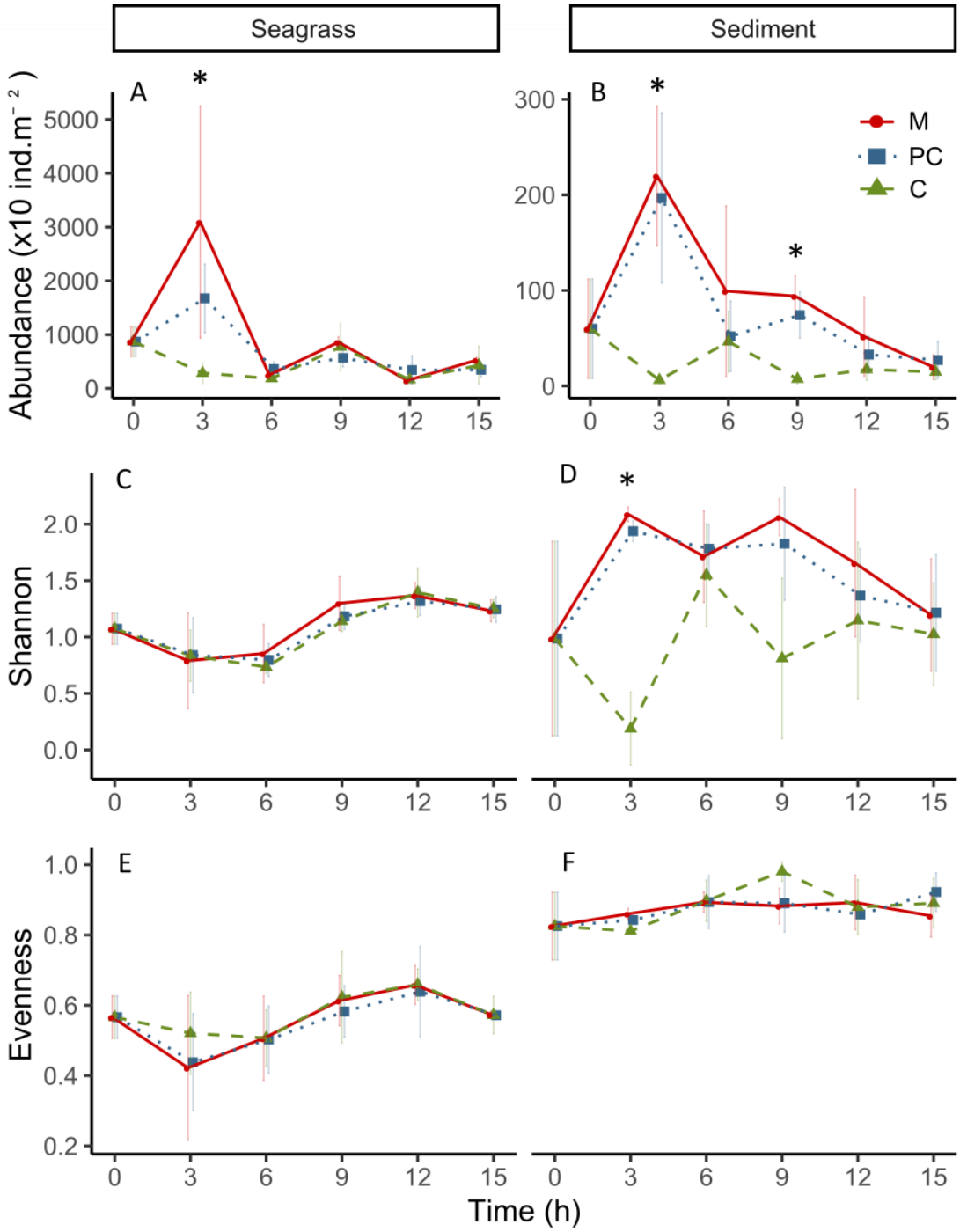

Fig. 4: Abundance of macrobenthic organisms (A and B, note the different scales for the two habitats), Shannon diversity index (C and D), and Pielou's equitability index (Evenness) on the seagrass meadow (A, C, and E) and bare sediment (B, D, and F) habitats. For each variable, dots represent average 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

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

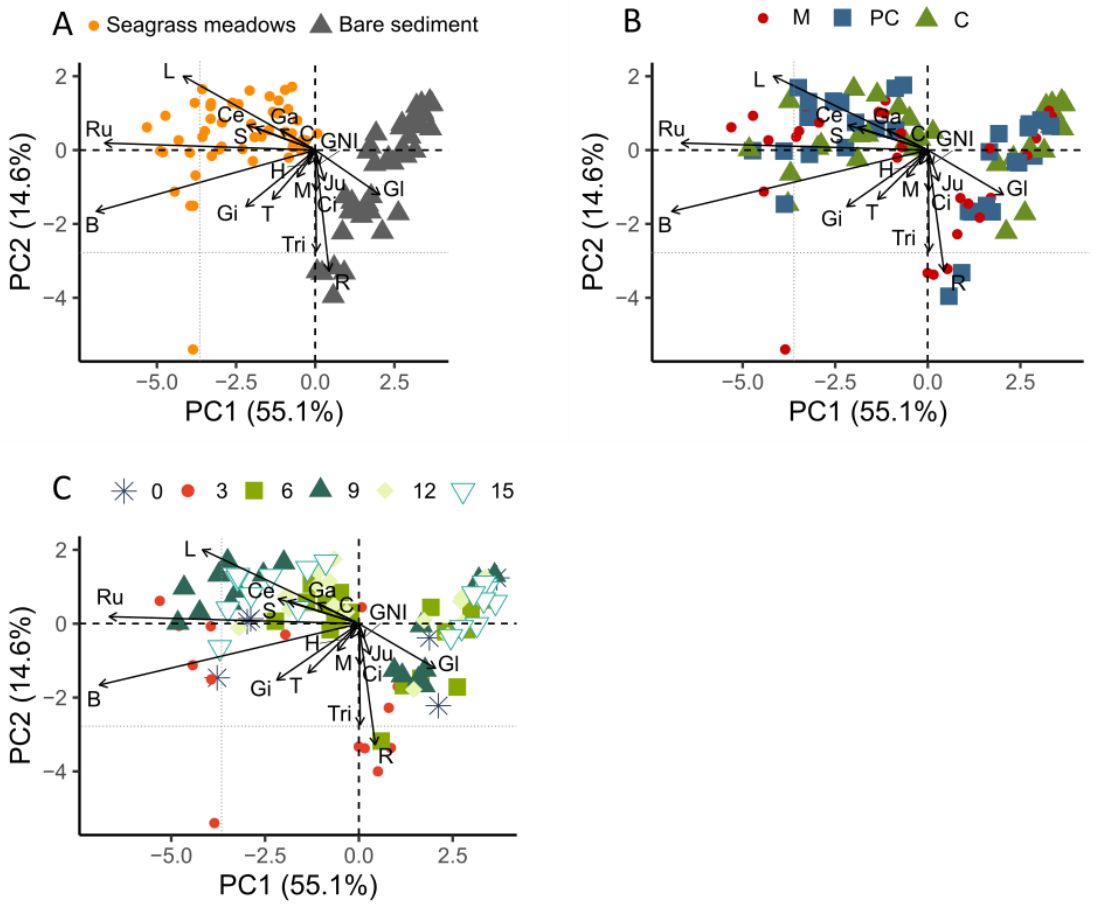

Fig. 5: Biplots of Principal Component Analysis (PCA). Samples (points) and taxa (arrows) are presented. In A, B, and C, samples are identified according to habitat, treatment (M: medusae, PC: procedure control, C: control), and sampling time (in h), respectively. Grey dotted lines are indicative thresholds to identify the samples with high Euclidean distance from the centre. For the sake of simplicity, taxa names are abbreviated (see Fig. 3 with taxa codes).

The results from BETADISPER did not detect significant changes in community dispersion over time (F= 0.7, p=0.6) or among treatments (F=2.5, p=0.08). However, the community dispersion

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

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

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

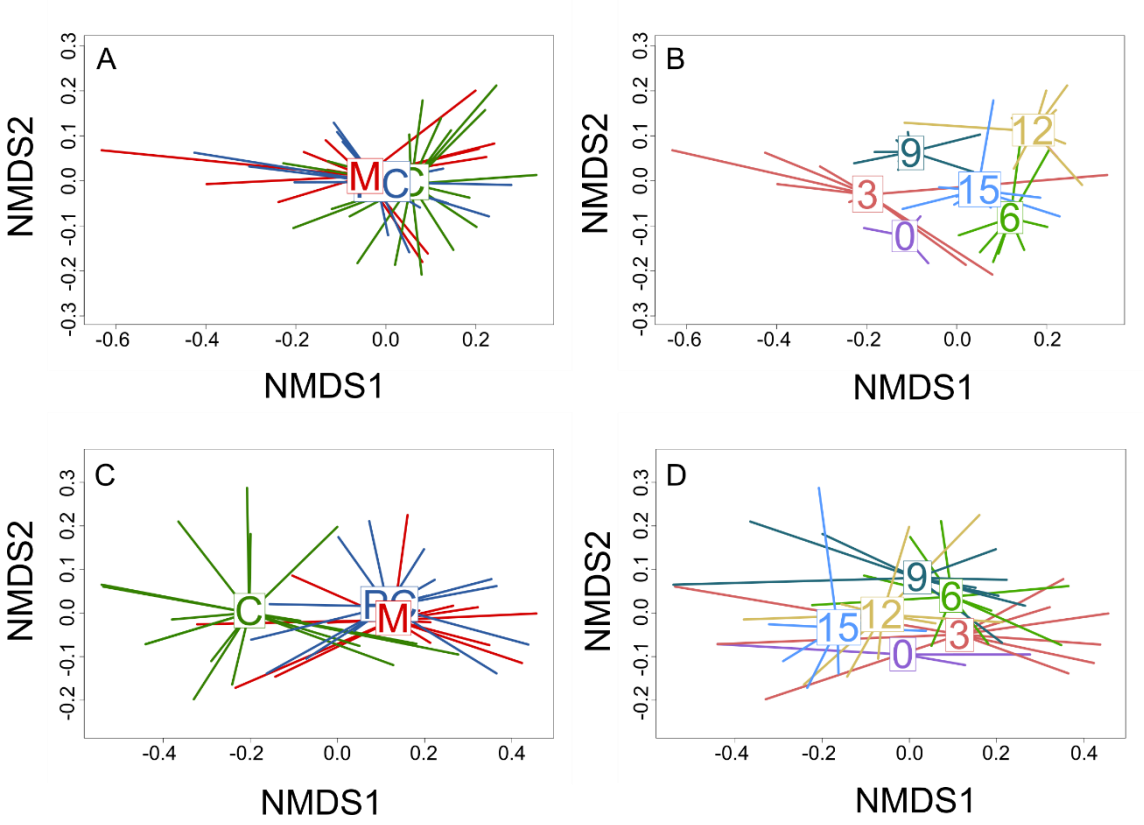

Fig. 6: Results from the Nonmetric Multidimensional Scaling (NMDS) analysis on the seagrass meadows (A and B) and the bare sediment habitats (C and D), showing the dispersion of the samples (lines) around the centroid of each group, by treatment (A and C): M: medusae, PC: procedure control, C: control;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

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

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

	Treatment		**Sampling time**		**Treatment: Sampling time**	
Seagrass meadows	**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

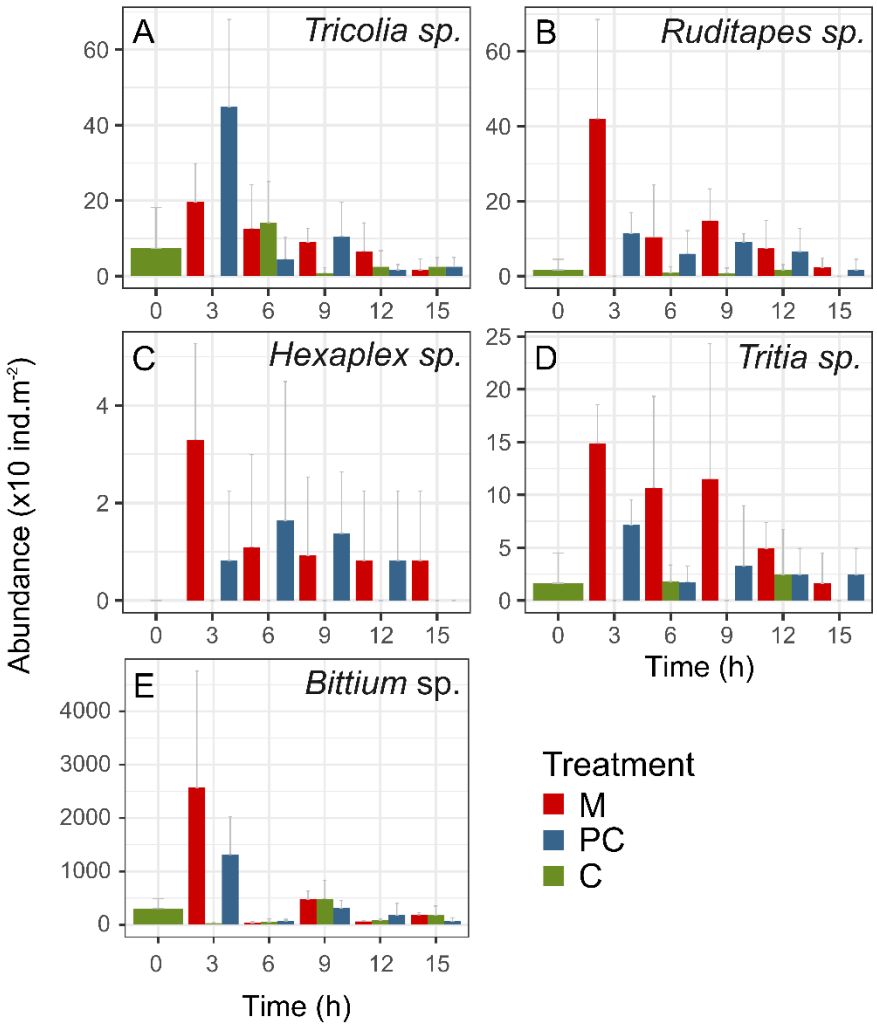

Fig. 7: Abundance of the macrobenthic organisms which showed significant contributions to the observed differences among treatments and sampling time (ManyGLM) on bare sediment (A to D) and seagrass meadows (E) habitats. Note the differences in scale between graphs.

4. Discussion

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

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

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

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

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

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

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

The results from our second experiment corroborate the limited contribution of macrobenthic organisms in the disappearance of jelly-falls in Thau. The lack of significant difference in community composition among the M and PC treatments indicates that the addition of jelly-falls to the seabed did not significantly disturb the community composition, either by attracting or repelling organisms. However, the species-specific analysis (i.e. ManyGLM), revealed potential positive responses of some particular taxa. Among those are the *Bittium* sp. in the seagrass meadows and the *Tritia* sp., *Hexaplex* sp., and *Ruditapes* sp. on the bare sediment. Indeed, peaks of their abundance were recorded, especially, for the M treatment at 3h, which co-occurred with the maximum in jellyfish biomass loss rates in our study. This might suggest a limited but still possible contribution of these macroorganisms consumption to the disappearance of dead medusae in the lagoon. Nevertheless, only the *Tritia* sp. (Nassariidae family; Galindo et al., 2016) revealed significant differences between the M and the PC treatments, indicating that, jelly-falls only significantly attracted this particular species, as also reported by Chelsky et al. (2016). Nassariidae species are common on soft sediment habitats and reported as herbivorous, carnivorous, but mainly as scavengers, feeding opportunistically on the available dead organic matter (Morton 2011). These organisms rapidly detect carrions from long distances and move fast towards the carcasses, but they leave it once they are satiated to avoid potential predators (Morton 2011). They appear to eat large amounts of organic matter (20 to 60% of their weight) in as fast as 8 minutes (Morton 2011; Lucena et al. 2012) and the amount of time they spend on feeding 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.

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

5. Conclusion

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

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

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The authors declare that they have no competing interests.

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