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Valentina Costa, Antonio Mazzola, Francesca Rossi, Salvatrice Vizzini. Decomposition rate and invertebrate colonization of seagrass detritus along a hydrodynamic gradient in a Mediterranean coastal basin: The Stagnone di Marsala (Italy) case study. *Marine Ecology*, 2019, 40 (6), pp.e12570. <10.1111/maec.12570>. <hal-02399814>

HAL Id: hal-02399814

<https://hal.science/hal-02399814v1>

Submitted on 14 Dec 2020

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1 **Hydrodynamics effects on decomposition rate and invertebrate colonization of seagrass detritus in a**
2 **coastal basin: the Stagnone di Marsala (Italy) case study**

3

4 **Decomposition of seagrass leaf litter**

5

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18 **Acknowledgements**

19 This study was supported by the Flagship Project RITMARE—Italian Research for the Sea—funded by the
20 Italian Ministry of Education, University and Research. We are grateful to A. Savona for field assistance and
21 E. A. Aleo for help with laboratory analyses.

22

23 **Abstract**

24 Seagrass leaf litter decomposition is a key component of marine carbon flow driven by both biotic and abiotic
25 factors, including water movement. In this study, we analyse *Posidonia oceanica* litter decomposition and
26 invertebrate colonization in three sites with different hydrodynamics in a coastal basin. Litterbags were put on
27 the seabed along a gradient of distance from the open-sea, implying a different level of water exchange. Leaf
28 litter mass loss and carbon and nitrogen concentration were analysed and density and biomass of benthic
29 invertebrates colonising litterbags were recorded after 3, 7, 14, 47, 101, 152 and 221 days. Results showed
30 that in the most sheltered site, the leaf litter decomposition rate, the invertebrate density and biomass and
31 the detrital carbon release were the lowest. The reduction of the decomposition rates of seagrass leaves in

32 the site characterised by low hydrodynamic forces may promote organic matter burial and carbon stocks,
33 emphasising the role of coastal basins such as ponds and lagoons as sinks of carbon and their viability for
34 blue carbon areas.

35

36 **Key-words:** seagrass detritus; litterbag; benthic invertebrate; carbon; nitrogen.

37

38 **Highlights**

- 39 - Seagrass decomposition was studied in sites with different hydrodynamic conditions in a coastal
40 basin
- 41 - Decomposition rate and nutrient release were slower in the site less exposed to the open-sea
- 42 - Benthic invertebrate density and biomass had their minimum in the site less exposed to the open-
43 sea
- 44 - Low decomposition may promote organic matter burial and carbon stocks in low hydrodynamic
45 condition

46

47 **1. Introduction**

48 Seagrass meadows are ecologically important because of their high primary productivity, provision of habitat
49 and supporting of high biodiversity levels (Hemminga & Duarte 2000). Seagrasses with mangroves and
50 saltmarshes, trap and sequester carbon, that in the last years has been referred as 'Blue Carbon'
51 (Nellemann et al. 2009). The estimates of organic carbon (C_{org}) sequestered in seagrass meadows, have
52 recognized them as global hotspots in the Blue Carbon global balance (Fourqurean et al. 2012). In the
53 Mediterranean Sea, the endemic species *Posidonia oceanica* (L.) Delile covers only 1-2% of the seabed
54 (25,000-50,000 km², Pasqualini et al., 1998), but produces up to 3,499 million tons of carbon annually
55 (Pergent et al. 1997) and represents the largest recognized pools of C_{org} stored in living seagrass
56 (Fourqurean et al. 2012). In seagrass meadows, the grazing pathway is highly variable, depending on the
57 study site and time of sampling, with a range between ~3% and 100% of net primary production directly
58 consumed by herbivores (Heck & Valentine 2006 and reference herein). The amount of primary production
59 not directly used becomes litter, which can enter the brown food web or be buried into the sediment (Cebrián
60 & Duarte 2001, Boudouresque et al. 2015). Therefore, seagrasses act as a significant source of C_{org} also
61 beyond the area directly occupied by the meadows, through the detrital biomass. Duarte & Krause-Jensen
62 (2017) pointed out as the potential sequestration of seagrass carbon exported beyond the meadows may
63 approach 30% of the carbon sequestered within meadows. Detritus act as faunal magnets (Duggins et al.
64 2016, Remy et al. 2017), attracting fungi and bacteria, but also benthic invertebrates that use them as food
65 and shelter (Heck et al. 2008, Remy et al. 2018). Detritus undergoes decomposition and recycling that allows
66 it to be channeled to higher trophic levels (Michel et al. 2015). The pathway undertaken by detrital leaves is a
67 crucial component of the flow of energy and matter regulated by seagrass meadows (Romero et al. 2006).
68 Despite the recognition of the importance of the detritus, a real estimate of the contribution of this
69 compartment to the Blue carbon global balance is unknown.

70 Biotic and abiotic variables regulate seagrass decomposition rate (e.g. Enríquez et al., 1993; Mateo and
71 Romero, 1996). Litter quality, such as carbon and nitrogen concentration, influence its decomposition and
72 palatability for consumers (Enríquez et al. 1993, Apostolaki et al. 2009). Abiotic conditions are known to
73 affect decomposition both directly, by influencing rates of biological reactions, and indirectly by modifying leaf
74 quality and/or consumer communities (Nicastro et al. 2012). Among physical variables, the reduced
75 hydrodynamics typical of coastal basins may decrease the mechanical action on the detritus, slowing down
76 the decomposition process, while the increase in nutrients and rise in temperature may stimulate and
77 facilitate the activity of heterotrophic bacteria (Mateo & Romero 1996, Lopez et al. 1998), accelerating the

78 decomposition, but with probably inverse effects at high temperature (Pedersen et al. 2011). Moreover, the
79 high environmental variability of coastal basins, in terms of daily and seasonal variation (Kjerfve 1994), can
80 affect invertebrate community composition. Evolution selects a small number of taxa capable of tolerating
81 this stressful condition, lowering community diversity while abundance and biomass increase (Arias & Drake
82 1994, Mistri et al. 2001), with potential consequences for the ecosystem functions. The role of benthic
83 invertebrates as direct detritus shredders and enhancers of microorganism activity is well recognized (Graca
84 1993), despite invertebrate abundance and decomposition rate are not always positively correlated (Dye
85 2006), as the macrofauna abundance seem to follow an exponential trend with an upper limit related to the
86 litter quality (Fazi & Rossi 2000). As the distribution of invertebrates in confined waters, like lagoons and
87 coastal basins, is strongly influenced by water movement (Guelorget & Perthuisot 1983, Constable 1999),
88 seagrass decomposition rate and therefore nutrients dynamics may respond in the same way.

89 In this experimental study, we deliberately added *P. oceanica* leaf litter across a gradient of hydrodynamics in
90 a Mediterranean semi-enclosed coastal basin and simultaneously followed the decomposition process, the
91 nutrient dynamics and the colonisation by benthic invertebrates. The specific objectives of the research were
92 (1) to test the null hypothesis of no significant differences of seagrass decomposition and invertebrates
93 colonization across a hydrodynamic gradient; (2) to analyse organic carbon and nitrogen dynamics during
94 seagrass decomposition.

95

96 **2. Methods**

97 **2.1 Study sites and experimental set-up**

98 The study was conducted in the Stagnone di Marsala, a semi-enclosed coastal basin (surface of 20 km²;
99 average depth of 1 m) in western Sicily (Italy) (Fig. 1). The basin is connected to the Mediterranean Sea by a
100 northern and a southern opening, the former narrower and shallower (400 m wide, 0.3-0.4 m deep) than the
101 latter (1200 m wide, 1.0-1.5 m deep). The sandy-muddy sediments are colonised by the seagrass
102 *Cymodocea nodosa* (Ucria) Ascherson. *P. oceanica* patches are present in the central part of the basin and a
103 natural *P. oceanica* reef emerges in the southern region (Tomasello et al. 2009), creating two
104 geomorphologically different sub-basins. The entire area is oligotrophic (Sarà et al. 1999). Three sites were
105 chosen according to their hydrodynamic regime with the same depth (0.8 m), vegetation coverage (*C.*
106 *nodosa* with *P. oceanica* patches) and sediment grain-size (sand 80-90%, silt/clay 5-15%, gravel 0-5%): Site
107 1 (N37° 52.284' E12° 27.517') in the central-northern basin, Site 2 (N37° 50.453' E12° 27.198') in the
108 southern basin and Site 3 (N37° 51.613' E12° 26.339') outside the basin (Fig. 1). The exposure level to the

109 open sea in the three sites was obtained from the Intertidal Dispersion Coefficient (IDC, La Loggia et al.,
110 2004). The IDC ($\text{m}^2 \text{s}^{-1}$) is a useful tool for characterising the dispersion of a point in the water body,
111 integrating data of, among others, water current velocity, wind shear stress and fetches: when the IDC is
112 high, water exchange is strong (hence residence time is short) (Cheng & Casulli 1992). A clear difference
113 was shown between the central-northern and the southern sub-basins (Fig. 1), with the latter showing higher
114 IDC values (about $23.8 \text{ m}^2 \text{ s}^{-1}$) than the former (about $11.2 \text{ m}^2 \text{ s}^{-1}$) (La Loggia et al. 2004). Since the selected
115 sites were located along a well-documented gradient within the basin, we used the factor Site as a proxy of
116 the hydrodynamic condition of the area.

117 Seagrass leaves were collected close to *P. oceanica* patches within the Stagnone di Marsala in May 2010.
118 Adult leaves naturally detached from the plants (due to ageing or mechanical action) were cut into 10 cm-
119 long fragments and only the central section was used, to minimise heterogeneity in thickness and toughness
120 (Mancinelli 2012). Aliquots of leaf fragments were dried at 60°C to constant weight, weighed ($3.000 \pm 0.001 \text{ g}$
121 initial dry mass) and enclosed in 1 mm mesh litterbags (10x10 cm). The mesh size of the litterbags was
122 chosen to reduce the amount of detritus lost from mechanical fragmentation but not limiting
123 macroinvertebrates colonization (Walker et al. 2001). Twenty-four litterbags were added to each site and
124 tethered to steel rods anchored to the bottom.

125 **2.2 Sampling and laboratory procedures**

126 The litterbags were deployed on June 11th 2010. After 6 hours, three bags per site (time 0) were collected.
127 Remaining bags were collected in triplicate at each site after 3, 7, 14, 47, 101, 152 and 221 days. Each bag
128 was carefully enclosed underwater in a plastic bag and preserved in a cooler for transportation to the
129 laboratory. At each sampling time, temperature (resolution: $\pm 0.01^\circ\text{C}$), salinity (± 0.01) and dissolved oxygen
130 concentration (DO, $\pm 0.01 \text{ mg l}^{-1}$) were measured in the seawater column above the litterbags in triplicate with
131 a HYDROLAB DS5 multiparametric probe.

132 In the laboratory, litterbags were gently washed and invertebrates inside the litterbags were carefully
133 removed. *P. oceanica* leaf fragments from each bag were dried (60°C , 72 h) and weighed (Dry Mass, DMDM,
134 $\pm 0.001 \text{ g}$). Subsamples were grounded and analysed for organic carbon (C%) and nitrogen (N%)
135 concentration using a Flash EA 1112 Thermo-Electron analyser.

136 Invertebrates were counted and identified at species level. Organisms were dried (60°C , 72 h) and weighed
137 (DM). List of all species identified was included in Table 1.

138 **2.3 Data elaboration and statistical analysis**

139 Differences in the mass loss, seagrass leaf litter variables (%C, %N and C:N ratio) and density and biomass
140 for each invertebrate group between sites during the experiment were tested via a one-way repeated-
141 measures ANOVA (RM-ANOVA): Site (3 levels) was the between-subject factor and Time (i.e. sampling
142 events) the repeated-measures (within-subject) factor.

143 Decomposition rate was estimated as the loss of dry mass during time and fitted to the exponential curve
144 (Petersen & Cummins 1974): $W_t = W_0 * e^{-kt}$, where W_t is the dry mass (g) remaining at time t (days), W_0 is
145 the initial dry mass, and k is the decomposition constant (day^{-1}). We used one-way ANOVA with Site (3
146 levels) as categorical factor to assess the statistical significance of the effect of Site (3 levels, $t=221$ days) on
147 decomposition rate.

148 Prior to ANOVAs, all data were checked for normality and homoscedasticity. In the event of significant effects
149 on the factors investigated, post-hoc comparisons were performed using Tukey's Honest Significant
150 Difference (Zar 1996). Univariate statistical analysis were performed with R version 3.5.1.

151 Differences in density and biomass of invertebrates species during the experiment were investigated at a
152 multivariate level, through analysis of variance based on permutations (PERMANOVA, Anderson, 2005),
153 using a two-way model with factors Site (3 levels, fixed) and Time (8 levels, random). Data were square-root
154 transformed to build a matrix of Bray-Curtis similarity coefficients. When the number of random permutations
155 in the PERMANOVA analysis was not sufficient to allow a reasonable permutation test, the p -value was
156 obtained using a Monte Carlo random sample from the asymptotic permutation distribution (Anderson 2005).
157 The similarity percentage routine (SIMPER) was used to highlight which invertebrate species provided the
158 largest contribution to dissimilarities between groups (Clarke & Warwick 2001). Multivariate analyses were
159 performed with PRIMER v6 software (Clarke & Warwick 2001).

160

161 **3. Results**

162 **3.1 Seawater column variables**

163 Seawater parameters were measured in the water column during the experiment. Temperature showed a
164 clear seasonal trend with a range of 13.3-27.9°C and with average higher values at Site 1 than at Site 2 and
165 Site 3 (23.4±4.9, 22.8±4.5 and 22.1±4.1°C, respectively). Salinity ranged from 38.0 to 48.0, with higher
166 values at Site 1 (overall mean: 44.8±4.0) than at Sites 2 and 3 (40.4±1.4 and 39.2±0.7, respectively).
167 Dissolved oxygen concentration (DO) ranged from 5.5 to 8.9 mg l^{-1} with the same average value in the three
168 sites 7.3±0.9 mg l^{-1} .

169 **3.2 Seagrass leaf litter decomposition**

170 Seagrass leaf litter decomposition was significantly affected by the factor Site (RM-ANOVA, $F_{2,14}=4.03$,
171 $p<0.05$). A rapid mass loss of *P. oceanica* leaf litter was observed at the first sampling date (0 days), with an
172 overall mean remaining weight of 2.3 ± 0.1 g (mean \pm s.d.) and no differences between sites (Tukey test,
173 $p>0.05$). More than 60 and 70% of leaf mass loss occurred after 221 d in Sites 2 and 3 respectively,
174 compared with a loss of only 40% in Site 1 (Fig. 2).

175 Overall, the decomposition process followed an exponential decay, with decomposition rate coefficients (k_{221})
176 significantly higher in Sites 2 (0.0030 ± 0.0004 day⁻¹, r^2 of the exponential regression line = 0.90) and 3
177 (0.0044 ± 0.0003 day⁻¹, $r^2 = 0.96$) than in Site 1 (0.0011 ± 0.0003 day⁻¹, $r^2 = 0.60$) (ANOVA, $F_{2,6}=76.34$,
178 $p<0.001$; Tukey test, $p<0.01$). No differences were observed between Sites 2 and 3.

179 **3.3 Seagrass leaf litter features**

180 Changes in nutrient concentrations (%C, %N and C:N ratio) were observed in seagrass leaf litter during the
181 experiment (Fig. 3). Despite the hydrodynamic condition did not affect C concentration of the detritus during
182 the decomposition (RM-ANOVA, $F_{2,14}=1.89$, $p>0.05$), the overall initial C concentration (average 38.2%)
183 decreased slightly, and at day 221 a lower C concentration was recorded at Site 3 ($33.2 \pm 0.3\%$) than at
184 Sites 1 and 2 (37.1 ± 0.7 and $35.0 \pm 1.1\%$, respectively) (Fig. 3; Tukey test, $p<0.01$). N concentration showed
185 a very narrow range of variation from $0.8\pm 0.1\%$ (Site 1, 101 days) to $1.3\pm 0.2\%$ (Site 2, 152 days) with no
186 significant differences between sites during the experiment (RM-ANOVA, $F_{2,14}=3.48$, $p>0.05$). C:N ratio
187 ranged from 29.1 ± 5.1 (Site 2, 152 days) to 49.0 ± 4.0 (Site 1, 101 days) with significant differences between
188 sites during the experiment (RM-ANOVA, $F_{2,14}=5.24$, $p<0.05$). At the beginning of the experiment C:N ratio
189 averaged 35.5 while at the end higher values were recorded at Site 1 than at Sites 2 and 3 (39.2 ± 1.8 , 32.8
190 ± 1.9 and 32.1 ± 2.7 , respectively) (Fig. 3; Tukey test, $p<0.05$).

191

192 **3.4 Invertebrate densities and biomass**

193 A total of 1964 individuals (379, 948 and 637 respectively at Site 1, 2 and 3) belonging to 3 Phyla were
194 recovered and identified: the Arthropoda was the phylum with the highest number of taxa (46 crustacean
195 species grouped in 3 orders, 40 species of Amphipoda, 4 species of Isopoda and 2 species of Tanaidacea),
196 followed by Mollusca (8 species grouped in 2 classes, 1 species of Bivalvia and 7 species of Gastropoda)
197 and Anellida (2 species belonging to Polychaeta class) (Tab. 1).

198 Density and biomass of the entire invertebrate community were significantly affected by the interaction Site x
199 Time (PERMANOVA, Tab. 2). Pairwise tests for the term Site x Time for Site factor showed significant
200 differences from 47 to 152 days, with Site 1 showing significantly lower values than the others (P(MC))

201 <0.05). In general, the average dissimilarity, in terms of density and biomass data, was always higher
202 between Site 1 and the others than between Sites 2 and 3 (SIMPER; Tab. 3). The invertebrate groups mostly
203 responsible for differences between sites belong to the Arthropoda for both density and biomass data: the
204 amphipod *Gammarus aequicauda* (Martynov, 1931) contributes always for more than 10% and 7% to this
205 dissimilarity, respectively for density and biomass data, followed by the tanaidacean *Chondrochelia savignyi*
206 (Krøyer, 1842), and the caprellid *Caprella acanthifera* (Leach, 1814) for density data and the isopod
207 *Cymodoce truncate* (Leach, 1814), the polychaetes *Nereis* sp. and the amphipod *Lysianassa caesarea* for
208 biomass data. (Tab. 3). Other species generally contributed less than 8% to the average dissimilarity
209 between sites (Tab. 3).

210 Colonization of litterbags started with the Gastropoda *Tricolia pullus* at Site 1 (day 0), while at 3 days with
211 Amphipoda [*G. aequicauda* and *Melita palmata* (Montagu, 1804)], Isopoda (*C. truncate*) and Tanaidacea (*C.*
212 *savignyi*) and Amphipoda [*Aora gracilis* (Bate, 1857), *C. acanthifera*, *G. aequicauda*, *Lysianassa costae*
213 (Milne Edwards, 1830), *Pseudoprotella phasma* (Montagu, 1804)], Tanaidacea (*L. savignyi*) and Gastropoda
214 [*Melarhappe neritoides* (Linnaeus, 1758)], respectively at Sites 2 and 3 (Fig. 4). Total density ranged from 0.1
215 \pm 0.2 to 13.4 \pm 6.3 (Site 1, 0 and 101 days), from 0.0 to 77.8 \pm 27.9 (Site 2, 0 and 101 days) and from 0.0 to
216 49.8 \pm 18.5 (Site 3, 0 and 152 days) individuals g⁻¹ DM of seagrass detritus (Fig. 4). Total biomass ranged
217 from 0.2 \pm 0.3 to 4.7 \pm 0.9, from 0.0 to 30.7 \pm 33.7 and from 0.0 to 22.4 \pm 15.2 mg g⁻¹ DM respectively at Site
218 1, 2 and 3 (0 and 221 days) (Fig. 5). Univariate analysis showed that the density of organisms changed
219 during the experiment, with significant differences between sites only for the Amphipoda group (RM-ANOVA,
220 F_{2,14}=3.97, p<0.05) (Fig. 4), while no significant differences in biomass data were reported (RM-ANOVA,
221 p>0.05) (Fig. 5).

222 The invertebrate community was dominated by the Arthropoda both in terms of density (up to 106 ind. g⁻¹
223 DM) and biomass (up to 65 mg g⁻¹ DM): Amphipoda density and biomass increased gradually reaching the
224 maximum at the end of the experiment at Site 2 (Figs. 4, 5); Isopoda showed the highest density at 101 days
225 at Site 2, while Tanaidacea showed the highest density and biomass at 101 days at Site 3 (Fig. 4, 5). Density
226 for Anellida was always below 8 ind. g⁻¹ DM, with the highest values of density and biomass at Site 3 at the
227 end of the experiment (Fig. 4, 5). Mollusca Bivalvia showed no changes during the experiment in terms of
228 density and biomass, while Gastropoda density showed high values at 101 days and the highest biomass at
229 the end of the experiment at Site 3 (Fig. 4, 5).

230

231 4. Discussion

232 4.1 Seagrass leaf litter decomposition and nutrient dynamics

233 Seagrass meadows are recognized as some of the most productive of the Earth's ecosystems (Fourqurean
234 et al. 2012), but most of the primary production is exploited only through detrital routes (Cebrián & Duarte
235 2001). Accordingly, in the Stagnone di Marsala, the bottom of which is covered by a dense *C. nodosa*
236 meadow and patchy *P. oceanica*, there is evidence for the role of seagrass-derived organic matter for
237 consumers through detrital pathways (Vizzini et al. 2013).

238 In this area, leaf litter decomposition rates (from 0.001 to 0.004 day⁻¹) were in the range reported for
239 seagrasses (from 0.001 to 0.110 day⁻¹; Harrison, 1989), despite the decomposition rate recorded for the
240 central part of the Stagnone was lower than previously observed values for *P. oceanica* (from 0.003 to 0.017
241 day⁻¹; Romero et al. 1992, Mateo & Romero 1996, Cebrián et al. 1997). The high variability of seagrass
242 decomposition rates reported in the literature may be ascribed to the different experimental conditions in
243 decomposition studies. As summarised by Harrison (1989), the length of the study (from days to years), the
244 use of different types of detritus (fresh or dried leaves), leaf age (green leaves lose mass faster than old
245 ones) and also the mesh size (smaller mesh reduce the amount of particles lost but affect colonization) are
246 among the conditions that may affect the decay rates. Leaf litter decomposition rates in this study exhibited a
247 high spatial heterogeneity that was not imputable to the experimental conditions (i.e. type of detritus, leaf
248 age), which were homogeneous at the beginning of the experiment. The *P. oceanica* decomposition rate was
249 2x and 4x higher respectively in the southern and in the external sites than in the central-northern site.
250 Despite, the low decomposition rate in the Site 1 could be ascribed to different experimental conditions
251 compared to other studies, this result highlights a clear spatial pattern in the decomposition dynamics within
252 the basin.

253 Based on C and N concentration in seagrass leaf litter, loss of organic nutrients from the detritus on a daily
254 basis was calculated as the total mass x nutrient concentration at the beginning of the experiment minus that
255 at the end divided by the number of experimental days (Wardle et al. 2002). Carbon release rates were 0.09
256 ± 0.01, 0.21 ± 0.01 and 0.26 ± 0.01 mgC g⁻¹ d⁻¹ in Sites 1, 2 and 3 respectively, showing the same spatial
257 pattern as for litter decomposition rates, with a higher loss outside the basin than in the internal sites. In
258 contrast, nitrogen released by seagrass detritus was constant at all sites (0.01 ± 0.00 mgN g⁻¹ d⁻¹).

259 Leaf detritus is a source of nutrients which return in soluble forms through decomposition (Harrison 1989,
260 Romero et al. 2006), but the dynamics of carbon and nitrogen regeneration during the decay process is
261 rather complex and, as suggested in the literature, there is no common pattern to nutrient loss (see
262 references in Romero et al., 2006), highlighting the uncoupling between nutrient release and the negative

263 exponential trend of mass loss (Petersen & Cummins 1974). As summarised in Romero et al. (2006), during
264 the first phase of decomposition (leaching), the labile components release nutrients that can be assimilated
265 by microbes colonising the detritus; when all the labile substrates are processed, nutrients from the dead leaf
266 tissues are released in inorganic and/or organic forms (which can be assimilated again by microbes) by
267 means of bacteria exoenzyme attack; during the last phase of decomposition, the refractory portion
268 decomposes very slowly, releasing only nitrogen, while most of the carbon remains (Kristensen 1994).
269 These expected dynamics of nutrients were partially matched in our study: the initial phase of labile nutrient
270 release was probably bypassed by the pre-drying treatment of leaf litter as organic molecules become less
271 easily degraded (Harrison 1989); the slow release of C (from ~38% to ~33%) was coupled with the stable
272 condition reported for the N concentration (from ~1.3% to ~0.8%), with the decrease of C related to the
273 decomposition of mobilizable carbohydrates, and the stable N values probably related to the accumulation of
274 microbial biomass that can be responsible for a high portion (75-100%) of the total nitrogen content in
275 decaying litter (Newell 1996). In addition, the slower loss of organic matter was previously reported for dead
276 leaves (used in this study) compared to fresh material (Harrison & Mann 1975) This dynamic of nutrient
277 release also explains the fact that the C:N ratio of detritus was remarkably high, exhibiting a wide range of
278 variation from ~30 to ~50, but was within the range reported for seagrass detritus (14-75; Enríquez et al.,
279 1993). Moreover, the higher C:N reported for the internal site during the experiment indicates that seagrass
280 detritus here becomes more recalcitrant to decomposition (Pirc & Wollenweber 1988) and more refractory to
281 digestion by consumers than in the other sites. Accordingly, the seagrass-derived organic matter largely
282 contributes to the sedimentary organic matter pool in the central part of the Stagnone di Marsala, as shown
283 by stable isotope data (Vizzini et al. 2013), pinpointing the role of the basin as a sink of organic carbon.

284 **4.2 Role of invertebrate community in seagrass leaf litter decomposition**

285 Leaf litter, as a particular benthic substrate, provides food to invertebrates and refuge from predators,
286 channelling marine macrophyte production to higher trophic levels through the detritus-based food web
287 (Lepoint et al. 2006). Most of the invertebrates living in *P. oceanica* detritus belong to the typical community
288 found in the meadows (Gambi et al. 1992, Sánchez-Jerez et al. 1999), despite the fact that some species
289 show specific adaptations to the detritus habitat (e.g. different body colouration for the isopod *Idotea* sp. and
290 the shrimp *Hyppolyte inermis*, Gallmetzer et al., 2005).

291 Despite the limitation due to the mesh size of the litterbags, colonization of the detritus by invertebrates is
292 generally a rapid process (Norkko & Bonsdorff 1996), as also shown in our study (overall colonization started
293 after three days), with the dominance of motile taxa (e.g. amphipods, isopods and tanaidaceans). During the

294 experiment, Amphipoda and Isopoda were responsible for among-site differences in the invertebrate
295 assemblages both in terms of density and biomass. The dominance of crustaceans in detritus accumulation
296 is well-documented (Gallmetzer et al. 2005), with amphipods and isopods being the main constituents of the
297 crustacean community of *P. oceanica* detritus (Wittmann et al. 1981, Remy et al. 2018). Crustaceans, and in
298 particular amphipods and isopods, are an abundant, widely distributed and ecologically important component
299 of benthic communities, exhibiting a high degree of niche specificity (Mancinelli & Rossi 2002, De-La-Ossa-
300 Carretero et al. 2012). In our study, *G. aequicauda* was responsible for among-site differences in the
301 macrofaunal assemblages both in term of densities and biomass. Within the amphipods, the *Gammarus*
302 genus is a highly opportunistic feeder group (defined as a facultative shredder by Cummins and Klug, 1979),
303 but with a certain degree of selectivity probably related to environmental characteristics (Friberg & Jacobsen
304 1994, Mancinelli & Rossi 2002). Based on stable isotope and/or gut content analysis, some species were
305 reported to directly feed on *P. oceanica* leaf litter within these species the amphipods *G. aequicauda* and
306 *Gammarella fucicola* (Remy et al. 2018), but also isopods of the genera *Idotea* and *Cleantis* (Lepoint et al.
307 2006, Sturaro et al. 2010) and some echinoderms as the holothurian *Holothuria tubulosa* Gmelin (Costa et
308 al. 2014). In particular, *G. aequicauda* relied up to 80% of its diet on *P. oceanica* leaf detritus (Michel et al.
309 2015, Remy et al. 2018), highlighting the crucial role of this species not only during the fragmentation
310 process but also in the transfer of seagrass detritus organic matter in the food chain.

311 Low density and biomass of the invertebrate community were recorded in the central part of the Stagnone di
312 Marsala, where carbon released by detritus was lower, seagrass detritus more recalcitrant (high C:N ratios)
313 and resistant to degradation (Enríquez et al. 1993) and, hence, the decomposition rate was reduced. The
314 central part of the Stagnone is characterised by reduced hydrodynamic condition (La Loggia et al. 2004),
315 which may influence seagrass decomposition both directly and indirectly. Hydrodynamic is known to
316 contribute to detritus fragmentation through direct mechanical action on seagrass leaves, increasing the
317 surface available for microbial colonization (Mateo & Romero 1997, Romero et al. 2006). Moreover, reduced
318 hydrodynamic could act not only limiting the loss of fine particles through the litterbag but also reducing the
319 aeration of the litter through water movement in very shallow basins is also responsible for wide variability in
320 seawater variables which, in combination with the poor nutritional value of detritus, may have limited
321 invertebrate (but also microbial) colonization and slowed down the decomposition process.

322

323 **5. Conclusions**

324 Seagrass decomposition rate varied at a small spatial scale in a semi-enclosed coastal basin, resulting faster
325 in the sites that are more exposed to the open-sea than in the internal part of the Stagnone di Marsala. The
326 Stagnone seems to act as a sink of organic matter wherein the slow recycling process enhances the
327 accumulation of refractory materials. Moreover, the peculiar environmental characteristics of the internal site
328 constrain invertebrate abundance and the more recalcitrant and refractory condition of the detritus results in
329 slower decomposition. Consequently, low decomposition rates of seagrass leaves in internal sites
330 characterised by low hydrodynamic forces may promote organic matter burial and carbon stocks,
331 emphasising the role of coastal basins such as ponds and lagoons as blue carbon areas (Nellemann et al.
332 2009).

333

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466

Table 1. List of all taxa identified in the three sites: Site 1, Site 2 and Site 3 (* / : presence/absence).

TAXA	SITE		
	1	2	3
Anellida			
Polychaeta			
	<i>Nereis</i> sp.	*	*
	<i>Terebella</i> sp.	*	*
Arthropoda			
Amphipoda			
	<i>Amphilochus</i> sp.	*	
	<i>Aora gracilis</i>	*	*
	<i>Aora</i> sp.	*	
	<i>Aora spinicornis</i>		*
	<i>Autonoe rubromaculatus</i>	*	*
	<i>Autonoe viduarum</i>	*	*
	<i>Caprella acanthifera</i>	*	*
	<i>Elasmopus brasiliensis</i>	*	*
	<i>Elasmopus pectenircus</i>	*	*
	<i>Elasmopus pocillimanus</i>	*	*
	<i>Elasmopus rapax</i>	*	*
	<i>Elasmopus</i> sp.	*	*
	<i>Erichthonius punctatus</i>	*	*
	<i>Gammarella fucicola</i>	*	*
	<i>Gammarus aequicauda</i>	*	*
	<i>Idunella pirata</i>	*	
	<i>Lembos</i> sp.	*	*
	<i>Lembos websteri</i>	*	*
	<i>Leptocheirus bispinosus</i>	*	*
	<i>Leptocheirus mariae</i>		*
	<i>Lysianassa caesarea</i>	*	*
	<i>Lysianassa costae</i>	*	*
	<i>Lysianassa</i> sp.	*	*
	<i>Maera grossimana</i>	*	*
	<i>Maera hirondellei</i>	*	*
	<i>Maera pachytelson</i>		*
	<i>Maera sodalis</i>	*	*
	<i>Maera</i> sp.	*	*
	<i>Melita bulla</i>	*	*
	<i>Melita hergensis</i>	*	*
	<i>Melita palmata</i>	*	*
	<i>Melita</i> sp.	*	*
	<i>Microdeutopus bifidus</i>		*
	<i>Microdeutopus chelifer</i>	*	*
	<i>Microdeutopus similis</i>		*
	<i>Microdeutopus</i> sp.	*	*
	<i>Microdeutopus stationis</i>	*	*
	<i>Orchomene grimaldii</i>		*
	<i>Pseudoprotella phasma</i>		*
	<i>Quadrimaera inaequipipes</i>	*	*
Isopoda			
	<i>Anthura</i> sp.	*	*
	<i>Cymodoce truncata</i>	*	*
	<i>Gnathia phallonajopsis</i>	*	*
	<i>Joeropsis brevicornis</i>	*	*
Tanaidacea			
	<i>Apseudopsis latreillii</i>		*
	<i>Chondrochelia savignyi</i>	*	*
Mollusca			
Bivalvia			
	<i>Cerastoderma glaucum</i>	*	*
Gastropoda			
	<i>Cerithium</i> sp.	*	*
	<i>Eucithara</i> sp.	*	*
	<i>Gibbula</i> sp.	*	*
	<i>Haminoea hydatis</i>	*	*
	<i>Melarhaphe neritoides</i>		*
	<i>Rissoa</i> sp.	*	*
	<i>Tricolia pullus</i>	*	*

469 Table 2. PERMANOVA results for the effects of factors Site and Time on density (individuals g⁻¹ DM of
 470 seagrass detritus) and biomass (mg g⁻¹ DM of seagrass detritus) of the invertebrate community. n.s.: p>0.05;
 471 *: p≤0.05; **: p≤0.01; ***: p≤0.001.

Source	df	Density (ind. g ⁻¹ DM)			Biomass (ind. g ⁻¹ DM)		
		MS	Pseudo-F	P	MS	Pseudo-F	P
Site	2	8082.80	6.34	***	9545.80	4.86	***
Time	6	9283.40	7.28	***	9982.30	5.09	***
Site*Time	12	2493.50	1.96	***	3198.10	1.63	***
Residuals	42	1275.10			1963.10		

472

473 Table 3. Results of the SIMPER analysis on density (ind. g⁻¹ DM) and biomass (mg g⁻¹ DM) data showing the
 474 contribution of invertebrate species to dissimilarity between sites during the experiment: AD/SD, ratio of the
 475 average dissimilarity to the standard deviation of dissimilarity for the particular species; Contr(%), percentage
 476 contribution to the dissimilarity. Cut-off: cumulative percentage 60%.

477

Density (ind. g ⁻¹ DM)				Biomass (ind. g ⁻¹ DM)			
Species	Average Dissimilarity	AD/SD	Contr(%)	Species	Average Dissimilarity	AD/SD	Contr(%)
Site 1 vs 2				Site 1 vs 2			
	65.59				74.39		
<i>Gammarus aequicauda</i>		0.91	13.29	<i>Gammarus aequicauda</i>		0.69	9.12
<i>Chondrochelia savignyi</i>		1.04	9.2	<i>Cymodoce truncata</i>		0.57	7.34
<i>Joeropsis brevicornis</i>		0.93	8.15	<i>Lysianassa caesarea</i>		0.7	7.31
<i>Gnathia phallonajopsis</i>		0.63	7.97	<i>Nereis sp.</i>		0.82	6.79
<i>Tricolia pullus</i>		0.22	6.93	<i>Tricolia pullus</i>		0.22	6.11
<i>Caprella acanthifera</i>		0.64	6.92	<i>Chondrochelia savignyi</i>		0.63	5.75
<i>Maera sodalis</i>		0.74	5.51	<i>Caprella acanthifera</i>		0.58	5.37
				<i>Gnathia phallonajopsis</i>		0.73	5.26
				<i>Maera sodalis</i>		0.7	5.22
Site 1 vs 3				Site 1 vs 3			
	63.38				74.38		
<i>Gammarus aequicauda</i>		0.74	12.19	<i>Gammarus aequicauda</i>		0.63	9.26
<i>Chondrochelia savignyi</i>		1.29	11.78	<i>Nereis sp.</i>		0.82	8.09
<i>Tricolia pullus</i>		0.23	7.54	<i>Tricolia pullus</i>		0.25	6.97
<i>Caprella acanthifera</i>		0.56	7.11	<i>Maera sodalis</i>		0.64	6.56
<i>Maera sodalis</i>		0.71	5.94	<i>Caprella acanthifera</i>		0.59	5.93
<i>Nereis sp.</i>		0.85	5.22	<i>Lysianassa costae</i>		0.74	5.39
<i>Lysianassa costae</i>		0.77	4.72	<i>Quadrinemaera inaequipipes</i>		0.61	5.17
<i>Quadrinemaera inaequipipes</i>		0.64	4.6	<i>Chondrochelia savignyi</i>		0.66	5.08
				<i>Lysianassa caesarea</i>		0.52	4.07
Site 2 vs 3				Site 2 vs 3			
	54.07				68.4		
<i>Gammarus aequicauda</i>		1.1	10.43	<i>Gammarus aequicauda</i>		0.89	7.93
<i>Caprella acanthifera</i>		0.62	8.41	<i>Lysianassa caesarea</i>		0.65	7.32
<i>Gnathia phallonajopsis</i>		0.69	8.27	<i>Cymodoce truncata</i>		0.57	6.52
<i>Joeropsis brevicornis</i>		1.02	7.95	<i>Caprella acanthifera</i>		0.63	5.79
<i>Chondrochelia savignyi</i>		0.95	7.94	<i>Gnathia phallonajopsis</i>		0.73	5.34
<i>Lysianassa costae</i>		0.73	5.23	<i>Gammarella fucicola</i>		0.7	5.05
<i>Gammarella fucicola</i>		0.71	4.69	<i>Lysianassa costae</i>		0.68	4.44
<i>Quadrinemaera inaequipipes</i>		0.72	4.22	<i>Chondrochelia savignyi</i>		0.62	4.34
				<i>Quadrinemaera inaequipipes</i>		0.72	4.2
				<i>Elasmopus pocillimanus</i>		0.46	3.65
				<i>Cerithium sp.</i>		0.57	3.59

478

479

480 **Figure captions**

481

482 Figure 1. Study area with sampling sites (Site 1, 2 and 3). The dotted line marks the separation between the
483 central-northern and the southern sub-basins (from La Loggia et al., 2004).

484

485 Figure 2. Dry mass (g) of *P. oceanica* leaf detritus remaining in the litterbags after 0, 3, 7, 14, 47, 101, 152,
486 221 days in the three sites. Exponential decay fitting lines were reported as black dotted (Site 1), grey dotted
487 (Site 2) and black full (Site 3) lines.

488

489 Figure 3. Mean (\pm s.d.) C%, N% and C:N of *P. oceanica* leaf detritus remaining in the litterbags after 0, 3, 7,
490 14, 47, 101, 152, 221 days in the three sites.

491

492 Figure 4. Total density (ind. g^{-1} DM of detritus, mean \pm s.d.) and mean density (ind. g^{-1} DM) of each
493 invertebrate group (A, Anellida Polychaeta; B, Arthropoda Amphipoda; C, Arthropoda Isopoda; D, Arthropoda
494 Tanaidacea; E, Mollusca Bivalvia; F, Mollusca Gastropoda) found in the litterbags during the experiment in
495 the three sites.

496

497 Figure 5. Total biomass (mg g^{-1} DM of detritus, mean \pm s.d.) and mean biomass (mg g^{-1} DM) of each
498 invertebrate group (A, Anellida Polychaeta; B, Arthropoda Amphipoda; C, Arthropoda Isopoda; D, Arthropoda
499 Tanaidacea; E, Mollusca Bivalvia; F, Mollusca Gastropoda) found in the litterbags during the experiment in
500 the three sites.

501

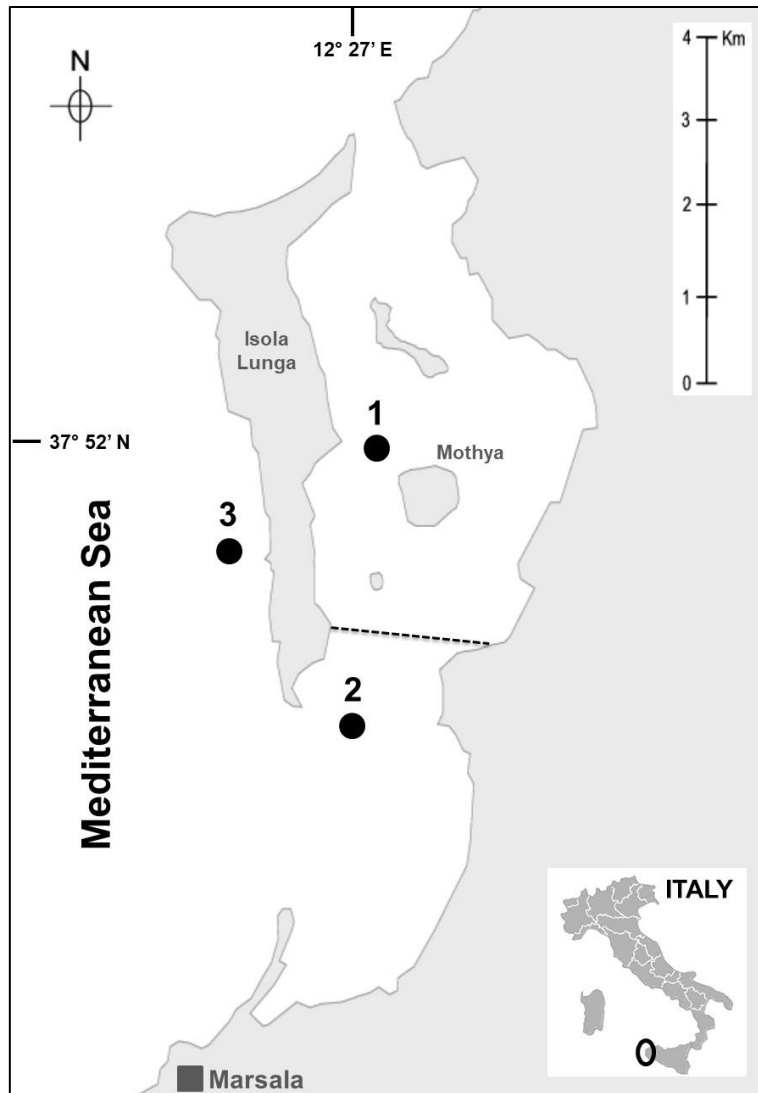


Fig. 1

502

503

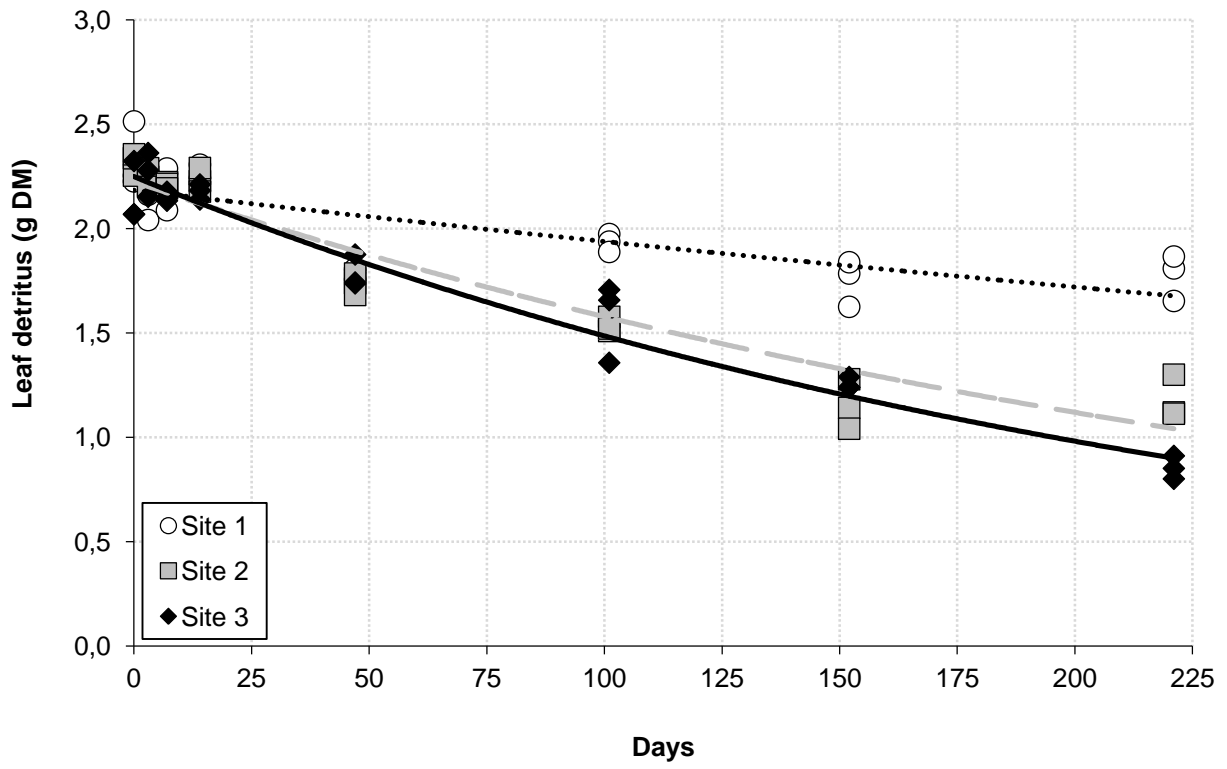
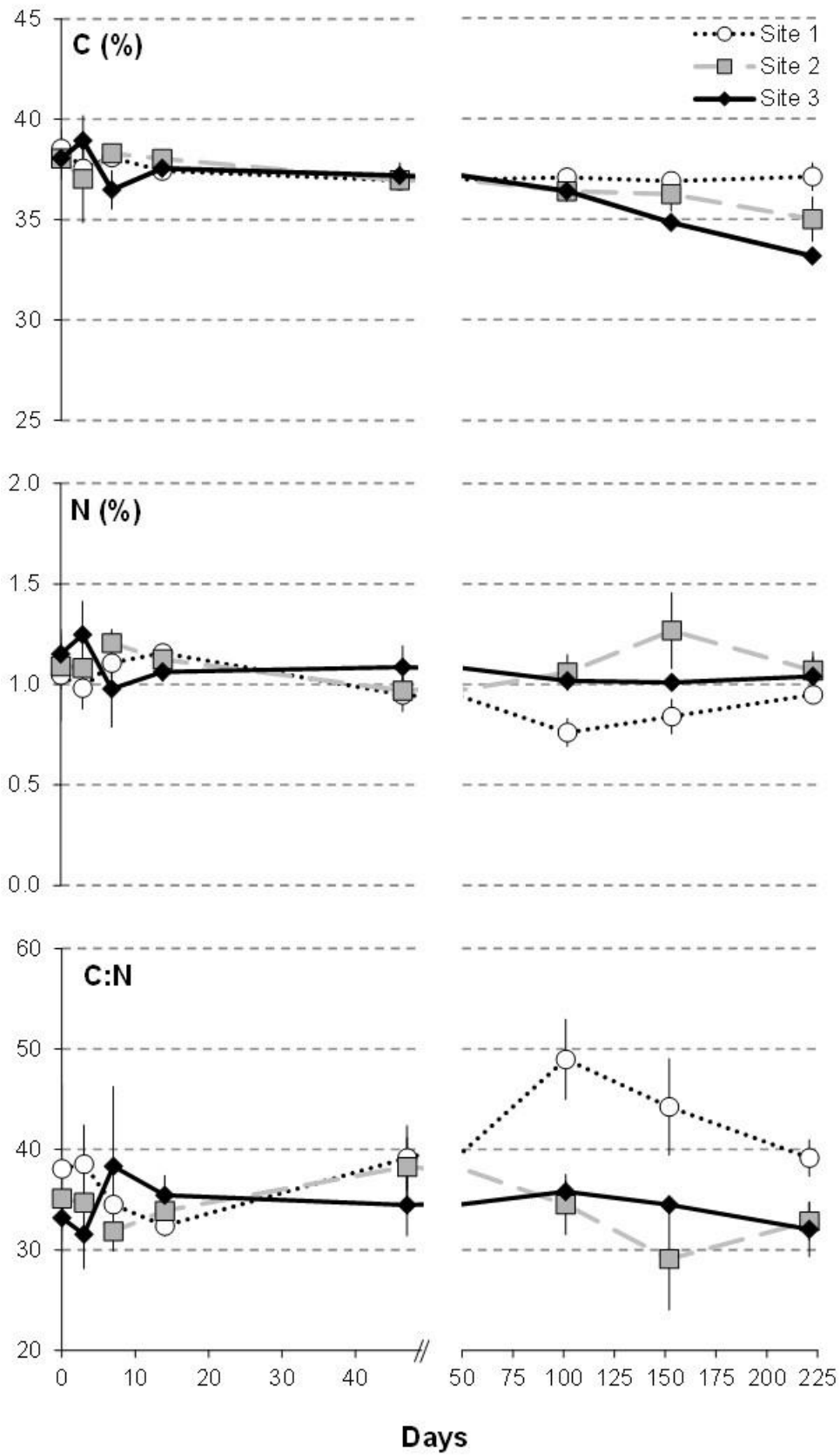


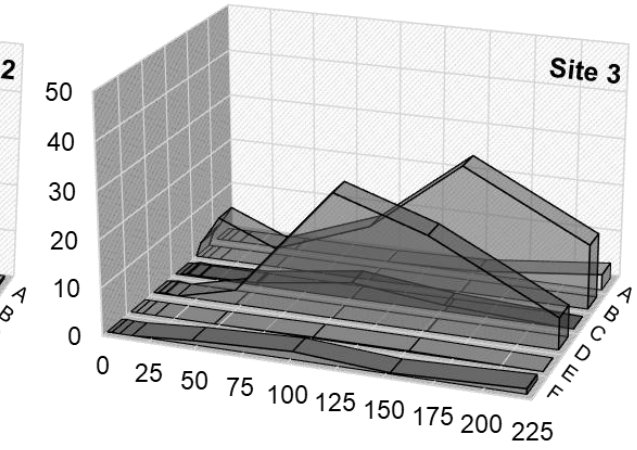
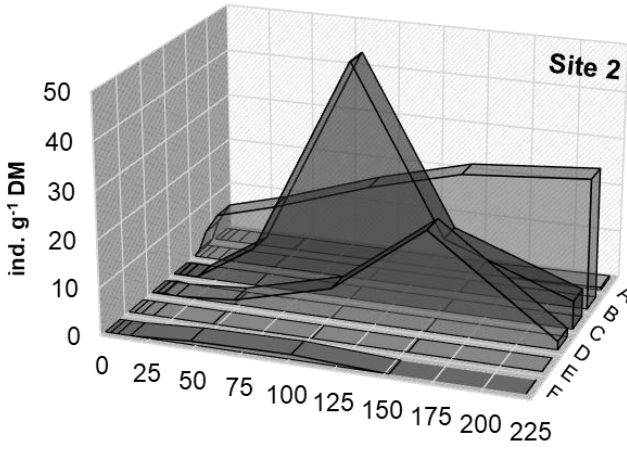
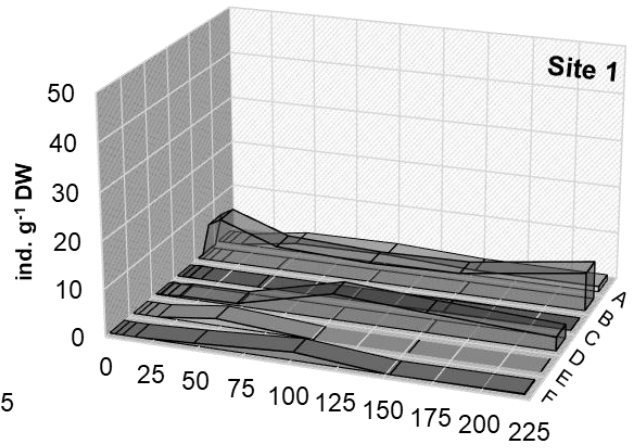
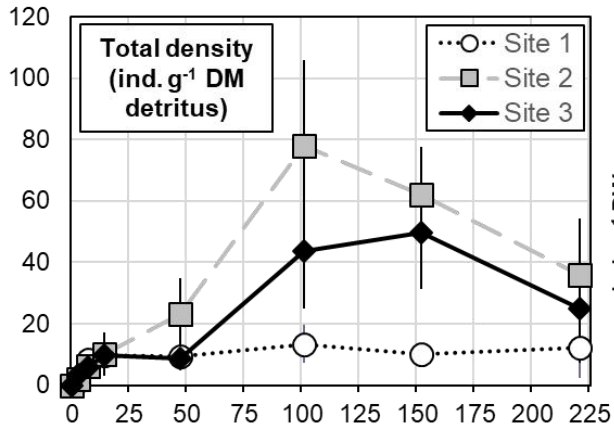
Fig. 2



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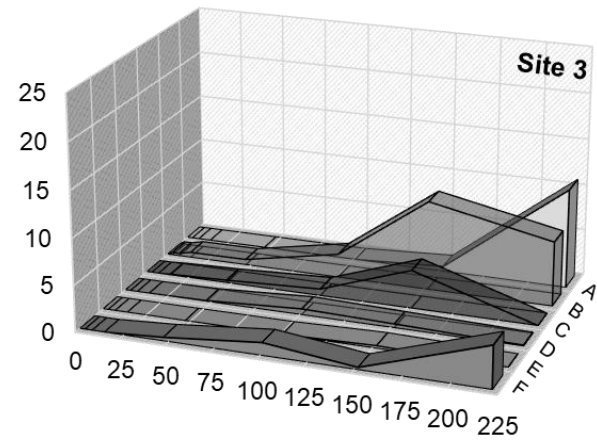
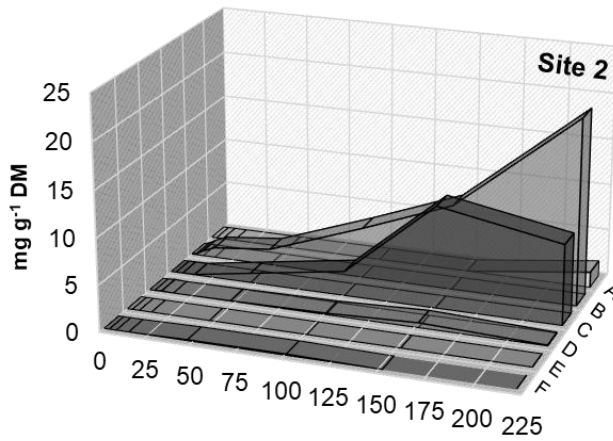
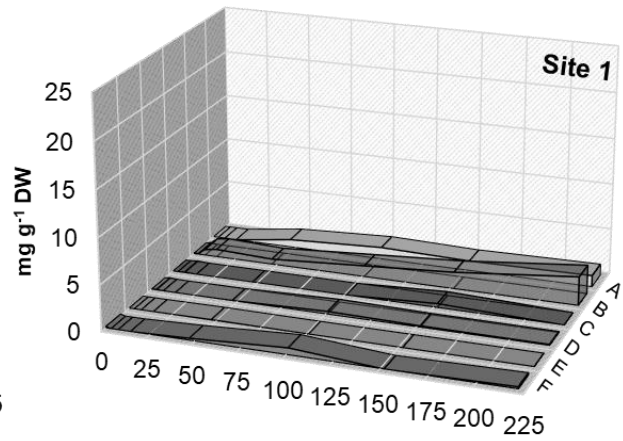
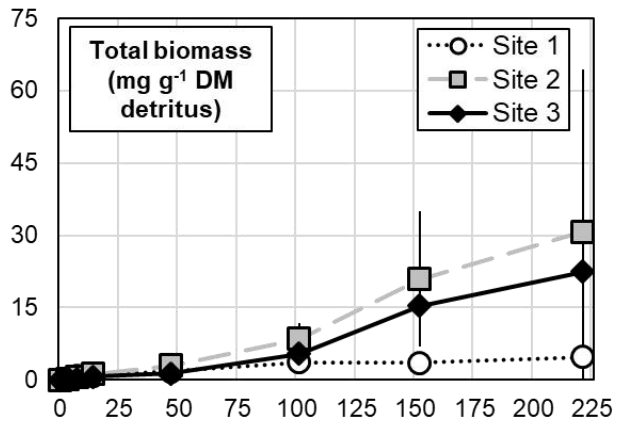
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Fig. 3



Days

Fig. 4



Days

Fig. 5