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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-02399814>

Submitted on 14 Dec 2020

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

Decomposition of seagrass leaf litter

Valentina Costa^{1,2*}, Antonio Mazzola^{1,3}, Francesca Rossi⁴, Salvatrice Vizzini^{1,3}

¹Department of Earth and Marine Sciences, University of Palermo, CoNISMa, Via Archirafi 18, 90123 Palermo, Italy

²Current address: Department of Biology & CESAM, University of Aveiro, Campus Universitário de Santiago, 3810-193, Aveiro, Portugal

³CoNISMa, Interuniversity National Consortium for Marine Sciences, Piazzale Flaminio 9, 00196 Roma, Italy

⁴Université Côte d'Azur, CNRS, FRE 3729 ECOMERS, Nice, France

* Corresponding author.

E-mail address: vale.costa@gmail.com

Acknowledgements

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

Abstract

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

1. Introduction

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

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

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

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

2. Methods

2.1 Study sites and experimental set-up

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

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

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

2.2 Sampling and laboratory procedures

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

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

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

2.3 Data elaboration and statistical analysis

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

Decomposition rate was estimated as the loss of dry mass during time and fitted to the exponential curve (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 the initial dry mass, and k is the decomposition constant (day^{-1}). We used one-way ANOVA with Site (3 levels) as categorical factor to assess the statistical significance of the effect of Site (3 levels, $t=221$ days) on decomposition rate.

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

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

160

161 **3. Results**

162 **3.1 Seawater column variables**

Seawater parameters were measured in the water column during the experiment. Temperature showed a 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 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 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). Dissolved oxygen concentration (DO) ranged from 5.5 to 8.9 mg l^{-1} with the same average value in the three 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 $0.8\pm0.1\%$ (Site 1, 101 days) to $1.3\pm0.2\%$ (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 [*Melarhaphe 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

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

4.2 Role of invertebrate community in seagrass leaf litter decomposition

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

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

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

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

472

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		

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	65.59			Site 1 vs 2	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 phallanajopsis</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 phallanajopsis</i>		0.73	5.26
				<i>Maera sodalis</i>		0.7	5.22
Site 1 vs 3	63.38			Site 1 vs 3	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 inaequipes</i>		0.61	5.17
<i>Quadrinemaera inaequipes</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	54.07			Site 2 vs 3	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 phallanajopsis</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 phallanajopsis</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 inaequipes</i>		0.72	4.22	<i>Chondrochelia savignyi</i>		0.62	4.34
				<i>Quadrinemaera inaequipes</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

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505

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Fig. 2

Fig. 3

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511

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Fig. 4

Days

Fig. 5