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INTERNSHIP REPORT

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Carbon fluxes in salt-marsh *Spartina maritima* communities, with a focus on two dominant arthropod species, *Arctosa fulvolineata* (Araneae, Lycosidae) and *Orchestia gammarellus* (Amphipoda, Talitridae)

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Introduction

In the context of the very rapidly changing climate, more than 70 countries, including the biggest polluters - China, the United States, and the European Union - have set a net-zero emissions target by 2050, covering more than three quarters of the global emissions (https://www.un.org/en/climatechange/net-zero-coalition). To reach this goal, most stakeholders will rely on specific carbon dioxide removal strategies to offset emissions that are unavoidable or difficult to reduce (IPCC, 2023). The world's ocean and coastal ecosystems are known as blue carbon sinks (the so-called blue ecosystems) because they can transfer and store carbon at very high rates for thousands of years, mainly in their sediments and in the biomass of living beings such as plants (Alongi, 2018). Seagrass, mangroves and salt marshes therefore provide a cost-efficient carbon dioxide removal opportunity based on their conservation and restoration with many co-benefits (Lester, 2023).

These ecosystems sequester ten times more carbon each year and store three to five times more carbon per equivalent area than tropical forests (McLeod et al., 2011 and Murray et al., 2011 respectively). Among these blue ecosystems, salt marshes provide the greatest long-term rate of carbon accumulation in sediment (210 gC m^{-2} $year^{-1}$) as compared to mangroves (139 gC m^{-2} $year^{-1}$) and seagrass meadows (83 gC m^{-2} $year^{-1}$) (Laffoley and Grimsditch, 2009). In addition, salt marshes provide many other benefits to human society in the form of ecosystem services (Barbier et al., 2011). These intertidal and coastal ecosystems are regularly flooded with salt or brackish water and dominated by salt-tolerant grasses, herbs and shrubs (Adam, 1993). They are among the most productive temperate ecosystems on Earth with a high primary production (up to 30 tonnes of dry matter per ha per year; Lefeuvre et al., 2000).

Marsh grasses contribute to the accumulation of organic matter and trapping of inorganic sediment (named “blue carbon”) (Turner et al., 2000). Once decomposed by microorganisms and arthropods, this organic matter can be exported to the sea following high tides, which is described as an outwelling process (Odum, 2000). High densities of arthropods, and notably decomposers such as amphipods, are supported by this high primary production of salt marshes (Schrama et al., 2012). Some of these arthropods are in turn widely consumed by other predatory arthropods such as spiders but also by other predators such as fish and birds. Also, salt marshes provide a critical habitat for various life stages of fishes which rise to the surface of the marsh at high tide to feed on invertebrates (Lafaille et al., 2000). For wading birds in

summer, they provide an important feeding habitat and a place to winter or a stopover for many migratory shore birds (Boorman, 2003).

La Rochelle is a city on the west coast of France and a seaport on the Bay of Biscay, a part of the Atlantic Ocean. This city aims to become the first urban coastal area in France to reach carbon neutrality by 2040 (https://www.larochelle-zerocarbone.fr/). To achieve this, a blue carbon research axis has been defined in the LRTZC (La Rochelle Territoire Zéro Carbone) project and aims to optimise the carbon sink functions of the surrounding wetlands and coastline in addition to improve coastal resilience. This project covers the entire urban agglomeration of La Rochelle, which represents thousands of hectares of blue ecosystems. Salt marshes form a very large area, with more than 6,000 ha of slike and 700 ha of schorre (Afonso, LRTZC project town of La Rochelle manager). Scientific members of the project have decided to study *in situ* carbon processes and fluxes at the various exchange interfaces through large-scale with the aim of establishing the first carbon budget for coasts and marshes in France. To achieve this, they have selected a well-known site to scientists, the Aiguillon Bay, as a study area for intertidal mudflats and retro-littoral marshes. An atmospheric Eddy Covariance (EC) station for the continuous measurement of CO_2 fluxes with the atmosphere at wetland scale was deployed and supported by some other *in situ* and laboratory measurements because understanding and quantifying these CO_2 fluxes are crucial to achieving the objective of carbon neutrality by 2040.

Blue ecosystems are subject to significant carbon fluxes and complex metabolic processes at the various exchange interfaces (air-water, air-sediment and sediment-water) which have been more or less quantified (e.g., Cole et al., 2007 and Aufdenkampe et al., 2011). Carbon dynamics in these ecosystems are controlled by a multitude of biogeochemical factors and processes, including autochthonous biological activity (primary production and respiration balance), physical processes (temperature control on CO_2 solubility), benthos-pelagos couplings, CO_2 exchanges with the atmosphere and horizontal advection of CO_2 with the tidal rhythm (exchanges with the terrestrial and oceanic environments). The autochthonous biological activity plays a key role in salt marshes particularly because of their high primary production. Atmospheric CO_2 is uptaken and assimilated by salt-marsh plants through photosynthesis. A part of this carbon will then be assimilated into the food web through consumption and stored whereas another part will be released by egestion, autotrophic (plant) and heterotrophic (microorganisms and animals) respiration (e.g., Keenan and Williams, 2018; Middelburg, 2019) and by outwelling process.

Among the various biological taxa involved in these carbon dynamics, terrestrial arthropods have received particularly poor attention, and their role is consequently largely unclear. However, arthropods can reach very high densities in salt marshes (i.e., more than 60 000 individuals per m^2, see Pétillon et al., 2005) and by their diversity likely constitute a key phylum for carbon transfer.

Thus, the main objective was the study of the contribution of dominant species of ground-dwelling arthropods to the carbon fluxes of the Aiguillon Bay salt marsh in *Spartina*-dominated habitats. First, we reconstructed the marsh trophic network (intertidal mudflats and retro-littoral marshes) using the C and N stable-isotope compositions of marsh components. These components collectively contribute to regulating the quantity of carbon captured and stored within ecosystems and exchanged with the atmosphere thanks to their functional integration of carbon into food webs. Based on this, the contribution of arthropods to the carbon fluxes was evaluated using the dominant species of the main trophic guilds in *in situ* mesocosm experiments. Only the detritic pathway was analysed. The effects were studied in relation to trophic guilds of arthropods and to animal density; two trophic groups were used, decomposers (amphipods) and predators of decomposers (spiders), in three treatments. The mesocosm experiment was conducted in *Spartina maritima* community, a pioneer species in the Aiguillon Bay, at the interface between the intertidal mudflat and the upper coast, which fixes the sediment and therefore allows the retro-littoral marshes to progress (Olivier et al., 2021).

Material and Methods

Study system and field site

Experiments were conducted on an expansive salt marsh in the National Nature Reserve of the Aiguillon Bay, Esnandes, France (46° 15 '19.0′ N, 1° 08' 16.0′ W). To precisely determine the marsh areas dominated by the perennial small cordgrass *Spartina maritima*, cartographic data produced by Paschal et al. (2023) was used. In order to select a homogeneous population in a healthy physiological state where flux measurements by the Eddy Covariance system (Polsenaere et al., 2012) was possible, several populations of *Spartina maritima* were prospected on the field in March 2023.

Natural history: knowing the players in the system

Life histories of salt-marsh arthropods

To determine herbivores, their natural enemies, and detritus feeders associated with salt-marsh habitats, all published articles and databases based on studies carried out in France on this subject were used, by consulting the electronic databases PubMed, Scopus, Web of Science and Google Scholar in March 2023. The terms "((salt marsh) AND (arthropod) AND (France))" were used. After searching the databases, 922 research and review articles were obtained but only 79 were selected for their relevance. The list of species concerning the most abundant arthropod taxa of each trophic guild (predators, phytophagous and detritivores) are shown in Table 1.

Table 1. List of dominant species living in salt marshes and associated trophic guilds:

	Family	Genus, species	Descriptor	Trophic guild
Amphipoda	Talitridae	*Orchestia gammarellus*	(Pallas, 1766)	detritivores
Araneae	Araneidae	*Argiope bruennichi*	(Scopoli, 1772)	predators
	Araneidae	*Neoscona adianta*	(Walckenaer, 1802)	
	Araneidae	*Larinioides cornutus*	(Clerck, 1758)	
	Dictynidae	*Argenna patula*	(Simon, 1874)	
	Linyphiidae	*Erigone longipalpis*	(Sundevall, 1830)	
	Linyphiidae	*Silometopus ambiguus*	(O. Pickard-Cambridge, 1906)	
	Lycosidae	*Arctosa fulvolineata*	(Lucas, 1846)	
	Lycosidae	*Pardosa purbeckensis*	(Linnaeus, 1758)	
	Tetragnathidae	*Pachygnatha degeeri*	Sundevall, 1830	
Coleoptera	Carabidae	*Bembidion normannum*	Dejean, 1831	
	Carabidae	*Bembidion minimum*	(Fabricius, 1792)	
	Carabidae	*Dicheirotrichus gustavii*	Crotch, 1871	
	Carabidae	*Pogonus chalceus*	(Marsham, 1802)	
	Staphylinidae	*Paederus littoralis*	Gravenhorst, 1802	
Heteroptera	Saldidae	*Saldula palustris*	(Douglas, 1874)	
	Saldidae	*Salda littoralis*	(Linnaeus, 1758)	
	Nabiidae	*Nabis pseudoferus*	Remane, 1949	
Heteroptera	Miridae	*Trigonotylus ruficornis*	(Geoffroy, 1785)	phytophagous
	Miridae	*Orthotylus moncreaffi*	(Douglas & Scott, 1874)	
Orthoptera	Tettigoniidae	*Conocephalus fuscus*	(Fabricius, 1793)	
	Tettigoniidae	*Conocephalus dorsalis*	(Latreille, 1804)	

Due to their high level of diet specialisation, herbivore arthropods in salt marshes are different according to the type of plant formation. For example, in pioneer formations of *Salicornia spp.* and *Spartina spp.*, a high slike fauna was found and mainly composed of Miridae. This environment is highly selective and will contain few species that are mostly halophilic. Arthropod communities associated with *Puccinellia spp.*, *Halimione spp.* and *Aster spp.* are more speciose in herbivores taxa with more Heteroptera. Finally, in the *Elytrigia* areas, in addition to the families mentioned above, different Orthopteran species and some Lepidopteran caterpillars were found.

The most abundant arthropod natural enemies of herbivores are generalist spiders, principally the lycosids *Pardosa purbeckensis* (around 4 ind/m^2) and *Arctosa fulvolineata* (less than 1 ind/m^2). Some orb-weaving spiders (Araneidae) are also generally found (e.g., *Argiope bruennichi*, *Neoscona adianta* and *Larinioides cornutus*). Some abundant Linyphiid species such as *Silometopus ambiguus* and *Erigone longipalpis* were also found. Carabid beetles can also play a role in the regulation of some small herbivores, especially *Bembidion spp.* and *Pogonus chalceus.*

The most abundant detritus feeders are amphipods (mean of 980 ind/m²) but a study has shown that springtails (mean of 5008 ind/m²) and mites (mean of 55302 ind/m²) are the most abundant (Pétillon et al., 2004). Isopods also appear to be present in important numbers in high part of the marsh.

Assemblages of arthropods in Spartina populations

Due to a lack of research on *Spartina* population, it was difficult to determine assemblages of arthropods species that live in this habitat, especially for herbivores. In order to improve the knowledge of arthropod species living in *Spartina maritima* areas, individuals collected with sweep nets during a preliminary study carried out in June 2022 by Amiar et al. (2022) have been identified (Table 2). This study was carried out on 6 different populations of the genus *Spartina*. This preliminary study showed very few phytophagous species in *Spartina* habitat with a high beta diversity between populations of *Spartina* and therefore did not allow us to determine abundant and specialised phytophagous species on *Spartina*.

Table 2. List of dominant phytophagous species living in *Spartina* populations:

	Family	Genus, species	Descriptor
Coleoptera	Chrysomelidae	*Cassida vittata*	Villers, 1789
Heteroptera	Lygaeidae	*Henesteris sp.*	
	Miridae	*Trigonotylus ruficornis*	(Geoffroy, 1785)
	Miridae	*Orthotylus moncreaffi*	(Douglas & Scott, 1874)
	Miridae	*Notostira elongata*	(Geoffroy, 1785)
Homoptera	Cixiidae	*Oliarus sp.*	
	Cicadellidae	species a	
	Cicadellidae	species b	
Orthoptera	Tettigoniidae	*Conocephalus fuscus*	(Fabricius, 1793)

Salt marsh food web of the Aiguillon Bay

To better understand the natural interconnection of food chains in the marsh trophic network of the Aiguillon Bay, the food web of this system was constructed using stable carbon isotopes

(^{13}C:^{12}C ratio) to define the origin of the carbon and stable nitrogen isotopes (^{15}N:^{14}N ratio) to define the trophic position of organisms depending on their sources. Collection and preparation of samples for isotopic analyses follow Skrzypek et al. (2022). Samples were precisely weighed (from 0.3 to 5 mg according to the type of sample) in a tin capsule for stable isotope analysis and were analysed using an elemental analyser (EA Isolink, Thermo Scientific, Milan, Italy) coupled with an isotope ratio mass spectrometer (Delta V Plus with a Conflo IV interface, Thermo Scientific, Bremen, Germany). The instrument was calibrated using certified reference materials (USGS-61 and USGS-63). Stable isotope ratios are expressed in delta δ notation, defined as parts per thousand (‰) deviation from a standard material; $\delta^{13}C$ or $\delta^{15}N$ = ([*Rsample/Rstandard*] – 1) x 1000, where R = $^{13}C/^{12}C$ or $^{15}N/^{14}N$.

In-ecosystem investigation using mesocosm experiments

Mesocosm: design and biophysical properties

Fifteen 50 x 50 cm mesocosms were built from a wooden frame covered with small-mesh nylon netting (800 µm). The mesocosms were buried to a depth of 40 cm and measured 1 m high. The net was buried at a depth of more than 10 cm. The fifteen mesocosms have been arranged in one line along the selected *Spartina* patch to offer them the same exposure conditions to wind and tide (Figure 1).

Figure 1. (A) Mesocosm distribution in the study area (B) Outside view of one mesocosm. (C) Inside view of one mesocosm.

Mesocosms were spaced at least 1.5 m apart to avoid any interference between them. Thanks to light sensors, incident light and temperature was measured with probes (HOBO Pendant data logger) on the mesocosms and its reduction due to the net (Figure 2).

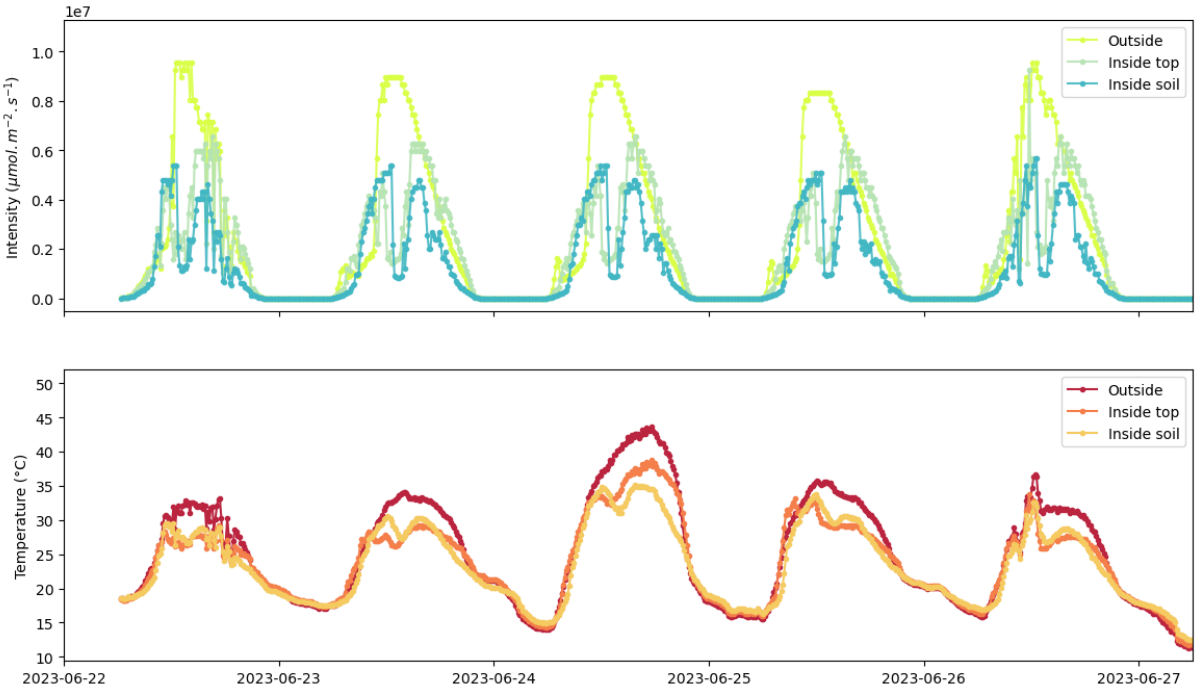

Figure 2. Light intensity (µmol.m^{-2}.s^{-1}) and temperature (°C) outside the mesocosm, inside the mesocosm at the apical level of the leaves and inside the mesocosm at the ground level over 5 days.

The tower-based Eddy covariance enabled us to obtain a footprint over the time of the experiment and the associated TPSP (Temperature, Pressure, Salinity Probe) multiparameter probes (NKE) allowed to estimate how long the mesocosms had been immersed in the water. A dry spell began in the second week and continued until the end of the experiment.

Mesocosm: treatments

Mesocosm experiments started in 2023, May 10th and were completed on June 23rd. At the start of the experiments, all arthropods, especially predators (e.g., crabs, spiders and carabids) present in the mesocosms were removed. It was not possible to remove benthic macrofauna, especially *Peringia ulvae*, meiofauna and microorganisms (i.e., bacteria) of sediment from mesocosms without severely disrupting vegetation and substrate. Then, *Spartina maritima* habitat was considered as vegetation (and sometimes green macroalgae attached to the vegetation), microorganisms, microphytobenthos, meiofauna (i.e., nematods, foraminifera) and benthic marine macrofauna (i.e., *Peringia ulvae*). At the end of the experiments, an evaluation of microorganisms, microphytobenthos, meiofauna and macrofauna was made. Each mesocosm was randomly assigned to one of the following three treatment groups (five mesocosms each): (1) controls to which no detritivores and predators were added; (2) amphipods (detritivore), 200 *Orchestia gammarellus* (corresponding to 2.11g in term of dry biomass) added to each

mesocosm; (3) amphipods (200 *Orchestia gammarellus*) and spiders, 8 *Arctosa fulvolineata* (corresponding to 0.16g in term of dry biomass) added to each mesocosm (Figure 3).

Figure 3. Pictures of *Orchestia gammarellus* (left) and of *Arctosa fulvolineata* (right). © C. Roy

Mesocosm density was within the range of naturally occurring amphipods densities. For spiders, the predation trait was increased by placing more spiders of this species in the mesocosm than in the natural area. The cocoons of the females were removed in order to avoid limiting predation. Amphipods were collected by vacuuming under marsh vegetation and spiders by hand collecting. Before being placed in the mesocosms, amphipods and spiders were globally weighed. At the end of the experiments, amphipods and spiders were collected, dried and globally weighed. Mortality and predation rates were calculated based on observed differences between amphipod and spider abundances between the different treatments at t_0 and t_{end}.

Spartina non-destructive biomass assessment

The aboveground biomass was harvested from 10 quadrats (0.5 m x 0.5 m) around the experimental area. A basic curve of mass vs. height was established by collecting 50 individual shoots in each quadrat in order to cover the maximum heights plants can reach. The height of each steam to the nearest 0.1 cm was measured on a standard meter stick and dried at 60 °C for 72 hours to obtain a constant weight.

Then, in three quadrats, the height of each of the ten tallest shoots to the nearest 0.1 cm was measured and the density of shoots taller than 10 cm was counted and their height stem to the nearest 0.1 cm was measured in order to improve the basic curve of mass vs. height. The biomass was then harvested; dried and weighed as seen before. The average height of the ten tallest shoots was used with the earlier curve to estimate the average individual mass of the tallest shoots. This mass was multiplied by the total stem number to estimate the total biomass $.m^{-2}$. To correct possible overestimation, the measured values of biomass were plotted against

the calculated possibly overestimated values. Thanks to this, the aboveground biomass of each mesocosm was calculated at t_0 and t_{end}.

At t_{end}, underground biomass of three mesocosms with different above-ground biomass was collected. The roots have been washed, dried at 60 °C for 72 hours and weighed.

Primary production and respiration balance in a Spartina maritima habitat

At t_0 and t_{end} CO_2 pressure was measured at the air/sediment interface (enclosed sediment area of 165 cm^2 down to 5-cm depth) using the closed-chamber method described in Migné et al. (2002). Air CO_2 concentration (ppm) changes were continuously monitored in the benthic chamber (0.8 L) continuously over an incubation period of 20 to 30 min, using an infrared gas analyser (IRGA Li-840A, LI-COR, Lincoln, NE, United States) connected to a datalogger (Li-1400, LI-COR) with a 30-s frequency. CO_2 flux was calculated as the slope of the linear regression of CO_2 concentration ($\mu mol.mol^{-1}$) against time (min) and expressed in mg $C.m^{-2}.h^{-1}$.

Transparent chambers were used to estimate the Net benthic Community Production [NCP; balance between the community GCP (Gross Community Production) and the Community Respiration (CR)]. Dark chambers were used to estimate the CR. Light and dark incubations were performed successively. Due to the tidal cycle duration, a maximum of 30 incubations were done in one day (15 transparent and 15 darks). The GCP expressed in mg $C.m^{-2}.h^{-1}$ was computed following Migné et al. (2002) (Eq. 1): GCP = NCP - CR. At t_0 these measures were carried out in the mesocosms before adding arthropods (to prevent arthropods escaping). At t_{end} arthropods were present during the measurements by benthic chambers. NCP and CR were expressed in $mmolC.m^{-2}.h^{-1}$ and NCP and CR was normalised by vegetation biomass only because animal biomass for CR (amphipods, spiders and *Peringia*) was low (less than 1% of total biomass). GCP was calculated from CR and NCP normalised data, following the equation seen above. These flows were expressed in $mmolC.m^{-2}.h^{-1}$.g dry matter.

Photosynthetic parameters of Spartina maritima

At t_0 and t_{end} photosynthetic parameters were measured using a Monitoring Pen (Photon systems instruments, Czech Republic). Rapid light curves (RLCs) were made to assess the photosynthetic activity, by exposing to 7 incremental steps of actinic light (30 s per step) ranging from 0 to 1000 µmol photons.$m^{-2}.s^{-1}$ (PAR, photosynthetically active radiation). The

measurement of RLCs was taken after 15 min dark-adaptation of one *Spartina* leaf per mesocosm. The photosynthetic efficiency (maximum quantum yield of PSII photochemistry) corresponding to the quantity of CO_2 fixed per photon absorbed was computed following Butler, 1978 (Eq. 2): efficiency of the PSII to light = F_v / F_m with F_v = F_m - F_0 (variable fluorescence) and F_m = maximal fluorescence intensity. These measurements were taken at the same time as those obtained by biomass assessment and benthic chambers.

Litterbag field experiment

At t_0, in order to estimate the decomposition of aboveground vegetation during the mesocosm experiment, *Spartina maritima* litter was made by recycling the dried stems obtained during non-destructive biomass assessment. Two types of litterbags were used, but no litterbag was placed in the control mesocosms in order to be able to carry out measurements in a mesocosm where no litter was added. In other mesocosm treatment, 2 litter bags with a size of 20 x 15 cm^2 containing about 25 g of dry aboveground material were placed. The first one is composed of nylon mesh with 800 µm diameter holes (accessible for the microorganisms like bacteria only) and the second one composed of plastic case with 1 cm diameter holes (accessible to the entire community). Each bag was individually weighted before and after adding litter. At t_{end} each bag with the rest of the litter was individually weighted. A tiny part of the remaining litter of each litterbag has been kept for enzyme activity measurements (see below). The remaining contents of each litterbag has been dried at 60°C for 72 hours and weighed.

Microbial enzymatic activities

At t_{end} two extracellular enzyme activities (EEA) involved in organic carbon cycle were assessed to determine the catabolic potential of microbial communities extracted from litter of litterbags: tyrosinase and fluorescein diacetate hydrolase (FDAse) activities. The extracellular enzymes of microorganisms such as bacteria enable the hydrolysis of organic matter. By degrading the cellulosic compounds (oligosaccharides) in lignocellulosic walls more efficiently, these organisms normally lead to a gradual enrichment of litter with organic matter derived from lignin. Tyrosinase is involved in the degradation of aromatic compounds such as tannins, phenolic acids and lignin (Zimmer, 2005). FDAse is a pool of enzymes including phosphatases, cellulases and lipases involved in the degradation of cellulose and carbohydrates (Guénon et al., 2017). It corresponds to the potential hydrolysis activity by different hydrolases. They therefore reflect the degradation of the most abundant constituents of leaf litter. For each

activity, two repeated assays were performed per litter sample. Tyronase activity was determined according to the modified method of Saiya-Cork et al. (2002) and FDAse activity was assessed according to the method of Schnürer and Rosswall (1982).

Community assessment by core sampling of Spartina maritima habitat

Different communities abundance and biomass were obtained from three cores made in the benthic chamber measurement zone in each mesocosm at t_{end}. A core of 2 cm + 1 cm deep and 1 cm diameter was made to assess the abundance of heterotrophic prokaryotes and a core of 1 cm deep and 2 cm diameter was made to assess microphytobenthos biomass. A core of 2 cm deep and 3 cm diameter was made to assess meiofauna abundance. At t_{end} macrofauna abundance was obtained by removing the top 5 cm of the sediment under the benthic chamber measurement zone to assess the abundance of amphipods and spiders present during the fluxes measurement and around the chamber zone to calculate predation and mortality rates). Amphipods and spiders have been dried at 60 °C for 72 hours and weighed.

At t_{end} heterotrophic prokaryotes (i.e., bacteria) abundance of sediment was measured by flow cytometry. Five milliliters of mesocosm sediment were fixed with 0.2 µm filtered formaldehyde solution (vol/vol, 2% final concentration) and freeze to N_2 liquid and stored at -80 °C. Then, cells were separated from the sediment and homogenised according to the protocol described by Lavergne et al. (2014). Briefly, one milliliter of sediment was diluted sequentially to 1/2000 (1:10, 1:100, 1:500, 1:1000 and 1:2000) in the detergent mix [0.01 M NaPp + Tween 80 (0.1% final conc.)] and was mixed by vortexing. Samples were then incubated at + 4°C for 30 min before sonication (60 W for 30 s). Finally, an aliquot of the sample was stained with SYBR Green I (1:10,000) for 15 min in the dark and was analysed by flow cytometry. The extraction step was repeated a second time (same settings as above) to improve cell counting.

At t_{end} the sediment biomass of chlorophyll a (µg Chl a. g dry sediment^{-1}) was used as a proxy for microphytobenthos (MPB) biomass. Chl a and phaeopigments were extracted and measured as previously described Herlory et al. (2004): spectrofluorimetric measurement (Turner TD-700 fluorometer) was performed on supernatant of sediment samples after lyophilisation, extraction (90% acetone, 12 h, + 4 °C, in the dark, continuous shaking) and centrifugation 10 min at 4000 ×g.

At t_{end} the sediment of the core were preserved in absolute ethanol (vol/vol). Samples (14 mL) were sieved through 45 µm sieve before staining with rose Bengal. All samples of macrofauna

were sieved through a 0.5-mm mesh, and organisms retained on the sieve were preserved in 70% ethanol. Meiofauna and macrofauna were counted and identified under a binocular loupe (Zeiss). The distinction between dead and live *Peringia ulvae* individuals was made by observing the presence of biofilm on the periostracum.

Stable carbon and nitrogen isotopes

At t_0 and t_{end}, a core of 2 cm deep and 2 cm diameter was made to measure stable isotopes on the predator and the preys but also for the different plant parts, litterbag litter (small and large mesh) and macro and microalgae present in the mesocosms. For each of these components, one replicate was made per mesocosm. Soil organic carbon was also analysed on the first and second cm in each mesocosm. For each mesocosm, a first stable isotopes measure was made on non-decarbonated sediment on the first and the second depth of the sample (one and one cm) to obtain the isotopic signature of nitrogen. Then, a second stable isotopes measure was made on the same sediment but containing a lot of carbonates. We decarbonated it with hydrochloric acid in order to obtain a correct isotopic signature of carbon.

Arthropod respiration rate

In the laboratory, dark chambers were used to estimate the CR of amphipods and spiders. Three replicates using 3 different lots (n= 20) of *Orchestia gammarellus* and 3 different lots (n= 8) of *Arctosa fulvolineata* were made. In each case and for each lot, measurements were taken with the clear chamber (similar to benthic chambers). To obtain the biomass, the individuals were then dried at 60°C for 72 hours and weighed to the nearest mg.

Statistical analyses

All calculations and statistical analyses were performed using R software version 4.3.1 (R Core Team, 2023). Litter degradation rate was calculated based on weight differences in litterbags between t_0 and t_{end} and expressed in % of dry matter loss. Chlorophyll a biomass (proxy of microphytobenthos biomass) in µg Chl a. g dry sediment^{-1} was converted to g C.m^{-2} using De Jonge, (1980). Heterotrophic prokaryotes abundance was converted to g C.m^{-2} using Pascal et al. (2008) and Bratbak and Dundas (1984). Meiofauna and macrofauna biomass were converted to g C.m^{-2} using stable carbon isotope results (carbon content. g of organisms^{-1}). *Peringia ulvae* flesh biomass was estimated for each mesocosm using Philippe et al. (2016).

The reconstruction of the food web of the Aiguillon Bay was made by using mean carbon $\delta^{13}C$ ($^{13}C/^{12}C$) and nitrogen $\delta^{15}N$ ($^{14}N/^{15}N$) of each dominant component of the Aiguillon Bay schorre. A delta of approximately 3.4 ‰ difference in nitrogen and 1 ‰ difference in carbon was used as values to make a distinction between the predator and its prey (De Niro and Epstein, 1978; Post, 2002).

Power regression was used to represent height of *Spartina maritima* individual shoots to dry weight of shoot. Linear regression was used to compare calculated and harvested biomass of *Spartina maritima*.

Prior to analysis, we checked normality using Shapiro-Wilk's method and homogeneity of variances. Comparison of samples from the two periods (t_0 and t_{end}) was considered as paired samples (two repetitions from the same mesocosm). Comparison of samples from one period was considered as unpaired samples because there was only one replicate per mesocosm and mesocosms are considered as independent (spaced at least 1m50 apart). However, litterbags were considered as paired (two per mesocosm).

For carbon fluxes, normality was only respected at t_0 for the different fluxes of spiders treatment and at t_{end} for all fluxes (except for NCP of control treatment). The homoscedasticity was respected only for CR and GCP of spiders treatment between t_0 and t_{end} (Fisher test) and for CR and GCP fluxes of treatments at t_{end} (Hartley test). Thus, in order to compare Net Community Production (NCP), Community Respiration (CR) and Gross Community Production (GCP) ($mmolC.m^{-2}.h^{-1}$.g dry matter) of the different treatments between t_0 and t_{end} two statistical tests were performed. Wilcoxon signed rank tests on paired samples were performed to compare carbon fluxes of the treatments between t_0 and t_{end} for all fluxes of control and amphipods treatments and only for NCP for spiders treatment. CR and GCP of spiders treatment was compared between t_0 and t_{end} using paired T-tests. To compare these fluxes at t_{end} between treatments (unpaired), we computed a Kruskal-Wallis test for NCP fluxes and one-way analysis of variance (ANOVA) for CR and GCP fluxes.

Photosynthetic activity of *Spartina* was compared according to treatment (control, spiders or amphipods) and to period (t_0 and t_{end}). We computed one-way analysis of variance (ANOVA) to compare treatment to a period and repeated measures ANOVA to compare treatment photosynthetic activity of t_0 to treatment photosynthetic activity of t_{end}.

Litter degradation rate at t_{end} of one type of litterbag according to treatment was compared by using Mann-Whitney tests. To compare litter degradation rate at t_{end} between litterbags type according to treatment, we computed Wilcoxon tests. Each enzymatic activity (FDAse and tyrosinase) was compared between litterbags type according to treatment using Wilcoxon tests. These enzymatic activities were also compared for each type of litterbag according to treatment by using Mann-Whitney tests.

Heterotrophic prokaryotes, meiofauna and macrofauna abundances of each mesocosm were compared at t_{end} between treatments using one-way analysis of variance (ANOVA) for Heterotrophic prokaryotes and macrofauna and Kruskal-Wallis test for meiofauna. Chl a and phaeopigments (used as a proxy of microphytobenthos biomass) were compared between t_0 and t_{end} using repeated measures ANOVA. They were also compared between treatments at t_0 or t_{end} using one-way analysis of variance (ANOVA).

Results

Natural history: knowing the players in the system

Salt marsh food web of the Aiguillon Bay

This reconstruction of the food web of the Aiguillon Bay showed an expected distribution of different system components. There was a clear difference between the shore vegetation with lower $\delta^{13}C$ and the *Spartina maritima* communities with higher $\delta^{13}C$ (Figure 4). Sediment, predators and prey were in the middle of these two groups in terms of $\delta^{13}C$.

In more details, predators such as the spiders *Arctosa fulvolineata* and *Pardosa purbeckensis* or the carabid *Pogonus chalceus* showed a high $\delta^{15}N$ (approx. 17‰). Detritivores such as *Orchestia gammarellu*s and *Porcellio scaber* showed similar $\delta^{15}N$ (approx. 14‰) and lower than spiders. These predators and detritivores showed a $\delta^{13}C$ similar and varying from -22/-24‰. More precisely, a delta of approximately 3.4‰ difference in nitrogen and 1‰ difference in carbon was observed between *Arctosa fulvolineata* and *Orchestia gammarellus*

Spartina maritima was one of the lowest plants in $\delta^{13}C$ with *Puccinellia maritima* (respectively -19 and -16‰). Spartina litter and roots were much lower in $\delta^{13}C$ (around -14‰). In contrast, these two *Spartina* components were higher in $\delta^{15}N$ in comparison to above ground *Spartina maritima* (around 8‰ versus 3‰).

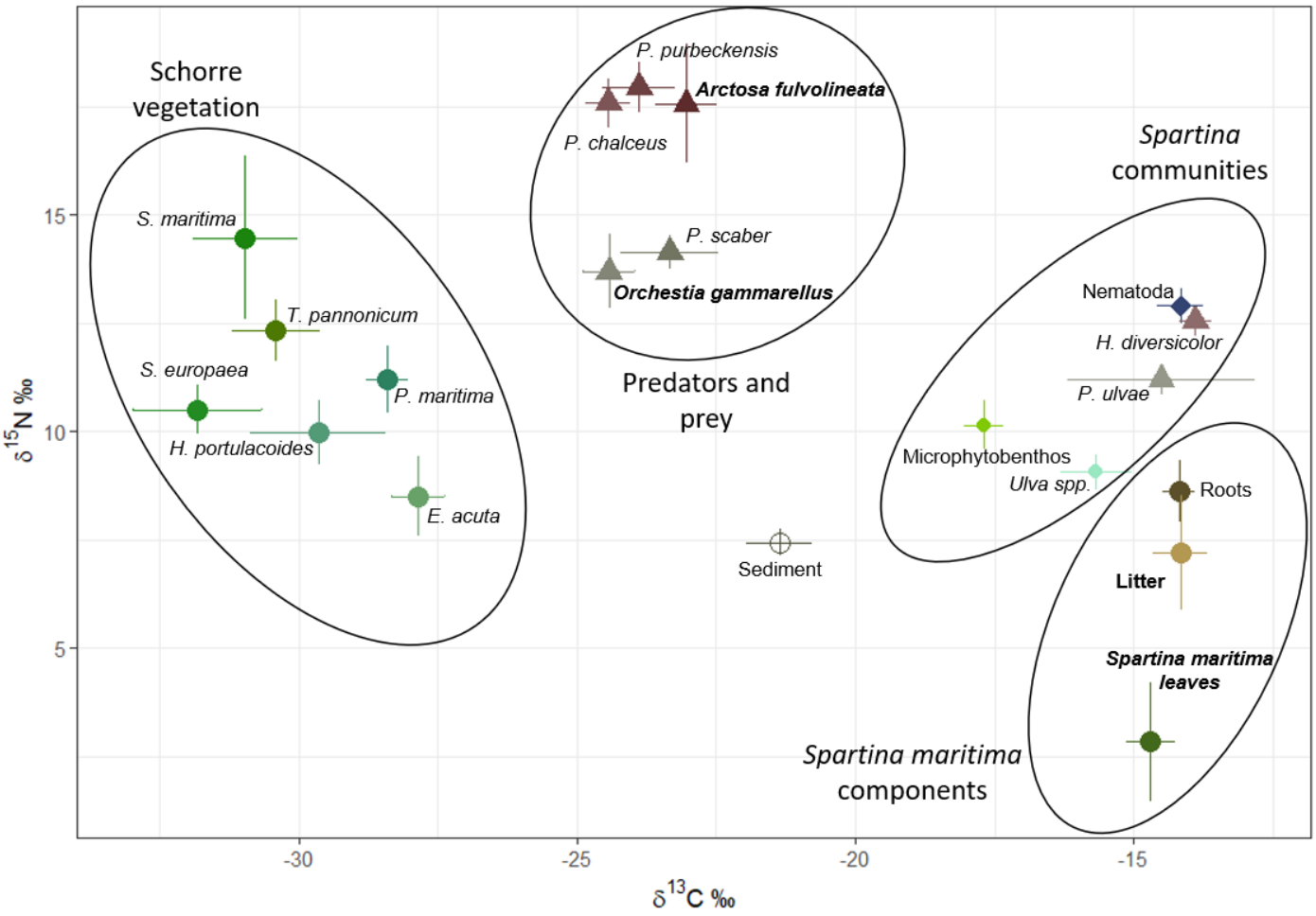

Figure 4. Food web representation: mean carbon $\delta^{13}C$ ($^{13}C/^{12}C$) and nitrogen $\delta^{15}N$ ($^{14}N/^{15}N$) for each dominant component of the Aiguillon Bay schorre. Sediment is the signature of stable isotopes of organic matter in the sediment. Schorre vegetation: *Suaeda maritima*; *Tripolium pannonicum*; *Salicornia europaea*; *Puccinellia maritima*; *Halimione portulacoides* and *Elytrigia acuta*. Predators and prey: *Pardosa purbeckensis*; *Pogonus chalceus* and *Porcellio scaber*. Spartina communities: *Hediste diversicolor* and *Peringia ulvae*.

In-ecosystem investigation using mesocosm experiments

Spartina non-destructive biomass assessment

The resulting calibration curves for *Spartina maritima* are shown as Figure 5. The power model showed a high R^2 value (more than 0.89). The use of a linear regression comparing measured biomass and calculated biomass based on ten tallest shoots showed that the use of the power regression equation (Figure 5) accurately predicted the measured biomass ($y = 1.0532x - 40.993$, $R^2 = 0.99$).

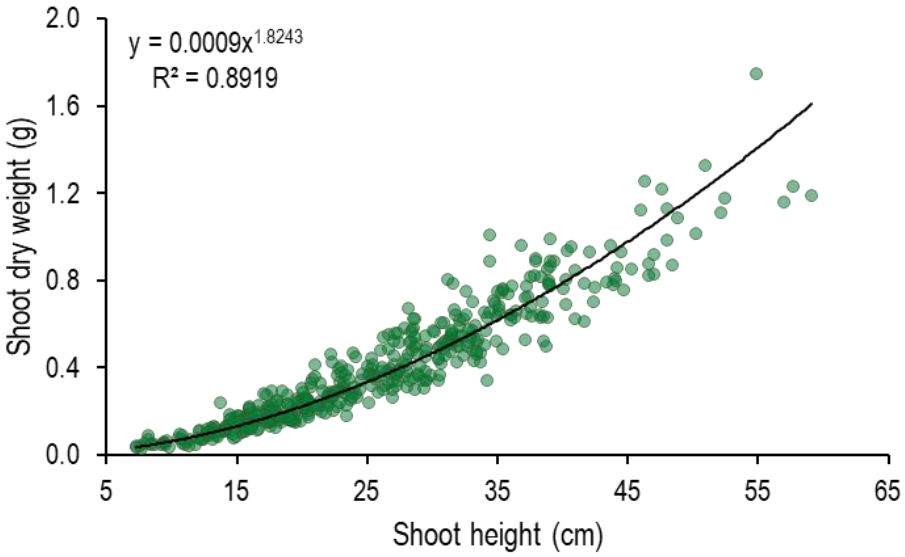

Figure 5. Power regressions relating height of individual shoots to dry weight of shoot for *Spartina maritima* (n=956). Alpha (transparency) value has been applied to all the points to visualise their distribution more clearly.

The use of a linear regression comparing measured biomass and calculated biomass based on ten tallest shoots showed that the use of the power regression equation (Figure 5) accurately predicted the measured biomass ($y = 1.0532x – 40.993$, $R^2 = 0.99$).

Total underground biomass in each mesocosm corresponded to 2.18 times the total aboveground biomass of the mesocosm.

Primary production and respiration balance, Spartina maritima habitat

Net community production relative (NCP) was always negative or close to 0 (Figure 6). NCP was lower in the mesocosms at the start of the experiment than at the end but with no significant difference. At t_{end}, NCP was very close to 0 for the control treatment, and negative in amphipods and spiders treatments (-0.012 ± 0.016 mmol $C.m^{-2}.h^{-1}.g^{-1}$ dry matter for both).

Community respiration (CR) was always positive. CR was higher in the mesocosms with amphipods and spiders in comparison to control mesocosm but with no significant difference. However, CR at t_{end} of the mesocosms with spiders was similar to control and higher with amphipods (Figure 6).

Gross Community production (GCP) was always negative or close to 0. GCP was higher in the mesocosms at the start of the experiment and lower in the mesocosms with amphipods and

spiders (Figure 6). At t_{end}, GCP was very close to 0 for the control treatment, and negative in amphipods and spiders treatments (-0.049 ± 0.027 and -0.047 ± 0.028 respectively). The GCP was statistically different between t_0 and t_{end} of spider treatment (Student's t-test,t = -3.10, df = 4, p= 0.036).

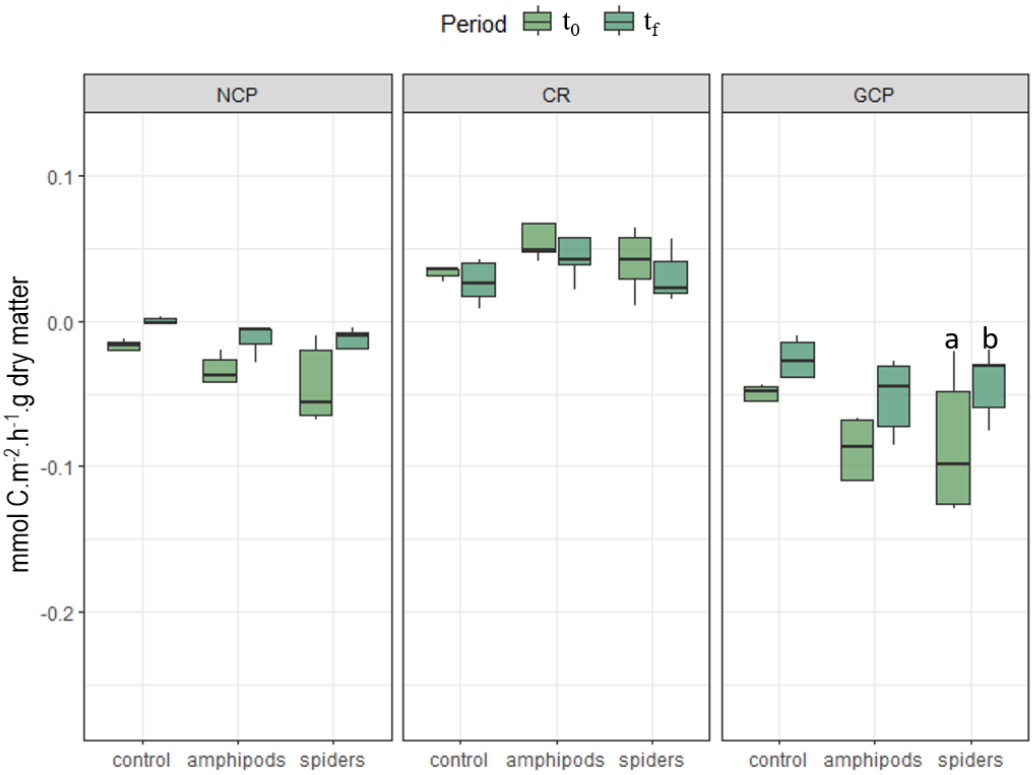

Figure 6. Comparison of Net Community Production (NCP), Community Respiration (CR) and Gross Community Production (GCP) (mmolC.m^{-2}.h^{-1}.g^{-1} dry matter) between t_0 (dark green) and t_{end} (light green) for each treatment (control, amphipods and spiders). The letters indicate a significant difference ($p < 0.05$) found after paired T-tests.

Photosynthetic parameters of Spartina maritima

An average value of 0.78 ± 0.020 was measured for the quantum efficiency of photosystem II (using the Monitoring Pen) of *Spartina maritima* at t_0 and an average value of 0.75 ± 0.021 at t_{end} corresponding to a high quantum efficiency (data not shown), which indicated a good physiological condition at t_0 and at t_{end}. No significant difference was observed between periods t_0 and t_{end} and between treatments.

Litterbag field experiment

Litter dry weight loss was always close to 60% ± 0.020% except for the large mesh litterbag from mesocosms with spiders where the degradation rate of the litter was lower (40% ± 0.020%)

(Wilcoxon test, p=0.049) (Figure 7). No significant difference was observed between the two litterbags types (small and large mesh) in amphipods treatment. Initial biomass of amphipods was reduced by predation rate (0.27) and "natural" mortality rate (0.29). This "natural" mortality rate was similar for spiders (0.25).

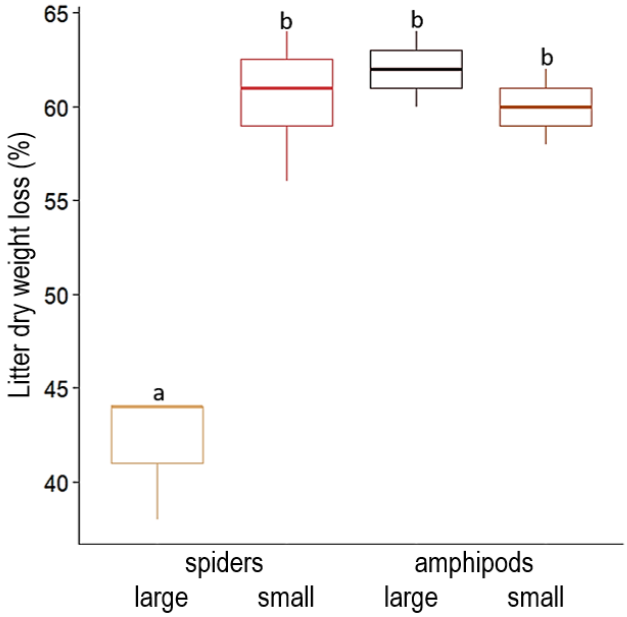

Figure 7. Comparison of litter dry weight loss (%) between t_0 (25 g) and t_{end} treatments (amphipods and spiders). The letters indicate a significant difference ($p < 0.05$) found after a Wilcoxon test.

Microbial enzymatic activities in litterbags (small and large)

FDAse and tyrosinase activities were statistically no different between the two litterbags types (small and large mesh) in amphipods and spiders treatments at t_{end}. No significant differences were found between treatments for FDAse activity (0.0112 ± 0.0026 U. g^{-1} dry matter) and tyrosinase activity (0.629 ± 0.136 U. g^{-1} dry matter).

Community assessment by core sampling of Spartina maritima habitat

Heterotrophic prokaryotes (i.e., bacteria) abundance was statistically no different between treatments at $t_{end.}$ Average abundance was high and was 2.39×10^{14} heterotrophic prokaryotes $.m^{-2}$.

Chl a was around 45 µg/g (± 30.56) at t_0 and 53 µg/g (± 34) at t_{end}. Phaeopigments was around 31 µg/g (± 8) at t_0 and 34 µg/g (± 16) at t_{end}. Chl a and phaeopigments (used as proxy of

microphytobenthos biomass) was statistically no different between treatments at t_{end}. The ratio phaeopigments/phaeopigments x Chl a was approximately around 40% for both periods, which means that 40% of the pigments were degraded, and 60% of the pigments were active.

At $t_{end.}$, no significant differences were found between treatments for meiofauna community. Over 98% of the meiofauna was represented by nematods and the average abundance was 1570 ± 942 meiofauna nematods.m^{-2}).

Concerning the macrofauna, the community was exclusively composed of *Peringia ulvae*. *Peringia ulvae* was distributed in abundance in all the mesocosms. Average abundance was 274 ± 158 individuals of *Peringia ulvae*.m^{-2}.

Stable carbon and nitrogen isotopes in amphipods and spiders used in the mesocosms

The isotopic data were used to produce a mass balance presented at the end of the report. No change was observed in the isotopic values of arthropods (amphipods and spiders) in the mesocosms between t_0 and t_{end} (data not shown). No change was observed in the amount of carbon in the mesocosm sediment and litter of litterbags (data not shown).

Arthropod respiration rate

The arthropod respiration rate was very similar between replicates, with a mean of CR of 1.59 ± 0.19 mmolC.m^{-2}.h^{-1}.g^{-1} dry matter for spiders and of 3.50 ± 0.45 mmolC.m^{-2}.h^{-1}.g^{-1} dry matter for amphipods.

Discussion

The contribution of the dominant arthropod species to the carbon fluxes in salt marsh has been studied for some trophic guilds – such as, detritivores (e.g., Zimmer et al., 2004, Rippel et al., 2022) and phytophagous (Denno, 1977 and Gustafson et al., 2006) but in few regions of the world only – such as the United States (see Denno). However, very few studies have included predators in their assessment of carbon fluxes (but see Graton and Denno, 2003), even though predators can play a very important regulatory role in salt marshes. As an example, *Pardosa littoralis* (Lycosidae) is the most abundant spider in the United States salt marshes, with densities frequently exceeding 200 individuals/m^2 (Denno et al., 2003) and this species has a consumption rate of 70 planthoppers/day (Döbel and Denno 1994). When studying the

decomposition process, these studies usually assess very few response variables and focus only on feeding and growth of detritivores or mass loss of litter for example.

The main objective was the study of the contribution of dominant species of ground-dwelling arthropods to the carbon fluxes of the Aiguillon Bay salt marsh in *Spartina*-dominated habitats. Then, *in*-situ investigations using mesocosm experiments were made in May-June 2023. Each mesocosm was randomly assigned to one of the following three treatment groups (five replicate of each condition): (1) controls to which no detritivores and predators were added; (2) amphipods (detritivore), 200 *Orchestia gammarellus* added to each mesocosm; (3) amphipods (200 *Orchestia gammarellus*) and spiders, 8 *Arctosa fulvolineata* added to each mesocosm. In this study, the ecosystem was studied using a mesocosm experiment in its entirety by assessing the contribution of autotrophic and heterotrophic organisms to the carbon fluxes. The dominant detritivore and predator in French salt marshes were used and several parameters influencing the decomposition process such as mass loss of litter, mortality rate, predation rate and enzymatic activity have been determined. The contribution to carbon storage of the dominant component of *Spartina* habitat has also been determined using stable carbon isotope. Unfortunately, the contribution of phytophagous was not possible in this study due to the absence of them in May 2023 (at the beginning of the mesocosm experiments).

In situ-ecosystem investigation using mesocosm experiments: conditions

The low filtration of light by the mesocosm mesh (14%) has made it possible to provide lighting very similar conditions to those found outside the mesocosm. *Spartina* has a very high growth rate, with an increase in biomass of 170% during the experiment combined with a very high photosynthetic activity (0.75 ± 0.021 at t_{end}). These values correspond to those described in the literature and are even a little higher (e.g., Padinha et al., 2000; Duarte et al., 2016)

On the basis of isotopic data, no variation was observed in *Orchestia gammarellus* and *Arctosa fulvolineata* stable carbon and nitrogen isotopes which means that they have been placed in mesocosms with optimum food conditions. These results are not surprising and are in accordance with the literature. Pétillon et al. (2009) have shown that *Arctosa fulvolineata* is specialised in predating amphipods and Moore et al. (1985) have shown that *Orchestia gammarellus* preferentially consumed algal material and litter of Poaceae, which are present in the *Spartina* habitat.

The dry spell, which covered almost the entire duration of the experiment, led to a significant lack of water supply to the mesocosms (underwater less than 10% of time). These climatic conditions led to a mortality rate of 0.29 for *Orchestia* and 0.27 for spiders.

Primary production, respiration balance and litter degradation in Spartina maritima habitat

Carbon fluxes i.e., Net Community Production (NCP), Community Respiration (CR), and Gross Community production (GCP) have been measured twice (t_0 and t_{end}) and related to aboveground vegetation biomass. NCP was always negative or close to 0 with an average rate of -0.027 ± 0.026 mmolC.m^{-2}.h^{-1}.g dry *Spartina* matter which means that community respiration is lower than photosynthesis.

Despite the presence or absence at varying densities of heterotrophic animals in mesocosms (i.e., *Orchestia gammarellus* ± *Arctosa fulvolineata* (according to treatment) and *Peringia ulvae*, meiofauna and heterotrophic prokaryotes), CR was very homogeneous between treatments over space and time with an average rate of 0.042 ± 0.022 mmolC.m^{-2}.h^{-1}.g dry *Spartina* matter. Amphipods, spiders and *Peringia*, meiofauna and heterotrophic prokaryotes, are therefore involved to a lesser extent in the respiration of the *Spartina* habitat. This low rate of participation in community respiration was confirmed at the laboratory where we obtained a respiration rate of 0.16 ± 0.03 mmolC.m^{-2}.h^{-1}.g dry matter for *Orchestia* and 0.041 ± 0.007 mmolC.m^{-2}.h^{-1}.g dry matter for *Arctosa fulvolineata*. In the sediment in the *Spartina* habitat, a large biomass of heterotrophic benthic prokaryotes (i.e., bacteria, an average of $2.39x10^{10}$) and microphytobenthos were present, which with the plant biomass actively probably participated in *Spartina* habitat respiration. Few studies have quantified the microphytobenthos respiration, Migné et al. (2009) showed that microphytobenthos respiration can be high, but with significant variations over time due to microphytobenthos migration and tidal conditions.

Gross community production (GCP) was always negative or close to 0 and higher at the start of the experiment with an average rate of -0.093 ± 0.064 mmolC.m^{-2}.h^{-1}.g dry *Spartina* matter at t_0 and an average rate of -0.047 ± 0.026 mmolC.m^{-2}.h^{-1}.g dry *Spartina* matter at t_{end}.

The high biomass production of *Spartina* leads to a formation of detritus that varies in quantity depending on the season in particular and it is thought that the flow of energy from primary producers in these systems is largely based on detritus (e.g., Silliman and Zieman 2001). In our experiment, the rate of litter degradation by amphipods without predators was 60%. The presence of *Arctosa fulvolineata* limited the density of prey (detritivores) with a predation rate

of 0.27 and thus the grazing of *Orchestia* on *Spartina* litter. The assessment of the microbial community part compared to the part of degradation by amphipods on litter degradation has not really been possible. As a reminder, litterbags used were not accessible to amphipods and spiders, but only to the microbial community (unlike the other litterbags accessible to the whole community). This means that the loss of litter mass of this type of litterbag is only due to microbial community and abiotic factors such as mechanical movements of water. However, the rate of litter degradation by the microbial community was very homogeneous between treatments over space (around 60%) and similar to those obtained in bags accessible to *Orchestia*. Several hypotheses may explain this such as the selection due to interaction with grazers of different microbial communities with different enzymatic arsenals for litter decomposition. In this study, measurement of the FDAse enzyme activity, which involves a pool of numerous hydrolases reflecting the whole microbial community (Guénon et al., 2017) and tyrosinase enzyme activity highlighting phenol oxidation activity involved in lignin and polyphenol degradation (Zimmer, 2005) were similar between both litterbags types (small or large) and treatments with an average enzyme activity of 0.0112 ± 0.0026 U. g^{-1} dry matter for FDAse and 0.629 ± 0.136 U. g^{-1} dry matter for tyrosinase which is in accordance with values obtained by Dhaou et al. (2022) in another blue ecosystem (here mangroves).

Understanding of the interactions between detritivores and the microbial community is crucial with regard to decomposition processes. The role of bacteria in the decomposition of plant litter is well known (e.g., Purahong et al., 2016; Krishna et al., 2017 and Yarwood, 2018) but the way in which a detritivore can influence the microbial community and therefore the decomposition process dynamic is largely unknown. Several studies suggested that the microbial community living on and within organic detrital particles is assimilated by detritivores. Hargrave (1970) was able to demonstrate that over 50% microbial community assimilation efficiency was done by an amphipod species and Barsdate et al. (1974) found that grazing on bacteria increased bacterial decomposition of *Poaceae* litter. However, in this present study, it seems that the presence of microbial grazers such as *Orchestia gammarellus* did not stimulate the microbial mineralization of *Spartina* litter. During the dry spell, amphipod behaviour could be changed, and they have taken refuge in the ground faults to protect themselves from desiccation. The amphipod rate degradation on the litter has therefore probably been reduced or even stopped during a long part of the experiment, but it is not possible to prove that (it is just a hypothesis).

Finally, no isotopic signature difference (same $\delta^{13}C$ and same $\delta^{15}N$) was observed in sediment of mesocosms over space and time. However, the isotopic signature of litter is different from

sediment signature and the degradation of litter by microorganisms and *Orchestia* has been shown. Thus, the degraded organic matter from litter was not integrated in the sediment but probably exported during the outwelling process (Odum, 2000).

The absence of phytophagous arthropods in the Aiguillon Bay at the start of the experiment has not made it possible to assess their contribution to carbon fluxes. However, the same experimental design with similar measures applied to phytophagous guild impact was reproduced in the *Spartina alterniflora* habitat of the Hoop Pole Marsh, North Carolina (East coast of the United States) under the supervision of Prof. Brian Silliman during May 2023 and still in progress. Two dominant species were used, the small phytophagous *Prokelisia marginata* and a small Linyphiid spider (*Grammonota vittata*). At the end of the experiments in France, many phytophagous species were present in the Aiguillon Bay including potentially the American species, used in Hoop Pole mash experiment, *Prokelisia marginata* which has already been observed in the Nouvelle Aquitaine administrative region. This species exclusively linked to the *Spartina* genus can cause significant damage and increase the *Spartina* detritus formation especially on *Spartina maritima* (Gustafson et al., 2006), which does not appear to have a very abundant specific phytophagous species in the Aiguillon Bay and which is already in the process of declining due to the presence of other invasive species such as *Spartina anglica* in the marsh (Joyeux and Corre, 2013).

Towards a Carbon mass balance in the mesocosm scale in May-June 2023

Spartina maritima covers a total of 57 ha in the Aiguillon Bay and plays a very important role in the advancement of the schorre (Olivier et al., 2021). The schorre is a major carbon dioxide removal strategy and its conservation and restoration are essential to reach La Rochelle carbon neutrality by 2040. Carbon fluxes of *Spartina maritima* communities are important at the marsh scale with a lower CR of 891± 448 molC.h^{-1} and a higher GCP of -1260 ± 454 molC.h^{-1}. The largest carbon storage is in underground *Spartina* biomass and above ground *Spartina* biomass (625 and 317 g.C.m^{-2} respectively). Then, heterotrophic prokaryotes represent a carbon storage of 12 g.C.m^{-2}, slightly more than the microphytobenthos which represents a carbon storage of 8 g.C.m^{-2} (see above Figure 8). Arthropods make a small contribution to carbon storage but we have shown that *Orchestia gammarellus* plays an important role in *Spartina* litter degradation. This species is able to degrade a large quantity of litter in a short space of time.

In order to fully understand the contribution of arthropods to carbon fluxes in salt marshes, it is important to repeat similar experiments in France with the dominant phytophagous arthropods and in the United States with the dominant detritivore. It is essential to determine the proportion of the detrital pathway in comparison with the phytophagous pathway.

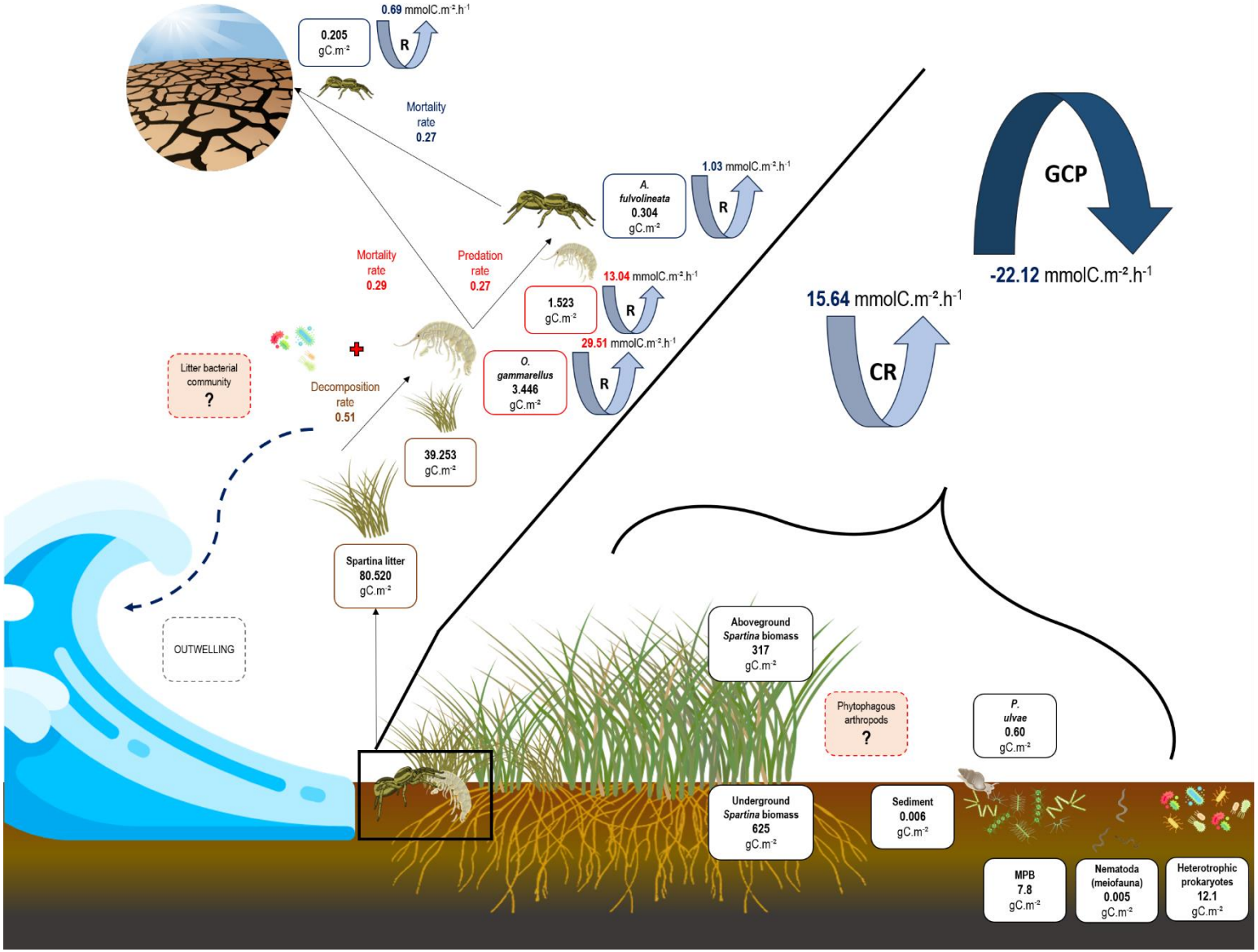

Figure 8. Mass balance of mean carbon fluxes and storage through the *Spartina maritima* habitat. Units are mmolC.m^{-2}.h^{-1} and gc.m^{-2} respectively. Abbreviations: GPP= Gross Community Production, CR= Community Respiration and R= respiration of *Arctosa fulvolineata* or *Orchestia gammarellus*. MBP= microphytobenthos.

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Abstract

Future climatic scenarios predict an increase in concentrations of atmospheric CO_2. *Spartina maritima* is a C_4 halophyte that is an important pioneer and ecosystem engineer in salt marshes of the Atlantic coast of southern Europe. A mesocosm experiment investigated the contribution of the *Spartina maritima* habitat i.e., vegetation, microorganisms, microphytobenthos, meiofauna and benthic marine macrofauna to the carbon fluxes. We measured NCP, CR, GPP of the habitat, *Spartina* biomass increase, chlorophyll fluorescence parameters, microphytobenthos biomass, macrofauna, meiofauna and heterotrophic prokaryotes abundance/biomass. A focus was made on two abundant components of the system i.e., the wolf spider *Arctosa fulvolineata* and its prey, the talitrid amphipod *Orchestia gammarellus* and their contribution to the detritic pathway. Two types of litterbags were used to assess the rate of litter degradation just by microbial community or by *Orchestia* (and microbial community). The litter degradation rate was measured with the presence or absence of the spider such as FDAse and tyrosinase enzymatic activities. CR for each species (amphipod and spider), predation and mortality rates were measured. Stable carbon and nitrogen isotopes were measured over time for all the components of the system. *Spartina maritima* habitat was a carbon sink over time with GPP higher than CR. Litter decomposition rate was high and modulated by the predation of spiders on the amphipods. The specific isotopic signature of the litter indicated that there was no integration of this degraded material in the sediment. The results suggest that the conservation and restoration of *Spartina maritima* habitat constitute an important carbon dioxide removal strategy.

Keywords: blue carbon, blue ecosystem, mesocosms, litterbag, detritic pathway, stable carbon and nitrogen isotopes

Résumé

Les scénarios climatiques prévoient une augmentation des concentrations de CO_2 atmosphérique. La Spartine maritime (*Spartina maritima*) joue un rôle pionnier dans les marais salés. Une expérience en mésocosme a permis d'étudier la contribution de son habitat aux flux de carbone, incluant la végétation, les micro-organismes, le microphytobenthos, la méiofaune et la macrofaune marine benthique. Nous avons mesuré le NCP (production nette de la communauté), le CR (respiration de la communauté) et le GCP (production brute de la communauté), l'augmentation de la biomasse de la plante, les paramètres de fluorescence de la chlorophylle, la biomasse du microphytobenthos et l'abondance/biomasse de la macrofaune, de la méiofaune et des procaryotes hétérotrophes. L'araignée-loup, *Arctosa fulvolineata* et sa proie, l'amphipode *Orchestia gammarellus* ont été utilisés afin d'évaluer leur contribution à la voie détritique. Deux types de sacs à litière ont été utilisés pour évaluer le taux de dégradation de la litière par la communauté bactérienne ou par *Orchestia*. Le taux de dégradation de la litière a été mesuré en fonction de la présence ou de l'absence de l'araignée, comme les activités enzymatiques de la FDAse et de la tyrosinase. La respiration de ces deux espèces et les taux de prédation et de mortalité ont été mesurés. Les isotopes stables du carbone et de l'azote ont été mesurés pour tous les composants du système. L'habitat de *Spartina maritima* a été un puits de carbone avec une GPP supérieure à la CR. Le taux de décomposition de la litière était élevé et modulé par la prédation des araignées sur les amphipodes. La signature isotopique spécifique de la litière indique qu'il n'y a pas eu d'intégration de produits de dégradation dans les sédiments. Les résultats suggèrent que la conservation et la restauration de l'habitat de *Spartina maritima* constituent une importante stratégie d'élimination du dioxyde de carbone.

Mots-clés : carbone bleu, écosystème bleu, mésocosmes, sacs à litière, voie détritique, isotopes stables du carbone et de l'azote