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Trophic ecology of macrofauna inhabiting seagrass litter accumulations is related to the pulses of dead leaves

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Abstract :

Accumulation of exported macrophytodetritus (AEM) represent unique habitats formed by the dead material originating from macrophyte ecosystems (e.g., seagrass, kelp, other seaweeds). AEM can be found everywhere, from the littoral zone to the deepest canyons, and from high to low latitudes. Seagrass AEMs are among the most common detrital accumulations found in marine environments, and sometimes include macroalgae wrack that has been ripped from the substrate. In the Mediterranean Sea, Posidonia oceanica (L.) Delile litter accumulations undergo pulses of new necromass all year, particularly in autumn, when dead leaves are shed. Here, macrofauna inhabiting AEM of Calvi Bay (Corsica, France) was sampled troughout an annual cycle (four seasons). By combining gut content examination and stable isotope analysis, we aimed to assess the effect of seasonal litter pulses on the trophic ecology of the dominant macrofauna species. Litter composition showed drastic variations throughout the sampling period, with the highest leaf litter quantity and contribution to AEMs in November. Dominant detritivores, herbivores, and omnivores responded positively to this increase by ingesting more seagrass material. A Bayesian stable isotope mixing model showed that the assimilation of carbon originating from seagrasses also increased. Additionally, isotopic niche modelling showed that consumer niches shifted towards seagrass isotopic composition in November. Predators did not shift their diet, but their isotopic composition was affected by the isotopic shift of their prey, demonstrating the transfer of seagrass carbon to higher trophic levels and the shift towards dead leaf material in the entire community. This response was, therefore, a rapid (days to weeks) parallel to that of the slow (months to years) decomposition of detrital material via physical alteration and microbial decomposition. This seemingly underestimated transfer route should be better characterised to understand the role of these seagrass beds in carbon sequestration in the marine environment.

Highlights

► Accumulations of *Posidonia* litter undergo pulses of dead leaves all year round, but particularly in autumn. ► Combining gut content and stable isotopes, we have assessed the effect of these pulses on litter macrofauna diet. ► Animals relied more on seagrass detritus in autumn, either directly or, in the case of predators, indirectly. ► The dominant consumers exhibited species-specific responses linked with their feeding strategies and ecological traits.

Keywords : Detritus, Seagrass, Resource pulse, Stable isotopes, Posidonia oceanica, Crustaceans, Mediterranean sea

1. INTRODUCTION

Marine macrophytes (i.e., salt marsh plants, seagrass, macroalgae) contribute significantly and globally to marine carbon fluxes and sinks through the necromass (i.e., detrital biomass) they generate and export to other habitats (Cebrian, 2002; Cragg et al., 2020; Mann, 1988; Ortega et al., 2019). In marine and brackish habitats, the accumulations of exported macrophytodetritus (AEM) can be found everywhere, from the littoral zone (Boudouresque et al., 2016; Mancinelli et al., 2005) to the deepest canyons (Samadi et al., 2010; Vetter and Dayton, 1998), and at all latitudes (Crawley et al., 2009; Filbee-Dexter et al., 2018; Norkko et al., 2004). AEMs are typically comprised of dead or photosynthetically active plant remains (e.g., seagrass, kelp, mangroves) but can also contain material of terrestrial origin (tree parts or other terrestrial plants) that are washed into the sea. Seagrass AEMs are among the most common accumulations found in marine environments. In these AEMs, seagrass detritus are sometimes mixed with drift macroalgal wrack that has been ripped from its substrate (Boudouresque et al., 2016; Hyndes and Lavery, 2005). Observations of such AEMs in the deep ocean (Wolff, 1976), nearshore canyons (Vetter and Dayton, 1998), or shallow areas (Boudouresque et al., 2016; Hyndes and Lavery, 2005) are common. Fossil seagrass AEMs are frequently found in Maastrichtian formations (66–72 × 10^6 years) for *Thalassocharis bosquetii* deposits (Jagt et al., 2019) and in the late Pliocene of Rhodes (3.6–2.6 × 10^6 years) for *Posidonia oceanica* litter deposits (Moissette et al., 2007).

Posidonia oceanica (L.) Delile is the dominant seagrass in the Mediterranean Sea and is the major contributor to AEMs in the area investigated in the current study (Calvi Bay, Corsica, NW Mediterranean). In the Mediterranean, AEM dynamics are primarily driven by the annual life cycle of *P. oceanica*, which shows a typical increase in leaf shedding in the autumn (Gobert et al., 2006; Romero et al., 1992). In addition to the seasonal biological dynamic, coastal AEMs are known to be highly variable in time, size, and composition. The disturbance frequency and intensity depend on local hydrodynamics (e.g., storm events in autumn), seafloor morphology or seascape features, and frequent exchanges with the beach (Mancinelli et al., 2005; Ricart et al., 2015; Simeone and De Falco, 2012; Simeone et al., 2013). These physical and biological dynamics generate stronger pulses of ‘new’ *Posidonia* necromass to AEMs in the fall. Resource pulses have been defined as “rare, brief and intense episodes of increased resource availability in space and time” (Ostfeld and Keesing, 2000). Thus, these biological and environmental drivers result in important temporal variations of AEM composition and abundance.

Posidonia oceanica AEMs are unique habitats that are colonised by abundant and diverse vagile meio- and macrofauna. The macrofauna of *P. oceanica* AEMs consists of up to 115 species but is dominated by a few crustacean taxa (Calizza et al., 2013; Como et al., 2008; Gallmetzer et al., 2005; Remy et al., 2018). The associated food web is dominated by species showing a mixed diet composed of various proportions of seagrass detritus, epiphytes growing on this detritus, and drift macroalgae (Remy et al., 2018). The fauna associated with litter contributes significantly to the decomposition of this material (Costa et al., 2019). Mesocosm experiments showed that the input of a moderate amount of dead *P. oceanica* leaves had large and rapid effects on macrofauna community (i.e., changes in specific diversity and total and relative abundances) (Costa et al., 2019; Remy et al., 2017b).

As AEM composition and abundance vary according to the pulse of dead material, food source identity, quality, and availability for the associated animal community, they potentially induce diet modifications in these consumers (Yang et al., 2008). Here, we aimed to assess the effect of litter inputs on the trophic ecology of five dominant macrofauna species from a seagrass AEM: the amphipods *Gammarus aequicauda* (Martynov, 1931), *Gammarella fucicola* (Leach, 1814), and *Melita hergensis* (Reid, 1939), and the shrimps *Athanas nitescens* (Leach, 1813) and *Palaemon xiphias* (Risso, 1816). These five macrofauna species are the most abundant throughout the year in the investigated AEMs (75% of the total individual abundance on yearly average). They span three trophic levels (primary consumers, omnivore, predator) and have contrasting feeding habits (detritivore, detritivore/herbivore, omnivore/herbivore, omnivore/predator, and predator, respectively) (Remy et al., 2018). Specifically, we hypothesised that 1) animals rely more on seagrass detritus when its availability increases (i.e., in fall) and that 2) different consumers exhibit species-specific responses linked with their contrasting feeding strategies and ecological traits. To address these hypotheses, we combined gut content and stable isotope analysis. Gut content analysis provides a high-resolution snapshot of recently ingested food, but does not provide any information on the actual assimilation of food sources. This can be challenging when dealing with poorly digestible food, such as seagrass detritus. Therefore, stable isotope measurements were used to complement this technique, bridge the gap between ingestion and assimilation, and provide a more accurate view of trophic interactions and energy flows.

2. MATERIALS AND METHODS

2.1. Sample processing

Litter samples were taken by SCUBA divers in August 2011, November 2011, March 2012, and May 2012 at two shallow (8–10 m) sampling sites near the STARESO oceanographic research station in Calvi Bay (42°35’N; 8°43’E, Corsica). The whole set of isotopic data (n = 19 species and N = 556 specimens in total) was published in Remy et al. (2018) to depict the structure of the food web associated with global macrophytodetritus accumulations, without considering temporal variation (data averaged over the whole year). Here, we re-used this dataset to investigate the temporal dynamics, focusing on the seasonal isotopic niche of the community (n = 19 species) and the dietary habits of the five dominant crustacean species (N = 331 individuals in total).

Litter and associated fauna samples (n = 6 per season and site) were collected by pushing a cylindrical PVC litter core (25 cm diameter, surface of 490 cm² used to report litter dry mass per m^{-2}) into the litter until the sediment surface was reached. The entire litter content inside the core was carefully collected manually and transferred into plastic jars that were sealed until further processing in the lab. Litter was then rinsed on stacked 10 mm and 1 mm sieves to facilitate macrofauna sampling. Potential benthic food sources (i.e., dead *Posidonia* and their epiphytes, drift macroalgae) and fauna were frozen (-20°C) until further analysis.

In the lab, the food sources collected in AEMs were separated into five categories: (1) dead *P. oceanica* leaf fragments, (2) drift brown algae, mainly ripped from adjacent rocky habitats, (3) drift red algae ripped from adjacent rocky habitats, (4) epiphytes (i.e., defined as sessile animals and algae living on dead seagrass leaves), and (5) living *P. oceanica* shoots uprooted from the seagrass meadow. All food sources were oven-dried (60°C for 96 h) and weighed to express the sampled amount in dry mass per square meter ($gDM.m^{-2}$), then were subsequently used for isotopic measurements. The ratio between dry epiphytes and leaf biomass was determined by scraping the first 25 dead leaves of each sample with a razor blade, then drying epiphytes and leaves and weighing them separately. The ratio between the two was then applied to the whole sample to extrapolate the total epiphyte dry mass.

2.2. Gut content analysis

Animals were dissected under a stereo microscope, and their gut contents were spread in a single layer over a microscope slide. Gut content analyses were performed under a stereo microscope (StemiC, Zeiss, Switzerland, magnification 50x) using the semi-quantitative technique described by Wilson and Bellwood (1997), which was adapted in this study for the very small gut contents of vagile invertebrates. Each microscope slide was superposed on a 4 cm^2 grid composed of 100 squares of 4 mm^2. Twenty-five of 100 squares were randomly chosen, and the dominant food item was identified in each square (Wilson and Bellwood, 1997). The dominant food items for this study were visually classified into five categories: (1) dead *P. oceanica* leaves, (2) living *P. oceanica* leaves, (3) other vegetal material, (4) animal material, and (5) unknown material. Once 25 squares were examined and the most dominant item was noted, the relative abundance (%) of each category was calculated. Organisms presenting an empty gut, or less than 10 squares containing one of the determined items, were excluded from further analyses.

2.3. Elemental and stable isotope analysis

After gut removal, the animals were dried for at least 96 h (60°C), ground to form a homogenous powder, and acidified under 37% HCl vapor for 24 h to eliminate the bias of carbonate isotopic composition on tissue isotopic composition. After acidification, samples were dried again for 48 h (60°C), ground, and put in tin cups prior to elemental and stable isotope analysis. The stable isotope ratio of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$), and the elemental composition (%C and %N) of both elements were determined for each individual using an isotopic ratio mass spectrometer (IsoPrime100, Elementar UK) interfaced in continuous flow with an elemental analyser (vario MICRO cube, Elementar). Isotope ratios for C and N were reported conventionally in permille (‰), using standard delta (δ) notation relative to their respective international standards, Vienna-Pee Dee Belemnite (V-PDB) and Atmospheric Air. Pure gases of CO_2 and N_2 were used as primary analytical standards and calibrated against certified reference materials, i.e., sucrose (IAEA-C6; $\delta^{13}C$

= -10.8 ± 0.5‰) and ammonium sulphate (IAEA-N2; δ^{15}N = 20.3 ± 0.2‰), obtained from the International Atomic Energy Agency (IAEA, Vienna, Austria). The analytical precision was assessed by procedural blanks, internal replicates (i.e., glycine and in-house crustacean and seagrass reference material), and isotopic certified reference material (i.e., IAEA-C6 and IAEA-N2). The standard deviations for replicate measurements were based on an in-house standard (amphipod crustacean powder) and were 0.1‰ for δ^{13}C and 0.2‰ for δ^{15}N.

2.4. Statistical analyses

To test for differences in the proportion of dead leaves in the gut contents and in δ^{13}C and δ^{15}N values among the consumers from different seasons, univariate two-way ANOVAs with species and date as factors were used. Tukey's multiple comparison test was then used to assess pairwise differences when ANOVAs revealed statistically significant effects. All test results were considered significant when p was ≤ 0.05. Statistical calculations were performed using PAST version 4.02 (Hammer et al., 2001).

Stable Isotope Bayesian Ellipses in R (SIBER) version 2.1.5 (Jackson et al., 2011) was used in R 4.0.1 (R Core Team, 2020) to generate bivariate standard ellipses representing the core isotopic niches of consumers. For each season, two sets of ellipses were generated. Population niches (i.e., species comparison) were computed using individual measurements for each of the five dominant species, and community niches were computed using the mean isotopic ratios of all 19 species as an input.

For mixing models, we aimed to assess seasonal variation in the reliance of dominant crustaceans inhabiting AEMs on different primary producers and/or organic matter sources, regardless of their trophic level. Models were therefore built using carbon stable isotopic ratios only and season-specific values for the isotopic ratios of consumers (individual measurements) and food items. Based on their δ^{13}C values (Remy et al., 2018), it was possible to distinguish four three benthic sources at the basis of the food web: 1.) dead *P. oceanica* leaves, 2.) a pool of epiphytes and brown macroalgae ripped from adjacent rocky habitats (mainly *Halopteris* spp. and *Dictyota* spp.), and 3.) red macroalgae ripped from adjacent rocky habitats. Trophic enrichment factors (TEFs; i.e., the net differences between consumer delta values and diet delta values) were taken from two published laboratory feeding experiments focusing on some of the studied species. The TEFs were 1.0 ± 0.4‰ for dead *P. oceanica* leaves (Remy et al., 2017a) and 0.2 ± 0.6‰ for other items (Michel et al., 2015). Models were built using simmr (stable isotope mixing models in R) 0.4.2 (Parnell et al., 2010, 2013) in R 4.0.1 (R

Core Team, 2020). The iteration number was set at 10^6 and burn-in size at 10^5. The model results are presented either as the full distribution of the posterior probability density function or as modes with a 95% credibility interval of the distribution.

3. RESULTS

3.1. AEM composition

Litter composition showed large variations throughout the sampling period (Figure 1). Averaged over the entire sampling period, dead *P. oceanica* leaves were by far the most abundant component of AEMs (813.0 ± 705.1 gDM.m^{-2}), followed by living *P. oceanica* leaves (168.6 ± 202.1 gDM.m^{-2}), epiphytes (93.8 ± 82.8 gDM.m^{-2}), dead *P. oceanica* rhizomes (53.3 ± 121.5 gDM.m^{-2}), and drift macroalgae (26.5 ± 37.6 gDM.m^{-2}). Dead *P. oceanica* leaves had the highest abundance in November 2011 and the lowest abundance in May 2012. Dead leaves were always the major component of the AEMs, representing on average proportions of 50 to 80% of litter biomass (Figure 1).

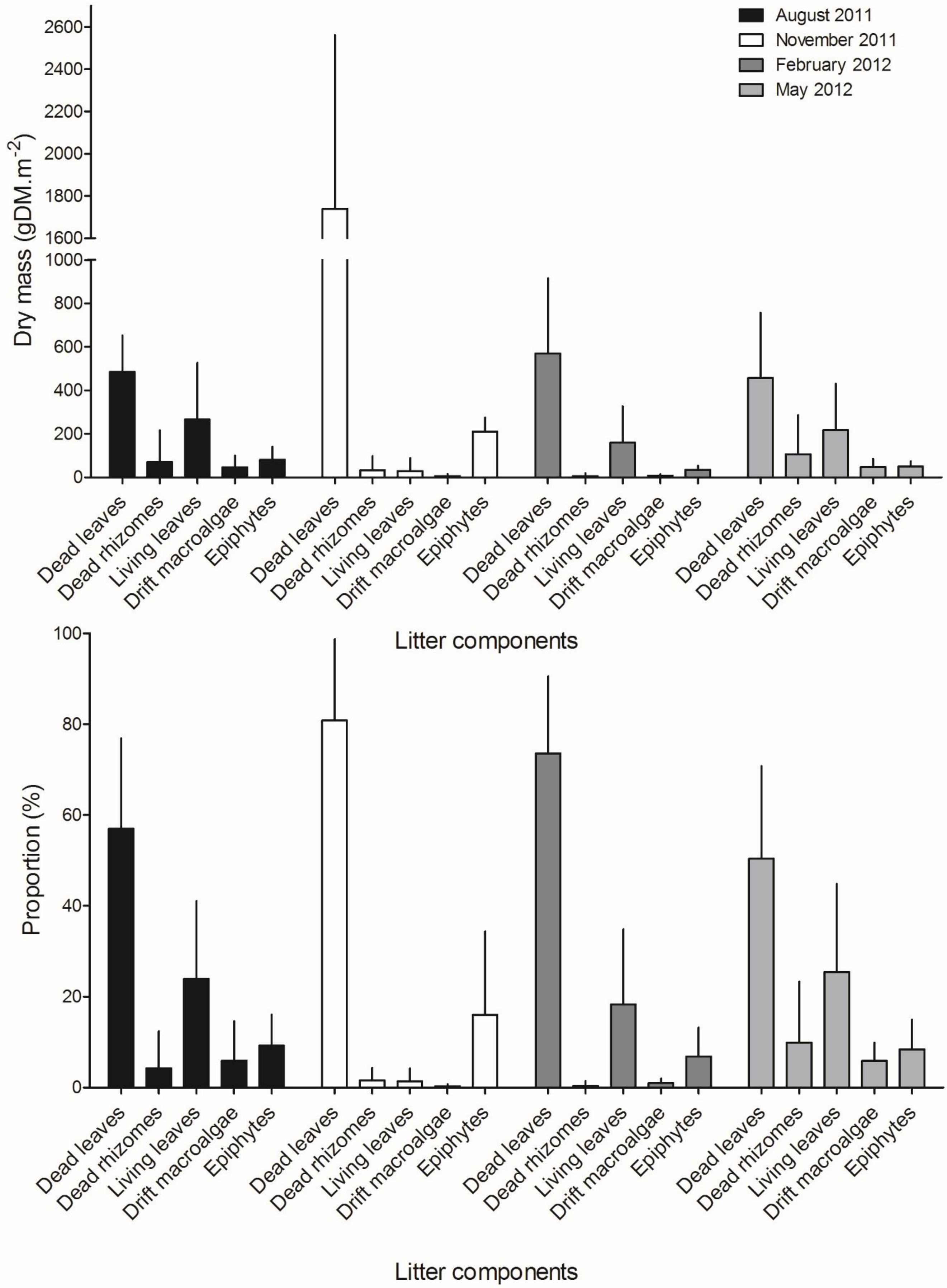
August 2011
November 2011
February 2012
May 2012
Dry mass (gDM.m^{-2})
0
200
400
600
800
1000
1600
1800
2000
2200
2400
2600
Dead leaves
Dead rhizomes
Living leaves
Drift macroalgae
Epiphytes
Litter components
Proportion (%)
0
20
40
60
80
100
Litter components

Figure 1: Composition of exported macrophytodetritus accumulations (AEMs) sampled in August 2011, November 2011, March 2012, and May 2012 (Calvi Bay, Corsica). Results are expressed as quantities (upper panel) and proportions (lower panel).

3.2. Gut content analysis

Green pieces (i.e., living) of *P. oceanica* shoots were never found in the gut contents of the five species investigated here. The gut contents of the five investigated species were clearly distinct (Figure 2). Guts of the detritivore amphipod, *Gammarus aequicauda*, were dominated by *P. oceanica* dead leaves. The detritivore/herbivore amphipod *Gammarella fucicola* showed various proportions of algae and seagrass detritus in its gut. The gut contents of the herbivore/omnivore amphipod *Melita hergensis* were dominated by algae material but also contained animal items. The omnivore/predator decapod *Athanas nitescens* had a larger proportion of animals in its diet, but also ingested dead seagrass material. The predator decapod *Palaemon xiphias* mostly ingested animal material.

Except for *P. xiphias*, all species ingested dead *P. oceanica* leaves (Figure 2). The proportion of this item in the gut contents differed significantly between species ($p < 0.001$, Table 1) and sampling dates ($p < 0.001$, Table 1). As shown by Tukey's multiple comparison test ($p < 0.001$), the proportion of dead leaves in the guts of *G. aequicauda*, *G. fucicola,* and *P. xiphias* guts differed significantly among the three species. *M. hergensis* and *A. nitescens* showed a similar proportion of *P. oceanica* dead leaves in their diet ($p > 0.2$) but differed markedly from that in the guts of *G. aequicauda*, *G. fucicola,* and *P. xiphias (*Tukey's multiple comparison test ($p < 0.001$).

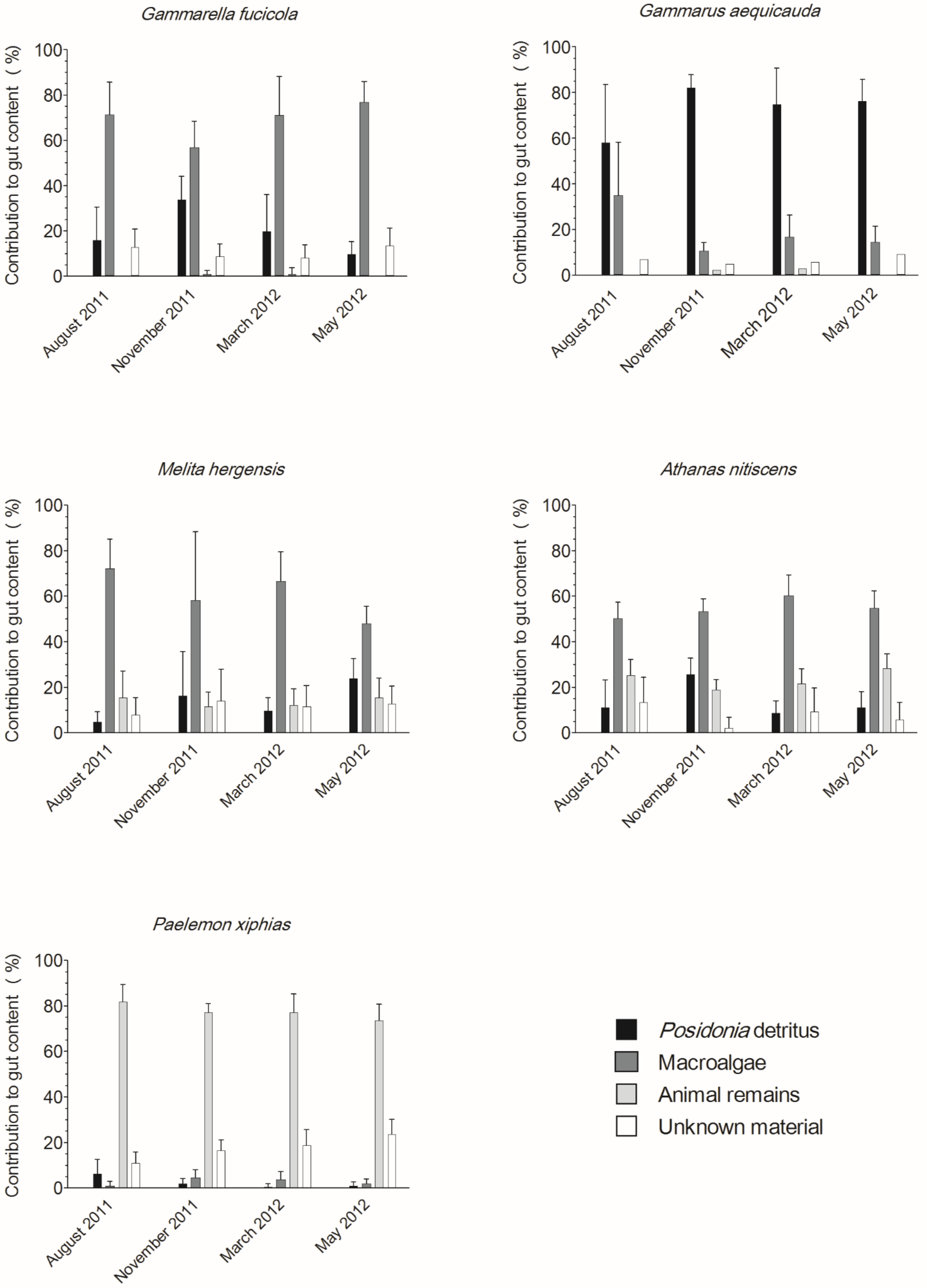
Gammarella fucicola
Gammarus aequicauda
Melita hergensis
Athanas nitiscens
Paelemon xiphias
Contribution to gut content (%)
0
20
40
60
80
100
August 2011
November 2011
March 2012
May 2012
■ *Posidonia* detritus
■ Macroalgae
■ Animal remains
□ Unknown material

Figure 2: Relative composition of gut contents of the five dominant species found in *Posidonia oceanica* AEMs sampled in August 2011, November 2011, March 2012, and May 2012 (Calvi Bay, Corsica).

The relative abundance of dead *P. oceanica* leaves in consumers' gut content changed over time, and the trends appeared to be species-specific (Figure 2). For *G. aequicauda*, the dead leaf contribution to gut content did not differ significantly across sampling times (Tukey's multiple comparison test, $p > 0.1$). For *G. fucicola*, the proportion of dead leaves in the gut was highest in November (33.7 ± 10.6%) and lowest in May (9.6 ± 5.6%) and significant differences were observed between August and the three other sampling dates (Tukey's multiple comparison test, $p < 0.05$ for all comparisons). For *M. hergensis,* the contribution of dead leaves to the total gut content was highest in May (23.9 ± 8.6%) and lowest in August (4.7 ± 4.6%), but the difference was only significant between February and May (Tukey's multiple comparison test, $p < 0.001$). For *A. nitescens*, the proportion of dead leaves in the gut content was highest in November (25.7 ± 7.1%) and lowest in February (8.7 ± 5.4%), and there were significant differences between August and November and between August and May (Tukey's multiple comparison test, $p < 0.05$). For *P. xiphias*, the proportion of dead leaves in the gut content was highest in August (6.3 ± 6.3%) and lowest in February (0.5 ± 1.5%) and there were no significant differences between sampling dates (Tukey's multiple comparison test, $p > 0.05$).

3.3. Community isotopic niches

Community isotopic niches (computed using all species analysed at each sampling date; Figure 3) clearly showed that $\delta^{13}C$ values of the whole community were less negative in November. Conversely, community isotopic niches in August, March, and May strongly overlapped.

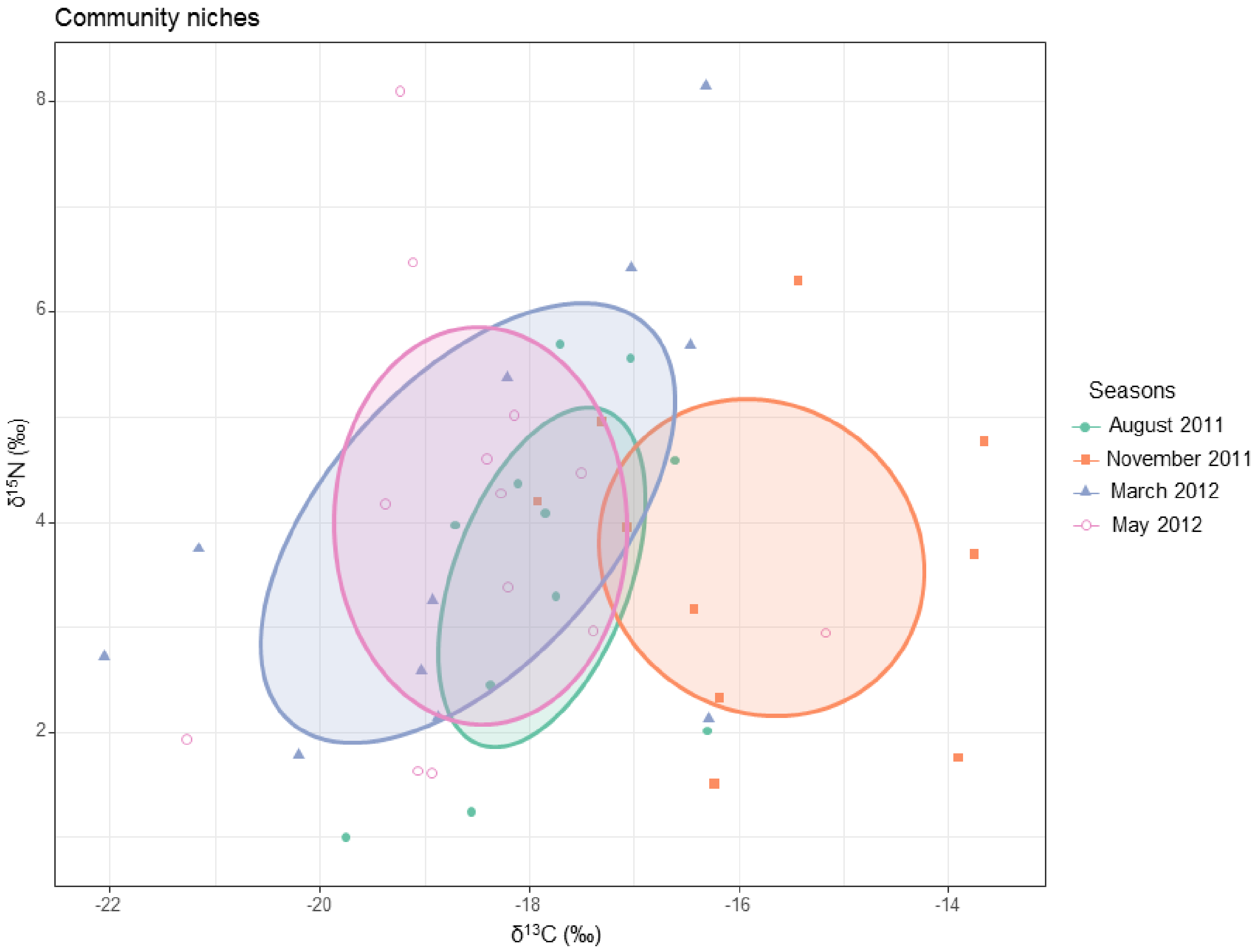

Figure 3: Community isotopic niches of macrofauna sampled in August 2011, November 2011, March 2012, and May 2012 in *Posidonia oceanica* AEMs (Calvi Bay, Corsica). Points are the mean of each species, and solid lines are standard ellipses.

3.4. Population isotopic niches

Average $\delta^{13}C$ and $\delta^{15}N$ values of consumers ranged from -20.7‰ (*M. hergensis*) to -13.7‰ (*G. aequicauda*) and from 0.2‰ (*G. fucicola*) to 6.7‰ (*P. xiphias*), respectively. Interspecific differences in both isotopic ratios were present ($p < 0.001$, Table 1). The $\delta^{13}C$ and $\delta^{15}N$ values differed significantly between *G. aequicauda*, *G. fucicola*, *M. hergensis*, *A. nitescens*, and *P. xiphias* (Tukey's multiple comparison test, $p < 0.01$ for all significant comparison), except for $\delta^{13}C$ values of *G. aequicauda* and *A. nitescens* (Tukey's multiple comparison test, $p < 0.001$).

Table 1: Results of the two-way ANOVA on the proportion of dead leaves in the gut content of consumers inhabiting exported macrophytodetritus accumulation and their $\delta^{13}C$ and $\delta^{15}N$ values. ***: $p < 0.001$

	% dead leaves					$\delta^{13}C$ values					$\delta^{15}N$ values				
	Sum of squares	df	Mean square	F	p	Sum of squares	df	Mean square	F	p	Sum of squares	df	Mean square	F	p
Species	193115	4	48279	309	***	579	4	144	323	***	907	4	227	424	***
Time	8341	3	2780	18	***	323	3	108	240	***	13	3	4	8	***
Time x Species	8420	12	702	4	***	123	12	10	22	***	38	12	3	6	***

The $\delta^{13}C$ and $\delta^{15}N$ values of consumers changed significantly over time ($p < 0.001$, Figure 4). For all species, the $\delta^{13}C$ values were the least negative in November. For *G. aequicauda*, $\delta^{13}C$ was the most negative in August and differed significantly between seasons (Tukey's multiple comparison test, $p < 0.01$), except between August and February. For *G. fucicola*, $\delta^{13}C$ values were the most negative in May. The $\delta^{13}C$ values taken for *G. fucicola* in November differed significantly from all other sampling dates (Tukey's multiple comparison test, $p < 0.001$), but there were no significant differences between the other sampling dates. For *M. hergensis*, the $\delta^{13}C$ values were highest in February. The $\delta^{13}C$ values taken in November differed significantly from all other dates, and those taken in February and May were also significantly different from each other (Tukey's multiple comparison test, $p < 0.001$). For *A. nitescens*, $\delta^{13}C$ values were the most negative in August, and were only significantly different between August and November (Tukey's multiple comparison test, $p < 0.001$). Finally, for *P. xiphias*, $\delta^{13}C$ values were the most negative in May with significant differences between all sampling dates (Tukey's multiple comparison test, $p < 0.001$), except between August and February (Tukey's multiple comparison test, $p > 0.1$).

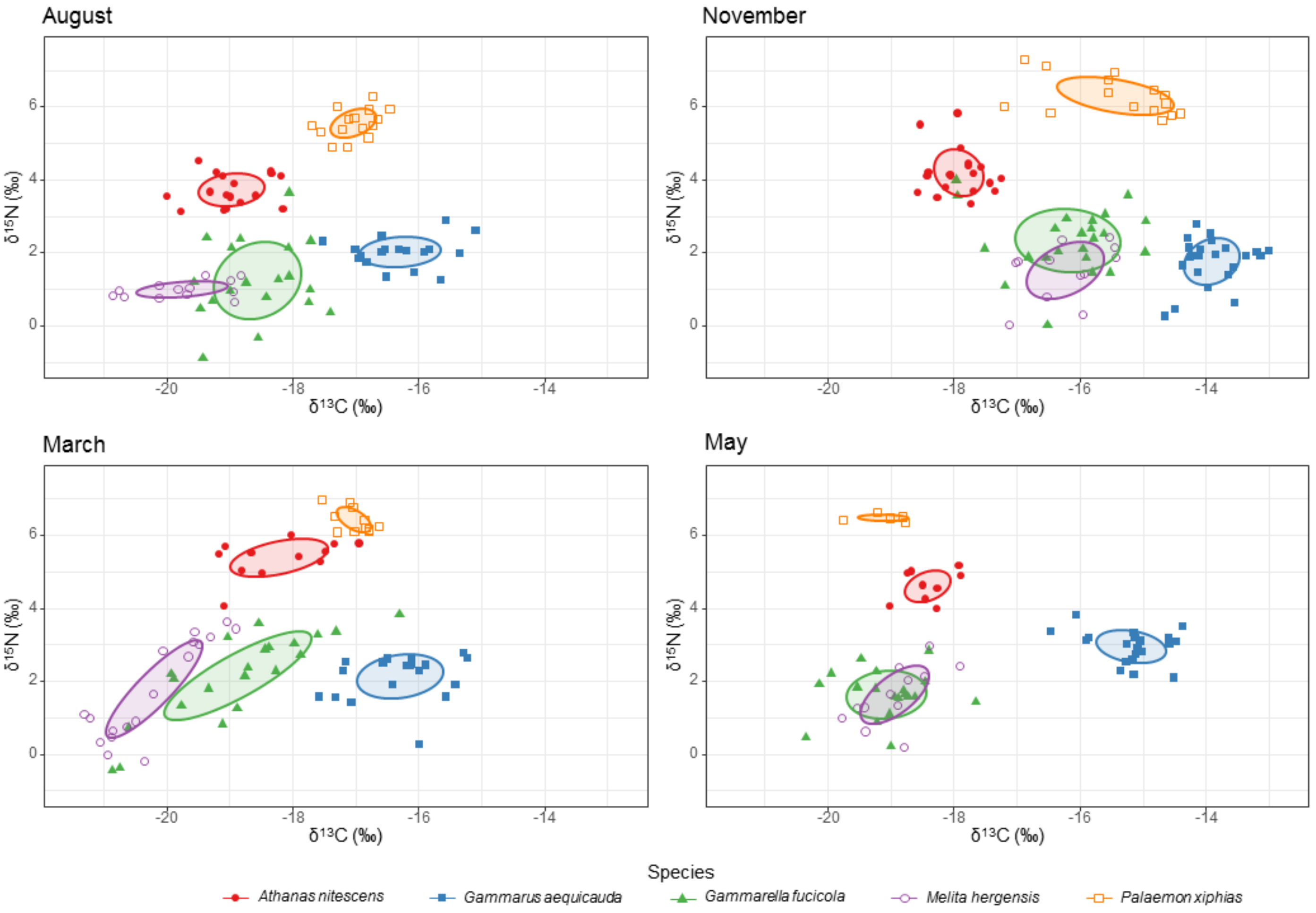

Figure 4: Population isotopic niches of five dominant macrofaunal consumers sampled in August 2011, November 2011, March 2012, and May 2012 in *Posidonia oceanica* AEMs (Calvi Bay, Corsica). Points are individual measurements, and solid lines are standard ellipses.

For $\delta^{15}N$ values, there was no consistent seasonal pattern common to all species. For *G. aequicauda*, $\delta^{15}N$ values were lowest in November and highest in May (Figure 4) and differed significantly between May and the other sampling periods (Tukey's multiple comparison test, $p < 0.001$). There were no significant differences between other sampling periods (Tukey's multiple comparison test, $p > 0.05$). For *G. fucicola*, $\delta^{15}N$ values were lowest in August and highest in November. The $\delta^{15}N$ values of *G. fucicola* measured in August differed significantly from all other sampling dates (Tukey's multiple comparison test, $p < 0.001$), but no significant differences were found between any other dates (Tukey's multiple comparison test, $p > 0.05$). For *M. hergensis*, $\delta^{15}N$ values were lowest in August and highest in May, but there were no significant differences between sampling dates (Tukey's multiple comparison test, $p > 0.05$). For *A. nitescens*, $\delta^{15}N$ values were lowest in August and highest in February. The differences in δ^{15}N values were only significant between February and August and between February and November (Tukey's multiple comparison test, $p < 0.001$). Finally, for *P. xiphias*, δ^{15}N values were lowest in August and highest in May, with no significant differences between sampling dates (Tukey's multiple comparison test, $p > 0.05$).

Population isotopic niches, modelled for the five dominant species using SIBER, were clearly distinct and never overlapped for *P. xiphias*, *G. aequicauda*, and *A. nitescens* (Figure 4). The isotopic niches of *M. hergensis* and *G. fucicola* were distinct from those of the three other species, but occupied closer positions in the isospace. According to the sampling dates, niches of *M. hergensis* and *G. fucicola* were adjacent (March), weakly overlapping (August), partly overlapping (November), or strongly overlapping (May) (Figure 4). Generally speaking, the isotopic niches of all consumers shifted towards less negative values in November.

3.5. Mixing model output

The mixing model output confirmed that the diet composition of the five dominant species changed over time (Figure 5). Moreover, dead leaves contributed, as a distal food source at the basis of the food web, to the nutrition of all species investigated here (Figure 5). All contributions in the following text are given as the mode [limits of the 95% credibility interval] of the relevant posterior probability density function.

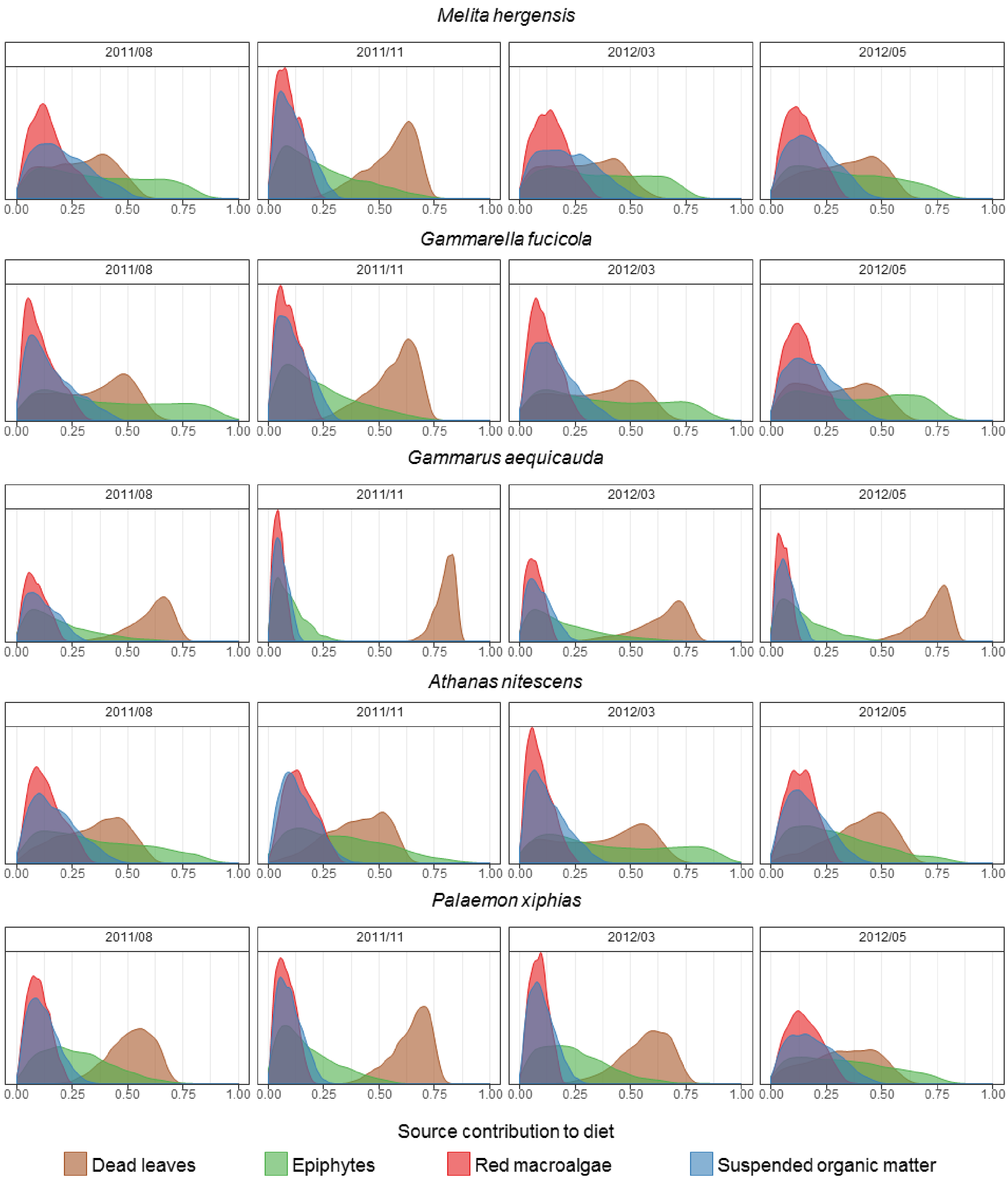

Figure 5: Relative contributions of four food items (dead *P. oceanica* leaves, their epiphytes and other drift photophilous green and brown algae, drift red algae, and suspended particulate organic matter) to the diet of five dominant macrofaunal consumers sampled in August 2011, November 2011, March 2012, and May 2012

in *Posidonia oceanica* AEMs (Calvi Bay, Corsica). The simmr output is presented as the full distribution of the posterior probability density function.

Dead *P. oceanica* leaves were the main contributor to the *G. aequicauda* diet in all seasons (Figure 5). This contribution was lowest in August (66% [39–74%]) and highest in November (83% [70–86%]). Compared to other amphipod species, inter-season changes in dead leaves comparisons varied little for *G. aequicauda*. Dead leaves were also an important food item for *G. fucicola* and *M. hergensis*, but their contribution varied more between sampling dates. Dead leaves were the main carbon source in November (63% [32–71%] for *G. fucicola* and 63% [30–71%] for *M. hergensis*). In all other seasons, both species co-relied on epiphytes, drift green and brown macroalgae, and dead leaves with a slight predominance of epiphytes and macroalgae. The diet of these *G. fucicola* and *M. hergensis*, as pictured by our mixing model, seemed quite similar.

For *A. nitescens*, the modelled contributions of dead leaves were also relatively important. Model solutions were dispersed for all sampling dates but varied relatively little between dates (45% [6–57%], 51% [11–60%], 55% [3–66%], and 49% [8–61%] for August, November, March, and May, respectively).

Finally, the simmr results suggested that dead leaves were the main organic matter source supporting the shrimp *P. xiphias* and its prey in all seasons but May. The importance of this food item peaked in November (70% [44–76%]).

4. DISCUSSION

Our results showed that the total abundance of AEMs, as well as their composition (i.e., relative proportions of the different fractions), changed over time. Dead *P. oceanica* leaves were found at each sampling date, but their abundance was particularly high in November. This continuous presence allows a relatively abundant animal community to develop in this particular habitat. The accumulations were mostly composed of dead *P. oceanica* leaves. Nevertheless, AEMs were very rare in March and May, and their abundance increased fourfold in November. This export was massive and occurred rapidly in relation to one or two major autumnal storms. This really corresponds to a pulse of ‘new’ resources for animals living in the accumulations. The shedding of dead *P. oceanica* leaves occurs mainly in September, and shed leaves stay in the meadow until major wind gusts occur and they are exported to other habitats (adjacent or not). This litter has already been colonised and affected by microbial decomposers, as it has been staying in the seagrass meadow for a few weeks. Nevertheless, the dead leaves found in accumulations in November were not fragmented and still supported an abundant epiphytic community, indicating that it should be considered relatively new compared to fragmented litter. There was a clear contrast between litter accumulated in November and that observed in March and May, with mixed recent litter and more degraded fragments.

The temporal evolution observed for the composition of AEMs was determined by the life cycle of *P. oceanica* (i.e., more important leaf production in spring, more important leaf abscission and fall in autumn) but also by hydrodynamics (occurrence of autumn storms, direction of waves and currents) and the local seascape (i.e., spatial ecosystem patterns, including local coastal morphology) (Gobert et al., 2006; Ricart et al., 2015; Simeone et al., 2013). Our study area, which is a sheltered bay with fine sand, accumulated litter from adjacent seagrass beds in October–November when autumnal storms occurred. There is a frequent exchange of material with the wrack washed up on the beach or forming *Posidonia* "banquettes" (i.e., seagrass berms) (Mateo et al., 2003; Simeone et al., 2013).

We hypothesised that animals would rely more on seagrass detritus when its availability increases (i.e., in autumn). Regarding this first hypothesis, our results suggest a clear relationship between the temporal variability of AEM composition and the diet of crustaceans dominating this habitat. Throughout the year, the organisms exploited multiple food items present in the litter accumulation (epiphytic algae and algae exported from adjacent habitats, animals, dead leaves of *Posidonia*). However, they seemed to respond to the massive arrival of dead leaves in autumn by shifting their dietary habits. We notably observed more seagrass consumption both in terms of ingestion (gut content analysis) and carbon assimilation (stable isotope analysis). The extreme abundance of this resource, despite poor digestibility, allows invertebrates that are capable of using them directly (or in an early phases of decomposition) to increase their biomass and abundance (Remy et al., 2017b). Moreover, this study demonstrates that resource increases induce diet modifications in some dominant macrofaunal herbivores, detritus feeders, and omnivores. This last observation mirrors findings about meiofauna living in the AEMs, as the three dominant species of harpacticoid copepods from AEMs also showed an increase in the proportion of carbon from seagrass in their diet (Mascart et al., 2018).

Here, community-wide isotopic niches showed a global shift of macrofaunal assemblages towards less negative δ^{13}C values (characteristic of seagrass tissues) in autumn. This suggests that, through multiple trophic linkages, the pulses of dead leaves could impact energy acquisition for the whole AEM community. Rapid temporal fluctuations of community structure and trophic interactions following the contributions of macrophytodetritus (seaweeds, leaves of trees, or seagrass) exist in many aquatic systems. For example, Majdi and Traunspurger (2017) showed that the isotopic niches of macrofauna and meiofauna colonising a stream in a temperate zone tended to shift towards isotopic values characteristic of tree leaf litter in autumn. This is, for example, the case of *Gammarus pulex*, a freshwater congener of *G. aequicauda.* Wallace et al. (1999) showed with a field experiment that the long-term exclusion of phytodetritus deposition could, in certain situations, drastically reduce the diversity, as well as secondary production, in a headwater stream. On a tidal flat in North America, Levinton and Stewart (1988) demonstrated the importance of the seasonal contributions of *Ulva* spp. wrack for intertidal annelids. These contributions influenced the dynamics of species succession and community structure, enhanced species diversity and abundance, and modified the basal structure of the food web (microphytobenthos *vs.* detrital food web) (Lopez and Levinton, 1987). Seasonal seaweed deposition is also important in saltmarsh mudflats (Kelaher and Levinton, 2003), and seagrass and macroalgae export has been shown to subsidise terrestrial ecosystems (Cardona et al., 2007; Colombini et al., 2009; Ince et al., 2007). Similar observations have also been reported for underwater accumulations of macroalgae litter (including kelp) (Crawley et al., 2009; De Betignies et al. 2020; Duggins et al., 2016; Norkko et al., 2004). Overall, macrophytodetritus subsidies (i.e., macroalgae, seagrass, and mangrove) appear to be ubiquitous and trophic pathway an important contributors to energy fluxes in aquatic ecosystems (Bouillon and Connolly, 2009; Heck Jr et al., 2008; Hyndes et al., 2014).

We hypothesised that the different consumers exhibit species-specific responses linked with their contrasting feeding strategies and ecological traits. Corroborating our second hypothesis, all dominant species were not affected in the same way by autumnal pulses of *Posidonia oceanica* detritus. The trophic niche of *G. aequicauda*, a detritivore species in AEMs (Remy et al., 2018), hardly seemed to change over time. However, *G. fucicola*, an herbivore/detritivore that dominated the assemblage (i.e., this species represented more than 50% of individual abundance in all samples), clearly showed greater reliance upon dead seagrass leaves, both in terms of gut content and stable isotopes. This was also, to some extent, the case for the two omnivores, *A. nitiscens* (as shown by gut contents) and *M. hergensis* (as shown by stable isotopes). Considering that these dominant species represent more than 75% (yearly average) of the animals present in AEMs, these shifts are likely to be relevant for community ecology. Interestingly, *Palaemon xiphias* also showed shifts in its isotopic ratios (Figure 4) and reliance on basal carbon sources (Figure 5) in November. Since *P. xiphias* is a predator (Remy et al., 2018), those shifts were unlikely to be related to the direct consumption of *P. oceanica* detritus. This was confirmed by our gut content analysis (Fig. 2). Instead, isotopic shifts might be caused by changes in the diet and increased litter consumption by *P. xiphias* prey, which notably feeds on *G. fucicola* (Remy et al., 2018). Therefore, the shift in *P. xiphias* isotopic ratios in November shows that changes in seagrass detritus carbon are channelled up to the predator level. This highlights the two main entry routes of seagrass material into the food web: (1) directly via the ingestion and assimilation of dead leaf material or (2) indirectly via the consumption of prey whose diet shifted to include more dead leaves. As mentioned above, we postulated that similar processes could explain how the ecological habits of the entire community are affected by sudden changes in AEM abundance and composition.

The decomposition of seagrass detritus is assumed to be slow (month to years, depending on the material nature and degradation conditions) (Mateo and Romero, 1996; 1997). Generally, decomposition increases the digestibility of seagrass detritus through the loss of phenolic compounds (Harrison, 1989). Without questioning this observation, we showed that some of this detritus was assimilated quickly (i.e., in a matter of weeks) by detritivores, without waiting for an advanced state of decomposition. The dead leaves observed in November were not yet fragmented or covered by living epiphytes. The incorporation of seagrass detrital organic matter into AEM's macrofaunal consumers could be not only significant (given the animal biomass observed and the proportion of seagrass in their diet) but also rapid (days to weeks) when compared to microbial decomposition processes (months to years). In this context, it could constitute an important and underestimated process for the Mediterranean coastal zone. AEMs are indeed frequented by local ichthyofauna feeding on small benthic invertebrates (Boudouresque et al., 2016). They could indirectly rely on seagrass detritus but also export organic matter, ultimately synthesised from this food source, to neighbouring areas. Furthermore, macrofaunal species living in the AEMs are also present in seagrass beds themselves (Michel et al., 2016), which implies that this mechanism of ‘express transfer’ from the detrital material to the animal biomass could also take place in the meadow itself. Overall, besides the degradation of detrital material via physical alteration and microbial decomposition, transfer through macrofauna appears as a parallel entry pathway for seagrass organic matter into the food web. It is likely that this transfer route should be better characterised to capture the complete role of seagrass beds in carbon sequestration in the marine environment.

CREDIT AUTHOR STATEMENT

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DATA & CODE AVAILABILITY

All data supporting the analyses from this paper are freely available at [XXX]. The code underlying isotopic niches and mixing model analyses, as well as Figures 3, 4, and 5, can be freely downloaded at https://doi.org/10.5281/zenodo.3903281.

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