ARTICLE

Coastal and Marine Ecology

Quantifying the direct and indirect relationships linking the environment, seagrass, and their associated fauna

Jade Millot[1] | **Jacques Grall**[1,2] | **Chirine Toumi**[1] | **Marion Maguer**[2] | **Aurélien Boyé**[3]

[1]LEMAR, Univ Brest, CNRS, IRD, Ifremer, Plouzané, France

[2]OSU IUEM, Univ Brest, CNRS, IRD, Plouzané, France

[3]IFREMER, Centre de Bretagne, DYNECO LEBCO, Plouzané, France

Correspondence
Jacques Grall
Email: jacques.grall@univ-brest.fr

Present address
Jade Millot, MARBEC, Univ Montpellier, Ifremer, IRD, CNRS, 34200, Sète, France.

Abstract

Foundation species such as seagrasses modulate critical ecosystem processes, promote biodiversity, and structure community spatial and temporal dynamics. Hence, they play a key role in mediating the response of biodiversity to environmental changes. The breadth of their contribution to biodiversity maintenance and the potential cascading effects of their alteration remain unclear as we lack a comprehensive understanding of the intricate mechanisms governing their response to environmental changes and that of their associated fauna. Indeed, the mechanisms involved are often studied in isolation or at scales that only provide incomplete representations of the complex functioning of these ecosystems. This study aimed to clarify the direct and indirect relationships linking the environment, seagrass, and their associated faunal assemblages, using structural equation modeling (SEM). To this end, we review the literature to derive theoretical models of the functioning of seagrass ecosystems and test them using long-term monitoring data covering 14 years of nine different *Zostera marina* seagrass beds across 500 km of coastline. We show that contradictory relationships and ambiguities regarding seagrass–biodiversity relationships emerge from the currently available literature (covering experimental, observational, and modeling studies). The SEM approach allowed us to clarify these direct and indirect relationships and resolve most ambiguities. In particular, we show that seagrass mediates the effect of the environment on its associated communities. However, this mediating effect is different, both qualitatively and quantitatively, for epifauna and infauna. Unexpectedly, the diversity of benthic macrofauna appeared to be controlled and promoted by the biomass rather than by the shoot density of the seagrass beds. We also provide quantitative estimates for the direct and cascading pathways linking seagrass biodiversity to environmental changes. Overall, by synthesizing, clarifying, and quantifying the multiple relationships linking a foundation species such as seagrass to its environment and associated biodiversity, we contribute to a better understanding of seagrass meadows

functioning and help predict the potential consequences of foundation species alteration on their associated fauna.

INTRODUCTION

Seagrass meadows are biogenic habitats that play a major role in the functioning and biodiversity of coastal ecosystems (Duffy, 2006). They actively contribute to nutrient cycling and act as carbon sinks (Duarte et al., 2010). On a small scale, seagrass aboveground structure reduces current velocity and traps particles, thus contributing with their inhabitants to increasing water quality through the filtration of suspended particles (Barbier et al., 2011; Maxwell et al., 2017). Seagrass's extensive root system also stabilizes sediments, reducing coastal erosion (Reidenbach & Thomas, 2018). Moreover, seagrass presence promotes biodiversity as it provides shelter together with abundant food sources for numerous species, while also acting as nurseries for many fish and invertebrate species (Duffy, 2006; Hughes et al., 2009; Lefcheck et al., 2018). Finally, seagrass beds have long been recognized for holding intense primary and secondary productivity that sustain complex food webs (Duarte et al., 2010).

The ecosystem functions and services provided by seagrass beds are globally and locally under severe threats. A global declining trend of seagrass coverage had been recorded until the 1980s (Dunic et al., 2021). Some historical and rapid losses were documented as caused by pandemics. For example, the so-called "wasting disease" led to the disappearance of 90% of the European *Zostera marina* populations in the early 1930s (Godet et al., 2008). However, most of the seagrass losses can be attributed to the global increase in human coastal occupancy and the pressure associated with human activities such as water quality degradation, benthic trawling, and urbanization (Dunic et al., 2021). Recently, following management measures aimed at improving water quality and reducing fishing pressure (Lefcheck et al., 2018; Turschwell et al., 2021), seagrass decline has been slowing down in southwestern Europe, and examples of local recovery have been reported (De los Santos et al., 2019; Dunic et al., 2021). However, it appears that seagrass loss currently remains greater than their gain, while their fragile restoration remains threatened by more frequent and intense extreme climatic events (Krause-Jensen et al., 2021).

Seagrass sensitivity to anthropogenic pressures makes them "sentinel" of the environment (Orth et al., 2006) that can be used to monitor the ecological status of coastal waters (Marbà et al., 2013). Furthermore, as their response to environmental changes has cascading effects on the whole functioning and biodiversity of coastal ecosystems, they are also "leverage" species whose conservation and management appear as a priority (Harley et al., 2006). Indeed, because they are leverage species, their disappearance or alteration has strong implications for the functioning of coastal ecosystems and their associated biodiversity (Airoldi et al., 2008; Hughes et al., 2009; Sunday et al., 2017). The extent of seagrass beds is therefore considered as an essential ocean variable (EOV) that would account for biodiversity trends at a global scale (Muller-Karger et al., 2018). Reaching a minimal surface of seagrass bed within an ecosystem then became a conservation target for numerous marine protected areas' (MPA's) management plans (Nicholson et al., 2021). Finally, seagrass meadows could play an important role in mediating the impact of future climate change on biodiversity (Bulleri et al., 2018; Harley et al., 2006).

At local scales, the ability of seagrass indicators to proxy ecosystem functioning and dynamics remains unclear. Indeed, too many uncertainties persist regarding the links between the habitat and its associated species (Airoldi et al., 2008; Boström, Jackson, & Simenstad, 2006; Boström, O'Brien, et al., 2006) as well as between species and ecosystem functioning (Snelgrove et al., 2014). Many experimental studies focused on understanding the links between seagrasses and their associated fauna and environment variations, with varying success. Thus, not all studies are unambiguous about the meaning or even the existence of direct relationships between these abiotic and biotic elements of seagrass ecosystems (Yang et al., 2013). Also, because they are often conducted on limited temporal and spatial scales, the findings of these studies are generally difficult to extrapolate to long-term processes (Witman et al., 2015; Yang et al., 2013). Moreover, our understanding of the links between seagrasses and their associated biodiversity is mostly focused on how these ecosystem engineers influence species richness (as for most engineering species; Miller et al., 2018; Romero et al., 2015). Despite efforts to better characterize the beta diversity (Whittaker, 1972) of seagrass meadows over recent years (e.g., Alsaffar et al., 2019; Boyé et al., 2017; Whippo et al., 2018), there are still

gaps in our understanding of how community composition and structure vary within and across seagrass meadows (Airoldi et al., 2008).

This study addresses the influence of environmental changes on benthic biodiversity and the mediating role of seagrass beds. To do so, it relies on data collected as part of the "Réseau Benthique" (REBENT), a monitoring network aimed at acquiring relevant knowledge of coastal benthic habitats, detecting long-term changes in coastal macrobenthic diversity, and understanding the influence of natural and anthropogenic constraints. It has been conducting dedicated monitoring programs over six different habitats along the Breton coastline since 2003 and is still doing so. Within this framework, nine intertidal *Z. marina* meadows from all over the region are monitored yearly for seagrass density size, biomass, as well as for associated epi- and infauna (macroinvertebrates). These data have already been used to study the structure and the functioning of the seagrass meadows and their associated fauna (Boyé et al., 2017, 2022; Toumi et al., 2023). These studies suggest that the structure and dynamics of epifauna and infauna communities, respectively occupying the above- and belowground biomass of the seagrass bed, are likely to be controlled by different factors (Boyé et al., 2017). They also provide insights into the responses of *Z. marina* (Boyé et al., 2022) and of its associated fauna (Boyé et al., 2017; Toumi et al., 2023) to the environmental changes that occurred over the last decades. However, they do not provide a holistic vision as well as quantitative estimates of how seagrass mediates the effect of abiotic changes on epi- and infauna macroinvertebrates.

With the specific aim of clarifying the direct and indirect relationships linking the environment, seagrasses, and their associated biodiversity, we used these long-term monitoring data to explore the following questions: (1) What is the direct influence of the environment on the structure and composition of the seagrass fauna? (2) How and to what extent the structure of seagrass beds mediates the response of the fauna to the environment? (3) Do epifauna and infauna respond differently to the characteristics of the seagrass bed and the direct and indirect effects of the environment? If so, what are the main drivers of the two compartments?

To address these questions, we start by building theoretical models of the direct and indirect relationships between epifauna or infauna, environmental drivers, and seagrass characteristics in intertidal environments, through a review of the existing literature. These theoretical relationships are then tested against empirical data using structural equation models (SEMs) (Lefcheck, 2016). Through sets of equations, SEMs allow quantifying direct and indirect links between variables, which can be both response and predictor. This innovative statistical tool has already shown its effectiveness in highlighting the complex relationships linking biogenic habitats to their environment and their associated biodiversity (e.g., in kelp forests; Miller et al., 2018). Two separate SEMs, focused on epifauna and infauna respectively, were built to qualitatively and quantitatively measure the direct and indirect relationships linking the environment, seagrass, and their associated fauna. We expect to identify different relationships between the two compartments and their environment (Boyé et al., 2017). We hypothesize that seagrass biomass and/or shoot density would be an important mediator of the effect of the environment on the epifauna (Boström et al., 2006a) and thus, that epifauna would be more tightly linked to seagrass characteristics and less to environmental conditions than infauna (Rodil et al., 2021). We expect more complex and indirect relationships for infauna, with potentially indirect effects of seagrass shoot density and aboveground biomass through organic matter content (Herkül & Kotta, 2009; Pearson, 1978) and drifting algae concentrations (Boström & Bonsdorff, 2000; Heery, 2018; Norkko et al., 2000). We forecast direct effects of seagrass belowground biomass on infauna (Orth et al., 1984) and a greater contribution of abiotic conditions, especially sediment characteristics on this compartment (Gray & Elliott, 2009; Sanders, 1958).

MATERIALS AND METHODS

Field sampling

Nine intertidal *Z. marina* beds distributed along the coastline of Brittany were monitored yearly between 2005 and 2019 (Figure 1). The whole set of sites covers a wide variety of environmental conditions, representative of the habitats of *Z. marina* beds (Boyé et al., 2022): from sheltered to highly exposed, growing on well-sorted sands to heterogenous muddy sediments.

Each seagrass bed was sampled yearly between the beginning of February and the end of March, which corresponds to the minimum growth period for *Z. marina* (Moore & Short, 2006). This sampling season thus limits the interannual variability of the measured morphological descriptors (Martínez-Crego et al., 2008). It also corresponds to a period before the minimum abundance and density of fauna, largely diminished after winter storms and before the recruitment of most species in the region (Grall, 2002). In order to take into account intra-meadow variability (Balestri et al., 2003), each meadow is sampled at three fixed points separated by about 200 m. Sampling includes sediment grain size analysis, biometry of the seagrass population together with infauna and epifauna

FIGURE 1   Location of the nine monitored *Zostera marina* beds.

abundance, and species composition. These parameters are then linked to environmental data extracted from models (see below, Appendix S1).

Study of the response of infauna and epifauna to environmental and seagrass variability

Construction of the theoretical models through literature review

The use of SEMs requires a limited selection of variables and the formulation of assumptions regarding the existence and direction of relationships between these variables (Grace & Irvine, 2020). This approach relies on the existing literature to identify major variables characterizing not only the seagrass bed, its environment, and associated fauna, but also on the relationships that link these variables together.

Two theoretical models, respectively centered on the infauna (Figure 2A) and the epifauna (Figure 2B), were

built, with every relationship being supported by one or more literature references (Appendix S2). Even if these models aim to derive general relationships from intertidal seagrass meadows, we targeted references from temperate intertidal *Z. marina* meadows except for relations poorly documented in this system. In addition, when the literature was unambiguous, we display the expected sign of the relationships (either positive or negative), in order to highlight expected results given in previous work and confront these theoretical relationships with the empirical data described below. As these models were built for intertidal meadows, light was not included as it is not expected to be a limiting factor in these environments (Boyé et al., 2022; Yang et al., 2013).

Acquisition and transformation of empirical data used to confront theoretical models

Fauna sampling

At each point and each year, epifauna was sampled at low tide by three 10-m-long, 1-m-wide, and 1-mm-mesh
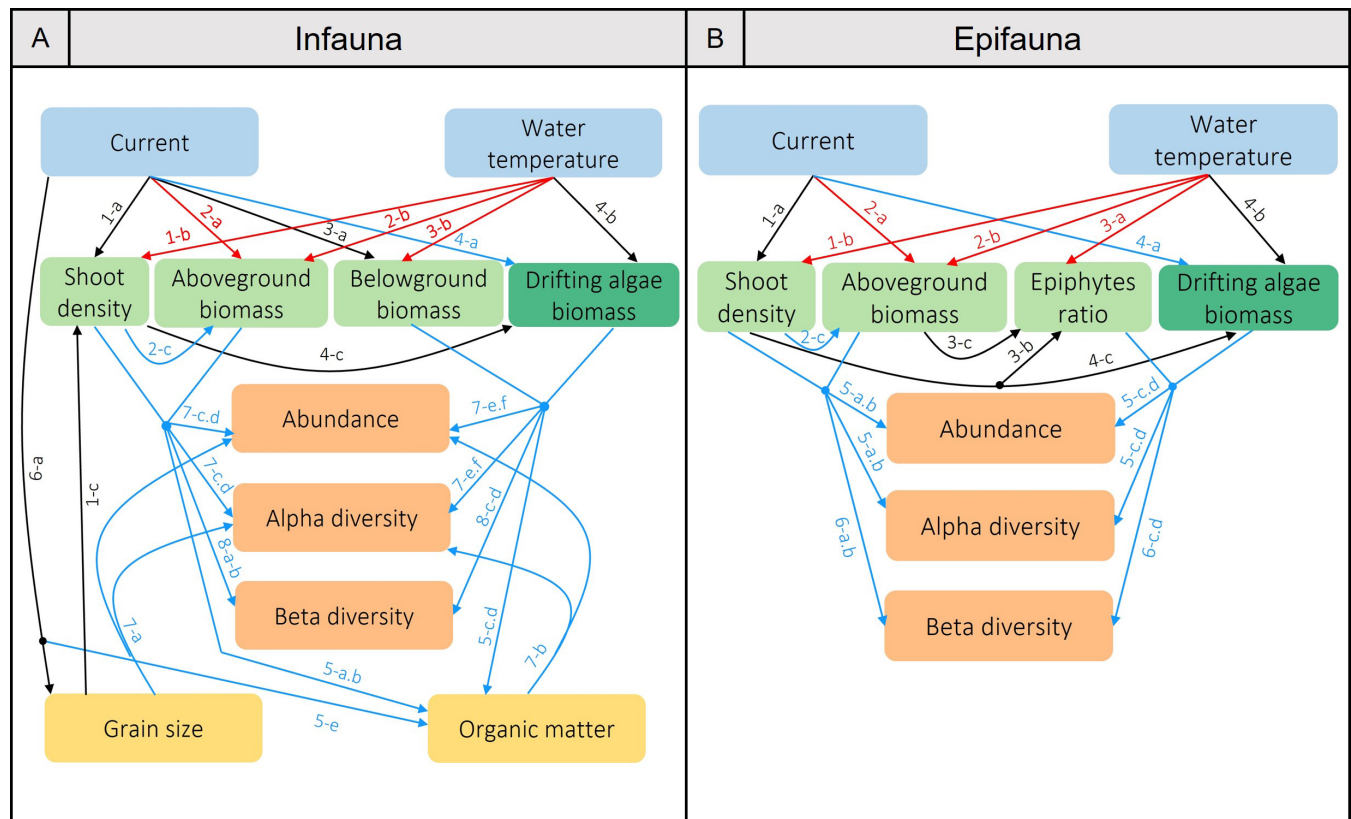
FIGURE 2 Model of hypothetical relationships of the "environment-seagrass-fauna" system based on literature review for (A) infauna and (B) epifauna. Hydrodynamic variables are in blue boxes, sediment-related variables in yellow boxes, *Zostera* biometry variables in light green boxes, macroalgal variables in the dark green box, and descriptors of the fauna in orange boxes. Arrows illustrate the relationships between the variables, black when positive, red when negative, and blue when the direction is ambiguous in the literature (Appendix S2).

push-net hauls. Infauna was sampled, at each point, by three 0.03 m² cores, sieved upon a 1 mm mesh size. Fauna samples were then fixed in 4% formalin. Sorting and identification to the lowest possible taxonomic level were performed in the laboratory (see www.rebent.org).

Epifaunal and infaunal species abundances were estimated at the site level by summing the abundances of the push-nets or core replicas. Two α diversity indices were derived: total number of species and the Shannon index. In order to study the variation of community composition across seagrass beds (beta diversity), two principal components analyses (PCAs) were calculated on the infauna and epifauna abundance data, respectively. Abundances were previously Hellinger-transformed (Legendre & Gallagher, 2001), to make the results comparable with previous studies on the communities of this habitat (Boyé et al., 2017).

Seagrass sampling

At each point and each year, all *Z. marina* shoots were collected within two 0.05-m² quadrats except in 2016 and 2017 where two 0.1 m² quadrats were used, without visible impacts on the time series. Sampling was processed in order to measure shoot density (number of shoots per square

meter) and above- and belowground biomass (in grams per square meter). On each shoot, biometry was further measured through leaf length and width (in millimeters), sheath length (in millimeters), number of leaves, and percentage of broken leaves (see Boyé et al., 2022, for details).

Additionally, within each quadrat, green, red, and brown macroalgae biomass (in grams per square meter) was quantified. The biomass of epiphytes (i.e., flora growing on *Zostera* leaves) was also measured on 10 randomly selected shoots at every sampling point, which was then expressed as a ratio between epiphyte biomass and *Zostera* aboveground biomass.

Sampling occasions with missing biometry data were excluded from our analysis. On the other hand, when only macroalgal biomass, belowground biomass, or epiphyte ratio was missing at a single sampling point out of three, values were estimated using the "*k*-nearest neighbor" (with *k* equal to 5) (Kowarik & Templ, 2016) method from the biometry data of the other sampling points.

Grain size data

At each point, a sediment core allowed for grain size and organic matter content assessment. Sediments were dried

in an oven (60°C for 24 h) and sieved on a range of sieve mesh sizes (<63, 63, 125, 500, and 2000 μm) and further weighed. These were then grouped into gravel (>2 mm; Fournier et al., 2012), sand (63 μm to 2 mm), and silt (<63 μm) fractions, while a sorting index was calculated (Trask index). Organic matter content was estimated by loss of material after combustion at 450°C for 5 h. All sampling occasions for which the whole sediment size data were missing were removed. When only the percentage of organic matter was missing, the missing value was estimated using the "k-nearest neighbor" method (with k equal to 5) from the granulometry data of the other sampling points.

Hydrology and meteorological data

Daily mean sea water bottom temperature (in degrees Celsius), current velocity (in meters per second), and salinity (practical salinity units) were extracted and computed from the ocean physic Multi-Year product IBI_REANALYSIS_PHYS_005_002 (Sotillo et al., 2015), downloaded from the E.U. Copernicus Marine Service platform (https://marine.copernicus.eu/) in September 2020. Sea water temperature and salinity were extracted from daily products that are available on a standard grid at 1/12° (~6–9 km; Appendix S1: Table S1) for 50 vertical levels, except for sea water bottom temperature which is only defined for one layer. Salinity was averaged across the 50 levels of the model (i.e., over the entire water column). Current velocity was extracted from hourly products (with the same spatial resolution) in order to properly account for tidal currents. However, those were only available for the surface layer. Hourly current velocities were computed by summing the squared eastward (uo) and northward (vo) velocities; then daily mean current velocity was obtained by averaging hourly current velocities. For the intertidal habitats, daily mean air temperature (in degrees Celsius), daily air temperature range (in degrees Celsius), and wind velocity (in meters per second) were extracted and computed from the SIM2 model of Météo-France (Le Moigne et al., 2020). This product is defined at an 8-km-grid resolution. The data were extracted and averaged in a buffer of radius equivalent to the resolution of the model around each point. For points where no model cell intersected the buffer, the radius of the buffer was changed to a radius equivalent to the resolution of the model plus the minimum distance of the point to the closest model cell. Values were estimated at the site level by averaging the data from the three points within each site.

Mean and SD of the above variables between the date of field sampling (always ranging between early February and late March) and the preceding November 1 were calculated at the site level and for each year. Such integration time was adapted not only to the response time of the seagrass variables considered here (i.e., 4–6 months;

O'Brien et al., 2018; Roca et al., 2016) but to that of the associated fauna (Lessin et al., 2019). This period was also selected to cover the period of winter storms typical of western European coasts (Leckebusch et al., 2006; Poppeschi et al., 2021) without considering summer and autumn conditions in the year prior to sampling, which were considered too distant in time to have relevant effects.

Fetch (expressed in kilometers) was calculated using the fetchR package, as the average length of nine radiating fetch segments (one every 10°) with a maximum distance for any fetch segment set to 300 km (using coastline data obtained from http://openstreetmapdata.com/data/land-polygon) (Seers, 2018).

Variable selection accuracy

Our variable selection was first based on literature review. However, additional statistical analyses proved necessary to specify and reduce the number of variables describing the final SEMs and reduce collinearity issues. Within each set of variables (granulometry, seagrass, hydrology, and meteorological data), we selected, for each pair of variables with Kendall's coefficient above a threshold of 0.7, only one variable out of the two, based on ecological considerations and expert knowledge. Then, the selected variables were fed into a PCA using all explanatory variables. The latter was used to select the final set of variables so as to limit multicollinearity while keeping the main compartments of interest from the theoretical models.

Alternative model assessment and final SEM building

All hypothetical relationships identified in the literature were translated in the form of a set of linear models in order to build the SEM following the methodological framework proposed by Lefcheck (2016). Given the breadth of the environmental gradients considered in this study (Boyé et al., 2022) and the number of explanatory factors already included in the models, we only included linear relationships in the models. The validity of the linear models was assessed for each response variable by studying the normality and homoscedasticity of the residuals. In order to meet these conditions, shoot density, biomass, abundance, and diversity index were log-transformed prior to the analyses. Macroalgal biomass variables and the epiphyte ratio required a stronger transformation to meet the model assumptions and were square-rooted. The whole set of variables was then standardized before fitting the models.

Fit accuracy of each tested SEM was estimated globally using Fisher's C statistic and locally by calculating the R^2 of each linear model included in the SEM (Lefcheck, 2016). Fisher's C statistic is based on a directed separation test (Shipley, 2013) that assesses whether claims of independence between unconnected variables in the theoretical model are realistic assumptions. Hypothetical relationships are considered consistent with the data if Fisher's C statistic follows a χ^2 distribution with $2k$ df (k being the number of links declared as independent, $p > 0.05$).

Based on the two initial theoretical models, several derived alternative models were tested in order to select the final models presented here. This selection process included removal and/or addition variables and relationships in order to best represent our initial alternative hypotheses, assess the sensitivity of our results to these initial choices, and adapt the models to the results of the directed separation test (Garrido et al., 2022). The set of equations that resulted in the SEM with the lowest Akaike information criterion (AIC) and that maximized the R^2 of the response variables was considered as the best representation (Garrido et al., 2022; Grace & Irvine, 2020). All relationships, including those nonsignificant, were retained in the two final models presented. In order to control for nonindependence of data between sites and years, these final SEMs were generated a second time using linear mixed-effects models. These latter models were not retained in the end as the addition of random "sites" and "years" factors increased the AIC.

All statistical analyses were performed with R 4.1.2 (R Core Team, 2021) using the packages piecewiseSEM v2.1.2 (Lefcheck, 2016), semEFF v0.6.0 (Murphy, 2022). Performance v0.9.0 (Lüdecke et al., 2021) was used to construct, validate, and interpret SEMs.

RESULTS

Construction of the theoretical models from the literature review

Expected presence and direction of relationships between the environment, the seagrass bed, and the associated infauna (Figure 2A) and epifauna (Figure 2B) were derived from the literature (Appendix S2). In the theoretical model describing the infauna, seagrass shoot density, seagrass aboveground biomass, seagrass belowground biomass, and drifting macroalgae were selected as the main factors likely to explain changes in the diversity and composition of this compartment. For epifauna, a different set of variables was used to describe the potential influence of seagrass, namely, seagrass shoot density, seagrass aboveground biomass, drifting macroalgae, and the epiphyte to aboveground biomass ratio.

It has to be noticed here that relationships as well as directions of the links between the environment and seagrass characteristics were mostly clearly set in the literature. In contrast, we found relationships regarding the influence of the environment and the seagrass bed on the fauna communities to be much more ambiguous.

Characterization of seagrass environment and associated fauna variability

The first two axes of the PCA conducted on the environmental variables (representing 54.7% of the total variance) were used to summarize the variability of the environmental conditions of the seagrass beds (Figure 3A,B). Axis 1 mainly describes variation of hydrological and meteorological conditions across sites while axis 2 depicts variation in the sediment granulometry of the beds (Figure 3A). Indeed, along the first axis, sampling sites are distinguished along a gradient of hydrodynamics and sea water temperature, with sheltered sites with variable temperatures such as Arradon or St. Malo on one side and exposed sites with more steady temperatures such as Sept-Iles, St. Marguerite, and Molène on the other side (Figure 3B). Axis 2 discriminates seagrass beds growing on heterogeneous sediments (Roscanvel, Callot) from sites characterized by well-sorted sands (Glénan, St. Marguerite and Molène; Figure 3B). Given these patterns of covariation in environmental conditions and our initial theoretical models (Figure 2), we selected mean current velocity and mean sea water temperature to describe the abiotic conditions in the final SEMs of infauna and epifauna. We added sediment mud content, gravel content, and sediment organic matter only in the final SEM of infauna. This selection reduces collinearity while preserving the main sources of variation of the environmental conditions observed across the seagrass beds.

Variations of macrofaunal communities were also described using PCA. The two first axes of the PCA conducted on infauna abundances explain 37.5% of the total variance (Figure 3C,D). The first axis strongly depends on the abundances of the polychaete *Spio* spp. (Fabricius, 1785), which isolates three sites from the others: Glénan, St. Marguerite, and Molène (Figure 3C,D). The second axis discriminates between two groups of three sites. St. Malo, Arcouest, and Arradon on the one hand are mainly characterized by abundances of the subsurface deposit feeders *Euclymene* spp. (Verrill, 1900) and the bivalve *Loripes orbiculatus* (Poli, 1795) (Figure 3C,D). On the other hand, Roscanvel, Callot, and Sept-Iles are dominated by the surface deposit feeders *Gammarella fucicola* (Leach, 1814) and *Aonides oxycephala* (Sars, 1862) (Figure 3C,D). These two axes hereafter referred to as "PC1: *Spio* spp." and "PC2: surface and subsurface deposit
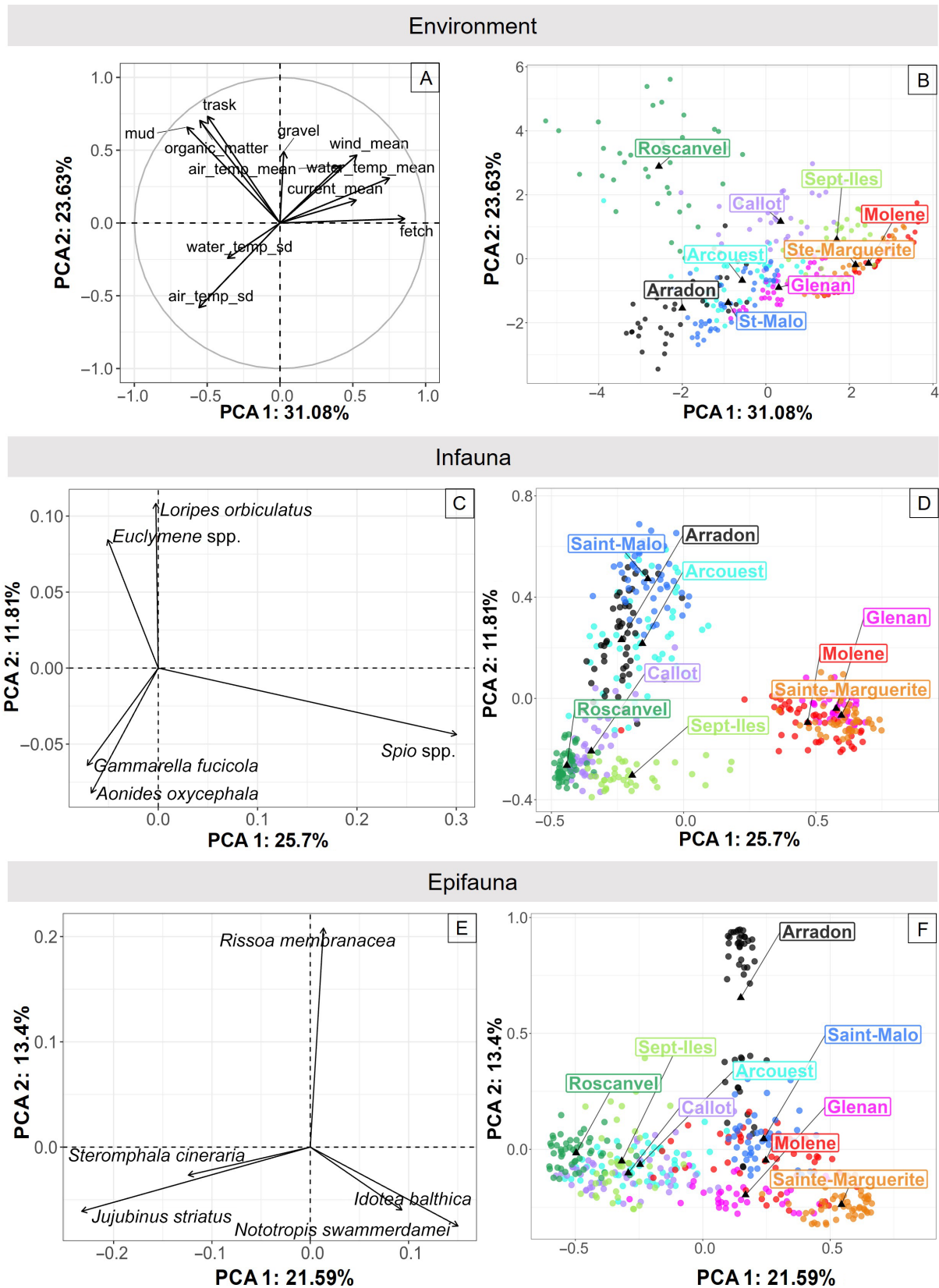
FIGURE 3 Principal components analyses (PCAs) of (A, B) environmental variables and Hellinger-transformed (C, D) infauna and (E, F) epifauna abundances. (A) Distance biplots of the environmental variables (in scaling 1) represented by the circle of equilibrium contribution. (C, E) Distance biplots (in scaling 1) representing the five main contributing infauna (C) and epifauna (E) species. (B, D, F) Distance biplot of the sites (in scaling 1) with colored dots representing every sampling point for each sampling year, and black triangles representing the sites with centroids.

feeders" were used to describe infauna compositional variation (beta diversity) in the final SEM dedicated to this compartment.

Regarding epifauna, the first two axes of the PCA explained 35% of the total variance (Figure 3E,F). The eight sites are homogeneously distributed along the first axis that is characterized on one side by the dominance of two non-opportunistic grazers, *Jujubinus striatus* (Linnaeus, 1758) and *Steromphala cineraria* (Linnaeus, 1758), and on the other side by two detritus feeders, *Idotea balthica* (Pallas, 1772) and *Nototropis swammerdamei* (H. Milne Edwards, 1830) (Figure 3E). The second axis is driven by the opportunistic grazer *Rissoa membranacea* (J. Adams, 1800), which distinguishes Arradon (highly dominated by this opportunistic species) from the other seagrass beds (Figure 3E,F). Thus, we selected these two axes to describe the beta diversity of epifauna in the final SEM modeling of this compartment. They are referred to as "PC1: non-opportunistic-detritivorous grazers" and "PC2: opportunistic grazers."

Direct and indirect responses of communities to environmental and seagrass variability

The two selected SEMs for infauna (AIC = 4185, χ^2 = 0.147, $p = 0.701$, Figure 4A,B) and epifauna (AIC = 4460, $\chi^2 = 1.113$, $p = 0.573$, Figure 4C) adequately model the variability of faunal composition across seagrass beds, in particular for infauna ($R^2 > 0.39$ for epifauna PC axes describing beta diversity, and >0.65 for infauna). On the other hand, variations in species richness, total abundance, and seagrass biometry are poorly explained (R^2 between 0.11 and 0.47). It also appears that infauna variations are better explained compared with epifauna variations, especially when accounting for abundance (higher R^2 for total abundance and PC axes for infauna and lesser improvement for species richness). For both faunal compartments, the theoretically strong role of macroalgal biomass (Figure 2) was not confirmed, as this variable was not retained in the final models (not explaining or being explained by any other variables; Figure 4).

Infauna final model

Variation of infauna appears mostly driven by direct effects of the environment, in particular with a major role of the sedimentary composition of the beds (Figure 4A). Indeed, species richness appears to be strongly and positively related to organic matter content of the sediment while abundances strongly decrease as the sediments become

muddier. On the other hand, gravel percentage moderately drives total abundance, species richness, and both community composition variables. Finally, infaunal species richness seems to be weakly governed by current velocity while a strong positive relationship is found between total abundance and mean sea water temperature.

The main direct relationship linking seagrass biometry to infauna is found between aboveground biomass and infauna total abundance, species richness and the dominance of surface and subsurface deposit feeders in the community (PC2). In contrast, no significant relationship was found between seagrass shoot density and infauna diversity. Only a weak, albeit significant, positive relationship was found between seagrass shoot density and the dominance of surface and subsurface deposit feeders in the community (PC2). Similarly, belowground biomass was weakly but significantly associated with the compositional gradient carried by *Spio* spp. abundances (PC1). More belowground biomass tends to reduce the dominance of *Spio* spp. in the community.

Part of the direct effects of seagrass on infauna is linked to the plant responses to its environment (Figure 4B), mediating the indirect effects of environmental conditions on infauna through its impact on seagrass biometry (Figures 4A,B and 5A). For instance, total abundance is driven by the indirect effect of mean current velocity (orange bar in Figure 5A): stronger velocities increase total abundance by promoting aboveground biomass (Figures 4A,B and 5A). This cascading pathway also influences the relative dominance of *Spio* spp. in the community (PC1), as the latter is tightly linked to total abundance. Interestingly, while there is a direct negative effect of mud content on total infauna abundance, there are indirect positive relationships between the two variables through the positive effects of mud content on both aboveground biomass and sediment organic matter content (Figures 4A,B and 5A). Although the resulting effect (indirect + direct) is still negative in the end, these indirect pathways moderate the extent of the negative direct effect of mud content on total abundance (Figure 5A). Similarly, while there is no direct relationship between mud content and species richness, they are indirectly related (positively) through the effect of mud content on organic matter content and on aboveground biomass. However, these indirect relationships are scarce and of lower intensity than direct relationships (Figure 5A).

Epifauna model

As for infauna, epifauna richness and composition appears mostly driven by the direct effects of the environment. For instance, total abundance and species richness
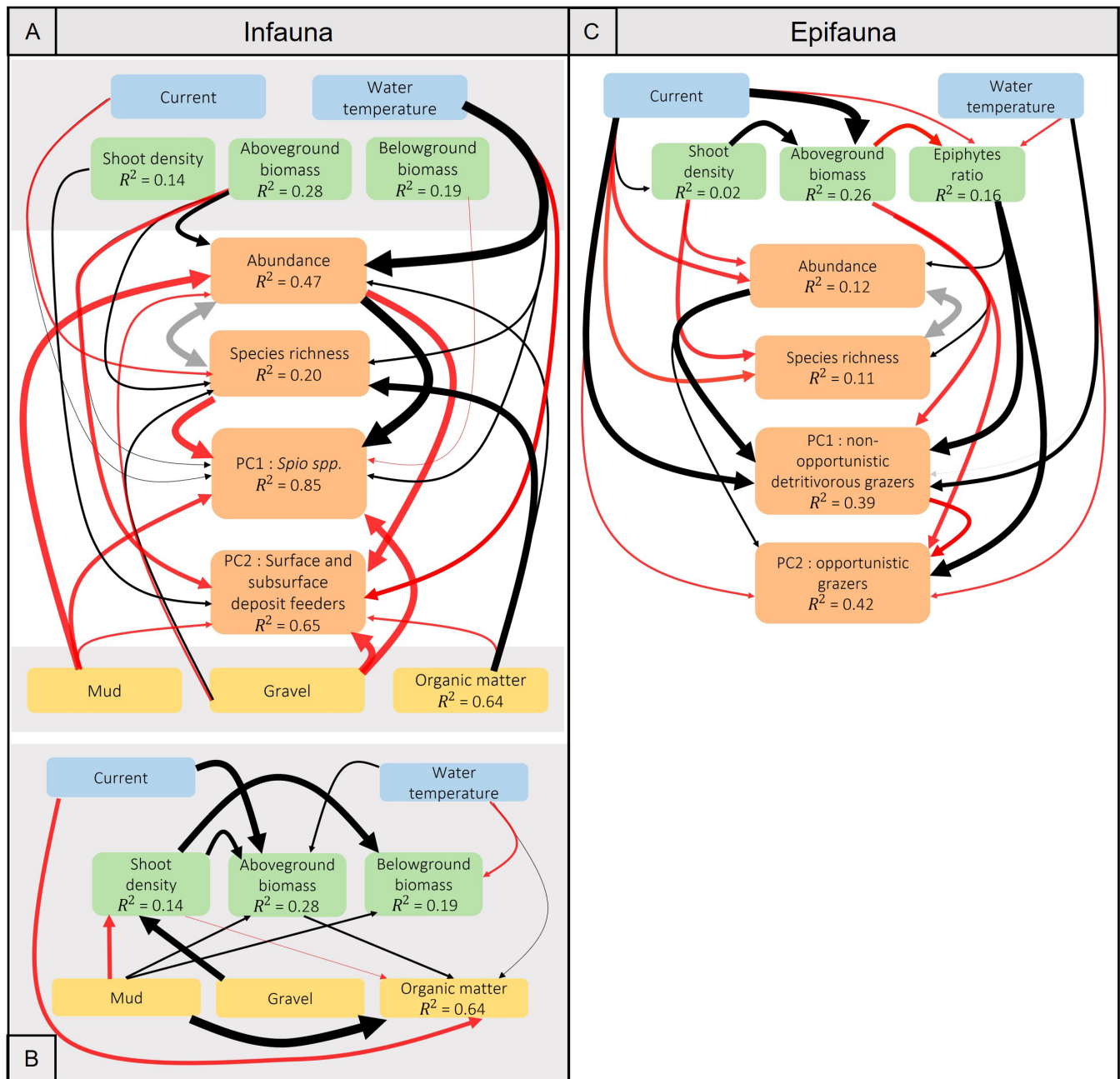
FIGURE 4 Structural equation model of the relationships between the environment, the seagrass bed, and the associated (A) infauna and (C) epifauna communities. Hydrological variables are represented in blue boxes, sediment-related variables in yellow boxes, seagrass biometry variables in green boxes, and finally infauna variables in orange boxes. Arrows symbolize the relationships between variables (positive and negative, respectively, in black and red) while residual correlations appear in double gray arrows. Nonsignificant relationships ($p < 0.05$) are not shown. The thickness of the arrows is proportional to the magnitude of the standardized regression coefficients for significant relationships (Appendix S3). (B) For the model on infauna, detailed relationships between environmental variables and seagrass biometry variables are represented separately for visual purposes.

of epifauna are strongly and negatively impacted by mean current velocity (Figure 4C). Sea water temperature does not significantly impact epifauna richness and total abundance (Figures 4C and 5B) but it is linked with community composition (Figure 4C). Compared with infauna, epifauna is more tightly linked to seagrass variables than infauna, whose responses were mostly governed by direct relationships with the environment, with few mediating effects of seagrass (Figure 5A,B). Yet, despite visible indirect pathways linking epifauna with its environment through seagrass characteristics (Figure 4C), most of them turn out to be nonsignificant
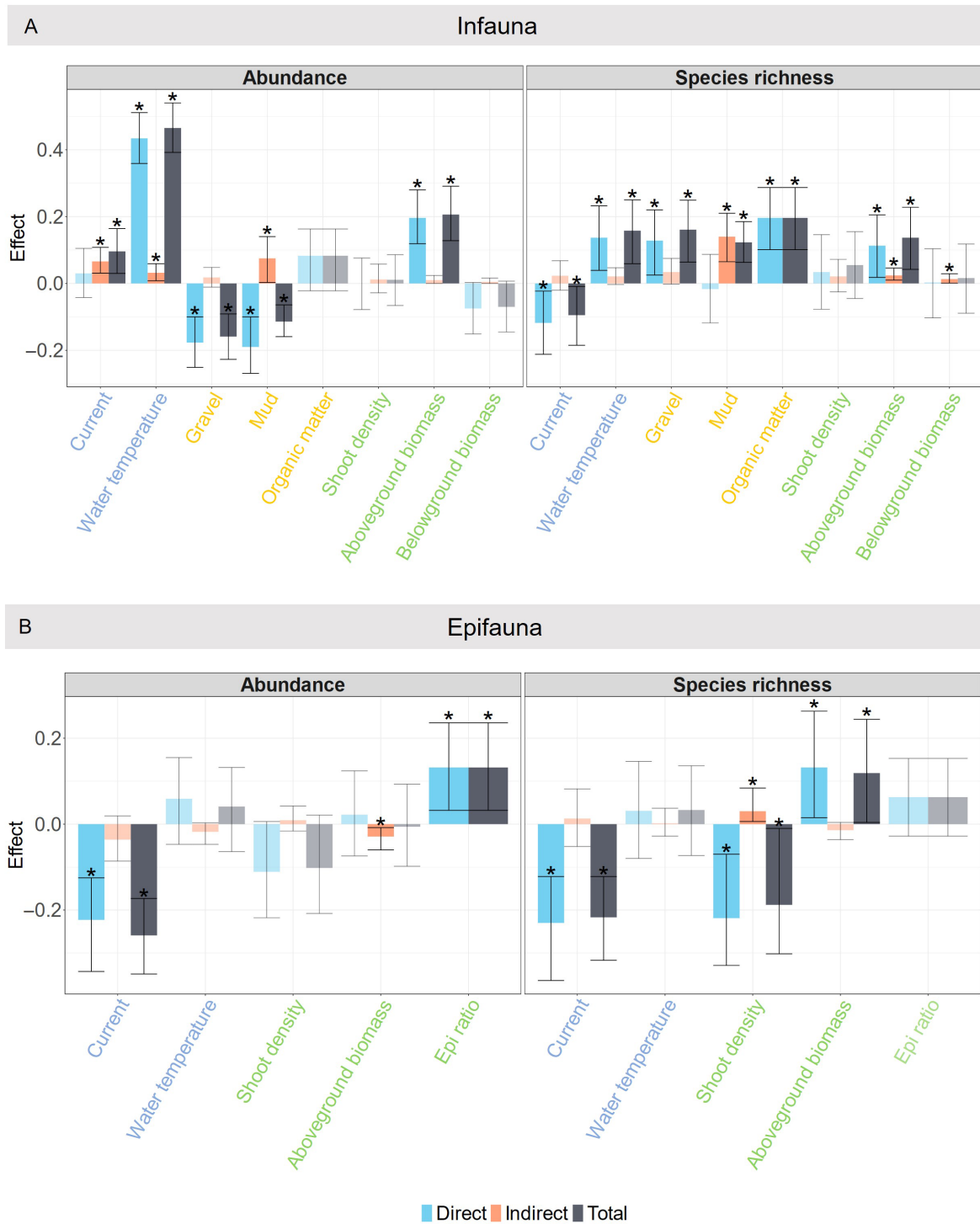
FIGURE 5 Quantification of direct, indirect, and total (direct + indirect) effects (standardized effect sizes) of seagrass and environmental variables on (A) infauna total abundance and species richness, and (B) epifauna total abundance and species richness. Significant effects are marked with a star and a solid bar. Note that confidence intervals are estimated here by bootstrap (Murphy, 2022) so that path significance might slightly differ from the models fitted with piecewiseSEM (Lefcheck, 2016) in Figure 4 (e.g. the negative effect of shoot density on epifauna abundance).

(Figure 5B). This can be explained by the pathways involved and the way the seagrass variables were constructed. Species richness is negatively related to

seagrass shoot density, even when accounting for its positive indirect effects, mediated by the positive (but weak) relationship between seagrass shoot density and

aboveground biomass (Figure 5B). In contrast, aboveground biomass is positively related to species richness. However, aboveground biomass has an indirect negative effect on epifauna abundance that is mediated by its trivial and negative relationship with the epiphyte ratio (which corresponds to epiphyte load divided by aboveground biomass). Indeed, the positive and direct influence of epiphyte load on total abundance is diminished by higher aboveground biomass. In addition, the epiphyte ratio directly promotes epifauna communities dominated by detritivores (PC1) (Figure 4C).

DISCUSSION

Because experimental studies are mostly conducted on a short time scale and locally, they often provide an incomplete representation of the complexity of a system (Witman et al., 2015). This may lead to conflicting results across experiments due both to replicability issues (Filazzola & Cahill, 2021) and to the scale-dependency of most ecological processes (Chase et al., 2018; Dixon Hamil et al., 2016). In agreement, we show here that contradictory relationships and ambiguities regarding seagrass–biodiversity relationships emerge from the literature currently available. Thus, we highlight the value of long-term monitoring for resolving these contradictions (Rodil et al., 2021; Yang et al., 2013) and upscaling available knowledge to broader scales, more relevant to inform conservation actions. We are aware that the consideration of nine intertidal seagrass beds variations upon time remains an incomplete surrogate of the complete gradient of environmental characteristics occupied by this habitat. Observations carried out on a larger number of meadows selected for their environmental characteristics would undoubtedly provide information proper to resolve the uncertainties that emerged from our study. Nonetheless, the diversity of environment encompassed in this study and the temporal scale of the data available provide a new and more holistic picture of the complex direct and indirect relationships governing macrofaunal diversity in seagrass meadows.

The SEM approach allowed to clarify direct and indirect relationships between a wide range of biological and environmental variables. In particular, regression coefficient assessment (Lefcheck, 2016; Yang et al., 2013) helped to remove ambiguity regarding the existence and magnitude of several competing hypothetical relationships. In particular, we expected that the infauna and epifauna would not be dependent on the same environmental factors (Boyé et al., 2017). In agreement, the structures of the relationships assessed by the SEMs for the two different communities as well as their

associated R^2 are different, which validates the choice to consider the two communities in two independent systems. In these models, infauna abundance and diversity, mostly explained by sediment grain size and sea water temperature, are both much better explained than epifauna abundance and species richness. Such an outcome agrees with that of Rodil et al. (2021) who also found that infaunal communities were primarily explained by sedimentary predictors, whereas epifaunal communities were mostly dependent on seagrass state. In our case, epifauna was more related to seagrass variables than infauna, but the main drivers of epifauna abundance and richness remain the direct effects of abiotic conditions.

These findings confirm and clarify the overall role of seagrasses in driving epifauna. They also help clarify and better quantify the link between infauna and seagrasses. Indeed, the mechanisms linking epifauna and infauna to seagrass habitat structure are numerous and complex (Chen et al., 2021; Duffy, 2006). Here, aboveground biomass directly increased the diversity of both communities. On the other hand, infauna did not respond to higher seagrass shoot density while epifauna responded negatively, which was unexpected given previous studies, especially for epifauna (Chen et al., 2021). Indeed, many studies conclude that the abundance and diversity of benthic communities increase in response to seagrass shoot density (Boström et al., 2006a; Rodil et al., 2021). Yet, it has to be noticed that these studies do not differentiate the effect of shoot density from the effect of aboveground biomass (assuming that high shoot density would lead to higher biomasses). Although these two variables are often confounded, their relationship might be highly variable (Vieira et al., 2018), to the point that they may be unrelated in some environments (Boyé et al., 2022). Here we show, in agreement with Attrill et al. (2000), that macrofauna patterns would be more dependent on the total amount of seagrass rather than on the number and/or size of plants. Hence, if shoot density is often used as an indicator of ecological status for seagrass beds (Marbà et al., 2013; Roca et al., 2016), it appears as a poor proxy of the diversity of the associated fauna.

The mechanisms underpinning this seagrass biomass effect may differ for infauna and epifauna. While it does not appear related to seagrass shoot density, it may still be related to other aspects of seagrass habitat complexity (Kovalenko et al., 2012). For instance, higher seagrass biomass may promote the establishment of secondary foundation species (Thomsen et al., 2018), which in turn could provide microhabitats whose variations are known to have a large influence on epifaunal assemblages (Chen et al., 2021). In agreement, we found positive relationships between epifauna and epiphytes. Given the monitoring design, the latter could only be expressed as a ratio with seagrass biomass (i.e., epiphyte to seagrass biomass

ratio). Indeed, we could not quantify the indirect effect of seagrass biomass that is mediated by epiphytic load. Yet, our result confirms the positive effects of epiphytes whose structure increases the complexity of the meadow (Edgar & Robertson, 1992; Thomsen et al., 2018) that constitutes a significant food source for numerous grazers (Bologna & Heck, 1999).

While a strong link between epifauna and aboveground seagrass biomass, mainly by the presence of epiphytes, has been frequently reported before (Chen et al., 2021), the direct dependence of infauna on this seagrass aboveground biomass has been less studied. Accordingly, the underlying mechanism remains unclear. Here, we accounted in the SEM for the indirect influence of aboveground biomass on infauna via the increase in the percentage of organic matter through seagrass decomposition (Herkül & Kotta, 2009). Yet, this indirect link did not contribute much to explain infauna abundance and richness, so other mechanisms seem involved in the direct relationship observed between seagrass aboveground biomass and infauna. The latter might result from indirect pathways omitted in our models that clearly do not consider the total range of primary production certainly useful to the infauna. For instance, *Zostera* leaves support considerable epiphyte production (including microphytobenthos) that might sediment directly or after consumption by epifauna (Chen et al., 2021; Jankowska et al., 2019). Aboveground seagrass biomass, as well as epiphyte-derived resources, would contribute as infauna food sources (Jankowska et al., 2019). Seagrass beds also contribute to increase infauna species recruitment of larvae by buffering the current (Boström & Bonsdorff, 2000). All these indirect links between aboveground biomass and infauna are not explicitly modeled in the presented SEM and may thus contribute to the direct linkage quantified here between the seagrass aboveground biomass and infauna.

While the present SEMs clarify and shed new light on the links between seagrasses and their associated fauna, some outcomes from our study contradict the literature. They might be explained by the specificities of the protocol used and of the meadows under study. According to Rodil et al. (2021), drifting macroalgae trapped within the seagrass habitat are highly efficient invertebrate transporters. Epifauna communities would then be stimulated by habitat heterogeneity provided by such additional food and shelter sources. However, algal mats create a very unstable environment in time and space. They have been reported to stress-out benthic fauna by generating anoxic conditions (Norkko et al., 2000) as well as by releasing toxic chemical compounds (Heery, 2018). We aimed at measuring and clarifying the influence of drifting macroalgae on associated faunal communities and expected to determine whether this facilitated species

transport would control epifauna composition by homogenizing spatial patterns (Quillien et al., 2015) or diversifying them (Rodil et al., 2021). Yet none of our SEMs found significant relationships between fauna and macroalgal biomass. The annual winter monitoring might be too punctual and thus poorly suited to detect transient signals such as the ephemeral and stochastic presence of algae (Rasmussen et al., 2013).

The lack of a relationship between mean current velocity and seagrass shoot density was also unexpected, especially when considering the strong positive relationship reported in Boyé et al. (2022), within the same set of data. Instead, we identified a strong relationship between high gravel content in the sediment and seagrass shoot density. We hypothesize that the integration of current conditions over 4–6 months may partially mask the effect of this factor. Indeed, large uncertainties remain regarding the response times of seagrasses to a wide variety of environmental factors (Roca et al., 2016). In addition, such response times might depend on the abiotic and anthropogenic variables considered (Roca et al., 2016). Gravels, which occur in high-exposure conditions (Paterson & Black, 1999), are representative of long-term hydrodynamic conditions (hydroclimate), which suggests that the effect of hydrodynamics on the seagrass habitat should be integrated over longer periods of time than those we selected.

The outcomes presented here thus depend on the variables and presumed relationships selected in the initial model. Only one-sided directions for each relationship are proposed since SEMs lack the ability to evaluate feedback loops (Lefcheck, 2016). As an example, the effects of current velocity on seagrass are considered here while the buffering effect of seagrass shoot density on hydrodynamics is not. Indeed, this process is considered to occur at a very small scale (meter) compared with the scale of the environmental data that we used in the model (Reidenbach & Thomas, 2018). A potential perspective would therefore be to test alternative models with different hypothetical directions for each relationship (when there are expected feedback loops or uncertainty regarding the expected direction in the literature) and then select the model best fitting the data according to some criteria such as AIC. Such a data-driven approach has been used by van der Heide et al. (2012) to show that large amounts of suspended particles could be trapped within the seagrass bed. In turn, water clarity was improved and seagrass growth was indirectly stimulated through remineralization. A complementary or alternative approach would be to use variables partitioning by time step, that is, environment at time t affecting the seagrass state at $t + 1$, which would then feedback to the environment at $t + 2$. Wu et al. (2018) modeled the

impact of dredging on seagrass beds using a similar process, taking into account the feedbacks it implies, especially on light availability.

Similarly, as in most SEMs built so far to explore the responses and effects of marine ecosystem engineers (Lamy et al., 2020; Miller et al., 2018; Yang et al., 2013), only linear relationships were considered. This choice was justified both by the number of factors included in the models (compared with the amount of data at hand), which limited our ability to include quadratic terms without saturating the SEMs, and by the breadth of the environmental gradients encompassed by our nine sampling sites. The latter only represent a fraction of the niche of *Z. marina* (Boyé et al., 2022) and its associated species (Gallon et al., 2017). Hence, we are unlikely to capture the full breadth of the expected bell-shaped species–environment relationships and expect linear processes to prevail in our case (Antão et al., 2022). Yet, nonlinear behaviors are expected both in the response of the seagrass to its environment (Dakos et al., 2019) and in its effect on its associated fauna (Boström, Jackson, & Simenstad, 2006). Provided sufficient data, our model and approach could easily be extended to include nonlinear relationships (Laliberté et al., 2014), which might prove necessary in other seagrass ecosystems.

Our understanding of the intricate mechanisms linking foundation species to their associated fauna in changing environments remains limited on many aspects (e.g., relationships with beta diversity - variation of community composition - and functional diversity remain understudied compared to species richness, presence of tipping points and cumulative effects, etc.) and for many foundation species (Airoldi et al., 2008; Dakos et al., 2019; Ellison, 2019). This, in turn, limits our ability to manage coastal biodiversity in the face of environmental change (Bulleri et al., 2018; Harley et al., 2006). Despite the limitations and perspectives highlighted above, this study contributes to a growing body of literature highlighting the usefulness and potential of SEM. Applied to both long-term monitoring and experimental data, SEM can help tease apart, identify, and quantify some of the many ecological processes controlled by foundation species (e.g., El-Hacen et al., 2018; Fields & Silbiger, 2022; Lamy et al., 2020; Lefcheck, 2016; Miller et al., 2018).

CONCLUSION

The effects of foundation species on ecosystems are expected to be species-specific (dependent upon the traits of the foundation species and the processes it controls) as well as context-dependent (Ellison, 2019). Beyond its case-specific interest, our approach, building on others before us (e.g., Miller et al., 2018; Yang et al., 2013), paves the way for a more systematic approach to confront our current theoretical understanding of the effect of foundation species to actual data. In addition, this method allows to scale-up our understanding of ecosystem functioning to be more relevant for management purposes. Generalizing this approach across ecosystems and environments is necessary to better grasp the role of foundation species (Ellison, 2019). In our case, some results contradicted with the literature dedicated to understanding single (isolated) links between fauna and their environment or fauna and seagrass bed structure. In particular, we propose that the diversity of benthic macrofauna would be controlled and promoted by the total aboveground biomass of the seagrass bed and not by seagrass shoot density. We also show that *Zostera*-associated infauna and epifauna are not driven by the same environmental factors and suggest that if they both respond to total aboveground biomass, they do so through different mechanisms. In the context of global biodiversity loss and alteration of the seafloor, further work will be needed to clarify the potential cascading effects caused by the decline of foundation species on biodiversity. Our approach contributes to such understanding for seagrass meadows and can provide a framework to explore the contributions of other foundation species.

CONFLICT OF INTEREST STATEMENT
The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT
Data and R scripts used to reproduce the analyses and the figures (Millot et al., 2023) are available from Zenodo: https://zenodo.org/records/10018511. The complete data from the REBENT monitoring program

(http://www.rebent.org/) are available in the Quadrige database: https://surval.ifremer.fr/Donnees/Cartographie-Donnees-par-parametre#/map.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.