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Positive contribution of macrofaunal biodiversity to secondary production and seagrass carbon metabolism

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Abstract

Coastal vegetated habitats such as seagrasses are known to play a critical role in carbon cycling and the potential to mitigate climate change, as blue carbon habitats have been repeatedly highlighted. However, little information is known about the role of associated macrofauna communities on the dynamics of critical processes of seagrass carbon metabolism (e.g., respiration, turnover, and production). We conducted a field study across a spatial gradient of seagrass meadows involving variable environmental conditions and macrobenthic diversity to investigate (1) the relationship between macrofauna biodiversity and secondary production (i.e., consumer incorporation of organic matter per time unit), and (2) the role of macrofauna communities in seagrass organic carbon metabolism (i.e., respiration and primary production). We show that, although several environmental factors influence secondary production, macrofauna biodiversity controls the range of local seagrass secondary production. We demonstrate that macrofauna respiration rates were responsible for almost 40% of the overall seafloor community respiration. Macrofauna represented on average >25% of the total benthic organic C stocks, high secondary production that is likely to become available to upper trophic levels of the coastal food web. Our findings support the role of macrofauna biodiversity in maintaining productive ecosystems, implying that biodiversity loss due to ongoing environmental change yields less productive seagrass ecosystems. Therefore, the assessment of carbon dynamics in coastal habitats should include associated macrofauna biodiversity elements if we aim to obtain robust estimates of global carbon budgets required to implement management actions for the sustainable functioning of the world's coasts.

KEYWORDS

benthic biodiversity, carbon stocks and flows, ecosystem functioning, macrofauna, respiration rates, seafloor metabolism, seagrass, secondary production

INTRODUCTION

Biodiversity loss is a global environmental challenge that threatens the functioning of ecosystems, undermines their inherent goods and services, and poses a severe risk to the well-being of future generations (UNEP, 2021). Given that biodiversity plays a largely functional role in nature (Hooper et al., 2005; Tilman et al., 1996), defining relationships between biodiversity and ecosystem productivity is key to understanding the consequences of biodiversity loss. The majority of the studies concerning biodiversity and ecosystem productivity have focused on the rates, trends, and drivers of primary production by autotrophs, because primary productivity is the foundation process of most ecosystems and food webs (Hooper et al., 2005). However, the relationships between primary consumers and ecosystem productivity in aquatic ecosystems are less well known, even though animals that have direct effects on ecosystem processes often face severe extinction threats (Duffy et al., 2003).

Different experimental studies have documented higher productivity in high-diversity plant assemblages (Flombaum & Sala, 2008; Liang et al., 2016; Oehri et al., 2017; Tilman, 2001), also in marine environments (Virta et al., 2019; Zedler et al., 2001). Similarly, increasing numbers of marine studies acknowledge the importance of macrofauna diversity in maintaining productive ecosystems (Duffy et al., 2017; Gamfeldt et al., 2005; O'Gorman et al., 2008). This situation has been highlighted particularly in coastal vegetated habitats, where secondary production (i.e., consumer incorporation of organic matter per time unit) is dominated by benthic macrofauna communities that mediate energy flow from primary producers to higher trophic levels (e.g., fish) and, therefore, they play a key role in the transfer of energy within coastal food webs (Dolbeth et al., 2012; Duffy et al., 2003, 2005; Rodil et al., 2020; Wong, 2018). Experimental evidence suggests that a more diverse primary consumer assemblage can be expected to enhance secondary production (Duffy et al., 2017). However, most of the marine studies on diversity–productivity relationships have mainly concentrated on small-scale experiments and laboratory-controlled conditions. Therefore, the answer to whether consumer diversity per se influences ecosystem properties such as secondary production in more natural open systems remains elusive.

Seagrass meadows are one of the best studied coastal vegetated habitats due to their global presence, relative accessibility in shallow waters, the key role in ocean carbon budgets, and rich biodiversity (Duarte et al., 2013a, 2013b; Fourqueran et al., 2012). The metabolic role of seagrass meadows has been investigated intensively because high rates of carbon capture, and subsequent biomass production, are one of the main processes by which seagrass affects carbon budgets (Attard et al., 2019; Duarte et al., 2013a, 2013b). Seagrasses are known as hotspots of macrofaunal diversity that contribute significantly to coastal processes such as respiration, productivity, nutrient cycling, and trophic transfer (Duffy et al., 2003; Lohrer et al., 2016; Rodil et al., 2020). Despite copious evidence linking carbon remineralization, nutrient efflux, and the activities of the benthic macrofauna (Snelgrove et al., 2018), the contribution of the macrofauna community to the seagrass carbon dynamics and the drivers behind it remain poorly understood (Macreadie et al., 2019). Seagrasses are among the most threatened marine habitats; current rates of loss of coastal plant communities and associated biodiversity can seriously compromise the capacity of seagrass to deliver climate change mitigation and adaption (Duarte et al., 2013b). As the incidence of species loss increases globally, there is an urgent need to link faunal diversity changes to ecosystem functions in field settings, so that consequences to ecosystem services can be better assessed and managed at the seascape scales.

Spatial heterogeneity influences key ecosystem features including biodiversity and several ecosystem processes (e.g., primary and secondary production), in both terrestrial and marine ecosystems (Cardinale et al., 2000; Griffin et al., 2009). Globally, seagrass meadows comprise heterogeneous seascape structures, differing in the composition and density of plant species and the biodiversity of the macrofauna across a strong range of environmental conditions (Duarte, 2000; Rodil et al., 2021a, 2021b), providing a unique platform for studying diversity–productivity relationships. Based on the known importance of biodiversity in sustaining the world's ecosystems (please refer to reviews in Hooper et al., 2012, Duffy et al., 2017), we hypothesize that macrofauna community diversity is a major driver of secondary production in natural seagrass habitats. We conducted a regional scale field study of multiple seagrass meadows with variable environmental conditions and macrobenthic diversity patterns established by natural community assembly processes to (1) estimate how much of the variability in seagrass macrofauna secondary production can be explained by macrofauna biodiversity after controlling for a set of environmental covariates, (2) determine the relationship between macrofauna diversity and ecosystem secondary production. Finally, given the global importance of seagrass meadows in coastal carbon cycling, and the macrofauna potential role in the functioning of key coastal carbon processes we consider it crucial to (3) quantify the macrofauna contribution to the seagrass carbon metabolism (i.e., respiration and primary production).

METHODS

Study sites

A range of seagrass meadows (11 sites, <4 m depth) dominated by *Zostera marina* L., but differing in the number, composition, and density of plant species (please refer to Rodil et al., 2021b) were studied across a 25-km distance along the southern shore of the Hanko Peninsula (Finland), nearby Tvärminne Zoological Station (59.844° N, 23.249° E) (Appendix S1: Figure S1). The seagrass meadows were sampled during peak biomass season (i.e., August–September 2017) during SCUBA diving. One site (TS) was sampled at the beginning (early August, TS_0) and end (late September, TS_f) of the campaign and used as a reference location (Appendix S1: Table S1).

Measuring seafloor community metabolism rates: AEC deployments

Seagrass community metabolism rates were measured *in situ* using the aquatic eddy covariance (AEC) technique (Berg et al., 2003). The AEC instrument consisted of a fast-response O_2 microsensor setup ($T_{90} \leq 0.3$ s) and an acoustic Doppler velocimeter (Vector, Nortek) that were mounted onto a tripod frame (Attard et al., 2019). The instrument was deployed for 1–4 days at each site and recorded O_2 concentration and water velocity data continuously at 32 Hz. The sensors were positioned ~35 cm above the seafloor and stood ~10 cm clear of the seagrass canopies. Additional sensors logged seabed photosynthetically active radiation (PAR) (LI-192, Li-Cor), water temperature and salinity (U24 HOBO), and dissolved O_2 concentration (U26 HOBO) every 15 min.

Benthic O_2 fluxes (mmol m^{-2} day^{-1}) were extracted from subsequent 15-min time windows of the raw 32 Hz data streams for vertical velocity and O_2 concentration following established protocols using the open-source package *sohfea* (www.dfmcginnis.com/SOHFEA). Daily metabolic rates were estimated for each 24 h period of data. The fluxes were then separated into daytime fluxes ($FLUX_{day}$; PAR > 0.0 µmol m^{-2} s^{-1}) and nighttime fluxes ($FLUX_{night}$; PAR < 0.0 µmol m^{-2} s^{-1}), and the PAR time series was used to determine the number of daylight hours (h_{day}). Daily gross primary productivity (GPP; mmol O_2 m^{-2} day^{-1}) was computed as $GPP = (FLUX_{day} + |FLUX_{night}|) \times h_{day}$. Respiration rates (R, mmol O_2 m^{-2} day^{-1}) were calculated as $R = |FLUX_{night}| \times 24$, and the net ecosystem metabolism (NEM, mmol O_2 m^{-2} day^{-1}) was computed as GPP/R.

Benthic biodiversity sampling: Measuring biotic and abiotic variables

At the end of each AEC deployment, we conducted a standardized survey (please refer to Rodil et al., 2019) to quantify dominant features of benthic biodiversity within the AEC footprint area (i.e., the seafloor area that contributes most of the O_2 flux registered). At each site, we sampled a circular seafloor area of ~80 m^2 to characterize the benthic biota contributing to seafloor O_2 flux dynamics (Rodil et al., 2019). Sixteen benthic samples were randomly taken per site (i.e., a total of 192 sampling units) to collect representatives of the main macrobenthic community components (i.e., plants and macrofauna). Therefore, we harvested all the vegetation (above and below ground) and associated epifauna by gently enclosing all plants within a quadrat frame (25 cm × 25 cm, $n = 16$) into net bags. We took benthic cores (Ø $= 5$ cm, 15 cm deep, $n = 16$) for macroinfauna at each site. Finally, we took six random sediment samples within the area using 100-ml syringes (Ø $= 3.5$ cm, 10 cm deep) for organic matter (OM) and pigments (surface sediment, 1 cm layer), and grain size (the rest of the sediment).

Large shell fragments were removed from grain-size samples and hydrogen peroxide was added (H_2O_2, 6%) to dissolve organic material before analysis. Samples were sieved (<63, 63, 125, 250, 500, 1000 and 2000 µm), the percentage dry weight of each fraction measured, and the mean grain size (µm; MGS) calculated using GRADISTAT (Blott & Pye, 2001). Homogenized surface sediment (0–1 cm) was analyzed for OM (%) as loss on ignition (3 h, 500°C). Sediment surface subsamples (~0.5 g) were analyzed spectrophotometrically for chlorophyll *a* (chl *a*) and phaeopigments (phaeo) (Shimadzu UV–VIS model) respectively (µg g^{-1}).

Macrobenthic community characterization

All the aquatic plants were measured (maximum length, cm), counted (shoots m^{-2}), and dried (60°C, 48 h, g m^{-2}). Seagrass C content (mg C m^{-2}) was estimated by applying species-specific conversion ratios (range from 35%–41% of dry weight) (Gustafsson & Norkko, 2019). We estimated the phototrophic carbon turnover rates (day^{-1}) from ratios of daily benthic GPP (mg C m^{-2} day^{-1}) and standing macrophyte biomass (mg C m^{-2}). Ephemeral algae associated with the aquatic plants were gently separated from the samples, dry mass was estimated (60°C, 48 h). Macrofauna abundance (individuals m^{-2}), ash-free dry mass (AFDM, mg m^{-2}), the number of taxa per site (i.e., taxon richness, TR), and the Shannon–Wiener $\log_e$-based index (H′) were determined. Macrofauna

AFDM was converted to C content (mg C m^{-2}) assuming a biomass organic content of 50% (Wijsman et al., 1999).

Estimation of macrofauna community respiration rates and secondary production

Macrofauna AFDM was used to estimate macrofauna community respiration rates and secondary production. Respiration rates per taxon were estimated using the Mahaut et al. (1995) formula for shallow water macrobenthos:

$$R = 0.017W^{0.844}$$

where R is the respiration (mg C day^{-1}) per taxon and W is the mean individual mass (mg C m^{-2}), valid for the temperature range 15–20°C. Daily R_{rate} for the total macrofauna community was calculated per site by multiplying the estimated R by the corresponding total abundance (individuals m^{-2}). Respiration rates were corrected for temperature assuming a Q_{10} of 2 and expressed as mg C m^{-2} day^{-1}.

We estimated secondary production using the empirical model of Edgar (1990). The water temperature ranges on which the model is based (5–30°C) were appropriate for our study, and the model was not based on data of mean annual biomass (Wong, 2018). Edgar's formula:

$$P = 0.0049B^{0.80}T^{0.89}$$

where P is the production of an individual macrobenthic animal (μg C day^{-1}), B is the body mass (μg AFDM), and T is the water temperature (°C). We calculated body mass by dividing total AFDM per taxon by the total abundance of that taxon (Wong, 2018). Daily secondary production for each taxon was estimated by multiplying the mean abundance per taxonomic group (m^{-2}) and referred to as P_{taxon} (mg C m^{-2} day^{-1}) to be used for multivariate analyses. Then, daily secondary production of the benthic community was estimated by summing the production of each taxonomic group and referred to as P_{total}.

Statistical analyses

A principal component analysis (PCA) for centroids (Euclidean distance, fourth-root transformed variables) was used to examine the spatial distribution of the seafloor community respiration (CR) in combination with PAR. Permutational analyses of variance (PERMANOVA; unrestricted permutation of raw data, Type III SS, 4999 permutations) were run to detect significant changes in the macrofauna AFDM across sites (site as a random factor, based on Euclidean dissimilarity measures and log[x + 1] transformed data).

We performed distance-based linear models (DistLM) to ascertain how much of the overall change (i.e., variance partitioning) in secondary production (i.e., P_{taxon} and P_{total}) was explained by macrofauna diversity including TR and Shannon-H′ while statistically controlling for the (log-transformed) biotic and abiotic covariates. DistLM were fitted using the stepwise selection procedure and R^2 criteria (4999 permutations). Distance-based redundancy analysis (dbRDA) was applied to visualize the position of the sites according to the productivity of the macrofauna assemblages (P_{taxon}) fitted to the significant predictor variables. Analyses were performed using PRIMER7 (Clarke & Gorley, 2015). Calculations for the mean TR and Shannon-H′ were performed using the "diverse" function.

We used the AEC flux-averaged measurements to establish simple regressions between macrofauna R_{rate} and the seafloor CR across sites. We used generalized linear models to establish relationships between P_{total} and macrofauna biodiversity metrics (TR and H′) based on the Gamma family (log-link) with a dispersion of 1 due to the exponential relationship. The normality (Shapiro test) and the variance (ncvTest) of the residuals were evaluated. Models were built using R 4.0.4 software (R Development Core Team, 2021). We used AFDM, R_{rate}, and P_{total} to quantify the macrofauna community contribution (g C m^{-2} day^{-1}) to the overall organic carbon metabolism estimated by the AEC (i.e., GPP and CR) across seagrass meadows.

RESULTS

Seafloor metabolism across seagrass meadows

The benthic O_2 flux data presented here consists of 1032 h of high-quality measurements distributed between the 11 sites. Flux data sets ranged in duration from 24 to 96 h (average = 69 h) (Appendix S1: Table S1). Daily GPP and CR were highly variable (Figure 1a; Appendix S1: Table S1), but always maintained a close 1:1 relationship (Figure 1b). This indicates that O2 production and consumption processes were tightly coupled (R^2 = 0.59) across spatial scales (Figure 1b). Net ecosystem metabolism varied across sites, showing both net heterotrophic (NEM <0) and net autotrophic (NEM >0) sites (Figure 1c; Appendix S1: Table S1). The PCA showed a spatial gradient of variation across seagrass sites related to the overall seafloor CR and PAR (Figure 1d). The first two axes of the PCA explained 85.5% of the direction of variation in the spatial distribution of the sites, with CR contributing mainly to the first axis (PC1 = 0.991)

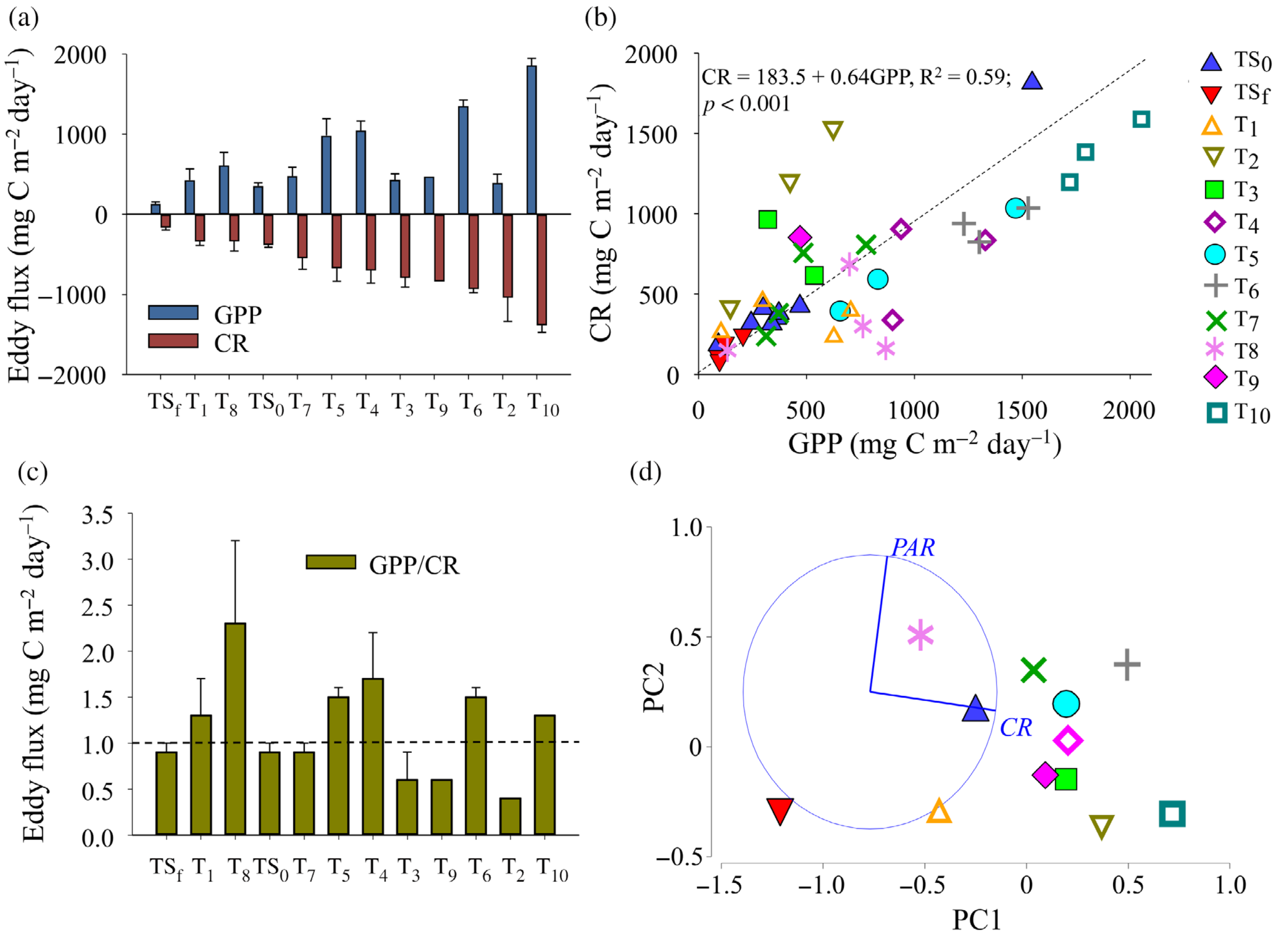

FIGURE 1 Seafloor metabolism: (a) mean (+SE) gross primary production (GPP) and community respiration (CR), (b) the relationship between GPP and CR across sites, (c) mean (+SE) net ecosystem metabolism (NEM = GPP/CR, dashed line indicates ratio ≥1) across sites (ordination based on principal component analysis [PCA]), and (d) PCA showing the spatial distribution of the seagrass sites in relation to CR and the photosynthetic active radiation (PAR) as a spatial covariate. (a, c) x axes values indicate site and sampling time

following a dominant gradient of variation for the sites (Figure 1a,d).

Macrofauna community biomass, secondary production, and respiration rates

Macrofauna AFDM showed significant differences (pseudo-$F_{11,180} = 16.63$; $p < 0.001$) across sites (Figure 2a; Appendix S1: Table S2). Consequently, P_{total} and R_{rate} showed a strong variability across sites (Figure 2b,c; Appendix S1: Table S2). Macrofauna P_{total} and R_{rate} ranged from 47.11 and 62.14 (T_1) to 303.11 and 466.96 (T_3) mg C m^{-2} day^{-1}, respectively (Figure 2b,c; Appendix S1: Table S2). We used the spatial distribution of increasing overall seafloor CR (Figure 1d) to plot macrofauna AFDM, R_{rate}, and P_{total}.

There was a strong spatial variability in terms of seagrass density and biomass across sites (Appendix S1: Figure S2, Table S3) (please refer to Rodil et al., 2021b). The seagrass sites with the highest plant AGDM (Appendix S1: Figure S2, Table S3) and macrofauna AFDM (i.e., T_3, T_9, and T_{10}) showed the highest P_{total} (>200 mg C m^{-2} day^{-1}) and R_{rate} (>300 mg C m^{-2} day^{-1}) (Figure 2a–c; Appendix S1: Table S2). As plant AGDM increased, so did macrofauna AFDM ($p < 0.001$), and consequently P_{total} and R_{rate} (Appendix S1: Figure S3). There was a spatial variability in terms of the sedimentary characteristics (Appendix S1: Table S3) across sites, with higher OM and chl *a* in the more protected sites (i.e., T_1–T_3 and TS) nearby the Station (Appendix S1: Figure S1) (Rodil et al., 2021b).

Variance partitioning of macrofauna secondary production

The DistLM model for P_{total} explained almost 30% of the variance in the data (Table 1). Macroalgal biomass,

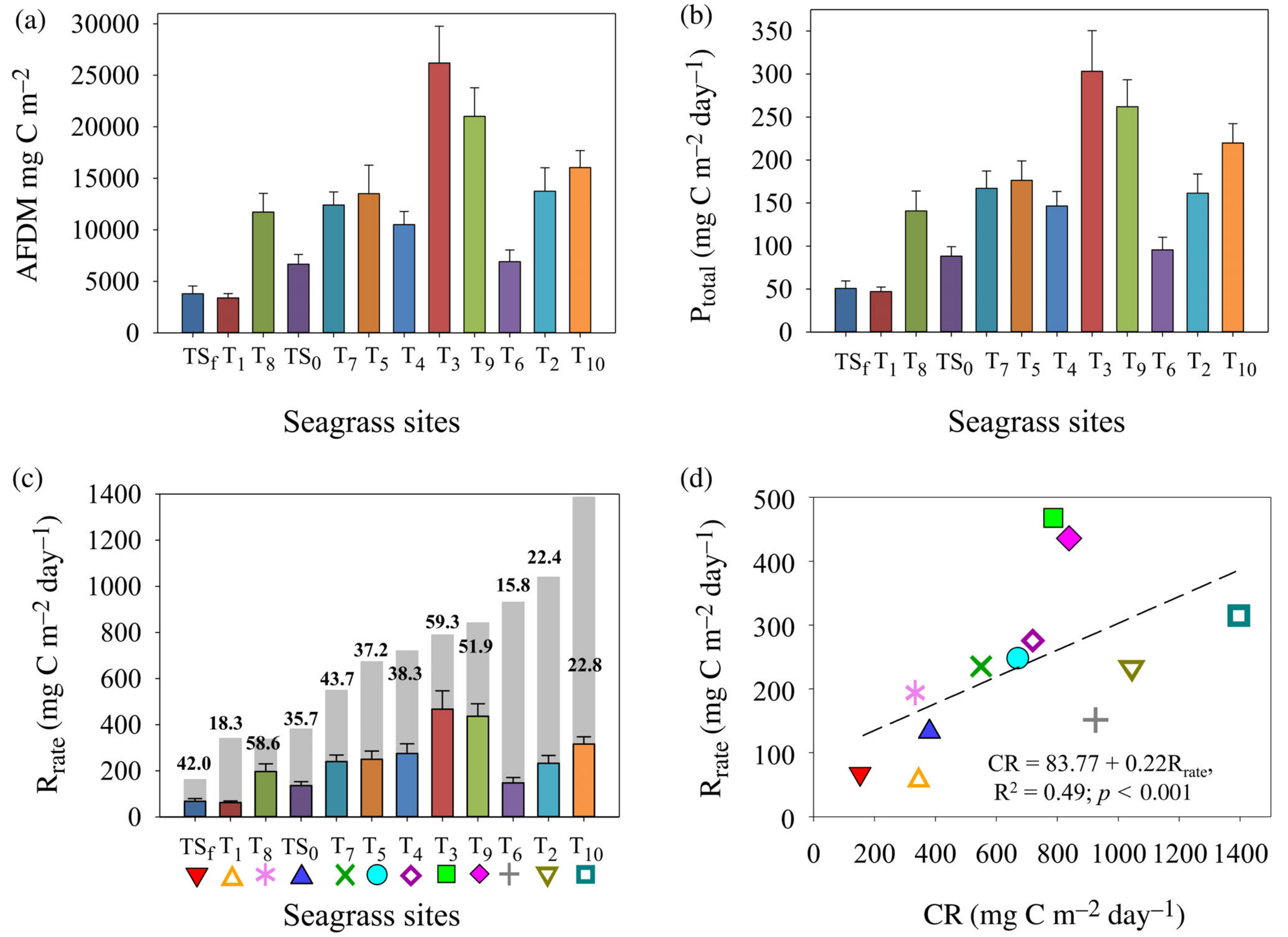

FIGURE 2 Macrofauna community: (a) ash-free dry mass (AFDM), (b) secondary production (P_{total}), (c) integrated seafloor respiration (in gray) and estimated macrofauna respiration rate (R_{rate}, bold numbers show % macrofauna relative contribution to the overall seafloor respiration), and (d) the relationship between overall seafloor community respiration (CR) and macrofauna respiration rate (R_{rate}). P_{total} is the daily secondary production of the benthic community

canopy height, sedimentary chl *a*, and grain size (>250 μm) were retained as significant determinants of P_{total} (14% of the variation). However, the largest significant part of the observed variation was explained by the number of taxa (15.5%) (Table 1). A significant part of the observed variation in P_{taxon} was explained by sedimentary predictors (13%), including pigments, OM and grain size, macrofauna diversity (TR explained 11.6% of the variability, and 12.2% if we use Shannon-H′ instead), and macrophytes explained less than 3% of the variability (Table 1). The first two dbRDA axes captured most of the salient patterns in the fitted model with 69.2% of the variability, and 18.9% of the total variation in the data cloud (Figure 3a). Observation of taxon scores relative to sites provided insight into taxa contributing to seagrass differences in community structure and their relationships to environmental conditions (Figure 3a; Appendix S1: Figure S4). The majority of the macrofauna community were macroinfauna individuals directly associated with the sediment and the dominant feeding mode was detritivore (Appendix S1: Figure S4, Table S4). Epifauna was less abundant and dominated by grazers (e.g., *Idotea* spp.) (Appendix S1: Figure S4, Table S4).

Macrofauna contribution to the seagrass organic carbon metabolism

The overall seafloor CR (mg C m^{-2} day^{-1}) estimated using the AEC technique was averaged across the same sites and during the same dates as for the macrofauna sampling (Appendix S1: Tables S1, S2). Therefore, we can provide an estimate of the relative macrofauna contribution to the CR across sites; higher than 50% at T_3, T_8, and T_9 and lower than 20% at T_6 and T_1 (Figure 2c; Appendix S1: Table S2). An increase in the CR was followed by a significant increase in R_{rate} across sites (Figure 2d). Similarly, an increase in CR showed a significant increase in

TABLE 1 Results of variation partitioning analysis (DistLM) quantifying the sequential effects of the specific contribution of macrofauna biodiversity (i.e., taxon richness or Shannon-H′), macrophyte attributes, and sedimentary predictors on macrofauna secondary production (i.e., total and taxon-specific assemblages; P_{total} and P_{taxon}) across seagrass sites

	Macrofauna P_{total} (Euclidean similarity matrix)				**Macrofauna P_{taxon} (Bray–Curtis similarity matrix)**			
Variables	**Pseudo-F**	p	R^2	ΣR^2	**Pseudo-F**	p	R^2	ΣR^2
Taxon richness[b]	34.97	<0.001	0.155	0.155	25.02	<0.001	0.116	0.116
Chlorophyll *a*	21.14	<0.001	0.085	0.240	3.60	<0.01	0.015	0.221
>250 μm	7.26	0.008	0.028	0.269	9.59	<0.001	0.043	0.159
Algal biomass	3.48	0.062	0.013	0.282				
Canopy height	3.53	0.062	0.013	**0.295**				
Phaeopigments					6.69	<0.001	0.029	0.188
Mean grain size					4.16	<0.001	0.018	0.206
Organic matter					3.41	<0.01	0.014	0.235
<63 μm					2.63	≤0.05	0.011	0.258
Chorda filum					2.98	<0.01	0.012	0.247
Canopy height					1.93	≤0.05	0.008	0.265
Above-ground dry mass					1.84	0.081[a]	0.007	**0.273**

Note: Total R^2 in bold. The position of the sites according to the predictor variables was plotted as dbRDA (Figure 3a). Daily secondary production for each taxon was estimated by multiplying the mean abundance per taxonomic group (m^{-2}) and referred to as P_{taxon} (mg C m^{-2} day^{-1}). Daily secondary production of the benthic community was estimated by summing the production of each taxonomic group and referred to as P_{total}.

[a] Marginally significant ($0.10 < p < 0.05$).

[b] If we use the Shannon-H′ diversity index: Pseudo-F = 26.32; $p < 0.001$, $R^2 = 12.2\%$.

P_{total} (Appendix S1: Figure S5). Macrofauna P_{total} was exponentially enhanced as diversity (TR and H′) increased (Figure 3b,c).

The seagrass meadows represented ~63% of the total benthic organic C stocks (30.2 g C m^{-2}), and the turnover rate was relatively fast (Figure 4). Across the seagrass sites, the seafloor's NEM was on average net autotrophic (NEM = 1.2; measured as GPP/CR), showing quite balanced means of GPP and CR (Figure 4). Ephemeral algae showed very low and highly variable biomass (on average 0.01 g C m^{-2}), assuming a C content of 28% (Bucholc et al., 2014) and sedimentary OM represented ~12% of the total benthic organic C stocks (Figure 4). The entire macrofauna community represented a mean biomass of 12.10 g C m^{-2} (i.e., >25% of the total benthic organic C stocks) and contributed on average ~38.7% of the overall seafloor CR (Figure 4). There was a high potential macrofauna production (P_{total} = 0.15 g C m^{-2} day^{-1}) introduced to upper trophic levels of the coastal food web, with a mean P/B ratio of 0.014 day^{-1} (Figure 4).

DISCUSSION

Benthic faunal diversity is ideal for exploring the relationships between biodiversity and ecosystem productivity, and carbon is the currency that connects the biodiversity of coastal ecosystems to climate change. Our study across a spatial gradient of seagrass meadows provides clear evidence that, under natural conditions, macrofauna diversity enhances secondary production, and emphasizes the key role of animals in coastal carbon metabolism. Consequently, the assessments of coastal carbon budgets need to include associated faunal communities and biodiversity elements that influence directly (e.g., grazing) and indirectly (e.g., respiration and biomass production) carbon production and transformation processes in coastal habitats.

Partitioning secondary production to macrofauna diversity

The variability of seagrass macrofauna community metrics (abundance, biomass, or richness) is typically explained by a composite of sedimentary and macrophyte characteristics (Hovel et al., 2002; Rodil et al., 2021b). The seagrass sites sampled in this study were arrayed along a heterogeneous gradient encompassing different seafloor environmental conditions. Therefore, we expected that a significant proportion of the macrofauna biomass-based productivity would be explained by sedimentary variables. Grain size reflects the local hydrodynamic conditions known to influence directly (e.g., erosion and

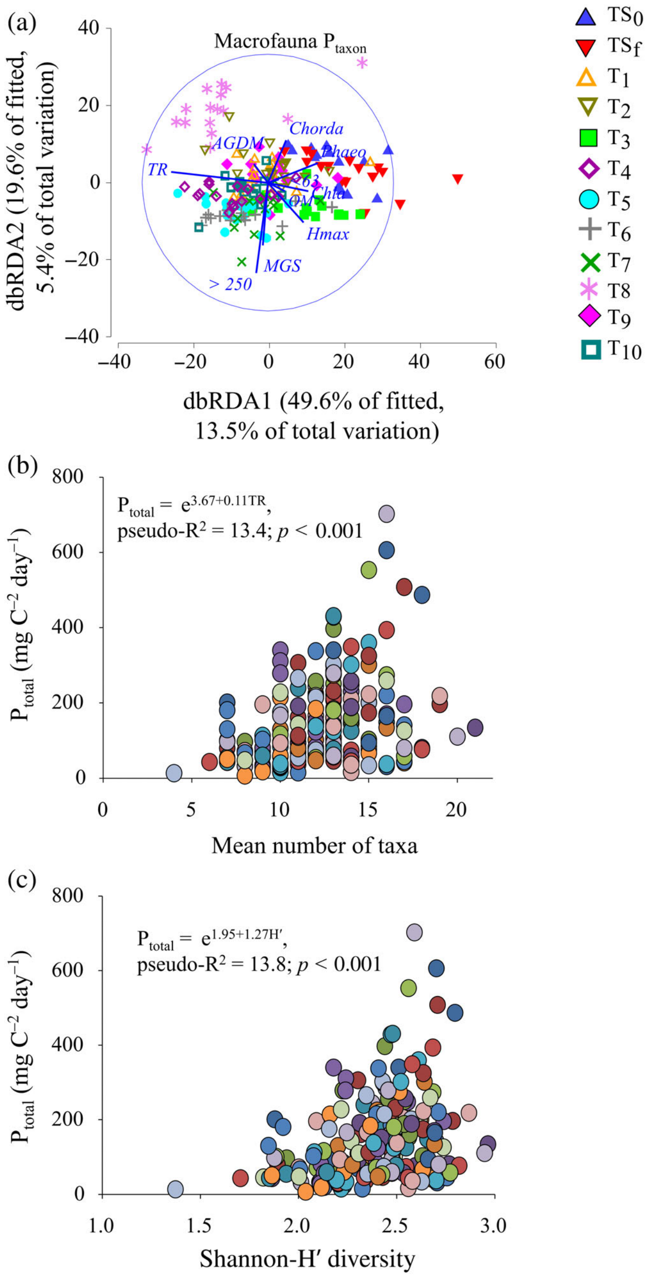

FIGURE 3 The distance-based redundancy analysis (dbRDA) ordination: (a) based on macrofauna secondary production per taxon (P_{taxon}) with overlaid environmental predictors as vectors (chlorophyll *a*, phaeopigments [Phaeo], organic matter (OM), mean grain size [MGS], <63 μm, >250 μm, canopy height [Hmax], aboveground plant biomass, algal biomass, and abundance of *Chorda filum*) in relation to taxon richness (TR) across seagrass sites (please refer to Table 1). The exponential relationship between secondary production of the benthic community (P_{total}) and (b) TR and (c) Shannon-H′ diversity

deposition) or indirectly (e.g., provision of food sources) the structure of soft-sediment macrobenthic communities (Herman et al., 1999). Organic matter and pigments are basic food resources for many macroinvertebrates (Duffy et al., 2005). Seagrass characteristics such as biomass or height are known to regulate the availability of food resources and provide shelter for macrofauna (Hovel et al., 2002). The role of *Chorda filum* (an epiphytic alga) on seagrass macrofauna is less known, although it is linked to the presence of dense meadows, and drifting algae are known to have a dominant role in explaining the variability of seagrass macrofauna (Rodil et al., 2021b).

We performed a field study across a gradient of seagrasses varying in both diversity and environmental characteristics to statistically isolate the effects of biodiversity from those of other biotic and abiotic drivers. We show that, under natural conditions, macrofauna diversity contributed at least as much as environmental conditions to the variability of secondary production (Figure 3).

The relationship between macrofauna biodiversity and secondary production

We know that a high-diversity assemblage of primary producers such as salt marshes, grasslands, forests, or aquatic microalgae can enhance primary production (e.g., Liang et al., 2016; Tilman et al., 2014; Virta et al., 2019; Zedler et al., 2001) even at the landscape scale (Oehri et al., 2017). Taxonomic and genetic diversity of seagrasses are known to enhance ecosystem functions such as carbon uptake, nutrient cycling, and O_2 production (e.g., Fourqueran et al., 2012; Gustafsson & Norkko, 2019; Rheuban et al., 2014). Whether macrofaunal diversity influences these ecosystem processes has been a knowledge gap preventing a complete understanding of the main drivers behind the productivity and carbon sequestration potential of seagrass meadows.

Despite some contradictory results, several studies conducted in different marine systems have shown that macrofauna diversity influences, both directly (grazing) and indirectly (biomass production), a variety of ecosystem processes and properties such as biogeochemical cycles and pools of OM (Baldrighi et al., 2017; Bolam et al., 2002; Duffy et al., 2003). Experimental studies using organisms from different trophic/functional groups (e.g., decomposers, ciliates, epigrazers) suggest that a more diverse consumer assemblage can enhance secondary production (Duffy et al., 2005; Gamfeldt et al., 2005; Naeem, 2002). Similarly, a recent meta-analysis showed that species richness increases community biomass production (Duffy et al., 2017). However, the potential positive relationships between consumer diversity and ecosystem productivity have been mostly limited to small-scale or controlled experimental conditions, and the answer to whether these patterns can be extrapolated to complex, real-world scenarios remains unclear. Nature's ecosystems provide critical goods

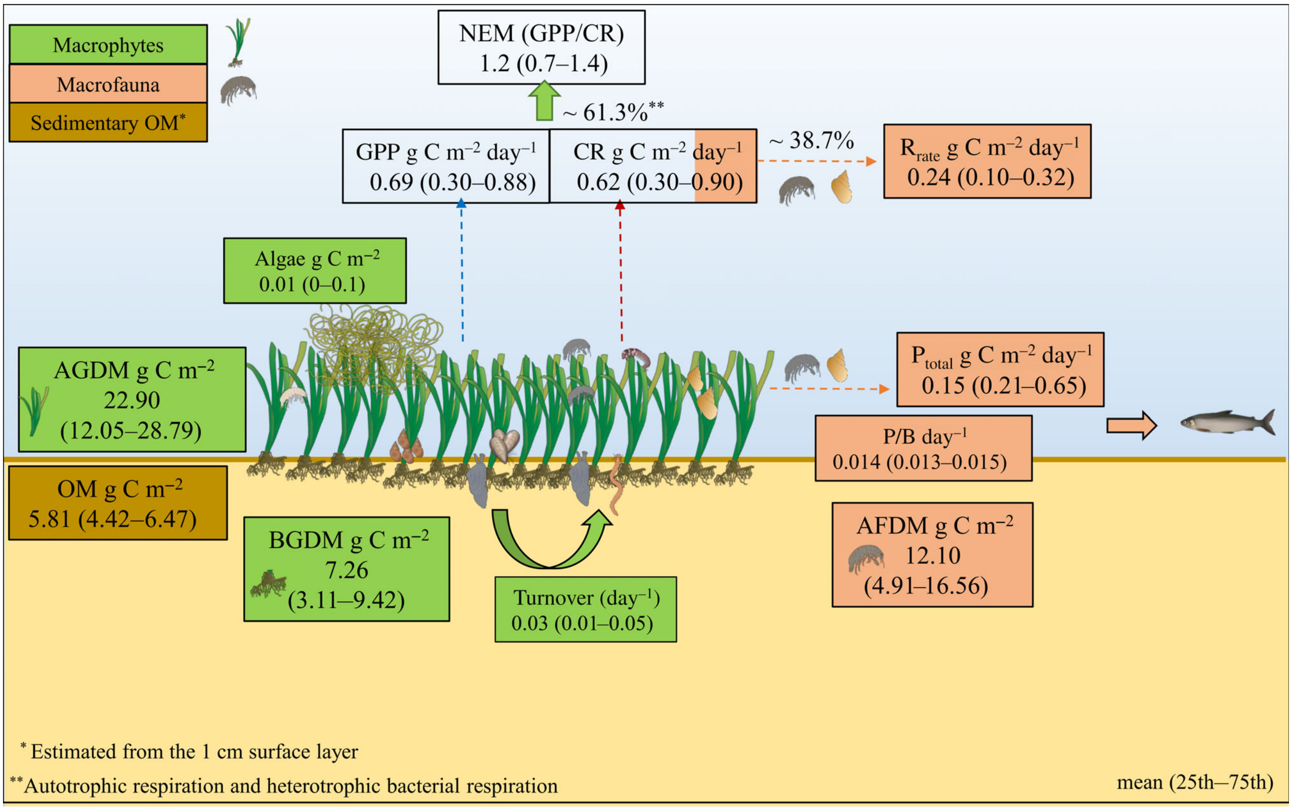

FIGURE 4 General budget showing the average contribution of the macrofauna community biomass (ash-free dry mass; AFDM), respiration (R_{rate}), secondary production (P_{total}), and P/B ratio, in relation to the contribution of the aquatic plants (i.e., above- and below-ground dry mass [AGDM and BGDM], gross primary production [GPP], community respiration [CR], net ecosystem metabolism [NEM], and turnover rates) to the seagrass carbon metabolism. OM: organic matter in the sediment. Images are courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/)

and services; therefore it is crucial to examine whether the biodiversity–productivity relationships identified in the laboratory or by systematic review also hold under natural conditions.

Our study reveals that higher macrofauna diversity is associated with higher secondary production. We show that secondary production was positively and exponentially related to macrofauna diversity across seagrasses. It follows that higher macrofauna diversity supports higher rates of seagrass productivity. It has been proposed (Gamfeldt et al., 2005; Loreau & Hector, 2001) that more diverse consumer assemblages can use their resources more efficiently because high richness can release a population from intraspecific competition allowing more efficient resource use among species (i.e., complementarity effects). Alternatively, more diverse consumer assemblages are more likely to have more efficient or highly productive species (i.e., selection effects), resulting in higher ecosystem functioning compared with less diverse assemblages. Our study showed a higher macrofauna abundance dominated by detritivores (Appendix S1: Table S4) in those seagrass sites with higher diversity (Appendix S1: Figure S6), probably revealing a positive selection effect (Loreau & Hector, 2001).

We highlight that the effect of benthic macrofauna on ecosystem productivity becomes more evident when biodiversity values are high, even in a low-diversity environment such as the Baltic Sea. Therefore, although variance partitioning results implied that some benthic environmental factors affect secondary production, the extreme lower and upper limits for seagrass productivity were naturally controlled by macrofauna biodiversity (Figure 3). The exponential shape of the relationship between macrofauna biodiversity and seagrass secondary production is different from the typically saturating relationship observed in laboratory experiments (Bolam et al., 2002; Duffy et al., 2003; Mora et al., 2014). The strength and the nature of biodiversity and ecosystem functioning relationships can differ broadly among habitats and between natural ecosystems and laboratory experiments (Hector et al., 2007; Mora et al., 2014). In laboratory conditions, the saturating relationship can be due to the presence of relatively few species, negative interactions among species, and/or the short duration of most experimental studies (Mora et al., 2014). However, large-scale observational studies on marine ecosystems have demonstrated non-saturating patterns of the relationship between biodiversity and functioning (Baldrighi et al., 2017; Danovaro et al., 2008). Natural ecosystems are inherently more complex than those indicated by experimental setups. Therefore, natural settings may reflect ecological processes that allow niche specialization and/or mature successional communities that already contain species with a higher production efficiency (Mora et al., 2014). Our field study supports the theoretical prediction of a positive influence of macrofauna on community biomass production (Duffy et al., 2017). We propose that enhanced secondary production at high macrofauna diversity is a robust ecological trend with potential generality across taxa and ecosystems. We suggest further *in situ* field studies across different coastal habitats and with different associated benthic fauna to validate the generality of these trends.

Macrofauna contribution to the seagrass organic carbon budget/metabolism

Benthic primary production in sedimentary habitats is mainly attributed to the phototrophic biomass (i.e., macrophyte and microphytobenthos), whereas CR can be related to a combination of photorespiration, bacterial respiration, and macrofaunal activity (Duarte et al., 2010; Glud, 2008; Rheuban et al., 2014). Our study shows that the macrofauna community was responsible on average for 38.7% of the overall seafloor CR across a gradient of seagrasses (Figure 4). Despite evidence strongly linking carbon remineralization, nutrient efflux, and the activities of the benthic macrofauna (Snelgrove et al., 2018), the contribution of macrofauna to seagrass carbon metabolism and the drivers behind it remain knowledge gaps (Macreadie et al., 2019). Theoretical studies have estimated a contribution of the benthic macrofauna to the CR of ~10%–30% (Wijsman et al., 1999). However, natural coastal systems typically present sharp spatial and temporal environmental gradients, and macrofauna exhibits large variation in terms of both community composition and diversity that can affect respiration rates (Rodil et al., 2020, 2021a). A previous *in situ* study estimated that ~25% of the seasonal seagrass respiration can be attributed to macrofauna respiration (Rodil et al., 2020). Our study shows that the majority of the seafloor CR (~61.3%) can be attributed to a combination of heterotrophic bacterial respiration and the large standing stock of autotrophic biomass. Typical microbial respiration rates inferred from laboratory measurements are similar, or even higher, to the estimates of macrofaunal respiration (Glud, 2008), and field studies attributed high respiration rates in seagrasses to bacterial respiration (Rheuban et al., 2014). If we account for microbial respiration at least a similar contribution as for macrofauna, then phototrophic respiration might be responsible for approximately one-fifth (i.e., 22.6%) of the overall seafloor CR, while representing most of the seafloor organic carbon stocks (i.e., 30.2 g C m^{-2}) (Figure 4). We need *in situ* measurements of microbial respiration to obtain accurate compartmentalization of the respiratory contribution of the different benthic community elements.

Determining the trophic status of seagrass meadows is crucial to quantifying their role in the global carbon budget (Berger et al., 2020), and understanding the impacts of their loss (Duarte et al., 2010). Our measurements estimated that GPP exceeded CR for most of the sites (9 out of 11; Figure 1). Therefore, most of the seagrass meadows were net autotrophic ($GPP/CR \geq 1$) consistent with the literature (e.g., Attard et al., 2019; Berger et al., 2020; Duarte et al., 2010; Rheuban et al., 2014). Macroinvertebrates undertake a vital function by transforming primary (plant) production into secondary (animal) production. Macrofauna biomass is in turn consumed by larger mobile species such as fish, ultimately limiting upper trophic levels (Duffy et al., 2003), stressing the importance of seagrasses to ecosystem functioning and as potential exporters of coastal productivity. The average macrofauna biomass (12.10 g C m^{-2}) represented approximately half of the seagrass AGDM organic carbon contribution, but it was almost two times higher than the seagrass BGDM (Figure 4). The high average values of secondary production (0.15 g C m^{-2} day^{-1}) and P/B ratio (0.014 day^{-1}) estimated for the macrofauna demonstrated the great importance of the macrofauna in the seagrass carbon budget. Our study showed high average secondary production, mainly because we sampled during the peak biomass season. However, previous secondary productivity values estimated seasonally for a seagrass meadow from the same area ranged between 0.02 and 0.13 g m^{-2} day^{-1} (Rodil et al., 2020), showing good agreement with faunal productivity estimates available in the literature (e.g., Dolbeth et al., 2012; Rodil et al., 2020; Wong, 2018). We provide empirical *in situ* evidence that the benthic macrofauna community is a strong driver of the organic carbon seafloor metabolism (in terms of stocks and flows) in a natural seagrass system, validating the importance of the benthic macrofauna communities in maintaining seagrass habitats and by extension coastal ecosystems.

CONCLUSIONS

Benthic macrofauna communities are key for regulating the basic functions that are responsible for the production of coastal ecosystem goods and services. We suggest that reductions of seagrass macrofauna biodiversity might be associated with exponential reductions of ecosystem productivity, with escalating consequences to higher trophic levels and the functioning of the entire coastal system. Our study provides critical context when assessing the impact of biodiversity loss due to climate change and anthropogenic stressors. Because seagrasses play a global role in ecological and biogeochemical processes, this study provides evidence that the conservation of seagrass macrofauna biodiversity is a priority for the sustainable functioning of the world's coasts. Integration of this perspective into global change policy is increasingly urgent as the Earth faces widespread and potentially irreversible ecosystem losses.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Rodil et al., 2021c) are available in Figshare at https://doi.org/10.6084/m9.figshare.16847458.v1.

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