

The Dynamic nature of carbon and oxygen benthic fluxes in seagrass habitats

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Abstract

Seagrass meadows are one of the most dominant vegetated ecosystems in temperate areas and contribute greatly to the carbon and oxygen cycles in coastal regions. However, their seasonal metabolism and how it varies along environmental gradients is rarely assessed and documented. Benthic chambers were used to measure carbon and oxygen fluxes during immersion in *Zostera marina* and *Nanozostera noltei* habitats and adjacent uncolonised sediments across part of their distribution range and at different times of year. Compared to bare sediments, seagrass increased both gross primary production through photosynthesis and oxygen consumption, probably by providing a complex habitat structure for the associated heterotrophic community. A seasonal trend was observed for all sites, with maximum benthic fluxes during warmer months (16.4 mmol h⁻¹ m⁻² for oxygen consumption and 28.4 mmol h⁻¹ m⁻² for dissolved inorganic carbon gross production). Using an extensive dataset combining oxygen and carbon flux assessments and the concomitant collection of habitat features (seagrass characteristics and environmental data), we showed that water temperature explained most of the variation in metabolism. We also provided quantitative estimates of Community Respiration Quotient (CRQ, between 0.63 and 1.49) and Community Photosynthetic Quotient (CPQ, between 0.88 and 1.43) two metrics characterizing benthic ecosystem functions, encompassing a wide range of environmental conditions and seagrass habitat features, making this study the first of such comprehensive and extensive coverage.

Keywords: benthic primary production, benthic respiration, oxygen, dissolved inorganic carbon, engineer species, *Zostera marina*, *Nanozostera noltei*

INTRODUCTION

Seagrass habitats play a key role in coastal ecosystems, representing local hotspots of species richness (Kindeberg et al., 2022; Pierrejean et al., 2023) and stimulating secondary production in, and around the area they colonise (Rodil et al 2020). Seagrasses have been highlighted for their potential role in reducing surface seawater CO₂ concentrations - thereby locally mitigating ocean acidification (e.g. Hendriks et al.; 2014; Ricart et al., 2021) - as well as in carbon storage and sequestration (Röhr et al. 2018; Christensen 2023), due to high rates of biological production and biomass accumulation. Healthy seagrass habitats tend to be net autotrophs due to an efficient photosynthesis/respiration ratio and are therefore efficient carbon sinks (Duarte and Cebrian, 1996; Gattuso et al., 1998). Conversely, a severe loss in seagrass shoot density (of 50–60%) has been shown to shift the entire habitat towards heterotrophy, due to decreased photosynthesis and respiration caused by lowered biomass, as well as increased microbial activity in the dead and decomposing biomass (Berger et al., 2020).

Over the last few decades, eutrophication, mechanical disturbance and climate change have been the main causes of seagrass decline worldwide (e.g. Orth and Carruthers, 2006). Some promising positive reversal trends have been observed in Europe, where management has created opportunities for recovery (Dunic et al., 2021). However, this vulnerability raises questions about the role these habitats play in both the overall functioning of coastal ecosystems, particularly with regard to carbon cycling. Empirical assessments of community metabolism are therefore essential to quantify the potential net effect of seagrass meadows of varying environmental states on carbon budgets. Accurate assessment of benthic metabolism in seagrass communities is however challenging, due to both the logistical complexity of the processes to be measured and their natural variability in time and space (Macreadie et al., 2014). Metabolism is highly mutable and dependant on a complex set of factors such as species, local biotic interactions, local hydrodynamics and associated physical characteristics, all of which vary seasonally and geographically (Ward et al., 2022). Temporal changes in seagrass morphometric traits and in associated species assemblages are also local drivers of seagrass metabolism over time (Delgard et al.; 2016; Rodil et al., 2022).

64 Comparative data using the same methodology to describe variations in seagrass metabolism at multiple
65 scales is still lacking. Temporal studies are often site-specific (Champenois and Borges; 2012; Ouisse et al.,
66 2010; Yarbrow and Carlson, 2008), whereas spatial variability is often reduced to season-specific approaches
67 (Asmala et al., 2019; Bravo and Grant, 2020). Moreover, most of the studies are performed in spatially stable
68 and homogeneous meadows, while meadows are known to be highly dynamic, with peripheral areas subject
69 to more variations (a.k.a. the “edge effect”, Hovel and Lipcius, 2001; Turrietta and Reidenbach, 2024), and
70 adjacent bare areas influenced by seagrass proximity (Muller et al., 2023). Few studies have evidenced an
71 edge effect on benthic fluxes in *Cymodocea nodosa* (Barrón et al., 2006) or *Nanozostera noltei* (formerly
72 *Zostera noltei*) (Delgard et al., 2016) habitats. The metabolic capacities of seagrass meadows are also
73 influenced by local features and environmental spatial gradients within the seagrass beds themselves (Ricart
74 et al. 2020).

75 This study aimed to investigate the variability in seagrass community benthic metabolism during immersion
76 within the distribution range of two seagrass species in France, *Zostera marina* Linnaeus, 1753, and
77 *Nanozostera noltei* (Hornemann) (Tomlinson and Posluszny, 2001), while accounting for local meadow-scale
78 fluctuations in these habitats. Three areas were investigated: the core and edge of the meadow as well as
79 adjacent bare sediment. Seasonal variations were considered by conducting sampling at five different time
80 periods over two years. We measured both oxygen (O₂) and dissolved inorganic carbon (DIC) fluxes at the
81 community level i.e by considering seagrasses and associated species.

82 Among benthic processes, primary production is often derived from O₂ measurements, which are more
83 accurate and easier to obtain continuously than carbon measurements. To infer about carbon cycling, O₂
84 values are then converted to carbon using the photosynthetic quotient, that is the molar ratio of the flux of O₂
85 released to the CO₂ assimilated during photosynthesis. A theoretical ratio of 1:1 is commonly used, without
86 appreciating the broad range of possible values (Trentman et al., 2023). This study also aimed to improve
87 estimates of carbon conversion based on O₂ production by conducting simultaneous O₂ and DIC
88 measurements..

89 To the best of our knowledge, this study is the first to deploy standardised *in situ* measurements, while
90 factoring in seasonal effect at different sites and habitats, varying both in terms of macrophyte cover (seagrass
91 vs bare) and meadow heterogeneity (stable vs dynamic area seagrass bed areas). Our results will help to
92 address the context-dependency of spatio-temporal fluctuations in seagrass metabolism, which is essential for

effectively incorporating seagrass habitats into broader-scale modelling efforts. Ultimately, these efforts are critical to scale up important ecosystem functions such as carbon cycle, and propose future scenarios, particularly in the context of global change.

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98 Study sites and sampling strategy

99 The functional role of seagrass during immersion was investigated by measuring DIC and O₂ fluxes at the
100 sediment-water interface in *Z. marina* and *N. noltei* habitats and adjacent bare areas at four sites across the
101 seagrass habitat distribution range along the French coasts (Dinard, Gulf of Morbihan, Bay of Arcachon and
102 Thau lagoon, Fig. 1). One important difference between the sites is the decreasing gradient in tidal amplitude
103 from the northernmost Dinard site to the southernmost site, with the tide being negligible at Thau. Thus, both
104 *Z. marina* and *N. noltei* are always submerged at Thau whereas *N. noltei* is intertidal at other sites. The
105 maximum temperatures also illustrate the north-south distribution gradient of the sites (Table 1).

106

107 **Table 1** - Location, annual water temperature variations, tidal regime and bed size at the four
108 study sites. Data retrieved from Lacoste et al. (2025).

	Coordinates (meadow core, longitude ; latitude		Bed size (ha)		Tidal regime	Seasonal water temperature range (°C)
	<i>Z. marina</i>	<i>N. noltei</i>	<i>Z. marina</i>	<i>N. noltei</i>		
Dinard	-2.043672 ; 48.633945	-2.198143 ; 48.603275	217	27	Mega	10-17.4
Gulf of Morbihan	-2.757894 ; 47.563187	-2.7552 ; 47.54044	812	544	Meso	9.7-18.6
Arcachon	-1.18967 ; 44.67773	-1.09645 ; 44.65625	56	3856	Meso	10.8-20.8
Thau	3.53828 ; 43.35232	3.57339 ; 43.3637	1295	125	Micro	8.6-24.9

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110 Nine benthic chambers were deployed seasonally by SCUBA-diving in each habitat (*Z. marina* and *N. noltei*,
111 Fig. 1) at the four sites between winter 2020 and spring 2021 (winter, summer, autumn 2020 and winter and
112 spring 2021). At each site, three spatio-temporal modalities were defined for each *Zostera* habitat, as gathered
113 from historical maps and/or area photographs where available, or based on local expert knowledge : (1) a
114 “core” area of the meadow where historic spatial data showed a stable meadow occurrence through time (at
115 least 10 years) (S modality), (2) a dynamic area of the meadow where fluctuating seagrass presence and
116 absence were observed over short alternating periods (D modality, not identified in Arcachon), and (3) an

117 “absent” constantly bare area adjacent to meadows where no seagrass has ever been observed (A modality)
 118 (Lacoste et al. 2024). Fluxes were measured in triplicate in each of these three discrete areas.

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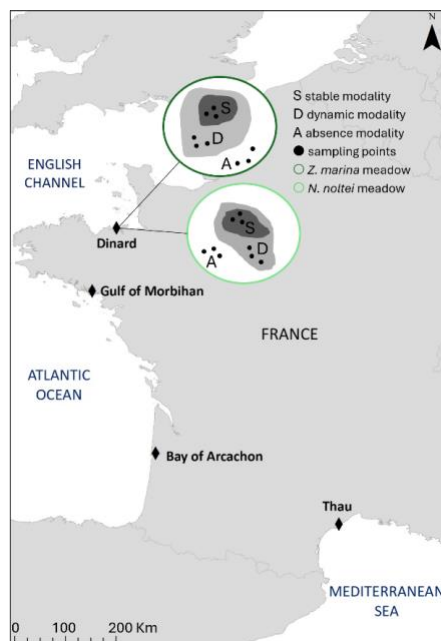


Figure 1 - Location of the four study sites in France. Nine flux measurements were carried out at each site in each habitat (*Z. marina* and *N. noltei*), in three modalities: (S) stable and (D) dynamic parts of the seagrass meadow and (A) adjacent bare area. Modality D could not be identified in Arcachon.

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Sediment-water fluxes measurement

139 Fluxes were measured during immersion using benthic chambers (0.13 m² surface area) during
 140 photosynthetic (transparent dome – light incubation) and respiratory (opaque dome - dark incubation) periods
 141 successively. The incubation time varied between 1.5 and 2.5 hours depending on the site and the season.
 142 Salinity was continuously recorded during light and dark incubations using a AQUALABO-C4E sensor. Oxygen
 143 and temperature were measured continuously (1 min frequency) within chambers using a HOBO ® U26-001
 144 logger. O₂ fluxes were calculated as the slope of the regression reported to incubation time and chamber
 145 surface area. Alkalinity and pH were measured at the beginning and the end of the incubation to calculate DIC
 146 fluxes as the difference in concentration, relative to incubation time and chamber surface area. pH was
 147 measured on board using a multi-parameter logger (WTW® Multi 3620 IDS) equipped with a pH sensor
 148 (WTW® IDS SensoLyt 900-P). Alkalinity (mol.kg⁻¹) was measured by pH-metric titration using the Titroline
 149 7000 (SI Analytics, Germany), according to Dickson et al. (2007). DIC was obtained from total alkalinity and
 150 pH using conversion from the seacarb package (Gattuso et al., 2024). It should be noted that this method is
 151 based on the assumption that no distinction is made between DIC production from respiration processes and
 152 DIC production or consumption associated with carbonate dissolution or precipitation. Oxygen and DIC fluxes

153 measured in dark conditions were expressed as community respiration (CR) whereas fluxes in light conditions
154 corresponded to the net community production (NCP). Gross community production (GCP) was obtained by
155 subtracting the CR from the NCP. Underwater photosynthetic photon flux density (PPFD, $\mu\text{mol m}^{-2} \text{s}^{-1}$) was
156 measured continuously in the chambers during the light incubation period using a spherical underwater
157 quantum sensor (LI-COR193).

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159 **Habitat characterization**

160 Habitat was characterized through the assessment of seagrass traits (shoot density, percentage cover, above
161 and below ground dry biomass and leaf area index), macroalgae dry biomass, organic matter content in the
162 sediment (loss on ignition method: 6h at 520°C), as well as density and ash free dry mass (AFDM) of infauna
163 collected in benthic chambers at the end of each incubation series. Macrofaunal samples were collected with a
164 small corer (0.05 m²) in the top 10 cm of the sediment. Organisms were sieved on 1 mm and identified to the
165 species level. AFDM was determined for the whole sample after burning 5h at 450°C. All detailed protocols
166 can be found in Lacoste et al. (2023). The results and their description, including the raw data and graphics,
167 can be found in companion papers (Lacoste et al., 2023, 2024, 2025), and are not therefore described in detail
168 in this article (but see Table 2 for partial results). The purpose of the data in the present study is to aid the
169 interpretation of the variability of the measured fluxes.

170 **Table 2** – Min and max values of organic matter in the sediment (OM %), shoot density (shoots
171 per m²) and macrofauna biomass (AFDM : ash free dry mass in g) measured in the meadows at
172 each site independently of season and modality (S and D)

	OM		Shoot density		Macrofauna AFDM	
	<i>Z. marina</i>	<i>N. noltei</i>	<i>Z. marina</i>	<i>N. noltei</i>	<i>Z. marina</i>	<i>N. noltei</i>
Dinard	1.5-18.7	0.7-4.2	31-1075	157-8800	0-208	3-1044
Gulf of Morbihan	2.6-29.2	2.1-8.2	0-262	198-10742	0-25	8-340
Arcachon	4.9-11.8	4.1-22.4	0-81	198-10544	3-55	0-624
Thau	3.6-7.6	2-6.4	0-225	199-4974	0-203	0-163

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174 **Data analysis**

175 Statistical analyses were performed using R v4.3.1 (R core team 2023). Statistical differences in CR and GCP
176 between sites and modalities were examined using linear mixed effect models with the package lme4 (Bates
177 et al., 2015), with Site and Modality as crossed fixed effects and Season as a random effect. The effect of
178 factors was considered significant when the null vs main effect models (using maximum likelihood estimation)

179 differed significantly (ANOVA $p < 0.05$). Where the effect of interaction was significant, the least-squares
180 means were calculated using the *emmeans* package (Lenth 2023) to test for inter- and intra-site differences
181 for each modality. The goodness of fit of the model was checked by examining the residual component (Quinn
182 and Keough, 2002).

183 The relationships between benthic metabolism (CR & GCP) and habitat characteristics and environmental
184 factors (independently of site and season) were explored separately for seagrass (S and D modalities) and
185 bare sediment (A modality). We employed multiple linear models with the stepwise selection procedure
186 (backward direction) of the *MASS* package (Venables and Ripley, 2002), to select the best model based on
187 the Akaike Information Criterion (AIC) (Akaike, 1973). Variables without a direct apparent effect on fluxes (e.g.
188 no direct effect of macrofauna on GCP) were discarded from the model. Absence of multicollinearity of
189 predictor variables was verified using variance inflation factors (final VIFs < 3).

190 Analyses were carried out on the basis of O₂ fluxes only (not DIC), given the continuous nature of O₂
191 measurement and the higher precision in the data. Complete results for three seasons (Summer and Autumn
192 2020 and Spring 2021 for all sites) were used. All considered GCP fluxes were measured at PPFD values
193 (Table 3) at or above photosynthetic saturation intensities for *Z. marina* and *N. noltei* according to the literature
194 (Plus et al. 2005, Léger-Daigle et al. 2022). Light was therefore not considered in the analysis assuming that
195 near maximal community fluxes were recorded.

196 In seagrass habitat, the community respiration (CRQ) and the community photosynthesis quotients (CPQ)
197 were calculated as the standardised major axis (Warton et al., 2006) of the regression between CR_{DIC} and
198 CR_{O₂} and between GCP_{O₂} and GCP_{DIC} respectively, using the *smatr* package (Warton et al., 2012).

199

200 **Table 3** - Mean underwater Photosynthetic Photon Flux Density (PPFD in $\mu\text{mol m}^{-2} \text{s}^{-1}$)
201 measured during flux experiments at each site and each season in *Z. marina* and *N. noltei*
202 habitats.

Site	Season	<i>Z. marina</i>	<i>N. noltei</i>
DN	2020 - Summer	331.9±25.2	404.6±219.9
	2020 - Autumn	296.2±48.6	257.5±67.2
	2021 - Spring	343.4±21.8	715.9±37.5
GM	2020 - Summer	777.1±173.1	1011.6±79.8
	2020 - Autumn	509.9±54.3	527.8±31.5
	2021 - Spring	506.3±35.9	1369.6±136.1
AC	2020 - Summer	585.3±24.3	944.9±255.5

	2020 - Autumn	182.1±0.4	684.4±371.4
	2021 - Spring	593.3±15.4	614.0±213.4
TH	2020 - Summer	371.3±70.5	743.6±108.5
	2020 - Autumn	280.0±30.4	100.2±4.5
	2021 - Spring	358.2±59.4	405.1±84.6

RESULTS

Common seasonal trend across sites

Diel variations of metabolism were observed for all habitats, with O₂ consumption in the dark and O₂ production during the light incubations (Fig. 2, 3). For both *Z. marina* and *N. noltei*, the main pattern of fluxes for all sites and all modalities consisted of higher values during the summer period, corresponding to the highest water temperature. Maximum values of CR were 16.39 mmol O₂ m⁻² h⁻¹ for *Z. marina* and 13.03 mmol O₂ m⁻² h⁻¹ for *N. noltei*, observed during summer in Thau and Arcachon respectively. Maximum values of GCP were 23.24 mmol O₂ m⁻² h⁻¹ for *Z. marina* and 28.39 mmol O₂ m⁻² h⁻¹ for *N. noltei* observed during summer in Gulf of Morbihan and Arcachon respectively. The lowest values of fluxes were generally observed during the winter, even though seasonal differences are less evident for the GCP as compared to the CR (Fig. 2, 3). In the presence of seagrass (Stable and Dynamic modalities) GCP values were always higher than CR (with the sole exception of Dinard during the summer). In the absence of seagrass (A modality), CR > GCP was observed several times (about 40% of the total fluxes), indicating that the measured heterotrophic processes were more important than the autotrophic process at the time of measurement.

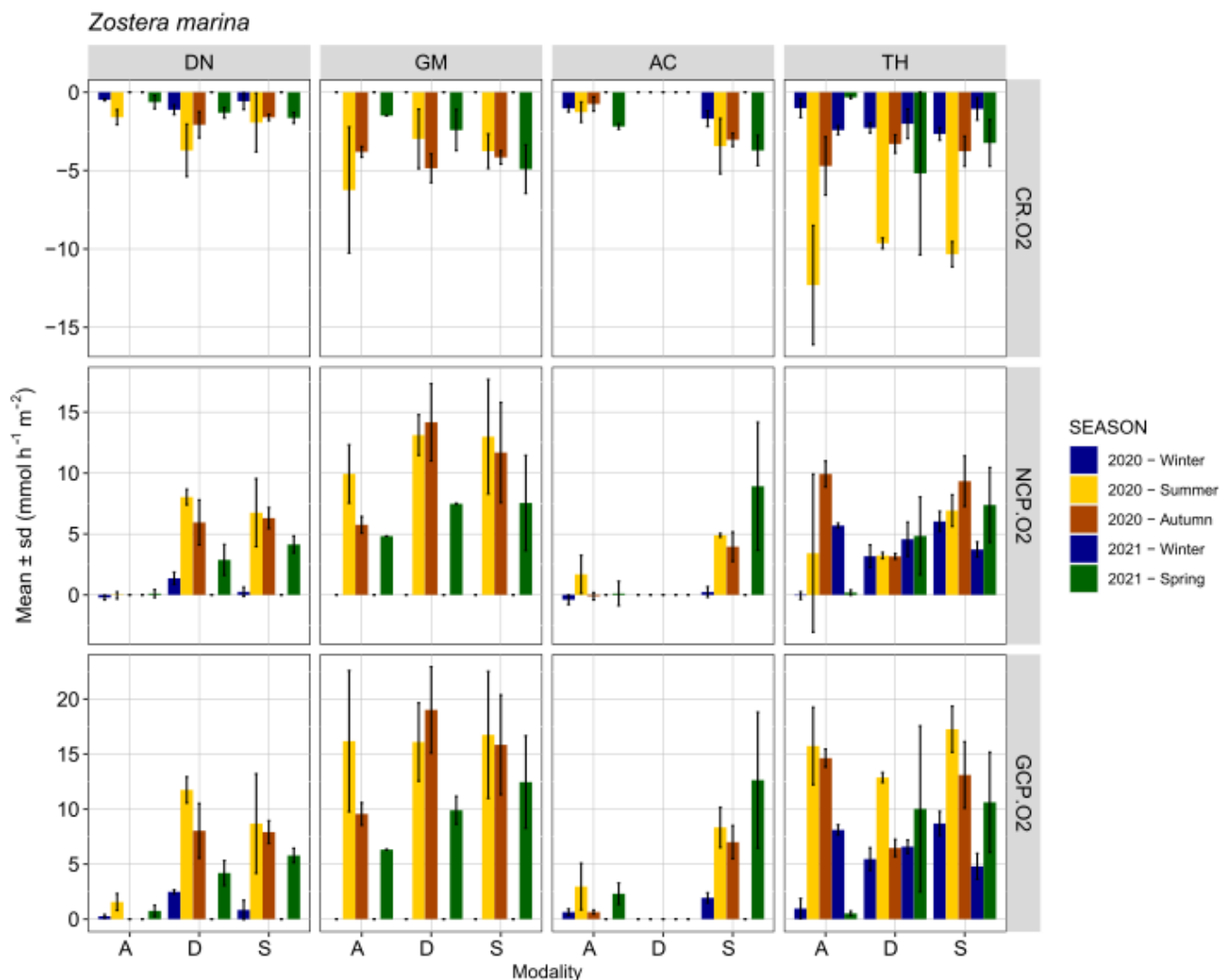


Figure 2 - Mean $\pm$ sd (n=3) community respiration (CR.O2), net community production (NCP.O2) and gross community production (GCP.O2) measured with the O₂ method for *Z. marina* during different seasons for three modalities: A: bare sediment, D: dynamic and S: stable, in Dinard (DN), Gulf of Morbihan (GM), Arcachon (AC) and Thau (TH).

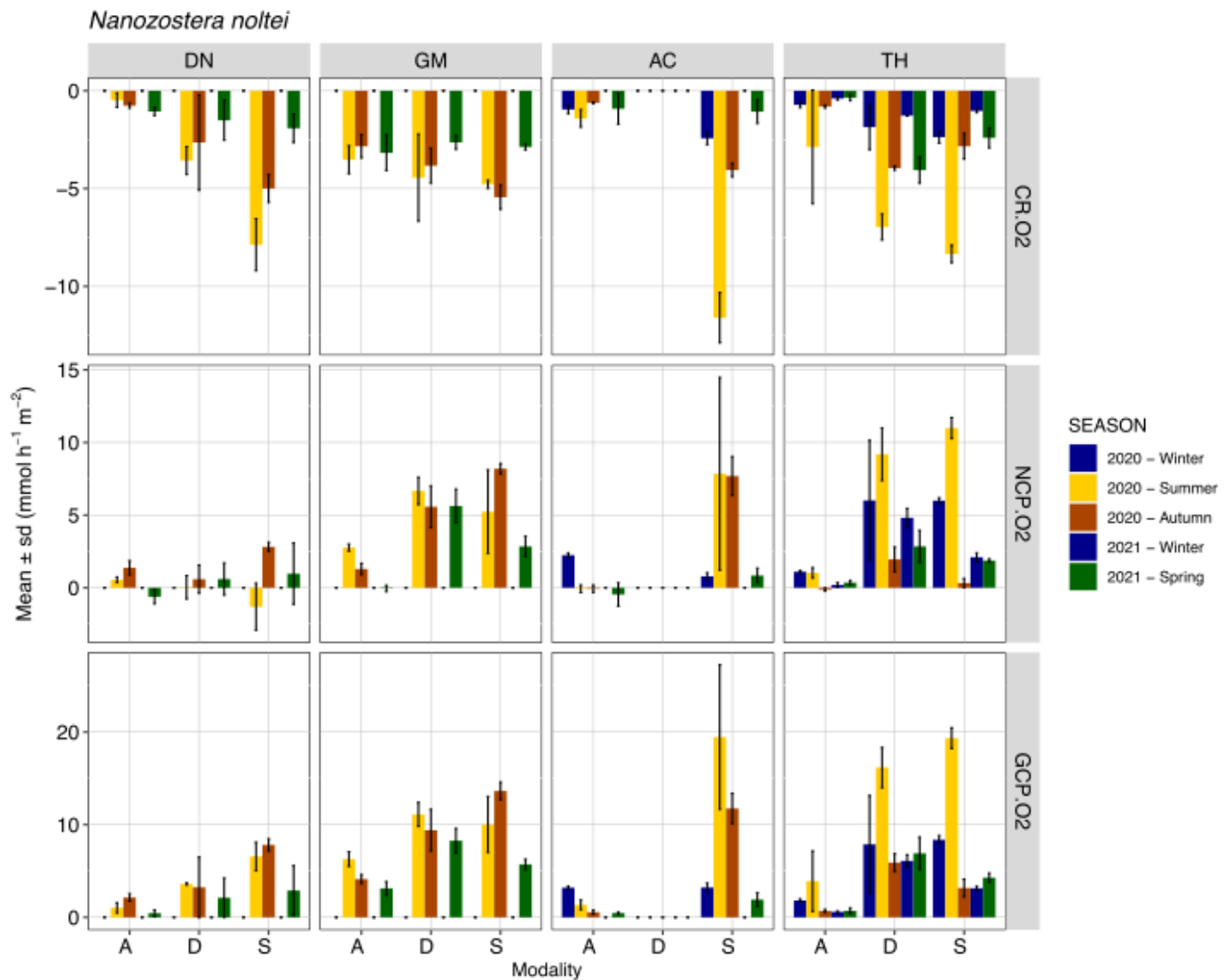


Figure 3 - Mean $\pm$ sd ($n=3$) community respiration (CR.O2), net community production (NCP.O2) and gross community production (GCP.O2) measured with the O₂ method for *N. noltei* during different seasons and for three modalities: A: bare sediment, D: dynamic and S: stable, in Dinard (DN), Gulf of Morbihan (GM), Arcachon (AC) and Thau (TH).

Spatial variability of sediment-water fluxes

The Site $\times$ Modality interaction was significant for both the CR and GCP fluxes in the *Z. marina* and *N. noltei* habitats (Table 4). Within *Z. marina* habitats, CR values were overall highest in Thau regardless of the modality (S and D), and GCP values were lower in Dinard and Arcachon compared to Gulf of Morbihan and Thau. For *N. noltei* GCP and CR were significantly lower in Dinard compared to Thau and Gulf of Morbihan. mean CR in *Z. marina* was not significantly affected by the within-habitat position. This absence of difference is likely due to important CR observed at modality A in Gulf of Morbihan and Thau. In *N. noltei*, CR was lower

in absence of seagrass (A modality), with no significant difference in the Gulf of Morbihan. In Dinard, there was also an effect of the within-habitat position (*N. noltei*), with higher CR in modality S (almost doubled in summer, Fig. 3).

Mean GCP was significantly lower in modality A of each species compared to the other two modalities (Fig. 2,3), except in Thau for *Z. marina* where an important biomass of macroalgae was observed in the bare sediment area in summer and winter (>300 mg.m² DW). Position within the seagrass bed (modality S vs. D) did not significantly influence GCP either for *Z. marina* or *N. noltei* , although large variations, by as much as double the value, were sometimes observed (Fig. 3).

With some exceptions, standard deviation was low (Fig. 2, 3), illustrating a good measurement repeatability through use of the benthic chamber method.

Table 4 - Results of the linear mixed effect models testing the effect of Site (N=4), Modality (N=3) and their interaction on community respiration (CR) and gross community production (GCP) during immersion in *Z. marina* and *N. noltei* habitats. Df: degrees of freedom, Chisq=chi-square value.

Species	Factor	CR			GCP		
		Df	Chisq	p	Df	Chisq	p-value
<i>Z. marina</i>	Site x Modality	13	44.018	<0.001	13	71.56	<0.001
<i>N. noltei</i>	Site x Modality	13	69.575	<0.001	13	76.431	<0.001

Influence of habitat on benthic metabolism at the sediment water interface

Explanatory variables of O₂ fluxes

Overall, water temperature was the most consistent significant factor across habitats and species (Table 5), explaining both CR and GCP. Other factors such as salinity, percentage of organic matter in the sediment and algal biomass showed variable significance depending on habitat and species (Table 5). Macrofauna (density) only had a significant effect on CR in *Z. marina* seagrass habitat (Table 5). Leaf biomass for both *Z. marina* and *N. noltei* and leaf area index for *N. noltei* were the two significant morphometric trait descriptors of GCP in seagrass habitats (Table 5).

Table 5 - Significant results of the multiple regressions testing the effect of measured environmental parameters on community respiration (CR) and gross community production (GCP) in *Z. marina* and *N. noltei* habitats. Habitat : seagrass = grouped dynamic and stable modalities (S, D), bare = modality A. Only significant models (*p-value* < 0.05) are presented (i.e. *N. noltei* GCP in bare sediment was not significant). Initial models, the relative importance of each predictor in the final models and number of samples (N) are reported in Table S1. F: Fisher statistic, RSE: residual standard error, adj. R²: adjusted R².

Species	Habitat	Model terms	Estimate	Std. Error	p-value
<i>Z. marina</i>	seagrass	1. CR : F=12.74 ; RSE= 1.19; adj. R ² =0.74			
		Water temperature	2.78×10^{-1}	5.34×10^{-2}	< 0.001
		Salinity	3.01×10^{-1}	9.24×10^{-2}	< 0.005
		Leaf biomass	9.22×10^{-3}	5.77×10^{-3}	ns
		Root biomass	2.87×10^{-3}	2.27×10^{-3}	ns
		% organic matter	1.15×10^{-1}	4.58×10^{-2}	< 0.05
		Infauna density	-3.19×10^{-4}	1.16×10^{-4}	< 0.05
<i>Z. marina</i>	bare	2. CR : F=13.93 ; RSE=1.62 ; adj. R ² =0.73			
		Water temperature	3.20×10^{-1}	8.01×10^{-2}	< 0.005
		Algal biomass	1.47×10^{-2}	3.46×10^{-3}	< 0.005
		% organic matter	2.16×10^{-1}	1.31×10^{-1}	ns
<i>Z. marina</i>	seagrass	3. GCP : F=7.81 ; RSE=3.42 ; adj. R ² =0.52			
		Water temperature	0.38×10^{-1}	1.45×10^{-1}	< 0.05
		Salinity	0.38×10^{-1}	2.54×10^{-1}	ns
		Shoot density	-5.74×10^{-3}	3.00×10^{-3}	ns
		Leaf biomass	3.40×10^{-2}	1.44×10^{-2}	< 0.05
<i>Z. marina</i>	bare	4. GCP : F=4.941 ; RSE=4.785 ; adj. R ² =0.36			
		Water temperature	4.30×10^{-1}	2.33×10^{-1}	ns
		Salinity	9.31×10^{-1}	4.16×10^{-1}	< 0.05
<i>N. noltei</i>	seagrass	5. CR : F=19.15 ; RSE= 1.091; adj. R ² =0.83			
		Water temperature	2.89×10^{-1}	4.40×10^{-2}	< 0.001
		Leaf Area Index	2.03×10^0	5.58×10^{-1}	< 0.005
		Algal biomass	-8.18×10^{-2}	2.17×10^{-2}	< 0.005
		% organic matter	-8.58×10^{-2}	5.45×10^{-2}	ns
		Infauna density	-8.69×10^{-5}	5.02×10^{-5}	ns
		Infauna AFDM	2.17×10^{-2}	1.18×10^{-2}	ns
<i>N. noltei</i>	bare	6. CR : F=4.81 ; RSE=0.83 ; adj. R ² =0.47			
		Water temperature	1.39×10^{-1}	4.85×10^{-2}	< 0.05
		Infauna density	1.85×10^{-4}	9.03×10^{-5}	ns
		Infauna AFDM	4.08×10^{-2}	1.99×10^{-2}	ns
<i>N. noltei</i>	seagrass	7. GCP : F=12.9 ; RSE=2.92 ; adj. R ² =0.67			
		Water temperature	0.38×10^{-1}	4.56×10^{-2}	< 0.01
		Leaf Area Index	34.6×10^{-1}	14.8×10^{-1}	< 0.05
		Algal biomass	-1.22×10^{-1}	5.57×10^{-2}	< 0.05
		Leaf biomass	4.44×10^{-2}	1.75×10^{-2}	< 0.05

Comparison of O₂ and DIC fluxes measurement: CR and CP quotients

Considering results from all seasons (Fig. 4) the community respiration quotient (CRQ) varied between 0.73 and 1.07 in *Z. marina* habitat and between 1.12 and 1.66 in *N. noltei* habitat (Table 6) with the slope significantly different from 1 in *N. noltei*. The regression slopes between GCP_{DIC} and GCP_{O₂} (CPQ) were different from 1 for both species with values between 1.01 and 1.41 for *Z. marina* and between 1.01 and 1.60 for *N. noltei*. Except for the CRQ in *Z. marina*, the deviation of the quotients from 1 indicated an imbalance between production and consumption processes.

For both species the CRQ was lower during spring (and summer) (Table 6). The CPQ was lower in autumn for *Z. marina* and in summer for *N. noltei* (Table 6). When considering each season separately, most of the regressions were not significant.

Table 6 - Estimation of the community respiration (CRQ) and community photosynthesis (CPQ) quotients from the standardized major axis using results from all four sites for grouped dynamic and stable modalities (S, D), per season, and for all seasons.

		Season	N	Slope	Lower limit	Upper limit	R ²	p
CRQ	<i>Z. marina</i>	2020 Winter	15	1.15	0.67	1.97	0.10	0.24
		2020 Summer	21	0.78	0.51	1.20	0.14	0.09
		2020 Autumn	21	1.49	1.04	2.15	0.40	0.002
		2021 Spring	21	0.63	0.40	0.98	0.08	0.20
		All seasons	78	0.88	0.73	1.07	0.28	<0.001
	<i>N. noltei</i>	2020 Winter	9	6.76*	3.09	14.77	0.06	0.50
		2020 Summer	21	1.33	0.86	2.05	0.13	0.11
		2020 Autumn	21	1.49	0.99	2.25	0.24	0.02
		2021 Spring	20	1.32	0.94	1.84	0.53	<0.001
		All seasons	71	1.36	1.12	1.66	0.34	<0.001
CPQ	<i>Z. marina</i>	2020 Winter	13	1.33	0.99	1.78	0.80	<0.001
		2020 Summer	21	1.39	1.01	1.91	0.55	<0.001
		2020 Autumn	21	0.88	0.62	1.26	0.44	0.001
		2021 Spring	20	1.29	0.86	1.96	0.26	0.02
		All seasons	75	1.19	1.01	1.41	0.46	<0.001
	<i>N. noltei</i>	2020 Winter	9	1.13	0.52	2.46	0.08	0.46
		2020 Summer	21	1.11	0.71	1.70	0.11	0.14
		2020 Autumn	20	1.43	0.91	2.24	0.12	0.14
		2021 Spring	17	1.15	0.68	1.94	0.005	0.79
		All seasons	67	1.27	1.01	1.60	0.13	0.003

*Outlying value excluded from mean calculation

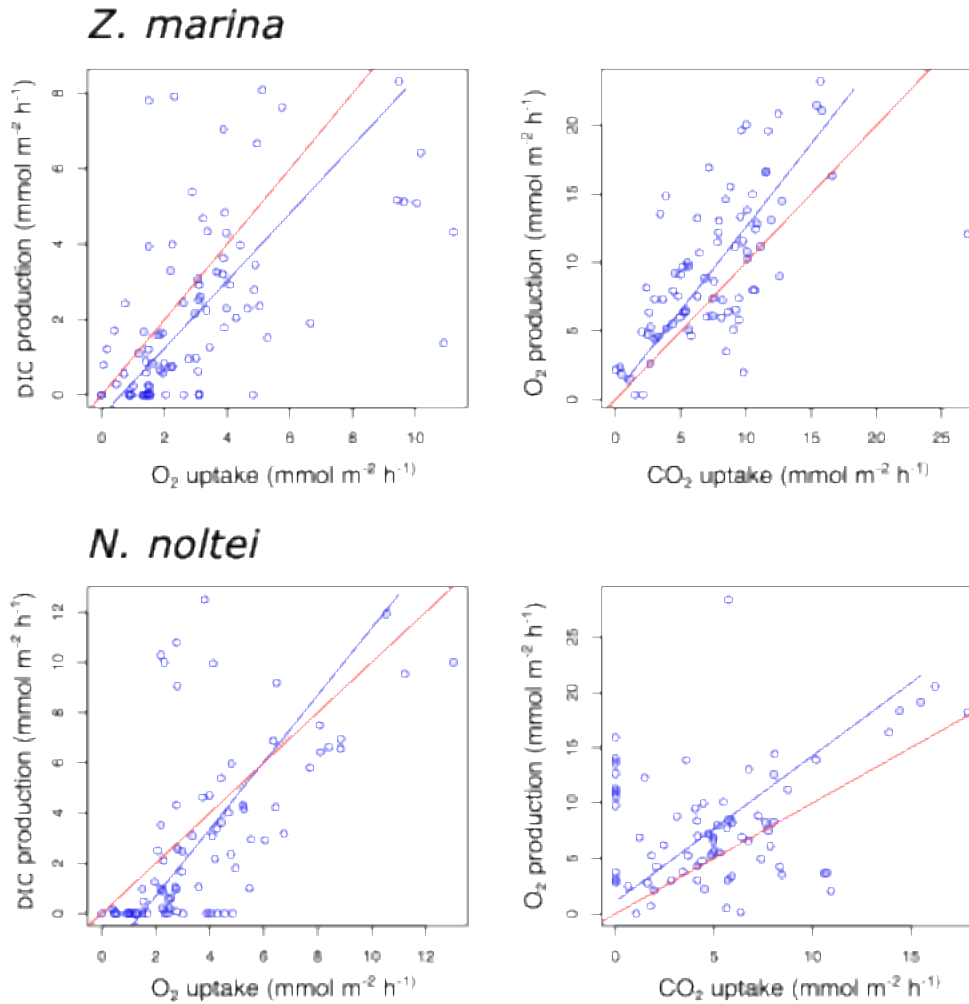


Figure 4 - Relationships between DIC production and O₂ uptake during dark (CRQ, left panels), and O₂ production and DIC uptake (CPQ, right panels) during light incubations for *Z. marina* (top panels) and *N. noltei* (bottom panels). The blue line is the linear regression fitted on the data. The red line corresponds to $y=x$.

DISCUSSION

Seagrass habitats play critical ecological roles in several ecosystem processes such as oxygen production via photosynthesis and O₂ release into the water, and carbon cycling regulation via DIC capture through photosynthesis, storing it in their biomass and sediments. The benthic chamber method presented here allows the estimation of instantaneous sediment-water exchanges at the community-level and has been widely used in different habitats and environments (e.g. Smith et al. 2009; Grenz et al., 2021; Ouisse et al., 2014). Using this methodology, we provided an extensive dataset of benthic O₂ and DIC fluxes for two emblematic seagrass species, *Z. marina* and *N. noltei*, covering a wide range of environmental conditions. The strength of this study

lies in the use of a standardized, common method deployed across four sites spread across a broad latitudinal gradient and over different seasons, allowing global analyses without bias.

Benthic metabolism at immersion in seagrass habitat

The community respiration (CR) and gross community production (GCP) values measured during this study are within the range of previous values obtained in temperate regions for these two species using the same method (Table 7). As observed in these studies, the highest values were obtained most of the time during the warmest periods, confirmed by the strong positive correlation between water temperature and fluxes. This is consistent with the general pattern of seagrass metabolism, which shows higher gross primary production during the summer months in both tropical and temperate ecosystems (Ward et al., 2022).

Overall, the benthic metabolic activity was enhanced in the presence of *Z. marina* and *N. noltei* compared to adjacent uncolonized sediments. Exceptions were observed in the Thau lagoon and the Gulf of Morbihan, where the fluxes were similar in the presence or absence of seagrass. This was mainly due to the presence of macroalgae, which may play a similar role to seagrass in increasing habitat complexity. This confirms the important role of seagrass (and macroalgae) as an ecosystem engineer - *sensu* Jones 1994, i.e. resource modifiers for other associated species - and their fundamental role in carbon and oxygen cycle (Fourqurean et al. 2012). This investigation brings additional confirmation that conservation efforts aimed at protecting and restoring seagrass habitats are essential for preserving the valuable ecosystem functions and services they provide. These results also highlight the need for habitat-specific measurements of benthic fluxes, often scarce in the literature to properly quantify habitat ecosystem functions. Together with habitat mapping, such information would provide a unique opportunity to capture the global functioning of coastal ecosystems.

Table 7 - Range of community respiration (CR) and gross community production (GCP) values measured using the immersed benthic chambers method and O₂ measurements throughout the distribution area of *Z. marina* and *N. noltei* over different seasons in existing literature.

Study	Habitat	Area	CR (mmol O ₂ m ⁻² h ⁻¹)	GCP (mmol O ₂ m ⁻² h ⁻¹)
This study	<i>Z. marina</i>	Multi sites (Atlantic & Thau lagoon)	0.05 to 16.4	0.16 to 23.2
	<i>N. noltei</i>		0.2 to 13.1	0.02 to 28.4
Ouisse et al. 2014*	<i>N. noltei</i>	Western English Channel	0.5 to 15	0.5 to 18
Martin et al. 2005*	<i>Z. marina</i>	Bay of Brest	2.5 to 5	3 to 13
Le Fur 2018*	<i>Z. marina</i>	Bages lagoon	5 to 10	15 to 30

Le Fur 2018*	<i>N. noltei</i>	Ayrolle lagoon	2.7 to 10	15 to 30
Plus et al. 2001	<i>N. noltei</i>	Thau lagoon	1.6 to 15.1	3.1 to 31.3
Asmala et al. 2019	<i>Undetermined eelgrass</i>	Baltic sea	0.1 to 3.8*	1.7 to 2.7
Camillini et al. 2021	<i>Z. marina</i>	Gulf of Finland	1.4 to 5.9	3.7 to 8.5

*Graphical estimation

Given the variability in morphological and biological traits of *Z. marina* between the four sites (Lacoste et al. 2025), one might have expected very different functional responses in terms of O₂ and DIC metabolism. On one hand, the morphological characteristics of *Z. marina* in Dinard have been described as adapted to stressful conditions (i.e. strong hydrodynamic conditions), with important shoot density and below-ground biomass for anchoring, with limited leaf surface area (see also Boyé et al. 2022). Conversely, the seagrass population that developed in the more turbid and calm conditions of Arcachon showed low shoot density but long and wide leaves, thereby maximizing their access to light. These different - and at the opposite of the ecological spectrum - strategies, expressed by different phenotypes, were not reflected in the ecological functioning at the community-level, since no significant difference was observed in the measured fluxes at immersion between these two sites. Similarly, the phenotypic difference observed for *Z. marina* at the modality scale in Dinard, with greater shoot density in the dynamic as opposed to the stable area, was not observed for fluxes. This is a sign of high phenotypic plasticity of this species, able to adapt to local conditions without altering its capacity to efficiently use resources. Seagrasses are however engineer species that host a highly diverse species assemblage, that include other primary producers such as epiphytes or microphytobenthos, as well as heterotrophic organisms, from bacteria to epifauna. Thus, GCP and CR derive from complex processes operated by different interacting organisms, and are also influenced by the environment (Rodil et al. 2021) such that seagrass characteristics alone may not be good proxies of ecosystem functioning.

Predicting flux variability at the global scale

In most cases, benthic metabolism differed markedly between vegetated areas and adjacent sediments. As such, we explored correlations between environment and fluxes separately within the meadow (modalities S and D), and in the bare area (modality A). Models in modality A were less well fitted than in seagrass, except for community respiration (CR) near *Z. marina* (R²: 0.74). The presence of macroalgae in Thau appears to have driven this correlation by increasing habitat complexity and possibly establishing heterotrophic

375 communities (Friedrich, 2012 and references therein). Considering the regression analysis, the role of
376 macrofauna does not appear to be the most important in our study, so other communities may be more
377 important. The positive role of temperature on CR in this modality suggests an important role of meiofauna
378 and bacteria inhabiting sediments and macroalgae, whose activity could be increased in warmer conditions
379 (Del Giorgio et al., 2006; Rivkin and Legendre, 2001). Conversely the poor prediction of gross community
380 production (GCP) in bare sediments may have suffered from the lack of quantification of primary producers
381 such as microphytobenthos, which could be an important contributor to photosynthesis in coastal areas
382 (Bartoli et al., 2003; Spilmont et al., 2006).

383 Of the total observed variance in benthic metabolic activity in seagrass, 52% to 83% was explained by the
384 factors considered in our measurements, the most important being temperature, leaf biomass and surface
385 area. This supports the direct effect of seagrass biomass on benthic primary production and respiration, as
386 previously shown in studies that have compared vegetated and nearby unvegetated sediments (Delgard et al.,
387 2016; Hume et al., 2011; Stutes et al., 2007). The positive effect of temperature on GCP is likely due to both
388 increased photosynthesis in warmer water and to co-correlation, with seasonally-driven morphometric
389 seagrass characteristics, in particular leaf growth. It should be noted that measurements were likely carried
390 out during the optimal temperature range for these species (Berger et al., 2020), with no apparent stress
391 during the studied period (Lacoste et al. 2025). Photosynthetic capacity is however known to start declining
392 above a certain temperature, together with plant biomass loss (Collier et al., 2017; Lee et al., 2007). We
393 therefore stress the importance of considering the evolution of seagrass benthic metabolism and their role in
394 benthic-pelagic coupling with respect to the increased sea water temperatures predicted under climate
395 change. This is particularly true at the distribution range edge of the species, such as in the Thau lagoon for *Z.*
396 *marina*.

397 Finally, given the lack of prediction of GCP variation in our model (R^2 : 0.52 and 0.67 for *Z. marina* and *N.*
398 *noltei*, respectively), one might expect to improve this predictability by quantifying other primary producers that
399 may contribute significantly to coastal primary production, such as epiphytes and microphytobenthos, as
400 mentioned above. It was for example previously found that epiphytic biofilm developing on seagrass leaves
401 have an effect on photosynthesis and respiration rate (Hansen et al. 2022) but that both bare leaves and
402 epiphytes might receive different amounts and nature of light, and thus respond differently to environmental
403 changes (Brush and Nixon, 2002). Despite this limitation, our dataset provides linear regression models that

can be used to make predictions about benthic metabolism in seagrass habitats under a given set of environmental conditions with knowledge of some seagrass morphometric traits.

The oxygen-carbon balance

Most existing studies of metabolic processes of macrophyte communities rely on measuring O₂ consumption and production rather than carbon (e.g. Barrón et al., 2006; Hansen et al., 2000; Santos et al., 2004), mainly due to the relatively straightforward measurement method of the former. The close correlation between DIC and O₂ release or demand due to respiration and photosynthesis at the water-sediment interface suggests that DIC and O₂ fluxes in sediments are closely coupled processes. As we are often more interested in carbon cycling, CO₂ uptake and release are therefore typically derived from O₂/CO₂ conversion, with the community photosynthesis quotient (CPQ) and community respiration quotient (CRQ) factors set to 1 which is the theoretical value expected. However, there are challenges in using this conversion factor when autotrophic and heterotrophic organisms coexist – such as in seagrass habitats – and for which situations the CRQ values tend to deviate from 1 (Trentman et al., 2023). For example, anaerobic reduction of sulphate may underestimate respiratory losses while overestimating net production. As part of this study, we have jointly estimated O₂ and DIC fluxes, providing a reliable estimate of CRQ and CPQ ratios across a large gradient of ecosystem variations spanning most of the *Z. marina* and *N. noltei* range in Europe.

The measured values of both CRQ and CPQ were within the range of values reported in the literature for seagrasses (Le Fur, 2018; Martin et al., 2005; Ouisse et al., 2014), deviating from 1. For all seasons combined, CPQ was > 1 for both species, indicative of higher O₂ production compared with DIC consumption. Such an imbalance may be due to several processes such as nitrate reduction processes releasing O₂ during biosynthesis associated with primary production (Trentman et al., 2023), or DIC consumption partly compensated by benthic alkalinity fluxes due to anaerobic processes. The CRQ was > 1 for *N. noltei*, indicating the possibility of organic matter decomposition using elements other than O₂ as terminal electron acceptors, such as nitrate or sulphate. This was also observed in winter and autumn for *Z. marina*, indicative of a potential increase of anaerobic processes during these periods. This hypothesis could be supported by the fact that seagrass meadows are known to be sites of high organic matter remineralisation, trapping and concentrating organic particles (Duarte et al., 2005).

Our results show that measuring O₂ fluxes only and assuming a CPQ of 1 would have led to overestimating community carbon assimilation in seagrass. For a better comprehension of community metabolism, it is therefore advised to measure O₂ and DIC fluxes simultaneously such that the ratio could inform on the biogeochemical processes mentioned above. Although our summary table (Table 6) provides a range of values for CRQ and CPQ at the scale of seagrasses distribution in France, predicting when and where quotients may vary as a function of environmental conditions requires further comparison of O₂ and DIC measurements at high sampling rates.

Conclusion

Seagrasses are key species in the functioning of coastal habitats, with their importance in carbon sequestration and ocean acidification mitigation now fully recognized. Accounting for spatial and temporal variability in metabolism is therefore particularly important for managers, given the growing interest in seagrass restoration and innovations towards nature-based solutions to mitigate ocean acidification and sequester carbon in the sediments. This study provides some clues and evidences to better understand whether gross community production and respiration vary predictably over time and at different spatial scales. To the best of our knowledge, this study is the first to deploy standardised *in situ* measurements, while factoring in seasonal effect at different sites and habitats, varying both in terms of macrophyte cover (seagrass vs bare) and meadow heterogeneity (stable vs dynamic area seagrass bed areas). At the global scale, some of the variability remains unexplained, probably due to the lack of direct quantification of certain community components, such as the microphytobenthos or the bacterial compartment. Functional diversity of macrofauna could also help explain part of the variability (Hillman et al. 2021). Site-specific models could actually increase the predictability of fluxes, but in most situations, data are scarce. The models proposed here therefore represent an imperfect alternative, which will nonetheless provide a better understanding of the role of seagrass beds in the functioning of coastal ecosystems. We also provide a reliable range of values with associated errors for converting O₂ to DIC when estimating seagrass carbon budgets from O₂ measurements. Ongoing global changes in environmental conditions and the extent of seagrass meadows will undoubtedly require additional efforts to estimate benthic metabolism as a function of environmental conditions and increasing water temperature.

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