

38 suitable and unsuitable plant morphometric traits for use as indicators. While traits such as
39 shoot density are used extensively, the current study shows that relative cover and LAI may
40 be much more reflective of ecological status. Temperature was the most influential factor on
41 LAI, and sediment structure modified competition between seagrasses with algae. The current
42 study highlights the importance of identifying site- and habitat-specific indicators. Future work
43 from our study will further evaluate the environmental pressures faced by these four sites to
44 characterize them based on conservation status.

45

46 **KEYWORDS:** interspecific boundary line, d_{grass} , seagrass meadows, efficiency of space
47 occupancy, ecological status, indicator, *Zostera marina*, *Nanozostera noltei*

48

49 1. INTRODUCTION

50 Seagrass meadows are one of the most productive ecosystems, providing numerous
51 ecosystem services, such as nutrient cycling, carbon sequestration, and prevention of
52 sediment suspension. They also act as bioengineers, providing structured habitats and
53 breeding grounds for a high diversity of fauna (Lefcheck et al., 2019; Unsworth et al., 2022).
54 Not only are they a global carbon sink, but their degradation can also contribute to carbon re-
55 emissions into the atmosphere. Seagrass meadows are, however, exposed to numerous
56 environmental stressors. About a third of European seagrasses were lost between 1869 and
57 2016 (de Los Santos et al., 2019) due to a combination of natural and anthropogenic
58 pressures. Ongoing anthropogenic pressures, including chemical pollution, eutrophication,
59 and fishing, can further slow their recovery or accelerate their deterioration. In fact, worldwide,
60 seagrass meadows are currently thought to be decreasing at 7% per year, a huge increase
61 compared to the mid-1900s, when seagrasses were decreasing at a rate of 0.9% per year
62 (Waycott et al., 2009). The conservation of seagrass meadows is, therefore, of high importance
63 (Pendleton et al., 2012).

64

65 Currently, several indicators are used to determine seagrass meadow status for management
66 and conservation purposes. These indicators are often selected for their sensitivity to
67 environmental changes. Lately, there has also been a growing interest in indicators for overall
68 ecosystem function. These indicators often include growth traits such as aboveground and
69 belowground biomass (Lyons et al., 2015) or shoot density. In Europe, an index called the
70 ecological quality ratio (EQR), proposed by the Water Framework Directive, is used (Auby et
71 al., 2018). It comprises three metrics: seagrass taxonomic composition, abundance/shoot
72 density (mainly density, according to Jones & Unsworth, 2016) and surface area extension.
73 While these metrics together provide a general overview of meadow status, some challenges
74 arise with seagrass taxonomic composition and abundance/shoot density. Species such as
75 *Zostera marina* (ZM) and *Nanozostera noltei* (NZN) do not always co-occur. For instance, in
76 many sites, NZN has not been observed to grow, and its absence does not necessarily reflect
77 a reduced meadow status. Taxonomic composition may, therefore, not always be a pertinent
78 metric for seagrass meadow status. Recent studies are also questioning the efficacy of shoot
79 density as an indicator. Boyé et al. (2022) described trade-offs in intertidal ZM between shoot
80 density and size that resulted in two plant phenotypes: those with high densities and low
81 aboveground-to-belowground ratios growing under high hydrodynamic and temperature
82 stress, and those with low densities and high aboveground biomass growing in more stable
83 conditions. Additionally, in a study of seagrass meadows in the British Isles, Jones & Unsworth
84 (2016) observed higher seagrass shoot densities in eutrophicated conditions. Finally, contrary
85 to common assumption, shoot density and aboveground biomass are not always correlated.

86 In fact, Olesen & Sand-Jensen (1994) discovered that maximum leaf biomass in ZM was not
87 associated to shoot density, and Cabaço et al. (2007) showed that, for NZN, biomass and
88 density were positively correlated only in nutrient-rich meadows.

89

90 Comparing the health of different seagrass meadows using currently proposed plant growth
91 parameters may, therefore, be misleading and can have implications for management. More
92 recently, a novel approach called the RESQUE (RESilience and QUality of seagrass
93 ecosystem) was studied in an attempt to combine several growth parameters, including leaf
94 surface and number, rhizome elongation, lower limit depth and cover, shoot density, and
95 epiphyte biomass, as well as the Conservation Index (Oprandi et al., 2021), into a single value
96 to define ecological status. The importance of many of these traits as reflective of seagrass
97 meadow status, however, has yet to be tested. Seagrasses exhibit phenotypic plasticity, and
98 their morphometric traits can vary both spatially and temporally depending on environmental
99 conditions, such as light availability, temperature, and nutrient concentrations (Bertelli et al.,
100 2021; Pazzaglia et al., 2021). Therefore, meadows at lower latitudes with higher temperatures
101 and lower hydrodynamics may have different morphometric traits compared to those at higher
102 latitudes with lower temperatures and higher hydrodynamics. In a previous study conducted
103 along the French coast, Lacoste et al. (2023a) showed that the ZM meadows in north Brittany
104 (Dinard) invested into shoot production and belowground biomass due to the strong tidal
105 currents of the region, while those in Arcachon Bay invested in leaves due to the limited light
106 conditions of the sheltered area. Even within the same region, clonal plants may modify their
107 phenotype to adapt to environmental conditions (Balestri et al., 2003). Not only may combining
108 all these traits into a single value bias the estimation of ecological status, but sampling and
109 measuring multiple traits can also be time-consuming.

110

111 Management efforts are also starting to focus not only on seagrass health but also on
112 associated benthic communities. Epifauna and endofauna form an integral part of the benthic
113 food web and have an important role in ecological processes. Seagrasses are competing with
114 benthic and planktonic algae, including the epiphytic community and macroalgae, for nutrients
115 and light. Epifaunal grazers and filter feeders control the development of these algae,
116 alleviating competition for seagrasses. Endofauna, on the other hand, play an important role
117 in sediment structuring and decomposition of organic matter (Gutiérrez et al., 2011). Despite
118 their different roles, epifauna and endofauna are also competing with each other for resources
119 (Schrijvers et al., 1996). More recent studies are exploring epifaunal and endofaunal species
120 richness and diversity, as well as functional trait diversity (AMBII, (Borja et al., 2000; Boyé et
121 al., 2017; Muller et al., 2023)) to determine overall ecosystem health. However, such studies
122 are complex, and observations differ between them. For instance, a higher epifaunal species

123 richness is not always associated with higher seagrass growth parameters. Additionally, as
124 discussed earlier, not all seagrass growth parameters (e.g., density) necessarily reflect
125 meadow health. It is, therefore, necessary to also characterize these biotic compartments.
126 Considering the complexity of seagrass ecosystems, an indicator reflecting seagrass meadow
127 ecosystem status would ideally integrate multiple metrics. In terms of management, however,
128 this can be time-consuming and expensive. An effective indicator for management is one that
129 is easy to measure, has been measured in the past, and is representative of the ecosystem
130 (Yen & Butcher, 1997).

131
132 Despite phenotypic variations in response to environmental conditions, efficient plants are
133 capable of packing more biomass per unit density (Vieira et al., 2018). The biomass-density
134 relationship has been widely studied for terrestrial plants and for algae to determine their
135 carrying capacities. Recently, (Vieira et al., 2018) defined such a relationship for seagrasses.
136 In a study including 2954 biomass-density observations of seagrasses, they defined an
137 interspecific boundary line (IBL) based on 500 of the most efficient plants worldwide. They
138 showed that the distance of seagrass meadow stands to the IBL (d_{grass}) was a useful ecological
139 indicator. However, the use of d_{grass} requires the collection and processing of samples for
140 determination of aboveground biomass, which can be both destructive and time-consuming.
141 Nevertheless, d_{grass} can be used as a reference to compare meadows across space and time
142 and to correlate with other biological and environmental variables. Integrating this parameter
143 into research studies for ecological status indicators can help bridge the knowledge gap
144 between available indicators and their reflection of overall ecosystem health. Such a study is
145 feasible when large sampling datasets are available, allowing for the comparison of different
146 meadow types.

147
148 Identifying an effective indicator for seagrass meadow status is clearly a complex and an
149 evolving research area that holds high value for management and requires a more nuanced
150 approach. The Life MarHa (Marine Habitats) project aims to determine a new-generation
151 indicator based on data collected from four sites (Dinard, Gulf of Morbihan, Arcachon, and
152 Thau) along the coast of France. The objectives of this study were to (1) determine the spatial
153 and temporal differences in seagrass efficiencies of space occupancy (Vieira et al., 2018), (2)
154 identify levels of ecological efficiency for the four sites, in comparison to each other, (3) identify
155 a relevant indicator for seagrass meadow status, and (4) determine associations between
156 different communities, including algae, seagrass, endofauna, and epifauna. This study will be
157 followed up in future by an exploration of environmental conditions and stressors, such as
158 fragmentation, surface area extension, fishing pressure, eutrophication, and pesticide
159 pollution, to characterize the four sites based on their conservation status.

160

161 **2. MATERIAL AND METHOD**

162 Details of the sample collection and processing, as well as descriptions of plant morphometry,
163 environmental conditions, and habitat structure, can be referred in Lacoste et al. (2023a) and
164 Lacoste et al. (2023b). The efficiencies of space occupancy of two seagrass species, *Zostera*
165 *marina* (ZM) and *Nanozostera noltei* (NZN), present in four coastal sites (Dinard [DN], Gulf of
166 Morbihan [GM], Arcachon [AC] and Thau [TH]; Fig. 1) of France were established by
167 measuring the distance of each stand to the interspecific boundary line. Two types of
168 modalities, that is, the stable or older meadow areas (Modality S) and the dynamic or younger
169 meadow areas (Modality D), were studied for all sites except for AC site, where a dynamic
170 meadow could not be defined (see Lacoste et al., 2003b). Levels of ecological status were
171 then defined for each of these modalities identified for the four sites.

172

173 The method section is structured into the following parts: (1) determination of the distance of
174 seagrass meadow stands to the interspecific boundary line (d_{grass}), (2) classification of the
175 different meadows and their modalities into levels of ecological efficiency using ordinal scaling,
176 (3) identification of patterns among the different biological variables for the selection of an
177 indicator, (4) determination of inter-site differences in sediment structure, and (5) determination
178 of inter- and intra-site differences in seagrass leaf carbon and nitrogen stoichiometry.

179

180 **2.1. Distance of the stands to the interspecific boundary line**

181 In the present study, the distance of the seagrass meadow to the interspecific boundary line
182 (d_{grass} ; (Vieira et al., 2018)) was used as a reference for assessing seagrass meadow health.
183 The interspecific boundary line (IBL) was calculated based on Vieira et al. (2018) as

184

$$185 \log_{10}B = \beta_0 + \beta_1 \log_{10}D,$$

186

187 where B represents biomass, D represents density, and β_0 (4.569) and β_1 (0.438) are the
188 coefficients for the seagrass IBL. These coefficients are established in the literature for algae,
189 seaweeds, and terrestrial plants.

190

191 Seagrass biomass and density data from the summer and autumn of 2020 and the spring and
192 winter of 2021 were used. The seagrass biomass-density points of each modality (S and D)
193 and season were plotted to visualize their position in relationship to the interspecific boundary
194 line. Plots were generated using the ggplot function of the vegan package (Oksanen et al.,
195 2022) in R (v 4.3.1; (R Core Team, 2023)). The points were then converted into an sf class
196 object, and the distance of each stand to the interspecific boundary line was calculated using

197 the `st_distance` function in R. A smaller value of d_{grass} indicates a higher efficiency of space
198 occupancy. Separate plots were created for ZM and NZN meadows.

199

200 Additionally, based on Cabaço et al.(2007), who found no correlation between biomass and
201 density except in disturbed/nutrient-rich meadows, regression analyses were performed to
202 determine the biomass-density relationships per site after pooling data from all seasons.

203

204 **2.2. Spatial and temporal differences in efficiency of space occupancy**

205 Using ordinal scaling for ecological classifications (Moreno et al., 2001), each modality (S or
206 D) per site was placed within one of four groups of efficiency of space occupancy. The
207 classification system used was as follows:

208

- 209 • Group 1 (minimum ecological status): $d_{\text{grass}} > M + 0.5SD$
- 210 • Group 2 (low ecological status): $d_{\text{grass}} = M$ to $(M + 0.5SD)$
- 211 • Group 3 (moderate ecological status): $d_{\text{grass}} = (M - 0.5SD)$ to M
- 212 • Group 4 (maximum ecological status): $d_{\text{grass}} < M - 0.5SD$

213

214 This scaling was first performed by averaging all seasons to obtain overall efficiency per
215 modality. Following this, scaling was performed to compare efficiencies for each season per
216 modality. For “all seasons”, therefore, M and SD , respectively, were the average and standard
217 deviations of d_{grass} calculated using data for all seasons from all sites. For “summer”, for
218 example, the M and SD were the average and standard deviation of d_{grass} calculated using
219 data for summer from all sites. The classification system is provided in Table 1.

220

221 **2.3. Correlations among biological variables**

222 Patterns in the data were explored using principal component analysis (PCA) in R. The
223 `factoextra` package (Kassambara & Mundt, 2020) was used. Correlations among different
224 variables were examined. These included d_{grass} , seagrass growth parameters (aboveground
225 biomass [SG_AG], belowground biomass [SG_BG], density [SG_density], leaf area index
226 [LAI], seagrass canopy height [SG_canopy_H], seagrass percentage cover [SG_cover],
227 number of leaves per shoot [SG_LfpSh], and average leaf surface area [SG_LSA]), algal
228 percentage cover (Algae_cover), total algal biomass (Algae), bare sediment relative cover
229 (Bare_sediment), endofaunal biomass, density and diversity indices (species richness
230 [Endo_SR], Pielou's evenness index [Endo_J], evenness derived from H [Endo_eve],
231 Simpson's inverse [Endo_Silnv], Shannon index [Endo_H]), as well as carbon (net primary
232 production [NCP_O2], carbon respiration [CR_O2]) and nutrient fluxes (f_{PO4} and f_{NH4}).

233

234 Throughout the article, the term “relative algal cover” refers to percentage algal cover on the
235 sediment surface, and the term “algae” refers to total pooled algal biomass, primarily
236 comprising drifting or floating filamentous algae.

237
238 To obtain a global understanding of patterns among biological variables, two initial PCA plots
239 were created by combining the data from all four seasons (summer and autumn 2020 and
240 spring and summer 2021) for ZM and NZN. In these plots, epifauna data were not included as
241 they were available only for autumn and winter 2020.

242
243 Additional PCAs were then plotted to view patterns for each season and provided in the
244 supplementary material. For autumn and winter, in addition to the variables described earlier,
245 epifaunal biomass, density and diversity indices (species richness [Epi_SR], Pielou’s evenness
246 index [Epi_J], evenness derived from H [Epi_eve], Simpson’s inverse [Epi_Silnv], Shannon
247 index [Epi_H]) were included in the analyses.

248
249 Additionally, for both ZM and NZN, two correlation plots were created. The first one was
250 created using autumn and winter data, pooling data from both modalities to determine
251 correlations between epifauna, seagrass, and algae. The second one was created using data
252 from all four seasons, pooling data from both modalities to determine correlations between
253 endofauna, seagrass, and algae. These plots were generated using the corrplot package (Wei
254 et al., 2021) in R.

255
256
257 Finally, the significance of correlations between d_{grass} and other biological variables were
258 determined using linear regressions to identify suitable indicators reflecting seagrass efficiency
259 of space occupancy. For this analysis, data for both ZM and NZN were pooled. When
260 correlations for the pooled data were not significant, data were tested separately for ZM and
261 NZN to determine any species-specific correlations. Spearman’s correlation analyses for
262 nonparametric data were performed in R.

263
264 **2.4. Inter-site variability in granulometry and organic matter content**
265 Sediment structure and grain size can significantly influence both seagrass and algal
266 development. To visualize sediment granulometry, bar plots were created. Since single
267 samplings were performed within each modality for summer and winter, only inter-site
268 differences were analysed using pooled data.

269

270 Plots were first generated to assess inter-site differences in the proportions of clay (size 2 to 5
271 μm) and sand (size 5 to 2000 μm) for ZM and NZN meadows (refer to supplementary material).

272

273 In the second analysis, sediment particles for the ZM and NZN meadows were grouped into
274 four size groups based on the Udden–Wentworth grade scale for sediments (Wentworth,
275 1922): 0 to 63 μm (mud fraction), 100 to 250 μm (very fine to fine sand), 400 to 800 μm (medium
276 to coarse sand), and 1000 to 2000 μm (very coarse sand). A PERMANOVA was then
277 performed using the `adonis2` function of the `vegan` package in R to identify inter-site differences
278 in the proportions of sediment size groups. Group dispersions were determined using the
279 `betadisper` function of the `vegan` package in R.

280

281 Organic matter content was also analysed using pooled data from all four seasons due to the
282 lack of replicates. A one-way ANOVA was conducted to determine inter-site differences,
283 followed by a pair-wise Tukey test. Data were tested for normality and homoscedasticity using
284 the Shapiro-Wilk and Bartlett tests, respectively, in R. When data did not meet these criteria,
285 log-transformation was applied.

286

287 **2.5. Stoichiometry of seagrass leaf tissue**

288 In the present study, the percentages of carbon (%C), nitrogen (%N), and molar carbon-to-
289 nitrogen (CN) ratios for the different sites were visualized using box plots to obtain information
290 on nutrient and light conditions. For both ZM and NZN, data were not available for spring and
291 winter 2021. Instead, data from winter 2020 and 2019 for ZM and NZN, respectively, were
292 used. This substitution should be interpreted with caution. For NZN, data were not always
293 available for all sites or seasons.

294 **3. RESULTS**

295 **3.1. Distance of the meadows to the interspecific boundary line**

296 Overall, during the periods of maximum growth (summer and autumn), the d_{grass} values were
297 smaller for the *Nanozostera noltei* (NZN) meadows than for the *Zostera marina* (ZM) meadows.
298 For both ZM and NZN, the d_{grass} values were lowest in spring, summer, or autumn depending
299 on the site and highest in winter (See Fig. 2, Fig. S1), ranging from as low as 1.07 in Modality
300 D of DN during autumn to as high as 2.4 in Modality S of AC during winter for the ZM meadows,
301 and from as low as 0.9 for Modality D of GM (during Autumn) and TH (during summer) to as
302 high as 3.3 in Modality S of AC during winter for the NZN meadows. Clearly, among all sites,
303 both the ZM and the NZN meadows of AC did the worst during winter.

304

305 **3.2. Classification of meadows based on efficiency of space occupation**

306 The ecological status of each modality based on their d_{grass} values is presented in Table 2.
307 Average d_{grass} values and their standard deviations are provided in the supplementary material
308 (Table S1).

309

310 Overall, except for AC, for which only a stable area was defined, the most or the least efficient
311 meadows were found in the dynamic zones rather than the stable. Based on the classification
312 of sites using ordinal scaling, among the ZM meadows, those in DN had the highest efficiency
313 of space occupancy (average score of Modalities S and D = 3.5), followed by AC with a score
314 of 3 and GM with a score of 2. TH had the least efficiency of space occupancy with a score of
315 1.5. Temporally, Modality D of DN performed the best irrespective of season, except for spring,
316 when AC had the highest efficiency among sites. Modality D of TH, on the other hand,
317 performed the worst during all seasons, except for winter, when AC performed the worst.

318

319 Among the NZN meadows, those in TH had the highest efficiency of space occupancy
320 (average score of 3.5), followed by GM with a score of 2.5 and DN with a score of 2. AC had
321 the least efficiency of space occupation with a score of 1. Temporally, Modality D of TH
322 performed the best, irrespective of season, except for autumn, when Modality D of GM
323 performed better. AC performed the worst in spring and winter of 2021, and Modality D of DN
324 performed the worst in summer 2020 and spring 2021.

325

326 Among the ZM meadows, a moderate positive correlation between biomass and density was
327 found for AC. Among the NZN meadows, moderate and strong positive correlations were found
328 for DN and AC, respectively (Fig. S2)

329

330 **3.3. Correlations between d_{grass} and biological variables**

331 **3.3.1. Global patterns in the data**

332 When data from all four seasons were combined, both ZM and NZN meadows showed clear
333 differentiation among sites (Fig. 3).

334

335 For ZM, the first two axes together explained more than 40% of the variability in the data. The
336 first axis, which explained 27% of the variability, separated DN (both Modalities S and D) on
337 the right from TH and GM (both Modalities S and D) on the left. Modality D of DN was
338 characterized by high relative seagrass cover, density, belowground biomass, and high
339 endofauna biomass. Modalities S and D of TH and GM were characterized by a high d_{grass} and
340 endofauna evenness. AC was characterized by a high canopy height, leaf surface area, and
341 number of leaves per shoot. Overall, DN was in a much better ecological state considering the

342 low d_{grass} and high plant growth parameters, whereas TH was the least efficient among the ZM
343 meadows.

344

345 For NZN, the first two axes together explained about 40% of the variability in the data. The first
346 axis, which also explained 27% of the variability, separated Modalities S and D of TH on the
347 right from Modalities S and D of DN and Modality S of AC on the left. Modality D of TH in
348 particular was characterized by a high relative seagrass cover, leaf area index, belowground
349 biomass, aboveground biomass, canopy height, leaf surface area and net primary production.
350 AC and DN were characterized by a high relative bare sediment cover, endofauna density and
351 d_{grass} . Modalities S and D of GM were characterized by a high endofauna species richness,
352 diversity, evenness (J) and inverse Simpson's index. Overall, TH was in a much better
353 ecological state compared with DN and AC, considering its low d_{grass} and high plant growth
354 parameters.

355

356 Season-wise PCA plots are presented in the supplementary data (Fig. S3 to S7).

357

358 **3.3.2. Relationships between epifauna, endofauna, algae and seagrasses**

359 Overall, epifauna and endofauna showed variable patterns in their relationship to seagrasses
360 depending on whether they occupied the ZM or the NZN meadow (Fig. S8 and S9).

361

362 For ZM, epifauna biomass and species richness (SR) tended to be positively associated mainly
363 with algal cover or biomass and with seagrass aboveground biomass but negatively associated
364 with all other seagrass parameters. Epifauna diversity was more strongly associated with
365 relative algal cover than with seagrass growth parameters or relative cover. Endofauna
366 biomass, density and SR, however, tended to be more positively associated with seagrass
367 growth parameters and negatively associated with algal biomass or relative algal cover.

368

369 For NZN, epifauna biomass and density were more positively associated with algal biomass
370 and cover as well as with seagrass leaf area index (LAI) and density. Although weak, epifauna
371 SR tended to be positively associated with algae and negatively with seagrasses. Epifauna
372 diversity was much more associated with seagrass belowground biomass among seagrass
373 growth parameters. The endofauna density and biomass, however, showed an opposite trend,
374 being negatively associated with both seagrasses and algal cover but positively with the
375 relative cover of bare sediments. Endofauna SR, however, was positively associated with
376 seagrass growth parameters but negatively with algae. Endofauna diversity was also much
377 more associated with seagrass aboveground and belowground biomass and seagrass relative
378 cover.

379

380 Ratios of epi- or endofauna biomass to drifting algal biomass can be referred to in the
381 supplementary material (Fig. S10 and S11).

382

383 **3.3.3. Identification of an indicator for seagrass meadow status**

384 When data from both ZM and NZN were pooled, linear regressions revealed that d_{grass} was
385 moderately or strongly negatively correlated with most seagrass growth parameters (SG_AG,
386 SG_BG, SG_density, SG_cover, and SG_LAI) and positively correlated with a few (SG_LSA
387 and SG_LfpSH) (Fig. 4). Canopy height did not exhibit a correlation with d_{grass} .

388

389 In terms of fauna, flux and relative algal cover, no meaningful correlations with d_{grass} were
390 observed when pooled ZM and NZN data were used, except for endofauna density, which
391 showed a moderately negative correlation with d_{grass} ($R = -0.46$, $p < 0.001$). When ZM was
392 studied separately, d_{grass} displayed moderate negative correlations with endofauna density (R
393 $= 0.51$, $p < 0.001$), endofauna biomass ($R = -0.4$, $p = 0.001$), and endofauna species richness
394 (SR) ($R = -0.5$, $p < 0.001$), and positive correlations with endofauna evenness ($R = 0.48$, $p <$
395 0.001) and algal cover ($R = 0.51$, $p < 0.001$). However, these correlations were absent or weak
396 when NZN was studied separately (Fig. S8 and S9).

397

398 Among the parameters strongly negatively correlated with d_{grass} and indicating a better
399 ecological status universally, seagrass cover and leaf area index (LAI) exhibited the highest R
400 values (respectively: $R_s = -0.71$ and -0.79 , $p_s < 0.001$).

401

402 **3.4. Inter-site variability in granulometry**

403 The sediment structure in both the ZM and NZN meadows was predominantly sandy,
404 comprising approximately 90% sand and 10% silt on average. AC exhibited the highest
405 proportion of silt, accounting for approximately 20% of the sediment composition, while TH had
406 the lowest proportion of silt, with only 3.3% for ZM and 1.9% for NZN (Fig. S12).

407

408 Significant differences in grain size distribution were observed between sites (PERMANOVA:
409 ZM meadows, $p = 0.01$; NZN meadows, $p = 0.02$) (Fig. 5). For the ZM meadows, DN was
410 distinct from the other sites, positioned on the negative end of the PC1 axis, while GM, AC,
411 and TH were clustered towards the positive end (Fig. 5). TH and GM, in particular, exhibited a
412 larger proportion of sand particles measuring 1000 to 2000 μm ($>50\%$), whereas AC had a
413 higher proportion of sand measuring 0 to 63 μm ($\sim 40\%$). DN showed a notably higher
414 proportion of sand particles measuring 100 to 250 μm ($\sim 60\%$). These patterns corresponded

415 closely to those observed in the principal component analyses (PCAs), wherein DN exhibited
416 smaller d_{grass} values and appeared separate from the other sites on PC1.

417

418 For the sediment structure in the NZN meadows, DN and AC were positioned on the positive
419 end of PC2 and were more similar to each other, as in the PCAs, where DN and AC displayed
420 large d_{grass} values and overlapped. GM was situated on the positive end of PC1 and the
421 negative end of PC2, while TH fell on the negative end of both PC1 and PC2. Similar to the
422 ZM meadows in DN and AC, the NZN meadows in DN and AC exhibited the highest proportion
423 of sand measuring 100 to 250 μm (~50%) and 0 to 63 μm (~40%), respectively. GM had
424 approximately 50% of sand particles measuring 1000 to 2000 μm (>50%), while TH had around
425 40% of sand particles measuring 100 to 250 μm . Notably, for TH, the sediment structure of the
426 NZN meadows differed significantly from that of the ZM meadows, with sand particles of 1000
427 to 2000 μm contributing to only about 30%.

428

429 Significant differences in organic matter were observed between sites (ZM, $p < 0.05$; NZN, p
430 < 0.001) (Fig. S13). In the ZM meadows, DN had a significantly lower organic matter content
431 compared to GM. In the NZN meadows, DN and TH had significantly lower organic matter
432 content compared to GM and AC. Additionally, the organic matter content in TH differed
433 significantly from that in DN.

434

435 **3.5. Stoichiometry of ZM**

436 The % carbon in the ZM meadows ranged from 33.7% (GM_S, Summer) to 40.6% (AC,
437 Summer) and the % nitrogen ranged from 1.6% (GM_S, Autumn) to 3.2% (TH_S, Summer)
438 (Table S2). In the NZN meadows, the % carbon ranged from 35.2% (TH_C, Summer) to 43.2%
439 (TH_D, Autumn), and the % nitrogen ranged from 1.5% (TH_S, Summer) to 3.6% (DN_D_
440 Summer). Among all the ZM meadows, those in TH, particularly Modality S, had CN ratios less
441 than 15 in summer and autumn. However, in winter 2020, TH had a CN of 25. Among all the
442 NZN meadows, those in DN, specifically Modality D, had CN ratios less than 15 in summer. In
443 all cases, the CN ratios less than 15 were driven by nitrogen content higher than 3%.

444

445 **4. DISCUSSION**

446

447 **4.1. Seagrass efficiencies of space occupancy**

448 The present study, conducted within the Life MarHa project, focused on establishing an
449 ecological indicator for seagrass meadows using data collected from samplings along the
450 English Channel and the Atlantic and Mediterranean coasts. The distance of the meadows to
451 the interspecific boundary line, derived from the biomass-density relationship of the most

452 efficient plants worldwide (Vieira et al., 2018), served as a reference. This approach aimed to
453 identify a suitable ecological indicator and to classify sites based on their ecological status.

454

455 Our study provides valuable insight into the ecological status of the seagrass meadows along
456 the coast of France and underscores the significance of d_{grass} as a reference for overall
457 seagrass health. The higher efficiency of space occupancy of *Nanozostera noltei* (NZN)
458 compared to *Zostera marina* (ZM) during autumn aligns with previous research by Vieira et al.
459 (2018). However, the larger d_{grass} values in our study compared to those of the most efficient
460 plants worldwide suggest that the studied seagrass meadows may be operating below their
461 carrying capacity.

462

463 The observation of a phalanx growth form, specific to environments with high hydrodynamic
464 conditions, in the ZM meadows of Dinard supports the findings of Boyé et al. (2022). Further,
465 the phalanx growth form coincided with a smaller d_{grass} , similar to (Vieira et al., 2018),
466 suggesting a good ecological status. The comparable efficiencies of space occupancy in the
467 dynamic and stable ZM meadows of Dinard, despite their significantly different biomasses and
468 densities in spring (Lacoste et al., 2023b) highlight the limitations of using individual growth
469 parameters as ecological indicators.

470

471 The positive correlations between biomass and density observed in sites with higher nutrient
472 content support the findings of Cabaço et al. (2007), reflecting disturbed environments. The
473 contrasting states of the ZM and NZN meadows in Thau further emphasize species-specific
474 responses to similar environmental conditions, with NZN demonstrating better overall
475 efficiencies.

476

477 The large d_{grass} values observed in the ZM meadow of Thau and the NZN meadows of
478 Arcachon and Dinard suggest their low ecological status, and underscore the importance of
479 environmental factors such as nutrient and light stress, sediment structure, temperature, and
480 competition with other species and algae in influencing seagrass health. Further exploration
481 and characterization of these environmental factors are crucial for a comprehensive
482 understanding of seagrass ecosystem dynamics and management.

483

484 Our analysis of the traits inversely correlated with d_{grass} provides valuable insights into suitable
485 indicators for seagrass meadow health. The findings suggest that LAI and relative seagrass
486 cover are more reflective of ecological status compared to aboveground biomass and density.
487 The potential of using simpler and less labour-intensive metrics such as seagrass cover, which

488 can be easily measured visually or through photo documentation by fieldworkers (see Lacoste
489 et al., 2023b), is highlighted.

490

491 LAI, aka canopy density, holds particular promise as an indicator due to its correlation with
492 both shoot density and aboveground biomass (Lebrasse et al., 2022). While its calculation may
493 pose some challenges, especially for submerged species, advancements in non-destructive
494 measurement methods, such as remote sensing using hyperspectral data, offer promising
495 avenues for its assessment (Chen et al., 2020; Hedley et al., 2017; Zheng & Moskal, 2009).

496

497

498 4.2. **Environmental factors affecting efficiency of space occupancy**

499 Vieira et al. (2018) showed that ZM, in particular, preferred the lower intertidal. This is in
500 contrast to observations in Dinard, where, due to the large tidal range, ZM has expanded
501 towards the upper intertidal and showed high efficiencies of space occupancy.

502 The co-occurrence of intertidal and subtidal species may hinder the extension of one species
503 into the habitat preferred by the other (Kim et al., 2020). In Bay du Prieuré of Dinard, the
504 absence of NZN appears to have facilitated the expansion of ZM into the upper intertidal.

505

506 Efficiencies of space occupancy generally decrease with depth, with ZM and NZN showing
507 higher efficiencies in shallower waters (Vieira et al., 2018). Despite the relatively shallow depth
508 (3 to 4 m below the mean sea level), the majority of ZM meadows exhibited d_{grass} values of 1.5
509 or higher, indicating reduced efficiency of space occupancy. Additionally, among both ZM and
510 NZN meadows, sites had d_{grass} values ranging from ~ 1 to greater than 2, depending on the
511 season. Depth was therefore not a significant factor contributing to differences in efficiencies
512 of space occupancy among the study sites.

513

514 Tidal regime also did not seem to significantly influence efficiency of space occupancy, as sites
515 with different tidal regimes displayed comparatively higher efficiencies depending on the
516 season. This underscores the complex interplay of various factors, including species
517 interactions, habitat availability, and environmental conditions and pressures, in determining
518 seagrass distribution and occupancy patterns.

519

520 The sediment structure appears to have played a significant role in shaping seagrass growth
521 and efficiency of space occupancy across the study sites. The higher proportion of fine sand
522 particles in Dinard may have contributed to reduced competition from algae, resulting in the
523 lower relative algal cover (Cahoon et al., 1999; Dalu et al., 2020). Conversely, in the ZM

524 meadows of both Thau and Gulf of Morbihan, the lower proportion of fine sand particles may
525 have facilitated colonization and competition by algae (Cahoon et al., 1999).

526

527 Although in the present study, environmental data were not available at the modality level,
528 plant stoichiometry, particularly carbon-to-nitrogen (CN) ratios, provided valuable insight into
529 nutrient and light conditions as well as seagrass quality (Duarte, 1990; Soissons et al., 2018).
530 Lower CN ratios suggest higher tissue nutrient concentrations, potentially rendering seagrass
531 leaf tissue more edible to consumers and indicating nutrient enrichment. Based on the
532 literature, %C less than 35 and %N greater than 3 suggest nutrient or light stress (Jones &
533 Unsworth, 2016; McMahon et al., 2013). Additionally, CN ratios below 20 are indicative of
534 reduced light environments, while ratios of 15 and below suggest light limitation (McKenzie et
535 al., 2012; McMahon et al., 2013).

536

537 The low CN ratios observed in the stable ZM meadow of Thau, along with the low efficiency of
538 space occupancy in the dynamic meadow, suggest a critical state for the entire ZM meadow.
539 Similarly, despite low competition with benthic algae in the NZN meadows of Dinard, low CN
540 ratios in the dynamic area suggest nutrient or light stress, indicating a critical state for this
541 meadow (Fourqurean et al., 1997; Jones & Unsworth, 2016). Shading by epiphytic algae may
542 have contributed to this stress.

543

544 The NZN meadow in Dinard exhibited high fluxes of ammonium NH_4 and phosphate PO_4 ,
545 further indicating nutrient enrichment. However, except for the CN ratio below 15 in the NZN
546 meadow of Dinard during summer, no clear patterns associating CN ratios with seagrass
547 efficiency of space occupancy were evident. This suggests that factors beyond light or nutrient
548 availability likely influence space occupancy efficiency.

549

550 In both the ZM meadow of Dinard and the NZN meadow of Thau, smaller d_{grass} values, larger
551 leaf area index (LAI), and CN ratios close to 20 across all seasons suggest an overall good
552 status and low nutrient and light stress. These meadows are likely not close to tipping points.
553 Compared to the ZM meadow in Thau, which had a high relative cover of algae and a low
554 efficiency of space occupancy, the NZN meadow of Thau had a low relative algal cover and a
555 high efficiency of space occupancy. The NZN meadow of Thau, in fact, also had a high algal
556 biomass, suggesting that efficiency of space occupancy is affected more by relative algal cover
557 than by drifting algal biomass in certain contexts.

558

559 The effect of environmental parameters on plant growth traits at the inter-site level has been
560 discussed in detail in Lacoste et al. (2023a). The strong correlation observed between leaf

561 area index (LAI) and d_{grass} in the present study suggests that LAI can serve as a proxy for d_{grass} .
562 LAI was found to be predominantly explained by water temperature (Figure 7 in Lacoste et al.,
563 2003a) across both ZM and NZN meadows, indicating that temperature is a key factor driving
564 seagrass efficiency of space occupancy, with higher temperatures being more favourable.

565
566 It is important to contextualize these findings within the temperature range observed in the
567 study area. The highest average temperature recorded was 24°C, which falls within the optimal
568 range for seagrasses. For temperate species like ZM, the optimal temperature range is
569 typically between 11.5°C and 26°C (Lee et al., 2007). The effects of temperature on LAI may
570 vary outside of this optimum range, potentially impacting seagrass efficiency differently (Sordo
571 et al., 2011).

572
573 The seasonal variations observed among seagrass species and sites further highlight the
574 importance of the period during which monitoring is carried out. Autumn is generally considered
575 the period of maximum growth and spring the period of minimum growth. Sampling programs
576 and experimental studies choose either the period of maximum growth (e.g., (Vieira et al.,
577 2018)) or the period of minimum growth to avoid the influence of seasonal variability (e.g. (Boyé
578 et al., 2022; Martínez-Crego et al., 2008; Moore & Short, 2006)). However, our study shows
579 that the same species can show seasonal variations in their efficiencies of space occupancy,
580 depending on the site. For example, compared with that of other sites, the low efficiency of
581 space occupancy of ZM in Arcachon and the high efficiency in spring may be a result of the
582 combined low salinity and high nitrogen content inducing competition with phytoplankton
583 (Lacoste et al., 2023b). Additionally, other seasonal pressures and environmental conditions
584 may contribute to such differences. These strong temporal variabilities among species, and
585 sites, stress the importance of determining site-specific characteristics in order to provide
586 suitable advice for management.

587 588 **4.3. Effect of habitat type on community structure**

589 Results from recent studies, such as those by Millot et al. (2023), emphasize the importance
590 of considering habitat structure, such as seagrass biomass, density, and leaf characteristics,
591 in relation to associated faunal communities for effective management effort. While shoot
592 density has traditionally been used as a proxy for seagrass ecological status, Millot et al. (2023)
593 suggest aboveground biomass as a better indicator due to its association with higher diversity
594 of both endofauna and epifauna.

595
596 In our study, specific associations between plant metrics and epifauna or endofauna
597 abundance (density or biomass), species richness (SR), and diversity were observed,

598 depending on the seagrass species inhabited. Such species-related differences in associated
599 communities has not, to the best of our knowledge, been described before. The stronger
600 association of epifauna with algae (relative cover and pooled biomass), however, has
601 previously been shown (Correia et al., 2022; Rodil et al., 2021).

602
603 The association of SR and abundance of both endofauna and epifauna with AG in the ZM
604 meadows is in line with (Millot et al., 2024). While endofauna are conventionally not thought to
605 be associated with seagrass aboveground biomass, the direct link observed between these
606 two compartments in (Millot et al., 2024) and the strong associations between seagrass growth
607 parameters and endofauna in our study suggest that endofauna are in fact associated with
608 seagrass shoot biomass.

609
610 Such links are pertinent, considering that high biomass can contribute to organic matter content
611 in the soils, which in turn can provide nutrients for endofauna. Contrary to these observations
612 for ZM, however, our study showed that AG was not strongly associated with epifauna in the
613 NZN meadows, highlighting the importance of taking into account species-specific differences
614 of associated communities.

615
616 The positive correlation of LAI with endofauna in the ZM meadows and with epifauna in the
617 NZN meadows highlight the importance and uniqueness of this parameter for consideration in
618 future monitoring and management programs.

619
620

621 4.4. Management of seagrass meadows

622 Seagrass meadows are highly complex ecosystems supporting a large biodiversity. While
623 individual and easy-to-measure indicators for overall seagrass status are being sought, our
624 study highlights the challenges of identifying such an indicator for management and the
625 importance of defining the goal of the management effort. The challenges are evident from the
626 significant inter-site differences observed in seagrass morphometric traits (see Table S3).

627
628 Additionally, an indicator for seagrass status may not be a suitable indicator for overall
629 ecosystem function. Faunal biodiversity, for example, may not sufficiently describe seagrass
630 status, and vice versa. Our study, as well as those by (Rodil et al. (2021) and (Correia et al.
631 (2022), suggest that algae are important structuring habitats for fauna, likely more than
632 seagrasses.

633

634 Conservation methods that aim to protect associated communities should, therefore, consider
635 natural drifting algae as part of the ecosystem process. However, drifting algae and relative
636 algal cover are both harmful to seagrasses as they compete for light and resources. Each
637 management program should, therefore, clearly define the goal and the target
638 species/community to be conserved, and all management programs should work in concert to
639 provide overall ecosystem protection.

640
641 Conservation efforts should also account for seagrass-specific ecosystem structures, as
642 meadows with high endofauna biomass may have relatively lower epifauna abundance and
643 vice versa through competition for resources (Schrijvers et al., 1996), especially when ZM and
644 NZN co-occur. Furthermore, deriving meadow- or habitat-specific indicators for ecosystem
645 function can provide valuable insight into seagrass ecological status and inform effective
646 management practices.

647
648 While relative cover and LAI were identified as suitable indicators for seagrass meadow health,
649 it is essential to exercise caution in interpreting these indicators, particularly in the context of
650 management strategies. Previous studies have shown that indicators such as standing stock
651 LAI that reflect a healthier meadow also correlated inversely with meadow resilience, requiring
652 more extreme management measures following disturbances (Soissons et al., 2014).

653
654 The importance of understanding the relationship between indicator metrics and ecosystem
655 resilience is, therefore, highlighted. In Soissons et al. (2014), recovery was measured after
656 mowing circular gaps of 0.5 m of aboveground biomass and removing them from the meadow.
657 The study's findings suggest that meadows with higher carbon stocks may require more
658 extensive recovery efforts following disturbances compared to those with lower biomass.

659
660 Indicators such as relative cover and LAI should, therefore, always be used alongside
661 comprehensive descriptions of environmental pressures to inform effective management
662 strategies for seagrass ecosystems.

663 664 **5. CONCLUSION**

665 The current study proposes efficiency of space occupancy as a key reference for selecting
666 ecological indicators for seagrass meadows. Seagrass relative cover and leaf area index (LAI)
667 were identified as strong correlates of efficiency of space occupancy and are suggested as
668 efficient metrics for assessing meadow status, surpassing traditional metrics such as shoot
669 biomass and density. However, it is emphasized that these indicators not be used in isolation
670 but be complemented with thorough environmental characterization.

671

672 Sediment structure and temperature, as well as nutrient status and light, were identified as
673 crucial factors influencing seagrass efficiency of space occupancy. Therefore, conservation
674 effort must consider these environmental parameters to better understand potential declines
675 in seagrass status.

676

677 The associations between epifauna in NZN meadows and endofauna in ZM meadows with LAI
678 highlight the importance of this metric as an ecological indicator. While relative cover and LAI
679 were found to be meaningful indicators for both ZM and NZN, the distinct characteristics and
680 environmental preferences of these seagrass species require species- and meadow-specific
681 conservation efforts.

682

683 The species-specific associations between fauna and seagrass growth traits highlight the need
684 for habitat-specific indicators, particularly when conservation of biodiversity is the primary
685 objective. Future research within the project will focus on evaluating environmental stressors
686 such as fishing pressure, pesticides, eutrophication, and meadow fragmentation to assess the
687 conservation status of these meadows and compare against seagrass efficiencies of space
688 occupancy. This holistic approach will provide valuable insight for the effective management
689 and conservation of seagrass ecosystems.

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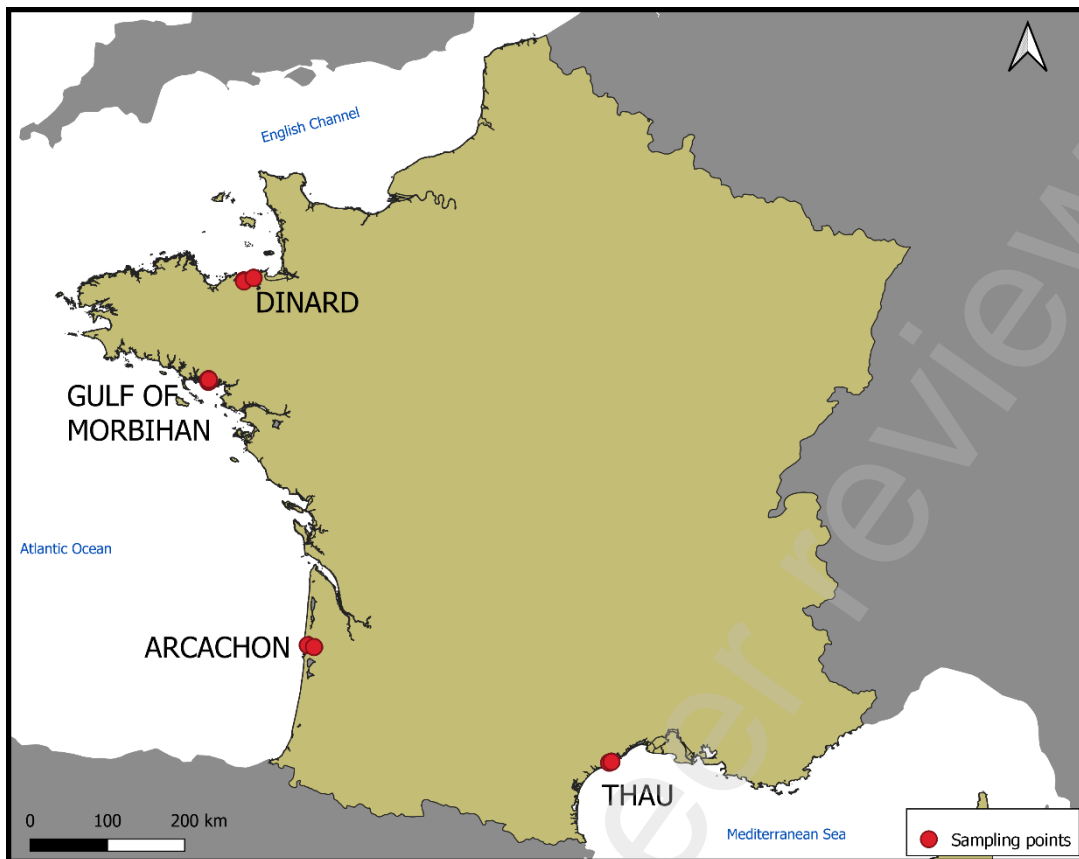
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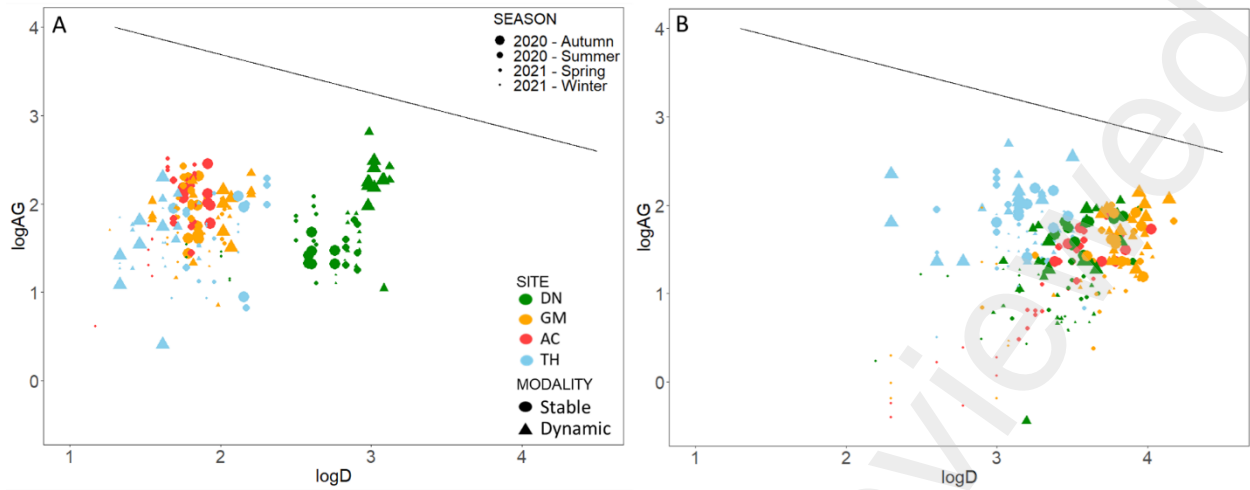
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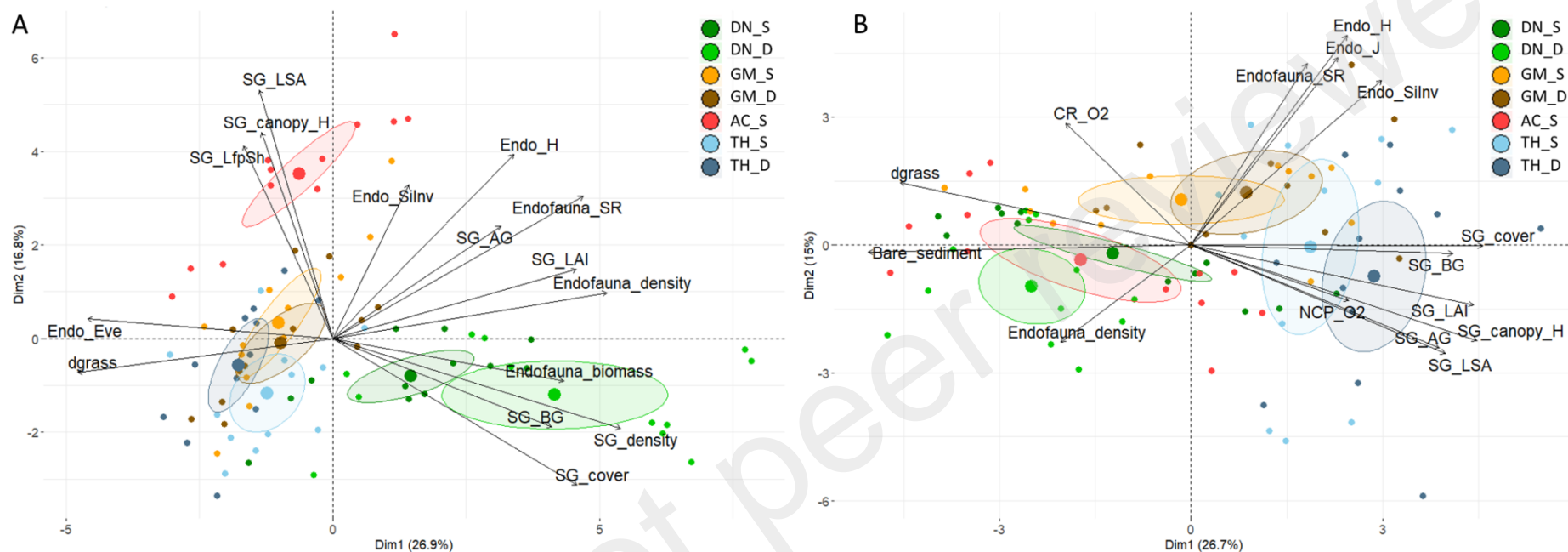
869 Fig. 1. Location of samplings within the framework of MarHa: Dinard (DN), Gulf of Morbihan
870 (GM), Arcachon (AC) and Thau (TH).



871 *Fig. 2. Position of seagrass meadows in relation to the interspecific boundary line (Vieira et al.,*
 872 *2018). Data are from summer and autumn 2020 and spring and winter 2021. A: Zostera*
 873 *marina, B: Nanozostera noltei. (DN: Dinard, GM: Morbihan, AC: Arcachon, TH: Thau).*

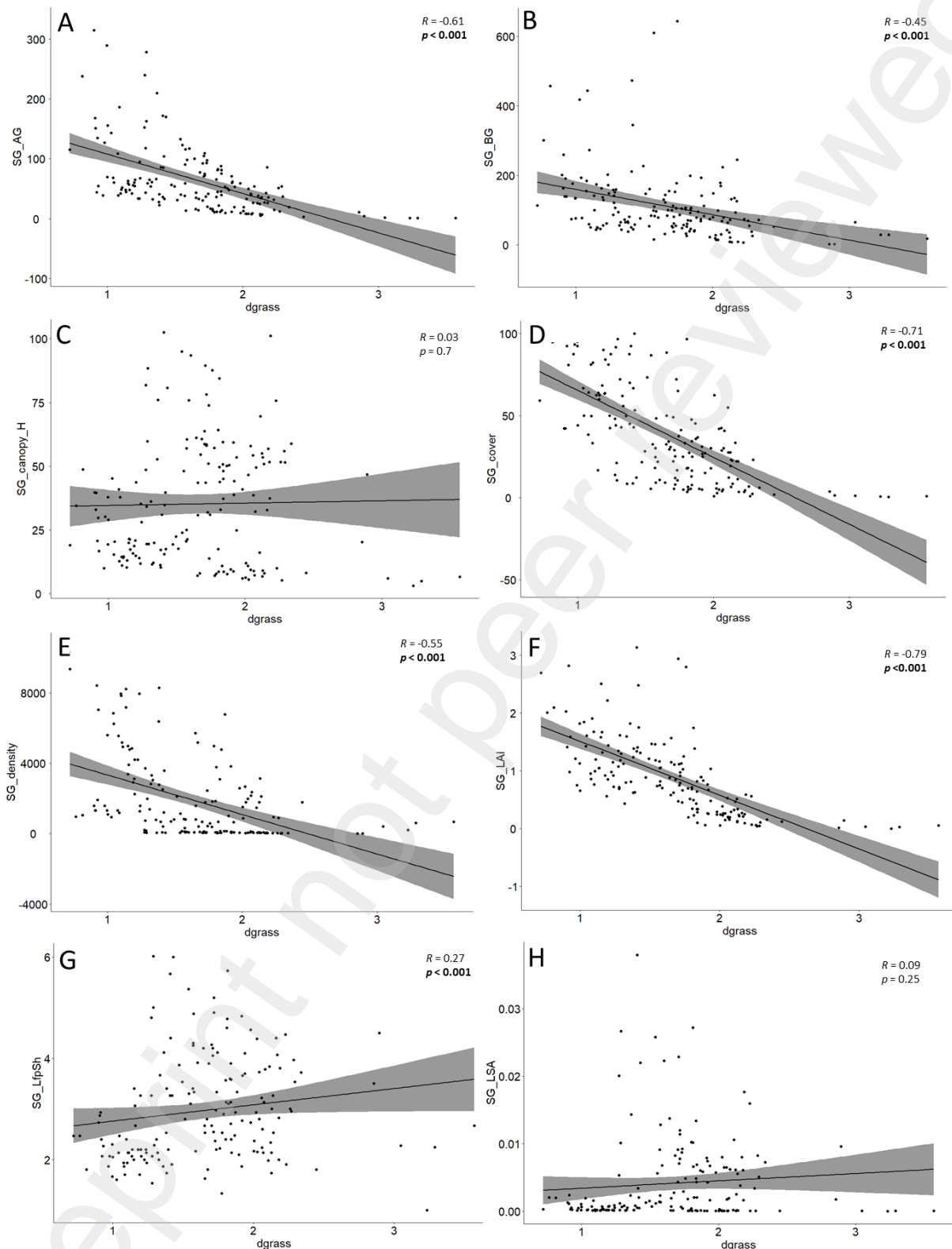
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877 Fig. 3. Principal components analyses (PCA) using data pooled from four seasons (summer and autumn 2020 and spring and winter 2021)
 878 performed for (A) *Zostera marina* and (B) *Nanozostera noltei* (DN: Dinard, GM: Morbihan, AC: Arcachon, TH: Thau ; S: Stable, D: Dynamic).
 879 Analyses were performed using distance of seagrass stands to the interspecific boundary line (d_{grass}), seagrass growth parameters (aboveground
 880 biomass [SG_AG], belowground biomass [SG_BG], density [SG_density], leaf area index [SG_LAI], seagrass canopy height [SG_canopy_H],
 881 seagrass relative cover [SG_cover], number of leaves per shoot [SG_LfPsh], and average leaf surface area [SG_LSA]), endofaunal biomass,
 882 density and diversity indices (species richness [SR], Pielou's evenness index [J], evenness derived from H [eve], Simpson's inverse [Silnv],
 883 Shannon index [H]), and carbon and nutrient fluxes (CR_O2, NCP_O2, fNH4, fPO4). Only the top 15 variables contributing to the variability are
 884 projected.

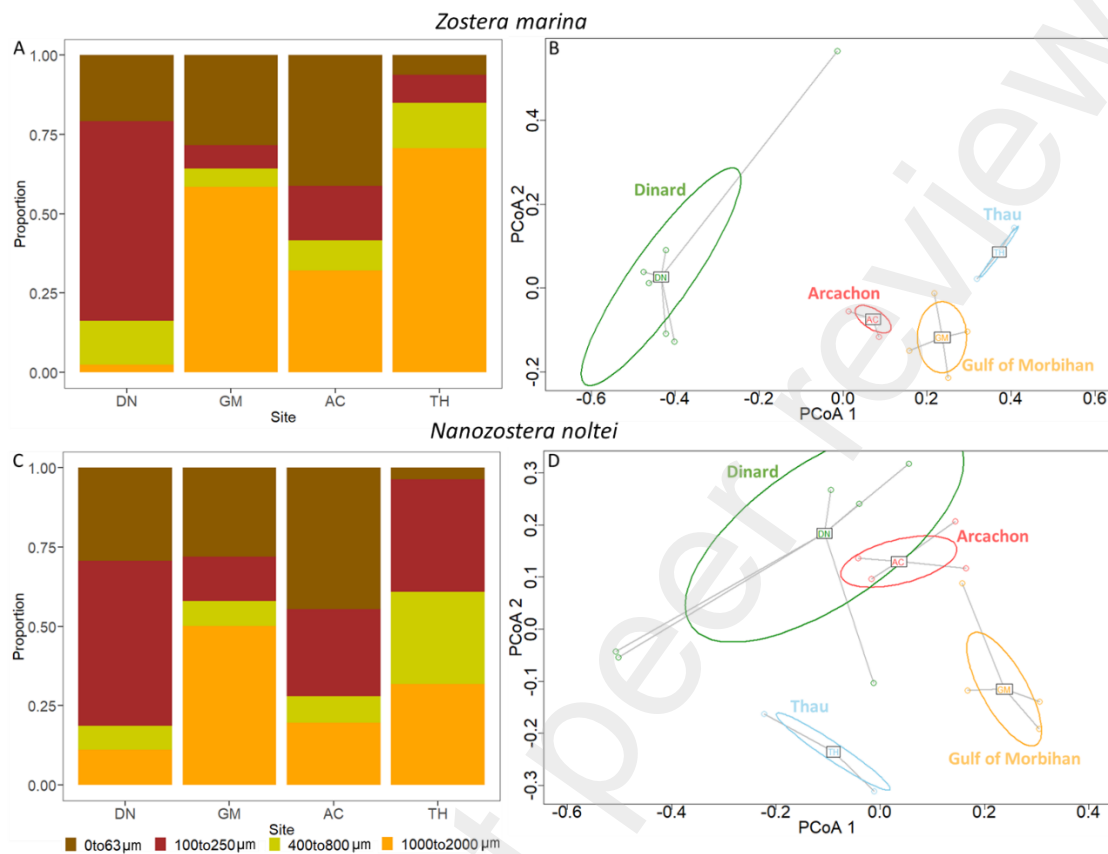


886 Fig. 4. Linear regressions using d_{grass} as the explanatory variable and plant growth parameters
 887 as the response (A: aboveground biomass [SG_{AG}], B: belowground biomass [SG_{BG}], C:
 888 canopy height [SG_{canopy_H}], D: cover [SG_{cover}], E: density [$SG_{density}$], F: leaf area

889 index [SG_LAI], number of leaves per shoot [SG_LfpSh], leaf surface area [LSA]). Analyses
890 are performed using data from both seagrass species, all sites, modalities and seasons.

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894 Fig. 5. Inter-site variability in sediment granulometry. A and C: Stacked barplots showing
895 distributions of different grain size groups for *Zostera marina* and *Nanozostera noltei*,
896 respectively. B and D: Dispersion plots showing inter-site differences in size structure of the
897 sediment. Data are available only for summer and winter. Because of the insufficient number
898 of replicates, data from all seasons and modalities (stable, dynamic and absence, (Lacoste et
899 al., 2023b)) were grouped together in the analyses.

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Table 1. Classification system of sites based on ordinal scaling of d_{grass} (ZM: *Zostera marina*, NZN: *Nanozostera noltei*)

ZM	4	3	2	1
All seasons	<1.51	1.51 to 1.8	1.8 to 2.02	>2.02
Summer 2020	<1.37	1.37 to 1.56	1.56 to 1.76	>1.76
Autumn 2020	<1.48	1.48 to 1.71	1.71 to 1.93	>1.93
Spring 2021	<1.41	1.41 to 1.70	1.70 to 2.0	>2.0
Winter 2021	<1.94	1.94 to 2.1	2.1 to 2.26	>2.26
NZN	4	3	2	1
All seasons	<1.23	1.23 to 1.55	1.55 to 1.9	>1.87
Summer 2020	<1.0	1.0 to 1.2	1.2 to 1.4	>1.39
Autumn 2020	<1.0	1.0 to 1.13	1.13 to 1.25	>1.25
Spring 2021	<1.55	1.55 to 1.8	1.8 to 1.97	>1.97
Winter 2021	<1.8	1.8 to 2.19	2.19 to 2.57	>2.57

913 **Note:** 4 = maximum ecological status, 3 = moderate ecological status, 2 = low ecological
914 status, 1 = minimum ecological status.

915 Table 2. Classification of meadows based on their efficiency of space occupancy (ZM: *Zostera*
916 *marina*, NZN: *Nanozostera noltei*; S: Stable, D: Dynamic)

ZM	DN		GM		AC	TH	
	S	D	S	D	S	S	D
All seasons	3	4	2	2	3	2	1
Summer 2020	2	4	3	2	2	2	1
Autumn 2020	2	4	2	2	3	2	1
Spring 2021	3	3	3	2	4	1	1
Winter 2021	2	4	2	3	1	3	2
NZN	DN		GM		AC	TH	
	S	D	S	D	S	S	D
All seasons	2	2	2	3	1	3	4
Summer 2020	3	1	3	3	2	3	4
Autumn 2020	2	2	2	4	2	2	3

Spring 2021	2	1	2	3	1	3	4
Winter 2021	2	3	2	3	1	3	4

917 **Note:** 4 = maximum ecological status, 3 = moderate ecological status, 2 = low ecological
918 status, 1 = minimum ecological status.

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