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**Drastic changes in tidal hydrodynamics following seagrass decline
and their seasonal variations in a shallow lagoon**

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18 **Abstract**

19 Seagrass meadows modify the flow structure and attenuate current velocities. Over the past
20 decades, seagrasses have drastically declined worldwide, reducing their capacity to regulate
21 flow conditions. Intertidal species have been particularly affected by this decline, yet there is
22 a lack of understanding regarding the influence of intertidal seagrass decline on the
23 hydrodynamics of shallow coastal lagoons. In this study we use a 3D flow-vegetation model
24 that accounts for the full effect of vegetation on mean and turbulent flow, as well as the action
25 of the flow on leaf bending, to study how tidal hydrodynamics respond to the seasonal and
26 multi-decadal changes in intertidal seagrass characteristics at a regional scale. The model is
27 applied to the Arcachon lagoon (France), which is colonized by extensive *Zostera* meadows
28 (*Zostera marina* and *Zostera noltei*). This study reveals that a short-leaf and flexible seagrass
29 species such as *Z. noltei* can regulate tidal hydrodynamics throughout the lagoon due to the
30 presence of broad and dense meadows on the tidal flats. In summer, seagrass decline leads to
31 a significant increase in flow velocities (+100%) on the tidal flats, but to a decrease in the
32 channels (-20%). However, in winter, the response of tidal hydrodynamics to the reduction in
33 seagrass coverage is far less pronounced. Comparison of various simulated scenarios reveals
34 that the multi-decadal decline of *Zostera* spp. with summer characteristics and the seasonal
35 loss between summer and winter lead to modifications in tidal flow parameters (current
36 velocities, tidal asymmetry, high tide water level) of comparable intensity.

37

38 **Keywords:** Tidal hydrodynamics, Seagrass decline, *Zostera* meadows, Coastal lagoons,
39 Numerical modeling, Arcachon lagoon

40

41 **1 Introduction**

42 Seagrasses have been recognized as effective buffers against physical stresses in many coastal
43 areas due to the protective services they provide to their ecosystem. They regulate
44 sedimentation and erosion processes, promoting deposition and mitigating the resuspension of
45 freshly deposited sediment thanks to their foliage, which effectively dampens hydrodynamic
46 energy (Ward *et al.*, 1984; Ganthy *et al.*, 2015). Additionally, their root system contributes to
47 seafloor stabilization and further limits sediment erosion (Hemminga and Duarte, 2000;
48 Ganthy *et al.*, 2011). Through these mechanisms, seagrass meadows affect seabed elevation
49 (Potouroglou *et al.*, 2017), mitigate erosion risks of the densely populated coastlines and
50 ensure the safety of the navigation by limiting the infilling of channels.

51 As current flows through vegetation, hydrodynamic drag resistance is exerted and turbulence
52 is generated, extracting momentum from the fluid (Gambi *et al.*, 1990; Lefebvre *et al.*, 2010;
53 Gao *et al.*, 2011). These processes result in the dissipation of wave energy (Anderson *et al.*,
54 2011) and the reduction of flow velocities (Peterson *et al.*, 2004), providing significant flood
55 risk mitigation services (Temmerman *et al.*, 2013). The drag force induced by vegetation is
56 highly dependent on the seagrass meadow characteristics (van Rooijen *et al.*, 2018) such as
57 leaf density (Fonseca and Cahalan, 1992; Nepf 1999; Koch and Gust, 1999; Abdelrhmann,
58 2003; Lefebvre *et al.*, 2010), leaf width (Nepf 1999; Abdelrhman, 2003), leaf length or
59 submergence ratio (Bouma *et al.*, 2005) and stiffness (Ghisalberti and Nepf, 2006).

60 Seagrass characteristics undergo perpetual changes, occurring at seasonal and multi-decadal
61 time scales. Marine phanerogams can experience strong seasonal variations throughout the
62 year (Auby and Labourg 1996), which have been shown to significantly affect current
63 velocities (Hansen and Reidenbach 2013; Kombiadou *et al.*, 2014; Moki *et al.*, 2020).

64 Seagrasses have also undergone severe loss worldwide, intensifying since 1990 (Orth *et al.*,
65 2006; Waycott *et al.*, 2009), to the extent that seagrass decline has been identified as one of
66 the most important decline on the planet (Orth *et al.*, 2006; Waycott *et al.*, 2009). Studies
67 focusing on the effects of vegetation loss on tidal flow (Vu *et al.*, 2017; Donatelli *et al.*, 2018;
68 Zhang *et al.*, 2019) have pointed out major changes in bottom shear stress and flow velocities.
69 Although seasonality and decline have concurrently affected the above-ground biomass and
70 impacted hydrodynamic conditions, the previous analysis only focused on one of these two
71 aspects. To the author's knowledge, due of the paucity of data regarding either the seasonal or
72 multi-decadal evolutions of the meadows at the study sites in previous research, the impacts
73 of seasonal changes and long term decline on tidal hydrodynamics have never been compared

74 at the scale of a coastal system. This study aims to bridge that gap. Considering the large
75 spatial and temporal scales at which these processes occur, numerical modeling appears to be
76 an efficient tool to perform such a study.

77 The Arcachon lagoon (France) shelters Europe's largest *Zostera noltei* meadow (Auby and
78 Labourg, 1996), which has been subject to comprehensive monitoring over the last 30 years
79 (Auby and Labourg, 1996; Ganthy *et al.*, 2013; Cognat *et al.*, 2018). This extensive dataset
80 encompasses both the seasonality of *Zostera* spp. and their decline that occurred during the
81 past three decades (Plus *et al.*, 2010). These data are used to force a 3D hydrodynamic model
82 and to conduct a scenario analysis, comparing two different states of the meadow (its pre-
83 decline and post-decline spatial extents) at two different seasons (summer and winter). This
84 work aims to address two main issues: (I) What is the relative impact of seasonal changes and
85 seagrass decline on tidal hydrodynamics? (II) How does the seasonal cycle of development of
86 the meadows affect the response of tidal hydrodynamics to seagrass decline?

87

88 **2 Study Area**

89 The Arcachon lagoon is a 174 km²-wide meso- to macro-tidal coastal lagoon located on the
90 French South–West coast (Figure 1). The lagoon is composed of a network of main,
91 secondary and inner channels separated by wide intertidal flats that occupy around 70 % of its
92 surface, namely 117 km². The tidal regime is semi-diurnal, with a tidal range varying from 0.8
93 m during neap tides to 4.6 m during spring tides. The Cap Ferret spit (Figure 1) acts as a
94 natural border between the lagoon and the open ocean. They are connected at the mouth
95 through two main channels, separated by the Arguin Bank (Figure 1). The sandy shoals and
96 banks prevent swell waves from entering the lagoon.

97 The lagoon is extensively colonized by *Zostera* meadows, i.e. *Zostera marina*, located along
98 the edges of the channels in the subtidal zone, and *Z. noltei*, which is found on the tidal flats
99 within the intertidal zone. Together, they covered around 40 % of the lagoon's surface in
100 1989. In this environment, *Z. noltei* follow an annual unimodal cycle (Auby and Labourg,
101 1996), with shoot density and above-ground biomass reaching their maximum during the
102 summer (maximum biomass is comprised between 110 and 150 g_{DW}.m⁻²) and their minimum
103 during the winter (minimum biomass varies between 40 and 80 g_{DW}.m⁻²), while shoot length
104 reaches a maximum at the end of summer or autumn (up to 20 cm) and a minimum in spring
105 (6 to 10 cm; Auby and Labourg, 1996). *Zostera* spp. have undergone a severe decline in the

106 Arcachon lagoon since 1988. The surface occupied by *Z. noltei* decreased by 33 % between
107 1989 and 2007, its spatial extent going from 68.5 km² to 45.7 km², while *Z. marina* decreased
108 by 74 % between 1988 and 2008, whose extent dropped from 3.7 km² to 1.0 km² (Plus *et al.*
109 2010).

110 The Arcachon lagoon also shelters high biodiversity, supporting fishing and shellfish farming
111 activities. Specifically, the lagoon is a hotspot for oyster production, with oyster farms
112 scattered in the lagoon and covering 7 % of the lagoon's surface, along with wild oyster reefs
113 colonizing another 3 %.

114

115 *Location for Figure 1*

116

117 **3 Methods**

118 **3.1 Model description**

119 MARS3D (Model for Applications at Regional Scale; Lazure and Dumas, 2008) is a 3D
120 hydrodynamic modeling software developed by IFREMER. The model solves the Navier-
121 Stokes equations under hydrostatic and Boussinesq hypothesis, using a finite difference
122 method with an Arakawa C-grid (Arakawa and Lamb, 1977) for the horizontal plane
123 associated with a vertical discretization of the water column using σ -coordinates. To prevent
124 vertical layers from becoming too thin in very shallow water, 3D computations are stopped
125 under a user-defined threshold of water level set as 0.75 m. Under this threshold, current
126 velocities are computed using the law of the wall. A wetting and drying scheme based on the
127 Flux Corrected Transport method (FCT) is also implemented in the model (Dumas and
128 Langlois, 2009), making the model suitable for application in an intertidal environment, such
129 as the Arcachon lagoon.

130 A new vegetation – flow module (so-called OBSTRUCTIONS module) was developed
131 (Kombiadou *et al.*, 2014) and recently improved (Ganthy *et al.*, Submitted) to account for the
132 influence of vegetation on the 3D flow. The action of vegetation on the flow is considered
133 through a loss of momentum, a production of turbulent kinetic energy and dissipation of
134 turbulence, represented as a sink term in the momentum equation and a source and sink term
135 in the $k - \varepsilon$ turbulence closure scheme, respectively.

136 The improvement of this module lies in representing the feedback between flow and leaf
137 bending, as described in Abdelrhman *et al.* (2007). The deflection of seagrass leaves under the
138 flow action, along with the subsequent changes induced by leaf bending on the structure of
139 the flow are both taken into account. For this purpose, each seagrass leaf is segmented, and a
140 force balance equation, accounting for drag, lift, weight and buoyancy forces, is applied on
141 each segment. Leaf bending is then computed solving the force balance equation iteratively
142 for each segment until the leaf height converges. Moreover, this module is able to consider
143 vertically varying leaf density and the presence of multiple vegetative species within a grid
144 cell, in agreement with Weitzman *et al.* (2015) who showed that it is fundamental to account
145 for primary as well as secondary vegetative species when studying the effects of vegetation on
146 hydrodynamics.

147

148 **3.2 Model application to the study site**

149 The MARS3D model uses nested grids with an increasing spatial resolution. The largest grid,
150 hereafter referred to as Rank-0, contains 3 sub-grids, namely Rank-1, 2 and 3; Rank-3 being
151 the finest and smallest grid. Rank-0 spreads from Lisbon (in the south) to Iceland (in the
152 north-west) and to Denmark (in the east), with a spatial resolution of 2500 meters. A tidal
153 forcing is used at the boundaries of the Rank-0 grid, based on the empirical tide solution
154 FES2012 (Carrère *et al.*, 2013). Rank-1 spreads from Parentis-en-Born (44.35 °N; -1.07 °W)
155 in the south, to Hourtins in the north (45.19°N; -1.06°W), with a 500-meter spatial resolution.
156 Rank-2 has a spatial resolution of 235 meters and includes the Arcachon lagoon and the near
157 open ocean up to a depth of around 50 meters. Rank-3 has a spatial resolution of 65 meters
158 and corresponds to a close zoom of the Arcachon lagoon.

159 Rank-0, 1 and 2 are simulated in 2D, but 3D modeling is adopted for Rank-3, in which case
160 the vertical dimension is subdivided into 15 layers. Note that vegetation is only considered in
161 Rank-2 and 3.

162

163 **3.3 Calibration and validation of tidal dynamics**

164 The Arcachon lagoon encompasses various geomorphologic entities and different sediment
165 types (Figure 2). Consequently, using a constant roughness length (z_0) fails to represent
166 seabed heterogeneity. Given the significant impact of roughness length on tide propagation
167 (Nielsen, 1992), this parameter needs to be carefully calibrated to account for the diverse

168 bottom features in this area. Note that calibration and validation are both performed using the
169 most recent bathymetry (from 2016).

170

171 **3.3.1 Calibration of the roughness length**

172 In this model, vegetation is directly taken into account on momentum and turbulence,
173 therefore the value of z_0 does not need to account for the presence of seagrass. This implies
174 that even within seagrass meadows, z_0 is representative of the bedforms and sediment types.
175 Calibration of the sediment roughness length is performed using a trial-and-error method and
176 the calibration values finally retained are presented in Figure 2.

177 For the main, secondary, and sandy channels (Figure 2), the roughness length is computed
178 using Soulsby's (1997) formulations (Eq. 1 to 3), based on the bedforms and mean grain size
179 provided by Bouchet (1968) for the Arcachon lagoon. The best results are obtained by
180 considering the secondary and sandy channels as sandy bottoms with ripple marks. In the
181 main channels, the roughness length is set to 2.72 mm, corresponding to a mixed sediment,
182 gravel-dominated, combined with coarse sand, and without ripple mark.

$$183 \quad z_0 = a_r(\Delta_r^2/\lambda_r) \quad (\text{Eq. 1})$$

184 With $a_r = 0.267$ (Nielsen, 1992), Δ_r the ripple height and λ_r the ripple wavelength, defined as:

$$185 \quad \lambda_r = 1000 D_{50} \quad (\text{Eq.2})$$

$$186 \quad \Delta_r = \lambda_r/7 \quad (\text{Eq.3})$$

187 Where D_{50} is the average sediment size (0.25 mm in the inner channels and 0.18 mm in the
188 sandy channels; Bouchet, 1968). However, according to the trial-and-error method, these
189 formulations prove inadequate to represent the bottom roughness in the inner channels and on
190 the tidal flats, where the bedforms are really small due to the presence of muddy sediments.
191 Therefore, z_0 is set to 0.2 mm in these areas to represent the roughness length of a silt bed
192 (Soulsby, 1983). The roughness length is also kept at 0.2 mm in the offshore areas because, in
193 deep water, z_0 has a weak impact on tide propagation. Regarding the oyster farms (Figure 2), a
194 6-mm roughness length is fixed based on a specific calibration analysis conducted in the
195 Marennes-Oléron bay (Ganthy, pers. com.).

196

197 **Location for Figure 2**

198

199 3.3.2 Model calibration and validation

200 Model calibration (Table 1) is performed at 3 sites (*GERM*, *COMP*, *EYRAC*; Figure 1) by
 201 comparing simulated water levels, tidal patterns and current velocities to the *in situ* data
 202 obtained by Ganthy (2011). Root-mean square error (RMSE) on predicted water levels varies
 203 between 0.10 m and 0.16 m and the absolute values of the mean error (ME) on high tide water
 204 levels range from 0.03 m to 0.14 m. Considering that the Arcachon lagoon is a meso- to
 205 macro-tidal environment, these errors on water levels appear very satisfactory. Average lags
 206 of the predicted high tide times are between -10 minutes and 14 minutes, which constitutes
 207 acceptable time lags given the semi-diurnal tide occurring in the lagoon. Current velocities are
 208 only available at *GERM*, where they reach about 1.2 m.s⁻¹ (Ganthy, 2011). At this site,
 209 RMSEs predicted on current velocities vary between 0.08 and 0.19 m.s⁻¹, providing a rather
 210 good agreement between the predicted and measured currents.

211

212 *Table 1: Synthesis of the calibration results. The calibration results are compared to the in-*
 213 *situ data obtained from Ganthy (2011) at Germanan and Comprian and provided by SHOM*
 214 *at Eyrac. The calibration results are presented using statistical indicators: the root mean*
 215 *square error (RMSE) and the mean error (ME).*

| | Eyrac Tide Gauge | | | GERM | | | COMP | | |
|-------------------------------------------|------------------|-------|-------|-------|-------|-------|-------|-------|-------|
| | Jun. | Aug. | Jan. | Jun. | Aug. | Jan. | Jun. | Aug. | Jan. |
| | 2010 | 2009 | 2010 | 2010 | 2009 | 2010 | 2010 | 2009 | 2010 |
| Water level - RMSE (m) | 0.10 | 0.12 | 0.14 | 0.13 | 0.15 | 0.16 | 0.12 | 0.14 | 0.14 |
| Residual Flow - RMSE (m.s ⁻¹) | - | - | - | 0.16 | 0.08 | 0.19 | - | - | - |
| High Tide time - ME (min) | +8 | +11 | +13 | -6 | -10 | +14 | -4 | -8 | +10 |
| High tide water level - ME (m) | +0.12 | +0.14 | +0.12 | -0.06 | -0.12 | +0.13 | -0.05 | -0.03 | +0.06 |

216

217 Model validation is carried out on water levels only, due to the lack of data available on
 218 current velocities. Water levels measured by Cognat *et al.*, (2018) between November 2015
 219 and November 2016 at nine sites distributed throughout the lagoon (Figure 1; blue circles) are
 220 used for comparison. Validation results are presented in Figure 3 and show a good fit between
 221 the model and the measurements, with the point cloud closely grouped around the identity line
 222 at most sites. Nonetheless, the predictions show a slight tendency to underestimate the
 223 observations. This can be explained by the inlet bathymetric data used for this calibration,
 224 which corresponds to the bathymetry of 1989 (and not 2016). The morphological evolutions
 225 that occurred at the inlet between 1989 and 2016 induced a slight increase in mean water level

226 at the lagoon scale (unpublished results). Although there is no available data on current
227 velocities for further validation of the model, this validation on water level proves that the
228 model accurately reproduces tide propagation in the entire embayment. Considering the
229 principle of mass conservation it can be safely assumed that tidal currents are also well
230 predicted.

231

232 **Location for Figure 3**

233

234 **3.4 Simulated scenarios**

235 To study the influence of seasonal changes and seagrass decline on tidal hydrodynamics, a
236 scenario analysis is performed. Four scenarios are defined (Table 2): a pre-decline period
237 (1988-1989) and a post-decline period (2012-2016), both simulated using seagrass
238 characteristics representative of summer and winter conditions (Table 3). These pre- and post-
239 decline periods are selected because they correspond to the oldest and most recent coverage
240 maps of *Zostera* meadows in our possession, presented in Figures 4.a and 4.b, respectively.
241 The methodology followed for the generation of these maps is described in Plus *et al.* (2010).
242 The seasonal characteristics of vegetation are averaged values computed from a dataset
243 gathering the results of extensive surveys conducted in the Arcachon lagoon (Auby and
244 Labourg, 1996; Ganthy *et al.*, 2013; Cognat *et al.*, 2018).

245

246 *Table 2: Configuration of the Zostera meadows used in the different simulated scenarios.*

| Name of the scenario | <i>Z. noltei</i> distribution | <i>Z. marina</i> distribution | Meadow's characteristics |
|----------------------|-------------------------------|-------------------------------|--------------------------|
| Summer 1989 | 1988 | 1989 | Summer |
| Summer 2016 | 2012 | 2016 | Summer |
| Winter 1989 | 1988 | 1989 | Winter |
| Winter 2016 | 2012 | 2016 | Winter |

247

248 In order to quantify the role of *zostera* meadows alone on the tidal flow, these scenarios are
249 run using the same simulation period, with only the vegetation characteristics being changed.
250 Simulation dates, parameters and bathymetry (from 2016) are kept identical for the different
251 simulations. The simulation period covers one spring-neap tidal cycle, spanning from March,
252 29th 2020 to April, 14th 2020. This period is selected because it corresponds to an extreme

253 spring-neap tidal cycle, namely a small neap tide and high spring tide, providing contrasting
 254 conditions for our analysis. The wind forcing used for the simulations is generated using the
 255 AROME weather model (Seity *et al.*, 2011) for the corresponding period.

256
 257 *Table 3: Seasonal characteristics of Zostera noltei and Zostera marina, obtained from*
 258 *averaging field data from Auby and Labourg (1996), Ganthy et al., (2013), Cognat et al.,*
 259 *(2018).*

| | | <i>Z. noltei</i> characteristics | | <i>Z. marina</i> characteristics | |
|----------------|--------------------|----------------------------------|---------|----------------------------------|--------|
| | | Summer | Winter | Summer | Winter |
| Leaf Length | (m) | 0.126 | 0.036 | 0.98036 | 1.15 |
| Leaf Width | (m) | 0.00113 | 0.00034 | 0.0084 | 0.0077 |
| Leaf Thickness | (m) | 0.0002 | 0.0002 | 0.001 | 0.001 |
| Leaf Density | (m ⁻²) | 73706 | 16295 | 568.96 | 220 |

260
 261
 262 **Location for Figure 4**

264 3.5 Metrics used to assess changes in tidal hydrodynamics

265 To obtain a representative and synthetic view of the hydrodynamic conditions resulting from
 266 the different scenarios, several parameters and indicators are selected:

- 267 - The mean high-tide water level ($H_{\text{hightide,tot}}$), computed over a spring-neap tidal cycle,
 268 provides a representation of tide propagation and valuable information regarding potential
 269 risks of coastal flooding.
- 270 - Tidal asymmetry factor (γ) characterizes tidal distortion and is obtained by computing the
 271 asymmetry in the duration of the ebb and flood tides, after Nidzieko (2010), as:

$$272 \quad \gamma = \frac{\frac{1}{N-1} \sum_{i=1}^N (n_i)^3}{\left[\frac{1}{N-1} \sum_{i=1}^N (n_i)^2 \right]^{3/2}} \quad (\text{Eq.4})$$

273 Where n_i is the time derivative of the sea surface elevation and N the number of samples of
 274 water level. This parameter provides details regarding tide propagation. If $\gamma < 0$, the tide is
 275 ebb-dominated, *i.e.* the ebb duration is shorter than the flood duration. If $\gamma > 0$, it characterizes
 276 a flood-dominated tide, with the flood duration shorter than the ebb duration.

- 277 - Near-bottom velocities, represented by the 75th percentile of velocities ($U_{\text{bot}_{p75}}$; m.s⁻¹)
 278 computed between 0 and 0.2 m above the seabed. This parameter provides information

279 regarding the high current velocities experienced by seagrass meadows, excluding the strong
280 current pulses that may occasionally occur.

281 - The scouring potential ($F_{0.165,Im}$), an adimensional coefficient whose computation is inspired
282 by standard formulations used in sedimentology to compute the erosion flux (Le Hir *et al.*,
283 2011). This coefficient provides a relevant description of the hydrodynamic forcing acting on
284 the vegetation meadows and the seabed. It allows the characterization of the global quantity of
285 hydrodynamic energy triggering erosion (or scouring) and leaf tear-off. This parameter is
286 computed as:

$$287 \quad F = \frac{\sum_{t=0}^n (f(t) - 1)}{N_{day}} \quad \text{with} \quad \begin{cases} f(t) = 0 & , \text{ if } \tau_F(t) \leq \tau_C \\ f(t) = \tau_F(t)/\tau_C & , \text{ if } \tau_F(t) > \tau_C \end{cases} \quad (\text{Eq.5})$$

288 With $\tau_F(t) = 1/2 \rho_{wat} C_D U_{bot}^2(t)$, where ρ_{wat} is the water density set as 1023 kg.m^{-3} , C_D is
289 the drag coefficient, set at 1.5, and U_{bot} is the bottom current velocity. τ_c is the critical bottom
290 shear stress above which erosion occurs. τ_c is computed the same way as τ_F but substituting
291 U_{bot} with the critical velocity $U_{bot,crit}$. $U_{bot,crit}$ is set as 0.165 m.s^{-1} , which corresponds to an
292 intermediate value between the critical velocities for leaf tear off and scouring (de los Santos
293 *et al.*, 2010), and the erosion of silt in the lagoon (Ganthy *et al.*, 2011).

294

295 **4 Results**

296 To limit the number of figures in the main body of the article, the changes in tidal
297 hydrodynamics are characterized solely through differences between the post- and pre-decline
298 scenarios (or summer and winter scenarios): $Var_{post} - Var_{pre}$ (or $Var_{sum} - Var_{win}$) and
299 percentage changes between these two scenarios: $(Var_{post} - Var_{pre}) / Var_{pre} \times 100$ (or $(Var_{sum} -$
300 $Var_{win}) / Var_{win} \times 100$). Additionally, the complete hydrodynamic results are presented for
301 each scenario in Appendix A, as they are essential for the interpretation of certain results.

302

303 **4.1 Impact of seasonality in pre-decline seagrass extent**

304 The influence of seasonality is studied by comparing scenarios *Winter 1989* and *Summer*
305 *1989*, and *Winter 2016* and *Summer 2016* (Table 2). For brevity, the seasonal changes are
306 only presented in the pre-decline configuration. The seasonality of *Zostera* meadows is
307 depicted through the Leaf Area Index (LAI; LAI = leaf density x leaf length x leaf width) and

308 is characterized by an increase in LAI between winter and summer on all the tidal flats (not
309 shown), in relation to the annual cycle of *Z. noltei* (Auby and Labourg, 1996) and *Z. marina*.
310 The responses of the tidal hydrodynamic parameters to the increase in LAI are presented as
311 differences in Figure 5 and percentage changes in Figure 6. The high-tide water level (Figure
312 5.a) decreases by approximately 1 cm across the entire lagoon between *Winter 1989* and
313 *Summer 1989*.
314 Seasonal development also has a distinct effect on tidal asymmetry (Figure 5.b), resulting in a
315 reduction in the flood duration on the tidal flats ($\Delta\gamma > 0.3$) and a subsequent increase in flood
316 velocities (not shown). Consequently, on the eastern tidal flats that are flood-dominated in
317 winter (Figure A.1.a and A.1.c), the flood dominance becomes more pronounced in summer.
318 On the western tidal flats, the reduction in flood duration turns the slightly ebb-dominated tide
319 in winter (Figure A.1.c) into a flood-dominated tide during the summer (Figure A.1.a).
320 Conversely, in the channels, the ebb duration shortens ($\Delta\gamma < 0$; Figure 5.b), enhancing the ebb
321 dominance (Figure A.1.c) and increasing ebb velocities (not shown).
322 The seasonal development of *Zostera* meadows induces a reduction in the 75th percentile of
323 bottom velocities on the tidal flats between winter and summer, ranging from 0.05 to 0.15
324 m.s⁻¹ (Figure 5.c), which corresponds to a 25 % – 60 % decrease in $U_{bot,p75}$ (Figure 6.a). A
325 similar tendency is observed for scouring potentials in the intertidal areas (Figure 5.d), with a
326 reduction in $F_{0.165,1m}$ of about 1000 % (Figure 6.b). Due to vegetation loss, the capacity of
327 vegetation to channelize the flow is diminished (Gao *et al.*, 2011), leading to an increase in
328 both $U_{bot,p75}$ and $F_{0.165,1m}$ in the eastern secondary channels and inner channels. In these areas,
329 $F_{0.165,1m}$ nearly doubles (Figure 6.b), and $U_{bot,p75}$ increases between 0.03 and 0.08 m.s⁻¹ (Figure
330 5.c), which corresponds to an intensification of bottom velocities as high as 20 % (Figure 6.a).
331 Note that the variations in tidal asymmetry, high tide water level, and scouring potential can
332 be observed up to the inlet, emphasizing the impact of seagrass decline at the whole lagoon
333 scale and not only in the areas where *Zostera* meadows decline.
334
335 The changes in current velocity due to the seasonal variations in *Zostera* meadows observed
336 in this study (ranging between 25 % and 60 %) appear lower than those reported by Moki *et*
337 *al.* (2020) in a very shallow lagoon extensively colonized by high-density *Z. marina* (ranging
338 between 50 % and 70 %). This difference can be explained by the fact that the Arcachon

339 lagoon is primarily colonized by *Z. noltei*, which has a lower capacity to attenuate flow
340 velocities than *Z. marina* due to its shorter and narrower leaves.

341

342 *Location for Figure 5*

343 *Location for Figure 6*

344

345 **4.2 Impact of decline in summer conditions**

346 The response of tidal flow parameters to the decline of *Zostera* meadows with summer
347 characteristics is assessed by comparing the scenarios *Summer 1989* and *Summer 2016*. The
348 results are illustrated in Figures 7 and 8, depicting differences and percentage changes,
349 respectively. Considering the decline of seagrasses, *Zostera* meadow coverage has decreased
350 on most of the tidal flats (Figure 4), especially in the eastern part of the lagoon, where the loss
351 exceeds 75 % and reaches up to 100 % in certain southeastern areas, leaving the sediment
352 totally exposed. This reduction in vegetation coverage induces an increase in the high-tide
353 water level between 1 and 2 cm throughout the lagoon (Figure 7.a). Although this change in
354 water level is not statistically significant, it reveals a tendency for tidal amplification.

355 A previous study (Donatelli *et al.*, 2019) demonstrated that vegetation, especially submerged
356 aquatic vegetation, enhances the flood dominance of coastal lagoons. Our results support this
357 previous observation by demonstrating that the presence of intertidal seagrasses accentuates
358 the flood dominance on the vegetated tidal flats (Figures A.1.a and b). Seagrass decline
359 induces a reduction in flood dominance on the mudflats ($\Delta\gamma < -0.3$; Figure 7.b, with $\gamma > 0$ in the
360 pre- and post-decline scenarios; Figures A.1.a and b), leading to a lengthening of the flood
361 duration and a reduction in flood velocities. In contrast, in the inner and secondary channels,
362 the tide remains ebb-dominated after decline ($\gamma < 0$ in the pre- and post-decline scenarios;
363 Figure A.1.a and b) but exhibits a reduction in ebb dominance ($\Delta\gamma > 0$; Figure 7.b), leading to
364 a lengthening of the ebb duration and a reduction in ebb velocities. To sum up, these findings
365 show that following the decline of *Zostera* meadows, the tide becomes more symmetrical
366 inside the lagoon, with the ebb-dominated channels becoming less ebb-dominated and the
367 flood-dominated tidal flats becoming less flood-dominated.

368 The decline of *Zostera* meadows also results in an increase in the 75th percentile of bottom
369 velocities (approximately by 75 %; Figure 7.c) and scouring potential (Figure 7.d) on most of
370 the tidal flats. In the southeastern part of the lagoon, where the vegetation coverage decreases

371 the most (Figure 4), hydrodynamic conditions significantly intensify, with $\Delta U_{bot_{p75}}$ reaching
372 0.15 m.s^{-1} (Figure 7.c), which corresponds to a twofold increase in $U_{bot_{p75}}$ (Figure 8.a), while
373 $F_{0.165,1m}$ increases by 2 to 3 orders of magnitude. In contrast, $U_{bot_{p75}}$ and $F_{0.165,1m}$ decrease in
374 the inner and eastern secondary channels. $F_{0.165,1m}$ is characterized by a tenfold reduction in
375 the inner channels and a 50 % reduction in the eastern secondary channels (Figure 8.b).
376 $U_{bot_{p75}}$ decreases by approximately 0.03 m.s^{-1} in the inner channels (20 % reduction; Figure
377 8.a) and by 0.12 m.s^{-1} in the eastern secondary channels (Figure 7.c).

378 Similarly to the influence of seasonal variations, the impact of seagrass decline is visible not
379 only on the vegetated tidal flats where vegetation has decreased but also throughout the rest of
380 the lagoon. In the main and western secondary channels (Figure 7.c), $F_{0.165,1m}$ increases by 10
381 % (Figure 8.b). Despite the increase in the coverage of *Zostera noltei* (Figure 4) west of *Ile*
382 *aux Oiseaux* (see Figure 1 for site location), a slight intensification of $U_{bot_{p75}}$ (0.05 m.s^{-1}) can
383 be noticed (Figure 7.c). However, in this area, $F_{0.165,1m}$ increases with seagrass development,
384 indicating the reduced ability of the flow to erode the finer sediments despite the
385 intensification of hydrodynamic conditions. Such a reduction in $F_{0.165,1m}$ is also well visible in
386 the north of the lagoon where vegetation has grown (Figure 7.d).

387 In response to the decline of *Z. marina* from the edges of several secondary channels (Figure
388 4), $U_{bot_{p75}}$ highly intensifies (Figure 7.c), particularly on the edges of the *Ile* and *Courbey*
389 channels (see Figure 1 for site locations), where it increases by 150 % (Figure 8.a). This
390 percentage change in bottom velocities is comparable to the changes induced by the decline of
391 *Z. noltei* in the areas this species decline the most. These findings reveal that the high density
392 of *Z. noltei*, as well as its wide extent, compensate for its small stature and high flexibility, to
393 the point that this species is capable of providing damping services comparable to a larger
394 species such as *Z. marina*. This corroborates the results from Bouma *et al.* (2005), who
395 demonstrated that high-density *Z. noltei* is capable of dissipating as much or more
396 hydrodynamic energy than the low-density *Spartina anglica*, a stiffer and taller species. Vu *et*
397 *al.* (2017) also showed that the complete loss of *Posidonia Oceanica* in a coastal bay resulted
398 in an increase in mean intense current velocity (above 0.30 m.s^{-1}) comprised between 50 %
399 and 80 %. Despite *Posidonia Oceanica* having longer and wider leaves than *Z. noltei*, the
400 changes in current velocities observed in our study are more important, being twofold where
401 seagrass decline is the most severe. Once more, this contrast can be explained first by the
402 much higher density of *Z. noltei* ($> 20,000 \text{ shoot.m}^{-2}$) than the density of *Posidonia Oceanica*
403 observed in their study (526 shoot.m^{-2}), and second by the consideration of bottom velocities,

404 which are more affected by vegetation than the depth-averaged velocities considered in Vu *et*
405 *al.*, (2017) .

406 *Location for Figure 7*

407 *Location for Figure 8*

408

409 **4.3 Impact of decline in winter conditions**

410 Finally, Figures 9 and 10 depict the response of tidal flow parameters to the decline of *Zostera*
411 meadows with winter characteristics (comparing the scenarios *Winter 1989* and *Winter 2016*),
412 presented as differences and percentage changes, respectively. Due to the high variability of
413 the annual cycle of *Zostera noltei* and its lower density during the winter, the differences in
414 biomass resulting from seagrass decline in this season are considerably smaller than what is
415 observed for similar rates of decline during the summer.

416 In this case, the impacts of seagrass loss on tidal hydrodynamics follow the same patterns of
417 change described for the summer decline (see the previous section) but exhibit changes of
418 much milder intensity. This is particularly evident in the high tide water level (Figure 9.a) and
419 tidal asymmetry (Figure 9.b), which are practically unaffected by the reduction in vegetation
420 coverage. The high tide water level increases by only a few millimeters (<5 mm; Figure 9.a),
421 while the modification of tidal asymmetry occurs only through a very slight reduction in the
422 ebb duration ($\Delta\gamma < 0$) on the eastern tidal flats (Figure 9.a).

423 The reduction in $U_{bot_{p75}}$ observed in the channels in the summer decline scenario (Figure 7.c)
424 is almost nonexistent when considering the seagrasses with their winter characteristics (Figure
425 9.c). Similarly, the increase in $F_{0.165,lm}$ is negligible (<1 %) in the main channels (Figure 10.b).
426 However, the reduction in the vegetation's ability to channelize the flow induced an
427 attenuation of $F_{0.165,lm}$ in most of the inner channels, in the range of 10 % (Figure 9.d). On the
428 tidal flats, $F_{0.165,lm}$ is characterized by a twofold increase (Figure 10.d) and a relatively
429 uniform rise in $U_{bot_{p75}}$ can be observed, approximately $0.04 \text{ m}\cdot\text{s}^{-1}$ (Figure 9c), which
430 corresponds to a 20 % intensification in the areas where vegetation decline the most (Figure
431 10.a).

432 In this season, *Z. marina* maintains its ability to dampen bottom velocities, as evidenced by
433 the 150 % increase in $U_{bot_{p75}}$ on the edges of the channels (Figure.10.a), a rate of increase
434 similar to that observed in the summer decline analysis (see the previous section; Figure 8.a).

435 *Location for Figure 9*

436 *Location for Figure 10*

437

438 **5 Discussion**

439 **5.1 Impacts of seagrass seasonality and decline**

440 Our findings highlight the significant impact of *Zostera* meadows on tidal hydrodynamics
441 within the Arcachon lagoon. Although *Zostera* meadows only colonize the tidal flats (*Z.*
442 *noletii*) and the edges of the channels (*Z. marina*), covering less than 50 % of the lagoon's total
443 surface, they regulate hydrodynamic conditions throughout the lagoon and up to the mouth.
444 This demonstrates that a small species like *Z. noletii*, despite its short stature and high
445 flexibility, can influence the flow at the system scale due to its large spatial extent and high
446 density. This effect is particularly visible in the eastern channels, where vegetation loss led to
447 a reduction in current velocities, resulting from the loss of its capacity to divert currents
448 around the canopy edges and to channelize the flow (Gao *et al.*, 2011; Nepf, 2012). This
449 reduction in channelization becomes clearly visible as a consequence of decline and
450 senescence, through the homogenization of the current velocities in the lagoon (Figure A.3).
451 Seasonal variations in *Zostera* meadows resulted in changes in tidal hydrodynamics of similar
452 intensity to those observed for the summer decline. In both cases, $\Delta U_{bot_{p75}}$ reaches $0.15 \text{ m}\cdot\text{s}^{-1}$
453 on the southeastern tidal flats and varies between $0.03 \text{ m}\cdot\text{s}^{-1}$ and $0.10 \pm 0.02 \text{ m}\cdot\text{s}^{-1}$ in the
454 eastern channels (Figure 5.c and 7.c). However, the response of tidal flow to the decline of
455 *Zostera* meadows with winter characteristics is less significant due to the smaller difference in
456 above-ground biomass between the pre- and post-decline scenarios (*Winter 1989* and *Winter*
457 *2016*), relative to the low biomass of *Z. noletii* during this season (Auby and Labourg, 1996).
458 Seagrass loss resulted in an increase in flow velocities on most of the tidal flats of
459 approximately 75 % considering the summer characteristics (Figure 8.a) and 20 %
460 considering the winter characteristics (Figure 10.a). These observations align with the rates of
461 attenuation previously reported for this *Z. noletii*, which can reach 87 % in summer conditions
462 (Ganthy *et al.*, 2015) and are estimated between 10 % to 20 % during winter (Widdows *et al.*,
463 2008). However, the later study demonstrated an attenuation capacity reaching a maximum of
464 50 % in summer, which appears lower than the rates simulated in this study. This difference
465 may be explained by the much higher leaf density at our study site, reaching $73,706 \text{ leaves}\cdot\text{m}^{-2}$
466 compared to $12,600 \text{ leaves}\cdot\text{m}^{-2}$ in the study by Widdows *et al.* (2008).

467 *Z. noltei* experiences significant seasonal variations, whereas the seasonality of *Z. marina* is
468 far less pronounced at our study site. The analysis of seagrass seasonality revealed that most
469 of the observed modifications in flow between summer and winter are associated with the
470 seasonal variations of *Z. noltei*. Nevertheless, due to the high rates of decline *Z. marina*
471 underwent and its weaker seasonal variations, the influence of its decline on bottom velocities
472 remains significant throughout the year.

473

474 **5.2 Implications for sediment dynamics**

475 Vegetation loss, through the modification of tidal hydrodynamics and a reduction in the
476 meadows' capacity to stabilize the substratum, very likely altered sediment dynamics in the
477 lagoon. On the mudflats, an intensification of scouring potential is expected to have increased
478 the erosion flux and the suspended sediment stock. Modification of tidal asymmetry, due to its
479 prominent role on sediment transport (Quaresma *et al.*, 2007), is anticipated to have led to the
480 redistribution of the different sediment classes. Considering the meadows in summer
481 conditions, seagrass decline lengthened the flood tide, meaning that the fine sediments
482 suspended during this phase can be maintained in suspension and driven for a longer time
483 (Quaresma *et al.*, 2007). In contrast, the coarser sediments are expected to deposit more easily
484 as flood velocities are reduced. This implies that, following the decline, finer sediments
485 should be transported towards the east end of the lagoon and accumulate there. This remark
486 aligns with the observations, which reported muddification of the tidal flats located along the
487 eastern coastline (Ganthy, pers. com.). Conversely, in the main channels, the ebb tide
488 lengthened, meaning that the fine sediments suspended in these areas should be exported out
489 of the lagoon for a longer time, whereas the coarser sediments should be deposited more
490 easily due to the reduction in ebb velocities. It is also anticipated that in relation to the
491 increased bottom velocities on the mudflats (Figures 8.a and 10.a), especially during the ebb
492 tide (not shown), all the classes of sediments will experience increased erosion. During
493 winter, however, the impact of seagrass decline on tidal asymmetry is much milder, and
494 during this season, no conclusion can be drawn regarding the impact of hydrodynamic
495 changes on sediment transport.

496

5.3 Implications for seagrass survival

Hydrodynamics was identified as one of the main stressor acting on *Zostera* meadows in the Arcachon lagoon (Cognat *et al.*, 2018). Consequently, the increase in hydrodynamic energy on the tidal flats induced by seagrass decline is expected to have caused direct damages to the meadows by tearing off leaves (Bouma *et al.*, 2005) and uprooting the plants. In turn, this effect may have initiated feedback mechanisms between the seagrass decline and the intensification of hydrodynamic conditions, contributing to the acceleration of the decline.

The intensification of hydrodynamic conditions and the subsequent increase in suspended sediment concentrations are well-known for their role in reducing light conditions in the bottom of the water column (Koch, 2001; Potouroglou *et al.*, 2017), thereby limiting the light available for photosynthesis. Consequently, the alteration of hydrodynamic conditions induced by seagrass decline likely had direct impacts on vegetation through mechanical destruction and also caused indirect damages to the meadows by establishing detrimental conditions for their survival. All these consequences are believed to have led to additional stresses acting on the *Zostera* meadows, collectively contributing to the acceleration of their decline.

513

514

515

6 Conclusions

This paper constitutes the first large-scale use of the 3D hydrodynamic model MARS3D accounting for the recently implemented effects of vegetation on the mean and turbulent flow, as well as the influence of the flow on leaf bending. Following model calibration and validation in the Arcachon lagoon, MARS3D was employed to investigate the impact of multi-decadal decline and seasonality of *Zostera* meadows on tidal hydrodynamics.

The results indicated that *Zostera* meadows exert control over tidal hydrodynamics across the entire lagoon, with observable flow modifications in unvegetated areas and up to the inlet in response to both decline and seasonal variations. More specifically, we showed that the short-leaf and flexible seagrass *Z.noltei* can regulate the hydrodynamics at the whole system scale due to its extensive presence on the tidal flats.

A comparison between different simulated scenarios revealed that the multi-decadal decline of *Zostera* spp. with summer characteristics and the seasonal loss resulted in modifications of

529 the tidal flow parameters of comparable intensity. Our results also highlighted the strong
530 seasonal dependence of the response of flow conditions to the decline of *Z.noltei*,
531 characterized by larger changes during summer when biomass peaks, compared to winter
532 when vegetation development is at its lowest.

533 The reduction in the coverage of *Zostera* meadows induced a homogenization of flow
534 characteristics between the tidal flats and the channels, attributable to the diminished
535 contribution of vegetation to the flow channelization. On the mudflats, an overall increase in
536 hydrodynamic energy and bottom velocities is observed between the pre- and post-decline
537 scenarios. These changes in tidal flow are also expected to have had significant consequences
538 on sediment dynamics, due to the increased bottom velocities that promote sediment
539 resuspension, along with the alteration of tidal asymmetry known to affect sediment transport.

540

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557

558 **Appendices**

559 **Appendix A: Spatial changes in tidal hydrodynamics**

560

561 *Location for Figure A.1*

562 *Location for Figure A.2*

563 *Location for Figure A.3*

564

565

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