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2 **Long-term trends of salinity in coastal wetlands: Effects of**
3 **climate, extreme weather events, and sea water level**

4 Running head: Salinity trends in coastal wetlands

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28

29 **Abstract**

30 Coastal freshwater ecosystems play major roles as reservoirs of biodiversity and
31 provide many ecosystem services and protection from extreme weather events.
32 While they are of particular importance worldwide, they are affected by a large
33 variety of anthropogenic threats, among which salinization has been less studied,
34 particularly regarding large temporal and spatial data sets based on real case
35 scenarios, while salinity can impact biodiversity and ecosystem functioning. In this
36 study, we investigated the variations of salinity across long-term (1996-2020) and
37 seasonal (monthly records) temporal scales and spatial (varying distance to the
38 coastline) scales in water bodies of two typical temperate coastal wetlands situated
39 on the Atlantic coast of France. We complemented our analyses with models of sea
40 water levels computed at both sites across 2000-2020. Our detailed data set allowed
41 for highlighting that salinity in ponds varied seasonally (higher during summer, due
42 to decreased precipitation and higher temperature), but also spatially (higher closer
43 to the seashore, which pattern increased through time). Over the long term,
44 decreased precipitation but not increased temperature induced increasing salinity.
45 We also highlighted contrasted long-term patterns of salinity changes on these two
46 coastal wetlands, with one site where salinity decreased over time linked to the
47 responses to marine flood, allowing to document the temporal dynamics of salinity
48 following a massive intrusion of sea water. Complementarily, at both sites, water
49 levels at high tides increased through time, a pattern which can induce additional
50 salinization. To our knowledge, our study is the first to investigate long-term
51 changes in salinity in coastal wetlands through natural processes (e.g. seaspray,

52 seasonal variations) and ongoing climate perturbations (e.g. marine surges linked to
53 extreme weather events, increased temperature and decreased precipitations).

54 Key-words: Brackish water, Marine submersion, Precipitation, Salinization, Seasonal
55 variations, Temperature

56

1. Introduction

57

58

59 Coastal wetlands are situated at the boundary between the land and the sea (Janas et
60 al., 2019). Despite a restricted extent of the interface between oceanic and terrestrial
61 biomes, coastal wetlands represent a significant surface area worldwide (Hopkinson
62 et al., 2019). While they play significant ecological roles (Davis et al., 2014; Hobohm
63 et al., 2021; Hopkinson et al., 2019), sheltering a large diversity of species and habitats
64 (Janas et al., 2019; Maynard and Wilcox, 1997) and serving a role of carbon
65 sequestration and protection of the terrestrial environment (Barbier et al., 2008; De
66 Battisti, 2021; Nelson and Zavaleta, 2012), coastal wetlands are currently affected by a
67 large variety of anthropogenic threats such as eutrophication, chemical pollution,
68 land use, invasive species, and ongoing modification of climatic conditions (Barua et
69 al., 2021; Martínez-Megías and Rico, 2021). Among these threats, changes in salinity
70 regimes (environmental salinization) across spatial and temporal scales relevant to
71 coastal wetlands have been less studied to date, despite the major role of this
72 environmental parameter in the functioning of these ecosystems (Herbert et al.,
73 2015).

74

75 Coastal ecosystems are naturally exposed to spatial and temporal variations of
76 salinity (Barua et al., 2021). Such natural variations of salinity (i.e. primary
77 salinization, Herbert et al., 2015) are linked to the specific geographic position of
78 coastal ecosystems, and notably the exchanges between terrestrial and oceanic

79 environments (Xue et al., 2013). The natural processes which affect variations of
80 salinity are primarily linked to landward aerial transport of dry or wet oceanic salts
81 (Zaman et al., 2018), such as sea-sprays (Benassai et al., 2005), and groundwater
82 intrusions and exchanges (Alcolea et al., 2019; Casamitjana et al., 2019; Coluccio et al.,
83 2021; Erostate et al., 2020; Kløve et al., 2011; Knighton et al., 1991; Meredith et al.,
84 2022; Tamborski et al., 2019; Visschers et al., 2022). As a consequence, coastal
85 ecosystems are characterized by spatial and temporal heterogeneity of salinity
86 (Estévez et al., 2019; Fu et al., 2021; Ghalambor et al., 2021; Ranjbar and Ehteshami,
87 2019). The spatial determinants of salinity are mainly linked to the proximity of salt
88 sources (i.e. distance to the coastline; Wu, Liu, and Huang, 2017) while salinity can
89 also change temporally from short- (hours) to longer temporal scales (years) (Ghosh
90 et al., 2013; Gutierrez and Johnson, 2010). Complementarily, climatic conditions (e.g.
91 temperature, rainfall, wind regimes) interact with salt deposition and can influence
92 variations of salinity (Morcillo et al., 2000; Perigaud et al., 2003). For instance,
93 salinity increases when evaporation exceeds precipitation (Hassani et al., 2021),
94 which might naturally occur seasonally (De Luis et al., 2009).

95

96 Coastal ecosystems are also susceptible to secondary salinization, the increase in salt
97 concentration caused by the direct actions of humans or their activities (Herbert et
98 al., 2015; Izam et al., 2021), because of several processes operating at different
99 temporal scales. First, ongoing climatic changes are expected to induce a significant
100 increase in sea level (Church and White, 2011; Domingues et al., 2008; Gornitz, 1995;
101 Herbert et al., 2015). Second, current climatic changes are expected to increase the

102 intensity and frequency of extreme events, such as marine storms and associated
103 surges (Dettinger, 2011; IPCC, 2022; Trenberth et al., 2015). Third, alterations of
104 hydric cycles due to changes in the magnitude and timing of precipitation (Martínez-
105 Megías and Rico, 2021; Neubauer and Craft, 2009) should affect freshwater inputs
106 and change evaporation rates (Herbert et al., 2015; Jeppesen et al., 2020; Mills et al.,
107 2013). Finally, other anthropogenic activities can directly lead to an increase in
108 salinity, such as groundwater pumping or water abstraction which have been shown
109 to increase sea water inundation and saline intrusion (Peters et al., 2021; Reid et al.,
110 2019). All of these processes and the associated increased salinity may severely
111 transform coastal areas (Knighton et al., 1991; Visschers et al., 2022), affecting habitat
112 structure through landward habitat shifts (Visschers et al., 2022), and biodiversity
113 through changes in geographic distribution (Brischoux et al., 2021; Gunter, 1956), and
114 in turn community structure (Anufrieva and Shadrin, 2018; Cunillera-Montcusí et
115 al., 2022; Ersoy et al., 2022; González-Sansón et al., 2022; Hart et al., 2003; Kendall et
116 al., 2022).

117

118 However, despite the major ecological impacts of salinization, the spatio-temporal
119 variations of salinity in coastal areas, and more importantly, their recent changes in
120 response to climatic modifications remain poorly known. Particularly, if salinity
121 variations in underground coastal water (Colombani et al., 2017; Mastrocicco et al.,
122 2021; Mastrocicco and Colombani, 2021) or large water bodies such as lagoons
123 (Casamitjana et al., 2019; Meredith et al., 2022) have been investigated, the impact on
124 smaller water bodies, relevant to coastal freshwater biodiversity such as ponds, and

125 considering different processes, is poorly understood. In order to better understand
126 these variations in salinity, it is essential to investigate the effects of environmental
127 factors that might influence salinization with high temporal resolution time series of
128 salinity measurements (Lee et al., 2022), such precise measurement lacking to date.
129 Such investigations are currently of crucial importance because they will allow
130 assessment of the extent of salinity variations in coastal environments (either natural
131 or induced by climate change), and thus to understand the consequences of these
132 changes on the resilience of these ecosystems.

133
134 In this study, we investigated the spatio-temporal variations of salinity across long-
135 term (decades) and fine temporal (monthly records) and spatial (varying distance to
136 the coastline) resolutions in water bodies of two typical temperate coastal wetlands
137 situated on the Atlantic coast of France. On both sites, water salinity was recorded
138 each month (for 24 years on 24 ponds in one site, and for 10 years on 31 ponds in the
139 other site). Based on these detailed data sets, our objectives were multiple. First, we
140 analysed the seasonal and spatial variations of salinity. We hypothesized that
141 salinity should be greater during summer because of reduced precipitation and
142 higher temperatures, and that salinity should be higher closer to the seashore
143 because of landward deposition of seaspray as well as exchanges (especially
144 groundwater exchanges) with the marine environment. Second, we analysed the
145 long-term changes in salinity and related these changes to concomitant variations in
146 precipitation and temperature in order to highlight potential effects of ongoing
147 climate change on this parameter. We hypothesized that increased temperatures and

148 decreased precipitation over time (Briffa et al., 2009; Schär et al., 2004) should
149 increase salinity levels across our time series. We also hypothesized that these long-
150 term changes should interact with the spatial variations of salinity, with
151 proportionally greater salinity increase closer to the seashore. Finally, we
152 complemented our analyses with models of sea water levels computed in front of
153 both sites across 2000-2020 in order to investigate whether fluctuation in this
154 parameter can contribute to further salinization through local inundations. We
155 hypothesized that sea water levels which occasionally provoke landward
156 inundations should increase in frequency and intensity over time.

2. Methods

2.1. Study sites and field procedures

Salinity of water bodies were measured on two coastal wetlands from the western coast of France: the « Réserve Naturelle Nationale de Moëze-Oléron » (45°53'33.36"N, 1°04'59.16"W, hereafter MO) and the « Réserve Naturelle Nationale du marais d'Yves » (46°2'40.735"N, 1°3'16.906"W, hereafter MY) (See figure 1). These two study sites, separated by ~15 km, are situated on the Atlantic coast of France (Département de la Charente-Maritime), an area characterized by a temperate climate. The two sites are natural reserves characterized by diverse habitat types which cover a continuum between intertidal sandy area, through salt and freshwater marshes; up to sand dunes and grasslands along with increasing distance from the seashore. On both sites, the presence of small water bodies (ponds) were favoured in order to improve biodiversity. Both sites span a similar surface area (218 ha for MO and 204 ha for MY, Fig. 1) and are relatively low (mean elevation: MY= 2.64 m ± 0.02 SE NGF; MO=2.90 m ± 0.01 SE NGF) coastal wetlands displaying a coastal sand dune (3.30 m high NGF both at MY and MO) situated near the high sea limit (see Lorrain-Soligon et al., 2021 for topographic profiles). Both sites were differentially hit by storm Xynthia (that occurred in 2010, Bertin et al., 2014): one site was completely submerged by sea water (MY), while many ponds at the other site (MO) were spared from the storm because they were protected by a second additional dune (see Lorrain-Soligon et al., 2021).

At MO, salinity of 24 ponds was measured (distance to the ocean: mean=564.52 m ± 59.99, min=57.69 m, max=1079.24 m, Figure 1) from January 1996 to December 2019.

181 At MY, the salinity of 31 ponds was measured (distance to the ocean: mean=564.29 m
182 \pm 24.95, min=186.83 m, max=836.76 m, Figure 1) from January 2010 (corresponding to
183 the sea water intrusion by storm Xynthia) to December 2019. These represent small
184 body of still water (<5000 m²), presenting similar characteristic of habitat types,
185 surrounding and aquatic vegetation, and depth (mean depth of ponds ranging from
186 ~0.5m to 1.5m). Some details on pond characteristics are given in Appendix A . On
187 each pond, the salinity was recorded once per month during 24 years (at MO) and 10
188 years (at MY). The salinity was recorded using a portable refractometer until 2000
189 (Cond 330i), and then using a conductimeter (YSI Professional Plus, ProQuatro
190 Multiparameter Meter, and Multi 340i with TetraCon 325 probe), and was repeatedly
191 measured at the same location for each pond (20 cm from the pond edge, 10 cm
192 below the water surface).

193

194 2.2. *Meteorological parameters*

195 We included yearly and monthly data of temperature and precipitation using the
196 *easyclimate* package (Moreno and Hasenauer, 2016) on R 3.6.3 (R Core Team 2020).
197 This package allows extraction of maximum temperature, which is expected to
198 influence evaporation, and total precipitation on a daily scale. We extracted these
199 data from La Rochelle meteorological station (46°9'0.684"N, 1°8'43.08"W) situated at
200 17.4 km and 26.6 km from MY and MO respectively, between 1996 and 2020. The
201 variations of these data across months are presented in Appendix B.

202

203 2.3. *Estimates of the water levels across 20 years*

204 To investigate the possible impact of changes in sea level on coastal wetland
205 salinization, we simulated the hydrodynamic circulation in the study area using the
206 numerical model SCHISM (Zhang et al., 2016), which solves the primitive equations
207 on unstructured grids using advanced numerical methods. We used a hydrodynamic
208 model because sea water levels strongly vary spatially while the only tide gauge
209 available over the studied period (La Pallice, see Figure 1) is located about 20 and 30
210 km to the North of both study sites. This spatial variability of water levels is due to
211 spatial variations of tides and storm surges. Thus, Dodet et al. (2019) showed that,
212 over the modelled domain and over the period 1998-2018, the mean tidal range
213 varied from 3.28 and 3.83 m and the maximum storm surge varied from 1.15 and 1.57
214 m. To a lesser extent, the tide gauge data has some gaps while the model is
215 continuous over the studied period. SCHISM was implemented in 2DH (two
216 dimensional horizontal, which means that the model uses one single layer on the
217 vertical) over the 'Pertuis Charentais' area with a spatial resolution ranging from
218 2000 m along the open boundary to 100 m near the shoreline, as described in Savelli
219 et al. (2019). The model starts at mean sea-level and uses a ramp of 1 day. A
220 sensitivity analysis reveals that the model converges when using longer ramps,
221 which is due to the small dimensions of the modelled domain. The model is forced
222 by amplitudes and phases of the 18 main tidal constituents, linearly interpolated
223 from the regional tidal model of Bertin et al. (2012) and fields of sea-level pressure
224 and 10 m winds originating from the CFSR reanalysis (Saha et al., 2010). The
225 hydrodynamic model used in this study is well-established and was previously
226 developed to compute sediment transport and morphological changes (Guerin et al.,

227 2016) and bed shear stress and biofilm resuspension in front of MO (Savelli et al.,
228 2019). The model was run over the period 2000-2020 and hourly time series of water
229 levels were extracted in front of each studied wetland. Due to the 2DH (two
230 dimensional horizontal) barotropic configuration, the model cannot capture long-
231 term changes in sea levels due to large-scale circulation patterns and global warming.
232 In order to account for these processes which are relevant at the scale of the studied
233 period (2000-2020), yearly mean sea levels observed at the nearby tide gauge of La
234 Rochelle (data available at <https://data.shom.fr/>) were computed and linearly
235 added to model outputs. This approach was validated against the available water
236 level data at La Rochelle tide gauge, which are reproduced with a root mean squared
237 discrepancy of 0.13 m (see Appendix C). Extreme water levels are only substantially
238 underestimated during Xynthia storm, mostly because the effects of short waves
239 were not accounted for in the simulation, as discussed in Bertin et al. (2014).

240

241 2.4. Statistical analyses

242 All statistical analysis were performed using R 3.6.3 (R Core Team, 2020) and Rstudio
243 v1.1.419. We computed Linear Models (LMs) or Linear Mixed Models (LMMs) using
244 the *lme4* (Bates et al., 2015) and *lmerTest* (Kunzetsova et al., 2017) packages. For all
245 test computed, models accuracy was tested using the *check_model* function from the
246 *performance* package (Lüdecke et al., 2020). When models did not fit the data, the
247 response variable was log transformed or log+1 transformed.

248 2.4.1. Seasonal variations of salinity

249 We investigated seasonal variations of salinity (all years combined), by computing
250 LMMs with each value of salinity recorded as dependent variables (log+1
251 transformed), month and its quadratic form as covariates, and pond as a random
252 effect. We also investigated the climatic drivers of these variations by computing
253 LMMs with mean salinity (measured for each month and each pond, all years
254 combined) as the dependent variable (log transformed), mean temperature or
255 precipitation as covariates, and pond as a random effect. As temperature and
256 precipitation were highly correlated ($\text{cor}=-0.145$, $\text{p-value}<0.001$) these variables were
257 tested in two separate models.

258 For these analyses, we calculated a mean temperature for each month (across the
259 study period) and a mean precipitation (mean of the sum of precipitations recorded
260 during each month across the study period).

261

262 2.4.2. Spatial variations of salinity

263 We analysed salinity records according to distance to the ocean of the ponds where
264 salinity was recorded, by computing LMMs with each value of salinity recorded as
265 dependent variables, distance to the ocean as the covariate (log+1 transformed), and
266 pond as a random effect.

267

268 2.4.3. Long term changes in salinity

269 Across the whole study period (January 1996 to December 2019 at MO, and January
270 2010 to December 2019 at MY), we evaluated long-term temporal trends of salinity by
271 computing LMMs with each value of salinity recorded as the dependent variable
272 (log+1 transformed), year as the covariate, and pond as a random effect.
273 Additionally, we investigated trends of maximum and minimum salinity (for all
274 ponds and all years: one value of maximum and minimum salinity for each pond
275 and each year), using either minimum or maximum salinity as dependent variables,
276 year as the covariate, and pond as a random effect. We also investigated the climatic
277 drivers of salinity trends, by computing LMMs with mean salinity (one value of
278 mean salinity for each pond and each year) as the dependent variable, mean
279 temperature across the year or total precipitation as covariates, and pond as a
280 random effect. Because previous analyses demonstrated that salinity recorded in
281 2010 at MY was exceptionally high due to the marine flooding driven by storm
282 Xynthia (Lorrain-Soligon et al., 2021), we removed this year from our analysis at MY,
283 in order to investigate only variations of salinity according to environmental
284 parameters under normal conditions.

285 Finally, to investigate whether the spatial gradient of salinity (distance to coastline)
286 changes across the study period, we extracted, for each year, the slope of the
287 relationships between salinity and distance to the ocean (see Appendix D), and
288 computed LMs with these slope as dependent variables, and year, temperature
289 (mean temperature of the year) or precipitation (sum of the precipitations of the year)
290 as a covariate.

291

292 2.4.4. Estimates of the high tides' water level

293 To investigate the variations of estimated water levels across the study period (2000-
294 2020 for both sites), we computed yearly-mean values of water levels exceeding 2.4
295 m/MSL (Mean Sea Level, the water level is thus given with respect to mean sea
296 level), which corresponds to spring tides. Indeed, under neap tides, the sea level is
297 too low to induce any flooding and salinization of the studied ponds. Although this
298 value is somehow arbitrary, it has no impact on inter-annual variability and upward
299 trend of sea levels.

300 We then computed LMs with these estimated water levels at high tides as dependent
301 variables, and year as a covariate.

302 **3. Results**

303 3.1. Seasonal variations of salinity

304 Across the whole study period, salinity varied seasonally (monthly variation),
305 according to a quadratic form, with maximum salinity attained in summer on both
306 sites (Figure 2, Table 1), and maximum values also attained in October and
307 November in MO (Figure 2, Table 1). In both sites, these variations were significantly
308 correlated to temperature, with salinity increasing with increasing temperature (MO:
309 Estimate=0.002, SE<0.001, t-value=14.780, p-value<0.001; and MY: Estimate=0.002,
310 SE<0.001, t-value=8.96, p-value<0.001), and to precipitation, with salinity decreasing
311 with increasing precipitation (MO: Estimate<-0.001, SE<0.001, t-value=-2.368, p-
312 value=0.019; MY: Estimate<-0.001, SE<0.001, t-value=-3.645, p-value<0.001).

313

314 3.2. Spatial variations of salinity

315 At MO and MY, salinity decreased with increasing distance to the ocean (MO:
316 Estimate<-0.001, SE<0.001, t-value=-3.41, p-value=0.003; MY: Estimate=-0.001,
317 SE<0.001, t-value=-2.048, p-value=0.050).

318

319 3.3. Long term changes in salinity

320 Across the whole study period, salinity decreased at MY, considering either mean,
321 minimum, or maximum values (Table 1). At MO, results were more complex with a
322 significant increase in minimal values of salinity across time (Table 1), and no

323 significant trends for maximal and mean values (Table 1). The long-term variations of
324 salinity were linked to precipitation, with salinity decreasing with increasing
325 precipitation at both sites (MO: Estimate<-0.001, SE<0.001, t-value=-3.562, p-
326 value<0.001; and MY: Estimate<-0.001, SE<0.001, t-value=-3.282, p-value=0.001), but
327 not to temperature (at MO: Estimate=-0.011, SE=0.016, t-value=-0.695, p-value=0.487;
328 and at MY: Estimate=0.066, SE=0.044, t-value=1.524, p-value=0.130).

329

330 Across years, the spatial gradient of salinity (slope of the relationships between
331 salinity and distance to the coastline) increased at MO (Estimate<-0.001, SE<0.001, t-
332 value=-7.449, p-value<0.001, Figure 3A), an effect that was marginally related to
333 decreased precipitation (Estimate<0.001, SE<0.001, t-value=1.881, p-value=0.073), but
334 not to temperature (p-value=0.238). At MY, there was no difference in the strength of
335 the spatial gradient of salinity (Estimate<0.001, SE<0.001, t-value=0.327, p-
336 value=0.752, Figure 3B), and no relationships with temperature or precipitation (both
337 p-values>0.269).

338

339 3.4. Estimates of the high tides' water level

340 In both sites, water levels at high tides increased over time (at MO: Estimate=0.002,
341 SE<0.001, t-value=4.735, p-value<0.001; at MY: Estimate=0.002, SE<0.001, t-
342 value=4.330, p-value<0.001; Figure 4). These data show that open water surface can
343 exceed the height of the protective coastal sand dunes during significant amount of
344 time (9 days at MO and 7 days at MY).

4. Discussion

Several studies have investigated contemporary long-term salinity changes in marine environments and highlighted contrasted patterns linked to variable freshwater inputs and evaporation patterns (Li et al., 2017; Lin et al., 2001; Meredith and King, 2005; Omstedt and Axell, 2003; Samuelsson, 1996; Tukenmez and Altiok, 2022). Very few studies have investigated such variations for freshwater or continental water bodies (Benjankar et al., 2021; Collins and Russell, 2009; Dugan and Arnott, 2022). To our knowledge, our study is the first to investigate long-term changes in salinity in coastal wetlands susceptible to salinization through natural processes (e.g. seaspray, Benassai et al., 2005) and ongoing climate perturbations (e.g. marine surges linked to extreme weather events, Nordio et al., 2023). Our detailed data set allowed for highlighting that salinity in ponds varied seasonally, being higher during summer months as well as until mid-autumn in one site, but also spatially, as salinity increase closer to the seashore. Importantly, this spatial gradient of salinity (which might be linked to landward salt deposition or groundwater intrusions) strengthened through time. These variations of salinity are linked to both increased temperature and reduced precipitations. Complementarily, in both sites, water levels at high tides increased through time, a pattern which can induce an additional source of salinization.

364

At both sites, salinity varied seasonally, with lowest salinity in winter and highest salinity in summer and until mid-autumn. Such seasonal variation was expected given the concomitant variations in climatic conditions (temperature and

368 precipitation) in temperate areas. Indeed, we showed that the seasonal variation of
369 salinity is driven both by temperature and precipitation, as salinity increased with
370 increasing temperature and decreasing precipitation (see also Appendix B). Both
371 variables are likely to affect evaporation patterns interactively (Hassani et al., 2021),
372 which naturally occur seasonally (De Luis et al., 2009). Additionally, because water
373 bodies are highly dependent on groundwater (Erostate et al., 2020; Kløve et al., 2011),
374 these seasonal variations can be explained due to groundwater discharge and water
375 recirculation which are known to affect surface water bodies (Casamitjana et al.,
376 2019; Rodellas et al., 2018; Sadat-Noori et al., 2016; Santos et al., 2012), and are also
377 known to vary seasonally (Sadat-Noori et al., 2016; Tamborski et al., 2019).

378

379 As expected from landward deposition of seaspray and groundwater exchanges, we
380 found that, overall, salinity was higher in coastal ponds situated closer to the
381 coastline, despite the small spatial extent of our study sites (situated from ~50m to
382 1000m from the coastline). Importantly, we found that, over time, the strength of this
383 spatial gradient of salinity increased significantly on one of our study sites (MO).
384 That is, the slope of the relationship between pond salinity and distance to the
385 coastline increased through time. This effect was mainly driven by increased salinity
386 closer to the seashore rather than by decreased salinity farther from the seashore,
387 which might be due to increase groundwater infiltration over time (Colombani et al.,
388 2017; Mastrocicco et al., 2021; Mastrocicco and Colombani, 2021). Such a result
389 highlights a remarkable spatial heterogeneity in the susceptibility of these coastal
390 ponds to salinization over a relatively small spatial scale. Complementarily, this

391 result reinforces the notion that ongoing climate change is currently inducing
392 significant salinization, and that this process strongly alters the spatial gradient of
393 salinity. Despite the strengthening of the spatial gradient of salinity, we did not
394 found a consistent trend of salinity over time, but found contrasted responses in our
395 two study sites. Indeed, in one of our study sites (MO), salinity (maximum and
396 mean) remains relatively stable across time, but minimum values of salinity
397 gradually increased through time (at a mean of 0.09 g.l⁻¹/year). This site was spared
398 from marine submersion linked to storm Xynthia due a protection dune (Lorrain-
399 Soligon et al., 2021), but minimal values still seems to be affected. The second site
400 however (MY), was completely submerged by storm Xynthia (Lorrain-Soligon et al.,
401 2021). Our salinity recordings started at the onset of this marine submersion and
402 documented the temporal dynamics of this parameter following a massive and brutal
403 intrusion of sea water. We showed that salinity was maximum following storm
404 Xynthia (due to sea water intrusion and increased salinity) and progressively
405 decreased through time to reach lower and temporally stable values at ~3 years post-
406 storm (see Lorrain-Soligon et al. [2021] for some salinity values recorded before
407 Xynthia). These lower values remained stable through time, although we emphasize
408 that the following 7 years are likely too short of a time scale to investigate potential
409 long-term changes in salinity. Importantly, other studies have shown that effects of
410 this marine submersion were long-lasting both for fluxes of marine elements (salt,
411 sediments, and organic matter) through the food web (Lorrain-Soligon et al., 2022)
412 and for the direct negative impact of salinization on biodiversity (Lorrain-Soligon et
413 al., 2021) In this study, while we emphasize a decrease in salinity following storm

414 Xynthia, the salinity levels recorded 7 years after the storm (7.23 g.l⁻¹ in 2017 and 4.16
415 g.l⁻¹ in 2018) are well beyond salinity levels recorded before the storm on the same
416 area (2.53 g.l⁻¹ in 2007, see Lorrain-Soligon et al., 2021). We thus highlighted gradual
417 as well as brutal changes in salinity in these coastal wetlands, which might both
418 impact coastal ecosystems (Delaune et al., 2021). Indeed, chronic salt exposure to
419 gradual increase in salinity might gradually transform coastal ecosystems through
420 acclimatory processes or epigenetic changes (Venâncio et al., 2022), while brutal
421 changes can induce species displacements or direct mortality (Lorrain-Soligon et al.,
422 2021).

423

424 Long-term variations in salinity are hypothesized to be mainly due to low
425 precipitation and excess evaporation linked to increased temperature (Al-Shammiri,
426 2002; Mills et al., 2013; Obianyo, 2019). Our results suggest that salinity increase may
427 be related to precipitation, while we failed to detect any influence of thermal
428 conditions, despite the strong effect of both parameters on seasonal variations of
429 salinity (see above). These results suggest that long-term salinization is primarily
430 driven by changes in the magnitude and the timing (seasonality) of precipitation, the
431 effects of which are strengthened by climate change and, notably, the increased
432 frequency of droughts (Herbert et al., 2015; Jeppesen et al., 2020; Mills et al., 2013).

433

434 Finally, the numerical modelling of sea levels and the computation of yearly-mean
435 values at high tides also shows a significant increase over time at both our study sites

436 (0.002 m.year⁻¹ through a 20 years' period, in both sites). This pattern is explained
437 firstly by the nodal tidal cycle (18.6 year period, which can influence sea water levels,
438 Baart et al., 2012; Royer, 1993; Yndestad et al., 2008), which reached a minimum in
439 2006 and maximum in 2015. The minimum values observed in 2003-2005 also
440 correspond to a period characterized by a weaker storminess in the region
441 (Chaumillon et al., 2019). Over the studied period, water levels increased by about
442 0.10 m. This increase is explained mostly by long term sea-level rise and, to a lesser
443 extent, by an increase in storminess from 2003-2005 to 2014-2017. More specifically,
444 these data show that open water surface can exceed the height of the protective
445 coastal sand dunes during significant amount of time. Such data highlight additional
446 risks of salinization through sea water inundations, which frequency has been shown
447 to increase with global changes in several areas of the globe (Dettinger, 2011;
448 Knutson et al., 2010; McLean et al., 2001; Nicholls et al., 1999; Trenberth et al., 2015),
449 even though they have not been formally tested in temperate areas. A previous study
450 have emphasized the importance of coastal sand dunes as a protection of coastal
451 wetlands against sea water intrusions (Lorrain-Soligon et al., 2021), but these natural
452 barriers may well prove inefficient in the long-term, given that by the end of this
453 century, global mean sea levels will most likely rise between 0.29m and 1.1m (IPCC,
454 2022).

455

456 Whatever the underlying causes, salinization is known to negatively affect the rich
457 biodiversity of coastal ecosystems (Bradley, 2009; Evans and Kültz, 2020; Hellebusi,
458 1976; Schultz and McCormick, 2012). Indeed, salinity higher than 4 g.l⁻¹ might

459 transform fungal and microbial communities (Canhoto et al., 2022), as well as
460 amphibian communities (Lorrain-Soligon et al., 2023), and salinities higher than 7 g.l⁻¹
461 can be detrimental for invertebrate communities (Venâncio et al., 2020) But
462 salinization will also affect hydrology by destabilizing the water column (Dugan and
463 Arnott, 2022; Koretsky et al., 2012) biogeochemistry (e.g. lack of oxygenation,
464 Ladwig, Rock, and Dugan, 2021; Dugan and Arnott, 2022), and soils characteristics
465 (Neubauer, Franklin, and Berrier, 2013). Taken together, these various consequences
466 of coastal wetland salinization suggest that salinity fluctuations are likely to
467 dramatically transform - and impact the functioning of - coastal ecosystems (Cañedo-
468 Argüelles et al., 2013; Cunillera-Montcusí et al., 2022; Denny, 1994; Herbert et al.,
469 2015; Visschers et al., 2022). Our study allows to emphasize that even ponds situated
470 farther from the seashore are at risk of salinization and should be considered when
471 planning conservation measure to mitigate this global change. Despite growing
472 interest on the outcome of human-induced salinization, we emphasize that the
473 consequences of these processes at large spatial and temporal scales are still to be
474 investigated (Cunillera-Montcusí et al., 2022), and can be site-specific. Further
475 research should focus on the impacts on biodiversity in relation to the spatio-
476 temporal salinity gradients. In addition, forecasting models should incorporate more
477 information on critical factors that might influence salinity changes, across large
478 spatial and temporal scales, not only for water bodies but also for soil, as terrestrial
479 salinization is a critical but overlooked process (Ayub et al., 2020; Greenway and
480 Munns, 1980; Rath and Rousk, 2015; Singh, 2016).

481

482 **5. Conclusion**

483

484 We highlighted both natural long-term changes in salinity in coastal wetlands (linked
485 to climatic conditions), but also the consequences of a marine submersion, inducing
486 brutal increase in salinity. Additionally, we demonstrated that salinity increased
487 closer to the seashore, probably due to exchanges with the marine environment
488 (through groundwater infiltration or sea-sprays), and this spatial gradient of salinity
489 is strengthen through time. Models of water levels at high tides further highlight a
490 temporal increase, suggesting a higher susceptibility to marine intrusion. We
491 emphasize the importance of recording long-term series for a large variety of
492 locations, as the salinity trends can be highly variable and site-specific.

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497

498 *Conflict of interest statement*

499 The authors declare that they have no conflict of interest.

500

501 *Author contributions*

502 **Léa Lorrain-Soligon:** Conceptualization ; Methodology; Formal analysis; Data
503 Curation; Writing - Original Draft ; Visualization. **Frédéric Robin:**
504 Conceptualization ; Writing - Review & Editing; Project administration; Funding
505 acquisition. **Xavier Bertin:** Methodology ; Formal analysis; Writing - Review &
506 Editing ; Visualization. **Marko Jankovic:** Investigation. **Pierre Rousseau :**
507 Investigation. **Vincent Lelong :** Investigation. **François Brischoux :**
508 Conceptualization ; Writing - Review & Editing; Supervision; Project administration;
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515

516 *Data* *Availability* *Statement*

517 The data that support the findings of this study will be made available upon request.

518

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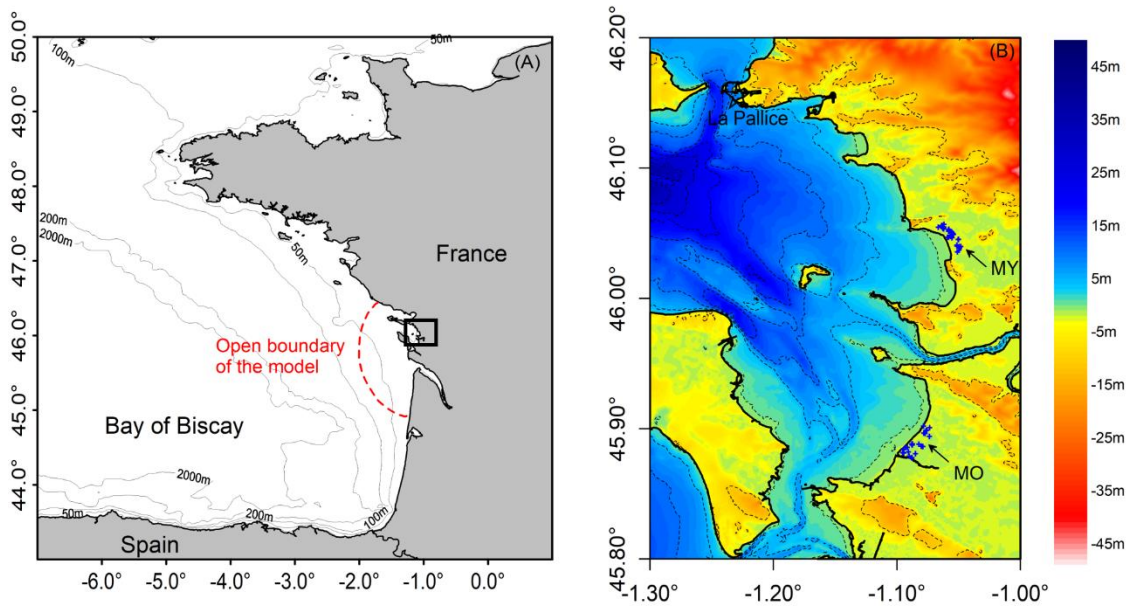
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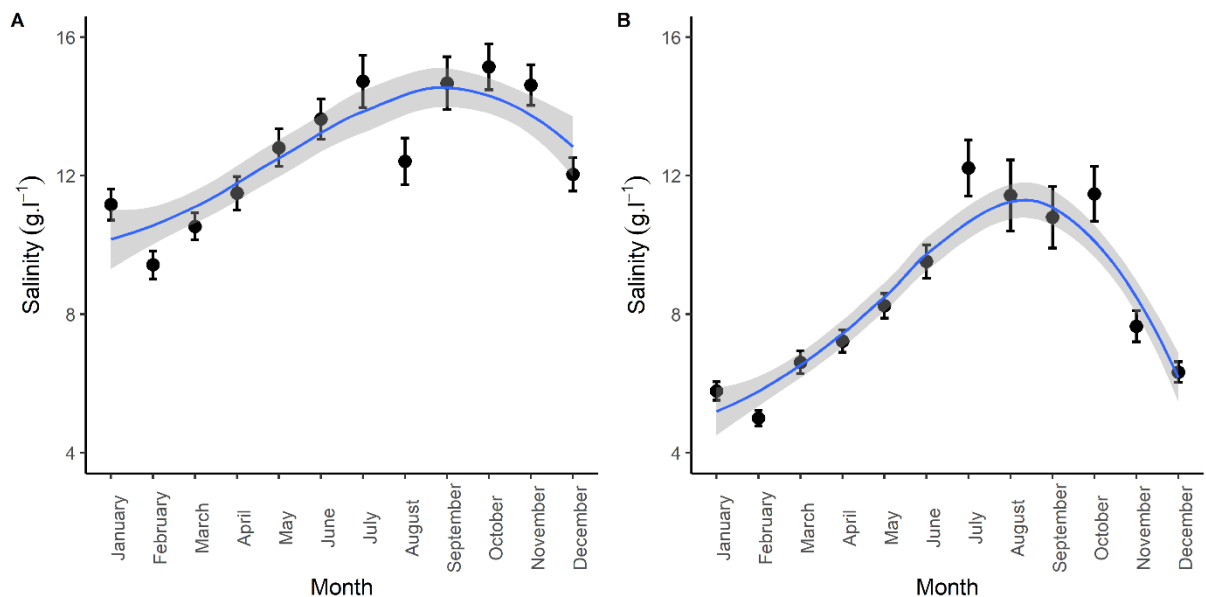
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870 Figure 1: (A) Map of the study area relative to Western France, including open
 871 boundary of the model run for estimated sea water levels, and (B) map representing
 872 the two study sites (MO and MY) and the study ponds (blue points), At MO, position
 873 of the study ponds ranged from 58 m to 1080 m from the seashore. At MY, position of
 874 the study ponds ranged from 187 m to 840 m from the seashore. La Pallice, where
 875 the tidal gauge and point use for climatic data are situated, is represented by a star.
 876 Bathymetry is indicated with the colour scale. MO (« Réserve Naturelle Nationale de
 877 Moëze-Oléron ») and MY (« Réserve Naturelle Nationale du marais d'Yves »).



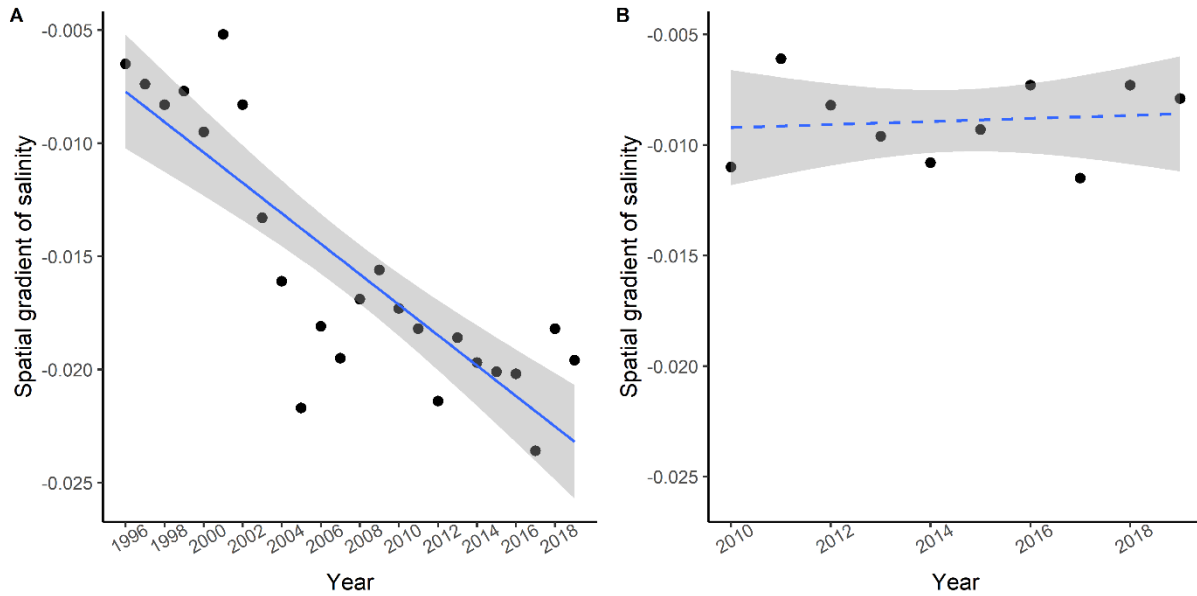
878

879 Figure 2: Variations of salinity by month at MO (A) and MY (B). Mean (24 years in
880 MO and 10 years in MY) \pm SE, and linear trend line \pm SE. MO : « Réserve Naturelle
881 Nationale de Moëze-Oléron » and MY : « Réserve Naturelle Nationale du marais
882 d'Yves »



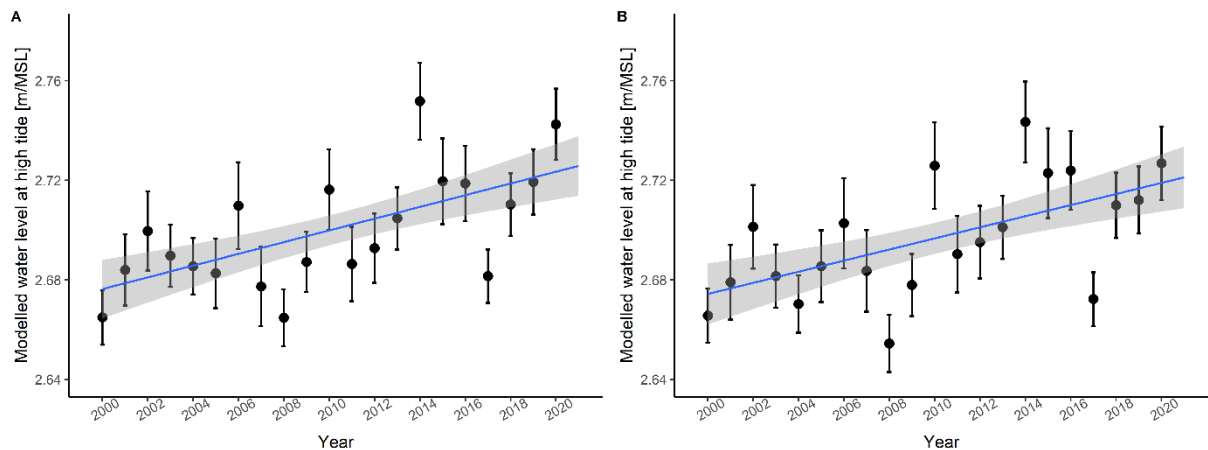
883

884 Figure 3: Variations of the spatial gradient of salinity (slope of the regression between
 885 salinity and distance to the ocean) through time, at MO (A) and MY (B). Mean (24
 886 years in MO and 10 years in MY) \pm SE. MO : « Réserve Naturelle Nationale de
 887 Moëze-Oléron » and MY : « Réserve Naturelle Nationale du marais d'Yves ». Dashed
 888 line represent a non-significant relation



889

890 Figure 4: Variations of water level at high tides by year at MO (A) and MY (B), given
891 in m/MSL (Mean Sea Level, the water level is thus given with respect to mean sea
892 level). Mean (20 years in both MO and MY) \pm SE. MO : « Réserve Naturelle Nationale
893 de Moëze-Oléron » and MY : « Réserve Naturelle Nationale du marais d'Yves »



894

895

896 Table 1: Effects of temporal scales (year, month and month²) on salinity at MO and
 897 MY (absolute values of salinity are log+1 transformed, not minimum and maximum
 898 values). MO : « Réserve Naturelle Nationale de Moëze-Oléron » and MY : « Réserve
 899 Naturelle Nationale du marais d'Yves »

Time scale	Site	Variable	Covariate	Estimate	SE	t- value	p- value
Seasonal	MO	Salinity	Month	0,006	<0,001	13,14	<0,001
	MO	Salinity	Month ²	-0,0003	<0,001	-10,41	<0,001
	MY	Salinity	Month	0,008	<0,001	13,47	<0,001
	MY	Salinity	Month ²	-0,0006	<0,001	-12,31	<0,001
Inter-annual	MO	Minimum salinity	Year	0,09	0,031	2,935	0,003
	MO	Mean salinity	Year	<0,001	<0,001	0,991	0,322
	MO	Maximum salinity	Year	-0,033	0,055	-0,606	0,545
	MY	Minimum salinity	Year	-0,481	0,042	-11,49	<0,001
	MY	Mean salinity	Year	<-0,001	<0,001	-30,48	<0,001
	MY	Maximum salinity	Year	-1,6161	0,106	-15,18	<0,001

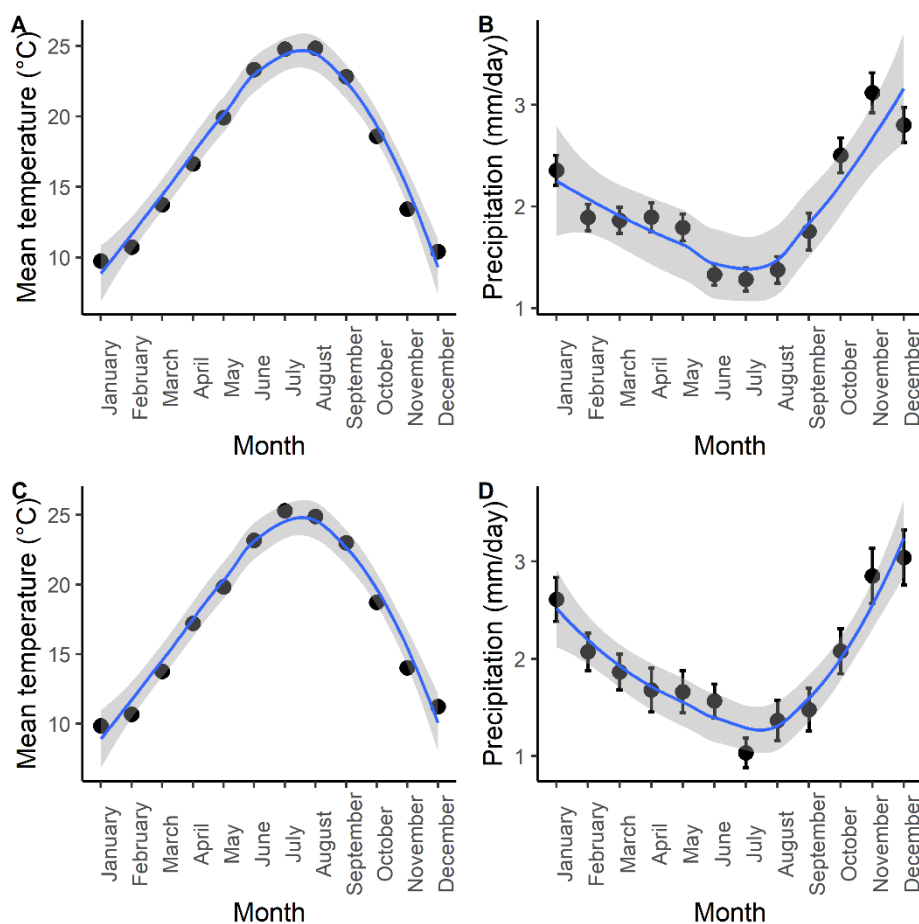
900

901 Appendix A: Ponds' characteristics: distance to the ocean, minimal, maximal and
 902 mean values of salinity (across 1996 to 2019 in MO and 2010 to 2019 in MY), and
 903 surface, estimated on QGIS 3.10. MO : « Réserve Naturelle Nationale de Moëze-
 904 Oléron » and MY : « Réserve Naturelle Nationale du marais d'Yves ».

Site	Pond	Distance to the ocean	Min salinity (g.l ⁻¹)	Max salinity (g.l ⁻¹)	Mean salinity (g.l ⁻¹)	Surface (m ²)
MO	1	57.68653298	1	45.2	19.5167832	339
	2	221.4873506	5	45.8	26.6501515	4312
	3	274.8322283	1.6	45.8	23.0836111	4238
	4	296.7595039	2	34.2	7.455	4169
	5	357.1932305	1	45	14.2644755	2198
	6	370.7487297	1	45.6	26.122027	980
	7	376.5774788	0.5	35.8	9.95729885	4482
	8	378.6115285	0.5	45.7	21.3752406	1490
	9	382.5761223	1	32.4	8.48732143	4548
	10	384.0366136	2.7	45.3	27.935731	1310
	11	432.344836	1	36.2	6.40893023	4867
	12	446.3393657	0.5	39	3.9247486	438
	13	459.340119	1.9	45	14.2698462	251
	14	464.1638429	2.5	45	24.4801714	4800
	15	498.3643205	1	28	7.17126168	5000
	16	606.0212352	3.5	45.7	24.5345856	4954
	17	722.1634794	0.9	33	5.64383621	680
	18	799.4838747	0.5	45	9.63150943	228
	19	867.3437206	0.5	42.2	6.85692641	4323
	20	952.6015984	1	35.1	7.01885246	3056
	21	1020.450705	0.7	31.8	7.25669604	4796
	22	1040.857566	1	16.8	5.5492511	400
	23	1060.621225	1	19	5.99704641	1105
	24	1079.242017	1	27	5.25384615	1296
MY	25	186.8311127	1.1	35	12.2680556	4198
	26	239.3743072	4	35.5	11.4866667	5000
	27	393.3444296	0	27.4	5.39384615	191
	28	420.0196351	5.1	40	16.1017241	1425
	29	450.0684786	1.2	19.4	7.61818182	209
	30	459.399225	1.5	31.2	7.93176471	237
	31	488.2280705	0.2	17.5	5.42686567	188
	32	489.0815413	0	28	9.81326531	190
	33	501.861769	0.5	15.8	5.159375	81
	34	506.4525037	0	26	6.48888889	153

35	511.6125876	0.4	40	5.13684211	134
36	512.4994544	1.4	30.1	9.32051282	288
37	531.4132802	2	37.7	10.9588235	67
38	534.7351455	0.4	15	4.96862745	270
39	535.2929692	0	14.5	5.30512821	154
40	582.5063774	2.5	24.8	8.99090909	686
41	589.1807029	2	26.6	9.05128205	1112
42	603.4902597	0.5	27.3	4.83802817	73
43	617.1999043	1	30.9	7.09710145	425
44	622.0270028	0.5	17.6	3.82878788	75
45	626.8756936	0	20.3	2.36136364	591
46	629.8770959	0	9	1.50483871	495
47	637.4923031	5.5	41.6	15.040404	611
48	638.8912086	3	43	13.1970297	5000
49	656.4141876	1.1	23.4	8.59275362	25
50	684.8357441	7.4	38	15.5056075	3200
51	710.1932236	0	7.2	1.74700855	1077
52	747.2916005	0	13	2.07586207	133
53	747.3792478	0	23.5	3.75042017	1056
54	772.7546576	1.7	24	6.03402062	1652
55	836.7616323	0	28	9.02842105	504

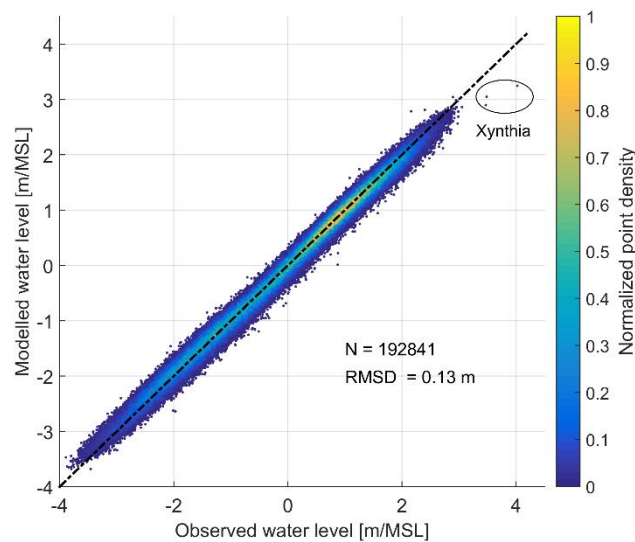
906 Appendix B: Variations of temperature (left column) and precipitations (right column)
 907 column) in MO (top line) and MY (bottom line). For both sites, these data span the
 908 study period considered (across 1996 to 2019 in MO and 2010 to 2019 in MY). We
 909 used the *easyclimate* package (Moreno and Hasenauer, 2016) on R 3.6.3 (R Core Team
 910 2020) to extract, on a daily scale, maximum temperature and total precipitation. We
 911 extracted these data from La Rochelle meteorological station (46°9'0.684"N,
 912 1°8'43.08"W) situated at 17.4 km and 26.6 km from MY and MO respectively. MO : «
 913 Réserve Naturelle Nationale de Moëze-Oléron » and MY : « Réserve Naturelle
 914 Nationale du marais d'Yves ».



915

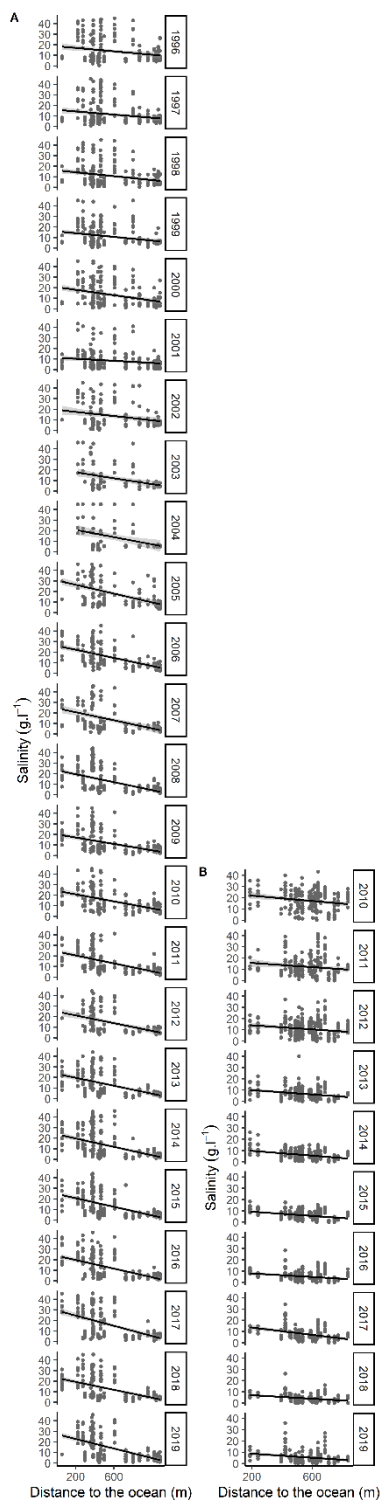
916

917 Appendix C: Comparison of observed water levels (available water level data at La
918 Rochelle tide gauge) and modelled water levels. Three estimated points were lower
919 than the observed values and corresponded to storm Xynthia. Extreme water levels
920 are only substantially underestimated during Xynthia storm, mostly because the
921 effects of short waves were not accounted for in the simulation, as discussed in Bertin
922 et al. (2014).



923

924 Appendix D: Variations of salinity with distance to the ocean across different years in
 925 at MO (A) and MY (B). MO : « Réserve Naturelle Nationale de Moëze-Oléron » and
 926 MY : « Réserve Naturelle Nationale du marais d'Yves ».



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