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

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ABSTRACT

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

1. Introduction

Coastal wetlands are situated at the boundary between the land and the sea (Janas et al., 2019). Despite a restricted extent of the interface between oceanic and terrestrial biomes, coastal wetlands represent a significant surface area worldwide (Hopkinson et al., 2019). While they play significant ecological roles (Davis et al., 2014; Hobohm et al., 2021; Hopkinson et al., 2019), sheltering a large diversity of species and habitats (Janas et al., 2019; Maynard and Wilcox, 1997) and serving a role of carbon sequestration and protection of the terrestrial environment (Barbier et al., 2008; De Battisti, 2021; Nelson and Zavaleta,

2012), coastal wetlands are currently affected by a large variety of anthropogenic threats such as eutrophication, chemical pollution, land use, invasive species, and ongoing modification of climatic conditions (Barua et al., 2021; Martínez-Megías and Rico, 2021). Among these threats, changes in salinity regimes (environmental salinization) across spatial and temporal scales relevant to coastal wetlands have been less studied to date, despite the major role of this environmental parameter in the functioning of these ecosystems (Herbert et al., 2015).

Coastal ecosystems are naturally exposed to spatial and temporal variations of salinity (Barua et al., 2021). Such natural variations of salinity (i.e. primary salinization, Herbert et al., 2015) are linked to the

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

Coastal ecosystems are also susceptible to secondary salinization, the increase in salt concentration caused by the direct actions of humans or their activities (Herbert et al., 2015; Izam et al., 2021), because of several processes operating at different temporal scales. First, ongoing climatic changes are expected to induce a significant increase in sea level (Church and White, 2011; Domingues et al., 2008; Gornitz, 1995; Herbert et al., 2015). Second, current climatic changes are expected to increase the intensity and frequency of extreme events, such as marine storms and associated surges (Dettinger, 2011; IPCC et al., 2022; Trenberth et al., 2015). Third, alterations of hydric cycles due to changes in the magnitude and timing of precipitation (Martínez-Megías and Rico, 2021; Neubauer and Craft, 2009) should affect freshwater inputs and change evaporation rates (Herbert et al., 2015; Jeppesen et al., 2020; Mills et al., 2013). Finally, other anthropogenic activities can directly lead to an increase in salinity, such as groundwater pumping or water abstraction which have been shown to increase sea water inundation and saline intrusion (Peters et al., 2021; Reid et al., 2019). All of these processes and the associated increased salinity may severely transform coastal areas (Knighton et al., 1991; Visschers et al., 2022), affecting habitat structure through landward habitat shifts (Visschers et al., 2022), and biodiversity through changes in geographic distribution (Brischoux et al., 2021; Gunter, 1956), and in turn community structure (Anufriieva and Shadrin, 2018; Cunillera-Montcusí et al., 2022; Ersoy et al., 2022; González-Sansón et al., 2022; Hart et al., 2003; Hintz and Relyea, 2019, Kendall et al., 2022).

However, despite the major ecological impacts of salinization, the spatio-temporal variations of salinity in coastal areas, and more importantly, their recent changes in response to climatic modifications remain poorly known. Particularly, if salinity variations in underground coastal water (Colombani et al., 2017; Mastrocicco et al., 2021; Mastrocicco and Colombani, 2021) or large water bodies such as lagoons (Casamitjana et al., 2019; Meredith et al., 2022) have been investigated, the impact on smaller water bodies, relevant to coastal freshwater biodiversity such as ponds, and considering different processes, is poorly understood. In order to better understand these variations in salinity, it is essential to investigate the effects of environmental factors that might influence salinization with high temporal resolution time series of salinity measurements (Lee et al., 2022), such precise measurement lacking to date. Such investigations are currently of crucial importance because they will allow assessment of the extent of salinity variations in coastal environments (either natural or induced by climate change), and thus to understand the consequences of these changes on the resilience of these ecosystems.

In this study, we investigated the spatio-temporal variations of salinity across long-term (decades) and fine temporal (monthly records) $\frac{1}{2}$

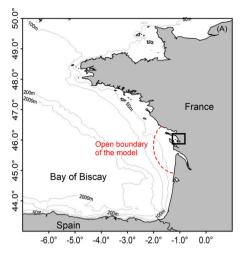
and spatial (varying distance to the coastline) resolutions in water bodies of two typical temperate coastal wetlands situated on the Atlantic coast of France. On both sites, water salinity was recorded each month (for 24 years on 24 ponds in one site, and for 10 years on 31 ponds in the other site). Based on these detailed data sets, our objectives were multiple. First, we analysed the seasonal and spatial variations of salinity. We hypothesized that salinity should be greater during summer because of reduced precipitation and higher temperatures, and that salinity should be higher closer to the seashore because of landward deposition of seaspray as well as exchanges (especially groundwater exchanges) with the marine environment. Second, we analysed the long-term changes in salinity and related these changes to concomitant variations in precipitation and temperature in order to highlight potential effects of ongoing climate change on this parameter. We hypothesized that increased temperatures and decreased precipitation over time (Briffa et al., 2009; Schär et al., 2004) should increase salinity levels across our time series. We also hypothesized that these long-term changes should interact with the spatial variations of salinity, with proportionally greater salinity increase closer to the seashore. Finally, we complemented our analyses with models of sea water levels computed in front of both sites across 2000–2020 in order to investigate whether fluctuation in this parameter can contribute to further salinization through local inundations. We hypothesized that sea water levels which occasionally provoke landward 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 Fig. 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 \pm 0.02 SE NGF; MO = 2.90 m \pm 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 = $564.52 \text{ m} \pm 59.99$, min = 57.69 m, max = 1079.24 m, Fig. 1) from January 1996 to December 2019. At MY, the salinity of 31 ponds was measured (distance to the ocean: mean = $564.29 \text{ m} \pm 24.95$, min = 186.83 m, max = 836.76 m, Fig. 1) from January 2010 (corresponding to the sea water intrusion by storm Xynthia) to December 2019. These represent small body of still water ($<5000 \text{ m}^2$), presenting similar characteristic of habitat types, surrounding and aquatic vegetation, and depth (mean depth of ponds ranging from $\sim 0.5 \text{ m}$ to 1.5 m). Some details on pond characteristics are given in Appendix A. On each pond, the salinity was recorded once per month during 24 years (at MO) and 10 years (at MY). The salinity was recorded using a portable reflactometer until 2000 (Cond 330i), and then using a conductimeter (YSI Professional Plus, ProQuatro Multiparameter Meter, and Multi 340i with



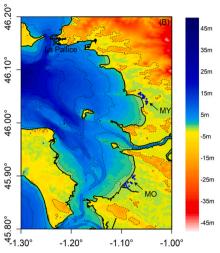


Fig. 1. (A) Map of the study area relative to Western France, including open boundary of the model run for estimated sea water levels, and (B) map representing the two study sites (MO and MY) and the study ponds (blue points). At MO, position of the study ponds ranged from 58 m to 1080 m from the seashore.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

TetraCon 325 probe), and was repeatedly measured at the same location for each pond (20 cm from the pond edge, 10 cm below the water surface).

2.2. Meteorological parameters

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

2.3. Estimates of the water levels across 20 years

To investigate the possible impact of changes in sea level on coastal wetland salinization, we simulated the hydrodynamic circulation in the study area using the numerical model SCHISM (Zhang et al., 2016), which solves the primitive equations on unstructured grids using advanced numerical methods. We used a hydrodynamic model because sea water levels strongly vary spatially while the only tide gauge available over the studied period (La Pallice, see Fig. 1) is located about 20 and 30 km to the North of both study sites. This spatial variability of water levels is due to spatial variations of tides and storm surges. Thus, Dodet et al. (2019) showed that, over the modelled domain and over the period 1998-2018, the mean tidal range varied from 3.28 to 3.83 m and the maximum storm surge varied from 1.15 to 1.57 m. To a lesser extent, the tide gauge data has some gaps while the model is continuous over the studied period. SCHISM was implemented in 2DH (two dimensional horizontal, which means that the model uses one single layer on the vertical) over the 'Pertuis Charentais' area with a spatial resolution ranging from 2000 m along the open boundary to 100 m near the shoreline, as described in Savelli et al. (2019). The model starts at mean sea-level and uses a ramp of 1 day. A sensitivity analysis reveals that the model converges when using longer ramps, which is due to the small dimensions of the modelled domain. The model is forced by amplitudes and phases of the 18 main tidal constituents, linearly interpolated from the regional tidal model of Bertin et al. (2012) and fields of sea-level pressure and 10 m winds originating from the CFSR reanalysis (Saha et al., 2010). The hydrodynamic model used in this study is well-established and was previously developed to compute sediment transport and morphological changes (Guerin et al., 2016) and bed shear stress and biofilm resuspension in front of MO (Savelli et al., 2019). The model was run over the period 2000–2020 and hourly time series of water levels were extracted in front of each studied wetland. Due to the 2DH (two dimensional horizontal) barotropic configuration, the model cannot capture long-term changes in sea levels due to large-scale circulation patterns and global warming. In order to account for these processes which are relevant at the scale of the studied period (2000–2020), yearly mean sea levels observed at the nearby tide gauge of La Rochelle (data available at https://data.shom.fr/) were computed and linearly added to model outputs. This approach was validated against the available water level data at La Rochelle tide gauge, which are reproduced with a root mean squared discrepancy of 0.13 m (see Appendix C). Extreme water levels are only substantially underestimated during Xynthia storm, mostly because the effects of short waves were not accounted for in the simulation, as discussed in Bertin et al. (2014).

2.4. Statistical analyses

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

2.4.1. Seasonal variations of salinity

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

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

2.4.2. Spatial variations of salinity

We analysed salinity records according to distance to the ocean of the ponds where salinity was recorded, by computing LMMs with each value of salinity recorded as dependent variables, distance to the ocean as the

covariate (log+1 transformed), and pond as a random effect.

2.4.3. Long term changes in salinity

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

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

2.4.4. Estimates of the high tides' water level

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

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

3. Results

3.1. Seasonal variations of salinity

Across the whole study period, salinity varied seasonally (monthly

variation), according to a quadratic form, with maximum salinity attained in summer on both sites (Fig. 2, Table 1), and maximum values also attained in October and November in MO (Fig. 2, Table 1). In both sites, these variations were significantly correlated to temperature, with salinity increasing with increasing temperature (MO: Estimate = 0.002, SE < 0.001, t-value = 14.780, p-value<0.001; and MY: Estimate = 0.002, SE < 0.001, t-value = 8.96, p-value<0.001), and to precipitation, with salinity decreasing with increasing precipitation (MO: Estimate < -0.001, SE < 0.001, t-value = -2.368, p-value = 0.019; MY: Estimate < -0.001, SE < 0.001, t-value = -3.645, p-value<0.001).

3.2. Spatial variations of salinity

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

3.3. Long term changes in salinity

Across the whole study period, salinity decreased at MY, considering either mean, minimum, or maximum values (Table 1). At MO, results were more complex with a significant increase in minimal values of salinity across time (Table 1), and no significant trends for maximal and mean values (Table 1). The long-term variations of salinity were linked to precipitation, with salinity decreasing with increasing precipitation at both sites (MO: Estimate $<-0.001,\ SE<0.001,\ t-value=-3.562,\ p-value<0.001;\ and MY: Estimate <math display="inline"><-0.001,\ SE<0.001,\ t-value=-3.282,\ p-value=0.001),\ but not to temperature (at MO: Estimate=-0.011,\ SE=0.016,\ t-value=-0.695,\ p-value=0.487;\ and\ at MY: Estimate=0.066,\ SE=0.044,\ t-value=1.524,\ p-value=0.130).$

Across years, the spatial gradient of salinity (slope of the relationships between salinity and distance to the coastline) increased at MO (Estimate $<-0.001,\,\mathrm{SE}<0.001,\,\mathrm{t\text{-}value}=-7.449,\,\mathrm{p\text{-}value}{<0.001},\,\mathrm{Fig.}\,3A),$ an effect that was marginally related to decreased precipitation (Estimate $<0.001,\,\mathrm{SE}<0.001,\,\mathrm{t\text{-}value}=1.881,\,\mathrm{p\text{-}value}=0.073),\,\mathrm{but}$ not to temperature (p-value =0.238). At MY, there was no difference in the strength of the spatial gradient of salinity (Estimate $<0.001,\,\mathrm{SE}<0.001,\,\mathrm{t\text{-}value}=0.327,\,\mathrm{p\text{-}value}=0.752,\,\mathrm{Fig.}\,3B),\,\mathrm{and}$ no relationships with temperature or precipitation (both p-values >0.269).

3.4. Estimates of the high tides' water level

In both sites, water levels at high tides increased over time (at MO: Estimate = 0.002, SE < 0.001, t-value = 4.735, p-value < 0.001; at MY: Estimate = 0.002, SE < 0.001, t-value = 4.330, p-value < 0.001; Fig. 4).

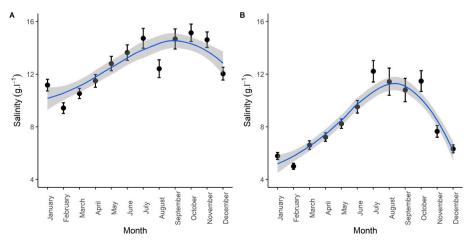


Fig. 2. Variations of salinity by month at MO (A) and MY (B). Mean (24 years in MO and 10 years in MY) \pm SE, and linear trend line \pm SE. MO: « Réserve Naturelle Nationale de Moëze-Oléron » and MY: « Réserve Naturelle Nationale du marais d'Yves »

Table 1

Effects of temporal scales (year, month and month²) on salinity at MO and MY (absolute values of salinity are log+1 transformed, not minimum and maximum values).

MO: « Réserve Naturelle Nationale de Moëze-Oléron » and MY: « Réserve 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	2935	0,003
	MO	Mean salinity	Year	< 0,001	< 0,001	0991	0,322
	MO	Maximum salinity	Year	-0,033	0055	-0,606	0545
	MY	Minimum salinity	Year	-0,481	0042	-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

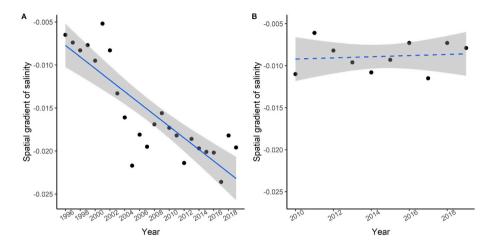


Fig. 3. Variations of the spatial gradient of salinity (slope of the regression between salinity and distance to the ocean) through time, at MO (A) and MY (B). Mean (24 years in MO and 10 years in MY) ± SE. MO: « Réserve Naturelle Nationale de Moëze-Oléron » and MY: « Réserve Naturelle Nationale du marais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

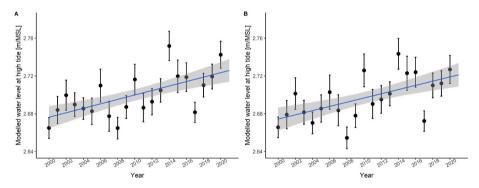


Fig. 4. Variations of water level at high tides by year at MO (A) and MY (B), given in m/MSL (Mean Sea Level, the water level is thus given with respect to mean sea level). Mean (20 years in both MO and MY) ± SE. MO: « Réserve Naturelle Nationale de Moëze-Oléron » and MY: « Réserve Naturelle Nationale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

These data show that open water surface can exceed the height of the protective coastal sand dunes during significant amount of 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.

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

As expected from landward deposition of seaspray and groundwater exchanges, we found that, overall, salinity was higher in coastal ponds situated closer to the coastline, despite the small spatial extent of our study sites (situated from ~50 m to 1000 m from the coastline). Importantly, we found that, over time, the strength of this spatial gradient of salinity increased significantly on one of our study sites (MO). That is, the slope of the relationship between pond salinity and distance to the coastline increased through time. This effect was mainly driven by increased salinity closer to the seashore rather than by decreased salinity farther from the seashore, which might be due to increase groundwater infiltration over time (Colombani et al., 2017; Mastrocicco et al., 2021; Mastrocicco and Colombani, 2021). Such a result highlights a remarkable spatial heterogeneity in the susceptibility of these coastal ponds to salinization over a relatively small spatial scale. Complementarily, this result reinforces the notion that ongoing climate change is currently inducing significant salinization, and that this process strongly alters the spatial gradient of salinity. Despite the strengthening of the spatial gradient of salinity, we did not found a consistent trend of salinity over time, but found contrasted responses in our two study sites. Indeed, in one of our study sites (MO), salinity (maximum and mean) remains relatively stable across time, but minimum values of salinity gradually increased through time (at a mean of $0.09 \text{ g l}^{-1}/\text{year}$). This site was spared from marine submersion linked to storm Xynthia due a protection dune (Lorrain-Soligon et al., 2021), but minimal values still seems to be affected. The second site however (MY), was completely submerged by storm Xynthia (Lorrain-Soligon et al., 2021). Our salinity recordings started at the onset of this marine submersion and documented the temporal dynamics of this parameter following a massive and brutal intrusion of sea water. We showed that salinity was maximum following storm Xynthia (due to sea water intrusion and increased salinity) and progressively decreased through time to reach lower and temporally stable values at ~3 years post-storm (see Lorrain-Soligon et al. [2021] for some salinity values recorded before Xynthia). These lower values remained stable through time, although we emphasize that the following 7 years are likely too short of a time scale to investigate potential long-term changes in salinity. Importantly, other studies have shown that effects of this marine submersion were long-lasting both for fluxes of marine elements (salt, sediments, and organic matter) through the food web (Lorrain-Soligon et al., 2022) and for the direct negative impact of salinization on biodiversity (Lorrain-Soligon et al., 2021) In this study, while we emphasize a decrease in salinity following storm Xynthia, the salinity levels recorded 7 years after the storm (7.23 g l^{-1} in 2017 and 4.16 g l^{-1} in 2018) are well beyond salinity levels recorded before the storm on the same area $(2.53 \text{ g l}^{-1} \text{ in } 2007, \text{ see Lorrain-Soligon et al., } 2021)$. We thus highlighted gradual as well as brutal changes in salinity in these coastal wetlands, which might both impact coastal ecosystems (Delaune et al., 2021). Indeed, chronic salt exposure to gradual increase in salinity might gradually transform coastal ecosystems through acclimatory

processes or epigenetic changes (Venâncio et al., 2022), while brutal changes can induce species displacements or direct mortality (Lorrain-Soligon et al., 2021).

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

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

Whatever the underlying causes, salinization is known to negatively affect the rich biodiversity of coastal ecosystems (Bradley, 2009; Evans and Kültz, 2020; Hellebusi, 1976; Schultz and McCormick, 2012). Indeed, salinity higher than 4 g l^{-1} might transform fungal and microbial communities (Canhoto et al., 2022), as well as amphibian communities (Lorrain-Soligon et al., 2023), and salinities higher than 7 g l⁻¹ can be detrimental for invertebrate communities (Venâncio et al., 2020) But salinization will also affect hydrology by destabilizing the water column (Dugan and Arnott, 2022; Koretsky et al., 2012) biogeochemistry (e.g. lack of oxygenation, Ladwig et al., 2021; Dugan and Arnott, 2022), and soils characteristics (Neubauer et al., 2013). Taken together, these various consequences of coastal wetland salinization suggest that salinity fluctuations are likely to dramatically transform - and impact the functioning of - coastal ecosystems (Cañedo-Argüelles et al., 2013; Cunillera-Montcusí et al., 2022; Denny, 1994; Herbert et al., 2015; Visschers et al., 2022). Our study allows to emphasize that even ponds situated farther from the seashore are at risk of salinization and should be considered when planning conservation measure to mitigate this global change. Despite growing interest on the outcome of human-induced salinization, we emphasize that the consequences of these processes at large spatial and temporal scales are still to be investigated (Cunillera-Montcusí et al., 2022), and can be site-specific. Further research should focus on the impacts on biodiversity in relation to the spatio-temporal salinity gradients. In addition, forecasting models should incorporate more information on critical factors that might influence salinity changes, across large spatial and temporal scales, not only for water bodies but also for soil, as terrestrial

salinization is a critical but overlooked process (Ayub et al., 2020; Greenway and Munns, 1980; Rath and Rousk, 2015; Singh, 2016).

5. Conclusion

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

Credit author statement

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

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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