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Some like it salty: Spatio-temporal dynamics of salinity differentially affect anurans and caudates in coastal wetlands

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Abstract

1. Coastal wetlands are naturally subjected to salinity, which is expected to increase through global climate changes. Most species will be affected by these changes, leading to major consequences for community structure and ecosystem functioning.
2. We investigated variation of salinity of temporary wetlands across spatial (1,000m from the ocean) and temporal (across three breeding season) scales relevant to coastal biodiversity and used amphibians (six species, sampled across one breeding season) as a model to investigate the consequences of the spatio-temporal variation of salinity in 24 ponds situated on the Atlantic coast of France.
3. We show that salinity is a highly dynamic environmental variable that varies widely both across spatial and temporal scales. The spatio-temporal dynamics of salinity are a critical factor structuring amphibian communities that affect the main amphibian phylogenetic groups (caudates vs. anurans) differently. Temporal variation in salinity disrupts the match between salinity selected by reproductive adults and those experienced later by their developing offspring, which negatively affect reproductive success.
4. Future changes in coastal salinity are likely to affect the structure and functioning of these ecosystems, excluding salt-intolerant species and eventually leading to less diverse communities of salt-tolerant species.

KEYWORDS

abundances, amphibians, life stages, reproductive success, species richness

1 | INTRODUCTION

Coastal wetlands are among the most diverse and productive ecosystems on earth (Hobohm et al., 2021). Situated at the interface between land and open sea (Janas et al., 2019), coastal areas are composed of a complex mosaic of biotopes concentrated across

restricted spatial scales, and shelter a large diversity of species and habitats (Janas et al., 2019; Maynard & Wilcox, 1997). In addition to their rich biodiversity (Maynard & Wilcox, 1997), coastal wetlands also provide ecosystem services with key role in oxygen and nutrient fluxes and primary production (Janas et al., 2019). However, coastal wetlands are particularly vulnerable to ongoing global

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changes (Barua et al., 2021; Hobohm et al., 2021; Martínez-Megías & Rico, 2021).

Among the various factors that affect these rich habitats, salinisation is an important – yet understudied – threat (Cunillera-Montcusí et al., 2022). Coastal wetlands are naturally subjected to spatially and temporally variable salinity mainly as a result of landward sea spray deposition, which creates a spatial and temporal salinity gradient (Benassai et al., 2005; Estévez et al., 2019; Fu et al., 2021; Ranjbar & Ehteshami, 2019). However, salinity is expected to increase locally as a result of several processes all linked to anthropogenic activities and ongoing climate changes (Le et al., 2019; Reid et al., 2019). In addition to the impacts linked to sea-level rise (Church & White, 2011; Vermeer & Rahmstorf, 2009), extreme storm events (Maxwell et al., 2019) and specific anthropogenic activities (i.e., groundwater pumping; Peters et al., 2021; Reid et al., 2019), salinity also can increase in temperate areas as a consequence of current modifications of climatic conditions (i.e., increased temperature and decreased precipitation; Çolak et al., 2022; Schroeder et al., 2017). Freshwater inputs to coastal wetlands are reduced because of decreasing riverine flows (Schroeder et al., 2017). Complementarily, evaporation can seasonally exceed precipitations – especially in spring and summer – and thus increase the salinity of coastal wetlands subjected to moderate salt input by sea sprays (Benassai et al., 2005). Taken together, all of these processes are expected to significantly affect the heterogeneity and associated spatio-temporal dynamics of salinity (Ghalambor et al., 2021).

The importance of considering salinisation and its consequences for wildlife is linked to the fact that most species have to regulate the osmolality of their body fluids in order to survive (Hoffmann et al., 2009; Potts, 1954). Most species display physiological mechanisms that aim at regulating water and ion fluxes to maintain homeostasis (i.e., osmoregulation; Evans & Kültz, 2020; Schultz & McCormick, 2012). These mechanisms are metabolically expensive and can trade-off with other functions (Herbert et al., 2015), and, ultimately, may jeopardise survival (Cañedo-Argüelles et al., 2013; Hall & Burns, 2002; Moorman et al., 1991). Although all trophic levels can be affected by increased environmental salinity (Hintz & Relyea, 2019), there is a wide variation in susceptibility among species (Castillo et al., 2018; Halse et al., 2003; Venâncio et al., 2022; Venâncio, Castro, Ribeiro, Antunes, Abrantes, et al., 2019), and among life stages (Paiva et al., 2020). In freshwater environments, early life stages of amphibians, mussels and zooplankton have been identified as the most sensitive taxa to salinity exposure, whereas some fish species, water moulds and macrophytes can be more tolerant (Venâncio et al., 2022). This species-specific susceptibility to salinity can have major consequences for ecosystem functioning (Cunillera-Montcusí et al., 2022). Indeed, susceptible species can avoid elevated salinity through habitat selection (Venâncio et al., 2020), thereby inducing shifts in home ranges size or location of intolerant species (O'Dell et al., 2021). Ultimately, these processes can reduce biodiversity (Hébert et al., 2022; Hintz & Relyea, 2019) and change community structure and composition (Findlay & Kelly, 2011; Hart et al., 2003; Hintz & Relyea, 2019; Venâncio, Castro, Ribeiro, Antunes, & Lopes, 2019).

Amphibian taxa are particularly susceptible to salinity (Venâncio et al., 2022). Indeed, amphibians are characterised by a relatively permeable skin that allows not only gas exchanges, but also ion and water fluxes (Hillyard et al., 2007; Wake & Koo, 2018), and relatively low dispersal abilities constraining movements when environmental conditions are harsh (Wells, 2007). As a consequence, amphibian species richness and distribution decrease with increasing salinity (Başkale & Kaya, 2009; Karraker et al., 2008; Smith et al., 2007), suggesting that salinity is a limiting factor for amphibian diversity (Hall et al., 2017). Conversely, some amphibian species have been shown to live and reproduce in habitats ranging from brackish to nearly marine (Greenwald, 1972; Hopkins & Brodie, 2015), which suggest that salt tolerance may not be as rare as it is been assumed previously, especially for species occurring in coastal habitats (Hopkins et al., 2016; Hopkins & Brodie, 2015), and that tolerances to salinity vary between species (Babbitt et al., 2006; Brown & Walls, 2013; Hopkins & Brodie, 2015; Hua & Pierce, 2013; Lorrain-Soligon et al., 2021).

In addition to these species-specific tolerances to salinity, amphibians also can display variable levels of tolerance to salinity within species. Indeed, most amphibians are characterised by a complex biphasic life cycle, with eggs and tadpoles developing in aquatic habitats and adults displaying various levels of terrestriality (Wells, 2007). Accordingly, eggs and larvae are less tolerant to elevated salinity than adults (Albecker & McCoy, 2017), and some evidence suggest that reproductive individuals can express habitat selection and avoid saline water for egg-laying (Albecker & McCoy, 2017; Haramura, 2008; Lorrain-Soligon, Robin, et al., 2022; Viertel, 1999) to improve their reproductive success (Lukens & Wilcoxon, 2020; Tornabene et al., 2021). Taken together, these elements suggest that variability in both within- and between-species susceptibility to salinity could be a major factor determining the structure of amphibian coastal communities (Lorrain-Soligon et al., 2021) and may significantly affect within- and between-species distribution across the spatial and temporal salinity gradient. However, the current literature lacks data on the effect of salinity across amphibian community (but see Lorrain-Soligon et al., 2021; Smith et al., 2007), across multiple sites and a long time scale, which is key to understanding how they will behave to the predicted increase in salinity.

In order to better understand how salinity changes naturally in coastal environments and how amphibians can respond to such spatial and temporal variation, we studied the amphibian community in a typical coastal wetland situated on the Atlantic coast of France, where amphibians are subjected to natural salinity variations. Firstly, we assessed the spatial (distance to the coastline) and temporal (seasonal across spring and summer) dynamics of salinity during 3 years in 24 coastal ponds. Secondly, on the same sites during one breeding season, we assessed amphibian presence and abundances across key life stages (adults, larvae and metamorphs) to investigate how community and diversity vary with salinity. Thirdly, we also investigated how the spatio-temporal dynamics of salinity can affect the fitness of individuals by quantifying malformations of larvae and metamorphs, as elevated salinity can alter embryonic and larval

development and induce malformations (Hopkins et al., 2013). We hypothesised that amphibian diversity should decrease with increasing salinity (Smith et al., 2007) as most amphibian species seem to be highly susceptible to salinity, that larvae should be present only in low-salinity ponds, as they are less tolerant to elevated salinity compared to adults (Albecker & McCoy, 2017), and that localised seasonal increase of salinity throughout the embryonic and larval development should negatively affect offspring quality because of the detrimental effects of salinity on development (Lukens & Wilcoxon, 2020; Tornabene et al., 2021).

2 | METHODS

2.1 | Study site and sampling

The study was carried out on a coastal wetland from the Eastern Atlantic coast (Réserve Naturelle Nationale de Moëze-Oléron, France, 45°53'33.36"N, 1°04'59.16"W). This site is composed of a continuum of habitat types (brackish and freshwater marshes and ponds) with increasing distance from the seashore (Figure 1).

We surveyed 24 ponds, during 32 sessions that occurred between 31/03/2021 and 12/07/2021 (Figure 1). Twenty ponds were prospected during 32 sessions, three ponds were prospected during three sessions, and one pond was prospected during 18 sessions. Each pond was prospected at an even number of night and day sessions. Successive sessions at each site were separated by a minimum of 24h and a maximum of 5 days. These ponds were chosen to express a large salinity gradient, which vary during the season. Characteristic of all ponds and number of visits are given in Table S1.

For each session, we measured water salinity (g/L) and temperature (°C) using a conductimeter (YSI Professional Plus) at 15 cm

deep. We also estimated the percentage of surface area covered by aquatic vegetation. Additionally, to complement our measures of salinity performed in 2021 and better assess the temporal variations of salinity, we aggregated data of pond salinity recorded once a month in April, May, June and July in 2018 and 2019 for 20 of the 24 ponds studied in 2021, using the same methodology as that used in 2021.

The surface area of each pond as well as its distance to the ocean at high tide were measured using QGIS 3.4.7. Both variables varied widely across our study sites (surface area 36–3,250m² [mean 490.47m² ± 159.21 SE]; distance to the ocean 30–796m [356.10m ± 47.64m SE]) but were not related to each other (Pearson correlation test: $r = -0.088$, $p\text{-value} = 0.712$).

For each prospection, we used three complementary survey methods to assess abundance of amphibian species. First, during diurnal surveys, we used binoculars at a distance of 10m from the pond edges to count individuals present on the whole water surface and on the edges of the ponds. Second, during diurnal and nocturnal sessions, we completed this survey by counting all individuals visible (≤ 2 m on land or in water) by slowly walking around the pond (with a headlamp at night), and searching under cover objects situated up to 2m from its edge on land to search for both hidden anurans and caudates. Finally, these visual surveys were complemented by direct sampling (using a net with fine mesh [1-mm]) to assess the presence of secretive larvae. To standardise this survey method, we sampled a pond according to its perimeter. We performed five dip netting manoeuvres every 10m. Such direct sampling also allowed us to ascertain whether individuals display malformations or abnormalities (Hopkins et al., 2013). We checked for the presence of malformation in all species and life stage captured, and these malformations consisted of oedema, axial malformations, reduced tail size, and skin infections. These complementary methods allowed us to assess the abundance of larvae, metamorphic or adult individuals for each species.

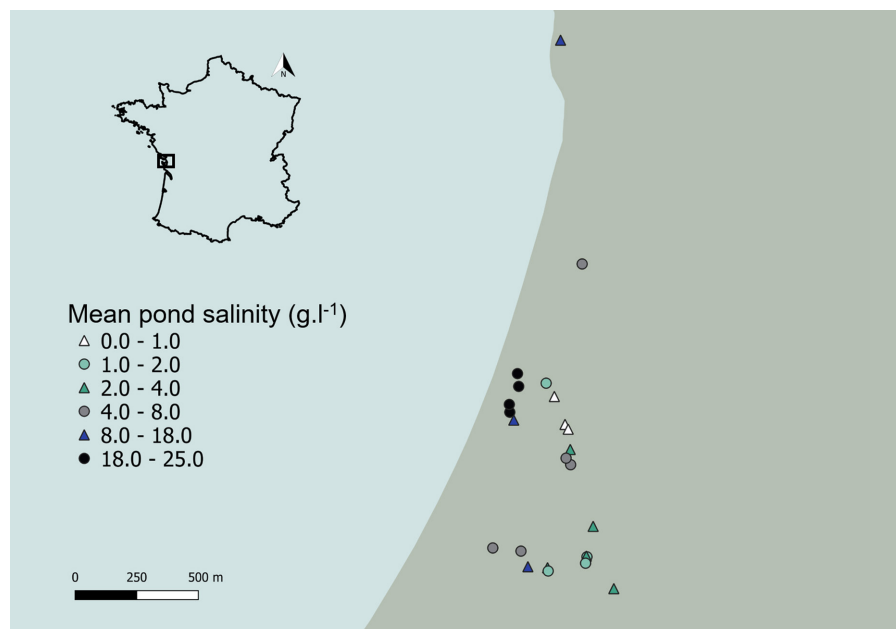


FIGURE 1 Location of the 24 study ponds in western France, with mean salinity during the whole study period (from 31/03/2021 to 12/07/2021).

This protocol led to the identification of six amphibian species (four anurans, two caudates): the green frog *Pelophylax* sp. (composed of a hybridogenic complex indistinguishable by sight; Dufresnes et al., 2017), the Mediterranean tree frog (*Hyla meridionalis*), the common parsley frog (*Pelodytes punctatus*), the Western spadefoot toad (*Pelobates cultripes*), the palmate newt (*Lissotriton helveticus*) and the marbled newt (*Triturus marmoratus*).

2.2 | Review of salt tolerance

We collected published data on salt tolerance in caudates and anurans obtained both during field studies and under laboratory conditions. We complemented the seminal review of Hopkins and Brodie (2015) with additional data published since then (Table S2). For consistency, we used the same methodology as Hopkins and Brodie (2015) to extract salinity data: "For every species where environmental salinity was measured at the time of field observation, we determined the maximum salinity concentration in which the animal was found. There are many measurement units used in the salinity literature, with very little standardisation or consistency (e.g., conductivity, specific conductance, mOsm/L, g/L, mg/ml, mequiv/L, specific gravity, ppt [parts per thousand], ppm [parts per million], psu [practical salinity unit]). To facilitate accurate comparison among species and studies, we converted all values into ppt (g/L Cl⁻). For those species whose salt tolerance had been experimentally examined in the laboratory, we determined the maximum upper limit of tolerance by arbitrarily defining this as the concentration of salt in which >50% of individuals survived. For non-lethal measures, we recorded the upper limit as that concentration which first caused a statistically significant negative effect." In addition, as in Hopkins and Brodie (2015), when a species had been found to occur in multiple salinities, we retained in our collection (see Table S2) the highest value.

These data were not used to perform quantitative statistical analyses, but we provide qualitative comparisons in Section 4 below.

2.3 | Data analysis

2.3.1 | Spatio-temporal variation in salinity

The spatio-temporal variation in salinity at our study sites was investigated with a linear mixed model (lmer) with salinity as a dependent variable, distance to the ocean, day of the year (the number of days since 01/01/2021), and their interaction as covariates, and pond as random effect, using all salinities measured during the 32 sessions. For clarity, only three dates are represented in Figure 2 corresponding to the beginning (31/03/2021), middle (20/05/2021) and end (12/07/2021) of the survey. To complement our measures of salinity performed in 2021 and to better assess the temporal variations

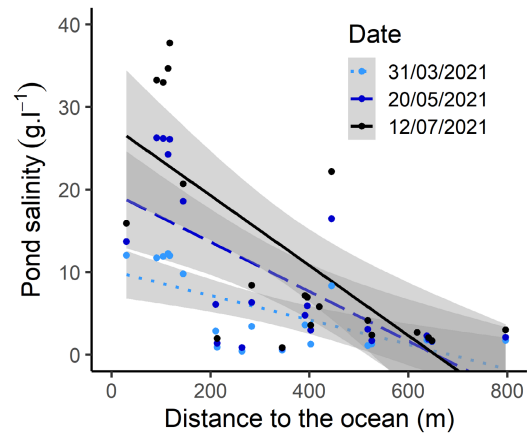


FIGURE 2 Spatial (according to distance to the ocean) and temporal (across surveys) variation of salinity on 24 coastal ponds. For clarity, only data corresponding to the beginning (31/03/2021), middle (20/05/2021) and end (12/07/2021) of the survey are represented. Points are observed values, lines indicate relationships with increasing distance from the seashore and grey shadings indicate 95% confidence intervals.

of salinity, we aggregated pond salinity data recorded in April, May, June and July in 2018 and 2019 for 20 of the 24 ponds studied in 2021 with all of the data recorded in 2021. The temporal variations of salinity were then investigated using lmer with distance to the ocean, day of the year, and their interaction as covariates, and pond and year as random effects. We previously tested for the effect of year to see if there was a difference in salinity between years, by setting a lmer with year as a dependent variable and pond as a random effect, but we found no variations between years (Sum Sq=32.356, $F_{1,771}=2.732$, $p=0.099$).

2.3.2 | Species presence and abundances

In order to model each species abundance, we used the N-mixture method of Royle (2004). This method allows estimating abundance of species using multiple counts of unmarked individuals, taking into account imperfect detection probability, and for variables influencing species detection and occupancy (Royle, 2004). For anuran species, we modelled for each species the estimated abundance of adults, metamorphs and larvae. Low sample sizes (three observations for each group) precluded these analyses for adult *P.punctatus* and adults and metamorphic individuals of *P.cultripes*. For caudate species, we modelled for each species the estimated abundance of adults and larvae. For the two groups (anurans and caudates), we also computed the same statistics using the abundance of all species considering each life stage separately (*Pelophylax* sp., *H.meridionalis*, *P.punctatus* and *P.cultripes* in anurans, and *L.helveticus* and *T.marmoratus* in caudates).

For each species and each developmental stage, we thus ran N-mixture models with the matrix of the 32 observations of the given

species and stage on the 24 study ponds, and tested a combination of models including, as variables explaining occupancy, maximum salinity recorded during the whole study period, its quadratic form, aquatic vegetation, the interaction between aquatic vegetation and either maximum salinity or the quadratic form of maximum salinity, and the additive effect of the surface area of the pond. Aquatic vegetation was always excluded during the model selection procedure. Maximum salinity was selected, instead of any other values of salinity, because maximum salinity represents the most constraining level of salinity that may influence habitat selection throughout the breeding season. It allows us to test whether adults could potentially predict temporal change in salinity that their larvae will experience later. For all models, we also tested if detection probability was temperature-dependent (using water temperature data recording at each pond during each prospection), as well as dependent on the day of the year (and its quadratic form, which was always excluded during the model selection procedure) or if it was constant over time. We used Poisson regression which fitted well our count data, except for the two caudate species, where abundance was lower and for which we used a zero inflated Poisson distribution. The best model was retained with selection by Akaike information criterion (AIC). The estimated abundances were represented using the package *ggeffects*.

In order to model the richness of amphibians' species, we used generalised linear mixed models (glmers) with Poisson or Zero Inflated Poisson distribution. We evaluated species richness of adults, larvae, metamorphs, and total (adults, larvae and metamorphs together) separately for anurans and caudates, and finally estimated total species richness regrouping all anuran species and all caudate species for all life stages. In our models, we included as covariates salinity measured at each prospection, its quadratic form, the interaction between aquatic vegetation and either salinity or the quadratic form of salinity, and the additive effect of the surface area of the study ponds. Pond was set as a random effect. We retained the best model with selection by AIC. The estimated specific richness were represented using the package *ggeffects*.

2.3.3 | Salinity and life stages

Differences in susceptibility (salinity tolerated by individuals) between life stages (analysed on all species grouped together) were investigated with lmer with salinity as a dependent variable (i.e., all pond salinities for prospection in which individuals were found – when no individuals were found, the pond and its associated salinity were not used in this analysis), day of the year (the number of days since 01/01/2021), life stages, and their interaction as dependent variables, with pond as random effect. This allowed us to highlight the mean salinity in which each life stage was found, and to compare with other life stages. We also provided empirical data on the minimum, maximum and mean pond salinity in which each life stage of each species were found, as well as the date of first and last observation (Table 1).

2.3.4 | Malformations occurrence

In order to assess the influence of pond salinity on occurrence of malformed individuals (analysed on all species grouped together), we used Poisson glmers with number of malformed individuals as a dependent variable, pond salinity or day of the year as a covariate, and pond as a random effect.

All statistical analysis were performed using R 3.6.3 (R Core Team, 2020) and Rstudio version 1.1.419.

3 | RESULTS

3.1 | Spatio-temporal variation of salinity

Considering only 2021, salinity varied with time (Sum Sq=3,353.9, $F_{1,24}=15.981$, $p<0.001$), distance to the ocean (Sum Sq=74.5, $F_{49,535}=17.406$, $p<0.001$), and their interaction (Sum Sq=1,307.3, $F_{49,535}=6.229$, $p<0.001$). Indeed, salinity decreased when distance to the ocean increased, but increased with date (Figure 2). During the whole survey, mean salinity among the five ponds closest from the ocean was of 22.19 g/L (± 2.18 SE) and mean salinity among the five ponds the farthest from the ocean was of 1.96 g/L (± 0.11 SE). Across our survey period, salinity ranged from 0.44 to 12.26 g/L at the beginning of the breeding season to 0.89 to 37.73 g/L at the end of the breeding season.

Data of salinity recorded in 2018, 2019 and 2021 in 20 study ponds yielded similar results, with salinity seasonally increasing in ponds (Estimate=0.072, SE=0.004, $t=20.346$, $p<0.001$), and increasing closer to the ocean (Estimate=-0.030, SE=0.006, $t=-4.631$, $p<0.001$), but no interaction between distance to the ocean and day of the year.

3.2 | Species presence and abundances

Overall, amphibians were present in 20 (83.33%) of the 24 surveyed ponds. Ponds that did not shelter any species during the whole breeding season were characterised by higher salinity both at the beginning (9.80 g/L ± 0.99 SE) and the end of the survey (30.45 g/L ± 9.56 SE). Detailed data on the minimum and maximum salinity for each species and life stages are given in Table 1.

Green frogs were found in high-salinity ponds (16.19 g/L for one individual and 15 g/L for two individuals). Except for these anecdotal observations, all anuran species were found in ponds where salinity was below 9 g/L (Table 1). In caudates, no individual was found in ponds where salinity exceeded 4 g/L (Table 1).

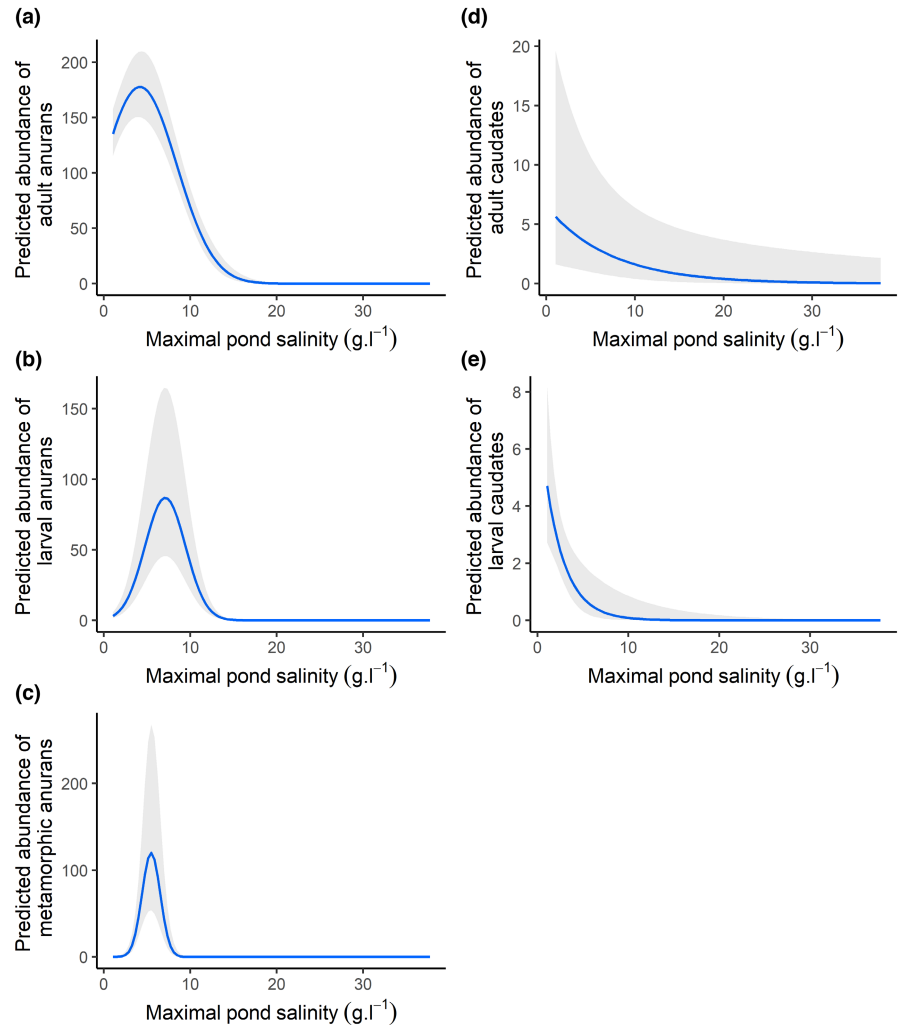
For all anurans species and all life stages, we found a significant quadratic response of abundance to maximum salinity, with abundance being higher at intermediate salinities (Figure 3A–C; Tables 2, S3). For some, but not all, anuran species, we also found that increasing pond surface area increased abundance of individuals (Tables 2, S3). Lastly, there was no effect of aquatic vegetation (alone or in

TABLE 1 Presence of each developmental stage of each species according to pond salinity (min, max and mean \pm SE).

Group	Species	Life stage	Salinity (g/L)			Average	SE	Number of ponds	Number of observations	Total number of individuals	Mean presence	First observation	Last observation
			Min	Max	Max								
Anurans	<i>Pelophylax</i> sp.	Adults	0.14	16.19	2.90	2.16	20	386	6,487	16.76	FD	LD	
		Larvae	1.23	8.96	4.23	2.04	6	66	794	12.03	03/05/2021	LD	
		Metamorphs	1.97	8.41	5.03	2.2	4	15	321	21.40	26/06/2021	LD	
<i>Hyla meridionalis</i>		Adults	0.4	7.85	2.71	1.77	16	77	256	3.21	FD	LD	
		Larvae	1.2	8.96	3.79	2.08	9	96	1,024	10.67	03/05/2021	25/06/2021	
		Metamorphs	1.66	8.96	5.1	2.14	6	20	260	13	07/06/2021	01/07/2021	
<i>Pelodytes punctatus</i>		Adults	3.66	4.22	3.87	0.3	1	3	3	1	11/04/2021	22/04/2021	
		Larvae	1.11	8.96	4.58	1.86	5	80	2,946	36.83	FD	26/06/2021	
		Metamorphs	3.88	8.96	6.6	1.29	5	25	339	13.56	09/05/2021	06/07/2021	
<i>Pelobates cultripes</i>		Adults	1.41	4.66	3.08	1.77	3	4	4	1	14/04/2021	03/05/2021	
		Larvae	5.11	8.96	6.94	1.34	2	13	105	8.08	07/06/2021	LD	
		Metamorphs	5.32	6.47	5.9	0.81	1	2	2	1	01/07/2021	06/07/2021	
Caudates	<i>Lissotriton helveticus</i>	Adults	0.44	2.4	1.12	0.63	3	10	10	1	FD	30/04/2021	
		Larvae	1.2	2.17	1.55	0.31	1	12	18	1.5	03/05/2021	25/06/2021	
		Adults	0.44	3.78	1.35	1.13	4	9	20	2.22	FD	03/05/2021	
	<i>Triturus marmoratus</i>	Larvae	1.2	2.25	1.67	0.31	2	28	103	3.68	03/05/2021	01/07/2021	

Note: We reported number of observations (i.e., the number of occasions on which species were encountered across the study period on all study sites), and the total number of individuals found, and the average number of individuals for the periods when observations were not zero (mean presence). FD stands for first day and indicates that a species (or a life stage) was already present when the surveys began (31/03/2021). LD stands for last day and indicates that a species (or a life stage) was still present when the surveys ended (12/07/2021).

FIGURE 3 Predicted abundance relative to salinity using N-mixture models for anurans (left panels) and caudates (right panels), in adults (a, d), larvae (b, e) and metamorphic individuals (c). Salinity was the main predictor in all cases, but for some species we also found a significant effect of pond surface (see Section 3 for details). Grey shadings indicate 95% confidence intervals. Note that as a result of variable richness and abundance, the scales of the y-axes are different. See Table S3 for details on analyses performed on each species separately.



interaction with salinity). Anuran detection probability also varied with temperature and day of the year (Table S3). In species in which day of the year had an effect, detection probability decreased when day of the year increased in adults, but increased with day of the year in larval and metamorphic individuals.

In caudates, abundance decreased strongly with increasing maximum salinity (Table 2; Figure 3D,E), but this effect was not significant in *Lissotriton helveticus* (Table S3). For *Triturus marmoratus*, we also found that increasing pond area decreased abundance of individuals (Table S3). Caudate detection probability also varied with temperature and day of the year (Table S3). In species in which day of the year had an effect, detection probability decreased when day of the year increased in adults, but increased with day of the year in larvae and metamorphic individuals. Lastly, there was no effect of aquatic vegetation (alone or in interaction with salinity).

Total species richness (for all stages of all species) followed a quadratic form, and was maximal for intermediate – temporally matched – salinities (Table 3). For all life stages, we observed that richness of anurans species was higher at intermediate salinities (quadratic effect), whereas richness of adult caudates and total

caudates decreased with increasing salinity (Table 3; Figure S1). We detected no significant relation between larval caudates and salinity. In adult anurans, we found that richness increased with the surface area of the pond (Table 3), but this variable was not retained in any other model. Lastly, there was no effect of aquatic vegetation (alone or in interaction with other variables) on species richness.

3.3 | Salinity and life stages

The salinity in which we found each species varied according to life stages (Sum Sq=13.827, $F_{4,598}=9.524$, $p<0.001$), date (Sum Sq=16.874, $F_{1,598}=46.491$, $p<0.001$), and their interaction (Sum Sq=13.630, $F_{4,598}=9.389$, $p<0.001$). In anurans, the salinity of the ponds where larvae or metamorphs were found was higher than that of adults because these life stages occurred later than adults at those sites (Figure 4). This pattern was corroborated by the highest mean salinity in which we found tadpoles and metamorphs compared to adults (Table 1). Comparatively, for caudates, larvae occurred later than adults, but the salinity in which adults and larvae were found was similar (Figure 4, Table 1).

TABLE 2 Environmental variables affecting abundance of anurans and caudates (all life stages analysed separately).

Group	Life stage	Environmental parameter	Estimated abundance			
			Estimate	SE	z	p
Anurans	Adults	Maximal salinity	0.19	0.038	4.95	<0.001
		Maximal salinity ²	-0.027	0.003	-8.05	<0.001
		Surface	0.001	<0.001	8.52	<0.001
		Temperature	0.042	0.005	8.69	<0.001
		Day of the year	-0.016	<0.001	-23.69	<0.001
	Larvae	Maximal salinity	1.323	0.162	8.15	<0.001
		Maximal salinity ²	-0.088	0.011	-7.96	<0.001
		Surface	0.002	<0.001	5.65	<0.001
		Temperature	0.109	0.012	8.8	<0.001
	Metamorphs	Maximal salinity	1.406	0.244	5.77	<0.001
		Maximal salinity ²	-0.096	0.021	-4.62	<0.001
		Surface	0.004	<0.001	9.39	<0.001
Temperature		0.245	0.018	14	<0.001	
Caudates	Adults	Maximal salinity	-0.139	0.06	-2.3	0.021
		Temperature	-0.104	0.058	-1.78	<0.001
		Day of the year	-0.058	0.014	-4.07	<0.001
	Larvae	Maximal salinity	-0.452	0.152	-2.97	0.002
		Temperature	0.092	0.034	2.72	0.006
		Day of the year	0.011	0.004	2.5	0.012

Note: Temperature and day of the year were used as covariates to model detection probability. Only variables retained in the best models are represented. See Table S3 for details on analyses performed on each species separately. Maximal salinity² indicate the quadratic form of maximal salinity.

TABLE 3 Environmental variables affecting species richness in anurans and caudates (all life stages combined or analysed separately).

Life stage	Species	Environmental parameter	Species richness			
			Estimate	SE	z	p
Total	Total (anuran and caudate)	Salinity	0.181	0.08	2.249	0.025
		Salinity ²	-0.025	0.006	-3.847	<0.001
	Anuran	Salinity	0.25	0.083	2.997	0.003
		Salinity ²	-0.029	0.007	-4.343	<0.001
	Caudate	Salinity	-0.635	0.279	-2.278	0.023
Adults	Anuran	Salinity	0.011	0.006	1.83	0.067
		Salinity ²	-0.002	<0.001	-4.318	<0.001
		Surface	<0.001	<0.001	2.815	0.005
	Caudate	Salinity	-2.239	0.691	-3.241	0.001
Larvae	Anuran	Salinity	1.334	0.25	5.346	<0.001
		Salinity ²	-0.095	0.022	-4.389	<0.001
	Caudate	Salinity	<-0.001	0.002	-0.235	0.814
Metamorphs	Anuran	Salinity	4.085	0.582	7.022	<0.001
		Salinity ²	-0.266	0.047	-5.647	<0.001

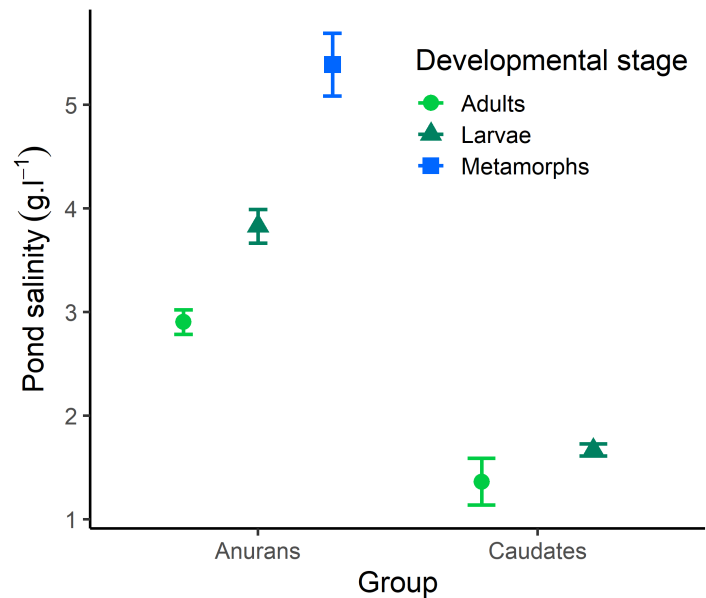
Note: Only variables retained in the best models are represented. Salinity² indicate the quadratic form of salinity.

3.4 | Malformations occurrence

We did not find any malformed individuals in caudates. Conversely, we found several malformed larvae and metamorphic individuals in

anurans ($N=17$, 0.35%). Malformations were diverse and included oedema, axial malformations, reduced tail size, and skin infections. In anurans, the number of malformed individuals increased with time (Estimate=0.035, SE=0.010, $t_{1,417}=3.415$, $p<0.001$) and increasing

FIGURE 4 Salinities (mean \pm SE) in ponds where different life stages of anurans (adults, larvae and metamorphs) and caudates (adults and larvae) occurred.



pond salinity (Estimate = 1.051, SE = 0.242, $t_{1,434} = 4.340$, $p < 0.001$), malformed individuals occurring solely in ponds wherein salinity was above 5 g/L.

4 | DISCUSSION

Overall, we show that salinity is a highly dynamic environmental variable that varies widely in coastal wetlands across spatial (up to 1 km) and temporal (spring and summer, across 3 years) scales relevant to local biodiversity. Using amphibians as a study model, we show that the spatio-temporal dynamic of salinity is a critical structuring factor of the community of these taxa. The most salient result from our study is the strong contrast between caudates and anurans, across all life stages. Indeed, caudates avoided brackish waters resulting in a strong decrease in richness and abundances with increasing salinity. Conversely, in anurans, richness and abundances were maximal for intermediate salinity, and decreased at around 8 g/L. In anurans, we found that larvae and metamorphic individuals developed in waters wherein salinity was higher than those selected by adults to reproduce, which can negatively affect reproductive success as exemplified by the decreased offspring quality (increased malformations) with increasing salinity.

4.1 | Spatio-temporal dynamics of salinity

Continental water bodies (i.e., rivers and lakes) have attracted considerable research effort to understand the consequences of freshwater salinisation (Cunillera-Montcusí et al., 2022), while marshes and ponds have been largely ignored to date despite their crucial role for biodiversity (Céréghino et al., 2014; Teixeira et al., 2014). In our study focused on such small water bodies, we found that salt concentration can vary widely, both spatially and temporally (Benjankar

et al., 2021; Collins & Russell, 2009). Spatial variations in salt concentration have already been shown in ponds (Benjankar et al., 2021), but never on such a small spatial scale (~1 km). In our study sites, salinity increased with decreasing distance to the ocean. This spatial variation is likely to be a result of exchanges between terrestrial and oceanic systems (Xue et al., 2013) and to the landward transport of sea spray (Benassai et al., 2005). Interestingly, we found a strong seasonal increase in pond salinity, presumably linked to increasing temperature and decreasing precipitations – and thus increasing evaporation – across spring and summer (Collins & Russell, 2009). We based our analyses across spring and summer during 3 years, and our results suggest that seasonal variation of salinity follows a predictable seasonal pattern. However, we emphasise that future studies are required to thoroughly quantify the seasonal variations of salinity (including autumn and winter) over longer-term (multiple years) in order to document whether current shifts in climatic conditions (i.e., temperature, precipitations, but also wind regimes that all interact to influence evaporative patterns; Richter & Xie, 2008) can affect the temporal variation of salinity and the hydroperiod in natural systems (Estévez et al., 2019; Ghalambor et al., 2021), and how such shifts will ultimately influence biodiversity.

4.2 | Variation in tolerance to salinity in coastal amphibians

Our results highlighted variable susceptibility between species suggesting different tolerance to salinity (Bray et al., 2019). We found very few effects of pond size and no effect of aquatic vegetation on amphibians' richness and abundance across all life stages (even if anuran richness and abundance was found to increase with increasing pond size, and caudate richness and abundance was found to decrease with increasing pond size), which emphasises the critical role of salinity as a structuring factor of the amphibian community.

Importantly, no species was found above 16 g/L which seems to constitute a threshold to amphibians' presence, and corroborate the global susceptibility to salinity in amphibians (Hopkins & Brodie, 2015). Taken together, our results point to a strong contrast between caudates and anurans across all life stages. In caudates, richness and abundance decreased strongly with small increments in salinity strengthening the fact that although few species can be salt-tolerant (Izzo et al., 2021; Licht et al., 1975), these taxa may be more susceptible to salt than anurans (Hopkins et al., 2013). Indeed, we found that anuran richness and abundance (across all life stages) were maximal for intermediate salinity (around 5–6 g/L) but also that some species occurred at remarkably high salinity. Such a contrast may be related to a weaker efficiency of the physiological mechanisms involved in osmoregulation in caudates as compared to anurans (i.e., reliance on urea, free amino acids and/or ionic concentrations in body fluids to reduce salt and water fluxes; Licht et al., 1975). To date, to the best of our knowledge, no study has formally compared mechanisms of osmoregulation and their associated efficiency between anurans and caudates. Complementarily, the seminal review of Hopkins and Brodie (2015), conducted for all life stages, suggested a slightly higher (but not significant) tolerance to salinity in anurans ($8.9 \text{ g/L} \pm 8.9 \text{ SD}$) than in caudates ($6.6 \text{ g/L} \pm 6.6 \text{ SD}$) in field studies; and a similar tolerance (respectively $9.0 \text{ g/L} \pm 6.6 \text{ SD}$ and $10.1 \text{ g/L} \pm 7.2 \text{ SD}$) under laboratory conditions. We have updated the review of Hopkins and Brodie (2015) with recent references and these new data point to similar patterns both in the field (mean tolerance in anurans $8.2 \text{ g/L} \pm 8.1 \text{ SD}$ and in caudates $6.3 \text{ g/L} \pm 6.0 \text{ SD}$) and under laboratory conditions (mean tolerance in anurans $8.1 \text{ g/L} \pm 6.0 \text{ SD}$ and in caudates $7.7 \text{ g/L} \pm 5.3 \text{ SD}$). As already highlighted in Hopkins and Brodie (2015), we believe this apparent discrepancy may be linked to bias in research effort between caudates and anurans. Indeed, the salt-tolerance of caudates seems less studied than it is in anurans (16 vs. 90 species studied in the field, 9 vs. 48 species studied under laboratory conditions; see Hopkins & Brodie, 2015). In addition, laboratory studies of salt-tolerance have used highly variable salinity conditions which preclude direct and straightforward comparisons (see also Hopkins & Brodie, 2015). In order to assess whether caudates and anurans universally differ in their salt-tolerance, we emphasise that future field studies should focus on both taxonomic groups where they co-occur, in a similar way to the current study. This also should be tested in sites where amphibian-specific richness is higher, because in our study site only six amphibian species are found, which limits computation of statistical analyses whenever specific richness is low. In addition, laboratory tests should be performed on similar test salinities in order to support large-scale comparisons. Finally, assessing whether caudates and anurans differ in osmoregulation mechanisms and associated efficiency will allow further crucial insights in order to understand putative differences in salt-tolerance and, thus, differential responses of these amphibian phylogenetic groups to environmental salinisation.

Interestingly, the higher tolerance of anurans to salinity in comparison to caudates fails to satisfactorily explain the quadratic

patterns we found across all life stages. Indeed, higher tolerance to salinity should have influenced the strength of the relationship between richness or abundances and salinity (i.e., the slope should be weaker in anurans) but not its shape (i.e., the quadratic effect of salinity and thus the lower richness and abundances of caudates at low salinity were unexpected). The fact that anurans seem to avoid fresh water may indicate weaker predation pressure (Velasco et al., 2019) or weaker pathogen transmission (such as chytridiomycosis; Clulow et al., 2018) in brackish water as compared to fresh water, which may induce habitat selection toward sites characterised by lower predation (i.e., lower abundances of crawfish) or pathogens in species that can tolerate moderate salinity (i.e., anurans) but not in salt-intolerant species (i.e., caudates). Finally, these patterns may reveal trade-offs linked to adaptive processes. Indeed, coastal anurans may have evolved specific physiological adaptations to promote life in hyperosmotic environments (Albecker & McCoy, 2019; Gomez-Mestre & Tejedo, 2003; Hopkins et al., 2016), notably through mechanisms that allow them to reduce salt intake (or increase excess salt excretion) and/or to increase water influxes (or reduce water effluxes, Lorrain-Soligon, Bichet, et al., 2022; Lorrain-Soligon, Robin, et al., 2022). In turn, these mechanisms may become maladaptive in hyposmotic water bodies because of elevated salt loss and excessive water influxes (Lorrain-Soligon, Bichet, et al., 2022), leading to massive oedema and mortality (L. Lorrain-Soligon, pers. obs). To date, we lack evidence to suggest that physiological mechanisms needed in hyperosmotic environments can affect performance in fresh water (Gomez-Mestre & Tejedo, 2003). Future studies should usefully investigate the mechanistic bases of the non-monotonic response of coastal anurans to environmental salinity. Whatever the underlying mechanisms, this non-monotonicity (somewhat similar to the "intermediate disturbance" hypothesis; Sheil & Burslem, 2013) appears to be a common pattern of response to salinity across a wide array of organisms [e.g., fish (Hieu et al., 2021), amphibians (Ahumada-García et al., 2018), invertebrates (Kefford et al., 2007), and plants (Sauer et al., 2016)].

4.3 | Seasonal increase in salinity and life-stages

Amphibian reproduction is negatively influenced by salinity (Karraker, 2007; Tornabene et al., 2021). For instance, salinity can directly affect sperm viability and fertilisation processes in these taxa characterised by external fertilisation (Green et al., 2021), and both field and experimental studies have shown that frogs avoid saline water for spawning (Albecker & McCoy, 2017; Viertel, 1999). In caudates, the salinities of ponds where larvae were found were similar to those of ponds where adults reproduced. Although larvae appeared later than adults, this emphasises the fact that adults selected low-salinity sites to reproduce characterised by a relatively moderate seasonal increase in salinity. Conversely, in anurans, tadpoles occurred when salinity was significantly higher than that experienced by reproductive adults. In this case, the seasonal increase in salinity induced a temporal disconnection between the salinity selected by

adults to reproduce and the salinity experienced by their developing offspring. In turn, the elevated salinity in which anuran larvae developed increased occurrence of malformations and abnormalities in both larvae and metamorphic individuals. This result dovetails well with previous laboratory studies which highlighted that increased salinity during embryonic and larval development induced malformations (Brady, 2013; Gosner & Black, 1957; Hopkins et al., 2013; Karraker, 2007), which ultimately decrease fitness and survival (Michel & Burke, 2011). Interestingly, the occurrence of malformed individuals (only found in anuran larvae and metamorphs) increased with increasing salinity and solely in sites wherein salinity exceeded 5 g/L. It is noteworthy that the proportion of malformed individuals we found remained very low, suggesting either that malformations increased mortality and/or susceptibility to predation (i.e., selective disappearance; Blaustein & Johnson, 2003) or that most larvae of coastal anurans were tolerant to salinity (Albecker & McCoy, 2019). Future studies are required to test for these hypotheses.

5 | CONCLUSION

Coastal aquatic ecosystems are naturally subject to salinity variation. In response to these variations, we show that species express different responses, affecting their distribution and their reproduction across the salinity gradient. Future changes in coastal salinity will be likely to affect the structure and functioning of freshwater ecosystems (Castillo et al., 2018). Indeed, even a small increase of salinity may be sufficient to induce changes in community structure and interspecific interactions (Venâncio, Castro, Ribeiro, Antunes, Abrantes, et al., 2019). Amphibian species seem to persist in saline habitats and can probably subsist in environments when gradual increase in salinity can promote adaptive responses (Delaune et al., 2021). Yet, brutal shifts in salinity (i.e., linked to extreme weather events; Lorrain-Soligon et al., 2021) may overcome population persistence (Venâncio et al., 2022). Colonisation by tolerant taxa and interactions between species will be key drivers of community persistence in salinised ecosystems (Kefford et al., 2016).

AUTHOR CONTRIBUTIONS

Conceptualisation: LLS, FR, FB. Developing methods: LLS, FB. Conducting the research: LLS. Data analysis: LLS, CB, FB. Data interpretation: LLS, FR, CB, FB. Preparation of figures & tables: LLS, CB, FB. Writing: LLS, FR, CB, FB.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

Data will be made available upon request.

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