




ORIGINAL RESEARCH

Life on the beach: Movements and growth of a coastal amphibian vary with distance to the sea

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Abstract

Proximity to the seashore is a critical structuring factor of coastal wetlands due to its influence on varying sources of nutrients (marine and terrestrial) and on the spatial gradient of salinity (higher salinity closer to the seashore). The spatial gradient of salinity may impact organisms because most organisms need to maintain an osmotic balance. Osmoregulation is energetically costly, and exposure to salinity should induce a trade-off in energetic allocation between osmoregulation and other competing functions such as growth rates and movement patterns. In this study, we used a capture–mark–recapture design during 3 consecutive years to investigate how distance to the sea influences growth rates and foraging movements (outside reproduction) in the western spadefoot toad (*Pelobates cultripes*), a typical coastal amphibian, in three populations from the French Atlantic coast. Growth rates were lower in larger individuals and in individuals living closer to the seashore. Distances travelled between captures were very limited (~20 m). Between years, these distances were larger for individuals located on the beach rather than inland, but were not influenced by body size or sex. Exposure to salinity and associated costs of osmoregulation may explain lower growth rates closer to the shoreline. The mechanisms underlying the effects of location on distances between captures remain to be identified, but may be related to foraging for abundant prey items on the wrack line. Our study confirms the remarkable terrestrial site fidelity in *P. cultripes*, which might be detrimental to coastal populations if localized perturbations affect coastal environments.

Introduction

Proximity to the seashore is a critical structuring factor of coastal wetlands (Hobohm et al., 2021; Levin et al., 2001; McLean et al., 2001). For instance, marine and terrestrial sources of nutrients, water, and organisms interact to affect functions of decomposition, nutrient cycling, and production (Levin et al., 2001; Snelgrove, 1997), which ultimately impact coastal communities and ecosystem functioning (Levin et al., 2001; Suchanek, 1994). More importantly, proximity to the seashore induces a spatial gradient of salinity with higher salinity (both in water bodies and on land) closer to the seashore (Lorrain-Soligon, Robin, Lelong, Jankovic, Barbraud, et al., 2022) because of progressive deposition of seasprays (Benassai et al., 2005). This spatial gradient of salinity is important insofar as most organisms need to maintain an osmotic balance between the salt concentration of the environment and cell

osmoregulation (Bradley, 2009; Hellebusi, 1976). Environmental increase in salinity disrupts this osmotic balance, and most organisms rely on osmoregulatory mechanisms to maintain homeostasis (Evans & Kültz, 2020; Lillywhite & Evans, 2021; Schultz & McCormick, 2012). Osmoregulation is energetically costly, and exposure to salinity will influence energetic allocation and induce a trade-off between osmoregulation and other competing functions such as growth, development, and reproduction (Herbert et al., 2015). Complementarily, because species vary in their tolerance to salt and dehydration (Arnott et al., 2023; Bentley, 2002; Herbert et al., 2015; Tadić et al., 2021), environmental salinity will negatively affect intolerant species in favor of tolerant species (Herbert et al., 2015; Radke et al., 2003), altering interspecific interactions (Herbert et al., 2015) and community structure (Hart et al., 2003).

Among the diverse fauna of coastal wetlands, amphibians are particularly susceptible to salinity (Hopkins et al., 2014;

Lorrain-Soligon, Robin, Lelong, Jankovic, Barbraud, et al., 2022; Tornabene et al., 2022). Such susceptibility to environmental salinity has been particularly well-studied for larval life stages, during which increased salinity has been shown to decrease survival (Albecker & McCoy, 2017; Chinnathamby et al., 2006; Christy & Dickman, 2002; Karraker et al., 2008; Sanzo & Hecnar, 2006; Tornabene et al., 2021), either prolong (Gomez-Mestre & Tejedro, 2003) or reduce larval development (Gomez-Mestre et al., 2004; Haramura, 2016; Lukens & Wilcoxon, 2020; Tornabene et al., 2021), reduce wet and dry mass (Tornabene et al., 2021), and reduce growth (Haramura, 2016; Lukens & Wilcoxon, 2020; Tornabene et al., 2021; Wood & Welch, 2015; Wu & Kam, 2009). In addition, larvae exposed to higher salinities express reduced foraging activity and behavior (Hall et al., 2017; Tornabene et al., 2021), altered responses to stimuli (Karraker, 2007; Sanzo & Hecnar, 2006), decreased swimming performance (Denoël et al., 2010; Haramura, 2016), and increased expression of erratic behaviors (Tornabene et al., 2021). Importantly, investigations of the influences of environmental salinity on post-metamorphic life stages have been comparatively less studied (Hopkins & Brodie, 2015), but salinity is known to negatively affect post-metamorphic individuals' physiological parameters (osmolality, immunity-related stress markers), body condition and locomotor performance (Lorrain-Soligon, Bichet, et al., 2022), as well as size- and sex-specific habitat selection (Lorrain-Soligon, Robin, Lelong, Jankovic, Barbraud, et al., 2022), along the spatial gradient of salinity generated by the distance to the coastline (Lorrain-Soligon, Robin, Lelong, Jankovic, Barbraud, et al., 2022).

Given these responses, it is expected that distance to coastline – and thus the spatial gradient of salinity (Lorrain-Soligon, Robin, Lelong, Jankovic, Barbraud, et al., 2022) – influences key life history traits of post-metamorphic coastal amphibians, namely, growth rates and movement patterns. Indeed, because of the energetic trade-offs between osmoregulation and other competing functions, exposure to environmental salinity should decrease the amount of energy available to growth. In addition to the energetic costs of osmoregulation, exposure to salt and dehydration negatively affect activity levels and movements (Feder & Londos, 1984; Lorrain-Soligon, Robin, Lelong, Jankovic, Barbraud, et al., 2022; Sinsch, 1990; Titon Jr et al., 2010), including resource acquisition (Feder & Londos, 1984; Yuqing et al., 2021), suggesting that osmotic costs should decrease movement patterns. Additionally, the size- and sex-specific habitat selection according to the spatial gradient of salinity generated by distance to coastline (Lorrain-Soligon, Robin, Lelong, Jankovic, Barbraud, et al., 2022) should impact growth and movement patterns. Indeed, growth rate curves are higher in newly metamorphosed individuals and lower in older individuals (Hota, 1994; Turner, 1962) and can vary with sex (Arantes et al., 2015; Hota, 1994; Wells, 2007). Additionally, dispersal distance has been shown to increase with body size (Denoël et al., 2018; Hillman et al., 2014), to be higher in juveniles (Bulger et al., 2003; Sinsch, 2014; Smith & Green, 2006), and to be sex-biased (Palo et al., 2004; Trochet et al., 2016).

In this study, we used a capture–mark–recapture design during 3 consecutive years (in autumn, outside the reproductive period of the species) to investigate how distance to the sea influences growth rates and foraging movements in the western spadefoot toad (*Pelobates cultripes*), in three populations from the French Atlantic coast. We posit that (1) growth rates should be higher in juveniles because growth rates decrease with increasing body size (Hota, 1994; Turner, 1962), growth rates should be higher in females because they reach larger body size than males of the same age (Hota, 1994; Wells, 2007), and that growth rates should be higher farther to the seashore according to the physiological constraint of salinity near the coast (Lorrain-Soligon, Robin, Lelong, Jankovic, Bustamante, et al., 2022), (2) movements (distance traveled) outside the reproductive season (i.e., linked to foraging, Jreidini & Green, 2022a; Jreidini & Green, 2022b; Pittman et al., 2014; Russell et al., 2005) should be higher in juveniles (Bulger et al., 2003; Smith & Green, 2006) and females (Trochet et al., 2016) to sustain higher growth rates (Hota, 1994; Wells, 2007) and should be lower near the seashore if exposure to salinity negatively affects activity (Feder & Londos, 1984; Lorrain-Soligon, Robin, Lelong, Jankovic, Barbraud, et al., 2022; Titon Jr et al., 2010), and (3) that individuals should express high site fidelity according to their ecology (Priol, 2015).

Materials and methods

Study species

The western spadefoot toad, *Pelobates cultripes*, is a nocturnal amphibian species, largely distributed across the Iberian Peninsula and occurring along the Mediterranean and Atlantic coasts of France (Leclair et al., 2005; Lizana et al., 1994; Lorrain-Soligon, Bichet, Robin, & Brischoux, 2022; Priol, 2015). This amphibian species is threatened (IUCN, 2015), and populations are currently declining across its range (Džukić et al., 2005; Rivière et al., 2019). In western France, habitats of *P. cultripes* are mainly located in coastal environments. However, the high salinity of potential reproduction habitats prevents individuals from colonizing coastal natural sites. Indeed, the species presence is negatively correlated with the salinity of the reproductive habitats, and reproduction mainly takes place in habitats with salinity ranging from <1‰ to 10‰, with a median of 2.5‰ (Thirion, 2014). Western spadefoot toads reproduce in early spring; and during the remaining of their life cycle, they are markedly terrestrial and take shelter in sandy soils during the day and forage at night (Speybroeck et al., 2018).

Study sites

We studied western spadefoot toad populations during 3 consecutive years (2020, 2021, and 2022) on three sites situated on the western coast of France: the 'Réserve Naturelle Nationale de Moëze-Oléron' (45°53'33.36" N, 1°04'59.16" W, hereafter MO), the 'Réserve Naturelle Nationale du marais d'Yves' (46°2'40.735" N, 1°3'16.906" W, hereafter MY), and the

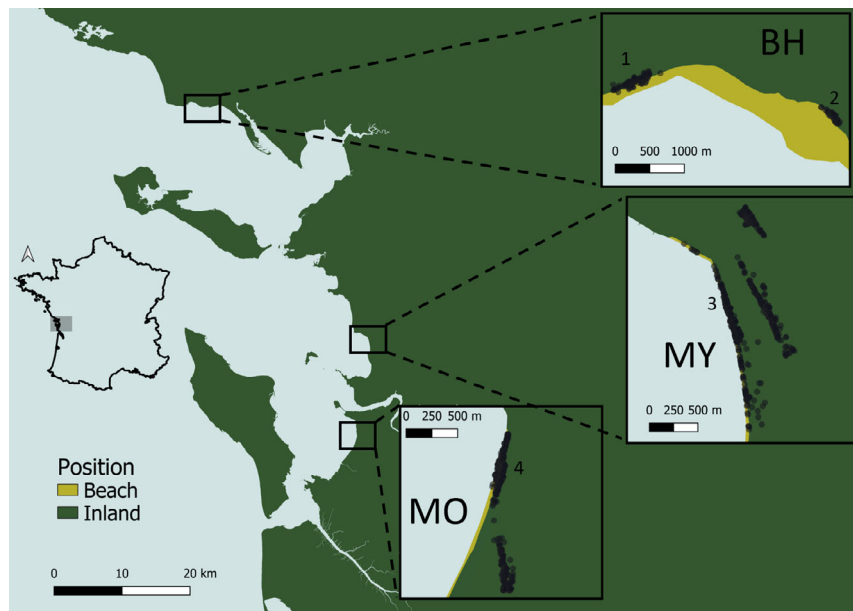


Figure 1 Map of the study areas and global situation in western France illustrating the three study sites [MO: ‘Réserve Naturelle Nationale de Moëze-Oléron’ ($N = 625$ captures and 138 recaptures); MY: ‘Réserve Naturelle Nationale du marais d’Yves’ ($N = 813$ captures and 181 recaptures); BH: ‘Réserve naturelle nationale de la casse de la Belle-Henriette’ ($N = 160$ captures and 38 recaptures)]. Points represent the position of captured individuals, either on the beach or inland. Numbers correspond to the close-up views displayed in Supporting Information Appendix S2.

‘Réserve Naturelle Nationale de la casse de la Belle-Henriette’ ($46^{\circ}20'37.32''$ N, $1^{\circ}21'59.76''$ W, hereafter BH; see Fig. 1). On these sites, prospected areas were situated from 0 to 665 m from the seashore. Prospected areas span 785 m width and 2400 m length in MY; 1450 width and 1600 m length in MO; 3400 m width and 243 m length in BH.

Field procedures

On each site, we conducted a capture–mark–recapture study in autumn (September–November), during 3 consecutive years (2020, 2021, and 2022). These surveys occurred outside the reproductive period (autumn), a period during which terrestrial activity is dedicated to foraging (Duguet, *et al.*, 2003). Each year, surveys were completed on at least three different occasions separated by 1–2 weeks (see Supporting Information Appendix S1), with teams of 5–10 people. All field surveys were carried out at night, between 21:00 h and 04:00 h when environmental conditions (temperature and humidity) favored their activity (Priol, 2015). Each captured individual was marked with a microchip (Trovan ID-100VB/1.4, United Kingdom). Our surveys lead to 1598 captures (see Supporting Information Appendix S1), representing 1241 individuals (948 individuals were captured once, 240 individuals were captured two times, 46 individuals were captured three times, four individuals were captured four times, two individuals were captured five times, and one individual was captured six times). Among recaptures, 209 occurred within the same year and 148 occurred across different years. At the first capture, 379

individuals were located on the beach and 862 inland. Overall, 507 individuals were located on the beach and 1091 inland.

All captured individuals were measured (snout-to-vent length [SVL], using a caliper [± 1 mm]) and weighted (Pesola, Switzerland spring scale [± 0.5 g]). Individuals were characterized as adults or juveniles based on their body size (individuals < 45 mm were classified as juveniles, (Lorrain-Soligon, Robin, Lelong, Jankovic, Barbraud, *et al.*, 2022)), and adults were sexed based on the presence of secondary sexual characters in males. Precise locations of capture were recorded with a Global Positioning System (Garmin GLO, United Kingdom) in order to assess distance to the sea at high tide, using the NNJoin extension in Qgis 3.10. We considered the same shoreline across years. Accordingly, we used capture locations to further qualify whether individuals were found in close proximity to the sea (“beach”) or further inland (“inland”). Prospected sites are constituted of 23.58% in BH, 5.68% in MY, and 11.59% in MO of beach habitats as compared to inland zones. Inland habitats are situated at a distance of 75 m to the shore in BH and 22 m to the shore in both MO and MY. Beach habitats were represented by the sandy shoreline without any vegetation. Inland habitats were situated beyond the beach line and represented, in the three sites, by sand dunes, covered by vegetation. The area covered by the beach habitat is limited in comparison to inland areas (see Fig. 1 and Supporting Information Appendix S2). While individuals can be found on the beach or inland, all breeding sites (ponds) are situated only inland [four ponds in BH (min salinity = 0 g.L^{-1} ; max salinity = 4.00 g.L^{-1} ; mean salinity = 0.57 g.L^{-1} ; min

distance = 190 m; max distance = 270 m; mean distance = 228.65 m), 24 ponds in MO (min salinity = 0.56 g.L⁻¹; max salinity = 6.36 g.L⁻¹; mean salinity = 3.21 g.L⁻¹; min distance = 56 m; max distance = 1188 m; mean distance = >490.75 m), and 22 ponds in MY (min salinity = 1.10 g.L⁻¹; max salinity = 7.37 g.L⁻¹; mean salinity = 4.00 g.L⁻¹; min distance = 29 m; max distance = 833 m; mean distance = 433.75 m)]. Interestingly, the salinity of these ponds increases closer to the seashore (Lorrain-Soligon, Robin, Lelong, Jankovic, Barbraud, et al., 2022). For clarity, we presented in Supporting Information Appendix S2 a better representation of captures according to beach and inland areas. Capture locations were also used to assess movements (distance traveled) of individuals between successive capture events. These distances were assessed both within the same year (209 observations) and across different years (148 observations) and were calculated as the Euclidean distance between successive capture locations (Data S1).

We evaluated growth solely in individuals who were recaptured during different years (148 observations; 76 observations occurring after 1 year, and 72 observations occurring after 2 years), as the difference of body size between capture events. Absolute growth rate was then corrected by the number of days elapsed between captures (mm.day⁻¹). Due to measurement errors, some individuals were characterized by negative growth rates. Importantly, these negative growth rates were only found in larger (adult) individuals (SVL > 50 mm) which are expected to express very low or no growth (Hota, 1994). Absolute errors (differences in size between two captures in individuals for which this difference was negative) were similar between individuals recaptured successively within field sessions (within the same year) and those recaptured among years (-3.390 vs. -3.567 mm, representing 5.538 vs. 5.435% SVL, respectively). This suggests that these measurement errors did not impede our ability to detect actual growth between different years, especially in smaller individuals in which growth rates were expected to be higher (Hota, 1994). For clarity, these negative growth rates were transformed to 0 in our final analyses, although maintaining negative growth did not qualitatively change the results.

Statistical analyses

We tested for differences in growth rate (mm.day⁻¹) across different years. To do so, we used a linear mixed model (lmm, package *lme4*) to evaluate the main effects of distance to the sea, location (on the beach or inland, location on the previous capture event being considered), body size at previous capture, sex and life stage (males, females, or juveniles), and their interactions (fixed effects) on the growth rate (response variable). Individual identity (as the same individual can be captured multiple times) as well as site (BH, MO, or MY) were used as random effects. These variables were selected by top-down selection (by *P*-value), and only the retained variables are presented in the final models (i.e., some variables were excluded during the selection procedure, and only the variables affecting the dependent variable are presented). As we found no differences in growth rates between sites (linear model,

package *MASS*: Sum Sq = 0.001, *F*-value = 1.787, *P*-value = 0.171, MO-BH: Estimate = 0.004, SE = 0.003, *t*-value = 1.326, *P*-value = 0.377, MY-BH: Estimate = 0.005, SE = 0.003, *t*-value = 1.698, *P*-value = 0.205, MY-MO: Estimate = 0.001, SE = 0.002, *t*-value = 0.554, *P*-value = 0.842), all sites were analyzed together (using site as a random effect, see above).

As individuals traveled larger distances between captures across different years than within the same year (linear mixed models; estimate = -5.970 m, SE = 1.992, *t*-value = -2.998, *P*-value = 0.003, see Supporting Information Appendix S3), statistical analyses of distances between captures across different years or within the same year were performed separately. We tested for the difference in distances between captures across different years and within the same year, for individuals who did not change location (inland-inland and beach-beach) and for individuals that change locations from beach to inland (beach-inland) or from inland to beach (inland-beach). To do so, we used an lmm to evaluate the main effects of session (within the same year or across different years) and change in location and their interactions (fixed effects) on distance traveled (response variable). Individual identity (as the same individual can be captured multiple times) as well as site (BH, MO, or MY) were used as random effects. We also tested if distance traveled was influenced by time (in days), separately for individuals captured across different years and within the same year. We used lms to evaluate the main effect of time (in days) (fixed effect) on distance traveled (response variable). Individual identity as well as site (BH, MO, or MY) were used as random effects. For individuals who were recaptured between years, we also tested the differences in distance traveled if they were recaptured after 1 year or after 2 years. We used an lmm to evaluate the main effect of time elapsed between recaptures (1 year or 2 years; fixed effect) on distance traveled (response variable). Individual identity as well as site (BH, MO, or MY) were used as random effects. As we found no differences in movements between sites (linear model: Sum Sq = 1561, *F*-value = 1.558, *P*-value = 0.121), all sites were analyzed together (using site as a random effect, see above and below).

Finally, we tested for variable influencing distances traveled, separately for distances performed across years or within years. To do so, we used an lmm to evaluate the main effect of distance to the sea, location (on the beach or inland), individuals' size at first capture, sex and life stage (males, females or juveniles) and their interactions (fixed effects), on distance (performed across years or within years) between captures (m). Individual identity as well as site (BH, MO, or MY) were used as random effects. These variables were selected by top-down selection (by *P*-value), and only the retained variables are presented in the final models (i.e., some variables were excluded during the selection procedure, and only the variables affecting the dependent variable are presented).

Additionally, for individuals who were recaptured both within the same year and across different years (for which we could compute both across-years and within-year movements), we investigated the relationships between the two sets of distances traveled, in order to test if individuals traveled more important distances across years than within year or if they

were consistent in their distance traveled, using Pearson's correlation test. We also tested for the relation between growth rates and distances between captures (across different years) using a Pearson correlation test.

All data analyses were performed using R 3.6.3 (R Core Team, 2020) and Rstudio v1.1.419.

Results

Growth rates

Growth rates were influenced by capture location (beach or inland), as well as the interaction between size and life stage. Growth rates were higher in individuals who were captured inland compared to those captured on the beach (Estimate = 0.003 mm.day⁻¹, SE = 0.001, *t*-value = 2.513, *P*-value = 0.013; Fig. 2A). Growth rates were lower in larger individuals (Estimate < -0.002 mm.day⁻¹, SE < 0.001, *t*-value = -6.756, *P*-value < 0.001), and this relationship was steeper in juveniles (Estimate = -0.020 mm.day⁻¹, SE < 0.001, *t*-value = -6.185, *P*-value < 0.001) than in adults (females: Estimate = -0.001 mm.day⁻¹, SE < 0.001, *t*-value = -5.540, *P*-value < 0.001; males: Estimate = -0.001 mm.day⁻¹, SE < 0.001, *t*-value = -2.956, *P*-value = 0.006). As a consequence, growth rates of juvenile individuals were significantly higher than those of adult individuals (compared to females: Estimate = 0.058 mm.day⁻¹, SE = 0.014, *t*-value = 4.272, *P*-value < 0.001; compared to males: Estimate = 0.061 mm.day⁻¹, SE = 0.019, *t*-value = 3.259, *P*-value = 0.003; Fig. 2B), but growth rates of adult males and females were similar (Estimate = 0.002 mm.day⁻¹, SE = 0.016, *t*-value = 0.136, *P*-value = 0.990; Fig. 2B).

Movements

Within year movements (distance travelled) varied from 0 m to 166.4 m (mean = 14.5 ± 1.5 SE; see Supporting Information Appendix S3). Distance traveled marginally, but not significantly, increased with time elapsed between captures (Estimate = 0.141 m, SE = 0.079, *t*-value = 1.777,

P-value = 0.079). None of the tested covariates influenced short-term (within the same year) distances traveled between successive captures (all variables excluded during the model selection procedure). Only 27 individuals (13%) changed location within the same year [beach to inland (*N* = 11) or inland to beach (*N* = 16), representing mean distances of 40.6 ± 12.2 m and 16.9 ± 2.8 m respectively, Supporting Information Appendix S3]. All other recaptured individuals (*N* = 182, 87%) were collected at the same location (either beach or inland, representing mean distances of 13.3 ± 1.7 m and 12.5 ± 1.5 m respectively, Supporting Information Appendix S3). Movements from beach to inland were significantly higher than any other movements (all *P*-values < 0.004, Supporting Information Appendix S3), but all other movements were similar (all *P*-values > 0.600, Supporting Information Appendix S3).

Across different years, distances between captures ranged between 0.6 m and 197.5 m (mean = 20.2 m ± 1.8 SE; see Supporting Information Appendix S3). Distances traveled for individuals recaptured after 1 year (76 recaptures, mean distance = 16.9 m ± 2.5 SE), or 2 years (72 recaptures, mean distance = 23.7 m ± 3.6 SE) were not significantly different from each other (Estimate = 6.375, SE = 4.559, *t*-value = 1.398, *P*-value = 0.164 considering differences in years and Estimate = 0.008 m, SE = 0.012, *t*-value = 0.645, *P*-value = 0.530 considering differences in days). These distances were influenced by capture location solely. Indeed, individuals initially captured on the beach moved further than those initially captured inland (Estimate = 8.177 m, SE = 4.228, *t*-value = 1.935, *P*-value = 0.047; Fig. 3). Similarly to short-term (within the same year) movements, only 21 individuals (14%) changed location [beach to inland (*N* = 5) or inland to beach (*N* = 16)], representing mean distances of 93.4 ± 33.8 m and 26.3 ± 4.2 m, respectively, Supporting Information Appendix S3). Distances traveled by individuals who moved from beach to inland were marginally (but not significantly) higher than distances traveled by individuals who moved from inland to beach (Estimate = 23.800 m, SE = 12.600, *t*-ratio = 1.890, *P*-value = 0.065). All other recaptured individuals (*N* = 127, 86%) were consecutively captured at the same

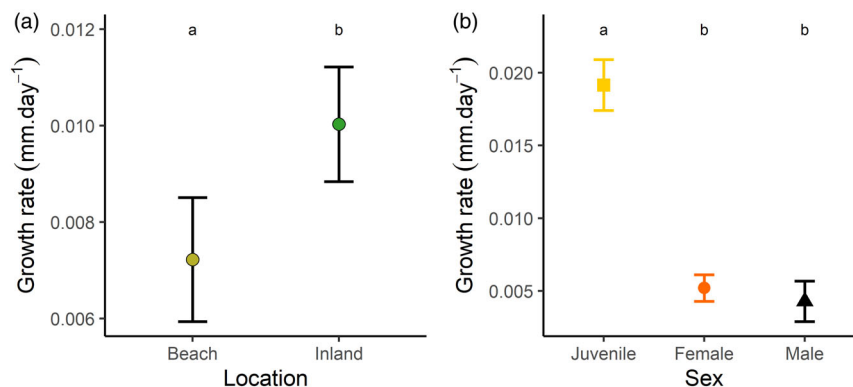


Figure 2 Growth rate (mm.day⁻¹) according to (A) location at the first capture [beach (*N* = 245) or inland (*N* = 112)] and (B) life stage and sex [Females (*N* = 197), Males (*N* = 74) and juveniles (*N* = 86)]. Mean ± SE. Different letters represent a significant difference at $\alpha = 0.05$.

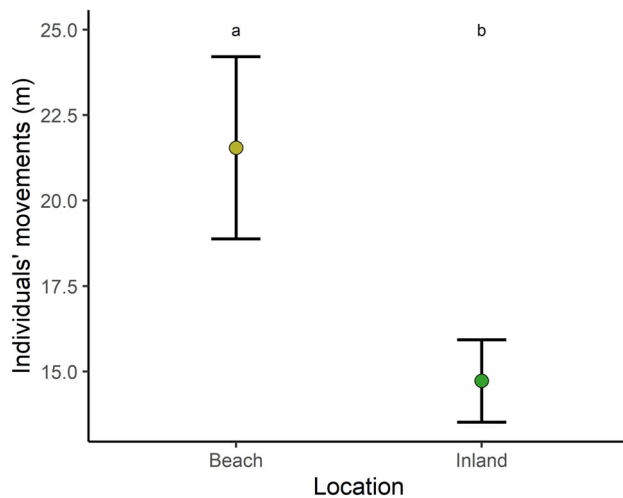


Figure 3 Distance between captures (across different years) according to the location at first capture [beach ($N = 245$) or inland ($N = 112$)]. Mean \pm SE. Different letters represent a significant difference at $\alpha = 0.05$.

location (either beach or inland, representing mean distances of 18.9 ± 2.0 m and 15.5 ± 2.4 m, respectively, Supporting Information Appendix S3). Movements from beach to inland were significantly higher than any other movements (all P -values < 0.001 , Supporting Information Appendix S3), but all others movements were similar (all P -values > 0.563 , Supporting Information Appendix S3).

Interestingly, in individuals for which we could compute both within-year and across-year movements, we found no significant relationships between the two sets of distances traveled ($\text{cor} = 0.282$, P -value = 0.091). Finally, growth was not related to distance traveled between captures ($\text{cor} = -0.001$, P -value = 0.997).

Discussion

In this study, we showed that, in coastal *P. cultripes*, both growth rates and distances traveled between captures were influenced by local environmental characteristics and were lower in individuals living closer to the seashore. As expected, we also showed that growth rates were lower in larger individuals. Outside reproduction, distances traveled between captures were very limited (~ 20 m) and were higher between years than within the same year. Between years, we found that these distances were larger for individuals located on the beach than for individuals located inland. Contrary to our predictions, these distances were not influenced by individual traits such as body size or sex.

Although growth of post-metamorphic amphibians remains understudied, it has been shown that growth rates were lower in larger individuals both among and within species (Cogalniceanu & Miaud, 2003; Hota, 1994). We found a similar pattern in our study species, with growth rates being higher in juveniles than in adults. In addition, growth rate has been identified

as one of the proximate causes of sexual dimorphism (Arantes *et al.*, 2015) and is expected to be higher in females because they reach a larger body size compared to males of the same age (Hota, 1994; Wells, 2007). Although we failed to detect an effect of sexual dimorphism on adult growth rates, it is plausible that such sex-dependent growth rates occur earlier, during the juvenile stage, when sexing individuals based on secondary sexual characteristics is not possible. Additionally, while females are usually larger than males (Hota, 1994; Wells, 2007), they probably reach maturity later, as found in a closely related species, *Pelobates fuscus* (Schmidt *et al.*, 2012), so that growth rates could be delayed. Finally, it is also plausible that such lack of sex effect on growth rates may be linked to measurement errors (see Materials and methods). Yet we emphasize that despite such, overall modest, measurement errors, we nonetheless were able to detect the expected size-dependent growth rates (Cogalniceanu & Miaud, 2003; Hota, 1994), suggesting that this minor bias did not generate spurious patterns. Future studies using molecular sexing are required to assess whether sexual dimorphism in growth rate occur prior to adulthood. In addition, future studies investigating the effects of age (through longer-term mark-recapture studies and/or the use of skeletochronology, Guarino *et al.*, 2003), in addition to body size, will allow a comprehensive understanding of the determinants of adult body size in this species.

According to our prediction, we found that growth rates were higher in individuals captured farther from the seashore, despite the fact that larger individuals – and thus with lower growth rates – are found farther from the shoreline (Lorrain-Soligon, Robin, Lelong, Jankovic, Barbraud, *et al.*, 2022). We suggest that lower growth rates near the shoreline are linked to the costs of osmoregulation related to the spatial gradient of salinity (Lorrain-Soligon, Robin, Lelong, Jankovic, Barbraud, *et al.*, 2022). Indeed, exposure to salinity induces energetic costs (Peña-Villalobos *et al.*, 2013) because the mechanisms involved in excreting excess ions and maintaining hydration are metabolically costly (Herbert *et al.*, 2015). Osmoregulation may thus limit energetic allocation to other organismal functions such as growth (Heino and Kaitala, 1999). Although the effects of salinity on growth have been widely studied in larval amphibians (Christy & Dickman, 2002; Lukens & Wilcoxen, 2020; Tornabene *et al.*, 2021; Wu & Kam, 2009), to the best of our knowledge, these effects have not been assessed in free-ranging post-metamorphic individuals. Alternatively, growth rates are widely dependant on prey availability, which may fluctuate according to local environmental conditions (Hota, 1994; Smith, 1976). As a consequence, higher growth rates farther from the seashore might be related to higher resource availability, notably as the trophic ecology of *P. cultripes* vary with distance to the sea (Lorrain-Soligon, Robin, Lelong, Jankovic, Bustamante, *et al.*, 2022). Yet we believe this hypothesis is unlikely as prey availability seemed very abundant on the beach where individuals forage for sand hoppers (*Talitrus saltator*) on the wrack line (Lorrain-Soligon, Robin, Lelong, Jankovic, Bustamante, *et al.*, 2022); L. Lorrain-Soligon pers. obs). As such, slower growth rate near the seashore, while food is abundant, may be due to salinity ingested by individuals via their food (and/or through their skin) when

they forage on the shoreline (Gutiérrez, 2014; Nagy *et al.*, 2021). Large-scale spatial variations of growth rates have already been highlighted in amphibians (linked to latitude and altitude; Morrison & Hero, 2003). Here, we highlighted a very short spatial extent of these growth rate variations (less than 1500 m). Importantly, this spatial gradient of growth rates dovetails relatively well with previous results showing that individuals found closer to the shoreline were smaller and more often juveniles (Lorrain-Soligon, Robin, Lelong, Jankovic, Barbraud, *et al.*, 2022). Such pattern might be a major phenomenon owing to the implications of growth rates and body size on life-history traits (Brown *et al.*, 2004; Brown & Sibly, 2006; Hildrew *et al.*, 2007).

Pelobates cultripes is known to express high site fidelity (Priol, 2015). Accordingly, we found that successive recaptures, either within or across years, occurred within very restricted distances (maximum values: 166.4 and 197.5 m, respectively). Although one can assume that individuals moving a larger distance may leave the limits of our study sites and thus be less likely to be detected, we emphasize that the extent of our study areas should allow us to record movements up to 3400 m in BH, 2400 m in MY, and 1600 m in MO. *Pelobates cultripes*, like many other amphibians, mainly migrate during the reproductive period (in spring) to and from breeding sites (Denoël *et al.*, 2018). Our study was performed in autumn, a period dedicated to foraging, so that these reproductive migrations occur outside the prospected period. In between these periods of reproductive migrations, where individuals express mainly foraging activity, individuals appeared relatively faithful to their terrestrial habitats. Although distances between captures were slightly higher between years than within the same year, interestingly, even between years, individuals appeared faithful to their terrestrial site, compared to the possible dispersion range of amphibian species (and particularly anurans). Indeed, Smith and Green (2005) found that, among 166 journal articles concerning 90 amphibian species, while 44% of the amphibian species moved no farther than 400 m, 5% were capable of movements greater than 10 km. When considering anurans only, nearly one-half (44%) of the anuran species displayed maximum dispersal distances greater than 1 km, and 7% of anurans were observed to have maximum dispersal distances greater than 10 km (Smith & Green, 2005). We did not study such dispersal movements, which considered displacements of populations from one site to another (Bailey & Muths, 2019; Cayuela *et al.*, 2017, 2020; Joly, 2019; Semlitsch, 2008). We thus highlighted that individual movements occur across a limited spatial scale. However, we cannot differentiate movements linked to reproduction (migration to ponds) from those expressed during non-breeding activities (resting; foraging), during which individuals could express diverging patterns (Bailey & Muths, 2019; Cayuela *et al.*, 2017; Joly, 2019). Although the spatial extent of movements can depend on individual traits (Cayuela *et al.*, 2020; Hillman *et al.*, 2014; Husté *et al.*, 2006; Sinsch, 2014; Trochet *et al.*, 2016), we failed to detect any effect of body size and sex on the distances between captures (see also Jreidini & Green, 2022a, 2022b; Smith & Green, 2006). Although it is likely that individuals move greater distances to reproduce

(Priol, 2015), our results suggest that individuals are able to return to a specific terrestrial site between reproductive events (see also Jreidini & Green, 2022b). Future studies are required to identify which environmental cues (i.e., odors, landmarks, positions of sun, moon and stars, and polarization patterns of the sky or magnetic fields, Sinsch, 1990) allow such marked site fidelity and if breeding migratory movements result in individuals moving larger distances to different sites.

As for growth rates, we found that distances between captures were dependent on the location of individuals. That is, individuals initially captured on the beach moved farther than their counterparts captured inland. These larger distances between captures may be related to movements linked to foraging. Indeed, sand hoppers (an important prey for toads located on the beach, see above) are situated on the wrack line, close to the seawater limit. It is plausible that toads captured on the beach shelter in the sand during the day at the upper beach limit and forage at night moving to the wrack line where sand hoppers, a mobile prey easily available, are located (Lorrain-Soligon, Robin, Lelong, Jankovic, Bustamante, *et al.*, 2022). Such hypothesis is consistent with the fact that distances between captures for individuals who moved from beach to inland were larger than those of individuals who moved from inland to beach. This may be related to movements to the beach which could be linked to foraging on abundant sand hoppers. Additionally, beaches represent open surfaces without obstacles for an amphibian which might facilitate movements (Brown *et al.*, 2006), while inland, landscape features such as vegetation may constrain amphibian movements (Sinsch, 2014). Yet we emphasize that these hypotheses need to be taken with caution as we did not monitor actual movements dedicated to foraging but only assessed distances between capture events. Nonetheless, the difference between the distances traveled by individuals captured on the beach or inland – similar within and across different years – strongly suggest that the environmental contrasts between these locations (e.g., salinity, resource availability, and habitat resistance to movements) may affect movement patterns. Future studies should investigate these movements at a finer temporal scale (i.e., using radiotracking, Coster *et al.*, 2014), or in coastal species moving larger distances, in order to test for these hypotheses.

Conclusion

Our study allows to demonstrate that location (beach or inland) affects growth rates and distances traveled between captures within the same year in a coastal amphibian. Exposure to salinity and associated costs of osmoregulation may well explain why individuals captured closer to the shoreline have markedly lower growth rates, a pattern that is remarkable given the spatial extent of our study sites. The mechanisms underlying the effects of location on distances between captures remain to be identified but may be related to foraging for abundant prey items on the wrack line. Our study confirms the terrestrial site fidelity in *P. cultripes*, a characteristic that may prove detrimental to coastal populations if localized perturbations linked to climate change (e.g., marine floods and rising

sea level) (Nicholls & Cazenave, 2010; Trenberth *et al.*, 2015) affect the coastal structure.

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Conflict of interest statement

The authors declare that they have no conflict of interest.

Author's contribution

LLS, FR, & FB conceptualized the study. All authors participated to data collection. LLS and FB analyzed the data and wrote the initial draft. All authors have reviewed and edited the manuscript and approved the final version.

Data availability statement

The data that support the findings of this study are available in the supplementary material of this article.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Number of surveys, number of captures, number of marked individuals, and number of recaptured individuals for each site.

Appendix S2. Close-up view of the capture points presented in Fig. 1, for a better identification of “beach” and “inland” areas. These captures were performed in BH (1,2), MY (3) and MO (4). See numbers in Figure 1. [MO: ‘Réserve Naturelle Nationale de Moëze-Oléron’ ($N = 625$ captures and 138 recaptures); MY: ‘Réserve Naturelle Nationale du marais d’Yves’ ($N = 813$ captures and 181 recaptures); BH: ‘Réserve naturelle nationale de la casse de la Belle-Henriette’ ($N = 160$ captures and 38 recaptures)]. Area of each sites are respectively 0.167, 0.056, 1.057, and 0.233 km² (for close up sites 1, 2, 3 and 4).

Appendix S3. (A) Distance between captures across different years and within the same year. Mean \pm SE. (B) Distance between captures across different years and within the same year, for individuals who did not change location (inland–inland and beach–beach) and for individuals that change locations from beach to inland (beach–inland) or from inland to beach (inland–beach) or from inland to beach (inland–beach). Mean \pm SE. Different letters represent a significant difference at $\alpha = 0.05$.

Data S1. Raw data representing the 1598 captures occurring from each individual captured during three consecutive years (2020, 2021, and 2022). These captures are identified by site (MO : ‘Réserve Naturelle Nationale de Moëze-Oléron’ [$N=625$ captures and 138 recaptures]; MY: ‘Réserve Naturelle Nationale du marais d’Yves’ [$N=813$ captures and 181 recaptures]; BH: ‘Réserve naturelle nationale de la casse de la Belle-Henriette’ [$N=160$ captures and 38 recaptures]), and date. Some individuals were captured only once (“C” for capture in the action column), while others were captured multiple time (“R” for recapture in the action column). Individuals were measured (SVL: Snout Vent Length, given in mm), weighted (mass, in g), and sex and age were assessed (based on size and the presence of secondary sexual characters). Each captured individual was marked with a microchip (Trovan ID-100VB/1.4, United Kingdom) and thus identified by a unique number (tag). For recaptured individuals only, we indicated session (intra or inter annual), duration relative to the previous capture event, position (on the beach or inland), distance to the ocean (m), distance travelled relative to previous capture (both relative [m] and corrected by number of days since precedent capture [m.day-1]), as well as growth relative to previous capture (both relative [mm] and corrected by number of days since precedent capture [mm.day-1]).