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The Mediterranean pond turtle shows resilience to extreme flood events

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ABSTRACT

In the present context of climate change and extreme weather events (EWEs), understanding the impact of flood events on Mediterranean riverine ecosystems is key for conserving landscapes while preserving local biodiversity. In this study, we examined the impact of a major flood that occurred in November 2014 on the Baillauray River (Southern France) where a population of the Mediterranean Pond Turtle *Mauremys leprosa* (Schweigger, 1812) was monitored from 2012 to 2022. Survival, recruitment, and transition probabilities were estimated before and after the flood using Pradel Robust-Design and Multistate models. Although turtle population size decreased by 16 % immediately after flooding, the adult population rapidly returned to its initial state with a balanced sex ratio. This study highlights that neither the structure nor the temporal dynamics of the adult population were altered over a ten year period underlying the fast resilience of the species. The flood however mainly impacted the spatial dynamics of the population by increasing downstream movements of turtles, which resulted in changes of their distribution along the river.

1. Introduction

Climate change has been reported to directly affect weather by increasing the frequency and the intensity of extreme weather events (EWEs) in most regions across the world (IPCC, 2022; Rahmstorf and Coumou, 2011). EWEs are characterized by fast and

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highly energetic changes in local environmental conditions (Peters et al., 2011). Changes in temperature and rainfall can exacerbate shifts in heatwaves and hydrological regimes, resulting in very short but massive floods and longer low-flow periods in some areas (Döll and Zhang, 2010) that strongly disturb riverine ecosystems (Messenger et al., 2021; Sabater, 2008). Climate change, by exacerbating flood events (Alfieri et al., 2017; Arnell and Gosling, 2016; Hirabayashi et al., 2013), alters rivers morphology, ecosystems functioning (Jentsch and Beierkuhnlein, 2008), and biodiversity (Doak et al., 2008; Sabater et al., 2023). The Mediterranean region is particularly at risk from climate change since it is warming 20 % faster than the average worldwide (United Nations Environment Programme, 2020), increasing the frequency and intensity of droughts (Somot et al., 2008), wildfires (San-Miguel-Ayanz et al., 2022), and floods (Llasat, 2021). Due to local microclimate, floods are even more frequent in some areas within the Mediterranean basin (Gaume et al., 2009; Llasat, 2021). Importantly, among the regions of critical importance for nature conservation, the Mediterranean basin hosts a great diversity of habitats and is considered as the second hotspot of global biodiversity (IUCN, 2023). There, beside climate change, floods mainly result from a combination of several factors such as urbanization of the catchment's areas, reduced soil moisture (Tremblay et al., 2019), and heavy rainfalls in the Northern part of the Mediterranean basin (Llasat, 2021). Yet the western part of the Mediterranean basin is most exposed to floods of high impact and magnitude, probably due to the influence of the oceanic climate (Gaume et al., 2016). Although understanding the impact of floods events on Mediterranean riverine ecosystems is key to conserving landscapes while preserving local biodiversity, studies reporting the demographic responses of wildlife to such extreme flood events in this region of the world remain scarce to date.

Floods affect aquatic species (Bodmer et al., 2018) with temporary or persistent impacts (Stickel, 1948). They may lead to individual death (Shine and Mason, 2004; Jones and Sievert, 2009), population displacements (Jones and Sievert, 2009), and population decline or extinction (Simpkins et al., 2015; Zhang et al., 2007; Neilson et al., 2020). Such impacts may vary with flood characteristics and temperature regimes, landscape features, but also with animals traits (Zhang et al., 2021). Indeed, animal species can exhibit specific physiological, behavioural, ecological, and demographic responses when faced with EWEs (Antão et al., 2020; Moritz and Agudo, 2013; Sergio et al., 2018). Life history traits such as longevity may affect animal capacity for resilience to climate change (Pacifiçi et al., 2017). In particular, long-lived animals that develop slowly and mature late (i.e., slow pace of life animals) appear to be less vulnerable to EWEs than short-lived ones (Morris et al., 2008). Because they express diverse life history traits and exhibit contrasted responses to EWEs, long-lived animals are relevant study models to investigate the medium- and long-term effects of climate change on wildlife.

Freshwater turtles are long-lived species with slow pace of life exploiting both terrestrial and aquatic habitats, making them potentially affected by landscape alterations in wetlands (Buhlmann and Gibbons, 2001; Burke and Gibbons, 1995). Of all recognized turtle species, about 50 % are threatened (Critically Endangered, Endangered, or Vulnerable) (Rhodin et al., 2021). A large variety of threats can affect population viability among turtles, including habitat loss and degradation (Pitt and Nickerson, 2012), invasive species (Van Dyke et al., 2019), diseases (Spencer et al., 2018), and human exploitation (Klemens, 2000). Climate change, which can even exacerbate EWEs, has been identified as a major driver of turtle population dynamics (Janzen, 1994; Janzen et al., 2018). Following long period of droughts, fires for instance, can alter individual body condition, survival, and population demographic structure, as reported in the European Pond Turtle *Emys orbicularis* (Linnaeus, 1758) (Cheylan and Poitevin, 1998) and in the Southern Western Pond Turtle *Actinemys pallida* (Seeliger, 1945) (Lovich et al., 2017). Extended drought periods have been reported to affect emigration and nesting behavior in the Pond Slider, *Trachemys scripta* (Thunberg, 1792) and in the Common Cooter *Pseudemys concinna floridana* (Le Conte, 1830) (Gibbons et al., 1983). Flood-induced displacements can lower mating and nesting rates, as illustrated in the Wood Turtle *Glyptemys insculpta* (Le Conte, 1830) (Jones and Sievert, 2009). Loss of vegetation and changes in water flow regimes further may disrupt the ability of turtles to find suitable resting and hiding sites (Moll and Moll, 2004). Finally, floods can exacerbate turtle mortality, especially in rocky streams compared to muddy streams, as shown in the Large-nosed Wood Turtle *Rhinoclemmys nasuta* (Boulenger, 1902), suggesting that the nature of the substrate may influence turtle resilience to EWEs (Garcés-Restrepo et al., 2019). It is thus important to study the consequences of flood events on turtles living in diverse landscapes over the long-term to set up the best conservation measures to reinforce species survival (Lamont et al., 2021).

The Mediterranean Pond Turtle *Mauremys leprosa* (Schweigger, 1812), whose distribution extends from North Africa (Libya, Tunisia, Algeria, and Morocco) to southern Europe (Spain, Portugal, and southern France), lives mainly in low flow rivers (Bertolero and Busack, 2017). This species has a high tolerance for elevated ambient temperatures, reduced water levels, high water salinity (Bertolero and Busack, 2017), and polluted waters (Le Gal et al., 2023). It has been classified as vulnerable in Europe by the International Union for Conservation of Nature (Van Dijk et al., 2004). In this study, we monitored a population of *M. leprosa* on the Baillaur River, South of France, over a ten-year period (2012–2022). This river experienced a major autumnal flood in November 2014, i.e., just in the beginning of the inactive season of the species, which enabled us to assess the impact of the flood using a robust BACI method. The previous large-scale flood dated back to October 1959 where the flow reached approximately $500 \text{ m}^3 \cdot \text{s}^{-1}$ (Michel, 1959). We therefore investigated along different sections of the river the demographic effects of this flood on turtles in terms of survival, recruitment, and transition rates. We predicted that (i) the flood would have a negative impact on turtle survival generating the expulsion of some individuals from the streams, as reported for *R. nasuta* (Garcés-Restrepo et al., 2019); (ii) the population would compensate for individual loss by increasing post-flood recruitment as reported for a population of *M. leprosa* in Spain after severe droughts (Keller, 1999); (iii) the impacts of flood would differ between river sections throughout its length due to contrasted topographic features, and (iv) the impacts of flood would differ between genders due to sex-related dispersal capacities (Owen-Jones et al., 2015; Otten et al., 2023).

2. Methods

2.1. Study area

The study was held on the Baillaury River, Pyrénées-Orientales region, South of France (Fig. 1), where the largest population of *M. leprosa* in France occurs (Courmont and De Sousa, 2011). The Baillaury River is a typical Mediterranean river that partially dries up in summer yet whose water level rises during seasonal rains. The water course is 8.5 kilometers long, shallow (0.5–1.50 m maximum), and narrow (0.5–5 m width). It rises in the Albera Massif at an altitude of 600 m and flows into the Mediterranean Sea at Banyuls-sur-Mer. It consists of a major bed and five tributaries. Three river sections were considered (Fig. 1): the first section (hereafter referred as section A), flows from 130 to 60 m above sea level over a cumulative length of almost five kilometers. Section B, which is a two-branch section, flows from 120 to 60 m above sea level over a cumulative length of six kilometers. It is hydrologically disconnected from section A by a concrete weir (Fig. 2.1). Part of that sector especially “Rec de Pouada” brook is quite narrow and rocky. Section C, which flows from 60 to 20 m above sea level over almost two kilometers, is hydrologically connected to section A. A flood controller was managed in its upper section to regulate water flows (Fig. 2.3).

2.2. Field data collection

The turtle population of the Baillaury River was monitored based on a Capture-Mark-Recapture (CMR) survey in 2012, 2013, 2015, 2016 and 2022. Turtles were captured using baited traps (50 × 30 cm), placed parallel to the shoreline where water was deep enough, and equipped with floats to prevent captured turtles from drowning. Capture sessions occurred generally from April to July, during the turtle activity season, with three sessions per year except in 2016 where four sampling sessions were carried out. They took place over two consecutive days, except in 2012 where they were accrued out over four days. Between 150 and 600 trap-nights were set out at each session along the entire river, with a capture effort varying between years depending on available human resources and water level (in total 1752 trapping days in 2012, 440 in 2013, 634 in 2015, 682 in 2016, and 700 in 2022). Captured turtles were marked using Cagle’s scute notching method (Cagle, 1939), measured (straight carapace length, ± 0.1 cm) using a Vernier calliper, and released at the site of capture. Sex was determined by examining secondary sexual characteristics such as plastron concavity and distance from the plastron notch to the cloaca opening (Pérez et al., 1979; Busack and Ernst, 1980; Meek, 1987; Fritz, 2003). Because individuals smaller than 80 millimeters body length did not have noticeable secondary sexual characteristics in the study population,

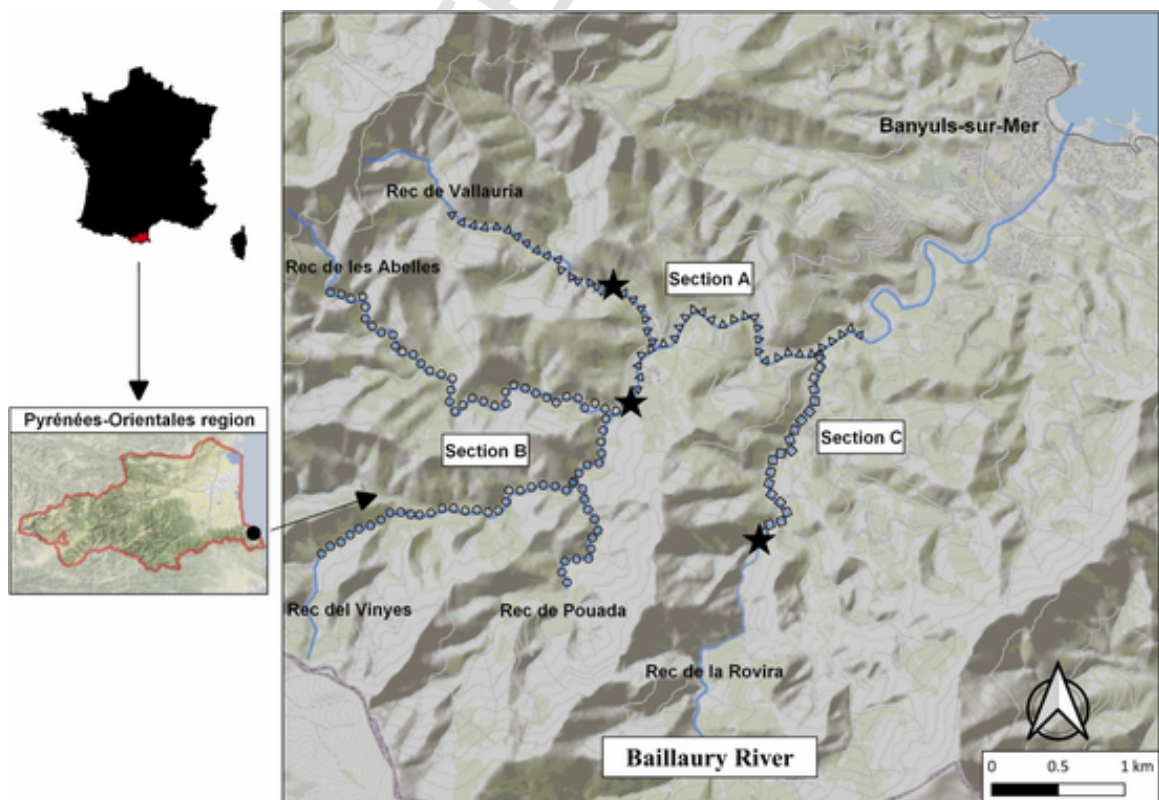


Fig. 1. Baillaury river in the vicinity of Banyuls-sur-Mer. Investigated river sections for turtles are illustrated by triangles (Section A), circles (Section B) and squares (Section C). Dark stars illustrate flood controllers. Note that the downstream portion of the river, which goes dry in summer, was not investigated for turtles.



Fig. 2. Photographs of the flood controllers between sections A and B (1), in the upper of section A (2) and in the upper of section C (3).

they were considered as juveniles. A ministerial authorization was granted for temporary captures by the DREAL Languedoc-Roussillon (nowadays DREAL Occitanie), and experiments were carried out in accordance with the U.K. animals (Scientific Procedures) Act, 1986 and associated guidelines, EU Directive 2010/63/EU for animal experiments.

During the night of 29–30 November 2014, heavy rainfall led to a massive flood resulting in a rise in water levels of up to five meters and a flow of $150 \text{ m}^3 \cdot \text{s}^{-1}$ (<https://hydro.eaufrance.fr/sitehydro/Y0105220/series>, accessed 2024/03/27). The mean daily flow of the Baillaury River rose from $0.001 \text{ m}^3 \cdot \text{s}^{-1}$ on November 2014, 29th, to $2.18 \text{ m}^3 \cdot \text{s}^{-1}$ on November 2014, 30th. The flood destroyed part of the vegetation along the Baillaury River, roads, and nearby vineyards, some of which were piled up in the riverbed (Fig. 3A and B).

2.3. Statistical analysis

Because turtle population stability has been reported to mainly depend on adult survival on the one hand (Frazer, 1992; Heppell, 1998; Olivier et al., 2010; Blamires and Spencer, 2013) and because small individuals were not marked on the other hand, only adults were considered for modeling population dynamics.

2.3.1. Robust-design models

The CMR data were modelled using Pradel Robust-design Survival and Seniority (Pradel, 1996) to test the impact of flood on the dynamic of the population by estimating the probability of capture (p), survival (φ), recruitment (b , inferred from the seniority as $b = 1 - \text{seniority}(\gamma)$) and population size (N). For these Robust-design models, capture and recapture probabilities were considered equivalent and closure tests were performed using CloseTest (Stanley and Burnham, 1999) to check intra-annual population closure. Since



Fig. 3. Photographs of the bed and banks of the Baillaury River, before (A) and after the 30-year flood of November 2014 (B).

capture effort has been reported to be a good predictor of capture probability for another freshwater turtle the European pond turtle, i.e., *E. orbicularis* (Owen-Jones et al., 2015), two models with either year effect or capture session effect on capture probability were developed.

Similarly because an influence of the 2014 flood on population dynamics was predicted, several models accounting different scenarios of survival ϕ and seniority γ were also developed: (i) ϕ and γ differ before versus after flood (referred as “bef/after flood”); (ii) ϕ and γ differ between before the flood, one and two years after the flood and returned to initial situation before the flood (referred as “bef-after1-after2-bef”); (iii) ϕ and γ differ between years with or without flood (referred as “with-without flood”), and (iv) ϕ and γ differ amongst years regardless flood occurred or not (referred as “year”). At last, because survival, capture, and recruitment probabilities have been reported to be sex-dependent in freshwater turtles (Olivier et al., 2010; Owen-Jones et al., 2015; Escoriza et al., 2020; Le Gal et al., 2023), the effect of sex alone or in addition with the other covariates were tested. Considering the large number of covariates, the number of models using all combinations was too high to be fitted exhaustively. Accordingly, we proceeded step by step as follows:

We first tested the covariates on capture probability, while the other parameters depended on the addition of year + sex (most complex models). Second, we kept the best model of capture probability, considered recruitment as year + sex dependent, and tested the different scenarios on the survival probability. Finally, we kept the best models of capture and survival probabilities, then tested the different hypotheses on recruitment. We thus obtained a set of 40 Pradel Robust-design Survival and Seniority models (Supplemental Table S1) that were all fitted using the software MARK 6.2 (White and Burnham, 1999) (Robust Design Pradel Seniority Full Likelihood p and c). Although this approach is not exactly a multimodel selection procedure, it allows the covariate effects to be explored while keeping the number of models fitted relatively low. We considered unequal time intervals between each occasion by mention it in set time intervals option. Models were compared using AICc and adjusted for small sample sizes (Burnham and Anderson, 2002).

Because several competing models had support, we used the AIC weight and a model Averaging procedure to obtain the average estimates (Burnham and Anderson, 2002). All estimates were provided with their confidence intervals (CI).

2.3.2. Multistate models

To test whether the 2014 flood differently impacted turtles across the river sections, the CMR data were also modelled using a multistate capture-recapture models (Nichols et al., 1994) with the states defined as the different river sections (A, B or C), by estimating the transition probability (Ψ) between river sections and the survival probability (ϕ). For the Multistate model, all intra-year captures were merged to build a yearly data set. When individuals were captured at two different locations in the same year, we only considered the last site of capture to be the most representative at the scale of the year. A Multistate goodness-of-fit test (Pradel et al., 2005) was performed using U-Care 2.3.2 (Choquet et al., 2009) to test trap-dependence and transience for multistate models.

For the same reasons as those reported earlier for the Robust-design models, several models with either year effect or capture session effect on capture probability were developed accounting different scenarios of Ψ : (i) Ψ differ before and after flood (referred as “bef/after flood”); (ii) Ψ differ before the flood, one and/or two years after the flood and returned to initial situation before the flood (referred as “bef-after1-after2-bef”); (iii) Ψ differ between years with or without flood (referred as “with-without flood”), and (iv) Ψ differ amongst years regardless flood occurred or not (referred as “year”). Similarly because different effects of the 2014 flood throughout the river length due to contrasted topography and to the presence / absence of flood controllers were predicted, effects of the river section (referred as “section”) on each parameter of the Multistate models (survival, recapture or transition probability) were tested alone, in addition or in interaction with the other covariates (year and sex). At last, because survival, capture, and dispersal probabilities have been reported influenced by the sex in freshwater turtles (Olivier et al., 2010; Owen-Jones et al., 2015; Escoriza et al., 2020; Le Gal et al., 2023), the effect of sex alone or in addition with the other covariates was tested.

Therefore, we first tested the covariates on recapture probability while survival probability depended on the addition of year + sex + section and transition probability depended on the interaction year*section, with sex in addition. Second, we kept the best model of recapture probability, considered the transition probability depending on the interaction year*section with sex in addi-

tion, and tested the different hypotheses on the survival probability. Finally, we kept the best models of capture and survival probabilities, and then tested the different hypotheses on transition probabilities. We thus obtained a set of 35 Multistate models (Supplemental Table S2) that were all fitted using the software MARK 6.2 (White and Burnham, 1999) (Multistate Recapture only). Models were compared using AICc and adjusted for small sample sizes (Burnham and Anderson, 2002). Because several competing models had support, we used the AIC weight and a model Averaging procedure to obtain the average estimates (Burnham and Anderson, 2002). All estimates were provided with their confidence intervals (CI).

3. Results

3.1. Raw captures during the sampling period

Between 2012 and 2022, a total of 377 individual turtles were marked on the Baillaury River, including 207 males and 170 females. Number of juveniles was low, i.e., 48, among which 91 % were only captured once. The Pradel Robust-design dataset consisted in 889 capture-recaptures of the 377 adult individuals (41 % were captured once, 25 % twice, 16 % three times, 7 % four times, 4 % five times, 3 % six times, 2 % seven times and 1 % more than seven times), and the Multistate dataset consisted of 606 capture-recaptures among which 253, 148, and 205 individuals were trapped across the river sections A, B, and C, respectively. Among the 377 individuals, 39 turtles transited between river sections (10 %), among which 34 transited between two sections and five between three sections. In 2012–2013, namely before the 2014 flood, 200 adult turtles were tagged. Out of the 200 individuals, 115 (57 %) were recaptured after the flood, including 58 (50 %) females. Out of the 115 individuals, 95 (83 %), including 48 females (51 %), were recaptured one or two years after flood (in 2015 and/or 2016) whereas only 20 (17 %), including 10 females (50 %), were recaptured eight years later (in 2022). Just after flood several individuals were found on the beaches of the Mediterranean coast in Banyuls-sur-Mer, and a turtle was even spotted at Paulilles beach, 3.5 kilometers further north.

3.2. Goodness-of-fit tests

The GOF test for multistate models was not significant ($z = 18.80$; $p = 0.28$) indicating adequation with the assumptions of the models (transience, trap-dependence, memory). Trap-dependence was not detected ($z = -1.30$; $p = 0.19$). Yet transience was marginally significant ($z = 2.25$; $p = 0.024$) for females only (females: $z = 2.00$; $p = 0.046$; males: $z = 1.19$; $p = 0.24$), indicating that a relatively high proportion of females were captured only once. Population closure test for Robust-design models, indicated that population was closed in 2012 ($\chi^2 = 1.53$, $p = 0.46$), 2013 ($\chi^2 = 1.64$, $p = 0.44$), 2015 ($\chi^2 = 0.46$, $p = 0.79$), 2016 ($\chi^2 = 3.86$, $p = 0.43$), and in 2022 ($\chi^2 = 4.41$, $p = 0.11$).

3.3. Effects of the flood on population dynamics

Seven Pradel Robust-design models were considered equivalent ($\Delta AICc < 2$) with a combined Akaike weight of 0.55 (Table 1). These models considered (i) an effect of session or session and sex on probability of capture; (ii) an effect of sex on survival probability; (iii) an effect of flood and sex, or sex only, on seniority probability. All fitted models are shown in the supplemental material (Appendix Table S1).

The capture probability depended on the capture session or on the capture session and individual sex. Capture effort positively influenced capture probability ranging from 0.06 (CI 0.04 – 0.11) to 0.54 (CI 0.45 – 0.62). Our model selection procedure did not support any effect of sex on recapture probability (Fig. 4).

Population size and sex ratio were affected by flood with a decrease in absolute and relative abundances of females in 2015 (16 %) and 2016 (27 %), whereas the total number of males remained around 100 individuals (Fig. 5). At the end of the study period (2022), the number of adults has returned to its initial level and the sex ratio was once again balanced as it was before the flood.

Table 1

Constraints, Akaike's information criterion (AICc), ($\Delta AICc$), Akaike weights (wi) and number of estimated parameters (K) for the 10 best Pradel Robust-design models obtained from 889 capture-recaptures of adults ($N = 377$). (ϕ) refers to the survival probability, (γ) refers to the seniority probability, (p) and (c) refer to the probability of capture and recapture, respectively, and (Fo) refers to the number of missed animals.

No.	Models	K	AICc	$\Delta AICc$	Wi
1	ϕ (sex) γ (sex) $p = c(\text{session})$ Fo(year + sex)	26	420.29	0.00	0.132
2	ϕ (sex) γ (sex) $p = c(\text{session} + \text{sex})$ Fo(year + sex)	27	420.81	0.52	0.102
3	ϕ (sex) γ (bef-after1-after2-bef + sex) $p = c(\text{session})$ Fo(year + sex)	28	421.29	1.00	0.080
4	ϕ (sex) γ (.) $p = c(\text{session})$ Fo(year + sex)	25	421.65	1.36	0.067
5	ϕ (sex) γ (bef/after flood + sex) $p = c(\text{session})$ Fo(year + sex)	27	421.84	1.55	0.061
6	ϕ (sex) γ (bef/after flood + sex) $p = c(\text{session} + \text{sex})$ Fo(year + sex)	28	422.13	1.84	0.053
7	ϕ (sex) γ (bef-after1-after2-bef + sex) $p = c(\text{session} + \text{sex})$ Fo(year + sex)	29	422.19	1.90	0.051
8	ϕ (sex) γ (with-without flood + sex) $p = c(\text{session})$ Fo(year + sex)	27	422.32	2.03	0.048
9	ϕ (sex) γ (bef-after1-after2-bef) $p = c(\text{session})$ Fo(year + sex)	27	422.51	2.22	0.044
10	ϕ (sex) γ (year + sex) $p = c(\text{session})$ Fo(year + sex)	29	3.76	2.47	0.038

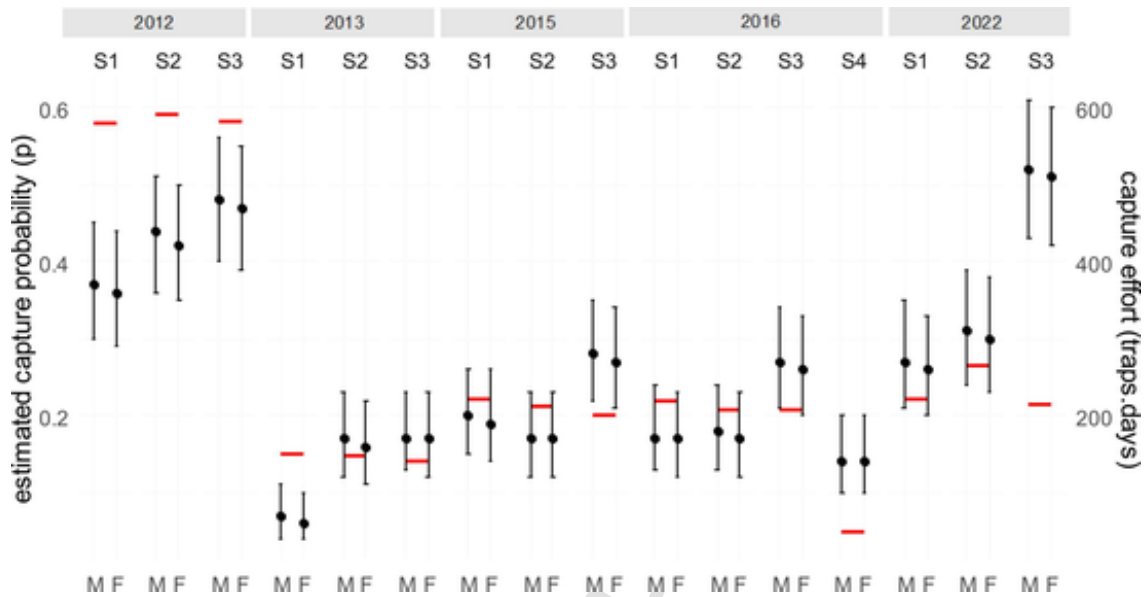


Fig. 4. Capture probability with 95 % confidence intervals (black dots and vertical lines) obtained by model averaging procedure from Pradel Robust-design models. Capture efforts for every capture session (S1, S2, S3, S4) are displayed as horizontal red lines.

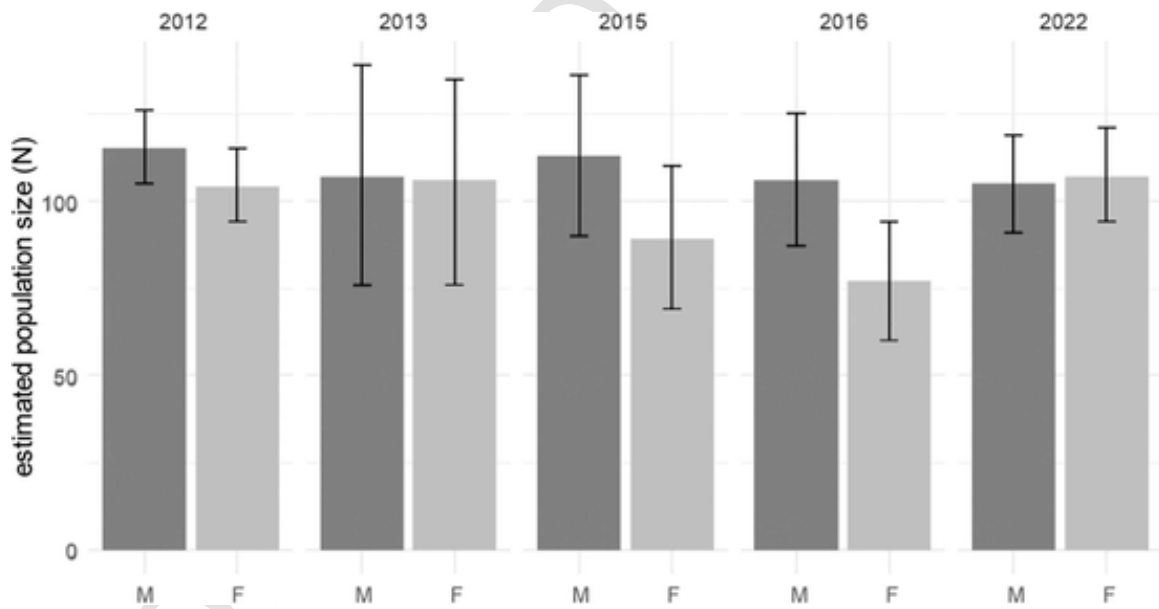


Fig. 5. Population size estimates and 95 % confidence intervals obtained by model averaging procedure from Pradel Robust-design models for male (dark grey) adults and female (light grey).

There was no significant effect of flood on survival rates calculated throughout the study period. Yet annual survival probability depended on individual sex, being higher for females (0.89, CI 0.85 – 0.92) than for males (0.85, CI 0.80 – 0.88).

The adult recruitment probability depended on flood (bef-after1-after2-bef) and on individual sex, being higher for males (0.15 per year, CI 0.12 – 0.18), than for females (0.11 per year, CI 0.09 – 0.14) (Fig. 6). The post-flood recruitment estimates calculated between 2015 and 2016 were associated to a large standard error.

3.4. Effects of flood on turtles depending of the river sections

Two Multistate models had the most support ($\Delta AICc < 2$) with a combined Akaike weight of 0.74 (0.49 for the first one and 0.25 for the second one ($\Delta AICc = 1.36$) (Table 2). Both of them considered: (i) effects of year on probability of recapture; (ii) an effect of

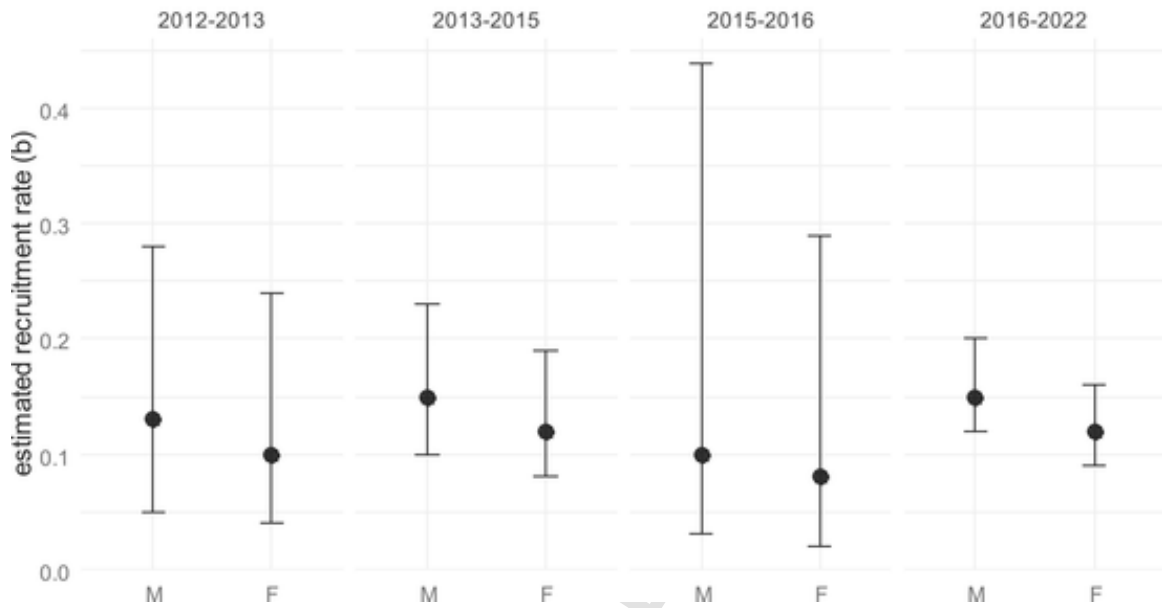


Fig. 6. Adult recruitment rate and 95 % confidence intervals obtained by model averaging procedure from Pradel Robust-design models.

Table 2

Constraints, Akaike’s information criterion (AICc), (Δ AICc), Akaike weights (wi) and number of estimated parameters (K) for the 10 best Multi-state models obtained from 606 capture-recapture (N = 377). (ϕ) refers to the survival probability, (c) refers to the probability of recapture, and (Ψ) refers to the probability of transition between sections.

No.	Models	K	AICc	Δ AICc	Wi
1	ϕ (sex) c(year) Ψ (bef/after flood*section)	15	1276.60	0.00	0.49
2	ϕ (bef/after flood + sex) c(year) Ψ (bef/after flood*section)	16	1277.96	1.36	0.25
3	ϕ (sex) c(year) Ψ (bef/after flood*section + sex)	16	1278.69	2.09	0.17
4	ϕ (bef/after flood + sex) c(year) Ψ (bef/after flood*section + sex)	17	1280.06	3.46	0.09
5	ϕ (sex) c(year) Ψ (with-without flood*section)	17	1287.71	11.11	0.00
6	ϕ (bef/after flood + sex) c(year) Ψ (with-without flood*section)	18	1289.12	12.52	0.00
7	ϕ (sex) c(year) Ψ (with-without flood*section + sex)	18	1289.76	13.16	0.00
8	ϕ (sex) c(year) Ψ (year*section)	26	1290.52	13.93	0.00
9	ϕ (bef/after flood + sex) c(year) Ψ (with-without flood*section + sex)	19	1291.15	14.56	0.00
10	ϕ (bef/after flood + sex) c(year) Ψ (year*section)	27	1292.00	15.40	0.00

sex and/or flood on annual survival probability; (iii) an effect of flood depending on river section on transition probability. All fitted models are shown in the supplemental material (Table S2).

Recapture probabilities depended on years, increasing from 0.40 (CI 0.31 – 0.50) in 2013 and 2015, to 0.51 (CI 0.40 – 0.62) in 2016, and to 0.60 (CI 0.30 – 0.84) in 2022. Our model selection procedure did not support any effect of sex on recapture probability.

Survival rates estimated by the MS models were nearly the same as those estimated by the RD models, being higher for females (0.90, CI 0.83 – 0.94) than for males (0.84, CI 0.78 – 0.89), regardless of the river section. The negative effect of flood on survival was not significant.

Transition probability differed before and after the flood according to the river sections. Between river sections A and B, whether upstream or downstream, transition probabilities did not differ significantly before (0.15, CI 0.06–0.32) and after (0.11, CI 0.06–0.20) the flood. Between river sections A and C, transition probabilities were higher after than before the flood. Yet there were no clear differences towards upstream from section A to C (from 0.04 (CI 0.01–0.23) to 0.12 (CI 0.06–0.21)) but significant differences towards downstream from section C to A (from 0 before to 0.10 (CI 0.05–0.20) after flood). Between river sections B and C (connected by A, i.e., transition across 3 sections, see Fig. 1), transition probabilities were also higher after than before the flood. There were clear differences in both directions, with transitions estimated from 0 to 0.13 (CI 0.06–0.27) from section B to C, and from 0 to 0.06 (CI 0.02–0.14) from section C to B (Fig. 7).

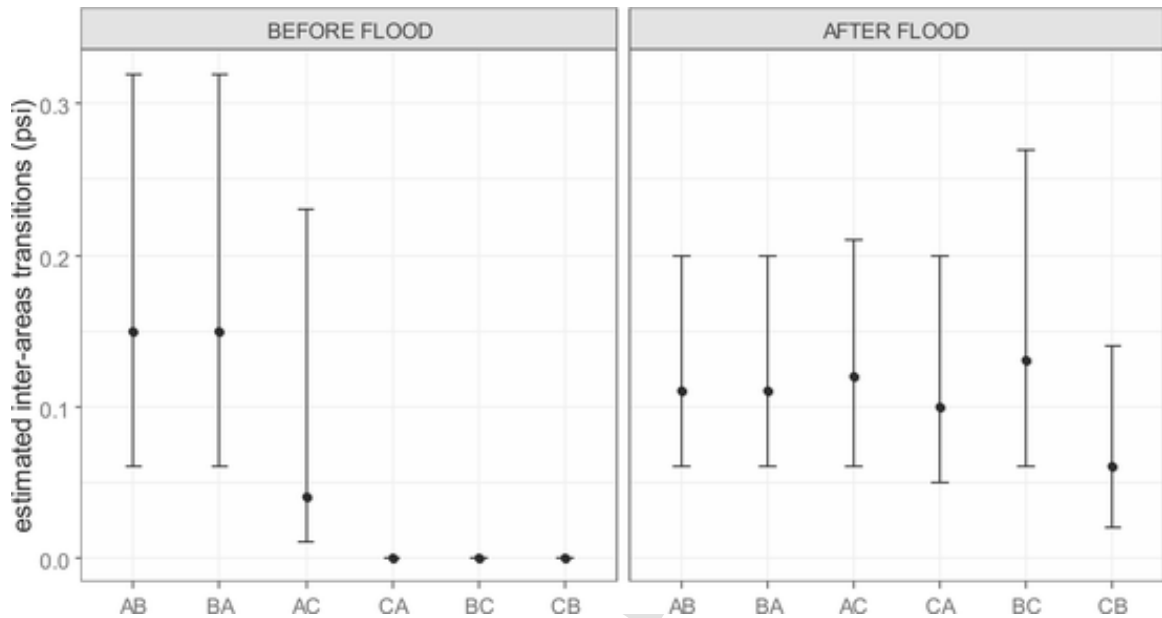


Fig. 7. Transitions probabilities between river sections and 95 % confidence intervals obtained by model averaging procedure from Multistate models.

4. Discussion

4.1. Consequences of the 2014 flood on turtles

This study highlights that the extreme flood occurring in November 2014 on the Baillaury River did neither alter the structure nor the dynamics of the adult population in the medium term. Although population size decreased immediately after flooding, the adult population rapidly returned to its initial state with balanced sex ratio. Because the turtle population is well isolated from the other known populations of Southern France, the nearest one being that of the Tech River located in the vicinity of the Boulou city, 20 kilometers far away (Courmont and De Sousa, 2021), recolonization from there could not be expected. However, the flood mainly impacted the spatial dynamics of the population by increasing the downstream movements of turtles, thus modifying their distribution throughout the river.

4.2. Capture probability and sampling effort

As we predicted, the capture effort was a good predictor of the capture probability that was estimated between 6 % and 54 %. Trapping effort varied amongst years, depending on availability of field staff, but also on river configuration since the summer droughts, i.e., low water levels, constrained the number of traps that could be deployed. Our results were also consistent with former studies reporting a positive correlation between trapping effort and total number of captured turtles and with the accuracy of the demographic parameters estimated in the same species (Le Gal et al., 2023) but also in *E. orbicularis* (Owen-Jones et al., 2015). This result thus highlights the importance of keeping capture efforts consistent and homogenous throughout years, especially for long term studies. A time step of five to ten years, excluding exceptional events, seems also sufficient for the long-term monitoring of a long-lived species such as *M. leprosa*.

4.3. Survival, recruitment and medium-term impact of flood

The survival of turtles in the Baillaury River was high (0.89 ± 0.03 for females and 0.85 ± 0.03 for males) and similar to that reported for the same species in other Mediterranean habitats such as the Fosseille River, another river of the area, deeper and wider yet more muddy due to pollution (0.88 ± 0.02 , Le Gal et al., 2023) and lagoons in south of Spain (0.87 ± 0.02 , Keller, 1997). Studies conducted on *G. insculpta* and in the Irwin's Snapping Turtle *Elseya irwini* (Cann, 1997) after floods also illustrated no negative effects on turtles (Jones and Sievert, 2009). As an explanation, it was suggested that turtles may use hibernacula as refuges and burrow to avoid extreme surface currents (Jones and Sievert, 2009). Our results however contrasted with those reported for *R. nasuta* living in rocky streams, i.e. an environment which is similar to the Baillaury River. Following heavy floods, lower survival was reported for *R. nasuta* in rocky streams than that reported for the same species in muddy streams, possibly because it is easier to escape or hide in mud substrates (Garcés-Restrepo et al., 2019). Females in the Baillaury River exhibited higher survival than males, which showed particularly low values for freshwater turtles in general (see Gibbons et al., 2000). The lower survival rate in males could be related either to their marked exploratory behaviors (emigration), making them more prone to exit the study area, or to their morphological

characteristics, males being smaller and lighter than females (Bakhouché et al., 2019; Muñoz, 2009) making them less prone to survive mechanical stress due to floods, but also predation. Importantly, higher mortality (or emigration) in males was compensated by higher male recruitment rate, leading to balanced population size and sex ratio on the medium term. Survival and recruitment were constant during the study period showing that the 2014 autumn flood had no effect, neither on survival rates nor on recruitment. Similar results were reported, yet after spring floods, in the Painted Turtle *Chrysemys picta* (Schneider, 1783) (see Jergenson et al., 2014), but also in the Northern Map Turtle *Graptemys geographica* (Le Sueur, 1817) and in *T. s. elegans* (see Pitt et al., 2021).

On a short term though, the 2014 autumn flood slightly altered population size, temporarily slightly unbalancing the sex ratio in favor of males (55 % and 57 % of males in 2015 and 2016, respectively), before population recovered and even increased with balanced sex ratio. Although flood events can destroy eggs and impair turtle recruitment (Janzen, 1994), our results underlined that reproduction was maintained since the population recovered over the medium-term, with the addition of new young individuals. Besides, we noted an important number of juveniles in 2015 and 2016 (about thirty) that may be related to an increase of nesting habitats along the river following flooding. An increase of juveniles after flood and/or drought was also observed by Keller (1999) on *M. leprosa*, by Pérez-Santigosa (2007) on both *M. leprosa* and *E. orbicularis*, and by Pitt et al. (2021) on *G. geographica*. Unlike fires that lead to massive mortality of young turtles, with repercussions in subsequent years in terms of recruitment due to hostile living conditions, i.e., absence of riparian vegetation and rarity of food resources (Cheylan and Poitevin, 1998), flood, which does not affect the survival of juveniles, supports population rejuvenation. It can even provide temporary and/or permanent wetlands for breeding and feeding aquatic species including turtles' prey (Mitsch and Gosselink, 2007), as illustrated by the observation of many fry the year after flood. Our study, along with previous studies, thus indicates that river turtles are able to cope with extreme flooding events. Resilience may be attributed to a combination of anatomical, physiological, and behavioral adaptations (Pitt et al., 2021).

4.4. Transition and short-term impact of flood

As a major outcome, our study shows that transitions between river sections were enhanced after the flood, mainly from sections C to A, and between sections B and C both ways (Fig. 7). This indicates that turtles were washed away by the flood, as also reported after extreme rainfalls for *R. nasuta* in similarly rocky streams (Garcés-Restrepo et al., 2019). Interestingly, some individuals were found out of the study area, i.e., on the sea beach and up to 3.5 kilometers far away from the river estuary, leading to a temporarily decrease in the population size. This indicates that turtles returned upwards, traveling up to eight kilometers, while dispersing between river sections. As a result, *M. leprosa* behaves as a river turtle, showing considerable ability to return to its home area when moved over long distances and also strong site fidelity (Otten et al., 2023). These movements appear to have occurred over a period of two years after the flood, since more than 90 % of the turtles recaptured post-flood (2015–2022) were recaptured in 2015 and/or 2016. Particularly, turtles were more recaptured in river sections A or C than in river section B. Section B was indeed the section the most affected by the flooding in terms of turtle habitat and, above all, by post-flood artificial development such as rearrangement of banks and removal of logjams, making this section the least favourable for turtles. As the flooding increased turtle movements between river sections, it may have served as a natural mechanism for animal dispersal. Flooding might therefore enable turtles to colonize new sites, promoting genetic mixing by gathering individuals from different initial river sections. This is supported by the fact that the largest populations of *M. leprosa* inventoried in France and Spain are located along the coastal fringe (Franch et al., 2015; Palacios et al., 2015; Courmont and De Sousa, 2021).

5. Conclusion

This study highlights the medium-term resilience of a population of *M. leprosa* to an extreme flood event that occurred during the turtle hibernation period. On the short term, we demonstrate the importance of extreme flooding events for the dispersal of turtles within a rocky river, with significant movements of individuals amongst river sections, but also beyond since some individuals could reach new sites northern up along the coasts. Despite the fact that size decreased immediately after the flood, the turtle population fully recovered both in size and structure within eight years, demonstrating the ability of turtles to return to their original area and state. This indicates the very importance of preventing building infrastructures impassable by turtles and aquatic wildlife in general during the implementation of river and bank management aimed at mitigating impacts of such extreme events.

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CRediT authorship contribution statement

Pauline Priol; Conceptualization, Methodology, Formal analysis, Investigation, Validation, Writing – Original Draft, Writing – Review & Editing, Supervision; Anne-Sophie Le Gal; Data curation, Visualization, Writing – Original Draft, Writing – Review & Editing; Olivier Verneau; Data collection, Review & Editing, Supervision, Funding acquisition; Jean-Yves Georges; Review & Editing; Alexis Santalucia; Data collection, Visualization, Review & Editing; Lionel Courmont; Conceptualization, Methodology, Investigation, Review & Editing, Supervision, Project administration, Funding acquisition.

Uncited references

Biber et al., 2023; Cardillo et al., 2005; Collins and Storfer 2003; Hershkovitz and Gasith 2013; Hunter and Hutchinson 1994; Lavorel et al., 2017; Nilsson et al., 2005; Piniewski et al., 2017; Tabari 2020.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Lionel Courmont reports financial support was provided by DREAL. Lionel Courmont reports financial support was provided by CD66. Lionel Courmont reports financial support was provided by SOPTOM. Lionel Courmont reports financial support was provided by GOR. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper

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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.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2024.e03177.

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