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Experimental biology of species range dynamics:

drivers of survival and dispersal in range-core and range-edge

invasive crayfish

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18 **Abstract**

Projecting and managing the future response of invasive species to global change requires a
20 mechanistic understanding of how climate and ecology jointly drive species demography and range
dynamics. Here, we use mark-recapture in replicated outdoor mesocosms to examine how survival
22 and dispersal, two key drivers of demography and range dynamics, respond to climate and ecology
in the invasive red swamp crayfish (*Procambarus clarkii*) along an invasion gradient. We show that
24 crayfish survival probability increased with (i) increasing body size at high (but not low) crayfish
density and (ii) with warmer temperatures, and decreased (i) with increasing body condition and (ii)
26 under higher crayfish density. Overland dispersal probability by crayfish increased with increasing
(i) body-size, (ii) body condition and (iii) temperatures. In contrast, crayfish from range-edge and
28 range-core habitats had similar survival and overland dispersal probabilities, suggesting no
evolution of their range-expansion potential along the invasion gradient. Our results highlight that
30 predicting species population dynamics and range shifts in a changing world requires accounting for
the joint contributions of climate, body size and ecological interactions. In local *P. clarkii*
32 populations, global warming will simultaneously promote both a numerical increase and a
geographic-range expansion, especially in populations dominated by large-bodied individuals. In
34 already-invaded ecosystems, we suggest that selective harvesting of large-bodied crayfish is a
management strategy that could reduce a population's range-expansion potential over both
36 ecological and evolutionary time scales.

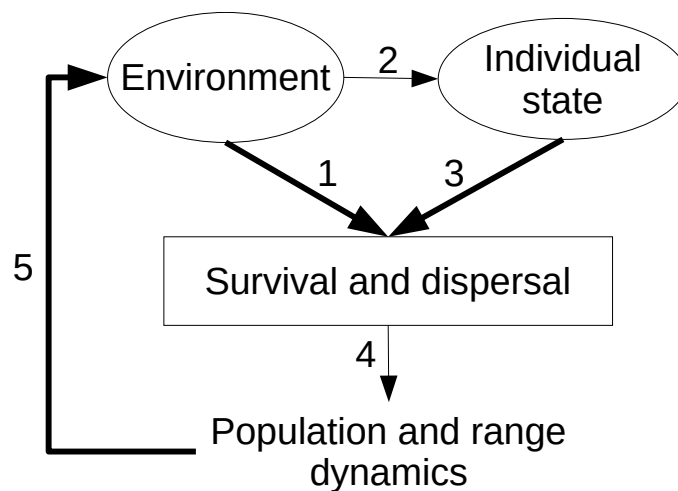
38 **Key words :** Density-dependent survival; Multistate mark-recapture model; Process-explicit
demographic models; Size-dependent dispersal.

40

INTRODUCTION

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How species geographic distributions will change in a near future is a central question in ecology, evolution, biodiversity conservation and the management of biological invasions. To date, our ability to answer this question often rests on correlative species distribution models, which provide a poor mechanistic understanding and, arguably, have a limited power to predict how organisms will respond to global change. Avoiding these problems requires explicit models of how ecological and evolutionary processes control geographic distributions (Briscoe et al. 2019). These process-explicit models draw heavily on population-dynamic models, and on how demographic rates, i.e., survival, reproduction and dispersal, respond to environmental change (Fig. 1).



52 **Fig. 1. Conceptual framework for process-explicit models of species range dynamics.** The environment
54 influences demographic rates either directly (Arrow 1), or indirectly through altering individual-state
56 variables through both phenotypic plasticity and natural selection (Arrow 2-3 sequence). Demographic rates
ultimately drive the dynamics of both population sizes and geographic ranges (Arrow 4). In turn, population
and range dynamics entail environmental alterations (Arrow 5). Bold arrows show causality links that are
directly investigated in the present study.

58

A host of environmental abiotic (e.g., climate) and ecological (i.e., density-dependent) factors
60 directly influence demographic rates, including survival and dispersal (Arrow 1 in Fig. 1, (Clobert

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et al. 2012). The environment may also influence individual-state variables (Arrow 2 in Fig. 1),
62 such as sex, body size or body condition which, in turn, also influence demographic rates (Arrow 2-
3 sequence in Fig. 1, Charlesworth, 1994; Clobert et al., 2012; Kooijman, 2010). Finally, in a
64 feedback loop, changes in demographic rates entail changes in population size and geographic
ranges (Arrow 4 in Fig. 1), i.e., changes in the environmental conditions experienced by individuals
66 (e.g., competition, predation, habitat quality, Arrow 5 in Fig. 1).

68 This feedback loop may be disrupted by global anthropogenic changes, which act at both the
environment and individual-state levels. At the environment level, climate warming alters
70 temperatures and precipitations, and the resultant oxygen, flow and sediment regimes in aquatic
ecosystems (IPCC 2021). At the individual-state level, a number of human activities, such as
72 harvesting, or their consequences, such as habitat fragmentation, are often selective on sex,
physiology, behaviour or body size (Edeline 2016).

74

An additional complexity layer comes from individual-state variables being potentially subject not
76 only to plastic changes in response to environmental alterations, but also to evolutionary changes. In
particular, emigration from the core habitat, or from the introduction point in the case of biological
78 invasions, often selects for increased dispersal propensity along the invasion gradient through
spatial sorting of the most dispersive phenotypes, and is further possibly a competition-avoidance
80 response where poorer competitors disperse from high-density core habitats to low-density marginal
habitats (Phillips et al. 2010; Burton et al. 2010). Hence, high dispersers and poor competitors are
82 likely to be overrepresented among immigrants at range edges. Results from spread experiments
support the prediction that increased dispersal evolves at range edges (Fronhofer and Altermatt
84 2015; Williams et al. 2016; Ochocki and Miller 2017), but evidence for reduced competitive ability
is mixed (Duckworth 2008; Hudina et al. 2015).

86

Unfortunately, however, the development of process-explicit models of geographic ranges that
88 would integrate these feedbacks is impeded by serious logistical and knowledge limitations. The
data needed to estimate demographic rates, as well as their environment- and state-dependency, are
90 hard and costly to acquire in the wild, and are thus typically lacking (Briscoe et al. 2019). Even
when present, such data may be poor if detection and/or recapture rates are low, or if population
92 size is small, resulting in inaccurate parameter estimation. A further obstacle to implementing
process-explicit models of species ranges is that eco-evolutionary feedback loops that may operate
94 during range expansion remain a frontier in biology and are poorly understood empirically (Miller
et al. 2020), which makes it uncertain which mechanisms should be incorporated into models.

96

In the present study, we propose to circumvent these logistical and knowledge limitations using
98 outdoor mesocosms and mark-recapture of wild-caught, range-core and range-edge animals. We are
not aware of any previous study of this kind in the field of species range dynamics. Specifically, we
100 tested the effects of key individual-state variables (sex, body size, body condition), climate
(temperature), ecology (population density) and geographic-range origin (core vs. edge of an
102 invaded area) on both survival and overland dispersal propensity in the cosmopolitan invasive red
swamp crayfish (*Procambarus clarkii*), which poses very serious management problems due to the
104 profound reorganizations it causes in recipient ecosystems (Twardochleb et al. 2013). In *P. clarkii*,
the factors that influence survival rates and dispersal syndromes remain relatively poorly
106 understood. However, as shown below, crayfish demographic rates and their predicted response to
individual-state variables, climate, ecology and geographic-range origin (see literature review in
108 Appendix 1) can be robustly quantified using mark-recapture in outdoor mesocosms. Our results
suggest that body size, population density, and water temperature are major drivers of demography
110 and geographic-range dynamics in the red swamp crayfish.

112

MATERIALS AND METHODS

114 **Study design**

Crayfish populations

116 *P. clarkii* originates from south-central USA (Louisiana and Texas) and was introduced to Europe
through both USA-to-Kenya-to-Europe and USA-to-Spain routes (Oficialdegui et al. 2019). We
118 used crayfish sampled from natural populations in the Brière area, north-western France, where
crayfish belonging to the USA-to-Kenya-to-Europe introduction route were introduced during the
120 early 1980's (Oficialdegui et al. 2019; Bélouard et al. 2019). Crayfish escaped from a farm and
invaded the nearby Brière marsh (90 km²), where they now form a large and genetically-
122 homogeneous population (Bélouard et al. 2019). From this range core, dispersers used streams,
ditches and, secondarily, overland dispersal to colonize ponds embedded in the surrounding
124 hedgerow landscape, where they founded multiple new populations that may be considered as
range-edge populations (Tréguier et al. 2018; Bélouard et al. 2019).

126

We sampled crayfish from three different range-core locations in the marsh (MB1, MB2 and MB3
128 as named in Bélouard et al. 2019), hereafter collectively referred to as “Range-core crayfish”, and
from three range-edge ponds. These pond populations are genetically-differentiated from the marsh
130 source population at neutral markers (CB7, I6 and I10 ponds in Bélouard et al. 2019), and are
hereafter collectively referred to as “Range-edge crayfish”. Further details on the populations used
132 in the experiment are provided in Appendix 2.

134 In addition to crayfish from the Brière, we sampled crayfish from a third locality, a pond located in
Rennes City (about 80 km away from the Brière, Appendix 2), hereafter referred to as an

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136 “Outgroup”. These Rennes crayfish have a genetic signature typical of the native range, suggestive
of an introduction route that differs from what has been described for the marsh of Brière
138 (Appendix 3). We used these Outgroup crayfish in order to standardize the density treatments in the
experiment (see below), and also because we were able to capture Range-edge crayfish only in
140 limited numbers.

142 *Crayfish sampling, marking and maintenance*

Crayfish in the Brière were sampled using non-baited traps on May 21st, 22nd and 24th 2019. Upon
144 capture, crayfish were determined as male or female from secondary sexual characters (first
pleopod pair transformed to gonopods in males), measured for body size (cephalothorax length to
146 the nearest mm, from the tip of the rostrum to the end of the cephalothorax), and weighted to the
nearest 10⁻¹g. Individual body condition was equated to the residual from a ln(Mass)-ln(Length)
148 regression performed on all individuals at once. Crayfish were individually marked using 8 mm
passive integrated transponders (Biomark HPT8 FDX PIT tags) inserted in the abdominal
150 musculature of the third abdominal segment in the ventral surface. Crayfish were then transported
to the PEARL, the INRAE experimental facility for aquatic ecology and ecotoxicology in Rennes
152 City, and stocked for 10 days in 8 m² mesocosms under a density of 15 crayfish m⁻². Stocking
conditions in mesocosms were designed so as to maximize crayfish welfare. Crayfish were provided
154 with an excess shelters made from PVC tubes, and were fed with fish food in excess (Le Gouessant,
Carpe Extrudée Coul 4). The same procedure was applied to Rennes crayfish, that were PIT-tagged
156 on April 24th and stocked for 40 days.

158 *Experimental mesocosms*

Experimental mesocosms were 28, three-m² circular tanks covered with nets to prevent avian
160 predation (Appendix 4A), and equipped with six artificial refuge traps (ART, Green et al. 2018).

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ARTs consisted in five PVC tubes (250 mm length) glued together and closed by a grid at one end
162 (Appendix 4B). ARTs were made from either 26.5 (3 ARTs) or 32.5 mm inner diameter tubes (3
ARTs), so as to fit with the needs of both small- and large-bodied crayfish. ARTs sank on the
164 bottom of the mesocosms and provided crayfish with shelters in excess (i.e., one tube provided one
shelter, 30 tubes per mesocosm). We initially did not introduce any sediments into the mesocosms,
166 but rapid algal sedimentation provided crayfish with some habitat structure at the bottom of the
mesocosms (Appendix 4A). Throughout the experiment, crayfish were mildly fed with 418 ± 11 mg
168 (mean \pm SD) of fish food per experimental mesocosm per week.

170 *P. clarkii* is able to colonize new habitats through overland movements (Huner and Barr 1991; Cruz
and Rebelo 2007; Ramalho and Anastácio 2015), and the propensities for overland movements and
172 in-stream dispersal are positively correlated in crayfish (Bubb et al. 2004; Moorhouse and
MacDonald 2011; Wutz and Geist 2013; Thomas et al. 2018). Therefore, we assumed that overland
174 movements in crayfish are part of a general dispersal syndrome (Clobert et al. 2012).

176 In order to measure crayfish dispersal propensity, each experimental mesocosm was equipped with
an exit trap requiring for trapping that crayfish actively walk out from water, i.e., that crayfish
178 initiate overland dispersal. Specifically, exit traps were made from a 50L bucket attached to the
inner wall of the mesocosm and hanging 30 cm underwater. Crayfish could climb a ramp made
180 from a plastic net and extending down from the bottom of the mesocosm and up to the rim of the
bucket (Appendix 4C). Crayfish falling into the trap could not escape back to the mesocosm. The
182 bottom of the bucket was pierced with holes to allow water circulation, and PVC tubes provided
trapped crayfish with shelters.

184

Experimental treatments and recapture

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186 On June 3rd 2019, we started the experiment by transferring crayfish into experimental mesocosms.
We introduced randomly-chosen Range-core and Range-edge crayfish at a constant density of 7
188 crayfish per mesocosm, and varied density by adding either 2 or 12 Outgroup crayfish, yielding two
density treatments (9 or 19 crayfish per mesocosm) and two range treatments (Range-core with
190 Outgroup or Range-edge with Outgroup) in a factorial design (7 replicate mesocosms per treatment,
392 crayfish in total). Experimental densities in our design (3.0 vs. 6.3 individuals m⁻²) were in the
192 high-range of naturally-observed densities, but were in line with experimental densities in the
literature (Appendix 5)

194

From June 5th 2019, both ARTs and exit traps were cleared at 1-7 days intervals (2.4 days mean \pm
196 0.8 SD). Recaptured crayfish were recorded for PIT tag number and were returned to their
mesocosm. Two live-recaptured crayfish had lost their tags during the course of the experiment (on
198 June 21st and August 7th). These were identified based on their sex, size and previous capture
histories, and re-tagged. On November 5th, after 153 days of experiment (63 recapture occasions),
200 mesocosms were drained and all surviving crayfish were recaptured and recorded for PIT tag
number.

202

Temperature

204 Air temperature during the experiment ranged from 3.9 to 39.4°C. Mean air temperature during a
recapture interval ranged from 9.3 to 26.9°C (Appendix 6). Water temperature in the mesocosms
206 was highly correlated with air temperature at a 5-hour lag (Appendix 6).

208

Data analysis

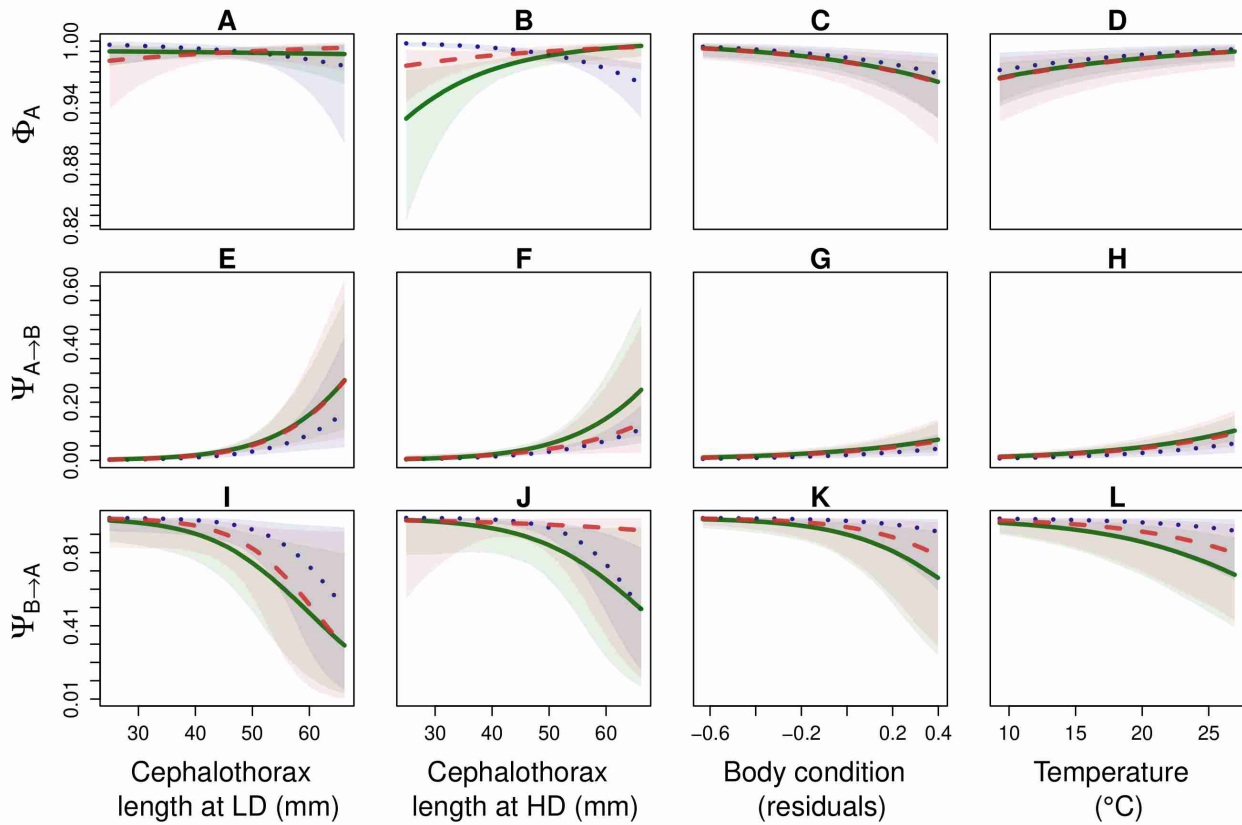
210 We estimated the effects of individual- and environment-level factors on crayfish survival and
overland dispersal probabilities using a multistate mark-recapture model in a state-space
212 formulation (Gimenez et al. 2012, Appendix 7). Briefly, the model allowed us to estimate the effects
of individual sex, body size (cephalothorax length, mm), body condition, geographic-range origin
214 (Range-core, Range-edge, Outgroup), density (9 or 19 crayfish mesocosm⁻¹), mean air temperature
(°C) and duration of time interval (days) between two capture occasions on individual (i) survival
216 probability in the mesocosm (Φ_A), (ii) probability to disperse from the mesocosm to an exit trap
($\Psi_{A \rightarrow B}$), and on (iii) “post-dispersal settlement probability” ($\Psi_{B \rightarrow A}$), i.e., on the probability
218 not to disperse after having dispersed at the previous recapture event. Non-symmetric patterns of
dispersal and post-dispersal settlement would be suggestive of a cost of dispersal in crayfish.

220

We fitted the model using Markov chain Monte Carlo (MCMC). Posterior parameter distributions
222 were largely insensitive to prior specification (Appendices 8-11). We tested for the significance of
posterior parameters through computing MCMC p-values as twice the proportion of the posterior
224 which sign was opposite to the sign of the posterior mode. We further evaluated the identifiability of
model parameters by computing the overlap between prior and posterior distributions. A high prior-
226 posterior overlap (PPO) indicates that information from the data is weak, such that the posterior
parameter distribution is strongly dependent on the prior distribution. A PPO greater than 35 % is
228 considered as indicative of a weak parameter identifiability (Gimenez et al. 2009).

230

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232 **Fig. 2. Predicted effects of body size-by-density interaction, body condition and temperature on**
 233 **crayfish survival probability Φ_A , dispersal probability $\Psi_{A \rightarrow B}$ and post-dispersal settlement**
 234 **probability $\Psi_{B \rightarrow A}$.** Lines represent median prediction, ribbons indicate 95 % credibility intervals. Green,
 235 solid lines: Range-core crayfish. Red, dashed lines: Range-edge crayfish. Blue, dotted lines: Outgroup
 236 crayfish. LD and HD stand for low and high crayfish density, respectively. All probabilities are for a
 237 transition interval of 2.4 ± 0.8 days (mean \pm SD). Predictions were made from parameters estimates of Eq.
 238 A7-3 by setting the Sex factor to female crayfish, and predictions for the effects of Body condition and
 239 Temperature were further made by setting the Density factor to HD.

240

242

244

246

RESULTS

248

Survival

250 Prior-posterior overlaps (PPOs) for all parameters in the survival sub-model were below 35 %,
indicating no major identifiability problem (Appendix 8A). In particular, none of the posteriors
252 associated with significant effects were weakly identifiable.

254 Crayfish survival probability during a time interval ranged from 0.9 to 1 (Figs. 2A-D). These high
probabilities were due to the short duration of a time interval (2.4 days on average). Over the entire
256 duration of experiment (153 days), 51.5 % of crayfish survived.

258 Larger-bodied crayfish had increased survival probability under high (but not low) density
conditions, a trend mostly present in Range-core crayfish (Figs. 2B vs. 2A, Appendix 9).
260 Specifically, average survival probability during a 2.4-day time interval was $9.57 \cdot 10^{-1}$ in the smallest
crayfish (24.9 mm cephalothorax length) and $9.98 \cdot 10^{-1}$ in the largest crayfish (66.2 mm,
262 probabilities predicted for Range-core female crayfish under high density, all other quantitative
covariates fixed to their average value).

264

Higher crayfish density (Figs. 2A vs. 2A, Appendix 9) and higher individual body condition (Fig.
266 2C, Appendix 9) both decreased crayfish survival probability. Note that the negative effect of
density on crayfish survival was weaker and not significant when evaluated as a main effect in a
268 model that did not include any interaction term (Appendix 10).

270 Warmer temperatures had a positive effect on crayfish survival probability (Fig. 2D, Appendix 9).
When all other quantitative covariates were fixed to their average value, raising mean temperature

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272 from its minimum (9.3°C) to its maximum (26.9°C) increased mean survival probability during a
2.4-day time interval from $9.81 \cdot 10^{-1}$ to $9.95 \cdot 10^{-1}$ (predictions computed for an average-sized, Range-
274 core female at low density).

276 There was no significant effect of the geographic-range origin on crayfish survival probability, nor
there was any significant range-by-body size, range-by-density or range-by-body size-by-density
278 interaction (Appendix 9). Note that we also tested for range-by-temperature and range-by-
temperature-by-density interactions and did not find any significant interaction (results not shown).

280

Dispersal

282 The identifiability of dispersal parameters was generally satisfying, with PPOs below 35 % except
for the outgroup-by-density interaction and for the range edge-by-density interaction (Appendix
284 8B). The probability for an individual crayfish to disperse to an exit trap during a time interval
ranged from 0.0 to 0.3 (Figs. 2E-H), while post-dispersal settlement probability ranged from 0.3 to
286 1 (Figs. 2I-L). Hence, crayfish were mainly sedentary during our experiment.

288 Dispersal probability was almost 0 in crayfish smaller than 45 mm in cephalothorax length, but
increased up to 0.1-0.3 in the largest-bodied individuals, a significant body-size effect (Figs. 2E and
290 2F, Appendix 9). Specifically, mean dispersal probability increased from $3.07 \cdot 10^{-3}$ in a small-bodied
crayfish (25 mm cephalothorax length) to $2.86 \cdot 10^{-1}$ in a large-bodied crayfish (66 mm, predictions
292 computed for a Range-core female at low density, all other covariates were fixed to their average
value).

294

Increasing body condition, as well as warmer temperatures, also had significantly positive effects
296 on crayfish dispersal probability (Figs. 2G and 2H, Appendix 9). When all other quantitative

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300 covariates were fixed to their average value, raising mean temperature from its minimum (9.3°C) to
302 its maximum (26.9°C) increased mean dispersal probability during a 2.4-day time interval from
304 1.17 10⁻² to 9.46 10⁻² (predictions computed for an average-sized, Range-core female at low density)

306 Neither crayfish density nor geographic-range origin did influence crayfish dispersal probability,
308 either directly or in interaction with body size (Figs 2e and 2f, Appendix 9).

310 The identifiability of model parameters for post-dispersal settlement probability was generally low,
312 since 9 over 16 parameters had prior-posterior overlaps exceeding 35 % (Appendix 8C). However,
314 the specific response of post-dispersal settlement to major covariates (body size, body condition and
316 temperature, as displayed in Fig. 2) was identifiable and looked generally symmetric to the response
318 of dispersal probability (Figs. 2I-L vs. 2e-h, Appendices 9 and 8C), suggesting that dispersing at
320 time t did not alter dispersal probability at time $t+1$ with respect to covariates.

DISCUSSION

322 Our study shows that mark-recapture in mesocosms allows for a robust estimation of demographic
324 parameters, and is thus an approach that may usefully complement field monitoring programs to
326 inform the parametrization of process-explicit models of geographic ranges. Our results suggest that
328 survival and dispersal are under the control of both individual-state and environment variables in *P.*
330 *clarkii*. Below, we first discuss these results separately for each set of variables, and then we discuss
the benefits of our findings for range-dynamics modelling and applied issues in invasive crayfish.

322 **Individual-state variables**

As expected (Appendix 1), a larger body size increased crayfish survival probability, but this effect
324 was significant only under a high crayfish density and in Range-core crayfish. This result highlights
density-dependent selection for a larger body size in *P. clarkii*, as previously reported in other taxa
326 (collembolans, fish and lizards), and presumably resulting from a dominance of large-bodied
individuals in interference competition and cannibalism (Edeline and Loeuille 2021). Accordingly,
328 larger-bodied crayfish dominate in competition for shelters (Figler et al. 1999), and crayfish with
larger chela have a higher probability of winning agonistic encounters (Graham and Angilletta
330 2020).

332 In mesocosms, a larger body size further had a strong positive effect on crayfish dispersal
probability, a finding that is in line with a previous report of overland movements being
334 predominantly performed by sexually mature (i.e., adult) individuals in *P. clarkii* (Ramalho and
Anastácio 2015). In *Pacifastacus leniusculus*, another invasive crayfish, both overland movements
336 and in-stream dispersal jointly increase with increasing body size (Bubb et al. 2004; Moorhouse and
MacDonald 2011; Wutz and Geist 2013; Thomas et al. 2018), suggesting that a larger body size is
338 associated with an elevated dispersal syndrome in crayfish.

340 This strong and taxonomically-conserved positive effect of body size on crayfish movements is
probably a response to multiple convergent selective pressures linked with physiological and
342 ecological constraints. A larger body size decreases the mass-specific energetic cost of transport of
both walking or running animals (Peters 1983), and further confers a higher body volume-to-surface
344 ratio which increases resistance to desiccation (Claussen et al. 2000; Antoł et al. 2021).
Additionally, walking speed also increases with body size (Claussen et al. 2000), and larger-bodied
346 dispersers thus have increased probability to find a water body before desiccation. Finally, larger-

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348 bodied individuals dominate in interference competition for food and contests for shelters (see
above), and thus probably also enjoy reduced costs of settlement during the colonization of novel
habitats. Together, these mechanisms confer larger-bodied crayfish with an increased benefit-to-cost
350 ratio of dispersal.

352 In accordance with the general expectation that increased energy stores decrease the survival cost of
long-distance movements (Appendix 1), we found that body condition was positively linked to
354 dispersal probability in crayfish. However, in contrast with our predictions, we found that a higher
body condition was also associated with a lower survival probability in mesocosms. A higher
356 nutritional status is associated with increased moulting probability in shrimps (Sharawy et al. 2019;
Lemos and Weissman 2021), and moulting entails increased mortality in crayfish (Taugbøl and
358 Skurdal 1992). In particular, newly-moulted crayfish have a soft shell and are strongly exposed to
predation.

360
Also contrary to our expectations (Appendix 1), survival and dispersal were both sex-independent
362 in *P. clarkii*. In *P. leniusculus*, dispersal was reported to be sometimes sex-independent (Bubb et al.
2004; Galib et al. 2022), and sometimes male-biased (Wutz and Geist 2013), which might suggest
364 that the sex-dependency of dispersal is context-dependent and versatile in crayfish.

366 Our predictions were also refuted regarding the effects of spatial sorting on *P. clarkii* competitive
ability and dispersal propensity (Appendix 1). Range-core and Range-edge crayfish did not differ in
368 either survival or dispersal probabilities, nor they did in their response to crayfish density variation.
Such an absence of any effect of the geographic-range origin agrees with previous results showing
370 no divergence for the fluctuating asymmetry of morphological traits among Range-core and Range-
edge crayfish populations in the Brière (Bélouard et al. 2019).

372

No phenotypic divergence despite divergence at neutral-genetic and geographic markers may result from both genetic and selective processes. Without selection, divergence in quantitative traits should equal the divergence at neutral marker loci. However, this equality does not hold for complex traits such as dispersal syndromes (Saastamoinen et al. 2018), because allelic interactions within (dominance) or between (epistasis) loci reduce the divergence at quantitative traits compared to the neutral expectation (Goudet and Martin 2007). Additionally, density-dependent selection in edge habitats may have rapidly erased the effects of spatial sorting to make Range-edge crayfish similarly dispersive and competitive as their Range-core counterparts. Strong density-dependent selection is particularly likely to occur in the “boom” phase of large demographic increase that sometimes immediately follows a colonization event, due to colonists arriving in an empty ecological niche with lots of resources available. Which of these different mechanisms best explains phenotypic similarity among Range-core and Range-edge crayfish in the Brière requires further investigation.

386

388 **Environment variables**

As expected (Appendix 1), *P. clarkii* density in mesocosms had a marginally-significant negative effect on the survival of Range-core crayfish. However, this effect was weaker than expected since it was not significant when evaluated simultaneously across all crayfish origins or sex. This weak density-dependence probably reflects limited density variation (from 3.0 to 6.3 individuals m⁻²) in presence of an excess of shelters (30 shelters for a maximum of 19 crayfish) in mesocosms. Accordingly, an average relationship between survival probability and stocking density for different experiment durations, as reconstructed from literature data (Appendix 12), predicts largely overlapping survival probabilities at 3.0 vs. 6.3 individuals m⁻² and for an average time interval of

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153 days corresponding to the duration of our experiment (range of predicted survival rates: 0.61-
398 0.83 at 3.0 individuals m⁻² and 0.56-0.78 at 6.3 individuals m⁻²). Hence, we conclude that the density
variation we applied in our experiment, although located in the upper range of naturally-observed
400 densities, entailed relatively mild changes in competition and, hence, resulted in weak effects on
survival and no effect on dispersal.

402

Finally, temperature was the only environment variable that had consistent effects on both survival
404 and dispersal during our experiment: both probabilities increased with increasing temperature. In *P.*
clarkii, somatic growth rate, which is a putative surrogate for survival rate, is maximal in the 22-
406 30°C temperature range (Westhoff and Rosenberger 2016), while overland dispersal seems maximal
at temperatures ranging from 16 to 24°C (Ramalho and Anastácio 2015). These temperatures will
408 more often be met in the future, as hot days will get hotter and more frequent. Under the SSP1-2.6
(low GHG emissions) or SSP5-8.5 (business as usual) scenarios of IPCC, our results project by
410 2081-2100 into a 1.5 or 5.2 % increase in *P. clarkii* monthly survival probability, and in a 14 or 44
% decrease in the number of days needed for *P. clarkii* to reach an overland dispersal probability
412 equal to 1 (Appendix 13).

414 **Implications for the management of invasive crayfish**

Correlative species distribution models based on climate envelopes predict that *P. clarkii* will
416 expand its geographic range in a warming world (Liu et al. 2011; Capinha et al. 2013; Zhang et al.
2020). Our study demonstrates the power of individual mark-recapture in mesocosms to provide a
418 mechanistic, demography-based understanding of the underlying processes, that may serve as a
starting point to building process-explicit models of range dynamics for this species (Fig. 3).

420

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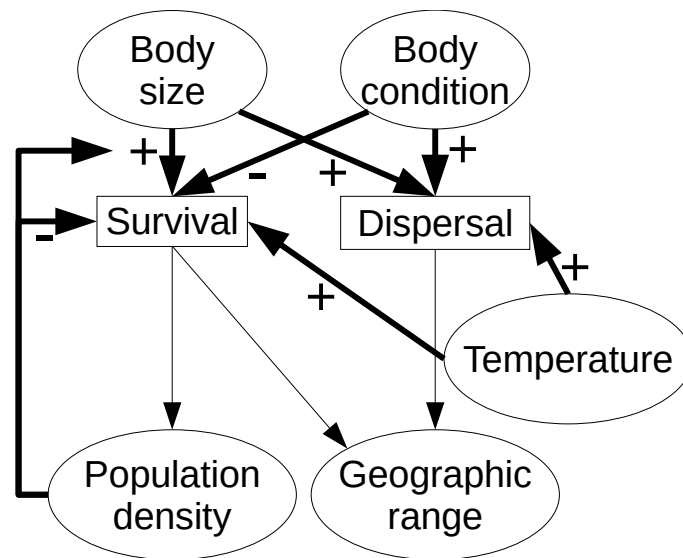


Fig. 3. Adaptation of the conceptual framework in Fig. 1 to *P. clarkii* range dynamics. Increased survival and dispersal are assumed to both increase the geographic range. Bold arrows indicate causality links that were investigated in the present study. The arrow pointing from population density to the positive effect of body size on survival indicates that this positive effect was present only under high crayfish density.

Future studies should extend the approach to couple mark-recapture in mesocosms with field-based count data from natural populations in integrated population models (Schaub and Kéry 2021). Ideally, future models should also account for multiple means of dispersal, because crayfish disperse not only actively, but also passively through human- or animal-mediated transport (Capinha et al. 2013; Anastácio et al. 2014; Acevedo-Limón et al. 2020). This new class of integrated, process-explicit models will provide more robust estimates of demographic rates under a wider range of ecological and climatic scenarios, potentially extending to interspecific interactions if possible (Dobler and Geist 2022; Geist et al. 2023), and, we feel, will represent high-class tools for the management of established invasive crayfish populations under global change.

Containment of crayfish range expansion could be reached by several management strategies. When prevention of dispersal is not possible, our results suggest that selective culling of large-bodied

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438 crayfish might represent a credible management alternative. Gherardi et al. (2011) wrote that
trapping was an inefficient management strategy for crayfish, because crayfish removal relaxes
440 competition and may stimulate rates of somatic growth and reproduction among survivors.
However, in size-structured animal populations, size-selective trapping of large-bodied, cannibal
442 individuals may instead result in increased densities of juveniles, and in increased competition, due
to relaxed cannibalism (Claessen et al. 2004). Additionally, over the long term, selective removal of
444 large-bodied individuals is expected to induce an evolutionary change towards smaller body sizes
and earlier maturation (Heino et al. 2015), which would not only cause crayfish to disperse less, but
446 would also potentially lower survival rates and decrease fecundity. If such harvest-induced
evolutionary changes are slowly reversible, then culling intensity could be relaxed after some years,
448 which would reduce management costs.

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