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Life-history phenology strongly influences population vulnerability to toxicants: a case study with the mudsnail Potamopyrgus antipodarum

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Abstract

One of the main objectives of ecological risk assessment is to evaluate the effects of toxicants on ecologically relevant biological systems such as populations or communities. However, the effects of toxicants are commonly measured on selected sub-individual or individual endpoints due to their specificity against chemical stressors. Introducing these effects into population models is a promising way to predict impacts on populations. Yet currently employed models are very simplistic and their environmental relevance needs to be improved to establish the ecological relevance of hazard assessment. This study with the gastropod *Potamopyrgus antipodarum* combines a field experimental approach with a modelling framework. It clarifies the role played by seasonal variability of life-history traits in the population's vulnerability to the alteration of individual performance, potentially caused by toxic stress. The study comprised three steps: *(i)* characterization of the seasonal variability of the life-history traits of a local population over 1 year with *in situ* experiments on caged snails, coupled with a demographic follow-up, *(ii)* development of a periodic matrix population model which visualizes the monthly variability of population dynamics, and *(iii)* simulation of the demographic consequences of an alteration of life-history traits (*i.e.*, fertility, juvenile and adult survival). The results revealed that demographic impacts strongly depend on the season when alterations of individual performance occur. Model analysis showed that this seasonal variability of population vulnerability is strongly related to the phenology of the population. We underline that improving the realism of population models is a major objective for ecological risk assessment, and that taking into account species phenology in modelling approaches should be a priority.

Keywords (limit 5 keywords):

Phenology, life-history, *in situ* caging, ecological risk assessment, population modelling

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1. Introduction

Biological effects of toxicants are most frequently assessed in terms of alteration of sub-individual or individual performance (*e.g.,* biomarkers) by means of bioassays or field monitoring. Nevertheless, for ecological risk assessment, these impacts on populations, communities and ecosystems are of primary concern [1-8]. Unfortunately, supplying an ecologically relevant assessment by measuring toxic impacts directly on these complex integrated systems is challenging, particularly because distinguishing toxicant impacts from the effects of other environmental factors or anthropogenic stressors can be difficult. One alternative methodology links the effects observed on individual-level endpoints measured in toxicity tests (in the laboratory or during *in situ* experiments) to impacts on populations [9-11]. However, a major problem is the complex relationship between the effects measured at the individual level and outcomes occurring at the population level [12-14]. Introducing the effects of toxicants on demographic parameters (*i.e.*, related to life-history traits) into population models is one way to investigate this relation and to anticipate impacts at the population level [10, 15-16]. In fact, such mechanistic ecological models provide a quantitative way of integrating multiple individual-level endpoints, including survival, growth and reproduction, in projections of population-level consequences such as changes in population abundance or growth rate [17].

A large number of studies have demonstrated the value of using demographic models in an ecotoxicological context (reviewed in Galic et al. 2010). However, despite attempts to use more elaborate modelling approaches that integrate environmental complexity [18-23], the ecological relevance of the population models involved is generally low. In fact, in the great majority of studies, demographic models are based on laboratory assays with species that are not representative of the ecosystems of interest (e.g. tropical fishes or daphnids for studies on lotic and temperate systems). These models are popular and useful tools for

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isolating the effects of a toxicant on the population growth rate [7], but they could fail to understand what occurs in the field on local populations [24]. In fact, the determinants of demographic sensitivity of populations are subject to strong variability (*e.g.,* interspecies and interpopulation variability of life cycle). This variability cannot be taken into account with overly simple demographic models [6, 18, 25-26]. Notably, these models do not capture the seasonal variability of population dynamics, even though several studies have underlined a seasonal variability of population vulnerability. A study on the crustacean amphipod *Corophium volutator* [27] showed that the same level of mortality impacts the population differently depending on the season at which mortality occurs. Similarly, in field studies on the amphipod *Leptocheirus plumulosus*, McGee and Spencer [28-29] highlighted a strong monthly variability of the sensitivity of the population growth rate to the different life-history traits. Thus, we need to develop population models which can integrate the seasonal variability of population dynamics to propose a more ecologically relevant assessment of the impact of toxicants on freshwater populations.

In the present study, we illustrate the strength of a field experimental approach (*in situ* caging and demographic follow-up) with a modelling framework (periodic matrix model) to decipher the role of seasonality in the vulnerability of populations to toxicants. The model organism is the widespread mudsnail *Potamopyrgus antipodarum* (Gray). We selected this species due to its sensitivity to a large range of chemicals for ecotoxicological tests in the laboratory [30-34] or in the field [35-36]. Notably, *P. antipodarum* is proposed to the Organization for Economic Cooperation and Development (OECD) as a relevant test species to assess the impacts of endocrine disruptors on freshwater molluscs [37]. In the first step we characterized the seasonal variability of the life-history traits of a population of *P. antipodarum* over 1 year, with experiments on caged snails and a demographic follow-up of the population. In the second step, we developed periodic matrix population models which

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allowed us to describe the demographic changes of this population and to picture the monthly variability of its dynamics. In the third step, we simulated the demographic consequences for this population of an alteration of life-history traits (*e.g.,* reduction in fertility, juvenile or adult survival), in order to illustrate the importance of the seasonal variability of population dynamics for ecological risk assessment of chemicals.

2. Material and methods

2.1. Biological data

P. antipodarum is a deposit-feeding gastropod which in Europe reproduces mainly by parthenogenesis of female populations [38]. We conducted a battery of experiments on a population on the Upper Rhône, in the Villebois reservoir (05°27′55.3 E; 45°46′30.7 N, Rhône, France). This site was selected because it contains durable populations of freshwater molluscs monitored for more than one decade [39] and because it was accessible all year round (the water-level fluctuations do not exceed 0.50 m during the year). Temperature was continuously recorded every 2 h using the Tinytag Aquatic 2® temperature logger.

To characterize the different life-history traits and the population dynamics of *P. antipodarum*, we used an *in situ* approach. Firstly, we conducted experiments with snails caged on the study site at different seasons for life-history trait quantification: fertility (*i.e.*, number of neonates produced per reproductive female per day) and growth (*i.e.*, increase of shell length (SL) of juveniles and adults). Secondly, we carried out a demographic follow-up based on a monthly population census to estimate the time-course in population characteristics: densities, SL structure and fecundity (*i.e.*, number of embryos in the brood pouch).

2.1.1. *In situ* caging experiments

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In situ caging experiments were conducted from October 2009 to November 2010 during 10 campaigns lasting 21 days. We measured contrasted environmental conditions between the different campaigns. In this way, mean water temperature, which is known to strongly influence *P. antipodarum* life-history traits [40-43], varied from 4.6 to 22.7 °C. We focused our experiments on measuring fertility and growth. During the year, we were able to study fertility during eight campaigns (insufficient numbers of adults during winter) and growth during seven campaigns (insufficient numbers of juveniles during three campaigns in summer and autumn). Snails were sampled and calibrated (*i.e.*, size selection) directly at the study site. Initial SL was measured each time with a sample of 30 snails. SL was measured between the apex and the distal extremity of the aperture under the binocular microscope, which corresponded to the maximal height of the shell. Initial SL varied from 2.28 (± 0.16) mm to 2.85 (± 0.34) mm for juveniles and from 4.38 (± 0.22) to 4.68 (± 0.34) for adults between the different campaigns.

Four replicates of 30 juveniles and four replicates of 50 adults were used for growth and fertility measurement. Snails were placed in polypropylene cylindrical containers (diameter, 10 cm; length, 12 cm) with pieces of net (mesh size, 100 µm) on perforations to allow water flow. Because *P. antipodarum* lives in the upper layers of the sediments [41], a 2-cm layer of sediment removed from the study site and sieved at 315 µm (*i.e.*, keeping out autochthonous snails) was added to the containers. Two containers with sediment but without snails were deployed for each campaign as control of the absence of autochthonous snails. Finally, containers were placed in a perforated protective case in polyvinylchloride (PVC) with fixing elements for the containers. The containers were placed on the bottom of the river, in close proximity to the site used for the demographic follow-up (see below) at a depth about 1.2 m. After the 21-day exposure period, juveniles and adults were fixed with 20% alcohol and measured in the laboratory in order to estimate the snails' daily growth rates. Neonates

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laid during the period were also fixed with 20% alcohol and counted under a binocular microscope. Then we estimated the fertility rates b (*i.e.*, number of neonates produced by snail per day) as follows:

$$b_i = \frac{n_i}{((l_{i,0} + l_{i,t})/2) \times t} \quad (1)$$

where b_i corresponds to the fertility rate of the replicate i; n_i to the number of neonates laid in the replicate i; t is the duration in days of the experiment (here t = 21 days for all assays); $l_{i,0}$ and $l_{i,t}$ are the number of living snails at the start and at the end of the experiment (here $l_{i,0}$ = 50 for all assays).

2.1.2. Demographic follow-up

A monthly demographic follow-up was performed from October 2009 to November 2010. For each month, snails were sampled in four stations along a 300-m transect at a depth from 0.50 to 1.5 m using a rectangular hand-net (25 × 18 cm); the total area sampled was 1 m². Samples were fixed on-site in 20% alcohol. Then we measured the SL of the snails present in a sub-sample corresponding to 9 out of 25 of the total sample in order to estimate monthly population densities and SL distributions. Considering 5% percentiles in SL distribution of juveniles, reproductive individuals and total individuals, we also determined, for each month, SL at birth, SL at maturity and maximum SL to provide guidance in the choice of the model's size classes. To estimate SL at maturity, we dissected 30 individuals covering a large range of sizes, and we counted the number of embryos in the brood pouch (*i.e.*, fecundity) according to the methodology described in Duft et al. [44]. This measurement also allowed us to calculate a relationship between SL and fecundity and to estimate the percentage of reproductive individuals for each adult class defined in the model.

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161 2.2. Modelling framework and demographic analysis

162

163 2.2.1. Definition of the population model

164 We used a periodic Lefkovitch matrix population model with five size classes [15, 45]
165 to capture the dynamics of the *P. antipodarum* population. Periodic matrix models [46-47] are
166 often used to study cyclical temporal variation (*e.g.*, seasonal or interannual) operated within
167 a single projection interval. The models take the form of periodic matrix products. We used
168 size class models, in contrast to most ecotoxicological studies in which age class (Leslie
169 models) or stage class models are employed [16]. We explain this choice with the following
170 arguments: *(i)* a valid method does not exist to determine the age of snails in field populations
171 for this species, *(ii)* we observed a strong correlation between SL and the life-history traits of
172 *P. antipodarum* (growth rate, maturity, fecundity) and *(iii)* in highly variable environments
173 (*e.g.*, contrasted seasonality), the life-history of individuals in such short-living species
174 strongly depends on their date of birth, which makes age a very weak predictor of biological
175 features. This model thus distinguishes two classes of juveniles (J1 and J2) and three classes
176 of adults (A1, A2 and A3). It integrates the heterogeneity of vital rates (survival, growth and
177 fecundity) between size classes throughout the year.

178 Let $n_i(k)$ be the number of individuals of size class i (i = 1 for J1, i = 2 for J2, i = 3 for
179 A1, i = 4 for A2 and i = 5 for A3) at the beginning of month k. The five $n_i(k)$ can be gathered
180 in a population vector $\mathbf{n}(k)$. Then we can define 12 monthly matrices $\mathbf{M}_k$ which link up the
181 population vectors $\mathbf{n}(k)$ between months k and k+1 as follows:

182 $$\mathbf{n}(k+1) = \mathbf{M}_k \, \mathbf{n}(k) \qquad (2)$$

183 with:

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$$\mathbf{M}_k = \begin{bmatrix} s_1(k)\left(1-\sum_{j>1} g_{1,j}(k)\right) & 0 & f_3(k)\sqrt{s_1(k)}\sqrt{s_3(k)} & f_4(k)\sqrt{s_1(k)}\sqrt{s_4(k)} & f_3(k)\sqrt{s_1(k)}\sqrt{s_5(k)} \\ s_1(k)\,g_{1,2}(k) & s_2(k)\left(1-\sum_{j>2} g_{2,j}(k)\right) & 0 & 0 & 0 \\ s_1(k)\,g_{1,3}(k) & s_2(k)\,g_{2,3}(k) & s_3(k)\left(1-\sum_{j>3} g_{3,j}(k)\right) & 0 & 0 \\ s_1(k)\,g_{1,4}(k) & s_2(k)\,g_{2,4}(k) & s_3(k)\,g_{3,4}(k) & s_4(k)\left(1-g_{4,5}(k)\right) & 0 \\ s_1(k)\,g_{1,5}(k) & s_2(k)\,g_{2,5}(k) & s_3(k)\,g_{3,5}(k) & s_4(k)\,g_{4,5}(k) & s_5(k) \end{bmatrix} \quad (3)$$

where $s_i(k)$ is the survival rate of the size class *i* during month *k*, $g_{i,j}(k)$ the transition rate between the size classes *i* and *j* during month *k*, and $f_i(k)$ the reproductive rate of the size class *i* during month *k*. The product of the 12 monthly matrices $\mathbf{M}_k$ leads to an annual periodic matrix $\mathbf{L}$, which links the population vector from year *t* to year *t*+1 as follows:

$$\mathbf{n}(t+1) = \left(\prod_{k=1}^{12} \mathbf{M}_k\right)\mathbf{n}(t) = \mathbf{L}\,\mathbf{n}(t) \quad (4)$$

To assess the seasonal variability of the demographic sensitivity of the population, we also defined four seasonal periodic matrices: $\mathbf{L_A}$ for autumn, $\mathbf{L_W}$ for winter, $\mathbf{L_{SP}}$ for spring and $\mathbf{L_{SU}}$ for summer. These matrices correspond to the product of the three monthly matrices $\mathbf{M}_k$ corresponding to each season (*i.e.*, September, October and November in autumn; December, January and February in winter; March, April and May in spring; and June, July and August in summer).

2.2.2. Parameter estimation

We estimated the reproductive rates $f_i(k)$ for the three size classes of adults (*i* = 3, 4 and 5) as follows:

$$f_i(k) = b_i(k)\,\rho_i(k)\,\Delta t(k) \quad (5)$$

where $b_i(k)$ corresponds to fertility (*i.e.*, number of neonates produced by reproductive female per day) for class *i* during month *k*, $\rho_i(k)$ to the percentage of females in reproduction in class *i* during month *k*, and $\Delta t(k)$ to the number of days of month *k*. $\rho_i(k)$ was estimated with data

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204 from the demographic follow-up (see above), and $b_i(k)$ was predicted with the mean monthly
205 water temperature, according to the relationship between mean temperature and fertility
206 established from outcomes of caging experiments. Because only one size class of adults was
207 used for *in situ* caging, we controlled the size effect between classes in the calculation of $b_i(k)$
208 using the relationship between SL and fecundity (*i.e.*, number of embryos in the brood
209 pouch), which is established from the demographic follow-up. Similarly, we calculated the
210 transition rates $g_{i,j}(k)$ using the relationship between growth and temperature estimated in *in*
211 *situ* caging experiments. Using the mean water temperature recorded during month *k*, we
212 predicted the growth of individuals with size at the limits of each class *i* between months *k*
213 and *k+1*, and then we estimated for each size class the proportion of individuals which stayed
214 in size class *i*, or which attained the larger size classes.
215 It is not possible to estimate the survival rates directly from field experiments. In fact,
216 mark and recapture methodologies, which are currently used for larger organisms (*e.g.*, fish,
217 mammals) are not easy to set up for *P. antipodarum* due to the difficulty marking the snails
218 durably. Alternatively, the survival rates observed with the caged snails were not ecologically
219 relevant (*e.g.*, lack of predation, competition). Therefore, to estimate the survival rates of
220 individuals for a month *k*, we compared the densities observed during the demographic
221 follow-up in month *k* to the theoretical densities predicted by the observed densities of month
222 *k−1* and the growth and reproductive rates of the individuals estimated for month *k−1*.
223
224 2.2.3. Model outcomes, elasticity analyses and simulations
225 The Lefkovitch matrix $\mathbf{L}$ is a primitive matrix and can be processed analytically as a
226 Leslie matrix. It presents a first dominant eigenvalue λ, corresponding to the asymptotic
227 population growth rate [15 , 48]. The right eigenvector w associated with this first eigenvalue
228 gives the asymptotic stable size structure. According to the first matrix used in the matricial

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product of the 12 monthly matrices $\mathbf{M}_k$, we can obtain the different SL structures at the end of each month of the year. The demographic elasticities were analyzed by simulation with the application of 10% reduction in each life-history trait successively (*i.e.*, survival of each class, fertility and growth) in order to estimate the subsequent relative reduction in the asymptotic population growth rate λ. To examine the between-season variability of population vulnerability, we also simulated the demographic consequences of different levels of alteration of life-history traits at different dates in the year. To accomplish this, reductions from 0% to 100% on fertility, juvenile survival and adult survival were applied to the three months corresponding to each season.

2.3. Statistical analyses

Statistical procedures and population models were all implemented with the R software [49]. Before using parametric analysis (ANOVA procedure), normality and homoscedasticity were checked using the Shapiro-Wilk test and the Bartlett test, respectively. To quantify growth of *P. antipodarum* snails in *in situ* caging, we fitted, independently for each caging experiment, a logistic model on SL data using the *nls* function, simultaneously considering the two categories of caged snails (juveniles and adults) as follows:

$$L(t) = \frac{Lmax}{1 + \left(\frac{Lmax}{Linit} - 1 \right) e^{(-r\,t)}} \qquad (6)$$

where $L(t)$ corresponds to the SL of snails at time t, $Lmax$ to the maximal SL of snails observed in the population, $Linit$ to the SL of the two categories of caged snails at the beginning of the experiment, r to the daily growth coefficient of the logistic model, and t to the time. We fixed $Lmax$ at 5.5 mm (maximum value observed during the demographic follow-up). No replicate effect was considered when fitting the logistic models (one per campaign), since no significant difference in SL of juveniles and adults were detected

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253 between replicates at the end of the test for each one of the seven campaigns. Concerning the
254 seasonal variability of fertility and daily growth, we fitted Gaussian relationships between
255 these life-history traits and water temperature using the *nls* function. For the demographic
256 follow-up, the influences of SL and month on fecundity were tested using linear modelling
257 including the interaction terms (ANOVA procedure).
258
259 **3. Results**
260
261 3.1. Seasonal variability of life-history traits
262 By means of *in situ* caging experiments, we recorded strong seasonal variability in the
263 production of *P. antipodarum* neonates, which varied from 0 to 0.8 neonates per female per
264 day. This seasonal variability in fertility was highly correlated with water temperature (Figure
265 3A). Thus, we fitted a Gaussian curve to describe fertility b_i (production of neonates per day
266 per reproductive female) as a function of mean water temperature θ (in °C) as follows:

267 $$b_i(\theta) = 6.92 \times e^{\left(\frac{17.91 - \theta}{3.85}\right)^2} \quad (7)$$

268 Fertility is optimal at a temperature of 17.91 °C. Concerning growth, here again we detected
269 strong seasonal variability of individual SL gains, in relation with the mean water temperature
270 (Figure 3B). We used nonlinear regression to fit a Gaussian relationship between growth
271 coefficient r and mean water temperature θ (in °C) as follows:

272 $$r(\theta) = 0.006 + 0.21 \times e^{\left(\frac{18.61 - \theta}{3.72}\right)^2} \quad (8)$$

273 In comparison with fertility, we added a constant parameter in order to take into account a
274 minimal daily growth rate different from 0. In fact, contrary to fertility, which was null during

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the caging with the lower temperature (Figure 3A), we observed that individuals grow even at low temperatures (Figure 3B). Growth is optimal at 18.61 °C.

Concerning the monthly demographic follow-up, the evolution of the population's SL structure is presented in Figure 1. The highest densities were observed in autumn (*e.g.*, more than 10,000 individuals per square metre in October and November) and the lowest in spring. Juveniles (*i.e.*, SL < 3.5 mm, size classes J1 and J2 of the model) are present throughout the year and account for the major part of the population, while adult densities (*i.e.*, SL > 3.5 mm, size classes A1, A2 and A3) show highly variable frequencies during the year. In fact, in winter and spring, the population comprises mainly juveniles, while in summer and autumn adults appear in the population. We estimated a SL at birth of 0.5 (0.1) mm, a SL at maturity of 3.5 (0.2) mm and a maximum SL of 5.2 (0.3) mm. According to these very weak standard deviations, we did not consider monthly differences in the SL at birth, at maturity and the maximum SL for the parameterisation of the population model. Concerning the percentage of individuals in reproduction (*i.e.*, females bearing embryos) $\rho_i(k)$, for all dates of the year, more than 90% of the individuals with a SL greater than 4.2 mm were reproductive. Individuals between 3.5 and 4.2 mm presented a seasonal variability: 50% of individuals were reproductive between November and May and 80% between June and October. We observe a strong positive relationship between SL and fecundity (Figure 2), with no seasonal effect (ANOVA test: interaction terms, $p > 0.1$; seasonal effect, $p > 0.81$; SL effect, $p < 10^{-15}$). In this way, we note that females of the model's A1 size class have a mean fecundity of 12.2 embryos; size class A2 females a mean fecundity of 24.3 embryos and size class A3 females a mean fecundity of 37.6 embryos.

3.2. Population model analysis

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299 Regarding parameter estimation, we report a strong between-class and between-month
300 variability of the reproductive rates $f_i(k)$. Between November and March, reproductive rates
301 were very low for all classes due to low water temperatures, while all size classes reproduced
302 between April and October. Depending on the size class and the month, reproductive rates
303 varied from 0.01 to 35.05 neonates per month per individual. Regarding the transition rates
304 $g_{i,j}(k)$, the majority of individuals stayed in their initial size class from month to month
305 during winter and spring, in contrast to summer and autumn, where growth was faster and a
306 great majority of individuals changed one or two size classes over 2 months. Adult survival
307 showed high monthly variability with very low survival rates between January and May and
308 higher survival rates in summer and autumn. Juvenile survival (for size classes J1 and J2) was
309 generally higher than adult survival, particularly in winter and spring. For some months, we
310 calculated survival rates higher than 1, in particular when densities of individuals were low
311 (uncertainty increased with small size samples). For the parameterization of the matrix model,
312 we tested two possibilities: *(i)* we applied the survival rates keeping the values higher than 1
313 (apparent survivals), or alternatively *(ii)* we fixed a ceiling level of 1 for maximum survival
314 rates. Despite differences in the absolute value of the asymptotic population growth rate λ, the
315 stable size distribution and elasticity pattern were very similar in both cases. For the following
316 results on model analysis, we chose to use survival rates capped at 1, but conclusions on the
317 demographic behaviour of the population remain unchanged with apparent survival rates.
318 In a first time, we calculated the asymptotic population growth rate λ with the annual
319 periodic matrix $\mathbf{L}$. We found a value of λ = 1.17. We also computed the stable size
320 distribution for the different seasons that we compared to the population structure observed
321 during the demographic follow-up (Figure 4). We noted good coherence between the model
322 and the field data. Thus, it appears that our mechanistic modelling framework can identify the
323 dynamics of the *P. antipodarum* population throughout the year. In a second time, we

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characterized the seasonal variability of the demographic fitness of the population by calculating the asymptotic population growth rate of the four periodic seasonal matrices ($\mathbf{L_A}$, $\mathbf{L_W}$, $\mathbf{L_{SP}}$ and $\mathbf{L_{SU}}$). We found 3-month λ values equal to 1.02 in autumn, 0.17 in winter, 0.16 in spring and 2.31 in summer. For comparison to the annual matrix $\mathbf{L}$, the standardization of λ to a 3-month time step supplies a value of 1.04. Thus, we underline a strong seasonal variability of snail population dynamics, with a potential growth of the population mainly in summer and autumn.

The elasticity analysis on the annual matrix $\mathbf{L}$ showed that the asymptotic population growth rate λ was more sensitive to relative changes in juvenile survival (S1 and S2) than to changes in the other life-history traits (Figure 5). The life-history trait corresponding to the second highest elasticity was adult survival (cumulative elasticities of S3, S4 and S5) followed by fertility. Concerning growth (Figure 5), we observe that the population growth rate was not sensitive to relative changes in this life-history trait. On the contrary, we note that a reduction of the daily growth rates strikingly increases the asymptotic population growth rate λ. We also performed elasticity analysis on the four seasonal matrices ($\mathbf{L_A}$, $\mathbf{L_W}$, $\mathbf{L_{SP}}$ and $\mathbf{L_{SU}}$) (Figure 6). These analyses reveal two contrasted patterns. On one hand, in spring and winter, the population growth rate was very sensitive to juvenile survival alteration but remained unchanged by reduction in adult survival or reproduction rates. Concerning growth, we observe, as for the annual model, that the reduction of this life-history trait increased the asymptotic population growth rate. On the other hand, in summer and autumn, the population growth rate was sensitive to changes in juvenile survival but also to changes in adult survival, fertility and growth.

Strong variability of population impacts (percentage of reduction of the population growth rate λ) can be seen when alterations of life-history traits at different seasons were integrated into the model (Figure 7). In fact, except for juvenile survival for which we noted

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that the population growth rate was highly affected for all seasons, concerning reproduction and adult survival, between-season differences were substantial. Indeed, the population was very sensitive to impacts on fertility in summer and particularly in autumn, but showed very low sensitivity in spring and winter, even for substantial fertility inhibitions. Furthermore, the population was very sensitive to impacts on adult survival in summer, even for very small inhibitions, but quite insensitive in the other seasons even for considerable inhibitions.

4. Discussion

4.1. Seasonal variability of life-history traits of *P. antipodarum*

We observed fluctuating densities during the year. The high-density pattern at the end of summer and autumn and the low-density pattern in winter and spring agree with previous data obtained during demographic follow-up conducted for *P. antipodarum* [41, 50]. Furthermore, these density variations during the year are consistent with the observations of a long-term follow-up of mollusc populations conducted in this study site (data not published for *P. antipodarum*). However, Schreiber et al. [51] observed the highest densities in spring and summer. This contrast with the present study can be explained by the delaying effect of temperature rise due to a large snow-melt upstream of the Rhône watershed. For Richards and Shin [52], these fluctuating densities are driven by density-dependent processes. Nevertheless, in populations with small temperature fluctuations, Quinn et al. [53] observed that densities are very stable during the year, and it is widely accepted that *P. antipodarum* population densities are generally strongly correlated with water temperature [50], consistent with our observations. The population in our case was primarily composed of juveniles, particularly in winter and spring, which agrees with previous data [51, 54]. In this way, the persistence of the population in winter is ensured by the survival of a reserve of juveniles. In summer and

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autumn, the population is composed of two cohorts, one with small juveniles and one with large adults. The size at birth, size at maturity and maximum size values are consistent with previous reports for this species [30, 51, 54-57]. Similar to Schreiber et al. [51], who observed 65% reproductive females in their population, we observed that the majority of females carried embryos. During dissections, we never observed males, as in other studies which stated that the vast majority of European populations of *P. antipodarum* are made up of parthenogenetic females [38] with a few exceptional males [58]. This explains why we did not integrate the sex ratio into our model.

The methodology of *in situ* caging implemented here throughout the year provides a useful tool to estimate life-history traits in the field (*e.g.*, realistic exposure conditions, good reproducibility of the assays) [59-60]. Until now, only a few studies have conducted *in situ* experiments with *P. antipodarum* [35-36, 61]. Here, we chose this methodology rather than a laboratory approach in order to obtain environmentally relevant data for the calibration of the population model. In fact, several factors are difficult to control in laboratory conditions, in particular the diet of *P. antipodarum*. Here, we report a strong seasonal variability in neonate production and growth rates. Several studies have shown that *P. antipodarum* life-history traits are strongly correlated with water temperature [40, 42]. The quality of the fits observed in Figure 3 confirms this pattern. The maximum fertility value (0.80 juveniles per day recorded during caging at a mean temperature of 17.5 °C) is higher than the values reported in other studies for this temperature range [30-31]. Nevertheless, all the studies which measured fertility directly (*i.e.*, counting production of neonates) were conducted during laboratory experiments, which probably do not offer optimal conditions for the reproduction of this species. To our knowledge, our study reports for the first time a direct *in situ* measurement of fertility. In fact, in *in situ* assays, fertility is usually estimated indirectly from fecundity (*i.e.*, counting of the number of embryos in the brood pouch) [35-36, 61]. This measure can

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399 provide useful information but it remains difficult to predict the realized reproduction of
400 individuals without information on laying dynamics. We estimated an optimal temperature of
401 17.9 °C for fertility. This value is consistent with previous laboratory studies [40, 42]. Schmitt
402 et al. [36] did not observe a relationship between temperature and fertility during different *in*
403 *situ* experiments, but the temperature range was very narrow compared to our experiments.
404 Concerning growth, we estimated an optimal value of 18.7 °C close to the fertility value.
405 Thus, water temperature between 17 and 19 °C appeared to provide optimal conditions for the
406 development of *P. antipodarum*.
407
408 4.2. Demographic insights from the population model analysis
409 The adequacy of the stable size distribution computed for each season with the
410 population size structure observed during the demographic follow-up (Figure 4) illustrates
411 that our modelling framework is able to reliably describe the dynamics of this *P. antipodarum*
412 population taking into account its particular phenology. The analysis of seasonal matrices
413 ($\mathbf{L_A}$, $\mathbf{L_W}$, $\mathbf{L_{SP}}$ and $\mathbf{L_{SU}}$), which simulate population dynamics under hypothetical scenarios of
414 eternal autumn, winter, spring or summer, allows us to underline substantial seasonal
415 variability in the demographic fitness of the population (quantified by the asymptotic growth
416 rate λ). On one hand, winter and spring are seasons with a potential population decrease, and
417 on the other hand, summer and autumn seasons have a high potential for a population
418 increase. This is explained by reproductive rates that are nearly zero in spring and winter
419 along with very low survival rates, in particular for adults.
420 With the annual model, we observed that the population dynamics is particularly
421 sensitive to changes in juvenile survival (Figure 5). This is consistent with the conclusions of
422 several demographic studies on *P. antipodarum* [30, 34, 62]. Pedersen et al. [30], when
423 studying the effects of the polycyclic musk HHCB on individual and population-level

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424 endpoints, observed that the asymptotic population growth rate of *P. antipodarum* is
425 approximately four times more sensitive to juvenile survival alteration than to adult survival,
426 and ten times more sensitive to juvenile survival alteration than to fertility inhibition.
427 Surprisingly, we noted that a reduction of the daily growth rate increased the asymptotic
428 population growth rate λ. This unexpected demographic outcome can be explained by the very
429 low survival rates of the last classes of adults for several months in spring and winter. Thus,
430 when the daily growth rate is decreased, individuals stay for more months in the first class of
431 adults with higher survival rates, which increases their cumulative reproductive value for the
432 population. This advantage for organisms with a low growth rate is similar to observations on
433 fish populations under fishing pressure, in which higher mortality rates lead to the selection of
434 individuals with lower growth ability [63-64]. With the seasonal models, we show an
435 important seasonal variability of the pattern of elasticities (Figure 6). In fact, in the same
436 manner as for the population dynamics, we can identify two contrasted periods. In spring and
437 winter, the population is mostly sensitive to the reduction in juvenile survival, while in
438 summer and autumn, the demographic sensitivity to juvenile survival reduction is
439 considerably reduced, and the population demography becomes more sensitive to the
440 alteration of other traits. This strong seasonal variability of population sensitivity is explained
441 by the phenology of the population: in winter and spring, maintenance of the population is
442 ensured by a stock of juveniles (no reproduction, high adult mortality), whereas in summer
443 and autumn, juveniles grow up, mature as adults, and therefore reproduce. Seasonal
444 variability of population sensitivity is also observed in the amphipod *Leptocheirus plumulosus*
445 using a field-based periodic matrix population model [28-29]. Thus, analyzing the elasticity of
446 periodic matrix models can provide valuable insights into the relative importance of the
447 demographic rates at different periods of year.
448

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449 4.3. Seasonal variability and field-based population models in ecological risk assessment

450 Despite the substantial seasonal variability of population demographic sensitivity, to
451 our knowledge, only a few ecotoxicological studies have addressed the temporal variability of
452 effects on population dynamics [27-29]. We roughly simulated reductions in fertility, juvenile
453 survival and adult survival at different seasons. Population impacts strongly depend on the
454 season at which toxic effects on individual performance occur (Figure 7). For instance, a time
455 window of high population vulnerability to reproductive alteration is focused in summer and
456 autumn, in contrast to winter and spring, for juvenile mortality. Thus, the development of
457 population models that integrate seasonality is a relevant way to increase our ability to project
458 toxic effects on individual performance into population demographic impacts. As an
459 illustration, when studying HHCB effects on *P. antipodarum*, Pedersen et al. [30] observed
460 significant effects on offspring production up to 42% reduction) but stated that such
461 inhibitions will not give rise to significant impacts on population dynamics. In spring and
462 winter, our simulations agree with this conclusion. However, in summer and particularly in
463 autumn, we anticipate considerable population consequences of such levels of fertility
464 inhibition. In fact, in autumn, we observed that a 40% reduction in fertility means a 30%
465 decrease of the asymptotic population growth rate (Figure 7). Similar to the great majority of
466 studies addressing population extrapolation, the life cycle is roughly parameterized from
467 laboratory data. In fact, life-history traits are often estimated in the controls of the
468 experiments and are not representative of life-history of local populations. Thus, with this
469 laboratory approach, models do not provide valuable information about potential
470 demographic consequences of toxicant impacts in field populations [30]. Laboratory
471 conditions are too favourable (*e.g.*, no predation or competition, water temperature is
472 constant) or in contrast, they fail to provide optimal conditions or complexity for all abiotic
473 and biotic parameters (*e.g.*, oxygenation, water flow, temperature, food, crowding effect). One

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474 way currently used to address such concerns about the ecological relevance of population
475 extrapolation consists in exploring a range of values of life-history traits and showing that
476 changes in the population growth rate are low. By this means, authors aim to assess the
477 robustness of their conclusions against divergence in life histories between laboratory and
478 wild populations. For example, Pedersen et al. [30] validated the robustness of their
479 population model by testing three scenarios: decrease in juvenile survival, decrease in
480 juvenile and adult survival, and decrease in juvenile survival, adult survival and fertility. But
481 the range of tested fluctuations is not at all "field-realistic" regarding our field observations:
482 (i) only 50% for fertility, whereas we showed in the *P. antipodarum* population that fertility is
483 very low during a great part of the year with greater reduction than in this study; and (ii) only
484 a 20% reduction in adult survival and a 90% reduction in juvenile survival, while we observed
485 that juvenile mortality is generally lower than adult mortality in the field. Thus, it appears that
486 a field-based approach can be of great interest to guarantee the relevance of hazard
487 assessment at the population level, and to provide realistic scenarios for exploring its
488 soundness with respect to between-population variability of life-histories.

489 Improving the ecological realism of population models is a major concern for
490 ecological risk assessment. Incorporating species phenologies is feasible with modelling
491 approaches and should be one priority when seeking to put the "eco into ecotoxicology" [2].

492

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494

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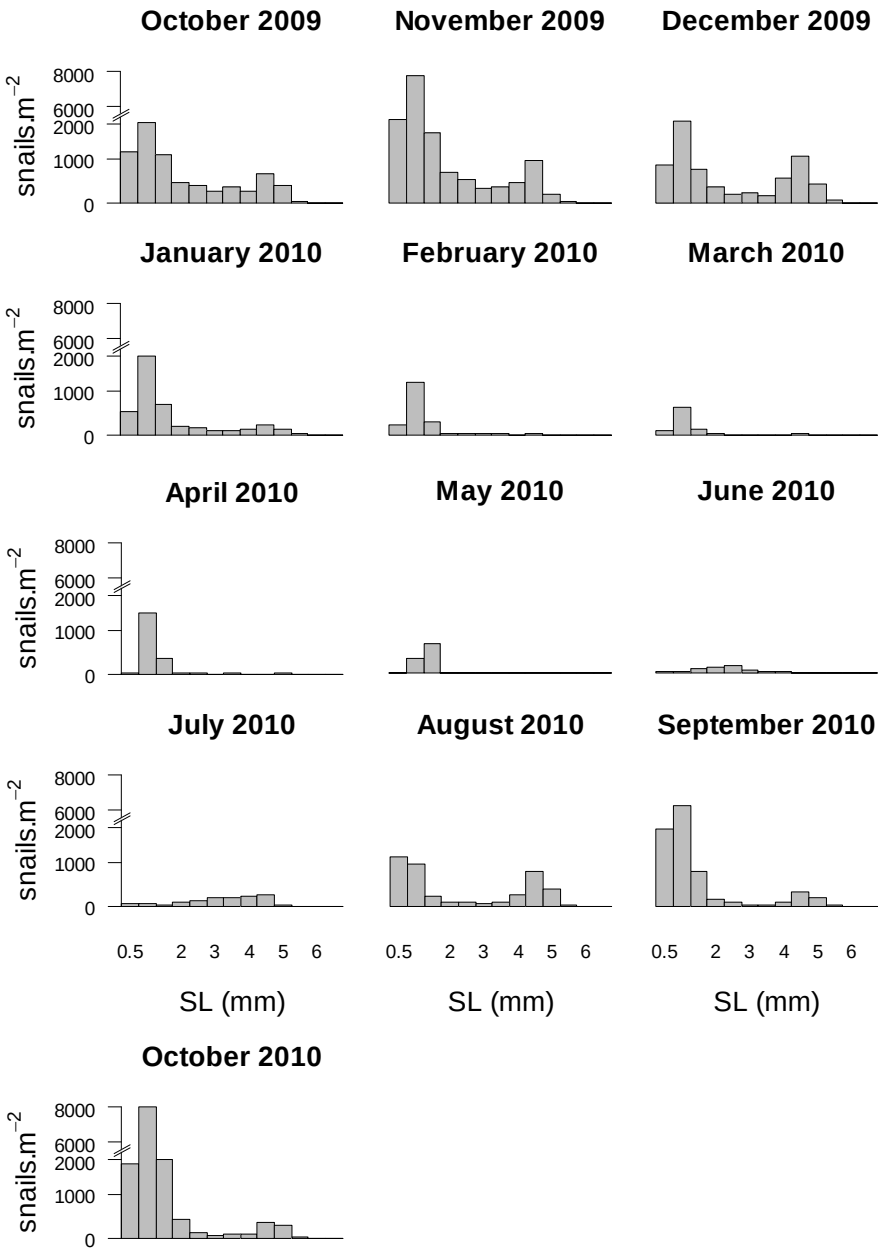

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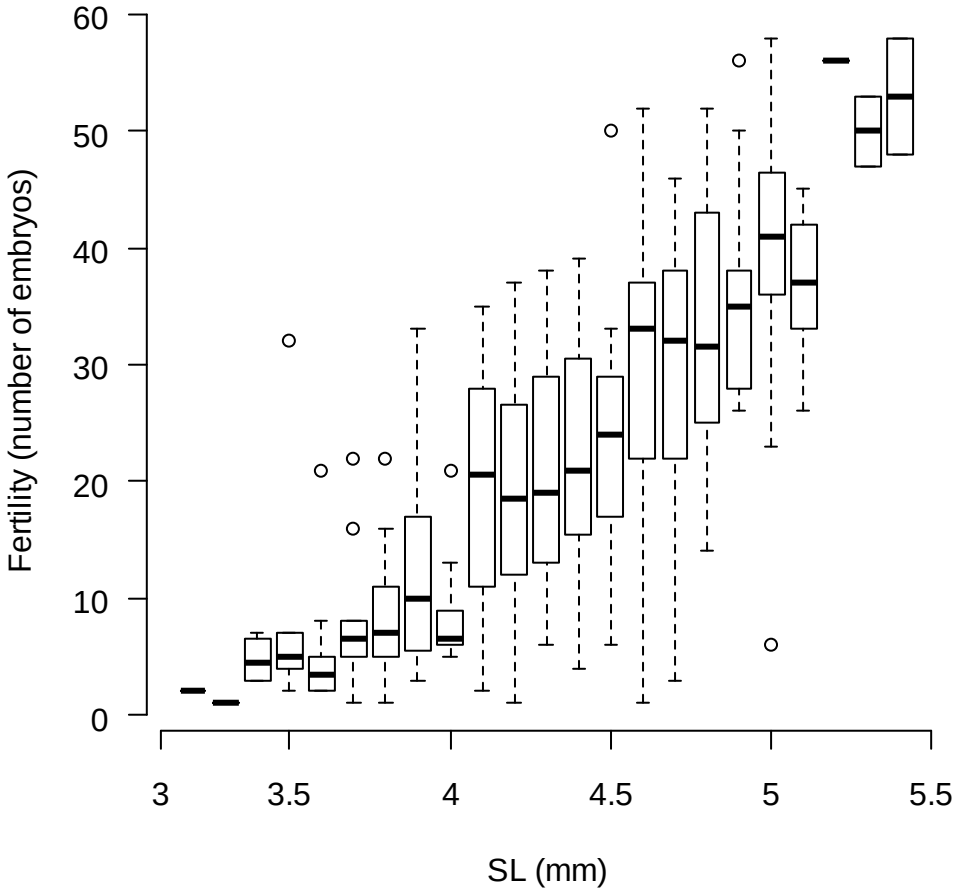

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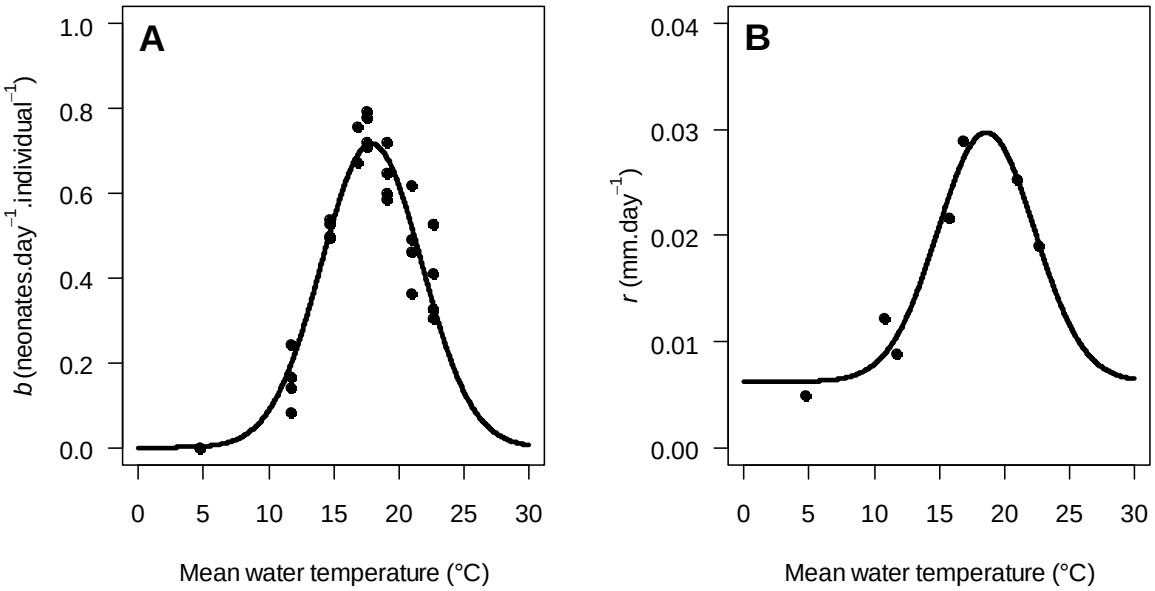

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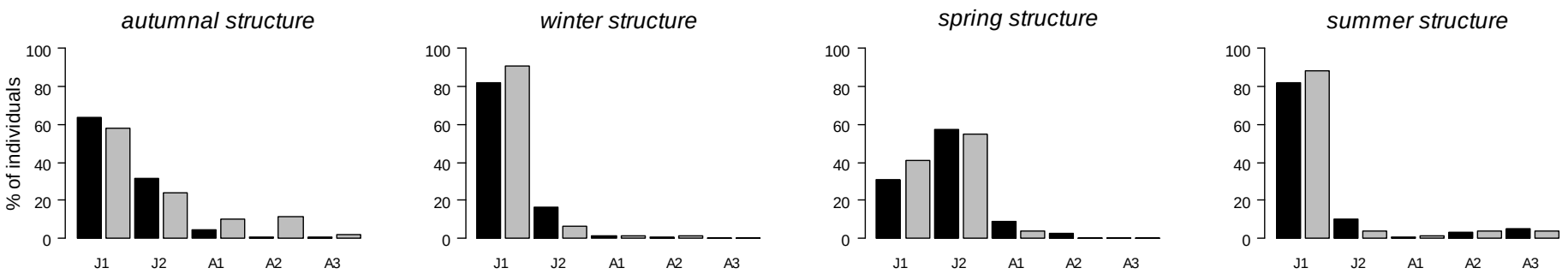

Figure 4.

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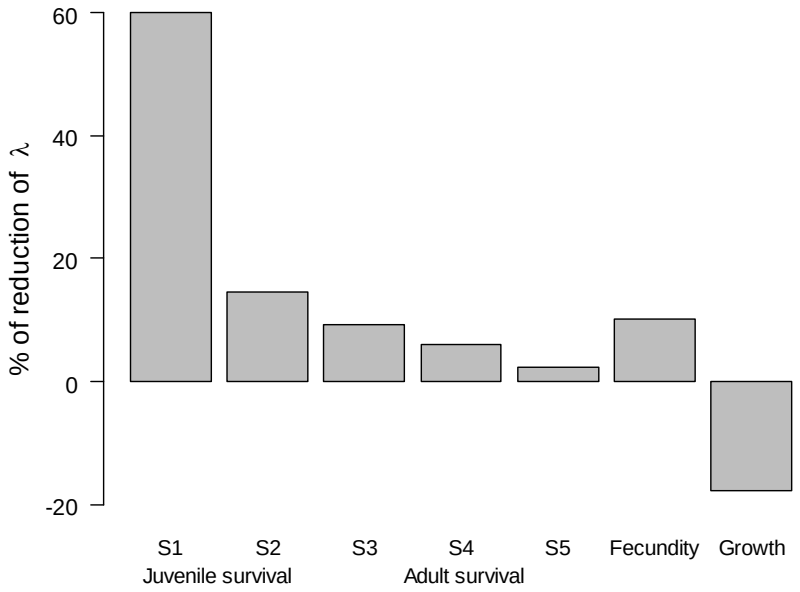

Figure 5.

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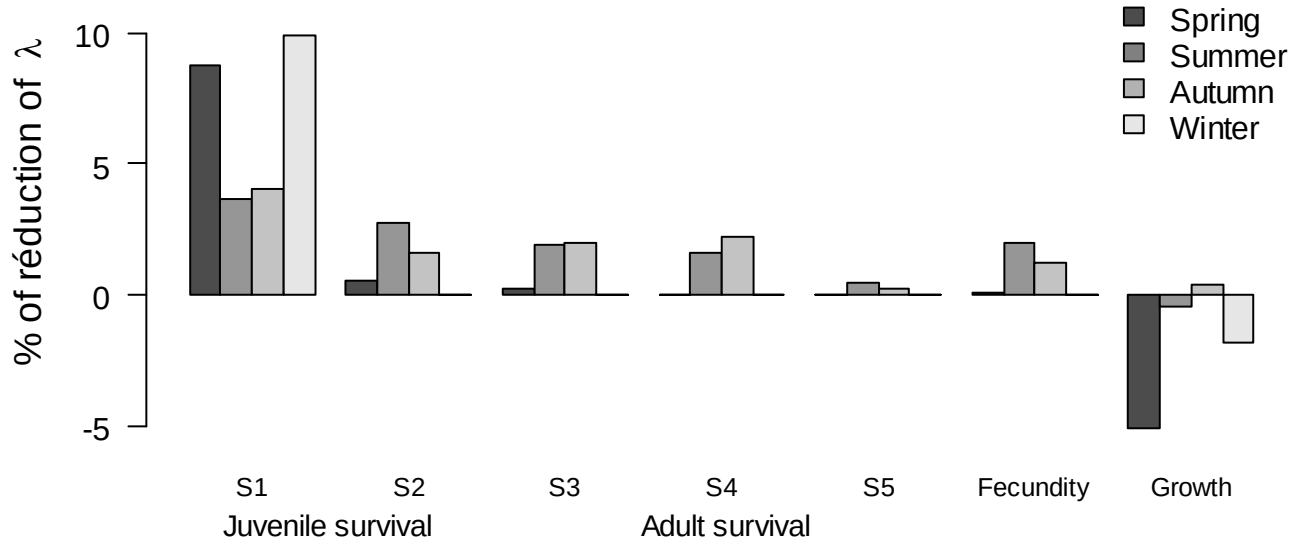

Figure 6.

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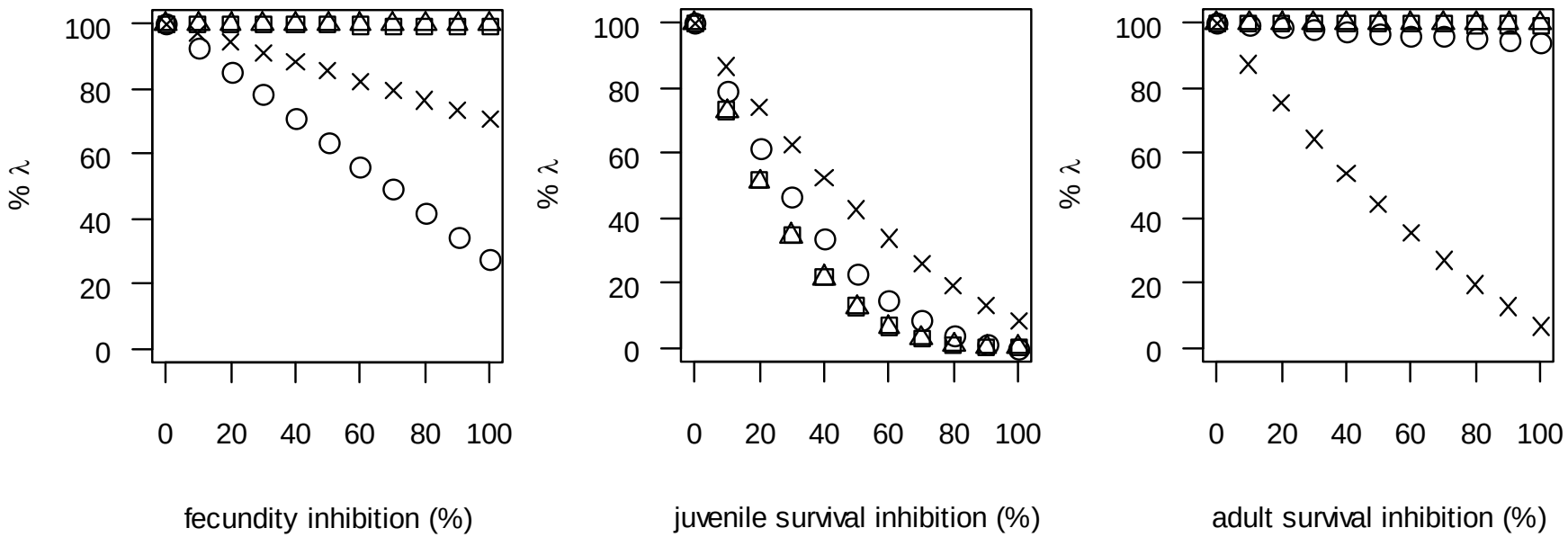

Figure 7.