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Probing of mortality rate by staying alive: The growth-reproduction trade-off in a spatially heterogeneous environment

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Abstract

1. In many annual plants, mollusks, crustaceans and ectothermic vertebrates, growth accompanies reproduction. The growth curves of these organisms often exhibit a complex shape, with episodic cessations or accelerations of growth occurring long after maturation. The mixed allocation to growth and reproduction has poorly understood adaptive consequences, and the life-history theory does not explain if complex growth in short-lived organisms can be adaptive.

2. We model the trade-off between growth and reproduction in a short-lived organism evolving in a metapopulation. Individuals occupy risky or safe sites throughout their lives, but are uncertain regarding the risk of death. Modelled organisms are allowed to grow and produce offspring at specified time points (moults), although we also consider scenarios that approximate continuous growth and reproduction.

3. Certain combinations of risky to safe sites select for strategies with mixed allocation to growth and reproduction that bet-hedge offspring production in safe and risky sites. Our model shows that spatially heterogeneous environments select for mixed allocation only if safe sites do not become the prevailing source of recruits, for example, when risky sites are frequent. In certain conditions, growth curves are multi-phasic, with allocation to growth that stops, remains constant or accelerates during adult life. The resulting complex growth curves are more likely to evolve in short-lived organisms that moult several times per adult life.

4. Our work shows that spatial heterogeneity can select for growth that accompanies reproduction and provides insights into the adaptive significance of complex growth curves. Short-lived crustaceans are particularly predisposed to exhibit complex growth patterns as an adaptive response to spatially heterogeneous environments. Our results suggest that standard statistical growth models assuming adult growth rate to only decelerate over life are not well suited to approximate growth curves of short-lived crustaceans.

KEYWORDS

body size, cladocerans, complex growth curve, indeterminate growth, mixed allocation, trade-off

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1 | INTRODUCTION

The evolution of growth tactics is key to understanding the diversity of life histories mediated by the body size of organisms (Gotthard, 2001; Kozlowski, 1996). The adaptive consequences of growth by mature plants, fish, amphibians, reptiles, crustaceans, mollusks and other invertebrates are far from being understood (Heino & Kaitala, 1999). Growth can be seen as an investment in future reproduction because the net amount of acquired resources scales positively with body size (Kozlowski, 2006; Peters, 1983). In an aseasonal environment, maximal fitness is reached by determinate growers that instantaneously switch the allocation of resources from growth to reproduction (Perrin & Sibly, 1993; Ziółko & Kozłowski, 1983). Seasonal environments select for indeterminate growth in perennials that switch multiple times per life between growth and reproduction but without periods of mixed allocation (Ejsmond, Czarnołęski, Kapustka, & Kozłowski, 2010; Ejsmond, Varpe, Czarnoleski, & Kozłowski, 2015; Kozłowski, 1999). Whereas multiple growth phases occur throughout the lives of perennial fish, crustaceans and mollusks (Dillon, 2000; Folkvord et al., 2014; Holmgren, 2003; Wada, Oba, Nakata, & Ito, 2008), annual plants, cladocerans and many short-lived indeterminate growers allocate resources to growth and reproduction simultaneously (Lynch, 1980; Sheehy, Mitchell, & Ferrer, 2004). This mixed allocation to growth and reproduction is an important determinant of the body size evolution in short-lived indeterminate growers and contributes to the considerable diversity of their growth curves (Lynch, 1980; Murugan & Job, 1982; Murugan & Sivaramakrishnan, 1973; Sheehy et al., 2004).

Several studies in life-history theory predict the growth of reproducing organisms, but these studies are often founded on simplifying assumptions that may alter the generality of the reported findings. For example, growth after maturity and mixed allocation were suggested to evolve in annual plants and cladocerans as an adaptive response to mortality rate or season lengths that fluctuate on a per generation basis (Gurney & Middleton, 1996; King & Roughgarden, 1982; Taylor & Gabriel, 1993; Wong & Ackerly, 2005). A fluctuating environment selects against an instantaneous switching from growth to reproduction because the production of a low number of offspring in some years drastically reduces the overall geometric mean fitness (Lewontin & Cohen, 1969). Mixed allocation to growth and reproduction bet-hedges against fluctuating environment and is predicted to evolve by the life-history work that assumes immediate offspring recruitment (Gurney & Middleton, 1996; King & Roughgarden, 1982; Taylor & Gabriel, 1993). This assumption contrasts with the fact that annual plants and cladocerans produce diapausing propagules that may recruit many years after the time they were released (Chambers & Macmahon, 1994; Hairston, 1996). The postponed recruitment bet-hedges against fluctuating environments as well, and current life-history theory does not explain the adaptive value of growth accompanying reproduction in organisms with diapausing offspring (see discussion in Wong & Ackerly, 2005). In plants, the mixed allocation to growth and reproduction is likely a consequence of the plant-herbivore arms race. The synthesis of non-degradable defensive chemicals that decrease the rate of vegetative parts loss due to herbivory selects for growth that accompanies reproduction (Janczur, 2009). Whereas this explanation seems plausible for plants, it cannot be applied to the majority of indeterminately growing animals. The proportional (linear) relationship between fecundity or mortality risk with reproductive allocation promotes a 'bang-bang' switch between growth and reproduction. However, the mixed allocation can be adaptive when birth rates, death rates or both scale nonlinearly with reproductive allocation (for details see. Johansson, Brannstrom, Metz, & Dieckmann, 2018; Leon, 1976; Sibly, Calow, & Nichols, 1985; Taylor, Gourley, Lawrence, & Kaplan, 1974). This general hypothesis, deriving growth tactics from a link between reproductive allocation, fecundity and mortality rate, awaits empirical verification; it is unclear to what extent taxa that share similar growth patterns are also similar with respect to the way vital rates scale with reproductive allocation. In contrast to our work, the aforementioned life-history literature, as well as taxa-specific studies reviewed in the discussion below, unrealistically assumes that growth tactics evolve in spatially homogenous environments.

Many short-lived indeterminate growers evolve in metapopulations of dynamic spatiotemporal structure. Plant-pathogen interactions can produce a dynamic mosaic of populations that undergo phases of local extinction and the colonization of annual species (Burdon & Thrall, 1999). Populations of cladocerans are connected by the migration of resting eggs, with occupied sites differing considerably with respect to the level of mortality risk, as these small organisms are capable of colonizing large water bodies but also temporary fishless ponds (Ebert, 2005). Similar structure of metapopulations, with patches differing in mortality risk, shapes the life-history evolution of other indeterminately growing crustaceans, such as short-lived amphipods (Munguia, Mackie, & Levitan, 2007; Wellborn, 1994; Wellborn & Broughton, 2008). The spatial variability in the mortality risk translates into demographic prospects that are not neutral to the evolution of body size. In fishless ponds, large daphnia species out-compete small ones (Ebert, 2005), with similar shifts to bigger body size reported in freshwater amphipods living in the absence of predators (Wellborn, 1994; Wellborn & Broughton, 2008). These size-shifts are driven by the fact that the lifetime expected offspring production is greater for those maturing late and with larger body size but only if conditions are safe (Kozlowski, 2006). Spatial variability in mortality risk imposes a dilemma on the adopted growth strategy as well as on the age and size at maturity of dispersing individuals. Our life-history model investigates the growth strategy of a short-lived organism that evolves in a spatially structured metapopulation.

In many adult fish, reptiles, cladocerans and plants, and also some mammals, the growth rate can periodically drop to zero, remain constant, or accelerate at certain periods of life (Bogin, 1999; Folkvord et al., 2014; Laver et al., 2012; Lynch, 1980; Murugan & Sivaramakrishnan, 1973; Rideout, Rose, & Burton, 2005; Sheehy et al., 2004; Xu et al., 2016). Complex shapes of growth curves are routinely associated with adverse conditions or sex reallocation

in hermaphroditic species (e.g. Higgins, Diogo, & Isidro, 2015). An alternative explanation links complex growth patterns with adaptive consequences of multiple shifts in the allocation of resources to growth and reproduction (Kozlowski, 2006). Complex shapes of growth curves in perennials often arise as a result of intensive growth occurring in years of skipped reproduction (Folkvord et al., 2014; Jørgensen, Ernande, Fiksen, & Dieckmann, 2006; Rideout et al., 2005). However, skipped reproduction has limited utility for explaining the origin of complex growth patterns in short-lived organisms. Annual plants and short-lived crustaceans, even when raised in a controlled environment or laboratory conditions, display multiphasic growth curves with growth that stops, remains constant, or accelerates at certain periods of adult life (Lynch, 1980; Murugan & Job, 1982; Murugan & Sivaramakrishnan, 1973; Sheehy et al., 2004). The phases of accelerating growth by adults, which are documented in studies on the individual growth trajectories of cladocerans, are sometimes associated with decreased egg production (Lynch, 1980; Murugan & Sivaramakrishnan, 1973). Whereas it is optimal to accelerate growth in the juvenile stage to compensate for adverse conditions experienced in young ages (Dmitriew, 2011), the adaptive consequences of periodical accelerations of growth by adults are unknown. Our work fills this gap by presenting how spatially heterogeneous environments can select for complex growth strategies in short-lived organisms.

Here, we model the evolution of growth strategies in a metapopulation that is spatially structured with respect to mortality risk. Because a reliable estimate of the risk of death by an individual may be elusive in natural environments, the only available information for organisms in the model is the fact of staying alive. To account for the fact that some indeterminate growers, for instance, cladocerans, enlarge their body sizes only when changing exoskeletons, our model considers a gradient of life histories differing with respect to the time interval between subsequent moults. However, we also included scenarios that approximate continuous growth. Our simulations show that heterogeneous environments with respect to mortality risk can select for growth accompanying reproduction and complex growth curves.

2 | MATERIALS AND METHODS

2.1 | The model

The presented model investigates the growth-reproduction trade-off in a short-lived organism (e.g. an invertebrate or annual plant) in which maturation does not preclude further growth. In our individual-based simulations, growth strategies evolve in a spatially heterogeneous environment with respect to mortality risk that cannot be sensed by an individual. A female starts her life as a randomly dispersed propagule in one of the two types of sites, namely, safe or risky, and remains there for the rest of her life. The environment is characterized by the proportion of risky sites S_R, with the frequency of safe sites given by $1-S_R$. We also consider homogenous environments with $S_R = 0$ and $S_R = 1$. Both

types of environments are characterized by a site-specific background mortality rate per generation, m_R for risky and m_S for safe environments. The species' generations are divided into n discrete time intervals, termed time episodes throughout the article (see below for details). All modelled life histories have the same time duration for the generation but the number of time episodes per generation may differ. The survival probability of a time episode, given by $p_R = e^{-\frac{m_R}{n}}$ for risky and $p_S = e^{-\frac{m_S}{n}}$ for safe type of habitat, is constant for an individual throughout its life. However, individual females that bear the same allocation strategy can live in different kinds of sites. The model assumes that in neither of the two types of habitats are organisms able to perceive cues about the mortality risk and death rate are independent on density. Whereas we present results for an environment with two different kinds of habitats, the diversity of growth strategies described in the results evolves also in a more complex setup with several types of habitats (Supporting Information Appendix S1).

Every generation is divided into n discrete time episodes in order to model the taxon-specific differences in the physiology of continuous vs. discrete growth; many arthropods, for example, cladocerans, can only grow while moulting and there are several moults per adult life. In other groups, as for instance in plants or mollusks, growth is continuous. In the model, the rate of allocation of resources is constant during a time episode $i = \{1, 2, ..., n\}$. An important feature of our model is that resources allocated to growth in a time episode i are mobilized and contribute to the body size increment at the beginning of the following time episode $i + 1$. Similarly, eggs produced over the episode i are released at the end of that time episode. The number of considered time episodes n per generation varies from 10, representing life histories of organisms that grow through several subsequent moults per life as cladocerans or many amphipods, to 80, which approximates physiology of taxa with continuous growth. The predictions of the model did not change when we assumed the number of episodes $n > 80$, although modelling of these scenarios was constrained by long computational times. As a base scenario, we assume 20 time episodes per generation.

The body size determines the net amount of resources P acquired per time episode i according to

$$P_i = \frac{k}{n} w_i^b \tag{1}$$

where w_i is the body size during the time episode i, k/n scales the net resource acquisition rate (described in more detail below) and b is the allometric exponent equal to 0.75. The allometric scaling of the net resource acquisition rate with body size to the power ca. 3/4 is well supported by empirical evidence (Glazier, 2005; Peters, 1983; Sibly & Brown, 2009). To maintain comparability of results from scenarios with different n, we scale the net resource acquisition rate P by assuming $k = 20$ in the examples presented below. The qualitative predictions of our work are robust with respect to the assumed parameter k, if the model is tested in a broad range of mortality rates. Similar properties of the parameter k to those found with our sensitivity analysis

were reported in other studies on evolution of body size (cf. Kozlowski, 2006; Kozłowski & Gawełczyk, 2002).

A female starts her life as one of 100,000 propagules randomly drawn from the pool of all eggs produced by individuals in the population with the birth rates being density independent. Initial body size w_0 equals 1 at time $i = 0$. Individuals in the metapopulation are characterized by allocation strategy α, given by the vector of numbers ranging from 0 to 1, with for example, α_2 matching an allocation decision into growth or $1\text{-}\alpha_2$ into reproduction over the second episode out of n episodes per generation. Body size increments are determined by the proportion of assimilated resources allocated to growth, with the body size in the next time episode given by.

$$w_{i+1} = w_i + \alpha_i P\left(w_i\right) \tag{2}$$

Note that, the rate of acquiring resources (Equation 1) increases with body size and growth should be seen as an investment in future reproductive potential. The production of eggs, strictly the allocation of resources to reproduction, by a female throughout her life is given by

$$V = \sum_{i=1}^{n} \left(1 - \alpha_i\right) P(w_{i-1}) v_i \tag{3}$$

where v is a binary vector that implements the death process removing females from the population. The vector v takes the value 0 for time episodes from i to n if randomly generated number $j_i \in \langle 0,1 \rangle$ is greater than the survival probability of one-time episode p_S for females inhabiting a safe site or p_R for those living in a risky site. In our model, generations do not overlap and all individuals die before the next generation starts. The used theoretical framework of individual-based simulations allowed us to model the evolution of growth strategies without the need of formulation of any fitness measure. However, the greatest chance for offspring recruitment had females with a strategy that enables production of the highest number of eggs.

The individual-based simulations allow us to model population of constant size with included stochastic effects occurring at recruitment of juveniles to the next generation. Produced eggs are released and diapause until the beginning of the next generation when 100,000 randomly recruited newborn individuals are placed in safe and risky places. The probabilities of getting into safe or risky site are equal to the proportion of risky (S_R) and safe sites ($1\text{-}S_R$) in the environment. We assume no egg mortality which leads to the same results as the random mortality of eggs. Allocation strategy, given by the vector α, is inherited from the mother and can change due to point mutations occurring with the probability 0.01 and the constant mutation step equal to 0.01, independently for every α_i. The mutation probability P and mutation step were set in order to maintain a variation of strategies in a population but also to keep feasible computation times. Simulations were initiated with vector $\alpha_i = 0.5$ for all time episodes i, but the conclusions of our work do not change when the initial vector α was set to other values. The evolution was simulated over 100,000 generations and longer simulation times did not affect the predictions of our work (see Figure S2 in Appendix S1). All calculations were performed with MATLAB 8.6 R2015b (MathWorks, Inc., Natick). The code for the algorithm used in this study is publicly available (see Data Availability Statement).

3 | RESULTS

The final evolutionary outcome of simulations run in homogenous environments is a resource allocation strategy that consists of a well-defined growth phase early in life and reproduction thereafter (Figure 1a). The duration of the growth period depends on the mortality risk, with larger body size attained in environments characterized by a low risk of death (Figure 1b). Allocation decisions with $\alpha_i < 0.9$ and $\alpha_i > 0.1$ were indistinguishable from pure growth ($\alpha_i = 1$) and pure reproduction ($\alpha_i = 0$) due to the persisting variability in α maintained by the stochastic character of our simulations (Figure 1a). Note that, although switching from growth to reproduction can be classified as a 'bang-bang' switch, one-time episode may be dedicated to mixed allocation if the optimal age/size of switching is placed within the time episode and not at its end (Figure 1a). To avoid the possibility of mixed allocation resulting from the stochastic character of our simulations, we defined that mixed allocation in our model as a strategy for which allocation decisions α_i fall between 0.1 and 0.9 for more than 15% of the time episodes per generation, that is, more than three per 20 episodes assumed in the base scenario.

A mixture of two types of sites, namely, risky and safe, with probabilities of an episode survival p_R and p_S, can select for mixed allocation. The mixed allocation occurs even though at each of these two types of sites a 'bang-bang' switching results in the highest expected offspring production (Figure 2a,b). Such simultaneous allocation to growth and reproduction is optimal in heterogeneous environments in which the proportion of risky sites S_R is high (Figure 2c). When the proportion of risky sites is low, females that are adapted to safe sites, that is, determinate growers that mature late and at a large size (cf. Figure 1), produce the prevailing proportion of recruits. In turn, the strategies adapted to safe sites over-compete strategies with mixed allocation that bet-hedge offspring production in safe and risky environments. The strength of selection for mixed allocation depends in a similar manner on the difference between survival prospects at safe and risky sites (Figure 2c and Figure S4 in Appendix S1). If the survival chance of one time episode is very high at safe sites in comparison to risky ones, natural selection promotes females that abruptly switch to reproduction late in life and after reaching a large body size (Figure 1). In turn, safe sites become the dominant source of recruits. However, when risky and safe sites are similar with respect to mortality risk, natural selection operates similarly as in homogenous environments where mixed allocation is selected against (Figure 2c). In other words, the mixed allocation to growth and reproduction is selected for when the degree of spatial heterogeneity is intermediate between homogenous and strongly structured environments at which safe sites become the dominant source of recruits (Figure 2c).
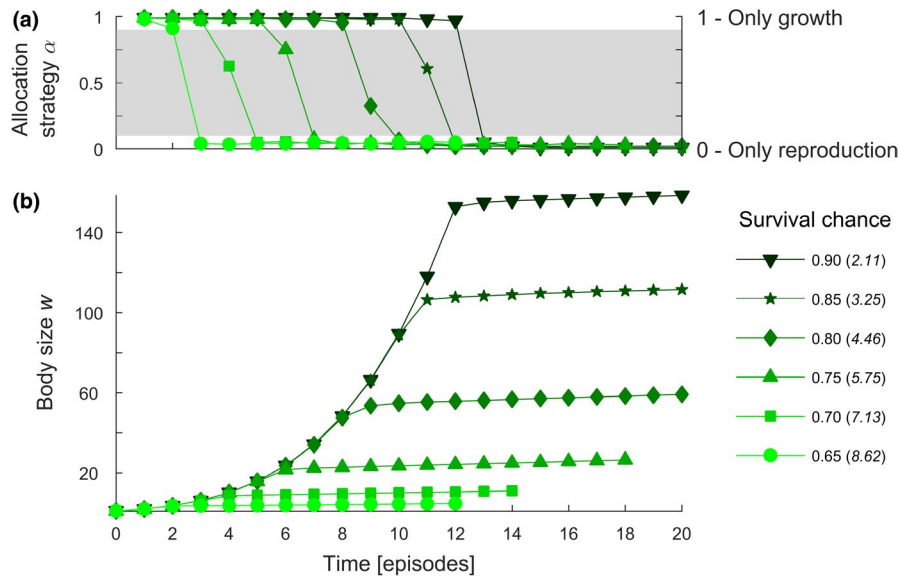
FIGURE 1 Allocation to growth and reproduction in homogenous environments. (a) In a homogeneous environment, modelled organisms switch the allocation of resources from growth to reproduction in less than three episodes of mixed allocation out of 20-time episodes per generation. Maturation occurs later when the survival probability increases. (b) Optimal size attained by the model animal increases in an exponential fashion along with increasing survival probability. (a, b) The legend provides information about the survival probability of one-time episode $p_R = p_S$ and the mortality rate per generation $m_R = m_S$ (italics). Allocation strategies and growth curves are presented for time episodes to which organisms survive with a probability >0.005. The presented allocation strategies are median values calculated across 20 simulation replicates

In heterogeneous environments that select for mixed allocation, the degree to which females accompany reproduction with growth depends on the difference between optimal size at safe and risky sites (Figure 3a,c vs. b,d and Figure S4 in Appendix S1). Under long periods of mixed allocation, the growth curves become complex with allocation to growth that remains constant or periodically accelerates during adult life (Figure 3b and the corresponding concave upward growth curves in Figure 3d). A female that has survived initial time episodes faces the dilemma of whether to keep growing or allocate to reproduction, and the only available information about risk is the fact that she is still alive. Females that exhibit complex growth are first pessimistic about their prospects and mature early. By living longer they become optimistic about local conditions, thus allocation to growth accelerates in the middle of their life span (Figure 3b,d). Females accelerate their growth only when the time episodes per generation are infrequent and long (Figure 4a,b vs. c,d), which obliges them to bet on their fate and set their allocation strategy for a relatively longer part of their maximal life span. Numerous episodes per generation, a proxy of continuous reproduction, allow females to make the allocation decisions frequently in life; the mixed allocation remains optimal but allocation to growth tends to only decrease over the adult life (Figure 4e,f).

Growth strategies with simultaneous allocation to growth and reproduction, including those with allocation to growth accelerating in the middle of life span, can evolve also in more complex environments that consist of several different types of sites (Figure S1 in Appendix S1).

4 | DISCUSSION

An organism unable to perceive reliable information about mortality risk must bet on its fate when deciding when to mature. In a heterogeneous environment, with respect to mortality risk, mixed allocation to growth and reproduction allows an organism to bet-hedge against maturing at a suboptimal time. In the presented model, growth accompanying reproduction evolves when 70% or more sites in the environment are risky (see Figure 2c), because safe sites select for large females capable of producing numerous offspring. Staying alive makes an organism more optimistic about its fate as it becomes more likely that it occupies a safe spot. This 'probing of mortality by living' becomes a selective force for mixed allocation as it permits the gradual building of size and reproductive potential. Probing of mortality in heterogeneous environments by staying alive has also been suggested to influence oviposition behaviour in parasitic insects (Tammaru, Javois, & Larsson, 2005).

Heterogeneous environments, with respect to mortality risk, that are stable over time but spatially structured, can select for indeterminate growth and mixed allocation to growth and reproduction in short-lived organisms. Previous contributions to life-history theory reveal that mixed allocation is an optimal bet-hedging strategy when mortality risk changes temporarily in a per generation basis (Gurney & Middleton, 1996; King & Roughgarden, 1982; Taylor & Gabriel, 1993; Wong & Ackerly, 2005). In our model, growth accompanying reproduction selected for in spatially heterogeneous environments also serves as a bet-hedging strategy because offspring produced by females are dispersed among risky and safe sites in the environment.
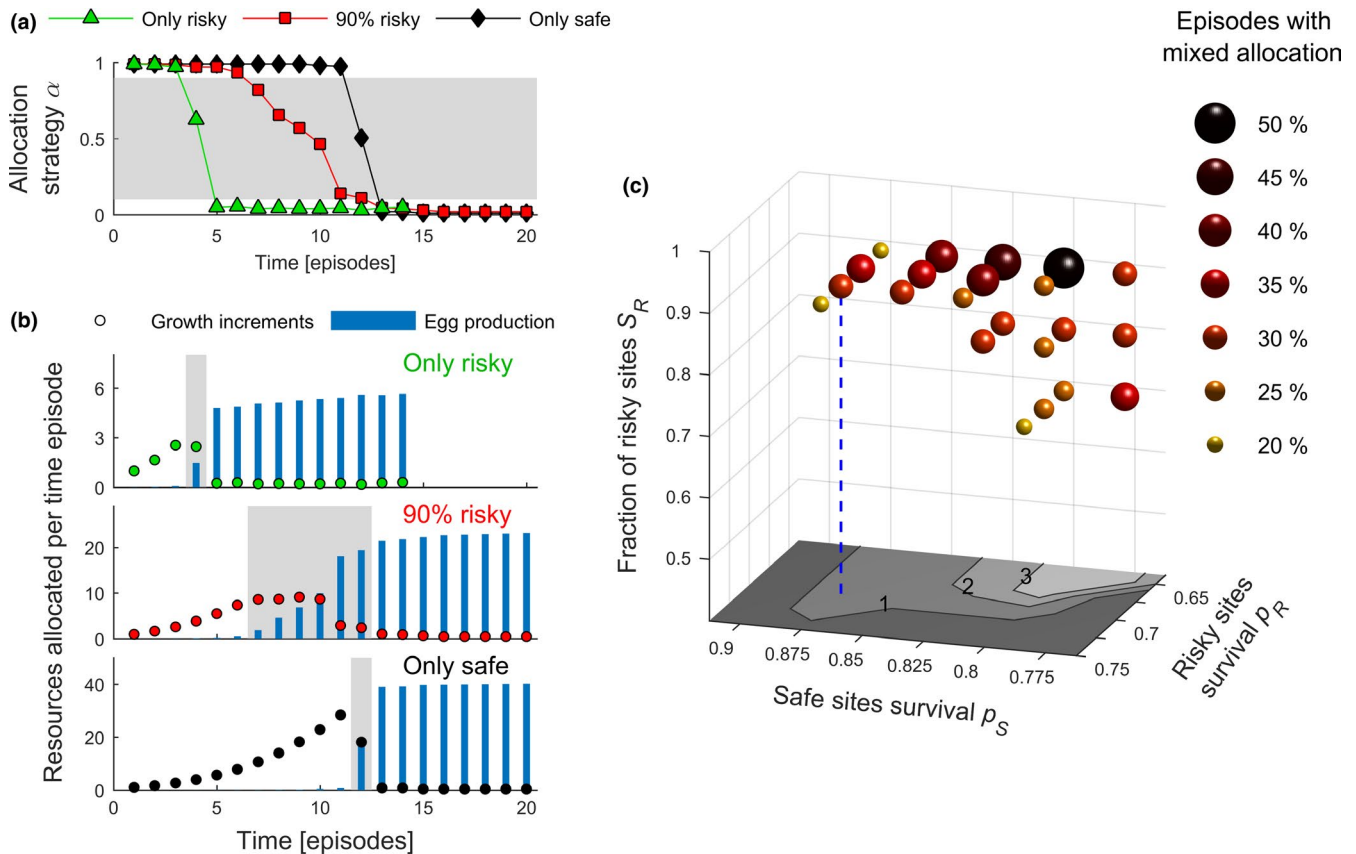
FIGURE 2 Optimal allocation strategies and resulting resource allocation patterns in homogenous and heterogeneous environments. (a) In a heterogeneous environment, the mixed allocation is selected for (red squares), whereas homogenous environments select for a 'bang-bang' switching (green triangles and black diamonds). (a, b) The shaded area depicts simultaneous allocation to growth and reproduction. The modelled environment consists of risky and safe sites with a survival probability of one-time episode equal to $p_R = 0.7$ and $p_S = 0.875$. Allocation strategies, growth increments and egg production are presented for episodes to which organisms survive with a probability >0.005. (c) The proportion of time episodes with mixed allocation per generation is illustrated by the coloured spheres (see the legend). The empty space matches scenarios with a 'bang-bang' switch (see the main text for the definition of mixed allocation). For certain combinations of survival probabilities p_S and p_R, the mixed allocation appears at more than one level of the considered proportion of risky sites S_R (the number of levels with mixed allocation is illustrated by the grey contour plot). The blue dashed line indicates the survival chance in risky and safe sites of the scenario investigated in a and b. (a–c) The presented allocation strategies are median values calculated across 20 simulation replicates. For illustration of individual variation in allocation strategies see Figure S3 in Appendix S1

Growth rate in the modelled females varies throughout life with periods of decelerating but also accelerating growth. Prolonged and variable allocation to growth by adults may produce complex growth curves that arise as an adaptation to spatially heterogeneous environments. Our study provides the first theoretical evidence of spatially heterogeneous environments selecting for complex growth curves. However, more work is needed to explore the evolution of growth strategies under complex spatiotemporal variation of the environment and with explicitly considered evolution of dispersal rate.

Living organisms undertake actions that are dependent on the cues and signals perceived from their environment, but the ability to perceive information about a determinant of vital rates can be elusive. Whereas food availability or thermal conditions translate to clear-cut physiological signals, mortality risk is much more difficult to be assessed for an organism, in particular when variable in space or time. However, individual life histories of short-lived indeterminate growers can be altered by cues of predator presence,

as for example, mechanical and visual stimuli, predator-derived kairomones or chemical odours of consumed prey (e.g. Czarnoleski, Muller, Kierat, Gryczkowski, & Chybowski, 2011; Lass & Spaak, 2003; Ślusarczyk & Rygielska, 2004). Mortality rate is an additive demographic parameter that can be divided into components that correlate with local conditions and the background mortality. In our work, females were unable to gather any information about mortality risk, but the conclusions are also valid if components of mortality rate correlate poorly with environmental conditions and cannot be perceived in a reliable manner.

There are several taxa-specific hypotheses on the evolution of growth following maturation that are worth mentioning. In plants, structural constraints of reproductive investment may lead to simultaneous growth and reproduction (Ioslovich & Gutman, 2005; Kozłowski & Ziółko, 1988). However, selection exerted by herbivores seems to be a more general explanation (see Janczur, 2009) as the great majority of plants synthesize defensive chemicals
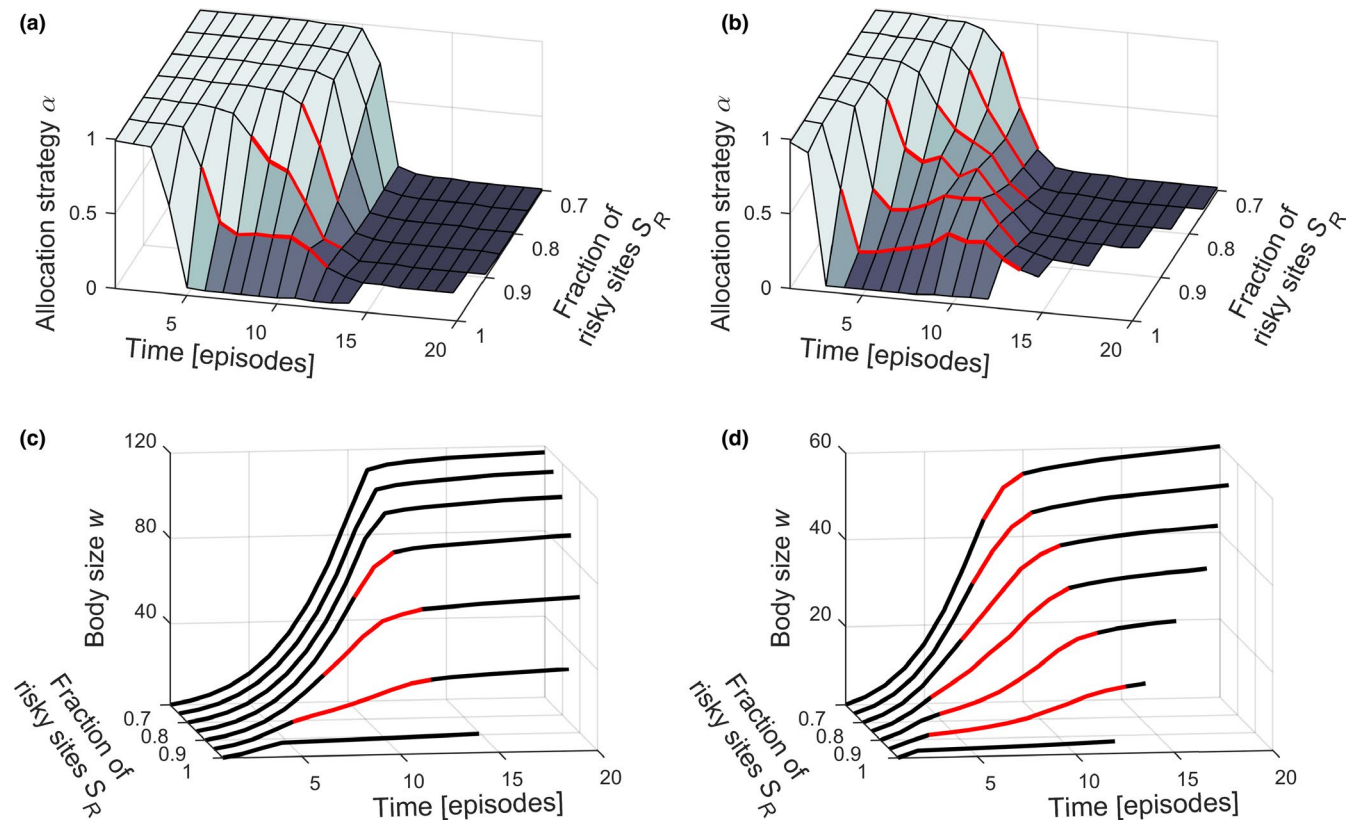
FIGURE 3 Allocation strategies and resulting growth curves in heterogeneous environments. (a, b) Resource allocation between growth (α = 1) and reproduction (α = 0) in relation to time. (a–c) Red lines illustrate time episodes and resulting growth phases arising due to mixed allocation to growth and reproduction. Survival probabilities of one-time episode in risky and safe sites are equal to 0.7 and 0.875 (a, c) or 0.65 and 0.825 (b, d). The degree to which growing organisms reproduce depends on the combination of mortality rates in risky and safe sites (compare a, c with b, d, see also Figure S5 in Appendix S1). More frequent safe sites in the environment selected for a 'bang-bang' switch and determinate growth (see main text). When the period of mixed allocation is long, the allocation to growth after maturation may accelerate over a certain part of life. The presented allocation strategies are median values calculated across 100 simulation replicates. For illustration of individual variation in allocation strategies see Figure S3 in Appendix S1. For clarity the figures present optimal allocation strategies in environments with a proportion of risky sites S_R > 0.7. Allocation strategies and growth curves are presented for time episodes to which organisms survive with a probability >0.005

to defend from herbivores (Ejsmond & Provenza, 2018; Foley & Moore, 2005; Strauss, Rudgers, Lau, & Irwin, 2002). Growth accompanying reproduction can also be optimal in populations that grow indefinitely, and age-specific mortality drops throughout life towards a constant value (Engen & Saether, 1994). However, the generality of the finding by Engen and Saether (1994) is unknown, as indeterminate growers rarely evolve in indefinitely growing populations, and unlimited population growth selects for an early maturation (Kozłowski, 1999). Our work adds spatial heterogeneity and metapopulational context to the list of evolutionary drivers of growth accompanying reproduction. Cladocerans, short-lived amphipods and other crustaceans that grow after maturation evolve in metapopulations that, similar to the modelled setup, consist of safe fishless ponds and risky water bodies inhabited by planktivorous fish (Ebert, 2005; Wellborn, 1994; Wellborn & Broughton, 2008). In the presented model, mixed allocation arises from a balance between offspring recruited from risky and safe sites. However, growth accompanying reproduction evolves also in more complex environments that consist of

several different types of habitats (see Supporting Information Appendix S1).

Growth that accompanies reproduction in short-lived water invertebrates has been suggested to evolve when both the assimilation of resources and mortality risk increase along with body size (Perrin, Sibly, & Nichols, 1993; Taylor & Gabriel, 1992). The death rates of many planktonic crustaceans are strongly affected by the activity of visual predators, with large species or individuals being exposed to a higher risk of death than small ones (Ebert, 2005; Gliwicz, Slusarczyk, & Slusarczyk, 2001; Slusarczyk, Ochocka, & Cichocka, 2012). However, intraspecific reactions of mortality risk to body size in planktonic crustaceans can be more complex. Large individuals can be selectively predated in amphipods (Wellborn, 1994), but in fast-swimming marine copepods older, and thus, larger, individuals are subjected to the lowest mortality risk on an intraspecific level (Eiane, Aksnes, Ohman, Wood, & Martinussen, 2002; Ohman, 2012; Ohman & Wood, 1996). The size dependence of mortality risk in aquatic environments may also depend on the type of predator, with visual and tactile predators being expected to select for opposed
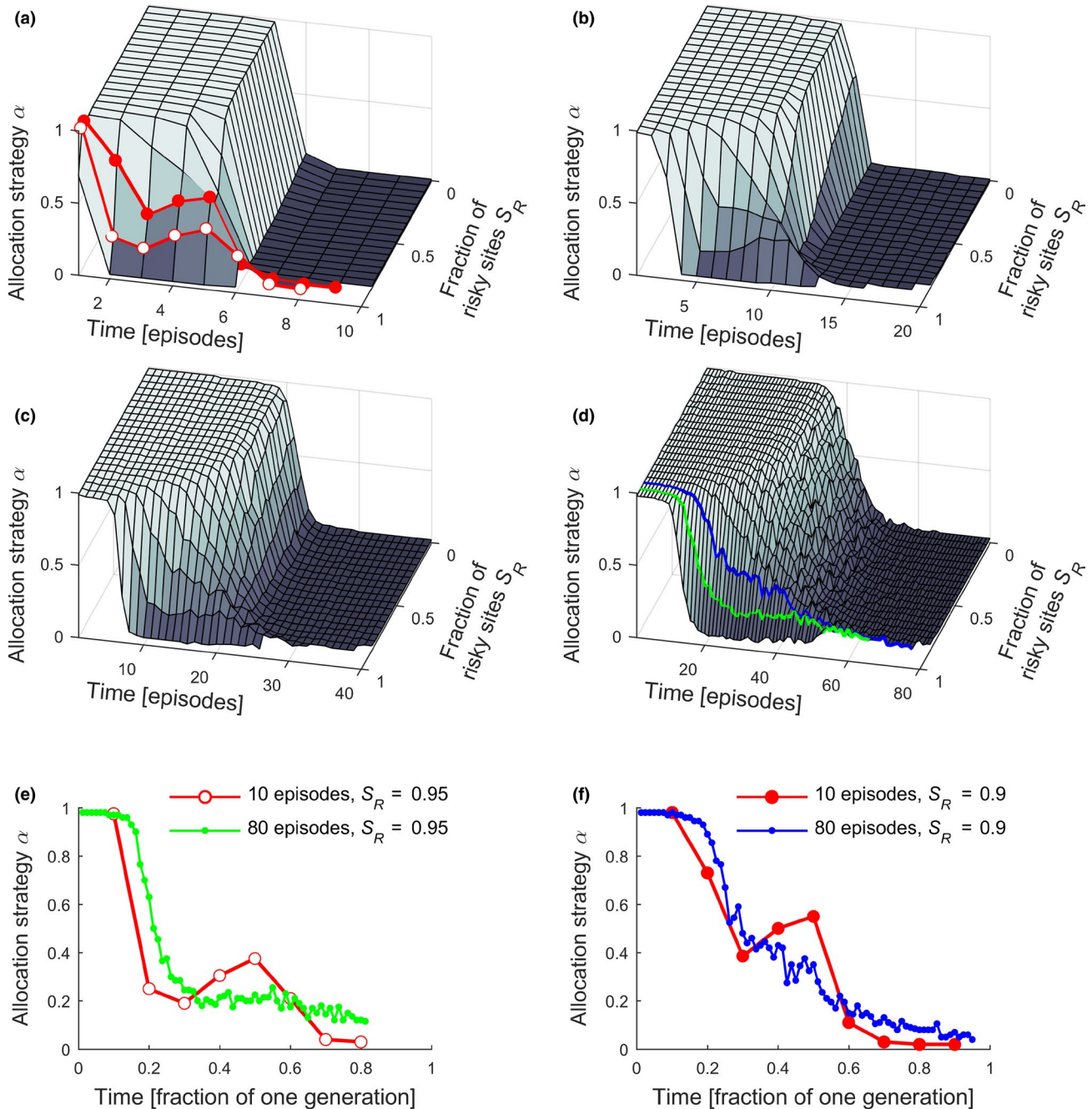
FIGURE 4 The effect of the number of time episodes per generation on the simultaneous allocation to growth and reproduction. (a–f) Resource allocation between growth ($\alpha = 1$) and reproduction ($\alpha = 0$) in relation to time. The colour of the lines in (a) and (d) match those presented in (e) and (f). Because the duration of the generation is the same for all modelled scenarios, time in (e) and (f) is expressed as a fraction of generation time. (a, b) Under the assumed low number of episodes per generation, the allocation to growth may periodically accelerate during adult life. (c, d) Scenarios with many time episodes per generation exhibit a greater stochastic variability of trajectories, as a suboptimal allocation within one-time episode can be compensated in an adjacent time episode(s) without a great change in resulting growth trajectory and offspring production. (e, f) Growth accompanying reproduction is selected for despite the assumed high number of episodes per generation. (a–f) The mortality rate per generation in risky and safe sites equals $m_R = 7.86$ and $m_S = 3.25$, respectively. This corresponds to the following probabilities of surviving one-time episode: (a) $p_R = 0.456$, $p_S = 0.722$; (b) $p_R = 0.675$, $p_S = 0.85$; (c) $p_R = 0.822$, $p_S = 0.922$ and (d) $p_R = 0.906$, $p_S = 0.960$. The presented strategies are median values calculated across 100 simulation replicates. Allocation strategies are presented for time episodes to which organisms survive with a probability >0.005

size spectra. Our work associates the diversity of growth patterns observed in planktonic crustaceans with the degree to which mortality risk varies in space. The theoretical concepts that link the evolution of mixed allocation with positive scaling of resource acquisition

rate and mortality rate predict that the rate of adult growth decelerates along with body size (e.g. Perrin et al., 1993). Shapes of growth curves of cladocerans, including those raised in laboratory conditions, can be complex with periodic termination or acceleration of

allocation to growth observed long after maturation (Lynch, 1980; Murugan & Sivaramakrishnan, 1973). Similarly, in our model, growth curves of adults can be complex due to periods of constant, accelerating or decelerating allocation to growth.

The diversity of growth tactics adopted by indeterminate growers stimulates the enduring discussion on the mathematical description of individual growth curves (von Bertalanffy, 1957; Czarnołęski & Kozłowski, 1998; Marshall & White, 2019). Models assume that the juvenile phase of growth is followed by an adult phase of growth during which growth rate decelerates in a negative exponential fashion (Boukal, Dieckmann, Enberg, Heino, & Jørgensen, 2014; Minte-Vera, Maunder, Casselman, & Campana, 2016; Quince, Abrams, Shuter, & Lester, 2008). However, these models do not capture the nature of complex growth curves that arise due to shifts in resource allocation, including episodic cessations or accelerations of growth (Lynch, 1980; Murugan & Job, 1982; Murugan & Sivaramakrishnan, 1973; Sheehy et al., 2004). In our model, allocation to growth that accelerates or remains constant throughout certain periods of adult life results in the complex shape of growth curves (see Figure 3c,d). Complex growth curves, routinely associated with adverse conditions in ecological literature, arise in the model as an adaptive response to spatial heterogeneity of the environment. These curves are more likely to arise when females in the model are able to enlarge their body size only during a moulting, and there are several moults per generation (see Figure 4). Cladocerans that enlarge their body size by changing exoskeleton through moulting (Ebert, 2005; Lynch, 1980) indeed display complex growth patterns (Lynch, 1980; Murugan & Job, 1982; Murugan & Sivaramakrishnan, 1973). Further studies are needed to investigate if high overhead costs of reproduction that cause females to reproduce discontinuously would also select for mixed allocation to growth and reproduction when environments are spatially heterogeneous.

To conclude, spatial heterogeneity with respect to mortality should be added to the list of factors that shape growth strategies of indeterminate growers. However, the modelled setup fits well with a life history of annuals or those with a shorter life cycle; more complex trade-offs need to be considered in the case of perennials (Ejsmond et al., 2015). The adults of short-lived organisms that moult during life can accelerate the allocation to growth as an adaptive response to heterogenic environments. Our work also shows that complex growth curves are more likely to evolve in short-lived organisms, when individuals need to change their exoskeleton to grow and there are only several moults per adult life.

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AUTHORS' CONTRIBUTIONS

All authors conceived the study and designed the model. A.E. wrote the code and ran the simulations. A.E. and M.J.E performed the analyses. M.J.E. drafted the paper with all authors contributing to writing.

DATA AVAILABILITY STATEMENT

The code for the computer program is available from the Zenodo open digital repository, accession number 3374420; https://doi.org/10.5281/zenodo.3374420 (Ejsmond, Kozłowski, & Ejsmond, 2019).

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REFERENCES

Bogin, B. (1999). Evolutionary perspective on human growth. *Annual Review of Anthropology*, *28*, 109–153. https://doi.org/10.1146/annurev.anthro.28.1.109

Boukal, D. S., Dieckmann, U., Enberg, K., Heino, M., & Jørgensen, C. (2014). Life-history implications of the allometric scaling of growth. *Journal of Theoretical Biology*, *359*, 199–207. https://doi.org/10.1016/j.jtbi.2014.05.022

Burdon, J. J., & Thrall, P. H. (1999). Spatial and temporal patterns in co-evolving plant and pathogen associations. *American Naturalist*, *153*, S15–S33. https://doi.org/10.1086/303209

Chambers, J. C., & Macmahon, J. A. (1994). A day in the life of a seed: Movements and fates of seeds and their implications for natural and managed systems. *Annual Review of Ecology and Systematics*, *25*, 263–292. https://doi.org/10.1146/annurev.es.25.110194.001403

Czarnołęski, M., & Kozłowski, J. (1998). Do Bertalanffy's growth curves result from optimal resource allocation? *Ecology Letters*, *1*, 5–7. https://doi.org/10.1046/j.1461-0248.1998.0007b.x

Czarnoleski, M., Muller, T., Kierat, J., Gryczkowski, L., & Chybowski, Ł. (2011). Anchor down or hunker down: An experimental study on zebra mussels' response to predation risk from crayfish. *Animal Behaviour*, *82*, 543–548. https://doi.org/10.1016/j.anbehav.2011.06.008

Dillon, R. T. (2000). *The ecology of freshwater mollusks*. Cambridge UK: Cambridge University Press.

Dmitriew, C. M. (2011). The evolution of growth trajectories: What limits growth rate? *Biological Reviews*, *86*, 97–116. https://doi.org/10.1111/j.1469-185X.2010.00136.x

Ebert, D. (2005). *Ecology, epidemiology and evolution of parasitism in Daphnia*. Bethesda, MD: National Library of Medicine.

Eiane, K., Aksnes, D. L., Ohman, M. D., Wood, S., & Martinussen, M. B. (2002). Stage-specific mortality of *Calanus* spp. under different predation regimes. *Limnology and Oceanography*, *47*, 636–645. https://doi.org/10.4319/lo.2002.47.3.0636

Ejsmond, A., Kozłowski, J., & Ejsmond, M. J. (2019). Data from: Probing of mortality rate by staying alive: The growth-reproduction trade-off in a spatially heterogeneous environment. *Zenodo*. https://doi.org/10.5281/zenodo.3374420

Ejsmond, M. J., Czarnołęski, M., Kapustka, F., & Kozłowski, J. (2010). How to time growth and reproduction during the vegetative season: An evolutionary choice for indeterminate growers in seasonal environments. *American Naturalist*, *175*, 551–563. https://doi.org/10.1086/651589

Ejsmond, M. J., & Provenza, F. D. (2018) Is doping of cognitive performance an anti-herbivore adaptation? Alkaloids inhibiting acetylcholinesterase as a case. *Ecosphere*, 9(2), e02129. https://doi.org/10.1002/ecs2.2129

Ejsmond, M. J., Varpe, Ø., Czarnoleski, M., & Kozłowski, J. (2015). Seasonality in offspring value and trade-offs with growth explain capital breeding. *The American Naturalist*, 186, E111–E125. https://doi.org/10.1086/683119

Engen, S., & Saether, B. E. (1994). Optimal allocation of resources to growth and reproduction. *Theoretical Population Biology*, 46, 232–248. https://doi.org/10.1006/tpbi.1994.1026

Foley, W. J., & Moore, B. D. (2005). Plant secondary metabolites and vertebrate herbivores - from physiological regulation to ecosystem function. *Current Opinion in Plant Biology*, 8, 430–435. https://doi.org/10.1016/j.pbi.2005.05.009

Folkvord, A., Jørgensen, C., Korsbrekke, K., Nash, R. D. M., Nilsen, T., & Skjæraasen, J. E. (2014). Trade-offs between growth and reproduction in wild Atlantic cod. *Canadian Journal of Fisheries and Aquatic Sciences*, 71, 1106–1112. https://doi.org/10.1139/cjfas-2013-0600

Glazier, D. S. (2005). Beyond the '3/4-power law': Variation in the intra- and interspecific scaling of metabolic rate in animals. *Biological Reviews*, 80, 611–662.

Gliwicz, Z. M., Slusarczyk, A., & Slusarczyk, M. (2001). Life history synchronization in a long-lifespan single-cohort Daphnia population in a fishless alpine lake. *Oecologia*, 128, 368–378. https://doi.org/10.1007/s004420100673

Gotthard, K. (2001). Growth strategies of ectothermic animals in temperate environments. In D. Atkinson, & M. Thorndyke (Eds.), *Environment and animal development: Genes, life histories and plasticity* (pp. 287–303). Oxford, UK: BIOS Scientific Publishers.

Gurney, W. S. C., & Middleton, D. A. J. (1996). Optimal resource allocation in a randomly varying environment. *Functional Ecology*, 10, 602–612. https://doi.org/10.2307/2390170

Hairston, N. G. (1996). Zooplankton egg banks as biotic reservoirs in changing environments. *Limnology and Oceanography*, 41, 1087–1092. https://doi.org/10.4319/lo.1996.41.5.1087

Heino, M., & Kaitala, V. (1999). Evolution of resource allocation between growth and reproduction in animals with indeterminate growth. *Journal of Evolutionary Biology*, 12, 423–429. https://doi.org/10.1046/j.1420-9101.1999.00044.x

Higgins, R. M., Diogo, H., & Isidro, E. J. (2015). Modelling growth in fish with complex life histories. *Reviews in Fish Biology and Fisheries*, 25, 449–462. https://doi.org/10.1007/s11160-015-9388-8

Holmgren, K. (2003). Omitted spawning in compensatory-growing perch. *Journal of Fish Biology*, 62, 918–927. https://doi.org/10.1046/j.1095-8649.2003.00086.x

Ioslovich, I., & Gutman, P. O. (2005). On the botanic model of plant growth with intermediate vegetative-reproductive stage. *Theoretical Population Biology*, 68, 147–156. https://doi.org/10.1016/j.tpb.2005.06.003

Janczur, M. K. (2009). Optimal energy allocation to growth, reproduction, and production of defensive substances in plants: A model. *Evolutionary Ecology Research*, 11, 447–470.

Johansson, J., Brannstrom, A., Metz, J. A. J., & Dieckmann, U. (2018). Twelve fundamental life histories evolving through allocation-dependent fecundity and survival. *Ecology and Evolution*, 8, 3172–3186. https://doi.org/10.1002/ece3.3730

Jørgensen, C., Ernande, B., Fiksen, Ø., & Dieckmann, U. (2006). The logic of skipped spawning in fish. *Canadian Journal of Fisheries and Aquatic Sciences*, 63, 200–211. https://doi.org/10.1139/f05-210

King, D., & Roughgarden, J. (1982). Graded allocation between vegetative and reproductive growth for annual plants in growing seasons of random length. *Theoretical Population Biology*, 22, 1–16. https://doi.org/10.1016/0040-5809(82)90032-6

Kozlowski, J. (1996). Optimal allocation of resources explains interspecific life-history patterns in animals with indeterminate growth. *Proceedings of the Royal Society B-Biological Sciences*, 263, 559–566.

Kozłowski, J. (1999). Adaptation: A life history perspective. *Oikos*, 86, 185–194. https://doi.org/10.2307/3546437

Kozłowski, J. (2006). Why life histories are diverse. *Polish Journal of Ecology*, 54, 585–605.

Kozłowski, J., & Gawełczyk, A. T. (2002). Why are species' body size distributions usually skewed to the right? *Functional Ecology*, 16, 419–432. https://doi.org/10.1046/j.1365-2435.2002.00646.x

Kozłowski, J., & Ziółko, M. (1988). Gradual transition from vegetative to reproductive growth is optimal when the maximum rate of reproductive growth is limited. *Theoretical Population Biology*, 34, 118–129. https://doi.org/10.1016/0040-5809(88)90037-8

Lass, S., & Spaak, P. (2003). Chemically induced anti-predator defences in plankton: A review. *Hydrobiologia*, 491, 221–239. https://doi.org/10.1023/A:1024487804497

Laver, R. J., Purwandana, D., Ariefiandy, A., Imansyah, J., Forsyth, D., Ciofi, C., & Jessop, T. S. (2012). Life-history and spatial determinants of somatic growth dynamics in Komodo Dragon populations. *PLoS ONE*, 7, e45398. https://doi.org/10.1371/journal.pone.0045398

Leon, J. A. (1976). Life histories as adaptive strategies. *Journal of Theoretical Biology*, 60, 301–335. https://doi.org/10.1016/0022-5193(76)90062-X

Lewontin, R. C., & Cohen, D. (1969). On population growth in a randomly varying environment. *Proceedings of the National Academy of Sciences of the United States of America*, 62, 1056–2000. https://doi.org/10.1073/pnas.62.4.1056

Lynch, M. (1980). The evolution of cladoceran life histories. *Quarterly Review of Biology*, 55, 23–42. https://doi.org/10.1086/411614

Marshall, D. J., & White, C. R. (2019). Have we outgrown the existing models of growth? *Trends in Ecology & Evolution*, 34, 102–111. https://doi.org/10.1016/j.tree.2018.10.005

Minte-Vera, C. V., Maunder, M. N., Casselman, J. M., & Campana, S. E. (2016). Growth functions that incorporate the cost of reproduction. *Fisheries Research*, 180, 31–44. https://doi.org/10.1016/j.fishres.2015.10.023

Munguia, P., Mackie, C., & Levitan, D. R. (2007). The influence of stage-dependent dispersal on the population dynamics of three amphipod species. *Oecologia*, 153, 533–541. https://doi.org/10.1007/s00442-007-0762-7

Murugan, N., & Job, S. V. (1982). Laboratory studies on the life cycle of Leydigia acanthocercoides Fisher (1854) (Cladocera: Chydoridae). *Hydrobiologia*, 89, 9–16. https://doi.org/10.1007/BF00017533

Murugan, N., & Sivaramakrishnan, K. G. (1973). The biology of Simocephalus acutirostratus King (Cladocera: Daphnidae)-laboratory studies of life span, instar duration, egg production, growth and stages in embryonic development. *Freshwater Biology*, 3, 77–83. https://doi.org/10.1111/j.1365-2427.1973.tb00063.x

Ohman, M. D. (2012). Estimation of mortality for stage-structured zooplankton populations: What is to be done? *Journal of Marine Systems*, 93, 4–10. https://doi.org/10.1016/j.jmarsys.2011.05.008

Ohman, M. D., & Wood, S. N. (1996). Mortality estimation for planktonic copepods: *Pseudocalanus newmani* in a temperate fjord. *Limnology and Oceanography*, 41, 126–135. https://doi.org/10.4319/lo.1996.41.1.0126

Perrin, N., & Sibly, R. M. (1993). Dynamic models of energy allocation and investment. *Annual Review of Ecology and Systematics*, 24, 379–410. https://doi.org/10.1146/annurev.es.24.110193.002115

Perrin, N., Sibly, R. M., & Nichols, N. K. (1993). Optimal growth strategies when mortality and production rates are size-dependent. *Evolutionary Ecology*, 7, 576–592. https://doi.org/10.1007/BF01237822

Peters, R. H. (1983). *The ecological implications of body size*. Cambridge, UK: Cambridge University Press.

Quince, C., Abrams, P. A., Shuter, B. J., & Lester, N. P. (2008). Biphasic growth in fish I: Theoretical foundations. *Journal of Theoretical Biology*, *254*, 197–206. https://doi.org/10.1016/j.jtbi.2008.05.029

Rideout, R. M., Rose, G. A., & Burton, M. P. M. (2005). Skipped spawning in female iteroparous fishes. *Fish and Fisheries*, *6*, 50–72. https://doi.org/10.1111/j.1467-2679.2005.00174.x

Sheehy, J. E., Mitchell, P. L., & Ferrer, A. B. (2004). Bi-phasic growth patterns in rice. *Annals of Botany*, *94*, 811–817. https://doi.org/10.1093/aob/mch208

Sibly, R. M., & Brown, J. H. (2009). Mammal reproductive strategies driven by offspring mortality-size relationships. *American Naturalist*, *173*, E185–E199. https://doi.org/10.1086/598680

Sibly, R., Calow, P., & Nichols, N. (1985). Are patterns of growth adaptive? *Journal of Theoretical Biology*, *112*, 553–574. https://doi.org/10.1016/S0022-5193(85)80022-9

Slusarczyk, M., Ochocka, A., & Cichocka, D. (2012). The prevalence of diapause response to risk of size-selective predation in small- and large-bodied prey species. *Aquatic Ecology*, *46*, 1–8. https://doi.org/10.1007/s10452-011-9376-6

Ślusarczyk, M., & Rygielska, E. (2004). Fish faeces as the primary source of chemical cues inducing fish avoidance diapause in *Daphnia magna*. *Hydrobiologia*, *526*, 231–234. https://doi.org/10.1023/B:HYDR.0000041599.56610.b4

Strauss, S. Y., Rudgers, J. A., Lau, J. A., & Irwin, R. E. (2002). Direct and ecological costs of resistance to herbivory. *Trends in Ecology & Evolution*, *17*, 278–285. https://doi.org/10.1016/S0169-5347(02)02483-7

Tammaru, T., Javois, J., & Larsson, S. (2005). When being alive implies being safe: variation in mortality rates can cause ovipositionselectivity to increase with age. *Oikos*, *111*, 649–653. https://doi.org/10.1111/j.1600-0706.2005.14226.x

Taylor, B. E., & Gabriel, W. (1992). To grow or not to grow: Optimal resource allocation for *Daphnia*. *American Naturalist*, *139*, 248–266. https://doi.org/10.1086/285326

Taylor, B. E., & Gabriel, W. (1993). Optimal adult growth of *Daphnia* in a seasonal environment. *Functional Ecology*, *7*, 513–521. https://doi.org/10.2307/2390126

Taylor, H. M., Gourley, R. S., Lawrence, C. E., & Kaplan, R. S. (1974). Natural selection of life history attributes: An analytical approach. *Theoretical Population Biology*, *5*, 104–122. https://doi.org/10.1016/0040-5809(74)90053-7

von Bertalanffy, L. (1957). Quantitative laws in metabolism and growth. *Quarterly Review of Biology*, *32*, 217–231. https://doi.org/10.1086/401873

Wada, S., Oba, T., Nakata, K., & Ito, A. (2008). Factors affecting the interval between clutches in the hermit crab *Pagurus nigrivittatus*. *Marine Biology*, *154*, 501–507. https://doi.org/10.1007/s00227-008-0944-9

Wellborn, G. A. (1994). Size-biased predation and prey life histories: A comparative study of freshwater amphipod populations. *Ecology*, *75*, 2104–2117. https://doi.org/10.2307/1941614

Wellborn, G. A., & Broughton, R. E. (2008). Diversification on an ecologically constrained adaptive landscape. *Molecular Ecology*, *17*, 2927–2936. https://doi.org/10.1111/j.1365-294X.2008.03805.x

Wong, T. G., & Ackerly, D. D. (2005). Optimal reproductive allocation in annuals and an informational constraint on plasticity. *New Phytologist*, *166*, 159–171. https://doi.org/10.1111/j.1469-8137.2005.01375.x

Xu, M., Jiang, L. B., Zhu, S., Zhou, C. G., Ye, M. X., Mao, K., … Wu, R. L. (2016). A computational framework for mapping the timing of vegetative phase change. *New Phytologist*, *211*, 750–760. https://doi.org/10.1111/nph.13907

Ziółko, M., & Kozłowski, J. (1983). Evolution of body size - an optimization model. *Mathematical Biosciences*, *64*, 127–143. https://doi.org/10.1016/0025-5564(83)90032-9

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