Temporal constraints on reproduction and growth in a seasonal environment

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Summary

The variety of life forms is one of the most striking phenomena that have stimulated research in evolutionary biology and ecology over recent decades. The crucial role in defining the most characteristic features of living organisms is dedicated to so-called life history traits (Stearns 1992, Roff 2002). Biological species are characterized by several life history traits such as lifespan, rate of ageing, sexual size dimorphism, but also traits investigated in this work: body size, growth rate, mode of reproduction, and timing and synchrony of breeding. Those traits define functional features of species with consequences going far beyond simple classification. From individual to the ecosystem level, life history traits affect physiology, behaviour but also interactions between species (Davies et al. 2012). Hence, the knowledge about how life history traits evolve is central for understanding important scientific questions but also practical ecological or conservation issues (Allen 2006, Jørgensen et al. 2007, Heino et al. 2015). The great meaning and the potential of our understanding of the sources of evolution of life history traits for understanding ecosystem functioning is the main motivation of my research presented in this thesis.

In my thesis I combine theoretical models and empirical work. I aimed at testing hypotheses on the evolution of life history traits in the context of one of the key life history compromises: the evolutionary trade-off between current and future reproduction (Williams 1966). My work was inspired by life histories of species living at a high-latitude Arctic ecosystem of Svalbard archipelago. The empirical part of my thesis, performed to test the predictions of my theoretical research, was conducted in Svalbard in years 2015-2020. The research questions regarding the evolution of body size, growth rate, mode of reproduction and, timing and synchrony of breeding presented in this thesis are oriented around the two subjects described below: the life history trade-off between current and future reproduction under temporal constraints generally and in a high latitude Arctic ecosystem particularly.

List of publications

PAPER I

Ejsmond A., Forchhammer M., Varpe Ø., Jónsson J.E., Jørgensen C. Nesting synchrony and clutch size in migratory birds: Capital versus income breeding determines responses to variable spring onset. The American Naturalist

(in review)

PAPER II

Ejsmond A., Jørgensen C. Modelling of reproductive success of eiders shows capital breeders can cope better under stochastically fluctuating than a stable food gain.

(manuscript)

PAPER III

Ejsmond A., Jørgensen C., Phenology of breeding in a capital breeding sea duck, common eider, is influenced by regional and local conditions

(manuscript)

PAPER IV

Ejsmond A., Kozłowski J., Ejsmond M.J. (2019) Probing of mortality rate by staying alive: The growth-reproduction trade-off in a spatially heterogeneous environment.

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Synthesis

Introduction

Life history trade-off under temporal constraints

Many life history traits are consequences of actions performed by organisms. The temporal aspect of performing these actions is key as growing, migration, reproduction, but also other processes, take time. In this thesis I focus on two major forces limiting the time available for organisms to perform various activities: seasonal time constraints and mortality risk. Some actions can only be performed in a certain period of year as performing them too late or too early drastically reduces fitness (Einum and Fleming 2000, Reznick et al. 2006, Jørgensen et al. 2006, Jørgensen and Fiksen 2006). Hence, the seasonal time constraints outline the periods of time within a year in which a given type of activity, e.g. reproduction or migration, has to be performed to avoid drastic decrease of fitness (Houston and McNamara 1999). The second type of temporal constraint explored in this thesis is related to the fact that all individuals die at some point but the life expectancy can differ considerably depending on biotic and abiotic conditions. The mortality risk outlines the expected lifespan i.e. the time period an average organism in the population can use to perform certain actions. By expected lifespan we mean an estimated value of lifespan averaged across all individuals in the population due to the stochastic character of mortality. The two described time constraints may depend on environmental conditions, display spatial variation or fluctuate year-to-year. However, both mortality risk and seasonal time constraints outline the time available for actions performed by individuals. The two mentioned sources of temporal constraints of life history evolution, i.e. seasonality and mortality rate, form a major subject of research and results presented in this thesis.

In this thesis I combine theoretical research and empirical field observations performed at high-latitude Arctic ecosystem to study the role and consequences of temporal constraints on life history evolution. In my research I investigate in particular the effects of temporal constraints caused by seasonal time constraints but the attention is also given to the spatiotemporal fluctuations of mortality rate that result in variation of the expected lifespan of individuals. Both variability in mortality rate and seasonal time

constraints are explored in the context of the evolutionary compromise between current and future reproductive success, to study evolution of body size, growth rate, mode of reproduction and, breeding synchrony and timing.

High-latitude Arctic ecosystem of Svalbard

The subject of my theoretical work was inspired by life histories of animals breeding at high-latitude Arctic ecosystems of Svalbard. Here, I briefly describe the species that inspired my work. However, a more detailed description of the biology of the species mentioned here is given in the parts of the thesis presenting the scientific context of the research questions (*see paragraphs below dedicated to description of trade-offs*).

The climatic conditions of Svalbard are termed Arctic semi-desert and characterized by low temperatures and low annual precipitation (Førland et al. 2011, Nordli et al. 2014). The unique climatic conditions of the Arctic are characterized by an annual daylight cycle, with polar night and polar day lasting around 4 months each. The light and temperature variation turn into a general annual freeze-thaw cycle, though due to specific climatic conditions, periodical melts can occur also during winter in certain parts of Svalbard archipelago. Apart of extreme seasonality and extremely short vegetative season, the Arctic is characterized by relatively fast climatic change. The forecasted changes in snow and sea ice melt dates make the Arctic, and so the phenology of organisms breeding at high latitudes, the most affected by the climate change on Earth (Høye et al. 2007, Etzelmuller et al. 2011, IPCC report 2013). The reported and forecasted change includes increasing mean temperature, thermal variation, and altered precipitation dynamics associated with earlier snow melt and increased duration of the snow-free period (Stone et al. 2002; Brown and Robinson 2011, Clark et al. 2014). All these make living organisms inhabiting Svalbard the ideal research subject for studying responses of life history traits to time constraints created by a seasonally changing environment, stochastically changing food supply and mortality rate.

The largest part of my dissertation is dedicated to studies of the trade-off between current and future reproductive success in a seasonal environment with optimization of timing of nesting and role of reserves in reproduction (**Paper I** and **II**). The models created to study evolution of these traits in seasonally changing environment were parameterized in order to resemble the life history of a migratory sea duck, the common eider (*Somateria*

mollissima). Some predictions derived from theoretical models based on the common eider life history were directly tested with empirical data (**Paper III**).

Second part of my work also investigates the trade-off between current and future reproduction under temporal constraint but the study subject is the growth strategy of annual organisms. The growth-reproduction trade-off considered in my work evolves under spatiotemporally variable mortality risk (**Paper IV**). The work was inspired by the life history and growth strategies of small freshwater crustaceans, as for example daphnids belonging to Cladocera or tadpole shrimps *Lepidurus arcticus*, that inhabit freshwater or slightly saline natural ponds of the Arctic. The main inspiration that link my theoretical work with life histories of freshwater crustaceans is related to variability in survival prospects that differ on year-to-year basis and spatially. Freshwater crustaceans inhabiting ponds of Svalbard experience strong spatiotemporal variation in mortality risk, as ponds differ with respect to the presence of its main predator – the Arctic char, *Salvelinus alpinus* (Jeppesen et al. 2001).

Life history trade-off between current and future reproductive success

The evolution of certain life histories usually means that alternative strategies have been selected against or outcompeted. This reasoning underlies the methodology of empirical and theoretical research in evolutionary ecology. Some combinations of life history traits, or components of fitness, as for example a combination of intensive reproduction with high longevity, or high growth rate maintained during periods of reproduction, are rarely observed. These negative correlations observed between some traits are due to the existing life history trade-offs and physiological constraints that outline the arena in which traits evolve (Garland 2014). There are several dozens of documented life history trade-offs that can affect fitness and evolution of life history traits (Stearns 1989). In this thesis, I present research on one of the key life history trade-offs that influence the lifetime reproductive effort, i.e. a compromise between current and future (expected) reproductive success (Williams 1966). The negative correlation between current and future reproduction is expected to arise when current reproductive effort and offspring production impose or increase costs that reduce future reproductive potential (Stearns 1992, Roff 2002). In general, the trade-off between current and future reproduction can

take different forms, as there are many types of activities that can be constrained by reproduction.

No matter the specific character of the discussed trade-off, it is governed by two biological features. First, resources available to organisms in natural populations are almost always limited (Stearns 1992). This limitation can be a consequence of various physiological or ecological features as for example, costs of digestion and assimilation (Weiner 1992), intra or interspecific competition, and infections by pathogens (Davies et al. 2012, Gotelli 2008). Assimilated resources used for reproduction cannot be utilized for other purposes, as for example growth, or stored to serve as an energy buffer during unpredictable environmental events. This limitation intensifies due to various temporal constraints that lead to a situation when time available for acquisition of the resources is restricted. Among temporal constraints, seasonal changes of food availability and environmental conditions are key determinants of resource acquisition and phenology in many species (Forrest and Miller-Rushing 2010). Resources need to be allocated in an optimal manner to growth, reproduction, storage, repairs of tissues etc. in order to maximize fitness (Stearns 1992, Roff 2002). Hence, the seasonal time limits the available resources available and create an important element of the trade-off between current and the future (expected) reproductive success.

The second important element of the trade-off between current and future reproductive success is a risk of death (Stearns 1992). No matter their physiological condition, ecological circumstances, or available resources, living organisms are uncertain about surviving to older ages. Mortality risk creates a time restriction on performed actions, including allocation to current reproduction (Kozlowski 2006). In natural populations mortality is a process with significant random component that may also depend on the age of the individual. The survival prospects of every individual in a given age can be described in a statistical manner by life expectancy, i.e. an average time an organism is expected to live, depending on its age and other characteristics (Stearns 1992). The life expectancy is also an important determinant of the trade-off between current and future reproduction. Postponement of reproduction and allocation of resources to activities that increase future offspring production can increase fitness only if the life expectancy at a given age is high enough. In other words, the survival probability to the moment of reproduction must be

high enough, so that the investment in future reproductive rate would payback in terms of fitness.

Because resources are limited and the death is unavoidable, organisms must decide whether to reproduce or perform actions that increase future rate of reproduction. To maximize fitness, they have to maximize the sum of currently produced recruits and the expected offspring production, or more precisely the number of recruits that will be produced in the future weighted by the probability of surviving to the age of reproduction (Williams 1966). The trade-off between current and future reproduction provides a powerful tool in explaining the great diversity of life history traits. For example, organisms that are expected to die relatively shortly after their birth would not evolve strategies that postpone reproduction, and hence would prioritize reproduction over growth. In turn, high mortality is expected to select for early maturation and small body size. Indeed, high mortality rate has been shown to increase tendency for early maturation, more intense reproduction early in life, and small body size (Reznick et al. 2006, Jeschke and Kokko 2009).

Breeding synchrony of capital and income breeding migratory birds

Bird life histories are distributed along a gradient of breeding synchrony (Magrath 1990; Spottiswoode and Møller 2004), and synchronous breeding can have far-reaching ecological consequences. For example, genetic diversity is increased in synchronous populations due to extra-pair paternity (Spottiswoode and Møller 2004). The degree of breeding synchrony can also affect functioning of ecosystems through the dynamics of food available to predators (e.g. Mwema et al. 2010). Synchronous breeding must provide fitness benefits high enough to outweigh high offspring mortality due to competition for food with peers (Mock and Parker 1997) or predators attracted by an abundant food source (e.g. Mwema et al. 2010). Hence, the question of why some bird species synchronize their breeding started a long-lasting discussion in ecology (Darling 1938). One of the prevailing explanations focuses on the benefits that females may achieve from breeding together. The fitness benefits of synchronous nesting include better opportunities for optimal partner choice and extra pair copulation (Ims 1990a; Spottiswoode and Møller 2004), more efficient defence or foraging in groups, and dilution of nest predation risk (Ims 1990b). Even though benefits from diluted predation have gathered strong support as a selective force for

synchronous breeding, they are often case-specific and claimed to have limited ability to serve as a general predictor of breeding synchrony (Ims 1990b).

In my research presented in this thesis I followed an alternative view according to which synchronization emerges from adjustment of individual breeding strategies to seasonal time constraints. There are clues that suggest a connection between seasonality and the degree of breeding synchrony of birds. With latitude as a proxy of season length, the timing of breeding in birds is more synchronized the further away from equator (Burr et al. 2016; Spottiswoode and Møller 2004). However, the latitudinal trend of reproductive synchrony only partially explains the variability of breeding timing. In my research of evolutionary causes of breeding synchrony, I investigated the role of reserves in reproductive strategy adopted by migratory species of birds.

Organisms adopt diverse strategies that allow them to store additional resources they can use for various purposes in the future. Living animals store nutrients and microelements (e.g. Rivero et al 2001), but usually lipid reserves constitute the prevailing mass of storage. Routinely, the role of reserves is associated with increased probability of survival during overwintering (Giacomini and Shutter 2013) or buffering unexpected fluctuations of the environmental conditions (Fischer et al 2009, Fischer et al 2011). The stored resources may also have great effects on fitness through production of recruits as organisms can increase the reproductive potential at the time offspring contribution to fitness is high (Varpe et al. 2007, Varpe et al. 2009, Ejsmond et al. 2015). Usage of reserves during breeding period is called capital breeding, whereas in income breeders, current acquisition of resources is used to cover costs of reproduction. There are examples of pure income and pure capital breeders, i.e. organisms that either use only reserves or only concurrent resource assimilation during reproduction, but the great majority of organisms adopt a mixed strategy of reproduction (Jönsson 1997, Stephens et al. 2009). The degree to which animals use reserves during reproduction introduces an important cause of variability in breeding strategies (Houston et al. 2007, Varpe et al. 2009, Pelisson et al. 2013, Ejsmond et al. 2015).

Storing of reserves can be seen as a form of the trade-off between current and future production of recruits. That is because acquired resources that are stored cannot be used for current production of offspring. Moreover, reserves form a pool of resources than can be relatively quickly allocated to cover costs of reproductive effort, but that also can be lost

without fitness payoff in case of death. The adaptive value of capital breeding results from a simple biological phenomenon: in seasonal environments offspring produced late in the breeding season have lower chances of recruitment than their conspecifics produced earlier (Einum and Fleming 2000; Reznick et al. 2006, Warner and Shine 2007). Resources stored prior to breeding can be used to cover reproduction costs at times when production of offspring governs high probability of recruitment (Varpe et al. 2007, Jørgensen et al. 2006, Ejsmond et al. 2015).

In my thesis I investigated how the described temporal constraint of recruit production caused by seasonal environments affect the timing of birth and breeding synchrony in migratory birds that adopt a capital or income breeding strategy. The terms income and capital breeding were first adopted to describe variation in breeding strategies of migratory birds by Drent and Daan (1980). Reserves are an important component of offspring production in a number of bird taxa such as ducks (eiders and other diving and dabbling ducks), geese, swans, waders, gulls, penguins, flamingos, owls, and even some passerine birds (Drent et al. 2006; Hobson and Jehl 2010; Krapu 1981; Kullberg et al. 2005; Langin et al. 2006; Mawhinney et al. 1999; Nolet 2006; Poisbleau et al. 2015; Rendón et al. 2011; Solonen 2014; Yates et al. 2010). My work was inspired by the biology of common eiders – a migratory sea duck breeding at high-latitude seasonal environments (Waltho and Coulson 2015). Common eider females are considered to apply a breeding strategy close to an extreme capital breeding. By intensively foraging prior to nesting, their stores alone can reach up to ca. 130% of the lean body mass (Milne 1976), and they terminate feeding completely during egg laying and 26 days of incubation (Parker and Holm 1990, Watson et al. 1993). Interestingly the king eider (*S. spectabilis*), a closely related species that also nests in the Arctic, is considered to apply a breeding strategy that is a mixture of income and capital breeding (Waltho and Coulson 2015). Females of king eiders need to concurrently acquire resources during egg laying and nesting (Waltho and Coulson 2015). The above described diversity of breeding strategies observed in eiders inspired my research during the PhD project. Consequently, in my models, described briefly below and in detail in **Papers I** and **II,** I considered income and capital breeders to test their responses to temporal constraints exerted by seasonal environment.

In migratory birds, capital breeding allows for reproduction at times that govern high chances of offspring recruitment (Barta et al. 2008). However, early breeding of capital

breeders can create a parent-offspring conflict (cf. Trivers 1974). That is because in birds that use reserves to boost reproductive allocation, the timing of breeding may impose a trade-off between reproductive capabilities of females and offspring survival (Barta et al. 2008). From an offspring perspective, it is often ideal to be hatched as early in the season as possible, because juveniles need time to achieve developmental milestones, e.g. ability to fly before autumn migration (Verhulst and Nilsson 2008, Barta et al. 2008). Hatching early increases the favorable time available for growth, and thus the survival chance of later stages, for instance first winter (Drent and Daan 1980, van der Jeugd et al. 2009). However, nesting onset in capital breeders restricts the time period between arrival and breeding used for foraging and as building-up reserves (e.g. Waltho and Coulson 2015, **Paper I**). Hence, breeding as early as possible is not necessarily optimal from the parents' perspective, who aim at maximizing the number of produced high quality eggs; mothers foraging for longer are able to produce more eggs but leave less time for offspring to develop (Rowe et al. 1994).

The described parent-offspring conflict concerns income and capital breeders but they are expected to respond differently, as for the optimal timing of their breeding but also as for other fitness components, as for example clutch size or recruitment probability. This evolution of the trade-off between current and future reproduction in seasonal environments is also expected to introduce differences between capital and income breeders in the degree of nesting synchronization. That is because capital breeders are more likely to postpone nesting and build up reserves, thus increasing their future reproductive success. Income breeders are expected to start reproduction immediately, as soon as conditions allow.

In my PhD project I have investigated the described set of hypotheses using an optimization model of life history of a migratory bird species that reproduces in a seasonal environment (**Paper I**). The model was inspired and parameterized in order to resemble biology and ecology of common eider. Birds arriving to the breeding grounds in advance of the breeding seasons were exposed to a seasonal environment with a declared date at which nesting could be initiated. To analyse responses of the optimal timing of migration and degree of breeding synchrony, I modelled income and capital breeders. The model emphasizes the time constraint imposed by length of season also through the probability of recruitment that decreases along with date of birth. Apart from modelling of

the response of nesting timing and breeding synchrony to variable length of breeding season and spring onset, the model provides data on clutch size produces by females in the population. The methods and results are described in **Paper I**.

Breeding synchrony of capital and income breeders under fluctuating food levels

In **Paper I**, I explored the model of breeding synchrony in capital breeding birds that migrate to breeding grounds. Capital breeders in the model are exposed to the trade-off between current and future recruits' production. After conditions allow for nesting, the modelled females can either start breeding or continue foraging and storing resources in order to increase number of eggs produced (**Paper I**). However, that model assumes that resource acquisition per day is constant, an assumption that departs from real natural conditions, in which individuals differ in the amount of food acquired per day (Houston and McNamara 1999). Similarly, common eiders foraging prior to breeding in Arctic ecosystems can experience temporal periods of starvation caused by harsh climatic conditions (Waltho and Coulson 2015).

Unpredictable fluctuations of daily food gain are an important determinant of birds' reproductive success and extensive variation of behavior and physiological responses has evolved to mitigate changes in body conditions driven by stochastic nature of food acquisition (Davies et al. 2012). Capital and income breeders among birds are expected to differently respond to food gain fluctuations. The random character of food acquisition, is expected to introduce a time lag before an individual can gather certain level of reserves which in turn can affect the decision on when to start nesting. The degree to which breeding synchrony, timing of nesting, clutch size and recruitment respond to stochastic fluctuations of food gain has been tested in the model of income and capital breeders described in this paragraph (**Paper II**). The daily food gain in the presented model fluctuates stochastically according to an assumed probability distribution. The considered strategies of breeding birds differ in the degree to which reproductive allocation during nesting period and incubation is covered from the reserves stored prior to breeding. The detailed description of the modelling of a capital and income breeding migratory birds is described in the paper attached to the thesis (**Paper II**).

Empirical data on breeding synchrony, timing of nesting and migration

Significant part of my work was dedicated to collecting data on timing of migration (6 years) and nesting (4 years) for the high-latitude breeding population of a long-lived and capital breeding sea duck, the common eider. This empirical part of my PhD project was performed on the west coast of Spitsbergen, in the vicinity of Longyearbyen. I performed daily counts of common eiders, during their spring arrival periods and breeding seasons. The collected data were analysed in relation to the climatic data and used to test if variation in arrival dates and dates of nesting onset in this species depend on large-scale climatic forces and local weather variation (**Paper III**). The analyses were performed separately for males and females to investigate sex-specific responses and phenological adaptations to high latitude Arctic environment. A part of the data on breeding synchrony and timing of nesting was used to test the prediction of the theoretical model of breeding synchrony in capital breeding migratory birds (**Paper I**).

Growth-reproduction trade-off under spatiotemporal variation of mortality risk

Body size is a primary determinant of life history evolution. Due to obvious physical constraints and natural selection, body mass at birth in multicellular organisms is almost always orders of magnitude lower than adult body size. This creates a challenging task for juveniles that need to acquire resources and take risk of death while growing before they mature and contribute to fitness by their reproduction. Whereas there is a great variability of resource acquisition rates dependent on physiological features, diet, life style, metabolic rate etc., there is also a general positive allometric relationship between amount of acquired resources and body size (Glazier 2005). Here allometric means that the rate of acquired resources increases slower than linearly.

Each juvenile organism has an evolutionary dilemma of how to allocate resources acquired and assimilated in a body mass-dependent manner. Postponement of maturation gives time and resources that can be used for growing and, as a consequence, increase the future reproductive potential. On the other hand, postponed maturation brings a risk that the investment in future reproduction by growing is lost in case death occurs prior to or shortly after maturation. Growth increases fecundity in future times and can be considered a long-term investment in future reproductive potential. In line with this reasoning, the

trade-off between growth and reproduction can also be understood as a form of the trade-off between current and future expected reproduction.

Apart of the fitness consequences of the time and resources dedicated to growth before maturation, the evolution of body size is affected also by the degree to which growth is continued after maturation. In some taxonomic groups of arthropods or entire group of birds, maturation terminates growth (determinate growers), whereas in fish, reptiles and many other indeterminately growing taxonomic groups the adults continue to grow (Heino and Kaitala 1999, Folkvord et al. 2014, Jørgensen et al. 2006, Jørgensen et al. 2008). So, the trade-off between growth and reproduction is not limited to determinate growers. Early life history models predicted that determinate growth is an optimal strategy fitness (Cohen 1971, Ziółko and Kozłowski 1983, Perrin and Sibly 1993). Later, numerous hypotheses have been proposed to explain circumstances at which growing adults can reach higher fitness than determinate growers. There are several hypotheses that explain how the trade-off between growth and reproduction evolving under seasonal environment can turn into indeterminate growth of perennial organisms, i.e. those living for longer than one year. These hypotheses have been reviewed in my work included in this thesis (see **Paper IV**).

There are numerous members of annual and short-lived organisms, as for example many crustaceans, that continue to grow after maturation. Tadpole shrimps that inhabit temporal and permanent ponds of Svalbard are indeterminate growers (Jeppesen et al. 2001). Freshwater ponds at high latitudes, are inhabited also by several species of cladocerans as for example *Daphnia pulex*, *D. pulicaria* or *D. longispina* (Hobæk et al. 1993, Luoto et al. 2016, Alfsnes et al. 2016) that also continue to grow after maturation. Females of daphnids in early instars allocate resources to growth but the structural body size, e.g. exoskeleton, increases in size to a various degree after maturation (Murugan and Sivaramakrishnan 1973, Taylor et al. 1974, Sibly et al. 1985, Taylor and Gabriel 1992, Taylor and Gabriel 1993). Their growth is characterized by high variability of individual growth rates in adult ages that result in complex shapes of growth curves, i.e. individual trajectories of body size changes along with age. Growth curves become complex for example due to growth rate that may drop close to zero in the middle of life. Importantly, cladocerans and many other organisms display complex growth patterns also under fully controlled laboratory environment i.e. the complex growth is a growth strategy rather than an effect

of variation in food availability or infection by pathogens (Murugan and Sivaramakrishnan 1973, Taylor et al. 1974).

The complex growth of perennial organisms, e.g. fish, arise also as an effect of skipped reproduction in some years during which adult growth rate is high (Folkvord et al. 2014, Jørgensen et al. 2006, Jørgensen et al. 2008). Causes of complex growth patterns in short-lived organism as daphnids are not as well understood. A large group of hypotheses that aim at explaining evolution of indeterminate growth in perennials do not apply to annual and short-lived organisms. There are hypotheses that link the degree to which short-lived organisms continue to grow as adults with fluctuations of season length (King and Roughgarden 1982, Taylor and Gabriel 1993, Gurney and Middleton 1996, Wong and Ackerly 2005), correlations between allocation to reproduction, fecundity, and mortality rate (Taylor et al. 1974, Leon 1976, Sibly et al. 1985, Johansson et al. 2018), or other factors (for review of hypotheses of indeterminate growth evolution see **Paper IV**).

Most existing studies of the evolution of indeterminate growth in short-lived organism assume that growth tactics evolve in spatiotemporally homogenous environments. This assumption does not match the biology of cladocerans and tadpole shrimps that display a high degree of indeterminate growth and inhabit complexes of temporary and permanent ponds that show high spatial and temporal variation in water level, isolation, and presence of predators (Ebert 2005). Due to seasonal and year-to-year fluctuations of water levels during melting periods, freshwater ponds of Svalbard are characterized by extreme spatiotemporal variation in hydrological conditions and predation intensity. The natural habitat of a high-latitude cladoceran creates a metapopulation complex of ponds that are interlinked over periods of melting and flooding. Isolated for the remaining time of year, this creates a mixture of predator-free/predator-occupied patches due to lack or presence of a fish predator, e.g. Arctic char (e.g. Jeppesen et al. 2001).

In my PhD work I created for the first time a model of evolution of growth strategies and body size of short-lived organism living in an environment with spatiotemporal variance in mortality risk. The modelled life history resembled life cycle of a cladoceran species inhabiting a metapopulation of ponds differing in presence of predators. The applied methods and results of this study are described below and in **Paper IV**.

Approach and aim of the thesis

Thesis aim

The general aim of the thesis is to link the evolution of body size, growth rate, and timing and synchrony of breeding with temporal constraints. My thesis shows how breeding and growth strategies are adaptations to temporal constraints and evolve under the trade-off between current and future reproduction (Williams 1966). The sources of the time constraint are the following: seasonal changes of the food availability, recruitment probability that depends on timing of birth, and spatiotemporal variability of mortality risk that limits life expectancy. The trade-off between current and expected offspring production takes specific forms of: storing-reproduction trade-off in modelling of breeding synchrony and timing of nesting in capital and income breeding migratory birds (**Papers I-III**), and growth-reproduction trade-off investigated in the work on the evolution of growth strategies and complex growth patterns in short lived crustaceans (**Paper IV**).

The specific aims concern testing of novel hypotheses. I hypothesized that capital and income breeding migratory birds display contrasting responses of their breeding synchrony and fitness components evolving under: seasonal time constraints (**Paper I**), and stochastic fluctuations of daily food gain (**Paper II**). The model predictions regarding the breeding synchrony of migratory birds was enriched with the analysis of the empirical data I gathered during the field observations conducted at a high Arctic ecosystem of Svalbard in years 2015-2020 (**Papers I** and **III**). Moreover, the empirical data were used to test hypotheses regarding timing of migration of common eiders in relation to climatic conditions (**Papers I** and **III)**. I also tested if growth strategies and body size of short-lived organisms evolve differently in stable and spatiotemporally variable life expectancy (**Paper IV**). To achieve the specific aims of the thesis, I constructed theoretical models designed to study evolution of the trade-off between current and expected reproduction (cf. Willimas 1966, Stearns 1992), and temporal constraints (Houston and McNamara 1999, Clark and Mangel 2000). The applied theoretical tools allowed for finding life history strategies that maximize fitness.

Research approach – modelling

Theoretical modelling is the main general approach used in my thesis to investigate the evolution of life history traits and test novel hypotheses. Theoretical investigation has a long history and fundamental role in the scientific investigation of evolution of biological traits. It is hard to imagine modern evolutionary biology without theoretical contributions at every stage of the discipline development. Classic models provoked questions and purified the intuition of scientists over the past century. Several simple theoretical models turned into extensive research avenues that arose as a consequence of the analysis of these theoretical contributions to the evolutionary biology. For example, one of the earliest models in evolutionary biology, the Wright-Fisher model, stimulated questions about fitness and the role of natural selection in maintaining genetic and biological diversity (Charlesworth and Charlesworth 2010). It also initiated the discussion about the quantitative role of genetic drift in evolution. The subsequent developments of the model by Wright and Fisher made scientists aware of the role of age structure, demography, and spatial structure in evolution of natural populations (Charlesworth 1994). Without development of demography in life history evolution we would not be aware of consequences of the evolution of traits that depend on natural selection forces that are age-specific (Stearns 1992, Roff 2002). Finally, annual routine models introduced by Houston and McNamara (1999), combined with dynamic optimization (Clark and Mangel 2000) and applied to ecological problems, enabled studying of life history adaptations to seasonal environments (McNamara and Houston 2008).

The modelling approach is very similar to an experimental scientific approach. Before implementing or creating a model, a scientist must know what is the ultimate aim for using theoretical tools in performed research. Similarly, as life history trade-offs and constraints outline the arena for evolution of life history traits, the discipline and planning define if the model will be a useful tool in testing a given research hypothesis. Complex models with numerous feedbacks incorporated and multitude mechanistic relationships can decrease the ability of understanding key mechanisms for obtained results. On the other hand, very simple models often fail to grasp the diversity of strategies, physiology, or biological circumstances that are relevant in natural conditions. The approach adopted in this thesis was to keep a rather low complexity of the models which facilitated

understanding of the mechanistic basis of results. However, the created models at the same time represented well biological circumstances, physiological constraints, and life history trade-offs of the modelled groups of organisms.

Research approach – empirical observations

A significant part of the workload during my PhD was dedicated to gathering empirical data on arrival dates and nesting onset of the migratory sea duck, the common eider, breeding in the Arctic. The empirical observations of nesting timing of females in the breeding colony of common eiders in Longyearbyen (Svalbard) were used to test the predictions of the models of breeding synchrony and timing of capital breeder and migratory birds (**Paper I**). Data of monitoring of arrival dates were used to perform further analysis of the degree of breeding synchrony and timing of spring migration dependence on climatic conditions (**Paper III**).

Methods

Theoretical models

Our knowledge about the diversity of body size, growth rates, modes of reproduction, or lifespan would be limited without application of models that link temporal constraints with life history trade-offs. In particular, the theoretical approach of investigation of the evolution of life history traits allows for manipulation of features by living organisms that can be studied only under large-scale and long-lasting empirical studies. By using models in this thesis, I was able to investigate synchrony of breeding under seasonal time constraints and fluctuating food gain in combination with investigation of important components of fitness such as clutch size or recruitment probability (**Papers I** and **II**). With models I was also able to investigate effects of natural selection acting over thousands of generations and on a large spatial scale of whole metapopulation (**Paper IV**). I have applied two numerical techniques of theoretical modelling: individual based evolutionary simulations and optimization models with dynamic programming in order to find life history strategies that maximize fitness. Below, I shortly describe these theoretical methods used in the modelling part of my work. A detailed description of methods used can be found in papers attached to the thesis (**Papers I, II** and **IV**).

Dynamic optimization and forward simulations

Life history theory shows that phenology of biological events in seasonally changing environments result from optimal timing of actions scheduled in order to maximize fitness (Houston and McNamara 1999). Due to the connection of phenology of actions with fitness the role of phenological responses of organisms is appreciated in ecology and evolutionary biology (Forrest and Miller-Rushing 2010). The resulting phenology of activities takes the form of routines that are performed by organisms within years and over the life. These so-called annual routines represent the optimal order of actions and allocation of resources to competing needs that maximize fitness, i.e. the number of descendants left far in the future (Houston and McNamara 1999, McNamara and Houston 2008).

The annual routine approach helps to investigate the role of seasonal time constraints in evolution of migration and timing of breeding (e.g. Barta et al. 2008,

Jørgensen et al 2006, Jørgensen and Fiksen 2006). However, because of their complex structure full annual routine models can be difficult to analyse. In my research I used a simplified version of an annual routine model in which optimal breeding strategy is calculated over a pre-breeding and breeding period. Chances of overwintering by adults in my model are assumed to be random and independent of the adopted breeding strategy whereas chances of juvenile overwintering depend of the timing of hatching. Optimal life history strategy in my model is calculated with the numerical optimization method of dynamic programming. The dynamic programing method was used to find a state dependent life history strategy that maximizes fitness by running optimization backwards in time (see Clark and Mangel 2000). State-dependence of the life history strategy modelled in my work means that a female bird initiates and terminates egg laying depending on the level of carried reserves (**Paper I**). In order to investigate breeding synchrony of migratory birds, clutch size, and recruitment probability the optimal strategy was calculated with dynamic programing as the first step. Next, I run individual based forward simulations of a population of females that follow the optimal strategy. By following individual life histories, I obtained information about breeding synchrony, clutch size produced by females, and recruitment probability of offspring (**Paper I**). The modified version of the framework described above that combined dynamic optimization with individual based forward simulations (**Paper I**) was also used to investigate the effect of stochastic fluctuations of food available on breeding synchrony (**Paper II**). In this model I assumed that the daily food gain is given by the probability distribution and birds optimize their breeding strategy taking into account the stochastic outcome of their foraging.

Simulation model

In order to obtain growth strategies in an environment with spatiotemporal variation of mortality rate, I created a simulation model of evolution (for details of the model description see **Paper IV**). In my model, I followed an individual based approach (individual based models, agent-based models) (Uchmański and Grimm 1996), i.e. my model concerned individual females and actions taken by each female during its life. I simulated subsequent generations of a population of females each carrying a genotypic value that sets the strategy on when to mature and about the degree to which to grow after maturation. The growth strategy, encoded in a form of vector of numbers, defined

phenotype of the individual and evolved due to mutations that occur in a random manner during reproduction. The most important feature of the model was the growth of female body size that determined the rate of reproduction. As females that were able to produce the greatest number of offspring over their life, had also highest chances that their offspring recruit to the next generation. Each female survived according to a survival probability characteristic for the site the female occupied. Spatial variation in mortality risk was modelled as the probability distribution of sites differing in mortality risk. The mortality risk in the environment fluctuated temporally year-to-year as the mortality risk of each site was randomly chosen. The individual-based simulation model allowed to find strategies of growth that maximize the number of produced offspring under spatiotemporally varying mortality risk.

Analysis of empirical data

The material for empirical data analysis was collected in Svalbard in years 2015-2020 from the shore of Adventjord and in nesting colony nearby Longyearbyen – the largest settlement in Svalbard archipelago (Norway, 78°-79°N, 11°-16°W). I performed counts of arriving common eiders during pre-breeding seasons between late March until early June along ca. 9 km of the coastline. The counts were performed with a high temporal resolution, i.e. with interval of 1-2 days. I also performed daily counts of common eiders in the breeding colony in Longyearbyen. The eiders in the colony were counted in years 2016-2019 form 1st May until end of July. The data of spring arrival and number of females in the colony were used for analysis of the timing of migration, breeding onset and breeding synchrony (**Paper I** and **III**). Due to relatively low number of studied years, the effect of climatic drivers on the eiders breeding phenology was tested one by one, to find potential correlations with climatic variables.

Summary of papers:
key findings and conclusions

Breeding synchrony of capital and income breeding migratory birds

In the **Paper I** we investigated the evolution of optimal timing of breeding to show how breeding synchrony, clutch size, and recruitment success co-vary systematically depending on whether the breeders use capital or income breeding strategy. There are two key forces responsible for the obtained results: (1) the trade-off between current and future recruit production that appears due to the evolutionary choice to breed or to store reserves for future reproduction, and, (2) the temporal constraint caused by restricted length of the breeding season. We showed for the first time that capital and income breeders display contrasting responses of breeding synchrony and clutch size to changes in timing of spring arrival. Capital breeders that start nesting early in years of early spring onset, breed in a less synchronous manner, produce smaller clutches, but each of their offspring has higher recruitment probability. Under early springs, income breeders produce larger clutches and do not change the degree of breeding synchrony. The prediction of less synchronous breeding of capital breeders in years with early nesting onset was confirmed by analysis of empirical data of common eider breeding synchrony in the Svalbard colony.

To conclude, the work showed for the first time that storing of reserves prior to breeding and using it later for reproduction introduces variation in nesting synchrony of migratory birds that adopt capital as opposed to income breeding. The model revealed that shifting onset of breeding periods to earlier dates by birds, often observed as a consequence of climate warming, is expected to introduce intraspecific variability in responses of clutch size; increasing clutch size of income breeders but decrease in clutch size of capital breeders along with warming. Our work provides important insights in changes of recruitment dynamics of migratory birds due to climate change (for details see **Paper I**).

Breeding synchrony of capital and income breeders under fluctuating food levels

Migratory birds that are capital breeders are exposed to an evolutionary choice after arriving to breeding grounds: whether to store reserves or start reproduction. This trade-

off is simplified in the case of income breeders, who do not store extensive reserves for reproduction and in perfectly predictable environment start nesting immediately after conditions allow (**Paper I**). In the **Paper II**, the assumption about constant resource acquisition was relaxed to check the vulnerability of the conclusions derived in the model with deterministic food gain (**Paper I**).

The conclusions about breeding synchrony of capital breeders and clutch size persisted after introducing stochastically fluctuating daily resource acquisition i.e.: the earlier the spring onset the more capital breeders decrease the degree of breeding synchrony and clutch size (**Paper I** and **II**). The effect of fluctuating food gain turned into reduced fitness of income breeders who, no matter the spring onset, produced on average smaller number of recruits than under deterministic daily food gain. However, for scenarios with early spring onset, capital breeders exposed to fluctuating food gain can produce on average more recruits per female than in scenarios with deterministic food gain (**Paper II**). That is because under intense stochastic fluctuations of food gain, unlucky individuals that often experience a low food gain are still able to produce a clutch due to their ability of buffering fluctuations with reserves. The lucky individuals that experienced high food gain frequently are capable of producing much larger clutches than under deterministic environments.

As a conclusion, the **Paper II** showed that under earlier spring onset and fluctuating food gain, capital breeding migratory birds can attain higher production of recruits and higher fitness than under deterministic environments. This result supports a common belief that capital breeding is an adaptation to stochastic fluctuations of the environment. However, a classic view that capital breeding helps to survive harsh periods during a year is significantly extended by our work, showing that under certain conditions capital breeding helps to make use of stochastic fluctuations and on average attain higher fitness per female than under deterministic environments.

Empirical data on breeding synchrony, timing of nesting and migration

The analysis of empirical data was directed to detect environmental correlates of the phenological measures of timing of migration, timing of breeding and degree of breeding synchrony (**Paper III**). I collected the data on phenology of nesting over 4 years, and for phenology of nesting over 6 consecutive years. The temporal scale of the gathered empirical data was too short for regular time-series analysis. Due to relatively low number of studied

years the effect of climatic drivers on breeding phenology was tested one by one, to find potential correlations with climatic variables. Detecting statistically significant drivers for the observed phenology was challenging and possible only in case of strong statistical associations between gathered data and extracted climatic variables. Hence, the analyses presented in **Paper III** provide rather an opening and exploratory inference, than a comprehensive empirical test of the predictions of the models presented in this thesis (**Paper I** and **II**). Though, the analyses presented in **Paper III** showed that migration timing of the studied population of common eiders, depends on the Arctic Oscillation Index. The analyses also suggest that timing of snow melt correlates with the timing of nesting onset by common eider females (**Paper III**).

Growth-reproduction trade-off under spatiotemporal variation of mortality risk

There are no studies that investigate the evolution of growth strategies under spatiotemporal variation in mortality risk. In order to model the trade-off between growth and reproduction in an environment under spatial variation of mortality risk we simulated individuals that as propagules can reach safe or risky sites in the environment. Because females in our model do not perceive cues regarding mortality risk they evolved a growth-reproduction strategy that bet-hedge offspring production in safe and risky sites. In a heterogenous environment in which risky sites are relatively frequent and females in safe sites do not become the prevailing source of recruits, the growth strategy that maximizes fitness includes growth in the adult phase. Under certain conditions, growth curves can become multi-phasic, with growth rate that slows down or even drops to zero during adult life.

In conclusion, our work showed for the first time that spatial heterogeneity and evolution of growth strategies in a metapopulation with year-to-year changes of mortality risk can select for indeterminate growth (i.e. growth continued in adults). As a result, evolution of growth strategies in a metapopulation context may lead to complex shape of individual trajectories of growth, in particular in organisms that moult (change exoskeleton) regularly during adult life.

General discussion and future perspectives

Breeding synchrony of income and capital breeding migratory birds

Life-history evolution theory assumes that adaptations to seasonality arise because individuals maximize fitness expressed as the number of offspring left far in the future (Houston and McNamara 1999). Individuals outcompete conspecifics that follow suboptimal phenological strategies through adaptive responses to the environmental constraints and fluctuations (Iwasa and Levin 1995). In the main part of my research I show that strong seasonal time constraints and fluctuations of food availability cause differences in responses of breeding synchrony, clutch size and recruitment of income and capital breeding birds (**Paper I** and **II**). That is because capital and income breeders optimize the trade-off between current and future reproduction in a different manner. However, my work does not consider fluctuations in seasonal effects that occur on a year-to-year basis. An important future direction for developing the theory on breeding synchrony of migratory birds should aim at including the year-to-year fluctuations in breeding season length and spring onset.

The simplifying assumption in my work about relatively constant climatic conditions between years cause fitness of migratory birds to be optimized without taking account of the risk of facing unfavorable conditions in harsh years. On the one hand, early arrival to breeding grounds provides high evolutionary payoffs such as longer breeding season or favorable territory. On the other hand, the advantage of early arrival trades-off with high risk of uncertain conditions faced under year-to-year fluctuations of climatic conditions for example due to late spring (Iwasa and Levin 1995) or mismatch with seasonal food source (Both and Visser 2001, van der Jeugd et al. 2009). In an environment with year-to-year fluctuations adaptive response can be plastic (McNamara and Houston 2008, Iwasa and Levin 1995). This plasticity has evolved as a response to the year-to-year fluctuations in local conditions. It is necessary to consider if normal year to year fluctuations in season length and spring onset are large enough to select for plastic phenological responses that can easily cope with changes in seasonality driven by climate change. That is why it is important to include the degree of stochastic variation between years in timing of climatic

events when considering phenological life history responses (Forchhammer et al. 1998, Forchhammer and Post 2000).

Responses of migratory birds to climatic change

Many birds live in habitats in which environmental factors, such as temperature and food availability, change over the year according to a seasonal cycle. In recent decades these seasonal cycles across the Earth has been disturbed due climatic changes. Shifts in phenological patterns of migratory birds were among the first documented signs of the impact changing climate exerted on biological life (Forchhammer et al. 1998; Crick and Sparks 1999; Dunn and Winkler 1999). The climate-driven changes in onset of conditions favorable for breeding, due to increased temperature or advanced snow melt, cause earlier migration and nesting as shown for diverse migratory bird species (Halupka and Halupka 2017, Høye et al. 2007, Drake and Martin 2018). Changes in timing of migration and breeding, driven by climatic change, can cause a cascade of diverse effects as for instance mismatches of bird phenology with seasonal food abundance, shifts in sex-specific migration patterns, altered host-parasite, or predator-prey interactions (Møller et al. 2010). This climatic change can also bring a more pronounced random variation of food availability.

One of the most important conclusions from my thesis, presented in detail in **Paper I** and **II**, is that income and capital breeding birds are expected to respond to climate induced spring advancement in a contrasting manner. Capital breeders are less synchronous in their breeding, produce smaller clutches, and attain higher chances of offspring recruitment in years with early arriving spring. They also attain higher fitness in years in which spring arrive early and food gain display pronounced random stochastic fluctuations. Income breeders do not change their nesting synchrony but produce larger clutches in years with early spring onset. Fluctuations of food gain always reduce fitness of income breeders. These conclusions have important implications for predicting the response of migratory birds to climatic change. Migratory birds differ with respect to the contribution of reserves to their reproduction, with pure capital and income breeding, modelled in **Paper I** and **II**, being the endpoints of the continuum observed in natural conditions. The degree to which a migratory bird species uses reserves in reproduction should be taken into account while

forecasting the impact of spring advancement on its breeding synchrony and population dynamics.

Effects of a warming climate on phenology are more pronounced at higher latitude: over the recent century the polar regions are characterized by the greatest spring advancement and rate of phenological change of diverse organisms (Høye et al. 2007, Post et al. 2018). Thus, more discussion is needed about the impact exerted by phenological shifts in breeding of migratory birds living at high latitudes, on their life history responses and trends in population number. The main biological consequence of warming at high latitudes is an advanced spring and longer vegetative season due to earlier snowmelt (Høye et al. 2007). A majority of migratory birds at high latitudes require snow-free ground or cavity entrance to reproduce, such that earlier snow melt may move the time of first possible breeding to earlier dates and extend the time window that can be used for breeding. It has been shown for birds breeding in temperate regions that more time given to offspring increases reproductive success as young birds must reach ability to fly early enough to migrate and successfully recruit (Verhulst and Nilsson 2008). Reproduction of birds at high latitudes is considered to be even more constrained by the length of breeding season than in temperate regions, as very short summers in the Arctic challenge offspring to develop and parents to prepare for autumn migration (e.g. Waltho and Coulson 2015). The analyses of empirical data presented in **Paper III** indicate that timing of snow melt is indeed an important correlate of the timing of nesting in high latitude Svalbard population of common eider investigated in my thesis.

In migratory birds the timing of spring migration is often the crucial for reproductive success (Both and Visser 2001, Ross et al. 2018). Taking a proper decision by a migratory bird on when to migrate and arrive to breeding grounds can be elusive if local climatic cues at wintering grounds or stopovers, that triggers spring migration, do not correlate well with altered climate at breeding grounds (e.g. Conklin et al. 2010, Senner et al. 2012). The empirical data collected in this project allowed to show that timing of migration of common eiders correlates with climatic conditions of Arctic Oscillation Index (**Paper III**). The presented analyses facilitate understanding of climatic context of migration of common eiders and help to predict a response of their spring migration to changing climate.

Modelling of common eider life histories in the context of emerging conservation issues

Costal marine ecosystems in several regions of the world face year-to-year episodic events of mass juvenile mortality and decreased recruitment of top marine predators (Sutherland et al. 2018, Gilbert 2018). These mass mortality episodes are associated with the deficiency of thiamine (vitamin B1) in juveniles (Balk et al. 2016). Thiamine is well known micronutrient essential for mitochondria functioning (Depeint et al. 2006) and nerve signaling in animals (Bâ 2008). The forecasted population decline of top marine predators due to deficiency of the thiamine deficiency has been identified as an emerging and one of the most important conservation issues of costal marine ecosystems (Sutherland et al. 2018, Gilbert 2018).

In recent years, there is a growing evidence that thiamine deficiency can cause drastic in magnitude impact on populations of top predators feeding almost exclusively on benthic organisms. A high juvenile mortality of ducklings, caused by thiamine deficiency, has been observed in common eiders - a top benthic predator of the costal marine ecosystems of the Northern Hemisphere (Balk et al. 2009, Mörner et al 2017). Recently observed massive deaths of sea birds in southern Sweden coast of the Baltic Sea accompanied with high mortality of common eider ducklings are also associated with thiamine deficiency-like symptoms (Svedäng et al. 2018). The thiamine deficiency syndrome occurring in common eiders deserves special attention due to two reasons. First, it concerns populations of an important top benthic predator of marine ecosystem of the Northern Hemisphere. Second, it shows that current approach focused on top fish predators and pelagic food webs is possibly too narrow to understand and remedy the disruption of marine ecosystems caused by low thiamine levels.

The models presented in **Papers I** and **II** provide an excellent material for development of a theoretical study that links levels of consumed thiamine and lifetime production of viable offspring by common eiders. An annual routine model of common eiders life history, with included elements of micronutrient consumption, would allow to predict the relationship between lifetime recruits production and levels or stochastic variation of the thiamine intake. The results presented in **Papers I** and **II** can serve as a null model for comparisons with the mentioned perspective study focused on limitations

of reproductive success by micronutrient consumption. The development of the presented theoretical framework (cf. **Papers I** and **II**) into model of the common eider reproductive success constrained by micronutrient availability, can help solving the big question in marine ecology about drivers of mass mortality of top predators caused by the thiamine deficiency.

Monitoring of migration and breeding in a population of common eiders in Svalbard

The empirical data on migration and breeding phenology of common eiders analysed in **Paper III** were gathered over years 2015-2020 in the vicinity of Longyearbyen. Low number of studied years considerably decreased the statistical power of the used analyses. However, with a limited range of studied seasons, I was able to document the Arctic Oscillation as the primary climatic force that influence the timing of migration of the studied population of common eiders. Monitoring of the common eider population continued in the future would increase the power of used statistical tests and provide a material for comprehensive analysis of impact of the climatic factors on phenology of migration and breeding of the common eiders.

Growth-reproduction trade-off under spatiotemporal variability in mortality risk

The model of the evolution of body size presented in **Paper IV** assumes spatiotemporal variation in mortality risk. The food availability in this model was assumed constant across sites in the metapopulation. As a future direction, I would like to add a spatiotemporal variation in resource gain, as in natural environments a mortality risk is often correlated with food availability. That is because feeding often means an increased exposure to predation risk. The concept of risky foraging has been recognized as an important factor in the evolution of body size (e.g. Abrams and Rowe 1996). However, the existing studies ignore the fact that most species in natural environments evolve as metapopulations, with sites within the metapopulation sometimes differing considerably with respect to food availability and predation risk. Adding spatial variation in gaining resources to the model presented in **Paper IV** is a promising future direction for this model development.

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

RESEARCH ARTICLE

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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

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 $1-\alpha_2$ 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 ($1-S_R$) 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 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).
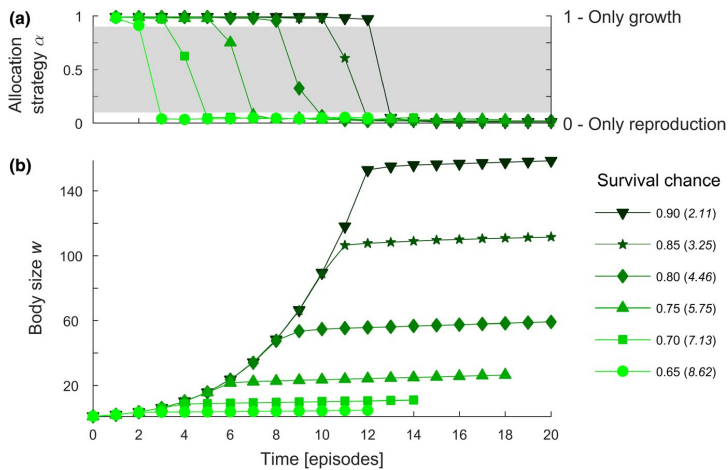
FIGURE 1 Allocation to growth and reproduction in homogenous environments. (a) In a homogeneous environment, modelled organisms switch the allocation of resources from growth to reproduction in less than three episodes of mixed allocation out of 20-time episodes per generation. Maturation occurs later 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 alloca-tion, 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 period-ically 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 mid-dle 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 environ-ments 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 het-erogeneous environment, with respect to mortality risk, mixed allo-cation 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 in-sects (Tammaru, Javois, & Larsson, 2005).

Heterogeneous environments, with respect to mortality risk, that are stable over time but spatially structured, can select for indeter-minate 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.
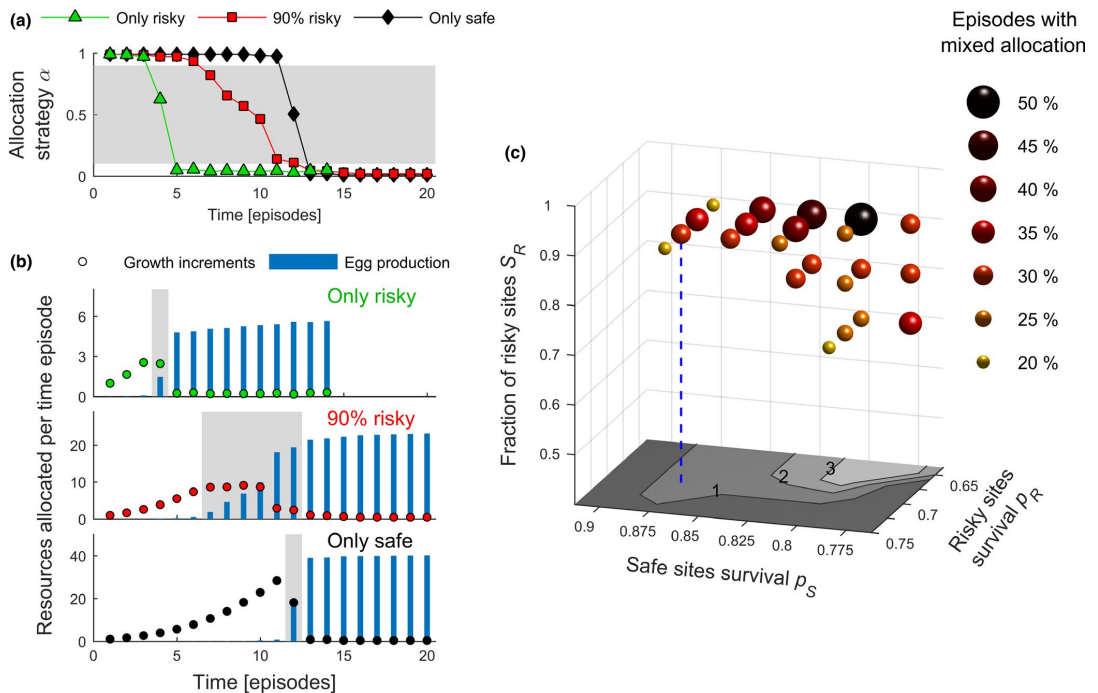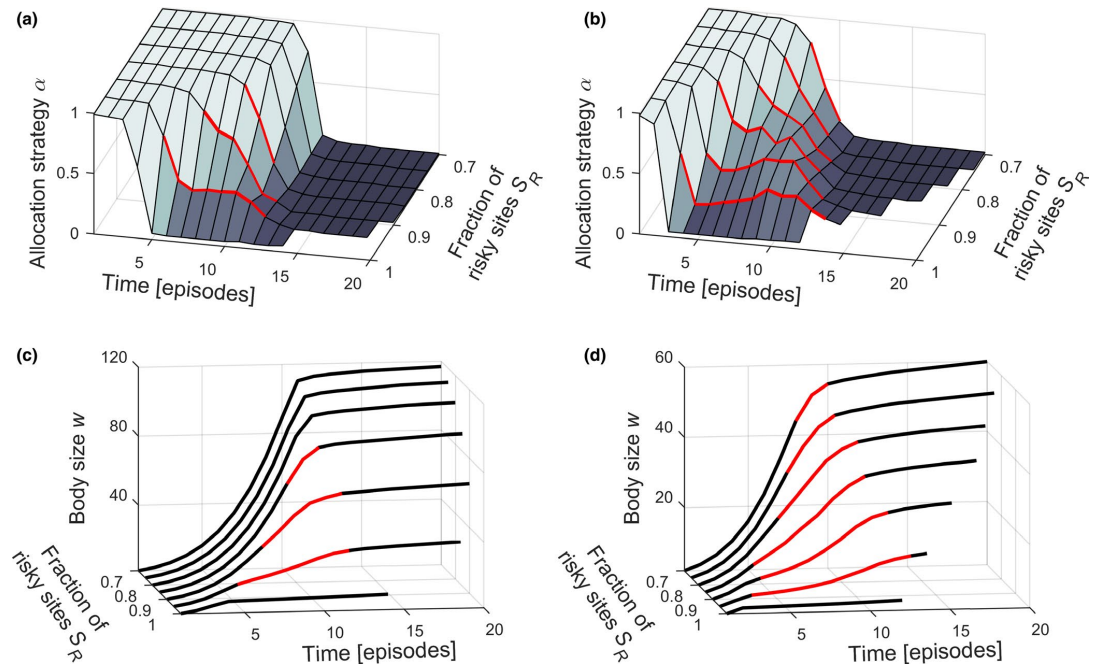
FIGURE 2 Optimal allocation strategies and resulting resource allocation patterns in homogenous and heterogeneous environments. (a) In a heterogeneous environment, the mixed allocation is selected for (red squares), whereas homogenous environments select for a 'bang-bang' switching (green triangles and 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 ($\alpha = 1$) and reproduction ($\alpha = 0$) 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
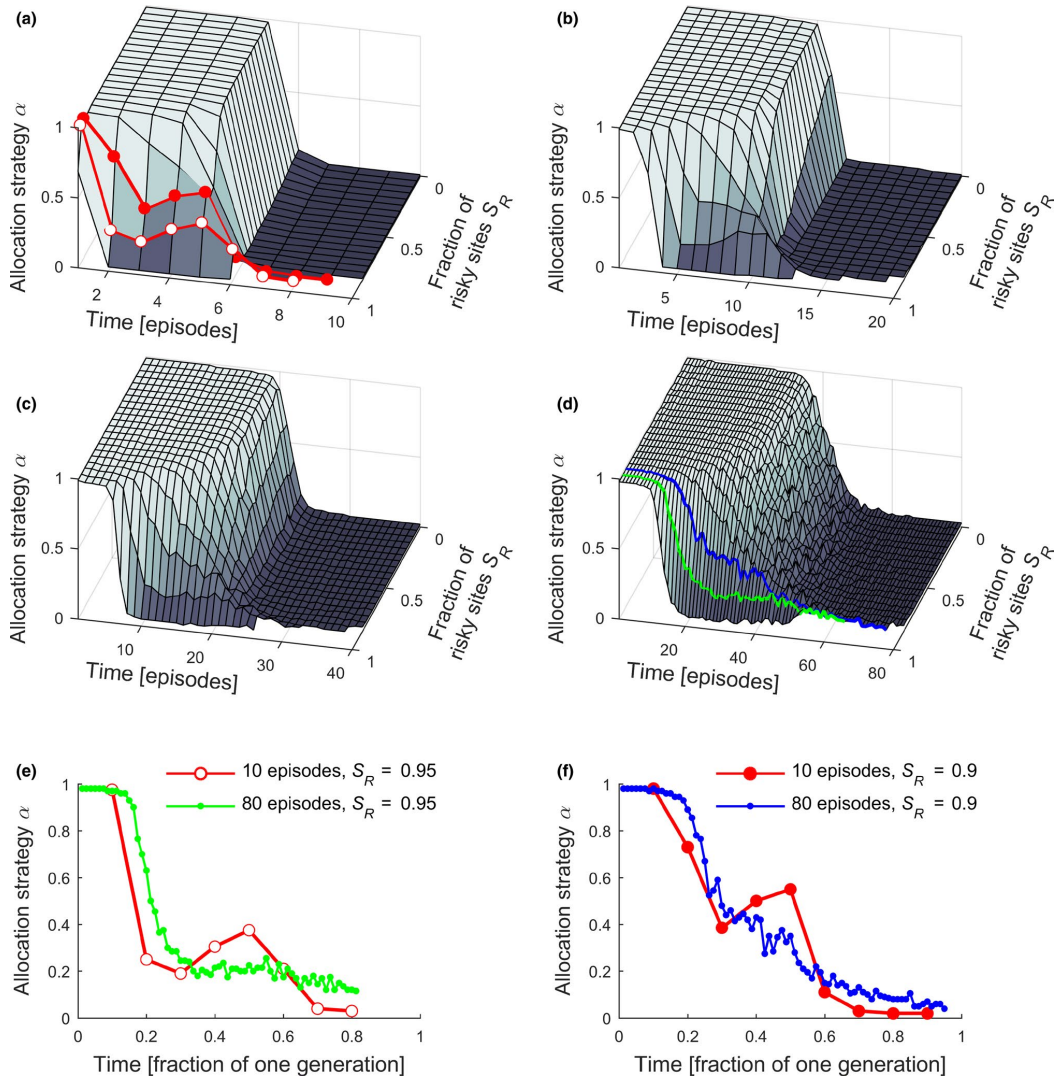
FIGURE 4 The effect of the number of time episodes per generation on the simultaneous allocation to growth and reproduction. (a–f) Resource allocation between growth ($\alpha = 1$) and reproduction ($\alpha = 0$) in relation to time. The colour of the lines in (a) and (d) match those presented in (e) 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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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Ejsmond A, Kozłowski J, Ejsmond MJ. Probing of mortality rate by staying alive: The growth-reproduction trade-off in a spatially heterogeneous environment.

Appendix 1

Sensitivity analysis of the model results to key parameters

Table of contents

1. *Evolution of growth strategies in an environment with several different kinds of habitats*

To increase generality of our findings presented in the main text we run simulations in a setup with several different kinds of habitats in the environment. The habitats differed with respect to the probability of surviving one time episode. At the start of every generation eggs were dispersed among sites in the environment. The probability of getting into each type of habitat was equal to the proportion of this habitat in the environment. All other model features as for instance division of generations into time episodes, processes of growth and reproduction were kept the same as in simulations presented in the main text (see the model description in the main text). The mixed allocation and complex growth curves evolve also when the environment consists of more than two types of sites (see Fig S1).
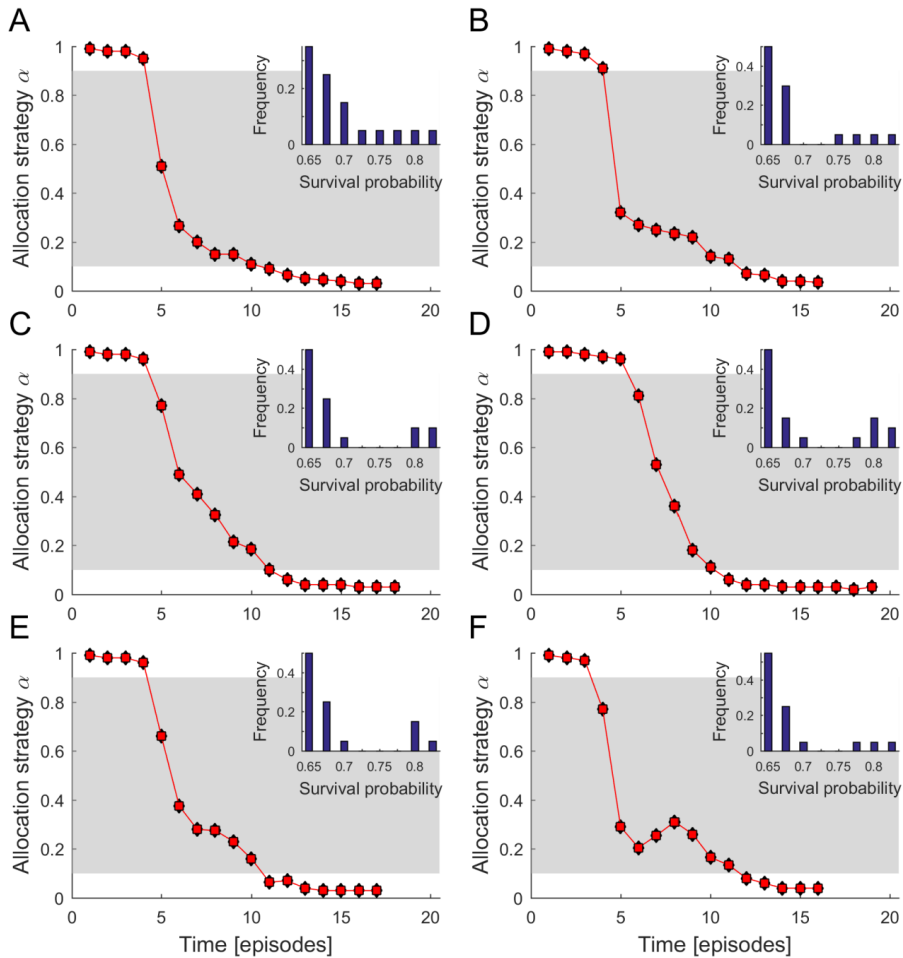
Figure S1. Evolution of mixed allocation to growth and reproduction in an environment with several different kinds of habitats in the environment. Resource allocation between growth ($\alpha=1$) and reproduction ($\alpha=0$) in relation to time presented for four exemplary scenarios simulated over 100 000 generations. The distribution of sites in the environment is illustrated by histograms (inserts). The shaded area depicts simultaneous allocation to growth and reproduction. Allocation strategies and growth curves are presented for time episodes to which organisms survive with a probability greater than 0.005. The presented allocation strategies are median values calculated across 100 simulation replicates.

2. *Sensitivity analysis of the model predictions to extended number of generations*
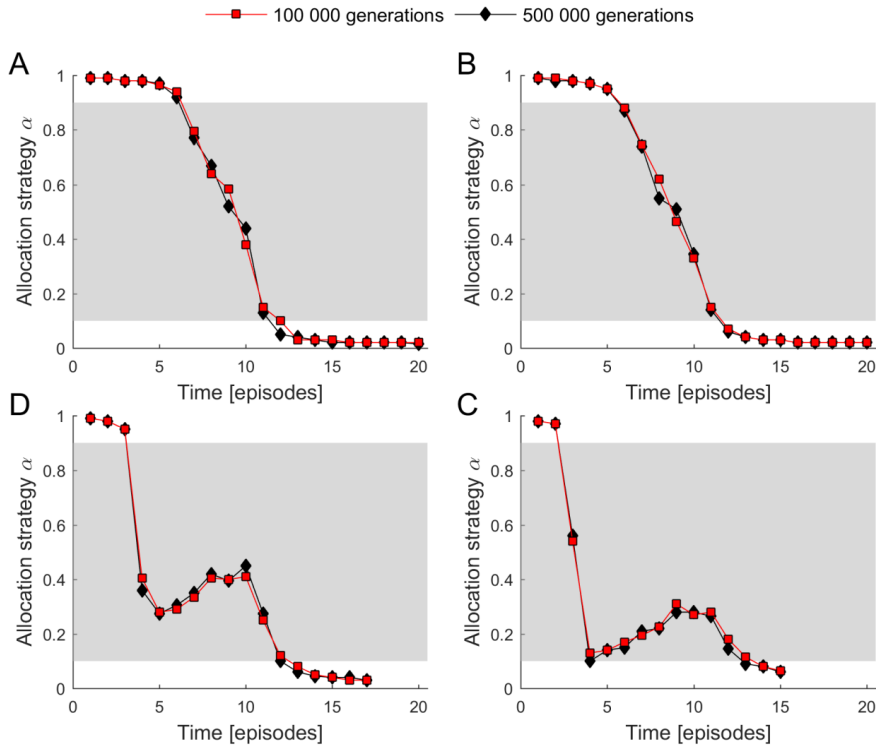

Figure S2. Sensitivity of the model predictions to the changes in simulation time frame. Resource allocation between growth ($\alpha=1$) and reproduction ($\alpha=0$) in relation to time for four exemplary scenarios simulated for 100 000 and 500 000 generations. The shaded area depicts simultaneous allocation to growth and reproduction. Survival probabilities of one time episode risky and safe sites are equal to $p_R=0.7$ and $p_S=0.875$ (A), $p_R=0.675$ and $p_S=0.85$ (B), $p_R=0.65$ and $p_S=0.825$ (C), $p_R=0.65$ and $p_S=0.825$ (D). The scenarios are characterized by the proportion of risky sites $S_R=0.9$ (A), $S_R=0.85$ (B), $S_R=0.95$ (C), $S_R=0.9$ (D). Allocation strategies and growth curves are presented for time episodes to which organisms survive with a probability greater than 0.005. The presented allocation strategies are median values calculated across 100 simulation replicates.

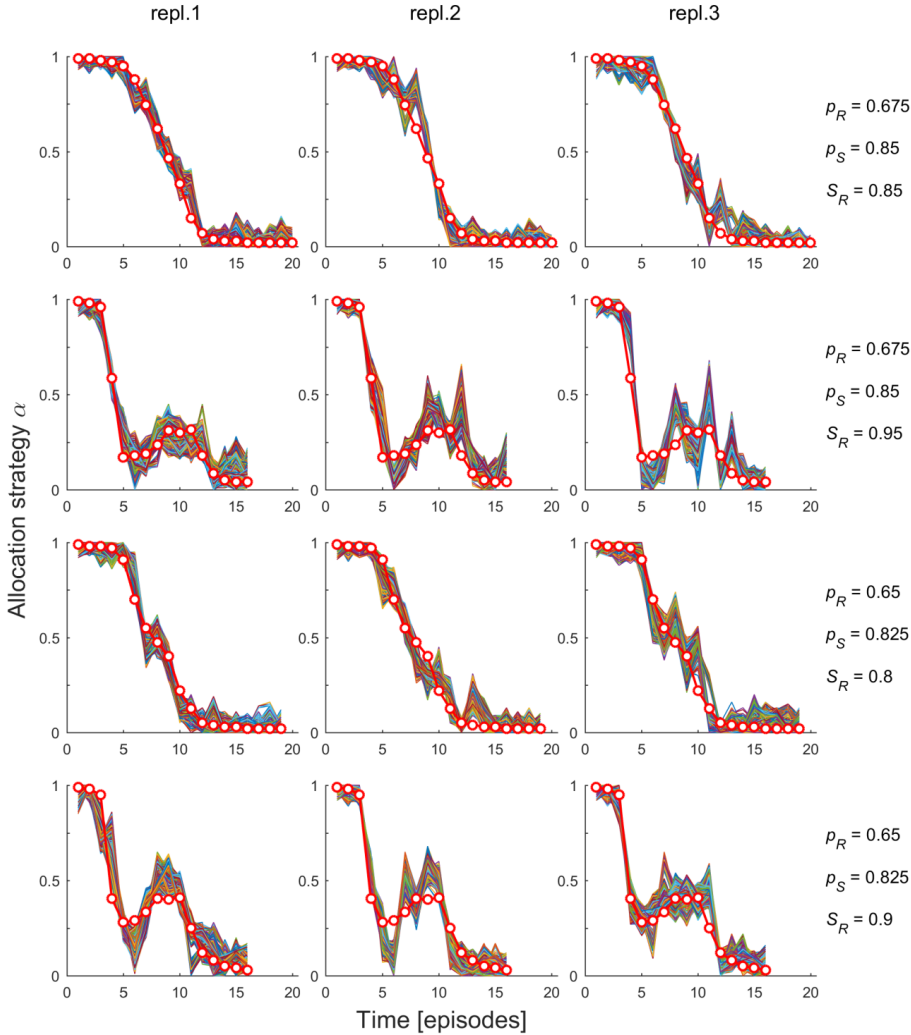### 3. *Individual variation of allocation strategies*

Figure S3. Individual variation in strategies of resource allocation. Resource allocation between growth ($\alpha=1$) and reproduction ($\alpha=0$) in relation to time for four exemplary scenarios (number of exemplary replications give above the panels). The fraction of risky sites in the environment S_R, survival probability in risky p_R and safe sites p_S, given on the right side of the panels. Thick red line with open circles match median values calculated across 100 simulation replicates. Thin lines match all individual strategies of resource allocation in the population for generation 100 000. Allocation strategies are presented for time episodes to which organisms survive with a probability greater than 0.005.

4. *Allocation strategies presented in a gradient of survival chances*
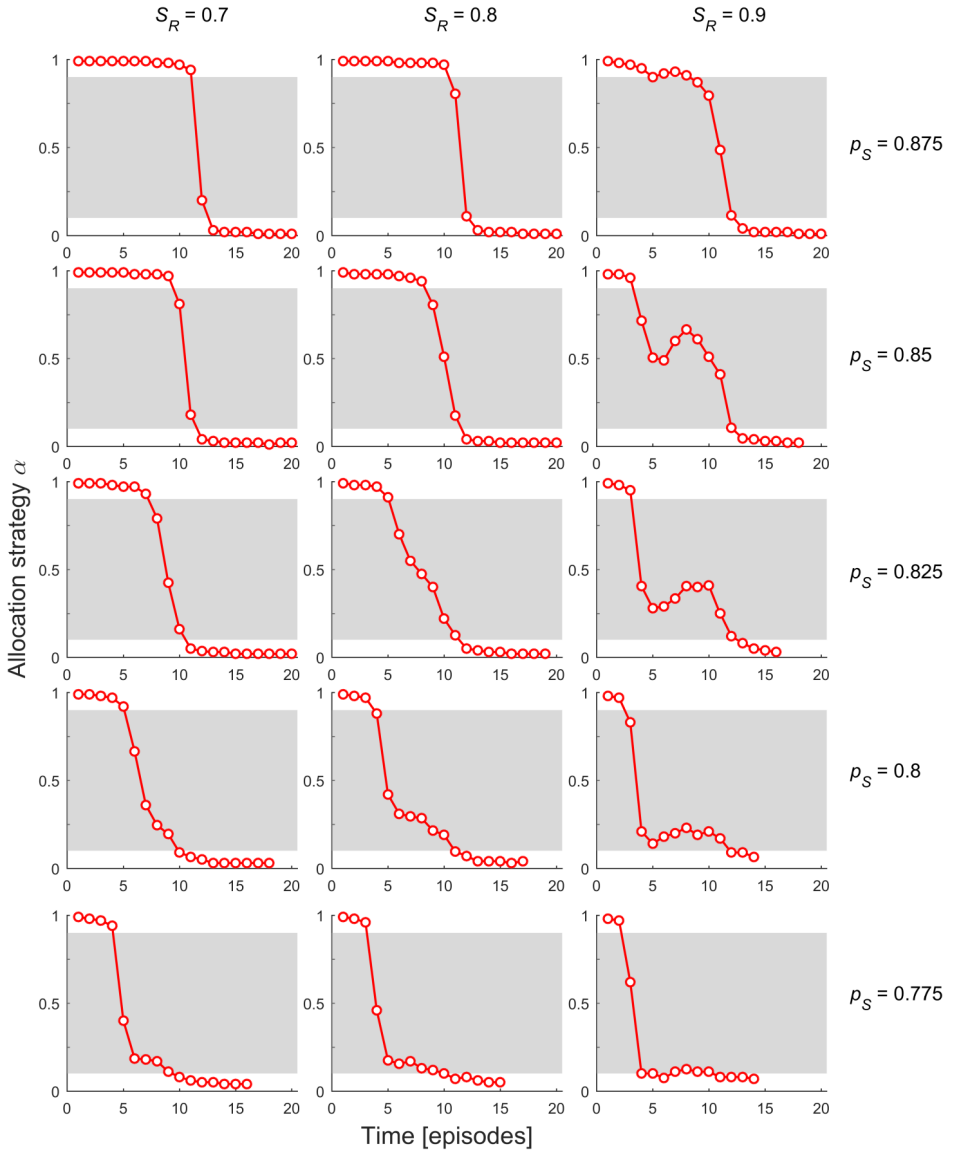

Fig. S4. Allocation strategies in heterogeneous environments differing with respect to risk of death in safe habitats. Resource allocation between growth ($\alpha=1$) and reproduction ($\alpha=0$) in relation to time. Survival probabilities of one time episode in risky sites p_R are are equal to 0.65. Survival probability of one time episode in safe sites p_S and proportion of risky sites in the environment S_R are given at the panels. The presented allocation strategies are median values calculated across 100 simulation replicates. Allocation

strategies are presented for time episodes to which organisms survive with a probability greater than 0.005.
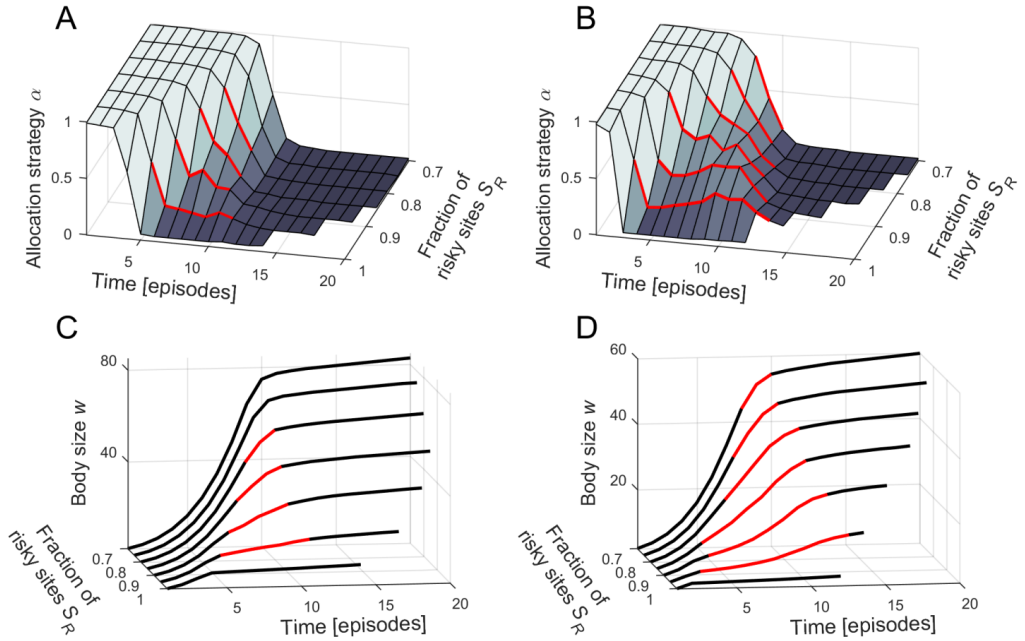

Fig. S5. Allocation strategies and resulting growth curves in heterogeneous environments. (A-B) Resource allocation between growth ($\alpha=1$) and reproduction ($\alpha=0$) in relation to time. (A-C) Red lines illustrate time episodes and resulting growth phases arising due to mixed allocation to growth and reproduction. Survival probabilities of one time episode in risky and safe sites are equal to 0.7 and 0.85 (A, C) or 0.65 and 0.825 (B, D). The presented allocation strategies are median values calculated across 100 simulation replicates. For clarity the figures present optimal allocation strategies in environments with a proportion of risky sites S_R greater than 0.7. Allocation strategies and growth curves are presented for time episodes to which organisms survive with a probability greater than 0.005.

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