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.
Functional Ecology 33: 2327-2337

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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 maturate 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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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.

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Nesting synchrony and clutch size in migratory birds: Capital versus income breeding determines responses to variable spring onset

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Abstract

Synchronous reproduction of birds has often been explained by benefits from nesting together, but this concept fails to explain observed intraspecific variation and climate-mediated changes of breeding synchrony. Here, we present a theoretical model of birds that store resources for reproduction (capital breeders) to show how breeding synchrony, clutch size and offspring recruitment respond to changes in timing of first possible breeding date. Our approach is based on individual fitness maximization when both pre-breeding foraging and offspring development are time-constrained. The model predicts less synchronous breeding, smaller clutch size, and higher chances for offspring recruitment in capital breeding birds that advance their nesting. For contrast, we also show that birds that need to acquire resources during egg laying (income breeders) do not change nesting synchrony but increase clutch size along with earlier breeding. The prediction of stronger nesting synchronization of capital breeders in years with late nesting onset is confirmed by empirical data on breeding synchrony of a high-latitude capital breeding sea duck, the common eider (*Somateria mollissima*). We predict that in warming high-latitude ecosystems, bird species that depend on stored reserves for reproduction are expected to desynchronize their nesting.

Keywords: clutch size, breeding synchrony, timing of breeding, capital breeding, Common eider, dynamic programming, warming

Introduction

The question of why some birds synchronize their breeding within the annual cycle is a long-debated subject in evolutionary ecology (Darling 1938). One type of explanations is focused on benefits achieved from breeding together, e.g. better opportunities for optimal partner choice, more efficient defense, group foraging, and dilution of nest predation risk (Ims 1990a; Ims 1990b; Spottiswoode and Møller 2004). The benefits from breeding at the same time must also 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). An alternative view is that synchronization emerges from adjustment of individual breeding strategies to seasonal time constraints. Comparative analyses of geographical trends in breeding synchrony, using latitude as a proxy for season length, show that nesting is more synchronized the further away from equator (Burr et al. 2016; Spottiswoode and Møller 2004). However, the latitudinal trend explains only part of the variability in reproductive synchrony (Stutchbury and Morton 2001, Burr et al. 2016).

On top of seasonality, a life-history approach is crucial for understanding the phenology of breeding. Juveniles need sufficient time to reach developmental milestones (e.g. fledging) early enough to successfully migrate and recruit (Verhulst and Nilsson 2008), and advancement of breeding by parents is expected to positively affect their fitness. However, in many bird species, the period before breeding serves as important determinant of body reserves that later contribute to reproduction (Chastel et al. 1995). Advancement of nesting thus increases prospects for offspring development and successful recruitment, but will at the same time shorten the time of pre-breeding foraging. This evolutionary dilemma, with its potential effect on breeding synchrony, clutch size, and offspring quality, concerns numerous bird species, and especially those that rely on stored reserves for breeding. This is referred to as "capital breeding" (cf. Drent and Daan 1980; Jönsson 1997), as opposed to "income breeding" in which reproduction is fueled with concurrent resource acquisition. A capital-breeding component has been shown to contribute to reproductive output in a number of species among ducks (eiders, 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).

Both capital and income breeding birds are expected to maximize the expected life-time number of offspring capable of recruiting. While early hatching is ideal from the perspective of each offspring's individual survival (Drent and Daan 1980), it is not necessarily optimal from the mother's perspective who can produce an extra chick if she gathers more reserves prior to breeding. This creates a trade-off between quantity of produced eggs and chance of each offspring's recruitment (Ejsmond et al. 2015). This trade-off constitutes a main challenge both for capital breeders who need to acquire the resources required for reproduction prior to breeding, and for income breeders who must forage during egg-laying in order to produce the full clutch of eggs. Species all along the continuum from income to capital breeders thus optimize timing of seasonal activities in order to maximize the expected number of recruits. Current literature focused on climate-driven changes in nesting phenology and clutch size lacks this diversity of strategies and its consequences for breeding and population dynamics.

Here, we follow a life history approach and develop a theoretical model to find the optimal timing of breeding that maximizes the expected number of successful recruits as proxy for fitness (Jørgensen and Fiksen 2006; Williams 1966). A seasonal time constraint is a key element in our model. We model pre-breeding behavior and breeding strategies in birds that vary in time of arrival to the breeding grounds. Offspring produced late in the season are assumed to have decreased chances of recruitment, so the timing of hatching affects fitness. This creates a life history trade-off between number of eggs produced and probability of offspring recruitment. Crucially, this trade-off and its consequences depend on whether the bird is a capital or an income breeder. Although our model considers pure capital and income breeders, the predictions portray two endpoints of a continuum and comparing them reveals the pros and cons of the two types of reproductive strategies. In our model, breeding synchrony emerges from optimization of timing and clutch size in a seasonal environment and the degree of synchrony results from individual breeding strategies that are conditional on the physiological state of females in the modelled population. Predictions of our model are compared with data on breeding synchrony of a high-latitude capital breeding and migratory sea duck, the common eider (*Somateria mollissima*).

Our modelling approach of comparing income and capital breeding birds allowed us to show that spring advancement is expected to trigger contrasting responses in these groups. The novelty of our paper is that we focus not only on optimal timing, but show how breeding synchrony, clutch size, and recruitment success co-vary systematically depending on whether the breeders use a capital or an income breeding strategy. The emergent breeding dynamics is mediated by the physiological state of individuals, their state-dependent decisions (Houston and McNamara 1999; McNamara and Houston 2008), and whether they can make use of a capital breeding strategy beyond income breeding. Our work elucidates how the breeding strategies adopted by birds are affected by changing spring phenology and have consequences for reproduction at the population level.

Methods

Model overview

The theoretical model focuses on the response of breeding synchrony and clutch size to shifting spring onset. We first describe the model for capital breeders, then explain how the income breeding model differs. Upon arrival at the breeding grounds, capital breeding females first gather required resources by building reserves, then reproduce. Females foraging for longer during the pre-breeding season are able to produce more eggs, but this leaves less time for offspring to develop. In turn, this results in lower per-offspring contribution to fitness. The key decisions are when to start and when to terminate egg laying in order to maximize fitness, where fitness is defined as the number of offspring multiplied with per-offspring recruitment probability (see below). Note that the words "decision" and "strategy" imply no conscious intent or cognitive planning but are used merely to describe physiological and behavioral responses that have evolved through natural selection. The decision of each female depends on the amount of reserves gathered so far and number of eggs already laid. After optimizing the state-dependent timing of nesting, the model simulates a population of females to quantify the distribution of breeding, clutch size, and probability of offspring recruitment. Whereas our work presents the model parameterized in order to resemble breeding biology of sea ducks, we also performed extensive sensitivity analyses to test the generality of our predictions (Supporting Information Appendix S1).

Optimization of capital breeding strategy

As an inspiration for model design of a capital breeder, we consider the breeding behavior of common eider females nesting in a high-latitude seasonal environment. The model spans the time between spring arrival at the breeding grounds and egg hatching. After migration in spring, the common eider females are in a lean condition and are unable to produce eggs without first foraging to build energy reserves (Waltho and Coulson 2015). Hence, in our model, all females have no energy reserves at the day of their spring arrival, i.e. minimal body reserves $S_{\min}=0$, and need to prepare for the upcoming reproduction by foraging prior to egg laying. We refer to this preparation period as the pre-breeding season. The total body mass of the modelled bird at day t consists of a lean body mass M_L plus reserves $S(t)$. Foraging and the corresponding daily gain w in energy reserves is given by $S(t+1)=S(t)+w$, with w parameterized according to Rigou and Guillemette (2010) and Korschgen (1977) (see Table 1 for the value of this and other parameters). Maximal body mass $M_{\max}$, i.e. the sum of lean body mass M_L and maximal reserves $S_{\max}$, was set consistent with observations that mass of reserves in common eider females can reach up to ca. 130% of the lean body mass (Milne 1976).

A female in good condition lays up to six eggs (Erikstad et al. 1993) with a rate of one egg per day (Watson et al. 1993), and we assume this to be the maximum clutch size, $n_{\max}$ (scenarios with $n_{\max}$ other than six are discussed in Supporting Information Appendix S1). After all eggs are laid, a female starts incubating her clutch (Waltho and Coulson 2015). We further assume that all eggs have the same size (Parker and Holm 1990; Waltho and Coulson 2015) and that egg size does not depend on female's body size or condition (Swennen and van der Meer 1992). Breeding females need to incubate eggs for 26 days (Parker and Holm 1990). For simplicity, we assume that the reserves used during incubation equal 50% of the energetic costs needed to produce the eggs (for egg mass and cost of incubation see Table 1). The costs of incubation being independent of clutch size are discussed in Supporting Information Appendix S1.

Egg laying in birds at high latitudes is constrained by access to nesting sites, e.g. due to timing of snowmelt (Chaulk and Mahoney 2012; Waltho and Coulson 2015). The key parameter in our model is the first possible breeding day b_s (Fig. 1A) (day of year). Females in our model arrive prior to the breeding season and can start egg laying at any day t on or after b_s (Fig. 1B). If females postpone egg laying, offspring have less time to develop before the autumn migration. We assume that the probability of offspring recruitment $f(t)$, is maximal at the first possible breeding day b_s of the earliest breeding season (among all investigated scenarios) and decreases linearly to 0 for those who hatch too late to develop to fledging with a physiological condition that allows autumn migration (Fig.1C). The assumption of decreasing probability of recruitment with the timing of hatching represents the reduced probability of successful offspring development along with the delayed post-breeding timing (Drent et al. 2003; Dunn 2004; Morrison et al. 2019).

The fitness measure V is a breeding female's expected number of recruits, i.e. the number of offspring weighed by their recruitment probability. A capital breeder in our model who decides to stop egg laying and start incubating obtains a fitness if breeding V_{incubate} (eq. 1). After incubation the offspring hatches, and the chance of recruitment f declines with time.

1. $V_{\text{incubate}}(t, n) = n\, f(t + i),$

where n is number of eggs laid and cannot exceed available resources divided by egg production costs, $S(t)/(cE)$. Hatching takes place i days after the last egg was laid and defines the offspring recruitment probability. A female who has not yet produced her maximum clutch size may alternatively decide to continue egg laying, which would lead to fitness if laying V_{lay}.

2. $V_{\text{lay}}(S, t, n) = V(S - cE, t + 1, n + 1),\ S \geq cE$

where E is the mass of one egg and c the multiplicative cost of producing and incubating it in units of energy reserves (see Table 1). The female may also continue foraging, which would influence prospects for future fitness due to increasing reserves, according to

3. $V_{\text{forage}}(S, t, n = 0) = V(S + w, t + 1, n = 0)$

where w is the daily increase in reserves and $S+w$ cannot exceed $S_{\max}$. The third argument $n = 0$ indicates that foraging is only available as long as no eggs have yet been laid; capital breeding females that have already initiated breeding ($n \geq 1$) were not allowed to forage ($V_{\text{forage}} = 0$). Reserves are constrained upwards by $S_{\max}$ (see Table 1). The model uses dynamic programming (cf. Clark and Mangel 2000) to fill in the matrix of V from the final day of the season and recursively for each day earlier. It does so by comparing V_{forage}, V_{lay} and V_{incubate} calculated on each day and for each level of energy reserves S and number of eggs laid:

$$4. \quad V(S,t,n) = \max\left[V_{\text{forage}}(S,t,n=0), V_{\text{lay}}(S,t,n)\,, V_{\text{incubate}}(t,n)\right]$$

In this way, the model optimizes the day t^* at which a capital breeding female initiates egg laying and day t^{**} at which female starts incubation, by maximizing V (see equation 3, Fig.1). At t^*, the female switches from foraging to reproduction, which thus determines the amount of reserves at breeding. At t^{**}, the female terminates egg laying, which sets the clutch size as one egg is laid per day. Note that the clutch size is not only determined by condition S because there may be not enough time for females nesting late to utilize all reserves for egg production.

Optimization of income breeding strategy

For income breeders we used the same parameterization regarding egg size, incubation time etc. as for the capital breeders. However, income breeding females were allowed to store reserves up to the level equal to production cost of one egg, i.e. $S_{\max}=cE$. Thus, while capital breeders can lay one egg per day, income breeding females need to set aside time to forage to produce another egg, and continue cycles of foraging and egg-laying until time t^{**}, when the 26-day period of incubation starts. Hence, the decision about starting incubation at t^{**} determines their clutch size. Income breeding females, in contrast to capital breeders, were allowed to forage and increase their reserves S no matter the number of eggs already laid, cf. eq. 3, which is then $V_{\text{forage}}(S,t,n) = V(S+w,t+1,n)$. Similarly to capital breeders, the optimal state-dependent strategy for an income breeder was found using dynamic optimization (see eq. 4).

Simulating populations of breeding females

To obtain distribution of nesting onset and other characteristics of the breeding population, we simulated a population of 10 000 females with normally distributed arrival dates. Behavior of the simulated females followed the state-dependent optimal strategy t^* and t^{**} obtained with backward optimization (equation 4). By following individual females arriving at different days, we obtained trajectories of individual reserve levels $S(t)$, day of breeding onset, and clutch size. We ran optimization and simulations for a range of arrival dates and three different scenarios of possible days of breeding onset b_s (Fig.1).

We contrast scenarios for different pre-breeding season lengths by varying day of first possible breeding onset b_s from an early (b_s=130) via intermediate (b_s=150) to late (b_s=170), and refer to these scenarios as spanning from early to late springs (for other arrival scenarios see Supporting Information Appendix S1). The model assumes normally distributed arrival dates (mean arrival day of year D_a= 90, SD=10 days) consistent with migration patterns for high-latitude populations of the common eider (Hanssen et al. 2016). The scenarios reflect the high seasonal variation observed in natural systems of diverse migratory bird species.

To test the generality of our predictions, we tested our model for a broad range of assumed maximal clutch size, incubation time, costs of egg production, distribution of arrival dates, and other key parameters to cover the biological variation and to explore whether conclusions are valid for other birds (Supporting Information Appendix S1). All calculations were performed with MATLAB (R2015b).

Empirical data: breeding synchrony of common eiders

The theoretical framework allows for predictions regarding changes in the degree of breeding synchrony with shifts in the first possible breeding date. By using gathered data on the degree of breeding synchrony we confronted our theoretical predictions with empirical patterns of breeding synchrony. We analyzed data from two high-latitude breeding colonies of common eider: Rif (Iceland, 65°N, 185-620 nests per year) and Longyearbyen (Svalbard, 78°N, 326-445 nests per year). The Iceland colony was monitored in years 1992-2013; nesting onset was defined as the day when at least one breeding female was observed (with 1 to 10 nests recorded at day of nesting onset during the long-term monitoring period of 20 breeding seasons, for details see Jónsson et al. 2017). In Svalbard, a clearly defined nesting area was counted daily in seasons 2016-2019. For both colonies, the degree of breeding synchrony was measured as the time interval between nesting onset and median nest day.

Results

Timing of nesting

The ability of storing reserves for clutch production allows capital breeding females to benefit from foraging prior to breeding (Fig 1). Among capital breeders, but not income breeders, some individuals therefore postponed breeding beyond the first possible day of nesting (Fig. 2). Initially, we focus on the strategy of capital breeding birds exposed to three scenarios differing in the first possible breeding day b_S (Fig. 2). When spring was early with rapid snowmelt, even an early arriving female was unable to gather sufficient reserves by the first possible day of nesting (Fig. 2A). Capital breeding females therefore postponed reproduction to forage beyond the first possible day of nesting. For intermediate spring onset, females that arrived early have amassed sufficient stores to produce the maximal number of eggs and start nesting as soon as conditions allow (Fig. 2B). Those who arrived late needed to postpone reproduction and foraged for longer to maximize expected number of recruits (Fig. 2B). Finally, when spring was late, the time window between arrival and first possible nesting gave enough time for all females, no matter their arrival date, to gather extensive energy reserves. Hence, all females reproduced as soon as conditions allowed and produced maximal clutch size (Fig. 2C).

Income breeders differed in that they started nesting earlier than the capital breeding strategy, except when spring was late and both capital and income breeders were forced to nest quickly to allow fledging and development prior to the autumn migration (Fig. 2). Although income breeders generally initiated nesting earlier than capital breeders, their chicks hatched later (Fig. 2) because income breeders had to forage for each consecutive egg laid.

Clutch size variability and breeding synchrony

The optimization of individual breeding tactics translates into breeding synchrony, clutch size variation and number of recruits per female recorded at the population level.

Income breeders synchronized nesting no matter the length of the pre-breeding season (Fig. 2A-C) because postponement of breeding by an income breeder brings no benefit in terms of clutch size as they cannot store extensive reserves. Additionally, late breeding leaves less time for clutch production, so when first possible breeding onset bs was late, income breeders had smaller clutch size, lower probability of recruitment, and in turn lower fitness measured by the expected number of recruits per female (Fig. 2A-C and Fig. 3B).

Reproductive synchrony and variation in clutch size are an outcome of the optimization of the trade-off between time dedicated to gathering reserves and offspring development. To facilitate interpretation of the model outcomes, we divided the gradient of the first possible breeding day bs into early, intermediate, and late spring onset, respectively (Fig. 3). When spring was early, capital breeders were not synchronized as there was significant variability in the condition among individuals at day bs (Fig. 2A). The average clutch size of capital breeders was low, but the probability of recruitment of the produced offspring was relatively high, and both these metrics varied among individuals in the population (Fig. 3, early spring onset). Among capital breeders in early springs, production of recruits per female was highest as the production of small clutches was accompanied with a high chance of offspring recruitment (cf. Fig. 2A-C, 3AB). When spring was intermediate, breeding synchrony and average clutch size of capital breeders were higher than when spring was early. Clutch size also showed greatest variability, but recruitment probability was lower compared with the scenarios of early spring onset (Fig. 3). When spring was late, the average number of eggs was high and the variation in clutch size very low among capital breeders (Fig. 3). Late breeding onset allowed most individuals to gather the reserves for maximum clutch size and breed immediately at day bs. The average probability of recruitment in the population was uniform but low (Fig. 3), as females in good condition had little possibility to advance breeding (Fig. 2C). When comparing early versus intermediate spring onset, capital breeders were able to buffer the drop in recruitment probability by increasing the number of produced eggs (Fig. 3AB). Income breeders cannot store reserves during the pre-breeding period and their egg numbers declined in late versus early springs, as opposed to capital breeders where clutch size was larger when spring was late (Fig. 2, 3).

Climate-induced shifts in breeding synchrony

Our model predicts trends in breeding synchrony, clutch size, and offspring recruitment that can be interpreted as responses to climate-mediated changes in the date of first possible breeding onset. Specifically, a shift from cold years with late breeding season towards warm years is expected to cause decreasing degree of synchrony in capital breeders, although income breeders are expected to remain synchronized (Fig. 2, 3). Warming is also expected to cause reduction of average clutch size among capital breeders, but an increase among income breeders (Fig. 2). Importantly, earlier spring onset is expected to increase probability of recruitment and production of recruits for both strategies (Fig. 3B and Fig. S8 in Supporting Information Appendix S1).

With gradually earlier spring onset, our model suggests that breeding biology will change in phases. For a capital breeding migratory bird with synchronous breeding, i.e. one corresponding with late spring onset in Fig. 3, the warming climate allows for earlier breeding and will initially bring no change to breeding synchronization and only little change to average clutch size (Fig. 3 right to center). For both capital and income breeders, the breeding onset is expected to shift to earlier dates with an increase in number of produced recruits (Fig. 3AB). An even earlier access to nesting sites (Fig. 3 from center to left) would cause nesting by capital breeders to be spread over time, with reduced clutch size, while only modest change is expected to occur for breeding onset. In contrast, income breeders would continue to nest earlier and earlier, and with larger, not smaller, clutch size (Fig. 2). The production of recruits by capital breeders is expected to increase only slightly in comparison to the increase in recruitment of income breeders (Fig. 3B). Under very warm conditions, in which breeding is possible almost right after arrival, capital breeders are expected to produce small clutches with high probability of recruitment (Fig. 3, left part) with variation in breeding dates being similar to the variation in arrival dates (cf. Fig. 2A).

Whereas parametrization of our model was inspired by the biology of common eiders, the sensitivity analysis (see Supporting Information Appendix S1) showed that the results described above regarding the response of breeding synchrony, timing of nesting, clutch size, and offspring recruitment to shifting spring onset would hold also in case of other capital breeding birds.

Empirical data

In both monitored colonies of the common eider, the degree of breeding synchrony was higher in years with later nesting onset (Fig. 4), as our model predicted for capital breeders. In the Svalbard colony, the first females started nesting as soon as snow melted, but synchrony varied. In years with late snowmelt, and consequently late breeding onset, the rate of increase in number of breeding females (and thus breeding synchrony) was higher than for early breeding onset (Fig. 4A). In the Iceland colony, the number of days until median nest decreased with the date of nesting onset across a dataset of 20 years (Fig. 4B).

Discussion

We have modelled capital and income breeding birds to show how their optimal breeding phenology differs in response to climatic variation in the onset of conditions that allow nesting. Our work predicted that in years when spring is early, both reproductive strategies would breed earlier and with higher success. In contrast, an earlier spring was characterized by diverging predictions for clutch size, which was lower for capital breeders but higher for income breeders, and nesting, which would be less synchronous among capital breeders but remain highly synchronized among income breeders. The reproductive adaptations of storing and preparing for egg production thus have contrasting consequences for these breeding characteristics. We show that the degree to which birds use storage gathered prior to breeding is crucial for predicting and interpreting demographic and ecological consequences. This is particularly relevant in light of the widespread changes in breeding phenology as spring has appeared progressively earlier over the last couple of decades; a trend that is projected to continue with climate change.

While we modelled capital and income breeding as two distinct reproductive strategies, it should be borne in mind that these are endpoints of a continuum where many species represent a strategy in between. There is also an underlying size gradient: small passerines cannot store significant reserves because that would entail high costs in terms of constrained flight ability and increased mortality risk (Kullberg et al. 2005). Birds weighing only a few grams are therefore commonly income breeders, defined as those species unable to produce a full clutch of eggs without feeding. In light of our model predictions, climate-induced changes in breeding ecology reported for small passerines cannot be extrapolated to larger species unless the role of reserves in reproduction is taken into account.

We first discuss optimal timing of nesting, which is the most straightforward prediction from our work. Early access to nesting sites leaves a longer post-breeding period, which is good for offspring survival and recruitment (Fig. 3AB). While income breeding requires little preparation and enables nesting onset soon after arrival, capital breeding necessitates a substantial pre-breeding foraging period and, in our model, approaches an asymptote for how early nesting can commence (Fig. 3B). Although observations from the common eider colony in Svalbard cover only four years (Fig. 4A), it was observed that the first females started egg-laying as soon as the nest site was snow free. In general, the warming climate has shifted reproduction in many bird species towards earlier nesting dates, which consequently has relaxed the constraints a short post-breeding time may impose on offspring development (Drent et al. 2003; Dunn 2004; Morrison et al. 2019). Such climate-driven changes have caused earlier nesting for many passerines and also other birds (Halupka and Halupka 2017), including in the high Arctic (Høye et al. 2007). The timing of breeding in some species is suggested to be tightly linked to peak of food availability. For example, offspring recruitment depends on a match with peak of insect abundance in many passerine birds that have advanced breeding in response to warming (Daan et al. 1989), an effect that is not included in our models. A similar trophic mismatch between offspring production and availability of high-quality food has been observed in capital-breeding snow geese (*Chen caerulescens*), where it resulted in reduced recruitment (Aubry et al. 2013; Dickey et al. 2008). However, in other species of capital-breeding geese, a match between the availability of high quality of food and timing of nesting was a poor determinant of offspring recruitment, as nesting in some populations took place much earlier than can be expected from timing adjusted to high-quality food peak (van der Jeugd et al. 2009). This points to a pivotal role of the mechanisms included in our model: temporal constraints on offspring development and building reserves prior to breeding.

Less straightforward is how earlier arrival of spring conditions desynchronizes nesting among capital breeders, but not among income breeders. Income breeders derive few benefits from the pre-breeding period as their stores are quickly maximized, and when spring conditions allow they can all start breeding. Whereas in our model income breeders appear highly synchronized, there are numerous mechanisms in real landscapes and populations, for example stochastic fluctuations of local weather or daily food gain, that introduce variation of nesting onset within the breeding colony or on spatial scales beyond it. Capital breeders require time to maximize their reserves and only when spring is late will all manage to do so and thus initiate nesting in a highly synchronized manner. If spring starts early, only those that arrived ahead of others in the population, or are in good condition from other reasons, will be ready to breed. Thus, variation among individuals in their stored capital translates into desynchronized breeding. Substantial year-to-year variation in breeding synchrony has been reported from seabird monitoring data, and our model helps interpret why synchrony is higher in years when breeding generally is later (Burr et al. 2016) as these species are mostly capital breeders. The empirical observations from the Svalbard and Iceland colonies of capital breeding common eiders fit the predicted change in degree of breeding synchrony: in both colonies we observed increased synchronization in years of late nesting onset (Fig. 4). It should be noted that in Iceland there is sufficient light for underwater foraging for mussels throughout the winter, and eiders can therefore overwinter there without a need for an energy-costly migration with a lightweight body. This may explain why the eiders in Iceland breed earlier than predicted by the model with Svalbard parameters, which represent the high Arctic summer much further north. In lapwings (*Vanellus vanellus*), a migratory bird, a long-term monitoring study spanning ca. 50 years of breeding phenology showed that timing of laying initiation moved to earlier dates, but the breeding synchrony, measured as difference between 1st and 10th laid egg, decreased with warmer spring temperatures (Both et al. 2005), which is consistent with our findings for capital breeders. In well-documented experimental studies on costs and benefits of laying date in European kestrel (*Falco tinnunculus*) and European coot (*Fulica atra*), early egg laying was beneficial but only individuals in good condition could afford to breed early (Brinkhof et al. 2002; Daan and Tinbergen 1997). Differences in condition can be further complicated by carry-over effects, as in the capital breeding pink-footed goose (*Anser brachyrhynchus*) for which body condition at a stop-over site along the migration route (Norway) determines reproductive success at the nesting site (Svalbard) (Drent et al. 2003). Because our model explicitly considers the time needed to gather stores for reproduction, it explains why capital breeding birds in good condition benefit from breeding early, but importantly also how females in poor condition are forced to breed later since they need to catch up with gathering stores to maximize fitness.

Even more interesting are the counterintuitive predictions about optimal clutch size, where earlier springs are associated with having larger clutches for income breeders but smaller for capital breeders. Key to understanding this result is to focus sharply on the trade-off between foraging prior to breeding and time available for offspring development after hatching. If spring is late, this trade-off is non-existent for capital breeders as most have already reached their maximal storage capacity, whereas income breeders experience the same trade-off brutally because each extra egg will require foraging that takes away crucial development time for the whole brood. Conversely, if spring is early, this same trade-off is relaxed for income breeders, whereas capital breeders suddenly experience a drop in post-breeding development time for all offspring if they continue foraging for another egg. This fits with observations among income-breeding passerines, which in warmer temperatures reproduce earlier and produce more offspring, in line with our model, or have increased chance for laying replacement or multiple clutches, which our model did not consider (Dunn 2004; Morrison et al. 2019; Morrison et al. 2015; Winkler et al. 2002). Contrast this with heavier passerines that may rely more on capital breeding, for example starlings (*Sturnus vulgaris*), which breed earlier but lay fewer eggs in warm years (Williams et al. 2015). Such a size gradient in capital breeding is also evident among boreal owls, where clutch size depends on food availability prior to breeding for large species but not for the small ones, who presumably respond more to current conditions (Lehikoinen et al. 2011). Unfortunately, we do not have data on clutch size for the eider colonies, a metric that is difficult to obtain for some groups, such as sea ducks including common eider, who have a high degree of conspecific brood parasitism in dense breeding colonies so that the number of eggs in the nest does not necessarily reflect the clutch size of the female (e.g. Waldeck et al. 2004). Thus, these data are not available for the focal eider populations to allow testing the model predictions.

It is further interesting to note how the relationship between clutch size and nesting date is different for capital breeding individuals within one season when compared to population averages across different years. Similar to the model by Rowe and colleagues (1994) for a single population of capital breeders under early spring onset, individual females in sufficient condition to breed early produced larger clutches than females breeding later in the season (see individual condition trajectories in fig. 2A). However, when different spring onsets are considered, capital breeders produced smaller clutches on average in years with early spring onset compared to late breeding onset (compare across fig. 2A-C, or see fig. 3A). In many bird species that breed earlier in warmer years, changes in reproductive performance, i.e. clutch size and offspring recruitment, tend to be more variable in response to increased temperature (reviewed in Dunn 2004). This aligns with the predictions from our model for capital breeders. We thus recommend that the role of reserves prior to reproduction should be considered when clutch size and breeding timing responses to warming are discussed.

Optimal responses in timing of breeding, synchrony, and clutch size translate into overall effects on expected number of recruits (see Fig. 3). These can be complex, as potentially many independent factors may interact and cumulatively affect probability of recruitment, and also make clear some of the limitations of our models. For example, seasonal trends in food quality are not yet considered but could affect offspring recruitment. The models further assume that conditions for the hatchlings remain unchanged with varying spring phenology, although matching the peak food for offspring needs is a major challenge for some species. Extrapolation beyond birds can be problematic as breeding timing of capital breeders in other taxa is shaped by trade-offs related to physiological features absent in birds, e.g. growth continued after maturation (Jørgensen et al. 2006), physiological limits of lactation (Houston et al. 2007), or diapause (Ejsmond et al. 2018). On the other hand, there are important factors that have been omitted in our model but are expected to have little effect on the model predictions. For example, in the model the only origin of variation in body condition is arrival date, although birds may differ in condition already on arrival. However, the conclusions derived from our work hold as long as there is pre-breeding variation in body condition, regardless of the mechanisms that introduce this variation.

The theoretical life-history approach applied in this study reveals that breeding synchrony and clutch size vary with shifting spring onset in ways that differ between capital and income breeders. Reproductive strategy, effects on individual condition, and a nuanced picture where several traits are interpreted in concert are therefore needed to predict how phenology and breeding strategies of birds have changed and will continue to be affected in warming ecosystems, including the Arctic.

Authors' Contributions

AE, CJ conceived the study, designed the model and wrote the code. AE ran the simulations and performed the analyses with input from ØV, CJ, MF. Data from Svalbard were collected by AE, MF. JEJ provided data from Iceland. AE drafted the paper and all authors contributed to writing.

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Tables and figures

Table 1. The model's parameters and their baseline values. The model was parametrized to resemble biology of the common eider with supporting references.

Parameter	Description	Unit	Value	Comments	References
N	Population size	–	10000		
M_L	Lean body mass	grams	1100	Mass with no reserves	Milne 1976
M_{max}	Maximal body mass	grams	2500	Mass with max reserves $M_{max}= M_L+ S_{max}$	Gabrielsen et al. 1991; Milne 1976
S_{max}	Maximal reserves	grams	1400	Body reserves	Gabrielsen et al. 1991; Milne 1976
w	Pre-breeding weight gain	$gram \cdot day^{-1}$	15	Estimated linear increase	Korschgen 1977; Rigou and Guillemette 2010
E	Egg mass	grams	110		Parker and Holm 1990; Waltho and Coulson 2015
L	Egg laying rate	–	1	Number of eggs laid daily	Watson et al. 1993
c	Coefficient accounting for costs of egg production	–	1.5	cost of egg production includes egg laying and incubation	
I	Incubation duration	days	26	Incubation starts after all eggs are laid	Parker and Holm 1990
D_a	Mean arrival date	day of year	90	Normal distribution, based on observed arrival dates	Hanssen et al. 2016; A. Ejsmond, personal observation
SD	SD for D_a	days	10		
b_s	Earliest possible breeding onset	day of year	130 to 170	Observed and reported early and late nesting	A. Ejsmond, personal observation; Waltho and Coulson 2015
D_e	Last possible laying date	day of year	240	Last day of laying that allow juveniles to develop before autumn migration	Waltho and Coulson 2015

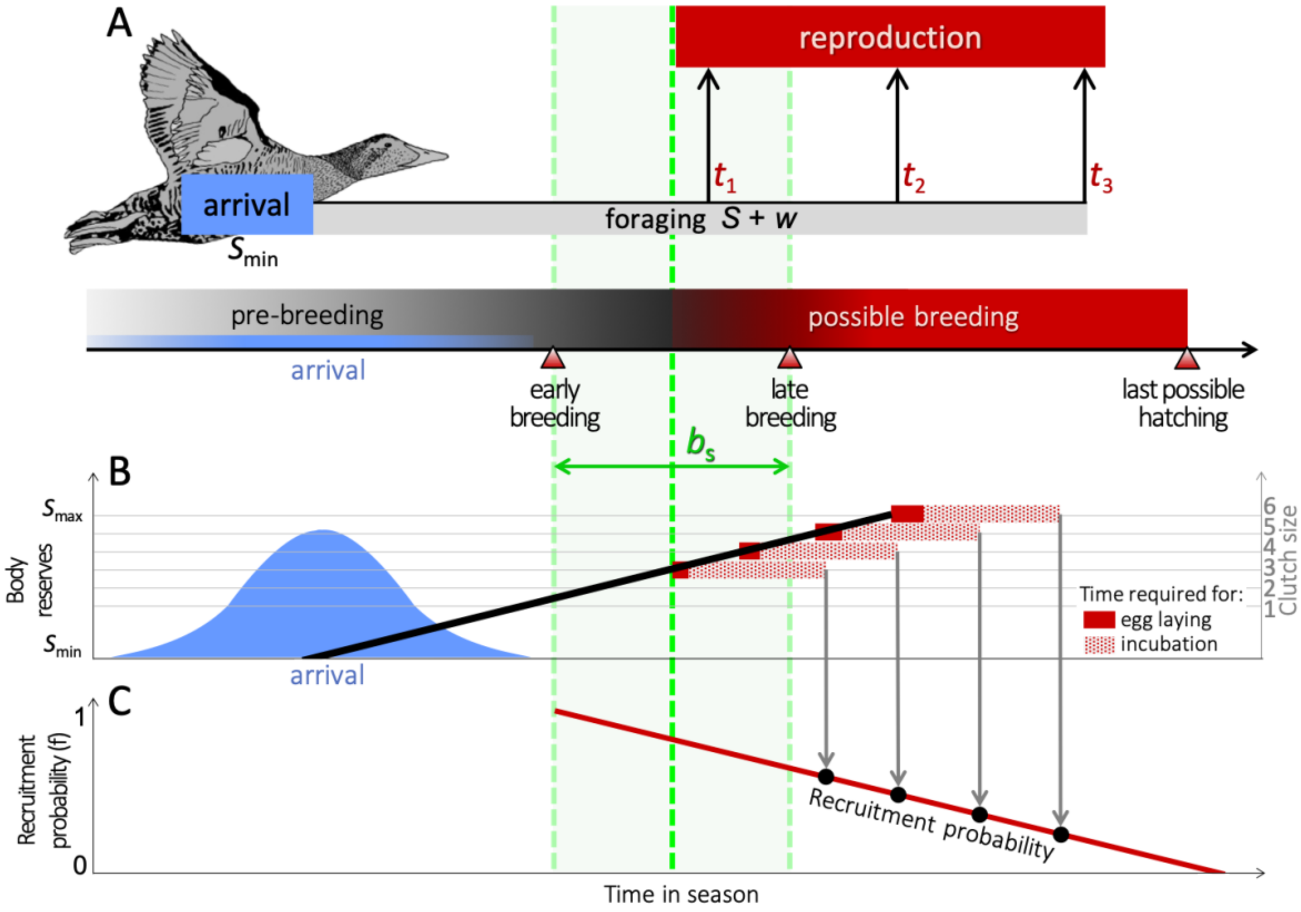

Fig. 1. Key components of the model. (A) The bird arrives at the breeding grounds in spring with minimal body reserves (S_{min}). The arrival is followed by resource acquisition, which increases mass of reserves S as the bird forages $S(t+1)=S(t)+w$, where w is a daily weight gain. The model optimizes timing of reproduction t that may take place from the day of first possible breeding b_s onwards (green lines). The model bird decides when to switch from foraging to egg laying and when to start incubation (t_1, t_2 and t_3 represent three hypothetical strategies differing in timing of nesting onset), while gathering more reserves postpones reproduction. (B) The body reserves increase until maximal body mass S_{max} is reached. Postponed reproduction allows for larger clutch size due to enlarged reserves, whereas the probability of recruitment f decreases. The distribution of arrival dates is depicted in blue. (C) The assumed recruitment probability f translates to probability of offspring recruitment that decreases from 1 at time b_s of the earliest scenario to 0. Thick black line in B exemplifies a trajectory of condition and clutch sizes mapped onto corresponding probability of recruitment in C.

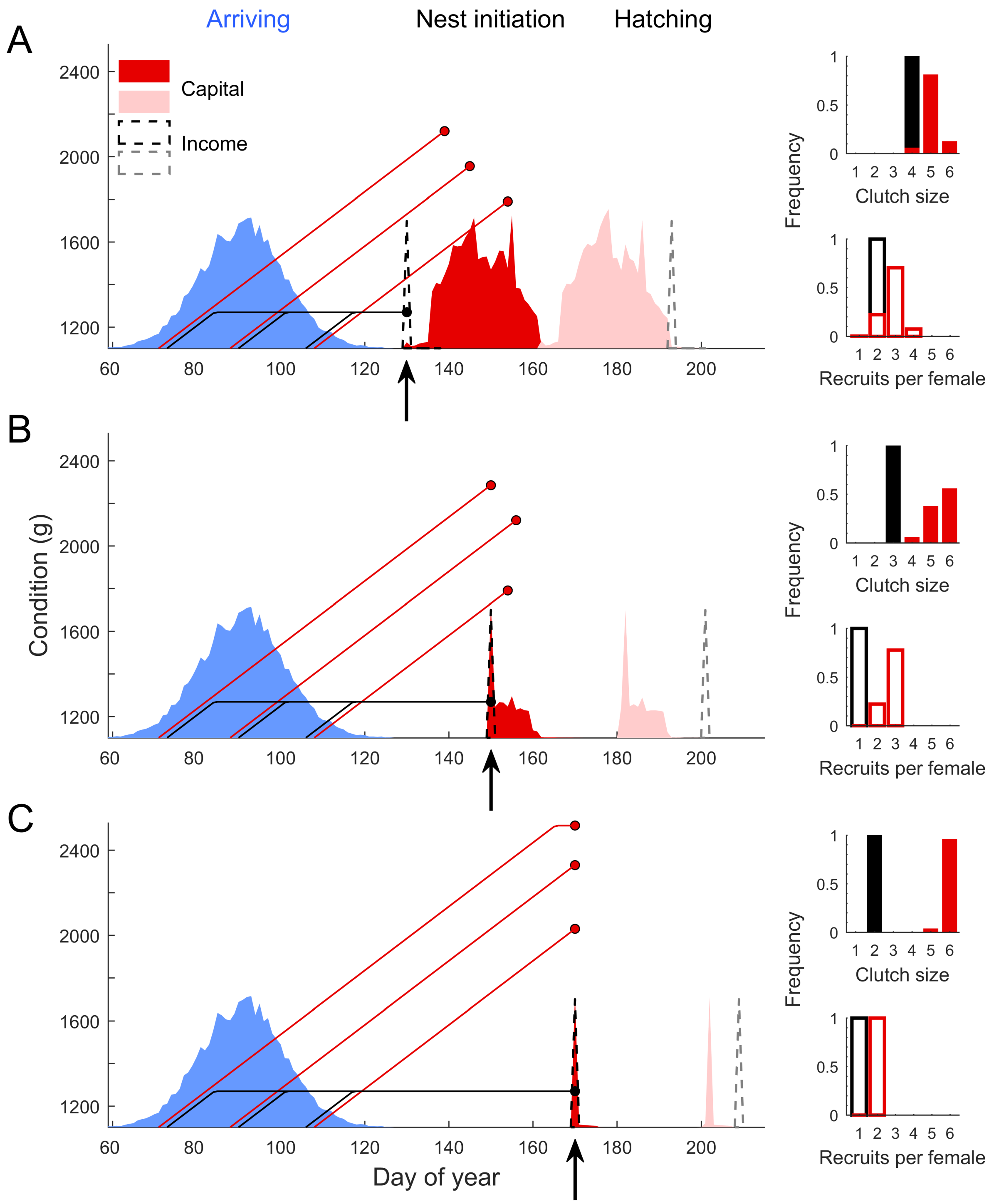

Fig. 2. Optimal breeding strategies in three considered scenarios of pre-breeding season length. Breeding dates, clutch size, probability of recruitment and the number of recruits per female presented for capital breeders (red) and income breeders (green). The main panels in the figure illustrate trajectories of body condition (solid red and dashed green lines) of females with given frequency distributions (frequency on y-axes) of: arrival dates (blue), nesting onset of capital breeders (red) and income breeders (green). Histograms

illustrate the distribution of clutch size, recruitment probability and recruits production in the simulated population. Panels in a row represent scenarios with first possible breeding day b_s (black dashed line) set to (A) short pre-breeding season with b_s=130, (B) intermediate pre-breeding season length b_s=150 and (C) long pre-breeding season b_s=170. The timing of arrival for the modelled population of 10,000 females (blue) is sampled from the normal distribution with mean arrival date D_a=90 and standard deviation SD=10.

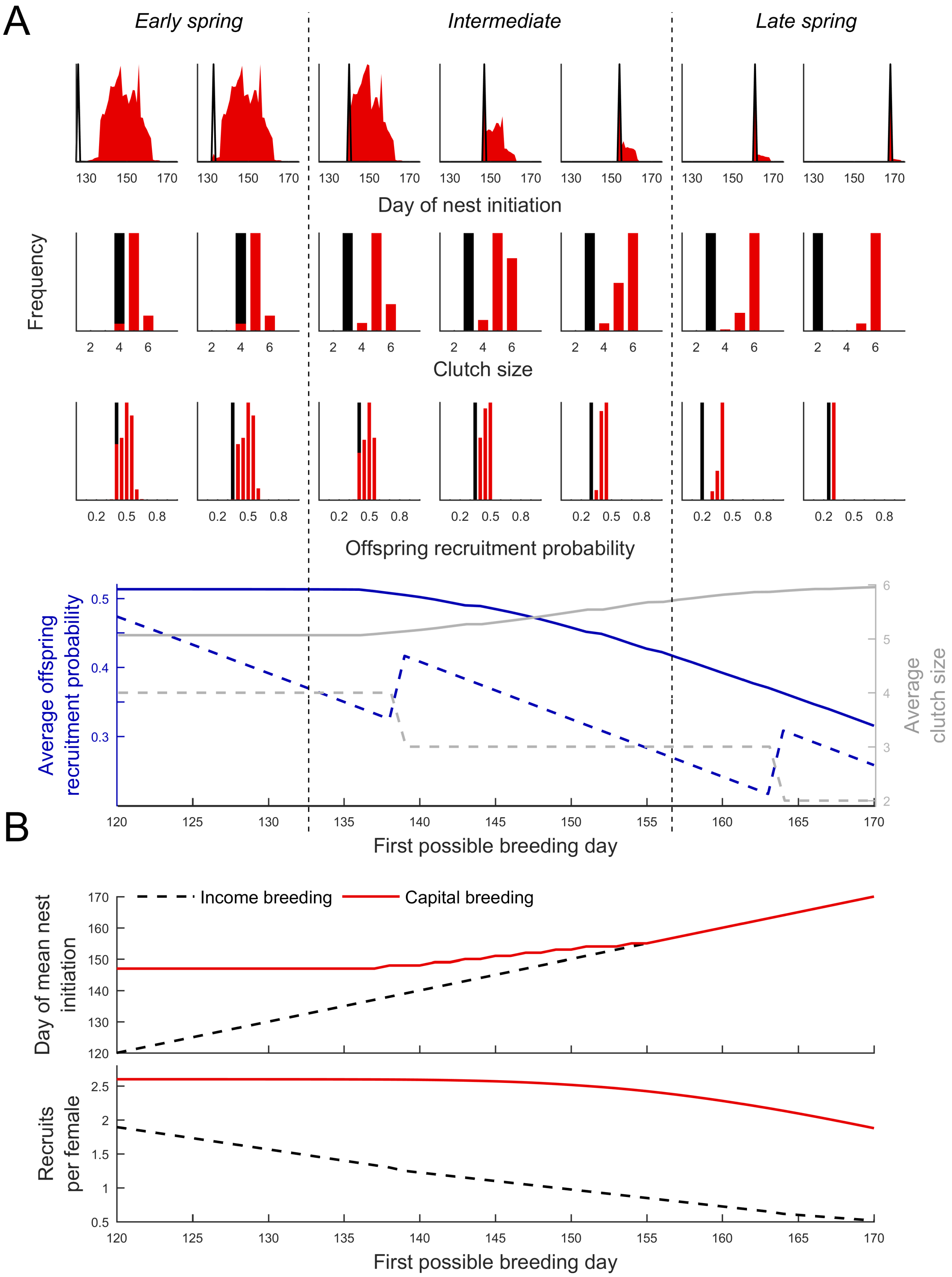

Fig. 3. Breeding components and the number of produced recruits for the modelled populations of females. (A) Breeding dates, clutch size, and probability of recruitment for capital breeder presented in gradient of first possible breeding day b_s. The figure is divided

into values of b_s corresponding to early, intermediate, and late spring onset. The position of normalized frequency distributions representing breeding onset, clutch size, and recruitment probability matches the time points specified by first possible breeding day axis. Average values of the breeding characteristics for modelled populations are represented by solid lines in the bottom panels. (B) Average breeding onset and recruits production by capital breeders compared with income breeders (see the legend) presented in gradient of first possible breeding day b_s.

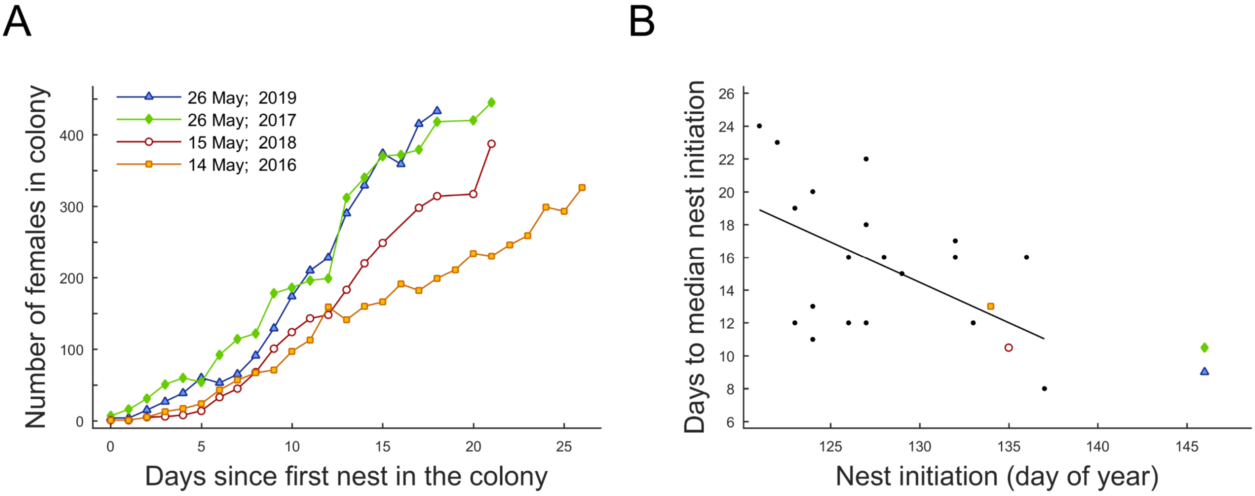

Fig. 4. Breeding synchrony in relation to timing of breeding in the monitored common eider populations. (A) The degree of breeding synchrony in the Svalbard colony presented for four years differing in first possible breeding day defined by the timing of snowmelt (first breeders start nesting when snow in the colony melts – visual observations). In years with late first possible breeding onset (2019, 2017), the breeding synchrony was high (steep increase in number of females) in comparison to years (2018, 2016) characterized by early access to nesting sites and early nesting onset. (B) The relation between the nest initiation date and time to median nest in the Iceland colony in years 1992-2013. In years with late nesting onset, there was a higher synchrony of breeding females than in years when nesting started early (slope: -0.49, p=0.015). For illustrative purpose, colored data points for years 2016-2019 from the Svalbard colony was added to the data from the Iceland colony (black dots) but were omitted from the regression analysis.

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Ejsmond A, Forchhammer M, Varpe Ø, Jónsson JE, Jørgensen C. Nesting synchrony and clutch size in migratory birds: Capital versus income breeding determine responses to variable spring onset.

Appendix 1

Model parametrization and sensitivity analysis of model outcomes to variable settings of model key parameters

Table of contents

1. Incubation costs

The main part of our work presents the model outcomes with costs of incubation assumed to be proportional to the number of produced eggs. The costs of incubation in the base scenario were set equal to 50% of the energetic value of the produced clutch (see the main text). Here we test scenarios with costs of incubation modelled as a constant overhead cost (see Fig S1-S2) and, in the later part of this chapter, we explore the effect of manipulated costs of egg incubation set proportional to the number of produced eggs (see Fig S3).

The higher the overhead costs, the more time is needed for improving condition to the level that allows reproduction (see Fig. 1 in the main text). Importantly, the general conclusion from our work, i.e. that breeding synchrony increases with later first possible breeding date, holds after the introduced incubation costs are kept independent on clutch size (Fig. S1). The higher the overhead cost of reproduction the later the average breeding onset, less eggs produced at average and lower probability of recruitment (Fig. S2A-C). Though, when costs of reproduction are very low the variation in average clutch size is very low as even the late arriving females are able to produce the maximal clutch size (Fig. S2A).

The main conclusions from our work did not change if the assumed costs of incubation were proportional to the number of eggs produced but set to a different value than 50% assumed for the baseline scenario (Fig. S3).

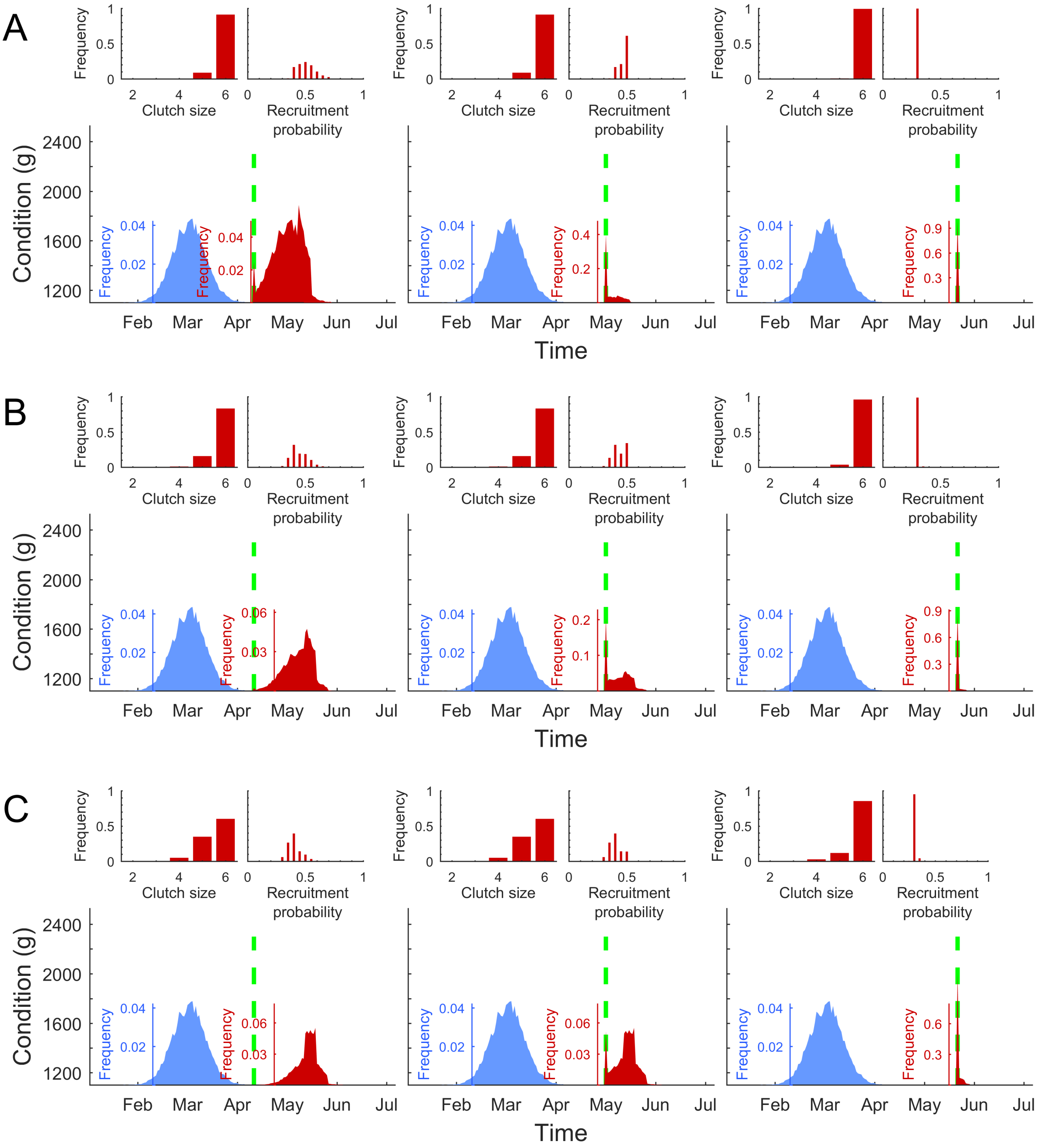

Fig. S1. Optimal breeding strategies in three scenarios with incubation modelled as an overhead cost equal to mass of 2 eggs (A), 3 eggs (B) and 4 eggs (C). Panels in the figure illustrate population of females with given distributions of arrival dates (blue) and nesting onset (red). Histograms illustrate the distribution of clutch size and probability of recruitment. Panels in a row represent scenarios with first possible breeding day b_s set to 130, 150 and 170 day indicated by the thick dashed green line. Other parameters defining timing of arrival, rate of condition gain, incubation time, maximal clutch size, etc., were assumed the same as in the main text.

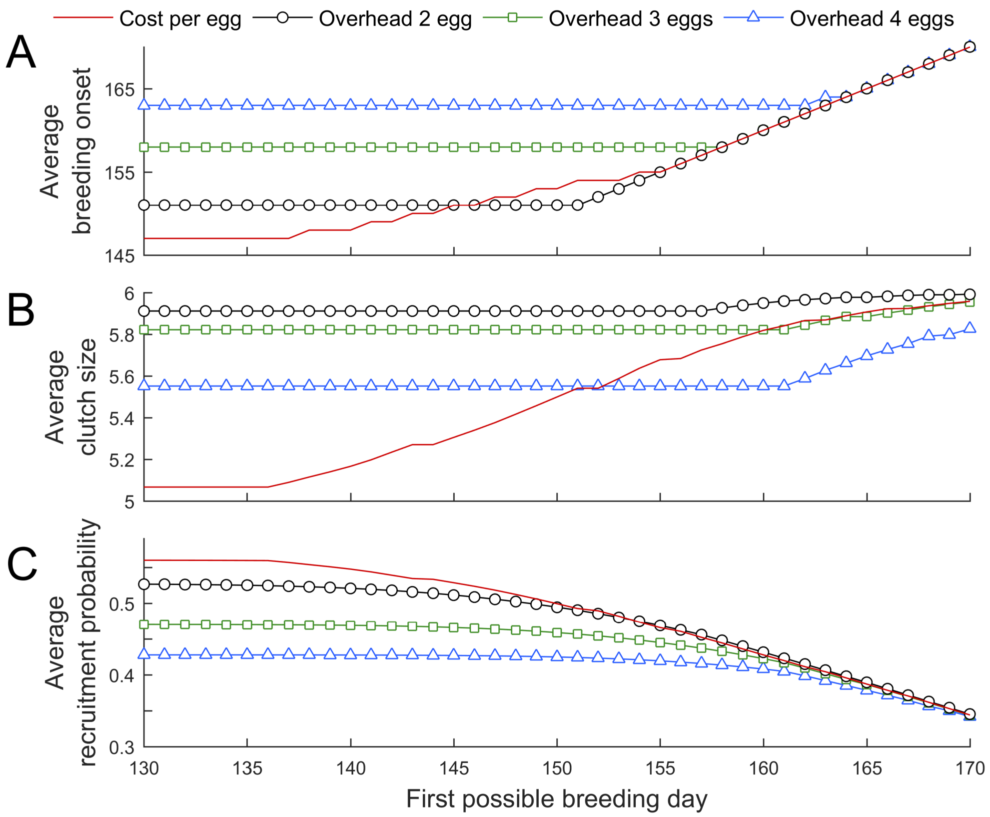

Fig. S2. The average breeding onset (A), clutch size (B) and probability of recruitment (C) presented in the gradient from first possible breeding day. To facilitate interpretation of the presented results we express the overhead costs of reproduction as the energetic value of the egg number (given in the legend). The scenario presented in the main text with cost of incubation proportional to egg number is illustrated by the red line. Other parameters defining timing of arrival, rate of condition gain, incubation time, maximal clutch size, etc., were assumed the same as in the main text.

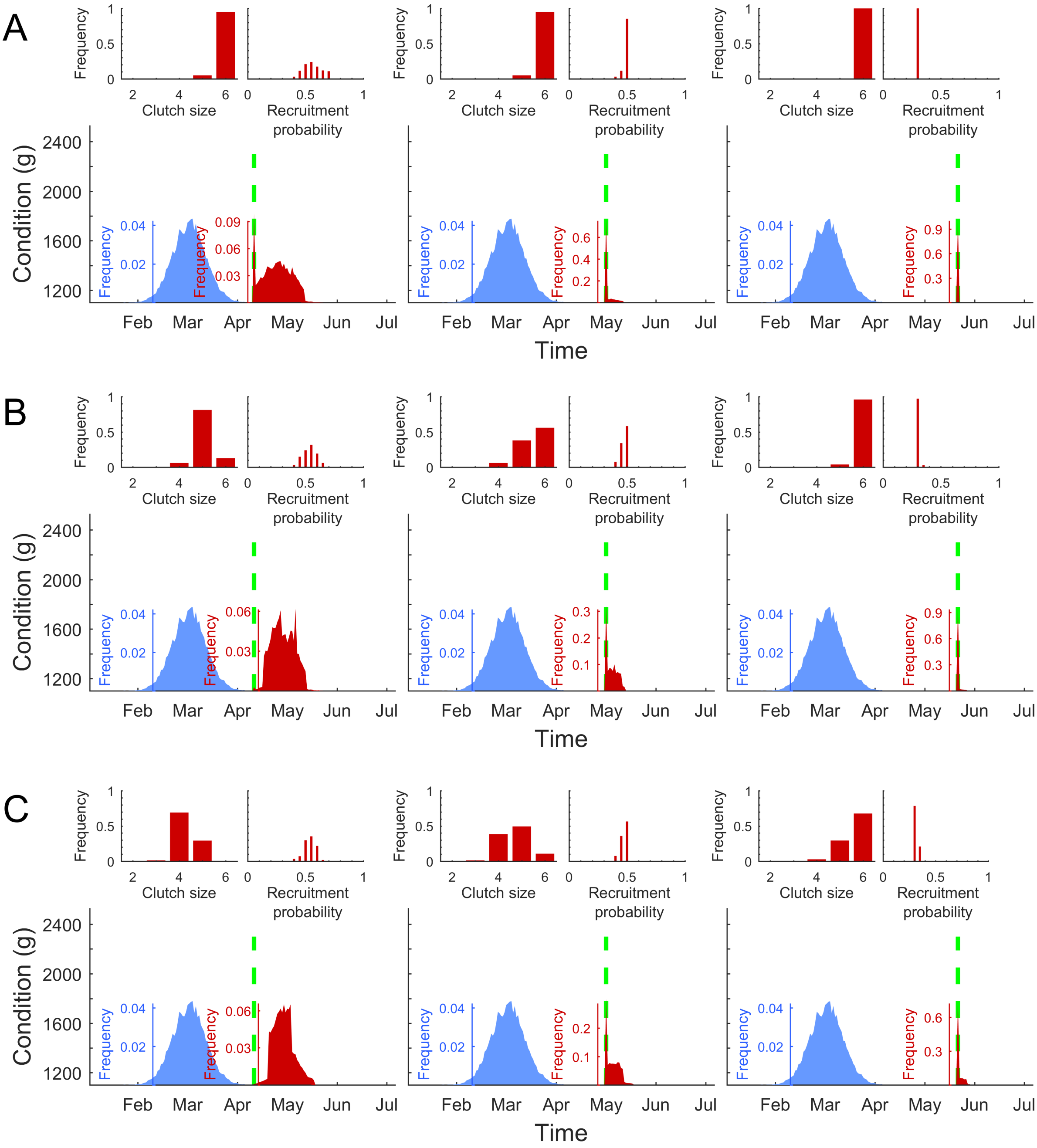

Fig. S3. Optimal breeding strategies in three scenarios with incubation cost set proportional to the number of eggs produces and set to 20% (A), 50% (B) and 80% (C) of the total mass of produced eggs. Panels in the figure illustrate population of females with given distributions of arrival dates (blue) and nesting onset (red). Histograms illustrate the distribution of clutch size and probability of recruitment. Panels in a row represent scenarios with first possible breeding day b_s set to 130, 150 and 170 day indicated by the thick dashed green line. Other parameters defining timing of arrival, rate of condition gain, incubation time, maximal clutch size, etc., were assumed the same as in the main text.

2. Rate of gaining resource

The rate females gain resource in the main part of our work was set to 15 g per day. In general, when the rate of condition gain during feeding phase is manipulated the conclusions of our work remain roughly similar regarding the degree of synchrony, average breeding onset and average probability of recruitment (Fig. S4A, C). However, when the rate of condition gain per day is lowered down females produce smaller clutches (Fig. S4B). For a short or intermediate pre-breeding period females try to compensate low rate of condition gain by foraging for longer (Fig. S4A). A very low rate of resource gain acts as an ecological or physiological constraint for females that are unable to gather enough resource to produce clutches close to the maximal levels allowed. On the other hand, a very high rate of resource gain corresponds to a scenario where females reproduce as early as possible and produce the maximal allowed clutch size (Fig. S4A, B).

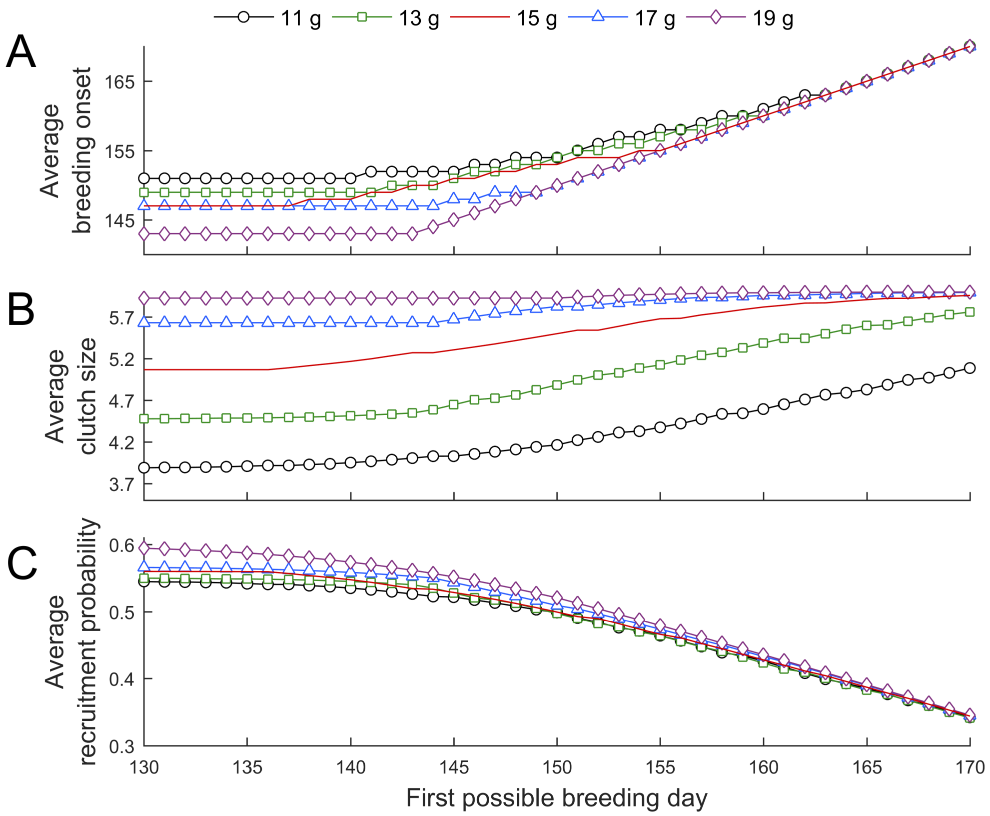

Fig. S4. The average breeding onset (A), clutch size (B) and probability of recruitment (C) presented in the gradient of first possible breeding day and rate of resource gain (given in the legend). The scenario presented in the main text assumes resource gain equal to 15 g per day and is illustrated by the red line. Other parameters defining timing of arrival, incubation time, maximal clutch size, etc., were assumed the same as in the main text.

3. Maximal clutch size

In the main part of our work we assumed that the modelled female can produce at maximum 6 eggs each of 110 g. To test the model predictions with respect to the maximal allowed clutch size we investigated scenarios in which females were allowed to produce between 4 to 10 eggs at maximum. The condition level needed to produce the maximal clutch size in all scenarios equalled 660 g, i.e. the weight of maximal clutch size in the main scenario. The assumed maximal cultch size did not affect the general conclusions presented in the main manuscript; that is, the variability of clutch size in the population decreases with the late first possible breeding onset no matter the assumed maximal clutch size (Fig. S5A). In the tested scenarios a long pre-breeding season cause females to start breeding late and produced offspring has at average low probability of recruitment (Fig. S5B).

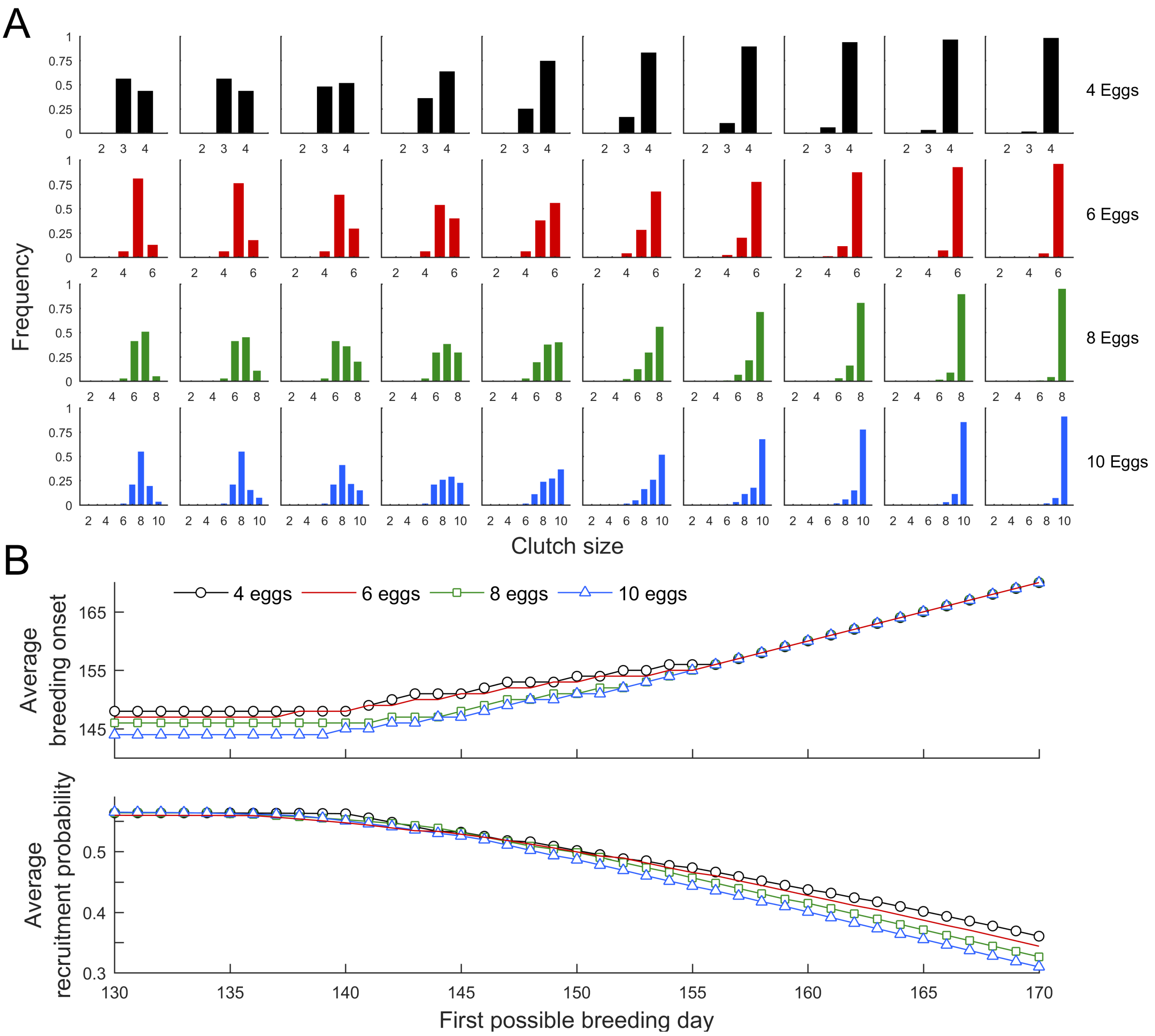

Fig. S5. The distribution of clutch size, average breeding onset and recruitment probability presented in the gradient of first possible breeding day. The considered scenarios differ with respect to the maximal clutch size (given at the right side of the panel rows and in the legend) but the total mass of maximal allowed number of eggs were kept the same for all scenarios. The histograms in the second row from the top (A) and the red line (B) matches the scenario presented in the main text that sets the maximal clutch size to 6 eggs. Other parameters defining timing of arrival, rate of condition gain, incubation time, etc., were assumed the same as in the main text.

4. Variation in timing of arrival

In the main text we present results for a population of females for which arrival dates are sampled from a normal distribution with the standard deviation SD=10 days. Here, we consider scenarios with populations of females differing with respect to the variability of the distribution of arrival dates (Fig. S6). The breeding synchrony is greater along with late first possible breeding day also in scenarios with population of arriving females drawn from both narrow and wide normal distribution (Fig. S6A-C).

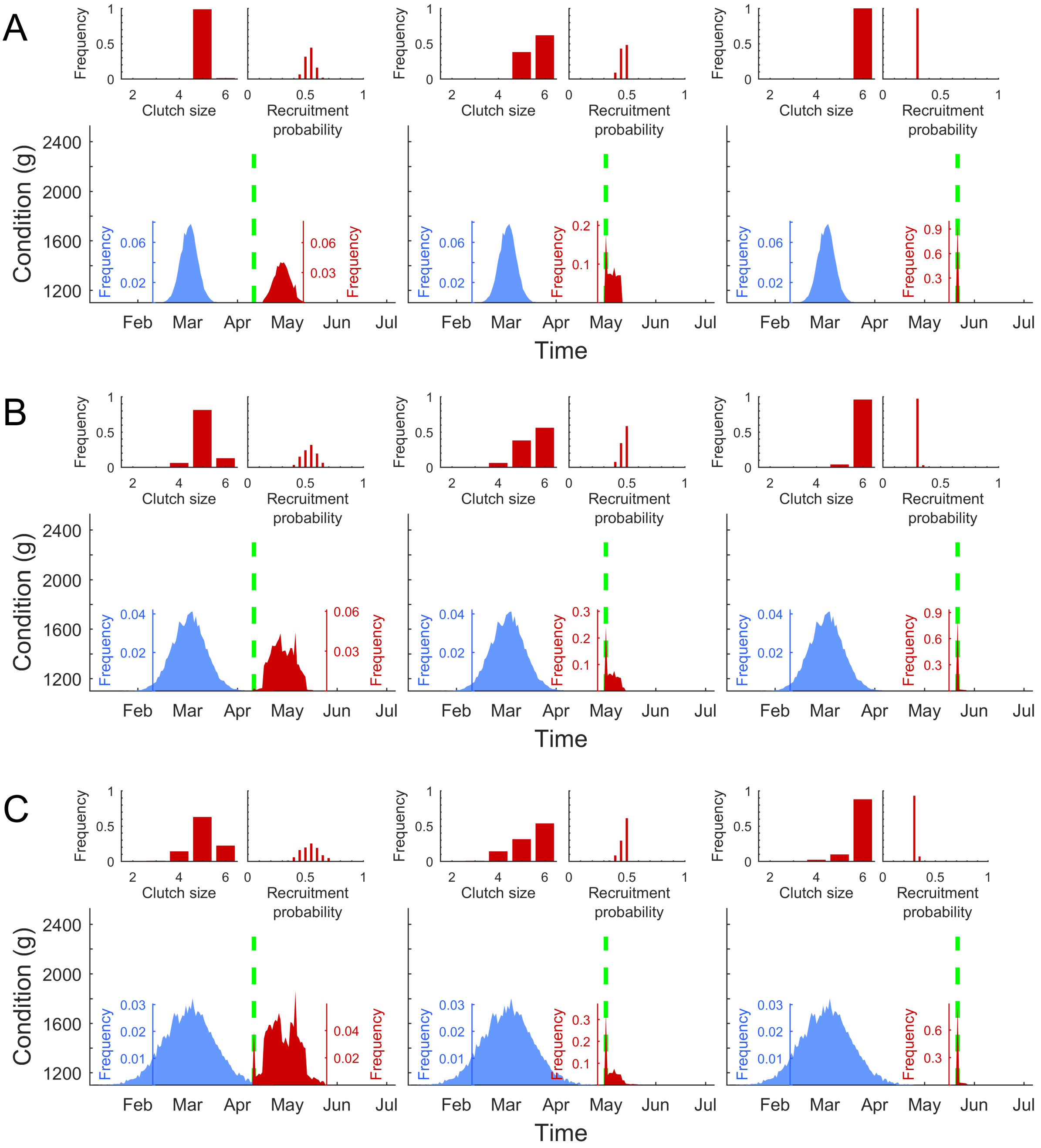

Fig. S6. Optimal breeding strategies in the three scenarios differing with respect to distribution of dates in arriving population of females: (A) standard deviation (SD) of 5 days, (B) SD=10 days and (C) SD=15 days. Panels in the figure illustrate population of females with given distributions of arrival dates (blue) and nesting onset (red). Histograms illustrate the distribution of clutch size and probability of recruitment. Panels in a row represent scenarios with first possible breeding day b_s set to 130, 150 and 170 day indicated by the thick dashed green line. Other parameters defining timing of arrival, rate of condition gain, incubation time, maximal clutch size, etc., were assumed the same as in the main text.

5. Incubation time

The main scenario assumes that female incubate eggs for 26 days (see the main text). In general, shorter or longer times of incubations assumed did not affected the direction to which nesting onset and breeding synchrony changes along with first possible breeding day (Fig. S7). However, when the pre-breeding season is short females compensate long incubation times by nesting earlier and producing smaller clutches (Fig. S7A, B). No matter the length of pre-breeding period incubation time pushes hatching of offspring for later, and hence, the longer the incubation time the lower the probability of recruitment (Fig. S7C).

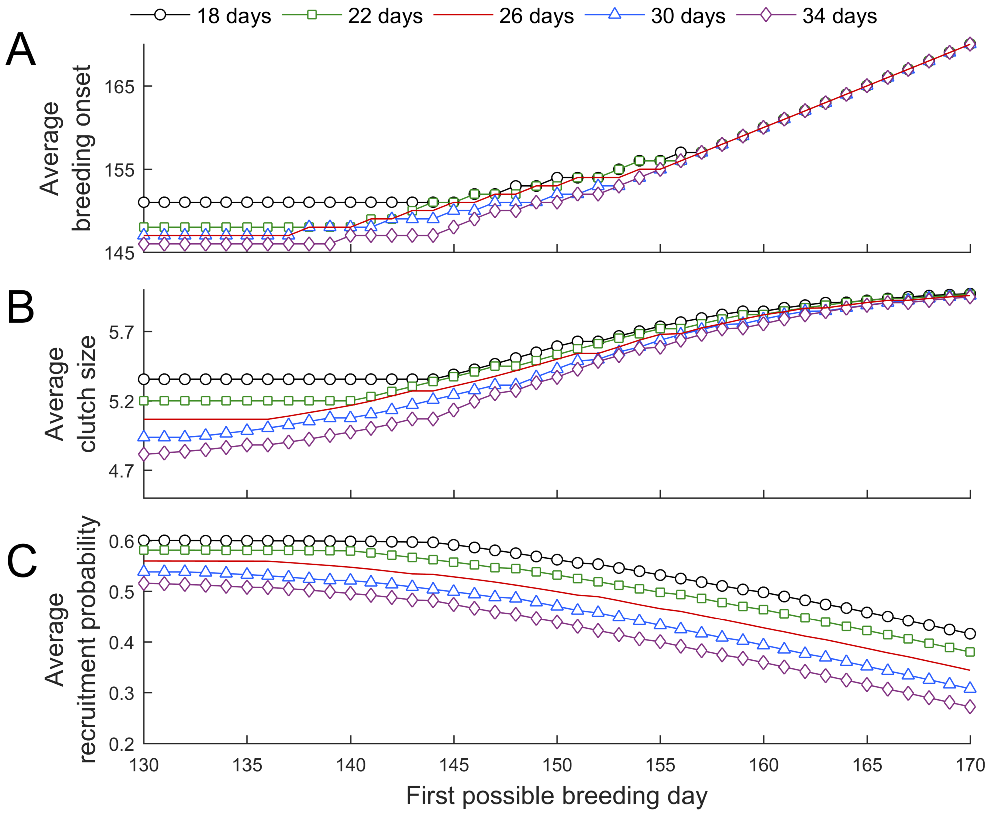

Fig. S7. The average breeding onset (A), clutch size (B) and probability of recruitment (C) presented in the gradient of first possible breeding day and incubation times (given in the legend). The red line matches the scenario presented in the main text that sets the incubation time for 26 days. Other parameters defining timing of arrival, rate of condition gain, maximal clutch size, etc., were assumed the same as in the main text.

6. Confronting with income breeders

Our work focuses on the breeding synchrony, clutch size and probability of recruitment of capital breeders that face the variable timing of the first possible breeding day b_s (Fig. S8). In contrast, income breeders do not change the degree of breeding synchrony along with data of first possible breeding b_s (Fig. S8). The postponement of breeding is used by capital breeders for gathering of extensive reserves, which takes time. Hence, the timing of breeding of capital breeders change only little along with change of first possible breeding b_s from 130 to 155 day. Income breeders cannot store reserves and their breeding timing scales linearly with b_s. The later the first possible breeding the more time can be dedicated to foraging and gathering reserves and hence capital breeders, but not income breeders, produce larger clutches with b_s moving to later dates (Fig. S8). Late first possible breeding day leaves less time to offspring to develop which negatively affect probability of offspring recruitment in capital and income breeders (Fig. S8). However, under late first possible breeding day the capital breeders can compensate low probability of recruitment with increased clutch size due to longer pre-breeding foraging. In turn, the number of recruits by capital breeding female decreases with b_s at much slower rate than in case of recruits produced by an income breeder (Fig. S8).

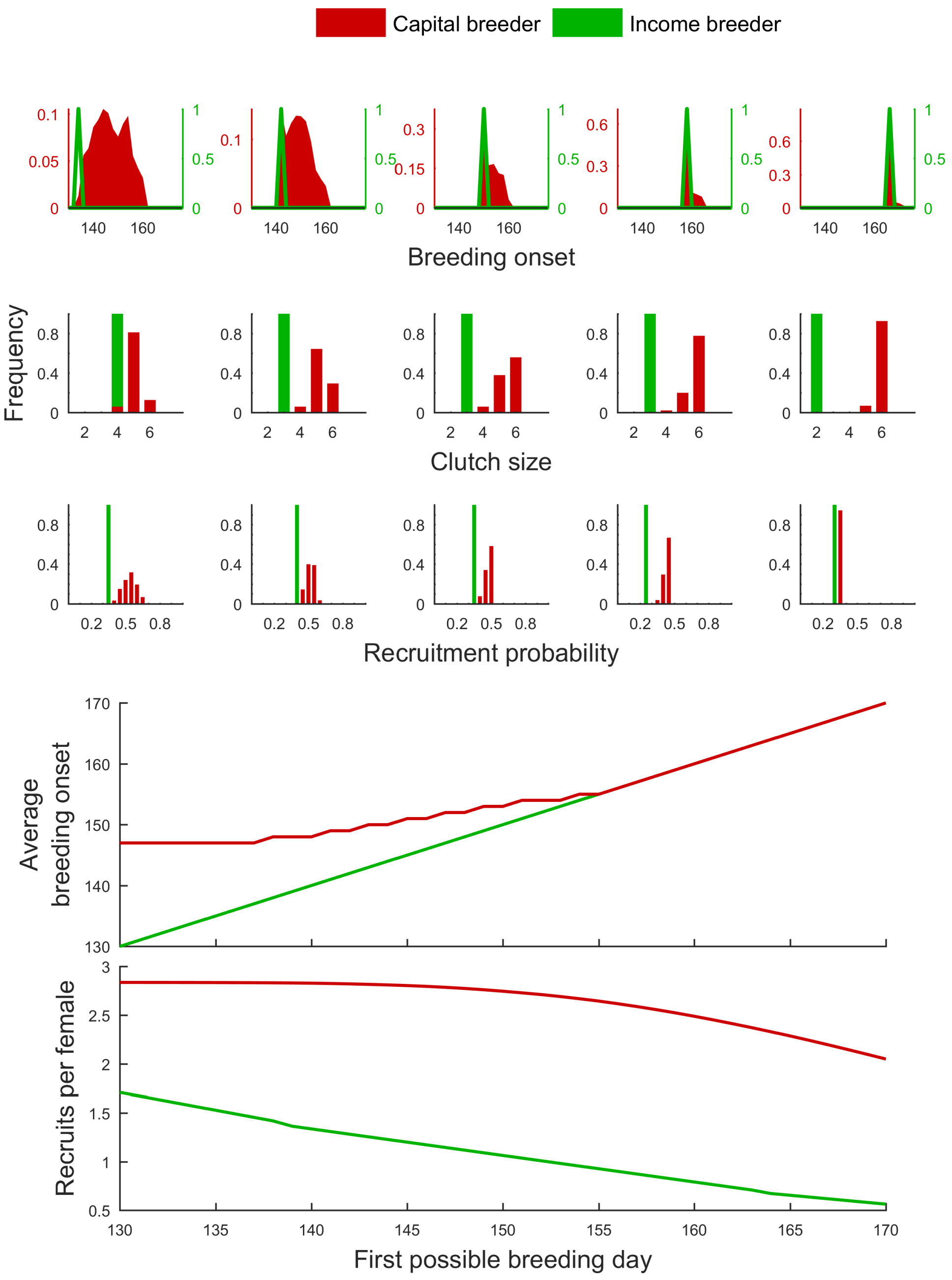

Fig. S8. Capital breeders contrasted with income breeders. Breeding dates, clutch size and recruitment probability in the modelled populations of capital breeding females (red) is contrasted with the income breeders (green). The position of histograms representing breeding onset, clutch size and probability of recruitment matches the time points specified by first possible breeding day axis. Average values of the breeding characteristics for modelled populations are represented by solid lines in the bottom panels. Timing of arrival, rate of condition gain, incubation time, maximal clutch size and other parameters were assumed the same as in the main text.

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PAPER II

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

(*manuscript*)

Modelling of reproductive success of eiders shows that capital breeders can cope better under a stochastically fluctuating than a stable food gain

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Abstract

Stochastic fluctuations of food gain are an important determinant of bird reproductive success and extensive behavior and physiological responses have evolved to mitigate the variable nature of foraging. Bird taxa exhibit a range of physiological features that diversify their breeding strategies, and may therefore differ in the way their reproductive success is impacted by stochastic fluctuations of food gain.

Here, we analyse a theoretical life-history model of migratory birds that store resources for reproduction (capital breeders), confronted with those who need to acquire resources during egg laying (income breeders). For capital breeders, foraging prior to breeding means a larger storage and clutch size, but for both strategies a postponement of nesting reduces chances of recruitment. As an inspiration for our work we refer to biology of two species of eider ducks nesting at high latitudes that differ in the degree to which storage contributes to their reproductive effort. The common eider (*Somateria mollissima*) gathers extensive reserves prior to reproduction, whereas king eider (*S. spectabilis*) is reported to rely on concurrently gathered food during egg laying and nesting. Our modelling approach is based on individual fitness maximization when both pre-breeding foraging and nesting period are time-constrained.

We found that birds exposed to stochastic fluctuations of food gain desynchronize nesting onset and start nesting later than under constant food intake. Whereas, the number of recruits by income breeders is always reduced when exposed to stochastic foraging, capital breeders may attain highest average fitness under stochastic conditions. Importantly, this increase in fitness along with fluctuations in food intake occur in years with early spring onset.

Whereas capital breeders are known to cope better than income breeders with fluctuating environments, we show for the first time that the mean recruitment of capital breeding migratory birds can be greater under stochastic fluctuations of food gain than under stable conditions. Because the warming climate has shifted reproduction of many migratory bird species towards earlier nesting dates, we predict that climatic change associated with a high degree of stochastic variation in food availability can promote migratory species that adopt a capital breeding strategy.

Keywords: clutch size, breeding synchrony, timing of breeding, capital breeding, Common eider, dynamic programming, warming

Introduction

Uneven distribution of food resources and its quality in space or time is an inevitable feature of ecological systems that force animals, including birds, to adopt various tactics to obtain resources (Davies et al. 2012). The diversity of foraging strategies results also from the fact that animals have limited information about the distribution of food in their environment and usually spend large amount of acquired resources and time to search for food (Krebs et al. 1977). In addition to that, numerous actions during foraging, e.g. searching, detecting, hunting and handling, have stochastic outcomes that strengthen the non-deterministic character of the foraging process. In ecological literature the random components of foraging are indeed considered as important drivers of optimal foraging and diversity of tactics adopted by animals (e.g. Stephens and Charnov 1982).

There is a multitude of behavioral and physiological adaptations in birds that help mitigate the stochastic changes in body condition and random outcomes of foraging. These responses differ in the degree of complexity, ranging from simple behavioral reactions, as for example leaving a poor-quality feeding patch, to significant life history shifts, e.g. abandoning the entire clutch by a parent in poor condition. Storing resources in a form of body reserves is a classic example of an adaptation that help to cope with fluctuations of food intake (Krebs et al. 1977, Fischer et al 2009, Fischer et al 2011). In birds, internal reserves play a role far beyond creating only a physiological buffer that helps to get through periods of potential starvation. In many birds, the time before breeding is used for gathering extensive reserves that later contribute to reproduction. This breeding strategy is called "capital breeding" and contrasted with "income breeding" i.e. a strategy in which reproduction is fueled with concurrent resource acquisition (cf. Drent and Daan 1980; Jönsson 1997). The degree to which reproductive strategy interacts with stochastic foraging, and the consequences of this interaction for reproductive success, are unexplored and important subjects in ecology and evolutionary biology.

Stochastic components play an important role in foraging of eiders. These sea ducks dive to feed on organisms living at the sea bottom. Diving for benthic organisms consume significant amounts of energy and eiders feeding on small prey need to collect several preys and to consume it underwater in order to cover costs of diving and searching for food

(Waltho and Coulson 2015). Hence, in poor quality areas the costs of searching for food can potentially outweigh the energetic gains from foraging. Stochastic variation of food gain in case of eiders biology means not only the random variation they experience, conditions for breeding or migration are other examples. These stochastic elements are expected to interact with reproductive strategy of eiders and lead to demographic consequences that are impossible to predict with consideration of deterministic foraging alone.

Females of common eider (*Somateria mollissima*) are a textbook example of capital breeders as they store extensive lipid reserves before nesting and use the internal reserves to boost reproductive effort and cover energetic costs of incubation (Drent and Dan 1980, Waltho and Coulson 2015). In contrast, the closely related king eiders (*S. spectabilis*) adopt a breeding strategy closer to income breeding as they keep foraging during egg laying and incubation (Drent and Dan 1980, Waltho and Coulson 2015). Stochastic variations in food gain is expected to be one of the most important forces that affect body condition of these species prior to and during the breeding season. In capital breeding species, variance in daily food gain prior to breeding would affect clutch size and ability to incubate eggs, but storing reserves before reproduction allow for buffering of unpredictable changes in body condition. In case of income breeders unexpected drops in body condition due to unsuccessful foraging can extend the period of egg laying and lead to reproductive failure. These differences of the two breeding strategies are expected to have consequences for mortality and fecundity, driven by stochastic variation in food gain.

A theoretical comparison of capital versus income breeding eider species during stochastic fluctuations in foraging serves as an excellent starting point for interpreting reproductive strategies of other bird species. That is because birds are a diverse group with respect to breeding strategy, with lipid reserves being to a various degree an important component of offspring production in a number of taxa (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). Changes in recruitment of eiders with reproductive strategies close to income and capital breeding and exposed to significant stochastic fluctuations of food gain can provide valuable predictions on how random foraging affect recruitment of bird species differing in the role of stored lipids in their reproduction.

Here we present a theoretical model in which population of income and capital breeding eiders are exposed to random variation in daily food gain. The consequences of random outcomes of feeding are considered in the context of limited time available for breeding. In our work the offspring of both capital and income breeders produced late in the season have decreased chances of recruitment, so the timing of hatching affects fitness. Capital breeders in our model can increase clutch size by postponing timing of nesting and pre-breeding foraging. This creates a life history trade-off between number of eggs produced and offspring quality. Income breeders need to forage continuously to produce subsequent eggs in the clutch. In our work we report how average nesting onset, breeding synchrony, clutch size and production of recruits of income and capital breeders respond to various scenarios of fluctuating food gain.

Methods

Model outline

In this work we present a life history optimization model (cf. McNamara and Houston 2008) that represent foraging and reproductive strategy of migratory birds that differ in the degree to which reserves gathered prior to breeding are used during egg laying and incubation. The model is based on Ejsmond et al. in review, and here we extend it with stochastically fluctuating daily food gain as birds are unable to predict the exact outcome of their feeding. Briefly, the modelled income and capital breeders arrive to breeding grounds with lean body condition and are able to start nesting as only when environmental conditions allow. In case of capital breeders, females foraging for longer before nesting are able to produce more eggs, but this leaves less time for offspring to develop. Income breeders need to keep foraging during egg laying and the length of the nesting period limits the maximal number of eggs that can be laid. In both capital and income breeders, postponement of nesting reduces the per-offspring contribution to fitness as timing of hatching affects recruitment probability.

The theoretical approach used here is based on a classic framework in life-history evolution built on the dynamic state-variable modelling and the dynamic programming method (Houston and McNamara 1999; Clark and Mangel 2000). We first use our model to find life history strategies that maximize fitness by running optimization backwards in time. By the term "strategy" we mean physiological and behavioral responses that have evolved through natural selection. The optimal state dependent life history strategy for input parameters defining the degree of stochastic fluctuation of daily food gain and seasonal time constraints is thereafter simulated in a population of individual females that follow the optimal strategy. Both stages of the modelling, i.e. backward optimization and forward simulations, are described in detail below. Whereas our model was parameterized in order to resemble breeding biology of eiders at high latitude Arctic ecosystem, the conclusions from our work are general and can be applicable to variable taxa of income and capital breeders among migratory birds.

Model inspiration

As an inspiration for model design, we consider the breeding behavior of two species of eider sea ducks, i.e. common eider and king eider, nesting in high-latitude seasonal environments. The considered eider species differ in the degree to which reproductive effort during nesting and incubation is covered from the reserves stored prior to breeding. Whereas common eider is considered to apply the breeding strategy close to an extreme capital breeding, king eider females are reported to forage during egg laying and nesting (citations, Waltho and Coulson 2015). Consequently, we modeled a strategy of an income breeder that needs to forage in a continuous manner in order to produce and lay eggs and a capital breeder who uses reserves gathered prior to breeding to produce eggs and cover costs of incubation.

Reproductive biology

Modelled females arrive at the breeding grounds and are in a lean condition after spring migration (Waltho and Coulson 2015). According to that, reserve level in arriving model females is $S_{\mathrm{min}}=0$. We refer to the period of pre-breeding foraging as the pre-breeding season. The total body mass of the modelled bird at day t consists of a lean body mass M_{L} plus reserves $S(\mathrm{t})$. The mass of reserves increases as an effect of foraging but the daily food gain in our model fluctuates stochastically (see details below). Maximal reserves S_{max} can reach up to 130% of the lean body mass, which is consistent with empirical observations (Milne 1976). Maximal clutch size was parameterized in order to cover interspecific variation in clutch size of both mentioned species of eiders (Erikstad et al.

1993, Waltho and Coulson 2015) with an egg-laying rate of one egg per day (Watson et al. 1993). We further assume that females produce eggs of the same size E=110 g (Parker and Holm 1990; Waltho and Coulson 2015) and incubate clutch for 26 days (Parker and Holm 1990). To cover incubation costs a female uses reserves equal 50% of the energetic costs needed to produce the eggs, i.e. cnE where n is clutch size, with c assumed to 1.5 in our study.

The key parameter in our model is the first possible breeding day b_s, i.e. the earliest possible day of the year on which nesting becomes possible. Timing of hatching determine probability of offspring recruitment f(t), set maximal at the first possible breeding day b_s of the earliest considered breeding season (among all investigated scenarios) and decreases linearly to 0 at time in which it is too late to develop for autumn migration. A decreasing probability of recruitment with the timing of hatching has been documented in several birds species (e.g. Drent et al. 2003; Dunn 2004; Morrison et al. 2019).

Stochastic foraging

The key element of our model is the stochastically fluctuating daily food gain w_i. The daily change in energy reserves for a foraging individual is given by $S(t+1)=S(t)+w_i$, with w_i that matches the net outcome of foraging, including energetic costs of searching, prey handling etc. Hence, net daily food gain w_i can turn negative for example in case of birds that forage in a poor patch and are unable to cover costs related to metabolism, locomotion, maintenance etc. We further assumed that the total reserves cannot be negative so if $S(t)+w_i<0$ then $S(t+1)$ is set to 0. An average net daily food gain for eiders in natural environment, and in our model as well w_a, is approximately 15g per day (Rigou and Guillemette 2010, Korschgen 1977). Due to the stochastic character of foraging, the daily net portion of acquired resources can vary in our model between x_1w_a and x_2w_a. Below we present results for x_1=-1 and x_2=3, which means that an unlucky individual can lose the mass of reserves equivalent to average daily food gain w_a and maximal net resource acquisition can be three times higher than w_a.

Each day for a bird that is foraging ends up with a certain outcome of foraging in terms of net food gain. We assumed that there are i=1, 2, … k foraging outcome types in our model with each that can happen with probability p_i and bring daily net food gain of w_i.

In the results presented below we show results for k=20 different types of the foraging outcome. Changing k to higher value, i.e. consideration of more foraging outcome types did not affect the result but prolong calculation times. The probabilities p_i that foraging bird will obtain food gain w_i was taken from a beta distribution. We used the beta distribution because it is defined on the interval [0,1] which, after rescaling, allowed us to keep the food gain within a predefined interval of x_1w_a and x_2w_a. We also assumed that the probability distribution of daily food gain is symetric i.e. shape parameters of the distribution α and β are equal. By setting the shape parameter of the distribution α, we were able to explore a broad range of scenarios differing in the variance but not the average of net daily food gain set to w_a in our model (see left column panel in Fig 1).

Backward optimization

The backward optimization procedure allowed us to find the reproductive strategy that maximizes fitness approximated in our model by the expected number of recruits V, i.e. the number of offspring weighed by their recruitment probability. However, capital and income breeders differ in their breeding strategy and in how fitness is calculated.

A capital breeder that starts incubation obtains a fitness if breeding V_{incubate} that depends on the number of eggs laid n (eq. 1). After incubation the offspring hatches, and the chance of recruitment f declines with time.

1. $$V_{\text{incubate}}(t,n) = n\,f(t+i),$$

where number of eggs laid cannot exceed $S(t)/(cE)$ and hatching takes place i days after the last egg was laid. A female that produced fewer eggs than $n_{\max}$ may continue egg laying, which would lead to fitness if laying V_{lay}.

2. $$V_{\text{lay}}(S,t,n) = V(S-cE, t+1, n+1),\ S \geq cE$$

The female may also continue foraging, which would influence prospects for future reproductive capabilities. However, the expected increase in reserves is given by the probability distribution, according to

3. $$V_{\text{forage}}(S,t,n=0) = \sum_{i=1}^{k} p_i V(S+w_i, t+1, n=0)$$

where w_i is the daily food intake of type i that occurs with probability p_i. The third argument n = 0 indicates that for capital breeders foraging terminates when first egg is laid.

Capital breeders were not allowed to store more reserves than S_{max}. The model compares and extract the maximal value out of V_{forage}, V_{lay} and V_{incubate} calculated on each day and for each level of energy reserves *S* and number of eggs laid:

$$4. \qquad V(S,t,n) = \max\left[V_{\mathrm{forage}}(S,t,n=0), V_{\mathrm{lay}}(S,t,n)\,, V_{\mathrm{incubate}}(t,n)\right]$$

The model optimizes the day *t** at which a capital breeding female initiates egg laying, by switching from foraging to reproduction, and day *t*** at which female starts incubation and terminates egg laying, which sets the clutch size.

In income breeders the maximal allowed reserves level was equal to production cost of one egg, i.e. $S_{\mathrm{max}}=cE$. Income breeders, that similarly to capital breeders are exposed to stochastically varying food gain, continue cycles of foraging and egg-laying until the time *t*** when the 26-day period of incubation starts. Onset of incubation in income breeders at *t*** thus determines clutch size. Income breeders were allowed to forage and increase their reserves *S* no matter the number of eggs already laid, (cf. eq. 3), which is then given by

$$5. \qquad V_{\mathrm{forage}}(S,t,n) = \sum_{i=1}^{k} p_i V(S + w_i, t+1, n)$$

The state-dependent reproductive strategy that maximizes fitness of income breeders was also found using dynamic optimization (see eq. 4).

Forward simulations

We simulated 10 000 females with normally distributed arrival dates to calculate average nesting onset, defined as the date of laying the first egg, breeding synchrony, clutch size and production of recruits by populations of females that adopt strategy of income or capital breeding. Behavior of the simulated females followed the state-dependent optimal strategy *t** and *t*** calculated with backward optimization (equation 4). We ran optimization and simulations for various assumed probability distributions of daily food gain w_i and different dates of first possible day of nesting onset b_s (Fig.1). The migration pattern of the modeled population of eiders (mean arrival day of year D_a= 90, SD=10 days) is consistent with empirical data on migration of high-latitude populations of common eider (Waltho and Coulson 2015, Hanssen et al. 2016). All calculations were performed with MATLAB (R2015b).

Results

The model compares breeding onset, synchrony and components of fitness for income and capital breeders exposed to various degrees of fluctuations of the net daily food gain w_i (Fig. 1, left column panel). In scenarios with fluctuating food, birds on average gained the same amount of food as in a deterministic environment, but fluctuations introduced variation in the body condition of individual as some would reach the desired level of reserves faster or slower than the average in the population (compare trajectories in Fig. 1C-D with 1A). Because the optimal strategies in both income and capital breeders strongly depended on time constraints related to the duration of breeding and pre-breeding season, the effect of the fluctuating food gain interacted with the timing of spring onset, determined by b_S in our model (Fig 1).

Timing of nesting and breeding synchrony

Postponement of the timing of nesting brought no benefits for income breeders in terms of fitness, as females are capable of gathering reserves sufficient to produce one egg only. In deterministic environment, income breeders started nesting right after the first possible breeding day b_S (Fig. 2A, the rightmost points). The only situation that caused income breeders to slightly delay the average nesting onset was a very early spring, when some late-arriving birds needed to forage beyond b_S to gather resources for their first egg (Fig. 2A, the light green line). The fluctuations of food gain introduced stochastic effects, and the greater the variance in food gain the longer the postponement in nesting onset (Fig. 2A). Because of fluctuations, some income breeders would need to gather resources for the first egg over a longer period than the average in the population (Fig. 1). Similarly, income breeders started nesting synchronously no matter the spring onset b_S tested, but the degree of synchrony was reduced if food gain fluctuated stochastically (Fig 2B).

The timing of nesting and synchrony of capital breeders displayed a more complex response than in case of income breeders. Capital breeders, in contrast to income breeders, may increase reserves and produce larger clutches by postponing reproduction and continuing foraging prior to nesting. The onset of nesting in capital breeders depended in particular on the spring onset, and the earlier b_S the greater the delay of nesting (Fig. 2C). This delay of nesting onset was further increased by fluctuations in food gain in a similar manner as observed in income breeders (Fig. 2C vs. 2A). The breeding synchrony of capital breeders depended in particular on spring onset b_s with greatest synchrony observed during late springs (Fig. 2D). Similarly to income breeders the high degree of fluctuations of food further desynchronized nesting onset of capital breeders (Fig. 2D).

Clutch size and offspring recruitment

No matter the fluctuations of food gain or spring onset, income breeders that are in body condition allowing laying of an egg, would always decrease their fitness by postponing nesting onset. Hence, only under early spring onset were income breeders capable of producing large clutches (Fig. 3A). However, early spring onset allowed not only production of large clutches (Fig. 3A) but earlier start of incubation and in turn high probability of recruitment (Fig. 3B). When food gain was deterministic, the maximal fitness was reached at a certain combination of clutch size and value of offspring at hatching (Fig. 3 A-B). Note that nearly all income breeders under deterministic environment applied the same breeding strategy, as variation in number of recruits per female was close to zero (Fig. 4A). However, when food gain fluctuated income breeders could produce on average smaller clutches with higher per offspring value or larger clutches with smaller per offspring value (Fig. 3A-B). The greater the variance in food gain, the greater the variation in fitness of income breeders (Fig. 4A). No matter if the clutch size of income breeders increased or decreased along with fluctuations, the number of recruits per female dropped when food availability changed stochastically (Fig. 4B).

Capital breeders needed to forage prior to nesting in order to breed and, in contrast to income breeders, produced largest clutches in seasons with late spring onset (Fig. 3A vs. 3C). However, nesting late and large clutches of capital breeders were associated with low probability of offspring recruitment (Fig. 3D). Under deterministic food gain capital breeders displayed variation in the number of recruits per female (Fig. 4C). This variation in the number of produced recruits was caused by the variability in the conditions of birds at b_s - individuals being in good condition started laying right away or just after b_s, whereas those in poor condition continued foraging beyond spring onset (Fig. 1). The variation of breeding characteristics of capital breeders under deterministic food gain was greatest for early spring onset (Fig. 4C). Under fluctuating food gain the reproductive synchrony of capital breeders decreases and the variation in number of recruits increased (Fig. 2D,

Fig. 4C). However, for scenarios with early spring onset capital breeders, but not income breeders, living under the fluctuating food gain could produce on average more recruits per female than in scenarios with deterministic food gain (Fig. 4B vs. D). This effect of greater fitness of capital breeders under fluctuating food gain than deterministic food gain was absent in scenarios in late spring onset (Fig. 4D).

Discussion

In our model, birds arrive at different times, and pre-breeding foraging introduces differences in the level of condition at the spring onset b_s. The difference in condition caused some capital breeders, but not income breeders, to forage far beyond b_s in years when spring arrived early (Fig. 2A vs C). That was because nesting onset and degree of synchrony in capital breeders are an outcome of the trade-off between time dedicated to pre-breeding foraging (building up the clutch size) and offspring recruitment determined by timing of hatching. In income breeders, this trade-off is absent and females tend to start nesting as soon as conditions allow. However, when food intake is stochastic both income and capital breeders spent more time on pre-breeding foraging and postponed their nesting. Whereas fluctuating food gain postponed and desynchronized nesting of both modelled strategies (Fig 2), capital breeders showed a greater tendency to desynchronize breeding along with fluctuations in food gain when spring started early (Fig. 2D). That is because in the scenario with early arriving spring, building up reserves took place during a period suitable for breeding. This allowed capital breeding females to adopt diverse solutions of the trade-off between clutch size, pre-breeding foraging, and probability of offspring recruitment determined by timing of hatching.

No matter if the clutch size of income breeders increased or decreased along with fluctuations, the number of recruits per female always dropped along with the degree of stochastic fluctuations of food intake (Fig. 4B). Income breeders were unable to compensate the mentioned drops in fitness. In capital breeders nesting in years with early spring, both average clutch size and recruitment chance increased along with fluctuations of food intake (Fig. 4C-D). Capital breeders were capable not only to compensate the effect of stochastic foraging, but also to attain higher fitness on average than when food gain was stable. However, the variance in the production of recruits by capital breeders increases along with fluctuations. That was because lucky individuals that experienced high food gain frequently were capable of producing large clutches just at or shortly after the early spring onset, which contributed to the high average clutch size (Fig. 3C). Unlucky individuals that frequently experienced low food gain by chance could still forage until they had gathered level of storage that allowed producing a clutch. When spring onset was late, a large proportion of arriving capital breeders gathered the maximal possible reserves before b_s, and strong fluctuations in food gain would cause these individuals to decrease in condition every time a bird experienced negative net food gain. As a consequence, the average fitness was lower than under stable conditions (Fig. 4D).

Whereas capital breeders are known to cope better than income breeders with fluctuating environments (Fischer et al 2009, Fischer et al 2011), our study shows for the first time that fitness of capital breeding migratory birds can increase with stochastic fluctuations of food gain. Importantly, this increase in fitness along with fluctuations in food intake occur in years with early spring onset. This result has important implications to the response of migratory birds to the observed environmental changes due to warming climates. Global warming has shifted reproduction of many migratory bird species towards earlier nesting dates, gradually relaxing the temporal constraints of offspring development (Drent et al. 2003; Dunn 2004; Morrison et al. 2019). With advancement of the breeding season, stochastic variation is also expected to play a more significant role in shaping reproductive success of migratory species (Forchhammer et al. 1998, Forchhammer and Post 2000). It is unknown how reproductive success of migratory birds would change along with increasing degree of fluctuating environments. Our study shows that predictions regarding the consequences of the stochastic fluctuations of food availability on fitness of migratory birds depended on the adopted breeding strategy. According to our study, capital breeders are expected to cope better and attain higher fitness when the degree of stochastic availability of food would increase.

Timing of nesting, clutch size and recruitment of capital and income breeders under fluctuations of food gain were modelled in individuals that differed in timing of spring migration and arrived with lean body condition. In our model, pre-breeding foraging introduces diversity of body condition at the date nesting can start but in natural conditions there are numerous forces that can affect the body conditions of females upon arrival.

Because what matters in our model is the body condition at the time environmental conditions allow nesting, the conclusions of our work hold also when birds arrive at the same day but differ in body condition on arrival. Our model is applicable to migratory but also non-migratory birds, as long as they exhibit pre-breeding variation in body condition before the environmental conditions allow nesting.

To conclude, our theoretical life history approach shows that fitness consequences of the adopted breeding strategy of migratory birds depend on the interaction between temporal constraints of reproductive success and stochastically varying environment. When resources are allocated in an optimal and a state-dependent manner to competing needs, the degree to which reserves are used during reproduction by migratory bird species become one of its key features. Importantly, the degree to which considered migratory bird species use lipids in their reproduction influence the predictions regarding fitness responses to changing environmental conditions.

Figures

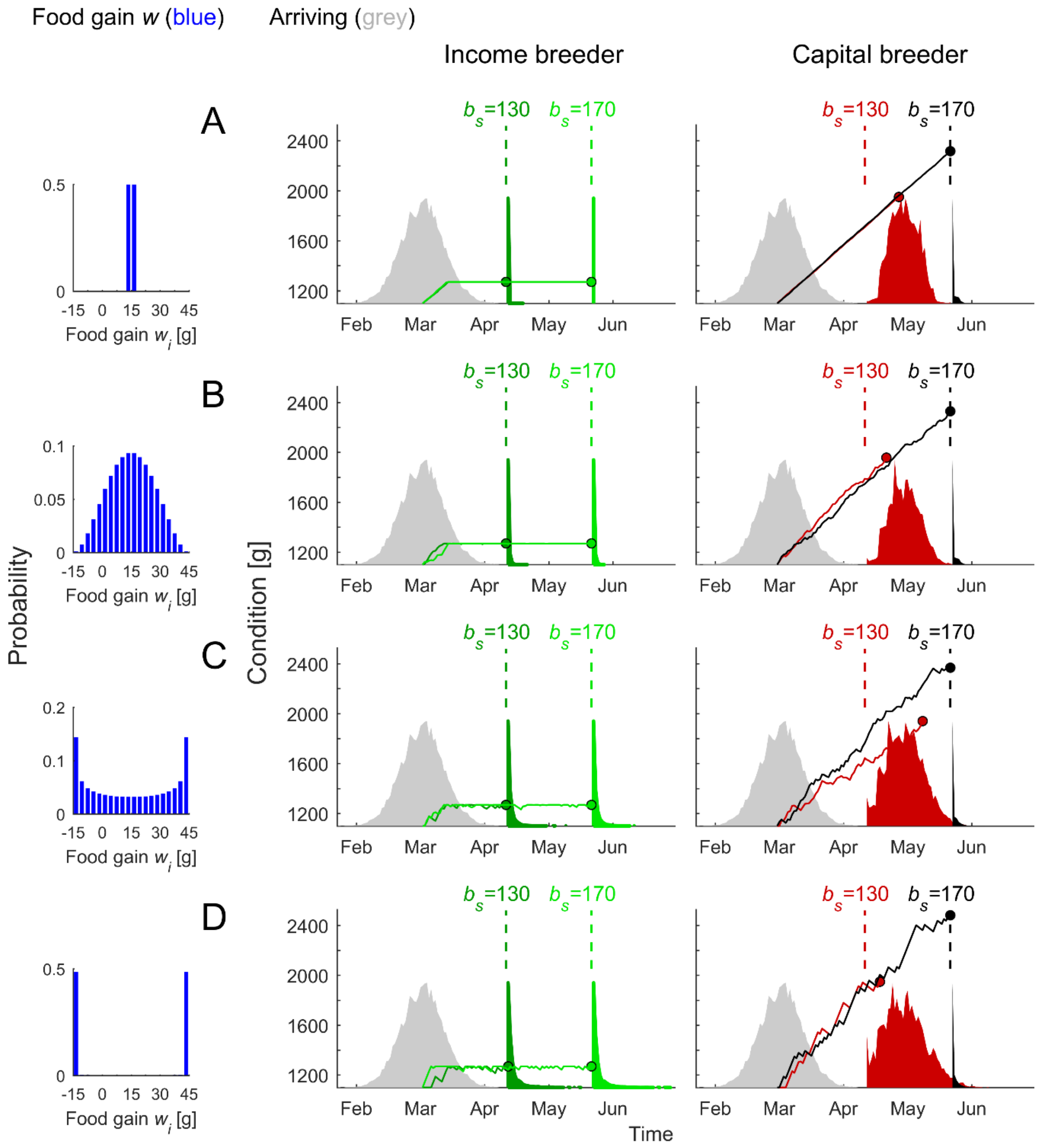

Fig. 1. Breeding onset presented for four example scenarios of fluctuating net food gain. Individual females of income breeders (middle column) and capital breeders (right column) optimize their breeding timing in response to assumed distribution of net daily food gain w_i (left column). Optimal strategies of females are presented for two scenarios differing in the time of first possible nesting b_s (see labels at the dashed lines in the middle and right column of panels). Trajectories show exemplary changes in body conditions by females

exposed to fluctuating net food gain (blue). The timing of arrival for the modelled population of 10,000 females (gray) is sampled from the normal distribution with mean arrival date D_a=90 and standard deviation SD=10. The stochastic fluctuations of daily net food gain were given by the beta probability distribution with shape parameter α =500 (A), α =3 (B), α =0.5 (C) and α =0.01 (D). Maximal and minimal net daily food gain were set to x_1=-1 and x_2=3 (see methods).

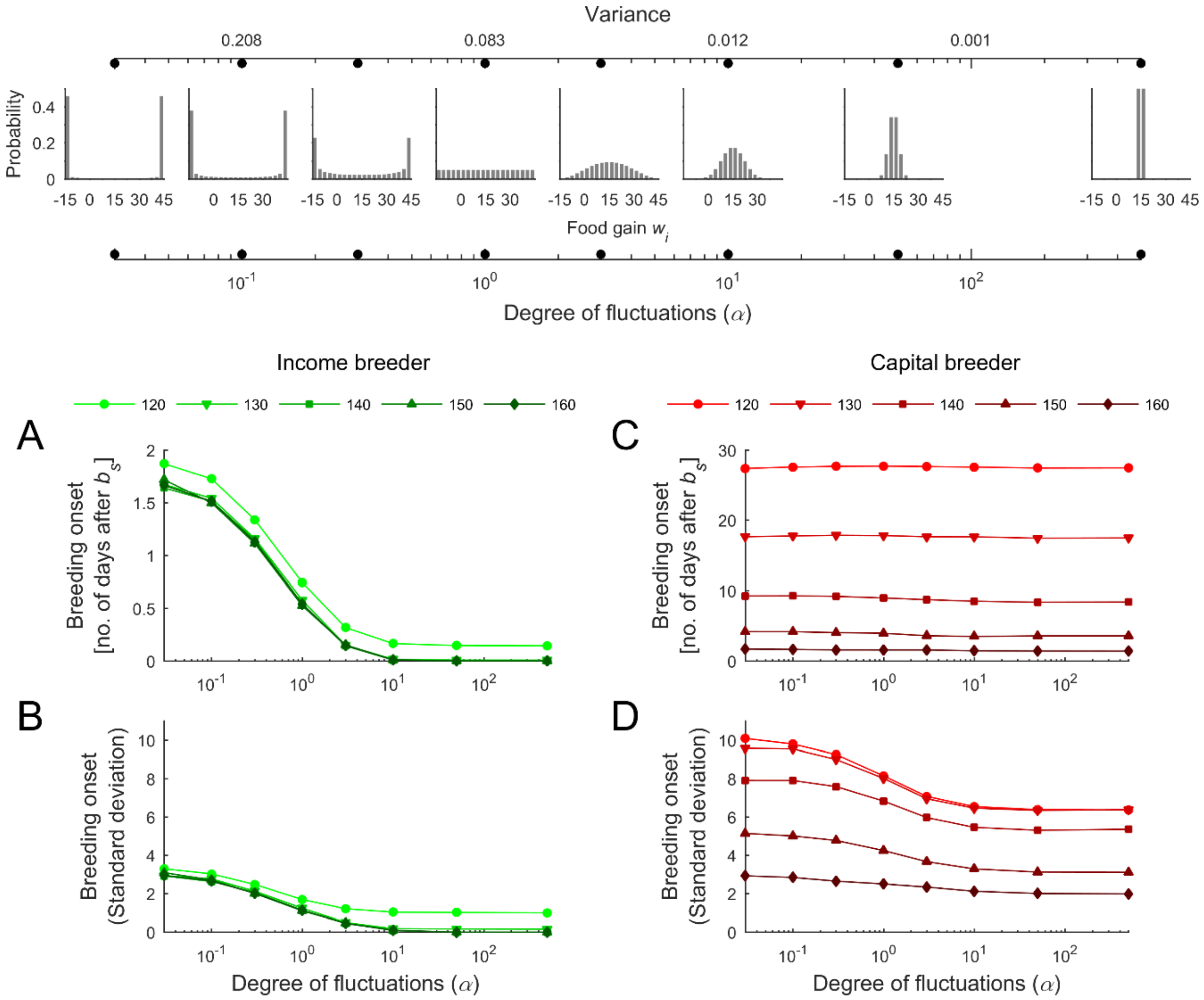

Fig. 2. Breeding onset and synchrony of populations exposed to fluctuating daily net food gain. Top panels present how the shape and variance of the net food gain distribution depends on parameter α. Black dots in top panels match values of α assumed for scenarios presented in panels A-D. (A, C) Average nesting timing given as relative to the first possible breeding day b_s and (B, D) the degree of breeding synchrony, approximated by the standard deviation of individuals breeding onset, are presented for income and capital breeders (see labels at the top of the panels). Presented scenarios differ in spring onset b_s (see the legend). (A-D) Clutch size and probability of recruitment are presented for intrapopulation variability of recruitment for income and capital breeders (see labels at the top of the panels).

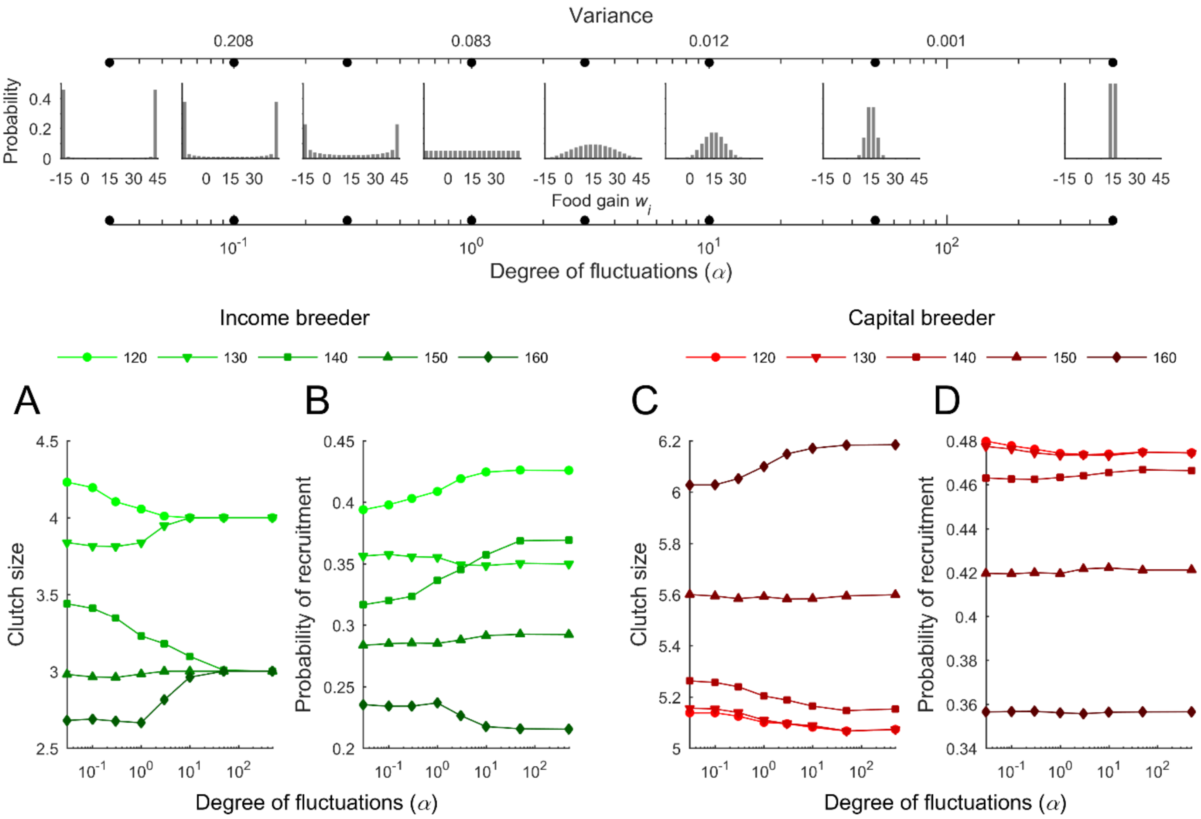

Fig. 3. Clutch size and probability of recruitment in populations exposed to fluctuating daily net food gain. Top panels present how the shape and variance of the net food gain distribution depends on parameter α. Black dots in top panels match values of α assumed for scenarios presented in panels A-D. (A, C) Clutch size and (B, D) probability of offspring recruitment are presented for income and capital breeders (see labels at the top of the panels). Presented scenarios differ in spring onset b_s (see the legend).

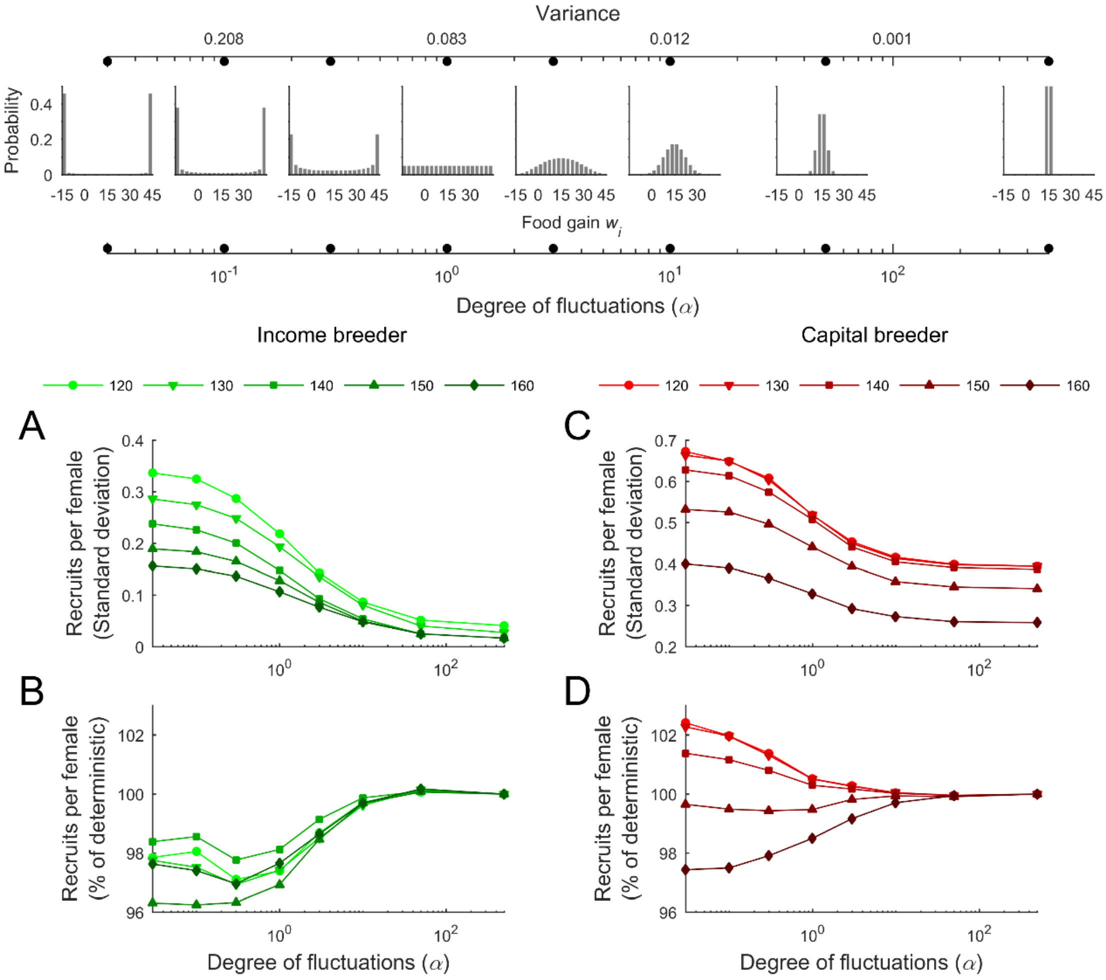

Fig. 4. Mean and variance of number of produced recruits in populations exposed to fluctuating daily net food gain. Top panels present how the shape and variance of the net food gain distribution depends on parameter α. Black dots in top panels match values of α assumed for scenarios presented in panels A-D. (A, C) Intrapopulation variability of recruitment and (B, D) average number of recruits expressed relatively to recruitment under deterministic food gain. Income and capital breeders are shown in separate columns (see labels at the top of the panels). Presented scenarios differ in spring onset b_s (see the legend).

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PAPER III

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

(*manuscript*)

Phenology of breeding in the capital breeding sea duck common eider is influenced by regional and local conditions

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Abstract

Migratory birds are the prevailing group of birds inhabiting the Arctic region. Their response to climatic change is crucial for understanding of present and future changes in functioning of the northernmost ecosystem of Earth. Hence, there is a growing interest in monitoring of phenology of migration and nesting of birds in the Arctic in relation to the climatic conditions. Here, we analyze data on spring arrival and nesting onset of a long-distance migratory sea duck common eider (*Somateria mollissima*).

The observations of arriving males and females were performed in Adventfjorden along ca. 9 km coastline, near Longyearbyen, Svalbard (78°13'N 15°33'E). The birds were counted with interval of 1-2 days from late March until early June in years 2015-2020. The observed birds overwinter in two wintering sites located ca. 1300 and 1700 km from the breeding grounds in Svalbard. Common eiders were counted also in the colony located outside Longyearbyen. Birds were counted daily in years 2016-2019 during breeding period. The data on timing of spring arrival were correlated with the Arctic Oscillation Index, while nesting onset were analysed for impact of several characteristics of snow, temperature, and wind conditions: annual maximum depth of snow, date of maximal snow depth, date of snow free conditions in spring, mean temperature, mean wind speed, and the number of days with wind speed over 8 m/s.

The data were presented graphically and statistically analysed. Due to relatively low number of studied years, the effect of climatic drivers on phenology was tested one by one, to find potential correlations with climatic variables. We found that migrations timing of the studied population of common eiders depends on the Arctic Oscillation Index, and that the timing of snow melt correlates with the timing of nesting onset by common eider females.

Our paper reports from the monitoring study that shows important correlations between timing of spring migration and nesting with climatic characteristics for a high latitude migratory species. Continuation of this monitoring would provide a material for a more comprehensive analysis of impact of the climatic factors on phenology of migratory birds nesting in the Arctic.

Keywords: clutch size, breeding synchrony, timing of breeding, capital breeding, Common eider, dynamic programming, warming

Introduction

Long-range migratory species depend on benign environmental conditions over large spatial scales to successfully complete their life cycles. Such migration is commonly a solution to seasonal environments, where individuals have evolved to schedule specific activities to particular locations over the year to maximize fitness (Barta et al. 2008). A typical migratory life cycle is divided into two or more phases separated by migration episodes, such that the timing of migration decisions, as well as any other biological events that have consequences for timing, become crucial for reproductive success and fitness (McNamara and Houston 2008).

Birds surpass most other groups of organisms in their capacity for migration. For migratory birds the timing of spring migration is a key factor shaping the duration of the breeding season with consequences for life history events throughout the year. Early arrival to breeding grounds provides not only more time for breeding and its preparations, but often involves also better access to favorable territories or mates. Being prepared early increases the probability of well-timed match between offspring needs and seasonal food sources (Both and Visser 2001, van der Jeugd et al. 2009). On the other hand, early arrival comes with a risk of uncertain conditions and misused time if spring starts late (Iwasa and Levin 1995). The phenology of breeding can be also subjected to other evolutionary compromises, as for example parent-offspring conflict (Trivers 1974, Ejsmond et al. *in review*). In some birds, early breeding means decreased reproductive capabilities of females but increased offspring survival (Lack 1968, Barta et al. 2008).

For migratory birds, favorable environmental conditions can be broken down into two consecutive challenges. The main criterion for success is that breeding itself is well timed. Since breeding is a composite phenomenon, it may vary between species and populations whether temporal constraints from the environment act most strongly on mating, nest-building, egg-laying, brooding, hatching, caring, fledging, and potentially other elements. For many species, the main success criterion is that eggs hatch when abundant food is available to feed the chicks (van der Jeugd et al. 2009, Dickey et al. 2008, Aubry et al. 2013, Ross et al. 2018). At high latitudes snow cover may prevent nest-building but also delay spring productivity more generally, so that it acts as a determinant for successful reproduction (Liebezeit et al. 2014).

Another important challenge is to time migration to arrive when breeding is optimal but not earlier. The advantage of early arrival can be outweighed by a risk of facing adverse conditions if spring starts late (Iwasa and Levin 1995). Long lasting adverse condition prior the breeding period may elevate mortality of adults, and decrease their body condition. Arriving to early would be also a waste of time that could be better spent for gathering internal reserves at the stop-over or overwintering grounds (Black et al. 2014, Lehikoinen and Sparks 2010). The decision of when to migrate is complicated by the obvious fact that it needs to be based on local cues at the overwintering area when the bird departs, although it is the conditions at the breeding area when it arrives that matter (Winkler et al. 2014). Hence, the studies that seek for spatial and temporal climatic correlates that enable such prediction are of high importance in understanding the drivers of phenologies of migratory birds.

Here we present observations of arrival and nesting dates from a population of a long-lived sea duck, the common eider (*Somateria mollissima*), breeding in the Arctic. The common eiders are a textbook example of a capital breeder constrained by the short summer available for breeding (Waltho and Coulson 2015). The eiders breeding in the Arctic need to migrate over a thousand of kilometers during spring migration to reach reproductive grounds, and upon arrival gather reserves for egg-laying and brooding (Hanssen et al. 2016). Common eider females rely on the reserves stored prior to nesting and do not eat during the ca. 25-day egg laying and incubation period (Parker and Holm 1990, Gabrielsen et al. 1991). Although studies of capital breeding consider females, a male also needs to refuel stores after the long migration to successfully defend his female from other males and accompany her to the nesting colony (Criscuolo et al. 2000). After arriving at the breeding grounds, both males and females forage intensively for several weeks before nesting begins (Waltho and Coulson 2015, Hansen et al. 2016). However, the time dedicated to foraging, i.e. the period between arrival and nesting onset, depends on climatic conditions due to year-to-year variability in climatic conditions. This variability in climate modifies the time available for common eiders to build the reserves needed for breeding, and local weather may thus affect both the efficacy of pre-breeding fatting and of success during the nesting period itself.

Strong environmental influences on optimal migration and breeding strategies need to be considered in the context of the forecasted climate change of high-latitude regions. The recorded and forecasted changes in dates of snow and sea ice melt portray polar regions as being most heavily affected by climate change (Førland et al. 2011, IPCC 2013, Nordli et al. 2014). Expected changes include increasing mean temperature 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). Many of these changes in weather pattern affect large regions and are slow to change, so that migrating birds potentially could sense effects at their overwintering grounds that are correlated with breeding conditions elsewhere. However, the advancement of spring due to Arctic warming is expected to accelerate over years as snow-free land surface decreases the albedo and further amplifies heating (Chapin et al. 2005).

For the common eider, the main biological consequences of warming at high latitudes are likely increased availability of feeding areas due to earlier sea ice melting and earlier accessibility to nesting sites due to earlier snowmelt. This in turn is expected to favour early-arriving birds, but it is unknown whether their energetic condition at the wintering grounds permits earlier departure, or whether there are local cues there that can inform them that early departure is beneficial. We thus use our counts of arriving to test the hypothesis that common eiders are capable of arriving earlier in years with more rapid spring phenology. We also focus on the breeding period, which is governed by local weather conditions having effects on pre-breeding foraging or on nesting itself.

In this study we present the analysis of the data obtained over 6 years of daily counts of a long-lived and capital breeding sea duck common eider during the spring arrival period. We also analyze observations of nesting eiders collected over 4 years. The data were analyzed in relation to the climatic data and timing of nesting to determine how the capital breeding species responses to changes in environmental conditions.

Methods

Study species and population

The study species is a capital breeding sea duck, the common eider. Our study concerns birds from a population breeding at high latitude Arctic ecosystem. Males and females from the analysed population forage in pre-breeding period in Adventfjorden and breed in a nearby nesting colony outside Longyearbyen, Svalbard (78°13'N 15°33'E). Common eiders breeding in Svalbard migrate from two wintering sites – Northern Norway and Iceland (Hanssen et al. 2016). These wintering grounds are located ca. 1300 and 1700 km from the breeding grounds in Svalbard. Common eider females arriving to breeding grounds can store up to ca. 130% of their lean body mass (Milne 1976). Such an extensive energy storage gathered prior to breeding season is used to cover costs of reproduction, as females lose up to 40% of their body mass during egg laying and 26-day incubation period (Parker and Holm 1990, Gabrielsen et al. 1991).

Arrival observations at the coast

The monitoring of arrival timing was carried out along ca. 9 km of coastline of Adventfjorden. The birds were counted at sea and on the shore from 26 fixed observation points on land (Fig. 1). The counts were performed with interval of 1-2 days in years 2015-2020 starting late March until early June. The common eiders are benthic feeders that dive, usually to less than 2 m, and only occasionally deeper than 10 m, to feed on mussels, crabs, sea urchins and other benthic invertebrates (Guillemette et al. 1993; Bustnes and Lønne 1997). The ducks spent up to a minute below the water surface per a single dive (Ydenberg & Guillemette 1991). Hence, each count was double-checked after around a minute in order to minimize errors of underestimated number of birds in a flock. In order to minimize risk of species misidentification, the birds were counted with binoculars and a scope. Common eiders look distinctly different from other birds at sea in this period, except of female king eiders (*Somateria spectabilis*), that are similar to common eider females from a distance. However, king eiders arrive in the Adventfjord later than the common eiders, and in smaller number. To distinguish between females of common and king eiders, we paid a particular attention to presence of diagnostic characters that allow for discriminating between the two species. From the high-resolution counts of eiders at sea we constructed the following metrics to describe the annual arrival dynamics: i) day of year when counts first exceed 3% of maximal number of males and females; ii) day of year when counts first exceed 50% of maximal number of males and females; iii) synchrony of arrival: number of days first exceeding 10 and 90% of maximal number of males and females. We used the day when counts exceed 3% of maximal number as a measure of beginning of spring arrival. This means we ignored a few first individuals observed at sea, because it is rather common that small number of eiders overwinter in west coast of Svalbard (Hanssen et al. 2016, G. Bangjord pers. comm.). Thus, these birds might have been noted at the very early counts.

Nesting observations at a breeding colony

Common eiders often breed in distinct colonies and generally show the tendency to return to the same nesting area year after year. One such a nesting colony outside Longyearbyen was monitored every day in years 2016-2019 (*n*=4) from 1 May to 30 July. The common eiders were counted with using binoculars and identified to sex. Because we used visual observations, we did not distinguish whether a female is in the phase of egg-laying or incubation. Hence, we used numbers of females observed within the clearly defined nesting area as a measure of nesting phenology. The counts run with a high temporal resolution at the nesting colony were used to calculate the following annual metrics: i) day of first nest in the colony (day of year); ii) day of median nest (day of year); iii) days between 10 and 90 percentiles as a measure of synchrony (days) (see Table 1). The day of first nest in the colony, assumed also as start of egg laying by a female, match the first moment at which a female was observed to occupy exactly the same nest location in the colony for more than 2 consecutive days.

Environmental data overview

For the data on spring arrival of eiders from the studied population, we focused on the effects of the large-scale atmospheric teleconnectivity, the Arctic Oscillation, which embraces conditions in wintering habitats, the breeding grounds in Svalbard, and the route between (Thompson & Wallace 1998, Deser 2000, Stenseth et al. 2003). For the timing of nesting we tested effects of several local factors, including weather data and snow conditions.

The Arctic Oscillation is a large-scale atmospheric phenomenon describing how cold Arctic air penetrates and interacts with more southerly air masses. It can be represented by a numerical index of atmospheric pressure anomalies along a latitudinal gradient towards the High Arctic. The Arctic Oscillation Index is hence an index of exchange of atmospheric mass between the Arctic and mid-northern latitudes. (Thompson and Wallace 1998, 2001). In its positive phase, lower sea-level pressure over the High Arctic pulls warmer and wetter air from south while Arctic air penetrates further south and the jet stream is undulating across latitudes, whereas, in the negative phase pressure remains high in the Arctic, keeping the Arctic cold and dry and separated from southerly air masses by a more stable jet stream (Stenseth et al. 2003). Specifically, when the index is high, strong polar vortex winds dominate and the Barents Sea is dominated by stormy weather with increased precipitation that affects Svalbard and the migration route. In contrast, a low Arctic Oscillation index is characterized by weaker trade winds and calmer weather in the Barents Sea and surroundings (Stenseth et al. 2003). Data (2015-2020) of the Arctic Oscillation winter index (January through March) were obtained from the Climate Prediction Center at the National Oceanic and Atmospheric Administration, USA (https://www.cpc.ncep.noaa.gov/products/precip/CWlink/daily_ao_index/ao.shtml).

For local weather conditions, we focused on the effects of snow, temperature, and wind during the period before and around nest initiation. Local weather data measured at the Longyearbyen Airport, i.e. ca. 10 km from the location of the breeding colony, were obtained from The Norwegian Meteorological Institute (https://www.met.no/en/free-meteorological-data). From these, we extracted the following metrics: i) recorded annual maximum depth of snow (cm), ii) day of year when maximum snow depth was recorded, iii) day of first observation of snow free conditions in spring, iv) the number of days between day of max snow depth and no snow cover. We also calculated measures of the prevailing weather conditions in the pre-breeding period i.e. between 15 April and 15 May: v) mean temperature, vi) mean wind speed between, and vii) number of days with wind speed over 8 m/s (see Table 1).

Statistical analyses

A challenge for detecting environmental drivers for the observed phenology in this study is that the sample size in terms of number of years observed was low for both arrival and colony data (4-6 years; see above). This means that drivers need to be tested one by one, and any association between variables need to be very strong for the test to approach common levels for statistical significance. The analyses therefore have the flavour of being somewhat exploratory in their character, but with such a limited sample size there are no other options. The time-series are also too short for regular time-series analysis with lagged temporal effects. We therefore retorted one-dimensional generalized linear models using the function glm() in R, which allows analysis of response variables with distributions different than the standard normal distribution. The glm() function was used to fit generalized linear models and we report the single linear predictor including its standard error distribution and statistical significance (R Core Team 2019). All statistical analyses were performed in R version 3.5.3 (R Core Team 2019).

Results

Timing of arrival and its global climatic correlates

Spring arrivals of common eiders began around day 90 in all years with dynamics of arrivals exceeding 3% and 50% of the number of arriving birds on average at 99 and 130 day of year, respectively (Table 1). Eiders from the studied populations usually completed their spring migration in slightly more than one month (Table 1). There was a tendency that maximum number of eiders increased from year to year over the documented period, but qualitatively arrival patterns look similar across years (Fig. 2.). The timing of migration, measured by the date of arrival of the half of the population, correlated with the Arctic Oscillation Index, i.e. the higher the Arctic Oscillation Index the later the males and females of common eider arrive to Adventfjord in spring (Table 2). Arriving females also tend to arrive in a more synchronous manner in years with higher Arctic Oscillation Index (Table 2).

Timing of nesting and its local climatic

Nesting, approximated by the presence of females in the colony (see Methods for details), began on average around day 142 with ca. 12 days needed for 90% of the breeding population to start their nesting (Table 1). A switch of the studied population from pre-breeding foraging to breeding corresponded with a switch of mean air temperatures to above zero levels (Fig. 3). Low number of studied years of breeding phenology decreased the power of the used statistical analyses. However, even with a limited range of four years data of monitoring, we were able to detect correlations between local climatic conditions and the timing of nesting, measured by the date at which half of the females in the colony was recorded (Table 3). Females postponed the timing of nesting in years with late snow-melt conditions characterized by first snow-free day, and likely the snow-melt period (Table 3)

Discussion

In this work what we refer to as arrivals are not necessarily the inflow of new birds to Svalbard, but counts at the coast where eiders spend weeks foraging prior to nesting. The counts thus include new arrivals as well as those already present, and our observations cannot distinguish between eiders that move to and from adjacent areas from those that are more stably resident in Adventfjorden. With those caveats, the birds counted at the coast are interpreted as the arriving population and its rate of increase assumed to reflect the rate of new arrivals. However, what matters the most from the perspective of reproductive biology is that the timing of spring arrival partially outlines the period available for foraging prior to nesting. In common eider, nesting onset terminates the mentioned time period available for improving body condition (Waltho and Coulson 2015). This in particular influences the reproductive capabilities of this capital breeders, i.e. a species for which the body reserves gathered prior to breeding are prevailing part of resources allocated to reproduction (cf. Drent and Daan 1980). Breeding as early as possible for capital breeders is not necessarily optimal from parents' perspective, who aim at maximizing the number of produced high quality eggs; mothers foraging for longer are able to produce more eggs but reduced the time left for offspring to develop (Rowe et al. 1994, Ejsmond et al. *in review*). The mentioned above evolutionary trade-offs interact with climatic and ecological factors which result in high intra- and interspecific variability of arrival timing of migratory birds.

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 in autumn 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 recover and prepare for autumn migration (e.g. Waltho and Coulson 2015). Hence, starting breeding early is a key component of fitness in migratory birds breeding at high latitudes.

In recent decades seasonal cycles of temperature and food availability across the Earth have been disrupted due to varies changes of climatic conditions. These changes of climatic conditions are uneven with pronounced differences in variation at wintering and stopover sites in comparison to more directional changes in breeding grounds of the Arctic. Choosing the right moment for spring migration can be challenging for birds migrating to Arctic areas in order to breed, as they need to relay on cues available at the wintering grounds or stopover sites located hundreds of kilometers from their breeding grounds. The degree to which climatic cues perceived at wintering and stopover sites represent conditions at breeding grounds can be low which makes taking the optimal decision on arrival timing elusive. Our work shows that timing of spring migration is related to Arctic Oscillation index. Although, our work does not answer the question if the arrival timing of the common eiders will change along with climatic warming of the Arctic, we believe that the strong correlation between migration phenology and Arctic Oscillation index is an important element that facilitate forecasting this response. Our analyses revealed also that the timing of snow melt tend to correlate with timing of nesting of common eiders. This relationship, considered in the light of forecasted changes of snow melt timing to earlier dates (Førland et al. 2011, IPCC 2013, Nordli et al. 2014), further adds to an expectation that climate warming can induce changes in phenology of migration and nesting of common eiders.

Among migratory birds, males often arrive on breeding areas earlier than females. This phenomenon, so called protandry, has been observed in songbirds, shorebirds and other groups (e.g. Hötker 2002, Coppack 2006, Zając 2015, Morbey and Ydenberg 2001). General and taxa-specific hypotheses have been proposed to explain the adaptive significance of this pattern (reviewed in Morbey and Ydenberg 2001). With reference to migratory birds, two hypotheses are given as the most relevant. The rank advantage hypothesis considers territorial species, in which the protandry is a consequence of male-to-male competition for territories (Ketterson and Nolan 1976, Myers 1981) and indirectly affects fitness (Morbey and Ydenberg 2001). The mate opportunity hypothesis (Wiklund &

Fagerström 1977; Iwasa et al. 1983; Parker & Courtney 1983, Kokko et al. 2006) assumes selection on males to arrive earlier than females in order to maximize chances for mating and provides direct fitness consequences for males (Wiklund and Fagerström 1977). It is because males compete for females and in case of sex-biased spring arrival, the chance for mating is usually improved more in males than in females (Kokko *et al.* 2006). Thus, protandry can be adaptive in migration to nesting area. The common eider, a monogamous migrant, is potentially protandrous. The sex-specific differences in timing of eiders spring arrival has, to our knowledge, not been investigated. While the rank advantage hypothesis does not apply to the common eider, there has been documented some cues, such as a male biased sex ratio in southern populations (Kilpi *et al.* 2003, Mosbech *et al.* 2006), suggesting a potential protandry in this species. Hence, also because of strong male-male competition, the mate opportunity hypothesis fits the life-history of this species. As a future direction we will use our data on arrival dates of males and females, and proportion of males in the arriving population to test elements and predictions derived from the mentioned hypotheses. We would also like to test if variation in arrival dates translates into dates of nesting onset which has not been addresses in the literature before (Hanssen et at. 2016).

To conclude, this paper presents exploratory analyses of empirical data on migration and breeding phenology of common eiders, collected in 2015-2020 nearby Longyearbyen (Svalbard). Our monitoring study run over few years allowed us to find some connection between local and global climatic conditions and common eiders phenology. Continuation of our monitoring study in the future would increase the power of used statistical tests and provide a material for comprehensive analysis of climate induced changes in phenology of migration and breeding of the common eider.

Figures and tables

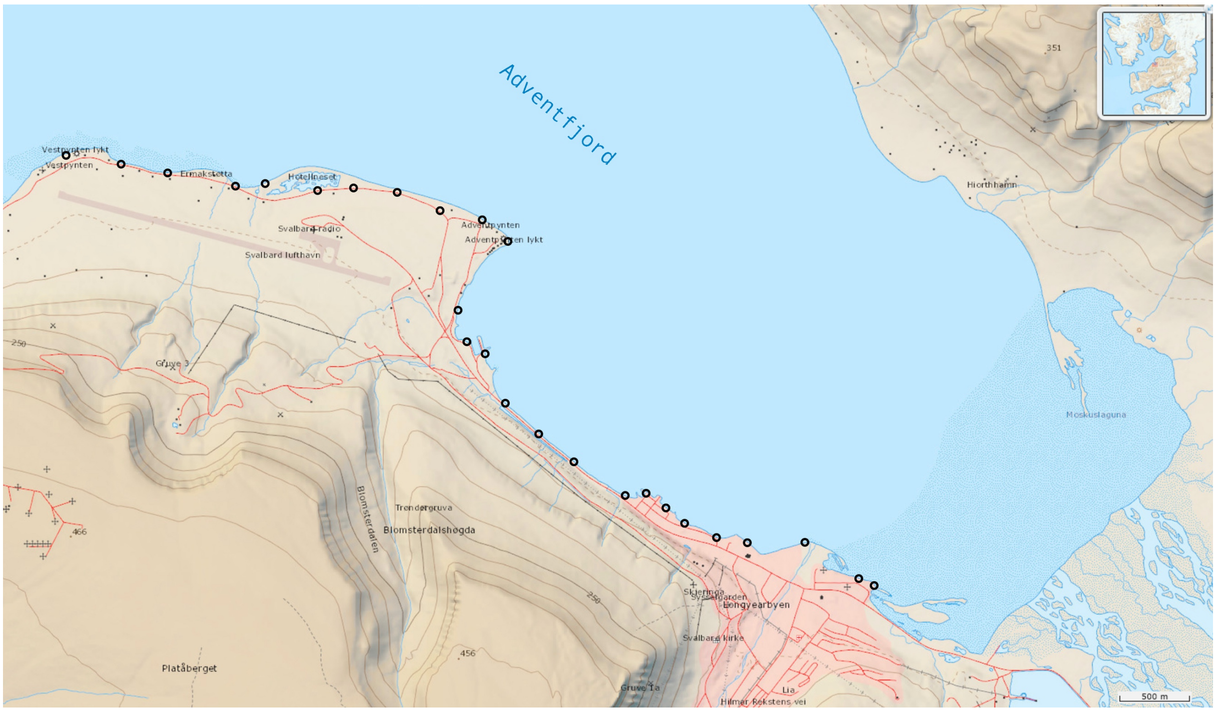

Fig. 1. Observation points in Adventfjord. The density of points was fixed in field so that eider flocks would not be overlooked due to various landforms.

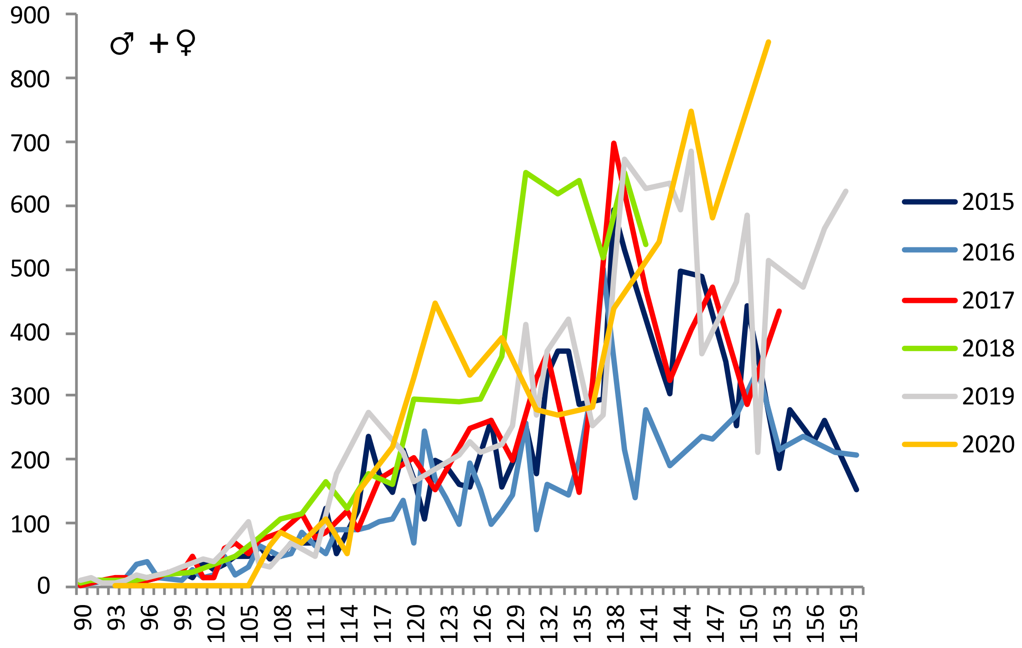

Fig. 2. Number of the observed common eiders in Adventfjord in 2015-2020 based on daily counts.

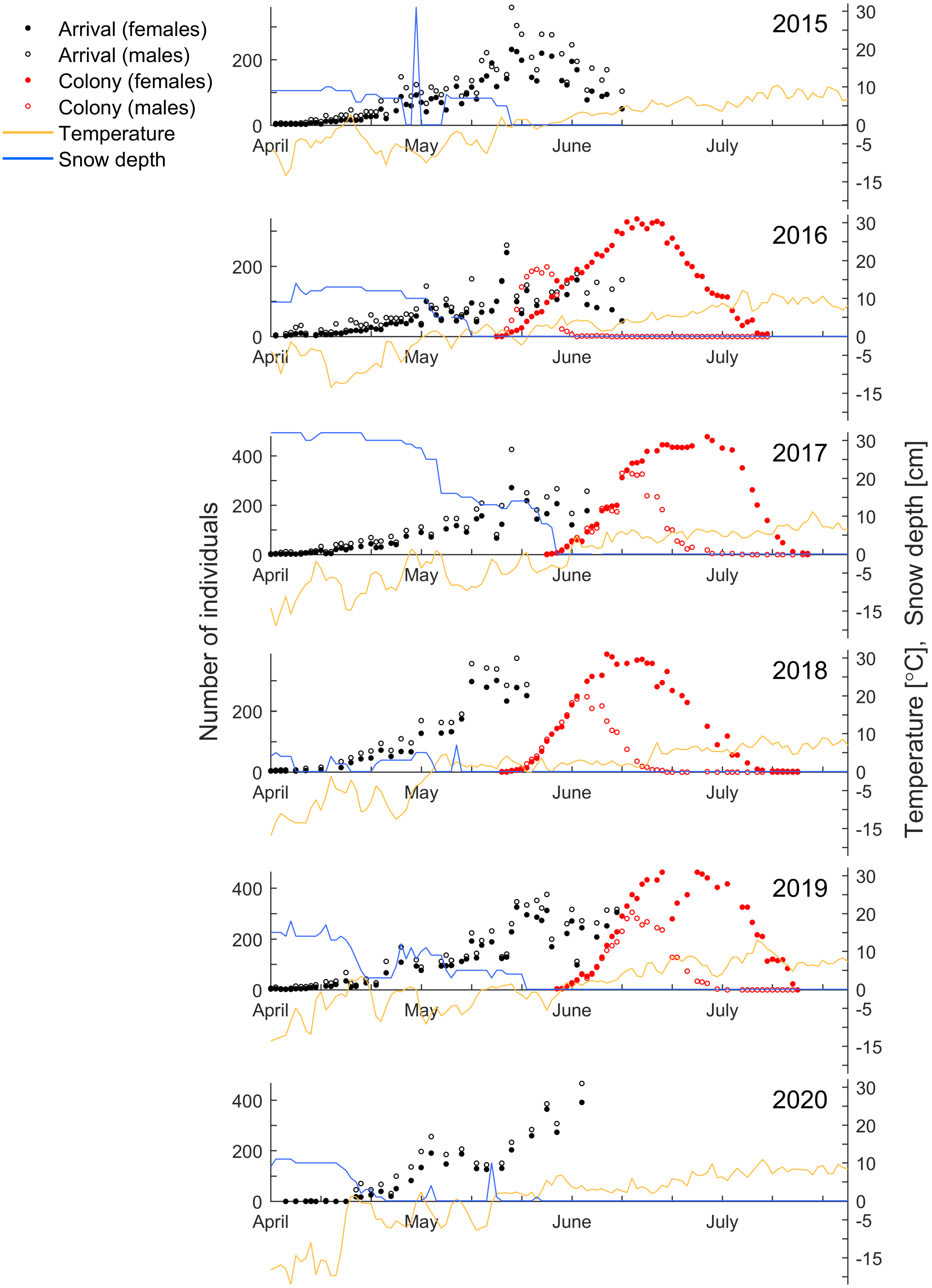

Fig. 3. Illustration of the number of observed common eider females and males in Adventfjord, during spring migration, and breeding colony presented along with local climatic data of mean temperature and snow depth (see legend).

Table 1. Metrics of arrival and breeding. Annual metrics calculated from arrival and breeding counts and used in statistical analysis. F = females, M = males.

	Unit	2015		2016		2017		2018		2019		2020	
Arrival phenology at the coast		**F**	**M**	**F**	**M**	**F**	**M**	**F**	**M**	**F**	**M**	**F**	**M**
First arrivals: Day when counts first exceed 3% of max	doy	99	96	94	93	98	98	102	98	99	96	108	105
Median arrival: Day when counts first exceed 50% of max	doy	131	131	123	121	130	132	126	127	131	131	139	139
Synchrony: Period between days first exceeding 10 and 90% of max	days	29	34	28	43	33	34	25	27	29	37	34	42
Breeding phenology in the nesting colony		**F**	**M**	**F**	**M**	**F**	**M**	**F**	**M**	**F**	**M**	**F**	**M**
First nesters: Day when counts first exceed 1% of max	doy			137	137	147	146	138	138	149	147		
Median nest: Day when counts first exceed 50% of max	doy			151	140	160	156	150	148	160	157		
Synchrony: Period between days first exceeding 10 and 90% of max	days			20	5	18	10	14	9	10	10		

Table 2. Relationship between global climatic conditions and timing of spring arrival. The outcomes of the analysis of large-scale Arctic Oscillation Index with arrival phenology of eiders to Adventfjorden. Relationships with statistical significance *p*<0.05 are given in bold and those with *p*<0.1 are given in italics.

		First arrivals (doy)		**Median arrival (doy)**		**Synchrony (days)**	
Driver	**Sex**	**Estimate**	***p***	**Estimate**	***p***	**Estimate**	***p***
Arctic Oscillation Index	Females	2.8±1.4	0.11	**4.4±0.5**	**<0.001**	*2.2±0.8*	*0.051*
	Males	*2.7±1.0*	*0.061*	**4.6±0.9**	**<0.01**	1.8±2.3	0.47

Table 3. Relationship between local climatic conditions and timing of nesting, and spring arrival. Outcome of statistical tests of potential drivers of nesting phenology in common eiders. From the four years of nest counts in the breeding colony we constructed simple annual metrics to describe breeding phenology. On these data (*n*=4) we performed general linear models on one metric at the time to identify statistically significant drivers for nesting phenology. Relationships with *p*<0.1 are given in bold.

		First nests (doy)		**Median nest (doy)**		**Synchrony (days)**	
Sex	**Environmental variable**	**Estimate**	***p***	**Estimate**	***P***	**Estimate**	***p***
Females	Max snow depth (cm)	0.37±0.28	0.31	0.39±0.20	0.19	0.10±0.27	0.75
	Day of max snow depth (doy)	−0.50±0.38	0.31	−0.49±0.31	0.26	0.09±0.37	0.83
	First snow-free day (doy)	0.48±0.19	0.13	**0.47±0.11**	**0.051**	−0.01±0.28	0.97
	Snow-melt period (days)	0.29±0.13	0.15	**0.28±0.08**	**0.076**	−0.02±0.17	0.90
	Mean temperature (°C)	−1.50 ±2.11	0.55	−1.64±1.78	0.45	−0.77±1.62	0.68
	Mean wind speed (m/s)	0.08±9.8	0.99	1.2±8.8	0.91	2.7±6.8	0.73
	Days of winds >8m/s (days)	2.3±1.9	0.35	2.3±1.6	0.28	−0.1±1.8	0.95
Males	Max snow depth (cm)	0.33±0.23	0.28	0.40±0.41	0.43	0.08±0.14	0.62
	Day of max snow depth (doy)	−0.42±0.33	0.34	−0.49±0.31	0.26	−0.02±0.20	0.93
	First snow-free day (doy)	0.42±0.15	0.11	0.52±0.34	0.27	0.11±0.13	0.50
	Snow-melt period (days)	0.25±0.11	0.15	0.27±0.24	0.38	0.05±0.09	0.66
	Mean temperature (°C)	−1.4±1.7	0.50	−2.2±2.6	0.48	−0.64±0.80	0.51
	Mean wind speed (m/s)	−0.27±8.4	0.98	−6.3±12	0.65	−3.4±3.0	0.37
	Days of winds >8m/s (days)	1.9±1.7	0.37	1.5±3.1	0.67	0±1	1

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PAPER IV

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RESEARCH ARTICLE

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 $i = \{1, 2, \ldots, n\}$. 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-α_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).

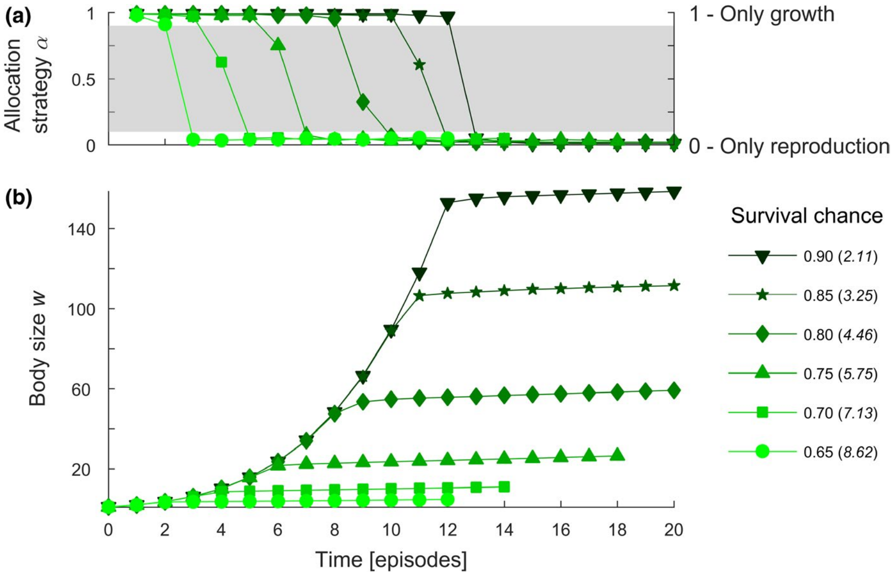

FIGURE 1 Allocation to growth and reproduction in homogenous environments. (a) In a homogeneous environment, modelled organisms switch the allocation of resources from growth to reproduction in less than three episodes of mixed allocation out of 20-time episodes per generation. Maturation occurs later 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 allocation, the degree to which females accompany reproduction with growth depends on the difference between optimal size at safe and risky sites (Figure 3a,c vs. b,d and Figure S4 in Appendix S1). Under long periods of mixed allocation, the growth curves become complex with allocation to growth that remains constant or periodically accelerates during adult life (Figure 3b and the corresponding concave upward growth curves in Figure 3d). A female that has survived initial time episodes faces the dilemma of whether to keep growing or allocate to reproduction, and the only available information about risk is the fact that she is still alive. Females that exhibit complex growth are first pessimistic about their prospects and mature early. By living longer they become optimistic about local conditions, thus allocation to growth accelerates in the middle of their life span (Figure 3b,d). Females accelerate their growth only when the time episodes per generation are infrequent and long (Figure 4a,b vs. c,d), which obliges them to bet on their fate and set their allocation strategy for a relatively longer part of their maximal life span. Numerous episodes per generation, a proxy of continuous reproduction, allow females to make the allocation decisions frequently in life; the mixed allocation remains optimal but allocation to growth tends to only decrease over the adult life (Figure 4e,f).

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

4 | DISCUSSION

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

Heterogeneous environments, with respect to mortality risk, that are stable over time but spatially structured, can select for indeterminate growth and mixed allocation to growth and reproduction in short-lived organisms. Previous contributions to life-history theory reveal that mixed allocation is an optimal bet-hedging strategy when mortality risk changes temporarily in a per generation basis (Gurney & Middleton, 1996; King & Roughgarden, 1982; Taylor & Gabriel, 1993; Wong & Ackerly, 2005). In our model, growth accompanying reproduction selected for in spatially heterogeneous environments also serves as a bet-hedging strategy because offspring produced by females are dispersed among risky and safe sites in the environment.

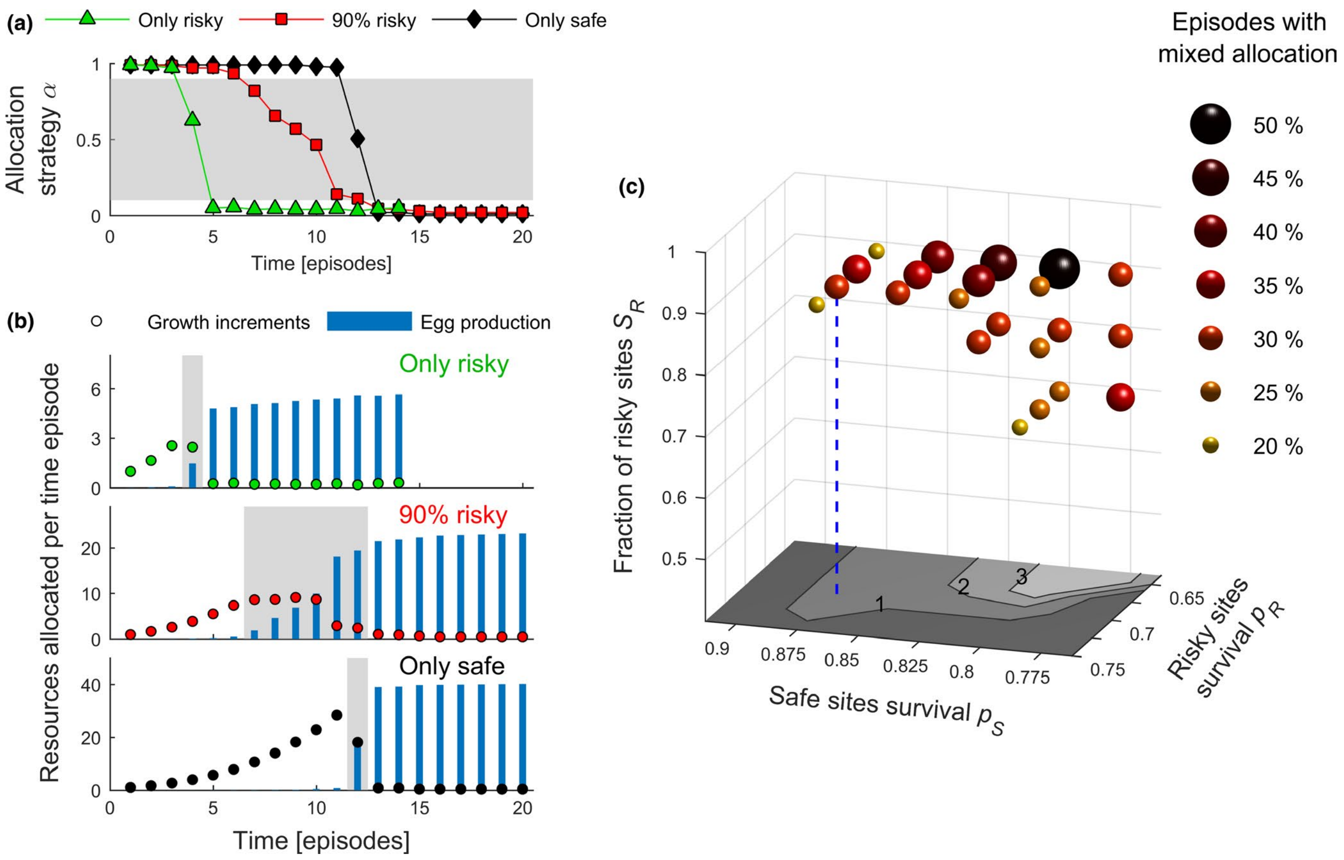

FIGURE 2 Optimal allocation strategies and resulting resource allocation patterns in homogenous and heterogeneous environments. (a) In a heterogeneous environment, the mixed allocation is selected for (red squares), whereas homogenous environments select for a 'bang-bang' switching (green triangles and black diamonds). (a, b) The shaded area depicts simultaneous allocation to growth and reproduction. The modelled environment consists of risky and safe sites with a survival probability of one-time episode equal to $p_R = 0.7$ and $p_S = 0.875$. Allocation strategies, growth increments and egg production are presented for episodes to which organisms survive with a probability >0.005. (c) The proportion of time episodes with mixed allocation per generation is illustrated by the coloured spheres (see the legend). The empty space matches scenarios with a 'bang-bang' switch (see the main text for the definition of mixed allocation). For certain combinations of survival probabilities p_S and p_R, the mixed allocation appears at more than one level of the considered proportion of risky sites S_R (the number of levels with mixed allocation is illustrated by the grey contour plot). The blue dashed line indicates the survival chance in risky and safe sites of the scenario investigated in a and b. (a–c) The presented allocation strategies are median values calculated across 20 simulation replicates. For illustration of individual variation in allocation strategies see Figure S3 in Appendix S1

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

Living organisms undertake actions that are dependent on the cues and signals perceived from their environment, but the ability to perceive information about a determinant of vital rates can be elusive. Whereas food availability or thermal conditions translate to clear-cut physiological signals, mortality risk is much more difficult to be assessed for an organism, in particular when variable in space or time. However, individual life histories of short-lived indeterminate growers can be altered by cues of predator presence, as for example, mechanical and visual stimuli, predator-derived kairomones or chemical odours of consumed prey (e.g. Czarnoleski, Muller, Kierat, Gryczkowski, & Chybowski, 2011; Lass & Spaak, 2003; Ślusarczyk & Rygielska, 2004). Mortality rate is an additive demographic parameter that can be divided into components that correlate with local conditions and the background mortality. In our work, females were unable to gather any information about mortality risk, but the conclusions are also valid if components of mortality rate correlate poorly with environmental conditions and cannot be perceived in a reliable manner.

There are several taxa-specific hypotheses on the evolution of growth following maturation that are worth mentioning. In plants, structural constraints of reproductive investment may lead to simultaneous growth and reproduction (Ioslovich & Gutman, 2005; Kozłowski & Ziółko, 1988). However, selection exerted by herbivores seems to be a more general explanation (see Janczur, 2009) as the great majority of plants synthesize defensive chemicals

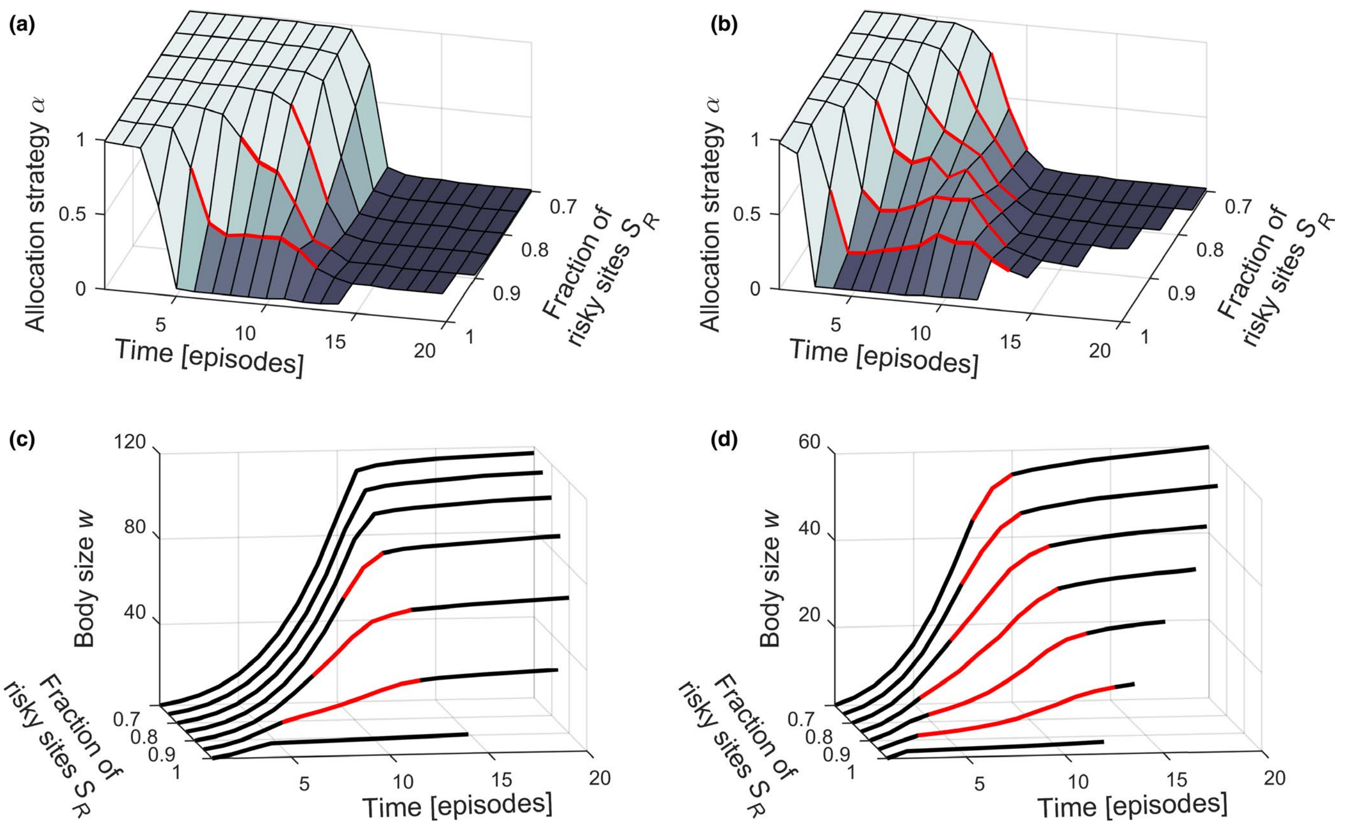

FIGURE 3 Allocation strategies and resulting growth curves in heterogeneous environments. (a, b) Resource allocation between growth (α = 1) and reproduction (α = 0) in relation to time. (a–c) Red lines illustrate time episodes and resulting growth phases arising due to mixed allocation to growth and reproduction. Survival probabilities of one-time episode in risky and safe sites are equal to 0.7 and 0.875 (a, c) or 0.65 and 0.825 (b, d). The degree to which growing organisms reproduce depends on the combination of mortality rates in risky and safe sites (compare a, c with b, d, see also Figure S5 in Appendix S1). More frequent safe sites in the environment selected for a 'bang-bang' switch and determinate growth (see main text). When the period of mixed allocation is long, the allocation to growth after maturation may accelerate over a certain part of life. The presented allocation strategies are median values calculated across 100 simulation replicates. For illustration of individual variation in allocation strategies see Figure S3 in Appendix S1. For clarity the figures present optimal allocation strategies in environments with a proportion of risky sites S_R > 0.7. Allocation strategies and growth curves are presented for time episodes to which organisms survive with a probability >0.005

to defend from herbivores (Ejsmond & Provenza, 2018; Foley & Moore, 2005; Strauss, Rudgers, Lau, & Irwin, 2002). Growth accompanying reproduction can also be optimal in populations that grow indefinitely, and age-specific mortality drops throughout life towards a constant value (Engen & Saether, 1994). However, the generality of the finding by Engen and Saether (1994) is unknown, as indeterminate growers rarely evolve in indefinitely growing populations, and unlimited population growth selects for an early maturation (Kozłowski, 1999). Our work adds spatial heterogeneity and metapopulational context to the list of evolutionary drivers of growth accompanying reproduction. Cladocerans, short-lived amphipods and other crustaceans that grow after maturation evolve in metapopulations that, similar to the modelled setup, consist of safe fishless ponds and risky water bodies inhabited by planktivorous fish (Ebert, 2005; Wellborn, 1994; Wellborn & Broughton, 2008). In the presented model, mixed allocation arises from a balance between offspring recruited from risky and safe sites. However, growth accompanying reproduction evolves also in more complex environments that consist of several different types of habitats (see Supporting Information Appendix S1).

Growth that accompanies reproduction in short-lived water invertebrates has been suggested to evolve when both the assimilation of resources and mortality risk increase along with body size (Perrin, Sibly, & Nichols, 1993; Taylor & Gabriel, 1992). The death rates of many planktonic crustaceans are strongly affected by the activity of visual predators, with large species or individuals being exposed to a higher risk of death than small ones (Ebert, 2005; Gliwicz, Slusarczyk, & Slusarczyk, 2001; Slusarczyk, Ochocka, & Cichocka, 2012). However, intraspecific reactions of mortality risk to body size in planktonic crustaceans can be more complex. Large individuals can be selectively predated in amphipods (Wellborn, 1994), but in fast-swimming marine copepods older, and thus, larger, individuals are subjected to the lowest mortality risk on an intraspecific level (Eiane, Aksnes, Ohman, Wood, & Martinussen, 2002; Ohman, 2012; Ohman & Wood, 1996). The size dependence of mortality risk in aquatic environments may also depend on the type of predator, with visual and tactile predators being expected to select for opposed

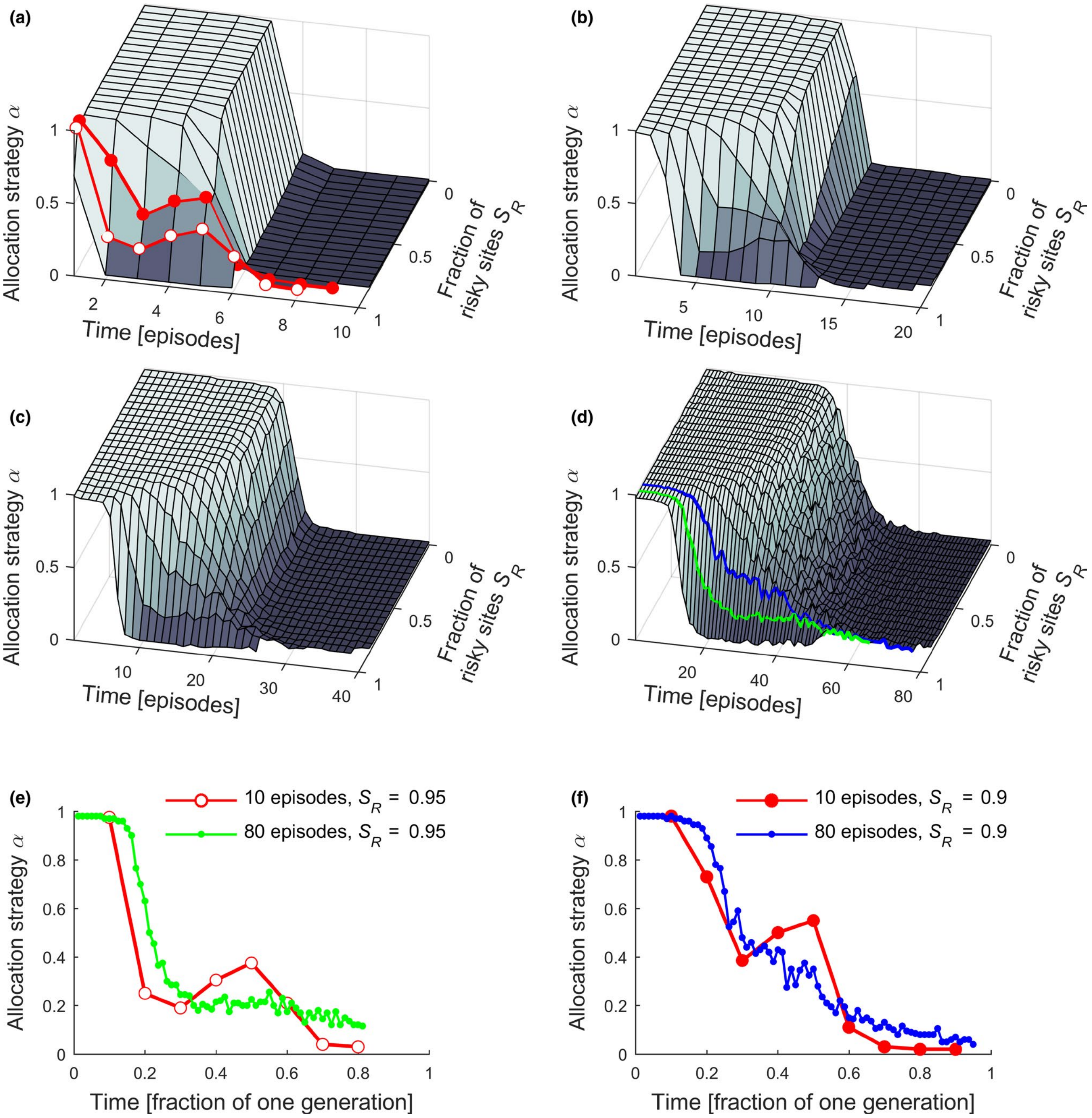

FIGURE 4 The effect of the number of time episodes per generation on the simultaneous allocation to growth and reproduction. (a–f) Resource allocation between growth (α = 1) and reproduction (α = 0) in relation to time. The colour of the lines in (a) and (d) match those presented in (e) and (f). Because 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.

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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).

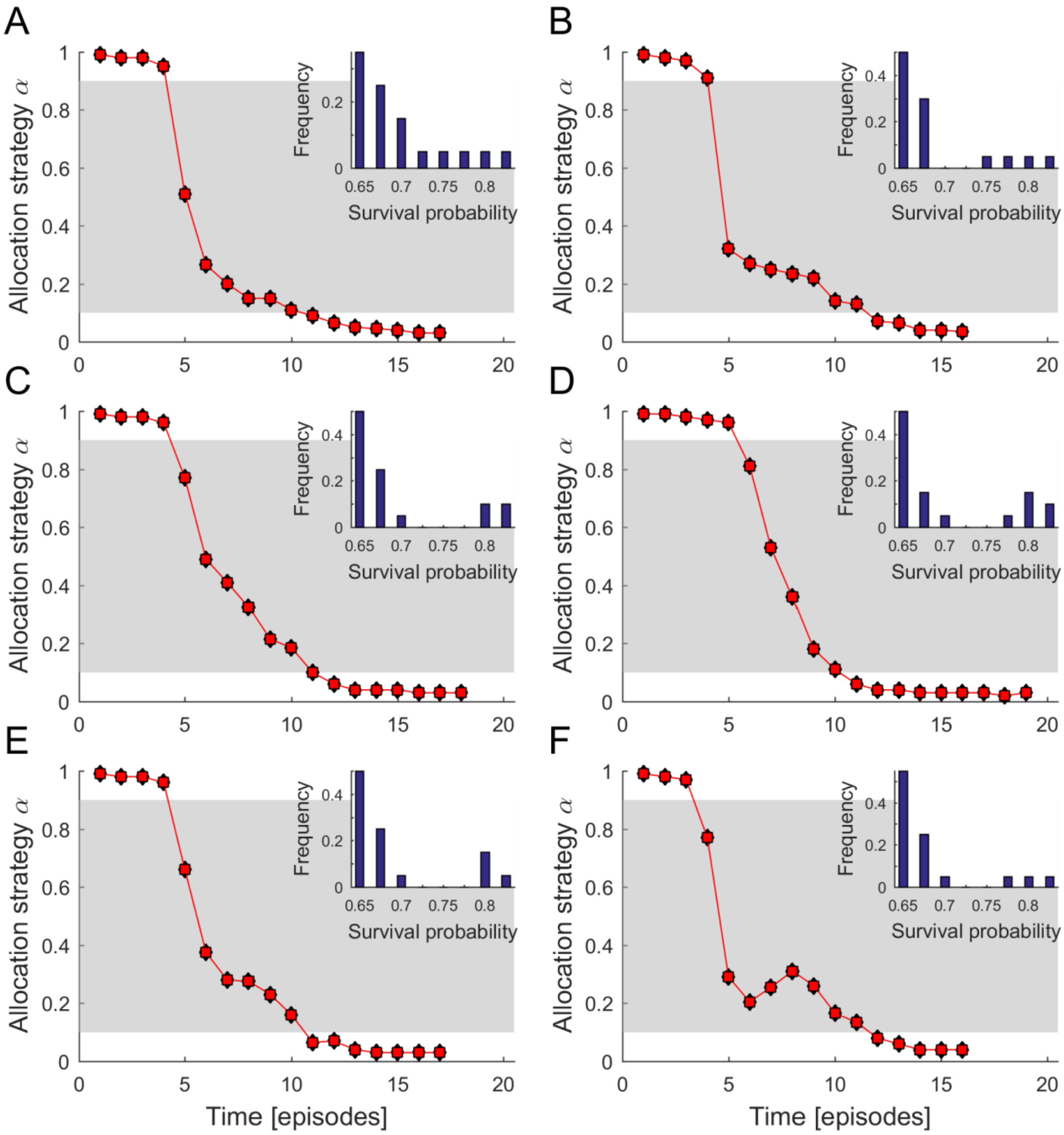

Figure S1. Evolution of mixed allocation to growth and reproduction in an environment with several different kinds of habitats in the environment. Resource allocation between growth (α=1) and reproduction (α=0) in relation to time presented for four exemplary scenarios simulated over 100 000 generations. 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*

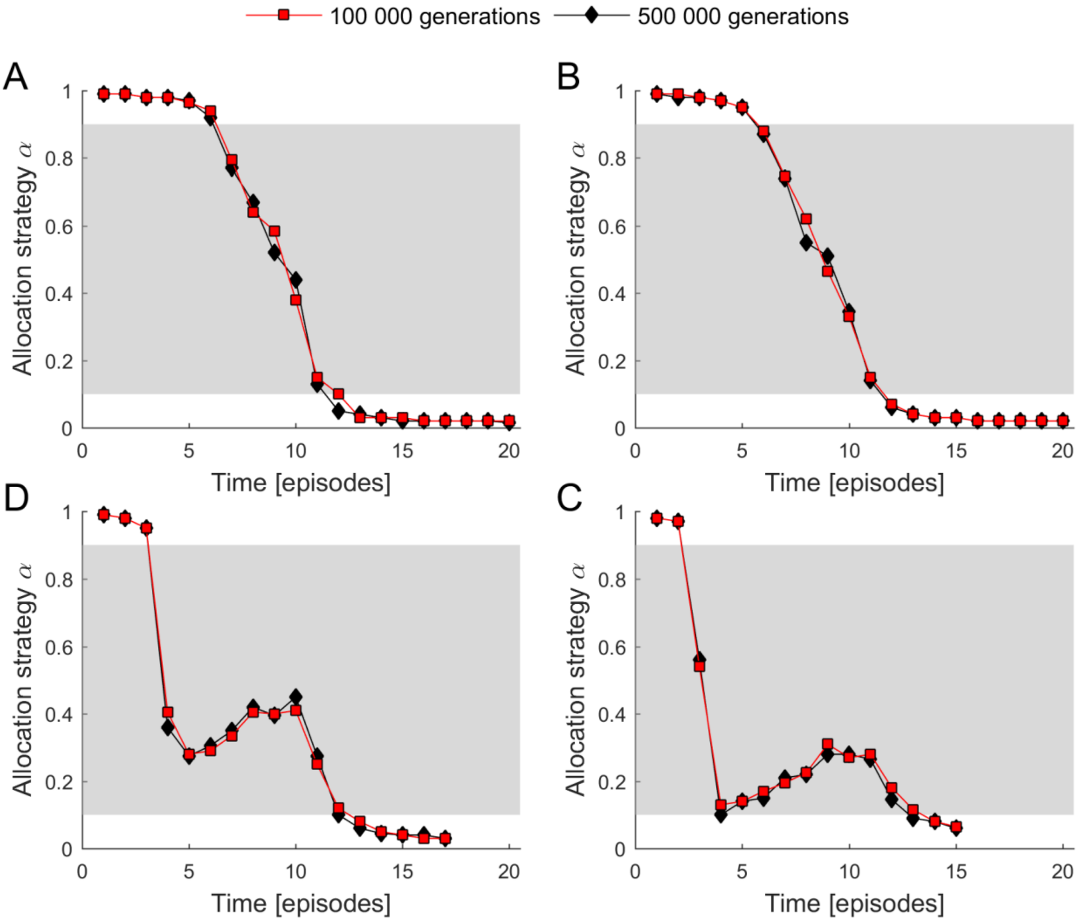

Figure S2. Sensitivity of the model predictions to the changes in simulation time frame. Resource allocation between growth (α=1) and reproduction (α=0) in relation to time for four exemplary scenarios simulated for 100 000 and 500 000 generations. The shaded area depicts simultaneous allocation to growth 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*

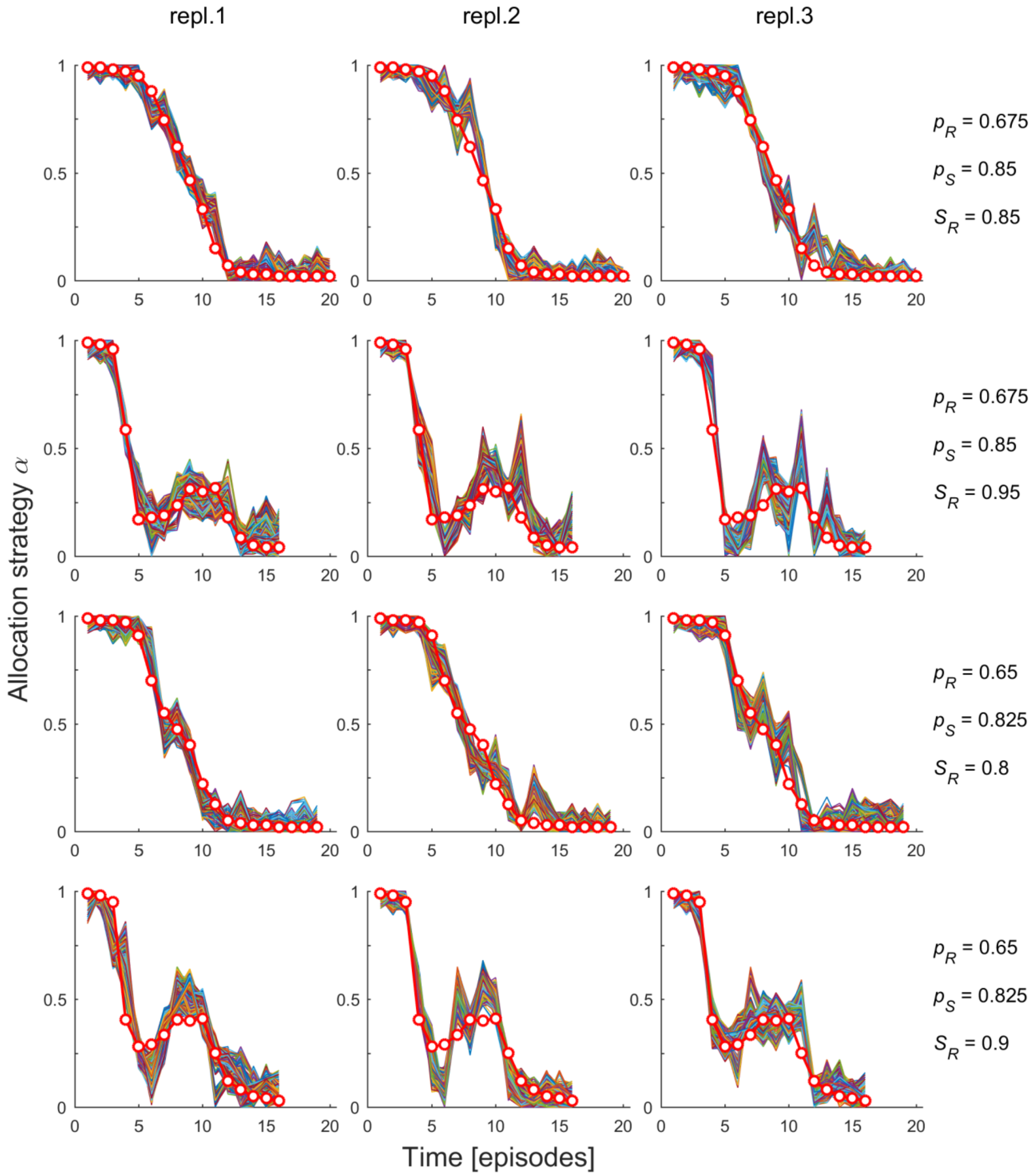

Figure S3. Individual variation in strategies of resource allocation. Resource allocation between growth (α=1) and reproduction (α=0) in relation to time for four exemplary scenarios (number of exemplary replications give above the panels). The fraction of risky sites in the environment S_R, survival 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***

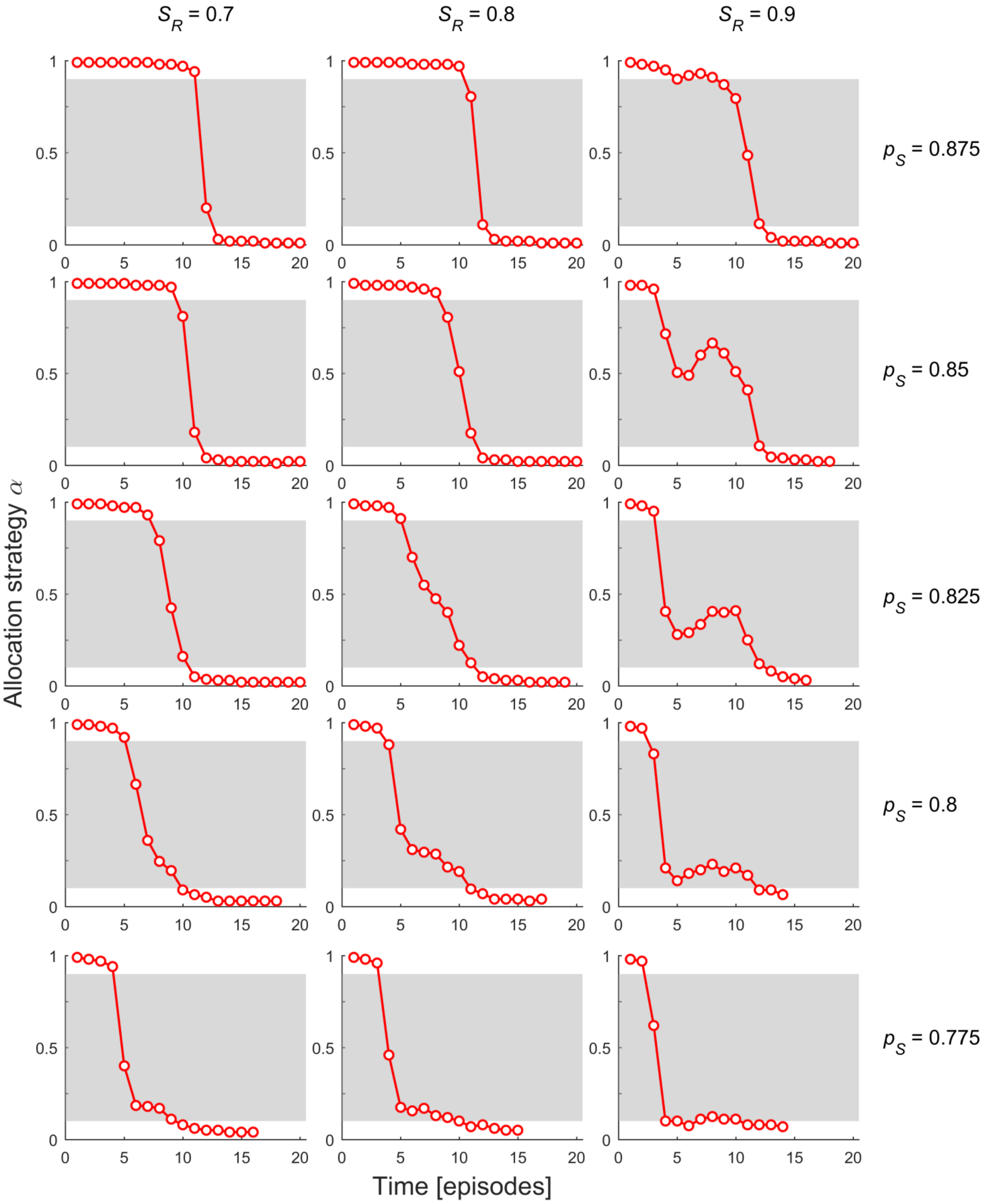

Fig. S4. Allocation strategies in heterogeneous environments differing with respect to risk of death in safe habitats. Resource allocation between growth (α=1) and reproduction (α=0) in relation to time. Survival probabilities of one time episode in risky sites p_R are are equal to 0.65. Survival probability 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.

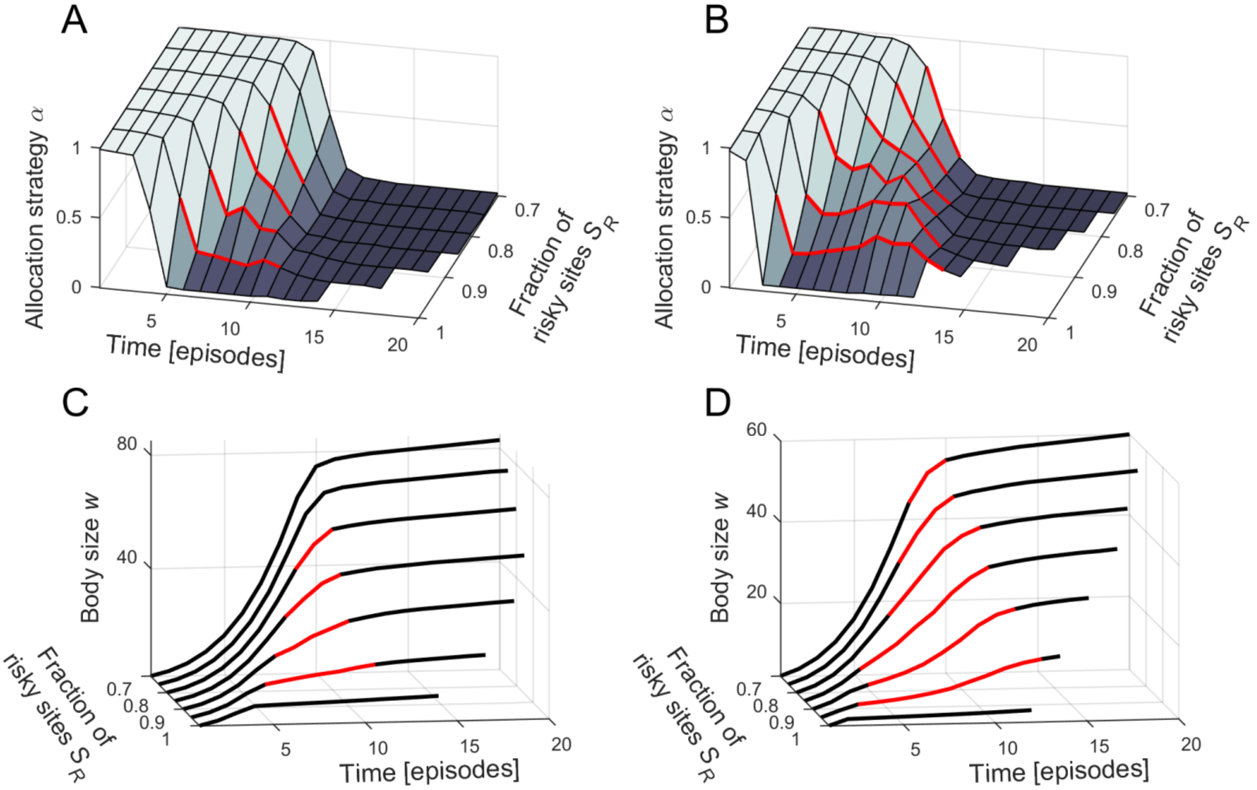

Fig. S5. Allocation strategies and resulting growth curves in heterogeneous environments. (A-B) Resource allocation between growth (α=1) and reproduction (α=0) in relation to time. (A-C) Red lines illustrate time episodes and resulting growth phases arising due to mixed allocation to growth and reproduction. Survival probabilities of one time episode in risky and safe sites are equal to 0.7 and 0.85 (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.