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RESEARCH ARTICLE

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Gradients of season length and mortality risk cause shifts in body size, reserves and reproductive strategies of determinate growers

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Abstract

1. The theory of life-history evolution investigates how growth-reproduction trade-offs drive evolution of body size in uni- and multivoltine (one or more generations per year) arthropods. Existing theory does not predict how the length of the feeding season (season length hereafter) affects body size in semivoltine (i.e., juvenile period longer than 1 year) determinate growers and usually ignores that uni- and semivoltine arthropods accumulate large reserves to cover costs of diapause and future reproduction.
2. Here, we present how the trade-offs between growth, storage and reproduction drive evolution of body mass and reproductive strategy in arthropods with determinate growth. Our life-history model concerns high-latitude marine copepods living in a strongly seasonal environment.
3. We find that small changes in season length and mortality rate translate into abrupt shifts in lean body mass (a proxy for body size). Body size shifts are caused by a change from multi- to uni- and semivoltine life cycles with semivoltine life histories selected for in short seasons and only if background mortality is low. Shifts in the number of generations per year do not translate into shifts in the mass of lipid reserves. The model predicts less reserves the shorter the winter. Season length alone is not a sufficient predictor of the degree of capital breeding. Storing for reproduction is strongly selected for under short season but low mortality rate. Hence, capital breeding contributes to fitness in uni- and semivoltine organisms whereas multivoltines are income breeders. We also show that storing reserves for diapause and capital breeding trades off with adult size of determinately growing arthropods.
4. Our results, in particular regarding optimal body size, reproductive strategy (income-to-capital breeding) and degree of storage are relevant to a number of determinate growers, including insects and crustaceans.

KEYWORDS

body composition, body size, *Calanus* copepods, capital breeding, determinate growth, life-history evolution, optimal allocation, season length

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1 | INTRODUCTION

A majority of the life-history trade-offs are mediated by organismal size (Stearns, 1992), and the evolution of body size has gained particular attention (Charnov, 1993; Kozłowski, 1992). The duration of the feeding season (referred to as season length below) and mortality risk are the two key drivers of the body size evolution in multi- and univoltine determinate growers as they limit time available for growth. Season length defines the period of resources acquisition and mortality determines life expectancy. Elevated background mortality, that is, the unavoidable core part of the death process that occurs independently on variation in body size or condition, leads to earlier maturation and smaller adult size (e.g., Abrams, Leimar, Nylin, & Wiklund, 1996; Kozłowski, 1992). Variation in season length generates body size clines with possible changes in the number of generations per year in multi- and univoltines (e.g., Kivela, Valimaki, & Gotthard, 2013; Roff, 1980). In determinate growers, shortening generations leaves less time for development and growth of juveniles which in turn negatively affect adult size (Roff, 1980). However, the classification of determinately growing arthropods into uni- and multivoltine (i.e., those with one or more than one generation per year) species does not grasp the life-history diversity of the group where some species spend several years in the juvenile period, such as the high-latitude copepod *Calanus hyperboreus*, wood feeding beetles of Cerambycidae or arctic moths *Gynaephora* spp. (Hirche, 1997; Morewood & Ring, 1998; Walczyńska, Dańko, & Kozłowski, 2010). Such semivoltine (i.e., with juvenile period longer than 1 year) determinately growing arthropods are represented by thousands of species of crustaceans and insects; many members of copepods (Copepoda), damselflies (Odonata), mayflies (Ephemeroptera), butterflies (Lepidoptera), beetles (Coleoptera) and stoneflies (plecoptera) are semivoltine (Corbet, Suhling, & Soendgerath, 2006; Lillehammer, Brittain, Saltveit, & Nielsen, 1989; Tammaru & Haukioja, 1996; Varpe, 2012; Walczyńska et al., 2010). Furthermore, we must aim to explain intraspecific variability of age at maturation in semivoltine species such as the beetle *Aredolpona rubra* (Walczyńska, 2010), damselflies *Coenagrion johanssoni* and *C. pulchellum* (Śniegula, Johansson, & Nilsson-Ortman, 2012; Śniegula, Nilsson-Ortman, & Johansson, 2012) or copepods *Calanus glacialis* and *Calanoides acutus* (Daase et al., 2013; Tarling, Shreeve, Ward, Atkinson, & Hirst, 2004). In only a couple of theoretical studies considering time constraints as triggers of life-history trade-offs, the juvenile period is allowed to last for longer than 1 year (e.g., McNamara, Welham, Houston, Daan, & Tinbergen, 2004; Walczyńska et al., 2010) and only few investigate how differences in adult size affect fitness. Altogether, current theory does not show how interaction between season length and mortality rate affects body size evolution in organisms that spend more than 1 year in juvenile stages.

Many uni- and semivoltine arthropods gather excessive lipid reserves to cover costs of overwintering and to contribute to future reproduction (capital breeding) (Conover, 1988; Kivela, Valimaki, Carrasco, Maenpaa, & Manttari, 2012; Tammaru & Haukioja, 1996; Varpe, Jørgensen, Tarling, & Fiksen, 2009). Reserves may constitute significant parts of the body and even influence adult mobility, as in flightless female winter moths (tribe Operophterini, Geometridae)

in which egg load created in the juvenile stage impede flight performance (Snaell et al., 2007). Adult size in semi- and univoltine determinately growing arthropods is an outcome of allocation of resources to growth and storage with time constraints being the core axis for the evolution of body size and reproductive strategies in these organisms. Models of evolution of adult size in determinate growers with explicit consideration of season length either do not consider allocation to storage (Kozłowski, 1992; Kozłowski & Wiegert, 1987), constrain the modelled organism with respect to maximal adult size (Sainmont, Andersen, Varpe, & Visser, 2014; Varpe, Jørgensen, Tarling, & Fiksen, 2007; Varpe et al., 2009) or force organisms to adopt income or pure capital breeding (Sainmont et al., 2014). These assumptions preclude investigations of the trade-off between growth, storage and reproduction. In the presented annual routine model, life history, adult size, reproductive strategy and the duration of the juvenile phase emerge from trade-off optimization through maximization of fitness. Our work shows the landscape of optimal life histories of determinate growers along gradients of season length and mortality rate. Three types of life histories emerge from our model: multivoltines (maturing early in the year of birth with their offspring reproducing in the same year), univoltines (maturing in the year of birth but with their offspring reproducing the next year) and semivoltines (maturing after the first year of life). The female copepods in our model produce eggs continuously and can potentially breed in more than 1 year if alive. Hence, our model allows generations to overlap. The overlapping generations and possible iteroparity reflects observed life-history diversity in marine copepods (see Materials and Methods) but also other crustaceans such as Decapoda and Ostracoda that do not grow after maturation and may breed over several years (Hartnoll, 1984). We do not assume season length to correlate with mortality rate but instead generate predictions in a broad space of parameters allowing for discussion of cases where mortality rate changes together with season length. The presented results, in particular regarding optimal size, reserves and reproductive strategy, are relevant to a number of determinately growing arthropods.

2 | MATERIALS AND METHODS

2.1 | Model organisms

Herbivorous zooplankton species are ideal for life-history investigations focused on time constraints and the trade-off between growth, storage and reproduction. They are exposed to strong variability in season length as their primary food source, marine algae, is available for a limited time period. For marine copepods, the duration of the feeding season (season length) declines the higher the latitude (Leu et al., 2015). Mortality risk also differs between populations as fish abundance, and light conditions vary between high and low latitudes (Langbehn & Varpe, 2017). Our life-history model is inspired by the interspecific differences in adult size, lipid reserves and reproductive mode (income-capital breeding) within calanoid copepods of the genus *Calanus* spp. (Varpe, 2012). The copepod species *Calanus finmarchicus*, *C. glacialis* and *C. hyperboreus*, constitute the dominant

group of primary grazers in Arctic and sub-Arctic seas, reaching up to 80% of the biomass in Arctic shelf seas (Blachowiak-Samolyk et al., 2008; Conover, 1988). They display life-history variability with respect to body size and age at maturity along a latitudinal gradient. Large and long-lived *C. hyperboreus* from the high Arctic reaches maturity in its second, third or fourth year of life whereas small *C. finmarchicus* from the North Atlantic can have up to two overlapping generations per year (Conover, 1988; Hirche, 1997). *C. glacialis* has intermediate body size and reaches maturity in its second year of life, with some populations being univoltine (Daase et al., 2013). Females of long-lived *C. hyperboreus* and *C. glacialis* can breed over more than 1 year (Hirche, 2013; Kosobokova, 1999). The life cycle of calanoid copepods involves winter diapause, preceded by accumulation of substantial reserves and descent to deep water layers (Conover, 1988). Calanoid copepods can be lipid rich with lipid reserves of some species like *C. hyperboreus* reaching 50%–70% of dry body mass. The variability in fat content is linked to the reproductive strategy as *Calanus* spp. cover the whole income-capital breeding continuum; with *C. hyperboreus* a pure capital breeder, *C. finmarchicus* predominantly an income breeder and *C. glacialis* a typical mixed capital and income breeder (Conover, 1988; Falk-Petersen, Mayzaud, Kattner, & Sargent, 2009; Hirche, 2013).

2.2 | The model

The model focuses on optimal annual routines (cf. Houston & McNamara, 1999; McNamara & Houston, 2008), that is, a set of actions that maximizes fitness for environmental periodicity of food

availability and temperature (season length). The optimal life-history arises as a consequence of actions undertaken by the model organisms. To model optimal annual routines in seasonal environments, we apply the theoretical framework that allows the time-related value of offspring to emerge from the model assumptions (see Supporting Information Appendix S1). In our model, the organism optimizes allocation of resources to growth, reproduction and storage as well as timing of diapause (Figure 1). By “diapause” we mean resting phase spent at depth with metabolic processes slowed down. Food availability and temperature are seasonal (Figure 2a) and the timing of actions matters. The optimal life histories in our model are state dependent, that is, actions depend on the lean body mass, reserves and time of year. The lean body mass in the modelled organisms cannot shrink and is a proxy of body size (see below) in the sense of structural tissue that is not including the reserves. We use the terms lean body mass and body size as synonyms. Rates of growth, development and metabolism were parameterized to resemble the physiology of *Calanus* spp. (see below and Supporting Information Appendix S1). However, conclusions regarding trends in body size and voltinism were not qualitatively affected if the assumed rates of physiological processes, for example, resource assimilation or maintenance costs, changed.

2.3 | Seasonal fluctuations of food availability, temperature and offspring value

Years in the modelled environment are divided into 360 days, and seasonality is driven primarily by food availability f but also by

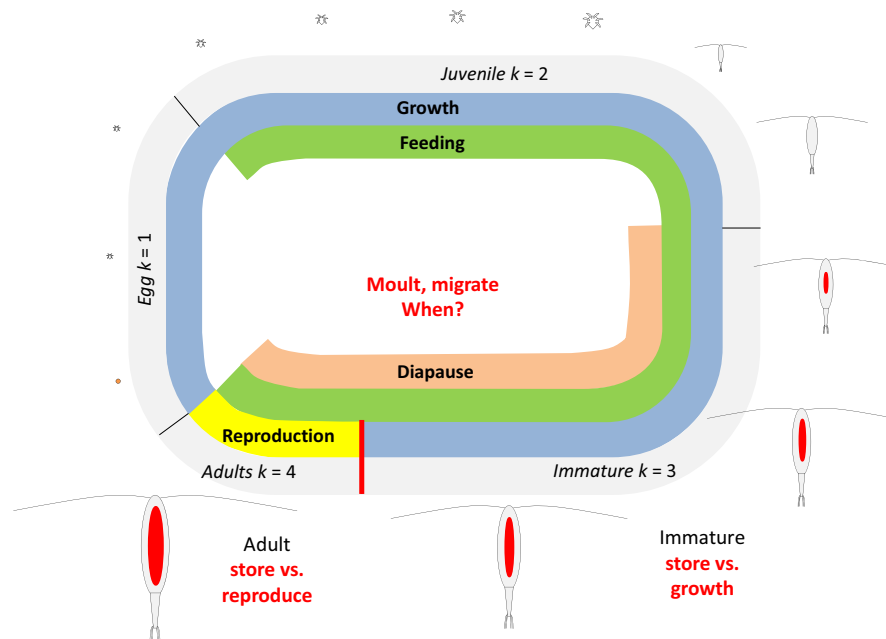


FIGURE 1 Schematic of the life cycle of the modelled female copepod with represented life stages (Egg-Adult). The size of drawings was scaled with the actual size of developmental stages in *Calanus glacialis*. Biological stages are represented along with the developmental stages (k) used in the model. The copepod's lipid sac is drawn in red. Colour fields represent the periods that can be dedicated for feeding, migration, growth and reproduction. Individuals in the immature and adult stages can descend to deep water layers and diapause at any time. Copepods in stages prior to the immature stage are unable to store reserves and suffer high mortality rate during winter. The immatures allocate energy between storage and growth whereas adults may divide the concurrent food intake between storage and reproduction. Reproduction rate in adults can be boosted by utilization of stored lipids (see the model description)

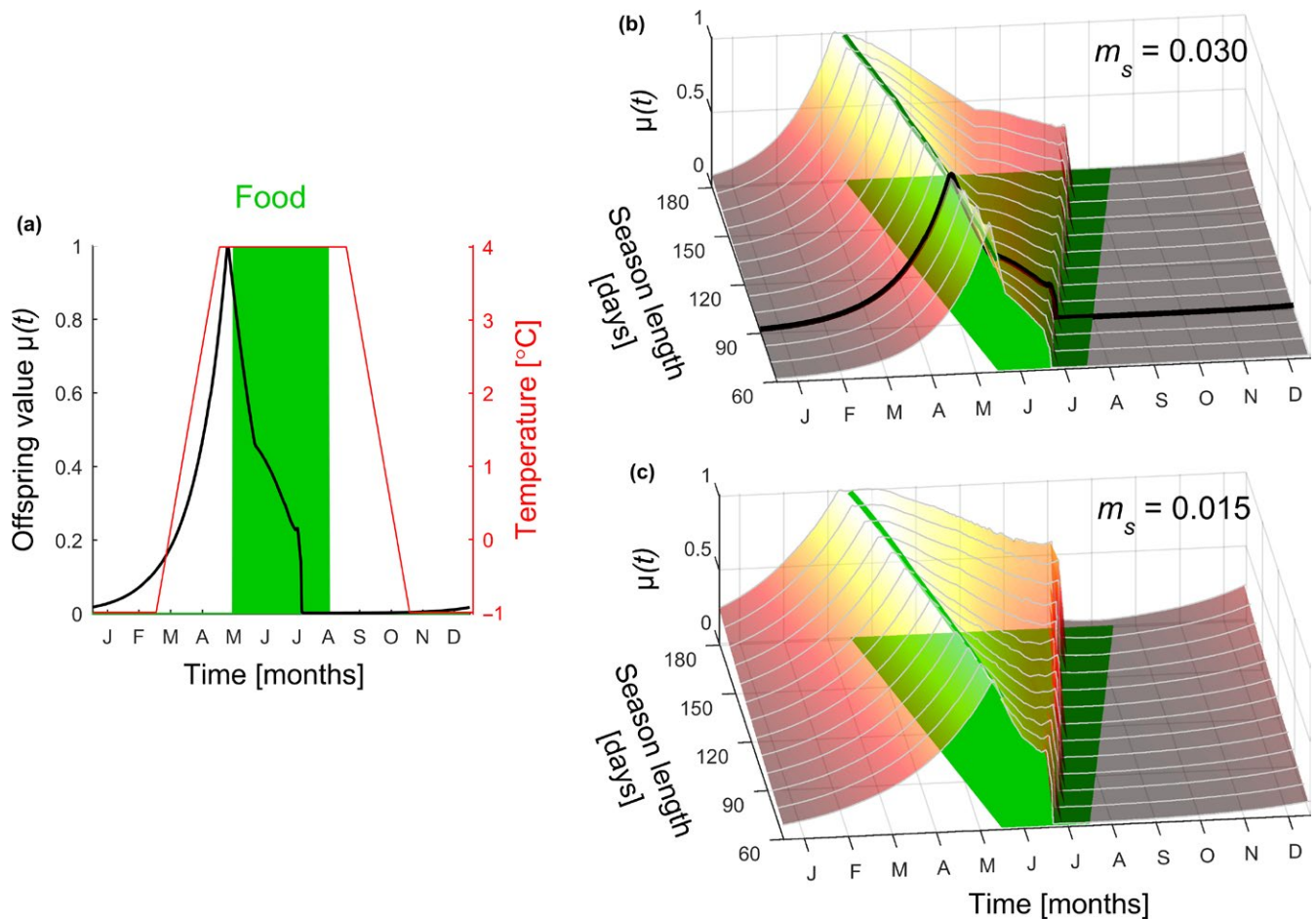


FIGURE 2 The components of modelled seasonality. (a) Food availability is depicted by the green rectangle and temperature by the red line. (a, b) Thick black line represents offspring value for an exemplary scenario in which food is available for 3 months and mortality rate at surface m_s equals 0.03. (b, c) The seasonal dynamics of offspring value changes with season length (ranging from 2 to 6 months), and mortality risk $m_s = 0.03$ (b) and 0.015 (c). Various lengths of the feeding period are outlined by the green patch. The thick green line in b and c indicates food onset mapped on the offspring value functions

changes in water temperature T (Figure 2a). To keep our model easy to follow, we assumed that food availability f , represented by the carbon mass of phytoplankton, is constant across the feeding season (see Supporting Information Appendix S1). The third seasonal component in our model is offspring value $\mu(t)$ which represents how offspring born at a given day contribute to fitness (see Figure 2), and is the outcome of the optimization process that emerges from the model assumption (see Supporting Information Appendix S1).

2.4 | Life history: development and physiology

Copepods of *Calanus* spp undergo complex development with eleven instars preceding the adult stage. We model the life history of a female copepod, from egg to adult, for simplicity divided into four functional stages $k \in \{1, 4\}$ (see Figure 1, Table 1). Growth and development in stages $k = 1$ and $k = 2$ (hereafter “egg” and “juvenile” stage) are determined by temperature and food availability only (see Supporting Information Appendix S1). For the stage preceding maturation, $k = 3$, hereafter “immature stage,” the model organism is

assumed able to modify the growth rate by optimally diverting resources to growth vs. storage (see Table 1 and details given below).

Individuals in all age classes are characterized by their lean body mass x [μg carbon] (body size or lean body mass hereafter) and immature and adult organisms ($k = 3$ and $k = 4$) can build reserves y [μg carbon]. These most developed stages are able to migrate between the feeding habitat of surface waters (active phase) and a refuge at depth (diapause) (see Figure 1) (e.g., Hirche, 1997). In the two-first functional stages ($k = 1$ and $k = 2$), the lipid reserves are not explicitly modelled.

To define net resource gain G [μg carbon·individual $^{-1}$ day $^{-1}$], we used literature data on food level-dependent assimilation rate $A(f)$ and maintenance costs M to parameterize mass-specific rates [μg carbon· μg carbon $^{-1}$ day $^{-1}$] (Supporting Information Appendix S1). Next, we assumed that the balance between assimilation and maintenance costs $A(f)-M$ scales with body size x and temperature T according to

$$G(x, f, T) = (A(f) - M) Q_{10}^{(T-T_{ref})/10} x^b \quad (1)$$

TABLE 1 The outline of state variables and activities that can be undertaken by the model organism in a given functional developmental stage k

Developmental stage; functional k (corresponding biological stage)	State (state variable)	Actions taken and allocation trade-offs (decision parameter)
Egg stage $k = 1$ (Egg-N2)	Lean body mass (x)	Food independent growth (no decisions)
Juvenile $k = 2$ (N3-C2)	Lean body mass (x)	Food-dependent growth (no decisions)
Immature $k = 3$ (C3-C5)	Lean body mass (x) Reserves (y) Surface vs. deep (n)	Grow vs. store (α) Migrate (θ) Moults to adults (γ)
Adult $k = 4$ (adult)	Lean body mass (x) Reserves (y) Surface vs. deep (n)	Reproduce vs. store (β) Migrate (θ)

Note. The respective biological stages of development (with reference to nauplii and copepodite stages), state variables and optimized decision parameters are given in parentheses.

with $Q_{10} = 2.5$ and b set to 0.75 (see Supporting Information Appendix S1).

2.5 | Mortality rate

The probability of surviving 1 day is given by $p = \exp(-m)$ where m matches the daily mortality rate. The model copepods suffer mortality rate m_s if staying in surface waters and m_d when diapausing at depth. Starving individuals with no reserves suffer the additional mortality $m_t = 0.003$ equivalent to monthly survival probability of 0.4. A key assumption in our model is that $m_d < m_s$, which fits with empirical estimates (Tarling et al., 2004). We present results when m_d is five times lower than m_s , that is, $m_d = m_s/5$. However, larger differences in mortality do not affect our conclusions. We consider a broad range of mortality rates in the surface habitat, $m_s \in (0.006, 0.036)$, to reflect conditions of variable environments and latitudes. The investigated daily mortality rates corresponded to a range from ca. 0.6 to 0.05 probability of surviving a 3-month period at the surface. Our model assumes no differences in stage-dependent mortality but the predicted trends in body size, reserves and voltinism would remain qualitatively unchanged as long as mortality of juveniles is higher than mortality of adults.

2.6 | Diapause, starvation and migration

Copepods with negative net gain $G < 0$ ($f = 0$, see Equation 1) use lipid reserves to cover maintenance costs according to

$$y(t+1) = y(t) + (1/C_r)G(x, f, T, n) \quad (2)$$

where n indicates whether the organism is diapausing ($n = 0$) or active in the surface waters ($n = 1$) and determines the costs of maintenance and mortality rate as staying in surface waters is more risky than diapause (see the above paragraph). We assumed that reserves y are used to cover maintenance with efficiency $C_r = 0.8$ (see Supporting Information Appendix S1), which means that $1 - C_r$ carbon is lost during the reserves mobilization. If the level of reserves y was insufficient to cover maintenance costs, that is, $y + (1/C_r)G(x,$

$T) < 0$, then mortality rate increases due to starvation by m_t and all stored reserves are utilized for maintenance $y(t+1) = 0$.

We assume that the migration imposes costs related to descent and ascent taking 1 day each. The mass of carbon necessary to cover costs of migrating down C_m [μg carbon] was set proportional to the total mass ($x+y$) of an organism according to $C_m(x, y) = -a(x+y)$ and taken from reserves, with $a = 0.2$ (see Supporting Information Appendix S1). The timing of migration is optimized, and when an animal migrates ($\theta = 1$), the reserves are reduced according to

$$y(t+1) = y(t) + (1/C_r)[C_m(x, y)] \quad (3)$$

An individual unable to cover the energetic cost of the descent (i.e., $y + C_m(x, y) < 0$) dies during migration. We assumed the ascent to be a passive process driven by positive buoyancy and lipid utilization (see Equation 1).

Immature individuals with positive carbon gain divide the surplus resources between allocation to growth and storage according to decision α (Equation 4).

$$\begin{aligned} y(t+1) &= y(t) + (1-\alpha)G(x, f, T) \\ x(t+1) &= x(t) + \alpha G(x, f, T) \end{aligned} \quad (4)$$

An increase in x positively affects the net carbon gain G (see Equation 1). Consequently, growth in our model should be considered an investment in future reproduction as individuals with larger lean body are able to assimilate resources and reproduce at higher rate (see below). Immature organisms ($k = 3$) in surface waters optimize timing of their moult to adult stage ($k = 4$) (see decision γ in Table 1).

2.7 | Life history, allocation and behaviour of adults

Adult organisms in the surface waters are able to build reserves and/or produce eggs. Those not reproducing can store reserves with a rate determined by carbon gain $G(x, f, T)$ (see Equation 1). Reproducing copepods utilize reserves, currently gained resources or both for offspring production. The maximal rate of reproduction R_p is given by

$$R_p = G(x, f, T) + C_r \min \left\{ \begin{array}{l} y \\ G_{\max} \end{array} \right. \quad (5)$$

where $\min \left\{ \begin{matrix} y \\ G_{\max} \end{matrix} \right.$ sets the amount of reserves that can be used to fuel reproduction in a given time unit. The ceiling is set by the maximal rate at which reserves can be utilized G_{\max} , which equals $C_r G(x, f_{\max}, T)$. The rate of reproduction is optimized through the decision parameter β (see Table 1) which sets the rate of egg production according to

$$R = \beta R_p \quad (6)$$

Allocation in adults is subject to a trade-off between reproduction and storage. If, for example, $\beta = 0$, an organism does not reproduce and current income is stored. If current gain is sufficient to cover offspring production $R \leq G$, then the organism gain reserves according to $y(t+1) = y(t) + [G(t) - R(t)]$. Otherwise, the organism utilizes reserves to cover reproduction according to $y(t+1) = y(t) + (1/C_r)[G(t) - R(t)]$.

2.8 | Fitness maximization

The fitness of a strategy V is the asymptotic growth rate of female copepods that follow the strategy and is calculated as the expected number of produced eggs weighted by offspring value $\mu(t_B)$ (see Supporting Information Appendix S1). The offspring value μ is equivalent to the normalized reproductive value at birth and is a function of the day of birth $\mu(t_B)$. To obtain $\mu(t_B)$ and to find the set of optimal allocation decisions maximizing fitness, we applied dynamic programming (see Houston & McNamara, 1999 and Supporting Information Appendix S1). All calculations were performed with MATLAB 7.9 (MathWorks, Natick, MA).

3 | RESULTS

3.1 | High contribution to fitness by early offspring

The dynamics of offspring value $\mu(t)$ that defines offspring contribution to fitness (Figure 2a), was primarily dependent on season length. When the season is short, the time window of high offspring value becomes narrow (Figure 2b,c). The best moment to be born falls just before the food onset, giving time for offspring to develop feeding ability on time (Figure 2). Releasing eggs far ahead of the bloom comes with additional costs to parents if also aiming to survive to the onset of the bloom; adults would need to either stay in the surface waters, utilize reserves and be exposed to high mortality risk or pay the costs of another migration.

3.2 | Size of adults emerges as a combination of mortality rate and season length

Before maturity, the modelled copepod grows to increase future fecundity (Equation 1). However, growth requires time and the organism consequently takes a mortality risk during this investment phase. The model predicts postponed maturation under low mortality rate m_s . However, the degree to which lean body mass changes

in response to different mortality rates interacts with season length. The shorter the feeding season, the less time for growth within a year, and time spent growing trades off with time necessary for gathering reserves that are later used to cover costs of migration, diapause and capital breeding. Thus, changes in mortality rate can move the optimal body size (lean body mass) to values that could only be achieved by changing the number of seasons dedicated to growth (Figure 3). This change could be a shortening or a prolongation of the life cycle. The vast change in body size in response to decreased risk comes about through a prolonged life cycle. Figure 3 illustrates how a relatively small change in mortality rate can cause a disproportionately large change in optimal lean body mass due to a switch from a 1- to a 2-year life cycle (Figure 3a-c) or from a 2- to a 3-year life cycle (Figure 3d-f). Discontinuous changes in total body mass ($x + y$), caused by the switch between an univoltine and a semivoltine life cycle, arise not only as an effect of the change in mortality but can also be caused by a change in season length without a change in mortality risk (see Figure 4a,b).

Under high mortality rate, the modelled copepod reaches maturity within the first year of life (e.g., Figure 3a) and has enough time for one or more generations per year (i.e., uni- or multivoltinism). Timing of offspring production matters, but for long seasons and high mortality, the offspring contribution to fitness μ is relatively high across the season (see Figure 2b) and mothers maximize expected offspring value not only through timing of offspring production but also by shortening their own development time and consequently maturing earlier. As a result, mothers shorten their growth phase and leave more time for offspring and subsequent generations, but reach smaller total body mass (lean body + reserves) (Figure 4c).

3.3 | Storing for diapause and capital breeding trades-off with growth

In general, the shorter the season, the more reserves are stored for winter diapause (Figure 5a) and reproduction is only fuelled, to a meaningful degree, with reserves when mortality is low (Figure 5b). That is because at high mortality the fitness benefit from capital breeding is lower because chances of survival to the following season are low and production of offspring by income breeding brings higher fitness benefits. Second, at low mortality copepods attain large body size and because costs of maintenance (metabolism) rise slower than linearly with lean body mass x (see Equation 1), small copepods pay higher costs of metabolism per unit of mass than larger ones. In turn, in small copepods proportionally smaller amounts of reserves are left after winter diapause for capital breeding, and particularly so when winters are long (i.e., when the feeding season is short). Storing for diapause and capital breeding leaves less time for growth. The shorter the season the higher the degree of capital breeding and the larger reserves, but less investment in lean body mass (Figure 5c-e). However, this trend can be disrupted if a change in lean body mass is associated with a switch to a lower number of generations per year which rapidly increases the time available for growth (Figures 5e and 4b).

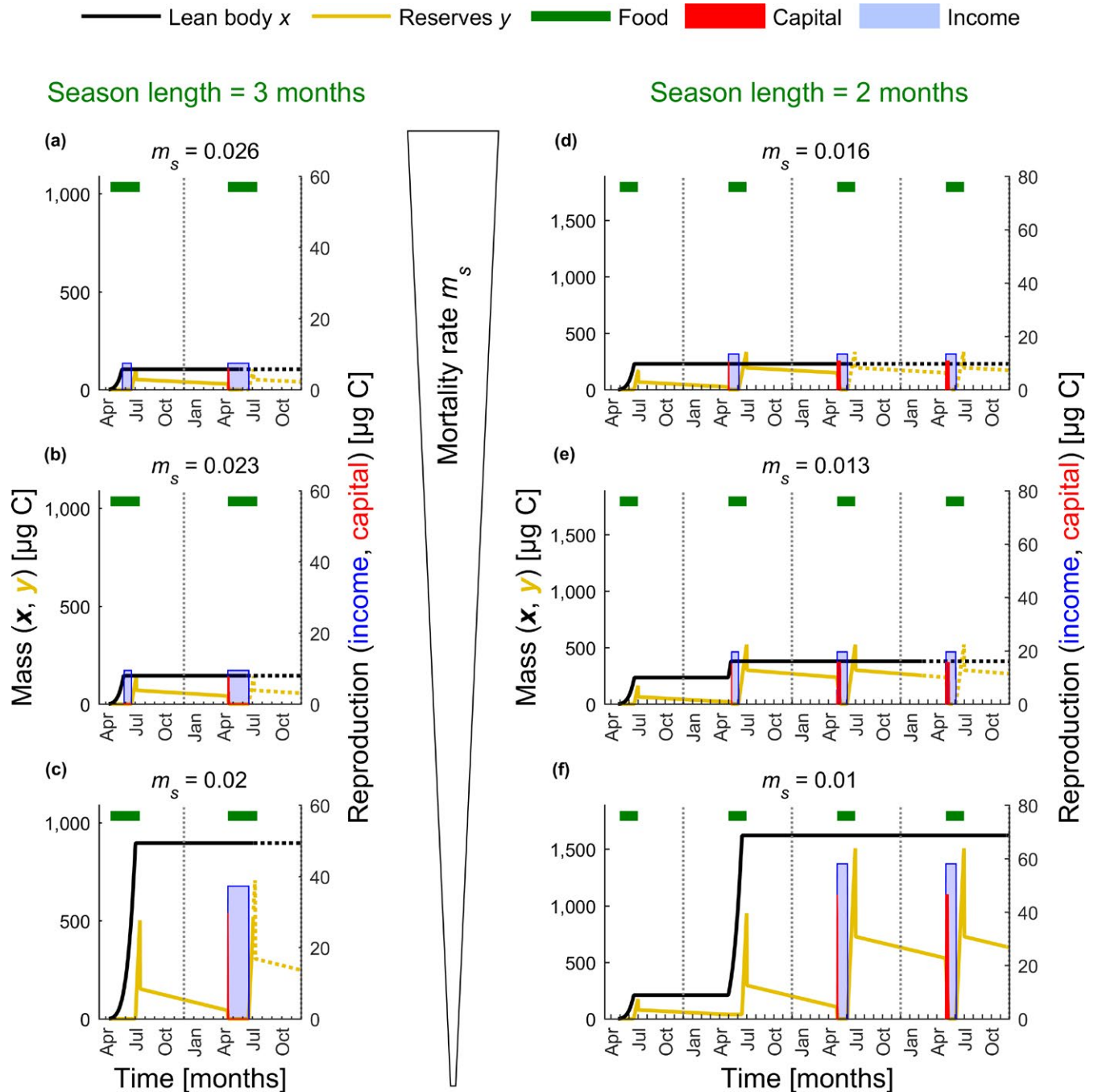


FIGURE 3 Lean body mass (body size), reserves and allocation strategies under decreasing mortality regime (schematically illustrated by the triangular shape). Decreasing mortality rate leads to a switch in age at maturation associated with a dramatic increase in body size and reserves: (a–c) a switch from 1- to 2-year life cycle for season length set to 3 months, (d–f) a switch from 2- to 3-year life cycle for season length set to 2 months. (a–f) Individual trajectories of lean body mass and reserves turn dotted when survival chance drops below 0.01. The ticks on the x-axis represent months. See red lines in Figure 4b that illustrate the position of the scenarios illustrated in a–f mapped on the full parameter space

4 | DISCUSSION

4.1 | Seasonality and adult body size

Variation in season length drives body size clines in determinate growers; a shorter season means less time available for growth unless the survival prospects are high enough so that maturation

can be postponed to the following season (see also Kozłowski & Wiegert, 1987; Walczyńska et al., 2010). Multivoltines differ from uni- and semivoltines with respect to the evolutionary forces underlying evolution of adult size. In uni- and semivoltines, the main selective force is the trade-off between allocation to growth, storage and reproduction optimized within a limited period of time (season).

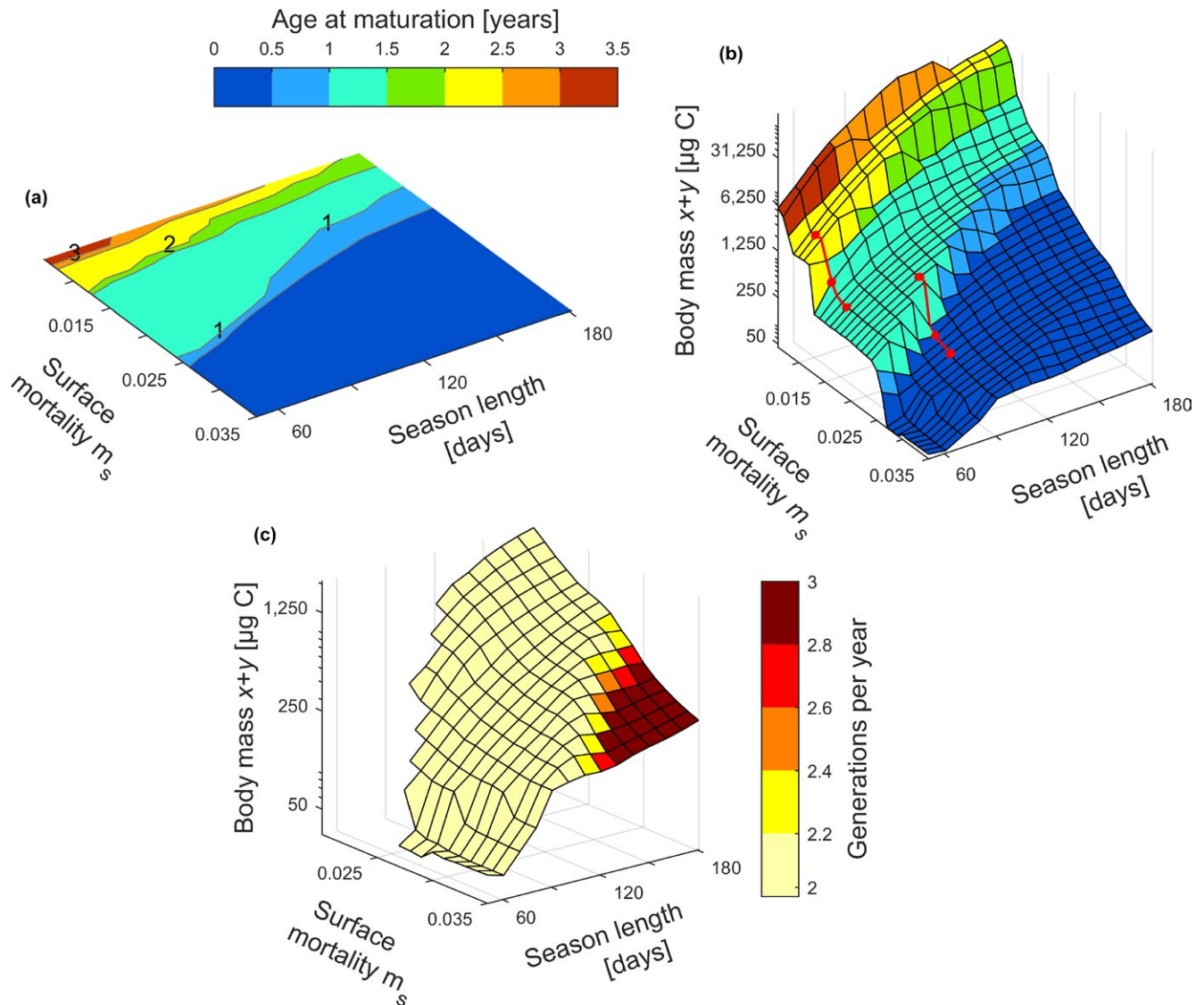


FIGURE 4 The age at maturity and total body mass (lean body + reserves) represented along gradients of background mortality rate in surface waters m_s and the duration of season length. Panels illustrate average characteristics for individuals born when offspring value $\mu > 0.9$, that is early in the season and with a high contribution to fitness. (a, b) The surface colours represent age at maturation. (b) Thick red lines match the combination of season length and mortality rate used to produce panels in Figure 3. (c) The surface colour indicates the average number of generations for multivoltine females born at $\mu > 0.9$. The number of generations was counted by following trajectories of individual females, their daughters and grand-daughters (see Supporting Information Figure S1). For clarity of presentation, panel c shows results for bivoltine and multivoltine life histories only

In multivoltines, the trade-off between growth and storage is a relevant selective force when the season is short (Figure 5e). However, the longer the season, the more important is the optimization of the number vs. length of generations (Figure 4c); high number of generations per year means early maturation and small body mass. Roff (1980) predicted body size shifts in multivoltine, semelparous arthropods arising from optimization of generation length, but he did not consider allocation to storage. Semelparity creates a strong selection force synchronizing timing of reproduction with season length. Furthermore, many models with assumed iteroparity and no reserves predict no shifts in body size in response to variations in season length (e.g., Abrams et al., 1996). However, low mortality

rate during diapause could significantly extend the period of growth (e.g., Kozłowski & Wiegert, 1987). Our results extend the predictions by Roff (1980) and show that for multivoltine life histories, even if generations are overlapping, the trade-off between generation length and number drives evolution of adult size in arthropods (see Figure 4c (this study), Kivela et al., 2013).

It would be incomplete to discuss the selection gradients in body size driven by season length without referring to the large-scale patterns observed across latitude—which for many environmental variables provide gradients of season length. The saw-tooth latitudinal clines in body size (shifts in adult size with latitude) documented in several species, such as crickets *Allonemobius fasciatus* (Mousseau

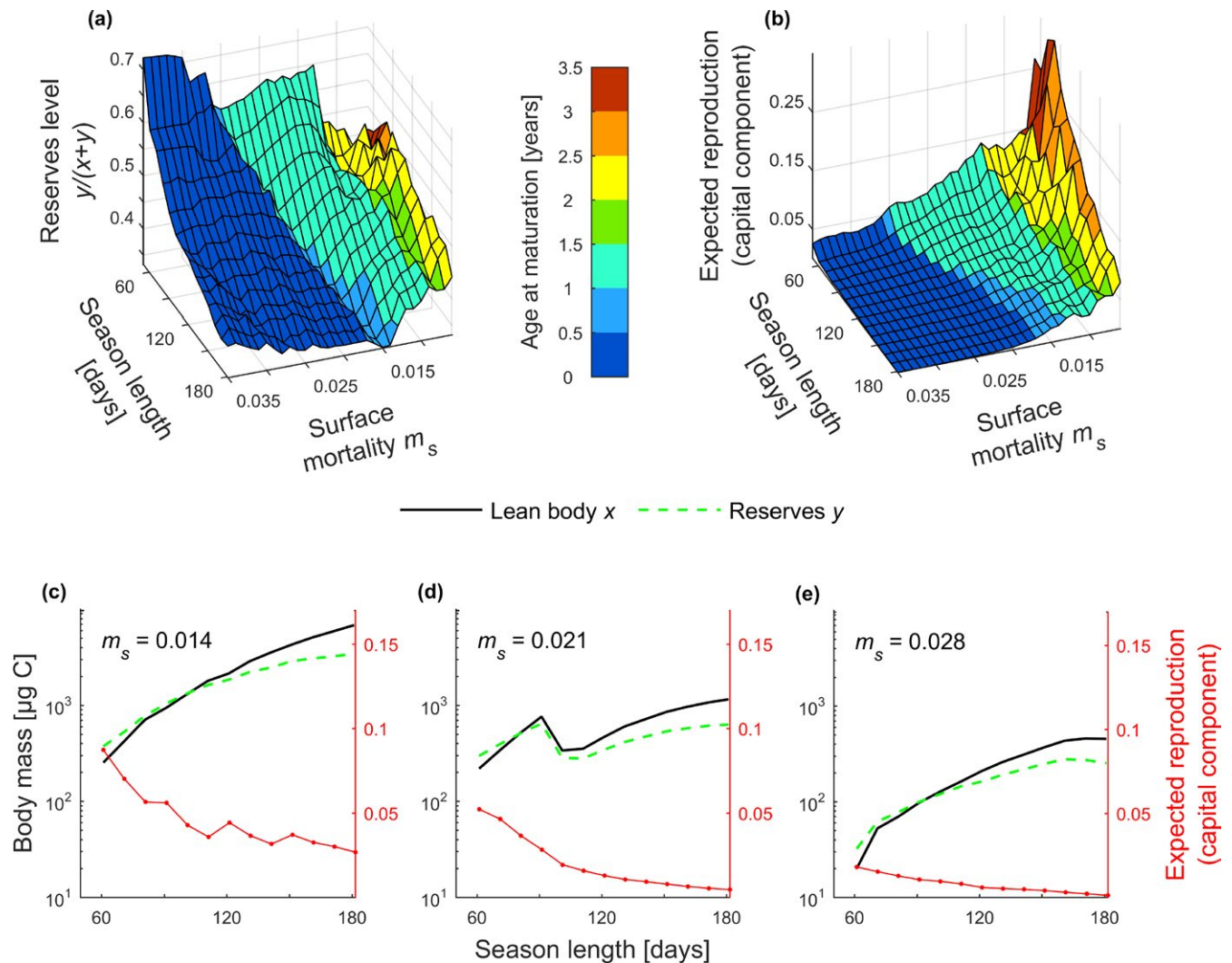


FIGURE 5 The level of reserves, the degree of capital breeding and body size (lean body mass) presented along gradients of background mortality rate in surface waters m_s and the duration of season length. (a, b) The surface colours in panels a and b represent age at maturation. (c–e) Lean body mass, reserves and degree of capital breeding for three exemplary gradients of season length, with season length and mortality risk assumed uncorrelated. (d) Note the shift in body size caused by the change in number of generations per year. Panels illustrate average characteristics for individuals born when offspring value $\mu > 0.9$, that is early in the season and with a high contribution to fitness

& Roff, 1989) or butterflies *Lycaena hippothoe* (Fischer & Fiedler, 2002), are not the prevailing pattern in arthropods (Horne, Hirst, & Atkinson, 2015; Shelomi, 2012). Instead, there are many examples of continuous change with latitude. For instance in some Geometridae moths size increases with season length (Kivela, Valimaki, Carrasco, Maenpaa, & Oksanen, 2011), whereas yellow dung flies (*Scathophaga stercoraria*) attain larger size at shorter seasons (Blanckenhorn & Demont, 2004). In general, the body size of many arthropods follow Bergmann's rule, that is, increases with latitude (Horne et al., 2015) or, as in insects, show an equiprobable Bergmann and converse Bergmann cline (Shelomi, 2012). Our model predicts a converse Bergmann cline or saw-tooth cline when background mortality and season length are uncorrelated (see Figure 5c–e). Overall, the predicted trends in body size depend on the assumed correlation between season length and mortality rate, which is similar to

predictions by Kozłowski, Czarnołęski, and Dańko (2004) for indeterminate growers.

4.2 | Evolution of voltinism

When season length does not correlate with mortality rate, the full continuum of life cycles from multi- to semivoltines can only be achieved by varying mortality risk (see Figure 4a). However, both short season length and in particular low background mortality select for semivoltine life histories in our model. The role of mortality rate for the postponed maturation in semivoltine determinate growers is described in several studies (e.g., Charnov, 1993; Kozłowski, 1992), but the effect of season length on the evolution of postponed maturation in determinate growers has not been discussed before. Our model predicts that semivoltine arthropods with much postponed

maturation would live only in safe environments and are more likely to be selected for when season length is short. Indeed, marine copepods or dragonflies at high latitudes are semivoltine in contrast to conspecifics living in temperate regions (Conover, 1988; Corbet et al., 2006). Stoneflies *Nemurella* sp. display intraspecific variability in voltinism with univoltine southern populations and semivoltine at higher latitudes (Lillehammer et al., 1989). Our predictions of the evolution of uni- and semivoltine life cycles in arthropods with overlapping generations extend the view by Kivela et al. (2013) derived for multivoltine species where season length is a major force driving the number of generations per year. Our model predicts that prolonged juvenile period in arthropods is more likely to evolve when short season length is associated with low mortality risk.

4.3 | Season length and mortality risk—implications for life histories of marine copepods

Large and lipid-rich copepods are selectively preyed on by fish and determine lipid and energy flow through marine ecosystems (Aksnes, Nejstgaard, Soedberg, & Sornes, 2004). There are so far few clear answers, as to how variation in season length affects the adult body size and body composition in marine copepods (Varpe, 2012). Arctic *C. hyperboreus*, maturing in their 3th-4th year of life, is ca. 4–5 times heavier than a *C. glacialis* maturing in its 2nd year of life, and more than 10 times heavier than bivoltine *C. finmarchicus* (Falk-Petersen et al., 2009), although intraspecific variability in body size exists (Choquet et al., 2018). The Bergmann cline observed in *Calanus* spp. in the Northern Hemisphere (Conover, 1988) fits with the predictions of our model only if mortality decreases along with season length. In other words, the further north the lower the mortality risk. Little is known about the latitudinal trends in survival rate of marine copepods, but the abundance of visual predators and light conditions may correlate negatively with season length and contribute to a lower risk of death at high latitudes (Aksnes et al., 2004; Langbehn & Varpe, 2017).

Our work contributes to the current discussion on climate-driven shifts in the life history of Calanoid copepods by showing that length of feeding season is not a sufficient factor for predicting body size, reproductive strategy and voltinism shifts. The role of background mortality rate cannot be underestimated and there is a need for a comprehensive analysis of how mortality risk changes along with feeding season duration in marine environments. Because we wanted to keep our work simple, we assumed background mortality independent of size. There is an ongoing discussion about the levels of mortality and the degree to which the risk of death changes with body size in marine copepods (Eiane, Aksnes, Ohman, Wood, & Martinussen, 2002; Ohman, 2012). The size dependence of risk may also depend on the type of predator with visual and tactile predators expected to select for opposed size spectra. Thus, instead of assuming size-dependent mortality we focused on the background component of mortality risk and considered optimal life histories with expected life duration ranging from few weeks to several years.

4.4 | Season length and capital breeding

Short season and large body size predispose arthropods for high degree of capital breeding in our model (see Figure 5b), but do not select for pure capital breeding (consistent with results by Varpe et al., 2009). Pure capital breeding has, however, evolved in many arthropods. Some *Neocalanus* spp. are pure capital breeders unable to feed in their adult stage (Miller, Frost, Batchelder, Clemons, & Conway, 1984). *Calanus hyperboreus* can also be regarded as a pure capital breeder (Hirche, 2013), but it is iteroparous in contrast to the semelparous *Neocalanus* spp. (see also Varpe & Ejsmond, 2018). The prevailing views about evolution of pure capital breeding in arthropods are based on verbal models (Bonnet, Bradshaw, & Shine, 1998; Jönsson, 1997) or assumed in theoretical work on life history of arthropods (e.g., Sainmont et al., 2014; Walczyńska et al., 2010). Overall, short seasons seem to select for a high degree of capital breeding—a boost in the rate of reproduction during a narrow time window, but are not sufficient for pure capital breeding to evolve in ectotherms. Separation of breeding and feeding grounds and high mortality related to feeding during reproduction are the strongest drivers responsible for evolution of pure capital breeding in ectotherms (Bonnet et al., 1998).

Marine and terrestrial arthropods are highly diverse with respect to degree of capital breeding but there is a prevailing representation of those who combine income and capital breeding (Daase et al., 2013; Javois, Molleman, & Tammaru, 2011; Kivela et al., 2012). In our work, capital breeding is indeed accompanied by income breeding and occurs at the beginning of the breeding season (cf. Varpe, 2017). Egg production in the later part of the breeding season is covered with incoming resources. Such a pattern has also been predicted by earlier life-history work (Ejsmond, Varpe, Czarnoleski, & Kozłowski, 2015; Varpe et al., 2009) and reported in several arthropods. Adult hawkmoths (*Amphion floridensis*) allocate carbon stored during the larval stage (capital) or acquired from nectar (income) to produce eggs, but the capital breeding component is only early in the breeding season (O'Brien, Schrag, & del Rio, 2000). Similar dynamics of a gradual decrease of the degree to which stored carbon is allocated to egg production has been observed in parasitic wasps (*Dinarmus basalis*) (Rivero, Giron, & Casas, 2001). Flesh flies of the Sarcophagidae family are mixed breeders in the first clutch and almost pure income breeders when producing the second clutch (Wessels, Jordan, & Hahn, 2010). Marine zooplankton members that combine capital and income breeding often use stored lipids early to produce eggs (e.g., Hirche & Kattner, 1993). This confirms the results by Varpe et al. (2007) and Ejsmond et al. (2015); the contribution of reserves to reproduction (capital breeding) is a relevant fitness component when a narrow time window is available for production of early offspring that is of high reproductive value.

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AUTHORS' CONTRIBUTIONS

M.J.E., J.S. and Ø.V. conceived the study. M.J.E., J.M.M. and Ø.V. designed the model. M.J.E. performed the analyses. M.J.E. and Ø.V. wrote the article.

DATA ACCESSIBILITY

The model outcomes are available at the Zenodo open digital repository (accession number 166313; <https://doi.org/10.5281/zenodo.166313>), Ejsmond, McNamara, Søreide, and Varpe (2018).

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