Research

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# Early is better: seasonal egg fitness and timing of reproduction in a zooplankton life-history model

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Timing of reproduction influences future prospects of offspring and therefore the reproductive value of parents. Early offspring are often more valuable than later ones when food availability and predation risk fluctuate seasonally. Marine zooplankton have evolved a diversity of life history strategies in response to seasonality. We present a state-dependent life history model for the annual and herbivorous high-latitude copepod *Calanoides acutus*. Individuals are characterised by four states; developmental stage, structural size, energy reserves and vertical location. There are two habitats, a surface habitat with seasonal predation risk and food availability, and a safer deep habitat with no food and low metabolism (diapause). Optimal life histories (diapause and energy allocation strategies) are found by dynamic programming. Seasonal egg fitness (reproductive value) emerges from the model and peak values are typically before the feeding season. Disentangling the fitness components, we conclude that seasonality in egg fitness is caused both by environmental seasonality in food and predation risk and by time-constraints on development and diapause preparation. Realised egg production, as predicted from population simulations, does not match the seasonal peak in offspring fitness but is delayed relative to peak egg fitness. We term this an 'internal life history mismatch' as constraints and tradeoffs cause sub-optimal birth dates for most eggs whereas mothers maximise their reproductive value by high number of eggs rather than few and optimally timed eggs. The earliest eggs have a disproportionately high contribution to population recruitment, emphasising the importance of early eggs and the need to understand seasonal patterns in offspring fitness.

Many plants and animals experience environmental conditions that allow growth or reproduction only during certain periods of the year. This is particularly evident at high latitudes, where strong seasonality in temperature and light leads to a short but often highly productive period of primary production. Herbivores have adapted their schedules of growth and reproduction accordingly.

Timing of reproduction is a life history trait of crucial importance for production of viable offspring and therefore for fitness. Examples are timing of egg laying in birds (Daan et al. 1990, Nilsson 1999), spawning in fish (Cushing 1990), and flowering in plants (Galen and Stanton 1991). The study of phenology has now gained increased interest because climate change may influence the timing of annual biological events (Both et al. 2006, Jonzén et al. 2006), and it is recognised that the whole life history must be studied to predict phenological changes (Visser and Both 2005). Life history decisions at one stage must be understood in light of their consequences for subsequent stages including offspring (Stearns 1992). The optimal timing of birth from the offspring's perspective may, however, differ from the optimal timing of reproduction from the parent's perspective. Examples include: the prudent parent whose residual reproductive value may increase by breeding later (Drent and Daan 1980); parents increasing fecundity by breeding later, at a cost of lower average offspring value (Rowe et al. 1994); and parents subject to seasonality in predation risk different from that of their offspring. In other words, life cycle constraints and tradeoffs may cause a mismatch between optimal time of birth vs optimal time to give birth, a parent–offspring conflict (Trivers 1974) over phenology.

Individuals in a population are not identical: their genes vary; they have experienced different environments; they are in different states or in different places; or they are born at different times of the year. Life history strategies are sensitive to such differences and often depend on the individual's state, such as body size, sex, energy reserves, and geographical position. Hence, optimal life history decisions vary within a population, and a state-dependent approach is desirable in studies of life histories and phenology (Rowe et al. 1994, McNamara and Houston 1996).

Here we adopt this state-dependent approach when modelling the life-history of a high-latitude marine copepod. Copepods form a large part of marine zooplankton and are abundant grazers on phytoplankton. Copepods are also the main prey of a range of higher trophic level organisms, including commercially important fish (Varpe et al. 2005). Consequently, understanding the life histories of copepods helps us understand the structure of pelagic marine ecosystems (Verity and Smetacek 1996). At high latitudes, herbivorous copepods have evolved strategies to cope with a short feeding season and a long unproductive winter (Conover 1988, Atkinson 1998, Lee et al. 2006), as well as seasonal predation risk (Kaartvedt 2000). Eggs are typically produced during spring, prior to or during the phytoplankton peak. For overwintering, one adaptation is to reside in deep-water with reduced metabolism and low exposure to predators; a state referred to as diapause (Hirche 1996). Because of environmental seasonality, the future prospects of an egg, and hence its fitness, are also expected to be seasonal, generating selection pressures on life-history traits determining timing and extent of egg production. Other factors than timing may influence egg fitness, such as egg size, but such factors are not incorporated in the present model (see Individual states).

To unravel the seasonal pattern of egg fitness, we built a dynamic state variable model (Houston and McNamara 1999, Clark and Mangel 2000) of a complete copepod life history. We designed the model for a given species (*Calanoides acutus*) and its specific environment (the Southern Ocean). This required a model rich in detail relevant to life history evolution of *C. acutus* and resembling species. In the model, life history tradeoffs emerge from built-in physiology and environmental constraints; a rare combination in theoretical life history models.

Here we focus on seasonal egg fitness and timing of reproduction and answer three main questions. 1) What is the seasonality in egg fitness? This can be answered because the model predicts reproductive value of individuals at all days of the year and for all developmental stages, including the egg. 2) How do fitness components, such as development rates, survival, and future reproduction, vary seasonally and thereby cause seasonality in overall egg fitness? These processes are quantified in population simulations of optimal life histories, which allow us to follow the fate of eggs laid at each and every day of the year. 3) Do the mothers produce eggs at the time of peak egg fitness, or is there a mismatch between the seasonality in egg fitness and egg production? Finally, we study the success of the produced eggs and compare early vs late eggs.

## The model

### Model species

*Calanoides acutus* is an abundant herbivorous copepod with circumpolar distribution in the Southern Ocean, the waters surrounding the Antarctic continent (Andrews 1966). *C. acutus* has a predominantly annual life cycle (Tarling et al. 2004). All stages are pelagic, eggs are produced near the surface in spring and subsequent development includes six nauplii stages (N1 to N6) and six copepodite stages (C1 to Adult) (Fig. 1). *C. acutus* has a seasonal migration between the feeding habitat (surface waters) and the diapause habitat (depths of 500–1500 m). Before diapause most individuals have reached C4 or older (Andrews 1966, Atkinson et al. 1997). While deep, most individuals moult to the adult stage and mating takes place before or during the spring ascent. Only females return to the surface (Andrews 1966, Atkinson et al. 1997), with sperm stored for the whole breeding season.

The life history model integrates laboratory and field data of *C. acutus* biology (and related species) with environmental data from the Scotia Sea (Fig. A1). In this region, *C. acutus* mainly completes its life cycle in one year (Tarling et al. 2004) and there are data on seasonal abundance and vertical distribution (Atkinson et al. 1997).

### Model overview

Here we give an overview of state variables, time scales, processes and model design. A detailed model description is available in Appendix 1 (figures and equations from the appendix are referred to with prefix 'A'). The modelling consists of two steps. 1) Optimisation by dynamic programming to find state-dependent optimal life history strategies given a set of parameters describing the environment. 2) Simulation of individuals and populations that follow the optimal life history strategy to describe individual characteristics and population dynamics.

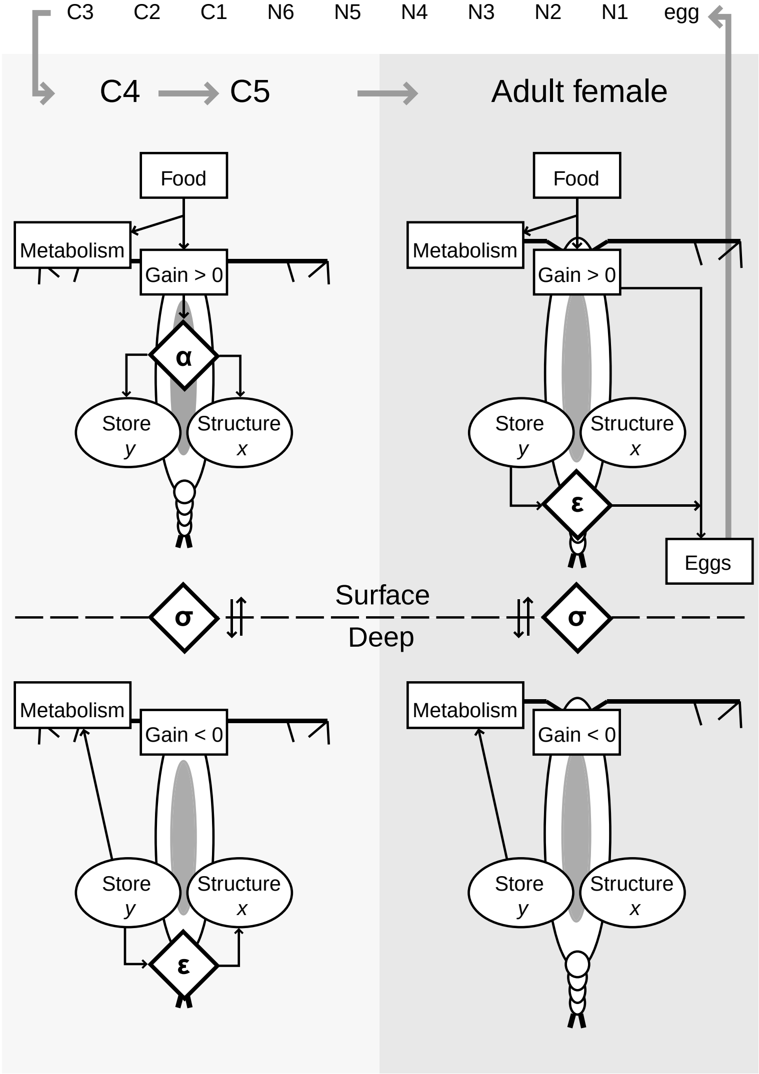


Fig. 1. Schematic overview of processes and decisions in a copepod life history model. Three life history decisions are optimised: allocation of carbon to store or structure α, the use of store ε, and habitat change σ (active in the surface, diapause while deep). Note that relevant decisions differ with stage and habitat. Migration costs are added to metabolism when changing from surface to deep habitat. Stores are used for metabolism if net carbon gain is negative (not shown for surface habitat). Development of early life-cycle stages (egg-C3, always in the surface) are modelled as temperature and food dependent stage transitions.

### *Individual states*

All individuals are characterised by time of the season (day of the year) as well as states related to development, condition and habitat (Fig. 1). The egg, all nauplii stages and the early copepodite stages are characterised by developmental stage only. Older stages are structured by three additional states. Two states describe body composition, presented as two compartments of carbon: structural body mass (representing development) and energy store (representing body condition) (Fig. 2). A third state is habitat. There are two habitats: a surface habitat with food during summer, high predation risk, and high routine metabolism; and a deep habitat with low predation risk, no food, and reduced metabolism characteristic of diapause (10% of surface metabolism).

Generally, parents may invest differentially in offspring depending on parent condition or time of the season. Examples include adaptive adjustments of offspring sex, size, condition, and even genetic constitution (haploid vs diploid). Here, we focus on timing of egg production, which may strongly influence egg fitness in seasonal environments. How other egg properties would influence development and survival in copepods would require an understanding of

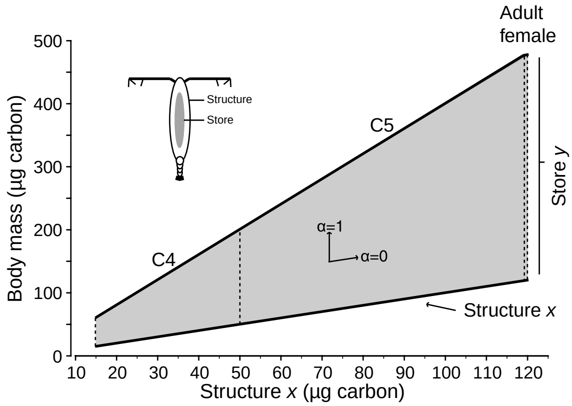


Fig. 2. Individual state space for a life history model of the copepod *Calanoides acutus*. Possible body masses are shown in grey: total body mass for given structural size x (irreversible) depends on the size of stores y (reversible). Maximum store is three times structure. An example is included of how the allocation decision α determines change in structure and store. In addition, store decreases if used for reproduction, structural growth or metabolism (Fig. 1). Individuals moult to the next stage at fixed structural mass. The state space captures common structure–store combinations for developmental stages from C4 to adult females. For simplicity, structural body mass of adult females is constant at 120 µg carbon whereas stores may vary. Details on how the state space is derived are available in Appendix 1.

stochasticity and patchiness in the food resource (Winemiller and Rose 1993) and a more detailed physiology of the early life stages and its consequences for starvation and predation. We acknowledge that other properties of the egg may vary with parent condition or time in season, but the tradeoff between egg size and numbers or other aspects of egg quality are not included in the present model (for some studies of variation in egg quality in free spawning copepods see Pond et al. 1996).

### *Environment*

The environmental processes include food availability, temperature, and predation risk, all with characteristic seasonality in the surface habitat but static in the deep habitat (Fig. 3). Phytoplankton, the primary food source of *C. acutus*, is represented by chlorophyll a (Chla) values derived from SeaWiFS satellite measurements (Fig. A1), and temperature is based on measurements at 50 m depth. Seasonality in surface predation risk is motivated by seasonal cycles in irradiation and its influence on predators relying on vision for hunting. The model has discrete time steps (1 day) and is run for the time needed to represent the entire life history (sometimes more than one year, for example when eggs are produced during unfavourable conditions).

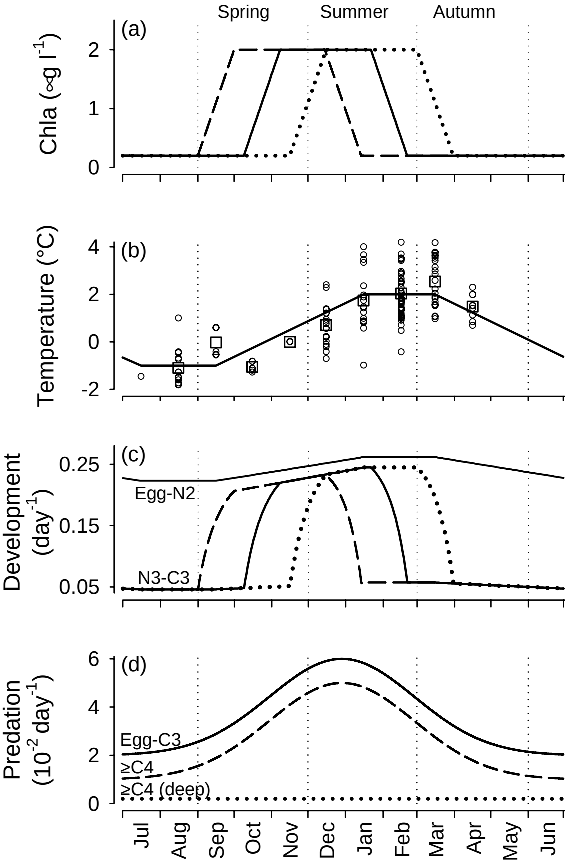


Fig. 3. Environmental forcing and development of young stages in a life history model of the Southern Ocean copepod *Calanoides acutus*. (a) Food availability in Chla units for an early, intermediate, and late feeding scenario. (b) Temperature in the surface habitat; model forcing (solid) based on measurements at 50 m depth, or nearest depth above (circles are data points, squares are monthly means). Data from stations in the World Ocean Atlas (http://www.nodc.noaa.gov) located in the reference area (Fig. A1). (c) Development as daily transition probabilities between stages (Eq. A5). Development is temperature-dependent for egg-N2, and temperature- and food-dependent for N3-C3 (seasonality depends on feeding scenario). (d) Predation rate for different stages and habitats.

### *Growth, development, and migration*

Individual processes include development, bioenergetics, energy allocation, and movement between the surface and deep habitat. The complete life cycle is modelled (Fig. 1). Development of early stages (egg-C3) is modelled as stage transitions (20 substages with daily transition probabilities). Development of egg, N1, and N2 is temperature-dependent, whereas development of subsequent stages also depends on food (Fig. 3c). For C4s, C5s, and adult females, net carbon gain (food intake) and bioenergetics determine potential rates of development, energy storing, and egg production (Fig. A2). Temperature influences growth and metabolism via a Q10 function. Net carbon gain is related to food availability (Chla) via a saturation function and subtraction of routine metabolism. Individuals divert net carbon gain to structure or store as determined by the optimal allocation α. There are constraints on potential size of structure and store (see State space, Fig. 2), and on rates for using stores.

Stores are used for egg production (adults) or for structural growth while deep (C4s and C5s). Optimal use of stores is determined by ε. When food intake is too small to cover metabolic costs, net carbon gain is negative and stores are used. When stores are empty there is elevated mortality caused by starvation. Adult females are assumed to remain at a constant structural size and therefore direct all net gain directly to egg production. The carbon mass of an egg is used to convert reproductive output (in carbon units) to fecundity (number of female eggs).

The optimised habitat switch σ contains information on when to move between the surface and the deep habitat (Fig. 1). Migration costs are paid at the time of descent (20% of total body mass).

### *Model design*

The model finds optimal energy allocation and timing of diapause based on maximization of reproductive value by dynamic programming (Eq. A7; Houston and McNamara 1999, Clark and Mangel 2000). This optimization method is a backward iteration process where reproductive value is found at any time of the year conditional on the individual's states, current actions, and optimal actions in the remaining life. The fitness measure used (based on McNamara 1991) can be explained as follows (Fiksen 1997). The optimization procedure starts by optimizing the number of offspring produced in the last generation. Due to different projections for development and survival, the eggs differ in the expected number of offspring they will give rise to. By now considering the last generation but one, the procedure uses this information and optimizes not only the number of eggs produced by individuals in different states at different times, but for each egg produced it also considers how many eggs that egg is expected to give rise to in the next generation. This process is then repeated, going backwards, for several generations until the life history strategy converges. The result is that the procedure optimizes the number of descendants far into the future. Optimizing this formulation of reproductive value that extends across several generations is, in the absence of frequency dependence and interannual environmental fluctuations (as in our model), identical to maximizing the population's long term growth rate (Houston and McNamara 1999). Accordingly, what we refer to as egg fitness is the expected number of descendants left far into the future, considered for one egg produced on a given day of the year. The actions maximising reproductive value determine the optimal life-history strategy schedule for growth, reproduction, and diapause. The approach allows us to stop at any point in the life cycle and ask what the individual should do to maximise its reproductive value. Generally, the later in the life cycle we ask this question, the higher the reproductive value because the individual is more likely to reach reproductive size successfully.

The backward iteration necessarily optimises strategies also for unlikely state combinations. In a second step we therefore simulate a population where individuals follow optimal strategies and the dominant state combinations emerge. By extensive bookkeeping we log the seasonal abundance of all stage- and state-combinations. The population simulations are therefore stage-structured, and for C4s, C5s and adult females, also structured by size (structure), condition (store), and habitat. Optimal strategies and population dynamics are found for three feeding scenarios: an early; an intermediate; and a late primary production season (Fig. 3a).

We perform experiments to follow the fate of eggs produced on any given day, and in Fig. 4 we illustrate how stochasticity in developmental time introduces variance within the cohort. In addition to following cohorts of eggs produced on a given day, we also perform full scale population dynamics which reveals the dynamics of the whole population. This virtual population can be sampled, analogous to empirical investigations, and results compared with observations. Here we focus on the timing of population level egg production and compare it with the seasonality in predicted egg fitness. With population simulations we also address the future contribution by early vs late eggs.

## Results and discussion

Results are presented in detail for the early feeding season scenario (Fig. 5 and 6). The intermediate and late scenarios are commented on briefly (Fig. 7), with details on fitness components given in Appendix 1 (Fig. A3).

### Reproductive value

The model predicts seasonal and state-dependent reproductive value of the optimal life history. There are three main trends in reproductive value related to stage, season, and condition (Fig. 5):

1. Reproductive value increases with developmental stage, because the individual is closer to reproduction (Fig. 5a).

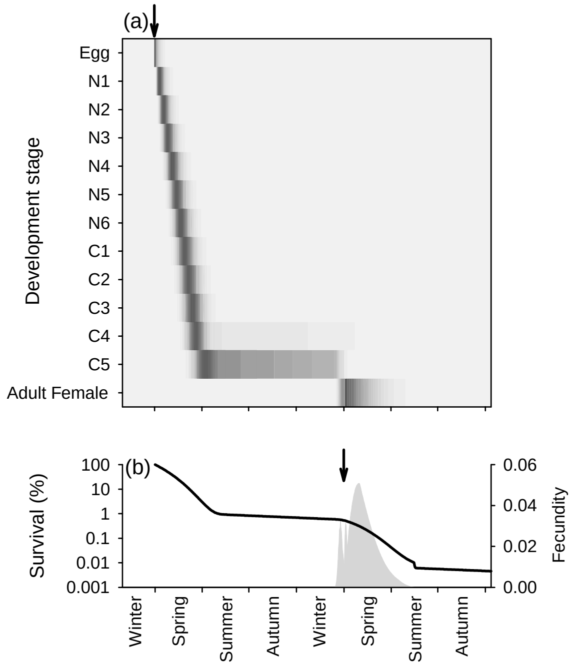
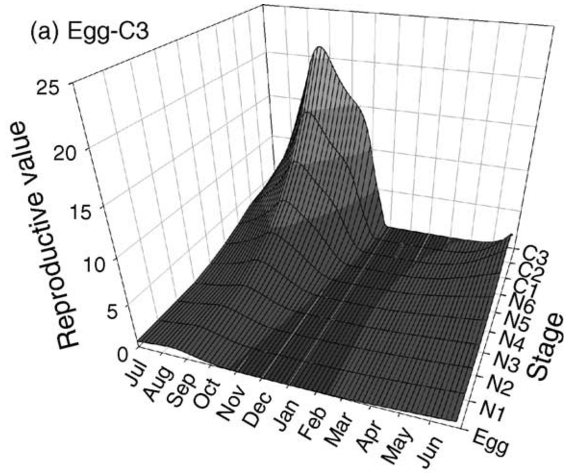


Fig. 4. Development, survival, and fecundity as predicted for a cohort of copepod eggs produced in early spring; arrows are one year apart and indicate the start date of the cohort (1 September). (a) Temporal distribution of egg, nauplii, and copepodites resulting from the egg cohort (relative abundances). Note that some individuals spend diapause as C4s but most as C5s. (b) Expected survival probability (line) and fecundity (eggs per individual; solid area) for the same cohort.

2. Reproductive value varies over the season. Early stages are increasingly time-constrained as the season progresses and development to a stage capable of diapause (C4 with some stores) becomes less likely. The resulting drop in reproductive value (Fig. 5a) is mainly an effect of survival probability, which is low in the surface (the only option of C3s and younger). Starvation is not the reason, as there is enough food for continued development also during winter, although at a slower rate. For an individual near maturity (Fig. 5b), reproductive value peaks in late winter and early spring. At this time there are good chances of reaching adulthood and reproduction. Later in the season there is a drop similar to that of younger stages. At this time an individual is too late to produce viable eggs. From then on, reproductive value increases gradually towards the next reproductive season.
3. Reproductive value increases with size of stores at all times (Fig. 5b). Individuals with small stores in winter will starve (lower right corner of Fig. 5b), and consequently have very low reproductive values. A minimum size of stores by the end of the feeding season is a prerequisite for preventing starvation during winter; for the C5s depicted in Fig. 5b this is about 40% of maximum storing capability. There are, however, additional benefits of larger reserves, as stores in addition to those needed for winter metabolism are used for egg production next spring or for structural growth during diapause.



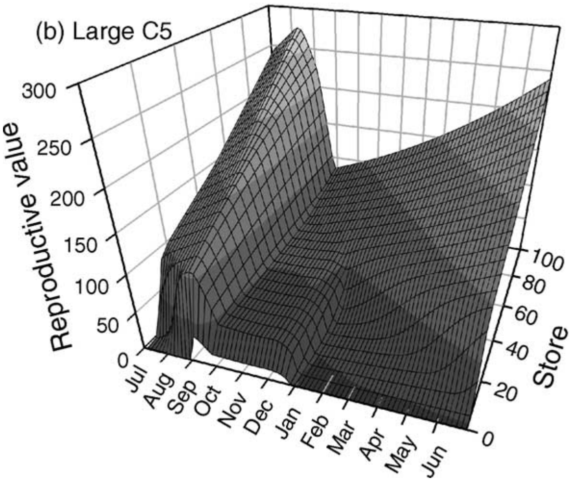


Fig. 5. Seasonality in reproductive value as predicted by a copepod life history model. (a) Early developmental stages (egg–C3), and (b) a nearly mature copepod (C5, $x = 110$) for all store values (% of maximum store) and in the optimal habitat. Data are from the early feeding season scenario. Plotted reproductive values are relative to the egg with maximum reproductive value and adjusted for the population growth rate.

## Egg fate and fitness components

Expected developmental time, diapause stage, survival, and fecundity are fitness components that vary

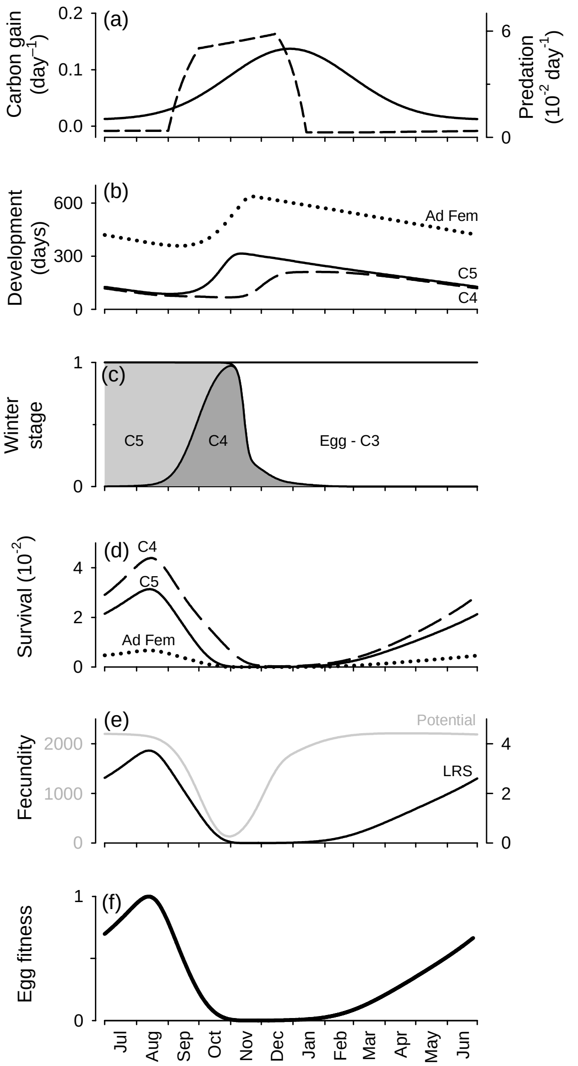


Fig. 6. Seasonality in fitness components and overall egg fitness predicted by a copepod life history model. (a) Carbon gain (broken line) and predation rate (solid line) of the early feeding scenario (cf. Fig. 3). (b-f) Expected fate of eggs produced at the different days (egg date) of the year. (b) Development time to specific stages (weighted average for the whole cohort). (c) Stage at mid-winter (1 July). (d) Survival probability until specific stages. (e) Potential fecundity (female offspring) of a single egg assuming no predation, and lifetime reproductive success (LRS) when predation is included. (f) Egg fitness measured relative to the egg with maximum reproductive value and adjusted for the population growth rate.

depending on when an egg is produced. We study these fitness components separately to disentangle the effects of each component on overall reproductive value. Cohorts of eggs, one for each day of the year (egg date), were followed (see Fig. 4 for a single cohort). Expected values of each fitness component for all egg dates are presented in Fig. 6.

*Development* (Fig. 6b). The shortest development time is predicted for eggs produced at the beginning or some time into the feeding season. There is a distinct rise in expected development time for eggs produced at a time when a given stage cannot be reached within the first year's feeding season; in these cases further development is postponed to the following year. Development to C5 obviously becomes time-constrained before development to C4. Maturity (adult female) during the first feeding season is not expected for any egg date. This is in agreement with the predominantly annual life cycle of this species (Tarling et al. 2004).

*Diapause stage* (Fig. 6c). C4s, C5s, and adult females may enter diapause (Fig. 1). The stage composition of the cohort at its first mid-winter varies with egg date. Eggs laid early develop to C5s before diapause. With later egg dates (already in the first half of the feeding season), the C5 stage is not reached and C4s dominate the diapause population. This change in winter stage reflects the stage-specific increase in development time (Fig. 6b). Eggs produced later are expected to overwinter as C3 or younger. These young stages stay in the surface habitat where they experience low food availability and high predation risk.

*Survival* (Fig. 6d). An egg's probability of survival until a given stage depends on egg date. Eggs produced prior to the feeding season have the best prospects for survival. Eggs with the highest survival probability are produced earlier than those with the shortest development time (Fig. 6b). There is a sharp decline in survival prospects as 1) the predation risk increases, and 2) the remaining feeding season becomes too short for development to a viable diapause stage.

*Fecundity* (Fig. 6e). Two measures of fecundity are presented: potential fecundity, which is an egg's expected number of female offspring assuming no predation (but including starvation) and one breeding season per female; and lifetime reproductive success (LRS), an egg's expected number of female offspring when predation risk is taken into account. For potential fecundity, starvation is the only risk of death. This is unrealistic, but illustrative.

Early eggs have time to develop to C5 and build large stores and are the individuals with the largest potential fecundity. Eggs produced later (September and onwards) are time-constrained and achieve lower potential fecundity because they enter diapause as C5s with smaller stores (which means fewer, if any, eggs produced from stores) or as C4s (no egg production based on stores and a need to use the early feeding season for growth and maturation). The potential fecundity is therefore reduced for both these fates. For egg dates when C4s become too small to enter diapause

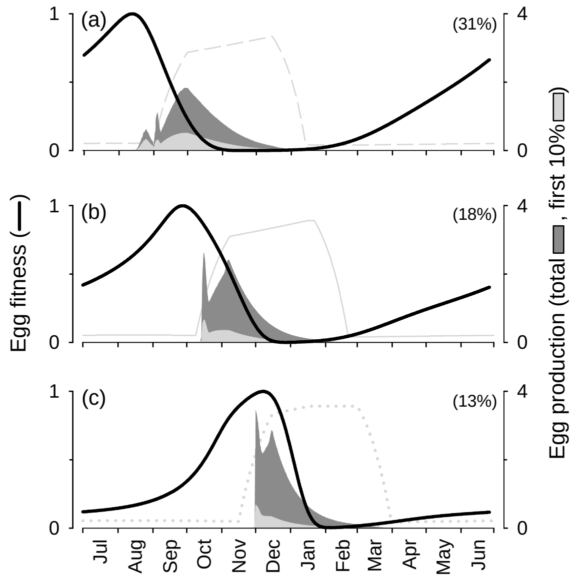


Fig. 7. Egg fitness and egg production for (a) the early, (b) intermediate, and (c) late feeding scenario. Egg production is derived from population simulations where individuals follow the optimal life history strategy, and are shown as daily population egg production as a percentage of total annual egg production. The 10% earliest eggs from the previous year contribute to a disproportionately large part of total egg production (contribution highlighted in light grey and given in parentheses). Seasonality in net carbon gain (grey line) is indicated (cf. Fig. 6 and A3).

or to make it through diapause, potential fecundity decreases because these individuals are likely to starve. Potential fecundity increases again for even later egg dates (November and onwards) because C3s or younger make it through the winter without starving. They may need two years to reach adulthood, but since potential fecundity does not include predation it shows that the individuals that survive can achieve maximum potential fecundity (right part, Fig. 6e).

LRS includes predation risk and obviously offers a more realistic perspective. Here, eggs produced late do poorly, whereas eggs produced some time prior to the feeding season are expected to have the largest LRS. The seasonality in LRS is similar to that of survival probability, pointing out the strong influence of mortality, including stage specific diapause capabilities, on reproductive success.

*Egg fitness* (Fig. 6f). Because fitness is evaluated far into the future, the move from LRS to total egg fitness amounts to including the LRS of the eggs produced in the first generation, the LRS of their eggs again, and iterate this process for future generations until the life history strategy converges. All fitness components presented above contribute to an egg's overall reproductive value. The seasonality in reproductive value is profound and gives clear predictions for when an egg should be laid from the offspring's perspective. Eggs laid about a month before the annual phytoplankton bloom have the best prospects (but see the late feeding season, Fig. 7c, A3). Eggs produced during the second half of the feeding season have very low reproductive values. There is a gradual increase in egg fitness towards the feeding season, and a marked decline when eggs are produced too late. Note also that food availability is still high by the time egg fitness has declined to virtually zero. The benefits of an early start are explained by two main factors: 1) escaping predation risk which is low early in the season and high later on; and 2) starting development early to reach a stage capable of diapause. Development may start prior to the bloom because the first nauplii stages develop without feeding, and the following stages may develop slowly on the pre-bloom food concentrations. Non-feeding nauplii stages are common in copepods and the first feeding stage varies between species (Mauchline 1998). Delayed first feeding allows development at times and places where food is lacking or not yet available (Miller et al. 1984, Saito and Tsuda 2000).

## Timing of egg production and the internal life history mismatch

We predict the timing and amount of population level egg production by simulating a population where individuals follow the optimal life history strategies. In the early scenario, egg fitness alone is a poor predictor of the timing of egg production. Most eggs are laid after the peak in egg fitness (Fig. 7a), when food is available for egg production. The simulations of single cohorts (Fig. 6) showed that eggs produced during the feeding season are likely to experience time constraints and will not reach a developmental stage or gain sufficient stores prior to the winter to allow early reproduction next spring. Hence, many of the late eggs will not produce eggs of high reproductive value themselves. Consequently, the model predicts an 'internal life history mismatch' as only a small fraction of the eggs is produced when the eggs have the highest fitness. High-value eggs must be produced by the use of energy reserves because the fitness peak is prior to the bloom. In the intermediate scenario this mismatch is even stronger, and no eggs are produced at the time of peak egg fitness (Fig. 7b). For the late scenario, however, there is high predation risk prior to the feeding season and a safer time window for feeding towards the end of the feeding season. This causes less of a mismatch between the seasonality in egg production and egg fitness (Fig. 7c), but a particularly rapid decline in egg fitness when eggs are produced too late (late December and onwards).

There are early peaks in egg production prior to or at the onset of the feeding season in all environments (Fig. 7). These early eggs are produced from internal stores (two first peaks in the early scenario and the first peak in the intermediate and late scenario). The later and more prolonged peak, as well as all subsequent egg production, is caused by direct use of food intake, and the peak appears because of high numbers of adult females combined with high food availability. The decline in egg production after the final egg production peak is caused by adult mortality and not by reduced food availability. This effect of predation causes a longer egg production period in the early compared to the intermediate and particularly the late scenario.

The predicted seasonality in egg fitness clearly suggests that early eggs are better. Early eggs are better also within the period when eggs are produced. Our population simulations suggest that the earliest 10% of eggs give rise to a disproportionately large part of next year's eggs (Fig. 7). For the early scenario, and in terms of eggs produced next year, an average egg among the earliest 10% is 4.1 times more valuable than an average egg among the remaining 90% (Fig. 7a). For the intermediate and late scenario the factor is 2.0 and 1.3, respectively. This illustrates the population level consequences of strong seasonality in egg fitness with particularly pronounced effects for the commonly occurring scenario where seasonal food availability (phytoplankton bloom) starts prior to the time of peak predation risk (Fig. 7a). The eggs produced next year by the earliest 10% of eggs are also, on average, earlier than those that follow from later eggs. The contribution by the earliest eggs is therefore even higher in terms of reproductive value than in terms of egg numbers (with factors as above now being 5.3, 2.3 and 1.5 for the early, intermediate, and late scenario, respectively).

## General discussion

### Why seasonal timing of reproduction?

From the offspring's perspective, there are at least three general drivers of annual rhythms in reproduction. 1) Food; as peak food demands of the offspring should coincide with high food availability (Both et al. 2006). This is the essence of the classical match–mismatch hypothesis (Cushing 1990). 2) Predation; as the offspring's prospects will vary when predation risk is seasonal (Vonesh 2005). 3) Habitat availability; as suitable habitat conditions influence the prospects of young at several stages in their development, such as nursing in ice-breeding seals (Lydersen and Kovacs 1999), ice-free waters for sea-going chicks (Murphy 1995), and development in wet ponds in amphibians (Tejedo 1992). Each of the factors above can have direct effects on phenology, or impose constraints such as developmental thresholds that affect phenology earlier in life.

Food availability and predation risk cause seasonality in egg fitness in the modelled copepod. Directly, food availability and predation determine the value of the productive season in summer. Indirectly, food and predation during winter sets developmental constraints. For instance, both the direct and indirect effects cause the high reproductive value of those reaching a viable diapause stage. The diapause constraint is one example of a general time-constraint of organisms in seasonal environments. For instance, late hatching nymphs of nymph-overwintering grasshoppers are smaller at the onset of winter and suffer higher winter mortality (Landa 1992). Birds migrating to high-latitude breeding sites offer another example. Their chicks must fledge and be prepared for a return migration before local conditions or migration conditions become too harsh (Cooke et al. 1984).

There are potential behavioural adaptations to such time constraints, as animals searching for food may accept higher risks to increase their growth rates (Houston et al. 1993). This must be mediated by the parents' feeding strategy in the case of the breeding bird. For copepods, potential options are reduced daily migration to depth or increased food searching activity. Behaviours at this time scale are not included in the present model, but have been explored in other models of zooplankton life histories (Fiksen 1997, Fiksen and Carlotti 1998).

Furthermore, an uncertain duration of the feeding season would, in some years, allow late offspring to develop to a viable diapause stage whereas even early offspring would have problems under harsh conditions in other years. The Chla data used here (Fig. A1) suggest inter-annual environmental variation in food abundance and duration of the feeding season. However, since optimal life history strategies in environments that vary interanually can not be predicted using optimization models such as ours (McNamara and Houston 1996, Houston and McNamara 1999), the model predictions must be interpreted for the specified environment only. Tarling et al. (2004) discuss the possible role of interannual variation in food availability, particularly in relation to the co-existence of 1-year and 2-year lifecycle phenotypes in the Scotia Sea population of *Calanoides acutus*.

The time constraints on development and growth are not caused solely by the need to be structurally prepared for diapause. There are three more factors: 1) diapause stages need sufficient energy reserves to avoid starvation; 2) energy reserves in excess of those needed for routine metabolism are beneficial for egg production next spring or structural growth while in diapause; and 3) reaching structurally large stages before diapause allows early maturation next year with production of high value offspring. Early eggs are more likely to achieve all of these effects. The link between an early start, subsequent size, and higher fitness is a widespread life history phenomenon (Reznick and Braun 1987, Landa 1992, Olsson and Shine 1997, Reznick et al. 2006).

Completing parts of development prior to the feeding season is beneficial when it implies reduced predation risk. This is predicted here, and the existence of non-feeding nauplii stages may therefore be an anti-predator adaptation as well as a response to time constraints on development. Seasonality in predation risk may select for growth and development at times of sub-optimal growth conditions. This tradeoff is evident in our model. Eggs produced early have maximum survival from egg to adult female (Fig. 6d), while development is quicker (meaning better growth conditions) for somewhat later eggs (Fig. 6b). The high value of early eggs is thus partly due to a risk-averse strategy. When comparing fitness consequences of early and late eggs, eggs produced several months prior to the feeding season have higher fitness than eggs laid even shortly into the feeding season.

## The match–mismatch hypothesis and the internal life history mismatch

For the commonly occurring early and intermediate ecological scenarios investigated in this paper, the model predicts an internal life history mismatch in the sense that most eggs are produced at times when they have relatively low fitness. The fact that only a small proportion of a population's egg production is produced at the time of peak offspring fitness is ecologically important. The classical match–mismatch hypothesis (Cushing 1990) suggests that timing of spawning remains fixed, reflecting the time of optimal developmental conditions for the offspring. In other words, the match–mismatch hypothesis implicitly assumes that breeding takes place at the peak in offspring fitness. This may have biased our views of marine life histories towards the offspring's perspective, neglecting the fact that parents maximise their own reproductive value (Einum and Fleming 2000), or that parents are constrained by food availability themselves. Both these factors explain the internal life history mismatch predicted here.

An internal life history mismatch need not lead to a mismatch, sensu Cushing (1990), as the latter tends to focus on the overlap between food availability and offspring demand. Observed overlap between food availability and young stages may seem good, as in our model, despite the internal life history mismatch between egg fitness and egg production. However, the model predicts benefits of an earlier start, but for reasons other than food availability. Here, seasonal predation risk and time constraints on development select for an earlier start. Both these factors are likely to be general.

We have shown that early eggs are better and we have predicted that some of the egg production is shifted prior to the feeding season in order to produce eggs of high fitness. Such early egg production relies on energy stores acquired the previous feeding season. Future analyses of this and similar models should focus on the importance of storage and early reproduction as a life history strategy (Reznick and Braun 1987, Reznick et al. 2006) and as a means of reducing an internal life history mismatch.

## Reproductive value and early eggs

Are we studying the winners? Here we predict that the earliest eggs contribute disproportionately to the production of future eggs. There are direct population level consequences of the seasonal egg fitness, and from the perspective of population recruitment it might be that these few but early eggs deserve our attention. We further predict that egg production may be low, as in the early scenario, when the successful offspring are born – those with the best chances of recruiting to the population and in turn producing viable offspring. Both predictions emphasise the importance of understanding patterns of individual reproductive value if our aim is to address future population consequences (Fisher 1930).

Given the high success of early eggs, we suggest an increased focus on processes at the time when high-value offspring are born. What, for instance, if adult copepods are cannibals on eggs early in the season (Ohman and Hirche 2001)? What if the ascent from diapause comes out of phase with the feeding habitat because of environmental changes primarily at the surface? Mismatch as a consequence of climate change is a well-documented phenomenon (Both et al. 2006), but there are also indirect evidence of rapid evolution of phenology, compensating for changes taking place in the feeding area (Jonzén et al. 2006). Our study suggests increased focus on the pre-bloom period in studies of marine copepods.

It would also be instructive to focus more on egg quality for zooplankton in general, such as variation in size and energy reserves of the egg. Egg size and quality may influence development time and survival probability, and consequently change the fitness of an egg, possibly including the seasonality in egg fitness. For pelagic fishes, the patchiness of the food resource may predict the tradeoff between size vs number of eggs

(Winemiller and Rose 1993). Variation in egg quality may therefore reflect adaptive strategies by parents. Egg size and content have been documented to vary seasonally (Pond et al. 1996), but we are not aware of studies on variation in egg size in relation to maternal state in free spawning copepods. A focus on egg states other than time of birth (egg date) would be a further step towards identifying the most successful strategies. Studies of salmon offer examples where egg quality (egg size) is studied in detail as well as the mothers' moulding of the offspring via the tradeoff between egg size and egg numbers (Einum and Fleming 2000).

## Guide to field studies and extended models

Reproductive values are difficult to obtain from field studies, particularly in systems where the fate of an individual is hard to follow, as for small pelagic species. The importance of early born offspring may therefore easily pass unnoticed, potentially also with the danger of concluding that the parent's strategy reflects what is best for the offspring and that total number of eggs (or other early stages) determine recruitment success. Field studies of zooplankton may contribute to a better understanding of temporal variation in reproductive value if cohorts of eggs are followed. Moving the research vessel with the currents, instead of along predetermined transects is one potential approach; another is fjord studies and mesocosms as laboratories for oceanic processes.

Some of the model predictions may also guide field or laboratory studies of copepod development and diapause. 1) For *C. acutus*, one basic study would be to determine development time to the first feeding stage. 2) We also suggest seeking a better understanding of the constraints that limit young stages from diapause. Potential causes are metabolic costs, migration costs, buoyancy costs, storage capability, and size-specific mortality.

Finally, we suggest that extensions of the model used here should test the consequences of letting adult females rebuild energy stores and prepare for a second diapause and breeding season. This may have consequences for some of the late egg production we predict and thereby the degree of mismatch between the timing of peak egg fitness and predicted egg production. The question also raises a fundamental life history question for copepods. Some species are known to be semelparous, in the sense of having one reproductive season (Miller et al. 1984), whereas others may be iteroparous and reproduce over several seasons (Miller et al. 1984, Kosobokova 1999). What are the ecological conditions and life history constraints that favour semelparity or iteroparity?

## Concluding remarks

We have studied the optimal life history of a high-latitude copepod experiencing seasonal food availability and predation risk. The reproductive value of an egg is predicted to be highly seasonal and the time of peak egg fitness depends on the interaction between food availability and predation risk. The highest egg fitness is predicted some time prior to the phytoplankton bloom. Studying fitness components separately allows us to conclude that seasonality in egg fitness is caused both by environmental seasonality (food and predation risk) and by the need to develop to a diapause stage towards the end of the feeding season, causing time-constraints. Despite being slow, development and growth prior to the feeding season are beneficial because of lower predation risk, and non-feeding initial stages may therefore be an anti-predator strategy. Finally, we have predicted an internal life history mismatch where mothers produce eggs later than the time of peak egg fitness. As a consequence, the earliest eggs, with the highest reproductive value, have the greatest importance to population recruitment despite their small initial numbers. We suggest a stronger focus on potential mismatch within life histories, and emphasise the need to study reproductive strategies as a component of complete life histories or annual routines.

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Appendix 1 is available online as Appendix O15893 at www.oikos.ekol.lu.se.