



The adaptive value of energy storage and capital breeding in seasonal environments

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Timing of reproduction in a seasonal cycle is a life history trait with important fitness consequences. Capital breeders produce offspring from stored resources and, by decoupling feeding and reproduction, may bend the constraints caused by seasonality in food or predation. Income breeders, on the other hand, produce offspring from concurrent food intake, with the disadvantage of less flexibility, but with high efficiency and no inventory costs of carrying stores. Here, we assess relative profitability of capital and income breeding in herbivorous zooplankton inhabiting seasonal, high-latitude environments. We apply a state-dependent life history model where reproductive values are used to optimise energy allocation and diapause strategies over the year. Three environmental scenarios were modelled: an early, an intermediate, and a late feeding season. We found that capital breeding was most important in the early season. Capital breeding ranged from 7–9% of the eggs produced but, because of the high reproductive value of early eggs, capital breeding ranged from 9–30% when measured in terms of reproductive value. The main benefit of capital breeding was reproduction prior to the feeding season – when the reproductive value of an egg peaked. In addition, capital breeding was also used to increase egg production rates at times of income breeding. For individuals born late in the season the model predicted a two-year cycle instead of the typical annual life cycle. These individuals could then reap the benefits of early reproduction and capital breeding in their second year instead of income breeding late in the first year. We emphasize the importance of evaluating reproductive strategies such as capital and income breeding from a complete life cycle perspective. In particular, knowing the seasonality in offspring fitness is essential to appreciate evolutionary and population-level consequences of capital breeding.

Individuals should allocate available resources such that individual fitness is maximized (Stearns 1992, Roff 2002). Allocating resources to current reproduction often has costs in terms of reduced future fitness, i.e. reduced residual reproductive value (RRV) (Williams 1966). There has been much attention on how the costs of reproduction influence RRV, as in studies manipulating the costs of reproduction and observing their effects on parental survival or future reproduction (Dijkstra et al. 1990). However, there are also costs of reproduction prior to breeding, many of which are linked to resource acquisition. These costs have received less attention in life history theory (Jönsson 1997, Jönsson et al. 1998) despite strong selection pressures operating on pre-breeding strategies.

Organisms allocate their limited resources to growth, maintenance, and reproduction. Energy storage, an important aspect of resource acquisition, may be viewed as a fourth category to which resources are allocated, albeit intermediately (Reznick and Braun 1987). Stores are linked to reproduction because energy reserves allow high rates of resource-transfer from parent to offspring, and reserves let reproduction take place at times or places with limited

access to food (Jönsson 1997, Bonnet et al. 1998). In many life cycles, resource acquisition is therefore part of a careful preparation for reproduction where the amount of stores acquired, ahead of breeding, links directly to expected fecundity. In seasonal environments, where feeding seasons are short and energy stores are central also for winter maintenance, fine-tuned energy storage strategies are particularly relevant.

Life cycles vary in their dependence on energy storage for reproduction – a part of life history evolution captured by the framework of capital and income breeding. Reproduction based on stored resources are referred to as ‘capital breeding’, whereas reproduction based on concurrent food intake is termed ‘income breeding’ (Stearns 1992, Jönsson 1997). Life history strategies are represented along the whole continuum from pure capital breeding to income breeding (Tamaru and Haukioja 1996, Meijer and Drent 1999, Jervis et al. 2005, Lee et al. 2006, Houston et al. 2007). Capital breeding has costs, such as energetic costs of carrying stores, but also survival costs, because foraging to acquire the stores needed for later reproduction typically involves elevated predation risk. These costs of reproduction, termed

pre-breeding costs (Sibly and Calow 1984, Jönsson et al. 1995, Jönsson 1997), must be traded against the benefits of capital breeding. Income breeders, on the other hand, have none of these costs because they do not delay the realization of reproductive value. Instead, they quickly turn available food into offspring, but with reduced flexibility because timing and rate of reproduction are constrained by food availability.

In his review, Jönsson (1997) suggested that theoretical analyses should evaluate the fitness consequences of capital and income breeding, and he stressed the importance of including foraging decisions as part of life history models. We take both challenges by using a state-dependent life history model where life history tradeoffs emerge from environmental constraints and inherent physiology, and where optimal annual routines can be predicted (McNamara and Houston 2008). Our context is the seasonal life history of a herbivorous copepod at high latitudes, and our model allows a novel quantification of capital versus income breeding by adopting a complete life-cycle perspective and using reproductive value as a fitness measure.

We demonstrate how the adaptive value of capital and income breeding varies between three environmental scenarios; an early, an intermediate, and a late feeding season. The environments consequently differ in the seasonal interaction between predation risk and food availability (primary production). The model predicts optimal strategies for energy allocation and timing of diapause. We present the population dynamics emerging from the optimal life history strategies, and we focus on the seasonal abundance of developmental stages as well as their timing of diapause – both factors influencing the potential for capital breeding. We then quantify the magnitude and importance of capital breeding, and we discuss the costs and benefits of capital breeding predicted by our zooplankton model. In particular, we focus on how seasonal changes in offspring fitness may drive capital breeding. Our predictions and conclusions are of relevance to all life histories with energy storage as part of a seasonal reproductive strategy.

The model

Here we give a brief introduction to the model organism as well as model structure and methodological philosophy. We have recently presented the full model description and analyzed the seasonality in egg fitness (Varpe et al. 2007, including the online Appendix O15893 at <<http://www.oikos.ekol.lu.se/appendix>>).

Model organism

Model parameters are for a high-latitude marine copepod, with special reference to *Calanoides acutus*, an abundant herbivorous copepod in the Southern Ocean with a predominantly annual life cycle (Tarling et al. 2004). High-latitude herbivorous copepods have evolved strategies to cope with a short feeding season and a long unproductive winter (Conover 1988, Atkinson 1998). One adaptation is a deep-water diapause (resting stage) with reduced meta-

bolism and low exposure to predators. *Calanoides acutus* produce eggs near the surface in spring and develop from egg to adult via six naupliar stages (N1 to N6) and six copepodite stages (C1 to adult, Fig. 1). Older stages (typically C4s and beyond) have a seasonal migration between the feeding habitat (surface waters) and the deep diapause habitat (Atkinson et al. 1997). *Calanoides acutus*, and copepods in general, have life history characteristics of both capital and income breeders (Hagen and Schnack-Schiel 1996, Lee et al. 2006). Energy stores are larger than needed for winter diapause, and surplus stores are used for maturation and early egg production (capital breeding). Later eggs are produced from concurrent phytoplankton grazing (income breeding). The feeding season is short and the timing of life cycle events are likely to be important (Varpe et al. 2007).

Model overview

The model predicts optimal state-dependent life history strategies based on maximization of reproductive value by

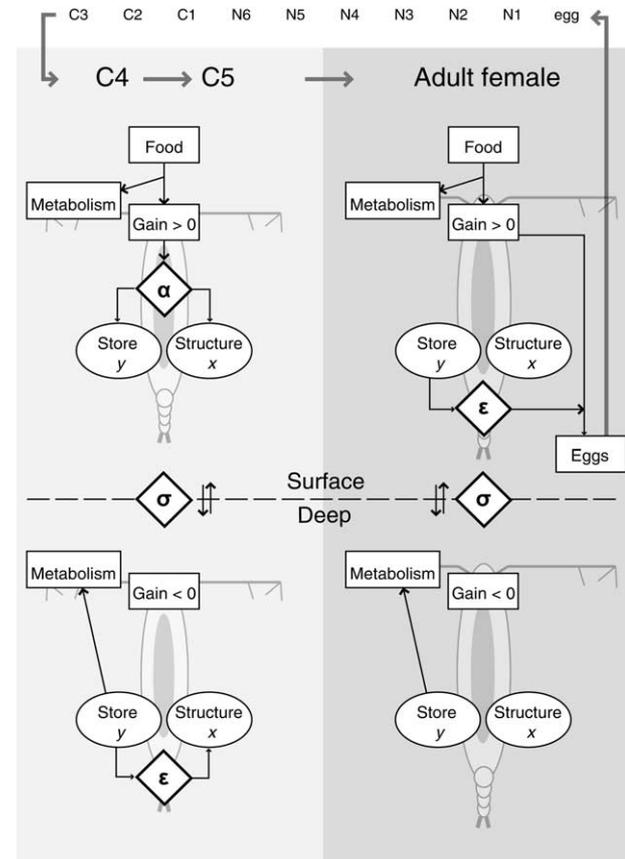


Figure 1. Processes and optimised decisions in a copepod life history model. The life cycle consists of the egg stage, six naupliar stages (N1–N6), and six copepodite stages (C1–C6), with C6 referred to as adults. There is a moult for each stage transition. Three life history decisions (diamonds) were optimised for each day of the year: allocation α of carbon to store or structure, the use of energy stores ϵ , and habitat change σ (active in the surface, diapause while deep). Relevant decisions differ with stage and habitat. The figure is from Varpe et al. (2007), which also contains a full description of the model.

dynamic programming (Houston and McNamara 1999, Clark and Mangel 2000). The model includes an entire life cycle from egg to adult, and the model has the capacity to determine any seasonality in offspring fitness (reproductive value) resulting from seasonal cycles in environmental variables such as food availability, predation risk, and temperature. In a recent study we showed marked seasonality in egg fitness; with peak fitness, and some egg production, occurring prior to the feeding season (Varpe et al. 2007).

Modelled individuals are characterized by states (developmental stage, structural body mass, energy store, and habitat; Fig. 1). Mortality depends on habitat, developmental stage, time of the season, and energy reserves. When stores are depleted the mortality rate is elevated, and the energetic costs of the autumn migration increase with body mass. Two habitats are available, a surface habitat, with seasonal cycles of food availability and predation risk, and a deep habitat where individuals experience low predation risk and enter an energy-conserving diapause. The model first finds the optimal energy allocation and diapause strategy for all state combinations and for each day of the year ($\sim 7.8 \times 10^6$ independent values). In a second step, we use a matrix model to simulate a population where individuals follow optimal strategies. From the population simulations we present realized seasonal stage composition, habitat use (deep or surface), and egg production. Importantly, we also track whether an egg is produced from capital or income breeding. Because the reproductive value of an egg is calculated in the model, we can use this information to quantify the value of capital and income breeding in terms of an egg's demographic projections. We can thereby assess the evolutionary importance of capital versus income breeding, and we do so for three environmental scenarios; an early, an intermediate, and a late feeding season.

Environmental forcing

We model typical high-latitude oceanic environments where seasonality in irradiance causes seasonality in food availability (phytoplankton), temperature, and predation risk – the latter motivated by the role of light for predators relying on vision for hunting. We explore three scenarios, where the seasonal cycle of food availability is shifted relative to the seasonality in predation risk (Fig. 2a, 3a, 4a). There are relatively safe temporal foraging windows if food is available early (Fig. 2a) or late (Fig. 4a) but, in the intermediate feeding season high food availability and high predation risk co-occur (Fig. 3a). The warming temperatures during spring and summer cause net carbon gain (growth rate) to increase slightly during the time of peak food availability. All seasonal trajectories are presented for a southern hemisphere ecosystem.

Here we focus on the effects of seasonality as predicted in deterministic environments. Even though inter-annual variation between years is likely, for instance variable onset of the feeding season, no equivalent to maximisation of descendants left far into the future exists when the environment is fluctuating (McNamara 2000). An analysis of the influence of inter-annual environmental variation

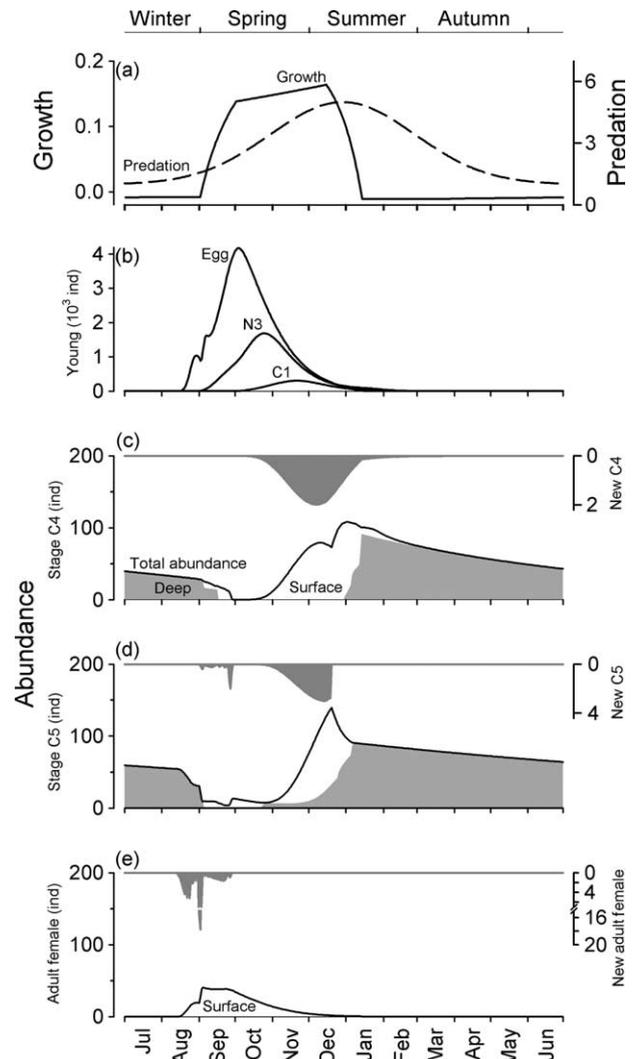


Figure 2. Early feeding season. The population dynamics predicted from simulations where individuals follow optimal life history strategies. The environment is seasonal, here with a feeding season prior to peak predation rates. (a) Potential carbon growth rate (day^{-1}) and predation rate (10^{-2} day^{-1}) of stages C4, C5, and adult female while in the surface habitat. (b–e) Seasonal abundance of eggs, nauplii and copepodite stages. Total abundance (black lines), which for C4s, C5s and adult females are separated for the deep (grey area) and surface (white area) habitat. Inflow of new individuals to a stage (upper part of panels c, d and e) is shown as daily percentage of annual total number of individuals recruited to that stage.

should therefore use other approaches, for instance individual-based models, often with less transparency and a reduced state space as a consequence.

We regard the early and intermediate feeding seasons as common for high-latitude copepods, and the late season as rarer. When presenting predicted life history trajectories, as revealed by population dynamics, we focus on the early scenario (Fig. 2), but point out where the two other scenarios differ (Fig. 3, 4). All scenarios are used when capital and income breeding are analyzed and compared (Fig. 5).

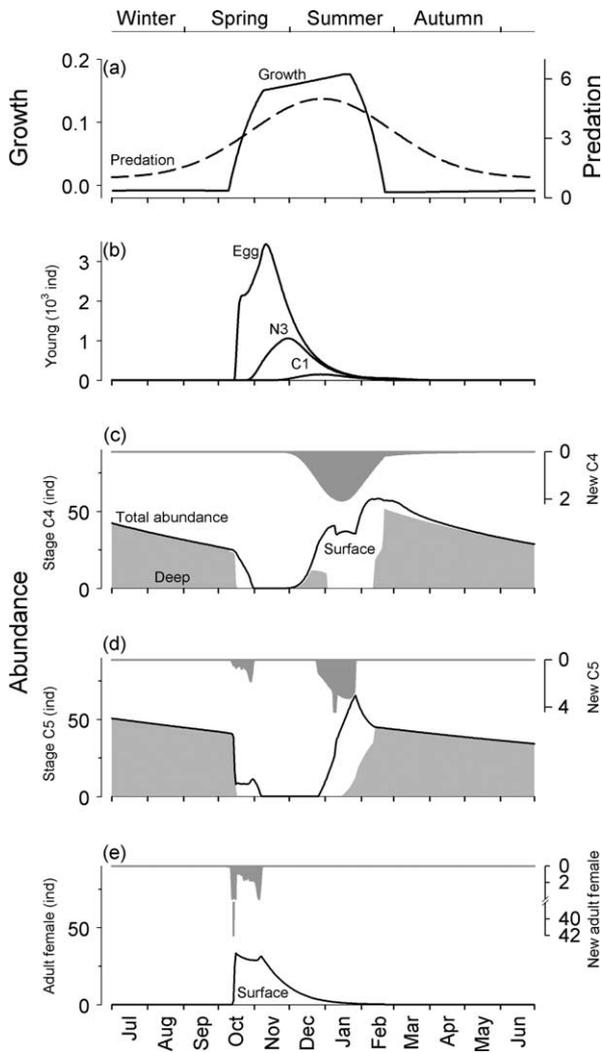


Figure 3. Intermediate feeding season, with legend otherwise as for Fig. 2.

Results

Life history

The main trends in the modelled life histories are as follows: Eggs are produced prior to and during the first half of the feeding season (Fig. 2b, 5a). Subsequent naupliar and copepodite stages follow (Fig. 2b), and the first individuals moult to C4 by the middle of the feeding season (Fig. 2c). From stage C4 and onward, individuals can allocate net gain to structure or store, or enter the deep habitat for diapause. The first C4s develop to C5s before diapause (Fig. 2d), whereas late C4s enter diapause in this stage. In wintertime, the population consists of similar proportions of C4s and C5s (Fig. 2c–d). The first adult females appear prior to the feeding season, in late August (Fig. 2e). The ascent from the deep diapause habitat to surface waters is not synchronized but depends on individual state. About half of the adult females appear prior to the bloom (they diapaused as C5) and some appear synchronously at the onset of the feeding season. The final recruitment to adult females is by copepodites that have to meet the energetic

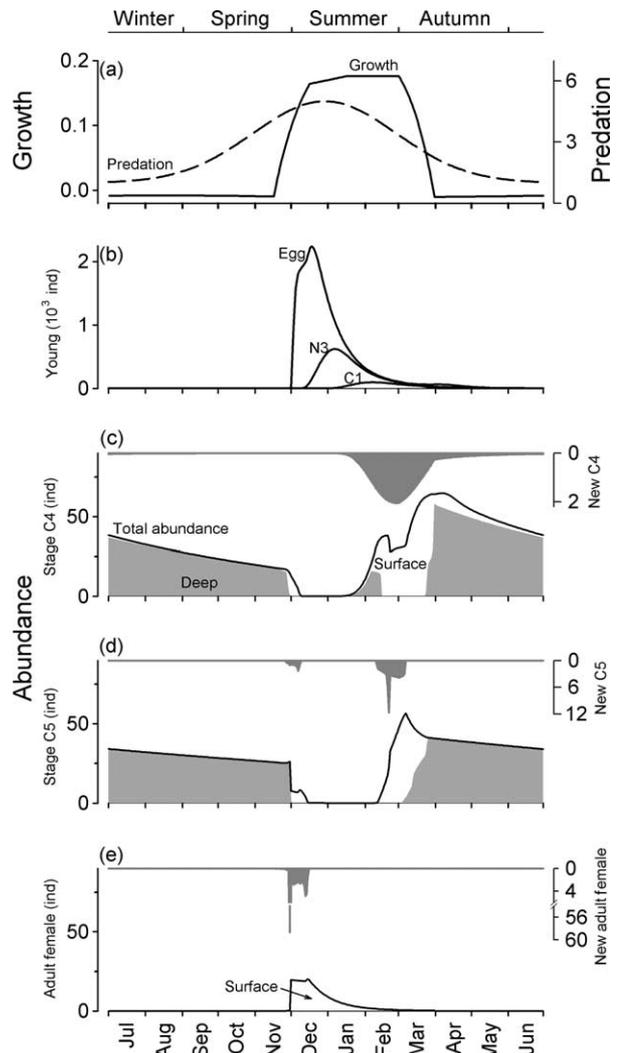


Figure 4. Late feeding season, with legend otherwise as for Fig. 2.

demands of moulting to adult females by feeding in surface waters. The number of adult females decreases as the season progresses, first due to predation, but after the feeding season also due to starvation (it is assumed that adult females do not rebuild stores as a preparation for a second winter).

Additional predictions from the early feeding season include: 1) some C4s remain in the surface habitat when the feeding season ends because their energy reserves are too small for diapause (Fig. 2c). Predation risk is high in the surface habitat and most of these C4s soon die. 2) The C4s ascend to the surface (left part of Fig. 2c) in two groups, about two weeks apart. The second group consists of the smallest C4s, both in terms of structure and stores (not shown). Their optimal strategy is to pass through two winters before moulting to the adult stage and breeding. During their second summer, they develop from C4 to C5 (during September/October in Fig. 2d) and descend early (October/November, Fig. 2d). Judged by their low abundance in November, they form only a small part of the adult population that ascends next year. 3) Generally, C5s are observed to enter diapause before C4s (December vs January; Fig. 2c–d).

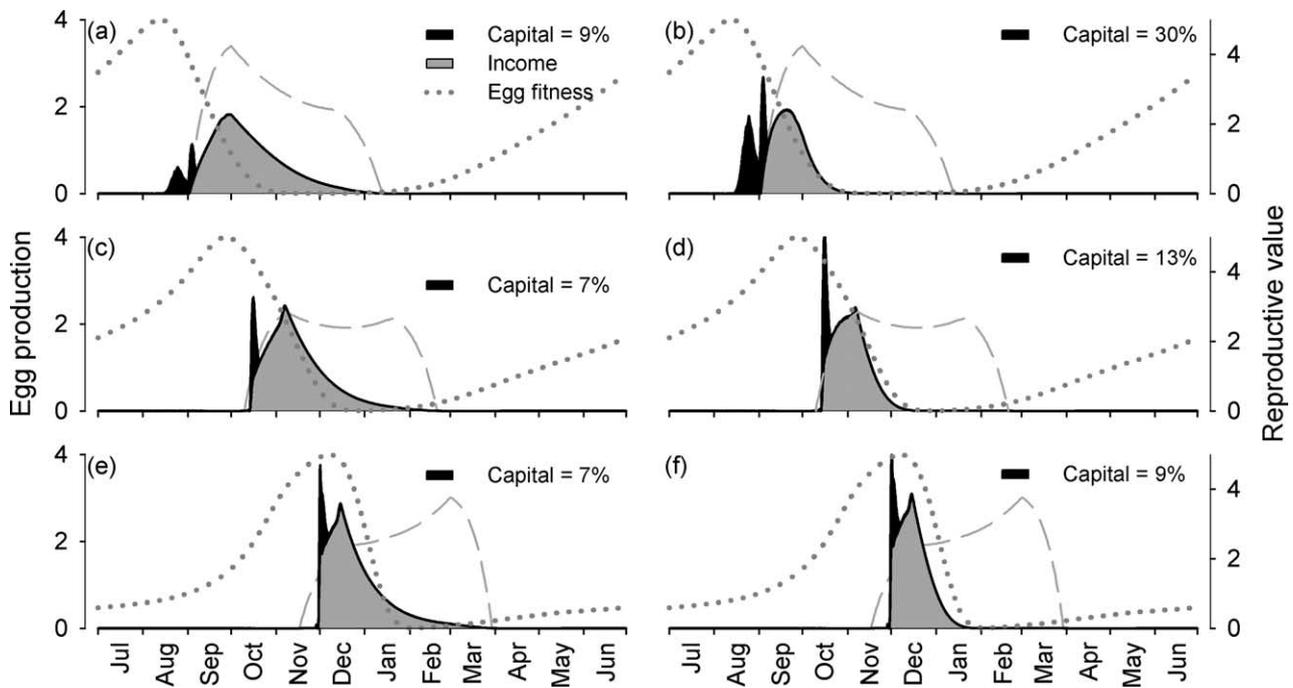


Figure 5. Egg production at the population level with capital and income breeding components separated. Number of eggs (left) and reproductive value (right) are shown as daily percentage of the annual total for the early (a, b), intermediate (c, d), and late feeding season (e, f). The percentage contribution from capital breeding is given on each graph. The ratio between growth rate and mortality rate in the surface habitat is indicated (broken grey line, no y-axis), as is the seasonal egg fitness (dotted, no y-axis) predicted by Varpe et al. (2007).

The intermediate and late scenarios deviate from the early scenario in some interesting ways: 1) the two-year life cycle is absent. 2) There is synchronous ascent by all adult females. 3) C4s perform anti-predator behaviour by an extra migration to the deep habitat during peak predation (dark area in December, Fig. 3c, and January/February, Fig. 4c). These individuals return to the surface and develop to C5s later in the same season before a new descent, this time for overwintering. 4) A large proportion of individuals (28%) in the late scenario does not develop to stages capable of diapause, and thus remains in stages younger than C4 at mid-winter. The proportions are 1% and 7% for the early and intermediate scenarios, respectively.

Capital and income breeding

As seen above, developmental history, life history constraints, and individual differences in physiological states render capital breeding an opportunity for some individuals and not for others. However, capital breeding is part of the reproductive strategy in all three modelled environments, but the amount of capital breeding differ between scenarios and depend on the method used to quantify capital breeding.

Number of eggs

The number of capital-bred eggs is low (7–9% of total egg production, Fig. 5a, 5c, 5e). Capital breeding takes place prior to the feeding season in the early scenario and at the beginning of the feeding season in all scenarios. Capital and income breeding are combined when stores and food are available at the same time, but as stores are depleted, egg

production can come only from income breeding. Income breeding increases toward the time of peak adult abundance (Fig. 5e) and declines as adult females die. For all scenarios, only about half the population are potential capital breeders – those individuals born sufficiently early in the season to diapause as C5 and with sufficient stores (Varpe et al. 2007).

Reproductive value

The importance of capital versus income breeding is better quantified by their contribution to reproductive value (number of eggs multiplied by their reproductive value, i.e. the expected contribution to future projections of population dynamics, Fig. 5b, 5d, 5f). Capital breeding accounts for 30% of total reproductive value produced when the feeding season is early; a threefold increase compared to the number of eggs produced. For the intermediate and late scenarios the proportion of capital breeding also increases, although less, when evaluated in terms of reproductive value. The increase in the proportion of capital breeding is caused by the generally high reproductive value of capital-bred eggs, and the lower value of most income-bred eggs.

Discussion

We have previously reported the population-level consequences of early egg production and analysed the fitness components that generate seasonality in egg fitness (Varpe et al. 2007). Here we focus on the later stages of the life cycle, including stage-specific seasonal abundances, timing

of diapause, generation time, and in particular the adaptive value of capital versus income breeding. Using a state-dependent life history model, we identify both capital and income breeding strategies in the same population. Depending on their date of birth, their state, and the environment, individuals either store energy and breed early so that offspring develop in time for the feeding season, or they skip energy storage and begin reproducing only as food becomes available. Individuals that begin the season as capital breeders continue to reproduce as income breeders. Among the most central findings are: 1) capital breeding is particularly profitable when egg fitness peaks prior to the feeding season; 2) the contribution of capital breeding to fitness is better quantified in terms of the reproductive value of eggs rather than just numbers of eggs; 3) for individuals born late in the feeding season, a two-year life cycle is predicted in environments where capital breeding is valuable; 4) the timing of the spring ascent is state-dependent with capital breeders migrating to the surface earlier than income breeders; 5) only overwintering C5s have the stores needed for capital breeding; and 6) both C4s and C5s are diapause stages, and in similar numbers. We structure the discussion of these findings in relation to the costs and benefits of capital breeding.

Costs of capital breeding

Pre-breeding costs of foraging

Foraging often involves elevated predation risk, and mortality is therefore a main pre-breeding cost (Jönsson et al. 1995). For a capital breeder, the decision to forage in order to build energy reserves is therefore part of a tradeoff between fecundity and adult survival, and for a pure capital breeder acquired stores would scale directly with expected fecundity. Among copepods, the *Neocalanus* spp. in the Pacific provide examples of pure capital breeders, as their adult stages are unable to feed (Miller et al. 1984).

Pre-breeding costs of energy storage are predicted in our model. Predation risk and routine metabolism are much reduced in the diapause habitat, but the copepods still stay in the surface long enough to store energy in excess of that needed for winter maintenance. At some point, however, further foraging comes at a larger risk than is gained through expected fecundity next spring. Many large C5s in the intermediate and late scenarios therefore enter diapause before the feeding season is over without using their full storage capacity (not shown) – a response to the relatively small value of capital breeding in these scenarios. Many C5s, however, acquire full stores when the feeding season is early, because capital breeding is more valuable. Under those conditions, store size is determined by a morphological constraint rather than the trade off between survival and fecundity (cf. Shine and Madsen 1997).

Inventory costs

There are two inventory costs in the model: a migration cost when entering diapause (proportional to total body mass), and a conversion cost when using stores for egg production or growth. Energetic costs of carrying stores are often more pronounced in birds and terrestrial animals compared to aquatic organisms, and inventory costs are generally higher in endotherms than in ectotherms (Bonnet et al. 1998).

Inventory costs can also be indirect, for example by interfering with locomotion and thereby reducing hunting or foraging efficiency or increasing predation mortality (Witter and Cuthill 1993). In copepods, predation pressures that increase with size (Eiane et al. 2002) may be an additional cost of energy storage not accounted for in our model.

Energy reserves may serve other functions before they are used for capital breeding, thereby increasing the adaptive value of energy storage. For instance, lipids serve as insulation in warm-blooded animals and buoyancy in aquatic animals (Hadley 1985). For copepods it has been suggested that lipid stores may be an energetically efficient mechanism to achieve neutral buoyancy at a preferred diapause depth (Visser and Jonasdottir 1999). However, the mechanism and its adaptive value are uncertain and much discussed (Campbell 2004, Fiksen et al. 2004, Irigoien 2004), and could constrain the evolution of capital breeding by selecting for narrow windows of optimal lipid stores. Clearly, one should keep alternative benefits and costs of storage in mind when evaluating pros and cons of capital breeding.

Mortality costs at the time of breeding

There can also be direct mortality costs of capital breeding, as when the capital breeders in our model ascend prior to the feeding season. They produce high value eggs, but must spend time in the risky surface waters during egg production and after stores are emptied but before income breeding can start. The extra fitness that these capital-bred eggs gain warrants the acceptance of higher predation risk (and higher metabolism) than in the diapause habitat. A retreat to the deep diapause habitat would serve as an escape from this waiting cost, but the metabolic migration costs makes such an escape suboptimal. Although not included in our model, anti-predator behaviours in the active surface phase, such as diel vertical migrations, may modify predation risk (cf. Fiksen 1997, Fiksen and Carlotti 1998) and therefore alter the costs and benefits of capital breeding.

Benefits of capital breeding

Timing of offspring production

In seasonal environments peak offspring fitness is typically early in the feeding season (Verhulst and Nilsson 2008). Often, individuals can better match this peak if they prepare by storing energy (Reznick et al. 2006). Accordingly, our model predicts the most pronounced capital breeding in the early scenario, where a pronounced peak in egg fitness is well ahead of the feeding season. In this scenario, peak egg fitness also coincides with low predation risk on adults (discussed below). Furthermore, some individuals that are cut off from the possibility of capital breeding in their first year opt for a two-year life cycle to reap the benefits of early capital breeding, thereby accepting another full year of mortality. *Calanoides acutus* has a predominantly annual life cycle, but a two-year life cycle is also observed (Tarling et al. 2004). The value of capital breeding may consequently be an important driver for a flexible life span in copepods. It is well known from other high-latitude copepods that the

duration of the life cycle varies (Conover 1988, Madsen et al. 2001).

Egg production prior to the phytoplankton bloom has been suggested to be important for high-latitude copepods, including *C. acutus* (Huntley and Escritor 1991, Hagen and Schnack-Schiel 1996). Proposed adaptive benefits include that juveniles will reach the first-feeding stages at the onset of the phytoplankton bloom (Allan 1976), and that they can develop at times of low predation risk (Varpe et al. 2007). However, a potentially counteracting cost is the risk of cannibalism on eggs and nauplii when food availability for adults is low (Ohman and Hirche 2001).

Reductions of foraging mortality

The decoupling of foraging and reproduction by capital breeding allows foraging to be concentrated to times when food can be acquired at low mortality costs (as indicated by the growth-per-mortality curves in Fig. 5). In the late scenario, there are such loopholes, with low costs of foraging when stores are built (prior to diapause), whereas foraging costs are high when income breeding takes place. Some capital breeding was therefore beneficial even though peak egg fitness coincided with the onset of the feeding season.

Risk-sensitive foraging also explains the summer retreat to the deep habitat predicted in the intermediate and late scenarios. With this migration, individuals circumvented the seasonal peak in predation risk, and postponed development and energy storage until later in the feeding season. Such retreats to deep waters have not been observed in marine copepods, possibly because other anti-predator responses are more effective, such as diel vertical migrations (Hays 2003). For freshwater copepods however, temporarily low food availability during mid-summer induced a resting phase, and feeding resumed when foraging conditions improved (Santer and Lampert 1995). The modelled copepod life cycles are variations on the general theme of migrations between rich feeding grounds, safe overwintering- and resting-areas, and suitable breeding grounds, observed for instance in turtles (Luschi et al. 2003), fish (Varpe et al. 2005) and birds (Meijer and Drent 1999).

Reductions of breeding mortality

Finally, capital breeding may also reduce the mortality costs during reproduction, in at least two ways. Firstly, by reducing predator exposure through the increased rates of reproduction obtained when capital and income breeding are used at the same time. This is an option when carrying stores have small costs in terms of foraging efficiency (cf. Cuthill and Houston 1997). Our model predicts a capital-based boosting of egg production rates in all scenarios, as a marked peak of capital breeding just when income breeding was starting. Secondly, capital breeding can also facilitate reproduction at times or places where adult predation risk is low, but food availability scarce. Low predation risk on adults contributed to the benefits of capital breeding in the early feeding season, where egg fitness is high at a time when predation is low for adults as well as offspring. A similar reduction of adult mortality may also be the driver for the purely capital breeding copepod species that feed in

surface waters but reproduce at depth in connection with the winter diapause (Miller et al. 1984, Ohman 1987).

How to quantify capital breeding: numbers or reproductive value?

When a life history is characterized by both continuous reproduction and seasonality in offspring fitness, counting the number of offspring is insufficient to evaluate the success of an individual, or the success of different strategies (Varpe et al. 2007). In our case, the number of eggs produced from capital breeding is low, but capital breeding is still contributing significantly to recruitment because the reproductive value of capital-bred eggs is high. This insight is gained because we allow reproductive values to emerge in a model with a full life cycle (Houston and McNamara 1999). For fieldwork, the corollary is that egg production rates only partly quantify the success of individual strategies and that recruitment cannot be predicted by egg numbers alone. Focusing on capital breeding can therefore help focus in on important constraints and processes that shape life history strategies and population dynamics.

Some recent studies have quantified the capital and income breeding proportions of reproduction. For instance, Gauthier et al. (2003) used stable isotope signatures in geese to estimate the contribution from endogenous reserves relative to the contribution of food plants eaten at the breeding grounds. Similarly, many other species combine capital and income breeding, for instance during different stages of parental care (Bowen et al. 1985). Casas et al. (2005) took a different perspective in studying the allocation strategy of an ectoparasite, finding that it was a capital breeder for lipids and an income breeder for sugars, with intermediate strategies for glycogen and proteins. As a final example, Houston et al. (2007) modelled offspring provisioning in seals, where strategies along the whole continuum of capital and income breeding were predicted. They quantified the contribution by maternal capital and maternal income to the offspring's energy, and predicted optimal strategies based on maximization of offspring production or maximization of offspring quality. Together, these studies point out some of the multidimensionality of capital and income breeding. We have added to this by pointing out the importance of seasonality in offspring fitness and the benefits of taking a life-cycle perspective in the analysis of capital breeding.

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