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Capital versus Income Breeding in a Seasonal Environment

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ABSTRACT: The allocation of resources between growth, storage, and reproduction is a key trade-off in the life-history strategies of organisms. A central dichotomy is between capital breeders and income breeders. Capital breeders build reserves that allow them to spawn at a later time independently of food availability, while income breeders allocate ingested food directly to reproduction. Motivated by copepod studies, we use an analytical model to compare the fitness of income with capital breeding in a deterministic seasonal environment. We analyze how the fitness of breeding strategies depend on feeding season duration and size at maturity. Small capital breeders perform better in short feeding seasons but fall behind larger individuals when the length of the feeding season increases. Income breeding favors smaller individuals as their short generation time allows for multiple generations within a year and thereby achieve a high annual growth rate, outcompeting capital breeders in long feeding seasons. Therefore, we expect to find a dominance of small income breeders in temperate waters, while large capital breeders should dominate high latitudes where the spring is short and intense. This pattern is evident in nature, particularly in organisms with a generation time of a year or less.

Keywords: income breeder, capital breeder, reproductive strategy, feeding season, spring bloom, life-history traits.

Introduction

In seasonal environments, the timing of resource allocation to reproduction has direct consequences for fitness and for population dynamics. In general, an individual can either allocate available resources to reproduction directly (income breeder) or build up reserves while resources are available and reproduce at some future date (capital breeder; Drent and Daan 1980; Stearns 1992; Jönsson 1997). An individual can also adopt a mixed strategy with income and capital co-occurring (Varpe et al. 2009) or concurrent food intake added to reserves stored before reproduction commences (Houston et al. 2007).

In constant (nonseasonal) environments, one can expect the income breeder to be the superior competitor as postponing breeding will not lead to better conditions for the offspring. However, this strategy becomes less effective when seasonality in resource availability and mortality risk shapes the fitness of an individual as a function of its time of birth (Varpe et al. 2009; Ejsmond et al. 2010). For example, for copepod species living in high-latitude seas, adverse conditions during the winter ensure a strong selection on the state of individuals at the end of the feeding season, underlining the hypothesis that offspring born late in the feeding season have a low fitness due to a lack of time to reach a suitable size to survive the winter (Varpe et al. 2007).

In this respect, capital breeding makes it possible to reproduce at a time and location that maximizes the fitness of their offspring (Jönsson 1997; Varpe et al. 2009). This strategy, however, is not without a risk, as in postponing reproduction, the adult (and its potential offspring) may perish in the meantime, illustratively referred to as a prebreeding cost of reproduction (Jönsson 1997; Jönsson et al. 1998).

Another trait that should be considered along with the income-capital breeding trait is the size of an organism, since size (e.g., for copepods; size at maturity or of eggs, or their ratio) is a key trait influencing fitness. In particular, adult size influences the ability to acquire resources, as well as mortality and metabolic rates, egg size influences fecundity, and relative size determines the time needed for offspring to grow to adulthood (Charnov 2001; Andersen et al. 2008). In seasonal environments, species have to time their maturation and their breeding strategy with the restricted duration of the feeding season. Within this context, a defining question is: what is the best breeding strategy (i.e., capital vs. income breeding) and maturity size as a function of the duration of the feeding season?

Copepod species of the genus *Calanus* found in the North Atlantic and the Arctic present a rich example of the diversity of reproduction strategies that similar species can adopt. Three dominant *Calanus* species in these waters display the full spectrum of resource allocation: *Calanus finmarchicus* is close to a pure income breeder, using con-

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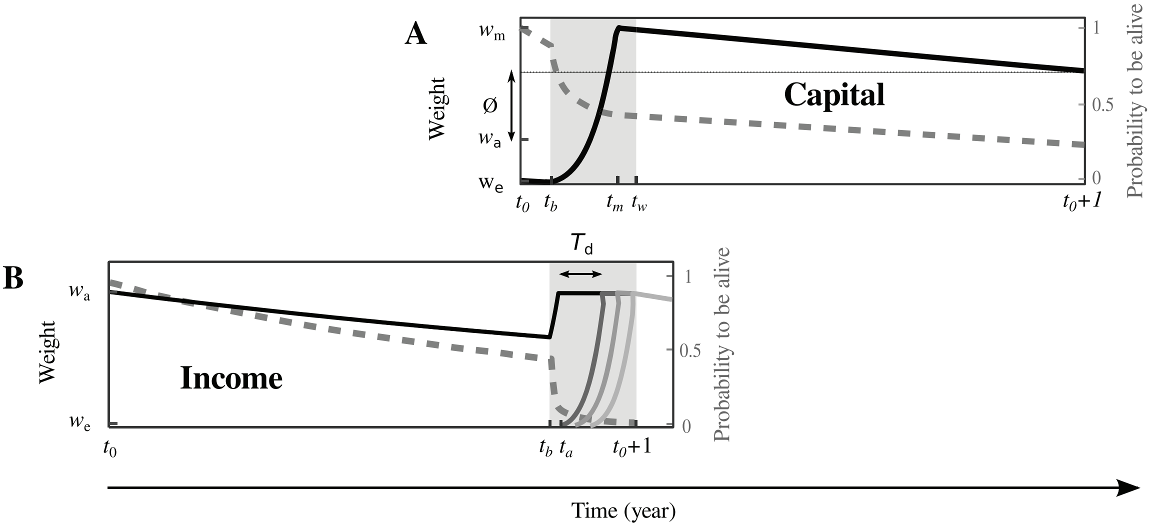

Figure 1: Weight (black lines) and probability to be alive (dashed gray lines) of capital (*A*) and income (*B*) breeders. *A*, Capital breeders are born at time t_0, grow during the feeding season (gray area) until they reach maximum size (w_m) at t_m and enter dormancy. The Ø represents the amount of weight converted to egg production. *B*, Income breeders start at adult size at the beginning of the winter (t_0), lose weight until the onset of the feeding season (t_b), after which they regain maturity at t_a. They spawn until the end of the feeding season, while their offspring reach the adult pool after their development time T_d. Additional generations are represented as shaded gray lines.

current food intake to produce eggs; *Calanus hyperboreus* is a pure capital breeder, spawning in very deep waters during the winter by using its reserves accumulated during the previous spring bloom; while *Calanus glacialis* adopts a mixed strategy, storing some reserves to spawn before the spring bloom and using the incoming food to spawn during the bloom as well (Conover 1988; Falk-Petersen et al. 2009). These three copepods are quite different in size, with *C. hyperboreus* being much larger than the two others. Although they display the same life cycle (they go through six stages of nauplii and five stages of copepodite before reaching adulthood), adopt similar strategies to avoid visual predation (diel vertical migration), and overwinter at depth, their centers of distribution differ: *Calanus finmarchicus* dominates the subarctic waters of the North Atlantic, *C. hyperboreus* the Arctic, and *C. glacialis* the continental shelf and the fjords of northern latitudes (Conover 1988).

Optimization models have highlighted the adaptive value of storage, capital breeding, and timing of reproduction for our understanding of within-species diversity and state-dependent life histories (Fiksen and Carlotti 1998; Varpe et al. 2009). We expect variability in breeding strategies and size to have evolved in response to spatial variability in environmental conditions, including seasonality in food availability and predation risk, similar to the pan-Arctic within-species diversity observed in *C. glacialis* (Daase et al. 2013). Several studies contrasting income versus capital breeding strategies have focused on relative trade-offs (e.g., cost benefit of carrying storage in ectotherm and endotherm species; Jönsson 1997; Bonnet et al. 1998; or on the pre- and postbreeding investment of the parents; Jönsson et al. 1998), but few have investigated how the environment shapes the success of these different breeding strategies within species and for closely related species. In a recent article, Stephens et al. (2014) found that an index of capital breeding for pinnipeds increases with stronger seasonality and a decreased predictability of the environment. Here, we pursue this line of investigation and show that the duration of the feeding season alone can select for breeding strategy and preferable size at maturity, also in organisms with short life spans.

We construct a simple life-history model of marine copepod species to use the species complex and strategy space to obtain insight into the general relevance for seasonal environments. The simple structure of the model allows us to obtain analytical solutions and perform a general analysis of (1) how the duration of the feeding season influences the success of capital versus income breeders and (2) how the relative fitness of these strategies varies with size at maturity.

Methods

We model the net reproduction of an individual and its offspring over one annual cycle for an income and a capital breeder in order to determine which of the two strategies has the highest fitness under given environmental con-

Table 1: Symbols and parameters used

	Description	Value	Units
Symbol:			
w	Weight of an individual		μg C
$P_{t_1 \to t_2}$	Probability to survive from t_1 to t_2		
r	Annual fitness		Individuals year^{-1}
μ	Mortality rate		Day^{-1}
w_a	Maturity weight		μg C
f	Feeding level	[0,1]	
μ_a	Mortality rate at adult size	$ah_f w_a^{1/4} + \mu_0$	Day^{-1}
θ	Reproductive investment		Individuals year^{-1}
Parameters:			
w_e	Egg weight	1	μg C
w_m	Maximum weight	$4w_a$	μg C
h_f	Factor for maximum consumption during the feeding season	1.01	μg C$^{1/4}$ day^{-1}
g_w	Reduction of h during winter	10	
h_w	Factor for maximum consumption during the winter	h_f/g_w	μg C$^{1/4}$ day^{-1}
μ_0	Size-independent background mortality	10^{-3}	Day^{-1}
ε_r	Conversion efficiency from adult to egg weight	.5	
f_c	Critical feeding level	.01	
a	Predation constant	.1	

Note: The units used are individuals, micrograms carbon (μg C), days, and years.

ditions. Our central focus is the length of the feeding season. Thus, the year is divided in two: the feeding season (spring) and the rest of the year (nominally termed "winter"), during which no food is available. For each strategy we first determine a life-cycle "bottleneck," a state (age, weight) that if not achieved by a particular date, for example, transition from winter to spring conditions, in the annual cycle will result in a negligible probability of survival. The fitness of a given strategy is set by the number of descendants from an individual 1 year later with the same state as the starting individual. All other things being equal, this measure will be identical to the annual population growth rate for a given state-date combination. We term this the "annual fitness."

For a capital breeder, breeding time is a clear bottleneck as it will spawn its entire production at a fixed time of the year. Hence we start the calculation with an egg born at time t_0 and follow its development, growth, and survival through the feeding season, its accumulation of reserves and descent into diapause, and its overwintering survival at depth, to calculate the number of eggs produced a year later. Thus, the fitness is set by the expected number of eggs produced at breeding time 1 year later (fig. 1*A*).

For an income breeder, the bottleneck is the size that an individual has to reach at the onset of winter. Failure to reach maturation would leave the individual with a low probability to survive the winter. The calculation starts with a mature individual at the end of the feeding season, and its weight and survivorship are followed through the winter and the next feeding season. This individual grows and reproduces and its fitness is the number of surviving descendants which reach maturity at the end of the following feeding season, discounted by the survivorship of the original individual during the previous winter. Note that the main advantage of income breeders here is the potential to have several generations per year. Even if the cycle measured for the two breeding strategies does not start with the same individual stage, the measures of fitness are nevertheless equivalent since we measure the full life cycle in both cases for the same annual environmental cycle.

Assumptions

Individual growth and mortality (μ) are allometrically related to body weight w. Maximum growth is $hw^{3/4}$ and modulated by available food (see table 1 for parameter descriptions and values) to give:

$$\frac{dw}{dt} = h(f(t) - f_c)w^{3/4}, \tag{1}$$

where h is the maximum consumption constant with units μg C$^{1/4}$ day^{-1}. The seasonal variation in food is described by the nondimensional feeding level $f(t)$ that denotes the

Table 2: Time interval as a function of individual characteristics

Trait, time interval	Value	Description
Capital:		
$t_b \rightarrow t_w$	$4\frac{w_a^{1/4}-w_e^{1/4}+h_w f_c}{h_w f_c+h_f(1-f_c)}$	Minimum feeding season duration to reach maturity size at the end of the year
$t_b \rightarrow t_m$	$\frac{4(w_m^{1/4}-w_e^{1/4})+h_w f_c(t_b-t_0)}{h_f(1-f_c)}$	Time to reach maturity size
Income:		
T_d	$4\frac{w_a^{1/4}-w_e^{1/4}}{h_f(1-f_c)}$	Development time
$t_b \rightarrow t_a$	$\frac{h_w f_c}{h_f(1-f_c)}(t_b - t_0)$	Time to regain maturity size after the winter

fraction of maximum consumption that is available from the environment. Level $f(t)$ is modeled as a boxcar function:

$$f(t) = \begin{cases} 1 & t_b < t < t_w \\ 0 & \text{otherwise} \end{cases}, \tag{2}$$

where t_b and t_w mark the start and the end of the feeding season. The critical feeding level f_c denotes the fraction of maximum consumption $hw^{3/4}$ used for standard metabolism and activity.

Mortality is likewise assumed to follow allometric scaling with exponent $-1/4$ (Peterson and Wroblewski 1984; Hirst and Kiørboe 2002; Brown et al. 2004):

$$\mu(w) = ahw^{-1/4} + \mu_0, \tag{3}$$

where μ_0 is a size-independent background mortality and a is a nondimensional constant characterizing the level of predation relative to the maximum consumption constant h. The presence of h in the predation mortality implies that faster growth (higher h) results in a higher mortality. This choice embodies a trade-off: faster growing individ-

Table 3: Equations for weight and probability to be alive

Trait, time interval	Weight at the end of the interval	Probability to survive the interval
Capital:		
$t_0 \rightarrow t_b$	$\left[-\frac{h_w f_c}{4}(t_b - t_0) + w_e^{1/4}\right]^4$	$\left(\frac{w_e}{w(t_b)}\right)^{-a/f_c} e^{-\mu_0(t_b-t_0)}$
Case 2:		
$t_b \rightarrow t_w$	$\left[\frac{h_f(1-f_c)}{4}(t_w - t_b) + w(t_b)^{1/4}\right]^4$	$\left(\frac{w(t_b)}{w(t_w)}\right)^{a/(1-f_c)} e^{-\mu_0(t_w-t_b)}$
$t_w \rightarrow t_0 + 1$	$\left[-\frac{h_w f_c}{4}(t_0 + 1 - t_w) + w(t_w)^{1/4}\right]^4$	$\left(\frac{w(t_w)}{w(t_0+1)}\right)^{-a/f_c} e^{-\mu_0(t_0+1-t_w)}$
Case 3:		
$t_b \rightarrow t_m$	w_m	$\left(\frac{w(t_b)}{w_m}\right)^{a/(1-f_c)} e^{-\mu_0(t_m-t_b)}$
$t_m \rightarrow t_0 + 1$	$\left[-\frac{h_w f_c}{4}(t_0 + 1 - t_m) + w_m^{1/4}\right]^4$	$\left(\frac{w_m}{w(t_0+1)}\right)^{-a/f_c} e^{-\mu_0(t_0+1-t_m)}$
Income:		
$t_0 \rightarrow t_b$	$\left[-\frac{h_w f_c}{4}(t_b - t_0) + w_a^{1/4}\right]^4$	$\left(\frac{w_a}{w(t_b)}\right)^{-a/f_c} e^{-\mu_0(t_b-t_0)}$
$t_b \rightarrow t_a$	w_a	$\left(\frac{w(t_b)}{w_a}\right)^{a/(1-f_c)} e^{-\mu_0(t_a-t_b)}$
T_d	w_a	$\left(\frac{w_e}{w_a}\right)^{a/(1-f_c)} e^{-\mu_0 T_d}$
$t_a \rightarrow t_a + T_d$	w_a	$e^{-\mu_a T_d}$

uals need to feed more and thereby face an increased risk of predation. On the other hand declining mortality with size (the $w^{-1/4}$ term) means that faster-growing individuals lower their mortality through their faster increase in size. This trade-off is a formulation of the classic "*M*/*K*" life-history invariant (Charnov 1993) for a size-dependent predation mortality and furthermore a consequence of size-spectrum theory, where consumption by predators is linked to the mortality of their prey (Andersen and Beyer 2006). The formulation of growth and mortality has the advantage that all parameters are nondimensional except the consumption constant h. See "Discussion" for alternative views on size-dependent mortality in zooplankton.

Above we have treated the maximum consumption constant h as a fixed constant. In reality, it differs between the feeding season (h_f) and the winter (h_w). We assume that the constant h is a factor g_w lower in winter than during the feeding season, such that $h_w = h_f/g_w$.

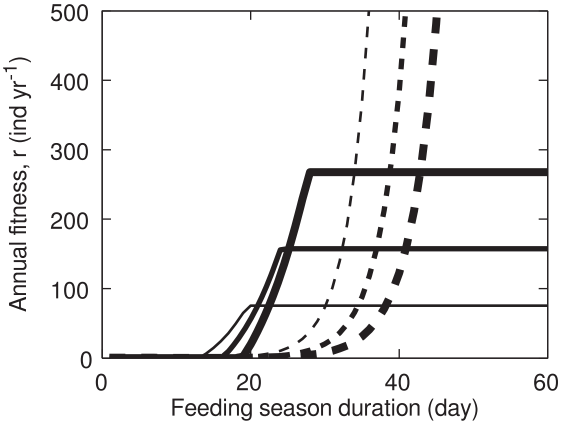

Figure 2: Fitness of capital (solid lines) and income breeders (dashed lines) for three different weights at maturity (thin line, $w_a = 300$ μg C; medium line, $w_a = 600$ μg C; and thick line, $w_a = 1{,}000$ μg C).

Elements of Fitness

Calculating annual fitness requires that the weight $w(t)$ and survival $P(t)$ of an individual is known. The increase in weight Δw during a time interval t_1 to t_2 (noted as "$t_1 \rightarrow t_2$") can be calculated by solving equation (1) (fig. 1):

$$\Delta w_{t_1\rightarrow t_2} = w(t_2) - w(t_1) = \left[\frac{h(f(t) - f_c)}{4}(t_2 - t_1) + w(t_1)^{1/4}\right]^4 - w(t_1). \tag{4}$$

The fourth power of the term in the parentheses is needed to maintain the dimensions of weight of the term, and it comes from the integration of equation (1).

Survival is determined partly by the declining mortality with size (eq. [3]) and partly by the increase in weight (eq. [1]). The survival during a time interval with constant feeding level f is found by solving $\mathrm{d}P/\mathrm{d}t = -\mu(w(t))\,P$ (fig. 1):

$$P_{t_1\rightarrow t_2} = \left(\frac{w(t_1)}{w(t_2)}\right)^{a/(f-f_c)} e^{-\mu_0(t_2-t_1)}. \tag{5}$$

From these two elements the annual fitness can be calculated as $r = P_{t_0\rightarrow t_0+1}\theta$, where θ is the adult reproductive investment (time is measured in years). The calculation of survival for the capital and income breeder is broken up into several time intervals, for example, the time from the beginning of the feeding season t_b to maturity t_a or maximum size t_m, derived from equation (4). These intervals are different for each strategy and are detailed in the following. The constituents of the fitness calculations for each strategy are listed in table 2 (time intervals) and table 3 (weights).

Capital Breeder

Capital breeders grow and accumulate reserves during the feeding season to be able to spawn during the winter before the next feeding season. We follow the development of an egg born at time t_0 with a weight w_e, and investigate the number of offspring produced at the same date the following year $t_0 + 1$. During the feeding season individuals grow until they either reach their maximum size w_m (at time t_m) or they reach the end of the feeding season at time t_w. In either event, the adults enter dormancy and are subject to winter conditions until spawning time at $t_0 + 1$.

We distinguish between three cases: (1) individuals have a weight lower than maturity size w_a at spawning time, that is, $w(t_0 + 1) < w_a$. This can happen if the individuals do not have time to mature during the feeding season ($w(t_w) < w_a$) or if the loss of weight during the winter is so large that the individual loses all its spawning capital (the interval of time $t_b \rightarrow t_w$ is shorter than the minimum feeding season duration specified in table 2). (2) Individuals do not reach maximum size during the feeding season but are still able to spawn, that is, $w_a < w(t_w) < w_m$. (3) Individuals reach maximum size and enter dormancy during the feeding season ($t_m - t_b < t_w - t_b$):

$$r = \begin{cases} 0 & \text{case 1} \\ P_{t_0 \to t_b} P_{t_b \to t_w} P_{t_w \to t_0+1} \theta & \text{case 2} \\ P_{t_0 \to t_b} P_{t_b \to t_m} P_{t_m \to t_0+1} \theta & \text{case 3} \end{cases}, \tag{6}$$

with reproductive investment

$$\theta = \varepsilon_r \frac{w(t_0 + 1) - w_a}{w_e}, \tag{7}$$

where ε_r is the reproductive efficiency and w_e is the weight of an egg.

Income Breeder

The fitness calculation for income breeders is more involved because not only do individuals reproduce throughout the feeding season but they may also have multiple generations per year (fig. 1*B*). For the income breeders, we follow the number of new adults over a year starting from the end of the feeding season. Two cases can be discerned depending on the duration of the feeding season: (1) individuals are unable to reach maturity during the feeding season, or they do but their offspring do not have time to reach adult stage; that is, ($w(t_0 + 1) < w_a$ or $t_w - t_b < t_a + T_d - t_b$, with T_d the development time from egg to adult); or (2) one or several generations of offspring reach adult stage before the end of the feeding season:

$$r = \begin{cases} 0 & \text{case 1} \\ P_{t_0 \to t_b} P_{t_b \to t_a} P_{t_a \to t_a + T_d} \theta & \text{case 2} \end{cases}. \tag{8}$$

In case 2, θ represents the rate at which adults are recruited to the population from successive generations founded by our focal animals. The rate of egg production and their probability to reach maturity during the feeding season of a single generation (r_p) is a function of the adult energy gain $[h_f(f - f_c)w_a^{3/4}]$, the conversion efficiency to egg production (ε_r), the egg weight (w_e), and of the probability for an egg to grow to adult size (P_{T_d}):

$$r_p = P_{T_d} \varepsilon_r \frac{h_f(f - f_c)w_a^{3/4}}{w_e}. \tag{9}$$

The number of adults follows a delay differential equation of the form:

$$\frac{dN(t)}{dt} = -\mu_a N(t) + r_p N(t - T_d), \tag{10}$$

where the first term on the right-hand side represents the mortality of the current adults and the second term the recruitment of offspring born a time T_d earlier and having now reached adult size with survival probability P_{T_d}. The term μ_a denotes adult mortality rate at constant adult size ($\mu_a = \mu(w_a)$). The term θ is then

$$\theta = \int_{t_a + T_d}^{t_0 + 1} \frac{dN(t)}{dt} dt. \tag{11}$$

As the food availability is constant during the feeding season, the number of adults at time $t - T_d$ is a constant proportion of the number of adults at time t: $N(t - T_d) = \lambda N(t)$, with λ a constant (details in online appendix "Delay Equation");

$$\lambda = \frac{W(r_p T_d e^{\mu_a T_d})}{T_d r_p}, \tag{12}$$

where W is the Lambert function.

The adult reproductive rate for the income breeder can then be written as

$$\theta = \exp\left[\left(\frac{W(r_p T_d e^{\mu_a T_d})}{T_d} - \mu_a\right)(t_0 + 1 - t_a - T_d)\right]. \tag{13}$$

Results

In a very short feeding season, neither the income nor the capital breeding strategy can maintain a positive annual growth rate (fig. 2). Small capital breeders have the highest annual fitness for short feeding seasons but are overtaken by the larger capital breeders as the season becomes longer. This is due to storage capacity, which is a constant fraction of maturity size. It is thus advantageous for a capital breeder to be as large as the length of the feeding season allows. The optimal maximum size in a given feeding season duration is

$$w_m^* = \left[\frac{h_f(t_w - t_b)(1 - f_c) - h_w f_c(t_b - t_0)}{4} + w_e^{1/4}\right]^4. \tag{14}$$

As the length of the feeding season increases it allows the income breeders to have several generations per season, leading to an exponential increase in their fitness. At a sufficiently long feeding season, income breeders outcompete capital breeders. The feeding season duration where this crossover occurs is a complicated function of the parameters (app B: "From Capital to Income Breeding"). Small income breeders outcompete larger ones as they reach maturity size faster and therefore can contribute more rapidly to the next generation and eventually have the opportunity to have a higher number of generations within a year. Therefore capital and income breeding strategies co-occur with a crossover between large and small maturity sizes. For the current parameters this occurs when the feeding season is around 30 days.

Sensitivity analyses on the main parameters used in this

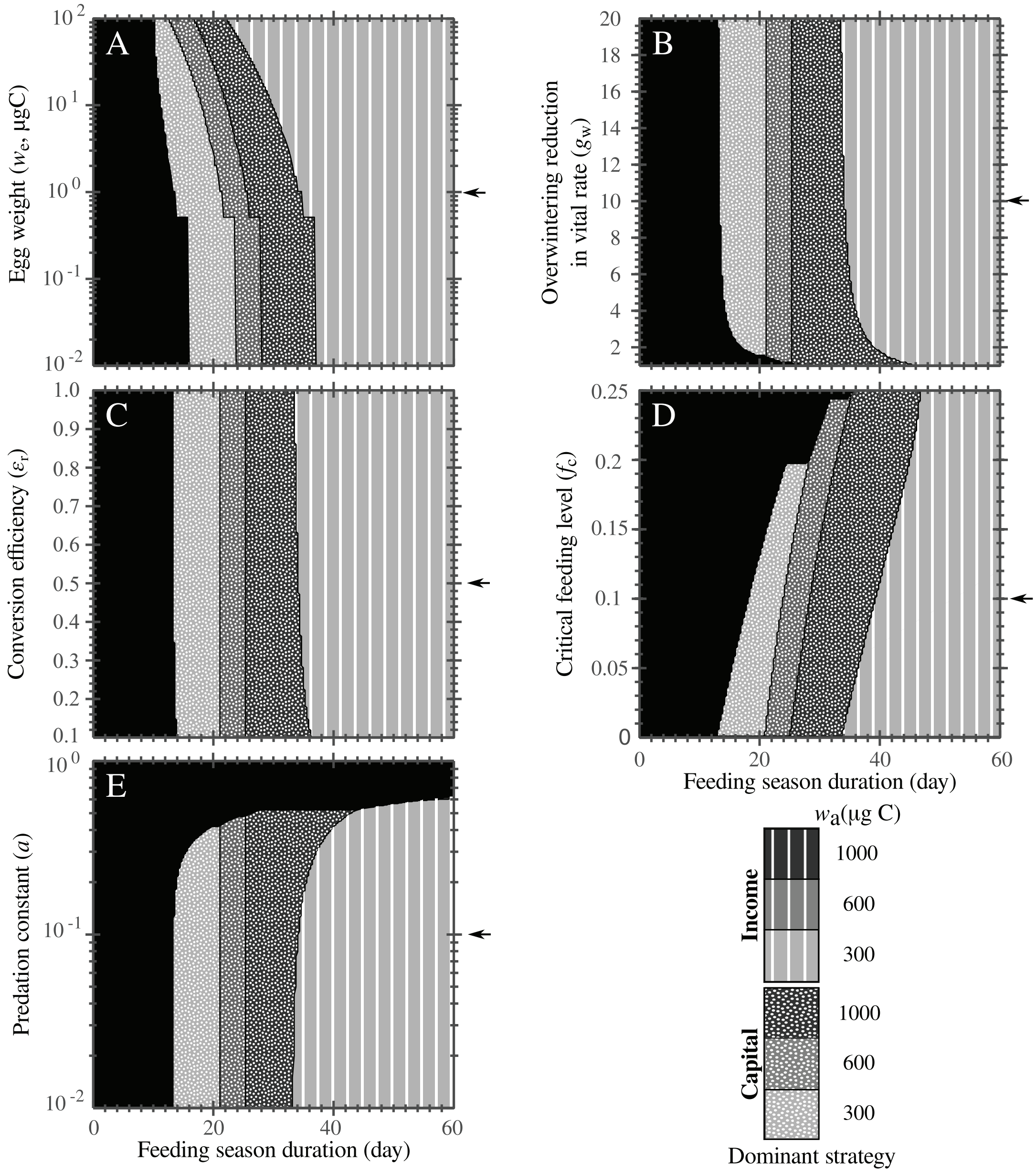

Figure 3: Dominance succession of income (vertical stripes pattern) and capital breeding (dots pattern) with different size at maturity (light gray, $w_a = 300$ µg C; medium gray, $w_a = 600$ µg C; and dark gray, $w_a = 1{,}000$ µg C), for variation in the egg weight (w_e; *A*); overwintering reduction in vital rate (g_w; *B*); conversion efficiency from individual weight to egg weight (ε_r; *C*); critical feeding level (f_c; *D*); and predation constant (a; *E*). Solid black areas indicate that strategies have zero fitness; the arrows indicate the values used in figure 2.

study reveal that the pattern of dominance by large capital breeders during short seasons and small income breeders during long seasons is quite robust (fig. 3). An increment in the critical feeding level increases the need of all the strategies for a longer feeding season (fig. 3*D*). Larger size at maturity (lower predation mortality compared to smaller individuals) makes a strategy less sensitive to an increase in the predation constant. Large capital breeders thus dominate over small income breeders through a longer window of feeding season durations (fig. 3*E*).

Discussion

We have demonstrated the relative success of two reproduction strategies (capital vs. income breeding) as a function of feeding season duration and how size at maturity interacts with breeding strategy in determining fitness. Capital breeders should be as large as possible to support maximum amount of reserves (supporting the speculation by Jönsson 1997) and generally perform well in short feeding seasons, while income breeders should be as small as possible to allow multiple generations within a year and take advantage of long feeding seasons.

Following this pattern, large capital breeders should be found at high latitude, while income breeders should dominate temperate waters. This is the case for the *Calanus* copepods in the North Atlantic and the Arctic: large *Calanus hyperboreus* dominate the Arctic by producing eggs at depth prior to the phytoplankton bloom (capital breeding), while *Calanus finmarchicus*, smaller and mostly an income breeder, dominate the subarctic of the North Atlantic where the phytoplankton bloom is longer (Conover 1988). Similarly, the copepods in the North Pacific follow the same pattern, with the capital breeders *Neocalanus* spp. dominating the area with short blooms while the smaller income breeders *Eucalanus* spp. have a southern distribution and are successful in the eastern subarctic gyre where the feeding season is prolonged due to local physical conditions (Miller et al. 1984; Tsuda et al. 2004). Further comparisons to other taxa require that individuals have the capacity to store reserves, to retreat in overwintering, and have the possibility for multiple generations within a feeding season. For example, mysids (shrimp-like crustaceans) fulfill the conditions. In the genera *Mysidopsis* and *Erythrops*, the species *M. didelphys* and *E. erythrophthalma*, both capital breeders (Tattersall 1969; Mauchline 1970; Buhl-Jensen and Fosså 1991) are found at higher latitudes of the North Atlantic than their smaller conspecifics of the same genus *M. gobbosa*, *M. angusta*, *E. elegans*, and *E. serrata* (Mauchline 1968, 1971).

Some of the patterns are also observed in species without multiple generations in a season; for example, although many fish species live longer than 1 year, breeding mode seems related to latitudinal gradients. McBride et al. (2013) analyzed fish reproduction strategies in relation to habitat. From this review, a latitudinal gradient can be made with fish in the temperate and subtropical area being mostly income breeders (e.g., the inland silverside *Menidia beryllina* or the bay anchovy *Anchoa mitchilly*), while the species inhabiting boreal latitudes are all capital breeders (e.g., the Atlantic and Pacific herring *Clupea harengus* and *Clupea pallasii*, haddock *Melanogrammus aeglefinus*, and the sea lamprey *Petromyzon marinus*). In temperate waters, both income and capital breeders are found (e.g., three-spined stickleback *Gasterosteus aculeatus* is an income breeder while the white crappie *Pomoxis annularis* is a capital breeder), and mixed strategies are common (e.g., European sprat *Sprattus sprattus*, northern anchovy *Engraulis mordax* or European sea bass *Dicentrarchus labrax*). However, this pattern is not without exceptions, for example the spiny chromis *Acanthochromis poluacanthus*, living in a tropical environment, is a capital breeder, and species present over a large range of latitude are found to be either income (e.g., mummichog *Fundulus heteroclitus*) or capital breeders (e.g., brown trout *Salmo trutta*). For many fish species, in particular larger ones, migrations constitute an important part of the life-history strategy which may be used as a means of moving between regions with different seasonal dynamics, for example, mackerel in the North Atlantic (Uriarte and Lucio 2001; Jansen and Gislason 2013), and a complete understanding of the income/capital breeding strategies for fish therefore also needs to consider migrations. Comparisons with larger species, for example, marine mammals, is more difficult, as long gestation and parental care, as well as in some cases extensive migrations, play important roles in the breeding strategy pay-off (Jönsson et al. 1998).

In this study, we have treated capital and income breeding as a dichotomy. However, there is a possibility that mixed strategies can be superior. Inspired by *C. hyperboreus*, we assumed capital breeders go into diapause before the end of the feeding season. They could, however, use the remainder of the feeding season to switch to an income breeding mode. While this may increase reproduction, the downsides are an increase in mortality and the possibility that their offspring will not reach a suitable stage before winter sets in. It is therefore beneficial to switch to income breeding if the remaining feeding time is longer that the development time and mortality is limited. Capital breeders could also target a multiyear cycle, which could allow them to maintain a positive growth rate in shorter feeding seasons. This strategy is adopted by the largest of the *Calanus* cousins, *C. hyperboreus* (Conover 1988; Swalethorp et al. 2011). On the income breeder side, offspring could go into diapause as soon as they reach adult size, prioritizing survival until next year instead of gambling on immediate production of offspring that may not reach a suitable size to overwinter (Kaartvedt 2000). Finally, a mixed strategy could allow the use of reserves for capital breeding before the feeding season, followed by income breeding when food appears as seen for *Calanus glacialis* (Hirche and Kattner 1993; Daase et al. 2013) and predicted by life history modeling (Varpe et al. 2009).

The pattern of success for income and capital breeders presented here and the speculation on mixed strategies rely on mortality decreasing with individual size. This allometric relationship is a general trend observed among organisms throughout the marine pelagic environment (Peterson and Wroblewski 1984; Hirst and Kiørboe 2002). This allows us to find analytic solutions to our problem. However, it has been argued that mortality could increase with stage among *Calanus* species (Eiane et al. 2002), especially in the presence of visual predators (Aksnes and Giske 1993). Higher mortality at larger size could induce smaller maturity size or the emergence of predation-avoidance strategies such as diel vertical migration (Lampert 1989; Ohman 1990; Sainmont et al. 2013), or a switch in feeding mode (ambush, cruise or filter feeding; Kiørboe et al. 1996; Visser and Fiksen 2013).

Predation mortality can also vary with seasons, for example, with an increase in predation pressure toward the end of the phytoplankton bloom with the increase in predator abundance (e.g., fish larvae), through seasonal presence of migrating fish predators (Kaartvedt 2000) or seasonal change in the performance of visually searching predators (Varpe and Fiksen 2010). In this situation, a mixed strategy could be beneficial and push individuals to find refuge while food is still available at the surface. This earlier overwintering balances a reduction in capital breeding energy storage over an increase in survivorship. Income breeder offspring could also have an advantage to overwinter as soon as they reach a suitable size instead of engaging another generation. Consideration of other mortality functions, either another allometric relationship or an intra-annual variation, would complicate the mathematical analysis beyond a level where it is possible to achieve analytical insight.

Here we have addressed a variable but predictable environment. In nature, interannual uncertainty is likely to affect the long term success of a population and could be calculated as the geometric mean of the successive year fitnesses (Yoshimura and Clark 1991; McNamara et al. 1995). If the uncertainty is on the timing of the beginning of the feeding season, the success of the capital breeders relies on their ability to time spawning with the feeding season (Varpe et al. 2007). In an unpredictable environment, animals should be larger than in a predictable environment, as they are more resilient to long winters and to a delay in food availability (Real and Caraco 1986). Interannual uncertainty and long winters could thus explain the size differences between similar animals adopting the same strategies (as suggested in a copepod study in the subarctic Pacific; Mackas and Tsuda 1999). For example, *C. finmarchicus* is found at higher latitudes in the Atlantic than its smaller cousin *Calanus helgolandicus* (Planque and Fromentin 1996), although they both are income breeders (Conover 1988). Thus, larger size at birth and at maturity could be responses to uncertain environments.

Our model assumes no feedback from the environment (density dependence) and no competition between income and capital breeders at different sizes (frequency dependence). Depending on how density dependence and frequency dependence operate, the fitness calculations could be more or less correct (Mylius and Diekmann 1995). Specifically, while the absolute value of our fitness estimate may be considerably off, we may expect the relative ranking of the various strategies to remain invariant to density dependent effects. Simulations of competing populations with explicit density-dependence would be needed to rigorously address this issue.

In conclusion, we demonstrated the succession of the capital followed by income breeder traits when the feeding season duration increases. Capital breeders should grow large while income breeder should remain small.

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APPENDIX A

Delay Equation

We look for a closed form for

$$\frac{\mathrm{d}y}{\mathrm{d}t} = ry(t-b) - \alpha y(t), \tag{A1}$$

with α, b, and r being constants. We approximate this equation by assuming that the number of adults at time $y(t-b)$ is a fraction of the population at time $y(t)$:

$$y(t-b) = \lambda y(t). \tag{A2}$$

Therefore, equation (A1) can be written as

$$\frac{\mathrm{d}y}{\mathrm{d}t} = (\lambda r - \alpha)y(t). \tag{A3}$$

We therefore have

$$y(t) = y(0)e^{(\lambda r-\alpha)t}. \tag{A4}$$

Similarly,

$$y(t-b) = y(0)e^{(\lambda r-\alpha)(t-b)} \tag{A5}$$

$$= y(t)e^{-(\lambda r-\alpha)b}. \tag{A6}$$

Or by definition $y(t-b) = \lambda y(t)$, λ is therefore the solution to

$$\lambda = e^{-b(\lambda r - \alpha)}. \tag{A7}$$

With $W(z)$ the Lambert function, the solution of the equation $z = W(z)e^{W(z)}$, we have

$$\lambda = \frac{W(bre^{\alpha b})}{br}. \tag{A8}$$

The solution of equation (A1) is therefore

$$y(t) = y(0)\exp\left[\left(\frac{W(bre^{\alpha b})}{b} - \alpha\right)t\right]. \tag{A9}$$

APPENDIX B

From Capital to Income Breeding

Capital and income breeders of the same size have equal fitness when the feeding season duration is

$$\Omega = 1 - \frac{4}{h_{\mathrm{w}}f_{\mathrm{c}}}(w_{\mathrm{a}}^{1/4} - e^{\beta-\sigma}), \tag{B1}$$

with β and σ as

$$\beta = \frac{1-f_{\mathrm{c}}}{4ah_{\mathrm{w}}}\left\{4(\mu_0 + \theta_{\mathrm{p}})(\xi + 1)w_{\mathrm{a}}^{1/4} \right. \tag{B2}$$

$$\left. - h_{\mathrm{w}}f_{\mathrm{c}}\left[\theta_{\mathrm{p}}(\xi + 1) - \ln\left(\frac{r}{K}\right)\right]\right\},$$

$$\sigma = W\left[\frac{(\mu_0 + \theta_{\mathrm{p}})(\xi + 1)(1 - f_{\mathrm{c}})}{ah_{\mathrm{w}}}e^{\beta}\right], \tag{B3}$$

and ξ, θ_{p}, and K as

$$\xi = \frac{h_{\mathrm{w}}f_{\mathrm{c}}}{h_{\mathrm{f}}(1 - f_{\mathrm{c}})}, \tag{B4}$$

$$\theta_{\mathrm{p}} = \frac{W(r_{\mathrm{p}}T_{\mathrm{d}}e^{\mu_{\mathrm{a}}T_{\mathrm{d}}})}{T_{\mathrm{d}}} - \mu_{\mathrm{a}}, \tag{B5}$$

$$K = w_a^{-a/[f_{\mathrm{c}}(1-f_{\mathrm{c}})]}e^{-\mu_{\mathrm{a}}T_{\mathrm{d}} - \theta_{\mathrm{p}}(\xi + T_{\mathrm{d}})}. \tag{B6}$$

The term r is the fitness of the capital breeder where they reach maximum size during the feeding season (case 3). For feeding seasons shorter than this, capital breeding is superior to income breeding.

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