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Life History Implications of Allocation to Growth Versus Reproduction in Dynamic Energy Budgets

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We compare the implications of determinate vs. indeterminate growth of a parthenogenetic iteroparous ectotherm at constant food density in the context of the dynamic energy budget theory, which specifies the tight links between life history traits, such as feeding, aging, growth and reproduction. We do a comparative analysis using, as measure of fitness, the life span reproduction, the population growth rate, and the conversion efficiency of food to biomass. When extrinsic mortality is constant, indeterminate growth cannot maximize fitness if measured by the population growth rate or the conversion efficiency, except when mortality is low, in which case both types of animals are similar. If the fitness measure is life span reproduction, indeterminate growth maximizes fitness even with constant mortality, provided it is not very high. When mortality decreases with size, indeterminate growth maximizes fitness for almost all measures of fitness. Finally, we suggest an evolutionary link between allocation strategies and expected life span. In populations of long living species, each type of animal can establish in the population of the other. In populations of short living species, determinate growers can invade, and displace, a population of indeterminate ones. However, when the mortality risk of organisms with small size is much higher than those of large size, indeterminate growers can be superior.

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1. INTRODUCTION

An organism can only acquire a limited amount of material and energy for which the physiological processes such as maintenance, somatic growth, development and reproduction compete. The study of energy allocation strategy between somatic growth and reproduction is central to life history theory. Since larger individuals tend to eat more than small ones and reproductive material is derived from food, a trade-off must exist between investment into growth and reproduction. Since aging relates to the action of free radicals and, therefore, to respiration, life span has direct links with energetics, and so with allocation strategies. The relative amount of energy allocated to reproduction differs from one species to another; even within a species, it can depend on environmental conditions. These relationships reveal an intimate coupling between various traits, which are realistically specified by a dynamic energy budget (DEB) model for the uptake and use of energy (Ross and Nisbet, 1990; Kooijman, 2000; Lika and Nisbet, 2000).

In the evolutionary studies of life history strategies it is often assumed that there exists some quantity related to fitness that is maximized by natural selection. Several alternative ways of measuring fitness exist (Stearns, 1992). The two most commonly used density independent fitness measures are the total number of offspring an individual produces over a lifetime and the population growth rate (Roff, 1992; Stearns, 1992; Charnov, 1993; Kozłowski, 1993; Engen and Sæther, 1994). When these measures are applied to the same life history model, different predictions usually result for optimal life history traits. The concept of fitness has played a central role in evolutionary ecology and the choice of fitness measure has been a matter of debate for quite some time. It is not at all obvious what traits precisely are favoured by evolution (Metz *et al*., 1992; Kozłowski, 1993; Mylius and Diekmann, 1995) and the choice should relate to invasion criteria, and so on feedback from the environment (Meszéna and Pásztor, 1990; Mylius and Diekmann, 1995).

Despite the debate over the appropriate fitness measure, a wide variety of models have been proposed to investigate the optimal allocation of resources to growth and reproduction. Simple models suggest that in a constant environment, the optimal strategy for an organism is the 'bang–bang' option of setting reproduction effort to 0 until a certain age at which growth ceases and all surplus energy is switched to reproduction (Perrin, 1992; Bulmer, 1994). Although the bang–bang strategy, also called determinate growth, occurs in nature, many organisms as diverse as perennial plants, most molluscs, echinoderms, and many fish are observed to exhibit simultaneous growth and reproduction (indeterminate growth). Both strategies frequently occur, even among rather phylogenetically related species: cladocerans sport indeterminate growth (*Daphnia magna* can grow by a factor two in length, that is a factor eight in volume, during the reproductive period), while copepods sport determinate growth. Several models have been proposed to explain indeterminate growth (Taylor and Gabriel, 1992, 1993; Perrin *et al*., 1993; Engen and Sæther, 1994; Gurney and Middleton, 1996; Heino and Kaitala, 1996).

Factors proposed to explain indeterminate growth include nonlinear trade-offs, age-specific mortality, size-dependent mortality and production rates (both increasing or both decreasing), and unpredictable environment [see reviews by Perrin and Silby (1993), Heino and Kaitala (1999)].

In this paper we compare the consequences of two allocation strategies in animals: indeterminate growth, where growth continues during the reproductive stage, and determinate growth, where growth is ceased during the reproductive stage. We assume that both animals are otherwise similar, and have no differences during the embryonic stage, where no food uptake occurs, and the juvenile one, where no allocation to reproduction occurs. Our analysis differs from similar ones known to us [e.g., Calow (1981), Iwasa and Cohen (1989), Kozłowski (1992, 1996), Roff (1992), Stearns (1992), Charnov (1993), Perrin and Silby (1993)], because we do not approach the topic using optimization arguments, but focus on the consequences of differences in strategies, using a framework where the different traits are coupled mechanistically. Since no fitness criterion exists that applies in every case, Stearns (1992) and Roff (1992) suggest more studies on how changing fitness definitions influence predictions about life history evolution. We consider here (1) the total number of offspring an individual produces over a lifetime, (2) the population growth rate, and (3) the efficiency of conversion of food into biomass. The last criterion is seldom mentioned because this efficiency is usually taken to be constant. Since we take account for maintenance requirements, however, this efficiency cannot be constant. Given a limited flux of available food, this efficiency determines population numbers and is, therefore, most relevant in an evolutionary perspective. In addition, we consider the problem of evolutionary stable strategies (ESS) in a spatially homogeneous population that receives a constant food input. A life history strategy is evolutionary stable (Maynard Smith, 1982) if a population following this strategy cannot be invaded, and displaced, by individuals that adopt another strategy. In our case a strategy is a choice of the partitioning of catabolic power to growth and reproduction.

In this paper, we consider a DEB model developed in (Kooijman, 2000, 2001; Nisbet *et al.*, 2000) and compare the two strategies for allocation to reproduction for a parthenogenetic iteroparous isomorphic ectotherm at constant food availability: a constant fraction allocation to reproduction by the indeterminate animal and a bang–bang allocation by the determinate one. We assume isomorphism. An isomorph does not change in shape during growth, which means that its surface area is proportional to its volume$^{2/3}$ and its length proportional to its volume$^{1/3}$. The restriction to parthenogenetic animals can rather easily be removed, and does not affect the conclusions. Some preliminary work has been reported in Kooijman (2000, pp. 293–297). We extend our work to include comparisons of reproductive traits under different type of mortalities and investigate the problem of ESS of the partitioning of catabolic power to growth and reproduction. Finally, we use the conversion efficiency of food into biomass as a fitness criterion, and compare the implications of the two energy allocation strategies.

Table 1. The assumptions that lead to the DEB model as formulated for multicellular animals.

1	Structural body volume and reserves are the state variables of the individual and they do not change in composition (strong homeostasis).
2	Food is converted into faeces and assimilates derived from food are added to reserves, which fuel all other metabolic processes. These processes can be classified in three categories: synthesis of structural body mass, and of reserves (including the embryonic reserves via reproduction), and processes that are not associated with synthesis of biomass. Products that leave the organism may be formed in direct association with these three categories of processes, and with the assimilation process.
3	If the individual propagates via reproduction (rather than via division), it starts in the embryonic stage that initially has a negligibly small structural body volume (but a substantial amount of reserves)
3a	The reserve density of the hatchling equals that of the mother at egg formation. Foetuses develop in the same way as embryos in eggs, but at a rate unrestricted by energy reserves.
4	The transition from embryo to juvenile initiates feeding, and from juvenile to adult initiates reproduction, which is coupled to ceasing maturation. The transitions occur when the cumulated energy invested in maturation exceeds a threshold value.
5	Somatic and maturity maintenance are proportional to structural body volume, but maturity maintenance does not increase after a given cumulated investment in maturation. Heating costs for endotherms are proportional to surface area.
6	The feeding rate is proportional to surface area and depends hyperbolically on food density.
7	The reserves must be partitionable, such that the dynamics are not affected; the use of reserves does not depend on food density; the reserve density at steady state does not depend on structural body volume (weak homeostasis).
8	A fixed fraction of energy, utilized from the reserves, is spent on somatic maintenance plus growth, the rest on maturity maintenance plus maturation or reproduction (the κ-rule).
9	Under starvation conditions, individuals always give priority to somatic maintenance and follow one of two possible strategies: they do not change the reserve dynamics (so continue to reproduce). They cease energy investment in reproduction and maturity maintenance (thus changing reserves dynamics). Some animals shrink during starvation, but do not gain energy from this.
10	Aging related damage accumulates in proportion to the amount of damage inducing compounds, which accumulate in proportion to the utilization rate. Apart from 'accidents', the hazard rate is proportional to accumulated damage density, death also occurs if somatic maintenance costs can no longer be paid.

We focus mainly on the application of the DEB model in evolutionary studies rather than the derivation of the model. For a full account of the model and justification of the assumptions (see Table 1) as well as tests against experimental data we refer to Kooijman (2000). The remainder of this article is organized as follows. In Section 2, we first briefly explain the general framework of the κ-rule model comprising food consumption, catabolic rate, transition from juvenile to adult stage and give the formulas used in this study. Thereafter, we present the different allocations of catabolic power to growth and reproduction. In Sections 3

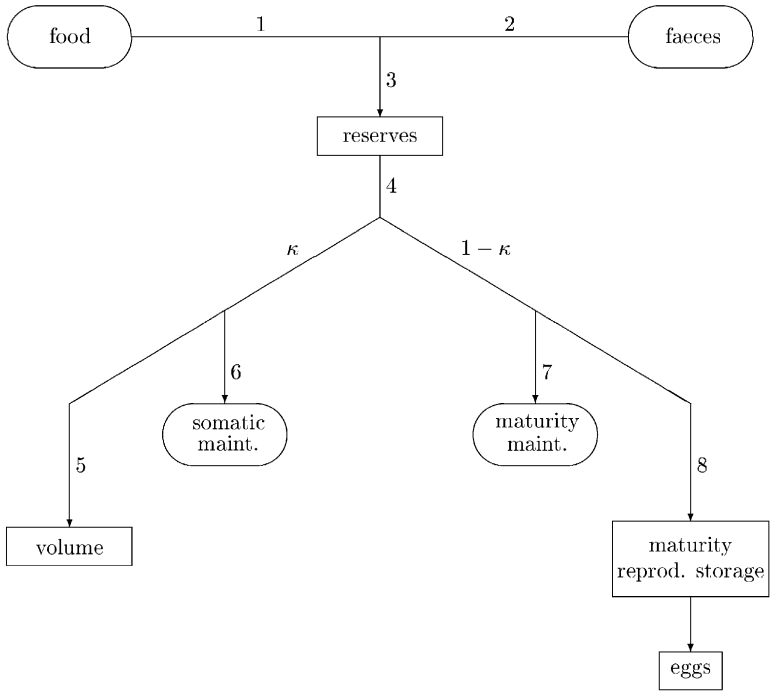
and 4 we present the results of the comparative analysis of the two energy allocation strategies and discuss them in light of previous work.

2. SUMMARY OF THE DEB MODEL

The DEB model uses differential equations to describe the rates at which the organism acquires energy from its environment and utilizes it for maintenance, growth, development and reproduction. These rates depend on the state of the organism and its environment. Two state variables specify the state of the organism: the structural body volume V and the energy reserves E. The use of volume as a state variable allows description of size related phenomena such as food uptake and growth. The existence of maintenance requirements, i.e., a continuous use of energy necessary to keep the organism alive, and observations indicating that individuals react slowly to sharp changes in feeding conditions imply the presence of an energy buffer. These and several other reasons necessitate the use of energy reserves as a state variable even in the most simple models. Free radicals that result from respiration cause irreparable damage to the DNA in organisms and have a direct relationship with aging [Kooijman (2000), Leeuwen *et al*. (2002) and references therein]. A third state variable, the accumulated damage, is required to specify the aging process.

An organism extracts energy from food which is added to the reserves and is subsequently used for growth (i.e., increase in structural body mass), maintenance (somatic and maturity), development or reproduction. Figure 1 shows the primary energy fluxes within the organism. By default, a constant fraction κ of the energy flowing out of the reserves is allocated to somatic functions (somatic maintenance and growth) and the remaining fraction to developmental and reproductive functions. In embryos and juveniles, the latter flow is used for maturation and for maintaining the achieved degree of maturity. We introduce two allocation strategies: the constant fraction allocation and the bang–bang allocation. The energy allocation rule (κ-rule) is the same for both strategies during the nonreproductive stages. The bang–bang allocation strategy adopted by a determinate organism assumes that growth ceases at puberty and all energy flowing out of the reserves is allocated to maintenance (somatic plus maturity) and reproduction.

The rate of change of the energy in reserves depends on the rate, $\dot{p}_A$, at which energy is assimilated from food, which follows a type II functional response, and the rate at which energy is utilized, $\dot{p}_C$, which is called the catabolic power. The assumptions in Table 1 imply that the dynamics of an organism are described by two differential equations: one specifies the dynamics of the structural body volume, V, and the other the dynamics of the reserve density, $[E]$, defined as the amount of reserves per unit of structural body volume. Reserve density has a maximum value $[E_m]$ which is independent of the size of the organism and the feeding conditions. The rate of change of reserve density is a first order process



1: ingestion 2: defecation 3: assimilation 4: utilization
5: growth 6: somatic maintenance 7: maturity maintenance 8: maturation/reproduction

Figure 1. Energy fluxes through an organism. The organism extracts energy from food which is added to the reserves and subsequently is used for somatic growth, maintenance (somatic and maturity), and maturation or reproduction. The rate at which energy becomes available for utilization (catabolic power) depends on its size and stored energy density. By default, a fixed fraction κ of the catabolic power is allocated to somatic maintenance and growth, and the remaining $1-\kappa$ to maturity maintenance and either maturation (for embryos and juveniles) or reproduction (for adults). Somatic maintenance has priority over growth. Reproduction ceases when the fraction $1-\kappa$ of energy is fully required for maturity maintenance.

at a rate inversely proportional to volumetric length $V^{1/3}$. Tables 2 and 3 list the model equations and all model variables and parameters. In the Appendix we give a brief derivation of the equations.

Solutions of the model equations represent the life history of individuals in a potentially variable environment. Once these equations have been solved, many other quantities can be calculated. We present only those needed in this study.

In a variable environment, one or more of the model parameters may vary with time. In this investigation, we assume that the environment is constant. Consequently, if the food density X, and therefore, the scaled functional response f are constant, the model simplifies. The reserve density will approach an equilibrium, that is, $[E] = f[E_m]$ and the structural volume $V(a)$ of an organism of age a is

Table 2. Equations of the κ-rule model for a growing organism.

State variables	V: structural body volume E: energy in reserve
Environment	X: concentration of food
Assimilation	$\dot{p}_A = \{\dot{p}_{Am}\} V^{2/3} f;\ f = (1 + X_K/X)^{-1}$
Maintenance	$\dot{p}_M = [\dot{p}_M] V$ (somatic) $\dot{p}_J = [\dot{p}_J] \min\{V, V_p\}$ (maturity)
Dynamics	$\frac{dV}{dt} = \kappa\{\dot{p}_{Am}\} \frac{V^{2/3}[E]/[E_m] - V/V_m^{1/3}}{\kappa[E] + [E_G]}$ $\frac{d[E]}{dt} = \frac{\{\dot{p}_{Am}\}}{V^{1/3}} \left(f - \frac{[E]}{[E_m]} \right)$
Hazard rate	$\dot{h}(t) = \frac{\ddot{h}_a}{\kappa V(t)} \int_0^t \left(V(t_1) - V(0) + \frac{[\dot{p}_M]}{[E_G]} \int_0^{t_1} V(t_2) dt_2 \right) dt_1$

given by the von Bertalanffy equation

$$V(a) = (V_\infty^{1/3} - (V_\infty^{1/3} - V_b^{1/3}) \exp\{-\dot{r}_B (a - a_b)\})^3, \tag{1}$$

where a_b and V_b are the age and volume at birth. $V_\infty^{1/3} = f V_m^{1/3}$ is the ultimate volumetric length of the organism at a given food level, $V_m^{1/3} = \frac{\kappa\{\dot{p}_{Am}\}}{[\dot{p}_M]}$ is the maximum volumetric length, and $\dot{r}_B \equiv (3[E_G] + 3\kappa f [E_m])^{-1} [\dot{p}_M]$ is the von Bertalanffy growth rate parameter which specifies how fast the organism approaches its ultimate size.

Embryo and juvenile stage. The equations describing the dynamics of V and $[E]$ (Table 2) with $f = 0$ also apply to embryos. The initial structural volume of an embryo is practically nil, so $V(0) = 0$. Although this implies that the initial energy density is infinitely large, the (absolute) initial energy in the egg, E_0, is finite. If the structural body volume at birth V_b is specified, then the initial energy in the egg is determined by the dynamic equations and the energy density at birth, $[E_b]$, which is assumed to be equal to that of the mother at egg formation (Assumption 3a). At steady state this means $[E_b] = f[E_m]$. Consequently, the age at birth a_b and the initial energy in the egg E_0 vary somewhat with the food density. The mechanism for the variation is that the use of reserves decreases with the reserve density, which increases the period required to reach a fixed size, while maintenance costs continue (Kooijman, 2000). This applies to both allocation strategies that we compare. For simplicity's sake, we take here age-at-birth a_b constant and $E_0 = ([E_G] + [E_m] f) V_b$. The latter approximation results by neglecting maintenance costs during the embryonic stage.

Up to the age at puberty a_p, the determinate animal is identical to the indeterminate one and its structural volume can be calculated from (1). The transition from juvenile to adult occurs when the cumulative investment into maturation exceeds a threshold value E_p. The catabolic power allocated to maturation is

Table 3. Table of frequently used symbols. Dots refer to rates (dimension: time^{-1}), square brackets [ ] and braces { } refer to quantities which are expressed per unit volume and per unit of surface area, respectively. In the dimension column, l means length, t time, e energy, # number.

Symbol	Dim	Interpretation
a, a_b, a_p, $a_\dagger$	t	Age, —at birth, —at puberty, —at death
t	t	Time
$\dot{\phi}(a)$	t^{-1}	Stable age distribution
V, V_b, V_p, V_∞, V_m	l^3	Structural body volume, —at birth, —at puberty, ultimate—, maximum—
E, E_0, E_p	e	Energy in reserve, initial energy in egg, energy in maturation at puberty
$[E]$, $[E_m]$, $[E_b]$	el^{-3}	Reserve density ($[E] = E/V$), maximum—, —at birth
$[E_G]$	el^{-3}	Volume-specific energy costs for growth
$\dot{p}_A$	et^{-1}	Assimilation rate
$\dot{p}_C$	et^{-1}	Catabolic power
$\dot{R}$	$\#t^{-1}$	Reproduction rate
N_R	#	Life span reproduction
X, X_K	mol l^{-3}	Concentration of food, saturation constant
f	—	Scaled functional response: $f = (1 + X_K/X)^{-1}$
$\dot{J}_{XS}$	mol t^{-1}	Supply flux of food
$\{\dot{J}_{XAm}\}$	mol $l^{-2}t^{-1}$	Surface area-specific food uptake rate
Y_{VX}	mol mol^{-1}	Conversion efficiency from substrate to biomass in terms of C-mol
$[\dot{p}_M]$, $[\dot{p}_J]$	$el^{-3}t^{-1}$	Volume-specific costs for somatic maintenance, —for maturity maintenance
$\{\dot{p}_{Am}\}$	$el^{-2}t^{-1}$	Surface area-specific maximum assimilation rate
$\dot{r}$, $\dot{r}_B$	t^{-1}	Population growth rate, von Bertalanffy growth rate
M_Q	#	Amount of damage
$\dot{h}$	t^{-1}	Hazard rate
$\ddot{h}_a$	t^{-2}	Aging acceleration
$\dot{m}$	t^{-1}	Extrinsic mortality rate: $\dot{m}(a) = \dot{m}_0 \left(\frac{V(a)}{V_b}\right)^{-\mu/3}$
$\dot{m}_0$	t^{-1}	Constant (or initial) mortality rate
μ	—	Rate of decrease of size-dependent mortality
κ	—	Fraction of catabolic power to growth + somatic maintenance
κ_R	—	Fraction of reproductive power fixed into embryonic reserves

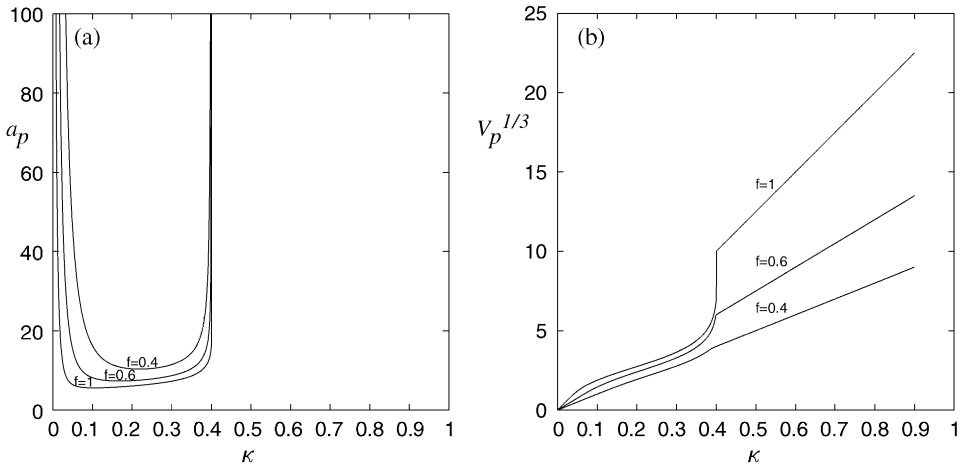


Figure 2. The age at puberty a_p (a) and length at puberty $V_p^{1/3}$ (b) as functions of the partition coefficient κ, for different food levels. Parameter values: see Table 4.

$(1-\kappa)\dot{p}_C(a) - [\dot{p}_J]V(a)$, where $[\dot{p}_J]$ represents the volume-specific costs for maturity maintenance. The age a_p and the length $V_p^{1/3}$ at puberty is then calculated from $E_p = \int_{a_b}^{a_p}((1-\kappa)\dot{p}_C(a) - [\dot{p}_J]V(a))da$ and (1). Substitution of (A.3) for the catabolic power gives for constant food density (where $[E] = f[E_m]$)

$$E_p = (1-\kappa)\, f\left(\{\dot{p}_{Am}\}\int_{a_b}^{a_p} V^{2/3}(a)da - [E_m](V(a_p) - V_b)\right) - [\dot{p}_J]\int_{a_b}^{a_p} V(a)da, \tag{2}$$

or equivalently

$$E_p = \frac{1-\kappa}{\kappa}[E_G](V(a_p) - V_b) + \left(\frac{1-\kappa}{\kappa}[\dot{p}_M] - [\dot{p}_J]\right)\int_{a_b}^{a_p} V(a)da. \tag{3}$$

If $[\dot{p}_J] = \frac{1-\kappa}{\kappa}[\dot{p}_M]$, the relationship (3) reduces to $E_p = [E_G](V(a_p) - V_b)\frac{1-\kappa}{\kappa}$, which reveals that $V_p \equiv V(a_p)$ does not depend on the scaled functional response f. The stage transition occurs when cumulative investment in maturation exceeds a fixed threshold, while at the same time, structural body volume exceeds a fixed threshold; age at puberty a_p does depend on f, however. For other values of $[\dot{p}_J]$, $V(a_p)$ does depend on f and κ, and stage transition no longer occurs at a fixed structural body volume.

Figure 2 illustrates how the age a_p and the length $V_p^{1/3}$ at puberty depends on the partitioning fraction κ for three different food levels. The value for κ for which the length at puberty does not depend on the feeding rate is $\kappa = (1 + [\dot{p}_J]/[\dot{p}_M])^{-1} = 0.4$ and is located on the boundary of the range for which maturity can be reached for this parameter combination (Table 4). For indeterminate growth, the volume at puberty at abundant food ($f = 1$) can differ up to a factor 8 from the

Table 4. Table of the parameter values frequently used in the numerical simulations.

Symbol	Dim	Value
a_b	d	2
$V_b^{1/3}$	mm	0.8
$E_p/[E_m]$	mm^3	10
$[E_G]/[E_m]$	—	0.02
$[\dot{p}_M]/[E_m]$	d^{-1}	0.1
$[\dot{p}_J]/[E_m]$	d^{-1}	0.15
$\dot{p}_{Am}/[E_m]$	mm d^{-1}	2.5
$\{\dot{J}_{XAm}\}$	$\text{mol mm}^{-2}\ \text{d}^{-1}$	3
$\ddot{h}_a$	d^{-2}	5×10^{-7}
κ_R	—	1

ultimate volume for this choice of parameter values. However, for low feeding rates, the ultimate size $V_\infty^{1/3} = f\kappa\frac{\{\dot{p}_{Am}\}}{\dot{p}_M}$ can drop below the size at birth $V_b^{1/3}$, as implied by the model assumptions. Somatic maintenance costs can only be paid by the neonate if $V_\infty \geq V_b$, and maturity can only be maintained by the neonate if $V_\infty \geq V_b \left(\frac{\kappa}{1-\kappa}\frac{[\dot{p}_J]}{[\dot{p}_M]}\right)^3$. Reproduction is only initiated if $V_\infty > V(a_p)$. Figure 3 illustrates all biologically meaningful combinations of f and κ, given the parameter values. The grey areas represent the values for f and κ where the organism can maintain itself and be reproductively active.

Adult stage. Although reproduction involves a series of events (e.g., births, oviposition), the energy flow to reproduction is regarded as a continuous and irreversible process. Because allocation of catabolic power to reproduction differs for the two allocation strategies, the specific formulas for the reproduction rate, $R(a)$, i.e., the average rate of offspring produced by an animal of age a, are given in the following subsections.

Survival probability. Free radicals that result from respiration cause irreparable damage to the DNA in organisms and have a direct relationship with aging [Kooijman (2000), Leeuwen *et al*. (2002) and references therein]. The hazard rate, $\dot{h}$, the probability per unit time that death occurs at a certain age, given survival to that age, is taken proportional to the density of accumulated damage, while the accumulated damage is proportional to damaged DNA, and this damage builds up proportional to the rate with which reserves are utilized. The latter rate directly relates to the respiration rate [see Appendix and Kooijman (2000, pp. 139–145) for details].

In addition to death caused by accumulation of damage-inducing compounds death will occur from extrinsic causes such as predation, accidents, and diseases. We will assume that the extrinsic mortality, $\dot{m}$, is either constant, $\dot{m}(a) = \dot{m}_0$ (independent of age or body size), or size-dependent. In the latter case, we

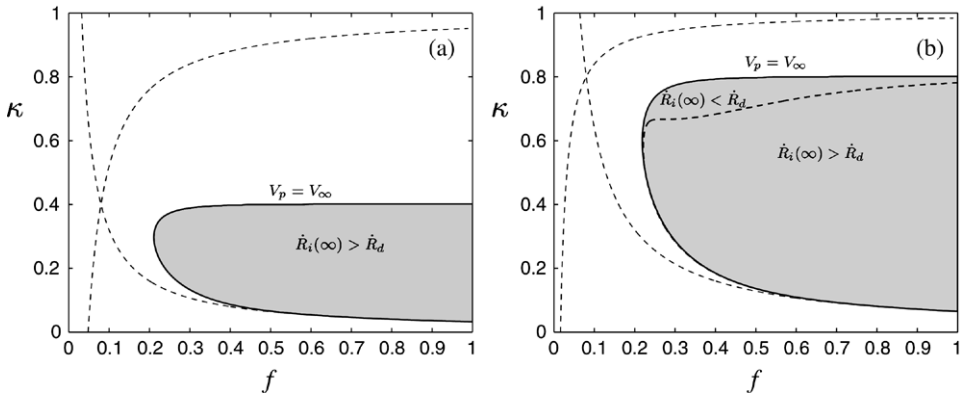


Figure 3. The dashed curves (a) and (b) represent boundaries for which the neonate just can pay somatic [curve (a)] and maturity [curve (b)] maintenance costs. The grey areas indicate combination of values for the scaled functional response f and the partitioning fraction κ, for which the organism is reproductively active; size at puberty equals the ultimate size at its border (solid lines). The fat dashed curve [in figure (a) coincides with the solid curve] represents values for f and κ where the ultimate reproduction rate of the indeterminate animal $\dot{R}_i(\infty)$ equals that to the determinate one $\dot{R}_d$. Parameter values: (a) $[\dot{p}_M]/[E_m] = 0.1\ \mathrm{d}^{-1}$, $[\dot{p}_J]/[E_m] = 0.15\ \mathrm{d}^{-1}$, (b) $[\dot{p}_M]/[E_m] = 0.2\ \mathrm{d}^{-1}$, $[\dot{p}_J]/[E_m] = 0.05\ \mathrm{d}^{-1}$; the rest of the parameters as in Table 4.

allow mortality to decrease with body length, $V^{1/3}$, according to the formula, $\dot{m}(a) = \dot{m}_0(V^{1/3}(a)/V_b^{1/3})^{-\mu}$, where $\dot{m}_0$ is the initial mortality rate and μ is a positive constant that measures how fast mortality decreases with size.

The total mortality rate is the sum of the hazard rate and the extrinsic mortality rate. The survival probability is then given by

$$\Pr\{\underline{a}_\dagger > a\} = \exp\left\{-\int_0^a (\dot{h}(t) + \dot{m}(t))dt\right\}, \tag{4}$$

where $a_\dagger$ is the age at death.

Life span. The mean life span $\mathcal{E}\underline{a}_\dagger$ of an animal relates to the hazard rate $\dot{h}$ and the extrinsic mortality rate $\dot{m}$ via the survival probability by the equation

$$\mathcal{E}\underline{a}_\dagger = \int_0^\infty \Pr\{\underline{a}_\dagger > a\}da. \tag{5}$$

Life span reproduction. For a reproduction rate $R(a)$, the life span reproduction N_R, i.e., the average number of offspring that an animal is expected to produce during its lifetime, amounts to

$$N_R = \int_{a_p}^\infty \dot{R}(a)\Pr\{\underline{a}_\dagger > a\}da. \tag{6}$$

Population growth rate. The population growth rate $\dot{r}$ at steady state is found from the Euler–Lotka equation

$$1 = \int_{a_p}^{\infty} \dot{R}(a)\Pr\{\underline{a}_\dagger > a\}\exp\{-\dot{r}a\}da. \tag{7}$$

2.1. ***Indeterminate growth.*** The constant fraction allocation strategy results in indeterminate growth; a constant fraction κ of catabolic power is allocated to somatic maintenance plus growth during all life stages. During the embryonic and juvenile stage, the remaining catabolic power is allocated to maturity maintenance plus maturation; the investment into maturation switches to reproduction after the cumulated energy investment into maturation exceeds a certain threshold E_p. Maturity maintenance $\dot{p}_J$ does not increase after the switch, but is proportional to volume at the switch (see Table 2). Somatic maintenance is always proportional to volume. Thus, energy allocation to reproduction equals the remaining catabolic power, $(1-\kappa)\dot{p}_C$, minus the cost of maintaining maturity, $[\dot{p}_J]V(a_p)$. The cost of producing an egg with energy content E_0 can be written as E_0/κ_R, where the dimensionless factor κ_R between 0 and 1 represents the fraction of production energy that is fixed in eggs; the fraction $1-\kappa_R$ dissipates and represents the overhead involved in the conversion from the reserve energy of the mother to the initial energy available to the embryo. Since these types of energy reserves are chemically related, the overhead is likely to be very small in most cases so that κ_R is close to 1. Thus the mean reproduction rate for ectotherms at age a is

$$\dot{R}(a) = \frac{\kappa_R}{E_0}((1-\kappa)\dot{p}_C - [\dot{p}_J]V(a_p)). \tag{8}$$

Substitution of equation (A.3) for the catabolic power into equation (8), for constant food density, gives the reproduction rate of the indeterminate animal

$$\dot{R}_i(a) = \frac{\kappa_R}{E_0}\left(\frac{(1-\kappa)f}{\kappa f/[E_G] + 1/[E_m]}\left(\frac{\{\dot{p}_{Am}\}}{[E_m]}V^{2/3}(a) + \frac{[\dot{p}_M]}{[E_G]}V(a)\right) - [\dot{p}_J]V(a_p)\right), \tag{9}$$

while the volume $V(a)$ is given by (1).

The hazard rate is given by equation (A.7) in the Appendix. If the aging acceleration is small enough, such that the period of substantial growth is short with respect to the life span, the hazard rate can be approximated for $a \geq a_p$ by

$$\dot{h}(a) = \frac{\ddot{h}_a[\dot{p}_M]}{2\kappa[E_G]}(a-a_p)^2. \tag{10}$$

2.2. ***Determinate growth.*** The bang–bang allocation strategy results in determinate growth. Determinate animals grow identically to indeterminate ones up to a certain volume $V(a_p)$, after which growth ceases and all catabolic energy is allocated to maintenance (somatic plus maturity) plus reproduction. The catabolic power for constant food density reduces to $\dot{p}_C = f\{\dot{p}_{Am}\}V^{2/3}(a_p)$. These lead to the reproduction rate of the determinate animal

$$\dot{R}_d = \frac{\kappa_R}{E_0}(f\{\dot{p}_{Am}\}V^{2/3}(a_p) - ([\dot{p}_M] + [\dot{p}_J])V(a_p)). \tag{11}$$

Up to the age at puberty a_p, the hazard rate of the determinate animal is identical to the indeterminate one and is given by equation (A.7). The hazard rate of an adult animal is derived similarly (see the Appendix), but the catabolic power is given by $\dot{p}_C = f\{\dot{p}_{Am}\}V^{2/3}(a_p)$. If the aging acceleration is small enough, such that survival up to puberty is almost sure, the hazard rate for the determinate animal can be approximated for $a \geq a_p$ by

$$\dot{h}(a) = \frac{\ddot{h}_a\{\dot{p}_{Am}\}f}{2[E_G]V^{1/3}(a_p)}(a - a_p)^2. \tag{12}$$

Note that the parameter κ can be interpreted as energy partition coefficient only up to the age at puberty. Increasing κ results in larger size at puberty which equals the ultimate size of the animal.

3. RESULTS

3.1. ***Comparison of reproductive traits.*** In this section we compare the life span, the reproduction rate, the life span reproduction, and the population growth rate for the two allocation strategies for constant food density.

The hazard rate, which reflects aging in our model, increases with age for both allocation strategies. This increase is caused by the accumulation of damage. Comparison of the approximate equations (10) and (12) shows that the hazard rate of the determinate animal exceeds that of the indeterminate one if $V_\infty > V(a_p)$, which is always the case. The assumption that death by aging is negligibly small till puberty obviously breaks down when the juvenile period becomes excessively large. We arrive at the same result when the formula derived in the Appendix is used [compare solid lines in Fig. 4(a) and (b)]. Total mortality rates (hazard rate plus extrinsic mortality rate) are qualitatively similar for both strategies [cf. Fig. 4(a) and (b)]. However, in the case of constant fraction allocation to growth there is a slower increase in mortality due to the combination of the lower risk of large animals and the decrease of specific oxygen consumption for increasing body size. Consequently, the life span of the indeterminate animal exceeds that of the determinate one [compare the locations of the arrows in Fig. 4(a) and (b)]. The effects of the functional response f and the partitioning fraction κ on life span are shown

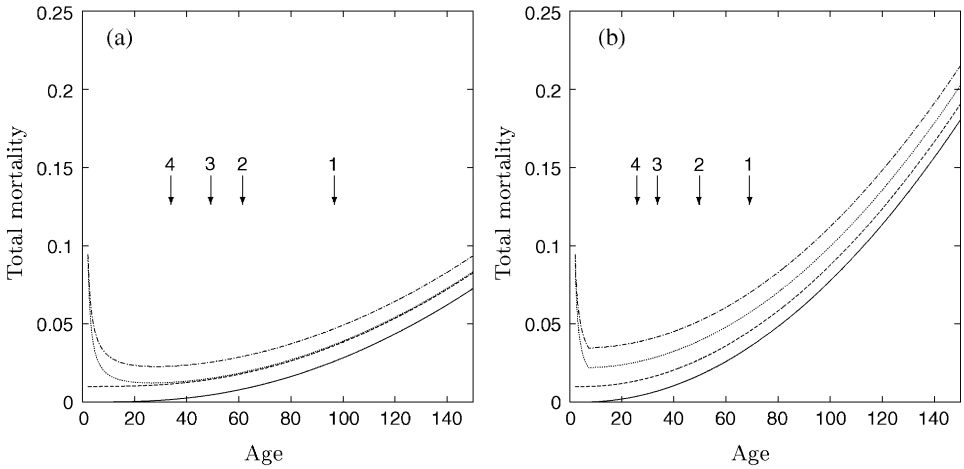


Figure 4. Age-dependence of total mortality rates for (a) an indeterminate animal and (b) a determinate animal, reflecting aging and extrinsic mortality at abundant food ($f = 1$) and with partitioning fraction $\kappa = 0.3$. The curves represent: aging only (1: —), aging and size-independent mortality (2: - - -, $\dot{m}_0 = 0.01$, $\mu = 0$), aging and size-dependent mortality (3: $\cdots$, $\dot{m}_0 = 0.1$, $\mu = 1.0$); (4: - · -, $\dot{m}_0 = 0.1$, $\mu = 0.7$). Arrows indicate the life span for the corresponding mortalities. Parameters: see Table 4.

in Fig. 5. Both type of animals, in a given food environment, can increase their life span by increasing κ [Fig. 5(a) and (b)]. On the other hand, for a given κ, the life spans increase as f increases [Fig. 5(c) and (d)] but the life span of the determinate animal may decrease for high values of f, when extrinsic mortality is low or absent.

From equations (9) and (11), we find that at the start of the adult period the reproduction rate of a determinate animal is always larger than that of an indeterminate one. For constant food density, the reproduction rate of a determinate animal is constant while that of an indeterminate increases with age to an asymptotic value. Assuming that aging allows, equation (9) with $V = V_\infty$ gives the reproduction rate of the fully grown indeterminate animal

$$\dot{R}_i(\infty) = \frac{\kappa_R}{E_0}\left(\frac{1-\kappa}{\kappa}[\dot{p}_M]V_\infty - [\dot{p}_J]V(a_p)\right). \tag{13}$$

A comparison of equations (11) and (13) gives that the ultimate reproduction rate of the indeterminate animal exceeds that of the determinate one if

$$(1-\kappa)V_\infty - \sqrt[3]{V_\infty V^2(a_p)} + \kappa V(a_p) > 0. \tag{14}$$

It turns out that if $\kappa < 1/2$, the inequality (14) holds for all biologically meaningful [i.e., $V_\infty \geq V_b$, $V_\infty \geq V_b\left(\frac{\kappa}{1-\kappa}\frac{[\dot{p}_J]}{[\dot{p}_M]}\right)^3$, and $V_\infty > V_p$] combinations of the parameters. If $\kappa \geq 1/2$, the reproduction rate of a determinate animal may exceed that of the fully grown indeterminate one for some biologically meaningful combinations of the parameters. This means that if the organism allocates a larger fraction of

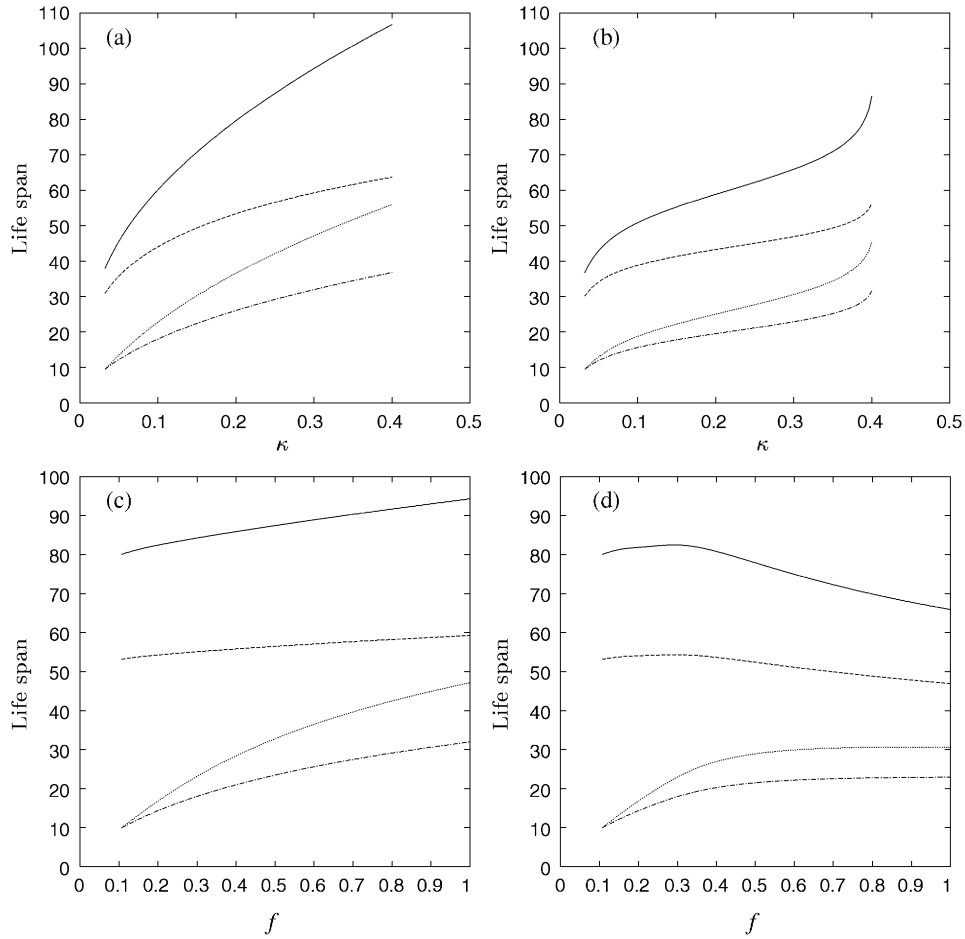


Figure 5. The life span of the indeterminate (a, c) and the determinate (b, d) animal as a function of the partitioning fraction κ at abundant food ($f = 1$) (a, b) and as a function of the functional response f with $\kappa = 0.3$ (c, d). The curves represent different mortality rates: aging only (—), aging and size-independent mortality (- - -, $\dot{m}_0 = 0.01$, $\mu = 0$), aging and size-dependent mortality ($\cdots$, $\dot{m}_0 = 0.1$, $\mu = 1$; - · -, $\dot{m}_0 = 0.1$, $\mu = 0.7$). Parameter values: see Table 4.

catabolic power to reproductive functions, then, assuming that aging allows, the indeterminate growth always results in higher ultimate reproduction rates.

Numerical simulations show that, in most cases, the ultimate reproduction rate of the indeterminate animal exceeds that of the determinate one for all biologically meaningful combinations of f and κ. One such case is shown in Fig. 3(a) where the parameters take the values given in Table 4. However, for some parameter values (e.g., high volume-specific costs for somatic maintenance and low volume-specific costs for maturity maintenance) the reverse holds for some combinations of food levels and allocation fractions [Fig. 3(b)]. These parameters affect the size at puberty (which equals the ultimate size of the determinate animal) as well as

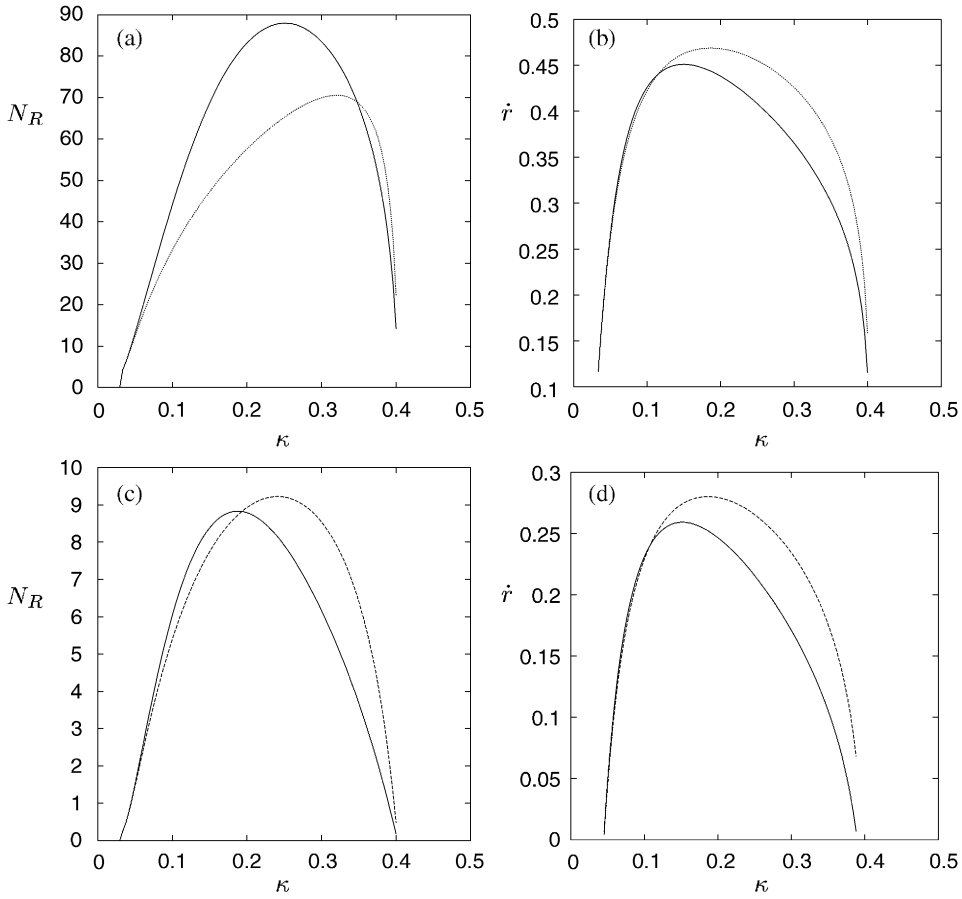


Figure 6. The life span reproduction N_R (a, c) and the population growth rate $\dot{r}$ (b, d) of the indeterminate (solid) and the determinate (dotted) animals as a function of the partitioning fraction κ at abundant food ($f = 1$). Upper panel (a, b): constant mortality ($\dot{m}_0 = 0.2$, $\mu = 0$). Lower panel (c, d): size-dependent mortality ($\dot{m}_0 = 0.5$, $\mu = 0.1$). Parameter values: see Table 4.

the ultimate size of the indeterminate animal in nonlinear ways; with the complex result as reported in Fig. 3(b).

The above analysis, justified by numerical simulations, implies that the life span reproduction N_R of an 'immortal' indeterminate animal is generally larger than that of a determinate animal, while the population growth rate $\dot{r}$ is larger for determinate growers. Determinate growth may lead to larger N_R for the large κ in the range of biological meaningful values, while indeterminate growth may lead to larger $\dot{r}$ for small κ. When extrinsic mortality and/or aging is applied the results do not change qualitatively. Figure 6 gives the life span reproduction and the population growth rate as a function of the partition coefficient at abundant food ($f = 1$) for different mortalities. Indeterminate growth leads to higher life span reproduction and population growth rate for small κ, while determinate growth leads to higher life span reproduction and population growth for large κ. The differences between the allo-

cation strategies for small κ are substantial for the life span reproduction, but small for the population growth rate. These differences get even smaller as f decreases.

If we assume that evolution maximizes N_R or $\dot{r}$ we find that the values of κ that maximize $\dot{r}$ are not affected considerably by the type and level of mortality, while the values of κ that maximize N_R decrease as mortality increases (independent of the type). In both cases the κ values of the determinate animal are larger than that of the indeterminate animal. Furthermore, for high levels of mortality the maximum N_R of the determinate animal may exceed that of the indeterminate animal [Fig. 6(c)]. The maximum $\dot{r}$ of determinate animals is higher than that of the indeterminate ones for all types and levels of mortality and food but for low food and mortality levels. In the latter cases, both animals are almost identical (maturation is delayed) and the difference is negligible for this choice of parameters.

3.2. ***ESS for allocation.*** We consider here the problem of what value of the partitioning of catabolic energy κ is evolutionary stable in determinate and in indeterminate populations, and whether an indeterminate individual with such a value of κ, can invade in a determinate population, and *vice versa*. To this end, we aim to determine the 'optimal' value of κ that minimizes f subject to the condition $N_R = 1$. A population of indeterminate (determinate) type animals having this optimum κ cannot be invaded, and displaced, by an indeterminate (determinate) type that partitions energy with a different value of κ. Moreover, the resulting values $f_{\min}$ tell which type of animal can invade into the population of the other, namely the type with the smallest value for $f_{\min}$. To determine the 'optimal' κ, we set $N_R = 1$ which gives a relationship between the values of the functional response f at which the organism can replace itself and the partitioning coefficient κ. We then find the value of κ for which f is minimum.

Figure 7 illustrates the values of the partitioning of catabolic energy κ which are evolutionary stable and the minimum value of f in determinate and indeterminate populations for different types of mortalities. We find that when mortality rates increase [e.g., $\dot{m}_0$ increases Fig. 7(a) or μ decreases Fig. 7(b)] the ESS values of κ decreases and the minimum functional response increases. For both allocation strategies the optimal age, a_p, at puberty decreases as mortality increases, meaning that short living species start reproduction earlier. When mortality is size-independent both types of animals are similar for small values of $\dot{m}_0$ [Fig. 7(a)], meaning that each type can establish in a population of the other type. The reason is that the condition that the life span reproduction equals one is only met in situations where the size at maturation almost equals the asymptotic size, and both allocation schemes are very similar indeed. For large values of $\dot{m}_0$ we observe small differences for this choice of parameters. In those cases, a determinate animal can invade, and displace, a population of indeterminate animals. In the case of size-dependent mortality we find that, when mortality rate is initially high and decreases fast with size, the reverse holds [Fig. 7(b)]; the indeterminate animal can invade, and displace, a population of determinate animals.

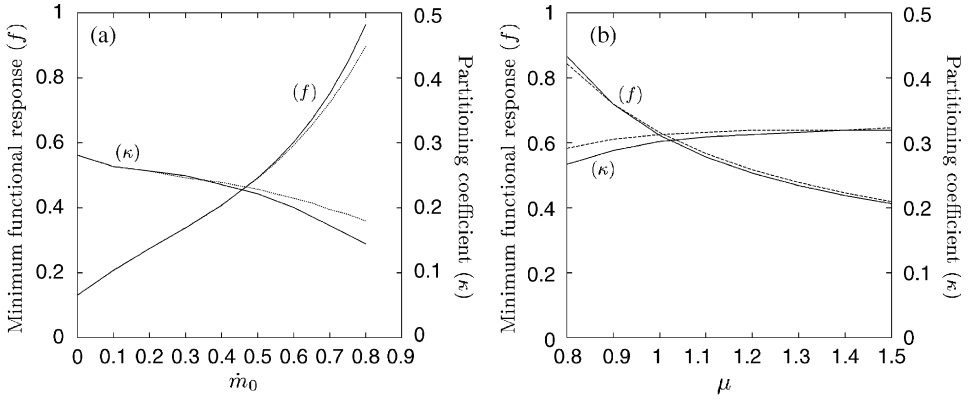


Figure 7. The evolutionary stable partitioning coefficient κ and the minimum value of f of the indeterminate (solid) and the determinate (dotted) animals as functions of different mortalities: (a) aging and size-independent mortality ($\dot{m} = m_0$) and (b) aging and size-dependent mortality ($\dot{m} = 1.6(\frac{V}{V_b})^{-\mu 3}$). Parameter values: see Table 4.

3.3. ***Conversion efficiency.*** In this section we compare the two allocation strategies in terms of conversion efficiency of food to biomass in steady state situations. Comparison on the basis of constant food density, implies an implicit mechanism for replacing food that has been eaten. A more realistic comparison is possible on the basis of a constant food flux, rather than a constant food density, assuming that food production is set by environmental conditions (such as light and nutrient availability). When food is supplied to a closed homogeneous volume with individuals, where no harvesting through intrinsic or extrinsic causes occurs, the population will grow to a size where food input just matches the maintenance needs of the individuals. In this situation, individuals neither grow nor reproduce. The conversion efficiency of food into biomass is then 0, because no biomass is produced. By increasing the harvesting rate we can increase, at least initially, the conversion efficiency.

Suppose that a population lives in a closed homogeneous volume that receives a food flux $\dot{J}_{XS}$, and assume that the age distribution among the individuals equals the stable age distribution $\dot{\phi}(a) = \Pr\{\underline{a}_\dagger > a\}/\mathcal{E}\underline{a}_\dagger$. The number of individuals, N, at steady state follows from equating the food supply flux to the amount that will be eaten

$$\dot{J}_{XS} = N f \{\dot{J}_{XAm}\} \mathcal{E} \underline{V}^{2/3}, \tag{15}$$

where $\mathcal{E}\underline{V}^{2/3} = \int_{a_b}^{\infty} \dot{\phi}(a) V^{2/3}(a) da$ is the mean surface area and $\{\dot{J}_{XAm}\}$ is the surface area-specific food uptake rate. The functional response, f, follows from the condition that the life span reproduction N_R equals 1 (each individual just replaces itself).

If an individual of size V is harvested at a probability rate $\dot{m} = \dot{m}_0 V^{-\mu/3}$ (where μ equals 0 for nonselective harvesting), the conversion efficiency in

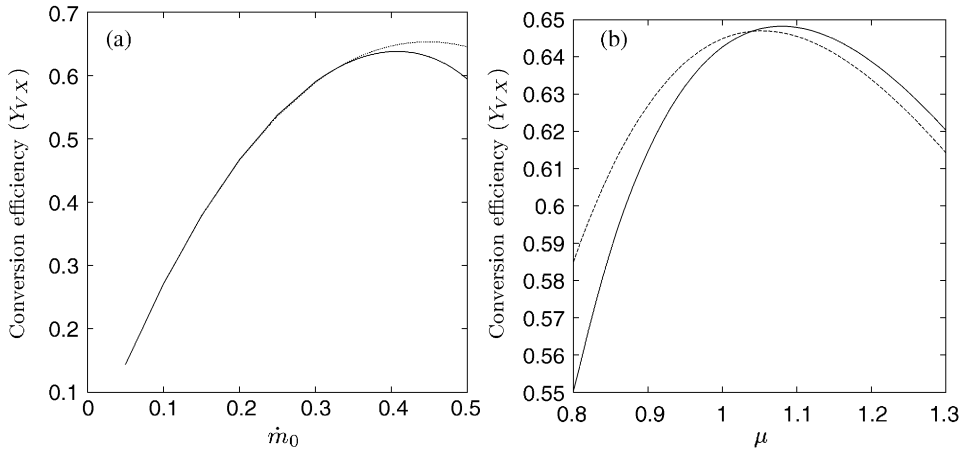


Figure 8. Effects of harvesting ($\dot{m} = \dot{m}_0(\frac{V}{V_b})^{-\mu/3}$) on the conversion efficiency Y_{VX} of the indeterminate (solid) and the determinate (dotted). (a) Nonselective harvesting ($\dot{m} = \dot{m}_0$) and (b) selective harvesting ($\dot{m} = 1.6(\frac{V}{V_b})^{-\mu/3}$). Parameter values: $\kappa = 0.36$, the rest of the parameters as in Table 4.

terms of C-moles of structural biomass per C-mole of substrate then amounts to $Y_{VX} = \dot{J}_{XS}^{-1} N \mathcal{E}\underline{\dot{m}V}$, where $N\mathcal{E}\underline{\dot{m}V}$, with $\mathcal{E}\underline{\dot{m}V} \equiv \int_{a_b}^{\infty} \dot{\phi}(a)\dot{m}(a)V^{2/3}(a)da$, is the harvested biomass. Using equation (15) to calculate the number of individuals at steady state, the conversion efficiency becomes

$$Y_{VX} = \frac{\mathcal{E}\underline{\dot{m}V}}{f\{\dot{J}_{XAm}\}\mathcal{E}\underline{V}^{2/3}}, \tag{16}$$

where f is the value of the functional response at which each individual can just replace itself. The system resembles a continuous culture, where input and output are decoupled.

The conversion efficiency depends on the harvesting rate as well as on the parameter κ. Determinate and indeterminate growth entails larger conversion efficiencies, respectively, for large and small values of κ in the range of biologically meaningful values. Figure 8 illustrates the effects of harvesting on the conversion efficiency. For both strategies, the conversion efficiency reaches a maximum value at intermediate harvesting rates. Furthermore, for nonselective harvesting the bang–bang allocation will lead to larger conversion efficiency at high harvesting rates. In contrast, when harvesting is much higher for small-sized than large-sized individuals, simultaneous growth and reproduction will lead to larger conversion efficiency.

4. DISCUSSION

Life history depends directly on how an organism allocates energy throughout its lifetime. DEB models describe the rates of acquisition and utilization of energy

by individuals and allow links between traits such as size-feeding and size-aging. By using DEB models, we ensure that energy-based trade-offs are incorporated into fitness measures. This paper illustrates the application of DEB models to life history theory. This is new and different from earlier approaches in the literature in that we use a DEB model to perform a comparative analysis of two strategies of energy allocation to growth and reproduction. We also use different fitness criteria and examine the effects of two types of mortality (constant mortality and mortality decreasing with size).

When we use the most popular density-independent measures of fitness, the life span reproduction N_R and the population growth rate $\dot{r}$, we find that independent of the measure of fitness and mortality (type or level), the values of the partition coefficient κ that maximize N_R or r are higher for determinate growth than those for indeterminate growth. Determinate growers can achieve maximum fitness by investing more to growth during development than the indeterminate growers. Furthermore, assuming that organisms adopt the value of κ that maximizes fitness, the maximum N_R may result from either determinate or indeterminate growth, depending on the level of mortality but not the type; the maximum $\dot{r}$ results from determinate growth, unless mortality and food levels are very low. Indeterminate growth maximizes N_R for low levels of mortality, because a substantial part of the life span is in the fully-grown phase, where the reproduction rate of indeterminate growers is higher. Determinate growth maximizes N_R for high levels of mortality and $\dot{r}$ because of the higher reproduction rate at the start of the adult period. In the case of population growth rate, the contribution of early offspring is more important than later offspring, since the early one reproduces earlier as well, the interest upon interest principle. Large population growth rates can be of ecological significance in spatially and temporally heterogeneous situations, where periods of rapid growth alternate with periods of (intense) random thinning.

The values of the partition coefficient κ that maximizes fitness are not affected considerably by changes in mortality rates, when $\dot{r}$ is the fitness criterion. However, this is not the case when N_R is used, where these κ values decrease when mortality rates increase. Our results are in agreement with those found by Taylor and Gabriel (1992) from maximizing only $\dot{r}$ and Fisken (1997), one of the rare papers that consider more than one fitness measure, from maximizing both $\dot{r}$ and N_R.

The indeterminate growth maximizes the conversion efficiency only by harvesting small-sized individuals preferentially. Fitness in terms of conversion efficiencies may be of interest to the analysis of ecosystem behaviour, provided that harvesting is a function of other populations.

In terms of invasion fitness, we studied the ESS for energy allocation as the lowest value of the functional response f, and consequently the lowest food density, at which an individual produces on average one viable offspring during its entire lifetime. In a constant environment, in cases where the population of long living species controls its own food density, both allocation strategies lead to very similar food densities, meaning that each type can establish in a population

of the other type. For short living species, individuals that follow the bang–bang allocation strategy can invade, and displace, a population of indeterminate type individuals. However, when mortality decreases with increasing body size, the indeterminate individuals can invade, and displace, a population of determinate individuals. Lika and Nisbet (2000) used a DEB model, which partitions energy according to a net production rule (net production equals assimilation minus maintenance), and studied the ESS of partitioning production energy to growth and reproduction in constant environment and constant mortality. They conclude that simultaneous lifetime allocation to growth and reproduction is optimal for short living species, while for long living species it is optimal to cease growth (not necessary at puberty) and continue to reproduce at a constant rate. The explanation of the difference in the predictions by the two DEB models is that the reproduction rate increases to a maximum at early ages in the net production model and declines to 0 as asymptotic size is approached, while reproduction rate increases with age (or size) in the present DEB model.

In an unchanging environment, simple models suggest that the optimal strategy for an organism is the determinate growth strategy (Perrin *et al*., 1993; Bulmer, 1994). Factors proposed to explain indeterminate growth include unpredictable environments (Taylor and Gabriel, 1993; Gurney and Middleton, 1996), age-specific mortality (Engen and Sæther, 1994), and size-dependent mortality and production rates (Taylor and Gabriel, 1992; Perrin *et al*., 1993). Our results show that an unpredictable environment is not needed to explain indeterminate growth. Nevertheless, in stochastic environments, indeterminate growth may be optimal under a much wider range of conditions. Engen and Sæther (1994) found that if mortality is a decreasing function of age, indeterminate growth is often optimal. This explanation is probably seldom applicable. Although age and size are usually correlated, age is not under evolutionary control (Heino and Kaitala, 1996, 1999), so mortality rates should not depend on age directly.

Perrin *et al*. (1993) extended previous results (Taylor *et al*., 1974; Gabriel, 1982; Sibly *et al*., 1985) and proved analytically that indeterminate growth can be optimal if production and mortality rates both increase or both decrease with size. This means that indeterminate growth either increases production rate at the expense of survival or increases survival at the expense of production. Production (net production) is determined by body size and is the total power devoted exclusively to growth and reproduction. Fitness was measured by the population growth rate. In simulations of a *Daphnia* model, Taylor and Gabriel (1992) found that growth after maturity can maximize the population growth rate when net production and survival rates increase with size, but growth after maturity is not optimal when survival rate decreases or is constant. Modelling clams, Heino and Kaitala (1996) could not explain indeterminate growth on the basis of life span reproduction if mortality decreases with size. They conclude that indeterminate growth may result from trade-offs and constraints related to the mass of offspring.

Our analysis shows that if mortality decreases with size, indeterminate growth maximizes almost all measures of fitness. However, if the fitness measure is life span reproduction, indeterminate growth may result even with constant mortality, provided it is not very high. Unlike Perrin *et al*. (1993), our result originates from an increased production (catabolic power) and a decreased mortality for indeterminate growers. Moreover, we explicitly take into account that the resulting size increase involves an increase in maintenance as well.

Our results show that for constant food density, indeterminate growth always leads to longer life span. The reason is in the decreasing specific oxygen consumption for increasing body size, an empirically well known phenomenon (Kleiber, 1932; Whithers, 1992), which is implied by the model assumptions listed in Table 1 (Kooijman, 2000) and the lower mortality risk of large-sized individuals. An indeterminate grower may increase its life span by directing energy away from reproduction. This type of individual is also more likely to survive a period of food shortage. Our conclusion underpins the findings of Masoro and Austad (1996) that a reduction of allocation to reproduction enhances survival during unpredictable short-term periods of starvation.

The present simple model for aging does not have the property of increasing the life span for low food density for indeterminates. Although it has been observed that food restriction slows aging (Finch, 1990), the strength of the present simple aging model is in revealing the role of energetics in the survival probability, though it is doubtful that aging is a major cause of death under field conditions. Nevertheless, more complex formulation should be used if research is geared towards answering questions concerning the evolutionary ecology of aging and longevity. Leeuwen *et al*. (2002) have developed a mathematical model based on the DEB theory, to describe the aging process that accounts for the effects of caloric restriction. This model is more complex and less tested, so far, against experimental data than the present model.

Our aim in this paper is to illustrate the application of DEB models to life history theory. This approach allows us to study questions concerning the evolution of lifetime reproductive allocation, optimal age and size at maturity, aging and longevity using a single modelling framework. In the present analysis we consider constant environments only. The full potential of DEB models for life history studies would be revealed in variable environments. The model does not consider the possibility of altering the partitioning of energy allocation to growth at maturity, which may occur in some species. We hope to deal with variable environments and variable allocation rules in future research.

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APPENDIX

In this appendix, we give a compact description of the basic equations for the DEB model used in this study, the κ-rule model.

An organism extracts energy from food which is added to the reserves and subsequently is used for somatic growth, maintenance, and development or reproduction. The rate of change of energy in the reserves is equal to the difference between the rate, $\dot{p}_A$, at which energy is assimilated and the rate, $\dot{p}_C$, at which energy is consumed by the bodily tissues (catabolic power); i.e., $dE/dt = \dot{p}_A - \dot{p}_C$. The organism ingests food at a rate that depends on its size and the food density (Assumption 6). The assimilation process involves uptake of food over the membrane surface and the subsequent transformation in reserve energy. The conversion efficiency of ingested food into reserve energy is assumed to be constant. Hence, the assimilation rate, $\dot{p}_A$, for an isomorph of volume V is

$$\dot{p}_A = \{\dot{p}_{Am}\} f V^{2/3}, \tag{A.1}$$

where $\{\dot{p}_{Am}\}$ represents the maximum surface area-specific assimilation rate, $f = (1 + X_K/X)^{-1}$ the scaled functional response, X the food density, and X_K the saturation constant.

The rate at which energy becomes available for utilization (catabolic power) depends on the organism's size and stored energy density. The reserve dynamics are a key concept in the model; they follow from the requirements stated in Table 1 (Assumption 7). These requirements lead [for details see Kooijman (2000, pp. 82–86)] to simple first-order dynamics for the reserve density, $[E] = \frac{E}{V}$,

$$\frac{d[E]}{dt} = \frac{\{\dot{p}_{Am}\}}{V^{1/3}} \left(f - \frac{[E]}{[E_m]} \right), \tag{A.2}$$

where $[E_m]$ is the maximum reserve density.

Using the chain rule for differentiation and equations (A.1) and (A.2), the catabolic power, $\dot{p}_C = \dot{p}_A - \frac{dE}{dt}$, can be written as

$$\dot{p}_C = [E] \left(\frac{\{\dot{p}_{Am}\}}{[E_m]} V^{2/3} - \frac{dV}{dt} \right). \tag{A.3}$$

As stated in Table 1 (Assumption 8), a fixed fraction κ of the catabolic power is allocated to somatic maintenance and growth, and the remaining $1 - \kappa$ to maturity maintenance and either maturation (for embryos and juveniles) or reproduction (for adults). Growth ceases when the fixed fraction κ of energy just meets somatic maintenance demands. Then, the organism may still continue to reproduce, provided the energy made available exceeds the requirements for maintenance. Reproduction ceases when the fraction $1 - \kappa$ of energy is fully required for maturity maintenance. When the default energy committed to somatic functions is insufficient to meet maintenance requirements deviation from the κ-rule is necessary, even if growth ceases. Depending on the species and

environmental factors, the individuals may continue to reproduce or they may cease energy investment to reproduction functions, increasing, thus, its survival period (Kooijman, 2000, pp. 227–230).

Thus, the catabolic power allocated to somatic maintenance and growth is $\kappa \dot{p}_C = [\dot{p}_M]V + [E_G]\frac{dV}{dt}$, where $[\dot{p}_M]$ and $[E_G]$ stand, respectively, for the volume-specific costs for maintenance and growth. Substitution of (A.3) gives the volume dynamics

$$\frac{dV}{dt} = \kappa\{\dot{p}_{Am}\}\frac{V^{2/3}[E]/[E_m] - V/V_m^{1/3}}{\kappa[E] + [E_G]}, \tag{A.4}$$

where $V_m^{1/3} = \frac{\kappa\{\dot{p}_{Am}\}}{[\dot{p}_M]}$ is the maximum volumetric length an isomorphic ectotherm can reach.

Now that growth has been specified, by substituting (A.4) into (A.3) we find that the catabolic power is given by

$$\dot{p}_C = \frac{[E][E_G]}{\kappa[E] + [E_G]}\left(\frac{\{\dot{p}_{Am}\}}{[E_m]}V^{2/3} + \frac{[\dot{p}_M]}{[E_G]}V\right). \tag{A.5}$$

In addition to the two state variables V and E, a third state variable, the accumulated damage, is also required to specify the aging process. The amount of damage-inducing compounds (changed DNA), M_Q, accumulates from value 0 in an embryo of age 0. The amount of damage changes at a rate proportional to utilization rate, so $\frac{dM_Q}{dt} \propto \dot{p}_C = ([\dot{p}_M]V + [E_G]\frac{dV}{dt})/\kappa$. The amount of damage-inducing compounds as a function of time is thus proportional to

$$M_Q(t) \propto \left([E_G](V(t) - V(0)) + [\dot{p}_M]\int_0^t V(t_1)dt_1\right)\Big/\kappa, \tag{A.6}$$

and the accumulated damage is $\int_0^t M_Q(t_1)dt_1$. The hazard rate, $\dot{h}(t)$, (the instantaneous death rate) is finally taken to be proportional to the accumulated damage density, which leads to

$$\dot{h}(t) = \frac{\ddot{h}_a}{\kappa V(t)}\int_0^t \left(V(t_1) - V(0) + \frac{[\dot{p}_M]}{[E_G]}\int_0^{t_1} V(t_2)dt_2\right)dt_1, \tag{A.7}$$

where the proportionality constant $\ddot{h}_a$, called aging acceleration, absorbs all the above proportionality constants.

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