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State-of-the-art review

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WHY LIFE HISTORIES ARE DIVERSE

ABSTRACT: Why do some animals weigh a fraction of a milligram and others many tons? Why do some animals mature after a few days and others need several years? Why do some animals grow and then reproduce without growing, while others continue growing after maturation? Why are growth curves so often well-approximated by von Bertalanffy's equation? Why do some animals produce myriads of tiny eggs and others produce only a few large offspring? Evolution of life histories is driven basically by the size-dependences of three parameters: the resource acquisition rate, metabolic rate and mortality risk. The combinations of size-dependences of this trio produce a plethora of locally optimal life histories, and even more sub-optimal strategies which must coexist with optimal ones in the real world. Additionally, selection forces differ depending on whether a population stays most of the time at equilibrium or in an expansion phase. Life history evolution cannot be understood without mathematical modelling, and optimization of life-time resource allocation is a powerful approach to that, though not the only one. Modelling outcomes from studies based on resource allocation optimization are presented here mainly as graphs.

KEY WORDS: optimality, mortality rate, production rate, age at maturity, growth curves, seasonality, body size, aging

1. INTRODUCTION

There is a great variability of body size in animals, body length ranging from a fraction of a millimetre in soil interstitial species, to tens-of-metres' giants such as blue whales. There is also huge diversity in offspring size, and although there is a general positive correlation between initial size and adult size, the ratio of offspring to adult sizes differs by orders of magnitude even between closely related species. Many such examples can be found in Echinodermata, with small eggs developing in feeding larvae and large eggs developing in non-feeding larvae (e.g. Lessios 1990, Hart 1996, Sewell and Young 1997), but egg size also varies enormously in fishes (e.g. Duarte and Alcaraz 1989, Froese and Pauly 2005). Some organisms, such as birds, mammals or insects, grow until maturity and then stay at roughly the same size. In many other groups, such as fish, amphibians, reptiles, some molluscs and some crustaceans, individuals keep growing even towards the end of life. In the latter group, most growth can occur either before or after maturation (e.g. Froese and Pauly 2005), and in some species there are even

inter-population differences in the shape of growth curves, suggesting differences in the fraction of final size attained at maturity (e.g. Czarnołęski *et al.* 2003, 2005). Organisms may grow rapidly or slowly, and may become senescent soon or late.

There is also a diversity of life history traits not considered in this paper. For example, offspring may be produced in clutches, sometimes repeated several times in a season, or born individually during some delimited period. The first mode requires some period of resource accumulation (capital breeders); in the second mode, current resource income may be sufficient (income breeders). Most species are iteroparous, that is, they produce multiple clutches during their lives, but semelparity, reproduction once before death, has evolved independently many times. The reasons for the evolution of these two modes are still not clear. That problem is not considered in this paper.

All multicellular organisms are descendents of a protist cell. Even when a common ancestor is not so distant, differences can be huge. The shrew and the elephant give a good example: they diverged quite recently on the geological time scale, but they differ many-fold in size, age at maturity and life span. Why such differences? The standard answer is that natural selection shaped the adult size, offspring size, schedule of growth etc., under different conditions for each species. This explanation is correct, but not satisfactory. It merely restates our belief that organisms living now are products of evolution. We need a much more specific answer that can, if not predict the size of an organism under given conditions, at least help us to understand the existing diversity of organisms' life history features.

We can say that any type of organism is constrained. For example, an arthropod cannot be too big because it would burst its exoskeleton; the maximum possible sizes differ between the land and aquatic forms. Size in insects may also be restricted due to inefficient oxygen delivery to the organs via the tracheal system. But most arthropods are far under that limit. Similarly, mechanical constraints impose maximum sizes on land quadrupeds, but that is not what eliminated the mammoths, and all land mammals living now are much smaller than mammoths.

Certainly there is a lower limit to egg size, but not too many species have eggs as small as those of the marine giant clam (*Tridacna gigas* (L.)), which weighs up to 250 kg and produces over 500 million eggs 0.1 mm in diameter (Braley 1989). In many systematic groups there are diverse mechanisms to increase initial size, which means that the optimum is usually far from the constraint. The same can be said of other life history traits: sometimes their values result from developmental, phylogenetic or physiological constraints, but more often they do not. We can say that natural selection for maximal lifetime reproductive success usually shapes the life history features of a given population in a given place.

Living things are self-replicating entities, and evolutionary success means the most effective passage of genome copies to further generations. The genetic program is responsible, directly or indirectly (e.g. through a genetically conditioned ability to learn), for all aspects of life. Living things are open thermodynamic systems called "dissipative structures". They can retain their complexity, or even increase it, because they dissipate energy. When they build tissues from simpler components, they locally decrease entropy at the cost of entropy of the surroundings, which increases through degradation of a large part of the captured energy (maintenance costs). After respiration stops, the now-dead organism dissipates rapidly and its entropy grows. Its corpse becomes nothing but food for other organisms. All multicellular organisms are mortal, and reproduction provides the only way to escape the catastrophe of total decay. Thus the ultimate "purpose" is to allocate resources to tissues of offspring, which carry copies of the genetic program further. Allocation to the organism's own mortal body is reasonable as an investment that can increase future offspring production; sooner or later, some or all surplus energy (not used for maintenance) is channelled to reproduction. Thus the first questions are when and how much to invest in the body's machinery in order to maximize lifetime reproductive success (fitness). Another question is how much of the resources to put into a single envelope of a copy of the genetic program in order to maximize fitness, or simply, how large an

individual offspring to produce, taking into account the unavoidable tradeoff between offspring size and number. Two other important questions are about the optimal growth rate and the optimal rate of resource capture for reproduction.

When the question on optimal adult size is raised, many papers consider only the gains and losses of a given size encountered by an adult. The best example, analyzed in more detail later, is the assumption that optimal size is the one that maximizes the production rate or fecundity (Sebens 1982, 1987, Reiss 1989, Brown *et al.* 1993). Such an assumption seems attractive but is misleading. The size of an organism is not *given* to the organism. It is *developed* by the organism, and development requires time, during which death is likely. Optimization of any life history trait must always be considered from the perspective of the entire lifespan.

Optimal resource allocation models seem appropriate for studies of life history evolution. They take into account the entire lifespan, and integrate the demographic and physiological properties of species. However, the model results must be considered a first approximation, not only because these models are still in a primitive state of development; more importantly, optimal solutions of evolutionary problems are not always evolutionarily stable. For a broader discussion of the applicability of the optimization approach, see Kozłowski (1999).

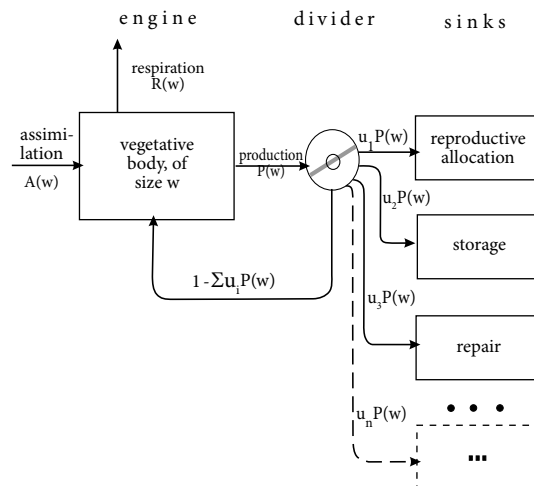
The next section gives an overview of life history evolution models, based on the prin-

ciple that optimal resource allocation maximizes fitness. The emphasis is on the role of seasonality, and also on ageing, which can be shaped by allocation of resources to repair. The role of the size-dependence of the mortality risk and production rate in an aseasonal environment is considered in Section 3. It is shown that this size-dependence is responsible for optimal adult size, offspring size, and even optimal foraging intensity under predator pressure. The evolution of life histories in a seasonal environment is considered in Section 4. The emphasis is on the resulting indeterminate growth, mimicking predictions of Bertalanffy's model, and the optimality of a reversible switch from growth to reproduction in consecutive years. Then, in Section 5, a classification of life histories is proposed, based on the level of mortality and such morphological traits as cell size and, indirectly, DNA amount. Finally in Section 6 some previous results are discussed in relation to the fitness measure, which differs between stable populations and populations that are almost constantly in an expansion stage.

2. OPTIMAL RESOURCE ALLOCATION MODELS: OVERVIEW

With allocation models such as illustrated in Fig. 1, investment decisions can be studied. It is assumed that organisms are limited by their available resources (usually considered in energy units) and must optimally compromise their allocation in order to maximize fitness. Energy may be limited

Fig. 1. Basic scheme of an allocation model. An organism consists of an “engine”, that is, a soma providing resources, and a “divider” which allocates surplus resources (not used for maintenance) back to the soma to allow growth, and to other “sinks” such as reproduction, storage and repair. The amount of surplus energy $P(w)$ depends on body size w . The proportions u_i of energy going to different sinks are subject to optimization in order to maximize fitness. In this paper, the simplest imaginable system is considered, with surplus energy allocated optimally between growth and reproduction. From Kozłowski (2000).



either by resource availability or by the ability of an organism to digest and assimilate food (Weiner 1992), and its acquisition rate $A(w)$ is dependent on organism size w , measured for simplicity in energy units. Acquired energy may be used for maintenance at rate $R(w)$, for tissue growth or storage, or for channelling to reproduction. Most allocation models do not distinguish between external and internal limitations on energy input. Additionally, it is usually assumed that maintenance costs are paid first, and that surplus energy, called the production rate $P(w)$, is a function of body size w as a result of the size dependence of the acquisition and maintenance rates.

Allocation models are built to find the optimal proportions of resources allocated into different sinks. These proportions change dynamically during the life span. Various mathematical methods not described in this review can be applied to find optimal solutions; the two most frequently used are the Pontryagin Maximum Principle (Pontryagin *et al.* 1962) and dynamic programming (Bellman 1957, Mangel and Clark 1989). Although the number of energy sinks considered is arbitrary, two of them must always be taken into account: reproduction and growth. This is because the reproductive allocation throughout life defines fitness, and growth changes the body size, an important determinant of the production rate and often also of the mortality risk. Storage is usually easy to define physiologically as the amount of fat in animals, or starch in plants. In life history, storage means at least two different things: a buffer of energy against an unfavourable season, or resources for future reproduction. The first kind of storage cannot be optimal in an ideally constant environment (no seasonal or stochastic changes in food access). This is because producing fat or starch and mobilizing such resources entail some cost; direct channelling of surplus energy to growth or reproduction must be more efficient. The second kind of storage can be considered the reproductive allocation. For example, reptiles often produce fat bodies that are later used up for yolk production. This case shows clearly that the terms “reproduction” and “reproductive allocation” are not synonymous. In allocation models,

reproduction means the release of earlier-accumulated resources.

The outcome of models considering optimal allocation of energy to growth and reproduction usually takes the form of switching curves that divide a plane defined by age and size axes into two parts; it is optimal to grow below the switching curve, and to reproduce above it (Fig. 2 A). In an aseasonal environment the switching curve is a straight line parallel to the age axis if there is no ageing (Fig. 2 B, upper left; e.g. Ziółko and Kozłowski 1983, Perrin and Sibly 1993). If mortality increases with age, the switching curve goes down because life expectancy decreases toward the end of life (Fig. 2 B, upper middle). In both cases determinate growth is optimal, because once an animal has crossed the switching curve it has no chance to be below it in the future. Resources used up for repair postpone ageing and in this way move the switching curve up (Fig. 2 B, upper right), but repair drains energy from growth, slowing it down. The change in these two curves causes them to cross later. Slower growth may last longer and produce an animal larger than in the case without repair, as illustrated in the figure, or growth can be so retarded that it is optimal to mature at a size smaller than in the case without repair. Optimal allocation of resources to repair is not considered explicitly in this paper; see Cichoń (1997) for this problem and Cichoń and Kozłowski (2000) for the effect of allocation to repair on the shape of mortality curves.

Instantaneous switching from growth to reproduction produces a growth pattern often called exponential, although in fact it should be described by a power equation with age raised to a power in the range 3–4. If size is expressed in energy units, the growth rate is equivalent to the production rate because all production is allocated to growth before maturation. There is a possible exception to the rule that optimal switching from growth to reproduction is instantaneous and irreversible in an aseasonal environment. Graded switching, discussed at the end of the next section, changes the shape of the growth curve, making it more similar to Bertalanffy's.

Seasonality has a strong effect on the shape of switching curves (Fig. 2 B, lower row). To model seasonality, the year is di-

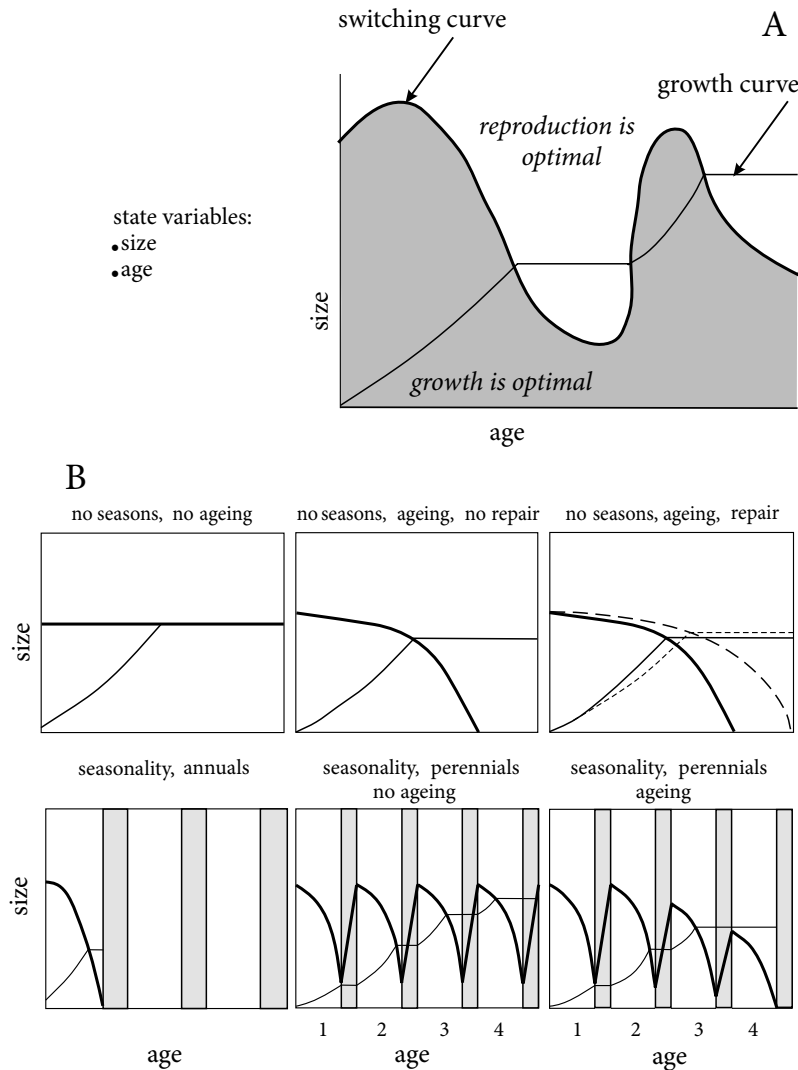


Fig. 2. Switching curves (thick lines) for different life styles resulting from models optimizing resource allocation to growth and reproduction. At the point where the growth curve (thin line; from production equation $P(w)$) reaches the switching curve, growth stops and all surplus energy is channelled to reproduction as long as the growth curve is above the switching curve. A – General scheme. B – Top row represents allocation in an aseasonal environment by organisms not ageing (left column), by organisms ageing and not allocating resources to repair (central column), and by organisms ageing and allocating resources to repair (dashed line in right column; solid line shows the case without repair for comparison). Bottom row represents allocation in a seasonal environment, with the years divided into favourable periods (unshaded) and unfavourable periods (shaded). Bottom left represents annual organisms; bottom middle and right represent iteroparous organisms - middle with unlimited life span (no ageing) and right with life limited to four years because of ageing. From Kozłowski *et al.* (2004), slightly modified.

vided into a favourable part when growth and reproduction are possible (called summer hereafter) and an unfavourable part when the energy balance equals zero or is even negative (winter). If the energy balance is negative in winter, it may be assumed that summer is shortened by a period necessary

to gain resources to balance winter expenditures, instead of explicitly considering storage allocation.

Annual organisms have monotonically decreasing switching curves, reaching zero at the end of summer (Fig. 2 B, lower left; e.g. Vincent and Pulliam 1980, Kozłowski

and Wiegert 1987). This is because it is optimal to use all surplus energy for reproduction (producing diapausing propagules) at the end of the season beyond which no life is expected.

If life extends longer than one season, the switching curves fall during summers and rise during winters (Kozłowski and Uchmański 1987, Kozłowski 1996b, Kozłowski and Teriokhin 1999). The switching curve never falls to zero at the end of a summer, except at the end of life, because for iteroparous organisms there is always some chance to survive and reproduce in the future (Fig. 2 B, lower row, middle and right). The elevation of the switching curve above the time/age axis at the end of a summer is positively related to the residual reproductive value (the expected number of offspring at the end of the season). The teeth on the curve mean that an organism that has crossed the switching curve and has reproduced is likely to be back below the switching curve at the beginning of the next season, thereby allowing growth to continue after maturation. Depending on the mortality schedule, such switching curves lead to either indeterminate growth that approaches an upper limit asymptotically if lifespan is unlimited (Fig. 2 B, lower middle), or growth that slows down and then stops completely after several years if the lifespan is limited (Fig. 2 B, lower right). Both forms of growth are called indeterminate here, because some part of growth is fulfilled after maturation.

3. OPTIMAL LIFE HISTORY IN AN ASEASONAL ENVIRONMENT

Life history optimization can be most easily modelled in an aseasonal environment. This is because absolute time is no longer important and the time axis can be identified with the age of an organism, which means that for a non-growing population it is not important when the offspring is born and only the expected lifetime offspring number matters. In further considerations it will be also assumed for simplicity that the resources allocated to reproduction are released continuously without any time lag (see Kozłowski 1996a for the consequences of removing this assumption), and that there is no ageing.

The first question is about optimization of the resource acquisition rate. Foraging may be risky because of predators, and if spots rich in resources are also dangerous, places not necessarily having maximum food abundance should be chosen. As shown by Werner and Anholt (1993), the optimal resource acquisition rate is the one that minimizes the mortality-rate-over-production-rate ratio. Mortality rate $m(w)$ is measured, for example, in d^{-1} units, and is related to survival in a standard way, i.e. probability of survival over the period t equals $\exp(-m(w)t)$. Production rate $P(w)$ is measured in, say, $J d^{-1}$ units. Thus the ratio $m(w)/P(w)$ has J^{-1} units and is a measure of mortality rate, but not the classic one per time unit, but a modified one per amount of surplus resources gathered. Minimizing $m(w)/P(w)$ before maturation, that is, during the growth phase of life, is equivalent to minimizing the death risk in the period necessary to reach a given size. It may be optimal to grow slowly and avoid risk or to grow rapidly and accept risk, depending on the exact shape of both functions $m(w)$ and $P(w)$. In the case of clones, minimization of the $m(w)/P(w)$ ratio during a size increase from, say, $1 J$ to $10 J$ means that the maximum number of clone members will reach size $10 J$. A similar interpretation can be applied to adult life: minimization of $m(w)/P(w)$ means minimization of the death risk per joule of energy allocated to reproduction. In other words, the expected amount of reproductive allocation will be maximized if the ratio is at minimum. Recall that minimization of m/P is optimal only for a non-growing population (see Section 6 for discussion of this point).

This reasoning can be extended to considerations of optimal maintenance costs: animals can increase the resource acquisition rate at the cost of increasing their metabolic rate, which can be denoted as $R(w, A(w))$. One possible way is to have a larger alimentary tract, which is usually very expensive. At what size is the rate of energy capture optimal? Because

$$P(w) = A(w) - R(w, A(w)) \quad (1)$$

an organism should acquire resources at the rate for which $m(w)/P(w)$ is at minimum, in both juvenile and adult life. The simple intu-

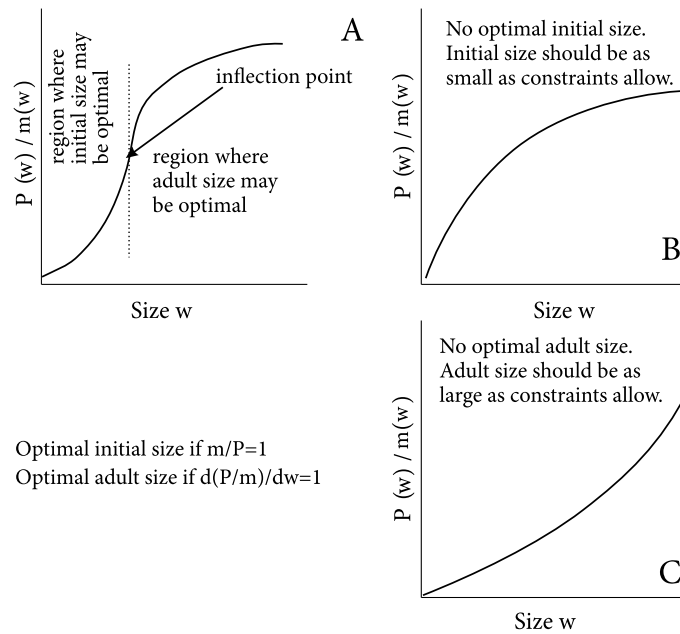


Fig. 3. Conditions for the existence of optimal initial and adult size. A – Both optima exist because the ratio P/m of production over mortality has an inflection point. B – Optimal initial size does not exist; it should be as small as design constraints allow. C – Optimal adult size does not exist; it should be as large as design constraints allow.

ition that at each size w the resource acquisition rate should be optimized in order to maximize the production rate $P(w)$ is misleading in general, and true only if increasing production does not intensify the mortality risk.

There is an obvious trade-off between offspring size and offspring number (Smith and Fretwell 1974). Resource allocation models also address the question of optimal offspring size. The condition necessary for offspring size (w_0) to be optimal is that

$$m(w_0)/P(w_0) = 1 \tag{2}$$

(Taylor and Williams 1984, Kozłowski 1996a). To show the sufficient condition, however, it is easier to consider not m/P , but its reciprocal P/m (Fig. 3). Condition 2 is also sufficient if the size satisfying it lies on the concave upward part of the $P(w)/m(w)$ curve, as shown in Fig. 3 A and C. If the relation of P/m with respect to body size is concave downward as in Fig. 3 B, there is no optimal offspring size, and very tiny propagules limited only by design constraints should be produced, as in the case of the giant clam, for example.

Optimal resource allocation models predict that the size at which it is optimal to switch from growth to reproduction in an aseasonal environment depends also on the $P(w)/m(w)$ ratio, and more exactly on the rate at which the ratio changes with size w measured in energy units (Kozłowski 1992, Perrin and Sibly 1993). The ratio P/m , expressed in joules, can be interpreted here as follows. In a constant environment, life expectancy at maturity for a non-ageing organism of adult size w_{opt} is equal to $1/m(w_{opt})$. Thus the P/m expresses the expected energy content of offspring produced during an average adult life. For non-ageing organisms, the optimal size at maturity (at switching from allocation to growth to allocation to reproduction) is the one satisfying the following condition:

$$\frac{d[P(w)/m(w)]}{dw} = 1 \tag{3}$$

(Perrin and Sibly 1993, Kozłowski 1996a). Equation (2) is a necessary but not sufficient condition for optimal adult size. Lifetime reproductive output will be maxi-

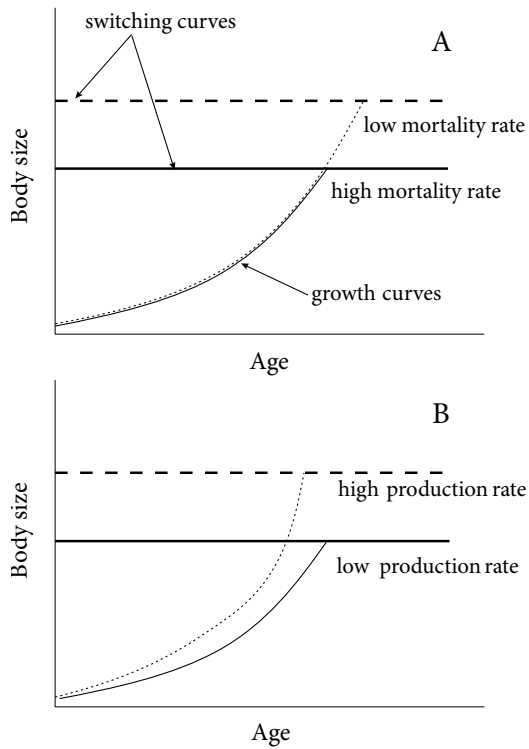


Fig. 4. The effect of mortality rate and production rate on optimal body size in an aseasonal environment for non-ageing animals. A – When two populations differ in mortality rate, optimal size is larger under low mortality, but growth rate is the same; as a result, age at maturity increases. B – When two populations differ in production rate, optimal size is larger under higher production rate, but growth rate also increases; as a result, age at maturity may stay the same or even decrease.

mized at the optimal size w_{opt} satisfying condition (3) only if the function $P(w)/m(w)$ is convex (concave downward) in the vicinity of w_{opt} , as shown in Fig. 3 B (Kozłowski 1996a). If there is no convex segment of the P/m ratio curve, there is no place for optimal adult size, which must be determined by design constraints (Fig. 3 C). Condition (3) has a very simple biological interpretation: it is optimal to allocate a joule of resources to growth if this growth increases the expected future reproductive output by more than one joule; otherwise it is better to allocate this unit of resources directly to current reproduction (Kozłowski 1992).

For size-independent mortality m , condition (3) simplifies to the form

$$\frac{dP(w)}{dw} = m \quad (4)$$

If the production rate curve is humped with respect to body size, that is, if it has a maximum for a given size, the simple but misleading intuition is that the size maximizing the production rate should be optimal, as assumed by Sebens (1982, 1987), Reiss (1989), or Brown *et al.* (1993). Such reasoning ignores the important role of the mortality risk in shaping optimal size – higher mortality decreases optimal size at maturity. Unless the mortality risk is negligible, the optimal size is always well below the one maximizing the production rate. It follows from (3) that mortality decreasing with size has a weaker effect on body size than size-independent mortality, and mortality increasing with size has a stronger effect. Thus, optimal size can reach the value maximizing the production rate, or even go beyond this point, only under a very strong decrease of mortality with size. In general, higher mortality means smaller optimal size (Fig. 4 A). Note that an increase or decrease of optimal adult size under the influence of mortality must simultaneously change age at maturity because growth rate remains unaltered.

According to conditions (3) and (4), the production rate (or more precisely its derivative), acts together with mortality to affect optimal size. The optimal size is larger under higher production when mortality risk remains the same (Fig. 4 B). When changes of the production rate are responsible for alterations of size at maturity, the growth rate changes as well, and larger size may be attained at the same age or even earlier.

Decisions for optimal life in an aseasonal environment are simple, and may be summarized in three rules: 1) always choose places, foraging intensity and physiology that keep the ratio of the mortality rate to production rate at a minimum for each body size; 2) mature at the size at which the derivative of the ratio of production rate to mortality rate equals one; 3) produce offspring of the size at which the ratio of the mortality rate to production rate equals one. Rule 2) is valid when the P/m is concave downward with re-

spect to body size, and rule 3) when the ratio is concave upward. Under other shapes, optima do not exist and constraints determine either initial or adult size. For both optimal initial and adult size to exist, the P/m ratio must have an inflection point: for small sizes it should be concave upward, then convex (concave downward). If there is more than one inflection point, multiple local optima for initial and/or adult size may exist. For possible consequences of multiple optima, see Kozłowski (1996a). For more information on size-structured interactions in aquatic systems see Persson and De Roos (2006).

Can simultaneous allocation of resources to growth and reproduction be optimal in an aseasonal environment?

Although instantaneous switching from growth to reproductive allocation is the rule, exceptions are possible, especially in aquatic ecosystems: if both the mortality rate and production rate increase with size, as in *Daphnia*, the switching curve may be humped (Fig. 5). Under instantaneous switching the growth curve would cross the switching curve to the left of the peak, but it would lead to a non-optimal solution (Perrin and Sibly 1993, Perrin *et al.* 1993). To maximize lifetime reproductive output, a period of mixed growth and reproduction, with the fraction of energy allocated to reproduction increasing steadily during growth, appears after a period of pure growth. During the period of mixed allocation, the growth trajectory follows a so-called singular arc, to cross the switching curve just at its peak. The resulting growth curves have a phase of rapid growth, which slows down after switching to mixed allocation. After the growth curve crosses the switching curve, all surplus resources should be allocated to reproduction. In such a case the switching curve should be interpreted as a line dividing the age-size plane into a field where only reproduction occurs and a field where growth occurs, possibly accompanied by reproduction (for the sufficient condition of a singular arc to occur, consult Perrin and Sibly 1993 and Perrin *et al.* 1993).

There are also other reasons for a graded switch between growth and reproduction based on some design constraints.

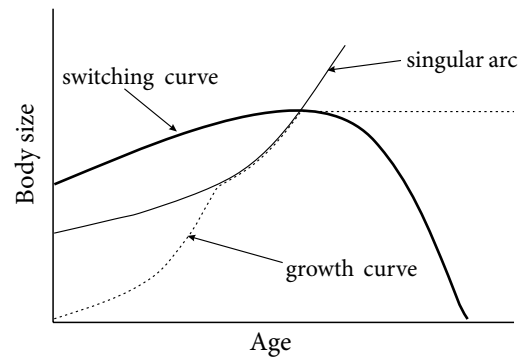


Fig. 5. Optimal growth trajectory when switching curve is humped, which is usually caused by both production and mortality increasing with size. Growth consists of three phases: 1) pure growth before the singular arc is reached; 2) mixed growth and reproduction in proportions allowing the curve to follow the singular arc and to cross the switching curve just at its peak; 3) pure reproduction without growth. From Kozłowski *et al.* (2004).

This means that without these constraints a graded switch would be sub-optimal. For example, gradual tissue maturation, unavoidable under real physiology, may slow down growth (Ricklefs 1979, Konarzewski 1988, Ricklefs 2003), which may lead to logistic, Richard's, or Bertalanffy's growth curves. This outcome resembles a graded switch. Developing reproductive structures may not be able to absorb the entire production previously used for growth. Under such a constraint, it may be optimal to start reproduction earlier and to continue growth together with reproduction (Kozłowski and Ziółko 1988); the resulting growth curves also have inflection points. For animals reproducing in large clutches, limits on the volume of the body cavity available for developing eggs may cause a graded switch (Rodhouse *et al.* 1988, Rodhouse and Hatfield 1990, Weeks 1996, Gunderson 1997, Stamps *et al.* 1998). A gradual switch from growth to reproduction should not be mistaken for the instantaneous but reversible switch described in the next section, although the result may look similar if the time scale is coarse (e.g. years instead of days).

4. THE EFFECT OF SEASONALITY

Optimal allocation of resources to growth and reproduction in perennial animals living in a seasonal environment was first studied by Kozłowski and Uchmański (1987), but only for the very specific case of constant mortality within a favourable season, with reproduction occurring just at the end of the season. Kozłowski and Teriokhin (1999) used the Pontryagin Maximum Principle (Pontryagin *et al.* 1962), which allowed them to include cases with mortality dependent on both the age of the organism and the season.

According to Kozłowski and Teriokhin's (1999) model, first reproduction appears at different ages and sizes, depending on winter and summer lengths, winter and summer mortality, and the size-dependence of the production rate (Fig. 6 and 7). Year after year following maturation, a larger and larger fraction of resources is allocated to reproduction, which means that growth slows down and the size approaches an asymptote. Asymptotic size and the proportion of growth before and after maturation also depend in perennial animals on mortality (Fig. 7; see Kozłowski and Teriokhin 1999 for more

examples). The general rule is that asymptotic size is lower under strong mortality, but the fraction of growth realized after maturation is especially sensitive to winter mortality. Species with low summer mortality and high winter mortality realize a large part of growth after maturation (Kozłowski and Teriokhin 1999). The growth curve is step-like (Fig. 8 A), but if each year is represented by one data point, the growth curve closely resembles Bertalanffy's growth curve (Fig. 8 B and C), albeit for reasons completely different from those suggested by von Bertalanffy (1957). In Bertalanffy's model, an increase of the catabolism rate faster than that of the anabolism rate (with respect to body size) is the mechanism responsible for slowing down growth, and equalization of these two processes defines the maximum size (Fig. 9 A). However, there is no surplus of anabolic over catabolic processes at the end of growth, which makes this model unrealistic, because producing offspring tissues represents anabolic processes. According to optimal resource allocation models, increasing the fraction of resources going to reproduction is responsible for slowing down growth, and the size at which it is optimal to allocate all surplus resources to reproduc-

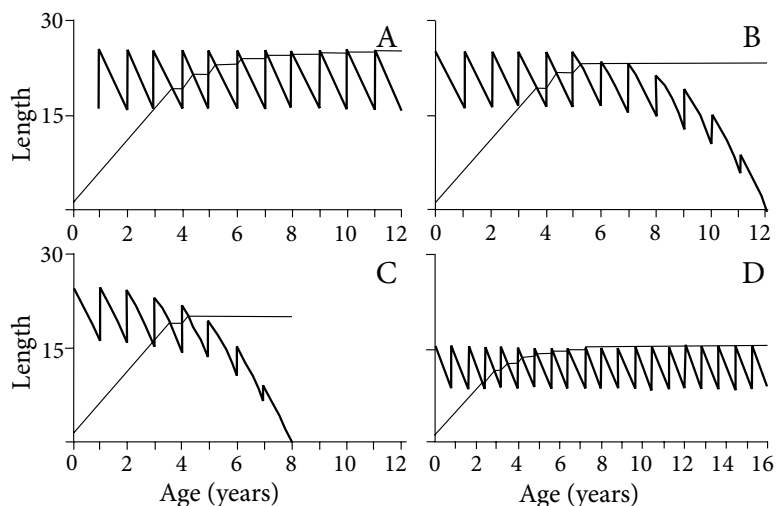


Fig. 6. The effect of life span and favourable season length on the optimal switching curve (thick line) and growth curve (thin line). Instantaneous mortality is 0.4 per year in the favourable season and 0.5 in the unfavourable season. Favourable season length is 50% of the year for figures A–C and 30% for D. Life span is unlimited for A and D, 12 years for B, and 8 years for C. Production rate is expressed by $30w^{0.67}$, where w is body size in energy units. Winters are cut out of the time axis. From Kozłowski and Teriokhin (1999).

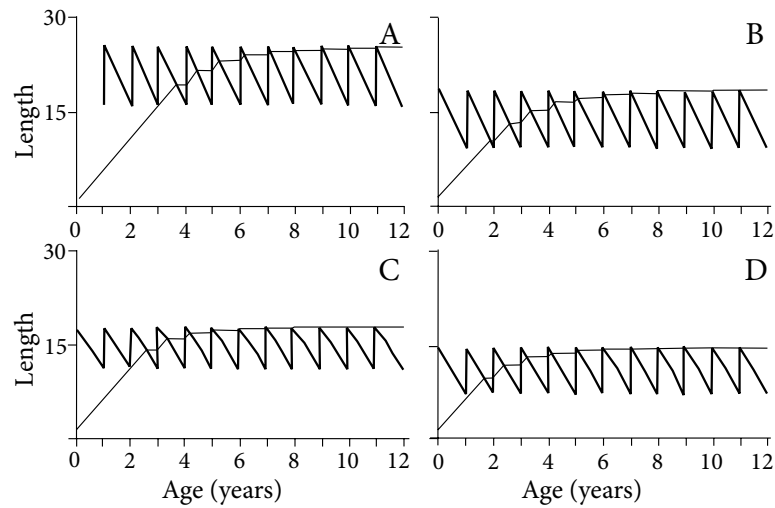


Fig. 7. The effect of mortality on the optimal switching and growth curves. Instantaneous mortality is (A) 0.4 per year in the favourable season and 0.5 in the unfavourable season, (B) 0.4 and 1.0, (C) 0.8 and 0.5, and (D) 0.8 and 1.0. Other parameters as for Fig. 6. From Kozłowski and Teriokhin (1999).

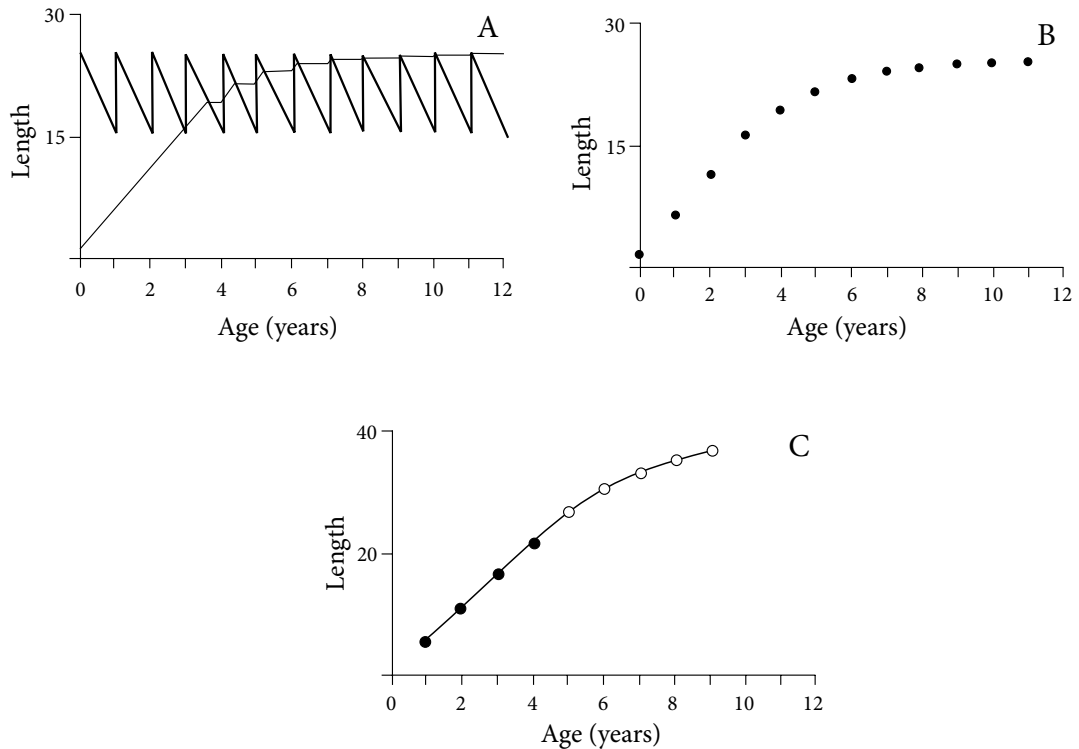


Fig. 8. A – Fig. identical to Figs 6 A and 7 A, showing step-like growth curve. B – Points showing body length when size is measured once per year, just before winter. C – Growth curve in fish *Chondrostoma nasus* in Wisłoka River, with closed symbols showing body length before maturation and open symbols showing body length after maturation; slowing of growth after some resources are diverted to reproduction is clearly visible. Data for Fig. C courtesy of M. Klich and A. Reczek – unpublished.

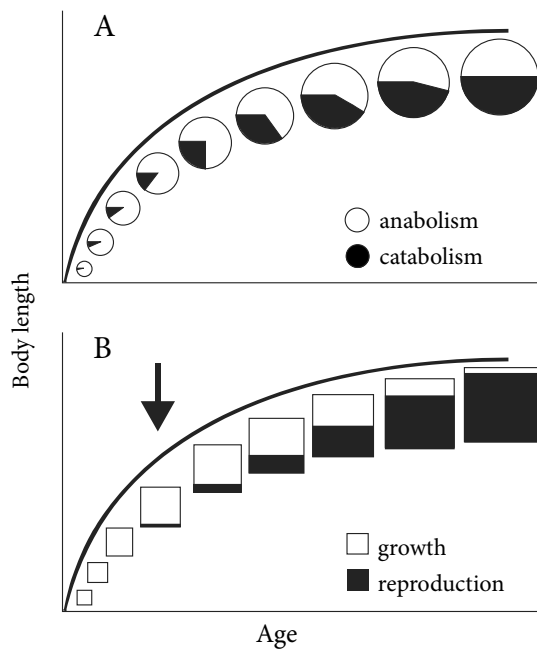


Fig. 9. In the Bertalanffy model (A) the growth rate of an individual equals the difference between its anabolism and catabolism rates (white and black areas, respectively), both of which increase with size and age; catabolism rises faster than anabolism does, leading to a decreasing-with-age growth rate which finally stops when catabolism offsets anabolism (black area equals white area). For body length, Bertalanffy's equation has the form $L_t = L_{max} (1 - \exp(-Kt))$, where L_t is body length at age t and K is the rate at which the asymptotic length L_{max} is approached. In the optimal resource allocation model (B) the amount of available resources (square) increases as an organism grows; slowing growth with age results from the optimal strategy – allocating an increasingly bigger fraction of the resources into reproduction than into growth (black and white areas, respectively). The resulting growth curve resembles the Bertalanffy curve. From Czarnołęski and Kozłowski (1998).

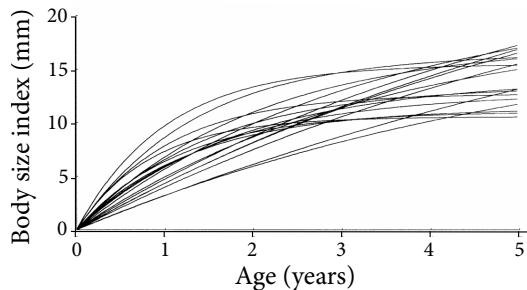


Fig. 10. Bertalanffy's growth curves fitted to data on age and body size index from 19 zebra mussel populations, mostly from northern Poland. The index is the cube root of the product of shell length, width and height. From Czarnołęski *et al.* (2003).

tion defines maximum size (Fig. 9 B). Bertalanffy's growth curve may differ substantially between populations or change through time quickly, as shown for zebra mussels (Fig. 10; Czarnołęski *et al.* 2003, 2005). As presented by Kozłowski (1996b), the resulting Bertalanffy-like growth curves show so-called Beverton-Holt (Beverton and Holt 1959) patterns: the mortality rate is positively correlated with Bertalanffy's growth constant, the mortality rate is negatively correlated with asymptotic length, and the growth constant is negatively correlated with asymptotic length. Such patterns have been described for fishes

(Fig. 11; Beverton and Holt 1959, Beverton 1992), reptiles (Shine and Charnov 1992, Shine and Iverson 1995) and zebra mussels (Czarnołęski *et al.* 2003, 2005).

In seasonal environments, the age and time scales are partially decoupled, and optimal placement of such events as laying clutches may have a crucial influence on fitness. Dynamic programming allows the researcher to include biological details almost without limits, and also to study the effect of stochasticity of environmental conditions. However, this application of dynamic programming still awaits broader exploitation.

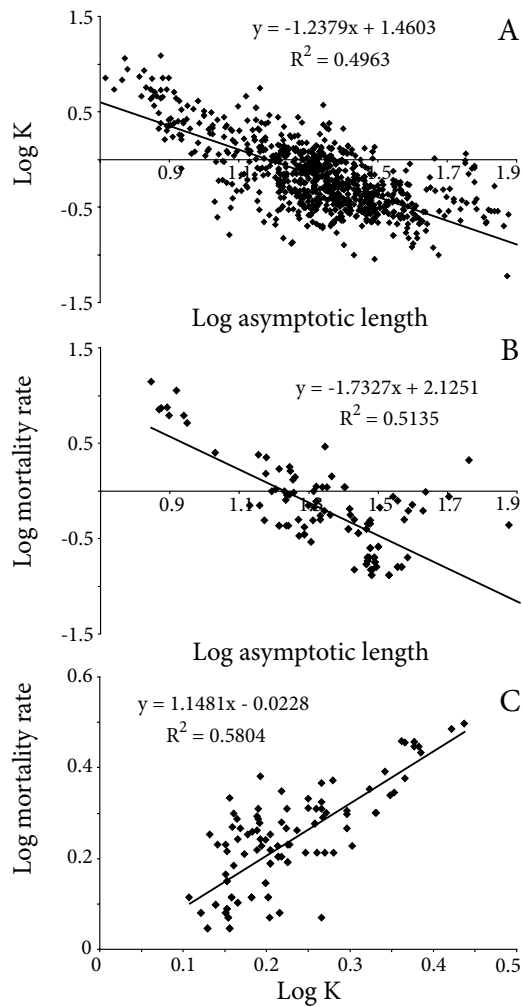


Fig. 11. Beverton-Holt pattern in fishes of the order Clupeiformes. A – negative relationship between two parameters of Bertalanffy's growth curve: growth constant K and asymptotic length L_{max} . B – negative relationship between the mortality rate and asymptotic length. C – positive relationship between the mortality rate and constant K . Data from FishBase (Froese and Pauly 2005).

5. SLOW VS. FAST AND WASTEFUL VS. FRUGAL LIFE STRATEGIES

5.1. Fast and slow life

The production rate increases with body size to a certain size, usually slower than linearly, and then may decrease. Thus there are diminishing returns of size increase, which means that the derivative of the production

rate with respect to body size is a decreasing function. An animal growing for a longer time to a larger size (but not exceeding the size determining the peak production rate) will be able to produce offspring at a higher speed, or more precisely, to allocate resources to offspring production at a higher rate. However, the longer growth phase and delayed maturation mean a lower probability of survival to reproduction, as discussed earlier. Together with the diminishing returns of enhanced productivity, it produces an optimal size maximizing the lifetime reproductive allocation, usually placed at a body size much smaller than the one maximizing production. Higher returns from the size increase are necessary to compensate heavy mortality, which means that the optimal size decreases when the mortality risk increases. This dependence of optimal size on mortality defines the slow-to-fast life continuum. Promislow and Harvey (1990) coined the term, but without precisely distinguishing between the role of mortality and the role of physiological differences between species (see next subsection).

An interesting phenomenon is expected if the production rate has a maximum with respect to body size and the mortality risk decreases rapidly with size. In such a case, the optimal size (defined by condition 3) may be larger than the one for which production is at maximum. Such gigantic species may have no natural enemies. Escaping predation this way has a side-effect, that is, decreased production, and low offspring production as a result. Species with such a strategy are very sensitive to additional sources of mortality, for example hunting by man. It is very likely that the gigantic mammals inhabiting North America disappeared after colonization of this continent by humans because intense hunting shifted the optimal size to the left of the size maximizing the production rate. This new optimum was not easily accessible from the old one placed at the gigantic size.

Even in a group of species having exactly the same functions defining the dependence of the metabolic and resource acquisition rates on body size, we still expect variability of optimal body sizes resulting from differences in mortality risk (Kozłowski 1992, Charnov 1993). Species with heavy mor-

tality are expected to be relatively small, to mature young and to die early. Species with a lower mortality risk are expected to grow longer to a relatively greater size, to mature late and to die late. The word “relatively” is used here, because mortality co-acts with the production rate in defining optimal life history features, as described in the next subsection.

5.2. Wasteful and frugal strategies

Animals of the same size may differ substantially in metabolic rates even between closely related species. As suggested years ago by Szarski (1983), cell size may be responsible for these differences: living things of the same size can be built of a smaller number of large cells or a larger number of small cells. Cell size has a very strong effect on the metabolic rate (e.g. Goniakowska 1973, Gregory 2001), because a large part of metabolic costs is used for preserving ionic gradients on cell membranes (Goniakowska-Witalinska 1976, Else and Hulbert 1987, Porter and Brand 1993) and the surface-to-volume ratio is higher for small cells. Szarski (1983) coined the term “wasteful strategy” for animals built of small cells, having a high metabolic rate, and able to process food rapidly. A wasteful strategy allows high offspring production under good food conditions, but also makes survival impossible in poor food conditions. The opposite strategy, which Szarski (1983) called the “frugal strategy”, is characterized by having large cells, a low metabolic rate, and a slow rate of food processing. Animals with such a strategy cannot produce offspring very rapidly even in good food conditions, but due to their low living costs can survive with little food. The frugal strategy also permits survival in hypoxic conditions. Obviously there is a full continuum between frugal and wasteful extremes.

Szarski (1983) noticed a correlation between cell size and the total amount of coding and non-coding DNA. His finding has been supported by more data, especially in recent years (Gregory 2001). Although the mechanism is still highly hypothetical, DNA amount is one of the determinants of nucleus size, nucleus size is one of the determinants

of cell size, and cell size is one of the determinants of specific metabolic rate. As a result, the correlation between DNA amount and metabolic rate is significant in mammals and birds (Vinogradov 1995, 1997), and probably also in many other groups. As shown by Kozłowski *et al.* (2003a), these relationships may underlie metabolic rate scaling.

Examples of frugal and wasteful strategies can be found among amphibians and fishes. Anurans have small cells and small genomes, whereas urodels often have very large cells and huge genomes (Roth *et al.* 1994, Jockusch 1997). Some miniature salamanders, especially from the group *Bolitoglossini*, consist of a relatively low number of very large cells, and have some very simplified organs including their brains, a very low metabolic rate, and slow development (Roth *et al.* 1994, 1997). Lungfishes, which survive long periods under hypoxic conditions, have very low metabolic rates and the largest genomes of all vertebrates (Gregory 2001), indicating very large cells.

Selective forces toward a size increase accompanied by a rapid or by a slow increase of metabolic rate are quite obvious. The second case may be exemplified by endangerment by gape-limited predators: an increase of size without a drastic increase of living costs may save life and increase fitness this way. The simplest mechanical way to increase size is through enlargement of the amount of non-coding DNA. Thus so-called “junk DNA” may often be junk only from the point of view of information content, but may play a fundamental role in shaping cell size/metabolic rate. A decrease or increase of DNA bulk may be a side-effect of very strong selection acting on body size.

The position on the wasteful-frugal strategy continuum, together with food availability, determines the size-dependence of the production rate $P(w)$, being the difference between the resource acquisition $A(w)$ and metabolic $R(w)$ rates. As shown in previous sections, the size-dependence of the production rate affects the optimal adult body mass. Thus, size in a given species is strongly affected by its position on the wasteful-frugal axis. In other words, body mass cannot be treated as an independent variable for the metabolic rate and resource acquisition rate,

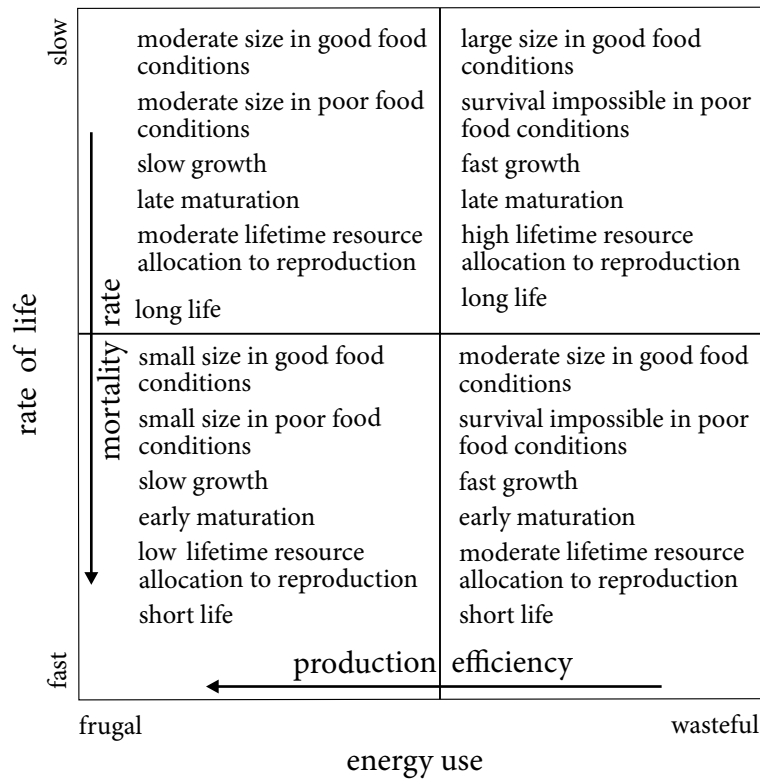


Fig. 12. Life history traits expected for the corners of frugal-wasteful and fast-slow continua. From Kozłowski *et al.* (2003b). See Section 5 for more detailed explanation.

as these traits co-vary with body size under the pressure of natural selection. The mortality risk is another factor strongly influencing the optimal body size, as discussed in the previous subsection. These two factors form a ...

5.3. ... two-dimensional array of life history strategies

Fig. 12 shows the life history traits expected at the frugal-fast, frugal-slow, wasteful-fast and wasteful-slow corners of the two-dimensional continuum. Large sizes are expected in animals having a slow life (low mortality) and a wasteful strategy. Such animals must live under good food conditions; they cannot live in permanently poor food conditions, although many mechanisms for surviving a temporary lack of resources are known: aestivation, hibernation and so on. Small sizes are expected in animals having a fast life (high mortality) and frugal strategies,

especially when they live in poor food conditions. Animals representing frugal strategies can produce offspring on poor resources, albeit slowly.

The terms “small size” or “large size” must be considered relative, characteristic for a given systematic group. A large spider is no bigger than a small mammal. We must also remember that giants can occur in a systematic group under strong negative size-dependence of mortality, as described earlier.

At this point some readers may recall the concept of r- and K-selection (MacArthur and Wilson 1967, Pianka 1970). There are similarities in the organisms’ features predicted under this concept and those shown in Fig.12. The two-way classifications (fast-slow and frugal-wasteful) presented here, however, are not refined versions of the r- and K-selection concept based on logistic equations, and assuming that r-selected organisms represent populations usually in an expanding phase, whereas K-selected organ-

isms represent populations usually at equilibrium. The classifications described in this section represent populations mostly at equilibrium. It is clear that the full spectrum of features traditionally assigned to *r*-selected organisms can be represented in stable populations. Although the features are similar, the causal system is different. For example, early maturation is caused in stable populations by a high mortality rate, but by the rate of population growth in expanding populations. In exponentially expanding populations age at maturity is completely independent of mortality, because high mortality rate is compensated by decrease of intrinsic population growth rate, and these two rates act in an additive way.

6. DISCUSSION

It was always clear that a perfect organism should mature early, live long (possibly forever) and reproduce at an enormous pace. Such a state is not possible because of the tradeoffs occurring in life history (Stearns 1992). Tradeoffs are what make life histories interesting. There are two traditions in the study of tradeoffs (Kozłowski 1991). In the first one, purely demographic, it is assumed that a change of one demographic parameter affects another demographic parameter. That is, a tradeoff is assumed between two demographic parameters. For example, increased reproduction impairs either future reproduction or survival. The second approach, represented in optimal allocation models, can be called physiologically demographic: the change of an organism's state is considered between the two parameters. Alteration of one demographic parameter changes the organism's state and in this way affects another demographic parameter (e.g. future reproduction or survival). For example, increased reproduction may slow down growth and in this way decrease body size or diminish storage. An organism may also save on its immune system and increase reproduction at the cost of survivability or future reproduction. Many other such tradeoffs can occur.

The second tradition, represented in this paper, gives a chance to integrate physiological ecology and the demographic approach. The tradeoffs are deduced from physiologi-

cal and behavioural properties of organisms, often studied for other purposes. Allocation models seem especially appropriate for working on life history tradeoffs, because they focus on very basic energetic limitations of organisms. A great deal of knowledge has accumulated on so-called ecological bioenergetics. Studies in this area have been done mostly without having in mind maximization of lifetime reproductive success. This is why the results usually cannot be applied directly in allocation models, although some of them can be adopted.

Both classes of models require some fitness measure, that is, a quantity to be maximized when optimal values of life history parameters are achieved. Although fitness is only a problem-solving tool and no general definition of the fitness measure is conceivable (Stearns 1992), the fitness measure for a given evolutionary problem cannot be arbitrary. This is because applying different fitness measures to the same problem often leads to different and sometimes even contradictory results (Mylius and Diekmann 1995, Pasztor et al. 1996). As suggested by Kozłowski (1999), the question is usually not "Is this or that measure correct?" but rather "What is the scope of applicability of a given model with a given fitness measure?" In this sense the choice of fitness measure should depend on the population's properties, especially on the character of density-dependent processes (Mylius and Diekmann 1995). In the models presented in this paper, lifetime reproductive allocation was taken as a measure of fitness. Under constant offspring size, which can be the subject of optimization as well (see Section 3), this measure is equivalent to the expected lifetime offspring production, also called net reproductive rate R . Such a measure is proper if populations are numerically stable and regulated by density-dependence early in life, for example through migration of juveniles (Kozłowski 1993, Mylius and Diekmann 1995). As shown by Benton and Grant (2000), in a stochastic environment, net reproductive rate R gives results closer to an evolutionarily stable strategy than the Malthusian parameter r does. Net reproductive rate is a completely unrealistic fitness measure for populations spending most of their

history in an expanding phase. The Malthusian parameter, called also the intrinsic population growth rate r , is the best candidate in such a case. The Malthusian parameter is the solution to the Euler-Lotka equation

$$1 = \int_0^{\infty} e^{-rt} l(t) m(t) dt \quad (5)$$

where t means age, $l(t)$ the probability of surviving to age t , and $m(t)$ fecundity at age t , with only female offspring taken into account. Maximization of R and r leads to completely different results on the role of mortality (Taylor and Gabriel 1992, Mylius and Diekmann 1995, Pasztor *et al.* 1996). As shown in this paper, if R is maximized, mortality has an enormous effect on optimal resource allocation, and as a result on life history traits such as age and size at maturity, and on the parameters of growth curves. On the other hand, if r is maximized, the mortality rate is not important. This is because r and the mortality rate act together additively, and higher mortality decreases r , making the sum of these two constant. Thus we should not expect differences in the mortality rate to be responsible for variation in life history traits in populations that are almost always in an expansion phase, with fast collapses occurring after depletion of resources.

The conclusion from these considerations is simple: models maximizing the lifetime reproductive allocation, a surrogate of lifetime offspring production, do not give universal predictions, but their range of applicability is broad enough to make them valuable, especially since they integrate demography with ecophysiology. There is a vast amount of evidence that mortality does shape life history traits (e.g. Charnov 1993, Reznick *et al.* 1996, Conover and Munch 2002, Czarnołęski *et al.* 2003, 2005). For populations regulated in a way that is not amenable either to R nor r as a fitness measure, the mortality rate plays a role in the evolution of life history traits, although less pronounced than in fully stable populations.

When we observe between-population differences in life history traits fitting predictions of optimization models, two possible mechanisms are possible: genetic differences between these populations, or phenotypic plasticity in response to some environmen-

tal clues. A mixture of these two mechanisms is likely as well. The important question of which mechanism prevails will be answered soon with molecular genetics methods. The mechanism based on phenotypic plasticity underlies so-called inducible defence, so common in aquatic environments in which chemical signals of a predator's presence can easily propagate (for review see Tollrian and Harvell 1998). To my knowledge, optimal resource allocation models have not been yet applied to inducible defence, although such an application is very promising and not very difficult to try, at least for the models described in Section 3. An inducible defence in its morphological form (e.g. Pijanowska 1991, Arnqvist and Johansson 1998, Boersma *et al.* 1998) or behavioural form, for example as represented by vertical or horizontal migration of plankton (e.g. Gliwicz 1986a, 1986b, Dawidowicz *et al.* 1990, Pijanowska 1993, Jachner 1995), is adopted to decrease mortality and has an adverse effect on production through either increased metabolic costs (e.g. cost of migration) or decreased acquisition of resources (e.g. through spending part of the day in less food-abundant places). There are also numerous examples of changes in life histories induced by predators (Riessen 1999, Slusarczyk 2001, Sakwinska 2002).

A thorough understanding of life history evolution is possible, at least at present, only for aseasonal environments (Section 3). Such environments may look like an abstraction to field biologists. There are two reasons to develop models for such conditions. First, the history of science (especially of physics) teaches us that it is very often fruitful to study simple systems first, then introduce more complexity step by step, after gaining deeper understanding of a system. Second, for short-lived multivoltine organisms, seasonality is unimportant for several generations, and only the last one, living before winter, has to "solve" the additional problem of when and how to produce a diapausing stage. Models of life history optimization in seasonal environments, although at a very preliminary stage at present, give us at least a qualitative insight into life history evolution. We understand why animals switch back and forth to growth and reproduction year af-

ter year, and why their growth slows down. Mistaken concepts that animals mature at the size for which growth slows down (e.g. Froese and Pauly 2005) can be replaced with the opposite view that growth slows down because animals allocate some energy to reproduction. Froese and Pauly (2005) argue that the concept of energy drainage for reproduction as the reason for slowing down growth should be rejected because smaller species attain a higher fraction of growth before maturation than large species. According to optimal resource allocation models there is no reason for the same fraction of growth to be realized before maturation: the asymptote is sensitive to the general mortality level, and the fraction of growth attained after maturation is sensitive to the difference between winter and summer mortality. Species with a large asymptotic length have low yearly mortality (Fig. 11 C), but if mortality is concentrated mainly in winter, the ratio of size at maturity to asymptotic size is low (Kozłowski and Teriokhin 1999).

7. CONCLUSIONS

Except for the extreme case of populations undergoing cycles of exponential growth and collapse, life history traits are co-shaped by the size-dependence of the mortality rate m and the size-dependence of production rate P , being the difference between the rate at which organisms acquire and spend resources ($A - R$). This is the main reason for the diversity of life histories in nature. In an idealized world the dependence of the m/P (or equivalently P/m) ratio on body size defines initial size, adult size and the growth rate (Section 3). The P/m ratio as a function of body mass may have a complex shape, which adds to the diversity of life histories, especially if we take into account that the production rate depends also on foraging behaviour, especially risk-avoiding behaviour. Seasonality adds much to the diversity of life histories (Section 4). Allocation to repair, with its optimal level dependent on external causes of mortality, is another confounding factor (Cichoń 1997).

Although life histories must be diverse, they are not chaotic. There are good correlations between different life history traits,

predicted by life history theory based on optimal resource allocation. For example, age at maturity correlates with mortality (Promislow and Harvey 1990) and with life expectancy (Harvey and Zammuto 1985, Sutherland *et al.* 1986) in mammals. There is a correlation between age and size at maturity in squamate reptiles (Promislow *et al.* 1992), and age at maturity correlates with mortality in this group (Shine and Charnov 1992). The Beverton-Holt pattern (Section 4) is another example of restrictions imposed on the variability of life history traits, and optimal resource allocation models have explained this pattern very well. As shown in Section 5 and Fig. 12, life history traits can be classified in a two-dimensional array with the axes defined by a fast-to-slow continuum dependent on the mortality risk, and a wasteful-to-frugal continuum dependent on physiological properties relying on cell size, in turn relying on DNA amount. Clearly, ecological, physiological and even cytological features integrate in defining optimal life history traits. Should we then be surprised by such high diversity?

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