

## Evolution of resource allocation between growth and reproduction in animals with indeterminate growth

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### Abstract

We review the recent theoretical developments explaining the evolution of age-schedules of reproduction in animals with indeterminate growth. Indeterminate growth, i.e. growth that continues past maturation and may continue until the end of life, is characteristic for a large number of invertebrate taxa (e.g. clams, cladocerans and crayfish) and 'lower' vertebrate taxa (e.g. fish, amphibians, lizards and snakes). Many plants also exhibit indeterminate growth, and we liberally include studies focused on plants when they can be interpreted in terms of animal life histories. We focus on different measures used to determine the fittest life histories, on indeterminate growth as a problem of resource allocation and on the effects of environment to the evolution of the resource allocation schemes.

### Introduction

Animals with indeterminate growth experience a life history trade-off in resource allocation between reproduction and growth throughout their lives (Stearns, 1992). Because fecundity usually increases with body size, there is also a trade-off between current and future reproduction in animals with indeterminate growth, even in the absence of survival costs of reproduction. Moreover, growth rates also tend to be size-dependent (Ware, 1980; Taylor & Gabriel, 1993). Allocation to reproduction within a given season has a profound influence on growth and fecundity in the future. Furthermore, resource allocation is also affected by 'environmental factors', such as changes in the availability of resources and the risk of dying. In general, these factors are age-, stage- or size-dependent, reflecting general ecological interactions such as

intra- and interspecific competition, predation and parasitism.

Resource allocation models offer an approach to study the evolution of resource allocation and age-schedules of reproduction in organisms with potentially indeterminate growth (Kozłowski, 1991). In these models reproductive output within a season is determined by the allocation decision, together with the amount of resources available. However, in simple models it often turns out that determinate – instead of indeterminate – growth strategy is optimal (see reviews by Kozłowski (1992) and Perrin & Sibly (1993), and an article by Engen & Sæther (1994)). Therefore, a fundamental question is why does indeterminate growth exist?

An individual must make an allocation decision every time it reproduces. Therefore, the lifetime allocation strategy is a complex trait. Mathematically lifetime allocation strategy has to be treated as a multidimensional vector, or as an infinite-dimensional function. Finding the optimal allocation strategy can be a daunting task, and many simplifying assumptions are necessary in order to keep the problem tractable for the analysis. One way to circumvent these difficulties is to assume that only age at maturity is evolving, and the resource allocation thereafter follows some fixed, predetermined

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rule, without specifying the factors that are responsible for indeterminate growth. The allocation strategy becomes one-dimensional, which makes the analysis simpler. In such a model, it is much easier to take into account ecological complications, such as density-dependent environmental feedback.

We begin by reviewing the methods used to determine the fittest life histories in general. We then discuss the problem of indeterminate growth, and review the effects of environment to the evolution of the resource allocation strategies.

### Measuring fitness

In order to formally analyse evolutionary processes one needs to identify the life history strategies that are favoured by natural selection (Parker & Maynard Smith, 1990). Until recently, the standard procedure was to assume that evolution maximizes some density-independent fitness 'measure' (Roff, 1992; Stearns, 1992). The most common measures used are expected lifetime fecundity,  $R_0$ , and intrinsic rate of increase,  $r$ , the latter defined by the Euler-Lotka equation. When applied to an identical life history model, density-independent  $R_0$  and  $r$  usually give different predictions for optimal life history traits. Evolution should not be driven by different and possibly conflicting rules, and thus, it has long been puzzling to ecologists and geneticists which one of these fitness measures, if any, should be regarded as the correct one (Kozłowski, 1993; Pásztor *et al.*, 1996). Furthermore, what is the relation of these fitness measures to theoretically sounder concept of invasion fitness, a population dynamics version of Maynard Smith & Price's (1973) evolutionarily stable strategy (ESS) concept (Metz *et al.*, 1992; Rand *et al.*, 1994; Ferrière & Gatto, 1995). Although the answers have been available for some time (Hastings, 1978; Charlesworth, 1994), Mylius & Diekmann (1995) and Metz *et al.* (1996a) finally clarified the problem. They showed that the fitness maximization approach may coincide with the invasion fitness concept only if population size is stable and if environmental feedback is one-dimensional – in practical terms, if there is only one density-dependent factor influencing population dynamics.

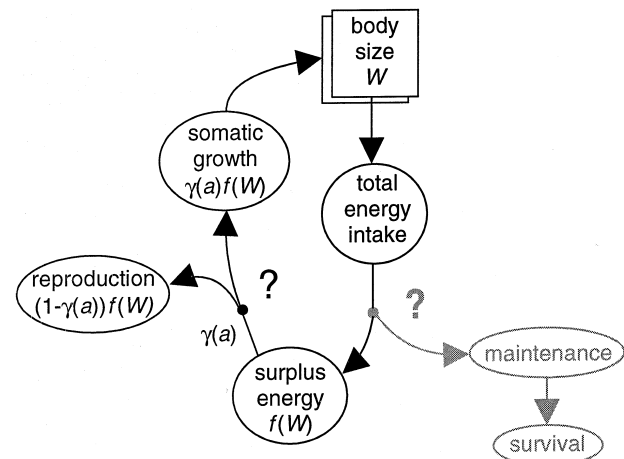
When environmental feedback is one-dimensional, the valid optimization criterion depends on the detailed form of the environmental feedback (Mylius & Diekmann, 1995; Metz *et al.*, 1996a). For example, if density dependence affects reproductive success only in a multiplicative manner (either because of density-dependent fecundity or because of density-dependent newborn survival), then, and only then, the valid optimization criterion is  $R_0$ . Similarly,  $r$  is valid if the only effect of density dependence is to increase mortality in all age-classes uniformly. A corollary result is that selecting a certain fitness measure means assuming implicitly a certain way in which density dependence affects the individuals in the population

under study. In particular, it implies assuming one-dimensional population regulation, which rules out the possibility of frequency-dependent selection and stable phenotypic polymorphisms (Heino *et al.*, 1998). Therefore, when interpreting the studies which have applied a certain density-independent fitness measure, it is important to recognize that the implicit assumptions may have strongly constrained the results and, furthermore, may be incompatible with the original problem.

### Evolution of lifetime reproductive allocation

Lifetime reproductive allocation can only be understood in terms of resource or energy allocation between reproduction and other competing needs, such as maintenance and growth (Fig. 1). Usually it is assumed that maintenance has priority over other needs. Empirical evidence from animals with indeterminate growth supporting this assumption is provided by Jokela & Mutikainen (1995). Energy in excess of maintenance is 'surplus' energy, which can be allocated between growth and reproduction (Ware, 1980; Roff, 1983). Simultaneous allocation of energy to growth and reproduction results in indeterminate growth. In perennial species it is also possible that indeterminate growth results from seasonal switching between allocation to growth only and allocation to reproduction only.

Indeterminate growth pattern implies that individuals must decide on how to allocate energy between growth and reproduction over all ages. The resulting optimization problem can be solved with help of Pontryagin's maximum principle (e.g. Perrin & Sibly, 1993), dynamic programming (e.g. Mangel & Clark, 1988), genetic



**Fig. 1** A schematic representation of an energy allocation model. Usually only allocation of surplus energy between reproduction and somatic growth is studied, while allocation to maintenance is simply ignored. Allocation to somatic growth results in positive feedback on body size.

algorithms (e.g. Sumida *et al.*, 1990) or simulated annealing (e.g. Blarer & Doebeli, 1996), provided that a valid optimization principle is available (see previous section). In stochastic environments, where simple optimization is not possible for structured models, individual-based models could be used to find out the allocation strategies favoured by selection. However, we are not aware of any such attempts.

The first models of allocation between growth and reproduction were focused on annual plants. In these models it was noticed that determinate growth patterns are always evolutionarily optimal (Cohen, 1971, 1976). This finding prompted the search for factors that could favour indeterminate growth. Cohen (1971, 1976) proposed that variable season length may select for graded change from allocation to growth to allocation to reproduction. Indeterminate growth could be seen as a special kind of bet-hedging strategy. This hypothesis was later confirmed theoretically by King & Roughgarden (1982), Amir & Cohen (1990) and Taylor & Gabriel (1993). Taylor & Gabriel (1993) included size-specific predation into the model and found that the highest level of adult growth occurred if mortality risk decreased with size.

The second explanation for indeterminate growth patterns is diminishing marginal returns from reproductive investment (Taylor *et al.*, 1974; León, 1976; Myers & Doyle, 1983; Sibly *et al.*, 1985). These models assume either that the cost of a single offspring increases as the investment for reproduction increases (that is, fecundity is a concave-down function of reproductive investment, at least for high levels of investment), or mortality is a concave-up function of reproductive investment. Reproductive investment is here measured either as the absolute investment of resources, or as the investment relative to the surplus energy. However, in most plausible mechanisms that could result in diminishing returns of reproductive investment, it is the reproductive investment relative to the current body size that matters (Heino & Kaitala, 1996). For example, in freshwater clams, increasing the volume of the clam larvae inside gill chambers interferes with feeding and respiration, which may incur costs in terms of reduced energy intake of the clam (Tankersley & Dimmock, 1993). Large individuals are able to brood more offspring than small individuals without a significant increase in the costs of brooding. Therefore, it is the investment relative to the current body size that matters. Similarly, high volume of eggs may impair the hydrodynamic properties of the fish (Wootton, 1990). Also the mechanisms resulting in diminishing returns from reproductive investment proposed by Myers & Doyle (1983) are best interpreted in terms of trade-offs between relative mass of offspring (or relative volume occupied by gonads) and mortality or fecundity.

Structural constraints may also be operating. Growth rate of the reproductive organs may be limited – it is feasible, especially when reproductive organs are small in

the initial stages of development, that they cannot absorb all surplus energy available (Kozłowski & Ziółko, 1988). Unless energy is stored for later use, or just wasted, indeterminate growth will result. Limitation of space for carrying eggs or larvae (Myers & Doyle, 1983; Perrin *et al.*, 1987; Heino & Kaitala, 1996) can also be regarded as a structural constraint. However, it is not a constraint in the strict sense because it should be possible to increase volume available for offspring, even though such increase would incur some costs. Hermit crabs often face space limitation, but it works in reverse: larger gastropod shells allowing body growth are often in short supply, which may force hermit crabs to allocate more energy to reproduction (Bertness, 1981).

Indeterminate growth was found to be optimal if both production and mortality rates increased with body size in simulations of a *Daphnia* model by Taylor & Gabriel (1992). Perrin *et al.* (1993; see also Perrin & Sibly, 1993) proved the result analytically; adult growth can also occur if both production and mortality decrease with size. Both of these situations may apply in nature.

In perennial species, seasonality of resource acquisition and reproduction may account for indeterminate growth: the optimal allocation pattern may include a number of seasons during which early season is devoted only to growth, and late season only to reproduction (Kozłowski & Uchmański, 1987). However, this result rests on the assumption that growth occurs before reproduction, such that the benefits of growth are received during the same season, before any mortality could take place (Doebeli & Blarer, 1997). If the timing of reproduction and growth is reversed, determinate growth results.

The above models assume that no somatic tissues are lost between growth seasons, which is a valid assumption for many animals. In many plants, however, parts of somatic tissues are lost during the winter, and spring regrowth starts with resources stored in stems and roots. Pugliese & Kozłowski (1990) showed that there is a critical level of proportion of persistent tissues below which no indeterminate growth should occur.

Engen & Sæther (1994) reported that age-specific mortality may favour indeterminate growth, if mortality decreases with age. However, this explanation is probably seldom applicable – usually mortality risk depends on size rather than on age. Although age and size are correlated, only size is under evolutionary control.

Most of the papers cited in this section do not consider density dependence, or make very simplifying assumptions on density dependence by using some density-independent fitness measure (see previous section). In rare occasions in which more than one fitness measure has been applied, different fitness measures yielded allocation strategies which were qualitatively similar (Blarer & Doebeli, 1996; Fiksen, 1997; Heino and Kaitala, personal observation). Maximizing  $r$  gave usually better fit with data than  $R_0$  in a model combining vertical migration and energy allocation in *Daphnia* (Fiksen,

1997). Simple density dependence as such does not select for indeterminate growth (Myers & Doyle, 1983; Vance, 1992); this is evident from the fact that the use of a certain fitness measure already implies a certain form of density dependence, i.e. one-dimensional environmental feedback.

Theories on resource allocation between growth and reproduction remain almost completely untested. Indeed, we are aware of only one experiment. Perrin (1989) set up an experiment to test whether size constraint was restricting reproduction in a cladoceran. The results of the experiment were equivocal, although more sophisticated theory might have shed new light on them. Bertness (1981) has shown that lack of larger gastropod shells may restrict body growth in hermit crabs and force them to allocate energy to reproduction instead. There is some empirical support for the hypothesis that trade-off between feeding and reproductive investment restricts reproductive allocation in freshwater clams (Tankersley & Dimock, 1993). Kozłowski and colleagues, using energy allocation models in which indeterminate growth results from seasonality, have derived predictions which match observed data very well: Kozłowski & Uchmański (1987) applied the model to two mollusc and one fish species, and were able to achieve a close agreement between observed and predicted growth curves. Further, Kozłowski & Teriokhin (1999) suggest that von Bertalanffy growth curves, which describe growth of many animals, result from optimal energy allocation in seasonal environments. Kozłowski's (1996) model also predicts interspecific life history patterns ('invariants') which are similar to those discussed extensively by Charnov (1993, 1997). However, alternative hypotheses have not yet been considered.

In summary, indeterminate growth can be favoured by ecological factors (varying length of growing season in annuals, seasonality as such in perennial species), or physiological factors (trade-offs and constraints limiting reproductive effort), or a combination of both of these factors (size-dependent mortality and production rates both increasing or decreasing).

Assuming that indeterminate growth is maintained by some factor, the theory allows a few generalizations. First, fraction of surplus energy allocated to growth (or fraction of season devoted to growth) usually decreases with age. Second, increasing mortality after newborn stage selects for earlier maturation and for decreased allocation to growth at any given age after maturation.

### Optimal age at maturity

The question of optimal age at maturity is a special case of the lifetime resource allocation problem. The simplification that energy allocation after maturation follows a predetermined rule makes the models more tractable from the analysis point of view. In particular, it is easier

to incorporate more complex and realistic ways of environmental feedback than in 'complete' allocation models. These simplified models implicitly assume that selection does not change the allocation rule after maturation. While this assumption obviously may be wrong, it may not be too unrealistic if strong nonlinear trade-offs effectively constrain the maximum reproductive effort. Nevertheless, it is the price which has to be paid for increased tractability.

Only few models based on energy allocation have been used in studying the evolution of age at maturity in animals with indeterminate growth. All these models assume the same allocation rule after maturation: the allocation to reproduction is such that the ratio of weight of sexual products to weight of the rest of the body is constant. In fisheries literature this measure is known as gonadosomatic index (GSI; Roff, 1992). Many fish obey GSI that is constant or slightly increases with size (see Table 1 in Roff, 1983). In the case of freshwater clams, relative glochidia mass is an analogous but more easily quantified measure. Optimal relative glochidia mass tends to increase with age in the clam model (Heino & Kaitala, 1996).

Roff (1983) developed a growth model based on energy allocation, and applied the model to the American plaice. Immature plaice had a constant growth increment per year, which implies that surplus energy is a certain function of size. Assuming that the same relation holds for mature fish, Roff's model predicts a growth curve which fits the observed growth curve very closely. However, instead of using the same energy allocation model to derive size-specific fecundities, Roff (1983) assumed that fecundity was a power function of size, estimated from empirical data. While this hybrid approach works for a fixed value of GSI, it is inappropriate for estimating fitness consequences of changes in GSI: increase in GSI results in decrease in size-at-age, but size-specific fecundity is not changed – unless the function for fecundity is adjusted properly. However, there is no need to use an external function for fecundity because the energy allocation model determines fecundity automatically. This simpler approach has been utilized by Perrin & Rubin (1990) and Heino & Kaitala (1997a,b). Perrin & Rubin (1990) were able to explain dome-shaped age-to-size reaction norm observed in fish using an energy allocation model, assuming that evolution maximizes density-independent  $R_0$ .

Heino & Kaitala (1997a,b) studied maturation in freshwater clams. They considered different, ecologically feasible ways in which density dependence could regulate clam populations. The alternative models have different ecological interpretations – resource competition or predation (Heino & Kaitala, 1997a) – and they may also reflect different priority rules of energy allocation (cf. Jokela & Mutikainen, 1995; Jokela, 1996). Depending on the way the population is regulated, an ESS age at maturity can maximize either density-

independent  $R_0$  or  $r$  – or neither one. More importantly, the predicted age at maturity in the clam populations depends on the method of population regulation – for realistic parameter values, an ESS age at maturity ranged between 3 and 11 years in different models (Heino & Kaitala, 1997a,b). Sensitivity of ESS maturation strategy to stochasticity also depends on the way in which population is regulated (Heino & Kaitala, 1997a).

Law & Grey (1989) developed an energy allocation model for the North-east Arctic cod. The difference to the models derived from Roff's (1983) model is in the growth function – juveniles follow a sigmoid instead of a linear growth curve. Law & Grey (1989) show the need to consider evolutionary consequences of harvesting. Current harvest patterns select for earlier maturity, which will result in decreasing sustainable yield. Indeed, trends towards earlier maturity have been observed in the North-east Arctic cod. Heino (1998) presents an extension of the analysis by Law & Grey (1989) which accounts for stochasticity and more complex harvesting strategies. The model displays the possibility that no single maturation strategy is an ESS. Instead, two or more maturation strategies might form a coalition that is able to resist invasions of all other maturation strategies, in which case the population becomes polymorphic with respect to age at maturity (cf. Metz *et al.*, 1996b; Geritz *et al.*, 1998).

## Discussion

Energy allocation models are powerful and theoretically sound tools for analysing problems related to evolution of life histories (Kozłowski, 1991). Although the bulk of the literature deals with the basic evolutionary problems, some applied issues in fisheries have also been studied. Ware (1980) studied stock and recruitment relationships in light of energy allocation models. Myers & Doyle (1983) and Kitahara *et al.* (1987) have used energy allocation models to estimate adult mortality rates from life history data. Evolutionary consequences of harvesting have been analysed by Law & Grey (1989) and Heino (1998) with energy allocation models.

One of the obstacles to the use of energy allocation models is that we seldom know the factors which maintain indeterminate growth patterns – presumably the model predictions are sensitive to assumptions on such factors. A way to overcome this difficulty is to assume that growth is indeterminate. Such an approach has the drawback that post-maturation evolutionary changes in allocation are neglected. Of course, this deficiency is shared by all models that focus on age at maturity only.

Other model classes also exist. Traditionally, in life history theory it has been assumed that fecundity is a simple function of size or age. In animals with indeterminate growth, current fecundity depends on size, which depends on past reproductive decisions. The models which use independently derived functions for fecundity

and size should therefore be used with care. While these models obviously have descriptive power (e.g. Kusano, 1982; Roff, 1984), it is essential to recognize that they can lead to spurious predictions if one function is changed independently of the other.

A third approach to life history evolution is that of life history invariants – products or ratios of certain life history parameters remaining approximately constant within some taxa (Charnov, 1993, 1997). Many of these invariants arise from very simple life history models assuming that optimal life histories maximize the density-independent lifetime reproductive success (Charnov & Berrigan, 1991; Jensen, 1996). When the simple invariants fail (Vøllestad *et al.*, 1993), more elaborated models may help (Mangel, 1996). None of the proposed life history invariants is based on models of energy allocation, which could provide a more functional interpretation of the invariants. However, Kozłowski (1996) used an energy allocation model to derive relations between random 'species' which resemble the proposed invariants. Nevertheless, the field of life history invariants has remained untouched by recent developments in life history theory, emphasizing the importance of details of environmental feedback (Mylius & Diekmann, 1995; Heino *et al.*, 1997, 1998).

The theories on evolution of energy allocation between growth and reproduction are approaching a mature stage. Remaining major theoretical challenges include a more careful consideration of the role of environmental feedback (possibly multidimensional), and energy allocation in stochastic environments for perennial species. Linking theory more closely with data has only begun and remains a major practical challenge.

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