



**Optimal Resource Allocation Between Growth and Reproduction in Clams:
Why Does Indeterminate Growth Exist?**

M. Heino, V. Kaitala

Functional Ecology, Volume 10, Issue 2 (Apr., 1996), 245-251.

Stable URL:

<http://links.jstor.org/sici?sici=0269-8463%28199604%2910%3A2%3C245%3AORABGA%3E2.0.CO%3B2-Q>

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

Functional Ecology is published by British Ecological Society. Please contact the publisher for further permissions regarding the use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/briteco.html>.

Functional Ecology

©1996 British Ecological Society

JSTOR and the JSTOR logo are trademarks of JSTOR, and are Registered in the U.S. Patent and Trademark Office. For more information on JSTOR contact jstor-info@umich.edu.

©2002 JSTOR

Optimal resource allocation between growth and reproduction in clams: why does indeterminate growth exist?

M. HEINO* and V. KAITALA

University of Helsinki, Division of Population Biology, P.O. Box 17, FIN-00014 University of Helsinki, Finland

Summary

1. That many animals and plants continue to grow after reproduction begins is a theoretically challenging evolutionary problem. We compare and extend the theories predicting intermediate resource allocation patterns. Our population dynamics model is developed for freshwater clams, which typically show considerable growth after maturity.

2. In the simulations, we used an age- and size-structured discrete-time resource allocation model, and applied dynamic programming algorithms to determine the resource allocation strategies that maximize fitness, measured as expected lifetime production of offspring, R_0 .

3. High levels of mortality select for early maturity and high reproductive effort.

4. Some adult growth is optimal in cases of size-dependent survival and production rates. However, this is not a sufficient explanation of the levels of adult growth observed.

5. We consider two trade-offs related to the mass of the offspring: one between relative glochidia mass (ratio of glochidia weight to the weight of the rest of the body) and production weight, and the other between relative glochidia mass and survival. In both cases, substantial adult growth is optimal, and the growth curves produced by the model are similar to those observed in clams. We discuss how these trade-offs are likely to arise in freshwater clams.

Key-words: Age-structure, dynamic programming, fitness, life-history, trade-offs

Functional Ecology (1996) **10**, 245–251

Introduction

Animals with indeterminate growth (e.g. fishes, snakes, lizards, and clams) experience life-history trade-offs between growth and reproductive effort, and between current and future reproduction. Reproduction requires energy, which then is not available for growth or maintenance. In many cases, growth ceases completely when reproduction begins, resulting in determinate growth. Such a growth strategy has been referred to in the literature as the 'bang-bang strategy', as opposed to the intermediate strategy where growth continues after maturity and is indeterminate (Perrin 1989; Sibly, Calow & Nichols 1985). In a wide class of life-history models the determinate (bang-bang) growth strategy is optimal (see reviews by Kozlowski 1992; Perrin & Sibly 1993; Engen & Sæther 1994).

Factors proposed to maintain indeterminate growth include size-dependent mortality and production rates

(Perrin, Sibly & Nichols 1993), age-specific mortality (Engen & Sæther 1994), unpredictable environment (King & Roughgarden 1982; Taylor & Gabriel 1993), and diminishing returns of reproductive investment (Taylor *et al.* 1974; León 1976). Structural constraints may also be operating, like the limited growth rate of the reproductive organs (Kozlowski & Ziolkowski 1988) and space-limitation of the brood-chamber in the daphnids (Perrin, Ruedi & Saiah 1987). Freshwater clams, which brood their young in gill chambers, may also face the space limitation during reproduction.

The annual reproductive potential of a mature individual usually depends on the individual's size (Ware 1980; Taylor & Gabriel 1993). In such a case, resource allocation along with age at maturity are expected to be crucial and evolutionarily sensitive life-history traits. In particular, the optimal resource allocation should be affected by age- or size-specific mortality or fertility patterns. Furthermore, these mortality or fertility patterns may be affected by such ecological factors as intra- and interspecific

competition, and by risks of predation, and by castrating parasitism.

We compare, with a model developed for freshwater clams, different life-history theories that predict intermediate resource allocation strategy. Freshwater clams typically show considerable growth after sexual maturity (Fig. 1). An appropriate test for a theory is its ability to produce a qualitative fit to the observed growth patterns. We carried out a dynamic study on resource allocation between growth and reproduction in animals with potentially indeterminate growth. Because of our interest in the factors maintaining intermediate resource allocation and indeterminate growth patterns commonly observed in both animals and plants, we developed, for our study, a general age-structured population dynamics model for freshwater clams. This allowed us to study the effects of age- and size-specific mortality patterns and trade-offs related to the volume occupied by the gonads or offspring on resource allocation. The fitness of the animals was measured as their lifetime production of offspring, R_0 . In a stable population, if density dependence affects the reproductive success in a multiplicative manner, density-independent R_0 is a valid fitness measure (Mylius & Diekmann 1995).

We develop the population dynamics model in the next section, with results presented in the Results section.

Population structure and evolutionary optimization problem

Here we describe the relevant life-history characteristics of freshwater clams. We then develop an age- and size-structured population dynamics model, and introduce the evolutionary optimization problem.

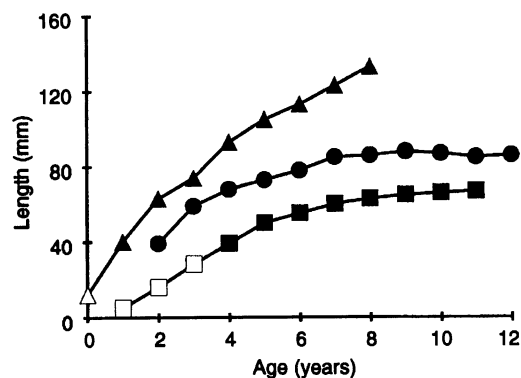


Fig. 1. Freshwater mussels *Anodonta* spp. show considerable growth after maturation, although such growth may eventually cease. Different species are indicated as follows: *A. woodiana* (triangles, data from Dudgeon & Morton 1983), *A. grandis* (boxes, Hanson *et al.* 1988) and *A. anatina* (circles, Taskinen & Valtonen 1995). White and black symbols denote immature and mature age classes, respectively.

Anodonta spp. may mature at the age of 1 year although maturity is usually delayed for some years (Dudgeon & Morton 1983; Hanson, Mackay & Prepas 1989; Taskinen & Valtonen 1995). Fertilization takes place in June (Jokela, Valtonen & Lappalainen 1991). The eggs are transferred to gill chambers, where they develop into glochidia larvae; glochidia, stored in gill chambers over winter, are released in spring (Jokela *et al.* 1991). They attach themselves to the fins and gills of common fish species, where they remain for some weeks, metamorphose, and finally detach and drop to the bottom. Post-larval mortality occurs predominantly during late winter (personal observation). Growth is fastest during the early season after which allocation of energy to reproduction increases (Jokela 1993). No growth occurs in winter.

AGE STRUCTURE AND REPRODUCTION

Consider a population of animals that reproduce seasonally once a year and in which the growth is potentially indeterminate. The population census takes place just before the release of offspring. Individuals may mature at any age, and allocation of the resources between growth and reproduction may change between years. The reproductive success of an individual is assumed to depend on the population density. Reproduction is followed by an overwintering period, during which survival is assumed to be independent of density.

Let k denote the index updating the reproduction – overwintering cycles. Let the subscript a denote the age class ($a=0, 1, \dots, a_{\max}$), and let a_M denote age-at-maturity. Assume that when reproduction begins during season k there are $X_a(k)$ individuals in age class a .

Assume next that a constant age-specific fraction μ_a of the overwintering individuals at age a survive over the overwintering period following the reproductive season k , to remain alive in the beginning of the reproductive season $k+1$. Then, the number of the overwintered individuals is

$$X_a(k+1) = \mu_{a-1} X_{a-1}(k), \quad a=1, \dots, a_{\max}. \quad \text{eqn 1}$$

Let $\sigma_a > 0$ denote age-specific per capita reproduction by mature individuals, that is, the number of young released at age a . Then the total number of offspring produced in the population is

$$x_0(k) = \sum_{a=1}^{a_{\max}} \sigma_a X_a(k), \quad \text{eqn 2}$$

where $\sigma_a = 0$ for $a \leq a_M$.

GROWTH STRATEGY

The relationship between age and size (length) is modelled by the following growth equation

$$L_0 = 0, \quad \text{eqn 3}$$

$$L_{a+1} = L_a + \Delta(L_a) \text{ mm for } a < a_M \quad \text{eqn 4}$$

and

$$L_{a+1} = L_a + S_g(L_a) \Delta(L_a) \text{ mm for } a \geq a_M, \quad \text{eqn 5}$$

where L_a is the length at age a , $\Delta(L_a)$ is the maximum growth at length L_a , a_M is age-at-maturity, and $S_g(L_a)$ is the growth strategy (i.e. the ratio of realized growth to maximum growth). Note that age-at-maturity refers to the age at which energy allocation to reproduction begins. Glochidia are released in our model one year later.

We next make the following assumptions:

- (1) a major part of the energy that is required in growth is used in developing the soft body parts, measured as body weight, W_a , at age a . (Note the distinction made here between the soft body parts and the shell.)
- (2) The energy required to produce a unit weight of glochidia is a constant proportion, c , of the energy required to produce a unit mass of body weight.
- (3) The maximum growth potential, Δ , is constant and independent of age or size. Growth is usually roughly linear in clams before maturity, which makes this simplification valid.

The body weight of the clams is assumed to depend on shell length as follows

$$W_a = 0.0025 L_a^3, \quad \text{eqn 6}$$

where length is given in mm and weight in mg. Thus, premature individuals increase their body weight as follows

$$\delta W_{L_a} = 0.0025 [(L_a + \Delta)^3 - L_a^3] \text{ mg}, \quad \text{eqn 7}$$

where δW_{L_a} is the increase in weight of a premature individual at size L_a . Mature individuals allocate their weight increase as follows

$$\delta W_{L_a} = 0.0025 [(L_a + S_g(L_a)\Delta)^3 - L_a^3] \text{ mg}, \quad \text{eqn 8}$$

where the growth strategy is constrained such that $0 \leq S_g(L_a) \leq 1$.

The unrealized increase in weight, the energy from which is used in reproduction, is

$$0.0025 [(L_a + \Delta)^3 - (L_a + S_g(L_a)\Delta)^3] \text{ mg}. \quad \text{eqn 9}$$

Recalling assumption 2, the weight of the glochidia produced at size L_a (and released at size L_{a+1}) is given as

$$\Psi_{L_{a+1}} = 0.0025 c [(L_a + \Delta)^3 - (L_a + S_g(L_a)\Delta)^3]. \quad \text{eqn 10}$$

Since we are not aware of estimates of the conversion rate, c , and because the unit does not affect the optimal growth strategies we assume that $c = 1$. Note also that equation 10 defines the equity $\sigma_a = \Psi_{L_a}$ (see equation 2).

EVOLUTIONARY OPTIMIZATION PROBLEM

The evolutionary optimization problem is one in which the optimal growth strategy S_g is determined

each year independently. Thus, the maximization of life-time production of offspring leads to the following dynamic programming problem

$$S_g(0), \dots, S_g(L_{a_{\text{MAX}}-1}) \sum_{a=1}^{a_{\text{MAX}}-1} L_a \Psi_{L_a} \quad \text{eqn 11}$$

such that equations 5 and 10, where the probability of surviving from birth to age a , l_a , is defined as follows: $l_0 = 1$, and $l_a = \mu_{a-1} l_{a-1}$, $a = 1, \dots, a_{\text{MAX}}$. Simulations are carried out by applying discrete-time dynamic programming algorithms (e.g. Mangel & Clark 1988, for details, see the Appendix).

Simulation results

Our main results deal with the trade-offs and constraints related to the volume occupied by the glochidia. For the purposes of comparison, however, we first show growth patterns produced by constant and size-dependent survival rates.

COMMON PARAMETERS

In simulation studies we used data from two different but closely related clam species occurring in freshwater rivers and lakes in the Boreal Forest zone, *Anodonta grandis* (Hanson *et al.* 1988, 1989, Jansen & Hanson 1991) in Canada, and *A. anatina* in Finland (Haukioja & Hakala 1978, Jokela 1993). No major differences in the life histories of these two species have been reported.

The growth potential Δ varies between different populations reflecting environmental variation. We assume here that $\Delta = 10$ mm, which was the case in the population studied by Hanson *et al.* (1988, 1989). The maximum age reported by Hanson *et al.* (1989) is 15 years, although no clams older than 12 years were caught alive. We assume here that $a_{\text{max}} = 12$ years.

Jansen & Hanson (1991) estimated that 0.007% of the glochidia produced will successfully attach to perch, which is a host during the clam's early parasitic stage, and that 0.0027% of the glochidia survive to age 2. We assume here that most of the mortality occurs during the first year, and that the survival rate of the new-born individuals to age 1 is $\mu_0 = 0.00003$. Survival-rate patterns for the other age classes are given below.

CONSTANT MORTALITY

When mortality is constant at all ages, an optimal resource allocation pattern is first to grow, then only to reproduce (Fig. 2). None of the cases shown in Fig. 2 led to indeterminate growth, although the resource-allocation strategy may have been intermediate during the year of maturation. The latter property was most likely due to the discrete time model used: optimal adult size cannot be achieved exactly at

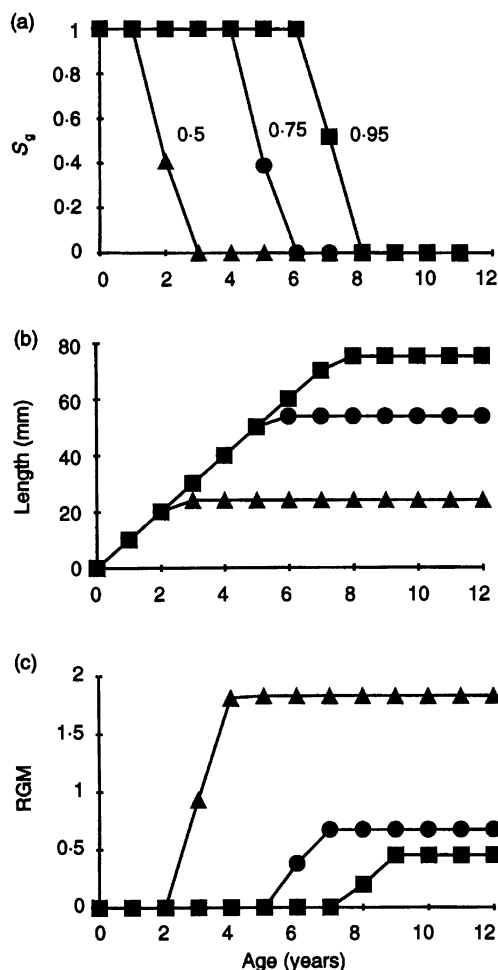


Fig. 2. Different constant, size- and age-independent annual survival rates μ (0.5, 0.75, and 0.95) may produce different optimal resource-allocation patterns, such that none of them leads to indeterminate growth. The proportion of surplus energy allocated to growth (S_g) decreases quickly at low survival rates ($\mu=0.5$), whereas high survival rates ($\mu=0.95$) make it optimal to mature late (a). The related growth patterns (b) and relative glochidia masses (ratio of glochidia weight to the weight of the rest of the body, RGM) (c) are also shown.

a certain age if the maximum growth potential is realized during each growth season. As expected, higher mortality leads to earlier maturation, higher reproductive effort, and smaller terminal size. All of this is accompanied by higher age-specific relative glochidia mass RGM, defined as the ratio of glochidia weight to the weight of the rest of the body (Fig. 2b). In the case of high mortality, the RGM becomes very high – the weight of the glochidia would exceed that of the rest of the body, which is unrealistic in the case of freshwater clams. In the absence of size-specific mortality, the growth potential (Δ) affects neither the allocation pattern nor the age-at-maturity, results which contradict those obtained by Engen & Sæther (1994).

SIZE-SPECIFIC MORTALITY

Muskrats are important predators of freshwater clams, and show size-specific preferences in their prey selec-

tion (Hanson *et al.* 1989; Jokela & Mutikainen 1995). Furthermore, the risk for castrating parasitism may to some extent be size-specific (Taskinen & Valtonen 1995). The effects of predation risk, are reported by Hanson *et al.* (1989), and are shown in Fig. 3 for $\mu=0.95$. The resource-allocation pattern is not qualitatively different from patterns observed under constant mortality. In the hypothetical case of heavy mortality, some growth is optimal for several years after maturation (Fig. 3). However, the growth curve is still very different from those curves observed in nature. Thus, it is evident that in freshwater clams size-specific mortality alone cannot be responsible for the substantial growth after maturation. This result holds for all ecologically realistic patterns of size-specific mortality, including mortality decreasing with size. When mortality decreases with size, the optimal strategy is always first to grow, then only to reproduce. Note again that early maturity leads to disproportionately large values for RGM.

TRADE-OFFS AND CONSTRAINTS CONCERNING THE MASS OF OFFSPRING

It is obvious from the analyses above that any organisms maturing early have a potentially very high reproductive output relative to their body mass. However, some organisms, such as clams, may not be able to realize fully their reproductive potential due to the limited capacity of their reproductive organs, to space limitations, decreased feeding efficiency, or decreased mobility, resulting in trade-offs related to reproductive effort.

The consequences of possible trade-offs among RGM, reproductive rate, and growth for clams are illustrated in Fig. 4. It is assumed that increase in the volume of glochidia inside female's gills decreases her feeding efficiency, leaving her of a smaller size and with less energy with gonads than without. Furthermore, this decreased feeding efficiency is assumed to decrease her annual growth potential Δ such that her annual growth potential is multiplied by the factor depending on the RGM, as seen in Fig. 4(a). Analyses of the three survival patterns show that if the survival rate is high ($\mu=0.95$), little is changed as compared to the unconstrained situation. However, when the survival rate is lower ($\mu=0.75$ or 0.5), several years of intermediate resource allocation strategy can be observed. The resulting growth curves resemble those observed in nature. Again, high mortality selects for earlier maturity.

Another possible cost associated with high volume of glochidia is increased mortality. In freshwater clams this trade-off may be realized as a risk for infection by castrating parasites associated with filter feeding. This trade-off results in indeterminate growth patterns (Fig. 5), which qualitatively fit those patterns observed in nature (Fig. 1). The results are also qualitatively similar to those seen in Fig. 4.

Discussion

Our explanation for indeterminate growth (see Trade-offs and constraints) relies on the following key assumption: a large volume of sexual products is costly. In freshwater clams this may be realized in different ways. Freshwater clams brood their young in gill chambers. Brooding is costly in terms of the efficiency of filter feeding: the efficiency of a gill with glochidia is 50% less than that of an empty gill in *Pyganodon cataracta* (syn. *Anodonta cataracta*) (Tankersley & Dimock 1993a). The RGM of this species is about 0.5; thus the trade-off curve in Fig. 4(a) is fairly realistic. Clams may attempt to compensate for decreased feeding efficiency by increasing filtration rate, which on the other hand, may increase

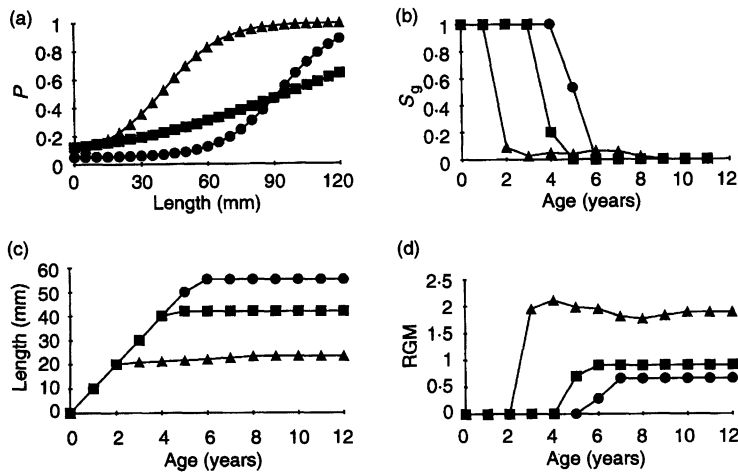


Fig. 3. Size-specific mortality affects optimal resource allocation. All three hypothetical annual predation risks studied increase with size of individuals (a). The dotted curve is an approximation of the predation risk reported by Hanson *et al.* (1989). Optimal resource allocation (b) and the resulting growth patterns (c) and RGM curves (d) are also shown.

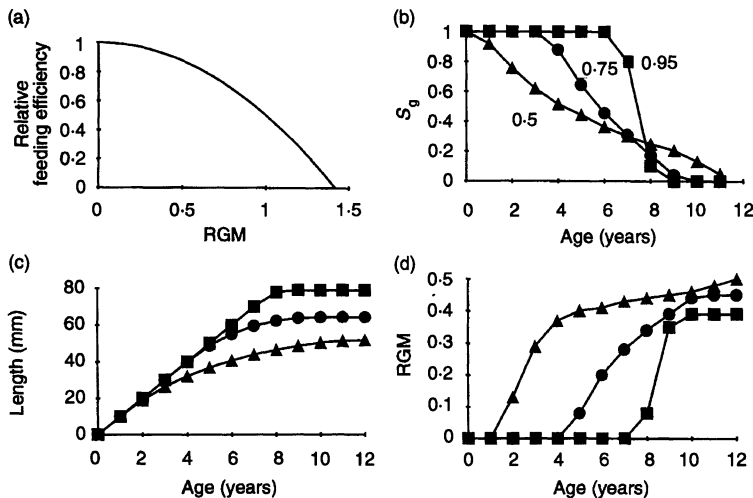


Fig. 4. The trade-off between RGM and the filtration efficiency of gills affects growth and reproduction. The growth potential Δ is multiplied by a factor describing the decreased efficiency of the gills (a). This trade-off results in intermediate resource allocation (b) irrespective of survival rates. Corresponding growth patterns (c) and RGM curves (d) are also shown. The three curves correspond to the different survival patterns given in Fig. 2(a).

the risk for castrating parasitism. Tankersley & Dimock (1993b) did not, however, observe any increase of filtration rate in gravid females.

The valves also set a physical upper limit for the size of brooding gills. More space for glochidia could be achieved with little additional investment in growth by an increasing shell obesity (width/length). Hence, many species are sexually dimorphic in the shape of the shell, the females having more convex valves. This has also been reported in *Anodonta* (Brander 1954). However, the shape of the shell may not be free to evolve due to its functional significance in burrowing, in locomotion and in maintaining a proper position on soft sediments. For example, Ghent, Singer & Johnson-Singer (1978) postulate that the flat, heavy shell of *Elliptio complanata* is responsible for its occurrence on hard shallow-water bottoms only, while the *Anodonta grandis* with its obese, light shell is restricted mainly to deep muddy bottoms in the lake they studied.

The cost of a large volume of sexual products may not be limited to freshwater clams only. In a fish, for example, a high volume of gonads may impair hydrodynamic properties and thus increase energy consumption, or decrease swimming speed. In both cases we expect the growth rate to decrease. High swimming speed is important for predators attacking highly mobile prey and for species which must search for sparsely occurring prey. High swimming speed is also needed to avoid being preyed upon.

Our model predicts that high values of RGM should be associated with high mortality and short life-span, and vice versa. In the case of freshwater clams, this also means that shell obesity and life-span should be inversely correlated. Although RGM displays wide variation in freshwater clams, it is not possible with the data available to link this variation to the expected life-span. The maximum value for RGM reported in *Anodonta* spp. is 1.0, although values between 0.20–0.50 appear to be typical (Huebner 1980; Jokela, Uotila & Taskinen 1993; J. Jokela, unpublished results). However, in *Lampsilis radiata* RGM is as low as 0.05 (Huebner 1980).

If the energy content of sexual products is high relative to that of the somatic tissues, i.e., the conversion rate c is low, the volume of the sexual products will not increase as much as expected. In *Anodonta*, although the energy content of gonads is high, the energy content of the gills with glochidia is low (Jokela *et al.* 1993). Another way to overcome the size constraint is by gradual release of sexual products. In freshwater clams this may apply to males only, since the period of brooding is relatively long in females.

Because male clams do not meet these constraints to the same extent as do females, we would expect male clams to have a higher reproductive effort-at-age and a lower growth rate after maturity. However, although the lack of published sex-specific growth curves prevents testing of this hypothesis, males are, nevertheless, usually smaller than females in *Anodonta woodiana* (Dudgeon & Morton 1983).

Although it is well established that the trade-off between reproductive effort and survival or reproductive output could lead to indeterminate growth, Myers & Doyle (1983) appear to be the first who have applied these trade-offs to practical models. However, they did not study other possible explanations. Moreover, most phenomena which may lead to trade-offs concerning reproduction relate the reproductive output to body size, rather than to somatic growth, as Taylor *et al.* (1974), León (1976) and Myers & Doyle (1983) assumed. Perrin *et al.* (1987) propose that, in a cladoceran, size constraint is responsible for indeterminate growth. Later, Perrin (1989) constructed a simple model of size constraint; however, his experimental data on a cladoceran did not support his model.

Engen & Sæther (1994) found that if mortality is a decreasing function of age, an intermediate strategy is often optimal, at least for some period of time. From the evolutionary point of view, although age- and size-specific mortalities are often correlated, it is very important to discern which is the primary ultimate source of mortality: individuals have some control over size-specific mortality via the growth strategy, but no control over age-specific mortality. It is difficult to imagine a biologically feasible situation in which age rather than size is the true vector of mortality decreasing with age. Mortality decreasing with size will not produce an intermediate strategy in our model.

Contrary to earlier studies (Kozłowski & Uchmanski 1987; Engen & Sæther 1994), energy allocation to reproduction is not always a monotonously increasing function, despite the fact that the underlying size-specific production and mortality functions are monotonous. However, the possible decrease in reproductive effort at some ages is

generally so low that it has no practical importance; the cost of being not optimal while following some monotonous allocation rule is usually negligible.

An important complication in the life-history theory is the role of stochasticity. Taylor & Gabriel (1993) using a *Daphnia* model showed that, in environments with stochastic variation, intermediate strategy is optimal under a much wider range of conditions than in constant environments. Nevertheless, our results show that environmental stochasticity is not needed to explain indeterminate growth. Size-dependent mortality and trade-offs among reproduction and other energy factors are also possible causes for this common life-history pattern.

Acknowledgements

We thank O. Diekmann and T. Kawecki for critical comments. We thank O. Diekmann, J. Jokela, J. Taskinen, and S.D. Mylius for providing manuscripts prior to publication.

References

- Brander, T. (1954) Über Geschlechtsdimorphismus bei europäischen Unionazeen. *Archiv für Molluskenkunde* **83**, 163–172.
- Dudgeon, D. & Morton, B. (1983) The population dynamics and sexual strategy of *Anodonta woodiana* (Bivalvia: Unionacea) in Plover Cove Reservoir, Hong Kong. *Journal of Zoology (London)* **201**, 161–183.
- Engen, S. & Sæther, B.-E. (1994) Optimal allocation of resources to growth and reproduction. *Theoretical Population Biology* **46**, 232–248.
- Ghent, A.W., Singer, R. & Johnson-Singer, L. (1978) Depth distributions determined with SCUBA, and associated studies of the freshwater unionid clams *Elliptio complanata* and *Anodonta grandis* in Lake Bernard, Ontario. *Canadian Journal of Zoology* **56**, 1654–1663.
- Hanson, J.M., Mackay, W.C. & Prepas, E.E. (1988) Population size, growth, and production of a unionid clam, *Anodonta grandis simpsoniana*, in a small, deep boreal forest lake in central Alberta. *Canadian Journal of Zoology* **66**, 247–253.
- Hanson, J.M., Mackay, W.C. & Prepas, E.E. (1989) Effect of size-selective predation by muskrats (*Ondatra zibethicus*) on a population of unionid clams (*Anodonta grandis simpsoniana*). *Journal of Animal Ecology* **58**, 15–28.
- Haukioja, E. & Hakala, T. (1978) Life-history evolution in *Anodonta piscinalis* (Mollusca, Pelecypoda). *Oecologia (Berlin)* **35**, 253–266.
- Huebner, J.D. (1980) Seasonal variation in two species of unionid clams from Manitoba, Canada: biomass. *Canadian Journal of Zoology* **58**, 1980–1983.
- Jansen, W.A. & Hanson, J.M. (1991) Estimates of the number of glochidia produced by clams (*Anodonta grandis simpsoniana* Lea), attaching to yellow perch (*Perca flavescens*), and surviving to various ages in Narrow Lake, Alberta (Canada). *Canadian Journal of Zoology* **69**, 973–977.
- Jokela, J. (1993) *The selective environment of a freshwater clam: causes of selection and evolution of a life-history strategy*. Ph.D. Dissertation, University of Turku, Finland (Reports from the Department of Biology, University of Turku, No. 32)

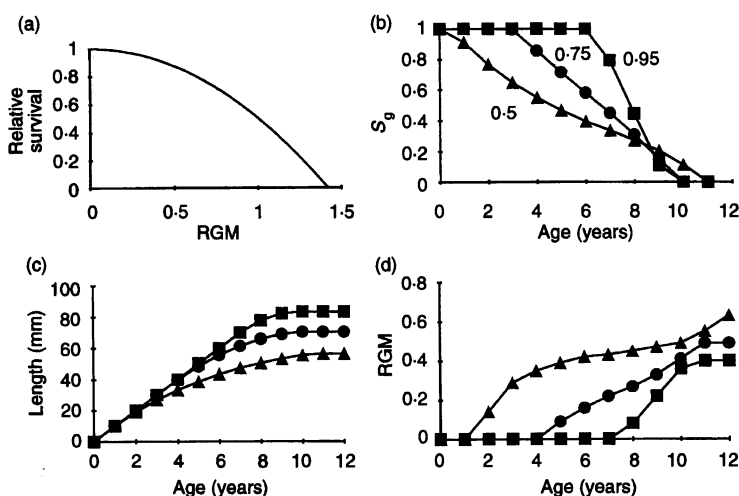


Fig. 5. The trade-off between RGM and survival will affect growth and reproduction. The survival rates of Fig. 2a are multiplied by a factor denoted as the relative survival, describing increased mortality due to the large volume of glochidia (a). This trade-off results in intermediate resource allocation (b). Corresponding growth patterns (c) and RGM curves (d) are also shown.

- Jokela, J. & Mutikainen, P. (1995) Effect of size-dependent muskrat (*Ondatra zibethica*) predation on spatial distribution of a freshwater clam, *Anodonta piscinalis* Nilss. (Unionidae, Bivalvia). *Canadian Journal of Zoology* **73**, 1085–1094.
- Jokela, J., Uotila, L. & Taskinen, J. (1993) Effect of the castrating trematode parasite *Rhipidocotyle fennica* on energy allocation of fresh-water clam *Anodonta piscinalis*. *Functional Ecology* **7**, 332–338.
- Jokela, J., Valtonen, E.T. & Lappalainen, M. (1991) Development of glochidia of *Anodonta piscinalis* and their infection of fish in a small lake in northern Finland. *Archiv für Hydrobiologie* **120**, 345–355.
- King, D. & Roughgarden, J. (1982) Graded allocation between vegetative and reproductive growth for annual plants in growing seasons of random length. *Theoretical Population Biology* **22**, 1–16.
- Kozłowski, J. (1992) Optimal allocation of resources to growth and reproduction: implications for age and size at maturity. *Trends in Ecology and Evolution* **7**, 15–19.
- Kozłowski, J. & Uchmanski, J. (1987) Optimal individual growth and reproduction in perennial species with indeterminate growth. *Evolutionary Ecology* **1**, 214–230.
- Kozłowski, J. & Ziolkowski, M. (1988) Gradual transition from vegetative to reproductive growth is optimal when the maximum rate of reproductive growth is limited. *Theoretical Population Biology* **34**, 118–129.
- León, J.A. (1976) Life histories as adaptive strategies. *Journal of Theoretical Biology* **60**, 301–335.
- Mangel, M. & Clark, C.W. (1988) *Dynamic Modeling in Behavioral Ecology*. Princeton University Press, Princeton.
- Myers, R.A. & Doyle, R.W. (1983) Predicting natural mortality rates and reproduction-mortality trade-offs from fish life-history data. *Canadian Journal of Fisheries and Aquatic Sciences* **40**, 612–620.
- Mylius, S.D. & Diekmann, O. (1995) On evolutionary stable life histories, optimization and the need to be specific about density dependence. *Oikos*, **74**, 218–224.
- Perrin, N. (1989) Reproductive allocation and size constraints in the cladoceran *Simocephalus vetulus* (Mueller). *Functional Ecology* **3**, 279–283.
- Perrin, N., Ruedi, M. & Saiah, H. (1987) Why is the cladoceran *Simocephalus vetulus* (Müller) not a 'bang-bang strategist'? A critique of the optimal-body-size model. *Functional Ecology* **1**, 223–228.
- Perrin, N. & Sibly, R.M. (1993) Dynamic models of energy allocation and investment. *Annual Reviews of Ecology and Systematics* **24**, 379–410.
- Perrin, N., Sibly, R.M. & Nichols, N.K. (1993) Optimal growth strategies when mortality and production rates are size-dependent. *Evolutionary Ecology* **7**, 576–592.
- Sibly, R., Calow, P. & Nichols, N. (1985) Are patterns of growth adaptive? *Journal of Theoretical Biology* **112**, 553–574.
- Tankersley, R.A. & Dimock, R.V., Jr. (1993a) The effect of larval brooding on the filtration rate and particle-retention efficiency of *Pyganodon cataracta* (Bivalvia: Unionidae). *Canadian Journal of Zoology* **71**, 1934–1944.
- Tankersley, R.A. & Dimock, R.V., Jr. (1993b) The effect of larval brooding on the respiratory physiology of the freshwater unionid mussel *Pyganodon cataracta*. *American Midland Naturalist* **130**, 146–163.
- Taskinen, J. & Valtonen, E.T. (1995) Age, size, and sex-specific infection of *Anodonta piscinalis* (Bivalvia: Unionidae) with *Rhipidocotyle fennica* (Digenea: Bucephalidae) and its influence on host reproduction. *Canadian Journal of Zoology* **73**, 889–897.
- Taylor, B.E. & Gabriel, W. (1993) Optimal adult growth of *Daphnia* in a seasonal environment. *Functional Ecology* **7**, 513–521.
- Taylor, H.M., Gourley, R.S., Lawrence, C.E. & Kaplan, R.S. (1974) Natural selection of life-history attributes: an analytical approach. *Theoretical Population Biology* **5**, 104–122.
- Ware, D.M. (1980) Bioenergetics of stock and recruitment. *Canadian Journal of Fisheries and Aquatic Sciences* **37**, 1012–1024.

Received 10 April 1995; revised 22 August 1995; accepted 23 August 1995

Appendix: Dynamic programming algorithm

The numerical algorithm for solving the dynamic programming problem (equation 11) is as follows. Let $R_0^*(L_a)$ denote the maximum expected residual production of offspring at age a and size L_a , after the offspring have been released at age a , and let $S_g^*(L_a), \dots, S_g^*(L_{a_{\text{MAX}}-1})$ denote the optimal resource allocation rules associated to $R_0^*(L_a)$. The dynamic programming algorithm is solved recursively backward in time (age) as follows:

1. Compute $R_0^*(L_{a_{\text{MAX}}-1})$ for all sizes $L_{a_{\text{MAX}}-1}$ ($0 \leq L_{a_{\text{MAX}}-1} \leq (a_{\text{MAX}}-1)\Delta$) from the following optimization problem

$$R_0^*(L_{a_{\text{MAX}}-1}) = \max_{S_g(L_{a_{\text{MAX}}-1})} \mu_{a_{\text{MAX}}-1} \Psi L_{a_{\text{MAX}}}$$

such that equation 10 is achieved.

2. Compute $R_0^*(L_a)$ for all sizes L_a ($0 \leq L_a \leq a\Delta$) from the following optimization problem

$$R_0^*(L_a) = \max_{S_g(L_a)} \mu_a [\Psi L_a + R_0^*(L_{a+1})]$$

such that equation 10 is achieved. Repeat this step backwards in time for all ages $a = a_{\text{MAX}} - 2, a_{\text{MAX}} - 3, \dots, 0$.

The precision used for the allocation strategy S_g was 1/250, and for the state variable (length) L_a , 1 mm. Linear interpolation was used when the state variable L_a fell between the grid values.