



Interim Report

IR-03-004

Unexpected Discontinuities in Life-History Evolution under Size-dependent Mortality

Barabara Taborsky (barbara.taborsky@esh.unibe.ch)
Ulf Dieckmann (dieckman@iiasa.ac.at)
Mikko Heino (mikko.heino@imr.no)

Approved by

Leen Hordijk
Director, IIASA

March 2003



The Adaptive Dynamics Network at IIASA fosters the development of new mathematical and conceptual techniques for understanding the evolution of complex adaptive systems.

Focusing on these long-term implications of adaptive processes in systems of limited growth, the Adaptive Dynamics Network brings together scientists and institutions from around the world with IIASA acting as the central node.

Scientific progress within the network is collected in the IIASA Studies in Adaptive Dynamics series.

- No. 1 Metz JAJ, Geritz SAH, Meszéna G, Jacobs FJA, van Heerwaarden JS: *Adaptive Dynamics: A Geometrical Study of the Consequences of Nearly Faithful Reproduction*. IIASA Working Paper WP-95-099 (1995). van Strien SJ, Verduyn Lunel SM (eds): *Stochastic and Spatial Structures of Dynamical Systems*, Proceedings of the Royal Dutch Academy of Science (KNAW Verhandelingen), North Holland, Amsterdam, pp. 183-231 (1996).
- No. 2 Dieckmann U, Law R: *The Dynamical Theory of Coevolution: A Derivation from Stochastic Ecological Processes*. IIASA Working Paper WP-96-001 (1996). *Journal of Mathematical Biology* 34:579-612 (1996).
- No. 3 Dieckmann U, Marrow P, Law R: *Evolutionary Cycling of Predator-Prey Interactions: Population Dynamics and the Red Queen*. IIASA Preprint (1995). *Journal of Theoretical Biology* 176:91-102 (1995).
- No. 4 Marrow P, Dieckmann U, Law R: *Evolutionary Dynamics of Predator-Prey Systems: An Ecological Perspective*. IIASA Working Paper WP-96-002 (1996). *Journal of Mathematical Biology* 34:556-578 (1996).
- No. 5 Law R, Marrow P, Dieckmann U: *On Evolution under Asymmetric Competition*. IIASA Working Paper WP-96-003 (1996). *Evolutionary Ecology* 11:485-501 (1997).
- No. 6 Metz JAJ, Mylius SD, Dieckmann O: *When Does Evolution Optimize? On the Relation Between Types of Density Dependence and Evolutionarily Stable Life History Parameters*. IIASA Working Paper WP-96-004 (1996).
- No. 7 Ferrière R, Gatto M: *Lyapunov Exponents and the Mathematics of Invasion in Oscillatory or Chaotic Populations*. *Theoretical Population Biology* 48:126-171 (1995).
- No. 8 Ferrière R, Fox GA: *Chaos and Evolution*. IIASA Preprint (1996). *Trends in Ecology and Evolution* 10:480-485 (1995).
- No. 9 Ferrière R, Michod RE: *The Evolution of Cooperation in Spatially Heterogeneous Populations*. IIASA Working Paper WP-96-029 (1996). *The American Naturalist* 147:692-717 (1996).
- No. 10 van Dooren TJM, Metz JAJ: *Delayed Maturation in Temporally Structured Populations with Non-Equilibrium Dynamics*. IIASA Working Paper WP-96-070 (1996). *Journal of Evolutionary Biology* 11:41-62 (1998).
- No. 11 Geritz SAH, Metz JAJ, Kisdi É, Meszéna G: *The Dynamics of Adaptation and Evolutionary Branching*. IIASA Working Paper WP-96-077 (1996). *Physical Review Letters* 78:2024-2027 (1997).
- No. 12 Geritz SAH, Kisdi É, Meszéna G, Metz JAJ: *Evolutionary Singular Strategies and the Adaptive Growth and Branching of the Evolutionary Tree*. IIASA Working Paper WP-96-114 (1996). *Evolutionary Ecology* 12:35-57 (1998).
- No. 13 Heino M, Metz JAJ, Kaitala V: *Evolution of Mixed Maturation Strategies in Semelparous Life-Histories: The Crucial Role of Dimensionality of Feedback Environment*. IIASA Working Paper WP-96-126 (1996). *Philosophical Transactions of the Royal Society of London Series B* 352:1647-1655 (1997).
- No. 14 Dieckmann U: *Can Adaptive Dynamics Invade?* IIASA Working Paper WP-96-152 (1996). *Trends in Ecology and Evolution* 12:128-131 (1997).
- No. 15 Meszéna G, Czibula I, Geritz SAH: *Adaptive Dynamics in a 2-Patch Environment: A Simple Model for Allopatric and Parapatric Speciation*. IIASA Interim Report IR-97-001 (1997). *Journal of Biological Systems* 5:265-284 (1997).
- No. 16 Heino M, Metz JAJ, Kaitala V: *The Enigma of Frequency-Dependent Selection*. IIASA Interim Report IR-97-061 (1997). *Trends in Ecology and Evolution* 13:367-370 (1998).
- No. 17 Heino M: *Management of Evolving Fish Stocks*. IIASA Interim Report IR-97-062 (1997). *Canadian Journal of Fisheries and Aquatic Sciences* 55:1971-1982 (1998).
- No. 18 Heino M: *Evolution of Mixed Reproductive Strategies in Simple Life-History Models*. IIASA Interim Report IR-97-063 (1997).
- No. 19 Geritz SAH, van der Meijden E, Metz JAJ: *Evolutionary Dynamics of Seed Size and Seedling Competitive Ability*. IIASA Interim Report IR-97-071 (1997). *Theoretical Population Biology* 55:324-343 (1999).
- No. 20 Galis F, Metz JAJ: *Why Are There So Many Cichlid Species? On the Interplay of Speciation and Adaptive Radiation*. IIASA Interim Report IR-97-072 (1997). *Trends in Ecology and Evolution* 13:1-2 (1998).

- No. 21 Boerlijst MC, Nowak MA, Sigmund K: *Equal Pay for all Prisoners/ The Logic of Contrition*. IIASA Interim Report IR-97-073 (1997). American Mathematical Society Monthly 104:303-307 (1997). Journal of Theoretical Biology 185:281-293 (1997).
- No. 22 Law R, Dieckmann U: *Symbiosis Without Mutualism and the Merger of Lineages in Evolution*. IIASA Interim Report IR-97-074 (1997). Proceedings of the Royal Society of London Series B 265:1245-1253 (1998).
- No. 23 Klinkhamer PGL, de Jong TJ, Metz JAJ: *Sex and Size in Cosexual Plants*. IIASA Interim Report IR-97-078 (1997). Trends in Ecology and Evolution 12:260-265 (1997).
- No. 24 Fontana W, Schuster P: *Shaping Space: The Possible and the Attainable in RNA Genotype-Phenotype Mapping*. IIASA Interim Report IR-98-004 (1998). Journal of Theoretical Biology 194:491-515 (1998).
- No. 25 Kisdi É, Geritz SAH: *Adaptive Dynamics in Allele Space: Evolution of Genetic Polymorphism by Small Mutations in a Heterogeneous Environment*. IIASA Interim Report IR-98-038 (1998). Evolution 53:993-1008 (1999).
- No. 26 Fontana W, Schuster P: *Continuity in Evolution: On the Nature of Transitions*. IIASA Interim Report IR-98-039 (1998). Science 280:1451-1455 (1998).
- No. 27 Nowak MA, Sigmund K: *Evolution of Indirect Reciprocity by Image Scoring/ The Dynamics of Indirect Reciprocity*. IIASA Interim Report IR-98-040 (1998). Nature 393:573-577 (1998). Journal of Theoretical Biology 194:561-574 (1998).
- No. 28 Kisdi É: *Evolutionary Branching Under Asymmetric Competition*. IIASA Interim Report IR-98-045 (1998). Journal of Theoretical Biology 197:149-162 (1999).
- No. 29 Berger U: *Best Response Adaptation for Role Games*. IIASA Interim Report IR-98-086 (1998).
- No. 30 van Dooren TJM: *The Evolutionary Ecology of Dominance-Recessivity*. IIASA Interim Report IR-98-096 (1998). Journal of Theoretical Biology 198:519-532 (1999).
- No. 31 Dieckmann U, O'Hara B, Weisser W: *The Evolutionary Ecology of Dispersal*. IIASA Interim Report IR-98-108 (1998). Trends in Ecology and Evolution 14:88-90 (1999).
- No. 32 Sigmund K: *Complex Adaptive Systems and the Evolution of Reciprocation*. IIASA Interim Report IR-98-100 (1998). Ecosystems 1:444-448 (1998).
- No. 33 Posch M, Pichler A, Sigmund K: *The Efficiency of Adapting Aspiration Levels*. IIASA Interim Report IR-98-103 (1998). Proceedings of the Royal Society London Series B 266:1427-1435 (1999).
- No. 34 Mathias A, Kisdi É: *Evolutionary Branching and Coexistence of Germination Strategies*. IIASA Interim Report IR-99-014 (1999).
- No. 35 Dieckmann U, Doebeli M: *On the Origin of Species by Sympatric Speciation*. IIASA Interim Report IR-99-013 (1999). Nature 400:354-357 (1999).
- No. 36 Metz JAJ, Gyllenberg M: *How Should We Define Fitness in Structured Metapopulation Models? Including an Application to the Calculation of Evolutionarily Stable Dispersal Strategies*. IIASA Interim Report IR-99-019 (1999). Proceedings of the Royal Society of London Series B 268:499-508 (2001).
- No. 37 Gyllenberg M, Metz JAJ: *On Fitness in Structured Metapopulations*. IIASA Interim Report IR-99-037 (1999). Journal of Mathematical Biology 43:545-560 (2001).
- No. 38 Meszéna G, Metz JAJ: *Species Diversity and Population Regulation: The Importance of Environmental Feedback Dimensionality*. IIASA Interim Report IR-99-045 (1999).
- No. 39 Kisdi É, Geritz SAH: *Evolutionary Branching and Sympatric Speciation in Diploid Populations*. IIASA Interim Report IR-99-048 (1999).
- No. 40 Ylikarjula J, Heino M, Dieckmann U: *Ecology and Adaptation of Stunted Growth in Fish*. IIASA Interim Report IR-99-050 (1999). Evolutionary Ecology 13:433-453 (1999).
- No. 41 Nowak MA, Sigmund K: *Games on Grids*. IIASA Interim Report IR-99-038 (1999). Dieckmann U, Law R, Metz JAJ (eds): The Geometry of Ecological Interactions: Simplifying Spatial Complexity, Cambridge University Press, Cambridge, UK, pp. 135-150 (2000).
- No. 42 Ferrière R, Michod RE: *Wave Patterns in Spatial Games and the Evolution of Cooperation*. IIASA Interim Report IR-99-041 (1999). Dieckmann U, Law R, Metz JAJ (eds): The Geometry of Ecological Interactions: Simplifying Spatial Complexity, Cambridge University Press, Cambridge, UK, pp. 318-332 (2000).
- No. 43 Kisdi É, Jacobs FJA, Geritz SAH: *Red Queen Evolution by Cycles of Evolutionary Branching and Extinction*. IIASA Interim Report IR-00-030 (2000). Selection 2:161-176 (2001).
- No. 44 Meszéna G, Kisdi É, Dieckmann U, Geritz SAH, Metz JAJ: *Evolutionary Optimisation Models and Matrix Games in the Unified Perspective of Adaptive Dynamics*. IIASA Interim Report IR-00-039 (2000). Selection 2:193-210 (2001).
- No. 45 Parvinen K, Dieckmann U, Gyllenberg M, Metz JAJ: *Evolution of Dispersal in Metapopulations with Local Density Dependence and Demographic Stochasticity*. IIASA Interim Report IR-00-035 (2000).
- No. 46 Doebeli M, Dieckmann U: *Evolutionary Branching and Sympatric Speciation Caused by Different Types of Ecological Interactions*. IIASA Interim Report IR-00-040 (2000). The American Naturalist 156:S77-S101 (2000).
- No. 47 Heino M, Hanski I: *Evolution of Migration Rate in a Spatially Realistic Metapopulation Model*. IIASA Interim Report IR-00-044 (2000). The American Naturalist 157:495-511 (2001).
- No. 48 Gyllenberg M, Parvinen K, Dieckmann U: *Evolutionary Suicide and Evolution of Dispersal in Structured Metapopulations*. IIASA Interim Report IR-00-056 (2000). Journal of Mathematical Biology 45:79-105 (2002).
- No. 49 van Dooren TJM: *The Evolutionary Dynamics of Direct Phenotypic Overdominance: Emergence Possible, Loss Probable*. IIASA Interim Report IR-00-048 (2000). Evolution 54: 1899-1914 (2000).
- No. 50 Nowak MA, Page KM, Sigmund K: *Fairness Versus Reason in the Ultimatum Game*. IIASA Interim Report IR-00-057 (2000). Science 289:1773-1775 (2000).
- No. 51 de Feo O, Ferrière R: *Bifurcation Analysis of Population Invasion: On-Off Intermittency and Basin Riddling*. IIASA Interim Report IR-00-074 (2000). International Journal of Bifurcation and Chaos 10:443-452 (2000).

- No. 52 Heino M, Laaka-Lindberg S: *Clonal Dynamics and Evolution of Dormancy in the Leafy Hepatic Lophozia Silvicola*. IIASA Interim Report IR-01-018 (2001). *Oikos* 94:525-532 (2001).
- No. 53 Sigmund K, Hauert C, Nowak MA: *Reward and Punishment in Minigames*. IIASA Interim Report IR-01-031 (2001). *Proceedings of the National Academy of Sciences of the USA* 98:10757-10762 (2001).
- No. 54 Hauert C, De Monte S, Sigmund K, Hofbauer J: *Oscillations in Optional Public Good Games*. IIASA Interim Report IR-01-036 (2001).
- No. 55 Ferrière R, Le Galliard J: *Invasion Fitness and Adaptive Dynamics in Spatial Population Models*. IIASA Interim Report IR-01-043 (2001). Clobert J, Dhondt A, Danchin E, Nichols J (eds): *Dispersal*, Oxford University Press, pp. 57-79 (2001).
- No. 56 de Mazancourt C, Loreau M, Dieckmann U: *Can the Evolution of Plant Defense Lead to Plant-Herbivore Mutualism*. IIASA Interim Report IR-01-053 (2001). *The American Naturalist* 158: 109-123 (2001).
- No. 57 Claessen D, Dieckmann U: *Ontogenetic Niche Shifts and Evolutionary Branching in Size-Structured Populations*. IIASA Interim Report IR-01-056 (2001). *Evolutionary Ecology Research* 4:189-217 (2002).
- No. 58 Brandt H: *Correlation Analysis of Fitness Landscapes*. IIASA Interim Report IR-01-058 (2001).
- No. 59 Dieckmann U: *Adaptive Dynamics of Pathogen-Host Interactions*. IIASA Interim Report IR-02-007 (2002). Dieckmann U, Metz JAJ, Sabelis MW, Sigmund K (eds): *Adaptive Dynamics of Infectious Diseases: In Pursuit of Virulence Management*, Cambridge University Press, Cambridge, UK, pp. 39-59 (2002).
- No. 60 Nowak MA, Sigmund K: *Super- and Coinfection: The Two Extremes*. IIASA Interim Report IR-02-008 (2002). Dieckmann U, Metz JAJ, Sabelis MW, Sigmund K (eds): *Adaptive Dynamics of Infectious Diseases: In Pursuit of Virulence Management*, Cambridge University Press, Cambridge, UK, pp. 124-137 (2002).
- No. 61 Sabelis MW, Metz JAJ: *Perspectives for Virulence Management: Relating Theory to Experiment*. IIASA Interim Report IR-02-009 (2002). Dieckmann U, Metz JAJ, Sabelis MW, Sigmund K (eds): *Adaptive Dynamics of Infectious Diseases: In Pursuit of Virulence Management*, Cambridge University Press, Cambridge, UK, pp. 379-398 (2002).
- No. 62 Cheptou P, Dieckmann U: *The Evolution of Self-Fertilization in Density-Regulated Populations*. IIASA Interim Report IR-02-024 (2002). *Proceedings of the Royal Society of London Series B* 269:1177-1186 (2002).
- No. 63 Bürger R: *Additive Genetic Variation Under Intraspecific Competition and Stabilizing Selection: A Two-Locus Study*. IIASA Interim Report IR-02-013 (2002). *Theoretical Population Biology* 61:197-213 (2002).
- No. 64 Hauert C, De Monte S, Hofbauer J, Sigmund K: *Volunteering as Red Queen Mechanism for Co-operation in Public Goods Games*. IIASA Interim Report IR-02-041 (2002). *Science* 296:1129-1132 (2002).
- No. 65 Dercole F, Ferrière R, Rinaldi S: *Ecological Bistability and Evolutionary Reversals under Asymmetrical Competition*. IIASA Interim Report IR-02-053 (2002). *Evolution* 56:1081-1090 (2002).
- No. 66 Dercole F, Rinaldi S: *Evolution of Cannibalistic Traits: Scenarios Derived from Adaptive Dynamics*. IIASA Interim Report IR-02-054 (2002). *Theoretical Population Biology* 62:365-374 (2002).
- No. 67 Bürger R, Gimelfarb A: *Fluctuating Environments and the Role of Mutation in Maintaining Quantitative Genetic Variation*. IIASA Interim Report IR-02-058 (2002). *Genetical Research* 80:31-46 (2002).
- No. 68 Bürger R: *On a Genetic Model of Intraspecific Competition and Stabilizing Selection*. IIASA Interim Report IR-02-062 (2002). *Amer. Natur.* 160:661-682 (2002).
- No. 69 Doebeli M, Dieckmann U: *Speciation Along Environmental Gradients*. IIASA Interim Report IR-02-079 (2002). *Nature* 421:259-264 (2003).
- No. 70 Dercole F, Irisson J, Rinaldi S: *Bifurcation Analysis of a Prey-Predator Coevolution Model*. IIASA Interim Report IR-02-078 (2002).
- No. 71 Le Galliard J, Ferrière R, Dieckmann U: *The Adaptive Dynamics of Altruism in Spatially Heterogeneous Populations*. IIASA Interim Report IR-03-006 (2003).
- No. 72 Taborsky B, Dieckmann U, Heino M: *Unexpected Discontinuities in Life-History Evolution under Size-Dependent Mortality*. IIASA Interim Report IR-03-004 (2003).

Issues of the IIASA Studies in Adaptive Dynamics series can be obtained at www.iiasa.ac.at/Research/ADN/Series.html or by writing to adn@iiasa.ac.at.

Contents

Introduction	1
Model Description	2
Life-history model	2
Evolutionarily optimal life histories	3
Model reduction.....	4
Results	5
Common features of optimal life histories	5
Influence of primary model parameters on optimal life histories	7
Influence of secondary model parameters on optimal life histories	10
Discussion.....	10
Appendix: Optimisation Algorithm.....	14
References	16

Abstract

In many organisms survival depends on body size. We investigate the implications of such size-selective mortality on life-history evolution by introducing and analysing a new and particularly flexible life-history model with the following key features: the lengths of growth and reproductive periods in successive reproductive cycles can vary evolutionarily, the model does not constrain evolution to patterns of either determinate or indeterminate growth, and lifetime number and sizes of broods are the outcome of evolutionarily optimal life-history decisions. We find that when size-dependent mortality is sufficiently strong, small changes in environmental conditions can lead to abrupt transitions in optimal life histories. Such discontinuous switching results from antagonistic selection pressures and occurs between strategies of early maturation with short reproductive periods and late maturation with long reproductive cycles. When mortality size-selective and the size-independent component is not too high, selection favours prolonged juvenile growth, thus allowing individuals to reach a mortality refuge at large body size before the onset of reproduction. When either component of mortality is then increased, the mortality refuge first becomes unattractive and eventually closes up altogether, resulting in short juvenile growth and frequent reproduction. Our results offer a new mechanism for the evolution of life-history dimorphisms.

About the Authors

Barbara Taborsky

Behavioural Ecology, University of Bern, Wohlenstrasse 50A, CH-3032

Hinterkappelen, Switzerland

and

Adaptive Dynamics Network, International Institute for Applied Systems Analysis, A-

2361 Laxenburg, Austria

and

Konrad Lorenz-Institut für Vergleichende Verhaltensforschung (KLIVV),

Savoyenstrasse 1a, A-1160 Vienna, Austria

Ulf Dieckmann

Adaptive Dynamics Network, International Institute for Applied Systems Analysis, A-

2361 Laxenburg, Austria

Mikko Heino

Institute of Marine Research, P.O. Box 1870 Nordnes, N-5817 Bergen, Norway

and

Adaptive Dynamics Network, International Institute for Applied Systems Analysis, A-

2361 Laxenburg, Austria

Acknowledgments

We are indebted for helpful comments by Thomas Ruf and Michael Taborsky on an earlier draft of this manuscript. BT was financed by the Austrian Science Fund, FWF (Grant No. P14327-BIO). UD received complementary funding by the Austrian Federal Ministry of Education, Science, and Cultural Affairs (Contract No. GZ 308.997/2-VIII/B/8a/2000). MH acknowledges financial support by the Academy of Finland (Project 45928).

Unexpected Discontinuities in Life-History Evolution under Size-dependent Mortality

Barbara Taborsky
Ulf Dieckmann
Mikko Heino

Introduction

Body size strongly influences survival in many organisms. Predation risk and over-winter survival, for example, may critically depend on body size (e.g. Sogard 1997). Yet, life-history evolution under size-dependent mortality is still not fully understood. Body size results from an ontogenetic growth process that, in turn, is influenced by size-dependent life-history decisions and ecological conditions (reviewed by Roff 1992). Size-dependent production rates are a key assumption of theoretical studies focusing on evolutionarily optimal patterns of energy allocation (reviewed by Kozłowski 1992 and Perrin & Sibly 1993). Consequently, body size has been identified as an important factor determining life-history decisions in many organisms (e.g. Roff 1992). However, size-dependent mortality rates have received surprisingly little attention in general models of life-history evolution. Even though some earlier investigations considered size-dependent mortality (Sibly *et al.* 1985; Kozłowski & Wiegert 1987; Vance 1992a,b; Perrin *et al.* 1993, Heino & Kaitala 1996), its general implications for evolutionarily stable patterns of growth and reproduction have not yet been systematically explored.

In this paper we introduce a flexible life-history model to investigate evolutionary patterns of growth and reproduction when both mortality and production rates can vary with body size. The model divides the lifetime of an individual into reproductive cycles, with each cycle comprising a period of somatic growth followed by a period devoted to reproduction. To avoid confounding interferences between evolving life-history patterns and those imposed by external influences, we consider non-seasonal environments. The model presented here is unusually versatile in that it allows the length of growth and reproduction periods to vary evolutionarily in all reproductive cycles. This flexibility allows us to encompass potential patterns of determinate and indeterminate growth in a single model. Also the expected number and size of broods can vary in the course of life-history evolution. Such generality has not been considered in earlier models, even

though considerable variation in inter-brood periods is well documented in nature (e.g. Reznick & Endler 1982).

We elucidate the dependence of optimal life-history decisions on the variation of three ecological factors, the growth potential of the environment, and the magnitude of the size-independent and size-dependent components of mortality. According to results by Sibly *et al.* (1985), Kozlowski & Wiegert (1987), Vance (1992a,b), and Perrin *et al.* (1993), gradual variation of these three factors is expected to translate into similarly gradual changes in evolutionarily optimal life histories. Surprisingly, however, our model shows that environmental changes of small magnitude may induce large and abrupt shifts in optimal life histories. Such shifts are associated with transitions from early maturation and short inter-brood intervals to late maturation and long reproductive cycles. Although similarly abrupt transitions are well known to occur in many non-linear dynamical systems (where they are referred to as catastrophic bifurcations; e.g. Abraham & Shaw 1992). It would appear that the potential for such discontinuities to prominently affect life-history evolution has previously been overlooked.

Model Description

Life-history model

We focus on organisms whose life history can be divided into alternating, non-overlapping periods of somatic growth and reproduction. Surplus energy (i.e. energy in excess of maintenance needs) is fully allocated either to somatic growth or to energy accrual for a clutch. At the end of each bout of growth and reproduction (hereafter termed ‘reproductive cycle’) energy invested in reproduction is fully released in form of offspring. The lengths of the time periods devoted to growth and reproduction are the evolving life-history variables in our model. No upper limit was imposed on the duration of these periods. The life-history “decisions” are state-dependent, with individual state being given by body size. Evidently, the length of the first growth period, which determines the immature period, cannot be zero. Subsequent growth periods may have zero lengths; if they are all zero, the growth pattern becomes determinate and no growth occurs after maturation.

Growth and reproduction. For simplicity, we assume that size at birth is zero. Size is measured as length and is denoted by s . The weight w of individuals is assumed to depend on their length according to a general allometric relation,

$$w = \alpha \cdot s^\gamma,$$

where α is a scaling constant and γ is the allometric exponent. Unless otherwise stated, we assume a cubic relationship between weight and length ($\gamma = 3$). We assume that growth is linear and occurs with a rate g throughout growth periods. Thus, during a

growth period of length T_g an individual increases its length by gT_g . This simple linear growth model implies that the size-specific weight production rate is $g \cdot \alpha \cdot \gamma \cdot s^{\gamma-1}$. During a reproductive period, all surplus production is allocated to reproduction. The resulting offspring are released at the end of such a period. Therefore, fecundity F is the product of this weight production rate and the time T_a invested into energy accrual, divided by the weight w_0 of an egg or newborn,

$$F(s, T_a) = \frac{g \cdot \alpha \cdot \gamma}{w_0} \cdot s^{\gamma-1} \cdot T_a \quad .$$

Survival. We assume that mortality depends on body length s according to the following relation,

$$m(s) = m_i + m_d \cdot \exp(-s/s_0) \quad ,$$

where the size-dependent mortality rate $m(s)$ is composed of a size-independent component m_i and a size-dependent component. The magnitude of the latter is determined by m_d , while the parameter s_0 characterizes at which length the size-dependent component of mortality drops to $1/e = 36.8\%$, relative to its value at size $s = 0$. The general shape considered for $m(s)$ is well applicable to a variety of empirically determined dependences of mortality on size (see Discussion). The survival probability P over a period of time from t_0 to t_1 is now given by

$$P = \exp\left(-\int_{t_0}^{t_1} m(s(t)) dt\right) \quad .$$

This equation can be simplified because size increments are constant during growth periods, and no growth occurs during reproductive periods. Thus, survival can be conveniently expressed in terms of size s at the beginning of a reproductive cycle and the durations T_g and T_a allocated to growth and reproduction, respectively,

$$P(s, T_g, T_a) = \exp\left(-\int_0^{T_g} m(s + gt) dt\right) \cdot \exp(-m(s + gT_g) \cdot T_a) \quad ,$$

where the two factors describe survival during growth and reproductive periods, respectively. Based on the chosen function m the remaining integral can be solved analytically. We allow for an additional instantaneous cost of reproduction M , which can be envisaged as the probability of females dying immediately after releasing their offspring.

Evolutionarily optimal life histories

We assume that density dependence acts multiplicatively on reproductive success. Under that assumption, the density of conspecifics does not influence the optimal life-history decisions of individuals, and the optimal reproductive strategy (corresponding to

an evolutionarily stable strategy or ESS) maximizes expected lifetime reproductive success (Mylius & Diekmann 1995).

The expected lifetime reproductive success R_0 is the sum of reproductive output from all reproductive cycles c , with the latter being given by the product of fecundity F_c in cycle c and survival probability P_c up to that cycle,

$$R_0 = \sum_{c=1}^{\infty} F_c \cdot P_c$$

with

$$F_c = F(s_c + gT_{g,c}, T_{a,c}) \quad \text{and} \quad P_c = (1 - M)^{c-1} \cdot \prod_{c'=1}^c P(s_{c'}, T_{g,c'}, T_{a,c'}) \quad ,$$

where s_c is the expected size at the onset of reproductive cycle c , and $T_{g,c}$ and $T_{a,c}$ are the life-history decisions in cycle c .

The optimisation algorithm used to find the ESS $(T_{g,1}^*, T_{a,1}^*, T_{g,2}^*, T_{a,2}^*, \dots)$ based on this expression is described in the Appendix.

Model reduction

At first sight, the model described above comprises eight free parameters: α , γ , w_0 , g , m_i , m_d , s_0 , and M . To simplify the further analysis, we extract the model's essential dimensionless parameters.

We first observe that two of the model parameters have no influence on the ESS: α and w_0 influence lifetime reproductive success only multiplicatively, and thus do not affect the qualitative dependence of R_0 on the evolving life-history variables. Without influencing the evolutionary analysis we can thus assume $\alpha/w_0 = 1$.

Four model parameters specify mortality and growth rates and have the dimensions of size (s_0), time^{-1} (m_i and m_d), and $\text{size} \times \text{time}^{-1}$ (g). Without any loss of generality, these four parameters can be combined into two dimensionless ratios,

$$r_i = m_i \cdot s_0 / g \quad \text{and} \quad r_d = m_d \cdot s_0 / g \quad .$$

By choosing convenient units for size (s_0) and time (s_0/g), we can now remove two of the four parameters: in the chosen units, both s_0 and s_0/g assume the value 1. Hence increases in r_i can result from a strengthening of the size-independent component of mortality, from a shallower decrease of mortality with size, and/or from a decrease in growth potential. Analogously, increasing values of r_d result from a strengthening of the size-dependent component of mortality, from a shallower decrease of mortality with size, and/or from a decrease in growth potential.

Thus by varying only three dimensionless parameters (r_i , r_d , and M) the model's full range of possible environmental settings can be explored. In addition, the allometric exponent γ can be altered. For reasons that will become evident in the course of the

further analysis, we refer to r_i and r_d as the model's primary parameters, and to M and γ as the model's secondary parameters.

Results

Common features of optimal life histories

Our analysis shows that in all model environments optimal life histories share several qualitative features. First and most importantly, in any given environment there is an optimal size: the optimal decision for any individual below this size is to grow to this optimal size, and the optimal decision of individuals at that size is to stay there. The optimal size is the same for all reproductive cycles during an individual's life because life-history decisions depend on size, but not on age *per se*. The optimal size is always reached in one continuous growth period in the first reproductive cycle, and thereby before the onset of reproduction. No further growth occurs after the first cycle. Hence, all optimal life histories in our model follow a pattern of determinate growth, even though we did not *a priori* constrain the mode of growth in any way.

Second, after attaining the optimal size, reproduction takes place in multiple bouts separated by periods during which energy is acquired to produce the next clutch. We thus obtain patterns of iteroparous reproduction, again without any *a priori* constraints on the mode of reproduction. Within an individual's life cycle, the optimal time spent on the acquisition of energy for reproduction is the same for all reproductive cycles because reproductive investment always starts out from the same optimal size.

According to these two qualitative features of optimal life histories, the life cycles of individuals are always divided into two main periods: (i) a pre-reproductive or immature period during which the optimal size is reached, and (ii) a reproductive or mature period, consisting of reproductive cycles of equal lengths, during which the lifetime reproductive success is accrued. In our model, optimal life histories can thus be described by only two life-history variables: the duration T_g^* of the first growth period ($T_{g,1}^* = T_g^*$, $T_{g,2}^* = T_{g,3}^* = \dots = 0$) and the duration T_a^* of the first and all subsequent reproductive periods ($T_{a,1}^* = T_{a,2}^* = \dots = T_a^*$).

Based on this result, the calculation of lifetime reproductive success can be greatly simplified. Survival to the end of the first growth period is $P_g = P(0, T_g, 0)$, survival over one reproductive cycle is $P_a = P(gT_g, 0, T_a)$, and fecundity in each cycle is $F_a = F(gT_g, T_a)$. The lifetime reproductive success of any candidate life history (T_g, T_a) can hence be evaluated as

$$R_0 = \frac{P_g P_a F_a}{1 - (1 - M) P_a} .$$

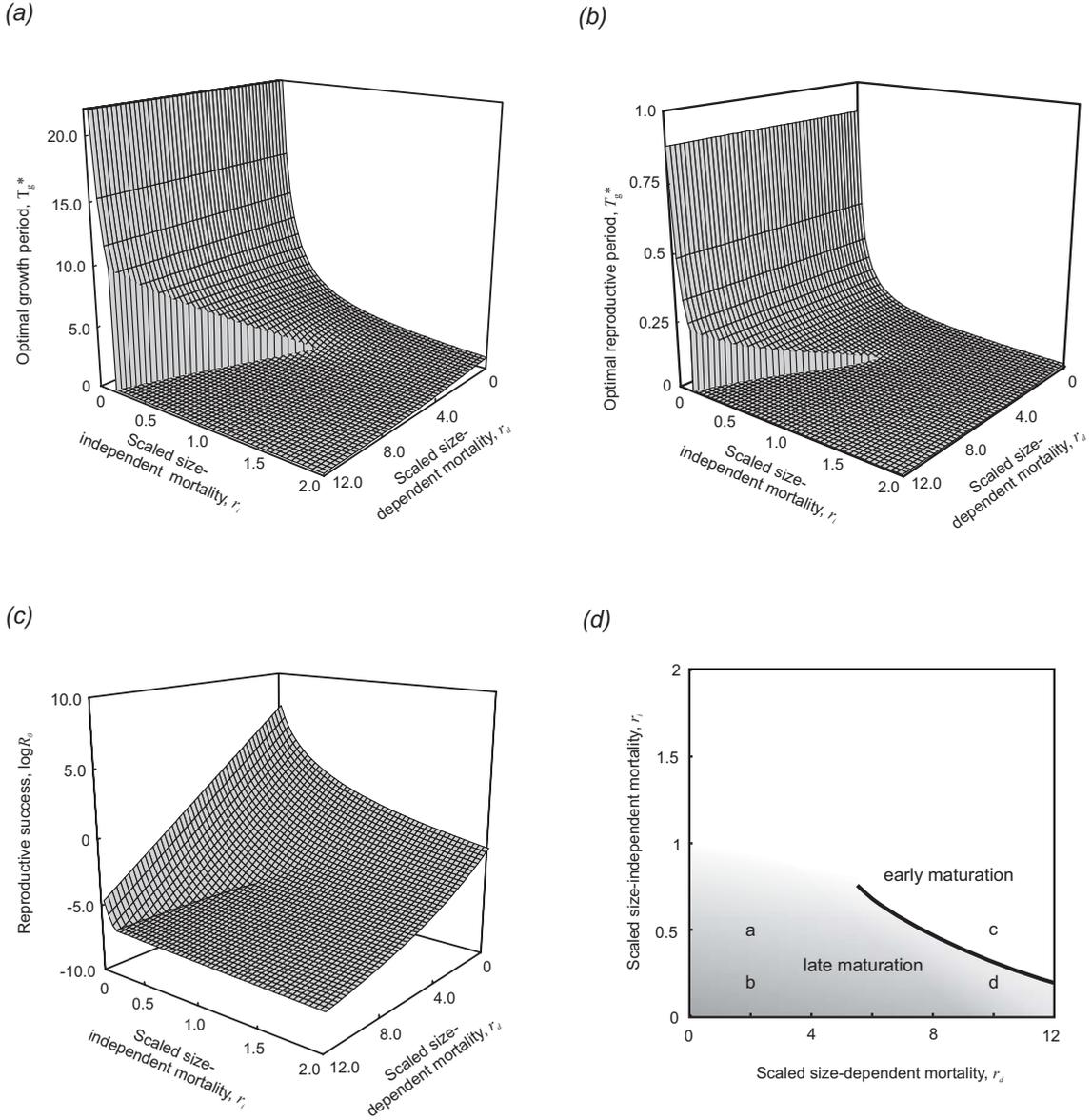


Figure 1. Influence of environmental parameters r_d and r_i on the evolutionarily optimal (a) time invested in growth, T_g^* , and (b) time invested in the accrual of energy for reproduction, T_a^* . (c) Resultant lifetime reproductive success R_0 . The black curve highlights the kink corresponding to the discontinuities in optimal life histories. (d) Schematic overview of life-history regimes. The black curve shows the location of discontinuous transitions of optimal life-history strategies T_g^* and T_a^* , while letters a-d indicate parameter combinations for which fitness landscapes are illustrated in Fig. 2. Other parameters: $M = 0.001$ and $\gamma = 3$.

The previously arduous optimisation task (see Appendix) is thus reduced to a two-dimensional problem. Optimal life histories can now be found easily, for example, by applying Powell's method (Press *et al.* 1992). The following results are based on this simplified algorithm. We first focus on cases in which the cost of reproduction, M , is small and the allometric exponent γ is set to its most likely value at $\gamma = 3$.

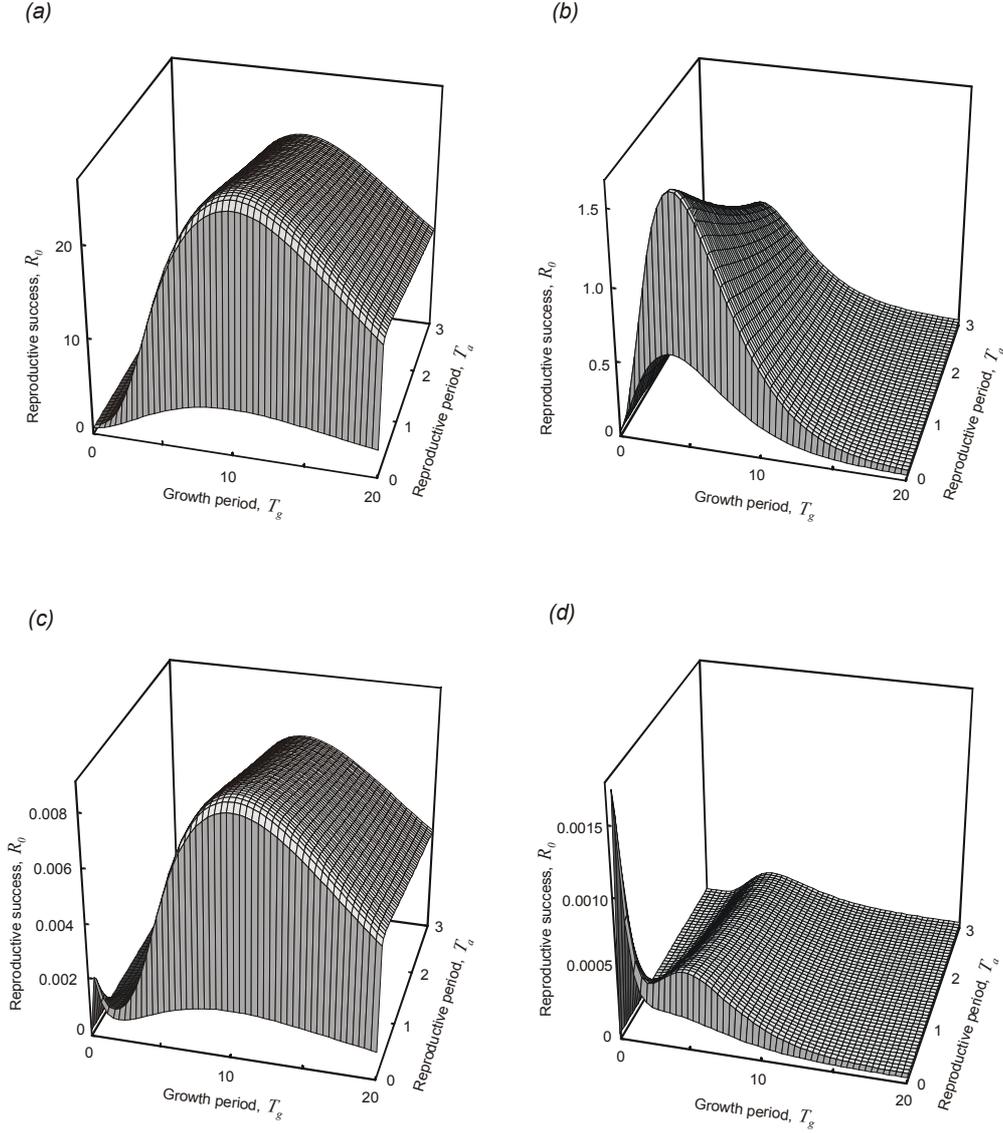


Figure 2. Lifetime reproductive success of all possible life-history strategies with $0.001 < T_g^* < 20$ and $0.001 < T_a^* < 3$ for (a) $r_d = 0.5$, $r_i = 2$; (b) $r_d = 0.2$, $r_i = 2$; (c) $r_d = 0.5$, $r_i = 10$; and (d) $r_d = 0.2$, $r_i = 10$. Note the drastic change in the relative magnitude of the two local maxima between panels (c) and (d) that straddle the life-history discontinuity in Fig. 1d. Other parameters: $M = 0.001$ and $\gamma = 3$.

Influence of primary model parameters on optimal life histories

We find that optimal life histories differ qualitatively for small and for large values of r_i (Fig. 1a,b). For small r_i , variation of r_d affects optimal strategies only weakly. Increasing r_i leads to a shortening of growth and reproductive periods. For larger r_i , both periods become shorter with an increase of r_i and r_d , with the effect of r_i being weaker than that of r_d .

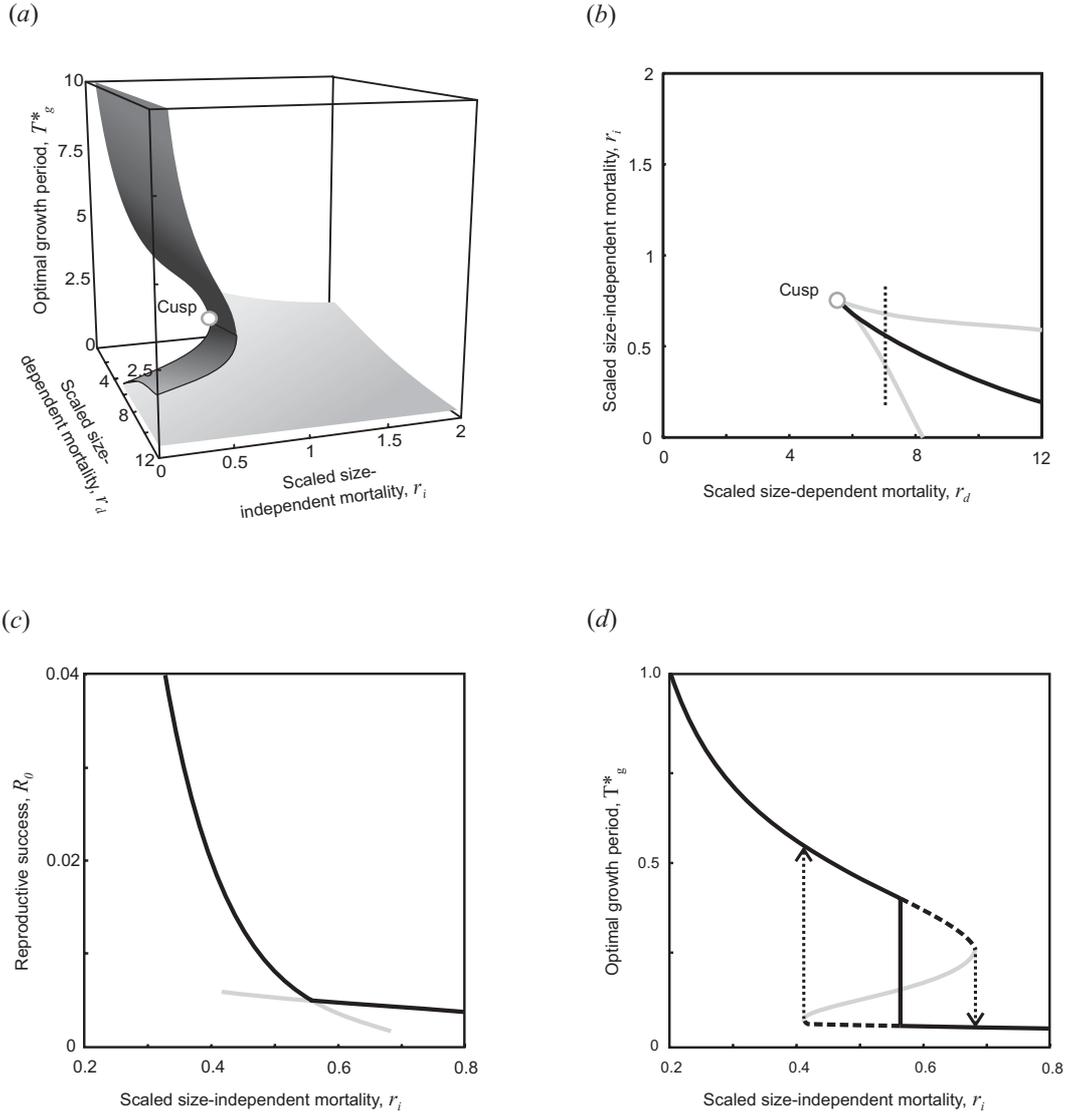


Figure 3. (a) The cusp bifurcation. The folded surface shows the variation of T_g^* with r_i and r_d . For some values of r_i and r_d , evolutionary equilibria are reached at three values of T_g^* . In these cases, the inner value corresponds to an unstable equilibrium (saddle; corresponding parts of surface outlined in black), whereas the outer values correspond to alternative evolutionary attractors at local fitness maxima. (b) Overview of evolutionary bifurcation curves. The black curve indicates the environmental conditions for which the two local fitness maxima swap rank. Grey curves describe the conditions that lead to the disappearance of one of the two local maxima through collision with the intermediate fitness saddle. As indicated by these bifurcation curves, the discontinuity found in our model represents a cusp bifurcation. The dashed line highlights the position of the cross-section illustrated in the subsequent panels. (c) Cross-section of Fig. 1c: variation of R_0 with r_i at $r_d = 7.0$ for the two local fitness maxima. The values R_0^* at the global fitness maximum are shown in black, and those of the alternative local maximum in grey. (d) Cross-section of Fig. 1a: variation of T_g^* with r_i at $r_d = 7.0$, showing the resulting discontinuous life-history switches. The continuous black curve highlights the position of global fitness maxima, and the grey curve that of fitness minima. The dashed curves describe the position of local fitness maxima that are not global fitness maxima. The vertical dotted lines indicate abrupt evolutionary transitions that result from the disappearance of a local fitness maximum. Other parameters: $M = 0.001$ and $\gamma = 3$.

For low r_d , increasing r_i leads to a gradual change from life histories with long growth periods and late maturation towards life histories with short growth periods and early maturation. For higher r_d , however, increasing r_i results in an unexpected abrupt transition between life histories with long and with short periods of growth and reproduction. This discontinuous switch of life-history strategies is accompanied by a kink in the fitness surface (Fig. 1c, black line). Fig. 1d summarizes the established optimal life histories schematically.

A closer look at the fitness of possible decisions in different sample environments illustrates what happens at the life-history switch. While for small r_d only a single fitness maximum exists (Fig. 2a,b), two local fitness maxima are present for larger r_d . At the life-history switch (i.e. along the black curve in Fig. 1d), these maxima are of equal height. For slightly larger r_i (above the black curve), life histories with short periods of growth and reproduction are globally optimal (Fig. 2c), while for slightly smaller r_i (below the black curve) this applies to long periods of growth and reproduction (Fig. 2d).

The so-called cusp bifurcation underlying all discontinuities described in this paper is shown in Fig. 3a. The resultant projection in Fig. 3b highlights the mortality conditions that allow for two locally optimal life histories (conditions within the grey wedge). To understand which one of these alternative evolutionary outcomes we should actually expect to observe in nature, we have to distinguish between two qualitatively different scenarios:

- If each candidate life history that is situated between the two local optima remains present in the system, or if immigrants constantly provide a sufficiently variable inflow of alternative life histories, or if feasible mutational steps are large enough, we expect that evolution can always attain the global optimum, since it ‘samples’ both fitness maxima. Such a population is expected to switch rapidly to the highest maximum, and such a life-history switch should occur just at those environmental conditions for which the fitness functions corresponding to the two local optima intersect (Fig. 3c).
- By contrast, if one assumes that adaptation is gradual and occurs through small changes in life-history strategies, it is unlikely that a population can track the globally optimal life history: this would require evolution to pass through a fitness minimum (grey line in Fig. 3d). Rather, such populations are expected to adhere to a locally optimal life history (stippled lines in Fig 3d) until it vanishes. Evolution to the other optimum is thus likely to occur only when, through ongoing environmental change, the tracked local fitness maximum disappears (by colliding, in one dimension, with the local fitness minimum, or, in two dimensions, with a fitness saddle). After such a collision, only the alternative fitness maximum remains, which the population can then attain through

directional selection, without any longer being impeded by the existence of an intermediate fitness minimum. Slow environmental change may thus drive a population's life history from one fitness maximum to another. If this occurs repeatedly through environmental fluctuations, the evolutionarily optimal life history exhibits a hysteresis.

Influence of secondary model parameters on optimal life histories

Above the effects of environmental parameters r_d and r_i were explored for fixed values of M (the instantaneous costs of reproduction) and γ (the allometric exponent in the size-fecundity relationship). The response of optimal life histories towards variation of r_d and r_i remains qualitatively the same when M and γ are varied.

Quantitatively, a reduction of the cost M results in shortening of the time invested in reproduction. At the limit in which the cost approaches zero, reproductive cycles become infinitely short, i.e. reproduction becomes continuous. Importantly, however, variation of M leaves the position of the cusp in the r_d - r_i -diagram (Fig. 1, 3a,b) essentially unaffected.

When decreasing the exponent γ , the tendency of evolutionarily optimal growth and reproductive periods to increase with r_d becomes more pronounced. For γ equal to 1, the cusp leaves the r_d - r_i -diagram (Fig. 1, 3a,b) at $r_d = 0$. The general importance of the life-history switches highlighted in this paper is underscored by the fact that even for γ smaller than 1 the dependence of life-history decision on the model's primary parameters remains discontinuous.

Discussion

Our model predicts discontinuous transitions between dissimilar life histories. We expect such discontinuities for a wide range of environmental conditions in which size-dependent components of mortality are sufficiently large and not dominated by size-independent components. They can occur both for locally adapting populations along environmental gradients in space and in evolving single populations through environmental change over time. In the course of transitions, life histories change abruptly from early maturation with frequent reproduction to late maturation with long reproductive cycles.

Qualitative jumps of life-history strategies along gradients in non-fluctuating environments were not observed in previous models of life-history evolution. Outside of the range of environmental conditions that lead to discontinuous transitions, in particular when size-dependent mortality is absent or weak, our model agrees with earlier findings by Kozłowski & Wiegert (1986) in that increasing size-independent mortality leads to a continuous decrease of immature growth and reproductive periods.

In a somewhat different context, evolutionary bifurcations were observed in reaction norms for morphological traits by van Dooren (2001), although this model considered dynamic environments with temporal oscillations in the fitness optimum, and a time lag between life-history decisions and their fitness consequences. To our knowledge, models of life-history evolution allowing for a level of flexibility in life histories similar to the model introduced here, with reproductive periods of arbitrary length, have not been analysed before. We have shown that, despite this flexibility, our model comprises only two salient environmental parameters and only two salient life-history variables, which provides an attractive compromise between generality and tractability.

The discontinuity predicted by our model may be interpreted biologically as the outcome of two antagonistic selection pressures: one for early maturation and almost continuous production of small clutches, and another for late maturation and the production of a few large clutches. To escape negative size-selective mortality, individuals may reach a “mortality refuge” by growing quickly to a large body size, i.e., without any delay incurred by reproduction. For example, some bivalve species start to reproduce only after growing to a refuge size at which they are safe from their major predator (Nakaoka 1998). Increasing levels of size-dependent mortality select for a prolongation of the initial growth period. At high mortality, however, long initial growth periods result in very low probabilities to survive to first reproduction. Eventually, an alternative life-history strategy based on short periods of growth and reproduction becomes evolutionarily optimal. Especially size-unselective mortality strongly selects for shorter immature growth periods and smaller sizes at maturation (Roff 1992; see Reznick *et al.* 1996 for an empirical example). In other words, in environments with sufficiently high size-dependent mortality and relatively low size-independent mortality, divergent selection pressures may create a mortality refuge that vanishes abruptly when mortality increases.

Evolutionarily optimal life histories as found in our model may be expressed by different genotypes, each adapted to a different environment, or by a single genotype exhibiting a reaction norm in response to the conditions of mortality and growth it actually experiences. In the latter case, populations with a bimodal distribution of life-history strategies are likely to exist under certain environmental conditions. There are a number of species which show marked differences in adult size and life history within a local area, ranging from normal forms to “dwarfs” with stunted growth (reviewed in Roff 1992). Usually, dwarfs mature earlier and live shorter than individuals with normal growth (Roff 1992). In some populations of fish (e.g. smelts *Osmerus* spp., Taylor & Bentzen 1993; Arctic charr *Salvelinus alpinus*, Parker *et al.* 2001; lake whitefish *Coregonus clupeaformis*, Trudel *et al.* 2001) and invertebrates (e.g. red-sea urchin *Strongylocentrotus franciscanus*, Botsford *et al.* 1994), the extremes at both ends of this size spectrum coexist sympatrically, with a truly bimodal distribution of normal and

dwarf forms. These coexisting life-history morphs can lie anywhere on a spectrum between ecological polymorphisms (through phenotypic plasticity) and genetically distinct groups without gene flow (Taylor & Bentzen 1993; evidence reviewed in Parker *et al.* 2001).

Even though we did not prescribe the growth pattern in our model in any way, optimal phenotypes exhibit determinate growth across all modelled environments. Previous life-history models found indeterminate growth to be optimal only under restrictive environmental conditions (e.g. unpredictable season length), physiological or morphological constraints, or age-dependent mortality (see reviews by Cichon 1999 and Heino & Kaitala 1999). The universal occurrence of determinate growth in our model was therefore not unexpected, as we did not include such specific assumptions.

Below we critically review the assumptions included in our analysis. Empirical relevance and checks of robustness are considered where possible, and alternative approaches are briefly discussed:

- Our results show that life-history strategies may change abruptly if mortality is modelled by the combination of a constant level and an exponential function of size. Such a relation in fact provided excellent fits to empirical data in species with size-dependent mortality (Hutchings 1993, F. Bashey, pers. comm.). Alternatively, size-dependent mortality can be modelled as a hyperbolic function, $m(s) = m_i + m_d / (1 + s/s_0)^\beta$. Owing to the additional parameter β a hyperbolic model allows more flexibility when fitting it to data. Assuming a hyperbolic function does not qualitatively alter the results presented here. For $\beta > 1$, two local fitness maxima and discontinuities in the global optimum always occur and, across all model environments, we find optimal life-history patterns with determinate growth.
- We assumed that the environmentally determined growth potential is constant throughout growth periods. The assumption of linear growth in length may appear simplistic. However, many ectotherms show linear growth of structural size in early life stages, sometimes even until maturation (American plaice *Hippoglossoides platessoides*, Roff 1983; cod *Gadus morhua*, Jørgensen 1992; fire salamander *Salamandra salamandra*, Alcobendas & Castanet 2000; freshwater clam *Anodonta grandis*, Hanson *et al.* 1988). We chose linear growth to avoid the impact of a predefined growth model on optimal life-history decisions. Any growth model depending on length or weight would inevitably influence the size-dependent life-history decisions of individuals (Czarnoleski & Kozłowski 1998).
- There is ample evidence that reproductive activities may reduce survival. For example, mating itself may reduce female survival, conspicuous reproductive

behaviours may increase predation risk, or a lowered body condition may enhance the susceptibility to stress and diseases (reviewed in Roff 1992). In the model, we expressed costs of reproduction in a very general way, as instantaneous costs affecting survival after the release of offspring. Costs of reproduction did not influence any model results qualitatively, but when approaching zero led to infinitely short reproductive periods.

- We assumed that fecundity was proportional to weight production rate (which is a power function of size; e.g. Roff 1983) and not limited by physiological or morphological constraints. When testing the robustness of the results to these two assumptions we found no qualitative change when (i) the allometric exponent of the size-weight relationship was varied, as long as it exceeded 1, and (ii) an upper bound for clutch weight was introduced that increased with maternal weight.

In summary, our assumptions about size-dependent mortality, growth mode, reproductive costs, and the nature of the fecundity-size relationship did not critically influence the model results. In particular the reported discontinuities in optimal patterns of growth and reproduction appear to be a very robust feature of life-history evolution under size-dependent mortality.

To conclude, our results show that in spatially heterogeneous or temporally varying environments small changes in mortality and/or growth conditions can induce drastic changes in optimal life histories. A generalist type may perform poorly under such conditions. The divergent selection pressures near the discontinuity may facilitate the emergence of distinct ecotypes, even when environmental conditions vary gradually. Our results could therefore offer a new mechanism for the emergence of ecological polymorphisms – which, in turn, may lead to genetic differentiation and eventually even lead to sympatric speciation.

Appendix: Optimisation Algorithm

We utilize a dynamic optimisation algorithm (see Houston & McNamara 1999; Clark & Mangel 2000) to determine optimal life histories. In our model, the optimal life-history decisions during a given reproductive cycle depend only on the size of an individual at the onset of the cycle (size is the only state variable, since there is no explicit age dependence of demographic rates), and on the fitness consequences of the decisions in the current cycle. The latter can be decomposed into (i) the fitness gain from the current cycle (i.e. the product of the survival probability to the end of the cycle and the fecundity realized then) and (ii) the fitness contributions from future reproductive cycles (given by the product of the survival probability to the end of the cycle and the reproductive value at that stage).

Reproductive values thus depend on all life-history decisions in an individual's future. Therefore, they are initially unknown and have to be found through a process of backward iteration. The general procedure can be summarized as follows. First, reproductive values for all relevant sizes are set to zero. Second, optimal decisions are determined for all relevant sizes, given the current estimates of size-specific reproductive values. Third, the estimates are updated with the reproductive values obtained as the result of the optimal decisions. Fourth, the second and third steps are repeated until convergence is achieved, that is, until reproductive values do not significantly change any more. From this, optimal decisions at all relevant sizes are determined.

More precisely, the following optimisation algorithm has been used in this study:

1. Initialise the optimisation procedure by setting to zero the reproductive values $R(s)$ for each of n evenly spaced sizes between $s = 0$ and $s = s_{\max}$.
2. For each size s , search for the life-history decisions $T_g(s)$ and $T_a(s)$ that confer the highest reproductive value,

$$(T_g(s), T_a(s)) = \arg \max_{(T_g, T_a)} R'(s, T_g, T_a) \quad ,$$

given the current size-specific reproductive values $R(s)$,

$$R'(s, T_g, T_a) = P(s, T_g, T_a) \cdot [F(s + gT_g, T_a) + R(s + gT_g)] \quad .$$

3. For each size s , replace $R(s)$ with $R'(s, T_g(s), T_a(s))$.
4. Repeat steps 2 and 3 until the convergence criterion,

$$\frac{1}{n} \cdot \sum_{s=0}^{s_{\max}} [(R(s) - R'(s, T_g(s), T_a(s))) / R(s)]^2 < c \quad ,$$

is met.

After convergence has been achieved, for each size s at the beginning of a reproductive cycle we obtained the optimal life-history decisions $T_g^*(s)$ and $T_a^*(s)$, together with the corresponding reproductive values $R^*(s)$. The optimal life history is then determined by forward iteration: starting at age and size zero at the onset of the first reproductive cycle, individuals grow and reproduce according to the obtained optimal life-history decisions.

To ensure that the global optimum has been identified in step 2 instead of a local one, we utilized a combination of exhaustive and simplex search (Press *et al.* 1992). The exhaustive search is used initially for searching for local maxima on a pre-defined grid of values (T_g, T_a) ; a subsequent simplex search is then used for fine-tuning the coarsely established globally optimal life-history decisions through local search. We used $n=100$ size classes, with s_{\max} (the largest size considered) re-set iteratively, when necessary, such that the maximum size corresponding to the optimal life history is within the range of 20% to 80% of s_{\max} . Quadratic interpolation was employed to obtain reproductive values for sizes falling between size bins, and a value of $c = 10^{-6}$ was used in the convergence criterion.

References

- Alcobendas, M. & Castanet, J. 2000. Bone growth plasticity among populations of *Salamandra salamandra*: Interactions between internal and external factors. *Herpetologica* **56**, 14-26.
- Abraham, L., Shaw, K. 1992 *Dynamics, The Geometry of Behaviour*. Redwood City: Addison-Wesley.
- Botsford, L.W., Smith, B.D. & Quinn, J.F. 1994. Bimodality in size distributions - the red sea urchin *Strongylocentrotus franciscanus* as an example. *Ecological Applications* **4**, 42-50.
- Cichon, M. 1999. Growth after maturity as a sub-optimal strategy. *Acta Oecologica* **20**, 25-28.
- Clark, C.W. & Mangel, M. 2000. *Dynamic State Variable Models in Ecology*. Oxford: Oxford Series in Ecology and Evolution.
- Czarnoleski, M. & Kozłowski, J. 1998. Do Bertalanffy's growth curves result from optimal resource allocation? *Ecology Letters* **1**, 5-7.
- 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.
- Heino, M. & Kaitala, V. 1996. Optimal resource allocation between growth and reproduction in clams: why does indeterminate growth exist? *Functional Ecology* **10**, 245-251.
- Heino, M. & Kaitala, V. 1999. Evolution of resource allocation between growth and reproduction in animals with indeterminate growth. *Journal of Evolutionary Biology* **12**, 423-429.
- Houston, A.I. & McNamara, J.M. 1999. *Models of Adaptive Behaviour*. Cambridge: Cambridge University Press.
- Hutchings, J.A. 1993. Adaptive life histories effected by age-specific survival and growth rate. *Ecology* **74**, 673-684.
- Jørgensen, T. 1992. Long-term changes in growth of Northeast Arctic cod (*Gadus morhua*) and some environmental influences. *ICES Journal of Marine Science* **49**, 263-277.
- 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. & Wiegert, R.G. 1986. Optimal Allocation of Energy to Growth and Reproduction. *Theoretical Population Biology* **29**, 16-37.
- Kozłowski, J. & Wiegert, R.G. 1987. Optimal age and size at maturity in annuals and perennials with determinate growth. *Evolutionary Ecology* **1**, 231-244.
- Mylius, S.D. & Diekmann, O. 1995. On evolutionarily stable life histories, optimization and the need to be specific about density dependence. *Oikos* **74**, 218-224.

- Nakaoka, M. 1998. Optimal resource allocation of the marine bivalve *Yoldia notabilis*: The effects of size-limited reproductive capacity and size-dependent mortality. *Evolutionary Ecology* **12**, 347-361.
- Parker, H.H., Noonburg, E.G. & Nisbet, R.M. 2001. Models of alternative life-history strategies, population structure and potential speciation in salmonid fish stocks. *Journal of Animal Ecology* **70**, 260-272.
- Perrin, N., Sibly, R.M. & Nichols, N. 1993. Optimal growth strategies when mortality and production rates are size dependent. *Evolutionary Ecology* **7**, 576-592.
- Press, W.H., Teukolsky, S.A., Vetterling W.T. & Flannery, B.P. (1992), *Numerical Recipes in C: The Art of Scientific Computing*, Second Edition, Cambridge University Press.
- Reznick, D. & Endler, J.A. 1982. The impact of predation on life history evolution in Trinidadian guppies (*Poecilia reticulata*). *Evolution* **36**, 160-177.
- Reznick, D.N., Rodd, F.H. & Cardenas, M. 1996. Life-history evolution in guppies (*Poecilia reticulata*: Poeciliidae). IV. Parallelism in life-history phenotypes. *The American Naturalist* **147**, 319-338.
- Roff, D.A. 1983. An allocation model of growth and reproduction in fish. *Canadian Journal of Fisheries and Aquatic Science* **40**, 1395-1404.
- Roff, D.A. 1992. *The Evolution of Life Histories. Theory and Analysis*. New York: Chapman & Hall.
- Sibly, R., Calow, P. & Nichols, N. 1985. Are patterns of growth adaptive? *Journal of theoretical Biology* **112**, 553-574.
- Sogard, S.M. 1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. *Bulletin of Marine Science* **60**, 1129-1157.
- Taylor, E.B. & Bentzen, P. 1993. Evidence for multiple origins and sympatric divergence of trophic ecotypes of smelt (*Osmerus*) in northeastern North America. *Evolution* **47**, 813-832.
- Trudel, M., Tremblay, A., Schetagne, R. & Rasmussen, J.B. 2001. Why are dwarf fish so small? An energetic analysis of polymorphism in lake whitefish (*Coregonus clupeaformis*). *Canadian Journal of Fisheries and Aquatic Science* **58**, 394-405.
- van Dooren, T.J.M. 2001. Reaction norms with bifurcations shaped by evolution. *Proceedings of the Royal Society London, Series B* **268**, 279-287.
- Vance, R.R. 1992a. Optimal Somatic Growth and Reproduction in a Limited, Constant Environment: Organisms with Determinate Growth. *Journal of theoretical Biology* **157**, 31-50.
- Vance, R.R. 1992b. Optimal Somatic Growth and Reproduction in a Limited, Constant Environment: The General Case. *Journal of theoretical Biology* **157**, 51-70.