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Interim Report

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Mothers determine offspring size in response to own juvenile growth conditions

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- 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).
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- 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).
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- 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).
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- 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).
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- 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).
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- 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). Journal of Evolutionary Biology 16:143-153 (2003).
- 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-00-57 (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: *Taking Stock: 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). *SIAM Journal on Applied Mathematics* 63:1378-1391 (2003).
- 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). *Evolution* 57:1-17 (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). *Proceedings of the Royal Society of London Series B* 270:713-721 (2003).
- No. 73 Gardmark A, Dieckmann U, Lundberg P: *Life-History Evolution in Harvested Populations: The Role of Natural Predation*. IIASA Interim Report IR-03-008 (2003). *Evolutionary Ecology Research* 5:239-257 (2003).
- No. 74 Mizera F, Meszéna G: *Spatial Niche Packing, Character Displacement and Adaptive Speciation Along an Environmental Gradient*. IIASA Interim Report IR-03-062 (2003). *Evolutionary Ecology Research* 5:363-382 (2003).
- No. 75 Dercole F: *Remarks on Branching-Extinction Evolutionary Cycles*. IIASA Interim Report IR-03-077 (2003). *Journal of Mathematical Biology* 47:569-580 (2003).
- No. 76 Hofbauer J, Sigmund K: *Evolutionary Game Dynamics*. IIASA Interim Report IR-03-078 (2003). *Bulletin of the American Mathematical Society* 40:479-519 (2003).
- No. 77 Ernande B, Dieckmann U, Heino M: *Adaptive Changes in Harvested Populations: Plasticity and Evolution of Age and Size at Maturation*. IIASA Interim Report IR-03-058 (2003). *Proceedings of the Royal Society of London Series B-Biological Sciences* 271:415-423 (2004).
- No. 78 Hanski I, Heino M: *Metapopulation-Level Adaptation of Insect Host Plant Preference and Extinction-Colonization Dynamics in Heterogeneous Landscapes*. IIASA Interim Report IR-03-028 (2003). *Theoretical Population Biology* 63:309-338 (2003).
- No. 79 van Doorn G, Dieckmann U, Weissing FJ: *Sympatric Speciation by Sexual Selection: A Critical Re-Evaluation*. IIASA Interim Report IR-04-003 (2004). *American Naturalist* 163:709-725 (2004).
- No. 80 Egas M, Dieckmann U, Sabelis MW: *Evolution Restricts the Coexistence of Specialists and Generalists - the Role of Trade-off Structure*. IIASA Interim Report IR-04-004 (2004). *American Naturalist* 163:518-531 (2004).

- No. 81 Ernande B, Dieckmann U: *The Evolution of Phenotypic Plasticity in Spatially Structured Environments: Implications of Intraspecific Competition, Plasticity Costs, and Environmental Characteristics*. IIASA Interim Report IR-04-006 (2004). *Journal of Evolutionary Biology* 17:613-628 (2004).
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- No. 85 Nowak MA, Sigmund K: *Evolutionary Dynamics of Biological Games*. IIASA Interim Report IR-04-013 (2004). *Science* 303:793-799 (2004).
- No. 86 Vukics A, Asbóth J, Meszéna G: *Speciation in Multidimensional Evolutionary Space*. IIASA Interim Report IR-04-028 (2004). *Physical Review* 68:041-903 (2003).
- No. 87 de Mazancourt C, Dieckmann U: *Trade-off Geometries and Frequency-dependent Selection*. IIASA Interim Report IR-04-039 (2004). *American Naturalist* 164:765-778 (2004).
- No. 88 Cadet CR, Metz JAJ, Klinkhamer PGL: *Size and the Not-So-Single Sex: disentangling the effects of size on sex allocation*. IIASA Interim Report IR-04-084 (2004). *American Naturalist* 164:779-792 (2004).
- No. 89 Rueffler C, van Dooren TJM, Metz JAJ: *Adaptive Walks on Changing Landscapes: Levins' Approach Extended*. IIASA Interim Report IR-04-083 (2004). *Theoretical Population Biology* 65:165-178 (2004).
- No. 90 de Mazancourt C, Loreau M, Dieckmann U: *Understanding Mutualism When There is Adaptation to the Partner*. IIASA Interim Report IR-05-016 (2005). *Journal of Ecology* 93:305-314 (2005).
- No. 91 Dieckmann U, Doebeli M: *Pluralism in Evolutionary Theory*. IIASA Interim Report IR-05-017 (2005). *Journal of Evolutionary Biology* 18:1209-1213 (2005).
- No. 92 Doebeli M, Dieckmann U, Metz JAJ, Tautz D: *What We Have Also Learned: Adaptive Speciation is Theoretically Plausible*. IIASA Interim Report IR-05-018 (2005). *Evolution* 59:691-695 (2005).
- No. 93 Egas M, Sabelis MW, Dieckmann U: *Evolution of Specialization and Ecological Character Displacement of Herbivores Along a Gradient of Plant Quality*. IIASA Interim Report IR-05-019 (2005). *Evolution* 59:507-520 (2005).
- No. 94 Le Galliard J, Ferrière R, Dieckmann U: *Adaptive Evolution of Social Traits: Origin, Trajectories, and Correlations of Altruism and Mobility*. IIASA Interim Report IR-05-020 (2005). *American Naturalist* 165:206-224 (2005).
- No. 95 Doebeli M, Dieckmann U: *Adaptive Dynamics as a Mathematical Tool for Studying the Ecology of Speciation Processes*. IIASA Interim Report IR-05-022 (2005). *Journal of Evolutionary Biology* 18:1194-1200 (2005).
- No. 96 Brandt H, Sigmund K: *The Logic of Reprobation: Assessment and Action Rules for Indirect Reciprocity*. IIASA Interim Report IR-04-085 (2004). *Journal of Theoretical Biology* 231:475-486 (2004).
- No. 97 Hauert C, Haiden N, Sigmund K: *The Dynamics of Public Goods*. IIASA Interim Report IR-04-086 (2004). *Discrete and Continuous Dynamical Systems - Series B* 4:575-587 (2004).
- No. 98 Meszéna G, Gyllenberg M, Jacobs FJA, Metz JAJ: *Link Between Population Dynamics and Dynamics of Darwinian Evolution*. IIASA Interim Report IR-05-026 (2005). *Physical Review Letters* 95:Article 078105 (2005).
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- No. 106 Durinx M, Metz JAJ: *Multi-type Branching Processes and Adaptive Dynamics of Structured Populations*. IIASA Interim Report IR-05-074 (2005). Haccou P, Jager P, Vatutin V (eds): *Branching Processes: Variation, Growth and Extinction of Populations*, Cambridge University Press, Cambridge, UK, pp. 266-278 (2005).
- No. 107 Brandt H, Sigmund K: *The Good, the Bad and the Discriminator - Errors in Direct and Indirect Reciprocity*. IIASA Interim Report IR-05-070 (2005). *Journal of Theoretical Biology* 239:183-194 (2006).
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Mothers determine offspring size in response to own juvenile growth conditions

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Through non-genetic maternal effects, mothers can tailor offspring phenotype to the environment in which young will grow up. If juvenile and adult ecologies differ, the conditions mothers had experienced as juveniles may better predict their offspring's environment than the adult environment of mothers. In this case maternal decisions about investment in offspring quality should be determined already during the juvenile phase of mothers. I tested this hypothesis by manipulating juvenile and adult maternal environments independently in a cichlid fish. Females raised in a poor environment produced larger young than females raised without food limitations, irrespective of the feeding conditions experienced during adulthood. This maternal boost was due to a higher investment in eggs, and to faster larval growth. Apparently mothers prepare their offspring for similar environmental conditions as they had encountered as juveniles. This explanation is supported by the distribution of these fish under natural conditions. Juveniles live in a different and much narrower range of habitats than adults. Therefore, the habitat mothers experienced as juveniles will allow them to predict their offspring's environment better than the conditions in the adult home range.

INTRODUCTION

Non-genetic maternal effects are widespread and strongly influence the fitness of mothers and offspring (reviewed in Mousseau & Fox 1998, Lindström 1999, Lummaa & Clutton-Brock 2002). Egg size (Bernardo 1996, Mousseau & Fox 1998) and quality (e.g. Schwabl et al. 1997, Blount et al. 2002) are important maternal effects, which can determine the entire life histories of offspring (Lindström 1999). Maternal effects may depend on maternal condition (e.g. Blount et al. 2002) and on the conditions in the current environment (Mousseau & Fox 1998, Lindström 1999) or during preceding breeding events (Reznick & Yang 1993).

While this appears to be adequate in some cases, in many animals successive life stages use different habitats (reviewed in Werner & Gilliam 1984) or they use resources differently within the same habitat (e.g. Lind & Welsh 1994). If juvenile and adult ecologies are uncorrelated, cues from the current conditions are a poor predictor of the environment offspring are likely to encounter (Bernardo 1996). In such cases the conditions a female encountered as juvenile may allow her to predict her offspring's environment with a much higher precision. Consequently, maternal investment decisions should be determined by a mother's early development (*sensu* Lindström 1999), but should be independent of the environmental conditions in which young are produced.

I tested this hypothesis experimentally with the African cichlid *Simochromis pleurospilus* by independently varying the resource availability of juveniles and adult females. In the field, I tested the prediction that the habitat use of adult females and juveniles differs, so that the environmental conditions experienced these stages are rather independent of each other.

MATERIALS AND METHODS

I raised 120 fish (among them 55 females) of the maternally mouthbrooding cichlid *Simochromis pleurospilus*, each in a separate tank, exposing aliquot numbers to high-food (H) and low-food (L) conditions (juvenile treatment, J) (see electronic Appendix A and Taborsky (2005) for details on experimental set-up). Fish were fed six days a week standardized agarose gel cubes containing an amount of Tetramin® flake food corresponding to 12% or 4% of mean body weight plus 5% *Spirulina* algae. I adjusted the food amounts to increasing body weight every 14 days. The juvenile treatment took on average 265 days and covered the period between independence of young (mean age 29 days) and the end of the first breeding attempt. Afterwards, half of all reproductively active females ($n=23$) were switched to the opposite treatment, while the remaining 23 females stayed on the original ration (adult treatment, A). Siblings were assigned alternately to high or low food ration as juveniles, and to switched or original ration during the adult treatment to achieve equal brood splitting. The resulting treatment groups were

denoted as HH ($n=13$), HL ($n=10$), LH ($n=11$) and LL ($n=12$). For each successive brood a female was mated with a different male (Taborsky (2005) gives details about schedules of male presence in female tanks). About 50% of females never raised a brood successfully despite spawning several clutches. Females remained in the adult treatment until they stopped to produce further clutches (mean reproductive lifespan in experiment: 264.5d; Taborsky 2005).

Brood care of *S. pleurospilus* consists of two phases, two weeks of continuous incubation when young use up yolk reserves ('1st incubation phase') and two weeks when young are periodically released from the mouth for feeding ('2nd incubation phase'). Total length (TL; nearest 0.5mm) and weight (W; nearest 0.01g) of females and young (TL: nearest 0.1mm, W: nearest 0.0001g) and weight of females and young were measured at the end of both incubation phases. I calculated Fulton's condition factor K as $K=100 \times W/TL^3$, and specific growth rates of young (SGR) as $\ln(TL_2/TL_1)/t$, where TL_1 , TL_2 are lengths at the beginning and end of the second incubation phase and t is the duration of this phase. As SGR depends on absolute size, it was corrected for TL_1 . The experiment lasted from November 2001 to May 2004. One clutch each was collected of all females that spawned during the last six months of this period (3HH, 4HL, 4LH, and 4LL females) to measure egg mass. Clutches could not be collected earlier, as this would have interfered with the measurement of reproductive rates of females (see Taborsky 2005). Mean clutch mass was calculated from individual egg dry mass measured to the nearest 0.0001g.

I calculated two-way analyses of variance with juvenile treatment (J) and adult treatment (A) as independent factors and individual females as independent units of analysis (using female means of clutch means). Female size and body condition was not related to size or weight of young after the 1st and 2nd incubation phase, and was therefore not included as a covariate in the ANOVAs.

I determined the size-frequency distribution of juveniles and females across the natural depth range of *S. pleurospilus* by transect counts along a 150-m stretch of pebble shore in Mbete Bay near Mpulungu, Zambia (see electronic Appendix A for details on survey methods). The mean distributions of four study years are presented here. In the lab experiment, females started to reproduce at a mean size of 5.7cm TL

(Taborsky 2005). Therefore, I considered individuals in size classes of ≤ 4.5 -5.4cm as 'juveniles' and individuals above 5.5cm as 'adults'.

RESULTS

When mothers had been raised with little food, offspring were on average 1.4mm larger at the end of brood care than when mothers had been well fed, irrespective of the ration mothers received during adulthood (Figure 1a; Table 1). The larger size of young was not explained by extended brood care, as the results did not change when controlling for the age of young (Table 1). Rather young of poorly-reared mothers grew faster during the second incubation phase (independent of their size at the beginning of this phase; Table 1). The condition factor K of young was not affected by treatment (Table 1), showing that faster growth was not compromised by a slower increase of body mass.

Young of poorly-raised mothers were already larger for their age after the first incubation phase (Figure 1b, Table 1), when larvae depend entirely on yolk reserves. Accordingly, females raised with little food laid eggs with a higher dry mass (ANOVA, $F_{1,13}=8.74$, $p=0.011$; Figure 1c). Egg mass was not related to female length (regression analysis: $R^2=0.02$, $p=0.64$, d.f.=1,13) or body condition ($R^2=0.04$, $p=0.52$, d.f.=1,12).

In their natural habitat, the majority of juveniles (<5.5 cm) stayed at a depth of 0.5m and were rarely found below 1m (median depth: 0.5m, inter quartile range (iqr) 0.5-1; Figure 2a,b). In contrast, fish of adult size occurred predominantly in deeper water (median: 1.5m, iqr 1.0-3.5; Figure 2a,b). Juvenile and adult habitat use differed with respect to depth distribution (Chi-square test, d.f.=5, $\chi^2=36.94$, $p<0.001$; frequencies ≥ 3 m were pooled because of low expected frequencies in these depths) and central tendency of depth distribution (Median test, d.f.=1, $\chi^2=11.16$, $p<0.001$).

Above 0.5m water depth, only small specimen (1.5–4.4cm were found). As they could not be counted by transect swimming, these numbers are not included in the results (separate data set of shallow-water counts given in electronic Appendix A).

DISCUSSION

At the end of broodcare, young of *S. pleurospilus* mothers raised on a poor diet were on average 8.8% longer than young of mothers raised without food limitation. This size difference is likely to affect offspring fitness, as even a size advantage of 3.3% can significantly increase the survival chances of fish larvae (McCormick & Hoey 2004). This is the first experimental evidence showing that maternal effects induced by pre-reproductive conditions can be similarly expressed in markedly different reproductive environments, while not being influenced by the conditions in which females produce their young. Moreover, the reported size differences of young were based on up to four successful broods spread over female reproductive life span, suggesting that such maternal effects can persist during the entire adulthood even in iteroparous, long-lived animals.

Poorly-raised females paid costs for producing larger young by having smaller clutches, while there was no indication for such a trade-off in females raised on the high-food diet (Taborsky 2005). If females raised on a poor diet had resulted in poorer quality adults than females raised on a rich diet, the former may have been more affected by the costs of reproduction than the latter.

S. pleurospilus females raised with little food apparently used two different mechanisms to boost the size of young. (i) They produced eggs with a higher energy content as indicated by higher egg dry mass. (ii) Young grew faster during the second incubation phase, when most yolk is used

up and they use already external food sources. The mechanism responsible for faster growth needs still to be clarified.

In several fish, insects and amphibians larger offspring have survival advantages under adverse growth conditions, while under benign conditions smaller young do equally well (Hutchings 1991, Mousseau & Fox 1998, Einum & Fleming 1999) or better (Kaplan 1992, Rotem et al. 2003). Therefore, the experimental results strongly suggest that *S. pleurospilus* females prepared their young for similar environmental conditions as they had encountered themselves as juveniles. In humans, it has been hypothesized that predicting the quality of the offspring environment incorrectly may have detrimental consequences for offspring health and survival (Bateson et al. 2004). The conditions mothers experienced as juveniles may predict their offspring's environment better than current environmental cues, if (i) environmental conditions for adults and juveniles vary independently, and (ii) juvenile conditions of successive generations are similar. When juveniles and adults have entirely different ecologies like in metamorphosing animals or anadromous fish, some species appear indeed to adjust offspring phenotype to their juvenile environment (Jonsson et al. 1996, Rotem et al. 2003) while others do not (Fox et al. 1995).

In contrast, juvenile and adult *S. pleurospilus* co-occur along the rocky shores of Lake Tanganyika use the same major food source, filamentous turf algae. However juveniles mainly live in shallow water using only a narrow range of water depths, while after maturity females mainly use deeper habitats for breeding (Figure 2a). The juvenile habitat has a high productivity of turf algae, while productivity varies by at least two orders of magnitude over the depth range inhabited by adults (Taborsky 1999). Because of this large variation the ability to predict food availability for offspring reliably is limited if females use cues from their ambient environment.

A much better estimate can be achieved if females use the growth conditions experienced during their own juvenile phase.

As differential habitat use of juveniles and adult is very widespread in animals, parents will often not be able to predict the conditions for the early life stages of offspring by using cues from their current environment. Therefore I predict that it is a common parental strategy to base decisions about the investment in individual offspring more strongly on the own early environment than on present conditions. When studying the origin and function of parental effects, it is hence inevitable to incorporate the influence on parents of the environment experienced during early development.

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Bateson, P., Barker, D., Clutton-Brock, T., Deb, D., D'Udine, B., Foley, R.A., Gluckman, P., Godfrey, K., Kirkwood, T., Lahr, M.M., McNamara, J., Metcalfe, N.B., Monaghan, P., Spencer, H.G. & Sultan, S.E. 2004 Developmental plasticity and human health. *Nature* **430**, 419-421.

Bernardo, J. 1996 Maternal effects in animal ecology. *Am. Zool.* **36**, 83-105.

Blount, J.D., Surai, P.F., Nager, R.G., Houston, D.C., Moller, A.P., Trewby, M.L. & Kennedy, M.W. 2002 Carotenoids and egg quality in the lesser black-backed gull *Larus fuscus*: a supplemental feeding study of maternal effects. *Proc. Roy. Soc. Lond. Ser. B* **269**, 29-36.

Einum, S. & Fleming, I.A. 1999 Maternal effects of egg size in brown trout (*Salmo trutta*): norms of reaction to environmental quality. *Proc. Roy. Soc. Lond. Ser. B* **266**, 2095-2100.

Fox, C.W., Waddell, K.J. & Mousseau, T.A. 1995 Parental host plant affects offspring life histories in a seed beetle. *Ecology* **76**, 402-411.

Hutchings, J.A. 1991 Fitness consequences of variation in egg size and food abundance in Brook Trout *Salvelinus fontinalis*. *Evolution* **45**, 1162-1168.

- Jonsson,N., Jonsson,B. & Fleming,I.A. 1996 Does early growth cause a phenotypically plastic response in egg production of Atlantic Salmon? *Func. Ecol.* **10**, 89-96.
- Kaplan,R.H. 1992 Greater maternal investment can decrease offspring survival in the frog *Bombina orientalis*. *Ecology* **73**, 280-288.
- Lind,A.J. & Welsh,H.H. 1994 Ontogenetic changes in foraging behaviour and habitat use by the Oregon garter snake *Thamnophis atratus hydrophilus*. *Anim. Behav.* **48**, 1261-1273.
- Lindström,J. 1999 Early development and fitness in birds and mammals. *Trends Ecol. Evol.* **14**, 343-348.
- Lummaa,V. & Clutton-Brock,T. 2002 Early development, survival and reproduction in humans. *Trends Ecol. Evol.* **17**, 141-147.
- McCormick,M.I. & Hoey,A.S. 2004 Larval growth history determines juvenile growth and survival in a tropical marine fish. *Oikos* **106**, 225-242.
- Mousseau,T.A. & Fox,C.W. 1998 The adaptive significance of maternal effects. *Trends Ecol. Evol.* **13**, 403-407.
- Reznick,D. & Yang,A.P. 1993 The influence of fluctuating resources on life-history patterns of allocation and plasticity in female guppies. *Ecology* **74**, 2011-2019.
- Rotem,K., Agrawal,A.A. & Kott,L. 2003 Parental effects in *Pieris rapae* in response to variation in food quality: adaptive plasticity across generations? *Ecol. Entomol.* **28**, 211-218.
- Schwabl,H., Mock,D.W. & Gieg,J.A. 1997 A hormonal mechanism for parental favouritism. *Nature* **386**, 231.
- Taborsky,B. 1999 Size-dependent distribution in littoral fish: optimization or competitive exclusion? In: *Behaviour and Conservation of Littoral Fishes* (Ed. by V.C. Almada, R.F. Oliveira & E.J. Goncalves), pp. 351-376. Lisboa, ISPA.
- Taborsky,B. 2005 The influence of juvenile and adult environments on life history trajectories. *Proc. Royal. Soc. Lond B*, doi:10.1098/rspb.2005.3347
- Werner,E.E. & Gilliam,J.F. 1984 The ontogenetic niche and species interactions in size structured populations. *Ann. Rev. Ecol. Syst.* **15**, 393-425

Figures

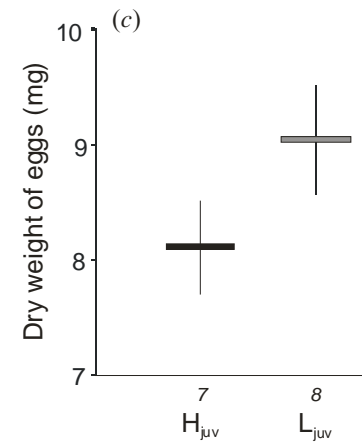
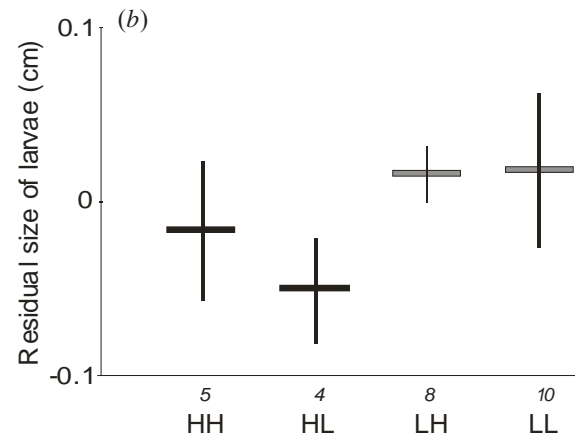
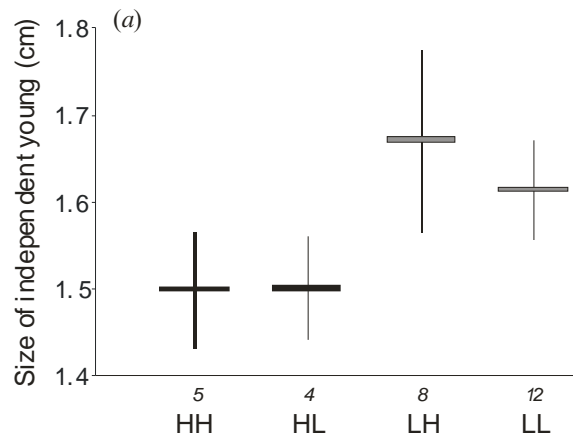
Figure 1. Total length of offspring at the end of (a) 2nd incubation phase, (b) 1st incubation phase (residuals of the model with offspring age as covariate are shown) and (c) egg dry mass of females (means \pm s.e. of brood means).

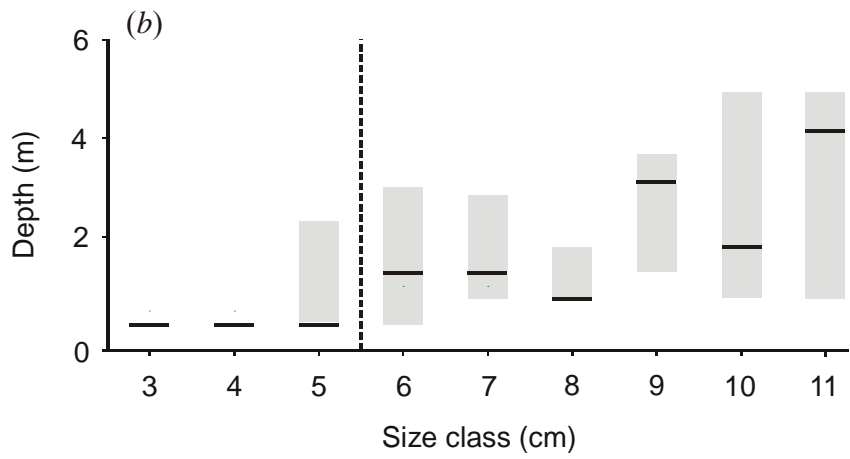
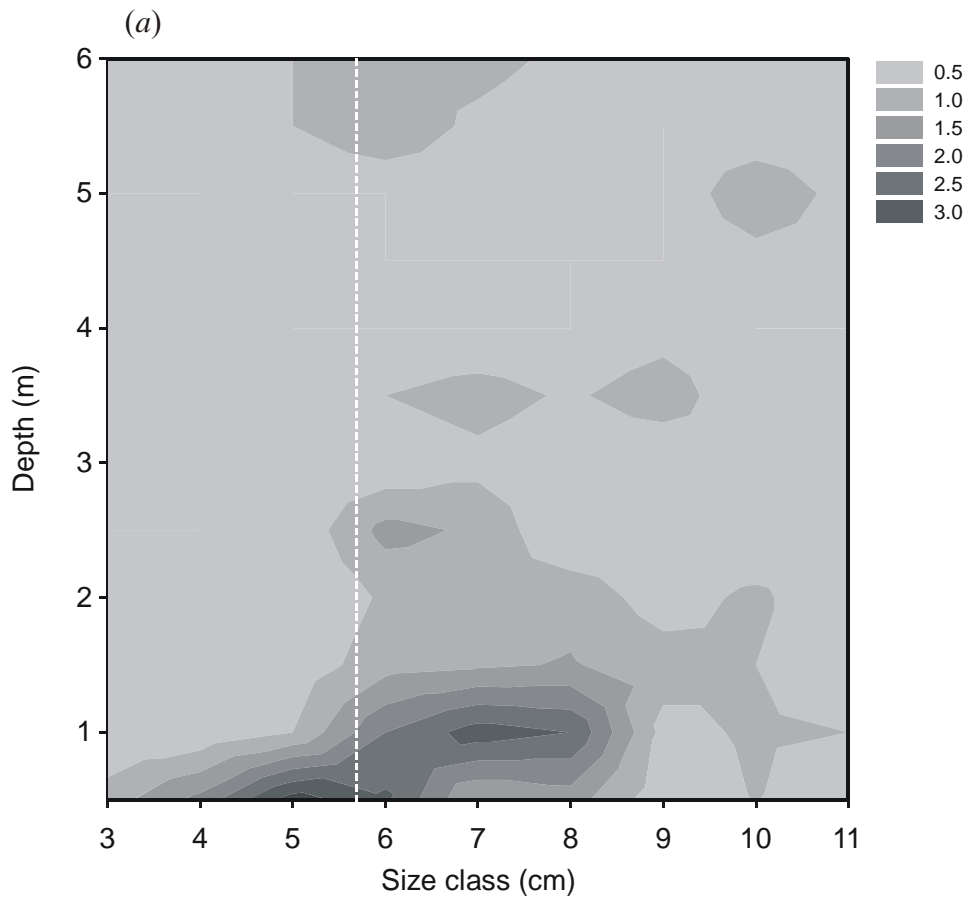
Figure 2. (a) Size-depth distribution of *S. pleurospilus* (mean of four study seasons); grey shades indicate frequencies of fish recorded for each size class and depth. (b) Medians and quartiles for the depth distributions of 1-cm size classes. Stippled lines indicate size at maturity.

Table 1. Analyses of variance testing for the effects of juvenile (J) and adult treatment (A) and their interaction on dependent variables associated with offspring phenotype of experimental females.

		<i>TL</i> after 2 nd inc. phase (cm)	<i>TL</i> after 2 nd phase corr. for age (cm)	<i>K</i> after brood care (g cm ⁻³)	<i>TL</i> after 1 st inc. phase corr for age	residual <i>SGR</i> * during 2 nd inc. phase (% day ⁻¹)
d.f.		3, 25	4, 24	3, 25	4, 22	3, 23
<i>R</i> ²		0.30	0.53	0.008	0.78	0.39
full model	<i>F</i>	3.64	6.80	1.07	19.42	4.91
	<i>P</i>	0.026	0.001	0.379	<0.001	0.009
covariate						
offspring age	<i>F</i>		11.63		64.0	
	<i>P</i>		0.002		<0.001	
main effects						
J	<i>F</i>	10.28	16.20	0.13	5.93	9.15
	<i>P</i>	0.004	<0.001	0.721	0.023	0.006
A	<i>F</i>	0.35	0.42	2.81	0.84	<0.001
	<i>P</i>	0.559	0.552	0.106	0.370	0.98
J × A	<i>F</i>	0.40	1.25	0.001	0.88	4.83
	<i>P</i>	0.530	0.274	0.975	0.359	0.038

*female means of residuals of the regression between *SGR* and initial *TL* of young (clutch means) at the beginning of the second incubation phase





Electronic Appendix A

Mothers determine offspring size in response to own juvenile growth conditions

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Study species

In *Simochromis pleurospilus* Nelissen (Subfamily: Tropheini), a mouthbrooding cichlid endemic to Lake Tanganyika, females produce clutches year-round and care for the young alone. Brood care consists of two phases; two weeks of continuous incubation when young only use yolk reserves are followed by another one to two weeks when young are periodically released from the mouth for feeding on the surrounding substrate. Afterwards, young are independent.

Experimental fish and housing

The experimental fish were recruited from 14 broods, bred from closely related parents (siblings and half-siblings) to minimize genetic variability. I raised 120 young *S. pleurospilus*, each in a separate 20-litre tank. Each 20-litre tank contained an internal biological filter and a clay flower pot half (10 cm diameter), both used as shelters by the fish, and a layer of river sand. Water temperature was kept at 27°C by controlled heating of the room temperature. The light:dark regime was set to 13h:11h including 10 min periods of dimmed light in the mornings and evenings to simulate natural light conditions at Lake Tanganyika. The sexes of the experimental fish could only be determined from an age of 5 to 6 month, when there were 55 females in the experimental population. Of these, 46 females (23 high-food and 23 low-food females) produced clutches of eggs during the experiment. These females were used in both the juvenile and the adult treatment phases. Of the 46 females, 23 females produced 'successful broods', i.e. they incubated and raised their young. The probability of successful incubation was not influenced by the food treatment (Taborsky 2005), and it is unknown why the remaining females always abandoned or swallowed their eggs.

Transition between juvenile and adult treatment

I switched the females from the juvenile to the adult treatment after their first breeding attempt. Most first-spawning females (37 of 46) interrupted incubation after 3.1 days (mean \pm 0.29 SE) and swallowed the eggs, a phenomenon generally observed in mouthbrooding cichlids. Only 9 females raised their first clutch. I wanted to ensure that all females were in the same developmental stage at the switch. Therefore, the day *after* the first breeding attempt was chosen as starting point for the adult treatment as first spawning is the first

unequivocal sign of maturity in these fish. Hence, the juvenile treatment period covered the entire phase of 'early development' (the time from birth to developmental maturity, Lindström 1999). Additionally it included a short period of ovary maturation before first spawning (2-3 weeks in Tropheini, Yanagisawa & Nishida 1991, B. Taborsky unpub. data, i.e., 6-7% of the juvenile treatment period), and in 9 females also incubation.

Of the 9 females that did raise the first clutch, six were switched to the opposite food level after incubation, according to the experimental protocol. As the first young of these 6 females were produced still under the previous (juvenile) food conditions, data of these clutches were analysed together with data of the respective non-switched groups whenever all four treatment groups were compared.

The majority (83%) of the 54 successful broods (produced by 23 females, mean: 1.9 broods \pm 0.18 SE per female, range 1-4), were produced during the adult treatment. Therefore, the timing of the treatment switch closely matched the divide between juvenile and adult stages of the experimental females.

Food source for young during adult treatment

Overall, clutch size increased with female size, while the latter was influenced by the food treatment (Taborsky 2005). In principle, it would be possible that the differences of growth rates during the second incubation phase have been caused by differential levels of density-dependent competition for the food rations provided daily. However, this possibility is unlikely because (i) larvae fed mainly on detritus and algae, which were plentiful in all tanks, and were thereby largely independent of the daily food rations and (ii) growth rates did not correlate with clutch size within treatments (except for the LH group, $r=-0.55$, $P=0.034$, $n=15$ individual broods).

Field survey

Data were collected along a 150m stretch of coastline in Mbete Bay at the southern tip of Lake Tanganyika about 1 km west of Mpulungu, Zambia. Data include counts of four study periods (25 Dec 96 to 26 Jan 97, 28 Jan to 2 Mar 98, 1 Mar to 10 Mar 2002, 1 Mar to 20 Mar 2003).

Before starting with the actual data collection each observer did several training trials allow for a direct comparison of count data collected by different observers. During these training trials, the observer first estimated the size of a randomly chosen focal individual, then he caught it and measured its total length to verify his estimate. At least 5 successive estimates had to be done correctly before an observer started to collect the data. This condition was usually fulfilled after very few training trials.

When conducting a transect count, the observer swam in parallel to the shoreline in constant water depth either by snorkelling or by SCUBA diving. Transects were conducted at each half depth meter between 0.5 and 6 m depth (12 transects per study period). Every 10 m along a transect the observer stopped, remained motionless for 2 min, counted all *S. pleurospilus* by once scanning the substrate and the water

column in a half-circle with a radius of 2 m. He then noted the size of each individual, which was estimated to the nearest 1.0 cm resulting size classes from 2.5-3.4 cm to 10.5-11.4 cm for females and juveniles. Male counts are not presented in this paper, as only the habitat use of females and juveniles is relevant for the focus of this study. Adult males were easily distinguished from juveniles and females by their bright colour pattern.

For further analysis the counts of all 15 positions of a transect were summed. Whenever a transect was repeated (all transects of 2002 and some transects in 1998), the counts of the repeated transects were averaged by taking the arithmetic mean.

The total numbers of juvenile fish detected during the transect counts was relatively low compared to the number of adults. This is because a large number of juveniles occurred above 0.5 m of depth, where the counting method described above is not feasible. To account for this problem, two additional counts were done in 2002 by walking on land along 100 m of shoreline in front of the study site (shore transects). For these transects fish were counted every 5 m on an area of a half-circle with 1 m radius. An additional size class (1.5-2.4 cm) was found during these counts. The numbers of fish in count 1 and 2, respectively, were 27 and 22 in size class 1.5 to 2.4 cm, 16 and 25 in class 2.5-3.4 cm and 7 and 9 in class 3.5-4.4 cm. No *S. pleurospilus* larger than 4.4 cm were found during these shore transects. As the counting method used in the shore transects is not directly comparable with the transects done by swimming, the results of these two additional transects were not included in the data presented in the 'Results' section.

References

- Lindström, J. (1999). Early development and fitness in birds and mammals. *Trends Ecol. Evol.* **14**, 343-348.
- Taborsky, B. (2005). The influence of juvenile and adult environments on life history trajectories. *Proc. Royal. Soc. Lond B*, doi: 10.1098/rspb.2005.3347
- Yanagisawa, Y. & Nishida, M. (1991). The social and mating system of the maternal mouthbrooder *Tropheus moorii* (Cichlidae) in Lake Tanganyika. *Jap. J. Ichthyol.* **38**, 271-282.