Ontogenesis

Eco-evolutionary perspective on life history complexity

Hin, V.

Bibliography

Abrams, P. A. 2009. When does greater mortality increase population size? The long history and diverse mechanisms underlying the hydra effect. Ecology Letters 12:462–474.

———. 2011. Simple life-history omnivory: responses to enrichment and harvesting in systems with intraguild predation. The American Naturalist 178:305–319.

Aguirre, J. D., M. W. Blows, and D. J. Marshall. 2014. The genetic covariance between life cycle stages separated by metamorphosis. Proceedings of the Royal Society B 281:20141091.

Aljetlawi, A. A., and K. Leonardsson. 2002. Size-Dependent Competitive Ability in a Deposit-Feeding Amphipod, *Monoporeia affinis*. Oikos 97:31–44.

Amundsen, P.-A. 1994. Piscivory and cannibalism in Arctic charr. Journal of Fish Biology 45 Suppl.:181–189.

———. 2016. Contrasting life-history strategies facilitated by cannibalism in a stunted Arctic charr population. Hydrobiologia pages 1–9.

Amundsen, P.-A., A. Klemetsen, and P. E. Grotnes. 1993. Rehabilitation of a stunted population of Arctic char by intensive fishing. North American Journal of Fisheries Management 13:483 – 491.

Amundsen, P.-A., R. Knudsen, and A. Klemetsen. 2007. Intraspecific competition and density dependence of food consumption and growth in Arctic charr. Journal of Animal Ecology 76:149–158.

Amundsen, P.-A., R. Knudsen, A. M. Kuris, and R. Kristoffersen. 2003. Seasonal and ontogenetic dynamics in trophic transmission of parasites. Oikos 102:285–293.

Amundsen, P.-A., M.-A. Svenning, and S. I. Siikavuopio. 1999. An experimental comparison of cannibalistic response in different Arctic charr (*Salvelinus alpinus* (L.)) stocks. Ecology of Freshwater Fish 8:43–48.

Andersen, K. H., N. S. Jacobsen, T. Jansen, and J. E. Beyer. 2016. When in life does density dependence occur in fish populations? Fish and Fisheries .

Andersson, J., P. Byström, D. Claessen, L. Persson, and A. M. De Roos. 2007. Stabilization of population fluctuations due to cannibalism promotes resource polymorphism in fish. The American Naturalist 169:820–829.

Bagenal, T. B. 1971. The interrelation of the size of fish eggs, the date of spawning and the production cycle. Journal of Fish Biology 3:207–219.

Banavar, J. R., J. Damuth, A. Maritan, and A. Rinaldo. 2002. Ontogenetic Growth: Modelling universality and scaling. Nature 420:626–627.

Banavar, J. R., A. Maritan, and A. Rinaldo. 1999. Size and form in efficient transportation networks. Nature 399:130–132.

Banavar, J. R., M. E. Moses, J. H. Brown, J. Damuth, A. Rinaldo, R. M. Sibly, and A. Maritan. 2010. A general basis for quarter-power scaling in animals. Proceedings of the National Academy of Sciences of the United States of America 107:15816–20.

Bascompte, J., and C. J. Melián. 2005. Trophic Modules for Complex Food Webs. Ecology 86:2868–2873.

Bassar, R. D., D. Z. Childs, M. Rees, S. D. Tuljapurkar, D. N. Reznick, and T. Coulson. 2016. The effects of asymmetric competition on the life history of Trinidadian guppies. Ecology Letters 19:268–278.

Baur, B. 1994. Inter-population differences in propensity for egg cannibalism in hatchlings of the land snail *Arianta arbustorum*. Animal Behaviour 48:851–860.

Berg, O. K., A. G. Finstad, P. H. Olsen, J. V. Arnekleiv, and K. Nilssen. 2010. Dwarfs and cannibals in the Arctic: Production of Arctic char (*Salvelinus alpinus* (L.)) at two trophic levels. Hydrobiologia 652:337–347.

Biro, P. A., and J. R. Post. 2008. Rapid depletion of genotypes with fast growth and bold personality traits from harvested fish populations. Proceedings of the National Academy of Sciences of the United States of America 105:2919–2922.

Boettiger, C., S. Chamberlain, D. Temple Lang, and P. Wainwright. 2016. rfishbase: R Interface to 'FishBase'. R package version 2.1.0.1. https://github.com/ropensci/rfishbase.

Boettiger, C., D. T. Lang, and P. C. Wainwright. 2012. rfishbase: Exploring, manipulating and visualizing FishBase data from R. Journal of Fish Biology 81:2030–2039.

Bøhn, T., O. T. Sandlund, P.-A. Amundsen, and R. Primicerio. 2004. Rapidly changing life history during invasion. Oikos 106:138–150.

Bokma, F. 2004. Evidence against universal metabolic allometry. Functional Ecology 18:184–187.

Bolnick, D. I. 2004. Can Intraspecific Competition Drive Disruptive Selection ? An Experimental Test in Natural Populations of Sticklebacks. Evolution 58:608–618.

Bonislawska, M., K. Formicki, A. Korzelecka-Orkisz, and A. Winnicki. 2001. Fish egg size variability: biological significance. Electronic Journal of Polish Agricultural Universities 4.

Borgstrøm, R., T. Isdahl, and M.-A. Svenning. 2015. Population structure, biomass, and diet of landlocked Arctic charr (*Salvelinus alpinus*) in a small, shallow high Arctic lake. Polar Biology 38:309–317.

Brose, U., T. Jonsson, E. L. Berlow, P. Warren, C. Banasek-Richter, L.-F. Bersier, J. L. Blanchard, T. Brey, S. Carpenter, M.-F. Cattin Blandenier, L. Cushing, H. Ali Dawah, T. Dell, F. Edwards, S. Harper-Smith, U. Jacob, M. E. Ledger, N. D. Martinez, J. Memmott, K. Mintenbeck, J. K. Pinnegar, B. C. Rall, T. S. Rayner, D. C. Reuman, L. Ruess, W. Ulrich, R. J. Williams, G. Woodward, and J. E. Cohen. 2006. Consumer-Resource Body-Size Relationships in Natural Food Webs. Ecology 87:2411–2417.

Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. Toward a Metabolic Theory of Ecology. Ecology 85:1771–1789.

Burgio, G., F. Santi, and S. Maini. 2005. Intra-guild predation and cannibalism between *Harmonia axyridis* and *Adalia bipunctata* adults and larvae: Laboratory experiments. Bulletin of Insectology 58:135–140.

Burton, T., S. S. Killen, J. D. Armstrong, and N. B. Metcalfe. 2011. What causes intraspecific variation in resting metabolic rate and what are its ecological consequences? Proceedings of The Royal Society B 278:3465–3473.

Byström, P., and J. Andersson. 2005. Size-dependent foraging capacities and intercohort competition in an ontogenetic omnivore (Arctic char). Oikos 110:523–536.

Byström, P., J. Andersson, A. Kiessling, and L. O. Eriksson. 2006. Size and temperature dependent foraging capacities and metabolism: Consequences for winter starvation mortality in fish. Oikos 115:43–52.

Byström, P., J. Andersson, L. Persson, and A. M. De Roos. 2004. Size-dependent resource limitation and foraging-predation risk trade-offs: growth and habitat use in young arctic char. Oikos 104:109–121.

Byström, P., P. Ask, J. Andersson, and L. Persson. 2013. Preference for Cannibalism and Ontogenetic Constraints in Competitive Ability of Piscivorous Top Predators. PLoS One 8:e70404.

Byström, P., L. Persson, and E. Wahlström. 1998. Competing Predators and Prey : Juvenile Bottlenecks in Whole-Lake Experiments. Ecology 79:2153–2167.

Cameron, T. C., and T. G. Benton. 2004. Stage-structured harvesting and its effects: An empirical investigation using soil mites. Journal of Animal Ecology 73:996–1006.

Caruso, T., D. Garlaschelli, R. Bargagli, and P. Convey. 2010. Testing metabolic scaling theory using intraspecific allometries in Antarctic microarthropods. Oikos 119:935–945.

Chesson, J. 1978. Measuring Preference in Selective Predation. Ecology 59:211–215.

Chesson, P. 2000. Mechanisms of Maintenance of Species Diversity. Annual Review of Ecology and Systematics 31:343–366.

Cheverud, J. M., J. J. Rutledge, and W. R. Atchley. 1983. Quantitative Genetics of Development : Genetic Correlations Among Age-Specific Trait Values and the Evolution of Ontogeny. Evolution 37:895–905.

Chiba, S., S. A. Arnott, and D. O. Conover. 2007. Coevolution of foraging behavior with intrinsic growth rate: risk-taking in naturally and artificially selected growth genotypes of *Menidia menidia*. Oecologia 154:237–246.

Claessen, D., and A. M. De Roos. 2003. Bistability in a size-structured population model of cannibalistic fish - A continuation study. Theoretical Population Biology 64:49–65.

Claessen, D., A. M. De Roos, and L. Persson. 2000. Dwarfs and Giants: Cannibalism and Competition in Size-Structured Populations. The American Naturalist 155:219–237.

———. 2004. Population dynamic theory of size-dependent cannibalism. Proceedings of the Royal Society of London B 271:333–340.

Clarke, A., and N. M. Johnston. 1999. Scaling of metabolic rate with body mass and temperature in teleost fish. Journal of Animal Ecology pages 893–905.

Crosetti, D., and C. A. Cordisco. 2004. Induced spawning of the thick-lipped mullet (*Chelon labrosus, Mugilidae, Osteichthyes*). Marine Life 14:37–43.

De Roos, A. M. 1988. Numerical methods for structured population models: the Escalator boxcar train. Numerical Methods for Partial Differential Equations 4:173–195.

———. 1997. A Gentle Introduction to Models of Physiologically Structured Populations. Chap. 6, pages 119–204 *in* S. Tuljapurkar and H. Caswell, eds. Structured-Population Models in Marine, Terrestrial, and Freshwater Systems, Structured-Population Models in Marine, Terrestrial, and Freshwater Systems. Springer, US.

———. 2016. PSPManalysis: A Matlab/R/C Package for Numerical Analysis of Physiologically Structured Population Models. https://bitbucket.org/amderoos/pspmanalysis.

De Roos, A. M., O. Diekmann, P. Getto, and M. A. Kirkilionis. 2010. Numerical Equilibrium Analysis for Structured Consumer Resource Models. Bulletin of Mathematical Biology 72:259–297.

De Roos, A. M., O. Diekmann, and J. A. J. Metz. 1992. Studying the Dynamics of Structured Population Models : A Versatile Technique and Its Application to Daphnia. The American Naturalist 139:123–147.

De Roos, A. M., J. A. J. Metz, and L. Persson. 2013. Ontogenetic symmetry and asymmetry in energetics. Journal of Mathematical Biology 66:889–914.

De Roos, A. M., and L. Persson. 2001. Physiologically structured models – from versatile technique to ecological theory. Oikos 1:51–71.

———. 2002. Size-dependent life-history traits promote catastrophic collapses of top predators. Proceedings of the National Academy of Sciences of the United States of America 99:12907–12912.

———. 2003. Competition in size-structured populations: mechanisms inducing cohort formation and population cycles. Theoretical Population Biology 63:1–16.

———. 2005. Unstructured Population Models: Do Population-Level Assumptions Yield General Theory? Chap. 3, pages 31–62 *in* K. Cuddington and B. Beisner, eds. Ecological Paradigms Lost. Routes of Theory Change. Elsevier Academic Press.

———. 2013. Population and Community Ecology of Ontogenetic Development. Princeton University Press, Princeton.

De Roos, A. M., L. Persson, and E. McCauley. 2003*a*. The influence of size-dependent life-history traits on the structure and dynamics of populations and communities. Ecology Letters 6:473–487.

De Roos, A. M., L. Persson, and H. R. Thieme. 2003*b*. Emergent Allee effects in top predators feeding on structured prey populations. Proceedings of the Royal Society of London B 270:611–8.

De Roos, A. M., T. Schellekens, T. Van Kooten, and L. Persson. 2008*a*. Stage-specific predator species help each other to persist while competing for a single prey. Proceedings of the National Academy of Sciences 105:13930–13935.

De Roos, A. M., T. Schellekens, T. Van Kooten, K. Van de Wolfshaar, D. Claessen, and L. Persson. 2007. Food-dependent growth leads to overcompensation in stage-specific biomass when mortality increases: the influence of maturation versus reproduction regulation. The American Naturalist 170:E59–76.

———. 2008*b*. Simplifying a physiologically structured population model to a stage-structured biomass model. Theoretical Population Biology 73:47–62.

De Ruiter, P. C., A. M. Neutel, and J. C. Moore. 1995. Energetics , Patterns of Interaction Strengths , and Stability in Real Ecosystems. Science 269:1257–1260.

DeAngelis, D. L., and W. M. Mooij. 2005. Individual-Based Modeling of Ecological and Evolutionary Processes 1. Annual Review of Ecology, Evolution, and Systematics 36:147–168.

Dercole, F. 2003. Remarks on branching-extinction evolutionary cycles. Journal of Mathematical Biology 47:569–580.

Dhooge, A., W. Govaerts, and Y. A. Kuznetsov. 2003. MATCONT: a MATLAB package for numerical bifurcation analysis of ODEs. ACM Transactions on Mathematical Software (TOMS) 29:141–164.

Diaz Pauli, B., M. Wiech, M. Heino, and A. C. Utne-Palm. 2015. Opposite selection on behavioural types by active and passive fishing gears in a simulated guppy *Poecilia reticulata* fishery. Journal of Fish Biology 86:1030–1045.

Dieckmann, U. 2002. Adaptive dynamics of pathogen-host interactions. Adaptive Dynamics of Infectious Diseases: In Pursuit of Virulence Management pages 39–59.

Dieckmann, U., and R. Law. 1996. The dynamical theory of coevolution: a derivation from stochastic ecological processes. Journal of Mathematical Biology 34:579–612.

Diehl, S., and M. Feißel. 2000. Effects of Enrichment on Three-Level Food Chains with Omnivory. The American Naturalist 155:200–218.

Diehl, S., and M. Feissel. 2001. Intraguild prey suffer from enrichment of their resources: a microcosm experiment with ciliates. Ecology 82:2977–2983.

Diekmann, O., M. Gyllenberg, and J. A. J. Metz. 2003. Steady-state analysis of structured population models. Theoretical Population Biology 63:309–338.

Diekmann, O., and J. A. J. Metz. 2010. How to lift a model for individual behaviour to the population level? Philosophical Transactions of the Royal Society B 365:3523–30.

Doebeli, M., and U. Dieckmann. 2000. Evolutionary Branching and Sympatric Speciation Caused by Different Types of Ecological Interactions. The American Naturalist 156:S77–S101.

Dunlop, E. S., M. Heino, and U. Dieckmann. 2009. Eco-genetic modeling of contemporary life-history evolution. Ecological Applications 19:1815–1834.

Dunlop, E. S., B. J. Shuter, and U. Dieckmann. 2007. Demographic and Evolutionary Consequences of Selective Mortality: Predictions from an Eco-Genetic Model for Smallmouth Bass. Transactions of the American Fisheries Society 136:749–765.

Dunn, J. R., and A. C. Matarese. 1987. A review of the Early Life History of Northeast Pacific Gadoid Fishes. Fisheries Research 5:163–184.

Durinx, M., J. A. J. Metz, and G. Meszéna. 2008. Adaptive dynamics for physiologically structured population models. Journal of Mathematical Biology 56:673–742.

Ebenman, B. 1992. Evolution in Organisms that Change Their Niches during the Life Cycle. The American Naturalist 139:990–1021.

Elgar, M. A., and B. J. Crespi. 1992. Cannibalism: ecology and evolution among diverse taxa. Oxford University Press.

Enberg, K., C. Jørgensen, E. S. Dunlop, M. Heino, and U. Dieckmann. 2009. Implications of fisheries-induced evolution for stock rebuilding and recovery. Evolutionary Applications 2:394–414.

Enberg, K., C. Jørgensen, E. S. Dunlop, Ø. Varpe, D. S. Boukal, L. Baulier, S. Eliassen, and M. Heino. 2012. Fishing-induced evolution of growth: concepts, mechanisms and the empirical evidence. Marine Ecology 33:1–25.

Enquist, B. J., E. P. Economo, T. E. Huxman, A. P. Allen, D. D. Ignace, and J. F. Gillooly. 2003. Scaling metabolism from organisms to ecosystems. Nature 423:639–642.

Eshel, I. 1983. Evolutionary and Continuous Stability. Journal of Theoretical Biology 103:99–111.

Ferrière, R., and S. Legendre. 2013. Eco-evolutionary feedbacks, adaptive dynamics and evolutionary rescue theory. Philosophical Transactions of the Royal Society B 368:20120081.

Fiegna, F., and G. J. Velicer. 2003. Competitive fates of bacterial social parasites: persistence and self-induced extinction of *Myxococcus xanthus* cheaters. Proceedings of the Royal Society of London B 270:1527–1534.

Finstad, A. G., P. A. Jansen, and A. Langeland. 2001. Production and predation rates in a cannibalistic Arctic char (*Salvelinus alpinus* L .) population. Ecology of Freshwater Fish 10:220–226.

Finstad, A. G., O. Ugedal, and O. K. Berg. 2006. Growing large in a low grade environment: size dependent foraging gain and niche shifts to cannibalism in Arctic char. Oikos 112:73–82.

Florø-Larsen, B., A. G. Finstad, O. K. Berg, and P. H. Olsen. 2014. Otolith size differences during early life of dwarf and cannibal Arctic char (*Salvelinus alpinus*). Ecology of Freshwater Fish 25:203–210.

Fox, L. R. 1975. Cannibalism in natural populations. Annual Review of Ecology and Systematics 6:87–106.

Fraley, C., and A. E. Raftery. 2002. Model-based clustering, discriminant analysis, and density estimation. Journal of the American statistical Association 97:611–631.

Froese, R., and D. Pauly. 2016. Fishbase. World Wide Web electronic publication. www.fishbase.org.

Futuyma, D. J., and G. Moreno. 1988. The Evolution of Ecological Specialization. Annual Review of Ecology and Systematics 19:207–233.

Gause, G. F. 1934. The struggle for existence. Williams and Wilkins, Baltimore.

Gerber, G. P., and A. C. Echternacht. 2000. Evidence for asymmetrical intraguild predation between native and introduced Anolis lizards. Oecologia 124:599–607.

Geritz, S. A. H., É. Kisdi, G. Meszéna, and J. A. J. Metz. 1998. Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. Evolutionary Ecology 12:35–57.

German, D. P., a. K. Gawlicka, and M. H. Horn. 2014. Evolution of ontogenetic dietary shifts and associated gut features in prickleback fishes (*Teleostei: Stichaeidae*). Comparative Biochemistry and Physiology, Part B 168:12–18.

Getto, P., O. Diekmann, and A. M. De Roos. 2005. On the (dis) advantages of cannibalism. Journal of Mathematical Biology 51:695–712.

Gillooly, J. F., J. H. Brown, G. B. West, V. M. Savage, and E. L. Charnov. 2001. Effects of Size and Temperature on Metabolic Rate. Science 293:2248–2251.

Giray, T., Y. A. Luyten, M. MacPherson, and L. Stevens. 2001. Physiological bases of genetic differences in cannibalism behavior of the confused flour beetle *Tribolium confusum*. Evolution 55:797–806.

Glazier, D. S. 2005. Beyond the '3/4-power law': variation in the intra- and interspecific scaling of metabolic rate in animals. Biological reviews of the Cambridge Philosophical Society 80:611–62.

———. 2006. The 3/4-power law is not universal: evolution of isometric, ontogenetic metabolic scaling in pelagic animals. BioScience 56:325–332.

———. 2009. Activity affects intraspecific body-size scaling of metabolic rate in ectothermic animals. Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology 179:821–828.

———. 2010. A unifying explanation for diverse metabolic scaling in animals and plants. Biological reviews of the Cambridge Philosophical Society 85:111–38.

Glazier, D. S., E. M. Butler, S. A. Lombardi, T. J. Deptola, A. J. Reese, and E. V. Satterthwaite. 2011. Ecological effects on metabolic scaling: Amphipod responses to fish predators in freshwater springs. Ecological Monographs 81:599–618.

Glazier, D. S., A. G. Hirst, and D. Atkinson. 2015. Shape shifting predicts ontogenetic changes in metabolic scaling in diverse aquatic invertebrates. Proceedings of the Royal Society B 282.

Gliwicz, Z. M. 1990. Food thresholds and body size in cladocerans. Nature 343:183–187.

Gould, S. J. 1966. Allometry and Size in Ontogeny and Phylogeny. Biological Reviews 41:587–638.

Gribbin, S. D., and D. J. Thompson. 1990. Asymmetric intraspecific competition among larvae of the damselfly *Ischnura elegans (Zygoptera: Coenagrionidae)*. Ecological Entomology 15:37–42.

Griffiths, D. 1994. The size structure of lacustrine Arctic charr (*Pisces: Salmonidae*) populations. Biological Journal of the Linnean Society 51:337–357.

Guill, C. 2009. Alternative dynamical states in stage-structured consumer populations. Theoretical population biology 76:168–78.

Gurney, W. S. C., E. McCauley, R. M. Nisbet, and W. W. Murdoch. 1990. The Physiological Ecology of Daphnia: A Dynamic Model of Growth and Reproduction. Ecology 71:716–732.

Gurney, W. S. C., and R. M. Nisbet. 1998. Ecological Dynamics. Oxford University Press, New York.

Gyllenberg, M., and K. Parvinen. 2001. Necessary and Sufficient Conditions for Evolutionary Suicide. Bulletin of Mathematical Biology 63:981–993.

Hammar, J. 1998. Evolutionary ecology of arctic char (*Salvelinus alpinus* (L.)). Intra- and interspecific interactions in circumpolar populations. Ph.D. thesis. University of Uppsala, Uppsala.

———. 2000. Cannibals and parasites: conflicting regulators of bimodality in high latitude Arctic char, *Salvelinus alpinus*. Oikos 88:33–47.

Hansen, P. J., P. K. Bjørnsen, and B. W. Hansen. 1997. Zooplankton grazing and growth: Scaling within the 2-2,000- body size range. Limnology and Oceanography 42:687–704.

Hardin, G. 1960. The Competitive Exclusion Principle. Science 131:1292–1297.

Heino, M., B. Díaz Pauli, and U. Dieckmann. 2015. Fisheries-Induced Evolution. Annual Review of Ecology, Evolution, and Systematics 46.

Heino, M., and U. Dieckmann. 2009. Fisheries-induced Evolution. Encylopedia of Life Science .

Hin, V., and A. M. De Roos. in prep. Evolution of Size-Dependent Intraspecific Competition Yields Paradoxical Predictions on the Scaling of Metabolism with Body Size. This thesis, chapter 2 .

Hin, V., T. Schellekens, L. Persson, and A. M. De Roos. 2011. Coexistence of Predator and Prey in Intraguild Predation Systems with Ontogenetic Niche Shifts. The American Naturalist 178:701–714.

Hirst, A. G., D. S. Glazier, and D. Atkinson. 2014. Body shape shifting during growth permits tests that distinguish between competing geometric theories of metabolic scaling. Ecology letters 17:1274–81.

Hirst, A. G., M. K. S. Lilley, D. S. Glazier, and D. Atkinson. 2017. Ontogenetic body-mass scaling of nitrogen excretion relates to body surface area in diverse pelagic invertebrates. Limnology and Oceanography 62:311–319.

Hjelm, J., and L. Persson. 2001. Size-dependent attack rate and handling capacity: inter-cohort competition in a zooplanktivorous fish. Oikos 95:520–532.

Hjelm, J., L. Persson, and B. Christensen. 2000. Growth, morphological variation and ontogenetic niche shifts in perch (*Perca fluviatilis*) in relation to resource availability. Oecologia 122:190–199.

Hjelm, J., G. H. van de Weerd, and F. A. Sibbing. 2003. Functional link between foraging performance, functional morphology, and diet shift in roach (*Rutilus rutilus*). Canadian Journal of Fisheries and Aquatic Sciences 60:700–709.

Holt, R. D. 1977. Predation, Apparant Competition, and the Structure of Prey Communities. Theoretical Population Biology 12:197–229.

Holt, R. D., and G. A. Polis. 1997. A Theoretical Framework for Intraguild Predation. The American Naturalist 149:745–764.

Hou, C., K. M. Bolt, and A. Bergman. 2011. A general model for ontogenetic growth under food restriction. Proceedings of the Royal Society B 278:2881–2890.

Hou, C., W. Zuo, M. E. Moses, W. H. Woodruff, J. H. Brown, and G. B. West. 2008. Energy Uptake and Allocation During Ontogeny. Science 322:736–739.

Hughes, D. J., and R. N. Huges. 1986. Metabolic Implications of Modularity: Studies on the Respiration and Growth of *Electra pilosa*. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences 313:23–29.

Huisman, J., and F. J. Weissing. 1999. Biodiversity of plankton by species oscillations and chaos. Nature 402:407–410.

ICES. 2015. Eggs and larvae dataset. http://www.ices.dk/marine-data/data-portals/Pages/Eggs-and-larvae.aspx. ICES, Copenhagen.

Jansen, P. A., A. G. Finstad, and A. Langeland. 2003. Size-scaling of zooplankton foraging in Arctic charr. Journal of Fish Biology 62:860–870.

Jobling, M., E. H. Jørgensen, A. M. Arnesen, and E. Ringø. 1993. Feeding, growth and environmental requirements of Arctic charr: a review of aquaculture potential. Aquaculture International 1:20–46.

Jusup, M., T. Sousa, T. Domingos, V. Labinac, N. Marn, Z. Wang, and T. Klanjšček. 2016. Physics of metabolic organization. Physics of Life Reviews 20:1–39.

Kamler, E. 2005. Parent-egg-progeny relationships in teleost fishes: An energetics perspective. Reviews in Fish Biology and Fisheries 15:399–421.

Kearney, M. R., and C. R. White. 2012. Testing metabolic theories. The American Naturalist 180:546–565.

Killen, S. S., D. Atkinson, and D. S. Glazier. 2010. The intraspecific scaling of metabolic rate with body mass in fishes depends on lifestyle and temperature. Ecology letters 13:184–93.

Killen, S. S., D. S. Glazier, E. L. Rezende, T. D. Clark, D. Atkinson, A. S. T. Willener, and L. G. Halsey. 2016. Ecological Influences and Morphological Correlates of Resting and Maximal Metabolic Rates across Teleost Fish Species. The American Naturalist 187:592–606.

King, J. R., and G. A. McFarlane. 2003. Marine fish life history strategies: applications to fishery management. Fisheries Management and Ecology 10:249–264.

Kiørboe, T., and A. G. Hirst. 2014. Shifts in mass scaling of respiration, feeding, and growth rates across life-form transitions in marine pelagic organisms. The American Naturalist 183:E118–30.

Kirkilionis, M. A., O. Diekmann, B. Lisser, M. Nool, B. P. Sommeijer, and A. M. De Roos. 2001. Numerical Continuation of Equilibria of Physiologically Structured Population Models. I. Theory. Mathematical Models and Methods in Applied Sciences 11:1101–1127.

Klefoth, T., C. Skov, J. Krause, and R. Arlinghaus. 2012. The role of ecological context and predation risk-stimuli in revealing the true picture about the genetic basis of boldness evolution in fish. Behavioral Ecology and Sociobiology 66:547–559.

Kleiber, M. 1932. Body Size and Metabolism. Hilgardia 6.

Klemetsen, A., P.-A. Amundsen, J. B. Dempson, B. Jonsson, N. Jonsson, M. F. O'Connell, and E. Mortensen. 2003. Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. Ecology of Freshwater Fish 12:1–59.

Knudsen, R., P.-A. Amundsen, and A. Klemetsen. 2002. Parasite-induced host mortality: Indirect evidence from a long-term study. Environmental Biology of Fishes 64:257–265.

Knudsen, R., K. Ø. Gjelland, A. P. Eloranta, B. Hayden, A. Siwertsson, P.-A. Amundsen, and A. Klemetsen. 2016. A specialised cannibalistic Arctic charr morph in the piscivore guild of a subarctic lake. Hydrobiologia pages 1–14.

Knudsen, R., A. Klemetsen, and F. Staldvik. 1996. Parasites as indicators of individual feeding specialization in Arctic charr during winter in northern Norway. Journal of Fish Biology 48:1256–1265.

Kock, K.-H. 1992. Antarctic Fish and Fisheries. Cambridge University Press.

Kondoh, M. 2008. Building trophic modules into a persistent food web. Proceedings of the National Academy of Sciences 105:16631–16635.

Kooi, B. W., and J. Van der Meer. 2010. Bifurcation theory, adaptive dynamics and dynamic energy budget-structured populations of iteroparous species. Philosophical Transactions of the Royal Society B 365:3579–90.

Kooijman, S. A. L. M. 1986. Energy Budgets Can Explain Body Size Relations. Journal of Theoretical Biology 121:269–282.

———. 2001. Quantitative aspects of metabolic organization: a discussion of concepts. Philosophical Transactions of the Royal Society of London. Series B, Biological sciences 356:331–49.

———. 2010. Dynamic Energy Budget Theory For Metabolic Organisation. Third edit ed. Cambridge University Press, Cambridge, UK.

———. 2014. Metabolic acceleration in animal ontogeny: An evolutionary perspective. Journal of Sea Research 94:128–137.

Kooijman, S. A. L. M., and J. A. J. Metz. 1984. On the dynamics of chemically stressed populations: the deduction of population consequences from effects on individuals. Ecotoxicology and environmental safety 8:254–274.

Kreutzer, C., and W. Lampert. 1999. Exploitative competition in differently sized Daphnia species: A mechanistic explanation. Ecology 80:2348–2357.

Lankford Jr., T. E., J. M. Billerbeck, and D. O. Conover. 2001. Evolution of Intrinsic Growth and Energy Acquisition Rates. II. Trade-offs with vulnerability to predation in Menidia menidia. Evolution 55:1863–1872.

Law, R. 2000. Fishing, selection, and phenotypic evolution. ICES Journal of Marine Science 57:659–668.

Lefébure, R., S. Larsson, and P. Byström. 2014. Temperature and size-dependent attack rates of the three-spined stickleback (*Gasterosteus aculeatus*); are sticklebacks in the Baltic Sea resource-limited? Journal of Experimental Marine Biology and Ecology 451:82–90.

Legendre, P. 2014. lmodel2: Model II Regression.

Levins, R. 1962. Theory of Fitness in a Heterogeneous Environment . I . The Fitness Set and Adaptive Function. The American Naturalist 96:361–373.

———. 1963. Theory of Fitness in a Heterogeneous Environment. II. Developmental Flexibility and Niche Selection. The American Naturalist 97:75–90.

Lewis, W. M. 1976. Surface/Volume ratio: implications for phytoplankton morphology. Science 192:885–887.

Lika, K., and R. M. Nisbet. 2000. A Dynamic Energy Budget model based on partitioning of net production. Journal of Mathematical Biology 386:361–386.

Ma, J., and S. A. Levin. 2006. The evolution of resource adaptation: How generalist and specialist consumers evolve. Bulletin of Mathematical Biology 68:1111–1123.

MacArthur, R. 1970. Species Packing and Competitive Equilibrium for Many Species. Theoretical Population Biology 1:1–11.

Maino, J. L., and M. R. Kearney. 2015. Ontogenetic and interspecific scaling of consumption in insects. Oikos 124:1564–1570.

Maino, J. L., M. R. Kearney, R. M. Nisbet, and S. A. Kooijman. 2014. Reconciling theories for metabolic scaling. Journal of Animal Ecology 83:20–29.

Makarieva, A. M., V. G. Gorshkov, and B.-L. Li. 2004. Ontogenetic growth: models and theory. Ecological Modelling 176:15–26.

———. 2009. Comment on "Energy uptake and allocation during ontogeny". Science 325:1206; author reply 1206.

Malmquist, H. J., S. S. Snorrason, S. Skulason, B. Jonsson, O. T. Sandlund, and P. M. Jonasson. 1992. Diet Differentiation in Polymorphic Arctic Charr in Thingvallavatn, Iceland. Journal of Animal Ecology 61:21–35.

Margulies, D., J. M. Suter, S. L. Hunt, R. J. Olson, V. P. Scholey, J. B. Wexler, and A. Nakazama. 2007. Spawning and early development of captive yellowfin tuna (*Thunnus albacares*). Fishery Bulletin 105:249–265.

Marquet, P. A., F. A. Labra, and B. A. Maurer. 2004. Metabolic Ecology: Linking Individuals to Ecosystems. Ecology 85:1794–1796.

Marshall, D. J., and S. G. Morgan. 2011. Ecological and evolutionary consequences of linked life-history stages in the sea. Current Biology 21:R718–R725.

Martin, B. T., T. Jager, R. M. Nisbet, T. G. Preuss, and V. Grimm. 2013. Predicting population dynamics from the properties of individuals: a cross-level test of dynamic energy budget theory. The American Naturalist 181:506–19.

Marty, L., U. Dieckmann, and B. Ernande. 2015. Fisheries-induced neutral and adaptive evolution in exploited fish populations and consequences for their adaptive potential. Evolutionary Applications 8:47–63.

Matsuda, H., and P. A. Abrams. 1994. Runaway Evolution to Self-Extinction Under Asymmetrical Competition. Evolution 48:1764–1772.

May, R. M. 1972. Will a large complex system be stable? Nature 238:413–414.

Mazancourt, C. D., and U. Dieckmann. 2004. Trade-Off Geometries and Frequency-Dependent Selection. The American Naturalist 164:765–778.

McCann, K., A. Hastings, and G. R. Huxel. 1998. Weak trophic interactions and the balance of nature. Nature 395:794–798.

McCann, K. S. 2011. Food Webs. Monographs in Population Biology. Princeton University Press.

McCauley, E., W. W. Murdoch, R. M. Nisbet, and W. S. C. Gurney. 1990. The physiological ecology of Daphnia: development of a model of growth and reproduction. Ecology 71:703–715.

McCauley, E., W. A. Nelson, and R. M. Nisbet. 2008. Small-amplitude cycles emerge from stage-structured interactions in Daphnia-algal systems. Nature 455:1240–1243.

McCauley, E., R. M. Nisbet, W. W. Murdoch, A. M. De Roos, and W. S. C. Gurney. 1999. Large-amplitude cycles of Daphnia and its algal prey in enriched environments. Nature 402:653–656.

Metz, J. A. J. 2012. Adaptive Dynamics. Pages 7–17 *in* A. Hastings and L. J. Gross, eds. Encyclopedia of Theoretical Ecology, Encyclopedia of Theoretical Ecology. California University Press.

Metz, J. A. J., and O. Diekmann. 1986. The dynamics of physiologically structured populations. Lecture notes in biomathematics .

Metz, J. A. J., S. A. H. Geritz, G. Meszéna, F. J. A. Jacobs, and J. S. Van Heerwaarden. 1995. Adaptive Dynamics: A Geometrical Study of the Consequences of Nearly Faithful Reproduction. Internation Institute for Applied Systems Analysis Working Paper .

Metz, J. A. J., R. M. Nisbet, and S. A. H. Geritz. 1992. How Should We Define 'Fitness' for General Ecological Scenarios? Trends in Ecology and Evolution 7.

Miller, T. E. X., and V. H. W. Rudolf. 2011. Thinking inside the box: Community-level consequences of stage-structured populations. Trends in Ecology and Evolution 26:457–466.

Moran, N. A. 1994. Adaptation and Constraint in the Complex Life Cycles of Animals. Annual Review of Ecology and Systematics 25:573–600.

Moses, M. E., C. Hou, W. H. Woodruff, G. B. West, J. C. Nekola, W. Zuo, and J. H. Brown. 2008. Revisiting a model of ontogenetic growth: estimating model parameters from theory and data. The American Naturalist 171:632–45.

Murdoch, W. W., C. J. Briggs, and R. M. Nisbet. 2003. Consumer-Resource Dynamics. Princeton University Press.

Murdoch, W. W., B. E. Kendall, R. M. Nisbet, C. J. Briggs, E. McCauley, and R. Bolser. 2002. Single-species models for many-species food webs. Nature 417:541–3.

Mylius, S. D., and O. Diekmann. 1995. On evolutionarily stable life histories, optimization and the need to be specific about density dependence. Oikos 74:218–224.

Mylius, S. D., K. Klumpers, A. M. De Roos, and L. Persson. 2001. Impact of intraguild predation and stage structure on simple communities along a productivity gradient. The American Naturalist 158:259–76.

Nakaya, F., Y. Saito, and T. Motokawa. 2003. Switching of metabolic-rate scaling between allometry and isometry in colonial ascidians. Proceedings of the Royal Society of London B 270:1105–1113.

Neuenfeldt, S., S. Neuenfeldt, F. W. Koster, and F. W. Koster. 2000. Trophodynamic control on recruitment success in Baltic cod: the influence of cannibalism. ICES Journal of Marine Science 57:309.

Neuheimer, A. B., M. Hartvig, J. Heuschele, S. Hylander, T. Kiørboe, K. H. Olsson, J. Sainmont, and K. H. Andersen. 2016. Adult and offspring size in the ocean: A database of size metrics and conversion factors. Ecology .

Nisbet, R. M., E. B. Muller, K. Lika, and S. A. L. M. Kooijman. 2008. From molecules to ecosystems through dynamic energy budget models. Journal of Animal Ecology 69:913–926.

Nissar, K. K. S., F. Rashid, G. G. Phadke, and A. Y. Desai. 2015. Reproductive biology of little tuna (*Euthynnus affinis*) in the Arabian sea. Ecology, Environment and Conservation 21:115–118.

Nurmi, T., and K. Parvinen. 2008. On the evolution of specialization with a mechanistic underpinning in structured metapopulations. Theoretical Population Biology 73:222–243.

———. 2013. Evolution of specialization under non-equilibrium population dynamics. Journal of Theoretical Biology 321:63–77.

Ohlberger, J., Ø. Langangen, E. Edeline, D. Claessen, I. J. Winfield, N. C. Stenseth, and L. A. Vøllestad. 2011. Stage-specific biomass overcompensation by juveniles in response to increased adult mortality in a wild fish population. Ecology 92:2175–2182.

Ohlberger, J., Ø. Langangen, N. C. Stenseth, and L. A. Vøllestad. 2012*a*. Community-Level Consequences of Cannibalism. The American Naturalist 180:791–801.

Ohlberger, J., T. Mehner, G. Staaks, and F. Hölker. 2012*b*. Intraspecific temperature dependence of the scaling of metabolic rate with body mass in fishes and its ecological implications. Oikos 121:245–251.

Ohlberger, J., G. Staaks, and F. Hölker. 2007. Effects of temperature, swimming speed and body mass on standard and active metabolic rate in vendace (*Coregonus albula*). Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology 177:905–916.

Okie, J. G. 2013. General Models for the Spectra of Surface Area Scaling Strategies of Cells and Organisms: Fractality, Geometric Dissimilitude, and Internalization. The American Naturalist 181:421–439.

Oksanen, L., S. D. Fretwell, J. Arruda, and P. Niemela. 1981. Exploitation Ecosystems in Gradients of Primary Productivity. The American Naturalist 118:240–261.

Olson, M. H., G. G. Mittelbach, and C. W. Osenberg. 1995. Competition between Predator and Prey : Resource-Based Mechanisms and Implications for Stage-Structured Dynamics. Ecology 76:1758–1771.

Palkovacs, E. P., and D. M. Post. 2008. Eco-evolutionary interactions between predators and prey: can predator-induced changes to prey communities feed back to shape predator foraging traits? Evolutionary Ecology Research 10:699–720.

Parvinen, K. 2005. Evolutionary Suicide. Acta Biotheoretica 53:241–264.

———. 2016. Evolution by natural selection to extinction. Evolutionary Ecology Research 17:743–756.

Parvinen, K., and U. Dieckmann. 2013. Self-extinction through optimizing selection. Journal of Theoretical Biology 333:1–9.

Pauly, D., and R. S. V. Pullin. 1988. Hatching time in spherical, pelagic, marine fish eggs in response to temperature and egg size. Environmental Biology of Fishes 22:261–271.

Persson, L. 1988. Asymmetries in competitive and predatory interactions in fish populations. Size-structured populations .

Persson, L., P.-A. Amundsen, A. M. De Roos, A. Klemetsen, R. Knudsen, and R. Primicerio. 2007. Culling prey promotes predator recovery–alternative states in a whole-lake experiment. Science 316:1743–6.

Persson, L., P. Byström, and E. Wahlström. 2000. Cannibalism and competition in Eurasian perch: population dynamics of an ontogenetic omnivore. Ecology 81:1058–1071.

Persson, L., D. Claessen, A. M. De Roos, P. Byström, S. Sjogren, R. Svanbäck, E. Wählstrom, and E. Westman. 2004. Cannibalism in a Size-Structured Population: Energy Extraction and Control. Ecological Monographs 74:135–157.

Persson, L., and A. M. De Roos. 2006. Food-dependent individual growth and population dynamics in fishes. Journal of Fish Biology 69:1–20.

———. 2012. Mixed competition–predation: potential vs. realized interactions. Journal of Animal Ecology 81:483–493.

———. 2013. Symmetry breaking in ecological systems through different energy efficiencies of juveniles and adults. Ecology 94:1487–1498.

Persson, L., A. M. De Roos, D. Claessen, P. Byström, J. Lövgren, S. Sjögren, R. Svanbäck, E. Wahlström, and E. Westman. 2003. Gigantic cannibals driving a whole-lake trophic cascade. Proceedings of the National Academy of Sciences of the United States of America 100:4035–4039.

Persson, L., and L. A. Greenberg. 1990. Juvenile Competitive Bottlenecks: The Perch (*Perca Fluviatilis*) -Roach (*Rutilus Rutilus*) Interaction. Ecology 71:44–56.

Persson, L., K. Leonardsson, A. M. De Roos, M. Gyllenberg, and B. Christensen. 1998. Ontogenetic Scaling of Foraging Rates and the Dynamics of a Size-Structured Consumer-Resource Model. Theoretical population biology 54:270–293.

Persson, L., A. Van Leeuwen, and A. M. De Roos. 2014. The ecological foundation for ecosystem-based management of fisheries: mechanistic linkages between the individual-, population-, and community-level dynamics. ICES Journal of Marine Science page fst231.

Peters, R. H. 1983. The Ecological Implications of Body Size. Cambridge University Press, Cambridge.

Pfennig, D. W. 1997. Kinship and Cannibalism. BioScience 47:667–675.

Pfennig, D. W., S. G. Ho, and E. A. Hoffman. 1998. Pathogen transmission as a selective force against cannibalism. Animal Behaviour 55:1255–1261.

Pfennig, D. W., M. L. G. Loeb, and J. P. Collins. 1991. Pathogens as a Factor Limiting the Spread of Cannibalism in Tiger Salamanders. Oecologia 88:161–166.

Pfennig, D. W., M. A. Wund, E. C. Snell-Rood, T. Cruickshank, C. D. Schlichting, and A. P. Moczek. 2010. Phenotypic plasticity's impacts on diversification and speciation. Trends in Ecology and Evolution 25:459–67.

Pimm, S. L., and J. C. Rice. 1987. The dynamics of multispecies, multi-life-stage models of aquatic food webs. Theoretical Population Biology 32:303–325.

Polis, G. A. 1981. The evolution and dynamics of intraspecific predation. Annual Review of Ecology and Systematics 12:225–251.

———. 1991. Complex Trophic Interactions in Deserts : An Empirical Critique of Food-Web Theory. The American Naturalist 138:123–155.

Polis, G. A., and R. D. Holt. 1992. lntraguild Predation: The Dynamics of Complex Trophic Interactions. Trends in Ecology and Evolution 7:5–8.

Polis, G. A., and C. A. Myers. 1985. A Survey of Intraspecific Predation among Reptiles and Amphibians. Journal of Herpetology 19:99–107.

Polis, G. A., C. A. Myers, and R. D. Holt. 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. Annual Review of Ecology and Systematics 20:297–330.

Post, D. M., and E. P. Palkovacs. 2009. Eco-evolutionary feedbacks in community and ecosystem ecology: interactions between the ecological theatre and the evolutionary play. Philosophical Transactions of the Royal Society B 364:1629–40.

R Core Team. 2015. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Rall, B. C., U. Brose, M. Hartvig, G. Kalinkat, F. Schwarzmüller, O. Vucic-Pestic, and O. L. Petchey. 2012. Universal temperature and body-mass scaling of feeding rates. Philosophical Transactions of the Royal Society B 367:2923–34.

Rankin, D. J., and A. López-Sepulcre. 2005. Can adaptation lead to extinction? Oikos 111:616–619.

Reichstein, B., L. Persson, and A. M. De Roos. 2015. Ontogenetic asymmetry modulates population biomass production and response to harvest. Nature Communications 6:6441.

———. in prep. Predator life history affects persistence times of predators and consumers in an intraguild predation system .

Reichstein, B., A. Schröder, L. Persson, and A. M. De Roos. 2013. Habitat complexity does not promote coexistence in a size-structured intraguild predation system. Journal of Animal Ecology 82:55–63.

Richard, R. 2014. Consumer Life History and Demography in Dynamic Environments. Ph.D. thesis. University of Calgary.

Richard, R., J. J. Casas, and E. McCauley. 2015. Sensitivity analysis of continuous-time models for ecological and evolutionary theories. Theoretical Ecology 8:481–490.

Ricklefs, R. 2003. Is rate of ontogenetic growth constrained by resource supply or tissue growth potential? A comment on West et al.'s model. Functional Ecology 17:384–393.

Robinson, B. W., and D. S. Wilson. 1996. Genetic variation and phenotypic plasticity in a trophically polymorphic population of pumpkinseed sunfish (Lepomis gibbosus). Evolutionary Ecology 10:631–652.

Robinson, B. W., D. S. Wilson, and G. O. Shea. 1996. Trade-Offs of Ecological Specialization: An Intraspecific Comparison of Pumpkinseed Sunfish Phenotypes. Ecology 77:170–178.

Roff, D. A. 1992. The Evolution of Life Histories Theory and Analysis. Chapman & Hall, New York.

Rudolf, V. H. W. 2007. The interaction of cannibalism and omnivory: consequences for community dynamics. Ecology 88:2697–2705.

———. 2008. Impact of cannibalism on predator-prey dynamics: size-structured interactions and apparent mutualism. Ecology 89:1650–1660.

Rudolf, V. H. W., and K. D. Lafferty. 2011. Stage structure alters how complexity affects stability of ecological networks. Ecology Letters 14:75–79.

Rudolf, V. H. W., N. L. Rasmussen, C. J. Diddle, and B. G. Van Allen. 2014. Resolving the roles of body size and species identity in driving functional diversity. Proceedings of the Royal Society B: Biological Sciences 281:20133203.

Rueffler, C., M. Egas, and J. A. J. Metz. 2006*a*. Evolutionary predictions should be based on individual-level traits. The American Naturalist 168:E148–E162.

Rueffler, C., T. J. M. Van Dooren, and J. A. J. Metz. 2006*b*. The Evolution of Resource Specialization through Frequency- Dependent and Frequency-Independent Mechanisms. The American Naturalist 167:81–93.

———. 2007. The interplay between behavior and morphology in the evolutionary dynamics of resource specialization. The American Naturalist 169:E34–E52.

Russel, F. S. 1976. The Eggs and Plankton Stages of British Marine Fishes. Academic Press, Oval Road, London.

Savage, V. M., J. F. Gillooly, W. H. Woodruff, G. B. West, A. P. Allen, B. J. Enquist, and J. H. Brown. 2004. The predominance of quarter-power scaling in biology. Functional Ecology 18:257–282.

Schluter, D. 1995. Adaptive radiation in sticklebacks: Trade-off in feeding performance and growth. Ecology 76:82–90.

Schluter, D., T. Price, and L. Rowe. 1991. Conflicting selection pressures and life history trade-offs. Proceedings of the Royal Society of London B 246:11–17.

Schröder, A., K. A. Nilsson, L. Persson, T. van Kooten, and B. Reichstein. 2009*a*. Invasion success depends on invader body size in a size-structured mixed predation-competition community. Journal of Animal Ecology 78:1152–62.

Schröder, A., L. Persson, and A. M. De Roos. 2009*b*. Culling experiments demonstrate size-class specific biomass increases with mortality. Proceedings of the National Academy of Sciences of the United States of America 106:2671–2676.

Schröder, A., A. van Leeuwen, and T. C. Cameron. 2014. When less is more : positive population-level effects of mortality. Trends in Ecology and Evolution 29:614–624.

———. 2015. Empirical support for different types of positive mortality effects. A reply to Abrams. Trends in Ecology and Evolution 30:180–181.

Sebens, K. P. 1987. The ecology of indeterminate growth in animals. Annual Review of Ecology and Systematics 18:371–407.

Sibly, R. M., J. H. Brown, and A. Kodric-Brown, eds. 2012. Metabolic Ecology A Scaling Approach. Wiley-Blackwell.

Smith, C., and P. Reay. 1991. Cannibalism in teleost fish. Reviews in Fish Biology and Fisheries 1:41–64.

Soudijn, F. H. 2016. Populations explosed to seasonal variability: from individual-level energetics to community dynamics. Ph.D. thesis. University of Amsterdam.

Sousa, T., T. Domingos, and S. A. L. M. Kooijman. 2008. From empirical patterns to theory: a formal metabolic theory of life. Philosophical Transactions of the Royal Society B 363:2453–2464.

Sousa, T., T. Domingos, J.-C. Poggiale, and S. A. L. M. Kooijman. 2010. Dynamic energy budget theory restores coherence in biology. Philosophical Transactions of the Royal Society B 365:3413–3428.

Steimle, F. W., W. W. Morse, P. L. Berrien, D. L. Johnson, and C. A. Zetlin. 1999. Essential Fish Habitat Source Document: Ocean Pout, *Macrozoarces americanus*, Life History and Habitat Characteristics. Tech. Rep. September, NOAA Technical Memorandum.

Stevens, L. 1989. The Genetics and Evolution of Cannibalism in Flour Beetles (Genus *tribolium*). Evolution 43:169–179.

Svanbäck, R., and D. I. Bolnick. 2007. Intraspecific competition drives increased resource use diversity within a natural population. Proceedings of the Royal Society B 274:839–844.

Svanbäck, R., and P. Eklöv. 2002. Effects of habitat and food resources on morphology and ontogenetic growth trajectories in perch. Oecologia 131:61–70.

———. 2003. Morphology dependent foraging efficiency in perch: a trade-off for ecological specialization? Oikos 102:273–284.

Svenning, M.-A., and R. Borgstrøm. 2005. Cannibalism in Arctic charr: Do all individuals have the same propensity to be cannibals? Journal of Fish Biology 66:957–965.

Ten Brink, H., and A. M. De Roos. 2017. A Parent-Offspring Trade-Off Limits the Evolution of an Ontogenetic Niche Shift. The American Naturalist 190.

Tilman, D. 1980. Resources: A Graphical-Mechanistic Approach to Competition and Predation. The American Naturalist 116:362–393.

———. 1982. Resource Competition and Community Structure. Monographs in population biology. Princeton University Press.

Toscano, B. J., V. Hin, and V. H. W. Rudolf. in press. Cannibalism Drives Coexistence, Competitive Exclusion And Loss Of Alternative Stable States In Intraguild Predation Systems. The American Naturalist (This thesis, chapter 4) .

Toscano, B. J., B. R. Rombado, and V. H. W. Rudolf. 2016. Deadly competition and life-saving predation: the potential for alternative stable states in a stage-structured predator–prey system. Proceedings of the Royal Society B 283:20161546.

Troost, T. A., B. W. Kooi, and S. A. L. M. Kooijman. 2005. When do mixotrophs specialize? Adaptive dynamics theory applied to a dynamic energy budget model. Mathematical Biosciences 193:159–182.

Van de Wolfshaar, K. E., A. M. De Roos, and L. Persson. 2006. Size-dependent Interactions Inhibit Coexistence in Intraguild Predation Systems with Life-History Omnivory. The American Naturalist 168:62–75.

Van der Meer, J. 2006. Metabolic theories in ecology. Trends in Ecology and Evolution 21:136–40.

Van Kooten, T., A. M. De Roos, and L. Persson. 2005. Bistability and an Allee effect as emergent consequences of stage-specific predation. Journal of Theoretical Biology 237:67–74.

Van Kooten, T., L. Persson, and A. M. De Roos. 2007. Size-Dependent Mortality Induces Life-History Changes Mediated through Population Dynamical Feedbacks. The American Naturalist 170:258–270.

Van Leeuwen, A., M. Huss, A. Gårdmark, M. Casini, F. Vitale, J. Hjelm, L. Persson, and A. M. De Roos. 2013. Predators with Multiple Ontogenetic Niche Shifts Have Limited Potential for Population Growth and Top-Down Control of Their Prey. The American Naturalist 182:53–66.

Vance-Chalcraft, H. D., J. A. Rosenheim, J. R. Vonesh, C. W. Osenberg, and A. Sih. 2007. The influence of intraguild predation on prey suppression and prey release: a meta-analysis. Ecology 88:2689–2696.

Vøllestad, L. A., and J. H. L'Abée-Lund. 1994. Evolution of the life history of Arctic charr *Salvelinus alpinus*. Evolutionary Ecology 8:315–327.

Wagner, J. D., M. D. Glover, J. B. Mosely, and A. J. Moore. 1999. Hereditability and fitness consequences of cannibalism in Harmonia axyridis. Evolutionary Ecology Research 1:375–388.

Wahlström, E., L. Persson, S. Diehl, and P. Byström. 2000. Size-dependent foraging efficiency, cannibalism and zooplankton community structure. Oecologia 123:138–148.

Wallace, J. C., and D. Aasjord. 1984. An investigation of the consequences of egg size for the culture of Arctic charr, *Salvelinus alpinus* (L.). Journal of Fish Biology 24:427–435.

Walters, C., and J. F. Kitchell. 2001. Cultivation/depensation effects on juvenile survival and recruitment: implications for the theory of fishing. Canadian Journal of Fisheries and Aquatic Sciences 58:39–50.

Webb, C. 2003. A Complete Classification of Darwinian Extinction in Ecological Interactions. The American Naturalist 161:181–205.

Werner, E. E. 1988. Size, scaling, and the evolution of complex life cycles. Pages 60–81 *in* B. Ebenman and L. Persson, eds. Size-structured populations. Springer-Verlag, Berlin Heidelberg.

———. 1994. Ontogenetic Scaling of Competitive Relations : Size-Dependent Effects and Responses in Two Anuran Larvae. Ecology 75:197–213.

Werner, E. E., and J. F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. Annual Review of Ecology and Systematics 15:393–425.

Werner, E. E., and D. J. Hall. 1977. Competition and Habitat Shift in Two Sunfishes (*Centrarchidae*). Ecology 58:869–876.

West, G. B. 1997. A General Model for the Origin of Allometric Scaling Laws in Biology. Science 276:122–126.

West, G. B., J. H. Brown, and B. J. Enquist. 1999. The fourth dimension of life: fractal geometry and allometric scaling of organisms. Science 284:1677–1679.

———. 2001. A general model for ontogenetic growth. Nature 413:628–631.

———. 2004. Growth models based on first principles or phenomenology? Functional Ecology 18:188–196.

White, C. R., M. R. Kearney, P. G. D. Matthews, S. A. L. M. Kooijman, and D. J. Marshall. 2011. A Manipulative Test of Competing Theories for Metabolic Scaling. The American Naturalist 178:746–754.

Wilbur, H. M. 1980. Complex life cycles. Annual Review of Ecology and Systematics 11:67–93.

———. 1988. Interactions between growing predators and growing prey. Pages 157–172 *in* B. Ebenman and L. Persson, eds. Size-structured populations. Springer-Verlag, Berlin Heidelberg.

Wilson, D. S., and M. Turelli. 1986. Stable Underdominance and the Evolutionary Invasion. The American Naturalist 127:835–850.

Winemiller, K. O., and K. A. Rose. 1992. Patterns of Life-History Diversification in North American Fishes: Implications for Population Regulation. Canadian Journal of Fisheries and Aquatic Sciences 49:2196–2218.

Wollrab, S., A. M. De Roos, and S. Diehl. 2013. Ontogenetic diet shifts promote predator-mediated coexistence. Ecology 94:2886–2897.

Yasuda, H., T. Kikuchi, P. Kindlmann, and S. Sato. 2001. Relationships Between Attack and Escape Rates, Cannibalism, and Intraguild Predation in Larvae of Two Predatory Ladybirds. Journal of Insect Behavior 14:373–384.

Yodzis, P., and S. Innes. 1992. Body Size and Consumer-Resource Dynamics. The American Naturalist 139:1151–1175.

Zera, A. J., and L. G. Harshman. 2001. The Physiology of Life History Trade-Offs in Animals. Annual Review of Ecology and Systematics 32:95–126.

Zuo, W., M. E. Moses, G. B. West, C. Hou, and J. H. Brown. 2012. A general model for effects of temperature on ectotherm ontogenetic growth and development. Proceedings of the Royal Society B 279:1840–6.

Summary

Ontogenesis: an eco-evolutionary perspective on life history complexity
In all organisms, ontogenetic development represents an essential life-history process that has major impacts on the interaction between an organism and its ecological environment. Ontogenetic development can be regarded as the collection of changes in the state of an individual that occur during its life, in terms of changes in size, shape, physiology, maturity status, or behavior. Ontogenetic development changes many ecological processes. For example, when organisms grow considerably during life, or undergo metamorphosis, small and large individuals often consume different types of food or live in different habitats. As such, ontogenetic development has consequences for both the type of ecological interactions (*e.g.* absence or presence of predation or competition) and the strength of ecological interactions (*e.g.* rates of predation or competitive ability). In turn, changes in ecological interactions during ontogenetic development have major implications for the dynamics of natural populations and communities.

However, there are conditions under which ontogenetic development, through its impact on the ecological interactions of individual organisms, does *not* affect the behavior of populations and communities. These are the conditions of *ontogenetic symmetry*. Ontogenetic symmetry describes how the strength of ecological interactions between an organism and its ecological environment, changes as the ontogenetic development of the organism unfolds. In case of ontogenetic symmetry, the change in ecological interaction strength happens in exact parity with the ontogenetic development of the organism. This creates a type of ecological *symmetry* between individuals that are at different stages of ontogenetic development. In case of a deviation from *ontogenetic symmetry*, the ecological interaction strength changes either faster, or slower, compared to the ontogenetic development of the individual. This is referred to as *ontogenetic asymmetry*. In the event of ontogenetic asymmetry, ontogenetic development will lead to a change in the ecological interaction strength of an organism, in a way that affects population and community dynamics.

The consequences of ontogenetic asymmetry for dynamics of natural populations and communities are well described, both in a theoretical and an empirical context. Furthermore, there are numerous indications that ontogenetic asymmetry pertains to most, if not all populations. However, the evolutionary aspects of ontogenetic asymmetry have not been studied. This thesis takes this step and focuses on the evolutionary origins of ontogenetic asymmetry. For this purpose, mathematical models are used that combine an accurate description of life-history processes (*i.e.* ontogenetic development, reproduction and mortality), with ecological interactions between different populations. The general question of this thesis, is whether and how evolution through natural selection will lead to ontogenetic asymmetry.

Chapter 2 and 3 describe the evolution of ontogenetic asymmetry in a simplified ecological system of a consumer species that lives of a single type of food (*i.e.* resource). Consumer individuals take up and assimilate food to meet the costs of metabolism. On top of that, they can invest energy in growth (both juveniles and adults are assumed to grow) and reproduction (only in case of adults). Because all consumer individuals compete for the single resource, ontogenetic asymmetry leads to a difference in competitive ability between individuals at different stages of ontogenetic development. A good competitor can take up and assimilate resources fast and also requires little energy for maintenance. Therefore, good competitors can spend a lot of energy on growth and reproduction, and this increases their fitness. A poor competitor has a low rate of resource uptake and high maintenance costs. When poor competitors have too little energy for maintenance, their mortality risk increases (starvation) and this leads to low fitness. Through a trade-off it is assumed that a good competitive ability in the juvenile phase, leads to poor competitive ability in the adult phase, and vice versa.

In chapter 2 and 3 it is shown that in this simplified setting, evolution of ontogenetic asymmetry neutralizes strong competitive differences. With the evolved type of ontogenetic asymmetry, individuals at different stages of development (*e.g.* juveniles versus adults), all require the same amount of food to meet their maintenance costs. Consequently, consumer individuals never suffer from starvation. However, differences in competitive ability do arise through differences in growth and reproduction rates. When either the juvenile phase of the life cycle, or juvenile mortality is increased, selection increases juvenile fitness (*i.e.* juvenile growth), at the expense of adult fitness (*i.e.* adult growth and reproduction). Vice versa, an extension of the adult phase of the life cycle, or increased adult mortality, leads to higher adult fitness, and lower juvenile fitness. However, this adaptive response is such that it does not lead to starvation in any part of the life cycle.

The evolved type of ontogenetic asymmetry does not match well with observations from nature. In many natural populations, individuals require different resource levels to cover their maintenance metabolism. Accordingly, strong competition between individuals in different life stages can induce starvation events. Concluding, the simple ecological setting as studied in chapter 2 and 3 does not explain the type of ontogenetic asymmetry that is observed in nature.

In chapter 4 and 5 it is studied whether the more complex ecological setting of life-history intraguild predation gives rise to the evolution of ontogenetic asymmetry. Intraguild predation describes the mixed predation/competition interaction between a predator and a prey species. Juvenile predators compete with the prey for a shared food source, while adult predators feed on the prey and, in addition, can cannibalize juvenile predators. The shift in diet from resource feeding to predation, implies a change in the type of ecological interaction and this leads to ontogenetic asymmetry. Cannibalism is another source of ontogenetic asymmetry, because it provides a food source for adult predators and leads to higher mortality for juveniles. Taking together the effects of cannibalism and diet shifts can lead to two types of ontogenetic asymmetry in the predator population when it is in equilibrium (*i.e.* population density does not change over time). Either the predator population becomes maturation-regulated, characterized by low juvenile growth rates and high juvenile mortality. Or the population becomes reproduction-regulated, characterized by low adult reproduction and high adult mortality. These two types are separated by ontogenetic symmetry, in which the predator population is neither reproduction, nor maturation regulated.

In chapter 4 it is shown that cannibalism is detrimental for the persistence of the intraguild predator, because it changes the ontogenetic asymmetry from reproduction-regulation into maturation-regulation. In case of maturation-regulation, competition of juvenile predators with consumers becomes too severe for stable predator persistence. Therefore, cannibalism leads to ecological extinction of predators by changing the type of ontogenetic asymmetry.

Chapter 5 describes the evolution of ontogenetic asymmetry in the intraguild predator, dependent on the level of cannibalism. In chapter 5 it is assumed that predators can evolve to increase resource feeding rates of juveniles (which decreases maturation regulation), or increase predation rates of adults (which decreases reproduction regulation). An ontogenetic trade-off between the life stages prevents simultaneous increase in resource feeding and predation rates. In absence of cannibalism, selection on this ontogenetic trade-off leads to an increase in specialization of one life stage, at the expense of feeding performance in the other life stage. Ultimately, increasing one type of specialization causes a shift in the community dynamics to a state in which predators can no longer persist. Consequently, selection on the ontogenetic trade-off in absence of cannibalism leads to evolutionary suicide of the intraguild predator. Cannibalism, however, prevents evolutionary suicide by stabilizing the selection on the ontogenetic trade-off in resource specialization.

In the more complex ecological setting of intraguild predation, ontogenetic asymmetry is also determined by the densities of consumers and resources. Selection on ontogenetic asymmetry leads to an ecological feedback on consumer and resource density. This feedback acts in opposite direction to the forces that drive selection (*i.e.* the amount and direction of ontogenetic asymmetry). Consequently, selection can act to decrease ontogenetic asymmetry, but due to the feedback in the ecological dynamics, selection might not be successful in doing so, or instead, even lead to more ontogenetic asymmetry. Furthermore, cannibalism can induce selection towards ontogenetic asymmetry, because the fitness benefits of cannibalism are greater when the population is in a maturation-regulated state. This is because juvenile density is high in such a state.

Concluding, in intraguild predation systems, the ecological persistence of predators depends crucially on the direction of ontogenetic asymmetry (chapter 4). Furthermore, selection of ontogenetic asymmetry can have unanticipated effects (evolutionary suicide; chapter 5). Increased ecological complexity through cannibalism can stabilize evolutionary dynamics and lead to ontogenetic asymmetry (chapter 5). Comparing these outcomes with the results described in chapter 2 and 3, shows that a certain amount of ecological complexity (as in the number and nature of ecological feedback loops) seems a prerequisite for the evolution of ontogenetic asymmetry.

The evolution of cannibalism can establish a novel ecological interaction and, as such, provides a route to increased ecological complexity in simple communities. Furthermore, cannibalism can inhibit persistence of intraguild predators on ecological timescales (chapter 4), but cannibalism can also stabilize evolutionary dynamics and prevent evolutionary suicide (chapter 5). It is therefore important to understand the conditions that inhibit or promote the evolution of cannibalism. Chapter 6 addresses this topic in the more applied and practical context of fisheries-induced evolution. A model for the population dynamics of cannibalistic Arctic char (*Salvelinus alpinus*), shows that fisheries-induced mortality promotes the evolution of cannibalism. Under low rates of mortality, cannibalism evolution is stabilized by the mortality costs associated with cannibalistic feeding. However, fisheries-induced mortality changes the stabilizing selection into positive directional selection to ever increasing rates of cannibalism. This leads to a double effect of mortality on the population. The fisheries-induced mortality decreases population biomass directly, but also selects for even higher rates of cannibalism, which further reduces population density.

Overall, this thesis combines complex ecological interactions with evolutionary processes that shape individual life histories. This combination has not been used often, but has the potential to provide insights on how complex life forms and ecosystems have coevolved and how they are maintained.

Samenvatting

Ontogenese: de ecologie en evolutie van complexe levensontwikkeling

Ontogenetische ontwikkeling is een essentieel proces in het leven van alle organismen en bepaalt in belangrijke mate de interactie tussen organismen en hun ecologische omgeving. Ontogenetische ontwikkeling kan worden beschouwd als de verzameling van veranderingen in afmeting, vorm, fysiologie, levensfase en gedrag, die plaatsvinden gedurende het leven van een organisme. Deze vorm van ontwikkeling is van grote invloed op allerlei ecologische processen. Zo leidt bijvoorbeeld groei in lichaamsgrootte of metamorfose vaak tot veranderingen in het dieet of habitat van het organisme. Op deze manier beïnvloedt ontogenetische ontwikkeling zowel de aard van de ecologische interactie (zoals de aanwezigheid van predatoren of concurrenten), als de sterkte van de ecologische interactie (de predatiedruk of de sterkte van competitie). Veranderingen in ecologische interacties als gevolg van ontogenetische ontwikkeling hebben grote gevolgen voor de dynamiek van natuurlijke populaties en levensgemeenschappen.

Er zijn echter bepaalde omstandigheden waarbij ontogenetische ontwikkeling, ondanks haar invloed op ecologische interacties van individuele organismen, geen effect heeft op de dynamiek van natuurlijke populaties en levensgemeenschappen. Onder zulke omstandigheden verkeert de populatie in een toestand van ontogenetische symmetrie. In het geval van ontogenetische symmetrie is de verandering in de sterkte van de ecologische interactie precies parallel aan de ontogenetische ontwikkeling van het organisme. Op deze manier ontstaat er een ecologische symmetrie tussen individuen die in verschillende stadia van hun ontogenetische ontwikkeling verkeren. Bij een afwijking van ontogenetische symmetrie neemt de sterkte van de ecologische interactie sneller toe of af, vergeleken met de ontogenetische ontwikkeling van het organisme. Dit wordt ook wel ontogenetische asymmetrie genoemd. Bij ontogenetische asymmetrie zorgt de ontogenetische ontwikkeling dus voor een verandering in de sterkte van de ecologische interactie, op een manier die van invloed is op de dynamiek van natuurlijke populaties en levensgemeenschappen.

Er zijn tal van aanwijzingen dat ontogenetische asymmetrie geldt voor de meeste, zo niet alle, populaties, en de gevolgen van ontogenetische asymmetrie op de dynamiek van populaties en ecosystemen worden tegenwoordig goed begrepen. De evolutionaire aspecten van ontogenetische asymmetrie zijn echter minder goed onderzocht. Het onderzoek in dit proefschrift richt zich daarom op de evolutionaire oorsprong en gevolgen van ontogenetische asymmetrie. Hiertoe worden wiskundige modellen gebruikt die een beschrijving van verschillende levensprocessen (bijv. ontogenetische ontwikkeling, reproductie en mortaliteit), combineren met een beschrijving van de ecologische interacties tussen verschillende populaties. De overkoepelende vraag van dit proefschrift is of, en op welke manier, evolutie door middel van natuurlijke selectie leidt tot ontogenetische asymmetrie.

In hoofdstuk 2 en 3 wordt de evolutie van ontogenetische asymmetrie in een gesimplificeerd ecosysteem onderzocht. Dit systeem bestaat uit een heterotrofe consument, die zich voedt met een enkele voedselbron. Consumenten gebruiken de energie van de voedselbron voor hun basale metabolisme. Bovenop de energetische kosten van het metabolisme investeren consumenten energie in lichaamsgroei (zowel juveniele als adulte consumenten kunnen groeien) en reproductie (alleen in het geval van adulten). Omdat alle consumenten afhankelijk zijn van dezelfde voedselbron, leidt ontogenetische asymmetrie tot concurrentieverschillen tussen individuen die in verschillende stadia van hun ontogenetische ontwikkeling verkeren. Een sterke concurrent kan snel voedsel opnemen en is weinig energie kwijt aan het basale metabolisme. Hierdoor kan een sterke concurrent veel energie besteden aan groei en reproductie, hetgeen de biologische fitness verhoogt. Een minder sterke concurrent neemt voedsel langzaam op en besteedt veel energie aan het basale metabolisme. Hierdoor kan een mindere concurrent weinig energie besteden aan groei en reproductie. Tevens kan te weinig energie zorgen voor een verhoogde sterftekans, wanneer er niet aan de kosten van het basale metabolisme wordt voldaan. Op deze manier hebben zwakke concurrenten een lage biologische fitness. Er wordt verder aangenomen dat er een trade-off bestaat tussen de concurrentiekracht in de juveniele fase en die in de adulte fase. Hierdoor leidt een verhoging van de concurrentiekracht in de juveniele fase, tot een verlaging van de concurrentiekracht in de adulte fase, en andersom.

In hoofdstuk 2 en 3 wordt beschreven dat in deze gesimplificeerde ecologische setting de evolutie van ontogenetische asymmetrie de sterke concurrentieverschillen in de populatie neutraliseert. Het type ontogenetische asymmetrie dat hierbij ontstaat zorgt ervoor dat individuen in verschillende fase van ontogenetische ontwikkeling (zoals juvenielen en adulten) dezelfde hoeveelheid voedsel nodig hebben voor hun basale metabolisme. Daardoor treedt er geen verhoogde mortaliteit op als gevolg van voedseltekort. Concurrentieverschillen zullen echter blijven bestaan door verschillen in groei- en reproductiesnelheid. Wanneer ofwel de lengte van de juveniele fase, ofwel de juveniele mortaliteit verhoogd wordt, verhoogt selectie de juveniele fitness (juveniele groeisnelheid), ten koste van de adulte fitness (adulte groei- en reproductiesnelheid). Andersom zal een verlenging van de adulte fase, of een verhoging van de mortaliteit onder adulten, leiden tot selectie voor verhoogde adulte fitness, ten koste van de juveniele fitness. Deze evolutionaire respons leidt echter in geen enkel deel van de levenscyclus tot extra mortaliteit als gevolg van voedseltekort.

Dit geëvolueerde type van ontogenetische asymmetrie komt echter niet goed overeen met observaties uit de natuur. In veel natuurlijke populaties verschillen individuen uit verschillende levensstadia in de hoeveelheid voedsel die ze nodig hebben voor hun metabolisme. In zulke populaties zorgt competitie tussen individuen uit verschillende levensstadia voor verhoogde mortaliteit. De simpele ecologische setting, zoals beschreven in hoofdstuk 2 en 3, kan dus niet de ontogenetische asymmetrie van natuurlijke populaties goed verklaren.

In hoofdstuk 4 en 5 wordt onderzocht of ontogenetische asymmetrie evolueert in de complexere ecologische setting van leeftijdsafhankelijke omnivorie. Er is sprake van omnivorie wanneer de predator, naast het prederen op de prooi, ook concurreert met de prooi om dezelfde voedselbron. Bij leeftijdsafhankelijke omnivorie beperkt deze competitie zich tot de juveniele levensfase van de predator, terwijl de predatie alleen plaatsvindt in de adulte levensfase van de predator. Daarnaast prederen adulte predatoren ook op hun eigen juvenielen (kannibalisme). De transitie van competitie (als juveniel) naar predatie (als adult) gedurende het leven van de predator, impliceert een verandering in de ecologische interactie en dit leidt tot ontogenetische asymmetrie. Ontogenetische asymmetrie ontstaat ook door kannibalisme van adulte predatoren, omdat het kannibalisme zowel een voedselbron voor adulten vormt als zorgt voor verhoogde mortaliteit onder juvenielen. Wanneer de populatie in evenwicht is (d.w.z. de populatiedichtheid verandert niet door de tijd) kunnen dieetverandering en kannibalisme zorgen voor twee soorten ontogenetische asymmetrie. De predatorpopulatie wordt ofwel gereguleerd door maturatie, met een lage juveniele groeisnelheid en hoge juveniele mortaliteit, ofwel gereguleerd door reproductie, met een lage reproductiesnelheid en hoge adulte mortaliteit. Ontogenetische symmetrie begrenst deze twee manieren van populatieregulatie, waarbij de predatorpopulatie noch door reproductie, noch door maturatie wordt gereguleerd.

In hoofdstuk 4 wordt beschreven dat kannibalisme nadelig is voor het voortbestaan van de predator, omdat het zorgt voor een transitie van reproductie- naar maturatieregulatie. In het geval van maturatieregulatie is de competitie tussen juveniele predatoren en prooien te sterk om het voortbestaan van de populatie veilig te stellen. Kannibalisme leidt dus tot het plaatselijk uitsterven van de predator door een verandering in het type ontogenetische asymmetrie.

In hoofdstuk 5 wordt de evolutie van ontogenetische asymmetrie bij de (omnivore) predator bestudeerd, afhankelijk van het niveau van kannibalisme. In hoofdstuk 5 wordt aangenomen dat evolutie, ofwel de concurrentiekracht van juveniele predatoren verhoogt (dit verlaagt de maturatieregulatie), ofwel de predatiedruk van adulte predatoren verhoogt (dit verlaagt de reproductieregulatie). Een trade-off tussen de verschillende levensfasen verhindert echter dat beide processen gelijktijdig toenemen. Wanneer er geen sprake is van kannibalisme, zal selectie op deze ontogenetische trade-off zorgen voor de specialisatie van een enkel levensstadium (ofwel juvenielen ofwel adulten specialiseren zich op hun voedselbron). Dit gaat ten koste van de mate van specialisatie binnen het andere levensstadium (respectievelijk het adulte of juveniele stadium). Uiteindelijk leidt dit tot een verandering in het ecologische evenwicht en tot het uitsterven van de predator. Selectie op de ontogenetische trade-off zorgt dus voor evolutionaire suïcide van de predator. Kannibalisme kan dit echter voorkomen door de selectie op de ontogenetische trade-off te stabiliseren.

In de complexere ecologische setting van leeftijdsafhankelijke omnivorie wordt de ontogenetische asymmetrie bepaald door de dichtheid van prooien en voedselbron. Selectie op ontogenetische asymmetrie zorgt via een ecologisch terugkoppelingsmechanisme voor veranderingen in de dichtheid aan prooien en voedselbron. De ecologische terugkoppeling werkt echter in tegengestelde richting ten opzichte van de selectiedruk. Hierdoor kan selectie die erop gericht is om de ontogenetische asymmetrie te verminderen, via de ecologische terugkoppeling leiden tot een toename van ontogenetische asymmetrie. Daarnaast kan kannibalisme leiden tot selectie voor ontogenetische asymmetrie, omdat de fitnessopbrengsten van kannibalisme groter zijn in een maturatie-gereguleerde populatie. Dit komt doordat in dit geval de juveniele dichtheid hoog is.

Samengevat, in systemen met leeftijdsafhankelijke omnivorie is het ecologische voortbestaan van predatoren afhankelijk van het type ontogenetische asymmetrie (hoofdstuk 4). Verder leidt selectie op ontogenetische asymmetrie tot onverwachte effecten (evolutionaire suïcide; hoofdstuk 5). Een toename van ecologische complexiteit, door de aanwezigheid van kannibalisme, stabiliseert de evolutionaire dynamiek en leidt tot ontogenetische asymmetrie (hoofdstuk 5). Indien men deze resultaten vergelijkt met de resultaten van hoofdstuk 2 en 3, dan lijkt een bepaalde mate van ecologische complexiteit (d.w.z. het aantal ecologische terugkoppelingen) een voorwaarde voor de evolutie van ontogenetische asymmetrie.

De evolutie van kannibalisme kan leiden tot een nieuwe ecologische interactie, en op deze manier bijdragen aan een toename van complexiteit in simpele ecologische gemeenschappen. Kannibalisme verhindert het voortbestaan van omnivoren op ecologische tijdschaal (hoofdstuk 5), maar stabiliseert ook de evolutionaire dynamiek en het voorkomt evolutionaire suïcide (hoofdstuk 5). Daarom is het belangrijk om te begrijpen welke omstandigheden de evolutie van kannibalisme remmen of juist bevorderen. Hoofdstuk 6 bestudeert dit onderwerp in de toegepaste context van visserij-geïnduceerde evolutie. Een model voor de populatiedynamiek van kannibalistische trekzalm (*Salvelinus alpinus*) laat zien dat visserij-geïnduceerde mortaliteit de evolutie van kannibalisme bevordert. Bij een lage mortaliteit wordt de evolutie van kannibalisme gestabiliseerd door de negatieve gevolgen van kannibalisme. Echter, bij een verhoging van de visserijdruk verandert deze stabiliserende selectie naar directionele selectie voor toenemende kannibalistische predatiedruk. Dit zorgt voor een tweeledig effect van mortaliteit. De visserij-geïnduceerde mortaliteit verlaagt direct de populatiedichtheid, maar selecteert tevens voor hogere predatiedruk door kannibalisme, wat zorgt voor een verdere afname van de populatiedichtheid.

In dit proefschrift wordt de bestudering van complexe ecologische interacties gecombineerd met de bestudering van evolutionaire processen die de levensontwikkeling van soorten bepalen. Deze benadering wordt nog niet veel gebruikt, maar levert mogelijk belangrijke inzichten op over hoe complexe levensvormen en ecosystemen zijn geëvolueerd en hoe deze blijven voortbestaan.

Author Contributions

2 **Evolution of Size-Dependent Intraspecific Competition Yields Paradoxical Predictions on the Scaling of Metabolism with Body Size**
Vincent Hin and André M. de Roos
VH and AMdR designed the research. VH analyzed the model and wrote first version of manuscript. VH and AMdR contributed to later versions of manuscript.

3 **Evolution of Metabolic Scaling**
Vincent Hin and André M. de Roos
VH and AMdR designed the research. VH analyzed the model and wrote first version of manuscript. VH and AMdR contributed to later versions of manuscript.

4 **Cannibalism and Intraguild Predation Community Dynamics: Coexistence, Competitive Exclusion and the Loss of Alternative Stable States.**
Benjamin J. Toscano, Vincent Hin and Volker H. W. Rudolf
BJT and VHWR designed the research. VH and BJT analyzed the model. BJT wrote first version of manuscript. BJT, VH and VHWR contributed to later versions of manuscript

5 **Cannibalism Prevents Evolutionary Suicide of Ontogenetic Omnivores in a Life History Intraguild Predation System**
Vincent Hin and André M. de Roos
VH designed the research, analyzed the model and wrote first version of manuscript. VH and AMdR contributed to later versions of manuscript.

6 **Fisheries-Induced Evolution in Cannibalism Promotes Collapses of Fish Populations**
Vincent Hin, André M. de Roos and Ulf Dieckmann
VH and UD designed the research. VH analyzed the model and wrote first version of manuscript. VH and AMdR contributed to later versions of manuscript.

Author Affiliations

Vincent Hin is at the:
Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam,
P.O. Box 94248, 1090 GE Amsterdam, The Netherlands

André M. de Roos is at the:
Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam,
P.O. Box 94248, 1090 GE Amsterdam, The Netherlands

Benjamin J. Toscano is at:
BioSciences, Rice University, Houston, Texas 77005, USA

Volker H. W. Rudolf is at:
BioSciences, Rice University, Houston, Texas 77005, USA

Ulf Dieckmann is at the:
Evolution and Ecology Program, International Institute for Applied Systems Analysis,
A-2361 Laxenburg, Austria