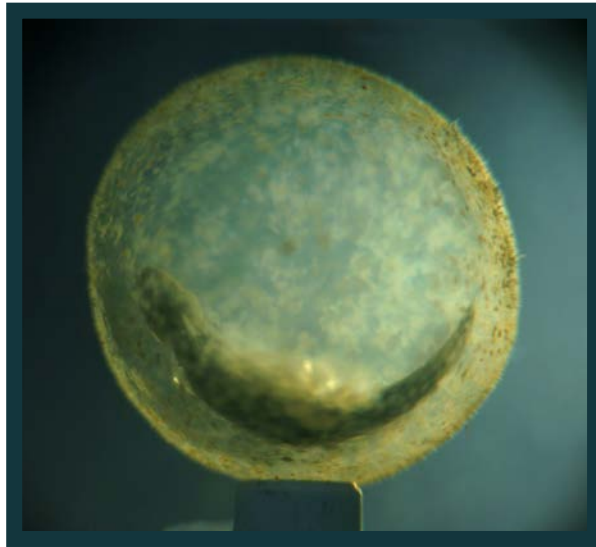


**DEVELOPMENTAL ENERGETICS
AND GAS EXCHANGE
IN AMPHIBIANS AND LUNGFISH**



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Ecology and Evolutionary Biology

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THE UNIVERSITY
of ADELAIDE

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Cover image: Australian lungfish (*Neoceratodus forsteri*) egg near hatching. The embryo lies quiescent at the bottom of the perivitelline fluid surrounded by membrane remnants. The surface of the egg is covered in debris and microscopic organisms.

LIST OF PUBLICATIONS:

Chapter 1. Effects of environmental oxygen on development and respiration of Australian lungfish (*Neoceratodus forsteri*) embryos

Chapter 1 is a co-authored paper published in *Journal of Comparative Physiology B*, and as such is written in plural thought. It is included with kind permission of Springer Science and Business Media under a license agreement with Casey A. Mueller (2673031019562). The paper can be cited as:

Mueller CA, Joss JMP, Seymour RS (2011) Effects of environmental oxygen on development and respiration of Australian lungfish (*Neoceratodus forsteri*) embryos. *Journal of Comparative Physiology B* **181**, 941-952. (DOI 10.1007/s00360-011-0573-3)

In this paper Jean Joss contributed to the initial concept of the study, permitted egg collection from the Macquarie Lungfish Laboratory and commented on a manuscript draft. Roger Seymour contributed to the initial concept and the development of ideas, helped with the experimental set up and commented on manuscript drafts. I collected the eggs, set up and ran the experiments, analysed the data and wrote the paper.

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Chapter 2. The energy cost of embryonic development in fishes and amphibians, with emphasis on new data from the Australian lungfish, *Neoceratodus forsteri*

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Chapter 4. The Regulation Index: a new method for assessing the relationship between oxygen consumption and environmental oxygen

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Chapter 5. The importance of perivitelline fluid convection to oxygen uptake of *Pseudophryne bibronii* eggs

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MANUSCRIPT IN PREPARATION:

Chapter 3. The trade-off between maturation and growth during accelerated development in frogs

Chapter 3 is a co-authored manuscript in preparation for journal submission and as such is written in plural thought.

In this chapter I collected the eggs, ran the experiments, analysed the empirical data and wrote the manuscript. Starrlight Augustine ran the DEB parameter estimation, wrote the appendix and provided comments on DEB theory, model results and the manuscript. Bas Kooijman also ran DEB parameter estimations and provided comments on DEB theory, the parameter results and the manuscript. Michael Kearney provided an introduction to DEB theory and commented on parameter estimation and the manuscript. Roger Seymour contributed to the initial concept of the study, helped with the experimental set up and commented on manuscript drafts.

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ABSTRACT

The development of amphibians and fishes is a complex process influenced by intrinsic and extrinsic factors. In this study I examine how energy use and gas exchange contribute to the success and rate of development in two Myobatrachid frogs, *Pseudophryne bibronii* and *Crinia georgiana* and the Australian lungfish, *Neoceratodus forsteri*.

1. Embryonic development of *N. forsteri* is affected by both temperature and oxygen level. Development time and the cost of development both decreased from 15 to 25 °C. At 20 °C survival and development rate were highest at oxygen partial pressures (PO₂) of 15 and 20.9 kPa. Hypoxia induced an early hatching age and stage and a decrease in hatchling mass. Breakdown of the vitelline membrane, which is stage-specific and unresponsive to PO₂ or temperature, allowed capsule conductance (GO₂) to increase, promoting oxygen uptake. The inherently low metabolic demand of *N. forsteri* results in an unusually low cost of development compared to other amphibians and fishes.
2. The partitioning and use of energy throughout development differs between *P. bibronii* and *C. georgiana* as modelled using dynamic energy budget theory. The aquatic *C. georgiana* reaches metamorphosis 1.7 times faster. The species switches energy partitioning at hatching to favour maturation over growth, producing less mass during development than *P. bibronii*. This appears to be a strategy for fast development, ensuring escape from the ephemeral pools in which *C. georgiana* develops. Along with faster development, *C. georgiana* demonstrates greater hypoxia tolerance, as measured by the regulation index. The regulation index, a new method developed to describe hypoxia response, is compared with previous methods, such as the environmental critical PO₂ (P_C) and shown to have advantages in describing the relationship between oxygen consumption and environmental PO₂.

3. The development of the perivitelline fluid in amphibians, which occurs as water is absorbed into the egg, can create a significant resistance to gas exchange. In the absence of convection created by cutaneous cilia, oxygen consumption of stage 17 – 19 *P. bibronii* dropped by 24%. At stage 27 the decline was only 14% due to muscular movements and a greater skin surface area in contact with the egg capsule.

4. Beyond the egg structures, oxygen transfer is strongly influenced by developmental gas exchange organs such as the skin and internal gills. Despite only taking 27 days to reach stage 27, compared to 39 days in *P. bibronii*, *C. georgiana* shows no significant adaptations in cardio-respiratory morphology that promote faster development. The species are similar in overall body volume and surface area and the skin is the major site for diffusive gas exchange, with the internal gills supplementing oxygen transfer, in both species. *P. bibronii* has a larger heart and greater internal gill tissue, but the volume of internal gill capillaries is the same. Rather than having a current function for gas exchange, the larger heart may function to promote the development of capillaries in the internal gills to match the greater larval growth of *P. bibronii* from stage 27.