

**Molecular phylogenetics and the evolutionary history of reproductive
strategies in benthic shallow-water octopuses
(Cephalopoda: Octopodinae)**

Thesis submitted by

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in February 2004

**for the degree of Doctor of Philosophy
in Zoology and Tropical Ecology
within the School of Tropical Biology
James Cook University**

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ABSTRACT

The adaptive nature of egg size and juvenile types is of fundamental interest to the life history theory of benthic marine invertebrates. One tenet of life history theory for these organisms predicts that the evolution and maintenance of dichotomous reproductive strategies is a fecundity-survival trade-off and environmental factors strongly influence the evolutionary history of these strategies. In this thesis I aimed to examine the evolutionary relationships among the benthic shallow-water octopuses (subfamily Octopodinae) using a molecular phylogenetic approach. The best phylogenetic hypothesis was then used in a comparative phylogenetic analysis to examine the evolutionary history of reproductive strategies. I was interested in examining whether evolutionary transitions in egg size have been influenced by macro-environmental variation during their evolutionary history.

A molecular phylogenetic analysis was used to reconstruct a broad-scale phylogeny of the benthic shallow-water octopuses from the amino acid sequences of two mitochondrial DNA genes: Cytochrome oxidase subunit III and Cytochrome *b* apoenzyme and, the nuclear DNA gene, Elongation Factor-1 α . Maximum Likelihood and Bayesian approaches were implemented to estimate the phylogeny and non-parametric bootstrap was used to verify confidence intervals for Bayesian topologies. Overall the genes used in this study were better suited to the examination of recent phylogenetic relationships, which has helped to resolve the relationships among closely related taxa, rather than deeper divergences among genera and species groups. The phylogenies revealed strong evidence that the genus *Octopus* is not a monophyletic group. Interestingly, a number of monophyletic sub-groups comprising closely related terminal taxa exist within the genus. Based on these findings it is clear that the systematics of the subfamily Octopodinae requires major revision. Deep relationships within this group remain only partially resolved and to improve resolution among distantly related species sequence data from conserved genes should be examined.

The dichotomous reproductive strategies that exist among species of the benthic shallow-water octopuses are an exceptional life history feature as they are only one of two groups within the Cephalopoda that maintain such a dichotomy. The reconstructed pattern of evolution in inferred juvenile types showed that the planktonic juvenile type

was ancestral among 22 species and three independent evolutionary transitions to the benthic juvenile type were observed with no subsequent reversals among taxa. The comparative phylogenetic analysis revealed that egg size covaries with variation in latitudinal gradient and more weakly with body size. These findings suggest that, evolutionarily, egg size is an adaptive trait that responds to a number of selection pressures including those associated with macro-environmental variation. Based on these results it is suggested that the dichotomy in egg sizes may be maintained by a fecundity-survival trade-off that responds to natural selection associated with the environmental conditions that a species inhabits.

Under the assumption that egg size and juvenile type are tightly correlated traits I propose a number of hypotheses regarding the evolution of reproductive strategies in octopuses. Small eggs and planktonic juvenile types are likely to be the ancestral states for shallow-water octopuses in general. Based on the covariation of egg size with latitudinal variation, inter-specific evolution in both egg size and juvenile type is likely to reflect adaptations to natural selection resulting from large-scale ecological factors; a finding that is consistent with benthic marine invertebrate life history theory. Large eggs and benthic juveniles may be an adaptation to high-risk conditions such as deep-sea and/or cold environments as supported by the tendency for transitions in reproductive strategy to occur most frequently in the direction of small egg size - planktonic juvenile type to large egg - benthic juvenile type. Evidence that egg sizes are constrained by phylogeny was observed, which may also indicate a constraint on reproductive strategies such that transitions in strategy are rare.

The dichotomous reproductive strategies that exist among species of the benthic shallow-water octopuses are an exceptional life history feature that is only observed in one other cephalopod family, the *Idiosepiidae*. Many other benthic marine invertebrates also maintain dual reproductive strategies between species and a large body of theory exists regarding how these traits have evolved and been maintained throughout evolutionary history. Using a comparative phylogenetic approach it was possible to investigate hypotheses generated by optimality models and experimental observations in an historical context and to examine the patterns of evolution in traits.

ACKNOWLEDGMENTS

I wish to thank my supervisors Professor Ross Crozier and Dr Mark Norman for their generous support and assistance throughout this thesis. Thanks to Ross for providing me with resources and an incredible working environment throughout my candidature. Thanks to Mark for the octopus samples that were used in this study as well as his unfaltering enthusiasm for all things cephalopodan. His assistance helped me to understand the biological context of an incredible group of animals even when they were often just tubes of DNA to me. I am extremely appreciative of the wealth of knowledge and constant encouragement that Ross and Mark have offered me during my candidature.

Special thanks to Ching Crozier for technical guidance in the lab. Her knowledge of molecular biology has been invaluable to my research capabilities. Thanks also to Wayne Mallet and Dominique Morrell from the High Performance Computing Facility at JCU for their technical assistance with the Unix system.

Thanks to all members of the Crozier lab over the years, particularly Mike and Janet Goodisman, Lynn Atkinson, Mike Henshaw, Rebecca Johnson, Cathy Oke, Ange Corrie, Angie Shuetrim, Line Bay, Rodrigo Esparza-Salas, Rika Raffiudin, Maria Chitotis and Melissa Carew. Also, thanks to Faye Christidis, and Heather and Simon Robson. All of these amazing people have offered me scientific guidance, assistance in assimilating to Townsville life, fun and much laughter during my candidature. Special thanks also to Simon Cook for his friendship and indisputable coffee breaks. These kept me level headed and somewhat sane when I was “so stressed out”. Thanks!

Thanks to Steve Delean for discussions of fundamental statistics and for reading through manuscripts of this thesis. You have inspired me to strive for excellence. Your constant support, friendship and love are beyond words. Thank you for everything.

Thank you to my wonderful family, Anna, John and Nicolle Guzik. Your unconditional love and words of encouragement have helped me throughout my candidature and my life. I have appreciated it.

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**STATEMENT ON SOURCES
DECLARATION**

I declare that this thesis is my own work and has not been submitted in any form for another degree or diploma at any university or other institution of tertiary education. Information derived from the published or unpublished work of others has been acknowledged in the text and a list of references is given.
