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

Thesis submitted by

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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-1α. 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.

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DECLARATION

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