AN EVALUATION OF GEOGRAPHIC VARIATION IN THE LIFE HISTORY AND BEHAVIOUR OF ANEMONEFISHES: A COMMON-GARDEN APPROACH

PhD thesis submitted by

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STATEMENT OF CONTRIBUTION OF OTHERS

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Abstract

The parameters of a species life history and performance do not vary independently. Co-varying traits provide the basis for hypotheses as to how individuals allocate energy, as populations genetically adapt to or phenotypically adjust to different environments. In coral reef fishes, the extent and underlying causes of such patterns across large geographic scales are poorly understood. Intraspecific phenotypic variation may be evident on a broad geographic scale, for example when comparing populations that are geographically isolated or those along a latitudinal cline. Such variation may be the consequence of local genetic variation due to natural selection, and/or it may reflect phenotypic and behavioural plasticity that is largely environmentally determined. Discriminating between these potential causes of local population differentiation is an important goal of evolutionary ecology. This study provides a comprehensive description of geographic life history variation (reproduction, growth, mortality) and performance (swimming ability) in a long-lived group of coral reef fishes (subfamily Amphiprioninae). It presents a unique evaluation of the degree to which life history and performance traits may be coupled, and determines whether these traits are environmentally induced *vs*. genetically determined by employing an integrated set of common-garden experiments.

Chapter two of this thesis describes a comparative field study that examined latitudinal differences in the life history characteristics of three species of anemonefishes (*Amphiprion melanopus*, *A. akindynos* and *Premnas biaculeatus*) among three locations, including Kimbe Bay in West New Britain, Papua New Guinea (5º30’S/150º05’E), and Lizard Island (14º40’S/145º28’E) and One Tree Island (23º30’S/152º05’E) on the Great Barrier Reef, encompassing 18^{o} of latitude. Life

history theory predicts that populations from higher latitudes should exhibit larger adult body sizes, but smaller size at age (i.e. slower growth). Concomitant with slow growth, a delay in sexual maturation is expected, which should be compensated through the fecundity advantage of a larger size and longer lifespan. As predicted, maximum age increased with increasing latitude in all three species. *A. melanopus* always had a higher maximum age than either *A. akindynos* or *P. biaculeatus* at each location, reaching 38 years at the highest latitude location. At this location, *A. melanopus* also had a larger adult body size, slower growth, lower mortality, greater proportional age and size at maturity and sex change, larger egg size and higher batch fecundity than at either of the lower latitude locations, and thus conformed well to life history theory. For the other two species, maximum body size was smaller at the higher latitude location, there were no differences among locations in growth and mortality rates, and no consistent trends in the timing of maturation or sex change. Thus, while longevity varied with latitude as expected in all three species, some of the other life history traits examined did not. The divergence in magnitude and direction of life history patterns among these species suggests that there are processes beyond simple trade-offs that determine life history strategies. I discuss the hypothesis that in anemonefishes, selection for flexibility in life histories imposed by a highly specialised habitat and rigid social structure may oppose selection over latitudinal environmental gradients.

Geographic variation in life history phenotypes between populations of a species is often assumed to reflect genetic divergence caused by natural selection. The relative contribution of genetic and environmental sources of phenotypic variation has never been determined in coral reef fishes. Yet, distinguishing between these sources of variation is fundamental to understanding the ecological and evolutionary significance of geographic life history variation. A conventional way of demonstrating the genetic basis of adaptive variation in the wild is to perform a common-garden experiment, in which individuals from different local populations are compared under identical environmental conditions established in a laboratory. This approach formed the basis of the following three chapters.

In *chapter three* I determined whether the latitudinal variation in maternal reproductive traits observed in the wild has a genetic basis or whether it represents a phenotypic response to the environment. Adult fishes of the three species were collected from three latitudes along the Great Barrier Reef (Lizard Island, Britomart Reef at 18º23'S/146º63'E and One Tree Island) and their reproductive performance was monitored in a common-environment for up to 3 years. Based on life history theory and previous field observations I predicted larger egg sizes, but lower egg numbers in populations from higher latitudes. However, size-specific egg size, fecundity and reproductive output did not differ among populations in any of the three species held under identical environmental conditions. Thus, any divergence in these traits observed among natural populations most likely results from environmentally induced plasticity, rather than genetic divergence.

The next chapter describes another common-garden experiment with a full-sib design to examine differences in early growth rates and growth plasticity and among the latitudinal populations described above. Temperature and food availability were manipulated under controlled laboratory conditions to determine whether there is intraspecific variation in growth plasticity in response to these two environmental factors. Given that environmental variability generally increases with latitude I expected that offspring from high-latitude populations should display greater levels of plasticity compared to their low-latitude counterparts. In all three species, mean growth rates differed significantly among populations and were consistent with the co-gradient variation hypothesis (i.e. offspring from low latitudes grew faster than offspring from high latitudes). Demonstrated under common-garden conditions, this implies that population-level variation in the growth capacity of juvenile anemonefishes has a genetic basis and should therefore respond to natural selection. Furthermore, significant genotype x environment interactions suggest the evolution of different growth reaction norms in response to temperature and food availability at different latitudes, although the variation did not always follow the predicted pattern. Overall, these results provide evidence for adaptive genetic differentiation for growth rate and growth plasticity in the early juvenile stages of these latitudinal populations.

Swimming abilities of larval fishes are important to their survival, potentially affecting their ability to avoid predators, obtain food and control dispersal and recruitment patterns. To date, no attempt has been made to quantify geographic and population-level differences in swimming performance of coral reef fishes. The aim of *chapter five* was to determine if, and to what extent, there is heritable variation for swimming performance among populations of the three anemonefish species across a latitudinal gradient. Flume-based trials were conducted to measure maximum sustainable swimming speeds (or U-crit) as an estimate of aerobic capacity of laboratory-reared pre-settlement larvae. My results confirmed that these fishes have different intrinsic swimming capabilities, such that offspring from high-latitude populations out-performed those from lower latitudes in all three species. These consistent behavioural differences between populations in the laboratory may reflect adaptive specialisation in response to latitudinal changes in coral reef environments. Mean swimming speeds were inversely related to mean body sizes among populations, suggesting that observed patterns may arise from a trade-off with growth rate. This demonstrates that developmental attributes and performance are interrelated in a complex fashion, with multiple selection pressures acting on multiple aspects of the phenotype, and that adaptation involves trade-offs among competing functions.

This study has shown that both phenotypic plasticity and genetic differentiation across environmental gradients may exist for important fitness-related traits in coral reef fishes. The high potential for gene flow and lack of obvious barriers to dispersal in these species does not appear to preclude local adaptation in life history and larval swimming capacity along a latitudinal gradient. These results are significant steps forward in resolving the evolutionary and ecological processes that explain the substantial variation in the life histories and behavioural abilities of coral reef fishes.

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