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The Importance of Fine-Scale Environmental Heterogeneity in Determining Levels of Genotypic Diversity and Local Adaptation

A thesis submitted in fulfilment of the requirements for the award of the degree

DOCTOR OF PHILOSOPHY

from the

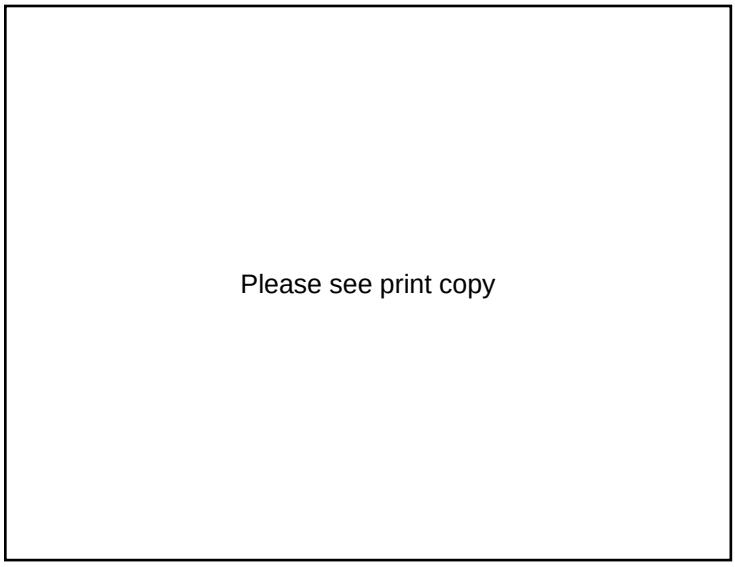
UNIVERSITY OF WOLLONGONG

by

Craig D. H. Sherman B. Sc. (Hons)

SCHOOL OF BIOLOGICAL SCIENCES

2006



The intertidal sea anemone *Actinia tenebrosa*. Photograph by A.M Martin

Certification

I, Craig D. H. Sherman, declare that this thesis, submitted in fulfilment of the requirements for the award of Doctor of Philosophy, in the School of Biological Sciences, University of Wollongong, is wholly my own work unless otherwise referenced or acknowledged. The document has not been submitted for qualifications at any other academic institution.

Craig Sherman
13 January 2005

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Abstract

Fine-scale environmental heterogeneity is predicted to be important in determining variation in genotypic diversity and in selection for important life history traits in natural populations. For example, theory suggests that organisms with complex life histories that involve both sexual and asexual modes of reproduction use sex to produce genotypically diverse and widely dispersed propagules for the colonisation of distant or unstable habitats, but rely on asexual reproduction to restock or maintain populations within their parental habitat. Such organisms should also have great potential for site-specific adaptation as multiple generations may compete within relatively static conditions. Surprisingly, little is still known about the importance of fine-scale genotypic variation and the degree of local adaptation within populations of clonal marine organisms.

In this study, I used two brooding corals (*Pocillopora damicornis* and *Seriatopora hystrix*) and one brooding sea anemone (*Actinia tenebrosa*), to test for evidence of fine-scale adaptation and the effects of environmental heterogeneity on variation in genotypic diversity. Using a combination of genetic and experimental techniques I assessed: i) if reproductive mode varies with environmental heterogeneity across habitats, ii) how genotypic diversity varies over fine spatial scales (centimetres and meters), and iii) if different clonal genotypes show evidence of fine-scale adaptation to specific habitats.

My data on the population genetics and mode of reproduction for the corals *P. damicornis* and *S. hystrix* did not support theoretical predictions. Brooded larvae from *P. damicornis* colonies collected in five reef habitats were all produced asexually. In contrast, brooded larvae of *Seriatopora hystrix* were sexually produced, with up to three sires contributing to some broods (r_p (±SE) = 0.32 ± 0.43), and almost half (46%) of the larvae resulting from self-fertilisation (mean outcrossing rates were t_m (±SE) = 0.54 ± 0.22). The population genetic structure of *S. hystrix* from One Tree Island matched that expected from the mating system; i.e. a high level of genetic subdivision due to restricted dispersal of gametes, and consistent heterozygote deficits within populations associated with inbreeding. However, populations of *P. damicornis* showed unexpectedly high levels of genotypic diversity and appear to be maintained by sexual reproduction; G_o/G_e ranged from 69 to 100% of that

expected for random mating within 14 sites across six habitats. Interestingly, at three sites in two habitats G_o/G_e ranged from 35 to 53%. Two of these sites were recently bleached, suggesting that asexual recruitment may be favoured after disturbance, although disturbance alone is probably insufficient to explain this species' continued investment in clonal reproduction.

Using a combination of variable microsatellite and allozyme markers, I assessed the genetic origin of brooded juveniles from adult *Actinia tenebrosa* collected from boulder and rock pool habitats to determine if the mode of reproduction varied with environment. Brooded juveniles displayed identical multi-locus genotypes to that of the brood parent, irrespective of habitat type or location. However, I found that the level of genotypic diversity varied widely among 19 *A. tenebrosa* populations across 2500km of its geographic range along the east coast of Australia. Some populations showing high levels of clonality while others displayed the level of genotypic diversity expected for sexual reproduction.

For *A. tenebrosa*, my results indicate that the importance of sexual and asexual reproduction may indeed vary among habitats with different levels of heterogeneity confirming predictions from evolutionary theory. Fine-scale genetic surveys ($<1m^2$) on the distribution of clones of *A. tenebrosa* revealed that clonal diversity was greater on individual boulders (71%) compared to rock pools (23%). However, samples collected over larger spatial scales ($25m^2$) revealed little difference in genotypic diversity between boulder (80%) and rock pool habitats (70%). Clones had limited distributions, although some could be spread throughout an entire habitat. With the exception of a single clone, I found no overlap of genotypes between boulder and rock pool habitats on the same rocky shore. This distinct segregation of genotypes to habitats within the same rocky shore may result either from highly limited dispersal of asexual propagules and/or fine-scale selection for certain genotypes in particular habitats.

To test for evidence of local adaptation to fine-scale environmental variation in different habitats, I reciprocally transplanted *A. tenebrosa* both within and between habitats. I found no evidence of adaptation of clones within habitats, with transplanted anemones performing

equally well to native anemones in terms of survivorship ($F_{1, 0.01} = 11.79$, $P = 0.075$), proportion of adults brooding juveniles ($F_{1, 0.01} = 0.40$, $P = 0.592$), mean number of juveniles/site ($F_{1, 2281} = 0.801$, $P = 0.068$), mean number of juveniles/brood ($F_{1, 12.2} = 1.238$, $P = 0.382$), and growth ($F_{1, 0.03} = 0.007$, $P = 0.942$). However, between-habitat transplants provided evidence that clones of *A. tenebrosa* are locally adapted at the habitat scale. Native anemones consistently out-performed foreign anemones transplanted from the adjacent habitat (survivorship $F_{2, 0.298} = 9.58$, $P < 0.001$; proportion adults brooding $F_{2, 0.139} = 3.12$, $P = 0.05$; mean number of juveniles/site $F_{2, 14039} = 3.90$, $P = 0.028$; growth $F_{2,} = 4.77$, $P = 0.014$).

In summary, the results from this study show little evidence that reproductive mode varies predictably among habitats for any of the three species tested. Furthermore, there appears to be a mismatch between the population genetic structure and the reproductive output for two of the three species. Level of genotypic diversity was shown to vary over different spatial scales, and with habitat to some degree, both in *P. damicornis* and *A. tenebrosa*, and transplant experiments provide evidence of fine-scale adaptation to specific habitats for *A. tenebrosa*. These results suggest that for some species, such as the brooding sea anemone *Actinia tenebrosa*, the importance of sexual and asexual reproduction may indeed vary among habitats with different environmental heterogeneity in the manner predicted by evolutionary theory.

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