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Willis, Bette Lynn (1987) *Morphological variation in the reef corals *Turbinaria esenterina* and *Pavona cactus*: synthesis of transplant, histocompatibility, electrophoresis, growth, and reproduction studies*. PhD thesis, James Cook University.

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CHAPTER 1. GENERAL INTRODUCTION

Observations of morphological variation in natural populations have inspired many of the classic studies which have led to our present understanding of evolutionary ecology. However, our present understanding of morphological variation in corals extends only as far as recognizing that it exists in many scleractinian species, and often at very high levels (variation in Eastern Australian corals recently described in Veron and Pichon, 1976, 1980, 1982; Veron *et al.*, 1977; Veron and Wallace, 1984). There has been recent speculation on the selective pressures which have produced this variation (Potts, 1983, 1984b, 1985), but the development of such theories is hampered by a lack of knowledge concerning the source of this variation (environmental versus genetic) and the genotypic structure of coral populations. Before questions regarding the significance of morphological variation in corals can be addressed, it is first necessary to determine whether the observed variation is genetic in origin or whether it reflects phenotypic plasticity.

Variation which is genetic in origin provides the prerequisite substrate for processes of natural selection, and hence for the evolution of species. Not only does genetic variation provide the flexibility for species to change through time, as formalized by Darwin, it also allows genetic differentiation to occur within populations at any given point in time (Antonovics *et al.*, 1971; Antonovics, 1971). Therefore the importance of genetic variability is not simply in its future potential for adaptation to changed environments. It may also be of immediate adaptive value to a species by facilitating the exploitation of a range of habitats. This may be especially important for sessile organisms living in spatially heterogeneous environments such as coral reefs (eg. Potts, 1984a).

In contrast, variability derived from phenotypic plasticity is not directly heritable (Grant, 1963). Therefore this source of variability is hidden from directional selection and the refining process of evolution. This suggests that rates of evolutionary

change will be retarded in traits where variation is due to phenotypic plasticity. However, phenotypic plasticity represents an immediate, non-genetic avenue of adaptation if the resulting variability increases fitness (Bradshaw, 1965). Hence this strategy may also be advantageous for sessile organisms, especially those, such as corals, with dispersive reproductive propagules likely to encounter a range of biotopes during settlement. Furthermore it provides a mechanism for change in unstable environments. The degree of phenotypic plasticity exhibited by a species is itself genetically determined (Jain, 1978). Thus, a complex suite of controls may underlie the expression of variation in natural populations.

In corals, the question of whether growth form variability is genetically determined or environmentally induced has remained largely unanswered, although opinions have oscillated from one extreme to the other over the years. Historically, systematists have used skeletal features of the calice and corallum to define species, and have tended to identify each morphological variant as a separate species¹. However, Wood Jones (1907) speculated that "though a definite inherent growth tendency is strongly implanted in the embryo, still the demands of the environment may call forth any type of vegetative growth." He radically suggested that "when the enormous variation in response to environment is recognised, the actual species are known to be but few". Stephenson and Stephenson (1933) refuted this reasoning stating, "The environment cannot call forth "any type of vegetative growth"; it can merely induce certain variations, within definite limits", and concluded that "species in the ordinarily accepted sense of the term do exist in many coral genera in considerable number". In reviewing the debate, Yonge (1968) stated, "a long controversy has ranged on the relative importance of growth forms as against species in these sedentary colonies which are so obviously subject to the major effects of wind, weather, exposure - and also depth", and arbitrated

¹Five previously defined species of *Turbinaria* (Bernard, 1896) have been synonymized into the presently defined species, *Turbinaria mesenterina* (Veron and Pichon, 1980). Three previously defined species of *Pavona* (Dana, 1846) have been synonymized into the presently defined species, *Pavona cactus* (Veron and Pichon, 1980).

that, "the final form of any coral is clearly the consequence both of genetic constitution and of environment", although no further evidence was presented.

When this project was initiated, clear demonstrations of either environmental or genetic control of growth form were lacking for corals. Several experimental studies involving transplantation of colonies to different depths and habitats had been performed (reviewed in Chapter 3, section 3.1), but results suggested that either these species were not phenotypically plastic, or, colonies were able to respond only marginally to the changed environment. As various aspects of the biology of corals have become known, an increasing number of parallels in demographic attributes affecting growth form have been drawn between corals and plants (eg. the sessile, modular nature of colonies and iterative process of growth (Harper and Bell, 1979), and mixed strategies of sexual and asexual reproduction (Williams, 1975)). In light of the abundant evidence of phenotypic plasticity in plants (Bradshaw, 1965), the apparent lack of phenotypic plasticity in the growth forms of corals merited further study.

A major objective of this study was to determine the extent to which phenotypic plasticity contributed to the morphological variation of the scleractinian corals, *Turbinaria mesenterina* and *Pavona cactus*. Morphological variation in corals may occur either at the level of individual corallites or at the level of the colony. This study is primarily concerned with variation at the colony level, and unless stated otherwise, phrases such as 'morphological variation' and 'growth form variation' will refer to the shape of colonies. Chapter 2 describes the range of morphological variation in these two species, and also the distribution of naturally occurring morphs with respect to variation in the physical environment. Surveys of growth form distribution provided background information for determining the sites for reciprocal transplant studies. Patterns in the physical data provided the context for interpreting the role of environmental variation in inducing morphological variation.

Chapter 3 describes reciprocal transplant studies undertaken to test for phenotypic plasticity in these two species. A change in growth form following the transplantation of a colony to a different habitat provides unequivocal evidence of plasticity. Where plasticity was found, further morphometric analyses were designed to determine the component of colony growth primarily responsible for the morphological change. Where plasticity was not found, further studies were undertaken to determine whether a genetic basis for the morphological variation could be demonstrated.

The genotypic structures of coral populations were unknown until recently (Stoddart, 1984a, 1984b). Despite characterization of the genotypic structure of populations of the morphologically variable coral, *Pocillopora damicornis* (Stoddart, 1984a, 1984b), genetic variation has not been related to morphological variation in a scleractinian coral. Previously, knowledge of coral population genetics was limited to the assumption that coral populations contained both single and replicated genotypes, because of the ability of many species to reproduce asexually (Highsmith, 1982). Histocompatibility tests used as bioassays to detect clonal population structures supported these predictions (Jokiel *et al.*, 1983; Neigel and Avise, 1983). Chapter 4 describes electrophoretic surveys and histocompatibility tests undertaken to characterize the genotypic structure of populations of *Pavona cactus* and *Turbinaria mesenterina*, and to determine whether populations contained replicated genotypes. The population of *Pavona cactus* at Eclipse Island was found to have a clonal structure, so further analyses were initiated to test for the presence of genotype-growth form associations. It was predicted that if all replicated genotypes exhibited the same growth form, despite large distances between colonies of the same genotype, then growth forms were primarily genetically determined. The electrophoretic survey also provided an independent test of the precision of the self-recognition response (the basis for histocompatibility tests) in these two corals.

The final two chapters provide further support for conclusions of environmental versus genetic determination of growth form reached in Chapters 3 and 4. In Chapter 5, growth strategies are compared between morphs to elucidate the mechanisms through which

colony morphology is determined and modified. The growth strategy for each species is subdivided into measurable components, such as rate of linear extension, angle of corallite addition and septo-costal thickness. Analyses of differences between morphs in these parameters, implicated which aspects of the growth process controlled colony morphology. Studies of the mechanisms underlying growth form variation in *T. mesenterina* and *P. cactus* were also undertaken for the potential insights they could offer into factors affecting calcification in corals, and the relationship between individual polyp growth and colony growth.

Although the 'one morph=one species' systematics of early taxonomists can be largely ignored, because of their lack of field experience and inability to correlate growth forms and habitats, the question of whether morphs actually interbreed still remains. In Chapter 6, further evidence of the taxonomic status of the morphs of *Turbinaria mesenterina* is presented. Data on the timing of gametogenesis and the release of gametes are analysed for evidence of reproductive isolation between morphs. Age at first reproduction, sex ratio, and polyp fecundity were also studied to assess whether divergence in reproductive strategies had occurred. It is known that at least one-third of the coral species found on the Great Barrier Reef release their eggs and sperm during an annual mass spawning period in late spring (Harrison *et al.*, 1984; Willis *et al.*, 1985; Babcock *et al.*, 1986). An alternative reproductive strategy is documented for *T. mesenterina*, and its implications for the proximate and ultimate controls on reproduction in corals are discussed.

In summary, the major objective of this project was to determine whether growth form variation in *Turbinaria mesenterina* and *Pavona cactus* reflected phenotypic plasticity, or underlying genetic differences. In structure, this thesis documents differences in the physical environment associated with the distribution of morphs, and then compares the experimental evidence for phenotypic plasticity versus genetic determination of growth form for each species. The mechanisms involved in varying colony morphology through differing growth strategies are analysed, and evidence concerning the existence of reproductive isolating mechanisms between morphs is evaluated.