GENOTYPIC DIVERSITY AND POPULATION STRUCTURE OF THE HAWAIIAN REEF CORAL, *PORITES COMPRESSA*

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1929-1964

ABSTRACT

The assessment of clonal diversity in populations of the endemic Hawaiian coral Porites compressa was undertaken using four independent assays of genotypic identity: colony morphology, immunocompatibility testing by tissue grafting, electrophoresis of soluble proteins, and chromatography of ultra-violet absorbing compounds. All methods were corroborative, but electrophoresis of soluble proteins provided the single most efficacious assay of genotypic diversity, with a 7-locus (21 alleles) system which was estimated to sufficiently resolve approximately 95% of clonal samples.

Populations of Porites compressa were demonstrated to have derived substantial contributions from both sexual and asexual modes of reproduction. Sexual reproduction in P. compressa was similar in most life history parameters to other Porites species that broadcast spawn. Age at first reproduction was estimated to be between 1.8 and 2.5 years. Mean oocyte diameters were approximately 250 um at spawning, with 10-30 eggs per polyp. Spawning was synchronized with full moon during summer months, and some colonies spawned over more than one night and over subsequent months. Planulae were competent to metamorphose after three days, and sibling juveniles which settled gregariously were often observed to fuse, suggesting that there may be ontogenetic changes in self-recognition responses in this species.

Production of asexual propagules by fragmentation was calculated to be between 35 and 96 fragments/m^2/year for a patchreef population of Porites compressa in Kaneohe Bay, Oahu. Fragment production was continuous through the year, with a 5-10 fold increase in summer months

due perhaps to increased activity of turtles near sheltering areas on the reef. Asexual propagules were large (1.5-151 cm^2) and survived for many weeks or months before "recruiting" or being lost from the fragment pool.

Spatial and/or numeric abundance of dominant and rare clones of Porites compressa could be explained, in part, by differences in measurable fitness parameters of growth rate and competitive ability. No significant differences in the propensity of clones to produce fragments were detected. The relationship between clonal abundance and single fitness correlates, however, was not a simple one. Clonal fitness is the sum of many life history and ecological characteristics of a genotype. Clonal abundance and distribution may also be effected by non-selective random physical processes leading to asexual colony replication and recruitment.

Genotypic diversity in six populations of Porites compressa was directly related to habitat disturbance histories. Highest diversity was found in populations which had been intensely or recently disturbed. In these populations, space was not limited and mean colony size was small (<500 cm^2), suggesting an early stage in population recolonization. In a stable, undisturbed population, low genotypic diversity revealed the extent of clonal replication of established genotypes. Unoccupied substratum was rare in this habitat, and average colony size was larger (>2000 cm^2). Single clones were distributed over small or large areas (<1 to >16 m^2) or distances (<1 to >90 m), and were numerically (>13% of total number of colonies) or spatially (>15% of total colony area) dominant.

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CHAPTER 1

INTRODUCTION

The influences of competition and disturbance on species diversity in communities of sessile marine invertebrates have been the subject of numerous discussions (Dayton, 1971; Levin, 1976; Jackson, 1977; Connell, 1978, 1983; Buss and Jackson, 1979; Russ, 1982; Paine and Levin, 1983; Paine and Suchanek, 1983). Genotypic diversity within populations which reproduce both sexually and asexually may also be effected by similar forces (Williams, 1975; Sebens and Thorpe, 1985).

Williams (1975) predicted in his Strawberry-Coral Model that species which reproduce asexually will be characterized by populations with a dominance of highly locally adapted genotypes representing those individuals with the best competitive ability and highest fitness. Clonal dominance has been shown to lead to a decline in genotypic diversity in plant populations due to the gradual elimination of less-fit genotypes by those which are competitively superior (Kays and Harper, 1974; Barkham and Hance, 1982; Aarssen and Turkington, 1985a).

The long-term evolutionary implications of clonal replication in species which reproduce asexually are far reaching. While the total number of genets (unique, sexually-derived individuals) in a population will determine overall genetic variability, the abundance and distribution of ramets (genotypically identical clonal replicates) may both reflect and contribute to the relative fitness of individual genotypes. Although plant population biology abounds in studies of the relative fitness of individual genotypes (Jennings and Aquino, 1968;

Fehr, 1973; Kalifa and Qualset, 1974; Turkington and Harper, 1979; Burdon, 1980; Burdon and Harper, 1980; Lovett Doust, 1981; Bazzaz, et al., 1982; Heywood and Levin, 1984), published reports on the importance of individual fitness to clonal diversity within animal species are few (Hebert, 1974; Sebens, 1983; Hoffmann, 1986).

The effects of physical disturbance on genetic diversity in populations of clonal species has been modelled by Sebens and Thorpe (1985), who predicted that intermediate disturbance or non-equilibrium situations will promote the highest levels of clonal diversity. Ayre (1984) found that clonal diversity was lowest in populations of the anemone, Actinia tenebrosa in the most stable habitats. Diversity is highest in plant populations when the environment is temporally or spatially heterogeneous (Harberd, 1963; 1967; Oinonen, 1967; Harberd and Owen, 1969; Kemperman and Barnes, 1976; Silander, 1979; Soane and Watkinson, 1979; Vasek, 1980; Lovett Doust, 1981; Fowler et al., 1983; Jefferies and Gottlieb, 1983; Room, 1983; Heywood and Levin, 1984; Hartnett and Bazzaz, 1985; Schmid and Harper, 1985). Clonal diversity in populations over a range of disturbance intensities has not been determined for any species of clonal marine invertebrates.

Asexual reproduction by fragmentation has been proposed to be a potentially important factor in the structuring of scleractinian coral populations (Highsmith, 1982). Coral fragments can be generated by storms (Stoddart, 1963; Maragos, et al., 1973; Randall and Eldredge, 1977; Highsmith, et al., 1980; Dollar, 1982), bioerosion (Tunnicliffe, 1978; Highsmith, 1980, 1981), fish grazing (P. Glynn, pers. comm.), or human activities such as fishing (Chesher, 1985), anchor damage (Davis,

1977), or reef-walking (Heyward and Collins, 1985a). Establishment of clonal fragments as physiologically independent colonies may result in an individual genotype being replicated one or more times in a population.

Although estimates of fecundity, mortality, and evolutionary relationships rely on the precise identification of individual genotypes and their distributions in clonal populations, the extent of asexual reproduction and its effect on population structure and dynamics have not been determined for most coral species. Stoddart (1984a,b, 1985, 1988) found that populations of the scleractinian coral, Pocillopora damicornis, in Australia and Hawaii were dominated by a small number of genotypes which were replicated by asexual production of fragments. In this brooding species, planula larvae may also be produced asexually and therefore be genetically identical to parent colonies (Stoddart, 1983a). Populations of the coral, Pavona cactus, show variation in number and distribution of clones at different sites (Willis and Ayre, 1984).

This dissertation attempts to rigorously define levels of clonality in populations of the endemic Hawaiian coral, Porites compressa, and to examine the ecological processes leading to clonal population structure. In Chapter 2*, methodologies for the assessment of clonal diversity in this species are developed and compared, and the distributions of ramets from eight clones within a 20 m^2 section of reef are determined.

*Major portions of the work presented in Chapter 2 have been published in Hunter and Kehoe (1985) and Hunter (1985).

In Chapter 3, the importance of both sexual and asexual production of propagules are quantified, and the sexual reproductive biology of P. compressa is described for the first time.

Differences in clonal growth rates and competitive ability have been documented in anemone and coral populations (Francis, 1973; Potts, 1976; Bigger, 1980; Purcell and Kitting, 1982; Sebens, 1983; Ayre, 1983, 1984, 1985; Rinkovich and Loya, 1983; Hidaka and Yamazato, 1984; Willis and Ayre, 1985; Fujii, 1987), but no attempts have been made to correlate differential fitness of clones to their relative abundances in any species of colonial marine invertebrates. In Chapter 4, a null model, which holds that clonal abundance is the result of random physical processes, is tested against a deterministic model for clonal dominance being the result of fitness differences as measured by growth rate and competitive ability in Porites compressa.

A common problem in studies addressing genetic diversity in clonal species has been a limited or uncertain ability of assays to adequately distinguish genotypes. In addition, population sampling in most studies may not have been sufficient in both intensity and scale to allow detection of clonal distributions and overall genotypic diversity. Chapter 5 presents and effort to resolve these methodological difficulties by development of an analytical estimate of the resolution power of an electrophoretic assay system and utilization of a nested-quadrate sampling design. These methods were then used to assess levels of clonal diversity in six populations of P. compressa in habitats of different age and disturbance histories.

CHAPTER 2

METHODOLOGIES FOR THE ASSESSMENT OF CLONAL DIVERSITY AND POPULATION STRUCTURE OF *PORITES COMPRESSA* ON A PATCHREEF IN KANEOHE BAY

INTRODUCTION

Asexual reproduction leading to the clonal replication of genotypes is a common life history trait in many plant and animal species (Jackson, 1977, 1985; Harper, 1981; Cook, 1983). The ability to differentiate genetically identical ramets from individuals belonging to other genets is critical to studies of populations of clonal organisms. For most clonal species in which asexually produced clonemates become physically separated, however, it is not possible to visually identify these ramets in order to trace clonal lineages, nor to distinguish them from genetically different members of the population. Evaluation of genetic diversity and the extent of clonal dispersal in these species is further complicated by the logistical difficulties of random and sufficient sampling.

Two methods have been utilized to examine population structure and genetic variation in corals: histocompatibility testing by tissue grafting and protein electrophoresis. Tissue grafting as a criterion of self-recognition has been used to assess clonal diversity in populations of *Montipora verrucosa* and *M. dilatata* (Jokiel *et al.*, 1983), *Acropora cervicornis* (Neigel and Avise, 1983), *Porites compressa* (Hunter and Kehoe, 1985), and *Pavona cactus* (Willis and Ayre, 1985;

Ayre and Willis, in press). Electrophoretic enzyme analyses have been utilized to quantify genetic variation in Pocillopora damicornis (Stoddart, 1983; 1984 a,b) and Pavona cactus (Willis and Ayre, 1985; Ayre and Willis, in press). Both of these methods have significant drawbacks in that they assay only a small subset of an entire genome (Stoddart, et al., 1985). In addition, both Heyward and Stoddart (1985) and Willis and Ayre (1985) have reported that electrophoretic analyses detected variability in tissues from coral colonies which were immunocompatible.

Because many ecological and evolutionary questions hinge on the precise identification of individual genotypes and their distributions in populations, it is important that the relative merits of assays for genetic variability be assessed, and any discrepancies in their results be resolved. Different methods may be more effective or appropriate for various species, and it may be misleading to draw conclusions for population parameters on the basis of a single assay.

The endemic hermatypic coral, Porites compressa, is one of the most numerically abundant and spatially dominant coral species in Hawaii. It is dioecious, reproducing sexually by broadcast spawning in summer (Chapter 3). Asexual reproduction by fragmentation has also been documented in this species by Maragos (1972), Dollar (1982), and Chapter 3. It forms extensive monospecific stands of contiguous but visually distinguishable colonies, and covers up to 100% of the periphery and slopes of reefs in Kaneohe Bay, Oahu (Maragos, 1972). Populations of P. compressa appear as patchworks of colonies of various sizes, colors, and growth forms. This study was initiated to

1) compare methodologies for analysis of clonal identity in P. compressa, 2) determine if morphologically identical colonies represent genetically identical (clonal) groups, and 3) quantify the contribution of asexual reproduction to the population structure of this species. Three independent assays were used to identify clonal genotypes: colony morphology, histocompatibility testing by grafting, and electrophoresis of soluble proteins. A method for analyzing intraspecific variation in ultra-violet absorbing compounds was developed and tested against results of the other three assays.

MATERIALS AND METHODS

The study area is a patch reef (#43, Roy, 1970) approximately 120 X 200 m in size, located in northern Kaneohe Bay on the northeast coast of Oahu, Hawaii. Depth of the reef at low tide is 1-2 m at the center and 4-5 m at the periphery. A channel 10-12 m deep surrounds the reef, separating it from the nearest patch reef by a distance of 20 m.

A 2 X 10 m transect was established in an east-west orientation on the leeward (southeast) side of the reef in an area which is uniform in depth and coral cover. The transect was permanently marked at four corners with stakes and subdivided into twenty 1 m^2 sections marked with surveying tape. A weighted 1 m^2 grid with 10 cm^2 divisions was used as a template to map the outlines of all coral colonies within each section. Colony borders were identified by a 2-3 mm zone of bare skeleton at the interfaces of adjacent colonies. Colony areas were estimated from mapping data with a Summagraphics XY digitizer.

COLONY MORPHOLOGY

Colony color, branch length and width, and distance between branches were used as visual markers for distinguishing different morphological types. Branch size and distance between branches were measured to the nearest cm and assigned to scalar classes (1=<1 cm, 2=1-2 cm, 3=2-3 cm, 4=>3 cm). Color was subjectively determined relative to other colonies. Some morphotypes had visually distinctive characteristics and were easily recognized, while others had subtle differences and were more difficult to differentiate. Approximately half (47%) of the colonies within the transect could be assigned to one of eight morphotypes.

IMMUNOCOMPATIBILITY

One large colony of each of the eight morphotypes was designated as a primary donor colony. Ten to 25 branches (minimum length > 3 cm) were broken from each donor colony and securely attached with pre-labeled cable ties to branches of other colonies assigned to 1) the same morphotype, 2) colonies of different morphotypes, or 3) the donor colony itself. All grafts were done in the field to avoid stress of transport and maintenance in the laboratory. (Porites compressa held in the laboratory often develop infestations of the corallivorous nudibranch, Phestilla sibogae). Grafts were removed from recipient colonies after two to six weeks and examined microscopically to determine the extent of tissue and skeletal fusion or tissue death. Grafting responses were scored after 14-21 days in summer months, and after 21-28 days in the winter when responses were slower to develop.

ELECTROPHORETIC ANALYSIS

Branches were removed from five different colonies of each of seven morphotypes (designated M3, M4, M5, M6, M7, M9, and M24). Only one colony could be assigned to Morphotype M8, so this was analyzed as a single sample. Tissue extracts were prepared from fresh branch tips which were first pulverized with a hammer and homogenized in an indicator-extractant buffer (Stoddart, 1983). Samples were covered with squares of Kim-wipe tissue to minimize contact of the filter paper wicks (Whatman #3) to mucus in the homogenate. Wicks were dipped into the homogenate which passed through the Kim-wipe tissue and loaded into starch gels (12% wt/vol Electrostarch, Lot 392). Gels were run at 50 mA for 6-8 h in a refrigerated (5^{o} C) chamber. Three buffer solutions were used: Tris-citrate (Selander et al., 1971, #5) for phosphoglucoisomerase (PGI), and glucose dehydrogenase (GDH); Tris-borate-EDTA (Selander et al., 1971, #6) for leucyl-glycyl-glycine and valyl-leucine peptidases (LGG and VL), and Tris-citrate-EDTA (Redfield and Salini, 1980) for phosphoglucomutase (PGM), malate dehydrogenase (MDH), and esterase (EST). Stains were prepared following the methods described by Redfield and Salini (1980) for PGI, GDH, PGM, MDH, and EST. The peptidases (LGG and VL) were stained using techniques from Nicholls and Ruddle (1973).

UV-ABSORBING COMPOUNDS

Tissue cores (0.7 cm diameter) were bored from the upper tips of branches removed from the tops of colonies. Five samples were taken from each of the same 36 colonies which were electrophoretically assayed, plus one additional colony (Morphotype Y) from outside the

transect. Sample preparation for high performance liquid chromatography (HPLC) followed the method of Dunlap and Chalker (1986). Cores were sequentially extracted three times in 70% aqueous methanol. Extracts were glass-fiber filtered, evaporated under vacuum to approximately 20% of original volume, and passed through a Waters C-18 Sep-Pak column to remove apolar residues. Volume was restored with 10% methanol. Compounds were separated by reverse-phase chromatography on a Brownlee Spheri-5 (25 cm) RP-8 column and eluted at 0.7 ml/min with 10% aqueous methanol and 0.1% acetic acid as the aqueous phase. Peaks were detected at 313 nm and relative ratios of compounds were calculated from integrated peak areas.

RESULTS

Porites compressa colonies occupied 86% of the total coral cover within the 2 X 10 m transect of the patchreef. The remaining area was occupied by Montipora verrucosa (9%), Pocillopora meandrina (<1%), Porites lobata (<1%), or sand and rubble (4%). Colonies comprising 61% of the total P. compressa cover were identified as belonging to one of eight morphotypes (Table 2.1). These 136 colonies represented 47% of the 291 P. compressa colonies within the 20 m^2. Three morphotypes (M3, M6, and M9) dominated the transect, together making up 40% of the total P. compressa area. There were no significant differences (ANOVA, Duncan's Multiple Range Test) in mean colony size between the eight morphotypes.

A total of 125 grafts were tied between colonies within the

transect. Autografts (within a colony) and isografts (between immunocompatible colonies) were characterized by complete fusion of coenenchyme and skeleton. Soft tissue fusion was evident for some grafts after four days, but a minimum of 14 days was found to be necessary for strong skeletal fusion between grafted branches. Some morphotypes (M3, M6, M9, and M24) fused as isografts more rapidly than others (4-5 days compared to 14 days). From 5-20 immunocompatible colonies were found for each of the donor colonies within the 2 X 10 m transect, with the exception of M8, for which none of 15 allografts resulted in fusion. Additional grafts outside of the transect identified immunocompatible colonies up to 90 m from the donor heads. All grafting results were transitive (i.e. if colony 3A fused with colonies 3B and 3C, then 3B also fused with 3C).

Graft rejections (allografts) exhibited an initial bleaching of the tissues in the contact zone, followed by subsequent tissue death, which resulted in a band of exposed skeleton 2-3 mm wide separating the tissues of the grafted branches. After several weeks, these bands usually became pink in color, perhaps due to bacterial invasion, and then developed into shallow grooves as the result of the growth of tissue on either side of the area of contact. For many grafts, partial overgrowth (3-6 mm) of the recipient, or more commonly, the donor branch was noted after 6-8 weeks. Pink or white bands and elevated calluses similar to those seen in experimental grafts were evident in contact zones between natural allografts of contiguous colonies in the field.

Grafts between colonies judged to be morphotypically identical

prior to grafting produced fusion responses in 81.6% of the tests. Grafts from donor colonies of morphotypes M5 and M8 to colonies which were morphologically similar but not identical produced most of the rejection responses. My ability to identify putative clonemates and to distinguish between morphotypes increased with familiarity with the eight clones, as subtle differences between the common morphotypes and similar but discernable colonies became easier to detect. No fusions occurred in grafts between colonies which were assigned a priori to different morphotypic groups.

Enzyme electrophoresis indicated polymorphisms for five of the seven loci examined (Table 2.2). EST and LGG exhibited inconsistent banding patterns for most samples, and were therefore omitted from the analysis. All colonies from each morphotype showed identical zymograms for the five polymorphic systems (PGI, GDH, PGM, MDH, and VL) assayed. Although no electrophoretic variants were detected within these morphotypes, an anomalous electrophoretic pattern for tissue removed from a colony which had been identified as M3 was found. On reexamination of this colony in the field, it was discovered that what was initially determined to be a single colony was actually two morphotypically similar colonies in close proximity. The two colonies were distinguishable by subtle differences in color and branch width, although, due to their particular growth form (branches closely oppressed), the zone demarcating the colony borders was not readily visible. A subsequent sample from the appropriate colony yielded banding patterns identical to the other representatives of morphotype M3. This finding prompted re-checking of all colony borders in the

mapped transect, but no other "mosaics" were discovered.

Seven UV-absorbing compounds were detected by high performance liquid chromatography of samples from 36 colonies of Porites compressa. Figure 2.1 gives examples of representative chromatograms obtained from four samples. Colonies produced chromatograms unique to each morphotype in the occurrence and relative proportions of the seven compounds. These "signatures" were statistically compared by transforming the areas under each peak to ratios relative to Peak G (Table 2.3). Each morphotype was significantly different (ANOVA, Duncan's Multiple Range Test) from all other morphotypes in the relative ratio of at least one peak.

DISCUSSION

Grafting results, enzyme electrophoresis, and analysis of UV chromatograms provided independent corroborative assays of genetic identity for colonies of each morphotype of Porites compressa examined. Each morphotype was found to be unique in its immunocompatibility traits, five-locus genotype, and suite of UV-absorbing compounds. No significant variability in immunological or biochemical traits was discovered among colonies within the defined morphotypes. These results strongly support the hypothesis that colonies which were recognized as being identical in gross morphological characters were representatives of genetically defined clones.

Immunocompatibility responses appear to be very specific and consistent characteristics of morphotypes of Porites compressa. Neigel and Avise (1983) provided operational definitions for self-recognition

systems derived from their work with Acropora cervicornis. Their criteria of multiple simultaneous modes of interaction, reproducible response, and fusion of autografts were met by P. compressa and were observed under both natural and experimental conditions. Neigel and Avise (1983) also suggested that, in the event of local settlement of sexually-produced siblings, grafts between related colonies might result in fusions if the sibling alleles for self-recognition were identical. It is possible that fusions between branches from P. compressa colonies which appeared to be morphotypically identical represented grafts between relatives sharing immunocompatibility alleles. Recently settled sibling juveniles of this species have been observed to fuse in laboratory cultures (see Chapter 3). Ontogenetic changes and the extent of variability in immunocompatibility response of corals deserve much further work.

The number of loci necessary to differentiate all of the genetic individuals in a population is difficult to determine a priori (but see Chapter 3). Most of the 28 pairwise-comparisons of the eight morphotypes electrophoretically assayed could be distinguished based on banding patterns obtained from one to three enzyme assays. However, identical zymograms for three enzyme systems were shared by morphotypes M4 and M7, M5 and M9, and M9 and M2, while two pairs of morphotypes (M5 and M6 and M6 and M7) shared banding patterns for four out of the five enzymes assayed. Therefore, five loci were necessary and sufficient to uniquely identify these eight clonal groups, although a larger number would probably be required if more morphotypes were surveyed.

No electrophoretic discrepancies between colonies which were

immunocompatible were detected. This is in direct contrast to the findings of other studies (Curtis et al., 1982; Heyward and Stoddart, 1985; Willis and Ayre, 1985) in which the results of grafting were compared electrophoretic assays of genetic identity. The self-recognition system may be more polymorphic in P. compressa than in other species for which immunocompatibility has been utilized as a tool for assessing genetic identity. Alternatively, electrophoretic variability may exist in other enzyme systems in P. compressa which have yet to be assayed. The resolution of these differences among species may lie in additional genetic comparisons allowed by further morphological or biochemical analyses.

Numerous compounds whose absorption maxima occur between 300-360 nm have been identified from a broad range of plants and animals (see Nakamura et al., 1982). These mycosporine-like amino acids probably have their precursive origin in the shikimic acid pathway of plants and, in corals and tridacnid clams, may be produced and transferred (exported or leaked) from the symbiotic zooxanthellae to the tissues of their hosts (B.Chalker, pers. comm.). UV-absorbing compounds vary in both kind and relative abundance between species of corals (Dunlap and Chalker, 1986), suggesting that the diversity of these compounds may be due to modification of molecular precursors within the animal tissues. That they also vary significantly between individuals of a single species has important potential for analysis of genetic identity.

A tremendous range of morphological diversity was documented for Porites compressa by Vaughan (1907). Brakel (1977) attributed the

continuous spectrum of variability in corallite characters of Jamaican Porites spp. to intense diversifying pressures of the environment. He found that colonies from different environments shared similar corallite structure, but did not determine whether or not any of the 140 colonies which he sampled may have been representatives of the same clone. Differences in degree of phenotypic plasticity in colonies of Montastrea annularis (Dustan, 1975; Foster, 1979) and Siderastrea siderea (Foster, 1979) transplanted to different environments suggest that the potential for intra-clonal variation is a species-specific characteristic. Jokiel (1985) found that branching morphology of a single Porites compressa colony changed when transplanted to various depths (0.5 to 7.0 m). In the present study, colonies of P. compressa from similar depths (approximately 3 m) in both leeward and windward areas of the study reef (distances of up to 100 m) showed little to no phenotypic variability (i.e. could be visually assigned to distinct clonal morphotypes), indicating that gross colony morphology in this species is under some genetic constraint, or, alternatively, that the patchreef is perceived as a very homogeneous or fine-grained environment.

Clones were represented by an average of 19 colonies per morphotype within the 20 m^2 transect. It is evident that asexual reproduction by fragmentation is an extremely important agent in structuring this patch reef population. No colonies smaller than 60 cm^2 were found, indicating that successful planular settlement may be a rare event in the space-limited area of the transect. Fragments may have a greater probability of survival in the face of competition for

space and light than small juvenile colonies (Highsmith, 1982). No correlations between morphological characteristics and the extent of clonal dispersal were apparent.

It is difficult to extrapolate the exact age of coral colonies from size alone due to the vagaries introduced by fragmentation, fusion and partial mortality (Hughes and Jackson, 1980) but approximations can be made. Given an annual linear growth rate of 3.5 cm/year (Jokiel, 1985), and the sizes of the smallest and largest coral heads within the transect (maximum diameter 8.8 and 97.3 cm, respectively), colony age ranged from about 2.5 to 15.5 years. Large colonies (diameter > 150 cm) which dominate the seaward edge of the reef may be well over 25 years old, and actual genet age may be much greater.

The results of this study demonstrate that colonies of Porites compressa are recognizable by a small set of morphological characters which, when rigorously applied, allows immediate identification of clonal replicates in the field. That physically separate clonemates may be visually identified is an important attribute of this species in that it considerably simplifies the evaluation of population structure. The distribution and enumeration of clones on a patch reef can be determined directly from visual censusing rather than by "blind" estimations from methods (i.e. grafting, electrophoresis) which require intensive sampling of the entire population.

This study also indicates that asexual reproduction by fragmentation is an important component of the life history of Porites compressa. The relative contributions of sexual and asexual reproduction in this species are described in Chapter 3.

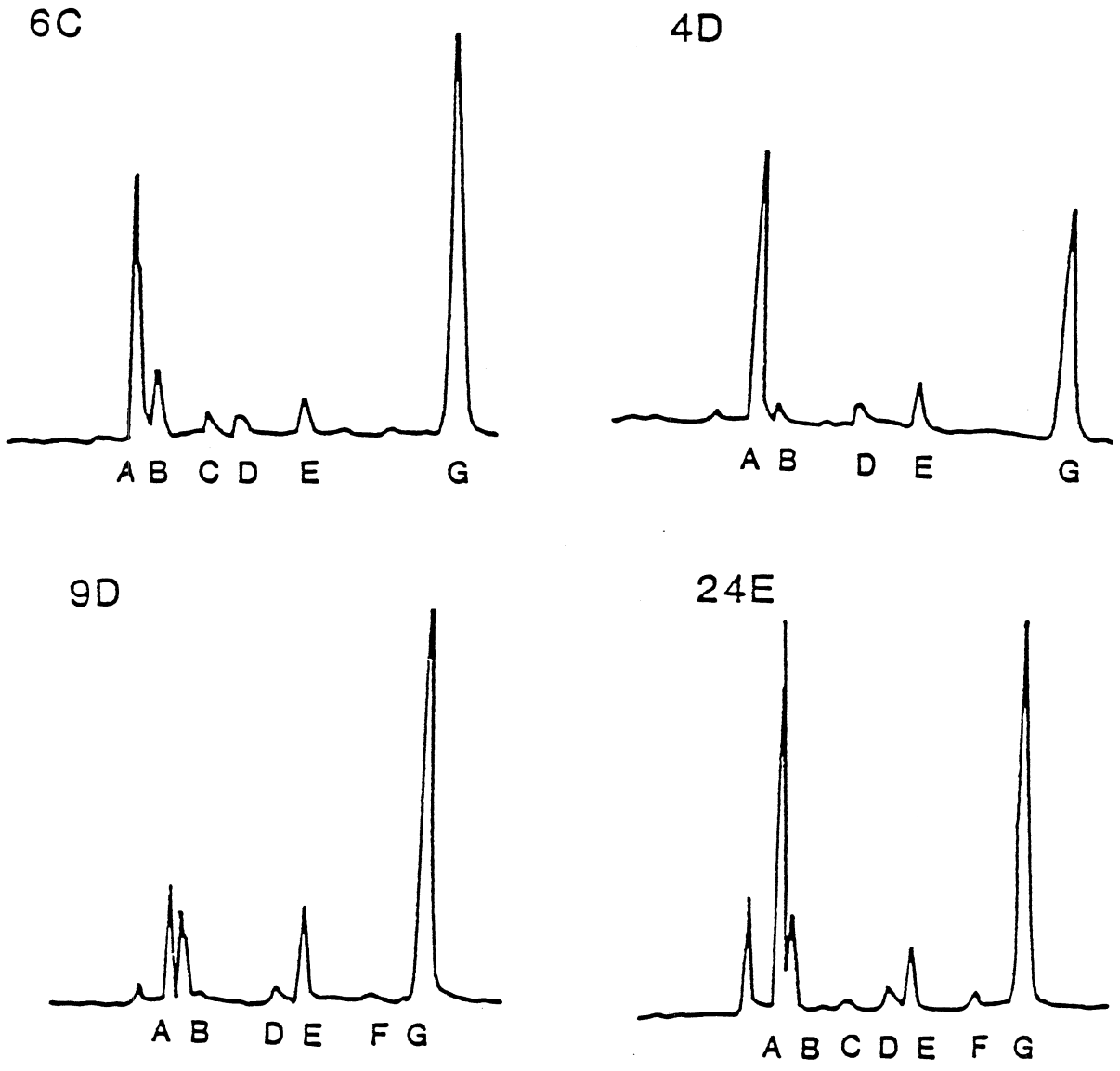


Figure 2.1. High performance liquid chromatographs representative of four of the eight morphotypes assayed.

Table 2.1. Morphological characteristics, spatial and numerical abundance, and mean colony size of eight morphotypes of Porites compressa in a 2 X 10 m transect on a patchreef in Kaneohe Bay, Oahu.

MORPHOTYPE	BRANCH LENGTH[a]	BRANCH WIDTH[b]	COMPACTNESS OF BRANCHES[c]	COLOR	% AREA IN 20 m^2	NUMBER OF COLONIES IN 20 m^2	MEAN COLONY SIZE (cm^2)
M3	2	2	2	tan	11.8	22	920
M4	1	2	1	yellow	7.4	15	800
M5	3	2	2	brown	7.1	17	800
M6	4	3	3	green	13.0	31	710
M7	2	1	2	tan	1.7	7	400
M8	4	2	4	ivory	1.3	1	260
M9	3	3	2	gold	15.5	38	690
M24	3	4	4	purple	4.1	7	980

[a] Length: 1 (<1 cm) 2 (1-2 cm) 3 (2^{-3} cm) 4 (>3 cm)

[b] Width: 1 (<1 cm) 2 (1-2 cm) 3 (2-3 cm) 4 (>^{3} cm)

[c] Compactness (distance between branch tips):

1 (<1 cm) 2 (1-2 cm) 3 (2-3 cm) 4 (>3 cm)

Table 2.3. Differences in the relative amounts of UV-absorbing compounds (Peaks A,B,C,D,E,F, and G) in eight morphotypes of Porites compressa. Letters represent significant differences (ANOVA, Duncan Multiple Range Test, $p>0.05$) in the ratios of the area under each peak relative to Peak G. The letter G indicates differences in absolute areas under Peak G (not a ratio).

M3	M4	M5	M6	M7	M9	M24	Y*
M3	E	AEFG	ACEG	G	ABEG	EB	A
M4		AEFG	ACEG	E	AG	E	AE
M5			CEF	AE	AE	AE	A
M6				AE	ACE	AEF	AC
M7					ABE	E	AE
M9						AE	D
M24							A

* Sample size=1; no statistical test performed.

Retention times for each peak: A=4 min, B=5 min, C=6 min, D=7 min, E=9 min, F=12 min, G=14 min.

TABLE 2.2. Banding patterns obtained from starch gel electrophoresis of five enzyme systems for eight morphotypes of Porites compressa.

	MORPHOTYPES							
	M3	M4	M5	M6	M7	M8	M9	M24
Enzymes:								
PGI	—							
	—	—		—	—	—	—	—
		—		—	—			—
	—	—	—	—	—			—
PGM					—		—	—
		—	—	—			—	—
	—	—			—	—		
GDH							—	—
	—	—	—	—	—			
						—		
MDH	—	—	—	—	—	—	—	—
			—	—	—		—	—
VL				—	—	—	—	—
	—	—	—	—	—	—	—	—

CHAPTER 3

SEXUAL REPRODUCTION AND ASEXUAL PRODUCTION OF FRAGMENTS IN THE SCLERACTINIAN CORAL, *PORITES COMPRESSA*

INTRODUCTION

Clonal organisms are those in which individual genets have the potential to produce genetically identical replicates of themselves (ramets) as well as sexually recombinant gametes that can form genetically unique zygotes (new genets) (Kays and Harper, 1974). Life history studies are critical to understanding the relative importance of both sexual and asexual modes of reproduction in clonal species (Williams, 1975; Harper, 1977; Cook, 1983; Jackson, 1985). Sexually and asexually produced offspring are expected to differ in a number of characteristics, including size, abundance and frequency of production, dispersal distance, and mortality rate (Williams, 1975). In corals, Highsmith (1982) proposed that the ability to fragment is adaptive in many species, and that there has been selection for morphological and life history characteristics which favor this ability.

Highsmith (1982) also suggested that many life-history parameters of corals that produce asexual offspring by fragmentation are opposite to those of non-fragmenting species. He attributed broadcast spawning (*vs.* brooding of larvae), low juvenile recruitment rates, high growth rate, large adult size, long life expectancy, and a reduced allocation of energy to sexual reproduction as characteristics of corals that

reproduce predominantly by fragmentation. However, there have been no studies which quantify the relative contributions of sexual and asexual reproduction within a coral species.

Porites compressa is one of the most abundant and competitively dominant scleractinian coral species in Hawaii (Maragos, 1972; Grigg, 1983). Little is known about its reproductive biology, although Stimson (1978) reported the presence of eggs in colonies from June-August and testes in February. Clonal diversity estimates from electrophoretic data demonstrated that asexual reproduction by fragmentation in this species produces viable propagules which recruit into local populations (Chapters 2 and 5). Populations of P. compressa vary from those with almost no clonal replication (recruitment is entirely sexual) to those in which some clones are widely and numerously distributed by the propagation of fragments. The present study is an investigation of sexual reproduction and asexual fecundity in P. compressa and the physical and ecological processes that may affect the recruitment of propagules generated by each mode of reproduction. The number, size, and frequency of fragments produced per unit area of reef through time and the relative propensity for fragmentation of different clones were measured for the patchreef population described in Chapter 2. Relative gamete maturity in both fragments and whole colonies were determined. In addition, the reproductive biology of P. compressa is described for the first time.

MATERIALS AND METHODS

ASEXUAL REPRODUCTION

Fragment production

The number of asexual propagules (fragments) generated on a reef over a period of one year was estimated by censusing three fragment "traps". One 4 m^2 and two 1 m^2 quadrates were permanently marked on a patchreef (#43, Roy, 1970) in northern Kaneohe Bay, Oahu, Hawaii. The 4 m^2 quadrate (A) was located on the central reef top in a topographical depression (approximately 3 m x 4 m) caused by a ship grounding two years prior to the beginning of the study. Both 1 m^2 quadrates (T1 and T2) were located on the reef slope in concavities where green sea turtles, Chelonia midas, were often observed to rest. Concavities are due to downslope slumping of large colonies resulting in the formation of crevices or gaps, and are generally surrounded on all sides by live Porites compressa colonies. Coral colonies on the bottom of concavities frequented by turtles have a characteristic worn-down appearance. The 1 m^2 quadrates were designed to estimate the contribution of turtles to fragment production on the patchreef. Quadrates were censused six to nine times, at 30 to 90 day intervals from May, 1987, through May, 1988. Fragments with live coral tissue were collected, and the total surface area and percentage live tissue cover of each fragment were estimated as the product of length and width measurements.

Clonal propensity for fragmentation

The hypothesis that numerically dominant clones have higher rates

of fragment production than rare clones was tested by measuring their relative propensity for fragmentation. Colonies of eight different genotypes were chosen from the windward and leeward sides (four from each site) of the reef. Three (leeward) clones were numerically dominant (7-31 per 20 m^2; Chapter 2), three (windward) clones were spatially abundant (colony diameter 1-3.3 m), and one clone from each site was "rare" (represented by only one colony). The "breaking strength" of six branches from each colony was estimated using a modification of the method of Jones and Demetropoulos (1968) and Polachek (1980). The force required to remove a branch from a parent colony was estimated by attaching a cable-tie connected to a hand-held fish scale 1 cm from the tip of a branch. Lateral pull was exerted on the scale and the force (measured as "weight" in kg) necessary to break the branch was recorded. Wet weight, volume displacement, and cross-sectional area across the plane of the break were measured for each broken branch. Ratios of branch weight to volume (ignoring the contribution of live tissue) were used as indices of skeletal density.

SEXUAL REPRODUCTION

The seasonality of gametogenesis and spawning were monitored in Porites compressa populations in Kaneohe Bay over a four year period, from 1984 to 1987. In 1987, branches from each of forty-five colonies were collected from north Kaneohe Bay (NKB, Patchreef #43) on 2 July, and from south Kaneohe Bay (SKB, Kokokahi fringing reef) on 8 July. Diameters of the two longest axes were measured for each colony. Polyps were microscopically examined for the presence of gonads

(swollen mesenteries) and stage of gamete development within mesenteries was recorded. Diameters of ten oocytes were measured from each female colony, and the presence or absence of zooxanthellae or germinal vesicles within eggs was noted. Testis squashes were used to determine male maturity, with head condensation, visibility of tails, and active spermatozoa swimming used as indicators of sequential stages of maturation.

In order to determine whether or not there is a "trade-off" between sexual and asexual modes of reproduction (e.g., whether fragments of varying sizes retain or lose their ability to reproduce sexually), maturity of gametes from different sixed fragments was compared to gametes from parent colonies from which the fragments were derived. Five to six fragments of varying size were broken from each of six large (> 0.5 m^2) colonies on the top of the reef slope on the leeward (southwest) side of Coconut Island in southern Kaneohe Bay on 20 April, 1987. Fragments were designated by letters (A-F) in increasing order of size. Each fragment was retied to its parent colony, with a sheet of black plastic separating the fragment from the parent colony to prevent re-fusion of tissue. All fragments were collected on 7 July, 1987, along with freshly removed branches from the parent colonies, and brought into the laboratory where their size and stage of gamete development were recorded.

RESULTS

ASEXUAL REPRODUCTION

Fragment production

A total of 576 Porites compressa fragments with a total live surface area of 4921.71 cm^2 were collected from the three census areas during the 12 months of this study (Table 3.1). The numbers of fragments produced in the turtle quadrates (0.35-0.46 per m^2/day) were significantly higher (t-test, $p < 0.001$) than in the reef top quadrate (0.07 per m^2/day) (Table 3.1). The large number of fragments found in the turtle quadrates is consistent with the supposition that turtles are a major cause of fragment production on this reef. Variation in number of fragments generated per day was also larger in the turtle quadrates, indicating that turtle visits or behaviors which cause fragmentation may be sporadic or seasonal, with the greatest activity occurring in summer months (Figure 3.1). Mean fragment size differed among the quadrates as well, with both whole fragment size and live tissue area more than twice as large in T1 as in the other two quadrates. Most fragments found within the turtle quadrates had similar branch morphologies and were assumed to have been derived from the colonies just above the quadrates.

Freshly broken Porites compressa branches that were held in flow-through seawater tables and observed over a period of months developed a film of diatoms and brown filamentous algae over the area of coral skeleton exposed by the break after 3-5 days. The beginning of regrowth of tissue over the break was noted after about one week, and the exposed skeleton was completely covered by tissue within 5-6 weeks.

Some coral fragments from each quadrate could be classified as "new recruits" (produced < 5 days prior to day of census) based on the presence of fresh breaks (no algal film overgrowth), or "rolling stones" which were completely covered by living coral tissue (produced >5 weeks prior to day of census) (Table 3.1). The occurrence of these younger and older fragments suggests a broad time frame over which fragments are viable.

The presence of "rolling stones" in quadrates where all fragments had been removed less than 4 weeks previously demonstrated that there was some movement of fragments into the quadrates from outside of the immediately surrounding area. The finding that there was no accumulation of fragments when traps were censused after longer time intervals suggests that fragments moved out of the quadrates as well.

Clonal propensity for fragmentation

There were no significant differences in skeletal density or breaking "strength" (Table 3.2) between the eight clonal genotypes tested (ANOVA, BMDP-7D program, $p=0.129$ and $p=0.412$, respectively). Branch morphology (as measured by the cross-sectional area at the point of breakage) did vary among clones (ANOVA, $p=0.014$), but correlations between break area and breaking "strength" over all samples combined was low ($r^2=0.12$). When compared within clones, correlations were higher for the leeward colonies ($r^2=0.41-0.68$) than for windward colonies ($r^2=0.07-0.28$). Windward colonies, which are larger and probably older, may have a greater variability in the degree of bioerosion within branches (due primarily to polychaetes and clionid sponges), and thus differences in the force needed to break branches,

than the smaller leeward colonies. Similarly, skeletal density and breaking "strength" had a low overall correlation coefficient (r^2=0.04), but in this case, within-clone r^2 values ranged from 0.01 to 0.76 with one leeward colony and one windward colony having the highest values (0.76 and 0.46, respectively).

SEXUAL REPRODUCTION

All Porites compressa colonies examined were gonochoric; 50 colonies representing 13 clones monitored over four years showed no evidence of sex change or hermaphroditism. Ovaries were first observed each year in early June. Oocytes were creamy white and ranged from one to nine per mesentery. Mean oocyte diameters (n=40) from Coconut Island reef flat colonies sampled on 9 June, 1987, were 150 $\pm$ 10 um and gradually increased in size to a maximum of 254 $\pm$ 29 um on 27 July, 1987. About one week prior to spawning, zooxanthellae were noted within the egg membrane in some oocytes, particularly those closest to the polyp mouth. Spawnings were inferred from the depletion of gametes from field-sampled colonies between 10-25 July, 1984 (full moon 13 July) and 29 July-12 August, 1985 (full moon 31 July). Colonies observed in the laboratory spawned on 23 June (full moon 21 June) and 21-22 July, 1986 (full moon 21 July). Field sampling indicated a third spawning period in August, 1986. In 1987, laboratory spawnings occurred during the week after full moon in July and August, but some colonies still had polyps with large and numerous eggs at the sampling just before full moon in September, indicating a third spawning event. No gametes were seen in any colonies after 7 September, 1987.

Testes were first noted in late May of each year, and appeared as translucent swellings within each mesentery of male colonies. As testes became mature (July-August), mesenteries enlarged to approximately 5-10 times their non-reproductive size and appeared opaque white. Spermatocyte and spermatid heads were irregular in outline. Tails became visible by early June in some colonies. Condensation of spermatid heads occurred one to two weeks prior to July spawnings. Mature spermatozoa were conical in shape, with 3 x 4 um heads and 70 um long tails. Active swimming of spermatozoa in testis squashes was evident about one week prior to spawnings in July, and most male colonies had active sperm through the rest of the summer.

Spawnings of colonies observed in the laboratory occurred at night between 2300 and 0030 hrs. Male and female colonies spawned up to three nights in a row. Eggs were neutrally buoyant. Eggs spawned at 2310 on 22 June, 1986 were experimentally fertilized with sperm released from a male colony at 2325; first cleavage was observed after 60 minutes. Two-celled embryos were crescent-shaped, and approximately 240 um in maximum diameter. After 3 h, second cleavage produced embryos with a tri-lobed appearance. Spherical gastrulae were observed after 18 h, concentrated near the water surface. Actively swimming planulae began to show photo-negative behavior between 24-48 h. After 3 days, planulae began to settle on dead coral rubble fragments placed in culture dishes. Tentacle buds were first seen on day 6, and skeletal deposition on day 8. Many larvae from sibling cultures settled gregariously, with as many as 30 polyps found with their body walls in contact on the bottom surface of pieces of rubble. Some

larvae settled on each other, and metamorphosed while still swimming by ciliary movement, forming "floating colonies" of up to 4 sibling polyps. Apparent tissue and skeletal fusion occurred in about 78% of polyps which settled adjacently on pieces of coral rubble (83 fused polyp-pairs/107 adjacent polyps). Groups of 2, 3, 4, and 7 fused sibling polyps behaved as integrated colonies, forming a common outer septal wall and showing no evidence of rejection after eight weeks of observation.

Reproductive parameters differed between the NKB and SKB populations sampled (Table 3.3). Mean colony size was almost an order of magnitude greater at the NKB site (2229.5 $\pm$ 1742 cm^2) than the SKB site (245.2 $\pm$ 210 cm^2), indicating that most NKB colonies are much older (see Chapter 5). The sex ratio was essentially equal for NKB (23 males:22 females), but determination of sex was not possible for 40% of the SKB colonies due to the absence of gonads (16 males:11 females:18 undeterminable). It is not known whether these colonies did not have gametes because they were immature or if they had spawned prior to the census. Some colonies throughout the sampled size range (18-812 cm^2) lacked recognizable gonads, although most (72%) of the undetermined colonies were smaller than the mean colony size at this site. Porites compressa colonies grow slowly during their first year after recruitment, reaching about 1-2 cm in diameter after twelve months (R. Fitzhardinge, pers. comm.). It is not known at what time their growth rates increase, but Polacheck (1978) reported a mean annual radial growth rate of 2.46 cm/year for larger colonies. Assuming this faster growth rate after one year, the smallest gravid colony sizes of 18 cm^2

(male) and 56 cm^2 (female) (Table 3.3) suggest that age at first reproduction is between 1.8 to 2.5 years in P. compressa. It is interesting to note that fragments larger than the minimum equivalent whole colony size for sexual reproduction (e.g., M1-E and M4-E) did not have fully developed testes and probably did not reproduce during the first year after fragmentation occurred.

At the SKB site, 31.8% of colonies greater than the median colony size (168 cm^2) were female, 36.4% were male, and 31.8% were unknown; below the median colony size, 13.6% were female, 36.4% were male, and 50% were unknown. For the NKB population, 59% of the colonies greater than the median size (1908 cm^2) were female as opposed to 36% below the median. Mean oocyte size was significantly larger (t-test, $p<0.001$) for the NKB population ($X=211 \pm 15.67$ um) than the SKB population ($X=199 \pm 7.60$ um), although egg size was not correlated with colony size in either population (NKB: $r^2=0.003$, SKB: $r^2=0.039$).

Sexual fecundity of experimentally produced fragments was a function of both the size and sex of a fragment. Two of the parent colonies in the field manipulation were female and four were male. (Gonads were immature at the start of the experiment, and sex could not be determined a priori). Number of eggs per mesentery varied between four and seven in controls and experimentally produced fragments, regardless of fragment size. Mean egg diameters of fragments were significantly different from the parent colonies only in the smallest fragments F-1A and F-2B) from the two female colonies (Table 3.4). Oocytes with zooxanthellae within them were found only in samples with mean egg diameters >220 um (Parent colonies, F-1E, F-2C,D).

Spermatogenesis appeared to be more affected by fragmentation than did oogenesis, and pattern and degree of disruption was different in each male colony (Table 3.4). Control branches (those removed from the colony on the day the experiment was ended) had actively swimming spermatozoa with readily visible tails and fully condensed heads. In Colony M-1, all fragments (A-E) had spermatids with uncondensed heads and a few with visible tails. Fragments from Colony M-2 had fully active spermatozoa (B-D), except for the smallest fragment (A) in which spermatids were not condensed and about 50% had visible tails. Larger fragments (D,E,and F) from Colony M-3 had mature spermatozoa, but the smaller fragments (A,C) had uncondensed spermatids with no tails, or spermatozoa with tails but not actively swimming (B). Only the largest fragment (F) from Colony M-4 had mature spermatozoa. Spermatids in fragments C and E had uncondensed heads and lacked visible tails; condensation of heads was beginning in B and D and tails were visible. Testes were undeveloped in all of the 14 polyps examined from Fragment M-4A.

DISCUSSION

Scleractinian coral populations exhibit high levels of genetic variability relative to many other invertebrate species (Nevo, 1978) despite the highly clonal population structures observed in the three species examined to date: *Pocillopora damicornis* (Stoddart, 1984a,b), *Pavona cactus* (Ayre and Willis, in press), and *Porites compressa* (Chapter 2 and 5). In *P. compressa*, sexual and asexual modes of reproduction each make significant contributions to population

structures (Fitzhardinge, 1985; Esquival, 1985; Chapter 5). Clonal genotypes are locally replicated through asexual reproduction by fragmentation, while genetic variability is maintained by recruitment of sexually-produced propagules with the concomitant introduction of new genotypes.

Coral fragments can be generated by storms (Stoddart, 1963; Maragos, et al., 1973; Randall and Eldredge, 1977; Highsmith, et al., 1980; Dollar, 1982), bioerosion (Tunnicliffe, 1978; Highsmith, 1980, 1981), fish grazing (P. Glynn, pers. comm.), or human activities such as fishing (Chesher, 1985), anchor damage (Davis, 1977), or reef-walking (Heyward and Collins, 1985a). During the year in which this study was conducted, there were no large storms which affected Patch-reef #43 (although there was a major flood in January, 1988, which killed corals on near-shore fringing reefs), and evidence of fragment-tation due to human activity on the study reef was negligible. Fragment production over the time period of this study was probably due primarily to bioerosion of branches and activity of the green sea turtle, Chelonia midas. Whether this was a "typical" year on this patchreef is conjectural. While rates of fragmentation caused by bioerosion and turtles are probably fairly constant, other agents of fragment production such as storms or human impact (e.g., boat groundings, destructive fishing practices) are unpredictable in both frequency and intensity.

Extrapolation of the number of fragments found within the 4 m^2 quadrate to the entire patchreef gives a total of 690,000 potential asexual propagules of Porites compressa generated within a one year

period on a 20,000 m^2 patchreef. If the turtle quadrates are included, the total extrapolated number of fragments could be as high as 1,920,000/year. However, the effects of turtles are localized; 17 concavities frequented by turtles were counted on the perimeter of Patchreef #43 and several have been noted on the reef top. Most fragmentation due to turtles is probably confined to these areas. Coral colonies adjacent to sites where turtles habitually rest may have a substantially greater potential contribution to the fragment pool. Analyses of clonal diversity down-slope from these sites could provide an estimate of the long-term impact of turtle-generated fragmentation on clonal population structure.

Long-term survivorship of P. compressa fragments was not followed in the present study, but the common occurrence of "rolling stones" suggests that up to 30% of generated fragments may survive at least 5-6 weeks. The finding that one out of three colonies in the NKB population is asexually derived (Chapter 5) suggests that a significant number of fragments persist, although the ultimate fates of individual asexual propagules and the proportion which recruit into the population are unknown. There was evidence for movement of fragments into and out of the censused traps, suggesting that fragments may disperse some distance from their parent colonies before reattaching or being lost from the viable fragment pool. Fragments may fall into crevices and interstices created by the thicket-like branching patterns of coral colonies where light may be a limiting factor to survival. Sedimentation and scouring may have deleterious effects on fragments which roll down the reef slope to the lagoon floor. Fragments which land in

contact with live colonies may either fuse with (if they are members of the same clone), be overgrown by, or outcompete the "host" colony. Fragments which land on bare, hard substratum probably have the best chance for survival.

The survivorship of experimentally-produced fragments of other ramose corals were measured for Montipora ramosa (approximately 62% for fragments >3 cm after 54 days; Heyward and Collins, 1985b), Acropora nasuta and A. formosa (100% for fragments >20 g after 120 days; Kobayashi,1984). Very low survivorships of storm-generated fragments were reported for small-branched ramose corals, Porites compressa (<1% after 14 days; Dollar, 1982) and Acropora cervicornis (53% after 3-9 days, <2% after 5 months; Knowlton, et al., 1981), while Acropora palmata, with larger branches, had higher survival (46% after 4 months; Highsmith, et al., 1980).

Most naturally produced fragments are probably not sexually viable. In the experimental fragment-fecundity study, the smallest fragments with normal gametogenesis were larger than all but a few of the fragments found in the censused traps. There appeared to be a "trade-off" between energy allocated to sexual reproduction and the metabolic requirements for survival in asexually produced fragments.

The hypothesis that observed differences in abundance of common and rare clones were due to differences in relative propensity for fragmentation as measured by breaking "strength" was not supported. Replicating the actual angle, strength, and manner in which fragments are naturally generated is not possible without empirical tests of the causative agents in situ. The methodology used to assess branch

breaking strength in this study had limitations in that it measured only the artificially applied horizontal force necessary to break branches from parent colonies. More refined methods might be better able to detect differences in propensity for fragmentation between clones. Alternatively, clonal dominance may be the result of differences in post-recruitment fitness.

The sexual reproductive biology of Porites compressa is similar to that described for other Porites species which broadcast spawn (Table 3.5). Broadcast spawning has been reported in six Porites species, three from the Great Barrier Reef (P. lobata, P. lutea, P. andrewsi; Kojis and Quinn, 1981), and three from Hawaii (P. compressa, P. lobata, P. evermanni; Hunter, unpubl.). The Great Barrier Reef Porites species spawn in the austral spring, and Hawaiian species spawn in summer. Oocyte sizes at spawning range between 200-280 um. All six species are stable gonochorists with the exception of P. andrewsi, for which a low incidence (3.7%) of hermaphroditism was reported (Kojis and Quinn, 1981). Three species, P. porites (Barbados; Tomascik and Sander, 1987), P. murrayensis (GBR; Kojis and Quinn, 1981), and P. lichen (Hawaii; G. Hodgson, pers. comm.), are dioecious brooders, with some incidence (2.7%) of hermaphroditism in P. porites (Tomascik and Sander, 1987). P. astreoides (Jamaica; Chornesky and Peters, 1987) is also a brooder, with about 50% of colonies being female and 50% hermaphroditic. Periodicity in spawning is linked to lunar cycles in P. andrewsi (1-10 days after full moon; Kojis and Quinn, 1981) and P. compressa (0-3 days after full moon; this study). Individual colonies of P. compressa spawned on more than one night each month, and over

one to three months. Hodgson (1985) reported laboratory spawnings and peaks in P. compressa planulae collected in plankton tows at both new and full moon in 1984.

Apparent fusion of recently metamorphosed primary coral polyps has been reported by a number of researchers (Stephenson, 1931; Edmondson, 1946; Harrigan, 1972; Richmond, 1985; this chapter). The cytological and immunological processes involved in these fusions, and whether fusion can occur under field conditions are unknown (Jackson, 1985). The genetic and ecological consequences of these potential "chimeras" require further investigation.

A summary of life history characteristics in eight species of Porites is presented in Table 3.6. Traits suggested by Highsmith (1982) to be associated with species that reproduce predominantly by fragmentation (broadcast spawning, low recruitment rates, large adult size, and long life expectancy) occur in P. compressa and P. andrewsi, which both have high rates of asexual recruitment (Kojis and Quinn, 1981; Chapters 2 and 5). However, these same traits occur in P. australensis, P. lutea, and P. lobata, species which rarely reproduce asexually (Kojis and Quinn, 1981; Harriott, 1983). P. porites, a brooding species, shows characteristics which are opposite to those of fragmenting species (sensu Highsmith, 1982), yet it has been reported to have high fragmentation rates, particularly in adverse environments (Tomascik and Sander, 1987). The present study has shown that numerical dominance of clones is not predictable from their relative ability to produce fragments. In light of these findings, the proposal by Highsmith (1982) that fragmentation itself is adaptive and that

there has been selection for particular life history traits in species which reproduce primarily by fragmentation cannot be supported.

Asexually produced offspring of Porites compressa differ greatly from sexually produced offspring in size, abundance, frequency of production, and dispersal potential (Table 3.5). These traits are consistent with the assumptions of Williams' (1975) model for the asexual proliferation of locally adapted genotypes in clonal populations. The hypothesis that clonal dominance of some genotypes on a reef is the result of post-recruitment differences in fitness is addressed in Chapter 4.

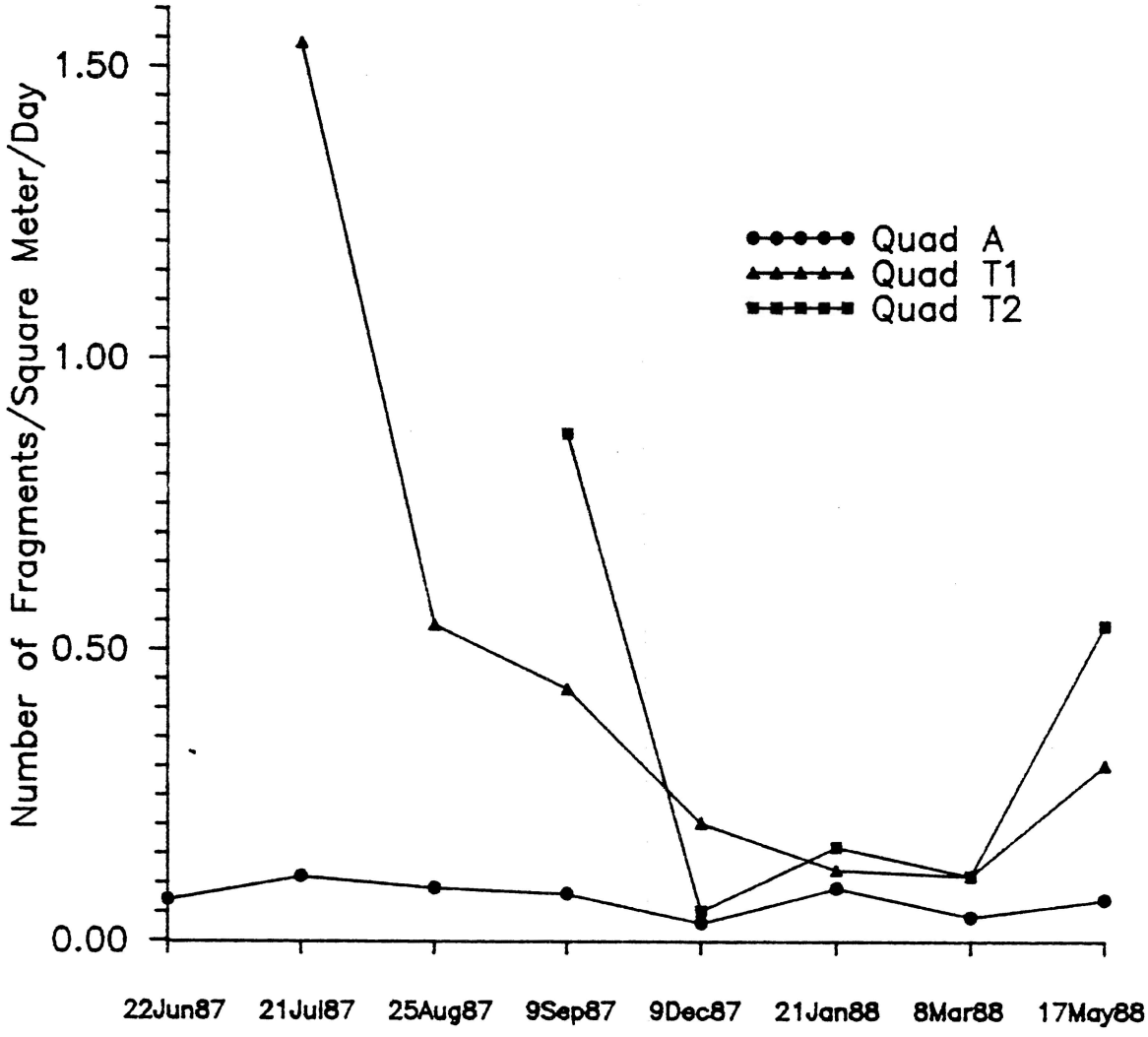


FIGURE 3.1. Number of fragments of Porites compressa generated per m^2 per day within three quadrats on Patchreef #43, Kaneohe Bay. Quad A was on the reef top (2 x 2 m), Quads T1 and T2 (1 m^2 each) were below concavities on the reef slope where turtles were observed to shelter.

TABLE 3.1. Number and size of fragments collected from three quadrats on Patchreef #43 between 21 May, 1987 and 17 May, 1988. a. Quadrate A (4 m^2) values were divided by four for comparison to T1 and T2 (1 m^2 quadrats). b. T1 and T2 quadrats. + = total on first day of collection. See text for description of "rolling stones" and "new recruits".

a.

Quadrate A	# Days	# Fragments	Number per m^2 per day	Total fragment area (cm^2) per day	Total live tissue area (cm^2) per day	Mean whole fragment size (cm^2)	Mean live tissue area (cm^2)	Rolling stones (%)	New recruits (%)
21 May 87	0	10.50	—	169.68+	101.78+	16.55	9.93	21.4	11.0
22 Jun 87	32	2.25	0.07	0.49	0.36	7.69	5.09	0	0
21 Jul 87	28	3.00	0.11	0.80	0.68	7.46	6.34	66.7	0
25 Aug 87	35	3.00	0.09	0.90	0.84	10.50	9.84	75.0	0
9 Sep 87	30	2.25	0.08	0.62	0.36	8.19	4.75	—	—
9 Dec 87	91	3.00	0.03	0.59	0.12	18.00	3.78	8.3	0
21 Jan 88	43	3.75	0.09	0.77	0.69	8.87	7.95	20.0	0
8 Mar 88	47	2.00	0.04	0.44	0.22	10.43	5.22	25.0	0
17 May 88	70	4.75	0.07	1.16	1.00	17.05	14.67	36.8	0
Total per year:		34.50		446.75	293.77				
Yearly mean:			0.07	0.72	0.53	11.64	7.51		
standard deviation:			0.02	0.22	0.29	4.07	3.28		

TABLE 3.1. (cont.)

	# Days	# Fragments	Number per m^2 per day	Total fragment area (cm^2) per day	Total live tissue area (cm^2) per day	Mean whole fragment size (cm^2)	Mean live tissue area (cm^2)	Rolling stones (%)	New recruits (%)
Quadrate T1									
22 Jun 87	0	101	—	3756.00+	1321.83+	23.20	10.99	8.9	2.0
21 Jul 87	28	43	1.54	48.46	20.46	31.55	13.32	2.3	4.7
25 Aug 87	35	19	0.54	8.23	4.98	15.17	9.17	21.1	0
9 Sep 87	30	13	0.43	7.58	3.50	17.50	8.07	—	—
9 Dec 87	91	18	0.20	2.19	1.78	11.08	9.00	5.6	0
21 Jan 88	43	5	0.12	2.05	2.05	17.60	15.48	0	0
8 Mar 88	47	5	0.11	12.53	3.63	117.80	34.12	0	0
17 May 88	70	21	0.30	5.61	3.20	18.69	10.67	14.3	0
Total per year:		225		6897.80	2818.60				
Yearly mean:			0.46	12.38	6.53	31.57	13.85		
standard deviation:			0.46	15.11	7.53	33.08	7.99		
Quadrate T2									
25 Aug 87	0	132	—	311.70+	142.60+	2.36	1.08	3.0	0
9 Sep 87	30	26	0.87	19.82	3.76	22.86	4.34	—	—
9 Dec 87	91	5	0.05	0.54	0.20	9.80	3.57	3.8	0
21 Jan 88	43	7	0.16	1.44	0.75	8.82	4.16	0	0
8 Mar 88	47	5	0.11	1.24	0.15	11.70	1.45	0	0
17 May 88	70	38	0.54	21.00	8.76	38.69	16.13	31.6	50.0
Total per year:		213		2545.45	925.95				
Yearly mean:			0.35	8.81	2.72	15.71	5.12		
standard deviation:			0.31	9.48	3.30	11.94	5.08		

TABLE 3.2. Means and standard deviations of measured parameters of propensity for fragmentation in eight clones of Porites compressa. Clones designated by numbers are leeward colonies, letters are windward. Sample size was five for each clone. * indicates rare clones.

Clone	Mean Skeletal Density (g/ml) (A)	Mean Break Area (sq.cm) (B)	Mean Breaking "Strength" (kg) (C)	Regression Coefficients Within Clones (A:C)	(B:C)
5	1.54 0.19	0.92 0.46	5.23 1.65	0.08	0.41
6	1.42 0.28	1.05 0.33	5.75 2.45	0.76	0.57
8 *	1.83 0.51	1.30 0.51	4.00 1.26	0.27	0.55
24	1.30 0.21	1.88 0.88	5.78 2.35	0.01	0.68
I	1.56 0.05	1.93 0.63	6.50 1.83	0.13	0.07
L	1.57 0.22	1.37 0.43	4.70 1.59	0.03	0.18
M	1.54 0.13	2.14 0.79	4.08 1.48	0.08	0.28
O *	1.54 0.20	2.12 0.81	4.92 2.23	0.46	0.08
Differences among clones:	n.s.	p=0.014*	n.s.		

TABLE 3.3. Colony size, sex, and oocyte diameters for NKB (2 July, 1987) and SKB (8 July, 1987) populations of Porites compressa.

NKB Colony Diameters (cm)		Area (sq.cm.)	Sex	Mean Oocyte Size (um) + std.dev.	
7	5	35	F	199.1	79.8
6	31	186	M		
25	11	275	M		
27	13	351	M		
21	23	483	F	277.7	144.1
23	26	598	F	226.2	61.9
27	27	729	M		
38	25	950	F	236.5	133.1
42	23	966	M		
39	25	975	M		
42	27	1134	F	—	
57	20	1140	F	225.2	32.7
30	40	1200	M		
34	37	1258	M		
40	32	1280	M		
33	39	1287	M		
24	57	1368	M		
74	19	1406	M		
74	20	1480	F	228.9	49.1
45	34	1530	M		
34	48	1632	F	243.8	101.4
38	50	1900	M		
36	53	1908	F	212.5	21.7
50	42	2100	F	249.1	97.4
57	37	2109	F	223.8	74.7
50	43	2150	F	214.5	21.3
55	40	2200	F	217.2	61.2
58	38	2204	M		
59	38	2242	F	—	
60	38	2280	M		
45	54	2430	M		
32	80	2560	M		
62	43	2666	M		
38	71	2698	F	242.7	45.1
45	60	2700	M		
50	60	3000	M		
89	35	3115	F	217.5	10.8
63	50	3150	F	266.8	77.7
71	45	3195	F	238.0	57.6
103	44	4532	F	247.2	32.8
117	43	5031	M		
65	78	5070	M		
82	64	5248	F	211.0	36.4
123	55	6765	F	220.9	45.3
113	78	8814	F	206.0	28.4
Pop. Means:		2229.5		211.0	15.7

SKB Colony Diameters (cm)		Area (sq.cm)	Sex	Mean Oocyte Size (um) + std.dev.	
6	3	18	M		
6	5	30	?		
6	7	42	?		
7	8	56	F	—	
7	8	56	?		
7	8	56	?		
10	6	60	M		
9	7	63	M		
8	8	64	?		
11	6	66	F	208.0	25.6
17	4	68	M		
7	11	77	?		
10	8	80	M		
9	9	81	?		
11	8	88	?		
8	12	96	?		
16	7	112	?		
16	8	128	M		
7	19	133	F	192.0	18.3
13	11	143	M		
14	11	154	M		
14	11	154	?		
14	12	168	M		
12	14	168	F	202.0	16.6
20	9	180	?		
16	12	192	F	194.0	25.4
18	11	198	?		
13	20	260	M		
20	13	260	?		
20	15	300	F	202.0	6.0
19	16	304	?		
34	9	306	F	—	
29	11	319	?		
21	17	357	M		
25	15	375	F	186.0	20.1
22	19	418	?		
20	23	460	M		
23	21	483	?		
22	22	484	F	206.0	15.6
25	21	525	F	—	
27	21	567	F	208.0	13.3
33	19	627	M		
28	23	644	M		
32	25	800	M		
28	29	812	M		
		245.15		199.0	7.6

TABLE 3.4. Oocyte size or spermatozoa development in experimentally-produced fragments of Porites compressa from two female (F1 and F2) and four male (M1-M4) colonies sampled on 7 July, 1987. Asterisks indicate significant differences in mean oocyte size between fragment and parent colony.

Colony #	Fragment #	Fragment size (g)	Stage of Gamete Development: Mean oocyte size (um)	Standard deviation	t-test * = p<0.05
F1		Parent	228	17.89	
	A	3.92	200	14.14	3.499*
	B	7.11	208	10.95	2.499
	C	7.61	212	17.88	1.949
	D	61.31	216	8.94	1.499
	E	86.51	232	10.95	0.499
	F	100.00	216	16.73	1.499
F2		Parent	232	27.13	
	A	7.52	212	17.89	1.648
	B	7.60	188	10.95	3.626*
	C	11.41	220	21.91	0.989
	D	25.58	220	14.14	0.989
	E	37.38	216	8.94	1.318
M1		Parent	1		
	A	3.63	4		
	B	4.68	4		
	C	5.81	4		
	D	11.67	4		
	E	21.83	4		
M2		Parent	1		
	A	7.94	4		
	B	12.74	1		
	C	38.45	1		
	D	126.50	1		
	E	140.62	1		
M3		Parent	1		
	A	12.83	4		
	B	13.65	3		
	C	19.68	4		
	D	42.27	1		
	E	67.57	1		
	F	122.01	1		
M4		Parent	1		
	A	3.66	5		
	B	4.10	2		
	C	6.67	4		
	D	24.67	2		
	E	33.44	4		
	F	106.71	1		

Stage of Spermatozoa:

1= Actively swimming
2= Condensed heads, tails visible not swimming
3= Heads not condensed tails visible
4= Heads not condensed tails not visible
5= No testes developed

TABLE 3.5. Life history characteristics of sexual and asexual propagules of eight species of Porites. Sources: a. Kojis and Quinn, (1981) Australia (GBR), b. Hunter, this study, Hawaii, c. Harriott (1983), Australia (GBR), d. Tomascik and Sander (1987), Barbados, e. Szmant (1986), Puerto Rico, f. Chornesky and Peters (1987), Jamaica.

	Mode of Reproduction	Size of Propagule	Number per 10 cm^2 colony/ per event	Frequency (peak)	Dispersal Potential	Mortality Rate of Propagules
P. andrewsi a	Sexual (eggs)	231 um	—	Annual (Feb.)	Broad	High
P. compressa b	Sexual (eggs) ,	254 um	215,000	Annual (Jun-Aug.)	Broad	High
P. australensis c	Sexual (eggs)	150 um	216,000	Annual (Oct.-Jan.)	Broad	High
P. lobata a	Sexual (eggs)	338 um	—	Annual (Dec.)	Broad	High
P. lutea a,c	Sexual (eggs)	297 um	216,000	Annual (Jan.-Feb.)	Broad	High
P. porites d	Sexual (planulae)	500-800 um	1200	Continuous (Nov.-Apr.)	Broad	Moderate
P. astreoides e,f	Sexual (planulae)	1000 um	50,000	Continuous (April)	Broad	Moderate
P. murrayensis a	Sexual (planulae)	401-872 um	—	Continuous (Nov.-Apr.)	Broad	Moderate
P. compressa b	Asexual (fragments)	X=9.09 cm^2 1.5-151 cm^2	1-6	Continuous (May-July)	Local (up to 90 m)	?

TABLE 3.6. Post-recruitment life history characteristics for eight species of Porites. Sources: a. Kojis and Quinn, (1981) Australia (GBR), b. Hunter, this study, Hawaii, c. Harriott (1983), Australia (GBR), d. Tomascik and Sander (1987), Barbados, e. Szmant (1986), Puerto Rico, f. Chornesky and Peters (1987), Jamaica.

	Mode of Reproduction	Juvenile Recruitment Rate	Adult Colony Size	Life Expectancy	Colony Growth Form	Propensity for Fragmentation
P. andrewsi d	Broadcast	Low	Large	Long	Branching	High
P. compressa f	Broadcast	Low	Large	Long	Branching	High
P. australensis e	Broadcast	Low	Large	Long	Encrusting/ Massive	Moderate
P. lobata d	Broadcast	Low	Large	Long	Encrusting/ Massive	Moderate
P. lutea d,e	Broadcast	Low	Large	Long	Encrusting/ Massive	Moderate
P. porites a	Brood	High	Large	Long	Branching	High
P. astreoides b,c	Brood	High	Small	Short	Encrusting/ Massive	Low
P. murrayensis d	Brood	High	Small	Short	Encrusting/ Massive	Low

CHAPTER 4

CORRELATES OF CLONAL FITNESS IN A SCLERACTINIAN CORAL, *PORITES COMPRESSA*

INTRODUCTION

Two alternative models can be invoked to explain patterns of clonal dominance in asexually reproducing species. The null model predicts that random physical processes account for the preponderance of a few clonal groups after many generations of sexual and asexual reproduction. In support of this hypothesis, Neigel and Avise (1983) found that the structure of two Caribbean populations of the coral *Acropora cervicornis* could be described simply by demographic and historical factors without assumptions of differential fitness or mortality among clonal genotypes.

A second, deterministic model is suggested by documentation of competition among clones (Ayre, 1983; Rinkovich and Loya, 1983; Hidaka and Yamazoto, 1984; Aarssen and Turkington, 1985b; Willis and Ayre, 1985). Locally superior genets may, with time, acquire limiting resources (such as space for sessile organisms) to the exclusion of less fit genets. This process can be visualized as proceeding from an ecologically "young" population in which all new recruits are derived from sexually-produced dispersive propagules which are genetically unique, to a more "mature" population in which asexual replication and competitive superiority of some locally adapted genets leads to dominance of a few clonal types (Williams, 1975; Sebens and Thorpe, 1985). Young and old populations will then differ in their overall

genetic variability due to differences in the relative contributions of sexual and asexual reproduction and the relative competitive abilities of each genet. Evidence in support of the deterministic model is the demonstration that the most dominant clones in a population are those with the highest local fitness.

Spatial and numerical dominance of clonal types have been documented for a patchreef population of the endemic Hawaiian coral, Porites compressa in northern Kaneohe Bay, Oahu, Hawaii (Hunter and Kehoe, 1985; Hunter, 1985; Chapters 2,5). This chapter addresses the assessment of relative clonal fitness in comparison to clonal abundance and distribution within a population in order to test the null and adaptive models of clonal population structure. The parameters chosen for estimation of fitness among clones were propensity for asexual reproduction by fragmentation (skeletal density, branch breaking force), whole colony and fragment growth rates, and whole colony and fragment competitive abilities. It has already been shown (Chapter 3) that no significant differences could be detected in the ability of clones to produce fragments.

Growth rate and competitive ability are fitness attributes which may affect clonal ability to acquire and maintain space on a reef where space is limiting. Clones that grow fastest are predicted to be spatially dominant in that they have the potential to spread over a greater area than slower growing clones. Competitive ability, although it may be correlated with or a partial consequence of growth rate in corals, is defined as the aggressiveness of colonies in inter-clonal contact (Rinkevich and Loya, 1983; Hidaka and Yamazato, 1984). In the

present study, growth and competitive ability of dominant and rare clones of Porites compressa were measured in experimental "common garden" arrays in two habitats (windward and leeward sites on a reef), as well as in situ.

MATERIALS AND METHODS

The study area was a patchreef (#43; Roy, 1970) in northern Kaneohe Bay. It was observed that colonies of Porites compressa on the windward (northeast) side of the reef were often very large (>4 m in diameter) and clones generally had few ramets, while leeward (southwest) colonies were generally smaller (< 1 m diameter) but clones were often composed of numerous ramets. The relative fitness of spatially or numerically abundant clones was compared to that of rare clones within and between two sites.

Eight clones were identified based on morphological, electrophoretic, and tissue-grafting assays (Chapter 2) and classified as rare (represented by a single clone within the study area) or abundant (>10 colonies/20 m^2 or colony size >4 m^2). Four clones (I, L, M, and O) were from the windward side of the reef and four (5, 6, 8, and 24) were from the leeward side. Clones 8 and O were rare, all others were numerically or spatially dominant.

Replication within common garden arrays allows both comparison of interactions among clones under identical environmental conditions and assessment of local fitness within clones growing in two different habitats. Ten branches were removed from each of the four windward and four leeward "parent" colonies. All branches were taken from the

center of parent colonies to avoid the potential effects of differential growth rates in various areas within a colony. The base of each branch was ground on an electric sander until smooth and flat. A 3 mm diameter hole was drilled into the base of each "nubbin", into which a 2 cm long peg of plexiglass rod was inserted. Each nubbin was then mounted on a 5 x 5 cm square plexiglass tile with a hole in the center through which the peg fit snugly, holding the nubbin in an upright position. Each tile was then affixed by two shorter pegs to a plastic array frame so that the edges of each tile were flush against the edges of adjacent tiles. Two frames of twenty nubbins (four rows of five) made up each experimental set (eight clones with five replicates each). Nubbins were arranged so that representatives of each clone were adjacent to every other clone at least twice within each set. Both sets were placed on the top of Patchreef #43 at approximately 3 m depth. One set was placed on the windward side and the other on the leeward side of the reef on 4 September, 1985.

Clones of Porites compressa have different branch morphologies (e.g., narrow vs. wide, short vs. long) and branches will therefore have various length:weight ratios. Measurement of linear extension does not take into account the extent of growth in all dimensions. Changes in overall branch weight may provide a better estimate of total growth, but it is unfeasible to measure weight of branches growing in situ. Therefore, growth of clones in the common garden arrays was measured as both change in buoyant weight (Jokiel, et al., 1978) and linear skeletal extension (Lamberts, 1978); linear extension rates only were used for in situ growth estimates.

Every three months for one year, the common garden arrays were retrieved from the field and returned to the laboratory in large tubs. Nubbins were weighed on a tray suspended from a balance so that the tray and coral sample were totally immersed in seawater. Before returning them to the field, each array was placed in a seawater table containg 20 ppm alizarin red dye for 8-12 h. Incorporation of the pink stain into the skeletons marked the outer skeletal surface of nubbins at each sampling date, allowing sequential measurements of linear skeletal deposition at the end of the experiment. Nubbin growth rates were calculated both as the percent change in mean buoyant weight and linear skeletal extension per three month period. Percent change rather than absolute size was used for comparisons to minimize any bias due to initial size differences among nubbins. Statistical differences in per cent increase in size within and between clones and sites were determined by analysis of variance (ANOVA), Tukey's studentized range tests, linear regression, and Kruskal-Wallis non-parametric one-way tests (SAS Institute, Release 5.18, Univ. of Hawaii Computer Center).

In situ growth rates were measured for the eight clones described above. Five branches on a colony of each clone were covered with large plastic bags secured at the openings with rubberbands. A vial of concentrated, pre-mixed alizarin dye was opened within each bag and the resulting seawater-dye solution mixed by gentle agitation of the bag. Bags were left on the coral colonies for 18-24 h. Stained branches were marked with vinyl-coated wire and collected for measurement of skeletal deposition after 120, 144, and 160 days.

Clonal competitive ability was assessed in the common garden

arrays at the end of one year by scoring the number of "wins", "losses", and "ties" in each between-clone contact. "Wins" (and reciprocal "losses") were scored when the tip or base of a nubbin overgrew any part of the tissue of an adjacent clone. "Ties" (=stand-offs) were recorded when tissues of two clones grew into contact but neither clone over-grew the other.

Few scorable inter-clonal contacts were found among the *in situ* windward clones. Therefore, analysis of competitive ability of whole colonies was done for leeward clones only. Colonies of each clone (with the exception of Clone 8) were numerous within a 20 m^2 leeward transect (Hunter and Kehoe, 1985). Areas of inter-clonal contact were searched and all observed interactions were recorded. "Wins", "losses", and "ties" were scored for inter-colony contacts between the four leeward clones used in the common garden arrays (#5, 6, 8, and 24) and four additional clones (#3, 4, 7, and 9) identified within the 20 m^2 transect using the same criteria for scoring as in the common garden arrays.

RESULTS

CLONAL GROWTH RATES

After three months, nubbins in the common garden arrays had grown in both length and width, with their bases spreading over the plexi-glass tiles. The relative amount of upward and lateral growth differed among clones. Nubbins began to ramify and to show distinct clonal morphologies (color, branch size, branching pattern) after about six months, implying a genetic basis for colony form.

Mean buoyant weight of nubbins in the common garden experiment increased by 50.8% in the first three month period (September-December) (Table 4.1). Growth of all clones slowed dramatically between December and March, with a mean increase in size of only 25.6%. Average growth rates of 55.8% (March-June) and 41.4% (June-September) brought the 12-month total mean increase in size to 173.65% for nubbins of all clones.

Over all clones in both sites, mean initial nubbin size of Clone M was significantly larger than for the other seven clones (ANOVA, $p=0.012$; Tukey's studentized range test). Initial nubbin sizes were not different within sites, between sites, or among clones between sites (ANOVA, $p>0.05$). There were significant differences among clones in mean percent increase in buoyant weight only at the three and six month censuses (Table 4.2a). After three months, Clone L nubbins had grown significantly faster than those from Clones 6, I, and 8; all other comparisons were non-significant. Clone L again grew faster than Clone 8 after 6 months. There were no correlations between growth rate and initial size (F-test, $p>0.05$) for any census period.

At the windward site, differences in mean growth rates of nubbins first became apparent after six months (Table 4.2b), with Clones O, L, and M growing gaster than Clones 6, I, and 8. However, after 12 months, only Clone M nubbins grew significantly faster than those of other clones (Clones M > 5, 6, 8, 24, and I). Significant differences in nubbin growth rate were found (Clone L > Clones 6 and 8) at the leeward site only at three and six month censuses.

There were no significant differences between sites in overall growth rate in any of the census periods (t-tests, $p<0.001$). Within

most clones, however, nubbins grew at significantly different rates (indicated by asterisks in Table 4.2a) between the windward and leeward sites. Nubbins in the windward array always grew slower, suggesting that large colony size on the windward reef may be due more to differences in local fitness of clones than to differences in habitat quality between the windward and leeward sites. The dominance of Clones M, L, and O in the growth rate hierarchies at both sites supports this finding.

Mean linear skeletal extension rates of nubbins ranged from 0.70 ± 0.11 cm/year (Clone O) to 1.86 ± 0.10 cm/year (Clone 5) in the common garden arrays (Table 4.3a). Linear growth was 2.7-4.6 times faster for in situ branches (Table 4.3a), ranging from 2.58 ± 0.47 cm/year (Clone 6) to 3.54 cm/year (single branch from Clone 8). In addition, hierarchies of relative growth rates based on in situ linear growth, and common garden buoyant weight and linear growth were substantially different, particularly for Clones 8, I, and O. Differences between relative growth in the common garden nubbins as measured by the two different methods may be due to the different branch morphologies of these clones. Clone 8 has thin, widely spaced branches, and linear extension would be expected to be greater than growth measured by change in weight. Conversely, Clones O and I have thicker and more closely spaced branches, so growth tends to be more massive and less linear.

Differences between linear growth of nubbins in the common garden arrays and branches on colonies in situ may be related to the relative local fitness of clones. Clone 8 had rapid linear growth but slow

increase in weight in the experimental arrays. It is a rare clone (no clonemates were found on the reef) and its competitive ranking is low (see next section). Clones O and I have more massive growth morphologies and grew slower in the common garden array than in situ. Clone I had the lowest percent increase in buoyant weight and is a poor competitor in inter-clonal encounters. Clone O increased more rapidly in buoyant weight and was high in the competitive rankings.

CLONAL COMPETITIVE ABILITY

After one year, 12 nubbins had been lost from the leeward arrays, and 11 from the windward (28.8% attrition). Of the remaining 76 potential between-clone contacts within the two experimental sets only 33 interactions could be scored, and 32 of these were from the leeward treatment. Because growth was much slower at the windward site, nubbins often did not come into contact with other clones on the arrays. This set was left on the reef for an additional three month interval, but vandalism precluded further analysis.

Within the 32 scored interactions, 30 were win-loss pairs and 2 pairs were ties (Table 4.4). Clone O was dominant or tied in all scored interactions (n=9), while Clone 8 was always out-competed (n=4). The competitive hierarchy among clones (L > O > 5 > M > I > 6 > 24 > 8) is statistically different (Spearman's rank correlation, $p<0.05$, Snedecor, 1956) from the rankings of relative growth rates (L > M > 5 > O > 24 > I > 8 > 6). It appears that clones that cover space fastest may not necessarilly be competitively superior in all inter-clonal contacts.

Examination of the leeward arrays suggested that inter-clone contact was avoided in many instances by growth being directed away from the adjacent clone. Often in the leeward arrays, where growth after 12 months caused crowding, nubbins of adjacent clones were observed to grow in such a way as to produce an inter-woven "canopy" much like those of trees in a forest. However, some clones (L and O, particularly), appeared to be more "aggressive" as evidenced by their growth morphology at points of contact with other clones. At these points, either the spreading bases of "aggressive" nubbins would be raised up and over the base of the "losing" clone or "winning" nubbin tips would begin to encircle the loser's nubbin.

The relative rankings of the four clones (5, 6, 8, and 24) scored in in situ competitive interactions (Table 4.5) were identical to their relative positions in the common garden hierarchies (Table 4.4). In situ competitive ability is strongly correlated with spatial and numerical abundances of clones within the 20 m^2 transect. The four most dominant competitors together make up 43.0% of the total areal coverage of the 20 m^2; the four least dominant clones make up a total of 18.9%. The most competitive clones also have moderate to high skeletal densities indicating a moderate to low propensity for fragmentation. However, Clones 3 and 7 (both poor competitors) have extremely low skeletal densities making them susceptible to fragmentation, but Clone 3 is abundant while Clone 7 is not. Growth rates of these clones were not determined, but it is possible that this or other fitness components could account for the disparity in their relative abundances. Clone 8 is a slow grower, poor competitor, poor frag-

menter, and poorly represented either in number of colonies or areal coverage.

DISCUSSION

Results of this study support the potential for a deterministic role of clonal fitness in structuring populations of the scleractinian coral, Porites compressa. Clones showed significant differences in growth rate and competitive ability, both in experimental common garden arrays and in situ. The three spatially dominant clones from the windward side of the reef grew faster (as measured by percent increase in weight) than leeward clones and were high in the competitve hierarchy; the small (rare) windward clone had the slowest growth rates and moderate competitve abilities. In situ competitive interactions reflected clonal fitness as represented by colony abundance: the most competitively dominant leeward clones were also the most abundant in number and areal coverage.

Relative growth rates and competitive hierarchies differed substantially between nubbins in the common garden arrays and whole colonies in situ. It appears that physiologically isolated branches may undergo a change in competitive status and growth rate as fragments, at least until they reattach as successful clonal propagules. This is similar to results (Chapter 3) which indicate that small fragments exhibit reduced fecundity when compared to whole colonies of the same clone.

Measures of percent increase in buoyant weight and linear growth produced different relative growth rate hierarchies. The clone with fastest linear growth in the common garden arrays (Clone 8), had very low percent increase in buoyant weight; the converse was true for Clone O. Acquisition of space on the reef may be more dependent on lateral spread than upward growth of colonies. For branching species, growth rates based on buoyant weight, which measures actual colony mass and therefore ability to occupy space, are probably better indicators of relative fitness than those based on linear extension.

Assessment of competitive ability based on aggressive interactions is problematical in this species. In situ, branches of colonies rarely are in contact, presumably due to growth being directed away from potential competitors. Observable borders between colonies that do come into contact are usually characterized by a zone of necrotic tissue approximately 2-5 mm wide, but it is often not possible at any one moment in time to determine which colony (if either) is "winning". Interactions in which one branch of Porites compressa can be found actually in the process of overgrowing another are rare, but may be important indicators of clonal competitive ability.

Fitness components other than growth and competitive ability may also prove to be important in the relative success of clones in coral populations. Propensity for fragmentation did not differ significantly among the clones tested (Chapter 3) and does not appear to be an attribute of clonal fitness in this species. However, the survivorship of fragments from individual clones was not addressed and could potentially be an important factor in the relative success of asexual clonal

propagation. Branch morphology (as it affects fragment survival), sexual fecundity, age to first reproduction, mortality rates, and physiological tolerances may all affect overall clonal fitness.

The null model, that clonal abundances and distributions are due to random physical processes, cannot be disproved. Random processes may play an important role in generating fragments and in opening up space for new recruitment of either sexual or asexual propagules, particularly in habitats where frequent disturbance causes arbitrary or wide-scale removal of clones. Degrees of clonality among populations with different disturbance histories are assessed in Chapter 5.

TABLE 4.1. Initial size and mean cumulative ratio of buoyant weight:initial size per census period for eight clones of Porites compressa in common garden arrays. Standard deviations are given in second row for each clone. Sample sizes for each census are shown in parentheses.

Clone:	Initial Weight (g)	3 Months	6 Months	9 Months	12 Months
5	3.71	.537	1.143	2.838	4.702
		.119	.402	.100	1.856
	(10)	(9)	(9)	(9)	(9)
6	3.94	.447	1.095	2.262	3.663
		.090	.215	.410	.656
	(10)	(9)	(9)	(8)	(8)
8	2.47	.418	1.019	2.331	3.654
		.135	.301	1.249	1.347
	(10)	(8)	(8)	(8)	(7)
24	3.83	.472	1.166	2.479	3.821
		.103	.332	.826	1.218
	(10)	(7)	(7)	(6)	(5)
I	3.44	.438	1.056	2.101	3.404
		.151	.315	.649	1.125
	(10)	(8)	(8)	(8)	(7)
L	3.60	.638	1.552	3.079	5.109
		.141	.406	.850	1.356
	(10)	(8)	(8)	(7)	(7)
M	5.74	.525	1.361	2.864	5.641
		.124	.386	.800	1.499
	(10)	(8)	(8)	(7)	(6)
O	4.16	.590	1.460	2.978	4.798
		.085	.259	.718	1.526
	(10)	(8)	(8)	(8)	(8)

TABLE 4.2. Hierarchies of initial size and percent increase in buoyant mass per quarter for eight clones of Porites compressa in common garden arrays. Clones are ranked in decreasing rate of growth. Lines connect clones which are not significantly different (Tukey's studentized range test). a. Overall hierarchies at both sites. Asterisks indicate significant differences (Kruskal Wallis, $p<0.05$) between growth rates at windward and leeward sites within clones. b. Hierarchies within sites. WA = windward array, LA= leeward array.

a.

Initial Size	Relative rankings in percent increase in size after: 3 months	6 months	9 months	12 months
M	* L	* L	* L	M
O	O	* O	* O	* L
6	* 5	* 5	M	O
24	M	M	* 5	* 5
5	24	* 24	* 24	24
L	* 6	* 6	8	* 6
I	* I	* I	* 6	8
8	8	* 8	* I	I

b.

Initial		3 months		6 months		9 months		12 months	
WA	LA	WA	LA	WA	LA	WA	LA	WA	LA
M	M	O	L	O	L	M	L	M	L
O	O	L	O	L	5	O	5	O	M
6	6	M	5	M	O	L	O	L	5
24	24	5	M	5	M	5	24	5	O
5	5	24	24	24	24	6	8	24	24
I	L	6	I	6	I	24	M	6	I
L	I	I	6	I	6	I	I	8	8
8	8	8	8	8	8	8	6	I	6

TABLE 4.3. a. Mean linear growth (cm/year) in eight clones of *Porites compressa*. Common garden samples were from individual nubbins after one year. *In situ* observations were from whole colonies stained in the field and collected after 120-206 days. b. Relative rankings of growth rate based on buoyant weight and linear extension in common garden arrays and *in situ*.

a.

Clone:	5	6	8	24	I	L	M	O	Overall Mean
Common Garden:									
Mean	1.857	0.757	0.940	0.800	0.750	0.783	0.817	0.700	0.926
s.d.	0.099	0.118	0.393	0.093	0.071	0.114	0.177	0.112	0.383
N	9	8	7	5	7	7	6	8	
In Situ:									
Mean	3.077	2.575	2.583	3.540	3.480	3.023	3.536	3.137	3.119
s.d.	0.435	0.471	0.701	—	0.357	0.561	0.367	0.548	0.392
N	12	7	9	1	3	12	10	9	

b.

Common Garden		*In Situ*
Buoyant Weight	Linear Growth	Linear Growth
M	8	24
L	M	M
O	24	I
5	L	O
24	5	5
6	6	L
8	I	8
I	O	6

TABLE 4.4. Win:loss records of competitive interactions among eight clones of Porites compressa in leeward common garden arrays. Clones are listed in order of their relative competitive rankings. Columns show number of wins/number of losses; rows show (reciprocal) number of losses/number of wins for each clone.

Clones:	L	O	5	M	I	6	24	8
L		1/0	1/2	0/2	0/1	0/2	0/1	0/1
O	0/1		0/2	=	0/2	0/2	0/1	=
5	2/1	2/0		0/2	0/2	=	0/1	---
M	2/0	=	2/0		0/1	0/2	---	0/1
I	1/0	2/0	2/0	1/0		---	0/1	---
6	2/0	2/0	=	2/0	---		---	0/1
24	1/0	1/0	1/0	---	1/0	---		0/1
8	1/0	=	---	1/0	---	1/0	1/0	

									Total:
Wins:	9	8	5	4	2	1	1	0	30
Losses:	2	0	4	4	6	6	4	4	30
Ties:	0	1	1	1	0	1	0	0	4
Interactions Scored:	11	9	10	9	8	8	5	4	64

TABLE 4.5. Win:loss records of *in situ* competitive interactions among eight clones of *Porites compressa* within a 20 m^2 transect on the leeward side of Patchreef #43 in Kaneohe Bay. Clones are listed in order of their relative competitive rankings. Columns show number of wins/number of losses; rows show (reciprocal) number of losses/number of wins for each clone. Scores for Clone 8 are in parentheses because interactions were with unidentified clones.

Clones:	5	9	6	4	24	3	7	8	
5		0/3	0/2	0/2	2/1	0/1	0/1	---	
9	3/0		1/1	2/2	0/1	0/1	0/1	---	
6	2/0	1/1		1/0	1/1	1/0	---	---	
4	2/0	2/2	0/1		1/0	0/1	---	---	
24	1/2	1/0	1/1	0/1		2/0	---	---	
3	1/0	1/0	0/1	1/0	0/2		---	---	
7	1/0	1/1	---	---	---	---	---	---	
									Total:
Wins:	7	5	3	3	3	2	0	(0)	23
Losses:	1	1	1	3	3	4	6	(4)	23
Ties:	0	0	2	1	1	0	0	(0)	4
Interactions Scored:	8	6	6	7	7	6	6	(4)	50
Percent cover within 20 m^2	7.1	15.5	13.0	7.4	4.1	11.8	1.7	1.3	61.9
Number of colonies within 20 m^2	7	38	31	15	7	22	7	1	138
Skeletal density (g/l)	1.54	1.39	1.42	1.77	1.30	1.10	1.10	1.83	

CHAPTER 5

GENOTYPIC VARIATION AND CLONAL STRUCTURE IN HAWAIIAN *PORITES COMPRESSA* POPULATIONS WITH DIFFERENT DISTURBANCE HISTORIES

INTRODUCTION

The potential for the production of asexual propagules by fragmentation in scleractinian corals been well documented in the past few years (Highsmith, 1980, 1982; Tunnicliffe, 1981; Bak and Criens, 1982; Bothwell, 1982; Kobayashi, 1984; Wallace, 1985; Willis and Ayre, 1985; Ayre and Willis, in press). Highsmith (1982) suggested that fragmentation of established colonies followed by recruitment of these clonal fragments would lead to considerably fewer genotypes than actual colonies on a reef. For populations of long-lived corals, Potts (1985) proposed that the persistence of a small number of successful clonal genotypes may place an evolutionary "drag" on speciation rates. Tests of these and other hypotheses concerning genetic variation and evolutionary relationships, as well as estimates of important life history parameters (e.g genet longevity and fecundity), rely on the precise identification of individual genotypes and their distributions in clonal populations.

Analysis of genetic structure of clonal populations presents three major methodological difficulties. First, assays used for identifying and distinguishing individuals must be sensitive enough to clearly resolve all genotypes sampled. Second, sampling of populations must be

sufficient in intensity and scale to allow detection of the presence and distribution of clonal replicates as well as unique genotypes. Third, most genetic analyses provide an estimate of genotypic diversity at only one moment in time; for long-lived species, sampling of populations at different successional stages or under various environmental regimes may provide a more complete description of the temporal characteristics of clonal population structure.

Several types of assays have been utilized to identify clonal structure in coral populations. Tissue grafting techniques were employed to detect clonal population structure in Montipora spp. (Jokiel, et al., 1983) and Acropora cervicornis (Neigel and Avise, 1983). However, later work by Heyward and Stoddart (1985), Resing and Ayre (1985), and Stoddart, et al. (1985) cautioned against the exclusive use of tissue grafting to determine clonal identity in corals because some colonies which fuse in grafts have been demonstrated to have different electrophoretic banding patterns.

Stoddart (1984a) identified clonal genotypes in populations of Pocillopora damicornis based on electrophoretic analysis of four loci (13 alleles) and found that diversity was approximately half of that expected for an exclusively sexually reproducing species. However, he was not able to evaluate the power of this multi-locus system to resolve all genotypes and suggested that the number of genets may have been underestimated.

Electrophoretic data were used in conjunction with morphotypic and histocompatibility assays to provide evidence of clonality and spatial clustering of genotypically identical colonies in Pavona cactus (Willis

and Ayre, 1985; Ayre and Willis, in press) and Porites compressa (Hunter, 1985; Chapter 2). Morphotypic assessment of intra-specific diversity in corals is confounded by phenotypic variation in some species, and by the inherent problems of quantifying the full range of individual morphological variation among genotypes. Similarly, effort involved in field work and time required for development of scorable results in histocompatibility testing limit the number of colonies which can be assayed, particularly in remote sites, areas which may be vandalized, or habitats which are accessible only at restricted times of the year.

For the present study, electrophoresis was chosen as the method which would allow analysis of a large number of colonies in a variety of habitats. The power of the multi-locus assay to resolve all genotypes sampled was tested by an electrophoretic survey of an aclonal "population" consisting of individuals all of which were known to have been derived from sexually produced larvae and were therefore assumed to be genetically distinct.

Sampling of clonal diversity in coral populations has been done either by random linear transecting (Stoddart, 1983a, 1984a,b; Willis and Ayre, 1985; Ayre and Willis, in press) or by arbitrary selection of colonies (Jokiel et al., 1983; Neigel and Avise, 1983). Random linear transects can provide good estimates of overall genetic diversity but cannot elucidate two-dimensional clonal distributions; arbitrary or haphazard sampling may detect common clones but will overestimate clonality if rare or small colonies have less chance of being sampled. A nested quadrate method designed to assess diversity in clonal plants

(Greig Smith, 1979) was modified for use in this study because of its utility in sampling both total genetic diversity and spatial distributions of clones in coral populations.

Intermediate levels of disturbance and non-equilibrium conditions have been proposed to create maximal species diversity in space-limited communities (Levin and Paine, 1974; Levin, 1976; Connell, 1978). Studies of species diversity in coral reef communities have supported the "intermediate disturbance" hypotheses (Grigg and Maragos, 1974; Dollar, 1982). Sebens and Thorpe (1985) modelled the effects of disturbance on genetic diversity in populations of species with sexual and asexual reproduction and predicted that intermediate disturbance or non-equilibrium situations will promote the highest levels of clonal diversity. In their model, Sebens and Thorpe (1985) equate low numbers of individuals (the result of high disturbance levels) with low genetic diversity. However, time since the last disturbance (reflected by the number of individuals which have been recruited) and spatial scale over which diversity is sampled (density of recruits) will affect assessment of overall genetic diversity within a population.

The hypothesis that was tested in the present study is that genetic diversity will be inversely related to environmental stability in the reef coral, Porites compressa, one of the most abundant scleractinian species in Hawaii. It occurs in a variety of habitats on all islands in the Hawaiian chain and often forms extensive monospecific stands. Cover frequently approaches 100% on the periphery and slope of reefs in Kaneohe Bay, Oahu and the west coast of the island of Hawaii (Maragos, 1972; Dollar, 1982). This dioecious species reproduces

sexually by broadcast spawning of eggs and sperm at full moon during summer (Chapter 3). Asexual propagules are produced continuously throughout the year by fragmentation (Chapter 3). In stable habitats, where unoccupied substratum is at a minimum, the opportunity for new recruitment of sexually derived individuals is spatially and temporally limited and locally adapted genotypes may become dominant. Populations such as these will be almost wholly structured by the processes of clonal replication and competition among clones, and genotypic diversity is predicted to be low. Populations in highly disturbed habitats are predicted to be composed primarily of sexually-derived recruits with a resultant high genotypic variability. In situations where periodic disturbances open new areas of bare substratum, opportunity exists for both new sexual recruits and storm-generated fragments to make inroads into the community. Here, diversity is predicted to be intermediate.

MATERIALS AND METHODS

STUDY SITES

Sampling was conducted within six populations, five on Oahu and one on the island of Hawaii (Figure 5.1). Criteria used to classify successional age and habitat stability in these populations are presented in Table 5.1.

Population NKB (North Kaneohe Bay) is a patch reef (#43; Roy, 1970), approximately 100 m X 200 m in size, in Kaneohe Bay on the windward coast of Oahu. This reef is characteristic of a physically

stable habitat, with low levels of environmental disturbance in the last 8000-12000 years since the formation of patchreefs in Kaneohe Bay (Roy, 1970). Coral cover approaches 95% on the reef top and slope and colonies of >4 m in diameter are common. Wave energy is low as reefs within the bay are protected from ocean swells by an extensive barrier system. The study reef, by virtue of its depth (>1 m at lowest tides) and distance from shore, is also relatively unaffected by freshwater flooding, an important periodic event in other areas of the bay (Banner, 1968; Hunter, unpubl.).

Population SKB (South Kaneohe Bay) is in the south basin of Kaneohe Bay, approximately 10 km from the NKB site. The top of this reef was dredged to a depth of approximately 3.3 m in the early 1940's for a seaplane runway (Roy, 1970). The south basin was also severely impacted by a major sewage outfall from the 1940's until 1978. During the period of sewage input, the benthic communities came to be dominated by filter-feeders, principally barnacles, sponges, and bivalves. Almost no corals were living in this area at the time of the diversion of the sewage outfall in 1978 (Smith et al., 1981); since that time a gradual 'recovery' of the bay has taken place (Maragos, et al., 1985). Most of the hard bottom is still bare space with small colonies of Porites compressa, Montipora verrucosa, and Pocillopora damicornis scattered over the substratum. Most colonies are small (<0.25 m diameter), and few have grown to an extent that they are in intra- or interspecific contact with other colonies. This site represents a very early stage in the successional progression back to the coral dominated communities that existed throughout the calm waters of Kaneohe Bay

prior to the 1940's (Smith, et al., 1973).

The MOS (Marv's Offshore Site) population is located on the outer barrier reef slope of Kaneohe Bay at a depth of approximately 15 m. This site is approximately 3 km from the NKB population and 7 km from the SKB site. Coral cover is less than 20% and is concentrated primarily in areas adjacent to ledges or other topographic features which may act to provide shelter from wave energy of winter storms and surge. Sizes of Porites compressa colonies are small (<0.25 m diameter) or intermediate (<1.0 m diameter).

Population LAN (Lanikai) is in the shallow (maximum depth < 3 m) lagoon of Kailua Bay, approximately 10 km south of Kaneohe Bay. Mokapu Peninsula separates the two bays. The fringing reef extends 1.25 km from shore, producing calm sea conditions, but there is considerable human impact (primarily boat anchoring, fishing, and sport diving) which may affect coral fragmentation rates. Porites compressa, P. lobata, P. evermanni, Montipora patula, and M. flabellata are the dominant species at this site, and there is a mixture of colony sizes from small to large (up to 3 m in maximum diameter).

Population BIK (Big Island, Kona) is in Kealakekua Bay, on the Kona coast of the island of Hawaii, at a depth of 15 m. This site was described by Dollar (1982) who reported that periodic storms caused extensive damage to the monospecific stands of P. compressa characteristic of this community. Fragmentation events occur as the result of such storms at least once every winter, although the intensity of storms varies greatly from year to year. Colony growth form in this population is thicket-like rather than the more compact

and discrete colonies found on Oahu, making colony size difficult to measure accurately. Coral cover of the substratum is high (>80%), but live tissue is restricted mainly to branch tips. The bases of branches are bare or covered by encrusting bryozoans, sponges, or tunicates.

The CI "population" (Coconut Island) consists of colonies growing on the vertical surface of a 30 m section of seawall on the southeast side of Coconut Island in south Kaneohe Bay, about 0.75 km from Population SKB. This population was selected to represent one in which all colonies were believed to be of sexual (planular) origin. This conclusion was based on the assumption that fragments could not lodge on the smooth vertical concrete face of the seawall.

SAMPLING

Samples of forty-five colonies each from the NKB, SKB, LAN, and BIK populations were collected following a nested quadrate sampling design (Figure 5.2a) modified from Greig Smith (1979). This sampling regime was chosen to enable an analysis of both fine-scale and large scale genetic variability in clonal populations, as well as to estimate the spatial scale of genet (clonal) distribution. Nested-quadrate sampling eliminates bias that would result from fixed-size quadrates which define the spatial scale over which clones can be detected. Sizes of the initial and final quadrates were determined from "sampling" a map of a 2 x 10 m area of the NKB patchreef (Hunter and Kehoe, 1985). The result of replicated random samples from this map of known clonal distributions are shown in Figure 5.2b. The index of diversity (D* = number of unique genotypes/number of colonies "sampled") drops between

a quadrate size of 0.5 m^2 and 1.0 m^2, and then rises gradually to a maximum at 16 m^2 the largest quadrate size "sampled". The apparent increase in genotypic diversity at the smallest quadrate size is due to the fact that in quadrates that are of the same spatial scale as the larger coral colonies (about 0.5 m^2), sampling of a single large colony will constrain the remainder of the samples taken to the small remaining area. This, coupled with the observation that nearest neighbors are rarely of the same clonal group, leads to a bias toward higher genotypic diversity in the smallest quadrates. (The apparent over-dispersion of clonemates at this scale is the result of fusion of genetically identical colonies which have grown into physical contact and thus become a single colony.) In the largest quadrates ("sampled" only once due to the limited coverage of the map), genotypic diversity is high. However, because the sample size was small and since clonemates have been found >100 m apart on this reef (Hunter and Kehoe, 1985) larger quadrates were chosen to maximize the chance of sampling total population diversity. Therefore, 1 m^2 and 256 m^2, respectively, were chosen as the smallest and largest quadrates necessary to assess both clonal and total genetic diversity.

Random numbers (1-100, 101-400, 401-1600, 1601-6400, 6401-25,600) generated by a hand calculator were used to plot point-locations of colonies to be sampled on graph paper. Five nested quadrates of increasing size (1 m^2, 4 m^2, 16 m^2, 64 m^2, and 256 m^2) were fitted over the plot so that five points fell within each of the first three nested quadrates, and 15 additional points were distributed in each of the fourth and fifth quadrates. The plot was then transposed to field

populations where the initial (1 m^2) quadrate was haphazardly placed. The colony under or closest to each pre-determined point was sampled.

Coral cover at the LAN site was patchy, so 45 colonies were haphazardly sampled at a depth of 2 m from a belt transect from west to east extending from approximately 20 m to 110 m from shore. The CI samples were collected from each of the first 45 colonies (>10 cm minimum diameter) encountered along a 30 m section of seawall. Maximum length and width measurements were taken for colonies in the NKB, SKB, and CI populations; the MOS, LAN, and BIK populations had many colonies with dead or encrusted bases, making colony boundaries (and thus size) difficult to determine.

GENETIC ANALYSIS

Six to 10 branch tips were removed from each colony. For each sample, some branches were kept alive in flowing sea water and the remainder were frozen at -80° C until analyzed.

Electrophoresis

Multi-locus genotypes were determined electrophoretically for all corals sampled. A total of 133 colonies from three populations sampled in 1986 (NKB, SKB, and BIK) were analyzed for five enzyme systems. The 269 colonies from the six populations sampled in 1988 were scored for seven loci.

Tissue extracts were prepared from fresh or frozen branch tips which were first pulverized between layers of plastic wrap with pliers and then homogenized in a spotplate in an indicator-extractant solution

of 10.0 g sucrose, 25 mg NADP, 0.1 g bromophenol blue and 0.1 ml mercaptoethanol (Stoddart, 1983a). Samples were covered with squares of Kim-wipe tissue to minimize contact of filter paper (Whatman #3) wicks to mucus in the homogenate. Horizontal starch gels (Electrostarch, 11.4% wt/vol. for 1986 samples; Sigma, 12.0% wt/vol for 1988 samples) were loaded with homogenates and run at 5° C. Three buffer solutions were used: Lithium hydroxide (LIOH) for phosphoglucoisomerase (PGI), phosphoglucomutase (PGM), and esterase-B (EST-B); Tris-citrate (TC-II) for malic enzyme (ME) and 6-phosphogluconate dehydrogenase (6-GPDH); and Tris-borate-EDTA (TVB-1) for glutamate dehydrogenase (GDH), malate dehydrogenase (MDH), valyl-leucine peptidase, leucyl-glycyl-glycine peptidase, and leucyl-tyrosine peptidase (VL, LGG, and LTY). Buffers and stains were prepared following methods described by Selander, et al. (1971), Redfield and Salini (1980), and Potts (unpublished). Recipes for buffers and stains are given in Appendix 5A. The 1986 samples were analyzed for GDH, LTY-1, LTY-2, LGG, and EST-B; 1988 samples were scored for PGI, PGM, ME, GDH, MDH, VL, and 6-PGDH. EST-B, LTY and LGG stains gave smeary or inconsistent bands in the later assays, possibly due to the change of starch used in the gels.

Analysis of electrophoretic data

Allelic and genotypic frequencies were determined for each population. An estimation of the power of the seven loci assayed to differentiate unique genotypes was done in two ways using genotypic data from the CI "population" in which each colony was assumed to be

the result of planular settlement and therefore represent a genetically unique individual. First, I calculated genetic diversity as a function of the mean number of unique genotypes recognized by each locus individually, then with the sequential addition of all possible combinations of two, three, four, five, six, and seven loci. A plot of diversity vs. number of loci is given in Figure 5.3. Secondly, the ratio of unique genotypes (44) to the total n (45) for the CI population provided an index (2.2%) of the probability of assigning genetically different individuals to the same multi-locus genotype. The magnitude of clonal replication (number of ramets per genet) within each population was assessed by comparing the observed genotypic diversity with that expected for a population reproducing solely by sexual means. Clonal membership was defined as all colonies which shared the same seven-locus genotype. For a population in which every colony is unique (e.g., no clonal replication), genotypic frequencies should conform to Hardy-Weinberg equilibria under the assumptions of random mating, recombination, and no selection. Observed genotypic diversity was calculated as:

$$G_O = 1/\sum_{x=0}^{N} f_x \cdot (x/N)^2$$

where f_x is the number of genotypes observed x times and N is the total sample size of each population (Stoddart and Taylor, 1988). It is influenced by departure from Hardy-Weinberg equilibrium and linkage disequilibrium. G_O was compared to the genotypic diversity G_e ($\tilde{G}$) expected under Hardy-Weinberg equilibrium which was calculated from a

simple binomial expansion of the frequencies of genotype classes using a program provided by J. Stoddart (Stoddart and Taylor, 1988). Degree of departure of $G_o:G_e$ from unity provides an index of deviation from both H-W equilibria and multi-locus linkage equilibrium. A population dominated by a small number of clonal types will have low $G_o:G_e$ ratios. $G_o:G_e$ approaches 1.0 as genotypic individuality is maximized. Diversity was also calculated as:

D=number of unique genotypes/N

D varies between 0 and 1, with 1 indicating a population where all colonies are unique (Hoffmann, 1986). Deviations of observed from expected levels of heterozygosity for each locus were calculated as:

$$H_d = (H_o - H_e)/H_e$$

where H_o is the observed proportion of individuals heterozygous at a locus) and $H_e = 1 - \quad x_i^2)$ where x_i is the frequency of the i^{th} allele at that locus. Mean heterozygosity per individual was calculated as:

$$\overline{H}_i = (\sum H_j/\text{total number of loci})/N$$

where H_i is the number of loci for which each individual is heterozygous, and N is sample size for each population. Chi-squared analyses were used to determine departures from single-locus Hardy-Weinberg equilibria. Genetic similarity among populations was calculated using Nei's (1978) unbiased index of genetic identity (I) using both unique and total allele frequencies. A cluster analysis was performed using UPGMA (unweighted pair-group method using

arithmetic averages; Sokal and Sneath, 1973). Numerical abundance and spatial distribution of genets and ramets were determined for the NKB, SKB, MOS, and BIK populations.

RESULTS

Interpretations of banding patterns were consistent with multiple allele systems described for other diploid species (Hopkinson et al., 1976). Corals examined to date have shown diploid chromosome structure (Heyward, 1985). For each locus, alleles were labeled alphabetically in order of decreasing electrophoretic mobility (Figure 5.3). Inferred subunit structures of the enzymes assayed were: PGI, GDH, VL, and 6-PGDH (dimers), PGM and MDH (monomers), and ME (tetramer). A dimeric subunit structure has been assigned to MDH for most species examined to date (Hopkinson, et al., 1976) but, in this and another study on corals (Stoddart, 1985), MDH banding patterns have been interpreted to indicate that heterozygotes stain for two distinct bands instead of one.

The seven enzyme systems (total of 22 alleles) used in the 1988 analyses resolved all but one of the 45 genotypes assumed to be unique in the CI population. A plot of the cumulative number of resolved genotypes against sequential addition of all permutations of loci appears to reach an asymptote between the sixth and seventh loci (Figure 5.4), indicating that the electrophoretic analysis was sufficient to identify and distinguish between essentially all clones in Porites compressa populations.

Table 5.2 gives allelic frequencies based on the total sample size for each population analyzed in 1988. All loci were polymorphic at every locus assayed, with the exception of 6-PGDH which was fixed in the MOS and BIK populations. Since the seven loci examined were adequate to assign each sample to a distinct clonal genotype, allele frequencies were also calculated from the unique genotypes found in each population (Table 5.3). Heterozygosity statistics are given for total sample sizes (Table 5.4) and unique genotypes (Table 5.5)

Significant departures from Hardy-Weinberg equilibria, based on unique genotypic frequencies, were detected in all populations at from one to three loci (Table 5.6). Most of the departures reflect heterozygote deficiencies, particularly for ME and VL.

Clonal distributions within each of the populations sampled by the nested quadrate design are shown in Figure 5.5. Sampled clone sizes within each population ranged from one to six colonies with means of 1.02 to 1.55 colonies/clone (Table 5.7). Distances between clonemates varied between populations, with BIK having both the closest (1.0 m) and most distant (16.5 m) colonies with identical multi-locus genotypes.

Figure 5.6 portrays the relative genotypic diversity observed in the six populations. For those populations sampled with the nested quadrate design, diversity within each quadrate is also shown. The curves delineate the various levels of diversity which were determined with increasing sample size and also provide information about the effective dispersal distributions of clones. At sample sizes of < 15 colonies (within an area of 16 m^2), measured diversity was 35-40 %

higher in the NKB population than for sample sizes > 30 (in 64 m^2). Distribution of clones was more extensive than 1 m^2, 4 m^2, or 16 m^2 in the MOS population, as evidenced by the abrupt drop in diversity for the larger quadrate sizes. The BIK population showed a high degree of clonal replication in the smallest quadrate (1 m^2), less in the intermediate sizes, and widely dispersed clones were again identified in the largest quadrate. Genotypes were distributed over all sampling scales in the NKB population, as shown by a steady decline in diversity with increasing quadrate and sample size, although the detection on clones leveled off in the largest quadrate (256 m^2).

A total of 212 seven-locus genotypes were recognized among the 269 colonies of Porites compressa scored in the 1988 samples giving a total diversity over all populations of G_O=163.20 (D=0.7881). For the 180 samples collected from Kaneohe Bay (NKB, SKB, CI, and MOS), G_O was 109.89 (D=.8280). Thirteen genotypes (4.8%) were found in more than one population (three in NKB and SKB, three in BIK and LAN, two in MOS and LAN, two in CI and SKB, and one each in SKB and LAN, MOS and BIK, and BIK and SKB). This overlap may reflect the limits of resolution (approximate error of 5%) of the seven-locus system for detection of individuals over the entire species. No genotypes were found in more than two populations.

As predicted by the disturbance hypothesis, genotypic diversity was highest in the CI and SKB populations, intermediate for BIK, MOS, and LAN, and lowest for NKB (Table 5.7). Genetic identity indices (I) varied from 0.8744 to 0.9868 (Table 5.8), and produced a dendrogram grouping the three Kaneohe Bay populations separately from the other

three, whether unique or total allele frequencies were used for calculation of I (Figure 5.7). Identity indices calculated from total N were lower, however, indicating an inherent bias in this statistic for comparisons of clonal populations.

Although colony size is not an accurate predictor of absolute age of a coral genet (e.g., some colonies may have been derived from fragments and therefore be genetically "older" than their size would indicate (Hughes and Jackson, 1980)), it can be used to provide a rough estimate of the minimum age of a colony if growth rates are known. Mean linear growth of colonies measured in NKB (3.1 cm/year; Chapter 3) and in south Kaneohe Bay (3.5 cm/year; Jokiel, 1985) suggests that colonies at both sites grow at about the same rate. Increase in whole colony size is perhaps better estimated by mean radial growth rate, which Polacheck (1978) measured as 2.46 cm/year for Porites compressa. Mean colony size was significantly greater (log transformed, t-test, $p<0.01$) for NKB samples (2586 $\pm$ 2079 cm^2 [mean $\pm$ standard deviation]; 10.3 years) than for SKB (366 $\pm$ 449 cm^2; 3.9 years), indicating that the NKB population is substantially older. Many (~35%) of the NKB colonies are derived from fragments, so that average genet age is probably much higher. Total area occupied per genet averaged 4156 $\pm$ 6128 cm^2 for NKB with a range of 1-6 colonies/clone and 383 $\pm$ 454 cm^2 for SKB (1-2 colonies/clone). There was no significant difference in mean colony size between one-colony clones ($X=2280 \pm 1398$ cm^2) and clones with more than one colony ($X=2478.00 \pm 1631$ cm^2) in the NKB population.

The five loci (total of 10 alleles) assayed in the 1986 samples

were not sufficient to resolve true clonal structure in the NKB, SKB, and BIK populations. Only 16 (NKB), 23 (SKB), and 26 (BIK) genotypes were detected within each population, yielding correspondingly low indices of diversity among the three populations (Table 5.9). The addition of one more locus (PGI:3 alleles) increased the total number of genotypes scored from 16 to 28 for the NKB populations and essentially doubled the diversity indices. (PGI produces clear bands for fresh tissue only in P. compressa, but only frozen SKB and BIK 1986 samples were available when this enzyme system methodology was worked out). Relative levels of diversity as measured by G_o and D changed from BIK > SKB > NKB to SKB > BIK > NKB in the 1986 and 1988 analyses, respectively.

DISCUSSION

Genotypic diversity and structure vary greatly among Porites compressa populations with different disturbance histories. Intensity, frequency, and length of time since the last disturbance event affect the detectable levels of genetic variation in these populations. Although quantification of absolute levels of disturbance is subjective, information about long-term changes in genetic structure can be gained from examination of populations at various successional stages.

Early successional populations are colonized (or recolonized) predominantly by sexual recruits (larvae which have been dispersed from other populations) and therefore have highest levels of diversity,

small colony size, and limited clonal distributions. The SKB population, presumably in the process of recovery from the effects of dredging in the 1940's, was essentially eliminated by algal overgrowth due to sewage enrichment and high turbidity from run-off and phytoplankton blooms in the 1960's and 1970's (Smith et al., 1973). This population had only two clones with more than one member among the 45 colonies sampled. These clonemates were found within 0.6 and 3.0 m of each other, the shortest distances between clonal replicates among any of the populations. Mean colony size of 366.3 cm^2 (mean diameter = 19.13 cm) extrapolates to an average age of approximately 3.9 years based on a radial growth rate of 2.46 cm/year (Polacheck, 1978). Sewage abatement began in 1978-1979, but new coral recruitment may not have occurred for several years due to residual organic fine sediment covering the bottom. (Smith, et al., 1981). Most colonies of recognizable size in the SKB population are probably between two and seven years old.

Populations which are well established but experience local or large-scale disturbances of intermediate intensity or frequency recruit from both sexual and asexual propagules (larvae and fragments, respectively) and therefore would have mixed or intermediate diversities and a mixed age-structure. New genotypes are introduced to the population by larval settlement on newly available substratum; established colonies replicate through fragmentation. MOS, LAN, and BIK populations were characterized by intermediate diversities, with clonemates scattered from 1.0 m to 16.5 m apart within the 32 m x 32 m sampling area. Unfortunately, it was not possible to consistently

measure colony size in these populations due to the thicket-like growth form (BIK) or the occurrence of many colonies with overgrown bases (MOS, LAN). Subjectively, there appeared to be a wide range of colony sizes (and presumably a broad age structure) in all three populations.

If lack of disturbance for long periods of time produces "climax" populations, then older populations in physically benign environments should be characterized by definite clonal structure and low genotypic diversity in coral species which can reproduce asexually by fragmentation. The NKB population had the highest number of colonies per clone (6), highest average clone size (1.5 colonies), and the lowest clonal diversity (29 genotypes in 45 colonies sampled) of all populations in this study. Clonemates were up to 15.9 m apart. Mean colony size in the NKB population of 2585 cm^2 (mean diameter =51 cm) suggests an average age of 10.3 years, although, if some colonies are the result of fragmentation of established genotypes, average genet age could potentially be one or two orders of magnitude greater. Colonies > 4 m in diameter occur on this reef, indicating ages of well over a century.

Vectors of clonal dispersal in all populations of Porites compressa are unknown, but it is likely that storm-generated waves and currents can move fragments or whole colonies large distances on the exposed coast of the Big Island (Dollar, 1982). In the calm conditions of Kaneohe Bay, however, the means by which fragments are broken and spread are less obvious. Huge colonies, weakened at their bases by bioeroders, have been seen to topple over on the slopes of patchreefs, generating fragments downslope (B. Tyler, pers. comm.; pers. obs.). Parrotfish in the Caribbean have been observed to disperse viable coral

fragments in their feces (P. Glynn, pers. comm.), but there are no large corallivores within the Bay capable of biting off entire branches of corals. Turtles have been seen frequently swimming above the reef and "resting" in crevices on the reef slope at the NKB site and may be responsible, along with the occasional anchor, for a great deal of coral fragmentation in some areas (see Chapter 4).

The long-term evolutionary implications of clonal replication in species which reproduce asexually are far-reaching. Changes in the abundance and distribution of ramets (genetically identical clonal replicates) affect the overall fitness of individual genotypes, while variation in the number of genets (unique, sexually derived individuals) will determine the total genotypic variability of the popuation. Decreased genotypic diversity may result in incipient speciation through isolation of populations with low effective numbers of individuals, or to extinction if the population is no longer able to track environmental changes because of reduced genetic resources (Levin and Wilson, 1978). In many marine invertebrate species with dispersive planktonic larvae, however, remote populations may act as reservoirs of genetic variability (Grassle and Grassle, 1978; Valentine and Ayala, 1978).

Gene flow and dispersal distances among coral reef species have been the subject of much recent research and ongoing debate (Jokiel, 1984; Williams, et al., 1984; Hodgson, 1985; Richmond, 1985; Bull, 1986; Leis, 1986; Oliver and Willis, 1987; Stoddart, 1988; Sammarco and Andrews, in press). Gene flow will affect the rates at which populations differentiate. Stoddart (1988) found that fringing reef

populations of Pocillopora damicornis in Western Australia were more genetically differentiated than those of patchreefs within Kaneohe Bay; he attributed these differences to a greater amount of larval connectivity among the Hawaiian reefs. Ayre and Willis (in press) reported a wide range of genetic relatedness (Nei's I = 0.72-0.98) among populations of Pavona cactus separated by approximately 1-1800 km on the Great Barrier Reef.

High genetic identities (Nei's I = 0.97-0.99) of the three Porites compressa populations sampled within Kaneohe Bay (NKB, SKB, and CI) suggest that gene flow occurs at least within the distances (0.75-6.2 km) between these sampling sites. Lanikai (LAN) and Big Island (BIK) populations were more similar to MOS (the site offshore from Kaneohe Bay) than to each other, suggesting that there may be some dispersal over much greater distances preventing isolation of these populations. However, the great longevity of many Porites individuals may also inhibit rates of population differentiation because of prolonged generation times (Potts, 1983, 1984).

Investigations of other anthozoan population structures have demonstrated significant clonality, particularly among species which are known to produce larvae asexually. The viviparous anemones, Actinia tenebrosa and A. equina, show very low levels of genotypic diversity in local populations (Black and Johnson, 1979; Ayre, 1983, 1984). Fujii (1987) using acrorhagial responses and sex ratios as indicators of clonal identity found that populations of the anemone, Anthopleura asiatica are dominated by a small number of clones, some of which may distributed over 5 km. Sebens (1982) and Ayre (1984)

reported higher clonal diversity in populations of sea anemones in unstable habitats.

Degree of clonality varies among coral species and among populations within species. Populations of Porites compressa (D values of 0.64-0.98) are much less clonal than those of Pocillopora damicornis (D values of 0.15-0.75) in Western Australia (25 populations) and Hawaii (8 populations) (Stoddart, 1984b, 1985). P. damicornis is hermaphroditic and broods planulae which may be asexually produced (Stoddart, 1983a). A large range of variation in clonal structure was found for Pavona cactus, a gonochoric broadcast spawner, with D values of 0.03-0.94 for six Great Barrier Reef populations (Ayre and Willis, in press).

Estimates of genetic diversity in clonal populations are dependent upon 1) resolution precision of the genetic assays used, and 2) scale of sampling. Electrophoretic assessments of genotypic diversity are severely limited by the lack of a priori methods for ascertaining the number of loci necessary to differentiate clones. In the present study, the power of the electrophoretic assay (7 loci, 23 alleles) to identify all genotypes in clonal populations was tested by comparison to its resolution ability in an aclonal population comprised of genetically unique colonies. Other studies that have addressed the genetic structure of anthozoan populations were hampered by the methodological difficulty of inadequate or uncertain resolution and were not able to fully differentiate all genotypes (Stoddart, 1984a: 4 loci, 13 alleles; Stoddart, 1984b: 5 loci, 15 alleles; Willis and Ayre, 1985: 4 loci, 12 alleles; Hoffmann, 1986, 1987: 5 loci, 11 alleles;

Ayre and Willis, in press: 4 loci, 17 alleles). Similarly, area and scale of sampling will affect estimated levels of diversity (e.g, Ayre and Willis, in press). The nested quadrate design utilized in the present study addressed the need for both fine-scale and broad-scale population sampling. Sufficient resolution and dimensionality of sampling are of critical importance in determining true genetic population structures of species which reproduce asexually.

Figure 5.1. Location of six sampling sites (NKB, SKB, CI, MOS, LAN, and BIK) of Porites compressa in Hawaii.

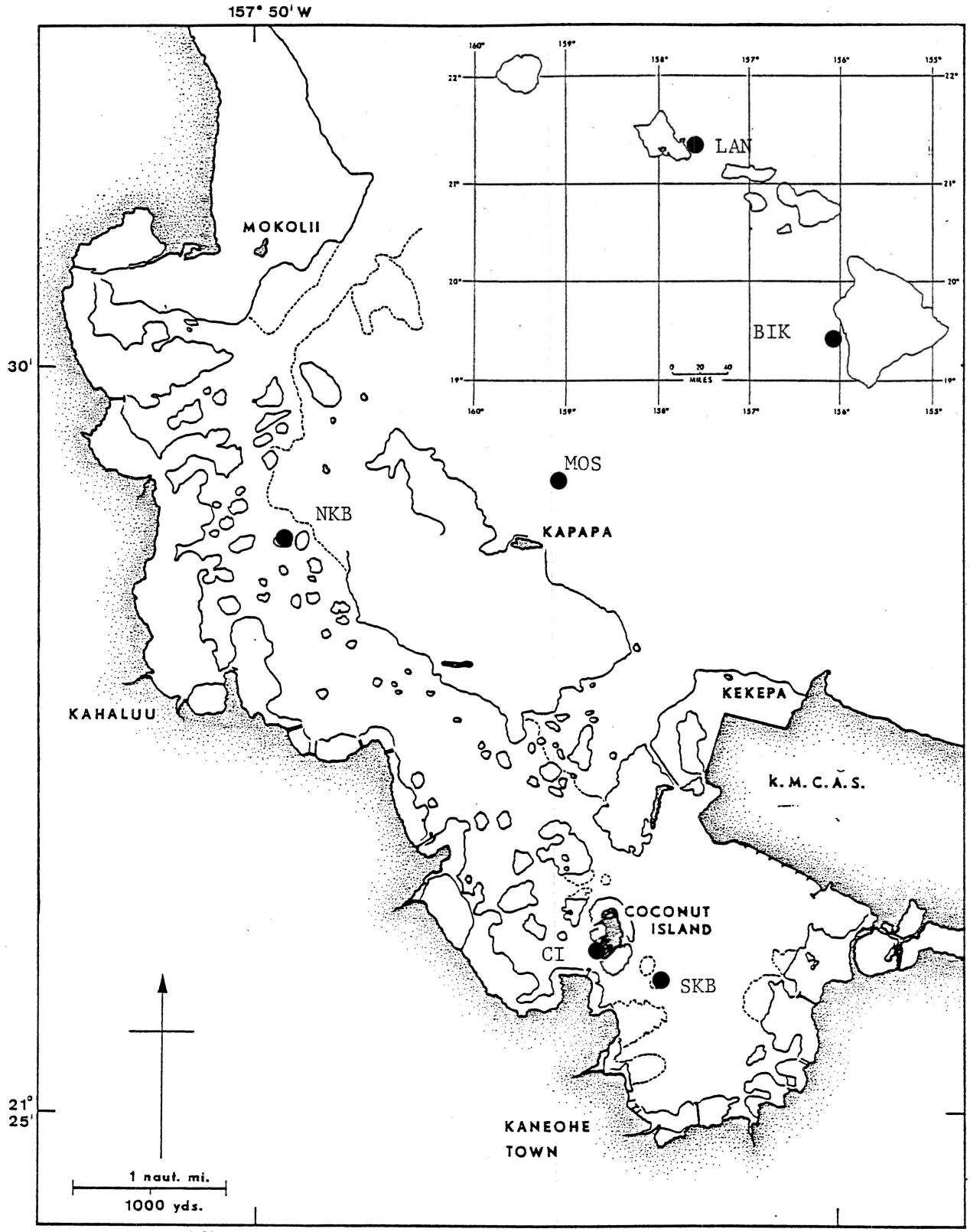
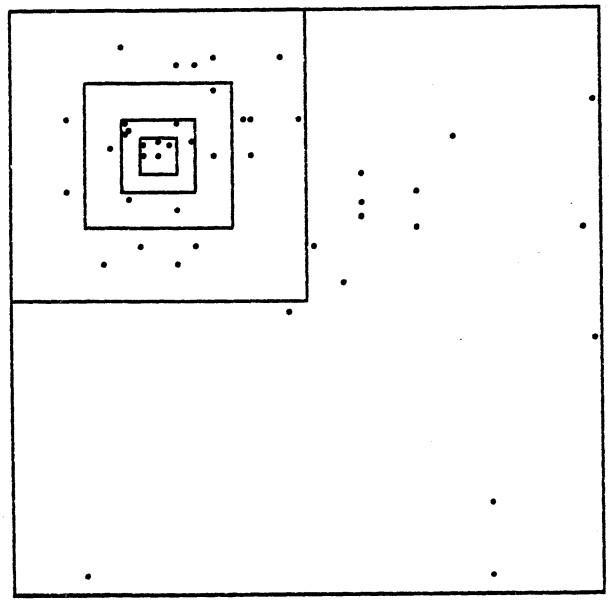

157° 50' W
30'
21°
25'
MOKOLII
LAN
BIK
0 20 40
MILES
MOS
NKB
KAPAPA
KEKEPA
KAHALUU
k. M. C. A. S.
COCONUT
ISLAND
CI
SKB
KANEOHE
TOWN
1 naut. mi.
1000 yds.

Figure 5.2 a. Diagram of Nested Quadrate sampling design used for the North Kaneohe Bay (NKB), South Kaneohe Bay (SKB), Marv's Offshore Site (MOS), and Big Island, Kona (BIK) populations. Smallest quadrate is one square meter. Each dot represents the location of a sample. b. Genotypic diversity (D*) estimated from "samples" from clonal distributions mapped by Hunter and Kehoe (1985).

a.



Quadrat #	Area (m^2)	Cumulative Number of Colonies Sampled
1	1	5
2	4	10
3	16	15
4	64	30
5	256	45

b.

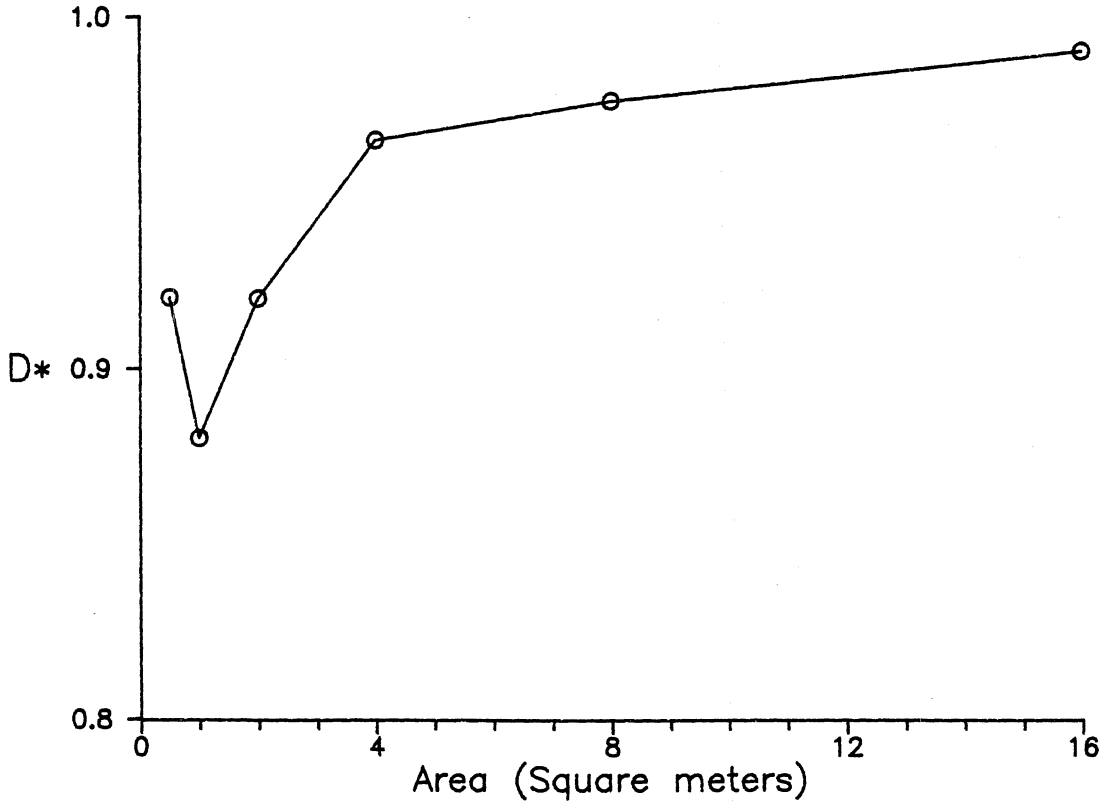
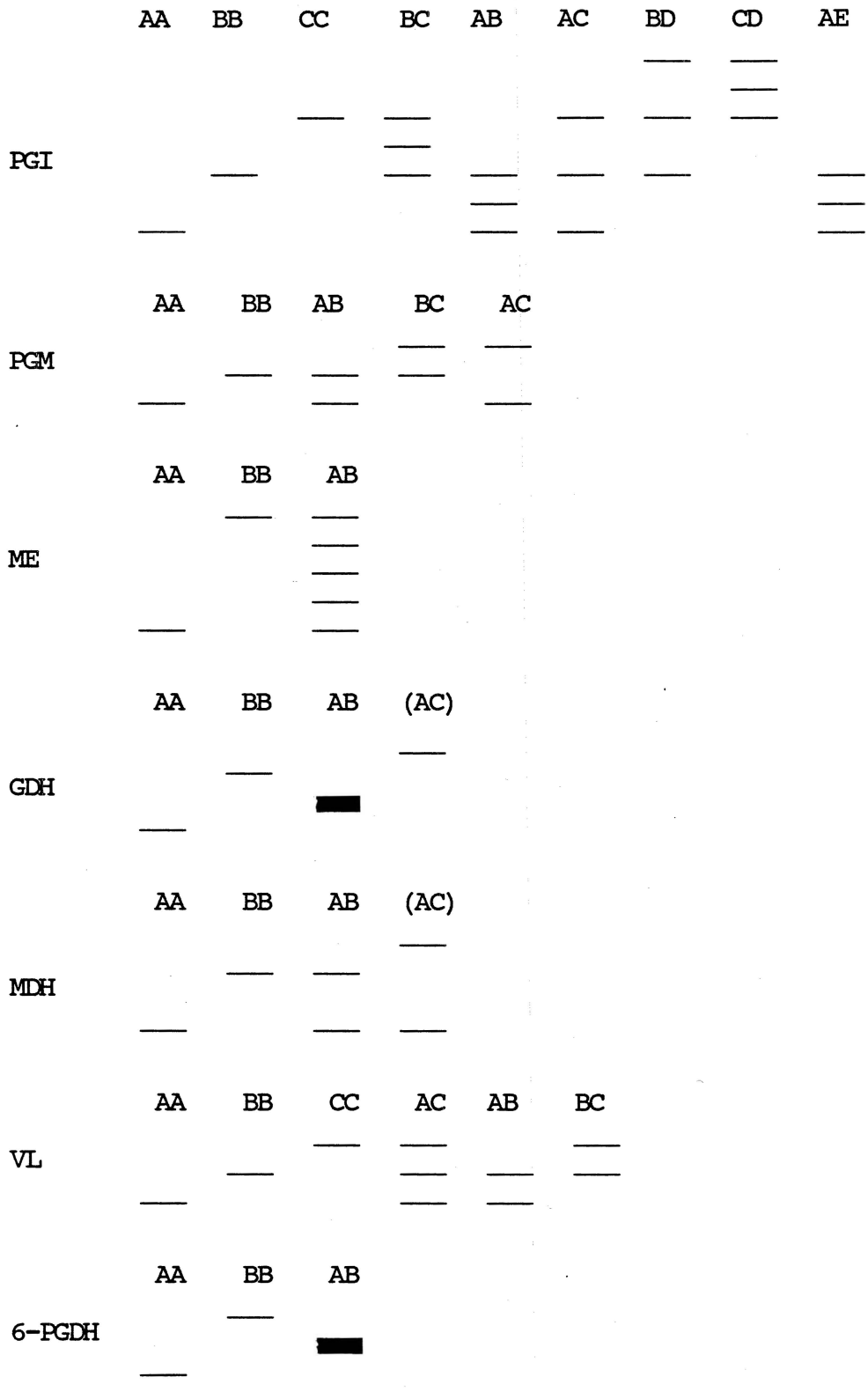


Figure 5.3. Banding patterns of seven enzyme systems scored for six populations of Porites compressa in 1988. Alleles were assigned letters in increasing order of mobility. Letters representing interpretation of genotypes are shown above each observed pattern. Genotypes in parentheses are tentative allele assignments.


AA
BB
CC
BC
AB
AC
BD
CD
AE
PGI
AA
BB
AB
BC
AC
PGM
AA
BB
AB
ME
AA
BB
AB
(AC)
GDH
AA
BB
AB
(AC)
MDH
AA
BB
CC
AC
AB
BC
VL
AA
BB
AB
6-PGDH

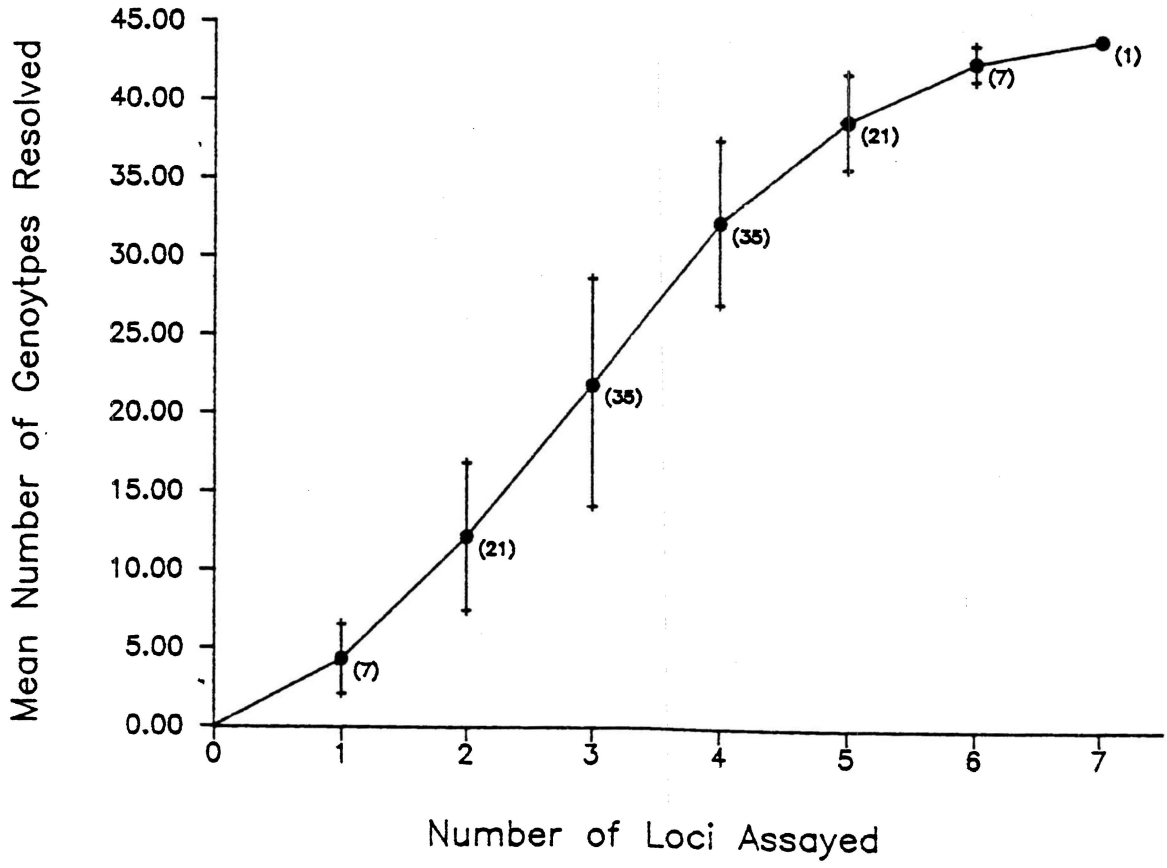


Figure 5.4. Mean number of unique genotypes resolved with the sequential addition of electrophoretic loci assayed in the Coconut Island (CI) samples. Bars show standard error. Numbers in parentheses indicate number of permutations of loci which were averaged to arrive at mean.

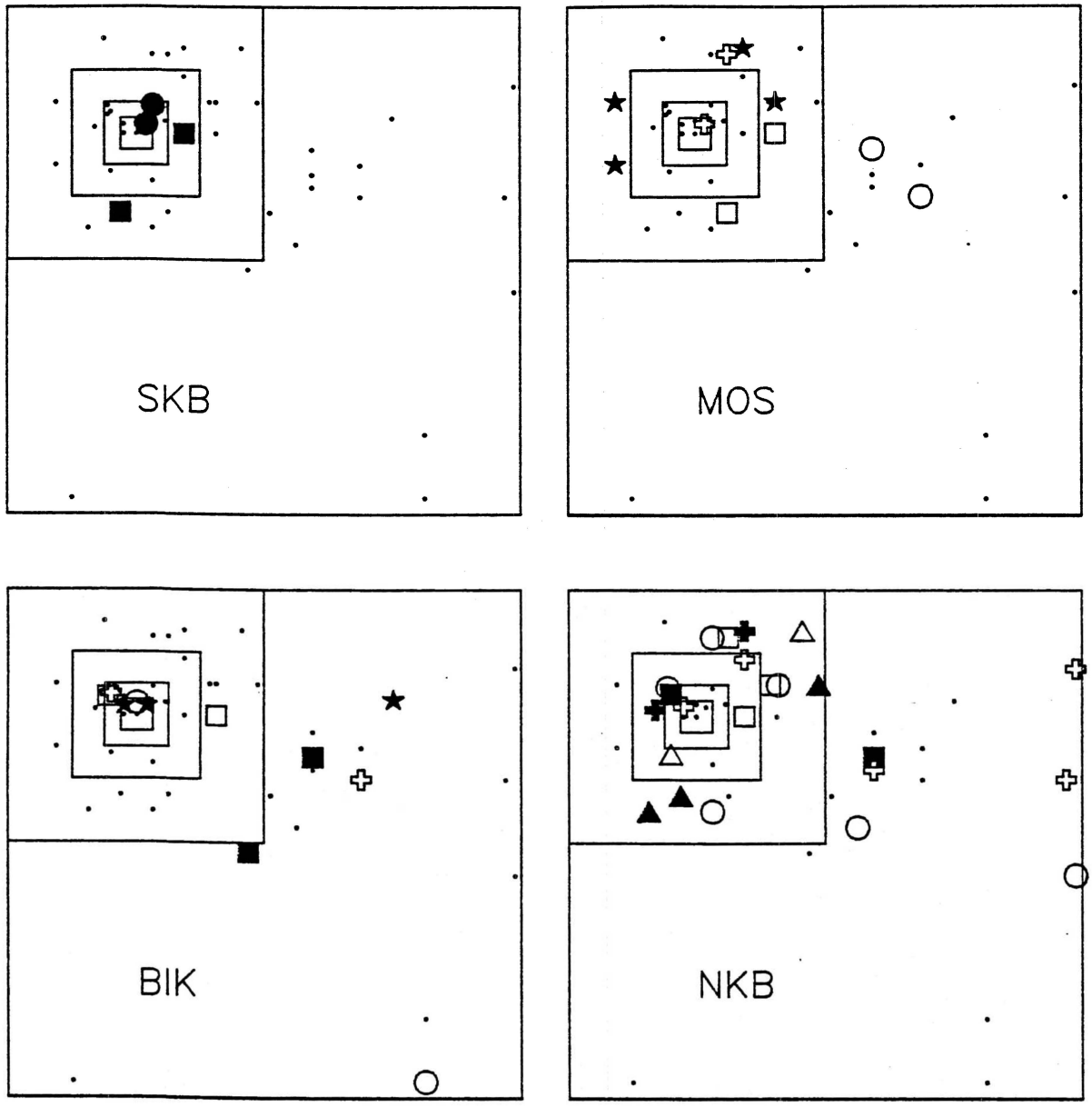


Figure 5.5. Distributions of clones within four populations of Porites compressa sampled by nested quadrat design. Dots indicate location of samples and symbols represent genotypes which occurred one or more times within a population. Numbers of replicated genotypes were: South Kaneohe Bay (2), Marv's Offshore Site (4), Big Island, Kona (5), and North Kaneohe Bay (7); all other genotypes were found only once in each population.

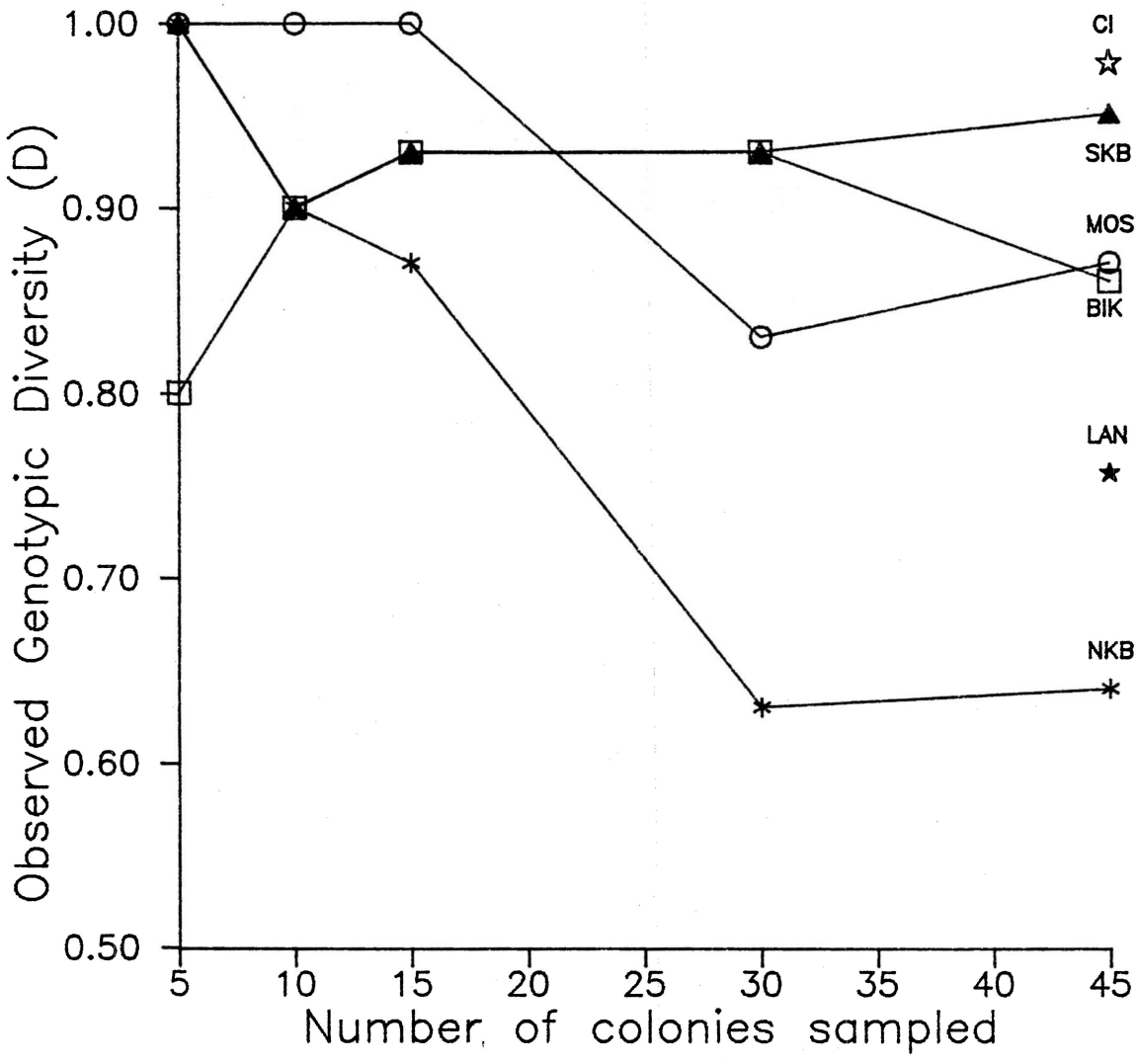
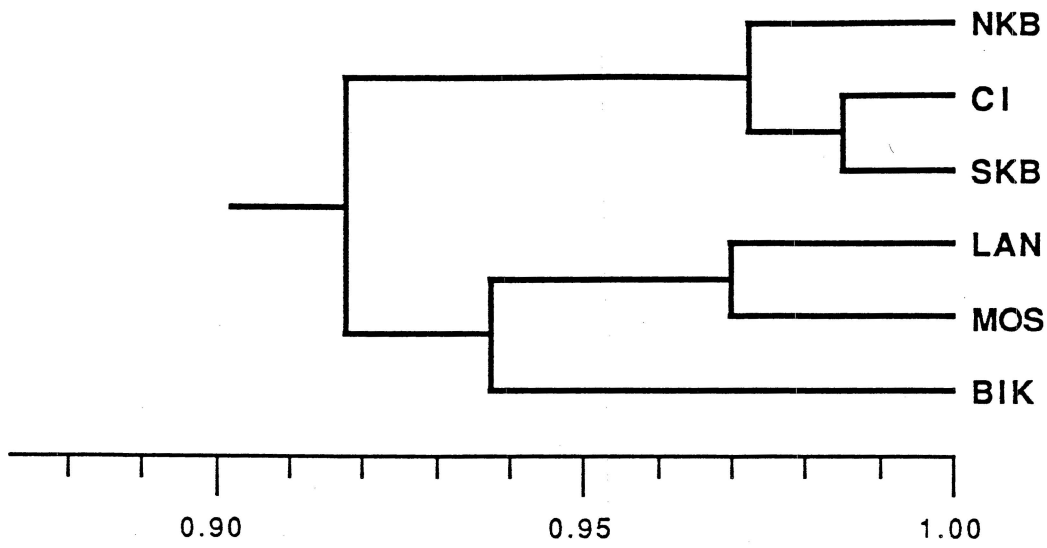


Figure 5.6. Observed genotypic diversity (D) as a function of number of colonies of Porites compressa sampled in four populations: North Kaneohe Bay (NKB), South Kaneohe Bay (SKB), Marv's Offshore Site (MOS), and Big Island, Kona (BIK).



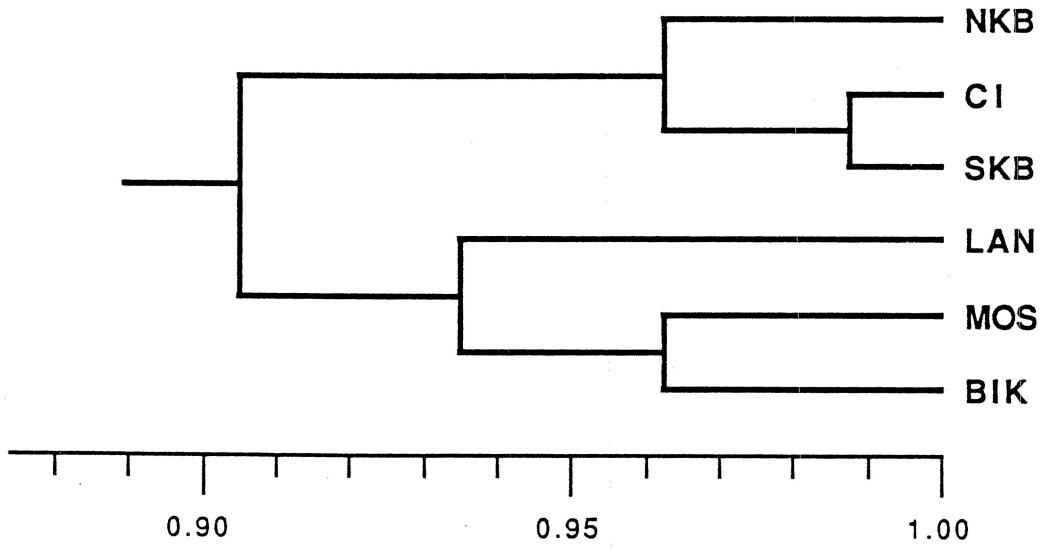


Figure 5.7 Dendrograms of genetic similarities of six populations of Porites compressa from Hawaii as determined by UPGMA. a. Based on allele frequencies of unique genotypes only. b. Based on allele frequencies calculated from total sample, including replicated genotypes.

Table 5.1. Estimates of levels of disturbance at six sampling sites: North Kaneohe Bay (NKB), Marv's Offshore Site (MOS), Big Island, Kona (BIK), Lanikai (LAN), South Kaneohe Bay (SKB), and Coconut Island (CI). Numbers are subjective evaluations of habitat stability and successional age criteria, based on scales of 1 to 10. A disturbance "index" was calculated as the total of all columns for each population.

A. largest colony diameters (1= >4 m, 5= 1-1.25 m, 10= <0.25 m),
B. percentage of unoccupied substratum (1= <10%, 5=4 0-50%, 10= >90%),
C. time since last major disturbance (1= >50 years, 5= 20-25 years, 10= <one year),
D. intensity of disturbance (1= "low", 5= "intermediate", 10= "high").

	A. Colony Size	B. Bare Substratum	C. Recency of Disturbance	D. Intensity of Disturbance	Disturbance "Index"
NKB	1	1	1	2	5
MOS	4	7	4	5	20
BIK	5	4	5	6	20
LAN	2	5	3	5	15
SKB	7	7	6	10	30
CI	10	9	8*	10*	36

* Colonies greater than 25 cm in diameter were not found on the seawall probably because they fall due to their own weight after reaching a particular size relative to their attachment area. As colonies of this size are approximately 3-5 years old, this was scored as a relatively frequent disturbance at a high level of intensity.

Table 5.2. Allele frequencies for seven loci assayed from six populations of Porites compressa in 1988. Frequencies are calculated from total sample, including clonal replicates. Alleles are designated in order of decreasing anodal mobility.

LOCUS	ALLELE	NKB (88)	SKB (88)	CI (88)	LAN (88)	MOS (88)	BIK (88)
	N=	45	45	45	45	45	44
PGI	A	0.478	0.367	0.456	0.722	0.522	0.523
	B	0.133	0.256	0.233	0.189	0.111	0
	C	0.389	0.356	0.289	0.089	0.367	0.477
	D	0	0.022	0.011	0	0	0
	E	0	0	0.011	0	0	0
PGM	A	0.555	0.344	0.333	0.700	0.789	0.841
	B	0.178	0.067	0.122	0.100	0.056	0.159
	C	0.267	0.589	0.533	0.200	0.155	0
	D	0	0	0.012	0	0	0
ME	A	0.278	0.267	0.333	0.211	0.111	0.330
	B	0.722	0.689	0.667	0.756	0.889	0.671
	C	0	0.044	0	0.033	0	0
GDH	A	0.389	0.478	0.422	0.489	0.367	0.375
	B	0.611	0.522	0.578	0.500	0.633	0.625
	C	0	0	0	0.011	0	0
MDH	A	0.622	0.722	0.711	0.711	0.557	0.716
	B	0.367	0.278	0.278	0.289	0.443	0.284
	C	0.011	0	0.011	0	0	0
VL	A	0.256	0.367	0.522	0.656	0.511	0.284
	B	0.744	0.600	0.478	0.122	0.215	0.318
	C	0	0.033	0	0.222	0.273	0.398
6-PGDH	A	0.987	0.844	0.933	0.889	1	1
	B	0.011	0.156	0.067	0.111	0	0

Table 5.3. Allele frequencies for seven loci assayed from six populations of Porites compressa in 1988. Frequencies are calculated from unique genotypes, omitting clonal replicates. Alleles are designated in order of increasing anodal mobility.

LOCUS	ALLELE	NKB (88)	SKB (88)	CI (88)	LAN (88)	MOS (88)	BIK (88)
	N=	45	45	45	45	45	44
PGI	A	0.466	0.384	0.466	0.686	0.577	0.487
	B	0.172	0.256	0.239	0.200	0.115	0
	C	0.362	0.349	0.273	0.114	0.308	0.513
	D	0	0.012	0.011	0	0	0
	E	0	0	0.011	0	0	0
PGM	A	0.466	0.349	0.341	0.700	0.769	0.855
	B	0.190	0.070	0.125	0.043	0.064	0.148
	C	0.315	0.581	0.523	0.257	0.168	0
	D	0	0	0.011	0	0	0
ME	A	0.259	0.279	0.341	0.228	0.121	0.342
	B	0.741	0.674	0.659	0.729	0.872	0.658
	C	0	0.044	0	0.043	0	0
GDH	A	0.448	0.500	0.432	0.457	0.397	0.395
	B	0.552	0.500	0.568	0.529	0.603	0.605
	C	0	0	0	0.014	0	0
MDH	A	0.603	0.756	0.716	0.700	0.513	0.697
	B	0.379	0.279	0.273	0.300	0.488	0.303
	C	0.017	0	0.011	0	0	0
VL	A	0.362	0.372	0.534	0.643	0.573	0.276
	B	0.638	0.593	0.466	0.129	0.218	0.316
	C	0	0.035	0	0.229	0.269	0.408
6-PGDH	A	0.983	0.837	0.932	0.871	1	1
	B	0.017	0.163	0.068	0.129	0	0

Table 5.4. Expected (H_e) and observed (H_o) heterozygosities per locus and mean heterozygosity per individual (H_i) calculated from total samples (including clonal replicates) for six populations of Porites compressa collected in 1988.

LOCUS	NKB (88)	SKB (88)	CI (88)	LAN (88)	MOS (88)	BIK(88)
PGI						
H_e	0.60	0.65	0.65	0.44	0.58	0.50
H_o	0.31	0.64	0.67	0.49	0.58	0.45
PGM						
H_e	0.59	0.53	0.59	0.46	0.35	0.27
H_o	0.49	0.44	0.40	0.58	0.24	0.27
ME						
H_e	0.40	0.45	0.44	0.30	0.20	0.44
H_o	0.24	0.31	0.53	0.27	0.13	0.34
GDH						
H_e	0.49	0.49	0.49	0.51	0.47	0.47
H_o	0.48	0.51	0.40	0.56	0.29	0.43
MDH						
H_e	0.48	0.40	0.42	0.41	0.49	0.41
H_o	0.40	0.38	0.44	0.44	0.43	0.34
VL						
H_e	0.38	0.50	0.50	0.51	0.62	0.66
H_o	0.33	0.38	0.33	0.07	0.48	0.07
6-PGDH						
H_e	0.02	0.26	0.13	0.20	0.00	0.00
H_o	0.01	0.04	0.09	0.22	0.00	0.00
MEAN H_i	0.326	0.384	0.385	0.369	0.341	0.273
MEAN He	0.423	0.469	0.460	0.415	0.386	0.392
MEAN Ho	0.323	0.386	0.409	0.375	0.308	0.273

Table 5.5. Expected (H_e) and observed (H_o) heterozygosities per locus and mean heterozygosity per individual (H_i) calculated from unique genotypes (omitting clonal replicates) for six populations of Porites compressa collected in 1988.

LOCUS	NKB (88)	SKB (88)	CI (88)	LAN (88)	MOS (88)	BIK(88)
PGI						
H_e	0.62	0.67	0.65	0.48	0.56	0.50
H_o	0.41	0.66	0.65	0.54	0.61	0.45
PGM						
H_e	0.63	0.53	0.59	0.44	0.38	0.25
H_o	0.45	0.44	0.41	0.57	0.21	0.24
ME						
H_e	0.38	0.47	0.45	0.42	0.22	0.45
H_o	0.17	0.16	0.55	0.26	0.15	0.32
GDH						
H_e	0.49	0.50	0.55	0.51	0.48	0.48
H_o	0.59	0.53	0.41	0.49	0.33	0.47
MDH						
H_e	0.49	0.35	0.41	0.42	0.50	0.42
H_o	0.38	0.37	0.43	0.43	0.46	0.34
VL						
H_e	0.46	0.51	0.50	0.52	0.62	0.66
H_o	0.34	0.37	0.34	0.06	0.41	0.08
6-PGDH						
H_e	0.03	0.27	0.13	0.22	0.00	0.00
H_o	0.03	0.05	0.09	0.26	0.00	0.00
MEAN H_i	0.325	0.389	0.393	0.367	0.300	0.271
MEAN He	0.445	0.471	0.468	0.429	0.394	0.394
MEAN Ho	0.340	0.369	0.416	0.371	0.311	0.271

Table 5.6. Deviations from expected levels of heterozygosity, with significance of departures from Hardy-Weinberg equilibria calculated from unique genotypes in six populations of Porites compressa.

LOCUS	NKB	SKB	CI	MDS	LAN	BIK	Total +	Total −
PGI	−0.335*	−0.021	+0.047	+0.101	+0.139	−0.105	3	3
PGM	−0.287*	−0.168	−0.312*	−0.455**	+0.292	−0.043	1	5
ME	−.550**	−0.650***	+0.214	−0.312*	−0.380	−0.298	1	5
GDH	+0.185	+0.070	−0.249	−0.304	−0.050	−0.009	2	4
MDH	−0.229	+0.061	+0.046	−0.075	+0.020	−0.190	3	3
VL	−0.254	−0.269*	−0.315*	−0.335*	−0.890***	−0.880***	0	6
6-GPDH	+0.021	−0.829***	−0.285	N.A.	+0.147	N.A.	2	2

* $p < 0.05$
** $p < 0.01$
*** $p < 0.001$

N.A. not applicable (fixed alleles)

Table 5.7. Summary of genotypic diversity and clonal distributions in six populations of Porites compressa. N = number of samples per population, G_o = observed genotypic diversity, G_e = expected genotypic diversity, and D = # unique genotypes/N.

	NKB (88)	SKB (88)	CI (88)	IAN (88)	MDS (88)	BIK (88)
# Genotypes	29	43	44	34	39	38
N	45	45	45	45	45	44
G_o	17.92	41.32	43.10	28.57	32.15	33.44
G_e	42.02	43.74	43.45	42.09	40.61	39.35
$\pm$ S.E.	1.64	1.06	1.27	1.66	1.83	1.85
G_o:G_e	0.427	0.947	0.994	0.679	0.791	0.849
D	0.644	0.956	0.978	0.756	0.867	0.864
Frequency of Clone Size:						
6	1	0	0	0	0	0
5	1	0	0	0	0	0
4	0	0	0	0	1	0
3	2	0	0	2	0	1
2	3	2	1	7	3	4
1	22	41	43	25	35	33
Distance between Clonemates (meters)						
Minimum	1.1	0.6	N.D.	N.D.	1.6	1.0
Maximum	15.9	3.0	N.D.	N.D.	6.0	16.5

Table 5.8. Nei's unbiased indices of genetic identity for six populations of *Porites compressa* in Hawaii. a. Based on unique genotypes, b. Based on total sample.

a.

	NKB	SKB	CI	MOS	LAN	BIK
NKB	1					
SKB	0.9734	1				
CI	0.9764	0.9868	1			
MOS	0.9400	0.9679	0.9177	1		
LAN	0.9208	0.9071	0.9370	0.9729	1	
BIK	0.9250	0.8744	0.8849	0.9551	0.9272	1

b.

	NKB	SKB	CI	MOS	LAN	BIK
NKB	1					
SKB	0.9619	1				
CI	0.9602	0.9882	1			
MOS	0.9320	0.8991	0.9190	1		
LAN	0.8860	0.8825	0.9147	0.9489	1	
BIK	0.9350	0.8759	0.8904	0.9625	0.9206	1

Table 5.9. Allelic frequencies for six loci of Porites compressa in three populations in Hawaii collected in 1986 based on total sample (and also from unique genotypes for NKB). N = number of samples per population, G_o = observed genotypic diversity, and D = # of unique genotypes/N.

LOCUS	ALLELE	NKB (86)	NKB (86) (Unique)	SKB (86)	BIK (86)
PGI	A	0.511	0.429	--	--
	B	0.178	0.232	--	--
	C	0.311	0.339	--	--
	D	0	0	--	--
	E	0	0	--	--
GDH	A	0.411	0.446	0.409	0.477
	B	0.589	0.554	0.591	0.523
LGG	A	0.822	0.821	0.909	0.932
	B	0.178	0.179	0.091	0.068
EST-B	A	0.289	0.321	0.555	0.614
	B	0.711	0.679	0.445	0.386
LDY-1	A	0.489	0.500	0.250	0.364
	B	0.511	0.500	0.750	0.636
LDY-2	A	0.512	0.500	0.227	0.477
	B	0.488	0.500	0.773	0.523
# Loci assayed		6	6	5	5
N		45	45	44	44
Mean H_e		0.380	0.392	0.378	0.418
Mean H_o		0.170	0.179	0.045	0.052
# of Genotypes:					
	(w/o PGI)	16	16	23	26
	(w/PGI)	28	28	--	--
G_o	(w/o PGI)	11.29	11.29	14.89	19.36
	(w/PGI)	22.27	22.27	--	--
D=	(w/o PGI)	0.356	0.356	0.511	0.578
	(w/PGI)	0.622	0.622	--	--

APPENDIX 5A. PROTOCOL FOR ENZYME ELECTROPHORESIS FOR PORITES COMPRESSA

Extraction:

1. Fresh tissue is best and necessary for many systems (PGI, PGM, MDH, MPI, ME). Esterases and peptidases often stain better for frozen tissue.

2. Whole fresh branch tips are shaken to remove excess seawater, placed between double layers of plastic wrap and crushed with pliers. The squashed tissue is then homogenized on a spot plate with approximately equal volume of Stoddart's (1983) Indicator/Extractant (0.1 ml mercaptoethanol, 10.0 g sucrose, 0.1 g bromophenol blue, 25 mg NADP/100 ml water, plus 1 g EDTA). Each spot is covered with a square of Kim-Wipe to minimize contact with mucus, and sample is absorbed onto Whatman #3 wicks.

Gels/Buffers:

1. Either Electrostarch Lot 392 (32 g/280 ml) or Sigma S4501 (33.5 g/ 280 ml) starch is used. Gels are run at 5° C under a cake pan of ice.

2. The systems utilized have given best results in the following buffer systems:

Enzyme	Buffer
PGI	LIOH
PGM	LIOH or TM
ME	TC-II
GDH	TVB-1
MDH	TVB-1 or TM
PEPS	TVB-1 or TC-I
6-GPDH	TC-II
EST	LIOH

3. Recipes (per liter):

LIOH (Selander, et al., 1971; #2)

gel:	0.12 g	lithium hydroxide
pH=8.3	1.19 g	boric acid
	5.58 g	tris
	1.44 g	citric acid
electrode:	1.2 g	lithium hydroxide
pH=8.1	11.8 g	boric acid

TC-I (Potts, unpubl.)

gel:	0.97 g tris
pH=6.7	0.63 g citric acid
electrode:	27.00 g tris
pH=6.3	18.07 g citric acid

TC-II (Selander, et al., 1971; #5)

gel:	2.77 g tris
pH=8.0	1.10 g citric acid
electrode:	83.20 g tris
pH=8.0	29.98 g citric acid

TM (Selander, et al., 1971; #9)

gel:	1:9 dilution of electrode
pH=8.0	
electrode:	12.10 g tris
pH=8.0	11.60 g maleic acid
	3.72 g EDTA
	2.03 g $MgCl_2$

TVB-1 (Selander, et al., 1971; #6)

gel:	1:9 dilution of electrode
pH=8.0	
electrode:	60.6 g tris
pH=8.0	40.0 g boric acid
	6.0 g EDTA

3. Stains: (*all catalogue numbers are for Sigma chemicals)

EST (E.C. 3.1.1)
Staining buffer-50 ml 0.2M NaH_2PO_4 pH=7.0

*N-8505	α-Napthyl Acetate (1.5% solution in 50% acetone)	2 ml
F-0250	Fast Blue BB (after 20 minutes) (in 20 ml distilled water)	50 mg

GDH (E.C. 1.4.1.3)
Staining buffer-50 ml 0.2M Tris-HCL pH=8.0

G-1626	Glutamic acid	400 mg
N-0505	NADP (5 mg/ml)	1 ml
M-2128	MTT (10 mg/ml)	0.5 ml
P-9625	PMS (5 mg/ml)	1 ml

MDH (E.C. 1.1.1.37)
Staining buffer-50 ml 0.2M Tris-HCl pH=8.0

M-0805	Na-Malate solution (1M=13.4 g malic acid pH=7.5 12.4 g $NaCo_3$) 100 ml	5 ml
N-7004	NAD (5 mg/ml)	1 ml
	MTT	0.5 ml
	PMS	1 ml

ME (E.C. 1.1.1.40)
Staining buffer-50 ml 0.2M Tris-HCl pH=8.0

Na-Malate solution	2 ml
$MgCl_2$ 0.1M	5 ml
NADP	1 ml
MTT	0.5 ml
PMS	1 ml

PEPTIDASES (E.C. 3.4.4.)
Staining buffer-20 ml 0.1M Phosphate buffer pH=7.0
25 ml 4% agarose overlay

L-0501	Leucyl tyrosine	
V-1625	Valyl leucine	10 mg
	Leucyl glycyl glycine	
A-5147	L-amino acid oxidase	2 mg
P-8125	Peroxidase	1 mg
D-3252	O-dianisidine (dissolve in 2 ml 10% HCl or 20% ethanol)	10 mg

6-PGDH (E.C. 1.1.1.44)
Staining buffer-50 ml 0.2M Tris-HCl pH=8.0

P-7877	6-Phosphogluconate	40 mg
	NADP	1 ml
	MTT	0.5 ml
	PMS	1 ml

PGI (E.C. 5.3.9.1)
Staining buffer-25 ml 0.2M Tris-HCl pH=8.0
25 ml 4% agarose overlay

F-3627	Fructose-6-Phosphate	20 mg
	$MgCl_2$	5 ml
	NADP	1 ml
	MTT	0.5 ml
	G-6-PDH	30 units
	PMS	1 ml

PGM (E.C. 2.7.5.1)

Staining buffer-25 ml 0.2M Tris-HCl pH=8.0
25 ml 4% agarose overlay

G-1259	Glucose-1-Phosphate	100 mg
	$MgCl_2$	1 ml
	NAD	1 ml
	MTT	0.5 ml
	G-6-PDH	1 ml
	PMS	1 ml

APPENDIX 5B. Multi-locus genotypes of Porites compressa colonies sampled in six populations in Hawaii in 1988.

TABLE 5.10

a. North Kaneohe Bay (NKB) Collected 25 Jan(#1-18), 2 Feb(#19-36), 15 Feb(#37-45).

SAMPLE	DIAM.1 (cm)	DIAM.2 (cm)	AREA (cm^2)	LOCI: PGI	PGM	ME	GDH	MDH	VL	6-PGDH
1	30	60	1800	BC	C	B	B	A	B	A
2	33	12	396	A	AB	B	B	B	B	A
3	47	31	1457	A	AB	B	B	B	B	A
4	25	25	625	A	AB	B	B	B	B	A
5	44	28	1232	B	C	B	AB	B	AB	A
6	33	16	528	AC	AC	A	AB	A	B	A
7	35	28	980	B	C	B	AB	AB	AB	A
8	83	58	4814	A	BC	AB	B	AB	AB	A
9	46	38	1748	A	BC	B	AB	AB	A	A
10	44	70	3080	A	BC	AB	B	AB	AB	A
11	90	57	5130	B	C	B	AB	A	AB	A
12	69	54	3726	C	A	AB	AB	AB	B	A
13	95	60	5700	C	A	AB	AB	AB	B	A
14	00	100	10000	C	A	AB	AB	AB	B	A
15	19	75	1425	AC	A	A	AB	AB	AB	A
16	84	33	2772	A	AB	B	B	A	B	A
17	34	27	918	AB	AB	B	B	A	AB	A
18	53	55	2915	A	AB	B	B	A	B	A
19	19	31	589	AC	AC	A	AB	A	B	A
20	29	19	551	C	A	B	A	AB	AB	A
21	77	50	3850	A	AB	B	B	AB	B	A
22	15	22	330	A	AB	B	B	A	B	A
23	42	45	1890	AB	A	B	A	A	A	AB
24	65	66	4290	C	A	AB	AB	A	B	A
25	63	36	2268	AC	AC	B	AB	B	AB	A
26	50	30	1500	AC	C	B	AB	B	B	A
27	43	12	516	A	AC	B	A	B	B	A
28	45	50	2250	C	A	AB	AB	A	AB	A
29	50	30	1500	C	A	B	A	B	AB	A
30	60	43	2580	A	BC	AB	B	A	AB	A
31	26	20	520	C	A	B	A	A	B	A
32	80	42	3360	AC	BC	A	AB	AD	B	A
33	40	26	1040	B	C	B	AB	A	AB	A
34	70	45	3150	AC	BC	B	AB	AB	B	A
35	70	70	4900	C	A	AB	AB	AB	B	A
36	100	80	8000	A	AB	B	B	A	B	A
37	60	70	4200	A	AC	A	B	AB	AB	A
38	40	30	1200	A	AB	B	B	A	B	A
39	10	20	200	AB	A	B	B	A	A	A
40	45	25	1125	AC	AC	A	AB	A	B	A
41	40	45	1800	C	A	B	A	AB	AB	A
42	70	70	4900	C	A	AB	AB	AB	B	A
43	80	65	5200	AC	A	B	A	AB	B	A
44	60	40	2400	C	A	AB	AB	AB	B	A
45	50	60	3000	AC	A	A	AB	A	A	A

TABLE 5.10 (cont.)

b. South Kaneohe Bay (SKB) Collected 8 March(#1-18), 5 April(#19-45).

SAMPLE	DIAM.1 (cm)	DIAM.2 (cm)	AREA (cm^2)	LOCI: PGI	PGM	ME	GDH	MDH	VL	6-PGDH
1	38	24	912	C	A	AB	AB	A	B	A
2	16	15	240	BC	A	A	AB	AB	AB	A
3	14	12	168	C	C	B	B	A	B	A
4	6	5	30	BC	AC	AB	AB	A	AC	A
5	19	9	171	BD	AC	B	B	AB	AB	A
6	8	5	40	C	C	B	B	A	B	A
7	10	10	100	BD	AC	B	B	AB	AB	A
8	52	30	1560	A	C	AB	A	AB	B	B
9	13	9	117	C	AC	B	AB	A	A	A
10	15	15	225	B	C	B	AB	B	AB	A
11	15	22	330	AC	C	A	A	A	AB	A
12	11	9	99	AC	AB	B	AB	A	AB	B
13	21	20	420	AC	AC	A	AB	A	B	A
14	23	20	460	AB	BC	AB	AB	AB	B	A
15	13	11	143	AC	C	AB	B	A	B	A
16	23	15	345	B	C	A	A	AB	AB	A
17	35	22	770	BC	AC	B	AB	A	A	A
18	10	3	30	AB	AC	B	B	B	B	AB
19	31	21	651	A	A	B	AB	A	AB	A
20	8	9	72	C	AB	AB	B	B	B	A
21	20	16	320	B	AC	B	AB	AB	B	A
22	5	7	35	AB	AC	B	AB	A	B	A
23	20	24	480	AB	C	B	AB	A	AC	A
24	6	15	90	AB	AC	B	A	AB	AC	A
25	26	25	650	AC	A	AB	B	A	A	A
26	20	14	280	A	C	B	A	AB	A	A
27	7	5	35	AC	C	B	B	AB	B	AB
28	9	12	108	AC	C	C	AB	B	B	A
29	26	45	1170	C	C	B	B	AB	B	A
30	16	16	256	AB	C	AB	AB	AB	B	A
31	23	14	322	AB	AC	A	AB	A	A	A
32	12	4	48	AC	AB	B	AB	AB	A	A
33	12	19	228	BC	BC	AB	B	A	A	A
34	14	8	112	AC	C	B	B	A	AB	A
35	30	23	690	B	A	AB	A	A	AB	A
36	8	10	80	A	C	C	A	A	AB	B
37	16	3	48	AC	C	B	A	AB	AB	B
38	8	6	48	AC	AC	B	A	A	A	A
39	17	11	187	AC	A	AB	AB	A	B	B
40	18	8	144	A	BC	B	A	AB	B	A
41	36	17	612	AB	AC	B	AB	A	AB	B
42	50	48	2400	AC	C	AB	AB	AB	B	A
43	24	13	312	AC	A	B	AB	A	B	A
44	9	9	81	AB	C	AB	AB	AB	AB	A
45	31	28	868	C	AC	AB	AB	A	B	A

TABLE 5.10 (cont.)

c. Cocoanut Island Collected 21 March, 1988.

SAMPLE	(CI) DIAM.1 (cm)	DIAM.2 (cm)	AREA (cm^2)	PGI	PGM	ME	GDH	MDH	VL	6-PGDH
1	9	13	117	A	C	B	AB	A	B	A
2	12	15	180	AC	B	AB	AB	A	AB	B
3	5	8	40	AB	B	AB	B	AB	AB	A
4	5	11	55	A	BD	B	B	B	B	A
5	4	8	32	AC	C	B	A	AB	B	A
6	10	15	150	AB	AC	A	AB	AB	AB	A
7	16	10	160	AB	C	B	B	A	B	A
8	6	6	36	A	C	AB	AB	A	A	A
9	7	12	84	AC	A	AB	AB	A	B	A
10	7	8	56	AC	C	B	AB	A	AB	A
11	12	13	156	AC	A	AB	AB	A	AB	A
12	14	17	238	A	AB	AB	AB	A	AB	A
13	7	8	56	AC	C	AB	AB	AB	A	A
14	12	12	144	A	AB	AB	AB	AB	A	A
15	4	6	24	B	AC	B	B	AB	B	A
16	4	5	20	BC	AC	AB	A	AB	B	A
17	4	5	20	AC	C	B	B	AB	AB	A
18	8	11	88	AC	A	A	B	B	AB	AB
19	5	5	25	AB	AC	AB	A	AB	B	AB
20	5	6	30	AC	C	B	B	A	B	A
21	4	6	24	AC	A	B	A	A	A	A
22	5	7	35	AC	A	B	A	A	AB	A
23	8	11	88	C	BC	AB	AB	AB	B	A
24	7	12	84	AB	C	AB	B	A	A	A
25	5	7	35	BC	AB	AB	AB	AB	AB	A
26	6	6	36	A	A	B	AB	A	AB	A
27	11	12	132	A	AC	AB	A	A	A	A
28	12	12	144	AC	C	AB	B	A	AB	A
29	13	13	169	CE	AC	AB	A	A	AB	A
30	4	11	44	B	AC	B	B	AB	AB	A
31	5	10	50	AB	A	AB	AB	A	B	A
32	4	6	24	AC	BC	AB	B	A	B	A
33	12	13	156	AC	C	B	AB	AB	A	A
34	4	8	32	B	A	B	A	AB	A	A
35	8	10	80	AB	C	AB	B	A	A	AB
36	8	8	64	C	C	B	B	AB	B	A
37	13	15	195	C	C	B	B	AB	B	A
38	9	11	99	BC	C	AB	A	A	AB	A
39	10	13	130	B	AC	A	AB	B	A	AB
40	8	10	80	AD	C	AB	B	A	B	A
41	9	11	99	AB	C	AB	B	AB	B	A
42	14	11	154	AB	AC	B	AB	AB	A	A
43	10	13	130	AC	AC	AB	A	AD	A	A
44	18	20	360	A	AC	AB	AB	AB	A	A
45	15	11	165	BC	BC	B	B	A	A	A

TABLE 5.10 (cont.)

d. Marv's Offshore Site Collected 28 April, 1988. (MOS)

SAMPLE	LOCI: PGI	PGM	ME	GDH	MDH	VL	6-PGDH
1	C	C	B	AB	B	B	A
2	A	C	B	A	A	C	A
3	AC	A	B	B	A	C	A
4	AB	A	B	A	A	A	A
5	AC	A	B	B	A	AB	A
6	A	A	AB	AB	AB	B	A
7	AB	A	B	A	A	A	A
8	C	A	B	B	A	AC	A
9	C	A	B	B	A	AC	A
10	A	A	B	AB	A	AC	A
11	AC	A	A	AB	AB	AC	A
12	C	A	B	B	A	AC	A
13	A	C	B	A	A	AC	A
14	AC	A	B	AB	AB	AB	A
15	C	A	B	B	A	AC	A
16	AC	A	B	B	B	B	A
17	AC	A	B	B	B	AC	A
18	AC	A	B	AB	B	AC	A
19	AC	A	B	B	AB	C	A
20	AC	A	B	B	AB	AB	A
21	C	A	B	B	AB	AB	A
22	AC	AC	B	B	A	AB	A
23	AB	A	AB	A	AB	C	A
24	AB	AC	A	B	AB	C	A
25	AC	AC	B	B	AB	AB	A
26	AC	AC	B	B	AB	AB	A
27	AB	AC	B	A	B	A	A
28	AB	AC	B	AB	B	A	A
29	AC	A	AB	B	AB	C	A
30	AB	A	B	AB	B	A	A
31	C	A	B	B	AB	AB	A
32	AC	AB	AB	AB	AB		A
33	A	A	B	A	AB	AB	A
34	AC	B	AB	B	AB	A	A
35	A	A	B	AB	B	AC	A
36	A	A	B	AB	B	A	A
37	C	A	B	B	A	B	A
38	A	AB	B	A	A	AB	A
39	BC	AC	B	AB	AB	A	A
40	A	A	B	B	B	A	A
41	AC	A	B	AB	AB	A	A
42	A	A	AB	A	AB	C	A
43	A	A	B	B	AB	AB	A
44	AB	AB	B	A	A	A	A
45	AB	AC	B	B	AB	A	A

TABLE 5.10 (cont.)

e. Ianikai, Collected 22 May, 1988.

	LOCI:						
SAMPLE	PGI	PGM	ME	GDH	MDH	VL	6-PGDH
1	AB	A	B	B	AB	B	A
2	A	AC	A	AB	A	C	A
3	AB	AC	B	AB	A	A	A
4	BC	A	C	B	A	C	A
5	AB	AC	AB	A	AB	A	A
6	A	AC	AB	AB	A	A	A
7	A	A	B	AB	AB	A	A
8	A	AC	AB	AB	A	C	A
9	AC	A	A	A	A	A	AB
10	A	A	B	AB	AB	AC	A
11	A	AC	AB	B	B	AC	A
12	A	AC	AB	AB	A	A	A
13	AB	AC	B	AB	A	A	A
14	A	AC	AB	AB	A	A	A
15	AC	A	A	A	A	A	AB
16	A	AC	B	AB	A	C	A
17	A	AC	AB	B	B	A	AB
18	AB	AC	B	A	AB	A	A
19	AB	AC	AB	A	A	C	A
20	BC	AB	B	B	AB	A	A
21	AB	AC	AB	A	AB	A	A
22	A	A	B	AB	AB	B	A
23	AC	AC	B	B	A	AB	AB
24	AB	A	B	A	A	A	A
25	AB	AC	B	AB	A	B	A
26	AC	A	B	B	AB	A	AB
27	AB	A	B	B	AB	A	A
28	A	A	B	AB	B	A	AB
29	A	A	B	AB	AB	A	A
30	A	A	B	AB	A	A	A
31	A	AC	B	AB	AB	A	A
32	A	A	B	AB	AB	B	A
33	AB	AC	B	A	AB	A	AB
34	AB	AC	B	A	AB	A	AB
35	AB	AC	B	A	AB	A	AB
36	A	AC	AB	AB	A	C	A
37	A	A	B	B	A	C	A
38	AC	A	B	B	A	C	A
39	A	A	B	AB	AB	A	A
40	A	AC	B	AB	A	A	AB
41	A	A	B	AB	A	A	A
42	A	AC	B	AB	A	C	A
43	BC	AB	AB	BD	AB	A	A
44	A	A	A	AB	AB	B	A
45	AB	BC	BC	AB	AB	A	A

TABLE 5.10 (cont.)

f. Big Island, Kona, Collected 18 November, 1987.

SAMPLE	LOCI: PGI	PGM	ME	GDH	MDH	VL	6-PGDH
1	AC	A	B	AB	AB	B	A
2	C	A	B	B	A	A	A
3	AC	A	B	AB	A	B	A
4	C	AC	AB	AB	AB	A	A
5	A	A	AB	B	B	B	A
6	AC	A	B	B	AB	C	A
7	A	A	AB	B	A	A	A
8	C	A	A	AB	A	B	A
9	AC	A	AB	AB	A	A	A
10	AC	A	AB	A	AB	AC	A
11	AC	AC	B	B	A	C	A
12	C	A	B	B	AB	C	A
13	C	A	A	B	A	C	A
14	AC	A	B	A	AB	BC	A
15	AC	A	A	B	AB	C	A
16	C	A	A	AB	B	BC	A
17	C	A	AB	AB	AB	A	A
18	A	A	AB	B	A	A	A
19	C	A	B	AB	A	B	A
20	C	A	A	AB	AB	B	A
21	AC	AC	B	B	A	C	A
22	AC	A	B	AB	AB	A	A
23	A	A	B	B	A	B	A
24	C	A	B	B	A	C	A
25	A	A	AB	AB	A	C	A
26	AC	A	B	AB	AB	B	A
27	AC	AC	B	B	A	B	A
28	A	AC	B	AB	A	C	A
29	A	A	AB	B	A	A	A
30	AC	A	AB	B	AB	A	A
31	A	A	B	B	A	C	A
32	AC	AC	B	B	B	C	A
33	A	AC	AB	A	AB	C	A
34	A	AC	AB	A	AB	C	A
35	A	A	AB	A	A	B	A
36	AC	A	AB	AB	A	C	A
37	AC	A	B	A	AB	C	A
38	C	AC	B	A	A	A	A
39	AC	AC	B	B	A	B	A
40	A	A	A	AB	B	B	A
41	AC	AC	B	AB	A	C	A
43	A	A	B	AB	A	A	A
44	AC	C	A	AB	A	B	A
45	AC	AC	AB	AB	B	A	A

SUMMARY

The assessment of genetic identity in clonal populations can be undertaken using a number of methodologies. The "best" resolution of genotypes may be attained from independent and corroborative assays. In Porites compressa, electrophoresis of soluble proteins provides the single most efficacious assay of genotypic diversity, with a 7-locus (21 alleles) system which is estimated to resolve approximately 95% of clonal samples.

Populations of Porites compressa have been demonstrated to derive substantial contributions from both sexual and asexual modes of reproduction. Sexual reproduction in P. compressa is similar in most life history parameters to other Porites species that broadcast spawn. Age at first reproduction is estimated to be between 1.8 and 2.5 years. Mean oocyte diameters are approximately 250 um at spawning, with 10-30 eggs per polyp. Spawning is synchronized with full moon during summer months, and some colonies may spawn over more than one night and over subsequent months. Planulae are competent to metamorphose after three days, and sibling juveniles which settle gregariously have been observed to fuse.

Production of asexual propagules by fragmentation has been calculated to be between 35 and 96 fragments/m^2/year for a patchreef population of Porites compressa in Kaneohe Bay. Fragment production is continuous through the year, with a 5-10 fold increase in the summer due in part to increased activity of turtles near sheltering

areas on the reef. Asexual propagules are large (1.5-151 cm^2) and may survive for many weeks or months before "recruiting" or being lost from the fragment pool.

Spatial and/or numeric dominance of some clones of Porites compressa can be explained, in part, by measurable local fitness parameters of growth rate and competitive ability. No significant differences in the propensity of clones to produce fragments were detected. The relationship between clonal abundance and single fitness correlates, however, is not a simple one. Clonal fitness is the sum of many life history and ecological characteristics of a genotype. Clonal abundance and distribution may also be effected by non-selective random physical processes leading to asexual colony replication and recruitment.

Genotypic diversity in six populations of Porites compressa is directly related to habitat disturbance histories. Highest diversity is found in populations which have been intensely or recently disturbed and are in the process of recolonization. In these populations, space is not limited and direct competition among clones is rare. In stable, undisturbed populations, clonal replication of established genotypes leads to lower diversity. Unoccupied substratum is rare in these habitats, and competition for space may result in the elimination of clones with slower growth rates or poor competitive ability. Single clones may be distributed over small or large areas (<1 to >16 m^2) or distances (<1 to >90 m), and may be numerically (>13% of total number of colonies) or spatially (>15% of total colony area) dominant.

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