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GENOTYPIC VARIATION AND CLONAL STRUCTURE IN CORAL POPULATIONS WITH DIFFERENT DISTURBANCE HISTORIES

CYNTHIA L. HUNTER*
Hawaii Institute of Marine Biology,
University of Hawaii, Kaneohe, HI 96744

Abstract.—Genotypic diversity in six populations of the endemic Hawaiian reef coral, *Porites compressa*, was directly related to habitat-disturbance history. The highest diversity (lowest amount of clonal proliferation) was found in populations that had been intensely or recently disturbed. In these populations, space was not limited and mean colony size was small (< 500 cm^2), suggesting early stages of recolonization. In an undisturbed, protected habitat, lower genotypic diversity was a result of a significant degree of clonal replication of established genotypes. Unoccupied substratum was rare in this habitat, and average colony size was large (> 2500 cm^2). Populations in intermediately disturbed habitats showed intermediate levels of diversity and clonal structure as a result of the combined contributions of sexual and asexual reproduction. Individual clones were distributed over small areas (< 4 m^2) or distances (< 1 m) in young populations, and more broadly (> 256 m^2) and over longer distances (> 90 m) in the older, undisturbed population. Interpretations of life-history parameters and estimates of total genetic variability in species that have the potential to reproduce asexually are dependent upon an assessment of the overall clonal structure of populations. The power of genotypic assays to reliably detect clonal versus unique colonies, as well as the spatial scales over which clonal populations are sampled, are critical to such assessments.

Key words.—Clonal structure, disturbance, genotypic diversity, scleractinian corals.

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Determinations of the abundance and distribution of asexually derived ramets in clonal populations are critical to assessments of genetic variability, estimations of important life history-parameters, and testing of hypotheses concerning most aspects of evolutionary change within and among clonal species (Hughes 1989). Estimates of genetic identity and divergence among populations may be biased by the contributions of clonal replicates to calculated allele frequencies (Stoddart 1984a; Ayre and Willis 1988). Estimates of diversity in populations will also depend on the spatial scale over which clonal distributions are measured and the precision and efficacy of assays used to distinguish clones (Hoffmann 1986; Ellstrand and Roose 1987; Mladenov and Emson 1990).

Factors that may affect genotypic diversity within populations include the relative levels of production, recruitment success, and survival of sexual versus asexual propagules (Hughes 1989). The influences of these factors may vary both among and within species, and will be dependent on the various environmental regimes and physical disturbances experienced by populations. Physical disturbances cause mortality among sessile individuals, opening new space for recruitment from both sexual and asexual sources. Disturbances may also accelerate the production of asexual propagules, particularly in organisms that reproduce by fragmentation such as sponges (Wulff 1985), gorgonians (Lasker 1990), corals (Tunnicliffe 1981; Highsmith 1982), asteroids (Crump and Barker 1985), and ophiuroids (Mladenov and Emson 1990).

For most clonal species, it may be expected that new or highly disturbed habitats will be colonized initially by sexually derived recruits. [Important exceptions may include species with parthenogenetically or asexually produced larvae, for example, the reef coral *Pocillopora damicornis* (Stoddart 1983, 1988).] Genotypic diversity will remain (maximally) high with continued recruitment of sexually derived propagules until either (1) established genotypes begin producing asexual propagules, or (2) competitive interactions among established clones exclude or eliminate less-fit genotypes. In stable or mature habitats, locally adapted clones may propagate asexually and become dominant through competitive advantage, thereby minimizing the availability of unoccupied substratum and limiting opportunities for recruitment of new genotypes. Populations such as these are expected to be almost wholly structured by the processes of clonal replication and competition, with a re-

* Present address: Botany Department, University of Hawaii, 3190 Maile Way, Honolulu, HI 96822.

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sultant decrease in genotypic diversity. In situations where periodic disturbances create new areas of bare substratum, opportunities may occur for both new sexual recruits and asexually produced propagules to become established in the population. Genotypic diversity in these habitats should then depend on the frequency and intensity of disturbance as factors in the creation of available space, and the relative success of sexual and asexual recruitment.

The effects of disturbance on genotypic diversity within populations of species with both sexual and asexual modes of reproduction have been modeled by Sebens and Thorne (1985). Their models predict that intermediate disturbance or nonequilibrium situations will promote the highest levels of clonal diversity under a variety of conditions (Sebens and Thorne 1985, p. 387). Population projections for two clonal species showed increasing genotypic diversity with higher levels of disturbance. Direct analysis of clonal diversity in populations at different successional stages or under various environmental regimes can test these model predictions and provide a more thorough description of the overall spatial and/or temporal characteristics of clonal population structure within a species (Ellstrand and Roose 1987). In the present study, the relationship between genotypic diversity and disturbance history was investigated in populations of the scleractinian coral, *Porites compressa.*

Materials and Methods

Porites compressa is one of the most abundant scleractinian corals in Hawaii and occurs in a variety of habitats on all islands in the Hawaiian chain. This endemic species often forms extensive monospecific stands, with total cover approaching 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). *P. compressa* is gonochoric, reproducing sexually by broadcast spawning of eggs and sperm at full moon during summer (Hunter 1988). Asexual propagules are produced continuously throughout the year by fragmentation of branches from parent colonies (Hunter and R. Kinzie unpubl. data).

Sampling was conducted within six sites, five on Oahu and one on the island of Hawaii (fig. 1). These sites were chosen a priori to represent a range of disturbance regimes of various recency and intensity. Criteria used to classify successional age and habitat stability in these populations are presented in table 1. Colony size was measured at and perpendicular to the maximum diameter of each colony sampled. At the three sites within Kaneohe Bay (NKB, SKB, and CI), colonies displayed compact and discrete growth forms; however, colonies at the KBO, LAN, and HAW sites were thicketlike, with live tissue restricted mainly to distal branch tips. Although colony borders could not always be accurately determined at these sites, colony sizes were estimated as ranging from 0.5 to 1.0 m in maximum diameters. The percentage of unoccupied substratum (sand, bare rock, algal turf, or calcareous algae) was visually estimated. Disturbance histories for each site were compiled from the available literature, personal observations, and interviews with local residents. Because various types of disturbances differ in their impacts on fragment production and the opening of new space, an index was developed that incorporated both disturbance intensity and recency into a single descriptor for each site.

The three sites located within Kaneohe Bay, Oahu, are protected from storms and swells by an extensive barrier reef system. Age of patch reefs within the bay has been estimated at 8000 to 10,000 years (Roy 1970). The North Kaneohe Bay site (**NKB**) is nearest to the mouth of the bay, and subject to occasional gentle swells. Because of its depth and distance from shore, however, this site has not been affected by subaerial exposure, freshwater flooding events, or pollution characteristic of near-shore fringing reefs in the bay (Banner 1968; Jokiel et al. in press). The reef at the South Kaneohe Bay site (**SKB**) was dredged to a depth of 3.3 m in the early 1940s for a seaplane runway (Roy 1970). The south end of the bay was also severely affected by a major sewage outfall from the 1940s until 1978, when the outfall was diverted offshore. At that time, there were almost no corals living in the south basin because of high turbidity and algal overgrowth (Smith et al. 1981), but a gradual recovery of the coral community began as eutrophication diminished (Maragos et al. 1985). A nearby site (**CI**) consisted of colonies growing on the vertical surface of a 30-m section of concrete seawall built 20 to 25 years ago. This site was selected to represent a population in which all colonies were assumed to be of sexual (planular) origin because of the difficulty of an asexual fragment attaching to the smooth vertical face of the wall. This assumption was supported by the lack of colonies greater than 25 cm in diameter on the wall, prob-

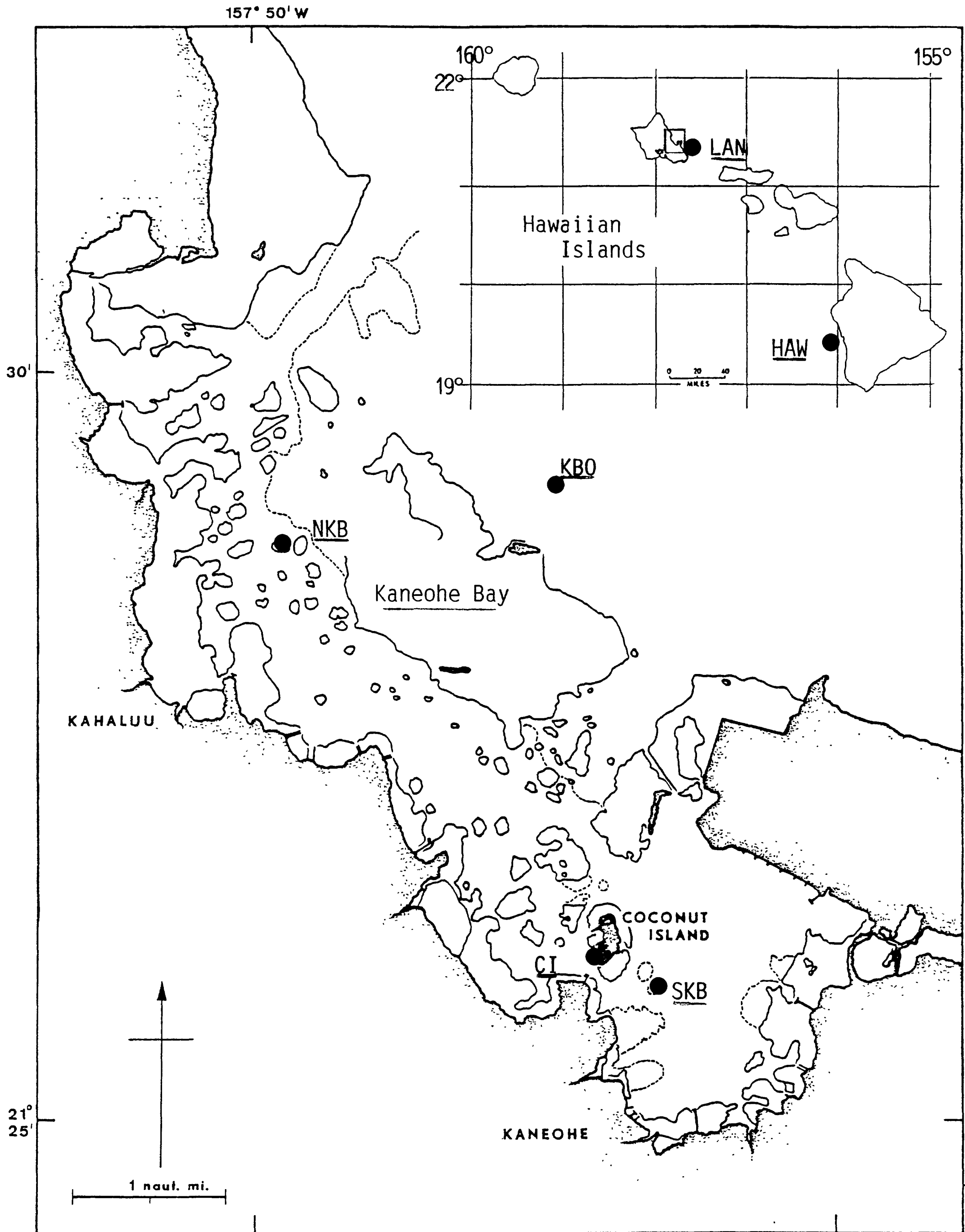


FIG. 1. Location of six sampling sites (NKB, SKB, CI, KBO, LAN, and HAW) of *Porites compressa* in Hawaii.

ably because the weight of larger colonies exceeds the strength of their basal attachments.

A fourth site (**KBO**) was located on the outer slope of the barrier reef across the mouth of Kaneohe Bay. This reef slope is exposed to swells generated by prevailing tradewinds and occasional winter storms. The **LAN** site was located in the bay immediately south of Kaneohe, on a fringing reef that extends 1.25 km from shore. This area typically has calm sea conditions close

TABLE 1. Characteristics of sampling sites for six populations of *Porites compressa*: North Kaneohe Bay (NKB), South Kaneohe Bay (SKB), Coconut Island (CI), Kaneohe Bay, Offshore (KBO), Lanikai (LAN), and Kealakekua Bay, Hawaii (HAW).

Site	Reef type (depth)	Maximum colony diameter	Unoccupied substratum	Intensity of disturbance	D_I†	Time since disturbance	D_T‡	Disturbance index ($\Sigma D_I/D_T$)
NKB	patch reef (2–3 m)	4.5 m	<5%	low	1	chronic§	.02	50
SKB	patch reef (2–3 m)	0.5 m	50%	low	1	chronic	.02	150
				very high	1000	10 yr; 40 yr‖	10	
CI	retainment wall (< 1 m)	0.2 m	80%	low	1	chronic	.02	383
				very high	1000	3–5 yr#	3	
KBO	fore reef (12–15 m)	*	65%	low	1	chronic	.02	80
				moderate	10	1–4 yr**	1	
				high	100	5 yr‡‡	5	
LAN	back reef (2–3 m)	*	75%	low	1	chronic	.02	60
				moderate	10	1–35 yr††	1	
HAW	fore reef (12–15 m)	*	35%	low	1	chronic	.02	74
				moderate	10	1–4 yr**	1	
				high	100	6 yr‡‡	7	

* Colony borders not distinct; actual colony sizes not determinable.

† D_I (intensity of disturbance) values were assigned on an exponential scale from 1 to 1000: 1 = low intensity, occasional branch tips broken, little space made available for new recruits (sexual or asexual); 10 = moderate intensity, numerous branches broken, some new space made available; 100 = high intensity, entire colonies broken and dislodged from substratum, substantial new space available; and 1000 = very high intensity, total mortality of all colonies, all space available.

‡ D_T values indicate the minimum time (in years) since last disturbance. D_T for chronic disturbance was estimated at 0.02 yr (approximately weekly), although levels may vary seasonally and among sites. Relative chronic disturbance among sites was subjectively evaluated as LAN > HAW > NKB > SKB > KBO > CI.

§ "Chronic" disturbance is that caused at frequent (daily) intervals by physical impacts of fish, turtles, or human activities (divers, boat anchors, fishing tackle, and nets) resulting in colony breakage and production of fragments.

‖ The top of this reef was dredged to a depth of 3.3 m depth in 1939. Severe eutrophication of the South Bay occurred between 1963 and 1978; sewage diversion in 1978 was followed by a rapid recolonization by scleractinian corals.

Colonies are lost from this population when they exceed a size that can be supported by their basal attachments on the sea wall; time since this "disturbance" was estimated from the sizes of remaining colonies on the wall.

** Average return time of storms of moderate intensity, generating wave heights of 3 to 5 m is 1 to 4 yr (Dollar 1982); wave height data for the KBO site were provided by Naval Ocean Systems Center (S. Henderson pers. comm. 1990).

†† From 1951 to the present, shoreline accretion and erosion at this site (measured at ±46 m; Hwang 1981) was accompanied by substantial local transport of sand resulting in continuous burial and scour of hard substratum and small colonies.

‡‡ Average return time of "severe" storms generating waves of 5 to 7 m is 40 yr; such storms impacted the KBO site in March 1983 (Naval Ocean Systems Center; S. Henderson pers. comm. 1990) and the HAW site in January 1980 (Dollar 1982).

to shore but has been subjected to considerable sand movement with continuous scour and burial of corals. Periodic storms have caused extensive damage to the monospecific stands of *P. compressa* characteristic of the HAW reef slope site, on the island of Hawaii, with approximate intervals of 4 ("intermediate" intensity) to 40 ("severe" intensity) years (Dollar 1982). All sites have been subject to chronic, low intensity disturbances from human impacts, primarily boat anchoring and fishing, as well as natural bioerosion and collisions from fish and turtles that result in fragmentation of colonies.

Sampling Methodology

Samples of 45 colonies each from the NKB, SKB, KBO, and HAW populations were collected following a nested quadrat sampling design 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 extent of individual genets (clones). Nested-quadrat sampling eliminates bias that would result from fixed-size quadrats that otherwise define the spatial scale over which clones can be detected.

Random numbers were used to plot point locations of colonies to be sampled. Five random points were drawn from each of the first three nested quadrats (1 m^2, 4 m^2, 16 m^2), and 15 points each from the fourth and fifth quadrats (64 m^2 and 256 m^2). An area of 256 m^2 within each field population was marked by stakes and

TABLE 2. Enzymes assayed for populations of *Porites compressa* in Hawaii.

Enzyme	E.C. no.*	Number of alleles	Subunit structure	Electrophoretic buffer†
	1986 assays			
Esterase-B (EST-B)	3.3.3.–	2	monomer	2
Leucyl-glycyl-glycine peptidase (LGG)	3.4.–.–	2	dimer	6
Leucyl-tyrosine peptidase (LTY-1,2)	3.4.–.–	2,2	dimer	6
Glutamate dehydrogenase (GTDH)	1.4.1.2	2	?	5
	1988 assays			
Glutamate dehydrogenase (GTDH)	1.4.1.2	3	?	5
Glucose-6-phosphate isomerase (GPI)	5.3.1.9	5	dimer	2
Malate dehydrogenase (MDH)	1.1.1.37	3	dimer	2
Malate dehydrogenase-NADP+ (MDH-P)	1.1.1.40	2	tetramer	5
Phosphoglucomutase (PGM)	5.4.2.2	3	monomer	2
Phosphogluconate dehydrogenase (PGDH)	1.1.1.44	2	dimer	5
Valyl-leucine peptidase (VL)	3.4.–.–	3	dimer	6

* Hillis and Moritz (1990).
† Buffer recipes from Selander et al. (1971).

the plotted points were located within the resultant grid. Colonies under or closest to each predetermined point were sampled. Because coral cover at the LAN site was patchy, 45 colonies were haphazardly sampled from a 2-m-wide belt transect extending approximately 20 m to 110 m perpendicular to shore. CI samples were collected from each of the first 45 colonies (> 10 cm minimum diameter) encountered along a 30-m section of seawall. The NKB, SKB, and HAW populations were sampled in 1986. All six populations were sampled in 1988.

Genetic Analysis

Six to 10 branch tips were removed from each colony sampled. As freezing affected activity of some enzymes, half of the branches were maintained alive in flowing sea water while the remainder were frozen at −80°C until assayed.

Electrophoresis.—Multilocus genotypes were determined electrophoretically for all corals sampled (table 2). A total of 133 colonies from the three populations sampled in 1986 was analyzed for five enzyme systems. The 269 colonies from six populations sampled in 1988 were scored for seven loci. Tissue extraction methods followed those of Stoddart (1983), and buffers and stains were prepared following methods of Selander et al. (1971), Redfield and Salini (1980), and D. Potts (unpubl. data). Horizontal gels utilized Electrostarch (11.4% wt/vol) for 1986 samples and Sigma starch (12.0% wt/vol) for 1988 samples. Descriptions of enzyme assays used for *P. compressa* samples are given in table 2. The 1986 samples were scored for GTDH, LTY-1, LTY-2, LGG, and EST-B; 1988 samples were scored for GPI, PGM, MDH-P, GTDH, MDH, VL, and PGDH. EST-B, LTY, and LGG stains gave smeared or inconsistent bands in the 1988 assays, possibly because of the change of starch used in the gels, and could not be reliably scored.

Analysis of Electrophoretic Data.—Allelic and genotypic frequencies were determined for each population. An estimation of the power of the seven loci to differentiate unique genotypes was done in two ways, both based on genotypic data from the CI population in which each colony was assumed to be the result of settlement of sexually produced planula larvae and therefore genetically unique. First, diversity was calculated as a function of the mean number of unique genotypes that were resolved by each locus individually (Hoffmann 1986). The sequential addition of the total number of genotypes resolved with all possible combinations of two, three, four, five, six, and seven loci provided a plot of observed diversity versus cumulative number of loci assayed (fig. 2). Second, the ratio of repeated genotypes to total sample size for the CI population provided an index of the probability of assigning genetically different individuals to the same multilocus 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 by any colonies that shared the same seven-locus genotype. For a population in which every colony is unique (e.g., no clonal

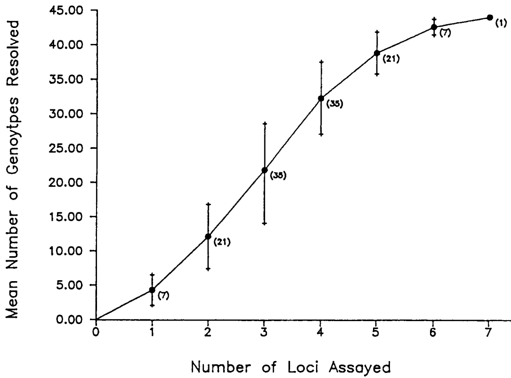


FIG. 2. Mean number of unique genotypes resolved with the sequential addition of electrophoretic loci assayed in the Coconut Island (CI) samples. Bars show standard error. Numbers in parentheses indicate the number of permutations of loci that were averaged to arrive at the means.

replication has occurred), genotypic frequencies should conform to Hardy-Weinberg equilibria under the assumptions of random mating, recombination, and no selection. Observed genotypic diversity was calculated as

$$G_0 = 1 \Big/ \sum_{x=0}^{N} f_x \cdot (x/N)^2$$

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. Observed genotypic diversity (G_o) was compared to the genotypic diversity expected under Hardy-Weinberg equilibrium G_e ($\tilde{G}$), calculated from a simple binomial expansion of the frequencies of genotype classes using a program provided by J. Stoddart to P. Mladenov (pers. comm. 1987). Degree of departure of G_o:G_e from unity provided an index of deviation from both H-W equilibria and multilocus linkage equilibria. A population dominated by a few clonal types will have low G_o:G_e ratios, and G_o:G_e approaches unity as genotypic individuality is maximized.

To facilitate comparisons with genetic studies of other plant and animal populations (e.g., Parker 1979; Hoffmann 1986; Ellstrand and Roose 1987), diversity was also calculated three additional ways: (1) as D, the complement of Simpson's Index (SI) (Simpson 1949):

$$D = 1 - \mathrm{SI} = 1 - \sum n_i(n_i - 1)/N(N - 1),$$

where n_i is the number of individuals belonging to the ith clone, and N is the total number of individuals sampled per population; (2) as $D^* =$ the number of unique genotypes/N; and (3) as E, a measure that allows scaled comparisons among populations with different clone sizes and sample sizes (Parker 1979), calculated as

$$E = (D_{\mathrm{obs}} - D_{\mathrm{min}})/(D_{\mathrm{max}} - D_{\mathrm{min}})$$

Both D^* and D vary between 0 and 1, with 1 indicating a population where all colonies are unique. E, which estimates evenness, also ranges from 0 ($D_{\mathrm{obs}} = D_{\mathrm{min}}$, complete unevenness) to 1 ($D_{\mathrm{obs}} = D_{\mathrm{max}}$, complete evenness).

RESULTS

Resolution of Genetic Diversity

Interpretations of banding patterns for *Porites compressa* were consistent with multiple allele systems described for other diploid species (Harris and Hopkinson 1976; Hillis and Moritz 1990). Most gels produced distinct and clear bands for all assays with the exception of those stained for GTDH and MDH. Interpretations of these gels were made with caution, and assays for each coral sample were repeated until consistent results were attained.

GTDH has been variously interpreted among different taxa as a dimer (Harris and Hopkinson 1976), a tetramer (Hillis and Moritz 1990), and a hexamer (D. Ayre pers. comm. 1986). Based on molecular weight and SDS-PAGE mobility of the purified GTDH enzyme from the staghorn coral *Acropora formosa,* Catmull et al. (1987) determined that the subunit structure is probably tetrameric. For *P. compressa,* diffuse bands intermediate in migration to those interpreted as representing the two homozygous states were scored as heterozygotes but were not resolved sufficiently to determine subunit structure. Similarly, resolution of MDH, reported to be dimeric in other plant and animal species examined (Harris and Hopkinson 1976; Hillis and Moritz 1990) was poor for many samples of *P. compressa*; two (often smeared) bands were interpreted in this study as the heterozygous condition, with the (normally) third band presumably masked by the band staining for either the A or B allele. *Pocillopora damicornis* has shown a similar anomalous banding pattern for heterozygotes at the *MDH* locus (Stoddart 1985). All loci assayed were polymorphic within each population of *P. com-*

TABLE 3. Comparisons of estimates of genotypic diversity between samples of *Porites compressa* assayed at different loci. G_O, observed genotypic diversity, and D*, number of unique genotypes/*N*.

	No. of loci assayed	No. of alleles found/ population	No. genotypes	G_O	D^*
NKB					
1986	5	10	16	11.29	0.356
(w/GPI)	6	13	28	22.27	0.622
1988	7	16	29	17.92	0.644
SKB					
1986	5	10	23	14.89	0.511
1988	7	19	43	41.32	0.956
HAW					
1986	5	10	26	19.36	0.578
1988	7	15	39	34.60	0.886

pressa, with the exception of *PGDH,* which was fixed in the KBO and HAW populations.

The seven enzyme systems (total of 21 alleles) used in the 1988 analyses resolved all but one of the 45 genotypes assumed to be unique in the CI population. The probability of assigning genetically different individuals of *P. compressa* to the same multilocus genotype using these assays (Type II error) was thus estimated at 2.2%. A plot of the cumulative number of resolved genotypes against sequential addition of all permutations of loci approaches an asymptote between the sixth and seventh loci (fig. 2). However, variations in local gene frequencies dictate that more loci may be required to identify and distinguish between all clones in all populations.

The five loci (ten alleles) assayed in the 1986 samples were not sufficient to resolve true clonal structure in the NKB, SKB, and HAW populations (Hunter 1985). Only 16 (NKB), 23 (SKB), and 26 (HAW) genotypes were detected among the 45 samples from NKB and 44 samples each from SKB and HAW populations, yielding correspondingly low indices of diversity among the three populations (table 3). The addition of one more locus (*GPI*: 3 alleles) increased the total number of genotypes scored from 16 to 28 for the NKB population and essentially doubled the diversity indices. *GPI* produced clearly resolvable bands for fresh tissue in *P. compressa,* but only frozen samples were available for *GPI* analyses for SKB and HAW in 1986. Estimated relative levels of diversity as measured by G_o and

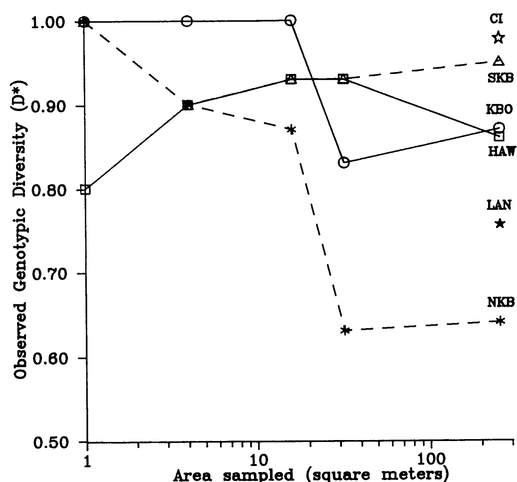


FIG. 3. Observed genotypic diversity (D^*) as a function of total area sampled in four populations of *Porites compressa*: North Kaneohe Bay (NKB), South Kaneohe Bay (SKB), Coconut Island (CI), Kaneohe Bay, Offshore (KBO), Lanikai (LAN), and Kealakekua Bay, Hawaii (HAW).

D^* changed from HAW > SKB > NKB to SKB > HAW > NKB in the 1986 and 1988 analyses, respectively.

Variation among Populations

Genotypic diversity and structure varied among *Porites compressa* populations (table 4). Proportions of asexually derived colonies ($1 - D^*$) ranged from 4% in the SKB population to 36% at the NKB site. Although most recruitment at the SKB site was apparently from sexual propagules, two genotypes were represented by two colonies each suggesting that asexual propagation can begin relatively soon after establishment of a population. The two sets of clonal replicates were within 0.6 to 3.0 m of their clone mates, the shortest distances of clone mates among any of the study sites. In contrast, the NKB population had the lowest clonal diversity (29 genotypes in 45 colonies sampled), the highest number of colonies per clone (6), and the highest average clone size (1.55 colonies) of all populations in this study. Sampled clone mates were up to 15.9 m apart. The KBO, LAN, and HAW populations were characterized by intermediate diversities, with proportions of asexually derived colonies ranging from 11 to 24%, and clone mates were scattered from 1.0 to 16.5 m apart within the 256 m^2 sampling areas.

The relative genotypic diversities observed in

TABLE 4. Summary of genotypic diversity and clonal distributions in six populations of *Porites compressa* sampled in 1988. *N*, number of samples per population; G_O, observed genotypic diveristy; G_e, expected genotypic diversity; D^*, number of unique genotypes/*N*; *D*, 1 − Simpson's Index; and *E*, scaled evenness value (see text for formulas); N.D., no data.

	NKB	SKB	CI	LAN	KBO	HAW	Mean ± SD
N	45	45	45	45	45	44	
No. of genotypes	29	43	44	34	39	39	38.00 ± 5.65
G_O	17.92	41.32	43.10	28.57	32.15	34.60	35.47 ± 7.74
G_e	42.02	43.74	43.45	42.09	40.61	39.35	41.88 ± 1.67
±SE	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	0.879	0.786 ± 0.209
D^*	0.644	0.956	0.978	0.756	0.867	0.886	0.848 ± 0.127
D	0.966	0.998	0.999	0.987	0.991	0.994	0.989 ± 0.012
E	0.851	0.999	0.999	0.946	0.801	0.896	0.918 ± 0.082
Clone size	Frequency						
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	3	
1	22	41	43	25	35	35	
Mean no. colonies/clone	1.55	1.05	1.02	1.32	1.15	1.13	
±SD	1.24	0.21	0.15	0.59	0.54	0.41	
Distance between clonemates (m)							
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	

six populations of *P. compressa* are portrayed in figure 3. For those populations sampled with the nested quadrat design (NKB, SKB, KBO, HAW), the various levels of diversity observed with increasing numbers of colonies and total area sampled provide descriptions of the effective dispersal distributions of clones. In the NKB population, clone mates were found within all quadrat sizes greater than 1 m^2. Clone mates in the KBO population were distributed over a wider area than detected by the 1 m^2, 4 m^2, or 16 m^2 quadrats but were most apparent at 32 m^2 as evidenced by an abrupt drop in relative clonal diversity within this quadrat. The HAW population showed a high degree of clonal replication in the smallest quadrats (1 m^2 and 4 m^2), less in the intermediate sizes, and widely dispersed clones were again identified in the largest quadrat. Clone mates were found only in quadrats less than 32 m^2 in the SKB population. It should be noted that the sampling regime was not designed to detect *all* clones or the distributions of *each* genotype in a population but rather to provide a reasonable estimate of levels of clonal replication at each site.

A total of 212 unique seven-locus genotypes was 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 the Kaneohe Bay area (NKB, SKB, CI, and KBO), G_o was 109.89 ($D^* = 0.8280$). Thirteen genotypes (4.8%) were found in more than one population (three shared between NKB and SKB, three between HAW and LAN, two between KBO and LAN, two between CI and SKB, and one each between SKB—LAN, KBO—HAW, and HAW—SKB). This overlap reflects the limits of resolution of the seven-locus system for detection of individuals over the entire species. No genotype was found in more than two populations.

Genet Size and Distributions

Sampled genet sizes within each population ranged from one to six colonies with means of 1.02 to 1.55 colonies/clone (table 4). Clonal distributions within each of the populations sampled by the nested quadrat design are shown in figure 4. Distances between clone mates varied within and among populations, with HAW having both the closest (1.0 m) and most distant

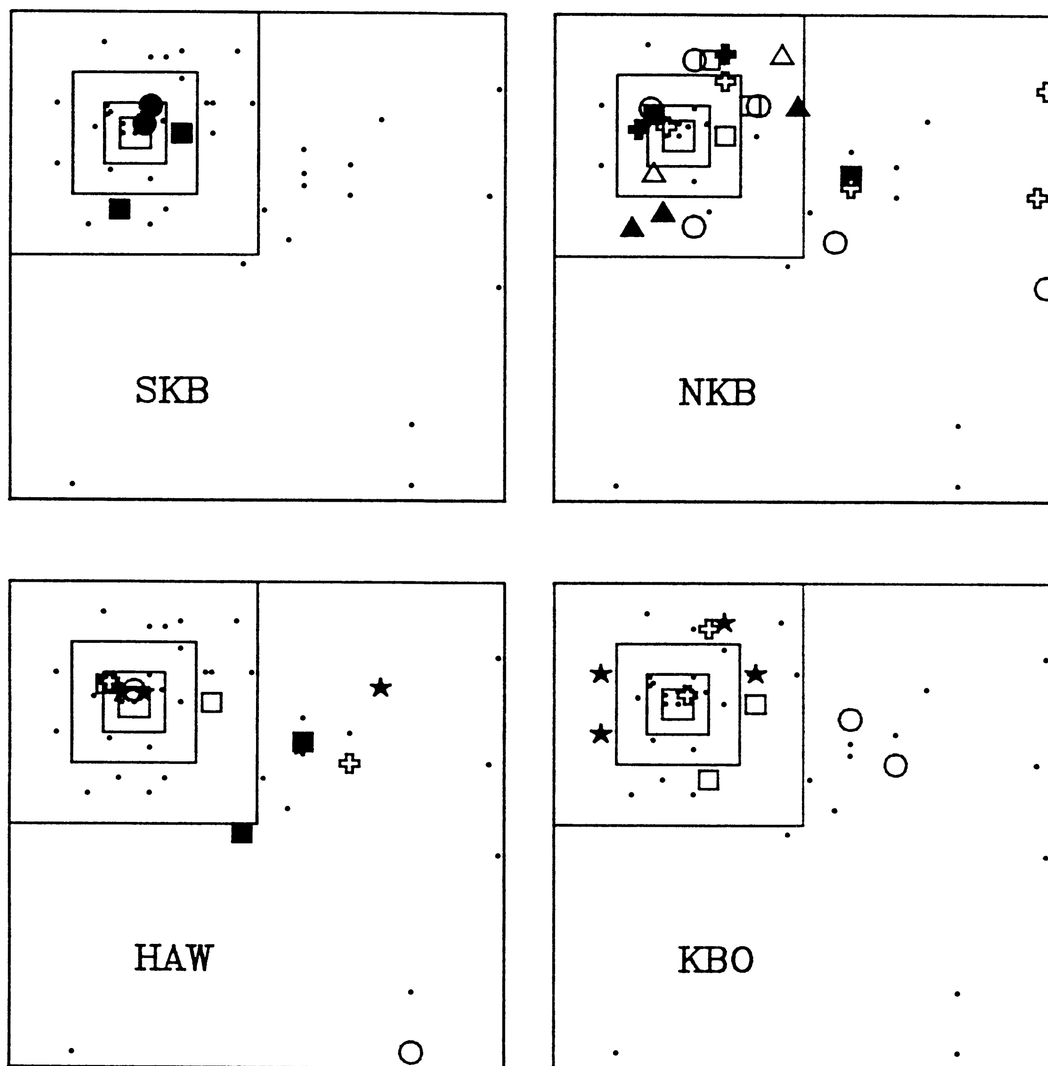
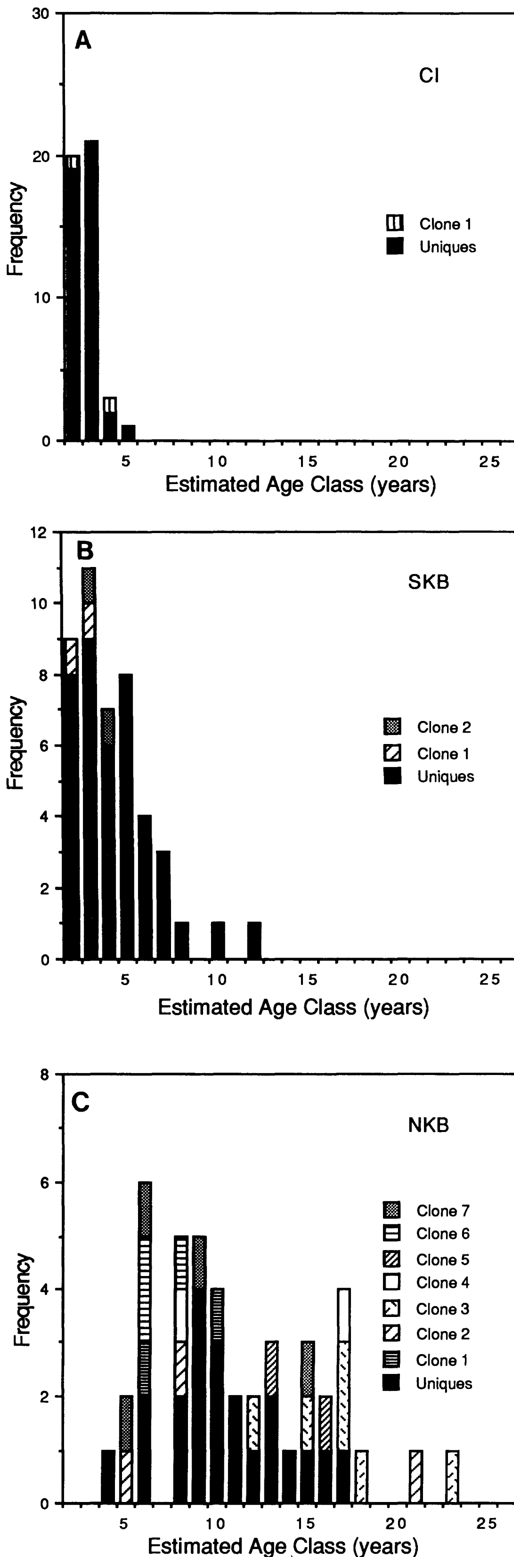


FIG. 4. Distributions of clones within four populations of *Porites compressa* sampled by nested quadrat design. Dots indicate location of samples from genotypically unique colonies; symbols represent genotypes that occurred two or more times within a population. Numbers of replicated genotypes were: South Kaneohe Bay (2), Kaneohe Bay, Offshore (4), Hawaii (5), and North Kaneohe Bay (7); all other genotypes were found only once in each population.

(16.5 m) colonies with identical multilocus genotypes.

Mean colony size was significantly different (log-transformed, *t*-tests, $P < 0.01$) among each of the sites (NKB = 2586 ± 2079 cm^2, SKB = 366 ± 449 cm^2, CI = 96 ± 70 cm^2) within Kaneohe Bay. Although colony size is not always an accurate predictor of absolute age of a coral genet (Hughes and Jackson 1980; Hughes and Connell 1987), it can provide a rough estimate of the minimum age of a colony if growth rates are known. Mean linear growth of *Porites compressa* colonies measured in NKB (3.1 ± 0.39 cm/yr; Hunter 1988) and in south Kaneohe Bay (3.5 ± 0.40 cm/yr; Jokiel 1985) suggests that colonies at both sites grow at about the same rate. With the assumption that a new sexual recruit grows to a diameter of 1 to 2 cm in its first year (Fitzhardinge 1985) and that colonies have a mean radial growth rate of 2.46 cm/yr (Polacheck 1978), approximate colony age structures were generated for each site (fig. 5A–C). Ages of



sampled colonies ranged from 4 to 23 yr at the NKB site, from 2 to 12 yr at the SKB site, and 2 to 5 yr for colonies on the wall at the CI site. Clonally derived colonies were restricted to the smaller age classes at SKB (fig. 5B) but were distributed across all age classes at the NKB site (fig. 5C).

Mean colony size at the SKB site extrapolated to an average age of approximately 3.9 yr. Mean colony size in the NKB population suggested an average age of 10.3 yr, although genet age could be substantially higher if recruitment was from an asexually derived fragment of an established clone. Several colonies greater than 4 m in diameter occur at this site (although none fell under the randomly assigned sampling points of the survey), suggesting ages of well over a century.

Total area occupied per genet averaged 4156 $\pm$ 6128 cm^2 for NKB with a range of one to six colonies/clone as compared to 383 $\pm$ 454 cm^2 for SKB with one to two colonies/clone. There was no significant difference in mean colony size between one-colony clones ($\bar{x}$ = 2280 $\pm$ 1398 cm^2) and clones with more than one colony ($\bar{x}$ = 2478 $\pm$ 1631 cm^2) in the NKB population.

Disturbance Indices and Genotypic Diversity

Criteria describing each of the six sites were ranked and statistically compared with ranks for the respective genotypic diversities for each population (table 5). Depth, wave exposure, percentage of unoccupied substratum, the period of time (D_T) since disturbance events of low, moderate, or high intensity, or the combined mean for all disturbance indicators at each site did not reflect the observed levels of clonal diversity in this range of habitats. However, genotypic diversity was significantly correlated ($P < 0.05$) with colony size, maximum disturbance intensity (D_I), and the time since disturbance events of maximum (very high) intensity. In addition, relative genotypic diversity was correlated with the disturbance index that incorporated both time and intensity of disturbance (D_I/D_T).

←

FIG. 5. Frequency of age-class distributions as approximated by size of sampled colonies of *Porites compressa* at three sites (NKB, SKB, CI). For details of age-class estimates, see the text.

Discussion

Analysis of genotypic diversity in natural populations of clonal species allows for a retrospective assessment of the relative success of sexual and asexual recruitment within and among populations. The potential for the production of asexual propagules by fragmentation in scleractinian corals has been well documented (Highsmith 1980, 1982; Tunnicliffe 1981; Bak and Criens 1982; Bothwell 1982; Kobayashi 1984; Heyward and Collins 1985; Wallace 1985). Highsmith (1982) suggested that recruitment of asexually produced clonal fragments would lead to considerably fewer genotypes than actual colonies on a reef. Model simulations of population structure for the reef coral, *Acropora cervicornis,* Neigel and Avise (1983) predicted that catastrophic disturbances combined with low rates of sexual recruitment could be important factors affecting levels of genotypic diversity. In the present study, the frequencies and distributions of replicated genotypes demonstrated that clonal diversity in natural populations of *Porites compressa* depends on both recency and intensity of disturbance events.

The introduction of new genotypes through sexual recruitment is apparently rare in most species of clonal corals (Fadlallah 1982; Neigel and Avise 1983; Stoddart 1984a). However, numbers of sexual recruits may equal or exceed those produced asexually by fission of adult colonies of *Agaricia lamarcki* and *Leptoseris cucullata,* respectively (Hughes 1988). Sexual recruitment in *P. compressa* averaged approximately 1.6 new recruits/m^2/yr on artificial settling blocks in Kaneohe Bay (Fitzhardinge 1985). The long-term survival rates of such recruits are unknown, but may be assumed to be even lower in areas where available substratum is limited because of the presence of established adult coral colonies or other sessile species. Rates of asexual reproduction through fragmentation have been estimated at 96 propagules/m^2/yr for *P. compressa* on the NKB reef, although the long-term fates of these fragments have not been directly observed (Hunter unpubl. data).

The relatively high levels of genotypic diversity of *P. compressa* compared to other clonal corals (table 6) suggests that recruitment and persistence of sexual propagules remains important in this species even in populations with low levels of disturbance. Alternatively (or in addition) to the contributions of sexual recruitment to ge-

Table 5. Relative rankings of genotypic diversity and population site characteristics for *Porites compressa* at six sites. r_s, Spearman rank correlation coefficients; *P*, exact probabilities (two-tailed test). See text and table 1 for description of sites and ranking methods. D_I, maximum intensity of disturbance, D_T, time since last disturbance of indicated intensity.

Site	Genotypic diversity rank	Reef depth	Colony size	Unoccupied substratum	Wave exposure	D_I (max)	D_T for Low	Mod	High	Very high	Disturbance index $\Sigma D_I/D_T$	Mean disturbance rank
CI	1	6	1	1	5.5	1.5	6	4	4.5	1	1	3.15
SKB	2	4	2	4	5.5	1.5	4	4	4.5	2	2	3.35
HAW	3	1.5	4*	5	1.5	3.5	2	2	2	4.5	4	3.00
KBO	4	1.5	4*	3	1.5	3.5	5	2	1	4.5	3	2.90
LAN	5	4	4*	2	3.5	5	1	2	4.5	4.5	5	3.55
NKB	6	4	6	6	3.5	6	3	4	4.5	4.5	6	4.75
r_s		−0.309	0.941	0.486	−0.478	0.971	−0.600	−0.293	−0.034	0.845	0.943	0.487
P		0.552	0.005	0.329	0.338	0.001	0.208	0.573	0.949	0.034	0.005	0.329

* Estimated; actual colony sizes not determinable.

TABLE 6. Genotypic diversity (D^*, number of clones/number of individuals; mean for all populations assayed) of clonal invertebrates as determined by isozyme studies utilizing various numbers of loci and alleles.

Taxon	Number of populations	Number of loci	Number of alleles	D^* (range)	Reference
Cnidaria					
Scleractinia					
Pavona cactus	1	4	13	.25	Willis and Ayre 1985
Pavona cactus	9	4	17	.35 (.03–.94)	Ayre and Willis 1988
Pocillopora damicornis					
Hawaii	8	4	16	.24 (.09–.35)	Stoddart 1985
Australia	25	4	13	.40 (.15–.75)	Stoddart 1984a
Porites compressa	6	7	23	.85 (.64–.97)	present study
Actiniaria					
Actinia equalis	2	10	16	.47 (.40–.53)	Ayre 1984
Actinia tenebrosa	9	3	6	.14 (.08–.52)	Black and Johnson 1979
Actinia tenebrosa	27	10	19	.21 (.09–.30)	Ayre 1984
Metridium senile	23	5	11	.70 (.13–.95)	Hoffmann 1986
Oulalia muscosa	9	6	30	~1 (NA)	Hunt and Ayre 1989
Sagartia elegans	8	14	NA	.61 (.41–.73)	Shaw 1991
Echinodermata					
Asteroidea					
Coscinasterias calamaria	14	6	14	.20 (.05–.44)	Johnson and Threlfall 1987
Ophiuroidea					
Ophiocomella ophiactoides	1	5	17	.90	Mladenov and Emson 1990
Ophiocoma pumilla	1	5	11	.67	Mladenov and Emson 1990
Ophiactis savigny (in sponge)	1	5	22	.10	Mladenov and Emson 1990
Ophiactis savigny (in algae)	1	5	22	.56	Mladenov and Emson 1990

NA = data not available.

notypic diversity, competitive networks among established clones may prevent complete competitive dominance by a single genotype (Rinkevich and Loya 1983). Similarly, microscale heterogeneity may generate differential selective pressures within a single population, so that no one genotype becomes dominant (Burdon 1980). Disturbance events may occur often enough across or within populations, relative to a species' generation time, to prevent domination of space by locally adapted clonal genotypes. Furthermore, the selective settlement responses of coral planulae (Wallace 1985) may enhance their survivorship relative to nonselective asexual recruitment of fragments. These factors may act alone or in conjunction to allow the coexistence of several clones and maintain relatively high genotypic diversity in this species.

Investigations of other invertebrate population structures, including anthozoans, have demonstrated a broad range of genotypic diversity (table 6), from populations that are almost completely dominated by single clones (Black and Johnson 1979; Mladenov and Emson 1990) to those with no evidence of asexual reproduction (Hunt and Ayre 1989). Histocompatibility assays suggested that fragmentation is important in vegetative propagation of the gorgonian, *Plexaura* A, but not in its congener, *Plexaura homomalla* (Lasker and Coffroth 1985). 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 few clones, some of which may be distributed over 5 km. Physical disturbance and unstable habitats have been suggested to contribute to higher clonal diversity in some anemones (Sebens 1982; Ayre 1984) and asteroids (Crump and Barker 1985). In contrast, zoanthid species may exhibit a decrease in clonal propagation with increasing levels of disturbance (Karlson 1991).

Interpretation of analyses of genetic structure in clonal populations is complicated by two major methodological difficulties. First, assays used for identifying and distinguishing individuals must be sensitive enough to clearly resolve all genotypes sampled. In addition, 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. Several types of assays have been utilized to identify clonal structure in coral populations. Tissue grafting techniques were employed to delineate clonal diversity in *Montipora* spp. (Jokiel et al. 1983) and *Acropora cervicornis* (Neigel and Avise 1983). 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 that fuse in grafts have been demonstrated to have dissimilar electrophoretic banding patterns. Stoddart (1984a) identified clonal genotypes in populations of *Pocillopora damicornis* based on electrophoretic analysis of four allozyme loci (13 alleles) and found that genotypic diversity in this species, which is reported to asexually produce larvae as well as fragments (Stoddart 1983), was less than half of that expected for an exclusively sexually reproducing species. However, the power of this four-locus system to resolve all genotypes of *Pocillopora damicornis* could not be evaluated, and Stoddart (1984a, 1988) suggested that the total number of genets may have been underestimated.

Interpretations of electrophoretic assessments of genotypic diversity in clonal species have been severely limited by the lack of a priori methods for ascertaining the number of loci necessary to differentiate clones. Studies that have addressed the genetic structure of marine invertebrate populations have utilized relatively few loci to describe clonal diversity (table 6). A plot of mean genotypic diversity (D^*) versus the number of alleles assayed shows a significant linear correlation for studies of coral and anemone populations (fig. 6), suggesting that assays utilizing more (or more polymorphic) loci may be better able to detect all or most unique genotypes in populations of cnidarians. In contrast, genotypic diversity and number of alleles assayed showed no apparent trend in studies of echinoderm populations. In the present study, the power of the electrophoretic assay to resolve all genotypes was tested by its application to an aclonal population consisting of individuals that were all derived from sexually produced larvae and therefore assumed to be genetically distinct. This test, along with the high G_o:G_e values and low (4.8%) proportion of overlapping genotypes among populations, suggests that the assays used were sufficient to resolve most clones of *Porites compressa.*

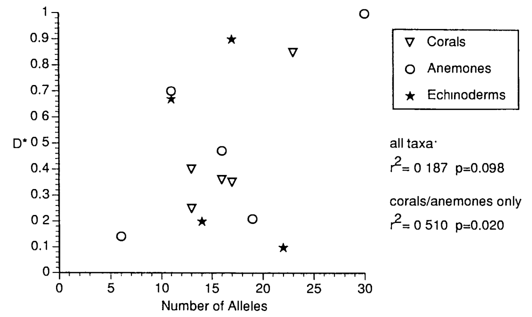


FIG. 6. Genotypic diversity (D^*) as a function of numbers of alleles assayed in studies of populations of clonal invertebrates (cnidarians and echinoderms, as in table 6).

Just as the scales of observation in space and time can result in different levels of predictability of ecological diversity (Jackson 1991), area and scale of sampling will affect estimated levels of genotypic diversity within populations (Willis and Ayre 1985; Ayre and Willis 1988). Sampling of clonal diversity in coral species has been done either by random linear transecting (Stoddart 1983, 1984a,b; Willis and Ayre 1985; Ayre and Willis 1988), by assay of colonies at fixed distances (Neigel and Avise 1983), or by arbitrary selection of colonies within patches (Jokiel et al. 1983). Linear transects can provide good estimates of overall genetic diversity, but they cannot elucidate two-dimensional clonal distributions; haphazard sampling may detect common clones but will overestimate clonality if rare or small colonies have less chance of being sampled. A nested sampling design applied to populations within a range of disturbance regimes was useful in the present study for elucidating both total genetic and genotypic diversity of the reef coral, *Porites compressa,* as well as the fine-scale and broad-scale patterns of clonality within this species.

In summary, physical factors may differentially alter the population structure of clonal species by affecting the relative production and long-term recruitment success of sexually and asexually produced propagules. Although studies of species diversity in coral reef communities have supported an "intermediate disturbance" hypothesis (Grigg and Maragos 1974; Connell 1978; Dollar 1982; Grigg 1983), genotypic diversity within the dominant coral species assessed in this study appears to be directly related to recency and severity of disturbance. The resolution power of both the genetic assay and the scale of sampling require careful consideration

when applied to ecological and evolutionary studies of clonal species.

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LITERATURE CITED

Ayre, D. J. 1984. The effects of sexual and asexual reproduction on geographic variation in the sea anemone *Actinia tenebrosa*. Oecologia 62:222–229.

Ayre, D. J., and B. L. Willis. 1988. Population structure in the coral *Pavona cactus*: Clonal genotypes show little phenotypic plasticity. Marine Biology 99:495–505.

Bak, R.P.M., and S. R. Criens. 1982. Experimental fusion in Atlantic *Acropora*. Marine Biology Letters 3:67–72.

Banner, A. H. 1968. A freshwater "kill" on Hawaiian coral reefs. Hawaii Institute of Marine Biology Technical Report 15, University of Hawaii, Manoa.

Black, R., and M. S. Johnson. 1979. Asexual viviparity and population genetics of *Actinia tenebrosa*. Marine Biology 53:27–31.

Bothwell, A. M. 1982. Fragmentation, a means of asexual reproduction and dispersal in the coral genus *Acropora*—a preliminary report. Pp. 137–144 *in* E. D. Gomez et al., eds. The reef and man: Proceedings of the Fourth International Coral Reef Symposium, Manila, The Philippines, 18–22 May 1981. Marine Sciences Center, University of Quezon City, The Philippines.

Burdon, J. J. 1980. Intraspecific diversity in a natural population of *Trifolium repens*. Journal of Ecology 68:717–735.

Catmull, J., D. Yellowless, and D. J. Miller. 1987. $NADP^+$-dependent glutamate dehydrogenase from *Acropora formosa*: purification and properties. Marine Biology 95:559–563.

Connell, J. 1978. Diversity in tropical rain forests and coral reefs. Science 199:1302–1310.

Crump, R. G., and M. F. Barker. 1985. Sexual and asexual reproduction in geographically separated populations of the fissiparous asteroid *Coscinasterias calamaria*. Journal of Experimental Marine Biology and Ecology 88:109–127.

Dollar, S. J. 1982. Wave stress and coral community structure in Hawaii. Coral Reefs 1:71–81.

Ellstrand, N. C., and M. L. Roose. 1987. Patterns of genotypic diversity in clonal plant species. American Journal of Botany 74:123–131.

Fadlallah, Y. H. 1982. Reproductive ecology of the coral *Astrangia lajollaensis*: sexual and asexual patterns in a kelp forest habitat. Oecologia 55:379–388.

Fitzhardinge, R. 1985. Spatial and temporal variability in coral recruitment in Kaneohe Bay (Oahu, Hawaii). Proceedings of the Fifth International Coral Reef Symposium 4:373–377.

Fujii, H. 1987. The predominance of clones in populations of the sea anemone *Anthopleura asiatica*. Biological Bulletin 172:202–211.

Greig Smith, P. 1979. Pattern in vegetation. Journal of Ecology 67:755–779.

Grigg, R. 1983. Community structure, succession and development of coral reefs in Hawaii. Marine Ecology Progress Series 11:1–14.

Grigg, R., and J. Maragos. 1974. Recolonization of hermatypic corals on submerged lava flows in Hawaii. Ecology 55:387–395.

Harris, H., and D. A. Hopkinson. 1976. Handbook of enzyme electrophoresis in human genetics. North-Holland, Amsterdam, Netherlands.

Heyward, A. J., and J. D. Collins. 1985. Fragmentation in *Montipora ramosa*: the genet and ramet concept applied to a reef coral. Coral Reefs 4:35–40.

Heyward, A. J., and J. A. Stoddart. 1985. Genetic structure of two species of *Montipora* on a patch reef; conflicting results from electrophoresis and histocompatibility. Marine Biology 5:117–122.

Highsmith, R. C. 1980. Passive colonization and asexual colony multiplication in the massive coral *Porites lutea*. Journal of Experimental Biology and Ecology 46:55–67.

———. 1982. Reproduction by fragmentation in corals. Marine Ecology Progress Series 7:207–226.

Hillis, D. M., and C. Moritz. 1990. Molecular systematics. Sinauer, Sunderland, Mass.

Hoffmann, R. J. 1986. Variation in contributions of asexual reproduction to the genetic structure of populations of the sea anemone, *Metridium senile*. Evolution 40:357–365.

Hughes, R. N. 1989. A functional biology of clonal animals. Chapman and Hall, London.

Hughes, T. P. 1988. Long-term dynamics of coral populations: contrasting reproductive modes. Proceedings of the Fifth International Coral Reef Symposium, Townsville 2:721–725.

Hughes, T. P., and J. H. Connell. 1987. Population dynamics based on size or age? A reef coral analysis. American Naturalist 129:818–829.

Hughes, T. P., and J.B.C. Jackson. 1980. Do corals lie about their age? Some demographic consequences of partial mortality, fission, and fusion. Science 209:713–714.

Hunt, A., and D. J. Ayre. 1989. Population structure in the sexually reproducing sea anemone *Oulactis muscosa*. Marine Biology 102:537–544.

Hunter, C. L. 1985. Assessment of clonal diversity and population structure of *Porites compressa*. Proceedings of the Fifth International Coral Reef Symposium, Tahiti 6:69–74.

———. 1988. Genotypic diversity and population structure of the Hawaiian reef coral, *Porites compressa*. Ph.D. diss. University of Hawaii, Manoa.

Hwang, D. 1981. Beach changes on Oahu as revealed by aerial photographs. University of Hawaii Technical Report HIG-81-3:71–75.

Jackson, J.B.C. 1991. Adaptation and diversity in reef corals. BioScience 41:475–482.

Johnson, M. S., and T. J. Threlfall. 1987. Fissiparity and population genetics of *Coscinasterias calamaria*. Marine Biology 93:517–525.

Jokiel, P. L. 1985. Growth of the reef coral *Porites compressa* on the Coconut Island reef, Kaneohe Bay. Pp. 101–110 *in* P. L. Jokiel et al., eds. Population biology of coral reefs. Hawaii Institute of Marine Biology, Technical Report 37.

Jokiel, P. L., W. H. Hildemann, and C. H. Bigger. 1983. Clonal population structure of the reef coral *Montipora*. Bulletin of Marine Science 33:181–187.

Jokiel, P. L., C. L. Hunter, S. Taguchi, and L. Watarai. Freshwater kill on coral reefs in Kaneohe Bay, Hawaii. Coral Reefs. *In press.*

Karlson, R. H. 1991. Fission and the dynamics of genets and ramets in clonal cnidarian populations. Hydrobiologia 216/217:235–240.

Kobayashi, A. 1984. Regeneration and regrowth of fragmented colonies of the hermatypic corals *Acropora formosa* and *Acropora nasuta*. Galaxea 3:13–23.

Lasker, H. R. 1990. Clonal propagation and population dynamics of a gorgonian coral. Ecology 71: 1578–1589.

Lasker, H. R., and M. A. Coffroth. 1985. Vegetative reproduction, clonal spread, and histocompatibility in a caribbean gorgonian. Proceedings of the Fifth International Coral Reef Congress 4:331–336.

Maragos, J. E. 1972. A study of the ecology of Hawaiian reef corals. Ph.D. diss. University of Hawaii, Manoa.

Maragos, J. E., C. Evans, and P. F. Holthus. 1985. Reef corals in Kaneohe Bay six years before and after termination of sewage discharge. Proceedings of the Fifth International Coral Reef Symposium, Tahiti 4:189–194.

Mladenov, P. V., and R. H. Emson. 1990. Genetic structure of populations of two closely related brittle stars with contrasting sexual and asexual life histories, with observations on the genetic structure of a second asexual species. Marine Biology 104: 265–274.

Neigel, J. E., and J. C. Avise. 1983. Clonal diversity and population structure in a reef-building coral, *Acropora cervicornis*. Evolution 37:437–453.

Parker, E. D. 1979. Ecological implications of clonal diversity in parthenogenetic morphospecies. American Zoologist 19:753–762.

Polacheck, T. 1978. The population biology of four common Hawaiian corals. Master's thesis. University of Hawaii, Manoa.

Redfield, J. A., and J. P. Salini. 1980. Techniques of starch gel electrophoresis of penaeid prawn enzymes (*Penaeus* spp. and *Metapenaeus* spp.). CSIRO Division of Fisheries, Report 116.

Resing, J., and D. J. Ayre. 1985. The usefulness of the tissue grafting bioassay as an indicator of clonal identity in scleractinian coral (Great Barrier Reef, Australia). Proceedings of the Fifth International Coral Reef Symposium, Tahiti 6:75–81.

Rinkevich, B., and Y. Loya. 1983. Intraspecific competitive networks in the Red Sea coral *Stylophora pistillata*. Coral Reefs 1:161–172.

Roy, K. J. 1970. Change in bathymetric configuration, Kaneohe Bay, 1882–1969. University of Hawaii Sea Grant Publication 70-6, HIG 70-15.

Sebens, K. P. 1982. Asexual reproduction in *Anthopleura elegantissima* (Anthozoa: Actinaria): seasonality and extent of clones. Ecology 63:434–444.

Sebens, K. P., and B. L. Thorne. 1985. Coexistence of clones, clonal diversity, and the effects of disturbance. Pp. 357–398 *in* J.B.C. Jackson et al., eds. Population biology and evolution of clonal organisms. Yale University Press, New Haven, Conn.

Selander, R. K., M. H. Smith, S. Y. Yang, W. E. Johnson, and J. B. Gentry. 1971. Biochemical polymorphism and systematics in the genus, *Peromyscus*. I. Variation in the old-field mouse (*Peromyscus polionotus*). Studies in Genetics VI. University of Texas Publications 7103:43–90.

Shaw, P. W. 1991. Effects of asexual reproduction on population structure of *Sagartia elegans* (Anthozoa:Actinaria). Hydrobiology 216/217:519–525.

Simpson, E. H. 1949. Measurement of diversity. Nature 163:688.

Smith, S. V., W. J. Kimmerer, E. A. Laws, R. E. Brock, and T. W. Walsh. 1981. Kaneohe Bay sewage diversion experiment: perspectives on ecosystem responses to nutritional perturbation. Pacific Science 35:279–395.

Stoddart, J. A. 1983. Asexual production of planulae in the coral *Pocillopora damicornis*. Marine Biology 81:19–30.

———. 1984a. Genetical structure within populations of the coral *Pocillopora damicornis*. Marine Biology 81:19–30.

———. 1984b. Genetic differentiation amongst populations of the coral *Pocillopora damicornis* off Southwestern Australia. Coral Reefs 3:149–156.

———. 1985. Biochemical genetics of *Pocillopora damicornis* in Kaneohe Bay, Oahu, Hawaii. Pp. 133–150 *in* P. L. Jokiel, R. H. Richmond, and R. Rogers, eds. Population biology of coral reefs. Hawaii Institute of Marine Biology, Technical Report 37.

———. 1988. Coral populations fringing islands: larval connections. Australian Journal of Marine and Freshwater Research 39:109–115.

Stoddart, J. A., D. J. Ayre, B. Willis, and A. J. Heyward. 1985. Self-recognition in sponges and corals? Evolution 39:461–463.

Stoddart, J. A., and J. Taylor. 1988. Genotypic diversity: estimation and prediction of samples. Genetics 118:705–711.

Tunnicliffe, V. 1981. Breakage and propagation of

the stony coral *Acropora cervicornis*. Proceedings of the National Academy of Sciences, USA 78:2427–2431.

Wallace, C. C. 1985. Reproduction, recruitment and fragmentation in nine sympatric species of the coral genus *Acropora*. Marine Biology 88:217–233.

Willis, B., and D. J. Ayre. 1985. Asexual reproduction and genetic determination of growth form in the coral *Pavona cactus*: biochemical, genetic, and immunogenic evidence. Oecologia 65:516–525.

Wulff, J. L. 1985. Dispersal and survival of fragments of coral reef sponges. Proceedings of the Fifth International Coral Reef Congress, Tahiti 5:119–124.

Corresponding Editor: J. Jackson