# SPECIES-SPECIFIC POPULATION STRUCTURE OF CLOSELY RELATED CORAL MORPHOSPECIES ALONG A DEPTH GRADIENT (5–60 M) OVER A CARIBBEAN REEF SLOPE

*M. J. A. Vermeij and R. P. M. Bak*

## ABSTRACT

We investigated the use of demographic characteristics to differentiate between closely related coral species that are difficult to distinguish morphologically and genetically. We looked at colony size and density in six morphospecies of the coral genus *Madracis* in Curaçao (Netherlands Antilles). Colonies of all species (n = 1585), including individuals as small as 0.01 $cm^2$, were measured in 30 × 1 m belt transects over a reef slope at 5, 10, 20, 30, 50 and 60 m depth. This resulted in a detailed description of species population structures over depth. Temperature, light, sedimentation and water movement were recorded. Our survey showed *Madracis* to be one of the most abundant coral genera (mean of 9.2 colonies $m^{-2}$) at the reef slope. The size frequency distributions were species specific and provide us with a set of characteristics, in addition to traditional morphological and genetic species classifications, to distinguish between coral taxa. Species density (n $m^{-2}$) and mortality rates differed between morphospecies and within morphospecies among depths, suggesting that population density is under environmental control (selective environment). Population structure, in terms of size frequency distribution, remained stable over depth and appears to be largely dependent on differences in species-specific life-history strategies (developmental environment). The population structure of all *Madracis* species changed only at the upper and lower margin of their distribution. These changes were similar in all species: (1) Densities of populations decreased, resulting in 'saw-shaped' size distributions; (2) Overall variation in un-transformed colony size distributions, expressed as coefficient of variation (CV), decreased while the variation in log-transformed size-distributions, which is indicative of the time a colony is present on the reef, increased; (3) Decreasing skewness ($g_1$) in untransformed size-distributions indicated that the proportion of smaller colonies decreased within the population; (4) The relative differences in the contribution of larger individuals to the total population surface increased, indicated by higher values for the Gini-coefficient (G); and (5) Mean colony sizes, after range standardization of size-data, became larger than 0.12. Life-history strategies partially overlap for morphospecies sharing the same colony morphology. Population turnover rates differed between species present at the same depth, ranging between >100 yrs for *Madracis senaria* to five yrs for *Madracis decactis*, which reflects species-specific susceptibility to environmentally induced mortality.

The distribution of coral colonies on a reef depends on the life history characteristics (e.g., growth, regeneration, larval production) of the coral species involved and heterogeneously distributed abiotic environmental factors. These factors interact and the relative contribution of factors stimulating coral growth (light, availability of dissolved $CaCO_3$, presence of zooplankton, substrate availability) and factors inhibiting coral growth (competition, sedimentation, disturbance, high temperature, or salinity) change with depth. The interaction of these environmental factors results in a composed environmental-gradient to which species have to adapt. This adaptation ranges from specialization to generalism. Specialists dominate restricted parts of the environmental gradient because of their highly successful adaptation to local abiotic factors which results in high reproductive or competitive success. Generalists are typically less successful, but compensate

for this by surviving over a broader gradient, dealing with a greater variety of environmental factors.

Understanding which life-history strategy a coral species has adopted to deal with the interacting environmental factors along a reef slope requires detailed demographic descriptions performed along such slopes. Observed changes indicate the nature and direction of adaptation, which provides insight in the coral's life-history strategy. Understanding the changes in demographic behavior is crucial to understanding coral population dynamics and only complete descriptions of a coral's environmental preferences and related demographic responses allow speculation on possible changes in population structure to environmental change, or its adaptations to survive on an evolutionary time-scale. However, studies describing the demographic structure of coral communities often focus on changes in a subset of the population (such as the larger adult colonies) and are mostly performed at one depth, or over limited vertical scales in shallow water. Since species are likely to have adapted differently to the environmental gradient, species' fitness can have their optima at different depths or habitats (Stearns, 1992). Therefore, comparing different species along a horizontal gradient may produce biased data since the behaviour of adapted vs less adapted species is compared. Detailed information on the demographic behaviour along broad environmental gradients is scarce. Such data would be valuable in understanding the changes in community of coral species in a three-dimensional reef setting. Field data are needed to provide the absolute boundaries of the environmental range in which a coral species survives because it gives the limits of a coral's adaptation to an over-all fitness gradient.

Demographic data in corals are based on colony size and colony numbers. The size of a colony represents the net result of growth, partial mortality and regeneration and is not necessarily related to age, which is traditionally used to describe demographic processes (Caswell, 1989). Bak and Meesters (1998) showed that for relatively small corals the assumption that size and age are related seems valid. This allows the assessment of their population composition without age- or size-related effects confounding interpretation. Changes in demographic data of small coral species along a large vertical gradient are therefore believed to be informative of the species' reaction to a changing environmental gradient based on its life-history strategy and the suite of environmental factors involved.

The Caribbean coral genus *Madracis* currently comprises six species described by Wells (1973a,b) and Vermeij et al. (in press). Small colony size, significant and species-specific morphological plasticity as well as large environmental tolerance characterize the genus (Wells, 1973a; Fenner, 1993; Bruno and Edmunds, 1997). This makes this genus well suited to address the questions: (1) Do differences in the population structure between closely related coral species exist? (2) Do such differences reflect the taxonomic variation within the genus? (3) How are changes in environmental conditions with depth, reflected in the colony size distributions? (4) How do recruitment and mortality affect the colony size distributions and abundance?

To answer these questions, we studied the population structure of six closely related species; *Madracis mirabilis, M. carmabi, M. senaria, M. decactis, M. formosa* and *M. pharensis,* in relation with environmental characteristics at the fringing reef off Curaçao, Netherlands Antilles over a depth gradient from 5–60 m.

## Materials and Methods

Distribution.—In 1998, all data were collected at one site, Buoy 1, near the Caribbean Marine Biological Station (CARMABI), Curaçao, Netherlands Antilles (12°05′N, 69°00′W). This is a well-studied site, representative of a reef on Curaçao's leeward coast (Bak, 1975, 1977; Van den Hoek et al., 1978; Van Duyl, 1985; Van Veghel, 1994; Meesters et al., 1997). To record coral populations 30 × 1 m belt-transects were laid out along isobaths parallel to the shore at 5, 10, 20, 30, 50 and 60 m depth (Babcock, 1991). All *Madracis* colonies in a belt transect were identified to species and each colony size (total $cm^2$ living tissue) was measured. Colonies are defined as any autonomous, free-standing coral skeleton with living tissue. A colony divided by partial mortality into separate patches of living tissue, but structurally still one entity, was considered to be one colony (Bak and Meesters, 1998). The size of all colonies was determined by counting the number of 1 $cm^2$ squares on a flexible transparent plastic grid laid over the living surface of the colony.

Colonies smaller than 2 $cm^2$, which corresponds to a circle with a diameter of 1.6 cm, were considered to be juveniles. Their distance to the closest colony of the same species and colormorph was measured to obtain an indication of their origin (settled planulae or fragmentation). Fragmentation results in small distances between juvenile colonies and their parents. All colonies were marked and revisited one yr later to determine colony mortality. No data were collected on mortality for *M. mirabilis* and *M. formosa* since their populations contain many small unattached fragments (<1 cm) that are impossible to tag.

Morphospecies Definition.—We used the morphological descriptions from Wells (1973a,b) for *M. mirabilis, M. senaria M. formosa. Madracis pharensis* and *M. decactis* were classified according to their colony morphology corresponding to the proposed ecotypes by Fenner (1993): encrusting and nodular colonies were classified as *M. pharensis* and *M. decactis,* respectively. One particular morph of *M. decactis* showed characteristics of both *M. decactis* (10 septs) and *M. formosa* (branching morphology). To distinguish this morph in our measurements we indicate this morph as a new species, *M. carmabi* (Vermeij et al., this issue).

Environmental Parameters.—Irradiance (μEin $m^{-2}$ $s^{-1}$, wavelength 400–700 nm) was measured at 1200 hrs November 1, 1998 under a cloudless sky and no wind using a cosine LI-192SA underwater quantum sensor (LI-COR) connected to a LI-1000 data-logger (LI-COR) in a portable underwater housing. The light coming straight from above and the light in a 90° angle to this direction, pointing from the reef, were measured. Temperature was recorded daily at 1200 hrs using continuum SEAMON Mini temperature-loggers (Hugrun ehf. 1995–1998) at 5, 15, 30 and 50 m depths for 1 yr. An indication of overall water movement was obtained using the 'clod-card' technique (Jokiel and Morrissey, 1993). Wall patching compound cones (ca 91 g) were attached to the bottom at each depth in two different habitats: on top of the substrate and against vertical walls (n = 4, for each habitat). Information on sedimentation was taken from De Kluiver (unpubl. data) who used cylindrical sediment-traps (see Van Veghel, 1994 for technical details).

Definition of Population Statistics.—The equality in size among colonies of a species present at the same depth was investigated using various measurements of size hierarchies that are used in terrestrial plant demography (reviewed by Weiner and Solbrig, 1984, Bendel et al., 1989). The Gini coefficient (G; $0<G<1$) indicates the inequality among contributions of population members to an overall population characteristic (e.g., total surface covered by one species at a certain depth or the next generation's gene pool). A value closer to one indicates greater inequality in contributions of the population members to the population characteristic consisting of the summed contribution of all its members. Skewness ($g_1$) is an indicator of a distribution's shape around the mean that is invariant to both scale and location. If skewness is non-zero, the distribution is asymmetric. A positive value then indicates a long right tail; a negative value, a long left tail. The skewness of a coral population can be indicative of the fraction of small relative to bigger colonies within the population. It is therefore related to the input of new individuals and the longevity of the colonies (Bak and Meesters, 1998). The coefficient of variation (CV) given by the sample standard deviation divided by the sample mean, is a measure of variation in populations (relative precision). The

CV is invariant to scale changes ($x \rightarrow ax$), but is not invariant to location changes ($x \rightarrow a+x$; Bendel et al., 1989). Since all morphospecies have different average sizes (i.e., vary in their location on the size-scale) we standardised size data before calculating the coefficient of variation (CV). This eliminates the location effect (Prairie and Bird, 1989). The data were range-standardized by assigning a size value 1 to the largest colony and the sizes of smaller colonies were expressed proportionate to this value.

G, CV and $g_1$ were computed first for raw, untransformed size distributions. Such distributions are very skewed and log transformation of colony size results in approximate normal distributions of size frequencies (Bak and Meesters, 1998), which allows better comparisons between populations due to increased descriptive resolution in the smaller size classes (Bak and Meesters, 1998; Vermeij and Bak, 2000). After transformation, distributions can be interpreted rather as age than size-distributions resulting from a balance between juvenile input and adult longevity (Bak and Meesters, 1998; Vermeij and Bak, 2000). These transformed distributions were analysed using the descriptive statistics CV, and $g_1$, which provide insight in the demographic processes structuring the distribution. Analyzing log transformed size distributions using CV is only allowed if one assumes that one is studying a new population consisting of ages rather than sizes. The calculation of CV in a variable that is already expressed in a new relative measure, i.e., by log transformation is not allowed (Sokal and Rolf, 1980). The size distribution of each species for each depth was given as percentages of the population falling into (logarithmic) size classes. Classes were identical for all depth/species combinations studied. The use of percentages reflects the shape of a size frequency distribution independent of the total number of individuals comprising the population.

## Results

Environmental Parameters.—The distribution of all species is given in Figure 1A, environmental gradients are shown in Figure 1B–D.

Irradiance decreased with depth (Fig. 1B) as: Irradiance (% surf. light) = $-23.1 \times \ln(\text{depth}_{(m)}) + 91.9$, $r^2 = 0.93$). Above-surface irradiance ranged between 1400–1800 µEin $m^2\ s^{-1}$, which was representative for cloudless days. The dimensionless vertical attenuation-coefficient (k') was −0.063. The proportion between light received in the two reef microhabitats, top positions vs vertical positions decreases slightly with depth ($r^2 = 0.33$, $P < 0.001$, $n = 541$) with the light coming from the side being on average 38.0 % (SD 9.2%, depth range 0.5–50 m) of the amount of light coming from above.

Water movement differed significantly between depths (Fig. 1C, ANOVA, $df = 7$, $F = 30.44$, $P < 0.01$). Water movement decreases exponentially with depth and becomes constant below 25 m. Water movement was on average 7.8% lower at vertical positions than at top positions for all depths (SD: 3.5%, n= 8 depths) but this difference was not significant for any depth (ANCOVA, $df = 1$, $F = 0.35$, $P > 0.56$).

Temperature at all depths is expressed as the difference between local temperature and the temperature at 5m to correct for seasonal changes in water temperature (Fig. 1D). The average yearly water temperature (1200 hrs) at 5 m was 27.91ºC (SD 0.97, n = 365). Significant differences in temperature between depths were found (ANOVA, $df = 3$, $F = 594.00$, $P < 0.05$). The highest fluctuation in temperature occurred at 50 m, possibly due to a thermocline moving up and down the reef slope around 50 m.

Vertical Distribution and Abundance.—The abundance of each species differed between depths ($n/m^2$; Kruskal-Wallis test, $H > 17.78$, $df = 4$, $P < 0.005$), and for all depths differences in abundance existed between the species (Kruskal-Wallis test, $H > 22.77$, df 2–4, $P < 0.001$). From the depth where a species is most abundant, its numbers decrease

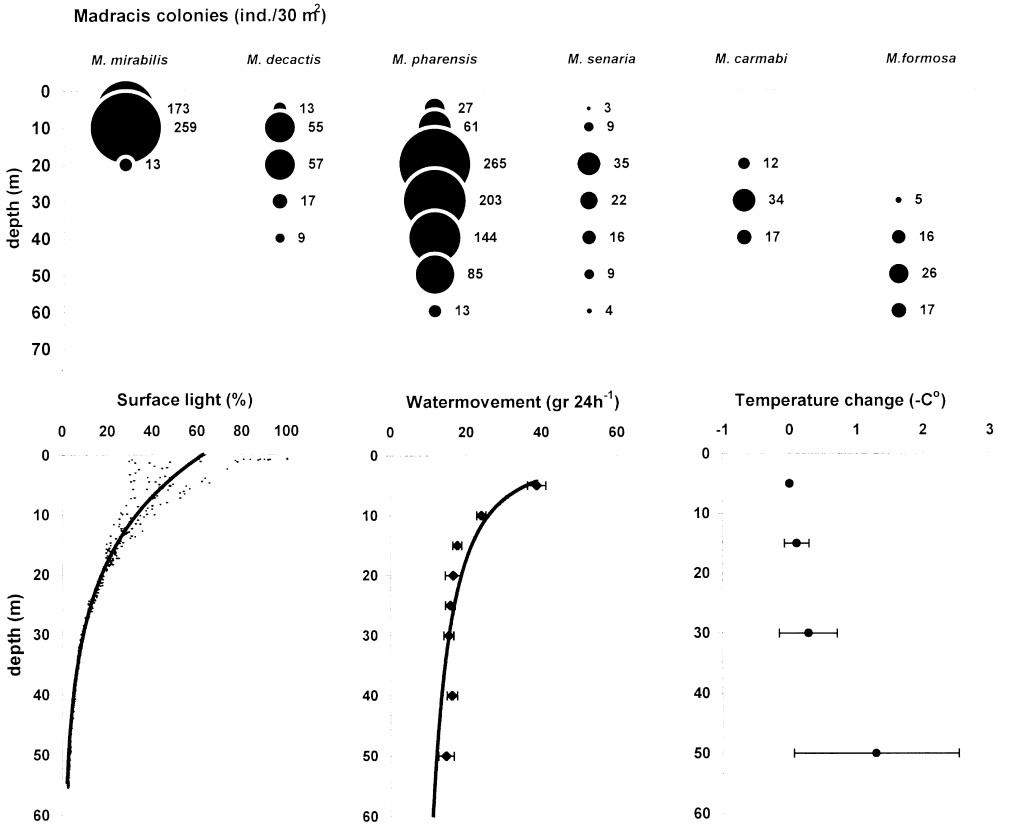



Figure 1. (a) Distribution of the different *Madracis* species over the reef-slope at Buoy 1, Curaçao . (b) The distribution of the abiotic factors light (μEin $m^{-2}$ $s^{-1}$). (c) water movement (g $d^{-1}$), and (d) temperature change (°C) are given over the same slope (mean ± SD).

in both shallower and deeper directions, resulting in bell-shaped distribution patterns over depth. Most species occurred over a restricted part of the 5–60 m depth range but *M. pharensis* and *M. senaria* were found over the entire depth range. These species were dominant members of the coral community at greater depths (>35m) and were still present in the deep reef zone (80–100 m) together with *Stephanocoenia michelinii, Agaricia* spp. and *Montastraea cavernosa* (Vermeij, pers. obs.). The occurrence of *M. pharensis* and *M. senaria* over this entire depth range (1–>100 m) is a unique characteristic for zooxanthellate corals. At 100 m they survive with only 0.2% surface light, which is among the lowest reported for colonial zooxanthellate scleractinian corals (Sheppard, 1982, and references therein).

Size Frequency Distributions.—In Figure 2A the untransformed size-frequency distributions are shown for all *Madracis* species for all depths. At 60 m *M. pharensis, M. senaria* and *M. formosa* occurred at densities that were too low to allow construction of size-frequency distributions (n per 30 $m^2 < 14$). Although all size-frequency distributions were highly skewed to the right (mean skewness 4.03, SD = 2.45) differences between species were evident. The consistency of these differences over the depth gradient suggests that population structure greatly depends on species-specific characteristics. Log-transformation of the data removes this asymmetry considerably (mean skewness decreased to −0.10; SD = 2.45), and improves the normality of the distributions (Fig. 2B). Eleven distributions out of 27 (41%) became non-significantly different from a normal distribution (Fig. 2B, Kolmogorov-Smirnov test with Lilliefors adjustment; $P > 0.05$). Analyzing the shape of the size-frequency distribution over the logarithmic size-classes, (Fig. 2B) we find that populations of the same species over its depth range are 1.7 times as similar as populations of different species within the same depth. The mean correlation coefficient (Spearman rank) for the intraspecific comparisons over depth is 0.84 (SD = 0.14; n = 15) while it is 0.49 (SD = 0.25; n = 16) for different species within the same depth. These correlation coefficients differ significantly (Mann-Whitney U-test, U = 15.00, $P < 0.001$). Fig. 3 demonstrates the consistency of the species size frequency pattern over the depth gradient and illustrates the important role of species-specific characteristics.

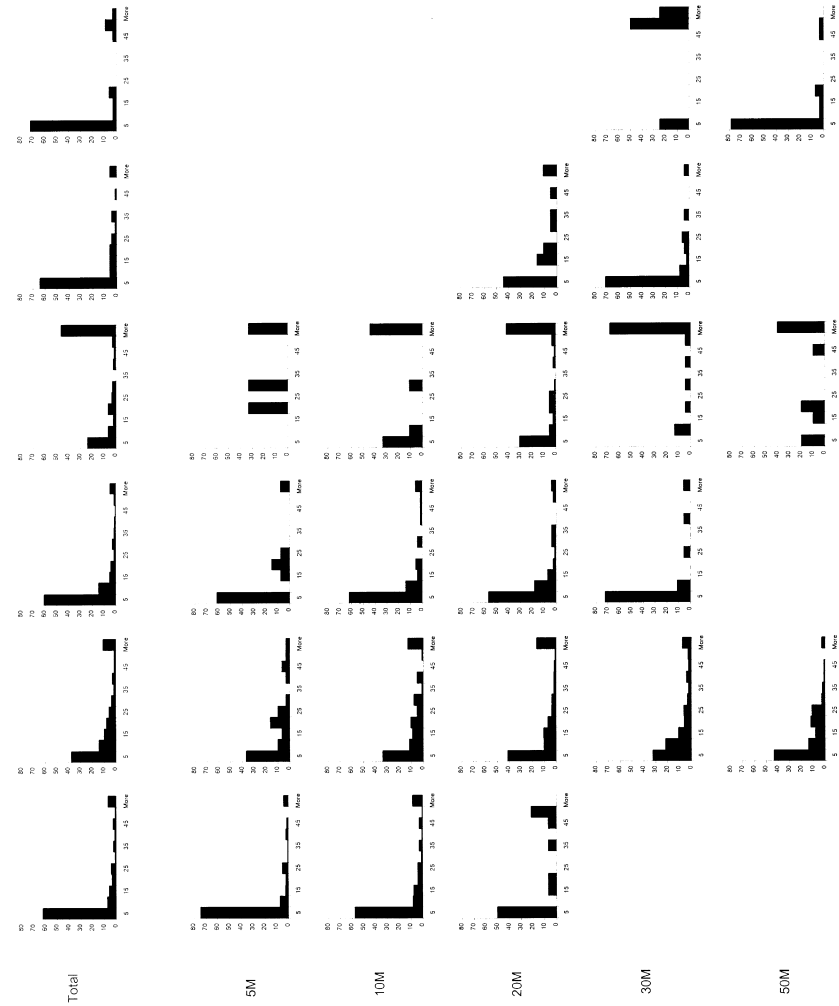
Non-Transformed Size Distributions (NTD) and Population Composition Parameters.—A demographic overview of colony size, total colony surface and coral density is shown for each depth and each species in Table 1. The descriptors Gini-coefficient (G), coefficient of variation (CV) and skewness ($g_1$) are shown for untransformed and $g_1$ and CV for log-transformed size-frequency distributions.

*Colony Size (NTD)*.—Mean colony size differed between *Madracis* species (Kruskal-Wallis ANOVA, $H > 14.12$, $P < 0.001$) and was independent of depth for all species (Kruskal-Wallis ANOVA, $H > 0.42$, $P > 0.43$). Although there was no gradual decrease in colony size towards the ends of a coral's distribution, the smallest mean colony size generally corresponds to habitats where species were least abundant (Table 1). Since the maximum colony size in populations depends on stochastic factors, the 95$^{th}$ percentile is preferred as a better indication of maximum colony size when comparing species (Soong, 1993; Meesters et al., 2001).

*Gini-Coefficient (NTD)*.—Gini-coefficients (G in Table 1) describe the inequality among contributions of individual members to an overall population characteristic. Values of G near 1 indicate great inequality and the minimum of zero indicates equal contributions of all population members.

Table 1. Distribution parameters of untransformed and log-transformed size data for all *Madracis* species present within 5 depths (5, 10, 20, 30 and 50 m). Standard demographic information is given in the first six columns (mean colony size [$cm^2$], standard deviation colony size [$cm^2$], 95-percentile colony size [cm2], total surface population surface [$cm^2$], total number of colonies [n], mean density [n $m^{-2}$], standard deviation density [n $m^{-2}$]. In the second part the distribution parameters of nontransformed size data (NTD) are given: Gini-coefficient ($G_{NTD}$), Coefficient of variation ($CV_{NTD}$) and Skewness ($g_{1NTD}$)and for log-transformed size data (LTD): Coefficient of variation ($CV_{LTD}$) and Skewness ($g_{1\,LTD}$).

| Species | Depth | Colony size ($cm^2$) | | | | Density (n $m^{-2}$) | | | Untransformed | | | Log-transformed | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | mean | SD | 95% | Total surface | n | mean | SD | $G_{NTD}$ | $CV_{NTD}$ | $g_{1\,NTD}$ | $CV_{LTD}$ | $g_{1\,LTD}$ |
| *M. mirabilis* | pooled | 14.2 | 31.5 | 66 | 6,932 | 487 | – | – | 0.25 | 2.20 | 5.9 | 0.40 | 0.30 |
| | 5 | 10.6 | 36.4 | 55 | 1,600 | 151 | 5.77 | 10.34 | 0.20 | 3.40 | 8.80 | 0.41 | 0.64 |
| | 10 | 15.7 | 29.2 | 121 | 5,065 | 322 | 8.63 | 13.15 | 0.27 | 1.90 | 3.30 | 0.38 | 0.21 |
| | 20 | 19.0 | 20.6 | 50 | 267 | 14 | 0.43 | 1.70 | 0.48 | 1.08 | 0.60 | 0.55 | −0.24 |
| *M. decactis* | pooled | 12.9 | 30.5 | 60 | 2,375 | 184 | – | – | 0.27 | 2.37 | 5.35 | 0.27 | −0.07 |
| | 5 | 12.1 | 19.2 | 71 | 157 | 13 | 0.43 | 1.41 | 0.15 | 1.59 | 2.72 | 0.62 | 0.13 |
| | 10 | 14.9 | 38.0 | 60 | 1,057 | 71 | 1.83 | 2.73 | 0.25 | 2.60 | 5.01 | 0.45 | 0.40 |
| | 20 | 11.5 | 25.5 | 48 | 942 | 82 | 1.90 | 2.29 | 0.30 | 2.22 | 5.60 | 0.29 | −0.47 |
| | 30 | 12.1 | 26.7 | 36 | 218 | 18 | 0.57 | 1.63 | 0.32 | 2.30 | 3.56 | 0.54 | 0.89 |
| *M. pharensis* | pooled | 23.8 | 57.3 | 97 | 16,928 | 759 | – | – | 0.34 | 2.40 | 11.99 | 0.25 | −0.52 |
| | 5 | 17.8 | 20.4 | 49 | 533 | 30 | 0.90 | 1.83 | 0.49 | 1.20 | 2.27 | 0.38 | −0.77 |
| | 10 | 29.2 | 54.6 | 100 | 2,221 | 76 | 2.03 | 2.62 | 0.33 | 1.87 | 4.01 | 0.28 | −0.82 |
| | 20 | 28.9 | 76.9 | 105 | 8,275 | 326 | 8.83 | 7.37 | 0.32 | 2.66 | 10.70 | 0.33 | −0.24 |
| | 30 | 20.3 | 34.4 | 75 | 4,639 | 229 | 6.77 | 5.02 | 0.38 | 1.70 | 5.33 | 0.24 | −1.03 |
| | 50 | 13.0 | 17.4 | 32 | 1,260 | 97 | 2.83 | 2.36 | 0.44 | 1.40 | 3.62 | 0.47 | −0.26 |
| *M. senaria* | pooled | 96.3 | 120.8 | 351 | 13,899 | 132 | – | – | 0.35 | 1.50 | 4.00 | 0.41 | −0.91 |
| | 5 | 89.6 | 113.1 | 220 | 269 | 3 | 0.10 | 0.40 | 0.83 | 1.30 | – | 1.34 | – |
| | 10 | 77.0 | 107.9 | 300 | 693 | 9 | 0.30 | 0.84 | 0.46 | 1.40 | 1.50 | 0.83 | −0.07 |
| | 20 | 92.4 | 204.4 | 332 | 9,056 | 88 | 1.17 | 1.60 | 0.31 | 1.70 | 4.30 | 0.48 | −0.68 |
| | 30 | 123.3 | 122.3 | 400 | 2,713 | 22 | 0.73 | 1.55 | 0.56 | 1.00 | 1.76 | 0.51 | −0.60 |
| | 50 | 116.8 | 144.9 | 396 | 1,168 | 10 | 0.30 | 0.65 | 0.49 | 1.20 | 1.10 | 0.56 | −0.47 |
| *M. carmabi* | pooled | 12.4 | 24.3 | 63 | 829 | 67 | – | – | 0.29 | 1.96 | 4.00 | 0.50 | 0.52 |
| | 20 | 23.1 | 38.0 | 66 | 415 | 18 | 0.40 | 1.83 | 0.38 | 1.60 | 2.91 | 0.81 | 0.02 |
| | 30 | 8.5 | 15.5 | 33 | 414 | 49 | 1.13 | 6.02 | 0.32 | 1.80 | 3.12 | 0.48 | 0.63 |
| *M. formosa* | pooled | 10.7 | 17.2 | 49 | 342 | 32 | – | – | 0.34 | 1.60 | 1.84 | 0.64 | 0.60 |
| | 30 | 39.3 | 25.0 | 56 | 157 | 4 | 0.17 | 0.59 | 0.99 | 0.70 | −1.90 | 0.67 | −1.99 |
| | 50 | 6.6 | 11.6 | 42 | 185 | 28 | 0.87 | 2.16 | 0.37 | 1.80 | 2.88 | 0.63 | 0.64 |


M. mirabilis
M. pharensis
M. decactis
M. senaria
M. carmabi
M. formosa
Total
5M
10M
20M
30M
50M
More

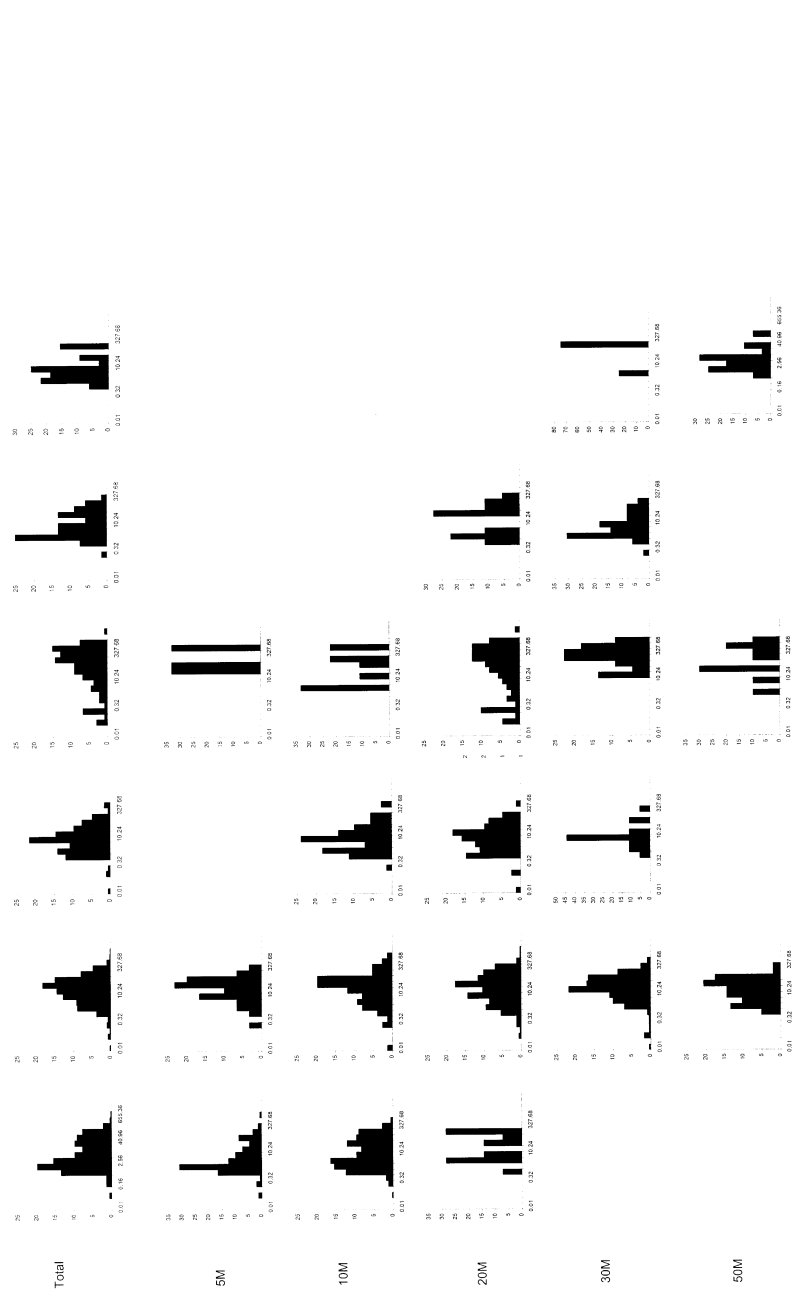



Figure 2. Size frequency distributions of all *Madracis* species at 5 depths (5, 10, 20, 30, 50 m and pooled; total) on (a) *(opposite page)* normal and (b) logarithmic scales at Buoy 1, Curaçao. Y- axis is population composition in % of total individuals and x-axis is size classes in $cm^2$. Note that the range of the y-axes differs between graphs.

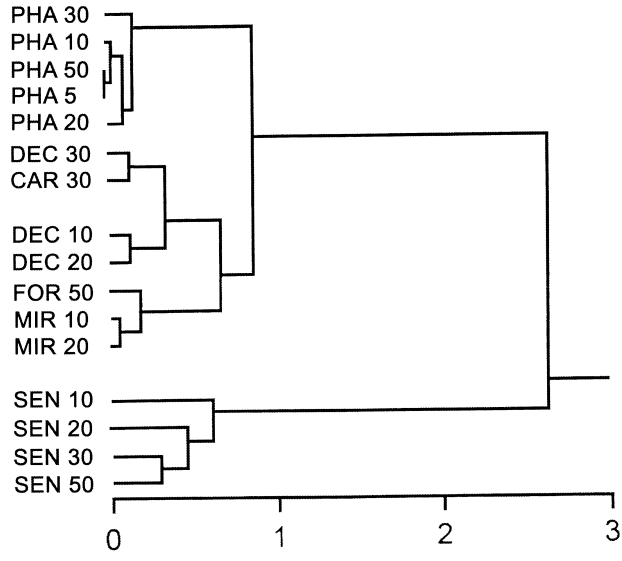



Figure 3. Cluster diagram (using complete linkage and gamma as distance metric) showing the high degree of similarity between the size distributions of the different *Madracis* species. Similarity between populations of the same species proved to be nearly twice as high as between species.

We calculated G from the individual colony sizes and the total surface area of a species' population (i.e., the summed surface of all individuals per depth). Values ranged between approximately 0.20–0.50 for all species. This indicates that total population surface, or related parameters, e.g., the genetic composition of a next generation is largely determined by the large contributions of a relatively small number of larger colonies. The influence of larger individuals is different for branching and encrusting species. For the (semi) branching species *M. mirabilis*, *M. formosa, M. decactis* and *M. carmabi* 21% of the larger individuals contribute 80% to the population's surface. For the encrusting species (*M. pharensis*, *M. senaria*) this value increases and 30% of the individuals correspond to 80% of the population's surface. Differences between species arise in the 50% of the population containing the largest individuals. The contribution of the first 50% of the population, containing the smaller colonies, to the total population surface is identical between species.

The hypothesis that G is related to density (which we used as a measure of the suitability of the habitat) was tested for each species against the null-hypothesis $r^2 = 0$ and a significant negative relation was found: $r^2 = 0.60$, SD = 0.25; Mann-Whitney U-statistic = 25.00; $P < 0.005$). This indicates that the relative unevenness of individuals increases at depths where they are least abundant. The increase in G is higher for species characterized by a relatively large fraction of large colonies in their populations, such as *M. senaria*. This is caused by the sensitivity of G to shifts away from the mode, or zero in a distribution (Bendel et al., 1989). In general, low G values indicate a stable size distribution where the number of individuals gradually decreases from the smallest size class towards successive size categories.

*Coefficient of Variation (NTD).*—The coefficient of variation (CV in Table 1) allows the comparison of variation present in coral populations, irrespective of differences in mean colony size. Factors affecting the size of a colony should be reflected in an in-

creased variability in the population and translated to increased values for CV (Bak and Meesters 1998). The variation in colony size increased with abundance for all species ($r^2 = 0.30$, $P < 0.02$; $n = 21$).

*Skewness (NTD).*—Skewness ($g_1$ in Table 1) is a measure of the symmetry of a distribution around its mean. If skewness is nonzero, a distribution is considered asymmetric. A positive value indicates a long right tail, i.e., most individuals are found on the left side of a distribution whereas a negative value corresponds to a long left tail. All *Madracis* populations in Figure 2A are skewed to the right indicating that juveniles dominated the populations for all species. *M. senaria* populations differed from this pattern and were characterized by lower $g_1$ values indicating a lower proportion of small individuals in the population. When the populations from all depths are pooled, *M. pharensis* has the highest overall $g_1$ (12.0) indicating a large fraction of individuals in the smallest size classes. This relative proportion of small colonies is successively lower for *M. mirabilis* ($g_1 = 5.9$) and *M. decactis* ($g_1 = 5.4$), followed by *M. senaria* ($g_1 = 4.0$), *M. carmabi* (4.0) and *M. formosa* ($g_1 = 1.8$). For all species a positive relation exists between abundance and high values of $g_1$ ($r^2 = 0.51$; $P < 0.001$; $n = 19$). This indicates that the small colony fraction becomes proportionally more dominant with increasing density.

For all *Madracis* populations, skewness and the average colony size after range-standardization are negatively related ($R^2 = 0.94$, $P < 0.001$, $n = 19$; Fig. 4). The average colony size after standardization reflects the overall similarity of all colonies within a population relative to the largest colony. Since the largest colony has size 1 by definition, high average values correspond to high similarity of all other colonies to this colony.

This relation is shown in Fig. 4 where populations of species at the limits of their depth range correspond to average standardized size values greater than 0.12. Low values for $g_1$ and average standardized size values greater than 0.12 are therefore indicative of populations in marginal habitats, e.g., the outer limits of a species distributional range.

Log Transformed Size Distributions (LTD) and Population Composition Parameters.—After log transformation (Fig. 2B), relative dominance of intermediate sizes and increased resolution in the smaller size classes provide better information on the smallest (0–5 $cm^2$) size classes in the data set (Fig. 2A). As for the mean size in untransformed data, log-transformed mean size was significantly different between species (Kruskal-Wallis test, $H > 127.24$, $P < 0.001$, $n = 1585$). The increased similarity to a normal distribution results in overall lower values for CV and $g_1$ in the transformed data set. Variation in transformed populations is approximately 4.4 times lower than variation in untransformed populations because of the reduced influence of a small fraction of larger colonies. A peak shows up in the 0.08–0.16 $cm^2$ size class for *M. senaria.* This species spawns large amounts of planulae in November (Vermeij et al., 2003) and we believe that the peak corresponds to recruited planulae since we collected most data during December 1998 and January 1999. A bimodal distribution was evident for the branching species, *M. mirabilis,* after log-transformation. Bimodality appears to be indicative of the presence of structurally weak medium-sized colonies in a population. These colonies either break apart (i.e., fragmentation) or are structurally supported by neighboring colonies in monospecific beds, resulting in the large colony sizes. The log-transformed size distribution, used as a proxy of the population's age distribution (Vermeij and Bak, 2000), is allowed for small coral species (Bak and Meesters, 1998).

*Coefficient of Variation (LTD).*—After transformation the value of CV was used to assess the variability in age rather than size in a population. The disproportionate contri-

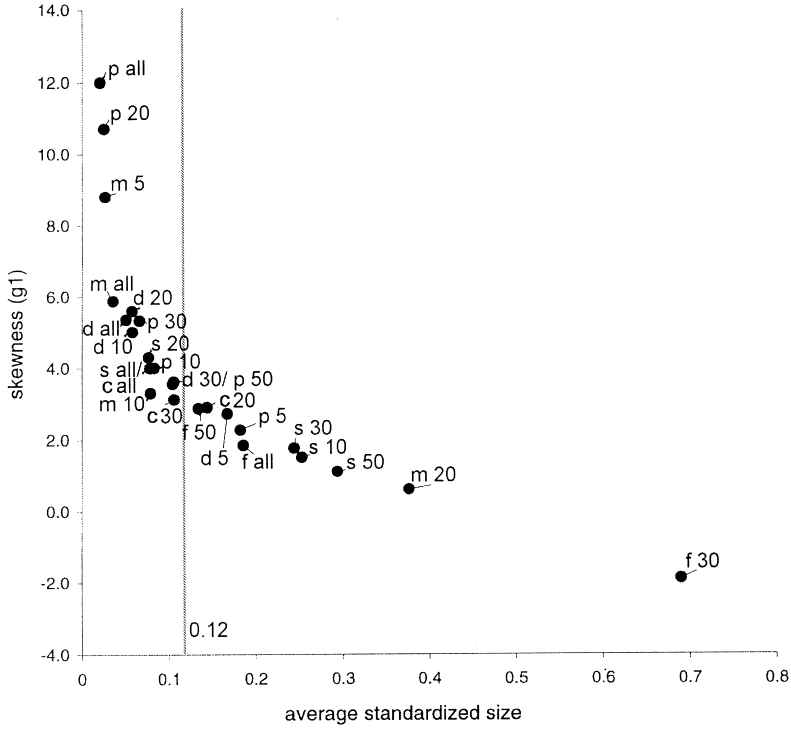



Figure 4. The relation between skewness ($g_1$, NTD) and the dimensionless mean standardized size for all possible species-depth combinations for *Madracis*. Note the increased dispersion and presence in the right part of the graph, representing coral populations near the end of their vertical range, along the horizontal axis (mean standardized size) compared to the vertical scale (skewness). Populations with a mean standardized size higher than 0.12 all correspond to populations in marginal habitats. Letters and numbers indicate species and depth (m). All= all depths pooled. D = *M. decactis*, F = *M. formosa*, M = *M. mirabilis*, C = *M. carmabi*, P = *M. pharensis* and S = *M. senaria*.

bution of large individuals to the population variability in untransformed distributions was reduced. After transformation CV became negatively related to abundance ($R^2$ = 0.35; $P < 0.007$; n = 19) and unrelated to colony size ($R^2 = 0.04$, $P > 0.38$, n = 19). In theory, the value of CV depends on the population size. However, we calculated that this error becomes <1% of the total variation when $n > 12$ and therefore is acceptable. There is a clear relation between the structural complexity of a coral species and its size variation (colony surface relief and CV; $R^2 = 0.69$, $P < 0.01$, n = 6). This shows that branching species have higher CV values than encrusting species, probably because of their greater susceptibility to physical disturbance.

*Skewness (LTD).*—This statistic is most useful in describing transformed populations since it illustrates the deviations from the normal distribution ($g_1 = 0$). This distribution results from a balance between juvenile input ($g_1$ increases) and adult longevity ($g_1$ decreases). After transformation, 8 of the 19 populations (42%) remained positively skewed indicating that relatively more colonies were present in the smallest size classes.

Negative values for $g_1$ indicate a high relative proportion of larger colonies in a distribution and were found for the encrusting species *M. pharensis* and *M. senaria*.

Positive $g_1$ values were mainly found for the branching species *M. mirabilis* and *M. formosa* where small colonies still dominated the population after transformation. The dominance of small colonies may be the result of fragmentation, which is facilitated by the branching morphology of these species.

MORTALITY.—Mortality rates were generally low (Table 2), probably due the absence of catastrophic events such as storms during the interval between the surveys. Higher mortality related to low density for *M. decactis* and *M. pharensis*. No dead colonies for *M. senaria* were found after one yr. Assuming a steady population state, i.e., the number of individuals remains the same, the number of surviving new recruits needed to compensate for the lost colonies is low. For *M. decactis*, 0.20 colonies $m^{-2}$ $yr^{-1}$, and for *M. pharensis,* 0.07 colonies $m^{-2}$ $yr^{-1}$ are needed to replace the dead colonies (all depths pooled).

Based on the yearly colony mortality we calculated the time needed for half of the population to die assuming no input of new individuals and density independent mortality. These halftimes are given in Table 2 and differed between species.

JUVENILE COLONIES.—Two processes are responsible for the supply of juveniles to a population: recruitment and fragmentation. The number of juveniles of each species is given in Table 3 for all depths. To estimate the contribution of each source to the smallest size class we measured the distance between each juvenile and the closest colony (>>2$cm^2$) of the same species. We assume that this distance will be small on average in case of fragmentation and larger if settlement is the dominant source of juveniles.

The abundance of juvenile *Madracis* colonies (n = 484) reflected the abundance of the adult fraction of the populations for all species at all depths ($R^2 = 0.82$, $P < 0.05$, $n = 5$). In Fig. 5, the proportion of juveniles within different distance classes is given for each depth. Below a depth of 30 m, a sharp increase occurs in the number of juvenile colonies present in the 32 cm+ distance category. The decrease in the proportion of juveniles within close distance to large colonies may result from a reduced role of fragmentation with depth as a source of new individuals.

## DISCUSSION

This study shows that structure in coral populations is variable, but highly dependent on species-specific characteristics. The size-frequency distributions of *Madracis* species were species-specific. These general patterns were distorted at the margins of species depth distributions. In all species towards the end of a species depth distribution: (1) Densities of populations decreased resulting in 'saw-shaped' size distributions; (2) Overall variation in un-transformed colony size distributions, expressed as coefficient of variation (CV), decreased, while the variation in log-transformed size distributions, which is indicative of the time a colony has been present on the reef, increased; (3) Decreased skewness in untransformed size distributions ($g_1$) indicated that the proportion of smaller colonies decreased within the population; (4) The relative inequality in the contribution of these larger individuals to the total population surface increased and is indicated by higher values for the Gini-coefficient (G); and (5) Mean colony sizes became larger than 0.12 (after range standardization of size-data).

The similarity in population composition (0.84) for all *Madracis* species along their vertical range suggests tolerance to a changing environment. The distribution pattern differs among species indicating that they have adapted differently to the range of interacting environmental factors over a depth gradient (light, sedimentation, water move-

Table 2. Mortality rates of three *Madracis* species: *M. decactis*, *M. pharensis* and *M. senaria*. Mortality is expressed as whole colony mortality after 1 yr and in the last colum the period needed for half of the population to die is given as a measure of the population's temporal stability.

| Species | Depth | Mean colony size ($cm^2$) | Mortality (colonies $yr^{-1}$) | Colonies (n) | 50% population mortality (yrs) |
|---|---|---|---|---|---|
| *M. decactis* | pooled | 12.9 | 5.9 | 185 | 11.7 |
| | 5 | 12.1 | 0.0 | 13 | >100 |
| | 10 | 14.9 | 5.7 | 71 | 12 |
| | 20 | 11.5 | 5.4 | 82 | 13 |
| | 30 | 12.1 | 13.3 | 19 | 5 |
| *M. pharensis* | pooled | 23.8 | 2.6 | 758 | 27 |
| | 5 | 17.8 | 4.0 | 30 | 17 |
| | 10 | 29.2 | 5.2 | 76 | 13 |
| | 20 | 28.9 | 1.1 | 326 | 61 |
| | 30 | 20.3 | 2.4 | 229 | 28 |
| | 50 | 13.0 | 5.1 | 97 | 13 |
| *M. senaria* | pooled | 96.3 | 0.0 | 132 | >100 |
| | 5 | 89.6 | 0.0 | 3 | >100 |
| | 10 | 77.0 | 0.0 | 9 | >100 |
| | 20 | 92.4 | 0.0 | 88 | >100 |
| | 30 | 123.3 | 0.0 | 22 | >100 |
| | 50 | 116.8 | 0.0 | 10 | >100 |

ment and temperature). Broad adaptation results in generalist species (*M. pharensis* and *M. senaria*) whereas a limited depth range indicates specialists (e.g., *M. mirabilis* and *M. formosa*).

Our results correspond to the findings of Meesters et al. (2001), who found that coral populations on degraded sites become dominated by large colonies. The finding that the shift towards larger colonies in a population is found along vertical (this paper) as well as

Table 3. The number of juvenile colonies (surface < 2 $cm^2$) within the isobathic 30 $m^2$ transects at various depths for all species.

| Species | Depth (m) Number of colonies | 5 | 10 | 15 | 20 | 30 | 40 | 50 |
|---|---|---|---|---|---|---|---|---|
| *M. decactis* | | 3 | 23 | 30 | 26 | 1 | 1 | 0 |
| *M. mirabilis* | | 91 | 25 | 5 | 0 | 0 | 0 | 0 |
| *M. pharensis* | | 3 | 15 | 63 | 62 | 42 | 30 | 15 |
| *M. senaria* | | 0 | 0 | 0 | 21 | 0 | 0 | 1 |
| *M. carmabi* | | 0 | 0 | 0 | 6 | 15 | 0 | 0 |
| *M. formosa* | | 0 | 0 | 0 | 0 | 0 | 2 | 4 |
| Total | | 97 | 63 | 98 | 115 | 58 | 33 | 20 |

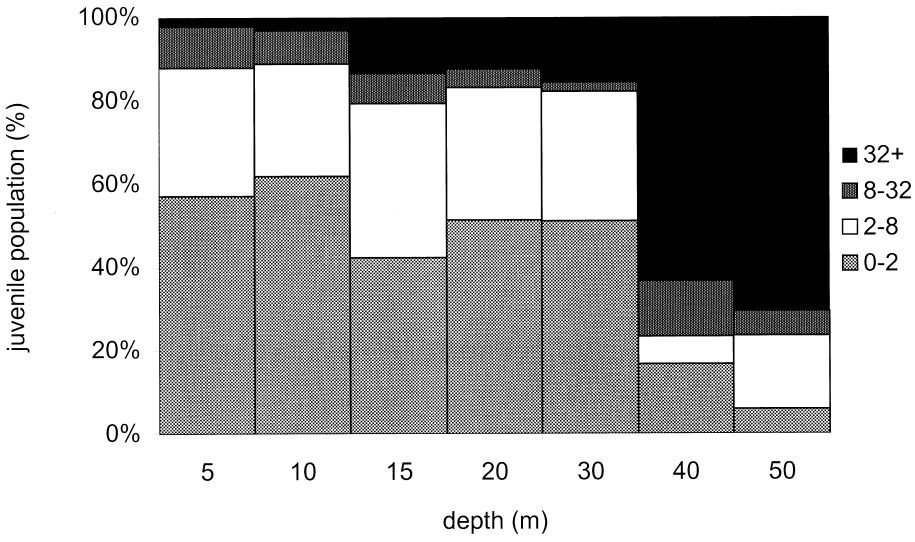



Figure 5. Origin of juvenile colonies over a depth gradient (all *Madracis* species pooled). The distance between juvenile colonies from larger colonies is indicative of their origin. Fragmentation results in short distances between juveniles and their supposed adults whereas settling juveniles correspond to larger distances.

horizontal spatial scales (Meesters et al., 2001) indicates the general usefulness of skewness ($g_1$) in assessing the status of coral populations. Since increased domination of larger individuals corresponds to increased negative skewness, it can be used to characterize populations growing under these sub-optimal conditions, i.e., in marginal habitats. In addition, we propose the use of the mean colony size based on standardized untransformed size data as an additional indication to characterize these populations (Fig. 4). This method expands the ability to distinguish marginal populations, dominated by larger individuals and already characterized by low $g_1$ values, because of its higher descriptive range, i.e., resolution. Based on our *Madracis* study we find that average standardized mean sizes (ASMS) higher than 0.12 correspond to populations in marginal habitats. The extent to which this value can be used for other species needs study.

Increasing G-coefficients towards a species distribution limit indicate a less structured contribution of population members to an overall characteristic resulting from 'saw-shaped,' or unstructured size distributions (Fig. 2A,B). The change in G strongly depends on changes of the mode from zero in a distribution (Bendel et al., 1989). In populations where many juveniles ensure the mode to be near zero (e.g., *M. mirabilis*, *M. decactis*), changes in G are expected to be smaller than in populations where this fraction is relatively small (e.g., *M. senaria*, *M. formosa*). Although reference values are needed to determine the change in G for each species, its change can be used as a third method to characterize populations in marginal habitats. In summary, we can conclude that coral populations in marginal habitats are mathematically characterized by: (1) low and negative values for $g_1$ (NTD); (2) mean colony sizes larger than 0.12 for range-standardized sizes; (3) increased G-values; and (4) high CV for log-transformed size distributions. This expands the number of possible statistics to study coral populations (Bak and Meesters 1998, 1999).

Colony density appears to be an important species characteristic under environmental control (selective environment) in contrast to population structure, which is determined by species-specific life-history strategies (developmental environment). It often remains difficult to determine if and which demographic processes are under density-dependent control. The few studies dealing with density dependence in corals or other clonal marine animals focus mainly on the effects of mortality and recruitment in populations and not the shape of its size distribution (Karlson et al., 1996; Tanner, 1999). For *Madracis* species, high densities correspond to a higher number of small colonies (high positive $g_1$), a structured population (low G) and low mortality. Our findings also indicate a relation between colony density and the statistics describing the size distribution. For the untransformed and transformed data sets all statistics show similar trends with abundance except for skewness in the log-transformed data set. In this set, $g_1$ approached values near zero for all species-depth combinations indicating a close resemblance to a normal distribution ($g_1 = 0$). The increased normality must result from a balance between adult (partial) mortality and juvenile input/survival. This also explains the consistency of the size distributions within species over an environmental gradient. Such species specificity of $g_1$ (LTD) has been demonstrated by Meesters et al. (2001). For *Madracis* species negative $g_1$ values (LTD) characterize the encrusting species *M. pharensis* and *M. senaria* whereas branching species have positive $g_1$ values. This suggests a general relation between colony morphology and life-history strategy with a larger fraction of relatively large colonies dominating in encrusting species. Increased adult longevity, or reduced input of juveniles, due a reduced role of fragmentation in the life history strategy of encrusting growth morphs, can explain this observation.

Meesters et al. (2001) suggest that the dominance of larger individuals in marginal habitats confirms the asymmetric competition hypothesis derived from terrestrial botany (Begon, 1984). This dominance could also result from a decrease in the number of suitable spots within the habitat mosaic at a certain depth. The first planulae settling in these spots, grow and occupy space preventing further settlement. The resulting population will consist of the few larger initial colonies and a reduced proportion of juveniles due the unavailability of suitable substratum.

*Madracis* species are closely related (Wells, 1973a,b; Fenner, 1993) and four species show genetic exchange: *M. pharensis*, *M. decactis*, *M. formosa* and *M. carmabi* (Diekmann et al., 2001). The similarity between distributions of the same species is twice as high compared with other species (Spearman rank correlation coefficients 0.84 *versus* 0.49). This is remarkable given their genetic relatedness. It indicates that changes in life history strategies or differential environmental plasticity possibly precede genetic fixation in the formation of new species.

Our study shows the poor overlap of the three paradigms (i.e., morphometrics, genetics and ecological characterization) that are currently used to study corals. Variation in one of these fields does not necessarily match with variation in the others, which is illustrated by results from our study. For example, the only morphological difference between *M. pharensis* and *M. senaria*, both found along a broad depth range (0–100+ m), is found at calyx level (*M. senaria* possesses six exert septa) but their life-history strategies differ. An abrupt end on the right side for *M. senaria* size frequencies in Fig. 2B suggests that catastrophic events results in whole colony mortality for this species. Catastrophic mortality rather than increasing levels of partial mortality prevents indeterminate growth in this species (Bak and Meesters, 1998). The relatively high number of large colonies in its

population, the low susceptibility to overall and partial mortality suggest that *M. senaria* is a species with a 'Phalanx' life history strategy (sensu clonal terrestrial plants Platt, 1975; Connell, 1978). Higher variation within the population (CV, NTD) suggests that colony size and population build-up of *M. pharensis* is more susceptible to environmental disturbance than in *M. senaria*. Furthermore, we found higher population turnover rates for *M. pharensis* and a significant decrease in juveniles generated by fragmentation with depth. Given these characteristics, *M. pharensis* seems best described as a generalist with a 'Guerilla' life history (Platt 1975; Connell 1978). The different life-history strategies of *M. pharensis* and *M. senaria* allow them to survive over a large depth range (5–60+ m) and indicate the ability of both species to deal with interacting structuring factors along a broad environmental range (water movement, light, temperature) using different strategies.

*Madracis pharensis* is often regarded as an ecomorph of *M. decactis,* because they overlap in colony morphology and corallite characteristics (Zlatarski and Estalella, 1982; Fenner, 1993). In our study *M. pharensis* and *M. decactis* showed different size distributions over the reef slope. *Madracis decactis* was not found below 30 m, indicating that demographic differences can exist between species that are not easy to distinguish using morphological or genetic criteria. Nodular and encrusting colony morphologies can be different developmental pathways of the same species that are adaptive, i.e. increase fitness, in different habitats (Moran, 1992). Most *M. decactis* colonies (≈ 70%) prefer positions on top of the substrate, whereas most *M. pharensis* colonies (≈ 90%) occur in cryptic positions on the reef (Fenner 1993; Vermeij and Bak, 2002). Within the syngameon or species-complex (Veron 1995), *M. decactis* prefers the advantages of high light availability while *M. pharensis* could be a fugitive morph. Increased fitness due to reduced sediment stress or escaping the disadvantages of overcrowded habitats (Denno and Roderick 1990) drives its occupation of a new cryptic habitat. The sharing of early morphological pathways (polyp architecture) between *M. pharensis* and *M. decactis*, prior to morphological divergence at colony level, results in shared characteristics. We hypothesize that *M. pharensis* is a species currently evolving as a refuge strategy morph of *M. decactis*. The occupancy of a new habitat associated with high relative fitness may explain the high numbers of *M. pharensis* on the reefs of Curaçao.

Because of its low density it was impossible to determine the size distribution for the new *Madracis* species, *M. carmabi*. Morphological and genetic data from Diekmann et al. (2001) suggest that this species is a hybrid between the *M. decactis/pharensis*-complex and *M. formosa*. *Madracis carmabi* is only found around 30 m, which is intermediate between the depth distributions of *M. formosa* and *M. decactis.* This suggests the presence of a hybrid zone (Futuyma, 1986) between *M. decactis* and *M. formosa*. In this case, morphological, genetic, and ecological data all correspond. Results obtained by using one of the three paradigms to describe coral behavior can be translated to the other two, but that this is not necessarily true in all cases (e.g., *M. pharensis* vs. *M. decactis*).

We conclude that for *Madracis* species size distributions are species-specific. While morphological and genetic relatedness have resulted in ongoing debate on the status of some *Madracis* species, we show the usefulness of size distribution analyses to successfully analyze and clarify differences between the supposed species.

Size distributions are twice as similar within populations of the same species as among species. The statistics G, CV, $g_1$ and mean colony size, after range-standardizing size data, provide mathematical information on the size-distributions and the similar change

observed for all species at the margins of their distributional range. General patterns arise when populations occur near the margins of their vertical distributions. These characteristic changes can be analyzed using the aforementioned statistics, emphasizing their usefulness in the study of coral populations at the limit of their environmental tolerance and in degraded environments.

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ADDRESSES: (M.J.A.V.) *University of Amsterdam, IBED, P.O.Box 94766, 1090 GT, Amsterdam, The Netherlands and Caribbean Institute for Management and Research of Biodiversity, Piscaderabaai z/n, P.O.Box 2090, Willemstad, Curaçao, Netherlands Antilles.* CURRENT ADDRESS: *Cooperative Institute for Marine and Atmospheric Science (CIMAS) at the Rosenstiel School of Marine and Atmospheric Science (RSMAS) of the University of Miami, 4600 Rickenbacker Causeway, Miami, Florida 33149.* (R.P.M.B.) *Netherlands Institute for Sea Research (NIOZ), P.O. Box 59, 1790 AB Den Burg, Texel, The Netherlands. E-mail: <rbak@nioz.nl>*. CORRESPONDING AUTHOR: (M.J.A.V.).