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*Article*

# Juvenile Coral Abundance Has Decreased by More Than 50% in Only Three Decades on a Small Caribbean Island

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**Abstract:** A comparison of the community structure of juvenile hermatypic corals of 2 to 37 m depth at the fringing reefs of Curaçao between 1975 and 2005 shows a decline of 54.7% in juvenile coral abundance and a shift in species composition. *Agaricia* species and *Helioseris cucullata,* the most common juveniles in 1975, showed the largest decline in juvenile abundance (a 9 and 120 fold decrease in density respectively) with *Helioseris cucullata* being nearly extirpated locally. In 2005, *Porites astreoides* contributed most colonies to the juvenile coral community, increasing from 8.2% (in 1975) to 19.9% of the total juvenile community. Between 1975 and 2005, juveniles of brooding species decreased in relative abundance while the abundance of juveniles of broadcast spawning species increased or remained the same. These data illustrate the magnitude of the changes that have occurred in only three decades in the composition of juvenile coral communities.

**Keywords:** recruitment; degradation; phase-shift; *Helioseris cucullata*; brooder

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## 1. Introduction

Over the past 30 years, coral cover on Caribbean reefs has declined from approximately 50% to 10% [1]. A similar, though less dramatic decline, occurred in Curaçao, in the Southern Caribbean. On the leeward side of Curaçao, coral cover declined from approximately 40% to 20% between 1973 and 2003 [2]. Both in Curaçao [3], and across the Caribbean [4–6], coral cover decline has been attributed to the combination of habitat degradation, sedimentation, and eutrophication that result from local industrial activity and near-shore residential and tourist developments. While the decline in coral cover has been documented for reef systems around the world [7], other changes to coral community structure are less well documented, largely due the absence of long-term studies (*i.e.*, datasets over 20 years old) and relevant historic information.

The maintenance and recovery of coral communities depends on the successful establishment, early survival and subsequent growth of coral planulae [8] and overall recruitment success differs between species under the same environmental conditions [9–11]. Variation in local coral recruitment rates is caused by variation in the composition of the local benthic habitat [8,12,13] as well as the size of the adult source population [8,14]. In addition, the total number of coral recruits, juveniles and adults in a given location will decrease during episodic disturbance events such as storms [15]. Recruitment failure can halt, delay or even prevent coral community maintenance and recovery [12,16,17].

Variability in recruitment across several decades (*i.e.*, between 1963 and 1992) has been quantified in the Pacific (Great Barrier Reef: [15]; Hawaii: [17]) but a decline in recruitment rates following changes in adult abundance was not observed. On the Great Barrier Reef local recruitment rates depended primarily on the availability of open space [15], whereas in Hawaii they depended on adult cover in the preceding year [17]. Such seemingly conflicting observations can be explained by differences in the open/closed nature of the study system under consideration [18]. For the Caribbean, there is little information on decadal variation in recruitment rates. Hughes and Tanner [16] showed that the recruitment rates of three dominant coral species in Jamaica declined between 1977 and 1993. They suggested increased algal cover and a decline in the species' source populations as drivers of the decline in recruitment rates through time. On Curaçao, Bak *et al.* [2] witnessed a 50% decline in coral cover over a 30-year time period from 1973 to 2003. Similarly, Vermeij [10] observed a 5.16-fold decline in coral recruitment to artificial substrata when comparing data taken during 1979–1981 with data taken over the period 1998 to 2004.

"True" recruitment, *i.e.*, the combined outcome of settlement and early post-settlement mortality, is difficult to monitor due to the temporal variability in larval supply, and the problems in finding and identifying true coral settlers, which are less than 2 mm in diameter; [8]). Growth rates collected for various species at Curaçao [10] indicate that coral colonies up to 4 cm in diameter can be up to 13 years old. Juvenile densities are therefore not indicative of recent and potentially stochastic recruitment dynamics, but rather represent the integrated outcome of settlement and postsettlement survivorship over much longer time periods (*i.e.*, greater than 10 years). The fact that juvenile densities represent the integration of approximately ten years of recruitment means that measurements of juvenile abundance are less subject to dramatic interannual fluctuations.

In this article, we compare the abundance and distribution of juvenile corals on Curaçao's leeward reefs in 2005 with a similar data set from 1975 from the same Caribbean island [19]. Using this

uniquely detailed historical ecological data on juvenile corals, we quantify the changes that have occurred in the abundance and composition of Caribbean juvenile coral communities over a thirty year period.

## 2. Materials and Methods

### *2.1. Sampling Methodology*

The abundance of juvenile corals (maximum diameter 4 cm) was determined at six reefs along the Curaçao coast, including the two sites that were studied using similar methods in 1975 [19]: Buoy I (12°07'34"N–68°58'32"W) and Buoy III (12°07'34"N–68°58'41"W). The other sites are: Santa Martha Bay (12°16'04"N–69°07'47"W), Snake Bay (12°08'21"N–68°59'53"W), Piscadera (12°07'21"N–68°58'16"W) and Water Factory (12°06'32"–68°57'16"W). For details on all sites, see [20]. At each site the abundance of juveniles was determined in four depth zones (following the original sampling design described in [19]): the shallow terrace zone (3–9 m), the drop-off zone (9–17 m), the upper slope zone (17–26 m) and the lower slope zone (26–37 m).

At each depth we counted, identified, and measured all juvenile hermatypic corals within a 0.25 m × 0.25 m quadrant that was moved along a 5 m long transect so that all juveniles in a total area of 1.25 $m^2$ were quantified for each transect. In each depth zone, a minimum of eight transects were haphazardly placed, avoiding sand patches and dense monospecific beds of the yellow pencil coral *Madracis mirabilis*.

### *2.2. Species Identification*

Because of the difficulty of identifying some of the smallest juveniles to species level, they were binned at the genus level for the following species: *Madracis* spp. (*i.e.*, *M. decactis*, *M. pharensis* and *M. senaria*), *Siderastrea* spp. (*i.e.*, *S. siderea* and *S. radians*, *Montastraea* spp. (*i.e.*, *M. annularis*, *M. faveolata* and *M. franksi*) and *Agaricia* spp. (*i.e.*, *A. agaricites*, *A. humilis* and *A. fragilis*). Finally, because solitary juvenile polyps of *Scolymia lacera* and *Mussa angulosa* look very similar, they were grouped as "*Mussa* sp./*Scolymia* sp.". Juveniles of the hydrozoan *Millepora* spp. (*i.e.*, fire coral) were also included in our surveys.

### *2.3. Statistical Analyses*

For each species, estimates of juvenile abundance in 2005 were correlated against depth to determine if a possible relationship existed between the abundance of their juveniles and depth. Potential differences in the distribution of juveniles (all species combined) across space in terms of depth and site were further investigated using a nested ANOVA.

The original site-by-site abundance data from Bak and Engel [19] were lost, therefore we could not compare our data to the 1975 data on a site-by-site basis. From the 1975 dataset, only island-wide averages for all species × depth combinations were available. To compare our two datasets, juvenile density for both sampling periods was first recalculated as the number of individuals per $m^2$ using depth zones, rather than sites, as replicates. We then compared juvenile abundance in 1975 and 2005 using a one way ANOVA using "year" as a predictor variable. In taking this approach, we make the

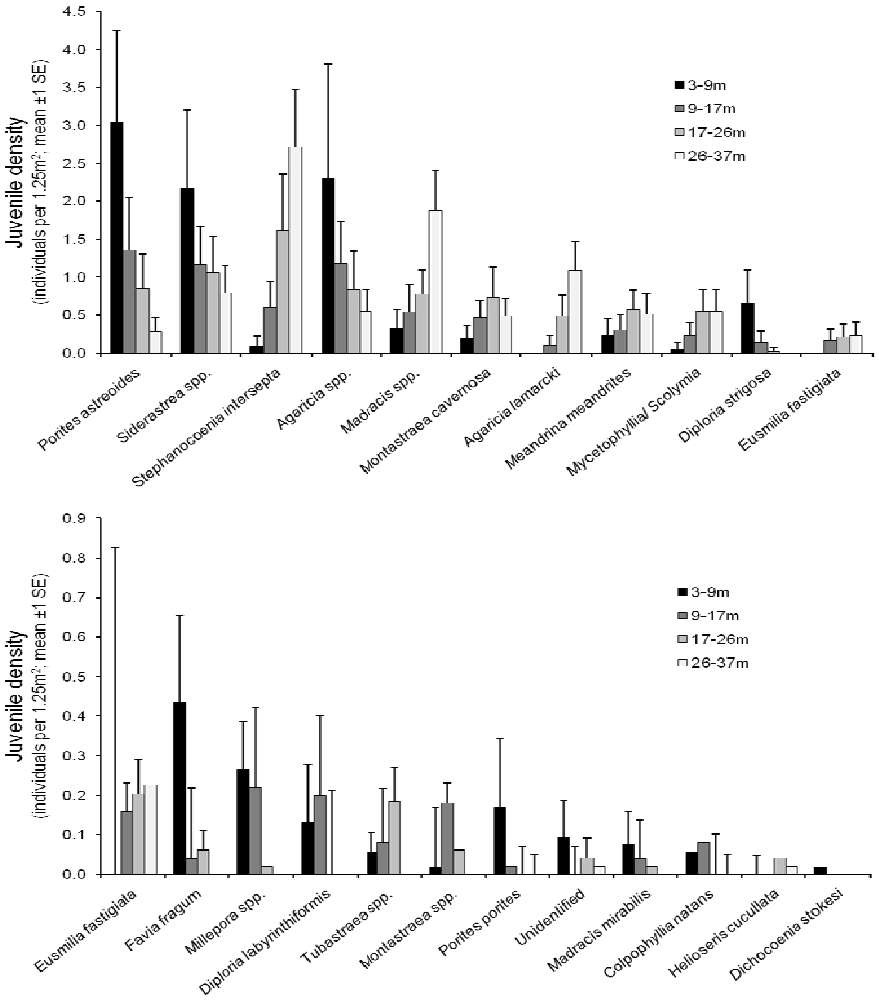
assumption that the data of Bak and Engel [19] provided an average estimate of juvenile abundance along the central leeward coast of Curaçao. To create an appropriate dataset for comparison, we focused our study in 2005 to sites that were also along the central portion of the leeward coast of the island. For more information on the composition of Curaçao's reef communities around the island [20].

## 3. Results

### *3.1. Juvenile Abundance and Distribution in 2005*

In 2005, the species *Agarica* spp., *Porites astreoides*, *Stephanocoenia intersepta* and *Siderastrea* spp. were the four most abundant types of coral juveniles on the reefs of Curaçao at depths between 3 and 37 m (Figure 1) and collectively accounted for 58.1% of all juveniles observed (n = 544). Brooding species thus dominated the juvenile community. The most dominant juveniles of broadcast spawning species were *Montastraea cavernosa* (5.4%) and *Colpophyllia natans* (0.3%).

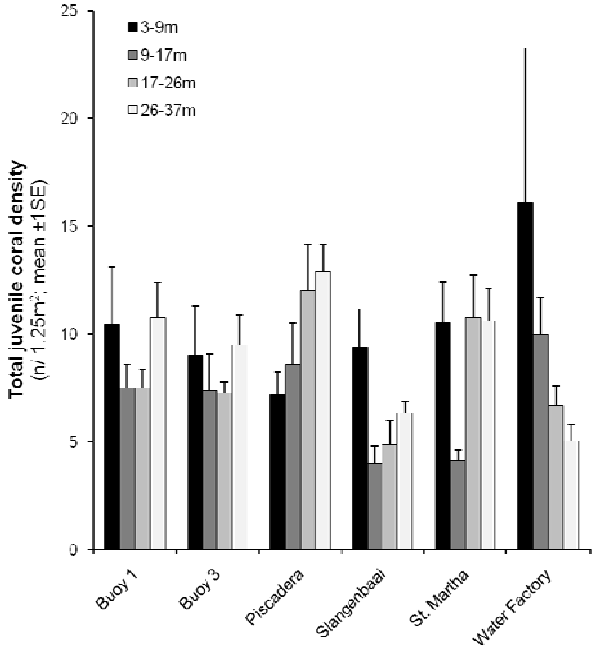
**Figure 1.** Distribution and density of juvenile hermatypic corals on Curaçao in 2005. Bars indicate the species' abundance per depth and are averaged for all six sites. Error bars indicate standard errors (SE). Species are ranked from high to low abundance. Note that the scale of the y-axis was adjusted for the bottom graph which depicts the abundance of the rarest coral species observed in this study.



The abundances of juvenile corals of some species reduced with increasing depth (Figure 1; *Porites porites, P. astreoides, Siderastrea* sp.*, Agaricia* sp., *Diploria strigosa, Diploria labyrithiformis, Favia fragum, Millepora* sp., *Madracis mirabilis, C. natans*, *Dichocoenia stokesi*; $-0.42 < r < -0.15$, $p < 0.001$, $n = 32$). Other species increased in abundance with increasing depth (Figure 1); *S. intersepta, Madracis* sp.*, Montastraea cavernosa, Agaricia lamarcki, Meandrina meandrites, Mycetophyllia/Scolymia* sp.*, Eusmilia fastigiata* and *Helioseris cucculata* ($0.17 < r < 0.54$, $p < 0.02$, $n = 32$). *Montastraea* sp. and *Tubastrea coccinea* showed no clear change in abundance over the depth range considered, *i.e.*, 3–37 m ($-0.01 < r < -0.07$; $p > 0.30$, $n = 32$). Similarly, the relative occurrence of juvenies from broadcast spawning and brooding species did not change with depth. See [19] for species' depth distributions in 1975.

When all species were pooled, no spatial differences in juvenile density across sites could be detected (Nested ANOVA, $F_{18,177} = 1.88$, $p = 0.10$), although the relationship between density and depth varied significantly across sites (Nested ANOVA, $F_{5,177} = 1.88$, $p < 0.01$). All possible relationships between depth and juvenile density were observed for at least one site (Figure 2) suggesting that the distribution of juvenile corals with depth is partially dependent on local environmental factors at the scale of individual sites.

**Figure 2.** Average number of juvenile hermatypic corals (all species pooled) per square meter for all six sites and all four depth zones in 2005. Error bars indicate standard errors (SE).




### *3.2. Historic Comparisons: 1975 and 2005*

Across all sites and depths, juvenile coral density averaged 15.3 individuals per m² in 1975 [19] and 6.9 per m² in 2005. Using depth zones as replicates, the overall decline in mean coral juvenile abundance was highly significant (ANOVA, $F_{1,6} = 39.85$, $p < 0.001$). Juvenile abundance decreased through time for every depth zone. This trend was driven by the reduction in juvenile abundance of

brooding species, whereas the density of juveniles of broadcasting species remained stable or increased (Figure 3). The change in juvenile density thus varied among species (Figure 4).

**Figure 3.** Densities of juvenile hermatypic corals (all species pooled) for brooding and broadcasting species in 1975 and 2005 followed by the net absolute change in density. Each set of three bars represents one depth zone. Different colours inside each bar correspond to brooding (white) and broadcast spawning species (grey).

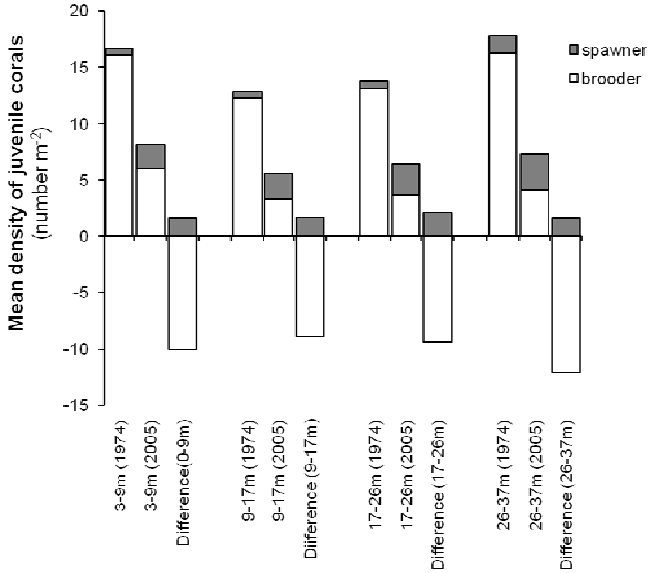
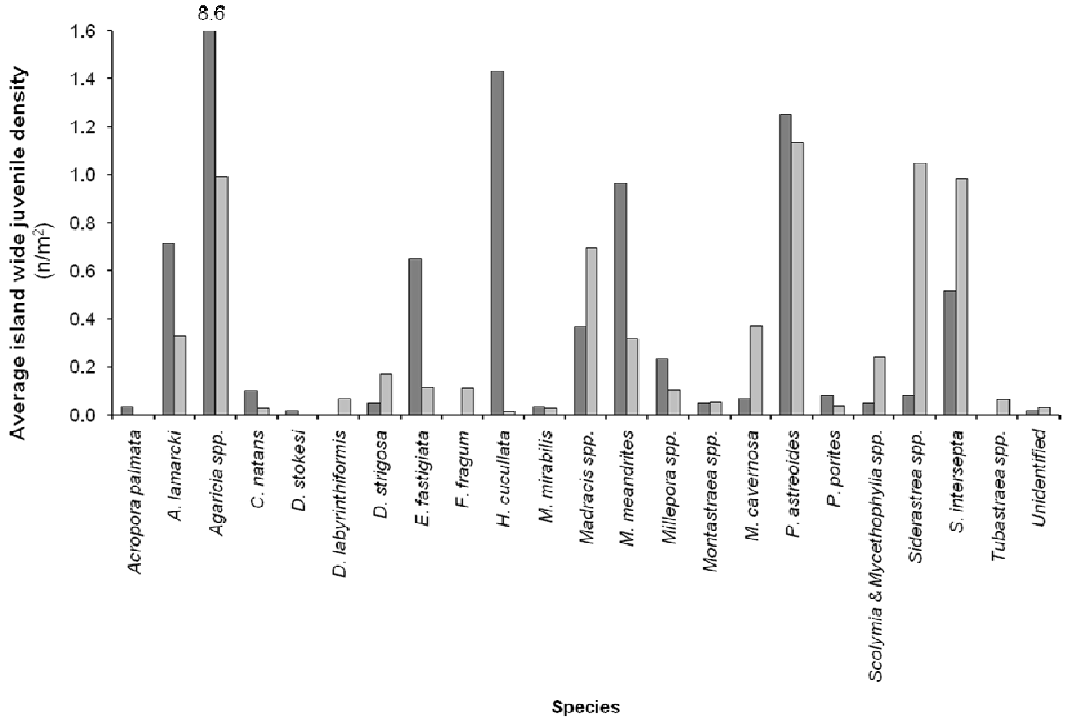
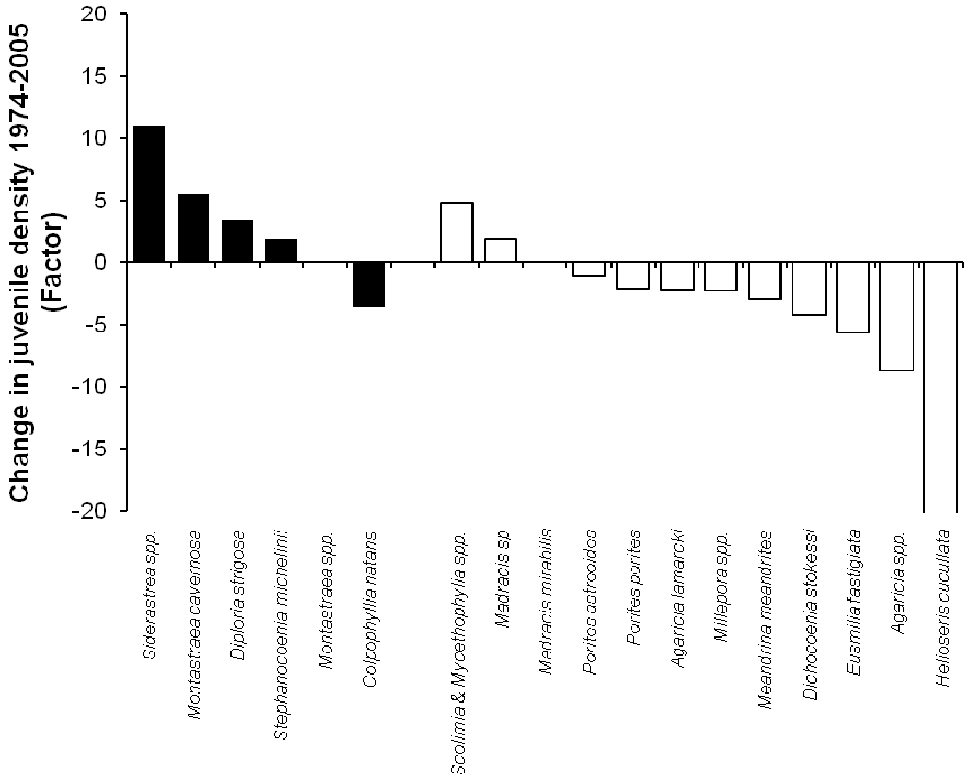



**Figure 4.** Density of juvenile hermatypic corals (all species pooled) in 1975 and in 2005. Different coloured bar correspond to juvenile density in 1975 (dark gray) and 2005 (light grey).



From 1975 to 2005, *Agaricia* spp. experienced the most dramatic decline, from 56.1% of the total juvenile population in 1975 (n = 518) to 14.3% of the total juvenile population in 2005 (n = 50). Despite this reduction, *Agaricia* spp. was still one of the most abundant juvenile coral taxa in 2005. The most dramatic decline was observed for *Helioseris cucullata*, which declined from 9.4% to 0.2% of the total juvenile population. *Siderastrea* spp. show the largest positive change, increasing from 0.5% to 13.3% of the total juvenile population (Figure 4). Therefore, despite the overall decline in juvenile coral abundance, juveniles of some coral species were found in higher densities in 2005 than in 1975 (Figure 5). Notably, six species have increased in abundance (*i.e.*, number of colonies per $m^2$) since 1975. Four of these species (66.7%) are broadcast spawners. Brooders account for the majority (90%) of the species that were less abundant in 2005 (n = 10).

**Figure 5.** Relative change in the density of juvenile hermatypic corals between 1975 and 2005 with species grouped by reproductive mode. Factor is a dimensionless number indicating the number of times individuals of a certain species are more or less abundant in 2005 compared to their density in 1975. Broadcast spawning species are shown in black; brooding species in white. The change in density of *Helioseris cucullata* juveniles (*i.e.*, −120 fold) exceeds the scale in this graph).




## 4. Discussion

This study provided a comparison of the community structure of coral juveniles along the coral reefs of Curaçao's leeward shore, along the depth gradient from 3 m to 37 m. Juvenile coral densities on Curaçao in 2005 (average of 6.9 individuals per m² across depths) were 1–5 times higher than the densities measured on other Caribbean islands over the last 15 years [21,22], but these values were still lower than those historically measured in the Caribbean region [19,23,24]. The distribution of species

across the depth gradient we examined in 2005 (Figure 1) parallels the historical data collected on the same reefs in 1975 [19]. Juvenile coral community composition varied minimally between sites, which is unsurprising due to the uniform nature of the reefs along the central part of the leeward coast of Curaçao [20]. Most of the coral juveniles belonged to four taxa: *Porites*, *Siderastrea*, *Stephanocoenia* and *Agaricia*, which together accounted for 63.4% of all juveniles observed (n = 544).

The abundance of juveniles serves as a proxy measurement of the integrated outcome of settlement, post-settlement survivorship and disturbance across a multiple year time period. We observed that this metric, total juvenile abundance, declined by 54.7% overall between 1975 and 2005. Importantly, we quantified coral *juveniles* that were on average approximately 13 yrs old [10] rather than recruits (*i.e.*, coral settlers < 4 mm in diameter). Therefore, the temporal fluctuations that affect recruit supply [8] are less pronounced in the overall abundance of juveniles and the observed decline in juvenile abundance is unlikely to be an artifact from sampling the highly variable recruitment process at the beginning and end of a 30 yr period. Importantly, the decrease of juvenile corals was observed consistently in four different depth zones between 3 and 37 m. (Figure 3). The declining abundance of coral recruits described here on multi-decadal timescales [10], as well as the decreasing densities of coral juveniles on other islands in the Caribbean [16], and decreased growth rates of juvenile corals [25], together suggest that conditions for the successful establishment and growth of coral recruits and juveniles have worsened in recent decades.

Within this dim picture overall, certain species have suffered disproportionately, and are now virtually absent from Caribbean reefs. In our study, juveniles of *Helioseris cucullata* (formerly known as *Leptoseris cucullata*) comprised 8.3% of the juvenile population in 1975, making them the second most common juvenile species on Curaçaoan reefs. By 2005, *H. cucullata* decreased in absolute abundance 120-fold, *i.e.*, from an average of 1.43 juveniles per square meter in 1975 to 0.01 in 2005. In three decades, a once abundant species nearly disappeared from the local species pool. Similar observations were made on Jamaica where recruitment rates of *H. cucullata* and adult cover of this species both approached zero during the late 1980s [16], while it was known as a dominant species in the juvenile community previously [26,27]. Because this species has a relatively short life span, recruitment is crucial to maintain its population through time [16]. While overall coral recruitment rates appear to have declined over the last three decades, *H. cucullata* most clearly shows how a once abundant species all but disappeared from Caribbean reefs in a little over three decades.

In the Caribbean, members of the genus *Agaricidae* typically dominate juvenile coral communities. The abundance of this brooding species, and *Porites* spp. in 2005 echoes the shift seen in the community structure of other Caribbean reefs (e.g., [28–30]) from long-lived broadcast spawning species to brooding species that are characterized by shorter lifespans and a weedy life history strategy. Importantly, Agaricids have always been the most dominant taxa in juvenile coral communities on Curaçao [19], and on other Caribbean reefs [16,24,31]. Thus, the idea that brooding specie are increasing in dominance is supported by the *relative* increase in their abundance compared to other coral species. Despite an increase in relative abundance, the absolute numbers of Agaricid juveniles was nevertheless lower in 2005 compared to 30 years earlier (Figure 5).

The corals that presently dominate the adult coral community of Curaçao are members of the *Montastraea* species complex, *Colpophylia natans*, and *Diploria* species [32]. Juvenile abundances of these broadcast spawning species were extremely low in 2005, however similar observations were

made over 25 years ago [19,23]. This suggests that low absolute abundance of juveniles *per se* is not necessarily indicative of recent recruitment failure, but rather a characteristic of long-lived species with infrequent recruitment success. Surprisingly, the absolute density of juveniles of some broadcast spawning species was 2–11 times higher in 2005 than in 1975 (Figure 5) and the same species dominate juvenile communities elsewhere in the Caribbean [21,24,33].

Bak and Engel [19] described three main ecological strategies for corals: massive, long-lived species with infrequent recruitment, short-lived opportunists with high recruitment rates and species whose propagation depends on vegetative rather than sexual reproduction. Interestingly, all but one of the broadcast-spawning species that occurred in higher densities in 2005 in our study were species in which the males release sperm *prior* to egg release by the females [34]. Therefore, female colonies from these species release *fertilized* eggs or embryos rather than unfertilized eggs (as is the case for "true" broadcasters). Releasing embryos rather than unfertilized eggs combines benefits of obligate broadcast spawning (*i.e.*, large numbers of outcrossed offspring) and brooding strategies (*i.e.*, increased fertilization success). Based on our observation, this should be considered a fourth life history strategy, distinct from the three described by Bak and Engel. Besides the clear difference in spawning behavior, our data show that corals with this ecological strategy are more robust in degraded habitats than "true" broadcast spawning species.

The observation that some species are now occurring in greater densities whereas others have declined indicates that species-specific factors affected the coral community's response to altered environmental conditions between 1975 and 2005. An increase in juvenile density for some broadcasting species (*Siderastrea* spp., *Montastraea cavernosa*, *Diploria strigosa* and *Stephanocoenia michelinii*) suggests that space availability could be important in driving their local abundance since the total cover of adult corals of these same species declined by approximately 50% on Curaçao over the same time period [2].

For species with brooding reproductive strategies, habitat degradation (e.g., increased coverage of benthic algae and the increased abundance of potentially pathogenic microbes) [35]) and/or a reduction of the adult pool can explain the decreased densities of juveniles [30]. Brooders generally recruit close to parental colonies [8,21] and they are therefore less likely to escape degraded habitats whose quality declined after their parent colonies established themselves on a given reef. Brooding species, therefore, could therefore be more severely affected by habitat degradation at a reef-by-reef scale. In contrast, broadcast species have the ability for long distance dispersal which allows their planulae to establish themselves outside locally degraded habitats.

In conclusion, whereas many studies have quantified coral degradation by measuring coral cover, few studies have considered how early life history processes contribute to such changes. Based on our data, we suggest that juvenile coral abundance is a useful measure of reef "health" as it reflects the relative success or failure of reef functional processes (recruitment, growth and survival) on a timescale meaningful to both ecology and conservation [36]. While the 54.7% decline in juvenile abundance observed between 1975 and 2005 can both be a cause and a consequence of the decline in adult coral cover on these reefs, it indicates that fundamental processes required for population maintenance and recovery are operating at rates well below their historic baselines. Historical baselines like the one described here clearly illustrate that recent inventories of coral juveniles alone are not sufficient to understand the changes that have occurred on Caribbean reefs over multiple

decades. The near-disappearance of once abundant species, such as *Helioseris cucullata*, in the relatively short time span of 30 years would have been missed if only recent surveys were considered. In addition, the apparent shift from broadcasting species to brooding species could only be falsified through the use of historic data. The overall decline in juvenile coral abundance in Curaçao over a period of 30 years is representative of the profound changes that are taking place in the structure of juvenile coral communities region-wide. Reduced in numbers and subject to increasing stress, these juvenile populations face the heavy burden of serving as the next generation of corals on Caribbean reefs.

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