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Long-term Shifts in Coral Communities On Shallow to Deep Reef Slopes of Curaçao and Bonaire: Are There Any Winners?

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Tropical coral reefs are among the most biologically diverse and economically important ecosystems on earth. Nevertheless, we found dramatic changes in coral communities on the reef slopes of Curaçao and Bonaire since 1973. Cover and abundance declined for virtually all coral species. The data show a shift from communities dominated by framework building species (e.g., *Orbicella* spp.) to communities consisting of small opportunistic, phenotypically plastic, species, including few remaining structural colonies. *Madracis mirabilis, Porites astreoides, Diploria strigosa*, and *Agaricia lamarcki* are at present modest winners in the coral assemblage, although overall cover declined also for these species. Increased frequency and intensity of events inducing coral mortality and ongoing reduction in suitable hard substratum, provided by the remnants of large colony building species, could reduce the chance of these species to remain winners in the longer run. The observed loss in coral cover and the shift from larger structural to smaller opportunistic species reduced reef carbonate production by 67% and therewith, in combination with a trend toward smaller coral colonies, reef complexity. Alarmingly, reefs at upper-mesophotic depths (30–40 m) did not escape the general degradation of the coral community. The negative effects are larger around densely populated areas where local stressors are adding to degradation caused, for instance, by region wide mass bleaching. Without proper conservation and management this already dramatic degradation will continue and turn more and more coral species into losers.

Keywords: coral, coral community dynamics, reef degradation, carbonate production, Caribbean, anthropogenic stress

INTRODUCTION

Tropical reefs are among the most biologically rich ecosystems on earth providing income for millions of people through fisheries, tourism and coastal protection (Moberg and Rönnbäck, 2003). On tropical reefs scleractinian corals are largely responsible for the architectural complexity due to the deposition of calcium carbonate and thereby provide habitat, food, and refuge for many taxonomic groups. Over the past decades corals reefs have been degrading worldwide at unprecedented rates (Gardner et al., 2003; Bak et al., 2005; Pandolfi and Jackson, 2006). Deteriorating coastal water quality (Rogers, 1990; Williams et al., 2002; Vega-Thurber et al., 2014), overexploitation of herbivores (Jackson et al., 2001) and anthropogenic induced climate change (Glynn, 1996; Aronson et al., 2002a; Wilkinson and Souter, 2008) are generally associated with this ubiquitous decline in coral cover (Jackson et al., 2014). These stressors negatively impact coral resilience, impeding the ability of corals to cope with disease, bleaching or physical disturbance, which in turn affects their competitive position with respect to other reef organisms such as macroalgae or sponges (Vega-Thurber et al., 2014; Zaneveld et al., 2016). Aforementioned developments are suggested to cause shifts in coral communities from assemblages dominated by framework building corals to a dominance of more persistent and opportunistic non-framework building species (e.g., Green et al., 2008; Alvarez-Filip et al., 2011a; Darling et al., 2012; Perry et al., 2015).

Whether coral species are likely to become winners or losers in the changing reef environment depends strongly on their specific life-history traits (Knowlton, 2001; Van Woesik et al., 2011). In an attempt to predict what species are likely to be lost and what species may be more persistent, several studies have divided species over groups based on shared characteristics such as: way of propagation, growth rate and thermo-tolerance (e.g., Edinger and Risk, 2000; Murdoch, 2007). Recently, Darling et al. (2012) divided 147 coral species from tropical reefs all over the world over four main groups: competitive, weedy or ruderal, stress-tolerant and generalist. This grouping was based on 11 functional traits. In the early 1970s coral reefs were still generally dominated by stress-tolerant, competitive and generalist species. It is hypothesized, however, that coral communities are shifting toward species assemblages comprising mainly of phenotypically plastic weedy species and some persistent framework building (stress-tolerant, generalist) species (Darling et al., 2012; Grottoli et al., 2014; McClanahan et al., 2014; Perry et al., 2015). Since the frequency and intensity of events inducing coral mortality (e.g., bleaching and hurricanes) is predicted to increase, recovery and adaptation will become progressively more difficult for all coral species (Hoegh-Guldberg, 1999; Van Woesik et al., 2011; McClanahan et al., 2014). As a consequence, the contribution of corals in benthic reef communities will likely decrease even further and the most stress susceptible coral species may disappear entirely at many reefs (Knowlton, 2001; Hoegh-Guldberg et al., 2007). Predicting trajectories of coral community change, however, is extremely complex due to the numerous factors involved (Hughes and Tanner, 2000; Done et al., 2010). Additionally, shifts in coral communities may occur slowly and are therefore often difficult to distinguish (Pauly, 1995). There appears to be a consistent lack of long-term temporal quantitative data documenting the trajectories of different species in the coral community.

Here, we provide data on the coral community dynamics at reefs on the southern Caribbean islands of Curaçao and Bonaire. Over the course of the studied time series human populations in the Caribbean increased from 27 million in 1973 to approximately 43 million in 2015 (United Nations, Department of Economic and Social Affairs, Population, Division, 2015). As a consequence, the Caribbean basin experiences chronic decline of water quality and overexploitation of fish (Siung-Chang, 1997; Jackson et al., 2014). Due to climate change and increasing sea water temperature, Caribbean corals have been exposed to mass bleaching events in 1998 (Aronson et al., 2002a), 2005 (Wilkinson and Souter, 2008; Eakin et al., 2010) and 2010 (Alemu and Clement, 2014). Furthermore, White Band Disease greatly reduced the cover of *Acropora* spp. from the late seventies to the mid-eighties, which negatively impacted rates of calcification and architectural complexity of the shallow reef (Gladfelter, 1982; Aronson and Precht, 2001). Additionally, herbivory was greatly reduced due to the mass-mortality of the *Diadema antillarum* sea-urchin in 1983 (Bak et al., 1984), formerly important in controlling the densities of competitive algae (De Ruyter Van Steveninck and Bak, 1986).

In comparison to other tropical regions (e.g., the Pacific), the Caribbean has relatively few coral species (Veron, 2014). As a consequence, certain ecologically relevant traits of specific species may be lost more rapidly in the Caribbean compared to other regions (Nyström, 2006). In many Caribbean sites the cover of corals providing complex 3D reef structure, mostly *Orbicella* spp. (= *Montastraea*, *sensu* Budd et al., 2012) and *Acropora* spp. was already strongly reduced over the past decades (Van Duyl, 1985; Aronson and Precht, 2001; Bruckner and Bruckner, 2006). The calcification balance on many of these reefs may currently have shifted toward net erosion which will result in the reduction of architectural complexity (Alvarez-Filip et al., 2009; Kennedy et al., 2013; Perry et al., 2013). This may drastically alter reef functioning and lead to loss of biodiversity as well as a reduction in important ecosystem services for coastal human population such as wave protection and food security (Moberg and Rönnbäck, 2003; Alvarez-Filip et al., 2009, 2011b; Graham and Nash, 2013; Newman et al., 2015).

On degrading Caribbean reefs, phenotypically plastic corals such as *Madracis* spp., *Porites* spp., *Siderastrea* spp. or *Agaricia* spp., are expected to replace species controlling reef structure like *Acropora* spp. and *Orbicella* spp. (Pandolfi and Jackson, 2006) and become dominant in coral communities (Jackson, 2001; Aronson et al., 2002b; Green et al., 2008; Perry et al., 2015). These species are, however, often small and generally not capable of fulfilling the important ecological functions provided by large framework building species (Bellwood et al., 2004; Nyström, 2006; Alvarez-Filip et al., 2013; Perry et al., 2013). Moreover, it may be expected that in the long run opportunistic weedy species (Darling et al., 2012) will also disappear since no coral species appears to be effectively insensitive to anthropogenic impact (McClanahan et al., 2014). We aim, on the basis of images from 18 time series collected at five reef sites in Bonaire and Curaçao, and covering up to 40 years, to (1) determine temporal and spatial changes in dominant coral species, (2) link observed trajectories of the coral community to the life-history strategies of large framework building species and opportunistic weedy species, (3) estimate the relative loss of carbonate production due to changes in coral species composition and cover over time, and finally (4) discriminate between the winners and losers on these Caribbean coral reefs.

MATERIALS AND METHODS

Site Description and Procedure for Image Collection

The spatio-temporal dynamics of coral reef communities at four southern Caribbean sites were tracked based on photographic records spanning a period of more than 40 years (Bak and Nieuwland, 1995; Bak et al., 2005). The survey sites are located at the leeward side of the islands of Curaçao: Carmabi Buoy One (sites I and II) and Carmabi Buoy Two (site III); and Bonaire: Karpata (site IV) (**Figure 1**, **Table 1**). The leeward fringing reef on both islands is characterized by a shallow reef terrace that transitions into a seaward slope with a drop off that varies from less than 20° to vertical (Bak, 1975; Van Duyl, 1985). At each site four permanent quadrats (9 m^2) were set out and marked in 1973 on the fore-reef slope at 10, 20, 30, and 40 m depth, one quadrat at each depth. The 10 m quadrats were too deep to cover the *Acropora palmata* and *Acropora cervicornis* zones, which are both situated, if present, on the shallow reef terrace at less than 10 m depth (Bak, 1977). Surveys were conducted with variable intervals between 1973 and 2014 and comprised of collecting overview images complemented by a series of detail recordings. In addition to the four main sites a fifth site, Awa Blancu (AB), located at the far south-eastern side of Curaçao, was included with a quadrat positioned at 10 m (since 1983) and 20 m (since 1992) depth. AB is located relatively far upstream of any urban areas and therefore suffers relatively less local anthropogenic disturbance (Gast et al., 1999; Lapointe and Mallin, 2011) (**Figure 1**). This series was used as a relatively pristine reference to the shallow fore-reef slope (10–20 m) of sites I-IV which lie downstream of densely populated areas and close to outlet bays (Van Duyl, 1985). Per series, a maximum of 9 years was analyzed (**Table 1**).

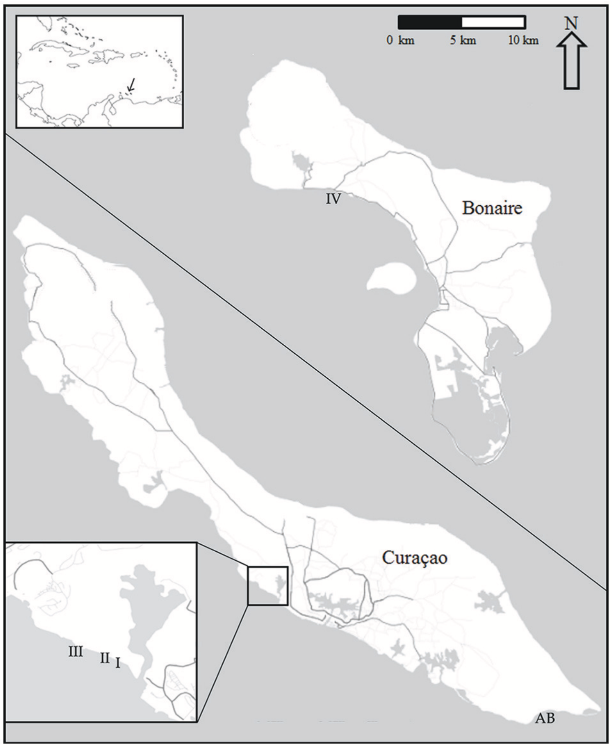

FIGURE 1 | Quadrat locations at Curaçao (I-III, AB) and Bonaire (IV). Including their position in the wider Caribbean sea (top left). Enlarged section at the lower left corner shows in detail the position of sites I-III on Curaçao.

Coral Community Characteristics

All coral colonies that were present in a quadrat were recorded. A coral was considered an individual colony when the tissue was distinctly separated in space from the tissue of any neighboring corals. When a colony was located on the edge of the quadrat only the area within the actual 9 m^2 quadrat was included in the survey. Fitted image overlays including all coral colonies were created in Photoshop CC 2015 (Adobe) and Scion Image v4.0.3.2. Actual live surface area (cm^2) and colony outline (cm) were extracted from the overlay images and used as general metrics for coral colony size. The ratio between colony outline and live surface area of each colony was used as a measure for colony shape (shape index). Larger round colonies have a relatively low shape index. Partial mortality, particularly in larger colonies (Type II, *sensu* Meesters et al., 1996), or exposure to competing organisms leads to a relatively larger outline compared to the surface area, resulting in a higher shape index. Colonies were identified to species level, but because the different *Orbicella* species (*O. annularis, O. faveolata, O. franksi*) could not be separated reliably in retrospect, they were grouped into the *Orbicella* complex. For the same reason there was no further distinction made between the species *Madracis pharensis*, *M. formosa, M. senaria*, and *M. decactis*, which were grouped together under the *Madracis* taxonomic spp. complex. As a baseline, the classification system proposed by Darling et al. (2012) was used to *a priori* subdivide the coral species. The class "stress-tolerant," however, proved at times confusing and was replaced by "large framework building." This class included the entire *Orbicella* species complex, in contrast to Darling et al. (2012) who categorized *O. faveolata* and *O. franksi* as "generalists." "Weedy" species are here referred to as opportunistic.

Statistical Analyses

The original data consists of a matrix where each row represents a single coral colony in a certain quadrat at a certain year and columns display surface area, outline, shape and specific site characteristics of each colony. This set was used to acquire the total number of colonies in each quadrat. Subsequently, the total planar cover per species was calculated for each quadrat and expressed as a percentage of the total quadrat area (9 m^2). Before statistical multivariate analysis the influence of less dominant species was increased by applying a square-root transformation. Non-metric Multi-Dimensional Scaling (nMDS) was used as a tool to display community development over time at each depth averaged over sites I-IV and also for AB at 10 and 20 m. To test for a directional development of the community composition over time a seriation routine (Clarke and Warwick, 1994) was conducted in the multivariate software program Primer-e v7.0.9 (RELATE function with $M = 9999$ simulations). This procedure allows testing of similarity of a community distance (sub)matrix to a model matrix based on the Spearman rank correlation coefficient (Kendall, 1948; Clarke and Warwick, 1994) and provides a measure (*Rho*) for linearity in temporal community development. A *Rho*-value close to 1 is indicative of a linear development over time. Similarly, a second

TABLE 1 | Survey site characteristics.

Island	Site	Code	Longitude	Latitude	Years	Depth (m)
Curaçao	Buoy One	I	−68°97′532.0″W	12°12′585.0″N	73;75;83;92;97;02;08;12;14	10;20;30;40
		II	−68°97′652.0″W	12°12′655.0″N	73;75;83;92;97;02;08;12;14	10;20;30;40
	Buoy Two	III	−68°97′778.3″W	12°12′723.4″N	73;75;83;92;97;02;08;12;14	10;20;30;40
	Awa Blancu	AB	−68°78′381.2″W	12°04′029.9″N	83;92;08;12;14	10
					92;02;08;12;14	20
Bonaire	Karpata	IV	−68°34′413.2″W	12°20′998.0″N	73;75;83;92;97;02;08;12;14	10;20;30;40

All years a site was visited (Years) and depths (m) at which permanent quadrats were positioned. Years visited are shown as the last two numbers of the year. Sites I–IV were first visited in 1973. The time series at Awa Blancu 10 and 20 m have a different start, namely 1983 and 1992, respectively.

stage routine was applied to submatrices of specific sites per depth to reveal consistencies or variations in temporal patterns of development in community composition among sites (Clarke et al., 2006). A positive correlation in the pattern of development of two time series will result in a high *Rho*-value. Temporal variation in colony size distributions were determined based on univariate measures of colony size, namely, mean size, skewness and kurtosis (Mardia, 1970), because changes in size frequency can be related to shifts in coral communities (Bak and Meesters, 1998). The difference in mean colony size at sites I-IV over time (of all colonies) was assessed by two-way ANOVA for each depth based on fourth-root transformed data, with year (start and end) and site as categorical variables. Assumptions for ANOVA were confirmed visually (Zuur et al., 2007). Subsequently Post Hoc (Tukey HSD with Bonferroni correction) tests were applied to compare colony size at the start and end in each individual quadrat. Sites were also compared with reference site AB using a different starting year (since 1983 and 1992 for 10 and 20 m resp.). Various diversity indices were computed for each quadrat and year: Shannon-Wiener diversity index (Shannon and Weaver, 1949), Simpson's diversity index (Simpson, 1949), Pielou's evenness (Pielou, 1969) and total number of species. Statistical testing of other community characteristics (e.g., no. of colonies, no. of species, diversity indices, skewness, kurtosis) was inappropriate because this would result in only one replicate value per quadrat. With the exception of the RELATE and Second stage routines all analyses were performed in the R programming environment v3.2.3 (R Core Team, 2014). Within R the following packages were used: vegan (Oksanen et al., 2016) and moments (Komsta and Novomestky, 2015).

Carbonate Production

The relative contribution of the coral community to reef carbonate production in kg $CaCO_3$ m^{-2} y^{-1} in a quadrat at each measured point in time was estimated based on total planar cover of each species. Species-specific or nearest equivalent species accretion rates were adapted from the *ReefBudget* method as proposed by Perry et al. (2012), who acquired the various rates from the available literature. Since our data on coral cover was extracted from 2D-images the obtained estimates will be an underestimation compared to the *ReefBudget* method where 3D surface is included. Moreover, the *ReefBudget* method provides calcification rates for shallow reefs between 5 m and 10 m depth. In order to compensate for the decrease in carbonate production with increasing depth a correction was applied to rates of carbonate production in quadrats at greater depth (Equation 1).

$$G = \frac{G_m\, exp(-\, km)}{G_m} \tag{1}$$

Where G_m is the carbonate production at maximum light intensity at the surface, k the extinction coefficient (0.05, Bosscher and Schlager, 1992) and m the depth at which the quadrat is located.

RESULTS

Consistencies and Variability in Trajectories of Community Change

The coral community at the four main sites I-IV has since 1973 developed in a constant uni-directional degrading way (**Figure 2**, **Table 2**), which is illustrated in the nMDS plot by the generally linear arrangement of points (years) along the y-axis (**Figure 2**). This suggests a directional trend in community development gradually moving away from (upwards in **Figure 2**) the initial community compositions at the start of the time series, irrespective of depth. The first axis indicates a clear effect of depth caused by strong variations in community composition across the depth gradient. The trajectories at greater depths (30 and 40 m) were very similar (**Figure 2**). At AB, change in community development was less pronounced compared to sites I-IV (**Figure 2**, **Table 2**), particularly at 20 m depth. The line of 10 m at the reference site AB was arranged relatively close to the average for sites I-IV at 10 m, suggesting similarity in community composition. At AB 10 m the community in 2014 resembled the community of 1997–2002 at sites I-IV, implying a time lag in reef degradation. A longer time lag was observed for 20 (**Figure 2**). Also, the community at AB 20 m appears to be more different from sites I-IV (**Figure 2**). At 20 m (recorded since 1992) the high, albeit not significant, *Rho*-value (0.926, $p = 0.087$) indicated linear development in coral community composition, but AB covered a shorter time period and less surveys were included. High *Rho*-values and non-significant p-values appear to be contradicting, but are likely the result of the low number of time points. In such a case more emphasis may be put on the *Rho*-value (Clarke and Warwick, 1994), but these values should be interpreted with caution.

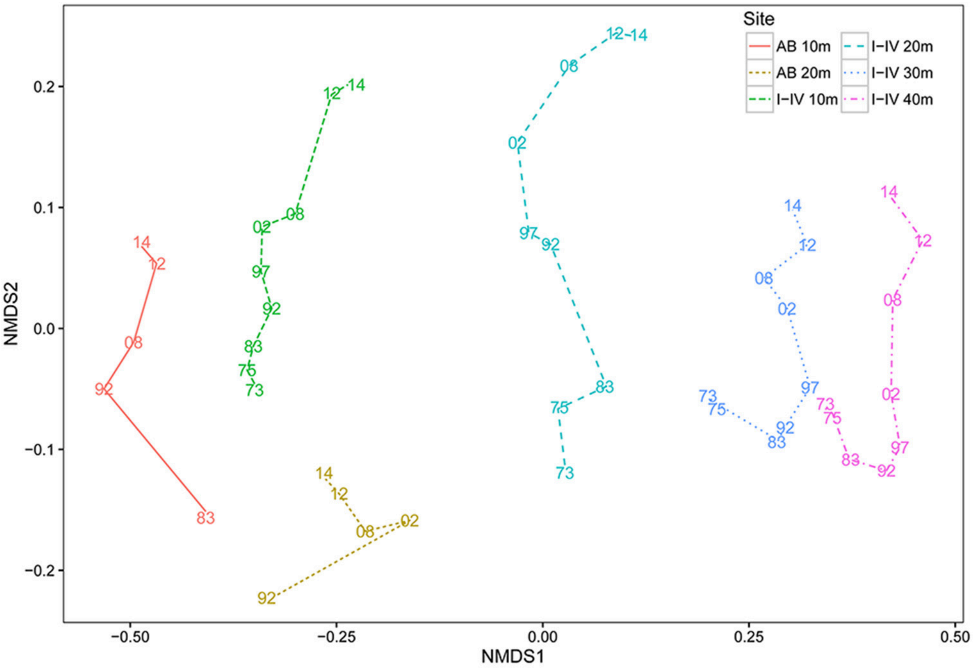

FIGURE 2 | Coral community dynamics on Curaçao and Bonaire. Non-metric Multi-Dimensional Scaling ordinations (nMDS) displaying mean community development over time of sites I-IV, separated by depth (I-IV-10 m, I-IV-20 m, I-IV-30 m, I-IV-40 m) and the reference site Awa Blancu 10 and 20 m (AB-10 m and AB-20 m). Each color-line type combination corresponds to a specific site-depth combination. Lines represent the degree and direction of community change between two surveys. All surveys are labeled as the last two numbers of the year a survey was conducted. The closer the distance between two points, the more similar in composition they are.

Overall, the total area covered by hard corals (**Figure 3A**) declined on average from 33.8% in 1973 to 10.1% in 2014 over the main sites (I-IV), resp. 95% confidence intervals: 25.7–42.9 and 6.9–14.5. The observed decline was highly comparable among depths but was greatest at 20 m depth, showing a decrease of 78.9% from 43% in 1973 to 9.1% cover in 2014 (**Figure 3A**). In comparison coral cover at 10, 30, and 40 m depth in 1973 was 42, 33, and 23% and declined by 68.9, 63.5, and 58.6% respectively to 13, 12, and 9.5% cover in 2014. This indicates a pronounced reduction in coral cover along the entire depth gradient studied. In comparison, coral cover at AB declined by 31% at 10 m and 49% at 20 m depth since 1983 and 1992, resp. (**Figure 3A**, **Table 3**). The mean percentage of change in cover at these two depths at sites I-IV, over the same time-span as AB, was much larger with 71% (10 m) and 76% (20 m), resp. 95% confidence intervals: 24–96 and 73–78.

Analogous with the decline in coral cover the total number of coral colonies decreased in the majority of the quadrats, particularly between 1973 and 1983 (**Figure 3B**, **Table 3**). At 10 m depth the number of colonies initially decreased almost exponentially in the first decade, but subsequently the number stagnated and finally started increasing again after the late 1990s (**Figure 3B**). This pattern was largely driven by the dynamic *M. mirabilis,* which has been a dominant species at 10 m depth (**Figure 4**), but through time proved to be highly variable in the number of colonies and cover. By 2014, *M. mirabilis* had increased in density at sites III and IV, and also at AB (steep increase in **Figure 3B**), while an obvious decrease was observed at site I. After 1983 the number of colonies on mesophotic depths (30 and 40 m) remained relatively constant until the late 1990s, after which a gradual decline was observed.

In addition to the decline in the number of colonies (**Figure 3B**), the community at sites I-IV has generally shifted to a relative dominance by smaller colonies in 2014 compared to 1973 (**Figure 3C**, **Table 3**). At 10 m, 20 m and 40 m a significant difference was observed between years [$F_{(1)} = 78, p < 0.001, F_{(1)} = 22, p < 0.001$ and $F_{(1)} = 7, p < 0.01$, resp.] and sites [$F_{(3)} = 97, p < 0.001, F_{(3)} = 17, p < 0.001$ and $F_{(3)} = 8, p < 0.001$, resp.]. At 30 m a significant difference was only found between sites [$F_{(3)} = 12, p < 0.001$]. A Post Hoc test comparing sites including AB showed significant larger colonies at AB in 1992 at 20 m depth (all $p < 0.001$), but by 2014 a dramatic decrease resulted in values that are comparable to those at sites I-IV (**Figure 3C**, **Table 3**). At 10 m depth, only site I differed significantly from AB in 1983 and 2014 ($p < 0.05$). Reduced mean colony size over time is in part a consequence of the loss of large colony building species such as *Orbicella* spp. and a still relatively high number of small colonies of, for instance, *M. mirabilis* (**Figure 5**). Both the *Orbicella* complex (dominant on the shallow fore-reef) and *A. lamarcki* (dominant on the deep fore-reef) showed a shift toward smaller colonies (**Figure 5**). This shift is also shown by an increased positive skewness for many quadrats, including AB, in 2014 compared to the beginning of the time series (**Table 3**). In contrast to the two other dominant species, the opportunistic

TABLE 2 | Linearity of community development over time for each individual quadrat by depth.

Depth	Site	*Rho* (*p*-value)
10	I	**0.678 (0.001)**
	II	**0.861 (0.001)**
	III	**0.891 (0.001)**
	IV	**0.911 (0.001)**
	AB	0.370 (0.328)
20	I	**0.843 (0.001)**
	II	**0.899 (0.001)**
	III	**0.688 (0.002)**
	IV	**0.905 (0.001)**
	AB	0.926 (0.087)
30	I	**0.936 (0.001)**
	II	**0.814 (0.001)**
	III	**0.792 (0.001)**
	IV	**0.851 (0.001)**
40	I	**0.710 (0.001)**
	II	**0.797 (0.001)**
	III	**0.910 (0.001)**
	IV	**0.696 (0.002)**

The degree of seriation (Rho) was based on the relative cover of all species present within a quadrat (I–IV and reference site AB). Strong linearity in development results in Rho-values close to 1. Significant Rho-values are given in bold, respective p-values in parentheses.

M. mirabilis does not show a clear shift in colony size, but more a general loss in the number of colonies (**Figure 5**). Coral colony "shape" (outline:area) appears to represent a shift from larger round colonies to smaller and more complexly shaped colonies (**Figure 3D**). This is likely a consequence of increased occurrence of partial colony mortality. Partial mortality may result in a relatively large increase in outline compared to a minor decrease in total surface area.

Trends in Species Composition

Over the course of the period surveyed (1973–2014) a total of 30 scleractinian coral species were recorded in the quadrats. After combining the various *Madracis* and *Orbicella* species into two groups 24 species/complexes remained (**Table 4**). The number of species declined in the majority of the quadrats between 1973 and 2014 (**Figure 3E**, **Table 3**). In 2014 opportunistic species accounted for 62% of the total coral cover, compared to 53% in 1973 at sites I-IV. At AB, framework building species kept dominating the coral community at both 10 and 20 m, accounting for 52% and 85%, respectively, of the total coral cover in 2014 (Table S3). The cover of competitive species (*Acropora* spp. and *Dendrogyra cylindrus*) in the quadrats was negligible. Highest coral diversity was generally found around 20 m depth and lowest at 40 m depth (**Table 3**, **Figure 3E**). A relatively low, but significant, correlation (*Rho*) was found among multiple sites, including AB, at the shallow (10–20 m) fore-reef (Table S1). This observation coincides with a clear variation in species composition and trajectories of coral community development between these sites, particularly regarding the dominance of *M. mirabilis*, *Orbicella* spp. or *Montastraea cavernosa* (**Figure 4**). In comparison, the species composition at 30 and 40 m depth was highly comparable among sites, with an overall dominance of *Agaricia lamarcki* (**Figure 4**), which resulted in strong correlations between all sites (Table S1).

In 1973 the coral community on the shallow fore-reef (10 m and 20 m) at sites I-IV was overall dominated by *Orbicella* spp. (28%), *A. agaricites* (20%) and *M. mirabilis* (17%) (Table S2). By 2014, *M. mirabilis* had become the dominant species (28%), followed by *Orbicella* complex (16%) and *A. lamarcki* (12%). The latter confirms the absence of obvious shifts in species composition but instead a general decline in cover of all species. It does, however, also show the increased relative importance of *M. mirabilis* with respect to other species at the most shallow quadrats over the more recent years (**Figure 4**). At 10 m depth evenness increased in most quadrats in 2014 compared to 1973 (**Table 3**) which is indicative of a more equal contribution of the species present to total coral cover. This is largely a consequence of the decline in cover of the both initially dominant *M. mirabilis* and *Orbicella* complex (**Figure 3**). On the deep fore-reef (30 and 40 m) the coral community was dominated by *A. lamarcki* throughout the studied period (63% in 1973, 77% in 2014) resulting in generally low evenness scores (**Table 3**). In 1973, *Montastraea cavernosa* (13%), *Siderastrea siderea* (6%), and *Stephanocoenia michelini* (6%) followed *A. lamarcki* in cover. These same species were still dominating the community in 2014: *M. cavernosa* (8%), *S. michelini* (6%) and *S. siderea* (3%), but all had declined in total cover.

Some species appear relatively persistent, and include both framework building species (*Colpophyllia natans, S. michelini, Meandrina meandrites, Diploria strigosa*) and opportunistic species (*M. mirabilis, A. lamarcki, Madracis* complex, *Porites astreoides*). These species showed either an increase in cover, a decrease of less than 10% or they had newly emerged in multiple quadrats. An increase in the cover of certain species over time was almost exclusively observed on the shallow reef and no species consistently increased in all quadrats in which it was initially present (Table S2). Species that were dominant in 1973 but declined consistently in the majority of the quadrats included: *Orbicella* complex, *Eusmilia fastigiata, M. cavernosa, Mycetophyllia* spp., *S. siderea* and *A. agaricites, M.* complex, *M. meandrites, S. michelini* (Table S2).

Comparable to the main quadrats (I-IV), the *Orbicella* spp. and *M. cavernosa* declined strongly at both depths at AB. At 10 m there was a clear increase in cover of *M. mirabilis* and a less distinct increase in *M. meandrites*. All other species showed a considerable decline. At 20 m, with the exception of *Porites porites, S. siderea* and *S. michelini*, all species declined in cover. A particularly strong decline occurred in the *Orbicella* complex (71%) and *C. natans* (100%). Nevertheless, *Orbicella* spp. still covered 12% of the total quadrat at both depths in 2014.

Temporal Change in Coral Calcium Carbonate Production

The consistent decline in coral cover inherently caused a reduction in the estimated rates of coral carbonate production

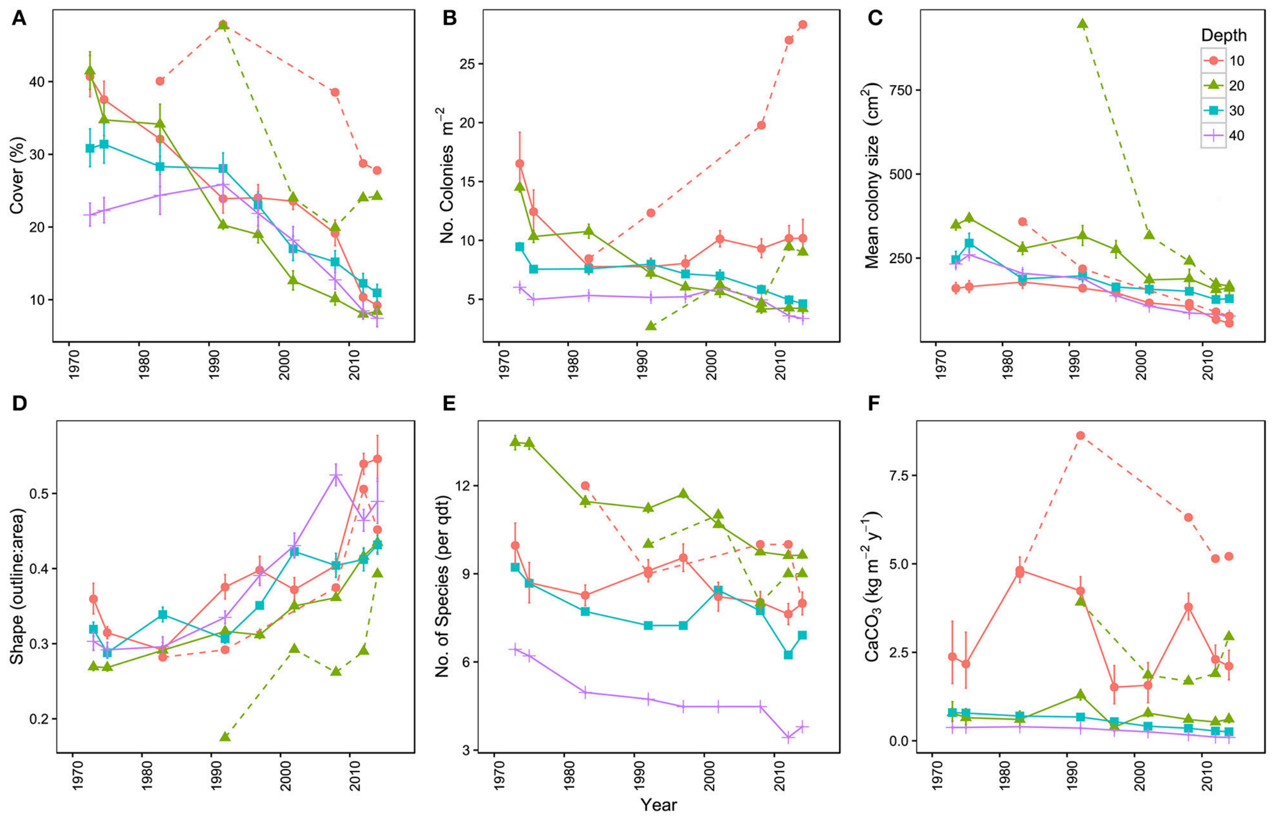

FIGURE 3 | Temporal trends in the coral communities on Curaçao and Bonaire. (A) mean percentage of the 9 m^2 quadrat covered by hard coral, **(B)** mean number of coral colonies per m^2, **(C)** mean colony size (cm^2), **(D)** mean colony shape index represented by the outline:area ratio of corals, **(E)** mean number of hard coral species in the quadrats and **(F)** mean carbonate production (kg m^{-2} y^{-1}) of the coral community. Points represent the mean of the four main locations (I–IV) at a surveyed point in time. Each color represents a specific depth. Dashed lines represent the reference site Awa Blancu (AB) at 10 and 20 m depth. All means are provided with their respective 95% confidence intervals.

in 2014 compared to 1973 (**Figure 3F**). The estimated mean contribution of corals to carbonate production (kg $CaCO_3$ m^{-2} y^{-1}) over all quadrats declined by 72% from a mean of 2.5 kg m^{-2} y^{-1} in 1973 to 0.8 kg m^{-2} y^{-1} in in 2014, respective 95% confidence intervals: 0.7–4.3 and 0.02–1.6. The three species that accounted for the highest cover also contributed most prominently to the estimated coral calcification: *M. mirabilis*, *Orbicella* complex and *A. lamarcki* in both 1973 and 2014. In 1973, coral carbonate production was highest at 10 m depth (**Figure 3F**, **Table 3**), with a mean of 6.7 kg m^{-2} y^{-1}, largely due to the high cover of the two rapidly calcifying species *M. mirabilis* (rate: 29 kg m^{-2} y^{-1}) and *Orbicella* spp. (rate: 14 kg m^{-2} y^{-1}) (**Table 3**). Particularly the 97% decline in *Orbicella* complex cover has resulted in a considerable decrease in calcification by 2014. Total coral calcification decreased with depth (**Figure 3F**) and at different depths a decline occurred over time (**Table 3**). The reduction in coral cover at 20 m depth at AB resulted in a decline in estimated coral calcification from 3.7 kg m^{-2} y^{-1} (1983) to 2.9 kg m^{-2} y^{-1} (2014), which is still high compared to sites I-IV (**Table 3**). Due to the vast increase in *M. mirabilis* at AB the total estimated coral calcification at 10 m depth had increased here slightly since 1983 (**Table 3**).

DISCUSSION

Since the early 1970s the coral communities of Curaçao and Bonaire have changed significantly in coral cover and species composition. Total cover has declined and colonies have generally become smaller on both the shallow (10–20 m) and upper-mesophotic reef (30–40 m). In particular, initially dominant framework building species such as *Orbicella* spp., *M. cavernosa* and *S. siderea,* lost significant cover, a trend that occurs throughout the wider Caribbean region (Bruckner and Bruckner, 2006; Edmunds and Elahi, 2007; Jackson et al., 2014). Concurrently, the relative cover of some phenotypically plastic so-called weedy species (*sensu* Knowlton, 2001) moderately increased since 1973. The observed shift also took place at the reference site Awa Blancu (AB) which is located far upstream and relatively distant from anthropogenic disturbances along the coast of Curaçao (**Figure 1**), but less distinct.

Overall, reef degradation was less pronounced at Awa Blancu (**Figure 2**). A noticeable difference with the shallow reef of sites I-IV was that *Orbicella*, over time, remained the dominant genus at AB with still relatively high cover by 2014 (13% and 11% of the total quadrat at 10 and 20 m respectively).

TABLE 3 | Summary of coral community characteristics.

Site	Depth (m)	Cover (%)		Number of colonies m^{-2}		Number of species		Skewness Skewness		Kurtosis Kurtosis		Mean colony size (cm^2)		Shannon diversity		Simpson diversity		Evenness		CaCO$_3$ production (kg m^{-2} y^{-1})	
		1973	**2014**	**1973**	**2014**	**1973**	**2014**	**1973**	**2014**	**1973**	**2014**	**1973**	**2014**	**1973**	**2014**	**1973**	**2014**	**1973**	**2014**	**1973**	**2014**
I	10	48.5	1.1	54	4	5	3 (1)	6.4	1.5	55.9	4.8	47.5	**24.1**	0.45	0.62	0.25	0.38	0.13	0.18	12.95	0.28
II		22.7	5.9	8	6	10	10 (4)	2.4	3.3	8.4	13.9	143.0	**31.8**	1.69	1.81	0.75	0.78	0.48	0.52	2.37	0.51
III		37.0	24.0	11	27	13	13 (1)	3.7	4.2	19.5	26.5	141.6	**31.7**	1.77	1.47	0.75	0.65	0.51	0.42	3.86	4.86
IV		62.8	22.2	12	14	14	9 (1)	3.4	3.2	16.0	15.4	206.0	**107.5**	1.31	1.33	0.54	0.65	0.37	0.38	7.78	4.51
AB**(1983)**		40.1	27.8	76	225	12	8	4.6	4.9	24.5	36.0	273.6	**45.4**	1.32	1.15	0.58	0.62	0.37	0.33	4.7	5.2
I	20	34.6	8.7	18	4	13	11	4.1	5.5	23.6	32.0	118.5	61.8	2.13	1.45	0.85	0.62	0.61	0.41	2.07	0.42
II		32.9	5.6	14	2	15	7	7.5	1.3	67.4	3.1	106.0	140.8	2.31	1.57	0.87	0.76	0.66	0.45	1.66	0.22
III		34.9	16.6	12	7	12	11 (1)	2.2	3.9	8.2	21.8	150.4	130.1	2.03	1.59	0.84	0.72	0.58	0.46	1.45	0.68
IV		70.6	5.6	14	6	14	10	2.1	3.7	8.1	18.2	339.0	**54.1**	1.97	2.11	0.80	0.86	0.56	0.60	2.70	0.26
AB**(1992)**		47.6	24.2	24	81	10	9	4.4	4.2	20.7	22.9	516.7	**70.4**	1.20	1.50	0.53	0.71	0.34	0.43	3.72	2.94
I	30	22.4	4.4	7	3	10	8 (1)	3.1	4.3	13.6	20.9	152.6	**47.0**	1.88	1.54	0.80	0.70	0.54	0.44	0.69	0.13
II		19.7	14.2	8	5	8	8 (2)	3.4	3.5	16.5	17.2	113.0	108.0	1.44	1.27	0.68	0.60	0.41	0.36	0.54	0.34
III		31.0	9.6	12	5	9	7	4.8	2.4	29.6	8.8	91.3	94.5	0.99	1.07	0.42	0.52	0.28	0.31	0.65	0.20
IV		60.0	20.2	11	5	10	5	2.5	2.5	8.6	9.9	259.5	243.2	1.28	0.59	0.59	0.30	0.37	0.17	1.52	0.44
I	40	12.9	1.4	6	2	7	4	4.3	2.1	22.5	7.4	110.4	39.2	1.32	0.98	0.64	0.58	0.38	0.28	0.30	0.03
II		17.6	6.9	5	4	6	6	4.1	3.1	21.1	11.2	91.0	**26.5**	0.86	0.70	0.40	0.34	0.25	0.20	0.30	0.09
III		36.1	18.4	8	4	8	2	3.3	3.1	14.0	14.6	121.0	138.9	0.46	0.16	0.18	0.07	0.13	0.05	0.46	0.20
IV		25.0	11.3	5	3	5	4 (1)	5.3	2.6	32.7	10.2	206.5	117.0	1.21	0.58	0.63	0.35	0.34	0.17	0.48	0.14

Percentage coral cover of each 9 m^2 quadrat; number of colonies per square meter; number of species present per quadrat, newly appeared species in 2014 are given in parenthesis; skewness; kurtosis and mean colony size (cm^2) over all colonies that were present in the quadrat. A significant (Post-Hoc test, $p < 0.05$) decline in the mean colony size in an individual quadrat over time is indicated by a bold value in 2014. Community diversity indices include: Shannon-Wiener diversity index, Simpson index and Pielou's evenness scores for species contribution. Estimated coral calcium carbonate (CaCO$_3$) production in kg m^{-2} y^{-1} of the coral community. All characteristics are given for 1973 and 2014 by depth and site (I–IV). For the reference site AB values are provided for their respective first year of visit: 10 m (1983), 20 m (1992).

FIGURE 4 | Spatio-temporal dynamics in coral community composition on Curaçao and Bonaire. Bars represent the coral cover at surveyed points in time in the 9 m^2 quadrats. Bars are subdivided (stacked) by species. Competitive species are given in shades of yellow (virtually absent), framework building species in blue and opportunistic species in red/purple. Sites are listed as I-IV (main sites) and AB (reference site Awa Blancu) indicated along the top and the depths (10, 20, 30, and 40 m) given on the right side of the panel. Detailed characteristics per quadrat can be found in Tables S2, S3.

Moreover, the coral communities at AB remained dominated by framework building species throughout the times series. This is in contrast to sites I-IV, where opportunistic species have become dominant. The latter suggests that coral communities along the leeward coast near urban areas and outlet bays (I-IV) receive additional stress on top of stress factors acting on a larger scale (i.e., regional or worldwide), at least down to 20 m depth. Since the start of our time series both Curaçao and Bonaire have experienced significant human population expansion (50% increase on Bonaire since 2001) as well as increased tourism (CBS Curaçao 2015, http://www.cbs.cw; CBS Dutch Caribbean 2015 www.rijksdienstcn.com). Both have consequently led to extensive development of the coastal area. Factors associated with coastal development such as pollution, turbidity and sedimentation negatively impact coral recruitment and survival by smothering corals or reducing the ability of corals to cope with diseases, bleaching or spatial competition (e.g., Meesters et al., 1992; Nugues and Roberts, 2003; Fabricius, 2005; Jackson et al., 2014; Vega-Thurber et al., 2014). Similar to many tropical regions, sewage water on Curaçao and Bonaire is generally insufficiently treated or even largely untreated before it is discharged (Buth and Ras, 1992; Lapointe and Mallin, 2011). Indeed, along the coast of Curaçao clearly higher nutrient concentrations have been found at sites I-III compared to Fuik bay, which is located near Awa Blancu (Gast et al., 1999; Govers et al., 2014). Elevated nutrient levels have also been found at Karpata (IV) on Bonaire during measurements in 2012 and 2013 (Slijkerman et al., 2014). The observed spatial variation in coral community degradation may therefore reflect the impact of persevering stress factors associated with coastal urbanization around more densely populated areas. These results suggest that implementation of thorough local conservation and management strategies, such as the implementation of properly working sewage treatment plants, will benefit local reef health and retard reef degradation. In addition, stronger recreational diving regulation may be useful since approximately 75% of the stay-over tourists on Bonaire are divers (IVM report 2013; http://www.rijksdienstcn.com), undoubtedly having a local impact on the reef (e.g., Hawkins et al., 1999; Lamb et al., 2014). Comparable data are lacking for Curaçao. It is clear that supporting data on specific effects of the

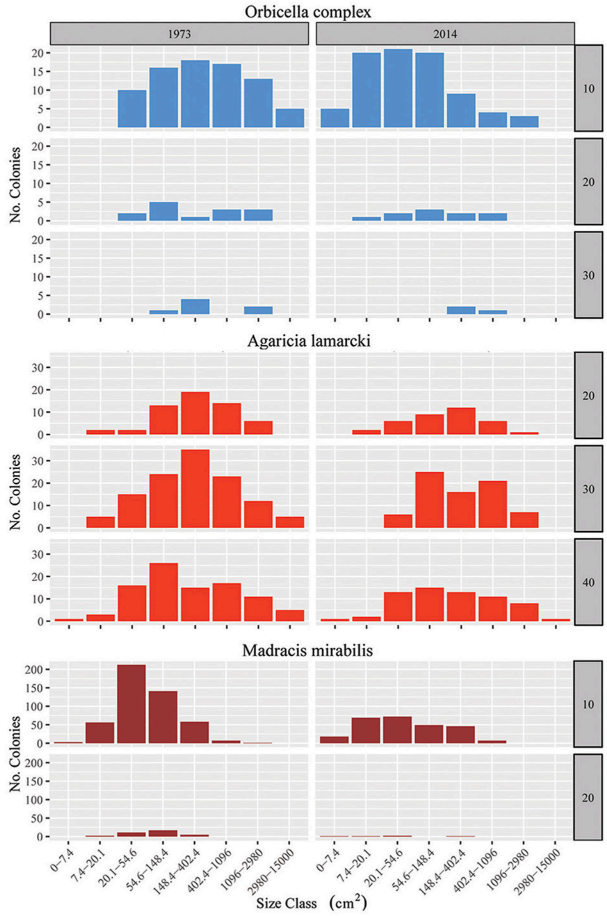

FIGURE 5 | Colony size frequency distribution for the three most prominent species: *Orbicella* spp., *Agaricia lamarcki* and *Madracis mirabilis*. Total number of colonies in 9 m^2 quadrats in 1973 (start time series) and 2014 (end) summed over the four main sites (I–IV) on a log scale (8 size classes), at different depths (when the species was present). Scale size varies for the different species. Species color codes correspond to the colors given in Fig. 4. For supporting data, also on the other species, see Figure S1 and Tables S2, S3.

TABLE 4 | Species specific life-history strategy and cover.

Species	Life history strategy	Cover (%)	
		1973	2014
Acropora cervicornis	Competitive	0	0
Dendrogyra cylindrus	Competitive	0.01	0
Orbicella complex	Framework building	14.1	9.8
Dichocoenia stokesii	Framework building	0.06	0
Dichocoenia stellaris	Framework building	0	0
Montastraea cavernosa	Framework building	10.6	7.6
Stephanocoenia michelini	Framework building	6.4	9.1
Siderastrea siderea	Framework building	4.3	3.1
Eusmilia fastigiata	Framework building	3.3	0.7
Colpophyllia natans	Framework building	2.7	5.1
Diploria strigosa	Framework building	0.81	0.35
Diploria labyrinthiformis	Framework building	0.02	0
Meandrina meandrites	Framework building	4.2	2.3
Porites porites	Opportunistic	0.08	0
Madracis complex	Opportunistic	2.4	0.8
Madracis mirabilis	Opportunistic	8.1	17.6
Mycetophyllia aliciae	Opportunistic	1.2	0.25
Mussa angulosa	Opportunistic	0.16	0
Mycetophyllia ferox	Opportunistic	0.1	0
Scolymia lacera	Opportunistic	0	0
Porites astreoides	Opportunistic	1.4	2.3
Leptoseris cucullata	Opportunistic	0	0
Agaricia lamarcki	Opportunistic	29.8	35.8
Agaricia agaricites	Opportunistic	9.9	5.2

Overview of all encountered species with their respective life history strategy and mean contribution (percentage) to the total coral cover at the start (1973) and end (2014) across the four main time series (I–IV). A cover of 0% at 1973 and 2014 means the species was observed at some point between both years. Detailed characteristics per quadrat can be found in Tables S2, S3.

various local stressors will be essential for proper implementation of conservation strategies, but at present such data is very limited or even absent.

The observed general decline in cover and abundance of corals not only occurred among reef building species, but included also most opportunistic species (e.g., *P. porites, Mycetophyllia* spp., *A. agaricites* and *Madracis* spp.). A few species, in particular *M. mirabilis, A. lamarcki* and *P. astreoides*, however, appear to be more resilient and their decrease in cover and abundance was less distinct (**Figure 4**, Table S2). This is confirmed by observations throughout the Caribbean (Green et al., 2008; Anderson et al., 2014; Perry et al., 2015). Nevertheless, these species seem to decline when the overall coral cover in the quadrat was substantially reduced. Like many coral species, *M. mirabilis* can not easily settle on loose substratum such as sand or rubble (Bak and Criens, 1981; Nagelkerken et al., 2000). Presumably, *M. mirabilis* relies on substratum provided by other species after mortality to settle or expand. Indeed, we found an increase in cover of *M. mirabilis* in quadrats where large colony building species (e.g., *Orbicella* complex) used to be dominant but died and left available hard substratum. Contrastingly, in quadrats where larger species were not initially present the cover of *M. mirabilis* remained low or even declined (e.g., site I, 10 m). This implies that survival of this species is all but certain. According to predictions (e.g., Darling et al., 2012), several larger framework building species such as *S. michelini* and *M. meandrites* indeed appear to be relatively persistent (stress-tolerant *sensu* Darling et al., 2012) and were not readily lost over time. Though their average cover declined in all quadrats, they continued to contribute to total quadrat cover by 2014 (**Figure 3**). *D. strigosa* even newly appeared in several shallow quadrats and seems relatively stress-tolerant (**Figure 3**, Table S2). If, however, the observed declining trend continues, it is likely that even these species will eventually disappear. Also, it remains to be seen whether the apparently opportunistic weedy species will be sufficiently tolerant to cope with the generally expected increase in frequency and severity of catastrophic events (Van Woesik et al., 2011; McClanahan et al., 2014). Historic records (e.g., van Woesik et al., 2012) show that even opportunistic species can become regionally extinct, as a consequence of large-scale climate disturbances. At the present rate of decline (**Figure 3A**) total coral cover on the reef slopes of Curaçao and Bonaire is expected to have dropped below 1% by 2030.

Evidently, the decline in colony size and shift toward dominance of smaller colonies is largely caused by a decline in abundance of species that potentially form large colonies such as the *Orbicella* spp. (**Figure 5**). This was most apparent on AB at 20 m which was originally dominated by many large *Orbicella* colonies (Table S3). The observed shift in colony size of *Orbicella*, *A. lamarcki* and most other species is largely a result of partial mortality of large colonies. Coral growth or tissue regeneration may be impeded by increased spatial competition between corals and other benthic organisms such as algae or benthic cyanobacterial mats (Hughes, 1994). Meesters et al. (1997a) describe two types of lesion in coral tissue: the so-called type I, where the lesion is completely enclosed by tissue; and type II, most frequently observed, where the lesion is located at the edge of the colony. The observed increase in the ratio of colony outline and live surface area of coral colonies (**Table 3**) could be an indication of the incapability of the coral to reclaim substratum after such a type II lesion (Meesters et al., 1997b). Partial mortality will generally result in a larger loss of surface area than colony outline, thus leading to a higher shape-ratio. A possible effect on colony size distribution caused by increased recruitment can be neglected since no new recruits were present in 2014. *M. mirabilis* may at present be the sole species to show recruitment within the quadrats. Fragmentation, however, makes it difficult to distinguish actual new *M. mirabilis* recruits. Nevertheless, the relative increase in abundance of opportunistic species in the past decade has contributed to a higher density of small colonies (Knowlton, 2001; Darling et al., 2012).

An important consequence of reduced coral cover is the loss of reef structural complexity and associated loss of biodiversity, but also coastal protection and human food security (e.g., Alvarez-Filip et al., 2009; Newman et al., 2015). In many of the studied quadrats, coral cover has approached or dropped below the 10% level. This point has been suggested as the threshold after which carbonate accretion will be surpassed by erosion and architectural complexity is being lost (Perry et al., 2013). Following this rationale, nine out of the 16 main quadrats would currently be in an eroding state (**Table 3**). Indeed, the estimated carbonate production has decreased considerably since 1973 in virtually all quadrats, largely attributed to the general reduction of coral cover and in particular the loss of large calcifying species such as *Orbicella* spp. (Perry et al., 2015). The relative decline in carbonate production was highly comparable across depths, with the exception of 10 m. At 10 m depth the degree by which carbonate production changed over time was generally lower and largely driven by the temporal dynamics in cover of the rapidly calcifying *M. mirabilis.* High *M. mirabilis* cover may compensate some of the reduction in production but it cannot be considered an important framework builder able to compensate for the loss of structural complexity provided by large calcifying species (such as *Orbicella* spp. and *Acropora* spp.) (Alvarez-Filip et al., 2011a). Moreover, opportunistic rapidly calcifying species such as *M. mirabilis* are typically absent at greater depths.

Diversity indices may reflect a gradient of decreased disturbance with greater depth. According to the intermediate disturbance theory highest community diversity is found at intermediate disturbance (Connell, 1978). Over the depth range studied, highest diversity occurred at 20 m depth both in 1973 and 2014, which could be indicative of intermediate disturbance level. At 10 m depth, high disturbance likely impacted all but the most resistant species such as *M. mirabilis* or *P. astreoides*, resulting in a low diversity. Both natural (e.g., hurricanes) and anthropogenic disturbances (e.g., eutrophication and run-off) generally have the highest impact on the more shallow reef. Particularly the anthropogenic stress has intensified over the past decades likely putting more stress on the most shallow reef zones (< 20 m). The generally low diversity of coral communities at greater depth (>20 m), in particular at 40 m, might indicate that these reefs experience lower levels of disturbance (e.g., declined water quality, reduced herbivory and hurricanes). Following the intermediate disturbance theory, reefs with low disturbance are characterized by dominant competitors (Connell, 1978). Indeed, the deeper reefs of Curaçao and Bonaire were dominated by *A. lamarcki* consistently between 1973 and 2014. In addition, low light intensities at greater depth likely support a generally lower diversity of species. Although, the reefs at greater depths may initially have experienced less disturbance (Bak et al., 2005) an obvious degrading trend was nevertheless observed, in particular since approximately 1990. A decline in cover and abundance of coral, including *A. lamarcki* may suggest that stress on these reefs has recently been increasing. Lapointe and Mallin (2011), for instance, found evidence for land-based sewage inputs reaching the deeper reef (18 m) near urban areas on Curaçao. Nutrient measurements on reefs below 18 m are virtually absent, but eutrophication may be reaching greater depths as well. The observed deep community dynamics of the recent years may, however, not be linked (anymore) to the absence of disturbance, but simply be the outcome of one strong competitor (*A. lamarcki*) and a generally limited pool of species at greater depths. The absence of weedy species such as *M. mirabilis* here may impede a shift to a more opportunistic coral community as seen on the shallow reef. Such species are simply unable to settle at these depths due to factors such as low light intensity. As yet no new opportunistic candidate has settled and with *A. lamarcki,* still dominant though steadily declining as well, the prospect for recovery of mesophotic coral communities on reefs appears to be very limited.

In conclusion, we found that coral communities of Curaçao and Bonaire have seen dramatic changes since 1973. Overall coral communities were heavily degraded by 2014. Phenotypically plastic and opportunistic species have increased and *M. mirabilis, A. lamarcki, P. astreoides* and *D. strigosa* may at present be considered very modest winners among the Caribbean coral assembly. These species, however, are unlikely to remain winners in a compromised habitat where suitable substratum for settlement is lost and disruptive events may become more frequent and severe, nor will they be able to provide the same structural complexity as the species from the near past (e.g. *Orbicella* spp.). The reefs at mesophotic depths (30–40 m) do not escape the general degradation of the coral community. Degradation was less evident away from urban areas. This suggests that local management, such as the provision of proper sewage treatment and run-off prevention, can have a positive effect on the general health and survival of coral reef communities. Although, the upsurge of some opportunistic species may provide a glimmer of hope for coral communities proper conservation and management will be essential to keep coral species from turning collectively into losers.

AUTHOR CONTRIBUTIONS

Data collection: RB, EM, and GN; Data analysis: DD, EM, RB, and GN; Interpretation of the data: DD, EM, FV, and RB; Drafting work: DD; Critical revision: EM, FV, RB, and GN; Final approval: EM and FV; Agreement to be accountable for all aspects of the work: DD, EM, FV, RB, and GN.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: http://journal.frontiersin.org/article/10.3389/fmars.2016.00247/full#supplementary-material

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