Size-frequency distribution of coral assemblages in insular shallow reefs of the Mexican Caribbean using underwater photogrammetry

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ABSTRACT

The characterisation of changes in coral communities depends heavily on systematic monitoring programs and the collection of necessary metrics to assess reef health. Coral cover is the most used metric to determine reef health. The current organizational shift in coral requires the evaluation of complementary metrics, such as colony size and frequency distributions, which help to infer the responses of the coral populations to local stress or larger scale environmental changes. In this study, underwater digital photogrammetry techniques were used to assess the live cover of all coral colonies ≥ 3 cm^2 and determine the size-frequency distribution of the dominant species in the shallow reefs of the Cozumel Reefs National Park (CRNP). In addition, the minimum sampling area (m^2) needed to obtain a representative sample of the local species pool was estimated. Areas between 550 and 825 m^2 per reef were photographed to generate high-resolution digital ortho-mosaics. The live area of the colonies was digitised to generate community matrices of species and abundance. EstimateS software was used to generate accumulation curves and diversity (Shannon H') at increasing area intervals. Chi-Square tests (χ^2, $p = 0.05$) were used to compare the observed *vs* estimated species richness. Spearman's coefficients (r_s), were calculated to correlate the increase in sampling area (m^2) *vs* H', and the Clench's function was used to validate the observed richness ($R^2 = 1$ and $R > 90\%$). SIMPER analysis was performed to identify dominant species. Comparisons in terms of abundance, coral cover and size-frequencies were performed with Kruskal-Wallis (H test, $p = 0.05$), and paired Mann-Whitney (U test, $p = 0.05$). In order to obtain 90% of the species richness, a minimum sampling area of 374 m^2 is needed. This sampling area could be used in shallow Caribbean reefs with similar characteristics. Twelve (mainly non-massive) species: *Agaricia agaricites, A humilis, A. tenuifolia, Eusmilia fastigiata, Meandrina meandrites, Montastrea cavernosa, Orbicella annularis, Porites astreoides, P. porites, Pseudodiploria strigosa, Siderastrea radians* and *S. siderea*, were dominant in terms of abundance and coral cover. A significant increase ($p < 0.05$) in the number of colonies and live coral (m^2) was observed from north to south of the study area. Furthermore, a wide

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intraspecific variation of size-frequency, even between adjacent reefs, was also observed. The size-frequency distributions presented positive skewness and negative kurtosis, which are related to stable populations, with a greater number of young colonies and a constant input of recruits. Considering the increase in disturbances in the Caribbean and the appearance of a new coral disease, digital photogrammetry techniques allow coral community characteristics to be assessed at high spatial resolutions and over large scales, which would be complementary to conventional monitoring programs.

INTRODUCTION

Coral reefs are among the most ecologically and economically productive marine ecosystems. However, over the last four decades the condition of reefs around the world has declined severely (*Raeaka-Kudla, 1997*; *Mumby & Harborne, 2010*). Coral reefs are locally and regionally subjected to a wide range of natural and human stressors, including overfishing, coastal development, algal blooms, disease outbreaks, invasive species, hurricanes and the effects of climate change, which have generated dramatic shifts in the community structure and composition (*Glynn, 1984*; *Hoegh-Guldberg, 1999*; *Gardner et al., 2003*; *Bellwood et al., 2004*; *Carpenter et al., 2008*; *Obura & Grimsdith, 2009*). The environmental goods and services obtained from coral reef ecosystems (e.g., coastal protection against hurricanes, food and income for local communities) are seriously threatened (*Moberg & Folke, 1999*; *Hoegh-Guldberg et al., 2007*; *Franklin et al., 2018*). The synergy of multiple stress factors has driven a phase shift that has altered the balance between corals and algae, which is characterised by the loss of coral cover and a substantial increase in macroalgae (*Jackson et al., 2014*). In addition, other shifts in the hierarchical dominance of coral species have occurred in the Caribbean. The previously dominant reef-builders, such as the branching species, *Acropora cervicornis* and *A. palmata*, or massive corals such as the *Orbicella* complex, have been disproportionately susceptible to several disturbances (e.g., bleaching events, disease outbreaks, among others) (*Bruckner & Bruckner, 2006*; *Weil, Croquer & Urreiztieta, 2009*), and opportunistic, small-sized coral species, such as *Agaricia agaricites* and *Porites astreoides*, have increased in abundance, dominating the current coral assemblages throughout the Caribbean (*Alvarez-Filip et al., 2013*; *Estrada-Saldívar et al., 2019*).

Recently, new stress factors have appeared in the Caribbean region, including the atypical massive arrival of *Sargassum spp*, observed over the last few years (*Rioja-Nieto & Álvarez Filip, 2018*; *Cabanillas-Terán et al., 2019*), and the emergence of a new coral disease observed for the first time in Florida's coral reefs (*Florida Department of Environmental Protection, 2019*), locally known as "White syndrome" in the Mesoamerican Reef System (MAR) (*Sociedad Mexicana de Arrecifes Coralinos, 2015*). White syndrome has expanded rapidly, affecting a wide number of scleractinian corals species, among them important

reef-building species (e.g., *Orbicella sp, Colpophyllia natans, Pseudodiploria sp*, among others). The rapid expansion of this disease threatens the marine biodiversity and socio-economic activities of the region (*Precht et al., 2016*; *Van Woesik & Randall, 2017*; *Healthy reefs, 2019*) and could lead to new shifts in the condition and structure of coral assemblages. Conservation strategies are critical to maintain the health and environmental services of coral reefs. These strategies depend heavily on the different methods employed to obtain metrics which are used to assess the condition of the coral reef communities (*Hughes et al., 2010*; *Turner et al., 2015*), and are collected as part of monitoring programs and local action plans.

Most monitoring programs have focused on the trajectory of coral cover loss (*Jackson, 1997*; *Gardner et al., 2003*), on the partial or total mortality of key coral species (*Aronson & Precht, 2001*), or on the coral-macroalgae balance (*Knowlton, 2001*; *Kramer, 2003*). In the majority of these studies, coral cover is the most used metric to assess coral communities and determine the health of a reef (*Gardner et al., 2003*; *Hodgson et al., 2006*; *Hill & Wilkinson, 2004*). However, coral cover by itself, does not provide information on other important aspects of the community structure and dynamics, or the ecological mechanisms that lead to changes in the coral assemblages (*Smith et al., 2005*; *Grimsditch et al., 2017*). Several studies have highlighted the ecological value of complementary metrics to coral cover, such as colony size and their size frequency distribution, to evaluate the condition of the coral communities and reef health (*Meesters et al., 2001*; *Harris et al., 2014*; *Mumby & Harborne, 2010*). In corals, life-history processes, such as reproduction and mortality, are related to size (*Meesters et al., 2001*) and seem to be affected by subtle environmental changes. Consequently, the size structure of corals is an important driver of the population dynamics (*Bak & Meesters, 1998*). Size-frequency distributions can help to understand the responses of the population to conditions of local stress or larger scale environmental changes (*Hughes & Jackson, 1980*; *Hughes, 1984*). Furthermore, size-frequency data make it possible to analyse ecological processes such as recruitment, fecundity and mortality, in retrospect as well as the potential community responses to disturbances (*Meesters et al., 2001*; *Vermeij & Bak, 2003*; *Adjeroud, Penin & Carroll, 2007*; *McClanahan, Ateweberhan & Omukoto, 2008*; *Gilmour et al., 2013*; *Turner et al., 2015*; *Grimsditch et al., 2017*).

The conventional methods for recording coral cover are based on collecting the information directly *in situ*, using line transect replicas (*Loya, 1972*; *Porter, 1972*; *English, Wilkinson & Baker, 1997*; *Hill & Wilkinson, 2004*). Along each transect, systematically distributed points are used to record and count each colony of the coral species and the data are subsequently transformed to obtain cover percentages (e.g., *Lang et al., 2010*). The standard method to assess size-frequency distributions, is to measure each colony *in situ* with a ruler or a measuring tape (*Burgess et al., 2010*; *Victor et al., 2009*; *Richardson & Voss, 2005*; *Smith et al., 2005*). Recently, underwater digital photogrammetric techniques and Structure-from-Motion (SfM) algorithms (*Longuet-Higgins, 1981*; *Smith, Carrivick & Quincey, 2015*; *Carravick, Smith & Quincey, 2016*), have been increasingly used for the assessment of coral reef communities across several spatial and temporal scales (*Burns et al., 2015a*; *Burns et al., 2016*; *Edwards et al., 2017*; *Rossi et al., 2019*). These techniques allow the construction of accurate two (2D) and/or three-dimensional (3D) ortho-mosaics at a

very high spatial resolution (few centimetres), which make it possible to characterise the structure of the coral community at scales as small as the size of a coral polyp (*Burns et al., 2015a*; *Burns et al., 2015b*; *Royer et al., 2018*).

In this study we used underwater digital photogrammetry, SfM algorithms and spatial analysis, henceforth referred to as photogrammetry techniques, to assess the live coral cover (m^2) and to describe the size-frequency distribution of the coral species of six assemblages in shallow reefs of the Cozumel Reefs National Park (CRNP). These reefs are distributed along a north to south gradient of decreasing urban growth and increasing reef development. In addition, we explored the size of the minimum sampling area (m^2) required to obtain a representative sample of the local species pool (maximum species richness in a minimum area). Cozumel's reefs are some of the most important reef systems in the Mexican Caribbean and are among the healthiest of the MAR (*McField et al., 2018*). Our results could provide support to the current monitoring programs in the Mexican Caribbean (and elsewhere in the region) and establish a baseline for long-term surveys based on digital photogrammetry, facilitating the ongoing assessment of local and regional coral reef condition.

MATERIALS & METHODS

Study area

The Cozumel Reefs National Park (CRNP) is administered by the National Commission of Natural Protected Areas (CONANP), which is the main government institution responsible for the management and conservation of protected areas in Mexico. With an extension of c.a. 12,000 ha, most reefs are located around the south east, south and south west coast of Cozumel Island, in the Mexican Caribbean (Fig. 1). The fringing reefs follow a marked north-south gradient of increasing reef structural complexity and habitat diversity, where larger massive coral structures, mainly of the *Orbicella* complex, can rise several metres above the seafloor (*Fenner, 1988*; *Muckelbauer, 1990*; *Jordán, 1988*; *Jordán-Dahlgren & Rodríguez-Martínez, 2003*; *Rioja-Nieto, Chiappa-Carrara & Sheppard, 2012*). The seascape consists of a mixture of sandy beds, fringing reefs, patch reefs, coral colonies on hard substrate, seagrasses and macroalgae (*Rioja-Nieto & Sheppard, 2008*). The reefs of the CRNP are considered to have the highest coral cover of all the reefs of the MAR (*McField et al., 2018*). Urban development is concentrated in San Miguel town (Fig. 1), and a few hotels and beach clubs distributed along the southwest of the island. The main economic activities are mostly related to tourism. Local authorities reported that in 2017 c.a. 5 million tourists visited the island, making Cozumel one the most visited islands in the Caribbean (*Cruz-Vázquez, Rioja-Nieto & Enríquez, 2019*). Cozumel is considered one of the best areas for SCUBA diving, and the marine protected area is heavily visited by people who engage in a variety of recreational activities (*Rioja-Nieto & Álvarez Filip, 2018*).

Data collection and construction of ortho-mosaics

Between February and March 2018, six reefs distributed across the western area of the CRNP were visited: Paraiso (PA), Chankanaab (CH), Yucab (YU), Cardona (CA), Francesa (FR) and Colombia (CO) (Fig. 1). The reefs are distributed c.a. 30 kms along the southwest
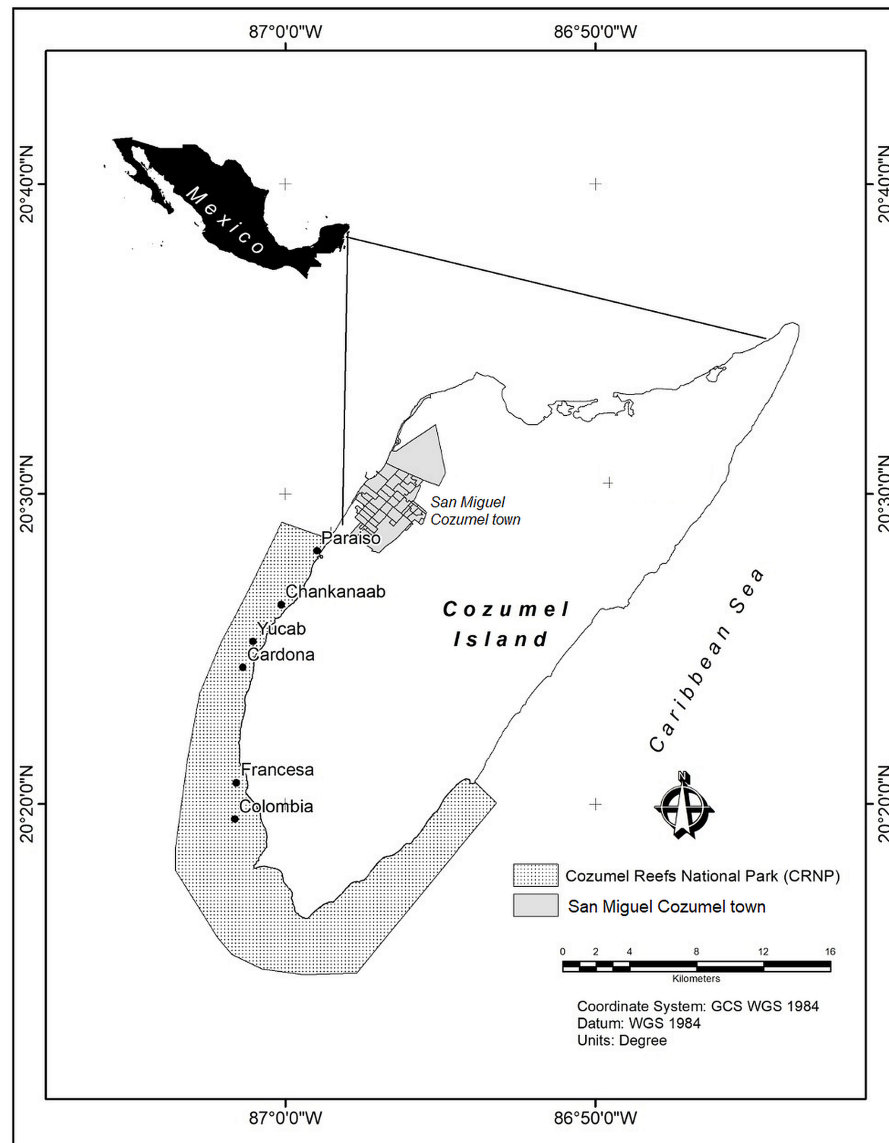
Figure 1 **Study area.** Cozumel Reefs National Park (CRNP). Reefs sampled from north to south were: Paraiso (PA), Chankanaab (CH), Yucab (YU), Cardona (CA), Francesa (FR) and Colombia (CO).

coast of the protected area and were chosen considering their location and their relative proximity to the main urban area (San Miguel Cozumel town). The reefs closest to the town were Paraíso and Chankanaab, while the reefs furthest from the town were Francesa and Colombia. The reefs selected in the central region of the study area were Yucab and Cardona. The sites selected for this study corresponded to the shallow reef front habitat, whose average depth varies from 7.3 m (Cardona and Paraiso) to 14.1 m (Yucab). For each site, transects ($n = 3$) of 30 m in length separated by 20 to 30 m, were placed parallel to the coast following the reef's development. Along each transect, marks made of polyvinyl (0.6×0.6 m), four at the corners and one at the centre of the transect, were placed to delineate a rectangular plot

c.a. five m wide (at least 150 m^2). The plot was divided at the middle mark and photographed by two divers (each focusing on one half of the plot), swimming in a gridded pattern at a constant speed of c.a. 5 m/min. Photographs were taken two metres above the average depth of the reef bottom (*Edwards et al., 2017*). The depth at the beginning and at the end of each transect was recorded using a standard dive computer. To obtain the photographs, two Canon G12 10-megapixel cameras (Canon WP-DC34) in waterproof housing were used. The settings used were: 4:3 frame size, at a 28 mm default focal length. We set the camera options to self-timer to automatically shoot ten times continuously (1 fps), before taking a new series of images. This ensured a high overlap (>80%) across and along images, which is necessary to construct ortho-mosaics via SfM algorithms (*Pix4D, 2019b*. https://support.pix4d.com/hc/en-us/sections/200591059-Manual). Pix4Dmapper (4.3.x) software was used to process images and to construct ortho-mosaics from photographs. This software follows three basic steps: (1) initial processing (internal/external camera orientation and sparse cloud creation), (2) point cloud and mesh generation, and (3) Digital Surface Model (DSM) and ortho-mosaic construction. Considering that the images obtained have no geolocation, and it is difficult to obtain accurate ground control points underwater, the marks (or quadrants of 0.60 × 0.60 m) were used as a contrast measurement of length to transform the model to absolute measurements (*Pix4D, 2019a*. https://support.pix4d.com/hc/en-us/articles/205360375-How-to-scale-a-project). The precision of the ortho-mosaic constructed was between 0.0015 and 0.0067 m of the computed length error. Ortho-mosaics were exported to ArcGIS 10.6 (*Environmental Systems Research Institute ESRI, 2017*) for analysis. The sections for each plot were joined along the central mark, using the spatial adjustment extension. This resulted in one ortho-mosaic for each plot (total $n = 3$ plots per reef). A great effort was made to maintain the width of the plots. However, this varied due to local current conditions and the lack of a visual reference to delimit the sides of the plots. CONANP, Dirección del Parque Nacional "Arrecifes de Cozumel" provided permits (F00.9/DPNAC/360/18) for this study.

Data analysis

Shapefiles associated with each of the ortho-mosaics were constructed by digitising the area covered with live coral tissue of all the colonies recorded ≥ 3 cm^2. Data matrices were generated from the identification of species to obtain the colonies' abundance, species richness (*S*) and cover (cm^2) of each site. The species were identified following the criteria of the AGRRA protocol (*Lang et al., 2010*; *Kramer, 2003*) and the *Human & Deloach (2002)* keys. In accordance with *Loya (1972)*, a coral colony was considered as a set of polyps interconnected by live tissue, detached and growing regardless of neighbouring colonies. When coral colonies presented portions clearly separated without live tissue and/or the calcareous skeleton was visibly eroded or overgrown by another benthic group (e.g., macroalgae), every living portion was considered as an independent colony. In the cases where corals showed growth in patches or large clumps (e.g., *Porites porites* and/or *Agaricia tenuifolia*), extreme care was taken to digitise the living tissue, avoiding the dead areas of the colony in order to consider these clumps as one single colony.

To assess whether the areas sampled at each reef were large enough to register a representative local species pool, accumulation curves were estimated (*Moreno & Halffter, 2000*; *Moreno & Halffter, 2001*; *Ma, Tarmi & Helenius, 2002*; *Chittaro et al., 2010*). For each plot, the number of colonies per cell on a 1×1 m mesh was obtained by using scripts written in Matlab and an envelope procedure known as Convex Hull (Jarvis's or Wrapping Algorithm, see *Graham, 1972*; *Andrew, 1979*; *Kirkpatrick & Seidel, 1986*). Community matrices of species richness and abundance were then constructed. EstimateS V9.10 (*Colwell, 2013*), was used to generate species accumulation curves and to obtain the corresponding Shannon diversity values (H'), based on 100 randomised iterations without replacement (*Gotelli & Colwell, 2011*; *Gotelli & Chao, 2013*). The curves were subjected to increases of 25 m^2 (up to the maximum area sampled in each site), using a non-parametric Bootstrap procedure. A Bootstrap estimator was chosen as it proved to be the most precise of the seven estimators given by default in the Estimate software during previous tests. The Bootstrap estimator was the least biased (low mean error -ME-), with the highest precision (low variance -VAR-) and accuracy (low mean standard error -MSE-). The performance of the estimators was evaluated following the criteria of *Hellmann & Fowler (1999)* and *Walther & Moore (2005)*. A Chi-Square goodness-of-fit test (χ^2, $p = 0.05$) was used to compare the observed richness against the richness estimated by Bootstrap for each reef. Spearman's rank coefficients (r_s), were calculated to correlate ($p = 0.05$) the sampling effort (area in m^2) and diversity values.

To model the relationship between the sampling effort and the number of species observed, the data were fitted to the asymptotic Clench model (*Jiménez-Valverde & Hortal, 2003*; *Gómez-Anaya et al., 2014*). The model equation used to estimate the number of predicted coral species for each reef was: $S(x) = ax/(1 + bx)$, where x is a measure of sampling effort, $S(x)$ is the predicted number of species at effort x, a represents the rate of increase at the beginning of sampling, b is a parameter related to the form of the accumulation curve and a/b is the asymptote. To fit the model, the mean number of species per sample was used from community matrices (*Colwell, 2013*). The model fit was obtained using the non-linear estimation module in STATISTICA V10 (*StatSoft, 2011*), applying the Simplex and Quasi-Newton methods for parameter estimation. The theoretical effort required (nq) for each inventory was then calculated with the equation: $nq = q/[b \cdot (1 - q)]$, where q is the relative proportion of the list of species to be detected (*Jiménez-Valverde & Hortal, 2003*). The first approach to the curve asymptote or the total number of species predicted (calculated as a/b) and the coefficient of determination (R^2), which is a descriptive measure of the proportion of explained variance, were also obtained for each reef.

The distribution of the abundance of colonies and live coral cover (m^2) per reef was analysed and statistically compared by means of similarity analyses (One-way ANOSIM, 9999 permutations, $p = 0.05$). For both parameters, similarity matrices based on the Bray-Curtis coefficient were generated and transformed with the square root (*Clarke & Warwick, 1994*). Subsequently, the size-frequency percentages (%) of each reef were distributed in 12 size-classes with ranges of 200 cm^2. The largest size class corresponded to colonies >3,800 cm^2. Non-parametric Mann–Whitney U test analyses ($p = 0.05$, 95%
of confidence, STATISTICA V10, *StatSoft, 2011*) were performed to compare the size-frequency distributions between reefs. The data were logarithmically transformed prior to analysis.

SIMPER analyses (*Clarke & Warwick, 1994*) were performed to identify the coral species that together contributed 90% of the abundance and total live coral cover. A group of twelve species was identified, which in combination formed the dominant species assemblages of each reef. The analyses were performed in PRIMER 6.1.13 and PERMANOVA+ (*Clarke & Gorley, 2006*). The size-frequencies of the dominant species were subsequently plotted in 12 size classes (cm2) (see Fig. S1 for the size-class ranges for each species). Colony size data were logarithmically transformed, analysed graphically and compared statistically. In accordance with *Bak & Meesters (1997)* and *Bak & Meesters (1998)*, the logarithmic transformation of coral-size data produces a clear representation of population structure in scleractinian corals. Size distributions of transformed data have a better resolution and reflect an approximate size-frequency distribution more closely than distributions of non-transformed data. Size-distributions were statistically contrasted via one-way non-parametric Kruskal-Wallis analyses (H test, $p = 0.05$, 95% of confidence) and subsequently significant differences in the size frequency distribution between reefs were obtained from post-hoc tests based on pairwise comparisons using Mann–Whitney ($p = 0.05$, 95% of confidence). A set of parameters related to the shape of the size-frequency distributions was analysed. Mainly the Skewness (g1) and the Kurtosis (g2), among other distribution parameters (such as, maximum size, 95th percentile and central tendency measures), were explored to describe the colony-size distributions of the dominant species population (*Sokal & Rohlf, 1995*; *Zar, 1999*).

RESULTS

There were no significant differences (X^2 test, $p > 0.05$) between the observed and estimated species obtained from the Bootstrap estimator (Figs. 2A, 2C, 2E, 2G, 2I and 2K). The diversity (H' index values) (Figs. 2B, 2D, 2F, 2H, 2J and 2L), was also positively correlated to the increase in the area sampled (Spearman coefficient, $r_s > 85\%$, $p < 0.05$). Both the curves of richness and diversity values increased rapidly from 25 to 150 m². In all cases, the asymptotic phases began c.a. 300 m², until stabilizing almost entirely around 400 m² (Fig. 2). The only exception was Cardona (Fig. 2G), where the curve began to stabilize after 450 m², which seems to be related to the presence of a few rare species, such as *Scolymia sp.,* which was only observed in this reef and *A. palmata*, which was only recorded in Cardona and Colombia. The maximum value of diversity varied from 1.83 (± 0.03) to 2.2 (± 0.04), between Chankanaab and Colombia, respectively (Table 1). The values of the determination coefficients (R^2 close to 1) and the high predicted species richness ($R > 90\%$) indicate a good model fit, which suggests that sampling an area of 300–400 m² is sufficient to obtain a representative and highly reliable record of coral species richness (Table 1). The number of predicted species (a/b) was very close to the total species richness observed at each reef (with a difference of less than one species). Using photogrammetry techniques, an average area of 374 m² (standard deviation SD = 48.1 m²) is necessary to
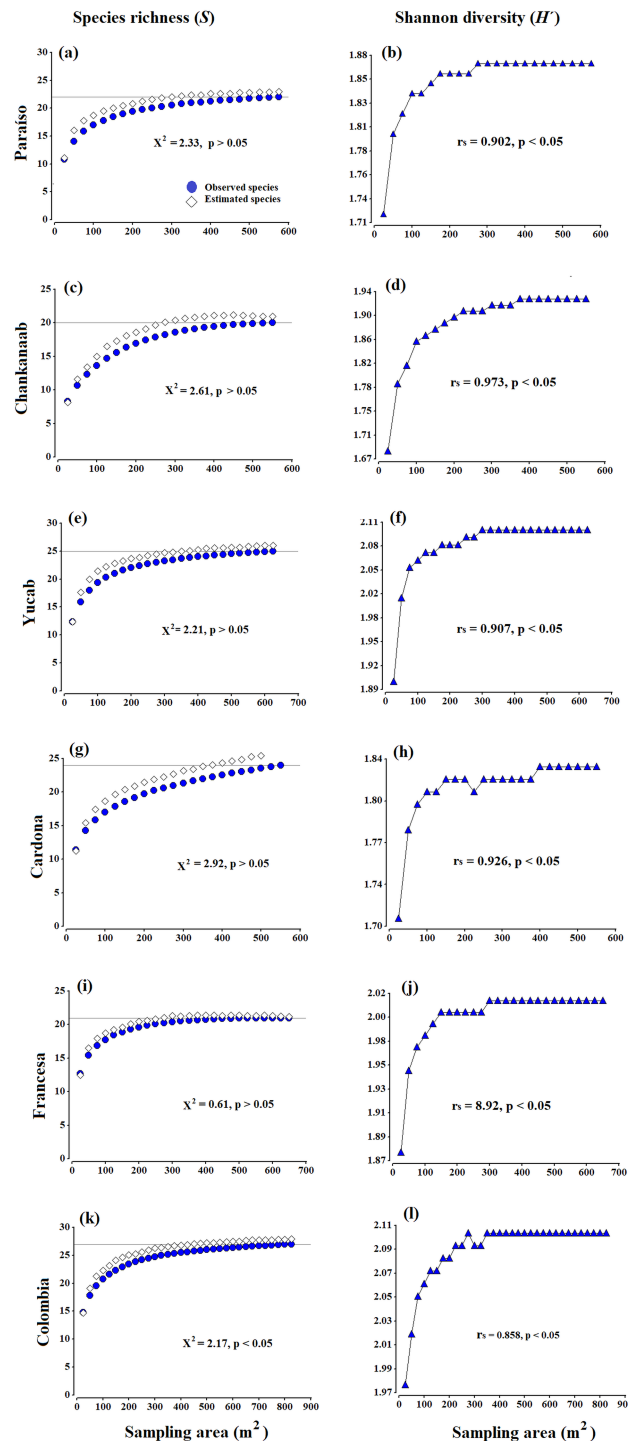
Figure 2 Accumulation species curves. Observed species *vs* estimated species (A, C, E, G, I, K) and Shannon diversity index values (H') (B, D, F, H, J, L), obtained from the Bootstrap estimator. A Chi-square goodness-of-fit test was used to compare the observed richness against estimated richness (X^2, $p = 0.05$, 95% confidence). The Spearman correlation coefficent (r_s) ($p = 0.05$, 95% confidence) was used to correlate the sampling effort (area in m^2) and Shannon diversity index values (H'). The grey horizontal line represents the total number of species observed in each site.

Table 1 Values obtained from the species accumulation curves according to Clench's function.

Reef	S_{obs}	H'	a	b	R^2	R (%)	(a/b)	(nq)
Paraiso	22	1.87	0.7056	0.0290	0.994	98.8	22.8	309
Chankanaab	20	1.83	0.3980	0.0181	0.992	98.4	21.9	495
Yucab	25	2.10	0.8092	0.0249	0.995	99.1	25.9	361
Cardona	24	1.93	0.6113	0.0248	0.974	94.9	24.6	362
Francesa	21	2.10	1.1001	0.0300	0.995	99.1	21.6	299
Colombia	27	2.20	0.9639	0.0351	0.983	96.6	27.3	256

Notes.

Site sampled (Reef), species observed (Sobs), diversity values (H'), a and b values, determination coefficient (R^2), explained model variance R (%), number of predicted species (a/b), and the theoretical sampling (nq) to capture 90% of the predicted species richness. The theoretical effort (nq), was calculated according to the equation: $nq = q/[b(1-q)]$, where $q =$ the relative proportion of the list of species to be detected (*Jiménez-Valverde & Hortal, 2003*).
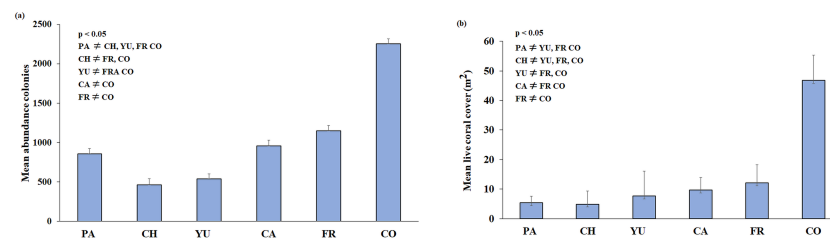
Figure 3 (A) Mean colony abundance and (B) Mean live coral cover. One-way similarity analyses (ANOSIM, 9999 permutations, P value $= 0.05$). Bars represent the Standard Error ($\pm$SE). The significant differences between reefs are indicated on the upper left side ($p < 0.05$). Paraiso (PA), Chankanaab (CH), Yucab (YU), Cardona (CA), Francesa (FR) and Colombia (CO).

record 90% of the coral species in the shallow reefs of Cozumel. This is also supported by the accumulation curves of richness and diversity (Figs. 2B, 2D, 2F, 2H, 2J and 2L). In general, the area recommended to record a high percentage of species (e.g., $nq = 90\%$), proved to be less than the total area sampled in the surveyed reefs.

Coral assemblages

A total of 3,775 m^2 (0.38 ha) of reef development was characterised from ortho-mosaics, of which 260 m^2 (or 6.8% of the total sampled area) was covered by live coral. The precision of the obtained ortho-mosaics was between 0.0015 and 0.0066 m of the computed length error. In total, 18,661 colonies and 32 species of scleractinian corals were recorded (Table 2). The sampling area for each reef ranged from c.a. 550 m^2 at Chankanaab and Cardona to 825 m^2 at Colombia reef. The lowest species richness (20) was observed at Chankannab and the highest (27) at Colombia. Colombia also showed the highest abundance of colonies and live coral cover ($p < 0.05$). Chankanaab had the lowest abundance of all the sampled sites (Fig. 3A, $p < 0.05$). The lowest live coral cover was observed at Paraiso, Chankanaab and Cardona (Fig. 3B, $p < 0.05$). In general, a significant increase ($p < 0.05$) in the number of coral colonies and live coral cover is observed from north to south of the study area.

The size-frequency distribution (Figs. 4A–4F) showed that >80% of the colonies in all reefs were distributed in small size-classes ($\leq$200–400 cm^2). Significant differences in size

Table 2 List of coral species recorded on six reefs of the CRNP. List of coral species recorded on six reefs of the CRNP. Sampling area (m^2), Species richness (S), Colonies abundance (n), Standardised live coral cover (% of total area). The code used is in accordance with the AGGRA protocol (see https://www.agrra.org/training-tools/coral-training/).

	Paraíso		Chankanaab		Yucab		Cardona		Francesa		Colombia	
Sampling area (m^2)	575		550		625		550		650		825	
Species richness (S)	22		20		25		24		21		27	
Colonies abundance (n)	2,572		1,390		1,620		2,867		3,446		6,766	
Standardised live coral cover (% of total area)	2.9		2.5		3.8		5.4		5.7		17.2	
Spp name/code	*n*	*m²*	*n*	*m²*	*n*	*m²*	*n*	*m²*	*n*	*m²*	*n*	*m²*
Agaricia agaricites AAGA	635	3.14	428	4.53	280	2.92	1,422	9.69	1,218	7.56	1,702	14.6
Agaricia fragilis AFRA	1	0.0024			14	0.15			7	0.07	25	0.13
Agaricia humilis AHUM	168	0.62	11	0.11	13	0.08	55	0.2	96	0.52	96	0.65
Agaricia lamarcki ALAM	6	0.02									13	0.21
Acropora palmata APAL							1	0.0021			1	0.01
Agaricia tenuifoila ATEN	12	0.23	6	0.34	20	0.37	21	1.24	191	3.35	877	50.88
Colpophyllia natans CNAT					1	0.08					3	0.05
Dendrogyra cylindrus DCYL											8	0.44
Diploria labyrinthiformis DLAB	21	0.25	6	0.17	2	0.07	8	0.18	5	0.04	9	0.2
Dichocoenia stokesii DSTO					3	0.01	2	0.01	3	0.03		
Eusmilia fastigiata EFAS	63	0.26	97	0.35	58	0.27	99	0.59	255	1.28	98	0.38
Favia fragum FFRA	12	0.01	3	0.0048	4	0.0042	42	0.04	30	0.03	26	0.04
Isophyllia rigida IRIG					9	0.09	1	0.01	4	0.06	5	0.08
Mancina areolata MARE	8	0.03			1	0.0035						
Montastraea cavernosa MCAV	80	1.23	77	1.57	104	1.94	104	2.64	58	1.36	127	3.57
Madracis decactis MDEC	2	0.0041	1	0.0034	13	0.07	12	0.04	12	0.07	43	0.17
Meandrina jacksoni MJAC			2	0.08	2	0.02						
Meandrina meandrites MMEA	16	0.31	8	0.17	14	0.4	2	0.04	7	0.05	6	0.07
Mycetophyllia sp MYCE	4	0.01							2	0.02	6	0.05
Orbicella annularis OANN	47	0.28	31	0.45	28	0.59	195	3.5	215	3.65	716	13.9
Orbicella faveolata OFAV	8	0.21	11	0.18	2	0.27	12	1.34	9	0.63	66	4.25
Orbicella franksi OFRA	4	0.08	1	0.0031	1	0.02	1	0.03			15	0.76
Porites astreoides PAST	713	2.66	245	1.81	317	2.35	295	2.21	102	0.53	1,090	10.47
Pseudodiploria clivosa PCLI			3	0.11	9	0.37	5	0.04			7	0.05
Porites furcata PFUR					12	0.24	9	0.03	41	0.51	68	1.12
Porites porites PPOR	18	0.07	6	0.05	436	9.21	233	2.18	794	13.37	1430	33.31
Pseudodiploria strigosa PSTR	26	0.83	4	0.22	15	0.61	16	0.43	17	0.38	25	0.43
Solenastrea bournoni SBOU			5	0.0047			2	0.05				
Scolymia sp SCOL							1	0.00025				
Isophyllia sinuosa SINT	1	0.01									1	0.13
Siderastrea radians SRAD	72	0.31	136	0.48	54	0.17	34	0.12	122	0.39	81	0.51
Siderastrea siderea SSID	655	5.63	309	4.07	208	2.77	295	4.43	258	2.48	222	3.96
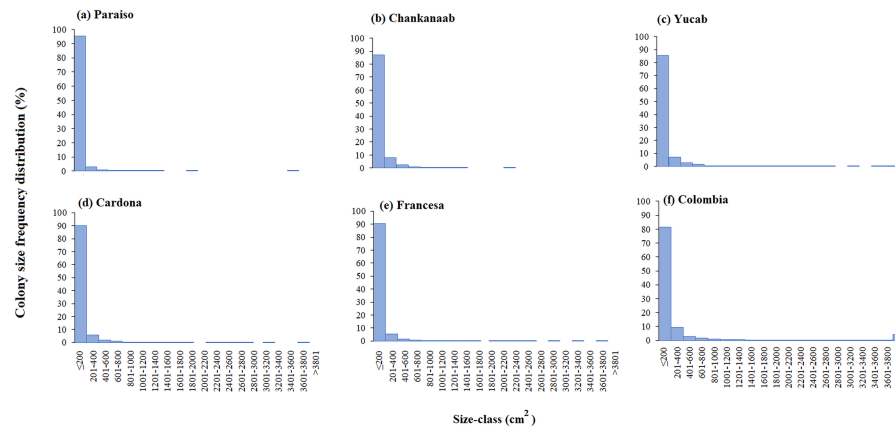
Figure 4 Coral colony size frequency distribution (%) by reef (A-F). Significant differences were found between Chankanaab (B) and Colombia (F) (W = 87.0, $p < 0.05$) and between Yucab (C) and Colombia (F) (W = 8.15, $p < 0.05$).

distribution were observed between Colombia and Chankannab (W = 87.0, $p < 0.05$), and Yucab (W = 8.15, $p < 0.05$). A group of twelve species proved to be dominant in terms of abundance (Figs. 5A, 5C, 5E, 5G, 5I and 5K) and live coral cover (Figs. 5B, 5D, 5F, 5H, 5J and 5L). In alphabetical order these were: *Agaricia agarites, A humilis, A. tenuifolia, Eusmilia fastigiata, Meandrina meandrites, Montastrea cavernosa, Orbicella annularis, Porites astreoides, P. porites, Pseudodiploria strigosa, Siderastrea radians* and *S. siderea*. The largest contributions, in terms of abundance, corresponded to sub-massive species, with small and medium sizes, such as *A. agaricites, P. astreoides* and *S. siderea*. In terms of coral cover the greatest contributors were *A. tenuifolia* and *P. porites*, whose foliose and digitiform morphologies tend to form large colony clumps. This dominant coral group represented 34% of the total species richness recorded. *A. agaricites*, was the only species within this group that contributed to both abundance and coral cover at all reefs. *S. siderastrea* and *P. astreoides* contributed in terms of abundance at all reefs, but not in terms of coral cover for Colombia and Francesa. *M. meandrites* and *P. strigosa* were only present in the dominant group of live coral cover at Paraíso. *O. annularis*, an important reef-building coral species for Caribbean reefs, was only present in the dominant species group in terms of abundance and/or coral cover at Cardona, Francesa and Colombia. Species considered as important reef-building corals (e.g., *O. faveolata* or *A. palmata*), in general showed very low contributions (<5%).

The number of colonies recorded by species and size-frequency distribution (non-transformed size data) in twelve independent size-classes for each species are shown in Fig. S1. A wide intraspecific variation between reefs was observed. In general, the colonies were concentrated in the smallest size-classes and declined markedly towards the largest size-classes. Abundant living colonies ≥ 3 cm^2 (viable fragments or small recruits) were recorded for several species such as, *A. tenuifolia, E. fastigiata, P. porites, S radians* and *S. siderea*. The largest colonies recorded corresponded to *P. strigosa* (2,135 cm^2), *M. cavernosa*
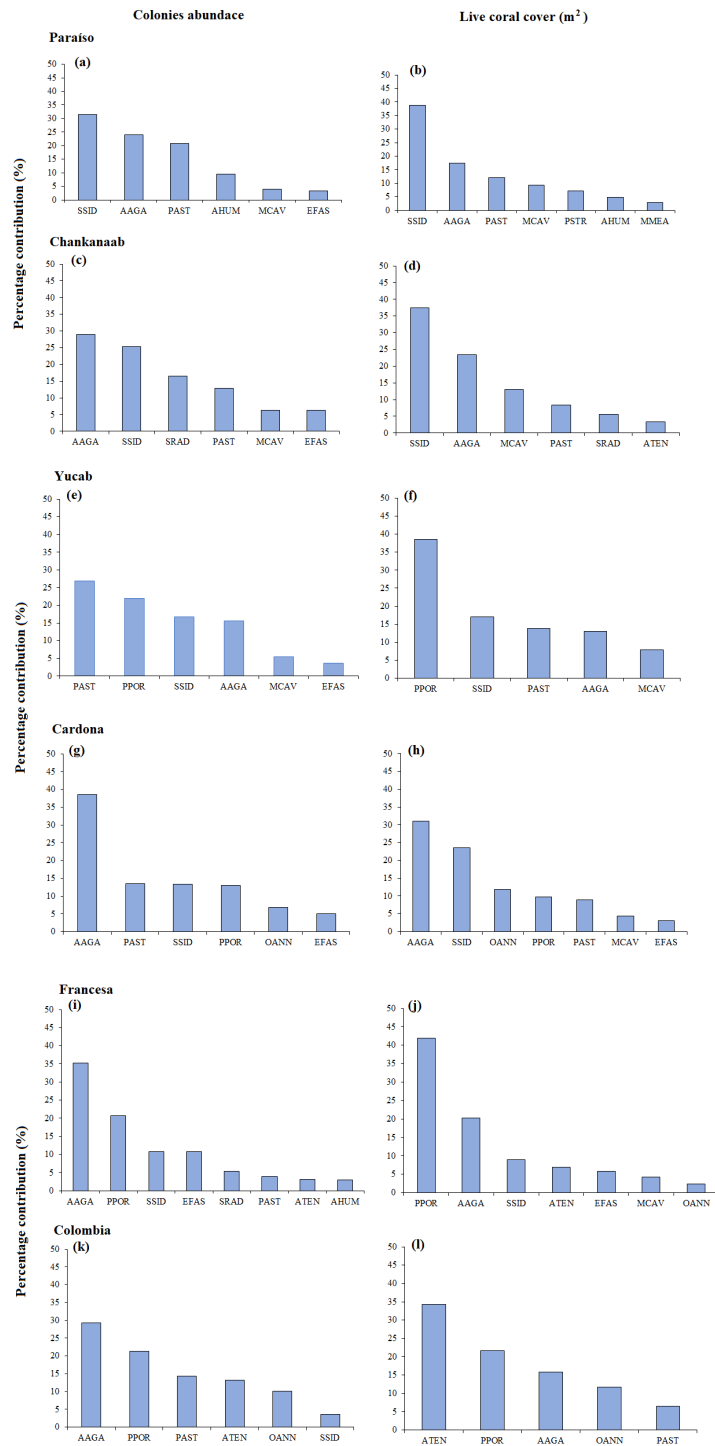
Figure 5 SIMPER analysis. Dominant species assemblages that contributed with 90% of the abundance of colonies (A–K) and live coral cover (m^2) (B–L) of each reef. *Agaricia agaricites* (AAGA), *A. humilis* (AHUM), *A. tenuifolia* (ATEN), *Eusmilia fastigiata* (EFAS), *Montastrea cavernosa* (MCAV), *Meandrina meandrites* (MMEA), *Orbicella annularis* (OANN), *Porites astreoides* (PAST), *P. porites* (PPOR), *Pseu-dodiploria strigosa* (PSTR), *Siderastrea radians* (SRAD) and *S. siderea* (SSID).

(3,176 cm^2), *O. annularis* (4,670 cm^2), *P. astreoides* (8,478 m^2), *P. porites* (14,378 cm^2) and *A. tenuifolia* (17,106 cm^2) (see Table S1).

The 95th-percentile size was used as a distribution parameter to determine the maximum colony size of the coral population (see *Soong, 1993*; *Meesters et al., 2001*). In this study, the colony size at the 95th-percentile varied considerably for the same species between sites, even for adjacent reefs (Table S1). For example, in the case of *A. agaricites*, the maximum colony size at the 95th percentile was twice as large at Chankanaab as in Paraiso (326.2 cm^2 and 141.5 cm^2, respectively). For other species, such as *A. tenuifolia*, the maximum colony size at the 95th percentile varied up to an order of magnitude, with 393.9 cm^2 at Yucab and almost 3,000 cm^2 at Colombia (see Table S1). The size data were logarithmically transformed (*Soong, 1993*; *Bak & Meesters, 1997*; *Bak & Meesters, 1998*), analysed graphically and compared statistically. The distribution of the size-frequency of the dominant species is shown in Figs. 6A–6M, and the probability of the data being normally distributed (Kolmogorov–Smirnov normal test using -KS-, $p = 0.05$), is shown in Table S1. The frequency distribution parameters indicated that the size-distribution of the species was not symmetrical around the mean. The species of the dominant group, *A. humilis, E. fastigiata, P. astreoides, P. strigosa* and S. radians showed mainly a negative skewness for most reefs. Those that presented mainly positive skewness were *A. tenuifolia, O. annularis, P. porites* and *S. siderea*. Others, such as *E. fastigiata, P strigosa, S. radians,* and *M. meandrites* presented distributions with skewness that were highly variable between reefs (Figs. 6A–6M and Table S1). A unidirectional tendency to shift from negative to positive skewness from north to south across the study area was observed for *P. astreoides.* Predominantly negative or platykurtic kurtosis was observed in the size-distributions of *A. agaricites, E. fastigiata, M. cavernosa* and *P. strigosa* across all reefs (Table S1). The colonies' size range (Figs. 6N–6Y) increased in a north-south direction ($p < 0.05$) for *A. agaricites, A. humunis, A. tenuifolia, O. annularis, P. astreoides* and *P. porites* (Figs. 6N, 6O, 6P, 6T, 6U and 6V, respectively). Significant differences (H test, $p < 0.05$) were also observed in *M. meandrites, E. fastigiata*, and *S. radians*. However, these species showed no size distribution pattern on a latitudinal gradient. *M. cavernosa, P. strigosa and S. siderea* did not present significant differences between reefs. These species were more homogenously distributed among reefs in terms of the median size range (Figs. 6R, 6X and 6Y, respectively).

DISCUSSION

The colony coral cover (m^2) and the structure and pattern of the corals' size-frequency distribution revealed important characteristics of the structure and composition of the coral assemblages in the shallow reefs of Cozumel. The live coral cover (m^2) quantified from using underwater photogrammetry techniques, resulted in lower percentages when compared to those estimated by the most used conventional methods of observation *in situ* in the Caribbean region. Twelve coral species were significantly dominant in terms of abundance and live cover (in alphabetical order): *Agaricia agarites, A humilis, A. tenuifolia, E. fastigiata, M. meandrites, M.cavernosa, O. annularis, P. astreoides, P. porites, P. strigosa, S. radians* and *S. siderea.* Both the abundance and live coral cover increased along a
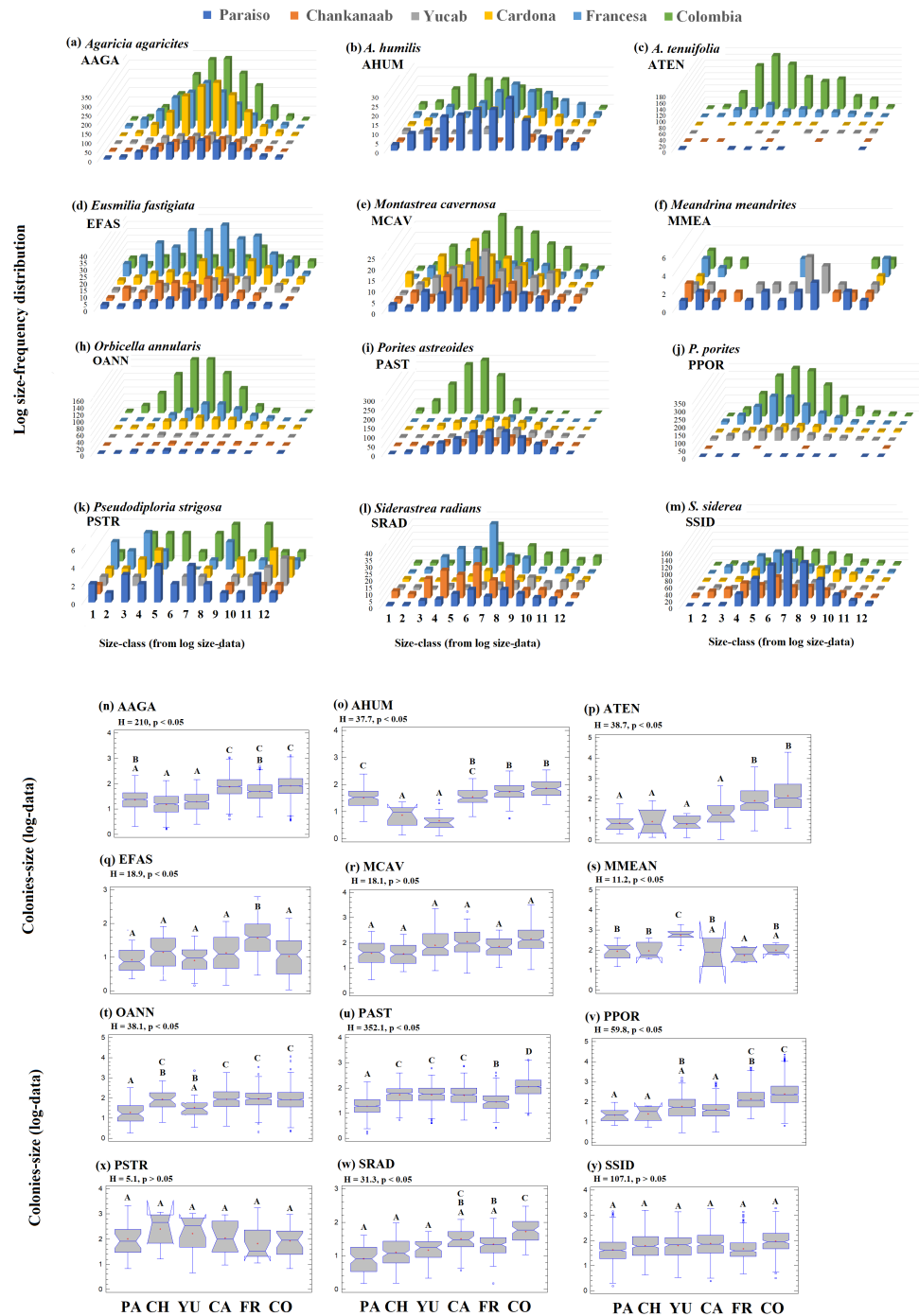
Figure 6 **Frequency-distribution.** Log size-frequency distribution of the twelve dominant species (A–M) and intraspecific contrast between of the colonies-size distribution by reefs (N-Y). Different letters indicate significant differences (Kruskal-Wallis *H* test, *p* = 0.05, 95% confidence). Sites: Paraíso (PA), Chankanaab (CH), Yucab (YU), Cardona (CA), Francesa (FR) and Colombia (CO). The size classes (1–12), correspond to the class ranges of Fig. S1. *Agaricia agaricites* (AAGA), *A. humilis* (AHUM), *A. tenuifolia* (ATEN), *Eusmilia fastigiata* (EFAS), *Montastrea cavernosa* (MCAV), *Meandrina meandrites* (MMEA), *Orbicella annularis* (OANN), *Porites astreoides* (PAST), *P. porites* (PPOR), *Pseudodiploria strigosa* (PSTR), *Siderastrea radians* (SRAD) and *S. siderea* (SSID).

north-south gradient for some species. Species with the highest number of colonies do not always contribute the largest live coral cover. For example, *A. tenuifolia* was not among the most abundant species on the reefs located to the north of the study area. However, this species was dominant on the reefs located in the south of the protected area, with the highest abundance in Francesa, and highest coral cover in Colombia. In Colombia reef, *A. tenuifolia* and *P. porites* were also determinant in the significant differences observed in live coral, with low abundance but high cover. Unlike other coral reefs, at Colombia, large colonies of these species were recorded forming extensive clumps. For most colonies, the size-frequency of the species ranged from ≥ 3 to around 400 cm^2, corresponding to the first size-class respectively for each dominant species. A minimum sampling area of c.a. 380 m^2 is suggested in order to facilitate the use of digital photogrammetry techniques to characterise coral reefs in the Caribbean.

Underwater digital photogrammetry techniques, have recently been applied to map and assess several attributes of coral assemblages, such as cover, condition, growth and structure (*Lirman et al., 2007*; *Westoby et al., 2012*; *Gintert et al., 2012*; *Burns et al., 2015b*; *Edwards et al., 2017*; *González-Rivero et al., 2017*; *Gintert et al., 2018*). Here, the high resolution of the obtained ortho-mosaics allowed a high number of colonies to be quantified, and the real area covered by live coral in colonies from 3 cm^2 to be estimated. The coral reefs of the CRNP have been well characterised and monitored since the early 1990's (e.g., *Jordán, 1988*; *Fenner, 1988*; *Fenner, 1991*; *Fenner, 1999*; *Alvarez-Filip et al., 2009*; *Alvarez-Filip et al., 2011*; *Reyes-Bonilla, Millet-Encalada & Álvarez Filip, 2014*; *McField et al., 2018*). The species richness recorded, corresponded to >80% (32) of the species previously reported. When comparing the percentage of live coral cover estimated in this study to recent assessments in the CRNP (see *Reyes-Bonilla, Millet-Encalada & Álvarez Filip, 2014*; *Barranco et al., 2016*; *Loreto-Viruel et al., 2017*; *McField et al., 2018*), the results were considerably lower. Coral cover ranged between 2.5 and 17.2%, with a mean live cover of 6.2% ($\pm$SE $= 1.8$), where previous studies establish a coral cover between 11 and 25% (average 20%). Considering that no major disturbances (e.g., hurricanes, disease) were observed during sample times and that the characterised reefs are the same used in previous studies, the difference in coral cover seems to be related to the sampling method used. Registering information *in situ* is possibly the most widely used technique to monitor reefs in the Mexican Caribbean (e.g., AGRRA protocol, Healthy Reefs Initiative -HRI, *Lang et al., 2010*; *McField et al., 2018*). In comparison, the high-resolution of the ortho-mosaics, allows a more precise quantification of the area covered by living coral tissue (cm^2). Although substantial post-processing time was required for the analysis of each colony, the live tissue can be estimated from colonies of a few centimetres in size (e.g., fragmented colonies or small recruits) to large adult colonies, thus encompassing a wide range of spatial scales (e.g., a few centimetres to tens or hundreds of metres). The difference observed between the coral cover reported in previous studies from *in situ* estimates (mentioned above), against those obtained here, may suggest an overestimation by the traditional methods. However, it is not easy to determine whether one method or the other results in an underestimation or overestimation of coral cover. This needs to be carefully evaluated through the contrast of cover data acquired from the
most commonly used evaluation methods (e.g., transect line), against those obtained by digital photogrammetry, which until now has not been explored.

Locally the species richness and diversity values obtained were representative of each reef studied. This was supported by the observed and estimated species richness obtained via the Bootstrap procedure for each reef. The Bootstrap curves did not differ significantly (X^2, $p > 0.05$) and showed strong and positive correlations (Spearman r_s) between the diversity ($H' > 1.80$) and increase in sampling area. The data fit to the Clench model and the subsequent estimated theoretical effort required (nq), suggested that an average area of c.a 380 m^2 is appropriate to record at least 90% of the local coral species pool in the shallow reefs of Cozumel, using underwater digital photogrammetry. The area sampled at each reef was larger than the average suggested. Therefore, the observations are reliable to assess the species richness, live coral cover and the colony size structure of the coral assemblages of the shallow reefs in the CRNP. Considering that in recent years, the use of photogrammetry techniques (from digital photography and video) in underwater monitoring has increased, the estimation of an average sampling area to record a representative sample of the local coral richness, is relevant. This should help to improve the efficiency of future ecological sampling (e.g., significantly reduce work in the field, permit more sites to be surveyed, save time collecting data, reduce bottom-time underwater, save money, among others) (*Lirman et al., 2007*; *Burns et al., 2015a*; *Burns et al., 2015b*). The average minimum sampled area (m^2) estimated in this study, could be applied to reefs of similar characteristics in the Caribbean, for example in terms of the depth range and reef-development.

A complementary monitoring program based on digital photogrammetry could allow changes in live coral cover area, colony growth, mortality, and recruitment of coral species and other important benthic groups to be described at a resolution of centimetres over extensive areas. In this study, the assessments were performed on six shallow reefs at different depths (between 6 and 14 m). Fringing shallow reefs border most of the continental and insular shores of the Mexican Caribbean and are common in other areas of the Caribbean Sea (*Jordán-Dahlgren & Rodríguez-Martínez, 2003*). Therefore, our results could be considered as representative of fringing shallow reefs in the region. In the CRNP, high species richness, a large number of colonies, and a wide range of coral colony sizes were obtained using photogrammetry. These are key components for coral populations demographic studies and the determination of general reef health (*Meesters et al., 2001*; *Lang et al., 2010*; *Mumby & Harborne, 2010*; *McField et al., 2018*). The results highlighted that the minimum and maximum size recorded for a single species varied substantially even when the reefs were located next to one another. In general, the greatest size-frequencies (>80%), were distributed among small size classes ≥ 3 to ≤ 400 cm^2. Most of the frequency distribution of the species between reefs had a positive skewness, which is considered as proxy of greater abundance of young colonies and a constant input of coral recruits (*Bythell, Bythell & Gladfelter, 1993*; *Soong, 1993*; *Lewis, 1997*; *Meesters et al., 2001*; *Kenyon et al., 2006*). The predominance of negative kurtosis or platykurtic (non-peaked distribution) and wide standard deviations observed in the dominant species of this study, are also indicative of a high variation in colony size and suggest stable coral populations in demographic terms. In contrast, the shape of the size-distributions of a similar group

of species in degraded reefs, were negatively skewed, with extremely positive kurtosis, suggesting limited recruitment and a low frequency of large adult colonies (see *Meesters et al., 2001*).

Other parameters used to describe the size-frequency distribution, such as the mean colony size, provide information about coral life-history strategies, such as growth and reproduction (*Soong & Lang, 1992*). The wide intraspecific variation between reefs observed, was in accordance with other studies where variations in the mean size between species and reef sites were up to an order of magnitude. The maximum colony size (based on the 95th percentile), has been correlated with reproductive traits such as the size at reproductive maturity of many conspicuous coral species of the Caribbean region (*Soong, 1993*). Previous studies have demonstrated that different species reach maturity at different sizes (*Szmant-Froelich, Reutter & Riggs, 1985*; *Szmant, 1986*; *Rinkevich & Loya, 1986*; *Babcock, 1984*; *Babcock, 1991*; *Pareja-Ortega & Quan-Young, 2016*). In small species such as *S. radians*, puberty starts c.a. 10 cm^2, and in medium size species, such as *M. cavernosa*, it starts at 20 cm^2 and for *P. astreoides* and *S. siderea* between 70–100 cm^2 (*Soong, 1993*; *Meesters et al., 2001*).

Here, the mean colony size of the species mentioned above comparatively exceeds the estimated size of reproductive maturity, which suggests that populations are in a healthy state of development. The reproductive strategies of corals and the habitat characteristics with respect to colony size, are decisive in the structuring of coral populations (*Szmant, 1986*; *Hall & Hughes, 1996*). The reproductive stage of small and medium size species starts early, they brood larvae and have relatively high rates of recruitment, whereas the large species are reproductively mature much later. When large sizes are reached, then these species release gametes during spawning events (*Szmant, 1986*; *Richmond & Hunter, 1990*; *Hall & Hughes, 1996*). Likewise, colony mortality rates have been inversely related to colony size (e.g., *Hughes & Jackson, 1980*; *Hughes & Jackson, 1985*; *Hughes & Connell, 1987*). The larger colonies are more susceptible to partial mortality than smaller colonies (*Soong & Lang, 1992*; *Soong, 1993*; *Meesters, Wesseling & Bak, 1997*). High partial colony mortality of large colonies has a negative effect on the larger size classes by decreasing their proportions and simultaneously increasing the proportion of colonies in the medium-sized classes. In addition, the fission or fragmentation of large colonies due to high physical stress can substantially increase the number of colonies in small-sized classes (*Hughes & Jackson, 1980*; *Jaramillo-González & Acosta, 2009*). The implications of these processes on the demographic dynamics of coral populations have been difficult to determine and have not yet been quantified in detail, primarily because of their complicated modular construction and growth. The partial mortality, fission and colony fusion can confuse any simple relationship between the size and age of the corals and mask the origin of individuals in size distribution analysis (*Hughes & Jackson, 1980*).

The ecological features found in this study, that relate to the size-frequency distribution of the dominant species of the shallow reefs in the CRNP, agree with the distributions described above for small and medium species. Most of these species (e.g., *A. agaricites, P. astreoides, M. cavernosa, O. annularis* and *S. siderea*) lead the current hierarchical shifts in species dominance in the coral assemblages of the Caribbean reefs (*Reyes-Bonilla,*

Millet-Encalada & Álvarez Filip, 2014; *Barranco et al., 2016*; *González-Barrios & Alvarez-Filip, 2018*; *Estrada-Saldívar et al., 2019*), and are considered to have a limited capacity to substantially contribute to the reef framework (*Alvarez-Filip et al., 2011*; *Graham & Nash, 2013*; *González-Barrios & Alvarez-Filip, 2018*). Nevertheless, the population characteristics of the dominant species in terms of their contribution to abundance, live coral cover and size-frequency distributions, imply healthy, stable and potentially resilient coral populations (*Loya, 1976*; *Connell, 1978*; *Soong, 1993*; *Bak & Meesters, 1998*; *Meesters et al., 2001*; *Richardson & Voss, 2005*; *Grimsditch et al., 2017*).

A wide intraspecific variation among reefs was identified in terms of the size-frequency distribution. However, mean abundance and live coral cover and colony size distribution, increased from north to south for most of the dominant species, which might be related to anthropogenic disturbance. Numerous studies have documented the presence of fewer colonies of small size classes in reefs closer to heavily urbanized coastal areas, with high levels of pollution, sediment load and fishing pressure (*Meesters et al., 2001*; *Vermeij & Bak, 2003*; *Adjeroud, Penin & Carroll, 2007*; *McClanahan, Ateweberhan & Omukoto, 2008*; *Crabee, 2009*). Colonies of smaller species which grow faster and have shorter generation times, apparently find relatively acceptable conditions for their development and persistence in unstable environments (*Meesters, Wesseling & Bak, 1997*). On the other hand, some species, such as *S. siderea* and *P. strigosa*, and particularly *M. cavernosa*, showed similar patterns of size-frequency distribution in all reefs. These species seem to be less sensitive and /or better adapted than other species to local stress factors, which could be related to the pressure level and proximity to urban development sources that potentially influence the intraspecific variation observed (*Rogers, 1990*; *Guzman & Holst, 1993*; *Guzmán, Burns & Jackson, 1994*; *Meesters et al., 2001*). These species could play an important role as wide scale indicators in tracking changes in current coral communities.

CONCLUSIONS

The size frequency distribution of coral species has rarely been studied in the field due to the underwater technical requirements and huge effort required to collect colony size data in large areas. The ortho-mosaics obtained from photogrammetry provide repeatable, high resolution measurements that can be used to track coral assemblages in the short term at very fine (cm) scales. We conclude that new complementary tools and simple metrics need to be included in current evaluation programs in order to detect short-term changes in coral assemblages. The suggested average sampling area of c.a 380 m^2 can help in terms of logistic resources in future evaluations of coral communities using photogrammetry techniques. Likewise, it is suggested that this minimum sampling area is applicable to shallow reefs in the Caribbean region with similar environmental characteristics (depth range and reef-development). However, the minimum area suggested for shallows reefs must be flexible when a deeper, speciose or complex reef is the target. The underwater photogrammetric techniques applied here, revealed important features of the coral assemblages of the shallow reefs in the CRNP. Small, non-reef-building coral species dominate and a wide range of intraspecific variation between reefs with respect to the abundance, live coral and in

particular the size-frequency distributions was observed. Local environmental factors seem to act differentially from north to south of the study area, with respect to their proximity to the main urban development. The shape and parameters of the frequency distributions of most dominant species exhibited positive skewness and negative kurtosis, which in addition to the coral cover and colony abundance suggest that the coral populations are stable. However, the frequency of the colonies was mainly limited to small size classes with few large colonies, and reef building species were very scarce. Potential changes in the organization of current coral species can be expected in the short term, related to a relatively new outbreak of a coral disease locally known as "White syndrome". When this study was carried out, coral diseases were not observed. In the CRNP, White syndrome disease was reported for the first time late in the summer of the same year. This disease has rapidly caused the death of a wide variety of coral species. It has been estimated that main reef-building species have been affected (more than 20 coral species), with live coral cover decreasing dramatically (up to c.a. 40% less live coral in some coastal reefs in the Mexican Caribbean) (Technical report, Cozumel reefs situation, Parque Nacional Arrecifes de Cozumel, CONANP, 2019). In order to obtain robust estimates of community change in terms of live coral cover (m^2) and size-structure over time, digital photogrammetry techniques should be used as complementary tools to traditional methods.

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Competing Interests

The authors declare there are no competing interests.

Author Contributions

- Roberto C. Hernández-Landa, Erick Barrera-Falcon and Rodolfo Rioja-Nieto conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft.

Field Study Permissions

The following information was supplied relating to field study approvals (i.e., approving body and any reference numbers):

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Data Availability

The raw data are available in the Supplemental Files.

Supplemental Information

Supplemental information for this article can be found online at http://dx.doi.org/10.7717/peerj.8957#supplemental-information.

REFERENCES

Adjeroud M, Penin L, Carroll A. 2007. Spatio-temporal heterogeneity in coral recruitment around Moorea, French Polynesia: implications for population maintenance. *Journal of Experimental Marine Biology and Ecology* **341(2)**:204–218 DOI 10.1016/j.jembe.2006.10.048.

Alvarez-Filip L, Carricart-Ganivet JP, Horta-Puga G, Iglesias-Prieto R. 2013. Shifts in coral-assemblage composition do not ensure persistence of reef functionality. *Scientific Reports* **3**:3486 DOI 10.1038/srep03486.

Alvarez-Filip L, Dulvy NK, Côte IM, Watkinson AR, Gill JA. 2011. Coral identity underpins architectural complexity on Caribbean reefs. *Ecological Applications* **21(6)**:2223–2231 DOI 10.1890/10-1563.1.

Alvarez-Filip L, Dulvy NK, Gill JA, Côte IM, Watkinson AR. 2009. Flattening of Caribbean coral reefs: region-wide declines in architectural complexity. *Proceedings of the Royal Society B: Biological Sciences* **276**:3019–3025 DOI 10.1098/rspb.2009.0339.

Andrew AM. 1979. Another efficient algorithm for convex hulls in two dimensions. *Information Processing Letters* **9(5)**:216–219 DOI 10.1016/0020-0190(79)90072-3.

Aronson RB, Precht WF. 2001. White-band disease and the changing face of Caribbean coral reefs. In: Porter JW, ed. *The ecology and etiology of newly emerging marine diseases. Developments in hydrobiology*. vol. 159. Dordrecht: Springer DOI 10.1007/978-94-017-3284-0-2.

Babcock RC. 1984. Reproduction and distribution of two species of *Goniastrea* (Scleractinia) from the Great Barrier Reef Province. *Coral Reefs* **2**:187–195.

Babcock RC. 1991. Comparative demography of three species of scleractinian corals using age- and size-dependent classifications. *Ecological Monographs* **61**:225–244 DOI 10.2307/2937107.

Bak RPM, Meesters EH. 1997. Population structure as a response of coral communities to global change. *American Zoologist* **39**:56–65.

Bak RPM, Meesters EH. 1998. Coral population structure: the hidden information of colony size-frequency distributions. *Marine Ecology Progress Series* **162**:301–306 DOI 10.3354/meps162301.

Barranco LM, Carriquiry JD, Rodríguez-Zaragoza FA, Cupul-Magaña AL, Villaescusa JA, Calderón-Aguilera LE. 2016. Spatiotemporal variations of live coral cover in the northern Mesoamerican Reef System, Yucatan Peninsula, Mexico. *Scientia Marina* **80(2)**:000–000 DOI 10.3989/scimar.04294.23A.

Bellwood D, Hughes T, Folke C, Nyström M. 2004. Confronting the coral reef crisis. *Nature* **429**:827–833 DOI 10.1038/nature02691.

Bruckner AW, Bruckner RJ. 2006. The recent decline of Montastraea annularis (complex) coral populations in western Curaçao: a cause for concern? *Revista de BiologÃa Tropical (International Journal of Tropical Biology* **54(Suppl. 3)**:45–58.

Burgess SC, Osborne K, Sfiligoj B, Sweatman H. 2010. Can juvenile corals be surveyed effectively using digital photography?: implications for rapid assessment techniques. *Environmental Monitoring and Assessment* **171**:345–351 DOI 10.1007/s10661-009-1282-1.

Burns JHR, Delparte D, Gates RD, Takabayashi M. 2015a. Utilizing underwater three-dimensional modelling to enhance ecological and biological studies of coral reefs. *The International Archives of the Photogrammetry, Remote Sensing and Spatial Information Sciences* **XL-5/W5**: 2015 Underwater 3D Recording and Modeling, 16–17 April 2015, Piano di Sorrento, Italy.

Burns JHR, Delparte D, Gates RD, Takabayashi M. 2015b. Integrating structure-from-motion photogrammetry with teospatial software as a novel technique for quantifying 3D ecological characteristics of coral reefs. *PeerJ* **3**:e1007 DOI 10.7717/peerj.1077.

Burns JHR, Delparte D, Kapono L, Belt M, Gates RD, Takabayashi M. 2016. Assessing the impact of acute disturbances on the structure and composition of a coral community using innovative 3D reconstruction techniques. *Methods in Oceanography* **15–16**:49–59 DOI 10.1016/j.mio.2016.04.001.

Bythell JC, Bythell M, Gladfelter EH. 1993. Initial results of a long-term coral reef monitoring program: impact of Hurricane Hugo at Buck Island Reef National Monument, St. Croix U.S. Virgin Islands. *Journal of Experimental Marine Biology and Ecology* **172(1–2)**:171–183 DOI 10.1016/0022-0981(93)90096-7.

Cabanillas-Terán N, Hernández-Arana HA, Ruiz-Zárate M, Vega-Zepeda A, Sanchez-González A. 2019. *Sargassum* blooms in the Caribbean alter the trophic structure of the sea urchin *Diadema antillarum*. *PeerJ* **7**:e7589 DOI 10.7717/peerj.7589.

Carpenter KE, Abrar M, Aeby G, Aronson RB, Banks S, Bruckner A, Chiriboga A, Cortés J, Delbeek JC, Devantier L, Edgar GJ, Edwards AJ, Fenner D, Guzmn HM, Hoeksema BW, Hodgson G, Johan O, Licuanan WY, Livingstone SR, Lovell ER, Moore JA, Obura DO, Ochavillo D, Polidoro BA, Precht WF, Quibilan MC, Reboton C, Richards ZT, Rogers AD, Sanciangco J, Sheppard A, Sheppard C, Smith J, Stuart S, Turak E, Veron JE, Wallace C, Weil E, Wood E. 2008. One-third of reef-building corals face elevated extinction risk from climate change and local impacts. *Science* **321(5888)**:560–563 DOI 10.1126/science.1159196.

Carravick J, Smith M, Quincey D. 2016. *Structure from motion in the geosciences.* Chichester: Wiley-Blackwell, 208.143.

Chittaro PM, Kaplan IC, Keller A, Levin PS. 2010. TradeOffs between species conservation and the size of marine protected areas. *Conservation Biology* **24(1)**:197–206 DOI 10.1111/j.1523-1739.2009.01323.x.

Clarke KR, Gorley RN. 2006. *PRIMER v6: user manual/tutorial (plymouth routines in multivariate ecological research).* Plymouth: PRIMER-E.

Clarke KR, Warwick RM. 1994. *Changes in marine communities: an approach to statistical analyses and interpretation.* Plymouth: Natural Environment Research Council.

Colwell RK. 2013. *EstimateS: statistical estimation of species richness and shared species from samples. Version 9.* Storrs: Department of Ecology & Evolutionary Biology, University of Connecticut Persistent URL http://purl.oclc.org/estimates.

Connell JH. 1978. Diversity in tropical rain forests and coral reefs. *Science* **199(4335)**:1302–1310 DOI 10.1126/science.199.4335.1302.

Crabee MJC. 2009. Scleractinian coral population size structures and growth rates indicate coral resilience on the fringing reefs of North Jamaica. *Marine Environmental Research* **67(4–5)**:189–198 DOI 10.1016/j.marenvres.2009.01.003.

Cruz-Vázquez C, Rioja-Nieto R, Enríquez C. 2019. Spatial and temporal effects of management on the reef seascape of a marine protected area in the Mexican Caribbean. *Ocean & Coastal Management* **169(1)**:50–57 DOI 10.1016/j.ocecoaman.2018.12.005.

Edwards C, Yoan E, Gareth W, Pedersen NE, Zgliczynski BJ, Gleason ACR, Smith JE, Sandin SA. 2017. Large-area imaging reveals biologically driven non-random spatial patterns of corals at a remote reef. *Coral Reefs* **36**:1291–1305 DOI 10.1007/s00338-017-1624-3.

English S, Wilkinson C, Baker V. 1997. *Survey manual for tropical marine resources.* Townsville: Australian Institute of Marine Science, 378.

Environmental Systems Research Institute (ESRI). 2017. ArcGIS desktop: release 10.6 Redlands, CA 5A remote sensing of reef environments.

Estrada-Saldívar N, Jordán-Dalhgren E., RodrÃguez-Martìnez RE, Perry C, Alvarez-Filip L 2019. Functional consequences of the long-term decline of reef-building corals in the Caribbean: evidence of across-reef functional convergence. *Royal Society Open Science* **6**:190298 DOI 10.1098/rsos.190298.

Fenner D. 1988. Some leeward reefs and corals of Cozumel, Mexico. *Bulletin of Marine Science* **42**:133–144.

Fenner DP. 1991. Effects of Hurricane Gilbert on coral reefs, fishes, and sponges at Cozumel. exico. *Bulletin of Marine Science* **42(1)**:133–144.

Fenner D. 1999. New observations on the stony coral (Sclerac-tinia, Milleporidae and Stylasteridae) species of Belize (Central America) and Cozumel (Mexico). *Bulletin of Marine Science* **64**:143–154.

Florida Department of Environmental Protection. 2019. Stony coral tissue loss disease response. *Available at* https://floridadep.gov/rcp/coral/content/stony-coral-tissue-loss-disease-response (accessed on October 2019).

Franklin GL, Torres-Freyermuth A, Medellin G, Allende-Arandia ME, Appendini CM. 2018. The role of the reef–dune system in coastal protection in Puerto Morelos (Mexico). *Natural Hazards and Earth System Sciences (NHESS)* **18**:1247–1260 DOI 10.5194/nhess-18-1247-2018.

Gardner TA, Cote IM, Gill JA, Grant A, Watkinson AR. 2003. Long-term regionwide declines in Caribbean corals. *Science* **301**:958–960 DOI 10.1126/science.1086050.

Gilmour JP, Smith LD, Heyward AJ, Baird AH, Pratchett MS. 2013. Recovery of an isolated coral reef system following severe disturbance. *Science* **340(6128)**:69–71 DOI 10.1126/science.1232310.

Gintert B, Gleason ACR, Cantwell K, Gracias N, Gonzalez M, Reid RP. 2012. Third-generation underwater landscape mosaics for coral reef mapping and monitoring. In: *Proceedings of the 12th international coral reef symposium, Cairns, Australia, 9–13 July.*

Gintert BE, Manzello DP, Enochs IC, Kolodziej G, Carlton R, Gleason CR, Gracias N. 2018. Marked annual coral bleaching resilience of an inshore patch reef in the Florida Keys: a nugget of hope, aberrance, or last man standing? *Coral Reefs* **37**:533–547 DOI 10.1007/s00338-018-1678-x.

Glynn PW. 1984. Widespread coral mortality and the 1982–1983 El Niño warming event. *Environmental Conservation* **11(2)**:133–146 DOI 10.1017/S0376892900013825.

Gómez-Anaya JA, Novelo-Gutiérrez R, Ramírez A, Arce-Pérez R. 2014. Using empirical field data of aquatic insects to infer a cut-off slope value in asymptotic models to assess inventories completeness. *Revista Mexicana de Biodiversidad* **85(1)**:218–227 DOI 10.7550/rmb.36978.

González-Barrios FJ, Alvarez-Filip L. 2018. A framework for measuring coral species-specific contribution to reef functioning in the Caribbean. *Ecological Indicators* **95**:877–886 DOI 10.1016/j.ecolind.2018.08.038.

González-Rivero M, Harbone AR, Herrera-Reveles A, Bozec YM, Rogers A, Friedman A, Ganase A, Hoegh-Gulberg O. 2017. Linking fishes to multiple metrics of coral reef structural complexity using three-dimensional technology. *Scientific Reports* **7**:13965 DOI 10.1038/s41598-017-14272-5.

Gotelli NJ, Chao A. 2013. Measuring and estimating species richness, species diversity, and biotic similarity from sampling data. In: Levin SA, ed. *Encyclopedia of biodiversity*. Second Edition. Vol. 5. Waltham: Academic Press, 195–211.

Gotelli NJ, Colwell RK. 2011. Estimating species richness. Chapter 4. In: Magurran AE, McGill BJ, eds. *Biological diversity frontiers in measurement and assessmentin.* New York: Oxford University Press Inc.

Graham NAJ, Nash KL. 2013. The importance of structural complexity in coral reef cosystems. *Coral Reefs* **32**:315–326 DOI 10.1007/s00338-012-0984-y.

Graham RL. 1972. An efficient algorithm for determining the convex hull of a finite planar set. *Information Processing Letters* **1**:132–133 DOI 10.1016/0020-0190(72)90045-2.

Grimsditch G, Pisapia C, Huck M, Karisa J, Obura D, Sweet M. 2017. Variation in size frequency distribution of coral populations under different fishing pressures in two contrasting locations in the Indian Ocean. *Marine Environmental Research* **131**:146–155 DOI 10.1016/j.marenvres.2017.09.017.

Guzmán HM, Burns KA, Jackson JBC. 1994. Injury, regeneration and growth of Caribbean reef corals after a major oil spill in Panama. *Ecology Progress Series* **105**:231–241 DOI 10.3354/meps105231.

Guzman HM, Holst I. 1993. Effects of chronic oil-sediment pollution on the repro-duction of the Caribbean reef coral Slderastrea aderea. *Marine Pollution Bulletin* **26**:276–282 DOI 10.1016/0025-326X(93)90068-U.

Hall VR, Hughes TP. 1996. Reproductive Strategies of modular organisms: comparative studies of reef-building corals. *Ecology* **77(3)**:950–963 DOI 10.2307/2265514.

Harris A, Wilson S, Graham N, Sheppard C. 2014. Scleractinian coral communities of the inner Seychelles 10 years after the 1998 mortality event. *Aquatic Conservation: Marine and Freshwater Ecosystems* **24(5)**:667–679 DOI 10.1002/aqc.2464.

Healthy reefs. 2019. Consultorìa –asistencia tècnica para la ejecuciòn del plan de acciòn del sìndrome blanco en arrecifes del caribe mexicano. *Available at https://www. healthyreefs.org/cms/consultoria-asistencia-tecnica-para-la-ejecucion-del-plan-de-accion-del-sindrome-blanco-en-arrecifes-del-caribe-mexicano/* (accessed on April 2019).

Hellmann JJ, Fowler GW. 1999. Bias, precision, and accuracy of four measures of species richness. *Ecological Applications* **9**:824–834 DOI 10.1890/1051-0761(1999)009[0824:BPAAOF]2.0.CO;2.

Hill J, Wilkinson C. 2004. *Methods for ecological monitoring of coral reefs. Version 1, 1-116.* Townsville: Australian Institute of Marine Science..

Hodgson G, Hill J, Kiene W, Maun L, Mihaly J, Liebeler J, Shuman C, Torres R. 2006. *Instruction manual: a guide to coral reef monitoring.* Pacific Palisades: Reef Check Foundation.

Hoegh-Guldberg O. 1999. Climate change, coral bleaching and the future of the World's coral reefs. *Marine and Freshwater Research* **50**:839–866.

Hoegh-Guldberg O, Mumby PJ, Hooten JA, Steneck RS, Greenfield P, Gomez E, Harvell CD, Sale PF, Edwards AJ, Caldeira K, Knowlton N, Eakin CM, Iglesias-Prieto R, Muthiga N, Bradbury RH, Dubi A, Hatziolos ME. 2007. Coral reefs under rapid climate change and ocean acidification. *Science* **318**:1737–1742 DOI 10.1126/science.1152509.

Hughes TP. 1984. Populations dynamics based on individual size rather than age. *The American Naturalist* **123**:778–795 DOI 10.1086/284239.

Hughes TP, Connell JH. 1987. Dynamics Based on Size or Age? A Reef-Coral Analysis. *The American Naturalist* **129(6)**:818–826 DOI 10.1086/284677.

Hughes TP, Jackson JBC. 1985. Population Dynamics and Life Histories of Foliaceous Corals. *Ecological Monographs* **55(2)**:141–166 DOI 10.2307/1942555.

Hughes TP, Graham NAJ, Jackson JBC, Mumby PJ, Steneck RS. 2010. Rising to the challenge of sustaining coral reef resilience. *Trends in Ecology & Evolution* **25**:633–642 DOI 10.1016/j.tree.2010.07.011.

Hughes TP, Jackson JBC. 1980. Do corals lie about their age? Some demographic consequences of partial mortality, fission, and fusion. *Science* **209**:713–715 DOI 10.1126/science.209.4457.713.

Hughes TP, Jackson JBC. 1985. Population Dynamics and Life Histories of Foliaceous Corals. *Ecological Monographs* **55(2)**:141–166 DOI 10.2307/1942555.

Human P, Deloach N. 2002. *Reef fish identification, Florida, Caribbean, Bahamas.* Jacksonville: New World Publications Inc., 481.

Jackson JBC. 1997. Reefs since Columbus. In: *Proceedings of the Eighth International Coral Reef Symposium, 1.* 97–106.

Jackson JBC, Donovan MK, Cramer KL, Lam VV (eds.) 2014. *Status and trends of Caribbean coral reefs: 1970–2012.* Gland: Global Coral Reef Monitoring Network, IUCN DOI 10.13140/2.1.4868.6726.

Jaramillo-González J, Acosta A. 2009. Comparación temporal en la estructura de una comunidad coralina en primeros estados de sucesión, Isla de San Andrés, Colombia. *Boleín de Investigaciones Marinas y Costeras* **38(2)**:29–53.

Jiménez-Valverde A, Hortal J. 2003. Las curvas de acumulación de especies y la necesidad de evaluar la calidad de los inventarios biológicos. *Revista Ibérica de Aracnología* **8**:151–161.

Jordán E. 1988. Arrecifes profundos de Cozumel. *Anales del Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma, Mèxico* **15(2)**:195–208.

Jordán-Dahlgren E, Rodríguez-Martínez RE. 2003. The Atlantic coral reefs of Mexico. In: Cortés J, ed. *Latin American coral reefs.* Amsterdam: Elsevier Science, 131–158 DOI 10.1016/B978-044451388-5/50007-2.

Kenyon JC, Vroom PS, Page KN, Dunlap MJ, Wilkinson CB, Aeby GS. 2006. Community structure of hermatypic corals at French Frigate Shoals, Norhtwestern Hawaiian Island: Capacity for resistance and resilience to selective stressors. *Pacific Science* **60**:153–175 DOI 10.1353/psc.2006.0006.

Kirkpatrick DG, Seidel R. 1986. The ultimate planar convex hull algorithm. *SIAM Journal on Computing* **15(1)**:287–299 DOI 10.1137/0215021.

Knowlton N. 2001. The future of coral reefs. *Proceedings of the National Academy of Sciences of the United States of America* **98(10)**:5419–5425 DOI 10.1073/pnas.091092998.

Kramer PA. 2003. Synthesis of coral reef health indicators for the western Atlantic: results of the AGRRA program (1997–2000). Atoll Res. Bull. In: Lang JC, ed. *Status*

of coral reefs in the Western Atlantic: results of initial surveys, Atlantic and Gulf Rapid Reef Assessment (AGRRA) program. 496: Atoll Research Bulletin 1–55.

Lang JC, Marks KW, Kramer PA, Kramer PR, Ginsburg RN. 2010. AGRRA protocols version 5.4. *Available at* http://www.agrra.org/method/methodhome.html.

Lewis JB. 1997. Abundance, distribution and partial mortality of the massive coral Siderastrea siderea on degrading coral reefs at Barbados, West Indies. *Marine Pollution Bulletin* **34**:622–627 DOI 10.1016/S0025-326X(96)00184-1.

Lirman D, Gracias N, Gintert B, Gleason A, Reid R, Negahdaripour S, Kramer P. 2007. Development and application of a video-mosaic survey technology to document the status of coral reef communities. *Environmental Monitoring and Assessment* **125**:59–73 DOI 10.1007/s10661-006-9239-0.

Longuet-Higgins HC. 1981. A computer algorithm for reconstructing a scene from two projections. *Nature* **293**(5828):133–135 DOI 10.1038/293133a0.

Loreto-Viruel RM, Merediz-Alonso G, García-Beltran G, Bezaury-Creel JE, Loreto-Viruel A, Hernández-Siller A, Lazcano-Barrero MA. 2017. Amigos de Sian Ka'an. Serie documentos "Arrecifes Insulares" de quintana roo. DOI 10.13140/RG.2.2.26614.29763.

Loya Y. 1972. Community structure and species diversity of hermatypic corals at Eliat, Red Sea. *Marine Biology* **13**:100–123 DOI 10.1007/BF00366561.

Loya Y. 1976. Settlement, mortality and recruitment of a red sea scleractinian coral population. In: Mackie GO, ed. *Coelenterate ecology and behavior*. Boston: Springer DOI 10.1007/978-1-4757-9724-4_10.

Ma MH, Tarmi S, Helenius J. 2002. Revisiting the species–area relationship in a semi-natural habitat: floral richness in agricultural buffer zones in Finland. *Agriculture, Ecosystems & Environment* **89**:137–148 DOI 10.1016/S0167-8809(01)00325-5.

McClanahan TR, Ateweberhan M, Omukoto J. 2008. Long-term changes in coral colony size distributions on Kenyan reefs under different management regimes and across the 1998 bleaching event. *Marine Biology* **153**:755–768 DOI 10.1007/s00227-007-0844-4.

McField M, Kramer P, Álvarez Filip L, Drysdale I, Rueda-Flores M, Giró-Petersen A, Soto M. 2018. 2018 Report card for the mesoamerican reef. Healthy reefs initiative (http://www.healthyreefs.org). DOI 10.13140/RG.2.2.19679.36005.

Meesters EH, Hilterman M, Kardinaal E, Keetman M, DeVires M, Bak RPM. 2001. Colony size-frequency distributions of scleractinian coral populations: spatial and interspecific variation. *Marine Ecology Progress Series* **209**:43–54 DOI 10.1016/j.marenvres.2017.09.017.

Meesters EH, Wesseling I, Bak RPM. 1997. Coral colony tissue damage in six species of reef-building corals: partial mortality in relation with depth and surface area. *Journal of Sea Research* **37**(1–2):131–144 DOI 10.1016/S1385-1101(96)00004-4.

Moberg F, Folke C. 1999. Ecological goods and services of coral reef ecosystems. *Ecological Economics* **29**:215–233 DOI 10.1016/S0921-8009(99)00009-9.

Moreno CE, Halffter G. 2000. Assessing the completeness of bat biodiversity inventories using species accumulation curves. *Journal of Applied Ecology* **37**:149–158 DOI 10.1046/j.1365-2664.2000.00483.x.

Moreno CE, Halffter G. 2001. On the measure of sampling effort used in species accumulation curves. *Journal of Applied Ecology* **38**:487–490 DOI 10.1046/j.1365-2664.2001.00590.x.

Muckelbauer G. 1990. The shelf of cozumel, mexico: topography and organisms. *Facies* **23(1)**:185–200 DOI 10.1007/BF02536713.

Mumby PJ, Harborne AR. 2010. Marine reserves enhance the recovery of corals on caribbean reefs. *PLOS ONE* **5(1)**:e8657 DOI 10.1371/journal.pone.0008657.

Obura DO, Grimsdith G. 2009. Resilience assessment of coral reefs—assessment protocol for coral reefs, focusing on coral bleaching and thermal stress. In: *IUCN working group on climate change and coral reefs.* Gland: IUCN, 70.

Pareja-Ortega S, Quan-Young L. 2016. Evaluación de la gametogénesis y fecundidad de corales escleractinios: orbicella annularis, pseudodiploria strigosa y siderastrea siderea, en Isla Fuerte (Bolívar), Colombia. *Actualidades Biológicas* **38(104)**:5–13 DOI 10.17533/udea.acbi.v38n104a01.

Pix4D. 2019a. *Available at https://support.pix4d.com/hc/en-us/articles/205360375-How-to-scale-a-project* (accessed on March 2019).

Pix4D. 2019b. *Available at https://support.pix4d.com/hc/en-us/sections/200591059-Manual* (accessed on March 2019).

Porter JW. 1972. Patterns of species diversity in Caribbean Coral Reefs. *Ecology* **53(4)**:668–673 DOI 10.2307/1934781.

Precht WF, Gintert BE, Robbart ML, Fura R, Van Woesik R. 2016. Unprecedented disease-related coral mortality in Southeastern Florida. *Scientific Reports* **6**:31374 DOI 10.1038/srep31374.

Raeaka-Kudla ML. 1997. The global biodiversity of coral reefs: a comparison with rainforest. In: Reaka-Kudla ML, Wilson DE, Wilson EO, eds. *Biodiversity II: understanding and protection our natural resources.* Washington: Joseph/National Academy Press, 83–108.

Reyes-Bonilla H, Millet-Encalada M, Álvarez Filip L. 2014. Community structure of scleractinian corals outside Protected Areas in Cozumel Island, Mexico. *Atoll Research Bulletin* **601(601)**:1–16 DOI 10.5479/si.00775630.600.

Richardson LL, Voss JD. 2005. Changes in a coral population on reefs of the northern Florida Keys following a coral disease epizootic. *Marine Ecology Progress Series* **297**:147–156 DOI 10.3354/meps297147.

Richmond RH, Hunter CL. 1990. Reproduction and recruitment of corals: comparisons among the Caribbean, the Tropical Pacific, and the Red Sea. *Marine Ecology Progress Series* **60**:185–203, 19 DOI 10.3354/meps060185.

Rinkevich B, Loya Y. 1986. Senescence and dying signals in a reef building coral. *Experientia* **42**:320 DOI 10.1007/BF01942521.

Rioja-Nieto R, Chiappa-Carrara X, Sheppard C. 2012. Effects of hurricanes on the stability of reef—associated landscapes. *Ciencias Marinas* **38(1a)**:47–55.

Rioja-Nieto R, Álvarez Filip L. 2018. Coral reef systems of the Mexican Caribbean: Status, recent trends and conservation. *Marine Pollution Bulletin* **140(2019)**:616–625 DOI 10.1016/j.marpolbul.2018.07.005.

Rioja-Nieto R, Sheppard C. 2008. Effects of management strategies on the landscape ecology of a Marine Protected Area. *Ocean & Coastal Management* **51(5)**:397–404 DOI 10.1016/j.ocecoaman.2008.01.009.

Rogers CS. 1990. Responses of coral reefs and reef organisms to sedimentation. *Marine Ecology Progress Series* **62**:185–202 DOI 10.3354/meps062185.

Rossi P, Castagnetti C, Capra A, Brooks AJ, Mancini F. 2019. Detecting change in coral reef 3D structure using underwater photogrammetry: critical issues and performance metrics. *Applied Geomatics* 1–15 DOI 10.1007/s12518-019-00263-w.

Royer JP, Nawaf MM, Merad D, Saccone M, Bianchimani O, Garrabou J, Ledoux J-B, Lopez-Sanz A, Drap P. 2018. Photogrammetric Surveys and Geometric Processes to Analyse and Monitor Red Coral Colonies. *Journal of Marine Science and Engineering* **6**:42 DOI 10.3390/jmse6020042.

Smith LD, Devlin M, Haynes D, Gilmour JP. 2005. A demographic approach to monitoring the health of coral reefs. *Marine Pollution Bulletin* **51(2005)**:399–407 DOI 10.1016/j.marpolbul.2004.11.021.

Smith MW, Carrivick JL, Quincey DJ. 2015. Structure from motion photogrammetry in physical geography. *Progress in Physical Geography: Earth and Environment* **40(2)**:247–275 DOI 10.1177/0309133315615805.

Sociedad Mexicana de Arrecifes Coralinos. 2015. *Available at* http://www.somac.gov.mx (accessed on September 2019).

Sokal RR, Rohlf FJ. 1995. *Biometry: the principles and practice of statistics in biological research*. Third Edition. New York: W.H. Freeman and Co.

Soong K. 1993. Colony size as a species character in massive reef corals. *Coral Reefs* **12**:77–83 DOI 10.1007/BF00302106.

Soong K, Lang JC. 1992. Reproductive integration in reef corals. *The Biological Bulletin* **183(3)**:418–431 DOI 10.2307/1542018.

StatSoft, Inc. 2011. STATISTICA (data analysis software system), version 10. *Available at* http://www.statsoft.com.

Szmant AM. 1986. Reproductive ecology of Caribbean reef corals. *Coral Reefs* **5**:43–53 DOI 10.1007/BF00302170.

Szmant-Froelich A, Reutter M, Riggs L. 1985. Sexual reproduction of Favia fragum (esper): Lunar patterns of gametogenesis, embryogenesis and planulation in Puerto Rico. *Bulletin of Marine Science* **37(3)**:880–892.

Turner JA, Polunin NVC, Field SN, Wilson SK. 2015. Measuring coral size-frequency distribution using stereo video technology, a comparison with in situ measurements. *Environmental Monitoring and Assessment* **187**:234–244 DOI 10.1007/s10661-015-4431-8.

Van Woesik R, Randall CJ. 2017. Coral disease hotspots in the Caribbean. *Ecosphere* **8(5)**:Article e01814 DOI 10.1002/ecs2.1814.

Vermeij MJA, Bak RPM. 2003. Species-specific population structure of closely related coral morphospecies along a depth gradient (5–60 m) over a Caribbean reef slope. *Bulletin of Marine Science* **73(3)**:725–744.

Victor S, Golbuu Y, Yukihira H, Van Woesik R. 2009. Acropora size-frequency distributions reflect spatially variable conditions on coral reefs of Palau. *Bulletin of Marine Science* **85**:149–157.

Walther BA, Moore JL. 2005. The concepts of bias, precision and accuracy, and their use in testing the performance of species richness estimators, with a literature review of estimator performance. *Ecography* **28(6)**:815–829 DOI 10.1111/j.2005.0906-7590.04112.x.

Weil E, Croquer A, Urreiztieta I. 2009. Yellow band disease compromises the reproductive output of the Caribbean reef-building coral Montastrea faveolata (Anthozoa, Scleractinia). *Diseases of Aquatic Organisms* **87(1–2)**:45–55 DOI 10.3354/dao02103.

Westoby MJ, Brasington J, Glasser NF, Hambrey MJ, Reynolds JM. 2012. 'Structure-from-Motion' photogrammetry: a low-cost, effective tool for geoscience applications. *Geomorphology* **179(2012)**:300–314 DOI 10.1016/j.jembe.2005.12.009.

Zar JH. 1999. *Biostatistical analysis*. Fourth Edition. Upper Saddle River: Prentice Hall.