

Newcastle University

MSc in Tropical Coastal Management

MST8005 Research in Coastal Management

2009-10

Paper

**The Influence of Coral Colony Definitions on the Outcomes of Colonial Scleractinian
Size Frequency Distribution Studies**

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Marine Ecology Progress Series

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The Influence of Coral Colony Definition on the Outcomes of Colonial Scleractinian Size Frequency Distribution Studies

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Abstract: Coral colony size frequency distributions are increasingly popular as a method of reviewing and monitoring coral populations. Colonial corals can exhibit partial mortality, forcing studies which measure colony size to define exactly what is meant by an individual colony. This study calculated size frequency distributions for massive *Porites* populations inside and outside the Napantao Fish Sanctuary Marine Protected Area (MPA) in Sogod Bay, Philippines, and in an intermediate zone. Three definitions of colony were used. Under the first, colony size was measured as the total skeletal surface area regardless of partial mortality. Under the second, only the area of living tissue was included for each contiguous skeleton. Under the third, patches of living tissue more than 3cm apart were treated as separate colonies even if occupying the same skeleton. Conclusions about the differences between the populations inside and outside the MPA were dependent on the definition used, highlighting the importance of this decision in such studies. It is possible that this methodological choice influences the effectiveness of a study in detecting specific demographic changes within coral populations, such as increased incidence of partial mortality or reduced recruitment. Size frequency distribution sampling regimes may benefit from measuring colonies in more than one way.

Key Words: Scleractinian • Population structure • Experimental design • Size-frequency distribution • Partial mortality

INTRODUCTION

Coral reef ecosystems are being degraded globally as a result of human activities (Pandolfi *et al* 2003). Percentage cover and biodiversity of hard corals have both been used extensively as reef health monitoring methods since such investigations began (Brown 1988). Until comparatively recently, the range and relative frequency of colony sizes within coral populations had been less widely used as a source of information for such studies (Bak & Meesters 1998; although see e.g. Hughes 1984, Babcock 1991). Scleractinian size frequency distributions are now generally considered to contain pertinent information about demographic processes and therefore the health of coral reefs, and have featured in studies into, for example, the effects of epizootic disease outbreak (Richardson & Voss 2005); the effects of large-scale bleaching events (McClanahan *et al* 2008); and the effectiveness of marine reserves (Mumby & Harbourne 2010). Size frequency distributions have also been compared between species (e.g. Meesters *et al* 2001), reproductive modes (Vermeij *et al* 2007, Nozawa *et al* 2008) and locations (e.g. Oigman-Pszczol & Creed 2004; Adjeroud *et al* 2007; Guzner *et al* 2007; Crabbe 2009).

The sampling techniques used to collect the data for size frequency distributions vary between studies. Three aspects of the experimental design in particular have the potential to introduce error into results by misrepresenting the proportions of small and large colonies. The first of these is the treatment of colonies which fall partly inside and partly outside the study area. As the probability of a colony crossing an edge of the survey area increases with colony size, the decision to include or exclude all such colonies will skew the size frequency distribution. The mathematics of this issue, including proposed solutions, have been covered elsewhere (Zvuloni *et al* 2008).

A second issue relates to the specific measurements taken, and the way in which they are used to calculate a comparative size for each colony. Many studies approximate colonies to simple geometric shapes, which is an accurate method for approximating surface area for most coral genera (Naumann *et al* 2009). Some size frequency distributions are based on measurements other than surface area such as geometric mean radius (Guzner *et al* 2007), maximum linear dimension (Smith *et al* 2005, Elahi & Edmunds 2007), width of colony intercepted by line transect (McClanahan *et al* 2008) or an alternative size index formulated by the author (Oigman-Pszczol & Creed 2004).

The third important aspect of experimental design which varies between studies is the result of the colonial nature of most scleractinians. The population dynamics of colonial corals are affected not only by recruitment, growth and mortality, but also by fission, partial mortality, and fragmentation (Hughes & Jackson 1985). That coral size is decoupled from coral age is not necessarily a limitation in itself, as many biotic and abiotic processes appear to be better related to colony size than colony age (Meesters *et al* 2001). However, partial mortality can lead to separate patches of living tissue on one coral head. In such cases, samplers must decide whether the area to be measured includes the entire coral skeleton; the total living surface area on the entire skeleton; or each separate patch of living tissue individually.

The purpose of this study was to attempt to quantify the influence which this last decision might have on the results of size frequency distribution studies, in relation to the influence of such factors on coral demography as might be examined using such techniques. Specifically, colony size measurements were taken from spatially proximate sites under different levels of marine protection using each of the colony definitions described above. Differences between the methodologies are examined in the context of differences between levels of protection.

The Napantao Fish Sanctuary is a Marine Protected Area (MPA) covering approximately 5 hectares of coral reef habitat on the east coast of Sogod Bay in the Philippines. Established by the Southern Leyte Provincial Government in 1996, the MPA is enforced by “Bantay Dagat” (lit. Fish Guardian) teams from the local community (Coral Cay 2010). All forms of fishing, anchoring and speedboat use are banned, and divers must pay a small fee to dive within the MPA. The MPA is surrounded by a 25m-wide buffer zone, within which line fishing only is permitted. The waters outside this buffer zone are subject to destructive fishing practices and anchoring.

Massive species of the *Porites* genus were selected as the study taxon as the simple shape makes partial mortality comparatively easy to identify and measure. Although the individual species of massive *Porites* cannot be distinguished in situ (Adjeroud *et al* 2007), as a taxonomic group it is readily identified and has been used in previous size frequency studies (e.g. McClanahan *et al* 2008, Adjeroud *et al* 2007). The species of massive *Porites*

known to be present in the Philippines include *P. lobata*, *P. lutea*, *P. australiensis*, *P. solida* and *P. mayeri* (Raymundo *et al* 2005).

METHODS

Study Sites

Sogod Bay is a major geographical feature of Southern Leyte province in the Eastern Visayas region of the Philippines. Surveys were carried out in and around the Napantao MPA (10° 3' 57.54" N; 125° 8' 2.10" E) on the east coast of the bay (Fig. 1).

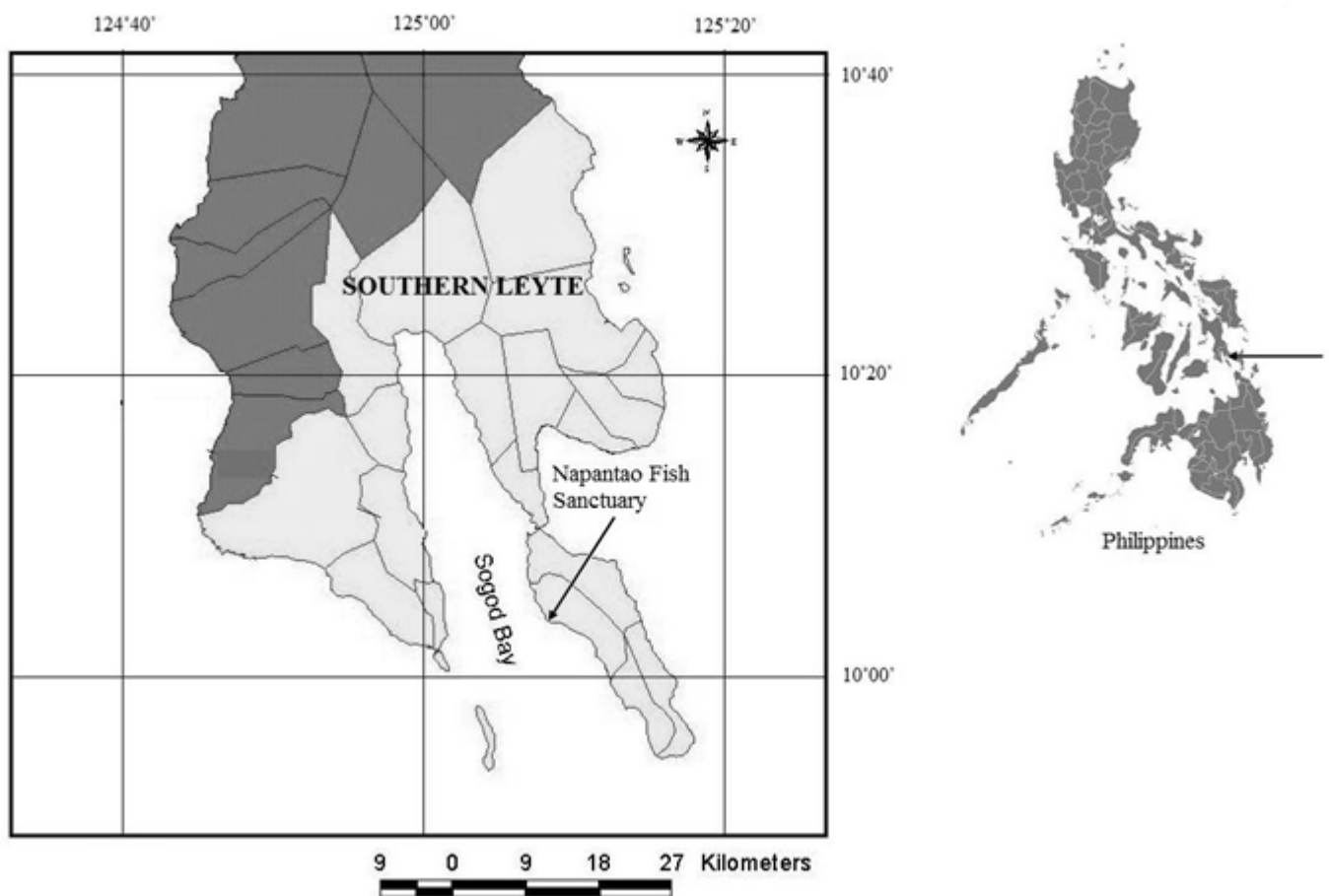


Figure 1. Location of the study area within the Philippines. The lighter area is the province of Southern Leyte. (Source: Coral Cay 2008).

The boundaries of the MPA defined the first site (referred to hereafter as ‘fully protected’), within which all forms of fishing and anchoring have been banned for 14 years. For 25m north of the MPA, line fishing only is allowed – this area defined the second site (referred to hereafter as ‘partially protected’). North of this 25m swath is subject to destructive fishing practices, and formed the third site (referred to hereafter as ‘unprotected’).

Survey Methods

A series of 1 x 20m haphazardly positioned belt transects were carried out parallel to the shore to a maximum depth of 5m. Ten transects were conducted at the fully protected and unprotected sites. Due to the small size of the site, only five transects were conducted at the partially protected site.

Measurements were taken to the nearest cm using a tape measure of any live massive *Porites* colony at least partially within the transect. Three initial measurements were taken for every colony, and included the entire skeleton: widest horizontal diameter (r_1); widest horizontal diameter in the direction perpendicular to the first measurement (r_2); and maximum height (r_3).

Colony surface areas were calculated using three different definitions of colony. For the first approach, referred to hereafter as 'total', a colony was considered to include the entire contiguous skeleton. Surface area was calculated by approximating the shape of the colony to a semi-ellipsoid using the following formula:

$$SA = \frac{2\pi r_1 r_2 r_3}{3}$$

Where r_1 = r_2 ; r_2 = r_3 ; r_1 = r_2 ; r_1 = r_3 (Klamkin 1971).

The second approach, referred to hereafter as 'summed', defined the surface area of a colony as the total surface area of living tissue on a contiguous skeleton. Where a colony had patches of partial mortality, the surface area of these patches was subtracted from the total area calculated above. Where a colony had patches of living tissue, the surface area of these was totalled. Patches of partial mortality and patches of living tissue were treated as two-dimensional, and measured in the widest dimension and perpendicular to the widest dimension. The area of such patches was approximated by multiplying together the two measurements taken. Where a colony exhibited no partial mortality, the surface area was calculated as above.

The third approach, referred to hereafter as 'separate', considered any patches of living tissue more than 3cm apart to be distinct individuals even if occupying the same skeleton. The surface area of colonies without partial mortality, or without patches of living tissue more than 3cm from any other living tissue, was calculated as above.

Analysis

The data were treated as nine separate datasets, one for each methodology at each site. Logarithmic transformation of colony size data increases resolution of smaller size classes, produces a more useful graphical representation of the data, and produces distributions which can be compared within and between species (Vermeij & Bak 2002). Normality of ln-transformed data was tested using the Shapiro-Wilk test. The distributions of ln-transformed datasets were compared between sites and between methodologies using the Kolmogorov-Smirnov 2-way test.

Non-transformed data also contains useful information about population demographics. Descriptive statistics were calculated for each set prior to transformation, including mean, skewness, and coefficient of variation. All statistical analyses were conducted using MyStat 12 (SYSTAT Software inc. 2007).

RESULTS

Characteristics of ln-Transformed Data

After ln transformation, all nine datasets became negatively skewed, representing a higher proportion of samples in the larger size classes (Table 1). Data from the fully protected site was the least negatively skewed under all methodologies, and data from the partially protected site was the most negatively skewed under all methodologies. Skewness also varied within sites under different methodologies (Figure 2).

Using the Shapiro-Wilks normality test, the transformed data from the fully protected site were normally distributed under the ‘total’ and ‘summed’ methodologies. The transformed data from the partially protected and unprotected sites were not normally distributed under any methodology (Table 1).

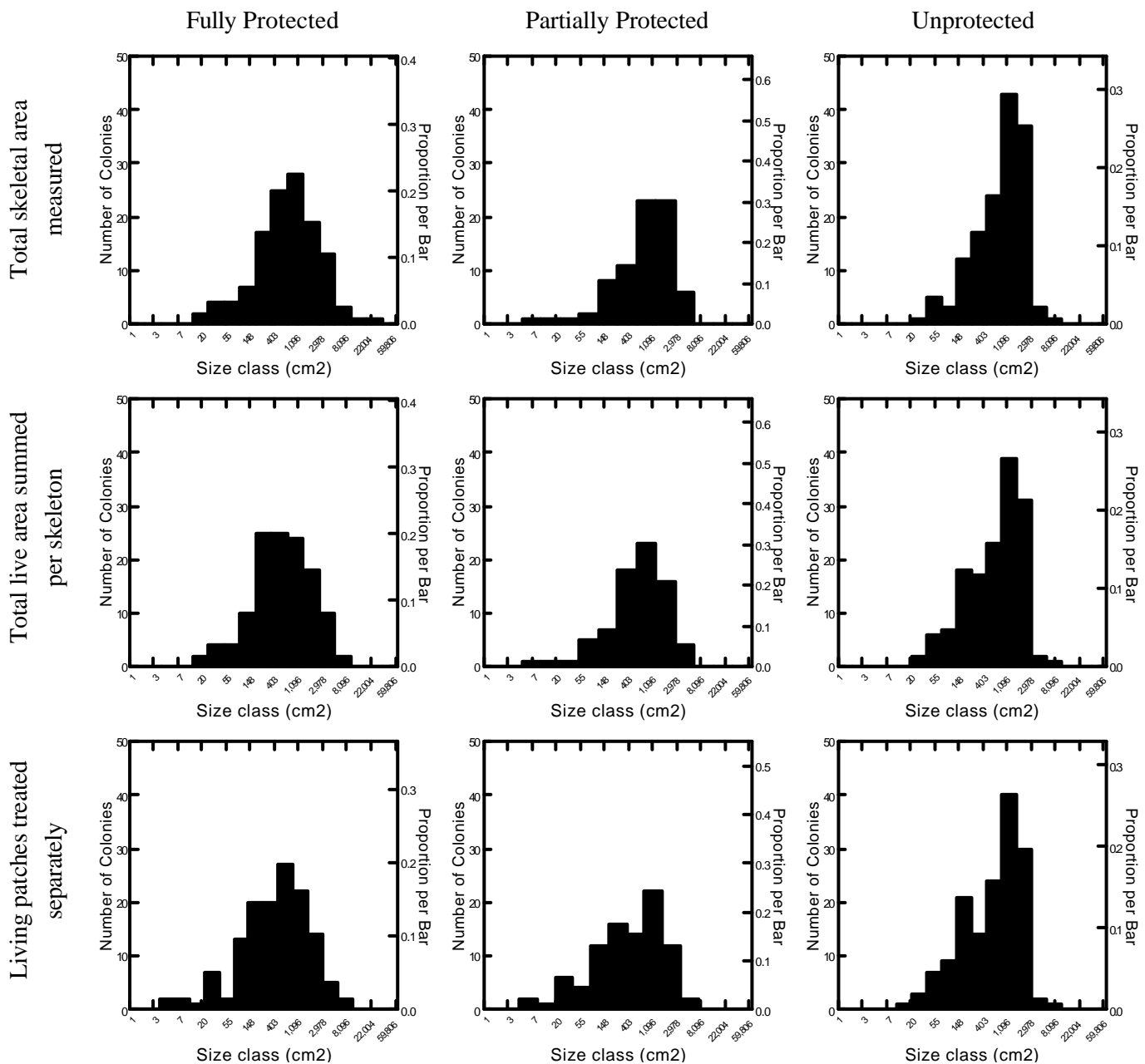


Figure 2. *Porites* spp. Size frequency distributions of colonies collected from fully protected, partially protected and unprotected populations under three different methodologies. Note logarithmic size classes.

Table 1. *Porites spp.* Descriptive statistics for ln-transformed colony size data. g_1 : skewness; norm: p-value of Shapiro-Wilks normality test; n: number of colonies. FP = Fully Protected; PP = Partially Protected; UP = Unprotected.

Methodology	Site	g_1	norm	n
<i>total</i>	FP	-0.236	0.566	124
	PP	-1.445	0.000	76
	UP	-0.935	0.000	146
<i>summed</i>	FP	-0.303	0.345	124
	PP	-1.145	0.000	76
	UP	-0.685	0.000	146
<i>separate</i>	FP	-0.742	0.001	137
	PP	-0.800	0.001	91
	UP	-0.752	0.000	152

The distributions were compared using the Kolmogorov-Smirnov (K-S) 2-way test. Due to the nature of the K-S test, results are identical whether using transformed or untransformed data. The results are divided into comparisons between methodologies and comparisons between sites.

Comparisons Between Methodologies

The differences between methodologies were site-specific (Table 2). There were significant differences between the ‘total’ and ‘separate’ methodologies at the fully and partially protected sites, and between the ‘summed’ and ‘separate’ methodologies at the partially protected site. There was no significant difference between methodologies at the unprotected site.

Table 2. *Porites spp.* p-values resulting from Kolmogorov-Smirnov test comparison of the distributions of the ln-transformed data from each site under different experimental methodologies. FP = Fully Protected; PP = Partially Protected; UP = Unprotected. ‘*’ indicates that the distributions produced by the two methodologies are significantly different at 95%.

	FP		PP		UP	
	total	summed	total	summed	total	summed
summed	0.714	n/a	0.404	n/a	0.424	n/a
separate	0.019*	0.324	0.000*	0.028*	0.098	0.944

Comparisons Between Sites

The differences between sites were affected by the methodology used in one instance (Table 3). Under all methodologies, there was a significant difference between the partially protected and unprotected sites, and no significant difference between the fully and partially protected sites; however there was a significant difference between the fully protected and unprotected sites under the ‘total’ methodology only.

Table 3. *Porites spp.* p-values resulting from Kolmogorov-Smirnov test comparison of the distributions of the ln-transformed data from each methodology at different sites. FP = Fully Protected; PP = Partially Protected; UP = Unprotected. '**' indicates that the distributions from the two sites are significantly different at 95%.

	total		summed		separate	
	FP	PP	FP	PP	FP	PP
PP	0.167	n/a	0.597	n/a	0.901	n/a
UP	0.019*	0.000*	0.147	0.000*	0.082	0.006*

Characteristics of Untransformed Data

Mean colony surface area varied between 780cm² and 1415cm² across all sites and methodologies (Table 4). At all sites, the mean colony surface area was smallest under the 'separate' methodology and largest under the 'total' methodology. Of the three sites, fully protected had the largest mean colony surface area under the 'total' methodology, while unprotected had the largest mean colony surface area under both the 'separate' and 'summed' methodologies.

All untransformed size frequency distributions were positively skewed at all sites, representing a high proportion of smaller colonies. The distribution from the fully protected site was the most positively skewed under all three methodologies (Table 4). The unprotected site showed comparatively little difference in skewness between methodologies (ranging from 1.350 – 1.570), the partially protected site showed some variation (ranging from 0.869 – 1.554) and the fully protected site showed most variation in skewness (ranging from 2.448 – 6.103).

Coefficient of variation was greatest at the fully protected site under all methodologies, with the largest difference under the 'total' methodology. Data from the partially protected and unprotected sites exhibited comparatively similar coefficients of variation (Table 4).

A total of 346 colonies were measured under the 'total' and 'summed' methodologies. Of these, 124 were at the fully protected site, 76 at the partially protected site, and 146 at the unprotected site. The total number of colonies increased to 380 colonies under the 'separate' methodology (Table 4).

Table 4. *Porites spp.* Descriptive statistics for untransformed colony size data. μ : mean colony surface area (cm²); g_1 : skewness; g_2 : kurtosis; CV: coefficient of variation; n: number of colonies. FP = Fully Protected; PP = Partially Protected; UP = Unprotected.

Methodology	Site	μ	g_1	g_2	CV	n
<i>total</i>	FP	1415	6.103	48.686	1.809	124
	PP	1163	0.869	0.180	0.781	76
	UP	1182	1.350	3.669	0.761	146
<i>summed</i>	FP	984	2.448	7.100	1.198	124
	PP	934	1.394	1.858	0.892	76
	UP	1043	1.539	4.589	0.854	146
<i>separate</i>	FP	891	2.574	7.910	1.291	137
	PP	780	1.554	2.298	1.061	91
	UP	1002	1.570	4.674	0.887	152

Summary of Transect Results

The mean skeletal area per transect was similar across all three sites (Table 5). The mean area of partial mortality per transect at the fully protected site was more than double that at the unprotected site. The partially protected site averaged the highest number of colonies per transect under all methodologies, and the fully protected site the most.

Table 5. *Porites* spp. Summary of transect results for each site.

	Site		
	Fully Protected	Partially Protected	Unprotected
Number of transects	10	5	10
Mean colonies / transect (total/summed)	12.4	15.2	14.6
Mean colonies / transect (separate)	13.7	18.2	15.2
Mean skeletal area / transect	17,549 cm ²	17,676 cm ²	17,270 cm ²
Mean living tissue / transect	12,205 cm ²	14,201 cm ²	15,227 cm ²
Mean partial mortality / transect	5,344 cm ²	3,475 cm ²	2,043 cm ²

DISCUSSION

One use of size frequency distributions has been to compare coral populations over space or time. The results of this study show that it is possible for the outcome of such comparisons to be influenced by experimental design decisions. The size frequency distribution of massive *Porites* colonies inside the Napantao MPA does not appear significantly different to that of the colonies in nearby unprotected waters when only living tissue is measured. There is, however, a significant difference between the distributions when the surface area of the entire skeleton is included (Table 3).

Under the ‘total’ methodology, the size frequency distribution of the fully protected colonies appears to be normally distributed (Table 1), indicating that more than half of colonies are in or above the modal size class. The distribution from the unprotected area has the same modal size class but shows fewer colonies larger than this class, and is correspondingly non-normal and more negatively skewed.

The difference between the two distributions found under the ‘total’ methodology therefore appears to be the result of an absence of larger colonies in the unprotected area. It has been suggested that partial mortality only is only an important phenomenon in larger colonies, becoming enormously more prevalent in colonies larger than the modal size class of a log-transformed size frequency distribution (Bak & Meesters 1998). There may be a lower incidence of partial mortality in the unprotected area due to the comparatively small number of colonies above the modal size class. That the colonies in the MPA exhibited more than twice the area of mortality per transect than those in the unprotected area (Table 4) is consistent with this hypothesis.

The ‘summed’ and ‘separate’ methodologies effectively treat large colonies with a high proportion of partial mortality as small colonies. The large colonies which make up the difference between the two distributions under the ‘total’ methodology might therefore be treated as small colonies under the other methodologies, reducing the difference between the distributions and altering the conclusions of the study.

The characteristics of the untransformed distributions agree with the result of many other size frequency distribution studies that coral population structure tends to be positively skewed (e.g. Meesters *et al* 2001; Elahi & Edmunds 2007; McClanahan *et al* 2008). An unresolved issue in the literature is whether increased stress affects coral size frequency distributions in a predictable way. In particular, whether stresses such as fishing, bleaching, disease, sedimentation and a marginal environment cause an increase in negative skewness and mean colony size (e.g. Bak & Meesters 1999, Meesters *et al* 2001) or a reduction in both (e.g. Fong & Glynn 1998, Oigman-Pszczol & Creed 2004; McClanahan *et al* 2008). The former would suggest that such stresses have a greater impact on small colonies or recruitment, the latter that large colonies are more seriously affected. Alternatively, such changes in the size frequency distribution of a population could conceivably depend on the specific combination of stresses, or be unrelated to stress in any predictable way.

The results of the ‘total’ methodology suggest a significant difference between the MPA and unprotected areas, with the unprotected population exhibiting a more negative skewness. However, although it seems likely that the unprotected site is subject to greater fishing pressure and physical damage, it is entirely possible that this does not translate into greater stress for massive *Porites* populations. As it is uncertain whether the two populations are under different levels of stress, it is not possible to speculate on which of the two hypotheses described above these results support.

The partially protected population does not appear significantly different to that inside the MPA under any methodology, but is significantly different to the unprotected population under all methodologies. Although this does not provide any evidence for the health of the populations, it does suggest that the differences between inside and outside the MPA may be related to physically destructive processes rather than the removal of fish – the partially protected site is fished, but not using destructive techniques. However, firm conclusions cannot be made due to the small size of the site and limited number of transects conducted.

The partially protected site showed the largest proportional increase in number of colonies under the ‘separate’ methodology (up to 91 from 76, Table 4). This represents a relatively high number of colonies divided by partial mortality into patches of living tissue more than 3cm apart, and may explain why the partially protected site showed significant differences between the ‘separate’ and ‘summed’ methodologies when the other sites did not (Table 2).

One factor influencing the choice of colony definition is the potential for sampler error in the field. It is often difficult to determine the extent of an individual skeleton, due to the potential for fusion, mechanical fragmentation, or erosion of areas which have undergone partial mortality. Under the ‘total’ and ‘summed’ methodologies, colony boundary definition is open to sampler bias. The ‘separate’ methodology more clearly defines the edge of colonies by setting a maximum distance between patches before they are considered separate, giving samplers a measurable rule to follow. Under all three methodologies, the sampler may potentially misidentify species. As transects were positioned haphazardly, there was also potential for sampler bias in the positioning of transect start locations. Finally, the smaller the colony the higher the chance it will not be observed by the sampler, leading to a possible under-representation of small colonies in any size frequency distribution study; this in particular is a potential source of error in the present study as sites were surveyed by snorkelling.

In addition to sampler bias, the proportion of smaller colonies may be underestimated by the inclusion of all colonies overlapping transect edges. Such colonies were included to maximise the number of colonies analysed; however large colonies are more likely to extend over the transect edge and so will be overrepresented by such a methodology (Zvuloni *et al* 2008). A final source of error is the equation used to calculate colony surface areas. It is possible that larger colonies are less accurately represented by a semi-ellipsoid than small colonies, although the effects of this error source are difficult to ascertain. As noted above, simple geometric shapes generally provide accurate estimates of colony surface area (Naumann *et al* 2009).

Size frequency distribution studies operate on the assumption that such distributions contain useful information about demographic processes in coral populations. There is some disagreement as to whether size is well correlated with age in colonial corals (Bak & Meesters 1998), although some life history characteristics such as growth rates (Elahi & Edmunds 2007) and partial mortality (Vermeij & Bak 2002) may be better correlated with size in any case.

The differences between the distributions produced by the three definitions of colony reflect the demographic processes which they are incorporating. For example, the ‘total’ methodology ignores partial mortality entirely (except where it is the cause of fragmentation, as described above), and yet in this study revealed differences between populations which were not detected by the other methodologies. The ‘summed’ methodology potentially reduces the correlation between size and age by not distinguishing between small, healthy colonies and large colonies with partial mortality. However, given the importance of partial mortality as a demographic process, and the possibility that area of living tissue is a better indicator of many aspects of coral health than age, the size distributions produced in this way may be more useful. The ‘separate’ methodology further decouples size and age in a theoretical sense, but is conceivably the colony definition with the lowest probability of sampler bias.

CONCLUSIONS

This study shows that the results of size frequency distribution studies can be significantly influenced by fundamental and often overlooked experimental design decisions. Care must be taken when comparing studies which were carried out using different definitions of colony. Due to the complexity of coral life history processes, it can be difficult to extract meaningful demographic information from size frequency distributions. It may be beneficial for future studies to utilise multiple definitions of colony to maximise the information gathered about populations and allow a broader analysis. For example, by carrying out the ‘summed’ sampling regime but additionally recording partial mortality on each coral skeleton, considerably more information about the population can be gathered with minimal additional effort. Size frequency distributions certainly have the potential to convey useful information about coral populations, but must be considered within the context of the specific experimental design used to generate them.

Acknowledgements. I thank Coral Cay Conservation and all the volunteers and staff at the Napantao expedition for their time, effort and logistical support. The research was partially funded by an NERC studentship. I also thank C Sweeting and N Polunin at Newcastle University for their help and advice throughout this project.

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