Decadal comparison of a diminishing coral community: a case study using demographics to advance inferences of community status

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The most common coral monitoring methods estimate coral abundance as percent cover, either via *in situ* observations or derived from images. In recent years, growing interest and effort has focused on colony-based (demographic) data to assess the status of coral populations and communities. In this study, we infer changes in coral communities from two separate data sets (photo-derived percent cover estimates, 2002-12, and opportunistic *in situ* demographic sampling, 2004 and 2012) in order to more fully understand the decade-scale changes observed at a small, uninhabited Caribbean island. Photo-derived percent cover documented drastic declines in coral abundance including disproportionate declines in *Orbicella* spp*.* While overall *in situ* estimates of total coral density were not different between years, densities of several rarer taxa were. *Meandrina meandrites* and *Stephanocoenia intersepta* increased while *Leptoseris cucullata* decreased significantly, changes that were not discernable from the photo-derived cover estimates. Demographic data also showed significant shifts to larger colony sizes (both increased mean colony sizes and increased negative skewness of size frequency distributions, but similar maximum colony sizes) for most taxa likely indicating reduced recruitment. *Orbicella* spp. differed from this general pattern, significantly shifting to smaller colony sizes due to partial mortality. Both approaches detected significant decadal changes in coral community structure at Navassa, though the demographic sampling provided better resolution of more subtle, taxon-specific changes.

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6 cover, either via *in situ* observations or derived from images. In recent years, growing interest
7 and effort has focused on colony-based (demographic) data to assess the status of coral
8 populations and communities. In this study, we relied on two separate data sets (photo-derived
9 percent cover estimates, 2002-12, and opportunistic *in situ* demographic sampling, 2004 and
10 2012) to more fully infer decadal changes in coral communities at a small, uninhabited
11 Caribbean island. Photo-derived percent cover documented drastic declines in coral abundance
12 including disproportionate declines in *Orbicella* spp. While overall *in situ* estimates of total
13 coral density were not different between years, densities of several rarer taxa were. *Meandrina*
14 *meandrites* and *Stephanocoenia intersepta* increased while *Leptoseris cucullata* decreased
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19 differed from this general pattern, significantly shifting to smaller colony sizes due to partial
20 mortality. Both approaches detected significant decadal changes in coral community structure at
21 Navassa, though the demographic sampling provided better resolution of more subtle, taxon-
22 specific changes.

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34   INTRODUCTION:

35   Coral cover and community composition have been established as the standard metrics

36   for reef monitoring programs. Visual census techniques have been around for decades (Stoddart

37   & Johannes 1978), and gained early recognition for their utility in understanding population

38   dynamics (Hughes 1984) and disturbance/recovery dynamics (e.g., Done 1985). These

39   techniques provide a valuable, albeit general, overview of the status of reef communities, but

40   offer little insight on the processes that drive the observed patterns. Coral cover also carries

41   relatively low signal:noise ratio in depauperate reef areas (e.g. <10% or even 1-2% cover) as is

42   characteristic of many modern Atlantic/Caribbean reefs (Jackson et al. 2014), making change

43   detection difficult without substantive (and perhaps unrealistic) increase in sample size (Molloy

44   et al. 2013). As a result, there has been increasing interest (and implementation) in expanding

45   from simple percent cover to more refined, process-based measures.

46   Coral demographic parameters have only recently been included in comprehensive coral

47   monitoring programs but may be a valuable supplement to percent cover data, as a demographic

48   approach offers species-specific and mechanistic insights into observed changes in percent cover.

49   Regional programs in south Florida (e.g., Smith et al. 2011; and Florida Reef Resillience

50   Program, frrp.org/coral-monitoring) and internationally (e.g., Atlantic and Gulf Rapid Reef

51   Assessment: Lang & Ginsburg 2006; IUCN: Obura & Grimsditch 2009) began implementing

52   colony based size and density measures in the early-mid 2000s. There is a wealth of ecological

53   theory to support analysis and interpretation of coral colony-based demographic data (Bak &

54   Meesters 1998; Vermeij & Bak 2002) whereby changes in the size structure of a population is

55   used to infer underlying ecological processes. Meanwhile, the collection of such data over large

56   programs and time frames carries some potential challenges such as inter-observer variation in

57   detection (especially of small corals), uncertainty in species identification (especially of small

58   colonies), and consistently delineating colony boundaries in populations with large amounts of

59   partial mortality.

60   In this study, we analyze coral information derived from both percent cover data and

61   from demographic data collected at haphazardly selected reef sites to examine temporal change

62   in coral status at Navassa, a small, uninhabited Caribbean island. Reefs in this area have suffered

63   severe disturbances, including hurricane impacts, severe disease outbreaks, and mass bleaching

64   over the past decade resulting in a drastic loss of live coral cover (Miller et al. 2008a). We

65   present coral percent cover data using standard photo-quadrat techniques (collected in 2002,

66   2004, 2006, 2009, 2012) in parallel with a separate coral demographic data set collected in 2004

67   and 2012. Our purpose is not to compare between these sampling methods per se, as choice of

68   method is influenced not only by practical considerations (level of effort, etc) but also the type of

69   information desired and applicability within a habitat type. Rather, we examine these data sets

70   (the only *in situ* data available from reefs of this uninhabited island) in parallel to address two

71   questions: 1) Are observed changes in coral community status consistent between these two data

72   sets (i.e. cover versus colony density and size structure); and 2) Does the demographic data

73   provide insights on processes underlying observed changes that are not evident from the cover

74   data alone?

75   METHODS:

76   The small oceanic island of Navassa (18.40°N, -75.01°W) is a component of the United

77   States National Wildlife Refuge system located approximately 55 km off the southwest tip of

78   Haiti. Though uninhabited, it is frequently visited by Haitian subsistence fishers. Reef

79   development mostly occurs on the narrow shelf along the leeward southwest coast of the

80   somewhat triangular island, whereas low-relief reef communities are found along the exposed

81   north coast (Fig 1). Benthic habitats along the windward east coast mainly consist of rubble

82   bottom. Due to its remoteness, there has been no structured monitoring program at Navassa.

83   Instead, episodic, opportunistic cruises have gathered both demographic and photoquadrat/cover

84   data. The opportunistic cruises were not intentionally designed to provide a rigorous comparison

85   across methodologies. Thus, here we leverage the only available data for a remote Caribbean

86   reef system starting from a relatively unimpacted baseline (Miller & Gerstner 2002) by laying

87   out parallel observations derived from two separate coral sampling schemes, collected within

88   coherent time and habitat strata, to examine the observed differences to determine what

89   meaningful and complementary inferences can be discerned.

90   *Photoquadrat data*

91   A set of sites along the southwest shelf of Navassa (depth 18-34m), was sampled with

92   haphazardly-placed, photoquadrats in 2002, 2004, 2006, 2009, and 2012. In 2002 and 2004 the

93   sites were haphazardly selected (but always targeting reef habitats along the southwest coast) by

94   necessity, as no habitat maps were available. Within the logistic constraints of working from a

95   single large ship with multiple cruise objectives, effort was made to disperse these sites

96   throughout the southwest shelf reef habitats. Later, the development of habitat maps from efforts

97   on the 2004 cruise (Miller et al. 2008b) enabled the stratified-random selection of sampling sites

98   in 2006, 2009, and 2012, similarly restricted to patch- and slope- reef habitats along the

99   southwest coast in order to be comparable to sets of sites sampled in earlier years. Although the

100   means of site selection varied between sample years, a relatively high sampling intensity (hence

101   a representative sample given the restriction of habitat strata) was accomplished in each year

102   (e.g., >2 sites km^{-2} shelf area in 2004, >4 sites km^{-2} shelf area in the other years, e.g., Fig 1b).

103   Photoquadrats were placed by taking five fin kicks in a haphazard direction from the

104   prior quadrat and then tossing the quadrat forward while the diver's eyes were closed, yielding

105   approximately 6-8 m distance between quadrats. Each photoquadrat was comprised of a 1m^2

106   image and a close-up of each quadrant of the quadrat (to provide a clearer image for reference to

107   aid in coral identification), for a total of five images per quadrat. Benthic community structure

108   was analyzed by overlaying each 1m^2 picture with 100 (2002-4) or 50 (2006-12) random point

109   counts (reduced over time because large numbers of points per frame do not contribute to

110   improved power; Aronson et al. 1994; Houk & Van Woesik 2006) using CPCe software (Kohler

111   & Gill 2006). Corals were identified to species when possible, genus if not. Eight to ten quadrats

112   were analyzed per site.

113   Variation over time in percent live coral cover was analyzed for the community as a

114   whole (all species summed) as well as for the most common individual taxa (*Orbicella* spp.

115   [primarily *O. faveolata*], *Agaricia* spp. [primarily *A. agaricites*], and branching *Porites*) via

116   separate one-way ANOVAs on ranks followed by Dunn's post-hoc tests for differences among

117   individual years. To make parallel, taxa-specific comparisons in percent cover as for the density

118   data (described below), we additionally performed separate Mann-Whitney rank sum tests to test

119   for differences in cover for each of three rarer taxa (*Siderastrea siderea*, *Meandrina meandrites*,

120   and *Stephanocoenia intersepta)* between 2004 and 2012.

121   *Coral demographic data*

122   In 2004 and 2012, coral colonies were surveyed at a separate set of haphazardly selected

123   reef sites (Table 1; including a subset of the stratified-random photoquadrat sites in 2012), with

124   effort to disperse these sites among the patch reef and slope reef habitats of the southwest and

125   north coasts (Fig 1). This demographic sampling was accomplished via belt transects (15m x

126   0.5m [2004] or 10m x 1m [2012]), with short dive times due to deep depths sometimes dictating

127   a smaller sample area. The actual area sampled was recorded for each transect and used to

128   standardize colony density (as # colonies m^{-2}). Within each belt transect, every colony (defined

129   as all tissue sharing a single skeletal unit, even if multiple live tissue isolates were divided by

130   areas of dead skeleton) was identified to species, and size was recorded for most colonies

131   (*Porites astreoides*, was tallied for density but not sized in 2012 due to dive time constraints). In

132   2004, a clear acetate grid was overlaid the colony and used to estimate projected live colony area

133   directly. In 2012, the dimensions of each colony (maximum diameter and the diameter

134   perpendicular to the maximum) and a visual estimate of its projected % live area were recorded

135   *in situ* as was deemed more consistent to apply among multiple observers and to conform to

136   regionally established protocols (AGRRA; http://www.agrra.org/method/methodhome.html). To

137   compare colony areas with those measured in 2004, a circular area (2-dimesional, projected) was

138   estimated with a diameter that was the average of the two diameters measured, and adjusted for

139   the estimated % live area of the colony (adjusted circular area). While the adjusted circular area

140   and acetate grid are different means to estimate area, all field methods represent approximations

141   and these are both reasonable, comparable methods. Other efforts specifically aimed and

142   comparing different geomentric approximations for coral colony size/area have shown negligible

143   differences (e.g., between using a circular versus elliptical approximation for 2d colony area;Van

144   Woesik et al. 2011). Colonies of less than 2 cm diameter (3.14 cm^2 area) were excluded from

145   subsequent analyses to account for potential observer bias in the detection of small colonies and

146   inherent difference in detectability between years or transects due to variable cover of the

147   macroalga, *Lobophora variegata*. Identification uncertainties for the smaller juveniles also

148   dictated pooling of certain taxa (mostly to genus, though *Porites* was delineated into branching

149   and mounding morphologies; see list in Fig 3).

150   For both coral density and multivariate community structure analyses, only transects

151   located along the southwest (leeward) coast of the island between 18 – 34 m depth were included

152   to standardize the sampled habitat in these analyses where including replicates in different

153   habitats would increase variance and decrease power. A smaller sampling effort did occur along

154   the north coast in each year (Table 1), but the reef habitats and benthic assemblage found here

155   are substantively distinct (Miller et al. 2008b) relative to the more-developed southwest reefs.).

156   However, since the colonies along the north and southwest coasts clearly do not represent

157   distinct populations (being separated by < 1 km distance) and sampling effort was similar

158   between years (Table 1), all colonies available (including the north coast) were pooled for the

159   within-taxa size frequency analyses (described below) where pooling habitats helped boost

160   sample size.

161   Coral density was tallied for each transect (n=17 for 2004, 18 for 2012) along the

162   southwest coast for 15 taxa in each year to generate mean abundance estimates of coral species

163   found in Navassa's high relief reef habitat. Univariate Mann-Whitney rank sum tests (or t-tests)

164   were used to test for univariate differences in density between years for each taxon and for total

165   coral density using transects as replicates. To characterize potential differences in coral

166   assemblage structure between 2004 and 2012, we calculated Bray-Curtis similarities on species

167   density estimates among all transects after square-root transforming the data to reduce the

168   influence of highly dominant taxa (Clarke & Warwick 2001). A non-metric Multi-Dimensional

169   Scaling (nMDS) plot was created to visualize differences in coral composition of transects

170   between years while Analysis of Similarity (ANOSIM) was used to determine significance of

171   these differences. Similarity Percentage (SIMPER) analysis was applied to identify which taxa

172   were most influential in determining significant difference between years (PRIMERe v. 6.0).

173   In analyzing potential differences in size structure of coral populations, we focussed on

174   taxa with n > 30 colonies sized in each year. Colony areas were ln-transformed (Vermeij and

175   Bak 2002) and histograms constructed for each sampled year (2004 and 2012). Descriptive

176   statistics were calculated and the distribution of colonies among size classes was compared

177   between years via Kolmogorov-Smirnov tests for each taxa. Taxa not consistently measured in

178   2012 (due to dive time constraints [i.e. *Porites astreoides*]) are not included in analyses of size

179   frequency.

180   Lastly, the individual colony areas (measured taxa only) for each transect were summed

181   by taxa and divided by the transect area. This yields a demographically-derived estimate of coral

182   cover (as coral area) to provide an integration of the (potentially contrasting) density and size

183   differences among taxa. This allows visualization of contrasts in assemblage composition

184   according to different 'currencies' (density versus area occupied) within the same demographic

185   data set.

186   This research was conducted under Navassa National Wildlife Refuge Special Use

187   Permits #41529-2002-10, #41529-2004-12 and #41529-2006-03, #41529-2009-01, and #41529-

188   2012-001 from the US Fish and Wildlife Service.

189   RESULTS:

190   *Photoquadrat data*

191   The average photo-derived coral cover along the southwest coast of Navassa declined

192   from 34% in 2002 to 9.6% in 2012. 2002 and 2004 do not differ significantly from each other,

193 but they both are significantly higher than the subsequent three survey years (Fig 2, Dunn's post-

194 hoc pairwise comparisons). *Orbicella* spp. (predominantly *O. faveolata*) constituted about three-

195 quarters (0.76) of total coral cover in 2002, but only one fifth (0.20) of coral cover in 2012 with

196 the steepest (and statistically significant) decline between 2002 and 2004, prior to the

197 demographic sampling (Fig 2). In contrast, the other two taxa with the highest cover showed

198 more gradual declines and retained similar proportional representation of total cover over the

199 same time frame (0.20 to 0.23 for *Agaricia* spp. and 0.19-0.23 for branching *Porites*) (Fig 2).

200 *Coral demographic data*

201 In contrast to total photo-derived coral cover, total coral density along the southwest

202 coast did not differ between 2004 and 2012 (Table 1, t-test p=0.33). However, significant

203 differences in species composition did occur (Global R=0.308; significance level of 0.1%; Fig 3)

204 with *S. siderea*, *A. agaracites*, branching *Porites*, *Leptoseris cucullata*, and *Orbicella* spp. being

205 the taxa contributing foremost to the dissimilarity between the two years, cumulatively

206 contributing 45% of the total dissimilarity (SIMPER analysis). When analyzed separately

207 (univariate Mann-Whitney rank sums tests), *A. agaricites, L. cucullata,* and *Orbicella* spp. all

208 showed significant univariate decreases in density whereas branching *Porites* did not show any

209 significant difference between 2004 and 2012 (Fig 4). Coral species exhibiting significantly

210 higher colony density in 2012 included one common species, *S. siderea*, and two rarer species,

211 *Stephanocoenia intersepta* (formerly *S. michelini*) and *Meandina meandrites* (Fig 4). In

212 comparison, the photo-derived coral cover similarly captured a significant increase between 2004

213 and 2012 in *S. siderea* (from 0.41 to 0.97% cover; U=57, p=0.039), but no significant change

214 was detected for *M. meandrites* (0.10 to 0.20%; U=100, p=0.864) nor *S. intersepta* which was

215   not identified in any of the photoquadrats in 2012, though it was detected at low abundance (a

216   mean of .013%) in 2004.

217   Robust coral size frequency distribution comparisons (n ≥100 colonies) were obtained for

218   four taxa and for another four taxa based on smaller sample sizes (n=30-99) (Table 2; three

219   additional taxa were recorded but lacked sufficient sample size for comparisons between years).

220   All four of the taxa with larger sample sizes show significant changes in size frequency

221   distributions between 2004 and 2012 (Fig 5a-d, Table 2). *Orbicella* spp. populations showed

222   smaller mean colony size (985 cm^2 in 2004 to 347 cm^2 in 2012), while branched *Porites* spp., *S.*

223   *siderea*, and *A. agaracites* had larger mean colony sizes. Of the four taxa with lower sample

224   size, only *L. cucullata* showed a significant difference (Fig 5e, Table 2), in this case shifting to a

225   larger mean colony size. Skewness shifted from positive to negative for four of the taxa (*A.*

226   *agaricites*, branched *Porites*, *L. cucullata*, and *S. intersepta*) indicating increased under-

227   representation of small (or over-representation of large) colonies in these populations (Table 2;

228   Vermeij et al. 2007).

229   Pooling the area occupied by measured corals, juxtaposed with their cumulative density

230   (Fig 6) aids in integrating the contrasting patterns of decreased cover, stable density, and

231   contrasting size changes among taxa. The calculated area occupied by these corals in 2012 is

232   less than half of that in 2004, despite only small (insignificant) change in colony density.

233   Additionally, individual taxa show contrasting patterns between area and density units, due to the

234   influence of different size structure. While *Orbicella* spp. showed small losses (a factor of 0.36)

235   in density between 2004 and 2012, its losses in calculated area were extreme (less than one tenth

236   remained due to loss of large colonies). In contrast, *S. siderea* showed much greater increases in

237   density (tripled) than in area occupied (due to increased abundance constituted by small colonies

238   occupying little area). Meanwhile, some taxa (e.g., *A. agaricites*) showed approximately

239   proportional changes in both units (Fig 6).

240   DISCUSSION:

241   The overall decline in coral cover and lack of resilience displayed among Caribbean reefs

242   over the past decades is well described in the literature. A large meta-analysis covering sites

243   throughout the Caribbean from 1970-2012 (Jackson et al. 2014) provides context for the changes

244   described here in Navassa reefs in the later portion of this interval. This meta-analysis indicates

245   the mean corrected coral cover for deeper reefs (5-20m depth, 88 locations) over three time

246   periods declined from 32.6% (1970-1983) to 19.4% (1984-1998) to 16.5 (1999-2012)(Jackson et

247   al. 2014, Part 1, Table 3, p.67). Though most of our Navassa sampling sites in all years were

248   deeper than 20m, the initial coral cover documented at Navassa's southwest reefs in this study

249   was 34% in 2002, corresponding with the Caribbean-wide average several decades earlier.

250   Subsequently, a 20% absolute decline in Navassa coral cover occurred over a period of just four

251   years, whereas the Caribbean- wide mean decline of only 16% absolute took two decades. While

252   coral cover at Navassa does appear to have remained robust for a longer duration in the absence

253   of local development and human habitation, acute disturbance events of global stressors such as

254   thermally-induced coral bleaching (Miller et al. 2011) and coral disease (Miller & Williams

255   2006) have coincided at Navassa with at least as great a magnitude of decline at a much more

256   rapid pace than the regional average.

257   We acknowledge several caveats to the data presented here when interpreting our

258   findings. The sites sampled in most cases were haphazardly chosen. However, all sites sampled

259   in both data sets were constrained by habitat type for each temporal comparison (e.g., to deep

260   patch and bank reefs on the southwest coasts for coral density). The total shelf area at Navassa is

261   small and the relative density of sampled sites was adequate to detect differences between years

262   in both cover and demographic parameters. The demographic data were collected

263   opportunistically to supplement % cover monitoring data, not as planned repeat monitoring or a

264   methods comparison. Furthermore, our sampling in both years was constrained by a limited

265   number of dives per cruise to survey the coral community, not shaped by an objective power

266   analysis nor optimal spatial allocation of samples (e.g., Smith et al. 2011). The sampling effort

267   (i.e. person dives and area covered) was fairly similar between both data sets in 2004, but

268   somewhat higher for the demographic data in 2012 (Table 1). Given this non-homogenous field

269   sampling, we took a conservative approach to our analyses. Our analytical approach has been to

270   filter the demographic data in conservative ways to avoid potential bias in the primary

271   comparison between years i.e., excluding (e.g. small sizes) or pooling (e.g. nominal spp

272   identifications into higher taxa groups) data whenever there was uncertainty in comparability.

273   Given this sub-optimal data set, interesting and significant differences between years are evident

274   from the demographic data (Fig 4, Table 2) that are not resolvable from the more traditional and

275   more frequent coral cover data.

276   Significant loss in coral cover occurred while total coral density remained unchanged, as

277   substantially lower colony abundance of some taxa (mainly *Orbicella* spp) was offset by

278   significantly higher density of other, typically smaller taxa. These taxa with higher density

279   include both the common *S. siderea* (for which increase was also apparent from the more

280   frequent photo-derived cover data), as well as two rare species for which changes in photo-

281   derived cover were not discernable (*M. meandites* and *S. intercepta*). High recruitment rates

282   have similarly been reported for these three species in other studies (e.g., Huntington & Lirman

283   2012; Vermeij et al. 2011). Historic studies of juvenile coral assemblages in Curaçao indicate *M.*

284   *meandrites* ranking 4th and *S. intersepta* 7th in terms of relative abundance within the total

285   juvenile population (Bak & Engel 1979). For *M. meandrites*, our 2004 mean density of 0.09

286   colonies m^2 is congruent with that reported by Pinzon and Weil (2011) measured in southwest

287   Puerto Rico in 2002-3, as is a negative skewness of its size distribution. However, this species

288   showed a decrease in juvenile density in Curaçao between 1979 and 2005 (Vermeij et al. 2011),

289   and we are unaware of other published reports of significant increasing abundance trends for this

290   species as observed at Navassa (Fig 4). Interestingly, *L. cucullata*, a significant 'loser' in colony

291   abundance in the current study, has showed a similar drastic decrease in juvenile density in both

292   Curaçao (as *Helioseris cucullata;* (Vermeij et al. 2011) and Jamaica (Hughes & Tanner 2000).

293   The size frequency data showed that some species shifted significantly toward larger

294   colonies, and others toward smaller size. The loss of very large *Orbicella* spp. colonies is most

295   likely attributable to substantial mortality associated with disease and bleaching events between

296   2004 and 2006 (Miller et al. 2011; Miller & Williams 2006). The most drastic difference in size

297   distribution among the taxa examined was a strong shift to larger colonies in branching *Porites*.

298   The reason for this remains unclear, but a reduction in recruitment combined with growth of

299   colonies through time (from a modal diameter of 3 cm to a modal diameter of 14 cm in eight

300   years, Fig 5B) seems plausible, given no significant change in density (Fig 4). Alternatively, it is

301   possible that a substantial shift in species representation within this morphological group may

302   have occurred (e.g., more *P. porites* and less of the small *P. furcata* and/or *P. divaricata*). We

303   do not think this explanation likely due to substantial representation by both small and larger

304   morphs in both sampling years, and recent genetic evidence has failed to support these three as

305   distinct species (Prada et al. 2014).

306   We considered the sampling efficiency of collecting both percent cover and demographic

307   data in deep water reefs where bottom time is limiting. The present data sets were collected with

308   roughly comparable levels of in-water effort per unit sample (at the depths and dive times

309   available for these deep reefs, a single diver was able to complete either one demography

310   transect or a set of photoquads, each method surveying ~ 10 m² of the seafloor, Table 1),

311   though there are clear tradeoffs in both the amount of post-processing effort required and aspects

312   of statistical power related to ten replicate photoquads versus a single transect that yields data on

313   a large but variable number of coral colonies. The consequences of these replication differences

314   will depend on the types of analyses attempted. Fundamentally, the methods pose different

315   questions-- % cover provides a picture of the overall coral community composition and enables

316   comparison across other competing benthic taxa (algae, sponges, etc), whereas demographic

317   surveys are necessarily species inventories aimed at characterizing populations. For sampling of

318   deep water reefs, the decision to use photoquads, demography transects, or both methods should

319   be based on the underlying questions motivating the survey.

320   Demographic and percent cover approaches can both pose pitfalls. For example,

321   increasing frequencies of small colonies can result from beneficial processes such as recruitment

322   of new colonies or undesirable processes such as partial mortality resulting in small remnant

323   colonies. Meanwhile, a single massive colony is not functionally equivalent (in terms of habitat

324   value, susceptibility to various threats, nor fecundity) to many small colonies but might be

325   represented as equal in terms of percent cover. Photoquadrats do not necessarily sample every

326   coral in the area surveyed, and can have poorer resolution or detectability for rare, small, or

327   similar-appearing species. For example, we were not able to quantify *L. cucullata* abundance

328   reliably from our photos (likely mis-identified as *Agaricia* spp., or present in cryptic locations

329   not visible in top-down photographs) whereas it was easily distinguishable in the field. Hence,

330   the significant loss of this species (sixth most common taxon in 2004) would not have been

331   detected from photoquadrat sampling alone.   The decline of *L. culcullata*, also reported in

332   Curacao (Vermeij et al. 2011) and Jamaica (Hughes & Tanner 2000), is likely the most

333   substantial collapse of a Caribbean coral species since *Acropora* spp. but has largely gone

334   unnoticed due to predominance of photographic monitoring approaches.

335   Most long-term coral monitoring efforts have relied solely on percent cover to quantify

336   abundance, community structure, and changes through time. This approach has been sufficient

337   to detect changes over long time frames (De'ath et al. 2012) and the drastic losses over short time

338   frames due to recent acute disturbances on Atlantic/Caribbean reefs (e.g., Coelho & Manfrino

339   2007; Miller et al. 2009). Significant declines are relatively easy to detect from a baseline of

340   50% cover, but change detection likely requires much greater sampling effort from a baseline

341   signal of 10%, or even much lower for individual coral species, as characterizes most modern

342   Caribbean reefs (e.g., Gardner et al. 2003; Ruzicka et al. 2013). Within the photoquadrat data set

343   reported here, significant change is detectable over less than a decade in coral percent cover and

344   even in the few dominant individual coral taxa (Fig 2). However, given the low percent coral

345   cover in Navassa by the end of the study period, it seems highly unlikely that future changes in

346   total coral cover (either continued decline from a low baseline or, hopefully, recovery), let alone

347   individual taxa, will be detectable over the next decade without substantially greater sampling

348   effort if relying on photoquadrat sampling alone. For example, Molloy et al. (2013) performed

349   intensive power analyses to determine the number of photoquadrats/points required to detect 1%

350   per annum recovery in coral cover and concluded this scale of recovery was essentially

351   impossible to detect with their most intensive photoquadrat protocols (250 quadrats per site, 50

352   points per quadrat). While traditional percent cover data such as from photoquadrats provides

353   crucial information on the status of the 'other 90%' of the reef that is not hard coral, it may

354   provide relatively less information for corals, especially when they are at low abundance. By

355   supplementing photoquadrat data with minimal demographic sampling we were able to detect

356   increased densities of several species over eight years. The collection of colony-based (i.e.

357   demographic) data provide additional metrics, greater resolution and analytical power (e.g.,

358   hundreds of colonies for many taxa in an effort such as this, rather than a cover estimate of, e.g.,

359   <1%), and a valuable mechanistic insight as to the population dynamics driving coral population

360   changes. Hence, a combined approach employing both photoquadrat data with demographic data

361   may be the most informative to track changes in benthic reef communities at low coral

362   abundances.

363

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Summary effort and density

In-water effort for 2004 and 2012 demographic ('Demo') and photoquadrat (PQ) sampling including number of sites, transects or photoquadrats and person-dives. Area (m^2) indicates the cumulative area of transects (demo) or quadrats sampled. The total number of colonies sampled and the colony density (# colonies/m^2) are also given under the demographic section.

1 Table 1. In-water effort for 2004 and 2012 demographic ('Demo') and photoquadrat (PQ)
2 sampling including number of sites, transects or photoquadrats and person-dives. Area (m^2)
3 indicates the cumulative area of transects (demo) or quadrats sampled. The total number of
4 colonies sampled and the colony density (# colonies/m2) are also given under the demographic
5 section.

Year	Location	PQ # sites	PQ area	PQ person - dives	Demo # sites	Demo # transects	Demo person -dives	Demo area	# col	Overall Density (SE)
2004	SW	14	149	16	13	17	13	111.5	1227	11.48 (1.06)
	N*				6	7	6	50.5	351	7.07 (0.56)
2012	SW	12	125	13	8	18	20	166.5	1711	10.17 (0.80)
	N*				4	6	5	51	316	6.18 (0.46)

7 *Transects from the north coast are included only in the size frequency analyses (Table 2, Fig 4)

Size frequency data

Coral colony size frequency summary statistics from Navassa demographic sampling in 2004 and 2012, based on ln(colony area [cm^2]). P-values are given for Kolmogorov-Smirnov tests comparing distributions between the two years. Three sections indicate groups of taxa with progressively lesser N's. Histograms for taxa that are significantly different are shown in Fig 5. Taxa as in Fig 4.

		2004						2012							
		Count	Mean	Median	Var	S.D.	Skewness	Count	Mean	Median	Var	S.D.	Skewness	p	KS
−	Aaga	438	3.89	3.74	2.24	1.50	0.24	365	4.28	4.46	1.48	1.22	-0.53	<0.001	3.51
	Orb spp	183	5.82	5.99	2.64	1.62	-0.42	100	5.08	5.45	2.22	1.49	-0.77	<0.001	2.04
	Por Branched	212	2.73	2.20	2.09	1.45	1.36	199	4.32	4.64	1.94	1.39	-0.45	<0.001	5.30
	Ssid	154	2.85	2.48	1.63	1.28	1.18	422	3.12	2.98	1.59	1.26	0.47	<0.001	2.32
=	Efas	36	3.44	2.94	2.96	1.72	0.61	45	3.70	3.50	2.27	1.51	0.87	0.31	0.97
	Lcuc	87	3.05	3.04	1.18	1.09	0.27	30	3.70	4.14	1.95	1.40	-0.37	0.00	1.76
	Mcav	31	3.63	3.30	3.36	1.83	0.78	46	3.59	3.42	2.21	1.49	0.30	0.81	0.64
	Sint	41	3.40	3.30	1.51	1.23	0.53	96	3.53	3.50	1.54	1.24	-0.03	0.19	0.83
≡	Dipl spp*	5	6.95	7.90	2.60	1.61	0.46	5	6.49	6.63	2.21	1.49	0.07	n/a	n/a
	Mmea	12	4.36	4.43	1.45	1.21	-0.17	57	4.63	4.73	2.17	1.47	-0.43	n/a	n/a
	Mycet spp	18	3.54	3.47	1.58	1.26	0.46	11	3.37	3.65	1.67	1.29	0.07	n/a	n/a

1   *Includes recently reclassified *Pseudodiploria strigosa* (Budd et al. 2012)

Sample Location

Map showing location of Navassa Island in the greater Antilles. Insets show the specific location of demographic sites (a) and photoquadrat sites (b) that were sampled in 2004 and 2012. Photoquadrat sites sampled in the other years were similarly dispersed among reef habitats of the southwest coast (i.e., 2004 and 2012 are shown as representative examples). Site locations are superimposed on satellite imagery showing reef distribution along the Navassa shelf (IKONOS image provided by DigitalGlobe).

Cuba

Haiti

Jamaica

Navassa Is

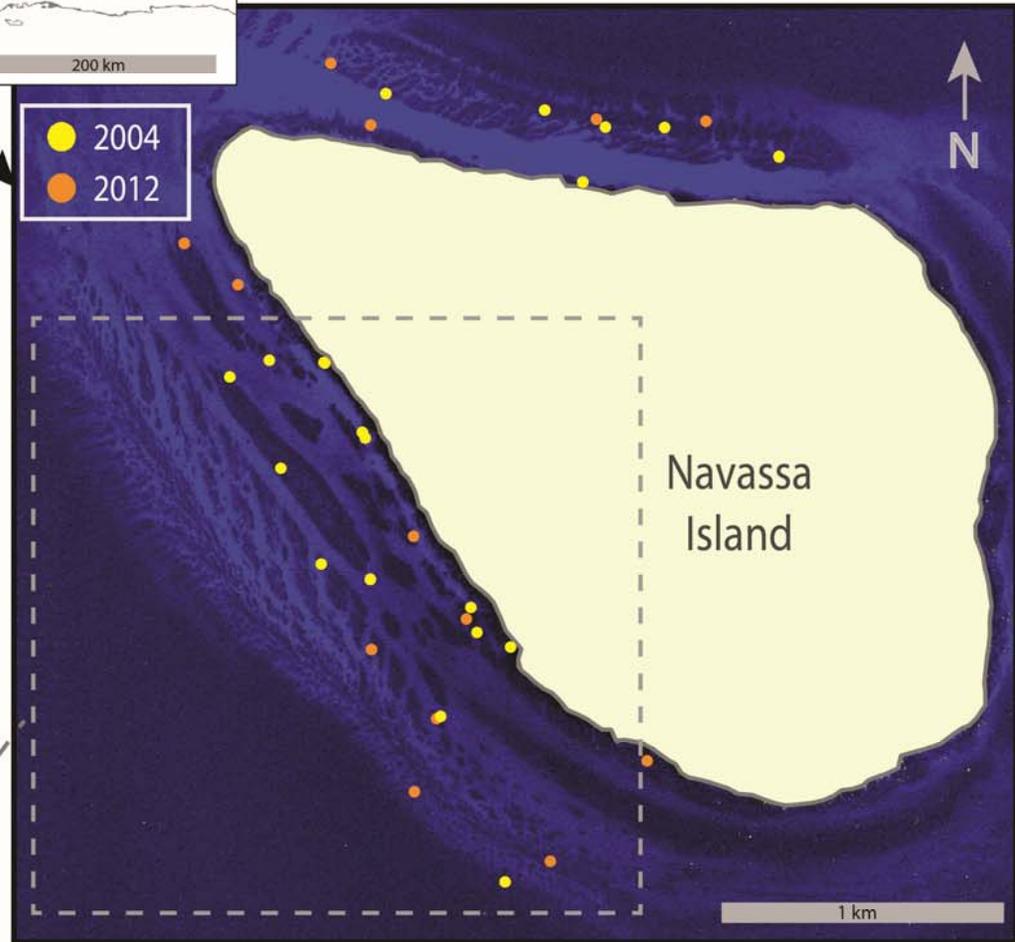
200 km

a) Demographic sites

● 2004
● 2012

N

Navassa Island

1 km

b) Photoquadrat sites

Navassa Island

N

▲ 2004
▲ 2012

1 km

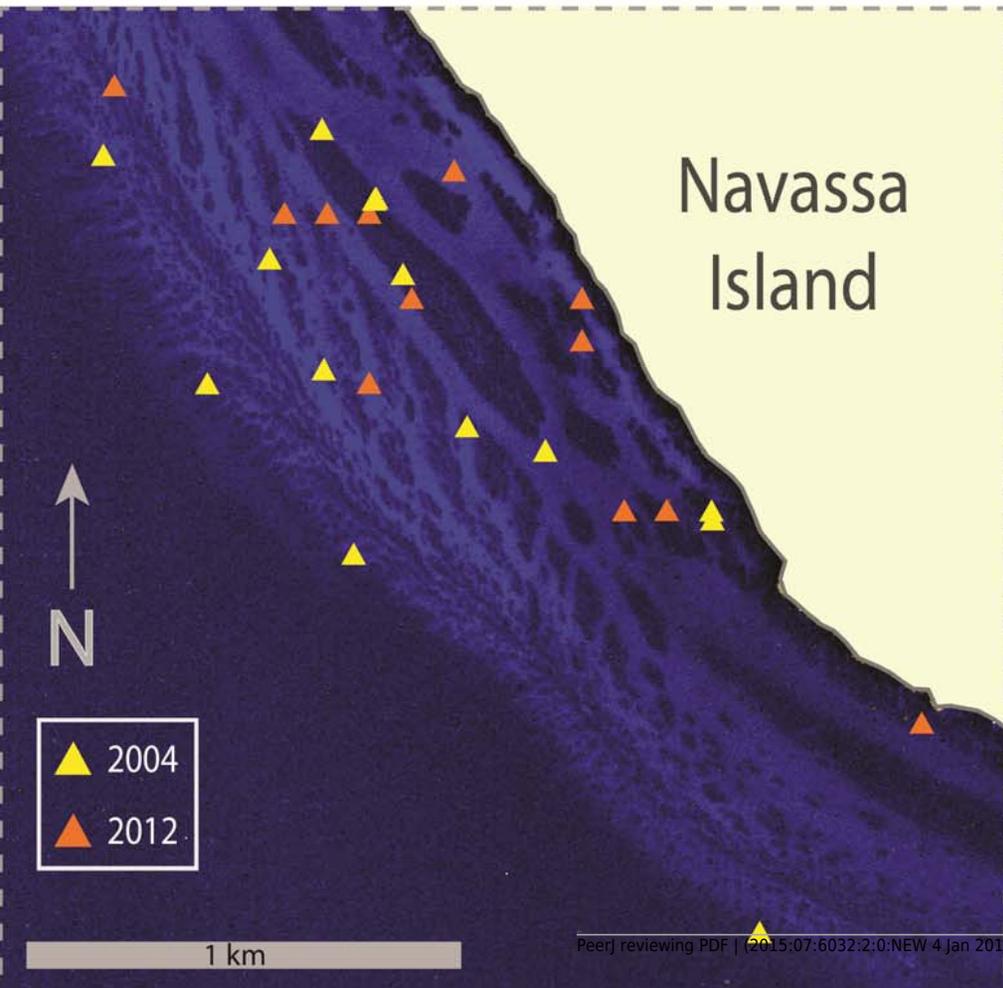
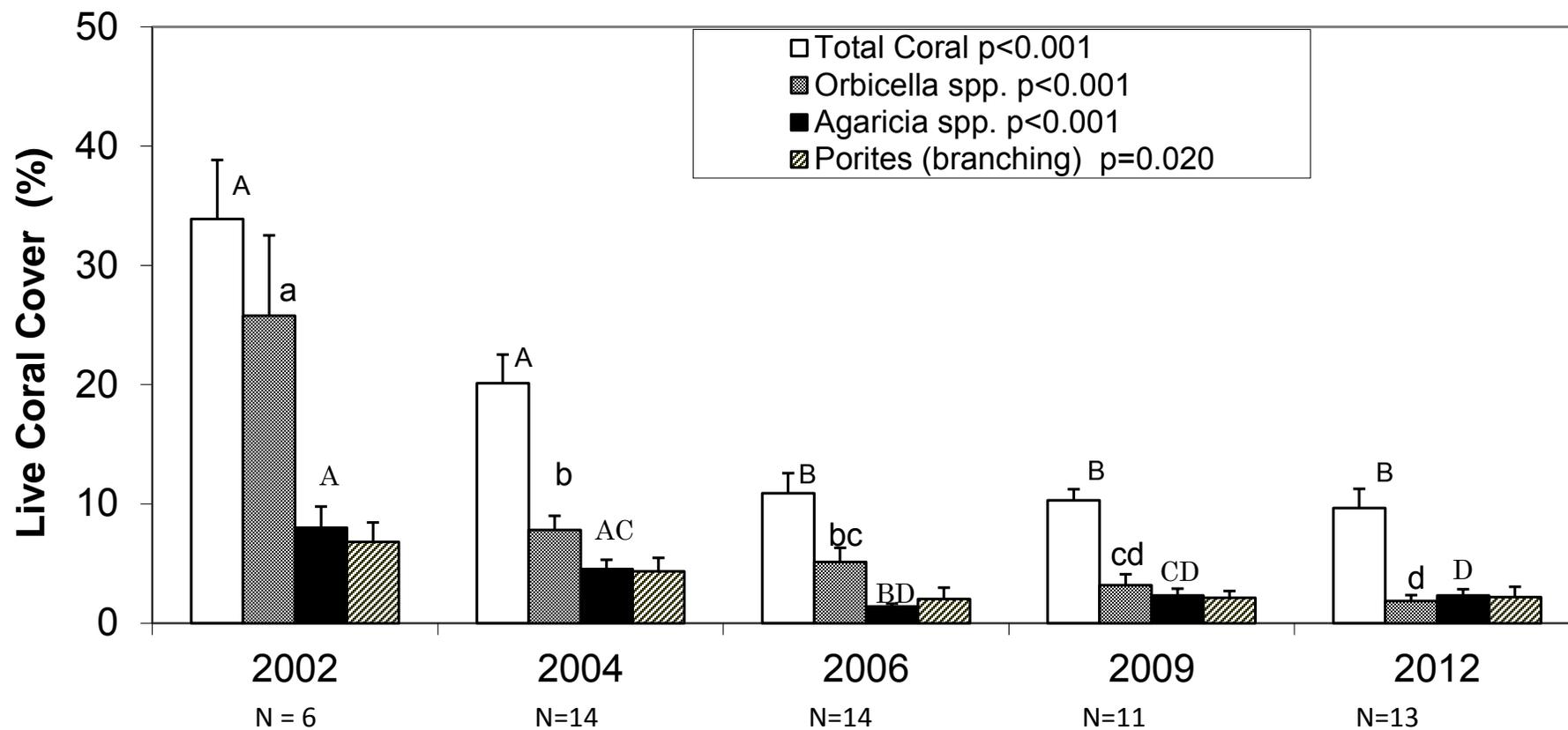
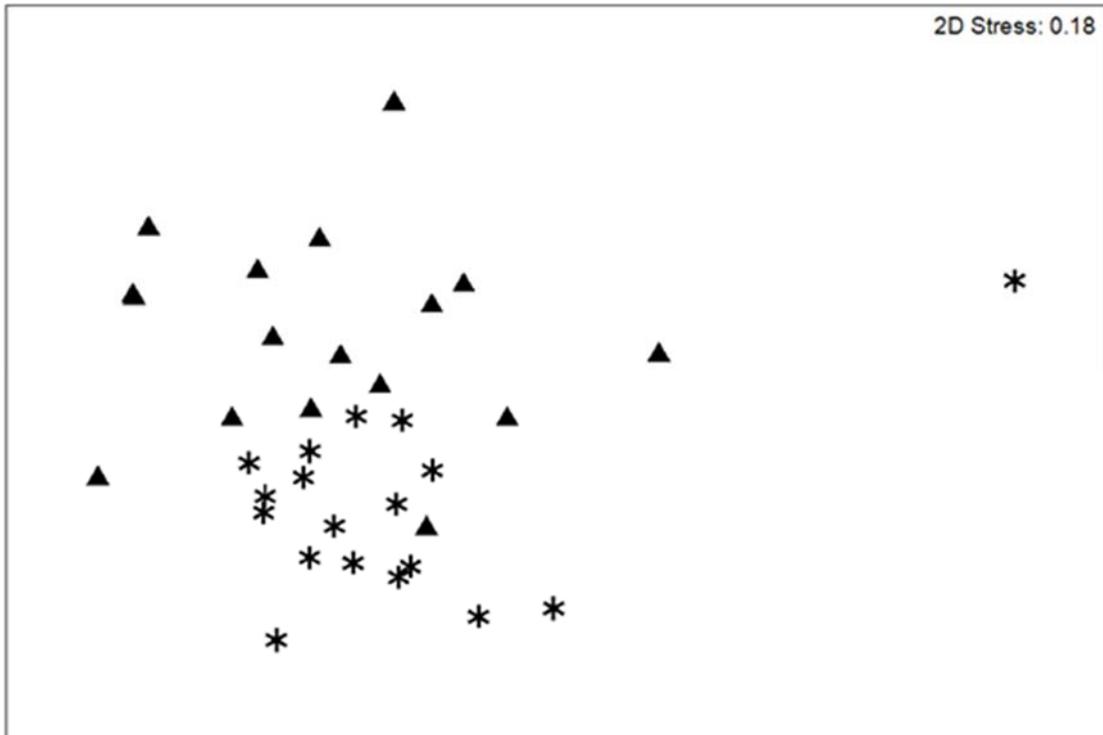



Photo-derived percent cover

Percent cover (+ 1SE) for total scleractinian corals and for the three most abundant coral taxa in Navassa photoquadrats over time. The three most abundant taxa are *Orbicella* spp. (predominantly *O. faveolata*), *Agaricia* spp. (dominated by *A. agaricites*), and branching *Porites* (*P. porites*, *P. furcata*, and *P. divaricata*). P-values in legend from separate one-way ANOVA on ranks for each taxa across time. N (number of sites) is given for each year under the axis. Similar letters over each set of bars indicate no statistical difference in post-hoc comparisons for a given taxa across time. Note that *Orbicella* spp. cover had declined most before 2004, whereas the other two taxa (and total coral cover) continued declining through 2006.

Community change

nMDS scaling plot for coral demographic transects sampled on the southwest coast of Navassa in 2004 (triangles) and 2012 (asterisks). Although the somewhat high stress level indicates that this 2-dimensional rendering is not a perfect representation of the similarity among samples, ANOSIM indicates significant change in coral community structure (based on square-root transformed colony density) between the two years (Global R=0.308; significance level of 0.1%).

Colony density by taxa

Colony density for coral taxa (mean + 1SE; n=17, transects in 2004 and 18 in 2012) in the demographic sampling of sites along the southwest coast of Navassa. *indicates significant difference between the two years as determined by Mann-Whitney rank sum test (p<0.05). Orb spp = *Orbicella* spp. (predominantly *O. faveolata*); Mcav = *Montastraea cavernosa*; Dipl spp = *Diploria* (includes recently reclassified *Pseudodiploria strigosa,* (Budd et al. 2012)) species; Por branched = branched *Porites* spp (*P.porites, P.furcata, P.divaricata*); Por Mound = mounding *Porites* species (predominantly *P.astreoides*); Ssid=*Siderastrea siderea*; Sint = *Stephanocoenia intersepta*; Mmea = *Meandrina meandrites*; Aaga=*Agaricia agaricites*; Other Ag= *Agaricia* species other than *A.agaricites*; Lcuc = *Leptoseris cucullata*; Efas = *Eusmilia fastigiada*; Mycet spp= *Mycetophyillia* species; Madr = *Madracis* species; Other = other scleractinians.

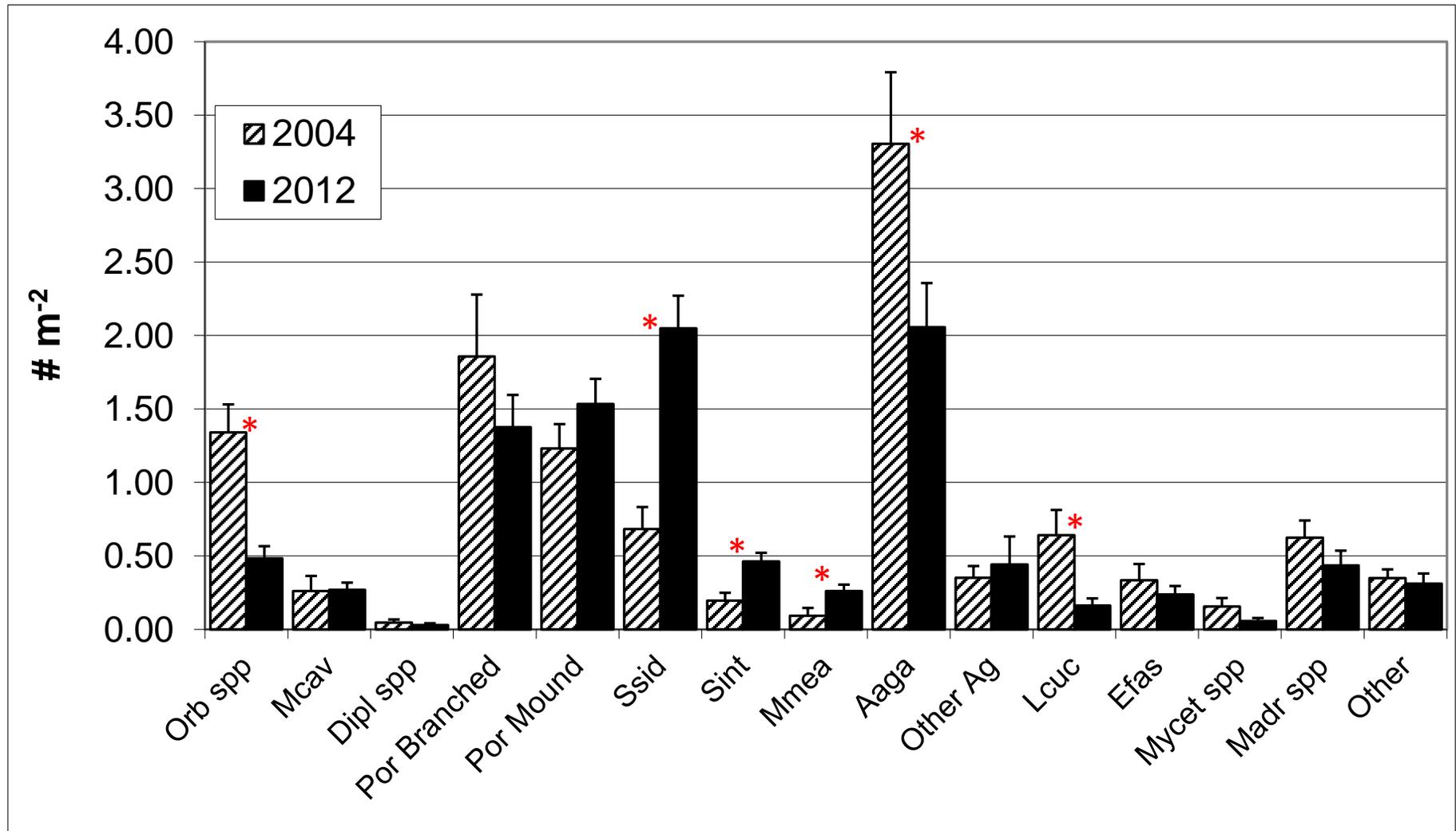
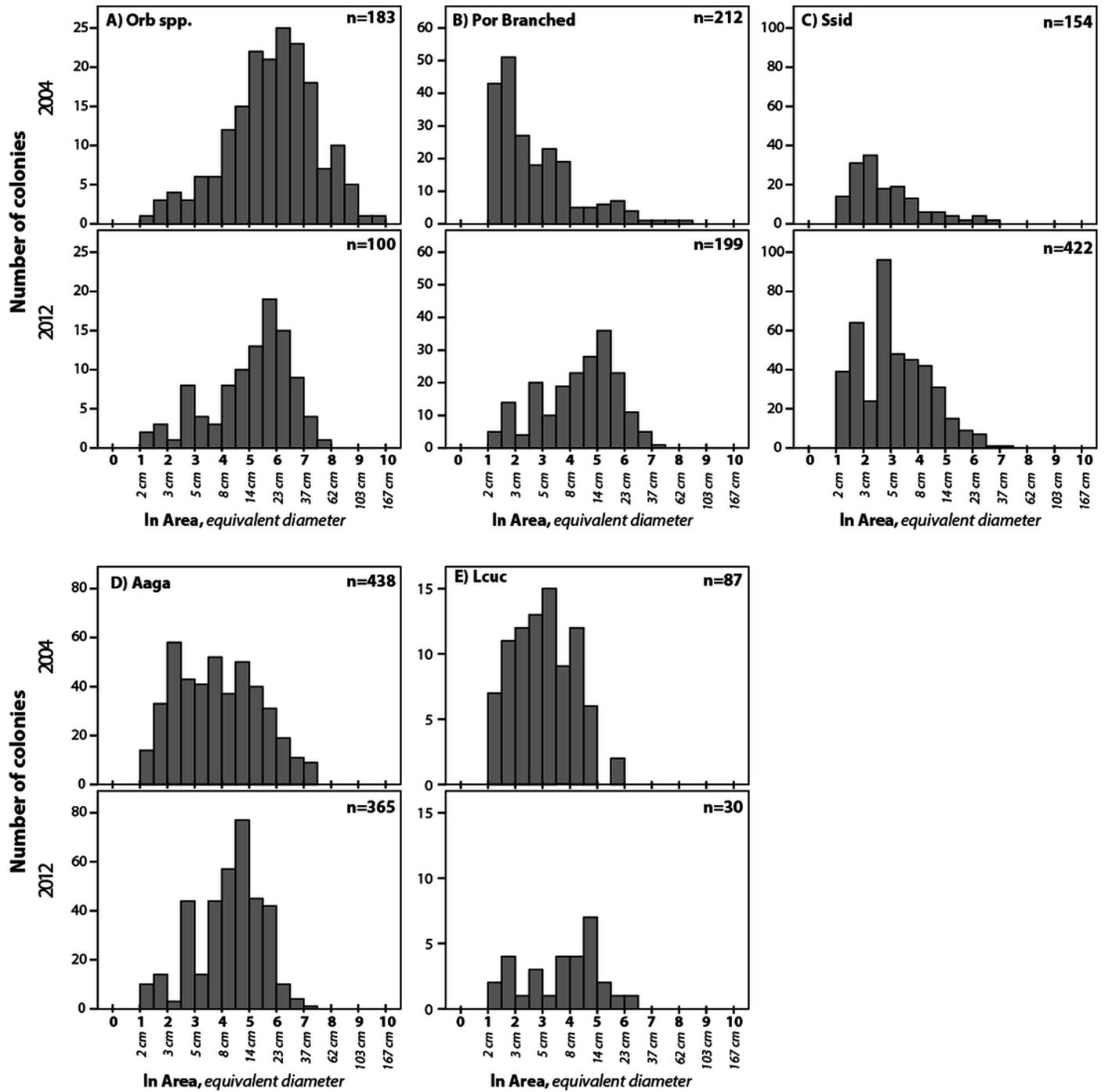
5

Size frequency distributions

Fig 5. Size frequency distributions for five taxa that showed significant difference between 2004 and 2012. Size bins are expressed as ln (colony area in cm^2). Corresponding colony diameters (for calculated circular area) are shown below the x-axis for scale. Summary statistics given in Table 2. Taxa as in Fig 4.

Area occupied by taxa

A comparison of coral composition (sized taxa only) for southwest sites based on demographic data expressed as density (A) and as area back-calculated by summing the area occupied by each of these sized colonies (B). Taxa abbreviations as in Fig 4.