Variation in size-frequency distributions of branching corals between a tropical versus sub-tropical reef

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ABSTRACT: Diversity in the life history of corals plays a critical role in shaping coral assemblages and reef habitats. Given difficulties in quantifying key demographic rates, valuable insights into life histories of corals are often inferred based on size-frequency distributions. The present study compares size-frequency distributions of branching coral taxa between Lord Howe Island, a sub-tropical reef, and Heron Island, in the southern Great Barrier Reef. Size-frequency distributions were markedly different among coral species but also varied among locations. Log-transformed size-frequency distributions of the majority of species were negatively skewed, reflecting the high levels of mortality among the smaller size classes and the persistence of the larger colonies. Among species, there were marked differences in kurtosis, reflective of fundamental variation in coral life histories; *Acropora yongei* had the lowest kurtosis, indicative of fast growth and high population turnover. Between locations, there was a higher proportion of smaller colonies at Heron Island, which was consistent across all coral taxa, suggesting a greater incidence of mortality at Heron Island. Size-frequency distributions provide important insights on the life-history dynamics of coral species and should be monitored over time to test how coral populations and communities will respond to global climate change, especially at high-latitude reefs.

KEY WORDS: Population · Life-history traits · Growth · Mortality · Colony size

INTRODUCTION

The structure and dynamics of coral populations and communities vary greatly in time and space (Done 1999), and improved understanding of the causes of this variation is critically important in projecting effects of climate change and other anthropogenic disturbances on coral assemblages and reef habitats. Inherent differences in the life-history characteristics of different coral species (e.g. the mode of reproduction, recruitment, growth and longevity) have an important role in shaping coral assemblages and structuring reef habitats. Fast-growing branching corals play an important role as the primary habitat-forming species (e.g. Coker et al. 2014). However, branching corals (e.g. *Acropora*, *Pocillopora* and *Sty-*

lophora) are also the most susceptible to severe disturbances (Hughes & Connell 1999, Marshall & Baird 2000) but are nonetheless very common because they are able to rapidly colonise reef habitats following disturbance (Highsmith 1982, Tunnicliffe 1983, Hughes et al. 1992, Hall & Hughes 1996). In contrast, other growth forms such as massive and columnar are far less dynamic, having slower growth and lower rates of population turnover, but are also more resistant to most major disturbances (Connell 1973). As a consequence, it is unclear how coral communities might change due to increasing incidence of disturbances (Pandolfi et al. 2011), including climate change.

The resilience of coral species to sustained and ongoing disturbances, incorporating both resistance

and recovery potential, is fundamentally dependent on key life-history characteristics, including the mode of reproduction and rates of recruitment as well as size-specific growth and survival (Hughes & Tanner 2000). Moreover, any changes in demographic rates brought about by changes in environmental conditions and/or disturbance regimes will directly affect the vulnerability and local persistence of individual species (Bak & Meesters 1999, Gilmour et al. 2013). However, there is a paucity of demographic data for individual coral species and populations, largely due to the effort required to directly quantify key demographic rates (Connell et al. 2004). An alternative method of inferring spatial, temporal or taxonomic differences in life histories is to simply assess size- and/or age-structure. For scleractinian corals (like all colonial organisms), demographic rates (e.g. fecundity, growth and mortality) are strongly dependent on colony size (Connell 1973, Hughes 1984, Hughes & Jackson 1985, Soong 1993), as opposed to age. Consequently, there is an increasing number of studies reporting on the size-structure of coral populations in a range of geographic locations (e.g. Persian Gulf [Bauman et al. 2013] and Chagos [Pratchett et al. 2013]).

Size-frequency distributions can be highly variable within and among coral populations (Adjeroud et al. 2007). Interspecific differences in size structure reflect inherent differences in life-history characteristics, especially growth and mortality (e.g. Adjeroud et al. 2007). However, variability in size-frequency distributions essentially results from disparities in the rates of recruitment, the subsequent persistence within a given size class, or growing into a larger size class, in addition to shrinking into a smaller size class due to partial mortality, or whole colony mortality (Bak & Meesters 1998). In addition, fragmentation can move colonies back in a size class, resulting in a preponderance of smaller colonies (Highsmith 1982, Wallace 1985). For colonial organisms, the growth of the colony is potentially indeterminate (Jackson 1977, Jackson & Hughes 1985). However, extrinsic factors such as available space, competition, disturbances, sedimentation and high temperatures can limit the capacity for growth and thus the advance to the next size classes or, in the case of significant partial mortality, actually lead to negative growth (Connell 1973, 1978). Therefore, factors that influence coral growth, such as light, carbonate saturation and available substrate, are counteracted by factors inhibiting growth (Vermeij & Bak 2003).

In general, the size-frequency distributions of coral populations are positively skewed, with the popula-

tions composed mainly of smaller colonies and relatively few large colonies (Hughes & Jackson 1985, Babcock 1991, Soong 1993, Bak & Meesters 1998). Log-transforming the size distribution thus results in a more normally distributed size-frequency distribution and increases resolution among smaller size classes (Meesters et al. 2001). However, not all coral populations exhibit a normally distributed log-transformed size structure; high levels of mortality will especially alter the population structure, reflected in changes in the coefficient of variation (CV), skewness and kurtosis of the frequency distribution (Bak & Meesters 1998). For example, following bleaching on Australia's Great Barrier Reef (GBR), fast-growing *Acropora* had negatively skewed size-frequency distributions, dominated by larger colonies (Linares et al. 2011).

Coral demographics will change with spatial and temporal gradients in environmental conditions, which should be reflected in contrasting size-frequency distributions among distinct populations (Bak & Meesters 1998). Knowledge of disturbance regimes can greatly increase the ability to infer demographic processes and contrast life histories, although background disturbances may cause unknown variation in the size-frequency distribution. At Lord Howe Island (off New South Wales), the 2 main processes known to structure the coral communities are the seasonal proliferation of macroalgae (Hoey et al. 2011) and a temperature-induced bleaching (Harrison et al. 2011). Macroalgae can cause fine-scale partial mortality to big colonies and whole colony mortality to small colonies, whereas bleaching is a large-scale disturbance that adversely affects branching morphologies (Marshall & Baird 2000, Loya et al. 2001) and larger colonies (McClanahan et al. 2008), as smaller colonies are less susceptible (Brandt 2009). In addition, on the GBR, disturbances such as tropical cyclones and crown-of-thorn starfish outbreaks cause the majority of coral mortality (Osborne et al. 2011).

The aim of the present study was to compare the size-frequency distributions of 5 species of branching corals between a tropical location, Heron Island, and a subtropical location, Lord Howe Island. At Lord Howe Island, growth rates of corals are lower than their tropical conspecifics (Harriott 1999). Therefore, the coral populations should be more peaked and centralized, resulting in a positive kurtosis, due to lower probability of transitioning through the size classes. In addition, the frequent disturbance regime at Heron Island would result in smaller colonies compared to Lord Howe Island. Subtropical locations

have been proposed as refugia in the face of climate change (Greenstein & Pandolfi 2008), and understanding variations between locations and among species will allow us to understand which species and what locations are likely to be most resilient to ongoing effects of climate change.

MATERIALS AND METHODS

Study sites

Subtropics: Lord Howe Island

The present study was conducted at Lord Howe Island, which is close to the southern limit of coral reef formation in the Pacific Ocean (Kleypas et al. 1999). Lord Howe Island is located 700 km south from the GBR, and local coral assemblages comprise only a fraction (83 of 356) of coral species that are found on the GBR (Harriott et al. 1995). To explore the size-frequency distributions of common coral species at Lord Howe Island, sampling was conducted at 2 sites, Horseshoe Reef (31° 32.554′ S, 159° 3.704′ E) and North Bay (31° 31.273′ S, 159° 2.773′ E), both of which are situated within the extensive lagoon on the western side of the island (Fig. 1). The lagoon encompasses the highest coral cover (40 %) around Lord Howe Island, and both sites are relatively shallow (<4 m) (Harriott et al. 1995). Despite low species diversity, the reefs have complex physical structures dominated by branching and column-forming species. Due to the homogenous depth in the lagoon, the spatial comparisons are restricted to between sites as opposed to among depths.

Southern GBR: Heron Island

To facilitate a spatial comparison between Lord Howe Island and the GBR, sampling took place at Wistari Reef. Wistari Reef is in the Capricorn and Bunker region of the southern GBR on the leeward side of Heron Island, Queensland (Fig. 1). It is situated 67 km northeast of Gladstone and 1137 km from Lord Howe Island. Heron Island

comprises 72 % of coral species found on the GBR (NOAA 2013). To match the topography of Lord Howe Island, sampling was restricted to 4 m depth at 2 sites (Wistari East: 23° 26.1′ S, 151° 53.12′ E; Wistari West: 23° 26.35′ S, 151° 52.01′ E), located 1 km apart running east west along the northern crest of the lagoonal platform. Both sites are similar in topography comprised of interconnecting reefs and bomboras (shallow submerged reefs, shallow rocks or sand banks).

Disturbance regimes

Heron Island is much more exposed to cyclones than Lord Howe Island. On average, the Capricorn Bunker Group is affected by one major cyclone every 4 yr (Flood 1986). Analyzing the database of past tropical cyclone tracks from the Australia Bureau of Meteorology (2013), 34 cyclone tracks were recorded from 1904 to the present within 50 km of Heron Island. The last cyclone reported within that distance was in 1994. In contrast, only 18 cyclones have
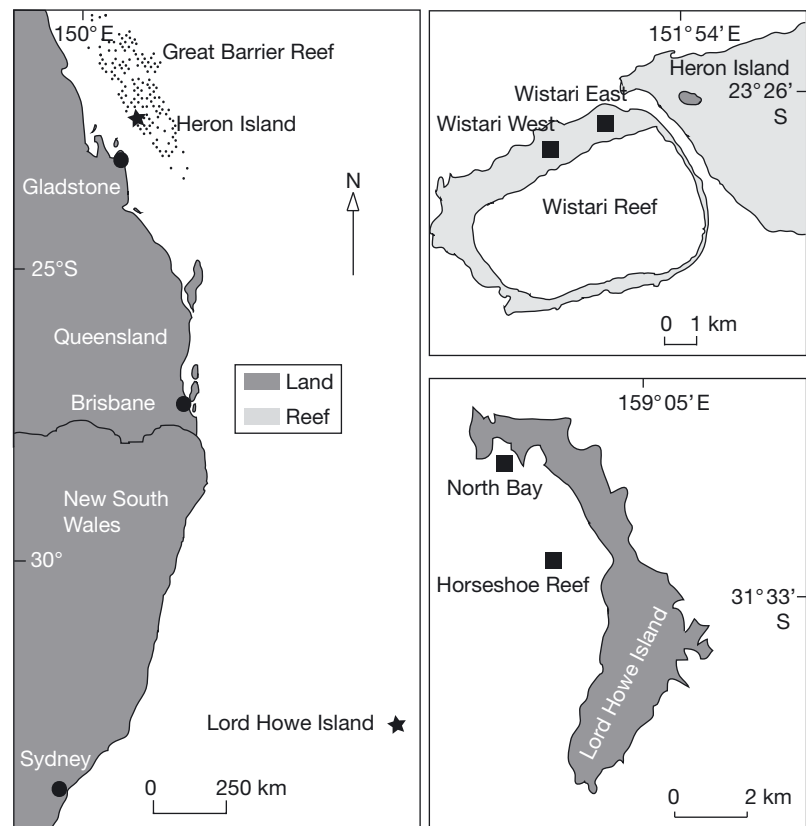

Fig 1. Study sites (■) at 2 sampling locations in Australia: subtropical Lord Howe Island and tropical Heron Island

passed within 50 km of Lord Howe Island during that same time period, with the last one occurring in 1967 (Australia Bureau of Meteorology 2013).

Another major disturbance to directly affect coral reefs is mass bleaching, which is increasing in frequency, extent and severity with ocean warming (Hoegh-Guldberg 1999). The first major bleaching recorded on the GBR was in 1998 (Baird & Marshall 1998), which affected Heron Island. Since then, bleaching has been documented in 2002 (Franklin et al. 2006), August 2003 (Hoegh-Guldberg et al. 2005), 2004 (Fine et al. 2005), a mild bleaching event in January to May 2006 (Ortiz et al. 2009) and February 2009 (MacKellar & McGowan 2010). In contrast, the only bleaching events at Lord Howe Island were documented by Harrison et al. (2011), who stated that coral bleaching did occur in 1998 but was most severe in 2010.

Study species

Lord Howe Island

At the subtropical location, we sampled *Acropora yongei*, *Pocillopora damicornis*, *Isopora cuneata*, *Stylophora pistillata* and *Seriatopora hystrix*. Species were identified using Veron & Stafford-Smith (2000). These species were selected based on their relatively high local abundance and contrasting morphologies, which are likely related to changes in their inherent life-history characteristics (Bak & Meesters 1998). Most of the species are branching, except *I. cuneata* which forms blades with laterally compressed extensions. The size-frequency distributions of *I. cuneata*, *S. hystrix* and *S. pistillata* have never before been examined.

Sampling was undertaken from 24 to 30 March 2011. Three researchers swam in a uniform direction parallel to the shore sampling every colony encountered in an area encompassing 100 m^2. All visible colonies were sampled. Colony diameter ranged from 1 to 810 cm, i.e. both adults and juveniles are included in the size-frequency distributions. In total, 1200 colonies were sampled: 585 at Horseshoe Reef and 615 at North Bay. For every colony sampled, the longest diameter and the perpendicular diameter of the coral colonies were recorded. Individual colonies were defined as autonomous, freestanding coral skeletons with live tissue (Bak & Meesters 1998). If the colony tissue was separate (e.g. because of partial mortality) but the colony remained one morphological entity, it was considered a single colony. Meas-

urements of colony dimensions were taken based on the maximal extent of intact and recognisable skeleton. The percentage of partial mortality was estimated *in situ* and subtracted from the total surface area to determine the amount of live tissue on each colony.

Heron Island

At the tropical location, we sampled *Pocillopora damicornis*, *Isopora cuneata*, *Stylophora pistillata* and *Seriatopora hystrix*. *Acropora yongei* does not occur at Heron Island, so the staghorn coral *A. muricata* was chosen for comparison. *A. muricata* often forms large monospecific thickets making size structure analysis difficult. However, these fragmented thickets at Wistari Reef are on the sand at >4 m outside of the depth chosen to match the study site at Lord Howe Island. Therefore, the size-frequency distribution of *A. muricata* is unreflective of the breadth of coral cover of these large thickets at the deeper depths.

Sampling was undertaken from 22 to 26 April 2013. The same sampling methodology performed at Lord Howe Island was implemented at Heron Island. At Wistari North and Wistari South, 444 and 435 corals were sampled, respectively, totalling 879 colonies. The relative density of colonies for each study species were quantified along replicate (n = 5) 10 × 2 m belt transects at each site and location.

Statistical analysis

Estimates of average diameter were used to approximate the 2-dimensional surface area of every coral colony, following Linares et al. (2011). Size-frequency distributions were then constructed based on the estimated living surface area for each coral species at each site. The intervals for the size-frequency distributions were chosen to encompass the largest breadth of colonies for direct comparison among the species and locations. Due to the large variation in colony size, the colonies of *Pocillopora damicornis*, *Seriatopora hystrix* and *Stylophora pistillata* that did not attain the large size of *Acropora* spp. or *Isopora cuneata* were grouped for comparison, allowing a more in-depth comparison among species. The size-frequency distributions of the smaller corals ranged for the untransformed data from 100 to >2000 cm^2. *Acropora* spp. and *I. cuneata* size-frequency distributions ranged for the untransformed

data from 500 to >10 000 cm^2. The colony size data were log$_{10}$ transformed to normalize the distribution and increase the resolution of the highly abundant smaller size classes, following Bak & Meesters (1998). The intervals for the log-transformed data ranged from 0.0 to 6.0 log-transformed colony size (cm^2). The size-structure for each species was directly compared between each species and each site, then between locations, using a 2-sample Kolmogorov-Smirnov (KS) test. In addition, the percentage of average partial mortality was calculated for each size class. A Student's t-test was used to look for variation in partial mortality. A 2-way ANOVA was used to assess variation in colony size between sites and locations. To determine specific differences among species from the ANOVA results, a Tukey's post hoc test was utilized. To compare the coral species' mean colony size between locations, a Student's t-test was performed

Descriptive statistics

Variation in the size structure of corals (within and among species) was compared based on (1) geometric mean, (2) CV, (3) skewness (g_1) and (4) kurtosis (g_2) following Bak & Meesters (1998). The geometric mean provides relative measures of colony size providing information on reproductive output (Hall & Hughes 1996). The CV describes the variation in the data set and allows for comparisons irrespective of the mean. Skewness describes the proportion of individuals in the population that are smaller or larger than the mean. If the skewness is negative, the population is skewed to the left, with a relatively larger proportion of colonies in the larger size classes than in the smaller size classes (Bak & Meesters 1998). Conversely, if the skewness if positive, then the population is skewed to the right, containing a large number of individuals in the smaller size classes than in the large size classes. Kurtosis describes whether the data is peaked or flat relative to the normal distribution and may reflect the transition through the size classes. If kurtosis is positive, the distribution is leptokurtic, which is peaked and highly centralized around the mean, indicative of slower population growth (Adjeroud et al. 2007). If kurtosis is negative, the distribution is platikurtic with a wide peak around the mean.

RESULTS

A total of 1856 corals were sampled during the present study (Table 1). Mean densities of corals were generally higher at Heron Island compared to Lord Howe Island, except for *Isopora cuneata* (Table 1).

While all coral populations had a large number of colonies in the smaller size classes, there were differences in the size-frequency distributions among species and between locations (Figs. 1 & 2). Given the prevalence of smaller colonies, all size-frequency distributions were positively skewed using the untransformed data. All distributions had the largest drop in numbers through the smallest size classes. By log-transforming the data, the size-frequency distributions became more normally distributed compared to the untransformed data.

Table 1. Statistical summary of the size-frequency distributions (using log-transformed colony size) for 6 coral species sampled at tropical (Heron Island) and/or subtropical (Lord Howe Island) locations. The sample size (n), density, log-transformed mean colony size, coefficient of variation (CV), skewness (g_1), kurtosis (g_2), and probability of being normally distributed (Kolmogorov-Smirnov p-value) are specified. For *Isopora cuneata*, statistics are given for each site at Lord Howe Island (HS: Horseshore Reef, NB: North Bay), since there were significant site effects (2-sample KS test, p < 0.05)

Species	Location	n	No. per m^2	Mean colony size (cm^2)	CV	g_1	g_2	p
Acropora yongei	Lord Howe	146	0.04	3.23	78	0.23	−0.50	<0.01
Acropora muricata	Heron Island	173	0.21	3.26	78	0.92	0.61	<0.01
Isopora cuneata	Lord Howe HS	100	0.20	3.06	57	−1.24	1.92	<0.01
	Lord Howe NB	100	0.21	2.72	76	−0.66	−0.15	ns
	Heron Island	153	0.19	2.51	26	−0.50	0.48	<0.05
Pocillopora damicornis	Lord Howe	236	0.27	2.49	29	−0.84	0.78	<0.01
	Heron Island	182	0.43	1.79	22	−0.31	−0.47	<0.05
Seriatopora hystrix	Lord Howe	240	0.18	2.05	27	−0.54	0.51	ns
	Heron Island	155	0.23	1.85	21	−0.03	0.08	<0.05
Stylophora pistillata	Lord Howe	177	0.13	2.17	34	−0.87	0.49	<0.01
	Heron Island	194	0.33	1.89	22	−0.38	−0.04	ns

For all species at Lord Howe Island, there was no significant effect of site, except for *Isopora cuneata* (2-sample KS test, p < 0.05). A few larger colonies of *I. cuneata* were observed at Horseshoe Reef, leading to a larger mean colony size and resulting in the significant variation between the sites. To display the variation among species and locations, the data were pooled between sites (Figs. 2 & 3). At Heron Island, there was no significant effect of site (2-sample KS test, p > 0.05) for all species, and the data were pooled between sites. Comparing between Lord Howe Island and Heron Island, there was a significant variation in the size-frequency distributions for each species (2-sample KS test, p < 0.05).

The staghorn *Acropora* spp. were the largest corals recorded for each site. There was a significant difference in colony size among species at Lord Howe Island (2-Way ANOVA, $F_{4,989} < 0.01$, p < 0.01) but not between sites (2-way ANOVA, $F_{1,989} = 0.17$, p = 0.683). Based on the Tukey's post hoc test, the colony size of *A. yongei* for both Horseshoe Reef and North Bay was significantly greater than that of all other species. Similarly at Heron Island, there was a significant difference in colony size among species (2-way ANOVA, $F_{4,847} = 4.52$; p = 0.001) but not between sites (2-way ANOVA, $F_{1,847} = 1.791$, p = 0.181). Based on Tukey's post hoc test, the colony size of *A. muricata* was significantly greater than that of all other species. Comparing between locations, the mean
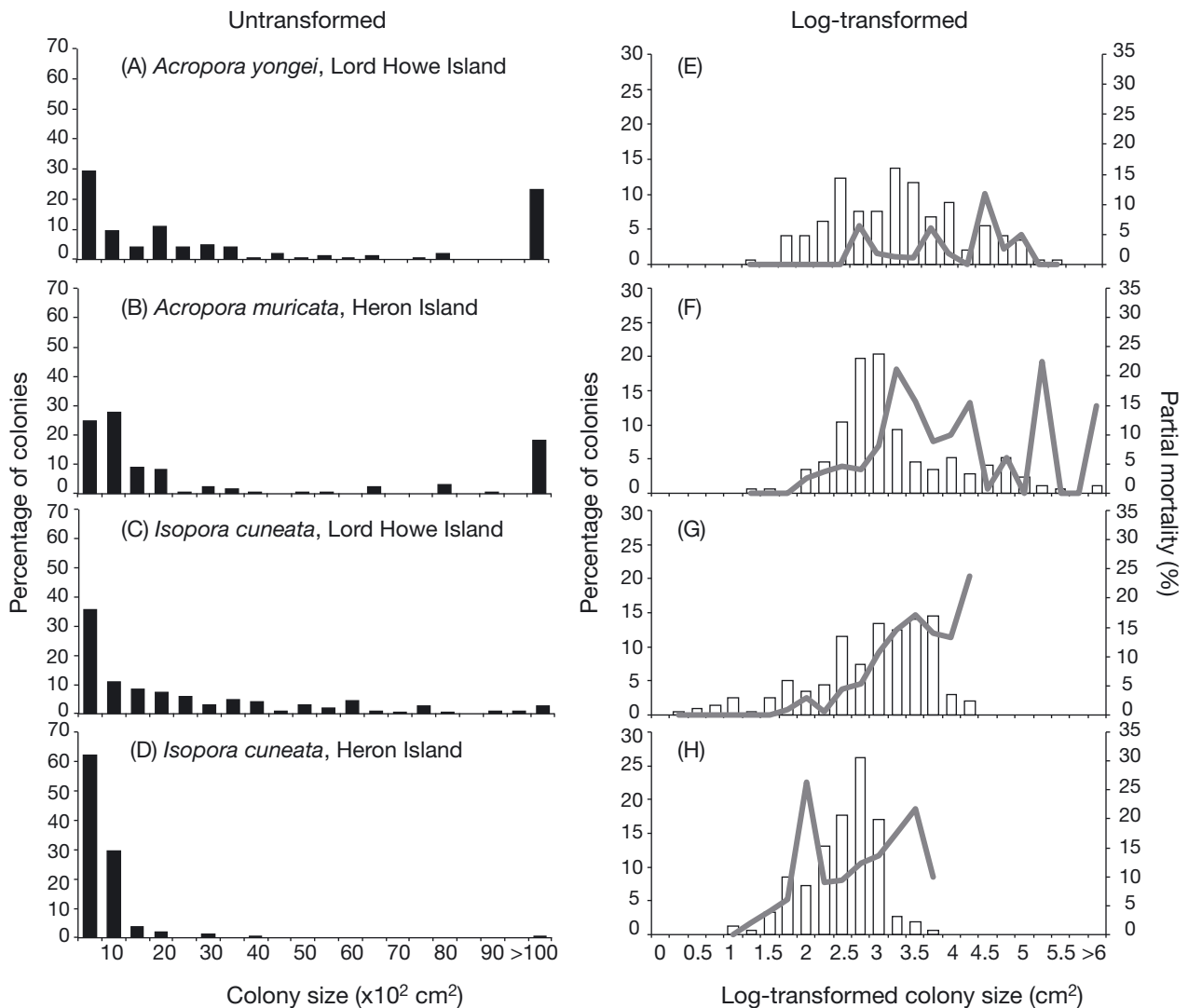

Fig. 2. (A–D) Untransformed and (E–H) log-transformed size-frequency distributions of (A,E) *Acropora yongei*, (B,F) *Acropora muricata* and (C,D,G,H) *Isopora cuneata* at (A,C,E,G) Lord Howe Island and (B,D,F,H) Heron Island. The grey line indicates average partial mortality (%) for each size class
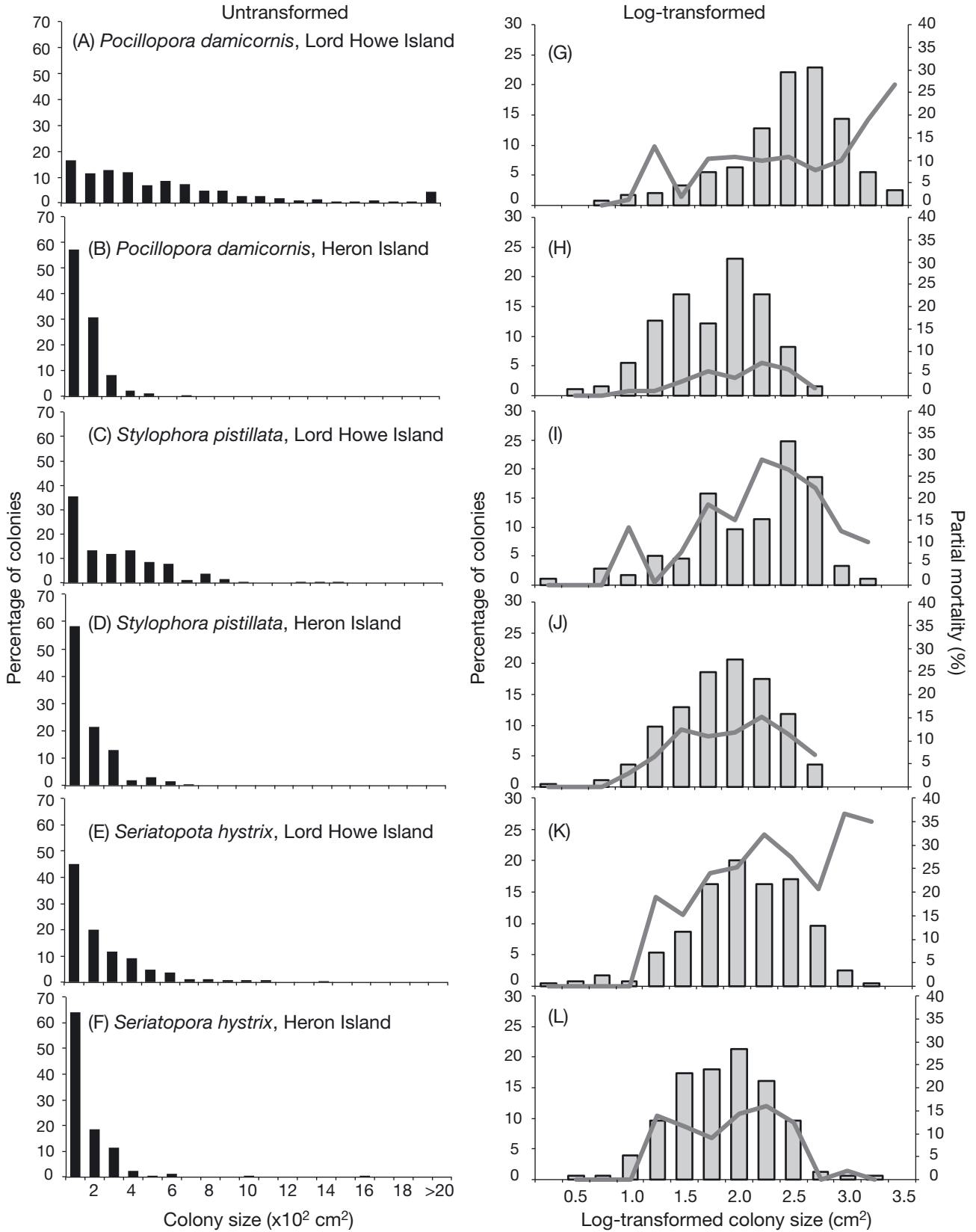
Fig. 3. (A–F) Untransformed and (G–L) log-transformed size-frequency distributions of (A,B,G,H) *Pocillopora damicornis*, (C,D,I,J) *Stylophora pistillata* and (E,F,K,L) *Seriatopora hystrix* at (A,C,E,G,I,K) Lord Howe Island and (B,D,F,H,J,L) Heron Island. The grey line indicates average partial mortality (%) for each size class
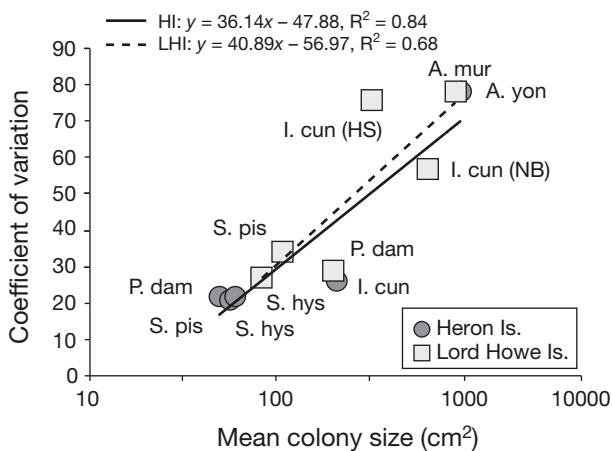
Fig. 4. Comparison of coefficient of variation (CV) and mean colony size for both Lord Howe Island (LHI) and Heron Island (HI) corals, *Acropora muricata* (A. mur), *Acropora yongei* (A. yon), *Isopora cuneata* (I. cun), *Stylophora pistillata* (S. pis), *Seriatopora hystrix* (S. hys), and *Pocillopora damicornis* (P. dam). *I. cuneata* had significant variation at Lord Howe Island, and therefore, the CV was plotted for both Horseshoe Reef (HS) and North Bay (NB)

colony size for *A. muricata* at Heron Island and *A. yongei* at Lord Howe Island did not differ significantly (Student's *t*-test, p > 0.05). However for all other species, the colony size was significantly larger at Lord Howe Island (Student's *t*-test within species, p < 0.05).

Acropora muricata and *A. yongei* both had a larger percentage (23 and 18%, respectively) of colonies in the largest class size (>10 000 cm^2) compared to the other species (Fig. 2). *Isopora cuneata* at Lord Howe Island and Heron Island had a few colonies (1 to 2%) in the largest size class. The largest discrepancy between locations comes from the percentage of colonies in the smallest size class; *I. cuneata* at Heron Island had almost twice (62%) as many colonies in the smallest size class (500 cm^2) compared to the same species at Lord Howe Island (35%). For *Pocillopora damicornis* at Lord Howe Island, 16% of the colonies were in the smallest size class (100 cm^2) compared to 57% at Heron Island, a 3-fold increase (Fig. 3). Similarly for *Stylophora pistillata*, there was almost double the number of colonies in the smallest size class at Heron Island (58%) compared to Lord Howe Island (35%). Colonies of *Seriatopoa hystrix* were the smallest ones recorded at both locations, and not surprisingly this species had the greatest number of colonies in the smallest size class (64% at Heron Island, and 45% at Lord Howe Island).

Predominantly, the percentage of partial mortality increased as the colonies became larger. Partial mor-

tality significantly varied between Lord Howe Island and Heron Island (Student's *t*-test within species, p < 0.05) for all species except *Isopora cuneata* (Student's *t*-test, p > 0.05). Partial mortality in the staghorn *Acropora* species was greater at Heron Island than at Lord Howe Island (Student's *t*-test, *t* = 3.824, p < 0.01) (Fig. 2E,F). Conversely, partial mortality was greater at Lord Howe Island compared to Heron Island for *Pocillopora damicornis* (*t* = −3.988, p < 0.01), *Stylophora pistillata* (*t* = −3.966, p < 0.01) and *Seriatopora hystrix* (*t* = −5.019, p < 0.01) (Fig. 3G–L).

To further analyse the distributions, the descriptive statistics of the log-transformed colony size data were evaluated among species and between locations (Table 1). The first descriptive statistic, the geometric mean, significantly varied among species (ANOVA, $F_{5,6} = 8.51$, p < 0.05): *Acropora muricata* had the greatest mean colony size (3.26 cm^2), similar to that of *A. yongei* (3.23 cm^2), and *Seriatopora hystrix* at Heron Island had the smallest mean colony size (1.85 cm^2). The geometric mean size was greater at Lord Howe Island for all species except *Isopora cuneata*. The CV varied greatly, ranging from 21 for *S. hystrix* at Heron Island, to 78 for both *Acropora* species (Fig. 4). There was a positive correlation of the CV and mean colony size (Fig. 4). With the log-transformed data, all coral species were negatively skewed or skewed to the left, except *A. yongei* and *A. muricata*. The total range of skewness (g_1) was −1.24 (for *I. cuneata* at Horseshoe Reef) to 0.92 (for *A. muricata*). Kurtosis (g_2) displayed the greatest range, being negative for *A. yongei* (−0.50) and highly positive (1.92) for *I. cuneata* at Horseshoe Reef. In addition, the KS test for normality was significant (p < 0.05) for all species after log-transformation except for *I. cuneata* at North Bay, *S. hystrix* at Lord Howe Island and *Stylophora pistillata* at Heron Island. Therefore, the hypothesis that the distributions are normally distributed was only accepted for these latter 3 coral populations.

DISCUSSION

The present study is the first to explicitly compare size-frequency distributions of corals between a subtropical and tropical reef. Untransformed size-frequency distributions for all coral species, regardless of location, were strongly and positively skewed, reflecting a preponderance of smaller size classes (Figs. 2 & 3). Similar positively skewed size-frequency distributions are apparent for virtually all coral species and all study locations (e.g. Hughes &

Jackson 1985, Meesters et al. 2001). However, equivalent coral taxa exhibit more strongly skewed size-frequency distributions at Heron Island, on the GBR, than at the subtropical location, Lord Howe Island. Assuming a constant supply of recruits to the population (i.e. no recruitment failure), strong positively skewed size-frequency distributions are generally considered to reflect higher mortality, especially among smaller colonies (Babcock 1991, Hughes & Tanner 2000). Accordingly, changes in the abundance of colonies between successive size classes were much greater for small colonies than for larger colonies. The trend of high mortality among the smaller size classes is consistent with known declines in the probability of whole colony mortality with increases in colony size (Hughes et al. 1992).

Growth is strongly temperature-dependent (e.g. Lough & Barnes 2000) and is likely to lead to variation in size-frequency distributions along large-scale latitudinal gradients. Compared to tropical locations, coral growth at Lord Howe Island is slower (Harriott 1999), and this may be reflected in the size-frequency distributions. Highly centralized, peaked distributions may represent a slower transition through the size classes as a result of slower growth rates (Adjeroud et al. 2007). However, for most coral taxa in our study, the size-frequency distributions were more peaked at Heron Island than at Lord Howe Island. This suggests that high mortality of the small and large colonies may be more dominant in structuring the size-frequency distributions at tropical locations than growth rates.

The magnitude of differences in the growth rates among coral species contributed to the variation in size-frequency distributions; *Acropora yongei* grew at least 2-fold faster than all other corals at Lord Howe Island during the summer (Anderson et al. 2012). These differences demonstrate apparent life-history trade-offs whereby fast-growing corals, such as *A. yongei*, that easily fragment have a high rate of mortality, especially in smaller size classes. Fragmentation causes corals to regress in size classes, contributing to a large number of corals in the smaller size classes (Wallace 1985). Similar trends of partial mortality were observed for *A. muricata* at Heron Island. The fast growth of *Acropora* spp. allows fast population turnover and persistence of larger colonies as they escape the risk of whole colony mortality (Hughes et al. 1992). Growth rates of corals are slower on Lord Howe Island compared to tropical reefs (Harriott 1999). However, the variations in life histories among corals are preserved between temperate and tropical reefs, despite this difference in growth rate.

Partial mortality is crucial in determining the size of coral colonies, as death of part of the living tissue can cause colonies to regress in size (Hughes 1984), similar to fragmentation (Wallace 1985). In our study, partial mortality increased with increasing size classes, supporting results from other studies and locations (e.g. Babcock 1991, Bak & Meesters 1998). The increase in partial mortality in relation to colony size was similar among the species suggesting the factors causing partial mortality (e.g. sedimentation, predation) are similar regardless of locations. However, partial mortality of *Pocillopora damicornis*, *Stylophora pistillata* and *Seriatopora hystrix* was greater at Lord Howe Island than at Heron Island. Despite the reduced partial mortality at Heron Island, colonies were generally smaller at Heron Island, suggesting a greater incidence of whole colony mortality. These results are similar to those of Bauman et al. (2013), who recorded a smaller mean colony size in the southern Persian Gulf than in the northern Gulf, which experiences greater chronic and acute disturbances.

The increased frequency of partial mortality with increasing size reflects an increased frequency of exposure to disturbances at both locations, despite their very different regimes of disturbance. The similarity suggests that there is a comparable frequency of disturbances affecting colonies at small scales on both temperate and tropical reefs, such as predation, fragmentation, sediment accumulation and competitive interactions, but the frequency is likely to be greater at Lord Howe Island as indicated by the greater partial mortality among the majority of corals. At temperate locations, seasonal competition with macroalgae can lead to mortality in small corals and cause partial mortality in larger corals. However, it is unclear if the macroalgae directly colonised the colonies causing mortality, or if the colony bleaches (Harrison et al. 2011), killing a portion of the colony which is then invaded by its space competitor (Crossland 1984, Hoey et al. 2011). At Heron Island, increased frequency of cyclones and crown-of-thorn-starfish outbreaks (Osborne et al. 2011) can lead to increased incidence of whole colony mortality.

Once log-transformed, the size-frequency distributions of all coral species were negatively skewed, and the majority of the corals had positive kurtosis, displaying over-centralized, peaked distributions. Skewness was reflective of the variation in disturbance regimes between a subtropical and tropical location, in addition to partial mortality. *Isopora cuneata*, *Pocillopora damicornis*, *Seriatopora hystrix* and *Stylophora pistillata* were negatively skewed at

both locations. However, the degree of skewness was less at Heron Island compared to Lord Howe Island, suggesting a lower probability of transitioning to the larger size classes (Adjeroud et al. 2007) due to a higher disturbance regime at the tropical location.

Positive kurtosis indicates high mortality of small and large colonies or slow transitioning through the size classes as a result of slow colony growth (Adjeroud et al. 2007). The flat size-frequency distribution of *Acropora yongei* at Lord Howe Island is characteristic of the genus' fast growth and high population turnover, as reported for *A. hemprichii* in the Red Sea (Guzner et al. 2007). Interestingly, kurtosis was positive at Heron Island for *A. muricata*. At Heron Island, increased incidence of disturbance is likely causing greater mortality to the smaller size classes, leading to the peaked distribution. A negative kurtosis was observed in *Acropora* spp. following a bleaching event in Kenya, where the size-frequency distribution shifted from positive to negative kurtosis (McClanahan et al. 2008). At Lord Howe Island, the first reported mass-bleaching of corals was recorded in 2010 and caused only moderate (up to 25%) coral mortality (Harrison et al. 2011, Hoey et al. 2011). There is limited evidence of any other major disturbances which typically affect tropical locations (e.g. outbreaks of crown-of-thorns starfish and severe tropical storms; Osborne et al. 2011) affecting these coral assemblages. Therefore, the characteristic fast growth of *A. yongei* is likely structuring its size-frequency distribution at Lord Howe Island, as opposed to disturbances.

The CV displayed marked variation among the coral species relative to colony size (Fig. 4). The present study contradicts that of Bak & Meesters (1998), who found the CV to be negatively related to the mean size of the coral species, whereas for the coral species in the present study, the CV was positively related (Fig. 4). However, a major difference between the studies was the species used: Bak & Meesters (1998) analysed massive or encrusting species. In the present study, the CV was similar among locations when compared to mean colony size, as evident in the similar slopes between Heron Island and Lord Howe Island, suggesting similar variance among coral populations at each location as the colonies increase in size. A higher CV has been associated with a very high proportion of very small corals (Bak & Meesters 1998), suggestive of large fluctuations in recruitment and mortality of the smaller size classes. At Lord Howe Island, however, the coral populations are sustained by very low and presumably fairly constant levels of recruitment (Hoey et al. 2011). Recruit assemblages at Lord Howe

Island tend to be dominated by the Family Pocilloporidae, Family Poritidae and sub-genus *Isopora* (Harriott 1992, Hoey et al. 2011), which all release brooded planulae (Harriott 1992). This is a stark contrast to the GBR where mass-spawning corals recruit in much higher abundances than brooding corals (Hughes et al. 1999). However, such shifts in the predominant reproductive strategies (towards brooding) of corals at peripheral locations have been well documented (Baird et al. 2009).

In conclusion, the size-frequency distributions of corals at Lord Howe Island and Heron Island varied greatly among species, yet they were all mostly negatively skewed and flattened distributions. The major exceptions were the fast-growing *Acropora* spp. The variations in the size-frequency distributions between locations were strongly suggestive of variation in local disturbance regimes. Smaller mean colony size at Heron Island demonstrated the more severe disturbance regime at this location. Recorded incidence of partial mortality was greatest at Lord Howe Island, but this may reflect the longer time to repair injuries due to slower coral growth at tropical locations (Harriott 1999) rather than increased rates of injury. These results strengthen our understanding of inter-specific variation in size-frequency distribution as a result of inherent life-history strategies. Ongoing research to investigate the size-structure at Lord Howe Island over time, thus analyzing changes in the coral communities, will be vital in determining the fate of corals at this high-latitude reef. This will help to identify whether subtropical reefs will provide important refugia for tropical reef corals subject to increasing effects of global climate change.

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