

1 *Colony size frequency distribution across gradients of reef health in disturbed coral reefs in*
2 *Northeast Peninsular Malaysia*

3 **Gilles Gael Raphael Bernard¹, Alexandra Lucie Kellam¹, Sebastian Szereday^{1,2*}**

4 ¹Coral Reef Research and Monitoring Project, Lang Tengah Turtle Watch (LTTW), Jalan
5 Bukit Tunku 17, Bukit Tunku, 50480, WP. Kuala Lumpur, Malaysia.

6 ²Social Enterprise for Coral Reef Conservation and Restoration, Coralku Solutions, Jalan
7 Burhanuddin Helmi, Taman Tun Dr Ismail, 60000 WP. Kuala Lumpur, Malaysia.

8 *** Correspondence:**

9 Sebastian Szereday

10 sebastian@coralku.org

11

12 **Author contribution:** SS conceived the study. GGB, ALK and SS collected the data. GGB
13 and SS designed analysis. GGB analysed the data and wrote the original draft. SS rewrote and
14 edited the original draft. All authors edited and approved the final draft and agreed to submit
15 for publication.

16 **Abstract**

17 Coral reefs globally are experiencing chronic stress leading to the deterioration of health and
18 functionality. Analysis of size frequency distribution (SFD) of hard corals enables post hoc
19 assessments of major demographic events (e.g., recruitment and mortality) that follow
20 ecological disturbances. Here, we present an evaluation of current reef health, SFD and
21 recruitment of 37 morpho-taxa in Northeast Peninsular Malaysia. Results highlight stress
22 viable demographic structure of massive taxa (e.g., massive *Porites*) and significant differences
23 of SFD across gradients of reef health, whereby degraded sites were predominantly
24 characterized by negatively skewed (e.g., large colonies) and leptokurtic (e.g., high population
25 turnover) distribution of dominant hard coral taxa. Ultimately, results suggest that locally coral
26 reef degradation can exceed tipping points, after which annual monsoon conditions and
27 degraded reef substrates interact to reinforce and manifest negative feedback loops, thereby
28 impeding demographic recovery, and altering coral SFD and population assemblage.

29 **Keywords:** Demography, Size frequency distribution, Hard Corals, Malaysia, Coral
30 Recruitment, Coral Cover, Community Composition, Ecosystem Disturbance, Chronic
31 Stressors, Marine Ecology

32 **1. Introduction**

33 Coral reefs have entered a crucial decade in which climate change associated extremes (e.g.,
34 global ocean warming and cyclones) are posing an existential threat to coral reef survival
35 worldwide (Hughes et al. 2017a, 2017b). Multiple, synchronous and synergistic disturbances
36 of natural (e.g., seasonal storms) and human origin (e.g., overfishing, nitrification, coastal
37 development) are having a direct impact on coral reefs worldwide and their population viability
38 (Hughes and Connell 1999; Bellwood et al., 2004; Harborne et al., 2016). Population dynamics,
39 function and resilience of ecosystems are co-determined by the reproductive viability of a
40 population, driven by the rates of births and deaths, and the amount of sexually mature
41 individuals (Weinstein and Pillai, 2015). Inherent demographic variations across time and
42 space are the results of events altering these processes, whereby present-day demographic
43 structures can hold clues over time and extent of past system-wide perturbations (Swedlund,
44 1978). In clonal organisms, such as hard corals, responses and adaptations to environmental
45 disturbances are reflected in the size frequency distribution (SFD) of individual populations
46 (Bak and Meesters, 1998), and these often vary greatly among taxonomic groups (Meesters et
47 al., 2001). Moreover, size-dependent mortality following large-scale disturbances such as coral
48 bleaching and tropical storms (Loya et al., 2001; Baird and Marshall, 2002) likely dictates
49 shifts in population assemblage and size structure (Massel and Done, 1993; McClanahan et al.,
50 2001; Anderson and Pratchett, 2014). Modifications in the distribution and frequency of
51 particular size groups can assert major changes in hard coral community assemblages with
52 cascading impacts on the structural habitat of reef species, and therefore, on the functional and
53 economic value of coral reefs (Graham, 2014; Darling et al., 2017). Thus, disturbance intensity
54 and frequency, as well as taxon-identity and population size structure co-determine the
55 resilience and trajectory of coral reefs (Bak and Meesters, 1998, 1999; McClanahan et al.,
56 2008; Darling et al., 2013; Dietzel et al. 2020).

57 The study of age-size relationships of sedentary organisms such as trees (dendrology) has
58 been well-established to identify fluctuations and disturbances in the biophysical environment
59 (Fonti et al., 2009; Loader et al., 2010). Similar methods (e.g., sclerochronology) have been
60 applied to coral reef research to reconstruct historic environmental variability (Barnes, 1970;
61 Hudson et al., 1976; Lough and Cantin, 2014). However, identifying age-size relationships in
62 scleractinian corals remains challenging due to fragmentation and partial mortality of
63 individual colonies, as well as fusion of genetically different colonies (Hughes and Jackson,
64 1980; Babcock, 1991). The scleractinian demographic structure and SFD is highly variable
65 across fine spatial scales such as individual reefs and across multiple depths (Adjeroud et al.,

66 2007, 2015; Kramer et al., 2020), but is an appropriate method to study scleractinian
67 population dynamics and status in field-assessments (Hughes and Connell, 1987). Indeed,
68 vital functional traits that underpin the functioning and resilience of coral reefs, such as
69 fecundity, growth, partial and total mortality (Darling et al., 2012), are influenced by colony
70 size rather than age (Hughes and Jackson, 1985; Hall and Hughes 1996). Therefore, colony
71 SFD is suitable to compare inter- and intra-specific variation in community size structure as
72 to provide insights into past ecosystem wide disturbance events (Bak and Meesters, 1998),
73 and to elaborate on demographic strategies of scleractinian taxa that underline changes in
74 coral cover and reef health (Miller et al., 2016). Ultimately, SFD assessments are viable tools
75 to estimate the impacts of multiple and synchronous stressors on scleractinian assemblages
76 and populations (Fong and Glynn, 1998; Smith et al., 2005), particularly when historical and
77 qualitative data sets are absent and parochial. Considering the multitude of present stressors
78 on coral reefs (Hughes and Connell, 1999; Bellwood et al., 2004; Hughes et al., 2017b), as
79 well as the lack of demographic assessments in field studies, SFD and demographic structure
80 assessments are urgently required to understand ecological changes in hard coral communities
81 under continuous environmental stress (Edmunds and Riegl, 2020).

82 In 2003, the average coral cover in the Indo-Pacific was reduced to approximately 22 %, after
83 decreasing annually by 1-2 % between the 1980s and 2003 (Bruno and Selig, 2007). However,
84 the percent coral cover metric is not conclusive and cannot detect significant changes in the
85 capability of coral reefs to recover and maintain ecosystem functioning (Hughes et al., 2010;
86 Edmunds & Riegl, 2020), as shifts in cover are underlined by changes in demographic and size
87 structure (Miller et al., 2016; Dietzel et al., 2020). Despite high regional diversity of hard coral
88 species (Huang et al., 2015), and high economic value of coral reefs (Kamarruddin et al., 2013;
89 Sukarno et al., 2015), data on Malaysian hard coral reefs is limited to benthic cover assessments
90 with a focus on hard coral reef coverage and taxonomic richness (Harborne et al., 2000).
91 Qualitative and quantitative information on hard coral communities, particularly coral
92 recruitment, general demographic studies and studies detailing community size structure, are
93 distinctively lacking or are unavailable in Malaysia (Praveena et al., 2012). As coral reefs in
94 Peninsular Malaysia are in a state of decline (Toda et al., 2007; Reef Check Malaysia, 2019),
95 studies are required to determine stochastic shocks and pulses that underpin population
96 dynamics and recovery, such as overall demographic structure (e.g., ratio of coral recruitment
97 and sexually mature individuals). In view of limited historical data and in consideration of
98 current disturbance regimes, determining the size-frequency distributions can serve as a post

99 hoc assessment of demographic events (mortality, recruitment, population turnover), to provide
100 insights into demographic shifts and to elaborate future trajectories.

101 Two theories have been suggested to explain shifts and non-equilibria states of hard corals
102 demographics. Firstly, a transition towards relatively more abundance of large colonies has
103 been demonstrated in the Caribbean (Bak and Meesters, 1999; Meesters et al., 2001; Miller et
104 al., 2016) and the Great Barrier Reef (Dietzel et al., 2020), particularly post multiple large-
105 scale disturbance events. In contrast, a shift towards relatively more small colonies has been
106 documented in French Polynesia (Adjeroud et al., 2015), in the western Indian Ocean
107 (McClanahan et al., 2008), and in the in the Red Sea (Riegl et al., 2012), whereby constant
108 impulses of coral recruitment were suggested to further drive shifts in SFD in the Red Sea and
109 partially in French Polynesia. Moreover, persistent ecosystem-wide disturbance shocks and
110 chronic stress exposure systematically narrow colony size ranges and homogenize community
111 size structures (Cannon et al., 2021). Consequently, this study investigated 1.) SFD and
112 demographic structure in Northeast Peninsular Malaysia across a continuum of reef health (e.g.,
113 cover, diversity, density, etc.), which results from biophysical reef site conditions (e.g., leeward
114 vs windward), and negative impacts of anthropogenic origin (sewage, coastal development,
115 overfishing and rising SST). Secondly, we investigated 2.) present patterns of coral recruitment,
116 to determine whether recent stochastic impulses of coral recruitment possibly resulted in the
117 present demographic structure (Riegl et al., 2012). Ultimately, these findings highlight 3.) hard
118 coral assemblages and taxa that are potentially more tolerant of multiple stressors and are more
119 likely to persist under current and future scenarios of persistent (human) impacts. Hereby, post
120 hoc evidence for the second hypothesis (shift to smaller colonies) should highlight recently
121 established populations (e.g., after disturbance) of any given taxa with a homogenous size
122 structure, composed of smaller colonies and a peaked distribution (*sensu* McClanahan et al.,
123 2008; Riegl et al., 2012), whereas potentially stress tolerant taxa should present with a more
124 evenly distributed spectrum of size classes (*sensu* Adjeroud et al., 2015). Additionally, reefs at
125 advanced stages of degradation should be characterized by highly centralized distribution of
126 predominantly weedy taxa and a preponderance of large colonies (e.g., disturbance ‘survivors’;
127 *sensu* Meesters et al., 2001; Dietzel et al., 2020). Lastly, intra-specific differences in SFD
128 should be well defined across gradients of reef health, (*sensu* Bauman et al., 2013), to
129 accurately highlight whether taxon identity or reef conditions underline the hard coral SFD.
130 This study represents the first analysis of the demographic structure and SFD of scleractinian

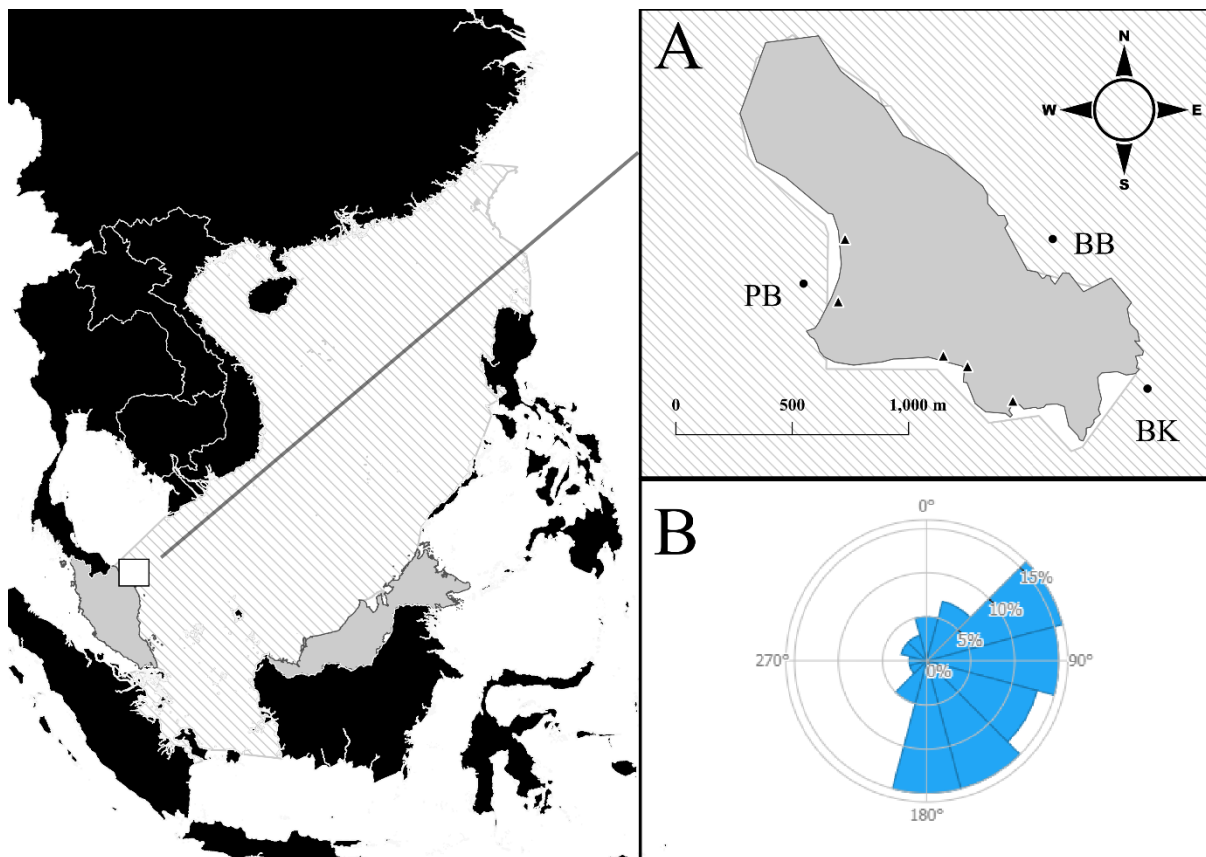
131 taxa in Peninsular Malaysia to date and provides fundamental insights to guide future
132 management of hard coral reefs in Peninsular Malaysia.

133 **2. Methods**

134 2.1 Study location

135 Fieldwork and data collection was carried out between September and October 2019 around
136 Pulau Lang Tengah (Pulau=Island) in Northeast Peninsular Malaysia (5°47'49.7"N,
137 102°53'45.0"E) (Figure 1). Pulau Lang Tengah is included in the Pulau Perhentian and Pulau
138 Redang marine park, and is legally protected from resource extraction and fishing (Praveena et
139 al., 2012). However, monitoring of fishing activities and enforcement of policies is limited
140 (Kimura et al., 2022). Despite legal protection from fishing pressure, over- and illegal fishing
141 is a significant problem in Malaysia (Stodbuzki et al., 2006, Asia-Pacific Economic
142 Cooperation, 2008; Ghazali et al., 2019). Low numbers of herbivorous reef fish have been
143 documented around Pulau Lang Tengah, whereby total herbivorous fish abundance was lowest
144 at leeward sites (Chew, 2018, unpublished data), suggesting elevated pressure on leeward coral
145 reef resilience and colony size in view of reduced herbivorous grazing (McClanahan et al.,
146 2001; Green and Bellwood, 2009). Thus, three sites along a set of human stressors and along a
147 wind gradient were selected: Pasir Besar (PB), Batu Kucing (BK) and Batu Bulan (BB),
148 whereby BB and BK are windward facing fringing reefs, and PB is a leeward lagoon (Figure
149 1A-B). Wind frequency and direction were determined by using web-based monitoring
150 products (Global Wind Atlas 3.0). In addition, all sites are subjected to the annual Northeast
151 Monsoon (November to February), which intensifies hydrodynamic conditions and increases
152 wave intensity; factors that are known to consequentially influence scleractinian colony SFD
153 (Madin and Connolly, 2006; Madin et al., 2012, 2014). Moreover, the leeward shore has been
154 extensively developed (Figure 1A), supposedly resulting in physical degradation of adjacent
155 coral reefs (Praveena et al., 2012), as well as untreated sewage discharge from nearby resorts,
156 further pressuring leeward reef assemblages (Wooldridge et al., 2012; Reef Check Malaysia,
157 2019). Physical reef degradation may further result in larger quantities of mobile substrate (e.g.,
158 coral rubble) which impede natural reef recovery due to sedimentation and physical
159 interference (Fox et al., 2019; Wolfe et al., 2021). Ultimately, there is a clear delineation of
160 local site pressures with markedly higher negative anthropogenic impacts on leeward coral
161 reefs, steering from the close proximity of leeward coral reefs to the source of the disturbance
162 (e.g., beach resorts) and subsequent secondary impacts (Fisher et al., 2008). Lastly, regional

163 ecosystem wide disturbance events that likely impacted scleractinian SFD at all sites, such as
164 coral bleaching (McClanahan et al., 2001, 2008), have been recorded across the entire east
165 coast of the Malayan Peninsula in 1998 (Kushairi, 1998), in 2010 (Tan and Heron, 2011; Guest
166 et al., 2012) and in May 2019 at all sites around Pulau Lang Tengah before data collection
167 (Szereday and Affendi, 2022). Moreover, tropical cyclone Pabuk significantly reduced live
168 hard coral cover in January 2019 in Northeast Peninsular Malaysia (Reef Check Malaysia,
169 2019; Safuan et al., 2020), suggesting probable impacts on hard coral SFD regionally.
170 Subsequently, any observed differences in SFD and general coral reef health may partially be
171 the result of synergistic impacts from coral bleaching (e.g., 1998 and 2010), hydrodynamic
172 disturbances (e.g., cyclone Pabuk 2019, annual monsoon), sedimentation (amplified by
173 physical degradation after coastal development), overfishing, eutrophication and fundamental
174 differences in hard coral assemblages and colony spatial-competition. Therefore, our deliberate
175 study design attempted to highlight differences in hard coral SFD across a continuum of reef
176 health and under various sets of local and regional stressor agents. This determined focus on
177 site differences (e.g., comparing degraded to healthier reef sites) is essential as historical data
178 on coral reef health and population size structure are unavailable for Northeast Peninsular
179 Malaysia, and baseline comparisons to studies prior to the occurrence of mass disturbances is
180 not possible. Hereby, it is important to note that healthier reef sites do not necessarily reflect
181 pristine conditions of former reefs, and this study represents a post hoc analysis of possible
182 demographic events that steered from human disturbances.



183

184 **Figure 1** | Location of Pulau Lang Tengah (A) in Northeast Peninsular Malaysia and within
185 the South China Sea basin (dashed line area). Survey sites are shown by circles and
186 abbreviations (PB – Pasir Besar; BK – Batu Kucing; BB- Batu Bulan). A wind frequency rose
187 (B) illustrates wind direction and frequency at island scale. Locations marked with triangles
188 along the shoreline demarcate coastal development sites (e.g., beach resorts).

189

190 2.1. Benthic surveys and reef health indicators

191 At each site, benthic surveys were conducted along three 50 meters transects (measure tapes)
192 laid parallel to the shore (Figure 1) and across multiple depths: shallow (4-8 m), intermediate
193 (8-12 m) and deep (15-20 m). Transect lines were anchored with weights to ensure maximum
194 tape stretch and to follow the reef contour. Surveys were performed by three divers in equal
195 proportion to reduce observer bias. Each transect consisted of one 50 meters line intercept
196 transect (LIT) and one 30 x 1 m belt transect. To reduce spatial sampling biases, belt transects
197 were broken up into six 5 x 1 m subsets at randomized points along the 50 m transect, and were
198 split equally across both sides of the tape (total of 15 x 1 m per side). Belt transect data was
199 used to determine scleractinian colony size frequency distribution and various reef health
200 indicators (e.g., density and diversity), whereas LITs were used to measure benthic substrate
201 composition in order to further approximate reef health (Teichberg et al., 2018). Hereby, non-

202 living substrate included sand, rock, recently killed corals and coral rubble, and following live-
203 benthic substrates were recorded: hard corals, soft corals, sponges, sea anemones, algae, giant
204 clams, zoanthids and corallimoprhs, as well as smaller benthic organisms (e.g., organ pipe
205 corals, fern corals, etc.). All living benthic substrates recorded during LITs were measured from
206 the colonies edge-to-edge and to the nearest centimetre, occasionally requiring the use of a
207 reference stick to perpendicularly project the colony edges onto the measure tape. This resulted
208 in complete measurements of colony length along the substrate rather than shortened intercept
209 measurements, whereas non-living substrates were recorded to the nearest centimetre by
210 measuring the intercept length. Subsequently, the sum of all recorded lengths along the transect
211 tape exceeded the actual 50 meters transect length. Therefore, following formula was applied
212 to calculate percent benthic coverage of a benthic substrate group (e.g., hard coral cover), where
213 TL is the standard 50 meters transect length:

214

$$215 \quad \text{Hard Coral Cover} = \frac{\sum \text{Hard Coral Lengths}}{\sum \text{Living Substrate Lengths}} * (TL - \sum \text{Non - Living Substrate Length})$$

TL

216

217 Note, hard coral cover includes the percent cover of *Heliopora spp.* colonies, due to their reef
218 building function on Indo-Pacific reefs. (Colgan, 1984). Individual hard coral colonies were
219 defined as autonomous, free-standing coral colonies with live tissue. Autonomous colonies
220 with fragmented live tissue resulting from partial colony mortality were considered a single
221 colony (Bak and Meesters, 1998), and the amount of partial mortality was visually estimated
222 in steps of 5% relative to the total colony surface area. Lastly, LIT measurements of hard coral
223 colony length were used to measure minimum and maximum colony length in addition to size
224 class that were recorded during belt transects.

225 Further indicators of reef health, such as taxonomic richness, evenness and colony density of
226 various size groups as well as colony size (Fisher et al., 2008), were calculated for each site
227 based on belt transect data to highlight coral reef health across sites. Belt transects increased
228 sampling size, accuracy, and reduced sampling errors of LITs, which are not suitable to detect
229 very small colonies (e.g., < 3 cm) (Obura and Grimsditch, 2009). Along belt transects, the size
230 of each hard coral colony encountered (including octocoral *Heliopora spp.*), was recorded by
231 measuring their maximum horizontal and linear extension with a graduated reference pipe.
232 Colony size classes were based on Obura and Grimsditch (2009): 0-2.5 cm, 2.5-5.0 cm, 5-10

233 cm, 10-20 cm, 20-40 cm, 40-80 cm, 80-160 cm, 160-320 cm and colonies > 320 cm. Here,
234 colonies in the two smallest size classes (< 5cm) were considered recruits. Furthermore, to
235 reduce Type 1 and Type 2 sampling errors (Zvuloni et al., 2008), only colonies whose centre
236 was within the belt were recorded (Nugues and Roberts, 2003), in addition to colonies with at
237 least 40% of colony surface area inside the belt.

238 Taxonomic identification was performed using the Coral Finder 3.0 (Kelley, 2016), and the
239 unique morphological appearances of individual colonies were recorded. Differences in SFD
240 and demographic structure can be detected on taxon level, and greater taxonomic resolution
241 may lead to more pronounced differences. However, correct identification of species during in-
242 water surveys based on morphological characteristics remains challenging. Therefore, to obtain
243 optimal resolution while minimizing identification biases, survey analysis of SFD and
244 demographic structure was conducted on distinctive morphological and taxonomic levels (e.g.,
245 *massive Porites*, *encrusting Porites*), henceforth referred to as morpho-taxon. This resolution
246 is suitable to describe demographic structure and SFD driven by taxon identity and functional
247 traits (growth, fecundity, etc.), which are phylogenetically conserved on genus and
248 morphological level (Darling et al., 2012; Alvarez-Noriega et al., 2016). In addition, *Porites*
249 species with an encrusting plate and up-growths (exclusively comprising *Porites rus* and
250 similar species), were grouped together due to their distinctive morphology and are hereafter
251 referred to as *Porites spp. (rus)*. Comparison of SFD on morphological level was based on
252 seven groupings: branching forms (e.g. arborescent, digitate, corymbose, hispidose), massive
253 forms (massive and sub-massive), encrusting (flat crust), encrusting with up-growths (e.g.,
254 crusts with short vertical branches and with columns), laminar forms (e.g. vase, plate, foliose),
255 columnar colonies and solitary (free-living) colonies.

256 2.2. Size frequency distribution (SFD) and statistical analysis

257 Data and statistical analyses were performed in R software (R Core Team, 2020). Prior to
258 analysis, non-normality of the SFDs was formally tested with Shapiro-Wilk tests (SW, package
259 ‘RVAideMemoire’) (Hervé, 2021). To reduce non-normality, colony sizes were \log_{10}
260 transformed by using the middle value of each size class (the middle value used for the size
261 class > 320 cm was 480 cm). The log transformed SFD distribution of morphological groups
262 and morpho-taxa was compared among sites and depths. Hereby, we used Anderson-Darling
263 (AD) k-samples tests (package ‘kSamples’) (Scholz and Zhu, 2019), to compare intra-
264 morphological and intra-taxonomic SFD differences across sites. Anderson-Darling (AD) k-

265 samples tests were conducted with the assumption that all samples came from the same
266 distribution, and p-values were adjusted with the Bonferroni correction method (Abdi, 2017).
267 Moreover, the AD test was chosen as it is a non-parametric test, it reliably detects small
268 variations, it is applicable to discrete distributions, and requires less data to reach sufficient
269 statistical power in order to detect differences between varying sample sizes. (Engmann and
270 Cousineau, 2011). As size classes are non-continuous, the second version was used with 10,000
271 simulations based on random splits of the pooled samples to estimate the exact conditional p
272 values. Hereby, for each computed analysis, a minimum sample size of seven colonies was
273 applied. Significant differences in scleractinian colony size were explored using non-
274 parametric Kruskal-Wallis tests (KW, package ‘stats’, R Core Team, 2021) to explore
275 differences within groups (e.g., site specific morphological groups), and Mann-Whitney-
276 Wilcoxon tests (MW, package ‘stats’) to explore differences between two sampling
277 populations (e.g., morpho-taxonomic comparisons). The distribution curves of SFD were then
278 analysed with descriptive statistical measures to investigate skewness (g_1) and kurtosis (g_2)
279 (package ‘moments’) (Komsta and Novomestky, 2015). Here, positive skewness identifies a
280 dominance of small colonies and a negatively skewed distribution results from predominance
281 of large colonies. Kurtosis identifies the peakedness of a distribution near its central mode and
282 highlights whether the distribution tails contain extreme values. A peaked distribution is
283 leptokurtic ($g_2 > 0$; dominance of a few consecutive size classes), and a distribution flatter than
284 a normal distribution is platykurtic ($g_2 < 0$; higher variation in size class abundance). Skewness
285 and kurtosis were divided by their respective standard errors to determine whether the values
286 were significantly different from the normal distribution (Cramer, 1997; Wright and
287 Herrington, 2011):

288

$$289 \quad SE \text{ Skewness} = \sqrt{\frac{6(n-2)}{(n+1)(n+3)}}$$

290
291

and

$$292 \quad SE \text{ Kurtosis} = \sqrt{\frac{24n(n-2)(n-3)}{(n+1)^2(n+3)(n+5)}}$$

293 Here, a distribution was significantly different from the normal distribution if the Z-value of
294 the skewness and kurtosis statistic was $> \pm 2$. Moreover, variations in colony size were

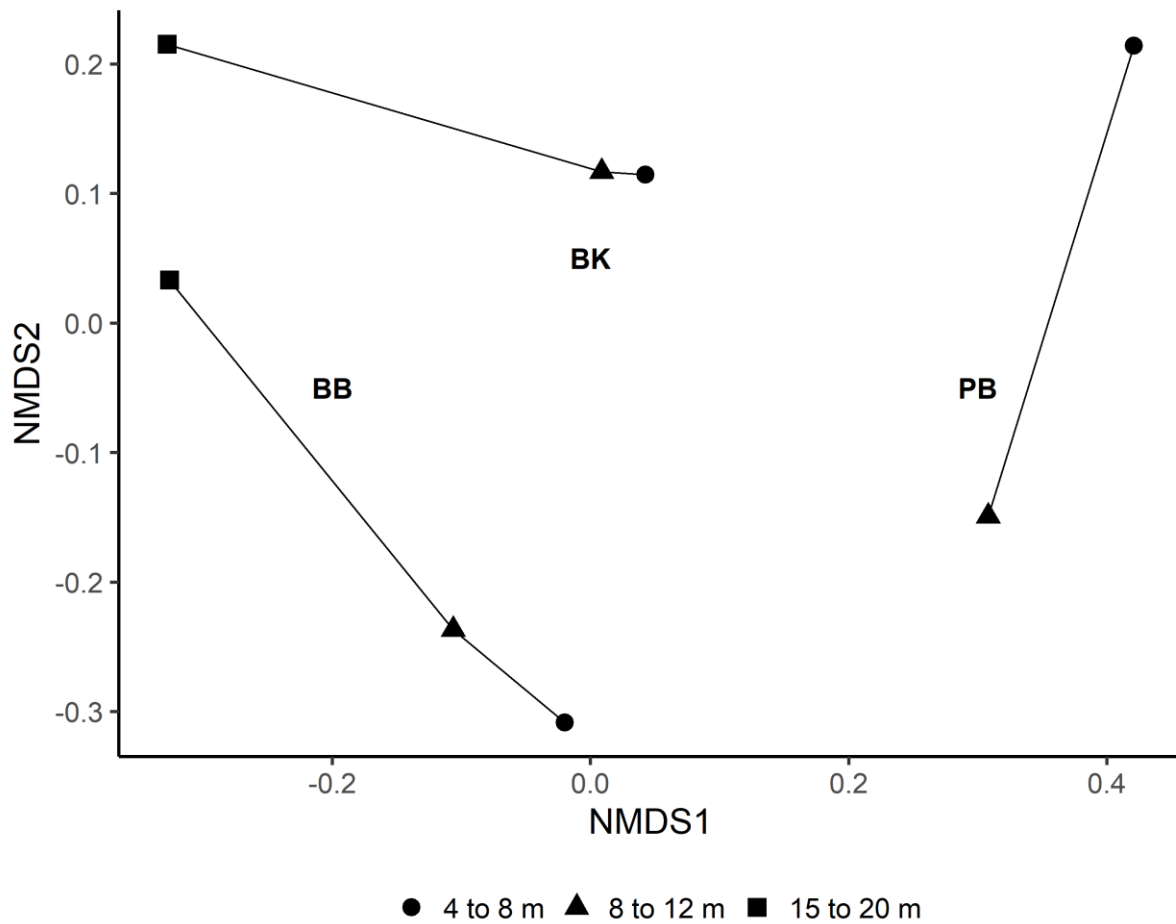
295 expressed by the coefficient of variation (CV), low values suggesting low variation in colony
296 size, and we further quantified the 10th and 90th percentile of each log-transformed colony size.
297 Finally, differences in morpho-taxonomic assemblages across sites and depths were visualized
298 using a non-metrical multidimensional scaling (NMDS) visualization in a Bray-Curtis
299 dissimilarity matrix, modelled with the package ‘vegan’ (Oksanen et al., 2020) in R software.

300 **3. Results**

301 **3.1. Benthic surveys and reef health**

302 Benthic surveys revealed substantial difference in coral assemblages across sites and depth
303 (Figure 2). All reef health indicators including hard coral density, diversity and percent hard
304 coral cover were consistently lower at leeward PB (Table 1), and increased along the reef health
305 and wind gradient from PB (leeward, least wind exposed) to BK and BB (most wind exposed).
306 Accordingly, hard coral cover was lowest at PB (8.78%), followed by BK (14.94%) and was
307 highest at BB (43.37%). Consistent with the hard coral cover gradient from PB to BB, benthic
308 cover at leeward PB (48.11 % sand and 39.61 % coral rubble) and windward BK (41.87 % sand
309 and 32.03 % coral rubble), was markedly more dominated by non-living substrate compared to
310 windward BB (14.37 % sand and 11.82 % coral rubble). At island scale, benthic cover was
311 dominated by sand (34.78 %) and rubble (27.82 %), and island wide hard coral cover was 22.26
312 %. Regardless of sites, hard coral cover declined with increasing depth (Supplementary S1).
313 Island wide hard coral density corresponded to 15.06 (colonies / m²), following the same
314 gradient as hard coral cover, with the lowest density at leeward PB (9.21 colonies / m²), to
315 windward BK (10.26 colonies / m²), and BB (highest density, 25.71 colonies / m²). The
316 Shannon Index of morpho-taxa increased from leeward PB to BK and BB (2.45, 2.70 and 3.15,
317 respectively).

318



319

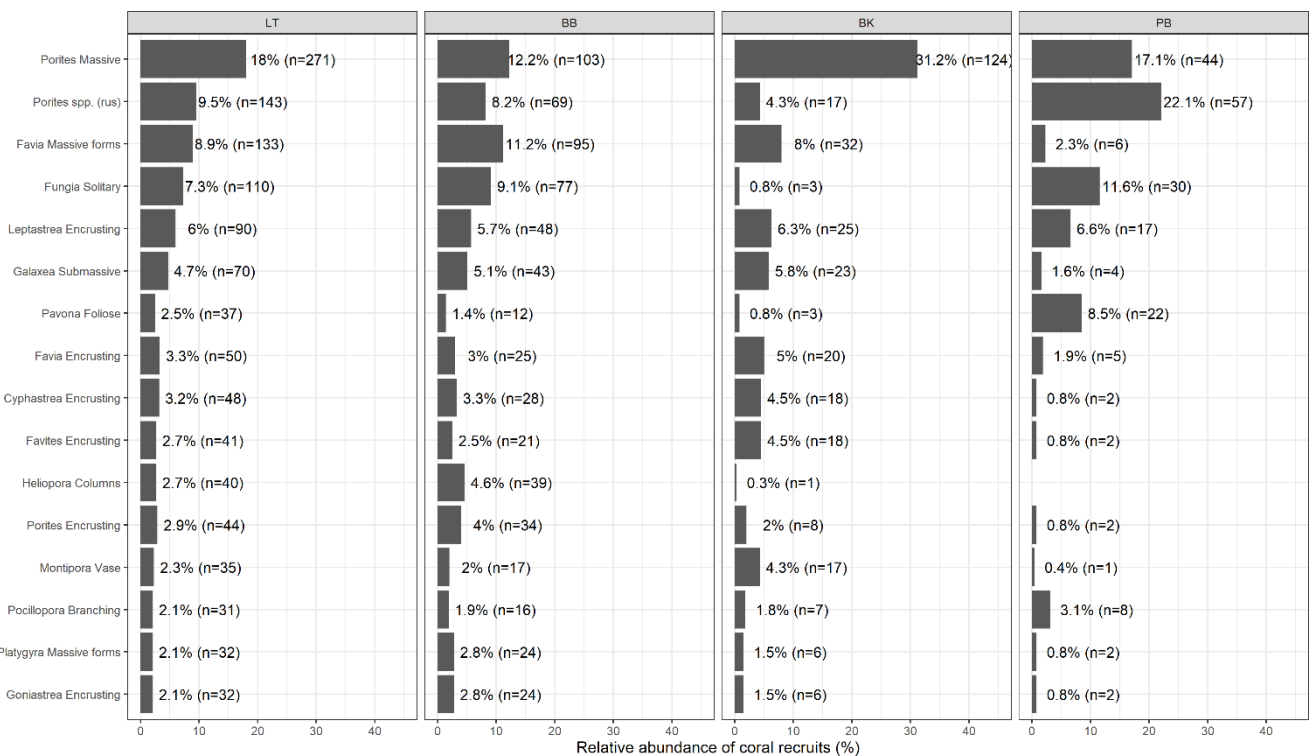
320 **Figure 2** | Hard coral community assemblage similarity is presented as a function of depth and
321 site in a non-metric multidimensional scaling (NMDS) ordination plotted on Bray-Curtis
322 dissimilarity matrices (2D). Each line represents a survey site (BB-Batu Bulan; BK-Batu
323 Kucing, PB-Pasir Besar) and markers present the morpho-taxonomic assemblage at the
324 respective site and depth, where close proximity of markers highlights similarities in hard coral
325 community assemblages. Note, no hard coral colonies were recorded at 15 to 20 meters of
326 depth at Pasir Besar (PB).

327

328 3.2. Demographic structure and recruitment

329 Sub-adult colonies as well as coral recruits dominated the scleractinian demographic structure
330 around Pulau Lang Tengah, whereby sub-adults accounted for 47.08% (n=1,914) and recruits
331 for 36.94% (n=1,502) of surveyed colonies (n=4,066). This general dominance of small sized
332 colonies was further highlighted by the low abundance (0.19 colonies / m²) of large colonies
333 (>80 cm) and was largely consistent across sites (Table 1). However, more intact sites hosted a
334 higher amount of large and small colonies, and the mean colony size of morpho-taxa was
335 different across taxa and sites, whereby the coefficient of variations of colony size varied from
336 62.59% at BK, 54.48% at BB and 46.68% at PB (Table 1). Secondly, there were notable

337 variations in the abundance of coral recruits across sites (Supplementary S2), whereby the
 338 relative recruitment density was substantially higher at windward BB (9.40 recruits / m²) than
 339 at BK (4.42 recruits / m²) and PB (2.87 recruits / m²) (Table 1). Furthermore, coral recruitment
 340 was disproportionately dominated by few taxa (Figure 3). On morpho-taxonomic level, recruits
 341 of massive *Porites* (18.0% of total recruitment, 3.01 recruit / m²) and *Porites spp. (rus)* (9.5%,
 342 1.59 recruits / m²) were most abundant, followed by massive *Favia* (8.9%, 1.48 recruits / m²),
 343 solitary corals *Fungia* (7.3%, 1.22 recruits / m²), and encrusting *Leptastrea* (6.0%, 1.00 recruits
 344 / m²) (Figure 3).



345

346 **Figure 3** | Percentage of relative coral recruitment is presented for the 16 most abundant hard
 347 coral morpho-taxa. The abundance of recruits (<5.0 cm) of each morpho-taxon is shown
 348 relative to the total number of recruits at regional (LT-Pulau Lang Tengah), and reef scale (BB-
 349 Batu Bulan; BK-Batu Kucing, PB-Pasir Besar).

350

351 The abundance of recruits relative to the respective abundance of adults varied considerably
 352 across sites for numerous morho-taxa (Supplementary S2).

353 3.3. Scleractinian size frequency distribution (SFD)

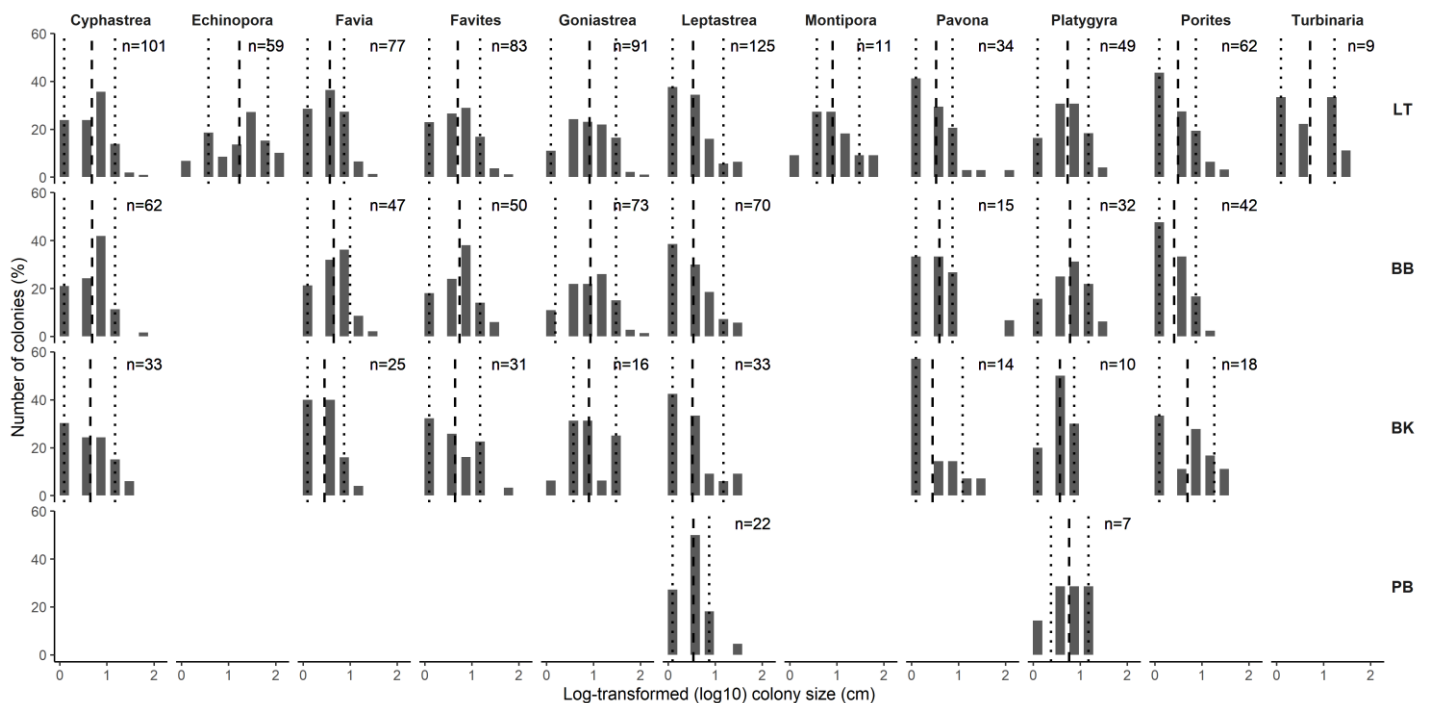
354 All log-transformed size-classes frequency distributions (SFDs) by morphology and site were
 355 non normal (SW tests $p < 0.01$). Similarly, most of SFDs by morpho-taxon and sites were non
 356 normal (74 % at BB (n=34), 81 % at BK (n=21), 87 % at PB (n=15)). Scleractinian colony size

357 was highly variable across and within sites. For instance, 273 of 561 (48.66%) morpho-
358 taxonomic colony size comparisons at BB (Mann-Whitney-Wilcoxon test), 63 of 210 at BK
359 (30.00% of pairs) and 67 of 105 (63.81% of pairs) were significantly different (electronic
360 supplementary data).

361 Sample size was sufficient to test 37 morpho-taxa for differences in SFD across sites and within
362 sites. Of these, 10 morpho-taxa were tested at all three sites, 13 at two sites and 14 at one site
363 (Table 2, Supplementary Table S3), resulting in 70 morpho-taxonomic SFD tests across sites
364 ($n=3,799$ colonies). Of the 70 morpho-taxonomic tests, SFD was positively skewed for 30
365 morpho-taxa, whereby only four were positively skewed at all sites (*encrusting Leptastrea*,
366 massive *Lobophyllia*, encrusting *Pavona* and massive *Porites*) (Figure 4 and Figure 5). Of 39
367 negatively skewed size frequency distributions, eight were negatively skewed at all three sites:
368 submassive *Galaxea*, *Porites spp (rus)*, encrusting *Platygyra*, massive *Platygyra*, hispidose
369 *Acropora*, laminar *Montipora*, solitary *Fungia* and massive *Symphyllia* (Table 2, Figure 4-6).
370 Massive *Leptoria* was neither positively, nor negatively skewed ($g_1=0.00$). Morpho-taxa tested
371 at only one site are shown in the supplementary material Table S3.

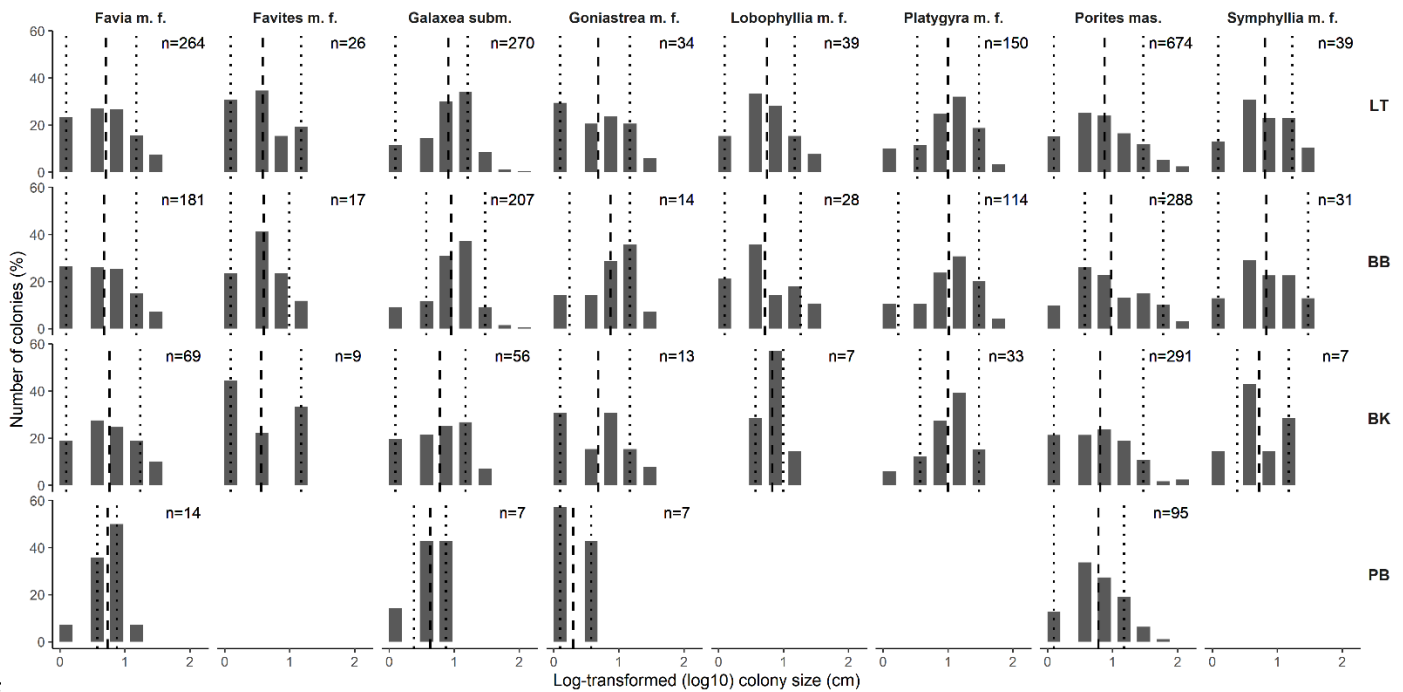
372 SFD of the following 11 morpho-taxa varied across sites: corymbose *Acropora*, encrusting
373 *Cyphastrea*, encrusting *Favia*, massive *Favia*, encrusting *Favites*, massive *Favites*, encrusting
374 *Goniastrea*, massive *Goniastrea*, foliose *Pavona*, *Pocillopora*, encrusting *Porites* (Table 2).
375 Here, there were significant differences across sites for five morpho-taxa with varying SFD
376 across sites: corymbose *Acropora* (AD k-test $p<0.001$), massive *Goniastrea* (AD k-test $p\leq 0.01$)
377 and *Pocillopora* (AD k-test $p<0.05$), encrusting *Porites*, (AD k-test $p<0.001$), and encrusting
378 *Favia*. Furthermore, significant differences in SFD were found for taxa whose SFD was
379 negatively skewed at all three sites, such as submassive *Galaxea* (AD k-test $p<0.001$), *Porites*
380 *spp. (rus)* (AD k-test $p<0.001$) and solitary *Fungia* (AD k-test $p<0.001$). Of morpho-taxa with
381 positive SFD at all three sites, massive *Porites* showed significant differences in size
382 distribution across sites (AD k-test $p<0.001$). Overall, leeward PB was more dominated by
383 negatively skewed morpho-taxa (11 of 15, 73.33%) than BK (11 of 21, 52.38%) and BB (18 of
384 34, 52.94%). Similarly, leeward PB was more leptokurtic compared to BB and BK (Table 1):
385 PB 40.00% leptokurtic morpho-taxa, 9.52% at BK, and 17.65% at BB. In addition to morpho-
386 taxonomic SFD differences across sites, there were further differences in morpho-taxa SFD
387 within sites, with 28.16% (158 of 561) of morpho-taxonomic SFD pairs being significantly
388 different at BB, 10.47% (22 of 210) at BK and 49.52% (52 of 105) at PB (electronic
389 supplementary data).

390 The Z-statistics of the SE Skewness of all 70 tested morpho-taxa revealed a significantly
 391 different SFD from the normal distribution for eight morpho-taxa ($Z > \pm 2$), and the Z-statistics
 392 of the SE kurtosis highlighted significantly different SFD ($Z > \pm 2$) for nine morpho-taxa (Table
 393 2). Noteworthy, hispidose *Acropora* at PB, solitary *Fungia* at PB and encrusting *Pavona* at BB
 394 ($g_1=1.45$, $g_2=2.50$, $CV=87.00\%$) were both, significantly skewed and peaked. Here, hispidose
 395 *Acropora* and solitary *Fungia* were significantly skewed towards larger colonies ($g_1= -2.18$ and
 396 -1.49 , respectively), colony size was highly centralized (leptokurtic, $g_2=5.25$ and 0.87 ,
 397 respectively), and less diverse ($CV=28.09\%$ and $CV=38.99\%$, respectively). In contrast to PB,
 398 kurtosis of solitary *Fungia* at BB was negative (platykurtic; $g_2= -1.45$, $CV=67.76\%$). At BB,
 399 all nine massive morpho-taxa were platykurtic, whereby massive *Favia* ($g_2= -0.98$,
 400 $CV=63.57\%$) and massive *Porites* ($g_2= -0.69$, $CV=52.68\%$) were significantly platykurtic
 401 (Table 2). At BK, kurtosis was significant for massive *Favites* ($g_2= -1.62$, $CV=88.79\%$). In
 402 addition to encrusting *Pavona*, encrusting *Turbinaria* at BB was the only other encrusting
 403 morpho-taxa with significant kurtosis ($g_2= -1.48$, $CV= 84.48\%$) (Supplementary S3). Skewness
 404 was significantly negative for massive *Platygyra* at BB ($g_1= -0.61$) and BK ($g_1= -0.85$), *Porites*
 405 *spp. (rus)* at PB ($g_1= -0.43$) and submassive *Galaxea* at BB ($g_1= -0.59$). Encrusting *Leptastrea*
 406 was significantly positively skewed at BK ($g_1=0.80$).



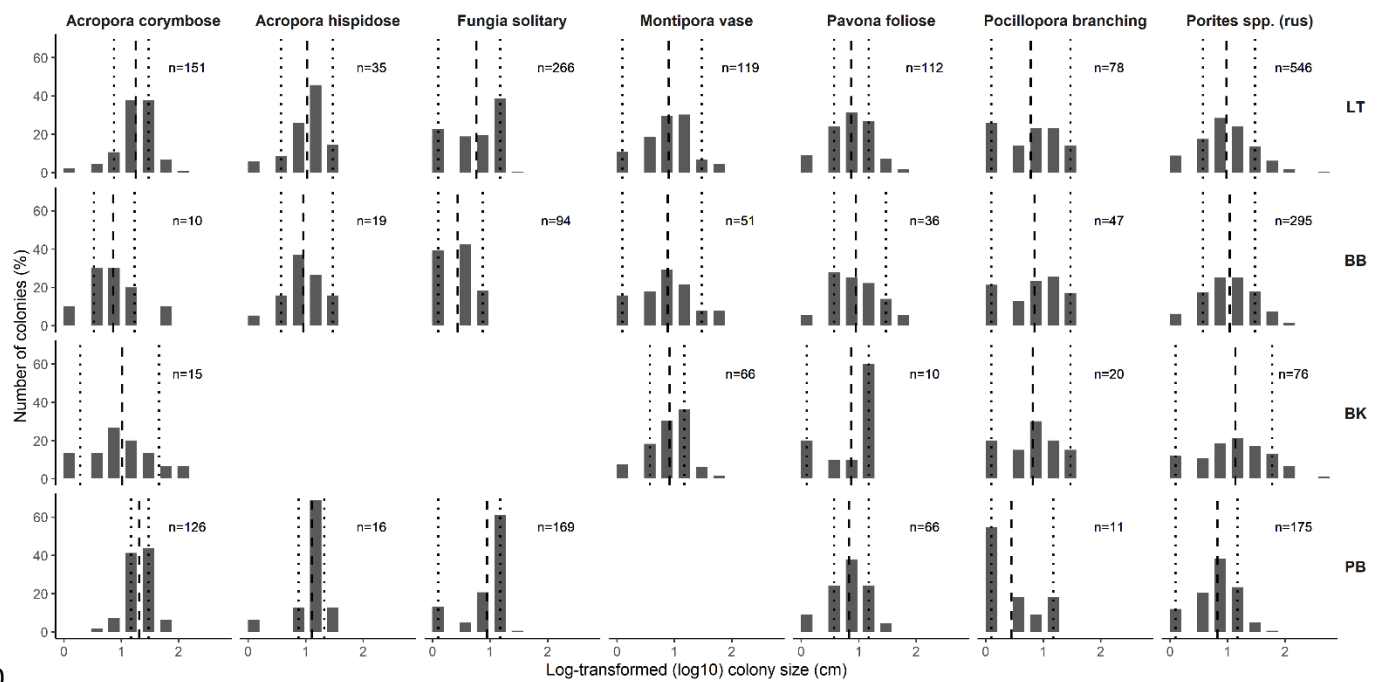
408 **Figure 4** | Log-transformed size frequency distribution (SFD) of encrusting hard coral morpho-
 409 taxa at reef scale at three sites (BB-Batu Bulan; BK-Batu Kucing; PB-Pasir Besar) and on
 410 island scale (LT-Lang Tengah), in Northeast Peninsular Malaysia. Dotted lines present the 10th
 411 and 90th percentile, respectively, and the dashed line shows the mean of the distribution.

412



413

414 **Figure 5** | Log-transformed size frequency distribution (SFD) of massive hard coral morpho-
 415 taxa at reef scale at three sites (BB-Batu Bulan; BK-Batu Kucing; PB-Pasir Besar) and on
 416 island scale (LT-Lang Tengah), in Northeast Peninsular Malaysia. Dotted lines present the 10th
 417 and 90th percentile, respectively, and the dashed line shows the mean of the distribution.
 418 Abbreviations: m.f – massive forms (includes submassive and massive); subm.- submassive;
 419 mas.- massive.



420

421 **Figure 6** | Log-transformed size frequency distribution (SFD) of hard coral morpho-taxa at reef
 422 scale at three sites (BB-Batu Bulan; BK-Batu Kucing; PB-Pasir Besar) and on island scale (LT-

423 Lang Tengah), in Northeast Peninsular Malaysia. Dotted lines present the 10th and 90th
424 percentile, respectively, and the dashed line shows the mean of the distribution.

425

426 **4. Discussion**

427 4.1. Benthic surveys and reef health

428 Benthic surveys showed marked and consequential differences in reef health based on benthic
429 substrate composition and general reef health indicators (Table 1). All indicators (e.g.,
430 taxonomic diversity and richness, colony density, hard coral cover, and colony size CV), were
431 lower at leeward PB and higher at windward BB. Live hard coral cover was markedly low at
432 leeward PB (8.78%), where coastal development possibly resulted in physical reef degradation
433 (Figure 1). In addition, herbivorous fish abundance is reportedly lower at PB than BK and BB
434 (CK. Lynn, unpublished data, 2018). Conceivably, secondary impacts from low abundance of
435 herbivorous fish (McClanahan et al., 2001; Green and Bellwood, 2009), sewage discharge and
436 sedimentation rates may persistently impact coral reef health at leeward sites (Wooldridge et
437 al., 2012; Duckworth et al., 2017; Reef Check Malaysia, 2019), resulting in lower hard coral
438 colony diversity, abundance and less variable colony size at leeward PB (Table 1). Although
439 historical data is not available and temporal analysis of percent live hard coral cover is not
440 possible, the disproportionately high amount of coral rubble at PB (39.61 %) compared to BB
441 (11.82 %), and the declining trend of coral reef health and cover across Peninsular Malaysia
442 (Toda et al., 2007; Praveena et al., 2012; Reef Check Malaysia, 2019), suggests that much of
443 the observed differences in benthic substrate composition and reef health indicators are
444 substantially driven by human activity. As such, coral reefs in close proximity to coastal
445 developments are particularly impacted, and a clear gradient of reef health is evident and
446 subsequent differences in coral assemblages are consequential (Table 1 and Figure 2).

447 4.2. Demographic structure and recruitment

448 Coral recruitment was dominated by a few morpho-taxa, such as massive *Porites*, *Porites spp.*
449 (*rus*), massive *Favia* and solitary *Fungia* (Figure 3, Supplementary S2 and S4). According to
450 findings by Riegl et al. (2012), constant recruitment impulses and declines in colony size after
451 mass disturbance events underpin demographic structure, and McClanahan et al. (2001; 2008)
452 further demonstrated that SFD significantly shifts to smaller colonies after mass ecological
453 disturbance (e.g., coral bleaching) and due to chronic stress (e.g., overfishing). Accordingly,
454 chronically disturbed reef environments should host a larger amount of recruits and sub-adult

455 colonies, but may also be constrained by high post-settlement mortality (Chong-Seng et al.,
456 2014). Pulau Lang Tengah's reefs are chronically stressed by human impacts, and during this
457 study we identified a generally high number of coral recruits (e.g., 36.94% of the surveyed
458 population), and smaller sized sub-adult colonies (e.g., < 20.00 cm; 47.08% of the surveyed
459 population). Moreover, reef scale assessments further revealed that healthier and more intact
460 sites (here BB) were hosting a higher abundance of both, larger (adult) and smaller colonies
461 (sub-adult and recruits), as compared to more degraded sites such as BK and PB (Table 1).
462 However, the general demographic structure was consistent across sites, as smaller coral
463 colonies of 10-20 cm in size were the most preponderant (Table 1). Presumably, this
464 preponderance of smaller colonies may be the result of extrinsic demographic factors such as
465 large-scale disturbance events that eliminated larger colonies and induced shifts in the
466 abundance and dominance of individual taxa (Meesters et al., 1996; Bak and Meesters, 1998,
467 1999). Correspondingly, after large-scale disturbance events, such as the 1998 and 2010 mass
468 bleaching events (Kushairi, 1999; Tan and Heron, 2011), morpho-taxa such as massive *Porites*
469 have started to replace formerly dominant taxa such as *Acropora* and *Montipora* (Brown, 1997;
470 Toda et al., 2007). Preconditions for such taxon-specific shifts would be visible in the taxon's
471 current SFD and would be specifically highlighted by a platykurtic distribution. Furthermore,
472 in view of skeletal growth rates of 2.0 cm / year of massive *Porites* colonies measured in nearby
473 (~10 km) Redang Island (Tanzil et al., 2013), and considering the time elapsed since the last
474 mass coral bleaching events with significant mortality rates (nine and 21 years, respectively),
475 impulses of post-disturbance recruitment are likely to have contributed to the preponderance
476 of smaller size groups and the co-aligned dominance of a few taxa, such as massive *Porites*,
477 and *Porites spp. (rus)*. (Table 1, Supplementary S4). Such findings are similar to studies from
478 the Red Sea and French Polynesia (Riegl et al., 2012; Adjeroud et al., 2015), where the
479 demographic structure was dominated by recruits and small colonies on reefs that suffered
480 recent and frequent ecological disturbances. On the other hand, frequent disturbances and
481 chronic stressors may have induced a decline in general colony size. For instance, in Kiribati,
482 chronic and multiple stressors resulted in a decadal and general decline in colony size of the
483 six most dominant taxa, declining to an average size of between 10-20 cm, (Cannon et al.,
484 2021), and further resulted in the dominance of taxa such as *Porites spp. (rus)*. These
485 observations are supported by contrasting colony sizes across gradients of reef health, as all
486 major taxa (except for corymbose *Acropora* and solitary *Fungia*), were larger at healthier
487 windward BB than at PB (Table 2). Nonetheless, pre-existing conditions specific to each reef
488 site, and conditions resulting from ecological disturbances (e.g., substrate suitability and

489 availability), are likely further determining recovery on reef-scale, and are key in understanding
490 the demographic structure and resilience of hard corals on individual reefs.

491 For significant shifts in the mix of taxa and SFD to occur after mass disturbance due to
492 successful coral recruitment, ample and suitable substrate is necessary to prevent high post-
493 settlement mortality (Chong-Seng et al., 2014). If unavailable, selective pressures may result
494 in recruitment bottlenecks in favour of fewer taxa that are capable of successful recruitment in
495 unfavourable environments, such as rubble dominated reefs. We investigated successful coral
496 recruitment by quantifying the abundance of coral recruits (Table 1, Figure 3), in view of site-
497 specific benthic substrate composition. Our results suggest that coral recruitment abundance
498 and diversity was consistent with patterns of site-specific coral reef health. As such, coral
499 recruitment was lowest at PB and highest at BB (Table 1, Supplementary S2). Presumably, the
500 bottom-substrate composition of the reef mosaic strongly impacts coral recruitment at reef
501 scale (Chong-Seng et al., 2014). For instance, at PB, coral rubble and sand were the most
502 dominating substrates (Table 1). Coral rubble in particular, is tagged as a coral recruitment
503 inhibitor and thus prevents the establishment of mature colonies, resulting in demographically
504 unviable populations (Raymundo et al., 2007; Wolfe et al., 2021), and in the preponderance of
505 a few taxa, that are able to reproduce and settle in such environments, such as solitary *Fungia*,
506 foliose *Pavona*, massive *Porites* and *Porites spp. (rus)*. Conversely, studies from the tropical
507 Pacific suggest that the recruitment abundance of *Acropora*, *Pocillopora* and *Porites* are
508 correlated with the abundance of adults. (Penin and Adjeroud, 2013; Bramanti and Edmunds,
509 2016). This may partially explain why dominant adult morpho-taxa are further dominating the
510 recruitment pool, and recruitment dominance of individual taxa such as *Acropora*, *Porites* and
511 *Fungia* was noted in Peninsular Malaysia on artificial reefs and on *in-situ* tiles (Rani et al.,
512 2015; Hanapiah et al., 2017). Lastly, species-specific recruitment mortality rates may further
513 explain the dominance of a few morpho- taxa (Smith, 1992).

514 4.3. Scleractinian colony size frequency distribution across reef health

515 It is important to note that historical records of hard coral SFD are unavailable for Peninsular
516 Malaysia and therefore retrospective conclusions about disturbance induced shifts in SFD are
517 not feasible, neither is it possible to retrospectively ascertain the importance of disturbance
518 events on the present demographic SFD. This study intended to create a baseline reference for
519 future studies, but it must be noted that changes in demographic structure are subject to strong
520 spatio-temporal patterns and variability (particularly coral recruitment), and conclusions are

521 only momentarily. Further and repeated studies on species-specific level are needed to quantify
522 the impacts of global and local stressors on demographic structure in order to highlight the
523 subsequent changes in community assemblages of hard corals (Edmunds and Riegl, 2020).

524 To determine present variations in hard coral demography and population viability in view of
525 chronic disturbances and human stressors, it was necessary to compare SFD across reefs in
526 various stages of reef health and across reefs subjected to the same overarching stressors. We
527 compared hard coral SFD across three reef sites, which were in good (BB > 40% hard coral
528 cover), fair (BK > 20% hard coral cover) and degraded conditions (PB < 20% hard coral cover)
529 (Table 1). SFD of 11 morpho-taxa was varied across sites, eight morpho-taxa were negatively
530 skewed at all three sites, and four taxa were positively skewed at all sites (Table 2, Figures 4-
531 6). We found evidence for both proposed theories of shifts to either large or small colonies. For
532 instance, on island scales, this study recorded a preponderance of small to medium sized corals
533 (Table 1), which possibly resulted from a recent demographic disturbance event followed by
534 recruitment (e.g., massive *Porites* as described above), and could further reflect the
535 consequences of chronic and multiple stress, similar to reefs in Kiribati (Cannon et al., 2021).
536 Variations in SFD were highly heterogenic across morpho-taxa, however, we found
537 pronounced differences with morpho-taxa across reef health (Table 2, Figures 4-6), which offer
538 insights into the impacts of various site stressors on taxon-specific SFD (Bauman et al., 2013).
539 Overall, the most degraded site (PB) was dominated by colony SFD shifted to larger colonies,
540 a more leptokurtic distribution, low recruitment density, as well as generally lower hard coral
541 abundance and diversity (Table 1-2, Figure 3). Moreover, the taxonomic assemblage here was
542 dominated by weedy taxa (Supplementary S5). These findings thus partially confirm postulates
543 by Meesters et al. (2001) and Dietzel et al. (2020), who argued that degraded reefs are
544 characterized by large colonies and low colony size variability, leading to a depression in
545 recruitment and subsequent reef replenishment. Nevertheless, whereby our results highlight the
546 limited demographic viability of more disturbed sites (Table 2, Figures 4-6), results further
547 revealed differences in SFD of numerous morpho-taxa across sites. As such, some morpho-
548 taxa were larger at healthier sites (here BB) compared to degraded sites. For instance, whereas
549 submassive *Galaxea* was negatively skewed at all sites, skewness was only significant at BB,
550 where it attained its largest size on average (Table 2). Massive *Platygyra* was significantly
551 skewed towards larger colonies at healthier sites, and both taxa were abundant as recruits
552 (Figure 3). SFD of encrusting taxa such as encrusting *Favia* were significantly different at BB
553 (good condition and negative distribution) compared to BK (fair condition and positive

554 distribution). Thus, negative skewness is not in immediate association with reef degradation
555 (*sensu* Meesters et al., 2001; Miller et al., 2016; Dietzel et al., 2020), but is taxon-dependent
556 and likely due to the inherent life-history strategies of present taxa. Possibly, resistance to
557 environmental stress, such as heat stress and subsequent bleaching, favours negative skewness
558 and larger size of taxa that are more tolerant to such conditions (Bauman et al., 2013).
559 Submassive *Galaxea* is locally a more bleaching tolerant taxon (Szereday and Affendi, 2022),
560 and possibly attains larger size on reefs with intact framework and sufficient substrate (such as
561 BB), whilst taxa susceptible to heat stress are reduced in size and are filtered out (McClanahan
562 et al., 2001, 2008), offering vacant substrate for growth and reducing spatial competition.

563 Contrasting the indicators of reef health against colony SFD, it is plausible that coral reef
564 degradation results in a SFD tipping point, where fewer morpho-taxa are able to maintain viable
565 demographic populations as coral reef degradation deteriorates the reef substrate and structure,
566 and ultimately exacerbates the loss of colonies. Such factors are also possible drivers of phase
567 shifts, where complex reef assemblages are replaced by rudimentary and weedy taxa
568 (McWilliam et al., 2020). Indeed, site-specific variations of hard coral SFD are due to the reef-
569 specific presence of chronic stressors, as well as life-history traits, that enable certain coral taxa
570 to persist under chronic and multiple stress (Darling et al., 2012, 2013). Chronic disturbances
571 and mortality shocks would result in a leptokurtic distribution of impacted taxa at disturbed
572 sites, and generally in platykurtic distribution of tolerant taxa, especially at healthier sites
573 (Bauman et al., 2013). Weedy morpho-taxa such as solitary *Fungia* and foliose *Pavona*
574 dominated the assemblage on the most degraded reef site (PB) (Figure 2), in addition to
575 corymbose and hispidose *Acropora*, as well as *Porites spp. (rus)*. Moreover, high population
576 turnover is characterized by leptokurtic distribution and is associated with frequent
577 disturbances (Kayal et al., 2015), noted for these taxa, with the exception of *Porites spp.(rus)*.
578 In contrast, platykurtic distribution was predominantly characteristic of massive taxa,
579 particularly at less degraded sites, and was significant for massive *Favia*, solitary *Fungia*,
580 massive *Porites* at BB, and massive *Favites* at BK (Table 2).

581 The current state of coral reef health and the biophysical interaction of monsoon waves with
582 the predominant reef substrates (e.g., coral rubble, live hard coral), provides a diagnostic
583 glimpse into the consequences of severe reef degradation, and offers further explanation of
584 demographic tipping points of individual reef sites. In this realm, natural recovery is
585 significantly impeded due to biophysical interactions, as in Pulau Lang Tengah specifically, the
586 northeast monsoon winds induce strong wind and wave action (Figure 1B), which establishes

587 a system in a state of hysteresis (*sensu* Hughes et al., 2010), where the excessive amount of
588 coral rubble, sand and monsoon waves interact to trigger further decline in hard coral colony
589 abundance, due to sedimentation and physical fragmentation. This state of hysteresis
590 hypothetically prevents successful larvae settlement and development, as suggested by the low
591 rates of recruitment and the high substrate cover of rubble and sand at PB. Thus, the
592 combination of reinforcing factors increases colony mortality and possibly further reduces the
593 local larvae source pool. Secondly, such reinforcing feedbacks increases the amount of mobile
594 substrate that acts as the degenerating agent. Therefore, once reef substrate degradation reaches
595 a critical level at which the proposed reinforcing mechanisms interact in a strong feedback
596 loop, demographic recovery is reduced and only taxa with beneficial life-history strategies and
597 physical properties with high hydro-mechanical tolerance, are able to persist. For instance,
598 hispidose *Acropora* (e.g., *Acropora longicyathus*), is known to persist well in coral rubble
599 fields (Veron et al., 2022), which may be due to colony morphology as well as life-history
600 characteristics, such as quick growth, density dependent recruitment and asexual reproduction
601 by fragmentation. Indeed, Szereday and Affendi confirmed a high dominance of this taxon at
602 PB during repeated annual surveys (Szereday and Affendi, 2022). Secondly, solitary *Fungia*
603 was particularly dominant in Lang Tengah's coral rubble fields, likely due to the non-sessile
604 lifestyle and colony shape that enables survival in shallow turbulent waters (Jokiel and Cowdin,
605 1976), as well as secondary life-history strategies (*sensu* Darling et al., 2013), which imply that
606 this taxon can benefit from degraded and unproductive environments. Thus, SFD of solitary
607 *Fungia* was significantly different between BB and PB (Table 2). At PB the dominance of
608 larger *Fungia* colonies was underlined by leptokurtic distribution and negative skewness, in
609 sharp contrast to BB. Other negatively skewed taxa at PB were corymbose *Acropora* and
610 *Porites spp. (rus)*. SFD of *Porites spp. (rus)* at PB contrasted BB and BK, as at healthier sites
611 it was more evenly distributed and thus demographically more viable. Although this taxon
612 occurs in very dense coral carpets and visibly contributes to the local leeward reef frame
613 building, high physical fragmentation was observed at PB, which is likely a result of human
614 disturbances (e.g., coastal development, sedimentation), and subsequently weakens the reef
615 frame and magnifies wave induced sedimentation. Furthermore, in the case of corymbose
616 *Acropora*, the lack of small colonies as well as low coral recruitment numbers may be due to
617 unsuitable substrate. With increasing degradation and annually occurring monsoon waves,
618 fragmentation possibly increases due to wave action and collision with mobile rubble. Indeed,
619 studies suggest that such broken fragments have limited reattachment and survival success in
620 rubble fields (Cameron et al., 2016). Occurrence in high density and mono-specific coral

621 carpets may provide enough robustness to withstand monsoon waves, but the lack of suitable
622 substrate would impede reef-wide larvae dispersal (Chong-Seng et al., 2014), which would be
623 otherwise warranted due to high adult abundance (*sensu* Bramanti and Edmunds, 2016).
624 Equally, asexual reproduction is hindered as reattachment of broken coral fragments is directly
625 influenced by fragment size and the benthic substrate composition (Smith & Hughes, 1999).
626 Therefore, it is possible that only larger fragments of certain growth-form (e.g., hispidose
627 branching) can quickly reattach to the reef matrix, causing lower colony size range and result
628 in the observed leptokurtic distribution. Ultimately, in environments dominated by an annual
629 monsoon and mobile substrates, the present demographic structure of these taxa represents a
630 severe reproductive barrier, threatening long-term population viability (Kramer et al., 2021).
631 This may also partially explain why only four taxa (corymbose *Acropora*, solitary *Fungia*,
632 massive *Porites* and *Porites spp. (rus)*) dominated ~70% of the assemblage at PB, in contrast
633 to BB, where 11 taxa constituted ~70% of the assemblage (Supplementary S5), while SFD was
634 significantly more negative here than compared to less degraded sites (Table 1). Conclusively,
635 such reefs are compromised in their capacity to suppress the movement and resuspension of
636 sand and rubble, reinforcing hysteresis between sedimentation and monsoon waves, resulting
637 in the survival of only larger colonies in dense clusters (e.g., corymbose *Acropora*, foliose
638 *Pavona*, *Porites spp. (rus)*), and with leptokurtic distribution (e.g., solitary *Fungia*, corymbose
639 and hispidose *Acropora*).

640 Despite indication that SFD can re-balance after mass disturbance such as hurricanes and coral
641 bleaching (Crabbe, 2009), the presented system of hysteresis and the complex interaction of
642 biophysical drivers would prevent significant recovery and result in depleted rubble
643 environments, as well as in reef assemblages with significant deficits in functional trait
644 diversity (McWilliam et al., 2021), leading to a loss of reef complexity and diversity, regardless
645 of whether SFD shifts towards a negatively or positively distributed SFD. Substrate
646 stabilization has shown to be a viable tool to increase hard coral cover (Fox et al., 2019), but
647 scalability remains an issue (Williams et al., 2018), and with continuous anthropogenic heating
648 (Szereday and Affendi, 2022), such management tools may soon become unviable.
649 Nonetheless, several taxa showed high absolute abundance, high recruitment rates and an
650 evenly distributed demographic structure, which is further coherent with findings from other
651 regions (e.g., French Polynesia), highlighting taxa that might be able to persist under
652 continuous stress and environmental degradation. For instance, while massive colonies were
653 generally smaller at PB compared to BB and BK, no clear differences in distribution metrics

654 (colony size CV, skewness and kurtosis) were discernible across sites for massive taxa
655 (Supplementary S6), which suggests general resistance to prevailing conditions at all sites and
656 less selective pressure on colony size and SFD. In French Polynesia, massive *Porites* has been
657 shown to be more resistance to perturbations due to size-structure homogeneity (Adjeroud et
658 al., 2007, 2015), typically due to low individual turnover, high longevity and resistance to
659 environmental perturbations (Kayal et al., 2015). Here, characteristics of massive *Porites* were
660 high recruitment rates and a stable demographic structure (as indicated by insignificant
661 skewness and significant platykurtic distribution), similar to the central Pacific (Adjeroud et
662 al., 2015). This was further true for several massive taxa (e.g., *Favia*, *Porites*, *Platygyra* and
663 *Goniastrea*), whereby dominance and steadiness of massive taxa can be explained by longevity
664 and fecundity (Alvarez-Noriega et al., 2016), as well as hydrodynamic stability (Madin et al.,
665 2014). In Kiribati, *Porites spp. (rus)* increased in relative abundance after multiple disturbances
666 to dominate the reef assemblage (Cannon et al., 2021), emerging as a more tolerant and stress
667 resistant taxon. Indeed, *Porites spp. (rus)* colonies have shown acclimation potential to turbid
668 and nutrient-rich environments by diversifying strategies for energy acquisition to facilitate
669 persistence (Padilla-Gamiño et al., 2012). Considering the high levels of sedimentation and the
670 probable sewage discharge by nearby resorts at PB, such energy acquisition strategies may co-
671 explain the persistence of *Porites spp. (rus)* at PB. Ultimately, dominant morpho-taxa (e.g.,
672 massive *Favia*, columnar *Heliopora*, massive *Porites*, *Porites spp. (rus)*) displayed high levels
673 of recruitment, absolute abundance, platykurtic distribution and were neither negatively nor
674 positively skewed at significant levels (Table 2). This indicates population stability and low
675 individual turnover rates, which further highlight demographic viability and tolerance to
676 perturbations. However, only the two *Porites* taxa were able to persist in significant numbers
677 at the severely degraded site, highlighting the selective pressure of the proposed tipping point.

678

679 **5. Conclusion**

680 In conclusion, healthier sites were richer in hard coral cover, recruitment, abundance and
681 diversity (Table 1). Chronic and widespread stress represents selective pressures on successful
682 recruitment, in favour of a limited amount of morpho-taxa that survive disturbance as adults
683 and reproduce successfully (e.g., massive *Porites*, *Porites spp. (rus)*), or are morpho-taxa that
684 are generalist, cryptic or weedy (e.g., solitary *Fungia*, encrusting *Leptastrea*, foliose *Pavona*).
685 Ultimately, such assemblages are significantly different compared to healthier and more intact
686 reef sites (e.g., PB vs BB) (Figure 2). Under multiple disturbance regimes and chronic stress,
687 a sharp decline in the abundance of all size classes is likely (Dietzel et al., 2020; Cannon et al.,

688 2021), in addition to a shift towards weedy and generalist taxa (e.g., all three taxa of *Porites*,
689 and massive taxa such as *Favia*, *Favites Platygyra*, *Lobophyllia*, and *Symphyllia*), which are
690 tolerant and more adaptable to unfavorable conditions (Darling et al., 2012; Adjeroud et al.,
691 2015; McWilliam et al. 2020). Overall, the study confirmed the advantages of inferring
692 demographic processes from population size structure in hard corals. Using size-class
693 frequency distribution analysis, in combination with common reef health indicators, the study
694 provided a solid baseline for future monitoring of hard coral reef health at fine scale in
695 Peninsular Malaysia, providing essential information for conservation assessments and
696 management actions (Edmunds and Riegl, 2020). Ultimately, we suggest that hard coral
697 demographic collapse is not a single-direction process. Much rather, structural demographic
698 changes of taxa are subjected to a two-step filter. For instance, if taxa survive disturbances and
699 are still fecund, whilst given a suitable degree of substrate availability, an initial shift towards
700 recruitment and sub-adult dominated populations may be observed, accompanied by the
701 elimination of non-tolerant and larger colonies susceptible to disturbances such as cyclones,
702 overfishing and coral bleaching. If multiple disturbances persist in systems with reinforcing
703 feedback loops (e.g., unconsolidated substrate coupled with monsoon waves), colony mortality
704 and fragmentation rates will continue to increase and create unfavorable environments for
705 demographic recovery and viability. We conclude that such reinforcing disturbance regimes
706 are applying strong selective pressure on hard coral taxa, resulting in the survival of only the
707 largest and most stress tolerant taxa with fewer functional traits, thus impoverishing the coral
708 reef assemblage. Therefore, the reduction of the abundance of all size groups and a shift
709 towards large colonies and weedy taxa may be the second step of a demographic continuum,
710 where SFD of individual taxa is regionally determined by biophysical interactions (such as
711 waves, colony shape and sedimentation), life-history traits, and the nature and persistence of
712 stressor agents.

713 **Acknowledgments**

714 We are thankful to Summer Bay Resort, Lang Tengah Island, for supporting our research with
715 generous in-kind contributions. We are grateful to Albert Apollo Chan from the Department of
716 Fisheries Malaysia (DoF) for endorsing the publication of this manuscript, under permit
717 number Prk.ML.630-7Jld.5 (21). Special thanks is owed to Joseph A. Henry for providing
718 critical suggestions that greatly improved the manuscript. The revision, writing and editing of
719 this manuscript was supported with a research writing residency at Rimbun Dahan.

720 **Disclosure of funding**

721 This research did not receive any specific grant from funding agencies in the public,
 722 commercial, or not-for-profit sectors. However, the researchers were supported in-kind by
 723 Summer Bay Resort, Lang Tengah Island, and received financial and non-financial support by
 724 Lang Tengah Turtle Watch and Coralku Solutions.

725 **Declaration of interests**

726 The authors declare that they have no known competing financial interests or personal
 727 relationships that could have appeared to influence the work reported in this paper.

728

729 **Table 1** | Summary and comparison of benthic substrates, coral reef health indicators and
 730 demographic variables of hard corals across survey sites around Pulau Lang Tengah, Northeast
 731 Peninsular Malaysia. Batu Bulan and Batu Kucing are windward facing sites, and Pasir Besar
 732 is leeward facing. Highlighted in grey are demographic variables that are significantly different
 733 from the mean distribution.

734

	Lang Tengah	Batu Bulan	Batu Kucing	Pasir Besar
Number of genera	40	33	30	24
Number of morpho-taxa	72	58	46	38
Number of colonies (n)	4066	2314	923	829
Shannon Index (H)	3.15	3.17	2.70	2.45
Shannon Index (H) recruits (<5 cm)	3.06	3.10	2.63	2.60
Recruit colonies / m ² (<5 cm)	5.56	9.40	4.42	2.87
Sub-adults colonies / m ² (≥5-20 cm)	7.09	11.61	4.38	5.27
Adult colonies / m ² (>20-80 cm)	2.23	4.37	1.28	1.03
Large colonies / m ² (>80 cm)	0.19	0.33	0.18	0.04
Mean colony size _{log} cm (SD)	0.87 (0.48)	0.88 (0.48)	0.80 (0.50)	0.89 (0.42)
Colony size coefficient of variation % (CV)	54.79	54.48	62.59	46.68
Skewness (g ₁) (Z-value)	0.03 (0.78)	0.07 (1.38)	0.19 (2.36)	-0.35 (-4.13)
Kurtosis (g ₂) (Z-value)	-0.39 (-5.09)	-0.40 (-3.94)	-0.47 (-2.94)	-0.25 (-1.48)
% hard coral cover	22.26	43.37	14.94	8.78
% other living benthos	4.94	12.61	0.90	0.99
% coral rubble	27.82	11.82	32.03	39.61
% sand	34.78	14.37	41.87	48.11
% dead hard corals	2.45	4.34	1.39	1.63

735

736 **Table 2** | Size frequency distribution (SFD) metrics of scleractinian morpho-taxa at surveyed
 737 sites (BB-Batu Bulan; BK-Batu Kucing; PB-Pasir Besar) around Pulau Lang Tengah in
 738 Northeast Peninsular Malaysia. Anderson-Darling k-sample statistics show significant intra-

739 taxonomic differences across sites. Highlighted in grey are the skewness and kurtosis
740 distributions that are significantly different from the normal distribution as based on the Z-
741 value $> \pm 2$.

742

Morpho-taxon	Site	n	Size (±SD)	10 ⁴ 90th	90th	Δ (Z)	CV (%)	CV%	AD	k-test
<i>Acropora corymbose</i>	BB	10	0.86 ± 0.46	0.53	1.44	0.42 (0.72)	0.12 (0.16)	53.18		p < 0.001
	BK	15	1.01 ± 0.56	0.29	1.66	0.07 (0.14)	-0.48 (-0.61)	55.22		p < 0.001
	PB	126	1.31 ± 0.24	1.18	1.48	-0.41 (-1.94)	0.50 (1.22)	18.01		p < 0.001
<i>Favia massive</i>	BB	181	0.68 ± 0.43	0.10	1.18	0.05 (0.30)	-0.98 (-2.81)	63.57		ns
	BK	69	0.76 ± 0.43	0.10	1.24	-0.09 (-0.33)	-0.87 (-1.64)	56.05		ns
	PB	14	0.73 ± 0.26	0.57	0.88	-0.79 (-1.49)	0.87 (1.12)	35.24		ns
<i>Galaxea submassive</i>	BB	207	0.95 ± 0.38	0.57	1.48	-0.59 (-3.49)	0.51 (1.55)	40.05		p < 0.001
	BK	56	0.78 ± 0.43	0.10	1.18	-0.32 (-1.02)	-0.93 (-1.63)	54.75		p < 0.001
	PB	7	0.63 ± 0.28	0.38	0.88	-0.93 (-1.52)	-0.07 (-0.11)	44.25		p < 0.001
<i>Goniastrea massive</i>	BB	14	0.87 ± 0.41	0.24	1.18	-0.71 (-1.33)	-0.38 (-0.48)	47.29		p ≤ 0.01
	BK	13	0.68 ± 0.47	0.10	1.18	-0.03 (-0.05)	-1.18 (-1.51)	69.07		p ≤ 0.01
	PB	7	0.30 ± 0.26	0.10	0.57	0.29 (0.47)	-1.92 (-2.9)	84.62		p ≤ 0.01
<i>Leptastrea encrusting</i>	BB	70	0.54 ± 0.42	0.10	1.18	0.52 (1.86)	-0.65 (-1.23)	78.18		ns
	BK	33	0.52 ± 0.45	0.10	1.18	0.80 (2.05)	-0.36 (-0.53)	87.25		ns
	PB	22	0.54 ± 0.35	0.10	0.88	0.53 (1.17)	0.66 (0.87)	64.16		ns
<i>Pavona foliose</i>	BB	36	0.95 ± 0.42	0.57	1.48	0.08 (0.22)	-0.47 (-0.70)	43.96		ns
	BK	10	0.87 ± 0.45	0.10	1.18	-0.98 (-1.69)	-0.72 (-0.96)	52.05		ns
	PB	66	0.83 ± 0.34	0.57	1.18	-0.47 (-1.64)	0.01 (0.02)	40.83		ns
<i>Platygyra encrusting</i>	BB	32	0.78 ± 0.39	0.10	1.18	-0.30 (-0.76)	-0.60 (-0.87)	50.51		ns
	BK	10	0.57 ± 0.28	0.10	0.88	-0.63 (-1.09)	-0.62 (-0.82)	49.95		ns
	PB	7	0.76 ± 0.38	0.38	1.18	-0.54 (-0.87)	-0.67 (-1.01)	50.18		ns
<i>Pocillopora</i>	BB	47	0.85 ± 0.48	0.10	1.48	-0.40 (-1.2)	-1.05 (-1.72)	56.33		p < 0.05
	BK	20	0.82 ± 0.46	0.10	1.48	-0.31 (-0.67)	-0.92 (-1.21)	56.28		p < 0.05
	PB	11	0.45 ± 0.45	0.10	1.18	0.67 (1.18)	-1.15 (-1.50)	99.59		p < 0.05
<i>Porites spp. (rus)</i>	BB	295	1.04 ± 0.44	0.57	1.48	-0.12 (-0.82)	-0.26 (-0.95)	42.20		p < 0.001
	BK	76	1.14 ± 0.59	0.10	1.78	-0.07 (-0.24)	-0.36 (-0.71)	51.37		p < 0.001
	PB	175	0.83 ± 0.37	0.10	1.18	-0.43 (-2.34)	-0.07 (-0.19)	44.33		p < 0.001
<i>Porites massive</i>	BB	288	0.98 ± 0.52	0.57	1.78	0.21 (1.44)	-0.69 (-2.47)	52.68		p < 0.001
	BK	291	0.81 ± 0.50	0.10	1.48	0.20 (1.43)	-0.45 (-1.62)	61.64		p < 0.001
	PB	95	0.78 ± 0.38	0.10	1.18	0.01 (0.05)	-0.29 (-0.63)	49.35		p < 0.001
<i>Acropora hispidose</i>	BB	19	0.96 ± 0.36	0.57	1.48	-0.46 (-0.95)	0.11 (0.14)	37.02		ns
	PB	16	1.11 ± 0.31	0.88	1.33	-2.18 (-4.28)	5.25 (6.75)	28.09		ns
<i>Cyphastrea encrusting</i>	BB	62	0.69 ± 0.37	0.10	1.18	-0.13 (-0.45)	-0.06 (-0.11)	54.30		ns
	BK	33	0.65 ± 0.44	0.10	1.18	0.10 (0.27)	-1.08 (-1.59)	68.23		ns
<i>Favia encrusting</i>	BB	47	0.65 ± 0.36	0.10	1.00	-0.19 (-0.57)	-0.54 (-0.89)	54.46		p ≤ 0.01
	BK	25	0.46 ± 0.33	0.10	0.88	0.26 (0.60)	-1.00 (-1.37)	72.96		p ≤ 0.01
<i>Favites encrusting</i>	BB	50	0.74 ± 0.39	0.10	1.18	-0.23 (-0.70)	-0.51 (-0.86)	52.30		ns
	BK	31	0.64 ± 0.47	0.10	1.18	0.31 (0.78)	-0.75 (-1.08)	72.71		ns
<i>Favites massive</i>	BB	17	0.60 ± 0.35	0.10	1.00	-0.09 (-0.19)	-0.84 (-1.08)	58.35		ns
	BK	9	0.56 ± 0.50	0.10	1.18	0.31 (0.52)	-1.62 (-2.20)	88.79		ns
<i>Fungia solitary</i>	BB	94	0.44 ± 0.30	0.10	0.88	-0.01 (-0.02)	-1.45 (-3.10)	67.76		p < 0.001
	PB	169	0.95 ± 0.37	0.10	1.18	-1.49 (-8.04)	0.87 (2.41)	38.99		p < 0.001
<i>Goniastrea encrusting</i>	BB	73	0.93 ± 0.45	0.19	1.48	-0.11 (-0.39)	-0.36 (-0.69)	48.58		ns
	BK	16	0.90 ± 0.42	0.57	1.48	0.08 (0.16)	-0.80 (-1.03)	46.06		ns
<i>Lobophyllia massive</i>	BB	28	0.72 ± 0.45	0.10	1.27	0.14 (0.33)	-0.97 (-1.36)	62.18		ns

	BK	7	0.83 ± 0.21	0.57	1.00	0.13 (0.22)	-0.61 (-0.92)	24.97	ns
<i>Montipora laminar</i>	BB	51	0.88 ± 0.48	0.10	1.48	-0.03 (-0.09)	-0.52 (-0.87)	54.00	ns
	BK	66	0.92 ± 0.36	0.57	1.18	-0.53 (-1.83)	0.27 (0.49)	39.07	ns
<i>Pavona encrusting</i>	BB	15	0.6 ± 0.52	0.10	0.88	1.45 (2.79)	2.50 (3.2)	87.00	ns
	BK	14	0.45 ± 0.48	0.10	1.09	0.92 (1.72)	-0.51 (-0.65)	105.8	ns
<i>Platygyra massive</i>	BB	114	1.01 ± 0.44	0.24	1.48	-0.61 (-2.72)	-0.16 (-0.36)	43.18	ns
	BK	33	1.00 ± 0.36	0.57	1.48	-0.85 (-2.18)	0.52 (0.77)	35.48	ns
<i>Porites encrusting</i>	BB	42	0.41 ± 0.33	0.10	0.88	0.40 (1.15)	-1.14 (-1.80)	79.98	p < 0.001
	BK	18	0.70 ± 0.50	0.10	1.27	-0.01 (-0.02)	-1.33 (-1.72)	71.54	p < 0.001
<i>Symphylia massive</i>	BB	31	0.83 ± 0.42	0.10	1.48	-0.18 (-0.46)	-0.76 (-1.10)	50.31	ns
	BK	7	0.72 ± 0.39	0.38	1.18	-0.19 (-0.31)	-0.89 (-1.35)	53.49	ns

743

744 References

745 Abdi, H. (2007). Bonferroni and Šidák corrections for multiple comparisons. *Encyclopedia of*
746 *measurement and statistics*, 3, 103-107.

747 Adjeroud, M., Mauguit, Q., & Penin, L. (2015). The size-structure of corals with contrasting
748 life-histories: A multi-scale analysis across environmental conditions. *Marine*
749 *Environmental Research*, 112, 131–139.

750 <https://doi.org/https://doi.org/10.1016/j.marenvres.2015.10.004>

751 Adjeroud, M., Pratchett, M. S., Kospartov, M. C., Lejeusne, C., & Penin, L. (2007). Small-
752 scale variability in the size structure of scleractinian corals around Moorea, French
753 Polynesia: patterns across depths and locations. *Hydrobiologia*, 589(1), 117–126.

754 <https://doi.org/10.1007/s10750-007-0726-2>

755 Álvarez-Noriega, M., Baird, A. H., Dornelas, M., Madin, J. S., Cumbo, V. R., & Connolly, S.
756 R. (2016). Fecundity and the demographic strategies of coral morphologies. *Ecology*,
757 97(12), 3485–3493. <https://doi.org/10.1002/ecy.1588>

758 Anderson K.D., & Pratchett M. S. (2014). Variation in size-frequency distributions of
759 branching corals between a tropical versus sub-tropical reef. *Marine Ecology Progress*
760 *Series*, 502, 117–128. <https://www.int-res.com/abstracts/meps/v502/p117-128/>

761 Asia Pacific Economic Cooperation, Fisheries Working Group. (2008). Assessment of
762 impacts of illegal, unreported and unregulated (IUU) fishing in the Asia-pacific. *APEC*
763 *Secretariat*, Singapore.

764 Babcock, R. C. (1991). Comparative Demography of Three Species of Scleractinian Corals
765 Using Age- and Size-Dependent Classifications. *Ecological Monographs*, 61(3), 225–
766 244. <https://doi.org/https://doi.org/10.2307/2937107>

767 Baird, A. H., & Marshall, P. A. (2002). Mortality, growth and reproduction in scleractinian
768 corals following bleaching on the Great Barrier Reef. *Marine Ecology Progress*
769 *Series*, 237, 133-141.

- 770 Bak, R. P. M., & Meesters, E. H. (1998). Coral population structure: the hidden information
771 of colony size-frequency distributions. *Marine Ecology Progress Series*, 162, 301–306.
772 <https://www.int-res.com/abstracts/meps/v162/p301-306>
- 773 Bak, R. P. M., & Meesters, E. H. (1999). Population Structure as a Response of Coral
774 Communities to Global Change1. *American Zoologist*, 39(1), 56–65.
775 <https://doi.org/10.1093/icb/39.1.56>
- 776 Barnes, J. D. (1970). Coral Skeletons: An Explanation of Their Growth and Structure.
777 *Science*, 170(3964), 1305–1308. <https://doi.org/10.1126/science.170.3964.1305>
- 778 Bauman, A. G., Pratchett, M. S., Baird, A. H., Riegl, B., Heron, S. F., & Feary, D. A. (2013).
779 Variation in the size structure of corals is related to environmental extremes in the
780 Persian Gulf. *Marine Environmental Research*, 84, 43–50.
781 <https://doi.org/https://doi.org/10.1016/j.marenvres.2012.11.007>
- 782 Bellwood, D. R., Hughes, T. P., Folke, C., & Nyström, M. (2004). Confronting the coral reef
783 crisis. *Nature*, 429(6994), 827–833. <https://doi.org/10.1038/nature02691>
- 784 Bramanti, L., & Edmunds, P. J. (2016). Density-associated recruitment mediates coral
785 population dynamics on a coral reef. *Coral Reefs*, 35(2), 543–553.
786 <https://doi.org/10.1007/s00338-016-1413-4>
- 787 Brown, B. E. (1997). Coral bleaching: causes and consequences. *Coral reefs*, 16(1), 129-138.
788 <https://doi.org/10.1007/s003380050249>
- 789 Bruno, J. F., & Selig, E. R. (2007). Regional decline of coral cover in the Indo-Pacific:
790 Timing, extent, and subregional comparisons. *PLoS ONE*, 2(8).
791 <https://doi.org/10.1371/journal.pone.0000711>
- 792 Cameron, C., Pausch, R., & Miller, M. (2015). Coral recruitment dynamics and substrate
793 mobility in a rubble-dominated back reef habitat. *Bulletin of Marine Science*, 92(1), 123-
794 136. <https://doi.org/10.5343/bms.2015.1030>
- 795 Cannon, S. E., Aram, E., Beiateuea, T., Kiareti, A., Peter, M., & Donner, S. D. (2021). Coral
796 reefs in the Gilbert Islands of Kiribati: Resistance, resilience, and recovery after more
797 than a decade of multiple stressors. *PLoS ONE*, 16(8 August), 1–29.
798 <https://doi.org/10.1371/journal.pone.0255304>
- 799 Chong-Seng, K. M., Graham, N. A. J., & Pratchett, M. S. (2014). Bottlenecks to coral
800 recovery in the Seychelles. *Coral Reefs*, 33(2), 449–461. [https://doi.org/10.1007/s00338-](https://doi.org/10.1007/s00338-014-1137-2)
801 [014-1137-2](https://doi.org/10.1007/s00338-014-1137-2)
- 802 Colgan, M. W. (1984). *The Cretaceous Coral Heliopora (Octocorallia, Coenothecalia)- a*
803 *Common Indo-Pacific Reef Builder. BT- Living Fossils* (N. Eldredge & S. M. Stanley
804 (eds.); pp. 266–271). Springer New York. [https://doi.org/10.1007/978-1-4613-8271-](https://doi.org/10.1007/978-1-4613-8271-3_33)
805 [3_33](https://doi.org/10.1007/978-1-4613-8271-3_33)
- 806 Crabbe, M. J. C. (2009). Scleractinian coral population size structures and growth rates
807 indicate coral resilience on the fringing reefs of North Jamaica. *Marine Environmental*

- 808 *Research*, 67(4), 189–198.
809 <https://doi.org/https://doi.org/10.1016/j.marenvres.2009.01.003>
- 810 Cramer, D. (1997). *Basic Statistics for Social Research: Step-by-step Calculations and*
811 *Computer Techniques Using Minitab*. London: Routledge
- 812 Darling, E. S., Alvarez-Filip, L., Oliver, T. A., McClanahan, T. R., & Côté, I. M. (2012).
813 Evaluating life-history strategies of reef corals from species traits. *Ecology Letters*,
814 15(12), 1378–1386. <https://doi.org/10.1111/j.1461-0248.2012.01861.x>
- 815 Darling, E. S., Graham, N. A. J., Januchowski-Hartley, F. A., Nash, K. L., Pratchett, M. S., &
816 Wilson, S. K. (2017). Relationships between structural complexity, coral traits, and reef
817 fish assemblages. *Coral Reefs*, 36(2), 561–575. [https://doi.org/10.1007/s00338-017-](https://doi.org/10.1007/s00338-017-1539-z)
818 [1539-z](https://doi.org/10.1007/s00338-017-1539-z)
- 819 Darling, E. S., McClanahan, T. R., & Côté, I. M. (2013). Life histories predict coral
820 community disassembly under multiple stressors. *Global Change Biology*, 19(6), 1930–
821 1940. <https://doi.org/https://doi.org/10.1111/gcb.12191>
- 822 Dietzel, A., Bode, M., Connolly, S. R., & Hughes, T. P. (2020). Long-term shifts in the
823 colony size structure of coral populations along the Great Barrier Reef. *Proceedings of*
824 *the Royal Society B: Biological Sciences*, 287(1936), 20201432.
825 <https://doi.org/10.1098/rspb.2020.1432>
- 826 Duckworth, A., Giofre, N., & Jones, R. (2017). Coral morphology and sedimentation. *Marine*
827 *Pollution Bulletin*, 125(1–2), 289–300. <https://doi.org/10.1016/j.marpolbul.2017.08.036>
- 828 Edmunds, P. J., & Riegl, B. (2020). Urgent need for coral demography in a world where
829 corals are disappearing. *Marine Ecology Progress Series*, 635, 233–242.
830 <https://doi.org/10.3354/MEPS13205>
- 831 Engmann, S., & Cousineau, D. (2011). Comparing distributions: the two-sample anderson-
832 darling test as an alternative to the kolmogorov-smirnov test. *Journal of applied*
833 *quantitative methods*, 6(3), 1-34.
- 834 Fong, P., & Glynn, P. W. (1998). A dynamic size-structured population model: does
835 disturbance control size structure of a population of the massive coral *Gardineroseris*
836 *planulata* in the Eastern Pacific? *Marine Biology*, 130(4), 663–674.
837 <https://doi.org/10.1007/s002270050288>
- 838 Fonti, P., von Arx, G., García-González, I., Eilmann, B., Sass-Klaassen, U., Gärtner, H., &
839 Eckstein, D. (2010). Studying global change through investigation of the plastic
840 responses of xylem anatomy in tree rings. *New Phytologist*, 185(1), 42–53.
841 <https://doi.org/https://doi.org/10.1111/j.1469-8137.2009.03030.x>
- 842 Fox, H. E., Harris, J. L., Darling, E. S., Ahmadi, G. N., Estradivari, & Razak, T. B. (2019).
843 Rebuilding coral reefs: success (and failure) 16 years after low-cost, low-tech
844 restoration. *Restoration Ecology*, 27(4), 862–869. <https://doi.org/10.1111/rec.12935>

- 845 Fisher, W. S., Fore, L. S., Hutchins, A., Quarles, R. L., Campbell, J. G., LoBue, C., & Davis,
846 W. S. (2008). Evaluation of stony coral indicators for coral reef management. *Marine*
847 *Pollution Bulletin*, 56(10), 1737–1745. <https://doi.org/10.1016/j.marpolbul.2008.07.002>
- 848 Ghazali, F., Talaat, W. I., Rahman, A., & Rusli, H. (2019). Malaysian efforts in combating
849 iuu fishing: A legal and policy review*. *Journal of East Asia and International Law*,
850 12(2), 387–400. <https://doi.org/10.14330/jeail.2019.12.2.09>
- 851 Global Wind Atlas 3.0. (2021). <https://globalwindatlas.info/> [Accessed October 24, 2019]
- 852 Graham, N. A. J. (2014). Habitat Complexity: Coral Structural Loss Leads to Fisheries
853 Declines. *Current Biology*, 24(9), R359–R361.
854 <https://doi.org/10.1016/j.cub.2014.03.069>
- 855 Green, A. L., & Bellwood, D. R., (2009). *Monitoring functional groups of herbivorous reef*
856 *fishes as indicators of coral reef resilience. A practical guide for coral reef managers in*
857 *the Asia Pacific Region*. IUCN working group on Climate Change and Coral Reefs.
858 IUCN, Gland, Switzerland. 70 pages.
- 859 Guest, J. R., Baird, A. H., Maynard, J. A., Muttaqin, E., Edwards, A. J., Campbell, S. J., et al.
860 (2012). Contrasting patterns of coral bleaching susceptibility in 2010 suggest an
861 adaptive response to thermal stress. *PLoS ONE*, 7(3).
862 <https://doi.org/10.1371/journal.pone.0033353>
- 863 Hall, V. R., & Hughes, T. P. (1996). Reproductive Strategies of Modular Organisms:
864 Comparative Studies of Reef- Building Corals. *Ecology*, 77(3), 950–963.
865 <https://doi.org/https://doi.org/10.2307/2265514>
- 866 Harborne, A. R., Rogers, A., Bozec, Y.-M., & Mumby, P. J. (2017). Multiple Stressors and
867 the Functioning of Coral Reefs. *Annual Review of Marine Science*, 9(1), 445–468.
868 <https://doi.org/10.1146/annurev-marine-010816-060551>
- 869 Hervé, M. (2021). RVAideMemoire: Testing and Plotting Procedures for Biostatistics. R
870 package version 0.9-79. <https://CRAN.R-project.org/package=RVAideMemoire>
- 871 Huang, D., Licuanan, W. Y., Hoeksema, B. W., Chen, C. A., Ang, P. O., Huang, H., Lane, D.
872 J. W., Vo, S. T., Waheed, Z., Affendi, Y. A., Yeemin, T., & Chou, L. M. (2015).
873 Extraordinary diversity of reef corals in the South China Sea. *Marine Biodiversity*,
874 45(2), 157–168. <https://doi.org/10.1007/s12526-014-0236-1>
- 875 Hudson, J. H., Shinn, E. A., Halley, R. B., & Lidz, B. (1976). Sclerochronology: A tool for
876 interpreting past environments. *Geology*, 4(6), 361–364. [https://doi.org/10.1130/0091-7613\(1976\)4<361:SATFIP>2.0.CO;2](https://doi.org/10.1130/0091-7613(1976)4<361:SATFIP>2.0.CO;2)
- 878 Hughes, T. P., Barnes, M. L., Bellwood, D. R., Cinner, J. E., Cumming, G. S., Jackson, J. B.
879 C., Kleypas, J., van de Leemput, I. A., Lough, J. M., Morrison, T. H., Palumbi, S. R.,
880 van Nes, E. H., & Scheffer, M. (2017b). Coral reefs in the Anthropocene. *Nature*,
881 546(7656), 82–90. <https://doi.org/10.1038/nature22901>

- 882 Hughes, T. P., & Connell, J. H. (1987). Population Dynamics Based on Size or Age? A Reef-
883 Coral Analysis. *The American Naturalist*, 129(6), 818–829.
884 <https://doi.org/10.1086/284677>
- 885 Hughes, T. P., & Connell, J. H. (1999). Multiple stressors on coral reefs: A long -term
886 perspective. *Limnology and Oceanography*, 44(3part2), 932–940.
887 https://doi.org/https://doi.org/10.4319/lo.1999.44.3_part_2.0932
- 888 Hughes, T. P., Graham, N. A. J., Jackson, J. B. C., Mumby, P. J., & Steneck, R. S. (2010).
889 Rising to the challenge of sustaining coral reef resilience. *Trends in Ecology and*
890 *Evolution*, 25(11), 633–642. <https://doi.org/10.1016/j.tree.2010.07.011>
- 891 Hughes, T. P., & Jackson, J. B. C. (1980). Do Corals Lie About Their Age? Some
892 Demographic Consequences of Partial Mortality, Fission, and Fusion. *Science*,
893 209(4457), 713–715. <https://doi.org/10.1126/science.209.4457.713>
- 894 Hughes, T. P., & Jackson, J. B. C. (1985). Population Dynamics and Life Histories of
895 Foliose Corals. *Ecological Monographs*, 55(2), 141–166.
896 <https://doi.org/https://doi.org/10.2307/1942555>
- 897 Hughes, T. P., Kerry, J. T., Álvarez-Noriega, M., Álvarez-Romero, J. G., Anderson, K. D.,
898 Baird, A. H., Babcock, R. C., Beger, M., Bellwood, D. R., Berkelmans, R., Bridge, T.
899 C., Butler, I. R., Byrne, M., Cantin, N. E., Comeau, S., Connolly, S. R., Cumming, G.
900 S., Dalton, S. J., Diaz-Pulido, G., ... Wilson, S. K. (2017a). Global warming and
901 recurrent mass bleaching of corals. *Nature*, 543(7645), 373–377.
902 <https://doi.org/10.1038/nature21707>
- 903 Jari Oksanen, F., Blanchet, G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., &
904 Wagner, H. (2018). vegan: Community Ecology Package. R package version 2.5-3.
- 905 Jarque, C. M., & Bera, A. K. (1980). Efficient tests for normality, homoscedasticity and serial
906 independence of regression residuals. *Economics letters*, 6(3), 255-259.
907
- 908 Jokieli, P. L., & Cowdin, H. P. (1976). Hydromechanical adaptation in the solitary free-living
909 coral *Fungia scutaria*. *Nature*, 262(5565), 212–213. <https://doi.org/10.1038/262212a0>
- 910 Kamarruddin, I., Osman, N. H., Ahmad, A., Abdullah, S. S., & Chan, A. A. (2013). PULAU
911 REDANG MARINE PARK: Management Effectiveness And Total Economic Value,
912 Department of Marine Park Malaysia, Ministry of Natural Resources and Environment,
913 Putrajaya, Malaysia, 1-101.
- 914 Kayal, M., Vercelloni, J., Wand, M. P., & Adjeroud, M. (2015). Searching for the best bet in
915 life-strategy: A quantitative approach to individual performance and population
916 dynamics in reef-building corals. *Ecological Complexity*, 23, 73–84.
917 <https://doi.org/https://doi.org/10.1016/j.ecocom.2015.07.003>
- 918 Kelley, R. (2016). Indo Pacific Coral Finder, 3rd Edition. Townsville: BYOGUIDES.

- 919 Kimura, T., Chou, L. M., Huang, D., Tun, K., & Goh, E. (2022). Status and Trends of East
920 Asian Coral Reefs: 1983–2019. *Global Coral Reef Monitoring Network, East Asia*
921 *Region*.
- 922 Komsta, L., & Novomestky, F. (2015). moments: Moments, cumulants, skewness, kurtosis
923 and related tests. R package version 0.14. [https://CRAN.R-](https://CRAN.R-project.org/package=moments)
924 [project.org/package=moments](https://CRAN.R-project.org/package=moments)
- 925 Kramer, N., Tamir, R., Eyal, G., & Loya, Y. (2020). Coral Morphology Portrays the Spatial
926 Distribution and Population Size-Structure Along a 5–100 m Depth Gradient. *Frontiers*
927 *in Marine Science*, 7(July), 1–13. <https://doi.org/10.3389/fmars.2020.00615>
- 928 Kushairi, M. M. R. (1998). The 1998 bleaching catastrophe of corals in the South China Sea.
929 *Proc. JSPS Joint Seminar on Marine and Fisheries Sciences, Bali, Indonesia, 1998*.
930 <http://ci.nii.ac.jp/naid/10018463620/en/>
- 931 Loader, N. J., Helle, G., Los, S. O., Lehmkuhl, F., & Schleser, G. H. (2010). Twentieth-
932 century summer temperature variability in the southern Altai Mountains: A carbon and
933 oxygen isotope study of tree-rings. *The Holocene*, 20(7), 1149–1156.
934 <https://doi.org/10.1177/0959683610369507>
- 935 Lough, J. M., & Cantin, N. E. (2014). Perspectives on Massive Coral Growth Rates in a
936 Changing Ocean. *The Biological Bulletin*, 226(3), 187–202.
937 <https://doi.org/10.1086/BBLv226n3p187>
- 938 Loya, Y., Sakai, K., Yamazato, K., Nakano, Y., Sambali, H., & Van Woesik, R. (2001).
939 Coral bleaching: The winners and the losers. *Ecology Letters*, 4(2), 122–131.
940 <https://doi.org/10.1046/j.1461-0248.2001.00203.x>
- 941 Madin, J. S., Baird, A. H., Dornelas, M., & Connolly, S. R. (2014). Mechanical vulnerability
942 explains size-dependent mortality of reef corals. *Ecology Letters*, 17(8), 1008–1015.
943 <https://doi.org/10.1111/ele.12306>
- 944 Madin, J. S., Hoogenboom, M. O., & Connolly, S. R. (2012). Integrating physiological and
945 biomechanical drivers of population growth over environmental gradients on coral reefs.
946 *Journal of Experimental Biology*, 215(6), 968–976. <https://doi.org/10.1242/jeb.061002>
- 947 Massel, S. R., & Done, T. J. (1993). Effects of cyclone waves on massive coral assemblages
948 on the Great Barrier Reef: meteorology, hydrodynamics and demography. *Coral Reefs*,
949 12(3), 153–166. <https://doi.org/10.1007/BF00334475>
- 950 McClanahan, T. R., Ateweberhan, M., & Omukoto, J. (2008). Long-term changes in coral
951 colony size distributions on Kenyan reefs under different management regimes and
952 across the 1998 bleaching event. *Marine Biology*, 153(5), 755–768.
953 <https://doi.org/10.1007/s00227-007-0844-4>
- 954 McClanahan, T., Muthiga, N., & Mangi, S. (2001). Coral and algal changes after the 1998
955 coral bleaching: Interaction with reef management and herbivores on Kenyan reefs.
956 *Coral Reefs*, 19, 380–391. <https://doi.org/10.1007/s003380000133>

- 957 McWilliam, M., Pratchett, M. S., Hoogenboom, M. O., & Hughes, T. P. (2020). Deficits in
958 functional trait diversity following recovery on coral reefs. *Proceedings of the Royal*
959 *Society B: Biological Sciences*, 287(1918), 20192628.
960 <https://doi.org/10.1098/rspb.2019.2628>
- 961 Meesters E.H., Hilterman M., Kardinaal E., Keetman M., deVries, M., & Bak R.P.M. (2001).
962 Colony size-frequency distributions of scleractinian coral populations: spatial and
963 interspecific variation. *Marine Ecology Progress Series*, 209, 43–54. [https://www.int-](https://www.int-res.com/abstracts/meps/v209/p43-54/)
964 [res.com/abstracts/meps/v209/p43-54/](https://www.int-res.com/abstracts/meps/v209/p43-54/)
- 965 Miller, M., Williams, D. E., Huntington, B. E., Piniak, G. A., Vermeij, M. J.
966 A. (2016). Decadal comparison of a diminishing coral community: a study using
967 demographics to advance inferences of community status. *PeerJ*, 4,
968 e1643. <https://doi.org/10.7717/peerj.1643>
- 969 Hanapiah, M. F., Saad, S., Mukai, Y., & Ahmad, Z. (2017). Relationship between adult
970 abundance and successive coral recruitment density in the Tioman Island Marine Park,
971 Malaysia. *Zoology and Ecology*, 27(3–4), 328–334.
972 <https://doi.org/10.1080/21658005.2017.1396793>
- 973 Obura, D. O., & Grimsdith, G. (2009). Resilience Assessment of Coral Reefs – Assessment
974 protocol for coral reefs, focusing on coral bleaching and thermal stress. IUCN working
975 group on Climate Change and Coral Reefs. IUCN, Gland, Switzerland. 70 pages.
- 976 Padilla-Gamiño, J. L., Hanson, K. M., Stat, M., & Gates, R. D. (2012). Phenotypic plasticity
977 of the coral *Porites rus*: Acclimatization responses to a turbid environment. *Journal of*
978 *Experimental Marine Biology and Ecology*, 434–435, 71–80.
979 <https://doi.org/https://doi.org/10.1016/j.jembe.2012.08.006>
- 980 Penin, L., & Adjeroud, M. (2013). Relative importance of recruitment and post-settlement
981 processes in the maintenance of coral assemblages in an insular, fragmented reef system
982. *Marine Ecology Progress Series*, 473, 149–162. [https://www.int-](https://www.int-res.com/abstracts/meps/v473/p149-162/)
983 [res.com/abstracts/meps/v473/p149-162/](https://www.int-res.com/abstracts/meps/v473/p149-162/)
- 984 Praveena, S. M., Siraj, S. S., & Aris, A. Z. (2012). Coral reefs studies and threats in
985 Malaysia: A mini review. *Reviews in Environmental Science and Biotechnology*, 11(1),
986 27–39. <https://doi.org/10.1007/s11157-011-9261-8>
- 987 Rani, M., Saad, S., Khodzori, F. A., Ramli, R., & Yusof, M. (2015). Scleractinian coral
988 recruitment density in coastal water of Balok, Pahang, Malaysia. *Jurnal Teknologi*, 77.
989 <https://doi.org/10.11113/jt.v77.6730>
- 990 Raymundo, L. J., Maypa, A. P., Gomez, E. D., & Cadiz, P. (2007). Can dynamite-blasted
991 reefs recover? A novel, low-tech approach to stimulating natural recovery in fish and
992 coral populations. *Marine Pollution Bulletin*, 54(7), 1009–1019.
993 <https://doi.org/https://doi.org/10.1016/j.marpolbul.2007.02.006>
- 994 Reef Check Malaysia. (2019). *Status of Coral Reefs in Malaysia, 2019*.
995 <http://www.reefcheck.org.my/media-information/annual-survey-reports>

- 996 Riegl, B. M., Bruckner, A. W., Rowlands, G. P., Purkis, S. J., & Renaud, P. (2012). Red Sea
997 coral reef trajectories over 2 decades suggest increasing community homogenization and
998 decline in coral size. *PLoS ONE*, 7(5), 5–11.
999 <https://doi.org/10.1371/journal.pone.0038396>
- 1000 RStudio Team (2021). RStudio: Integrated Development Environment for R. RStudio, PBC,
1001 Boston, MA URL <http://www.rstudio.com/>. [Accessed April 1, 2021]
- 1002 Safuan, C. D. M., Roseli, N. H., Bachok, Z., Akhir, M. F., Xia, C., & Qiao, F. (2020). First
1003 record of tropical storm (Pabuk - January 2019) damage on shallow water reef in Pulau
1004 Bidong, south of South China Sea. *Regional Studies in Marine Science*, 35(January
1005 2019), 101216. <https://doi.org/10.1016/j.rsma.2020.101216>
- 1006 Scholz, F., & Zhu, A. (2019). kSamples: K-Sample Rank Tests and their Combinations. R
1007 package version 1.2-9. <https://CRAN.R-project.org/package=kSamples>
- 1008 Smith, S. R. (1992). Patterns of coral recruitment and post-settlement mortality on bermuda's
1009 reefs: Comparisons to caribbean and pacific reefs. *Integrative and Comparative Biology*,
1010 32(6), 663–673. <https://doi.org/10.1093/icb/32.6.663>
- 1011 Smith, L. D., Devlin, M., Haynes, D., & Gilmour, J. P. (2005). A demographic approach to
1012 monitoring the health of coral reefs. *Marine Pollution Bulletin*, 51(1–4), 399–407.
1013 <https://doi.org/10.1016/j.marpolbul.2004.11.021>
- 1014 Smith, L. D., & Hughes, T. P. (1999). An experimental assessment of survival, re-attachment
1015 and fecundity of coral fragments. *Journal of Experimental Marine Biology and Ecology*,
1016 235(1), 147–164. [https://doi.org/https://doi.org/10.1016/S0022-0981\(98\)00178-6](https://doi.org/https://doi.org/10.1016/S0022-0981(98)00178-6)
- 1017 Stobutzki, I. C., Silvestre, G. T., Abu Talib, A., Krongprom, A., Supongpan, M., Khemakorn,
1018 P., Armada, N., & Garces, L. R. (2006). Decline of demersal coastal fisheries resources
1019 in three developing Asian countries. *Fisheries Research*, 78(2–3), 130–142.
1020 <https://doi.org/10.1016/j.fishres.2006.02.004>
- 1021 Sukarno W., Nor Hasni O., Abdul Rahim G.Y., Azhar A., Muntalib J., Mohd. Ridzuan M. A.,
1022 Fitra A. Z. and Chan, A. A., 2015, Pulau Perhentian Marine Park Total Economic
1023 Value & Management Effectiveness, Department of Marine Park Malaysia, Ministry
1024 of Natural Resources and Environment, Putrajaya, Malaysia, 151 pages.
- 1025 Swedlund, A. C. (1978). Historical Demography as Population Ecology. *Annual Review of*
1026 *Anthropology*, 7(1), 137–173. <https://doi.org/10.1146/annurev.an.07.100178.001033>
- 1027 Szereday, S., & Yang Amri, A. (2022). Highly variable response of hard coral taxa to
1028 successive coral bleaching events (2019-2020) and rising ocean temperatures in
1029 Northeast Peninsular Malaysia. *BioRxiv*, 2021.11.16.468775.
1030 <https://doi.org/10.1101/2021.11.16.468775>
- 1031 Tabachnick, B. G., & Fidell, L. S. (1996). *SPSS for Windows workbook to accompany large*
1032 *sample examples of using multivariate statistics*. Harper Collins College Publishers.

- 1033 Tan, C. H., & SF, H. (2011). First observed severe mass bleaching in Malaysia, Greater Coral
1034 Triangle. *Galaxea, Journal of Coral Reef Studies*, 13(1), 27-
1035 28. <https://doi.org/10.3755/galaxea.13.27>
- 1036 Tanzil, J. T. I., Brown, B. E., Dunne, R. P., Lee, J. N., Kaandorp, J. A., & Todd, P. A. (2013).
1037 Regional decline in growth rates of massive Porites corals in Southeast Asia. *Global*
1038 *Change Biology*, 19(10), 3011–3023. <https://doi.org/https://doi.org/10.1111/gcb.12279>
- 1039 Teichberg, M., Wild, C., Bednarz, V. N., Kegler, H. F., Lukman, M., Gärdes, A. A., Heiden,
1040 J. P., Weiland, L., Abu, N., Nasir, A., Miñarro, S., Ferse, S. C. A., Reuter, H., & Plass-
1041 Johnson, J. G. (2018). Spatio-temporal patterns in coral reef communities of the
1042 Spermonde Archipelago, 2012-2014, I: Comprehensive reef monitoring of water and
1043 benthic indicators reflect changes in reef health. *Frontiers in Marine Science*, 5(FEB),
1044 1–18. <https://doi.org/10.3389/fmars.2018.00033>
- 1045 Toda, T., Okashita, T., Maekawa, T., Alfian, B. A. A. K., Rajuddin, M. K. M., Nakajima, R.,
1046 Chen, W., Takahashi, K. T., Othman, B. H. R., & Terazaki, M. (2007). Community
1047 structures of coral reefs around peninsular Malaysia. *Journal of Oceanography*, 63(1),
1048 113–123. <https://doi.org/10.1007/s10872-007-0009-6>
- 1049 Veron, J. E. N., Stafford-Smith, M. G., Turak, E., & DeVantier, L. M. (2022). Corals of the
1050 World: *Acropora longicyathus*. [Accessed 20th January 2022, version 0.01 (Beta).]
1051
- 1052 Weinstein, J., & Pillai, V. K. (2015). *Demography: The science of population*. Rowman &
1053 Littlefield.
- 1054 Williams, S. L., Sur, C., Janetski, N., Hollarsmith, J. A., Rapi, S., Barron, L., Heatwole, S. J.,
1055 Yusuf, A. M., Yusuf, S., Jompa, J., & Mars, F. (2019). Large-scale coral reef
1056 rehabilitation after blast fishing in Indonesia. *Restoration Ecology*, 27(2), 447–456.
1057 <https://doi.org/https://doi.org/10.1111/rec.12866>
- 1058 Wolfe, K., Kenyon, T. M., & Mumby, P. J. (2021). The biology and ecology of coral rubble
1059 and implications for the future of coral reefs. *Coral Reefs*, 40(6), 1769–1806.
1060 <https://doi.org/10.1007/s00338-021-02185-9>
- 1061 Wooldridge, S. A., Done, T. J., Thomas, C. R., Gordon, I. I., Marshall, P. A., & Jones, R. N.
1062 (2012). Safeguarding coastal coral communities on the central Great Barrier Reef
1063 (Australia) against climate change: Realizable local and global actions. *Climatic*
1064 *Change*, 112(3–4), 945–961. <https://doi.org/10.1007/s10584-011-0229-z>
- 1065 Zvuloni, A., Artzy-Randrup, Y., Stone, L., van Woesik, R., & Loya, Y. (2008). Ecological
1066 size-frequency distributions: how to prevent and correct biases in spatial sampling.
1067 *Limnology and Oceanography: Methods*, 6(3), 144-153.