Fluctuations in coral reef fish densities after environmental disturbances on the northern Great Barrier Reef

Zegni Triki Corresp., [1] , **Redouan Bshary** [1]

[1] Institute of Biology, University of Neuchâtel, Neuchâtel, NE, Switzerland

Corresponding Author: Zegni Triki
Email address: zegni.triki@unine.ch

Global warming is predicted to increase the frequency and or severity of many disturbances including cyclones, storms, and prolonged heatwaves. The coral reef at Lizard Island, part of the Great Barrier Reef, has been recently exposed to a sequence of severe tropical cyclones (i.e., Ita in 2014 and Nathan in 2015) and a coral bleaching in the year 2016. Reef fishes are an essential part of the coral reef ecosystem, and their abundance is thus a good marker to estimate the magnitude of such disturbances. Here, we examined whether the recent disturbances at Lizard Island had an impact on the coral reef fish communities. To do this, we examined fish survey data collected before and after the disturbances for potential changes in total fish density post-disturbance. Also, by sorting fish species into eleven functional groups based on their trophic level (i.e., diet), we further explored the density changes within each functional group. Our findings showed an overall decline of 68% in fish density post-disturbance, with a significant density decrease in nine of eleven trophic groups. These nine groups were: browsers, corallivores, detritivores, excavator/scrapers, grazers, macro-invertivores, pisci-invertivores, planktivores, and spongivores. The piscivores, on the other hand, were the only “winners”, wherein their density showed an increase post-disturbance. These changes within functional groups might have a further impact on the trophodynamics of the food web. In summary, our findings provide evidence that the fish assemblage on the reefs around Lizard Island was considerably affected by extreme weather events, leading to changes in the functional composition of the reef fish assemblage.

Title: Fluctuations in coral reef fish densities after environmental disturbances on the northern Great Barrier Reef

Authors: Zegni Triki* & Redouan Bshary

Affiliations:

Institute of Biology, University of Neuchâtel, Emile-Argand 11, 2000 Neuchâtel, Switzerland

***Correspondence to** Zegni Triki, zegni.triki@unine.ch

Abstract

Global warming is predicted to increase the frequency and or severity of many disturbances including cyclones, storms, and prolonged heatwaves. The coral reef at Lizard Island, part of the Great Barrier Reef, has been recently exposed to a sequence of severe tropical cyclones (i.e., Ita in 2014 and Nathan in 2015) and a coral bleaching in the year 2016. Reef fishes are an essential part of the coral reef ecosystem, and their abundance is thus a good marker to estimate the magnitude of such disturbances. Here, we examined whether the recent disturbances at Lizard Island had an impact on the coral reef fish communities. To do this, we examined fish survey data collected before and after the disturbances for potential changes in total fish density post-disturbance. Also, by sorting fish species into eleven functional groups based on their trophic level (i.e., diet), we further explored the density changes within each functional group. Our findings showed an overall decline of 68% in fish density post-disturbance, with a significant density decrease in nine of eleven trophic groups. These nine groups were: browsers, corallivores, detritivores, excavator/scrapers, grazers, macro-invertivores, pisci-invertivores, planktivores, and spongivores. The piscivores, on the other hand, were the only "winners", wherein their density showed an increase post-disturbance. These changes within functional groups might have a further impact on the trophodynamics of the food web. In summary, our findings provide evidence that the fish assemblage on the reefs around Lizard Island was considerably affected by extreme weather events, leading to changes in the functional composition of the reef fish assemblage.

Introduction:

The recently observed increase in frequency and magnitude of extreme weather events is attributed to anthropogenic global warming (Cai et al., 2014; Cheal et al., 2017; Hughes et al., 2018). Such extreme events are a great threat to coral reefs worldwide (Hughes et al., 2017). Coral reefs are one of the world's most diverse ecosystems, with fish as an essential component. Losing live corals can thus have severe impacts on the diversity and stability of this ecosystem (Bellwood et al., 2006; Pratchett et al., 2008, 2011; Munday et al., 2008). For instance, one of the threats of extreme weather events to coral reefs is the prolonged El Niño cycles and the resulting coral bleaching. El Niño is a naturally occurring climatic event that brings warm water towards the Indo-Pacific. A recent prolonged El Niño event led to an increase in seawater temperatures (Cai et al., 2014; Hoegh-Guldberg & Ridgway, 2016). In these conditions, overstressed coral tissues expel their intracellular symbionts "zooxanthella" (i.e., symbionts from which corals gain their different pigmentations) which causes bleaching. The resulting bleached corals may die if they do not re-establish the symbiotic relationship with the zooxanthella within a range of six months post-bleaching (DiazPulido & McCook, 2002). In addition to the threat of coral bleaching, cyclones can also be destructive due to the formation of strong waves that can damage exposed coral reef fields (Cheal et al., 2017). Both cyclones and coral bleaching can thus result in environmental degradation and habitat loss (Pizarro et al., 2017; Hughes et al., 2017).

Using fish assemblages, diversity, and abundance, researchers can evaluate the biological integrity and quality of a given habitat (Karr, 1981; Ganasan & Hughes, 1998). Several studies, for instance, showed that fish abundance could be negatively affected by environmental

disturbances due to climate change, either directly through abiotic factors such as temperature and ocean acidification (Ferrari et al., 2011; Browman, 2016), or indirectly through habitat loss (Munday et al., 2008). Thus, changes in fish abundance should provide reliable information on habitat quality.

Habitat degradation is known to have a negative impact on overall fish density (Munday, 2004; Wilson et al., 2008b, 2010). Bellwood et al. (2004) argue that further insights can be gained from analysing fish functional groups but only in addition to knowing the cause and extent of the habitat degradation. Therefore, exploring potential changes at the level of fish groups that share the same function (i.e., functional group) might yield additional information about the mechanism and effect of the impact. For instance, three main functional groups displaying herbivore dietary traits (i.e., corallivores, excavator/scrapers, and grazers) can play an important role in coral reef recovery. The functional role of these three herbivores is complementary, and together their presence on the reef can play a role in its resistance to disturbances (Bellwood et al., 2004). In addition to the densities of herbivorous fishes, other factors also play a major role in coral reef resistance and recovery, such as the complexity of coral structure and water depth (Graham et al., 2015).

A suitable location to explore potential changes in fish abundance and functional groups after environmental disturbances is Lizard Island (Pizarro et al., 2017; Emslie, Cheal & Logan, 2017; Triki et al., 2018). The island is located in the northern Great Barrier Reef (GBR), Australia, within a marine reserve. The island was impacted by a sequence of extreme weather events three years in a row: In April 2014, Cyclone Ita hit Lizard Island (Pizarro et al., 2017), reaching an

intensity of category 5 on the Australian scale (Puotinen et al., 2016). In April 2015, the island was again exposed to another severe cyclone, Cyclone Nathan, a severe category 4 cyclone (Pizarro et al., 2017). And finally, in February/March of 2016, the GBR was affected by a massive coral bleaching event, resulting in more than 60% bleached coral cover (Hughes et al., 2017).

In this study, we asked in to what extent fish communities would change as a function of environmental disturbances at Lizard Island. To do so, we compared fish densities before and after disturbances both overall and by functional group. We expected to find a decline in fish species that rely directly or indirectly on live corals for their diet (Wilson et al., 2006). In contrast, due to the colonisation of dead corals by microalgae (Cheal et al., 2010) we expected an increase in the abundance of various herbivorous fish species specialised on such algae (Randall, 1961).

Methods:

Field site and fish census:

The study was conducted on the reef around Lizard Island, Great Barrier Reef, Australia (14.6682° S, 145.4604° E). The study was carried out at two locations: Mermaid Cove and Northern Horseshoe reefs. Mermaid Cove forms a continuous fringing reef of approximatively 35,000 m^2 (i.e., estimated from maps: https://www.freemaptools.com/area-calculator.htm), with a depth range from 1 to 7 m. The reef is located in a small bay on the northern side of Lizard Island. The other location, Northern Horseshoe reef, is also a continuous reef consisting of a coral garden of approximately 17,000 m^2, with a depth range from 1 to 4 m. The reef is located on the western side of the island (see Figure 1). After the 2014 and 2015 cyclones, the reef at

106 Mermaid Cove was heavily damaged. Northern Horseshoe reef, however, had been protected
107 from these two cyclones due to its location within the lagoon (Pizarro et al., 2017; Lizard Island
108 Research Station directors, personal communication). The coral bleaching event in 2016 affected
109 all the reefs around Lizard Island including our two study sites.
110
111 We used underwater visual fish census methods based on earlier studies by Wismer et al. (2014)
112 and Triki et al. (2018). Within each location, the observer swam ten replicates of a 30 m transect
113 line on the reef flat. Due to the different shape of the reef at the two locations, the transect line
114 was placed parallel to the reef crest at Mermaid Cove, whereas at Northern Horseshoe it was
115 placed parallel to the shoreline (Following methods in Wismer et al., 2014). Along the 30 m
116 transect line the observer first recorded the number of all large visible fish (i.e., species with
117 body total length TL > 10 cm) on a 5 m wide area, then the number of small visible fish (i.e.,
118 species with body TL ≤ 10 cm) on a 1m wide area. Each of the ten transect replicates, within
119 each location, were sampled at least 10 meters apart from each other to minimise possible
120 resampling of the same individuals. Only adult fish were surveyed, and their species was
121 identified. Overall, there were 163 species identified in our survey (Table S1). All fish counts
122 (i.e., large and small fish) were scaled per 150 m^2 to facilitate further statistical analyses.
123
124 The fish surveys from the two study locations were collected at the same time of day in a similar
125 way between June and August within each year of data collection. Data were collected at
126 Mermaid Cove in 2011 (in Wismer et al., 2014), 2016 (in Triki et al., 2018), and 2017. At
127 Northern Horseshoe, the fish census was conducted in 2014, 2016 (in Triki et al., 2018) and
128 2017. We labelled the data collected in 2011 (i.e., from Mermaid Cove) and 2014 (i.e., from

Northern Horseshoe), as fish survey before disturbances. Subsequently, the fish surveys in 2016 and 2017 were labelled as data after the disturbances (as in Triki et al., 2018).

Fish species were then categorised into functional groups based on the species' trophic level (Butterfield & Suding, 2013; Brandl et al., 2016). We sorted fish species into 11 trophic-functional groups (Table 1). The categorisation into dietary functional groups followed methods in studies by Wernberg et al. (2013) and MacNeil et al. (2015) (see Table S1 in the Supplementary material). For the few species for which trophic level was missing from these studies, we completed information from the FishBase (Froese & Pauly, 2016).

Statistical analyses:

All data analyses and figures were generated by using the Software R version 3.5.1. All the recorded fish species were included in the present analyses. Fish counts on each transect represented fish abundance. Therefore, the transect line was the statistical unit in our sample size. Overall, we ran two statistical models. We fit the first model to test for the overall change in total fish abundance before and after the disturbances. It was a General Linear Model (GLM), with a negative binomial distribution. The model had fish abundance as the response variable, while the period before and after the perturbation was fitted as a predictor with data collection site as a covariate. The model had the following structure: fish abundance ~ period of data collection + site. The model assumptions were checked with visual plots with the function `influencePlot()` in R language.

The second model tested for potential changes in the abundance within the eleven trophic-functional groups. Here, we fitted a zero-inflated negative binomial distribution due to the presence of many zeros in the count data. The zeros refer to the absence of some functional groups in the transects. The site identity was fitted as a covariate to control for potential differences between the two sites (R. Slobodeanu, personal communication). The model had the following function: fish abundance ~ functional group * period of data collection + site. As *post hoc* analyses for the second model, we ran least-squares means analyses with the function `emmeans()` from the package (`emmeans` in R language). The `emmeans()` function uses the Tukey method by default for multiple comparisons. The reported pseudo R-squared in the results are the Nagelkerke (Cragg and Uhler) values generated with the `nagelkerke()` from the package (`rcompanion` in R language) (see Liu, Zheng & Shen, 2008). For further details about statistical tests, R packages and script, please refer to our statistical script in the Figshare repository (DOI: 10.6084/m9.figshare.4990919).

Ethical note:

The Animal Ethics Committee of the Queensland government (DAFF) approved the project (CA 2016/05/970 and CA 2017/05/1063).

Results:

Fish census data showed that total fish abundance significantly declined after the environmental disturbances (ANOVA: $N = 60$, estimate = -1.239, $X^2 = 52.885$, $p < 0.001$, pseudo R-squared = 0.49, Figure 2), despite differences between the two study sites (ANOVA: $N = 60$, estimate = 0.519, $X^2 = 9.583$, $p = 0.002$). On the other hand, fish functional groups provided more details

on where the decline in fish density occurred, with a significant interaction of the trophic-functional group and the period of data collection (ANOVA*:* $N = 660$, $X^2 = 68.899$, pseudo R-squared = 0.66, $p < 0.001$, Figure 3). *Post hoc* tests showed that ten out of the eleven functional groups went through a significant change in fish abundance after the disturbances, of which nine showed a decline (the contrast before – after): browsers (estimate= 1.534, $z = 3.427$, $p < 0.001$); corallivores (estimate= 2.099, $z = 2.418$, $p = 0.015$); detrivores (estimate= 15.784, $z = 3.610$, $p < 0.001$); excavator/scrapers (estimate= 8.904, $z = 4.308$, $p < 0.001$); grazers (estimate= 11.836, $z = 2.617$, $p = 0.009$); macro-invertivores (estimate= 3.580, $z = 2.195$, $p = 0.030$); pisci-invertivores (estimate= 1.133, $z = 2.337$, $p = 0.020$); planktivores (estimate= 102.06, $z = 4.340$, $p < 0.001$); and spongivores (estimate= 39.951, $z = 3.479$, $p < 0.001$). Only piscivores showed a significant increase in abundance (estimate= -0.662, $z = -2.277$, $p = 0.022$), while micro-invertivores were the only functional group that did not show any significant changes (estimate= 6.956, $z = 1.152$, $p = 0.249$).

Discussion:

We identified a substantial decline in the density of reef fishes at Lizard Island following a sequence of severe tropical cyclones and coral bleaching. We documented a 68 % decline in fish densities; a percentage close to what Wilson et al. (2006) found in their meta-analysis of 17 independent studies on fish density after environmental disturbances, in which an average decline of 62 % was observed in fish density within three years after disturbances including cyclones and coral bleaching. These findings are in line with previous studies suggesting that the loss of coral cover would lead to a reduction in fish density (Jones et al., 2004; Russ & Leahy,

198 2017; Pratchett et al., 2018). It suggests that the recorded decline in the present study might be
199 due to the loss of coral cover. Cyclones usually destroy the reef structure, which would impede
200 corals from possible rapid recovery (Cheal et al., 2002). Also, coral recovery might be
201 compromised if the reef is repeatedly exposed to tropical cyclones over short-time intervals
202 (De′ath et al., 2012; Puotinen et al., 2016). In addition to damage from cyclones, bleaching can
203 reduce coral cover (DiazPulido & McCook, 2002). Recently, Stuart-Smith et al. (2018)
204 documented a 51 % coral cover loss at the GBR after the 2016 bleaching event. Subsequently, it
205 is expected that habitat loss would lead to a decline in fish abundance (Pratchett et al., 2011;
206 Brandl et al., 2016). We acknowledge an important caveat in the present study: we were unable
207 to incorporate information about the benthic habitat structure and benthic communities. This
208 information would provide more insight into the fluctuations in reef-dependent fish communities
209 (Goren & Spanier, 1985; Holbrook, Schmitt & Stephens, 1997; Russ & McCook, 1999; Wismer,
210 Hoey & Bellwood, 2009; Pizarro et al., 2017; Prazeres, Roberts & Pandolfi, 2017; Renfro &
211 Chadwick, 2017). Also, due to the absence of data on the benthos, the significant effect of "site"
212 in our model is virtually impossible to interpret (see Supplementary Fig. S1 and Fig. S2).
213 Nevertheless, the significant decline in fish densities recorded here can still inform us about the
214 effect of extreme weather events on fish assemblages (Wilson et al., 2006).
215
216 Assessing fish density according to their trophic-functional groups showed a substantial decline
217 in nine out of eleven functional groups. This suggests that most fish, regardless of their trophic
218 affiliation, were susceptible to the disturbances. Nevertheless, the piscivore group was the only
219 group to benefit from such disturbances. It is possible that due to the damage of reef structure
220 and the resulting destruction of shelters, piscivores (i.e., reef-associated predators) would gain

easy access to prey, from which they could benefit and thereby increase their numbers. Also, it is possible that bleached corals might no longer be suitable shelters for coral-dwelling species (Coker, Pratchett & Munday, 2009; Pratchett et al., 2011), nor appropriate camouflage background for small-bodied prey. As a consequence, predators would easily recognise their prey (Phillips et al., 2017), which would eventually change the assemblage structure of these predatory fishes (Emslie, Cheal & Logan, 2017). Nevertheless, such an increase might be transient in time and eventually be followed by a decline due to decreased numbers of prey. Also, the erosion of corals skeleton over time might result in a reduction of shelter and hunting options for ambush predators (Kerry & Bellwood, 2012).

Graham et al. (2011) predicted that micro-invertivores are one of the trophic-functional groups most vulnerable and macro-invertivores the least vulnerable to climate disturbances. Here, the micro-invertivores were the only group without apparent changes from pre- to post-disturbance. A potential explanation for this divergence is that micro-invertivores may show high functional redundancy, where losses in particular species can be replaced by population increases in other species that share a similar function (Micheli & Halpern, 2005; Brandl et al., 2016). Furthermore, we note that the decline in browsers, corallivores and pisci-invertivores, as well as the increase in piscivores documented in this study, differ from previous results also collected around Lizard Island (Ceccarelli, Emslie & Richards, 2016; Brandl et al., 2016). One potential explanation is that those previous studies used post-disturbance data collected in early 2015, i.e. only a few months after hurricane Ita hit the island, while we collected data 2-3 years after another cyclone and the El Niño event took place. A potential additional factor could be that the

243 previous studies collected data in 3m and 9m depth, while our data include shallow areas of 1-
244 2m depth.
245
246 The trophic-functional groups that were most abundant pre-disturbance, the planktivores and
247 spongivores, also showed a decline in numbers post-disturbances (Figure 3). For instance,
248 planktivores are mainly damselfish that are often highly coral-associated species (Feary et al.,
249 2007; Wilson et al., 2008a), wherein habitat loss might explain the decline in their numbers.
250 Such losses can be detrimental to the ecosystem balance, mainly because the planktivores play
251 an important role in transferring nutrients from the pelagic environment onto the reef (Pace et al.,
252 1999; Fisher et al., 2015). Spongivores also have a significant role in protecting corals by feeding
253 on overgrowing sponges, thereby reducing coral-sponge competition (Hill, 1998). The decrease
254 in fish density in the other functional groups: browsers, detritivores, grazers, and
255 excavators/scrapers, can also have severe consequences on the health and resilience of corals
256 after disturbances. These trophic-functional groups feed on macro-algae, which prevent the latter
257 from over-colonising the corals. Their functional role is hence beneficial for coral resilience,
258 coral settlement, and growth (Green & Bellwood, 2009; Cheal et al., 2010; Rasher, Hoey & Hay,
259 2013).
260
261 **Conclusion**
262
263 Environmental disturbances are expected to increase in frequency and magnitude due to global
264 warming. Here we found that such environmental events were followed by reductions in fish
265 densities across multiple trophic-functional groups around Lizard Island. These findings add to

the data that shows that future coral reef fish communities are susceptible to significant changes on this island. Supported by the larger scale fish assemblage changes across the GBR shown by Hughes et al. (2018). It suggests that such losses can impact the functionality and stability of these communities (Green & Bellwood, 2009; Rasher, Honey & Hay, 2013).

Acknowledgement

We kindly thank the staff of Lizard Island Research Station for their support and friendship, R. Slobodeanu for his assistance with the statistical analyses, and J. McClung and Y. Emery for their contribution with proofreading.

276 **References:**

277 Bellwood DR, Hoey AS, Ackerman JL, Depczynski M. 2006. Coral bleaching, reef fish community
278 phase shifts and the resilience of coral reefs. *Global Change Biology* 12:1587–1594. DOI:
279 10.1111/j.1365-2486.2006.01204.x.
280 Bellwood DR, Hughes TP, Folke C, Nyström M. 2004. Confronting the coral reef crisis. *Nature*
281 429:827–833. DOI: 10.1038/nature02691.
282 Brandl SJ, Emslie MJ, Ceccarelli DM, T. Richards Z. 2016. Habitat degradation increases
283 functional originality in highly diverse coral reef fish assemblages. *Ecosphere* 7:e01557.
284 DOI: 10.1002/ecs2.1557.
285 Browman HI. 2016. Applying organized scepticism to ocean acidification research. *ICES Journal*
286 *of Marine Science: Journal du Conseil* 73:529–536. DOI: 10.1093/icesjms/fsw010.
287 Butterfield BJ, Suding KN. 2013. Single-trait functional indices outperform multi-trait indices in
288 linking environmental gradients and ecosystem services in a complex landscape. *Journal*
289 *of Ecology* 101:9–17. DOI: 10.1111/1365-2745.12013.
290 Cai W, Borlace S, Lengaigne M, Rensch P van, Collins M, Vecchi G, Timmermann A, Santoso A,
291 McPhaden MJ, Wu L, England MH, Wang G, Guilyardi E, Jin F-F. 2014. Increasing
292 frequency of extreme El Nino events due to greenhouse warming. *Nature Climate*
293 *Change* 4:111–116. DOI: 10.1038/nclimate2100.
294 Ceccarelli DM, Emslie MJ, Richards ZT. 2016. Post-Disturbance Stability of Fish Assemblages
295 Measured at Coarse Taxonomic Resolution Masks Change at Finer Scales. *PLOS ONE*
296 11:e0156232. DOI: 10.1371/journal.pone.0156232.

297 Cheal A, Coleman G, Delean S, Miller I, Osborne K, Sweatman H. 2002. Responses of coral and
298 fish assemblages to a severe but short-lived tropical cyclone on the Great Barrier Reef,
299 Australia. *Coral Reefs* 21:131–142. DOI: 10.1007/s00338-002-0227-8.
300 Cheal AJ, MacNeil MA, Cripps E, Emslie MJ, Jonker M, Schaffelke B, Sweatman H. 2010. Coral–
301 macroalgal phase shifts or reef resilience: links with diversity and functional roles of
302 herbivorous fishes on the Great Barrier Reef. *Coral Reefs* 29:1005–1015. DOI:
303 10.1007/s00338-010-0661-y.
304 Cheal AJ, MacNeil MA, Emslie MJ, Sweatman H. 2017. The threat to coral reefs from more
305 intense cyclones under climate change. *Global Change Biology* 23:1511–1524. DOI:
306 10.1111/gcb.13593.
307 Coker DJ, Pratchett MS, Munday PL. 2009. Coral bleaching and habitat degradation increase
308 susceptibility to predation for coral-dwelling fishes. *Behavioral Ecology* 20:1204–1210.
309 DOI: 10.1093/beheco/arp113.
310 De'ath G, Fabricius KE, Sweatman H, Puotinen M. 2012. The 27–year decline of coral cover on
311 the Great Barrier Reef and its causes. *Proceedings of the National Academy of Sciences*
312 109:17995–17999. DOI: 10.1073/pnas.1208909109.
313 DiazPulido, McCook G. 2002. The fate of bleached corals: patterns and dynamics of algal
314 recruitment. *Marine Ecology Progress Series* 232:115–128. DOI: 10.3354/meps232115.
315 Emslie MJ, Cheal AJ, Logan M. 2017. The distribution and abundance of reef-associated
316 predatory fishes on the Great Barrier Reef. *Coral Reefs*:1–18. DOI: 10.1007/s00338-017-
317 1573-x.

318 Feary DA, Almany GR, Jones GP, McCormick MI. 2007. Coral degradation and the structure of
319 tropical reef fish communities. *Marine Ecology Progress Series* 333:243–248. DOI:
320 10.3354/meps333243.
321 Ferrari MCO, Dixson DL, Munday PL, McCORMICK MI, Meekan MG, Sih A, Chivers DP. 2011.
322 Intrageneric variation in antipredator responses of coral reef fishes affected by ocean
323 acidification: implications for climate change projections on marine communities. *Global*
324 *Change Biology* 17:2980–2986. DOI: 10.1111/j.1365-2486.2011.02439.x.
325 Fisher J a. D, Casini M, Frank KT, Möllmann C, Leggett WC, Daskalov G. 2015. The importance of
326 within-system spatial variation in drivers of marine ecosystem regime shifts.
327 *Philosophical Transactions of the Royal Society of London B: Biological Sciences*
328 370:20130271. DOI: 10.1098/rstb.2013.0271.
329 Froese R, Pauly D. 2016. Editors. 2016. FishBase.World Wide Web electronic publication.
330 www.fishbase.org, version (06/2016).
331 Ganasan V, Hughes RM. 1998. Application of an index of biological integrity (IBI) to fish
332 assemblages of the rivers Khan and Kshipra (Madhya Pradesh), India. *Freshwater Biology*
333 40:367–383. DOI: 10.1046/j.1365-2427.1998.00347.x.
334 Goren M, Spanier E. 1985. The communities of benthic fish in foul bay (tiran island, red-sea).
335 *Oceanologica acta* 8:471–478.
336 Graham NAJ, Chabanet P, Evans RD, Jennings S, Letourneur Y, Aaron MacNeil M, McClanahan
337 TR, Öhman MC, Polunin NVC, Wilson SK. 2011. Extinction vulnerability of coral reef
338 fishes: Reef fish extinction vulnerability. *Ecology Letters* 14:341–348. DOI:
339 10.1111/j.1461-0248.2011.01592.x.

340 Graham NAJ, Jennings S, MacNeil MA, Mouillot D, Wilson SK. 2015. Predicting climate-driven
341 regime shifts versus rebound potential in coral reefs. *Nature* 518:94–97. DOI:
342 10.1038/nature14140.
343 Green AL, Bellwood DR. 2009. *Monitoring functional groups of herbivorous reef fishes as*
344 *indicators of coral reef resilience: a practical guide for coral reef managers in the Asia*
345 *Pacific region*.
346 Hill MS. 1998. Spongivory on Caribbean reefs releases corals from competition with sponges.
347 *Oecologia* 117:143–150. DOI: 10.1007/s004420050642.
348 Hoegh-Guldberg O, Ridgway T. 2016. Coral bleaching hits great barrier reef as global
349 temperatures soar. *Green Left Weekly*:10.
350 Holbrook SJ, Schmitt RJ, Stephens JS. 1997. Changes in an Assemblage of Temperate Reef Fishes
351 Associated with a Climate Shift. *Ecological Applications* 7:1299–1310. DOI:
352 10.1890/1051-0761(1997)007[1299:CIAAOT]2.0.CO;2.
353 Hughes TP, Anderson KD, Connolly SR, Heron SF, Kerry JT, Lough JM, Baird AH, Baum JK,
354 Berumen ML, Bridge TC, Claar DC, Eakin CM, Gilmour JP, Graham NAJ, Harrison H, Hobbs
355 J-PA, Hoey AS, Hoogenboom M, Lowe RJ, McCulloch MT, Pandolfi JM, Pratchett M,
356 Schoepf V, Torda G, Wilson SK. 2018. Spatial and temporal patterns of mass bleaching of
357 corals in the Anthropocene. *Science* 359:80–83. DOI: 10.1126/science.aan8048.
358 Hughes TP, Kerry JT, Álvarez-Noriega M, Álvarez-Romero JG, Anderson KD, Baird AH, Babcock
359 RC, Beger M, Bellwood DR, Berkelmans R, Bridge TC, Butler IR, Byrne M, Cantin NE,
360 Comeau S, Connolly SR, Cumming GS, Dalton SJ, Diaz-Pulido G, Eakin CM, Figueira WF,
361 Gilmour JP, Harrison HB, Heron SF, Hoey AS, Hobbs J-PA, Hoogenboom MO, Kennedy

362 EV, Kuo C, Lough JM, Lowe RJ, Liu G, McCulloch MT, Malcolm HA, McWilliam MJ,
363 Pandolfi JM, Pears RJ, Pratchett MS, Schoepf V, Simpson T, Skirving WJ, Sommer B,
364 Torda G, Wachenfeld DR, Willis BL, Wilson SK. 2017. Global warming and recurrent mass
365 bleaching of corals. *Nature* 543:373–377. DOI: 10.1038/nature21707.
366 Jones GP, McCormick MI, Srinivasan M, Eagle JV. 2004. Coral decline threatens fish biodiversity
367 in marine reserves. *Proceedings of the National Academy of Sciences* 101:8251–8253.
368 DOI: 10.1073/pnas.0401277101.
369 Karr JR. 1981. Assessment of Biotic Integrity Using Fish Communities. *Fisheries* 6:21–27. DOI:
370 10.1577/1548-8446(1981)006<0021:AOBIUF>2.0.CO;2.
371 Kerry JT, Bellwood DR. 2012. The effect of coral morphology on shelter selection by coral reef
372 fishes. *Coral Reefs* 31:415–424. DOI: 10.1007/s00338-011-0859-7.
373 Liu H, Zheng Y, Shen J. 2008. Goodness-of-fit measures of R^2 for repeated measures mixed
374 effect models. *Journal of Applied Statistics* 35:1081–1092. DOI:
375 10.1080/02664760802124422.
376 MacNeil MA, Graham NAJ, Cinner JE, Wilson SK, Williams ID, Maina J, Newman S, Friedlander
377 AM, Jupiter S, Polunin NVC, McClanahan TR. 2015. Recovery potential of the world's
378 coral reef fishes. *Nature* 520:341–344. DOI: 10.1038/nature14358.
379 Micheli F, Halpern BS. 2005. Low functional redundancy in coastal marine assemblages. *Ecology*
380 *Letters* 8:391–400. DOI: 10.1111/j.1461-0248.2005.00731.x.
381 Munday PL. 2004. Habitat loss, resource specialization, and extinction on coral reefs. *Global*
382 *Change Biology* 10:1642–1647. DOI: 10.1111/j.1365-2486.2004.00839.x.

383 Munday PL, Jones GP, Pratchett MS, Williams AJ. 2008. Climate change and the future for coral
384 reef fishes. *Fish and Fisheries* 9:261–285. DOI: 10.1111/j.1467-2979.2008.00281.x.
385 Pace ML, Cole JJ, Carpenter SR, Kitchell JF. 1999. Trophic cascades revealed in diverse
386 ecosystems. *Trends in Ecology & Evolution* 14:483–488. DOI: 10.1016/S0169-
387 5347(99)01723-1.
388 Phillips GAC, How MJ, Lange JE, Marshall NJ, Cheney KL. 2017. Disruptive colouration in reef
389 fish: does matching the background reduce predation risk? *Journal of Experimental*
390 *Biology* 220:1962–1974. DOI: 10.1242/jeb.151480.
391 Pizarro O, Friedman A, Bryson M, Williams SB, Madin J. 2017. A simple, fast, and repeatable
392 survey method for underwater visual 3D benthic mapping and monitoring. *Ecology and*
393 *Evolution* 7:1770–1782. DOI: 10.1002/ece3.2701.
394 Pratchett MS, Hoey AS, Wilson SK, Messmer V, Graham NAJ. 2011. Changes in Biodiversity and
395 Functioning of Reef Fish Assemblages following Coral Bleaching and Coral Loss. *Diversity*
396 3:424–452. DOI: 10.3390/d3030424.
397 Pratchett MS, Munday P, Wilson SK, Graham NA, Cinner JE, Bellwood DR, Jones GP, Polunin NV,
398 McClanahan TR. 2008. Effects of climate-induced coral bleaching on coral-reef fishes.
399 *Ecological and economic consequences. Oceanography and Marine Biology: Annual*
400 *Review* 46:251–296.
401 Pratchett MS, Thompson CA, Hoey AS, Cowman PF, Wilson SK. 2018. Effects of Coral Bleaching
402 and Coral Loss on the Structure and Function of Reef Fish Assemblages. In: *Coral*
403 *Bleaching*. Ecological Studies. Springer, Cham, 265–293. DOI: 10.1007/978-3-319-75393-
404 5_11.

405 Prazeres M, Roberts TE, Pandolfi JM. 2017. Shifts in species abundance of large benthic
406 foraminifera Amphistegina: the possible effects of Tropical Cyclone Ita. *Coral Reefs*
407 36:305–309. DOI: 10.1007/s00338-016-1497-x.
408 Puotinen M, Maynard JA, Beeden R, Radford B, Williams GJ. 2016. A robust operational model
409 for predicting where tropical cyclone waves damage coral reefs. *Scientific Reports* 6.
410 DOI: 10.1038/srep26009.
411 Randall JE. 1961. Overgrazing of Algae by Herbivorous Marine Fishes. *Ecology* 42:812–812. DOI:
412 10.2307/1933510.
413 Rasher DB, Hoey AS, Hay ME. 2013. Consumer diversity interacts with prey defenses to drive
414 ecosystem function. *Ecology* 94:1347–1358. DOI: 10.1890/12-0389.1.
415 Renfro B, Chadwick NE. 2017. Benthic community structure on coral reefs exposed to intensive
416 recreational snorkeling. *PLOS ONE* 12:e0184175. DOI: 10.1371/journal.pone.0184175.
417 Russ GR, Leahy SM. 2017. Rapid decline and decadal-scale recovery of corals and <Emphasis
418 Type="Italic">Chaetodon</Emphasis> butterflyfish on Philippine coral reefs. *Marine*
419 *Biology* 164:29. DOI: 10.1007/s00227-016-3056-y.
420 Russ GR, McCook LJ. 1999. Potential effects of a cyclone on benthic algal production and yield
421 to grazers on coral reefs across the central Great Barrier Reef. *Journal of Experimental*
422 *Marine Biology and Ecology* 235:237–254. DOI: 10.1016/S0022-0981(98)00180-4.
423 Stuart-Smith RD, Brown CJ, Ceccarelli DM, Edgar GJ. 2018. Ecosystem restructuring along the
424 Great Barrier Reef following mass coral bleaching. *Nature* 560:92–96. DOI:
425 10.1038/s41586-018-0359-9.

426 Triki Z, Wismer S, Levorato E, Bshary R. 2018. A decrease in the abundance and strategic
427 sophistication of cleaner fish after environmental perturbations. *Global Change Biology*
428 24:481–489. DOI: 10.1111/gcb.13943.
429 Wernberg T, Smale DA, Tuya F, Thomsen MS, Langlois TJ, de Bettignies T, Bennett S, Rousseaux
430 CS. 2013. An extreme climatic event alters marine ecosystem structure in a global
431 biodiversity hotspot. *Nature Climate Change* 3:78–82. DOI: 10.1038/nclimate1627.
432 Wilson SK, Burgess SC, Cheal AJ, Emslie M, Fisher R, Miller I, Polunin NVC, Sweatman HPA.
433 2008a. Habitat utilization by coral reef fish: implications for specialists vs. generalists in
434 a changing environment. *Journal of Animal Ecology* 77:220–228. DOI: 10.1111/j.1365-
435 2656.2007.01341.x.
436 Wilson SK, Fisher R, Pratchett MS, Graham N a. J, Dulvy NK, Turner RA, Cakacaka A, Polunin
437 NVC. 2010. Habitat degradation and fishing effects on the size structure of coral reef fish
438 communities. *Ecological Applications* 20:442–451. DOI: 10.1890/08-2205.1.
439 Wilson SK, Fisher R, Pratchett MS, Graham N a. J, Dulvy NK, Turner RA, Cakacaka A, Polunin
440 NVC, Rushton SP. 2008b. Exploitation and habitat degradation as agents of change
441 within coral reef fish communities. *Global Change Biology* 14:2796–2809. DOI:
442 10.1111/j.1365-2486.2008.01696.x.
443 Wilson SK, Graham N a. J, Pratchett MS, Jones GP, Polunin NVC. 2006. Multiple disturbances
444 and the global degradation of coral reefs: are reef fishes at risk or resilient? *Global*
445 *Change Biology* 12:2220–2234. DOI: 10.1111/j.1365-2486.2006.01252.x.

446 Wismer S, Hoey A, Bellwood DR. 2009. Cross-shelf benthic community structure on the Great
447 Barrier Reef: relationships between macroalgal cover and herbivore biomass. *Marine*
448 *Ecology Progress Series* 376:45–54.
449 Wismer S, Pinto AI, Vail AL, Grutter AS, Bshary R. 2014. Variation in Cleaner Wrasse Cooperation
450 and Cognition: Influence of the Developmental Environment? *Ethology* 120:519–531.
451 DOI: 10.1111/eth.12223.
452

Figure 1(on next page)

Lizard Island group map.

The map is showing the two study sites: Mermaid Cove reef as Site 1 and Northern horseshoe reef as Site2. Modified from *Triki et al. 2018, Global Change Biology* (© 2017 John Wiley & Sons Ltd).

PeerJ
Manuscript to be reviewed

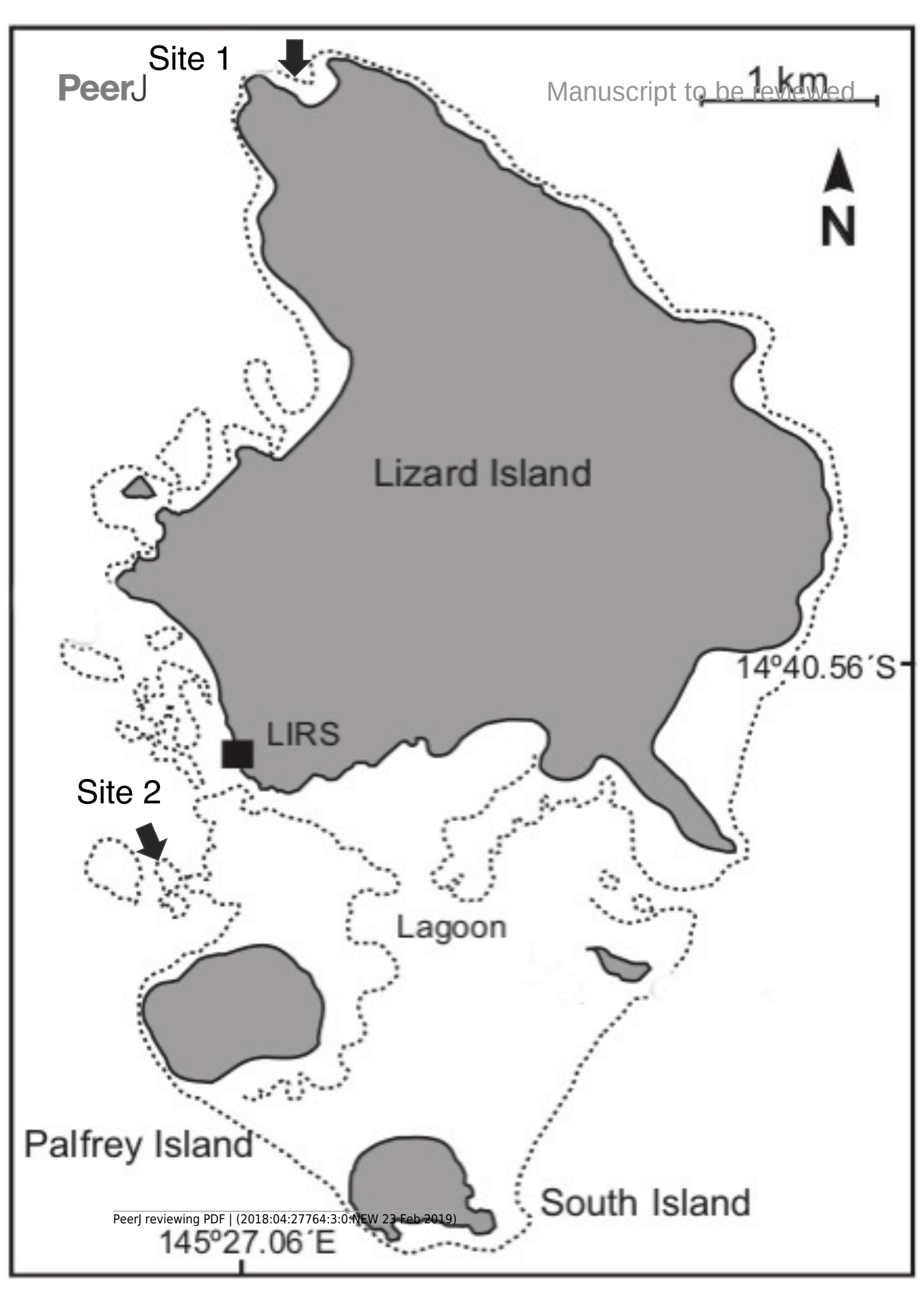

Figure 2(on next page)

Total fish abundance.

Boxplots are displaying median and interquartile of total fish abundance before (n=20) and after (n=40) the environmental disturbances (i.e., cyclones and coral bleaching). Negative binomial Generalised Linear Model: *** $p < 0.001$.

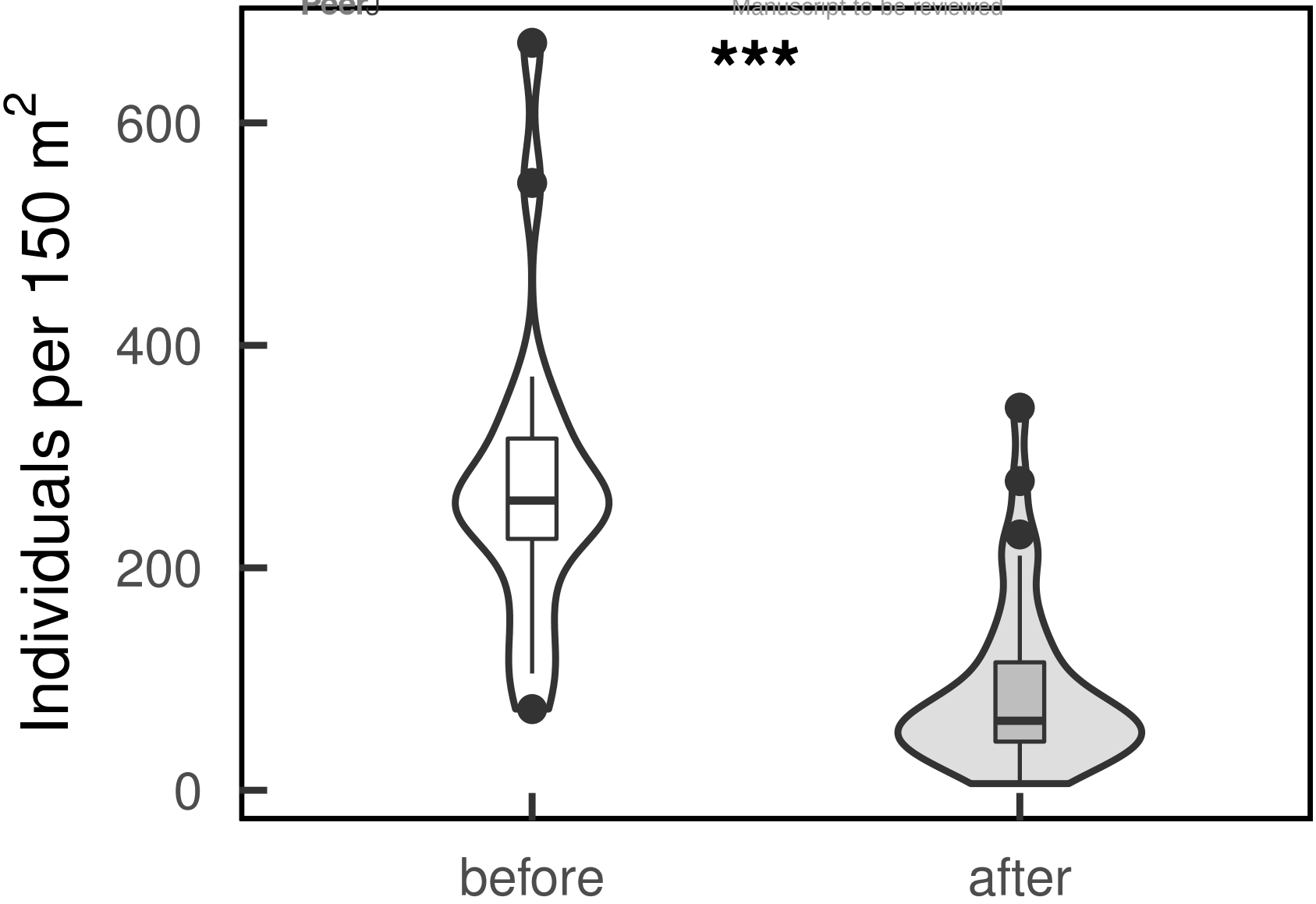
***
Individuals per 150 m2
600
400
200
0
before
after

Figure 3(on next page)

Fish abundance per trophic-functional groups

Boxplots are displaying median and interquartile of fish abundance within trophic-functional groups showing eventual changes from before (n = 20) to after (n = 40) the environmental disturbances (i.e., cyclones and coral bleaching). Note that due to the high variation in fish counts per functional group, the y-axes do not have the same scale. Post hoc analyses of a Zero-inflated negative binomial model showing differences between before and after the perturbations within each functional group: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

PeerJ Manuscript to be reviewed

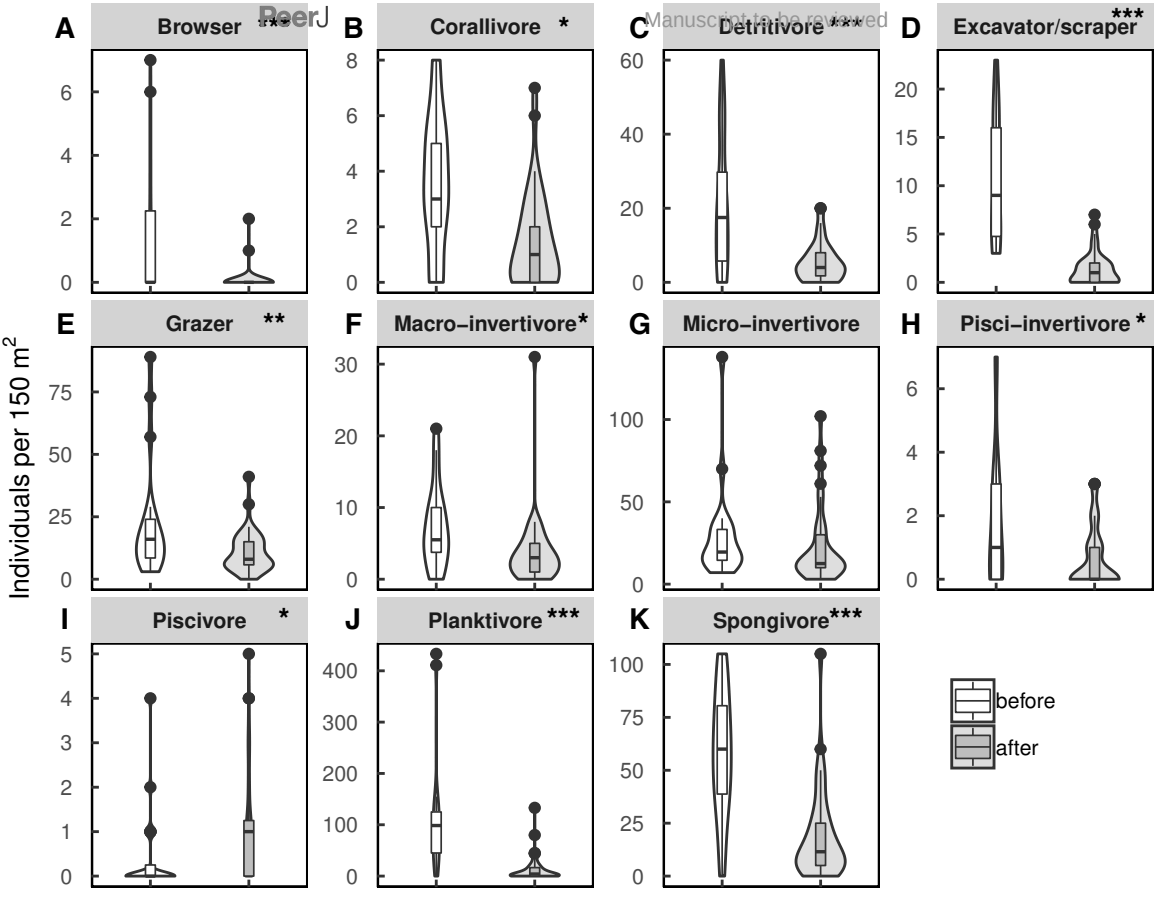

Table 1(on next page)

Dietary functional trait used in sorting fish species into trophic-functional groups.

Trophic-functional group	Diet	Example
Browsers	Macro-algae	*Naso unicornis*
Corallivores	Corals	*Chaetodon aureofasciatus*
Detritivores	Dead organic material "detritus"	*Ctenochaetus striatus*
Excavators/scrapers	Remove reef substrate while looking for living material	*Chlorurus spilurus*
Grazers	Fast-growing macro-algae "turf algae"	*Siganus doliatus*
Macro-invertivores	Large invertebrates	*Balistapus undulatus*
Micro-invertivores	Small invertebrates	*Coris batuensis*
Pisci-invertivores	Fish and invertebrates	*Lethrinus olivaceus*
Piscivores	Fish	*Epinephelus merra*
Planktivores	Plankton	*Abudefduf sexfasciatus*
Spongivores	Sea sponges	*Pomacanthus sexstriatus*

1