Seasonal shifts in the competitive ability of macroalgae influence the outcomes of coral–algal competition

Kristen T. Brown1,2†, Dorothea Bender-Champ1,2, Ove Hoegh-Guldberg1,2,3 and Sophie Dove1,2

1School of Biological Sciences, 2Australian Research Council Centre of Excellence for Coral Reef Studies, and 3Global Change Institute, The University of Queensland, St Lucia, Queensland 4072, Australia

†Present address: Department of Biology, University of Pennsylvania, Philadelphia, PA 19104, USA.

Understanding the effects of natural processes on coral–algal competition is an important step in identifying the role of macroalgae in perturbed coral reef ecosystems. However, studies investigating coral–algal interactions are often conducted in response to a disturbance, and rarely incorporate seasonal variability. Here, naturally occurring coral–algal interactions were assessed in situ four times a year over 2 years across eight sites spanning diverse benthic communities. In over 6500 recorded coral–algal interactions, cyanobacteria and turf algae were found to be the most damaging regardless of season, resulting in visible damage to coral in greater than 95% of interactions. Macroalgae that primarily compete using chemical mechanisms were found to be more damaging than those that compete using physical mechanisms (e.g. abrasion), with both groups demonstrating decreased competitive ability in summer. While crustose coralline algae were the least damaging to competing coral, during summer, it became three times more competitive. Our results demonstrate that the competitive ability of macroalgae and the outcomes of coral–algal competition can fluctuate in seasonal cycles that may be related to biomass, production of chemical defences and/or physical toughness. The results of this study have important implications for understanding the trajectory and resilience of coral reef ecosystems into the future.

1. Background

Macroalgae from coral reef ecosystems vary in space and time owing to a combination of biotic (e.g. herbivory) and abiotic
(e.g. temperature, wave action) processes [1–3]. Anthropogenic activities, such as land-clearing and fertilization for agriculture, the loss of herbivores because of overexploitation or thermal stress, can disrupt the natural balance leading to reductions in reef-building coral and increases in macroalgal cover [4,5]. An increase in the abundance of macroalgae can lead to increases in coral–algal competition [6,7], which may play an important role in the degradation of coral reefs [8]. Given rapidly shifting coral reef ecosystem dynamics [9], macroalgae and their interactions with corals are more relevant than ever.

On the Great Barrier Reef, macroalgae display latitudinal, regional, within reef and seasonal patterns. Generally, macroalgal abundance increases latitudinally from north to south, longitudinally from offshore to inshore, within a reef system from the reef slope to reef flat and in the austral winter and spring [2–4,10,11]. In reef systems that are relatively unaffected by anthropogenic disturbances (e.g. eutrophication, overfishing), seasonal shifts in water motion, temperature, light and nutrients are the principal drivers of algal abundance [1,2,12,13]. While seasonality has been found to influence the frequency of coral–algal contact [2], it is not known if seasonal shifts in algal abundance relate to the competitive ability of macroalgae.

Competition between coral and macroalgae may take either of two forms: direct aggressive behaviour or indirect defensive behaviour [14]. Several prominent competitive mechanisms, reviewed by McCook et al. [14] and Chadwick & Morrow [15], include pre-emption, overgrowth, smothering, abrasion, shading, allelopathy and microbial enhancement (figure 1). Studies mostly demonstrate negative impacts of direct contact by macroalgae, resulting in reductions to coral growth, calcification, fecundity and survivorship [16–19]. Macroalgal growth, pigmentation and chemical defences can also be compromised by contact with corals [20,21]. A number of studies have determined that the outcomes of coral–algal interactions are dependent on a range of factors, including the kind of coral and algae involved, the size and growth form of the coral colony and the proportion of macroalgae in contact with the coral [2,22–26]. Investigations into whether seasonal changes can alter the competitive ability of macroalgae.

Our study investigates whether the outcomes of coral–algal competition are influenced by seasonal changes in environmental conditions on the reef system Heron Reef (23.442° S, 151.914° E), on the southern Great Barrier Reef. Heron Island is a small (800 × 300 m) offshore coral cay with a large platform reef environment that is also home to a tourist resort and scientific research station (University of Queensland). Owing to being 50 km offshore and being protected by the Great Barrier Reef Marine Park Authority since 1975, impacts from eutrophication and sedimentation owing to agriculture are non-existent, as is the overharvesting of herbivores [27]. Heron Reef was among the least affected reefs from the cumulative footprint of 2016–2017 coral bleaching events on the Great Barrier Reef [28]. Therefore, macroalgal dynamics were principally driven by pronounced seasonal oscillations in environmental conditions such as temperature and light [2].

We assessed naturally occurring coral–algal interactions in situ four times a year over 2 years (2015–2016) across eight sites spanning the geomorphological habitats of Heron Reef. By examining a range of habitats across seasons, we are able to catalogue a comprehensive set of interactions that include diverse
coral and macroalgal communities [2,29] (table 1). With this information, we investigated which macroalgal groups or types are the most damaging to competing coral, and within these groups, if the competitive ability of macroalgae varies with season. The results of this study provide a better understanding of the mechanisms by which coral and macroalgae compete and the seasons in which macroalgae are the most competitive.

2. Methods

A total of eight surveys, representing each austral season twice, were conducted during the 2 year period between January 2015 and November 2016. Surveys were performed across the same eight sites during each visit to incorporate the breadth of coral and macroalgal communities that naturally occur across the geomorphological habitats of Heron Reef [2,29] (electronic supplementary material, figure S1). Coral–algal interactions were recorded using a modified line intercept approach first described by Barott et al. [38] and subsequently modified by Brown et al. [2]. At each site, 3 × 15 m transects were established coursing north, east and west from a permanent reference point. Within a 1 m belt, every coral colony was examined and any colony that was physically touching algae identified and recorded (figure 1). A single coral colony could be involved in multiple competitive interactions with different macroalgal taxa or groups [24]. The types of interacting corals and macroalgae were recorded to genus level, with the exception of cyanobacteria, turf algae, articulate and crustose coralline algae (CCA), which generally cannot be identified to genus level in situ [39].

The outcome of each interaction was recorded, with the three outcomes being: 1, coral overgrowing algae (coral ‘winning’); 2, algae overgrowing coral resulting in discoloration to the coral (coral ‘losing’); and 3, seemingly neutral (figure 1; see also fig. 2 in [22] and fig. 3 in [25]) [22,24,25]. Pigmentation loss at the interaction zone was clearly distinguishable from any other irregularities found on coral colonies (figure 1). Where macroalgae were covering coral, it was removed to determine the outcome in the area underneath, as not all contact by macroalgae results in discoloration to the competing coral [19,25,36]. Individual colonies were not tracked through time; therefore, the long-term fate (i.e. beyond one season) was not investigated in this study. Seasonal means for benthic cover, temperature and irradiance for the study period are reported in Brown et al. [2].

In order to determine which type of macroalgae is most damaging to coral, macroalgae were separated into categories by group/taxa or primary competitive mechanism. This included the commonly regarded functional groups: articulate coralline algae (ACA), CCA, Halimeda, turf algae and cyanobacteria [39] (table 1 and figure 2). While cyanobacteria are not taxonomically considered ‘algae’, this group of photosynthetic bacteria (colloquially referred to as blue-green algae or microalgae) are prominent competitors to corals and often included in studies of coral–algal

| group or taxa               | growth form or genera                          | references       |
|-----------------------------|-------------------------------------------------|------------------|
| articulate coralline algae (ACA) | e.g. Amphiroa                                   |                  |
| chemical                    | Amanzia, Asparagopsis, Chlorodesmis, Dictyota, Laurencia, Lobophora, Padina, Plocamium | [30–32]          |
| crustose coralline algae (CCA) | e.g. reef crest (Porolithon, Lithophyllum), reef slope (Lithothamnion, Mesophyllum) | [33]             |
| cyanobacteria               | e.g. Lyngbya                                    |                  |
| Halimeda                    | e.g. reef flat (H. discoidea, H. macroloba), reef slope (H. heteromorpha, H. macrophysa) | [34,35]          |
| physical                    | Arrainvillea, Caulerpa, Chnoospora, Codium, Colpomenia, Dictyosphaeria, Hydroclathrus, Hypnea, Sargassum, Turbinaria, Valonia | [16,36,37]      |
| turf algae                  | e.g. Feldmannia                                 | [26]             |

Table 1. Groups of macroalgae. (Within each group or taxa, genera indicate recorded taxa, where ‘e.g.’ refers to commonly observed taxa from Heron Reef. Chemical macroalgae compete through the transfer of allelochemicals via direct contact, whereas physical macroalgae compete primarily using physical mechanisms (e.g. abrasion).)
Calcifying macroalgae of the genus *Halimeda* were not separated by species but included a range of small- and large-segmented species common across Heron Reef, including: *Halimeda discoidea*, *Halimeda heteromorpha*, *Halimeda macroloba* and *Halimeda opuntia*, among others [34,35]. All other macroalgae were further differentiated into two groups: (i) those that compete primarily through chemical mechanisms, or (ii) those that compete primarily through physical mechanisms based on the literature (table 1). 'Chemical' macroalgae compete through the transfer of allelochemicals via direct contact, and are often considered the most damaging to competing coral [19,23,30]. On the other hand, macroalgae that compete primarily using physical mechanisms (e.g. abrasion) are often found to result in no visible effects (e.g. coral bleaching) to competing coral [19,23,36].

### 2.1. Statistical analyses

The outcome of coral–algal competition was explored using generalized linear mixed effect models with a binomial distribution (`glmmer` within the *lmer4* package) [40]. Outcome was evaluated as the binary state, with neutral/coral ‘winning’ (1) assessed against coral ‘losing’ (0). We fit all possible model combinations using the predictor variables: (i) season (spring, summer, autumn, winter), (ii) algal group (ACA, CCA, chemical, cyanobacteria, *Halimeda*, physical, turf algae), and (iii) interactive effect of season and algal group (electronic supplementary material, table S1). The interaction between season and algal group was further explored by investigating the proportion of coral colonies losing (number of coral colonies losing/total number of interactions) using a linear mixed effects model. Site was included as a random effect in all models. Models were compared and the best model was selected using Akaike information criterion for small sample sizes (AICc) and AICc weight ($\omega$) (electronic supplementary material, table S1).

The significance of fixed effects and their interactions was determined using an analysis of variance with a type III error structure (`Anova` in *car* package [41]). Significant interactive effects were followed by pairwise comparison of estimate marginal means using the *emmeans* package with Tukey HSD adjusted $p$-values [42]. Data were tested for homogeneity of variance and normality of distribution through graphical analyses of residual plots for all models. All statistical analyses were done using R v. 4.0.0 software [43], and graphical representations were produced using the package *ggplot2* [44].

### 3. Results and discussion

A total of 6589 coral–algal interactions were recorded over the 2 year study at Heron Reef, representing 30 coral and 24 macroalgae taxa or groups (table 1). The majority of interactions (4031 or 61%) were recorded...
as coral losing, with 2279 (35%) scored neutral and only 279 (4%) of interactions identified as coral winning.

Cyanobacteria and turf algae were the most damaging to competing coral regardless of season (figure 2; electronic supplementary material, tables S2–S4). Interactions with cyanobacteria resulted in visible damage to 100% of coral colonies involved in interactions, whereas interactions with turf algae resulted in visible damage to 95.4–99.6% of colonies (electronic supplementary material, table S4). While some cyanobacteria are opportunistic and among the first to colonize recently dead coral, other cyanobacteria can actively overgrow and outcompete coral [38]—the latter of which is most consistent with our observations (figure 2). Turf algae and cyanobacteria are effectively able to damage coral through hypoxia, altering microbial communities or trapping sediments [45–48], making them among the most damaging benthic competitors [6,24,25]. Many cyanobacteria also produce toxic secondary metabolites that are used to deter herbivory and fouling, which may contribute to their competitive success [47,49,50].

Macroalgae that compete using chemical mechanisms were generally more damaging than macroalgae that compete primarily using physical mechanisms; however, these effects varied by season \((p = 0.006, \text{figure 2; electronic supplementary material, tables S3 and S4})\). Allelopathic macroalgae were significantly more damaging in winter and spring, with visible damage observed in 94.5% and 90.2% of interactions compared to only 70.8% in summer (figure 2; electronic supplementary material, table S4). Macroalgae that compete primarily through physical mechanisms displayed a non-significant shift in competitive ability, with the percentage interactions resulting in visible damage decreasing to just over half (56.2%) in summer from three-quarters (72.4–77.3%) in all other seasons (figure 2; electronic supplementary material, table S4). The increase in competitive ability in winter and spring directly coincides with the seasons in which macroalgal abundance is highest [2,11]. The increased cover not only multiplies the frequency of coral–algal contact [2], but increases macroalgal biomass per unit area, or the thickness of the macroalgal cover [11,51]. In the seasons when macroalgae are most abundant, macroalgae can cover large areas and completely surround or smother coral (figure 1), which may contribute to their competitive success. In summer, the interaction of high temperature and high light has been shown to reduce the abundance of macroalgae at Heron Reef [2] and elsewhere across the Great Barrier Reef, increasing temperatures are negatively correlated to macroalgal abundance [52]. In addition to the warmer conditions that coincide with summer leading to a decline in macroalgal cover, these conditions may also reduce (i) the production of chemical defences [53] and/or (ii) physical toughness [54], ultimately decreasing the competitive ability of both chemically rich and physically tough macroalgae.

Previous studies that have not considered seasonal shifts in competitive ability have also found chemically rich macroalgae to be more damaging than macroalgae that are physically tough [17,23,30]. The effects of physically competitive macroalgae, however, are dependent on macroalgal density, duration of contact and thalli structure [19,51,55]. The group of macroalgae defined as ‘physical’ in this study included a range of genera (greater than 10; table 1) representing diverse thalli structures from mat-forming (e.g. Colpomenia) to clumped and rubbery (e.g. Hypnea) to erect and abrasive (e.g. Turbinaria). A previous study that compared mat-forming and canopy-forming macroalgae on coral found that mat-forming algae (e.g. Hydroclathrus) significantly reduce light (by 96%) and dissolved oxygen (by 26%), with thicker algal mats resulting in the greatest mortality [51]. Although canopy-forming macroalgae (e.g. Sargassum) also significantly decreased light availability, these algae allowed for greater water exchange, resulting in minimal effects to understory corals [51]. Macroalgae that grow in flat dense mats (e.g. Colpomenia, Hydroclathrus) or clumps of rubbery branches (e.g. Hypnea, Chnoospora) are often seasonal, lasting only a few weeks in spring [2,10,11]. However, these ephemeral macroalgae may result in the greatest physical damage to competing corals owing to their ability to cover large areas and completely surround or smother coral [11,51] (figure 1). While perennial species often receive the most attention, future studies should incorporate ephemeral types of macroalgae as they may play an elusive, yet important role in coral reef ecosystem degradation.

Coral colonies were the most successful against ACA, Halimeda and CCA. In summer, a greater proportion of corals were losing against CCA when compared with all other seasons \((p = 0.006, \text{figure 2; electronic supplementary material, tables S3 and S4})\). At Heron Reef, the abundant CCA species Porolithon onkodes was found to display maximum vertical growth and calcification in spring, with Lewis et al. [56] suggesting that P. onkodes may direct resources towards competition as opposed to growth in summer. The reasoning of Lewis et al. [56] is supported by the results presented in this study, where contact with CCA resulted in visible damage to competing coral in approximately 30% of interactions in summer, compared to only 0–5% in all other seasons (figure 2; electronic supplementary material, table S4). ACA and Halimeda displayed no seasonal shifts in competitive ability (figure 2; electronic supplementary material, tables S3 and S4), with a previous study also
finding no temporal changes in the competitive ability of *H. heteromorpha* [36]. ACA was more damaging than *Halimeda*, with 33.5–43.9% of coral colonies losing interactions with ACA when compared with 3.2–14.5% for *Halimeda* (figure 1; electronic supplementary material, tables S3 and S4). While both ACA and *Halimeda* are articulate and calcareous, other types of macroalgae were often observed growing on ACA, potentially creating a harmful multi-species assemblage. *Halimeda* has been found to be less damaging than other macroalgal groups in a number of previous studies from the Indo-Pacific [25,46,57]. In the Caribbean, however, *Porites* and *Agaricia* were found to bleach in 90–95% of interactions with *H. opuntia* [21]. Although *Halimeda* is characterized as chemically rich [19,21,58], competition with coral has been shown to compromise the chemical defences of *Halimeda* [21]. Furthermore, older, strongly calcified portions are generally less chemically active than new, less calcified segments [58]. Chemical defences decrease quickly, only 48 h after production; therefore, exposure to the most harmful allelochemicals may be limited [58]. Although no visible damage was observed, persistent (e.g. greater than two months) contact with *Halimeda* has been shown to lead to reductions in calcification rates of competing coral [36]. Similarly, Tanner [16] found that by removing competing algal assemblages including *Halimeda*, coral did better, resulting in increased coral cover and a twofold increase in fecundity. The results of Tanner [16] and Brown et al. [36] highlight the complexity of these interactions, and reinforces that the methodology used in this study is limited in its resolution. The effects of coral–algal contact go beyond visible effects and should be the focus of future studies.

4. Conclusion

Seasonality has long been considered an important driver of macroalgal biomass and composition [11,12]. Most coral reef research, however, has not incorporated seasonal variability adequately into ecological assessments and experiments [59]. By investigating a reef system comparatively unexposed to anthropogenic impacts, we demonstrate here that macroalgae has the ability to alter its competitive ability in seasonal cycles that can be related to abundance. It remains to be determined whether seasonal shifts in biomass, the production of chemical defences and/or physical toughness are responsible for the patterns we observed. If we are to comprehensively understand coral–algal competition in natural yet changing settings, future studies could explore seasonal variability in anthropogenically disturbed reef environments, with a focus on the long-term fate of these types of interactions. Nevertheless, this study contributes to our understanding of the complicated dynamics influencing the outcomes of coral–algal interactions, which have important implications for understanding the trajectory and resilience of coral reef ecosystems into the future.

Ethics. Research was conducted under Great Barrier Reef Marine Park Authority Research permits G14/37212.1 and UQ008/2014c.

Data accessibility. The datasets and scripts generated/analysed for this study can be found as an electronic notebook on https://github.com/imkristenbrown/RSOS_2020.

Authors’ contributions. K.T.B. conceived the ideas and designed the methodology, K.T.B. and D.B.-C. carried out the study and collected field data, K.T.B. analysed the data and wrote the first draft of the manuscript, and all authors contributed to the interpretation and final version of the paper. All authors agreed to be listed and gave final approval for publication.

Competing interests. We declare we have no competing interests.

Funding. This work was supported by the Australian Research Council (ARC) Centre of Excellence for Coral Reef Studies CE140100020 (O.H.-G. and S.D.) and an ARC Laureate Fellowship FL120100066 (O.H.-G.). It was also supported by funding from XL Catlin (O.H.-G.), the Holsworth Wildlife Research Endowment-Equity Trustees Charitable Foundation and the Ecological Society of Australia (K.T.B.), the PADI Foundation (K.T.B.) and a XL Catlin Seaview Survey scholarship (K.T.B.).

Acknowledgements. We would like to thank Michelle Achlatis, Aaron Chai, Tania Kenyon, Andreas Kubicek, Matheus A. Mello-Athayde and Rene M. van der Zande for support in the field as well as the staff of Heron Island Research Station.

References

1. Littler MM, Littler DS, Brooks BL. 2006 Harmful algae on tropical coral reefs: bottom-up eutrophication and top-down herbivory. *Harm. Algae* 5, 565–585. (doi:10.1016/j.hal.2005.11.003)
2. Brown KT, Bender-Champ D, Kubicek A, van der Zande R, Achlatis M, Hoegh-Guldberg O, Dove SG. 2018 The dynamics of coral-algal interactions in space and time on the southern Great Barrier Reef. *Front. Mar. Sci.* 5, 181. (doi:10.3389/fmars.2018.00181)
3. Diaz-Pulido G, McCook LJ, Larkum AW, Lotze HK, Raven JA, Schaffelke B, Smith JE, Steneck RS. 2007 Vulnerability of macroalgae of the
Great Barrier Reef to climate change. The Great Barrier Reef Marine Park Authority, Townsville. See http://146.116.27.35/pslp/handle/11017/540.

4. De’ath G, Fabricus K. 2010 Water quality as a regional driver of coral biodiversity and macroalgae on the Great Barrier Reef. Ecol. Appl. 20, 840–850. (doi:10.1890/08-2231.1)

5. Diaz-Pulido G et al. 2009 Doom and boom on a resilient reef: climate change, algal overgrowth and coral recovery. PLoS ONE 4, e5239. (doi:10.1371/journal.pone.0005239)

6. Haas A, El-Zabadah M, Wild C. 2010 Seasonal monitoring of coral–algae interactions in fringing reefs of the Gulf of Aqaba, Northern Red Sea. Coral Reefs 29, 93–103. (doi:10.1007/s00338-009-0556-y)

7. Connell JH, Hughes TP, Wallace CC, Tanner JE, Harns KE, Kerr AM. 2004 A long-term study of competition and diversity of corals. Ecol. Monogr. 74, 179–210. (doi:10.1890/0012-9615(2004)074[0179:ALTSOC]2.0.CO;2)

8. McCook L. 1999 Macroalgae, nutrients and phase shifts on coral reefs: scientific issues and management consequences for the Great Barrier Reef. Coral Reefs 18, 357–367. (doi:10.1007/s003380050213)

9. Hughes TP et al. 2018 Global warming transforms coral reef assemblages. Nature 556, 492–496. (doi:10.1038/s41586-018-0401-2)

10. Ceccarelli DM et al. 2018 Rehabilitation of coral reefs through removal of macroalgae: state of knowledge and considerations for management and implementation. Rest. Ecol. 26, 827–838. (doi:10.1111/rec.12852)

11. Schaffelle B, Klumpp D. 1997 Biomass and productivity of tropical macroalgae on three nearshore fringing reefs in the central Great Barrier Reef, Australia. Bot. Mar. 40, 373–384. (doi:10.1515/botm.1997.40.1-6.373)

12. Atebewerban M, Bruggemann J, Breeman A. 2006 Effects of extreme seasonality on community structure and functional group dynamics of coral reef algae in the southern Red Sea (Eritrea). Coral Reefs 25, 391–406. (doi:10.1007/s00338-006-0109-6)

13. Ferrari R, Gonzalez-Rivero M, Ortiz JC, Mummy PJ. 2012 Interaction of herbivory and seasonality on the dynamics of Caribbean macroalgae. Coral Reefs 31, 683–692. (doi:10.1007/s00338-012-0889-9)

14. McCook L, Jompa J, Diaz-Pulido G. 2001 Competition between corals and algae on coral reefs: a review of evidence and mechanisms. Coral Reefs 19, 400–417. (doi:10.1007/s003380010029)

15. Chadwick NE, Morrow KM. 2011 Competition among sessile organisms on coral reefs. In Coral reefs: an ecosystem in transition (eds Z Dubinsky, N Stambler), pp. 347–372. Dordrecht, The Netherlands: Springer.

16. Tanner JE. 1995 Competition between scleractinian corals and macroalgae: an experimental investigation of coral growth, survival and reproduction. J. Exp. Mar. Biol. Ecol. 190, 151–168. (doi:10.1016/0022-0981(95)00027-0)

17. Jompa J, McCook L. 2003 Coral-algal competition: macroalgae with different properties have different effects on corals. Mar. Ecol. Prog. Ser. 258, 87–95. (doi:10.3354/meps258087)

18. Ferrari R, Gonzalez-Rivero M, Mummy PJ. 2012 Size matters in competition between corals and macroalgae. Mar. Ecol. Prog. Ser. 467, 77–88. (doi:10.3354/meps109953)

19. Rasher DB, Hay ME. 2010 Chemically rich seaweeds poison corals when not controlled by herbivores. Proc. Natl Acad. Sci. USA 107, 9683–9688. (doi:10.1073/pnas.0912095107)

20. Nagues MM, Delvoye L, Bak RP. 2004 Coral defence against macroalgae: differential effects of mesenterial filaments on the green alga Halimeda opuntia. Mar. Ecol. Prog. Ser. 278, 103–114. (doi:10.3354/meps278103)

21. Longo GO, Hay ME. 2015 Does seaweed–coral competition make seaweeds more palatable? Coral Reefs 34, 67–96. (doi:10.1007/s00338-014-1230-6)

22. Barott KL, Williams GJ, Vermeij MJ, Harris J, Smith JE, Rohwer FL, Sandin SA. 2012 Natural history of coral–algae competition across a gradient of human activity in the Line Islands. Mar. Ecol. Prog. Ser. 466, 1–12. (doi:10.3354/meps09784)

23. Bonaldo RM, Hay ME. 2014 Seaweed–coral interactions: variation in seaweed algalopaty, coral susceptibility, and potential effects on coral resilience. PLoS ONE 9, e85786. (doi:10.1371/journal.pone.0085786)

24. Swieten T, Vermeij MJ. 2016 Competitive interactions between corals and turf algae depend on coral colony form. PLoS ONE 4, e10484 (doi:10.7717/peerj.10484)

25. Brown KT, Bender-Champ D, Bryant DE, Dove SG, Hoegh-Guldberg O. 2017 Human activities influence benthic community structure and functional group dynamics of mesenterial filaments on the green alga Sinularia cruciata (Alcyonacea). Mar. Ecol. Prog. Ser. 556, 9688. (doi:10.1007/s00279-016-01775-y)

26. Fong J, Lim ZW, Baum AG, Villacvetvett S, Lian LM, Yip ZT, Todd PA. 2019 Allelopathic effects of macroalgae on Pocillopora acuta coral larvae. Mar. Environ. Res. 151, 104745. (doi:10.1016/j.marenvres.2019.06.007)

27. Barott K, Smith J, Dindoale E, Haryat M, Sandin S, Rohwer F. 2009 Hyperspectral and physiological analyses of coral-algal interactions. PLoS ONE 4, e8403. (doi:10.1371/journal.pone.0080043)

28. Senecke RS, Dethier MN. 1994 A functional group approach to the structure of algal–dominated communities. Oikos 69, 476–498. (doi:10.2307/545860)

29. Bates D et al. 2018 Package ‘lme4’, version 1.1-7. See https://github.com/lme4/lme4/.

30. Fox J et al. 2012 Car: companion to applied regression, Vienna, Austria: R Foundation for Statistical Computing. See https://cran.r-project.org/web/packages/car.

31. Lenth R. 2018 emmeans: Estimated marginal means, aka least-squares means. R package version 1.4.7. See https://cran.r-project.org/web/packages/emmeans.

32. R Core Team. 2014 R: A language and environment for statistical computing, Vienna, Austria: R Foundation for Statistical Computing. See https://cran.r-project.org/web/packages/bootstrap.

33. Wickham H. 2016 ggplot2: create elegant data visualisations using the grammar of graphics. R package version 3.2. See http://cran.r-project.org/web/packages/ggplot2.

34. Barott KL, Rodriguez-Mueller B, Youle M, Marhaver KL, Smith JE, Rohwer FL. 2012 Microbial to reef scale interactions between the reef-building coral Montastraea annularis and benthic algae. Proc. R. Soc. B 279, 1655–1664. (doi:10.1098/rspb.2011.2155)

35. Barott KL, Rodriguez-Brito B, Janusikiewicz J, Marhaver KL, Smith JE, Keeling P, Rohwer FL. 2011 Microbial diversity associated with four functional groups of benthic reef algae and the reef-building coral Montastraea annularis.
47. Morrow K, Paul VJ, Liles M, Chadwick N. 2011 Allelochemicals produced by Caribbean macroalgae and cyanobacteria have species-specific effects on reef coral microorganisms. *Coral Reefs* **30**, 309–320. (doi:10.1007/s00338-011-0747-1)

48. Jompa J, McCook LJ. 2003 Contrasting effects of turf algae on corals: massive *Porites* spp. are unaffected by mixed-species turfs, but killed by the red alga *Anotrichium tenue*. *Mar. Ecol. Prog. Ser.* **258**, 79–86. (doi:10.3354/meps258079)

49. Titlyanov E, Yakovleva I, Titlyanova T. 2007 Interaction between benthic algae (*Lyngbya bouillonii*, *Dictyota dichotoma*) and scleractinian coral *Porites lutea* in direct contact. *J. Exp. Mar. Biol. Ecol.* **342**, 282–291. (doi:10.1016/j.jembe.2006.11.007)

50. Paul V, Cruz-Rivera E, Thacker R. 2001 Chemical mediation of macroalgal-herbivore interactions: ecological and evolutionary perspectives. In *Marine chemical ecology* (eds JB McClintok, BJ Baker), pp. 227–265. Boca Raton, FL: CRC Press.

51. Haut C, Fabricius KE, Schaffelke B, Humphrey C. 2010 Chemical and physical environmental conditions underneath mat-and canopy-forming macroalgae, and their effects on understory corals. *PLoS ONE* **5**, e12685. (doi:10.1371/journal.pone.0012685)

52. Smith JN, Mongin M, Thompson A, Jonker MJ, De’ath G, Fabricius KE. 2020 Shifts in coraline algae, macroalgae, and coral juveniles in the Great Barrier Reef associated with present-day ocean acidification. *Global Change Biol.* **26**, 2149–2160. (doi:10.1111/gcb.14985)

53. Sudatti DB, Fujiit MT, Rodrigues SV, Torra A, Pereira RC. 2011 Effects of abiotic factors on growth and chemical defenses in cultivated clones of *Laurencia dendroidea* J. Agardh (Ceramiales, Rhodophyta). *Mar. Biol.* **158**, 1439–1446. (doi:10.1007/s00227-011-1660-4)

54. Graba-Landry AC, Loffler I, McClure EC, Pratchett MS, Hoey AS. 2020 Impaired growth and survival of tropical macroalgae (*Sargassum* spp.) at elevated temperatures. *Coral Reefs* **39**, 475–486. (doi:10.1007/s00338-020-01909-7)

55. River GF, Edmunds PJ. 2001 Mechanisms of interaction between macroalgae and scleractinians on a coral reef in Jamaica. *J. Exp. Mar. Biol. Ecol.* **261**, 159–172. (doi:10.1016/S0022-0981(01)00266-0)

56. Lewis B, Kennedy EV, Diaz-Pulido G. 2017 Seasonal growth and calcification of a reef-building crustose coralline alga on the Great Barrier Reef. *Mar. Ecol. Prog. Ser.* **568**, 73–86. (doi:10.3354/meps12074)

57. Atapattu SS. 2009 The effect of two common reef organisms on the growth of the common reef coral *Acropora formosa*. *Mar. Biodivers. Rec.* **2**, e61.

58. Hay ME, Fenical W. 1988 Marine plant-herbivore interactions: the ecology of chemical defense. *Annu. Rev. Ecol. Syst.* **19**, 111–145. (doi:10.1146/annurev.es.19.110188.001043)

59. Bruno JF, Precht WF, Vismann P, Alonson RB. 2014 Coral reef baselines: how much macroalgae is natural? *Mar. Pollut. Bull.* **80**, 24–29. (doi:10.1016/j.marpolbul.2014.01.010)