Coral restoration is only practical when local human pressure levels are low

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Abstract

Coral reefs are threatened by interacting local (fishing, coastal development) and global (climate change) stressors that degrade coral cover. Adding coral to the reef (coral restoration) is gaining prominence as a management strategy, however it is unclear whether restoration alone can ensure self-sustaining high coral cover under interacting stressors. We assess how much restoration is needed for a self-sustaining healthy coral reef using a mathematical model and real-world restoration case studies. We find that a reef with low macroalgal cover and high coral recruitment requires low restoration to ensure self-sustaining high coral cover but as nutrient enrichment and fishing increase, more restoration is required. Thus, if the reef is facing high local human stressors, restoration is unlikely to ensure self-sustaining high coral cover, suggesting that under such conditions conservation resources should first be allocated towards reducing the impact of stressors, prior to any restoration.

Keywords: Coral Reef, Restoration, Mathematical Modelling, Nutrient Enrichment, Fishing, Management Planning

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1 Introduction

Coral reefs face numerous imminent threats to their survival, at the global level from bleaching events, ocean acidification, and damage from severe storms (Cheal et al., 2017; Van Hooidonk et al., 2014), and at the local level from over-fishing (Roberts, 1995), nutrient enrichment (Szmant, 2002) and sedimentation (Bartley et al., 2014). These stressors have halved living coral levels worldwide since the mid-20th century, and could lead to between 70-99% of reefs experiencing bleaching-related degradation by 2100. (Frieler et al., 2013; Van Hooidonk et al., 2016; Bindoff et al., 2019). The amount of loss differs between regions, but some reef regions, like the Florida Keys, have been extremely degraded (Baums et al., 2022). Efforts to combat decline in coral health have included reducing fishing levels through gear restrictions or periodic fishing limits, erosion reduction through run-off control, and the restoration of degraded coral reefs (Clark and Edwards, 1995). Coral restoration is the process of adding coral fragments or coral larvae to a region in an attempt to directly raise coral cover (Bostrm-Einarsson et al., 2020).

The same stressors which suppress coral often allow benthic organisms such as macroalgae to grow more easily. The increased ability of these organisms to compete with coral, under these stressors, causes reefs to change from coral dominated to non-coral dominated ecosystems (Hughes, 1994). This is particularly concerning because coral reefs are thought to have multiple "stable states", including some stable states dominated by macroalgae instead of coral (Knowlton, 1992; Mumby et al., 2007; Fung et al., 2011) which support lo fish biodiversity (Rogers et al., 2014; Graham and Nash, 2013).

Multiple stable states (MSS) exist when a single ecosystem can support two or more stable communities (Knowlton, 1992). In coral reef ecosystems, the two main stable states discussed are coral-dominated states and macroalgal-dominated states (Lang and Chornesky, 1990; Knowlton, 1992; Mumby et al., 2007). Coral reef MSS were first modeled by Mumby et al. (2007), predictions from which have been empirically supported by experimental evidence (Schmitt et al., 2019) and empirical data (Rogers and Miller, 2006; Cheal et al., 2010; Graham et al., 2015). Further theoretical research has extended these methods

to understand the relationship between coral and macroalgae with respect to larval dispersal (Elmhirst et al., 2009; McManus et al., 2021; Greiner et al., 2022*b*) and other stressors such as sedimentation and nutrient enrichment (Fung et al., 2011).

MSS are particularly relevant in the context of coral loss and restoration because coral competition with algae for space is a known threat to the growth of newly-dispersed coral (Birrell et al., 2008). Widespread restoration activities have attempted to reduce coral loss, (Clark and Edwards, 1995; Bostrm-Einarsson et al., 2020) but they are incredibly costly (Bayraktarov et al., 2016)and have seen mixed levels of success (Hein et al., 2017; Bostrm-Einarsson et al., 2020). Large-scale restoration studies have not been feasible due to the difficulty of adding more than a small percent of coral cover to a large reef system (Bostrm-Einarsson et al., 2020). Additionally, even in restoration studies that did find high survivorship of out-planted coral, bleaching events proved to be a challenge (Smith et al., 2019), and maintenance (such as clearing microalgae from nursery corals (Knoester et al., 2024) or removing corallivores (Rogers and Plagnyi, 2022)) was required.

These shortcomings highlight a key factor for managers: the importance of theoretical work *prior* to beginning restoration activities to assess the viability of the plan. Coral reef restoration may be an appropriate conservation management plan for certain reefs but not all (Banaszak et al., 2023). Coral reef managers should use feasibility modeling to determine when restoration is appropriate, as is done in other conservation initiatives. Well-documented examples of this include population viability analyses (e.g. Boyce (1992); Coulson et al. (2001); Brook et al. (2000)) which have contributed to the famously successful re-introduction of species like wolves and Peregrine falcons (Ebenhard, 2000) and management strategy evaluation methods in fisheries (e.g., Mapstone et al., 2008; Bunnefeld et al., 2011; Punt et al., 2016). In the case of coral reef conservation, we argue here that we can use simplified models of coral reef dynamics to take the internal dynamics and stressor levels of a coral reef into account so as to assess which reefs will be most benefited by restoration methods.

We use a simple model of coral reef cover to provide widely-applicable advice for successful coral restoration. We consider under which stressor levels restoration is appropriate

by determining how stressor levels interact with the coral cover of the system. This helps determine whether achieving and maintaining a coral-dominated stable state is possible, or if the system is likely to regress to a degraded state. We modify a standard model from Mumby et al. (2007) and consider stressors including fishing levels, nutrient enrichment, and the amount of coral larval dispersal into the focal reef. We then use two case studies as examples for how this modeling approach could be applied in specific situations. Overall, our goal is to provide insights and guidelines for applying models to better inform the rapidly growing field of coral reef restoration.

2 Methods

To assess which conditions support restoration as a reasonable management method for coral reefs, we developed a simple model to determine the minimum coral cover that restoration efforts would need to achieve, under varying levels of interacting stressors and coral larval recruitment, to allow a reef to attain and maintain a coral-dominated state with coral cover $C > 30\%$ and macroalgal cover $M < 30\%$ (i.e. a self-sustaining healthy coral reef state). To determine what minimum coral cover is required for this, we use a linear stability analysis to find stable equilibria (attractors) of the system. Then, we simulate a range of trajectories from different initial conditions and parameter combinations (representing different stressor levels) to determine the basins of attraction associated with each attractor. These basins of attraction allow us to understand which initial conditions and parameter combinations allow the system to trend towards a coral-dominated attractor, and therefore, attain and maintain a coral-dominated state (i.e. restoration "success"). Finally, we used real-world restoration examples from the literature as case studies to demonstrate the application of this approach in real systems, and make quantitative predictions of restoration success in these cases.

Our mathematical model of a reef is based on the Mumby et al. (2007) model, to which we added an explicit coral larval dispersal term to allow us to model coral dispersing into the focal reef (based off of the Elmhirst et al. (2009) model). The model describes how herbivorous grazing on macroalgae and turf, natural coral mortality, coral larval disper-

sal, and spatial competition processes on the reef change the relative cover of coral (C), macroalgae (M), and turf algae (T) through time (see Figure 1, and equations (S1a–S1c)). In our model, the amount of C coming into the focal reef is determined by the coral larval dispersal rate (z). z is higher when more coral larvae are dispersing into the focal reef; for the sake of this study we will equate a higher z value with healthier connected reefs, but we acknowledge that the health of the focal reef and ocean current patterns also play a role in changing the value of z. We also consider how C and M compete for space on the reef (denoted by parameter a), which can be affected by nutrient enrichment (Szmant, 2002). If the reef experiences high levels of nutrient enrichment, M's ability to out-compete C grows via an increase in a. Finally, both T and M are removed from the reef through the process of grazing, g, by some implied grazing species (e.g. parrotfish), which can then make room for dispersing coral larvae to land and settle. For more information on the model and analysis see the Supplemental Information (8.1).

We wanted to assess how different stressors would change restoration success, so we simulated changes in the rate of macroalgal-coral competition a, dispersal of coral larvae z and grazing rate g (Table 1) to approximate changes in nutrient enrichment levels, health of connected reefs, and fishing levels (respectively) (Figure 1). We varied these parameters continuously, but for some analyses they are binned as 'low', 'medium', and 'high', and performed a fully factorial comparison across all three variables. We also wanted to assess if the percentage cover of C, M, and T affected restoration success due to inherent non-linearities, so we compared a thorough sampling of possible starting combinations of the three state variables and observed how that impacted the final state of the reef. From this, we determined, at each parameter combination, what the minimum initial coral cover value was that would lead the focal reef to trend to a self-sustaining healthy coral reef state from any starting C cover value (Figure 2). We then quantified how that minimum initial coral cover value changed if we focused only on low, medium or high initial macroalgal cover values (Figure 3).

We used two restoration case studies as examples for how this model could prove useful in a real-world context. To do this, we used the model (Equations (S1a–S1c), Figure 1) to

simulate reefs based on empirically-derived parameters for the case studies to determine whether restoration activities changed reefs' tendencies to attain a self-sustaining healthy coral reef state. We used data from Hein et al. (2020), who tracked not only the restoration activities of sites, but also the general conditions of the region containing the sites. We compared two different case studies: the New Heaven Reef Conservation Program (NHRCP) on the Thai island of Koh Tao, and The Nature Conservancy project (TNC) on St Croix, US Virgin Islands. We compiled data from each of these programs, and translated the information about the reefs into ranges of parameter values that could be used in our model. For coral cover and macroalgal cover, we gathered proportions directly from the project data (Hein et al., 2020), but for other important parameters in the model, we inferred from categorical information on each study (Jaleel, 2013; Hein et al., 2015). We used information on herbivore abundance to inform our grazing parameter, g, nutrient enrichment levels to inform our macroalgal-coral competition parameter, a, and immigration level of coral larvae to inform our coral larval dispersal measurement, z, (Table 2). Once we extracted the parameter values, we simulated each of the case studies across a factorial set of simulations across possible parameter combinations. This allowed us to assess the new starting point for the system and determine whether the increase in coral cover attained through the restoration program described, without altering any of the stressors in the region, would allow for the system to attain a self-sustaining healthy coral reef state in the future.

3 Results & Discussion

We found that to ensure self-sustaining healthy coral reefs, grazing rate was the most important variable. At low and medium grazing rates, as the macroalgal-coral competition value increases and the coral larval recruitment rate decreases, the minimum initial coral cover value needed for the reef to be able to achieve and maintain a healthy state (i.e. possible to trend to a coral-dominated stable state with coral levels $C > 30\%$, but also have macroalgae levels $M < 30\%$) from any initial macroalgal cover value, increaseswhen the grazing rate is low, there are some competition and recruitment values at which no minimum initial coral cover level is sufficient. When initial macroalgal cover levels are

considered explicitly, it is evident that as initial macroalgal cover levels increase, the minimum initial coral cover level needed for the reef to achieve and maintain a healthy state increases or the chance of the reef trending to such a state at those parameter values is not possible (Figure 3). As macroalgal-coral competition increases, the minimum grazing rate, recruitment rate, initial minimum coral cover level and initial macroalgal cover level at which attaining a self-sustaining healthy coral reef state is possible increases smoothly (Figure S3) (the analogous is true as coral larval recruitment rate increases, (Figures S2 and S4)).

These results encourage paying specific attention to grazing levels on a reef, through explicit measurement of grazing rate on different benthic substrates, not just grazer biomass levels (Graham and Nash, 2013). This is likely because the behaviour of the system appears to change drastically as shift between grazing levels, while changing macroalgal-coral competition or coral larval recruitment levels leads to more linear/predictable outcomes. However, when it is not possible to make changes to grazing, increasing the levels of coral larval recruitment (e.g. by improving the health of surrounding reefs) will provide new parameter spaces for healthy reef states at any initial coral level (Figure S2). Conversely, reducing the nutrient input of the system (or any other factor that increases coral's competitive ability) will reduce the amount of initial coral required to reach a healthy state (Figure S1). Having a reef start from low coral cover or restoring a reef to have ¿ 40% coral cover is hard ((Souter et al., 2021; van Woesik and Kratochwill, 2022; Tebbett et al., 2023).), so it is important to consider maintaining high grazing values, low macroalgal-coral competition values and high recruitment values to ensure that a low starting coral cover level can be sufficient to encourage the system to trend to a self-sustaining healthy state.

Even at reasonably high levels of coral cover (15% and 60% respectively), neither of the two case studies (TNC, NHRCP; see Table 2) is likely to achieve and maintain a coral-dominated state in the context of this model because of low grazing and low coral larval recruitment (Figure 4). If we interpret the TNC case study at these parameter values and macroalgal cover, restoration efforts in this region would need to increase the coral cover to 30-40% for the reefs to trend to a healthy state (Fig. Figure 3) and 50-60% if

the macroalgal cover were to increase (Fig. Figure 2, Figure 3). However, in the NHRCP scenario coral cover was quite high (60%), so it is surprising that all of the restoration cases seem likely to fail (Figure 4). This result of our simulations is likely a product of very low levels of herbivore abundance and unusually high levels of nutrient enrichment combined with essentially zero coral larval recruitment in the NHRCP system. Therefore, even though a large number of corals were out-planted, there are few avenues for them to successfully compete against algae. While the TNC system showed limited opportunities to regain a healthy state, its ability to do so where the NHRCP was unable to is likely due to its coral larval recruitment and lower nutrient enrichment, because higher enrichment increases macroalgae's competitive advantage over coral (Figure 4). Thus, our results show that restoration is only a viable long-term solution if other measures are taken to counteract the challenges the out-planted coral will encounter as they grow and attempt to sustain their population independently on a reef.

This model was developed from other models (most notably, (Mumby et al., 2007)) whose conclusions have been shown to fit real world systems in the Caribbean (Hughes, 1994; Rogers and Miller, 2006; Nystrm et al., 2000) and in the Indo-Pacific (Graham et al., 2015; Schmitt et al., 2019; Cheal et al., 2010; DONE, 1992). However, it is not a perfect analog to a real reef system because the base model (Mumby et al., 2007) was built to investigate how changing the grazing level affects the benthic cover of the reef system. Thus, our finding that varying the grazing parameter vastly alters restoration success (more than any other parameter, compare Figure 2 with Figures S1 and S2) may be slightly overblown and should be assessed through field experiments in real reef systems. Nevertheless, the importance of maintaining grazing species has been shown consistently on real reef systems (Hixon and Brostoff, 1996; Robinson et al., 2020), so it is clearly a very important process in maintaining coral reefs. Also, this model focused on the capacity of restoration to restore coral cover and the metrics of 'healthy' was built around coral cover level. We focused on this aspect because this model is built for investigating changes in benthic cover and because coral cover is known to be an important indicator of reef health (Obura et al., 2019; Birrell et al., 2021), but it is not the only indicator (e.g. reef structural complexity, overall

biodiversity, high ecosystem service provision, etc; (Graham and Nash, 2013; Rogers et al., 2014; Daz-Prez et al., 2016; Darling et al., 2017; Ford et al., 2018)) and might not be the most relevant for a particular coral restoration case study. Further modeling and fieldwork studies should investigate whether the conclusions of this study change when alternative metrics of success are investigated.

While we could not find any case studies (with all important parameters reported) that showed a strong promise of increase in percentage coral cover, we do not think that there are no cases where restoration is useful, but it is essential to identify such cases. Our results here reinforce the notion that restoration of degraded or stressed reefs is an expensive band-aid solution that is unlikely to produce desired results (Hughes et al., 2023). They also show that increasing coral larval recruitment, increasing herbivorous grazing, and decreasing macroalgal-coral competition (e.g. via decreasing nutrient enrichment) allows the system to trend to healthy self-sustaining coral reef states ($> 30\%$ coral cover, $< 30\%$ macroalgal cover) (Figure 2). If a reef starts from low macroalgal cover, even lower initial coral cover is sufficient for the system to trend to healthy states (Figure 3). When coral larval recruitment and grazing are lower and nutrient enrichment is higher, oftentimes reefs need $> 70\%$ coral cover for the reef to trend to a healthy state (Figure 2) which is unrealistic in most real systems (Souter et al., 2021). These results are echoed in the few small-scale restoration studies which comment on the environmental condition and the amount of other benthic organisms on the reefs throughout the restoration process, which find that reefs with high immigration and connectivity to thriving reefs as well as reefs with low nutrient enrichment or fishing pressures can benefit from restoration (Cinner et al., 2018; Anthony et al., 2020; Hein et al., 2020). Therefore, our results encourage restoring fish biomass to an acceptable level on a reef prior to any restoration activities, as this allows reefs to recover to a healthier state. Additionally, carefully managed fish stocks can act both as a buoy to coral and as a harvestable resource for the communities that live near these reefs. The process of identifying potential candidate reefs for restoration should include developing a model that incorporates more specific knowledge of a given reef as well as the capacity of the community and other involved stakeholders to maintain restoration efforts.

Our results show that the best method for achieving self-sustaining healthy coral reefs is to first reduce nutrient enrichment on reefs, increase grazing, and increase coral cover on well-connected reefs (through similar methods) to increase recruitment values (Greiner et al., 2022*a*,*b*). Pursuing these actions before pursuing coral restoration efforts helps avoid wasting resources on reefs with little to no herbivore abundance or recruitment–which is paramount for conserving resources while effectively protecting coral reefs.

4 Conclusion

We find that coral restoration is most practical and feasible when a coral reef is experiencing low levels of human pressures (low fishing, low pollution) and has low macroalgal cover and high coral larval recruitment. The best candidates for coral restoration are reefs that have low coral cover but are otherwise unaffected by local human pressures – i.e. reefs that have recently been hit by cyclones or bleaching events but otherwise have low stressor levels and thus have large amounts of dead coral that has not yet been overgrown by algae. However, even in such an ideal case it is important to consider whether the reef with the newly dead coral remains healthy enough to recover on its own and whether adding more coral would be a waste of effort (e.g. important to use coral that are thought to be resilient/resistant to bleaching in areas thought to be at high risk of future bleaching events, (Barshis et al., 2013)). In this era of drastic global change, especially for coral reefs, we do not have the time or resources to waste effort on healthy coral reefs or on management methods that will not be able to help improve reef condition in a meaningful and self-sustaining way. Mathematical models, when integrated appropriately with empirical data and co-designed with reef managers, are an effective way to quickly hypothesize which management method would be most effective on a particular reef. Using mathematical models to assess the efficacy of management methods beforehand is common practice in the management of many systems (species introductions, fisheries, etc.; (Knight, 2012; Hilborn and Walters, 1992)) and has been shown to be effective. Thus, we implore the coral reef management community to use mathematical models such as this one to assess whether coral restoration alone will give their coral reef the best chance of surviving into the future, or whether they

should aim to first reduce local human pressures.

5 Acknowledgement

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6 Data Availability Statement

Data sharing is not applicable to this article as no new data were created or analyzed in this study. All code to reproduce the analyses here can be found on GitHub:

https://github.com/colebrookson/coral-restoration/releases/tag/v1.0.0

7 Tables & Figures

Model Parameters			
Term	**Description**	**Values**	**Restoration Importance**
r	Rate of coral larval overgrowth on turf algae	0.55	
z	Dispersal rate of coral into the reef	0-0.99	The health of nearby reefs will strongly affect the success of coral dispersal into the focal reef, and hence the amount of new coral to supplement the recently transplanted coral.
d	Natural mortality rate of coral	0.24	
a	Rate of macroalgal-coral competition	0-0.99	The rate at which macroalgae will succeed in overgrowing coral changes with increases in nutrient influx to a reef (Elmhirst et al., 2009). If a reef has high nutrient enrichment levels, macroalgae will overgrow coral at higher rates.
g	Rate of grazing on algae	0-0.99	Herbivore numbers on reefs will impact restoration since if grazing is low or absent, there is no removal of macroalgae. (Elmhirst et al., 2009).
γ	Rate of macroalgae overgrowth on turf algae	0-0.77	

Table 1: Parameter values and details for the set of differential equations used to simulate the coral reef system. Variables that are considered levers for conservation action (z, a, and g) are explained with respect to their usefulness in conservation.

Restoration Case Studies							
Case Study	**Herbivore Abundance**	**Nutrient Enrichment**	**Coral Larval Dispersal**	**Unrestored Coral Cover**	**Unrestored Macroalgal Cover**	**Restored Coral Cover**	**Restored Macroalgal Cover**
TNC	low $0 \leq g \leq 0.2$	low $0 \leq a \leq 0.2$	low* $0 \leq z \leq 0.2$	10%	15%	15%	13%
NHRCP	low** $0 \leq g \leq 0.2$	high $0.4 \leq a < 1$	0% $0 \leq z \leq 0.2$	25%	0%	60%	0%

Table 2: Information from our case studies, translated into model parameters. *Too low to measure pre- and post-restoration. ** Assuming low based on inference of high fishing rates from other studies in this area (Jaleel, 2013; Hein et al., 2015).

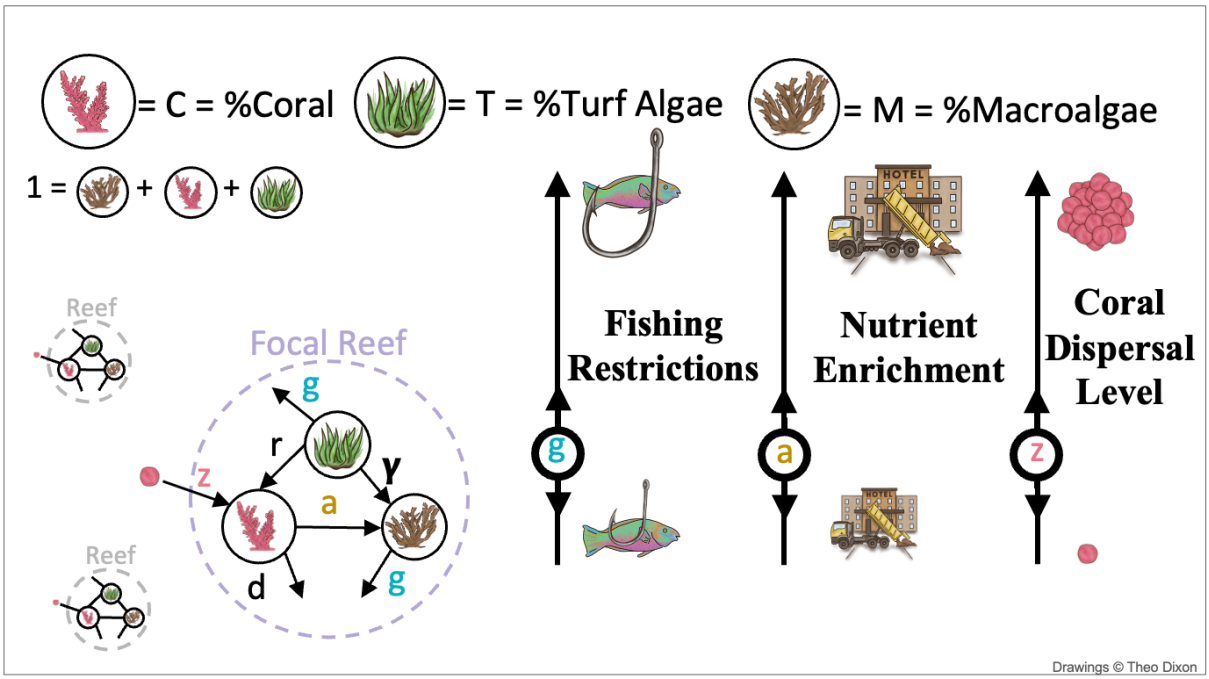

Figure 1: Conceptual figure of the model and how it represents the coral reef. We consider the reef as being covered entirely by coral (C), macroalgae (M) and turf algae (T). For simplicity, we say that (T) represents turf but this state variable essentially represents any space-filling benthic organism that can be settled on by coral larvae and consumed by herbivores (in some similar models it represents free space - see (Blackwood et al., 2018)). The focal reef is a discrete area that may be surrounded by other discrete reefs from which coral can disperse to/from. The transition between the three types of cover is modulated by the lettered parameters next to the arrows. The process of coral growth over turf algae (r), macroalgal growth over coral (a), and dispersal of coral larvae to the focal reef (z) and natural coral mortality (d) describes coral growth, while macroalgae can outgrow turf algae (γ). The colours of the different anthropogenic effects relate to the parameters in the model coloured the matching colour. For more detail see SI methods.

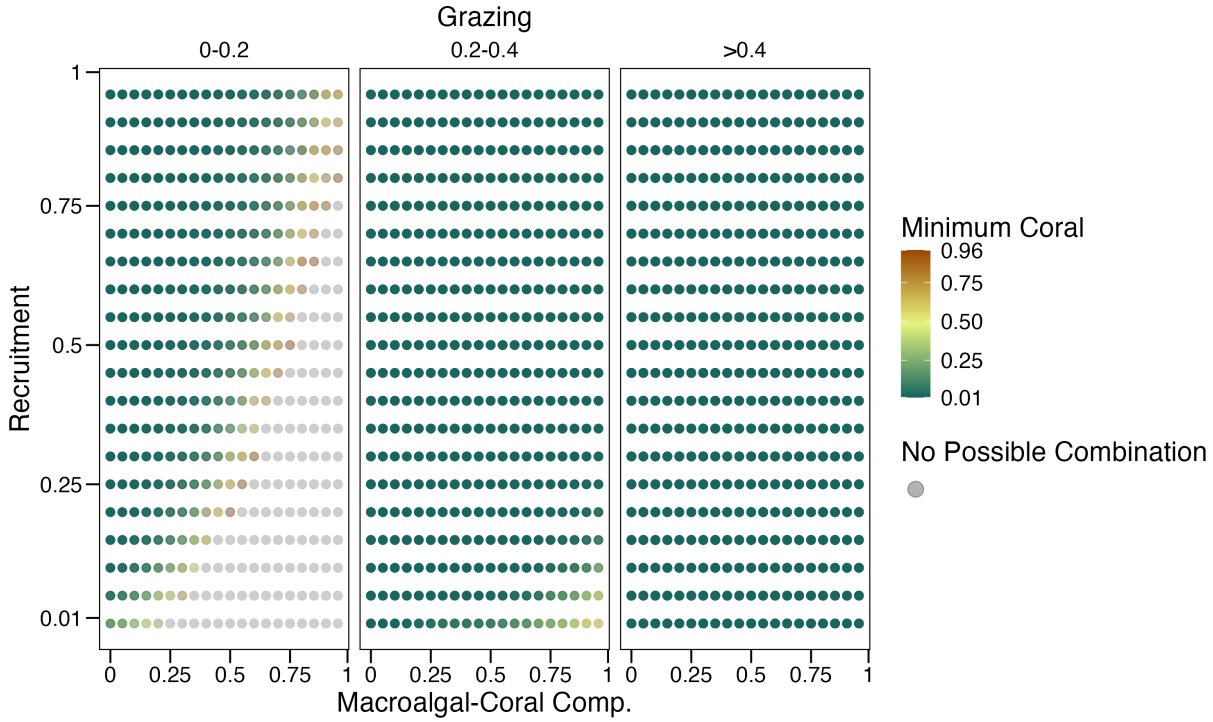

Figure 2: Each point represents the minimum amount of initial coral cover for the given parameter combinations, such that all initial values of macroalgae result in the reef being in a "healthy self-sustaining coral reef state" (i.e., trending towards a stable state with >30% coral cover & <30% macroalgae cover). Light grey points indicate that no possible parameter combination or initial condition results in the reef being in a "healthy self-sustaining coral reef state".

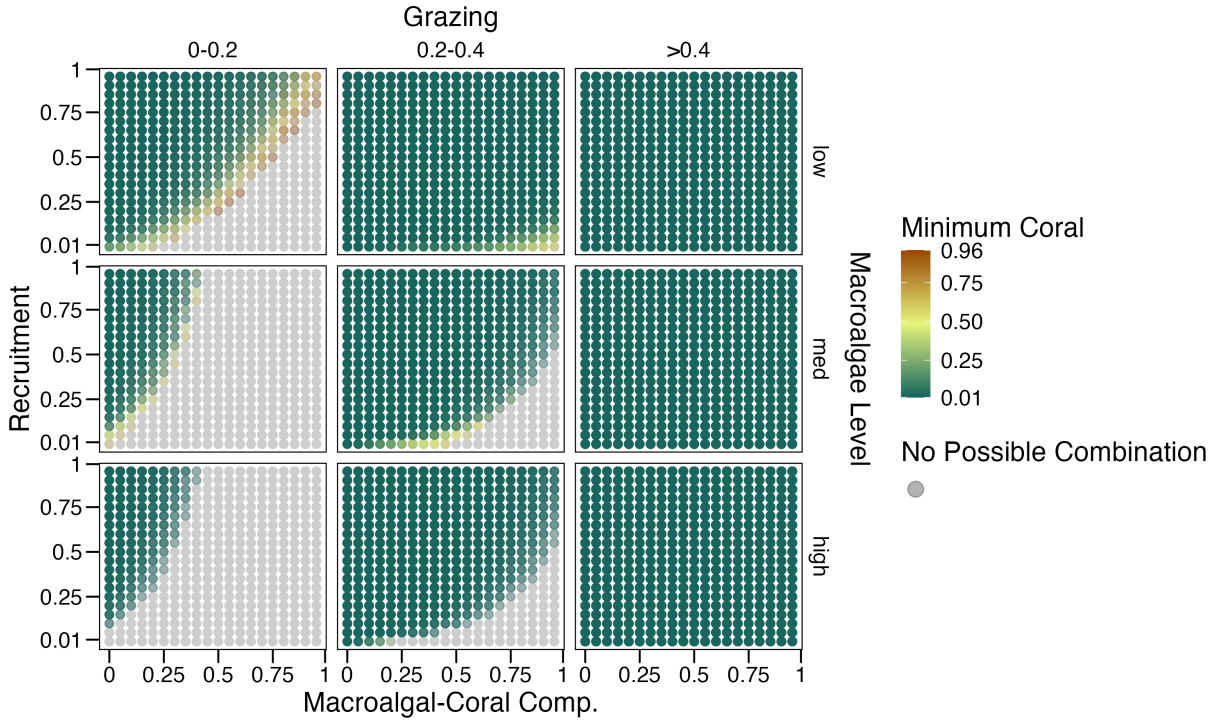

Figure 3: Each point represents the minimum amount of initial coral cover for the given parameter combinations, such that certain initial values of macroalgae result in the reef being in a "healthy self-sustaining coral reef state" (i.e., trending towards a stable state with >30% coral cover & <30% macroalgae cover). The values on the right y-axis depict whether the initial values of macroalgae considered are low (0-33%), medium (33-66%) or high (¿66%). Light grey points indicate that no possible parameter combination or initial condition results in the reef being in a "healthy self-sustaining coral reef state".

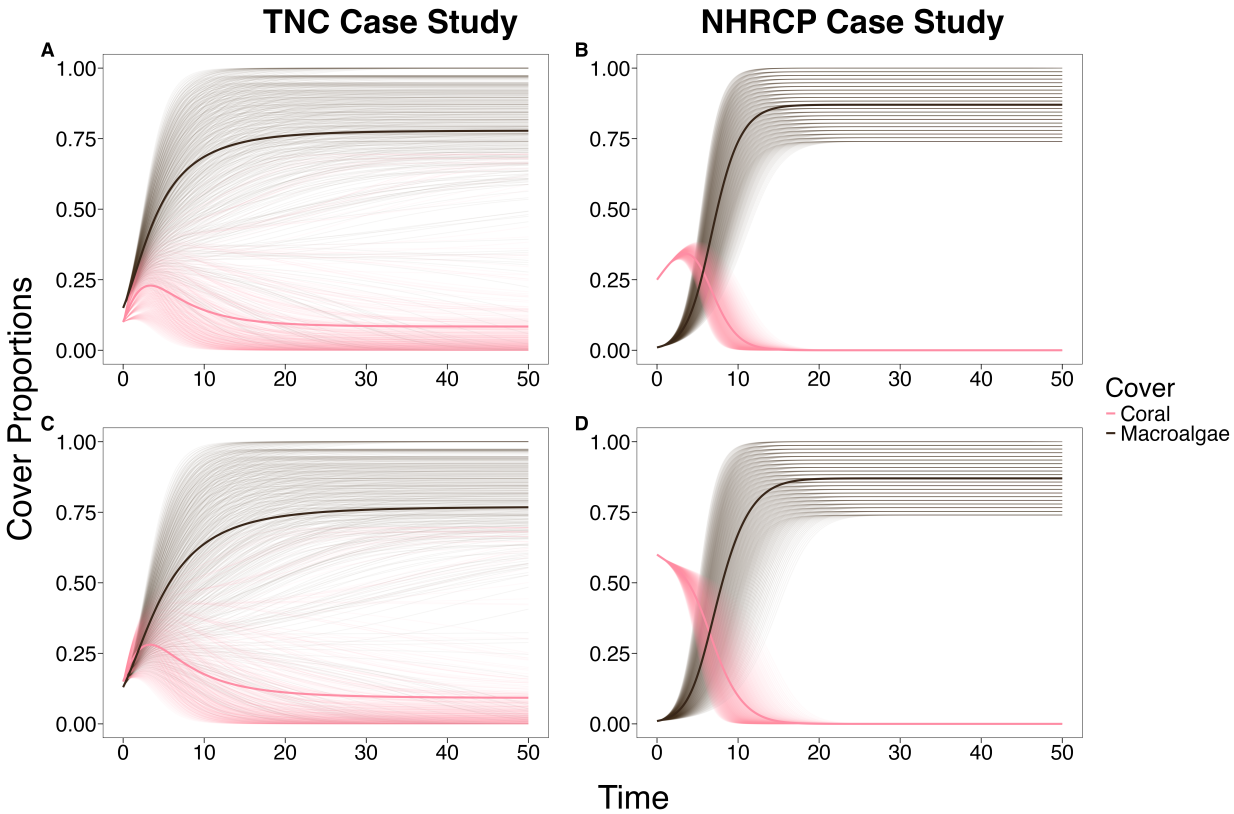

Figure 4: Restoration case studies before coral restoration (first row) and after (second row). A) and C) depict the the St. Croix reefs in the Nature Conservancy (TNC) case study, and B) and D) depict the New Heaven Reef Convservation Program (NHRCP) on the Thai island of Koh Tao.

References

Anthony, K. R., K. J. Helmstedt, L. K. Bay, P. Fidelman, K. E. Hussey, P. Lundgren, D. Mead, I. M. McLeod, P. J. Mumby, and M. Newlands. 2020. Interventions to help coral reefs under global changeA complex decision challenge. Plos one, **15**:e0236399. URL https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0236399. Publisher: Public Library of Science San Francisco, CA USA.

Banaszak, A. T., K. L. Marhaver, M. W. Miller, A. C. Hartmann, R. Albright, M. Hagedorn, P. L. Harrison, K. R. W. Latijnhouwers, S. Mendoza Quiroz, V. Pizarro, and V. F. Chamberland. 2023. Applying coral breeding to reef restoration: best practices, knowledge gaps, and priority actions in a rapidly-evolving field. Restoration Ecology, **31**:e13913. URL https://onlinelibrary.wiley.com/doi/abs/10.1111/rec.13913. _eprint: https://onlinelibrary.wiley.com/doi/pdf/10.1111/rec.13913.

Barshis, D. J., J. T. Ladner, T. A. Oliver, F. O. Seneca, N. Traylor-Knowles, and S. R. Palumbi. 2013. Genomic basis for coral resilience to climate change. Proceedings of the National Academy of Sciences, **110**:1387–1392. URL https://pnas.org/doi/full/10.1073/pnas.1210224110.

Bartley, R., Z. T. Bainbridge, S. E. Lewis, F. J. Kroon, S. N. Wilkinson, J. E. Brodie, and D. M. Silburn. 2014. Relating sediment impacts on coral reefs to watershed sources, processes and management: A review. Science of the Total Environment, **468**:1138–1153. URL https://www.sciencedirect.com/science/article/pii/S0048969713010681?casa_token=NP2v3GLhgngAAAAA:-ZK5lDWuoyM0RSoQN96k5eyez2QJKHQfgkgyGunIW8ZrrKhQisRq2_oWsTWXiRPaxYFxz1QtfQ. Publisher: Elsevier.

Baums, I. B., V. F. Chamberland, N. S. Locatelli, and T. Conn. 2022. Maximizing Genetic Diversity in Coral Restoration Projects. In M. J. H. van Oppen and M. Aranda Lastra, editors, Coral Reef Conservation and Restoration in the Omics Age,

pages 35–53. Springer International Publishing, Cham. URL https://doi.org/10.1007/978-3-031-07055-6_3.

Bayraktarov, E., M. I. Saunders, S. Abdullah, M. Mills, J. Beher, H. P. Possingham, P. J. Mumby, and C. E. Lovelock. 2016. The cost and feasibility of marine coastal restoration. Ecological Applications, **26**:1055–1074. URL https://esajournals.onlinelibrary.wiley.com/doi/10.1890/15-1077.

Bindoff, N. L., W. W. Cheung, J. G. Kairo, J. Arstegui, V. A. Guinder, R. Hallberg, N. Hilmi, N. Jiao, S. Karim, and L. Levin. 2019. Changing ocean, marine ecosystems, and dependent communities. URL https://ri.conicet.gov.ar/handle/11336/233328. Publisher: Cambridge University Press.

Birrell, C. L., L. J. McCook, B. L. Willis, and G. A. Diaz-Pulido. 2008. Effects of benthic algae on the replenishment of corals and the implications for the resilience of coral reefs. In Oceanography and marine biology, pages 31–70. CRC Press. URL https://www.taylorfrancis.com/chapters/edit/10.1201/9781420065756-4/effects-benthic-algae-replenishment-corals-implications-resilience-coral-reefs-chico-

Birrell, C. L., E. Sola, R. H. Bennett, D. van Beuningen, H. M. Costa, J. J. Sitoe, N. Sidat, S. Fernando, E. S. Darling, and N. A. Muthiga. 2021. A Summary of the WCS Knowledge on the State of Coral Reefs in Mozambique. URL https://programs.wcs.org/databases/doi/ctl/view/mid/33065/pubid/DMX3958800000.aspx. Publisher: Wildlife Conservation Society.

Blackwood, J. C., C. Okasaki, A. Archer, E. W. Matt, E. Sherman, and K. Montovan. 2018. Modeling alternative stable states in Caribbean coral reefs. Natural Resource Modeling, **31**:e12157. URL https://onlinelibrary.wiley.com/doi/abs/10.1111/nrm.12157. _eprint: https://onlinelibrary.wiley.com/doi/pdf/10.1111/nrm.12157.

Bostrm-Einarsson, L., R. C. Babcock, E. Bayraktarov, D. Ceccarelli, N. Cook, S. C. Ferse, B. Hancock, P. Harrison, M. Hein, and E. Shaver. 2020. Coral restorationA systematic review of current methods, successes, failures and future directions. PloS

one, **15**:e0226631. URL https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0226631. Publisher: Public Library of Science San Francisco, CA USA.

Boyce, M. S. 1992. Population Viability Analysis. Annual Review of Ecology and Systematics, **23**:481–497. URL https://www.annualreviews.org/doi/10.1146/annurev.es.23.110192.002405.

Brook, B. W., J. J. O'Grady, A. P. Chapman, M. A. Burgman, H. R. Akakaya, and R. Frankham. 2000. Predictive accuracy of population viability analysis in conservation biology. Nature, **404**:385–387. URL https://idp.nature.com/authorize/casa?redirect_uri=https://www.nature.com/articles/35006050&casa_token=Ldxat5t9VNcAAAAA:R_8nKIz8hFziwJAHfhaYfESpdaepwzb70onSI971sT8diTkJSMtT1NUeE6qTDyNG3WREBmsNfjRueQE9xhs. Publisher: Nature Publishing Group UK London.

Bunnefeld, N., E. Hoshino, and E. J. Milner-Gulland. 2011. Management strategy evaluation: a powerful tool for conservation? Trends in Ecology & Evolution, **26**:441–447. URL https://www.cell.com/trends/ecology-evolution/abstract/S0169-5347(11)00133-9. Publisher: Elsevier.

Cheal, A. J., M. A. MacNeil, E. Cripps, M. J. Emslie, M. Jonker, B. Schaffelke, and H. Sweatman. 2010. Coralmacroalgal phase shifts or reef resilience: links with diversity and functional roles of herbivorous fishes on the Great Barrier Reef. Coral Reefs, **29**:1005–1015. URL https://doi.org/10.1007/s00338-010-0661-y.

Cheal, A. J., M. A. MacNeil, M. J. Emslie, and H. Sweatman. 2017. The threat to coral reefs from more intense cyclones under climate change. Global Change Biology, **23**:1511–1524. URL https://onlinelibrary.wiley.com/doi/10.1111/gcb.13593.

Cinner, J. E., E. Maire, C. Huchery, M. A. MacNeil, N. A. J. Graham, C. Mora, T. R. McClanahan, M. L. Barnes, J. N. Kittinger, C. C. Hicks, S. DAgata, A. S. Hoey, G. G. Gurney, D. A. Feary, I. D. Williams, M. Kulbicki, L. Vigliola, L. Wantiez, G. J. Edgar, R. D. Stuart-Smith, S. A. Sandin, A. Green, M. J. Hardt, M. Beger, A. M. Friedlander,

S. K. Wilson, E. Brokovich, A. J. Brooks, J. J. Cruz-Motta, D. J. Booth, P. Chabanet, C. Gough, M. Tupper, S. C. A. Ferse, U. R. Sumaila, S. Pardede, and D. Mouillot. 2018. Gravity of human impacts mediates coral reef conservation gains. Proceedings of the National Academy of Sciences, **115**. URL https://pnas.org/doi/full/10.1073/pnas.1708001115.

Clark, S. and A. J. Edwards. 1995. Coral transplantation as an aid to reef rehabilitation: evaluation of a case study in the Maldive Islands. Coral reefs, **14**:201–213. URL https://idp.springer.com/authorize/casa?redirect_uri=https://link.springer.com/article/10.1007/bf00334342&casa_token=fiqW7GLjBJsAAAAA:RFfFlm_EvvFsV2lNkMWgI135Ez_uUDMXkksAf-WwEyqgv4vQt98tr1xl_O7sEur0LyOUmF7nzJhy6tVqyo8. Publisher: Springer.

Coulson, T., G. M. Mace, E. Hudson, and H. Possingham. 2001. The use and abuse of population viability analysis. Trends in Ecology & Evolution, **16**:219–221. URL https://www.cell.com/trends/ecology-evolution/fulltext/S0169-5347(01)02137-1. Publisher: Elsevier.

Darling, E. S., N. A. J. Graham, F. A. Januchowski-Hartley, K. L. Nash, M. S. Pratchett, and S. K. Wilson. 2017. Relationships between structural complexity, coral traits, and reef fish assemblages. Coral Reefs, **36**:561–575. URL https://doi.org/10.1007/s00338-017-1539-z.

Deysher, L. and T. A. Norton. 1981. Dispersal and colonization in *Sargassum muticum* (Yendo) Fensholt. Journal of Experimental Marine Biology and Ecology, **56**:179–195. URL https://www.sciencedirect.com/science/article/pii/002209818190188X.

DONE, T. 1992. Constancy and Change in some Great Barrier Reef Coral Communities: 198019911. American Zoologist, **32**:655–662. URL https://doi.org/10.1093/icb/32.6.655.

Daz-Prez, L., F. A. Rodrguez-Zaragoza, M. Ortiz, A. L. Cupul-Magaa, J. D. Carriquiry,

E. Ros-Jara, A. P. Rodrguez-Troncoso, and M. d. C. Garca-Rivas. 2016. Coral Reef Health Indices versus the Biological, Ecological and Functional Diversity of Fish and Coral Assemblages in the Caribbean Sea. PLOS ONE, **11**:e0161812. URL https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0161812. Publisher: Public Library of Science.

Ebenhard, T. 2000. Population viability analyses in endangered species management: the wolf, otter and peregrine falcon in Sweden. Ecological bulletins, pages 143–163. URL https://www.jstor.org/stable/20113254?casa_token=SiTS1pKfrQ8AAAAA:je5Z3D6yDTOiy0BxJ1qjoW4uqdVZvQvHbausv0Oe1ZNx3r0hDZmyjdeheHfTPHhOx7d5SCN3z06XZsm3Ej8TYP Publisher: JSTOR.

Elmhirst, T., S. R. Connolly, and T. P. Hughes. 2009. Connectivity, regime shifts and the resilience of coral reefs. Coral Reefs, **28**:949–957. URL https://idp.springer.com/authorize/casa?redirect_uri=https://link.springer.com/article/10.1007/s00338-009-0530-8&casa_token=zlnBpDKmnkMAAAAA:Gg7Sg0Y01Z5ErZUzRDHnfD55yZEuntITXzGKCDLhT6ntfYvW3Sg4cxQMTDYpFA3FcRBVDORyiMyXVqqHH9c. Publisher: Springer.

Ford, A. K., A. Eich, R. S. McAndrews, S. Mangubhai, M. M. Nugues, S. Bejarano, B. R. Moore, C. Rico, C. Wild, and S. C. A. Ferse. 2018. Evaluation of coral reef management effectiveness using conventional versus resilience-based metrics. Ecological Indicators, **85**:308–317. URL https://www.sciencedirect.com/science/article/pii/S1470160X1730626X.

Frieler, K., M. Meinshausen, A. Golly, M. Mengel, K. Lebek, S. D. Donner, and O. Hoegh-Guldberg. 2013. Limiting global warming to 2 C is unlikely to save most coral reefs. Nature Climate Change, **3**:165–170. URL https://idp.nature.com/authorize/casa?redirect_uri=https://www.nature.com/articles/nclimate1674&casa_token=7G10SVvRHI8AAAAA:BUFFwtaFcFyQXnYGwv3bbVohGVtcOySjAKZ7d8qv6VeL1TpDIlHf5BVTuOQ-arc6Pz91jINyLJ7jhfNy. Publisher: Nature Publishing Group UK London.

Fung, T., R. M. Seymour, and C. R. Johnson. 2011. Alternative stable states and phase shifts in coral reefs under anthropogenic stress. Ecology, **92**:967–982. URL http://doi.wiley.com/10.1890/10-0378.1.

Graham, N. A., S. Jennings, M. A. MacNeil, D. Mouillot, and S. K. Wilson. 2015. Predicting climate-driven regime shifts versus rebound potential in coral reefs. Nature, **518**:94–97. URL https://idp.nature.com/authorize/casa?redirect_uri=https://www.nature.com/articles/nature14140&casa_token=zctFXMLj3zQAAAAA:oldTNpl7XaFh8fS37MHR8QDAnzlIro3EHCmSEVWvqKSYzcFHd-nPxsHdYnGEOR1vnpO34PuLi7PJfh_NEtE. Publisher: Nature Publishing Group UK London.

Graham, N. A. and K. L. Nash. 2013. The importance of structural complexity in coral reef ecosystems. Coral reefs, **32**:315–326. URL https://idp.springer.com/authorize/casa?redirect_uri=https://link.springer.com/article/10.1007/s00338-012-0984-y&casa_token=4lSXs3YxJhwAAAAA:i_5mIQB9V0bQCSAP-XAka2K77BmXBjLu8fHq8jpQNTsRMKWkxFxMz80C0iZDcQV7AkDAI9QYvAliMuXBbJA. Publisher: Springer.

Greiner, A., M. Andrello, E. Darling, M. Krkoek, and M. Fortin. 2022*a*. Limited spatial rescue potential for coral reefs lost to future climate warming. Global Ecology and Biogeography, **31**:2245–2258. URL https://onlinelibrary.wiley.com/doi/10.1111/geb.13571.

Greiner, A., E. S. Darling, M.-J. Fortin, and M. Krkoek. 2022*b*. The combined effects of dispersal and herbivores on stable states in coral reefs. Theoretical Ecology, **15**:321–335. URL https://idp.springer.com/authorize/casa?redirect_uri=https://link.springer.com/article/10.1007/s12080-022-00546-w&casa_token=n3yuRwjw0vUAAAAA:xVK5xOs-ej9W1ApDvdVRNZaVt7gzKrmRw8PBOcMt_Im2yLmxJQyNiK1R_ykNLDWpLH0kB4tzeppqjW1n8wQ. Publisher: Springer.

Hein, M. Y., R. Beeden, A. Birtles, N. M. Gardiner, T. Le Berre, J. Levy, N. Marshall, C. M. Scott, L. Terry, and B. L. Willis. 2020. Coral restoration effectiveness: multiregional

snapshots of the long-term responses of coral assemblages to restoration. Diversity, **12**:153. URL https://www.mdpi.com/1424-2818/12/4/153. Publisher: MDPI.

Hein, M. Y., J. B. Lamb, C. Scott, and B. L. Willis. 2015. Assessing baseline levels of coral health in a newly established marine protected area in a global scuba diving hotspot. Marine Environmental Research, **103**:56–65. URL https://www.sciencedirect.com/science/article/pii/S0141113614001949.

Hein, M. Y., B. L. Willis, R. Beeden, and A. Birtles. 2017. The need for broader ecological and socioeconomic tools to evaluate the effectiveness of coral restoration programs. Restoration Ecology, **25**:873–883. URL https://onlinelibrary.wiley.com/doi/10.1111/rec.12580.

Hilborn, R. and C. J. Walters. 1992. Stock and Recruitment. In Quantitative Fisheries Stock Assessment, pages 241–296. Springer US, Boston, MA. URL http://link.springer.com/10.1007/978-1-4615-3598-0_7.

Hixon, M. A. and W. N. Brostoff. 1996. Succession and Herbivory: Effects of Differential Fish Grazing on Hawaiian CoralReef Algae. Ecological Monographs, **66**:67–90. URL https://esajournals.onlinelibrary.wiley.com/doi/10.2307/2963481.

Hughes, T. P. 1994. Catastrophes, Phase Shifts, and Large-Scale Degradation of a Caribbean Coral Reef. Science, **265**:1547–1551. URL https://www.science.org/doi/10.1126/science.265.5178.1547.

Hughes, T. P., A. H. Baird, T. H. Morrison, and G. Torda. 2023. Principles for coral reef restoration in the anthropocene. One Earth, **6**:656–665. URL https://www.sciencedirect.com/science/article/pii/S2590332223001896.

Jaleel, A. 2013. The status of the coral reefs and the management approaches: The case of the Maldives. Ocean & Coastal Management, **82**:104–118. URL https://linkinghub.elsevier.com/retrieve/pii/S0964569113001440.

Knight, T. M. 2012. Using Population Viability Analysis to Plan Reintroductions. In J. Maschinski, K. E. Haskins, and P. H. Raven, editors, Plant Reintroduction in a Changing Climate, pages 155–169. Island Press/Center for Resource Economics, Washington, DC. URL http://link.springer.com/10.5822/978-1-61091-183-2_9.

Knoester, E. G., M. H. Groenendijk, A. J. Murk, and R. Osinga. 2024. Some like it dirty: Less frequent nursery cleaning can reduce reef restoration costs with limited negative effects on coral performance. Ecological Engineering, **201**:107209. URL https://www.sciencedirect.com/science/article/pii/S0925857424000338.

Knowlton, N. 1992. Thresholds and multiple stable states in coral reef community dynamics. American Zoologist, **32**:674–682. URL https://academic.oup.com/icb/article-abstract/32/6/674/95955. Publisher: Oxford University Press UK.

Lang, J. C. and E. A. Chornesky. 1990. Competition between scleractinian reef corals-a review of mechanisms and effects. Ecosystems of the world, **25**:209–252. URL https://pascal-francis.inist.fr/vibad/index.php?action=getRecordDetail&idt=19736343.

Mapstone, B. D., L. R. Little, A. E. Punt, C. R. Davies, A. D. M. Smith, F. Pantus, A. D. McDonald, A. J. Williams, and A. Jones. 2008. Management strategy evaluation for line fishing in the Great Barrier Reef: Balancing conservation and multi-sector fishery objectives. Fisheries Research, **94**:315–329. URL https://www.sciencedirect.com/science/article/pii/S0165783608002269.

McManus, L. C., D. L. Forrest, E. W. Tekwa, D. E. Schindler, M. A. Colton, M. M. Webster, T. E. Essington, S. R. Palumbi, P. J. Mumby, and M. L. Pinsky. 2021. Evolution and connectivity influence the persistence and recovery of coral reefs under climate change in the Caribbean, Southwest Pacific, and Coral Triangle. Global Change Biology, **27**:4307–4321. URL https://onlinelibrary.wiley.com/doi/10.1111/gcb.15725.

Mumby, P. J., A. Hastings, and H. J. Edwards. 2007. Thresholds and the resilience of Caribbean coral reefs. Nature, **450**:98–101.

URL https://idp.nature.com/authorize/casa?redirect_uri=https://www.nature.com/articles/nature06252&casa_token=6NFMMcmjJKUAAAAA:yqZKrkisf3fXmcw2iqjAcw0oz2Co7bsmSkukC-w34yOhMR1E3yVfLBeiFoImUTBBE3ReQYBQ-iWmmgiNn3E. Publisher: Nature Publishing Group UK London.

Nystrm, M., C. Folke, F. Moberg, M. Nystrm, C. Folke, F. Moberg, M. Nystrm, C. Folke, and F. Moberg. 2000. Coral reef disturbance and resilience in a human-dominated environment. Trends in Ecology & Evolution, **15**:413–417. URL https://www.cell.com/trends/ecology-evolution/abstract/S0169-5347(00)01948-0. Publisher: Elsevier.

Obura, D. O., G. Aeby, N. Amornthammarong, W. Appeltans, N. Bax, J. Bishop, R. E. Brainard, S. Chan, P. Fletcher, T. A. C. Gordon, L. Gramer, M. Gudka, J. Halas, J. Hendee, G. Hodgson, D. Huang, M. Jankulak, A. Jones, T. Kimura, J. Levy, P. Miloslavich, L. M. Chou, F. Muller-Karger, K. Osuka, M. Samoilys, S. D. Simpson, K. Tun, and S. Wongbusarakum. 2019. Coral Reef Monitoring, Reef Assessment Technologies, and Ecosystem-Based Management. Frontiers in Marine Science, **6**. URL https://www.frontiersin.org/journals/marine-science/articles/10.3389/fmars.2019.00580/full. Publisher: Frontiers.

Punt, A. E., D. S. Butterworth, C. L. de Moor, J. A. A. De Oliveira, and M. Haddon. 2016. Management strategy evaluation: best practices. Fish and Fisheries, **17**:303–334. URL https://onlinelibrary.wiley.com/doi/abs/10.1111/faf.12104. _eprint: https://onlinelibrary.wiley.com/doi/pdf/10.1111/faf.12104.

Roberts, C. M. 1995. Effects of Fishing on the Ecosystem Structure of Coral Reefs. Conservation Biology, **9**:988–995. URL https://conbio.onlinelibrary.wiley.com/doi/10.1046/j.1523-1739.1995.9051332.x-i1.

Robinson, J. P. W., J. M. McDevittIrwin, J. Dajka, J. HadjHammou, S. Howlett, A. GrabaLandry, A. S. Hoey, K. L. Nash, S. K. Wilson, and N. A. J. Graham. 2020. Habitat and fishing control grazing potential on coral reefs. Functional Ecology, **34**:240–251. URL https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2435.13457.

Rogers, A., J. L. Blanchard, and P. J. Mumby. 2014. Vulnerability of coral reef fisheries to a loss of structural complexity. Current Biology, **24**:1000–1005. URL https://www.cell.com/current-biology/pdf/S0960-9822(14)00318-2.pdf. Publisher: Elsevier.

Rogers, C. S. and J. Miller. 2006. Permanent 'phase shifts' or reversible declines in coral cover? Lack of recovery of two coral reefs in St. John, US Virgin Islands. Marine Ecology Progress Series, **306**:103–114. URL https://www.int-res.com/abstracts/meps/v306/p103-114/.

Rogers, J. G. D. and . E. Plagnyi. 2022. Culling corallivores improves short-term coral recovery under bleaching scenarios. Nature Communications, **13**:2520. URL https://www.nature.com/articles/s41467-022-30213-x. Publisher: Nature Publishing Group.

Schmitt, R. J., S. J. Holbrook, S. L. Davis, A. J. Brooks, and T. C. Adam. 2019. Experimental support for alternative attractors on coral reefs. Proceedings of the National Academy of Sciences, **116**:4372–4381. URL https://pnas.org/doi/full/10.1073/pnas.1812412116.

Smith, K. M., T. G. Payton, R. J. Sims, C. S. Stroud, R. C. Jeanes, T. B. Hyatt, and M. J. Childress. 2019. Impacts of consecutive bleaching events and local algal abundance on transplanted coral colonies in the Florida Keys. Coral Reefs, **38**:851–861. URL https://doi.org/10.1007/s00338-019-01823-7.

Souter, D. e. ., S. e. . Planes, J. e. . Wicquart, M. e. . Logan, D. e. . Obura, and F. e. . Staub. 2021. Status of coral reefs of the world: 2020 : executive summary. URL https://bvearmb.do/handle/123456789/3190. Accepted: 2023-08-22T01:05:42Z Publisher: Global Coral Reef Monitoring network (GCRMN) and International Coral Reef Initiative (ICRI).

Stiger, V. and C. E. Payri. 1999. Spatial and temporal patterns of settlement of the brown macroalgae Turbinaria ornata and Sargassum mangarevense in a coral reef on

Tahiti. Marine Ecology Progress Series, **191**:91–100. URL https://www.int-res.com/abstracts/meps/v191/p91-100/.

Szmant, A. M. 2002. Nutrient enrichment on coral reefs: Is it a major cause of coral reef decline? Estuaries, **25**:743–766. URL https://doi.org/10.1007/BF02804903.

Tebbett, S. B., S. R. Connolly, and D. R. Bellwood. 2023. Benthic composition changes on coral reefs at global scales. Nature Ecology & Evolution, **7**:71–81. URL https://www.nature.com/articles/s41559-022-01937-2. Publisher: Nature Publishing Group.

Van Hooidonk, R., J. Maynard, J. Tamelander, J. Gove, G. Ahmadia, L. Raymundo, G. Williams, S. F. Heron, and S. Planes. 2016. Local-scale projections of coral reef futures and implications of the Paris Agreement. Scientific reports, **6**:1–8. URL https://www.nature.com/articles/srep39666/1000. Publisher: Nature Publishing Group.

Van Hooidonk, R., J. A. Maynard, D. Manzello, and S. Planes. 2014. Opposite latitudinal gradients in projected ocean acidification and bleaching impacts on coral reefs. Global Change Biology, **20**:103–112. URL https://onlinelibrary.wiley.com/doi/10.1111/gcb.12394.

van Woesik, R. and C. Kratochwill. 2022. A global coral-bleaching database, 19802020. Scientific Data, **9**:20. URL https://www.nature.com/articles/s41597-022-01121-y. Publisher: Nature Publishing Group.