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Social plasticity and limited resilience of coral-dwelling gobies (genus *Gobiodon*) to climate change: outlook for coral-fish mutualisms in a changing world

Catheline Yasmin Magali Froehlich

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**Social plasticity and limited resilience of coral-dwelling gobies
(genus *Gobiodon*) to climate change: outlook for coral-fish
mutualisms in a changing world**

Catheline Yasmin Magali Froehlich

Supervisors:

Marian Y.L. Wong, Mark Downton, O. Selma Klanten

This thesis is presented as part of the requirement for the conferral of the degree:
Doctor of Philosophy

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Abstract

Climate change is rapidly altering ecosystems on a global scale, and coral reefs are particularly vulnerable to climate-induced disturbances. Coral reefs depend on mutualisms with their foundation species, i.e. corals, and yet most of the literature has focused on their mutualisms with only one type of symbiont (algae). Little is known about how coral-fish mutualisms respond to climatic disturbances, and yet cyclones and heatwaves are increasingly devastating coral reefs. We urgently need to assess how coral-fish mutualisms respond to disturbances as changes in mutualisms have the potential for causing ecosystem-level changes. Yet fish in coral-fish mutualisms have often been overlooked in studies regarding environmental disturbances. There are multiple aspects of the life history, behaviour, and movement of fish that may impact their mutualisms with corals. Here, I investigated (1) whether both symbionts in coral-fish mutualisms respond similarly to climatic disturbances, and (2) what mechanisms from the fish perspective are likely responsible for how coral-fish mutualisms respond to climatic disturbances. I used a model coral-fish mutualism between coral hosts from the genus *Acropora* and coral-dwelling gobies from the genus *Gobiodon* in which both organisms provide important benefits for the resilience of each partner. I implemented a comparative approach by investigating multiple goby and coral species encountered in study locations to provide genus-wide understandings of how their coral-goby mutualisms are impacted by climatic disturbances. Particularly important is that gobies can live in social groups and living in groups can improve coral maintenance. Accordingly, first I provided a comprehensive review on how climate change is impacting the sociality of coral reef fish as the sociality of these taxa have only recently been investigated. Studies have shown that climate change affected the habitat and physiology of fishes, and each of these effects impacted their sociality. The review highlighted key changes to the sociality of these fish depending on how corals respond to disturbances, like reduction in coral size, shifts in coral communities, and health of corals. Secondly, I set the scene by monitoring coral-goby mutualisms throughout four extreme disturbances in the northern Great Barrier Reef (GBR): two cyclones and two heatwaves that caused mass bleaching events. In the aftermath and after a few years of recovery, there were more coral species, but corals were almost three times smaller. For gobies though, there were two times fewer coral species, there were fewer gobies, and most corals became absent of gobies when previously most were occupied. Alarming, this study highlighted that gobies declined far more than corals and were far slower to recover than their hosts. Finally, I used a combination of observational and manipulative studies to investigate the potential for coral gobies to exhibit plasticity in their host use, sociality, and movement in relation to disturbances. Following the same four extreme disturbances, I found that gobies shifted hosts to the newly abundant coral species. Although exhibiting host plasticity may be an advantage in the short-term, using alternative coral hosts may reduce the fitness of gobies, i.e. their growth rates. I then investigated whether gobies shifted their social tendencies to live in groups or in pairs following these four extreme disturbances in the northern GBR and following a single extreme disturbance in the southern GBR. Gobies no longer lived in groups, rarely in pairs, and primarily lived as solitary individuals after the four disturbances, whereas there was relatively little change in their social tendencies after the single disturbance. This study suggests that if consecutive disturbances become the norm, gobies may continue to decline if they primarily stay solitary

as they need to live in pairs to breed. I then completed another study to investigate how predation risk, coral size and health, and number of group members affected the movement of gobies. I translocated gobies *in situ* into corals with varying sizes, number of individuals, and health. I replicated the study in a relatively undisturbed environment in Papua New Guinea, and in the highly disturbed environment following the four extreme disturbances in northern GBR. Regardless of the disturbance state, gobies preferred to face high costs of predation and did alter their movement based on coral size, health, or number of group members, even when predation risk was higher in disturbed environments. This suggests that gobies do not alter their movement plasticity based on environmental disturbances even though predation risk is heightened. This means that gobies exhibited host and social plasticity, but they did not exhibit movement plasticity to disturbances. I found that each mechanism of plasticity was likely responsible for a reduced recovery potential of gobies compared to their coral hosts. By combining the findings from each chapter of the thesis, I suggest that coral-fish mutualisms are highly vulnerable to climate change as fish experience barriers to recovery via host, social, and movement plasticity. Future conservation strategies should address declines in fish in order to maintain coral-fish mutualisms important for coral health.

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List of Publications Included as Part of the Thesis

Style of Thesis;

The thesis has been prepared as a Thesis by Compilation style, as outlined for the University of Wollongong. In light of this, there may be unavoidable repetition among introduction, methods, and discussion of several chapters.

Chapter 2: Literature Review

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Author Contributions: C.F. – conceptual framework, manuscript writing. O.K. – conceptual framework, manuscript editing. M.W. – conceptual framework, manuscript editing.

Chapter 3: Data Chapter

Published.

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Chapter 4: Data Chapter

In review (September 2022) in Ecology & Evolution.

Froehlich, C.Y.M., Klanten, O.S., Hing, M.L., Dowton, M., and Wong, M.Y.L. *Submitted.* Delayed recovery and host specialization may spell disaster for coral-fish mutualisms.

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Note: The preprint is available at: **Froehlich CYM, Klanten OS, Hing ML, Dowton M, Wong MYL.** 2022. Delayed recovery and host specialization may spell disaster for coral-fish mutualism. :2022.06.01.494455. doi:10.1101/2022.06.01.494455.
<https://www.biorxiv.org/content/10.1101/2022.06.01.494455v1>.

Chapter 5: Data Chapter

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Froehlich, C.Y.M., Heatwole, S.J., Klanten, O.S., Hildebrandt, C.A., Smith, J.O., Hing, M.L. and Wong, M.Y.L. *In prep.* Maintenance of social structures of coral-reef fishes on a geographic scale.

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Chapter 6: Data Chapter

Published.

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Certification

I, Catheline Froehlich, declare that this thesis submitted in fulfilment of the requirements for the conferral of the degree Doctor of Philosophy, from the University of Wollongong, is wholly my own work unless otherwise referenced or acknowledged. This document has not been submitted for qualifications at any other academic institution.

Catheline Froehlich

3rd May 2023

List of Names or Abbreviations

LI = Lizard Island, northern Great Barrier Reef, Australia

OTI = One Tree Island, southern Great Barrier Reef, Australia

PNG = Kimbe Bay, Papua New Guinea, Australia

COTS = crown-of-thorn starfish

PERMANOVA = permutational analyses of variance

SIMPER = similarity percentage analyses

GLMM = generalized linear mixed model

LMM = linear mixed model

GLM = generalized linear model

LM = linear model

VGLM = multinomial logistic regression model

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Fig 3.2. Effects of consecutive climate disturbances on coral and goby populations. Changes in *Acropora* **a** richness (n = 279), and **b** average diameter (n = 244), **c** percent goby occupancy (n = 244) and *Gobiodon* **d** richness (n=279), and **e** group size (n = 230) per transect (n = sample size per variable) before and after each cyclone (black cyclone symbols) and after two consecutive heatwaves/bleaching events (white coral symbols) around Lizard Island, Great Barrier Reef, Australia. Error bars are standard error. Fish and coral symbols above each graph illustrate the change in means for each variable among sampling events from post-hoc tests. Figures were illustrated in R (v3.5.2)(R Core Team 2018) and Microsoft Office PowerPoint 2016.

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Fig 3.4. Shifts in communities of corals and gobies throughout consecutive climate disturbances. The changes in communities along transects (n=279) before and after each cyclone (black cyclone symbols) and after two consecutive heatwaves/bleaching events (white coral symbols) at Lizard Island, Great Barrier Reef, Australia, for **a** *Acropora* corals and **b** *Gobiodon* gobies visualized on non-metric multidimensional scaling plots. Each colored point represents a single transect, black points represent bootstrapped averages (avg), and points closer together are more similar in species composition than points further apart. Figures were illustrated in PRIMER-E software (v7, <https://www.primer-e.com/>) and Microsoft Office PowerPoint 2016.

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heatwaves), **b** the 10 most common coral hosts and **c** their goby symbionts experienced drastic changes in abundances. Abundances after each cyclone were not significant but were significant after the last disturbances, and thus we display changes post-disturbances. Error bars are standard error. Percentages above bars represent the proportion of corals that were occupied by gobies during that particular survey year.

Fig 4.2. Host specificity of *Gobiodon* gobies in *Acropora* coral hosts changed following multiple disturbances. Proportion of all *Acropora* species used by the 10 most common *Gobiodon* species from surveys: pre-disturbances (2014), after cyclone Ita (2015), after cyclone Nathan (2016), after two back-to-back heatwaves/bleaching events (2018), and 3 years post-disturbances (2020). Letters above each bar represent host use differences among sampling years that are significantly similar to one another within species, and asterisks represent host occupation that is significantly different from all others within a species.

Fig 4.3. Changes in preferred *Acropora* host (s) for each *Gobiodon* gobies following multiple disturbances. Completed surveys before disturbance (2014), after cyclone Ita (2015), after cyclone Nathan (2016), after two back-to-back heatwaves (2018), and 3 years post-disturbances (2020). Coral hosts are organized from top to bottom to illustrate changes from most abundant to least abundant corals after disturbances. Green arrow highlights coral species that increased in abundance after disturbances, and red arrow highlights coral species that decreased in abundance after disturbances. Green box signifies gobies that did not change their preferred host until after heatwaves.

Fig 5.1. Sociality framework that tests whether ecological factors affect animal societies at four levels of variation and what rank of vulnerability is given to the sociality for the taxa based on how many variations have negative responses. Colony = all individual(s) living together in a society; # = number.

Fig 5.2. Forms of sociality of all species **a** by all three locations and pre-/post-disturbances for two locations and **b** by coral size. PNG = Papua New Guinea; LI = Lizard Island; OTI = One Tree Island; data outlined in black line is post-disturbance(s).

Fig 5.3. Sociality index of each species at different locations including repeat visits pre- and post-disturbance(s).

Fig 5.4. Synergistic relationship between group size, size of dominant, and coral size for group-forming *Gobiodon* gobies and their *Acropora* coral hosts. Yellow arrows identify significant effect ($p < 0.05$), and crossed out dashed lines represent no significant effect ($p \geq 0.05$).

Fig 5.5. Distribution of size ratios between rank 1&2 (rankstep1), and rank2&3 (rankstep2) of single species colonies of *Gobiodon* species. Note: no rankstep2 data for *G. brochus*, *G. erythrospilus*, *G. histrio*, and *G. oculolineatus* due to insufficient data; the size differences between the same species of

goby pictures are illustrated to scale based on rankstep means.

Fig 5.6. Size ratio between rank 1 and rank 2 individuals of *Gobiodon* species within single species colonies that were revisited at **a** Papua New Guinea (Sep-Nov 2018 and May-June 2019) and **b** Lizard Island before and after disturbances and follow up visit (Jan-Feb 2014, Jan-Mar 2020 and Jan-Mar-2021).

Fig 5.7. **a** Sex dominance of species visited at Lizard Island in 2020 vs. 2021, and **b** revisited the following year to see whether any sex outgrew the other in 2021. Note: no male outgrew the female in any goby colony (green).

Fig 5.8. Proportion of intermixed ranks **a** and bigger species as rank 1 **b** within size-based hierarchies of mixed species colonies of *Gobiodon* and their grouping composition **c**. PNG = Papua New Guinea; LI = Lizard Island; OTI = One Tree Island; year after the location label is the year sampled; data outlined in thick black line was taken post-disturbance while all other data was taken pre-disturbance.

Fig 5.9. Size ratios between each rankstep within the size-based hierarchies of mixed species colonies of *Gobiodon* gobies. Note: rankstep i = ratio between rank_(i) and rank_(i+1) individuals; the size differences between individuals of goby pictures are illustrated to scale based on rankstep means.

Fig 6.1. Experimental design: a focal goby was translocated into a dead coral adjacent to an unfamiliar live coral of similar size to offer two habitat health options: dead coral vs. live coral. Six treatment combinations were used to account for two habitat sizes and three habitat saturation levels.

Fig 6.2. Frequency of gobies' final location in relation to habitat health (live/red coral or dead/grey coral), saturation and size.

Fig 6.3. **a** Most common outcome for coral gobies that were translocated into a dead coral away from their home coral. Thin dashed arrow represents translocation, solid arrows represent expected outcomes, and the circle crosses out the least popular outcome. **b** Final location of focal gobies in relation to the distance to travel and return to their home coral.

Chapter 1: General Introduction

1.1. Impacts of climate change in coral reef ecosystems

Ecosystems around the world are being increasingly challenged by the frequency and intensity of climatic disturbances (Camill 2010; Turner 2010; Emanuel 2013; Hughes *et al.* 2017). Many ecosystems have not returned to their pre-disturbance states for several decades now and are not recovering fully from repeated disturbance (Burrows *et al.* 2011; Roff & Mumby 2012; Russell *et al.* 2012; Vergés *et al.* 2014; He & Silliman 2019). Accordingly, understanding how the flora and fauna of ecosystems are responding to these recurring and extreme disturbances is critical to conserving the integrity of ecosystems (Kiers *et al.* 2010; AghaKouchak *et al.* 2018; Sergio *et al.* 2018; Denton & Gokhale 2019). Studies often focus on foundation species, i.e. those that strongly influence the structure of ecosystems, to assess the extent of changes to ecosystems as these are the building blocks of ecosystems, e.g. conifers, kelps, and corals (Angelini *et al.* 2011; Denton & Gokhale 2019). Many foundation species exhibit mutualistic relationships (i.e. in which both organisms benefit), and such relationships have the potential for causing ecosystem-level shifts or disruptions if the mutualisms change (Wilson *et al.* 2006; Kiers *et al.* 2010; Turner 2010; Six *et al.* 2011). Whether mutualisms with foundation species will change as climatic disturbances are occurring more frequently will likely have large implications for the future of many ecosystems.

Coral reef ecosystems are particularly vulnerable to disturbances. In the past two decades they have experienced heightened frequencies and severities of cyclones and heatwaves on an unprecedented global scale (Carpenter *et al.* 2008; Emanuel 2013; Hughes *et al.* 2017, 2019a). The mutualism between corals and Symbiodiniaceae algae are at the core of corals bleaching from heatwaves (Lesser 2006; Baker *et al.* 2008). Corals bleach when their mutualistic relationship with the algae break down during acute environmental stress, but this mutualism can recover if corals regain the algae, thus surviving through continued environmental disturbance (Lesser 2006; Baker *et al.* 2008; Bay *et al.* 2016; Claar *et al.* 2020). However, coral reefs are experiencing disturbances at an increasing frequency that may not allow coral-algal mutualisms to persist continuously overtime and may cause coral community shifts if coral recruitment cannot offset devastating loss in coral cover (Hughes *et al.* 2017, 2018a, 2019a). As founders of coral reefs, corals also exhibit mutualisms with far less studied symbionts, like bacteria, fishes, and crabs (Munday *et al.* 1999; McKeon *et al.* 2012; Thompson *et al.* 2015). Recent studies report that these other organisms can play critical roles in coral health (Pratchett *et al.* 2000; Pratchett 2001; Dirnwoeber & Herler 2013; Chase *et al.* 2020b), e.g. coral-fish mutualisms can reduce bleaching susceptibility of corals (Chase *et al.* 2018). Further research to understand how these mutualisms respond to disturbances is critical as other symbiotic relationships may reduce the impacts of cyclones and heatwaves on corals.

Fish in mutualisms with corals are experiencing heightened stress from environmental disturbances that threaten their coral habitat, thermal tolerance, and longevity (Munday *et al.* 2007; Bellwood *et al.* 2012;

Rodgers *et al.* 2017; Rivest *et al.* 2019). Fish smaller than 50 mm, i.e. cryptobenthic fishes, tend to be overlooked in reef surveys, thus missing many potential changes to trophic levels following disturbances (Ahmadia *et al.* 2012; Brandl *et al.* 2018). Only in the last decade have studies begun to uncover the vast diversity and ecological niche breadth of cryptobenthic fishes and the impacts of degrading habitat on these fishes (Ahmadia *et al.* 2012; Brandl & Bellwood 2014b; Brandl *et al.* 2018, 2019b). Small, coral-dwelling cryptobenthic fishes in particular are experiencing acute stressors as cyclone damage and coral bleaching directly reduces the quality of their habitat (Bonin *et al.* 2009; Wong 2010; Hing *et al.* 2019). These fishes often exhibit high site fidelity to their host (Munday *et al.* 1997) and provide important mutualistic benefits to their coral hosts, like sediment and toxic algae removal, improved growth, increased water movement, and corallivore deterrence (Lassig 1981; Holbrook *et al.* 2008; Dixon & Hay 2012; Dirnwoeber & Herler 2013; Chase *et al.* 2018, 2020b). Thus coral-fish mutualisms have the potential for improving the resilience of corals to continued disturbances.

Recent studies have begun uncovering the impacts of climate change (here referring to increasing water temperatures, severe heatwaves, and storm activity) on coral-dwelling fishes and provided some potential implications for their coral-fish mutualisms. Depending on the fish taxa, some fishes like damselfishes are willing to reside in dead corals (Wismer *et al.* 2019), whereas others like gobies will only reside in live corals of the genus *Acropora* (mainly plate corals and some branching) (Bonin *et al.* 2009 Munday 1999). Cyclone activity damages corals, especially *Acropora* corals which are prone to breaking and tumbling during storms (Harmelin-Vivien 1994; Cheal *et al.* 2017; Madin *et al.* 2018). A previous study reported that the destruction of these preferred coral hosts did reduce goby numbers, especially those of group living gobies (Hing *et al.* 2018).

Since coral-dwelling fishes increase water movement within coral branches, such movement can reduce the bleaching susceptibility of corals in short heatwaves (Chase *et al.* 2018). The bleaching and death of coral hosts have been linked to reduced populations of damselfishes that occupy branching corals (Bonin *et al.* 2009). Heatwaves can cause mass loss of coral habitat by reducing overall coral cover which in turn will result in lower coral recruitment (Hughes *et al.* 2019a). Particularly, acroporid corals are some of the most vulnerable coral taxa to bleaching, storms and cyclones (Roff & Mumby 2012; Hughes *et al.* 2019a). Accordingly, corals and fish in mutualisms are facing acute stress from climate change as coral loss is substantial in recent years (Cheal *et al.* 2017; Hughes *et al.* 2017, 2018a). However, the response of their coral-fish mutualisms collectively has yet to be examined.

1.2. Mechanisms of responses of coral-fish mutualisms to climate change

Habitat is a limiting resource for coral-dwelling fishes and thus plays a critical role in many aspects important to these fishes, like life history, behaviour, and movement (Faulkes *et al.* 1997; Duffy & Macdonald 2010; Wong & Buston 2013; Hing *et al.* 2017; Branconi *et al.* 2020). Therefore, there are likely several mechanisms associated with aspects of coral habitat affecting fish, and this may impact how

coral-fish mutualisms respond to disturbances. As climate change is making environments more challenging (Camill 2010; Turner 2010; Emanuel 2013; Hughes *et al.* 2017), it is important to understand whether organisms exhibit plasticity in relation to how their habitat responds to these changes. Plasticity is the ability to change particular characteristics or behaviour in order to accommodate for environmental condition. Mechanisms of plasticity related to their habitat can thus provide insights into how coral-dwelling fishes respond to disturbances, and what implications such mechanisms have for their mutualisms.

Coral-dwelling fishes reside in corals and the type of coral habitat is important for these fish as continued disturbances may impact some types of habitat more than others (Douglas 1998; Kiers *et al.* 2010; Bonin 2012). How these fish use the coral habitat is important in understanding what type of habitat (e.g. morphology, size, shape, species, or health of habitat) is critical for coral-dwelling fishes. For example, coral-dwelling damselfishes reside among and above the coral branches and are continuously swimming to stay in place (Chase *et al.* 2020a). Damselfishes may even move among a group of corals in a small area and use degraded or dead corals as habitat depending on the fish size and age (Wismer *et al.* 2019; Chase *et al.* 2020a; Pratchett *et al.* 2020; Rueger *et al.* 2021a). Coral reef cardinalfishes will stay within and above coral branches the majority of the day and require live corals (Rueger *et al.* 2014, 2018). Cardinalfishes will have one primary home coral, but will often move to a few other corals as well (Rueger *et al.* 2014, 2018). Coral-dwelling gobies primarily reside deep within the coral branches and rest directly on the branches by using their single pelvic fin that acts as a suction. Gobies remain usually within a single coral colony and never reside within dead corals, although they will remain within partially bleached corals (Bonin *et al.* 2009; Wong & Buston 2013; Froehlich *et al.* 2021; Froehlich pers. obs.). The species of corals for these coral-dwelling fishes is also important (Munday 2001; Gardiner & Jones 2005) as certain coral species provide different characteristics, e.g. more interbranch space, that will improve movement, feeding efficiency, and growth of fish (Munday 2001; Caley & Munday 2003; Pereira & Munday 2016). The type of coral habitat available is affected by climate change, because corals become truncated, bleached, and some corals species may be more vulnerable to population decline from climatic disturbances (Douglas 1998; Kiers *et al.* 2010; Bonin 2012; Madin *et al.* 2018; Hughes *et al.* 2019a). The type of coral habitat will therefore play a role in how these fish are able to maneuver among and within the corals, how much these fish are able to grow, and how they may respond to climate change.

Host specialization (i.e. using one or two specific species only as hosts rather than using a variety of species as hosts) is a common phenomenon for many taxa and provides one potential mechanism in which symbiont fish may respond to climate change (Munday *et al.* 1999; Bonin 2012; McKeon *et al.* 2012; Thompson *et al.* 2015). If coral-dwelling fishes display plasticity with respect to selecting host species, then there is the potential for improved recovery, i.e. returning to the same behaviors, phenotypes, and populations size as pre-disturbances, following disturbances as some hosts are more susceptible to disturbances than others (Douglas 1998; Kiers *et al.* 2010; Bonin 2012). Alternatively, host plasticity may reduce overall resilience of fish since they may exhibit reduced fitness, e.g. growth rates,

when living in less preferred host species (Munday 2001; Caley & Munday 2003). There is also the potential for hosts to incur improved benefits, e.g. improved nutrition and protection, when particular symbiont species inhabit them (Douglas 1998; Kiers *et al.* 2010; Sensenig *et al.* 2017). Whether fish exhibit host plasticity will then impact their own resilience and that of their hosts, thus having the potential to affect how coral-fish mutualisms respond to climate change.

As environmental disturbances strongly affect coral reef ecosystems, and habitat is often a predictor of social living in many taxa, the social structure of fishes may need to be plastic for continued survival (Schradin *et al.* 2018). The sociality, i.e. their tendencies to associate in groups, of coral-dwelling fishes and other habitat specialist fishes in particular is experiencing indirect stressors as climatic disturbances reduce the quality of their habitat, which is important for the group-living of many taxa (Bonin *et al.* 2009; Wong 2010; Hing *et al.* 2019). Larger habitat often allows for more fish to live in groups by reducing conflict among individuals (Fautin 1992; Elliott & Mariscal 2001; Buston 2003a; Wong 2011; Chausson *et al.* 2018; Barbasch *et al.* 2020). More individuals within a group will also improve the maintenance and defence of the host (Foster 1985; Rueger *et al.* 2021a). As climatic disturbances often reduce the size of habitat in coral reefs, and coral-dwelling fishes tend to exhibit high site fidelity (Munday *et al.* 1997), they are ideal model organisms to study social plasticity and impacts of environmental disturbances. An assessment of what has already been studied regarding how the sociality of coral reef fishes is affected by climate change would be beneficial to understanding potential implications to their overall resilience to these disturbances.

Within the study of sociality, there are several scales at which to assess impacts of an organism's environment on their sociality. On a large scale, the tendency to live solitarily, in pairs, or in groups may be impacted by the condition of an environment and level of disturbance that it exhibits (Faulkes *et al.* 1997; Avilés *et al.* 2007; Lantz & Karubian 2017; Hing *et al.* 2018). For example, some social taxa have evolved an affinity for group living in challenging environments, i.e. the life insurer hypothesis (Queller & Strassmann 1998), as seen in *Synalpheus* sponge-burrowing shrimp, birds, and Australian rodents (Duffy & Macdonald 2010; Jetz & Rubenstein 2011; Firman *et al.* 2020). Alternatively, challenging environments may not be suitable for group-living in social animals, and instead animals may have evolved to live in groups in stable environments, as seen in hornbills (Gonzalez *et al.* 2013). On a smaller scale, the ways in which animals cooperate, e.g. size hierarchies and aggression (Wong *et al.* 2008; Ang & Manica 2010b, a; Rueger *et al.* 2021a), may be affected by ecological variation (Harwood & Avilés 2013; Pratchett *et al.* 2020). For example, habitat degradation may affect which individual disperses first within a group based on their size hierarchy (Pratchett *et al.* 2020). However, a clear pathway is lacking in which to test social plasticity of organisms to ecological factors, like habitat characteristics and environmental disturbances.

Social behaviour studies need to confirm sociality observations of particular taxa over many geographic locations, as intraspecific variations in sociality are affected by environmental conditions (Schradin *et al.* 2018). Social plasticity may be exhibited within a species or within a genus due to environmental

circumstances (Schradin *et al.* 2018; Hing *et al.* 2019). Without confirming social plasticity of discrete populations, we cannot properly predict changes to sociality from environmental disturbances. Accordingly, a comparative approach is important to understand at what scale sociality may vary within a species and within a genus in order to assess changes to sociality on large ecological scales like environmental conditions. Since the sociality of coral-dwelling fishes is closely linked to the characteristics of their host, if these fishes exhibit social plasticity on large environmental scales, there may be associated implications for their coral-fish mutualisms.

Characteristics of their habitat and environment may also impact the movement decisions of coral-dwelling fishes. Whether fish remain in one habitat or move to other habitat is often linked to the benefits of philopatry and costs of ecological constraints (Selander 1964; Emlen 1982; Stacey & Ligon 1991; Hing *et al.* 2017; He *et al.* 2019). By remaining in a group, an individual will have more access to several benefits like improved longevity, breeding rights, and high quality habitat, i.e. benefits of philopatry (Emlen 1982; Stacey & Ligon 1991). However, if habitat quality is reduced, then group-living may become an unpopular lifestyle (Wong 2010). To date, habitat size has been investigated as an indicator for movement decisions of some habitat specialist fishes (Parry 1973; Woolfenden & Fitzpatrick 1978; Buston 2004; Wong *et al.* 2007). However, other aspects of habitat quality, like health of habitat, have not been investigated. Remaining in a group may also be important to offset costs of movement from ecological constraints like habitat saturation (Selander 1964; Emlen 1982; Gonzalez *et al.* 2013; He *et al.* 2019; Branconi *et al.* 2020). To increase individual survival and fitness, cooperating peacefully in groups could be a beneficial alternative to dispersing and facing high predation risk (Wong *et al.* 2007). If available habitat is already saturated, then the ability to join a group could be the best strategy, especially if the habitat is of high quality, e.g. large size (Hing *et al.* 2017; Schradin *et al.* 2018). Additionally, movement decisions of fish have only been investigated in healthy environments. Yet, cryptobenthic fish often exhibit high predation risk in disturbed environments (Parry 1973; Woolfenden & Fitzpatrick 1978; Buston 2004; Wong *et al.* 2007), thus there is the potential for movement plasticity for coral-dwelling fishes depending on the state of the environment. Accordingly, whether fish exhibit movement plasticity to habitat characteristics and conditions of the environment will likely impact their own resilience from climatic disturbances.

1.3. Model species: coral-dwelling gobies from the genus *Gobiodon* inhabiting corals from the genus *Acropora*

For my PhD thesis, I aim to elucidate the plasticity and resilience to challenging environments for some of the more cryptic fishes in coral-fish mutualisms: coral-dwelling gobies from the genus *Gobiodon*. There are more than 20 species in the *Gobiodon* genus with varying degrees of sociality (Hing *et al.* 2018, 2019), and each predominantly reside in *Acropora* corals (Munday *et al.* 1999; Froehlich *et al.* 2021). The species of *Acropora* corals inhabited is important for some gobies as it can influence their growth (Munday 2001; Pereira & Munday 2016). *Acropora* corals are one of the most threatened coral species by bleaching, storms and cyclones and there is far less available *Acropora* habitat after these disturbances

(Harmelin-Vivien 1994; Hughes *et al.* 2019a). Already, cyclones have reduced group size of several group-forming coral gobies and coral sizes (Hing *et al.* 2018). Heatwaves cause mass bleaching in *Acropora* corals (Hughes *et al.* 2017; Madin *et al.* 2018), yet the effects of bleaching on goby populations have yet to be studied. Gobies provide important services to coral hosts that improve their fitness by removing toxic algae and sedimentation, reducing bleaching susceptibility, and deterring corallivores with their own toxic skin (Dixon & Hay 2012; Dirnwoeber & Herler 2013; Chase *et al.* 2018, 2020). In return, gobies receive shelter, food and nesting sites from their coral hosts (Kuwamura *et al.* 1994; Wong & Buston 2013). Accordingly, their coral-fish mutualism has the potential for improving the resilience of both symbiotic partners to disturbances.

For gobies, recolonization of degraded habitats depends on multiple factors relating to settlement, movement and the social tendencies of gobies. Gobies tend to remain in the coral (i.e. site fidelity) they settle in as post-larval juveniles after a short larval dispersal stage (Munday *et al.* 1998; Green *et al.* 2015; Hing *et al.* 2018). Gobies are some of the most specialized cryptobenthic fishes as they experience host specificity, sometimes down to a single coral species (Munday *et al.* 1997; Munday 2004a). Competition exists for particular host coral species as particular hosts increase fitness and competitive advantages for specific goby species (Munday *et al.* 1997; Munday 2001, 2004a). Host plasticity may thus potentially play a role in the resilience to challenging environments as some *Acropora* species are more susceptible to bleaching than others (Hughes *et al.* 2019a). Habitat availability is also an important indicator of sociality for gobies as they exhibit high site fidelity (Munday *et al.* 1997; Dirnwöber & Herler 2007; Hing *et al.* 2018, 2019). Some goby species live primarily in pairs whereas others tend to live in groups (Hing *et al.* 2018, 2019), and the effects of large scale ecological impacts on their sociality are only recently being studied. For example, Hing *et al.* (2019) found that ecological impacts play a larger role in their sociality than phylogenetic signals, and that cyclones have the potential for reducing their sociality moving forward (Hing *et al.* 2018). However, we know that gobies cooperate in groups via size hierarchies with a breeding pair and smaller subordinate nonbreeders queuing for breeding status (Buston 2003b; Buston & Cant 2006; Wong & Buston 2013; Branconi *et al.* 2020). Gobies may also alter their tendency to live in pairs or groups depending on the quality of their habitat (Hing *et al.* 2018, 2019). Gobies are expected to remain philopatric to the coral they settled in as post-larval juveniles due to the high predation risk that they face associated with movement as they are less than 6 cm in length (Wong & Buston 2013; Hing *et al.* 2017; Brandl *et al.* 2018). Gobies and corals thus provide an excellent model mutualism for investigating how environmental disturbances affect coral-fish mutualisms.

1.4. Thesis Outline

With this thesis I developed and expanded our knowledge of how disturbances affect coral-fish mutualism by investigating coral-goby mutualisms in geographic locations that differed in disturbance regimes. Recently, two back-to-back cyclones (2014 Ita, 2015 Nathan) and the two biggest consecutive mass bleaching events (2016, 2017) devastated reefs in the northern Great Barrier Reef, Australia. A further heatwave (2020) caused mass bleaching in the southern Great Barrier Reef as well. The

environmental climate of the Great Barrier Reef provides an ideal system to test how coral and coral goby assemblages are affected by climatic events. In the north in Papua New Guinea, climatic disturbances have rarely affected the reefs, and there were no disturbances affecting the reefs during the study period; thus this reef environment provided me with the opportunity to study coral-goby mutualisms in relatively undisturbed environments. Accordingly, these study areas were ideal environments for investigating the impacts of climatic disturbances on coral-fish mutualisms. By using the model mutualism of *Gobiodon* gobies and *Acropora* corals, my thesis aimed to answer the following question:

How do coral-fish mutualisms respond to climatic disturbances and what are potential mechanisms from the fish perspective that explain such responses?

I aimed to answer this question via a combination of a review, observational and manipulative studies:

The sociality of coral reef fishes and their links to coral habitat has only recently been investigated, and these fishes are some of the most vulnerable social taxa to climate change. I provide an extensive review in chapter 2 on how the sociality of coral reef fishes may be impacted by environmental disturbances. I link key aspects of their coral habitat and their physiology to potential consequences of environmental stressors. This literature review provides an essential foundation on which to investigate how climate change is affecting the sociality of fishes in coral reef ecosystems.

In chapter 3 (published), I assess whether corals and gobies respond similarly to climatic disturbances in order to investigate the recovery potential of their coral-fish mutualisms. I monitor populations of all species of *Acropora* corals and *Gobiodon* gobies throughout four devastating and consecutive disturbances at Lizard Island, northern Great Barrier Reef: two category 4 cyclones (2014, 2015), and two heatwaves causing mass bleaching (2016, 2017). I compare community-based metrics for corals and gobies throughout these disturbances.

In chapter 4 (in review), I investigate the potential for gobies to exhibit host plasticity as a mechanism that may explain their responses to climatic disturbances. I monitor which *Acropora* coral hosts are used by each *Gobiodon* gobies throughout the same four climatic disturbances at Lizard Island as in chapter 3. I also return 3 years post-disturbances to assess whether host plasticity exists during their recovery phase from disturbances.

In chapter 5, I introduce a framework for assessing the extent that social plasticity may be influenced by various ecological factors, e.g. habitat characteristics and environmental conditions. I present four levels of variation within sociality that range from large scale to small scale in order to investigate potential impacts of ecology at a defined taxonomic group level as well as a species level. I then use the framework on *Gobiodon* gobies to investigate impacts of geographic location and climatic disturbances on their sociality and link their mutualisms with corals as an additional layer of ecology. To complete this study, I monitor the sociality of multiple gobies species in the undisturbed environment in Kimbe Bay, Papua

New Guinea, and compare it to the disturbed environments at Lizard Island, which experienced a high disturbance regime, and at One Tree Island, southern Great Barrier Reef, which experienced a moderate disturbance regime.

In chapter 6 (published), I assess the potential for gobies to exhibit movement plasticity in relation to different characteristics of their coral habitat that may be affected by climatic disturbances. Each habitat characteristic is linked to the tendency for gobies to stay in a coral host or disperse, as well as the tendency for gobies to live in social groups. Accordingly, the study links the benefits of philopatry and ecological constraints to the costs of movement, which are key aspects of sociality. I use a manipulative experiment *in situ* at the undisturbed environment in Kimbe Bay to investigate the movement decisions of a goby, *Gobiodon quinquestrigatus*, in relation to the characteristics of *Acropora* coral hosts. To determine whether the condition of the environment affected the movement decisions of the same species, I repeat the study in Appendix 1 at the heavily disturbed environment of Lizard Island after multiple disturbances.

It is important to note that the thesis is a compilation of published and prepared manuscripts to be submitted. Accordingly, there is unavoidable repetition among chapters.

Chapter 2: Literature Review: A review of how environmental disturbances affect social behaviours of coral reef fishes

2.1. Introduction

Animals have evolved a variety of social organisations to better exploit their niche resources and counter many stressors (Queller & Strassmann 1998; Duffy & Macdonald 2010; Bourke 2014; Hing *et al.* 2017; Nowicki *et al.* 2018b; Firman *et al.* 2020; Rueger *et al.* 2021a). Sociality—which can be defined as conspecifics cooperating in pairs or groups—is either preserved in a species, or may exhibit plasticity depending on ecological circumstances (Emlen 1982; Duffy & Macdonald 2010; Schradin *et al.* 2018; He *et al.* 2019). As environmental changes are intensifying on a global scale, a key question is whether sociality will be fixed or plastic in response to these global stressors (Avilés *et al.* 2007; Duffy & Macdonald 2010; Coker *et al.* 2013; Gonzalez *et al.* 2013; Thompson *et al.* 2019; Froehlich *et al. in prep*). Social taxa may switch to solitary lifestyles, conversely assimilate into larger groups, or instead face extinction if they are unable to cope with these stressors and exhibit no social plasticity (Faulkes *et al.* 1997; Munday 2004b; Avilés *et al.* 2007; Lantz & Karubian 2017; Schradin *et al.* 2018; Thompson *et al.* 2019; Froehlich *et al. in prep*). Alternatively, exhibiting no social plasticity could be an advantageous strategy, if for example group-living species are less habitat selective, have higher individual fitness, and/or exhibit enhanced population connectivity that will replenish degraded environments (Munday 2000; Wilson & Hölldobler 2005; Cowen *et al.* 2006; Rubenstein & Lovette 2007; Duffy & Macdonald 2010; Avilés & Harwood 2012; Nalepa 2015). Social plasticity will play a role in determining how species respond to environmental changes (Komdeur & Ma 2021) as these stressors are intensifying into the future (Turner 2010; Hughes *et al.* 2018b).

Some of the most susceptible taxa to environmental change are coral reef fishes (Munday 2004b; Munday *et al.* 2008; Ahmadi *et al.* 2012; Cheal *et al.* 2017; Brandl *et al.* 2018; Hughes *et al.* 2018a; Froehlich *et al.* 2021), of which several exhibit a variety of social systems (Hourigan 1989; Brandl & Bellwood 2013, 2014a; Wong & Buston 2013; Fox *et al.* 2015; Hing *et al.* 2017). Some species will exclusively live in pairs, some will be paired for nonbreeding activities but will associate in groups for breeding, some will live in groups with limited cooperation, whereas others will be organized in highly cooperative societies (Warner 1995; Krause *et al.* 2000; Wong & Buston 2013; Fox *et al.* 2015; Pajmans *et al.* 2019; Thompson *et al.* 2019). In recent decades, there have been growing efforts to uncover the sociality of coral reef fishes, and they are providing several unique aspects of social evolution (Wong & Buston 2013; Rueger *et al.* 2021a). Groups of coral reef fishes are generally composed of unrelated individuals, unlike other social taxa, owing to a larval dispersal stage (Kolm *et al.* 2005; Buston *et al.* 2007), although there is some potential for minimal relatedness in some species (Gerlach *et al.* 2007; Selwyn *et al.* 2016; Rueger *et al.* 2020, 2021b). Coral reef fishes rarely exhibit alloparental care besides as a consequence of brood parasitism in damselfishes or breeding male mortality in anemonefishes (Tariel *et al.* 2019; Phillips

et al. 2020). Unlike most other animals, paternal care is widespread in fish (Goldberg *et al.* 2020). Several species can change sex while some cannot, which play roles in sex ratios in groups (Godwin *et al.* 2003; Godwin 2009; Wong & Buston 2013; Goikoetxea *et al.* 2017). Several species, like damselfishes, coral-dwelling gobies, hawkfishes, wrasses, and angelfishes, cooperate peacefully through size-based hierarchies in which subordinates control their growth to remain smaller than their adjacent rank and may even forgo or delay reproduction to avoid conflict (Thresher 1979; Hoffman 1985; Kane *et al.* 2009; Ang & Manica 2010b; Rueger *et al.* 2021a). Accordingly, the sociality of coral reef fishes is a growing research area that is providing new insights into social evolution.

There are many benefits and costs of living in groups for coral reef fishes and there is the potential for a variety of factors to affect this cost-benefit balance. Living in groups can increase foraging benefits and shared territory defense, delay senescence, improve fitness and reproductive output (Clifton 1990; Hing *et al.* 2017; Killen *et al.* 2017). Living in groups can also have a ‘calming effect’ on individuals that reduces their metabolic demand, as seen in damselfishes (Nadler *et al.* 2016a). Since there is little kinship in coral reef fishes, living in groups increases mate availability. However, living in groups may also reduce reproductive opportunities or delay reproduction for some individuals, as seen in coral-dwelling gobies and anemonefishes (Wong & Buston 2013; Rueger *et al.* 2021a). Such costs may be acceptable if the benefits of remaining philopatric to groups allow individuals to access limited resources like habitat or localized food sources, particularly if they can inherit breeding or territories once they become dominant individuals (Buston 2004). Conversely, for foraging fish species, prey availability may affect the tendency to live in pairs, as seen in some butterflyfishes (Brandl & Bellwood 2013, 2014a; Nowicki *et al.* 2018b). The formation or loss of groups may thus be a response to competition for limiting resources. Another important aspect of sociality is that dispersing away from groups would then incur high costs from not only losing access to key resources, but also facing heightened predation risks (Manassa *et al.* 2013; Hodge *et al.* 2018; Guerra *et al.* 2022). As the benefits and costs of sociality are modulated by several social and environmental factors, there may be an advantage to exhibiting social plasticity if certain limiting factors are altered.

There are many aspects of the environment of coral reef fishes that play a role in their sociality, and several of these aspects are becoming increasingly affected by environment changes at an alarming rate. Coral reefs are well known for their extensive live substrate, e.g. corals, sponges and anemones, and these substrates are limiting resources for sociality of several coral reef fishes (Brandl & Bellwood 2013; Hing *et al.* 2018; Thompson *et al.* 2019). The agitation of water around coral reefs from storm activity can however displace or damage live substrate, which may alter the benefits of group-living (Cheal *et al.* 2017; Hing *et al.* 2018). Communication is key to cooperating in groups, and water is an excellent medium for olfactory cues, electroreception, and sound transmission (Tricas & Webb 2016; Marshall *et al.* 2019; Rivest *et al.* 2019). Communication uses a variety of physiological functions in fish, and the poikilothermic nature of fish allows them to thrive in certain temperature ranges (Biswal *et al.* 2021). The temperature of oceanic waters tends to fluctuate less than air temperatures, especially at coral reefs, which explains why climate change can greatly impact coral reefs and fish physiology (Johansen & Jones 2011;

Hughes *et al.* 2017; Donelson *et al.* 2018). Oceanic water is an excellent medium at absorbing carbon dioxide causing ocean acidification, which can affect the physiology of fish (Munday *et al.* 2009, 2014). There are extensive networks of coral reefs around the world and some species migrate through ontogeny or to form groups for breeding during certain times of the year (Warner 1995). Coral reefs are also prone to oceanic currents, which have the potential for large-scale population connectivity while at the same time limiting the development of kin groups due to larval dispersal stages (Cowen *et al.* 2006; Jones *et al.* 2007). However coral reefs are becoming increasingly prone to a variety of threats, including climatic events like cyclones and heatwaves, oil spills, ocean acidification, fishing practices, invasions, logging, sedimentation, and habitat degradation (Parsons 1992; Salvat 1992; Bellwood *et al.* 2004; Munday *et al.* 2008; Hamilton *et al.* 2017; Wong *et al.* 2018; Brandl *et al.* 2019a; Hutchings *et al.* 2019). There is the potential for environmental disturbances to alter social behaviours of fish by changing group membership, access to limiting resources, physical and spatial structure of habitat, predation rates, connection among reef systems, and fish physiology (Parsons 1992; Munday *et al.* 2009; Selwyn *et al.* 2016; Colchen *et al.* 2017; Seebacher & Krause 2017; He *et al.* 2019; Hing *et al.* 2019; Takeshita *et al.* 2021). However, only a few studies have directly assessed the link between environmental disturbances and the social behaviour of coral reef fishes (Croft *et al.* 2003; Coker *et al.* 2013; Hing *et al.* 2019; Thompson *et al.* 2019), and only a few have investigated behavior in general (Pratchett *et al.* 2018).

Here we highlight what is currently known and what knowledge gaps need to be addressed to understand how environmental disturbances (both abiotic and biotic with special emphasis on environmental change) affect the sociality of coral reef fishes. We review the existing literature to investigate how the sociality of coral reef fishes (1) may be affected by direct changes to their ecology, and (2) by indirect changes to their physiology. Changes to their ecology have provided several insights into how reef substrate alterations (from abiotic and biotic factors), connections among coral reef systems (abiotic factors) and community shifts (abiotic and biotic factors) may affect social plasticity (Hing *et al.* 2017; Pecl *et al.* 2017; Hodge *et al.* 2018; He *et al.* 2019). Changes to individual physiology have been less studied, yet recent studies on olfactory organs, energy costs and reproduction (primarily from abiotic factors) suggest that group membership, parental care, and reproductive success may be affected (Takegaki & Nakazono 1999; Albers 2012; Donelson *et al.* 2016). As we find multiple lines of evidence linking environmental disturbances and the sociality of coral reef fishes, we urge coral reef research and management to include research on sociality into coral reef conservation.

2.2. Effects of Habitat Disturbances & Community Shifts on Sociality

Coral reef ecosystems are changing at an alarming rate due to anthropogenic disturbances, and fish may need to adapt their behaviours in order to persist (Pankhurst & Munday 2011; Hughes *et al.* 2017; Hing *et al.* 2018; Wong *et al.* 2018). There are abiotic and biotic stressors affecting the live substrate and community structures of coral reef ecosystems, including: stronger and more frequent climatic events, erosions and sedimentations, recurrent outbreaks of crown-of-thorn starfish (COTS), overfishing, species invasions (Syms & Jones 2000; Daskalov *et al.* 2007; Babcock *et al.* 2016; Hixon *et al.* 2016; Hughes *et al.*

al. 2017; Pecl *et al.* 2017; Hughes *et al.* 2019a). Each threat changes the structural integrity and survival of corals, affects fish community diversity, and alters several factors that are important for behavioural processes (Jones & Syms 1998; Keith *et al.* 2018; Wong *et al.* 2018; Hing *et al.* 2019; Hughes *et al.* 2019a). Fish communities are often dependent upon coral habitat for shelter, prey availability, and other resources, and they provide reciprocal benefits to their coral shelter (Kuwamura *et al.* 1994; Thompson *et al.* 2007; Cole *et al.* 2009; Gochfeld 2010; Dixon & Hay 2012; Dirnwoeber & Herler 2013; Wong & Buston 2013; Chase *et al.* 2018). The degradation of essential coral habitat may alter the benefits and costs of sociality (He *et al.* 2019; Hing *et al.* 2019), which could in turn change the social behaviours of several reef fishes.

Relationships between the reef habitat, fish communities, and fish behaviours are important for the conservation of coral reef ecosystems (Great Barrier Reef Marine Park Authority 2019). However, social behaviour of reef fishes are often overlooked in these discussions (Great Barrier Reef Marine Park Authority 2019). Fish communities provide important ecosystem services to reef habitat (Gochfeld 2010; Dixon & Hay 2012), yet fish are often reliant on several characteristics of reef ecosystems that are only available in optimal conditions, e.g. habitat quality and predator-prey balance (Thompson *et al.* 2007, 2019; Hing *et al.* 2019). For example, pairing behaviour in *Chaetodon* species is dependent on healthy coral habitat, and deviations from pair formations indicate ocean deterioration (Reese 1981). Changes in benefits of different social systems could thus have profound effects on reef systems (Keith *et al.* 2018). To understand the plasticity of social systems associated with environmental factors, I review the effects of (1) habitat alterations, (2) population connectivity, and (3) changes to fish communities on social behaviour of coral reef fishes (Box 2.1).

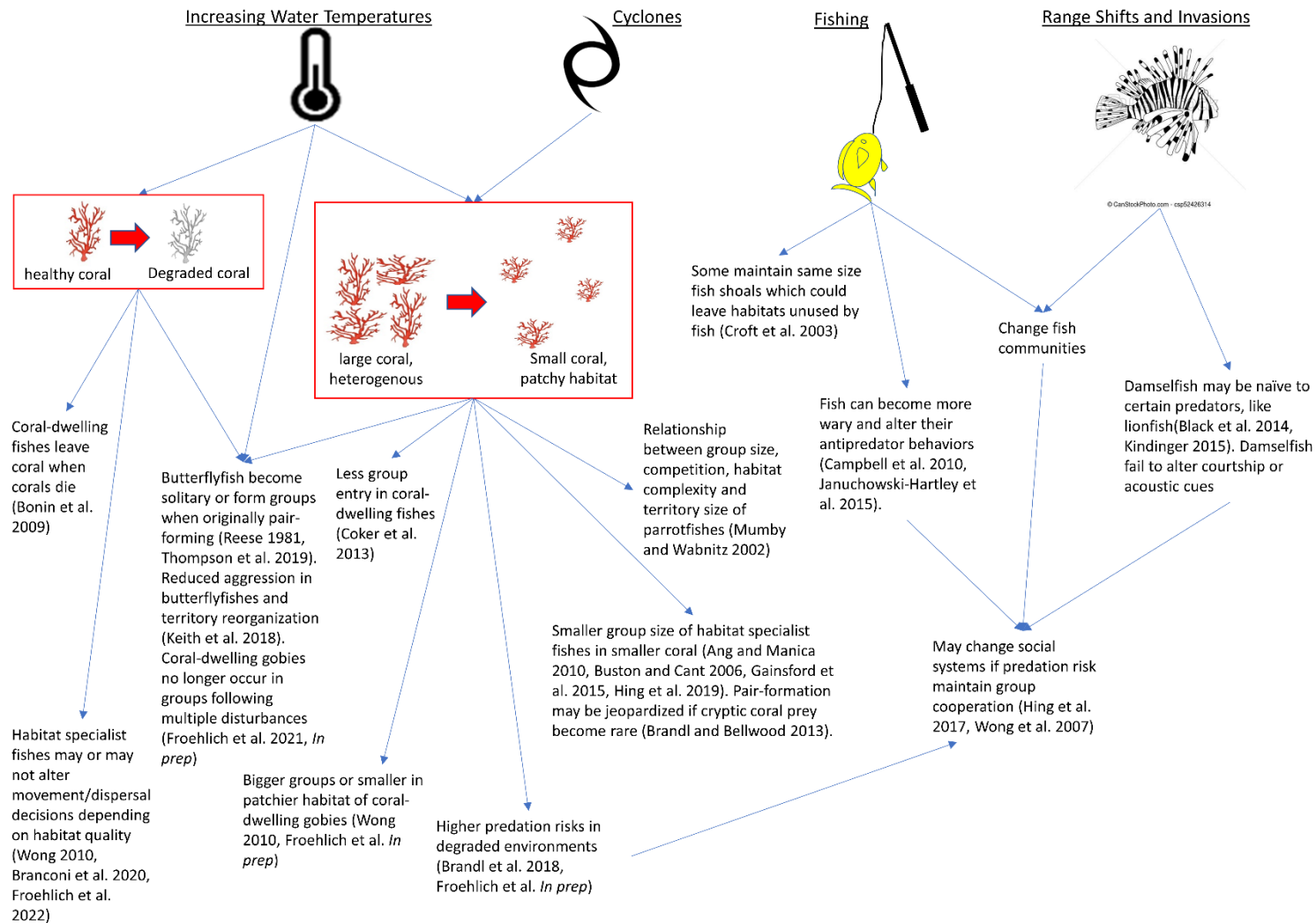
2.2.1. Habitat Alterations: Climatic Activity, Erosion & Crown-of-Thorn Starfish

Fish are often dependent on live substrate like corals and anemones for shelter, foraging, and other resources, and living in groups provides the opportunity to reduce competition for this limiting resource (Jones & Syms 1998; He *et al.* 2019; Thompson *et al.* 2019; Rueger *et al.* 2021a). Yet live reef substrate is being degraded by several environmental stressors, and such changes are altering the benefits of sociality. Widespread and frequent climatic events are reducing the number and size of large coral, reducing coral recruitment, and making recovery at minimum a decade-long process (Kayanne *et al.* 2002; Gilmour *et al.* 2013; Hughes *et al.* 2019a). Reef erosion and nutrient runoff increase coral degradation and sedimentation (Hallock & Schlager 1986; McCulloch *et al.* 2003). Nutrient runoff and ocean acidification intensifies outbreaks of COTS, which predate excessively on corals and devastate large areas in the Indo-Pacific (Brodie *et al.* 2005; Babcock *et al.* 2016; Kamya *et al.* 2017; Pratchett *et al.* 2017a). Together, these disturbances reduce available habitat, complexity of coral reefs, and live coral cover. As coral habitats are altered, fish societies that are dependent on healthy coral cover will face acute stressors, and fish may need to adjust their social behaviours accordingly (Jones & Syms 1998; He *et al.* 2019).

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resources, and living in groups provides the opportunity to reduce competition for this limiting resource (Jones & Syms 1998; He *et al.* 2019; Thompson *et al.* 2019; Rueger *et al.* 2021a). Yet live reef substrate is being degraded by several environmental stressors, and such changes are altering the benefits of sociality. As disturbances transform reefs into patchier habitat, fish can prevent additional group entry (Coker *et al.* 2013). Reduced entry could be a consequence of habitat decline, which could further affect population density and social stability if predation limits dispersal abilities and survival of evicted individuals (Thompson *et al.* 2019), as was previously predicted by Reese (1981). Smaller fish are more heavily predated upon in degraded environments as there is less habitat complexity and fewer hiding spots (Almany 2004; Ahmadi *et al.* 2012; Brandl *et al.* 2018; Froehlich *et al. in prep*). Another explanation is that the social transmission of predator alarm cues are reduced in degraded environments for some damselfish species, as seen in *Pomacentrus amboinensis*, although not for others like *Pomacentrus nagasakiensis* (Chivers *et al.* 2016). Heavily disturbed environments also experience higher rates of sedimentation and decreased habitat complexity, which reduces feeding efficiency (Brandl & Bellwood 2013; Newport *et al.* 2021). For butterflyfishes, surgeonfishes, and rabbitfishes that forage on reef substrate, like corals or algae growing on corals, there is a convergence in snout morphology with pair-formation compared to living solitary or in groups (Brandl & Bellwood 2013). Pair-formation may not be conserved when live and complex substrate becomes scarce, as seen in some butterflyfishes following coral loss (Thompson *et al.* 2019). As reef substrate is continuously disturbed on a large scale, species may no longer benefit from living in groups or pairs if resources limiting sociality become scarce and less complex (He *et al.* 2019; Froehlich *et al. in prep*).

Box 2.1. Studied links between physical disturbances and social systems of coral reef fishes.



Several fishes that depend on live corals and anemones for shelter are known to form complex social systems that are linked to the quality (e.g. size and health) and saturation of their live habitat (Thompson *et al.* 2007; Bonin *et al.* 2009; Coker *et al.* 2013; Nadler *et al.* 2014; Untersteggaber *et al.* 2014; Gainsford *et al.* 2015; Hing *et al.* 2019). However the quality of live substrate is diminishing with continued disturbances (Cheal *et al.* 2017; Hughes *et al.* 2017). For habitat specialist fishes, larger habitat allows the dominant member in size-hierarchy societies to grow larger, which allows more individuals to join the group (Buston & Cant 2006; Ang & Manica 2010b; Gainsford *et al.* 2015) (Box 2.1). When their habitat dies, coral-dwelling fishes will often leave their corals (Bonin *et al.* 2009). If their habitat instead survives but is smaller, groups may simply become smaller if their habitat becomes saturated with individuals beyond the levels for peaceful cooperation (Hing *et al.* 2019). Alternatively, smaller and patchier habitat could increase the need for individuals to live in groups as less viable habitat exists (Wong 2010) (Box 2.1). Patchier habitat may also increase group size because corals may be bigger in general in patchier habitat than continuous habitat (Nadler *et al.* 2014). Individuals may alter their movement decisions to disperse or remain philopatric depending on habitat characteristics (Wong 2010; Branconi *et al.* 2020). Alternatively, individuals may prefer familiarity of hosts or mates over habitat with high quality and reduced saturation regardless of habitat degradation (Froehlich *et al.* 2022, *in prepb*). Habitat quality can also be linked to behavioural plasticity when habitat becomes saturated, because boldness can be linked to group size (Belgrad & Griffen 2017), but this needs to be tested empirically in reef fishes. In corallivore butterflyfishes, reduced aggression is observed after bleaching because the quality of their coral food is diminished, and behavioural trait changes can then alter territory size and group cohesion (Keith *et al.* 2018). The quality and saturation of coral reef habitat is thus important in maintaining social systems of several reef fishes.

Changes in coral communities can also have profound impacts on behaviour of several fishes due to competition for coral hosts. Increased fitness can be incurred by inhabiting specific coral host species (Holbrook & Schmitt 2002; Pereira & Munday 2016; Khan *et al.* 2017). Competition between individuals for habitat resources may increase as particular hosts degrade, and previously peaceful cooperation may no longer be viable if habitat is limited further (Robertson 1995; Munday 2004a; Wong *et al.* 2007; McCormick *et al.* 2017). For example, mating systems are controlled by the number of hiding spots for damselfish (Fricke 1980), and some habitats may provide better shelter than others. The specific habitat type, even down to the coral species, could change fish group composition due to intraspecific competition (Munday 2001; Hing *et al.* 2019; Froehlich *et al.* *in review*). Some fish, like *Pomacentrus moluccensis* damselfish even change from using a variety of coral species in cooler temperatures, to specializing in one or two coral species only in elevated temperatures (Matis *et al.* 2018). However, corals species vary in their susceptibility to environmental disturbances, including elevated temperature, sedimentation, eutrophication, and also storm damage (Schoffin 1993; Fabricius 2011; Erftemeijer *et al.* 2012; Cheal *et al.* 2017; Hughes *et al.* 2019a; Froehlich *et al.* 2021, *in review*). Since some coral species decline more than others, fish will compete for particular coral host species that provide better resources (Munday 2004b; Froehlich *et al.* *in review*). Bigger groups could potentially provide a stronger competitive front, thus excluding new individuals from entering the groups, but this has yet to be tested

on coral specialists. Alternatively, to remove competitive pressures or adapt to changing coral communities, some fish may simply change their preferred coral hosts and disperse (Munday 2001; Froehlich *et al. in review*). Host plasticity, movement behaviour, and social circumstances could together shed light on adaptability to environmental disturbances, as seen in coral-dwelling gobies (Froehlich *et al. 2022, In review, in prepa, In prepb*). Thus, understanding the link between competition, social systems, and shifts in coral communities may illuminate potential social plasticity in some coral reef fishes.

2.2.2. Population Connectivity, Recruitment & Movement

Population connectivity and movement capabilities of coral reef fishes are important to understand potential resilience of reef fishes and the plasticity of social systems (Jones *et al. 2009*). Without gene flow between reefs, populations may suffer from bottleneck effects that become more acute after habitat alterations (Shearer *et al. 2009*; Chong-Seng *et al. 2014*; Oppen *et al. 2015*), threatening extinction (Hutchings & Reynolds 2004; Jones *et al. 2007*; Mumby & Hastings 2008). Population bottlenecks could be further increased if reef fishes exhibit limited movement post-settlement (Munday 2004b; Froehlich *et al. in prep*). If strong gene flow exists between large geographic areas and some post-settlement movement is observed, then social structures could also be presumably conserved within a species. Alternatively, separate populations could be using different social strategies to adapt to environmental differences (Schradin *et al. 2018*; Froehlich *et al. in prep, in prepc*). Population connectivity and post-settlement movement can provide important insights into variations of sociality.

Larval dispersal increases connectivity in marine systems, and generally results in unrelated kin-based groups (Saenz-Agudelo *et al. 2012*). Some new recruits can even recognize their parents and prefer to settle away from them (Munday *et al. 2009*). Settling juveniles also prefer to settle away from degraded habitats (Coppock *et al. 2013*), which could result in bottleneck effect and connectivity problems (Box 2.1). There are several examples that counter the generalization that larval dispersal results in a lack of kinship in coral reef fishes (Berumen *et al. 2012*; Selwyn *et al. 2016*). As a result, self-recruitment is observed in *Amphiprion percula* and *Chaetodon vagabundus* (Berumen *et al. 2012*), and may lead to potential relatedness of individuals within groups. For example, siblings of the marine goby *Coryphopterus personatus* settle together, producing a chaotic genetic patchiness in a small area (Selwyn *et al. 2016*). One potential explanation for cohort settlement and self-recruitment is that parental care increases larvae size and development before larval dispersal (Selwyn *et al. 2016*). The size advantage may allow larvae to hover together over their natal reef once they enter the planktonic stage (Selwyn *et al. 2016*). Population connectivity and recruitment patterns could then play a role in social mechanisms, especially if relatedness is more prevalent than expected.

Population connectivity studies have been vital in the installation of marine reserves across the globe (Martínez *et al. 2019*), yet temporary aggregations and territory sizes of adult reef fishes can also provide important insights for area protection (Erisman *et al. 2017*). Social behaviours are crucial to understand movement patterns of adults because temporary aggregations and territory size are important for mating success in reef fishes (Fox *et al. 2015*). Protected areas increase densities of both exploited and non-

exploited species, and these benefits vary depending on ontogeny and the social behaviour of fishes—like solitary individuals, facultative schoolers, or obligate schoolers (Claudet *et al.* 2010). Some fish alter their social behaviour and territory size with age, from group spawning in large home ranges to harem-forming in small home ranges (Afonso *et al.* 2008). For several parrotfishes, territory size is related to group size, competition and habitat complexity (Mumby & Wabnitz 2002) (Box 2.1). For rabbitfishes, social systems may change during spawning season, and marine reserves may not be able to account for the temporary migrations that are important for mating aggregations (Fox *et al.* 2015). For example, *Siganus doliatus*, a coral reef rabbitfish, associates in monogamous pairs throughout the year, except during large migrations to aggregations around the moon cycle (Fox *et al.* 2015). These short-term and long-distance movements suggest mating only occurs in temporary aggregations, whereas monogamous pairing is instead a strategy for vigilance and foraging success (Fox *et al.* 2015). Temporary associations in large groups are observed across many coral reef fishes for spawning, and these associations call for the improvement of protected areas to encompass short-term spawning habitats (Erisman *et al.* 2017). The causes for social systems and the length of social associations need to be identified for the proper allocations of space for protection (Afonso *et al.* 2008; Fox *et al.* 2015). Protected areas can provide important recovery zones for coral reef fishes (Planes *et al.* 2009), but the social behaviour of reef fishes need to be included in the planning of marine protected areas (Green *et al.* 2015).

2.2.3. Changes in Fish Communities: Fishing, Range Shifts, & Invasions

Anthropogenic changes to coral habitat are altering fish communities and societies. Fishing, range shifts, and invasions change the community composition of reef fishes on many levels (Koslow *et al.* 1988; Wilson *et al.* 2010; Hixon *et al.* 2016; Pecl *et al.* 2017). Each change can impacts social behaviour of fish by altering the benefits and costs of sociality, such as perceived risks of predation and resource limitations (Hing *et al.* 2017; Hodge *et al.* 2018). In turn, functional niches can be affected by shifts in sociality, which can impede important mechanisms for ecosystem functioning, e.g. trophic cascades or maintenance of foundation species (Brandl & Bellwood 2014b; Pecl *et al.* 2017). Shifts in fish communities thus can jeopardize the maintenance of animal societies, which could lead to additional stressors on ecosystem health.

Fishing can have species-specific consequences or more widespread effects that destabilize whole ecosystems and fish societies (Wilson *et al.* 2010; Neuheimer & Grønkjær 2012; Hixon *et al.* 2014; Slade & Kalangahe 2015). Aside from habitat destruction and loss of auditory functioning that are linked to dynamite fishing (Slade & Kalangahe 2015; Pacini *et al.* 2016), behaviour of fish is susceptible to increased fishing threats. Fishermen exploit the social behaviour of fish (like schooling or spawning aggregations) to increase their fishing output just like predators, and can devastate populations rapidly, especially since fish are often naïve to fishing pressure (Parrish 1999; Frisch *et al.* 2019). Fishing reduces densities of populations and could alter group size of schools, but some species still maintain similarly-sized shoals (Croft *et al.* 2003) (Box 2.1). By maintaining group size, less habitat may be exploited, resulting in changes in other ecosystem aspects (Croft *et al.* 2003). In contrast, some fish have learned to alter their movement patterns to reduce fishing risk (Januchowski-Hartley *et al.* 2015; Alós *et al.* 2016),

which could alter their antipredator behaviours (Campbell *et al.* 2010; Januchowski-Hartley *et al.* 2015) (Box 2.1). As a result, higher mortality could occur, and may potentially affect group size if predation risk is an ecological constraint for group living (Heg *et al.* 2004; Hing *et al.* 2017). Increased wariness can then as a consequence change community composition and reduce coral reef ecosystem functioning as predation responses are affected (Januchowski-Hartley *et al.* 2015). As fish become exploited by heavy fishing pressure, community composition may change, and some fish may alter their shoaling behaviours while others remain socially inflexible.

Several fish are changing their range and moving to cooler waters as the sea temperature is rising, and these shifts can change local fish communities and shoaling behaviours (Feary *et al.* 2014; Booth *et al.* 2018; Day *et al.* 2018). Range shifts and invasions have very similar effects in that endemic species are often naïve to these intruders (Feary *et al.* 2014). Competition for resources and predation risks are important threats that are introduced as non-endemic species increase their range (Smith *et al.* 2016). Not only does the community composition change due to these threats (Day *et al.* 2018), but the social behaviour of fishes is based on the risk of predation and the availability of resources (Hing *et al.* 2017) (Box 2.1). As competition and predation increase, several fish may need to adapt their behaviour to avoid local or even broadscale extinctions (Schradin *et al.* 2018). In some areas, vagrants and natives develop mixed shoals (Smith *et al.* 2018), which could affect the social organisation within shoals (Krause *et al.* 2000). Mixed-species shoals develop if conspecific densities are low, but this has yet to be studied in response to environmental drivers (Paijmans *et al.* 2019). As several fishes continue to alter their range and invasions increase in response to anthropogenic disturbances, other reef fishes may need to adapt to these stressors in order to persist in these ecosystems.

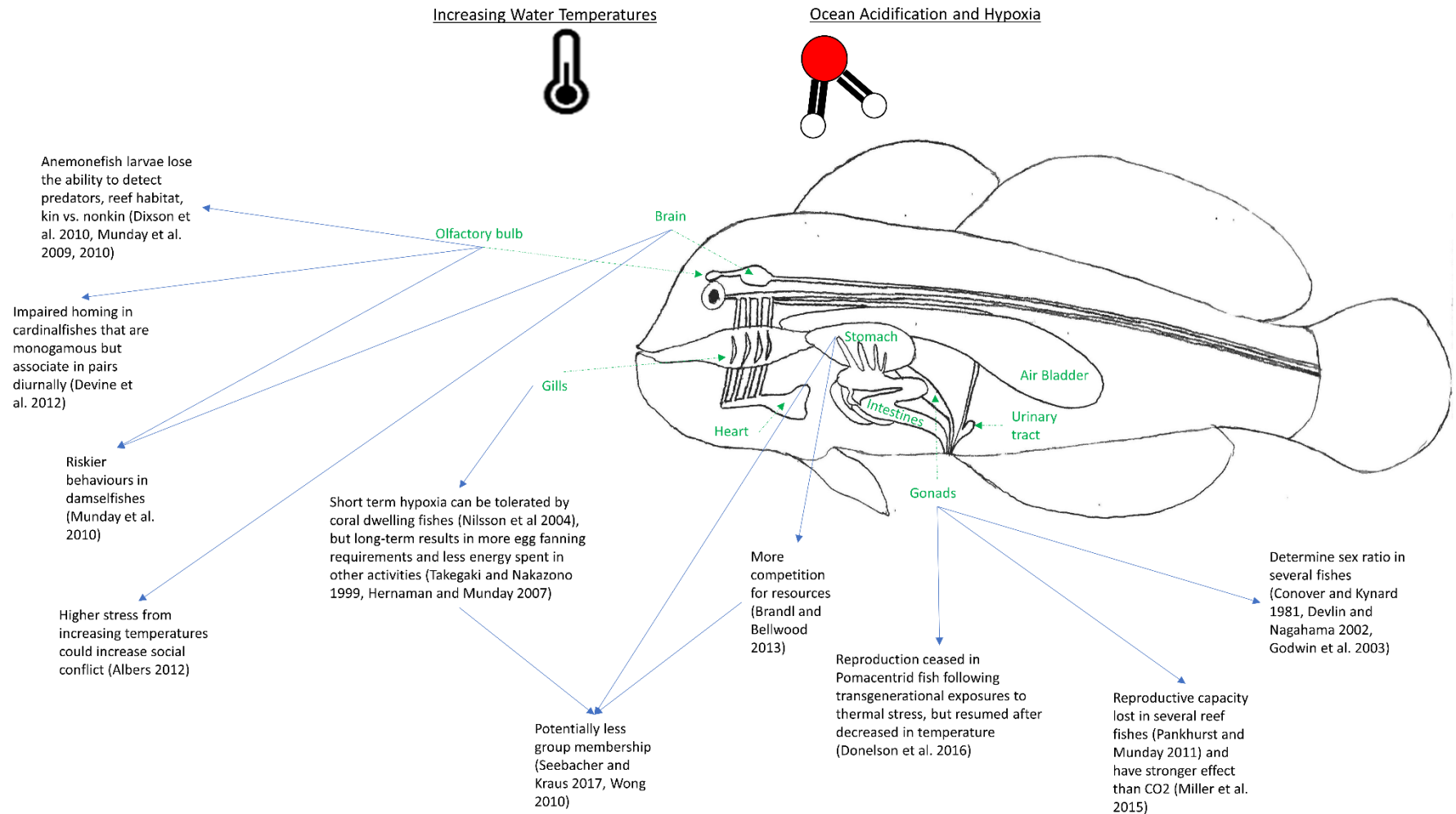
One of the most successful invasions in coral reef ecosystems is the introduction of lionfish to the Caribbean, which is drastically changing the composition of endemic fishes (Hixon *et al.* 2016). Lionfish have recently also reached the Mediterranean Sea (Kletou *et al.* 2016). Prey naivete is high when such successful invasive predators are introduced into a system, resulting often in heightened mortalities and possible local extirpation (Rocha *et al.* 2015; Ingeman 2016). Damselfishes in the Caribbean are common prey of the invasive lionfish, yet damselfish fail to alter their courtship or acoustic behaviours to lionfish presence (Black *et al.* 2014; Kindinger 2015) (Box 2.1). Damselfish may be unable to alter their mating behaviour, because damselfish may be unable to detect the scent and visual cues of invasive lionfish. However, where lionfish are native (i.e. Indo-Pacific coral reefs), experienced coral reef fish, such as coral gobies, are threat sensitive and alter their behaviour accordingly (Marsh-Hunkin *et al.* 2013). The successful invasion of lionfish into the Caribbean and Mediterranean, coupled with their broad salinity tolerance (Jud *et al.* 2015) make them a threat to many reef systems because native reef fish are unable to detect lionfish and alter their cues and social behaviours.

2.3. Disturbances & Fish Physiology: Effects on Sociality

Direct effects of temperature and hypoxia on sociality have yet to be studied extensively in coral reef

fishes. However studies on freshwater brown trout and danio (zebrafish) fish found a loss in group formations as temperatures increased, reducing group cohesion and possible survival (Bartolini *et al.* 2015; Colchen *et al.* 2017). Further research is needed to disentangle possible changes to social organisation of coral reef fishes from a physiological perspective of climate change. In an excellent review of the effects of climate change on sensory pathways, Rivest *et al.* (2019) highlights the vulnerability of cue signal reception and transmission, and the consequences to social communication. Studies have already touched upon physiological effects of abiotic stressors like ocean acidification, hypoxia, and increasing temperatures, and several of these effects suggest indirect changes to sociality of coral reef fishes (Sale 2002; Nilsson *et al.* 2004; Munday *et al.* 2009; Donelson *et al.* 2016). Accordingly, environmental stressors and potential links to sociality are discussed below with a focus on (1) physiological costs to the olfactory organ, (2) energy costs and stress changes, and (3) reproduction and sex change consequences (Box 2.2).

Box 2.2. Studied links between environmental stressors, physiological changes, and social systems of coral reef fishes. Note: organs are not drawn to scale.



2.3.1. Physiological Costs to the Olfactory Organ

Physiological consequences to the olfactory sensory system have the potential to affect survival and important social interactions of coral reef fishes (Box 2.2). The olfactory organ is responsible for many pivotal processes in marine fishes, and it is one of the first sensory organs to become fully developed (Treloar *et al.* 2010). Olfactory organs play an important role in not only communication, predator detection, and homing, but also settlement, host recognition and imprinting (Arvedlund & Nielsen 1996; Wright *et al.* 2005; Treloar *et al.* 2010; Paris *et al.* 2013; Roux & Lecchini 2015). The recognition of olfactory cues is key for the social communication for coral reef fishes (Sale 2002). As an example for habitat-specialist fishes, it is important for social individuals to differentiate between vacant coral hosts and corals occupied with conspecifics, and to differentiate between kin and the sex of conspecifics (Sweatman 1983, 1988; Dixon & Jones 2018). Olfactory cues are important for linking these complicated mechanisms since the ocean provides a medium for effective chemical transport (Munday *et al.* 2009; Dixon *et al.* 2010; Dixon & Hay 2012; Roux & Lecchini 2015). Unfortunately, many studies have found impairments to the functioning of this sensory organ in relation to ocean acidification and increasing temperatures, and these impairments could affect social communication and stability (e.g. Sale 2002; Nilsson *et al.* 2004; Munday *et al.* 2009; Donelson *et al.* 2016).

The inhibition of the olfactory sensory organ affects all ontogenetic phases in fish, and is particularly problematic for larval settlement and kinship (Munday *et al.* 2009; Dixon *et al.* 2010; Devine *et al.* 2012). In high CO₂ conditions induced by reducing pH levels, larvae lose the ability to chemically sense predators, differentiate between parent and non-parent, and detect natal reef habitat (Munday *et al.* 2009; Dixon *et al.* 2010) (Box 2.2). There is some disagreement on the extent that ocean acidification affects chemical cues of fish (Clark *et al.* 2020; Munday *et al.* 2020; Clements *et al.* 2022), yet potential ramifications of chemical cue break down are vast. Replenishment of reef fish larvae is also diminishing due to riskier behaviour of fish when exposed to acidification (Munday *et al.* 2010) (Box 2.2). The mode of impairment is important to further understand how ocean acidification can lead to changes in behaviour. Interestingly, physical changes to the morphology of the olfactory organs are not observed, which suggests possible interruptions to the chemosensory signaling pathways instead of growth defects in the organ compartments themselves (Munday *et al.* 2009). For species that live in groups of non-kin assemblages, such impairments can have dire costs to their social systems as individuals lose the ability to differentiate between kin and non-kin and may allow for more inbreeding (Munday *et al.* 2009). Olfactory impairment also reduces the ability to detect livable habitat (Munday *et al.* 2009), which may lead to catastrophic drops in recruitment and the formation of social groups if larval settlement is unsuccessful.

Adult fish experience similar physiological impairments to their olfactory systems due to ocean acidification, which could lead to changes in preferred habitat, threat sensitivity, and homing. Coral-dwelling fishes have a harder time finding their preferred habitat when exposed to elevated CO₂ (Devine & Munday 2013). This could lead to potential changes in species distributions, reduced growth (as preferred habitat tends to increase growth rates), and even survival (Munday 2004b; Devine & Munday 2013). Changes in growth rates could lead to pronounced changes in sociality, especially for those species

that live in size hierarchies (Buston & Cant 2006; Wong & Buston 2013; Hing *et al.* 2017). Alternatively, in fish taxa where larger species tend to live in smaller groups due to habitat limitations, if they experience slower growth then they may live in larger groups (Hing *et al.* 2019). Predator sensitivity could also be impaired, and individuals may instead disperse, thus reducing group size and further exposing individuals to higher mortality rates (Heg *et al.* 2004; Hing *et al.* 2017). On the other hand, fish may stay philopatric, but may lack threat sensitivity and no longer defend their territory, thus potentially exposing all members (including eggs) to heightened predation (Heg *et al.* 2004). Homing can also be impaired in adult cardinalfishes by ocean acidification (Devine *et al.* 2012) (Box 2.2). Cardinalfishes associate in pairs within aggregations (Gardiner & Jones 2010; Rueger *et al.* 2018), and they exhibit large diurnal movements on a daily basis (Devine *et al.* 2012; Rueger *et al.* 2014). As homing becomes impaired in temporary movers, they will be unable to associate into their stable aggregations and could have reduced spawning success (Afonso *et al.* 2008). Thus, similar to the effects of impairment in larval olfactory systems, adults face physiological consequences of ocean acidification that could interrupt key processes for sociality.

2.3.2. Energy Costs & Stress Changes

Warming sea temperature, ocean acidification and oxygen depletion are increasing the energy costs of fish (Qin *et al.* 2018), and may affect the costs associated with sociality. Interestingly, some fish with swim bladders can actually survive in hypoxic or air-exposed environments for a few hours at a time (Nilsson *et al.* 2004). Short-term hypoxic tolerance may exist due to fish either recycling retained water droplets across gills or breathing through the skin (Nilsson *et al.* 2004). However, prolonged exposures to hypoxic environment can have huge consequences on the metabolism and stress hormones of fishes (Box 2.2). Plausible links are discussed below between energy costs and stress hormone changes from environmental disturbances and sociality consequences. Further studies need to corroborate these links as few studies have directly addressed whether environmental disturbances change social behaviour of coral reef fishes by changing their stress and energy costs.

Environmental disturbances may alter metabolic costs and may impact foraging, which are linked to the sociality of fishes (Johansen & Jones 2011; Killen *et al.* 2021). Due to the poikilothermic nature of fish, increasing temperatures will increase metabolic rates, which lead to additional food intake requirements (Qin *et al.* 2018). For example, as cryptic food is a limiting resource for the sociality of several families of biting reef fishes, group sizes may change as higher metabolic rates alter competition (Brandl & Bellwood 2013). Some individuals may become less active for energy conservation while others may become more active to increase foraging or seek better habitat (Seebacher & Krause 2017). Reduced group membership and social associations could result as individuals are required to move further for foraging success (Seebacher & Krause 2017) (Box 2.2). For example, social behaviour within shoals may be altered from changes in energy requirements, which could alter behavioural cohesion (Killen *et al.* 2017). Alternatively, bigger groups may be necessary for predator vigilance as shoaling species need to cover more distances for foraging (Brandl & Bellwood 2013). The extent of group-living may thus be altered when foraging behaviour changes as a response to changing metabolism.

Higher metabolic rates may also result in added aggression in size-hierarchical societies, especially if food resources become limited (Buston & Cant 2006; Buston & Wong 2014). Alternatively, there may only be changes to the growth of individuals from ocean acidification due to poorer body condition into the future without affecting how individuals cooperate for those in size-based hierarchies (McMahon *et al.* 2019). Smaller groups could be a consequence if metabolic changes limit growth potential, as the size of dominant individuals is linked to group size for some habitat specialist fishes (Fautin 1992; Elliott & Mariscal 2001; Buston 2003b; Wong 2011; Chausson *et al.* 2018; Barbasch *et al.* 2020; Rueger *et al.* 2021a), although not for all (Froehlich *et al. in prep*). Thus, food requirements will play important roles in the maintenance of sociality for fishes, and environmental disturbances may threaten this important balance.

Offspring care requirements may also change due to hypoxia, which could affect group membership. As hypoxia increases, parents may be required to fan their eggs more, which would make parental care more costly, as seen in *Valenciennea longipinnis* gobies (Takegaki & Nakazono 1999). Although parental care does not include feeding and other practices usually observed in terrestrial animals, egg fanning is key for hatching success for many marine organisms (Hernaman & Munday 2007). With increasing fanning demands, parents and group members will be required to spend extra energy away from other activities that are crucial to their own survival for the proper development of eggs (Hernaman & Munday 2007). Energy costs of egg fanning from hypoxia could result in loss of group membership as the requirements for brood care begin to outweigh the benefits of philopatry (Wong 2010).

Environmental disturbances may also increase the stress hormone levels, which may alter sociality further (Qin *et al.* 2018). There is some plasticity in endocrine and neuroendocrine mechanisms, which could play important roles in the aggression-sociality continuum (Kelly & Vitousek 2017). Since group-living species have important networks between individuals within a group (Seebacher & Krause 2017), changes in stress and emotions could lead to network and group fissions. Higher stress that leads to more aggression may especially threaten societies in which peaceful cooperation is integral to group maintenance (Wong *et al.* 2007). In societies where aggressive traits increase with individual dominance in groups, increasing social conflicts may result in smaller groups, as seen in freshwater rainbowfish (Colléter & Brown 2011). Higher stress could elicit aggression changes, which could affect social behaviours (Albers 2012; Matthews & Wong 2015) (Box 2.2). These changes in emotional levels could be indicators of changes to social structures for many fish as temperature threatens coral reef ecosystems. Living in groups can also have a ‘calming effect’ on the metabolism as stress levels are reduced (Parker Jr. 1973; Trune & Slobodchikoff 1976; Martin *et al.* 1980; Nadler *et al.* 2016a), yet environmental disturbances may cause social isolation (Lassig 1983; Yoon *et al.* 2011; Froehlich *et al. in prep*). Such isolation could change the body condition and metabolism of isolated individuals, and ocean acidification may heighten these responses (Nadler *et al.* 2016a, b). Thus, there are direct and indirect links between stress hormones and sociality from environmental disturbances.

2.3.3. Reproduction & Sex Change Consequences

There are many reproductive benefits to group living (Hing *et al.* 2017), yet increasing temperatures and ocean acidification may hinder the continued mating benefits of group living in marine fishes. In a laboratory study, *Acanthochromis polyacanthus* damselfish cease reproduction following transgenerational exposures to high temperatures (Donelson *et al.* 2016). However, if temperature is reduced for these exposed individuals, reproduction resumes (Donelson *et al.* 2016) (Box 2.2). Loss in reproductive capacity is observed in several other fishes following warming (Pankhurst & Munday 2011; Biswal *et al.* 2021), and increasing temperatures have stronger effects on reproduction than increasing CO₂ (Miller *et al.* 2015) (Box 2.2). As temperatures continue to increase, reproduction itself may no longer be a beneficial effect of group living, and individuals may choose to disperse from groups in order to seek cooler waters. Alternatively, sociality may be so strong in some species that fish may stay in groups even in higher temperatures, as demonstrated by temperate three-spine sticklebacks (Cooper *et al.* 2018). There is however some potential for temperature adaptation when investigating gene expression, as seen in a common coral reef spiny chromis damselfish (Veilleux *et al.* 2018). If in fact coral reef fish exhibit inflexibility in sociality, then reproduction may decrease, and fishes could become heavily threatened as water temperatures increase.

Tolls on reproductive capacity, along with other related life history and environmental factors, could destabilize reef fish populations at an unprecedented level as temperatures increase. For several species, delayed senescence and maturity are a consequence of living in fish societies (Buston & García 2007), as has also been confirmed in insect societies (Keller & Genoud 1997). Delayed maturity and longer life often develop due to low mortality rates in groups (Keller & Genoud 1997). Fecundity also increases with age since many fish grow indefinitely (Keller & Genoud 1997; Hixon *et al.* 2014). In several coral reef societies, suppression of maturity can be important to group cohesion, which delays reproductive output (Jones 1987). Since group living reduces mortality rates, increases fecundity, and parental care, extreme life spans can increase species success (Keller & Genoud 1997). However, environmental changes can affect growth, reproduction, and predation (Dixson *et al.* 2010; Pankhurst & Munday 2011; Donelson *et al.* 2016; Qin *et al.* 2018; Spinks *et al.* 2022), and societies may collapse entirely. More individuals may die before maturity is even reached, and only species that have a short life cycle and early maturation may survive (Brandl *et al.* 2018). Similarly, for shoaling fishes, growth, deteriorating body condition and earlier maturation may result from a combination of increasing temperatures and heavy fishing pressure (Neuheimer & Grønkjær 2012; Pratchett *et al.* 2017b). As age-dependent fecundity is important for several exploited species (Hixon *et al.* 2014), reduced gamete production and recruitment could shrink groups even further. Thus, reproductive success is being threatened in many social species due to increasing temperatures and other environmental stressors.

Temperature can alter the sex of some fishes (Ospina-Álvarez & Piferrer 2008), which may affect reef fish societies that are dependent on sex allocation patterns (Godwin *et al.* 2003). Although sex determination and sex change can be controlled through social context (Godwin *et al.* 2003; Hobbs *et al.* 2004), temperature determines sex in several marine fishes (Conover & Kynard 1981; Devlin &

Nagahama 2002; Godwin *et al.* 2003) (Box 2.2). An increase in temperature will accordingly change sex ratios, which could have profound impacts on reproductive success of fish societies (Conover & Kynard 1981; Devlin & Nagahama 2002; Godwin *et al.* 2003). Sex change is known to occur from changing stress hormone levels for some species (Goikoetxea *et al.* 2017; Todd *et al.* 2019). Fish may have to adapt their social organisations according to sex ratios, which could be especially relevant in societies where one sex dominates others. However, in bidirectional sex-changing species (e.g. *Gobiodon* gobies), sex ratios may not play a critical role in their social structure (Kappus & Fong 2014), as long as temperature does not impact their sex-changing abilities (Spinks *et al.* 2022). Additionally, there is some evidence that parents can alter the sex of their offspring to mitigate effects of climate change (Donelson & Munday 2015). Thus, sex changes could result from increasing temperatures in some reef fishes, and sex ratios may or may not affect social organisations depending on reproductive characteristics and adaptability of different coral reef fishes.

2.4. Conclusion and future recommendations

Environmental disturbances change the reefscape, water temperature, chemistry, and faunal communities in coral reef systems (Brodie *et al.* 2005; Munday *et al.* 2008; Slade & Kalangahe 2015; Day *et al.* 2018; Hing *et al.* 2018). Several of these effects alter the behaviour and physiology of fishes. Remarkably few studies have investigated direct links between environmental disturbances and the sociality of coral reef fishes (Coker *et al.* 2013; Hing *et al.* 2019; Thompson *et al.* 2019; Froehlich *et al. in prep*). Some of the problems with investigating these links are that we have yet to identify why several reef fish species evolved social living (Hing *et al.* 2017). For example, pair-forming in rabbitfishes was thought to be a mechanism of reproduction, but observations of large-scale migrations to form short-term aggregations have questioned this mechanism (Fox *et al.* 2015). Some potential causes of social evolution were discovered when observational studies found changes in social structures of butterflyfishes and coral-dwelling gobies with relation to environmental stressors like climatic disturbances (Hing *et al.* 2019; Thompson *et al.* 2019; Froehlich *et al. in prep*). However, fish societies are diverse and have yet to be well understood. A critical step forward has been the introduction of a framework to assess the effects of ecological factors, like habitat characteristics and environmental disturbances, on multiple levels of variation within sociality (Froehlich *et al. in prep*). With the implementation of the framework, we can then identify what level of variation within sociality is most vulnerable to environmental disturbances in order to inform future conservation efforts.

This literature review has highlighted several potential avenues that could indicate changes in social systems from disturbances, but several need to be studied further. Most avenues discussed have been elucidated by indirectly linking studies related to impacts of disturbances on local reef and habitat condition and impacts on the physiology of fish with relation to their sociality. Additional work is needed to directly assess the impacts of environmental disturbances on sociality via these different avenues. It would be particularly interesting to know whether sociality is conserved within a species at different locations and whether it is linked to genetic signaling. For example, population connectivity studies could

be coupled with social behaviour in order to understand the extent of sociality geographically. The degree that a species exhibits social plasticity will be an indicator of its resilience in these challenging environments (Schradin *et al.* 2018). Accordingly, links between social information, population dynamics, and community responses will provide evidence that sociality can predict ecosystem resilience (Gil *et al.* 2018). Thus, studying how social systems of coral reef fishes respond to environmental stressors will provide a better understanding of the recovery potential of reef ecosystems.

Chapter 3: Data Chapter: Uneven declines between corals and cryptobenthic fish symbionts from multiple disturbances

Published in Scientific Reports.

3.1. Abstract

With the onset and increasing frequency of multiple disturbances, the recovery potential of critical ecosystem-building species and their mutual symbionts is threatened. Similar effects to both hosts and their symbionts following disturbances have been assumed. However, we report unequal declines between hosts and symbionts throughout multiple climate-driven disturbances in reef-building *Acropora* corals and cryptobenthic coral-dwelling *Gobiodon* gobies. Communities were surveyed before and after consecutive cyclones (2014, 2015) and heatwaves (2016, 2017). After cyclones, coral diameter and goby group size (i.e., the number of gobies within each coral) decreased similarly by 28-30%. After heatwave-induced bleaching, coral diameter decreased substantially (47%) and gobies mostly inhabited corals singly. Despite several coral species persisting after bleaching, all goby species declined, leaving 78% of corals uninhabited. These findings suggest that gobies, which are important mutual symbionts for corals, are unable to cope with consecutive disturbances. This disproportionate decline could lead to ecosystem-level disruptions through loss of key symbiont services to corals.

3.2. Introduction

Multiple disturbances over short periods can disrupt important ecological processes and threaten the persistence of ecosystems (Turner 2010; Hughes *et al.* 2018b). From species survival to population bottlenecks and trophic disruptions, such consecutive disturbances may transform entire environments (Carson 1990; Turner 2010; Brandl *et al.* 2018; Hughes *et al.* 2018b). The ability for ecosystems to recover depends on the frequency and intensity of multiple events, which are predicted to increase with climate change (Turner 2010; Hughes *et al.* 2018a). Species interactions within complex environments can deteriorate in an accelerated fashion as a result (Turner 2010). Whether organisms persist in the short-term during extreme consecutive disturbances will determine their recovery potential and that of associated organisms (Kiers *et al.* 2010; AghaKouchak *et al.* 2018; Sergio *et al.* 2018). We need to understand whether ecological relationships are resilient to consecutive disturbances in order to better align future strategies for ecosystem conservation (Kiers *et al.* 2010; Denton & Gokhale 2019).

Mutualism occurs in many taxa and may be one such ecological relationship that proves fragile from consecutive disturbances (Kiers *et al.* 2010; Denton & Gokhale 2019). Mutual symbioses are observed in all environments and promote life in otherwise inhospitable areas (Denton & Gokhale 2019). A small shift in environmental conditions may change the nature of such relationships, like mutualism becoming parasitism, or relationships ceasing if one symbiont becomes locally threatened (Kiers *et al.* 2010). Climate-driven disturbances can lead to break downs of mutualisms like those responsible for preventing

seagrass degradation (De Fouw *et al.* 2016), maintaining myrmecophyte-dominated savannahs (Sensenig *et al.* 2017), sustaining coral survival (Baker *et al.* 2018), and promoting microbe-assisted biodiversity (Six *et al.* 2011; Denton & Gokhale 2019). Collapse of mutual symbioses may have flow-on effects by destabilizing habitats and causing deleterious ecosystem consequences (Kiers *et al.* 2010; Six *et al.* 2011). For example, as mutualism breaks down, corals can become more susceptible to stress due to a lack of symbiont services, resulting in fewer corals that provide habitat for other associated species like invertebrates and other fishes, and then these habitats may continue to destabilize as a negative feedback loop exists between reduced coral cover and reduced presence of reef associated species. Studies need to assess the consequences of disturbances on mutual symbioses in order to predict flow-on effects to ecosystems.

Mutually beneficial taxa are especially vulnerable to climate-driven disturbances, but most of the research is primarily focused on an ecosystem's foundation species instead of associated animals, as seen in coral reefs (Cheal *et al.* 2017; Hughes *et al.* 2017, 2018b, 2019a). As the frequency and intensity of storms and heatwaves are increasing, corals are being exposed to disturbances in rapid succession (Cheal *et al.* 2017; Hughes *et al.* 2017, 2019a). Up to 11% of coral reef fishes depend on live corals for survival through food, settlement and shelter (Jones *et al.* 2004; Pratchett *et al.* 2008). In return, coral-associated fishes promote coral resilience by reducing disease, algal growth, and increasing nutrient cycling (Chong-Seng *et al.* 2011; Dixon & Hay 2012; Dirnwoeber & Herler 2013; Chase *et al.* 2018; Pryor *et al.* 2020). However, disturbance studies are largely focused on corals (Cheal *et al.* 2017; Hughes *et al.* 2017, 2019a). If fish symbionts decline disproportionately from climate-driven impacts (Wilson *et al.* 2006), then corals will be exposed to additional threats as there is little functional overlap in coral reefs (Brandl & Bellwood 2014b). Disproportional declines in corals and their mutualistic symbionts may lead to ecosystem shifts (Morais *et al.* 2020) if consecutive disruptions become the norm (Hughes *et al.* 2018a).

Here, we examined the impacts of multiple climate-driven disturbances on the persistence of coral-fish symbioses using the most susceptible reef-building corals (genus *Acropora*) (Estrada-Saldívar *et al.* 2019; Hughes *et al.* 2019a) and their mutually beneficial inhabitants, cryptobenthic coral-dwelling gobies (genus *Gobiodon*) (Dixon & Hay 2012; Dirnwoeber & Herler 2013). In return for shelter, breeding sites and food from corals (Kuwamura *et al.* 1994; Wong & Buston 2013), gobies remove harmful seaweed, deter corallivores, and increase nutrient cycling (Dixon & Hay 2012; Dirnwoeber & Herler 2013; Chase *et al.* 2018) (Fig 3.1A). Gobies are often overlooked in disturbance studies because they are small and time-intensive to survey, yet as cryptobenthic fishes they are critical to the trophic structure of coral reefs (Brandl *et al.* 2018). We surveyed coral and goby communities throughout four consecutive disturbances at Lizard Island, Great Barrier Reef, Australia. Within four years, the reef experienced two cyclones (2014, 2015), and two unprecedented heatwaves that caused widespread bleaching (2016, 2017) (Hughes *et al.* 2019b). Our study quantified the additive impacts of cyclones and heatwaves on the persistence of corals and their goby symbionts over a short space of ecological time.

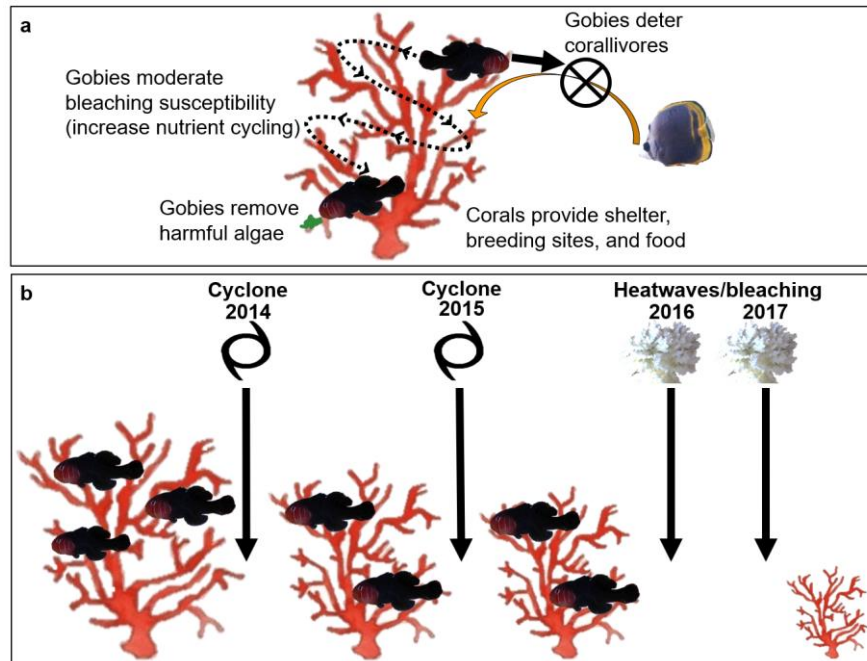


Fig 3.1. Drastic shifts to the mutual symbiosis of corals and cryptobenthic coral-dwelling gobies following multiple disturbances. **a** Benefits that each symbiont receives from the mutual symbiosis (Kuwamura *et al.* 1994; Dixon & Hay 2012; Dirnwoeber & Herler 2013; Wong & Buston 2013; Chase *et al.* 2018). **b** Summary of the findings highlighting changes to corals and gobies from each consecutive disturbance with coral-dwelling gobies from the genus *Gobiodon* in scleractinian corals from the genus *Acropora*. Reductions in coral size are drawn to scale and relative to changes in means among disturbances. Figures were illustrated in Microsoft Office PowerPoint 2016.

3.3. Methods

3.3.1. Study Location and Sampling Effort

The study was completed at Lizard Island, Great Barrier Reef, Queensland, Australia (14° 40.729' S, 145° 26.907' E, Supplementary Fig 3.1). Four climatic events affected Lizard Island from 2014 to 2018. Cyclone Ita hit in April 2014, and Cyclone Nathan hit in March 2015 (Supplementary Fig 3.1). The following year (2016), the first extensive mass-bleaching event spanned March to April, and a second extensive mass-bleaching event spanned February to May 2017. A total of 17 sites were first visited in February 2014 before climatic events. After the first cyclone 10 sites were revisited in January-February 2015, 15 sites in January-February 2016 (after second cyclone), and 17 sites in February-March 2018 (after back-to-back heatwaves).

3.3.2. Survey Method

At each site, goby and coral communities were surveyed visually within 1 m on either side of 30-m line transects by two experienced scuba divers in 2014 (n = 59 transects) and were repeated in 2018 (n = 40).

Transects were completed in 2015 (n = 73) and 2016 (n = 107) using a different method: cross-transects—two 4-m x 1-m belt transects laid in a cross around a focal colony. Not all sites were surveyed during each sampling event due to weather conditions, and cyclones scoured sections of reef to bare rock after their impact. Transects at all sites were completed on the reef flat, crest, and slope and were within 1 to 6-m in depth. In 2018, random searching for up to one hour (in addition to the transects) was also completed in several areas (n = 28 searches) to determine whether goby species that were missing were simply absent from transects or were instead likely locally extirpated from Lizard Island. For all methods, when a live *Acropora* coral was encountered, the coral was identified to nominal species following Veron *et al.* (2018) and measured along three dimensions: width, length, and height (Kuwamura *et al.* 1994). A bright torch light (Bigblue AL1200NP) was shone in the coral to quantify the number of goby residents and the *Gobiodon* species inhabiting each coral. Gobies were delineated either as adults or recruits depending on their coloration and size. The study was performed in accordance with relevant guidelines and regulations, including ARRIVE guidelines, under the University of Wollongong Animal Ethics protocol AE1404 and AE 1725 and under research permits issued by the Great Barrier Reef Marine Park Authority (G13/36197.1 and G15/37533.1).

3.3.3. Data Analysis

Univariate analyses were completed to assess changes in the following variables per transect (as a single sample) throughout disturbances: adult goby species richness, average adult goby group size per coral, percent occupied coral, coral species richness, average coral diameter (the three coral dimensional measurements were averaged to calculate an average diameter)(Kuwamura *et al.* 1994). Goby and coral richness were count data with several zero data points after multiple disturbances. As such, richness variables were each analysed using zero-inflated generalized linear mixed model designs (GLMER: using poisson family) among sampling year (fixed factor) and site (random factor). The following variables were continuous variables and as such were analysed using linear mixed model designs (LMER) amongst the sampling year (fixed) and site (random): average coral diameter, average goby group size, and percent occupied corals. Variables analysed with LMER were transformed as required to meet normality and homoscedasticity, which were determined using Q-Q plots, histograms, and residuals over fitted plots. Tukey's tests were used for differentiating between statistically significant levels within factors. For each univariate analysis, outliers were investigated if their standard residuals fell outside of 2.5 standard deviation from 0 and were subsequently removed. A maximum of 7 outliers were removed for any given analysis. All analyses were completed in R (v3.5.2)(R Core Team 2018) with the following packages: tidyverse (Wickham *et al.* 2019), lme4 (Bates *et al.* 2015), lmerTest (Kuznetsova *et al.* 2017), LMERConvenienceFunctions (Tremblay & Ransijn 2020), piecewiseSEM (Lefcheck 2016), glmmTMB (Brooks *et al.* 2017), emmeans (Lenth *et al.* 2020), DHARMA (Hartig & Lohse 2020), and performance (Lüdtke *et al.* 2021).

Community composition was analysed separately for corals and gobies. To take into account the different survey techniques, samples were standardized to create proportional abundance as follows: for each survey, we divided each count per species by the total abundance of all species. Only adult gobies were

included in the analyses. Communities were analysed with permutational analyses of variance (PERMANOVA). Communities were compared against sampling year (fixed factor) and were controlled for site (random factor) with permutational analyses of variance in PRIMER-E software (v7). Type I error was included because of the unbalanced design with uneven transects per year. Community differences were bootstrapped to a 95% region for a total of 150 bootstraps per year and were visualized on non-metric multidimensional scaling plot. When statistical differences were observed, similarity percentage analyses (SIMPER) were performed to determine what species contributed to the differences observed. Species contributions were cut off to the top 75% of species that contributed the most to differences observed. See supplemental table 3.1 for all statistical outputs of univariate and multivariate analyses.

3.4. Results and Discussion

3.4.1. *Host and mutual symbionts decline at different rates following consecutive cyclones and bleaching*

Before and after disturbances, we surveyed *Acropora* corals known to host *Gobiodon* coral gobies along line (30 m) and cross (two 4 m by 1 m belt) transects. In February 2014, prior to cyclones and bleaching events, most of these *Acropora* corals were inhabited by *Gobiodon gobies*. Gobies were not found in corals under 7-cm average diameter, therefore we only sampled bigger corals. The vast majority of transects (95%) had *Acropora* corals. On average there were 3.24 ± 0.25 (mean \pm standard error) *Acropora* coral species per transect (Fig 3.2A) and a total of 17 species were observed among all 2014 transects. Average coral diameter was 25.4 ± 1.0 cm (Fig 3.2B), with some corals reaching over 100 cm. Only 4.1 ± 1.4 % of corals lacked any goby inhabitants (Fig 3.2C). On average there were 3.37 ± 0.26 species of gobies per transect (Fig 3.2D) and a total of 13 species among all 2014 transects. In each occupied coral there were 2.20 ± 0.14 gobies (Fig 3.2E), with a maximum of 11 individuals of the same species.

In January-February 2015, 9 months after Cyclone Ita (category 4) struck from the north (Supplementary Fig 3.1), follow-up surveys revealed no changes to coral richness ($p = 0.986$, see Supplementary Table 3.1 for all statistical outputs) relative to February 2014, but corals were 19% smaller ($p < 0.001$, Fig 3.2A-B). Cyclonic activity may have damaged existing corals (Madin *et al.* 2018), which might explain smaller corals. Alternatively, corals may have died from cyclonic damage (Madin *et al.* 2018), but previously undetected corals (less than 7-cm average diameter threshold for surveys) may have grown and accounted for finding smaller corals and no changes to species richness. After the cyclone, gobies occupied 76% of live corals, which meant that occupancy dropped by 19% ($p < 0.001$, Fig 3.2C). Goby richness did not change after the first cyclone relative to February 2014 ($p = 0.997$, Fig 3.2D). However, goby group sizes (i.e., the number of gobies within each coral) were 28% smaller ($p < 0.001$), with gobies mostly occurring in pairs, and less so in groups (Fig 3.2E). Smaller groups were likely due to their coral hosts being smaller than before the cyclones as there is an indirect link between group size and coral size (Hing *et al.* 2018).

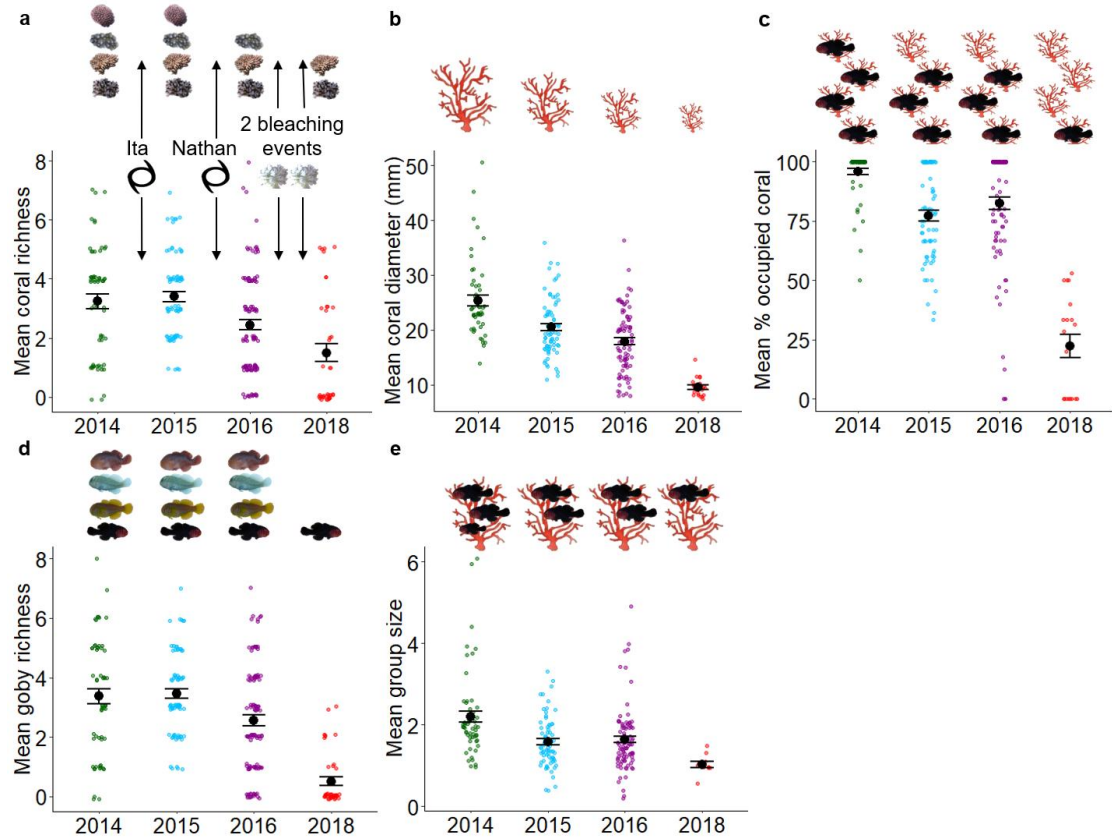


Fig 3.2. Effects of consecutive climate disturbances on coral and goby populations. Changes in *Acropora* **a** richness (n = 279), and **b** average diameter (n = 244), **c** percent goby occupancy (n = 244) and *Gobiodon* **d** richness (n=279), and **e** group size (n = 230) per transect (n = sample size per variable) before and after each cyclone (black cyclone symbols) and after two consecutive heatwaves/bleaching events (white coral symbols) around Lizard Island, Great Barrier Reef, Australia. Error bars are standard error. Fish and coral symbols above each graph illustrate the change in means for each variable among sampling events from post-hoc tests. Figures were illustrated in R (v3.5.2)(R Core Team 2018) and Microsoft Office PowerPoint 2016.

In January-February 2016, 10 months after Cyclone Nathan (category 4) struck from the south (Supplementary Fig 3.1), our follow-up surveys revealed 26% fewer coral species ($p = 0.008$), and 13% smaller corals ($p = 0.029$) relative to February 2015 (Fig 3.2A-B). Many corals were damaged (personal observations), and bigger corals were likely heavily damaged and disproportionately reduced in size. As *Acropora* corals vary in several morphological traits such as branch thickness, such characteristics might alter their susceptibility to cyclonic damage (Scoffin 1993; Madin *et al.* 2018) and likely explain a decrease in coral richness. There was no change to coral occupancy by gobies relative to February 2015 ($p = 0.167$, Fig 3.2C). Goby richness however did not mirror declines to their coral hosts as there was no change relative to February 2015 ($p = 0.060$, Fig 3.2D). Goby group size did not change relative to February 2015 and most individuals occurred only in pairs ($p = 1.000$, Fig 3.2E). Since the second cyclone did not add additional changes to coral occupancy, goby richness or goby group size, gobies may have exhibited some ecological memory (Hughes *et al.* 2019b) from the first cyclone. However, when combining the effects of consecutive cyclones, coral and goby symbioses were disrupted substantially.

Coral hosts were 30% smaller relative to 2014 (pre-disturbances), 25% of hosts were uninhabited compared to only 4% in 2014, and goby group size remained the same as after the first cyclone whereby gobies were no longer living in groups, instead living in pairs (Fig 3.1B). These acute disturbances had effects lasting longer than 10 months and will likely require many years to return to pre-disturbance status (Cheal *et al.* 2017).

Unfortunately, there was no time for recovery from cyclones before two prolonged heatwaves caused widespread bleaching in March-April 2016 and February-May 2017 (Supplementary Fig 3.1). Ten months after the second bleaching event (Jan-Feb 2018), we returned to Lizard Island and rarely found live corals along our transects. Half (50%) of the transects lacked any living *Acropora* corals compared to just 5% of transects before any disturbance (2014). There were 39% fewer coral species ($p = 0.009$) relative to February 2016, with only 1.5 ± 0.31 species per transect (Fig 3.2A). Corals were 47% smaller than in February 2016 ($p < 0.001$, Fig 3.1B&2B), averaging 9.57 ± 0.39 cm coral diameter (maximum 21 cm). Acroporids were also the most susceptible family to bleaching from these back-to-back heatwaves across the Great Barrier Reef and their coral recruitment was at an all-time low (Hughes *et al.* 2018b, 2019a). Since corals were lethally bleached during the prolonged heat stress only a few acroporids species survived these consecutive events (Álvarez-Noriega *et al.* 2018). Such declines and extensive bleaching from the 2015-2016 heatwave were also observed in many areas around the world (Hughes *et al.* 2018a; Majumdar *et al.* 2018).

After consecutive heatwaves, coral gobies faced even more drastic declines than their coral hosts in all our survey variables. Of the few live corals recorded, most ($77.7 \pm 4.8\%$) corals lacked gobies compared to just 4% without gobies pre-disturbance (2014), and 24% after cyclones ($p < 0.001$, Fig 3.2C). For the first time, only after heatwaves, we observed a change in goby richness with 80% fewer goby species per transects relative to February 2016 ($p < 0.001$, Fig 3.2D), even though consecutive cyclones did not affect goby richness. Alarming, goby group size decreased to such an extent that gobies were no longer found in groups ($p = 0.036$), rarely in pairs ($n = 3$), and the few observed occurred singly (Fig 3.2E). For these long-living, monogamous, and nest brooding fishes (Munday 2004a; Wong & Buston 2013), finding gobies predominantly without mates suggests that reproduction likely ceased or was significantly delayed for most individuals in the population (Wong & Buston 2013). An interruption in mate pairing likely led to extremely low recruitment and turnover rates in gobies from climatic disturbances.

Gobies declined substantially more than coral hosts after consecutive heatwaves, leaving most corals uninhabited (Fig 3.1B). Although communities still had not recovered from cyclonic disturbances before prolonged heatwaves, we suspect that heatwaves had more devastating impacts on gobies than cyclones. Gobies have a strong tendency to stay in the same coral they settle in as recruits (Wong 2010) as long as the coral is alive (Bonin *et al.* 2009), yet many may have unsuccessfully attempted to find other corals once their coral was lethally bleached (Brandl *et al.* 2018). Unlike gobies, other coral-dwelling fishes, like damselfish recruits, successfully adopted alternative habitat, including dead corals (Wismer *et al.* 2019). Gobies did not adopt alternative habitat and were surprisingly absent from most living corals.

Importantly, goby richness did not change after consecutive cyclones and only changed after heatwaves. Thus coral host death likely is not the only stressor and gobies may have suffered physiological consequences from prolonged environmental disturbances (Munday *et al.* 2009; Dixon *et al.* 2010; Devine & Munday 2013). Although gobies can survive short exposures of hypoxia (Nilsson *et al.* 2004), extended periods of reduced wind-induced mixing and thermal stress may jeopardize physiological functioning (Donelson *et al.* 2016; Qin *et al.* 2018). Indeed, reef fishes can lose the ability to detect predators, kin, and habitat (Munday *et al.* 2009; Dixon *et al.* 2010; Devine & Munday 2013), and to reproduce from environmental stress (Donelson *et al.* 2016). Gobies likely lost similar functioning from heatwaves leading to high mortality and little goby turnover, which left many healthy corals unoccupied. A lack of mutual goby symbionts following consecutive disturbances suggests that coral hosts may begin experiencing additional threats to their recovery (Dixon & Hay 2012; Dirnwoeber & Herler 2013; Chase *et al.* 2018). Such declines and potential physiological consequences may also hold true for other coral-dwelling organisms, like symbiotic xanthid crabs (McKeon *et al.* 2012). Since acroporid corals are crucial foundation species for coral reef ecosystems, greater declines in their symbionts from multiple disturbances may reduce the persistence of corals and destabilize habitats over large scales.

3.4.2. Communities of goby symbionts exhibit greater changes than communities of coral hosts from multiple disturbances

In February 2014, before the consecutive climatic events, we recorded 17 species of *Acropora* corals known to be host *Gobiodon* coral gobies, with the most common being *A. gemmifera*, *A. valida*, *A. millepora*, *A. loripes*, *A. nasuta*, *A. intermedia*, *A. tenuis*, and *A. cerealis*. Thirteen species of *Gobiodon* gobies were recorded, with the most common being *G. rivulatus*, *G. fuscoruber*, *G. brochus*, *G. histrio*, *G. quinquestrigatus*, and *G. erythropsilus*. Each disturbance changed the assemblages of both corals ($p < 0.001$, Fig 3.3A) and gobies ($p < 0.001$, Fig 3.3B), yet the changes in both corals and gobies did not mirror each other since communities among sampling events did not aggregate similarly (Fig 3.3).

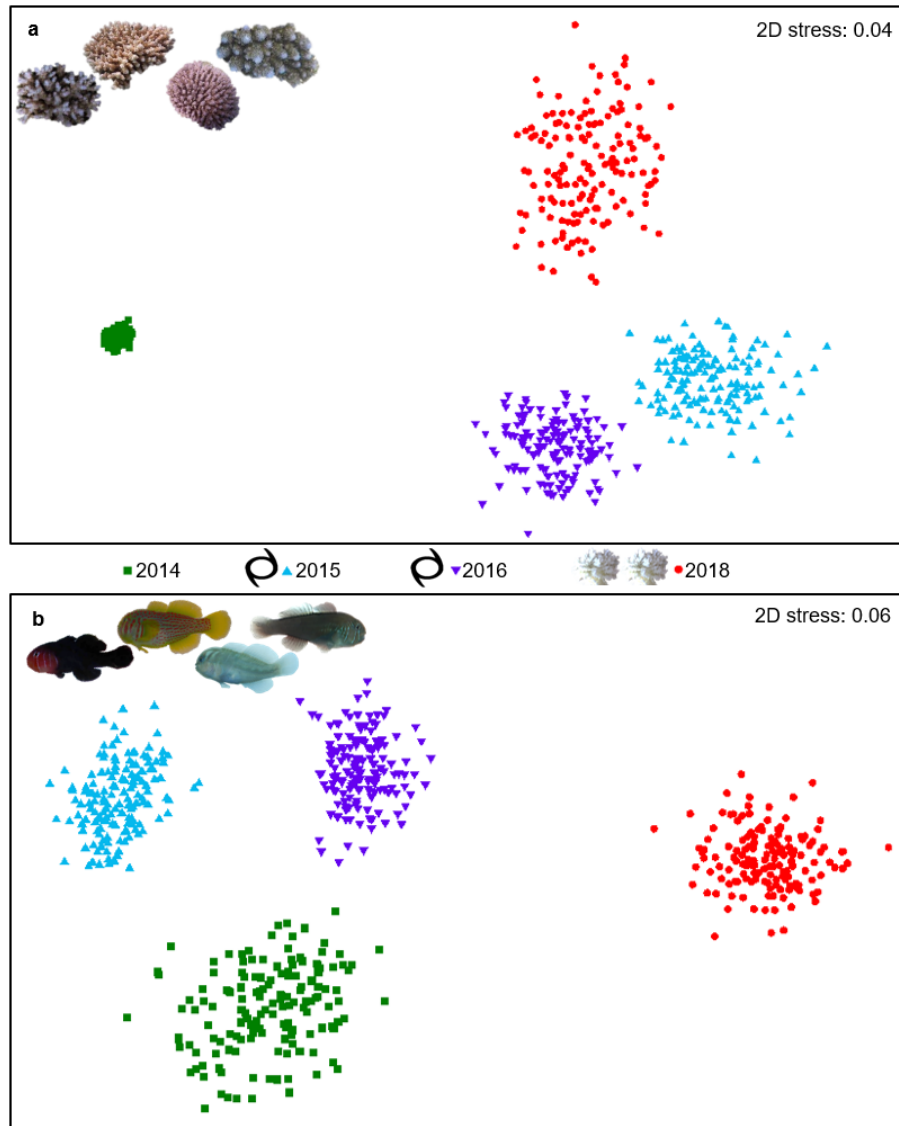


Fig 3.3. Shifts in communities of corals and gobies throughout consecutive climate disturbances. The changes in communities along transects ($n=279$) before and after each cyclone (black cyclone symbols) and after two consecutive heatwaves/bleaching events (white coral symbols) at Lizard Island, Great Barrier Reef, Australia, for **a** *Acropora* corals and **b** *Gobiodon* gobies visualized on non-metric multidimensional scaling plots. Each colored point represents a single transect, black points represent bootstrapped averages (avg), and points closer together are more similar in species composition than points further apart. Figures were illustrated in PRIMER-E software (v7, <https://www.primer-e.com/>) and Microsoft Office PowerPoint 2016.

After the first cyclone, 11 *Acropora* species were found, and the common species increased in proportional abundance relative to February 2014 ($p = 0.009$, Fig 3.3A&3.4A). The previously rare species *A. valida* increased in proportional abundance as well. However, *Acropora intermedia*, which was previously recorded in several transects, was no longer observed; this is likely due to its branches being long and thin, thus highly susceptibility to damage (Madin et al. 2018). Goby assemblages were also altered after the first cyclone ($p = 0.003$, Fig 3.3B), and the proportional abundance of the common

species differed in response relative to 2014 (Fig 3.4B). The proportion of *G. histrio* and *G. rivulatus* in transects increased compared to 2014, and so did the proportion of their preferred hosts, *A. nasuta* and *A. gemmifera*, respectively (Fig 3.4)(Munday et al. 1999). However, the proportion of *G. fuscoruber* decreased even though its common host, *A. millepora* (Munday et al. 1999), was recorded more frequently than several other corals (Fig 3.4). *Gobiodon fuscoruber* is a group-living species, and it is possible that as group size decreased, they were outcompeted for coral hosts by other species (Munday et al. 2001). Two rare gobies were no longer recorded (*G. citrinus* and *G. okinawae*), and both preferred *A. intermedia* (Munday et al. 1999), which also disappeared. Since species of both corals and gobies had mixed responses to the cyclone, there may be some positive effects of an intermediate level of disturbance for those species that increased in proportional abundance, specific to the intermediate disturbance hypothesis (Connell 1978).

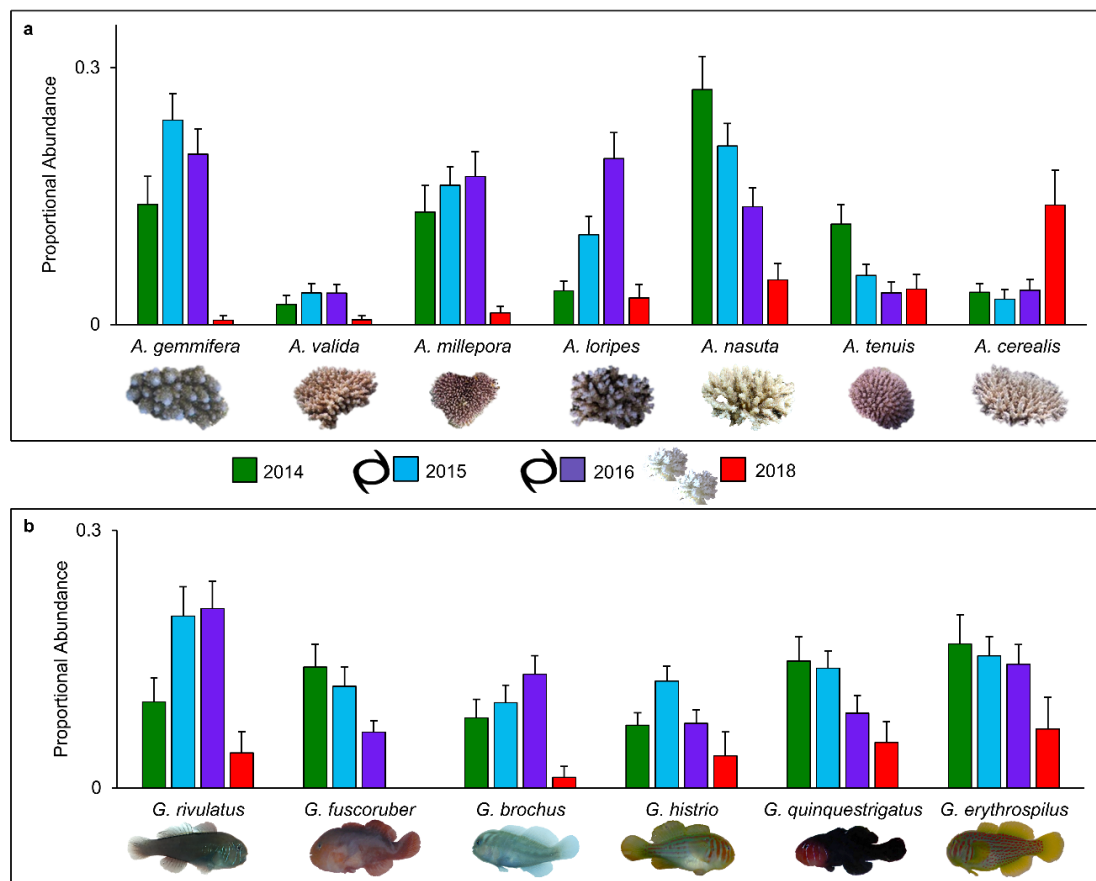


Fig 3.4. Changes in abundance of coral and goby species before and after each consecutive climate disturbances. The proportional abundances for the most common species within each transect (n=279) for **a** *Acropora* corals and **b** *Gobiodon* gobies is shown before and after each disturbance around Lizard Island, Great Barrier Reef, Australia: effect of each cyclone (black cyclone symbols) and combined effect of two consecutive heatwaves/bleaching events (white coral symbols). Proportional abundances were calculated by taking the count per species per transect divided by the total count among all species observed per transect. Visualized here are the proportional abundances pooled per sampling event for the most common species. Figures were illustrated in Microsoft Office PowerPoint 2016.

After the second cyclone, we found mixed results in coral assemblages ($p < 0.001$, Fig 3.3A). Although 15 *Acropora* species were found after the second cyclone (5 more than after the previous cyclone) and no species were locally extirpated, only *A. loripes* became more common (Fig 3.4A). Several of the most common corals (i.e. *A. gemmifera*, *A. nasuta*, *A. tenuis*) decreased in proportional abundance after the second cyclone (Fig 3.4A). Goby communities were altered once again ($p < 0.001$, Fig 3.3B), this time with fewer species increasing in proportional abundance and more species decreasing (Fig 3.4B). However, all *Gobiodon* species were encountered, even *G. citrinus* and *G. okinawae* that originally disappeared after the first cyclone. *Gobiodon brochus* increased in proportional abundance and so did its common host *A. loripes* (Munday et al. 1999). However, *G. rivulatus* increased even though its preferred host *A. gemmifera* decreased (Fig 3.4)(Munday et al. 1999).

After consecutive bleaching events, the reef was left with few corals, most of which were very small in size. Although the coral community after bleaching was distinct from each disturbance sampling event ($p < 0.001$), all disturbed communities aggregated closely together compared to the pre-disturbance community (2014, Fig 3.3A). After bleaching, the most coral species were recorded (22 in total) compared to all other sampling events. Although coral richness per transect was the lowest after bleaching (Fig 3.2A), the coral community as a whole was more diverse and was made up of more coral species. A few *A. intermedia* were again recorded after none were observed following the first cyclone, along with 9 rare and previously unrecorded *Acropora* species. However, some species were no longer observed, e.g. *A. divaricata* (previously rare), *A. granulosa* (previously rare), and *A. humilis* (previously common). Many of the common coral species became rare after bleaching (Fig 3.4A). In coral reefs, *Acropora* are one of the most susceptible coral genera to cyclone damage and bleaching in a warming climate (Madin et al. 2018; Hughes et al. 2019a), which explains such steep declines in many *Acropora* species. Surprisingly, *A. cerealis*, which was previously rare, had since increased in proportional abundance despite multiple disturbances (Fig 3.4A). In other areas though, such as the Andaman Bay, *A. cerealis* was one of the most lethally bleached species (Majumdar et al. 2018). Regional differences in thermal plasticity and coral recruitment may have disproportionately affected the survival thresholds of identical species.

Coral gobies were more dramatically affected by consecutive bleaching than corals. Goby communities after bleaching were the most distinct ($p < 0.001$), while communities from all other sampling events aggregated closer together (Fig 3.3B). Every goby species declined after bleaching (Fig 3.4B), and half of the species were no longer recorded. Some species were locally extirpated, including *G. citrinus* (previously rare), *G. sp. D* (previously rare), *G. bilineatus* (previously common), and *G. fuscioruber* (previously common, Fig 3.4B). None of the locally extirpated species were observed during random searches. Only 6 species remained, and no previously unrecorded species were observed. As expected, gobies were never found in dead corals, as they can only survive in live corals (albeit surviving in stressed corals (Bonin et al. 2009)). These findings highlight the greater impact that multiple disturbances have on symbiont communities, especially when disturbances are a mix of acute (short-term) and prolonged (long-term) events. Although we cannot assess the effects of cyclones compared to heatwaves since they

occurred in succession, we can clearly show that multiple disturbances affect corals and gobies differently. We observed a loss of biodiversity for gobies from multiple disturbances, whereas their coral hosts were more diverse even though fewer corals were recorded, and they were smaller.

The study demonstrates the effects that multiple disturbances have on reef ecosystems down to the level of important mutualisms. Disturbance studies have primarily focused on the disturbance effects to corals (Madin et al. 2018; Hughes et al. 2019a, b), yet cryptobenthic fishes are often overlooked (Brandl et al. 2018). We may be missing effects of disturbances on fishes that could have flow-on effects on the whole ecosystem, especially since cryptic fishes make up a large part of reef biodiversity and are crucial prey for many taxa (Brandl et al. 2018). This study is one of few multi-year studies to record species-level changes in cryptobenthic fishes from multiple consecutive disturbances. Intriguingly, although corals and gobies responded similarly at first to the initial two cyclones, they then diverged in their responses after additional stress from heatwaves. Here we show that gobies declined faster on a community and species level than their coral hosts, which will likely leave corals exposed to algal growth, poor nutrient cycling, and corallivory (Dixon & Hay 2012; Dirnwoeber & Herler 2013; Chase et al. 2018) (Fig 3.1). The unwillingness of gobies to use alternative habitat in the short-term may drastically reduce their resilience to disturbances, threatening localized extinction (Munday 2004b). Declines from a single disturbance have the potential for a resilience, but multiple events will require long-term recovery (Hing et al. 2018; Madin et al. 2018) as most corals are uninhabited after consecutive disturbances (Fig 3.1B). Although the disturbances in this study were compounded, heatwaves may have had an even stronger effect on gobies since goby communities differed the most after the heatwaves, whereas coral communities remained similarly diverse after each disturbance. Without the added benefits of gobies, surviving corals will likely experience further threats to survival (Dixon & Hay 2012; Dirnwoeber & Herler 2013; Chase et al. 2018). Multiple disturbances may even cause ecosystem shifts when the foundation species of the environment, such as hard corals, face extreme declines (Kiers et al. 2010). If mutual symbionts show greater declines than corals, important processes may be exacerbated, further jeopardizing the recovery potential of an ecosystem's foundation species.

3.4.3. Future implications for symbiotic relationships from multiple disturbances

Our study demonstrates that consecutive disturbances result in uneven declines between mutual symbionts, and this has the potential for exposing surviving hosts to additional threats if their mutual and cryptic inhabitants disappear. As mutualisms break down, organisms that rely on these mutualisms may become more vulnerable to multiple disturbances and there may be ecosystem-level disruptions as a result (Wilson et al. 2006; Kiers et al. 2010; Turner 2010; Six et al. 2011), especially as climate-driven events become more frequent (Hughes et al. 2018a). Although the length and type of the disturbance play important roles in disturbance impacts, few studies have examined the effect of multiple disturbances (Johnstone et al. 2016; Madin et al. 2018; Hughes et al. 2019b). If successive threats become the norm, a system will already be stressed before a second event strikes, leading to greater consequences (Madin et al. 2018). Population bottlenecks will inevitably follow (Carson 1990) and threaten the survival of many organisms globally (Sergio et al. 2018). Flow-on effects will affect closely-associated organisms,

especially for those that depend on feedback loops with symbionts (Kiers *et al.* 2010). In each ecosystem, species are responding differently to disturbances, and mutually beneficial relationships are being tested (Kiers *et al.* 2010). Our study suggests that multiple disturbances will likely leave ecosystem builders exposed to additional threats if their cryptic symbionts fail to recover.

Chapter 4: Data Chapter: Delayed recovery and host specialization may spell disaster for coral-fish mutualism

In review/submitted to Ecology Letters.

4.1. Abstract

Mutualisms are prevalent in many ecosystems, yet little is known about how symbioses are affected by ecological pressures. Here we show delayed recovery for 13 coral-dwelling goby fishes (genus *Gobiodon*) compared with their host *Acropora* corals following 4 consecutive cyclones and heatwaves. While corals became twice as abundant 3 years post-disturbances, gobies were only half as abundant relative to pre-disturbances and half of the goby species disappeared. Although gobies preferred particular coral species, surviving goby species shifted hosts to newly abundant coral species when their preferred hosts became rare. As host specialization is key for goby fitness, shifting hosts may have negative fitness consequences for gobies and corals alike and affect their survival in response to environmental changes. Our study is an early sign that mutualistic partners may not recover similarly from multiple disturbances, and that goby host plasticity, while potentially detrimental, may be the only possibility for early recovery.

4.2. Introduction

In the face of climate change, multiple consecutive disturbances are becoming increasingly prevalent globally, and ecosystem stability is being threatened as a result (Turner 2010; Hughes *et al.* 2018). Relationships between organisms are important for maintaining ecosystem balance and diversity during these challenging times, especially when one of these organisms is a habitat-forming foundation species, e.g. conifers, kelps, and corals (Angelini *et al.* 2011; Denton & Gokhale 2019). Mutually beneficial symbioses (here termed ‘mutualisms’) often promote the survival of foundation and partner species, but anthropogenic disturbances are adding extreme pressures on these relationships (de Fouw *et al.* 2016; Denton & Gokhale 2019). A key question to arise is: will organisms in mutualisms respond similarly to consecutive disturbances, and what factors are important in the persistence of both partners (Marquis *et al.* 2014)?

For symbioses in which one organism relies on the other for limiting resources like food and shelter, the host species is a key determinant of the fitness of its symbiotic partner (mediated through growth, feeding, and reproductive advantages) (Hughes *et al.* 2000; Munday 2001). The benefits that the host incurs from their symbiotic partner may also vary with the species of the partner, e.g. specialized nutrients and protection (Douglas 1998; Kiers *et al.* 2010; Sensenig *et al.* 2017). However, as disturbances are intensifying and occurring more frequently, some host species are being disproportionately affected than other hosts (Douglas 1998; Kiers *et al.* 2010; Bonin 2012). In response, symbiotic partners may leave their host if it becomes unhealthy (Sensenig *et al.* 2017; Pratchett *et al.* 2020), or they may stay and facilitate their mutual recovery (Kiers *et al.* 2010; Marquis *et al.* 2014; Chase *et al.* 2018).

On coral reefs, corals are host to many mutually symbiotic organisms, such as microbes, *Symbiodinium* algae, crabs and coral-dwelling fishes (Munday *et al.* 1999; McKeon *et al.* 2012; Thompson *et al.* 2015). These symbiotic partners often specialize on particular host coral species, which they may leave or stay during environmental stress (Munday *et al.* 1999; Bonin 2012; McKeon *et al.* 2012; Thompson *et al.* 2015). Little is known about how climate change affects these mutualisms and the degree of host specialization by symbiotic partners, despite the importance of these ecological partnerships. For example, coral-fish symbioses are important for coral health because fish protect corals from toxic algae, sedimentation, predation, and stagnant hot water build-up (Lassig 1981; Dixon & Hay 2012; Dirnwoeber & Herler 2013; Chase *et al.* 2018, 2020b). Often, coral-dwelling fishes specialize on different hosts and vary to what extent they are specialized: some only live in 1-3 species (host specialist), while others use 4-11 coral species (host generalist) (Munday 2001; Caley & Munday 2003; Bonin 2012). Host specialization by coral-dwelling fishes likely affects how both symbiotic partners recover given that climatic disturbances affect some hosts more than others (Hughes *et al.* 2019; Froehlich *et al.* 2021).

Since fish provide important services for the health and growth of corals (Penin *et al.* 2010; Dixon & Hay 2012; Dirnwoeber & Herler 2013; Chase *et al.* 2018, 2020b), the ability for fish to shift hosts may result in some coral hosts becoming unoccupied and thus more vulnerable to disturbances. Coral-dwelling fish, like gobies, damselfishes, and coral crouchers, remain primarily within the branches of corals and can reduce several stressors that corals face during and after disturbances. For example, coral-dwelling fishes lessen bleaching susceptibility of their coral hosts by aeration of water among the branches even while sleeping (Goldshmid *et al.* 2004; Chase *et al.* 2018). Coral-dwelling gobies remove harmful competing seaweed and damselfishes remove sediment on coral branches (Dixon & Hay 2012; Chase *et al.* 2020b), which are both known coral stressors that are heightened after climatic disturbances (Hughes *et al.* 2007; Erftemeijer *et al.* 2012). Surviving corals are also more heavily targeted by predation after disturbances (Kokita & Nakazono 2001; Pratchett *et al.* 2004), but coral-dwelling gobies can actually deter corallivores with their toxin (Lassig 1981; Dirnwoeber & Herler 2013). Corals will grow faster with inhabiting damselfishes than without fish present (Holbrook *et al.* 2008), and growth is critical after disturbances as corals often become heavily damaged and truncated (Madin *et al.* 2018). As each of these coral stressors are heightened from disturbances, how fish respond with their host use may leave some corals less resilient if they become unoccupied.

Here, our 7-year study (2013-2020) shows that coral-dwelling gobies (genus *Gobiodon*) either disappeared or shifted their occupation of host corals (genus *Acropora*) after an unprecedented succession of disturbances with limited recovery periods: 2 category 4 cyclones (2014, 2015) and 2 prolonged heatwaves (2016, 2017) which caused extensive coral bleaching. By surveying gobies and their coral hosts before and after each disturbance, and then 3 years post-disturbances, we found that gobies fared far worse than corals, with a distinct time lag in the early signs of recovery of gobies compared to corals (Froehlich *et al.* 2021). Previous studies have shown trade-offs between goby fitness and host specificity, with particular coral hosts improving growth and survival of specialist gobies compared to generalist

gobies (Munday 2001; Caley & Munday 2003). Accordingly, the shifts in host occupation (i.e. host plasticity) coupled with a lag in recovery of gobies will likely hamper fitness of both parties during the crucial and early stages following disturbances (Penin *et al.* 2010; Dixon & Hay 2012; Dirnwoeber & Herler 2013; Chase *et al.* 2018, 2020).

4.3. Methods

4.3.1. Study Location

All sampling was completed at reef sites within Lizard Island, Great Barrier Reef, Queensland, Australia (-14.687264, 145.447039, Suppl. Fig 4.1). Lizard Island was affected by four extreme climatic events annually from 2014 to 2017: cyclone Ita (category 4) in April 2014, cyclone Nathan (category 4) in March 2015, heatwave causing a mass-bleaching event from March to April 2016, and a second heatwave causing a mass-bleaching event from February to May 2017 (Fig 4.1A). Sites were visited before these events in February 2014 (n = 18 sites), after the first cyclone in January-February 2015 (n = 16), after the second cyclone in January-February 2016 (n = 19), after both heatwaves in February-March 2018 (n = 22), and 3 years after the last disturbance in January-March 2020 (n = 24) (Fig 4.1A). Not all sites were sampled each year due to weather conditions and scouring effects of cyclones that left some sites with only bare rock.

4.3.2. Sampling Method

Surveys were completed at each time point for the presence of *Gobiodon* goby spp. within *Acropora* coral spp. There were two types of surveys used: (1) in 2014, 2018, and 2020, corals were surveyed 1 m on either side of 30-m transects, and (2) in 2015 and 2016, corals were surveyed 1 m on either side of 4-m cross-transects (Hing *et al.* 2018; Froehlich *et al.* 2021). In addition, since very few corals were encountered along transects after the four disturbances, random searches occurred in 2018 and 2020. When a live *Acropora* coral was encountered, the coral was identified nominal to species following Veron *et al.* (2018), and was measured and averaged along its width, length, and height (Kuwamura *et al.* 1994). Only corals at least 7 cm in average diameter were included in surveys, because smaller corals were never found occupied by gobies (Froehlich *et al.* 2021). The coral was searched for a *Gobiodon* species using a bright torch light (Bigblue AL1200NP), and the species and number of individuals were noted. Individuals were identified as adults or juveniles based on coloration and size. The study was completed under the animal ethics protocols AE1404 and AE1725 from the University of Wollongong, and research permits G13/36197.1, G15/37533.1 and G18/41020.1 issued by the Great Barrier Reef Marine Park Authority.

4.3.3. Data analysis

For changes in coral and goby populations, we used data from transects only since random searches did not follow any particular transect techniques. The following variables had many zero data points per

transect after multiple disturbances, and accordingly were compared among survey yr (fixed factor) and site (random factor) with a generalized linear mixed model (GLMER: poisson family) using a zero-inflated model: coral richness and abundance, adult goby richness and abundance, and juvenile goby richness and abundance. Note: for all abundance variables, only line transects in 2014, 2018, and 2020 were used to remove transect type bias in abundances. The following variables were compared among survey yr (fixed factor) and site (random factor) with linear mixed models (LMER): average coral diameter, coral occupancy (whether occupied or unoccupied by *Gobiodon* spp.), and adult goby group size (juveniles were not included because they were observed moving between coral heads). All analyses were completed in R (v3.5.2) (R Core Team 2018) with the following packages: tidyverse (Wickham *et al.* 2019), lme4 (Bates *et al.* 2015), lmerTest (Kuznetsova *et al.* 2017), LMERConvenienceFunctions (Tremblay & Ransijn 2020), piecewiseSEM (Lefcheck 2016), glmmTMB (Brooks *et al.* 2017), emmeans (Lenth *et al.* 2020), DHARMA (Hartig & Lohse 2020), and performance (Lüdtke *et al.* 2021). Coral and goby communities for the 10 most common species of each genus were compared among survey yr (fixed factor) and site (random factor) with a permutational analysis of variance (PERMANOVA) in Primer-E software (v7).

For host specificity analyses, we used data from transects and random searches. Data for particular species were removed for years in which the species was observed less than 8 times in order to allow for enough observations to assess host specificity use. Three out of the 13 goby species observed in the surveys were excluded for host specificity analysis since they were consistently too rare (*G. citrinus*, *G. okinawae*, and *G. sp. D*). The corals inhabited per goby species were then combined within current zones per year. Coral species inhabited were compared among goby species (fixed factor) and survey yr (fixed factor) using PERMANOVA. The following covariable was added to the analysis which was calculated from the first survey pre-disturbances (2014): specificity continuum (proportion of occurrences in which only one coral species was used per goby species [continuous variable, 0-1]). PERMANOVAs were repeated (without the covariable as it is correlated with the following factors) to individually include each of the following explanatory factors calculated from the first survey pre-disturbances (2014): coral richness specificity (fixed factor, host specificity category per goby species on the basis that goby conspecifics used up to 3 coral species [specialist] versus more than 3 coral species [generalist]), proportional coral specificity (fixed factor, host specificity category per goby species on the basis that 75% or more goby conspecifics used a single coral species [specialist] versus less than 75% of gobies used a single coral species [generalist]), and sociality index of each goby species (fixed factor: asocial or social as calculated in Hing *et al.*, 2018). Note: the goby species factor was nested within each of the factors in the later PERMANOVAs.

4.4. Results

4.4.1. Goby Recovery is Lagging Behind the Recovery of their Coral Hosts

Throughout these consecutive disturbances and 3 years post-disturbances, we surveyed 36 species of

Acropora coral hosts used by 13 species of coral-dwelling gobies (*Gobiodon*) known to occur at Lizard Island, Great Barrier Reef, Australia (-14.687264, 145.447039, Fig 4.1A). Less than one year after the last disturbance (2018), coral and goby abundances, richness, coral diameter and occupancy, and goby group size were at an all-time low (Suppl. Fig 4.2, $p < 0.001$, see Supplementary Table 4.1 for all statistical results). Three years post-disturbances (2020), there were signs of recovery for corals as coral abundance and richness were higher than previously recorded, but corals remained extremely small and were rarely occupied by gobies (Suppl. Fig 4.2). Goby richness and abundances were still very low, and gobies continued to occur singly whereas they were living in pairs or in groups pre-disturbances (Suppl. Fig 4.2). However, the number of juvenile goby species and their abundance improved (Suppl. Fig 4.2).

We focused specifically on the abundance of the 10 most commonly used coral hosts and 10 most common goby species and found that not all goby and coral species responded in the same way. Abundances were different among years ($p < 0.001$, Fig 4.1B), with eight coral species becoming extremely rare after disturbances, which was not surprising because 50% of the transects lacked corals compared to only 5% before disturbances (Froehlich et al. 2021). However there was recovery 3 years post-disturbances when only 17% of transects lacked corals. Surprisingly, two coral species became more abundant immediately after disturbances even though they were rare before (*A. cerealis* and *A. selago*). These species became at least 10 times more abundant 3 years post-disturbances than pre-disturbances (Fig 4.1B). In general, more corals were found without goby partners post- compared to pre-disturbances (Fig 4.1B).

For gobies though, it was a different story. Several species were still absent three years post-disturbances (2020) (Fig 4.1C). Three species disappeared altogether from our survey sites immediately after disturbances (*G. cf. bilineatus*, *G. fuscuber*, and *G. oculolineatus*), and an additional two species (*G. aoyagii*, and *G. rivulatus*) became rarely sighted 3 years post-disturbances (Fig 4.1C). Of those species that disappeared, three were already rare before disturbances, but one was originally the most common species surveyed (*G. fuscuber*). Only one goby (*G. axillaris*) returned to its pre-disturbance abundance in 2020 i.e. had fully recovered, while the remaining half that were still observed were still at 50% pre-disturbance abundances (Fig 4.1C).

4.4.2. Some Gobies Showed Plasticity in their Host Specificity

Pre-disturbances, each goby species usually inhabited a range of coral species with minimal overlap among goby species ($p < 0.01$), but this variation in host specificity was affected by the climatic disturbances ($p < 0.01$, Suppl. Fig 4.3, Fig 4.2). Not all gobies responded the same in terms of host occupation throughout the disturbances ($p < 0.01$; Fig 4.2), although there were no marked differences in particular coral species occupied by host specialists versus host generalists ($p > 0.50$; Fig 4.2).

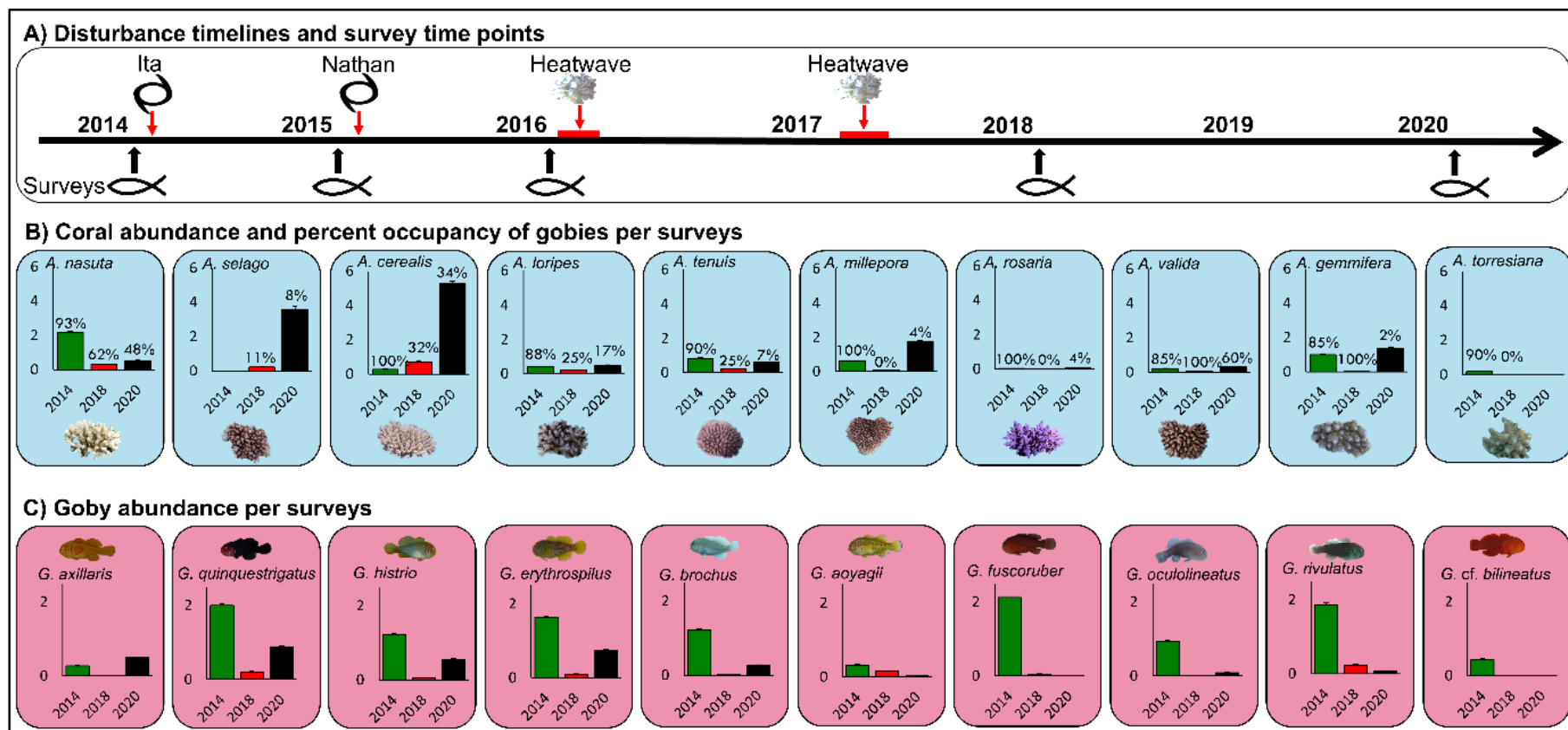


Fig 4.1. Multiple disturbances changed the mean abundance per transect of *Acropora* corals (blue) and their symbiotic *Gobiodon* gobies (red). **a** Following consecutive disturbances (2 cyclones and 2 heatwaves), **b** the 10 most common coral hosts and **c** their goby symbionts experienced drastic changes in abundances. Abundances after each cyclone were not significant but were significant after the last disturbances, and thus we display changes post-disturbances. Error bars are standard error. Percentages above bars represent the proportion of corals that were occupied by gobies during that particular survey year.

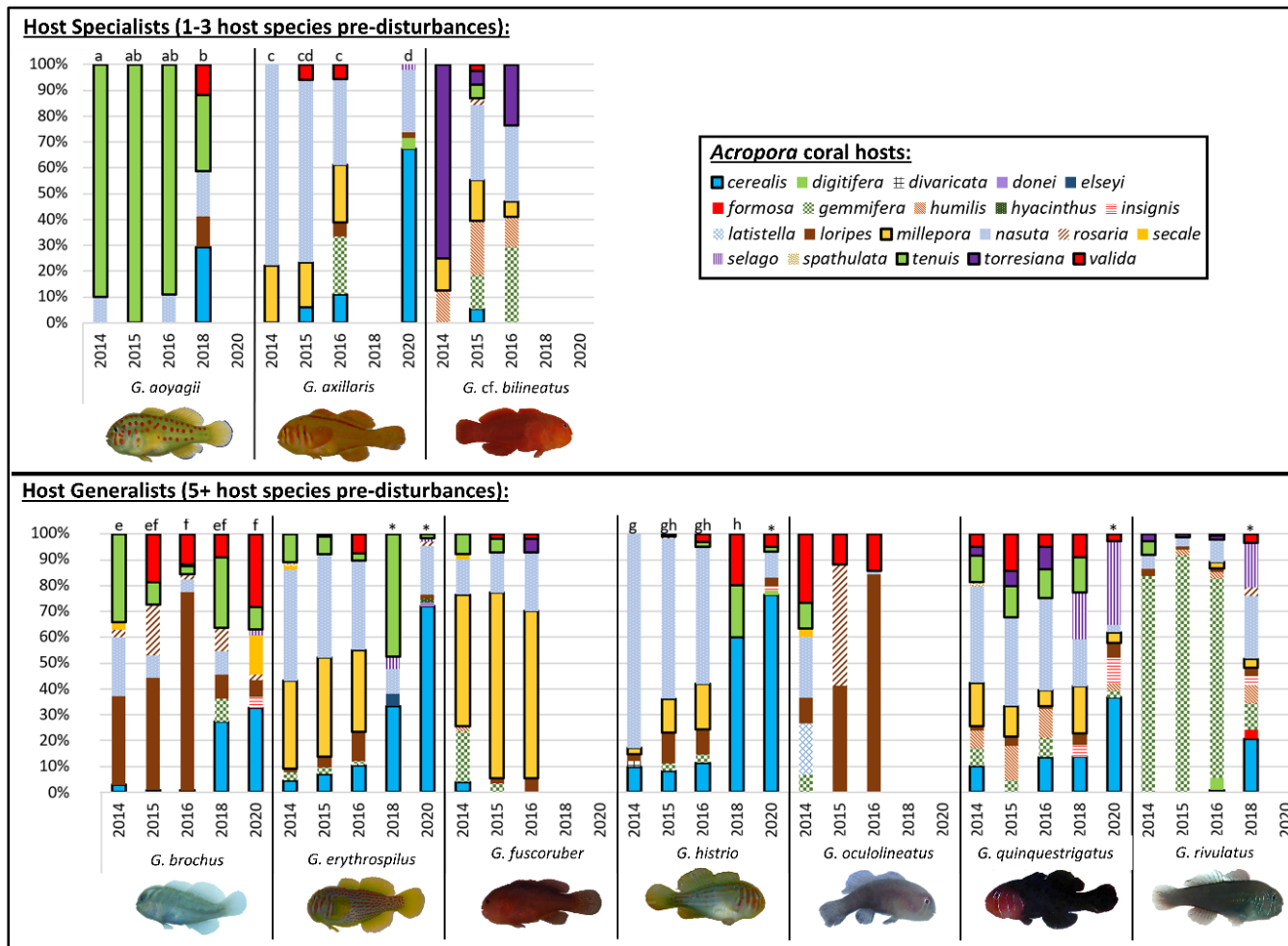


Fig 4.2. Host specificity of *Gobiodon* gobies in *Acropora* coral hosts changed following multiple disturbances. Proportion of all *Acropora* species used by the 10 most common *Gobiodon* species from surveys: pre-disturbances (2014), after cyclone Ita (2015), after cyclone Nathan (2016), after two back-to-back heatwaves/bleaching events (2018), and 3 years post-disturbances (2020). Letters above each bar represent host use differences among sampling years that are significantly similar to one another within species, and asterisks represent host occupation that is significantly different from all others within a species.

Host specialists, i.e. *G. aoyagii*, *G. axillaris*, and *G. cf. bilineatus*, occupied 1-3 host species pre-disturbances but each species occupied their own range of host species (Fig 4.2). Cyclones had minimal effects on host occupation, but there were marked changes after heatwaves. Post-disturbances, host specialists either disappeared or occupied more host species than previously observed (Fig 4.2). Of the three host specialists, *G. aoyagii* was the only species that was present after disturbances (2018), but it switched to being a host generalist occupying 5 coral species. Three years post-disturbances, *G. aoyagii* disappeared, but *G. axillaris* was observed once again and was a generalist occupying 5 coral species.

The other seven goby species were host generalists inhabiting between 5 to 10 coral host species pre-disturbances (Fig 4.2). Cyclones had minimal effect on host occupation, but heatwaves again caused noticeable changes. Post-disturbances, out of the seven host generalists, 5 goby species were still present and all but *G. histrio* remained host generalists, although *G. histrio* was only observed 10 times (Fig 4.2). Even three-years post disturbances, generalists continued occupying a wide range of hosts, including *G. histrio* again, although another generalist *G. rivulatus* had disappeared (Fig 4.2).

To index host specificity along a continuum instead of finite categories (host specialist vs. generalist), we calculated the proportion of occurrences that a goby species only occupied one coral species. We found that this index affected the range of hosts occupied throughout disturbances ($p < 0.01$); i.e., goby species that tended to occupy only one coral species occupied different coral species to goby species that tended to occupy several coral species. However, regardless of being a host generalist or host specialist, each goby species occupied a single coral species in higher proportion over others (Fig 4.3). Gobies occupied a particular host between 35-90% of the time, although host specialists tended to occupy one host species more often than host generalists. For host specialists, 90% of *G. aoyagii* occupied *A. tenuis*, 75% of *G. axillaris* occupied *A. nasuta*, and 75% *G. cf. bilineatus* occupied *A. torresiana* (Fig 4.2&4.3). For host generalists, 30% of *G. brochus* occupied *A. loripes* and 30% occupied *A. tenuis*, 40% of *G. erythrospilus* occupied *A. nasuta*, 50% of *G. fuscoruber* occupied *A. millepora*, 80% of *G. histrio* occupied *A. nasuta*, 25% of *G. oculolineatus* occupied *A. valida*, 35% of *G. quinquestrigatus* occupied *A. nasuta*, and 80% of *G. rivulatus* occupied *A. gemmifera* (Fig 4.2&4.3). Therefore, *A. nasuta* was the most commonly occupied host for four goby species, whether they were host specialists or generalists (Fig 4.3).

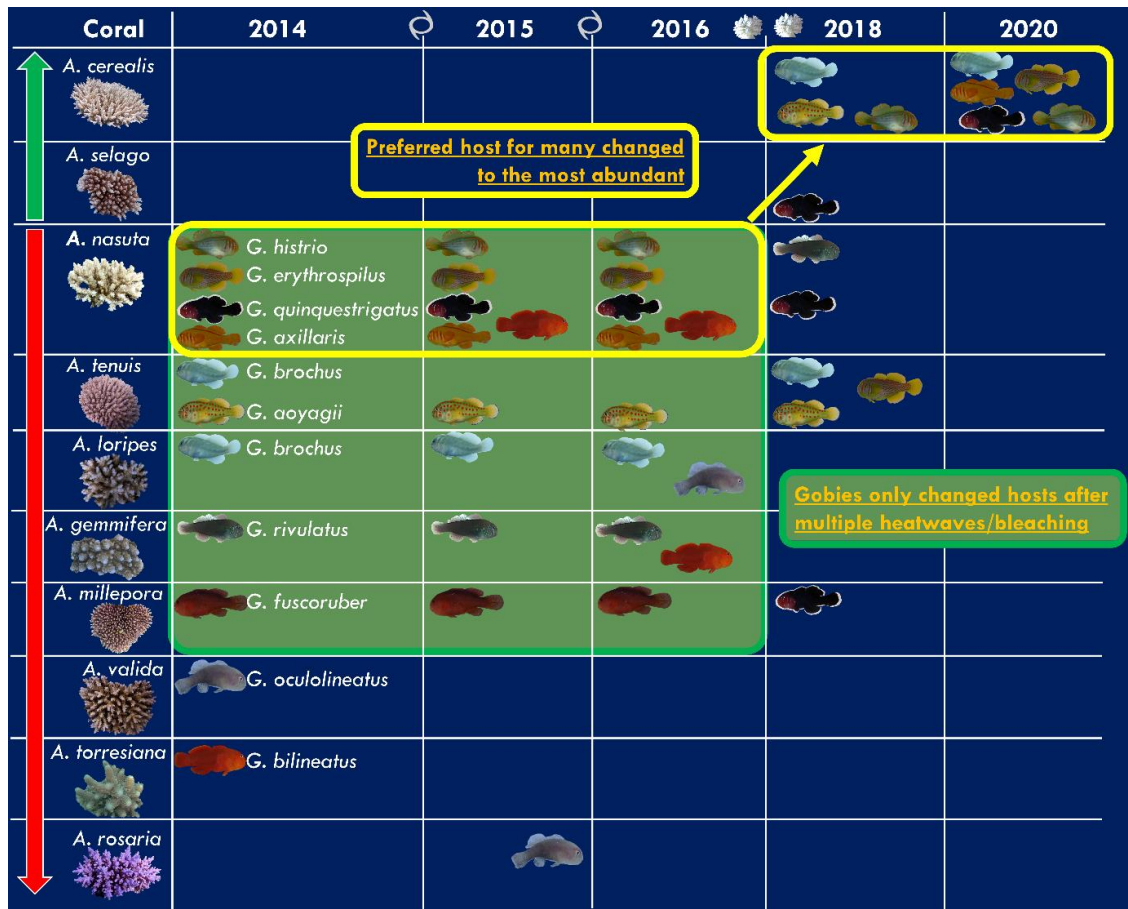


Fig 4.3. Changes in preferred *Acropora* host (s) for each *Gobiodon* gobies following multiple disturbances. Completed surveys before disturbance (2014), after cyclone Ita (2015), after cyclone Nathan (2016), after two back-to-back heatwaves (2018), and 3 years post-disturbances (2020). Coral hosts are organized from top to bottom to illustrate changes from most abundant to least abundant corals after disturbances. Green arrow highlights coral species that increased in abundance after disturbances, and red arrow highlights coral species that decreased in abundance after disturbances. Green box signifies gobies that did not change their preferred host until after heatwaves.

After the two cyclones, there was little change in in proportional occupancy of different coral hosts, suggesting that cyclones did not alter host specificity (Froehlich *et al.* 2021) (Fig 4.3). However after heatwaves, gobies shifted their host use, and often this shift mirrored the change in coral community. Many gobies switched from the previously popular *A. nasuta* to the newly abundant *A. cerealis* (Fig 4.1&4.3). Out of the remaining goby species post-disturbances, *Gobiodon aoyagii* began occupying *A. tenuis* and *A. cerealis* each 25% of the time, *G. histrio* switched to occupying the newly abundant *A. cerealis* 60% of the time, and three others (*G. brochus*, *G. erythrospilus*, and *G. rivulatus*) were also found more often in *A. cerealis* than previously observed (at least 20% of the time). The occupation of any particular host coral was not above 45% for any goby species after heatwaves, except for *G. histrio*.

Three years post-disturbances, there was little change in the number of hosts occupied by each goby species, but the majority of gobies were primarily occupying *A. cerealis* as it was the most abundant (Fig

4.1&4.3). *Gobiodon axillaris* was observed once again but switched host to *A. cerealis* 65% of the time (Fig 4.2&4.3). For *G. histrio* and *G. erythropsilus*, both species switched to *A. cerealis* (75% and 70% respectively), others like *G. brochus* switched to *A. cerealis* albeit to a lesser extent (30%), and *G. quinquestrigatus* switched to using both *A. cerealis* (35%) and *A. selago* (30%). Accordingly, even three years post-disturbances, most gobies used *A. cerealis* over other coral species (Fig 4.3).

4.5. Discussion

As multiple disturbances are becoming the norm, we find that mutualisms on coral reefs are not responding as a collective unit. Our 7-year study shows that *Acropora* corals are faring far better than their goby inhabitants (genus *Gobiodon*) 3 years after back-to-back climatic events (2 cyclones and 2 heatwaves) (Froehlich *et al.* 2021). However, not all coral species responded the same to disturbances, suggesting that habitat use plays a key role in the decline of gobies. Indeed, some goby species shifted their host use after disturbances, although that shift may be a potential downfall to their fitness in the long-term as they were not occupying their preferred hosts (Munday 2001; Caley & Munday 2003). Accordingly, host use is a strong indicator of the slower recovery of goby inhabitants compared to their coral hosts, although it may not always lead to goby population resilience in the long-term.

Nine months post-disturbances, populations of corals and gobies were each devastated, but gobies declined at least three times more than corals, and most corals were devoid of gobies (Froehlich *et al.* 2021). After 3 years of recovery time, coral hosts became twice as abundant and speciose compared to pre-disturbances, although coral sizes were three times smaller than pre-disturbances. Reduced competition for space among corals may have allowed a surge in abundances within a few years of recovery, yet corals also had to compete with fast growing algae and high incidences of corallivory (Baird & Hughes 2000; Penin *et al.* 2010). For gobies though, half of the species became rare or absent 3-years post-disturbances, including two previously abundant species, *G. fuscus* and *G. rivulatus*. There were four times fewer adult gobies compared to pre-disturbances. Gobies were never found in dead corals (Bonin *et al.* 2009). In addition, these gobies were living singly, which suggested extremely low turnover rates since gobies need to live in pairs or groups to reproduce (Wong & Buston 2013). Since corals remained very small, gobies may have been unable to pair and breed as they need larger corals to do so (Kuwamura *et al.* 1996). Gobies may be facing a population bottleneck (Sergio *et al.* 2018) due to the inability to form pairs over multiple years. Alarming, 75% of corals no longer hosted gobies post-disturbances compared to just 5% pre-disturbances (Froehlich *et al.* 2021). No single coral species was ever occupied more than 60% of the time post-disturbances, whereas several species had been previously occupied up to 100% of the time pre-disturbances. Even with 3 years of recovery time, 75% of corals were still devoid of gobies. Such a lag in goby population recovery is dire for the mutualism of corals and gobies. Coral-dependent fishes are predicted to decline substantially with climate change (Buchanan *et al.* 2016), and gobies are a striking example of this phenomenon.

Given that habitat specificity likely plays a key role in the continued prevalence of coral and goby

symbioses, our finding that half the gobies disappeared is a cause for concern. Initially, one third of the goby species inhabited just 2-3 host species (i.e. host specialists), while others occupied a broader range of hosts (i.e. host generalists) (Munday *et al.* 1999; Munday 2000; Dirnwöber & Herler 2007). Two out of the three host specialists were absent 3 years post-disturbances, which suggests that host specialists may be less resilient to disturbances (Dirnwöber & Herler 2007; Hof *et al.* 2012; Ainsworth & Drake 2020). However, three out of seven host generalists disappeared as well, suggesting that host specificity may not be an indicator of vulnerability to disturbances, as shown in plant-pollinator interactions in temperate forests (Vázquez & Simberloff 2002). The extent and severity of disturbances and the differential susceptibility among specific corals may instead affect how particular species respond.

Although goby host generalists occupied a broad range of hosts, each host generalist still used one coral species over others, just like host specialists. The disappearance of half of the goby species mirrored the decline in their most occupied coral hosts immediately after cyclones and heatwaves. Thus, despite being an advantage during stable periods, primarily using only one type of habitat may be a significant disadvantage during unstable periods (Munday 2000; Feary 2007). Even more alarmingly, many goby species stayed rare or disappeared despite the host species they used prior to disturbances increasing in abundance 3 years post-disturbances. For example, *G. fuscoruber* and *G. rivulatus*, both initially host generalists, disappeared even though their previously used hosts, *A. millepora* and *A. gemmifera* respectively, reappeared in higher abundance 3 years post-disturbance. Yet, *G. axillaris*, which was a host specialist that primarily used *A. nasuta*, initially disappeared 1 yr post-disturbance, but then returned 3 years post-disturbance and switched to occupying *A. cerealis* as it became more abundant. Our findings suggest that some gobies exhibit host plasticity with regard to the single most occupied host species, and that there is no clear advantage of being a host specialist or host generalist. Yet, whether gobies are able to remain on their previously occupied host species or shift to newly available host species is key to their recovery.

Other aspects of the biology and ecology of coral-dwelling gobies may be adding to their limited recovery from climatic disturbances. Due to a larval dispersal stage, coral reef fishes have the potential for larvae to be supplied from locations far away through stochastic replenishment (Munday *et al.* 1998; Green *et al.* 2015; Hing *et al.* 2018). However, broadscale disruptions to larval supply are likely occurring as climatic disturbances have broadscale reach and such disruptions have already been shown in *Acropora* corals as well (Hughes *et al.* 2019a). Coral-dwelling gobies may even experience higher disruptions to larval supply compared to corals as their larvae may be settling closer to their natal habitat than expected, as seen in other coral reef fishes (Gerlach *et al.* 2007; Selwyn *et al.* 2016; Rueger *et al.* 2020, 2021b). Limited recovery in coral-dwelling gobies may also be a consequence of their social tendencies to live in pairs or groups depending on the species (Hing *et al.* 2018). Out of the ten *Gobiodon* species that we focused on in our study, two were known to live in groups (*G. fuscoruber* and *G. rivulatus*), and both species became extremely rare after disturbances. Habitat constraints may explain a decline in group-living species, as larger corals can house more goby individuals (Hing *et al.* 2018). Since corals were substantially smaller after disturbances, group-living species were likely at a disadvantage. Accordingly,

it is possible that group-living species are less resilient to climatic disturbances, although this needs to be studied further with more species and at more locations.

Although unoccupied corals are on the rise and may be able to survive in the short term, a prolonged lack of mutualistic goby partners may increase their vulnerability to external threats in the long-term since gobies provide beneficial services to corals (Penin *et al.* 2010; Dixson & Hay 2012; Dirnwoeber & Herler 2013; Chase *et al.* 2018, 2020b). However, it is possible that other goby species may shift hosts in the short-term, given the host plasticity observed in some species. Such host shifts may increase coral resilience but potentially decrease goby fitness, since goby growth rates are higher in certain coral species (Munday 2001; Caley & Munday 2003). Certain inhabiting species may also be less effective at promoting resilience of hosts (Douglas 1998; Visser & Gienapp 2019), as seen in acacia ant-plant mutualisms following fire disturbance (Sensenig *et al.* 2017) and bark beetle-fungus symbioses with thermal stress (Six *et al.* 2011). While the capacity for host shifts may promote initial short-term survival of both partners, the long-term fitness of both gobies and corals may decline over time unless other coral symbionts fill the symbiont niche (Bonin 2012; McKeon *et al.* 2012; Thompson *et al.* 2015). Inhabiting fishes are particularly important for the resilience of their coral host to thermal stress (Chase *et al.* 2018), as is also seen in *Populus tremuloides* host plants with ants and aphids (Marquis *et al.* 2014). As coral-dwelling fish reduce bleaching susceptibility and impacts of sedimentation of coral hosts (Chase *et al.* 2018, 2020b), their decline may potentially spell disaster for coral resilience. Future studies should quantify recovery rates of corals with or without fish inhabitants to further determine how much coral-dwelling fishes contribute to the resilience of corals.

Our study is an early warning sign that mutually symbiotic partners may not recover at similar rates, and, while the capacity for host plasticity may be key for immediate survival, it may not improve resilience to future environmental and other stressors. Given that disturbances are occurring more frequently than ever before (Turner 2010; Hughes *et al.* 2018a), the mutualism between coral hosts and gobies may not be able to persist after continued disturbances, leaving both organisms susceptible to additional stress. Mutualism break downs are being observed in various environments, e.g. seagrass beds (De Fouw *et al.* 2016), tidal environments (Dunkley *et al.* 2020), and myrmecophyte habitats (Kiers *et al.* 2010). As mutualisms are predicted to change drastically moving forward (Kiers *et al.* 2010), such changes could even have knock-on effects on ecosystem stability (Wilson *et al.* 2006; Kiers *et al.* 2010; Turner 2010; Six *et al.* 2011). Whether symbionts exhibit host plasticity to changing environments is a key factor to understanding the potential resilience of corals and coral reef ecosystems to climate change.

Chapter 5: Data Chapter: Multiple levels of social variation through time, space, and disturbance regimes: a case study with coral-dwelling gobies, genus *Gobiodon*

5.1. Abstract

The evolution of sociality in many animals does not follow a strong phylogenetic signal, suggesting that ecological and environmental factors play a greater role in the development of animal societies. For some social animals, living in groups may not always be the best strategy depending on different environmental factors. In light of this, we have established a sociality framework that identifies four levels of variation in social organisation that vary from large-scale to fine-scale and can each be related to various ecological and environmental factors: (1) forms of sociality, (2) degree of sociality, (3) social plasticity, and (4) within-group plasticity. We modelled this framework by quantifying the four levels of variation over time, space and disturbance regime using multiple species of coral-dwelling gobies from the genus *Gobiodon*. Gobies are particularly interesting model system as they vary in social structure, show within-group cooperation and form a mutualistic relationship with their coral hosts which are vulnerable to climatic disturbances. We found that gobies varied in forms of sociality – from being solitary, to paired or group-living depending on location and disturbance regime. With regards to degree of sociality, gobies exhibited low or moderate degrees of sociality, and this was influenced by location or disturbance regime depending on species. Gobies were more often solitary or pair-forming than group-forming (which became extremely rare) in a high disturbance regime whereas they were more often found in groups in a moderate disturbance regime. With regards to social plasticity, gobies exhibited social plasticity in relation to the size of their coral hosts, which was reduced due to climatic disturbances. Lastly, gobies did not exhibit within-group plasticity in sociality, as there were no changes to the structure of size-based hierarchies or sex allocation patterns with location or disturbance regime. By combining the four levels of variation, we find that the sociality of coral-dwelling gobies is extremely vulnerable to environmental disturbances. By using our structured framework, we were able to identify which levels of social variation were subject to environmental factors like location and disturbance and hence this framework provides an excellent tool for predicting the future responses of animal societies to environmental stressors.

5.2. Introduction

In the animal kingdom, many species live in groups in order to reap some type of advantage, such as predation avoidance, improved territory defense, better survival in harsh conditions, increased mate availability, improved habitat quality, and enhanced offspring resilience (Queller & Strassmann 1998; Duffy & Macdonald 2010; Hing *et al.* 2017; Nowicki *et al.* 2018a; Firman *et al.* 2020; Rueger *et al.* 2021a). Social living is common in many taxa, and is often characterized by convergent evolution with little phylogenetic signaling even within closely related species, but not for all taxa (Faulkes *et al.* 1997; Shultz *et al.* 2011; Rivera *et al.* 2014). Instead, group living and social behaviours are often dependent on

ecological pressures that alter the benefits of social living (Emlen 1982; Duffy & Macdonald 2010; Hing *et al.* 2017; He *et al.* 2019). However, there is often no clear distinction made between multiple levels of social variation in relation to an organism's ecological and social environment when in fact differences in sociality can be measured at different scales. Here, we introduce a multi-level sociality framework that identifies four levels of social variation that highlight the extent of sociality amongst social species from large to fine-scale variation: (1) forms of sociality (i.e. proportion of individuals that live solitarily, in pairs, or groups), (2) degree of sociality (i.e. whether species are found strictly in one form of sociality), (3) social plasticity (i.e. ability to change group size based on local ecological or social contexts), and (4) within-group plasticity (i.e. ability to change social structure and hierarchy maintenance). This framework can be applied to many social taxa and is particularly interesting for those exhibiting high reproductive skew in which mature individuals forgo their own reproduction in order to cooperate in groups as nonbreeders. Thus, elucidating these four levels of social variation will be key to understanding the influences of ecological factors on animal societies.

At the largest scale, the first level of variation within the framework is the form of sociality exhibited, here defined as the proportion of individuals in the population that are solitary, in pairs, in single species groups (i.e. >2 group members) or in mixed species colonies (>1 individual of 2+ species). The allocation of single species groups can be separated further if it is important to differentiate between different types of groups, e.g. if reproductive skew varies substantially like in eusocial versus noneusocial societies. Mixed species colonies are defined as any colony that exhibits at >1 species of the same taxa. The taxa of interest can either be defined down to a species level or can be quantified for any broader level, such as genus, depending on the question. The proportion of individuals living solitarily, in pairs, or groups can be impacted by ecological conditions, e.g. variability of environment (Faulkes *et al.* 1997; Avilés *et al.* 2007; Lantz & Karubian 2017; Hing *et al.* 2018). By quantifying the proportion of individuals living in the different forms of sociality, we can assess whether ecological factors of varying scales will impact the tendency to live solitarily, in pairs or in groups. The form of sociality provides an overview of what proportion of individuals live in groups depending on external ecological, social and environmental pressures, and its strength lies in the ability to quantify this fairly easily for taxa level of interest (Fig 5.1).

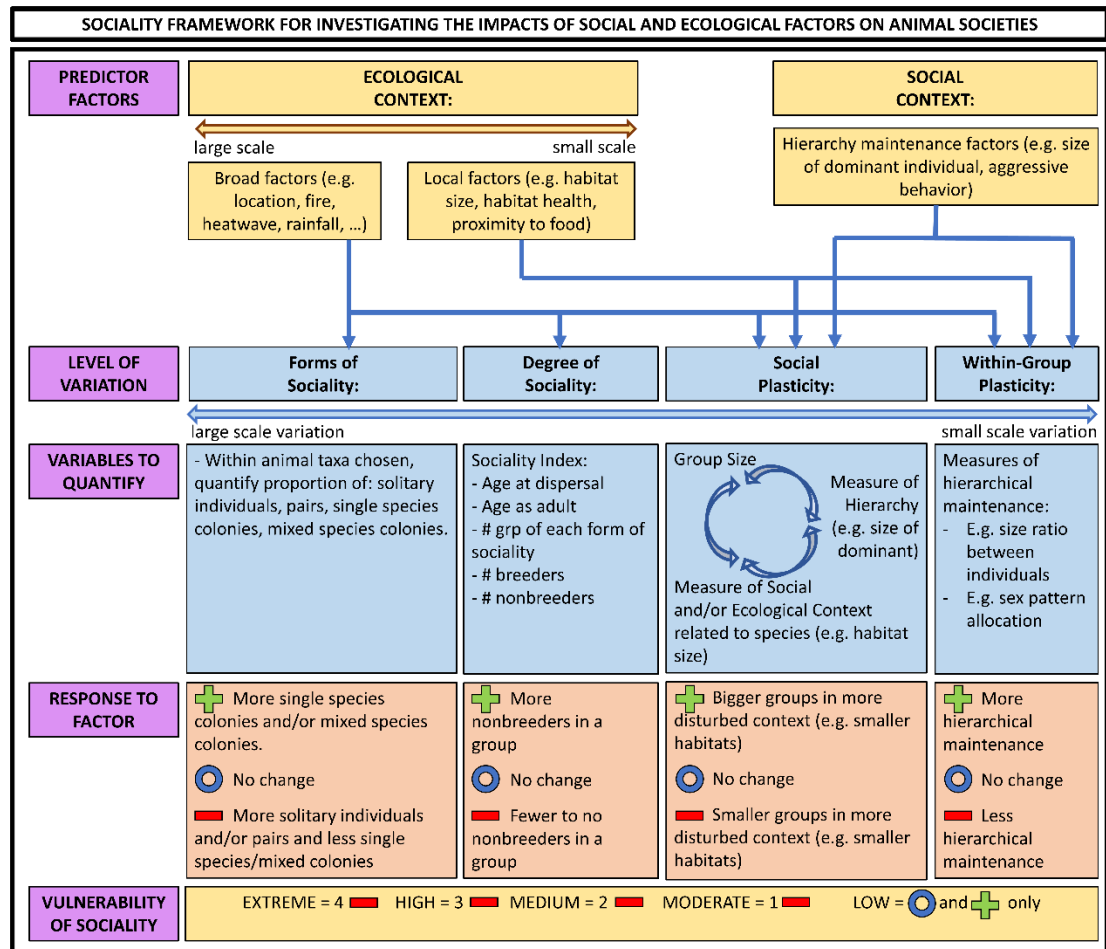


Fig 5.1. Sociality framework that tests whether ecological factors affect animal societies at four levels of variation and what rank of vulnerability is given to the sociality for the taxa based on how many variations have negative responses. Colony = all individual(s) living together in a society; # = number.

The second level of variation in the framework, the degree of sociality, is defined as the tendency for a given species in a given population to be strictly solitary, pair-forming or group-forming. The degree of sociality can be measured via the sociality index, identified by Avilés and Harwood (2012) and adapted by Hing et al. (2018). The sociality index calculates a value on a scale from 0 (solitary living) to 1 (exclusively group-forming) for a species based on the dispersal of the species, the proportion of groups in a population, and the proportion of breeding and nonbreeding individuals within colonies. There is a 0.5 threshold in which species below this threshold are pair-forming and those above are group-forming (Avilés & Harwood 2012; Hing *et al.* 2018). Therefore any given species is assigned just one value that encompasses how social (or not) that species or population of a given species is, as well as the degree of reproductive skew exhibit by that species. For a species with the highest degree of sociality, i.e. sociality index close to 1, individuals live strictly in eusocial groups, as seen in naked mole rats, ants, and termites (Wilson & Hölldobler 2005; Avilés & Harwood 2012; Nalepa 2015). Similarly, species with the lowest degree of sociality, i.e. sociality index close to 0, are strictly solitary, e.g. dune mole rats, platypus, and solitary sandpipers (Oring 1973; Griffiths 1988; Avilés & Harwood 2012). Values closer to 0.5 are for species that exhibit a mix of social organisations within the population, such as pair-forming and group-

forming, e.g. marine shrimp, social spiders, and many birds (Duffy & Macdonald 2010; Jetz & Rubenstein 2011; Avilés & Harwood 2012). The degree of sociality therefore provides a value of how social a species is without too much consideration of the degree to which that species could show flexibility in its social arrangements within a set environment, i.e. equivalent to an average degree of sociality exhibited by the species or population of that species, rather than a variance. The degree of sociality can then be calculated for different populations that vary in ecological conditions (e.g. season, geographic area, disturbance regime). Accordingly, the degree of sociality allows us to determine whether a particular form of sociality is consistently the form of sociality that is exhibited, or whether large scale environmental conditions allow for different degrees of sociality (Fig 5.1).

The third and yet finer level of variation in sociality is social plasticity, defined as the extent to which the group size of a species or population flexibly changes in response to local conditions, such as smaller scale ecological or social variables (adapted from Teles *et al.* 2016). For example, within a population, group sizes of many coral-reef fishes varies with the size of their coral or anemone habitat, and in some cases with the size of the largest, most dominant individual within a group (Buston & Cant 2006; Wong, 2011; Rueger *et al.* 2021). Larger habitat allows more individuals to live together as there is more space and resources to reduce conflict, and larger groups in turn can promote an increase in size of the habitat via mutualistically mediated benefits (Buston & Cant 2006; Wong, 2011; Rueger *et al.* 2021). In addition, the size of the largest individual can dictate the number of smaller subordinates that live within the group owing to rules of the hierarchy (Buston 2003b; Buston & Cant 2006; Branconi *et al.* 2020). Therefore, unlike the degree of sociality which essentially provides just one value to describe overall sociability of a species or population, social plasticity describes how flexible a species or population is to changes in the environment, such as disturbance regimes (Hing *et al.* 2018; Froehlich *et al.* 2021).

Finally, the smallest level of social variation relates to within-group plasticity in sociality, here defined as the degree of conflict and cooperation between individuals within groups and its higher-level consequences through its influence on group structure. In all societies, conflict over rank, resources and reproduction is unavoidable. For some societies, peaceful cooperation by subordinates is maintained through social constraint mechanisms, such as sex, size and maturity regulation, which can be influenced by ecological, social and environmental factors (Ghiselin 1969; Lassig 1977b; Warner 1988; Rubenstein 2007; Wong & Buston 2013; Hing *et al.* 2019). For this level of social variation, the variables that regulate social cooperation for particular species can be quantified and related to ecological and social factors. For taxa that exhibit sex allocation patterns, influences of environmental conditions and stressors like rainfall variability, temperature and pollutants have been shown to affect these patterns (Devlin & Nagahama 2002; Oldfield 2005; Rubenstein 2007; Ospina-Álvarez & Piferrer 2008). For example, female superb starlings change their offspring sex allocations based on their own body condition in relation to rainfall variability (Rubenstein 2007). For taxa that exhibit size-based hierarchies, influences of temperature and ocean acidification have been shown to impact some aspects of individual growth (Matthews & Wong 2015; McMahon *et al.* 2019). For example, temperature influences the extent to which subordinates control their own growth in relation to their immediate dominants for Eastern

mosquitofish (Matthews & Wong 2015). Such fine scale variation in social structure can thus be compared among many environmental factors to elucidate whether within-group plasticity exists in relation these factors.

Here, we applied this multi-level sociality framework to understanding how and why sociality varies in coral-dwelling gobies from the genus *Gobiodon*, which contains more than 13 species (Munday *et al.* 1999). Within a single colony, defined as all gobies living within a single coral host, gobies exhibit various forms of sociality ranging from solitary, pair-forming to group-forming (Hing *et al.* 2018) and may even live in mixed species colonies (i.e. with congeners, Froehlich *pers. obs.*). The composition of these mixed species colonies has yet to be quantified, but they provide an additional layer of social complexity as congeners reside and breed within the same habitat. Gobies do not form groups with kin as they have a 3-week larval dispersal stage and then settle into coral colonies as subordinate non-breeders with unrelated individuals (Brothers *et al.* 1983; Wong & Buston 2013; Rueger *et al.* 2021b). Within groups, individuals cooperate via peaceful cooperation within a size-based hierarchy, and only a monogamous pair breeds (Wong & Buston 2013). Group sizes mainly depend on ecological factors, like coral size (Hing *et al.* 2019), and potentially on social factors, like body sizes of the largest individual, as seen in *Paragobiodon xanthosomus* and *Amphiprion percula* (Fautin 1992; Elliott & Mariscal 2001; Buston 2003b; Wong *et al.* 2007; Wong 2011; Barbasch *et al.* 2020; Rueger *et al.* 2021a). Within the genus, there is only a weak phylogenetic signal for sociality (Hing *et al.* 2019), which suggests that environmental factors play a substantial role in sociality. *Gobiodon* gobies occur across a range of areas in the Indo-Pacific Ocean, which allows us to test the influences of both large-scale environmental factors, like acute cyclones and heatwaves, and small-scale factors on the structure of their societies (Munday *et al.* 1999; Hughes *et al.* 2018a; Froehlich *et al.* 2021).

Specifically, we investigated how and why sociality varies by decidedly examining each of the 4 levels of sociality in these coral gobies. We used data spanning multiple time points and three different reef systems which experienced varying disturbance regimes. To use the framework, we (1) compared the forms of sociality exhibited across the *Gobiodon* genus among coral size, time, locations and disturbance regimes. We then (2) assessed the impacts of these environmental factors on the three other levels of variation - the degree of sociality, social plasticity, and within-group plasticity - for each individual species and then performed comparisons of these variables among species. Finally, we took a closer look at mixed species colonies and investigated which species composed these colonies and quantified the within-group plasticity of these colonies among locations and disturbance regimes. Finally, we combined the results of each sociality metric to identify the vulnerability rank of the sociality of coral-dwelling gobies (Fig 5.1).

5.3. Methods

5.3.1. Site Description

The study was conducted at three different reef systems in the Indo-Pacific, the northern, central and southern reef systems. The northern reef system is made up of four inshore reefs in Kimbe Bay, West New Britain, Papua New Guinea (PNG) (-5.42896°, 150.09695°). This PNG reef system has remained relatively undisturbed since an initial trip we conducted in Sep-Nov 2018. The central reef system is made up of multiple small reefs around Lizard Island (LI), Queensland, Australia (-14.687264°, 145.447039°). The LI reef was relatively undisturbed in early 2014 but was affected by four extreme climatic disturbances on an annual basis: category 4 cyclones Ita (2014), Nathan (2015), and two mass bleaching events (2016 and 2017). More recently, LI has sustained mild bleaching events (2020, 2021, and 2022, a.k.a. few patches of corals bleaching) and is in a continued state of disturbances with little time for proper recovery (Froehlich pers. obs., Pratchett et al. 2021). The southern reef system is within an enclosed lagoon at One Tree Island, Queensland, Australia (OTI, -23.506565°, 152.090954°). The OTI reef system was relatively undisturbed in 2019 but suffered from mass bleaching events in 2020 with very minimal bleaching in 2022.

5.3.2. Sampling Techniques and Intervals

All fieldwork was conducted either on SCUBA or snorkel at each reef system. Two types of sampling techniques were used for the study. The first technique involved conducting surveys along 30 m line transects to search all corals within 1 m on either side of the transect. The second sample technique involved haphazardly sampling corals at each reef system. When a coral was encountered, a bright torch light (Bigblue AL1200NP) was used to search for goby occupants. Within each coral, the number of gobies (i.e. group size), life stage of gobies, and goby species were noted. Goby life stage was recorded as either breeding adults (two largest adults), non-breeding adults (all other adults smaller than 2 breeders but larger than juveniles), and juveniles (a.k.a. recruits) depending on their coloration and size. Coral diameter was measured along three axes (length, width, and height), and an arithmetic average was taken to indicate coral size (i.e. average coral diameter; Kuwamura et al. 1994). Corals under a minimum of 7 cm average diameter were excluded because gobies were never found in such small corals (Froehlich et al. 2021). Gobies were collected from a random selection of corals from each sampling technique in order to quantify body size. During collection, a clove oil anesthetic solution (clove oil, 70% ethanol, and seawater) was sprayed over the coral and fish were wafted out with hand nets (Munday & Wilson 1997). Each fish was placed in a Ziploc bag full of seawater and measured for standard length (mm, ± 0.1 mm) using handheld calipers. During later collections (as noted below), fish were also sexed and injected with a unique visible implant elastomer identification tag (Northwest Marine Technology, Inc., Anacortes, Washington, USA) (Munday 2001). Fish were then returned unharmed to their coral. On later trips, goby colonies containing tagged fish were revisited and re-collected to note coral size, group size, fish size and sex.

Sampling was completed at LI before climatic disturbances (Feb 2014) and three years after the four major climatic events (Jan-Mar 2020). During 2020, gobies were tagged with elastomer and sexed, and then the same colonies were revisited one and two years later (Jan-Mar 2021 and Jan-Apr 2022). Haphazard sampling was completed at PNG during one sampling event (Sep-Nov 2018) in which gobies

were tagged with elastomer and were revisited six months later (May-June 2019). Haphazard sampling was completed at OTI before climatic disturbances (Jan-Feb 2019) and two years later (Mar-Apr 2022) after mass coral bleaching had occurred.

The study was performed in accordance with relevant guidelines and regulations, including PREPARE and ARRIVE guidelines, under the University of Wollongong Animal Ethics protocol AE1404, AE 1725, and AE2117 and under research permits issued by the Great Barrier Reef Marine Park Authority (G13/36197.1, G15/37533.1 and G18-41020.1) and the Papua New Guinea Research Visa Permit AA654347.

5.3.3. Data Analysis

5.3.3.1. Form of Sociality – Single Species Pairs, Single Species Groups, Mixed Species

Gobies encountered during transect surveys and haphazard searches were included for analysis and were categorized into form of sociality as follows: one individual living alone (solitarily), living in pairs with conspecifics only (single species pairs), living in groups with conspecifics only (single species groups), and living with congeners (mixed species). Only corals with a minimum of 10 cm average diameter were included because that was the minimum size of corals measured during haphazard searches. The effect of location (i.e. reef) (fixed factor) on the form of sociality of gobies were analysed using multinomial logistic regression models for two analyses: (1) compare locations in relatively undisturbed conditions (i.e. before climatic disturbances = PNG2018, LI2014, OTI2019), (2) compare locations before and after being disturbed by climatic disturbances (i.e. pre-disturbances = LI2014 & OTI2019, post-disturbances = LI2020, LI2022 & OTI2022), and (3) compare Lizard Island between the two post-disturbance time points (LI2020 and LI2022). For each multinomial model, the baseline reference level for the response variable was a solitary individual in order to test whether the predictors affected the probability of falling into alternative response levels compared to the baseline. Juveniles were included in the analysis unless they were solitary individuals as they were not evicted by adults. All analyses were completed in R (v4.2.0) (R Core Team 2022) and R Studio (2022.02.2+485) (RStudio Team 2022) with the following packages: tidyverse (Wickham *et al.* 2019), VGAM (Yee 2010), car (Fox & Weisberg 2019), and rcompanion (Mangiafico 2016).

5.3.3.2. Degree of Sociality - Sociality Index

We calculated the sociality index for each species in which there were a minimum of 5 colonies of the species in any single location at each survey time point, including pre- and post-disturbance. The sociality index was adapted from Avilés and Harwood (2012) as follows:

$$S = \frac{\frac{A_d}{A_a} + \frac{N_g}{N_g + N_p + N_i} + \frac{I_n}{I_r + I_n}}{3}$$

where A_d = age of dispersal (i.e. settlement), A_a = age of adulthood, N_g = number of groups, N_p = number of pairs, N_i = number of solitary individuals, I_n = number of reproducing (dominant) adults, I_r = number

of non-reproducing (subordinate) adults. The numerator is comprised of three components: the proportion of the life cycle spent in a colony, the proportion of groups encountered, and the proportion of subordinates (nonbreeding) individuals (respectively). We followed guidelines set out in Hing *et al.* (2018) to calculate biologically-relevant assumptions of the numerator. *Gobiodon* gobies spend only 22-41 days in the larval dispersal stage (Brothers *et al.* 1983), which equates to the age of settlement. Once gobies settle into a coral (after their larval dispersal), they rarely move between corals unless they are evicted or their mate dies (Munday *et al.* 1998; Wong *et al.* 2007), and their life spans multiple years (Munday 2001). Accordingly, we set the maximum proportion of life cycle spent in a colony (i.e. A_d/A_a) to 1, which is biologically realistic even if there is some natural variation. We then calculated the sociality index for each species at each location and time point, and categorized them alongside the threshold of 0.5 as either pair-forming (< 0.5) or group-forming (≥ 0.5). Note, we did not calculate sociality indices for mixed species colonies.

5.3.3.3. Social Plasticity: Group Size – Size of the Dominant – Coral Size

To investigate the determinants of social plasticity, we only calculated the relationship for goby species that were group-forming as per sociality indices (i.e. > 0.5), and of which we collected a minimum of 30 colonies. We excluded any mixed species colonies. The analysis of the synergistic relationship between group size, size of the dominant individuals and coral size was repeated for each variable by placing each as the focal response variable in the model. The effect of the size of the dominant and coral size on group size were analysed using a generalized linear model using the poisson distribution. The effect of the group size and coral size on the size of the dominant individual were analysed using a linear model. The effect of the size of the dominant and group size on the coral size were analysed using a linear model. Location was included as a fixed factor in each analysis and analyses were repeated per species separately. The variables and models were assessed for normality and homoscedasticity via g Q-Q plots, histograms, and residuals over fitted plots, and were transformed as required. If outliers fell outside of 2.5 standard deviation from 0, then they were subsequently removed. All analyses were completed in R (v4.2.0) (R Core Team 2022) and R Studio (2022.02.2+485) (RStudio Team 2022) with the following packages: tidyverse (Wickham *et al.* 2019), lme4 (Bates *et al.* 2015), lmerTest (Kuznetsova *et al.* 2017), LMERConvenienceFunctions (Tremblay & Ransijn 2020), piecewiseSEM (Lefcheck 2016), and emmeans (Lenth *et al.* 2020).

5.3.3.4. Within-group plasticity: Size Ratios

To investigate the size ratios, we only included goby colonies in which all individuals were collected and were found in single species colonies. Otherwise, we would not have been able to confirm the correct rank placement of each individual in the hierarchy. Size ratios were calculated by dividing the standard length (SL) of the lower rank individual by the standard length of the upper rank individual (e.g. $SL_{\text{rank2}}/SL_{\text{rank1}}$) (Wong *et al.* 2007). The effect of coral size (covariable), group size (covariable), species (fixed factor) and location (fixed factor) on the size ratio between rank 1 and rank 2 individuals (i.e. rankstep 1) were analysed with generalized linear models with family quasibinomial. The analyses were repeated for the size ratio between rank 2 and rank 3 individuals (i.e. rankstep 2). At two locations, goby colonies

were revisited in consecutive sampling events (PNG 2018 & 2019, LI 2020 & 2021); for these repeat visits, size ratios were calculated for rankstep 1 but not for further ranks as there were not enough colonies with minimum of 3 individuals per species. The effect of coral size (covariable), group size (covariable), species (fixed factor), location (fixed factor), and year (fixed factor) on the size ratio for rankstep 1 was analysed with generalized linear models with family quasibinomial. We had enough samples to compare size ratios of rankstep 1 at Lizard Island pre- (2014) and post-disturbances (2021 and 2021). Accordingly, we investigated the effects of coral size (covariable), group size (covariable), species (fixed factor) and pre- vs. post disturbance (fixed factor) on the size ratios of rankstep 1 at Lizard Island. The variables and models were assessed for normality and homoscedasticity via g Q-Q plots, histograms, and residuals over fitted plots, and were transformed as required. If outliers fell outside of 2.5 standard deviation from 0, then they were subsequently removed. Models were selected based on the Akaike Information Criterion (AIC). All analyses were completed in R (v4.2.0) (R Core Team 2022) and R Studio (2022.02.2+485) (RStudio Team 2022) with the following packages: tidyverse (Wickham *et al.* 2019), lme4 (Bates *et al.* 2015), car (Fox & Weisberg 2019), LMERConvenienceFunctions (Tremblay & Ransijn 2020), piecewiseSEM (Lefcheck 2016), emmeans (Lenth *et al.* 2020), and ggpubr (Kassandra 2020).

5.3.3.5. Within-group plasticity: Sex Dominance in Breeding Partners

For single species colonies that were revisited at LI in 2020 and 2021, the sex of the dominant individual (rank 1) was identified on repeated trips. The sex ratio of rank 1 males to rank 1 females was compared to differ from unity 1:1 with a 1-sample proportions test with continuity correction. The effects of species (fixed factor) and year (fixed factor) on the ratio of rank 1 females to rank 1 males within breeding partners was compared analysed using generalized linear models with the binomial family. All analyses were completed in R (v4.2.0) (R Core Team 2022) and R Studio (2022.02.2+485) (RStudio Team 2022) with the following packages: stats (R Core Team 2022), car (Fox & Weisberg 2019), and rcompanion (Mangiafico 2016).

5.3.3.6. Mixed Species Colonies: Social Structure and Composition

Across all locations, goby colonies containing mixed species were used to calculate three categorical response variables that measured whether the mixed species colony: (1) had different species intermixed within hierarchical ranks—e.g. rank 1,3,5 were species A and rank 2,4,6,7 were species B (yes, intermixed) versus rank 1-4 were species A and rank 5-7 were species B (no, not intermixed); (2) had the biggest species as the rank 1 individual (yes or no; biggest species as defined by Hing *et al.* 2019); and (3) was composed of solitary individuals, pairs or groups of each species, or a combination of each. The main effect of location (fixed factor) on the mixed species response variable was analysed using multinomial logistic regression models for each response variable separately. Mixed species colonies were only observed and not collected post-disturbance, therefore no pre- versus post-disturbance analyses were completed for response variables 1 and 2. For comparing the composition of mixed species colonies (response variable 3) pre- versus post-disturbances, not enough mixed species colonies were found post-disturbance at LI, but there were enough found for collected at OTI. The effect of pre- vs. post-

disturbance (fixed factor) on the composition of mixed species colonies at OTI was analysed using a multinomial logistic regression model. For each multinomial model, the baseline reference level for the response variable was as follows: (1) intermixed rank reference: no, (2) bigger species as rank 1 reference: no, and (3) mixed composition reference: solitary individuals. Juveniles were included in the analysis unless they were solitary individuals. All analyses were completed in R (v4.2.0) (R Core Team 2022) and R Studio (2022.02.2+485) (RStudio Team 2022) with the following packages: tidyverse (Wickham *et al.* 2019), VGAM (Yee 2010), car (Fox & Weisberg 2019), and rcompanion (Mangiafico 2016).

Size ratios for each rankstep within mixed species colonies were calculated for up to rankstep 8 due to large group sizes in mixed species colonies. Initially, size ratios were calculated per species within mixed species colonies in order to test whether their size ratios were the same as those in single species colonies. The effect of coral size (covariable), group size (covariable), rankstep (fixed factor), species (fixed factor), location (fixed factor) and single vs. mixed species group (fixed factor) on the size ratios (separated by species in mixed species colonies) was analysed with a generalized linear model with family quasibinomial. Then, size ratios were calculated within ranks regardless of species, because we confirmed that in fact their size ratios did not match up to single species colonies (latter analysis) and species were intermixed within mixed species colonies (analysis previous paragraph). The effect of coral size (covariable), group size (covariable), rankstep (fixed factor) and location (fixed factor) on the size ratios (regardless of species in mixed species colonies) was analysed with a generalized linear model with family quasibinomial. Both size ratio models were assessed for normality and homoscedasticity via g Q-Q plots, histograms, and residuals over fitted plots, and were transformed as required. If outliers fell outside of 2.5 standard deviation from 0, then they were subsequently removed. All analyses were completed in R (v4.2.0) (R Core Team 2022) and R Studio (2022.02.2+485) (RStudio Team 2022) with the following packages: tidyverse (Wickham *et al.* 2019), lme4 (Bates *et al.* 2015), car (Fox & Weisberg 2019), LMERConvenienceFunctions (Tremblay & Ransijn 2020), piecewiseSEM (Lefcheck 2016), emmeans (Lenth *et al.* 2020), and ggpubr (Kassandra 2020).

5.4. Results

The abundance of *Gobiodon* species differed at each location and some species were sometimes not found in sufficient abundance at a given location for each analysis. For example, a latitudinal decline in opposite directions has previously been reported for *Gobiodon histrio* and *Gobiodon erythropsilus* (Munday *et al.* 1999), which we also observed in the current study; i.e. *G. histrio* occurred at PNG and LI (lower latitude) but was extremely rare at OTI (higher latitude), whereas *G. erythropsilus* was never found at PNG but occurred at LI and OTI. Therefore, not all species could be used in each analysis.

5.4.1. Form of Sociality – Single Species Pairs, Single Species Groups, Mixed Species

We compared the form of sociality exhibited by gobies among locations by comparing the number of corals that had gobies living alone (i.e. solitarily), living in pairs with conspecifics (i.e. single species pairs), living in groups with conspecifics (i.e. single species groups), and living with congeners (i.e. mixed species). We used all species observed for these analyses. Before any climatic disturbances, the form of sociality differed among locations (see Suppl. Tabs 6.1-4 for all statistical outputs, here Suppl. Tab 5.1, $p < 0.01$). There were far more mixed species colonies at OTI than any other location, and there were more single species groups at LI than at other locations (Fig 5.2). Beyond these differences, single species pairs were most common at each location (Fig 5.2). Solitary individuals were found in the smallest corals, followed by single species pairs, then mixed species colonies, and then single species groups were found in the biggest corals.

There was a significant interaction between location and pre/post-disturbances on the form of sociality ($p < 0.01$, Fig 5.2). At OTI, there were substantially more solitary individuals and less pair-forming individuals post disturbance compared to pre-disturbance, but the proportion of single species groups and mixed species colonies remained similar pre- and post-disturbance (Fig 5.2). At LI, there were also substantially more solitary individuals and fewer single species pairs post-disturbance than pre-disturbance, but single species groups and mixed species colonies became extremely rare post-disturbance even though that differed slightly among 3-yr and 5-yr mark post-disturbance ($p < 0.001$, 2020 v. 2022, Fig 5.2). In 2020, ~70% of gobies were solitary compared to just under 25% pre-disturbances, and the remainder were living pair-forming except for a single occurrence of a mixed species colony. In 2022, there were fewer solitary gobies (~50%), and others lived in pairs except for 5 single species groups (1%) and 5 mixed species colonies (1%). At PNG, there was a similar proportion of solitary and paired individuals as at OTI pre-disturbances, but there were only slightly more mixed species colonies than single-species colonies (Fig 5.2).

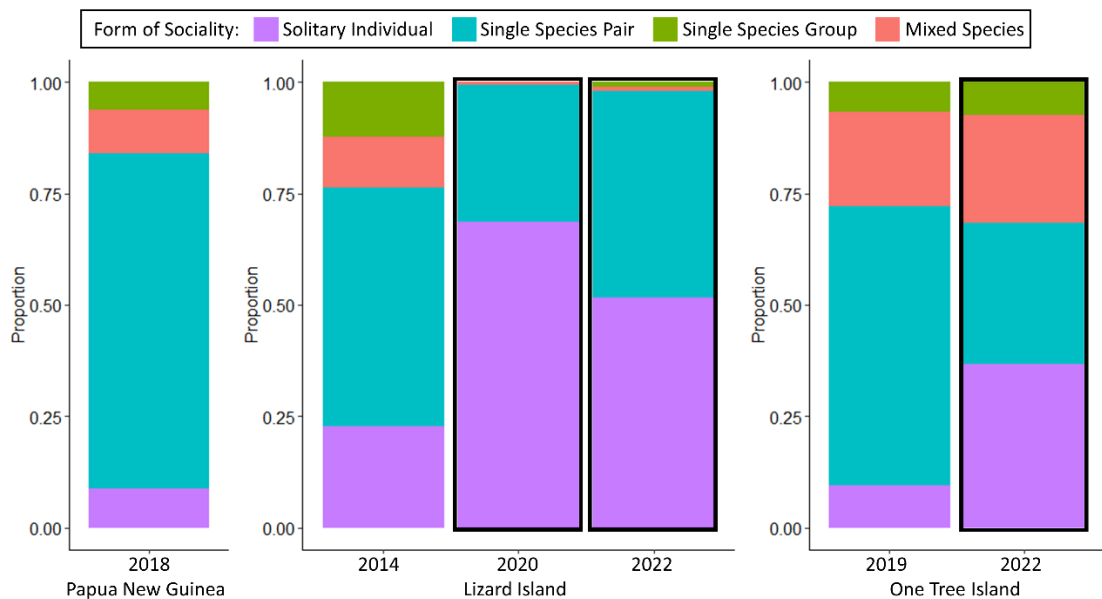


Fig 5.2. Forms of sociality of all species by all three locations and pre-/post-disturbances for two locations. PNG = Papua New Guinea; LI = Lizard Island; OTI = One Tree Island; data outlined in black line is post-disturbance(s).

5.4.2. Degree of Sociality - Sociality Index

By calculating sociality indices among locations for each species (minimum of 5 colonies) we found that pair-forming species exhibited low degrees of sociality and remained pair-forming as per Hing et al. (2018), even post-disturbances (Fig 5.3). Interestingly, *Gobiodon quinquestrigatus* was pair-forming at all locations, although it was just shy of reaching the 0.5 threshold for group-forming at PNG (Fig 5.3). Other species also varied from the distinct pair-forming value of 0.33 as some nonbreeding subordinates were accepted into a pair depending on the locations for several species. However, some species that were originally group-forming switched to pair-forming, thus suggesting that group-forming species have moderate degrees of sociality with subordinates being accepted less often post-disturbances (Fig 5.3). *Gobiodon citrinus* was the only species to remain group-forming regardless of location or disturbance and to have the most subordinates in groups (highest sociality indices) even post-disturbance, although the species was rarely encountered and only found in enough numbers for sociality index calculation post-disturbance at OTI. *Gobiodon fuscoruber* was initially group-forming at all locations, although with a lower sociality index, except PNG where it was classed as pair-forming pre-disturbance. The species remained group-forming post-disturbance at OTI with little change to their index. The species was however too rare at LI post-disturbances. *Gobiodon rivulatus* was another species that had the highest sociality index and had many subordinates in a group at LI pre-disturbance but became exclusively pair-forming and not accepting subordinates at LI post-disturbances. At PNG pre-disturbances, the species also occasionally accepted some subordinates, just falling shy of 0.5 sociality index. However, the species was exclusively pair-forming at OTI pre-disturbances, and instead occasionally accepted subordinates at OTI post-disturbances (Fig 5.3).

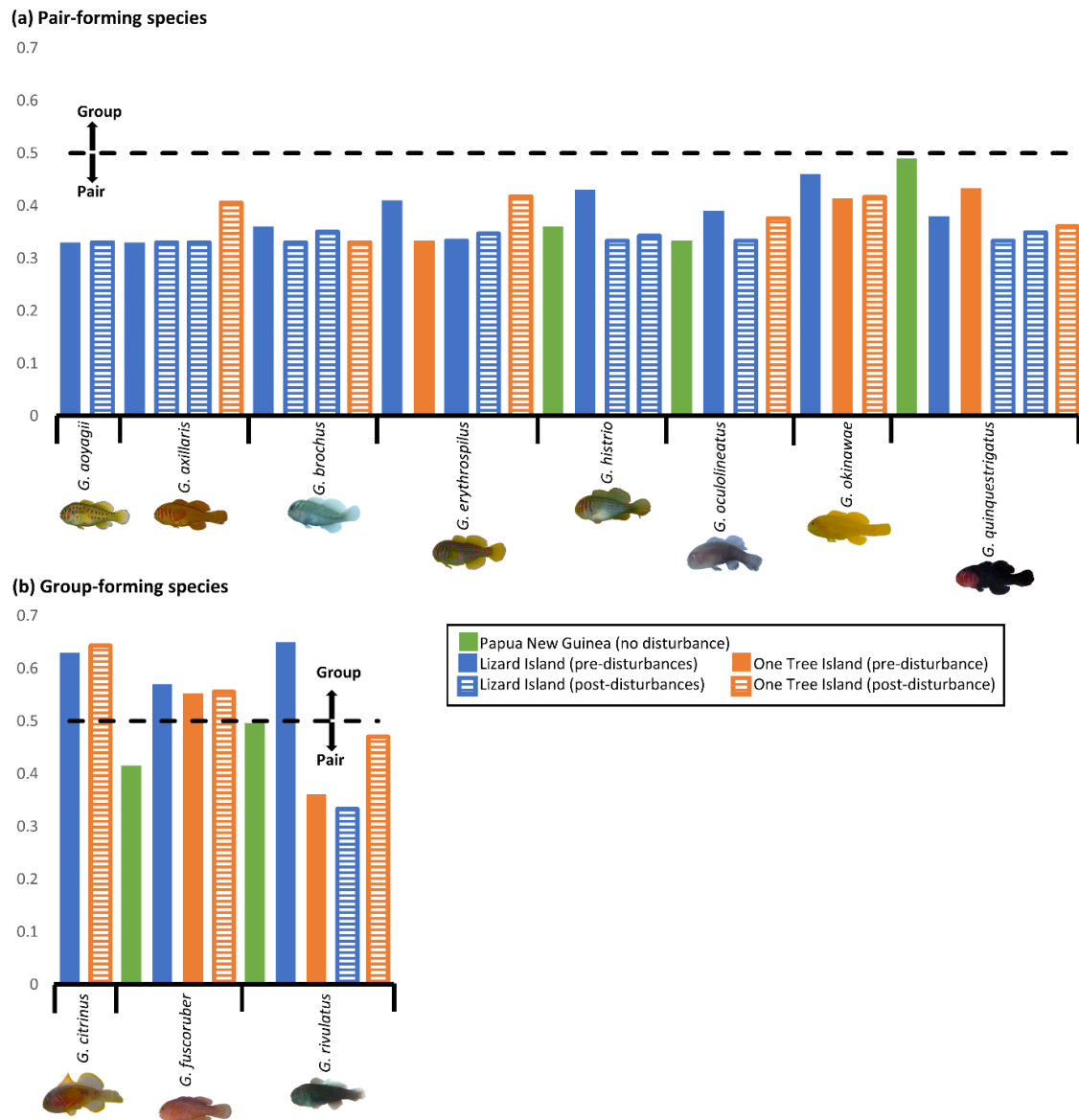


Fig 5.3. Sociality index of each species at different locations including repeat visits pre- and post-disturbance(s).

5.4.3. Social Plasticity: Group Size – Size of the Dominant – Coral Size

We were able to compare 2 group-forming species at 2 locations (LI, OTI) with sufficient sample size (i.e. *G. fuscoruber*, and *G. rivulatus*). We investigated the relationship between group size, size of dominant individual, and coral size (Fig 5.4). For both species, group size was related to coral size (Suppl. Tab 5.2, $p < 0.01$), but was not related to the size of the dominant individual or location ($p > 0.40$). The size of the dominant individual was related to coral size for both species ($p < 0.05$), and to group size and location for *G. rivulatus* ($p = 0.03$, $p < 0.01$, respectively), but was not related to group size nor location for *G. fuscoruber* ($p > 0.36$). Coral size was related to group size and the size of the dominant for both species ($p < 0.01$), but was not related to location for either species ($p > 0.14$). There was no interaction between any of the variables for each analysis ($p > 0.27$). Note: no analyses were completed to compare these size relationships pre- versus post-disturbance as colonies were primarily

made up of pairs at LI post-disturbance, and no colonies were collected at OTI post-disturbance.

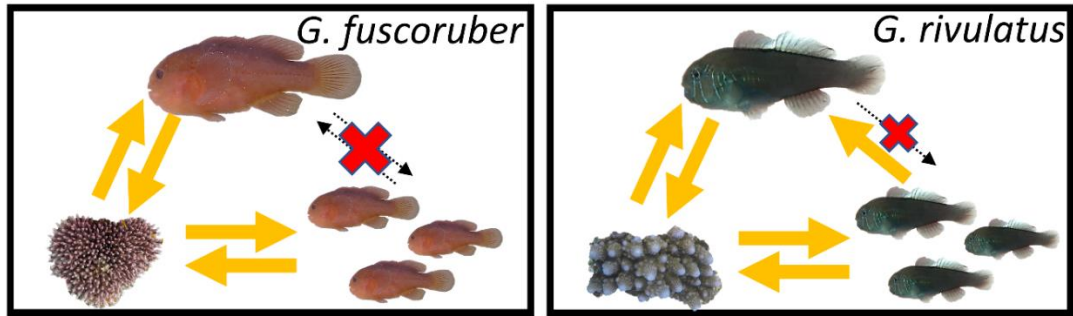


Fig 5.4. Synergistic relationship between group size, size of dominant, and coral size for group-forming *Gobiodon* gobies and their *Acropora* coral hosts. Yellow arrows identify significant effect ($p < 0.05$), and crossed out dashed lines represent no significant effect ($p \geq 0.05$).

5.4.4. Within-group plasticity: Size Ratios

We compared the size ratios between rank 1 and rank 2 (i.e. rankstep 1) for six species (*G. erythrospilus*, *G. fuscuscoruber*, *G. histrio*, *G. oculolineatus*, *G. quinquestrigatus*, and *G. rivulatus*) that were found at multiple locations with enough sample size (i.e. without *G. brochus*). Mean size ratio for rankstep 1 ranged from 0.88 and 0.94 ± 0.01 -0.02 among all species (Fig 5.5). Size ratios for rankstep 1 were not related to coral size (Suppl. Tab 5.3, $p = 0.94$), group size ($p = 0.09$), species ($p = 0.15$) nor location ($p = 0.52$), and there was no interaction between any predictors ($p = 0.24$). Since there was no effect of location, we then included a seventh species, *G. brochus*, that was only found at one location (LI). Including *G. brochus* did not change the outcome of the model with size ratios for rankstep 1 being unrelated to coral size ($p = 0.21$), group size ($p = 0.25$), and species ($p = 0.12$).

For size ratios between rank 2 (second breeder) and 3 (first nonbreeder) (i.e. rankstep 2), we did not have enough colonies with rank 3 individuals for four of the seven species (*G. brochus*, *G. erythrospilus*, *G. histrio*, and *G. oculolineatus*), so these species were excluded. Further, we pooled the size ratios for rankstep 2 for the other 3 species among locations, because there were not enough samples per location and location did not affect size ratios for rankstep 1. The size ratio for rankstep 2 trended similarly to that for rankstep 1 for most species (Fig 5.5). Size ratios for rankstep 2 were related to coral size ($p = 0.003$), group size ($p = 0.003$), and was barely significant among species ($p = 0.05$). Rank 3 tended to be much smaller for *G. quinquestrigatus* (rankstep 2 mean = 0.63 ± 0.11) than other species (rankstep 2 mean ranging from 0.85 to 0.90 ± 0.03 -0.08). Smaller rank 3 individuals for *G. quinquestrigatus* suggests that the species is primarily pair-forming, but that breeders will tolerate nonbreeders occasionally if they are far smaller in size (Fig 5.5). Some of the nonbreeders were close to juvenile size, but other were adult-sized.

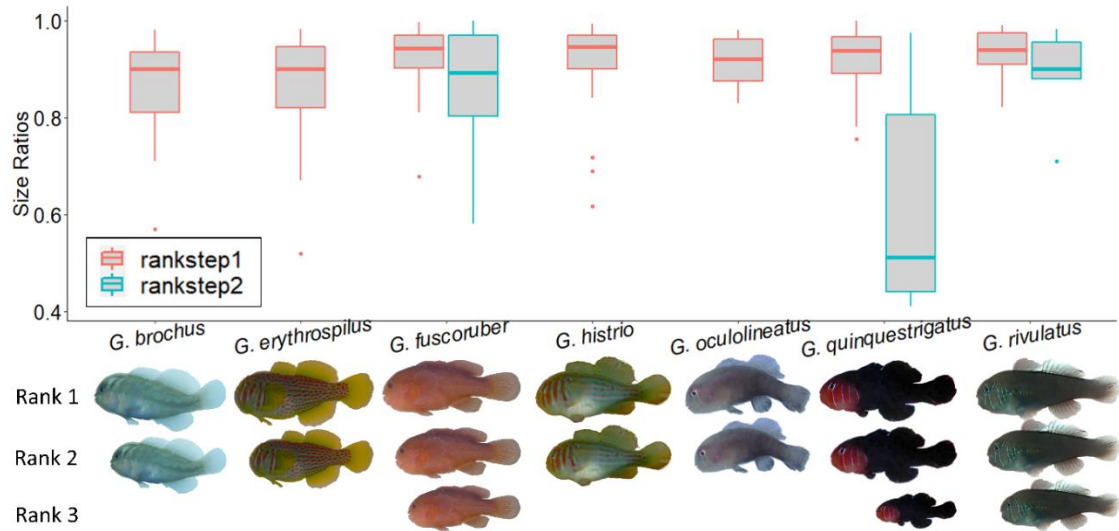


Fig 5.5. Distribution of size ratios between rank 1&2 (rankstep1), and rank2&3 (rankstep2) of single species colonies of *Gobiodon* species. Note: no rankstep2 data for *G. brochus*, *G. erythrospilus*, *G. histrio*, and *G. oculolineatus* due to insufficient data; the size differences between the same species of goby pictures are illustrated to scale based on rankstep means.

We revisited LI and PNG in consecutive years (LI2020 and LI2021, PNG2018 and PNG2019), and calculated the size ratio for rankstep 1 if both dominant individuals tagged in the first trip were still present in the following trip. The size ratios for rankstep 1 were related to coral size ($p = 0.02$), but not to group size ($p = 0.76$), species (0.30), location ($p = 0.37$), nor year ($p = 0.09$), and there were no interactions ($p > 0.07$). The time between visits at LI was one year compared to only six months at PNG, and yet there was no effect of location or interaction with year on the size ratios. Although the effect of year was not significant, there is a trend for rank 1 and rank 2 individuals to converge in size overtime (Fig 5.6).

When comparing the size ratio of rankstep1 pre- and post-disturbances at Lizard Island, we only had enough samples from *G. brochus*, *G. erythrospilus*, *G. histrio*, and *G. quinquestrigatus*. The size ratio of rankstep 1 was related to coral size ($p < 0.01$), but not to group size ($p = 0.06$), species ($p = 0.19$), nor pre- vs. post-disturbance ($p = 0.29$), and there was no interaction ($p = 0.20$).

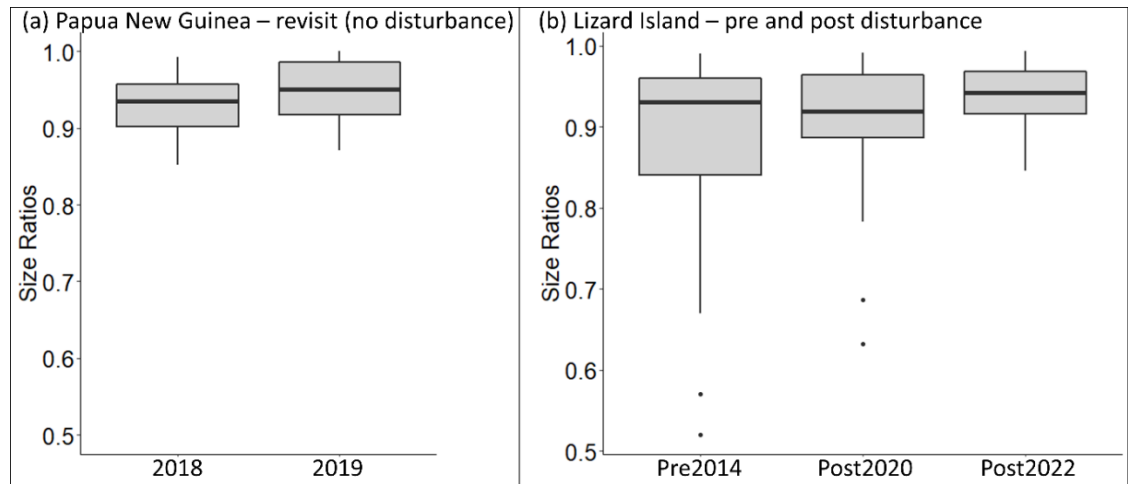


Fig 5.6. Size ratio between rank 1 and rank 2 individuals of *Gobiodon* species within single species colonies that were revisited at **a** Papua New Guinea (Sep-Nov 2018 and May-June 2019) and **b** Lizard Island before and after disturbances and follow up visit (Jan-Feb 2014, Jan-Mar 2020 and Jan-Mar-2021)

5.4.5. Within-group Plasticity: Sex Dominance Between Breeding Partners

Sex dominance was only identified during trips to LI in 2020 and 2021. We compared sex dominance in goby colonies at LI in 2020 and 2021, only if both dominant individuals tagged in 2020 were still present in 2021. There were five goby species found in high enough abundance to determine whether sex dominance existed for rank 1. In 2020, 120 colonies were identified for sex dominance, and 42 colonies were revisited in 2021. From both years combined, the sex ratio between rank 1 females and rank 1 males was 1:0.70 which differed significantly from unity 1:1 (Suppl. Tab 5.3, $p = 0.02$). There was also a difference among years ($p < 0.01$) in 2020, the ratio of female to male rank 1 was 1:1.05 among species (Fig 5.7). However, in the same colonies in 2021, females often outgrew males, and the sex ratio was 1:0.36 female to male rank 1 individuals for all species (Fig 5.7). The male never outgrew the female in any colonies (Fig 5.7). There was no difference in the ratio of female to male rank 1 individuals among species ($p = 0.30$) and no interaction between species and year ($p = 0.29$).

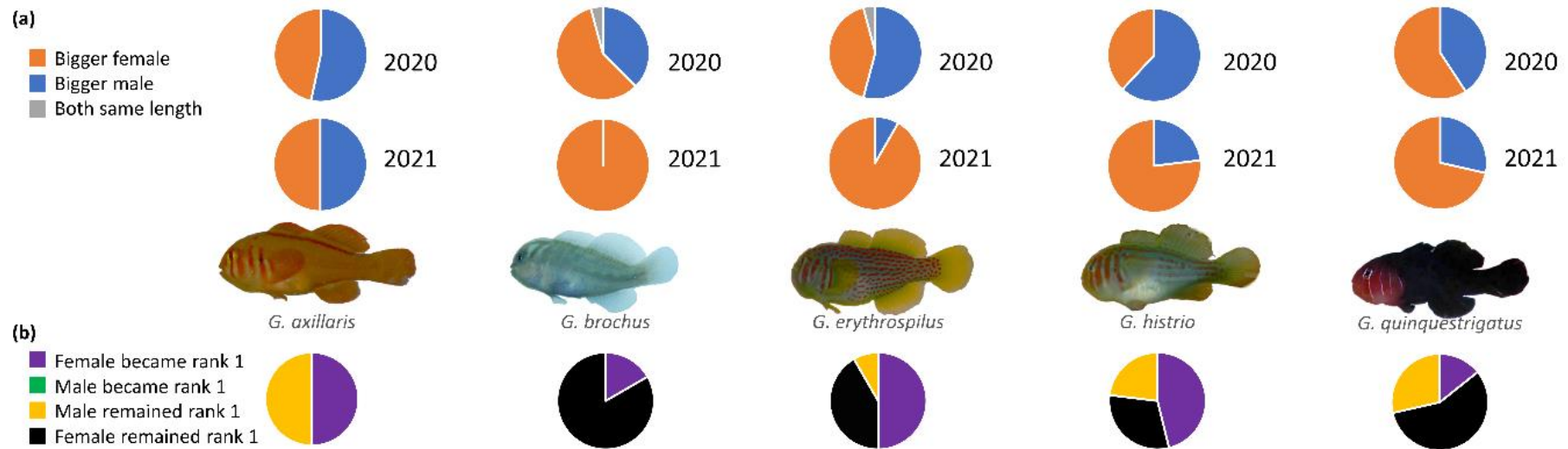


Fig 5.7. **a** Sex dominance of species visited at Lizard Island in 2020 vs. 2021, and **b** revisited the following year to see whether any sex outgrew the other in 2021. Note: no male outgrew the female in any goby colony (green).

5.4.6. Mixed Species Colonies: Social Structure and Composition

Although we did not sex individuals to confirm they were reproductively active, we did find two nests containing eggs each being guarded by a pair of different species within the same coral on more than one occasion. It is also important to note that no mixed species colonies were collected post-disturbance at any of the locations, therefore no pre- versus post-disturbance analyses were completed for hierarchy and size ratio analyses. When quantifying the size-based hierarchy within mixed groups, we found that different species were intermixed within the ranks just under 50% of the time with no difference among locations (intermixed e.g. rank 1,3,5 were species A and rank 2,4,6,7 were species B, Suppl. Tab 5.4, $p = 0.91$, Fig 5.8A, Fig 5.9). The rank 1 individual within mixed groups was generally the bigger species (as defined by Hing et al. 2019) approximately 75% of the time with no pattern among locations ($p = 0.93$, Fig 5.8B).

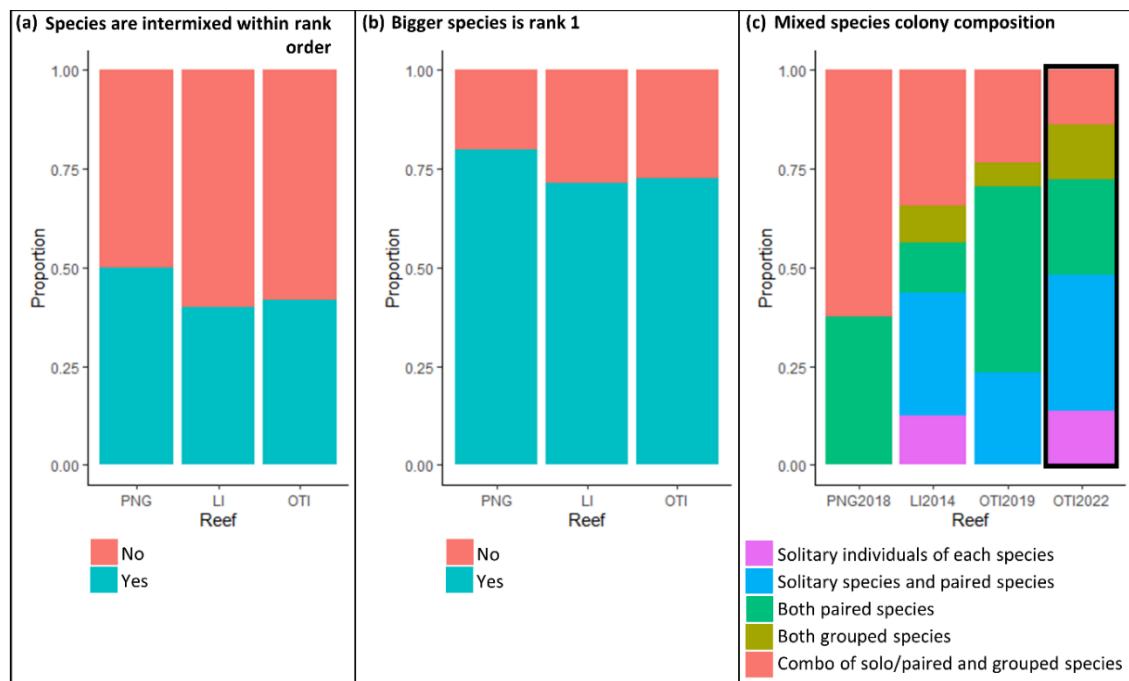


Fig 5.8. Proportion of intermixed ranks **a** and bigger species as rank 1 **b** within size-based hierarchies of mixed species colonies of *Gobiodon* and their grouping composition **c**. PNG = Papua New Guinea; LI = Lizard Island; OTI = One Tree Island; year after the location label is the year sampled; data outlined in thick black line was taken post-disturbance while all other data was taken pre-disturbance.

When we calculated the size ratios between each rank within mixed species colonies, there were sufficient large groups to compare ranksteps 1-8 (i.e. from rank 1 down to rank 9). The size ratio of each rankstep in mixed species colonies differed by coral size (Suppl. Tab 5.2, $p < 0.01$), group size ($p = 0.02$), but not by rankstep ($p = 0.10$) or location ($p = 0.11$). There was no interaction between any of the variables. We found that when size ratios were separated per species, size ratios within mixed species colonies were smaller on average (0.88 ± 0.01) than those for that same species in single species colonies (0.91 ± 0.01 , $p < 0.01$), which supports the finding that species were intermixed within mixed species colonies. We then compared size ratios of mixed species colonies, regardless of species, to single species colonies and found

no difference between mixed or single species colonies ($p = 0.22$, Fig 5.5&5.9).

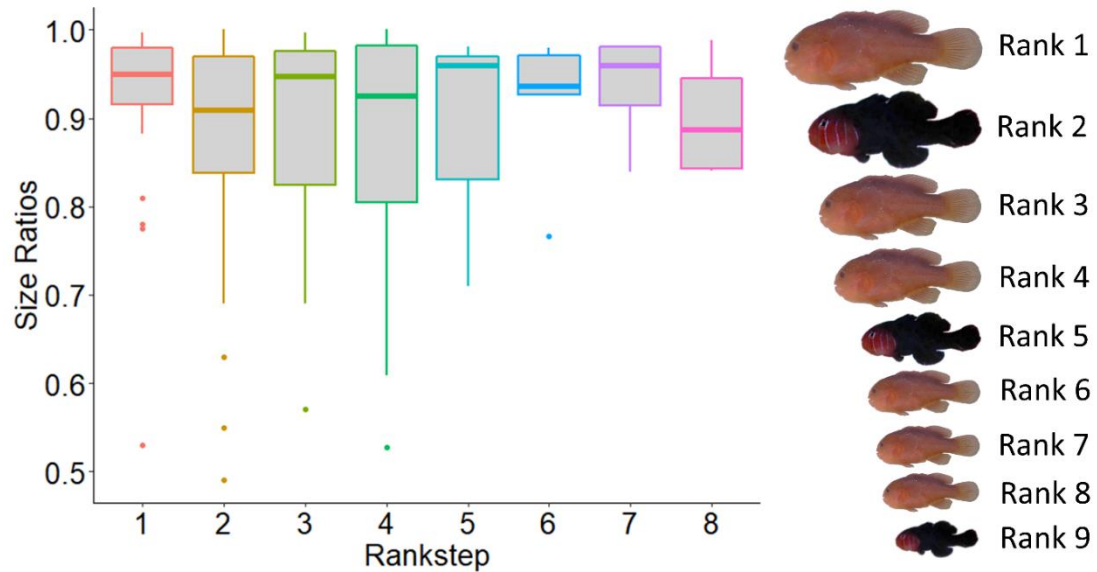


Fig 5.9. Size ratios between each rankstep within the size-based hierarchies of mixed species colonies of *Gobiodon* gobies. Note: rankstep i = ratio between rank $_{(i)}$ and rank $_{(i+1)}$ individuals; the size differences between individuals of goby pictures are illustrated to scale based on rankstep means.

Pre-disturbances, mixed species colonies were composed of solitary, pair-forming and/or group-forming species with no difference in proportion among locations (Suppl. Tab 5.4, $p = 0.69$, Fig 5.8C). There was also no difference in mixed species composition pre- or post-disturbance at OTI ($p = 0.58$, Fig 5.8C). Note, not enough mixed species colonies were found at LI post-disturbance, therefore LI was not compared for disturbance effect. Mixed species colonies were primarily made up of two species (88%), followed by three species (10%), and there was only a single colony of four species (1%, Suppl. Tab 5.4). Every *Gobiodon* species observed were found in a mixed species colony at least at one time point (Suppl. Tab 5.4). However, the most common mixed species colonies were made up of *G. fuscoruber*-*G. quinquestrigatus* colonies (23%) followed by *G. fuscoruber*-*G. rivulatus* colonies (10%) and then *G. oculolineatus*-*G. quinquestrigatus* colonies (9%, Suppl. Tab 5.5). The single most common species in mixed species colonies was *G. fuscoruber* (55%) followed by *G. rivulatus* (43%) and *G. quinquestrigatus* (41%, Suppl. Tab 5.4). The following species were found with similar proportions within mixed species and single species colonies: *G. citrinus*, *G. fuscoruber*, *G. oculolineatus*, and *G. sp.D*; all other species observed occurred more often in single species colonies than in mixed species colonies (Suppl. Tab 5.5).

5.5. Discussion

Following our sociality framework, we investigated and identified to what extent ecological, environmental and social factors affected the four levels of social variation in coral-dwelling gobies in the *Gobiodon* genus. We chose large-scale environmental factors, namely location and disturbance regime, as our primary ecological factors, smaller-scale ecological factors, namely habitat characteristics like habitat

size, and social factors, namely body size of the largest group member. Each level of variation outlined in the framework (i.e. forms of sociality, degree of sociality, social plasticity, within-group plasticity) guided our assessment of ecological and social factors. By following the framework, we found that location and disturbance regimes played substantial roles in the forms of sociality within the genus and the degree of sociality for certain species, with gobies tending away from group-forming under high disturbance regimes. In contrast, social plasticity and within-group plasticity were not directly affected by these large-scale factors but were instead indirectly affected by changes to coral size, which is heavily reduced from disturbances. From these findings, we established that societies of coral-dwelling gobies are at an extremely high risk of being vulnerable to climatic disturbances. Accordingly, this framework allowed us to identify the impacts of multiple ecological factors on animal societies over different scales.

With respect to the form of sociality, studying multiple goby species within the *Gobiodon* genus enabled us to investigate how sociality in the whole genus was affected by environmental factors. In the northern location at Kimbe Bay, Papua New Guinea, gobies tended to form pairs; in the central reef location at Lizard Island, Australia gobies tended to form single species groups; and in the southern location at One Tree Island, Australia, gobies tended to form mixed species colonies. This gradient may indicate a latitudinal shift in social systems, as seen in ground-nesting bees (Dew *et al.* 2018) and birds (Arnold & Owens 1998). Reef type may potentially explain such differences in location; for example, the movement of goby larvae may be limited in a lagoonal reef like at One Tree Island and prompt the formation mixed species colonies in order to reduce the potential for inbreeding (Selwyn *et al.* 2016). It should be noted though that we did not sample at multiple reefs at each latitude, hence limiting our ability to draw conclusions as to the major underlying causes of this latitudinal variation.

Additionally, disturbance regime was a strong predictor of sociality, with high disturbance regimes reducing the propensity for group-living as gobies were found either living solitarily or in pairs after these disturbances. After moderate disturbance regimes, gobies were also primarily living solitarily and less often in pairs, but the same proportion of groups were still found compared to pre-disturbances. Finding many gobies living solitarily is a cause for concern as pairs are needed for breeding. Gobies may be choosing to live solitarily due to the new availability of empty and small corals. Such a loss in sociality under disturbance regimes is likely due to the extreme decline in populations of gobies following particularly extreme events (Hing *et al.* 2018; Froehlich *et al.* 2021). An important advantage to living in pairs instead of groups during periods of population decline may be the ability to breed sooner and more often as their life span is likely diminished particularly from extreme disturbances (Froehlich *et al.* 2021). Therefore, queuing to breed during times of increased mortality may allow far fewer individuals to breed than during stable environments. Alternatively, gobies could have reaped the benefits of safety by numbers and breeding sooner in mixed colonies, yet no mixed colonies were found after high disturbance regimes. A lack of groups may instead be a consequence of smaller corals (Rueger *et al.* 2021a), as seen in passerine birds (Lantz & Karubian 2017). The loss of sociality after climatic disturbances may also be related to reduced food resources, as seen in butterflyfishes (Thompson *et al.* 2019). Environmental factors are therefore important predictors for the form of sociality within the genus of *Gobiodon*.

The impacts of location and disturbance regime were also observed to reduce the degree of sociality within each goby species, with two patterns emerging. Several species showed low degrees of sociality and tended to live in pairs (0.33-0.49) regardless of location or disturbance regime, which agrees with labelling these species as pair-forming as per Hing *et al.* 2018 and 2019. These species primarily lived in pairs, although some accepted nonbreeding subordinates, even in low disturbance regimes albeit not in high disturbance regimes. On the other hand, group-forming species (Hing *et al.* 2018 and 2019) showed moderate degrees of sociality (0.33-0.65) that fluctuated between group-forming or pair-forming depending on the year, location and disturbance regime, and patterns were not always similar among species. The degrees of sociality fluctuated post-disturbance depending on the species and their occurrence. The two group-living species that had the highest degrees of sociality, i.e. most subordinates in a group, at one location, *G. citrinus* and *G. rivulatus*, either continued occurring in groups with many subordinates, or became pair-forming after disturbances, respectively. The third group-living species, *G. fuscuber*, was group-living at most locations pre-disturbances and after low disturbance regimes, although with less subordinates. However, it is important to note that *G. citrinus* and *G. fuscuber* disappeared after high disturbance regimes at Lizard Island (Froehlich *et al.* 2021). Thus, living strictly in groups may not be advantageous for gobies depending on large-scale environmental factors.

Our findings do not provide support for the life insurer hypothesis of sociality (Queller & Strassmann 1998), as gobies have lower degrees of sociality in challenging environments, i.e. high disturbance regimes. Some limited fluctuation in the degree of sociality (0.59-0.81) was also observed in social spiders *Anelosimus eximius* and *Anelosimus guacamayos* among location and year, respectively, but these group-forming species remained group-forming (Avilés & Harwood 2012). Naked mole-rats living in groups have some of the highest degrees of sociality and are strictly eusocial, like the *Heterocephalus glaber* (0.95) and *Fukomys damarensis* (0.80-91) (Avilés & Harwood 2012). As gobies exhibit low to moderate degrees of sociality, environmental conditions play a large role in their tendencies to remain in groups. Our study suggests that gobies likely evolved social living in stable environments, in order to reap benefits of larger coral habitats, but will live with less subordinates and in primarily in pairs in challenging environments, thus negating the life insurer hypothesis.

When addressing smaller variations in sociality, we found that group-forming gobies were not socially plastic in relation to location, but they were socially plastic with respect to habitat size. This demonstrates that coral size is a limiting resource for gobies as corals became smaller after climatic disturbances (Hing *et al.* 2018, 2019; Madin *et al.* 2018; Froehlich *et al.* 2021). Gobies are less social when corals are smaller, which is a common consequence of climatic disturbances. The most social of the species studied at all locations, *G. fuscuber*, had a two-way positive relationship between coral size and size of the dominant, and coral size and group size, but there was no relationship between size of the dominant individual and group size. This suggests that social constraints on group size, namely the size of the largest dominant individual, has less of an influence on group size than ecological factors like coral size. For *G. rivulatus* on the other hand, group size did affect the growth of the dominant individual, but not

vice versa. There was however little impact of location on any of these relationships. For *P. xanthosoma* and *A. percula*, all three variables (group size, habitat size, and size of dominant) were affected by one another, suggesting strong social plasticity based on habitat size and social context (Buston & Cant 2006; Wong, 2011; Rueger et al. 2021). Studies on social spiders provide an interesting look at social plasticity in the form of other ecological and social factors. For example, social spiders are socially plastic to prey sizes and group sizes, and their hunting abilities are also affected by these factors (Harwood & Avilés 2013, 2018). Social plasticity therefore appears to vary depending on the taxa studied and the ecology of the taxa, and such variation allows for investigation on the impacts of large-scale factors as well.

For within-group plasticity, we found that size ratios and sex dominance ratios of gobies were not directly affected by environmental factors like location and disturbance. We found that the hierarchies within *Gobiodon* groups are similar to within *Paragobiodon* groups (Wong et al. 2007, 2008); in a goby colony the two dominant individuals are slightly different in size with a bigger rank 1 individual (1:0.88 to 1:0.92) regardless of species or location. Although males are often the bigger individual at first, females will outgrow males more than half of the time, owing to their growth rate advantage (Nakashima *et al.* 1996; Munday *et al.* 2006). Initially a bigger male allows for better paternal care and offspring success in the first breeding year, but then a bigger female allows for more offspring in a single egg clutch (Nakashima *et al.* 1996). Gobies also have bi-directional sex change which allows either individual to change sex if their mate dies and they find a new partner (Nakashima *et al.* 1996; Munday *et al.* 1998; Sunobe *et al.* 2017). This suggests that while a bigger female is advantageous in the long run, it does not limit the group to be strictly matriarchal, as seen in anemonefish, *Amphiprion percula* (Wong & Buston 2013; Buston & Wong 2014; Rueger *et al.* 2021a).

When considering variation in size ratios in colonies, specifically between rank 2 and 3, we found that their size ratio is similar to that between the breeding individuals (rank 1 and rank 2) for most species (0.9 to 0.93), except *G. quinquestrigatus*. For the latter species, rank 3 nonbreeders were far smaller than the rank 2 individuals (0.64). This is not entirely surprising as *G. quinquestrigatus* was living primarily in pairs, suggesting limited tolerance of breeders for any non-breeders. Size ratios between these two ranks were affected by coral size. Therefore, living in groups may be costly for nonbreeders as they must remain far smaller than breeders, making living in groups potentially an advantage only in large corals (Hing *et al.* 2019; Rueger *et al.* 2021a). In strictly group-forming species however, breeders are tolerant of nonbreeders and appear to allow nonbreeders to grow larger (Rueger *et al.* 2021a).

When investigating the within-group composition of mixed colonies, we found that that different species were often interspersed in ranks within the hierarchy. Interestingly though, the size ratios between ranks remained the same regardless of which species were adjacent in ranks, and regardless of location, but was affected by coral size. When factoring in the clear size differences between goby species, with some species growing larger on average than others (Hing *et al.* 2019), we found that bigger species tended to occupy the rank 1 position (i.e. largest individual) in mixed species colonies, regardless of location. Accordingly, this suggests that growth regulation is critical for peaceful cooperation, whether it be in

single species colonies or mixed species colonies. With a larger coral, higher ranks may be able to grow bigger, then allowing additional individuals to cooperate within the size-based group. There was no particular trend for mixed species colonies to be composed of only pair-forming individuals, groups, or a combination of both, and this was not affected by location or disturbance regime. However, there appears to be some advantage to living in mixed species colonies for some species, e.g. *G. fuscovuber*, *G. quinquestrigatus* and *G. rivulatus*, which did so more than others (Ellis & Good 2006). By far the most common mixed species colony was composed of *G. fuscovuber* and *G. quinquestrigatus* and this particular pairing may not necessarily have to do with the size differences between species as neither is particular smaller than the other (Hing *et al.* 2019). One potential advantage of living with congeners may be that individuals can reach breeding status quicker (Rueger *et al.* 2021a). In fact, we did find two sets of eggs guarded by different sets of species within the same mixed species colony on multiple occasions. Yet, even in mixed species colonies, we often found more than 2 individuals of the same species. Instead, an alternative advantage is that living in mixed species colonies means territory defence against predators is shared amongst more individuals, thus decreasing the load of each individual while still allowing for reproduction (Goodale *et al.* 2017; Rueger *et al.* 2021a). Gobies in mixed species colonies are likely reaping the benefits of both faster breeding rights and greater territory defence while maintaining size-based hierarchies for cooperation. It is also possible that there is no advantage of mixed species colonies over single species colonies. Future studies comparing egg clutch sizes and territory defence among single species and mixed species colonies would be important in identifying the benefits of living in mixed species colonies.

In each of the four levels of variation, we found direct and indirect impacts of climatic disturbances, suggesting an extremely high vulnerability rank to loss of sociality (Fig 5.1). The form of sociality and degrees of sociality were each negatively affected by high disturbance regimes. Social plasticity and within-group plasticity were not directly affected by disturbances, but instead were indirectly reduced due to a decrease in coral size. Since disturbances drastically diminish the sizes of available corals (Hing *et al.* 2018, 2019; Madin *et al.* 2018; Froehlich *et al.* 2021), the social plasticity and within-group sociality are indirectly vulnerable to disturbances. Accordingly, each level of variation in coral-dwelling goby societies is vulnerable to disturbances, highlighting an extremely poor outlook for these gobies.

By quantifying the four levels of variation, the sociality framework introduced here provides a flexible yet robust assessment of social organisation of animal societies along different scales of ecological and environmental factors. Depending on the factors of interest, each level of variation can be quantified at a defined spatial and temporal scale. The framework can identify limiting resources that will play huge roles in the formation and maintenance of animal societies. The framework is particularly useful as it requires only monitoring of group sizes, measures of cooperation, e.g. size and sex of individuals within groups, and measures of ecological and social factors of interest, e.g. habitat size and proximity to other groups, without requiring manipulative experimentation (although this would be encouraged). The levels of variation (i.e. forms of sociality, degree of sociality, social plasticity, and within-group plasticity) as well as the social and ecological factors can be easily adapted to the life history, cooperation, and ecology

of the social taxa (e.g. Fig 5.1). The framework can be adapted for any species and many different factors, including larger-scale ones like spatiotemporal and disturbance factors, thus making observational data a powerful tool for predicting the social organisation and plasticity of many taxa into the future. By assessing how each level of variation is affected by ecological factors, the metrics can then be integrated to identify the vulnerability rank of the societies studied.

Chapter 6: Data Chapter: Habitat health, size and saturation do not alter movement decisions in a social coral reef fish

Published in Animal Behaviour.

6.1. Abstract

While habitat is often a limiting resource for group-living animals, we have yet to understand what aspects of habitat are particularly important for the maintenance of sociality. As anthropogenic disturbances rapidly degrade the quality of many habitats, site-associated animals are facing additional stressors that may alter the trade-offs of moving or remaining philopatric. Here we examined how **habitat health, size and saturation** affect movement decisions of a coral-dwelling goby, *Gobiodon quinquestrigatus* (Five-Lined Coral Goby), that resides within bleaching-susceptible *Acropora* coral hosts. To assess effects of habitat health, we translocated individuals far from their home corals into dead corals with the choice of adjacent healthy corals. To assess effects of habitat size and saturation, we manipulated coral sizes and the number of residents in healthy corals. Remarkably, 55% of gobies returned home regardless of treatment, 7% stayed in the new coral, and the rest were not found. Unlike other coral reef fishes, habitat factors did not affect how costs of movement influence group-living decisions in this species. These obligate coral-dwelling fishes preferred to home instead of choosing alternative habitat, which suggests a surprising awareness of their ecological surroundings. However, disregarding alternative high-quality habitat is concerning as it may affect population persistence under conditions of rapid habitat degradation.

6.2. Introduction

Social animals often live in specific microhabitats, like tunnels for mole rats, sponges for shrimp, tree cavities for hornbills, and cnidarians for reef fishes (Faulkes *et al.* 1997; Duffy & Macdonald 2010; Gonzalez *et al.* 2013; Wong & Buston 2013). For many social animals, such habitat provides access to food, mates, territory and breeding sites (Lassig 1976; Woolfenden & Fitzpatrick 1978; Kokko & Ekman 2002), and therefore represents a key limiting resource (Faulkes *et al.* 1997; Duffy & Macdonald 2010; Wong & Buston 2013). As such, habitat can play a key role in the evolution and maintenance of sociality since habitat factors are known to modulate decisions of individuals from many taxa to remain in groups as a nonbreeder or move to breed elsewhere (Selander 1964; Emlen 1982; Stacey & Ligon 1991; Hing *et al.* 2017; He *et al.* 2019).

According to the ecological constraints hypothesis (Emlen 1982), delaying reproduction to remain in groups outweighs moving to other habitat to breed independently due to high costs of movement and habitat saturation (Selander 1964; Emlen 1982; Gonzalez *et al.* 2013; He *et al.* 2019; Branconi *et al.* 2020). Movement imposes substantial costs because of predation risk and energy expenditure, especially if alternative habitat is already saturated (Arnold & Owens 1998). Alternatively, when reproduction of

low ranking individuals is suppressed, moving to less saturated habitats could mean reaching breeding positions sooner (Selander 1964; Wong 2010). Hence for social animals, the trade-offs between dispersing and remaining philopatric are likely driven by both habitat saturation and costs of movement. Alternatively, the benefits of philopatry hypothesis suggests that remaining in groups enables access to high quality habitat, which can increase survival and long-term reproduction (Emlen 1982; Stacey & Ligon 1991). Habitat quality is often inferred via habitat size, and larger habitats typically support larger groups due to the additional space and resources available for supporting more individuals and reducing conflict (Parry 1973; Woolfenden & Fitzpatrick 1978; Hing *et al.* 2018). Lower ranking individuals may even forgo reproduction to reap the benefits of remaining in larger habitat (Woolfenden & Fitzpatrick 1978; Wong & Buston 2013).

While studies have focused primarily on the role of habitat size as a measure of quality (Parry 1973; Woolfenden & Fitzpatrick 1978; Buston 2004; Wong *et al.* 2007), other parameters clearly dictate habitat quality and hence the degree of movement and sociality of animals. For social animals residing in living habitats, as is seen in shrimp inhabiting sponges (Duffy & Macdonald 2010), ants inhabiting plants (Stapley 1999), and fish inhabiting cnidarians (Wong & Buston 2013), movement decisions may depend on the health of their ‘host’ habitat. Given that habitat degradation is occurring at an alarming rate due to environmental and anthropogenic disturbances (Turner 2010; Hughes *et al.* 2018a), investigating the role of habitat health is necessary for a holistic understanding of how habitat promotes sociality (He *et al.* 2019). Linking the interaction between habitat health, size, and saturation to the movement and sociality of habitat-specialists is especially important since threats of habitat degradation and mortality are increasing. Therefore, we urgently need to assess the interplay between multiple habitat factors on movement decisions in order to predict and potentially mitigate the social consequences of environmental degradation.

However, we cannot assume that the same reasons for living in groups for habitat-dependent animals apply to all species within similar taxa. For example, from a global analysis, birds were thought to remain social in order to withstand challenges of variable environments (Jetz & Rubenstein 2011). However, this general conclusion does not apply universally; for example, habitat saturation in stable environments may instead explain why hornbills (Bucerotidae) cooperate in groups (Gonzalez *et al.* 2013). Recently, studies on coral reef fishes in the families of Gobiidae and Pomacentridae have provided important insights into the ecological constraints theory and benefits of philopatry (Taborsky & Wong 2017; Rueger *et al.* 2021a). Several species in both families reside exclusively within corals and anemones in pairs or groups and cooperate peacefully via size hierarchies by controlling individual growth (Buston 2003a; Wong *et al.* 2007; Rueger *et al.* 2021a). Critically, although these species are typically considered site-attached, habitat size and saturation have been shown to affect the movement decisions of *Paragobiodon xanthosoma* (Emerald Coral Goby; Gobiidae) and *Amphiprion percula* (Orange Clownfish; Pomacentridae) whereby individuals trade off costs of movement for larger or less saturated habitats (Wong 2010; Branconi *et al.* 2020). It is therefore possible that habitat factors could influence movement decisions of other coral reef fishes with similar habitat needs and social structures.

Here we investigated how multiple ecological factors, namely habitat health, size, and saturation, influence the movement decisions of a coral-dwelling goby, *Gobiodon quinquestrigatus* (Five-Lined Coral Goby). Like the closely related *Paragobiodon xanthosoma*, *Gobiodon* species provide an excellent model system for testing predictions about how ecological factors influence social behaviour since groups are also organized in size hierarchies and these fish reside within branches of living cnidarians, specifically acroporid corals (Munday 2001; Bonin *et al.* 2009). *Gobiodon* species have also been documented to move between corals, although such movements are thought to only occur if conditions in their coral become unfavourable, e.g. eviction by group members or mate death (Munday *et al.* 1998). Unlike *Paragobiodon xanthosoma*, *G. quinquestrigatus* are classified as facultatively social because group-living only occurs when coral hosts are large enough, whereas pair-forming occurs when corals are small (Hing *et al.* 2019). Such facultative sociality is useful because it enables us to examine and manipulate the potential factors promoting group- over pair-formation. In line with the ecological constraints and benefits of philopatry hypotheses, we completed an *in situ* manipulative experiment to test the predictions that these gobies would prefer to move to a: (1) healthy versus dead coral, (2) larger coral, and (3) less saturated coral (smaller groups) to improve breeding opportunities.

6.3. Methods

6.3.1. Site location

All experiments were conducted *in situ* using SCUBA during two trips (Sep-Nov 2018 and May-Jun 2019) at four inshore reefs near Mahonia Na Dari Research and Conservation Centre in Kimbe Bay, West New Britain, Papua New Guinea (-5.42896°, 150.09695°). A total of 132.17 hours of SCUBA diving were required per person in a diving pair to complete the study *in situ*.

6.3.2. Experimental design

Our experiments involved removing a goby from its home coral and translocating it into a dead coral that was situated adjacent to a live coral. To set up these experiments, dead corals of *Acropora kimbeensis* were opportunistically located on the reef. These dead corals were of two size categories: small (11.2-cm avg. diameter) and large (17.3-cm avg. diameter), as calculated by taking the arithmetic average across three axes of each coral to indicate coral size (Kuwamura *et al.* 1994). We then randomly searched for similarly-sized live corals that contained *G. quinquestrigatus* individuals. To set up one trial, a dead coral was placed within 10 cm of the similarly-sized live coral (Fig 6.1, Suppl Fig 6.1A,B & 6.2). In neighbouring corals (within a 10-m radius), we then located a ‘focal’ *G. quinquestrigatus* individual that was smaller (16.9-mm avg. standard length, range: 12.2-22.5 mm) than gobies in the live coral (next to the dead coral). Selecting a smaller goby was important to reduce potential eviction by residents because gobies peacefully cooperate within groups by maintaining size-based hierarchies (Wong *et al.* 2007). The focal goby was removed from its original home coral using a clove oil anesthetic solution and hand nets

(Munday & Wilson 1997) and injected with a unique visible implant elastomer identification tag (Northwest Marine Technology, Inc., Anacortes, Washington, USA) (Munday 2001). The focal goby was then translocated into the dead coral (Fig 6.1), and we revisited trials daily for up to 7 days to determine where the focal goby subsequently moved.

Since the dead coral was adjacent to the live coral, this gave the focal goby the choice of a dead or live coral (thereby examining the effect of habitat health). To simultaneously assess effects of habitat size, the dead and live corals were size-matched in each trial (small or large, Fig 6.1). In addition, to investigate the role of habitat saturation, treatments were carried out using both small and large coral sizes under three levels of habitat saturation (Fig 6.1): (i) no residents, (ii) one bigger conspecific, or (iii) two bigger conspecifics in the live coral. Accordingly, a total of six treatment combinations were trialed: three levels of habitat saturation for two levels of habitat size (Fig 6.1). Ten trials were completed per treatment combination, totaling sixty trials (sample size power = 0.952: $n = 10$ trials per combination, factor 1 = 2 treatments, factor 2 = 3 treatments, effect size = 0.3, $\alpha = 0.5$). For each trial, a different focal fish and live coral were used.

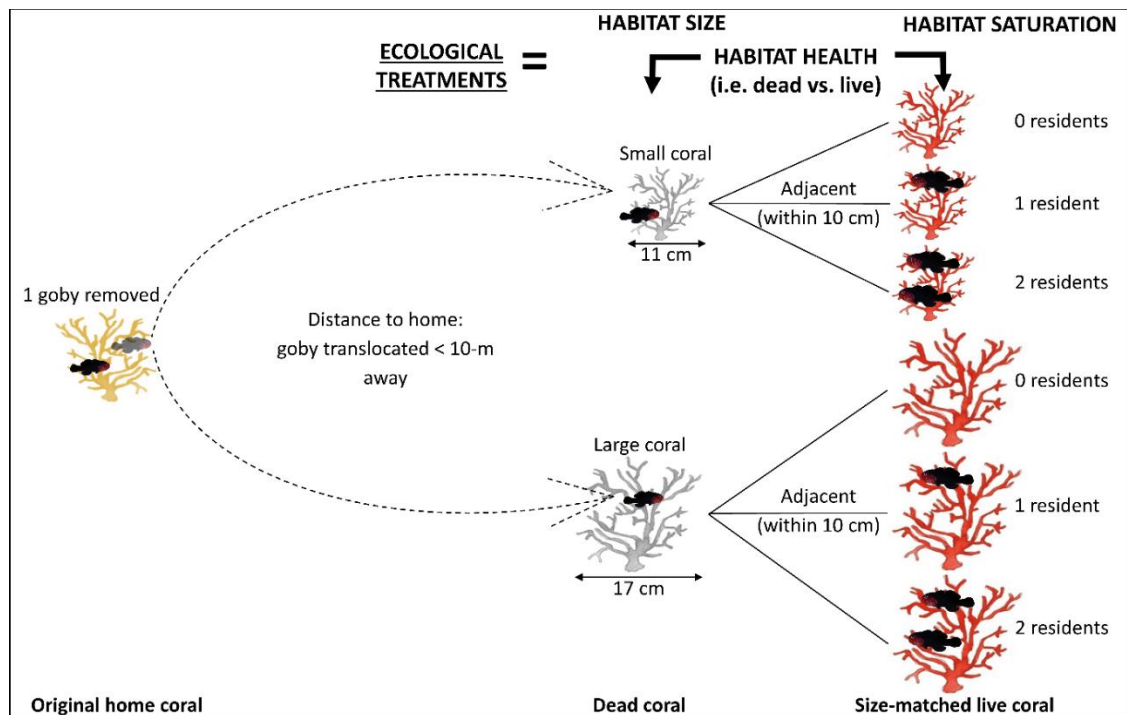


Fig 6.1. Experimental design: a focal goby was translocated into a dead coral adjacent to an unfamiliar live coral of similar size to offer two habitat health options: dead coral vs. live coral. Six treatment combinations were used to account for two habitat sizes and three habitat saturation levels.

To set up enough trials, we located sufficient numbers of live corals containing one or two residents, so we did not need to manipulate group sizes for habitat saturation treatments of one or two gobies. However, there were not enough empty live corals for the treatment with no residents (Fig 6.1), so we removed all residents from live corals to simulate the lowest saturation level. Removed residents were housed at the Mahonia Na Dari Research and Conservation Centre in a 15l bucket with an air stone, given

pellet food twice a day, and received a 25% water change daily. Residents were returned to their home corals 48hrs later.

Before each trial, the focal goby was removed from its home coral and given 5 min to recover in a seawater-filled bag underwater. To start a trial, the focal goby was translocated into the dead coral that was covered in a net to allow the fish to settle in the dead coral without potentially darting away (Suppl Fig 6.1C). The goby was given a further 5 min to settle before the net was removed. Initially, the focal gobies were observed for 30 min by a scuba diver *in situ* and recorded using a video camera (GoPro 5) for the first 24 trials. However, during these initial observations we noticed that focal gobies rarely moved from the dead coral so subsequent trials only included a 5-min observation by a scuba diver once the net was removed. In the following days, to confirm whether and where focal gobies had moved, the dead coral, the adjacent live coral, and the home coral were checked daily for two weeks. From these observations, it became apparent that gobies not located within the first week were never located, hence thereafter experimental plots were revisited daily for up to 7 days. Since most gobies moved within the first 24hrs (Suppl Fig 6.2), if a focal goby stayed in either the dead coral or the unfamiliar live coral for 48hrs, their choice was recorded, and the goby was then returned to its home coral.

To assess where the focal goby moved and whether any movement decisions were based on the level of saturation of neighbouring corals in the study plot, we surveyed all *Acropora* corals larger than 7-cm in diameter (Froehlich *et al.* 2021) within a 10-m radius from the dead coral in each trial. Additional covariables were recorded and accounted for in data analysis (see Suppl Tab 6.1).

6.3.3. Data analysis

The effect of habitat health (live or dead) on the final location of focal gobies was compared using a chi-squared goodness-of-fit test with the null hypothesis that gobies would equally prefer the dead or live coral, or leave the experimental setup. The effects of the six treatment combinations on the final location of the focal goby (i.e., in dead coral, in live coral, goby not located, returned to home coral) were compared using multinomial logistic regression models. For each multinomial model, the baseline reference category level was finding the focal goby in the dead coral, and the models tested whether the different predictors affected the odds of falling into each alternative category level relative to the baseline. Both habitat size (small or large) and habitat saturation (0, 1, or 2 residents) were included as fixed factors along with the following covariables: distance to home coral, number of gobies in home coral, proportion of uninhabited corals within 10-m radius, and average group size of conspecifics in inhabited corals within 10-m radius. Recruits (i.e. individuals that newly settled onto the reef after a planktonic larval stage were distinguished from juveniles and other life stages by distinct colour and markings, Hing *et al.* 2018) in the home coral were not included in analysis, because recruits often move between corals before settlement (Froehlich pers. obs. & Hing *et al.*, 2018). Whether movement entailed high costs was tested by comparing the probability of locating the focal goby (moved successfully) versus not locating the focal goby (moved unsuccessfully) after 7 days, using a chi-squared goodness-of-fit test. Data analysis was completed in RStudio (RStudio Team 2020) with R v4.0.1 (R Core Team 2020) packages:

VGAM (Yee 2010), car (Fox & Weisberg 2019), tidyverse (Wickham *et al.* 2019), and rcompanion (Mangiafico 2016).

6.3.4. Ethical note

The study was completed in accordance with PREPARE and ARRIVE guidelines and approved under the University of Wollongong animal ethics protocols AE1404 and AE1725 and Papua New Guinea Research Visa Permit AA654347. Before undertaking the full study, we completed a successful pilot test in Papua New Guinea in September 2018. We ran a power analysis to determine the optimal sample size for each trial (see Methods – Experimental Design). Each fish was only used once to minimize stress and to avoid confounding the results. We collected individuals with hand nets and clove oil to minimize impacts on other surrounding fauna and flora (Frisch *et al.* 2007). Fish were placed in large plastic bags (30 by 40cm) to limit contact and stress on animals. We tagged, measured, and relocated fish within 20 min to minimize distress. Fish were less than 4 cm in length, and bags received new water every 5 min to replenish water quickly. To limit stress from handling, fish were released directly from plastic bags into their corals. Animals were monitored for up to 5 min after release to confirm they had returned to normal behaviours. For fish placed in captivity for up to 48 hrs, enrichment in the form of coral skeletons were placed for shelter. Fish were monitored 5 times per day. Pairs of fish living together underwater were placed together in captivity in order to reduce stress through mate familiarity.

6.4. Results

We completed 24 trials in 2018 and 36 trials in 2019 (total = 60 trials). Movement decisions of focal gobies were not dependent on habitat size ($p = 0.93$, see Suppl Tab 6.1 for all statistical outputs, Fig 6.2), or saturation ($p = 0.88$, Fig 6.2). Surprisingly, only four gobies remained in the experimental plot: one goby stayed in the dead coral and three moved into the live coral (Fig 6.2). Therefore, most focal gobies (93%, $n = 56$) did not remain in the dead coral or move to the adjacent live coral, rejecting our hypothesis that movement decisions were affected by habitat health ($p < 0.001$, Fig 6.2). Instead, 55% of focal gobies ($n = 33$) were located back in their home coral, which was up to 10-m away (Fig 6.3A). Gobies that returned home travelled between 0.6 to 9 m (Fig 6.3B). While most returned home within 1 day, some took up to 7 days (Suppl Fig 6.3). The remaining 38% of gobies ($n = 23$) could not be located anywhere in the dead coral, live coral, home coral, or in any of the corals within a 10-m radius despite thorough searches. This therefore suggests that they did not survive and thus faced high costs of movement as the number of individuals located were similar to the number of individuals not located ($p = 0.18$). None of the other measured covariables were related to movement decisions ($p > 0.12$).

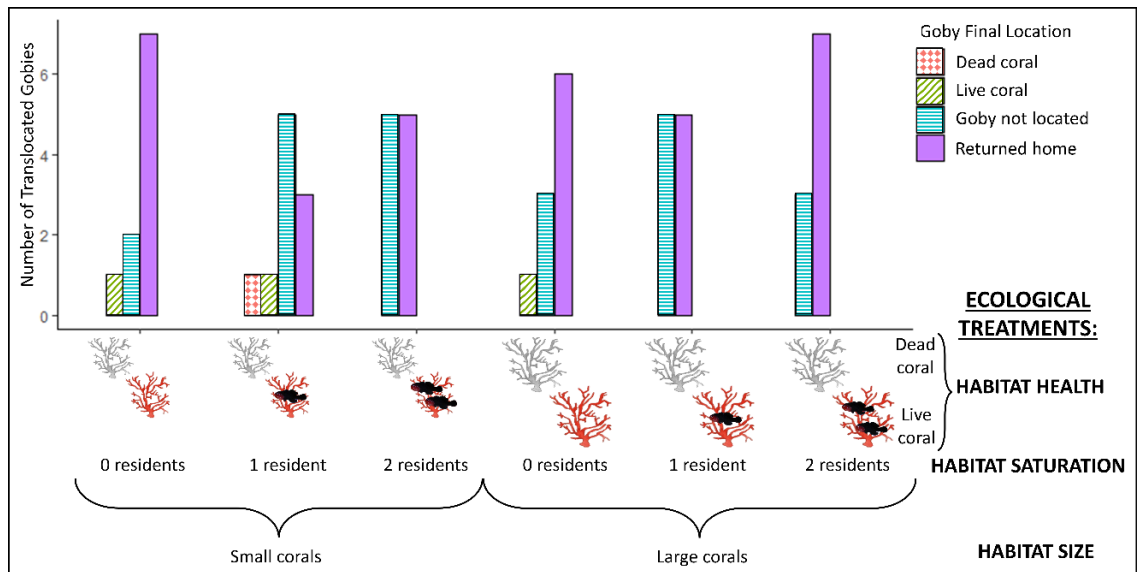


Fig 6.2. Frequency of gobies' final location in relation to habitat health (live/red coral or dead/grey coral), saturation and size.

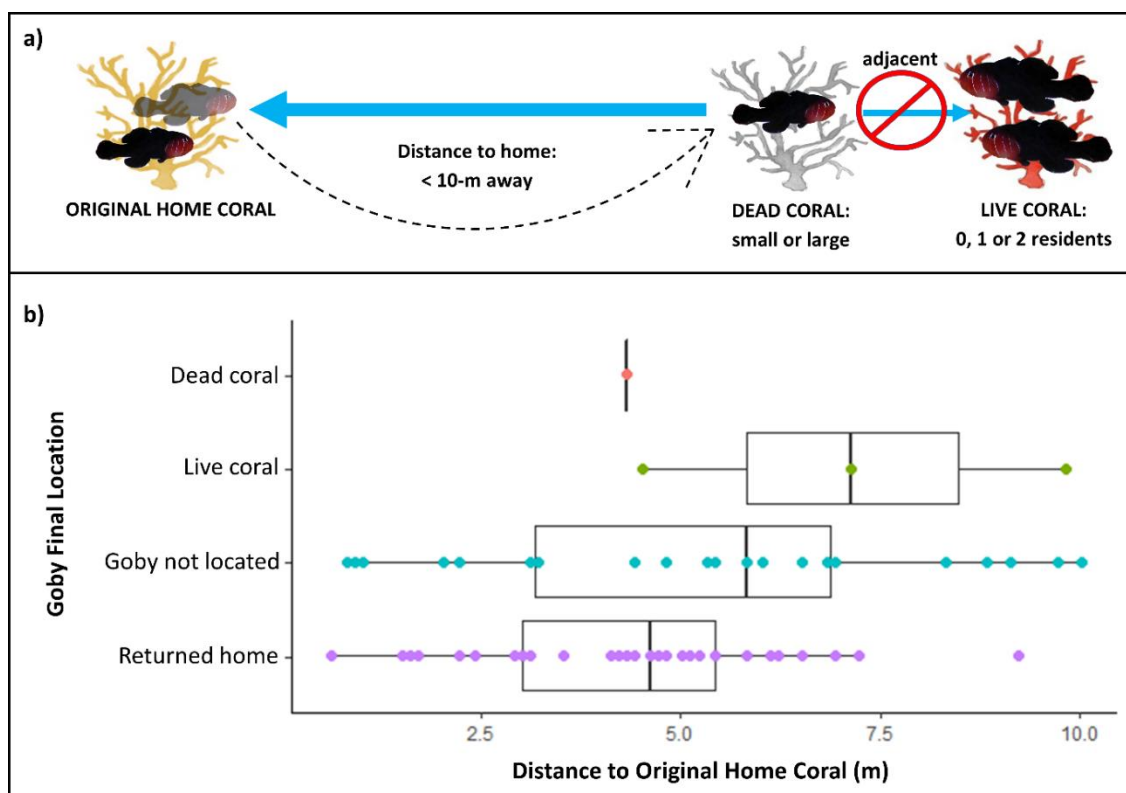


Fig 6.3. **a** Most common outcome for coral gobies that were translocated into a dead coral away from their home coral. Thin dashed arrow represents translocation, solid arrows represent expected outcomes, and the circle crosses out the least popular outcome. **b** Final location of focal gobies in relation to the distance to travel and return to their home coral.

6.5. Discussion

By experimentally manipulating three ecological factors (habitat health, size, and saturation), we simultaneously tested multiple components of two hypotheses of sociality: ecological constraints (costs of movement and habitat saturation) and benefits of philopatry (habitat health and size). Surprisingly, when these small-bodied fish were translocated up to 10-m away, they preferentially returned to their home coral instead of moving into an alternative live coral nearby (within 10 cm). This preference occurred despite high apparent costs of movement (38% chance of mortality). In contrast, movement decisions were not related to habitat health, size, and saturation, contradicting the hypothesized role of ecological factors on movement. Instead, these findings highlight an unsung role of habitat familiarity and benefits of homing in movement decisions in this social fish.

For other social reef fishes, previous studies have demonstrated that habitat factors influence the movement decisions of individuals, thereby promoting sociality (Wong 2010; Branconi *et al.* 2020). Numerous studies found positive correlations between habitat size and group size (Fautin 1992; Wong 2011; Chausson *et al.* 2018; Hing *et al.* 2018, 2019; Barbasch *et al.* 2020), demonstrating the important role of habitat in determining levels of sociality. In addition, habitat saturation influences dispersal and grouping decisions in the coral goby *Paragobiodon xanthosoma* (Wong 2010) whereby individuals preferentially move to adjacent corals of low saturation (low risk of movement). Furthermore, since coral gobies and damselfishes only inhabit relatively healthy corals and leave highly degraded and dead corals (Feary 2007; Feary *et al.* 2007; Bonin *et al.* 2009; Pratchett *et al.* 2020), we expected coral health to influence movement decisions. However, the current study demonstrated that none of these habitat factors (health, size, and saturation) influenced the movement of *G. quinquestrigatus*. Instead, gobies remarkably returned home even though i) they were often reinstated as nonbreeding subordinates at home, ii) there were opportunities to breed immediately in nearby corals that were healthy, large, and had low saturation, and iii) there were high costs of returning home due to the long distances and risks of predation. Future studies manipulating these factors in controlled laboratory settings may be useful to complement this experiment, however the fact that our study was conducted *in situ* provides a more realistic assessment of the role of habitat factors on movement decisions.

Why do *G. quinquestrigatus* individuals facing high costs of movement return home when other social reef fish species, such as *P. xanthosoma* and *Amphiprion percula*, prefer to join alternative groups instead (Wong 2010; Branconi *et al.* 2020)? Homing ability has already been demonstrated in *G. histrio* (Wall & Herler 2009), as well as other cryptobenthic and reef fishes (White & Brown 2013; Streit & Bellwood 2017), suggesting broader benefits of homing. However, the anemonefish *A. percula* only homed when distances to travel home were small (0.5 m) and never when ecological constraints were heightened and travel distances reached 5 m (Branconi *et al.* 2020). Interestingly, even though *G. quinquestrigatus* are at least one third smaller than anemonefish, they preferred to home despite longer distances (up to 10 m) and high costs of movement (estimated 38% mortality). Resident crabs within alternative corals (Vytopil & Willis 2001) may have deterred some of the translocated gobies as they are known to be aggressive

towards introduced gobies (Lassig, 1977), however resident crabs were not always present in all alternative corals (Froehlich pers. obs). Instead, perhaps *G. quinquestrigatus* home due to the benefits of associating with familiar conspecifics, like in social damselfishes (Jordan *et al.* 2010). Returning to a well-established social hierarchy (Griffiths *et al.* 2004; Branconi *et al.* 2020) means avoiding costs of re-establishing dominance, like immediate eviction and possible mortality from enhanced aggression by unfamiliar residents (Wong *et al.* 2007; Wong & Balshine 2011). In our study, we translocated fish that were smaller than those found in alternative corals in order to reduce potential conflict within the hierarchy should they have chosen the adjacent coral, however returning to familiar conspecifics may still outweigh costs of movement. Importantly, since gobies in our study returned home even if they were the only one residing in that coral, there may be benefits of returning to a familiar host habitat, as seen in the cardinalfish *Sphaeramia nematoptera* (Rueger *et al.* 2018). Cardinalfishes move hundreds of meters daily and return to the same host, but host fidelity is more important than mate fidelity because new mates are common (Rueger *et al.* 2018). Gobies, in contrast, may move temporarily between corals as juveniles, but eventually select a particular host and only leave that coral if conditions become unfavourable, like host death, the queue to inherit a breeding position is too long, or their mate dies (Kuwamura *et al.* 1996; Munday *et al.* 1998; Bonin *et al.* 2009; Wong 2010). This site fidelity suggests that certain aspects of their particular coral habitat may enhance their fitness (Munday 2001). Thus, choosing an alternative host could be less advantageous than attempting to return to their familiar home coral.

Our study revealed that not only are coral gobies clearly specialized to a particular type of habitat, but also to specific sites that they are familiar with. Such specificity might prove disadvantageous under conditions of rapid habitat degradation, particularly due to cyclones and bleaching (Hing *et al.* 2018; Hughes *et al.* 2018a; Froehlich *et al.* 2021), because maintaining plasticity in habitat utilization would enable these fish to reside in any habitat available following environmental disturbances (Pratchett *et al.* 2020). However, unlike other social fishes, *G. quinquestrigatus* opted to pay high costs of movement by returning to their familiar corals rather than adopting other suitable corals nearby. Such interspecific differences may disproportionately alter the maintenance of sociality among species as their habitats are degrading at alarming rates. Since our study site was located on a relatively undisturbed reef system, perhaps the homing of gobies reflects the overall reef condition. Hence, focal individuals may only restrict movements and adopt alternative habitat if their reef system is overall degraded. Further research investigating whether degrees of disturbance affect movement and grouping decisions would be important for predicting the impacts of environmental change on social species.

6.5.1. Conclusions

While habitat factors are thought to play an important role in movement decisions, here we show that habitat saturation, size and health do not influence the use of alternative hosts by coral gobies when their home habitats are still viable. Our study offers new insights into movement decisions in this obligate coral dwelling fish. Instead of forming new groups or inhabiting alternative corals of high quality, this social fish opts to swim long distances to return to their familiar home coral. These findings suggest that habitat, mate and/or social group familiarity drives homing behaviour in coral gobies. Since movement decisions

will likely have ramifications for the maintenance of sociality, the tendency to home may subsequently influence the formation and maintenance of social groups in this species. In addition, this study indicates that future changes due to climate change, such as habitat degradation and fragmentation, will likely alter the costs and benefits of movement, with implications for the maintenance of sociality and persistence of populations under future conditions.

Chapter 7: General Discussion and Conclusion

Sociality in habitat specialist fishes is a promising field of study that provides an important ecological link between mutualisms, social living, and climate change. Observational and manipulative studies have provided a substantial amount of information concerning the potential for climate change to affect the coral-fish mutualisms and the sociality of these fishes (e.g. Wong 2010; Hing *et al.* 2018, 2019; Pratchett *et al.* 2020; Froehlich *et al.* 2021, 2022). For my dissertation, I aimed to answer how coral-fish mutualisms respond to climatic disturbances and what potential mechanisms from the fish perspective may explain such responses. I found that environmental disturbances may break down coral-fish mutualisms (Froehlich *et al.* 2021, *In review*), and I identified multiple mechanisms that explain such impacts on the fish symbionts with focus on how coral loss affects the fish symbiont (Froehlich *et al.* 2022, *In review*, *in prepa*, *In prepb*). I investigated a coral-fish mutualism with one of the coral genera that is most susceptible to climate change (e.g. cyclones, heatwaves, and crown-of-thorn starfish predation), even though it is a fast growing and branching coral (Pratchett *et al.* 2017a; Hughes *et al.* 2018a, 2019a; Madin *et al.* 2018). By investigating the mutualism between coral-dwelling gobies from the genus *Gobiodon* and scleractinian corals from the genus *Acropora*, I was able to use a multi-species comparative approach with long-term datasets to understand to what extent gobies are affected by disturbances. Such comparative studies within a genus and among different taxa are critical for uncovering the factors that affect mutualisms (Kiers *et al.* 2010; Angelini *et al.* 2011; Rueger *et al.* 2021a). In the following discussion, I first highlight the major findings from my thesis, and then provide an extended discussion on key findings from my thesis.

7.1. Major Findings

To investigate the impacts of environmental disturbances on coral-goby mutualisms, I first set the scene with population monitoring studies (Chapter 3 and 4). I found that after multiple and extreme climatic disturbances, i.e. cyclones and bleaching, gobies declined far more than their coral hosts (Froehlich *et al.* 2021). Corals showed signs of early recovery, whereas gobies lagged behind (Froehlich *et al.* *in review*), suggesting that coral-fish mutualisms could break down in response to repeated environmental stressors.

I then investigated whether gobies displayed plasticity to environmental disturbances using different mechanisms (Chapter 4, 5 and 6). Through observational studies, I found that gobies exhibited host and social plasticity based on environmental stressors, although that varied among goby species (Froehlich *et al.* *in review*, *in prepa*). After disturbances, some goby species were able to shift from their preferred coral host species (Froehlich *et al.* *in review*), but that may not be to their advantage due to lower fitness benefits in less optimal host species (Munday 2001; Caley & Munday 2003). After repeated and extreme disturbances, gobies stopped living in groups, and most were living alone (Froehlich *et al.* *in prep*), which is a cause for concern as gobies need to live in monogamous pairs to reproduce (Nakashima *et al.* 1996; Wong & Buston 2013). Through a manipulative experiment using one goby species, I found that

Gobiodon quinquestrigatus did not exhibit movement plasticity in relation to habitat disturbance or sociality (Froehlich *et al.* 2022, *in prepb*). This goby species preferred to face a high cost of movement rather than using alternative hosts, even in disturbed environments in which the cost of movement was even higher (Froehlich *et al.* 2022, *in prepb*). By combining these findings, I find that coral-fish mutualisms may break down as environmental disturbances (regimes) are increasing in the future and gobies may not display sufficient plasticity in ways that are necessary for recovery. If environmental conditions further deteriorate, the long-term outlook for coral-goby mutualisms is bleak, especially for *Gobiodon* species. Future management of coral reefs will likely benefit from including coral-fish mutualisms in their conservation efforts.

7.2. Gobies are far less resilient than corals to climatic disturbances

As climatic disturbances are occurring more frequently and with higher intensity in recent years, coral reef ecosystems are particularly vulnerable to degradation (Harmelin-Vivien 1994; Cheal *et al.* 2017; Hughes *et al.* 2018a; Smale *et al.* 2019). Since corals are foundation species of coral reef ecosystems (Angelini *et al.* 2011), the fact that corals benefit from the presence of small cryptic fish living within their branches suggests that these fish play key roles in coral reef communities (Penin *et al.* 2010; Dixon & Hay 2012; Dirnwoeber & Herler 2013; Brandl *et al.* 2018; Chase *et al.* 2018, 2020b). Yet these cryptobenthic fishes are often overlooked in disturbance studies on coral reefs (Brandl *et al.* 2018). Accordingly, in chapter 3 and 4, I completed comparative studies to investigate how climatic disturbances affected the mutual survival of cryptic gobies and their coral hosts for multiple *Gobiodon* species living within *Acropora* coral hosts. By monitoring the populations of corals and gobies at Lizard Island, Great Barrier Reef, Australia, throughout four disturbances; 2 cyclones (2014, 2015) and 2 mass-bleaching (2016, 2017) events, my results highlighted that multiple disturbances have detrimental effects on the mutualism between corals and coral-dwelling gobies. The mutualistic partners did not respond the same, albeit both declining substantially.

At first, after the initial disturbance, there were similar changes in population metrics of corals and gobies. Then after multiple disturbances, gobies declined far more than their coral hosts, and half of the goby species disappeared. Gobies became rare during our monitoring as most corals were unoccupied, and gobies were occurring singly. Three years post-disturbances, despite corals faring better than gobies by exhibiting a steep increase in coral richness and abundance, almost double that of pre-disturbances, gobies in contrast were still only a quarter as abundant compared to pre-disturbances. However, corals were at least 60% smaller and thus likely limited the number of gobies able to live within their branches as goby group size is affected by coral size (Hobbs & Munday 2004; Hing *et al.* 2018, 2019; Froehlich *et al.* *in prep*). This suggests that gobies likely faced additional pressures that may have led to a lack of reproduction and recruitment potential (Wong & Buston 2013; Donelson & Munday 2015; Qin *et al.* 2018). These uneven population level responses to multiple disturbances highlight the extent that repeated disturbances affect coral-fish mutualisms (Froehlich *et al.* 2021).

The findings from both chapters 3 and 4 suggest that the outlook for coral and goby mutualisms are bleak. If gobies continue to exhibit high rates of decline and slower recovery than their coral hosts, fewer corals will be inhabited by cryptic gobies into the future. Although there are several organisms that have symbioses with corals, if one becomes absent then their ecological niche will likely not be replaced by others (McKeon *et al.* 2012; Thompson *et al.* 2015). There may also be flow-on effects to the wider community and ecosystem within coral reef systems if mutualisms break down (Wilson *et al.* 2006; Kiers *et al.* 2010; Turner 2010; Six *et al.* 2011; Marquis *et al.* 2014). Following these studies, a critical step is to identify why the coral-fish mutualisms are breaking down and why in particular fish are far less resilient than corals. Protection of coral reef ecosystems should include the management of cryptobenthic fish species as they have been mostly disregarded thus far.

7.3. Potential mechanisms affecting coral-fish mutualisms from a cryptic goby fish perspective

7.3.1. Some gobies exhibit host plasticity, but that may not be to their advantage

One potential mechanism to explain why gobies declined far more than corals from multiple disturbances is that gobies prefer particular coral species over others, i.e. host specificity. Many studies have found that host specificity will dictate which species are more resilient to climate change than others (Dirnwöber & Herler 2007; Hof *et al.* 2012; Ainsworth & Drake 2020). Species that only use a small range of hosts (1-3 host species, host specialists) will perish due to their limited host range, whereas species that use a wide range of hosts (4+ host species, host generalists) will display higher plasticity to disturbances (Dirnwöber & Herler 2007; Hof *et al.* 2012; Ainsworth & Drake 2020). Anemonefishes and gobies are site-attached and will never leave their live hosts even if the host becomes unhealthy, but these fish will not remain on dead hosts, a.k.a. dead corals and anemones (Bonin *et al.* 2009; Wong & Buston 2013; Froehlich *et al.* 2021). Coral-dwelling damselfishes on the other hand are not necessarily site attached, and will disperse depending on the health status of the coral hosts, but juveniles are willing to live on dead corals if necessary (Wismer *et al.* 2019; Pratchett *et al.* 2020). Therefore, we cannot assume that site-attached fishes respond the same to environmental changes.

I explored the host plasticity mechanism in chapter 4 to understand whether different goby species showed plasticity to host use throughout the same 4 extreme climatic disturbances at Lizard Island. Even three years post-disturbances, gobies exhibited a delayed potential for recovery compared to their coral hosts. Over 75% of corals were devoid of goby inhabitants 3 years post-disturbances, compared to only 5% pre-disturbances, and half of the goby species remained rare or locally extirpated. The few remaining goby species switched their preferred coral hosts to mirror coral community changes that occurred as a result of the climatic disturbances. Not all coral species were impacted the same by disturbances, and while most acroporid corals declined after disturbances, some species flourished and reached abundances far greater than before. Since gobies have different preferences for particular host species, this suggests that host plasticity is key to gobies surviving disturbances when coral communities change (Froehlich *et*

al. in review).

Interestingly, the degree to which gobies survived was not strongly related to the range of coral hosts they used prior to any disturbances. Consequently, both the host specialist and host generalist species disappeared after multiple disturbances, and remaining species from both categories switched to newly abundant coral host species. This suggests that host specialization (i.e. host specialist vs. generalist) per se does not predict whether gobies are resilient to disturbances. Instead, the tendency for each goby species to prefer one particular host species over others is a plasticity response to disturbances. Pre-disturbances, each goby species preferred one host species over others, with most preferring *A. nasuta*. However, as many host species declined substantially post-disturbances, goby species that remained post-disturbances primarily switched to a newly abundant coral species, *A. cerealis*. Accordingly, gobies exhibit host plasticity to their single most preferred host species, regardless of whether they are host generalist or specialist (Froehlich *et al. in review*).

Exhibiting host plasticity may seem to be an advantage in order to survive repeated disturbances, but gobies are still far less resilient than their coral hosts. One potential explanation is that post-disturbance competition for available hosts is heightened as gobies are now primarily competing for the same newly available host species (*A. cerealis*). There are a select few goby species that are stronger competitors and can evict other species from their host coral species of choice, e.g. *G. histrio* is a superior competitor over *G. brochus* (Munday 2001; Hobbs & Munday 2004). Competition may be a driver for slow recovery in gobies, however, I found many available and unoccupied coral hosts 3 years post-disturbances, including the newly common *A. cerealis*. Instead, fitness benefits that gobies incur from using particular host species may be reduced from having to use a newly common host (Munday 2001; Caley & Munday 2003). Although gobies are able to change hosts, particular host species provide gobies with optimal growth rates, i.e. fitness benefits (Munday 2001; Caley & Munday 2003). Thus, in the short term, shifting hosts may be an advantage to surviving disturbances, but in the long term, it likely will result in slower recovery rates for gobies. Accordingly, host plasticity of gobies may be key to the delay in their recovery compared to coral hosts (Froehlich *et al. in review*).

7.3.2. Gobies exhibit social plasticity in response to extreme disturbances, which may reduce recovery potential

As the tendency to live in social groups varies for several social animals based on different ecological factors, another mechanism responsible for the decline in gobies may be based on their degree of social plasticity in response to disturbances. Social taxa may not exhibit any social plasticity, and remain truly group-forming regardless of ecological factors, as seen in naked mole rats, ants, and termites (Wilson & Hölldobler 2005; Avilés & Harwood 2012; Nalepa 2015). Alternatively, social taxa may display social plasticity to ecological factors, but their responses to factors like disturbances will vary based on why they evolved a social living system (Duffy & Macdonald 2010; Jetz & Rubenstein 2011; Avilés & Harwood 2012; Gonzalez *et al.* 2013). For several taxa, sociality (i.e. living in groups) evolved in challenging environments, as seen in marine shrimp, social spiders, and many birds (Duffy & Macdonald

2010; Jetz & Rubenstein 2011; Avilés & Harwood 2012), i.e. the life insurer hypothesis (Queller & Strassmann 1998). On the other hand, sociality instead evolved in stable environments in other taxa, such as hornbills (Gonzalez *et al.* 2013). Accordingly, the latter species will likely become far less social into the future as environments are becoming more challenging due to climate change (Turner 2010; Hughes *et al.* 2018b). Thus, the ability for animals to exhibit social plasticity as a response to climate change will become an important indicator of their resilience to continued disturbances in the future.

Accordingly, in Chapter 5, I have addressed whether gobies exhibit social plasticity to disturbances, and whether that may be an explanation for the reduced resilience of gobies compared to corals. In order to assess this, I introduced a framework that investigated at what levels of variation within sociality do social animals exhibit plasticity to ecological factors (Froehlich *et al. in prep*). I demonstrated that the framework was successful at identifying at what levels of variation gobies exhibit social plasticity to location, time, and disturbances. By modelling the framework on gobies, I was able to show that the framework is easily adaptable to any social taxon based on its life history and ecological characteristics, and that small-scale as well as large-scale ecological factors can be investigated simultaneously. The framework is particularly useful as it only requires the quantification of observational data to investigate ecological impacts on all levels of variation within sociality. Accordingly, this framework could be a powerful tool to investigate whether social animals exhibit social plasticity to ecological factors.

Upon testing the framework on gobies, I found that gobies do not exhibit plasticity at all levels of variation within sociality, and that only certain levels are impacted by disturbances (Froehlich *et al. in prep*). I investigated their social plasticity before and after climatic disturbances of cyclones and bleaching at different locations that exhibit different disturbance regimes: Kimbe Bay in Papua New Guinea (no disturbance), Lizard Island (4 extreme disturbances = high disturbance regime) and One Tree Island both on the Great Barrier Reef, Australia (one extreme disturbance = moderate disturbance regime). Gobies exhibited different forms of sociality at the genus level based on disturbances: solitary (rare as pair-living is necessary for breeding), pairs, single species groups, and mixed species groups. After high disturbance regimes, gobies switched to either pair-forming or solitary living and were rarely observed in groups. Monogamous pairing is critical for successful reproduction in this genus (Nakashima *et al.* 1996; Wong & Buston 2013). When I compared sociality at the species level, I found that some species (like *G. axillaris*, *G. brochus*, *G. erythrospilus*, *G. histrio*) always lived in pairs regardless of disturbance regime or location. On the other hand, other species (like *G. fuscuber*, *G. rivulatus*) tended to live in groups in stable environments, and only in certain locations, but switched to pair-forming after high disturbance regimes. Thus pair-forming and group-forming species exhibit different degrees of sociality, but only group-forming species exhibited plasticity in their degrees of sociality to disturbances (Froehlich *et al. in prep*).

Upon investigation of smaller-scale variation in sociality, I found that group-forming species (e.g. *G. fuscuber*, *G. rivulatus*) will alter their group size based on the size of their coral host and partially based on the size of the largest individual in a group. Since cooperation within goby groups is maintained by

size hierarchies and via monogamous breeding from a single male-female pair (Ang & Manica 2010b; Wong & Buston 2013; Buston & Wong 2014), I assessed even finer scale variation within their social groups. I found that disturbances and location did not impact the sex-based dominance or size ratios between individuals. Accordingly, large-scale factors of disturbance and location impact large-scale levels of variation in sociality with regards to the tendency for gobies to live in pairs or groups, but they do not impact small-scale factors that are responsible for maintaining cooperation within groups. This suggests that the mechanisms by which gobies cooperate within groups (i.e. size-based hierarchies and sex allocation patterns) are robust to disturbances (Froehlich *et al. in prep*).

It is important to note though that group-forming species became far rarer than pair-forming species after extreme disturbances, which suggests that social living may be a disadvantage with increasing rates of climatic disturbances (Froehlich *et al. in prep*). My study suggests that gobies likely evolved social living in stable environments, in order to reap benefits of larger coral habitats, i.e. negating the life insurer hypothesis (Queller & Strassmann 1998). Looking ahead, I find that group-living is a disadvantage for gobies in times of increased and repeated climatic disturbances and that pair-forming will likely become their preferred lifestyle for the future. Although some gobies display social plasticity to disturbances, that may not be to their advantage as climate change is becoming increasingly devastating. Alarmingly, far more gobies are living solitarily after repeated disturbances than before (Froehlich *et al. in prep*), but they need to be in pairs to breed (Nakashima *et al.* 1996; Wong & Buston 2013). This is likely due to the availability of smaller corals after disturbances, with gobies choosing to settle alone in a coral instead of joining another for pairing. Combined, these results suggest that gobies are far less resilient than their coral hosts to repeated disturbances due to their limiting social plasticity.

7.3.3. Gobies do not exhibit movement plasticity, which increases predation risk post-disturbances

I explored a third mechanism that may explain why gobies are slower to recover than their host corals. I investigated whether gobies exhibit movement plasticity depending on habitat and environment factors. For such site-attached animals like habitat specialist fishes, ecological constraints, costs of movement, and benefits of philopatry affect their movement decisions and tendencies to stay in groups or disperse (Wong 2010; Branconi *et al.* 2020). Habitat is a limiting resource for these social animals (Faulkes *et al.* 1997; Duffy & Macdonald 2010; Wong & Buston 2013; Froehlich *et al.* 2021, *In review*), and habitat characteristics are known to play roles in their movement decisions (Selander 1964; Emlen 1982; Stacey & Ligon 1991; Hing *et al.* 2017; He *et al.* 2019). Having access to habitat of high quality and low saturation are important predictors of movement decisions of site-attached animals (Selander 1964; Parry 1973; Woolfenden & Fitzpatrick 1978; Emlen 1982; Stacey & Ligon 1991; Arnold & Owens 1998; Wong 2010). Often a key explanation for social living in many taxa is that their small size makes them ideal predation targets (Thompson *et al.* 2007; Wong 2011; Hing *et al.* 2019). Movement would then incur high predation risks and should only be undertaken under conditions in which predation risk is reduced and movement is far more beneficial than benefits of philopatry (Arnold & Owens 1998; Branconi *et al.* 2020). Thus, movement decisions are strongly tied to their social living decisions.

In chapter 6, I explored the potential for movement plasticity in one goby species, *G. quinquestrigatus*. I completed the study at Kimbe Bay, which provided me with the opportunity to investigate movement plasticity of this goby species based on habitat characteristics of their *Acropora* coral host under relatively undisturbed environmental conditions. Since habitat characteristics have been shown to dictate movement decisions of other habitat specialist fishes (Wong 2010; Branconi *et al.* 2020), I translocated a *G. quinquestrigatus* individual into an alternative coral host up to 10 m away with varying degrees of health, size and saturation. Accordingly, an individual goby would have had to face high costs of movement to attempt to return home. Unlike other habitat specialist fishes though (Wong 2010; Branconi *et al.* 2020), *G. quinquestrigatus* chose to face high costs of movement and return home regardless of any habitat characteristics (Froehlich *et al.* 2022). Such a lack of movement plasticity and attempting to return home (55% of the translocated gobies) resulted in high predation risk, with more than a third of gobies (38%) no longer found. These findings suggest that the benefits of returning to a familiar home and/or familiar mates far outweigh the costs of movement (Froehlich *et al.* 2022).

I then assessed whether gobies would alter their movement decisions based on the conditions of the environment. In times of high disturbance regimes, small-bodied animals become easier targets for predation as environments become less complex and there are less opportunities for shelter (Almany 2004; Ahmadi *et al.* 2012). Accordingly, in Appendix 1, I repeated the study from Chapter 6 using the same species, *G. quinquestrigatus*, and same experimental design, except that I completed it in the highly disturbed environment at Lizard Island after the 2 cyclones and 2 heatwaves (Chapter 3, 4). Gobies still did not prefer to remain in the alternative hosts and instead attempted to return home, although predation risk was far higher in this disturbed environment, with more than half of gobies no longer found (Froehlich *et al.* *in prep*). The willingness to return home in disturbed environments suggests that gobies still do not exhibit movement plasticity be it in disturbed or undisturbed (see above) environments.

Gobiodon quinquestrigatus prefer to face high costs of movement and return home to their original coral hosts, instead of choosing alternative hosts with varying degrees of habitat size, health and saturation. Such results are unlike other habitat specialist fishes, i.e. *Paragobiodon xanthosomus* and *Amphiprion percula*, which prefer low costs of movement and choose alternative hosts of large size and low saturation (Wong 2010; Branconi *et al.* 2020). Alarming, *G. quinquestrigatus* did not alter their movement decisions in disturbed environments even though predation risk was even higher. It would be useful to repeat these experiments with other *Gobiodon* species in order to confirm whether the genus as a whole does not exhibit movement plasticity to habitat characteristics or disturbances. It should be noted that I did use a species (*G. quinquestrigatus*) that is one of the most common species at all three locations studied and remained common pre- and post-disturbances (Froehlich *et al.* 2021, *In review, in prep*). Accordingly, I suggest that the lack of movement plasticity in gobies results in higher predation risk in disturbed environments, which is one key mechanism for why gobies are slower to recover than their coral hosts after disturbances.

7.4. General Conclusion

7.4.1. Coral-fish mutualisms are fragile to climatic disturbances

My thesis provides a critical assessment of not only how mutualisms respond to climate change, but what mechanisms may be responsible for such responses. In order to investigate one of the mechanisms, I introduce a powerful framework for the assessment of ecological impacts on multiple levels of variation within sociality (Froehlich *et al. in prep*). I use a model coral-fish mutualism that has provided several breakthroughs for social evolution in recent years (Hing *et al.* 2018, 2019; Rueger *et al.* 2021a) as marine taxa have only recently become the focus of sociality research (Buston 2003a; Wong 2010; Wong & Buston 2013; Branconi *et al.* 2020; Rueger *et al.* 2021a). By focusing on essential questions around the resilience of gobies, my thesis is also one of few to investigate consequences of climatic disturbances on overlooked species like small cryptic fishes that live in mutualism with coral hosts. We have yet to understand how significant the loss of gobies may be to coral resilience, but my thesis finds that gobies decline far more than their coral hosts and that coral loss is a strong indicator of goby decline.

My thesis suggests that coral-fish mutualism may break down as a consequence of climatic disturbances in coral reef ecosystems. Gobies decline far more than their coral hosts after multiple climatic disturbances, and their road to recovery is far slower than I observed in corals (Froehlich *et al.* 2021, *In review*). I find three mechanisms of plasticity for gobies that are likely drivers of their slower recovery. (1) Gobies exhibit host plasticity by switching to less preferred hosts after disturbances, and although that might be beneficial in the short term, in the long term this likely reduces their growth rates in the less preferable hosts (Froehlich *et al. in review*). (2) Gobies display social plasticity to disturbances, but post-disturbance they are switching to pair-forming and alarmingly more solitary living, which reduces reproductive capability if and when they find a breeding mate (Froehlich *et al. in prep*). (3) Gobies do not exhibit movement plasticity (undisturbed and disturbed habitats) and even prefer to face heightened predation in heavily disturbed environments in order to attempt to return home instead of using alternative coral hosts (Froehlich *et al.* 2022, *in prepb*). Each mechanism can affect the resilience of coral-dwelling gobies, but the social plasticity shift to pair-forming and most often solitary living is the most detrimental mechanism hindering short-term resilience of gobies due to the lack of reproduction. The inability for gobies to exhibit movement plasticity is the next most detrimental mechanism since it results in higher predation rates. Finally, the ability for gobies to exhibit host plasticity can be detrimental long-term, but provides a short-term ability for gobies to be plastic to changes in the coral community. Throughout my thesis, I find that these three mechanisms are likely predictors of poor resilience in gobies, and coral hosts may no longer be occupied by gobies in the future if climate change continues to intensify. Such an outlook provides the potential for other mutualisms to be fragile to climate change, as ecosystems are changing rapidly with repeated disturbances becoming the norm (Turner 2010; Hughes *et al.* 2018b).

7.4.2. Future research recommendations

There is the potential for additional mechanisms to be responsible for the lower resilience in fish

compared to corals. There may be a latitudinal shift in the social plasticity of gobies as seen in ground-nesting bees (Dew *et al.* 2018) and birds (Arnold & Owens 1998), which might impact how gobies respond socially to disturbances. I only compared one reef at any given latitude and suggest that additional reef systems be investigated at each latitude. It would be beneficial to add locations that exhibited different disturbance regimes at each latitude. To complement my thesis, future work should also investigate whether there is a gene flow mechanism that limits the resilience of gobies compared to their coral hosts (Froehlich *et al. in prep*). As gobies have a larval dispersal stage (3 weeks), there is the potential for population connectivity in the Indo-Pacific (Brothers *et al.* 1983; Horne *et al.* 2008). If instead there is limited gene flow in the Indo-Pacific (Schluessel *et al.* 2010; Klanten *et al.* 2020), it would explain the likelihood of a slow recovery of gobies at Lizard Island, as all the neighboring reef systems were also devastated by the same disturbances (cyclones and bleaching). Goby populations may also be exhibiting population bottlenecks from such extreme disturbances and reduce resilience (Carson 1990; Sergio *et al.* 2018; Froehlich *et al. in prep*). Thus, I suggest that genetic diversity should be investigated pre- and post-disturbances to complement population genomic studies. Such studies would then be able to highlight whether latitudinal and gene flow mechanisms are responsible for the slower resilience/recovery of gobies.

Another critical step forward is to identify to what extent host corals will have reduced survival without the presence of gobies. Since *Acropora* coral hosts are some of the most vulnerable coral taxa to climate change (Hughes *et al.* 2018b, a, 2019a), the presence of gobies may in fact play a major role in improving resilience of host corals into the future. There may also be flow-on effects of changes to mutualistic relationships across coral reef ecosystems (Wilson *et al.* 2006; Kiers *et al.* 2010; Turner 2010; Six *et al.* 2011; Marquis *et al.* 2014). As climatic disturbances are predicted to increase both in power and frequency in the future (Emanuel 2013; Hughes *et al.* 2018a), we urgently need to assess the impacts of goby occupancy on coral host resilience. By understanding how critical these fish are to corals in coral-fish mutualisms, conservation and management methods should be developed in order to help preserve gobies and their hosts.

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Appendices

Appendix 1: Gobies do not exhibit movement plasticity to disturbances and face higher predation risks

A.1.1. Purpose

To investigate whether *Gobiodon quinquestrigatus* alters its movement decisions based on habitat health, size, and saturation in highly disturbed environments.

A.1.2. Methods

I repeated the same experimental design and methods from chapter 6, except the difference is this study was completed at a highly disturbed environment: 3 years post-disturbances from 2 extreme cyclones (2015, 2016) and 2 mass-bleaching events (2016, 2017) at Lizard Island, Queensland, Australia. Data analysis was exactly the same as detailed in chapter 6. The study was performed in accordance with relevant guidelines and regulations, including PREPARE and ARRIVE guidelines, under the University of Wollongong Animal Ethics protocol AE1404 and AE 1725 and under research permit issued by the Great Barrier Reef Marine Park Authority G18-41020.1 and the Papua New Guinea Research Visa Permit AA654347.

A.1.3. Results & Discussion

All trials were completed from Jan-Feb 2021 at Lizard Island in a disturbed state (total = 60 trials). Gobies did not base their movement decision on habitat size ($p = 0.69$); see Tab A.1.1 for all statistical outputs; Fig A.1.1), or saturation ($p = 1.00$; Fig A.1.1). The number of gobies located versus no longer located did not significantly differ ($p = 0.44$). No gobies stayed in the dead coral or moved into the adjacent live coral, and instead 4 gobies moved into other corals within 10 m, therefore gobies rejecting that gobies would move based on habitat health ($p < 0.001$; Fig A.1.1). However, the remaining gobies either returned home 38% of the time ($n = 23$) or were no longer located 55% of the time ($n = 33$). Distance to home did not affect whether gobies went home, were found in other corals, or were no longer located ($p = 0.05$; Fig A.1.2). These findings suggest that the cost of movement is higher in disturbed environments as 55% of gobies were no longer located in disturbed environments, compared to only 38% in healthy environments (Froehlich *et al.* 2022).

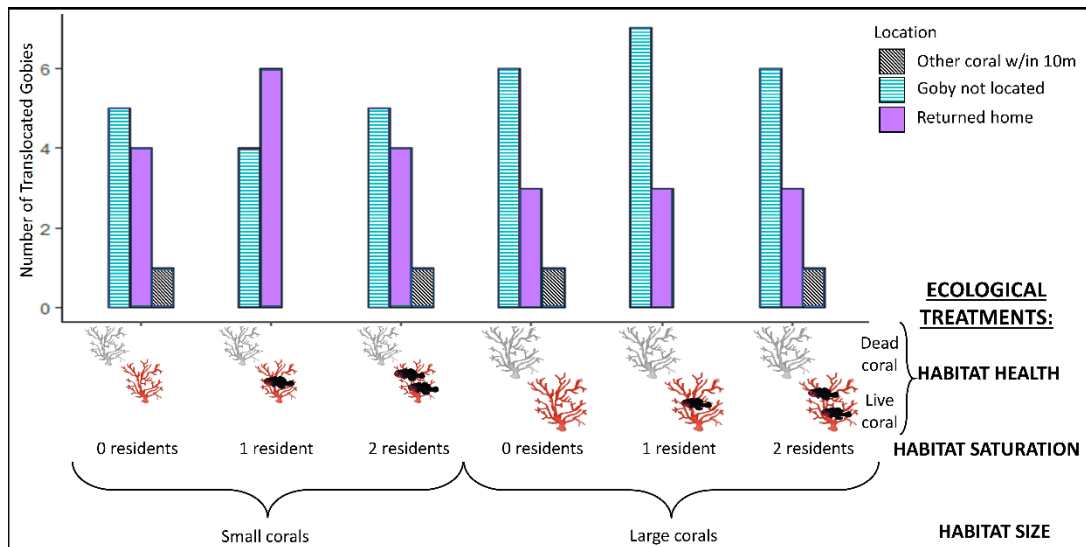


Figure A.1.1. Frequency of final location decisions by gobies based on habitat health, size and saturation at a disturbed site. w/in = 10 m.

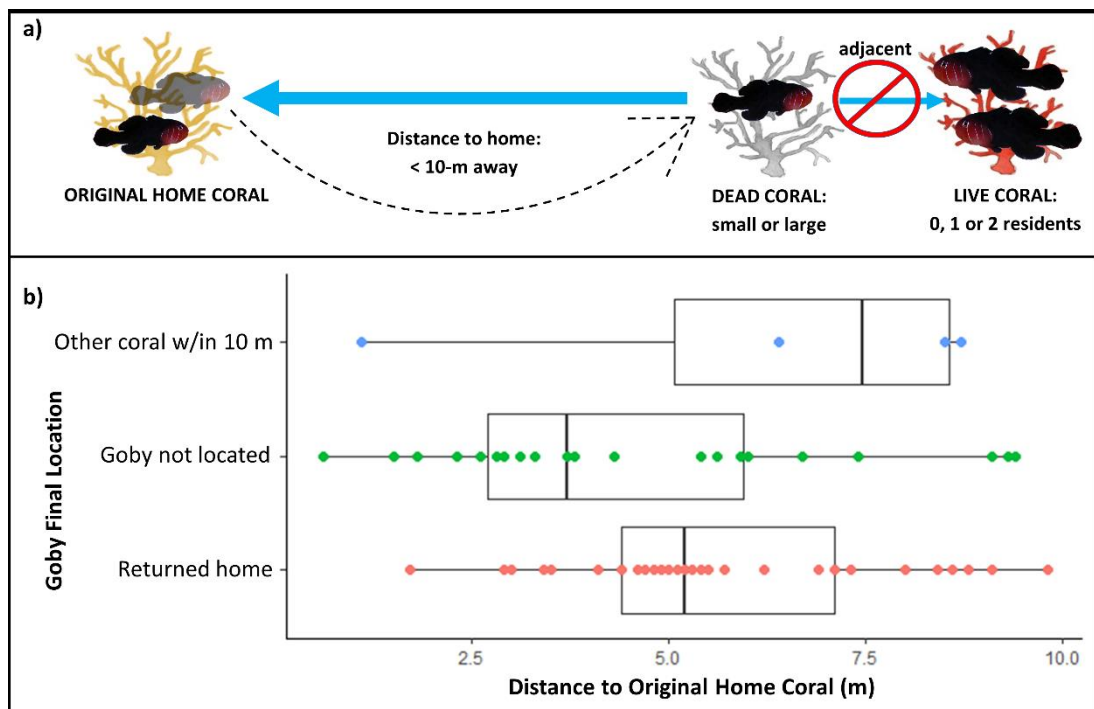


Figure A.1.2. **a** Expected (blue) versus actual (blue not crossed out) outcomes from the movement decisions of gobies translocated from their home coral at a disturbed site. **b** Outcome of gobies based on distance translocated away from their home coral. w/in = 10 m.

Table A.1.1. Statistical outputs of all analyses for the translocation of coral-dwelling goby *Gobiodon quinquestrigatus* in relation to habitat health, size and saturation at a disturbed site. “Avg.” means average; “Prop.” means proportion; “within 10-m” refers to the survey completed in a 10-m radius around each experimental setup; “N/A” means not applicable.

Response variable	Predictor variable	Factor Type	Model Test	df	χ^2 value	p-value	pseudo R-squared Statistic	Test Value
focal goby final location (3 levels: other coral within 10m, not located, returned home)	habitat health	N/A	chi-squared goodness-of-fit test	2	21.7	< 0.0001	N/A	N/A
if goby was located or not located	cost of movement	N/A	chi-squared goodness-of-fit test	1	0.6	0.4386	N/A	N/A
focal goby	habitat size	fixed	multinomial	4	2.2228	0.6949	McFadden	0.0561
final location	habitat saturation	fixed	logistic	6	0.6487	0.9955	Cox and Snell (ML)	0.0936
(categorical variable: 4 levels)	interaction: habitat size x saturation	fixed	regression model	4	0.4479	0.9784	Nagelkerke (Cragg and Uhler)	0.1133
	model likelihood ratio test			10	5.8995	0.8236		
focal goby	distance to intruder home coral	covariable	multinomial	2	5.9781	0.0503	McFadden	0.1225
final location	habitat size	fixed	logistic	3	3.6204	0.3055	Cox and Snell (ML)	0.1933
(categorical variable: 4 levels)	habitat saturation	fixed	regression	5	0.6610	0.9850	Nagelkerke	0.2338
	interaction: habitat size x saturation	fixed	model	4	0.5064	0.9729	(Cragg and Uhler)	
	model likelihood ratio test			12	12.8880	0.3773		

Appendix 2: Additional publications during PhD candidature

Froehlich, C.Y.M. 2022. What happens during a cyclone? The perspective of a reef fish. *In: Coral reefs of Australia: perspectives from the water's edge, Chapter 4: Understanding the Fundamentals of Coral Reefs*. CSIRO publishing, Australia.

Froehlich, C.Y.M., Wong, M., Klanten, O.S. 2021. Photos from the field: why losing these tiny, loyal fish to climate change spells disaster for coral. *The Conversation*. <https://theconversation.com/photos-from-the-field-why-losing-these-tiny-loyal-fish-to-climate-change-spells-disaster-for-coral-167119>

Rueger T., Branconi, R., **Froehlich, C.Y.M.**, Heatwole, S.J., Wong, M.Y.L., and Buston, P.M. 2021. The next frontier in understanding the evolution of coral reef fish societies. *Frontiers in Marine Science*. 8:665780. doi: 10.3389/fmars.2021.665780.

Appendix 3: Statement of Contribution of Others

The PhD candidate conceived, completed, and wrote all material within the thesis, however co-authors played integral roles in each section. As clearly defined in section “List of publications included as part of the thesis,” each co-author contributed particular tasks to each section.

Candidate Signature
Catheline Froehlich

Primary Supervisor Signature
Marian Wong

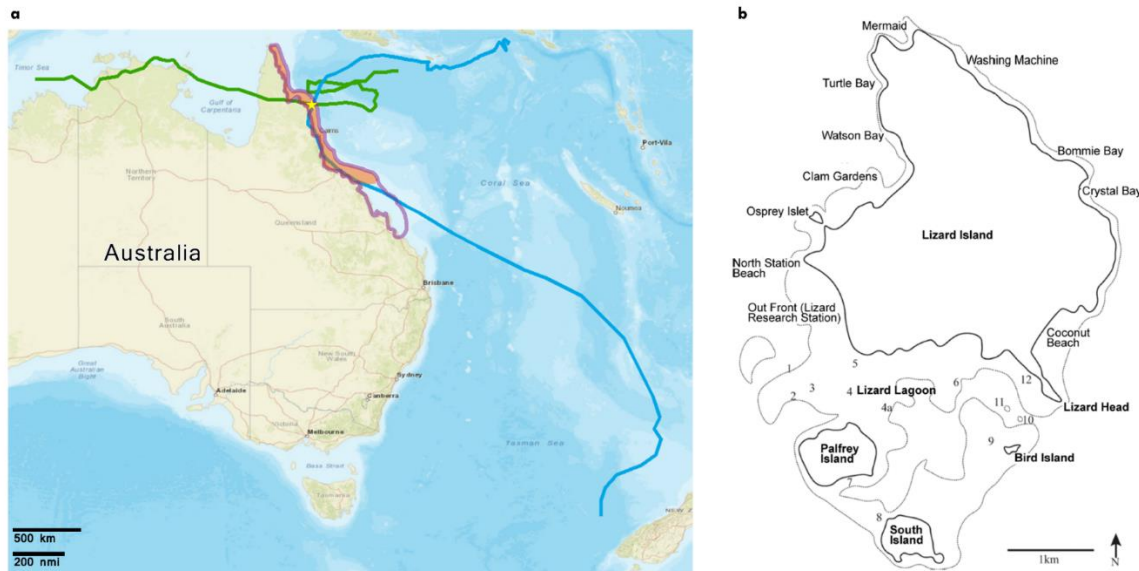
Secondary Supervisor Signature
Mark Dowton

Tertiary Supervisor Signature
O. Selma Klanten

Head of Postgraduate Studies Signature
Phillip Byrne

Other Supplementary Materials

Supplementary Material for Chapter 3:

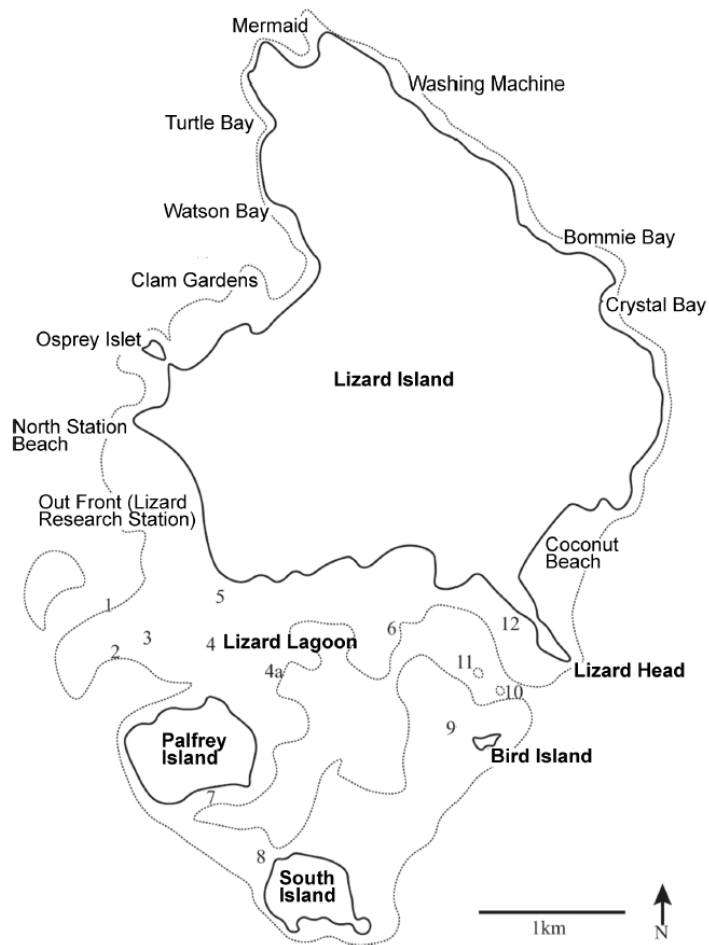


Supplementary Figure 3.1. Map and location of consecutive climate disturbances affecting Lizard Island, QLD, Australia. **a** Map of Australia created in ArcGIS (source: Esri, DeLorme, HERE, Garmin, USGS, Intermap, iPC, NRCAN, Esri Japan, METI, Esri China (Hong Kong), Esri (Korea), Esri (Thailand), MapmyIndia, Tomtom, NGCC, OpenStreetMap contributors, and the GIS User Community) with cyclone tracks of Ita 2014 (blue line) and Nathan 2015 (green line) sourced from the Australian Government Bureau of Meteorology (<http://www.bom.gov.au/cyclone/history/tracks/beta/?region=sh>), with areas overlayed to show impacts of coral bleaching from 2016 (orange shaded area) and 2017 (purple outlined area). Lizard Island is highlighted with yellow star. Bleaching areas were adapted from two papers (Hughes *et al.* 2017, 2019a). **b** Map of Lizard Island (-14.687264, 145.447039) created in Adobe Illustrator® (v2020). Numbers represent discrete sites as follows: Big Vickey's Reef (1); Vickey's Reef (2); Horseshoe Reef (3); Palfrey Reef (4±4a); Loomis Reef (5); Trawler (6); Picnic Beach (7); Ghost Beach (8); Bird Island Reef (9); Entrance Bommie (10); Bird Bommie (11); Lizard Head (12).

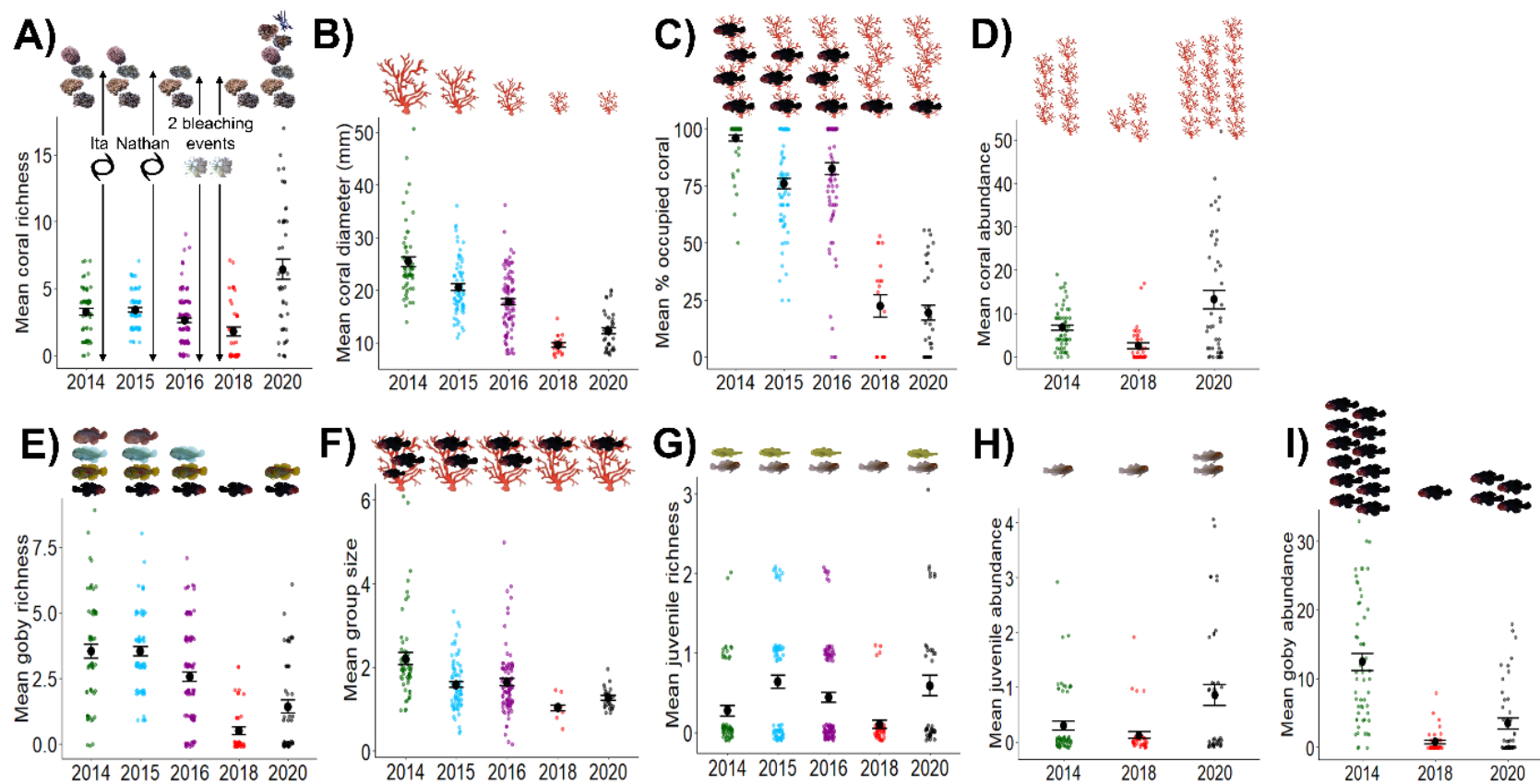
Supplementary Table 3.1. Statistical output of all univariate and multivariate analyses for changes in *Acropora* corals and coral-dwelling *Gobiodon* gobies following multiple disturbances. Corals and gobies were surveyed before (Feb 2014) and after each cyclone (Jan-Feb 2015, Jan-Feb 2016) and consecutive bleaching (Feb-Mar 2018) around Lizard Island, Great Barrier Reef, Australia. CI means confidence interval.

Response Variable	Model	Predictor variable	Factor Type	df	Model Statistic	Test-value	p-value	R-squared	Pairwise Comparison	Pairwise Statistic	Test-value	P-value	Lower 95% CI	Upper 95% CI
Coral Richness	GLMM poisson	Year Site	fixed random	3	χ^2 (chi-squared)	35.418	< 0.0001	0.147 marginal	2014, 2015	t-ratio	-0.34	0.9864	-0.307	0.236
									2014, 2016		2.658	0.0412	0.007	0.53
									2014, 2018		4.875	0.0001	0.349	1.137
									2015, 2016		3.203	0.0083	0.059	0.55
									2015, 2018		5.09	<.0001	0.383	1.174
									2016, 2018		3.18	0.0089	0.089	0.86
Average Coral Diameter log-transformed	LMM	Year Site	fixed random	3	F-value	67.207	< 0.0001	0.5874422 conditional	2014, 2015	t-ratio	6.6	<.0001	0.19419	0.445
									2014, 2016		9.572	<.0001	0.31755	0.553
									2014, 2018		13.334	<.0001	0.72185	1.07
									2015, 2016		2.797	0.0285	0.00863	0.223
									2015, 2018		8.406	<.0001	0.39888	0.754
									2016, 2018		7.086	<.0001	0.2923	0.629
Coral Assemblage	PERMANOVA	Year Site	fixed Random	(3,259) (16,259)	pseudo-F	10.361 2.7032	0.0001 0.0001	N/A	2014, 2015	t-value	5.8509	0.0001	N/A	N/A
									2014, 2016		4.0838	0.0001		
									2014, 2018		4.6241	0.0001		
									2015, 2016		1.7032	0.0092		
									2015, 2018		1.704	0.0066		
									2016, 2018		2.1477	0.0002		
Goby Richness	GLMM poisson	Year Site	fixed random	3	χ^2 (chi-squared)	99.332	< 0.0001	0.524 marginal	2014, 2015	t-ratio	0.195	0.9974	-0.249	0.289
									2014, 2016		2.545	0.0555	-0.004	0.512
									2014, 2018		7.999	<.0001	1.277	2.496
									2015, 2016		2.512	0.0602	-0.007	0.475
									2015, 2018		7.886	<.0001	1.254	2.478
									2016, 2018		6.975	<.0001	1.027	2.237
Average Goby Group Size log-transformed	LMM	Year Site	fixed random	3	F-value	12,877	< 0.0001	0.2007437 conditional	2014, 2015	t-ratio	4.308	0.0001	0.1420	0.569
									2014, 2016		4.645	<.0001	0.1603	0.564
									2014, 2018		5.088	<.0001	0.3688	1.133
									2015, 2016		0.088	0.9998	-0.1802	0.193
									2015, 2018		2.683	0.0389	0.0140	0.776
									2016, 2018		2.709	0.0364	0.0172	0.760
Percent Occupied Coral	LMM	Year Site	fixed random	3	F-value	79.009	< 0.0001	0.6253415 conditional	2014, 2015	t-ratio	5.876	<.0001	10.88	28
									2014, 2016		4.394	<.0001	5.55	21.5
									2014, 2018		15.143	<.0001	59.63	84.2
									2015, 2016		-2.066	0.1674	-13.37	1.5
									2015, 2018		10.739	<.0001	39.84	65.1
									2016, 2018		12.625	<.0001	46.45	70.4
Goby Assemblage	PERMANOVA	Year Site	fixed Random	(3,259) (16,259)	pseudo-F	5.8348 2.2043	0.0001 0.0001	N/A	2014, 2015	t-value	1.709	0.0061	N/A	N/A
									2014, 2016		1.777	0.0042		
									2014, 2018		2.9856	0.0001		
									2015, 2016		2.1039	0.0008		
									2015, 2018		3.6387	0.0001		
									2016, 2018		2.7908	0.0001		

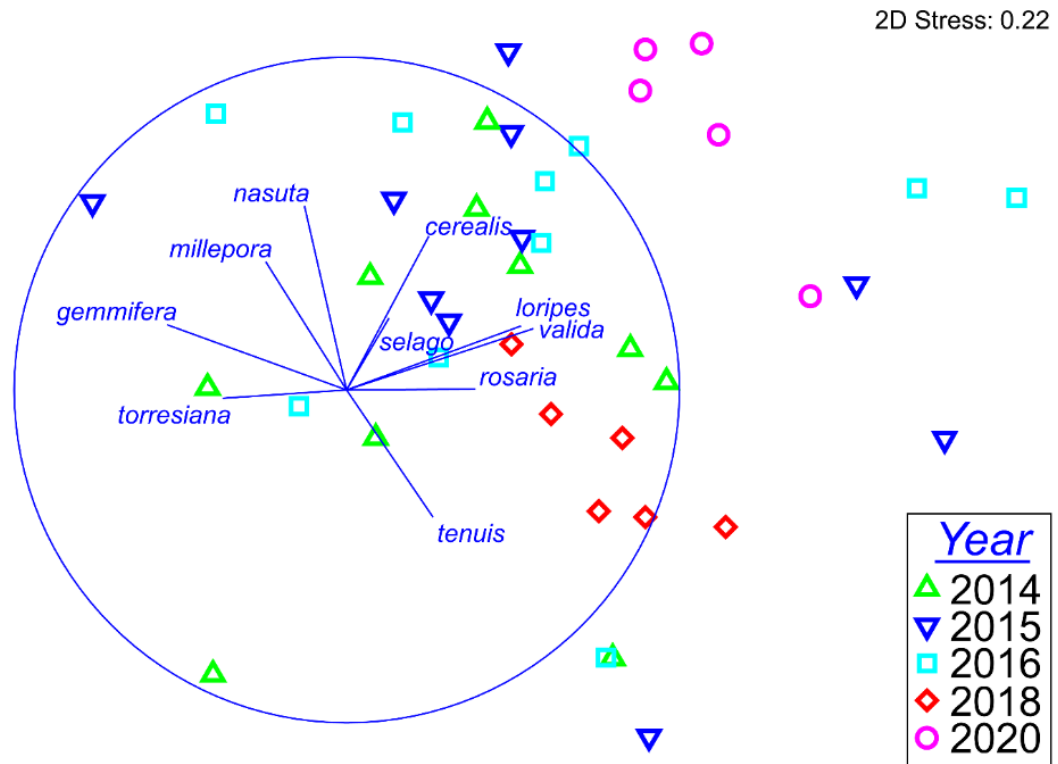
Supplementary Material for Chapter 4:



Supplementary Fig 4.1. Map of Lizard Island, QLD (-14.687264, 145.447039). Numbers represent discrete sites as follows: Big Vickey's Reef (1); Vickey's Reef (2); Horseshoe Reef (3); Palfrey Reef (4±4a); Loomis Reef (5); Trawler (6); Picnic Beach (7); Ghost Beach (8); Bird Island Reef (9); Entrance Bommie (10); Bird Bommie (11); Coconut Head Reef (12).



Supplementary Fig 4.2. Multiple disturbances affect the populations of *Acropora* corals and *Gobiodon* gobies. **a** Coral richness, **b** diameter, **c** occupancy by gobies, and **d** abundances, **e** adult goby richness and **f** group size, **g** juvenile goby richness, and the abundance of **h** juvenile gobies, and **i** adult gobies per transect before and after each cyclone (black spiral symbol), after heatwaves/bleaching (white corals), and 3 yrs post-disturbances. Abundances (**d,h,i**) were only calculated in 2014, 2018, and 2020 due to differences in transect methodology. Symbols above data points depict changes in means as identified through post-hoc testing. Error bars are standard error.



Supplementary Fig 4.3. Coral assemblages inhabited by each goby species following multiple disturbances. Multidimensional scaling plot illustrating surveys were completed: before (2014), after Cyclone Ita (2015), after cyclone Nathan (2016), after two back-to-back bleaching events (2018), and 3 yr after disturbance (2020). Each point represents the diversity of corals used by each goby species within a single survey time period. Points closer together are more similar in coral assemblages than points further apart. Overlaid are the direction in which *Acropora* coral species are most abundant, and the closer the trajectory is to reaching the outer circle, the most abundance of that species is explained in that direction.

Supplementary Material for Chapter 5:

Supplementary Table 5.1. Statistical output of forms of sociality analyses. VGLM = multinomial logistic regression model

Response Variable	Model	Predictor variable	Factor Type	df	Model Statistic	Test-value	p-value	R-squared statistic	Test value
Sociality Status pre-disturbances only (categorical variable: 4 levels)	VGLM	location	fixed	6	χ^2 (chi-squared)	24.45	0.0004*	McFadden	0.023
					Sample size	n = 529		Cox and Snell (ML)	0.500
								Nagelkerke	0.056
Sociality Status pre and post-disturbances (categorical variable: 4 levels)	VGLM	location	fixed	3	χ^2 (chi-squared)	50.69	< 0.0001*	McFadden	0.109
		pre/post	fixed	3		109.36	< 0.0001*	Cox and Snell (ML)	0.209
		location x pre/post	fixed	3		42.42	< 0.0001*	Nagelkerke	0.236
					Sample size	n = 1239			
Sociality Status x year post-disturbance at Lizard Island (categorical variable: 4 levels)	VGLM	year	fixed	3	χ^2 (chi-squared)	18.93	0.0002*	McFadden	0.022
								Cox and Snell (ML)	0.040
					Sample size	n = 791		Nagelkerke	0.047

Supplementary Table 5.2. Statistical output of social plasticity analysis. GLM = generalized linear model, LM = linear model.

Response Variable	Model	Predictor variable	Factor Type	df	Model Statistic	Test-value	p-value	R-squared statistic	Test value
Group Size for <i>G. rivulatus</i> (includes all coral species)	GLM	average coral diameter	covariable	1	χ^2 (chi-squared)	8.78	0.006*	marginal	0.267
		size of dominant individual	covariable	1		7.66	0.29		
		reef	factor	2		5.82	0.40		
		coral diam x dominant size	interaction	1		5.79	0.85		
					Sample size	n = 37			
			Outliers removed	n = 1					
Size of Dominant Individual for <i>G. rivulatus</i> log-transformed (includes all coral species)	LM	average coral diameter	covariable	1	F-value	4.37	0.045*	marginal	0.423
		group size	covariable	1		5.10	0.03*		
		location	factor	2		5.93	0.007*		
		coral diam x group size	interaction	1		0.62	0.44		
					Sample size	n = 37			
			Outliers removed	n = 1					
Coral Diameter for <i>G. rivulatus</i> log-transformed (includes all coral species)	LM	size of dominant individual	covariable	1	F-value	7.84	0.009*	marginal	0.522
		group size	covariable	1		21.76	<0.0001*		
		location	factor	2		2.13	0.14		
		dominant size x group size	interaction	1		0.0008	0.98		
					Sample size	n = 37			
			Outliers removed	n = 0					
Group Size for <i>G. fuscoruber</i> (includes all coral species)	GLM	average coral diameter	covariable	1	χ^2 (chi-squared)	3.91	0.0002*	marginal	0.412
		size of dominant individual	covariable	1		3.68	0.63		
		location	factor	2		3.60	0.96		
		coral diam x dominant size	interaction	1		2.69	0.34		
					Sample size	n = 31			
			Outliers removed	n = 2					
Size of Dominant Individual for <i>G. fuscoruber</i> fourth-root transformed (includes all coral species)	LM	average coral diameter	covariable	1	F-value	6.33	0.02*	marginal	0.207
		group size	covariable	1		0.58	0.45		
		location	factor	2		1.07	0.36		
		coral diam x group size	interaction	1		0.21	0.65		
					Sample size	n = 31			
			Outliers removed	n = 0					
Coral Diameter for <i>G. fuscoruber</i> log-transformed (includes all coral species)	LM	size of dominant individual	covariable	1	F-value	13.86	0.001*	marginal	0.629
		group size	covariable	1		23.94	<0.0001*		
		location	factor	2		1.69	0.21		
		dominant size x group size	interaction	1		1.30	0.27		
					Sample size	n = 31			
			Outliers removed	n = 0					

Supplementary Table 5.3. Statistical output of within-group plasticity, i.e. size ratio and sex dominance analyses. GLM = generalized linear model.

Response Variable	Model	Predictor variable	Factor Type	df	Model Statistic	Test-value	p-value	R-squared statistic	Test value
Rankstep1 Size Ratios for single species colonies without <i>G. brochus</i> all locations fourth power transformation	GLM quasibinom	average coral diameter	covariable	1	χ^2 (chi-squared)	25.95	0.94		
		group size	covariable	1		25.53	0.09		
		location	fixed	2		25.34	0.52		
		species	fixed	5		23.08	0.15		
		location x species	interaction	8		21.56	0.24		
					Sample size	n = 164			
					Outliers removed	n = 3			
Rankstep1 Size Ratios for single species colonies with <i>G. brochus</i> all locations fourth power transformation	GLM quasibinom	average coral diameter	covariable	1	χ^2 (chi-squared)	26.17	0.21		
		group size	covariable	1		25.98	0.25		
		species	fixed	6		24.49	0.12		
					Sample size	n = 175			
					Outliers removed	n = 5			
Rankstep2 Size Ratios for single species colonies all locations	GLM quasibinom	average coral diameter	covariable	1	χ^2 (chi-squared)	4.53	0.003*		
		group size	covariable	1		3.76	0.003*		
		species	fixed	3		2.61	0.05		
					Sample size	n = 175			
					Outliers removed	n = 0			
Rankstep1 Size Ratios for single species colonies between year at LI and PNG only fourth power transformation	GLM quasibinom	average coral diameter	covariable	1	χ^2 (chi-squared)	11.57	0.02*		
		group size	covariable	1		11.56	0.76		
		species	fixed	4		11.09	0.30		
		location	fixed	1		11.02	0.37		
		year	fixed	1		10.73	0.09		
		species x location	interaction	1		10.41	0.07		
		species x year	interaction	4		9.93	0.29		
		location x year	interaction	1		9.93	0.81		
					Sample size	n = 114			
					Outliers removed	n = 3			
Rankstep1 Size Ratios for single species colonies pre vs. post disturbance LI only fourth power transformation	GLM quasibinom	average coral diameter	covariable	1	χ^2 (chi-squared)	16.79	0.001*		
		group size	covariable	1		16.34	0.06		
		species	fixed	3		15.73	0.19		
		pre/post years	fixed	2		15.41	0.29		
		spp x pre/post years	interaction	6		14.32	0.20		
					Sample size	n = 124			
					Outliers removed	n = 4			

Suppl. Tab. 5.3 (cont'd)

Response Variable	Model	Predictor variable	Factor Type	df	Model Statistic	Test-value	p-value	R-squared statistic	Test value
Size Ratios among ranksteps for mixed species colonies fourth power transformation	GLM quasibinom	coral size	covariable	1	χ^2 (chi-squared)	40.83	0.002*		
		group size	covariable	1		38.71	0.008*		
		rankstep	fixed	7		35.36	0.14		
		location	fixed	2		34.03	0.11		
		coral size x rankstep	interaction	7		32.49	0.65		
		group size x rankstep	interaction	7		30.13	0.35		
		coral size x group size	interaction	1		29.92	0.41		
		Sample size				n = 119			
Outliers removed				n = 0					
Size Ratios among ranksteps for comparison of single vs. mixed species colonies per species fourth power transformation	GLM quasibinom	coral size	covariable	1	χ^2 (chi-squared)	76.43	0.06		
		group size	covariable	1		75.57	0.04*		
		rankstep	fixed	6		69.24	< 0.0001*		
		species	fixed	6		67.76	0.31		
		location	fixed	2		66.67	0.07		
		mix/single colony	interaction	1		63.93	< 0.0001*		
		location x mix/single	interaction	2		63.22	0.18		
		rankstep x mix/single	interaction	6		61.36	0.18		
Sample size				n = 307					
Outliers removed				n = 4					
Size Ratios among ranksteps for comparison of single vs. mixed species colonies regardless of species fourth power transformation	GLM quasibinom	coral size	covariable	1	χ^2 (chi-squared)	88.71	0.038*		
		group size	covariable	1		88.58	0.45		
		rankstep	fixed	7		77.97	< 0.0001*		
		location	fixed	2		77.06	0.13		
		mix/single spp colony	fixed	1		76.73	0.22		
		location x mix/single spp	interaction	7		75.02	0.36		
		coral size x rankstep	interaction	7		72.46	0.12		
		group size x rankstep	interaction	1		72.29	0.36		
coral size x group size	interaction	2	71.39	0.13					
Sample size				n = 338					
Outliers removed				n = 5					
Sex Dominance divergence from unity 1:1	type of test: 1-sample proportions test with continuity correction								
	males: n = 62 AND females: n = 89				1	χ^2 (chi-squared)	5.12	0.024*	
Sex Dominance for single species colonies	GLM	species	fixed	4	χ^2 (chi-squared)	4.88	0.30	McFadden	0.105
	binomial	year	fixed	1		13.48	0.0002*	Cox and Snell (ML)	0.645
at LI only: 2020 vs. 2021		species x year	interaction	4		4.97	0.29	Nagelkerke	0.645
						Sample size	n = 162		

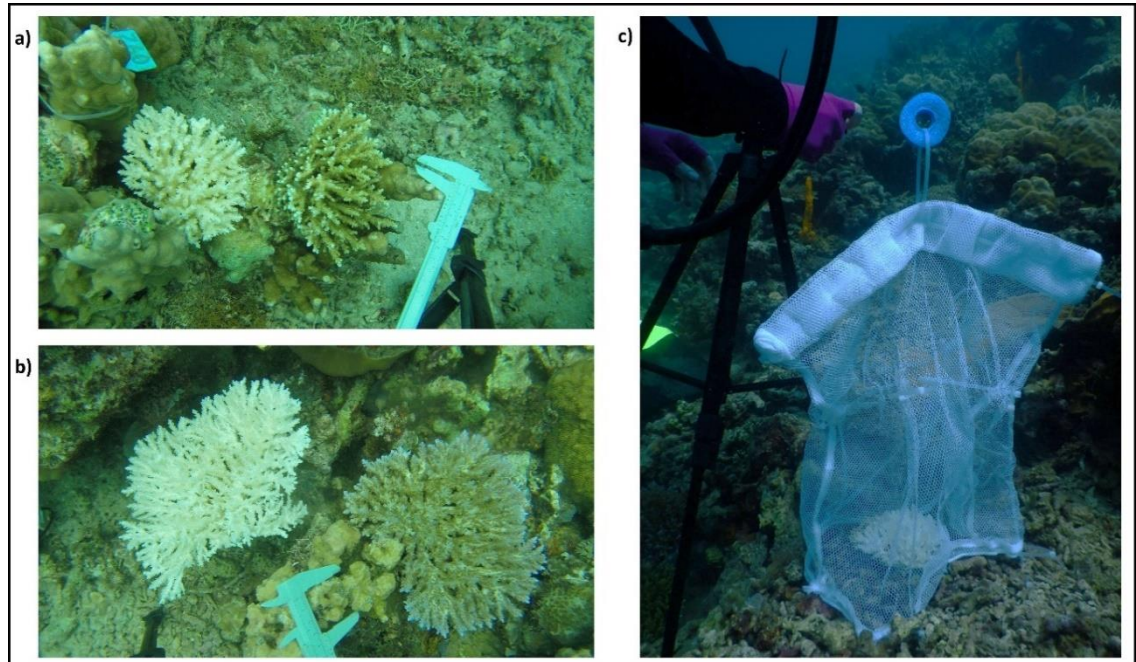
Supplementary Table 5.4. Statistical outputs of mixed species colony compositions. VGLM = multinomial logistic regression model.

Response Variable	Model	Predictor variable	Factor Type	df	Model Statistic	Test-value	p-value	R-squared statistic	Test value
Mixed Species: Intermixed Ranks Within Hierarchy? (only pre-disturbance data available):Yes or No	VGLM	location	fixed	2	χ^2 (chi-squared)	0.19	0.91	McFadden Cox and Snell (ML) Nagelkerke	0.004 0.005 0.007
					Sample size	n = 38			
Mixed Species: Bigger Species Is Rank 1? (only pre-disturbance data available):Yes or No	VGLM	location	fixed	2	χ^2 (chi-squared)	0.15	0.93	McFadden Cox and Snell (ML) Nagelkerke	0.004 0.004 0.006
					Sample size	n = 37			
Mixed Species: Composition of Colony only pre-disturbance	VGLM	location	fixed	2	χ^2 (chi-squared)	5.59	0.69	McFadden Cox and Snell (ML) Nagelkerke	0.110 0.272 0.288
					Sample size	n = 57			
Mixed Species: Composition of Colony: OTI only pre vs post-disturbance	VGLM	pre vs. post disturbance	fixed	2	χ^2 (chi-squared)	2.89	0.58	McFadden Cox and Snell (ML) Nagelkerke	0.051 0.142 0.149
					Sample size	n = 46			

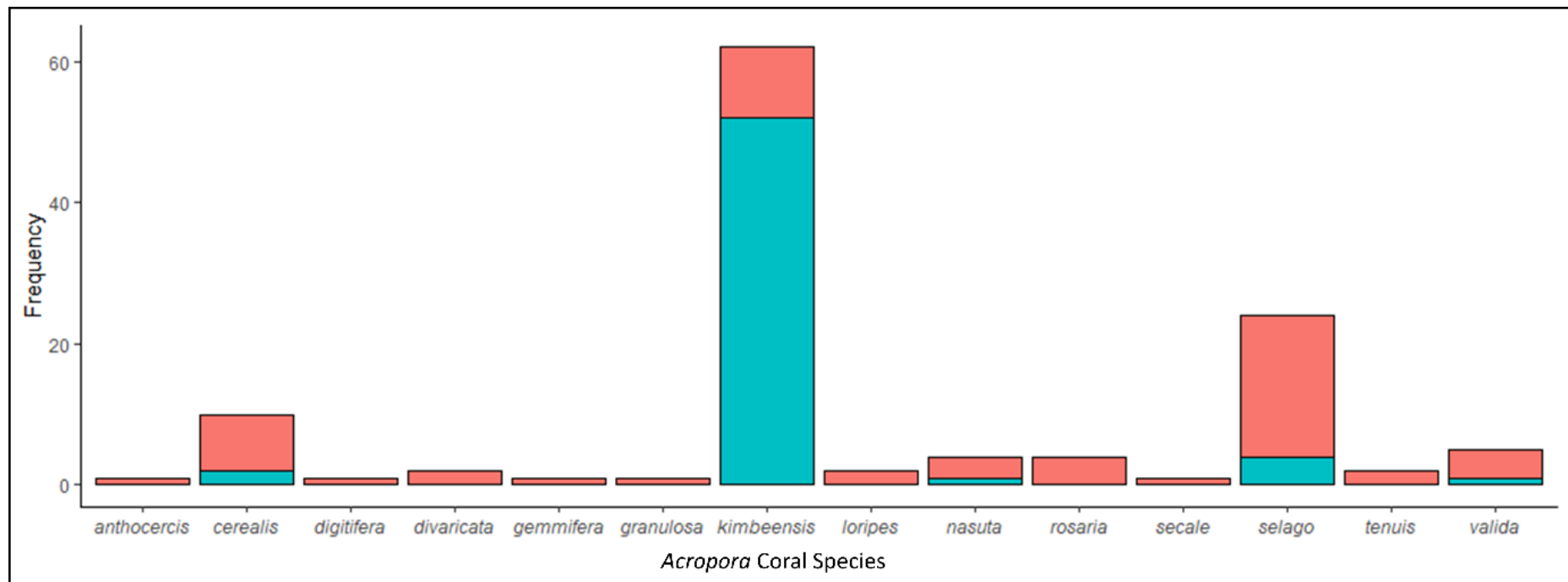
Supplementary Table 5.5. *Gobiodon* species compositions in mixed species colonies.

Mixed Species: Species Composition	Count	Species	Count in Mixed Colony	Count in Single Species Colony	# Species in Mixed Colony	Count
<i>G. axillaris</i> & <i>G. erythrospilus</i> & <i>G. fuscoruber</i> & <i>G. oculolineatus</i>	1	<i>G. axillaris</i>	3	19	Two species	76
<i>G. axillaris</i> & <i>G. rivulatus</i>	2	<i>G. brochus</i>	7	17	Three species	9
<i>G. brochus</i> & <i>G. erythrospilus</i>	2	<i>G. c.f. fulvus</i>	1		Four species	1
<i>G. brochus</i> & <i>G. rivulatus</i>	5	<i>G. citrinus</i>	3	3		
<i>G. c.f. fulvus</i> & <i>G. quinquestrigatus</i>	1	<i>G. erythrospilus</i>	12	42		
<i>G. citrinus</i> & <i>G. fuscoruber</i> & <i>G. okinawae</i>	1	<i>G. fuscoruber</i>	47	45		
<i>G. citrinus</i> & <i>G. okinawae</i>	1	<i>G. histrio</i>	6	44		
<i>G. citrinus</i> & <i>G. sp.D</i>	1	<i>G. oculolineatus</i>	21	27		
<i>G. erythrospilus</i> & <i>G. fuscoruber</i>	6	<i>G. okinawae</i>	6	10		
<i>G. erythrospilus</i> & <i>G. fuscoruber</i> & <i>G. oculolineatus</i>	1	<i>G. quinquestrigatus</i>	35	83		
<i>G. erythrospilus</i> & <i>G. oculolineatus</i>	1	<i>G. rivulatus</i>	37	70		
<i>G. erythrospilus</i> & <i>G. rivulatus</i>	1	<i>G. sp.D</i>	4	5		
<i>G. fuscoruber</i> & <i>G. oculolineatus</i>	4					
<i>G. fuscoruber</i> & <i>G. oculolineatus</i> & <i>G. quinquestrigatus</i>	1					
<i>G. fuscoruber</i> & <i>G. oculolineatus</i> & <i>G. rivulatus</i>	1					
<i>G. fuscoruber</i> & <i>G. okinawae</i> & <i>G. quinquestrigatus</i>	1					
<i>G. fuscoruber</i> & <i>G. quinquestrigatus</i>	20					
<i>G. fuscoruber</i> & <i>G. quinquestrigatus</i> & <i>G. rivulatus</i>	2					
<i>G. fuscoruber</i> & <i>G. rivulatus</i>	9					
<i>G. histrio</i> & <i>G. oculolineatus</i>	1					
<i>G. histrio</i> & <i>G. quinquestrigatus</i>	2					
<i>G. histrio</i> & <i>G. rivulatus</i>	3					
<i>G. oculolineatus</i> & <i>G. quinquestrigatus</i>	1					
<i>G. oculolineatus</i> & <i>G. quinquestrigatus</i> & <i>G. rivulatus</i>	2					
<i>G. oculolineatus</i> & <i>G. rivulatus</i>	8					
<i>G. oculolineatus</i> & <i>G. sp.D</i>	1					
<i>G. okinawae</i> & <i>G. quinquestrigatus</i>	2					
<i>G. okinawae</i> & <i>G. sp.D</i>	1					
<i>G. quinquestrigatus</i> & <i>G. rivulatus</i>	3					
<i>G. sp.D</i> & <i>G. rivulatus</i>	1					

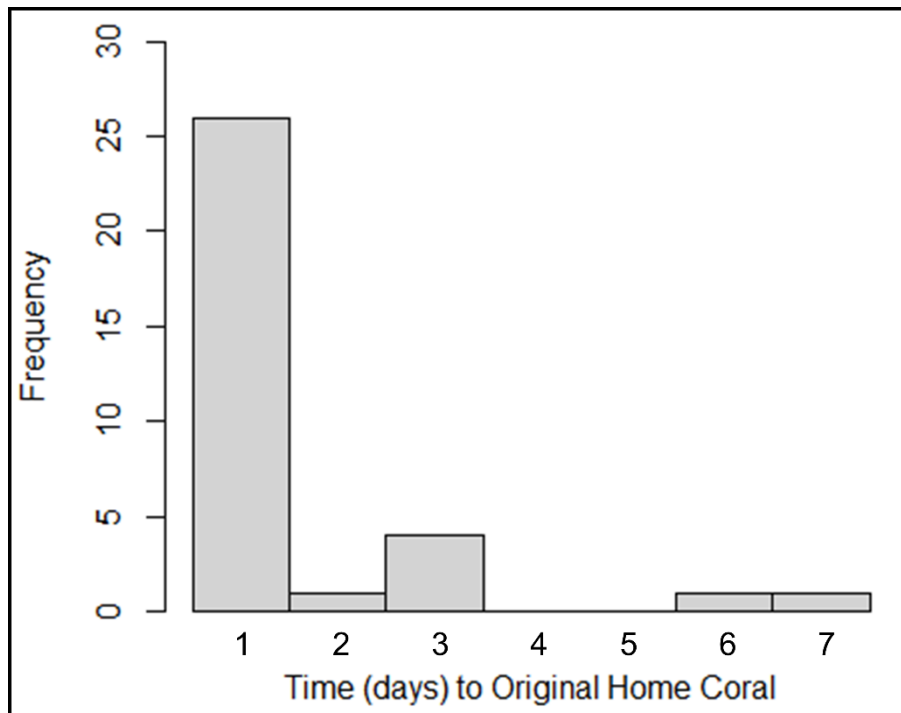
Supplementary Material for Chapter 6:



Supplementary Figure 6.1. The dead coral (white) and unfamiliar live coral were size matched for: **a** small corals and **b** large corals. **c** A net was placed around the dead coral for 5 min at the start of each trial and subsequently removed.



Supplementary Figure 6.2. Frequency of *Acropora* species that were used in the experiment for the home coral (red) and the unfamiliar live coral (blue).



Supplementary Figure 6.3. Number of days that focal gobies took to return home successfully.

Supplementary Table 6.1. Statistical outputs of all analyses for the movement decisions of coral dwelling gobies *Gobiodon quinquestrigatus* in relation to covariables and treatments. Additional covariables not discussed in detail in the manuscript are also included here. Habitat size means coral size, and habitat saturation means the number of gobies in the unfamiliar live coral. “Avg.” means average; “Prop.” means proportion; “within 10-m” refers to the survey completed in a 10-m radius around each experimental setup; “N/A” means not applicable.

Response variable	Predictor variable	Factor Type	Model Test	df	χ^2 value	p-value	pseudo R-squared Statistic	Test Value
focal goby final location (4 levels: dead coral, live coral, not located, returned home)	habitat health	N/A	chi-squared goodness-of-fit test	3	48.533	< 0.0001	N/A	N/A
if goby was located or not located	cost of movement	N/A	chi-squared goodness-of-fit test	1	1.7857	0.1814	N/A	N/A
focal goby final location (categorical variable: 4 levels)	habitat size	fixed	multinomial	5	1.3730	0.9272	McFadden	0.1132
	habitat saturation	fixed	logistic	8	3.7300	0.8806	Cox and Snell (ML)	0.1870
	interaction: habitat size x saturation	fixed	regression model	6	1.0330	0.9843	Nagelkerke (Cragg and Uhler)	0.2228
	model likelihood ratio test			15	12.4230	0.6467		
focal goby final location (categorical variable: 4 levels)	distance to intruder home coral	covariable	multinomial	3	1.9815	0.5763	McFadden	0.3808
	number of fish in intruder home coral	covariable	logistic	3	0.7351	0.8649	Cox and Snell (ML)	0.5016
	prop. uninhabited corals within 10-m	covariable	regression	3	1.0015	0.8009	Nagelkerke (Cragg and Uhler)	0.5976
	avg. group size of conspecifics in corals within 10-m	covariable	model	3	0.7680	0.8571		
	habitat size	fixed		5	2.4247	0.7878		
	habitat saturation	fixed		8	3.8077	0.8740		
	interaction: habitat size x saturation	fixed		6	2.0385	0.9161		
	model likelihood ratio test			27	41.7860	0.0346		
focal goby final location (categorical variable: 4 levels)	distance to intruder home coral	covariable	multinomial	3	4.0416	0.2570	McFadden	0.1885
	habitat size	fixed	logistic	4	0.6953	0.9519	Cox and Snell (ML)	0.2915
	habitat saturation	fixed	regression	8	4.1305	0.8452	Nagelkerke	0.3473
	interaction: habitat size x saturation	fixed	model	6	1.1887	0.9774	(Cragg and Uhler)	
	model likelihood ratio test			18	20.6800	0.2959		
focal goby final location (categorical variable: 4 levels)	number of fish in intruder home coral	covariable	multinomial	3	0.4837	0.9225	McFadden	0.2012
	habitat size	fixed	logistic	4	0.9593	0.9159	Cox and Snell (ML)	0.3079
	habitat saturation	fixed	regression	8	3.9462	0.8619	Nagelkerke	0.3668
	interaction: habitat size x saturation	fixed	model	6	1.1645	0.9786	(Cragg and Uhler)	
	model likelihood ratio test			18	22.0770	0.2286		
focal goby final location (categorical variable: 4 levels)	unfamiliar live coral average diameter	covariable	multinomial	3	0.0769	0.9945	McFadden	0.1139
	habitat size	fixed	logistic	5	1.2397	0.9410	Cox and Snell (ML)	0.1881
	habitat saturation	fixed	regression	8	3.6473	0.8875	Nagelkerke	0.2240
	interaction: habitat size x saturation	fixed	model	6	1.0695	0.9828	(Cragg and Uhler)	
	model likelihood ratio test			18	12.5000	0.8204		
focal goby final location (categorical variable: 4 levels)	intruder home coral average diameter	covariable	multinomial	3	2.4219	0.4896	McFadden	0.1460
	habitat size	fixed	logistic	4	1.5723	0.8138	Cox and Snell (ML)	0.2344
	habitat saturation	fixed	regression	8	3.7882	0.8757	Nagelkerke	0.2792
	interaction: habitat size x saturation	fixed	model	6	0.6783	0.9949	(Cragg and Uhler)	
	model likelihood ratio test			18	16.0220	0.5910		
focal goby final location (categorical variable: 4 levels)	number of corals within 10-m	covariable	multinomial	3	3.2425	0.3557	McFadden	0.1463
	habitat size	fixed	logistic	5	2.3435	0.7999	Cox and Snell (ML)	0.2348
	habitat saturation	fixed	regression	8	4.2744	0.8316	Nagelkerke	0.2797
	interaction: habitat size x saturation	fixed	model	6	1.9181	0.9271	(Cragg and Uhler)	
	model likelihood ratio test			18	16.0550	0.5887		
focal goby final location (categorical variable: 4 levels)	reef sampled	covariable	multinomial	9	2.5301	0.9801	McFadden	0.1668
	habitat size	fixed	logistic	5	1.9122	0.8612	Cox and Snell (ML)	0.2629
	habitat saturation	fixed	regression	8	3.7378	0.8800	Nagelkerke	0.3131
	interaction: habitat size x saturation	fixed	model	6	1.2359	0.9751	(Cragg and Uhler)	
	model likelihood ratio test			24	18.2980	0.7883		

Suppl. Tab. 6.1 (cont'd)

Response variable	Predictor variable	Factor Type	Model Test	df	χ^2 value	p-value	pseudo R-squared Statistic	Test Value
focal goby final location (categorical variable: 4 levels)	avg. group size in corals within 10-m	covariable	multinomial	3	2.3528	0.5025	McFadden	0.1382
	habitat size	fixed	logistic	5	1.5734	0.9044	Cox and Snell (ML)	0.2233
	habitat saturation	fixed	regression	8	3.9323	0.8632	Nagelkerke	0.2660
	interaction: habitat size x saturation	fixed	model	6	1.1439	0.9796	(Cragg and Uhler)	
	model likelihood ratio test			18	15.1610	0.6509		
focal goby final location (categorical variable: 4 levels)	prop. corals within 10-m with conspecifics	covariable	multinomial	3	5.6503	0.1299	McFadden	0.2267
	habitat size	fixed	logistic	5	2.5984	0.7616	Cox and Snell (ML)	0.3394
	habitat saturation	fixed	regression	8	4.5473	0.8047	Nagelkerke	0.4043
	interaction: habitat size x saturation	fixed	model	6	1.1184	0.9807	(Cragg and Uhler)	
	model likelihood ratio test			18	24.8750	0.1284		
focal goby final location (categorical variable: 4 levels)	avg. group size of conspecifics in corals within 10-m	covariable	multinomial	3	2.8486	0.4156	McFadden	0.1444
	habitat size	fixed	logistic	5	1.7018	0.8887	Cox and Snell (ML)	0.2320
	habitat saturation	fixed	regression	8	4.1718	0.8413	Nagelkerke	0.2764
	interaction: habitat size x saturation	fixed	model	6	1.2342	0.9752	(Cragg and Uhler)	
	model likelihood ratio test			18	15.8410	0.6037		
focal goby final location (categorical variable: 4 levels)	prop. uninhabited corals within 10-m	covariable	multinomial	3	0.9194	0.8207	McFadden	0.1226
	habitat size	fixed	logistic	5	1.3318	0.9316	Cox and Snell (ML)	0.2008
	habitat saturation	fixed	regression	8	3.6067	0.8907	Nagelkerke	0.2392
	interaction: habitat size x saturation	fixed	model	6	1.0074	0.9853	(Cragg and Uhler)	
	model likelihood ratio test			18	13.4490	0.7642		
focal goby final location (categorical variable: 4 levels)	empermental depth (unfamiliar live coral)	covariable	multinomial	3	2.5315	0.4696	McFadden	0.1390
	habitat size	fixed	logistic	5	1.4310	0.9209	Cox and Snell (ML)	0.2245
	habitat saturation	fixed	regression	8	3.9675	0.8600	Nagelkerke	0.2674
	interaction: habitat size x saturation	fixed	model	6	1.0879	0.9821	(Cragg and Uhler)	
	model likelihood ratio test			18	15.2530	0.6445		
focal goby final location (categorical variable: 4 levels)	year of experiment	covariable	multinomial	3	0.2992	0.9602	McFadden	0.1229
	habitat size	fixed	logistic	5	1.3776	0.9267	Cox and Snell (ML)	0.2013
	habitat saturation	fixed	regression	8	3.2511	0.9176	Nagelkerke	0.2398
	interaction: habitat size x saturation	fixed	model	6	0.9905	0.9860	(Cragg and Uhler)	
	model likelihood ratio test			18	13.4850	0.7620		
focal goby final location (categorical variable: 4 levels)	intruder goby standard length	covariable	multinomial	3	2.6132	0.4552	McFadden	0.2765
	habitat size	fixed	logistic	5	2.5858	0.7635	Cox and Snell (ML)	0.4240
	habitat saturation	fixed	regression	8	5.1707	0.7392	Nagelkerke	0.4908
	interaction: habitat size x saturation	fixed	model	6	1.1977	0.9770	(Cragg and Uhler)	
	model likelihood ratio test			33	30.3440	0.6000		
focal goby final location (categorical variable: 4 levels)	unfamiliar live coral species	covariable	multinomial	12	2.3849	0.9985	McFadden	0.1727
	habitat size	fixed	logistic	5	0.3060	0.9975	Cox and Snell (ML)	0.2708
	habitat saturation	fixed	regression	8	3.3812	0.9082	Nagelkerke	0.3227
	interaction: habitat size x saturation	fixed	model	6	0.2565	0.9997	(Cragg and Uhler)	
	model likelihood ratio test			27	18.9510	0.8718		
focal goby final location (categorical variable: 4 levels)	intruder home coral species	covariable	multinomial	39	2.1569	1.0000	McFadden	0.3711
	habitat size	fixed	logistic	5	1.6304	0.8976	Cox and Snell (ML)	0.4927
	habitat saturation	fixed	regression	8	4.5299	0.8064	Nagelkerke	0.5869
	interaction: habitat size x saturation	fixed	model	6	1.6188	0.9512	(Cragg and Uhler)	
	model likelihood ratio test			54	40.7150	0.9092		