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**Sub-lethal effects of coral loss and habitat
degradation on coral reef fishes with specific
emphasis on *Chaetodon* butterflyfishes**

Thesis submitted by
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In April 2023

For the degree of Master of Philosophy in Natural and Physical Sciences
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Acknowledgments

In 2015 I was in Lombok learning to surf, and my favourite quote from my Indonesian instructor was “never try, never know”. I really took this on board and nearly died several times during my surfing adventures. After surviving, I took this philosophy on in all aspects of my life, and that brought me to undertaking a Master of Philosophy. I am now at the finish line and could not have reached this point without the support of many people.

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Statement on the contribution of others

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Chapter	Contributor	Nature of assistance
Chapter 2	Morgan Pratchett ¹	Conceptual, writing, editorial, data collection
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	Peter Cowman ¹	Data analysis, editorial
	Shaun Wilson ²	Writing, editorial, data collection
Chapter 3	Morgan Pratchett ¹	Conceptual, writing, data collection
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	Samuel Matthews ¹	Data analysis, editorial
Chapter 4	Morgan Pratchett ¹	Writing, editorial, data collection
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In addition to above named persons who co-authored published thesis chapters, the following people assisted with data and specimen collections: Ciemon Caballes, Simon Wever, Michael Berumen, Andrew Cole, Rebecca Lawton and Deborah Pratchett.

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Abstract

Widespread and extensive degradation of coral reef ecosystems, which is characterised by declines in abundance (cover) of hard corals, shifts in benthic composition, and declines in structural complexity, have considerable effects on coral reef fishes. The rate and extent of coral reef degradation is however, increasing due to escalating effects of climate change and other anthropogenic pressures. Changing environmental and habitat conditions on coral reef fishes are expected to affect an increasing range of reef-associated fishes, with potential consequences for biodiversity, productivity and ecosystem function. Effects of reef degradation and coral loss are likely to be particularly pronounced for specialized fishes that rely on corals for food and/ or shelter, including coral-feeding butterflyfishes. However, susceptibility of fishes may vary not only with patterns of resource use, but also inherent variation key biological attributes, such as sociality. This thesis explores effects of sustained and ongoing environmental and habitat changes (namely coral loss) on coral reef fishes, focussing explicitly on sublethal (e.g., behavioural and physiological) responses that might precede, and contribute towards, apparent declines in the local abundance of fishes following acute episodes of coral loss.

In Chapter 2, the effects of mass coral bleaching (and associated changes in the structure of tropical reef habitats) on the structure and function of reef fish were examined by testing for variation in responses of fishes within and among 19 distinct functional or trophic groups. To explicitly test for response diversity and compensatory dynamics among reef fishes, data were compiled from a variety of studies that have quantified species-specific declines in abundance of fishes prior to, and then 1-7 years after distinct episodes of coral loss. This chapter also reported on changes in feeding rates and diet, physiological condition, and growth of fishes, that were exposed to extensive corals loss, which may forewarn of longer-term impacts on individual survival and population viability. While the effects of coral depletion caused by climate-induced coral bleaching was of primary interest, data were taken from all studies that have explored changes in the abundance of fishes following acute episodes of coral loss, regardless of the cause. The main group of fishes that consistently exhibited pronounced and often very rapid declines in abundance following localised coral depletion were obligate coral-feeding fishes. Declines in the abundance of coral-feeding fishes are directly attributable to prey depletion and subsequent starvation, reflected in initial declines in their physiological condition. Where coral bleaching and/or coral mortality reduces the availability of coral prey, declines in the abundance of coral-feeding fishes are often preceded or accompanied by declines in individual condition or fitness. Declines in individual condition may occur regardless of shifts in diet breadth and composition, demonstrating that fishes are susceptible to changes in coral composition even if there is only moderate change in the

overall abundance (or cover) of corals. Aside from coral-feeding fishes (e.g., butterflyfishes), there has been very limited consideration of behavioural or physiological responses to coral loss and reef degradation. It is apparent however, even by just looking at population-level responses, that extensive coral loss affects a very broad range of different fish species.

Coral loss and reef degradation are among the foremost threats to coral reef fishes, especially for highly specialised species with specific reliance on live corals. Aside from affecting the carrying capacity of local environments, declines in the quality and quantity of critical reef habitats are likely to lead to changes in behaviour, condition, and fitness of individual fishes. Chapter 3 of this thesis explored changes in the sociality (specifically, the proportion of individuals observed in pairs) for coral reef butterflyfishes over several decades, in the northern Great Barrier Reef. During the study period where there were significant disturbances that reduced coral cover, there were also sustained declines in abundance of many butterflyfish species. Across five species of pairing butterflyfishes (*Chaetodon baronessa*, *C. lunulatus*, *C. citrinellus*, *C. auriga* and *C. vagabundus*), the overall proportion of individuals in pairs varied among the three surveys (2002, 2009, and 2017) and was positively correlated with live coral cover. This pattern was most apparent for, and largely driven by changes in sociality of *C. baronessa*. Declines in incidence of pairing may suggest that pairing is untenable as prey becomes limiting, or elevated rates of adult mortality increasingly disrupt patterns of sociality. Disruptions to sociality, and thereby reproductive systems, may add to population declines and greatly constrain subsequent recovery and resilience of populations. For other more generalist or non-coral feeders, the relative incidence of pairing actually increased due to disproportionate declines in abundance of solitary individuals. This chapter shows that coral loss and reef degradation can have important effects on the sociality of reef fishes, though it remains to be tested whether species with more complex or atypical sociality are more or less susceptible to coral loss.

The chevron butterflyfish, *Chaetodon trifascialis*, is among the most specialised coral-feeding fishes, and while it is known to be very susceptible to extensive depletion of its preferred coral prey (tabular *Acropora* spp.), their specific responses to changing coral cover are poorly understood. The purpose of Chapter 4 was to test for variation in territorial behaviour and condition of *C. trifascialis* relative to spatial variation in coral cover across four mid-shelf reefs on the Great Barrier Reef. Explicit consideration was also given to the territorial arrangement and interactions among sympatric individuals, with a view to better understanding the sociality of this species. Variation in overall coral cover (which ranged from 26.5–73.4% among sites) as well as cover of tabular *Acropora* (13.3–44.8%) had limited effect on the territoriality or body condition of *C. trifascialis*. Rather, individual variation in territoriality was attributable to differences in sex and size of fish. Male *C. trifascialis* were generally larger and also had larger territories than female counterparts. They also interacted with conspecifics

(and congenics) much more than females. Taken together, these results support previous assertions that *C. trifascialis* is harem. There was, however, limited evidence that male territories encompassed the territories of >1 female. It is possible therefore, that generally low levels of coral cover (especially, limited abundance of tabular *Acropora*) may constrain the complex sociality of this species and thereby limit local reproduction capacity and recovery potential.

It is well established that extensive coral loss (whether caused by mass-bleaching, severe tropical storms, or outbreaks of invertebrate corallivores) results in significant declines in abundance across a broad range of different reef fishes. The research presented in this thesis suggests that such effects may be underpinned by variety of sublethal effects, such as changes dietary selectivity, territoriality, and sociality. These behavioural changes may moderate or exacerbate declines in the local abundance of coral reef fishes subject to coral loss and habitat degradation. However, apparent changes in the physiological condition of fishes with varying abundance of coral prey or habitat clearly demonstrate their susceptibility to coral loss. In all, this thesis shows that extensive coral loss will have significant and far-reaching effects on reef-associated species, and especially those species that are highly specialised and strongly coral-dependent. This provides significant imperative for reducing greenhouse gas emissions, to reduce the incidence and severity of future mass coral bleaching events, while also addressing other more localised disturbances that contribute to coral loss and reef degradation.

Table of contents

Acknowledgments.....	ii
Statement on the contribution of others	iii
Abstract.....	iv
Table of contents	vii
List of tables	ix
List of figures.....	x
Chapter 1: General Introduction.....	1
1.1: Environmental and habitat change on coral reefs	1
1.2: Responses of coral reef fishes to coral loss and reef degradation	3
1.3: Sociality and its importance in coral reef fish ecology	4
1.4: Coral reef butterflyfishes	5
1.5: Objectives and thesis outline.....	7
Chapter 2: Effects of Coral Bleaching and Coral Loss on the Structure and Function of Reef Fish Assemblages	10
2.1: Introduction	10
2.2: Coral bleaching and changes in the structure of reef habitats	13
2.2.1: Bleaching selectivity and changes in coral composition	13
2.2.2: Coral loss and increasing predominance of alternative habitat-forming taxa	15
2.2.3: Coral loss versus declines in topographic complexity	16
2.3: Declines in abundance of reef fishes and loss of biodiversity and function	17
2.3.1: Interspecific variation in vulnerability to coral bleaching and depletion	18
2.3.2: Loss of biodiversity and function	22
2.3.3: Effects of coral reef degradation on tropical fisheries production	25
2.4: Changes in the behaviour and fitness of reef fishes.....	27
2.4.1: Behavioural changes	29
2.4.2: Effects of coral bleaching versus coral loss on individual fitness of fishes.....	30
2.5: Conclusions	31
Chapter 3: Changes in sociality of butterflyfishes linked to population declines and coral loss	33
3.1 Introduction	33
3.2 Materials and methods	35
3.2.1 Study location and history of disturbances	35

3.2.2 Study species.....	36
3.2.3 Field sampling	37
3.2.4 Statistical analysis	38
3.3 Results	38
3.3.1 Changes in sociality	40
3.4 Discussion.....	41
Chapter 4: Territoriality and condition of Chevron Butterflyfish (<i>Chaetodon trifascialis</i>) with varying coral cover on the Great Barrier Reef, Australia.....	46
4.1 Introduction	46
4.2 Methods	49
4.2.2 Behavioural observations	51
4.2.3 Fish collections	51
4.2.4 Individual condition	52
4.2.5 Coral cover	53
4.2.6 Statistical analysis	53
4.3 Results	54
4.3.1 Fish collections	54
4.3.2 Territories and coral cover	56
4.3.3 Behavioural observations	56
4.3.4 Body condition	57
4.4 Discussion.....	57
Chapter 5: General Discussion	66
5.1: Changes in the sociality of fishes with habitat degradation.....	67
5.2: Future directions	69
References	70
Appendices.....	92
Appendix A: other publications during candidature	92

List of tables

Table 2.1

Sub-lethal effects of mass-coral bleaching and coral depletion on coral reef fishes, highlighting A) behavioral shifts associated with declines in the local abundance, cover or diversity of corals, and B) consequences for individual fitness, such as declines in condition and growth.

Table 3.1

Chaetodon species present at Lizard Island, showing their classification to sociality types by Yabuta and Berumen (2014), as well as the percentage of fish (mostly mature individuals) recorded in pairs from different studies and locations.

Table 4.1

Reefs visited in 2017 with GPS coordinates for sites and month of the year that site was visited

Table 4.2

Proportional cover of different coral genera/ families at each of 11 sites where we documented sociality for a distinct group of *C. trifascialis*. *Acropora* corals were further divided into tabular *Acropora* and other *Acropora*, reflecting the strong feeding preference of *C. trifascialis* for tabular *Acropora* (e.g., Pratchett 2005). Standard Error (SE) indicated in parentheses. Shannon's diversity index (Shannon 1948) shows species diversity for each group and can be read as: low diversity (<1.5), medium diversity (1.5<2.5) and high diversity (>2.5)

Table 4.3

Variation in biological and environmental characteristics among 11 distinct groups of *C. trifascialis*, sampled across 4 different reefs (Fig. 1). "*" indicate groups that exhibit nested territories, which may be indicative of harem mating

Table 4.4

Variation in the areal extent of territories of *C. trifascialis* modelled as a function of "Sex", "Size", and cover of "Acropora" (or overall cover of all corals as an alternate model) within individual territories, using a linear mixed effects model (lme), where all models include "Group" as a random effect. Alternative models were compared using Akaike's information criterion corrected for small sample sizes (*AICc*), while also accounting for changes in degrees of freedom (*df*). The adjusted R^2 (*adj R^2*) is shown for each model, and the best model shown in bold

List of figures

Figure 2.1

Effects of coral loss on biodiversity (species richness) of coral reef fishes. The relationship between change in species richness (%) is plotted against increasing declines (%) in local coral cover, based on data extracted from 30 independent studies, categorized according to the major (but not exclusive) cause of localized coral loss. Confidence intervals (~95%) for the General Additive Model were calculated using a continuous set of predictor variables ($n = 1,000$), with the MGCV package in R.

Figure 2.2

Standardised responses of A) Obligate corallivores and B) Croppers and browsers to significant (>10%) declines in coral cover. Species-specific responses are calculated based on their proportional decline in abundance divided by proportional declines in live coral cover, and averaged across multiple studies, where possible. Standard errors are calculated based on variation in responses among studies.

Figure 2.3

Variation in standardized responses to coral loss (proportional change in the abundance of individual species divided by proportional declines in local coral cover) for 19 functional (trophic) groups of reef fishes. Responses are predominantly negative showing the broad range of fishes that decline in abundance following coral loss.

Figure 3.1

Temporal (1995-2017) changes in coral cover at Lizard Island, averaged across four zones (flat, crest, slope and base) at four sites (North Reef, Washing Machine, Lizard Head and South Island). Declines in coral cover (from 1995 to 2002 and 2011 to 2017) are attributable to major disturbances that occurred during these periods, including outbreaks of crown-of-thorns starfish (1995-1999, 2009-2015), severe tropical cyclones (2014, 2015) and mass coral bleaching (2016).

Figure 3.2

Changes in sociality and abundance of butterflyfishes among sample years, and relative to temporal changes in coral cover (in order from left to right), for **a** all species combined, **b** *Chaetodon baronessa*, **c** *Chaetodon lunulatus*, **d** *Chaetodon citrinellus*, **e** *Chaetodon auriga* and **f** *Chaetodon vagabundas*.

Figure 4.1

Relative size and position of individual territories for *Chaetodon trifascialis*, recorded across 11 sites at 4 reefs on the Great Barrier Reef, Australia. Colours on left-bottom panel indicate Great Barrier Reef Marine Park Authority zonation (GBRMPA). Elford Reef was zoned “conservation zone”, while all other locations were within “habitat protection zones”. Right panels showing territory maps are grouped by reef, each coloured polygon is an individual fish (yellow, female; blue, male; and grey, unknown sex or juvenile). Inset shows the method used to quantify territory area for each focal individual.

Figure 4.2

Chaetodon trifascialis gonads stained with Mayer’s hematoxylin and Young’s eosin. (a) mature male showing stages of spermatogenesis: oc) spermatocytes; ti) spermatids; and zo) spermatozoa, zoomed section inset (b) high magnification (40x) of spermatozoa; (c) mature female showing ripe stage 4 oocytes; and (d) immature female showing only stage 1 and 2 oocytes. Numbers denote stage of oocyte development: 1) previtellogenic, perinucleolar; 2) previtellogenic, cortical alveoli beginning formation; 3) early vitellogenic; and 4) mid vitellogenic. Scale bars are in mm.

Figure 4.3

Box plots showing sex related differences in body size (total length in mm) and territory size (area in m²) of *Chaetodon trifascialis*. Sex is unknown for those individuals that evaded capture or were immature (grey).

Figure 4.4

Relationship between size (total length in mm) of *C. trifascialis* and A) territory size (area in m²) and B) frequency of interactions, with separate relationships shown for males (blue), females (orange), and those individuals for which sex is unknown (grey).

Figure 4.5

Frequency of congeneric interactions recorded during observations (total 1,080 minutes) of *Chaetodon trifascialis* (n = 54).

Chapter 1: General Introduction

Coral reefs are renowned for their exceptional biodiversity and productivity (e.g., Sale 1977; Connell 1978; Hughes 1989; Knowlton et al. 2010), which are variously attributed to the specific environmental and habitat conditions that characterise coral reef ecosystems. At local scales, for example, the high diversity and complexity provided by habitat forming hard (order Scleractinia) corals often moderates environmental conditions (eg. Provides refuge from UV irradiance – Kerry and Bellwood 2017) to tolerable levels for a range of species, moderates biological interactions, and allows for increased co-existence among reef-associated species (Beukers and Jones 1998; Bruno et al. 2003; Bonin et al. 2015). Accordingly, the local abundance and diversity of reef-associated species often increases with the diversity and abundance (cover) of hard corals (e.g., Bell and Gazlin 1984; Roberts and Ormond 1987; Bouchon-Navaro and Bouchon 1989; Gratwicke and Speight 2005; Graham and Nash 2012). Coral reef ecosystems are however, being increasingly exposed to major disturbances and anthropogenic pressures (Bellwood et al. 2019), and corresponding changes in environmental and habitat conditions are threatening biodiversity and productivity (Wilson et al. 2006; Bell et al. 2013).

Perennial threats to coral reef ecosystems (e.g., overfishing, sedimentation, and eutrophication) are now also being compounded and exacerbated by increasing effects of global climate change (Hughes et al. 2017; Bruno et al. 2019). The degradation of coral reef ecosystems are most apparent based on sustained and ongoing declines in the cover of hard corals, which have been documented in most major coral reef regions (e.g., Arabian Gulf – Burt et al. 2013; Riegl et al. 2018; central Indian Ocean – Graham et al. 2006; Sheppard et al. 2020; Great Barrier Reef – De'ath et al. 2012; Mellin et al. 2019; Caribbean – Gardner et al. 2003). Coral loss, and corresponding changes in the physical structure of coral reef habitats, further affects the broad range of organisms that associate with coral reefs (Wilson et al. 2006; Stella et al. 2011). Most notably, marked declines in the abundance and diversity of coral reef fishes have been documented following acute and extensive coral loss (Jones et al. 2004; Wilson et al. 2006; Munday et al. 2008; Pratchett et al. 2008a; Alvarez-Filip et al. 2015; Cheal et al. 2017; Bargahi et al. 2020), especially when local coral cover is reduced to <10% (Wilson et al. 2006; Holbrook et al. 2008).

1.1: Environmental and habitat change on coral reefs

The plight of coral reefs has been highlighted by recent effects of unprecedented, punctuated disturbances, and most particularly, extensive and widespread mass bleaching and coral mortality associated with pan-tropical temperature extremes (Hughes et al. 2018a;

Eakin et al. 2019). However, the current condition and status of many of the world's coral reef ecosystems (Öhman et al. 1993; Gardner et al. 2003; Bellwood et al. 2004; Wilkinson 2004; Jackson et al. 2014) reflects a long-history of disturbances and anthropogenic pressures that have not only directly contributed to habitat degradation but undermined the resilience of key habitat-forming species (Pandolfi et al. 2003; Bellwood et al. 2004; Mellin et al. 2019). Notably, reef degradation and coral loss have occurred over several decades in various reef systems (e.g., Gardner et al. 2003; De'ath et al. 2012; Precht et al. 2019). The rate and extent of habitat degradation is, however, increasing as expansive and pervasive anthropogenic pressures (e.g., intensified fisheries, human visitation, catchment modification, pollution, and climate change) combine and affect an increasing proportion of coral reefs (Harborne et al. 2017; Bellwood et al. 2019; Bauman et al. 2022).

Major disturbances affecting coral reef ecosystems, including climate-induced mass-bleaching and severe tropical storms (hurricanes, typhoons or cyclones), generally damage or kill reef-building and habitat-forming corals (Hughes et al. 2018; Madin et al. 2018; Pisapia et al. 2019), thereby contributing to coral loss. However, the immediate and instantaneous effects of elevated coral mortality are also compounded and conflated by prolonged suppression of coral growth and replenishment (Done et al. 2010; Gilmour et al. 2013; Bonesso et al. 2017; Hughes et al. 2019), which constrains the recovery and resilience of disturbed assemblages. Chronic and ubiquitous changes in environmental and habitat conditions further constrain growth and recovery of corals (e.g., Thompson and Dolman 2010; Gil et al. 2016; Ortiz et al. 2018), such that rates of coral recovery are declining while the frequency and severity of disturbances are increasing (e.g., Hughes et al. 2018). Reduced rates of coral settlement and growth and/ or increased incidence of disturbances will limit opportunities for coral recovery (Osborne et al. 2011; Johns et al. 2014) contributing to sustained declines in coral cover and persistent low cover of corals.

Aside from causing elevated coral mortality and corresponding declines in live coral cover, increasing incidence of both chronic and acute disturbances will have a major influence on the biological and physical structure of coral reef habitats (Wilson et al. 2006; Pratchett et al. 2008). In the extreme, extensive coral loss often coincides with declines in topographic complexity of reef habitats (Pratchett et al. 2008a; Alvarez-Filip et al. 2009) and proliferation of macroalgae (or seaweeds) or alternative early colonisers of consolidated reef substrates (Norström et al. 2009; Hughes et al. 2010; Graham et al. 2014; Tebbett et al. 2023). However, there are also likely to be significant changes in the relative abundance and dominance of different coral species (Alvarez-Filip et al. 2013; Pratchett et al. 2020; McWilliam et al. 2020), which can have significant effects on the structure and function of coral reef ecosystems.

Given marked inter-specific differences in the susceptibility and resilience of corals to acute and chronic disturbances (Hughes et al. 2018b), increasingly disturbed coral

assemblages are likely to represent new and alternative configurations of coral species (Darling et al. 2013; Graham et al. 2014; Zinke et al. 2018). Most major disturbances (e.g., severe tropical storms and mass-bleaching) disproportionately affect erect branching coral species, such as *Acropora* (Loya et al. 2001; McClanahan et al. 2004; Madin and Conolly 2006; Pratchett et al. 2008). However, the predominance of coral taxa in the aftermath of major disturbances is influenced as much (if not more) by the differential recovery (specifically, interspecific variation in growth and recruitment) capacity of corals, as it is the differential susceptibility among taxa (Connell 1978; Jackson and Hughes 1985; Baker et al. 2008; Darling et al. 2013). The capacity of corals to recover (regardless of whether they have fast or slow growth and high or low recruitment) will, however, be conditional upon the scale, frequency and severity of disturbances (Pratchett et al. 2020). As such, directional shifts in the structure of coral assemblages will depend on the specific local context and disturbance regime.

1.2: Responses of coral reef fishes to coral loss and reef degradation

It is well established that extensive coral loss (whether caused by mass-bleaching, severe tropical storms, or outbreaks of invertebrate corallivores) results in significant declines in abundance across a broad range of reef fishes (Munday 2004, Sano 2004, Bellwood et al. 2006a, Pratchett et al. 2008, 2011b) and corresponding declines in the diversity of reef fish assemblages (Wilson et al. 2006). However, it is still unclear how apparent effects of coral loss are compounded or conflated by changes in the biological and physical structure of coral reef habitats (Pratchett et al. 2008a). It is unequivocal that live coral represents a critical and important resource for many reef-associated fishes, especially those fishes that depend on corals for food, shelter or settlement (Williams 1986; Munday 2000; Jones et al. 2004; Pratchett et al. 2006; Froehlich et al. 2021, 2022). For many other fishes, however, live coral may be largely irrelevant, except in contributing to habitat diversity and topographic complexity (Roberts and Ormond 1987; Garpe et al. 2006; Graham and Nash 2013). Discerning the independent effects of coral loss (as distinct from topographical collapse) may be possible by assessing the short-term responses of fishes to biological disturbances (e.g., mass coral bleaching) that cause extensive coral mortality while largely unaffected the structure of coral habitats (Wilson et al. 2006). Recent and extensive mass coral bleaching (e.g., Hughes et al. 2018), therefore, provides a unique and important opportunity to further assess the consequences of extensive coral mortality on reef-associated fishes.

Declines in the abundance and diversity of reef fishes in the aftermath of punctuated disturbances and extensive coral loss provides compelling evidence that live coral is critically important habitat for many reef fishes (Wilson et al. 2006). Declines in the abundance of reef fishes on degraded reef habitats, which may be highly protracted (Graham et al. 2007;

Pratchett et al. 2008a) are however, likely to be preceded or accompanied by changes in the individual behaviour and fitness of reef fishes. Declines in the abundance of coral-dwelling fishes, for example, are attributed to compromised health of the individual fishes and increased susceptibility to predation following extensive coral loss (Sano et al. 1984, 1987; Jones et al. 2004; Pratchett et al. 2008b). However, there has been very limited research on sublethal effects of such disturbances (but see Coker et al. 2009, 2013), especially compared to extensive research on changes in the abundance and diversity of fishes following punctuated disturbances and extensive coral loss (reviewed by Wilson et al. 2006, Pratchett et al. 2008a, 2011b).

Sublethal effects are those that, while not immediately causing the death of an organism, can contribute to a reduction in function or physiological condition of the organism such that they have reduced fitness and may exhibit protracted declines following the effect. This can include changes to behaviour such as switching prey to a less calory dense species when the preferred prey is lost, or reduced in abundance, due to disturbance (Wen et al. 2016; Hempson et al. 2017). The switching of prey to more readily available but less calory-dense sources causes a reduction in physiological condition which has flow-on effects on individual health and reproductive fitness (Pratchett et al. 2004; Brooker et al. 2013a). Alternatively, if fish do not change their feeding preference when their favourite food is lost, they can become locally extirpated (Brooker et al. 2014). These changes in the individual behaviour and condition of fishes with varying abundance of specific corals may forewarn of longer-term impacts on individual survival and population viability, but also help to understand the specific nature and importance of strong associations with live corals.

1.3: Sociality and its importance in coral reef fish ecology

The sociality of reef fishes (more specifically, the group typology and nature of social relationships among individuals within a population) is an important biological attribute that has significant influence on the local distribution, abundance, and habitat-use for reef fishes (e.g., Hing et al. 2018). The stability and maintenance of social groups may also influence reproductive potential (Whiteman and Côté 2004; Nowicki et al. 2018a), and thereby influence resilience and recovery of fishes in the aftermath of major disturbances and habitat degradation. This is important, because changes in habitat condition and structure may serve to disrupt sociality of fishes. For obligate coral-dwelling fishes, for example, the size and occurrence of breeding pairs is constrained by the availability of sufficiently large coral hosts (e.g., Kuamura et al. 1994). The coral dwelling goby, *Paragobiodon xanthosomus*, lives in groups with subordinate fish that are not sexually mature (reproductive suppression) choosing to live in a high-quality coral where they will not have a chance to breed, rather than a lower quality coral where they would be a dominant, reproductive member of the group (Fricke 1980;

Wong 2010; but see also Froelich et al 2022). Group sociality could involve either a dominant individual living with a number of individuals of the opposite sex, and sexually immature subordinates who are constrained by both social and ecological factors (poor alternatives) (Branconi et al 2020). Declines in the size and/ or abundance of suitable coral hosts may, therefore, greatly constrain the reproductive capacity and population persistence of coral-dwelling fishes (Munday 2004), with disproportionate effects on specialist species that occupy only a very limited suite of different corals. Despite increased variability in group typology and increased opportunities for mating, constraints of habitat availability on local reproduction may be even more pronounced for group forming fishes (Hing et al. 2018). Hing et al. (2018) showed that declines in local size and abundance caused by recurrent storms had disproportionate effects on group forming species of coral-dwelling goby, whereas pair-forming species were relatively resilient to changing availability of coral hosts, because they were able to maintain their social organisation in much smaller coral hosts than group forming species. The generality of this finding is, however, unknown, owing to limited studies of the effects of coral loss on sociality of fishes.

1.4: Coral reef butterflyfishes

Butterflyfishes (family Chaetodontidae) are a speciose and diverse group of marine fishes, characterised by deep compressed bodies, small mouths, strong jaws and bristle-like teeth (Bellwood and Pratchett 2014). Most, but not all, butterflyfishes are strongly associated with coral reefs (Bellwood et al. 2010). Moreover, many coral reef butterflyfishes (at least 61 species of the 79 species that are generally associated with coral reefs) feed on corals, with ~25 feeding primarily, if not exclusively on corals (Cole et al. 2008; Cole and Pratchett 2014). As such, butterflyfishes are the predominant group of coral reef fishes that consume corals, potentially representing an important and critically underrepresented trophic link on coral reefs (Cole et al. 2008). More importantly, however, their reliance on corals for food makes butterflyfishes extremely sensitive to changes in the quality and quantity of corals (Cole et al. 2008). Coral reef butterflyfishes also rely on live corals for habitat, especially at settlement (Pratchett et al 2008b).

Coral reef butterflyfishes, especially *Chaetodon* species, are broadly classified as obligate, facultative, or non-coral feeders (Harmelin-Vivien and Bouchon-Navaro 1983, Pratchett 2005; Cole and Pratchett 2014), which is intended to reflect their differential reliance on corals and vulnerability to coral loss (Pratchett et al. 2006b, 2008a). Butterflyfishes for which corals represent >80% of the diet (e.g., >80% of bites are taken from live corals; Pratchett 2005) are considered to be obligate coral feeders (Pratchett 2005; Cole and Pratchett 2014) and have been shown to be disproportionately affected by extensive coral loss (Bouchon-Navaro et al. 1985; Pratchett et al. 2008a). Approximately one-third of coral

reef butterflyfishes are obligate coral feeders (Cole and Pratchett 2014) and obligate coral feeding species are often the predominant butterflyfishes recorded in coral-dominated habitats. Among obligate coral-feeding butterflyfishes there are marked differences in dietary breadth and selectivity. *Chaetodon trifascialis*, for example, is an extreme specialist, which feeds almost exclusively on tabular *Acropora* (Pratchett 2005) and even though it will readily feed on alternate prey, cannot survive without access to *Acropora* corals (Berumen and Pratchett 2008). In contrast, *Chaetodon lunulatus* feeds on a wide diversity of corals (Berumen et al. 2005, Pratchett 2005), and has been shown to modify its diet composition with changes in availability of different coral prey (Pratchett et al. 2004). This variability in dietary selectivity and ecological versatility is reflected in the differential susceptibility of obligate coral-feeding fishes to localised coral loss (reviewed by Pratchett et al. 2008a; Wilson et al. 2014).

For facultative coral-feeding butterflyfishes, corals constitute 20-60% of their diet (Pratchett et al. 2008a), but even though those species that consume relatively limited amounts of coral (e.g., *Chaetodon kleinii*) display consistent declines in abundance following extensive coral loss. This suggests that the proportional use of coral prey by different species of butterflyfishes does not necessarily reflect their differential reliance on corals, nor vulnerability to coral loss. Even though they exploit a greater diversity of different prey items, facultative corallivores may be nonetheless reliant on corals to provide essential nutrients and/or provide a mixed diet to maximise assimilation efficiency (Birkeland and Neudecker 1981). Even some non-coral feeding butterflyfishes (e.g., *Chaetodon auriga*), for which corals represent <5% of their diets, consistently decline in abundance following localised coral loss, (Pratchett et al. 2015b). In analysing the responses of butterflyfishes to coral loss, Wilson et al. (2014) suggested that dietary specialisation was more important than the relative consumption of coral prey in accounting for inter-specific differences in susceptibility. There may also be other biological attributes (e.g., differences in sociality) that affect the extent to which butterflyfishes are sensitive to changes in coral cover.

Many butterflyfish are pair forming, although this can vary by geographic location (Yabuta and Berumen 2014). The strength of heterosexual pair bonds may vary seasonally with pairs more frequently swimming together during the reproductive season (eg. *C. lunulatus*, *C. ornatissimus*, *C. plebius*; Yabuta 2007). Nowicki et al (2018b) showed that pairs stay together and re-pair quickly after their partner is removed. During the short term (~9days) following a re-pairing the new pair show more conflict with each other than the original two individuals (Nowicki et al 2018b). This conflict is an extra use of energy that could be better used to forage and shows that there are benefits to remaining with the same partner, rather than switching regularly. While pairing is often thought to be between male and female for reproductive benefits, several species of Chaetodontidae have been shown to pair when immature (Fricke 1986) and with partners of the same sex (Gore 1983). Whether for

reproduction or not, this social arrangement has been shown to confer benefits to both individuals through enhanced predator vigilance and increased foraging (Brandl and Bellwood 2014; 2015).

Aside from being the most specialised butterflyfish, the sociality of *C. trifascialis* is also atypical of *Chaetodon* butterflyfishes (Yabuta and Berumen 2014). Whereas most *Chaetodon* butterflyfish are pair-forming (Yabuta and Berumen 2014; Brandl and Bellwood 2015; Nowicki et al. 2018a) and presumed to be monogamous (Whiteman and Côté 2004; Yabuta and Berumen 2014), *C. trifascialis* is mostly observed as solitary individuals and considered to be polygamous (Yabuta and Kawashima 1997). Polygamous and harem species may be particularly susceptible to breakdowns in sociality (*sensu* Lung and Childress 2007; Whiteside et al. 2016), because females rely on dominant males for competitive defence and predator vigilance. There has however, been very limited research on spatiotemporal variation in the sociality of butterflyfishes.

1.5: Objectives and thesis outline

The overarching objective of this thesis was to advance understanding of the specific effects of sustained and ongoing environmental and habitat changes on coral reef fishes, focussing explicitly on sublethal (e.g., behavioural and physiological) responses that might precede, and contribute towards, apparent declines in the local abundance of fishes following acute episodes of coral loss (e.g., Pratchett et al. 2004). Given their strong reliance on live corals as both food and habitat (Wilson et al. 2014), this research is focussed on coral feeding *Chaetodon* species. However, before presenting original research on the biology of *Chaetodon* butterflyfishes (i.e. Chapters 3 and 4), Chapter 2 provides an overview of the contemporary knowledge and understanding of the effects of coral loss across coral reef fishes more broadly. The specific objectives of each of the formative chapters of this thesis, as well as their independent and novel contributions to understanding responses of fishes to changing habitat conditions, are outlined in-turn.

Chapter 2 explores effects of coral bleaching and coral loss on reef fishes, based on reported changes in the abundance of fishes following acute disturbances and extensive coral loss. This review builds on similar previous reviews (e.g., Wilson et al. 2006, Pratchett et al. 2008) by assessing standardised responses across individual fish species, which relate proportional changes in the abundance of fish to the extent of coral loss that has occurred, mostly due to climate-induced coral bleaching. The emphasis on coral bleaching reflects its' increasing importance as the foremost cause of episodic coral loss on coral reefs (e.g., Hughes et al. 2018a). This review focuses on variation in standardised responses within and among 19 different functional (trophic) groups, showing that extensive coral bleaching and coral loss results in declines in the abundance of fishes across virtually all functional groups

examined (Fig. 2.3). This review also outlines the variety of sublethal effects of coral loss and reef degradation on reef fishes that have been documented in previous (and mostly very recent) studies (Table 2.1).

Chapter 3 explores changes in the sociality of *Chaetodon* butterflyfishes over an extended period, during which, there were significant disturbances that reduced coral cover and caused declines in abundance of many different butterflyfishes. Most species of butterflyfishes are pair-forming (Yabuta and Berumen 2014; Brandl and Bellwood 2015; Nowicki et al. 2018a), and paired individuals not only have increased reproductive opportunities, but higher feeding efficiency and greater access to limited resources (Brandl and Bellwood 2014). It is also possible, however, that declines in resource availability will undermine the benefits and persistence of pairs (Reese 1981). Declines in incidence of pairing following coral loss may suggest that pairing is untenable as prey becomes limiting, or elevated rates of adult mortality increasingly disrupt patterns of sociality. Disruptions to sociality, and thereby reproductive systems, may further contribute to declines in the abundance of butterflyfishes following major disturbances and extensive coral loss and greatly constrain subsequent recovery and resilience of populations.

Whereas most *Chaetodon* butterflyfish are pair-forming and presumed to be monogamous (Whiteman and Côté 2004; Yabuta and Berumen 2014), *Chaetodon trifascialis* predominantly occurs as solitary individuals and is potentially polygamous (Yabuta and Kawashima 1997). *Chaetodon trifascialis* is also among the most specialised species of butterflyfish (Pratchett 2005), though their distribution and diet may reflect their competitive dominance and increased access to prey corals (Blowes et al. 2013). The purpose of **Chapter 4** was to explore variation in the sociality and physiological condition of *C. trifascialis* among reefs and sites with varying coral cover and composition. Specifically, we investigated how i) territory size, ii) sociality, iii) aggression, and iv) individual condition of *C. trifascialis* varied with local coral cover. This research will not only improve understanding of the specific sociality of *C. trifascialis* but establish the extent to which specialisation and/ or sociality may influence the susceptibility of fishes to reef degradation and coral loss. Highly specialist fishes are likely to be particularly vulnerable to disturbances and resource depletion (e.g., Munday 2004), but other important biological traits (e.g., sociality; Hing et al. 2018) may also influence their vulnerability.

The research presented in this thesis is expected to significantly advance understanding of the effects of reef degradation and coral loss on reef associated fishes, and especially *Chaetodon* butterflyfishes. *Chaetodon* butterflyfishes are expected to be directly and substantially affected by reef degradation, owing to their specific reliance on corals for food and settlement (Pratchett et al. 2008a). However, susceptibility to disturbances may vary not only with patterns of resource use, but also with inherent variation key biological attributes,

such as sociality. Despite the fundamental role of sociality in resilience and persistence of fishes (Nowicki et al. 2018b), and likely effects of disturbances and habitat degradation on the stability and persistence of social groups (Reese 1981; Hing et al. 2018), there is yet to be any research on changes in the sociality of butterflyfishes associated with major disturbances or varying coral cover.

Chapter 2: Effects of Coral Bleaching and Coral Loss on the Structure and Function of Reef Fish Assemblages¹

2.1: Introduction

Mass coral bleaching, caused by elevated ocean temperatures, has now emerged as a major, if not the single most important, contributor to elevated rates of coral mortality (Hughes et al. 2017; Donner et al. 2018; Eakin et al. 2018; Oliver et al. 2018), greatly accelerating the degradation of coral reef ecosystems throughout the world. Coral reefs have been subject to increasing anthropogenic disturbances and threats throughout the last few decades (if not centuries), resulting in sustained declines in the cover or abundance of scleractinian corals and corresponding shifts in the structure of reef habitats (Hughes et al. 2003; Alvarez-Filip et al. 2011b). Climate change (specifically resulting in coral bleaching) is almost always considered, along with a variety of other more localized anthropogenic disturbances and threats, as a key contributor to sustained and ongoing coral loss (e.g., De'ath et al. 2012). However, mass coral bleaching has previously been considered to be a relatively minor, though emerging and increasingly important, contributor to coral loss, especially relative to other major disturbances such as severe tropical storms and outbreaks of coral predators (Pratchett et al. 2011b; De'ath et al. 2012). The extent and severity of the latest (2014–2017) global bleaching event (Hughes et al. 2017, 2018a), as well as successive years of severe bleaching in many locations, have firmly heralded in an era where global climate change is the foremost threat to coral reef ecosystems.

What makes coral reef ecosystems particularly vulnerable to climate change is that reef-building (scleractinian) corals are both very sensitive to elevated temperatures (Jokiel and Coles 1990; Smith and Buddemeier 1992; Berkelmans 2018; Stanley and van de Schootbrugge 2018) and fundamental to the structure and function of coral reefs (Bellwood et al. 2004; Pratchett et al. 2015a). Scleractinian corals are the building blocks of coral reefs, not only contributing to reef accretion (Pratchett et al. 2015a) but also forming complex habitats which support a high diversity of fishes (Coker et al. 2014) and other reef-associated organisms (Stella et al. 2011). The importance of scleractinian corals is particularly apparent

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given marked declines in the abundance and diversity of coral reef fishes following acute and extensive coral loss (Jones et al. 2004; Wilson et al. 2006; Pratchett et al. 2008a; Munday et al. 2008; Cheal et al. 2017) caused by severe tropical storms (hurricanes, typhoons and tropical cyclones), outbreaks of coral predators and mass coral bleaching. Such effects are particularly pronounced when coral cover falls below 10% (Wilson et al. 2006; Holbrook et al. 2008), suggesting that $\geq 10\%$ coral cover is necessary to maintain ecological functions that support diverse assemblages of coral reef fishes.

Many coral reef fishes rely on scleractinian corals for food (Cole et al. 2008), habitat (Coker et al. 2014) and/or settlement (Jones et al. 2004; Coker et al. 2012). However, the range of coral reef fishes that decline in abundance following extensive coral depletion (60–75%) far exceeds that which are known to have an explicit and direct reliance on scleractinian corals (Jones et al. 2004; Graham et al. 2007; Pratchett et al. 2011c; Cheal et al. 2017). The broadscale ecosystem consequences of extensive coral loss suggest that we have overlooked some important ecological benefits of coral-rich habitats for reef fishes (e.g., Dixon et al. 2014; Pratchett et al. 2015b). For example, extensive coral depletion may effectively remove major odour cues that are used by reef fishes and corals to orientate towards and settle within coral reef habitats (Dixon et al. 2014). The effects of coral loss on the biodiversity and abundance of reef-associated organisms may also be compounded by declines in topographic complexity (Syms and Jones 2000; Wilson et al. 2006; Graham et al. 2009; Coker et al. 2012), which occurs due to erosion and decomposition of dead coral skeletons (Sheppard et al. 2002) and disproportionate loss of key habitat forming corals (Graham et al. 2006; Alvarez-Filip et al. 2011b). Importantly, high levels of structural complexity increase habitat area and moderate key ecological interactions (e.g., competition and predation) contributing to increased species packing, as well as facilitating coexistence of large numbers of diverse species (Gratwicke and Speight 2005).

In this chapter, we revisit the effects of mass coral bleaching (and associated changes in the structure of tropical reef habitats) on the structure and function of reef fish assemblages. In particular, this chapter will investigate the ecological and economic consequences of declines in the abundance of fishes, based on the selectivity of effects within and among different functional groups, as well as testing for compensatory dynamics necessary to maintain key ecological functions following species declines or losses (Houlahan et al. 2007). It is well established that extensive coral depletion (whether caused by mass coral bleaching, tropical cyclones or outbreaks of invertebrate corallivores) results in significant declines in abundance across a broad range of reef fishes (Pratchett et al. 2011c) and overall declines in diversity of fish assemblages (Wilson et al. 2006). However, it is still not known whether far-reaching declines in the abundance of coral reef fishes will compromise ecological functions and especially those functions that are fundamental in maintaining ecosystem resilience

(Bellwood et al. 2003; Hoey and Bellwood 2009). Importantly, net declines in the abundance or performance of ecologically important reef fishes may lead to feedbacks that inhibit recovery and reassembly of coral-dominated habitats (Graham et al. 2015) and/or further exacerbate the degradation of coral reef environments (Hoey and Bellwood 2011).

The extent to which declines in the abundance and diversity of fishes will cause ecological functions to be lost or compromised depends on the number of species that can perform a particular function (i.e., *functional redundancy*) as well as variation in responses to environmental perturbations among functionally equivalent fishes (i.e. *response diversity*) (Elmqvist T et al. 2003). Some fishes, particularly herbivorous or generalist species, actually exhibit increases in abundance following extensive coral loss (Jones et al. 2004; Bellwood et al. 2006; Pratchett et al. 2008a; Halford and Caley 2009; Cheal et al. 2017). Intuitively, species that are ecologically equivalent would be equally or similarly affected by perturbations that lead to loss of habitat complexity or resource depletion. For example, extensive coral depletion will lead to declines in coral prey across all species of corallivores, though different species may be more or less affected depending on their degree of dietary specialization (Pratchett et al. 2008a). Functionally equivalent species may also differ in the extent to which they are adversely affected by small-scale or patchy habitat disturbances based on differences in the scales at which they associate with reef habitats (Nash et al. 2016). To maintain ecosystem function, however, significant declines in the abundance of key ecological species must be offset by compensatory increases in the abundance of species that can perform, or contribute to, the same function, though compensatory dynamics are rarely observed in most ecosystems (Houlahan et al. 2007). To explicitly test for response diversity and compensatory dynamics among reef fishes, data were compiled from a variety of studies that have looked at species-specific declines in abundance of fishes before and then 1-7 years after distinct episodes of coral loss, following Pratchett et al. (2011c). While we were primarily interested in the effects of coral depletion caused by climate-induced coral bleaching, data were taken from all studies that have explored changes in the abundance of fishes following acute episodes of coral loss, regardless of the cause. Each species of fish was independently assigned one of four primary functional groups based on their trophic function (i.e. carnivores, omnivores, corallivores and herbivores). Species were subsequently assigned to secondary functional groups based on feeding mode, diet and behaviour to reflect their role in ecosystem processes and/or differential sources of their prey. Response diversity and compensatory dynamics were then assessed based on the distribution of responses (changes in abundance) for fishes within 19 distinct functional or trophic groups.

2.2: Coral bleaching and changes in the structure of reef habitats

Coral reefs are among the most vulnerable ecosystems to global climate change (Walther et al. 2002), owing to the magnitude and severity of habitat loss that occurs during severe mass bleaching episodes (Hughes et al. 2017, 2018a). The scale and magnitude of coral loss caused by pantropical mass bleaching events eclipse all other major acute disturbances (e.g., tropical cyclones, outbreaks of coral predators and coral disease) that have contributed to coral declines around the world. Generally, it is the cumulative effects of multiple discrete disturbances, which may or may not be increasing in incidence, that have caused coral declines in major reef regions (Gardner et al. 2003; De'ath et al. 2012). These disturbances tend to occur at the scale of individual reefs or reef clusters. However, large-scale mass bleaching is unequivocally linked to sustained increases in global sea surface temperatures (Heron et al. 2016), which may be compounded by ocean-scale climatic features (e.g., El Niño events). In 1998, for example, mass coral bleaching was reported on coral reefs throughout the Indo-Pacific and in the Caribbean (Wilkinson 2000) and killed 75– 99% of corals across the worst affected regions (Goreau et al. 2000; Graham et al. 2006). This event contributed greatly to increased recognition of climate change as a significant threat to coral reef ecosystems (Hoegh-Guldberg 1999) and motivated many of the foremost studies on ecosystem effects of severe coral bleaching and coral loss (Graham et al. 2006, 2008). Graham et al. (2008) surveyed fish assemblages at 66 sites across the western Indian Ocean in the aftermath of the 1998 bleaching and assessed changes in the size structure and taxonomic composition of fish assemblages by comparing results with surveys conducted prior to the bleaching (in 1990– 1998). The key finding from this study was that spatial management arrangements provided no protection against mass coral bleaching and subsequent effects of coral loss on reef fish assemblages. It was also apparent that mass coral bleaching had disproportionate impacts on small bodied (<20 cm total length) reef fishes (Graham et al. 2008). Beyond that, the effects of the 1998 bleaching event (on both coral and fish assemblages) were highly variable (Graham et al. 2008), requiring much greater consideration of the specific changes to coral reef habitats that are caused by mass coral bleaching. It is also important to realise that mass coral bleaching was even more widespread in 2014– 2017 than in 1998 (Hughes et al. 2017, 2018a), though the impacts of these latest pantropical bleaching events are yet to be fully realised.

2.2.1: Bleaching selectivity and changes in coral composition

The specific effects of mass coral bleaching on coral reef fishes will depend on the magnitude (extent and severity) and selectivity of coral loss. All scleractinian corals are susceptible to bleaching at some level, but certain genera, such as *Stylophora*, *Pocillopora*, *Acropora* and *Montipora*, tend to be much more susceptible, based on the proportion of

colonies and species that bleach (McClanahan et al. 2004; Hoey et al. 2016) and are also more likely to die once bleached (Baird and Marshall 2002). The selectivity of mass coral bleaching declines with increasing severity (Hughes et al. 2017), whereby there are very few corals that can withstand prolonged exposure to extreme temperatures. During moderate bleaching events, however, bleaching and mortality may be restricted to a few specific coral taxa (Baird and Marshall 2002). For the most part, it is branching corals that tend to exhibit higher rates of bleaching and mortality (Baker et al. 2008), though it is unknown whether this reflects a taxonomic bias in coral morphology (McCowan et al. 2012) or inherent physiological properties of massive or robust corals that increase resistance and resilience to coral bleaching (Loya et al. 2001). Taxonomic differences in susceptibility to bleaching can vary spatially and temporally (Guest et al. 2012; Pratchett et al. 2013), depending on depth and habitat, the recent thermal history, hydrodynamics and endosymbiont associations. Moreover, increasing incidence of coral bleaching will not necessarily favour those coral species that are most resistant to bleaching (Hughes et al. 2003; Baker et al. 2008). Rather, directional shifts in the composition of coral assemblages will depend on both rates of colony-level mortality due to bleaching (relative to normal background rates of whole colony mortality) and the differential recovery capacity of species. Importantly, corals with rapid growth and high rates of population turnover may be relatively unaffected by recurrent bleaching (Linares et al. 2011), compared to slow-growing coral species that invest significant energy in maintenance and persistence. Declines in the species richness of coral assemblages can directly impact on diversity of fish assemblages (Messmer et al. 2011), though there are specific coral taxa that are particularly important in providing food and habitat resources and also make disproportionate contributions to topographic complexity of reef habitats (Coker et al. 2012). Corals vary in the extent to which they provide effective habitat for reef fishes mainly due to differences in gross morphology (e.g., branching versus encrusting or massive colonies), though some specialist coral-dwelling fishes only occupy very specific corals and clearly distinguish within or among coral species (Munday 2001; Messmer et al. 2011; Noonan et al. 2012). The corals that are most important in providing habitat for highly specialised coral-dwelling fishes (including digitate *Acropora*, *Stylophora* and *Pocillopora* corals; Coker et al. 2014) are particularly susceptible to coral bleaching. Some of the more bleaching-resistant corals, such as branching *Porites spp.*, are also important in providing habitat for a wide range of fishes (Richardson et al. 2017), but they tend to be occupied by less specialized species that use a wide range of different corals (Gardiner and Jones 2005; Coker et al. 2014). Coral specialists are, by definition, expected to have a much stronger reliance on live corals and are more vulnerable to any changes in coral availability (Munday 2004; Pratchett et al. 2012). Given the close association of many specialist reef fishes with *Acropora* and *Pocillopora* corals, selective depletion of these corals may be just as devastating as a wholesale loss of

scleractinian corals, affecting both the availability of preferred habitats and topographic complexity. Even if these corals are generally resilient to recurrent bleaching, temporary declines in the availability of critical habitats may have devastating effects for fishes that are directly reliant on specific coral hosts (Munday 2004).

2.2.2: Coral loss and increasing predominance of alternative habitat-forming taxa

While moderate bleaching is likely to cause directional shifts in the structure of coral assemblages (described above), severe episodes of mass bleaching affect a significant proportion of scleractinian corals (Hughes et al. 2017) and are likely to lead to extensive and widespread declines in coral cover. Such reductions in the abundance or cover of corals within shallow reef environments may be accompanied by increases in abundance of other alternative habitat-forming organisms, such as macroalgae (Hughes et al. 2010), though this depends on the specific environmental settings and relevant constraints on macroalgal growth and coral dynamics (Chong-Seng et al. 2014). Accordingly, there have been documented increases in the abundance of herbivorous fishes following widespread coral loss and concomitant increases in cover and biomass of macroalgae (Jones et al. 2004; Pratchett et al. 2008a; Cheal et al. 2017). In some instances, high densities of herbivores can prevent proliferation of macroalgae even after extensive coral depletion. However, fisheries exploitation has reduced the abundance of herbivorous fishes in many reef regions, compromising their capacity to respond to increasing cover and growth of macroalgae (Rasher et al. 2013). Once established, shifts from coral to macroalgal dominance may be reinforced by reduction in grazing and increased production of algal propagules (Hoey and Bellwood 2011) as well as constraints on recovery and replenishment of coral assemblages (Hughes et al. 2007). Moreover, the estimated biomass of herbivorous fishes needed to promote recovery of coral-dominated habitats (>180 kg per hectare) is much greater than what is required to prevent the initial proliferation of macroalgae and exceeds the estimated biomass of herbivorous fishes in most reef regions (Hoey et al. 2016).

Fundamental shifts in the dominant habitat-forming biota within tropical reef environments will significantly affect the behaviour, abundance and composition of coral reef fishes. While there are some species of reef-associated fishes that will benefit from increased cover and biomass of macroalgae (Dahlgren and Eggleston 2000; Wilson et al. 2010, 2017), fishes that feed, shelter or recruit to live corals are likely to disappear from reefs dominated by macroalgae (Jones et al. 2004). Importantly, macroalgae do not provide the same level of habitat structure and complexity as scleractinian corals, and the overall abundance and diversity of fishes on algal dominated reefs are much lower, compared with coral-dominated habitats (Sano 2001). In the Seychelles, Graham et al. (2015) showed that the biomass of herbivorous fishes was highest on reefs with high levels of underlying structural complexity

and this, in turn, was a major determinant of whether reefs recovered (rather than undergoing a regime shift to macroalgae) following the 1998 mass coral bleaching. While data on overall biomass of fishes was not presented for coral- versus macroalgae-dominated reefs (Graham et al. 2015), restoration of the functional integrity of reefs that recovered will likely have significant ecological and economic benefits, such as increased contribution to local fisheries production.

2.2.3: Coral loss versus declines in topographic complexity

Mass coral bleaching is categorised (along with outbreaks of coral predators and coral diseases) as a biological or non-structural disturbance (Wilson et al. 2006) whereby corals are killed without directly modifying their physical structure, at least in the short term. Physical or structural disturbances (e.g., tropical cyclones), meanwhile, cause immediate reductions in both live coral cover and topographic complexity of the reef framework by dislodging and/or breaking apart coral skeletons (e.g., Madin and Connolly 2006). Structural disturbances are generally thought to have much more pronounced and far-reaching effects on reef fishes compared to biological disturbances, because coral loss is compounded by declines in structural complexity (Wilson et al. 2006) and it is sometimes difficult to identify the independent contributions of coral loss versus topographic collapse (Pratchett et al. 2008a; Graham and Nash 2013). In at least some cases, coral loss appears to have greater influence on abundance of fishes than declines in structural complexity (Komyakova et al. 2013), while loss of coral diversity is the foremost driver of declines in diversity of reef fishes (Messmer et al. 2011; Holbrook et al. 2015). Moreover, extensive coral depletion can lead to declines in structural complexity, regardless of whether it is caused by biological or physical disturbances; coral colonies that have died due to bleaching (or other biological disturbances) are immediately subject to physical and biological forces that cause skeletal erosion and decomposition (Glynn 1997; Sheppard et al. 2002; Ferrari et al. 2017b), leading to inevitable, though sometimes protracted, declines in structural complexity (e.g., Sano et al. 1987). There are, however, instances where habitat complexity is provided by underlying substrate rugosity and is independent of coral loss (Pratchett et al. 2008a; Emslie et al. 2014), which may actually buffer fish assemblages during periods of coral loss.

The timing and sequence of decomposition and structural collapse of dead coral skeletons have only rarely been explicitly studied, but it is increasingly apparent that this is a gradual and ongoing process (Ferrari et al. 2017b), rather than an acute and delayed effect of coral mortality. Notably, delayed declines in the abundance and diversity of fishes, which may be apparent >3 years after extensive coral depletion (Pratchett et al. 2008a), have been at least partly attributed to lags in declines in topographic complexity following extensive coral mortality (Graham et al. 2006). The extent to which coral reef habitats are actually vulnerable

to structural collapse also varies, depending on the extent to which coral assemblages are dominated by branching species, variation in the structural integrity of corals (even among different branching species), localised differences in the factors that promote physical and biological erosion and the relative contribution of contemporary coral growth versus underlying reef structure to topographic complexity (Pratchett et al. 2008a; Cheal et al. 2017).

2.3: Declines in abundance of reef fishes and loss of biodiversity and function

Much of the current understanding regarding the effects of mass coral bleaching on coral reef fishes comes from studies that have documented species-specific changes in abundance of fishes before and after specific bleaching events (e.g., Graham et al. 2008). While the results of such studies are dependent on the specific timing of surveys and especially the time elapsed following mass coral bleaching (Pratchett et al. 2009), the magnitude of species losses is broadly comparable to the effects of coral depletion caused by tropical cyclones, outbreaks of crown-of-thorns starfish and experimentally imposed disturbances (Fig. 2.1). Where coral mortality was >60%, the number of species recorded along belt transects or within point counts generally declined, although there was considerable variation among studies, with some documenting limited or even positive changes in diversity of fishes when coral mortality was >80%. Notably, extreme levels of species loss (60% decline in species richness) occurred following near-complete coral loss, regardless of what caused this coral mortality. However, moderate levels of coral loss had limited or positive effects on the local diversity of reef fishes (Fig. 2.1) which may reflect increases in the abundance and diversity of generalist fishes following initial loss of corals and corresponding increases in habitat heterogeneity (Wilson et al. 2006). It is important, however, to consider species-specific responses of fishes to mass coral bleaching, to understand which species are affected and potential impacts on ecosystem function and fisheries production (e.g., Brandl et al. 2016).

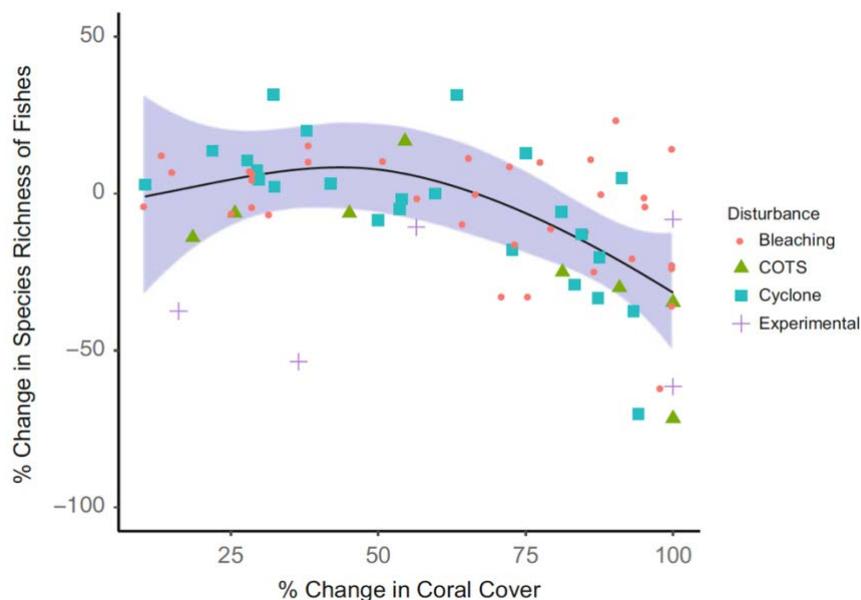


Figure 2.1 Effects of coral loss on biodiversity (species richness) of coral reef fishes. The relationship between change in species richness (%) is plotted against increasing declines (%) in local coral cover, based on data extracted from 30 independent studies (see Pratchett et al. 2009 for details), categorised according to the major (but not exclusive) cause of localised coral loss. Confidence intervals (~95%) for the general additive model were calculated using a continuous set of predictor variables (n = 1000 simulations), with the MGCV package in R.

2.3.1: Interspecific variation in vulnerability to coral bleaching and depletion

Fishes vary in their responses to habitat perturbations (and potential resource depletion) due to varying levels of ecological specialisation and differential reliance on specific resources (e.g., coral prey), their capacity to use alternative habitats or resources following changes in resource availability, their distribution relative to areas of major impacts and variation in the scales at which they associate with coral reef habitats (Pratchett et al. 2011c). The main group of fishes that consistently exhibit pronounced and often very rapid declines in abundance following localised coral depletion are obligate coral-feeding fishes (Wilson et al. 2006, 2014; Emslie et al. 2011; Fig. 2.2). Declines in the abundance of coral-feeding fishes are directly attributable to prey depletion and subsequent starvation, reflected in initial declines in their physiological condition (Pratchett et al. 2004). Coral-feeding fishes are initially attracted to bleached, diseased or injured corals, though they will preferentially feed on healthy (unbleached corals) in the longer term (McIlwain and Jones 1997; Cole et al. 2009). This suggests that the nutritional quality of corals declines soon after they bleach. The eventual mortality of bleached corals will then further constrain prey availability for obligate coral-feeding fishes. Accordingly, virtually all corallivorous fishes (including soft-coral feeders) exhibit significant declines in abundance, probably reflecting high rates of mortality, as opposed to movement among habitats, following localised coral depletion (Emslie et al. 2011; Wilson et al. 2014; Fig. 2.2). While localised declines in the abundance of these fishes may

result from movement, the potential to find more suitable habitats is likely to be very limited, especially given the spatial extent of major mass bleaching events (e.g., Hughes et al. 2017). Even if fishes are able to find relatively undisturbed reef environments, high levels of aggression among coral specialists (e.g., coral-feeding butterflyfishes, Blowes et al. 2013) are likely to constrain the invasion of new habitats by displaced individuals. Moreover, individual fishes are likely to persist within their established home ranges for some time after corals have bleached and died (Pratchett et al. 2004), which would further limit their ability to ultimately outcompete conspecifics and invade new habitats.

For fishes with an explicit and direct reliance on corals (e.g., for food and habitat), declines in abundance are often disproportionate to levels of local coral depletion. For example, *Chaetodon trifascialis* is often locally extirpated following relatively low (14%) levels of coral depletion. The standardised response (which explicitly accounts for proportional coral loss) for *C. trifascialis* is, therefore, as low as -5. Such disproportionate declines in the abundance of these fishes reflect high selectivity in coral use as well as the sensitivity of preferred coral species to mass coral bleaching and other major disturbances. *Chaetodon trifascialis* is among the most highly specialised of coral reef fishes (Pratchett 2014), feeding almost exclusively on tabulate *Acropora* as well as a few other select species (e.g., *Acropora florida*). Accordingly, declines in the abundance of *C. trifascialis* relate to declines in the abundance of their major prey (tabulate *Acropora*), rather than overall declines in live coral cover. Other relatively specialised corallivores (*C. plebeius*, *C. baronessa* and *Oxymonacanthus longirostris*) also exhibit disproportionate declines in abundance following significant (>10%) reductions in local coral cover (Fig. 2.2). The only corallivorous fish that has been seen to increase in abundance following coral depletion is *Labropsis xanthonota*, for which densities of recruits actually increased (albeit from very low densities) following mass coral bleaching in Chagos (Graham et al. 2008).

Concern about the loss of key functional groups on coral reefs mostly centres around herbivorous fishes, largely due to their role in preventing and potentially reversing macroalgal overgrowth (Hughes et al. 2007; Hoey and Bellwood 2011). While all herbivorous fishes ostensibly consume and remove algae, they perform different and complimentary roles in helping reefs to resist shifts to alternate states and reassemble following disturbances. Specific differences in the feeding mode of herbivorous fishes, as well as variation in body size, group size and home ranges, suggest that each and every species of herbivorous fish may have a subtly different role in preventing or reversing proliferation of macroalgae following extensive coral depletion (Mouillot et al. 2014). Certainly, there are some individual species that contribute disproportionately to specific functions. For example, overfishing of the excavating parrotfish, *Bolbometopon muricatum*, has resulted in a near total loss of external bioerosion on several Indo-Pacific reefs (Bellwood et al. 2003, 2012) even though there are

several other excavating species on these reefs. In many regions, fisheries exploitation represents the foremost threat to herbivorous fishes (Graham et al. 2011), though it is also apparent that at least some herbivorous fishes decline in abundance following extensive coral depletion (Fig. 2.2). While some herbivorous fishes do increase in abundance following coral depletion, presumably responding to increases in the areal extent and/or productivity of algae, these responses are not consistent either within or among species. Most notably, there are several species of acanthurids (e.g., *Acanthurus lineatus* and *A. tennentii*) that have exhibited contrasting responses (increases versus decreases in abundance) to coral loss in different studies conducted at different locations. Moreover, apparent declines in the abundance of several species of croppers and browsers (Fig. 2.2) are based on results from just one study location. Such vagaries in responses of herbivorous fishes to changes in resource availability may reflect the role of irregular larval supply and recruitment in facilitating population increases. However, rapid increases in the abundance of some fishes almost certainly reflect the aggregation and movement of fishes into degraded reef habitats (Hart et al. 1996), which may also be constrained by local densities and distributions of fishes.

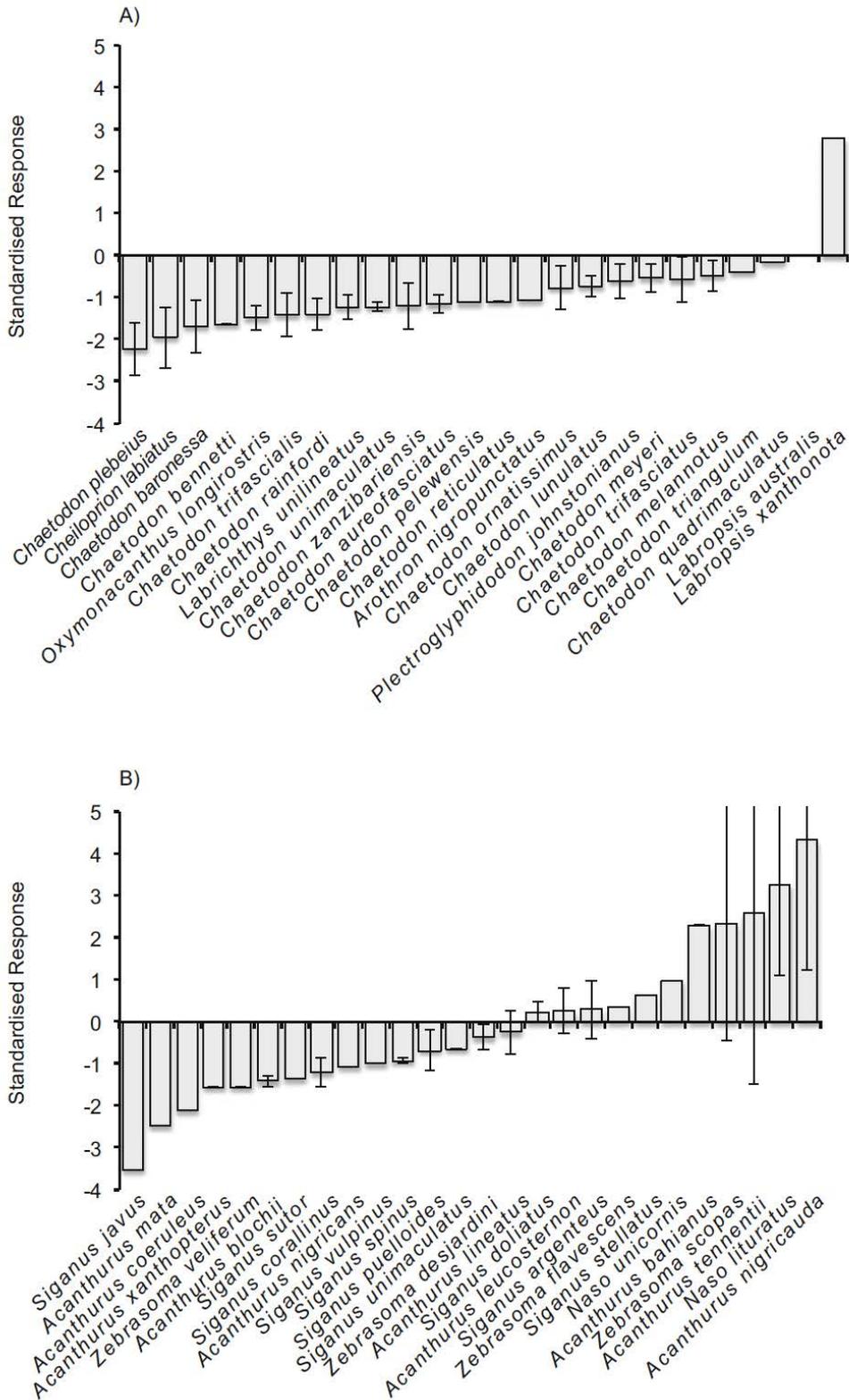


Fig. 2.2 Standardised responses of (a) obligate corallivores and (b) croppers and browsers to significant (>10%) declines in coral cover. Species-specific responses are calculated based on their proportional decline in abundance divided by proportional declines in live coral cover and averaged across multiple studies, where possible. Standard errors are calculated based on variation in responses among studies.

2.3.2: Loss of biodiversity and function

The extent to which declines in the abundance of fishes will constrain key ecological functions depends on the functional identity of component species and the variation in responses to coral loss among species that contribute to similar functions. For fishes that are directly reliant on corals for food, it is to be expected that entire functional groups will respond similarly to the localised depletion of scleractinian corals (e.g., Pratchett et al. 2011c). However, the responses of other groups are much less clear. For herbivorous fishes, several studies have reported increases in the abundance of specific species or groups following large-scale reductions in coral cover (e.g., Adam et al. 2011; Gilmour et al. 2013), and previous meta-analyses have shown that the majority of species that respond positively to coral loss are herbivorous fishes, though such effects may be relatively short-lived (Wilson et al. 2006; Pratchett et al. 2008a). As discussed previously, increases in the abundance of herbivorous fishes are generally attributed to increased cover and availability of turfing algae, which rapidly colonise dead coral skeletons (Mumby and Steneck 2008). When large numbers of corals die, there may also be a significant, though temporary, input of nutrients that actually increase algal productivity and growth. However, beneficial effects of increased food availability following the loss of live corals may be more than offset by declines in the availability of preferred settlement habitats and increased intensity of competition and predation within degraded reef habitats.

Comparisons of the standardised responses to coral loss for each of 19 distinct functional (or trophic) groups show that while there was considerable variation in the response of individual species within each group, the net effect is a decline in abundance for 18 of the 19 functional groups examined (Fig. 2.3). The only exception was the macroalgal browsers (*Naso* spp. and *Siganus* spp.) that show a net positive response to coral loss. Interestingly, these browsing fishes do not associate with live coral or structurally complex areas at settlement, instead settling to areas of coral rubble (e.g., *Naso unicornis*, Doherty et al. 2004) or dense macroalgae, predominantly Sargassum (e.g., *Siganus* spp., Hoey et al. 2013; Evans et al. 2014). This, coupled with the increased availability of algal resources following coral mortality (Diaz-Pulido and McCook 2002), suggests these species are not reliant on live coral and may actually prosper in habitats with depauperate coral cover.

Although the net response of most functional groups to coral loss was negative, there was considerable variation among species within each group. This variation likely reflects differences in the intensity and/or nature of the disturbance, the temporal scale over which the changes were quantified and the longevity of the species and the reliance of individual species on live coral for settlement, food and/or shelter. For example, many scraping and excavating parrotfishes settle to macroalgal (Green 1998) or mangrove habitat (Dorenbosch et al. 2006), yet other species, such as the bumphead parrotfish *Bolbometopon muricatum*, settle to

branching *Acropora* (Hamilton et al. 2017). The reliance of *B. muricatum* on live coral at settlement is of particular concern as, when present, it overwhelmingly dominates the process of external bioerosion on reefs (Bellwood et al. 2003, 2012), and as such the loss of corals could undermine this ecological process. Similarly, differences in settlement habitat are evident within other function groups. For example, the piscivorous coral trout *Plectropomus leopardus* settles to rubble habitats (Light and Jones 1997), while the congener *P. maculatus* settles to branching *Acropora* (Wen et al. 2013). Predicting the effects of coral loss on the functional composition of reef fish assemblages is complex. Despite some fishes appearing to be largely unaffected by coral loss (Emslie et al. 2017) or even thriving following coral loss (e.g., Adam et al. 2011), the net effect of extensive coral depletion on almost all functional groups is negative (Fig. 2.3). Although changes in the abundance do not account for differences in the functional contribution of individual species, the prevalence of negative impacts suggests ongoing coral loss is likely to compromise the functioning and productivity of coral reefs, especially given cumulative effects of multiple disturbances (Brandl et al. 2016).

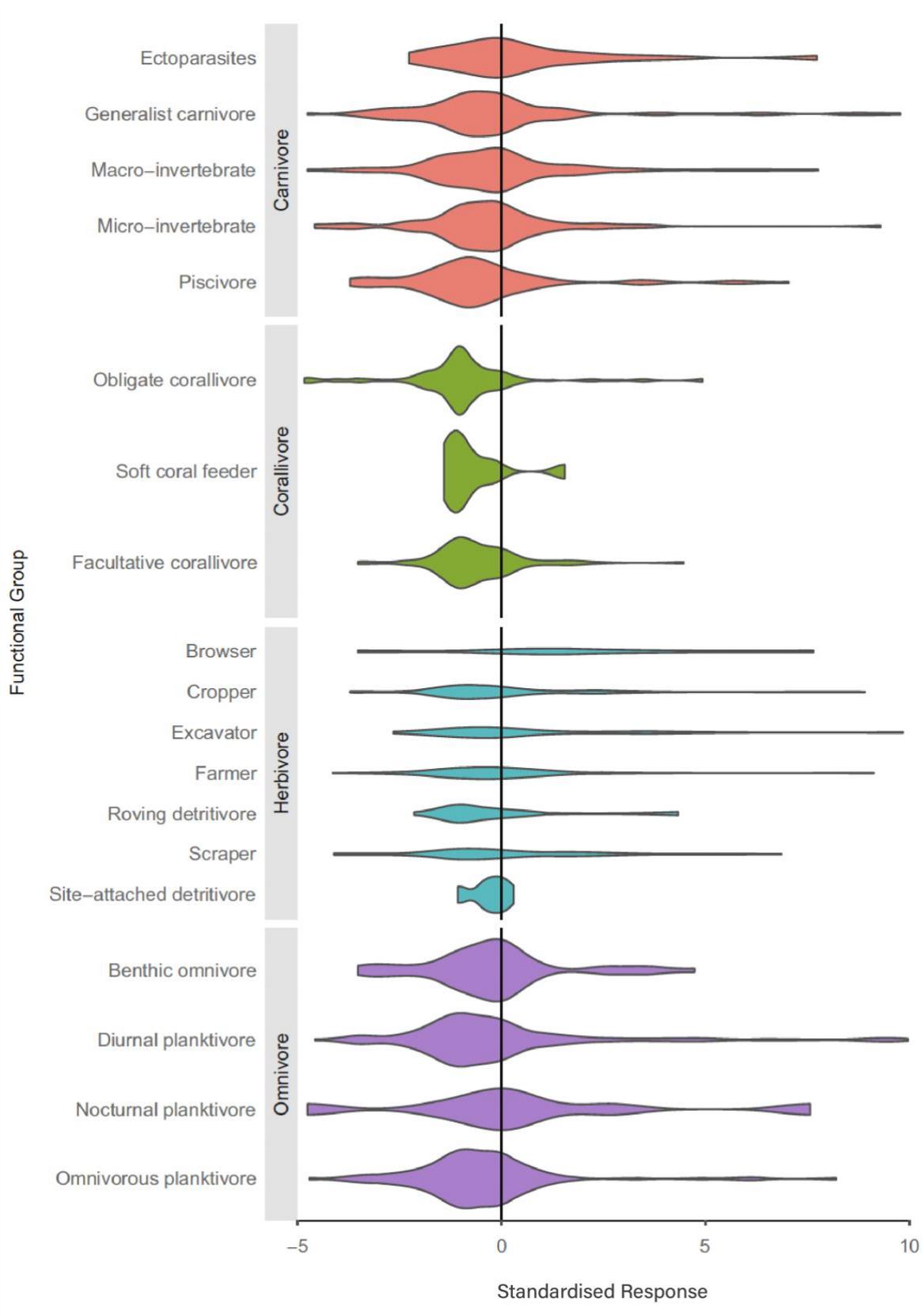


Figure 2.3 Variation in standardised responses to coral loss (proportional change in the abundance of individual species divided by proportional declines in local coral cover) for 19 functional (trophic) groups of reef fishes. Responses are predominantly negative showing the broad range of fishes that decline in abundance following coral loss

2.3.3: Effects of coral reef degradation on tropical fisheries production

Coral reef ecosystems are a major contributor to tropical coastal fisheries production, with coral reef fishes accounting for up to 65% of coastal fisheries production in the tropical Pacific (Bell et al. 2013). Coral reef fisheries typically target multiple species across almost all trophic levels, including piscivores, invertivores and herbivores (Dalzell et al. 1996). Differential effects of coral bleaching and depletion across major functional groups are, therefore, expected to cause changes in catch composition, if not declines in overall fisheries production. Cheung et al. (2013) showed that there have been marked shifts in catch composition for tropical fisheries from the 1970s to 2006. These changes are related to changing thermal regimes, differential thermal sensitivities of tropical fishes and increasing redistribution of fishes to match changing climatic envelopes (Cheung et al. 2010). However, significant and widespread habitat degradation due to increasing incidence and severity of mass coral bleaching will also have consequences for coral reef fish and fisheries (Pratchett et al. 2011a; Bell et al. 2013). By 2100, the combined effects of habitat degradation and ocean warming, together with ocean acidification, are projected to cause a 20– 50% decline in sustainable fisheries production of demersal fishes from tropical coastal environments across Pacific Island countries and territories (Pratchett et al. 2011a). These projected declines are mostly linked to ongoing habitat loss across coral reef, seagrass and mangrove habitats, though the projected rates of habitat loss (e.g., 50% decline in mean coral cover by 2035) may have been overly conservative given the habitat loss that is likely to have occurred during recent pantropical mass coral bleaching events. Projected declines in coral reef fisheries productivity caused by climate change could equate to losses of up to US\$8.4 billion per annum by the year 2100 (Speers et al. 2016). Given the increasing demand for fish with significant increases in human population across tropical island nations, the degradation of coral habitats from bleaching poses a major threat to future food security (Bell et al. 2018).

The specific effects of coral bleaching on fisheries species and production remain equivocal (Brander 2007; Cinner et al. 2013), given difficulties in discerning climatic signals against background fluctuations in catch and effort (McClanahan et al. 2002; Grandcourt and Cesar HS 2003). Graham et al. (2007) found declines in the size structure of fisheries target species following extensive mass bleaching in the Seychelles. It is also clear that extensive coral depletion, especially when combined with declines in topographic complexity, can impact on the abundance of large-bodied reef fishes and fisheries target species (Pratchett et al. 2011a, 2017). Most fishes that associate with live coral are small-bodied (Coker et al. 2014) and are not typically targeted by fishers. Reduced abundance of these small-bodied fish can, however, impact on prey availability for larger piscivorous species (Wen et al. 2016). For example, reduced abundance of coral-dwelling planktivores following bleaching resulted in an increased benthic, rather than pelagic, isotopic signature in the barred-cheek coral trout,

Plectropomus maculatus (Hempson et al. 2017). This shift in dietary composition was also associated with declines in individual condition, potentially attributable to declines in resource availability within degraded reef systems (Hempson et al. 2018). This may explain why densities of these *P. maculatus* covary with fluctuations in live coral cover (Williamson et al. 2014), though coral habitats are also important for growth and survival of newly settled individuals (Wen et al. 2013) which feed on benthic invertebrates that are generally more prevalent in the presence of live corals.

Previous studies (and meta-analyses) on the susceptibility of reef fishes to coral depletion and changes in the structure of reef habitats emphasised the vulnerability of small-bodied species (Wilson et al. 2006; Graham et al. 2008), which often have closer association with benthic habitats and explicitly utilise complex habitats to moderate exposure to predators. However, more recent analyses show that species with large body size are equally vulnerable to coral depletion and reef degradation as their smaller-bodied counterparts (Pratchett et al. 2014b), though there may be significant lags in the time required for such declines to become apparent. The mean and modal standardised responses to coral loss for all groups of carnivorous fishes, which include many large-bodied piscivores and macro-invertebrate feeders, were negative (Fig. 2.3). The mechanistic basis for such declines is likely to be complex and vary among species. However, high coral cover and topographic complexity may be critical to the feeding success of many ambush predators, such as groupers (Kerry and Bellwood 2012). Some larger-bodied fisheries species (e.g., *Bolbometopon muricatum*) may also rely on specific corals or coral-rich habitats for settlement (Rogers et al. 2014; Hamilton et al. 2017), even though adults are only loosely associated with coral habitats, which would explain why extensive coral depletion results in protracted declines in the abundance of these species. The overall importance of corals (cf. algae or other reef habitats) for inducing settlement or promoting survival of newly settled fishes is still largely unknown (but may have been greatly underappreciated, Jones et al. 2004), as habitat requirements for many juvenile coral reef fish are yet to be established (Wilson et al. 2010).

Dramatic shifts in the species composition, abundance and biomass of reef fishes are likely to occur following shifts from coral- to macroalgae-dominated systems (Chong-Seng et al. 2014; Ainsworth and Mumby 2015; Graham et al. 2015), which may become increasingly common following severe mass coral bleaching and will have obvious connotations for fisheries production. Most notably, the abundance of many traditional fisheries species is suppressed on reefs dominated by macroalgae (Ainsworth and Mumby 2015). There are, however, other fishes that are very abundant on reefs with high cover of macroalgae (Graham et al. 2014), which might still sustain high fisheries productivity, albeit based on a different suite of species (Ainsworth and Mumby 2015). Exploring new fishing opportunities and adapting to changes in resource availability may help to close the gap between productivity of

coral reef fisheries and increasing fisheries demands in tropical island countries (Bell et al. 2018). Embracing such changes must, however, take account of the ecological importance of some fishes and balance the needs for fisheries production versus contributions of fishes to ecosystem function. If, for example, fisheries capitalise on the increased abundance of herbivorous fish that can occur following mass coral bleaching (Wilson et al. 2006; Pratchett et al. 2008a), this may undermine the capacity for recovery and reassembly of coral-dominated habitats (Bozec et al. 2016).

2.4: Changes in the behaviour and fitness of reef fishes

While there are many studies that have documented changes in the abundance and diversity of fishes on reefs affected by coral bleaching and coral loss (Graham et al. 2008), sublethal effects of such disturbances have often been overlooked. However, fishes may respond to coral bleaching and coral loss in ways other than absolute changes in their local abundance (Table 2.1). These differences in feeding rates and diet, physiological condition and growth may forewarn of longer-term impacts on individual survival and population viability but understanding sublethal effects of coral depletion may also help to elucidate how and why reef fishes associate with coral-dominated habitats. For example, *Chaetodon auriga* declines in abundance following localised coral loss (Bouchon-Navaro Y et al. 1985; Pratchett et al. 2015b) despite feeding very little, if at all, on scleractinian corals throughout much of its geographical range. Moreover, *C. auriga* preferentially settles to near-shore patch reef habitats with limited cover of live corals (Pratchett et al. 2008b), questioning why this species would be negatively affected by coral depletion. However, Pratchett et al. (2015b) showed that feeding rates of *C. auriga* (on non-coral substrates) increase with increasing coral cover. This suggests that corals support increased abundance of prey items (such as small crustaceans and other cryptofauna living within the algal turfs) consumed by *C. auriga*. The cryptofauna associated with algal turfs is an important contributor to the trophic dynamics of shallow reef systems (Kramer et al. 2013), and though it is unknown whether high coral cover increases overall productivity of cryptobenthic assemblages or favours only specific species consumed by *C. auriga*, this is a potentially important link in understanding the far-reaching effects of mass coral bleaching and coral depletion on coral reef fishes.

Table 2.1 Sublethal effects of mass coral bleaching and coral depletion on coral reef fishes, highlighting (A) behavioural shifts associated with declines in the local abundance, cover or diversity of corals and (B) consequences for individual fitness, such as declines in condition and growth

(A) Behavioural Shifts

Effect	Observed change	Time frame	Species and data source(s)
Feeding on bleached corals	Preferential feeding on bleached corals	Hours to days	<i>Labrichthys unilineatus</i> (McIlwain and Jones 1997; Cole et al. 2009)
	Preferential feeding on bleached corals	Hours to days	<i>Chaetodon baronessa</i> (Cole et al. 2009)
	Active avoidance of bleached corals	9 days	<i>Chaetodon plebeius</i> (Pisapia et al. 2012)
Overall bite rates	Increased with increasing coral cover	Space for time comparison	<i>Chaetodon auriga</i> (Pratchett et al. 2014b)
	No difference	Space for time comparison	<i>Chaetodon vagabundus</i> (Pratchett et al. 2014b)
Shifts in dietary composition	Reduced intake of benthic invertebrates	1-2 years	Juvenile <i>Plectropomus maculatus</i> (Wen et al. 2016)
	Increased intake of herbivorous fishes	3-7 years	<i>Plectropomus maculatus</i> (Hempson et al. 2017)
	Increased use of massive corals	2 years	<i>Chaetodon lunulatus</i> (Pratchett et al. 2004)
	No change despite loss of preferred prey	1 year	<i>Oxymonacanthus longirostris</i> (Brooker et al. 2014)
Territoriality and aggression	Larger territories with declining coral cover	Space for time comparison	<i>Labrichthys unilineatus</i> (McIlwain and Jones 1997)
	Larger territories and reduced aggression at low coral cover	Space for time comparison	<i>Chaetodon baronessa</i> (Berumen and Pratchett 2006)
	Increased inter- vs intraspecific aggression in degraded habitats	20 days	<i>Pomacentrus moluccensis</i> , (Kok et al. 2016)
Susceptibility and exposure to predators	Failure to respond to predator odour cues on dead corals	Immediate	<i>Pomacentrus amboinensis</i> (Lönngstedt et al. 2014)
	Failure to respond to conspecific alarm cues in degraded habitats	Immediate	<i>Pomacentrus moluccensis</i> and <i>Chromis viridisi</i> (Ferrari et al. 2017a)
	Water for dead corals impedes escape responses	Immediate	<i>Pomacentrus amboinensis</i> , <i>P. chrysurus</i> , <i>P. wardi</i> , (McCormick and Allan 2017)
	Dead coral impedes social learning and predator recognition	Immediate	<i>Pomacentrus amboinensis</i> , <i>P. nagasakiensis</i> (Chivers et al. 2016)
	Higher strike rates by predators on prey fishes against bleached corals	Immediate	<i>Pomacentrus moluccensis</i> , <i>Dascyllus aruanus</i> (Coker et al. 2009)

(B) Consequences for individual fitness

Effect	Observed change	Time frame	Species and data source(s)
Physiological condition	Declines in condition when feeding on sub-optimal prey	2 years	<i>Chaetodon lunulatus</i> (Pratchett et al. 2004)
	No differences between bleached versus unbleached corals	Space for time comparison	<i>Dascyllus aruanus</i> (Coker et al. 2015)
	No change, despite increased use of suboptimal habitats	1 month	<i>Chrysiptera parasema</i> , <i>Dascyllus melanurus</i> (Feary et al. 2009)
Spawning	Lack of spawning for fishes deprived of access to preferred prey	3 weeks	<i>Oxymonacanthus longirostris</i> (Brooker et al. 2013)

Effect	Observed change	Time frame	Species and data source(s)
Growth rates	Limited growth following extensive depletion of coral prey	1 year	<i>Oxymonacanthus longirostris</i> (Kokita and Nakazono 2001)
	Growth rates directly related to tissue cover of coral hosts	1 month	<i>Chrysiptera parasema</i> , <i>Dascyllus melanurus</i> (Feary et al. 2009)
	No difference when feeding on bleached versus unbleached corals	23 days	<i>Chaetodon aureofasciatus</i> , <i>C. lunulatus</i> (Cole et al. 2014)

2.4.1: Behavioural changes

Mass coral bleaching and associated changes in the structure of reef habitats have important and far-reaching effects on the availability of prey resources and not only for those fishes that feed directly on live corals (Wen et al. 2013; Pratchett et al. 2015b). Where possible, fishes would be expected to respond to changes in resource availability by altering their dietary intake and feeding behaviour (e.g., Pratchett et al. 2004). However, diets of some highly specialist species are inflexible (Berumen and Pratchett 2008; Brooker et al. 2014), making them extremely susceptible to prey depletion. Even for fishes that can modify dietary intake in accordance with changing prey availability, this may have significant consequences for individual fitness and long-term survival. Following mass coral bleaching in the central Great Barrier Reef, Australia, Pratchett et al. (2004) showed that *Chaetodon lunulatus* increased its intake of bleaching-resistant coral species. This shift in diet composition enabled adult fishes to persist following the bleaching, though it did have consequences for physiological conditions (Pratchett et al. 2004), which may, in turn, affect longer-term survival and reproductive output (discussed below). Reductions in live coral cover also increase the area over which corallivores forage (e.g., McIlwain and Jones 1997; Kokita and Nakazono 2001), potentially increasing competitive encounters and exposure to predators.

One of the foremost explanations put forward to explain high abundance and diversity of fishes in coral-rich habitats is the extent to which high levels of habitat diversity and complexity will moderate outcomes of competition and predation (Almany 2004a). This hypothesis is not readily testable, because the persistence and coexistence of multiple species depend on the outcomes of numerous biological interactions over extended time scales, rather than the changes in the absolute intensity of competition and predation. It would be expected, however, that resource competition would become more intense (especially among coral-dependent fishes) following local coral depletion. Similarly, predation rates might be expected to increase with coral loss and declines in fine-scale topographic complexity of reef habitats (Almany 2004a). Thus far, there has been limited evidence of increased intensity of competition among reef fishes following coral loss (Table 2.1). One of the more unexpected consequences of coral loss is that fishes appear to be much more susceptible to predation

when corals bleach and die (Coker et al. 2009; Chivers et al. 2016; Ferrari et al. 2017a; Table 2.1), attributable to both changes in habitat structure and apparent changes in the behaviour of fishes in degraded reef environments. Notably, Chivers et al. (2016) showed that water that has passed over dead and degraded corals impedes social learning and predator recognition among the damselfish, *Pomacentrus amboinensis*. Lönnstedt et al. (2014) suggested that dead coral masks the odours of potential predators. Accordingly, field experiments showed that damselfish (*P. amboinensis*) associated with dead coral hosts did not exhibit characteristic sheltering within corals when exposed to the odour of a predator but did so upon seeing the predator. Interestingly, *P. amboinensis* is one of the few coral-dwelling damselfishes that is commonly found on dead coral hosts, especially after major disturbances (Pratchett et al. 2012), and these effects may be even stronger for obligate coral-dwelling species.

There has been comparatively little research on the specific behavioural responses of fishes to host coral bleaching or mortality (but see Coker et al. 2009, 2013). It is implicitly assumed, for example, that declines in the abundance of coral-dwelling fishes following extensive and widespread coral loss are due to elevated rates of individual mortality, due to compromised health of the individual fishes and increased susceptibility to predation (Sano et al. 1984, 1987; Jones et al. 2004; Pratchett et al. 2008b), which may be compounded by declines in local settlement rates (Feary et al. 2007). However, Coker et al. (2009) showed that prey fishes associated with bleached corals are much more susceptible to predation compared to conspecifics living on unbleached corals, which was attributed to both visual and chemical camouflage provided by live coral tissues. Even if predation rates are not actually any higher for fishes on bleached corals, it is possible that increased exposure to predators may provide significant motivation for coral-dwelling fishes to rapidly vacate bleached coral hosts (Sano et al. 1987; Coker et al. 2009). This might also explain the reluctance of fishes to settle on bleached corals (e.g., Feary et al. 2007).

2.4.2: Effects of coral bleaching versus coral loss on individual fitness of fishes

Where coral bleaching and/or coral mortality leads to depletion of resources for reef fishes, species losses are likely to be preceded or accompanied by declines in individual condition or fitness (Kokita and Nakazono 2001; Pratchett et al. 2006b; Brooker et al. 2013). Kokita and Nakazono (2001) documented localised extirpation of *Oxymonacanthus longirostris* over 2 years following coral bleaching in Okinawa, Japan (see also Brooker et al. 2014). However, even before these fishes disappeared, growth rates were severely compromised (Kokita and Nakazono 2001), reflecting limited access to their preferred coral prey, *Acropora*, which had succumbed to the bleaching and died. Experimental studies conducted by Brooker et al. (2013) also showed that constrained access to preferred coral

prey by breeding pairs of *O. longirostris* resulted in reproductive failure. It is also possible that declines in the nutritional quality of coral prey may occur even during bleaching, due to rapid depletion of lipid reserves (but see Pisapia et al. 2012). Some coral-feeding fishes will initially target bleached corals over healthy coral prey, potentially due to increased mucous production or limited tissue retraction, but preferentially target healthy corals over colonies subject to prolonged bleaching (Cole et al. 2009). It is clear that corallivorous fishes will consume bleached corals, but protracted feeding on bleached corals may constrain nutritional intake. However, Cole et al. (2014) found no apparent differences in the growth rates of juvenile butterflyfishes that were restricted to feeding on bleached versus healthy corals for 23 days. The findings suggest that bleaching *per se* may have limited effects on corallivorous reef fishes (see also Bonin et al. 2009; McCormick et al. 2010). Rather, it is the subsequent mortality of bleached coral colonies that impacts on food availability leading to declines in the physiological condition and ultimately the survival of corallivorous fishes.

Aside from coral-feeding fishes (e.g., butterflyfishes), coral-dwelling fishes have the most direct and explicit reliance on corals (Pratchett et al. 2012) and are extremely vulnerable to local depletion of their specific coral hosts (Munday 2004). Many coral-dwelling fishes vacate their coral hosts as soon as they bleach, let alone die (Feary et al. 2007; Coker et al. 2012). Redistribution of coral-dwelling fishes among remnant coral hosts may moderate the susceptibility of these fishes to host coral depletion, though overall densities often decline in approximate accordance with the proportional loss of preferred coral habitats (Wilson et al. 2008; Pratchett et al. 2012). The proximate causes of declines in the abundance of coral-dwelling fishes following host coral mortality remain largely unknown. Explicit comparisons of the physiological condition of several different species of coral-dwelling damselfishes (Table 2.1) constrained to living on bleached versus healthy coral hosts reveal little or no differences. This suggests that declines in the abundance of coral-dwelling fishes within habitats subject to host coral depletion are due to extrinsic processes (e.g., predation) rather than intrinsic factors. However, sublethal effects of coral depletion need to be considered across a much wider range of reef fish species.

2.5: Conclusions

Highly diverse and productive assemblages of coral reef fishes rely on the combination of high abundance (cover) and diversity of scleractinian corals, as well as high levels of topographic complexity, which is often provided by high coral growth. Mass coral bleaching, which can cause extensive coral loss, will, therefore, have significant effects on the structure and function of reef fish assemblages (e.g., Graham et al. 2006, 2008; Wilson et al. 2006), with potential consequences for fisheries production and coral reef resilience. The loss of entire functional groups that comprise multiple species may appear unlikely. However,

biodiversity of coral reef fishes is not equally apportioned among different functional groups (Mouillot et al. 2014). There are also entire functional groups that respond similarly to coral bleaching and coral loss, such that certain ecological functions will be severely compromised, if not lost altogether (Graham et al. 2011). It is now clear that effects of coral bleaching and associated coral loss extend well beyond those species traditionally thought to have specific reliance on corals for food and shelter (e.g., butterflyfishes, damselfishes, gobies). In extreme cases, the abundance and species richness of fishes may decline >60% following extensive coral depletion and topographic collapse of reef habitats, combined with increasing dominance of non-coral biota. The spatial extent of mass bleaching events is also far greater than other major disturbances, potentially threatening widespread species with extinction. This provides significant imperative for reducing greenhouse gas emissions, to reduce the incidence and severity of future mass coral bleaching while also addressing other more localised disturbances that contribute to coral loss and reef degradation.

Chapter 3: Changes in sociality of butterflyfishes linked to population declines and coral loss²

3.1 Introduction

Coral reef ecosystems are subject to significant and increasing pressures (Hughes et al. 2018a), resulting in sustained coral loss and habitat degradation (e.g., Bruno and Selig 2007; De'ath et al. 2012). On Australia's Great Barrier Reef, for example, coral cover declined by 50%, from 28.0% in 1985 to 13.8% in 2012 (De'ath et al. 2012). Coral loss was further exacerbated by recent cyclones (Wolff et al. 2016; Cheal et al. 2017) and unprecedented back-to-back years (2016 and 2017) of mass coral bleaching (Hughes et al. 2017, 2018a). Given their important contributions to habitat structure, depletion of scleractinian corals threatens the biodiversity, productivity and functioning of coral reef ecosystems (Pratchett et al. 2008a; Chapter 2). Most notably, acute declines in live coral cover, caused by severe large-scale disturbances, have been linked to significant reductions in the abundance and diversity of coral reef fishes (Jones et al. 2004; Wilson et al. 2006; Pratchett et al. 2008a; Hoey et al. 2016). Coral loss is also often accompanied by declines in the structural complexity of coral reef habitats, which can further contribute to declines in the abundance and diversity of coral reef fishes (Graham et al. 2006; Wilson et al. 2006; Pratchett et al. 2008a).

Declines in the abundance of reef fishes following extensive coral depletion are variously ascribed to declines in prey availability (Pratchett et al. 2008a), habitat loss (Munday 2004) reductions in habitat complexity and availability of shelter (Almany 2004b; Graham et al. 2006), or changes in chemical cues (Dixson et al. 2014; Chivers et al. 2016), necessary for settlement or predator detection. Rapid and pronounced declines in the abundance of fishes fundamentally reflects increased rates of mortality, due to compromised health of the individual fishes and/or increased susceptibility to predation (Sano et al. 1984, 1987; Jones et al. 2004; Pratchett et al. 2008a), which may be compounded by declines in local settlement rates (Feary et al. 2007). However, changes in local reef habitats may also induce changes in the behaviour, condition and fitness of individual fishes, which might further contribute to population declines (Khan et al. 2017; Pratchett et al. 2018 - Chapter 2). Most obviously, coral-

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feeding fishes have been shown to alter their feeding behaviour in the aftermath of severe coral loss, either expanding the range of corals they consume (Pratchett et al. 2004) or increasing the areal extent of feeding territories to account for declines in prey abundance (Kokita and Nakazono 2001). Despite these changes in feeding, reduced access to preferred prey resources may result in reduced growth, reproductive failure and long-term declines in the abundance of specialist coral feeders (Kokita and Nakazono 2001; Pratchett et al. 2008a; Brooker et al. 2013).

Butterflyfishes (family Chaetodontidae) are among the most specialised group of coral reef fishes, and many species are directly reliant on live corals (Wilson et al. 2014; Bellwood et al. 2015). Most notably, Chaetodon butterflyfishes are the predominant group of fishes that feed on corals (Cole et al. 2008), and many species take >80% (and up to 100%) of bites from live corals (Cole and Pratchett 2014). For these obligate coral-feeding butterflyfishes (sensu Reese 1977), declines in abundance following major episodes of coral loss are generally attributed to prey depletion and starvation (Bouchon-Navaro Y et al. 1985; Williams 1986; Sano et al. 1987). While obligate corallivores are the first and worst affected by episodes coral loss, declines in the abundance of facultative and non-coral-feeding butterflyfishes have also been recorded during extreme coral depletion (Cole and Pratchett 2014; Pratchett et al. 2015b), reflecting further important (albeit weaker or indirect) reliance on live corals. While many studies have documented fluctuations in abundance of Chaetodon butterflyfishes linked to changes in local coral cover (Williams 1986; Sano et al. 1987; Halford et al. 2004), the biological processes and mechanisms (e.g., changes in individual condition, reproductive output or population structure) underlying these changes in population size have rarely been considered (but see Pratchett et al. 2004).

The purpose of this study was to test for changes in the sociality (defined herein as the group typology and nature of social relationships among individuals within a population; Dunbar and Shultz 2010) of *Chaetodon* butterflyfishes associated with changes in coral cover at Lizard Island, in the northern Great Barrier Reef. More specifically, we explore whether there was an increase or decrease in the incidence of pairing associated with changes in habitat quality and population size. Most species of butterflyfishes (> 80%) form pairs (Brandl and Bellwood 2014), which is generally attributed to reproductive benefits of extended mate-guarding, though pair bonding also enhances resource defence in these fishes (Nowicki et al. 2018b). Even among pair-forming species, there are a portion of individuals that occur as solitary individuals (Table 3.1). Solitary butterflyfishes presumably have reduced opportunities to reproduce, but their physiological condition is also lower compared to paired individuals (Nowicki et al. 2018a), which benefit from increased feeding efficiency and monopolisation of areas with abundant prey resources (Righton 1998; Berumen et al. 2005; Nowicki et al. 2018b). Paired individuals may therefore be more resilient to coral loss. If so, solitary

individuals may be disproportionately affected during habitat perturbations, and we would expect apparent increases in the incidence of pairing. It is also possible, however, that declines in resource availability will undermine the benefits and persistence of pairs (Reese 1981). Importantly, fishes must feed over increasingly larger areas as prey becomes limiting, and at some point, territoriality and aggression become largely untenable (Kokita and Nakazono 2001; Berumen et al. 2005). Also, if mortality is independent of sociality, we would expect an inevitable increase in the incidence of solitary individuals, especially where reduced densities and increased dispersion of individuals will constrain re-pairing. If coral loss and population declines do disrupt sociality, concomitant effects on reproduction and population replenishment might explain protracted declines in the abundance of butterflyfishes in the aftermath of major disturbances (Pratchett et al. 2006b).

3.2 Materials and methods

3.2.1 Study location and history of disturbances

To document long-term changes in the sociality of *Chaetodon* butterflyfish, underwater visual surveys were conducted at Lizard Island (northern Great Barrier Reef; 14.6645° S, 145.4651° E) in January 2002, February 2009 and February 2017, as part of a longer-term study looking at changes in butterflyfish and benthic assemblages since 1995. During the course of this study, reef habitats at Lizard Island were subject to several major disturbance events, including successive outbreaks of crown-of-thorns starfish (Pratchett 2005; Uthicke et al. 2015), two severe tropical cyclones (Ceccarelli et al. 2016; Hing et al. 2018; Madin et al. 2018), and elevated temperatures that caused mass coral bleaching (Richardson et al. 2018).

Table 3.1: *Chaetodon* species present at Lizard Island, showing their classification to sociality types by Yabuta and Berumen (2014), as well as the percentage of fish (mostly mature individuals) recorded in pairs from different studies and locations. “*” indicates instances with limited sample size.

Species	Sociality	Location	Pairing (%)	Reference
<i>Chaetodon aureofasciatus</i>	2b	Southern GBR	<9	(Reese 1975)
<i>Chaetodon auriga</i>	5	Red Sea	60	(Fricke 1986)
		Southern Japan	48	(Yabuta 2007)
		Southern GBR	<39	(Reese 1975)
		Marshall Islands	73	(Reese 1975)
		Central Pacific	53	(Reese 1975)
		French Polynesia	77	(Bouchon-Navaro 1981)
<i>Chaetodon baronessa</i>	1a	Southern Japan	55*	(Yabuta 2007)
		Northern GBR	78	(Nowicki et al. 2018b)
		Southern GBR	70	(Reese 1975)
<i>Chaetodon citrinellus</i>	1a	Southern Japan	86	(Yabuta 2007)
		Marshall Islands	59	(Reese 1975)
		French Polynesia	87	(Bouchon-Navaro 1981)
<i>Chaetodon ephippium</i>	1a	Southern Japan	48*	(Yabuta 2007)
		Southern GBR	66	(Reese 1975)

Species	Sociality	Location	Pairing (%)	Reference
		Marshall Islands	75	(Reese 1975)
		Central Pacific	67	(Reese 1975)
		French Polynesia	80	(Bouchon-Navaro 1981)
<i>Chaetodon kleinii</i>	1b	Southern Japan	80	(Yabuta 2007)
<i>Chaetodon lineolatus</i>	4	Red Sea	86	(Fricke 1986)
		Southern Japan	50*	(Yabuta 2007)
		Southern GBR	<34	(Reese 1975)
<i>Chaetodon lunula</i>	4	Southern Japan	20*	(Yabuta 2007)
		Marshall Islands	63	(Reese 1975)
		French Polynesia	51	(Bouchon-Navaro 1981)
<i>Chaetodon lunulatus</i>	1a	Southern Japan	95	(Yabuta 2007)
		Northern GBR	84	(Nowicki et al. 2018b)
		Central GBR	68	(Pratchett et al. 2006a)
		Southern GBR	84	(Reese 1975)
		Marshall Islands	76	(Reese 1975)
		Central Pacific	53*	(Reese 1975)
		French Polynesia	94	(Bouchon-Navaro 1981)
<i>Chaetodon melannotus</i>	2b	Red Sea	50	(Fricke 1986)
		Southern Japan	17*	(Yabuta 2007)
		Southern GBR	<12	(Reese 1975)
<i>Chaetodon plebeius</i>	6	Southern Japan	82	(Yabuta 2007)
		Northern GBR	<10	(Nowicki et al. 2018b)
		Southern GBR	<7	(Reese 1975)
<i>Chaetodon rafflesi</i>	1a	Southern Japan	85	(Yabuta 2007)
<i>Chaetodon rainfordi</i>	2b	Northern GBR	<12	(Nowicki et al. 2018b)
		Southern GBR	<4	(Reese 1975)
<i>Chaetodon speculum</i>	2a	Southern GBR	<28	(Reese 1975)
<i>Chaetodon trifascialis</i>	2a	Red Sea	7	(Fricke 1986)
		Southern Japan	25	(Yabuta 2007)
		Northern GBR	<20	(Nowicki et al. 2018b)
		Southern GBR	<7	(Reese 1975)
		Marshall Islands	<18	(Reese 1975)
		French Polynesia	<14	(Bouchon-Navaro 1981)
<i>Chaetodon ulietensis</i>	4	French Polynesia	57	(Bouchon-Navaro 1981)
<i>Chaetodon unimaculatus</i>	1d	Southern Japan	73	(Yabuta 2007)
		Southern GBR	76	(Reese 1975)
		Marshall Islands	71	(Reese 1975)
		Central Pacific	83	(Reese 1975)
		French Polynesia	77	(Bouchon-Navaro 1981)
<i>Chaetodon vagabundus</i>	1a	Southern Japan	75	(Yabuta 2007)
		Northern GBR	71	(Nowicki et al. 2018b)
		Southern GBR	65	(Reese 1975)
		French Polynesia	75	(Bouchon-Navaro 1981)

3.2.2 Study species

A total of 18 species of *Chaetodon* butterflyfishes have been recorded within shallow reef habitats at Lizard Island (Blowes et al. 2013). Eight of these species are considered pair-

forming, whereby the majority of individuals occur in pairs (Table 3.1), though it is largely unknown whether these species are monogamous (Nowicki et al. 2018a). Some of the remaining species do occasionally form pairs, though pair bonds appear relatively weak, and the reproductive sociality is unknown (Table 3.1). This study focused on five species of butterflyfishes (*Chaetodon auriga*, *C. baronessa*, *C. citrinellus*, *C. lunulatus* and *C. vagabundus*), reflecting broad differences in sociality. Primarily, however, these fishes were selected because they were sufficiently abundant at all survey periods to effectively quantify the incidence of pairing.

Where pairing is ostensibly for the purposes of reproduction, the incidence of pairing may vary seasonally, associated with changes in reproduction and spawning behaviour (Yabuta 2007). At lower latitudes, most butterflyfishes have been recorded to spawn year-round (Yabuta and Berumen 2014), though settlement on the GBR tends to be highest in late summer (February–March; Williams and Sale 1981), which may reflect increased reproductive effort and/or higher larval survivorship during this period. To account for possible changes in sociality, as well as minimizing and standardising the influence of immature individuals on occurrence of pairing, all surveys were conducted in January–February.

3.2.3 Field sampling

Butterflyfish and benthic assemblages were surveyed using five replicate 50-m transects in each of four reef zones (flat, crest, slope and base) at each of four study sites (North Reef, Washing Machine, Lizard Head and South Island) with a generally southerly (exposed) aspect. Transects were orientated parallel to the reef crest and run from a haphazardly selected starting point within each zone. During surveys, divers swam slowly (~ 5 m min⁻¹) along the transect path recording all butterflyfish species within a four-metre-wide path. All butterflyfishes were identified to species, as well recording their sociality, following Nowicki et al. (2018b). Coral cover and benthic composition were quantified along each transect, using either line-intercept or point-intercept methods. Up until 1999, benthic assemblages were surveyed along the first 10 m of each transect, recording the intercept length (to the nearest cm) of all distinct coral colonies or other sessile macrofaunal (including macroalgae that were > 5 cm tall), following Pratchett et al. (2006b). Areas of substrate that were not occupied by sessile macrofauna were then recorded as either sand, rubble or consolidated substrate. From 2002 onwards, the proportional abundance of different corals and other sessile macrofauna was recorded using point-intercept methods along the entire length (50 m) of each transect. A total of 100 uniformly distributed points (50 cm apart) were sampled along each transect, recording the identity of corals or any other sessile macrofauna (mostly to genera) underlying each point, or otherwise categorizing the substrate as either sand, rubble or consolidated substrate. These data were used to calculate proportional cover

of live corals (all taxa combined), with both methods expected to provide broadly comparable results for this relatively coarse metric.

3.2.4 Statistical analysis

To explore changes in sociality among survey periods (2002, 2009 and 2017) and with varying levels of overall coral cover, we calculated the proportion of individuals that occurred in pairs, as distinct from solitary individuals. Binomial generalised linear mixed models (GLMMs) were then fitted to the proportional data with a logit link function using the lme4 package (Bates et al. 2014) in R v3.4.4. GLMMs were fitted separately to the data for each of the five species (*C. auriga*, *C. baronessa*, *C. citrinellus*, *C. lunulatus*, and *C. vagabundus*) with the proportions being weighted by the total number of individuals for each transect, allowing proportion data to be interpreted as binomial trials where success is represented as pairing and a failure is solitary behaviour. In each model, zones were nested within sites as a random factor to account for potential differences in pairing between sites and within zones. Temporal changes in pairing behaviour and the effect of coral cover were assessed in two separate models due to the correlation between the two variables.

3.3 Results

Coral cover on the exposed reef front at Lizard Island, averaged across 4 study sites, ranged from 7.46% (± 0.66 SE) up to 25.15% (± 1.32 SE), through the course of this study (Fig. 3.1). Highest coral cover was recorded at the start of the study (1995), but then declined through the course of an outbreak of the Pacific crown-of-thorns starfish (*Acanthaster cf. solaris*) in 1996–1999 (Pratchett 2005), during which coral cover declined from 25.15% (± 1.32 SE) in 1995 to 12.55% (± 1.80 SE) in 2002 (Fig. 3.1). Thereafter, coral cover increased to 22.55% (± 1.20 SE) in 2009, before a renewed outbreak of crown-of-thorns starfish caused further coral loss. Between 2011 and 2017, coral cover declined 58% from 20.66% (± 1.32 SE) in 2011 to just 7.46% (± 0.66 SE) in 2017, associated with an ongoing outbreak of crown-of-thorns starfish, two major tropical storms (Tropical Cyclone Ita in 2014 and Tropical Cyclone Nathan in 2015; Hing et al. 2018) and mass coral bleaching in 2016 (Hughes et al. 2017; Richardson et al. 2018).

While coral cover increased from 2002 to 2009 at Lizard Island (Fig. 3.1), densities of *Chaetodon* butterflyfishes did not exhibit corresponding increases during this period. For the five species considered during this study (*C. auriga*, *C. baronessa*, *C. citrinellus*, *C. lunulatus* and *C. vagabundus*), overall densities were highest (6.56 ± 0.40 SE butterflyfishes per 200 m²) in 2002 and declined (albeit very slightly) to 2009 (6.24 ± 0.38 SE butterflyfishes per 200 m²), with lowest densities (3.90 ± 0.39 SE butterflyfishes per 200 m²) recorded in 2017. Changes in abundance from 2002 to 2017 were negligible for *C. auriga*, *C. citrinellus*, and *C.*

vagabundus (Fig. 3.2). In contrast, densities of both *C. baronessa* and *C. lunulatus* declined markedly through the course of this study. *Chaetodon lunulatus* was the most abundant species in 2002 with average densities of 2.35 (\pm 0.21 SE) butterflyfishes per 200 m² across all sites and zones. Densities of *C. lunulatus* declined 72% from 2002 to 2017, with declines most apparent from 2009 (2.11 \pm 0.20 SE butterflyfishes per 200 m²) to 2017 (0.67 \pm 0.13 SE butterflyfishes per 200 m²). *Chaetodon baronessa* was the only species that increased in abundance from 2002 (1.15 \pm 0.20 SE butterflyfishes per 200 m²) to 2009 (1.55 \pm 0.22 SE butterflyfishes per 200 m²), but exhibited a >85% decline in abundance through the course of this study and was the least abundant of the five species (0.16 \pm 0.06 SE butterflyfishes per 200 m²) in 2017 (Fig. 3.2).

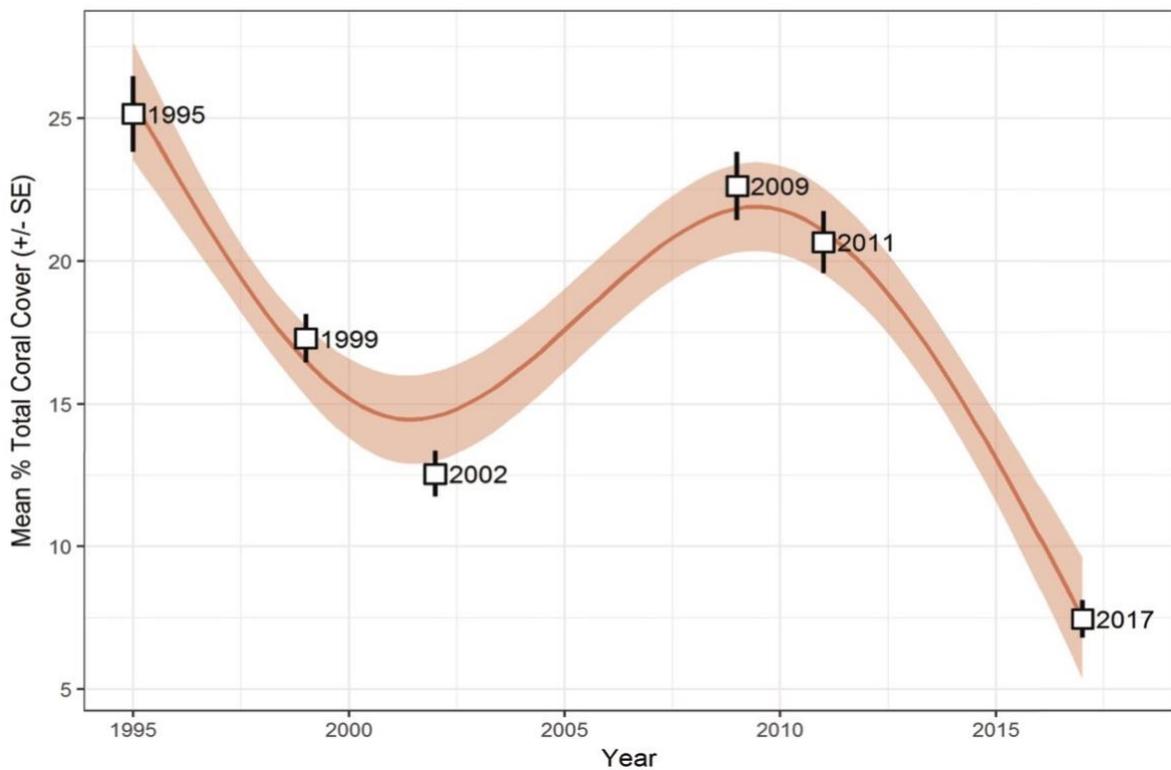


Figure 3.1: Temporal (1995–2017) changes in coral cover at Lizard Island, averaged across four zones (flat, crest, slope and base) at four sites (North Reef, Washing Machine, Lizard Head and South Island). Declines in coral cover (from 1995 to 2002 and 2011 to 2017) are attributable to major disturbances that occurred during these periods, including outbreaks of crown-of-thorns starfish (1995–1999, 2009–2015), severe tropical cyclones (2014, 2015) and mass coral bleaching (2016).

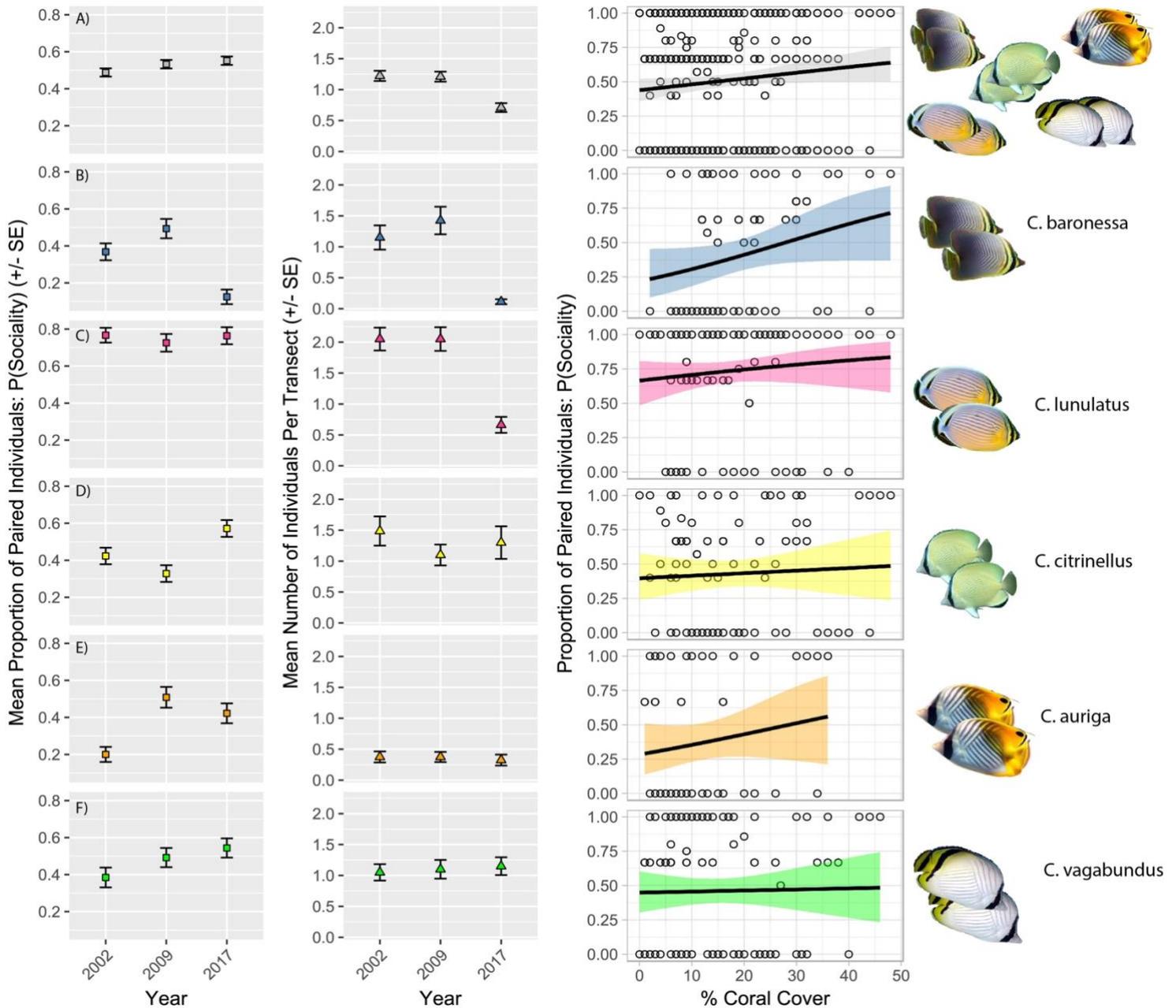


Figure 3.2: Changes in sociality and abundance of butterflyfishes among sample years, and relative to temporal changes in coral cover (in order from left to right), for **a** all species combined, **b** *Chaetodon baronessa*, **c** *Chaetodon lunulatus*, **d** *Chaetodon citrinellus*, **e** *Chaetodon auriga* and **f** *Chaetodon vagabundus*

3.3.1 Changes in sociality

The incidence of pairing (pooled among years) varied among the five study species, ranging from 55.6% for *C. citrinellus* up to 80.1% for *C. lunulatus*. The overall incidence of pairing was fairly consistent among the three survey periods, though there was a significant positive effect of coral cover on sociality (at the 95% confidence level) (Estimate = 0.63, 95% CI 0.028, 0.10), but this relationship varied between species ($p = 0.036$). This trend was most apparent for *C. baronessa* (Estimate = 0.061, 99% CI 0.014, 0.11). For *C. baronessa*, the

relative incidence of pairing actually significantly increased from 36.8% in 2002 up to 49.4.2% in 2009 (Tukey HSD; $p < 0.001$), corresponding with increases in coral cover and population size. The relative incidence of pairing for *C. baronessa* then declined markedly from 2009 to 2017 (Tukey HSD; $p = 0.006$) (Fig. 3.2) in line with marked population declines and coral loss. Only one pair of *C. baronessa* was recorded during the 2017 surveys (across 80 transects and 16,000 m²). Otherwise, we never saw more than a single solitary individual on any transect (200 m²) in 2017. The overall incidence of pairing in 2017 was just 12.5% (Fig. 3.2).

For *C. lunulatus*, marked declines in abundance through the course of this study (Fig. 3.2) did not affect the incidence of pairing ($p > 0.4$). Additionally, temporal changes in coral cover did not account for variation in the incidence of pairing (Estimate = 0.020, 95% CI - 0.019, 0.061).

The relative incidence of pairing effectively increased through the course of this study for *C. auriga*, *C. citrinellus* and *C. vagabundus* (Fig. 3.2) attributable to disproportionate declines in abundance of solitary individuals. Temporal differences in the incidence of pairing were most pronounced for *C. citrinellus*, where the incidence of pairing (57.2%) was significantly higher in 2017, compared to 2002 (42.3%; $p = 0.02$) and 2009 (32.8%; $p = 0.02$) (Fig. 3.2). For this species, densities of solitary individuals declined 53.1% from a mean of 0.80 (± 0.14 SE) individuals per 200 m² in 2002 down to 0.35 (± 0.08 SE) individuals per 200 m² in 2017. This decline was, however, offset by an increase (34.5%) in densities of paired individuals, suggesting that there was fundamental change in sociality (Fig. 3.2). Changes in sociality were not, however, explained by variation in coral cover for *C. citrinellus* (Estimate = - 0.0022, 95% CI - 0.025, 0.020), nor *C. auriga* (Estimate = 0.025, 95% CI - 0.025, 0.084) or *C. vagabundus* (Estimate = - 0.0089, 95% CI - 0.034, 0.016).

3.4 Discussion

Sociality is a fundamental aspect of animal behaviour (Dunbar and Shultz 2010), with important influences on foraging and/or reproductive success for coral reef fishes (Hing et al. 2018; Nowicki et al. 2018b). Ultimately, sociality may influence differential survival and resilience of fishes to large-scale disturbances or otherwise contribute to protracted declines in the abundance of fishes following severe habitat loss and degradation (Hing et al. 2018). This study revealed changes in sociality among Chaetodon butterflyfishes, linked to population declines and coral loss at Lizard Island, in the northern Great Barrier Reef. Lizard Island has been subject to multiple disturbances in the last few years (e.g., Richardson et al. 2018; Hing et al. 2018), culminating in extensive coral loss across the entire depth range (1–15 m) on fringing reefs that surround the island complex (Ceccarelli et al. 2016). Coral cover recorded in February 2017 (averaging 7.46% ± 0.66 SE across four zones at four sites) was the lowest recorded in the last two decades (since 1995), largely attributable to coral loss caused by two

recent and severe tropical cyclones (Ceccarelli et al. 2016), which was further superimposed by subsequent mortality of many remnant corals during elevated temperatures and mass coral bleaching in early 2016 (Hughes et al. 2017; Madin et al. 2018). Not surprisingly, there have been substantial declines in the abundance of butterflyfishes corresponding with recent coral loss, especially among those species with the strongest reliance on corals (see also Ceccarelli et al. 2016).

Coral-feeding butterflyfishes are frequently among the first and worst affected fishes during major disturbances and acute episodes of coral loss (Sano et al. 1987; Pratchett et al. 2008a; Ceccarelli et al. 2016). Many studies have documented species-specific declines in the abundance of *Chaetodon* butterflyfishes following outbreaks of crown-of-thorns starfish, mass coral bleaching and/or cyclones (Reese 1981; Bouchon-Navarro Y et al. 1985; Williams 1986; Pratchett et al. 2006b; Emslie et al. 2011), invariably showing disproportionate effects on obligate coral-feeding species, such as *C. baronessa* and *C. lunulatus*. However, despite the apparent effects of disturbances on the population structure and dynamics of butterflyfishes, none of these previous studies explicitly tested for changes in group typology or sociality during major disturbances and coral loss. Accordingly, there are limited prior expectations for how sociality might change with population declines and coral loss, though it has long been suggested that pairing incidence should be recorded for butterflyfishes (along with overall abundance and territory size) as a potential indicator of population viability and responses to changes in habitat condition (Reese 1981). Reese (1981) suggested that pair persistence and size-assortative mating is likely to be compromised in marginal or disturbed environments, ultimately resulting in fewer pairs and more solitary (unpaired) individuals.

Where sociality (mainly, pairing incidence) of *Chaetodon* butterflyfishes has been studied, the predominant group typology of species varies both spatially and temporally (Yabuta and Berumen 2014). *Chaetodon lunulatus* is among the most extensively studied species of butterflyfish and also exhibits the highest incidence of pairing (Yabuta and Berumen 2014). However, pairing incidence ranges from 53 to 95% among different geographic locations (Table 3.11). Variation in pairing incidence is even more pronounced for some other species, such as *C. plebeius* (Table 3.1), where 7% of individuals were recorded in pairs on the Great Barrier Reef (Reese 1975) versus 82% in Japan (Yabuta 2007). Explanations for these geographic differences in sociality will require explicit research (Yabuta and Berumen 2014), but is likely to vary with demography (Pratchett et al. 2006a), as well as prey availability and habitat condition. Pratchett et al. (2006b) showed that the size-specific onset of pairing in *C. lunulatus* coincides with reproductive maturation, which is size dependent, and this, in turn, may be affected by habitat quality and availability of preferred resources that promote rapid growth (Pratchett et al. 2006a; Berumen et al. 2012), along with inherent effects of water temperature.

The only species for which we recorded significant changes in sociality, that were also seemingly linked with population declines and coral loss, was *C. baronessa*. Notably, both population size and the incidence of pairing increased and then decreased in direct accordance with changes in coral cover. *Chaetodon baronessa*, like *C. lunulatus*, is an obligate coral feeder, but is the most specialized of the species considered in this study (Pratchett 2007). *Chaetodon baronessa* is also the most aggressive and competitively dominant of the species considered herein (Blowes et al. 2013), though it is not clear why this would make them any more sensitive to disturbances and coral loss. It is also unclear whether changes in sociality are a cause or consequence of observed population declines. In February 2017, the mean abundance of *C. baronessa* (0.16 ± 0.06 SE butterflyfishes per 200 m²) corresponded with less than one individual per site-zone combination, let alone one fish per transect. It is unknown whether remaining fishes were always solitary individuals or have lost their partner, and have failed to re-pair owing to the limited density and necessary dispersion of conspecifics. Under normal circumstances, these fishes may repair within hours or days of losing a partner (Nowicki et al. 2018b), but low levels of food availability and scarcity of mates are likely to limit opportunities for pairing. Given the extent of coral loss and associated declines in the abundance of *C. baronessa*, it seems likely that prey limitation severely constrained the capacity for multiple fishes to be sustained within the same feeding territory (Tricas 1989; Berumen et al. 2005) as well as reducing energetic incentives for territorial defence (Keith et al. 2018). Keith et al. (2018) documented widespread declines in territorial aggression among coral-feeding butterflyfishes following depletion of prey resources caused by extensive coral bleaching. The very low number of paired fishes recorded at Lizard Island in 2017 is further expected to limit reproductive output, potentially contributing to ongoing population declines while also constraining population replenishment and recovery.

While pairing in terrestrial species is often linked with monogamy and bi-parental care (Wilson 2000), the reproductive basis of pairing in fishes is equivocal, but often assumed (Whiteman and Côté 2004). For *C. lunulatus*, spawning is confirmed to occur exclusively among paired fishes (Yabuta 1997), and it is likely that other *Chaetodon* butterflyfishes that exhibit strong pair bonds (including *C. baronessa* and *C. vagabundus*) are also socially and reproductively monogamous (Yabuta 2007; Nowicki et al. 2018b). It is apparent, however, that pairing among fishes has benefits beyond reproduction (Fricke 1986; Brandl and Bellwood 2014, 2015; Nowicki et al. 2018a, b) and does not always reflect their reproductive mode. Both *C. auriga* and *C. citrinellus* exhibited relatively low levels of pairing (< 50%) from the outset, though pairing incidence actually increased over the course of the study with ongoing disturbances and sustained coral loss. Both these species exhibit low levels of aggression (Blowes et al. 2013), especially towards conspecifics (Berumen and Pratchett 2006), and solitary and/or paired individuals will occasionally come together to form transient, though pro-

social, groupings. This flexibility in sociality is difficult to explain from a reproductive perspective (Yabuta and Berumen 2014) and may suggest that pairing in these species has a largely non-reproductive basis (e.g., increased feeding efficiency or predator vigilance).

The ability to effectively and rapidly establish the sociality of butterflyfishes during in situ surveys has an important bearing on the results and conclusions of this study. Most notably, any limitations in detectability will bias results towards solitary records and underestimate pairing incidence. The relatively limited observation period used to assess sociality may also result in some fishes erroneously being categorised as solitary, especially where pair bonding is relatively weak and paired fishes only occasionally occur in close proximity (Reese 1975). The converse, where solitary fishes happen to be seen together and are erroneously considered to represent a pair, is unlikely, because such encounters often involve overt demonstrations of aggression (Blowes et al. 2013). Mostly however, paired butterflyfishes tend to remain in very close proximity (Yabuta 2002; Nowicki et al. 2018a). Yabuta (2002) conducted recurrent observations of select pairs of *C. lunulatus* totaling 3.9–13.6 h per pair and showed that paired fishes are located < 2 m apart for > 89% of time. Butterflyfishes are also very amenable to visual surveys, and one suggested benefit of pairing is the increased effectiveness of territorial defence through conspicuous advertising of partner affinity (Reese 1981). We cannot conclusively state that biases associated with inferring sociality from instantaneous observations of group typology are either minimal or consistent. An obvious extension of this current study would be to actually quantify changes in partner affinity and pro-social behaviour (sensu Nowicki et al. 2018a) associated with coral loss and habitat degradation. This would certainly help to resolve whether changes in sociality result from disruption to pair bonds or the loss of mates that eventually succumb to prey depletion and starvation.

Aside from *C. baronessa*, apparent changes in sociality for the *Chaetodon* butterflyfishes considered herein (*C. auriga*, *C. lunulatus*, *C. citrinellus*, and *C. vagabundus*) do not reflect predicted declines in the incidence of pairing following disturbances and habitat degradation (sensu Reese 1981). For *C. auriga* and *C. vagabundus*, limited changes in the incidence of pairing may reflect their limited reliance on coral prey; both these species rarely feed from the surface of live corals (at least in the western Pacific) and feed ostensibly on small motile invertebrates, such as polychaetes (Nagelkerken et al. 2009). Nonetheless, *C. auriga* (but not *C. vagabundus*) have been shown to decline in the aftermath of severe coral loss (Bouchon-Navaro Y et al. 1985; Pratchett et al. 2015b), attributed to indirect benefits of coral-rich habitats in supporting increased abundance of specific prey species. Accordingly, there were sustained declines in the abundance of solitary individuals for *C. auriga*, possibly reflecting the increased capacity of established pairs to monopolise the best feed grounds, allowing them to better withstand disturbances and habitat degradation. Similarly, for *C.*

lunulatus, there was no apparent effect of changing availability of coral prey on sociality, though there were marked declines in population abundance and disproportionate declines in abundance of solitary versus paired individuals.

While this study focused exclusively on pairing, *Chaetodon* butterflyfishes (and other reef fishes more generally) exhibit a broad array of socialites (Yabuta and Berumen 2014). *Chaetodon trifascialis*, for example, is most likely haeremic (Yabuta and Kawashima 1997), whereby extensive feeding territories of male individuals encompass non-overlapping territories of multiple female individuals (Yabuta and Berumen 2014). *Chaetodon trifascialis* is also the most specialized of obligate coral-feeding butterflyfishes (Pratchett 2005) and is disproportionately affected by coral loss (Pratchett et al. 2008a). It seems likely, however, that the reproductive activity and output for polygamous fishes will be more resilient to population declines than for monogamous pair-forming species, though this will also depend on the flexibility of social and reproductive systems. Comparative studies of ecologically equivalent species, which otherwise have contrasting socialites, would be interesting to explore links between sociality and population resilience.

In conclusion, this study shows that major disturbances and severe coral loss can impact on the sociality of *Chaetodon* butterflyfishes, though the specific effects vary among species. For *C. baronessa*, which is a highly specialized obligate coral-feeding species, there were apparent declines in the incidence of pairing, corresponding with population declines and coral loss. The breakdown in pair formation and persistence for *C. baronessa* likely reflects severe limitations in the availability of coral prey, potentially adding to population declines, while almost certainly limiting population replenishment and resilience. For other generalist and non-coral-feeding butterflyfishes, there were apparent increases in the incidence of pairing following severe coral loss, caused by disproportionate declines in solitary versus paired individuals. It appears therefore that pairing may confer increased resilience in some instances, though social bonds cannot be maintained during extensive loss of specific prey; After this point, disruptions to sociality may actually exacerbate population declines and undermine population resilience.

Chapter 4: Territoriality and condition of Chevron Butterflyfish (*Chaetodon trifascialis*) with varying coral cover on the Great Barrier Reef, Australia³

4.1 Introduction

Marine ecosystems are significantly degraded throughout the world, owing to increasing anthropogenic pressures on species and habitats (Roberts et al. 2002; Hoegh-Guldberg and Bruno 2010; Duarte et al. 2020). In particular, coral reef ecosystems are facing escalating threats due to global climate change (Cheal et al. 2017; Hughes et al. 2018a, 2020; Skirving et al. 2019), as well as other more direct anthropogenic disturbances (fishing pressure - Graham et al. 2017; declining water quality - Ortiz et al. 2018; MacNeil et al. 2019; and sedimentation - Pisapia et al. 2019). Increasing incidence, severity and diversity of disturbances is causing widespread declines in coral cover and habitat complexity (Alvarez-Filip et al. 2011a; Elliott et al. 2018; Sheppard et al. 2020). Moreover, most disturbances are highly selective in their effects, causing shifts in coral composition. For the most part it is erect branching corals, such as *Acropora* spp., that are disproportionately affected by major disturbances (population outbreaks of crown-of-thorns starfish, Pratchett et al. 2014a; coral bleaching, Hughes et al. 2018b; cyclones, Madin et al. 2018), though it is also important to take account of differential recovery capacity in the aftermath of such disturbances (McWilliam et al. 2020; Pratchett et al. 2020).

Coral depletion (Wilson et al. 2006; Pratchett et al. 2018 - Chapter 2), topographic collapse (Darling et al. 2017; Wilson et al. 2019), and shifts in coral composition (Richardson et al. 2018) all have important consequences for reef-associated organisms. Most notably, degradation of the biological and physical structure of coral reef ecosystems results in widespread declines in the abundance of fishes (Wilson et al. 2006; Pratchett et al. 2008a; Chapter 2), especially among those species that are explicitly reliant on live corals for food, shelter or recruitment (Feary et al. 2007; Wilson et al. 2008; Emslie et al. 2011; Khan et al. 2017). Foremost among fishes with direct reliance on live corals are *Chaetodon*

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butterflyfishes (family: Chaetodontidae), many of which have an obligate reliance on live corals for food (Cole et al. 2008; Bellwood et al. 2010; Pratchett 2014). Accordingly, rapid and pronounced declines in the abundance of *Chaetodon* butterflyfishes follow acute disturbances that cause extensive coral loss (Pratchett et al. 2006b; Graham et al. 2009; Emslie et al. 2011; Russ and Leahy 2017). In some instances, coral-feeding butterflyfish can adjust their diet to moderate short-term effects of coral depletion (Pratchett et al. 2004; Graham 2007; Feary et al. 2018; Keith et al. 2018), though prey switching can have consequences for energy stores and individual condition (Pratchett et al. 2004), ultimately resulting in long-term declines in abundance (Pratchett et al. 2006b; Graham et al. 2009). For highly specialised coral-feeding fishes, disturbances that cause extensive depletion of their specific prey (often *Acropora* spp.; Pratchett 2014) can lead to widespread extirpation (Kokita and Nakazono 2001; Emslie et al. 2011; Brooker et al. 2014).

The chevron butterflyfish, *Chaetodon trifascialis* Quoy and Gaimard 1825, is one of the most specialised corallivorous butterflyfish (Harmelin-Vivien and Bouchon-Navaro 1983; Harmelin-Vivien 1989; Irons 1989; Cole et al. 2008; Pratchett 2014). On Australia's Great Barrier Reef (GBR), for example, *C. trifascialis* has been reported to take more than 89% of bites from *Acropora* species (Pratchett 2005; Berumen and Pratchett 2008), and mostly from tabular *Acropora* (e.g., *A. hyacinthus*). Moreover, experimental tests of diet versatility revealed that *C. trifascialis* rapidly lose individual condition and die when restricted to feeding on non-preferred coral prey, specifically *Porites* spp. (Berumen and Pratchett 2008). Therefore, any disturbances, such as outbreaks of crown-of-thorns starfish (Pratchett et al. 2014a), cyclones (Madin et al. 2018), or severe coral bleaching (Hughes et al. 2018b), that cause extensive loss of *Acropora* spp. are likely to have marked effects on the individual condition, population viability and abundance of *C. trifascialis* (Pratchett et al. 2006b).

Aside from affecting individual condition and survival, and local abundance of *C. trifascialis*, spatial and temporal variation in the abundance (cover) of preferred coral species is likely to affect the behaviour of such specialist fish (Pratchett et al. 2018; Keith et al. 2018). For example, territoriality and levels of inter-specific aggression exhibited by butterflyfishes varies between areas of high and low coral cover, having fewer and less aggressive encounters in habitats where preferred coral prey is scarce (Berumen and Pratchett 2006a; Keith et al. 2018). *Chaetodon trifascialis* is a highly territorial and aggressive species, capable of monopolising access to preferred corals within their territory (Irons 1989; Reese 1989; Berumen and Pratchett 2006a; Blowes et al. 2013). However, aggression and territoriality have been shown to break down following localised prey depletion (Samways 2005; Keith et al. 2018), presumably because it is not feasible to defend more expansive territories needed to access limited prey. The breakdown in

territoriality may have further consequences for sociality and reproduction (Thompson et al. 2019 – Chapter 3).

Whereas most *Chaetodon* butterflyfish are pair-forming (Yabuta and Berumen 2014; Brandl and Bellwood 2015; Nowicki et al. 2018a) and presumed to be monogamous (Whiteman and Côté 2004; Yabuta and Berumen 2014), *C. trifascialis* is mostly observed as solitary individuals and considered to be polygamous (Yabuta and Kawashima 1997) whereby males have larger territories that encompass multiple small and distinct territories of females within their harem. Limited observations conducted previously in Sekisei lagoon, Yaeyama Islands, are consistent with polygamous and harem mating (Yabuta and Kawashima 1997). However, harem mating in teleost fishes is often linked to hermaphroditism and social suppression of sex-change (Robertson 1972; Godwin 2009), whereas there is yet to be conclusive evidence of sex change among butterflyfishes (Nowicki et al. 2018a). The breakdown in territoriality with declining or low coral cover (e.g., Samways 2005) may disrupt established social systems and lead to compromised mating and reproductive output. Coral loss and reef degradation have been shown to impact the sociality of pairing butterflyfishes (Thompson et al. 2019 – Chapter 3), leading to declines in the proportion of paired individuals. This likely has consequences for resource defence and acquisition, as well as reproduction (Brandl and Bellwood 2015; Nowicki et al. 2018a,b), potentially exacerbating population declines and eroding resilience to coral loss. Polygamous and harem species may be even more susceptible to sociality breakdown, because females in harems often rely disproportionately on dominant males for competitive defence and predator vigilance (Lung and Childress 2007; Whiteside et al. 2016). While links between sociality and vulnerability to disturbance have never been tested for *Chaetodon* butterflyfishes, it is apparent that *C. trifascialis* is among the most vulnerable species of butterflyfish to changing cover of corals (Wilson et al. 2014). *Chaetodon trifascialis* is relatively unique among butterflyfishes in terms of sociality (Yabuta and Berumen 2014) though vulnerability to coral loss is largely attributed to their dietary specialisation (Pratchett et al. 2008).

The purpose of this study was to explore variation in the sociality and physiological condition of *C. trifascialis* among reefs and sites with varying coral cover and composition. Specifically, we investigated how i) territory size, ii) sociality, iii) aggression, and iv) individual condition (measured based on hepatocyte vacuolation, following Pratchett et al. 2004) varied with local coral cover. Detailed studies of the territorial arrangement and interactions among individuals of different sexes may help to advance our understanding of the reproductive biology for *C. trifascialis* following Pratchett et al. (2014b) and assess the extent to which their specific sociality makes them more or less susceptible to coral loss and reef degradation.

4.2 Methods

This study was conducted in 2017 on Australia's Great Barrier Reef (GBR), in the aftermath of widespread and severe coral bleaching in 2016 (Hughes et al. 2017) and during an active outbreak of crown-of-thorns starfish, *Acanthaster cf. solaris* (MacNeil et al. 2017). Sampling was conducted at 4 distinct reefs within the central GBR, between Cairns and Townsville (Fig.4.1, Table 4.1). We had originally intended to extend sampling to reefs in the vicinity of Lizard Island in northern section of the GBR, where recent coral loss has been particularly pronounced (Madin et al. 2018). However, there were no *C. trifascialis* recorded during extensive reef-wide surveys at Lizard Island in 2017 (Pratchett et al. Unpub. Data). Ultimately, sampling was restricted to Elford Reef, located near Cairns, as well as Lodestone, Rib and Walker Reefs in the central GBR near Townsville (Fig. 4.1, Table 4.1). All reefs were mid-shelf reefs within Great Barrier Reef Marine Park Authority (GBRMPA) zones that allow recreational fishing.

At each reef, we established 1-4 study sites (Fig. 4.1), defined as relatively discrete areas of shallow (<10m depth) reef habitat that were occupied by one or more *C. trifascialis*. At each site, we systematically and sequentially observed all *C. trifascialis* to ascertain the size and relative position of their individual territories.

4.2.1 Territories

The spatial extent of individual territories for *C. trifascialis* was established by following each individual for 20-min, following Reese (1989) and Berumen and Pratchett (2006a). During observations, observers would follow the fish at a minimum distance of 2m. One observer would be assigned to each focal individual, up to 2 observers conducted observations simultaneously at the same site. During this time the maximum extent over which the fish travelled was marked out using weighted lengths of coloured flagging tape. Markers were placed only after the focal fish had moved away from the immediate area and there was no perceptible impact to the individuals' movements. All *C. trifascialis* (up to nine individuals) within each site were observed sequentially, with different coloured weighted flagging tape used to mark the extremities of each territory. After all individuals at a site had been observed for 20 minutes, transect tapes were laid out around the outermost markers (weighted flagging tape) of each territory to enable in situ sketches of the spatial relationship of territories, and measurements between markers to be taken. The areal extent of each territory was quantified by measuring the distance between each marker (to the nearest cm), dividing the entire area into the least number of adjacent triangles then using Heron's formula (Fig. 4.1).

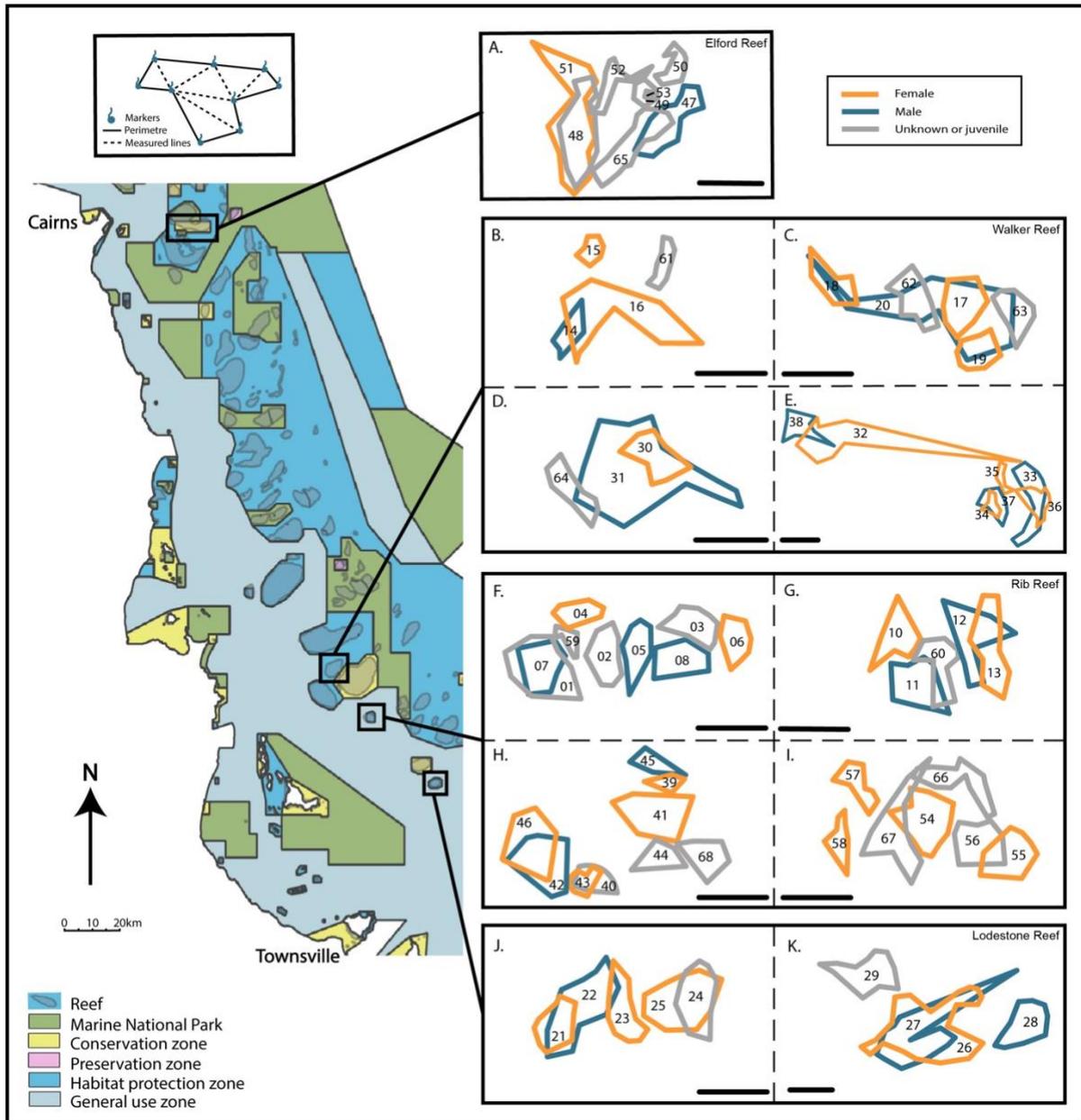


Fig. 4.1 Relative size and position of individual territories for *Chaetodon trifascialis*, recorded across 11 sites at 4 reefs on the Great Barrier Reef, Australia. Colours on left-bottom panel indicate Great Barrier Reef Marine Park Authority zonation (GBRMPA). Elford Reef was zoned “conservation zone”, while all other locations were within “habitat protection zones”. Right panels showing territory maps are grouped by reef, each coloured polygon is an individual fish (yellow, female; blue, male; and grey, unknown sex or juvenile). Inset shows the method used to quantify territory area for each focal individual.

Table 4.1. Reefs visited in 2017 with GPS coordinates for sites and month of the year that site was visited

Group	Reef	Month	GPS Co-ordinate	
			South	East
<u>A</u>	<u>Elford</u>	February	16.918000	146.281130
<u>B</u>	<u>Walker</u>	May	18.346583	146.733083
<u>C</u>	<u>Walker</u>	May	18.344883	146.733100
<u>D</u>	<u>Walker</u>	June	18.346800	146.733180
<u>E</u>	<u>Walker</u>	June	18.341020	146.735430
<u>F</u>	<u>Rib</u>	February	18.482410	146.864930
<u>G</u>	<u>Rib</u>	March	18.491350	146.872560
<u>H</u>	<u>Rib</u>	May	18.479492	146.865867
<u>I</u>	<u>Rib</u>	May	18.475850	146.870750
<u>J</u>	<u>Lodestone</u>	June	18.690730	147.092820
<u>K</u>	<u>Lodestone</u>	June	18.685380	147.104110

4.2.2 Behavioural observations

During the course of the focal observations to establish territorial extent of individual fish, observers also recorded all interactions involving the focal individual and other *Chaetodon* butterflyfishes (conspecifics and congeners). These interactions were classified as negative (aggressive) whenever the focal fish chased, or was chased by, another fish, or positive between conspecifics as this could be considered to confer positive reproductive benefits (or passive between congeners, with no reproductive benefit) whenever the focal fish exhibited co-ordinated swimming with conspecifics that came into close proximity, following Nowicki et al. (2018a, b). No attempt was made to keep track of the number of distinct individuals with which the focal individual interacted, and no specific consideration was given to the extent or duration of observed interactions (cf. Blowes et al. 2013). Rather, we simply tallied the number of positive versus negative interactions recorded during the 20-minute observation period.

4.2.3 Fish collections

Once all observations at a study site were completed, we attempted to collect all focal individuals by spearing. Collections were undertaken only after all observations were completed so as not to confound estimates of territory size or the nature and incidence of interactions. The identity of individual fishes was mostly assured based on variation in individual size, distinguishing markings (where present) and above all, their occurrence within the clearly delineated individual territories. Upon capture each individual was immediately placed in a separate plastic bag with a coloured marker corresponding to the colour used to mark their territory. All fish (contained within individual plastic bags) were then placed in an ice slurry for a minimum of 10-min, and euthanised by severing the spinal cord,

as detailed in ethics permit A2439. Each fish was measured (total length to the nearest mm) and dissected to remove the liver and gonads. Whole livers and gonads were preserved in 10% seawater buffered formalin for at least 7 days prior to histological analysis.

4.2.4 Individual condition

The preserved whole liver and gonad from each individual fish were embedded in paraffin, serially sectioning at 5 μ m, stained using Mayer's hematoxylin and Young's eosin and mounted on glass slides. Gonad tissues were carefully inspected (at 40x magnification) to distinguish developmental stages of male and female gonads. Mature males were identified by the presence of spermatozoa (Fig. 4.2a, b), and mature females by the presence of stage 3 and/or stage 4 oocytes (Fig. 4.2c). In particular, the entire area of sectioned tissues from each fish was carefully searched for evidence of transitional gonads (with simultaneous occurrence of both spermatozoa and oocytes), which would be indicative of sex change.

Individual condition for each individual fish was assessed by quantifying hepatocyte vacuolation in histological sections of liver tissue (following Pratchett et al. 2004; Hoey et al. 2007). Hepatocyte vacuolation is a simple and effective method for quantifying lipid storage, and hence body condition, in fishes (Theilacker 1978) and has been explicitly validated for *Chaetodon* butterflyfishes (Pratchett et al. 2004). To quantify proportion of vacuoles, we randomly took three replicate photographs (at 40x magnification) from distinct sections of the liver for each individual fish. All images were then transferred to ImageJ where a standardised grid of 84 points was overlaid on each image, the entire field of view for each image was occupied by a section of liver, so that all grid points were overlaid on tissue. The proportion of points (out of 84) overlaying hepatocyte vacuoles were then counted and pooled across the three photographs for each individual fish.

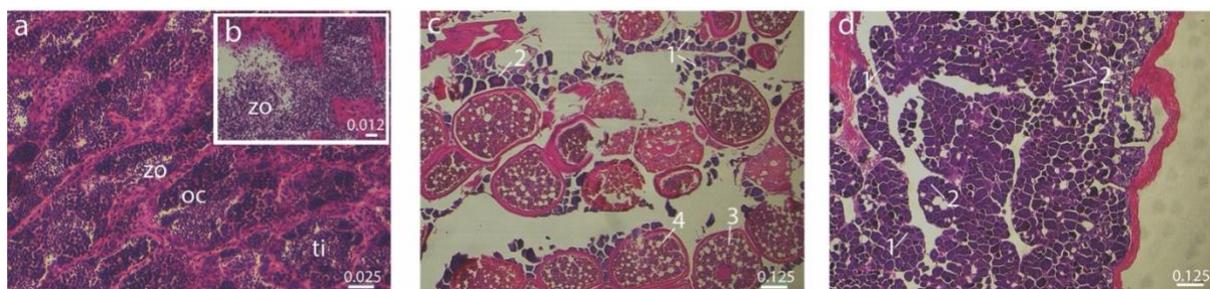


Fig. 4.2 *Chaetodon trifascialis* gonads stained with Mayer's hematoxylin and Young's eosin. **a** mature male showing stages of spermatogenesis: oc) spermatocytes; ti) spermatids; and zo) spermatozoa, zoomed section inset **b** high magnification (40x) of spermatozoa; **c** mature female showing ripe stage 4 oocytes; and **d** immature female showing only stage 1 and 2 oocytes. Numbers denote stage of oocyte development: 1) previtellogenic, perinucleolar; 2) previtellogenic, cortical alveoli beginning formation; 3) early vitellogenic; and 4) mid vitellogenic. Scale bars are in mm

4.2.5 Coral cover

To relate the biology and behaviour of *C. trifascialis* to total coral cover and the cover of preferred coral prey (tabular *Acropora*; Pratchett 2005) among sites, we quantified coral composition within the territories of each individual fish. Proportional cover of all major coral types was quantified using an average of 4.6 non-overlapping 1m² quadrats, with each quadrat divided into an 11x11 grid of evenly spaced points. Photographs (n=307, across 67 individual territories) were analysed using a manual point count in ImageJ. All live corals were distinguished to genus or family (Table 4.2), though *Acropora* corals were further divided into tabular *Acropora* species (mainly, *A. hyacinthus*) versus other *Acropora* spp., reflecting the strong feeding preferences and habitat associations of *C. trifascialis* for tabular *Acropora* on the GBR as reported previously (Pratchett 2005). In a small number of cases (11 out of 307 quadrats), the photograph did not effectively capture the entire quadrat area, and so the sample area and number of points was reduced accordingly, and the cover of each coral category/type expressed as a proportion.

4.2.6 Statistical analysis

To investigate any sex-related differences in body size a one-way ANOVA was used to compare total length among males, females, and individuals of indeterminate sex. Initial analyses were conducted with all samples (to make full use of available data, and explore potential biases among individuals of indeterminate sex). Post-hoc pairwise comparisons were then conducted (with Bonferroni correction) to explicitly test for differences in size between males and females. Linear mixed effects models fitted using the “nlme” package (Pinheiro et al. 2020) in R 3.3.2 (R Core Team 2016), were used to investigate the potential effects of sex (male, female and unknown), body size (TL mm), cover of tabular *Acropora*, and total coral cover on territory size (in m²). The cover of tabular *Acropora* and total coral cover were colinear so alternate models were used to test the contribution of these variables separately. All candidate models were compared using Akaike’s Information Criterion corrected for small sample sizes (AICc) following Burnham and Anderson (2002) (Table 4.4).

Generalized linear models (glm) using a Poisson distribution (log link function) were used to test for changes in the areal extent of territories (in m²), relative to the sex (male, female and unknown), size (TL mm) of individuals, and cover of tabular *Acropora* within individual territories. The frequency of different-types of interactions (including, i) aggressive interactions where focal individuals of *C. trifascialis* were the aggressor, ii) aggressive interaction where aggression was directed at the focal individuals of *C. trifascialis*, and iii) all positive (between conspecifics) or passive (between congeners) interactions were compared among species (including *C. trifascialis* and all other congeners with which these fish were seen to interact) using χ^2 , based on log-linear statistics. Models were fitted

as a to best represent counts of interactions, which ranged from 0-18). Alternative models were compared using $AICc$, while the adjusted R^2 of all models was also considered to assess the relative and absolute performance of alternative models. Similar analyses (glm) were also conducted to explore intrinsic and extrinsic factors that might contribute to variation in the condition of *C. trifascialis*, though models were fitted using a binomial distribution (logit link function) to best represent the proportional data for hepatocyte vacuolation.

4.3 Results

4.3.1 Fish collections

A total of 67 individual *C. trifascialis*, across 11 groups (or sites) were observed during the course of this study (Table 4.2). 46 out of 67 (68%) fish were successfully collected and processed to assess sex and condition. The remaining 21 individuals evaded capture and could not therefore be reliably sexed; there was also one individual for which the gonads were lost following spearing. Of those individuals that could be sexed ($n = 45$), 28 (62%) were female and 17 (38%) were male. Despite the female biased sex ratio (1.65:1), we did find that there were often >1 male within a group (Table 4.3; Fig. 4.1). The size of *C. trifascialis* collected ranged from 83mm TL to 148mm TL, with most individuals (75%) 120-140mm TL. Size differed significantly (1-way ANOVA, $F_{2,48} = 4.2$, $p < 0.01$) among males, females and those individuals of unknown sex (either because they evaded capture or were immature). While there was also substantial overlap in body size between females (83-140mm TL) and males (120-148mm TL), males (average TL = 133.5mm \pm 0.18 SE) were significantly ($p = 0.02$) larger than females (average TL = 119.0mm \pm 0.27 SE). The largest individual collected from each group was always male, though only females were collected at one site on Rib reef (i.e. Fig. 4.1).

Table 4.2 Proportional cover of different coral genera/ families at each of 11 sites where we documented sociality for a distinct group of *C. trifascialis*. *Acropora* corals were further divided into tabular *Acropora* and other *Acropora*, reflecting the strong feeding preference of *C. trifascialis* for tabular *Acropora* (e.g., Pratchett 2005). Standard Error (SE) indicated in parentheses. Shannon's diversity index (Shannon 1948) shows species diversity for each group and can be read as: low diversity (<1.5), medium diversity (1.5<2.5) and high diversity (>2.5)

Family	Genera	Group										
		A	B	C	D	E	F	G	H	I	J	K
Acroporidae	tabular <i>Acropora</i>	11.0 (3.0)	33.0 (4.8)	41.7 (3.3)	34.6 (6.6)	42.3 (3.8)	34.4 (3.0)	27.1 (0.9)	38.2 (3.6)	20.9 (5.1)	32.1 (4.1)	35.4 (5.5)
	other <i>Acropora</i>	18.0 (2.7)	20.1 (3.0)	15.8 (1.9)	16.0 (3.7)	21.0 (2.7)	27.0 (2.1)	16.8 (1.6)	20.4 (2.0)	27.9 (4.6)	16.8 (1.9)	15.5 (1.8)
	<i>Isopora</i>											0.1
	<i>Astreopora</i>			0.1						0.1		0.3
	<i>Montipora</i>	0.1	0.3	<0.1	0.1	2.4 (2.8)	2.6 (1.0)	0.5 (1.4)	0.1 (2.1)	0.4 (0.4)	0.4 (2.9)	0.2 (0.6)
Pocilloporidae	<i>Pocillopora</i>	2.0 (0.9)	0.4	0.6 (0.3)	0.4 (1.1)	0.3 (0.8)	1.5 (0.8)	1.7 (0.7)	0.7 (0.3)	0.1 (0.3)	1.2 (0.4)	2.6 (0.5)
	<i>Stylophora</i>	0.4 (0.6)					0.2 (0.2)	0.8 (0.4)	0.1 (0.3)			
	<i>Seriatopora</i>	0.2 (0.3)					0.1 (0.8)	<0.1				
Merulinidae	<i>Goniastrea</i>	0.3 (0.2)					0.1 (1.7)	0.1	<0.1	0.4 (0.5)	0.2 (1.2)	0.2 (1.2)
	<i>Echinopora</i>					0.2						
	<i>Favia</i>	0.1 (0.3)					0.1		0.1 (0.6)	<0.1		0.1
	<i>Favites</i>	0.3 (0.3)				0.1 (0.6)	<0.1	0.2 (0.8)		0.1	0.3 (0.3)	0.1 (0.4)
	<i>Leptoria</i>				0.1						0.2 (0.5)	<0.1
	<i>Platygyra</i>	0.2 (0.4)	0.2 (0.1)				0.2 (0.5)	0.1 (0.8)	<0.1	<0.1	0.1	0.1
	<i>Hydnophora</i>					0.5 (2.5)						
Diploastraeidae	<i>Diploastrea</i>									0.5 (3.3)	0.1	
Lobophyllidae	<i>Acanthastrea</i>	0.1								<0.1		0.1
	<i>Lobophyllia</i>	0.2 (0.6)						<0.1		0.5 (0.4)	0.1	<0.1
Poritidae	<i>Porites</i>	4.7 (1.1)	0.2 (0.6)	0.3 (0.6)	0.2	0.3 (0.6)	1.0 (0.4)	1.0 (0.4)	0.2 (0.2)	1.9 (1.6)	0.9 (0.7)	
	<i>Goniopora</i>	<0.1	<0.1									
Fungiidae											0.1	
Agariciidae	<i>Pavona</i>										<0.1	<0.1
Psammocoridae	<i>Psammocora</i>				0.1							
Total coral cover		37.4 (1.4)	54.2 (4.4)	58.6 (7.8)	51.4 (5.0)	67.0 (4.9)	67.2 (3.5)	48.3 (2.8)	60.0 (4.4)	52.2 (3.4)	52.9 (2.5)	55.0 (2.4)
<i>Acropora</i> spp. as a proportion of total coral cover		77.5	97.8	98.2	98.6	94.4	91.3	90.8	97.8	93.4	92.6	92.6
Shannon's diversity index		2.2	1.5	1.2	1.4	1.5	1.9	1.9	1.5	1.9	2.0	2.0

4.3.2 Territories and coral cover

The areal extent of territories of *C. trifascialis* ranged from 1.0 to 273.9m², with a mean of 51.6m² (± 6.6 SE). Among groups (sites), the average size of territories was highest (164.6m² ± 44.8 SE) at Lodestone, where average coral cover was 59.7% (± 6.6 SE), and lowest (34.9m² ± 44.8 SE) at Elford where coral cover was lowest (26.5%; Table 4.3). Coral cover was dominated by tabular and other *Acropora* spp., collectively accounting for 77.5% to 98.6% of total coral cover (Table 4.2). The abundance of other coral taxa was low, with Shannon's Diversity Index ranging from 1.2 to 2.2 across the eleven sites (Table 4.2.) The best model to explain individual variation in territory size for *C. trifascialis* included body size and sex, but not total coral cover or cover of tabular *Acropora* (Table 4.4). Males had generally larger territories (average = 71.3m²) compared to females (average = 56.6m²), though the two fish with the largest territories (>250m²) were both females (Fig. 4.3). Territory size increased with increasing size of fish, with the rate of increase tending to be greater for males than females or those individuals for which sex was unknown (Fig. 4.4).

4.3.3 Behavioural observations

The frequency of intra- and inter-specific interactions varied among individuals, ranging from 0 to 18 (mean = 4.76) interactions per 20-minute observation. The best model to explain individual variation in the frequency of interactions (all interactions, regardless of whether they were positive or negative and inter- or intra-specific) included sex, body size, and also territory area (Table 4.5). The number of interactions was positively related to fish size and territory area, but only among male individuals (Fig. 4.4b). Most interactions recorded (211/279; 75.6%) were intraspecific, and of these, most were positive or passive (Fig. 4.5).

The frequency of different types of interactions varied with species ($\chi^2 = 285.0$, df = 12, $p < 0.01$; Fig. 4.4). For the intraspecific interactions, most (173/211; 82.0%) were classed as positive (between conspecifics) or passive (between congeners) (e.g., swimming together) and only 38 (18.0%) were negative (involving aggression) (Fig. 4.4). Interactions recorded between *C. trifascialis* and other congeneric butterflyfishes predominantly involved aggression (62/68; 88.6%), and mostly involved *C. baronessa* (18/68; 26.5%) and *C. lunulatus* (19/68; 27.9%). However, interactions with *C. baronessa* were bi-directional, while interactions with *C. lunulatus* mostly involved *C. trifascialis* chasing individuals of *C. lunulatus*. Indeed, most congeners (all except *C. baronessa*) did not exhibit aggression towards *C. trifascialis* (Fig. 4.5).

4.3.4 Body condition

Hepatocyte vacuolation was used to compare body condition among 44 *C. trifascialis* that had intact livers, and ranged from 7.1% to 25.9% among individuals (mean = 15.6% \pm 0.7 SE). The best model to explain individual variation in proportional hepatocyte vacuolation of *C. trifascialis* included only body size (Table 4.5), though this model had low explanatory power (i.e., low R^2). It is apparent that highest levels of hepatocyte vacuolation were recorded among very small, and potentially non-reproductive, individuals. However, there was also significant variation in hepatocyte vacuolation among larger *C. trifascialis*, regardless of sex. Variation in condition of *C. trifascialis* was unrelated to differences in territory size or availability of their preferred coral prey, tabular *Acropora* (Table 4.5).

Table 4.3 Variation in biological and environmental characteristics among 11 distinct groups of *C. trifascialis*, sampled across 4 different reefs (Fig. 4.1). “*” indicate groups that exhibit nested territories, which may be indicative of harem mating.

Group	No. individuals	Average territory size in m ² (SE)	Sex ratio F:M	% cover of all corals (SE)	% cover of tabular <i>Acropora</i> (SE)
A	8	34.9 (14.5)	1:1	26.5 (9.3)	13.3 (6.9)
B *	4	36.7 (21.0)	2:1	58.2 (6.5)	31.4 (3.8)
C *	6	49.0 (19.9)	3:1	73.4 (4.6)	44.8 (5.7)
D	3	75.8 (46.2)	1:1	65.7 (4.6)	33.7 (2.2)
E	7	75.1 (31.6)	4:3	61.9 (2.6)	41.8 (3.5)
F	9	30.8 (5.7)	2:3	64.8 (5.4)	39.0 (4.3)
G	5	39.2 (3.7)	2:2	39.3 (12.1)	20.1 (5.7)
H	9	29.7 (6.7)	4:2	49.1 (3.4)	33.5 (2.8)
I	7	35.9 (5.9)	4:0	51.3 (4.7)	25.8 (3.8)
J	5	51.0 (8.9)	3:1	55.7 (7.4)	30.7 (6.2)
K	4	164.6 (44.8)	1:2	59.7 (2.3)	33.3 (3.0)
	67	51.6 (6.6)	27:17	53.9 (2.4)	31.6 (1.8)

4.4 Discussion

Territoriality among *Chaetodon* butterflyfishes is strongly linked to both resource defence and sociality (Tricas 1989; Roberts and Ormond 1992; Nowicki et al. 2018b). Notably, the predominance of pairing and putative monogamous mating systems among butterflyfishes is attributed, at least in part, to increased efficiencies in resource acquisition and territory defence by paired individuals (Roberts and Ormond 1992; Pratchett et al. 2006a; Nowicki et al. 2018b). However, *C. trifascialis* exhibits strong territoriality and aggression (Irons 1989; Blowes et al. 2013) despite being non-pair forming (Yabuta and Kawashima 1997). Explicit studies of sex-specific differences in territoriality and reproductive behaviour for *C. trifascialis* suggest that this species is harem with multiple discrete female territories nested within larger territories of dominant males (Yabuta and Kawashima 1997). However, this archetypal arrangement of harem territories has only been documented from one limited location involving just 3 males and 8 females (Yabuta and Kawashima 1997). In

our study, *C. trifascialis* were observed to occupy discrete territories that did not overlap with conspecifics known to be of the same sex (Fig. 4.1). It was also apparent that territory sizes of males were generally larger than that of females (Fig. 4.3). However, there was very limited evidence of nested territories, where large male territories encompassed smaller territories of one or more females. Of the 11 groups of *C. trifascialis* examined, only one group (Walker Reef; Fig.4.1, C) had a single large male territory encompassing the territories of 5 other smaller individuals, of which at least 3 were female (the other 2 evaded capture and therefore, were not sexed).

Table 4.4 Variation in the areal extent of territories of *C. trifascialis* modelled as a function of “Sex”, “Size”, and cover of “*Acropora*” (or overall cover of all corals as an alternate model) within individual territories, using a linear mixed effects model (lme), where all models include “Group” as a random effect. Alternative models were compared using Akaike’s information criterion corrected for small sample sizes (*AICc*), while also accounting for changes in degrees of freedom (*df*). The adjusted R^2 (*adj R^2*) is shown for each model, and the best model shown in bold.

Model	<i>df</i>	<i>AICc</i>	<i>adj R²</i>
Territory Size			
~ Sex * Size * <i>Acropora</i>	14	557.8	0.90
~ Sex * Size * All coral	14	560.6	0.90
~ Sex * Size	8	540.7	0.89
~ Size * <i>Acropora</i>	6	560.6	0.88
~ Size	4	551.7	0.88
~ Sex	5	642.3	0.12
~ <i>Acropora</i>	4	656.7	0.07
~ All coral	4	656.7	0.09

While it is clear that *C. trifascialis* has a social structure and mating system that is atypical of *Chaetodon* butterflyfishes (Yabuta and Berumen 2014), the evidence for harem mating in this species is equivocal. Across 11 social groups considered in this study, the average territory size of male *C. trifascialis* (71.3m²) was larger than that of females (56.6m²), but only by 25%. Even more unclear is support for protogynous sex change in *C. trifascialis*, which often underpins harem mating systems in fishes (Robertson 1972; Godwin 2009). Though there was broad overlap in the size of males versus females, the largest individuals (>110mm TL) recorded in this study were consistently male, and smaller individuals (<99mm TL) were consistently female. Moreover, all males were sexually mature, whereas many (57%) of females were immature. These patterns are consistent with socially mediated patterns of protogynous sex change (Todd et al. 2016), though we did not observe transitional gonads. While difficult to observe (Sadovy and Shapiro 1987), transitional gonads provide the best evidence for functional sex change in fishes, though it may require experimental manipulation of social groups to explicitly test whether *C. trifascialis* do or do

not change sex. The amount of dietary resources (i.e., live coral) required to sustain entire social groups of *C. trifascialis* during experimental tests of sex change in aquaria is probably prohibitive (*sensu* Hobbs et al. 2004), though it may be feasible to manipulate social groups *in situ*. More specifically, experimental removal of dominant males from seemingly archetypal harem groups combined with careful monitoring of behavioural shifts in remaining fishes may help to target fish that should be examined for evidence of sex change. It is possible however, that these fishes do change sex and the territorial arrangement of *C. trifascialis* is maintained through sex-specific suppression, whereby subordinate males expand their territories in response to removal of locally dominant males.

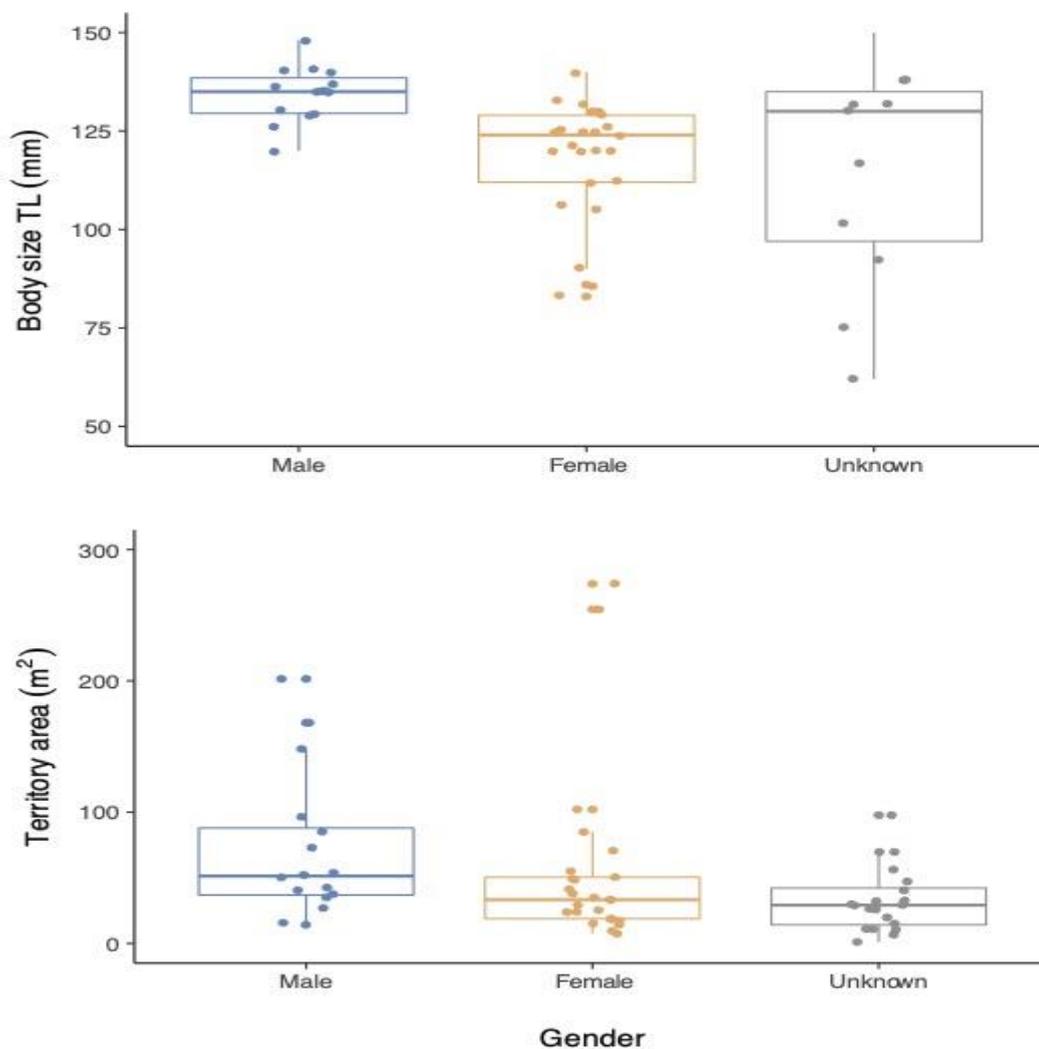


Fig. 4.3 Box plots showing sex related differences in body size (total length in mm) and territory size (area in m²) of *Chaetodon trifascialis*. Sex is unknown for those individuals that evaded capture or were immature (grey)

Although *C. trifascialis* are predominantly solitary (Nowicki et al. 2018a), our study has shown that they do interact frequently (and mostly positively) with conspecifics living in

their immediate area. The average number of conspecific interactions (equating to 11.1 interactions per hour \pm 1.5 SE) is three times that reported for generalist obligate corallivore, *C. austriacus* (Righton et al. 1998). This high level of social interaction is likely to have benefits for reproduction and collective fitness (Shuster and Wade 2003; Brandl and Bellwood 2015), regardless of social system. Moreover, our study suggests that seemingly stable territorial boundaries among sympatric individuals of *C. trifascialis* may be maintained more through mutual co-operation than intense intraspecific aggression (see also Roberts and Ormond 1992). Conversely these fishes do exhibit high levels of aggression towards congeners, and especially *C. baronessa*, reflecting already established competitive hierarchies (Berumen and Pratchett 2006; Blowes et al. 2013), where aggression is greatest among pairs of species with greatest overlap in resource use. However, unlike most previous studies on territoriality of *Chaetodon* butterflyfishes (e.g., Tricas 1989; Righton et al. 1998) we found no relationship between territory size and prey availability. The factors responsible for the specific size and arrangement of territories for *C. trifascialis* will therefore require further investigation, including detailed temporal studies to assess the persistence and stability of territorial boundaries, especially during changes in resource availability, caused by major perturbation to coral assemblages (e.g., Madin et al. 2018).

Vagaries in the arrangement of territories for *C. trifascialis* across the study locations considered herein may be linked to disruptions caused by recent disturbances and associated coral loss. Disturbances to coral assemblages have been most pronounced in the northern GBR, where there have been recurrent episodes of mass coral bleaching, severe tropical storms, as well as high densities of crown-of-thorns starfish (Hughes et al. 2017; Vanhatalo et al. 2017; Madin et al. 2018). *Chaetodon trifascialis* is reported to be particularly vulnerable to acute episodes of coral loss, even among obligate coral-feeding butterflyfishes (Berumen and Pratchett 2006b; Pratchett et al. 2006a; Emslie et al. 2011), which is widely attributed to their extreme dietary specificity (Berumen and Pratchett 2008). Importantly, declines in the abundance of *C. trifascialis* during major disturbances are often disproportionate to levels of coral loss (Pratchett et al. 2008; Wilson et al. 2014) because of their heavy reliance on corals (e.g., tabular *Acropora*) that are extremely vulnerable to most major disturbances (Pratchett et al. 2020). *Chaetodon trifascialis* has been recorded to feed on other corals (e.g., *Pocillopora* and *Montipora*) when *Acropora* is scarce (Irons 1989; Graham 2007; Keith et al. 2018), which may provide some capacity to cope with localised depletion of *Acropora* corals. However, we failed to record any *C. trifascialis* in habitats or on reefs with very low cover of *Acropora* (e.g., in the northern GBR), suggesting that either these fish are particularly reliant on *Acropora* corals on the GBR (see also Pratchett 2005; Berumen and Pratchett 2008) or disturbances that occurred in the northern GBR (Hughes et al. 2018b; Madin et al. 2018) were so severe as to simultaneously deplete cover of *Acropora*

and other alternative prey corals. In this study, *C. trifascialis* were recorded in areas where *Acropora* was the most abundant contributor to coral cover and there was low diversity of coral taxa (Table 4.2). Where *C. trifascialis* were recorded there was no evidence that variation in local coral cover affected either territorial behaviour (but see Wrathall et al. 1992; Righton et al. 1998) or individual condition (Berumen et al. 2005). Rather, body size (which covaried with sex) was the predominant factor accounting for differences in the areal extent of territories and the frequency of interactions of *C. trifascialis* considered in this study. This may suggest that *C. trifascialis* is resilient to all but very low levels of prey availability, and territoriality is determined more by the distribution, rather than abundance of prey corals (Righton and Mills 2006). However, shifts in the size and arrangement of feeding territories may have a critical influence on social interactions, with consequences for reproduction and population replenishment (Thompson et al. 2019 – Chapter 3).

Protracted declines in the abundance of obligate coral-feeding fishes have been recorded following acute disturbances that cause extensive coral depletion, which are attributed to ecological versatility and gradual depletion of energy reserves (Pratchett et al. 2006b; Graham et al. 2009). However, declines in the fitness of individuals may be compounded with changes in sociality (Hing et al. 2018), leading to protracted declines in population size. For pair-forming butterflyfishes, breakdowns in sociality can have consequences both for feeding efficiency and reproductive potential (Nowicki et al. 2018b), as well as potentially affecting predation risk (*sensu* Brandl and Bellwood 2015). However, group-living fishes (or those species with more complex sociality) may be even more vulnerable to disturbances, owing to increased social conflict (Keith et al. 2018; Hing et al. 2018). While *C. trifascialis* may be able to live in a wide range of different environments, so long as there is at least moderate abundance of preferred coral prey, it is possible that there are subtle changes in sociality that will impact long-term population persistence.

Aside from territoriality, we would expect variation in prey availability (e.g., the cover of tabular *Acropora* within feeding territories of each fish) to directly influence individual condition of *C. trifascialis* (*sensu* Pratchett et al. 2004; Berumen et al. 2005), especially given its dietary specificity (Berumen and Pratchett 2008). For example, Pratchett et al. (2004) showed that hepatocyte vacuolation, a measure of stored lipids, of the coral generalist *Chaetodon lunulatus* declined within 2 years after localised depletion of coral prey associated with mass coral bleaching. It is apparent however, that hepatocyte vacuolation can vary enormously among sympatric individuals (e.g., Montanari et al. 2017), possibly with changes in reproductive condition and spawning. Individual variation in the hepatocyte vacuolation of *C. trifascialis* could not be explained based on body size, but was highest among smaller individuals, which may be explained by their limited reproductive investment (Pratchett et al. 2006b). Hepatocyte vacuolation was also highly variable among larger

individuals, possibly reflecting differences in the timing and extent of spawning, as energy reserves in the liver may be rapidly mobilised for reproduction (e.g., Henderson et al. 1984; Craig et al. 2000).

The degradation of coral reef ecosystems and decline in abundance of live corals (Hughes et al. 2017; Wilson et al. 2019) poses a major threat to coral-dependent reef fishes. In particular, highly specialist fishes are considered particularly vulnerable to coral loss (Pratchett et al. 2008), but there are other important biological traits that will also influence the vulnerability of species to habitat perturbations and resource depletion (Hing et al. 2018). In the case of *C. trifascialis*, we only ever found groups in areas with moderate to high corals cover and a predominance of tabular *Acropora*. This suggests that these fish are highly reliant on this coral, at least on the GBR. However, there were relatively minor changes in individual behaviour and condition with spatial variation in overall coral cover. It is possible that the distribution and abundance of coral prey influences the territorial arrangement and subsequent social interaction among sympatric individuals, but much more work is needed to reconcile the complex sociality of this species.

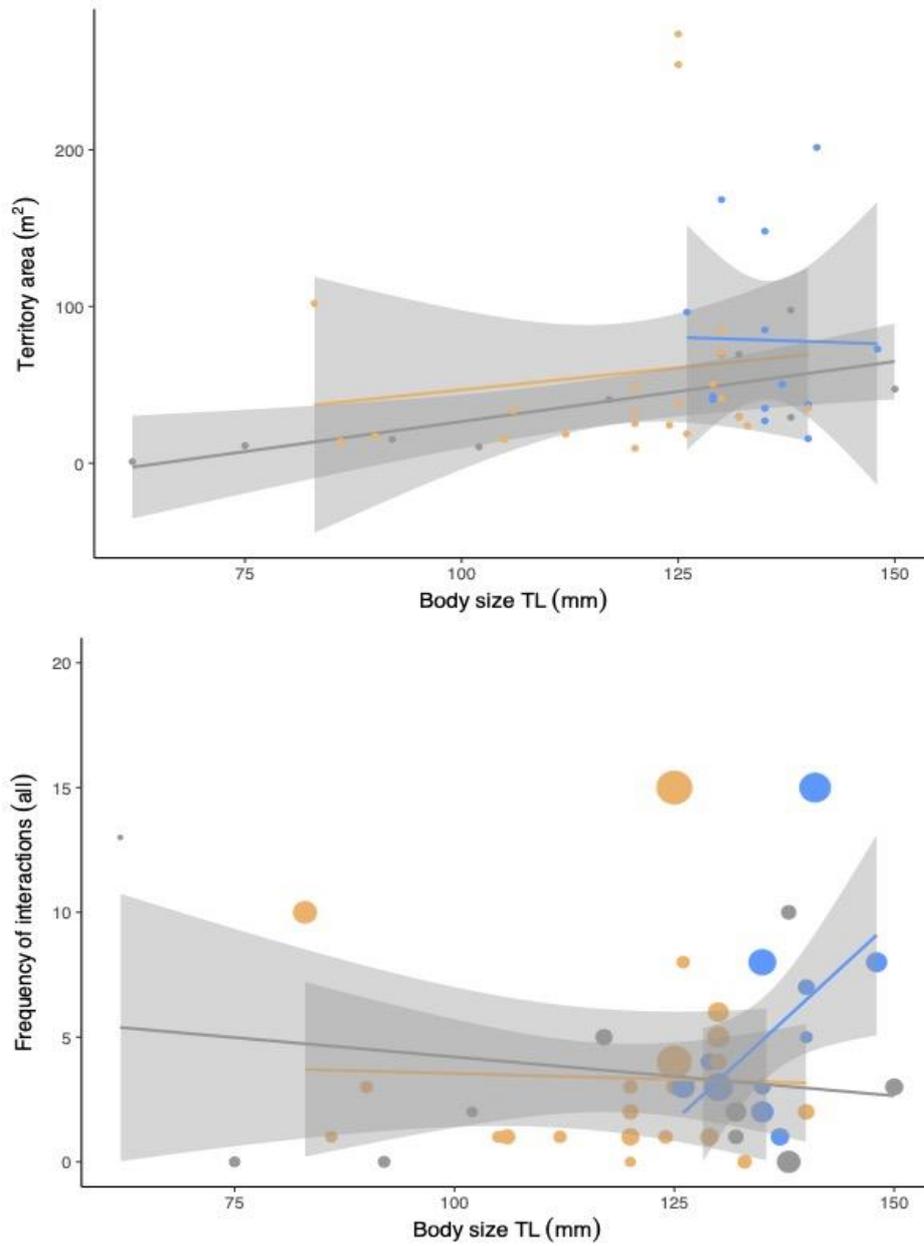


Fig. 4.4 Relationship between size (total length in mm) of *C. trifascialis* and A) territory size (area in m²) and B) frequency of interactions, with separate relationships shown for males (blue), females (orange), and those individuals for which sex is unknown (grey)

Table 4.5 Behaviour and condition of *C. trifascialis*, where all interactions and hepatocyte vacuolation were modelled as a function of “Territory” size, “Sex”, body “Size”, and cover of “*Acropora*” (presumed to represent prey availability) within individual territories, using generalized linear models (glm). Frequency of interactions (count data) was modelled using a Poisson distribution, while hepatocyte vacuolation (proportions) was modelled using a binomial distribution. Alternative models were compared using *AICc*, as for Territory size (Table 4). The adjusted R^2 (*adj R*²) is shown for each model, and the best model shown in bold.

Model	<i>df</i>	<i>AICc</i>	<i>adj R</i>²	<i>df</i>	<i>AICc</i>	<i>adj R</i>²
	Interactions (all)			Hepatocyte vacuolation		
~ Sex * Size * Territory * <i>Acropora</i>	24	278.3	0.95	20	102.5	0.04
~ Sex * Size * Territory	12	242.8	0.90	12	49.5	0.04
~ Sex * Size	6	276.0	0.69	6	27.8	0.04
~ Sex	3	318.5	0.09	3	20.3	<0.01
~ Size	2	282.5	0.57	2	17.4	0.05
~ Territory	2	282.4	0.47	2	17.9	<0.01
~ <i>Acropora</i>	2	321.3	<0.01	2	17.9	<0.01

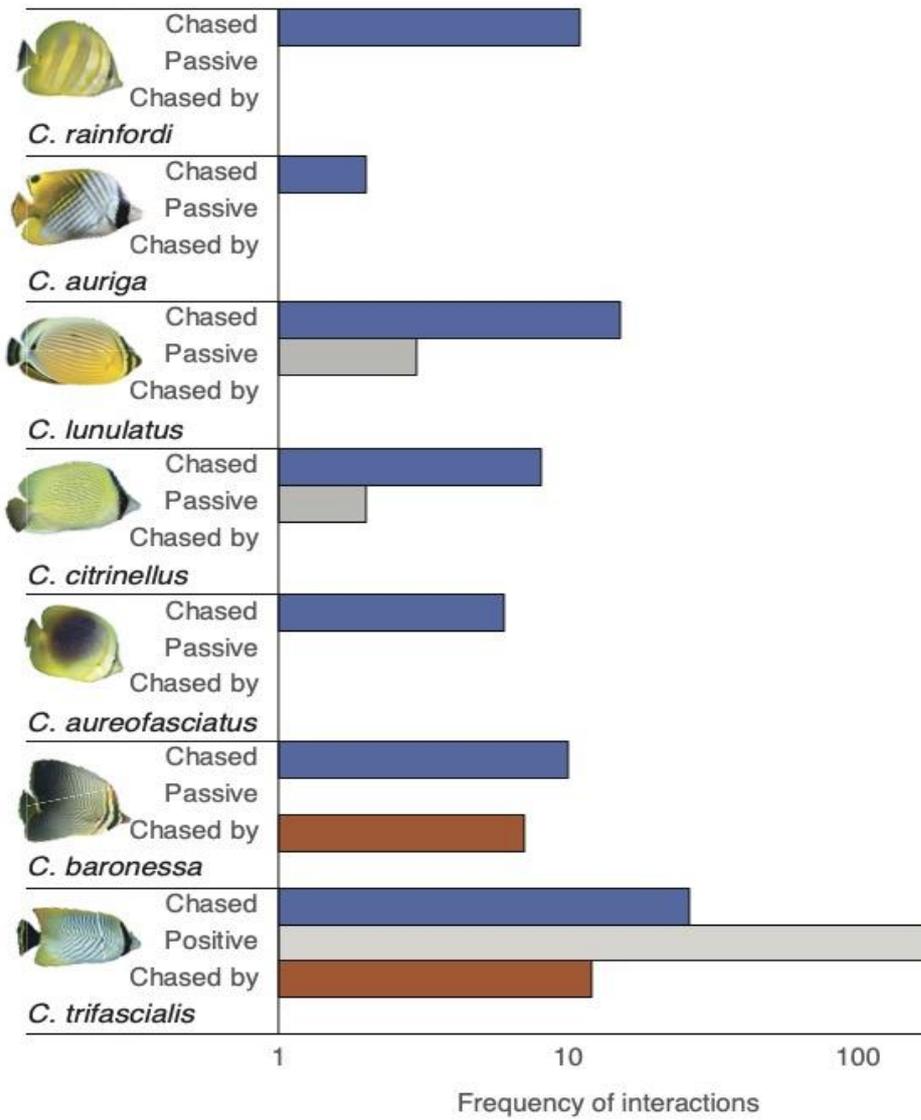


Fig. 4.5 Frequency of congeneric interactions recorded during observations of *Chaetodon trifascialis* (n = 54)

Chapter 5: General Discussion

Sustained and ongoing degradation of coral reef ecosystems, which is largely characterised by declines in overall abundance (cover) of hard corals, shifts in benthic composition, and declines in the structural complexity of reef habitats (e.g., Alvarez-Filip 2009; Graham et al. 2014; Mellin et al. 2019), have marked effects on reef-associated species, such as reef fishes (Jones et al. 2004; Wilson et al. 2006; Pratchett et al. 2008a, 2011c). Such effects are most apparent based on declines in the overall and individual abundance of a broad range of different fish species that rely on corals for food and/ or shelter following punctuated and extensive incidences of coral mortality (e.g., Pratchett et al. 2011c). These results emphasise the importance of corals for the biodiversity and productivity of reef fish assemblages (Wilson et al. 2006; Bell et al. 2013; Brandl et al. 2020), though the specific benefits that reef-associated fishes derive from corals are often very complex and vary among species (e.g., Coker et al. 2019; Pratchett et al. 2015b). Moreover, the specific responses of fishes to declines in the abundance of corals, and the limited extent of coral-dominated reef habitats (e.g., Coker et al. 2019; Hing et al. 2018; Thompson et al. 2021 – Chapter 4), still warrant much greater research attention. The research presented in this thesis shows that fishes may exhibit a diversity of behavioural and physiological changes in response to varying coral cover, which in some cases may undermine individual survival and population viability, ultimately resulting in longer-term changes in the local abundance (Pratchett et al. 2018 - Chapter 2; Thompson et al. 2019 – Chapter 3). For some reef-associated fishes, however, behavioural changes may moderate population declines in the face of changing habitat conditions, potentially obscuring their susceptibility to further coral loss and reef degradation.

Declines in the abundance of reef fishes in the aftermath of major disturbances and extensive coral loss are variously ascribed to declines habitat availability or complexity (Munday 2004; Almany 2004; Graham et al. 2006), reduced prey availability (Pratchett et al. 2008, 2015b), constraints on settlement success (Bonin et al. 2009; Coker et al. 2012; Chivers et al. 2016; Blandford et al. 2023), and/ or increased predator-induced mortality (Coker et al. 2009). However, these processes often result in protracted declines in the local abundance of reef-associated fishes (Pratchett et al. 2008a) and are likely preceded by changes in individual behaviour and/ or fitness. For obligate coral-dwelling fishes, for example, changes in the distribution, size, health, and/ or abundance of coral habitats necessitate a redistribution of individuals among available coral hosts (Coker et al. 2013; Hing et al. 2018; Pratchett et al. 2020). In these instances, the individual survival and overall abundance of fish are strongly moderated by social constraints on access to increasingly limited habitats (Coker et al. 2012; Pratchett et al. 2020). The social organisation of surviving individuals will also impact on their

reproductive potential (Hing et al. 2018) and subsequent contribution to population replenishment and recovery. Such effects are particularly apparent among group forming species that occupy distinct coral hosts, and these systems have significant utility for assessing causes and consequences of changes in sociality with ongoing habitat degradation (Hing et al. 2018; Pratchett et al. 2020). However, reef degradation and coral loss will likely have equally important effects on the distribution, habitat-use and subsequent sociality of other coral reef fishes, especially those with an obligate reliance on corals (Brooker et al. 2013; Hobbs 2013; MacDonald et al. 2021; Thompson et al. 2021- Chapter 4).

For coral-feeding fishes, the local distribution and abundance of individuals is intimately linked to the distribution of suitable coral resources (e.g., Anderson et al. 1981; Bouchon-Navaro et al. 1985; Pratchett and Berumen 2008; Brooker et al. 2013b). It is inevitable, therefore, that varying coral cover, and especially the distribution, size and abundance of preferred prey corals, will affect the local distribution and abundance of these fishes (Kokita and Nakazono 2001; Pratchett et al. 2006b; Brooker et al. 2014). However, responses of coral-feeding fishes to changing availability of coral prey may be initially much more subtle. If sufficiently generalist in their diet, coral-feeding fishes may feed on alternate coral prey (Pratchett et al. 2004; Hobbs 2013; MacDonald et al. 2021; Semmler et al. 2022) to the extent permitted by availability of, and accessibility to, these alternate coral prey (Blowes et al. 2013; Keith et al. 2018). Critically, changes in the overall abundance, and distribution of potential coral prey, will directly affect both inter- and intra-specific interactions among coral-feeding fishes (Keith et al. 2018, 2023), which vary greatly in their territoriality and aggressiveness (e.g., Blowes et al. 2013, 2017). Even if coral-feeding fishes can access alternate coral prey, and thereby withstand declines in availability of otherwise preferred coral prey (at least initially), this may still impact on individual condition (Pratchett et al. 2004), which may compromise longer-term survival or fitness, and ultimately lead to declines in abundance (Pratchett et al. 2006). Such effects may also be compounded by disruptions to sociality and consequent reproductive potential (Thompson et al. 2019- Chapter 3).

5.1: Changes in the sociality of fishes with habitat degradation

The sociality of fishes has a significant influence on their individual fitness, and especially their reproductive potential (Whiteman and Côté 2004; Nowicki et al. 2018a), which will in turn influence resilience and recovery of fishes in the aftermath of major disturbances and habitat degradation. Moreover, sociality of reef-associated fishes is likely to be affected by the condition and status of coral reef habitats (e.g., Hing et al. 2018; Thompson et al. 2019- Chapter 3). However, few studies have investigated the link between habitat degradation and sociality, let alone the potential feedback between sociality and reproductive potential, which may further amplify longer-term declines in abundance of fishes following habitat degradation

and extensive corals loss. For obligate coral-feeding butterflyfishes, which are known to have low individual survivorship in the aftermath of extensive coral loss (Sano et al. 1987; Pratchett et al. 2008a), it is to be expected that there will be widespread disruptions to established bonds and group typology.

The majority of butterflyfishes are pair forming (Yabuta and Berumen 2014, Nowicki et al. 2018b), such that habitat perturbations and declines in abundance are expected to result in fewer pairs and more solitary (unpaired) individuals (e.g., Reese 1981). While butterflyfishes can rapidly establish bonds with new partners following the loss of previous partners (Nowicki et al. 2018b), declines in overall abundance are likely to greatly reduce opportunities for re-pairing following extensive coral loss. Despite the fundamental role of sociality in resilience and persistence of fishes, and intuitive effects of coral depletion on the incidence of pairing among butterflyfishes (Reese 1981), there has been surprisingly limited research to test for changes in pairing of butterflyfishes (Thompson et al. 2019 – Chapter 3), or sociality more generally (Thompson et al. 2021 – Chapter 4). Thompson et al. (2019 - Chapter 3), showed that there was a reduced incidence of pairing for *C. baronessa* at Lizard Island, in the northern GBR, following recurrent disturbances, extensive coral loss and overall declines in their abundance. However, such changes were not apparent for other coral-feeding butterflyfishes, including *C. lunulatus*, despite apparent declines in their local abundance (Thompson et al. 2019 – Chapter 3). Much more work is required therefore, to understand when and why, pairing might be undermined by environmental and/ or habitat changes.

While reduced incidence of pairing will directly constrain mating opportunities for monogamous species, fishes with increasingly complex sociality may be even more susceptible to habitat degradation and coral loss (e.g., Hing et al. 2018). *Chaetodon trifascialis*, for example, is among the most susceptible species of butterflyfish to habitat perturbations and coral loss (Pratchett et al. 2018 – Chapter 2), and has the most specialised diet of all butterflyfishes, but also exhibits atypical sociality. While the evidence for harem mating in the northern GBR was equivocal (Thompson et al. 2021 – Chapter 4), the arrangement of territories recorded for *C. trifascialis* may be linked to recent disturbances and associated coral loss (e.g., Madin et al. 2018). It is apparent for example, that territory size of *C. trifascialis* does not necessarily scale with abundance of their preferred corals (mainly tabular *Acropora*), rather limited size and abundance of these corals will result in increasing separation among territories. Extensive coral loss and corresponding shifts in the size and arrangement of feeding territories are likely therefore, to have a critical influence on social interactions, with consequences for reproduction and population replenishment. If increasingly dispersed prey resources constrain territorial overlap for *C. trifascialis* and thereby disrupt their otherwise haemic social organisation, this is will further exacerbate their susceptibility to reef degradation and coral loss.

5.2: Future directions

Butterflyfishes are often considered to be unique among coral reef fishes, given their strong association with coral reefs habitats, and explicit dependence on live corals (e.g., Harmelin-Vivien and Bouchon-Navaro 1983; Halford et al. 2004; Pratchett et al. 2006). However, there are a very broad range of fishes that rely on corals for food (Cole et al. 2008), habitat (Coker et al. 2012), or settlement (Jones et al. 2004) and are adversely affected by extensive coral depletion (Sano et al. 1987; Jones et al. 2004; Pratchett et al. 2011). As such, responses of butterflyfishes to habitat degradation and coral loss may provide important insights into broad-scale and long-term effects of coral loss and reef degradation on coral reef fishes (Pratchett et al. 2009, 2011). In particular, differential responses among coral-feeding butterflyfishes to habitat degradation and coral loss are revealing key attributes (e.g., dietary specialisation; Pratchett et al. 2008a) that influence vulnerability or resilience to disturbance. There is therefore, significant imperative to further resolve inter-specific differences in resource use and dependence among coral reef butterflyfishes, potentially making use of new technologies (e.g., DNA metabarcoding; Coker et al. 2022) that will complement *in situ* feeding observations to establish diet breadth and overlap. This research also provides a unique and important opportunity to test for intrinsic versus extrinsic determinants of dietary specialisation, which is relevant for understanding the evolution of dietary specialisation and its role in extinction risk (Lawton et al. 2011).

Climate change represents the foremost threat to the structure and function of coral reef ecosystems, causing changes in the composition and abundance of habitat-forming corals over very large geographic scales (Hughes et al. 2018). Such changes in habitat structure clearly affect the local abundance of many reef-associated fishes (Pratchett 2008a), though the underlying basis for these responses and potential threats to the persistence of species throughout their range remain poorly understood. Extensive research on the ecology of butterflyfishes has already contributed greatly to understanding broader effects of environmental and habitat change on coral reefs, and remain a promising study group for addressing remaining knowledge gaps. Most obviously, coral reef butterflyfishes exhibit considerable diversity in their social organisation (Berumen and Yabuta 2014; Nowicki et al. 2018b) and provide an ideal opportunity to test the extent to which long-term pairing and monogamous breeding may confer increased resilience to changing habitat conditions. There is also a specific need for focussed research in the biology of butterflyfishes that do not form pairs, to better understand the nature and vulnerability of their social systems.

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Appendices

Appendix A: other publications during candidature

- Scott ME, Tebbett SB, Whitman KL, **Thompson CA**, Mancini FB, Heupel MR, Pratchett MS (2022) Variation in abundance, diversity and composition of coral reef fishes with increasing depth at a submerged shoal in the northern Great Barrier Reef. *Reviews in Fish Biology and Fisheries*. 32:941-962. doi:10.1007/s11160-022-09716-9
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