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THE SHORT- & LONG-TERM IMPLICATIONS OF MARINE RESERVES FOR FISHERIES ON CORAL REEFS

Thesis submitted by
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STATEMENT OF THE CONTRIBUTION OF OTHERS

All research presented in this thesis was conducted under the supervision of Sean Connolly, Geoff Jones, and David Williamson. Contributions to each chapter can be found in Table I.

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Table I Statement of contribution to individual chapters

Chapter	*Statement of Contribution*
Chapter 1: *General introduction*	JH wrote the chapter with feedback from SC, GJ, and DW
Chapter 2: *Fishery consequences of marine reserves: short-term pain for longer-term gain*	JH and SC conceived the research, with feedback from GJ and DW; JH developed the models under the supervision of SC and with feedback from Mike Bode; DW, GJ, Hugo Harrison, and Colin Wen provided coral trout and habitat data; JH wrote the first draft of the manuscript and SC, GJ, and DW contributed to revisions
Chapter 3: *Synergistic effects of marine reserves and harvest controls on the abundance and catch dynamics of a coral reef fishery*	JH conceived the research, with feedback from SC, GJ, and DW; JH developed the model under the supervision of SC; the Australian Institute of Marine Science, and Queensland Fisheries provided coral trout and catch data; JH wrote the first draft of the manuscript and SC, GJ, and DW contributed to revisions
Chapter 4: *Marine reserves increase the stability of fisheries in environmentally disturbed metapopulations*	JH, SC, GJ and DW conceived the research; JH developed the models under the supervision of SC; DW and GJ provided the coral trout and habitat disturbance data; JH wrote the first draft of the manuscript and SC, GJ, and DW contributed to revisions
Chapter 5: *General discussion*	JH wrote the chapter with feedback from SC, GJ, and DW

* Initials are JH = Jessica Hopf, SC = Sean Connolly, GJ = Geoff Jones, DW = David Williamson

ABSTRACT

Reserves are a popular tool in managing marine systems, and have well-established conservation benefits. However, since they are nearly always established in areas accessed by fishers, their impacts on fisheries are contentious. Reserve-fishery theory suggests that reserve implementation will often be a sub-optimal fisheries management action, while the observed level of biomass build-up within reserves is argued sufficient to compensate for the loss of fishable habitat. In this thesis, I have furthered our understanding of the impact of marine reserves on fisheries by addressing key knowledge gaps that have previously hampered our ability to link outcomes predicted from fishery-reserve theory with changes observed after reserve establishment.

Firstly, I examined the transient impacts of reserve establishment on fisheries and fished metapopulations. I considered a well-mixed larval pool model and a spatially explicit model based on coral trout (an important fishery species; *Plectropomus* spp.) metapopulation in the Great Barrier Reef Marine Park (GBRMP), Australia. I also symbolically explored a simplified, pseudo-spatial, age-unstructured model to elucidate the demographic mechanisms behind my results. When fishing pressure was reallocated relative to the area protected, yields decreased initially, then recovered, and ultimately exceeded pre-reserve levels. However, recovery time was on the order of several years to decades. If fishing pressure intensified to maintain pre-reserve yields, reserves were sometimes unable to support the increased mortality and the metapopulation collapsed. This was more likely when reserves were small, or located peripherally within the metapopulation. Overall, I found that reserves can achieve positive conservation and fishery benefits, but direct effort controls complementary to reserve implementation is essential.

Secondly, I tested a metapopulation model against observed fishery and population data for the coral trout in the GBRMP to evaluate how the combined increase in reserve area and reduction in fishing effort in 2004 influenced changes in fish stocks and the commercial fishery. I found that declines in catch, increases in catch rates, and increases in biomass observed since 2004 were substantially attributable to the integration of direct effort controls with the rezoning, rather than the rezoning alone. The combined management approach was estimated to have been more productive for fish and fisheries than if the rezoning had occurred alone, and comparable to what would have been

obtained with effort controls alone. My sensitivity analyses also indicated that the direct effort controls prevented initial decreases in catch per unit effort that would have otherwise occurred with the rezoning. My findings demonstrate that, by concurrently restructuring the fishery, the conservation benefits of reserves were enhanced and the fishery cost of rezoning the reserve network was socialised, mitigating negative impacts on individual fishers.

Lastly, I evaluated the effects that reserves can have on fisheries subject to environmental disturbances. I found that they can be beneficial, reducing the magnitude of temporal fluctuations in yields and biomass, and extending the time to disturbance-driven collapse. This was true whether the fishery was heavily exploited and reserves increased average yields, or moderately exploited and reserves decreased average yields. Appling my model to a disturbed coral trout metapopulation across a small reserve network in the GBRMP, I find that protecting a mix of disturbed and non-disturbed reefs consistently provided stability for both fish populations and fishery catches, under a range of dispersal and reserve coverage scenarios. Furthermore, more centralised reserves were the most beneficial for reducing disturbance driven fluctuations in yields and biomass. This shows that, regardless of whether reserves increase or decrease time-averaged fishery yields, they can stabilize fisheries and fished populations, enhancing the sustainability and predictability of fishery dynamics, and ensuring the consistency of ecosystem functions provided by fished populations.

Research in this thesis provides theory that is directly relevant to currently established reserves and explicitly tests the efficacy of a major reserve network. My results show that minimising, or negating, the impacts of reserves on fisheries can be achieved by continuing to directly manage fisheries when reserves are established. This combined approach will also support the recovery of fish biomass, thereby preventing metapopulation (and fishery) collapse, reducing the return time on fishery benefits, and increasing the long-term productivity of the system. Even in cases where reserves reduce overall yields, they can provide stability to fisheries by reducing variations in catch due to natural disturbances.

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Chapter 1:

GENERAL INTRODUCTION

1.1 Marine Reserves and Fisheries

Marine reserves, throughout this thesis referring to ‘no-take’ areas that exclude direct exploitative or destructive activities (Sale et al. 2005), are used worldwide in the management of marine environments and their resources (Watson et al. 2014). By restricting the proportion of area open to destructive activities, reserves aim primarily to conserve: maintaining or restoring areas to their ‘natural states’ of biodiversity and increasing resilience at an ecosystem-wide scale (Agardy 1994; Sale et al. 2005). Reserves are also commonly established with the goal of promoting sustainable fishing (Russ 2002; Sale et al. 2005), and benefits of protection for fishery targeted species have been demonstrated globally. Reserve populations exhibit increased biomass, density, and reproductive output compared to their fished counterparts (Gell & Roberts 2003; Halpern 2003; Lester et al. 2009; Edgar et al. 2014), and show shifts in size-, age-, and sex-distributions towards those expected under unfished scenarios (Armsworth 2001; White et al. 2013). Furthermore, larval dispersal (Harrison et al. 2012; Almany et al. 2013) and adult movement (Grüss et al. 2011a) among populations provide pathways for these benefits to be exported from reserves to unprotected populations.

While marine reserves are proving successful in conserving the biomass of targeted species within their boundaries, whether these benefits extend to fisheries (e.g. enhancing fishable biomass) is contentious. Since reserves are nearly always established in areas accessed by fishers, their implementation reduces the amount of accessible fishing ground (Russ 2002; Gell & Roberts 2003; Halpern & Warner 2003; Sale et al. 2005; De Freitas et al. 2013). This forces fishers to redistribute their effort into the areas that remain open (a phenomenon known as ‘fishery squeeze’), or else exit the fishery entirely (Halpern et al. 2004; Lédée et al. 2012; De Freitas et al. 2013). In order to benefit fishery yields, the reproductive output of reserves (including the survival of recruits) to fished populations needs to be large enough to more than compensate for the area lost (Sale et al. 2005). A number of empirical studies suggest that the large biomass build-up observed within reserves, which can be up to 500% (Lester et al. 2009), is sufficient to achieve this (Halpern et al. 2004; Harrison et al. 2012). However, the redistribution of fishing effort associated with reserve establishment increases fish mortality outside the protected areas, and shifts the structure of these non-protected populations towards smaller, less fecund individuals (Adams et al. 2000; Berkeley et al. 2004; Williamson et al. 2004; White et al. 2013). This creates spatial heterogeneity in the demographics of the metapopulation (e.g. non-linear changes in density-dependent juvenile survival: White 2009, or egg fertilization success: Chan et al. 2012), which can potentially offset any benefits accrued within reserves (Russ 2002; Halpern et al. 2004). Consequently, there is debate as to whether, and under what conditions, establishing marine reserves will actually benefit fisheries, and if not, then how to best mitigate costs (Gaines et al. 2010b; Brown et al. 2014; Buxton et al. 2014). The overall aim of this thesis is, therefore, to understand the impact of marine reserves on fisheries (focusing on catch and sustainability) and the metapopulation dynamics of fished populations.

To date, elucidating how marine reserves alter metapopulation dynamics and impact fisheries has been hampered by a lack of congruence between fishery-reserve theory and observed reserve effects (Sale et al. 2005; Gaines et al. 2010a; White et al. 2011). Due to the large complex nature of marine reserve systems, the majority of fishery-reserve theory has come from modelling studies, which allow for a range of scenarios (e.g. varying reserve designs) to be explored, without the costs (time or money), risks, or confounding factors associated with manipulating a large number of real world systems in different ways (Starfield 1997; White et al. 2011). These studies have focused on reserves as a potential strategy in fisheries management, finding that they can prevent metapopulation collapse brought about by high fishing rates, or uncertainties in stock estimates. However, if a moderate to light fishing pressure is maintained, then the profitability of long-term sustainable yields are likely to be sub-optimal with reserves (Russ 2002; Gerber et al. 2003; Hilborn et al. 2006; Fogarty & Botsford 2007), although there are exceptions (e.g. in species with strong post-dispersal density-dependence; Gaylord et al. 2005; White & Kendall 2007; White 2009). In contrast, empirical data on reserve effects typically come from reserves that have been designed and implemented primarily with conservation (rather than fishery management) objectives in mind, often as part of an integrative approach alongside other non-spatial management interventions (McCook et al. 2009; Graham et al. 2011). Furthermore, these observed data typically capture changes in fishable biomass and fishery-yields in the short-term after reserves have been established (Russ 2002; Graham et al. 2011; White et al. 2011), rather than changes to fisheries at equilibrium (which is the focus of most modelling studies; Gerber et al. 2003; White et al. 2011). Consequently, our ability to compare predictions of reserve impacts from theory to observed changes in fishery yields or catch rates is limited. This is problematic because it hinders testing reserve theory (e.g. evaluating whether reserves are impacting fisheries as predicted) and restricts adaptive management (e.g. altering future management actions to minimise negative reserve effects) (Sale et al. 2006; White et al. 2011).

In this thesis, I consider three key knowledge gaps in linking fishery-reserve theory with observed fishery catch and target species biomass changes that follow establishment of reserves. Firstly, by focusing on long-term equilibrium yields, most modelling studies have overlooked the short-term impacts of reserves on fishery yields, catch rates, and metapopulation biomass (but see White et al. 2013; Brown et al. 2014). Such long-term studies provide little or no insight into the dynamics that occur during the transient phase, nor any indication of the time taken to reach equilibrium conditions. This makes comparisons to empirical data on reserve performance measures (e.g. target species biomass and fishery catches) difficult, as those data are often transient, capturing the first 20 years after reserve establishment at best (Edgar et al. 2014). Furthermore, the few studies that have considered transient effects of reserves indicate that those transient effects may differ qualitatively from reserves' long-term effects (Ezard et al. 2010; White et al. 2013), and without short-term modelling studies for reference, changes observed after reserve establishment may be incorrectly assessed as indicating a failure to meet objectives, when in reality they reflect the initial stages of a longer-term trend towards reserve benefits (or vice versa; White et al. 2011). Consequently, the first aim of this thesis is to investigate the expected short-term response of a fished metapopulation to the establishment of a marine reserve network.

Secondly, reserves are commonly established alongside other management actions (e.g. as part of an integrated approach to marine conservation; Gaines et al. 2010a; Graham et al. 2011), yet explicit evaluations of the interactive effects of reserves and other management interventions are lacking. Long-term theoretical studies have demonstrated the potential of concurrent non-spatial management actions (e.g. direct fishery controls; Stefansson & Rosenberg 2005) to support biomass recovery, and prevent fishery collapse due to redistributed effort, after reserve establishment (e.g. Hilborn et al. 2006). However, empirical studies commonly overlook these synergistic effects and attribute changes primarily to reserves (e.g. Fletcher et al. 2015). This potentially over- or under-estimates the impact of reserve establishment. Elucidating the relative contributions of multiple influencing factors in large, complex systems, such as reserve networks, can be achieved by comparing the observed changes to a range of modelled scenarios (Sale et al. 2005; White et al. 2011), yet fishery-reserve studies of this nature are lacking. Therefore, the second aim of this thesis is to evaluate (by testing empirical data against models) how combined fishery management changes and increased reserve area contributed to observed short-term changes in fish biomass and commercial fishery catches.

Lastly, most fishery-reserve models are deterministic, assuming that the system does not experience variability, natural or otherwise, in demographic rates (e.g. adult or larval survival). In nature, however, reserves are established in areas subject to stochastic environmental fluctuations, such as storms or temperature variation, which may affect demographic rates (Short & Wyllie-Echeverria 1996; Hoegh-Guldberg et al. 2007; De'ath et al. 2012). It has been claimed that reserves can enhance metapopulation sustainability and persistence by promoting areas with healthy and productive ecosystems (Lauck et al. 1998; Graham et al. 2011). Certainly, the net gain in biomass observed within reserves (Lester et al. 2009; Edgar et al. 2014) is consistent with this conjecture. However, evidence that the biomass gains within reserves also support fishery stability and persistence in the face of natural disturbances is scarce. The third aim of this thesis is, therefore, to evaluate the sustainability of reserves for fisheries that are subject to environmental disturbances.

1.2 Thesis outline

In this thesis, I couple modelling approaches with empirical data to better understand the impacts that reserves have had, and can expected to have, on fisheries. I focus on coral trout (*Plectropomus* spp.) in the Great Barrier Reef (GBR), Australia, as a case study throughout the thesis, and use well informed metapopulation models to address knowledge gaps that are highly relevant to policy makers, fisheries, monitoring programs, conservationists, and others interested in reserve-fisheries theory. My three data chapters are stand-alone studies that have either been published (Hopf et al. 2016a, b), or are in preparation for submission (Chapter 4). They explore 1) the short-term consequences of marine reserves for fisheries, 2) the synergistic effects of combining marine reserves with active reductions in fishing pressure (which reduces reallocated effort), and 3) the long-term implications of reserves for fisheries subject environmental disturbances.

Coral trout (here referring to *Plectropomus* spp.; sub-family Epinephelidae) are useful model species for investigating the impacts of reserves on fisheries and fish populations. Similar to other tropical, exploited reef species, coral trout are relatively long-lived with asymptotic growth, are protogynous hermaphrodites (changing sex from female to male), and have relatively sedentary reef-associated adult populations connected through dispersing larvae. They are a target of both recreational and commercial fisheries throughout the Indo-Pacific region, and have consistently formed 30-40% of the commercial line fishery catch in the North-East Coast of Australia over the last 25 years (DAFF 2015). In this thesis, I have chosen to focus on coral trout in the GBR Marine Park (GBRMP), Australia, where fishers' access to coral trout populations was notably restricted by a rezoning in 2004 (which increased reserve coverage from 4.6% to 33%; GBRMPA 2003). Importantly, this system is data-rich. Data on coral trout commercial catch and effort since 1990 are readily available from the Queensland Fisheries' online Logbook Program (QFish; http://qfish.fisheries.qld.gov.au/). There has also been considerable research into coral trout demography (Mapstone et al. 2004b), life-history characteristics (Ferreira & Russ 1994; Russ et al. 1998), adult movement (Davies 1996; Zeller 1997; Zeller & Russ 1998), reproductive biology (Rimmer et al. 1994; Samoilys 2002), juvenile habitat use (Wen et al. 2013), and larval dispersal (Harrison et al. 2012), in the GBR, which provide robust demographic and dispersal parameter estimates for metapopulation models. In Chapters 2 and 4, which have spatially explicit components, I have focused on the coral trout metapopulation in the Keppel Island Group, GBR. Data on larval connectivity (Harrison et al. 2012) and habitat usage by juveniles (Wen et al. 2013) has recently become available for this area, which allows realised dispersal patterns to be included in the models. Furthermore, the Keppel Island Group has a history of natural disturbances, primarily fresh water inundation and elevated sea temperatures (Williamson et al. 2014), and is therefore a useful systems for considering reserve effects in stochastic environments.

In **Chapter Two**, I investigate the short-term response of a fished metapopulation to the establishment of a marine reserve network. I consider a comprehensive stage-structured model with both well-mixed and distance-dependent larval dispersal, as well as simplified symbolic model, to demonstrate how yields can expect to change in the first decades after reserves are implemented. I find that yields can be expected to decrease initially, but, after several years to decades, will recover and ultimately exceed pre-reserve levels. This, however, is only true if fishing effort is reallocated relative to the amount of area protected. Importantly, my results show that the fishery is vulnerable to collapse (rather than recovery and growth) immediately after reserves are established if fishing pressure is intensified to maintain pre-reserve yields (especially if reserves are small), or if reserves are placed peripherally within the metapopulation. My findings in this chapter demonstrate that reserves can achieve positive benefits over time for both fisheries and conservation, but that fisheries management complementary to reserve implementation is essential to support the recovery of newly protected metapopulations. Furthermore, it shows how the direction of trends observed in short-term empirical data on reserves may not indicate whether fishery state variables will be higher or lower in the longer term.

In **Chapter Three**, I test a coral trout metapopulation model against observed coral trout fishery data from the GBRMP, to evaluate how combined fishery management changes (effort reductions) and increased reserve area contributed to changes in fish stocks, and commercial fishery catches and catch rates, observed over the past decade. This chapter builds on my findings in chapter two and demonstrates a real world scenario in which fisheries management has been combined with reserve establishment to the benefit of both fish and fisheries. I disentangle the mechanisms driving trends observed in the GBRMP coral trout fishery, and find that declines in catch, increases in catch rates, and increases in biomass were substantially attributable to the integration of direct effort controls with reserves, rather than due to the increased reserve coverage alone. Furthermore, my results estimate that the combined management approach was more productive for both fish and fisheries than if reserves had occurred in isolation, and comparable to only controlling fishing effort. These findings have significant implications for both conservation and fisheries as they clearly show that the holistic management approach taken in the GBRMP enhanced the conservation benefits of reserves and socialised the fishery costs, mitigating negative impacts on individual fishers

Finally, in **Chapter Four**, I evaluate the long-term implications of reserves for fisheries that are subject to environmental disturbances that cause episodic mortality. I find that marine reserves can stabilize fishery yields, regardless of whether they increase or decrease average yields, but that this stabilization is dependent on where the reserve is placed and the degree of connectivity among the metapopulation. Protecting both disturbed and non-disturbed reefs, such as is the case for coral trout in the Keppel Islands region of the GBRMP, will not always provide the greatest benefits, but I found it to be the approach that most consistently reduced fluctuations in yields and biomasses, in both heavily and lightly exploited fisheries, and when reserve coverage was both low and high. My results here demonstrate that reserves act as insurance for fisheries, enhancing the sustainability and predictability of fishery dynamics, and ensuring the consistency of ecosystem functions provided by fished populations.

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Chapter 2:

FISHERY CONSEQUENCES OF MARINE RESERVES: SHORT-TERM PAIN FOR LONGER-TERM GAIN [1]

2.1 Introduction

Marine reserves that exclude extractive or destructive practices have become a common strategy for the conservation of marine systems (Russ 2002; Lester et al. 2009). Protected populations typically show an increase in biomass, density, average organism size, and species richness compared to those outside reserves (Lester et al. 2009; Edgar et al. 2014). How reserves affect fishery yields, however, is a matter of considerable controversy (Hilborn et al. 2004; Jones et al. 2007; Grüss et al. 2011b; White et al. 2011). Populations within reserves are connected to their harvested counterparts, either via adult movement (Russ & Alcala 2010; Grüss 2015) or larval dispersal (e.g. Harrison et al. 2012; Almany et al. 2013). This connectivity has been hypothesised to result in a net export of reserve benefits into the non-protected areas, subsidising fished populations (Roberts et al. 1991; Russ 2002; Sale et al. 2005). However, establishing reserves reduces the amount of available fishing ground, and fisheries typically redistribute their effort into the area remaining open ("fishery squeeze"; Halpern et al. 2004; De Freitas et al. 2013), increasing local fish mortality and potentially outweighing any recruitment benefits from reserves.

Theoretical assessments of how fish populations and fishery yields may be impacted by the establishment of reserves have often focused on long-term equilibrium consequences (Gerber et al. 2003; White et al. 2011). Such studies typically do not consider how quickly these conditions will be approached, or what kind of transient dynamics will occur before reaching equilibrium. However, any abrupt change in management, such as the establishment of marine reserves, is likely to perturb the system from its previous trajectory (Caswell 2001, 2007; Ezard et al. 2010). Before returning to

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a stable state, or achieving potential long-term benefits, the system will almost certainly experience transient dynamics with changes to both metapopulation size and structure (Ezard et al. 2010; White et al. 2013). This was demonstrated by White et al. (2013) who found that, following the removal of fishing pressure, initial fish densities within reserves may attenuate, amplify, or oscillate, depending on life-history traits, fishing pressure prior to reserve establishment, and the degree of larval input from external sources. These models, however, focus on local population dynamics within reserves. While transient dynamics are sometimes implicitly acknowledged in bioeconomic fisheries models (e.g. Holland & Brazee 1996; Sanchirico & Wilen 2001), the outcomes of these models still focus on the long-term equilibrium conditions of the system, which may take a long time to reach. The transient dynamics of entire metapopulations (including harvested and protected populations) in response to reserve establishment, and how these may impact fishery yields, remain relatively unexplored.

Understanding how metapopulations respond to reserve establishment in the short-term, and the associated yield implications, is also essential for monitoring and managing reserve networks. Empirical studies typically measure changes in biomass or population density after reserves are established (comparing inside-outside reserves or before-after implementation; White et al. 2011). Since few empirical studies have explicitly demonstrated a full recovery of biomass within reserves to near pre-harvest levels (but see Russ & Alcala 2010), these monitoring studies focus on systems undergoing transient dynamics. Without a greater theoretical understanding of transient dynamics, results from these empirical studies may be misleading. Changes in harvestable biomass observed immediately after reserve establishment may be due to transient dynamics, rather than reflecting longer-term outcomes. A greater understanding of the transient dynamics of metapopulations after reserve establishment would also benefit any process of adaptive management. Predicted outcomes are required to complement empirical data and drive adaptive changes, yet there is a paucity of metapopulation models that capture the short-term dynamics after reserve establishment (Gerber et al. 2005a; White et al. 2011).

Here, we investigate the short-term response of a fished metapopulation to the establishment of a marine reserve network. We focus on how expected yield biomass changes in the period following reserve implementation (transient dynamics), as well as the asymptotic growth rate (λ) as an indication of the direction of projected growth once transients subside (i.e. overall metapopulation increase or decline). Using coral trout (*Plectropomus* spp.) – an important fishery species throughout the Indo-Pacific – as a baseline life-history, we evaluate a well-mixed two-population model that considers two fishery scenarios; one where fishing effort remains constant following reserve establishment, but is redistributed into the area that remains open to fishing, and one where effort intensifies such that yield biomass remains constant. We then explore a simplified symbolic model to demonstrate that our results hold true under a broad range of conditions. Finally, we evaluate the effects of spatially-explicit dispersal in a heterogeneous environment, basing our metapopulation on the Keppel Island group in the southern section of the Great Barrier Reef Marine Park (GBRMP). Here, genetic studies have provided empirical estimates of larval dispersal (Harrison et al. 2012), enabling us to model reserve effects in a real geographic setting using a realised dispersal kernel.

2.2 Methods

2.2.1 Study species

Coral trout are large-bodied fishes that occur on coral reefs throughout the Indo-Pacific region. Like most other grouper species, they are heavily exploited by fisheries, and stocks have been depleted in many areas (Sadovy de Mitcheson et al. 2013). On the Great Barrier Reef (GBR), coral trout are the primary targets of commercial and recreational coral reef fisheries (Russ 1991). Coral trout share a number of life-history characteristics with a range of exploited reef fishes, making it a useful model genus for investigating the implications of reserves for reef fisheries. Coral trout are relatively long-lived with asymptotic growth, they are protogynous hermaphrodites (changing sex from female to male), and have relatively sedentary reef-associated adult populations connected through dispersing larvae (Harrison et al. 2012). There has been considerable research into coral trout demography (Mapstone et al. 2004b), life-history characteristics (Ferreira & Russ 1994; Russ et al. 1998), adult movement (Davies 1996; Zeller 1997; Zeller & Russ 1998), reproductive biology (Rimmer et al. 1994; Carter et al. 2014b), juvenile habitat use (Wen et al. 2013), and larval dispersal (Harrison et al. 2012) on the GBR. These studies provided robust demographic and dispersal parameter estimates for use in models.

2.2.2 Two-population model

For our baseline case, we used an age-structured, two population model, with the simplifying assumption that all larvae enter a common pool and are redistributed according to the proportional reef area occupied by each population. We assumed longevity of 14 years, age of first reproduction to be 2 years, an annual spawning/reproduction event, and that sex change occurred after the age of 5 years, in accordance with previous coral trout studies (Ferreira & Russ 1994; Ferreira 1995; Chan et al. 2012).

To model the effects of reserve implementation, we assumed that at the time of reserve establishment metapopulation abundances were at levels where density-dependent processes are negligible and that short-term metapopulation dynamics following the implementation of the reserve network are well approximated by a density-independent model (following White et al. 2013). We are confident that this assumption is reasonable for many fisheries, given that large predatory fish populations' biomasses are estimated to have been reduced to, on average, ~40% of pre-harvest levels (Juan-Jorda et al. 2011). Likewise, this assumption is applicable in the GBR where, prior to reserve implementation, coral trout biomass was depleted to ≤ 20% of the current densities observed within reserves (Williamson et al. 2004).

Metapopulation dynamics were described using a linear matrix model, following the vec-permutation matrix approach developed by Hunter & Caswell (2005). All parameter and variable descriptions can be found in Table 2.1. In its simplest form the model can be written

$$\mathbf{n}_{t+1} = \mathbf{M}\,\mathbf{n}_t,$$

where $\mathbf{M}$ is the metapopulation projection matrix and $\mathbf{n}_t$ is a vector of the fish abundance in the metapopulation at time t. Following Hunter & Caswell (2005), $\mathbf{M}$ is a function of both demographic and dispersal processes such that

$$\mathbf{M} = \mathbf{P}^{\mathrm{T}}\mathbb{D}\mathbf{P}\mathbb{B},$$

Table 2.1 Parameter and variable descriptions, values, and references (where applicable) used for the coral trout specific models. TP = Two-population model, KI = Keppel Islands spatially explicit model.

Symbol	Description	Value	Reference/Source
$\mathbf{n}_t$	Vector of abundances, at time t Sub elements $n_{i,a,t}$, where i, a, and t identifies the population, age, and time in years, respectively		
A_1	TP: Proportion of area occupied by population one (which becomes protected after establishment)	(0,1)	
A_R	KI: Proportional area of reef habitat within reserves (after establishment)	0.3281	Measured reef area in KI
y_f y_{fr}	Proportion of population caught per year before (f) and after (fr) reserve establishment	(0,1)	
$\mathbb{D}$	Dispersal block diagonal matrix. Diagonal sub-matrices $\mathbf{D}_a$, for age a		
H_y	Relative habitat parameter for destination reef y	(0,1)	Measured reef area in KI (Wen et al. 2013)
$\beta_{y,x}$	Probability of dispersing a given distance from reef x to destination reef y		See Appendix B
$\mathbb{B}$	Demography block diagonal matrix Diagonal sub-matrices $\mathbf{B}_i$, for population i		
L_a	Length of an individual of age a $L_a = L_\infty(1 - e^{-k[a-a_0]})$, where L_∞ = average asymptotic maximum body size, k = growth rate parameter, and a_0 = hypothetical age at which length is zero	50cm 0.459 -0.083	(Haddon 2001) (Chan et al. 2012)
W_a	Weight (g) of a fish of age a $W_a = g\,(L_a)^h$, where g = shape parameter h = shape parameter	0.0079 3.1570	(Ferreira & Russ 1994)
f_a	Per-capita fecundity of a fish of age a (assuming a 100% fertilization rate) $f_a = v\,(L_a)^w$, where v = shape parameter w = shape parameter	4.7559 2.6399	(Samoilys 2002)
Ψ_t	Proportion of eggs fertilised at time t $\Psi_t = 1 - e^{-R\sum \Omega_a W_a n_{i,a,t}}$, where R = fertility parameter Ω_a = proportion of fish age a that are males	8 $\Omega_{5\text{-}6} = 0.4103$ $\Omega_{7\text{-}8} = 0.5103$ $\Omega_{9\text{-}12} = 0.6103$ $\Omega_{13\text{-}14} = 0.7103$	(Chan et al. 2012)
m	Rate of adult mortality due to natural causes	0.3383	(Chan et al. 2012)
m_f	Rate of adult mortality due to fishing (m_{fr} = reallocated fishing pressure rate)	TP: (0,2) KI: 0.2307	(Ferreira & Russ 1992)
S_1	Probability of a juvenile surviving their first year (includes larval dispersal and juveniles mortality once on the reef)	(0,1)	

where $\mathbb{D}$ is a block diagonal matrix describing dispersal and recruitment to the adult population, $\mathbb{B}$ is a block diagonal matrix describing demography, and $\mathbf{P}$ is the vec-permutation matrix. Here we have assumed a pre-breeding census and that adult demographic processes occur before dispersal and survival through the first year. The block diagonals on the matrices $\mathbb{B}$ and $\mathbb{D}$ are 14 x 14 and 2 x 2 projection matrices for the demography of population i ($\mathbf{B}_i$) and dispersal of age a ($\mathbf{D}_a$), respectively.

Following the well-mixed assumption the matrix $\mathbf{D}_1$ (dispersal of juveniles; where the sub-element $d_{ij}^{(1)}$ is the probability that a larvae from population j settles in patch i) for the two-population model was

$$\mathbf{D}_1 = \begin{bmatrix} A_1\, S_1 & A_1\, S_1 \\ (1 - A_1)\, S_1 & (1 - A_1)\, S_1 \end{bmatrix},$$

where S_1 is the per-capita survival of larvae in the pelagic through to settlement as juveniles at the end of the first year, and A_1 is the area occupied by population one (by definition $A_2 = 1\text{-}A_1$). Dispersal matrices for all other ages ($\mathbf{D}_{2\text{-}14}$) are 2 x 2 identity matrices that accounted for the assumption that all adults within a population remained within that population over time.

We used two separate demography projection matrices ($\mathbb{B}$) to model demographic processes; the first described metapopulation demographics prior to reserve implementation (with fishing in all populations), and the other after implementation (with fishing pressure only in open populations). With the exception of whether adults were subject to fishing mortality (harvested) or not (protected), all populations were assumed to have identical demographic rates. To account for changes in fecundity with age we modelled fecundity (f_a) as a power function of length at age a (L_a), following the von Bertalanffy growth curve:

$$f_a = (1 - \Omega_a)\, v\, (L_a)^w,$$

where Ω_a is the proportion of fish aged a that are male, v and w are the functional shape parameters. Length at age a is defined as

$$L_a = L_\infty\left(1 - e^{-k[a-a_0]}\right),$$

where L_∞ is the average asymptotic maximum body size, k is the growth rate parameter, and a_0 is the hypothetical age at which length is zero. Following previous modelling studies on exploited hermaphroditic fishes (Heppell et al. 2006; Chan et al. 2012), we assumed a fixed rate of sex change with age, and that fertilization success at time t (Ψ_t) was a function of the male biomass:

$$\Psi_t = 1 - e^{R \sum \Omega_a W_a n_{i,a,t}},$$

where R is the fertility parameter, and the weight of a fish aged a (W_a) is defined as

$$W_a = g\,(L_a)^h,$$

with the functional shape parameters, g and h. While little is known about the functional form of sperm limitation in coral trout in particular, the asymptotic function has been shown to effectively approximate fertilization success in other pair-spawning hermaphroditic reef fishes (Petersen & Warner 2006).

Prior to the implementation of reserves, we assumed that all populations were subject to equal fishing pressure and that only fish aged ≥ 3 years were vulnerable to capture. This takes into account current size limits for harvested coral trout on the GBR, and is representative of the common management strategy of allowing adult fish one reproductive year before entering the fishery (Mapstone et al. 2004b). Hence, the demographic projection matrix for all populations prior to reserve implementation (**B**) was

$$\mathbf{B} = \begin{bmatrix} 0 & f_1 & f_2 & \cdots & \cdots & f_{14} \\ e^{-m} & 0 & 0 & \cdots & \cdots & 0 \\ 0 & e^{-m} & 0 & \ddots & \ddots & \vdots \\ \vdots & \ddots & e^{-m-m_f} & \ddots & \ddots & \vdots \\ \vdots & \ddots & \ddots & \ddots & \ddots & \vdots \\ 0 & \cdots & \cdots & \cdots & e^{-m-m_f} & 0 \end{bmatrix},$$

where m is the natural mortality rate and m_f the mortality rate due to fishing.

Reserves were implemented by setting fishing mortality to zero for those populations assigned protection. We rescaled the fishing mortality rate (m_f) by the proportion of reef area remaining open to fishing such that the rate of mortality due to fishing after reserve implementation was $m_{fr} = \frac{m_f}{(1-A_R)}$, where A_R is the proportion of area assigned protection. This assumes that fisheries respond by redistributing fishing effort from areas established as reserves to areas that remain open to fishing (Halpern et al. 2004). This fishery squeeze has been observed for both commercial and recreation fishers in many contexts (e.g. Suuronen et al. 2010), including on the GBR (De Freitas et al. 2013).

We calculated yield biomass at any point after reserve implementation as the proportional change in biomass caught per year relative to the expected yield biomass if reserves were never established. The proportion of the population caught per year (pre-reserves: y_f) was derived from the rate of fishing pressure integrated over the entire year, resulting in

$$y_f = \frac{m_f}{(m+m_f)}\left[1 - e^{(-m-m_f)}\right].$$

For yields after reserve establishment, we substituted m_f with m_{fr} (which is a function of A_R) to calculate the proportion caught (y_{fr}). As an indication of the direction of projected growth once transient dynamics stabilised, we calculated the metapopulation asymptotic growth from the leading eigenvalue of the post-reserves projection matrix.

2.2.3 Analytic model

To better understand the demographic mechanisms behind our results, we also symbolically explored a simplified, age-unstructured model with well-mixed larvae and fishing effort reallocated inversely proportional to the area that remains open to fishing (fishery squeeze). We focused on establishing whether, under these conditions, reserves will always 1) decrease yields initially, and 2) increase the asymptotic metapopulation growth rate; outcomes that occurred consistently in our baseline model (See Appendix A).

2.2.4 Target-yield scenario

We also considered the situation where pre-reserve biomass yields were held constant and the rate of fishing pressure after reserve implementation was a function of time, changing in response to changes in the density of harvestable fish. We refer to this as the ‘Target-Yield’ model. This is a plausible scenario for systems in which livelihoods may require maintaining a certain yield biomass (e.g. subsistence fisheries). In some simulations for this model, the biomass available was below the target-yield, in which case we assumed 100% of the harvestable fish were caught. Since this is a non-linear model, we calculate the metapopulation growth rate at each time step for this model as the total metapopulation size that year divided by the metapopulation size the previous year.

2.2.5 Keppel Islands spatially explicit model

To explore how results change with realistic patterns of dispersal, reef sizes, and spacing, we expanded the baseline two-population model to a spatially-explicit metapopulation model, based on the Keppel Islands coral trout metapopulation. We discretised adult fish populations in the Keppel Islands into 19 separate populations which span different management zones and are representative of the major reefs in the area (See Appendix Figure B1). All demographic processes, and hence all demographic projection matrices, were unchanged from the baseline two-population model.

To model distance-dependent connectivity among the 19 populations, we developed a dispersal kernel using parentage analysis data collected for coral trout in the Keppel Islands (Harrison et al. 2012). A negative exponential dispersal location function with a shape parameter value of 12.4km (95% CI [7.7, 30.7]) was the best fit to the data (See Appendix B). This function was then used to calculate the probability of dispersing a given distance from reef x to reef y ($\beta_{y,x}$). We assumed a closed metapopulation in that all larvae were sourced only from within the Keppel Islands.

The availability of suitable settlement habitat is thought to be an important driver of variations in juvenile abundances among reefs (Wen et al. 2013). Here, we used the total amount of reef flat area (the primary settlement zone for coral trout in the Keppel Islands), normalised relative to the reef with the largest suitable settlement area, as a proxy for the relative survival of juveniles among reefs (H_y). Hence size differences among reefs in the Keppel Islands only directly influenced juvenile survival in our model, and not adult survival or fecundity.

Therefore, the matrix $\mathbf{D}_1$ (dispersal of juveniles) of the metapopulation projection matrix ($\mathbb{D}$) for the Keppel Island specific model became

$$\mathbf{D_1} = \begin{bmatrix} \beta_{1,1}\,\mathrm{H_1}\,\mathrm{S_1} & \cdots & \beta_{1,19}\,\mathrm{H_1}\,\mathrm{S_1} \\ \vdots & \ddots & \vdots \\ \beta_{19,1}\,\mathrm{H_{19}}\,\mathrm{S_1} & \cdots & \beta_{19,19}\,\mathrm{H_{19}}\,\mathrm{S_1} \end{bmatrix}.$$

Similar to the two-population model, dispersal matrices for all other ages ($\mathbf{D}_{2\text{-}14}$) were 19 x 19 identity matrices, assuming no adult movement among reefs. Yields were calculated following procedures in the two-population well-mixed model above.

2.2.6 Model analysis

We assumed that at the time of reserve establishment the metapopulation had been fished for a sufficient time such that it reached an asymptotic state, with a stable growth rate (λ_1) and stable age/population distribution, following White et al. (2013). In addition, we assumed that the fishery population was approximately constant (i.e. neither growing nor declining) before reserve establishment ($\lambda_1 = 1.0$). To obtain $\lambda_1 = 1.0$, we varied S_1 (survival through to age one) simultaneously with the rate of fishing pressure. We chose to vary S_1 as, to the best of our knowledge, there is no quantitative data for this parameter, and coupled this with fishing pressure to explore over a range of potential fishery scenarios. We then used the stable age/population distribution from the pre-reserve projection matrices as initial conditions for the models, and ran models for 500 years, more than sufficient time to complete transient dynamics.

For all models we considered a broad range of reserve sizes (proportional area of metapopulation assigned protection). To achieve this in the Keppel Islands spatially explicit model, we used a random subset (~1500 per coverage range) of all possible combinations of reefs protected that gave 8-12%, 18-22%, 28-32%, and 38-42% of the total reef-flat habitat area covered by reserves. Here we assumed that all reefs had the same ratio of reef-flat area to crest and slope, hence the proportion of reef-flat protected directly corresponded to the proportion of total reef area protected. For the two-population well-mixed models we also considered a range of initial fishing pressures spanning from ~5% to ~60% of the metapopulation removed in a given year.

2.2.7 Sensitivity analysis

To evaluate the robustness of our results to the assumptions made, we ran a number of sensitivity analyses. Firstly, we tested the key assumption that transient dynamics are well approximated by a density-independent model by considering cases where juvenile survival depended on the biomass of adults (e.g. cannibalism of young; Appendix D.1.a). Secondly, we tested the sensitivity of our results to the assumption of an initial stable metapopulation growth rate (λ_1=1). For the baseline model we ran the models with λ_I fixed at 0.95 (declining metapopulation) and 1.05 (increasing metapopulation) prior to reserve establishment, rather than 1.00. For our target-yield model we considered the scenarios where the population was growing or declining moderately (~3%) prior to reserve implementation (Appendix D.1.b). Since setting λ_I=1 implies that first year survival and fishing pressure covary across these scenarios, we also tested the sensitivity of our model to these parameters individually (Appendix D.1.b). Finally, we considered a non-sex-changing population to test the sensitivity of the results to sex change (Appendix D.1.c).

The spatially explicit model differed from the well-mixed model in two respects: a realised dispersal kernel and heterogeneity in the availability of juvenile habitat. To evaluate how habitat heterogeneity influenced the outcomes of the Keppel Islands model, we considered a scenario with homogenous reef size and habitat quality (i.e. $H_y = 1$; Appendix D.1.d). To test the sensitivity of the outcomes to the estimated kernel shape parameter value, we also ran the model with dispersal kernel shape parameter values at the upper and lower 95% confidence intervals of the parameter estimate. This provided an indication of results under varying degrees of local retention (Appendix D.1.e).

2.3 Results

2.3.1 Two-population well-mixed scenario

When dispersing larvae were well mixed, yield biomass always decreased immediately after reserve establishment. However, reserves consistently increased the asymptotic metapopulation growth rate, and yields always recovered to pre-reserve levels and continued increasing thereafter (**Error! Reference source not found.**). Time to recovery ranged from 5-10 years under high fishing intensity, to several decades under more lightly fished scenarios. Increasing the proportion of area protected increased yield biomass attenuation, time to yield recovery, and the asymptotic metapopulation growth rate (**Error! Reference source not found.**). Greater fishing pressures also produced larger yield attenuations and increased gains in the asymptotic metapopulation growth rate. Yet, due to the increased benefit of protecting heavily fished systems, the recovery time was shorter than with lower fishing pressures. These trends followed expected biomass changes in the population; fished populations experienced initial decreases in biomass followed by recovery, while biomass in reserves increased immediately after reserve establishment (Appendix Figure C1).

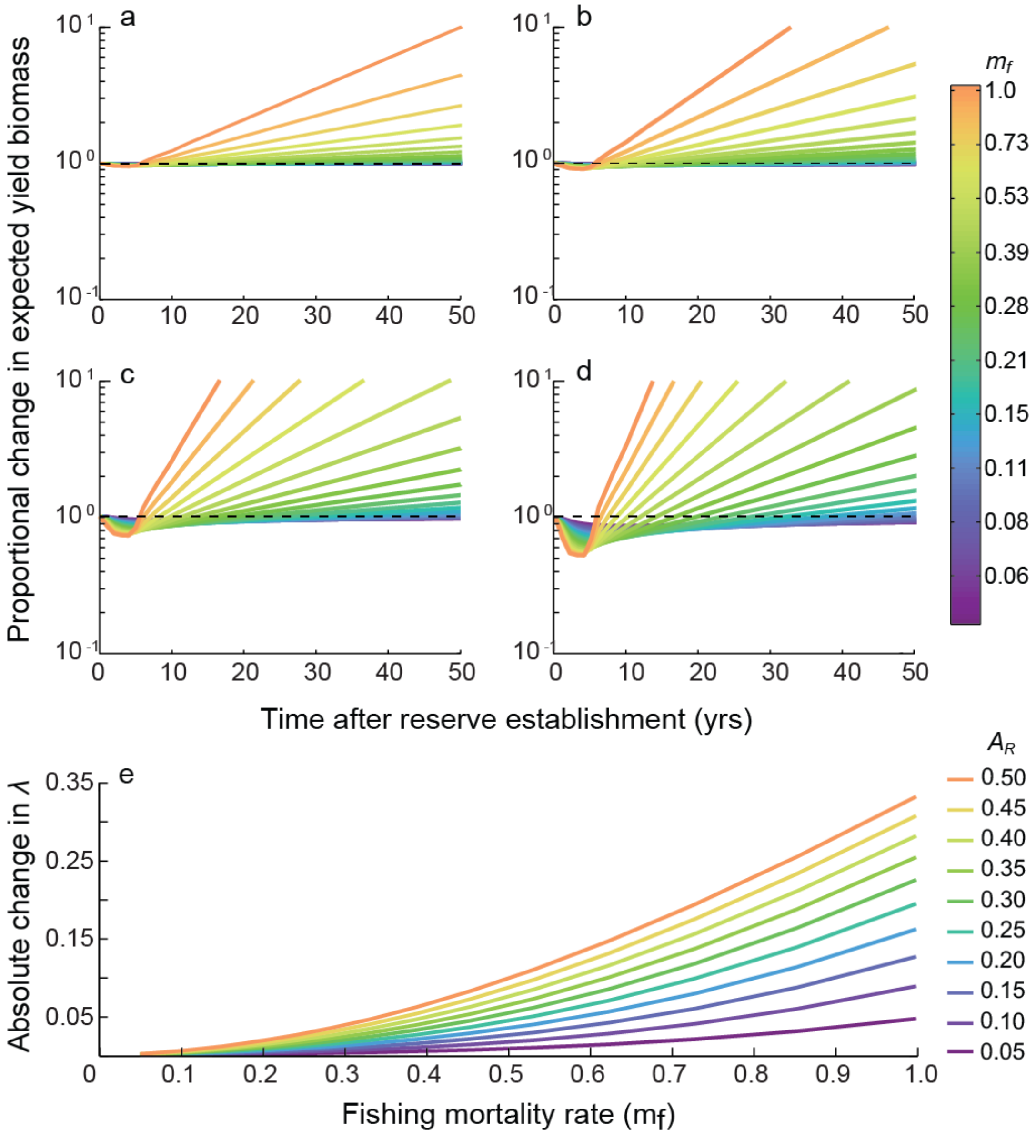

Figure 2.1 Short-term changes in yield biomass under a range of reserve sizes (5% [**a**], 10% [**b**], 30% [**c**], 50% [**d**]) and fishing pressures (m_f; colours), and (**e**) changes in asymptotic metapopulation growth rate (λ) as a function of fishing pressure (m_f) and different proportions of reserve coverage (A_R; colours), after reserve implementation. Larvae are well mixed among populations and fishing pressure post-reserves is reallocated proportional to the area that remains open to fishing.

2.3.2 Analytic model

Our symbolic analysis of a more simplified life-cycle demonstrated that yields always decreased initially and the asymptotic metapopulation growth rate always increased, independent of demographic parameter values (see Appendix A for proof). An important condition for this to be true, however, was that fishing effort remained constant following reserve establishment and was redistributed into the area that remained open to fishing. Under these conditions, there were fewer fish available to fishers immediately after reserve establishment, temporarily decreasing yield biomass. Average adult survival across the metapopulation, however, always increased with reserve establishment. This supported the recovery and growth of the metapopulation, leading to yield enhancements in the longer-term (Figure 2.1).

2.3.3 Target-yield scenario

When fishing effort was varied after reserve establishment to obtain a target-yield biomass, reserves were not always beneficial (Figure 2.2). In cases where target-yields were maintained after reserve establishment, the metapopulation had reduced asymptotic growth rates compared to those prior to reserve establishment. This was more likely to occur when reserves covered a small to intermediate proportion of the metapopulation (<50%) and when the metapopulation exhibited stable or declining growth prior to reserves (See Appendix D.2.b). The smaller the reserves however, the longer it took before yields could no longer be maintained and the metapopulation collapsed (Figure 2.2). Driven by the intensive increase in fishing pressure, a large initial reduction in reproductive productivity from harvested populations compromised population growth within small reserves and undermined their ability to support the metapopulation. Only when reserves were large (>50%) were reserve populations able to grow independent of larval supply from the harvested area and export enough larvae to support metapopulation growth, allowing yields to eventually recover to target levels.

2.3.4 Keppel Islands spatially explicit scenario

Including distance-decay in dispersal of larvae, and heterogeneity in habitat, among reefs increased variation in both the yield dynamics after reserve establishment, and the asymptotic metapopulation growth rate (Figure 2.3). In contrast to the well-mixed cases, there was an initial yield biomass increase in some simulations (certain reserve combinations), followed by yield decreases and slower recovery times. A subset of these

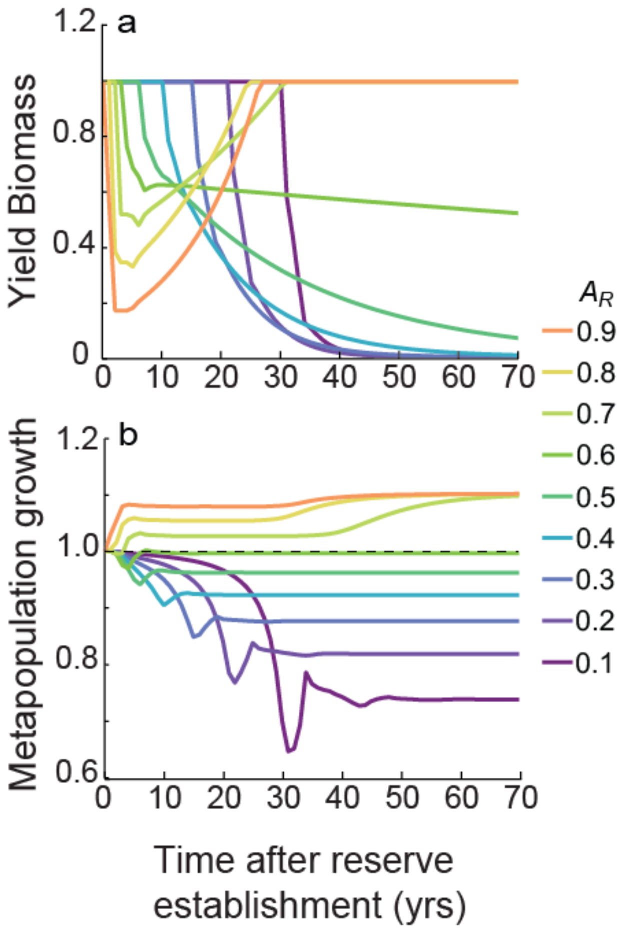

Figure 2.2 Short-term changes in (**a**) yield biomass, and (**b**) metapopulation growth after reserve implementation when fishing effort is varied overtime to maintain pre-reserve catch levels. Coloured lines indicate proportion of the area protected in reserves (A_R). Note; if available biomass was less that the target yield all individuals available were caught.

combinations generated reduced asymptotic metapopulation growth rates, with no yield recovery. Initial yield increases and reduced growth rates were more likely when the proportion of reef area protected was small (<12%) and when protected reefs were on average more peripheral to the rest of the metapopulation (Figure 2.4).

Due to the distance-decay in dispersal of larvae, more peripheral reefs had lower than average fishable biomasses prior to reserve establishment, compared to more central reefs (See Appendix Figure E1). When reserves encompassed these peripheral reefs, the proportion of biomass that was initially protected was less than the proportion of area protected. Since fishing effort was reallocated relative to reserve area, the increase in pressure was greater than the loss of biomass, and yields increased initially; i.e. the fishery was overcompensating for the true decrease in available biomass. This large initial removal in biomass combined with the reduced larval connectivity experienced by distant reserve reefs resulted in slow population recovery times (or a lack of recovery in some situations). We demonstrated that the overcompensation in the reallocation of fishing effort was the driving factor behind these results by considering the case where effort was reallocated relative to the proportion of biomass protected at the time of reserve implementation, rather than the area protected (See Appendix Figure E2).

Reserve combinations that included one large reef in particular (29% of the total reef area) had notable increases in their yield biomass attenuation and asymptotic metapopulation growth rate, relative to alternative combinations that protected the same amount of reef area (Figure 2.3). Increased local retention associated with distance-decay in dispersal meant that this reef initially supported a large proportion of the biomass relative to its area and, when protected, recovered more quickly than would have been the case if larvae were well-mixed. Hence the initial loss in yield biomass was greater, but asymptotic metapopulation growth rate was larger and the time until yield recovery and benefits was shorter.

2.3.5 Sensitivity analysis

Transient dynamics were well approximated by a density-independent model, especially when the metapopulation was moderately to heavily fished (e.g. fished to 20% virgin biomass before reserve establishment). If the assumption that the fishery was heavily fished when reserves were established is violated, then the longer-term yield recovery dynamics are overestimated by the density-independent model, relative to a density-dependent alternative (Appendix D.2.a). Our results were not qualitatively sensitive to first year survival rate or to the assumption that metapopulation growth was constant prior to reserve establishment (Appendix D.2.b), nor were they sensitive to whether the target species exhibited sex-change (Appendix D.2.c). For the target-yield model, our main findings - that intensifying fishing to maintain pre-reserve levels can cause metapopulation collapse - were more likely when the metapopulation was already in decline ($\lambda_1 < 1$), but were less likely when the metapopulation exhibited positive growth ($\lambda_1 > 1$; Appendix D.2.b). For the spatially explicit model, our sensitivity analysis demonstrated that the observed initial yield increases occurred regardless of whether individual reefs varied in size or were all of equal size (Appendix D.2.d). Furthermore, the effects of distance-decay in dispersal were exacerbated when self-recruitment to natal reefs (local retention) was increased (i.e. shorter mean dispersal distance), and reduced when the system became more well-mixed (i.e. longer mean dispersal distance; Appendix D.2.e).

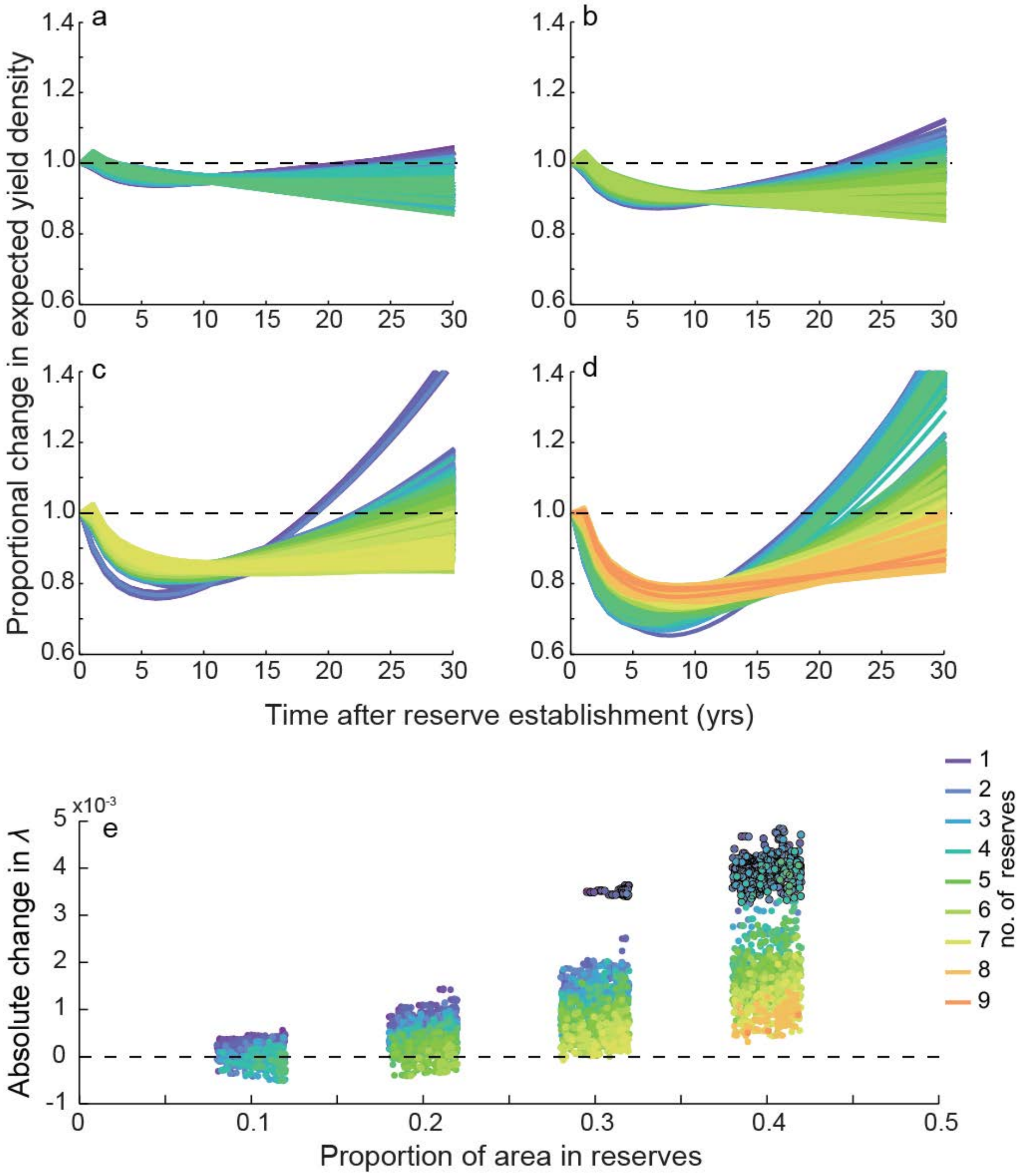

Figure 2.3 Short-term changes in yield biomass under a range of reserve sizes (8-12% [**a**], 18-22% [**b**], 28-32% [**a**], 38-42% [**d**]), and (**e**) changes in asymptotic metapopulation growth rate (λ), after reserve implementation for the Keppel Island spatially explicit model (distance-decay in larval dispersal and heterogeneous reef sizes). Individual points relate to different reserve combinations and only a random subset of all possible combinations is shown. Different colours indicate the number of reefs protected in a given combination (purple = 1 to orange = 9). Black edges indicate combinations that contain at least one disproportionally large reef in the reserve network.

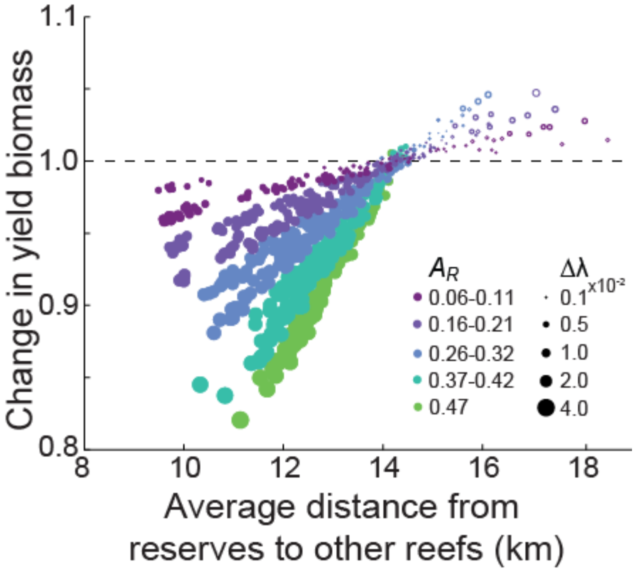

Figure 2.4 Proportional change in the first year yield compared to the average distance (km) of reserves to all other reefs in the metapopulation for a modified Keppel Island spatially explicit model, with homogenous reef sizes. Colours indicate the proportion of reef area protected in reserves (AR), and point size indicated the absolute change in asymptotic metapopulation growth with reserve establishment (Δλ). Open and filled points indicate a reduction and increase in asymptotic metapopulation growth rate with reserve establishment, respectively. Individual points are combinations of reefs and only a random subset of all possible combinations is shown.

2.4 Discussion

Our results show that, with realistic levels of larval dispersal, the establishment of marine reserves will generally result in initial reductions in fishery yields before compensation and yield recovery in the longer term. Previous studies have demonstrated that, given the magnitude of biomass increase expected within reserves, the export of larvae from reserves should be sufficient to compensate for the redistributed fishing pressure associated with reserve establishment, except in cases where larval dispersal distances are short (Halpern et al. 2010; Pelc et al. 2010). Our finding that yield recovery is possible is consistent with these studies; however, by focusing on the short-term transient dynamics, we demonstrate that fishery benefits may take decades to be realized as adult fish biomass accrues within reserves. Holland & Brazee (1996) recognised the potential costs associated with this lag, and considered optimal reserve designs that maximised cumulative profit over 60 years. They, however, assumed well-mixed larval dispersal and a constant fishing effort (subject to fishery squeeze after reserve establishment). We show that if these assumptions are violated, yield dynamics after reserve establishment become more sensitive to reserve design, and overfishing and metapopulation collapse may occur.

A key finding of our study is that during the initial period of biomass growth and recovery within reserves, the metapopulation may be vulnerable to collapse, especially if the population is overfished (negative population growth) or fished to the point where population growth is stable. This depends on both the response of fishers to the loss of harvestable area and the design of the reserve network. If fishers respond to the initial yield decreases by immediately increasing effort to maintain pre-reserve yields, then the increased fishing intensity outside reserves may compromise biomass accumulation within reserves (via reduced larval input from fished areas), resulting in metapopulation decline. This would be less of a concern if the metapopulation has limited larval mixing, as reserves will have higher levels of self-recruitment, and be less impacted by the increased adult mortality and reduced larval production in fished areas. Here, yield biomass would likely decrease faster, and take longer to recover, but metapopulation persistence would be more likely. Depending on the magnitude of increase in total effort, and the state of the fishery pre-reserves, it may take up to 50% area protected within reserves to avoid metapopulation collapse in well-mixed systems. This is a plausible concern for subsistence fisheries, where a lack of alternative livelihoods may force communities to maintain pre-reserve catch levels (akin to our ‘Target-yield’ model) and reserves are typically small so as to minimise impact on the fishery and to conform with community tenure arrangements (Agardy et al. 2011; Almany et al. 2013; Hamel et al. 2013).

Overfishing and metapopulation collapse is also a concern if fisheries overcompensate for the proportion of the biomass removed by fishing. In our models this occurred when the proportion of area protected was small (< 20%) and protection was given to reefs that supported lower than average pre-reserve biomass densities (due to their peripheral locations), but effort reallocation was redistributed relative to the area protected. This is a likely scenario for both recreational and commercial fisheries in systems such as the Great Barrier Reef Marine Park, where the distribution of fishers was relatively uniform across reefs prior to reserve implementation and spatial reallocation concentrated effort into the remaining area after reserves were established (Lédée et al.

2012; De Freitas et al. 2013). In cases where fishers focus their efforts in areas known to support higher fish biomass, protecting less productive reefs is less likely to result in overcompensation for biomass protected. These results highlight unexpected risks in protecting isolated or low-biomass reefs, complementing the argument that protecting de facto reserves (e.g. remote and/or inaccessible reefs) are unlikely to benefit metapopulation persistence (Gaines et al. 2010a).

Our results highlight the importance of fisheries management, complementary to reserve design, which acknowledges the short-term dynamics of reserve implementation. This is significant in two ways; 1) the monitoring of yields after reserves are established, and 2) management decisions that accompany reserve implementation. Similar to recent recommendations for monitoring biomass changes after reserve establishment (Moffitt et al. 2013; White et al. 2013), our results suggest that yield assessments should occur regularly and over long time periods after reserve implementation in order to avoid misjudging reserve efficacy. For example, in all of our simulations, yield trends in the first 5 - 10 years did not reflect those seen in the longer-term. Yield evaluations within the first decade following reserve establishment may suggest fishery yield losses when, in fact, insufficient time has passed for reserve benefits to manifest. Similarly, initial yield increases may actually reflect a system that is becoming overfished and likely to collapse in the future, as demonstrated in our spatially explicit model.

Given that short-term decreases in fishery yields are likely following reserve establishment, adopting additional fishery management strategies in conjunction with reserve implementation will help guard against population collapse as a result of effort squeeze. Fishers affected by reserves are often provided with compensation packages while they adjust to new management schemes, or buyouts if they exit the fishery entirely, and this process was adopted when the revised GBRMP zoning management plan was implemeneted in 2004 (FERM 2007; Sen 2010). These provisions, while intended as financial assistance to affected fisheries, also reduce the level of fishing pressure redistributed into the remaining harvestable areas. Our results demonstrate that this would support faster recovery of the metapopulation and decrease the time until yield benefits occur. Counter-intuitively, restructuring options for fisheries, such as licence buy-outs and compensation packages, are more important for metapopulation persistence when the proportion of area protected is small (< 50%), as this is when metapopulation collapse is more likely to occur.

Previous theoretical studies have primarily focused on comparing long-term sustainable yields under scenarios with reserves to those with more traditional fisheries management (i.e. direct actions that limit catch and effort; Gerber et al. 2003; White et al. 2011). The general consensus from these studies is that reserves will only benefit yields when the fishery is over-exploited. Here we have instead focused on short-term changes in yields and assessed how these transient dynamics are influenced by reserve design and changes in fishing effort. It is important to note that we made the assumption that the fishery was heavily exploited at the time reserves were established - as is the case for coral trout on the GBR and many other large predatory reef fishes (Juan-Jorda et al. 2011; Sadovy de Mitcheson et al. 2013) - and therefore well approximated by a density-independent model. In a less exploited fishery, our density-independent model still approximated the initial changes in yield biomass, but would likely overestimate yield recovery (see Appendix D.2.a).

Designing reserve networks within fishing grounds requires potential trade-offs between conservation and fishery objectives (Halpern & Warner 2003; Jones et al. 2007). As our results show, maintaining fishery objectives (e.g. target yield) and achieving conservation goals are not mutually exclusive, although they may occur on disparate temporal scales. More ambitious conservation goals (e.g. larger reserve coverage or protecting reefs that support higher fish biomass) are likely to have a greater initial impact on fishery yields, but will result in faster yield recoveries and reduce the probability of recruitment overfishing. As demonstrated in our spatially explicit model, single large reserves (compared to a number of smaller reserves) will also increase the magnitude of initial yield losses, but will support greater reserve growth and reduce the time period to yield recovery. Likewise, preventing fisheries from increasing effort beyond suitable reallocation levels will compromise yields and enhance conservation in the short-term, while reducing the time required for yield recovery. These are important considerations when designing, monitoring and managing marine reserve networks, and they are especially pertinent as marine reserve science moves towards effective linking of theoretical and empirical data to understand reserve effects and make informed adaptive management decisions.

Chapter 3:

SYNERGISTIC EFFECTS OF MARINE RESERVES AND HARVEST CONTROLS ON THE ABUNDANCE AND CATCH DYNAMICS OF A CORAL REEF FISHERY [2]

3.1 Introduction

Marine reserves are commonly established as part of an integrated approach to protect biodiversity and sustain fisheries (Graham et al. 2011; Watson et al. 2014). Hence, their establishment is often coupled with other management interventions (McCook et al. 2010; Graham et al. 2011) such as changes to the harvest strategies of local fisheries (e.g. active reductions in effort; McCook et al. 2010, or the exclusion of destructive fishing practices; Russ et al. 2004a; Graham et al. 2011). Whether reserves can enhance, or even maintain, sustainable yields is controversial (Gerber et al. 2003; Halpern et al. 2004; White et al. 2008; Harrison et al. 2012; Kerwath et al. 2013), and coincident management actions make the causal attribution of post-intervention changes in fisheries and fished populations difficult to resolve. Fishery-reserve theory suggests that non-spatial management actions can interact with reserves to significantly influence the expected fish biomass and fishery yields (Stefansson & Rosenberg 2005; Hilborn et al. 2006; Botsford et al. 2009b). Despite this recognition of the importance of other fishery management actions, empirical reserve studies have not estimated their contribution to stock and catch changes, and often assume such changes to be due primarily to the implementation of reserves (McClanahan & Mangi 2000; Graham et al. 2011; Emslie et al. 2015; Fletcher et al. 2015).

To address this knowledge gap, we quantitatively evaluated the relative impacts that concurrent reserve and non-reserve management changes had on observed post-intervention catch and population responses. Specifically, we examined the response of

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[2] This chapter is published as Hopf, J.K., Jones, G.P., Williamson, D.H. & Connolly, S.R. (2016). Synergistic effects of marine reserves and harvest controls on the abundance and catch dynamics of a coral reef fishery. *Curr. Biol.*, http://dx.doi.org/10.1016/j.cub.2016.04.022 The structure of the published manuscript has been modified for this thesis.

coral trout (*Plectropomus* spp.), the primary targets of the coral reef line fishery in Australia's Great Barrier Reef Marine Park (GBRMP), to a substantial increase in no-take reserve areas and coincident management actions to reduce fishing effort.

During the 2004 rezoning of the GBRMP, no-take reserve area was increased from 4.6% to 33% (Fernandes et al. 2005). To reduce the potential for fishery effort displacement to compromise the performance of the reserve network (GBRMPA 2003; FERM 2007), the Queensland Department of Agriculture and Fisheries (QDAF) implemented license buyouts, reduced the Total Allowable Catch of coral trout by ~30%, and introduced Individual Transfer Quotas (FERM 2007; Gunn et al. 2010), resulting in an approximate halving of the pre-rezoning effort (Mapstone et al. 2008; DAFF 2015). To understand the effects of these changes on catch, catch rates, and biomass of coral trout, we combined commercial fisheries catch data (DAFF 2015) and biomass monitoring data (Emslie et al. 2015) from the GBRMP with an age- and sex-structured two-patch metapopulation model (Chan et al. 2012; Chapter 2). Our model included 33% reserve coverage and a 50% reduction in effort (reflecting the 2004 GBRMP rezoning and direct fishery management changes; GBRMPA 2003; Mapstone et al. 2008; McCook et al. 2010), and was parameterised independently of the fisheries and monitoring data. We also ran the model under scenarios with reserves alone and with reduced effort alone, to evaluate how the GBR coral trout fishery and stocks would have performed under only spatial closures or direct effort management.

3.2 Methods

3.2.1 Catch, effort, and biomass data

We obtained the commercial catch (weight in tonnes) and effort (fishing days and active licences) data for coral trout from QFish (Queensland Fisheries' Information System) in March 2015 (DAFF 2015). QFish is an online repository for the catch and effort data (1990 to present) collected through the commercial fishers' logbooks program. We pooled catch and effort data by financial year for all fishing methods and across all regions for coral trout. Note that while we considered all fishing methods, the predominant fishing method for coral trout is line fishing (Emslie et al. 2015). We smoothed the post-2004 catch and effort data using a 3-year backwards moving average, and rescaled these data relative to 1996-2004 (pre rezoning and fishery restructure) average values. The limited available historical data suggests that from early 1980s to 1996 commercial fishing effort and catch on the offshore reefs steadily increased, coinciding with decreasing coral trout biomass (Leigh et al. 2014; Emslie et al. 2015). Effort substantially increased in the early 1990's with the rapid growth of the live fish export market (Welch et al. 2008), but stabilized after 1996, around the time Queensland Fisheries announced revisions of management of the coral trout fishery and aims to limit further expansion of the fishery (Mapstone et al. 2008; Leigh et al. 2014). Hence we used the 1996-2004 effort and catch data as our reference values prior to the rezoning and fisheries management changes.

We obtained coral trout biomass density estimates on the outer-reefs from long-term survey data, recently compiled by Emslie et al. (2015) for 1996 to 2012. Given that the majority of the GBR commercial reef fishery catch data is obtained from the outer-reefs (Leigh et al. 2014), we focused only on changes in populations in these areas. For biomass changes within reserves, we considered data only from reefs that were established as reserves in 2004, as opposed to reefs that had been protected since the 1980's (which totalled only 5% of the GBRMP area). The post-2004 biomass data was smoothed using a 3-year backwards moving average, and rescaled relative to pre-rezoning weighted average values. A backwards, rather than centred, moving average allowed smoothing without the influence of future biomass values, of which biomass in a given year is independent.

3.2.2 Metapopulation model

Our metapopulation model closely followed the two-population, stage-structured, well-mixed-larvae model used in Chapter 2, and was parameterised independently of the observed post-intervention biomass and catch data that were used to evaluate the model's performance. However, we included density-dependent juvenile survival (as a function of adult biomass) to regulate population growth and assess long-term outcomes. Adult biomass is known to affect juvenile survival in coral trout through cannibalism and pre-emption of territory space (St. John 1995; Samoilys 1997). We used the common Ricker stock-recruitment relationship to model first year survival in population *i* at time *t* ($s_{1,i,t}$):

$$s_{1,i,t} = -\mu_1 \, e^{-\mu_2 \sum_{a=2}^{14} A_i \, B_{i,a,t-1}}$$

where μ_1 is the density-independent survival of juveniles, μ_2 is the strength of density-dependence, A_i is the proportion of area in population i, $B_{i,a,\mathrm{t}-1}$ is the biomass of fish aged a in population i at the start of the year. As there are currently no empirical estimates for the density dependence parameters we used three covarying values of μ_1 and μ_2 that yielded unfished equilibrium biomass densities equal to historical levels of coral trout on the outer GBR reefs (Emslie et al. 2015). We considered weak, moderate, and strong combinations of these parameters that spanned a plausible range of parameter value sets. For detailed information on the life-history characteristics of coral trout, other demographic parameter estimates, and further justification of the density-dependent parameter range explored, see the Appendix G (including Table G.**2**).

To initialise the model, we assumed that the metapopulation was at equilibrium prior to the 2004 changes, and was fished, but not spatially protected. This is a reasonable assumption, given that biomass densities of harvested coral trout populations on the outer-reef were relatively stable in the decade before 2004 (Appendix Figure G1), and that only <5% of the GBR area was designated no-take. To quantify the baseline adult mortality due to fishing, we assumed that coral trout on the GBR had been depleted to ~20% virgin biomass before the management changes. We believe this to be a reasonable assumption given that biomass estimates within reserves in 2014 averaged ~7.5 kg.1000m^{-2}, while total biomass prior to 2004 averaged ~1.7 kg.1000m^{-2} (Figure 3 in Emslie et al. 2015). Note that using reserve values as indicators of virgin biomass likely underestimates the degree of exploitation of coral trout, since abundances were reduced by several major disturbances (Williamson et al. 2014), and poaching within reserves on the GBR (Davis et al. 2004) reduces densities within reserves compared to no-entry zones.

We considered three alternative management scenarios in the model: 1) 33% of the area was protected in reserves and effort was reduced by 50% (the real-word scenario), 2) 33% reserves and no effort reduction (rezoning without fishery restructuring), and 3) 50% effort reduction and no reserves (direct effort management only). We implemented 33% reserves by setting the fishing mortality rate (m_f) in the protected population to zero, and rescaling m_f in the harvested population to be inversely proportional to the area that remained open ($\frac{1}{1-0.33}$). This captured fishery squeeze, in which fishers respond to the zoning by redistributing effort from the now protected areas into the areas that remain open to fishing (Halpern et al. 2004). To implement effort reduction we halved the baseline fishing mortality rate, as per the effort data (DAFF 2015). In the scenario where both reserves and reduced effort were implemented, we first reduced the effort, then reallocated the decreased effort into the remaining open area. Simulations were run for 150 years, and the catch, CPUE, and population biomass densities at the each time step were scaled relative to the pre-2004 (initial) equilibrium values.

3.3 Results

Our combined model (33% reserve coverage and a 50% reduction in effort) successfully captured the increase in catch per unit effort (CPUE - impact on individual fishers; Figure 3.1a), the decrease in total catch (impact on fishery as a whole; Figure 3.1b), and the increase in overall population biomass density (impact on fish population as a whole; Figure 3.1c-e), observed in the decade since 2004. Our model closely tracks the empirical data up until 2009, at which point a series of environmental disturbances (cyclones, bleaching events, and flood plumes), which are not captured in our deterministic model, substantially reduced the abundance of coral trout on the GBR, and negatively affected commercial fisheries (Williamson et al. 2004; Tobin et al. 2010; Leigh et al. 2014; Emslie et al. 2015). Tropical cyclone (TC) Hamish (2009) and TC Yasi (2011), for example, resulted in significant declines in hard coral cover and fish densities (including coral trout), compared to unaffected reefs (GBRMPA 2011; Leigh et al. 2014; Emslie et al. 2015).

Neither of our single management scenarios modelled reflected the combined trends in observed CPUE, catch, and biomass data as effectively as the combined management scenario (Figure G1). Importantly, without the fishery restructure, sensitivity analysis indicates that individual fishers would have experienced decreased CPUE in the years following the 2004 re-zoning (green shading, Figure 3.2a), although the initial drop in catch as a whole would not have been as pronounced (green shading, Figure 3.2b). Biomass recovery after the rezoning would also have been markedly slower than observed, if not for the concurrent reduction in fishing effort (green shading, Figure 3.2c-e). In the absence of the rezoning, the direct effort reductions would have benefited fisheries slightly more than the combined approach (compare orange and purple shading,

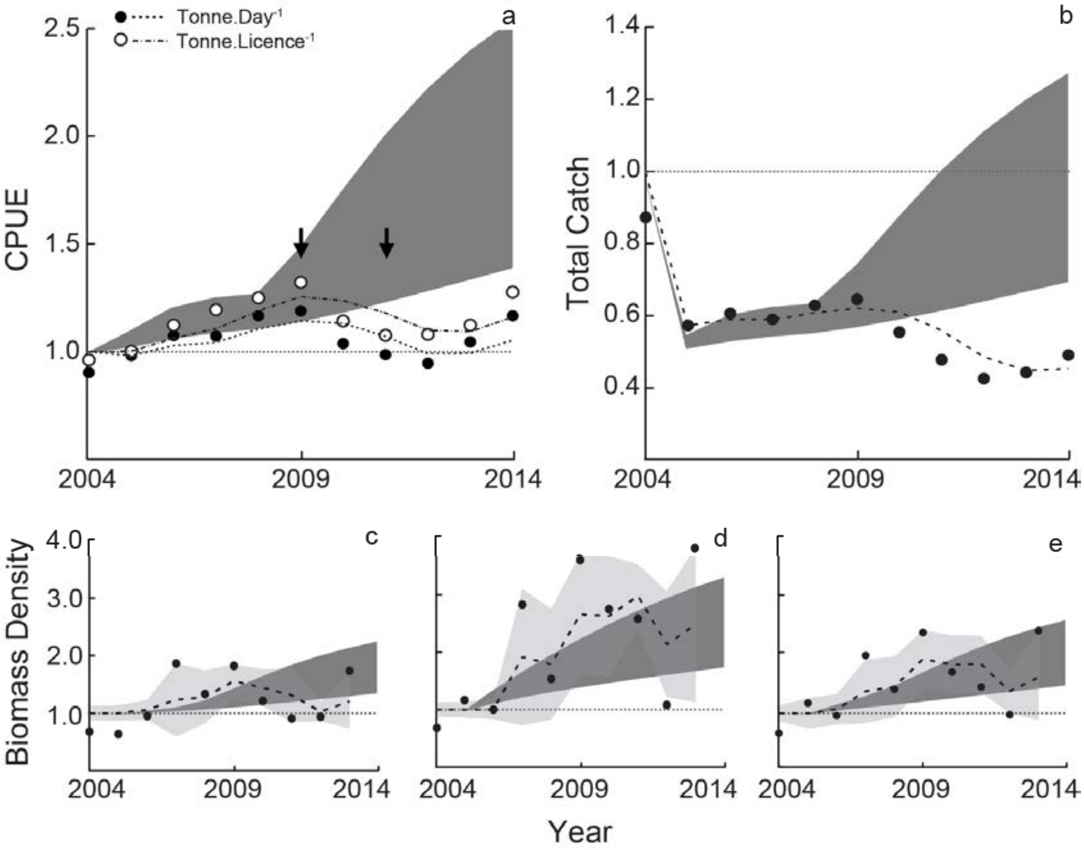

Figure 3.1 Observed (points and dashed lines) and modelled (dark-grey shading, which indicates the range of model outcomes for the density dependence strengths considered) changes in coral trout catch per unit effort (CPUE; tons per day and tons per license) (**a**), total catch (**b**), and biomass in fished areas (**c**), reserves (**d**), and the metapopulation (**e**) after the 2004 rezoning and fishery restructuring. Dashed lines are 3-year backward-moving averages, and light-grey shading captures the 95% confidence intervals on biomass estimates. Changes are relative to pre-2004 levels, and horizontal dotted lines indicate a pre-2004 business as-usual scenario. See also Figure G1.

Figure 3.2a-b); however, overall coral trout biomass would have recovered at a slower rate than with reserves (orange vs purple shading, Figure 3.2e).

All the scenarios that we considered resulted in long-term increases in CPUE, total catch, and biomass densities compared to a pre-2004 business-as-usual scenario (Figure 3.3). However, the combined management model projects a substantially more productive fishery and metapopulation in the long-term relative to pre-2004, indicating that the short-term observed decreases in overall catch are consistent with long-term catch benefits. Moreover, these long-term benefits are projected to be greater than could have been achieved with the rezoning alone: long-term catches and fish biomass are increased by

>20% in the former scenario relative to the latter (purple versus green shading; Figure **3.3**). The combined management approach was also slightly more beneficial for long-term metapopulation biomass than a strategy of reducing fishing effort alone (purple versus orange shading; Figure 3.3c-e). However, conversely, we project that the restructure alone (i.e., without reserves) would have produced the highest expected long-term catch rates and catches (orange shading; Figure 3.3a-b).

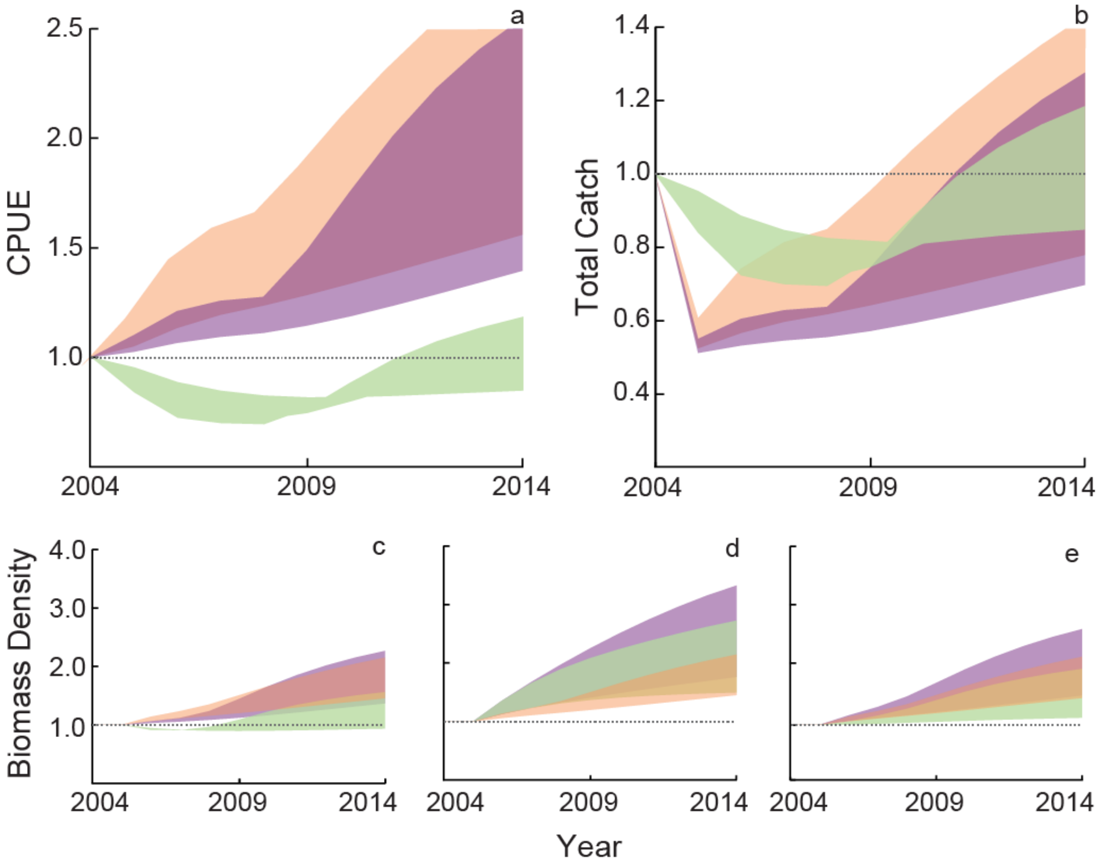

Figure 3.2 Changes, relative to pre-2004, in coral trout catch per unit effort (CPUE; tons per day and tons per license) (**a**), total catch (**b**), and biomass in fished areas (**c**), reserves (**d**), and the metapopulation (**e**) for different modelled management scenarios: reserves (33%) and reduced fishing effort (0.5) (purple), reserves only (green), and reduced effort only (orange). In all panels, shading indicates the range of model outcomes for the density dependence strengths considered. Horizontal dotted lines indicate a pre-2004 business-as-usual scenario. See also Figure G1.

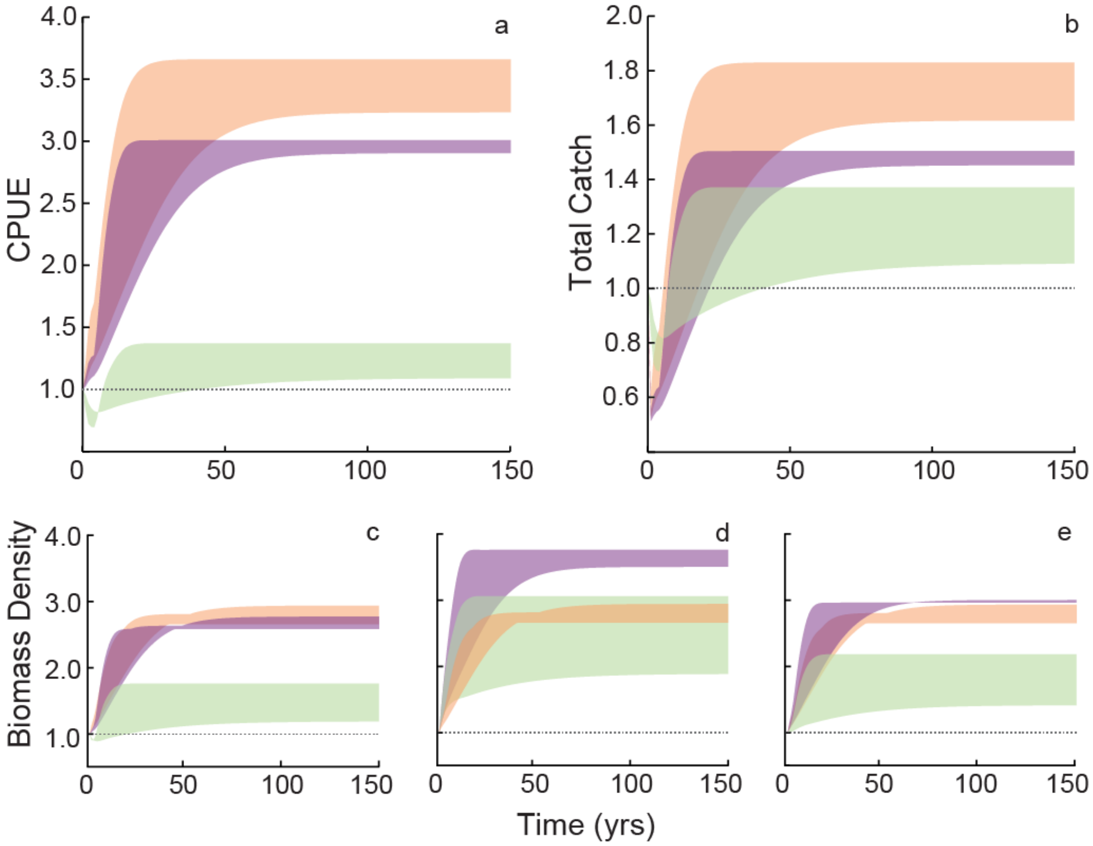

Figure 3.3 Predicted long-term changes, relative to pre-2004, in coral trout catch per unit effort (CPUE; tons per day and tons per license) (**a**), total catch (**b**), and biomass in fished areas (**c**), reserves (**d**), and the metapopulation (**e**) for different modeled management scenarios: reserves (33%) and reduced fishing effort (0.5) (purple), reserves only (green), and reduced effort only (orange). In all panels, shading indicates the range of model outcomes for the density dependence strengths considered. Dashed lines indicate a pre-2004 business-as-usual scenario.

3.4 Discussion

Since marine reserves are nearly always implemented in areas that support commercial, recreational, and/or subsistence fisheries (Allison et al. 2003; Fernandes et al. 2005; Graham et al. 2011), their establishment often creates conflict between fisheries and conservation management (Salomon et al. 2011). Modelling studies demonstrate that predicted long-term yields will typically, but not always, be less than those under classical fisheries management approaches (e.g. effort limits, catch limits; e.g. Hastings & Botsford 1999), if fishing pressure is near, or less than, that achieving maximum sustainable yield (MSY) (Gerber et al. 2003; Hart 2006; White 2009). If the fishery is overfished, however, reserves will tend to increase yields. Emerging theory also suggests that combining spatial and non-spatial management can help mitigate fishers' dissatisfaction with reserve establishment (Mapstone et al. 2008) and prevent collapse due to uncertainties in stock estimations or fishery-squeeze (Stefansson & Rosenberg 2005; Hilborn et al. 2006; Chapter 2). Although these studies are often parameterised using data from well documented fisheries (e.g. Stefansson & Rosenberg 2005; Hart 2006), the performance of such models is rarely explicitly compared with empirical data on post-intervention catch or population biomass dynamics (Gerber et al. 2003; White et al. 2011). Conversely, empirical studies comparing before/after or inside/outside reserves have documented both increased (Alcala et al. 2005; Kerwath et al. 2013) and decreased (Fletcher et al. 2015) yields in the years after reserves implementation. Such empirical studies have not separated the responses due to reserves versus those due to concurrent changes in direct fisheries management (Graham et al. 2011); rather, they have typically assumed that post-implementation changes were principally due to reserves (e.g., Apo Island, Phillippines; Russ et al. 2004a, the Great Barrier Reef [GBR]; Williamson et al. 2004, 2014; Emslie et al. 2015; Fletcher et al. 2015, and Mombasa Marine Park, Kenya; McClanahan & Mangi 2000).

By coupling a rigorously calibrated metapopulation model with empirical data, we were able to partition the effects of the management changes made in 2004, and show that coral trout stock and fishery changes in the GBRMP over the last decade are not solely, or even primarily, due to the rezoning. Rather, our sensitivity analysis indicates that the reduction in fishing effort reduced overall catches more than if the rezoning had occurred in isolation. By reducing the effects of "fishery squeeze", restructuring the fishery also supported a faster recovery of coral trout biomass, and prevented initial decreases in CPUE compared to a reserves-only scenario. Furthermore, the trends in the data were similar to those expected under the classical effort-control scenario typically favoured by opponents of the application of reserves in fishery management (Gerber et al. 2003; Hart 2006).

Our findings challenge a recent analysis suggesting that the GBRMPA rezoning was the primary driver behind the net loss in total catch of all species experienced since 2004, and that it was more detrimental to fisheries than initially suggested (Fletcher et al. 2015). Fletcher et al. (2015) compared within-GBRMP data to fishery data outside the GBRMP, but did not account for the substantial changes in fishing effort on the GBR (Hughes et al. 2016). Our results indicate that, without the direct effort controls, total catch losses due to the rezoning would have been much less than observed, but the cost of the rezoning would have been borne by individual fishers (via a short-term reduction in CPUE, which does not occur in either the empirical data or the combined model projections). Similarly, our results indicate that the role of rezoning in the recovery of top predators in reserves on the GBR is likely over-estimated in many ecological studies, which have tended to assume that reserves were the sole driver behind biomass changes (Williamson et al. 2004, 2014; Russ et al. 2008; McCook et al. 2009; Emslie et al. 2015).

A major finding from our study was that the active reduction of commercial fishing effort in the coral trout fishery shifted costs (the reduced overall catch) from individual fishers (whose CPUE increased) to the community (who bore the cost of the license buyouts that drove effort reduction), effectively socialising the impacts of the 2004-rezoning. Indeed, this was a primary aim of the GBRMPA's Structural Adjustment Package (GBRMPA 2003; FERM 2007; Gunn et al. 2010). Including fishing effort regulation alongside reserve establishment has been recommended in previous work, to increase fisher satisfaction and reduce the probability of overfishing (Stefansson & Rosenberg 2005; Hilborn et al. 2006; Mapstone et al. 2008; Botsford et al. 2009a; Chapter 2). In particular, prior to the rezoning, Mapstone et al. (2008) used a coral trout fishing simulation model to compare multiple effort-reserve regimes, recommending that reducing fishing effort with reserve establishment was most likely to satisfy all stakeholder identified targets. Our findings show that this combined management strategy reduced the impacts of spatial closures on transient CPUE responses and long-term sustainable yields, while maintaining conservation objectives (which often include non-fishery-related goals, such as to enhance ecosystem protection; Edgar et al. 2014; Watson et al. 2014; Emslie et al. 2015).

In the longer-term, the release of fishing pressure on the GBR coral trout metapopulation shifted the system away from overfished (~20% virgin biomass; Emslie et al. 2015), and brought the expected long-term yields closer to the MSY for the fishery. Since the system is no longer overfished, the combined scenario has a slightly lower equilibrium CPUE and total catch than with effort management alone. This lower equilibrium catch is consistent with many, but not all, theoretical studies of reserve impacts on fisheries (Gerber et al. 2003; Hart 2006; White 2009). From a fisheries perspective, effort control without spatial closures would have been the preferred management approach, since it produced higher long-term yields. However, effort controls alone have too often proven to be insufficient in maintaining sustainable stocks (Sale et al. 2005). A number of fishery modelling studies have shown how spatial closures, in conjunction with reductions in fishing effort (rather than as an alternative to), can enhance fishery efficacy and sustainability in the long-term (e.g. Stefansson & Rosenberg 2005; Hilborn et al. 2006). Our study explicitly demonstrates these benefits of combined management for a major commercial fishery.

Our findings have broader implications for the integration of reserve implementation and direct fishery controls on catch and effort. Reserves have been established alongside other management interventions in a number of other fisheries (Graham et al. 2011), including the Australian South East Fishery (FERM 2007), Indonesian's Apo Island subsistence fisheries (Russ et al. 2004a), and the Kenyan Mombasa Coral Reef Fishery (McClanahan & Mangi 2000), all of which are economically and ecologically important. In these and similar cases, it is likely that these interventions acted synergistically to influence the responses of the impacted fisheries and fished populations. It is important to note that where classical harvest strategies cannot be implemented or enforced, reserves alone can still deliver long-term conservation and fishery benefits in heavily exploited systems. Our study illustrates how to quantitatively evaluate the interactive effects of these interventions, and to effectively anticipate and plan for the impacts of reserve networks, in order to maximise the future benefits for both fish and fisheries.

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Chapter 4:

MARINE RESERVES INCREASE THE STABILITY OF FISHERIES IN ENVIRONMENTALLY DISTURBED METAPOPULATIONS

4.1 Introduction

Marine systems are subject to a variety of impacts ranging from direct anthropogenic pressures such as fishing and terrestrial run off, to natural disturbances including severe storms (cyclones/hurricanes) and dramatic fluctuations in temperature (Short & Wyllie-Echeverria 1996; Hoegh-Guldberg et al. 2007; De'ath et al. 2012). To mitigate against these impacts, marine reserves ('no-take' areas) have become a ubiquitous management tool (Russ 2002; Lester et al. 2009; Edgar et al. 2014), advocated for their potential to conserve biodiversity, rebuild fish stocks, and promote resilience to the increasing array of stresses on coastal marine ecosystems (Bohnsack 1996; Lauck et al. 1998; Sale et al. 2005; Graham et al. 2011). However, the implications of reserves for fisheries, and their ability to promote sustainable fishing in disturbed systems, are contentious issues (Gerber et al. 2002; Russ 2002; Hilborn et al. 2004; Sale et al. 2005; Fletcher et al. 2015; Hughes et al. 2016).

The biomass of targeted species typically increases after reserves are established (Lester et al. 2009; Russ & Alcala 2010; Edgar et al. 2014; Emslie et al. 2015), whereas most theoretical models predict that total catch will decrease, unless the fishery is heavily exploited (Russ 2002; Gerber et al. 2003; Hart 2006; Chapter 3). Despite these impacts on fishery yields, the net gain in biomass provided by reserves has been argued to provide insurance against overfishing, reduce the likelihood of disturbance driven fishery collapse, and promote long-term sustainability (Sale et al. 2005). Studies evaluating reserve-fishery interactions in a stochastic framework (such as in disturbed systems), however, are few (Gerber et al. 2003).

4.1.1 Environmental disturbance impacts

Environmental disturbances change the abundance and composition of fishes through directly impacting the growth and survival of fish (e.g. Wenger et al. 2012), or, more commonly, reducing the availability of suitable habitat (Jones & Syms 1998;

Fraterrigo & Rusak 2008). On coral reefs, for example, cyclones, elevated terrestrial run-off, and thermal bleaching reduce live coral cover (Osborne et al. 2011; De'ath et al. 2012). This removes an important source of food, habitat, and shelter for reef fishes, increasing their mortality (Jones & Syms 1998; Jones et al. 2004; Williamson et al. 2014; Emslie et al. 2015). As such, disturbances create temporal variations in fish abundance, with periods of population recovery following disturbance driven losses (Detenbeck et al. 1992; Jones & Syms 1998; Williamson et al. 2014; Emslie et al. 2015). If the intensity and frequency of disturbances is increased beyond certain thresholds, then the population can no longer fully recover between events and will eventually collapse (Thompson & Dolman 2010).

It has been hypothesised that marine reserves can buffer fished metapopulations against disturbance driven collapse by promoting areas with healthy and productive ecosystems, which can then export population subsidies to non-protected areas (Almany et al. 2009; Graham et al. 2011). For fished species, reserves increase average abundance, size, and therefore reproductive output, relative to populations that remain open to exploitation (Williamson et al. 2004; Russ & Alcala 2010; Micheli et al. 2012; Edgar et al. 2014). While reserves and fished areas typically exhibit similar damage to habitat (translating to similar initial losses in fish biomass) after severe disturbance events (Jones et al. 2004; Williamson et al. 2014), the increased reproductive capacity of exploited species within reserves is argued to shorten recovery times, thereby buffering populations against collapse due to episodic increases in mortality (Sale et al. 2005; Micheli et al. 2012).

In populations subject to disturbances that are fished, however, increased fishing pressure lengthens recovery times and increases variability in abundance (Beddington & May 1977; Hsieh et al. 2006). This has the capacity to undermine seemingly healthy stocks, as reduced stability may not yet be reflected by declining abundances (Hsieh et al. 2006). When reserves are established, fishing effort is reallocated into the non-protected areas (i.e., "fishery squeeze"; Halpern et al. 2004), and, as such, establishing reserves may further compromise the recovery and stability of non-protected populations. Consequently, whether the disturbance mitigation effect of reserves on protected sub-populations outweighs any compromising effects of fishery squeeze in the fished sub-populations is not intuitively obvious, either for fishery yields, or for population biomass.

4.1.2 Implications of reserve placement

Given that the effects of environmental disturbances in marine systems are rarely spatially uniform (Osborne et al. 2011), the placements of reserves is likely to affect their ability to safeguard against disturbance driven collapse (Maynard et al. 2015). The mechanisms of this are twofold. Firstly, it has been hypothesised that placing reserves in areas with relatively low exposure to disturbance will allow them to steadily build-up biomass and more effectively protect the ecosystem (Allison et al. 2003; Roberts et al. 2003; Maynard et al. 2015). However, under this approach fishing is concentrated into the more frequently disturbed populations, increasing their vulnerability to disturbance driven collapse (relative to a non-fished population; Hsieh et al. 2006). That the benefits of protecting relatively undisturbed populations outweigh the increased risks posed by fishing in disturbed areas has never been clearly demonstrated.

Secondly, reserve placement relative to the degree of connectivity (e.g. through larval dispersal) among populations is likely to influence the ability of reserves to provide insurance against disturbance driven collapse (Almany et al. 2009). For example, a distant (poorly connected) reserve is less likely to contribute to the recovery of a metapopulation than one that is highly-connected (Botsford et al. 2009a). Furthermore, increased spacing between reserves (or any population in a metapopulation) is likely to decrease the probability that multiple reserves are affected by a single disturbance event (risk-spreading). More distant reserves, however, have weaker connectivity, reducing the benefits provided by risk- spreading (Almany et al. 2009; Blowes & Connolly 2011). Yet, the consequences of these trade-offs between exposure and connectivity, for fisheries, and fished populations, are unclear.

4.1.3 Stochasticity in reserve-fishery theory

The few studies that have considered stochasticity in reserve-fishery interactions have focused on whether reserves can reduce the variability in catch that is inherent in fisheries (e.g. Lauck et al. 1998). Catch variability is often assumed to be driven by natural (and often large) fluctuations in recruits to the fishery (due to temporally varying larval and/or juvenile survival rates), and temporal variations in fishing pressure (i.e. episodic changes in adult mortality in the fished areas). Although some studies have concurrently considered stochasticity in other demographic rates such as fecundity and natural mortality (Mangel 2000; De Leo et al. 2015), most vary larval survival and/or mortality due to fishing at a temporal scale. In all cases, reserves have been shown to be an effective means of stabilizing catches and reducing the risk of fishery collapse (Lauck et al. 1998; Sladek-Nowlis & Roberts 1999; Mangel 2000; Pitchford et al. 2007; West et al. 2009; De Leo & Micheli 2015). These studies, however, are limited to two spatial ranges of stochasticity; 1) it is homogenous across all populations (i.e. episodic recruitment), or 2) it occurs only in fished populations (i.e. fluctuations in fishing effort) and is restricted into a smaller area when reserves are established. In contrast, natural disturbances are not spatially uniform; they can affect both reserve and fished areas, and they are unbounded by the establishment of reserves. We need to consider how these factors can influence the stabilising properties of reserves in the face of natural disturbance, so that we can further our understanding of the capacity of reserves to promote fishery stability and sustainability.

Here, I investigate the theoretical effects of marine reserves for fisheries in environmentally disturbed systems, and apply this to a coral reef fishery with a well-documented disturbance history. Specifically, I aim 1) to determine how marine reserves change the expected long-term impacts of environmental disturbances for fisheries and their targeted metapopulations, and 2) to understand the influence of reserve placement, in relation to larval connectivity and spatial heterogeneity in disturbances, on these reserve effects. Using coral trout (*Plectropomus* spp.) in the Keppel Island Group (southern Great Barrier Reef; GBR), as the case study, I first evaluate a two-population well-mixed-dispersal model that considers a range of disturbance regimes, including the case where increasing disturbance frequency and intensity causes the metapopulation to eventually go extinct. I then evaluate the impacts of reserve placement using a spatially-explicit dispersal model, based on reef arrangement and exposure to recorded disturbances in the Keppel Island Group.

4.2 Methods

4.2.1 Study species

Coral trout, here referring to *Plectropomus* spp., are target commercial and recreational species on coral reefs throughout the Indo-Pacific (Russ 1991; Sadovy de Mitcheson et al. 2013). They are closely associated with live coral, and changes in coral trout abundance often reflect changes in coral cover over space and time (Connell & Kingsford 1998; Kingsford 2008; Williamson et al. 2014). Coral trout share a number of life-history characteristics with other exploited reef fishes: they are relatively long-lived with asymptotic growth (Mapstone et al. 2004b), are protogynous hermaphrodites (changing sex from female to male; Samoilys 2002), and have relatively sedentary reef-associated adult populations connected through dispersing larvae (Davies 1996; Zeller & Russ 1998; Harrison et al. 2012), making them useful species for investigating the implications of reserves for fisheries. Furthermore, there has been considerable research into coral trout demography (Mapstone et al. 2004b), life-history characteristics (Ferreira & Russ 1994; Russ et al. 1998, 2004b), adult movement (Davies 1996; Zeller 1997; Zeller & Russ 1998), reproductive biology (Ferreira 1993; Rimmer et al. 1994; Carter et al. 2014a, b), habitat use (Kingsford 2008; Wen et al. 2013), and larval dispersal (Harrison et al. 2012) on the GBR, which provide robust demographic and dispersal parameter estimates for use in models.

4.2.2 Two-population model

For the baseline model I used a two-population, stage-structured matrix model that included well-mixed-larvae and density-dependent juvenile survival, following Chapter 3. I assumed a longevity of 14 years, age of first reproduction to be 2 years, sex-change dependent on mean age of the population, and a common larval pool from which larvae are proportionally redistributed according to reef area.

Larval production was a function of adult female fecundity at age a (f_a), and fertilisation success of adult males in population i at time t ($\Psi_{i,t}$) such that

$$f_a = v\,(L_a)^w$$

and

$$\Psi_{i,t} = 1 - e^{-R\,M_{i,t}}$$

where v, w, and R are shape parameters, L_a is the length of a fish age a, and $M_{i,t}$ is the proportion of the biomass in the population i that is male at time t. The probability that a female will change sex to a male ($\Omega_{i,a}$) at age a is a function of the mean age ($a_{m,i}$) of the local population i:

$$\Omega_{i,a} = (1 - e^{-q[a - a_{m,i} - a_o]})^{-1},$$

where q is the strength of the rate of sex-change, and a_o is an offset term, set so that unfished populations have a female to male ratio of 3 to 1 (following observed ratios on protected reefs; Ferreira 1995; Chan et al. 2012). To test the sensitivity of the results to the assumption of sex-change I also ran scenarios without sex-change, assuming a 1:1 female to male ratio in the metapopulation.

Given that juvenile survival in coral trout is influenced by adults through cannibalism and pre-emption of territory space (St. John 1995; Samoilys 1997) I assumed that density dependence occurs within the first year on the reef. Juvenile survival in population i at time t ($s_{1,i,t}$) was a function of the local adult biomass density at the start of the year, and followed the common Ricker stock-recruitment relationship:

$$s_{1,i,t} = -\mu_1 \, e^{-\mu_2 \sum_{a=2}^{14} B_{i,a,t-1}} ,$$

where $\sum_{a=2}^{14} B_{i,a,t-1}$ is the local adult biomass density, μ_1 is the density-independent survival of juveniles, and μ_2 is the strength of density-dependence. Currently, there are no empirical estimates for the density-dependent parameters, so I set μ_1 and μ_2 such that the average unfished equilibrium biomass was equal to a conservative estimate of total coral trout biomass densities in the absence of fishing on the GBR (Ayling & Choat 2008). See also Table 2.1 (Chapter 2), and Table G.**2** (Appendix G), for descriptions of parameters and parameter values.

In the absence of reserves, we assumed that all populations experienced the same fishing pressure and only fish aged ≥ 3 years were subject to fishing. This takes into account current size-limits for harvested coral trout on the GBR, and is representative of the common management strategy for a number of species of allowing adult fish one reproductive year before entering the fishery (Mapstone et al. 2004a).

I considered heavily fished and moderately fished scenarios, setting fishing pressures such that the metapopulation biomass without reserves was 20% and 50% of the virgin biomass, respectively. I consider these to be reasonable depletion levels given that the average biomasses of large predatory fishes are estimated to have been reduced to 40%, or less, their pre-harvest levels (Juan-Jorda et al. 2011), and biomass estimates of coral trout prior to the implementation of any reserves in the GBR were $\leq 20\%$ of the current densities observed within reserves (Williamson et al. 2004). In the models, reserves were implemented by setting the rate of mortality due to fishing in protected populations to zero, and rescaling fishing mortality in non-protected areas by the proportion of reef area remaining open to fishing. This assumes that fisheries respond to reserve establishment by concentrating their efforts into the remaining fishing ground ('fishery squeeze'), which has been observed in many recreational and commercial fisheries (Halpern et al. 2004; Suuronen et al. 2010; De Freitas et al. 2013).

We included the effects of environmental disturbance in adult mortality, assuming that adult natural survival decreased with a disturbance event. Initially we used a 50% reduction in adult natural survival, following the 50% decline in adult coral trout biomasses observed after disturbances in the Keppel Island group (Williamson et al. 2014), and explored a range of disturbance frequency regimes from no disturbances (deterministic model) to a 60% chance that a disturbance will occur in a given year (i.e. on average, one every 1.6 years). This encompassed plausible disturbance frequency regimes on the GBR given that freshwater inundation, for example, occurs at least once a year on inshore reefs (Maynard et al. 2015); although not all these events will result in large declines in live coral cover and reef habitat quality. To test whether the results were sensitive to disturbance intensities, I also considered the case where adult mortality increased up to 5 times the undisturbed rate (i.e. 20% of undisturbed survival rate) with disturbance. For this scenario I assumed that the chance of disturbance in a given year was 0.2 (roughly one ever 5 years). Whether a disturbance occurred in a given year was independent of prior disturbance history. Since increasing disturbance frequency and intensity lowers average long-term biomass, we varied the strength of density dependence (μ_2) so that virgin biomass densities were the same for all disturbance regimes considered.

I ran models for 2000 years, discarding the first 1000 years to remove any artefacts of the initial conditions. To evaluate the interactive effects of disturbances and reserves I calculated the mean and magnitude of fluctuations (expressed as coefficient of variation, a.k.a. the relative variance) in yield and metapopulation biomass experienced in the last 1000 years for 1000 iterations of each scenario.

4.2.3 Time to extinction

To evaluate whether reserves could increase the persistence of harvested species in disturbed systems, I considered scenarios where increased disturbance frequency and intensity cause the metapopulation to go extinct, when the metapopulation is heavily fished (~20% virgin biomass). For increased disturbance frequency I used a value for the strength of density dependence (μ_2) that allowed the metapopulation to persist under a 20% chance of disturbance, but ran the model with a 50% chance of disturbance (on average one every 2 years). For increased intensity I used a 20% change of disturbance, but increased mortality fivefold, relative to undisturbed natural mortality, with disturbance. I ran 1000 iterations for each scenario and calculated the time to fishery collapse (i.e. extinction) for both the heavily and moderately fished cases, under a range of reserve coverages.

4.2.4 Spatially explicit model

To determine the influence of reserve placement on yields and biomass changes in disturbed systems, I considered the scenario where only a portion of the metapopulation was subject to disturbances. I first focused on a scenario where larvae were well-mixed among the populations, and then expanded the baseline model to include distance dependent larval dispersal. For larval dispersal I used the coral trout dispersal kernel I developed in Chapter 2 (see Appendix B). To focus on disturbance effects, I assumed that all reefs are of equal sizes (c.f. Chapter 2, Appendix B).

I based the disturbance pattern on those seen in the Keppel Island Group, Southern Great Barrier Reef Marine Park, Australia. Here, live coral cover has fluctuated notably over the past decade and, on two occasions, decreased by ~30% in response to major disturbance events (coral bleaching in 2006, and freshwater flooding 2010/2011; Williamson et al. 2014). These disturbance-driven declines were independent of zonation (i.e. reserve or open), however, the furthest inshore, west (mainland)-oriented reefs were generally more heavily impacted by both bleaching and flood plume disturbances (David Williamson, unpublished data). Consequently, I set populations on west-oriented reefs as the disturbed areas, constituting half (10 out of 19 populations) of the metapopulation.

I used a disturbance regime with a 20% chance of disturbance in a given year, and a 50% reduction in adult survival with disturbance. Consistent with the previous section, I considered a heavily fished scenario, where the metapopulation had been fished to 20% virgin biomass prior to reserve establishment, and a moderately fished scenario at 50% virgin biomass without reserves. However, coral trout population estimates for reserve and non-reserve reefs in inshore areas of the GBRMP suggest that the heavily exploited case is the more likely scenario (Williamson et al. 2004, 2014). Since 2004, 6 out of 19

(~33%) reefs in the Keppel Island Group have been designated as no-take reserves. Similarly, across the entire GBRMP, approximately 33% of coral reefs have been protected within reserves since 2004 (McCook et al. 2010). However, I also evaluated alternate scenarios with low reserve coverage (~10%) and high reserve coverage (~50%). I considered three reserve scenarios that cover the range of possible reserve placements in relation to disturbance impacted areas; 1) half of the reserves were placed in disturbed and half on non-disturbed areas, 2) all reserves were placed in non-disturbed areas, and 3) all reserves were placed in disturbed areas. I evaluated up to 20 random combinations of reserve placements for each of these scenarios, and ran 100 iterations of each combination.

4.3 Results

4.3.1 Two-population well-mixed scenario

When disturbance is homogeneous across all populations, implementing reserves reduced the magnitude of fluctuations (as indicated by the coefficient of variation, hereafter CV) in long-term yields (black vs. coloured lines; Figure 4.1). This is true whether the fishery was heavily exploited (fished to 20% virgin-biomass prior to reserves) and reserves increased average yields (Figure 4.1a,b), or moderately exploited (fished to 50% virgin biomass) and reserves decreased average yields (Figure 4.1c,d). Reserve effects, however, were greatest under the higher fishing pressure scenario. Fluctuations in yields increased, and average long-term yields decreased, with increasing disturbance frequency (irrespective of reserve coverage). However, the stabilising effect of reserves was greater, and changes in time-averaged yields were smaller, under higher disturbance frequencies (Figure 4.1). Increasing disturbance intensity produced qualitatively identical trends (Appendix Figure H1), but fluctuations in yields increased exponentially with increasing intensity, rather than asymptoting, as with increasing frequency. Reserves also stabilized metapopulation biomass, reducing fluctuations both with increasing disturbance frequency and intensity (Appendix Figure H2 & H3). These qualitative results were not sensitive to the assumption that the species exhibited sex-change (Appendix Figure H4).

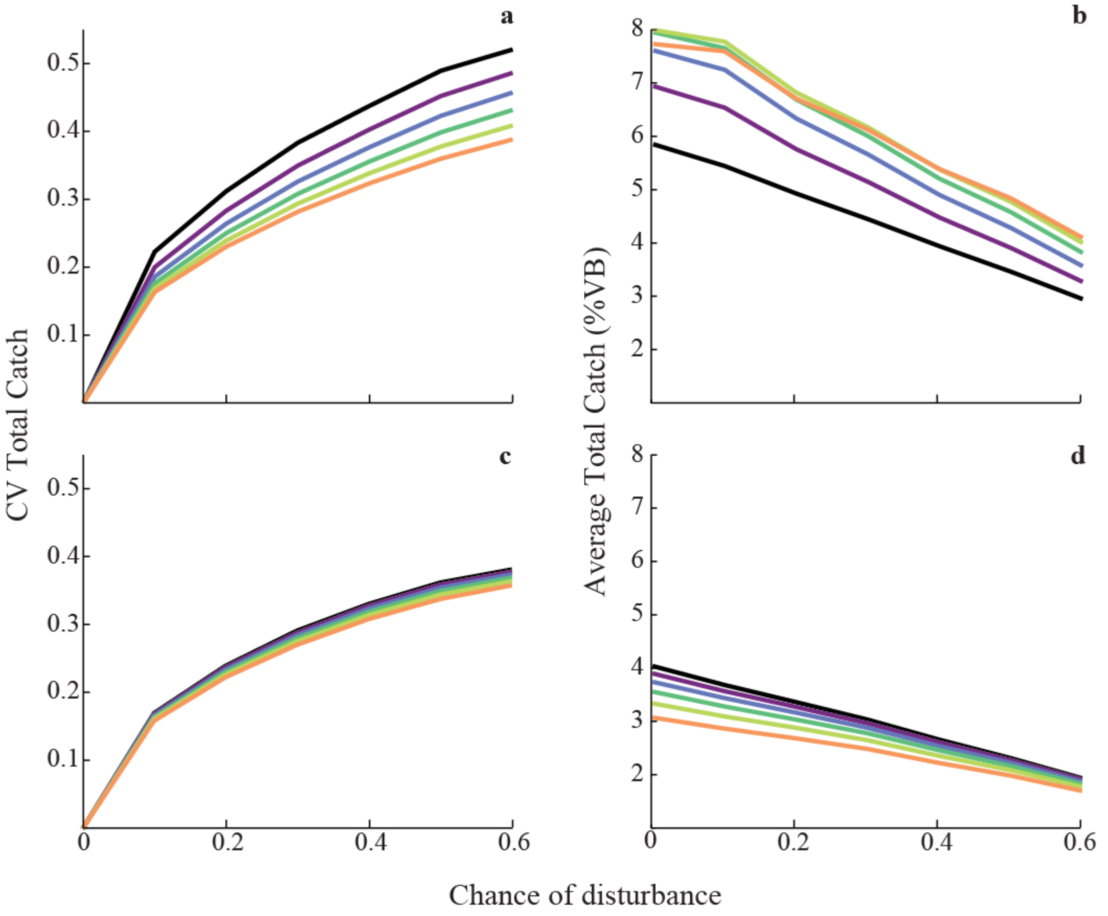


Figure 4.1 Change in the mean coefficient of variation (CV) and mean average (as a percentage of virgin biomass; %VB) of total catch with increasing disturbance frequency and varying reserve coverage, for a heavily fished system (20% virgin biomass without reserves; **a**, **b**), and moderately fished system (50% virgin biomass; **c**, **d**). Colours indicate reserve coverage from 0% (black) to 50% (orange) in increments of 10%. Means are of 1000 interactions, and total catch CV and average for each iteration are of the last 1000 years of the simulations.

When increased disturbance frequency and intensity caused metapopulation, and fishery, collapse, the time to extinction was notably lengthened with increasing reserve coverage (Figure 4.2a). This was also true when collapse was due to increasing disturbance intensity (Figure 4.2b).

4.3.2 Spatially explicit model

The ability of reserves to stabilise fisheries depended on where the reserves were placed, the level of fishing pressure, and the degree of larval connectivity among the metapopulation. When larvae were well mixed (square markers on left of panels in Figure 4.2), protecting only non-disturbed areas rarely reduced fluctuations in yields compared

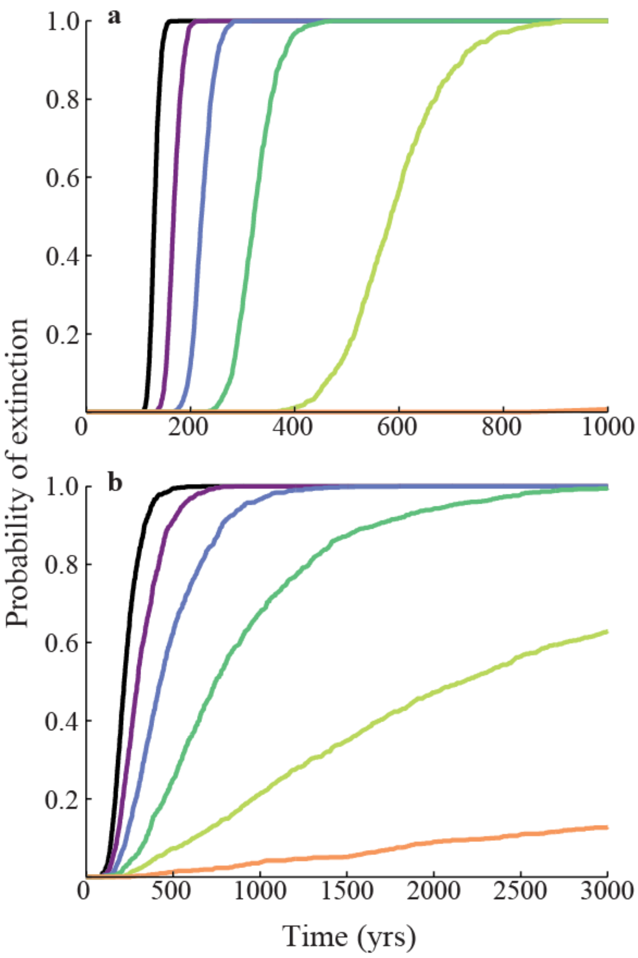


Figure 4.2 Probability of metapopulation extinction over time due to increased disturbance frequency (**a**), and increased disturbance intensity (**b**), with varying reserve coverage. Colours indicate reserve coverage from 0% (black) to 50% (orange) in increments of 10%.

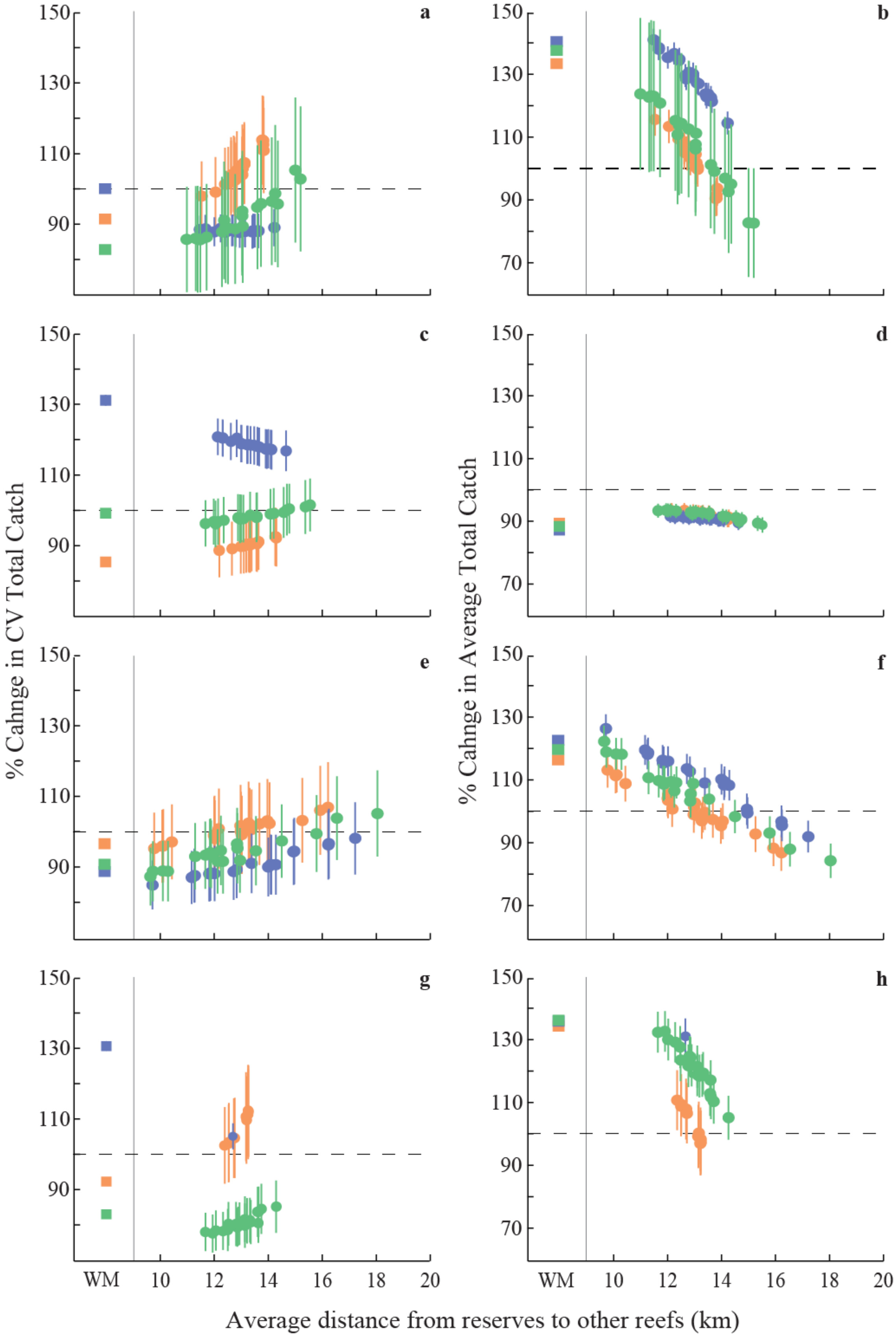
to a scenario without reserves (i.e., relative change in CV is <100% for blue square markers in Figure 4.2a,c,g). The exception was when reserve coverage was low (square markers Figure 4.2e). This approach however, typically produced time-averaged yield benefits that were equivalent or higher than the other reserve scenarios considered (square blue markers, Figure 4.2b,d,f,h). When larvae were well mixed, protecting only non-disturbed habitats also provided the largest reductions in metapopulation fluctuations (square blue markers, Figure 4.3a,c,e,g), and increases in time-averaged metapopulation biomass (square blue markers, Fig. 4b,d,f,h). In contrast, protecting only disturbed areas when larvae was well mixed always reduced fluctuations in yields (square orange markers, Figure 4.2a,c,e,g), but had minimal, or no, benefits to average yields (and gains to average metapopulation biomass; square orange markers, Figure 4.2 & 4.4 panels b,d,f,h), and increased fluctuations in metapopulation biomass (square orange markers, Figure 4.3a,c,e,g).

Protecting a combination of disturbed and non-disturbed populations typically reduced fluctuations in both yields (square green markers, Figure 4.2a,c,e,g) and metapopulation biomass (square green markers, Figure 4.3a,c,e,g) when larvae were well mixed. This was true for both heavily fished (square markers Figure 4.2a-b & Figure 4.3a-b), and lightly fished scenarios (square markers Figure 4.2c-d & Figure 4.3c-b), and when reserve coverage was low (square markers Figure 4.2e-f & Figure 4.3e-f) and high (square markers Figure 4.2g-h & Figure 4.3g-h). This combined disturbed-undisturbed protection approach also typically improved time-averaged yields (square markers Figure 4.2b,f,h), except when fishing pressure was moderate (square markers Figure 4.2d). The combined approach also improved time-averaged metapopulation biomass (square markers Figure 4.3b,d,f,h), compared to a non-reserve scenario.

Increasing the distance between reserves and other reefs (akin to decreasing larval dispersal distance) typically reduced stability in yields and biomass, and decreased time-averaged yield and biomass, irrespective of whether reserves protected disturbed or non-disturbed reefs, or a combination of both (round markers, Figure 4.2 & 4.4). Furthermore, when reserves were far from other reefs (~14 km or more), reserve establishment often decreased yields and biomass stability (relative CV > 100%), where they otherwise promoted stability when distances were short or larvae well-mixed (round markers, Figure 4.2a,c,e,g & Figure 4.3a,c,e,g). The exception to this is when reserves were placed only in non-disturbed reefs and fishing pressure is moderate; here catch is less destabilized than in a well-mixed scenario (compare round and square blue markers, Figure 4.2c).

→

Figure 4.3 Relative change in the coefficient of variation (CV; **a**, **c**, **e**, **g**) and average (**b**, **d**, **f**, **h**) total catch (both as percentage of the non-reserve scenario) in the Keppel Island Group, with increasing average distance from reserves to all other reefs in the metapopulation, for three reserve placement scenarios; 1) reserves only placed in disturbed reefs (orange), reserves placed only in non-disturbed reefs (blue), and reserves equally spaced between disturbed and non-disturbed reefs (green). Square symbols indicate a well-mixed (WM) larvae scenario. Reserve coverage is ~30% (**a** – **d**), ~10% (**e**, **f**), or ~50% (**g**, **h**), and fishing pressure is high (20% virgin biomass; **a**, **b**, **e** – **h**), or moderate (50% virgin biomass; **c**, **d**). Mean values (symbols) and standard deviations (lines) are of 100 interations, and total catch CV and average for each iteration are of the last 1000 years of the simulations. The horizontal dashed lines represents the no reserve (but still disturbed) scenario. For realtive CV, values above the dashed line indicate increases in temporal fluctuations, and below indicates decreases in fluctutations (increased stability), comapred to a no-reserve scenario. Note in panels **g** and **h**, there is only one possible combination of reserve placement when reserve coverage is high (50%) and reserves are placed only in non-disturbed reefs (blue). For a sumamry of results see Table 4.1 in the Discussion.


a
b
c
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e
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WM
10
12
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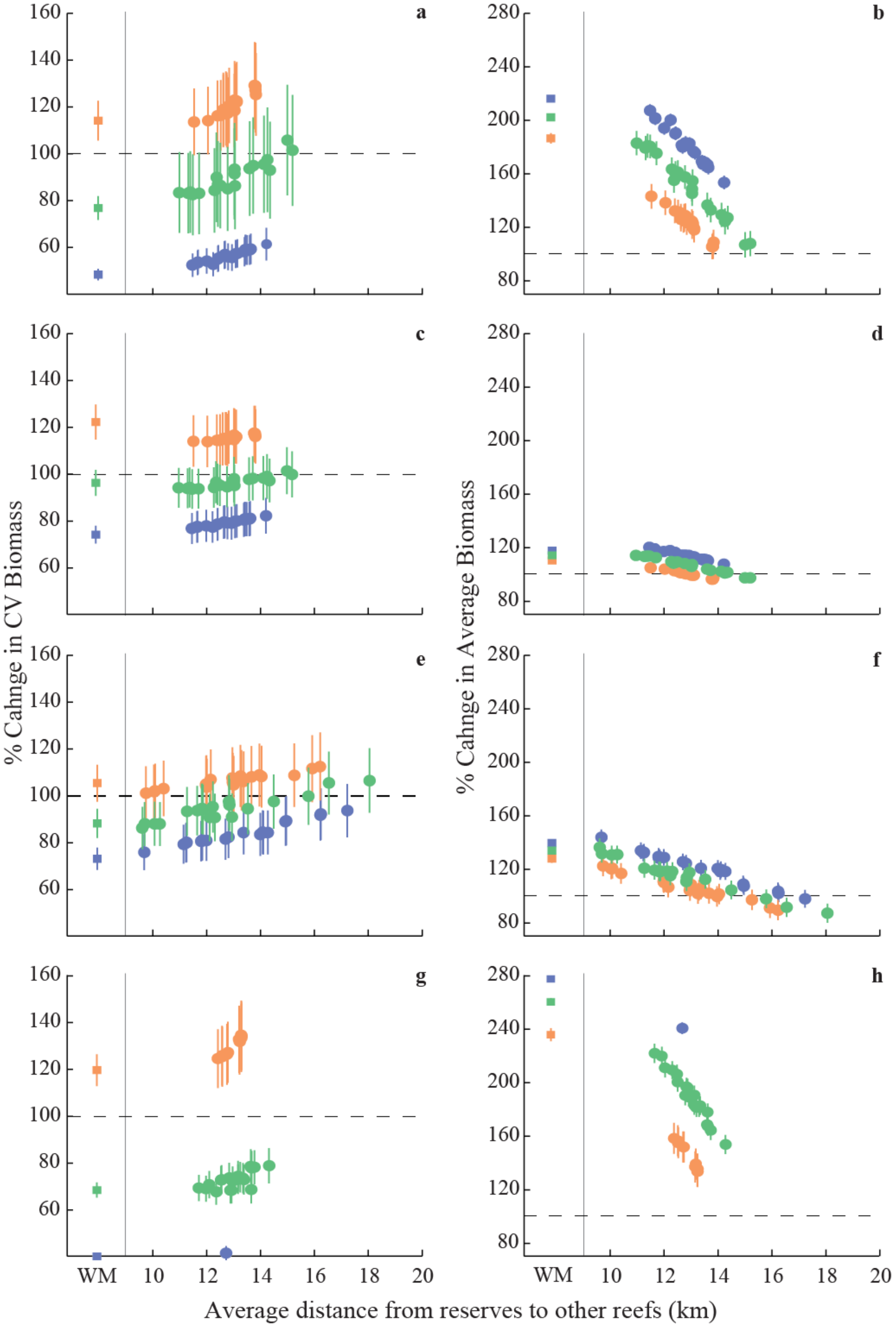
% Cahnge in CV Total Catch
% Cahnge in Average Total Catch
Average distance from reserves to other reefs (km)


a
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% Cahnge in CV Biomass
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160
140
120
100
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60
280
240
200
160
120
80
WM
10
12
14
16
18
20
Average distance from reserves to other reefs (km)

←

Figure 4.4 Relative change in the coefficient of variation (CV; **a**, **c**, **e**, **g**) and average (**b**, **d**, **f**, **h**) metapopulation biomass (both as percentage of the non-reserve scenario) in the Keppel Island Group, with increasing average distance from reserves to all other reefs in the metapopulation, for three reserve placement scenarios; 1) reserves only placed in disturbed reefs (orange), reserves placed only in non-disturbed reefs (blue), and reserves equally spaced between disturbed and non-disturbed reefs (green). Square symbols indicate a well-mixed (WM) larvae scenario. Reserve coverage is ~30% (**a** – **d**), ~10% (**e**, **f**), or ~50% (**g**, **h**), and fishing pressure is high (20% virgin biomass; **a**, **b, e** – **h**), or moderate (50% virgin biomass; **c**, **d**). Mean values (symbols) and standard deviations (lines) are of 100 interations, and biomass CV and average for each iteration are of the last 1000 years of the simulations. The horizontal dashed lines represents the no reserve (but still disturbed) scenario. For relative CV, values above the dashed line indicate increases in temporal fluctuations, and below indicates decreases in fluctutations (increased stability), comapred to a no-reserve scenario. Note in panels **g** and **h**, there is only one possible combination of reserve placement when reserve coverage is high (50%) and reserves are placed only in non-disturbed reefs (blue). For a sumamry of results see Table 4.2 in the Discussion.

4.4 Discussion

My results support the hypotheses that marine reserves provide the dual benefit of stabilising fishery yield and overall fish biomass, and can increase the persistence of metapopulations subject to environmental disturbances. By explicitly demonstrating that the stability provided by reserves is not outweighed by the increased fishing pressure outside reserves (due to fishery squeeze; Grüss et al. 2011b), I provide evidence for the common assertion that reserves act as insurance measures for fishery targeted species against disturbances (Bohnsack 1996; Sale et al. 2005). This reserve effect occurred when the fishery was heavily exploited and reserves increased average yields, and, to a lesser extent, when moderately exploited and reserves decreased average yields. I also show that, while focusing protection on areas less likely to be affected by disturbances is the most effective approach for promoting the stability and long-term persistence of metapopulation biomass (as often suggested to meet conservation objectives; Allison et al. 2003; Rodwell et al. 2003; Maynard et al. 2015), it can have mixed results for fisheries. Rather, achiving stability and supporting long-term persistance for both fish biomass and fisheries is more likely when protecting a mix of disturbed and non-disturbed areas.

A key finding from my study is that, by enhancing the sustainability and predictability (i.e. increased stability) of fishery dynamics, reserves provide an important, but often overlooked, service to fisheries. Reserves are typically viewed as beneficial to fisheries only in cases where high fishing pressures have reduced stocks to heavily-exploited levels, else they reduce long-term yields (Gerber et al. 2003; Sale et al. 2005; Hart 2006). I found that even in a moderately fished system, reserves can produce yields that are more consistently stable over time, and can prevent the collapse of the fishery due to increased disturbance frequency and intensity. This stability has economic benefits, because more consistent yields increase fishing efficiency, reduce costs, and provide economic sustainability (Lauck et al. 1998; Hsieh et al. 2006), all of which are potential trade-offs for any potential losses in average yields due to reserve establishment. These benefits have rarely been considered, because the performance of marine reserves is overwhelmingly modelled deterministically (Halpern & Warner 2003; Gerber et al. 2003; Sale et al. 2005), or measured empirically as changes to total yields, or catch per unit effort, averaged over space and/or time (e.g. Alcala et al. 2005; Fletcher et al. 2015).

As my results show, reserve placement, relative to a reef's exposure to environmental disturbances, is critical to the ability of reserves to stabilise fisheries (see columns in Table 4.1). I found that protecting a mix of disturbed and non-disturbed reefs consistently increased stability in both yields and fish biomass. Although not an explicit objective, such a coverage of a range of disturbance regimes was achieved through the Representative Areas Program (RAP) that resulted in the rezoning of the GBRMP in 2004 (Maynard et al. 2015), suggesting success in benefiting a range of stakeholders. From a conservation perspective, protecting areas at low risk of disturbance has always been assumed, or argued, to be the most beneficial for population persistence (Table 4.2; Allison et al. 2003; Roberts et al. 2003; Almany et al. 2009; Maynard et al. 2015), although Game et al. (2008) show that if most areas are consistently in a degraded state, then it is preferable to protect the high-risk areas. However, conservation-centric studies have typically assumed a 'scorched-earth' scenario, where all populations outside reserves are fished to the point that they no longer contribute to metapopulation dynamics, and as such ignore the impacts of, and impacts to, fisheries. My findings demonstrate that focusing protection solely on non-disturbed areas, while consistently the most beneficial for stabilising metapopulation biomass, had variable results for fisheries, and often resulted in increased fluctuations in yields, especially in well-mixed or moderately fished systems.

I also found that connectivity among metapopulations, the centrality of reserves, and the degree of reserve coverage, all play significant roles in the stabilising effect of reserves. This is especially true for fishery yields (see rows in Table 4.1). When larvae are well-mixed among the metapopulation, the variability in reproductive output created by disturbances are distributed evenly across all populations. Yet with distance-dependent dispersal, the disturbed natal reef may account for the majority of the variability in larval settlement (Harrison et al. 2012; Almany et al. 2013). I found that reserves in systems with relatively short larval dispersal distances (large distances between reserves) will tend to stabilise yields less (and in some cases destabilise yields), unless reserves are placed only in non-disturbed areas and reserve coverage is moderate to high (≥ 30%). If dispersal is less than well-mixed and reserves are placed only in non-disturbed areas then yields are, counterintuitively, more stable compared to a system with well-mixed (or long-dispersing) larvae.

Table 4.1 Summarised changes to the stability and long-term average value of fishery yields (relative to a non-reserve scenario) under a range of dispersal distances, reserve area, and fishing pressures when reserves protect a mix of environmentally disturbed and non-disturbed reef (mixed; see also green markers in Figure 4.2), protect only non-disturbed reefs (see also blue markers in Figure 4.2), or protect only disturbed reefs (see also orange markers in Figure 4.2). Bolded arrows indicate the best protection strategy (in terms of stability and changes in yields) for a given scenario.

			REEFS PROTECTED					
DISPERSAL DISTANCE	RESERVE COVERAGE	FISHING PRESSURE	Mixed		Non-disturbed only		Disturbed only	
			Stabl.	*Avg.*	*Stabl.*	*Avg.*	*Stabl.*	*Avg.*
Long (WM)	10%	High	↑↑	↑	**↑↑**	**↑**	↑	↑
	30%	High	**↑↑**	**↑↑**	↔	↑↑	↑	↑↑
	30%	Mod.	↔	↓	↓↓	↓	**↑**	**↓**
	50%	High	**↑↑**	**↑↑**	↓↓	↑↑	↑	↑↑
Short	10%	High	↓	↓	**↑**	**↓**	↓	↓
	30%	High	↓	↓	**↑**	**↑**	↓	↓
	30%	Mod.	↔	↓	↓	↓	**↑**	**↓**
	50%	High	**↑↑**	**↑**	↓	↑	↓	↔

Symbols indicates a ↓ ↓ = large decrease, ↓ = moderate decrease, ↓ = Small decrease, ↔ = no change, ↑ = small increase, ↑ = moderate increase, ↑↑ = large increase, and ↑↑↑ = very large increase. Mod. = Moderate, and WM = well mixed (comparable to long-dispersal distances)

Table 4.2 Summarised changes to the stability and long-term average value of total fish biomass (relative to a non-reserve scenario) under a range of dispersal distances, reserve area, and fishing pressures when reserves protect a mix of environmentally disturbed and non-disturbed reef (mixed; see also green markers in Figure 4.3), protect only non-disturbed reefs (see also blue markers in Figure 4.3), or protect only disturbed reefs (see also orange markers in Figure 4.3). Bolded arrows indicate the best protection strategy (in terms of stability and changes in biomass) for a given scenario.

Dispersal Distance	Reserve coverage	Fishing Pressure	Reefs protected					
			Mixed		Non-disturbed only		Disturbed only	
			Stabl.	*Avg.*	*Stabl.*	*Avg.*	*Stabl.*	*Avg.*
Long (WM)	10%	High	↑	↑	**↑↑**	**↑**	↓	↑
	30%	High	↑	↑↑	**↑↑**	**↑↑**	↓	↑↑
	30%	Mod.	↑	↑	**↑**	**↑**	↓	↑
	50%	High	↑↑	↑↑	**↑↑↑**	**↑↑**	↓	↑↑
Short	10%	High	↔	↓	**↑**	**↔**	↓	↓
	30%	High	↔	↑	**↑↑**	**↑↑**	↓	↑
	30%	Mod.	↔	↔	**↑**	**↑**	↓	↔
	50%	High	↑	↑	**↑↑↑**	**↑↑**	↓	↑

Symbols indicates a ↓ ↓ = large decrease, ↓ = moderate decrease, ↓ = Small decrease, ↔ = no change, ↑ = small increase, ↑ = moderate increase, ↑↑ = large increase, and ↑↑↑ = very large increase. Mod. = Moderate, and WM = well mixed (comparable to long-dispersal distances)

Previous studies modelling stochasticity have demonstrated that reserves can serve to hedge against inevitable variations, uncertainties, errors, and biases in fisheries assessments and management (Lauck et al. 1998; Sladek-Nowlis & Roberts 1999; Mangel 2000; West et al. 2009; De Leo & Micheli 2015). The majority of these studies focus on temporal variations in fishing pressure (but see Sladek-Nowlis & Roberts 1999), thereby assuming that reserve populations are experiencing less variation in mortality rates than the fished populations. While akin to my specific scenario of protecting only, and all, non-disturbed reefs in the spatially explicit model (blue markers, Figure 4.2g-h & Figure 4.3g-h), these scenarios are not directly comparable. When fishing pressure is temporally variable, stochasticity occurs across the entire metapopulation in the pre-reserve scenario and is then restricted (along with the fishery-squeeze) to the un-protected areas after reserve establishment. Yet, in my spatially explicit model, stochasticity (due to environmental disturbances) was spatially heterogeneous, and implementing reserves only reallocated the fishing pressure into the areas subject to temporal variations. This is perhaps why I found that reserves decreased catch stability when protecting all non-fluctuating (i.e. non-disturbed) areas (blue markers, Figure 4.2g), while previous studies have always found reserves to increase stability when fluctuations (due to fishing) are removed from a portion of the metapopulation. Consequently, this study demonstrates that (in contrast to stochastic fishing pressure) spatially heterogeneous and natural stochastic disturbances interact with reserve placement in ways that are not always advantageous for the stability and sustainability of fish populations and fisheries.

While this study has covered a range of possible scenarios, there are a number of caveats that warrant future attention. First, I have focused on disturbances that impact the survival of adult fishes. Juvenile fishes often have close associations with the benthos (e.g. Wen et al. 2013), and are also likely to also be impacted by the loss of habitat due to environmental disturbances. While the stabilising effects of reserves are still likely to occur if juveniles are impacted by disturbances (as is the case for stochasticity in larval dispersal and survival; De Leo & Micheli 2015), the consequences of reserve placement may vary from my results. This is especially true if juveniles undergo density dependent survival (which is likely for a number of targeted species; White et al. 2010), as spatial non-linear averaging among reserves and non-reserves (and among temporal fluctuations) may dampen or enhance stability. Second, I have assumed set probabilities for disturbance intensities and frequencies, rather than drawing from probability distributions. I chose this approach so as to simplify parameters in the model, and allow focus on the general effects of disturbances. However, exploration of changes in disturbance probability distributions over time, in the context of reserve-fishery interactions, may be warranted given that the likelihood of high-intensity disturbance events is projected to increase with climate change (IPCC 2014).

The impacts that reserves have on fisheries are often considered in terms of how reserves change long-term maximum sustainable yields, relative to catch regulations that are well-designed, well-managed, and commonly assume a degree of stability in the system (Gerber et al. 2003). The prevailing view is that, in most cases, reserves reduce yields. Yet, in reality, fishing takes place in stochastic environments (due to environmental disturbances, variability in fisher behaviour, and other sources of variation; Mangel 2000; Williamson et al. 2014; Emslie et al. 2015), and this compromises their stability and sustainability. Evidence is mounting that establishing reserves can mediate fluctuations in catch and targeted biomass, and reduce the chance of extinction (e.g. Pitchford et al. 2007; Leo et al. 2015), and this study contributes substantially to this by demonstrating that the stabilizing effects of reserves extend to buffering the metapopulation against environmental disturbances. However, given the spatial complexity of natural disturbances, care needs to be taken to ensure that a mix of disturbed and undisturbed areas are protected in order to support stable and sustainable fisheries and fish populations.

Chapter 5:

GENERAL DISCUSSION

This thesis provides new understanding of the impacts of marine reserves on fisheries and the dynamics of fished metapopualtions, addressing knowledge gaps that have previously limited our ability to interpret short-term changes, predict longer-term outcomes, and mitigate potentially negative impacts of reserves for fisheries in coral reef systems. Firstly, yields can be expected to decrease in the short-term after reserve establishment, and it may take years to decades to achieve biomass and yield recovery and benefits. Importantly, during this transient period, the metapopulation may be vulnerable to overfishing and collapse if excess fishing effort is not effectively managed. Secondly, combining fishing effort controls with a reserve network rezoning has yielded significant conservation and catch benefits in a major Australian fishery, beyond those achievable with the rezoning alone. The concurrent reduction in fishing effort successfully socialised the fisheries cost of rezoning, preventing the initial declines in catch rates that would have otherwise occurred. Thirdly, reserves can stabilize naturally disturbed fisheries and fished populations, thereby enhancing the sustainability and predictability of fishery dynamics. Importantly, this was true whether reserves increased or decreased average long-term expected yields. Throughout this thesis, however, I made a number of key assumptions that warrant discussion.

First, in all of my models I assumed that, prior to any management changes, the metapopulation was heavily fished, reduced to 20% virgin biomass (although in Chapter 4 I also considered a 50% virgin biomass scenario). As discussed throughout the thesis, this is a reasonable assumption for coral trout on the GBR as biomass densities prior to reserve establishment were approximately 20% of the current densities observed within the most strictly enforced no-take zones (Williamson et al. 2004; Ayling & Choat 2008). Similarly, most large predatory fishes are estimated to have been reduced to ≤ 40% their pre-harvest biomass (Juan-Jorda et al. 2011). The extent to which a population is fished, however, can have implications for the recovery potential with reserve establishment. In a heavily fished system (where biomass density is low), density-dependent processes are negligible and the population is primarily regulated by fishing pressure (Sánchez Lizaso et al. 2000; Rose et al. 2001). Here, there is a large potential for adult fish biomass, and reproductive productivity, within reserves to increase to a level where net export of larvae provides recruitment subsidies to surrounding fished areas and effectively compensates fishers for lost fishing ground, before density-dependent processes set-in (see Russ & Alcala 2010 for an empirical example of recovery to carrying capacity). In more moderately fished systems, however, both density-dependent processes and fishing regulate the population (Sánchez Lizaso et al. 2000; Rose et al. 2001), and there is less capacity for gains in biomass and larval export from reserves. This is exemplified in the long-term outcomes of Chapter 3: if the GBRMP coral trout fishery had remained heavily fished (no effort reduction), then the long-term catch and catch rate with reserves is greater than without (compare the dotted horizontal line and green shaded region, Figure 3.3a,b), but when the fishery was more moderately fished (with effort reductions), the reserve network reduced long-term catch and catch rates (compare orange and purple shading, Figure 3.3a,b).

Reserves also create non-linear averaging in density-dependent demographic rates such as juvenile survival and fecundity. The function of most density-dependent demographic rates are non-linear (e.g. Heppell et al. 2006; White 2009), and, therefore, changes in per-capita rates within reserves (due to increased biomass) will be disproportionate to those in the fished areas (due to decreased biomass from fishery squeeze). This causes the average per-capita rate across the metapopulation with reserves to differ from that without. For example, due to the declining exponential function of per-capita juvenile survival, the average survival of an individual juvenile will be greater with reserves compared to a no-reserve scenario (Figure 5.1; see also Chan et al. 2014 for a similar discussion on fertilization success). Since non-linear averaging affects the productivity of the system, it will also influence whether there is enough larvae exported from reserves to compensate fishers for reduced access to fishing grounds, and affect expected long-term yields (Gerber et al. 2003; Gaylord et al. 2005; White et al. 2008; White 2009). Reductions in long-term yields, for example, are less likely to occur in non-sex-changing species (Chan et al. 2012), but more likely to occur in species where juvenile survival depends on competition among juveniles, rather than adult biomass (White 2009).

Consequently, caution should be taken when applying the findings of this thesis to moderately and lightly fished systems, especially if the focal species are subject to different density-dependent processes than coral trout (I have assumed biomass density

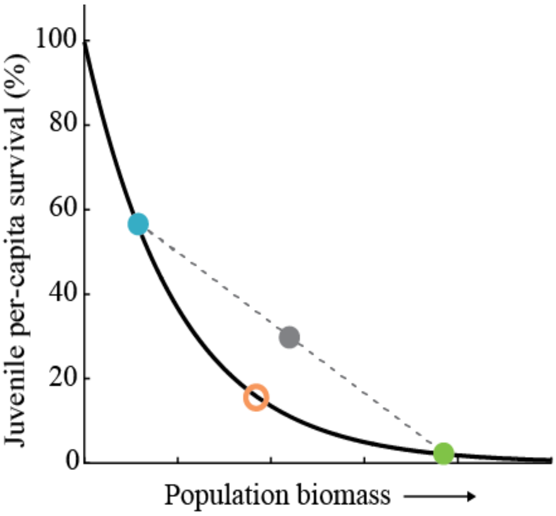

Figure 5.1 Per-capital juvenile survival (relative to density-independent survival) as a function of the local population biomass density (solid line). The orange (open) circle represents a fished population, without reserves, where population biomasses are homogenous. The filled circles represent the biomass densities in protected areas (increased biomass; green), fished areas (decreased biomass; blue), and the metapopulation average (grey), with reserve establishment. For simplicity, this represents a system where half the metapopulation has been protected. Due to the non-linear changes in sub-population biomasses, and the net increase in metapopulation biomass, the average per-capita survival of juveniles with reserves (grey filled circle), is greater than without (orange open circle).

affects per-capita juvenile survival and egg fertilization success; Chapters 3 & 4). For example, while reserves are likely to decrease yields initially (Chapter 2, 3, Appendix D.2.a), time until yield recovery, as well as the likelihood of yield benefits occurring, decreases with decreasing exploitation (see also Appendix D.2.a). Likewise, if the fishery is already well managed (archiving near its maximum sustainable yield), then effort reductions alongside reserve implementation are unlikely to mitigate short-term losses in catch and catch rates, and metapopulation collapse after reserve establishment (due to localised over-fishing; Chapter 2) would be less of a concern. However, ensuring that fishing effort continues to be maintained, and not increased, would still likely benefit the fishery. Finally, in Chapter 4 I demonstrated that the ability of reserves to stabilize yields and biomass in environmentally disturbed environments is retained (although lessened) in more moderately fished systems. This makes sense, as reserves, irrespective of their effects on yields, increase the net productivity of the system (through increasing total metapopulation biomass), thereby decreasing recovery times after disturbance. For this reason, it is also unlikely that the stabilizing benefits of reserves would be qualitatively affected by the type of density-dependence assumed. However, the type of density-dependent process exhibited by the focal species is likely to influence the magnitude of reduction in fluctuations with reserves. For example, a non-sex-changing sensitivity analysis in Chapter 4 shows that reductions in biomass and yields temporal variations were greater when fertilization success did not depend on relative male biomass (compare Figures 4.1a & H4a, and Figures H2a & H4c).

Second, I assumed that fishing pressure was evenly distributed across the metapopulation, and that whole reefs (which have represented individual populations) were delineated as either protected within a reserve, or open to fishing. In the GBRMP, fishing pressure is relatively uniform across all fished reefs (both before and after the 2004 rezoning; Lédée et al. 2012; De Freitas et al. 2013), and most reserves typically coincide with the natural segregation of habitats. These were, therefore, reasonable assumptions to make when addressing the objectives of this thesis. However, it common knowledge among fishers that more and larger fish can be found within reserves, and that this biomass can 'spill-over' into the areas immediately adjacent to a reserve (Russ et al. 2004a; Kellner et al. 2007). This is especially true when reserves do not encompass whole habitat areas (e.g. they protect only a portion of a reef, or a section of a continuous coastal habitat; Kellner et al. 2007), or when the target species is relatively mobile (e.g. sharks; Apostolaki et al. 2002; Grüss et al. 2011b). Consequently, fishers have been known to 'fish-the-line' (fishing immediately alongside a reserve boundary; Russ et al. 2004a; Kellner et al. 2007), thereby affecting the adult survival rate in the reserve subpopulation. For similar reasons, fishers can aggregate in non-protected areas known to be biomass 'hotspots' (e.g. regions of particularly healthy habitat, areas infrequently disturbed, or areas of high larval recruitment; Smith & Wilen 2003), especially when their preferred area becomes inaccessible as a reserve (De Freitas et al. 2013). This behaviour would result in a disproportionate increase in fishing-induced mortality in the more heavily fished areas.

A sensitivity analysis of the spatially-explicit Keppel Island model in Chapter 2, for example, demonstrated that if fishers reallocated effort according to the proportion of biomass (rather than area) lost to reserves, then collapse in the short-term due to overfishing was less likely (see Appendix E). In contrast, if fishing-the-line occurred, then the chance of metapopulation collapse immediately after reserve implementation could increase, as the growth of the protected population is compromised by the removal of adults from the population edges (as a side note, this would also likely apply to systems which are subjected to poaching in reserves). Alternatively, fishing-the-line could reduce the chance of collapse due to increased effort, by minimising initial fishery yield reductions (similar to incrementally increasing reserve coverage; Brown et al. 2014) and discouraging excess effort to maintain yields. Finally, by targeting areas of high biomass, fishers are more likely to focus on areas that experience less environmental disturbance.

If these areas are then protected within reserves, the large increase in fishing effort (which would be greater than if fishing pressure was homogenous prior to reserve establishment) in disturbed, unprotected areas could outweigh the biomass gains within reserves and offset the stabilizing benefits of reserves. This would be comparable to a situation in which reserves (i.e. areas with relatively low fishing pressure) in more disturbed habitats are shifted to relatively undisturbed areas, and the results from Chapter 4 suggest that, while always stabilising metapopulation biomass (compare orange to blue markers, Figure 4.3a,c,e,g), this could increase temporal variation in yields, especially if the system has well-mixed larvae and reserve coverage is large (>~20%) (compare orange to blue markers, Figure 4.2a,g), or the system is moderately fished (compare orange to blue markers, Figure 4.2c).

Third, I made the simplifying assumption that habitat quality, and therefore natural mortality rates, among reefs/populations was spatially homogenous (an exception being the spatially-explicit Keppel Island Group model in Chapter 4). Habitat quality can affect the survival of both juveniles (Wen et al. 2013) and adult fish (Jones & Syms 1998; Jones et al. 2004; Williamson et al. 2014). In Chapter 2, I considered variation in juvenile survival in the Keppel Island spatially-explicit model, reflecting observed variation in the amount of suitable recruitment habitat (i.e. reef/reserve size) available among reefs in the Keppel Island region (see also Appendix B). I found that protecting small, relatively distant, reefs increased the chance of metapopulation collapse in the short-term (assuming homogenous distribution of fishing pressure, and fishery squeeze). While the results from Chapter 2 were discussed in terms of reserve area, they could also be conceptualised in terms of juvenile habitat quality, with a large reserve and a small reserve equating to similar sized reserves protecting high and low quality habitats, respectively. Therefore, protecting poor-quality reefs (especially those located peripherally within the metapopulation), would likely also be detrimental for metapopulation, and fishery, recovery and increase the chance of metapopulation collapse. Chapter 2, however, considered short-term reserve effects, and used a density-independent model, focusing on heavily fished systems (Appendix D). For coral trout I have assumed that density-dependence affects juvenile survival (see Chapters 3 & 4 for justification). For moderately to lightly fished systems, or systems where effort has been concurrently reduced, variation in habitat quality is likely to also affect the strength of density-dependence (μ_2 throughout the thesis), with poor-quality habitat effecting stronger reductions in juvenile survival with increasing population biomass. Non-linear averaging among zones (protected vs. fished) and habitat qualities (good vs. bad) could potentially produce counter intuitive results for long-term yields and fishery stability, and would likely be subject to reserve placement. This is potentially a direction for future investigation.

Habitat quality can also affect the natural survival of adults (Jones & Syms 1998; Jones et al. 2004; Williamson et al. 2014), with a greater biomass of predatory fishes, such as coral trout, associating with better quality habitats (e.g. greater live coral cover; Kingsford 2008; Bunt & Kingsford 2014). Where reserves are placed, in relation to the habitat quality for adults (assuming only spatial and not temporal variation), is unlikely to create short-term dynamics that qualitatively differ from those due to variation in juvenile survival (as discussed in the previous paragraph). Likewise, the long-term effects of reserve placement, would be similar to the long-term average yields and biomasses changes seen in Chapter 4. That is, placing reserves in good quality habitats will tend to produce the greatest increases in yields and metapopulation biomass when fishing pressure is high (Figures 4.3b,d,h & 4.4b,d,h). However, when fishing pressure is moderate, reserve placement has little effect on the extent of yield losses (Figure 4.3d) and only slight benefits to biomass gains with reserves (Figure 4.4d).

I have, however, also assumed in this thesis that adults remain within their natal population (i.e. no adult migration). Yet it is possible that adult fishes (unlike juveniles) actively seek out better quality habitats, making small-scale migrations to preferred areas (Davies 1996; Connell & Kingsford 1998). This could impact the expected outcomes of reserves in temporally disturbed environments (Chapter 4). For example, if fish migration has a lower associated mortality than remaining in a disturbed habitat, placing reserves in disturbed areas may increase yields, as fish periodically migrate out of reserves, seeking more favourable and productive habitats. This however, would likely be unsustainable in the long-run as the adult export from reserves could undermine metapopulation persistence (as is the case for species with home ranges that extend beyond reserve bounders; Grüss et al. 2011a, b). The outcomes would also depend on the likelihood of an adult migrating and the additional risk of mortality associated with moving to better quality habitats (Grüss et al. 2011a, b), although estimates of these parameters are lacking.

5.1 Conclusions

Reserves are an increasingly popular tool in managing marine systems, yet their impacts on fisheries is contentious. Reserves are nearly always established in areas accessed by fisheries, and they have long been argued to be a sub-optimal fisheries management action. The results of this thesis broaden our understanding of the impact of reserves on fisheries and the metapopulation dynamics of fished populations. My findings reduce the gap between fishery-reserve theory and observed reserve effects by providing theory that is directly relevant to currently established reserves (Chapters 2-4), by explicitly testing the efficacy of a major reserve network (the GBRMP; Chapter 3), and by extending the relatively limited research on how stochasticity influences MPA performance (Chapter 4). Furthermore, my findings demonstrate that the conservation objectives of marine reserves need not be incompatible with effective fisheries management. Rather, they show that evaluating the interactive effects of reserves and direct fisheries management actions when designing new reserve networks is critical to enhancing the benefits for both fisheries and conservation in the future, and that reserve impacts on fisheries need to be considered in terms broader than simple changes in long-term yields (e.g. fishery sustainability and stability).

REFERENCES

Adams, S., Mapstone, B.D., Russ, G.R. & Davies, C.R. (2000). Geographic variation in the sex ratio, sex specific size, and age structure of *Plectropomus leopardus* (Serranidae) between reefs open and closed to fishing on the Great Barrier Reef. *Can. J. Fish. Aquat. Sci.*, 57, 1448–1458.

Agardy, T., di Sciara, G.N. & Christie, P. (2011). Mind the gap: Addressing the shortcomings of marine protected areas through large scale marine spatial planning. *Mar. Policy*, 35, 226–232.

Agardy, T.M. (1994). Advances in marine conservation: the role of marine protected areas. *Trends Ecol. Evol.*, 9, 267–270.

Alcala, A.C., Russ, G.R., Maypa, A.P. & Calumpong, H.P. (2005). A long-term, spatially replicated experimental test of the effect of marine reserves on local fish yields. *Can. J. Fish. Aquat. Sci.*, 62, 98–108.

Allison, G., Gaines, S., Lubchenco, J. & Possingham, H.P. (2003). Ensuring persistence of marine reserves: catastrophes require adopting an insurance factor. *Ecol. Appl.*, 13, 8–24.

Almany, G., Connolly, S., Heath, D., Hogan, J., Jones, G., McCook, L., Mills, M., Pressey, R. & Williamson, D. (2009). Connectivity, biodiversity conservation and the design of marine reserve networks for coral reefs. *Coral Reefs*, 28, 339–351.

Almany, G.R., Hamilton, R.J., Bode, M., Matawai, M., Potuku, T., Saenz-Agudelo, P., Planes, S., Berumen, M.L., Rhodes, K.L., Thorrold, S.R., Russ, G.R. & Jones, G.P. (2013). Dispersal of grouper larvae drives local resource sharing in a coral reef fishery. *Curr. Biol.*, 23, 626–630.

Apostolaki, P., Milner-Gulland, E.J., McAllister, M.K. & Kirkwood, G.P. (2002). Modelling the effects of establishing a marine reserve for mobile fish species. *Can. J. Fish. Aquat. Sci.*, 59, 405–415

Armsworth, P.R. (2001). Effects of fishing on a protogynous hermaphrodite. *Can. J. Fish. Aquat. Sci.*, 58, 568–578.

Ayling, A.M. & Choat, J. (2008). *Abundance patterns of reef sharks and predatory fishes on differently zoned reefs in the offshore Townsville region : Final report to the Great Barrier Reef Marine Park Authority Abundance patterns of reef sharks and predatory fishes on differently zoned.* Research Publication No. 91, Great Barrier Reef Marine Park Authority, Townsville (32pp).

Beddington, J.R. & May, R.M. (1977). Harvesting natural populations in a randomly fluctuating environment. *Science*, 197, 463–465.

Berkeley, S., Hixon, M., Larson, R.J. & Love, M. (2004). Fisheries sustainability via protection. *Fisheries*, 29, 23–32.

Beverton, R.J.H. & Holt, S.J. (1957) *On the Dynamics of Exploited Fish Populations*. United Kingdom Ministry of Agriculture, Food, and Fisheries Investigations S. 2 No. 19, 533 pp.

Blowes, S.A. & Connolly, S.R. (2011). Risk spreading, connectivity, and optimal reserve spacing. *Ecol. Appl.*, 22, 311–321.

Bohnsack, J. (1996). Maintenance and recovery of reef fishery productivity. In: *Reef Fisheries*. Chapman & Hall Fish and Fisheries Series (eds. Polunin, N.C. & Roberts, C.). Springer Netherlands, pp. 283–313.

Botsford, L., White, J., Coffroth, M., Paris, C., Planes, S., Shearer, T., Thorrold, S. & Jones, G. (2009a). Connectivity and resilience of coral reef metapopulations in marine protected areas: matching empirical efforts to predictive needs. *Coral Reefs*, 28, 327–337.

Botsford, L.W., Brumbaugh, D.R., Grimes, C., Kellner, J.B., Largier, J., O'Farrell, M.R., Ralston, S., Soulanille, E. & Wespestad, V. (2009b). Connectivity, sustainability, and yield: bridging the gap between conventional fisheries management and marine protected areas. *Rev. Fish Biol. Fish.*, 19, 69–95.

Brown, C.J., Abdullah, S. & Mumby, P.J. (2014). Minimizing the short-term impacts of marine reserves on fisheries while meeting long-term goals for recovery. *Conserv. Lett.*, 8, 180-189.

Bunt, C. & Kingsford, M. (2014). Movement, habitat utilization and behaviour of coral trout *Plectropomus leopardus* during and after the reproductive period on the southern Great Barrier Reef. *Mar. Ecol. Prog. Ser.*, 496, 33–45

Buxton, C.D., Hartmann, K., Kearney, R. & Gardner, C. (2014). When Is Spillover from Marine Reserves Likely to Benefit Fisheries? *PLoS One*, 9, e107032.

Carter, A.B., Russ, G.R., Tobin, A.J., Williams, A.J., Davies, C.R. & Mapstone, B.D. (2014a). Spatial variation in the effects of size and age on reproductive dynamics of common coral trout *Plectropomus leopardus*. *J. Fish Biol.*, 84, 1074–98.

Carter, A.B., Davies, C.R., Mapstone, B.D., Russ, G.R., Tobin, A.J. & Williams, A.J. (2014b). Effects of region, demography, and protection from fishing on batch fecundity of common coral trout (*Plectropomus leopardus*). *Coral Reefs*, 33, 751–763.

Caswell, H. (2001). *Matrix population models: construction, analysis, and interpreation*. Second edition. Sinauer Associates, Sunderland, Massachusetts, USA.

Caswell, H. (2007). Sensitivity analysis of transient population dynamics. *Ecol. Lett.*, 10, 1–15.

Chan, N., Connolly, S. & Mapstone, B. (2012). Effects of sex change on the implications of marine reserves for fisheries. *Ecol. Appl.*, 22, 778–91.

Connell, S.D. & Kingsford, M.J. (1998). Spatial, temporal and habitat-related variation in the abundance of large predatory fish at One Tree Reef, Australia. *Coral Reefs*, 17, 49–57.

DAFF. (2015). QFish Commercial Fishing Dataset. http://qfish.fisheries.qld.gov.au/.

Davies, C.R. (1996). *Inter-reef Movement of the Common Coral Trout,* Plectropomus leopardus. Research Publication No. 61, Great Barrier Reef Marine Park Authority, Townsville (50pp).

Davis, K.L.F., Russ, G.R., Williamson, D.H. & Evans, R.D. (2004). Surveillance and poaching on inshore reefs of the Great Barrier Reef Marine Park. *Coast. Manag.*, 32, 373–387.

De'ath, G., Fabricius, K.E., Sweatman, H. & Puotinen, M. (2012). The 27-year decline of coral cover on the Great Barrier Reef and its causes. *Proc. Natl. Acad. Sci.*, 109, 17995–17999.

De Freitas, D., Sutton, S. & Moloney, J. (2013). Spatial substitution strategies of recreational fishers in response to zoning changes in the Great Barrier Reef Marine Park. *Mar. Policy*, 40, 145–153.

De Leo, G.A. & Micheli, F. (2015). The good, the bad and the ugly of marine reserves for fishery yields. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.*, 370.

Detenbeck, N.E., DeVore, P.W., Nieme, G.J. & Lima, A. (1992). Recovery of template-stream fish communities from disturbance: A review of case studies and synthesis of theory. *Environ. Mangement*, 16, 33–53.

Edgar, G.J., Stuart-Smith, R.D., Willis, T.J., Kininmonth, S., Baker, S.C., Banks, S., Barrett, N.S., Becerro, M.A., Bernard, A.T.F., Berkhout, J., Buxton, C.D., Campbell, S.J., Cooper, A.T., Davey, M., Edgar, S.C., Försterra, G., Galván, D.E., Irigoyen, A.J., Kushner, D.J., Moura, R., Parnell, P.E. Shears, N.T., Soler, G., Strain, E.M.A. & Thomson, R.J. (2014). Global conservation outcomes depend on marine protected areas with five key features. *Nature*, 506, 216–220.

Emslie, M.J., Logan, M., Russ, G.R., Sweatman, H.P.A., Williamson, D.H., Ayling, A.M., Macneil, M.A., Ceccarelli, D., Cheal, A.J., Evans, R.D., Johns, K.A., Jonker, M.J., Miller, I.R., Osborne, K., Russ, G.R. & Sweatman, H.P.A. (2015). Expectations and outcomes of reserve network performance following re-zoning of the Great Barrier Reef Marine Park. *Curr. Biol.*, 1–10.

Ezard, T.H.G., Bullock, J.M., Dalgleish, H.J., Millon, A., Pelletier, F., Ozgul, A. & Koons, D.N. (2010). Matrix models for a changeable world: the importance of transient dynamics in population management. *J. Appl. Ecol.*, 47, 515–523.

Fisheries Economics, Research, and Management (2007). *A review of the business exit (licence buyout) assistance component of the Great Barrier Reef Marine Park structural adjustment package: final report*. Report of the Australian Government Department of the Environment. http://www.environment.gov.au/system/files/resources/6d31cd5f-5645-4ea7-bf00-a408f8c7f03c/files/gbrmp-adjustment-package.pdf.

Fernandes, L., Day, J., Lewis, A., Slegers, S., Kerrigan, B., Breen, D., Cameron, D., Jago, B., Hall, J., Lowe, D., Innes, J., Tanzer, J., Chadwick, V., Thompson, L., Gorman, K., Simmons, M., Barnett, B., Sampson, K., De'ath, G., Mapstone, B., Marsh, H., Possingham, H., Ball, I., Ward, T., Dobbs, K., Aumend, J., Slater, D. & Stapleton, K. (2005). Establishing representative no-take areas in the great barrier reef: Large-scale implementation of theory on marine protected areas. *Conserv. Biol.*, 19, 1733–1744.

Ferreira, B.P. (1993). Reproduction of the inshore coral trout *Plectropomus maculates* (Perciformes: Serranidae) from the Central Great Barrier Reef, Australia. *J. Fish Biol.*, 42, 831–844.

Ferreira, B.P. (1995). Reproduction of the common coral trout *Plectropomus Leopardus* (Serranidae: Epinephelinae) from the Central and Northern Great Barrier Reef, Australia. *Bull. Mar. Sci.*, 56, 653–669.

Ferreira, B.P. & Russ, G. (1994). Age validation and estimation of growth rate of the coral trout, *Plectropomus leopardus* (Lacepede 1802), from Lizard Island, Northern Great Barrier Reef. *Fish. Bull.*, 92, 46–57.

Ferreira, B.P. & Russ, G.R. (1992). Age, growth and mortality of the inshore coarl trout *Plectropomus maculatus* (Pisces: Serranidae) from the Central Great Barrier Reef, Australia. *Mar. Freshw. Res.*, 43, 1301–1312.

Fletcher, W.J., Kearney, R.E., Wise, B.S. & Nash, W.J. (2015). Large-scale expansion of no-take closures within the Great Barrier Reef has not enhanced fishery production. *Ecol. Appl.*, 25, 1187–119.

Fogarty, M.J. & Botsford, L.W. (2007). Population Connectivity and Spatial Management of Marine Fisheries. *Oceanography*, 20, 112–123.

Fraterrigo, J.M. & Rusak, J.A. (2008). Disturbance-driven changes in the variability of ecological patterns and processes. *Ecol. Lett.*, 11, 756–770.

Gaines, S.D., Lester, S.E., Grorud-Colvert, K., Costello, C. & Pollnac, R. (2010a). Evolving science of marine reserves: New developments and emerging research frontiers. *Proc. Natl. Acad. Sci.*, 107, 18251–18255.

Gaines, S.D., White, C., Carr, M.H. & Palumbi, S.R. (2010b). Designing marine reserve networks for both conservation and fisheries management. *Proc. Natl. Acad. Sci. U.S.A.*, 107, 18286–93.

Game, E.T., McDonald-Madden, E., Puotinen, M.L. & Possingham, H.P. (2008). Should we protect the strong or the weak? Risk, resilience, and the selection of marine protected areas. *Conserv. Biol.*, 22, 1619–1629.

Gaylord, B., Gaines, S., Siegel, D.A. & Carr, M.H. (2005). Marine reserves exploit population structure and life history in potentially improving fisheries yields. *Ecol. Apps.* 15, 2180–2191.

Great Barrier Reef Marine Park Authority (2003). *Summary report of the social and economic impacts of the rezoning of the Great Barrier Reef Marine Park*. Report of the Great Barrier Reef Marine Park Authority. http:// elibrary.gbrmpa.gov.au/jspui/handle/11017/381

Great Barrier Reef Marine Park Authority (2011). *Impacts of tropical cyclone Yasi on the Great Barrier Reef: a report on the findings of a rapid ecological impact assessment*. Report of the Great Barrier Reef Marine Park Authority. http://www.gbrmpa.gov.au/__data/assets/pdf_file/0008/8783/GBRMPA_ImpactsTC_Yasi_onGBRSept2011.pdf.

Gell, F.R. & Roberts, C.M. (2003). Benefits beyond boundaries: the fishery effects of marine reserves. *Trends Ecol. Evol.*, 18, 448–455.

Gerber, L.R., Beger, M., McCarthy, M.A. & Possingham, H.P. (2005a). A theory for optimal monitoring of marine reserves. *Ecol. Lett.*, 8, 829–837.

Gerber, L.R., Botsford, L.W., Hastings, A., Possingham, H.P., Gaines, S.D., Palumbi, S.R. & Andelman, S. (2003). Population models for marine reserve design: a retrospective and prospective synthesis. *Ecol. Appl.*, 13, 47–64.

Gerber, L.R., Kareiva, P.M. & Bascompte, J. (2002). The influence of life history attributes and fishing pressure on the efficacy of marine reserves. *Biol. Conserv.*, 106, 11–18.

Graham, N.A.J., Ainsworth, T.D., Baird, A.H., Ban, N.C., Bay, L.K., Cinner, J.E., Freitas, Debora, M.D., Diaz-pulido, G., Dornelas, M., Dunn, S.R., Pedro, I.J., Foret, S., Good, T.C. & Kool, J. (2011). From microbes to people : Tractable benefits of no-take areas for coral reefs. *Oceanogr. Mar. Biol.*, 49, 105–136.

Grüss, A. (2015). Modelling the impacts of marine protected areas for mobile exploited fish populations and their fisheries: what we recently learnt and where we should be going. *Aquat. Living Resour.*, 133, 107–133.

Grüss, A., Kaplan, D.M., Guenette, S., Roberts, C.M. & Botsford, L.W. (2011a). Consequences of adult and juvenile movement for marine protected areas. *Biol. Conserv.*, 144, 692–702.

Grüss, A., Kaplan, D.M. & Hart, D.R. (2011b). Relative impacts of adult movement, larval dispersal and harvester movement on the effectiveness of reserve networks. *PLoS One*, 6, e19960.

Gunn, J., Fraser, G. & Kimball, B. (2010). *Review of the Great Barrier Reef Marine Park Structural Adjeustment Package*. Report of the Australian Government Department of the Environment. http://www.environment.gov.au/system/files/resources/4b3d907c-a200-40c e-88b0-c377c371357f/files/gbrmp-sap-review.pdf.

Haddon, M. (2001). Stock-recruitment relationships. In: *quantitative methods in fisheries*. CRC Press Taylor & Francis Group, Boca Raston.

Halpern, B. (2003). The impact of marine reserves: do reserves work and does reserve size matter? *Ecol. Appl.*, 13.

Halpern, B., Gaines, S. & Warner, R. (2004). Confounding effects of the export of production and the displacement of fishing effort from marine reserves. *Ecol. Appl.*, 14, 1248–1256.

Halpern, B.S., Lester, S.E. & Kellner, J.B. (2010). Spillover from marine reserves and the replenishment of fished stocks. *Environ. Conserv.*, 36, 268–276.

Halpern, B.S. & Warner, R.R. (2003). Matching marine reserve design to reserve objectives. *Proc. R. Soc. London. Ser. B Biol. Sci.*, 270, 1871–1878.

Hamel, M.A., Andréfouët, S. & Pressey, R.L. (2013). Compromises between international habitat conservation guidelines and small-scale fisheries in Pacific island countries. *Conserv. Lett.*, 6, 46–57.

Harrison, H.B., Williamson, D.H., Evans, R.D., Almany, G.R., Thorrold, S.R., Russ, G.R., Feldheim, K.A., van Herwerden, L., Planes, S., Srinivasan, M., Berumen, M.L. & Jones, G.P. (2012). Larval export from marine reserves and the recruitment benefit for fish and fisheries. *Curr. Biol.*, 22, 1023–1028.

Hart, D. (2006). When do marine reserves increase fishery yield? *Can. J. Fish. Aquat. Sci.*, 63, 1445–1449.

Hastings, A. & Botsford, L.W. (1999). Equivalence in yield from marine reserves and traditional fisheries management. *Science*, 284, 1537–1538.

Heppell, S.S., Heppell, S.A., Coleman, F.C. & Koenig, C.C. (2006). Models to compare management options for a protogynous fish. *Ecol. Appl.*, 16, 238–249.

Hilborn, R., Micheli, F. & De Leo, G. (2006). Integrating marine protected areas with catch regulation. *Can. J. Fish. Aquat. Sci.*, 649, 642–649.

Hilborn, R., Stokes, K., Maguire, J.J., Smith, T., Botsford, L.W., Mangel, M., Orensanz, J., Parma, A., Rice, J., Bell, J., Cochrane, K.L., Garcia, S., Hall, S.J., Kirkwood, G.P., Sainsbury, K., Stefansson, G. & Walters, C. (2004). When can marine reserves improve fisheries management? *Ocean Coast. Manag.*, 47, 197–205.

Hoegh-Guldberg, O., Mumby, P.J., Hooten, A.J., Steneck, R.S., Greenfield, P., Gomez, E., Harvell, C.D., Sale, P.F., Edwards, A.J., Caldeira, K., Knowlton, N., Eakin, C.M., Iglesias-Prieto, R., Muthiga, N., Bradbury, R.H., Dubi, A. & Hatziolos, M.E. (2007). Coral reefs under rapid climate change and ocean acidification. *Science*, 318, 1737–42.

Holland, D.S. & Brazee, R.J. (1996). Marine reserves for fisheries management. *Mar. Resour. Econ.*, 11, 157-171.

Hopf, J.K., Jones, G.P., Williamson, D.H. & Connolly, S.R. (2016a). Fishery consequences of marine reserves: short-term pain for longer-term gain. *Ecol. Appl.*, 26, 818–829.

Hopf, J.K., Jones, G.P., Williamson, D.H. & Connolly, S.R. (2016b). Synergistic effects of marine reserves and harvest controls on the abundance and catch dynamics of a report synergistic effects of marine reserves and harvest controls on the abundance and catch dynamics of a coral reef fishery. *Curr. Biol.*, http://dx.doi.org/10.1016/j.cub.2016.04.022

Hsieh, C.H., Reiss, C.S., Hunter, J.R., Beddington, J.R., May, R.M. & Sugihara, G. (2006). Fishing elevates variability in the abundance of exploited species. *Nature*, 443, 859–62.

Hughes, T.P., Cameron, D.S., Chin, A., Connolly, S.R., Day, J.C., Jones, G.P., McCook, L., McGinnity, P., Mumby, P.J., Pears, R.J., Pressey, R.L., Russ, G.R., Tanzer, J., Tobin, A., Young, M.A.L., Russ, G.R., Tanzer, J., Tobin, A.J. & Young, A.L. (2016). A critique of claims for negative impacts of Marine Protected Areas on fisheries. *Ecol. Appl.*, 26, 637–641.

Hunter, C.M. & Caswell, H. (2005). The use of the vec-permutation matrix in spatial matrix population models. *Ecol. Modell.*, 188, 15–21.

IPCC (2014). *IPCC, 2014: Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Core Writing Team, R.K. Pachauri and L.A. Meyer (eds.). IPCC, Geneva, Switzerland, 151 pp.

St. John, J. (1995). Feeding ecology of the coral trout, *Plectropomus leopardus* (Serranidae) on the Great Barrier Reef, Australia. James Cook University.

Jones, G.P., McCormick, M.I., Srinivasan, M. & Eagle, J.V. (2004). Coral decline threatens fish biodiversity in marine reserves. *Proc. Natl. Acad. Sci. U.S.A.*, 101, 8251–3.

Jones, G.P., Srinivasan, M. & Almany, G.R. (2007). Population connectivity and conservation of marine biodiversity. *Oceanography*, 20, 100–111.

Jones, G.P. & Syms, C. (1998). Disturbance, habitat structure and the ecology of fishes on coral reefs. *Aust. J. Ecol.*, 23, 287–297.

Juan-Jorda, M.J., Mosqueira, I., Cooper, A.B., Freire, J. & Dulvy, N.K. (2011). Global population trajectories of tunas and their relatives. *Proc. Natl. Acad. Sci.*, 108, 20650–20655.

Kellner, J.B., Tetreault, I., Gaines, S.D. & Nisbet, R.M. (2007). Fishing the line near marine reserves in single and multispecies fisheries. *Ecol. Appl.*, 17, 1039–54.

Kerwath, S.E., Winker, H., Götz, A. & Attwood, C.G. (2013). Marine protected area improves yield without disadvantaging fishers. *Nat. Commun.*, 4, 2347.

Kingsford, M.J. (2008). Contrasting patterns of reef utilization and recruitment of coral trout (*Plectropomus leopardus*) and snapper (*Lutjanus carponotatus*) at One Tree Island, southern Great Barrier Reef. *Coral Reefs*, 28, 251–264.

Lauck, T., Clark, C.W., Mangel, M. & Munro, G.R. (1998). Implementing the precautionary principle in fisheries management through marine reserves. *Ecol. Appl.*, 8, S72–S78.

Lédée, E.J.I., Sutton, S.G., Tobin, R.C. & De Freitas, D.M. (2012). Responses and adaptation strategies of commercial and charter fishers to zoning changes in the Great Barrier Reef Marine Park. *Mar. Policy*, 36, 226–234.

Leigh, G.M., Campbell, A.B., Lunow, C.P. & Neill, M.F.O. (2014). *Stock assessment of the Queensland east coast common coral trout (*Plectropomus leopardus*) fishery*. Technical Report of the Queensland Department of Agriculture, Fisheries and Forestry. http://era.daf.qld.gov.au/4547/.

Lester, S.E., Halpern, B.S., Grorud-Colvert, K., Lubchenco, J., Ruttenberg, B.I., Gaines, S.D., Airam, S. & Warner, R.R. (2009). Biological effects within no-take marine reserves: a global synthesis. *Mar. Ecol. Prog. Ser.*, 384, 33–46.

Mangel, M. (2000). Irreducible uncertainties, sustainable fisheries and marine reserves. *Evol. Ecol. Res.*, 2, 547–557.

Mapstone, B., Carlos, G., Lunow, C.P. & Reid, A.E. (2004a). *Uncertainty in Length Measurements of Live Coral Trout: Implications for Compliance to and Enforcement of Minimum Legal Size Limits. CRC Reef Research Centre Technical Report No. 54.* CRC Reef Research Centre, Townsville.

Mapstone, B.D., Davies, C.R., Little, L.R., Punt, A.E., Smith, A.D.M., Pantus, F., Lou, D.C., Williams, A.J., Jones, A., Ayling, A.M., Russ, G.R. & Mcdonald, A.D. (2004b). *The effects of line fishing on the Great Barrier Reef and evaluations of alternative potential* *management strategies. CRC Reef Research Centre Technical Report No 52. CRC Reef Res. Cent. Tech. Rep. No 52.* CRC Reef Research Centre, Townsville, Australia.

Mapstone, B.D., Little, L.R., Punt, a. E., Davies, C.R., Smith, a. D.M., Pantus, F., McDonald, A.D., Williams, A.J. & Jones, A. (2008). Management strategy evaluation for line fishing in the Great Barrier Reef: Balancing conservation and multi-sector fishery objectives. *Fish. Res.*, 94, 315–329.

Maynard, J.A., Beeden, R., Puotinen, M., Johnson, J.E., Marshall, P., van Hooidonk, R., Heron, S.F., Devlin, M., Lawrey, E., Dryden, J., Ban, N., Wachenfeld, D. & Planes, S. (2015). Great Barrier Reef no-take areas include a range of disturbance regimes. *Conserv. Lett.*, DOI: 10.1111/conl.12198.

McClanahan, T.R. & Mangi, S. (2000). Spillover of exploitable fishes from a marine park and its effect on the adjacent fishery. *Ecol. Appl.*, 10, 1792–1805.

McCook, L.J., Almany, G.R., Berumen, M.L., Day, J.C., Green, A.L., Jones, G.P., Leis, J.M., Planes, S., Russ, G.R., Sale, P.F. & Thorrold, S.R. (2009). Management under uncertainty: guide-lines for incorporating connectivity into the protection of coral reefs. *Coral Reefs*, 28, 353–366.

McCook, L.J., Ayling, T., Cappo, M., Choat, J.H., Evans, R.D., De Freitas, D.M., Heupel, M., Hughes, T.P., Jones, G.P., Mapstone, B., Marsh, H., Mills, M., Molloy, F.J., Pitcher, C.R., Pressey, R.L., Russ, G.R., Sutton, S., Sweatman, H., Tobin, R., Wachenfeld, D.R. & Williamson, D.H. (2010). Adaptive management of the Great Barrier Reef: a globally significant demonstration of the benefits of networks of marine reserves. *Proc. Natl. Acad. Sci. U.S.A.*, 107, 18278–18285.

Micheli1, F., Saenz-Arroyo, A., Greenley, A., Vazquez, L., Montes J.A.E., Rossetto, M. & De Leo, G.A. (2012) Evidence that marine reserves enhance resilience to climatic impacts. *PLoS One*, 7, e40832.

Moffitt, E., White, J. & Botsford, L. (2013). Accurate assessment of marine protected area success depends on metric and spatiotemporal scale of monitoring. *Mar. Ecol. Prog. Ser.*, 489, 17–28.

Osborne, K., Dolman, A.M., Burgess, S.C. & Johns, K.A. (2011). Disturbance and the dynamics of coral cover on the Great Barrier Reef (1995-2009). *PLoS One*, 6, e17516.

Pelc, R.A., Warner, R.R., Gaines, S.D. & Paris, C.B. (2010). Detecting larval export from marine reserves. *Proc. Natl. Acad. Sci. U.S.A.*, 107, 18266–71.

Petersen, C.W. & Warner, R.R. (2006). Ecological context of reproductive behaviour. In: *Coral reef fishes: Dynamics and diversity in a complex ecosystem* (ed. Sale, P.F.). Gulf Professional Publishing, pp. 103–120.

Pitchford, J.W., Codling, E.A. & Psarra, D. (2007). Uncertainty and sustainability in fisheries and the benefit of marine protected areas. *Ecol. Modell.*, 207, 286–292.

Ricker, W.E. (1975) Computation and interpretation of biological statistics of fish populations. *Bull. Fish. Res. B. Can.* 191, 382 pp

Rimmer, M.A., Garrett, R.N. & Samoilys, M.A. (1994). In vitro fertilization of eggs of coral trout, *Plectropomus leopardus* (Serranidae), collected from an aggregation site on the Great Barrier Reef, Australia. *Bull. Mar. Sci.*, 54, 356–358.

Roberts, C.M., Branch, G., Bustamante, R.H., Castilla, J.C., Dugan, J., Halpern, B.S., Lafferty, K.D., Leslie, H., Lubchenco, J., Mcardle, D., Ruckelshaus, M. & Warner, R.R. (2003). Application of ecological criteria in selecting marine reserves and developing reserve networks selecting marine reserves and developing, *Ecol. Apps.* 13, 215–228.

Roberts, C.M., Polunin, N.C.V.C. & Roberts, M. (1991). Are marine reserves effective in management of reef fisheries? *Rev. Fish Biol. Fish.*, 1, 65–91.

Rodwell, L., Barbier, E., Roberts, C. & McClanahan, T.R. (2003). The importance of habitat quality for marine reserve fishery linkages. *Can. J. Fish. Aquat. Sci.*, 60, 171–181.

Rose, K.A., Cowan, J.H., Winemiller, K.O., Myers, R.A. & Hilborn, R. (2001). Compensatory density dependence in fish populations: importance, contoversy, understanding and prognosis. *Fish. Fish.*, 2, 293-327.

Russ. (1991). Coral reef fisheries: effects and yields. In: *The ecology of fishes on coral reefs* (ed. Sale, P.F.). Academic Press, San Diego, CA, pp. 601–634.

Russ, G., Cheal, A., Dolman, A. & Emslie, M. (2008). Rapid increase in fish numbers follows creation of world's largest marine reserve network. *Curr. Biol.*, 18, 514–515.

Russ, G.R. (2002). Yet another review of marine reserves as reef fishery management tools. In: *Coral Reef Fishes* (ed. Sale, P.F.). Acadmeic Press, Burlington, pp. 421–443.

Russ, G.R. & Alcala, A.C. (2010). Decadal-scale rebuilding of predator biomass in Philippine marine reserves. *Oecologia*, 163, 1103–6.

Russ, G.R., Alcala, A.C., Maypa, A.P., Calumpong, H.P. & White, A.T. (2004a). Marine reserve benefits local fisheries. *Ecol. Appl.*, 14, 597–606.

Russ, G.R., Lou, D.C. & Ferreira, B.P. (2004b). *A long-term study on populaiton structure of the coral trout* Plectropomu leopardus *on reefs open and closed to fishing in the central Great Barrier Reef. CRC Reef Research Centre Technical Report No. 3.* CRC Reef Research Centre, Townsville

Russ, G.R., Lou, D.C., Higgs, J.B. & Ferreira, B.P. (1998). Mortality rate of a cohort of the coral trout, Plectropomus leopardus, in zones of the Great Barrier Reef Marine Park closed to fishing. *Mar. Freshw. Res.*, 49, 507–511.

Sadovy de Mitcheson, Y., Craig, M.T., Bertoncini, A.A., Carpenter, K.E., Cheung, W.W.L., Choat, J.H., Cornish, A.S., Fennessy, S.T., Ferreira, B.P., Heemstra, P.C., Liu, M., Myers, R.F., Pollard, D.A., Rhodes, K.L., Rocha, L.A., Russell, B.C., Samoilys, M.A. & Sanciangco, J. (2013). Fishing groupers towards extinction: a global assessment of threats and extinction risks in a billion dollar fishery. *Fish Fish.*, 14, 119–136.

Sale, P.F., Cowen, R.K., Danilowicz, B.S., Jones, G.P., Kritzer, J.P., Lindeman, K.C., Planes, S., Polunin, N.V.C., Russ, G.R., Sadovy, Y.J. & Steneck, R.S. (2005). Critical science gaps impede use of no-take fishery reserves. *Trends Ecol. Evol.*, 20, 74–80.

Sale, P.F., Hanski, I. & Kritzer, J. (2006). The merging of metapopultion theory and marine ecology: establishing the historical context. In: *Marine Metapopulations* (eds. Kritzer, J. & Sale, P.F.). Elsevier Academic Press, London.

Salomon, A.K., Gaichas, S.K., Jensen, O.P., Agostini, V.N., Sloan, N.A., Rice, J., McClanahan, T.R., Ruckelshaus, M.H., Levin, P.S., Dulvy, N.K. & Babcock, E.A. (2011). Bridging the divide between fisheries and marine conservation science. *Bull. Mar. Sci.*, 87, 251-274

Samoilys, M.A. (1997). Movement in a large predatory fish: coral trout, *Plectropomus leopardus* (Pisces: Serranidae), on Heron Reef, Australia. *Coral Reefs*, 16, 151–158.

Samoilys, M.A. (2002). Reproductive dynamics of an exploited seranid on the Great Barrier Reef. Thesis. School of Marine and Tropical Biology, James Cook University, Townsville.

Sánchez Lizaso, J.L., Goñi, R., Reñones, O., García Charton, J. A., Galzin, R., Bayle, J.T., Sánchez Jerez, P., Pérez Ruzafa, A. & Ramos, A.A.. (2000). Density dependence in marine protected populations: a review. *Environ. Conserv.*, 27, 144–158.

Sanchirico, J.N. & Wilen, J.E. (2001). A Bioeconomic Model of Marine Reserve Creation. *J. Environ. Econ. Manage.*, 42, 257–276.

Sen, S. (2010). Developing a framework for displaced fishing effort programs in marine protected areas. *Mar. Policy*, 34, 1171–1177.

Short, F.T. & Wyllie-Echeverria, S. (1996). Natural and human-induced disturbance of seagrasses. *Environ. Conserv.*, 23, 17.

Sladek-Nowlis, J. & Roberts, C. (1999). Fisheries benefits and optimal design of marine reserves. *Fish. Bull.*, 97, 604–616.

Smith, M.D. & Wilen, J.E. (2003). Economic impacts of marine reserves: the importance of spatial behavior. *J. Environ. Econ. Manage.*, 46, 183–206

Starfield, A.M. (1997). A pragmatic approach to modeling for wildlife management. *J. Wildl. Manag.*, 61, 261–270.

Stefansson, G. & Rosenberg, A.A. (2005). Combining control measures for more effective management of fisheries under uncertainty: quotas, effort limitation and protected areas. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.*, 360, 133–46.

Suuronen, P., Jounela, P. & Tschernij, V. (2010). Fishermen responses on marine protected areas in the Baltic cod fishery. *Mar. Policy*, 34, 237–243.

Thompson, A.A. & Dolman, A.M. (2010). Coral bleaching: One disturbance too many for near-shore reefs of the Great Barrier Reef. *Coral Reefs*, 29, 637–648.

Tobin, A., Schlaff, A., Tobin, R., Penny, A., Ayling, T., Ayling, A., Krause, B., Welch, D., Sutton, S., Sawynok, B., Marshall, N., Marshall, P. & Maynard, J. (2010). *Adapting to change: minimising uncertainty about the effects of rapidly-changing environmental conditions on the Queensland Coral Reef Fin Fish Fishery. Final Report to the Fisheries Research & Development Corporation, Project 2008/103.* Fishing & Fisheries Research Centre Technical Report No. 11, James Cook University, Townsville, Australia (172pp.).

Watson, J.E.M., Dudley, N., Segan, D.B. & Hockings, M. (2014). The performance and potential of protected areas. *Nature*, 515, 67–73.

Welch, D.J., Mapstone, B.D. & Begg, G. A. (2008). Spatial and temporal variation and effects of changes in management in discard rates from the commercial reef line fishery of the Great Barrier Reef, Australia. *Fish. Res.*, 90, 247–260.

Wen, C.K.C., Almany, G.R., Williamson, D.H., Pratchett, M.S., Mannering, T.D., Evans, R.D., Leis, J.M., Srinivasan, M. & Jones, G.P. (2013). Recruitment hotspots boost the effectiveness of no-take marine reserves. *Biol. Conserv.*, 166, 124–131.

Wenger, A.S., Johansen, J.L. & Jones, G.P. (2012). Increasing suspended sediment reduces foraging, growth and condition of a planktivorous damselfish. *J. Exp. Mar. Bio. Ecol.*, 428, 43–48.

West, C.D., Dytham, C., Righton, D. & Pitchford, J.W. (2009). Preventing overexploitation of migratory fish stocks: The efficacy of marine protected areas in a stochastic environment. *ICES J. Mar. Sci.*, 66, 1919–1930.

White, C. (2009). Density dependence and the economic efficacy of marine reserves. *Theor. Ecol.*, 2, 127–138.

White, C. & Kendall, B.E. (2007). A reassessment of equivalence in yield from marine reserves and traditional fisheries managament. *Oikos*, 116, 2039–2043.

White, C., Kendall, B.E., Gaines, S., Siegel, D.A. & Costello, C. (2008). Marine reserve effects on fishery profit. *Ecol. Lett.*, 11, 370–9.

White, J., Samhouri, J. & Stier, A. (2010). Synthesizing mechanisms of density dependence in reef fishes: behavior, habitat configuration, and observational scale. *Ecology*, 91, 1949–1961.

White, J.W., Botsford, L.W., Baskett, M.L., Barnett, L.A.K., Barr, R.J. & Hastings, A. (2011). Linking models with monitoring data for assessing performance of no-take marine reserves. *Front. Ecol. Environ.*, 9, 390–399.

White, J.W., Botsford, L.W., Hastings, A., Baskett, M.L., Kaplan, D.M. & Barnett, L.A.K. (2013). Transient responses of fished populations to marine reserve establishment. *Conserv. Lett.*, 6, 180–191.

Williamson, D.H., Ceccarelli, D.M., Evans, R.D., Jones, G.P. & Russ, G.R. (2014). Habitat dynamics, marine reserve status, and the decline and recovery of coral reef fish communities. *Ecol. Evol.*, 4, 337–54.

Williamson, D.H., Russ, G.R. & Ayling, A.M. (2004). No-take marine reserves increase abundance and biomass of reef fish on inshore fringing reefs of the Great Barrier Reef. *Environ. Conserv.*, 31, 149–159.

Zeller, D.C. (1997). Home range and activity patterns of the coral trout Plectropomus leopardus (Serranidae). *Mar. Ecol. Prog. Ser.*, 154, 65–77.

Zeller, D.C. & Russ, G.R. (1998). Marine reserves: patterns of adult movement of the coral trout (*Plectropomus leopardus* (Serranidae)). *Can. J. Fish. Aquat. Sci.*, 55, 917–924.

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APPENDICES

Appendix A: ***Symbolic proofs of initial yield decrease and asymptotic metapopulation growth rate increase (Chapter 2)***

A consistent outcome of our models in Chapter 2 was that implementing reserves initially decreased yields, but they later recovered due to increased asymptotic growth rates. To better understand the demographic mechanisms behind our results, we reduced the model to a simple unstructured, well-mixed, two-population model, which we could explore symbolically. Here we use this model to determine the conditions under which reserves will always 1) decrease yields initially and 2) increase the asymptotic metapopulation growth rate, with fishing pressure reallocated proportional to the area protected within reserves.

Consider a simplified well-mixed two-population model, whose dynamics over time are described by;

$$N_{1,u,t+1} = b\,A\,N_{1,u,t} + b\,A\,N_{2,u,t} + S_F\,N_{1,u,t} \tag{A.1}$$

$$N_{2,u,t+1} = b\,(1-A)\,N_{1,u,t} + b\,(1-A)\,N_{2,u,t} + S_F\,N_{2,u,t} \tag{A.2}$$

$$N_{1,r,t+1} = b\,A\,N_{1,r,t} + b\,A\,N_{2,r,t} + S_U\,N_{1,r,t} \tag{A.3}$$

$$N_{2,r,t+1} = b\,(1-A)\,N_{1,r,t} + b\,(1-A)\,N_{2,r,t} + S_{FF}\,N_{2,r,t}\,, \tag{A.4}$$

where $N_{i,u,t}$, and $N_{i,r,t}$ is the biomass of population i (i = [1,2]) before (subscript u) and after reserve (subscript r) establishment respectively, b indicates the per-capita births, and A is proportion of habitat area assigned protection.

Prior to reserve establishment both populations are subjected to fishing, and per-capita adult survival ($S_F = e^{-m-m_f}$) is a function of the rate of both natural (m) and fishing mortality (m_f). After reserve establishment N_1 is protected as a reserve and adult survival in this population becomes $S_U = e^{-m}$ (mortality due to fishing removed). At the same time the fishing pressure experienced by the metapopulation prior to reserve establishment is redistributed into the area that remains open to harvesting, and adult survival in N_2 becomes $S_{FF} = e^{-m-\frac{m_f}{1-A}}$. This follows the assumption of 'fishery squeeze', as per Chapter 2.

Hence, the total metapopulation dynamics ($N_T = N_1 + N_2$) for each scenario are described by

$$N_{T,u,t+1} = b\, N_{T,u,t} + S_F\, N_{T,u,t} \tag{A.5}$$

$$N_{T,r,t+1} = b\, N_{T,r,t} + S_U\, N_{1,r,t} + S_{FF}\, N_{2,r,t}\ ; \tag{A.6}$$

growth of the metapopulation at time *t,* for each scenario, is

$$\frac{N_{T,u,t+1}}{N_{T,u,t}} = b + S_F \tag{A.7}$$

$$\frac{N_{T,r,t+1}}{N_{T,r,t}} = b + S_U(1 - p_t) + S_{FF}\, p_t, \tag{A.8}$$

where $(1 - p_t) = \frac{N_{1,r,t}}{N_{T,r,t}}$ & $p_t = \frac{N_{2,r,t}}{N_{T,r,t}}$ (note that p_t is the proportion of the metapopulation that is in the harvestable area at time *t*); and the yields at time *t*, with reserves and without reserves respectively, are

$$Y_{u,t} = y_f\, N_{T,u,t} = y_f\, (\, b\, N_{T,u,t-1} + S_F\, N_{T,u,t-1}\,)\text{, and} \tag{A.9}$$

$$Y_{r,t} = y_{fr}\, N_{2,r,t} = y_{fr}\, [\, b\,(1 - A)\, N_{1,r,t-1} + b\,(1 - A)\, N_{2,r,t-1} + S_{FF}\, N_{2,r,t-1}] \tag{A.10}$$

where y_f and y_{fr} are the proportion of fish caught per year with and without reallocated effort respectively. Note that without reserves both populations are fished, whereas only the second population is fished when reserves are present.

Proposition/Theorem A.1: Reserve establishment will reduce yields in the first year, relative to a scenario without reserves, that is $Y_{u,1} > Y_{r,1}$.

Proof: Since both populations are experiencing the same demographic rates without reserves, and the larvae are well mixed, the initial stable population distribution will reflect the area assigned each population, i.e. $N_{1,r,0} = A$ and $N_{2,r,0} = 1 - A$. This is assuming that the metapopulation has been fished for a time such that it has reached an asymptotic state prior to reserve establishment, as discussed in Chapter 2. Substituting $N_{1,r,0} = A$ and $N_{2,r,0} = 1 - A$ into equations A.9 & A.10 gives

$Y_{u,1} = y_f\ [\ b + S_F\ ]$, and

$$Y_{r,1} = y_{fr}\,[\,b\,(1-A)A + b\,(1-A)(1-A) + S_{FF}\,(1-A)]$$

$$= y_{fr}\,(1-A)\,[\,bA + b - bA + S_{FF}\,]$$

$$= y_{fr}\,(1-A)\,(\,b\; + S_{FF})\,.$$

For $Y_{u,1} > Y_{r,1}$ to be true, then

$$\frac{y_f}{y_{fr}} > \frac{b+S_{FF}}{b+S_F}(1-A) \qquad \text{(A.11)}$$

must also be true. That is, reserves will decrease yields initially whenever the change in the proportion of fish available to fishers in the first year (i.e. harvestable fish that have survived the previous year, plus births into the harvestable area) is less than the change in the proportion of fish caught per year with reserve establishment.

Assuming that fish are caught continuously throughout the year, the change in yield over time, before reserves are established, is described by

$$\frac{d\mathrm{Y}_{u,t,(\tau)}}{d\tau} = m_f\,\mathrm{N}_{u,T,(\tau)}\;,$$

where τ ($\tau = [0,1]$) is time within the year. Substituting in the abundance of fish at time τ during the year t+1:

$$\mathrm{N}_{u,T,(\tau)} = \mathrm{N}_{u,T,t}\,\mathrm{e}^{-(m+m_f)\tau},$$

and integrating with the initial condition that no fish have been caught at the start of the year gives the cumulative yield at the year ($\tau = 1$):

$$\mathrm{Y}_{u,t} = \mathrm{N}_{T,t}\,\frac{m_f}{(m+m_f)}\left[1-\mathrm{e}^{-(m+m_f)}\right].$$

Therefore, the proportions of fish caught in each scenario (y_f and y_{fr}) can be related to the survival of adults from fishing (S_F and S_{FF}) and the adult mortality rates (m_f and m) by the equations

$$y_f = \frac{m_f}{m+m_f}\,[\,1-S_F]\qquad , \qquad \text{and}$$

(A.12)

$$y_{fr} = \frac{\frac{m_f}{1-A}}{m+\frac{m_f}{1-A}}\left[1 - S_{FF}\right] \quad . \qquad \text{(A.13)}$$

Substituting equations A.12 & A.13 into inequality A.11 gives

$$\frac{\frac{m_f}{m+m_f}}{\frac{m_f/(1-A)}{m+m_f/(1-A)}}\,\frac{1-S_F}{1-S_{FF}} > \frac{b+S_{FF}}{b+S_F}(1-A)$$

$$\frac{m_f}{m+m_f}\,\frac{m+\frac{m_f}{1-A}}{m_f}\,\frac{1-S_F}{1-S_{FF}} > \frac{b+S_{FF}}{b+S_F}$$

$$\frac{m+\frac{m_f}{1-A}}{m+m_f}\,\frac{1-S_F}{1-S_{FF}} > \frac{b+S_{FF}}{b+S_F} \quad . \qquad \text{(A.14)}$$

Substituting in the survival terms $S_F = e^{-m-m_f}$ and $S_{FF} = e^{-m-\frac{m_f}{1-A}}$, into the left-hand-side of inequality A.14, gives the expression

$$\frac{m+\frac{m_f}{1-A}}{m+m_f}\,\frac{1-e^{-m-m_f}}{1-e^{-m-\frac{m_f}{1-A}}} \quad . \qquad \text{(A.15)}$$

The power series approximations for the exponential terms in expression A.15 are

$$e^{-m-m_f} \approx 1 + \left(-m - m_f\right) + \frac{\left(-m-m_f\right)^2}{2!} + \frac{\left(-m-m_f\right)^3}{3!} + \cdots \qquad \text{(A.16)}$$

$$e^{-m-\frac{m_f}{1-A}} \approx 1 + \left(-m - \frac{m_f}{1-A}\right) + \frac{\left(-m-\frac{m_f}{1-A}\right)^2}{2!} + \frac{\left(-m-\frac{m_f}{1-A}\right)^3}{3!} + \cdots \qquad \text{(A.17)}$$

Substituting the power series approximations A.16 & A.17 into expression A.15 gives

$$\frac{m+\frac{m_f}{1-A}}{m+m_f}\,\frac{1-e^{-m-m_f}}{1-e^{-m-\frac{m_f}{1-A}}} = \frac{m+\frac{m_f}{1-A}}{m+m_f}\,\frac{1-\left[\,1+\left(-m-m_f\right)+\frac{\left(-m-m_f\right)^2}{2!}+\frac{\left(-m-m_f\right)^3}{3!}+\cdots\,\right]}{1-\left[\,1+\left(-m-\frac{m_f}{1-A}\right)+\frac{\left(-m-\frac{m_f}{1-A}\right)^2}{2!}+\frac{\left(-m-\frac{m_f}{1-A}\right)^3}{3!}+\cdots\,\right]}$$

$$= \frac{m+\frac{m_f}{1-A}}{m+m_f}\ \frac{-(-m-m_f)-\frac{(-m-m_f)^2}{2!}-\frac{(-m-m_f)^3}{3!}-\cdots}{-\left(-m-\frac{m_f}{1-A}\right)-\frac{\left(-m-\frac{m_f}{1-A}\right)^2}{2!}-\frac{\left(-m-\frac{m_f}{1-A}\right)^3}{3!}-\ldots}$$

$$= \frac{m+\frac{m_f}{1-A}}{m+m_f}\ \frac{-(-m-m_f)}{-\left(-m-\frac{m_f}{1-A}\right)}\ \frac{1+(-m-m_f)+\frac{(-m-m_f)^2}{2!}+\frac{(-m-m_f)^3}{3!}+\cdots}{1+\left(-m-\frac{m_f}{1-A}\right)+\frac{\left(-m-\frac{m_f}{1-A}\right)^2}{2!}+\frac{\left(-m-\frac{m_f}{1-A}\right)^3}{3!}+\ldots}$$

$$= \frac{1+(-m-m_f)+\frac{(-m-m_f)^2}{2!}+\frac{(-m-m_f)^3}{3!}+\cdots}{1+\left(-m-\frac{m_f}{1-A}\right)+\frac{\left(-m-\frac{m_f}{1-A}\right)^2}{2!}+\frac{\left(-m-\frac{m_f}{1-A}\right)^3}{3!}+\ldots}$$

$$= \frac{1-e^{-m-m_f}}{1-e^{-m-\frac{m_f}{1-A}}} = \frac{S_F}{S_{FF}}$$ (Substituting the exponentials back in for the power series)

Therefore $\frac{m+\frac{m_f}{1-A}}{m+m_f}\ \frac{1-S_F}{1-S_{FF}} > \frac{b+S_{FF}}{b+S_F}$ becomes

$$\frac{S_F}{S_{FF}} > \frac{b+S_{FF}}{b+S_F}$$

$$\frac{S_F\ (b+S_F\ )}{S_{FF}\ (b+S_{FF}\ )} > 1 \qquad \text{(A.18)}$$

Since $S_F > S_{FF}$ (by definition), then inequality A.18 is always true and reserve establishment will, therefore, always decrease yields initially.

Proposition/Theorem A.2: Reserves will increase asymptotic metapopulation growth rate, relative to a scenario without reserves.

Proof: For growth at any time after reserve implementation to be greater than a scenario without reserves, then

$$\frac{N_{T,u,t+1}}{N_{T,u,t}} < \frac{N_{T,r,t+1}}{N_{T,r,t}} \qquad \text{(A.19)}$$

must be true. Therefore,

$$S_F < S_U\ (1-p_t) + S_{FF}\ p_t \qquad \text{(A.20)}$$

must also be true (substituting equations A.7 & A.8 into inequality A.19). That is, the growth rate of the metapopulation, at any time t, will be greater with reserves if the average survival in the metapopulation at that time is greater than the per-capita survival without reserves (which is analogous to the average survival in a homogenous metapopulation).

To establish whether asymptotic growth will be greater with reserves, we need to consider the metapopulation at its stable population distribution. Under these conditions,

$$S_F < S_U\,(1-p) + S_{FF}\,p\,, \tag{A.21}$$

where p (the asymptotic proportion of the metapopulation in the harvestable area after reserves are established) is obtained from the eigenvector associated with the leading eigenvalue of the metapopulation projection matrix, for the scenario with reserves.

To explore these conditions further, we substitute in the survival terms $S_U = e^{-m}, S_F = e^{-m-m_f}$, and $S_{FF} = e^{-m-\frac{m_f}{1-A}}$

into inequality A.21 giving

$$e^{-m-m_f} < e^{-m}\,(1-p) + e^{-m-\frac{m_f}{1-A}}\,p$$

$$e^{-m_f} < (1-p) + e^{-\frac{m_f}{1-A}}\,p$$

$$0 < 1 - e^{-m_f} + p\,(e^{-\frac{m_f}{1-A}} - 1)$$

$$p\,(1 - e^{-\frac{m_f}{1-A}}) < 1 - e^{-m_f}$$

$$p < \frac{1-e^{-m_f}}{1-e^{-\frac{m_f}{1-A}}} \tag{A.22}$$

The power series approximations for the exponential terms in inequality A.22 are

$$e^{-m_f} \approx 1 + (-m_f) + \frac{(-m_f)^2}{2!} + \frac{(-m_f)^3}{3!} + \cdots \tag{A.23}$$

$$e^{-\frac{m_f}{1-A}} \approx 1 + \left(-\frac{m_f}{1-A}\right) + \frac{\left(-\frac{m_f}{1-A}\right)^2}{2!} + \frac{\left(-\frac{m_f}{1-A}\right)^3}{3!} + \cdots \tag{A.24}$$

Substituting the power series approximations A.23 and A.24 into inequality A.22 gives

$$p \ < \frac{1-[\,1+\left(-m_f\right)+\frac{\left(-m_f\right)^2}{2!}+\frac{\left(-m_f\right)^3}{3!}+\cdots\,]}{1-[\,1+\left(-\frac{m_f}{1-A}\right)+\frac{\left(-\frac{m_f}{1-A}\right)^2}{2!}+\frac{\left(-\frac{m_f}{1-A}\right)^3}{3!}+\cdots]}$$

$$p \ < \frac{\left(-m_f\right)+\frac{\left(-m_f\right)^2}{2!}+\frac{\left(-m_f\right)^3}{3!}+\cdots]}{\left(-\frac{m_f}{1-A}\right)+\frac{\left(-\frac{m_f}{1-A}\right)^2}{2!}+\frac{\left(-\frac{m_f}{1-A}\right)^3}{3!}+\cdots}$$

$$p \ < \frac{m_f}{\frac{m_f}{1-A}} \ \frac{1+\left(-m_f\right)+\frac{\left(-m_f\right)^2}{2!}+\ldots]}{1+\left(-\frac{m_f}{1-A}\right)+\frac{\left(-\frac{m_f}{1-A}\right)^2}{2!}+\ldots}$$

$$p \ < (1-A)\frac{1-m_f+\frac{{m_f}^2}{2!}-\frac{{m_f}^3}{3!}+\cdots}{1-\frac{m_f}{1-A}+\frac{(\frac{m_f}{1-A})^2}{2!}-\frac{(\frac{m_f}{1-A})^3}{3!}+\cdots} \, . \tag{A.25}$$

To simplify further we can substitute the exponentials in inequality A.25 for the power series approximations A.23 and A.24 to give

$$p \ < (1-A)\left(\frac{e^{-m_f}}{e^{-\frac{m_f}{1-A}}}\right). \tag{A.26}$$

Note that, given $m_f > 0$ and $1-A \in [0,1]$, $\frac{e^{-m_f}}{e^{-\frac{m_f}{1-A}}} = \frac{S_F}{S_{FF}} > 1$, which reflects the magnitude of decrease in adult survival in the harvested area (due to reallocated fishing pressure) when reserves are established.

Therefore, for reserves to increase the asymptotic metapopulation growth rate, the proportion of area that remains open to harvest must be greater than the proportion of the metapopulation biomass in the harvestable area after reserve establishment, discounted by the reduction in adult survival in that area; i.e.

$$p\ \frac{S_{FF}}{S_F} < (1-A)\,. \tag{A.27}$$

Note that if

$$p < (1-A)\,, \tag{A.28}$$

is true, then inequality A.27 will also be true (since $\frac{S_{FF}}{S_F} < 1$). To simplify the algebra, we will focus on establishing whether inequality A.28 is true for our model.

To establish the value of p (the proportion of the metapopulation available to fishers) and determine if inequality A.28 is true for our model, we need to consider the asymptotic population distribution with reserves. This can be calculated from leading eigenvector of the matrix form of the coupled linear equations A.3 & A.4, which is

$$\mathbf{M} = \begin{bmatrix} b\,A + S_U & b\,A \\ b\,(1-A) & b\,(1-A) + S_{FF} \end{bmatrix}.$$

The eigenvalues (**λ**) and eigenvectors (**w**) associated with matrix **M** are

$$\boldsymbol{\lambda} = \begin{bmatrix} \lambda_1 & 1 \\ 1 & \lambda_2 \end{bmatrix}, \text{ where}$$

$$\lambda_1 = \frac{S_{FF} + S_U + b + \sqrt{2*S_{FF}*b - 2*S_{FF}*S_U - 2*S_U*b + {S_{FF}}^2 + {S_U}^2 + b^2 + 4*A*b(S_U - S_{FF})}}{2}$$

$$\lambda_2 = \frac{S_{FF} + S_U + b - \sqrt{2*S_{FF}*b - 2*S_{FF}*S_U - 2*S_U*b + {S_{FF}}^2 + {S_U}^2 + b^2 + 4*A*b(S_U - S_{FF})}}{2}, \quad \text{and}$$

$$\mathbf{w} = \begin{bmatrix} W_1 & 1 \\ 1 & W_2 \end{bmatrix}, \text{ where } W_1 = -\frac{S_{FF} + b - Ab}{b(1-A)} +$$

$$\frac{S_{FF} + S_U + b + \sqrt{2*S_{FF}*b - 2*S_{FF}*S_U - 2*S_U*b + {S_{FF}}^2 + {S_U}^2 + b^2 + 4*A*b(S_U - S_{FF})}}{2*b(1-A)}$$

$$W_2 = -\frac{S_{FF} + b - Ab}{b(1-A)} +$$

$$\frac{S_{FF} + S_U + b - \sqrt{2*S_{FF}*b - 2*S_{FF}*S_U - 2*S_U*b + {S_{FF}}^2 + {S_U}^2 + b^2 + 4*A*b(S_U - S_{FF})}}{2*b(1-A)}.$$

Since A, b, S_U, S_F, and S_{FF} are, by definition, positive values, λ_1 will always be the leading eigenvalue. Therefore, we will rescale its associated eigenvector (W_1) to sum to one, to determine the stable population distribution (**n**):

$$\mathbf{n} = \begin{bmatrix} 1-p \\ p \end{bmatrix} = \begin{bmatrix} \frac{W}{1+W} \\ \frac{1}{1+W} \end{bmatrix}.$$

Therefore $p = \frac{1}{1+W} = [\,1 - \frac{S_{FF} + b - Ab}{b(1-A)} +$

$$\frac{S_{FF} + S_U + b + \sqrt{2*S_{FF}*b - 2*S_{FF}*S_U - 2*S_U*b + {S_{FF}}^2 + {S_U}^2 + b^2 + 4*A*b(S_U - S_{FF})}}{2*b(1-A)}\,]^{-1}$$

$$= [\, 1 - \frac{\frac{S_{FF}}{b}+1-A}{(1-A)} +$$

$$\frac{\frac{1}{2b}(\, S_{FF} + S_U + b + \sqrt{2 * S_{FF} * b - 2 * S_{FF} * S_U - 2 * S_U * b \; + \; {S_{FF}}^2 + {S_U}^2 + b^2 \; + \; 4 * A * b(\, S_U - S_{FF})}\,)}{(1-A)}\,]^{-1}$$

$$=$$

$$[\, \frac{-\frac{S_{FF}}{b} + \frac{1}{2b}(\, S_{FF} + S_U + b + \sqrt{2 * S_{FF} * b - 2 * S_{FF} * S_U - 2 * S_U * b \; + \; {S_{FF}}^2 + {S_U}^2 + b^2 \; + \; 4 * A * b(\, S_U - S_{FF})}\,)}{(1-A)}\,]^{-1}$$

$$= \frac{(1-A)}{-\frac{S_{FF}}{b} + \frac{1}{2b}(\, S_{FF} + S_U + b + \sqrt{2 * S_{FF} * b - 2 * S_{FF} * S_U - 2 * S_U * b \; + \; {S_{FF}}^2 + {S_U}^2 + b^2 \; + \; 4 * A * b(\, S_U - S_{FF})}\,)}$$

(A.29)

Obviously this is not a neat solution for *p.* We know, however, that by definition $S_{FF} < S_U$, so we can substitute S_{FF} for cS_U (where $c \in [0,1]$) in equation A.29, giving

$$p = \frac{(1-A)}{-\frac{c\,S_U}{b} + \frac{1}{2b}[\, c\,S_U + S_U + b + \sqrt{2\,b\,c\,S_U - 2\,c\,{S_U}^2 - 2\,b\,S_U + \; c^2\,{S_U}^2 + {S_U}^2 + b^2 + 4\,A\,b\,S_U\,(1-c)}\,]}\,.$$

(A.30)

Substituting equation A.26 into inequality A.24 gives us

$$\frac{(1-A)}{-\frac{c\,S_U}{b} + \frac{1}{2b}[\, c\,S_U + S_U + b + \sqrt{2\,b\,c\,S_U - 2\,c\,{S_U}^2 - 2\,b\,S_U + \; c^2\,{S_U}^2 + {S_U}^2 + b^2 + 4\,A\,b\,S_U\,(1-c)}\,]} < \; (1 - A)$$

$$1 < -\frac{c\,S_U}{b} + \frac{1}{2b}\,[\, c\,S_U \; + \; S_U \; + \; b \, +$$
$$\sqrt{2\,b\,c\,S_U - 2\,c\,{S_U}^2 - 2\,b\,S_U + \; c^2\,{S_U}^2 + {S_U}^2 + \; b^2 + 4\,A\,b\,S_U\,(1-c)}\;]$$

$$2b\left(1 + \frac{c\,S_U}{b}\right) \; < \; c\,S_U + S_U + b \, +$$
$$\sqrt{2\,b\,c\,S_U - 2\,c\,{S_U}^2 - \; 2\,b\,S_U \; + \; c^2\,{S_U}^2 + {S_U}^2 + \; b^2 \; + \; 4\,A\,b\,S_U\,(1-c)}$$

$$2b + 2\,c\,S_U - \; c\,S_U - S_U - \; b \; <$$
$$\sqrt{2\,b\,c\,S_U \; - \; 2\,c\,{S_U}^2 - \; 2\,b\,S_U \; + \; c^2\,{S_U}^2 + {S_U}^2 + \; b^2 \; + \; 4\,A\,b\,S_U\,(1-c)}$$

$$b + c\,S_U - S_U < \sqrt{2\,b\,c\,S_U - 2\,c\,{S_U}^2 - 2\,b\,S_U + c^2\,{S_U}^2 + {S_U}^2 + b^2 + 4\,A\,b\,S_U\,(1-c)}$$

$$[\,b + S_U(c-1)\,]^2 < 2\,b\,c\,S_U - 2\,c\,{S_U}^2 - 2\,b\,S_U + c^2\,{S_U}^2 + {S_U}^2 + b^2 + 4\,A\,b\,S_U\,(1-c)$$

$$b^2 + 2\,b\,S_U(c-1) + {S_U}^2(c-1)^2 < 2\,b\,c\,S_U - 2\,c\,{S_U}^2 - 2\,b\,S_U + c^2\,{S_U}^2 + {S_U}^2 + b^2 + 4\,A\,b\,S_U\,(1-c)$$

$$b^2 - 2\,b\,S_U + {S_U}^2 + 2\,c\left(bS_U - {S_U}^2\right) + c^2{S_U}^2 < b^2 - 2\,b\,S_U + {S_U}^2 + 4A\,b\,S_U + 2c\,(bS_U - 2{S_U}^2) - 4A\,b\,S_U c + c^2\,{S_U}^2$$

$$0 < 4A\,b\,S_U - 4A\,b\,S_U c$$

$$0 < 1 - c$$

Since $c < 1$ is a condition of the system, $p < 1 - A$ is true, and it follows that $p\,\frac{S_{FF}}{S_F} < (1 - A)$ is also true. Therefore reserves will always increase the asymptotic metapopulation growth rate when fishing effort is reallocated inversely proportional to the area remaining available to fishers at the time of reserve establishment. Note that in this model the proportion of area protected is equal to the proportion of the metapopulation biomass which is protected at the time of reserve establishment, i.e. $\frac{N_{1,r,0}}{N_{T,r,0}} = A$ and $\frac{N_{2,r,0}}{N_{T,r,0}} = 1 - A$.

Appendix B: ***Developing a dispersal kernel for Coral Trout in the Keppel Islands group***

To estimate the dispersal location kernel for coral trout in the Keppel Island group, we used data from a recent parentage analysis study in which a portion of recruited juveniles sampled from a range of reefs (n = 19) were assigned to one of three natal reefs (Clam Bay, Middle Island, and Egg Rock; Figure B1; Harrison et al. 2012). We assumed that the number of juveniles that disperse among reefs is a function of the Euclidian distance between the natal and destination reefs and the availability and quality of settlement habitat at the destination reef. To describe dispersal among reefs, we fitted four dispersal location kernel functions (see below) commonly used in ecology (Almany *et al.*, 2013; Nathan et al., 2012). To determine the best fit function we considered the negative log-likelihood of observing the recorded number of juveniles that have travelled from their natal reefs to the destination reefs given different values of the kernel shape parameter (ϕ). The ϕ value with the minimum Akaike Information Criterion (corrected for finite sample size; AICc) value was taken as the best estimate of true ϕ, and the dispersal function with the minimum negative log-likelihood was considered the best fit function (all functions had the same number of parameters).

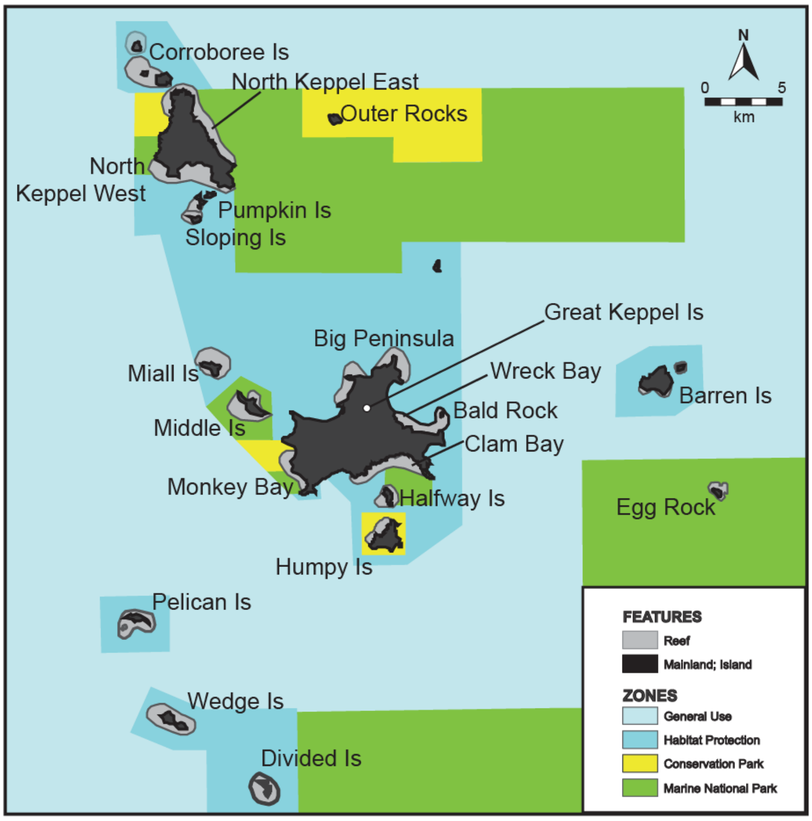


Figure B1 Keppel Island region showing major reef areas

The probability of a juvenile dispersing from its natal reef to a given destination reef ($\beta_{y,x}$) is either;

$$\beta_{y,x} = \frac{1}{2*\pi*\phi^2}\, e^{-\frac{D_{y,x}}{\phi}},$$

following Negative Exponential dispersal,

$$\beta_{y,x} = \frac{1}{\pi*\phi^2}\, e^{-\frac{{D_{y,x}}^2}{\phi^2}},$$

following Gaussian dispersal,

$$\beta_{y,x} = \frac{3}{2*\pi*\phi^2*\Gamma(\frac{2}{3})}\, e^{-\frac{{D_{y,x}}^3}{\phi^3}},$$

following Ribbens dispersal,

$$\beta_{y,x} = \begin{cases} \phi, & x = y \\ 1 - \phi, & x \neq y \end{cases},$$

assuming a proportion self-recruit and all other larval are distributed evenly among the other non-natal reefs (adjusted LPER dispersal, $\phi \in [0,1]$)

where $D_{y,x}$ is the Euclidian distance between reefs x (natal) and y (destination).

Recent work suggests that the recruitment of newly settled juvenile coral trout is greatly influenced by the availability of certain habitat types (Wen et al. 2013). As juveniles sampled for parentage analysis were post-recruitment, we accounted for the differences in the quantity and quality of settlement habitat among reefs by discounting the proportion of juveniles expected at a given reef ($\beta_{x,y}$) by a relative habitat parameter for each destination reef: H_y. Wen *et al.* (2013) demonstrated preferences by coral trout juveniles for habitats characterised by corymbose and arboresent *Acropora* on loose substrates (sand/rubble). Data suggests that, on average, these habitat types support 2.3 times the number of juveniles found on other habitat in the reef-flat (primary settlement reef zone; Wen *et al.* 2013). Total reef flat area (preferred and other) was measured for each destination reef in the Keppel Islands group and weighted by their preference by juveniles (2.3x for preferred and 1x for other). These values were then normalised relative to the reef with the maximum weighted settlement habitat to give H_y.

The habitat weighted probabilities were then discretised such all larvae from a given natal reef travel to one of the 19 destination reefs. This gives the probability of a juvenile from natal reef x dispersing to destination reef y and successfully establishing in their destination reef as

$$p_{y,x} = \frac{H_y * \beta_{y,x}}{\sum_{y=1}^{19} H_y * \beta_{y,x}}.$$

Models not accounting for juvenile habitat preference (but amount of habitat available) or amount of available habitat (preferred or otherwise), were also considered for each of the dispersal functions. A multinomial distribution best describes the sampling process where the probability of observing $\{J_{1,x}, J_{2,x}, \ldots, J_{19,x}\}$ juveniles from natal reef x (3 sampled natal reefs), in each of the 19 destination reefs (with N trials) was

$$P(\{J_{1,x}, J_{2,x}, \ldots, J_{19,x}\}) = \frac{N!}{(J_{1,x})!(J_{2,x})! \ldots (J_{19,x})!} p_{1,,x}{}^{J_{1,x}} p_{2,x}{}^{J_{2,x}} \ldots p_{19,x}{}^{J_{19,x}},$$

Since the multinomial coefficient (first term in the likelihood) is independent of the estimated parameter ϕ, we can follow convention and drop this constant from the likelihood. We maximised the product of likelihoods (sum of log-likelihoods) from all reefs, because only a subset of natal reefs was sampled and we required a generic kernel for the region. In doing so we assume that dispersal processes are the same for all larvae among all reefs. Hence the negative log-likelihood dispersal function for all natal reefs constrained becomes

$$\boldsymbol{L}(\phi \mid \{J_{1,1}, \ldots, J_{19,n}\}) = \sum_{x=1}^{3} -ln[p_{1,x}{}^{J_{1,x}} p_{2,x}{}^{J_{2,x}} \ldots p_{19,x}{}^{J_{19,x}}].$$

We calculated 95% confidence intervals for the best-fit ϕ values based on the likelihood ratio test.

To assess the validity of using one fitted kernel shape parameter value (ϕ) for all reefs in the Keppel Islands, we compared the constrained model to one in which ϕ were fitted separately to each of the three natal reefs (ϕ_1, ϕ_2, ϕ_3), and a combined likelihood calculated for the entire data set. All models were compared using AICc with the number of parameters being one for the constrained ϕ models, and three for the models in which ϕ was fitted separately for each natal reef, and a total sample size of 58 juveniles assigned parentage.

B.1 Results

Of the four candidate dispersal kernel functions fitted with a constrained shape parameter value (ϕ) for all natal reefs, a negative exponential kernel function was the best fit to the data (Figure B2, Table B.1). The Gaussian dispersal kernel function performed only slightly worse. All dispersal location kernel functions performed better than dispersal following an adjusted LPER assumption where the probability of dispersing among non-natal reefs was constant (i.e. was not a function of distance). This was true irrespective of whether juvenile habitat preference and/or habitat availability was included in the model. Models where separate ϕ values were fitted to each natal reef separately were comparable (ΔAICc < 1.4) or performed worse than the best-fit constrained model, where ϕ was fitted to all reefs simultaneously (Table B.1). This suggests that it is reasonable to assume a fixed ϕ for all reefs.

Overall, models which included both juvenile preference and availability of habitat performed slightly better than those that considered only the amount of settlement habitat present at each reef. Models that did not account for any difference in habitat availability and quality among reefs performed markedly worse than other models (Table B.1).

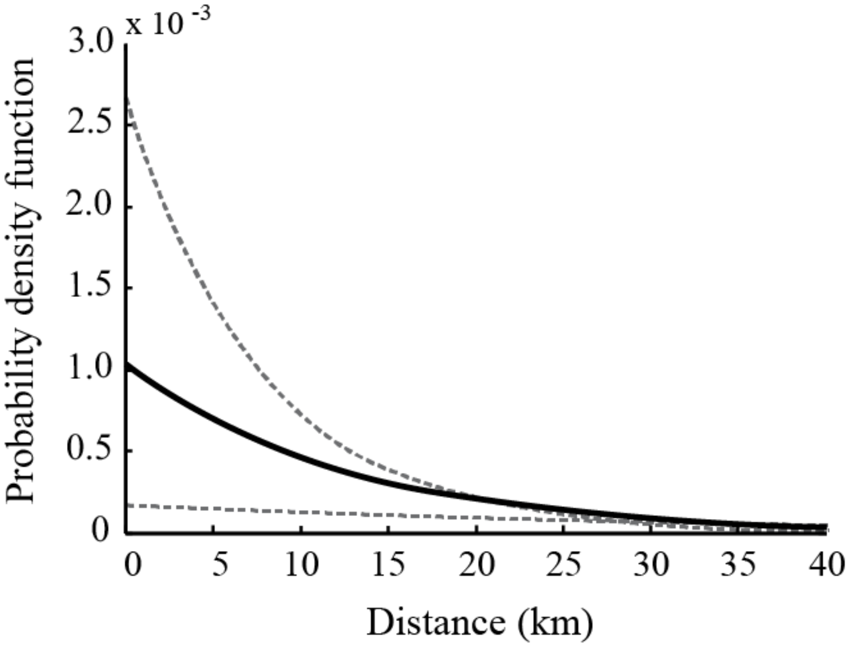


Figure B2 Best fit dispersal location kernel (negative exponential probability density function) for coral trout in the Keppel Islands, based on parentage analysis data and juvenile habitat preference data. Grey dashed lines indicate 95% confidence intervals for shape parameter value.

Table B.1 Best-fit dispersal kernel shape parameter values (ϕ), negative likelihood values (negLL) and second order Akaike's Information Criterion (AICc) for different dispersal functions when ϕ was fitted to all natal reefs simultaneously, and negLL and AICc values for when ϕ was fitted separately to all natal reefs. The number of parameters fitted was one for the constrained ϕ models and three for the models with separate ϕ for each natal reef. For habitat inclusion; 'full' includes the amount of preferred and other habitat available, 'area only' includes the total available habitat without accounting for juvenile preference in substrate type, and 'none' does not account for any difference in habitat availability or quality among reefs. ΔAICc values are relative to the overall best fit model. Bold indicates the most suitable fitted dispersal kernel function for the Keppel Island region.

		ϕ constrained for all reefs				**ϕ fitted separately to each reef**		
Dispersal location kernel	**Habitat inclusion**	**Best-fit ϕ**	**NegLL**	**AICc**	**Δ AICc**	**NegLL**	**AICc**	**ΔAICc**
Negative Exponential	**Full**	**12.38**	**112.27**	**226.59**	**1.31**	110.04	226.37	1.23
	Area only	11.66	115.72	233.49	8.21	113.23	232.74	7.60
	None	13.07	164.74	331.52	106.24	158.32	322.92	97.78
Gaussian	Full	18.30	113.97	229.98	4.70	109.43	225.14	0.00
	Area only	17.70	117.62	237.28	12.00	112.71	231.69	6.55
	None	18.78	166.91	335.86	110.58	158.96	324.21	99.07
Ribbens	Full	22.81	115.85	233.74	8.46	109.43	225.15	0.01
	Area only	22.15	119.72	241.48	16.20	112.76	231.79	6.65
	None	22.99	168.92	339.88	114.60	159.16	324.60	99.46
Adjusted LPER	Full	0.43	117.60	237.24	11.96	116.72	239.71	14.57
	Area only	0.45	121.90	245.84	20.56	120.90	248.07	22.93
	None	0.57	170.64	343.32	118.04	167.71	341.71	116.57

Appendix B References

Almany, G.R., Hamilton, R.J., Bode, M., Matawai, M., Potuku, T., Saenz-Agudelo, P., Planes, S., Berumen, M.L., Rhodes, K.L., Thorrold, S.R., Russ, G.R. & Jones, G.P. (2013). Dispersal of grouper larvae drives local resource sharing in a coral reef fishery. *Curr. Biol.*, 23, 626–630.

Harrison, H.B., Williamson, D.H., Evans, R.D., Almany, G.R., Thorrold, S.R., Russ, G.R., Feldheim, K.A., van Herwerden, L., Planes, S., Srinivasan, M., Berumen, M.L. & Jones, G.P. (2012). Larval export from marine reserves and the recruitment benefit for fish and fisheries. *Curr. Biol.*, 22, 1023–1028.

Nathan, R., Klein, E., Robledo-Arnuncio, J.J. & Revilla, E. (2012). Dispersal kernels: review. In: *Dispersal Ecol. Evol.* (eds. Clobert, J., Baguette, M., Benton, T.G. & Bullock, J.M.). Oxford University Press, Oxford, pp. 187–210.

Wen, C.K.C., Almany, G.R., Williamson, D.H., Pratchett, M.S., Mannering, T.D., Evans, R.D., Leis, J.M., Srinivasan, M. & Jones, G.P. (2013). Recruitment hotspots boost the effectiveness of no-take marine reserves. *Biol. Conserv.*, 166, 124–131.

Appendix C: ***Short-term changes in population biomass (Chapter 2)***

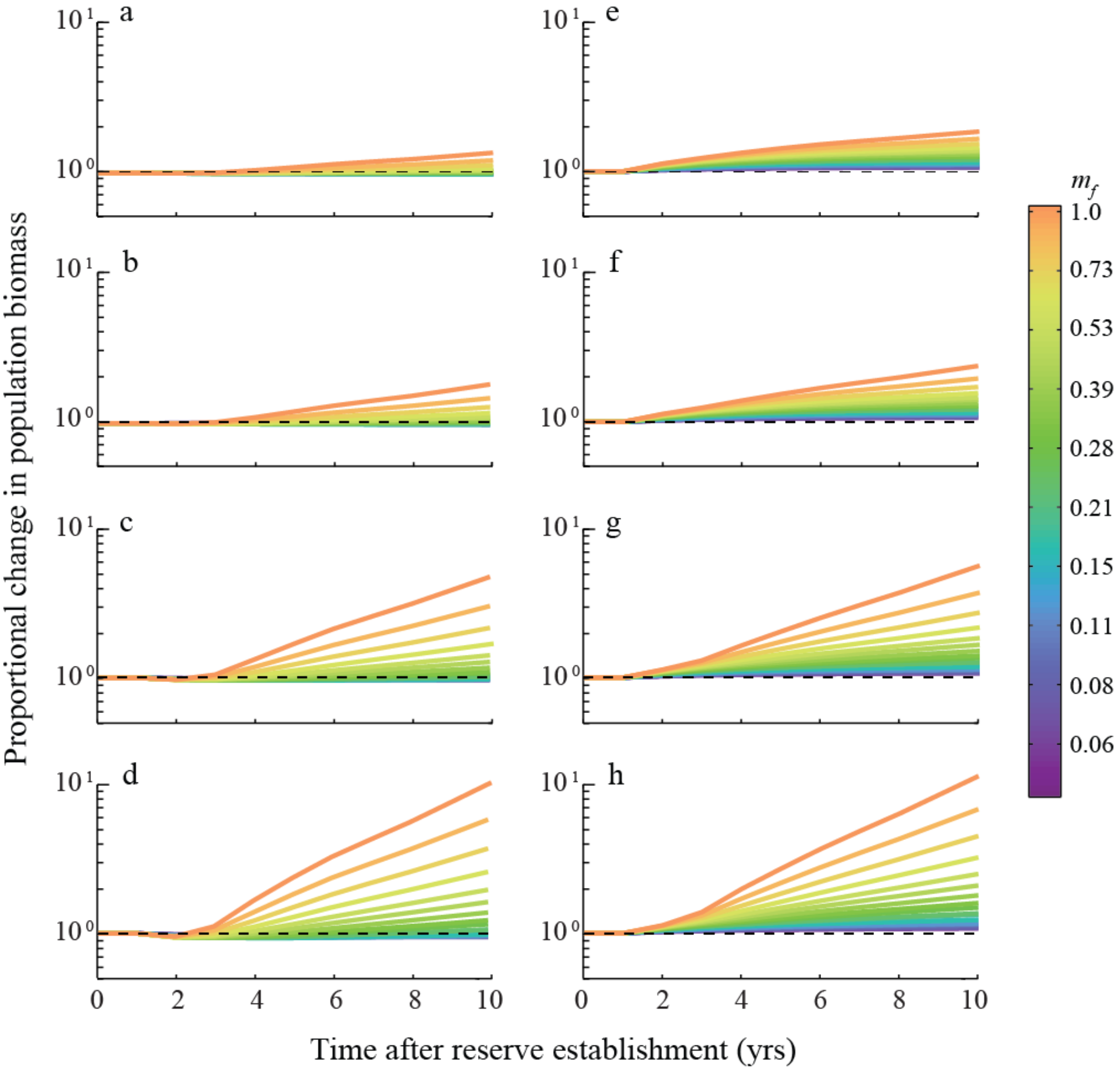


Figure C1 Short-term changes in population biomass for fished (**a, b, c, d**) and reserve (**e, f, g, h**) areas under a range of reserve sizes (**a, e** 5%; **b, f** = 10%; **c, g** = 30%; **d, h** = 50%) and fishing pressures (m_f; colours), after reserve implementation. Larvae are well mixed among populations, sex-change occurs in the population, and fishing pressure post-reserves is reallocated proportional to the area that remains open to fishing.

Appendix D: ***Sensitivity analysis (Chapter 2)***

D.1 Methods

D.1.a Sensitivity to linear approximation

In our models in Chapter 2 we made the assumption that the metapopulation was fished to a level such that density-dependent processes are negligible, and that transient metapopulation dynamics could be well-approximated by density-independent models. To test this assumption we considered the case where juvenile survival is regulated by the density of local adults (e.g. through cannibalism), which is a likely possibility for coral trout (St. John 1995). Here we used the well-mixed, age-structured model with sex-change, setting the proportion of area in reserves to reflect the current reserve coverage in the Keppel Island group (0.3281).

We modelled density-dependence following the common Ricker stock-recruitment relationship, with recruitment referring to recruitment to age one, not to the fishable stock. Specifically, survival to age one in a given population i at time t ($s_{1,i,t}$) was

$$s_{1,i,t} = -\mu_1 \, e^{\frac{-\mu_2}{A_i} \sum_{a=2}^{14} W_a \, n_{i,a,t-1}}$$

where μ_1 is the density-independent survival of juveniles, μ_2 is the strength of density-dependence, A_i is the proportion of area in population i, W_a is the weight of a fished aged a, and $n_{i,a,t-1}$ is the number of fished aged a in population i at the start of the year. We have used biomass instead of abundance as larger individuals are likely to have a greater per-capita density-dependent influence on juveniles due to their greater energy demands (Luppi *et al.* 2001). Weight parameter values were as per Table 2.1 in Chapter 2. Currently, there are no empirical estimates for the density-dependent parameters (μ_1 and μ_2), so we chose several values of μ_1 and μ_2 that yielded an equilibrium biomass that was equal to a conservative estimate of total coral trout biomass in the absence of fishing in the Keppel Islands (10800kg). Biomass estimates were based on biomass densities in green zones within the GBR (Williamson *et al.* 2004), multiplied by total reef area. We considered 'weak', 'moderate', and 'strong' sets of density-dependent parameters that spanned a plausible range of parameter value sets (e.g. values that caused the metapopulation to exhibit cyclic behaviour were considered unrealistic). Note that the greater μ_1 (strength of density-dependence) was, the larger μ_2 (density-independent survival) needed to be in order to obtain the unfished biomass, and that this increased juvenile survival required greater fishing pressures to reduce the stock.

The ability of linear models to approximate the transients of density-dependent models is argued to increase as the fishery becomes increasingly exploited (White *et al.* 2013). To test if this held true for our models, we considered scenarios in which the stock was depleted to ~20% and ~50% virgin biomass levels, when reserves were implemented. We considered 50% virgin biomass to be a lightly fished scenario, and 20% to be a more realistic scenario for most fisheries, given that the average biomasses of large predatory fishes are estimated to have been reduce to ~40% their pre-harvest levels (Juan-Jordá et al. 2011). Furthermore, biomass estimates of coral trout prior to the implementation of any reserves in the GBR (Williamson *et al.* 2004) suggest that the stock was depleted to ≤ 20% the current densities observed within reserves. Note that it is likely that 20% virgin biomass is an under-estimation of the degree of exploitation of coral trout, given the presence of poaching within reserves on the GBR (Davis *et al.* 2004) and that current densities within reserves are likely below those in an unfished scenario, as indicated by abundances in no-entry zones (Ayling & Choat 2008). To achieve the desired level of depletion, we altered the rate of mortality due to fishing (m_f). We then compared short-term outcomes to our density-independent model, set for the same rate of adult mortality due to fishing.

D.1.b Sensitivity to initial asymptotic metapopulation growth rate and first year survival

In our simulations we made the assumption that the metapopulation had been fished for a sufficient time such that it had reached an asymptotic state, with a stable growth rate (neither growing nor declining; $\lambda_1 = 1$). Here, we consider the sensitivity of four fishery and metapopulation metrics relevant to our results to small changes in λ_1, focusing on our baseline model (well-mixed larvae, fishery squeeze). These metrics were; 1) time to yield equivalence (time taken for yields to recover to their pre-reserve levels), 2) maximum yield attenuation (maximum proportional decrease in yields prior to yield recovery), 3) time to stable growth (time taken for the metapopulation to reach an asymptotic state), and 4) $\Delta\lambda$ (absolute change in the asymptotic metapopulation growth rate with reserve establishment, compared to before reserve establishment). In Chapter 2 we constrained $\lambda_1 = 1$ by varying S_1 (survival through to age one; a parameter for which there is no quantitative information) alongside different fishing pressure rates. Here we varied the models (well-mixed and Keppel Island specific) over a range of S_I (with a set fishing pressure) to obtain different λ_I values. Therefore, this sensitivity analysis also reflects the sensitivity of the metrics to changes in S_I.

In addition, we tested whether the results for our 'Target-yield' model were also robust to the assumption that the population was exhibiting zero growth at the time reserves were implemented. For this sensitivity analysis we again varied the S_I parameter value such that the population had reached asymptotic dynamics, but was either moderately (~3%) declining or growing prior to reserve establishment. We then compared the changes in metapopulation size, yield, and metapopulation growth rate in scenarios with and without reserves, relative to the population dynamics at the time reserves were implemented (in the Chapter 2 we used the stable pre-reserve values as our baseline).

In Chapter 2 we varied S_I simultaneously with the rate of fishing pressure (m_f) to maintain $\lambda_I = 1$ across different levels of m_f. Consequently, scenarios with higher fishing pressure had greater juvenile survival rates by definition. Therefore, in addition to testing the sensitivity of our results to changes in S_I, we also assessed whether the trends seen in our results were primarily driven by fishing pressure, and not an artefact of the covarying S_I, m_f values. We considered changes in the aforementioned metapopulation metrics (time to yield equivalence, maximum yield attenuation, time to stable growth, and $\Delta\lambda$), over the range of m_f values used in the Chapter 2, but with fixed S_I values. Three S_I values were considered (low, medium, high), which spanned the range of S_I values used in Chapter 2.

D.1.c Sensitivity to sex-change

Previous work suggests that sex-changing populations are unlikely to receive the same yield-enhancing benefits from reserve establishment as their non-sex-changing counterparts (Chan *et al.* 2012). However, those models focused on equilibrium conditions, regulated by density-dependent processes. In Chapter 2 we have focused on the short-term dynamics of a species that exhibits a protogynous sex-changing strategy. We tested the implications of including sex-change in our models by also considering cases without sex-change, assuming a 1:1 sex ratio. We ran a non-sex-change model for each of the scenarios in Chapter 2, i.e. a well-mixed two-population model, a target-yield model, and a Keppel Islands spatially explicit model. All other parameter values remained the same as per Chapter 2, with the exception of the rate of juvenile survival (S_1), which was varied to obtain a metapopulation growth rate of 1 prior to reserve establishment.

D.1.d Effects of heterogeneity in juvenile habitat

In our Keppel Islands spatially explicit models we accounted for the availability of suitable juvenile settlement habitat among reefs by assuming that this was primarily driven by reef size. To evaluate which aspects of our results were due to this heterogeneity in available habitat among reefs (versus distance-decay in dispersal), we also ran our Keppel Islands model with all reefs equal in size (i.e. homogenous in their habitat availability for settling juveniles). All other parameter values remained the same as per the Keppel Islands model in Chapter 2, with the exception of the rate of juvenile survival (S_1), which was varied to obtain a metapopulation growth rate of 1 prior to reserve establishment

D.1.e Effects of the strength of distance-decay in larval dispersal

For larval dispersal in our Keppel Islands spatially explicit models we used the best-fit kernel function and parameter values developed in Appendix B (above). To test the sensitivity of our results to our estimate dispersal fit we ran models at the upper and lower 95% confidence intervals of the estimate kernel parameter (ϕ) value. The upper ϕ value (30.7 km) is representative of dispersal that is relatively well-mixed among populations, whereas the lower ϕ value (7.7 km) represents a system with greater self-recruitment and less dispersal among populations. All other parameter values remained the same as per the Keppel Islands model in Chapter 2, with the exception of the rate of juvenile survival (S_1), which was varied to obtain a metapopulation growth rate of 1 prior to reserve establishment.

D.2 Results

D.2.a Sensitivity to linear approximation

Our density-independent model provided a good approximation of the short-term changes in yield biomass after reserve establishment, especially for cases in which the population had been reduced well below (~20%) its unfished biomass (Figure D1a). In all cases, the magnitude of initial yield attenuation was comparable between both the density-independent and density-dependent models (Figure D1). Yield recovery, however, was overestimated by the density-independent model when the population was less exploited (Figure D1b). This is due to the inability of the density-independent model to capture population dynamics as the long-term equilibrium conditions are approached, which would occur faster in a less exploited fishery. Our results match those of White *et al.* (2013), in that linear models are suitable approximations for the transient dynamics of heavily exploited populations after reserves are established, but are not suitable for evaluating long-term conditions.

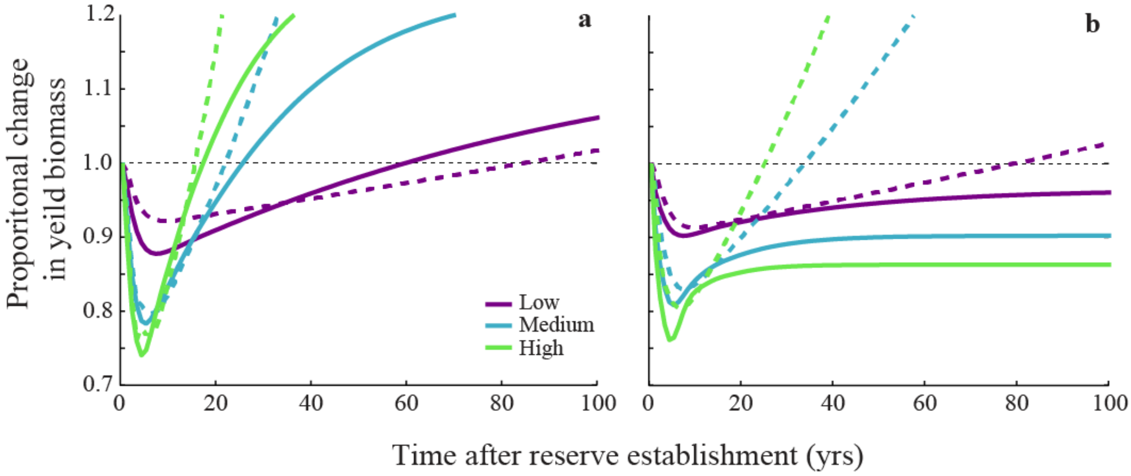


Figure D1 Short-term changes in yield biomass after reserve establishment, comparing models with density-dependence (solid lines) to those without (dashed lines), for fisheries with stocks depleted to (**a**) 20% and (**b**) 50% their virgin biomass. Colours indicate various strengths of density-dependence.

D.2.b Sensitivity to initial asymptotic metapopulation growth rate and first year survival

The outcomes of our models were not sensitive to the assumption that the population was stable (neither growing nor declining; $\lambda_1 = 1$) before reserves were implemented. This was true both when fishing effort remains constant but is reallocated into the area that remains open to fishing, and when effort intensifies to maintain pre-reserve yields. For our baseline model (well-mixed larvae, fishery squeeze), a ±10% change in λ1 occurred within an order of magnitude change in S1 (Figure D2). Over this range there was little change in any of the four metrics measured (Figure D3). This suggests that our main findings are robust for stable populations as well as those increasing or decreasing by up to 10% prior to reserve implementation. Further, it demonstrates that the results are not sensitive to the intrinsic per capita rate of increase of the population.

For the target-yield scenario, our main findings - that intensifying fishing to maintain pre-reserve levels can cause metapopulation collapse - held true when the metapopulation was already in decline ($\lambda_1 = 0.965$), but were less of a concern when the metapopulation exhibited positive growth ($\lambda_1 = 1.026$). When the population was declining prior to reserves, reserve establishment was only beneficial (increasing both yield and population growth) when reserves covered a large portion of the area (>50%; Figure D4). When reserves were small, their implementation was detrimental to the population, causing collapse to occur faster than the scenario without reserves (Figure D4). When population growth was positive, reserves were always beneficial in the longer-term, however larger reserves had a greater initial impact on yields (Figure D5). In this case the growth of the population mitigated any increased fishing pressure due to loss of fishing area. The implementation of reserves in a successfully recovering fishery, however, is markedly less likely to occur than in a declining fishery.

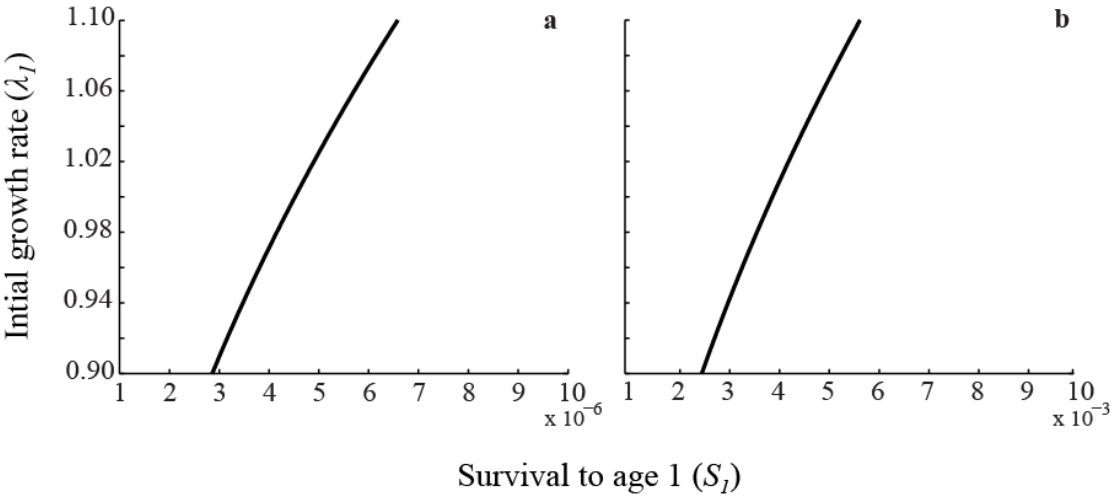


Figure D2 Change in initial metapopulation asymptotic growth rate (λ_1) over varying rates of survival to age 1 (S_1) for (**a**) the well-mixed model and (**b**) the Keppel Islands specific model. In both models 32.81% of the area is in reserves (actual reserve coverage in the Keppel Islands) and the fishing pressure rate is 0.2307.

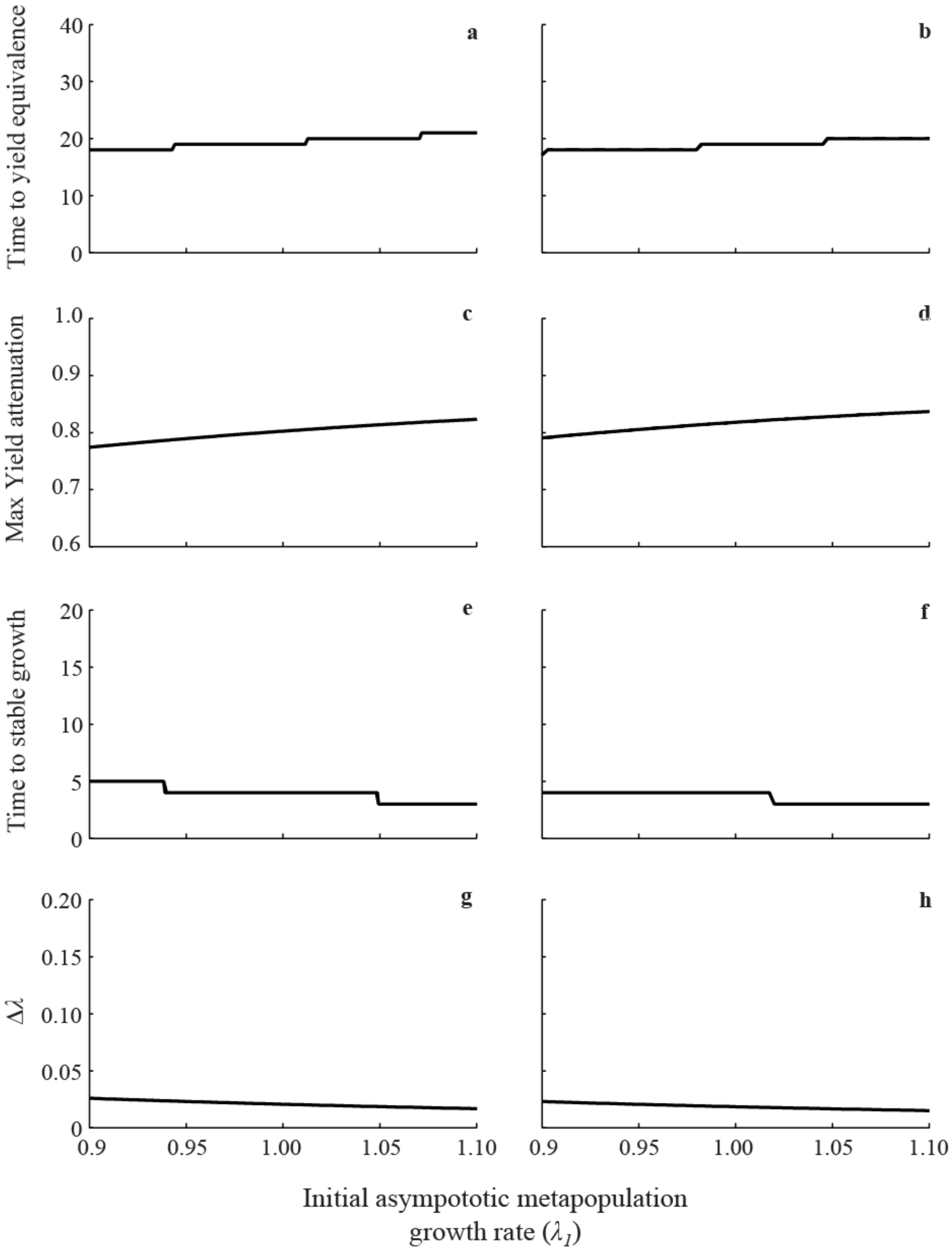


Figure D3 Sensitivity of changes in fishery and metapopulation metrics to changes in the pre-reserve asymptotic metapopulation growth rate (λ_1) for (**a, c, e, g**) the well-mixed model, and (**b, d, f, h**) the Keppel Islands spatially explicit model. In both models 32.81% of the area is in reserves (actual reserve coverage in the Keppel Islands) and the fishing pressure rate is 0.2307.

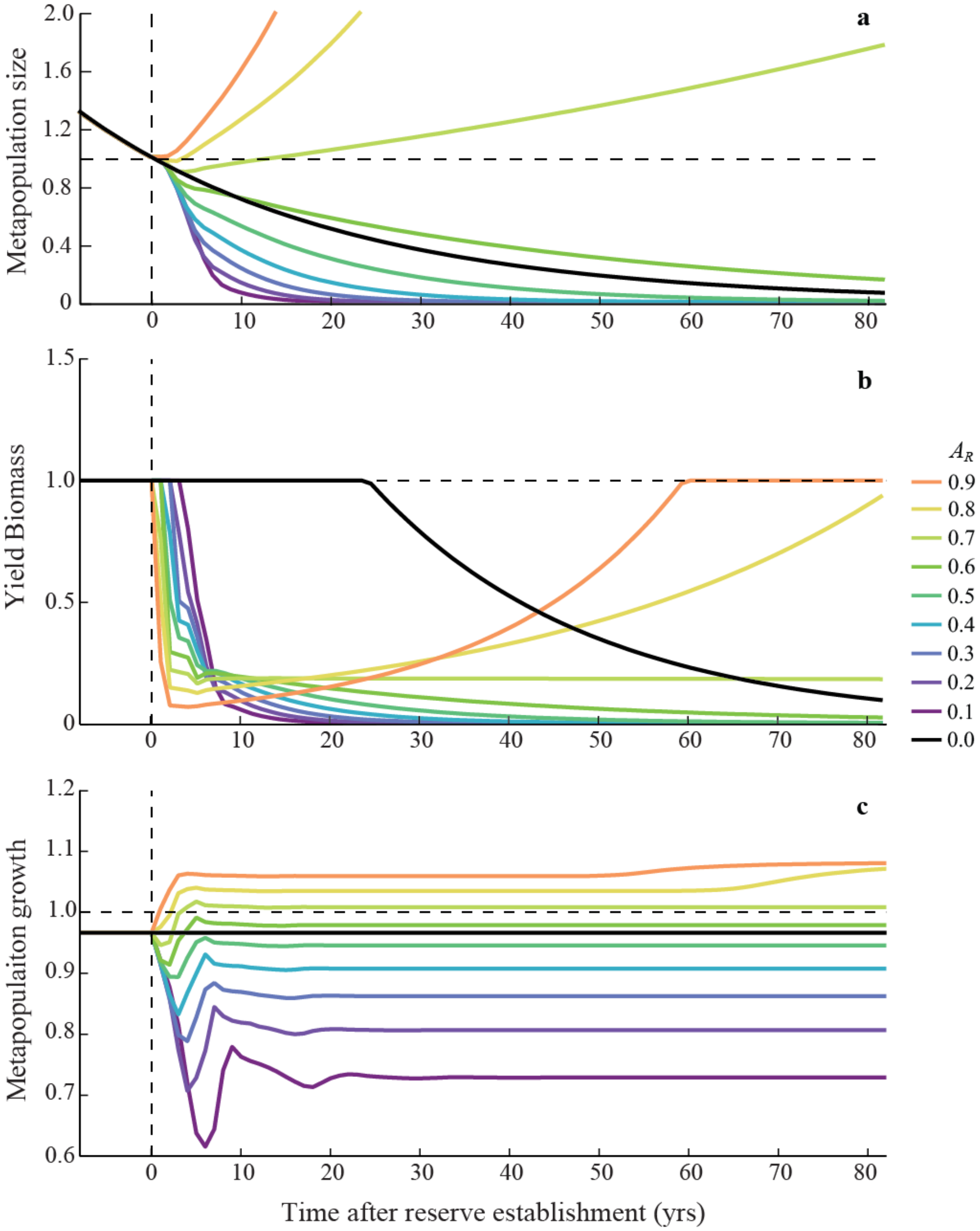


Figure D4 Short-term changes in total metapopulation size (**a**), yield biomass (**b**), and metapopulation growth (**c**), in a declining metapopulation ($\lambda_I = 0.965$) subject to a target-yield fishing scenario with (coloured lines) and without (black line) reserves. Metapopulation size (**a**) and yield biomass (**b**) are relative to the time at which reserves were implemented (time = 0). Vertical dashed lines indicate reserve implementation, horizontal dashed lines indicated stable yield and population size, and coloured lines indicate proportion of the area protected in reserves (A_R).

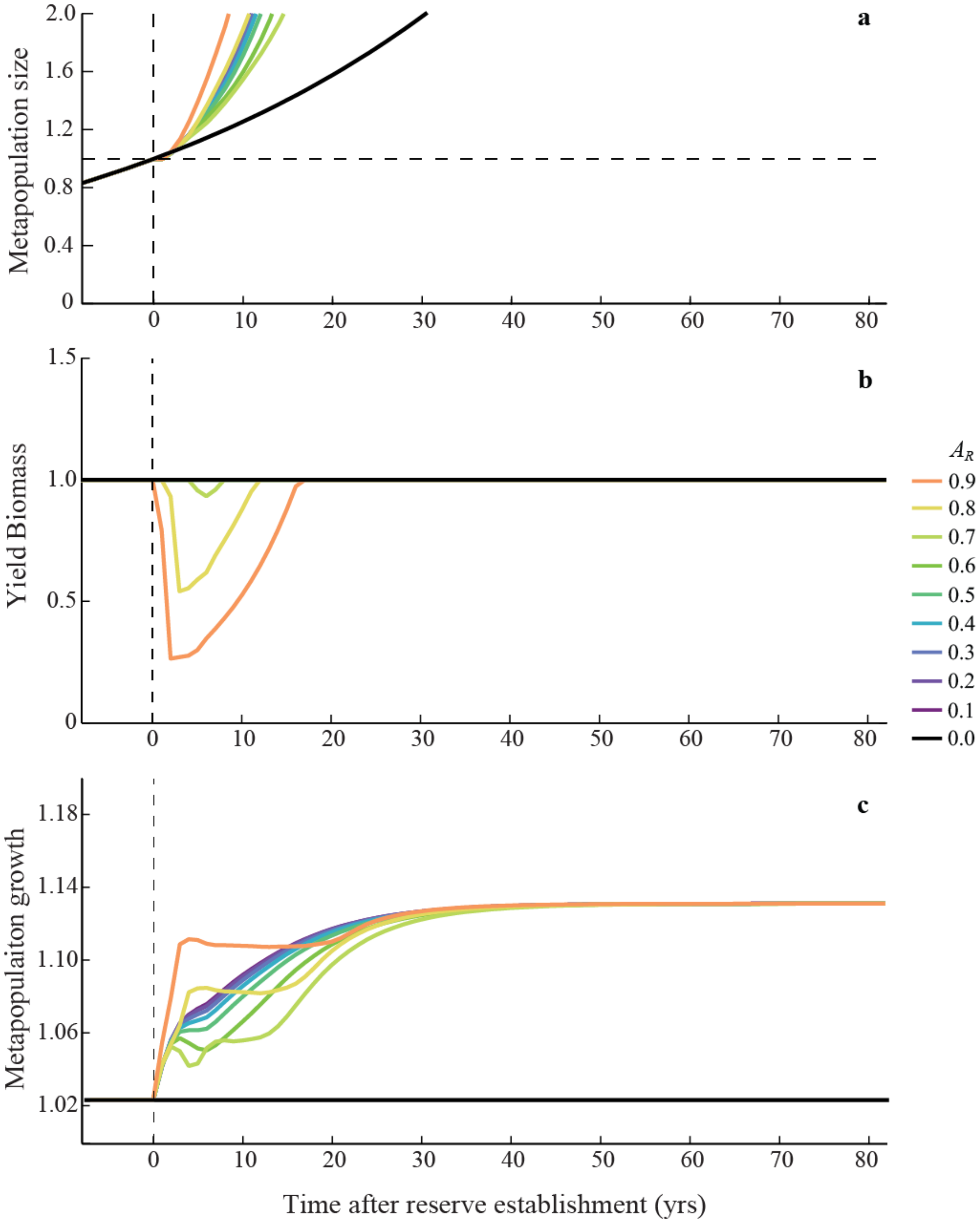


Figure D5 Short-term changes in total metapopulation size (a), yield biomass (b), and metapopulation growth (c), in a growing metapopulation (λ1 = 1.026) subject to a target-yield fishing scenario with (coloured lines) and without (black line) reserves. Metapopulation size (a) and yield biomass (b) are relative to the time at which reserves were implemented (time = 0). Vertical dashed lines indicate reserve implementation, horizontal dashed lines indicated stable yield and population size, and coloured lines indicate proportion of the area protected in reserves (AR).

Furthermore, the impacts of the strength of fishing pressure (i.e. that greater fishing pressures result in larger intial decreases in yeilds, but faster recovery times and greater asymptotic growth rates) were not confounded by the paired juvenile survival rate that we used to constrain $\lambda_1 = 1$. There were notable changes in the four metrics considered as fishing pressure increased and juvenile survival remained constant (Figure D6). These changes were consistent with our results in Chapter 2, and were independent of the magnitude of juvenile survival used (Figure D6).

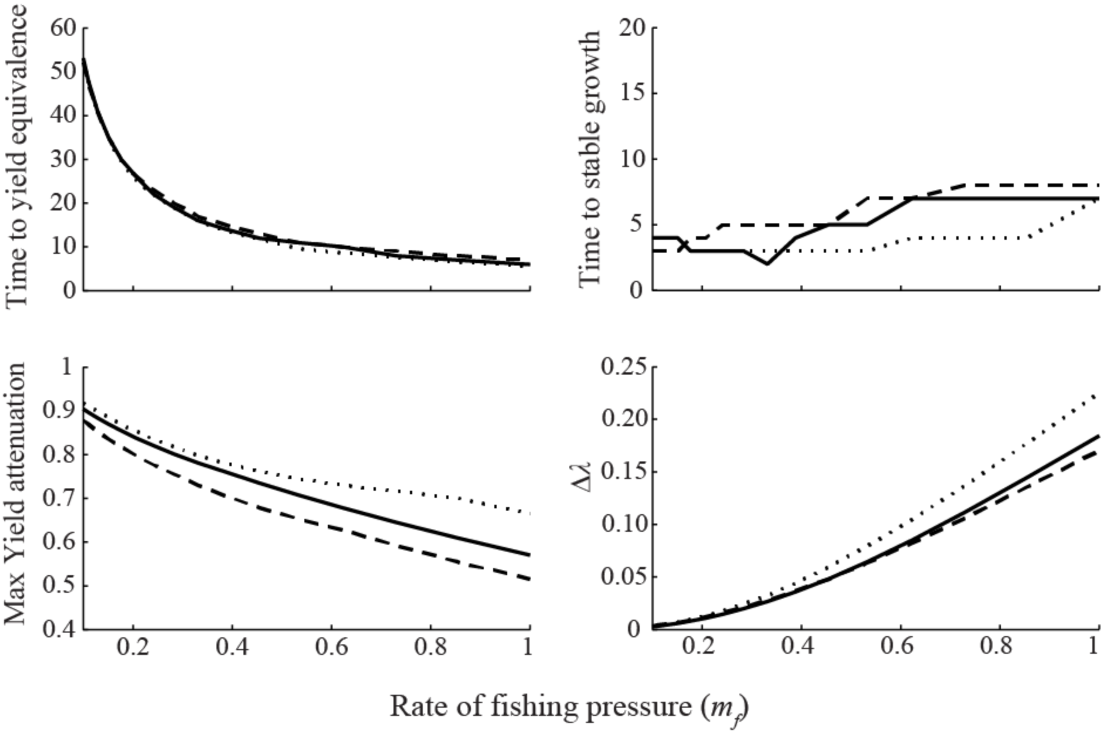


Figure D6 Sensitivity of changes in fishery and metapopulation metrics for the well-mixed model to changes in the fishing pressure rate (m_f) for fixed juvenile survival values. Dashed, solid, and dotted lines represent low (0.50×10^{-5}), medium (1.04×10^{-5}), and high (2.80×10^{-5}) juveniles survival rates. Proportion of area in reserves is set at 32.81% (actual reserve coverage in the Keppel Islands).

D.1.c Sensitivity to sex-change

Removing sex-change from our models had little impact on the outcomes of our study (Figure D7-D9). Without sex-change, reserve implementation decreased yields initially, but later allowed yields to recover and increase beyond pre-reserve levels. The non-sex-change models, however had slower yield recovery times, compared to those with sex-change, especially under high rates of mortality (Figure D7-D8). For sex-changing species, fishing impacts the reproductive output of the metapopulation in two ways; 1) it reduces the total number of reproductive adults, and 2) it skews the age structure towards younger/small individuals (predominately females), and, consequently, the remaining reproductive biomass is compromised by sperm limitation. For non-sex-changing species, fishing only reduces the total number of reproductive adults, but fertilization success remains uncompromised. Thus, protecting a portion of the metapopulation from fishing has a lesser positive impact on the net reproductive output of species that do not change sex, reducing the time to yield recovery and asymptotic metapopulation growth rate.

D.2.d Effects of heterogeneity in juvenile habitat

The main results of our spatially explicit Keppel Islands models – that initial yield increases, followed by slower recovery times were more likely when reserves were small and located peripherally within the metapopulation – did not markedly change when we considered a case where all reefs were homogenous in size. This suggests that the main source in variation among combinations of reefs that were protected (with distance-decay in larval dispersal) was due to their location relative to other reefs, rather than heterogeneity in habitat area (Figure D10).

D.2.e Effects of the strength of distance-decay in larval dispersal

The degree of dispersal among populations in our Keppel Islands spatially explicit models had little influence on the overall trends observed in Chapter 2 (Figure D11 & D12). Unsurprisingly, reducing the degree of connectivity among populations (lower 95% confidence limit of ϕ estimate) increased the proportion of reserve combinations that resulted in lowered asymptotic metapopulation growth rates and increased the time to yield recovery in those combinations that had positive growth (Figure D11). Furthermore, decreasing connectivity enhanced the yield and conservation benefits of protecting a single large reef compared to a number of small reefs. Conversely, increasing the degree of connectivity among populations reduced the potential for metapopulations to collapse (Figure D12), and the results were akin to those in the well-mixed, two-population model.

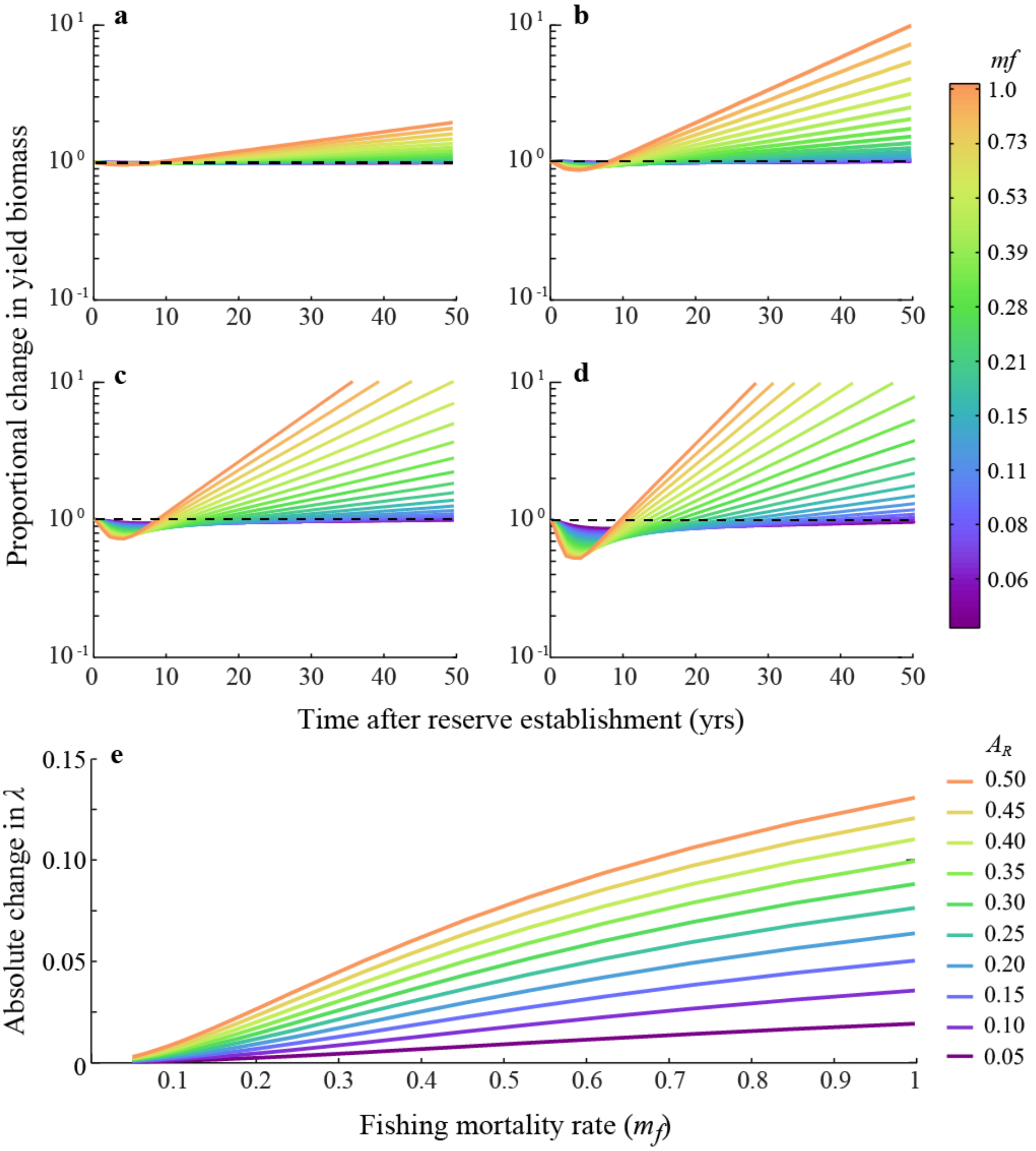


Figure D7 Short-term changes, for a non-sex-changing scenario, in yield biomass under a range of reserve sizes (**a** = 5%, **b** = 10%, **c** = 30%, **d** = 50%) and fishing pressures (m_f; colours), and (**e**) changes in asymptotic metapopulation growth rate (λ) as a function of fishing pressure (m_f) and different proportions of reserve coverage (A_R; colours), after reserve implementation. Larvae are well mixed among populations and fishing pressure post-reserves is reallocated proportional to the area that remains open to fishing.

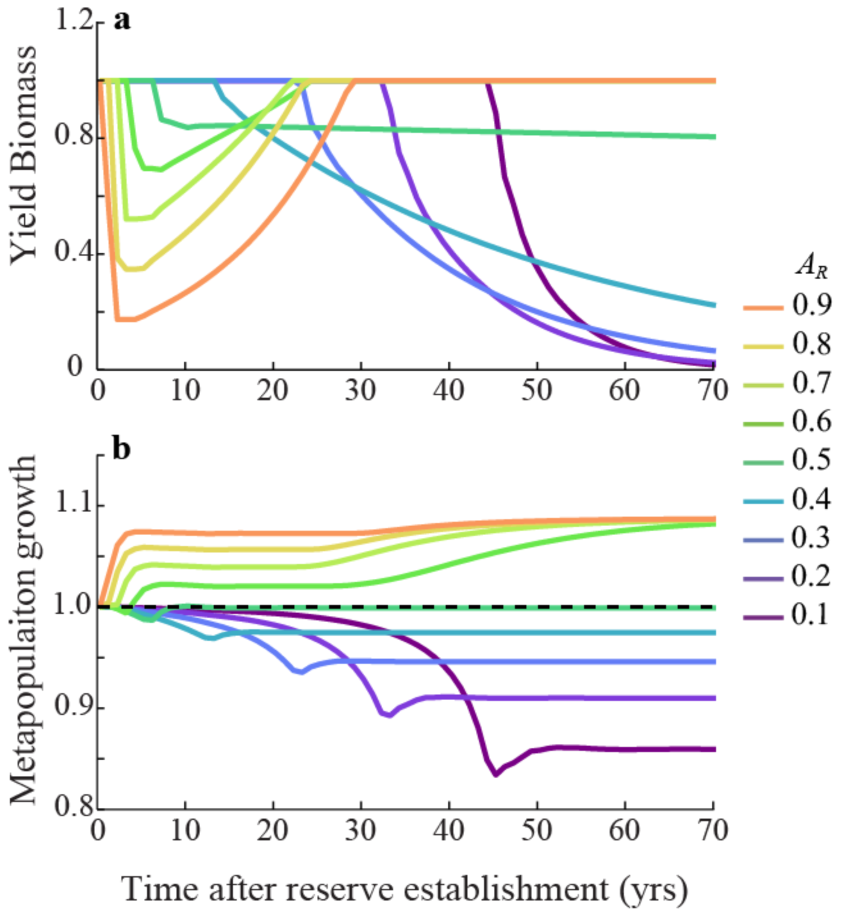


Figure D8 Short-term changes, for a non-sex-changing scenario, in (**a**) yield biomass, and (**b**) metapopulation growth after reserve implementation when fishing effort is varied overtime to maintain pre-reserve catch levels. Coloured lines indicate proportion of the area protected in reserves (A_R). Note; if available biomass was less that the target yield all individuals available were caught.

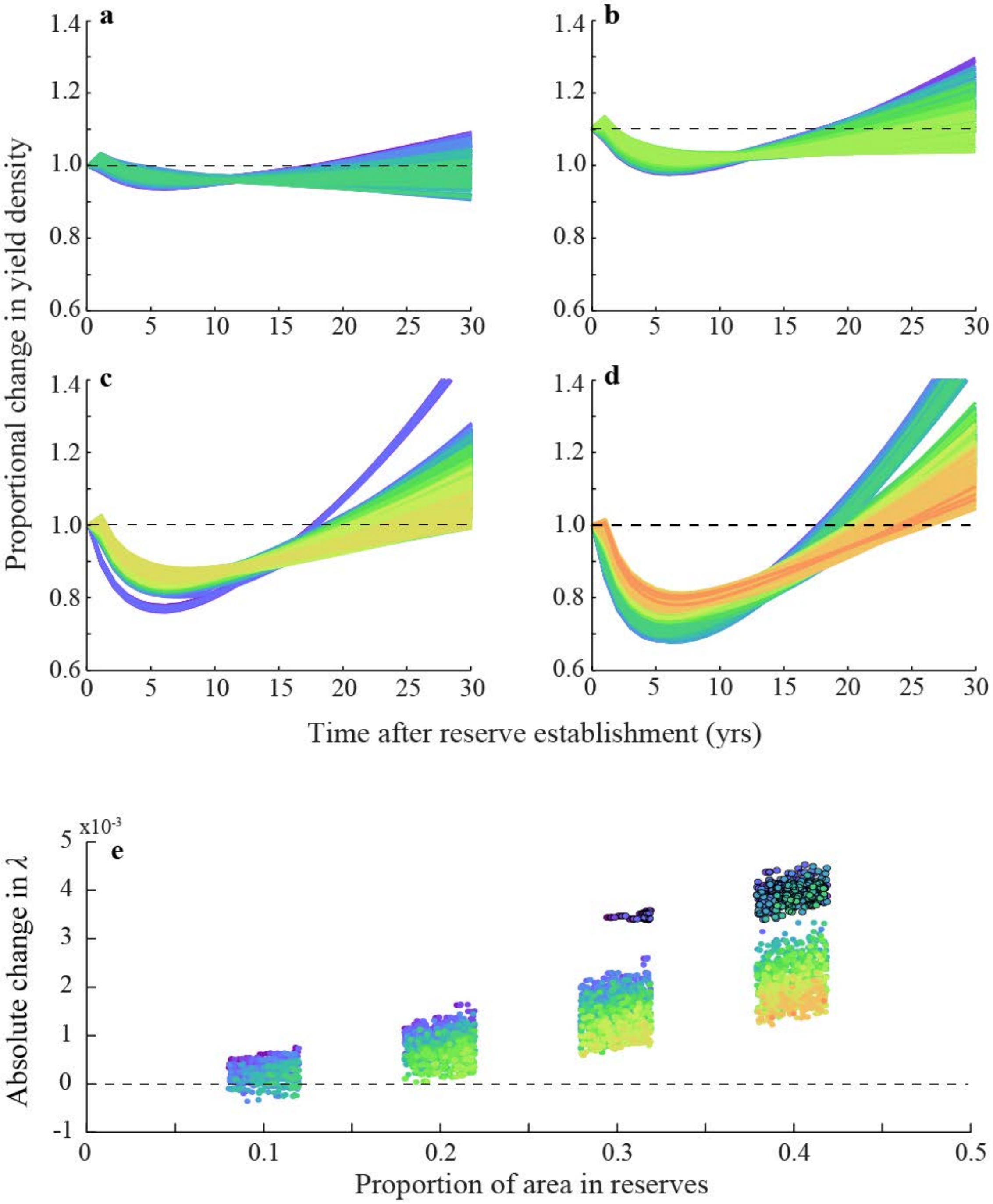


Figure D9 Short-term changes, for a non-sex-changing scenario, in yield biomass under a range of reserve sizes (**a** = 8-12%, **b** = 18-22%, **c** = 28-32%, **d** = 38-42%), and (**e**) changes in asymptotic metapopulation growth rate (λ), after reserve implementation for the Keppel Islands spatially explicit model (distance-decay in larval dispersal and heterogeneous reef sizes). Individual points relate to different reserve combinations and only a random subset of all possible combinations is shown. Different colour indicate the number of reefs protected in a given combination (purple = 1 to orange = 9). Black edges indicate combinations that contain a disproportionally large reef.

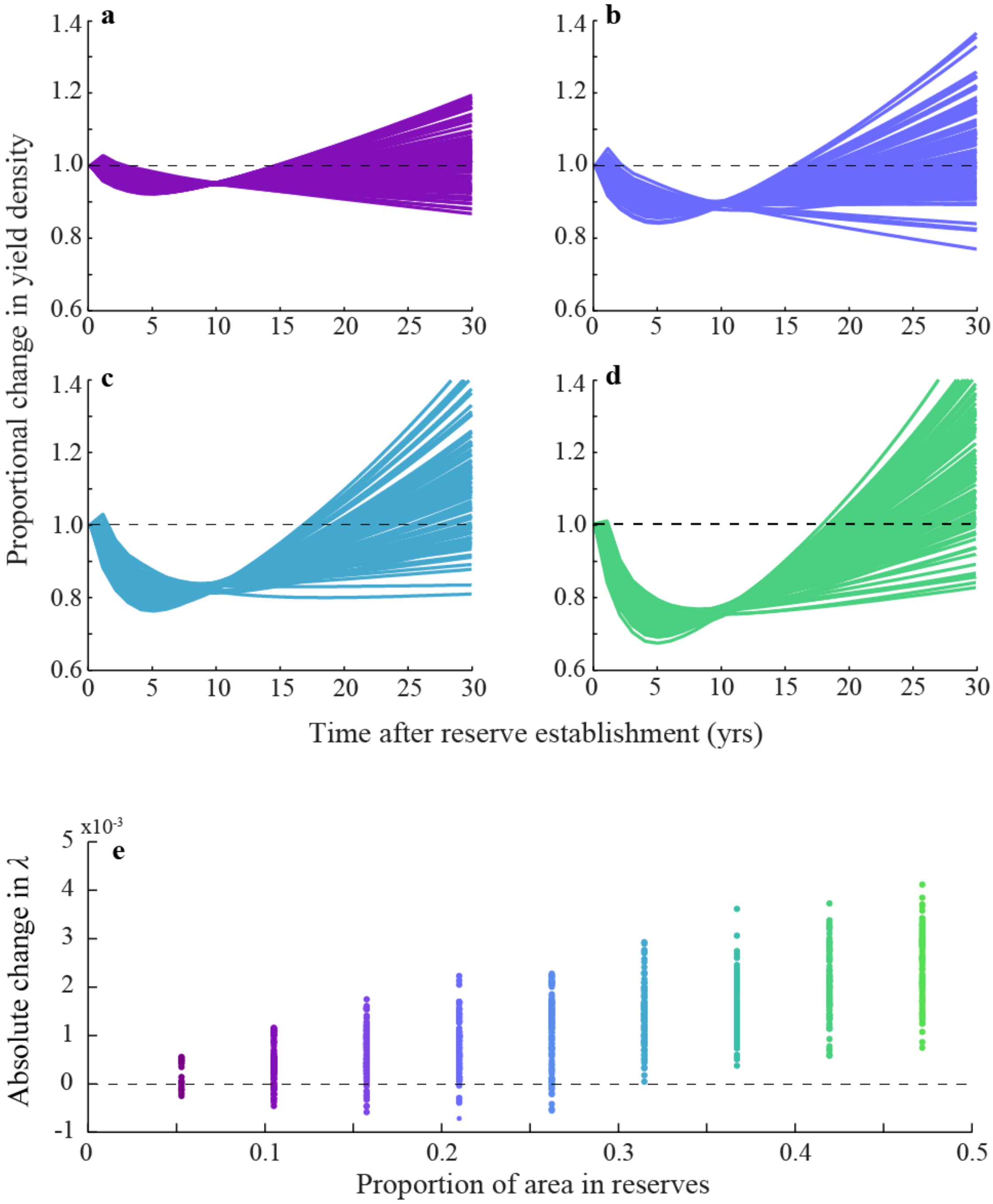


Figure D10 Short-term changes in yield biomass under a range of reserve sizes (**a** = 10.5%, **b** = 21.0%, **c** = 31.5%, **d** = 42.0%), and (**e**) changes in asymptotic metapopulation growth rate (λ), after reserve implementation for the Keppel Islands spatially explicit model (distance-decay in larval dispersal) with homogenous reefs. Individual points relate to different reserve combinations and only a random subset of all possible combinations is shown.

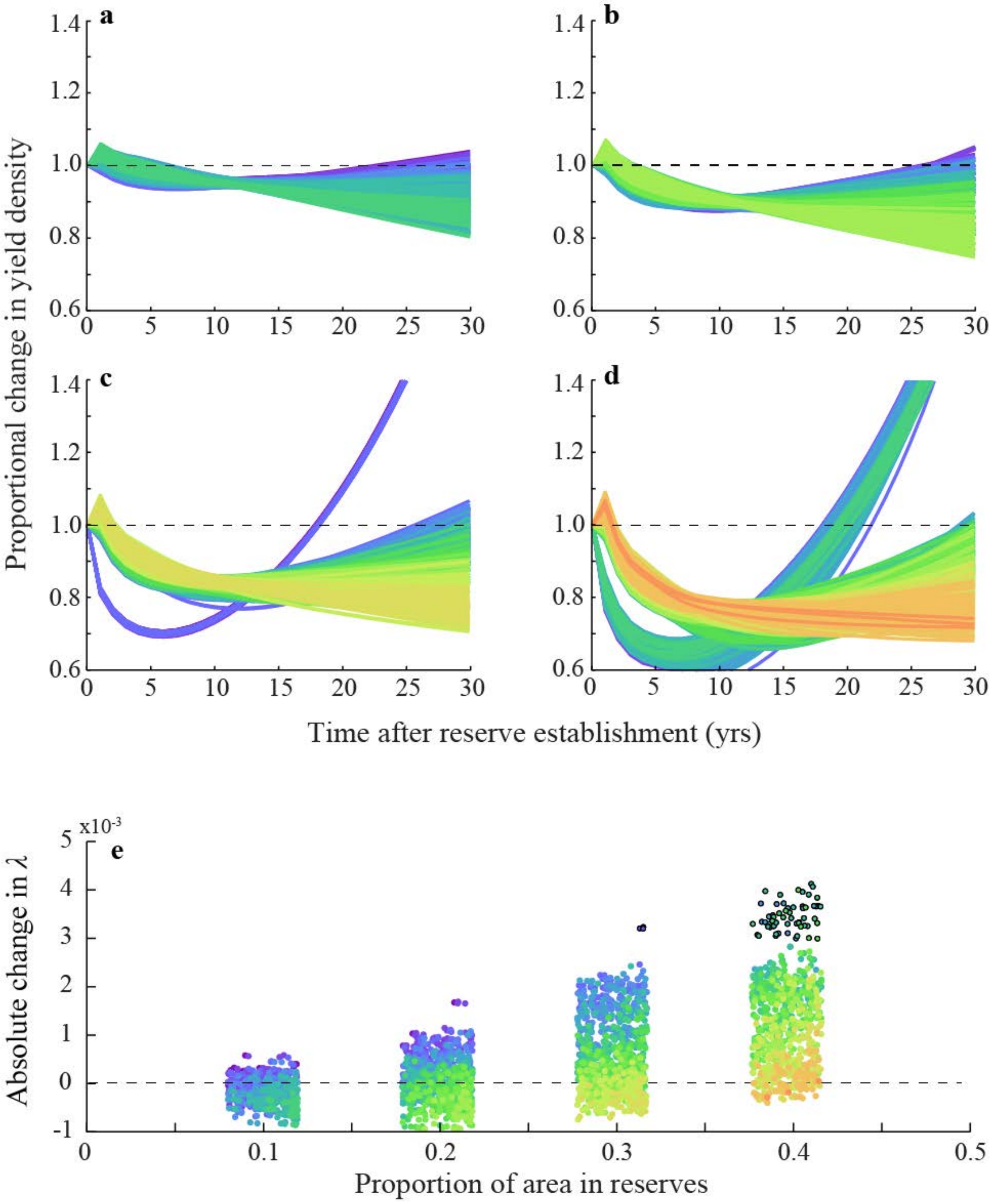


Figure D11 Short-term changes, when larval dispersal among populations is low, in yield biomass under a range of reserve sizes (**a** = 8-12%, **b** = 18-22%, **c** = 28-32%, **d** = 38-42%), and (**e**) changes in asymptotic metapopulation growth rate (λ), after reserve implementation for the Keppel Islands spatially explicit model (distance-decay in larval dispersal and heterogeneous reef sizes). Individual points relate to different reserve combinations and only a random subset of all possible combinations is shown. Different colour indicate the number of reefs protected in a given combination (purple = 1 to orange = 9). Black edges indicate combinations that contain a disproportionally large reef.

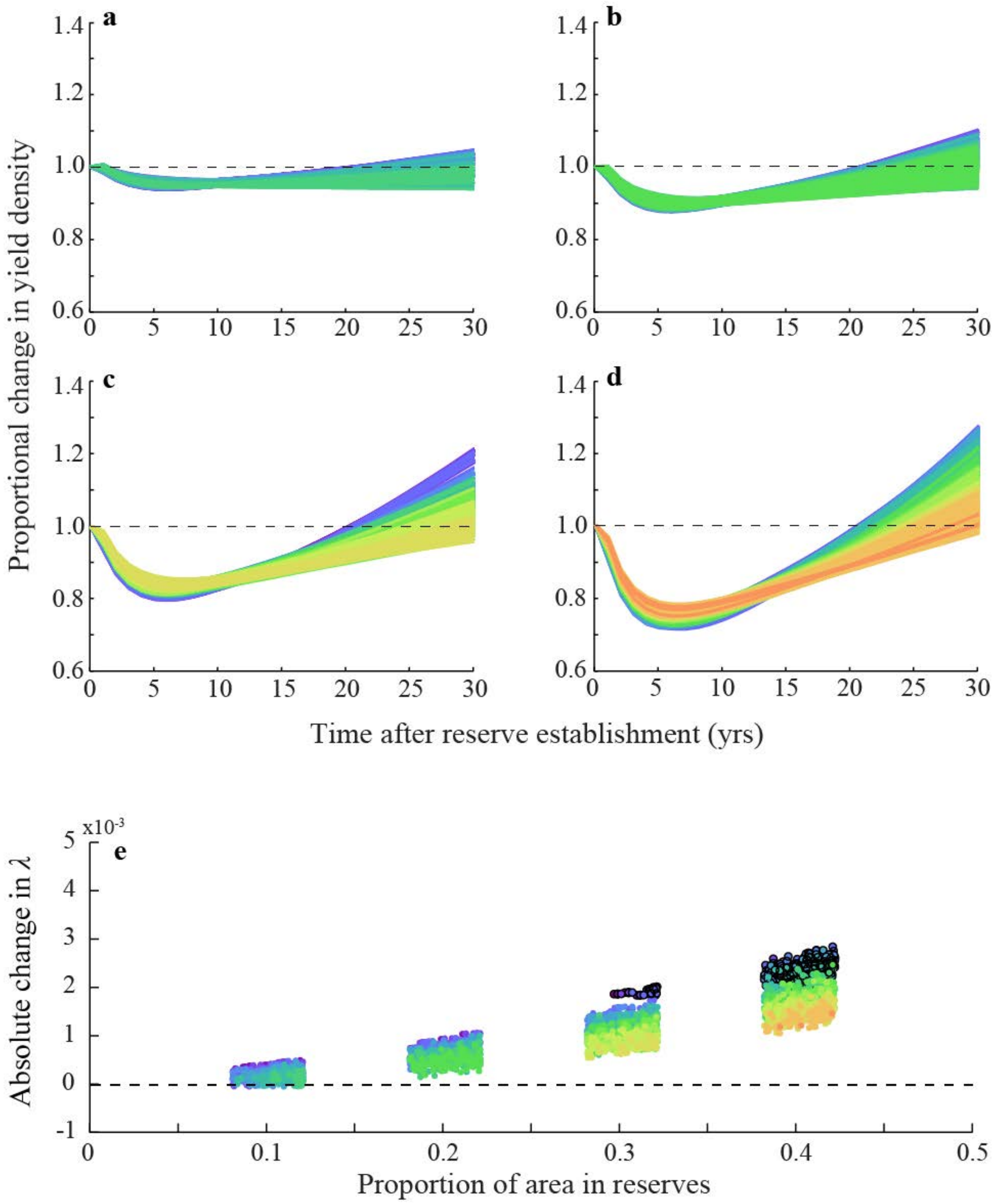


Figure D12 Short-term changes, when larval dispersal among populations is high, in yield biomass under a range of reserve sizes (**a** = 8-12%, **b** = 18-22%, **c** = 28-32%, **d** = 38-42%), and (**e**) changes in asymptotic metapopulation growth rate (λ), after reserve implementation for the Keppel Islands spatially explicit model (distance-decay in larval dispersal and heterogeneous reef sizes). Individual points relate to different reserve combinations and only a random subset of all possible combinations is shown. Different colour indicate the number of reefs protected in a given combination (purple = 1 to orange = 9). Black edges indicate combinations that contain a disproportionally large reef.

Appendix D References

Ayling, A.M. & Choat, J.H. (2008) *Abundance patterns of reef sharks and predatory fishes on differently zoned reefs in the offshore Townsville region.* Final Report to the Great Barrier Reef Marine Park Authority, Research Publication No. 91, Great Barrier Reef Marine Park Authority, Townsville.

Chan, N., Connolly, S.R. & Mapstone, B. (2012). Effects of sex change on the implications of marine reserves for fisheries. *Ecol. Appl.,* 22, 261–285.

Davis, K.L.F., Russ, G.R., Williamson, D.H. & Evans, R.D. (2004). Surveillance and Poaching on Inshore Reefs of the Great Barrier Reef Marine Park. *Coast. Manag.*, 32, 373–387.

Juan-Jordá, M.J., Mosqueira, I., Cooper, A.B., Freire, J., & Dulvy, N.K. (2011). Global population trajectories of tunas and their relatives. *PNAS,* 108, 20650-20655.

Luppi, T. A., Spivak, E. D., & Anger, K. (2001). Experimental studies on predation and cannibalism of the settlers of *Chasmagnathus granulata* and *Cyrtograpsus angulatus* (Brachyura: Grapsidae). *J. Exp. Mar. Biol. Ecol.,* 265, 29–48.

St. John, J. (1995). Feeding ecology of the coral trout, *Plectropomus leopardus* (Serranidae) on the Great Barrier Reef, Australia. *Thesis submitted in the School of Marine & Tropical Biology*, *Townsville, Australia*

White, J.W., Botsford, L.W., Hastings, A., Baskett, M.L., Kaplan, D.M. & Barnett, L.A.K. (2013). Transient responses of fished populations to marine reserve establishment. *Conserv. Lett.*, 6, 180-191

Williamson, D.H., Russ, G.R. & Ayling, A.M. (2004). No-take marine reserves increase abundance and biomass of reef fish on inshore fringing reefs of the Great Barrier Reef. *Environ. Conserv.*, 31, 149–159.

Appendix E: ***Reallocation of effort by biomass vs. reallocation by area (Chapter 2)***

A key finding of our study was that if fisheries overcompensated for the loss of access to harvestable area then the recovery of yields to pre-reserve levels was slow, or non-existent. This was more likely in when reserves were established on more peripheral reefs, which, due to the distance decay in dispersal, had lower than average proportions of the total metapopulation biomass at the time of reserve establishment (Figure E1). Here we demonstrate that a key aspect to this overcompensation was that fishing pressure was reallocated based on the proportion of area lost, yet the area lost was greater than the proportion of biomass lost. We show this by approaching the problem from two directions: 1) violation of the conditions of our analytical model (see Appendix A above), and 2) re-evaluating our Keppel Islands spatially explicit model with reallocated fishing pressure as a function of the biomass lost at the time of reserve establishment, rather than the area lost.

A key condition of our analytical model was that, due to 'fishery-squeeze', the reallocation of effort was inversely proportional to the area that remained open to harvest (1-A). Due to the assumption that larvae were well mixed among the populations, the area that remained open was also equal to the proportion of the metapopulation biomass that remained available to fishers at the time of reserve establishment (i.e. $\frac{N_{2,b,0}}{N_{T,b,0}} = 1 - A$ and $\frac{N_{1,b,0}}{N_{T,b,0}} = A$; see Proposition/Theorem A.1 In Appendix A). Under these conditions reserves always decrease yields initially, but increase the long-term asymptotic metapopulation growth rate (Propositions/Theorems A.1 & A.2). If the biomass protected is less than what is accounted for in the reallocation of fishing effort – which is what occurred in the Keppel Islands model – then these conditions are violated and the propositions/theorems A.1& A.2 no longer hold true.

To demonstrate the link between biomass lost and the reallocation of effort, we also re-analysed the Keppel Islands model with the rate of adult mortality due to reallocated fishing as

$$m_{fr} = \frac{m_f}{(1-B_r)},$$

where B_r is the proportion of the harvestable biomass available before reserves that was protected when reserves were implemented. This redistributes fishing effort spatially proportional to relative biomass on each reef. All other parameter values and methods remained the same as per the Keppel Islands model in Chapter 2, with the exception of the rate of juvenile survival (S_1), which was varied to obtain a metapopulation growth rate of 1 prior to reserve establishment. Here, all reserve combinations resulted in initial yields decreases, followed by yield recovery and growth within 10-20 years (Figure E2). Since effort was reallocated as per the biomass protected and not the area protected, there was no overcompensation for the loss of harvestable biomass. In other words, we recover the results proved for the analytical model in Propositions/Theorems A.1 & A.2.

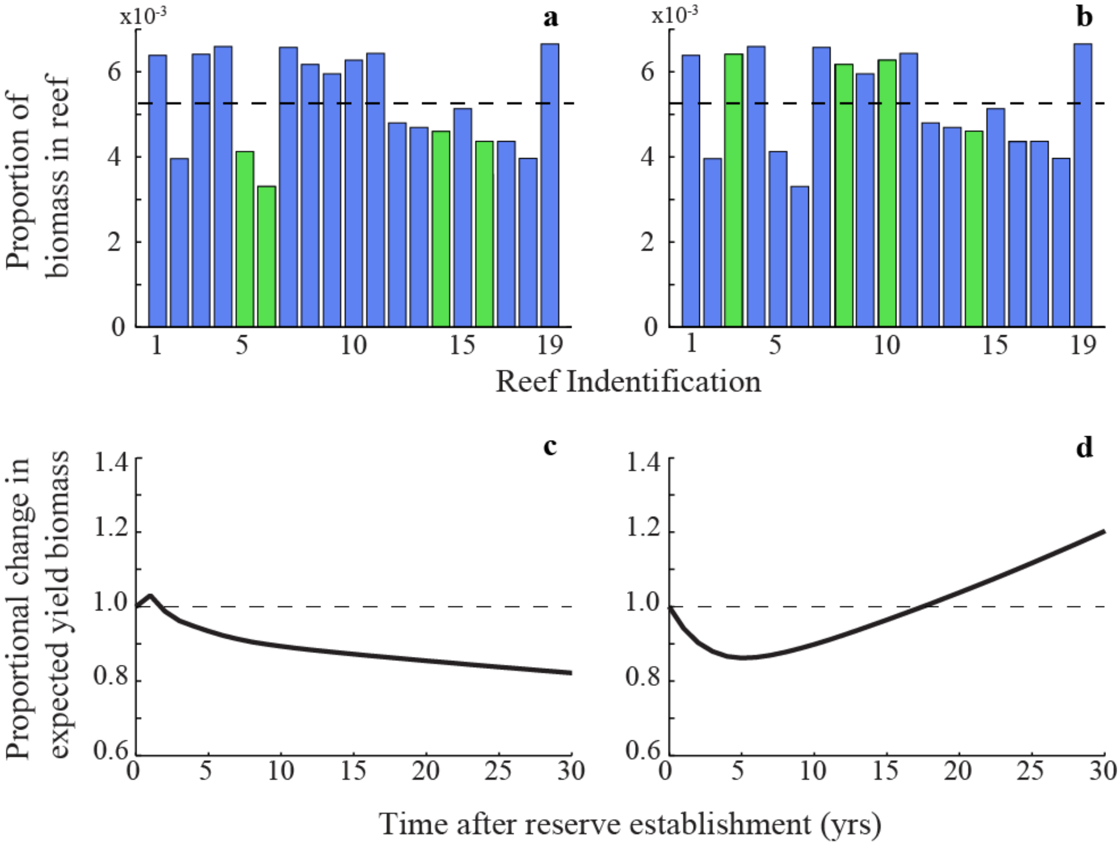


Figure E1 Example stable population distributions (**a, b**), and changes in yield biomass densities (**c, d**) over time, for a modified Keppel Islands spatially explicit model with homogenous reef sizes. In the left panels (**a, c**) four peripheral reefs were given reserve status, and, consequently, a smaller proportion of the biomass than proportion of the area was protected. For this scenario the asymptotic metapopulation growth was 0.9962. In the right panels (**b, d**) three central and one peripheral reef were given reserve status, with a larger proportion of the biomass than the area protected. For this scenario the asymptotic metapopulation growth was 1.0149. In panels **a** and **b**, green and blue bars indicate reserve and fished populations respectively and dashed line indicates average fishable biomass across all reefs.

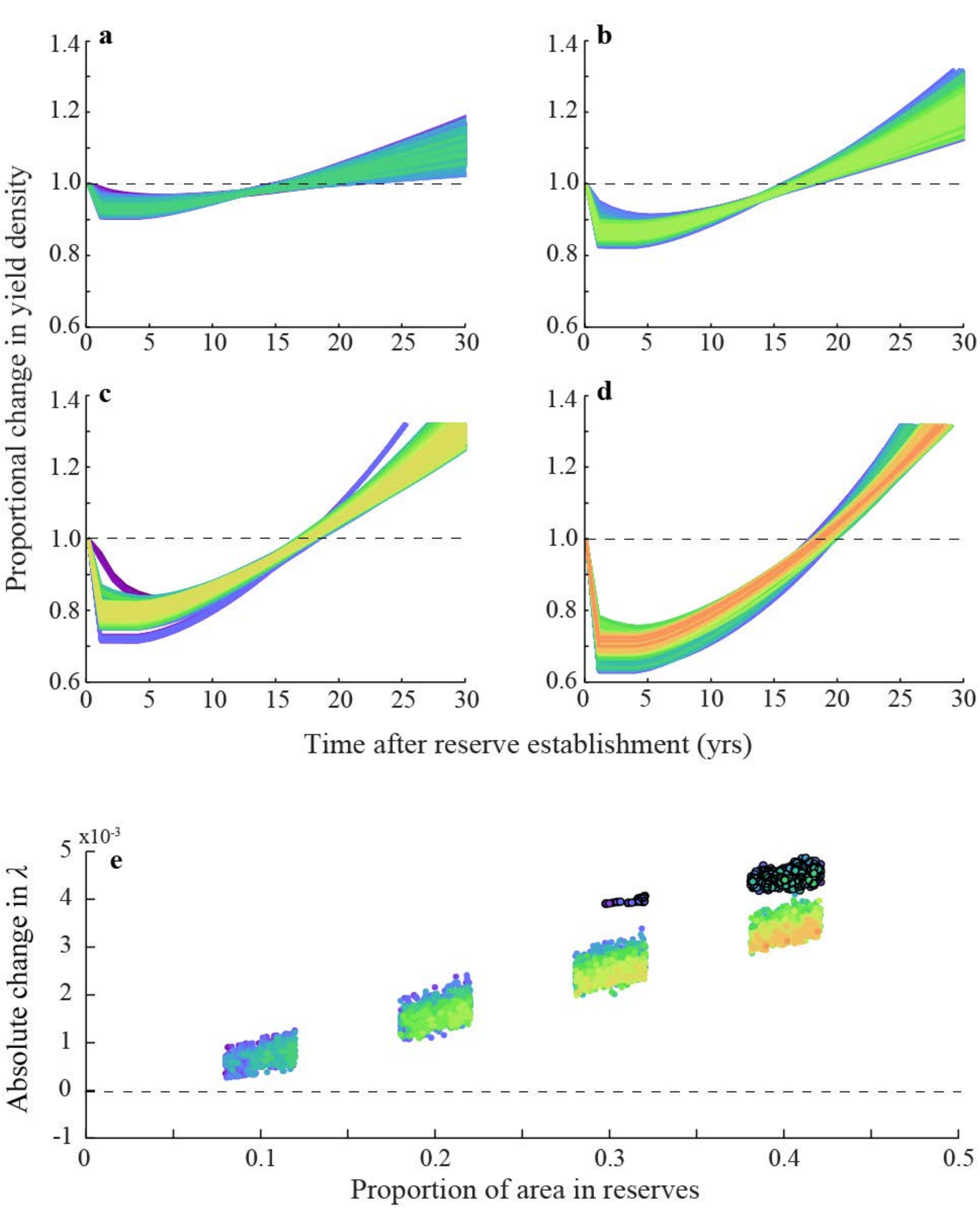


Figure E2 Short-term changes, when reallocated effort is proportion to biomass initially protected in reserves, in yield biomass under a range of reserve sizes (**a** = 8-12%, **b** = 18-22%, **c** = 28-32%, **d** = 38-42%), and (**e**) changes in asymptotic metapopulation growth rate (*λ*), after reserve implementation for the Keppel Islands spatially explicit model (distance-decay in larval dispersal and heterogeneous reef sizes). Individual points relate to different reserve combinations and only a random subset of all possible combinations is shown. Different colour indicate the number of reefs protected in a given combination (purple = 1 to orange = 9). Black edges indicate combinations that contain a disproportionally large reef.

Appendix F: ***Observed and predicted changes in coral trout catch, catch rates, and biomasses (Chapter 3)***

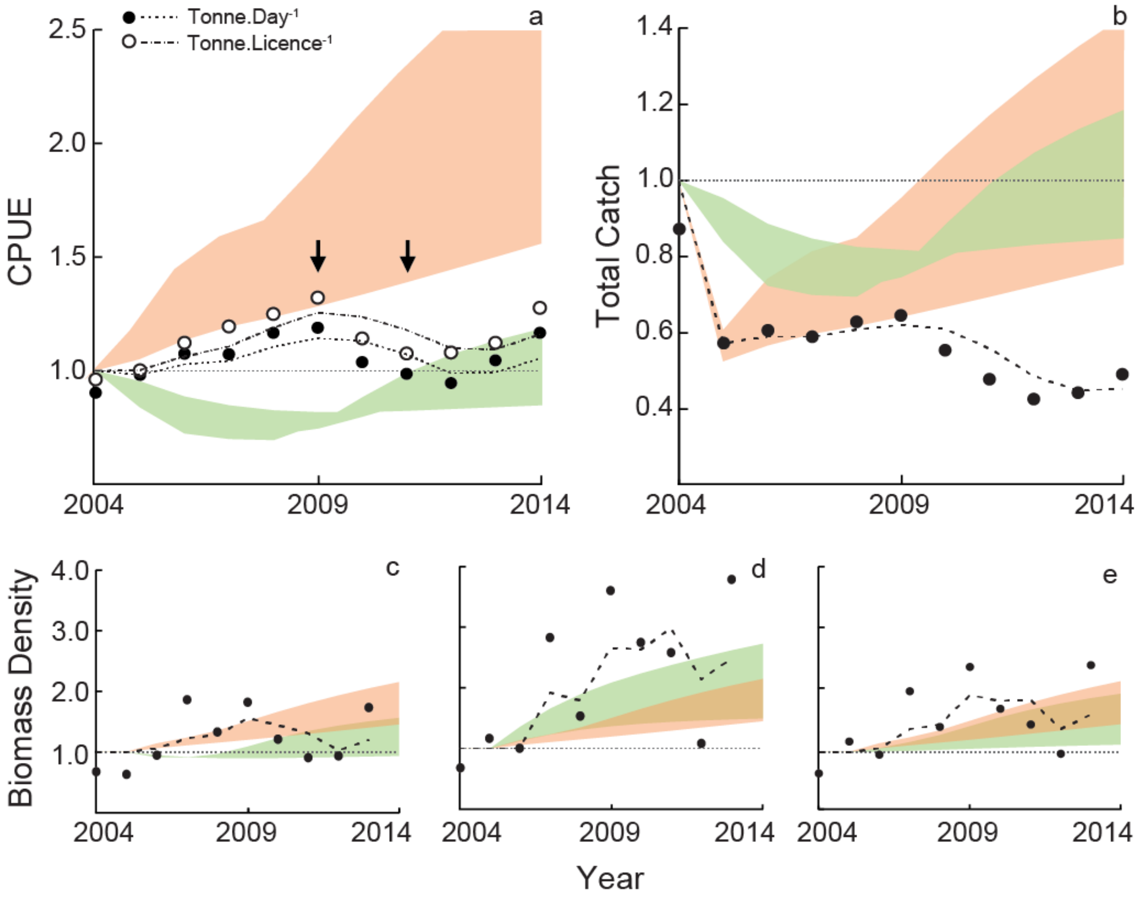


Figure F1 Observed (points & dashed lines) and modelled (coloured shading) changes in coral trout catch per unit effort (CPUE; tonnes per day and tonnes per licence) (**a**), total catch (**b**), and biomass in fished areas (**c**), reserves (**d**), and the metapopulation (**e**), after the 2004 rezoning and fishery restructuring. Colours indicate different modelled management scenarios; 33% reserves only (green), and reduced effort only (orange). In all panels shading indicates range of model outcomes for the range of density dependence strengths considered. Dashed lines are 3yr backwards moving averages, and light grey shading captures the 95% confidence intervals on biomass estimates. Horizontal dotted lines indicate a pre-2004 business as usual scenario.

Appendix G: ***Supplementary experimental procedures (Chapter 3)***

G.1 Study species

Coral trout (*Plectropomus* spp.) are a target fish of commercial fisheries on the GBRMP and throughout the Indo-Pacific region (Russ 1991) and have life-history characteristics similar to other tropical, exploited reef species. They are relatively long-lived with asymptotic growth, are protogynous hermaphrodites (changing sex from female to male), and display a metapopulation structure with relatively sedentary reef-associated adult populations connected through dispersing larvae. There has been considerable research into coral trout demography (Mapstone *et al.* 2004), life-history characteristics (Ferreira & Russ 1994; Russ *et al.* 1998), adult movement (Davies 1996; Zeller 1997; Zeller & Russ 1998), reproductive biology (Rimmer *et al.* 1994; Samoilys 2002), and larval dispersal (Harrison *et al.* 2102) on the GBR, providing robust parameter estimates for our models.

G.2 Model specifics

We described coral trout dynamics using an age-structured, sex-changing, two population model, with the simplifying assumption that all larvae enter a common pool and are redistributed according to the proportional reef area occupied by each population. We assumed longevity of 14 years, age of first reproduction to be 2 years, an annual spawning/reproduction event, and that sex-change from female to male was dependant on the mean age of the population. The model in its simplest form can be written as

$$\mathbf{n}_{t+1} = \mathbf{M}_t\, \mathbf{n}_t\,,$$

where $\mathbf{M}_t$ is the metapopulation projection matrix and $\mathbf{n}_t$ is a vector of the fish abundance in the metapopulation by age, sex, and population, at time *t*, where each time step is one year.

Following the vec-permutation matrix approach developed by Hunter & Caswell (2005), and used in Chapter 2, the matrix $\mathbf{M}_t$ is a function of both dispersal ($\mathbb{D}_t$ being a block diagonal matrix describing dispersal and recruitment to the adult population) and demographic ($\mathbb{B}_t$ being a block diagonal matrix describing demography) processes at time *t* such that

$$\mathbf{M}_t = \mathbf{P}^{\mathrm{T}}\mathbb{D}_t\mathbf{P}\mathbb{B}_t,$$

where **P** is the vec-permutation matrix. Here we have assumed a pre-breeding census and that adult demographic processes occur before dispersal and survival through the first year. The block diagonals on the matrices $\mathbb{B}_t$ and $\mathbb{D}_t$ are 14x14 and 2x2 projection matrices for the demography of population i ($\mathbf{B}_{i,t}$) and dispersal of age a ($\mathbf{D}_{a,t}$), at time t, respectively.

Following the well-mixed larvae assumption, the matrix $\mathbf{D}_1$ is

$$\mathbf{D}_{1,t} = \begin{bmatrix} A_1\, S_{1,1,t} & A_1\, S_{1,1,t} \\ A_2\, S_{1,2,t} & A_2\, S_{1,2,t} \end{bmatrix},$$

where $S_{1,i,t}$ is the per-capita survival of larvae in the pelagic through to settlement as juveniles at time t (see main text), and A_i is the area occupied by population i (by definition $A_1 + A_2 = 1$). Dispersal matrices for all other ages ($\mathbf{D}_{2\text{-}14}$) are 2x2 identity matrices which accounted for the assumption that all adults within a population remained within that population over time.

Per-capita survival of larvae ($S_{1,i,t}$; see Table G.**2**) is a function of the density-independent survival of juveniles (μ_1), and the strength of density-dependence (μ_2). Since empirical estimates for μ_1 and μ_2 are non-existent, we considered a plausible range of (μ_1, μ_2) pairs that yielded unfished equilibrium biomass densities equal to historical levels of coral trout on the outer GBR reefs (Emslie *et al.* 2015). The bounds of our (μ_1, μ_2) pairs were determined by realistic expectations of model behaviour. For example, if the density-independent survival of larvae, or the strength of density-dependence, was to too high, then the population would exhibit endogenously-driven cyclical behaviour, which is not observed in the empirical data (see, e.g., Figure G1). Conversely, if it was too low, then the population would not have been able to maintain itself under historical fishing pressures.

To model demographic processes we used two separate demography projection matrices ($\mathbb{B}_t$); the first described metapopulation demographics prior to the changes in management (with fishing in all populations), and the other after implementation (with fishing pressure only in A_2 if rezoning occurs). With the exception of whether adults were subject to fishing mortality (harvested) or not (protected), all populations were assumed to have identical demographic rates.

Prior to the rezoning and restructuring of the fishery, we assumed that all populations experienced the same fishing pressure and only fish aged ≥3 years were subject to fishing. This takes into account current size-limits for harvested coral trout on the GBR, and is representative of the common management strategy of allowing adult fish one reproductive year before entering the fishery (Mapstone *et al.* 2004). Since we needed to account for age-dependent sex-change, our demographic projection matrix comprised of submatrices ($\mathbf{b}_{y,z}$) describing the contribution of sex z to sex y (M = male, F = female). Hence, the demographic projection matrix for all populations prior to any management changes ($\mathbf{B}_{i,t}$) was

$$\mathbf{B}_{i,t} = \begin{bmatrix} \mathbf{b}_{\mathbf{F,F}} & \mathbf{b}_{\mathbf{F,M}} \\ \mathbf{b}_{\mathbf{M,F}} & \mathbf{b}_{\mathbf{M,M}} \end{bmatrix},$$

where

$$\mathbf{b}_{\mathbf{F,F}} = \begin{bmatrix} 0 & f_1\,\Psi_{i,t} & f_2\,\Psi_{i,t} & \cdots & \cdots & f_{14}\,\Psi_{i,t} & \\ e^{-m}(1-\Omega_{i,a}) & 0 & 0 & \cdots & \cdots & 0 & \\ 0 & e^{-m}(1-\Omega_{i,a}) & 0 & \ddots & \ddots & \vdots & \\ \vdots & \ddots & e^{-m-m_f}(1-\Omega_{i,a}) & \ddots & \ddots & & \vdots \\ \vdots & \ddots & \ddots & \ddots & \ddots & & \vdots \\ 0 & \cdots & \cdots & \cdots & e^{-m-m_f}(1-\Omega_{i,a}) & & 0 \end{bmatrix},$$

$$\mathbf{b}_{\mathbf{M,F}} = \begin{bmatrix} 0 & 0 & 0 & \cdots & \cdots & 0 & \\ e^{-m}\Omega_{i,a} & 0 & 0 & \cdots & \cdots & 0 & \\ 0 & e^{-m}\Omega_{i,a} & 0 & \ddots & \ddots & \vdots & \\ \vdots & \ddots & e^{-m-m_f}\Omega_{i,a} & \ddots & \ddots & & \vdots \\ \vdots & \ddots & \ddots & \ddots & \ddots & & \vdots \\ 0 & \cdots & \cdots & \cdots & e^{-m-m_f}\Omega_{i,a} & & 0 \end{bmatrix},$$

$\mathbf{b}_{\mathbf{M,M}}$ is a lower shift matrix, and $\mathbf{b}_{\mathbf{F,M}}$ is a zero matrix. Here f_a is the fecundity of females aged a, $\Psi_{i,t}$ is the fertilization success and $\Omega_{i,a}$ the probability of a female transitioning to a male in population i at time t, m is the natural mortality rate, and m_f the mortality rate due to fishing (see Table G.**2** for more detail).

After the rezoning and restructuring, the fishing mortality rate ($m_{f,s}$) changed depending on the scenario, and the proportion of fish caught (y_s), and yield biomass at time t ($Y_{,s,t}$) for each scenario s considered were as follows:

Scenario	**Fishing mortality rate**	**Proportion of fish caught**	**Yield biomass**
Rezoning & Restructure	$m_{f1} = \frac{m_f\,(1-d_e)}{A_2}$	$y_1 = \frac{m_{f1}}{(m+m_{f1})}\left[1-e^{(-m-m_f)}\right]$	$Y_{1,t} = y_1 \sum W_a n_{2,a,t}$
Rezoning only	$m_{f2} = \frac{m_f}{A_2}$	$y_2 = \frac{m_{f2}}{(m+m_{f2})}\left[1-e^{(-m-m_f)}\right]$	$Y_{2,t} = y_2 \sum W_a n_{2,a,t}$
Restructure only	$m_{f3} = m_f\,(1-d_e)$	$y_3 = \frac{m_{f3}}{(m+m_{f3})}\left[1-e^{(-m-m_f)}\right]$	$Y_{3,t} = y_3 \sum W_a n_{i,a,t}$

Here, d_e is the proportional decrease in effort due to the restructuring, W_a is the weight of a fish aged a, $n_{i,a,t}$ is the number of fished individuals in population i, aged a, and at time t. The proportion of fish caught in a given scenario (y_s) was derived from the rate of fishing pressure integrated over the entire year. For scenarios where reserves were implemented, we set fishing mortality to zero for population 1 (the "reserve" sub-population), and we rescaled the fishing mortality rate by the proportion of reef area remaining open to fishing. We calculated yield biomass at each point after the management changes as the proportional change in biomass caught per year relative to the yield biomass prior to any management changes.

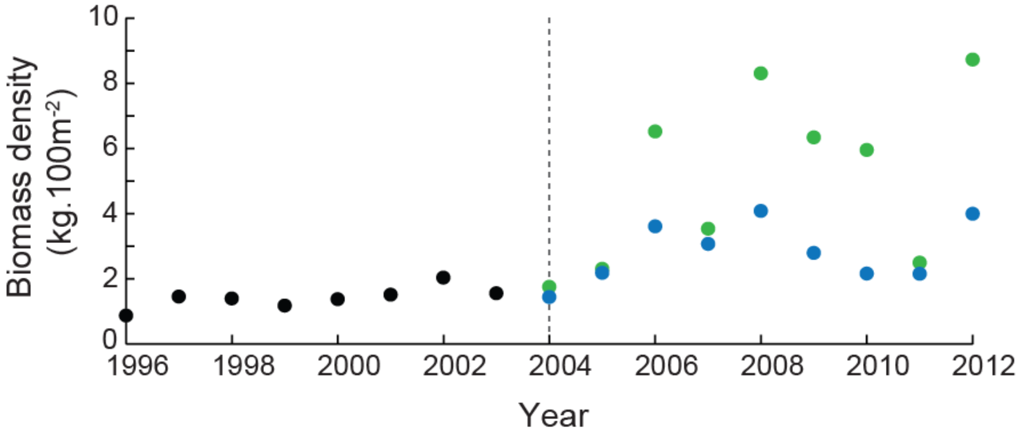


Figure G1 Changes in coral trout biomass densities on outer-shelf reefs of the GBRMP in fished reefs before (black points), and in reserves (green points) and fished areas (blue points) after the 2004 rezoning and fishery management changes.

Table G.2 Parameter descriptions, values, and references (where applicable) used for the models in Chapter 3, also see Chapter 2, Table 2.1.

Symbol	Description	Value	Ref.
A_1	Proportion of area occupied by population one (which becomes protected after establishment)	0.33	(GBRMPA 2003)
L_a	Length of an individual of age *a* $L_a = L_\infty(1 - e^{-k[a-a_0]})$, where L_∞ = average asymptotic maximum body size, k = growth rate parameter, and a_0 = hypothetical age at which length is zero	50cm 0.459 -0.083	(Haddon 2001; Chan *et al.* 2012)
W_a	Weight (g) of a fish of age *a* $W_a = g\,(L_a)^h$, where g = shape parameter, and h = shape parameter	0.0079 3.1570	(Ferreira & Russ 1994)
f_a	Per-capita fecundity of a female fish age *a* $f_a = v\,(L_a)^w$, where v = shape parameter, and w = shape parameter	4.7559 2.6399	(Samoilys 2002)
$\Omega_{i,a}$	Probability that a female fish age *a* in pop. *i* will change sex to male $\Omega_{i,a} = (1 - e^{-q[a- a_{m,i}-a_o})^{-1}$, where q = strength of sex change rate, $a_{m,i}$ = mean age of population *i*, and a_o = offset term, set so that unfished populations are 3:1 female to male	0.3369 (0,14) 7.9	(Ferreira 1995; Chan *et al.* 2012)
$\Psi_{i,t}$	Proportion of eggs fertilised in pop *i* at time *t* $\Psi_{i,t} = 1 - e^{-R\,M_{i,t}}$, where R = fertility parameter, and $M_{i,t}$ = proportion of pop. *i* biomass that is male at time *t*	8	(Chan *et al.* 2012)
m	Rate of adult mortality due to natural causes	0.3383	(Chan *et al.* 2012)
$s_{1,i,t}$	Survival of juveniles in population *i* at time *t* (includes larval dispersal and juveniles mortality once on the reef) $s_{1,i,t} = -\mu_1\, e^{-\mu_2 \sum_{a=2}^{14} A_i\, W_a\, n_{i,a,t}}$, where µ1 = density-independent survival^{++}, and µ2 = strength of density-dependence^{++}	[0.8, 1.65, 2.5]*10^{-5} [0.881 2.01 2.657] *10^{-8}	

++ μ_1 and μ_2 values are coupled and were set to unfished equilibrium biomass densities equal to historical levels of coral trout on the outer GBR reefs.

Appendix G References

Chan, N., Connolly, S. & Mapstone, B. (2012). Effects of sex change on the implications of marine reserves for fisheries. *Ecol. Appl.*, 22, 778–91.

Davies, C.R. (1996). *Inter-reef Movement of the Common Coral Trout,* Plectropomus leopardus. Research Publication No. 61, Great Barrier Reef Marine Park Authority, Townsville (50pp).

Emslie, M.J., Logan, M., Russ, G.R., Sweatman, H.P.A., Williamson, D.H., Ayling, A.M., Macneil, M.A., Ceccarelli, D., Cheal, A.J., Evans, R.D., Johns, K.A., Jonker, M.J., Miller, I.R., Osborne, K., Russ, G.R. & Sweatman, H.P.A. (2015). Expectations and outcomes of reserve network performance following re-zoning of the Great Barrier Reef Marine Park. *Curr. Biol.*, 1–10.

Ferreira, B.P. (1995). Reproduction of the common coral trout *Plectropomus Leopardus* (Serranidae: Epinephelinae) from the Central and Northern Great Barrier Reef, Australia. *Bull. Mar. Sci.*, 56, 653–669.

Ferreira, B.P. & Russ, G. (1994). Age validation and estimation of growth rate of the coral trout, *Plectropomus leopardus* (Lacepede 1802), from Lizard Island, Northern Great Barrier Reef. *Fish. Bull.*, 92, 46–57.

Great Barrier Reef Marine Park Authority (2003). *Summary report of the social and economic impacts of the rezoning of the Great Barrier Reef Marine Park*. Report of the Great Barrier Reef Marine Park Authority. http:// elibrary.gbrmpa.gov.au/jspui/handle/11017/381

Haddon, M. (2001). Stock-recruitment relationships. In: *quantitative methods in fisheries*. CRC Press Taylor & Francis Group, Boca Raston.

Harrison, H.B., Williamson, D.H., Evans, R.D., Almany, G.R., Thorrold, S.R., Russ, G.R., Feldheim, K.A., van Herwerden, L., Planes, S., Srinivasan, M., Berumen, M.L. & Jones, G.P. (2012). Larval export from marine reserves and the recruitment benefit for fish and fisheries. *Curr. Biol.*, 22, 1023–1028.

Hunter, C.M. & Caswell, H. (2005). The use of the vec-permutation matrix in spatial matrix population models. *Ecol. Modell.*, 188, 15–21.

Mapstone, B.D., Davies, C.R., Little, L.R., Punt, A.E., Smith, A.D.M., Pantus, F., Lou, D.C., Williams, A.J., Jones, A., Ayling, A.M., Russ, G.R. & Mcdonald, A.D. (2004). *The effects of line fishing on the Great Barrier Reef and evaluations of alternative potential management strategies. CRC Reef Research Centre Technical Report No 52. CRC Reef Res. Cent. Tech. Rep. No 52.* CRC Reef Research Centre, Townsville, Australia.

Rimmer, M.A., Garrett, R.N. & Samoilys, M.A. (1994). In vitro fertilization of eggs of coral trout, *Plectropomus leopardus* (Serranidae), collected from an aggregation site on the Great Barrier Reef, Australia. *Bull. Mar. Sci.*, 54, 356–358.

Russ. (1991). Coral reef fisheries: effects and yields. In: *The ecology of fishes on coral reefs* (ed. Sale, P.F.). Academic Press, San Diego, CA, pp. 601–634.

Russ, G.R., Lou, D.C., Higgs, J.B. & Ferreira, B.P. (1998). Mortality rate of a cohort of the coral trout, Plectropomus leopardus, in zones of the Great Barrier Reef Marine Park closed to fishing. *Mar. Freshw. Res.*, 49, 507–511.

Samoilys, M.A. (2002). Reproductive dynamics of an exploited seranid on the Great Barrier Reef. Thesis. School of Marine and Tropical Biology, James Cook University, Townsville.

Zeller, D.C. (1997). Home range and activity patterns of the coral trout Plectropomus leopardus (Serranidae). *Mar. Ecol. Prog. Ser.*, 154, 65–77.

Zeller, D.C. & Russ, G.R. (1998). Marine reserves: patterns of adult movement of the coral trout (*Plectropomus leopardus* (Serranidae)). *Can. J. Fish. Aquat. Sci.*, 55, 917–924.

Appendix H: ***Supplementary figures (Chapter 4)***

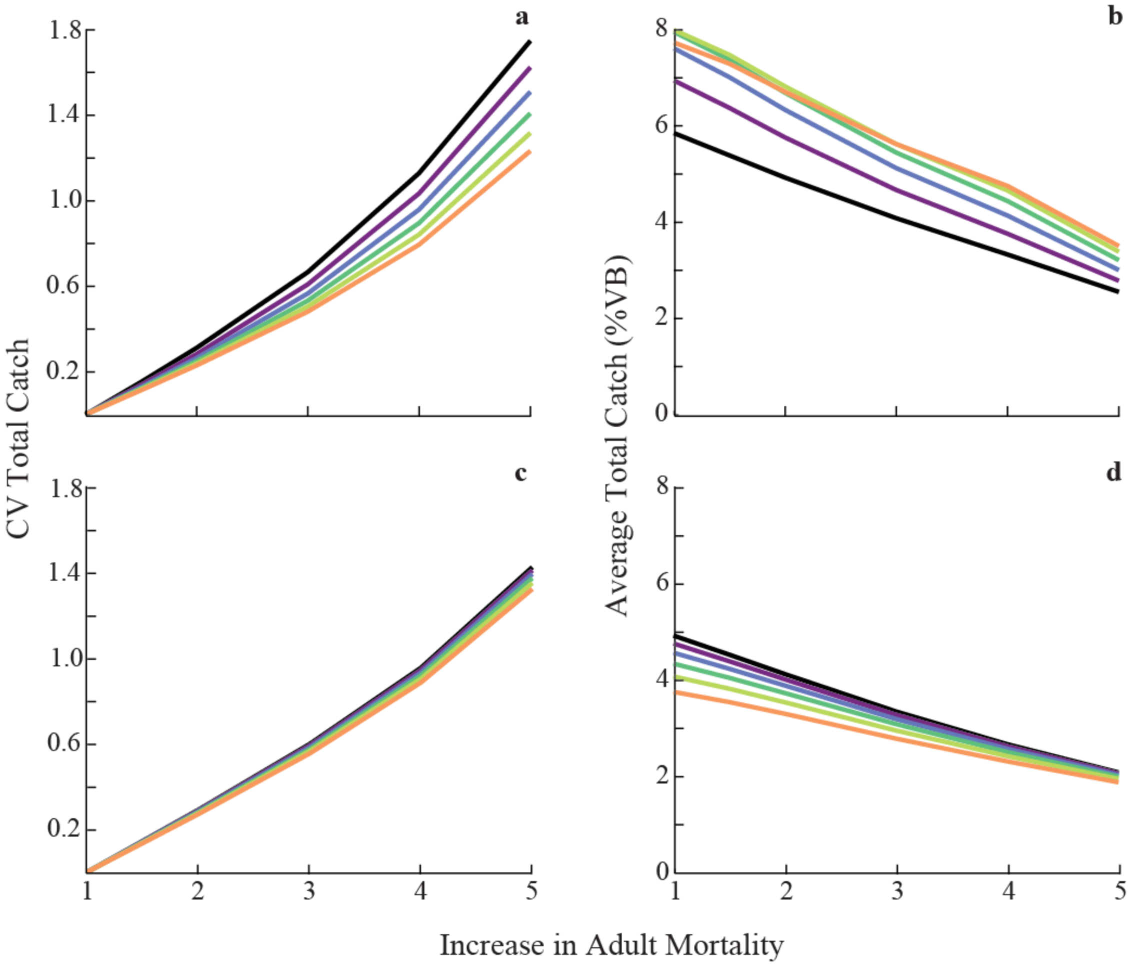


Figure H1 Change in the mean coefficient of variation (CV) and mean average (as a percentage of virgin biomass; %VB) of total catch with increasing disturbance intensity (increased adult mortality) and varying reserve coverage, for a heavily fished system (20% virgin biomass without reserves; **a**, **b**), and moderately fished system (50% virgin biomass; **c**, **d**). Colours indicate reserve coverage from 0% (black) to 50% (orange) in increments of 10%. Means are of 1000 interations, and total catch CV and average for each iteration are of the last 1000 years of the simulations.

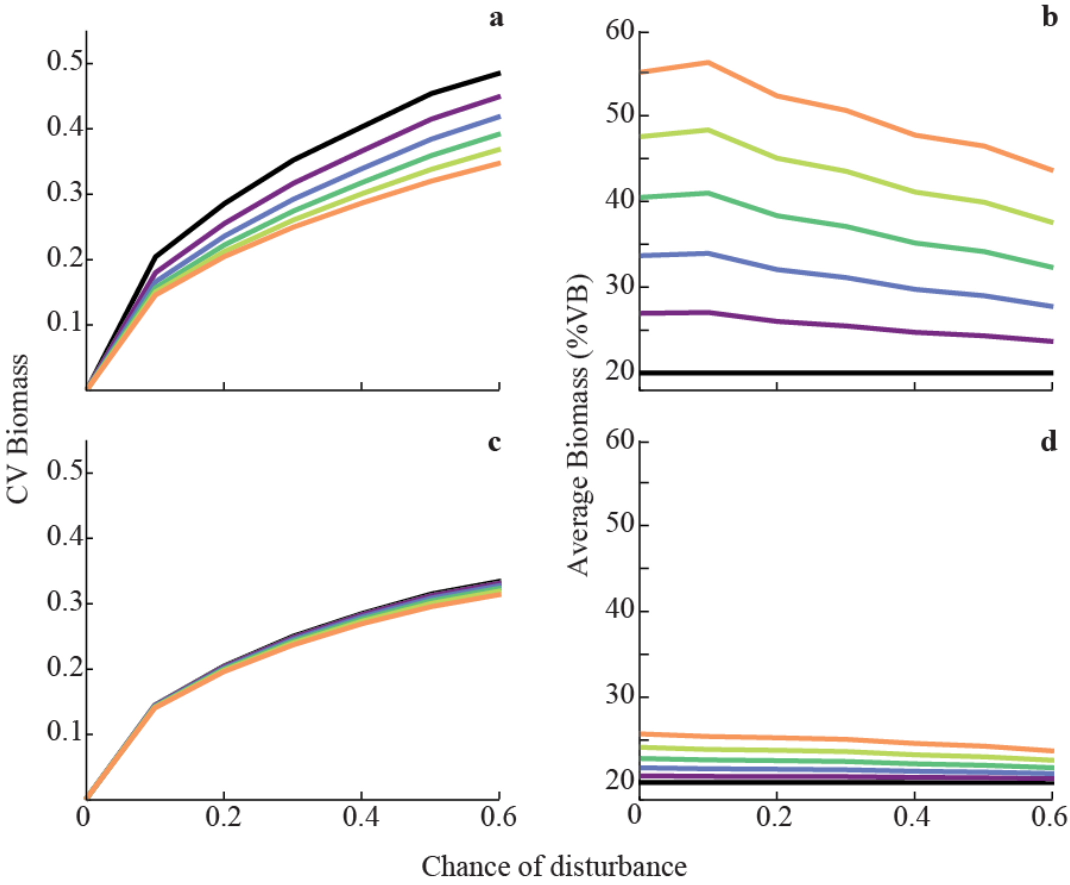


Figure H2 Change in the mean coefficient of variation (CV) and mean average (as a percentage of virgin biomass; %VB) of metapopulation biomass with increasing disturbance frequency and varying reserve coverage, for a heavily fished system (20% virgin biomass without reserves; **a**, **b**), and moderately fished system (50% virgin biomass; **c**, **d**). Colours indicate reserve coverage from 0% (black) to 50% (orange) in increments of 10%. Means are of 1000 interations, and biomass CV and average for each iteration are of the last 1000 years of the simulations.

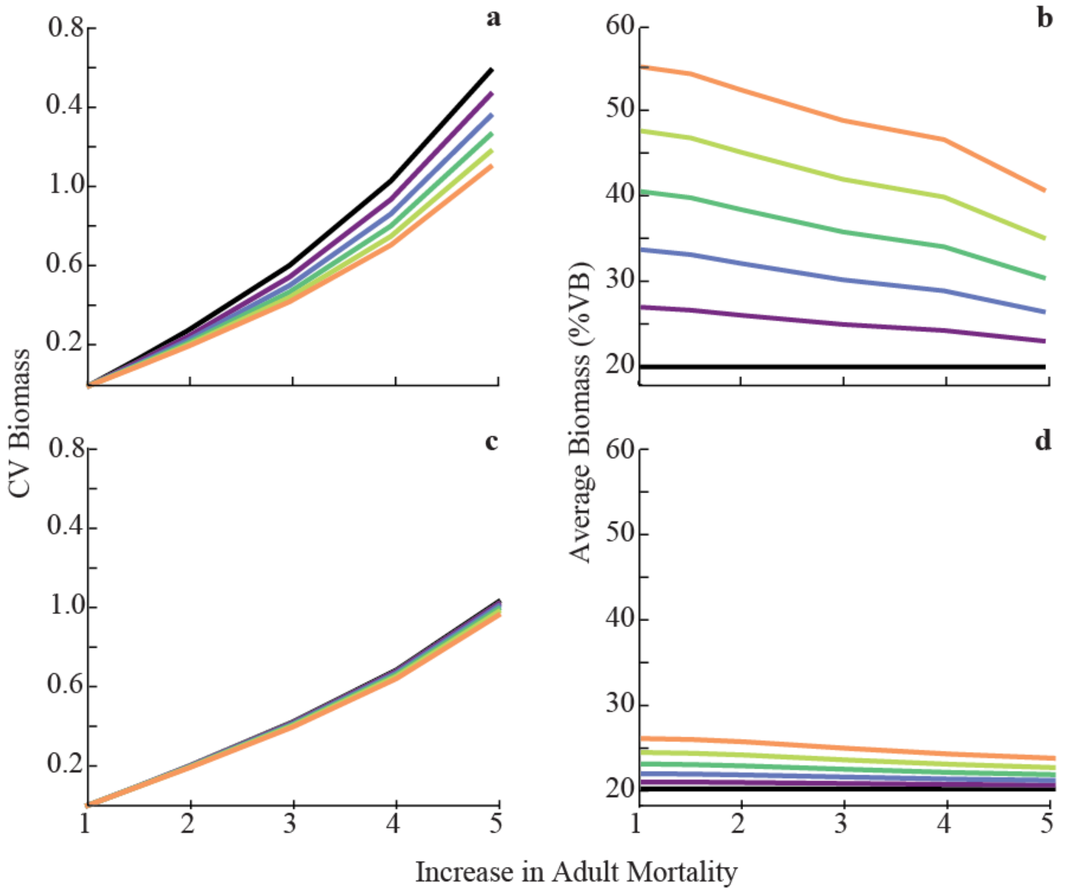


Figure H3 Change in the mean coefficient of variation (CV) and mean average (as a percentage of virgin biomass; %VB) of metapopulation biomass with increasing disturbance intensity (increased adult mortality) and varying reserve coverage, for a heavily fished system (20% virgin biomass without reserves; **a**, **b**), and moderately fished system (50% virgin biomass; **c**, **d**). Colours indicate reserve coverage from 0% (black) to 50% (orange) in increments of 10%. Means are of 1000 interations, and biomass CV and average for each iteration are of the last 1000 years of the simulations.

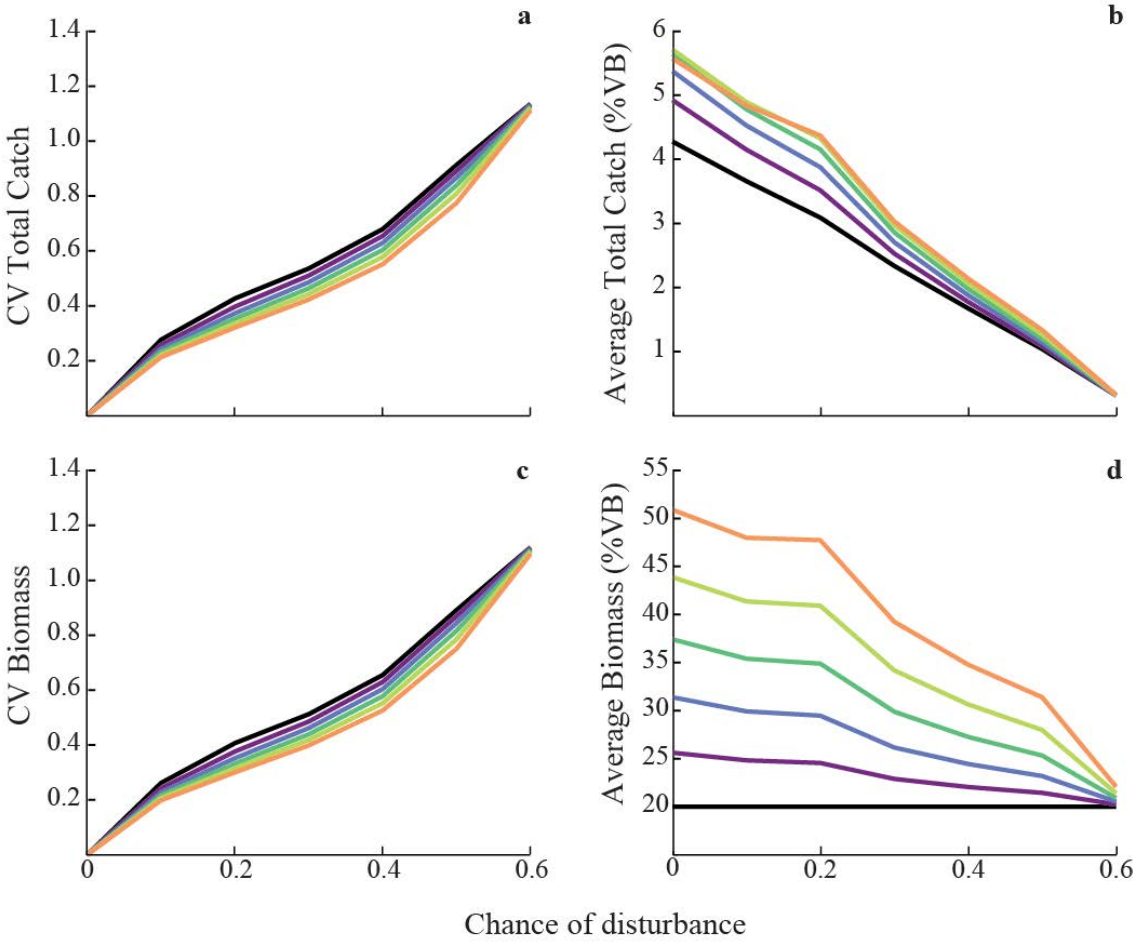
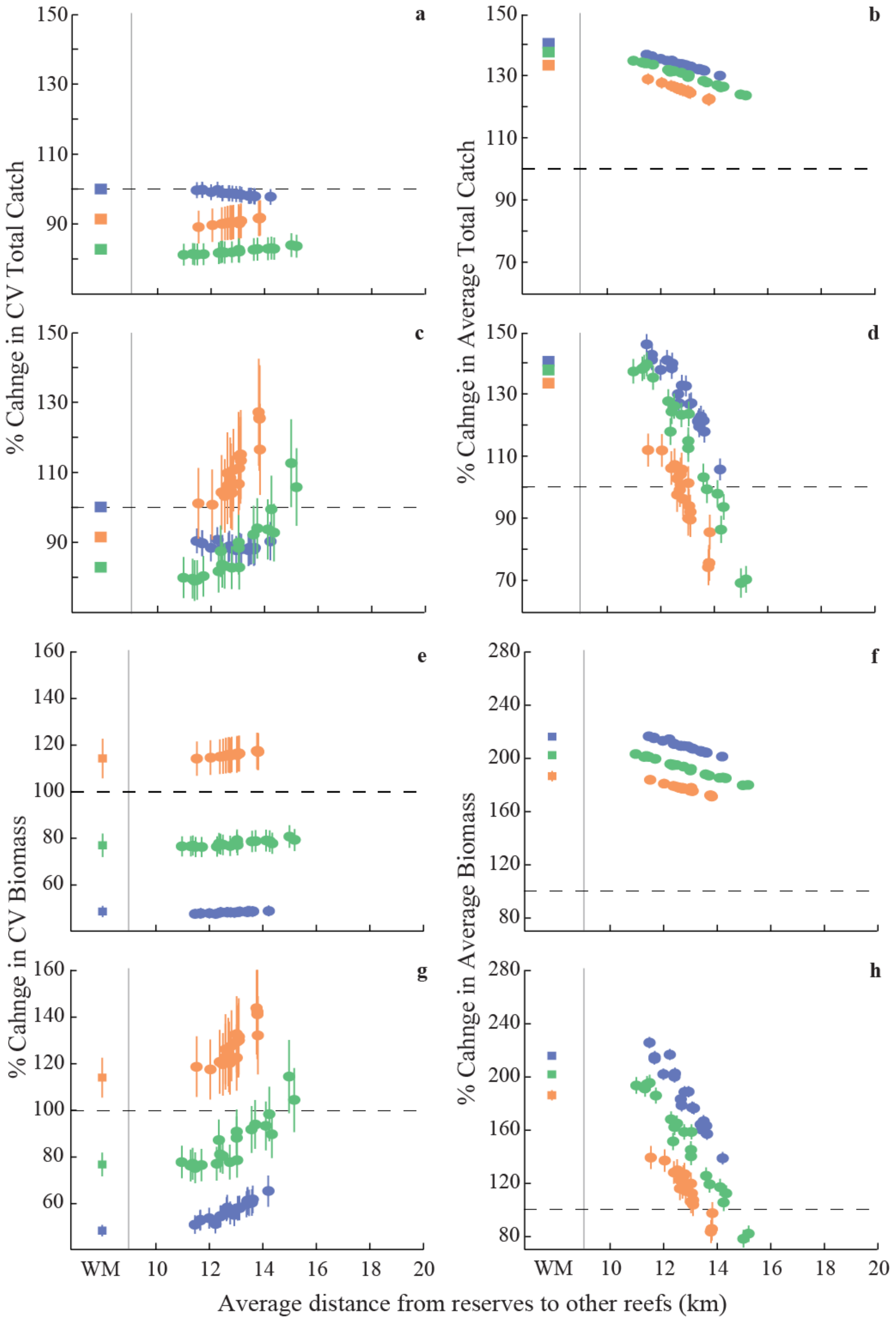


Figure H4 Change in the mean coefficient of variation (CV) and mean average (as a percentage of virgin biomass; %VB) of total catch (**a**, **b**) and metapopulation biomass (**c**, **d**) with increasing disturbance frequency (increased adult mortality) and varying reserve coverage, for a heavily fished (20% virgin biomass without reserves), non-sex-changing species. Colours indicate reserve coverage from 0% (black) to 50% (orange) in increments of 10%. Means are of 1000 interations, and total catch CV and average for each iteration are of the last 1000 years of the simulations.

→

Figure H5 Relative change in the coefficient of variation (CV) and average total catch and metapopulation biomass (as percentages of the non-reserve scenario) in the Keppel Island Group, with increasing average distance from reserves to all other reefs when larval disersal distance is long (**a**, **b**, **e**, **f**), and short (**c**, **d**, **g**, **h**) for three reserve placement scenarios; 1) reserves only placed in disturbed reefs (orange), reserves placed only in non-disturbed reefs (blue), and reserves equally spaced between disturbed and non-disturbed reefs (green). Square symbols indicate a well-mixed (WM) larvae scenario. Reserve coverage is ~30% and fishing pressure is high (20% virgin biomass). Mean values (symbols) and standard deviations (lines) are of 100 interations, and CV and average for each iteration are of the last 1000 years of the simulations. The horizontal dashed lines represents the no reserve (but still disturbed) scenario. realtive CV, values above the dashed line indicate increases in temporal fluctuations, and below indicates decreases in fluctutations (increased stability), comapred to a no-reserve scenario.


a
b
c
d
e
f
g
h
% Cahnge in CV Total Catch
% Cahnge in Average Total Catch
% Cahnge in CV Biomass
% Cahnge in Average Biomass
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100
80
60
280
240
200
160
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12
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18
20
Average distance from reserves to other reefs (km)

Appendix I: ***Statement of publication contributions***

Publication	*Nature and extent of the intellectual input of each author, including the candidate*	*I confirm the candidate's contribution to this paper and consent to the inclusion of the paper in this thesis*
Thesis Chapter 2: Hopf, J. K., Jones, G. P., Williamson, D. H. and Connolly, S. R. (2016) Fishery consequences of marine reserves: short-term pain for longer-term gain. *Ecol Appl*, 26: 818–829.	JH and SC conceived the research question, with feedback from GJ and DW; JH developed the models and ran sensitivity analysis; JH analysed the outputs, with assistance from SC, GJ, and DW; JH wrote the first draft and produced the figures; all co-authors contributed to revisions	Name: Geoff Jones Signature: Name: David Williamson Signature: Name: Sean Connolly Signature:
Thesis Chapter 3: Hopf, J. K., Jones, G. P., Williamson, D. H. and Connolly, S. R. (2016) Synergistic Effects of Marine Reserves and Harvest Controls on the Abundance and Catch Dynamics of a Coral Reef Fishery, *Curr. Biol.* http://dx.doi.org/10.1016/j.cub.2016.04.022	JH conceived the research, with feedback from SC, GJ, and DW; JH developed the model and analysed the outputs, with feedback from SC, GJ, and DW; JH wrote the first draft of the manuscript and produced the figures; all co-authors contributed to revisions	Name: Geoff Jones Signature: Name: David Williamson Signature: Name: Sean Connolly Signature: