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Habitat determinants of *Chaetodon* butterflyfish and fishery-targeted coral reef fish assemblages in the central Philippines

Thesis submitted by

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All data reported in this thesis were collected by Susannah Leahy, with the exception of:

(1) otolith increment numbers and widths (Chapter 3), which were collected by a commercial professional otolith ageing entity (Tropical Fish Ageing, Townsville) headed by Dr. Dongchun Lou;

(2) long-term fish and benthic monitoring data (Chapter 4), which were collected by Prof. Garry Russ from 1983 to 2014;

(3) remotely sensed imagery (Chapter 5), which was collected by the WorldView-2 satellite, which is owned and operated by DigitalGlobe. Imagery was purchased from the Australian WorldView-2 imagery provider GeoImage Pty. Ltd., with some basic pre-processing steps already completed.

Co-authors on current and future publications arising from this thesis made intellectual contributions to the manuscripts, in the form of guidance at the experimental design stage and the editing stage. Non-authors who provided important support for the thesis data chapters are: Prof. Rhondda Jones, Dr. Justin Rizzari, and Mr Mason Campbell, who acted as statistical "sounding boards" throughout the thesis; anonymous reviewers at Marine and Freshwater Research (Chapter 2) and Coral Reefs (Chapter 3), who provided helpful comments on earlier versions of the data chapter manuscripts; and Claro Renato Jadloc, who facilitated all of my fieldwork in the Philippines.

I am the primary author of three of the four publications arising from this thesis (Chapters 2, 3, and 5), as I conceived of each research question, designed the experimental approach, implemented the work, collected the data, carried out the statistical analyses, and wrote the manuscripts. I am the second author of the publication arising from Chapter 4, although the first author (G.R. Russ) and I have contributed equally to that manuscript. G.R. Russ designed the experimental approach in 1983, was awarded funding for the work, collected the data used in Chapter 4 over the course of 31 years of monitoring the study sites, and edited the manuscript produced from this data chapter. I carried out the statistical analyses on the dataset and prepared the manuscript for the chapter.

All of the research presented and reported in this thesis was conducted within the guidelines of the James Cook University Animal Ethics Committee (approval number A1803).

List of publications arising from this thesis

Leahy, S. M., G. R. Russ, and R. A. Abesamis. 2015. Primacy of bottom-up effects on a butterflyfish assemblage. Marine and Freshwater Research, 10.1071/MF15012

Leahy, S. M., G. R. Russ, and R. A. Abesamis. 2015. Pelagic larval duration and settlement size of a reef fish are spatially consistent, but post-settlement growth varies at the reef scale. Coral Reefs **34**:1283-1296, 10.1007/s00338-015-1330-y

Russ, G. R., and S. M. Leahy (*in review*). Rates and degrees of decline and recovery of corals and *Chaetodon* butterflyfish on Philippine coral reefs. Environmental Biology of Fishes

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General Abstract

Habitat availability and suitability are key factors determining the local abundance of a species and the structure of species assemblages. Nowhere is this more evident than in coral reef systems, where the availability, condition, and complexity of scleractinian corals are major determinants of the abundance, growth, and survival of both specialist and generalist coral reef fishes. Unfortunately, these shallow water habitats are also extremely vulnerable to destructive natural events such as cyclones, as well as anthropogenic environmental disturbances such as reduced water quality, overfishing and destructive fishing, and increased temperatures and reduced ocean pH associated with climate change. The deterioration of shallow water habitats is particularly pronounced in poor, developing nations such as those in the Coral Triangle, where marine biodiversity is high, but so are human population density and reliance on resource extraction. No-take marine reserves (NTMRs) are used throughout the region to reduce human impacts on coastal areas, and produce benefits for conservation, fisheries, or even both. This thesis aims to determine the habitat characteristics that drive the abundance, species richness, growth rates, and assemblage structure of coral reef fishes in order to inform placement of NTMRs, and to identify potential environmental stressors that may require more complex management strategies.

Identifying the full range of habitat characteristics that can influence coral reef fish is potentially highly complex. Thus, work reported early in this thesis was carried out on *Chaetodon* butterflyfish, which exhibit relatively well-known habitat associations, are highly sensitive to changes in habitat condition and habitat loss, and are not normally targeted by fishers, such that a *Chaetodon* response to habitat condition should not be confounded by fishing effects. Many *Chaetodon* butterflyfish

exhibit a particularly strong association with live coral cover, such that the abundance of obligate corallivorous *Chaetodon* butterflyfish has often been promoted for use as an indicator of coral reef health. The work presented in **Chapter 2** of this thesis tested the influence of a wide range of bottom-up (benthic resource) and top-down characteristics on the abundance of corallivorous and generalist *Chaetodon,* and overall *Chaetodon* species richness. This research reinforced certain well-established associations between *Chaetodon* butterflyfish and their habitats, such as increased abundance of obligate corallivores with increased availability of branching and tabular live coral and with increasing benthic rugosity, but also elucidated and quantified several less-known influences on *Chaetodon* abundance and diversity. One of these is that the negative effect of macroalgal cover on *Chaetodon* abundance and species richness is stronger and more directly influential than has previously been reported in the literature. Furthermore, *Chaetodon* were not affected by the density of large predators, but corallivorous *Chaetodon* were negatively influenced by the density of small predators (mesopredators), which are most likely affecting new recruits and juveniles. These results encourage the management of coral reefs to limit macroalgal growth (e.g. improve water quality and reduce fishing pressure on herbivores) and to control the abundance of mesopredators.

Habitat characteristics can influence not only the presence and abundance of a species, but also its physiology and development, with potential consequences for the survival and reproduction of each individual. **Chapter 3** extended previous research on the habitat associations of *Chaetodon* butterflyfishes to explore the effects of habitat condition on the growth rates of newly-settled fishes, using *Chaetodon vagabundus* as a model species. The data collected in this chapter also provided the first measure of pelagic larval duration and size-at-age estimates for *C. vagabundus* in this region, which has previously been used to model larval connectivity of coral reef fishes. I report that larval characteristics of *C. vagabundus* were consistent across the 80 km study region, but that site-level (1-5km) differences in habitat condition caused significant differences in early post-settlement growth rates for this species. High growth rates were associated with the known habitat preferences of juvenile *C. vagabundus* (rocky, low rugosity reef flats). However, the strongest habitat association was an unexpected, strongly negative influence of macroalgal cover on early growth rates, as well as evidence of reduced growth rates when density of juvenile conspecifics was high (i.e. negative density dependence). The significant negative influence of macroalgal cover in this region again emphasises the importance of management to control macroalgae, such as by improving water quality and reducing fishing pressure on herbivores.

Strong associations between coral reef fishes and their habitats can be used to assess fish responses to environmental disturbances and also to assess the duration of recovery periods of fish and benthos after disturbance. This is particularly true of *Chaetodon* butterflyfishes and measures of live coral cover. In **Chapter 4**, I identify the major drivers of the abundance of corallivorous and generalist *Chaetodon*, as well as overall *Chaetodon* species richness, and use them to assess the *Chaetodon* response to a range of environmental disturbance events and subsequent recovery periods over the course of 31 years of almost annual monitoring at two NTMRs and two fished sites at offshore islands in the Bohol Sea, in the central Philippines. Macroalgae was not present at the long-term monitoring sites. Instead, the abundance of generalist *Chaetodon* and *Chaetodon* species richness both exhibited a strong negative association with sand and rubble cover. In addition, the uniquely long and consistent monitoring provided the opportunity to quantify the effects of several major disturbance events (typhoons, crown of thorns (COTS) outbreaks, coral bleaching, and destructive fishing) and recovery periods, which saw disturbance events reduce cover of branching and tabular corals and the abundance of corallivorous *Chaetodon* on average by half in just 1-2 years, while recovery periods saw branching and tabular coral cover and abundance of corallivorous *Chaetodon* on average double in 11-12 years. The order of magnitude difference in the rate of recovery compared to the rate of decline is an important concern for reef managers and users. Furthermore, the NTMR status of the study sites did not significantly affect benthic cover or *Chaetodon* abundance, species richness, or assemblage structure, which serves as an important reminder that NTMRs are not a panacea for increasingly disturbed coral reefs.

Many coral reef fishes have much more complex habitat requirements than *Chaetodon* butterflyfishes. For example, some use a range of reef and non-reef habitats at different periods in their lives, and the spatial extent (i.e. area) of each habitat type, and their proximity to each other (i.e. connectedness) have been identified as significant drivers of the abundance and species richness of these coral reef fishes. **Chapter 5** combined extensive *in situ* collection of traditional habitat condition metrics, such as depth and percent cover of massive and encrusting corals, with remotely-sensed imagery that quantified the spatial extent and proximity of major habitat types (coral reef, seagrass beds, mangrove stands), to determine which variables most strongly influenced the presence/absence and biomass of several major coral reef fishery taxa at 19 inshore sites along the coast of Negros Oriental in the central Philippines. Study taxa included both heavily and lightly targeted species groups in order to provide relevant information to coastal resource managers in this region. I determined that NTMR protection and measures of habitat condition specific to each fish grouping (e.g. percent rubble cover for goatfish) were consistently strong predictors of species presence and biomass, while measures of habitat extent and connectedness were rarely significant drivers in this system. These results encourage the management of coastal resources to promote habitat health, and the placement of NTMRs in areas of high habitat quality rather than in marginal habitats in order to maximize their benefits to local fisheries.

This thesis emphasises the importance of managing coastal habitats, and coral reefs in particular, to prioritise habitat health and condition, such as improving water quality. In addition, it encourages the placement of NTMRs on healthy rather than degraded habitats in order to generate the greatest benefits to conservation and fisheries.

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Chapter 1: General Introduction

1.1. Context of the research

The association between organisms and their habitat is at the core of the study of ecology, with habitat defined as the range of physical, chemical, and biological environments in which a species can occur (Whittaker et al. 1973). Habitat availability and habitat suitability, or "quality", are therefore key factors determining the local abundance of a species and the structure of species assemblages.

A number of iconic cases demonstrate the importance of habitat – and habitat loss – to the abundance of a species. In the north-American Pacific Northwest, the abundance of the Northern Spotted Owl (*Strix occidentalis caurina*) declined dramatically in the 1980s as a result of logging of the old growth coniferous forests that it relies upon (Franklin et al. 2000). Similarly, in Nigeria, the Cross River gorilla (*Gorilla gorilla diehli*) has been in decline for decades, primarily as a result of destruction and fragmentation of the tropical moist forests where it is found (Eniang 2003). At Lizard island on the northern Great Barrier Reef, the abundance of obligate coral-dwelling gobies is closely related to the availability of host corals, and declined in response to a reduction in abundance of host corals following an outbreak of crown-of-thorns starfish in 1995 (Munday et al. 1997). Even – and perhaps, especially – primary producers are constrained by their own "bottom-up" limitations: phytoplankton (Menge 2000) through to the pedunculate oak (Hunter and Price 1992) respond to nutrient availability, temperature, and light.

However, other classic examples in the ecological literature appear to paint a different picture, demonstrating that "top-down" ecological processes such as predation and competition, and not "bottom-up" controls such as habitat, can be the key structuring agents of the local abundance of a species and the structure of species assemblages. Early research into interspecific interactions in marine systems demonstrated that interspecific competition (Connell 1961) and predation (Paine 1966) are key variables structuring the distribution of different species of barnacle in rocky intertidal systems. In the subtidal, observed changes in *Orca* feeding patterns in western Alaska caused sea otter populations to plummet, triggering a trophic cascade in which reduced predation pressure on herbivorous sea urchins led to overgrazing of kelp beds (Estes et al. 1998). In terrestrial systems, an equally iconic case study of key species interactions began with the increased abundance of wolves in Yellowstone National Park in the mid-1990s, which led to reduced abundance of elk and subsequent browsing activity by elk, allowing willows to recover as the dominant riparian plant (Ripple and Beschta 2004). Despite the charisma of these “top-down” examples, in which interspecific interactions are the central feature, it is important to remember that all of these interactions and trophic cascades operate on the background of habitat availability and suitability: for any of the observed species to be present, and to interact with one another, “bottom-up” influences such as temperature, precipitation (or water depth), nutrient availability, substrate composition, and dispersal potential from neighbouring habitats, among many other physical and biological factors, had to be suitable for those organisms, and to any key habitat-forming organisms that they rely upon. To add further complexity, “bottom-up” drivers can themselves be mediated by natural and anthropogenic disturbances to the environment (Connell et al. 1997, Menge 2000).

Nowhere is this more evident than in coral reef systems, where the availability, condition, and complexity of scleractinian corals is a major determinant of the abundance (Munday et al. 1997, Holbrook et al. 2000, Cheal et al. 2008), growth (Kokita and Nakazono 2001, Munday 2001), and survival (Holbrook and Schmitt 2002, Almany 2004a) of both specialist and generalist coral reef fishes (Wilson et al. 2006, Pratchett et al. 2015). It is important to note, however, that in coral reef systems, both top-down and bottom-up processes operate within the potential constraints of larval supply (Doherty and Williams 1988, Armsworth 2002, Sale 2004), which is highly variable in both space and time (Williams et al. 1994, Jones et al. 2009, Berumen et al. 2012a, Harrison et al. 2012). Furthermore, many species of "coral reef" fishes actually use non-coral habitats such as seagrass beds and mangrove stands at different times in their lives (Nagelkerken et al. 2000, Mellin et al. 2007, Nagelkerken 2009), such that assemblages of coral reef fish can actually be structured by the availability and condition of several different types of shallow water benthic habitats, as well as the spatial proximity of the different habitat types, known as seascape connectivity or habitat connectedness (Bradbury 1978, Nagelkerken et al. 2000, Dorenbosch et al. 2005, Olds et al. 2012a).

Unfortunately, shallow water benthic habitats such as coral reefs, seagrass beds and mangrove stands are also extremely vulnerable to destructive natural events such as cyclones (Harmelin-Vivien 1994), as well as to anthropogenic environmental disturbances such as reduced water quality from land use modifications (Brodie et al. 2012), overfishing and destructive fishing (Hughes 1994), and increased temperatures and reduced ocean pH associated with climate change (Veron et al. 2009b, Pratchett et al. 2011). The deterioration of shallow water habitats is particularly pronounced in poor, developing nations such as those in the Coral Triangle (Fig. 1.1A), where marine biodiversity is high, but so are human population density and reliance on extractive activities (Hoegh-Guldberg et al. 2009, McLeod et al. 2010, Burke et al. 2012). The Western Visayas region of the central Philippines (Fig. 1.1B), considered "the heart of the Coral Triangle" due to its particularly high coral and fish diversity and high levels of endemicity (Carpenter and Springer 2005, Veron et al. 2009a), faces all of the same stressors as coral reefs worldwide (Hughes et al. 2003, Pandolfi et al. 2005, Burke et al. 2011) in addition to an increased frequency and destructiveness of typhoons over recent years (Emanuel 2005, Marler 2014).

In an effort to mediate the effects of these stressors, coastal communities and local reef managers have implemented a number of no-take marine reserves (NTMRs) across the region (Alcala and Russ 2006, Horigue et al. 2012). NTMRs can produce a number of direct and indirect benefits (Lester et al. 2009), including increased abundance of fished species inside and near the border of reserves (Abesamis et al. 2006, Russ et al. 2015c), larval subsidy of fished areas (Cudney-Bueno et al. 2009, Harrison et al. 2012), and restored species interactions and ecological processes inside the reserve area (Graham et al. 2003, Mumby et al. 2007, Stockwell et al. 2009, Babcock et al. 2010). These positive changes to protected areas can increase the resistance and resilience of the local system to unavoidable external disturbances such as coral bleaching and typhoons, particularly for coral reef NTMRs that host large and diverse assemblages of herbivorous fishes (Hughes et al. 2007, Green and Bellwood 2009, Hughes et al. 2010).

Research into the effects of the deterioration and recovery of shallow water benthic habitats, and coral reefs in particular, can be challenging due to the sheer complexity of coral reef fish assemblages, and the diversity of coral reef fish responses to changes in coral reef condition. However, of all groups of coral reef fish, *Chaetodon* butterflyfishes have one of the strongest and best studied associations with benthic coral reef habitat (Reese 1981, Bozec et al. 2005, Pratchett et al. 2008b). In addition, *Chaetodon* are generally not targeted by artisanal fisheries (Lawton et al. 2013, Padin et al. 2013), making them favoured as an “indicator” taxon in the coral reef monitoring literature (Reese 1981, Bozec et al. 2005, Kulbicki and Bozec 2005). For these reasons, *Chaetodon* butterflyfish are an ideal model taxon for studies that assess coral reef fish response to changes in reef condition (Reese 1981, Öhman et al. 1998, Bozec et al. 2005, Kulbicki et al. 2005a).

Given that habitat availability, suitability, and connectivity are some of the key drivers of the structure of reef fish assemblages, and that NTMR protection can play a strong role in maintaining habitat condition into the future, the habitat composition of existing and future NTMRs must be an important consideration in the pursuit of both conservation and fisheries goals (Fernandes et al. 2005, Weeks et al. 2010, Nagelkerken et al. 2012, Ortiz and Tissot 2012, Olds et al. 2013). Decisions regarding the placement of future reserves should therefore be made with the best possible information on habitat availability (i.e. extent) and suitability (i.e. condition) for fish taxa of interest.

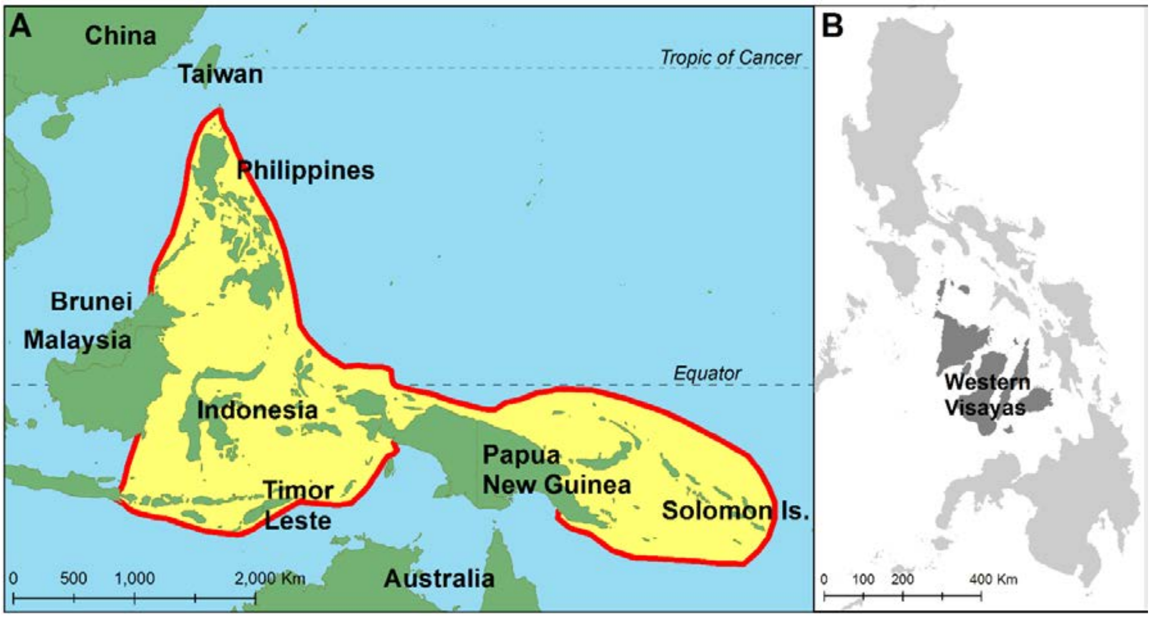

Figure 1.1. Map of **A** the Coral Triangle, and **B** the Western Visayas region of the Philippines.

1.2. Purpose and structure of the thesis

1.2.1. Aims and objectives

The ultimate goal of this thesis was to help inform decision-making on the placement of future no-take marine reserves (NTMRs) by determining the habitat-related drivers of abundance, species richness, and growth rates of coral reef fishes. To achieve this goal, the thesis addressed four main objectives:

(1) To identify and quantify the extent to which habitat condition drives the abundance and species richness of *Chaetodon* butterflyfish (**Chapter 2**). Butterflyfish were chosen as the focal taxon to address this research objective because they are highly sensitive to changes in habitat condition and habitat loss, and because they are not normally targeted by fishers, such that a *Chaetodon* response to habitat condition and changes in habitat condition should not be confounded by fishing effects.

(2) To identify and quantify the extent to which habitat condition drives early post-settlement growth rates of a *Chaetodon* butterflyfish, the model coral reef fish *Chaetodon vagabundus* (**Chapter 3**). *C. vagabundus* is commonly used as a model species in larval connectivity studies, but little is known about what happens to juveniles of this species once they settle onto the reef.

(3) To identify and quantify the extent to which habitat condition drives the abundance and species richness of *Chaetodon* butterflyfish through time, and to use these relationships to quantify the rate and magnitude of the decline and recovery of *Chaetodon* assemblages in response to a range of environmental disturbances, including extremely large changes to the benthic habitat, and under different levels of NTMR protection (**Chapter 4**).

(4) To identify and quantify the relative effects of habitat condition, extent, and connectedness (i.e. proximity) at driving the biomass of fishery-targeted coral reef fishes (**Chapter 5**). In order to make this work directly applicable to local coastal resource managers, study species were selected to represent a range of fishing pressures from artisanal fisheries (highly targeted and less-targeted species). Furthermore, in order to best quantify the relative effects of NTMR protection and habitat condition, extent, and connectedness, study species were also selected to represent a range of habitat usage patterns (species that use non-reef habitats and species that exclusively use reef habitats).

1.2.2. Approach to the thesis aims

The investigation into the *Chaetodon* response to habitat condition in **Chapter 2** took advantage of the spatial variation in habitat condition caused by a major typhoon to identify and assess the relative influence of major "bottom-up" (i.e. habitat) variables, as well as a possible "top-down" influence of predation. The subsequent study on the influence of habitat condition on the growth rates of young *Chaetodon vagabundus* in **Chapter 3** used relative otolith increment widths as a proxy for somatic growth. Spatial variation in growth rates was identified and correlated with spatial variation in habitat conditions, as well as variation in the density of predators and juvenile conspecifics.

This understanding of the relationship between *Chaetodon* butterflyfishes and habitat condition was then applied to a 31-year monitoring dataset to investigate the long-term stability of the butterflyfish-benthos relationship through time (**Chapter 4**). The complex natural disturbance and NTMR protection history of four different sites also allowed me to quantify the rate and extent of the response of *Chaetodon* abundance, species richness, and assemblage structure to habitat loss and recovery. The additional effects of habitat extent and connectedness were incorporated into a subsequent study in **Chapter 5**, in which field surveys of fish assemblages and benthic habitat condition were combined with spatially extensive and high-precision remotely-sensed assessments of habitat extent and connectedness to assess which factors were most important in structuring different types of fish assemblages, including fishery targeted versus less-targeted species, and species which use multiple habitats versus those that exclusively use reef habitats. In addition, **Chapter 5** showcases the value of remote sensing, spatial analysis, and advanced statistical modelling tools in ecological research, and their potential to produce powerful, practical information for direct use in the management of coral reefs. The General Discussion in **Chapter 6** brings together the results of each study and discusses their ecological and management implications.

Chapter 2: Identifying and quantifying the extent to which habitat condition drives the abundance and species richness of *Chaetodon* butterflyfish[1]

2.1. Abstract

The question of whether biological systems are maintained by top-down (i.e. predation) versus bottom-up (i.e. resource limitation) drivers is a recurring one in ecology. It is a particularly important question to address in the management of coral reefs, which are at risk from a variety of anthropogenic stressors. This study explicitly tests whether the abundance of different feeding guilds of coral-associated *Chaetodon* butterflyfishes are controlled by top-down or bottom-up drivers, and assesses the relative influence of all statistically significant drivers. Results indicate that the abundance and species richness of *Chaetodon* butterflyfishes are predominantly determined by bottom-up drivers. The abundance of corallivores is primarily driven by availability of branching and tabular live corals, while the abundance of generalists is most strongly influenced by a negative association with macroalgal cover. This study presents some evidence of weak top-down control on the abundance of corallivorous butterflyfish by mesopredators, but no such effects on generalist butterflyfish. These findings indicate that conservation of coral reefs for *Chaetodon* butterflyfishes must include management at a larger spatial scale in order to reduce the impact of coral reef

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stressors such as declining water quality and climate change, but should also include implementation of fisheries management tools in order to increase local herbivory.

2.2. Introduction

The question of whether biological systems are controlled by top-down (e.g. predation) versus bottom-up (e.g. availability of resources) processes is a difficult one to definitively answer, with much evidence for both cases (Estes et al. 1998, Pace et al. 1999, Richardson and Schoeman 2004, Ware and Thomson 2005, Myers et al. 2007, Frank 2008). The abundance and diversity of coral reef fishes are often thought to be largely controlled from the top down, in part because of a rich history of apex predator-induced trophic cascades (Myers et al. 2007, Baum and Worm 2009, Ferretti et al. 2010, Rizzari et al. 2014), and in part because of the importance of herbivorous fishes and invertebrates in controlling macroalgal growth and in maintaining a coral-dominated system (Hughes 1994, Bellwood et al. 2006, Mumby et al. 2006, Hughes et al. 2007). However, some members of the reef ecosystem are likely to be moderated by bottom-up processes, in particular, availability of food and benthic habitat for resource-specialists (Munday et al. 1997, Pratchett et al. 2006, Emslie et al. 2011). Furthermore, both top-down and bottom-up processes operate within the potential constraints of larval supply (Doherty and Williams 1988, Armsworth 2002, Sale 2004), which is highly variable in both space and time (Williams et al. 1994, Jones et al. 2009, Berumen et al. 2012a, Harrison et al. 2012).

Misunderstanding the dominant regulatory processes in an ecosystem can have important consequences for ecosystem persistence, as conservation of different ecosystem drivers can require very different management actions. For example, preservation of top-down processes on coral reefs has been achieved with the implementation of no-take marine reserves (Mumby et al. 2006, 2007, O'Leary et al. 2012) and fishing gear restrictions (Cinner et al. 2009). On the other hand, preservation of bottom-up processes requires management actions at a much larger spatial scale, such as changes to land-use practices to reduce sedimentation and nutrient enrichment (McCook 1999, Brodie et al. 2012), and identification of spatial refugia in the face of climate change (McClanahan et al. 2007, McLeod et al. 2010, Groves et al. 2012).

Reality is likely to be far more complex than this dichotomous description, such that both bottom-up and top-down processes are likely involved in maintaining ecosystem processes and components (e.g. Power 1992, Brett and Goldman 1997, Cury et al. 2000, Menge 2000). However, few studies have identified and quantified the relative influence of top-down and bottom-up processes on the abundance and diversity of coral reef fishes (but see Wilson et al. 2008), especially on the butterflyfishes (Chaetodontidae). The genus *Chaetodon* includes several distinct feeding guilds, which are generally assumed to be moderated solely by bottom-up processes, with obligate hard corallivores being most susceptible to changes in coral cover (Crosby and Reese 2005, Pratchett et al. 2006). However, reef fish populations are often strongly structured by mortality due to predation (Hixon 1991, Jones and McCormick 2002), which is particularly high immediately post-settlement and in juveniles (Webster 2002, Doherty et al. 2004, Almany and Webster 2006), and butterflyfish should be no exception to this.

The primary aim of this study was to quantify the relative influence of the top-down and bottom-up biotic and abiotic variables affecting the abundance and species richness of *Chaetodon* butterflyfishes along an extensive coastline in the central Philippines that was recently impacted by a severe tropical storm. This study used sheltered “control” sites and sites that had a gradient of benthic assemblage compositions likely generated by distance from the storm path to distinguish and quantify the effects of benthos and predator abundance on the *Chaetodon* assemblage. Findings are interpreted in the context of their implications for coral reef management techniques.

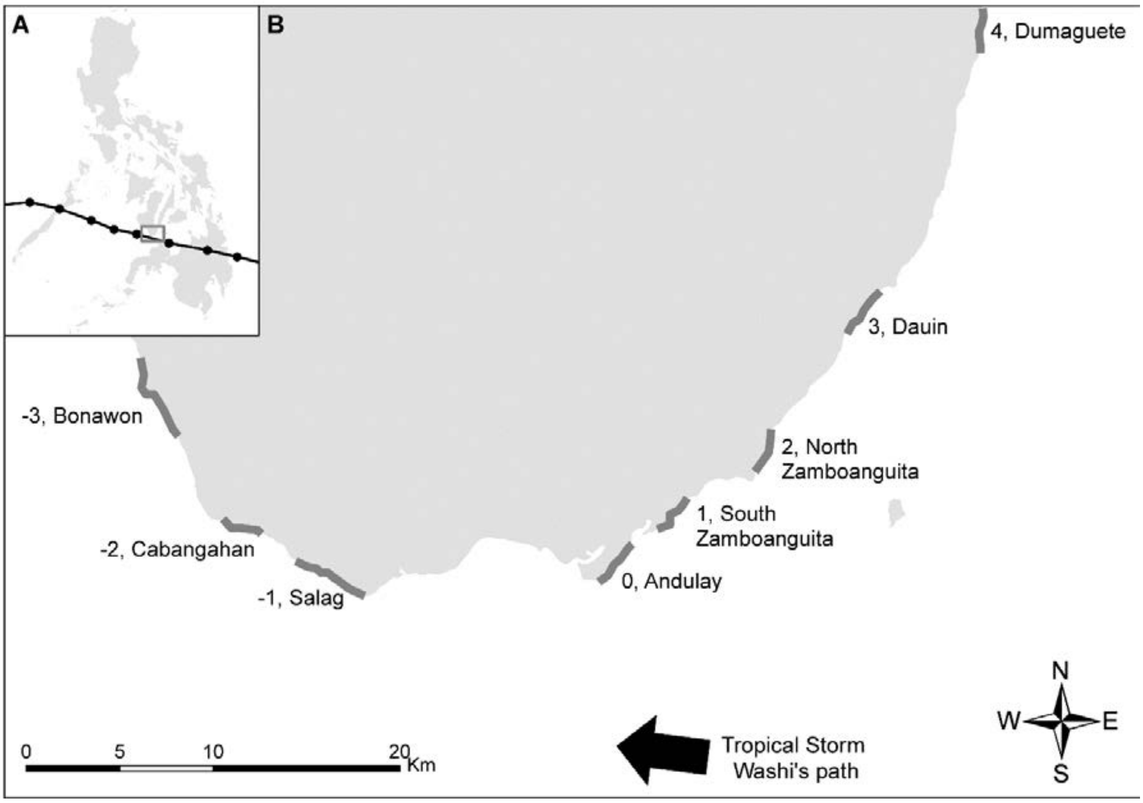


Figure 2.1. A Philippines, including the path of Tropical Storm Washi (black), and study region (dark grey). **B** Study region on the southern coast of Negros Oriental, in the Central Visayas region of the Philippines. Study sites are indicated in dark grey outline. Black arrow indicates the trajectory of Tropical Storm Washi. Tropical storm track data from United States Naval Research Laboratory Marine Meteorology Division (2011).

2.3. Methods

2.3.1. Description of field sites

The southern coastline of Negros Oriental, in the central Philippines, is characterised by intermittent, shallow, fringing coral reefs with lagoonal seagrass or coral beds and occasional remnants of mangrove stands (Yambao et al. 2001, DeVantier et al. 2004). Tropical Storm Washi (local name: Sendong) traversed this region in

December 2011, with devastating impacts on human communities and local ecosystems (Rasquinho *et al.* 2013).

A total of eight study sites were selected along the coast. The community of Andulay was very close to the path of Tropical Storm Washi and received the brunt of destructive winds and damaging waves on this coastline (Fig. 2.1), and is therefore designated as “site zero.” The other seven study sites were distributed approximately evenly west (sheltered from the storm) and east (exposed to the storm) around site zero, and are identified numerically based on their relative distance from the storm’s path (from -3 to +4, Fig. 2.1B). Site 4 coincides with a large urban centre, Dumaguete. Irregularities in the distance between sites were due to lack of reef environments (e.g. between sites -1 and 0, Fig. 2.1B), or to inaccessibility for political or logistical reasons (e.g. between sites 3 and 4, Fig. 2.1B).

2.3.2. Field surveys

Surveys of the benthos, the *Chaetodon* assemblage and potential *Chaetodon* predators were carried out at each site between 17 September 2012 and 11 December 2012, approximately 1 year after Tropical Storm Washi’s passage. Surveys were conducted on SCUBA on the reef crest and slope (3-15 m deep), as storm and cyclone effects are generally most distinctive on these reef zones (Harmelin-Vivien 1994). All benthivorous members of the *Chaetodon* genus and all predators >6 cm Total Length (TL) (certain members of the families Labridae, Lutjanidae, Pinguipedidae, Pseudochromidae, Serranidae, Scorpaenidae, and Synodontidae) were surveyed using 4 m wide 50 m belt transects (200 m^2 per transect). Between 5 and 11 replicate transects were surveyed at each site, depending on the spatial extent of the reef zone and its benthic heterogeneity. Benthic characteristics were recorded every 0.5 m using the Point

Intercept technique (English et al. 1994) on the return swim along each transect. An index of rugosity (as per Russ et al. 2005) was estimated on a scale from 0 (least rugose) to 4 (most rugose) at 10 m increments along each transect to provide a measure of benthic complexity.

2.3.3. Drivers of the benthic and predator assemblages

Boosted Regression Tree (BRT) models were built to assess spatial patterns, in particular the influence of position along the coast (*i.e.* distance from the storm) and survey depth, on the extent of major benthic components (branching and tabular live coral, massive and encrusting live coral, rubble, macroalgae, and rock), benthic complexity, and the abundance of small (6-10 cm TL) and large (>10 cm TL) predators. The small predator category (6-10 cm TL) was made up of mesopredators, which generally hunt for small prey items such as juvenile reef fishes within the reef matrix. Members of the large predator category (>10 cm TL) generally hunt for larger prey items above the reef matrix (Almany 2004a). BRTs produce similar outputs to traditional regression-based techniques, but are arguably better suited to ecological studies as they accommodate non-linear relationships, identify and exclude unimportant variables, and can automatically model interactions (De'ath 2007, Elith et al. 2008). BRTs were built and fitted in RStudio (RStudio 2013) using the *dismo* package (Elith et al. 2008), which is derived from the *gbm* package (Ridgeway 2015), but contains automated cross-validation and tree optimization protocols. Because model output was relatively insensitive to variation in key parameters, model parameters were derived to optimize biological meaningfulness and interpretability (Table 2.1). As such, tree complexity was limited to main effects and first-order interactions. A bag fraction <1 introduced stochasticity into the model in order to prevent model over-fitting; model output therefore varied slightly each time it was run. The percent deviance explained by each model (adjusted D^2) is analogous to an adjusted R^2, which penalises models for the addition of extra variables that increase model explanatory power due to chance alone. Dependent variables were untransformed, with the exception of macroalgal cover, which was fourth-root transformed in order to reduce the magnitude of a mean-variance relationship in the model residuals.

2.3.4. Drivers of the Chaetodon assemblage

BRT models were built to explain *Chaetodon* species richness, as well as the abundance of members of the two most common *Chaetodon* feeding guilds: obligate hard corallivores and benthic generalists (Table 2.2), hereafter referred to as "corallivores" and "generalists," respectively. Model parameters were similar to those used to model benthic components (Table 2.1). Predictor variables included depth and benthic components (branching and tabular live coral cover, massive and encrusting live coral cover, rubble cover, macroalgal cover, rock cover, and rugosity index), abundance of small (6-10 cm TL) predators, and abundance of large (>10 cm TL) predators. Collinearity between predictor variables was negligibly small ($-0.60 < r < 0.60$, Zuur et al. 2007). A simplification procedure was run to remove predictors that did not significantly improve the model (Elith et al. 2008, Harborne et al. 2012). Dependent variables did not require transformation.

Table 2.1. Parameters and properties of the boosted regression tree models for the benthic assemblage and the *Chaetodon* assemblage. CBCT indicates branching and tabular corals, CMCE indicates massive and encrusting corals.

Parameter	**Distribution family**	**Learning rate**	**Tree complexity**	**Bag fraction**	**Optimal number of trees**	**Final number of variables**	**Adjusted D^2**
CBCT cover	Gaussian	0.001	2	0.75	4050	2	45.7%
CMCE cover	Gaussian	0.001	2	0.75	6400	2	71.7%
Rubble cover	Gaussian	0.001	2	0.75	1700	2	47.9%
Macroalgal cover[i]	Gaussian	0.001	2	0.75	6950	2	52.8%
Rock cover	Gaussian	0.001	2	0.75	8900	2	64.9%
Rugosity	Gaussian	0.001	2	0.75	4500	2	53.6%
Small predator abundance	Poisson	0.001	2	0.75	3150	2	52.0%
Large predator abundance	Poisson	0.001	2	0.75	1850	2	41.0%
Corallivore abundance	Poisson	0.001	2	0.75	4900	6	72.9%
Generalist abundance	Poisson	0.001	2	0.75	4350	5	54.9%
Chaetodon species richness	Gaussian	0.001	2	0.75	3350	5	62.2%

[i] Macroalgal cover was fourth-root transformed in order to reduce the influence of a mean-variance relationship in the model residuals. No other dependent variables were transformed.

Table 2.2. Abundance of the benthic feeding members of the *Chaetodon* assemblage across the entire surveyed area (13,400 m^2). Only hard corallivores and generalists were included in the statistical analyses due to low abundances of the other feeding guilds (soft corallivores and non-corallivores). Feeding guild classification as per Findley and Findley (2001) and Cole et al. (2008).

Species by guild	Abundance
Hard corallivores	212
C. baronessa	93
C. lunulatus	88
C. octofasciatus	10
C. ornatissimus	13
C. reticulatus	6
C. trifascialis	2
Generalists	198
C. adiergastos	10
C. auriga	3
C. citrinellus	10
C. lineolatus	1
C. lunula	9
C. rafflesi	6
C. speculum	2
C. vagabundus	149
C. xanthurus	8
Soft corallivores	39
C. melannotus	1
C. ocellicaudus	4
C. punctatofasciatus	34
Non-corallivores	7
C. selene	7

2.4. Results

2.4.1. Drivers of the benthic and predator assemblages

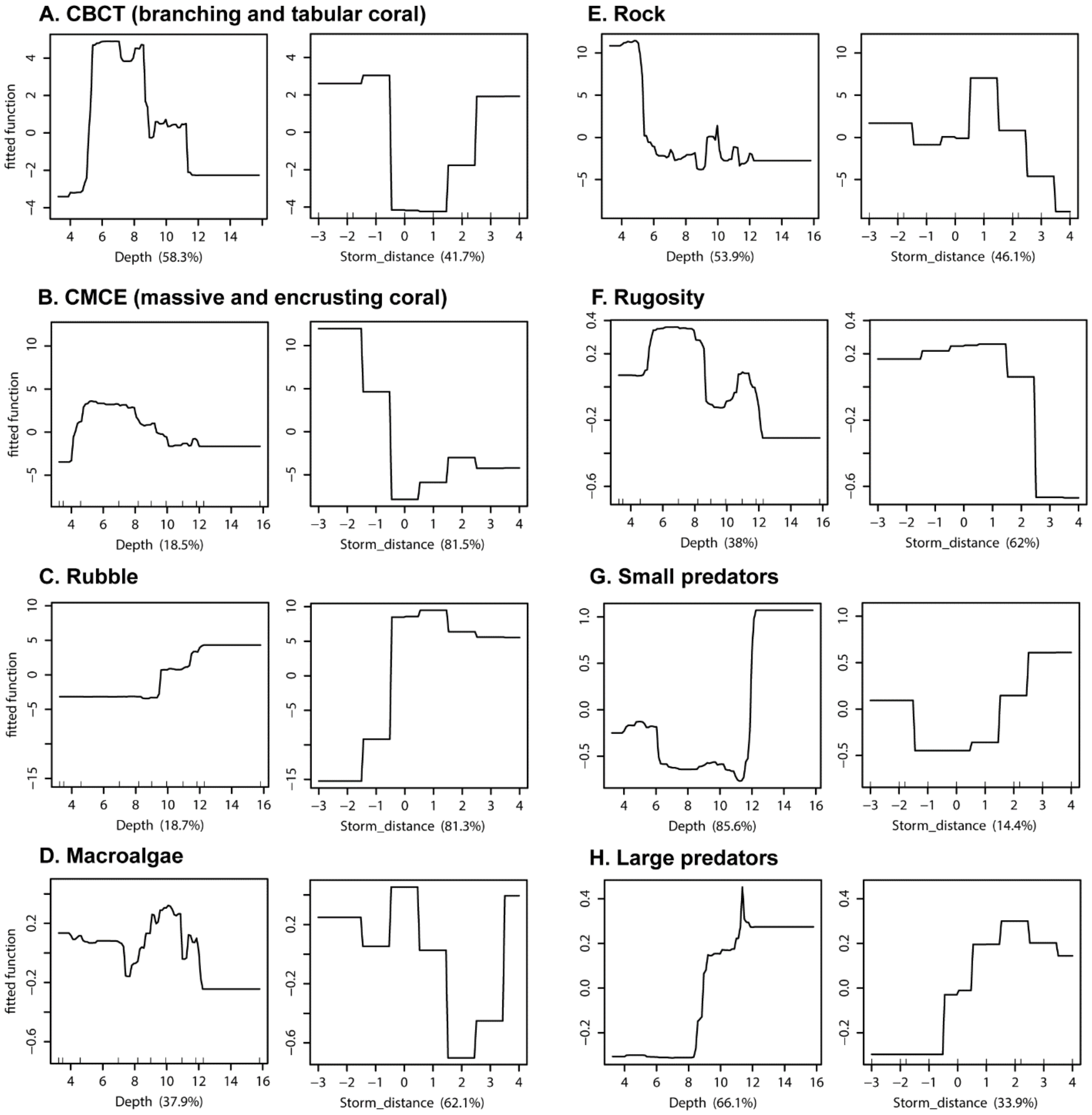
BRT models containing only distance from the storm and depth as explanatory variables captured between 41 and 72% of the variation in the main benthic components and the predator assemblage (Table 2.1). Branching and tabular coral cover was best explained by depth, while massive and encrusting coral cover was best explained by distance from the storm (Table 2.3). Both types of coral cover exhibited complex non-linear relationships with distance from the storm, with high coral cover at sites sheltered from the storm's impact (negative site numbers), a distinct low in coral cover at the site of the storm impact, and sequentially higher coral cover at each site further away from the storm impact (positive site numbers, Figs. 2.1, 2.2A, and 2.2B). Conversely, rubble cover was lowest at sheltered sites (negative site numbers), and exhibited a distinct peak near the site of the storm impact and gradual decline along the east-coast sites (positive site numbers, Figs. 2.1 and 2.2C). Macroalgal cover was also most strongly driven by position along the coast, in a complex spatial pattern with the highest peak in macroalgal cover at the site of the tropical storm (site 0, Fig. 2.2D). Rock cover was more strongly explained by depth rather than position along the coast, but exhibited a clear decline between sites 1 and 4 (Table 2.3, Fig. 2.2E). Rugosity (*i.e.* benthic complexity) was most strongly explained by position along the coast, with consistently high levels of rugosity at west coast sites, and a sharp decline along the east coast, between sites 1 and 4 (Fig. 2.2F). Patterns in the fitted function of each benthic component against depth approximated the reef profile in this region, with low complexity rock and macroalgal cover from 4-6 m, high complexity coral dominance (particularly branching and tabular morphologies) from 6-9 m, and intermediate to low complexity rubble and macroalgal dominance from 9-12 m (Fig. 2.2).

The predator assemblage was most strongly structured by depth (85.6% for small predators, Fig. 2.2G; 66.1% for large predators, Fig. 2.2H). Small predators were most common at depths >12 m, while large predators were most common at depths >8 m. Both sizes exhibited complex spatial patterns across the region: the abundance of small predators was particularly low at sites -1, 0, and 1 (Fig. 2.2G), while large predators appeared to be almost absent from the west coast (sites -3 to -1), and to increase in abundance from sites 0 to 2 (Fig. 2.2H).

Table 2.3. Percent deviance explained by each variable within the final Boosted Regression Tree model for each benthic component. CBCT indicates branching and tabular corals, CMCE indicates massive and encrusting corals.

	Distance from storm	**Depth**
CBCT	41.7	58.3
CMCE	81.5	18.5
Rubble	81.3	18.7
Macroalgae[i]	62.1	37.9
Rock	46.1	53.9
Rugosity	62.0	38.0
Small predators	14.4	85.6
Large predators	33.9	66.1

[i] Macroalgal cover was fourth-root transformed in order to reduce the influence of a mean-variance relationship in the model residuals. No other dependent variables were transformed


A. CBCT (branching and tabular coral)

B. CMCE (massive and encrusting coral)

C. Rubble

D. Macroalgae

E. Rock

F. Rugosity

G. Small predators

H. Large predators

Figure 2.2. Partial dependence functions for the two variables (distance from storm and depth) influencing the extent of each benthic component across the study region. **A** Branching and tabular live coral cover (CBCT), **B** massive and encrusting live coral cover (CMCE), **C** rubble cover, **D** fourth-root transformed macroalgal cover, **E** rock cover, **F** rugosity index, **G** abundance of small predators (6-10 cm), and **H** abundance of large predators (>10 cm).

2.4.2. Drivers of the Chaetodon assemblage

The *Chaetodon* assemblage was composed of 19 species of benthic feeding butterflyfish, and was numerically dominated by hard corallivores and generalists (Table 2.2). BRT models explained between 55 and 73% of the variation in the abundance of major *Chaetodon* feeding guilds, as well as species richness (Table 2.1).

Relationships between explanatory and dependent variables were generally nonlinear and frequently complex (Table 2.4, Fig. 2.3).

The obligate hard corallivore community was numerically dominated by *C. baronessa* and *C. lunulatus* (Table 2.2). The abundance of corallivores was most strongly structured by the availability of branching and tabular live coral cover (Table 2.4, Fig. 2.3A). Corallivore abundance exhibited a non-linear increase with increasing branching and tabular live coral cover until approximately 15% coral cover, after which corallivore abundance showed no further increases (Table 2.4, Fig. 2.3A). Corallivore abundance was also structured by a strong negative relationship with macroalgal cover; the abundance of corallivores demonstrated a sharp and persistent decline in response to quite low levels of macroalgal cover (1-15%, Fig. 2.3A). The abundance of corallivores was also associated with intermediate levels of rock cover (20-30%), and intermediate depths (6-9 m, corresponding with the depth of the coral-rich reef crest and upper slope on reefs in this region (Fig 2.2A and Fig. 2.2B). Corallivore abundance was also significantly associated with the abundance of small predators (6-10 cm TL), with increasing small predator abundance linked to decreased corallivore abundance (Fig. 2.3A). Corallivore abundance was also positively linked to the extent of massive and encrusting corals (Fig. 2.3A). Variables removed from the model due to lack of significance included rubble cover, benthic complexity, and the abundance of large predators (Table 2.4).

The generalist community was numerically dominated by *C. vagabundus* (Table 2.2). The abundance of generalists was significantly affected by five different explanatory variables, but most strongly by a negative relationship with macroalgal cover (Table 2.4, Fig. 2.3B). Generalists exhibited a sharp and persistent decline in response to very low levels of macroalgal cover (1-5%, Fig. 2.3B). Generalists also exhibited a positive relationship with rock cover, with beneficial and persistent effects of rock cover >20%, as well as a positive relationship with rugosity (Fig. 2.3B). The abundance of generalists had a complex and mostly negative relationship with the extent of branching and tabular corals, as well as a complex relationship with depth, with a peak between 9 and 11 m (Fig. 2.3B). Both measures of predator abundance were removed from the model due to lack of significant explanatory power, as were rubble and massive and encrusting coral cover (Table 2.4).

Chaetodon species richness was most strongly explained by a complex relationship with depth, with a peak in species richness occurring between 9 and 12 m (Table 2.4, Fig 2.3C). Species richness also demonstrated a strong negative relationship with macroalgal cover (Table 2.4, Fig. 2.3C). Weaker relationships with other variables included a positive relationship with rugosity. Species richness also exhibited a complex relationship with rock cover, with a peak in species richness at intermediate levels of rock cover (Fig. 2.3C), as well as a negative relationship with the abundance of small predators (Table 2.4, Fig. 2.3C). Both measures of live coral cover, as well as rubble and the abundance of large predators, did not significantly contribute towards explaining patterns of *Chaetodon* species richness (Table 2.4).

Table 2.4. Percent deviance explained by each variable within the final Boosted Regression Tree model for each descriptor of the *Chaetodon* assemblage. (+) Indicates a positive relationship, (-) indicates a negative relationship, (c) indicates a complex relationship, / indicates variables that were removed from the model because BRT protocols rated them as non-contributors to the model.

Parameter	**Corallivore abundance**	**Generalist abundance**	***Chaetodon* species richness**
Depth	12.8 (c)	14.1 (c)	31.5 (c)
Branching and tabular coral (CBCT)	32.3 (+)	15.3 (c)	/
Massive and encrusting coral (CMCE)	8.0 (+)	/	/
Rock	16.6 (c)	19.8 (+)	14.1 (+)
Rubble	/	/	/
Macroalgae	18.2 (-)	35.0 (-)	25.8 (-)
Rugosity / benthic complexity	/	15.8 (+)	14.8 (+)
Small predator abundance	12.1 (-)	/	13.7 (-)
Large predator abundance	/	/	/

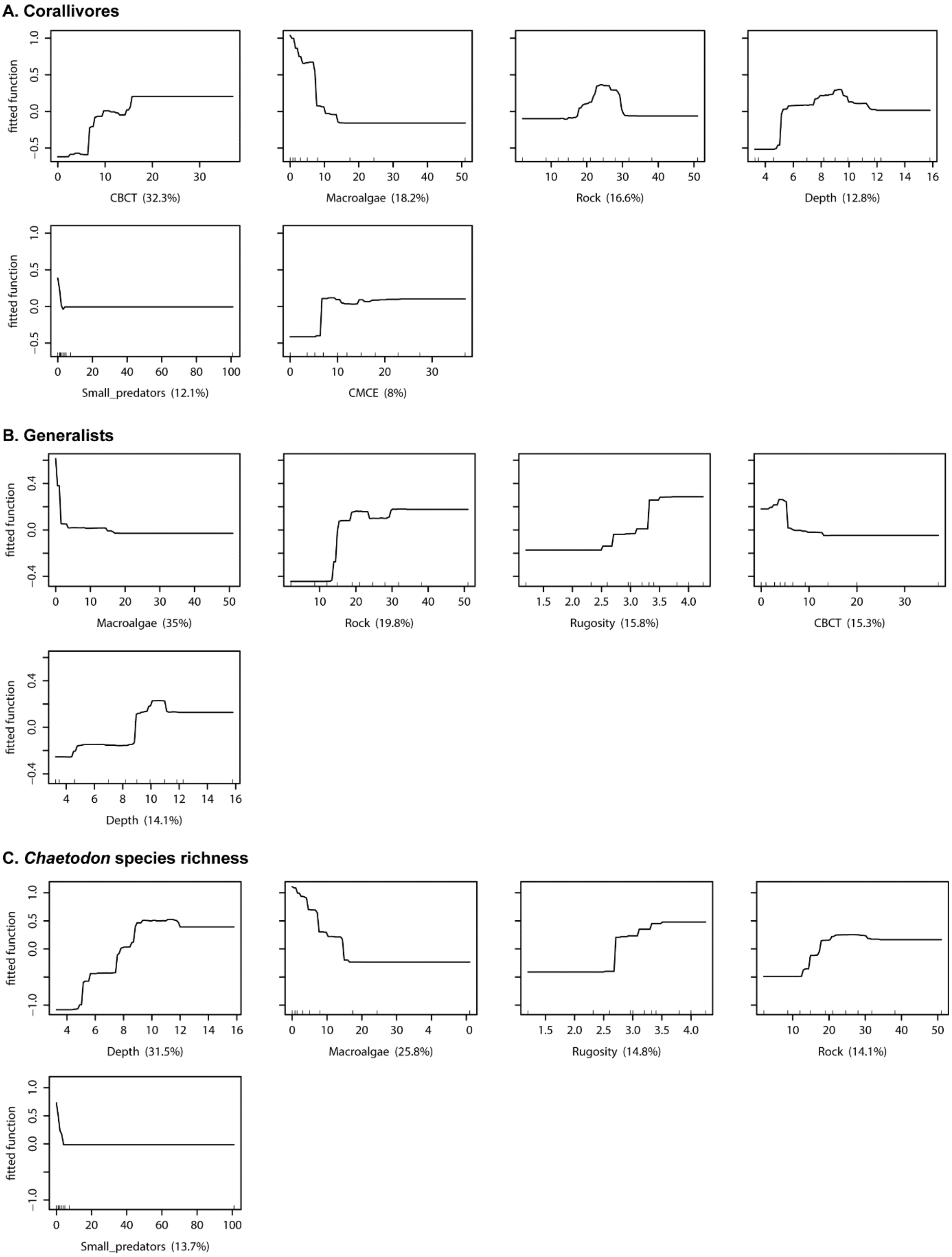


Figure 2.3. Partial dependence functions for all variables significantly influencing **A** the abundance of corallivorous *Chaetodon*, **B** the abundance of generalist *Chaetodon*, and **C** *Chaetodon* species richness across the study region. Variables are presented in order of decreasing relative influence. CBCT indicates branching and tabular corals, CMCE indicates massive and encrusting corals.

2.5. Discussion

This study provides an assessment of both the effects of bottom-up and top-down processes on *Chaetodon* butterflyfishes, and elucidates important ecological processes acting on this iconic coral reef taxon. The results indicate that overall, the *Chaetodon* assemblage is most strongly structured by a few key bottom-up (habitat) variables. Depth, macroalgal cover, rugosity, rock cover, and the extent of branching and tabular corals consistently re-occur as the strongest predictors of *Chaetodon* abundance and species richness (Table 2.4, Fig. 2.3). Suitable habitat for corallivores appears to be algal-poor, intermediate-cover rocky reefs between 6 and 10 m deep, with at least 15% cover of branching and tabular corals (Fig. 2.3A). Suitable habitat for benthic generalists is algal-poor, rocky and rugose reefs between 9 and 12 m deep, with as little live coral cover as possible (Fig. 2.3B).

The most striking finding was the strong negative effect of macroalgae on the butterflyfish assemblage. A negative relationship between macroalgae and reef fish abundance has generally been interpreted as a consequence of decreased live coral cover, without a direct cause-and-effect relationship between macroalgae and reef fish abundance (Done 1992, Hughes 1994, McManus and Polsenberg 2004, Mumby et al. 2006, Hughes et al. 2007). However, the results point to a considerable, and possibly more direct, negative algal effect on the butterflyfishes, particularly generalists, rather than simply a side-effect of the loss of live coral cover. This is a concerning finding, given that increases in macroalgal cover are a common outcome of acute disturbances such as storm events, as well as of chronic stressors such as overfishing of herbivores, destructive fishing practices, sedimentation and nutrient enrichment (Hughes 1994, Hughes and Connell 1999, Nyström et al. 2000, Fabricius 2005, Knowlton and Jackson

2008), all of which are common stressors in this region (Gomez et al. 1994, Hoegh-Guldberg et al. 2009, McLeod et al. 2010, Burke et al. 2012).

I hypothesise that the strong negative effect of macroalgae on the *Chaetodon* butterflyfishes was the result of two main factors. The first factor is unattractive olfactory cues emitted by the algae, which could have deterred larval fish settlement. Larval-stage reef fishes use many olfactory cues to select suitable settlement habitat (Kingsford et al. 2002, Dixson et al. 2008, Coppock et al. 2013), with coral cues being significantly more attractive than algal cues for many coral reef fishes (Lecchini et al. 2013). The second factor is reduced foraging options, with increasing macroalgal cover reducing availability of both coral and non-coral invertebrate prey. An extensive review by Stella *et al.* (2011) on non-coral invertebrate communities on coral reefs found that a high proportion of non-coral invertebrates were obligate coral associates (56%), with extremely high levels of specialisation (84% depended on just a single coral taxon, and predominantly fragile genera such as *Pocillopora* and *Acropora*). It is therefore possible that an increase in macroalgal cover may reduce the non-coral invertebrate community that generalist *Chaetodon* prey upon. However, neither of these factors can fully explain the low threshold levels (5% for generalists, 15% for corallivores) of the negative effect of macroalgal cover on butterflyfish abundance and species richness. The severity of the negative effects of macroalgal cover is surprising, and merits further investigation.

Although live coral (particularly branching and tabular morphologies) was an important predictor of corallivorous *Chaetodon* abundance, the benefits of branching and tabular coral cover on corallivore abundance were attained at only 15% cover of branching and tabular corals, which is much lower than has been found in other studies of deteriorated reef condition (Pratchett et al. 2006, Cheal et al. 2008). Furthermore, live coral cover exhibited a negative influence on generalist abundance, and was unrelated to overall *Chaetodon* species richness in this study. Research in other regions has found that live coral cover is an important predictor of *Chaetodon* species richness (in New Caledonia, Bozec et al. 2005; in the Chagos Archipelago, Graham 2007; and on the Great Barrier Reef, Halford et al. 2004, Pratchett et al. 2006), and the difference with our study may be due in part to the relatively high abundance of generalists in the *Chaetodon* assemblage in this region (Table 2.2).

The results of this study also contribute to growing evidence of the pre-eminence of measures of habitat complexity (e.g. rugosity and rock cover) over coral cover as a driver of butterflyfish abundance and diversity (Bozec et al. 2005, Graham et al. 2009, Tkachenko and Soong 2010). This may be particularly true in my study region, where high benthic complexity or rugosity was found at sites with high rock cover, and is therefore attributable to high levels of rugosity in the underlying dead coral and rocky reef structure (Fig. 2.2E and Fig. 2.2F). This underlying reef complexity is likely a major reason why the measure of rugosity used in this study was consistently high across most of the region, despite extremely low live coral cover and high rubble cover at the sites closest to the path of Tropical Storm Washi. The absence of a storm "fingerprint" on the benthic complexity in our study may also be a consequence of the depth range of our surveys (3-15 m), with deeper areas being less vulnerable to storm damage, and sometimes experiencing increases in rugosity due to the displacement of massive corals and rocks from the upper reef slope to the lower reef slope during storms (Harmelin-Vivien 1994). This depth effect may explain why the results of this study differ so strongly from studies on shallow reef slopes (6-9 m deep) on the Great Barrier Reef, which reported simultaneous reductions in live coral cover and benthic complexity as a result of physical storm damage (Emslie et al. 2008, 2011, 2014).

Some top-down control was suggested by the negative effect of small predators (6-10 cm) on the abundance of corallivorous butterflyfish and on overall *Chaetodon* species richness (Table 2.4, Fig. 2.3). Predators in this size range are considered mesopredators, and are largely responsible for the extremely high mortality seen in newly-settled and juvenile reef fishes (Holmes and McCormick 2010, Feeney et al. 2012). It is therefore likely that the negative effect of mesopredators on butterflyfish abundance is occurring at these early life stages, during which small butterflyfish are still vulnerable to small predators. The vulnerability of newly-settled and juvenile butterflyfish to predation is so strong that it is considered to be the main driver of the evolution and prevalence of false eyespots in juveniles of *Chaetodon* species (Neudecker 1989), whereas the large body size, lateral compression, extreme body depth, and long dorsal and anal spines on adult butterflyfish are thought to greatly limit predation risk for adult butterflyfishes (Hourigan 1989, Neudecker 1989). In addition, my data indicate that predation on *Chaetodon* juveniles is only significant for corallivorous species, and not for generalists. This is likely due to contrasting settlement site selection by members of the different feeding guilds, with dietary specialists such as corallivores needing to settle directly into deeper, coral-dominated habitats (Pratchett and Berumen 2008, Pratchett et al. 2008b) where they may be more prone to predation, whereas generalists can often settle into safer “nursery” habitats such as shallow, rocky subtidal areas where predator foraging success is much reduced (Dahlgren and Eggleston 2000, Nagelkerken et al. 2008, Kimirei et al. 2013) and then carry out an ontogenetic shift onto deeper reef areas (Pratchett and Berumen 2008, Clark and Russ 2012) when they have outgrown the “predation gauntlet” of mesopredators (Dahlgren and Eggleston 2000, Lecchini and Galzin 2005, Pratchett et al. 2008b).

The BRT models captured a great deal of the variation in *Chaetodon* abundances and species richness. However, there was still considerable unexplained variance in this system. Potentially the most important determinant of reef fish abundances and diversity is larval supply (Williams et al. 1994, Armsworth 2002, Sale 2004), which was not assessed in this study. While post-settlement habitat availability and preferences can strongly mediate adult abundances, they act on an initial pool of recruits that is not distributed evenly in space or time (Williams et al. 1994, Jones et al. 2009, Berumen et al. 2012a, Harrison et al. 2012). Initial work to elucidate patterns of larval connectivity in this region (Abesamis et al. *in prep*) will aid in understanding to what extent *Chaetodon* abundances are structured by larval supply versus post-settlement ecological factors such as those explored here.

While it is standard practice for ecological studies to assess and report the influence of a few key variables on a study species (Munday et al. 1997, Halford et al. 2004, Bozec et al. 2005, Pratchett et al. 2006, Graham 2007), it is much less common to quantify the relative influence of both bottom-up and top-down processes (but see Wilson et al. 2008). Exploring a much larger number of drivers, involving both bottom-up and top-down processes, is the only way to fully illustrate a complete ecological picture that can provide better information for management (e.g. Wilson et al. 2008). This study demonstrated that post-settlement *Chaetodon* abundance and species richness were overwhelmingly structured by bottom-up drivers. However, key benthic components such as live coral cover and macroalgal cover are themselves subject to both top-down (i.e. predation and herbivory, respectively) and bottom-up (e.g. nutrient enrichment, environmental disturbances to benthos) influences, which makes management of coral reef systems particularly complex. This study contributes to growing evidence that coral reefs must be actively managed using a combination of bottom-up and top-down approaches, in which large-scale stressors such as sedimentation, nutrient enrichment, ocean acidification and sea-surface warming are addressed (Pandolfi et al. 2005, Veron et al. 2009b, Brodie et al. 2012) to promote coral health and to reduce macroalgae-favouring conditions, while local-scale fisheries management is used to increase the abundance of herbivores (McManus et al. 2000, Mumby et al. 2006) and to control the abundance of mesopredators (Prugh et al. 2009).

Coral reef systems are especially vulnerable to multiple, interacting stressors, in which natural disturbance events are compounded by direct human activities and indirect climate-mediated stressors (Hughes et al. 2003, Veron et al. 2009b, Hoegh-Guldberg 2011). However, their proximity to many of the world's poorest, most resource-dependent coastal nations (Hoegh-Guldberg et al. 2009, Burke et al. 2012) and their importance to the livelihoods of millions of people (Hoegh-Guldberg et al. 2009, Burke et al. 2012, Foale et al. 2013) means that their persistence will require careful and holistic management (Hoegh-Guldberg et al. 2009, McLeod et al. 2010, Burke et al. 2012). Management, in turn, must be informed by high-quality research that assesses and exposes the major drivers of abundance and diversity in coral reef systems.

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Chapter 3: Identifying and quantifying the extent to which habitat condition drives spatial variation in post-settlement growth of a *Chaetodon* butterflyfish[2]

3.1. Abstract

Recent research has demonstrated that despite a pelagic larval stage, many coral reef fishes disperse over relatively small distances, leading to well-connected populations on scales of 0-30 km. Although variation in key biological characteristics has been explored on the scale of 100s to 1,000s of km, it has rarely been explored at the scale relevant to actual larval dispersal and population connectivity on ecological timescales. In this study, I surveyed the habitat and collected specimens (n=447) of juvenile butterflyfish, *Chaetodon vagabundus*, at nine sites along an 80-km stretch of coastline in the central Philippines to identify variation in key life history parameters at a spatial scale relevant to population connectivity. Mean pelagic larval duration (PLD) was 24.03 days (SE = 0.16 days) and settlement size was estimated to be 20.54 mm Total Length (TL; SE = 0.61 mm). Both traits were spatially consistent, although this PLD is considerably shorter than reported elsewhere. In contrast, post-settlement daily growth rates, calculated from otolith increment widths from 1 to 50 days post-settlement, varied strongly across the study region. Elevated growth rates were associated with rocky habitats that this species is known to recruit to, but were strongly negatively correlated with macroalgal cover and exhibited negative density dependence

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[2] Published as: Leahy, S. M., G. R. Russ, and R. A. Abesamis. 2015. Pelagic larval duration and settlement size of a reef fish are spatially consistent, but post-settlement growth varies at the reef scale. Coral Reefs **34**:1283-1296, 10.1007/s00338-015-1330-y

with conspecific juveniles. Larger animals had lower early (first 50 days post-settlement) growth rates than smaller animals, even after accounting for seasonal variation in growth rates. Both VBGF and Gompertz models provided good fits to post-settlement size-at-age data (n=447 fish), but the VBGF's estimate of asymptotic length (L_∞=168 mm) was more consistent with field observations of maximum fish length. These findings indicate that larval characteristics are consistent at the spatial scale at which populations are likely well-connected, but that site-level biological differences develop post-settlement, most likely as a result of key differences in quality of recruitment habitat.

3.2. Introduction

For many years, coral reef fish populations were thought to be "open" systems as a result of the long pelagic stage of many reef fish larvae (Williams et al. 1984, Caley et al. 1996, Mora and Sale 2002). This led to assumptions of homogeneity of fish populations and life history characteristics in space (Planes 2002). However, there is now extensive evidence that many coral reef fish larvae can disperse over small spatial scales, and even recruit to or near their natal reef (Jones et al. 1999, 2005, Almany et al. 2007). This information has often been used to demonstrate the larval supply benefits of no-take marine reserves (Jones et al. 2009, Berumen et al. 2012a, Buston et al. 2012, Harrison et al. 2012), but it may also help to explain the development and preservation of local population-level biological characteristics (Pineda et al. 2007, Sotka 2012). Surprisingly, despite the increasingly fine-scale resolution of population connectivity studies, exploration of the variability in population characteristics at similarly fine spatial scales appears to be relatively rare (but see Gust et al. 2002, Ruttenberg et al. 2005).

There is evidence that intraspecific, pre-settlement characteristics such as Pelagic Larval Duration (PLD) and settlement size can vary over spatial scales of 1,000s of km, with important consequences for potential dispersal distances, survival in the plankton, and post-settlement performance (Wellington and Victor 1992, Bay et al. 2006, Treml et al. 2012, Leis et al. 2013). Studies of variation in pre-settlement characteristics have thus far addressed fish populations at the island scale (Wellington and Victor 1992, Bay et al. 2006, Leis et al. 2013), and have not addressed the possibility of among-reef population substructure in key life history traits such as PLD and settlement size.

Much more is known about the "population regulating" effects of post-settlement processes (Caley et al. 1996, Armsworth 2002). There is consistent evidence that reef-scale variation in key habitat characteristics has important consequences for the survival and growth of reef fishes (Kerrigan 1994, Tupper and Boutilier 1995b). Survivorship of newly-settled fishes is often very low (Doherty et al. 2004, Almany and Webster 2006), and is influenced by a few key ecological factors such as predator density and predation risk (Almany 2004a, Holmes and McCormick 2006), density of competitors (Almany 2004a, McCormick 2012, McCormick and Weaver 2012), which can include conspecifics (Doherty et al. 2004, Hixon and Jones 2005, Boström-Einarsson et al. 2013), and availability of key habitat components (Tupper and Boutilier 1997, Feary et al. 2007) such as shelter (Almany 2004b). Survivors of this population bottleneck tend to exhibit a few key characteristics, such as high growth rates immediately post-settlement (Gagliano and McCormick 2007, Gagliano et al. 2007). Evidence of this growth rate can be found in inert structures such as otoliths (Panfili et al. 2009).

In this study, I used otolith ageing techniques to document and assess the spatial variability of key pre-settlement characteristics and the early post-settlement growth history of *Chaetodon vagabundus*, a common generalist butterflyfish which recruits to rocky intertidal habitats, at the scale of individual coral reefs along an 80-km coastline in the central Philippines. In addition, this study elucidates the ecological factors associated with the range of growth rates observed across our study region, and produces the first post-settlement size-at-age estimates for this species using traditional fisheries growth models (VBGF and Gompertz). The focal species in this study is regularly used to model coral reef fish connectivity in the Coral Triangle (Almany et al. 2007, Berumen et al. 2012a, Pratchett et al. 2014). Evidence of reef fish population connectivity is an important driver for improved reef management and the implementation of no-take marine reserves (Almany et al. 2007, Jones et al. 2009, Berumen et al. 2012a), but reef-scale variability in key life history traits for this species is not yet known. Thus, quantification of life history traits of *C. vagabundus* and of spatial variation in these life history traits at a scale that is directly applicable to management will add important detail to our understanding of population connectivity patterns beyond predicted or observed patterns of larval settlement.

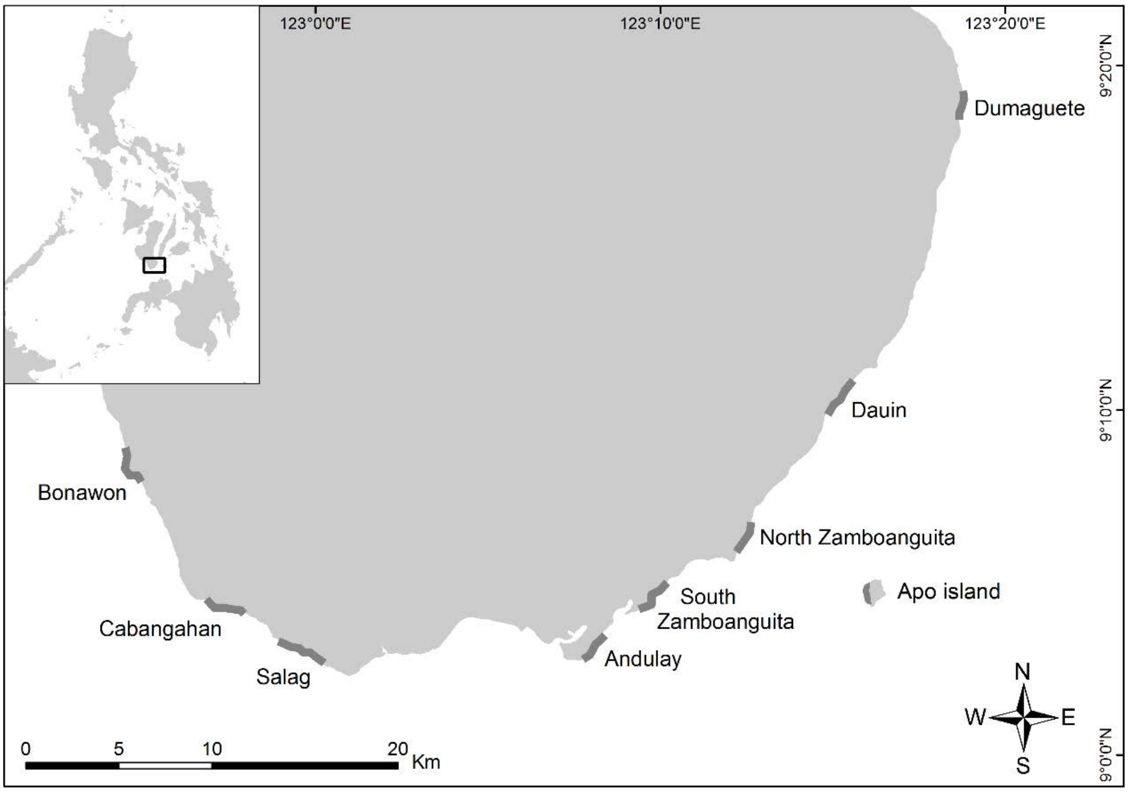

Figure 3.1. A Map of the Philippines, with study region delimited in black. **B** Study region on the southern coast of Negros Oriental, in the Visayas region of the central Philippines. Study sites are indicated in dark grey.

3.3. Methods

3.3.1. Study area

This study was conducted off the southern coast of Negros Island in the Visayas region of the central Philippines (Fig. 3.1A). This region is at the heart of the Coral Triangle, which is considered the world's epicentre of marine biodiversity (Roberts et al. 2002, Carpenter and Springer 2005). Over the past 40 years, management of Philippine coral reefs has increasingly relied on the use of no-take marine reserves to halt the decline in fisheries resources and biodiversity brought about by intense human extractive activities (Alcala and Russ 2006, White et al. 2006, Horigue et al. 2012). This study presents one component of ongoing research into reef fish population connectivity in the region, conducted at the reef scale (1-5 km) for ease of implementation by reef managers at the village scale.

Nearshore habitats in this area are characterised by intermittent, shallow, fringing coral reefs with lagoonal seagrass or coral beds and occasional remnants of mangrove stands (Yambao et al. 2001, DeVantier et al. 2004). Field surveys and fish sampling were carried out at nine sites (1-3 km each) unevenly distributed along 80 km of coastline, and including part of one offshore island (Apo island, Fig. 3.1B).

3.3.2. Study species

Chaetodon vagabundus is a generalist butterflyfish (Family: Chaetodontidae) common throughout the Indo-Pacific. In the study area, this species is generally not targeted directly by commercial or artisanal fisheries (BFAR 2010). It exhibits an ontogenetic habitat shift from shallow, rocky/dead coral intertidal, juvenile habitats to deeper, more coral-rich, adult habitats (Harmelin-Vivien 1989, Pratchett et al. 2008b, Clark and Russ 2012). Butterflyfish recruitment (settlement) in this region occurs throughout the year and peaks in recruitment are likely to occur from September to February, when water temperature is slightly lower (Abesamis and Russ 2010).

3.3.3. Specimen collection

Specimens of *C. vagabundus* were collected at nine sites along the southern coast of Negros between 7 October 2011 and 30 November 2012 (Fig. 3.1B). Fish were collected by spear gun and barrier net, and euthanized as per James Cook University animal ethics protocol A1803. Upon collection, total length (TL) of specimens was recorded and a small tissue sample was taken from the posterior portion of the dorsal fin or the caudal fin for genetic analysis in a separate study, thus precluding the use of standard length and weight in this study. For the present study, a minimum sample size of 15 specimens in each of three size classes ("juveniles": <50 mm, "sub-adults": 50 to 100 mm, "adults": >100 mm TL) was targeted at each site. However, sample size was unbalanced at some sites, either due to low availability of a size class and/or over-representation of abundant size classes. Specimens <50 mm were exclusively collected from the shallow, rocky/dead coral intertidal habitats to which they recruit (Pratchett et al. 2008b, Clark and Russ 2012), and specimens ≥50 mm were collected wherever they were encountered on the reef profile.

3.3.4. Otolith preparation and reading

Sagittal otoliths were extracted, cleaned of adhering tissue, and preserved dry. Thin transverse cross-sections of one otolith from each fish were produced by grinding down both the anterior and posterior ends of the otolith using increasingly fine sandpaper, then lapping film (as per Wilson and McCormick 1997). The resulting section was discarded if it did not include the otolith nucleus. Otolith cross-sections were read using transmitted light at 400x magnification. A single count of daily increments was conducted along the clearest axis (as in Plaza et al. 2013) from the otolith core to the outer edge by an experienced professional (Tropical Fish Ageing, Townsville, Australia). Otolith legibility was scored on a scale from 1 (unreadable) to 5 (excellent). Of the 455 otoliths prepared, 449 were considered legible (score of 2 or higher) and were used for further analyses.

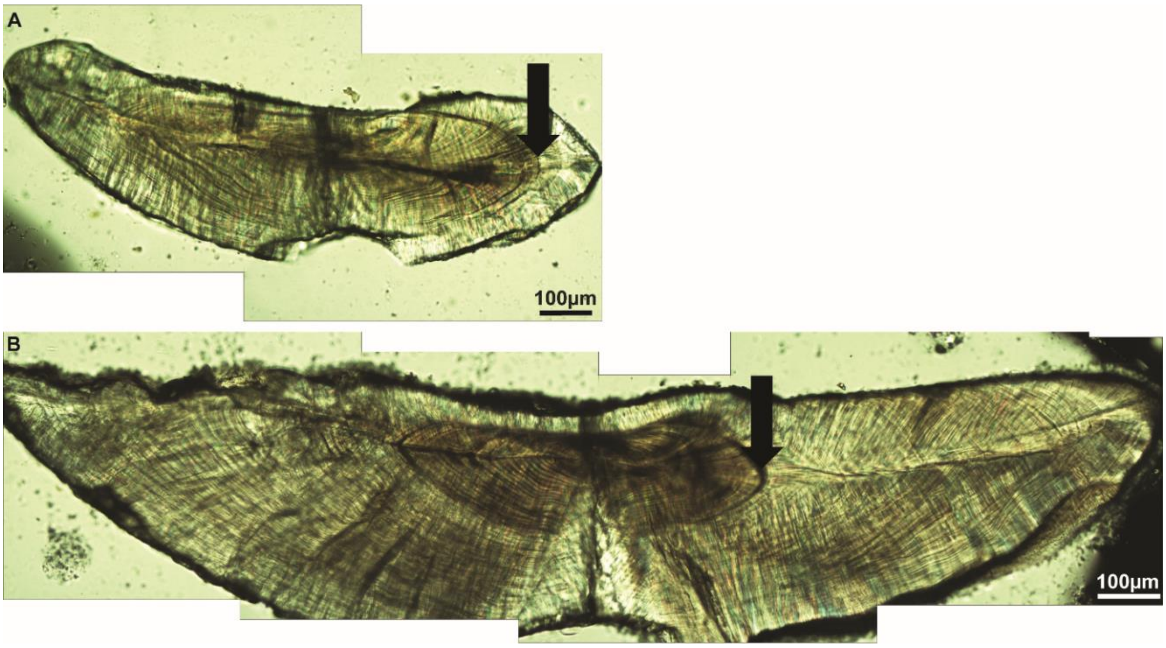

Figure 3.2. Sample transverse cross-sections of *Chaetodon vagabundus* otoliths, **A** individual with 30 day PLD and 31 days post-settlement, TL = 38 mm, **B** individual with 20 day PLD and 197 days post-settlement, TL = 100 mm. Settlement is indicated by large black arrows, and is visible as the abrupt change from wide daily increments (appear brown) to narrow daily increments (appear grey).

Chaetodon vagabundus exhibited a Type Ia settlement mark (Wilson and McCormick 1999): an abrupt change involving a single increment transition (Fig. 3.2A and Fig. 3.2B). The number of pre-settlement increments was recorded for specimens for which a settlement mark was unambiguous (n = 349). For specimens for which the settlement mark was unclear (n = 98), pre-settlement duration was assumed to be 24 days, which was both the mean and median of the pre-settlement duration in the remainder of the sample, for the purpose of calculating post-settlement age (total age – pre-settlement age) for use in statistical analyses. For a further two specimens that were newly-settled, total increment number was less than 24 days. Pre-settlement duration for those individuals was estimated as "total increments – 1" (i.e., it was assumed that these individuals were collected within 1 day after settlement). Pre-settlement duration was corroborated by another experienced otolith reader on a separate sample of juvenile *C. vagabundus* from the same region (Abesamis et al. *in prep*).

Where possible, post-settlement increment widths were measured along the clearest axis up to the 50th post-settlement increment using the image analysis program Optimas 6.5. Otolith radius along the measurement axis was recorded in order to standardise increment widths to relative increment widths (Plaza et al. 2013).

3.3.5. Surveys of juvenile conspecifics and recruitment habitat

The abundance of juvenile *Chaetodon vagabundus* (≤50 mm, estimated to be approximately <50 d post-settlement) in shallow or intertidal recruitment habitats (<1 m deep) was recorded at the same nine sites where specimens were collected (Fig. 3.1B). In order to avoid negative impacts of sampling on fish abundances in field surveys, surveys were either conducted prior to sampling or ≥4 months after sampling, thus allowing for the recruitment of several new cohorts before surveying. The abundance of juveniles (≤50 mm TL) of all species of *Chaetodon* and the abundance of all potential predators (>100 mm TL) of juvenile *Chaetodon* were surveyed simultaneously using 50 m belt transects estimated to be 4 m wide (200 m^2 $transect^{-1}$) laid out parallel to the coastline. Potential predators included certain members of the families Labridae, Lutjanidae, Pinguipedidae, Pseudochromidae, Serranidae, Scorpaenidae, and Synodontidae. Four to seven replicate transects were surveyed per site between 17 September 2012 and 11 December 2012. Benthic composition (live coral, volcanic or coralline rock, rubble, seagrass, macroalgae, sand, and all other) was recorded every 0.5 m using the Point Intercept technique (English et al. 1994) on the return swim along each transect. An index of rugosity (as per Russ et al. 2005) was estimated at 10 m increments to provide a relative measure of benthic complexity in the generally low-complexity recruitment habitat.

3.3.6. Data analysis

3.3.6.1. Pre-settlement characteristics

The effect of site on the PLD of *C. vagabundus* was assessed by comparing the fit of a linear mixed effects model with site treated as a random factor in the *nlme* package (Pinheiro et al. 2014) to the fit of a generalized least squares fixed-effects model that did not include the random site term (Table 3.1) in RStudio (RStudio 2013). The Akaike Information Criterion (AIC) of each model was used to determine whether the site term significantly improved the model's explanatory power (Zuur et al. 2009). Differences in AIC scores of ≤ 2 points are indicative of equally probable models, and indicate that the model with the fewest explanatory variables is most probable (Burnham and Anderson 2004). Sites for which fewer than ten PLDs could be accurately read from the otoliths were not included in this analysis (N = 8 sites remaining). Once the best model (including or excluding the "site" factor) was identified, a follow-up generalized least squares model was built to evaluate the possibility of size-selectivity (i.e. variation in PLD associated with TL at collection) and seasonality (i.e., variation in PLD associated with time of year of settlement) on the PLD of *C. vagabundus* (Table 3.2). Julian settlement date of *C. vagabundus* was used as a proxy for seasonal effects and was incorporated using two parameters: a sine harmonic term ($\sin(2\pi/365*\text{settlement date})$) and a cosine harmonic term ($\cos(2\pi/365*\text{settlement date})$) (Pinheiro and Bates 2000).

Settlement size for *C. vagabundus* and potential site-related differences in settlement size were assessed by comparing the fit of a generalized least squares fixed-effects model on fish TL without the site term, to the fit of a linear mixed effects model with site as a main effect, as well as to a linear mixed-effects model with site as an interaction with fish age (Table 3.1). Settlement size was considered to be the intercept of the regression of TL against post-settlement age in very young fish (≤ 200 days), i.e.

TL at age zero. Sites with fewer than ten very young fish (≤ 200 days) were not included in this analysis (N = 7 sites remaining). Despite linear growth rates being common for young coral reef fishes (Ferreira and Russ 1994, Choat and Axe 1996), including other members of the Chaetodontidae (Fowler 1989, Berumen 2005, Zekeria et al. 2006), the length-versus-age relationship in young *C. vagabundus* was best fitted by a quadratic term, such that

$$TL \sim Age^2 + Age \qquad \text{(Eq. 3.1)}$$

where *TL* is Total Length in mm and *Age* is the post-settlement age in days. For both the mixed effects and the fixed effects models, within-group heteroscedasticity structure was modelled using a power variance function, with *Age* as the variance covariate.

Table 3.1. Evaluation of model quality given the exclusion or inclusion of the factor site as a random main effect or interaction in models explaining (a) *Chaetodon vagabundus* pelagic larval duration (PLD, in days), (b) total length (in mm), and (c) log-transformed relative increment width. Best models were selected based on lowest AIC scores; when AIC scores differed by ≤ 2, the model with the fewest explanatory variables was considered best. Details of model-building approach in-text.

Dependent variable	Explanatory variables	Variance structure	Number of sites	Number of cases	AIC	Best model
(a) PLD	None	None	8	346	1,723.69	*
	Site	None	8	346	1,721.69	
(b) Total length[i]	Age^2 + Age	Heteroscedastic	7	324	2,187.56	*
	Age^2 + Age + Site	Heteroscedastic	7	324	2,187.17	
	Age^2 + Age * Site	Heteroscedastic	7	324	2,191.17	
(c) Log (Increment width)	Increment number	None	7	13,498	16,264.07	
	Increment number + Site	None	7	13,498	16,054.92	
	Increment number * Site	None	7	13,498	16,011.66	*

[i] Intercept of the Total Length model is equivalent to total length at age zero, i.e., settlement size

Table 3.2. Models evaluating possible size-selectivity and seasonality in the pelagic larval duration (PLD) and early post-settlement growth history of *Chaetodon vagabundus*. Abbreviations: "incr." represents "increment", "TL" represents "Total Length". Significant terms (at $p < 0.05$) are indicated in bold.

Dependent variable	Model R^2	Fixed explanatory variable	Variable's contribution to R^2	Coefficient value	Coefficient st. err.	t-value	*p*-value
PLD[i]	0.035	TL	0.016	-0.013	0.007	-2.006	**0.046**
PLD[i]	0.035	sin(settlement date)	0.003	-0.211	0.266	-0.796	0.427
PLD[i]	0.035	cos(settlement date)	0.017	0.611	0.252	2.422	**0.016**
Incr. width[ii]	0.244	Incr. number	0.074	-0.008	0.001	-12.152	**0.000**
Incr. width[ii]	0.244	TL	0.163	-0.007	0.000	-33.281	**0.000**
Incr. width[ii]	0.244	sin(Incr. date)	0.003	0.023	0.009	2.495	**0.013**
Incr. width[ii]	0.244	cos(Incr. date)	0.005	0.079	0.007	10.705	**0.000**

[i] Model: PLD ~ TL + sin(2π/365*Julian settlement date) + cos(2π/365*Julian settlement date)

[ii] Model: Log(increment width) ~ increment number * site + TL + sin(2π/365*Julian increment date) + cos(2π/365*Julian increment date)

3.3.6.2. Early post-settlement growth and habitat associations

Daily growth rates in juvenile *C. vagabundus* (≤ 50 mm) and potential site-related differences in daily growth rates were assessed by comparing the fit of a generalized least squares fixed-effects model on the relative increment widths of *C. vagabundus* between 0 and 50 days post settlement (N = 334 fish, N = 13,498 increments) without the site term, to the fit of a linear mixed effects model with site as a main effect, as well as to a linear mixed-effects model with site as an interaction with fish age (i.e. increment number; Table 3.1). Sites with <20 fish samples were not included in this analysis (N = 7 sites remaining). Relative increment widths were log-transformed in order to accommodate the exponential decay in increment widths with increasing increment number.

Once the best model (including or excluding the "site" factor) was identified, a follow-up non-linear mixed effects model was built to evaluate the possibility of size-selectivity (i.e., variation in early growth associated with fish TL at collection) and seasonality (i.e., variation in early growth associated with the time of year of growth) on the early growth rates of *C. vagabundus* (Table 3.2). The Julian date of formation of each otolith increment was used as a proxy for seasonal effects and was incorporated using two parameters: a sine harmonic term (sin(2π/365*increment date)) and a cosine harmonic term (cos(2π/365*increment date)) (Pinheiro and Bates 2000). Only fish for which all 50 days of post-settlement increments were available were included in the model (i.e. no fish younger than 50 days).

Significant site-related differences in the daily growth rates of juvenile *C. vagabundus* were explored further using Principal Components Analysis (PCA) in Statistica 12 (StatSoft). Relative increment widths were regressed against increment number, and the residuals of the regression were broken into 10 day brackets (1-10 days post-settlement, 11-20 days post-settlement, etc.). The average of each 10 day growth bracket at each site was resolved along Principal Components axes. Characteristics of juvenile *C. vagabundus* habitats (benthic composition, structural complexity, abundance of juvenile conspecifics, and abundance of potential predators) were averaged for each site, and then resolved along the same PC axes. Correlations between habitat and growth vectors were assessed for statistical significance at $p < 0.05$ and $p < 0.1$. The abundance of other species of *Chaetodon* was extremely low at all sites, and so was not included in the analysis.

3.3.6.3. Size-at-age estimates

Post-settlement, age-based growth parameters were calculated for the full data set using least-squares estimation and were optimised using the Levenberg-Marquardt algorithm in Statistica 12 (StatSoft). Size-at-age data were fitted to three models: the Gompertz function, the standard Von Bertalanffy Growth Function (VBGF), and the re-parametrised Von Bertalanffy Growth Function (rVBGF). For the Gompertz model, length L at age t is determined by

$$L_t = L_\infty \cdot e^{-e\,(G-gt)} \tag{Eq. 3.2}$$

where L_∞ is the theoretical asymptotic length, G is the initial growth rate, and g is the rate at which G declines . For the VBGF, length L at age T is determined by

$$L_T = L_\infty\left[1 - e^{-K\,(T-t_0)}\right] \tag{Eq. 3.3}$$

where L_∞ is the theoretical asymptotic length, K the rate at which L approaches L_∞ (also known as the curvature parameter), and t_0 is the theoretical point in time when the fish had length zero. For the rVBGF

$$L_T = L_y + \frac{\left[L_v - L_y\right]\left[1 - r^{2(T-y)(v-y)^{-1}}\right]}{1 - r^2} \tag{Eq. 3.4}$$

and

$$r = \frac{L_v - L_w}{L_w - L_y} \tag{Eq. 3.5}$$

where L_y, L_v, and L_w are the mean lengths at ages y, v, and w, with $w = \frac{y+v}{2}$.

Both the VBGF and the rVBGF provide the same model fit, however the VBGF estimates more traditional parameters (e.g. L_∞) that can readily be compared to fish growth models in the literature, while the rVBGF estimates biologically relevant parameters (Welsford and Lyle 2005). Longevity and mean maximum length were not estimated due to a sampling bias towards young animals.

3.4. Results

3.4.1. Pre-settlement characteristics

PLD in *C. vagabundus* ranged from 18 to 32 days, with a mean of 24.03 days (SE ±0.16 days), a median of 24 days, and a mode of 22 days (Fig. 3.3). PLD did not vary significantly among sites (Table 3.1). A statistically significant seasonal effect (i.e. variation in PLD due to time of year) was detected, but its influence was very weak ($R^2 = 0.017$; Table 3.2). Similarly, a significant, negative size-selective effect (i.e. larger animals had shorter PLDs) was detected, but its influence was also negligible ($R^2 = 0.016$; Table 3.2). Estimated settlement size for *C. vagabundus* was 20.54 mm TL (SE ± 0.61 mm), which did not vary significantly among sites (Table 3.1).

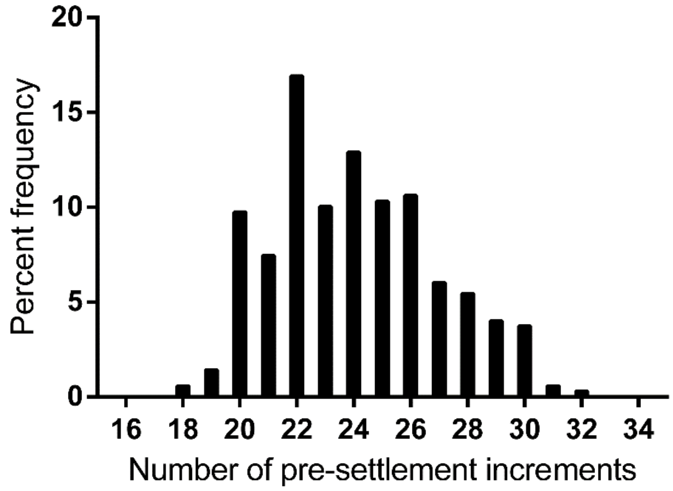

Figure 3.3. Frequency distribution of pre-settlement increments in *Chaetodon vagabundus* (n = 349).

3.4.2. Early post-settlement growth and habitat associations

Daily growth rates (i.e., log-transformed relative otolith increment widths in the first 50 days post-settlement) varied significantly among sites (Fig. 3.4; Table 3.1). The best model fit indicated a significant interaction effect, indicating the presence of significant among-site differences in both the intercept and the slope of the regression relationship (Fig. 3.4). Subsequent analyses indicated the presence of a negative, size-selective effect on early growth in *C. vagabundus* (i.e. larger animals had lower early growth rates) as well as a significant seasonal effect (i.e. variation in growth rates due to time of year; Fig. 3.5; Table 3.2). The size-selective effect was relatively strong ($R^2 = 0.163$), contributing more than two thirds of the model's explanatory power, whereas the two terms describing the seasonal effect were both extremely weak ($R^2 = 0.003$ and 0.005; Table 3.2).

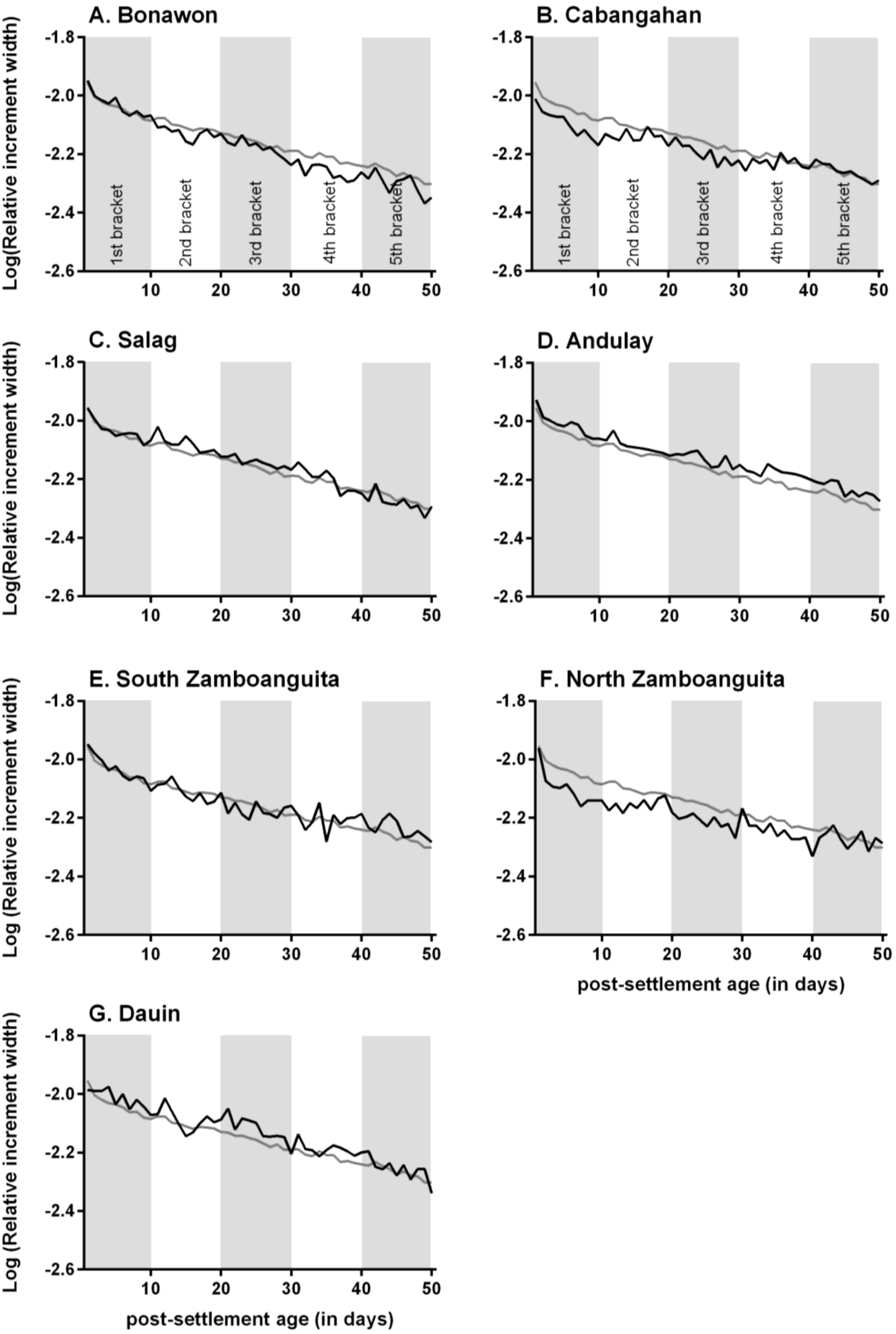

Figure 3.4. Mean log-transformed relative otolith increment width for the first 50 days post-settlement, by site. Sites are arranged geographically, from west to east. Grey line indicates regional mean, black line indicates site mean. "Brackets" are used to subdivide the 50 days post-settlement period into 10 day intervals for subsequent analyses.

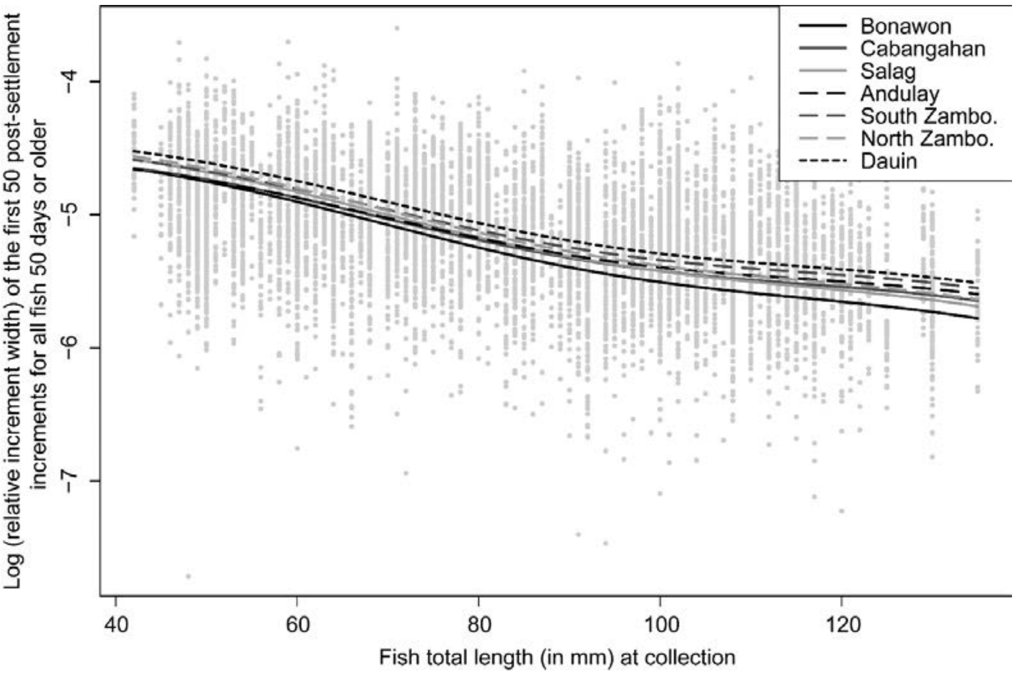

Figure 3.5. Raw data points and best-fit lines from the non-linear mixed effects model describing size-selectivity and seasonality on the early growth rates (log-transformed otolith increment widths for the first 50 days post-settlement) of *Chaetodon vagabundus* at seven sites (Table 3.2). Only fish for which all 50 days of post-settlement increments were available were included in the model. "Zambo." represents "Zamboanguita".

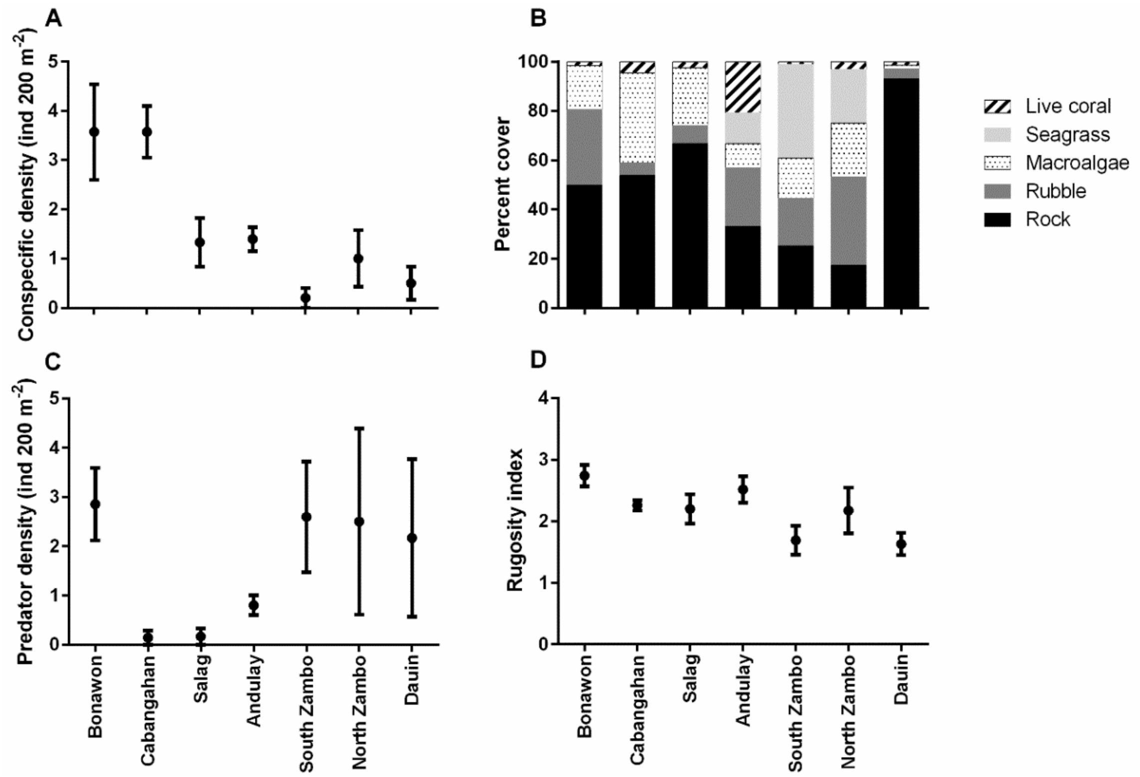

Figure 3.6. Characterization of *Chaetodon vagabundus* recruitment habitat at the seven sites for which juvenile growth history was available: **A** mean (± SE) density of juvenile conspecifics, **B** mean percent cover of major benthos, **C** mean (± SE) density of potential predators, **D** mean (± SE) rugosity index. Sites are arranged geographically, from west to east. "Zambo." represents "Zamboanguita".

Key characteristics of the recruitment habitat for *C. vagabundus* varied noticeably across the study region (Fig. 3.6). The density of juvenile conspecifics was highest at Bonawon and Cabangahan (Fig. 3.6A). Benthic composition across the region varied greatly, although most sites had high cover of rock and rubble, and most had low live coral cover (except Andulay; Fig. 3.6B). The density of potential predators was either low or highly variable (Fig. 3.6C), and the index of rugosity was relatively similar across the study region (Fig. 3.6D).

Resolution of the 10 day brackets of relative daily growth rates in multidimensional space was very high, with the first two Principal Components accounting for 95.7% of the variation in daily growth rates (Fig. 3.7). Growth rate brackets clustered in two quadrants of multidimensional space, with brackets 1, 2, and 3, representing post-settlement days 1 to 30, grouped particularly close together (Fig. 3.7A).

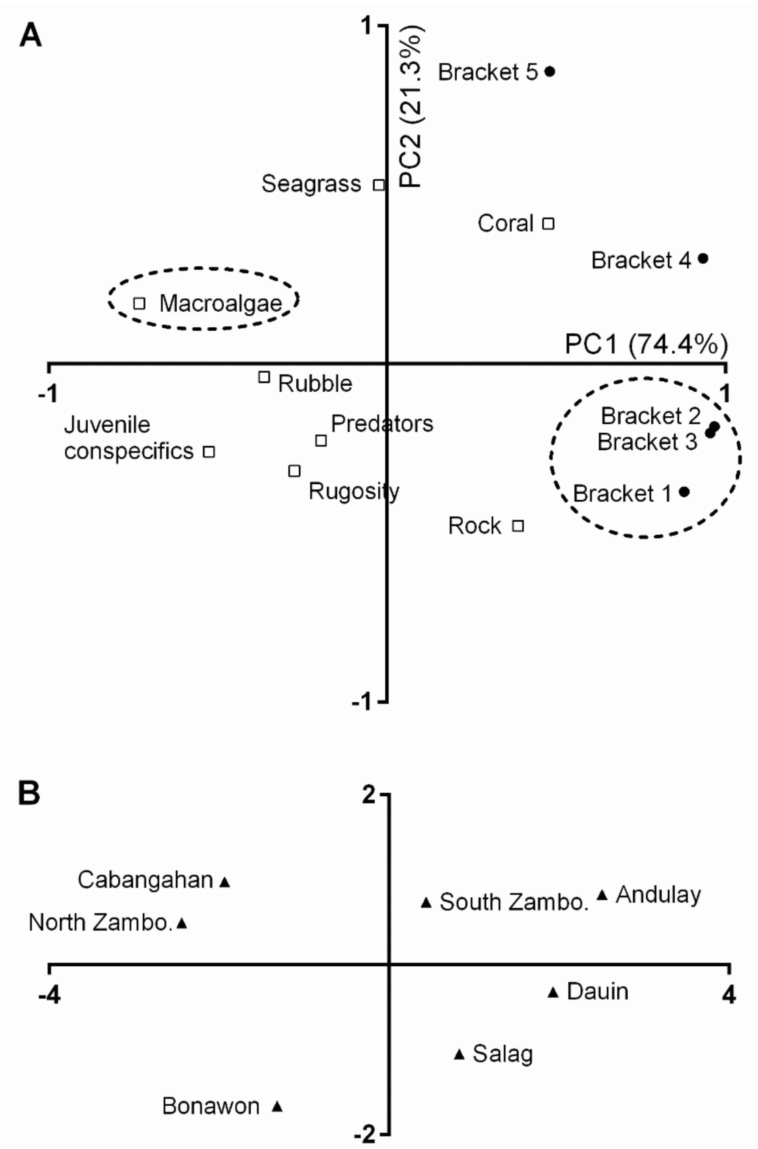

Figure 3.7. **A** Principal components analysis (PCA) of the residuals of the regression of daily growth rates of young *Chaetodon vagabundus* against otolith increment number, in 10-day brackets (filled circles), with resolution of supplementary habitat variables illustrated along the same axes (hollow squares). Dotted circles highlight significant growth-habitat correlations at $p < 0.1$. **B** Resolution of each site, when overlayed on the PCA growth vectors. “Zambo.” represents “Zamboanguita”.

Overlaying habitat variables on the growth vector PCA showed strong positive associations between growth in all brackets and rock cover, as well as coral cover (Fig. 3.7A, Table 3.3). Strong and consistently negative associations occurred between early post-settlement growth and macroalgal cover, rubble cover, and rugosity (Fig. 3.7A, Table 3.3), although only the negative correlation between macroalgal cover and growth in brackets 1-3 was statistically significant at $p < 0.1$ (Table 3.3).

Associations between juvenile growth and seagrass cover and the abundance of predators were much weaker and generally inconsistent (Fig. 3.7A, Table 3.3).

Site-level differences in growth rates identified by the mixed-effects model (Table 3.1) were illustrated by the resolution of sites along the PC axes, particularly PC1 (Fig. 3.7B). The highest growth rates were at Andulay and Dauin (Fig. 3.4D, Fig. 3.4G, and Fig. 3.7B), which were characterised by low macroalgal cover (Fig. 3.6B and Fig. 3.7A). Conversely, the lowest growth rates were encountered at Bonawon, Cabangahan, and North Zamboanguita (Fig. 3.4A, Fig. 3.4B, Fig. 3.4F, Fig. 3.5, and Fig. 3.7B), which were characterised by relatively high densities of conspecifics and high macroalgal cover (Fig. 3.6A and Fig. 3.6B).

Table 3.3. Subset of the correlation matrix between growth vectors (average post-settlement otolith increment growth residuals at each site, in 10 day brackets) and habitat variables (i.e., abundance of juvenile conspecifics and predators, cover of benthic components, and rugosity). ** indicates correlation was significant at $p < 0.05$; * indicates correlation was significant at $p < 0.10$.

	Bracket 1 (1-10 days)	**Bracket 2 (11-20 days)**	**Bracket 3 (21-30 days)**	**Bracket 4 (31-40 days)**	**Bracket 5 (41-50 days)**
Juvenile conspecifics	-0.385	-0.523	-0.410	-0.511	-0.513
Predators	0.143	-0.206	-0.208	-0.400	-0.166
Coral cover	0.303	0.375	0.354	0.550	0.609
Rubble cover	-0.090	-0.342	-0.455	-0.496	-0.089
Rock cover	0.363	0.413	0.616	0.302	-0.305
Macroalgal cover	**-0.827****	**-0.684***	**-0.746***	-0.527	-0.275
Seagrass cover	-0.060	-0.069	-0.285	0.052	0.524
Rugosity	-0.070	-0.220	-0.229	-0.362	-0.390

3.4.3. Size-at-age estimates

VBGF and Gompertz models fitted the size-at-age data for *C. vagabundus* equally well (Fig. 3.8, Table 3.4), but the higher asymptotic length (L_∞) predicted by the VBGF model is more consistent with field observations of maximum length in this species (up to 164 mm TL; R. A. Abesamis, *pers. obs.*). The higher asymptote in the VBGF was associated with a low curvature parameter K, which was double that of the equivalent

Gompertz term *g* (the rate at which the growth rate *G* declines with age; Table 3.4). Both models closely described the size-at-age trajectory of young (≤ 200 day old) *C. vagabundus* (Fig. 3.8, Table 3.4), and model assumptions were satisfied equally well for both models (Figs. 3.8C-F).

Using the rVBGF, *C. vagabundus* lengths at ages $y = 50$ days, $w = 225$ days, and $v = 400$ days were estimated to be 52.9 mm, 124.2 mm, and 151.4 mm, respectively (Fig. 3.8A). The rVBGF parameters could not be estimated for each site due to dissimilar age ranges among specimens collected from each site.

Table 3.4. Post-settlement size-at-age-based demographic model parameter estimates and model evaluation (R^2) for the VBGF model and the Gompertz function. For both models, length is expressed in mm and time is expressed in days.

Model	Parameters	Parameter estimates	R^2
VBGF	L_∞	168.2648	0.9415
	K	0.0055	
	t_0	-18.6340	
Gompertz	L_∞	147.2702	0.9427
	G	0.5960	
	g	0.0109	

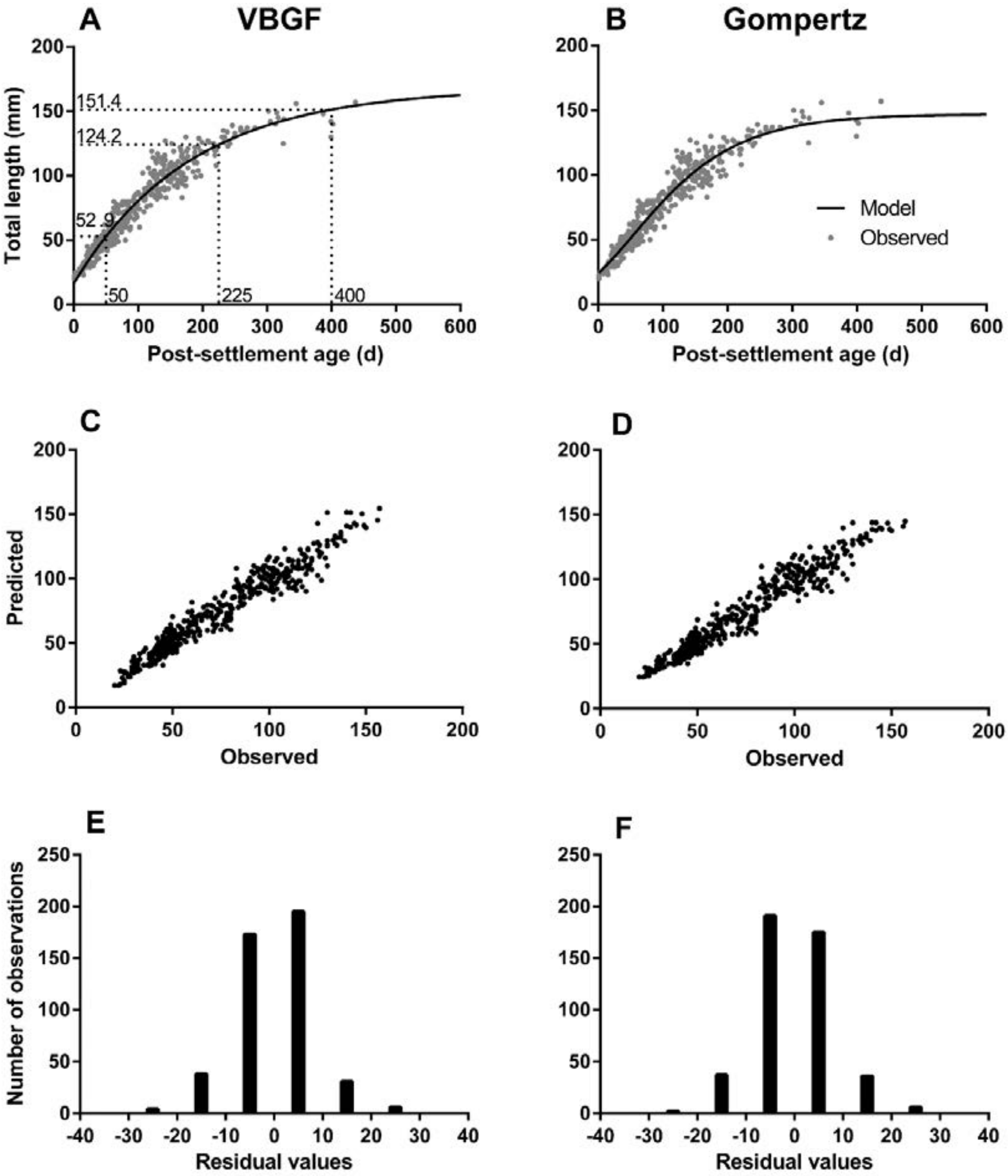

Figure 3.8. Post-settlement, size-at-age-based growth model fit to observed data for **A** the VBGF and **B** the Gompertz function; dotted lines on the VBGF panel indicate rVBGF length estimates at given ages. Assessment of model assumptions: distribution of predicted versus observed values for **C** VBGF and **D** Gompertz function, and distribution of residual values for **E** VBGF and **F** Gompertz function.

3.5. Discussion

3.5.1. Implications of spatial variation in post-settlement growth characteristics

This study identified significant spatial differences in early (≤ 50 days post-settlement) growth rates in *C. vagabundus*, and correlated these patterns with key environmental variables, thereby elucidating major growth, and probable survival-related, drivers for this species. The results of this study confirm that growth rates in very young *C. vagabundus* (1-50 days post-settlement) are significantly higher in the rocky environments with which they associate at or soon after settlement (Harmelin-Vivien 1989, Pratchett et al. 2008b, Clark and Russ 2012), and also adds significant detail to that association: that the strongest driver of early growth is actually a negative relationship with macroalgal cover, and that young *C. vagabundus* experience negative density-dependent effects on early growth by conspecific juveniles (Fig. 3.7, Table 3.3).

The negative relationship between early growth rates in *C. vagabundus* and macroalgal cover is somewhat surprising, given that the diet of juvenile *C. vagabundus* consists largely of non-coral invertebrates (50%) and filamentous algae (30%) (Harmelin-Vivien 1989). This suggests that a macroalgal-rich habitat could provide adequate nutrition for young *C. vagabundus* – although this seems not to be the case (Fig. 3.7, Table 3.3). It is possible that the strong negative association of macroalgae on early *C. vagabundus* growth rates was the result of reduced foraging options, with higher macroalgal cover limiting the availability of non-coral invertebrate prey (Stella et al. 2011), in addition to the dominance of potentially unpalatable macroalgal taxa in the shallow-water macroagal communities (e.g. *Bornetella nitida* and *Turbinaria ornata*). The distinct negative impact of macroalgal cover on this species may mean that assessment of macroalgal cover in juvenile habitats (<1 m deep) may provide a simple indicator of low growth rates in *C. vagabundus* recruits, with implications for potential lower survivorship and subsequent population patterns (Jones and McCormick 2002).

However, the non-significant, but distinctly negative correlation between very early growth rates in *C. vagabundus* and the density of conspecific juveniles indicates that interpreting growth and survivorship in this system may be more complex than simply assessing habitat quality parameters such as benthic cover. For many coral reef fishes, the presence of conspecifics is an important cue in settlement site selection (Sweatman 1983, Lecchini et al. 2005, Munday et al. 2009), but there is also extensive evidence indicating that resident fish can have negative effects on the recruitment (Almany 2003), survivorship (Almany 2004a, Doherty et al. 2004, Hixon and Jones 2005, Boström-Einarsson et al. 2013), and growth (Tupper and Boutilier 1995a) of conspecifics. The high specificity of *C. vagabundus*' recruitment habitat (Bouchon-Navaro 1981, Clark and Russ 2012) suggests that the negative effect of juvenile conspecific density on early growth in *C. vagabundus* is a true relationship rather than an artefact of migration of juveniles between habitats.

The presence of negative size-selectivity on early growth of *C. vagabundus* (Table 3.2, Fig. 3.5) was an unexpected finding, given the well-known declines in mortality rate with increasing size in many teleost fishes (Houde 1997). The negative effect of animal size on early growth rates was consistent across sites (Fig. 3.5), and was significantly, albeit very weakly, influenced by seasonal variation in early growth rates (Table 3.2). Although uncommon, negative size-selectivity is not unheard of in marine systems, with an extensive meta-analysis reporting that 23% of observations of selective pressure on body size were of negative size selection (Perez and Munch 2010). A possible explanation for selection against rapid growth rates is that rapid growth requires greater foraging time, and therefore increases exposure to predation (Gagliano et al. 2007).

Although it was not possible to assess site-level differences in VBGF, Gompertz, or rVBGF model parameters for *C. vagabundus* in this study, the strong site-level differences in early growth history suggest that, given a larger sample size and more even sampling effort, size-at-age model parameters for *C. vagabundus* would likely vary within this study region, as has been found in two parrotfishes, two surgeonfishes, and one damselfish at similar spatial scales (Gust et al. 2002, Ruttenberg et al. 2005). In addition, estimates of longevity for this species may also vary across the region as a result of site-specific differences in fishing intensity, as large *C. vagabundus* are vulnerable to passive fishing gears such as fish traps and gill nets (G. R. Russ and R. A. Abesamis, *pers. obs.*). Testing this hypothesis may prove difficult however, due to the logistical difficulties of collecting representative numbers of large adult *C. vagabundus* on the deep reef slopes (>18 m) where they are commonly encountered (R. A. Abesamis and S. M. Leahy, *pers. obs.*). The maximum age encountered in this study (437 days) is far lower than that found in other systems, with other members of this genus estimated to have longevities between 4 and 14 years on the northern Great Barrier Reef (Berumen et al. 2012b). This discrepancy may be in part due to the logistical difficulties of collecting large *C. vagabundus* in their deep reef slope habitats, and in part due to the locally low abundances of large *C. vagabundus* as a result of intensive, non-selective fishing in this region.

3.5.2. Implications of spatial consistency in pre-settlement characteristics

The PLDs reported in this study were consistent across the study area, and were in line with previous estimates of PLDs for the Chaetodontid family (range: 20-57 days, mean <40 days; Leis 1989), but were much lower than those reported for the same species from Papua New Guinea (38 days, Almany et al. 2007) and Japan (42 days, Soeparno et al. 2012). The discrepancy is too large to be explained solely by the addition of a 30 hour egg stage (Leis 1989) or of a 4 days period between egg spawning and yolk sac absorption, as reported in *C. nippon* (Suzuki et al. 1980), during which time otolith increment deposition may begin (Fowler 1989). The pre-settlement durations reported here are also unlikely to be artefacts of biased reading, as they were corroborated by another experienced otolith reader on a separate sample of juvenile *C. vagabundus* from the same region (Abesamis et al. *in prep*).

Similar magnitudes of intraspecific differences in PLDs have been reported for one species of wrasse and two species of damselfish (Wellington and Victor 1992) between sites almost 3,500 km apart in the Eastern Pacific. While Wellington and Victor (1992) found the shortest PLDs at higher latitude sites and the longest PLDs at equatorial sites, that is not the case for *C. vagabundus*, which displayed long PLDs at both high (Japan, Soeparno et al. 2012) and low (Papua New Guinea, Almany et al. 2007) latitudes, and short PLDs at an intermediate/low latitude (Philippines, this study). The short PLDs encountered in this study could not be attributed to seasonal variation ($R^2 = 0.017$; Table 3.2) and may instead be a result of a local adaptation to maximize recruitment in an extremely well-connected region, as has been observed in a damselfish (Bay et al. 2006).

While it has been hypothesised that lower PLDs improve larval survivorship by reducing exposure to predation in the plankton (Sponaugle 2009), within-cohort analyses of damselfishes have shown no differences between the PLD of post-recruitment survivors and the initial pool of settlers (Nemeth 2005, Gagliano et al. 2007), indicating no post-settlement survival-related benefits of shorter PLDs.

Similarly, we observed a statistically significant but non-influential ($R^2 = 0.016$) effect of TL on PLD of *C. vagabundus*. The large intraspecific difference in PLD between this study and those reported elsewhere (Almany et al. 2007, Soeparno et al. 2012) may be a result of the density and proximity of suitable settlement habitat in this study region, which, when coupled with a monsoonal environment in which prevailing winds change direction seasonally (Abesamis 2011, Abesamis et al. *in prep*), would make long PLDs unnecessary, if not unhelpful, to maintain the abundance of *C. vagabundus* populations across the region. These results underscore the importance of collecting local life history information when producing biological and ecological models for local application.

The settlement size reported in this study was consistent across the study region, and was similar to the average size at settlement for the Chaetodontidae as a whole (20 mm, Leis 1989). The implications of differences in size at settlement on subsequent growth and survival of recruits is unclear. Some studies have provided evidence of higher survivorship among larger settlers (McCormick and Hoey 2004), whilst others have shown evidence of higher survivorship among smaller settlers (Gagliano et al. 2007), with other studies finding no significant difference in survivorship associated with size at settlement (Hoey and McCormick 2004, Nemeth 2005), all within the same species of damselfish, *P. amboinensis*. The spatially consistent settlement size reported in our study does not clarify the debate above, but rather indicates that any selective pressure on settlement size in this species, whether positive or negative, is homogenous across the 80 km coastline surveyed in this study.

3.5.3. Implications for population connectivity

This study provides the first description of basic biological traits of a species already used as a model organism in several connectivity studies in the Coral Triangle (Almany et al. 2007, Berumen et al. 2012a), and identifies spatial consistency of its larval characteristics (PLD and settlement size) and spatial heterogeneity of post-settlement characteristics (daily growth rates). Given the extremely high mortality rate in young reef fishes (Doherty et al. 2004, McCormick and Hoey 2004, Almany and Webster 2006), the outcomes of even minor differences in growth and development rates may well have implications for the survival and reproduction of reef fishes (Jones and McCormick 2002). Therefore, while population connectivity studies in coral reef systems generally focus on parent-offspring connections and larval settlement patterns (Almany et al. 2007, Cowen and Sponaugle 2009, Abesamis 2011, Berumen et al. 2012a, Harrison et al. 2012, Abesamis et al. *in prep*), there is no guarantee that predicted or observed patterns of larval settlement equate to true patterns of survival, growth, and eventually reproduction. This study empirically demonstrates that early post-settlement growth rates of a model coral reef fish, *C. vagabundus*, can vary at scales of 1-5 km due to differences in habitat suitability, suggesting that any observed or predicted patterns in larval settlement are acted upon by post-settlement forces that have the potential to significantly alter post-settlement patterns of survival, and eventually reproduction of individuals.

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Chapter 4: Identifying and quantifying rates and degrees of decline and recovery of benthic habitats and *Chaetodon* butterflyfish[3]

4.1. Abstract

Environmental disturbances to benthic habitat on coral reefs can affect fish assemblages, with dietary specialists like coral-feeding *Chaetodon* butterflyfishes particularly sensitive to declines in hard coral cover. However, declines in density of *Chaetodon* due to declines in hard coral cover are usually documented for individual environmental disturbances, often with no, or limited, quantification of post-disturbance recovery. This study documents the effects of live hard coral loss and recovery on the *Chaetodon* assemblage for 31 years at four sites in the Philippines. This long-term "natural experiment" documents five environmental disturbance events (e.g. typhoons, coral bleaching, destructive fishing) that reduced live branching hard coral cover on average by 61% and density of corallivorous butterflyfish by 47%, with an average duration of decline of two years. This study also reports on five periods of hard coral and butterflyfish recovery, with an average 202% increase in branching hard coral cover over 11 years, and a 196% increase in density of corallivorous butterflyfish over 12 years. The density of butterflyfish was not significantly affected by marine reserve protection, and thus changes in butterflyfish density were most likely driven by change in benthic habitat. Assemblage structure of *Chaetodon* at each site was distinct, and

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[3] In review as: Russ, G. R., and S. M. Leahy (*in review*). Rates and degrees of decline and recovery of corals and *Chaetodon* butterflyfish on Philippine coral reefs. Environmental Biology of Fishes

remained remarkably consistent for 31 years, despite substantial declines and recovery of coral cover. The difference in rate of decline and rate of recovery of butterflyfish raises concerns for the persistence of this iconic coral reef taxon in the face of increasing frequency and intensity of environmental disturbances to coral reefs.

4.2. Introduction

Animal communities are strongly structured by the condition of their habitat, and are impacted by events that alter or damage their habitat (Menge and Sutherland 1987, Tilman et al. 1994). In marine systems, reef fish assemblages are altered by environmental disturbance events that cause large changes to the benthos (Halford et al. 2004, Wilson et al. 2006, Cheal et al. 2008, Emslie et al. 2008). Significant losses of live hard coral, particularly those that result in a reduction in habitat complexity, initially cause a significant reduction in the abundance of coral-associated fishes, especially among habitat and dietary specialists such as butterflyfishes (Pratchett et al. 2008a, Graham et al. 2009), and a shift towards rubble-associated taxa such as wrasses, parrotfish and goatfishes (Wilson et al. 2006, Cheal et al. 2008, Russ et al. 2015a, 2015b). The benthic community and the fish assemblage can recover to pre-disturbance states (Halford et al. 2004, Emslie et al. 2008, Graham et al. 2015), but recovery can often take years to decades (McClanahan 2000, MacNeil et al. 2015, Russ et al. 2015a).

In the Philippines, coral reefs are important sources of food security (Burke et al. 2012), but are in decline from a number of anthropogenic stressors, including increased storm intensity (Emanuel 2005, Marler 2014), thermal bleaching (McLeod et al. 2010), destructive fishing activity (McManus et al. 1997), and overexploitation (McManus 1997, Burke et al. 2012). In an attempt to mitigate the effects of these disturbances, coral reef managers in this region have implemented no-take marine reserves (NTMRs) as far back as the 1970s (Alcala and Russ 2006). NTMRs produce direct beneficial effects on coral reef fish communities by increasing the abundance of targeted species (Lester et al. 2009, Molloy et al. 2009), as well as indirect benefits by restoring ecosystem functioning (Babcock et al. 2010). In the Philippines, they also prevent the use of destructive fishing techniques (explosives, drive nets), and thus NTMRs can help maintain habitat complexity and coral cover (Fox and Caldwell 2006, Selig and Bruno 2010).

Of all groups of coral reef fish, *Chaetodon* butterflyfishes have one of the strongest and best studied associations with benthic coral reef habitat (Reese 1981, Bozec et al. 2005, Pratchett et al. 2008b). This is particularly true for obligate corallivores (Harmelin-Vivien 1989, Pratchett et al. 2006). In addition, *Chaetodon* are generally not targeted by artisanal fisheries (Lawton et al. 2013, Padin et al. 2013), making them favoured as an "indicator" taxon in some of the coral reef monitoring literature (Reese 1981, Bozec et al. 2005, Kulbicki and Bozec 2005, but see Öhman et al. 1998). However, *Chaetodon* can form a small component of trap and gillnet catches (G.R. Russ and S.M. Leahy, *pers. obs*.), and are also vulnerable to fishing techniques destructive to benthic habitat, such as drive nets and bombs (Russ and Alcala 1989, 1998).

Early studies of the relationship between coral cover and butterflyfish density and species richness began with dietary studies (Harmelin-Vivien and Bouchon-Navaro 1983, Sano 1989), and single-point-in-time field observations of associations of butterflyfish with particular coral types (Reese 1981, Öhman et al. 1998) and coral cover in general (Reese 1981, Bell et al. 1985). Field studies progressed to describing declines in butterflyfish density and species richness in response to environmental disturbances that substantially reduced coral cover (Sano et al. 1984, Halford et al.

2004, Jones et al. 2004, Pratchett et al. 2006, Cheal et al. 2008). More recent studies have described declines in butterflyfish density in response to multiple environmental disturbances (Wilson et al. 2006, 2014, Emslie et al. 2008, 2011) with an emphasis on how different types and intensity of environmental disturbances result in declines of butterflyfish to different degrees (Emslie et al. 2011). Studies that not only document declines of butterflyfish in response to reductions in coral cover, but also recoveries of both coral and butterflyfish, are far less common, simply because they require decades to document recoveries in cases of severe declines (Halford et al. 2004, Berumen and Pratchett 2006, Emslie et al. 2008),given that coral recovery can take decades (Graham et al. 2011, 2015) and many species of butterflyfish may live 5-15 years (Berumen et al. 2012b). Thus, our empirical knowledge of how rapidly butterflyfish density and species richness can decline when coral cover declines is relatively good, but our knowledge of the rates and degrees of recovery of butterflyfish populations subsequent to environmental disturbances of varying degree remains limited, simply because decadal-scale field studies of the butterflyfish-coral relationship are rare. Clearly, studies that document declines (often rapid) and subsequent recoveries (often slow) of butterflyfish density due to declines and recovery of coral cover provide a far more convincing empirical case than single-point-in-time correlations or short-term descriptions of fish decline due to coral decline.

This study investigates the effects of both declines and recovery of hard coral cover on local populations of *Chaetodon* butterflyfish in the central Philippines. Both fish and benthic communities were monitored almost annually at one NTMR site and one “control” fished site on each of two offshore Philippine islands, Apo and Sumilon (Fig. 4.1) between 1983 and 2014. Each site had its own unique management and environmental disturbance history, including destructive fishing, coral bleaching, a crown-of-thorns starfish (COTS) outbreak, and several typhoons (Russ and Alcala 1998, Russ et al. 2015a, 2015b). This study identifies major components of the benthic habitat that are key drivers of density and species richness of *Chaetodon* butterflyfish and uses them to identify potential benefits of long-term NTMR protection for this taxon. In addition, I quantify the responses of both benthos and butterflyfish to important environmental disturbance events and quantify post-disturbance recovery. Finally, I investigate the response of the *Chaetodon* assemblage to long-term NTMR protection and to change in key benthic habitat variables, and find that the assemblage structure of butterflyfish was remarkably consistent at each of the four sites over 31 years of monitoring, despite the environmental disturbances.

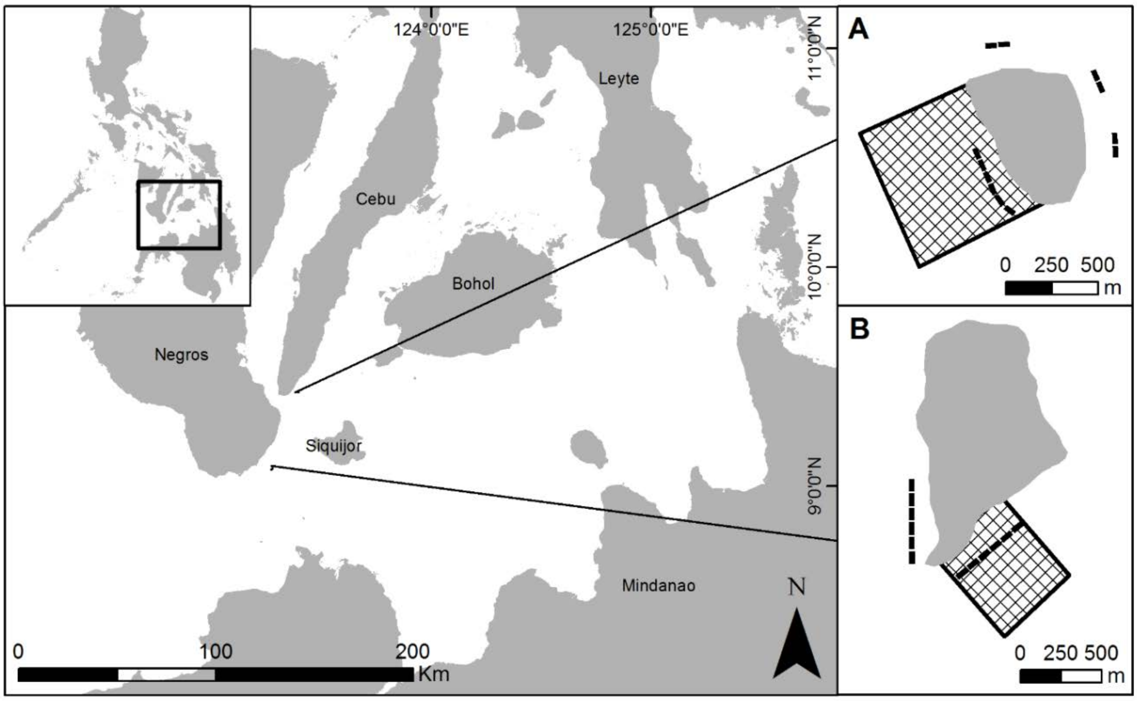


Figure 4.1. Location of the study sites in the central Philippines. Inset **A**: Sumilon island. Inset **B**: Apo island. Crosshatch indicates marine reserve area. Black rectangles indicate approximate positions of permanent 50 m by 20 m replicate transects for fish and benthic surveys.

4.3. Methods

4.3.1. Site description, reserve history, and environmental disturbance history

This study was conducted at four sites, located on two different islands in the central Philippines: Apo and Sumilon (Fig. 4.1). Butterflyfish and benthic communities were monitored almost annually for 31 years from 1983 to 2014 at one NTMR site and one "control" fished site on each island. However, both the fishing status and the sequence of environmental disturbance events at each site varied greatly (Russ et al. 2015a, 2015c).

Apo island is a small (74 ha) volcanic island located offshore of the major island of Negros (Fig. 4.1). It has a very small (15 ha) NTMR on its south-eastern side that was implemented in 1982 and has been maintained successfully since then (Alcala and Russ 2006). The use of destructive fishing techniques has been banned around the entire island since 1986 (Alcala and Russ 2006). Both the reserve and fished study sites at this island were impacted by the 1998 bleaching event (Raymundo and Maypa 2003). The west-facing reserve site was impacted by a tropical storm in early December 2010, by Severe Tropical Storm Washi in late December 2011 and by Super Typhoon Bopha in early December 2012 (Russ et al. 2015c).

Sumilon island is a very small (23 ha) coral island located offshore of the major island of Cebu (Fig. 4.1). It has a small (approx. 40 ha) NTMR on its western side that was implemented in 1974, but was subject to non-compliance, including the use of highly destructive fishing techniques such as explosives and drive nets (*muro ami*) in 1984 (Russ and Alcala 1998). Unrestricted fishing, but mostly using techniques non-destructive to the benthos, took place inside the reserve area between 1992 and 1994, and hook-and-line fishing was permitted in the reserve area from 1995 to 2001 (Alcala and Russ 2006). The reserve was affected by the 1998 coral bleaching event and a crown-of-thorns (COTS) outbreak, possibly beginning as early as 1997 (Russ et al. 2015a). The fished site was closed to all fishing between 1987 and 1991, and has been a hook-and-line fishing only site since 2009 (Russ et al. 2015c). It was impacted by Super Typhoon Bopha in December 2012 (Russ et al. 2015c).

4.3.2. Butterflyfish surveys

All benthic-feeding members of the genus *Chaetodon* were counted in underwater visual censuses (UVC) performed on SCUBA by the same observer (G.R.R.). Fish surveys were carried out in six 1,000 m^2 (50 m by 20 m) replicates on the reef slope (3-17 m in reserves, 9-17 m at fished sites) at each of the four sites. The positions of the replicates were the same every year, and surveys were performed at the same time every year (November/December) almost annually between 1983 and 2014. Juveniles (<5 cm TL) were not counted. *Chaetodon ocellicaudus* and *C. melannotus*, both predominantly soft corallivores (Cole et al. 2008), were treated as a species complex due to occasional misidentification early in the study.

4.3.3. Benthic surveys

Benthic surveys were conducted in the same reef slope areas as the fish surveys, and immediately following the fish surveys. Between 1983 and 1998, benthos was recorded using the point-intercept technique every 20 cm along a 50 m transect tape. Between 6 and 9 replicate benthic transects were conducted at each site in each year. From 1999 to 2014, the 1,000 m^2 (50 m by 20 m) of each replicate fish transect was subdivided into ten 10 x 10 m quadrats, and the cover of major benthic components within each quadrat was estimated by eye to the nearest 5%, while a structural complexity index (SCI) was estimated on a relative scale from 0 to 4. Benthic cover and SCI were then averaged across the ten quadrats to produce the percent cover and SCI for each 50 m by 20 m replicate. The benthic categories reported in this paper were consistent throughout the entire study period (1983-2014): branching and tabular corals (CBCT), massive and encrusting corals (CMCE), soft coral (SC), hard dead substratum (HDS), rubble, sand, macroalgae, and other. Sand and rubble cover were pooled into a single category (SaRu) for all analyses reported here. Values for the macroalgae and "other" benthic categories were extremely low (Russ et al. 2015b) and were therefore excluded from statistical analyses.

Table 4.1. Classification of types of benthic feeders of the *Chaetodon* assemblage recorded at the study sites.

Obligate hard corallivores	Generalists
C. baronessa	*C. adiergastos*
C. bennetti	*C. auriga*
C. lunulatus	*C. ephippium*
C. ornatissimus	*C. lineolatus*
C. trifascialis	*C. lunula*
	C. melannotus / *C. ocellicaudus* species complex
	C. mertensii
	C. punctatofasciatus
	C. rafflesi
	C. speculum
	C. ulietensis
	C. unimaculatus
	C. vagabundus

4.3.4. Data analysis

Boosted Regression Tree (BRT) models were built to identify the benthic variables (CBCT, CMCE, SC, HDS, SaRu, and SCI) that most strongly influenced *Chaetodon* species richness, as well as the density of the two most common *Chaetodon* feeding guilds: obligate hard corallivores and all other benthivores (Table 4.1), hereafter referred to as "corallivores" and "generalists", respectively. BRTs produce similar outputs to traditional regression-based techniques, but are arguably better suited to ecological studies as they accommodate non-linear relationships, identify and exclude unimportant variables, and can automatically model interactions (Elith et al. 2008). BRTs were built and fitted in RStudio (RStudio 2015) using the *dismo* package (Elith et al. 2008), which includes automated cross-validation and tree optimization protocols. Model parameters were derived to optimize biological meaningfulness and interpretability (tree complexity: 2, learning rate: 0.001, bag fraction: 0.75). A bag fraction <1 introduced stochasticity into the model in order to prevent model over-fitting.

Generalized Additive Mixed Models (GAMMs) were then used to assess the effects of NTMR protection and benthic composition on the density of corallivores, the density of generalists, and species richness of *Chaetodon* at each island (Apo and Sumilon). Fixed explanatory variables in the model were: the subset of benthic habitat variables that individually contributed >10% of the explanatory power of the BRT models above, as well as NTMR status and time (duration of protection). Replicate transects for each year were included as a random factor to account for non-independence of the transects in space and time. Separate GAMMs were built for each *Chaetodon* response variable at each island because of their strongly differing management and disturbance histories. Due to the complex management history at Sumilon island, duration of protection of Sumilon reserve did not correspond to chronological time. In addition, all surveys of Apo Reserve from 2012 onwards were extreme outliers (due to effects of the consecutive typhoons) and were excluded from this analysis. GAMMs were built and fitted in RStudio (RStudio 2015) using the *gamm4* package (Wood and Scheipl 2014), and model selection was carried out using the dredge routine from the *MuMIn* package (Barton 2015), which ranks models using the Akaike information criterion corrected for small sample sizes (AICc); low values of AICc are indicative of better model fit. The top three models for density of each *Chaetodon* guild and for species richness of *Chaetodon* at each island are presented here.

The *Chaetodon* response to both declines and increases of key benthic variables was then quantified over time periods of interest. To avoid calculations with zero values, a constant of 1 was added to all benthic habitat variables. Percent cover of each benthic component was then divided by 100, while SCI was divided by 5. Similarly, a constant of 1 was added to all fish response variables. Percent change in each variable over specified time periods was calculated as: (end value – start value)/start value *100.

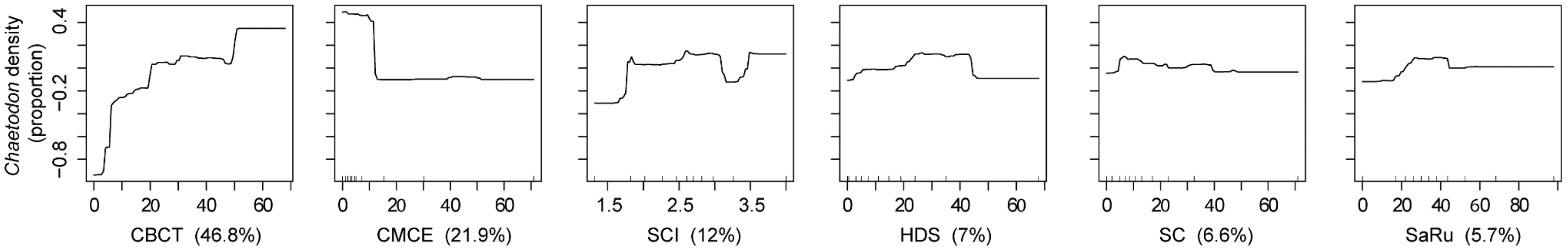
Spatial and temporal patterns in the assemblage structure of *Chaetodon* butterflyfish were explored using non-metric multidimensional scaling (nMDS) of a Bray-Curtis resemblance matrix based on square-root transformed *Chaetodon* densities. Similarly, spatial and temporal patterns in the benthos were explored using nMDS of a Euclidean distance resemblance matrix based on normalised $\log_{10}$-transformed percent cover of the major benthic components and SCI. Bray-Curtis distance is recommended for use with abundance data, while Euclidean distance is generally used for environmental data (Clarke et al. 2014). Complete-linkage CLUSTER analyses were also carried out on each resemblance matrix to illustrate statistical similarity groupings in each nMDS. The nMDS and CLUSTER analyses were conducted on mean fish density or percent benthic cover at each site within each year, i.e. all replicate surveys were averaged within each site within each year, in PRIMER v7 (Clarke et al. 2014). The association between benthic habitat variables and the assemblage structure of *Chaetodon* was then examined using permutational distance-based linear models (DistLM), implemented in the PERMANOVA+ extension of PRIMER v7 (Anderson et al. 2008). In DistLM, a resemblance matrix of a response dataset – in this case, assemblage structure of *Chaetodon* – is regressed against a set of potential explanatory variables – in this case, benthic characteristics. Explanatory variables were selected using a stepwise procedure. Only years for which both *Chaetodon* and benthic data were available were included in the nMDS, CLUSTER, and DistLM analyses.

4.4. Results

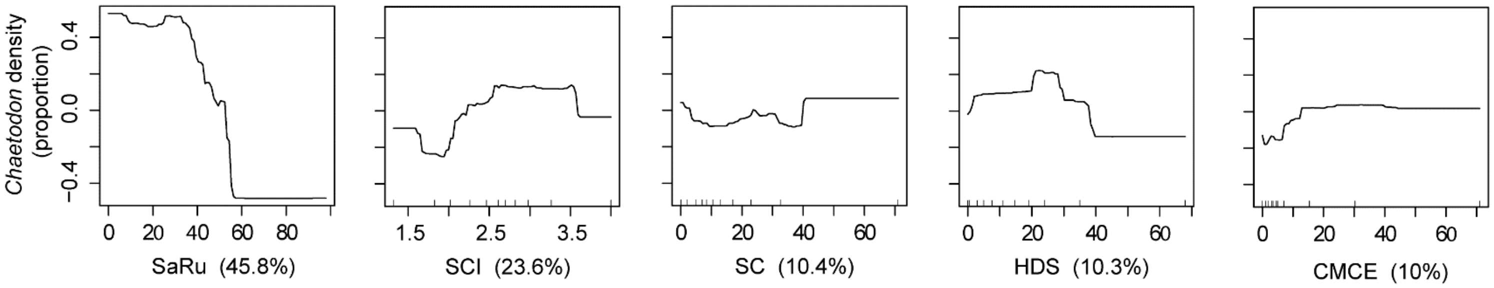
4.4.1. Association of *Chaetodon* guilds with benthos

Simplified BRTs captured 44%, 38%, and 43% of the variation in density of corallivores, density of generalists, and species richness of *Chaetodon*, respectively. Density of corallivores was strongly positively associated with cover of CBCT, had a weaker negative association with CMCE, a complex relationship with SCI, and weak complex relationships with all other benthic variables (Fig. 4.2A). CBCT, CMCE, and SCI each contributed >10% of the explanatory power of the BRT model for density of corallivores, and were therefore selected as key habitat variables in the follow-up GAMMs. Density of generalists was strongly negatively correlated with cover of SaRu, had a complex but mostly positive relationship with SCI, and weaker, complex relationships with several other habitat variables (Fig. 4.2B). Five benthic variables contributed >10% to the BRT model for density of generalists, and were selected for use in the follow-up GAMMs. Species richness of *Chaetodon* was best explained by a strong negative association with cover of SaRu (Fig. 4.2C), although positive associations with SCI and CBCT also contributed >10% to the BRT model and were therefore selected for use in the follow-up GAMMs.

A. Density of obligate hard corallivore *Chaetodon*



B. Density of generalist *Chaetodon*



C. Species richness of *Chaetodon*

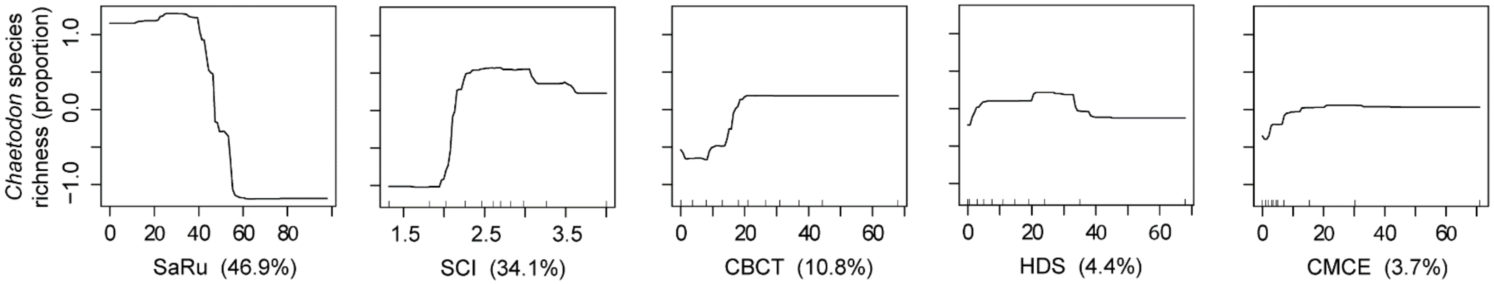


Figure 4.2. Partial plots of the relative contribution of benthic variables to Boosted Regression Tree (BRT) models for **A** density of obligate hard corallivores, **B** density of generalists, and **C** species richness of *Chaetodon*. Abbreviations: cover of sand and rubble (SaRu), cover of massive and encrusting coral (CMCE), cover of branching and tabular coral (CBCT), cover of soft coral (SC), cover of hard dead substratum (HDS), structural complexity index (SCI).

4.4.2. *Chaetodon* responses to NTMR status and benthic habitat change

An effect of NTMR protection should appear as a statistically significant NTMR Status*Time (duration of protection) interaction, together with a pattern of increase in fish density and/or species richness inside the NTMR relative to the fished site over time. Density and species richness of *Chaetodon* did not exhibit a response to NTMR protection at either of the study islands. Although GAMMs indicated a significant NTMR Status*Time interaction for corallivores at Apo island (Table 4.2), density of corallivores increased more at the fished site relative to the reserve, even when the post-typhoon years (2012-2014) were excluded (Fig. 4.3A). GAMMs also indicated a significant Status*Time interaction for density of generalists at Sumilon island (Table 4.2). This is likely a result of high variability in the density of generalists in the NTMR, including a period between 7-8 years of protection during which the density of generalists was greater outside the reserve than inside it. There was no clear increase in density of generalists in the Sumilon island NTMR over time (Fig. 4.3D).

GAMMs and examination of the temporal trends in density and species richness of *Chaetodon* indicated that the dominant explanatory effect was an inherent site-specific difference in benthos and assemblage structure of *Chaetodon* between NTMR and fished sites at each island, indicated by a significant “Status” main effect (Table 4.2). These inherent differences in benthos and *Chaetodon* assemblages between NTMR and fished sites existed before implementation of the NTMRs at each island (Fig. 4.3). Time (duration of protection) frequently recurred as an explanatory variable (Table 4.2) due to clear changes in density of *Chaetodon* over time in the study (Figs. 4.3A, 4.3B, and 4.3D). Benthic habitat variables were present in all of the top models, and, as in the BRT models, SCI was the most commonly recurring benthic variable in GAMMs explaining the density of corallivores and generalists (Table 4.2).

Table 4.2. Optimal generalized additive mixed models (GAMMs) for predicting density of obligate corallivores and generalists in the genus *Chaetodon* and species richness of *Chaetodon* at Apo and Sumilon islands. Top three models were selected based on minimization of the Akaike information criterion corrected for small sample sizes (AICc). AICc weights (*w*AICc) provide an estimate of the relative probability of each model. Adj. R^2: adjusted R^2 of each model.

Location	**Fish response**	**Model**	***df***	**AICc**	**ΔAIC**	***w*AICc**	**Adj. R^2**
Apo	Hard corallivores	Status*Time + Status + Time + SCI + CMCE	8	893.6	0.0	0.622	0.601
		Status*Time + Status + Time + SCI + CMCE + CBCT	10	894.0	0.4	0.323	0.638
		Status*Time + Status + Time + SCI	7	898.7	5.1	0.049	0.592
	Generalists	Status + SCI + HDS	5	1216.7	0.0	0.087	0.068
		Status + SCI	4	1216.9	0.2	0.079	0.064
		Status + SCI + HDS + SaRu	6	1218.3	1.6	0.038	0.065
	Species richness	CBCT + SaRu + SCI + Status	8	826.1	0.0	0.130	0.130
		CBCT + SaRu + Time	6	826.6	0.5	0.103	0.115
		CBCT + SCI + Status	7	826.7	0.6	0.097	0.133
Sumilon	Hard corallivores	Status + Time + SCI + CMCE	6	1000.1	0.0	0.292	0.260
		Status + Time + SCI	5	1000.6	0.5	0.232	0.256
		Status + Time + SCI + CMCE + CBCT	7	1001.9	1.8	0.117	0.255
	Generalists	Status*Time + Status + Time + SCI + SC + HDS + CMCE	11	993.2	0.0	0.368	0.585
		Status*Time + Status + Time + SCI + SC + HDS	10	994.1	0.9	0.235	0.578
		Status*Time + Status + Time + SCI + SC+ CMCE	9	995.8	2.6	0.098	0.581
	Species richness	Status + CBCT	5	711.1	0.0	0.186	0.639
		Status + CBCT + SaRu	6	711.6	0.5	0.146	0.637
		Status	4	712.7	1.6	0.086	0.638

Abbreviations: NTMR status (reserve or fished), time (duration of protection of reserve), cover of sand and rubble (SaRu), cover of massive and encrusting coral (CMCE), cover of branching and tabular coral (CBCT), cover of soft coral (SC), cover of hard dead substratum (HDS), structural complexity index (SCI) of the benthos.

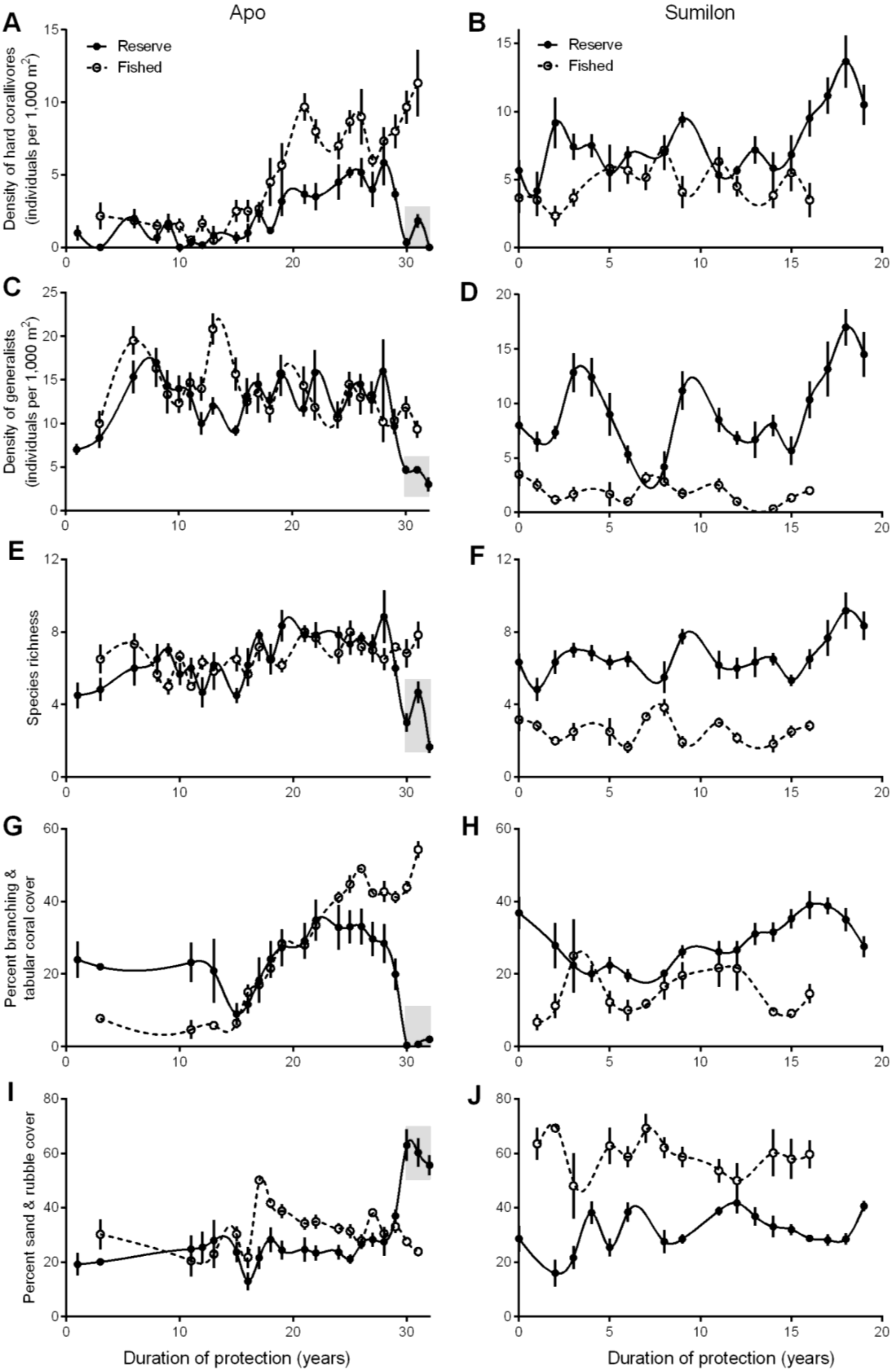


Figure 4.3. Mean (±SE) density and species richness of *Chaetodon* and cover of major benthic components plotted against duration of NTMR protection at paired reserve (black-fill circles, solid line) and fished (hollow circles, dashed line) sites at Apo and Sumilon islands. Trend lines are cubic splines. Grey box indicates outlying data points that were excluded from generalized additive mixed models (GAMMs). Note: for Sumilon island, "duration of protection" is not equivalent to chronological time.

4.4.3. Effects of environmental disturbances on coral reef benthos and *Chaetodon*

Seven specific environmental disturbance events that lead to coral decline were recorded during the 31 year study, of which five events severely impacted the cover of branching and tabular corals (CBCT) in particular (Table 4.3, Fig. 4.4). The two environmental disturbance events that affected benthic components other than CBCT were the mass bleaching event at Apo reserve in 1998, which predominantly affected CMCE (Table 4.3, Fig. 4.4A), and the mass bleaching event at the Apo fished site in 1998, which predominantly affected SC (Table 4.3, Fig. 4.4B). Both events had negligible or positive effects on the density and species richness of *Chaetodon* (Table 4.3, Fig. 4.5A and Fig. 4.5G).

In the five cases in which CBCT declined, density and species richness of *Chaetodon* declined as well, with declines often occurring in 1-2 years (Table 4.3, Fig. 4.5 and Fig. 4.6). Firstly, a local storm event at Apo reserve in 2010 caused a 29% loss of CBCT, a 33% increase in SaRu, and a 29-37% decline in density and species richness of *Chaetodon* (Fig. 4.4A and Fig. 4.5C). Secondly, back-to-back typhoons at Apo reserve in 2011 and 2012 resulted in a 93% loss of CBCT, a 27% reduction in SCI, and 68% increase in SaRu (Fig. 4.4A and Fig. 4.5E). Density and species richness of *Chaetodon* declined by 43-71% following these typhoons (Table 4.3, Fig. 4.5C and Fig. 4.5E). Thirdly, a 2-year period of use of fishing methods harmful to benthos (explosives and drive nets) at Sumilon reserve from 1983 to 1985 caused a 55% loss of CBCT and a 10% reduction in SCI (Fig. 4.4C and Fig. 4.6A). Density and species richness of *Chaetodon* dropped sharply during this period (Table 4.3, Fig. 4.6A). This was partly due to loss of benthic habitat, and partly to direct removal by non-selective fishing (Russ and Alcala 1989). Fourthly, an outbreak of COTS followed by mass coral bleaching at Sumilon reserve from 1994 to 1999 resulted in a 56% loss of CBCT, a 21%

reduction in SCI, and a coincident 45% increase in SaRu (Fig. 4.4C and Fig. 4.6C). Density of corallivores declined with a time-lag of approximately 3 years (Table 4.3, Fig. 4.4C and Fig. 4.6C). Fifthly, Super Typhoon Bopha struck the Sumilon fished site in 2012 and caused a 72% loss of CBCT and a 19% increase in SaRu (Fig. 4.4D and Fig. 4.6G). Only density of corallivores declined due to this typhoon event (Table 4.3, Fig. 4.6G).

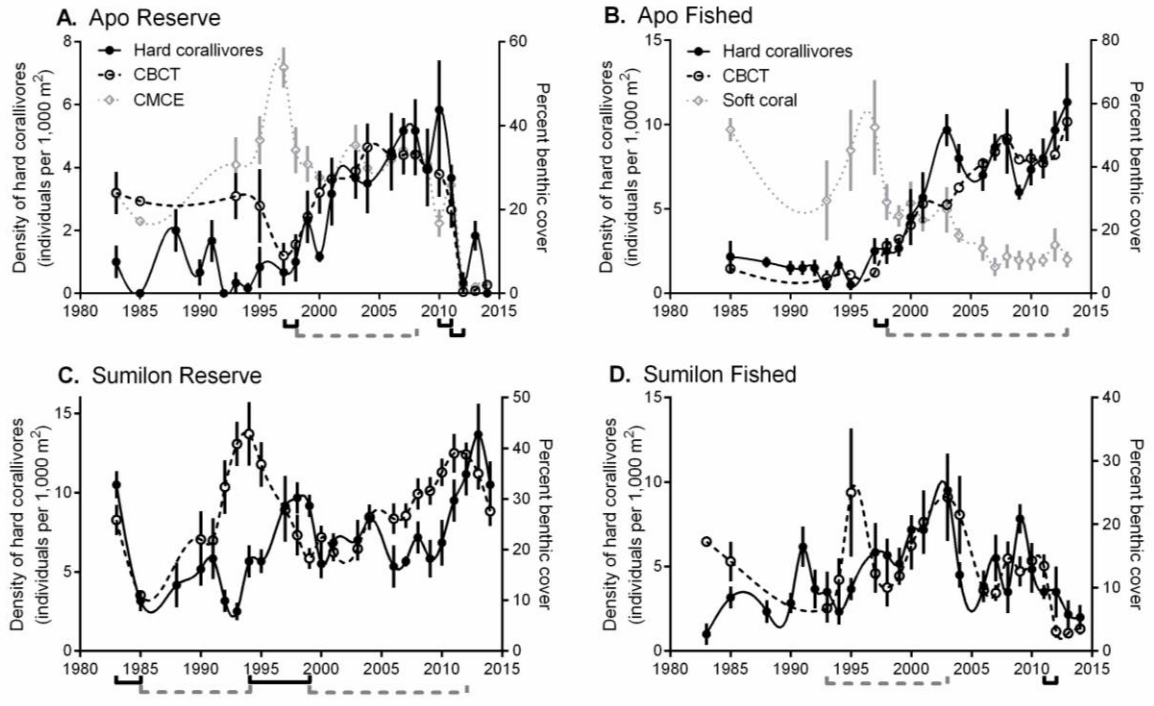


Figure 4.4. Long-term (1983-2014) mean (±SE) density of obligate hard corallivores in the genus *Chaetodon* (black-fill circles, black solid line), cover of branching and tabular coral (CBCT, hollow circles, black dashed line), and cover of important non-CBCT benthic components (hollow diamonds, grey dotted line) at NTMR and fished sites at Apo and Sumilon islands. Non-CBCT benthic components are massive and encrusting corals at Apo Reserve, and soft corals at Apo Fished. Trend lines are cubic splines. Under the x-axis, solid black brackets indicate periods of environmental disturbance to the benthos and dashed grey brackets indicate periods of recovery corresponding to the time periods presented in Table 4.3, Fig. 4.5, and Fig. 4.6. Environmental disturbances (black brackets) from left to right are: Apo Reserve - coral bleaching, local storm and back-to-back typhoons; Apo Fished - bleaching of soft corals; Sumilon Reserve - destructive fishing, COTS and coral bleaching; Sumilon Fished - super typhoon.

Figure 4.5. Percent change in benthos (black bars), density and species richness of *Chaetodon* (white bars) in response to environmental disturbances (left hand column) and periods of recovery (right hand column) at Apo Reserve and Apo Fished sites between 1983 and 2014. Different time intervals are provided for disturbance and recovery events where the *Chaetodon* response lagged behind benthic change. CBCT: cover of branching and tabular coral; CMCE: massive and encrusting coral; TS = Tropical Storm. Asterisks (*) highlight environmental disturbance events where the main benthic response was from a benthic component that was not CBCT.

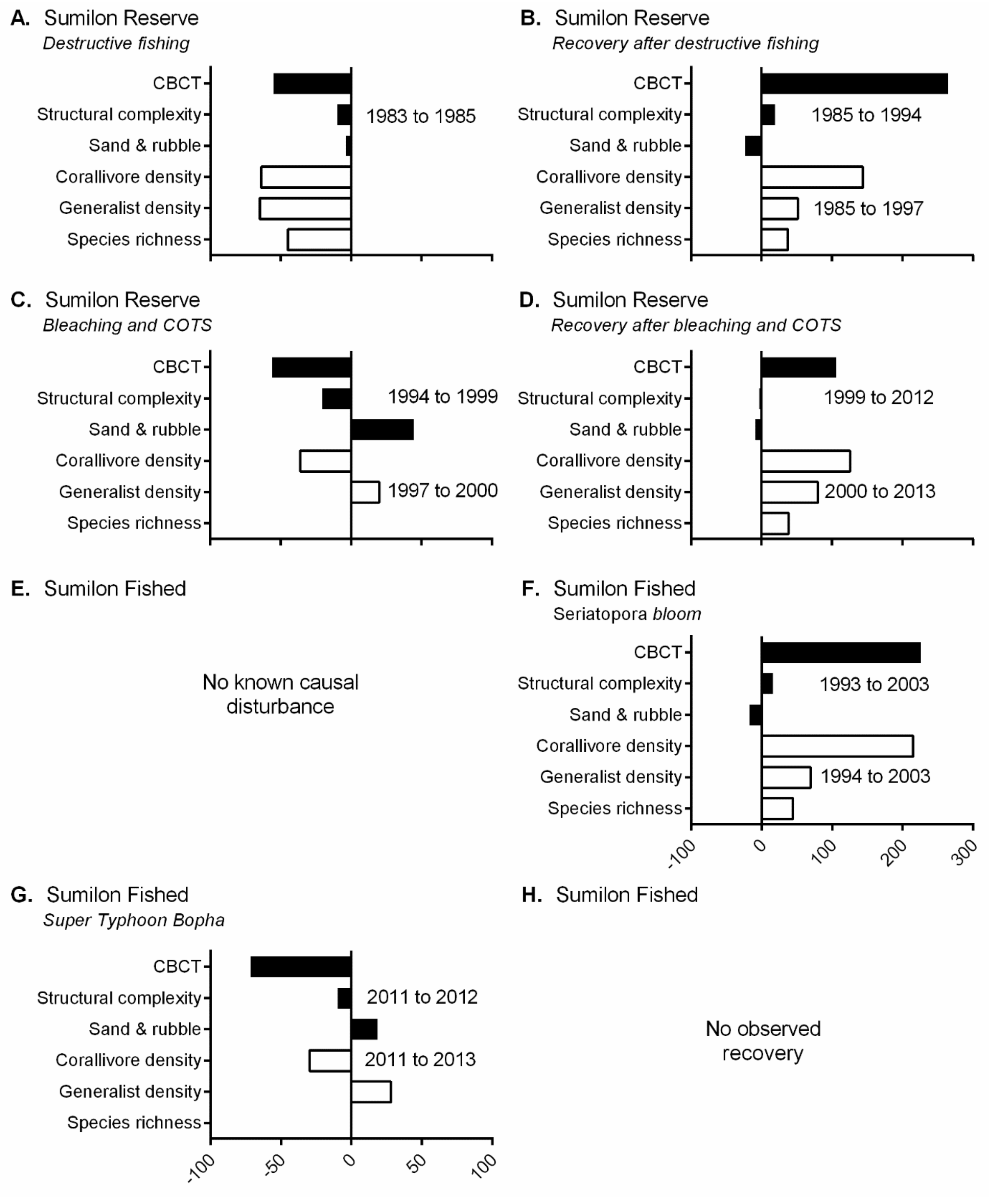


Figure 4.6. Percent change in benthos (black bars), density and species richness of *Chaetodon* (white bars) in response to environmental disturbances (left hand column) and periods of recovery (right hand column) at Sumilon Reserve and Sumilon Fished sites between 1983 and 2014. Different time intervals are provided for disturbance and recovery events where the *Chaetodon* response lagged behind benthic change. CBCT: cover of branching and tabular coral.

4.4.4. Recovery of coral reef benthos and *Chaetodon* after environmental disturbances

Four periods of coral recovery following disturbances and one period of coral growth without prior disturbance were observed during the study, and all resulted in large increases in the density of corallivores, but with recovery of corals and fish often taking over a decade (Table 4.3, Fig. 4.4). Firstly, cover of CBCT at Apo reserve increased by 169% in the decade following the 1998 bleaching of CMCE, changing the benthic cover at this site from CMCE-dominance to a roughly equal mix of CBCT and CMCE (Table 4.3, Fig. 4.4A and Fig. 4.5B). Density of corallivores increased by 242% during this decade, with more modest increases in density of generalists and species richness (Fig. 4.5b). Secondly, CBCT at the Apo fished site increased by 245% and SCI increased by 34% in the 15 years following the 1998 bleaching of SC, eventually replacing SC as the dominant benthic cover at this site (Table 4.3, Fig. 4.4B and Fig. 4.5H). Corallivore density increased by 252%, with a modest increase in species richness and a 23% decline in density of generalists over the same period (Table 4.3, Fig. 4.5H). Thirdly, the coral cover at Sumilon reserve recovered strongly after the destructive fishing. CBCT cover increased by 265% and SCI by 20% from 1985 to 1994 (Fig. 4.4C and Fig. 4.6B), while density of both feeding guilds of *Chaetodon* and species richness increased substantially during a slightly longer period (1985 to 1997, Table 4.3, Fig. 4.4C and Fig. 4.6B). Fourthly, CBCT cover increased by 106% from 1999 to 2012, recovering from the COTS outbreak and bleaching event at Sumilon reserve (Fig. 4.4C and Fig. 4.6D). Density of both feeding guilds of *Chaetodon*, as well as species richness, increased substantially during this time, with a 1 year temporal lag (Table 4.3, Fig. 4.4C and Fig. 4.6D). Fifthly, CBCT cover increased by 226% and SCI increased by 16% at the Sumilon fished site from 1993 to 2003 (Fig. 4.4D and Fig.

4.6F) due to an ephemeral bloom of fast-growing *Seriatopora* corals on the formerly sandy deep reef slope (G.R.R. *pers. obs.*), which were negatively impacted by the 1998 bleaching event, but recovered quickly (Fig. 4.4D). This caused a 215% increase in density of corallivores (Table 4.3, Fig. 4.4D), and more modest increases in density of generalists and species richness (Fig. 4.6F).

Table 4.3. Summary of the duration and percent change in cover of branching and tabular coral (CBCT), density of obligate corallivores in the genus *Chaetodon*, and *Chaetodon* species richness in response to major environmental disturbance and recovery events highlighted in Fig. 4.4 and illustrated in Figs 4.5 and 4.6. Italicised numbers describe changes to a benthic component other than CBCT (CMCE: massive and encrusting coral), and are not included in the calculated mean duration of and percent change. NA = not applicable.

Site	**Environmental disturbance**	**Decline**					**Recovery**				
		Duration of benthic change	**CBCT cover**	**Duration of fish change**	**Corallivore Density**	**Spp. Richness**	**Duration of benthic change**	**CBCT cover**	**Duration of fish change**	**Corallivore Density**	**Spp. Richness**
Apo Reserve	Bleaching of CMCE	*1 year (1997-1998)*	*-36% CMCE*	*1 year (1997-1998)*	*+20%*	*+30%*	10 years (1998-2008)	+169%	12 years (1998-2010)	+242%	+37%
Apo Reserve	Local Storm	1 year (2010-2011)	-29%	1 year (2010-2011)	-32%	-29%	No observed recovery		No observed recovery		
Apo Reserve	Back-to-back typhoons	1 year (2011-2012)	-93%	1 year (2011-2012)	-71%	-43%	No observed recovery		No observed recovery		
Apo Fished	Bleaching of soft coral	*1 year (1997-1998)*	*-44% SC*	*1 year (1997-1998)*	*0%*	*-11%*	15 years (1998-2013)	+245%	15 years (1998-2013)	+252%	+33%
Sumilon Reserve	Destructive fishing	2 years (1983-1985)	-55%	2 years (1983-1985)	-64%	-45%	9 years (1985-1994)	+265%	12 years (1985-1997)	+144%	+38%
Sumilon Reserve	Coral bleaching & COTS	5 years (1994-1999)	-56%	3 years (1997-2000)	-36%	0%	13 years (1999-2012)	+106%	13 years (2000-2013)	+126%	+39%
Sumilon Fished	*Seriatopora* “bloom”	NA		NA			10 years (1993-2003)	+226%	9 years (1994-2003)	+215%	+44%
Sumilon Fished	Super Typhoon	1 year (2011-2012)	-72%	2 years (2011-2013)	-30%	0%	No observed recovery		No observed recovery		
Means		**2 years**	**-61%**	**2 years**	**-47%**	**-23%**	**11 years**	**+202%**	**12 years**	**+196%**	**+38%**

4.4.5. Response of assemblage structure of *Chaetodon* to benthic change

Non-metric multidimensional scaling (nMDS) and overlaid CLUSTER analyses indicated that benthic communities were quite distinct at each of the four sites, and remained so for most of the study. There were no particular groupings in the data by island, but there was a slight difference according to NTMR status, with a higher composition of sand, rubble, and hard dead substrata at fished sites, and greater habitat complexity (SCI) and higher hard coral cover (CMCE and CBCT) at reserve sites (Fig. 4.7A). Three environmental disturbance events produced significant changes in the benthic communities. Firstly, the 1998 bleaching event at the Apo fished site caused the benthic community to shift from primarily soft coral to CBCT dominated (Fig. 4.4B and Fig. 4.7A). Secondly, the back-to-back typhoons in 2012 at Apo reserve caused a substantial change in the benthic community, from hard coral dominance with high structural complexity (SCI) to dominance by sand, rubble, and hard dead substratum, with low SCI (Fig. 4.7A). Thirdly, the 2012 typhoon effect at the Sumilon fished site caused a similar but smaller shift from low-medium coral cover to very high cover of sand and rubble (Fig. 4.7A).

Multidimensional scaling of the assemblage structure of *Chaetodon* indicated distinct assemblages at each site, with no clear island or NTMR effects, and little change in response to environmental disturbance events to the benthos, or to subsequent recoveries of the benthos (Fig. 4.7B). Assemblage structure of *Chaetodon* butterflyfish was remarkably distinct from site to site and this remained consistent throughout the study. The only exceptions to this spatial distinctness of assemblage structure occurred in the post-typhoon years (2012-2014) at Apo reserve and the Sumilon fished site (Fig. 4.7B).

Distance-based linear models (DistLM) indicated that most of the benthic habitat variables were key predictors of patterns in assemblage structure of *Chaetodon* butterflyfish (Table 4.4). Sand and rubble (SaRu) cover alone explained 14.8% of the variation in assemblage structure (Table 4.4). This may be a result of the numerical dominance of generalist *Chaetodon* in the study region (Fig. 4.3C and Fig. 4.3 D) which earlier analyses indicated were strongly negatively associated with SaRu (Fig. 4.2B and Fig. 4.2C).

Table 4.4. Summary of results of distance-based linear models (DistLM), based on Akaike information criterion corrected for small sample sizes (AICc).

Model	**AICc**	**R^2**	**Pseudo-*F***	***p* value**
SaRu, CMCE, CBCT, SC, SCI	561.61	0.400	4.456	0.001
SaRu, CMCE, CBCT, SC	563.96	0.366	5.841	0.001
SaRu, CMCE, CBCT	567.69	0.320	8.278	0.001
SaRu, CMCE	573.76	0.251	11.207	0.001
SaRu	582.49	0.148	14.444	0.002

Abbreviations: cover of sand and rubble (SaRu), cover of massive and encrusting coral (CMCE), cover of branching and tabular coral (CBCT), cover of soft coral (SC), structural complexity index (SCI).

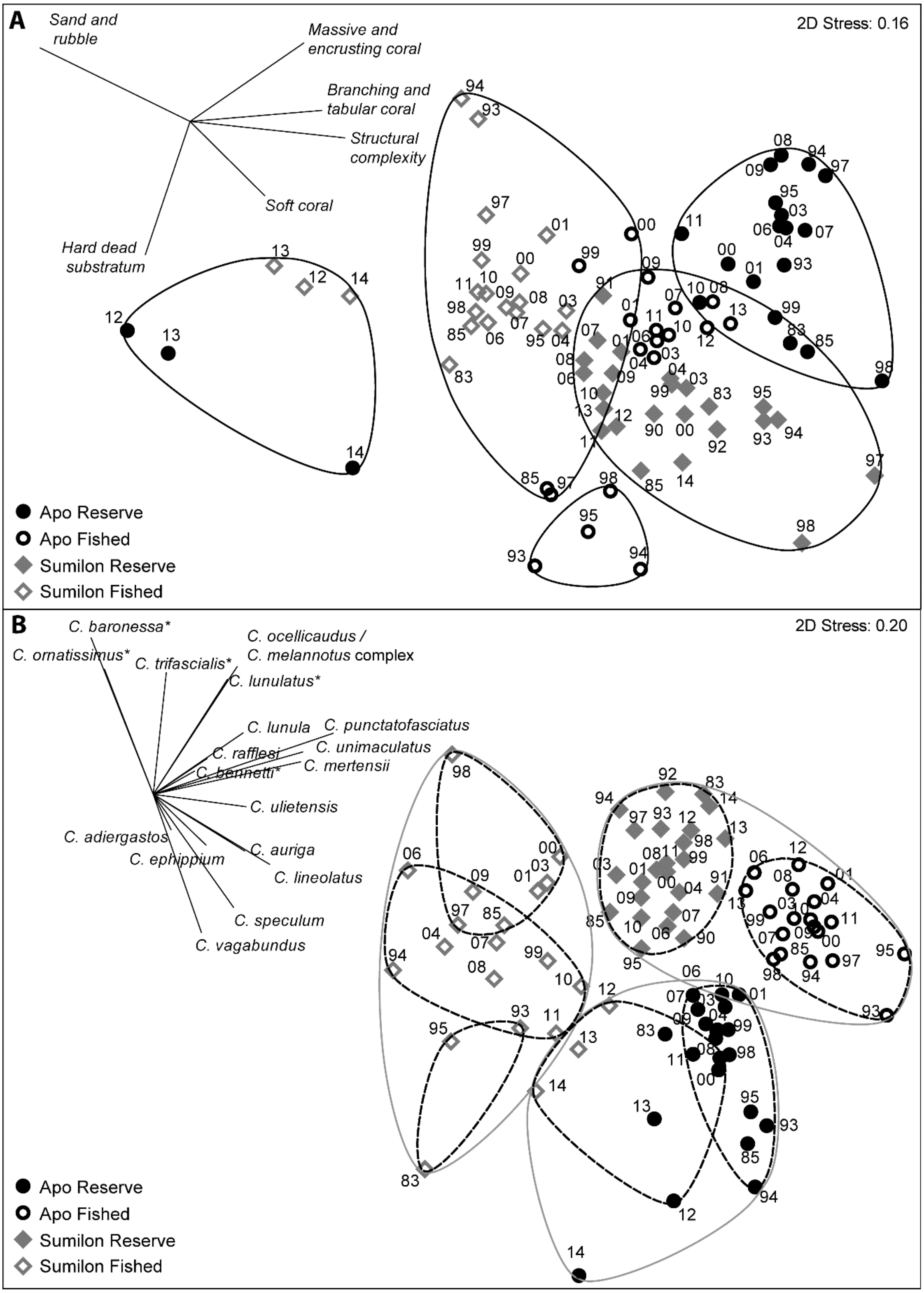


Figure 4.7. Non-metric multidimensional scaling (nMDS) of resemblance matrices for **A** benthic habitat characteristics and **B** density of the 18 species of *Chaetodon* surveyed in the study. Groupings indicate similarity clusters: 50% similarity (black solid line) in benthic composition; 30% (grey solid line) and 50% similarity (black dashed line) in *Chaetodon* assemblage structure. *Chaetodon* species with an asterisk in panel **B** are obligate hard corallivores. Vectors illustrate Pearson correlations between the variables (**A**: benthic, **B**: *Chaetodon*) and the ordination.

4.5. Discussion

This study utilised a “natural experiment” of 31 years duration to confirm the close association between cover of live branching hard corals and the density and species richness of *Chaetodon* butterflyfishes. The results of this study confirm that density of corallivorous butterflyfish and species richness of *Chaetodon* in general can decline rapidly (by 47% and 23%, respectively in just 2 years, n = 5 events, Table 4.3) when environmental disturbances cause coral cover to decline rapidly. However, unlike most other studies of the butterflyfish-coral relationship to date, this study also documents the recovery of corallivorous butterflyfish to former levels (Fig. 4.4), with an average 196% increase in density of corallivores and 38% increase in species richness of *Chaetodon* over an average 12 years of recovery (n = 5 recovery events, Table 4.3), depending on the severity of decline. In addition, these results demonstrated that neither coral cover nor butterflyfish are strongly affected by NTMR protection, even in a country like the Philippines, where coral reefs are classified as overfished (Newton et al. 2007). Apparent statistical effects of NTMR status and NTMR effects (status*time interaction, with positive effects through time) indicated that if anything, the NTMRs on Apo and Sumilon island were initially placed in areas with richer coral and *Chaetodon* communities than nearby fished sites. Thus, much of the difference in *Chaetodon* communities at NTMR versus fished sites was due to site-level differences in coral cover, while most changes in density and species richness documented in this study were most likely due to changes in benthos, not due to fishing.

Another novel outcome of this study was the demonstration that the assemblage structure of *Chaetodon* butterflyfish was not only spatially distinct among four sites (NTMR and fished locations at two separate islands), but that this distinctness persisted for 31 years, despite most of the sites being subjected to environmental disturbances that often changed the benthos, in most cases, substantially. This long-term persistence of assemblage structure is even more remarkable when one considers that sites were bombed and fished with drive nets (Sumilon reserve), subjected to a severe coral bleaching event (all four sites), affected by crown of thorns starfish (Sumilon reserve) and hit directly by typhoons (Apo reserve, Sumilon fished site). Given their strong trophic link with hard corals, the distinctness of the *Chaetodon* assemblages in space (among sites) was certainly largely driven by initial differences in benthic cover, particularly the relative cover of branching corals and sand/rubble (Fig. 4.7A). That said, while some of the environmental disturbances reported here were substantial and sustained enough to significantly alter the benthos, they were not able to transform one site-specific *Chaetodon* assemblage into that characteristic of another site (Fig. 4.7). I suggest that the reason for the distinctness of the *Chaetodon* assemblages in space and over time is a result of the distance between the two study islands (~ 30 km, Fig. 4.1). It is possible that they may not share the same supply and species composition of the larval pool (Jones et al. 2009, Buston et al. 2012). Differences in larval supply, and potentially self-recruitment at the scale of islands like Apo and Sumilon, could partly explain the unique and persistent assemblage structure of *Chaetodon* butterflyfish at sites with similar benthic habitats. Although there is some evidence from French Polynesia that *Chaetodon* assemblage structure can shift dramatically over time (Berumen and Pratchett 2006), the evidence of the persistence of assemblage structure presented here is far more convincing, based on data density (85 surveys at 4 sites, this study; 3 surveys at 1 site, Berumen and Pratchett 2006) as well as the statistical stability of the *Chaetodon* communities in each study (N = 18 species, this study; N = 7 species, Berumen and Pratchett 2006).

The change in density of corallivorous *Chaetodon* in response to two of the environmental disturbances and four of the periods of benthic recovery was lagged 1-3 years behind the change in cover of live branching coral (Fig. 4.5 and Fig. 4.6). The lagged responses to the environmental disturbances may be a result of initially sub-lethal effects of coral loss on *Chaetodon* (Pratchett et al. 2004, Wilson et al. 2006), or of dietary flexibility among some corallivorous *Chaetodon* (Berumen et al. 2005, Lawton et al. 2012) providing a buffer against initial declines in their favoured prey items. The lagged responses to benthic recovery are likely a result of the slow growth of the *Chaetodon* population due to lagged recruitment to the surveyed population (*Chaetodon* >5cm TL). This lagged recovery may be a necessary component of the recovery process, with only one period of *Chaetodon* recovery appearing to have little or no lag behind the associated period of benthic recovery (Apo fished site, 1998-2013, Fig. 4.4B and Fig. 4.5H).

This study contributes to a growing body of evidence on the importance of measures of habitat complexity (SCI) as a driver of butterflyfish abundance and diversity (Bozec et al. 2005, Graham et al. 2009), with SCI recurring in almost all of the top models describing *Chaetodon* density and species richness (Table 4.2, Fig. 4.2). However, the structural complexity index (SCI) used in this study included the complexity of the underlying reef structure (e.g caves in reef slope walls), and was therefore largely indicative of inherent site-level differences in structural complexity. Thus, the statistical significance of SCI as a driver of density and species richness of *Chaetodon* in this system was confounded with the site effect, and should be interpreted with caution. In addition, the measure of SCI used in this study was also relatively insensitive to disturbance events that altered hard coral cover, such that our estimates of the percent change in SCI as a result of environmental disturbances and periods of benthic recovery are very conservative estimates of actual change in structural complexity of the benthos.

The results of this study indicate that *Chaetodon* butterflyfishes are extremely vulnerable to environmental disturbance to their benthic habitats, and to reductions in the cover of live branching hard corals in particular, but also presents evidence that *Chaetodon* can recover from such disturbances (Table 4.3, Fig. 4.5 and Fig. 4.6). However, the large discrepancy between the time frames of decline due to disturbance and of recovery from disturbance is concerning, with important losses of *Chaetodon* density and species richness occurring on average in 2 years (range 1-3 years), but equivalent levels of population recovery taking on average 12 years (range 9-15 years), in many cases with a 1 year temporal lag between the onset of benthic recovery and the subsequent *Chaetodon* response (Table 4.3, Fig. 4.4, Fig. 4.5, and Fig. 4.6). The frequency of disturbance events is therefore of utmost importance in determining the long-term persistence of density and species richness of *Chaetodon*, with current predictions of increased frequency of high-intensity cyclones globally (Knutson et al. 2010), and in the West Pacific in particular (Emanuel 2005, Marler 2014) being cause for concern. With this in mind, management of coral reefs at the local scale should seek to eliminate or minimize all “controllable” disturbances (e.g. overfishing, destructive methods of fishing, land-based pollution) to ensure that reef assemblages have the highest chance of rapid recovery from disturbances such as storms – for example, with high water quality, abundant and diverse fish communities, and a well-connected marine reserve network for larval supply (Nyström et al. 2008, Hughes et al. 2010).

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Chapter 5: Identifying and quantifying the relative effects of habitat condition, extent, and connectedness at driving the biomass of fishery-targeted coral reef fishes[4]

5.1. Abstract

Coral reef ecosystems are under threat from multiple anthropogenic stressors, including climate change, deteriorating water quality, and overfishing. No-take marine reserves (NTMRs) are often proposed as a management tool to mitigate some of these stressors, and can help achieve both conservation and fisheries goals. There is increasing research emphasis on optimising the placement of NTMRs to maximise their benefits. This often involves *in situ* characterisation of benthic habitat suitability for a taxon or community of interest. Recently, spatial analysis tools have been used to demonstrate that spatial characteristics such as the extent, proximity, and connectedness of key reef and non-reef habitats can be important drivers of abundance of focal species. This study used a combination of *in situ* assessment of benthic habitat condition and remote sensing of habitat spatial characteristics to identify the most important drivers of the presence and biomass of six key foodfish groups both inside and outside NTMRs in the central Philippines. Foodfish groups were selected from four different families (goatfish, rabbitfish, snapper, and grouper) to represent a range of habitat uses and fishing mortalities. Results indicated that spatial variables such as the extent of coral

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[4] In preparation for submission to a peer-reviewed journal as: Leahy, S. M., G. R. Russ, and R. A. Abesamis (*in prep*). Quality over quantity: habitat condition is a stronger driver of fish biomass on coral reefs than habitat spatial extent and connectedness. Ecology

reef, the extent of seagrass beds, and connectedness of sites with mangrove stands were rarely significant drivers of fish presence or biomass, regardless of the fish group's known habitat uses. Instead, measures of benthic habitat condition or suitability for fish, such as depth and percent cover of benthic components specifically required by each fish group, were consistently better predictors of both foodfish presence and biomass. NTMR status was also a key predictor of foodfish biomass for five of six fish groups, and a key predictor of foodfish presence for three of six fish groups. The latter result suggests that these three groups are being overfished to the point of extirpation at fished sites in this region. The results of this study highlight the value of NTMRs in this system, and underscore the importance of collecting *in situ* information on benthic habitat condition to ensure conservation and fisheries objectives of NTMRs can be achieved.

5.2. Introduction

Shallow marine ecosystems around the world are under threat from multiple, interacting, direct and indirect anthropogenic stressors such as overharvesting, declining water quality, and climate change (Gray 1997, Halpern et al. 2007, 2008). Coral reef ecosystems are particularly vulnerable to degradation, given their proximity to many of the world's poorest, most resource-dependent coastal nations (Hoegh-Guldberg et al. 2009, Burke et al. 2012). Nowhere is this more true than the Coral Triangle, where coral reefs are a key component of the livelihoods of millions of people (Hoegh-Guldberg et al. 2009, Burke et al. 2012, Foale et al. 2013), but are in decline from a number of anthropogenic stressors, including increased storm intensity (Emanuel 2005, Marler 2014), thermally-induced coral bleaching (McLeod et al. 2010), destructive fishing activity, and overexploitation (Burke et al. 2012).

In an attempt to mitigate some of the effects of these disturbances, no-take marine reserves (NTMRs) have become an important management tool in the pursuit of both conservation and fisheries goals (Lubchenco et al. 2003, Lester et al. 2009, Gaines et al. 2010, Edgar et al. 2014). NTMRs produce direct beneficial effects on coral reef fish communities by increasing the abundance of targeted species (Lester et al. 2009, Molloy et al. 2009), as well as indirect benefits by preserving top-down processes on coral reefs (Mumby et al. 2006, 2007, O'Leary et al. 2012) and maintaining or restoring ecosystem functions (Babcock et al. 2010). NTMRs have also been shown to influence fisheries outside them by exporting adult fish, a process known as spillover (Russ and Alcala 1996, Abesamis and Russ 2005, Halpern et al. 2009). More recently, evidence has emerged that NTMRs also provide larval subsidy to fished areas (Jones et al. 2009, Berumen et al. 2012a, Buston et al. 2012, Harrison et al. 2012).

Optimising the placement and design of NTMRs, and marine protected areas in general, for maximum effectiveness has therefore become a research priority (e.g. Edgar et al. 2014, Green et al. 2014b). Current research focuses on the consequences of the two-phase life cycle of most coral reef fishes on the configuration of NTMRs. Firstly, evidence of the small modal larval dispersal distances of many coral reef fishes (Jones et al. 2009, Buston et al. 2012, Harrison et al. 2012, Almany et al. 2013) has fuelled a research emphasis on creating NTMR networks that are connected via larval supply, thus promoting the recovery and long-term persistence of local fish populations (Almany et al. 2009, Berumen et al. 2012a, Burgess et al. 2013, Green et al. 2014b) as well as providing recruitment subsidies to fisheries (Harrison et al. 2012). Secondly, evidence for use of non-reef habitats by reef-associated fishes at some time in their life cycles has been used to promote the inclusion of diverse, non-reef habitats in NTMRs (Ortiz and Tissot 2008, Unsworth et al. 2008, Nagelkerken et al. 2012, Honda et al.

2013, Olds et al. 2013), coincidentally supporting conservation targets for habitat representativeness in protected areas (Fernandes et al. 2005, Weeks et al. 2010, Green et al. 2014a).

The use of non-reef habitats by reef-associated fishes at some point in their life cycles is surprisingly common, and occurs as a result of a variety of life-history strategies. For example, some species settle from the plankton into shallow “nursery” habitats such as mangrove stands and seagrass beds before moving to coral reefs as subadults or adults (Ogden and Quinn 1984, Mumby 2006, Nakamura et al. 2008, Nagelkerken 2009). Other species predominantly spend their time on coral reefs, but can take advantage of tidal inundation of mangrove stands and seagrass beds to forage (Ogden and Quinn 1984, Nagelkerken et al. 2008, Unsworth et al. 2008). Some species may use mangrove stands or seagrass beds almost exclusively throughout their benthic lives, but are nonetheless categorised as coral reef associated in the literature (Lieske and Myers 2001, Allen and Erdmann 2012). Thus, the availability and proximity of key non-reef habitats, particularly mangrove stands and seagrass beds, to coral reefs can directly influence the abundance and biomass of fishes that use these non-reef habitats at particular life stages, or throughout their lives (Mumby et al. 2004, Dorenbosch et al. 2007, Olds et al. 2012a, Martin et al. 2015). This concept is sometimes referred to as “seascape connectivity” (Berkström et al. 2012, Olds et al. 2012a) or “habitat connectivity” (Fischer and Lindenmayer 2007, Lindenmayer et al. 2008). For the purpose of avoiding confusion with the term “connectivity”, which is often used in the context of larval dispersal, this study will use the term “habitat connectedness” (Bradbury 1978). The placement of NTMRs to incorporate habitat connectedness, by including non-reef habitats, or by being near non-reef habitats to provide some level of protection from exploitation, should therefore directly benefit species that use a range of shallow marine habitats, and in particular species that are targeted by fisheries (Mumby et al. 2004, Mumby 2006, Ortiz and Tissot 2012).

In this study, I explored the effect of spatial variables (coral reef area, seagrass bed area, coral reef connectedness to mangrove stands) and of several traditional metrics of benthic habitat condition (depth and percent cover of key benthic components) on the occurrence and biomass of exploited reef fishes with different patterns of reef and non-reef habitat usage in the central Philippines, with the goal of identifying which variables are most informative to the management of coral reefs. Artisanal fishing pressure on coral reef fishes in the Philippines is extremely intense (Alcala and Russ 2002, Green et al. 2004, Newton et al. 2007), and NTMRs are commonly used for conservation and fisheries management (Alcala 2001, Alcala and Russ 2006). Fish taxa assessed in this study were selected to represent a range of reef and non-reef habitat-use strategies and levels of fishing pressure. Data on the spatial extent and connectedness of major reef and non-reef habitat types at 19 study sites (9 NTMR sites, 10 fished sites) were collected using remote sensing techniques. Prior work on this topic has either solely assessed the effects of spatial habitat characteristics (e.g. Mumby 2006, Dorenbosch et al. 2007, Nagelkerken et al. 2012, Honda et al. 2013) or of measures of benthic habitat condition on reef fishes (e.g. Russ et al. 2005, Cheal et al. 2008, Emslie et al. 2008, Russ et al. 2015a). Only recently have researchers attempted to bring together both elements in order to determine the true drivers of reef fish abundance or biomass, and so far have been limited to using coarse metrics of benthic habitat condition such as “live coral cover” and “rugosity” (Olds et al. 2012a, Martin et al. 2015). This study reports that the presence and biomass of all fish groups, across all habitat needs and levels of fishing pressure, were overwhelmingly determined by NTMR protection and benthic habitat characteristics relevant to each fish group, such as percent cover of massive and encrusting corals and percent cover of rubble, rather than by measures of habitat availability (spatial extent) or connectedness. These results encourage the design of NTMRs to include high quality habitats, and the management of human activities to promote the health of coastal marine habitats.

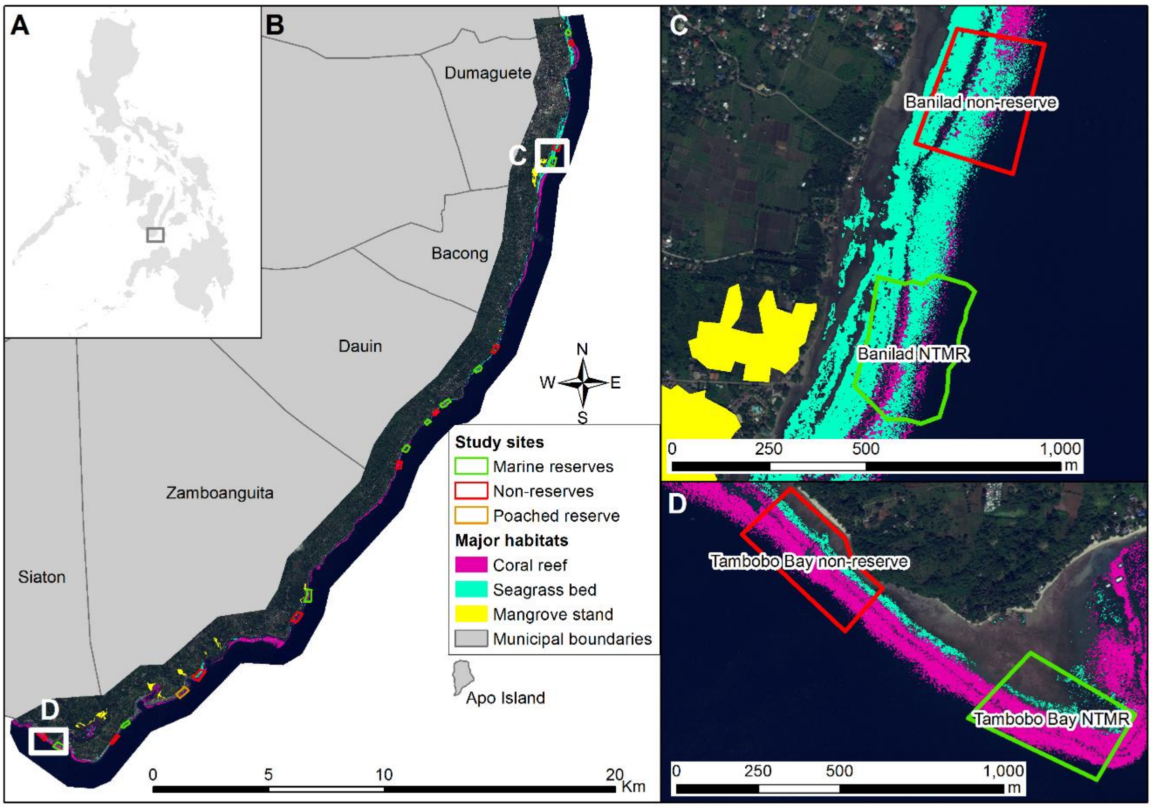

Figure 5.1. **A** Study region in the Philippines; **B** WorldView-2 Natural Colour Composite, including location of study sites, major benthic habitats (coral reef and seagrass beds) and location of insets **C** and **D**. Details of each site are available in Table 5.1. **C** and **D:** Site-scale examples of mapping of coral reefs, seagrass beds, and mangrove stands.

5.3. Methods

5.3.1. Description of field sites

This study was conducted off the southwest coast of Negros Island in the central Philippines (Fig. 5.1). The nearshore habitats in this area are characterised by intermittent, shallow, fringing coral reefs with lagoonal seagrass or coral beds and occasional *Nypa fruticans* plantations and remnants of mangrove stands (Yambao et al. 2001, DeVantier et al. 2004).

Table 5.1. Name and duration of protection of all NTMR study sites, and name of the nearby "control" non-reserve study sites with similar habitats. Sites are listed geographically, from north to south, and their exact locations are illustrated in Fig. 5.1.

Municipality	**NTMR study site**	**Years of NTMR protection** (as of 2014)	**Nearby non-reserve study site with similar habitats**
Dumaguete	Bantayan marine reserve	3	Piapi
	Banilad marine reserve	13	Banilad
Dauin	Lipayo North marine reserve (Atlantis resort)	9	Bulak
	District I marine reserve	14	Masaplod Norte[i]
	Masaplod Norte marine reserve	17	Masaplod Norte[i]
	Masaplod Sur marine reserve	15	Masaplod Sur
Zamboanguita	Basak South marine reserve	6	Guinsuan
	Lutoban marine reserve[ii]	Poached	Lutoban
Siaton	Andulay marine reserve	3	Andulay
	Tambobo Bay marine reserve	5	Tambobo Bay

[i] Masaplod Norte non-reserve site served as a control for two NTMR sites.
[ii] Lutoban marine reserve was actively poached during the study period.

A total of 19 study sites were selected along 50 km of coastline (Fig. 5.1): nine no-take marine reserve (NTMR) sites and 10 nearby non-reserve (fished) sites with comparable habitats (Table 5.1), including one NTMR that experienced regular poaching, and was therefore considered a fished site for the purpose of this study (A. Bucol and A.C. Alcala, *pers. comm.*). NTMRs ranged from 3 to 17 years of age at the time the surveys were conducted (2014). Sites were selected to represent a range of proximities to mangrove stands and a range of extents of seagrass beds in a fully crossed experimental design.

5.3.2. Field surveys of the fish and benthic assemblages

Reef-zone-stratified surveys of the benthos and key members of the foodfish assemblage were carried out at each site between 2 April and 7 May 2014. Reef zones were: inshore coral lagoon, seagrass bed, sargassum reef flat, rocky reef flat (< 3 m), reef crest (3-6 m), and reef slope (> 9 m). Not all reef zones occurred at all sites. Surveys were conducted on snorkel or SCUBA, as appropriate to depth.

The number and total body length (TL, in 5 cm increments) of a subset of species from the artisanal-fisheries-targeted families Mullidae (goatfish), Siganidae (rabbitfish), Lutjanidae (snapper), and Serranidae (grouper) were estimated using 4 m wide, 50 m long belt transects (200 m^2 per transect). Species were selected to represent a range of post-settlement life history strategies (Table 5.2). Benthic composition (branching and tabular live coral, massive and encrusting live coral, coralline or volcanic rock, rubble, sand, macroalgae, seagrass) was recorded every 0.5 m along the transect using the Point Intercept technique (English et al. 1994) on the return swim along each transect. An index of rugosity (as per Russ et al. 2005) was estimated at 10 m increments along the transect to provide a measure of benthic complexity, and an index of slope or gradient (as per Russ et al. 2005) was estimated at 10 m increments. Between 3 and 6 replicate transects were surveyed in each reef zone at each site depending on the spatial extent of the zone and its benthic heterogeneity, with generally 4 or 5 different zones present at each site.

Benthic habitat ground-truth data were collected on snorkel in the same general area as the benthic and fish surveys, between 1 April and 12 May 2014 using a handheld Garmin GPSMap 78. Point and polygon ground-truth data were converted to shapefile format using the Open Source software DNRGPS 6.1 (Minnesota Department of Natural Resources), and were randomly divided, at a ratio of approximately 67%:33%, into training and validation datasets using ArcMap 10.2 (ESRI).

Table 5.2. Study species, grouped by family and by life history strategy within each family, and the *a* and *b* parameters used to convert total length estimates to biomass estimates. Species groups are based on ecological notes in Allen and Erdmann (2012). Species marked with an asterisk (*) have been assigned to a guild based on field observations of their habitat usage in this study region, rather than on reports from the literature. All estimates of *a* and *b* are from Kulbicki et al. (2005b) unless otherwise designated.

Species group	*a*	*b*	Species group	*a*	*b*
Goatfish that only use reef habitats			**Goatfish that use non-reef habitats at some stage in their life cycle**		
Parupeneus crassilabris	0.010470[i]	3.110[i]	*Parupeneus barberinus**	0.01310	3.122
Parupeneus cyclostomus	0.01242[ii]	3.00[ii]	*Parupeneus indicus*	0.01420	3.114
Parupeneus multifasciatus	0.01140	3.211			
Parupeneus pleurostigma	0.01190[ii]	3.00[ii]			
Snapper that only use reef habitats			**Snapper that use non-reef habitats at some stage in their life cycle**		
Lutjanus biguttatus	0.01413[i]	2.980[i]	*Lutjanus argentimaculatus*	0.02800	2.844
Lutjanus bohar	0.01560	3.059	*Lutjanus ehrenbergii*	0.01072[i]	2.960[i]
Lutjanus decussatus	0.01413[i]	2.980[i]	*Lutjanus fulviflamma*	0.02050	2.960
Lutjanus fulvus	0.02110	2.974	*Lutjanus gibbus*	0.01310	3.138
Lutjanus lutjanus	0.01820	2.969	*Lutjanus kasmira*	0.00840	3.247
Lutjanus monostigma	0.02220	2.913	*Lutjanus quinquelineatus*	0.01460	3.100
Lutjanus rivulatus	0.00840	3.260			
Grouper that only use reef habitats			**Rabbitfish that use non-reef habitats at some stage in their life cycle**		
Anyperodon leucogrammicus	0.00140	3.548	*Siganus canaliculatus*	0.01200[ii]	3.011[ii]
Cephalopholis argus	0.00930	3.181	*Siganus corallinus*	0.00230	3.821
Cephalopholis boenak	0.01460	3.019	*Siganus fuscescens*	0.01370	3.068
Cephalopholis urodeta	0.02820	2.818	*Siganus guttatus*	0.01740[ii]	3.00[ii]
Cephalopholis microprion	0.01175[i]	3.050[i]	*Siganus lineatus*	0.02190	2.998
Cephalopholis miniata	0.01070	3.114	*Siganus spinus**	0.01500	3.093
Cephalopholis sexmaculata	0.01150	3.109	*Siganus vermiculatus*	0.01900[iii]	3.100[iii]
Epinephelus coeruleopunctatus	0.01800	2.938	*Siganus virgatus*	0.01040	3.272
Epinephelus fasciatus	0.01380	3.041			
Epinephelus merra	0.01500	2.966			
Epinephelus ongus	0.01900	2.928			

[i] Modelled by Froese et al. (2013)

[ii] From FishBase database (Froese and Pauly 2015)

[iii] From Gundermann et al. (1983)

5.3.3. Remotely sensed imagery collection and processing

Imagery from two adjacent multispectral satellite passes of the study region were acquired by the WorldView-2 instrument on 14 December 2014, one at 2:20:25 UTC (10:20:25 local time) with a 27.4° off-Nadir angle, and the other at 2:20:36 UTC (10:20:36 local time) with a 24.5° off-Nadir angle, coinciding with an extreme low tide (+0.15 m). Although ground-truth data predate the satellite imagery by 8 months, no significant environmental disturbance events occurred in the intervening period. The WorldView-2 images were provided by GeoImage Pty Ltd as Archived Ortho-Ready Standard Level 2A imagery in UTM coordinates (datum WGS84, zone 51 N) at 16-bit radiometric resolution. The WorldView-2 sensor has eight spectral bands in the visible and near-infrared spectrum (Table 5.3) at 1.84 m spatial resolution, and panchromatic imagery at 0.46 m resolution when viewed at nadir.

Table 5.3. Spectral range of the WorldView-2 sensors.

Band number	Band name	Wavelength range (nm)
X	Panchromatic	450 – 800
1	Coastal	400 – 450
2	Blue	450 – 510
3	Green	510 – 580
4	Yellow	585 – 625
5	Red	630 – 690
6	Red Edge	705 – 745
7	Near InfraRed 1	770 – 895
8	Near InfraRed 2	860 – 1,040

Delivered imagery was orthorectified, radiance calibrated, radiometrically balanced, and pan sharpened (University of New Brunswick algorithm) by the imagery provider (GeoImage Pty Ltd) in Geomatica (PCI Geomatics). Atmospheric conditions were homogenous across the study area, thus allowing the use of atmospheric correction using Dark Object Subtraction (Collin and Hench 2012) in ENVI 5.2 (Exelis). The two corrected and sharpened satellite passes were then mosaicked, including colour balancing of the spectral range of the smaller first pass based on the area of overlap of the two passes. Sun glint removal algorithms were not implemented because water surface condition was relatively calm at the time the imagery was captured, and because standard sun glint removal protocols (e.g. Hedley et al. 2005) can incorrectly alter the spectral profiles of areas where reflectance in the Near-Infrared (NIR) includes benthic reflectance rather than water-leaving reflectance alone, such as dry habitats and shallow submerged habitats (Hedley et al. 2005). A land mask was not implemented as the satellite image was collected at a time of extreme low tide (+0.15 m), and thus would have excluded aerially exposed intertidal habitats from the classification procedure. Instead, a land and optically deep water mask was hand-drawn in ArcMap 10.2 (ESRI) based on visual inspection of the satellite imagery and was implemented prior to spectral classification (Fig. 5.2).

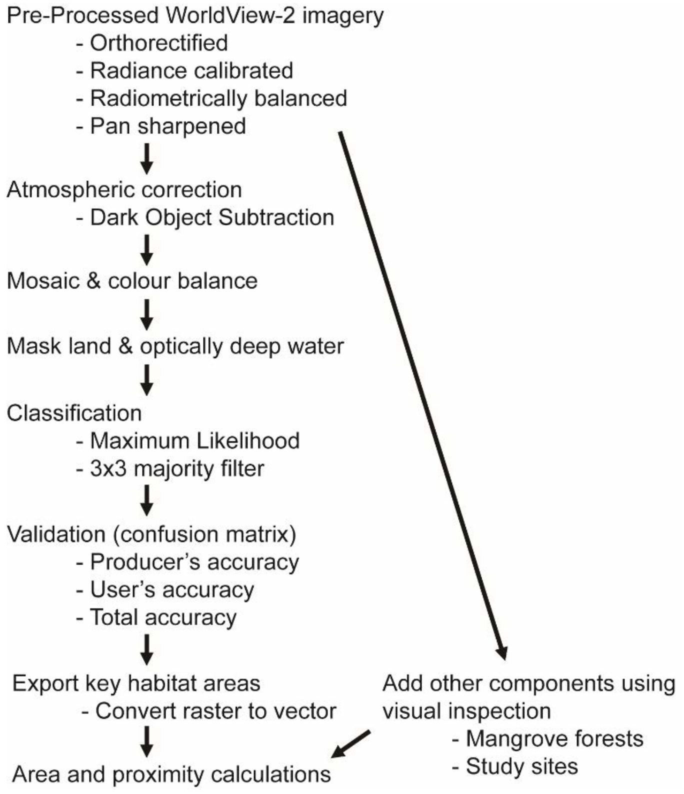

Figure 5.2. Methodological protocol followed in processing WorldView-2 imagery to produce quantitative spatial data on habitat area and connectedness in the study region.

Table 5.4. Number of training and testing pixels, producer's accuracy, and user's accuracy for the 13 benthic habitat classes used in Maximum Likelihood classification, including thresholds for depth-stratified benthic habitat classes. Depth thresholds have been adjusted to account for tide height at time of image acquisition. Asterisks (*) indicate classes exported for use in fish biomass analyses.

Class	Number of training pixels	Number of testing pixels	Producer's accuracy	User's accuracy
To be excluded				
Cloud	168,939	77,867	41.77%	100.00%
Optically deep water	5,741,969	3,361,626	94.59%	99.98%
Suspended sediment	33,699	21,263	83.78%	96.31%
Terrestrial surfaces	176,135	107,091	81.88%	90.40%
Key benthic habitats				
*Deep coral reef (>5 m)	25,660	14,606	76.32%	5.79%
*Shallow coral reef (<5 m)	26,489	13,078	83.74%	92.85%
*Deep seagrass (>5 m)	17,128	9,092	95.60%	68.97%
*Shallow seagrass (<5 m)	11,545	6,336	77.05%	83.61%
Deep sand (>5 m)	885,628	569,587	61.84%	81.86%
Shallow sand (<5 m)	22,618	12,432	89.64%	87.94%
Coral rubble	28,260	17,965	97.38%	68.72%
Algal reef	7,743	3,572	83.62%	73.97%
Sargassum bed	7,910	3,928	84.19%	91.71%

A total of 36 spectral indices were used to distinguish benthic habitat classes: all eight WorldView-2 spectral bands (Table 5.3), and the 28 band ratios calculated between each pair of bands. A Maximum Likelihood classification with a probability threshold of 0.0001 was used to resolve a total of 13 different habitat classes. Four classes represented spectral features to be excluded (Table 5.4); six classes represented depth-stratified versions of key benthic habitat types, and the remaining three classes represented benthic habitat types that only occurred in shallow water (Table 5.4). Using depth-stratified classes accommodates differences in the spectral signatures of the same benthic habitat at different depths (Collin et al. 2013, Reshitnyk et al. 2014). Region-of-interest (ROI) polygons for habitat classes designed to be excluded (Table 5.4) were manually drawn in ArcMap 10.2 (ESRI) based on visual inspection of the imagery and local expertise, and were also split 67%:33% into training and validation datasets. A 3x3 majority filter was applied to the classification product to reduce speckling. A confusion matrix was then constructed to calculate producer's, user's, and total accuracy for the filtered classification product, using the ground-truth data set aside as a validation dataset (Table 5.4).

Four main habitat components were extracted from the filtered classification product and converted to vector format for ease of manipulation: shallow seagrass, deep seagrass, shallow coral, and deep coral. The location of mangrove stands and of all 19 study sites were drawn in vector format in ArcMap 10.2 (ESRI) using visual inspection of the satellite imagery (e.g. visible marker buoys indicating marine reserve perimeters) and field notes (Fig. 5.1C and Fig. 5.1D). The area (in ha) of all coral and seagrass within each site was calculated in ArcMap 10.2 (ESRI). A unitless mangrove connectedness index (C_S), adapted from Lin (2008), was calculated for each site:

$$C_s = \sum_i^n \frac{Area_i}{Distance_i} \qquad \text{(Eq. 5.1.)}$$

Where n is the number of mangrove stands within 2.5 km of Site S, $Area_i$ is the area (in ha) of a given mangrove stand within 2.5 km of Site S, and $Distance_i$ is the shortest in-water distance (in km) of that mangrove stand from Site S. Connectedness indices ranged from 0 (no mangrove stands within 2.5 km of a site) to 390 (extensive mangrove stands immediately adjacent to a site). A seagrass connectedness index was not produced as some seagrass was present at all sites.

5.3.4. Data analysis

Fish species density by size class data were converted to biomass estimates using the length-weight equation formulated by Bohnsack and Harper (1988):

$$W = a * TL^b \qquad \text{(Eq. 5.2.)}$$

where W is the fish weight (in grams), TL is the midpoint of the estimated total length size class (in cm), and a and b are species-specific constants (Table 5.2). Biomass estimates for each species were pooled into biomass estimates for six species groups based on similar life histories within each family (Table 5.2) for increased statistical power. Despite this, biomass estimates for grouper that use non-reef habitats and for rabbitfish that exclusively use reef habitats were extremely zero-inflated (>90%), and were therefore excluded from further analysis (Table 5.2).

Field-collected benthic habitat variables were explored for collinearity (i.e. correlation) prior to analysis. When high levels of collinearity ($r > |0.60|$) existed between two variables, one of the variables was omitted from further analysis (Zuur et al. 2007). Where possible, only variables that were collinear with multiple others were removed. In this way, the estimated slope of each field survey was discarded due to its strong collinearity with depth, and estimated rugosity was discarded due to its strong positive collinearity with percent cover of rock and percent cover of massive and encrusting coral, and strong negative collinearity with percent cover of seagrass. In further analyses, significant statistical effects of massive and encrusting coral cover and rock cover should therefore be interpreted with caution, as they may in fact reflect a fish response to benthic rugosity or habitat complexity, rather than to the nature of the benthic substratum.

Boosted Regression Tree (BRT) models were then built to identify the subset of non-collinear field-collected benthic habitat variables (depth and percent cover of branching and tabular live coral, massive and encrusting live coral, coralline or volcanic rock, rubble, sand, macroalgae, and seagrass) that most strongly influenced the biomass of each fish group (Table 5.5). The subset of benthic habitat variables that individually contributed >10% of the explanatory power of the BRT models were used as explanatory variables in subsequent models of fish biomass. BRTs produce similar outputs to traditional regression-based techniques, but are arguably better suited to ecological studies as they accommodate non-linear relationships, identify and exclude unimportant variables, and can automatically model interactions (Elith et al. 2008). BRTs were built and fitted in RStudio (RStudio 2015) using the *dismo* package (Elith et al. 2008), which includes automated cross-validation and tree optimization protocols. Model parameters were derived to optimize biological meaningfulness and interpretability (tree complexity: 2, learning rate: 0.001, bag fraction: 0.6). A bag fraction <1 introduced stochasticity into the model in order to prevent model over-fitting. Continuous benthic variables were standardised prior to analysis to prevent numerical instabilities and to improve model convergence (Zuur et al. 2009).

Table 5.5. Percentage deviance explained by each benthic habitat variable in the Boosted Regression Tree (BRT) model of the biomass of each fish group. By convention, variables are presented in order of decreasing influence. Key benthic variables (contributing >10% to the BRT model) were used in later Generalized Additive Mixed Models (GAMMs) to explain the presence/absence and biomass of each fish group. Abbreviations: branching and tabular coral (CBCT), massive and encrusting coral (CMCE), "ns": non-significant.

	Goatfish that only use reef habitats	**Goatfish that use non-reef habitats**	**Rabbitfish that use non-reef habitats**	**Snapper that only use reef habitats**	**Snapper that use non-reef habitats**	**Grouper that only use reef habitats**
Key benthic variables	Rubble (31.0%) CMCE (21.4%) Depth (14.0%) Macroalgae (12.5%)	Depth (47.0%) Sand (20.1%) Rock (12.9%) CBCT (12.4%)	CMCE (48.4%) Sand (28.3%) Macroalgae (23.3%)	Depth (51.3%) Macroalgae (13.0%) Sand (12.1%)	Sand (67.3%) Depth (14.8%) CMCE (12.2%)	Depth (57.5%) CMCE (42.5%)
Low-contributing benthic variables	Seagrass (8.1%) Rock (7.0%) CBCT (3.4%) Sand (2.5%)	CMCE (7.5%) Rubble (ns) Macroalgae (ns) Seagrass (ns)	Rock (ns) Depth (ns) Rubble (ns) Seagrass (ns) CBCT (ns)	CMCE (9.1%) CBCT (6.6%) Rubble (4.6%) Rock (3.0%) Seagrass (0.3%)	Rubble (5.8%) Rock (ns) Macroalgae (ns) CBCT (ns) Seagrass (ns)	Macroalgae (ns) CBCT (ns) Rubble (ns) Sand (ns) Rock (ns) Seagrass (ns)

The effect of NTMR protection and key environmental variables on the biomass of each fish group was assessed using zero-adjusted Gamma-distributed generalized additive mixed models (ZAG GAMMs or hurdle GAMMs) using the *gamm4* package (Wood and Scheipl 2014) in RStudio (RStudio 2015). Study site was treated as a random factor to account for potential spatial dependency among surveys conducted at the same site (Zuur et al. 2009). Fixed explanatory variables in the model were: NTMR status, spatial extent of coral (in ha), spatial extent of seagrass (in ha), mangrove connectedness index (unitless), and the subset of influential benthic habitat variables identified by the BRTs above. Spatial extent of coral and seagrass areas were not standardised by site area in order to avoid complexity in data interpretation (e.g. percent coral cover ≠ percent of a site that is coral reef area). Preliminary analyses indicated that standardising or not standardising the spatial extent variables did not alter the outcome of the statistical analyses.

The Gamma distribution is uniquely suited to continuous data that can only be positive, such as biomass (Zuur et al. 2009). However, it cannot accommodate zero values, such that the analysis must be carried out in a two-step process: (1) the occurrence of zero and non-zero biomass values are modelled using a Bernoulli distribution, (2) the values of the non-zero biomass estimates are modelled using a Gamma distribution (Zuur et al. 2012). Additive mixed models (GAMMs) were used instead of traditional linear mixed models (GLMMs) in order to account for potential non-linearity in the relationship between explanatory and response variables (Zuur et al. 2014). Given the large number of variables assessed in this study, a more conservative significance threshold of $p < 0.01$ was used in the interpretation of the models to reduce the risk of type I error.

5.4. Results

5.4.1. Remotely-sensed imagery

Overall classification accuracy for the satellite imagery was 88.67%. Producer's accuracy, which is a measure of how many validation pixels were correctly classified, ranged from 41.77% to 97.38% across all classes. Producer's accuracy for the four classes used for later analysis of fish biomass trends (deep coral, shallow coral, deep seagrass, shallow seagrass) ranged from 76.32% to 95.60% (Table 5.4). User's accuracy, which is a measure of how many pixels classified as class *N* are likely to actually be class *N* in the real world, ranged from 5.79% to 100.00% across all classes, with almost all classes achieving >68% user's accuracy. User's accuracy for the four classes used for later analysis of fish biomass trends ranged from 5.79% to 92.85% (Table 5.4). The extremely low user's accuracy for the deep coral class is of concern, but was attributable to extensive misclassification of non-coral areas, particularly deep sand, as deep coral (errors of commission, Goodman et al. 2013) at locations far from the 19 study sites, where field data were limited or absent. Visual inspection of the distribution of the deep coral class at each the 19 study sites indicated that the classification was reliable within and near the 19 sites.

5.4.2. Fish biomass determinants

5.4.2.1. Goatfish that only use reef habitats

Boosted Regression Trees (BRTs) identified the most influential benthic habitat variables for this fish group as (1) percent rubble cover, (2) percent massive and encrusting coral cover, (3) depth, and (4) percent macroalgal cover. Several other variables significantly, but weakly, influenced the biomass of goatfish that only use reef habitats, and were omitted from further analyses (Table 5.5).

Subsequent analyses indicated that the presence of goatfish that only use reef habitats was influenced significantly by depth and cover of massive and encrusting corals, with goatfish most likely to be encountered at intermediate depths and in the presence of high cover of massive and encrusting corals (Table 5.6). None of the metrics of habitat extent or connectedness significantly influenced the presence of this fish group. The biomass of goatfish that only use reef habitats was positively and significantly influenced by NTMR protection (Fig. 5.3B), depth, and cover of massive and encrusting corals. Biomass of goatfish that only use reef habitats was greatest at intermediate levels of rubble cover, and was reduced in the presence of large extents of seagrass beds (Table 5.6).

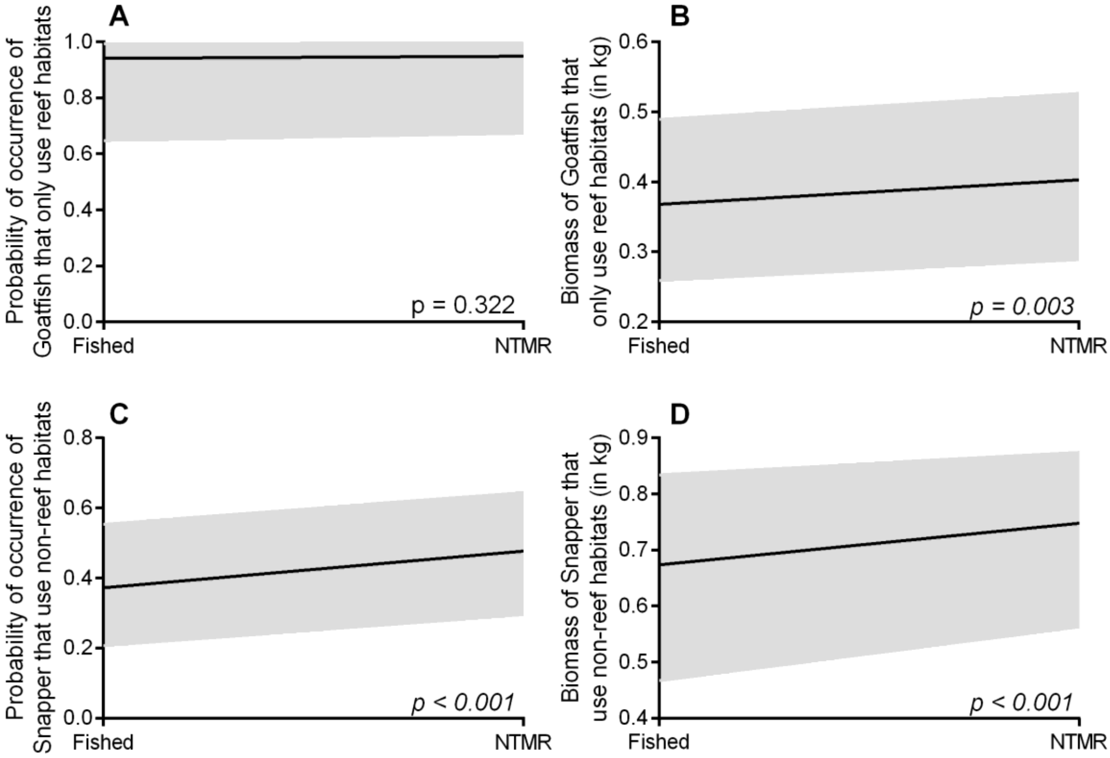

Figure 5.3. Modelled probability of occurrence (i.e. presence/absence) and biomass of goatfish that only use reef habitats, a lightly fished group (panels **A** and **B**), and of snapper that use non-reef habitats, a much more heavily fished group (panels **C** and **D**). Grey bands are 95% confidence intervals of the model. Note that y-axis scales differ among panels.

5.4.2.2. Goatfish that use non-reef habitats at some stage in their life cycle

The most influential benthic habitat variables for this fish group were depth, percent cover of sand, percent cover of rock, and percent cover of branching and tabular corals (Table 5.5). Subsequent analyses indicated that goatfish that use non-reef habitats were most likely to be present at intermediate depths, and at low levels of branching and tabular coral cover (Table 5.6). Their biomass was highest at greater depth and when rock cover was high, and was not significantly influenced by NTMR protection (Table 5.6). None of the metrics of habitat extent or connectedness significantly influenced the presence or the biomass of goatfish that use non-reef habitats.

5.4.2.3. Rabbitfish that use non-reef habitats at some stage in their life cycle

The most influential benthic habitat variables for this fish group were percent massive and encrusting coral cover, sand cover, and macroalgal cover (Table 5.5). Subsequent analyses demonstrated that the presence of rabbitfish that use non-reef habitats exhibited a positive relationship with percent macroalgal cover, and a complex sinusoidal relationship with mangrove connectedness index (Table 5.6), in which rabbitfish were most likely to be present at sites with extremely low or relatively high connectedness to mangroves, and least likely to be present at sites with intermediate or extremely high connectedness to mangroves. The biomass of rabbitfish that use non-reef habitats was positively influenced by NTMR protection and cover of massive and encrusting corals, and peaked at sites with intermediate extents of coral reef area (Table 5.6).

5.4.2.4. Snapper that only use reef habitats

The most influential benthic habitat variables for this fish group were depth, percent macroalgal cover, and percent sand cover (Table 5.5). Follow-up hurdle GAMMs indicated that snapper that only use reef habitats were most likely to be present inside NTMRs, at greater depth, and when macroalgal cover was minimal. Their biomass was greatest inside NTMRs and at greater depth (Table 5.6). None of the metrics of habitat extent or connectivity influenced the presence or the biomass of snapper that only use reef habitats significantly (Table 5.6).

5.4.2.5. Snapper that use non-reef habitats at some stage in their life cycle

The most influential benthic habitat variables for this fish group were percent sand cover, depth, and percent cover of massive and encrusting corals (Table 5.5). Subsequent analyses demonstrated that snapper that use non-reef habitats were most likely to be present inside NTMRs (Fig. 5.3C), and when massive and encrusting coral cover was highest. Their biomass was greatest inside NTMRs (Fig. 5.3D), at intermediate depths, and when sand cover was greatest (Table 5.6). None of the metrics of habitat extent or connectivity influenced the presence or the biomass of snapper that only use non-reef habitats significantly (Table 5.6).

5.4.2.6. Grouper that only use reef habitats

The most influential benthic habitat variables for this fish group were depth and percent cover of massive and encrusting corals (Table 5.5). Follow-up hurdle GAMMs indicated that grouper that only use reef habitats were most likely to be present inside NTMRs, at intermediate depths, and when cover of massive and encrusting corals was high (Table 5.6, Fig. 5.4). Their biomass was greatest inside NTMRs and at greater depths (Table 5.6). None of the metrics of habitat extent or connectivity significantly influenced the presence or the biomass of grouper that only use reef habitats (Table 5.6, Fig. 5.4).

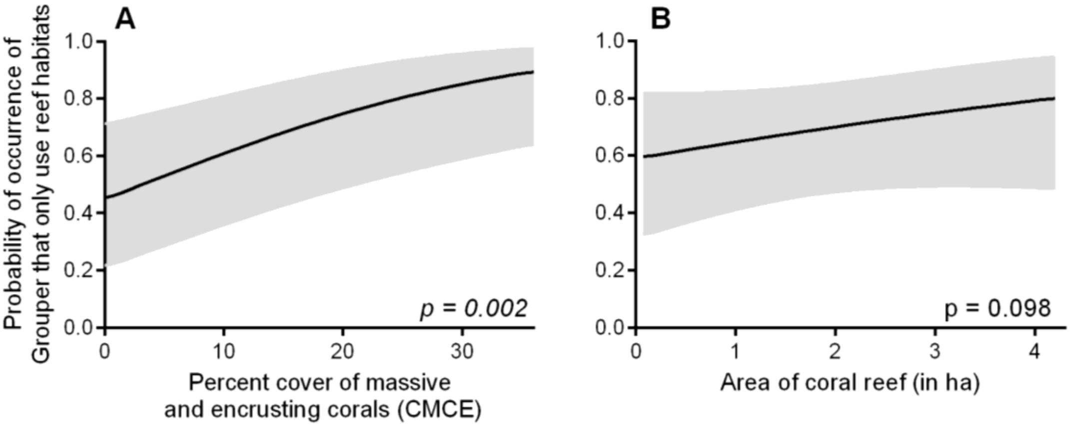

Figure 5.4. Modelled probability of occurrence (i.e. presence/absence) of grouper that only use reef habitats, as associated with **A** percent cover of massive and encrusting corals (CMCE, statistically significant at $p < 0.01$) and **B** area of coral reef (in ha, statistically non-significant at $p < 0.01$), including 95% confidence intervals (grey bands).

Table 5.6. Hurdle GAMMs evaluating the effects of no-take marine reserve (NTMR) protection, habitat extent (coral reef area, seagrass bed area), habitat connectedness with mangrove stands ("Mangrove"), and influential benthic substrate variables identified by BRT analyses. Abbreviations: massive and encrusting corals (CMCE), branching and tabular corals (CBCT). Statistically significant (*p*<0.01) effects are indicated in bold font. Asterisks (*) are used to denote levels of statistical significance (**<0.001; 0.001<*<0.01). Estimated values for each variable indicate the magnitude and direction of its relationship with the fish response. For smoothed variables, the shape of the smoothed relationship, the F-statistic, and the effective degrees of freedom (EDF, a measure of the amount of smoothing applied to the variable, where an EDF of 1 indicates a linear relationship) are reported. Some of the modelled trends presented here are illustrated in Figs. 5.3 and 5.4 to aid in their interpretation.

	Bernoulli model: presence/absence						**Gamma model: biomass**					
	Effect	**df**	**Estimate**	**SE**	**z**	***p***	**Effect**	**df**	**Estimate**	**SE**	**z**	***p***
Goatfish that only use reef habitats	Intercept	1	1.194	0.908	1.315	0.188	Intercept	1	-1.252	0.133	-9.408	**<0.001****
	NTMR	1	1.378	1.390	0.991	0.322	NTMR	1	0.563	0.189	2.973	**0.003***
	Coral area	1	0.469	0.659	0.713	0.476	Coral area	1	-0.074	0.090	-0.823	0.411
	Seagrass area	1	-0.261	0.826	-0.316	0.752	Seagrass area	1	-0.441	0.115	-3.829	**<0.001****
	Mangrove	1	-0.074	0.863	-0.086	0.932	Mangrove	1	0.064	0.115	0.554	0.580
	Rubble	1	0.576	0.288	1.999	0.046	Rubble	2.908	Intermediate peak		6.940	**<0.001****
	CMCE	2.608	Positive		27.62	**<0.001****	CMCE	1	0.241	0.066	3.638	**<0.001****
	Depth	2.486	Intermediate peak		16.24	**<0.001****	Depth	1	0.223	0.067	3.308	**0.001***
	Macroalgae	1	0.515	0.230	2.238	0.025	Macroalgae	1	-0.116	0.076	-1.522	0.130
Goatfish that use non-reef habitats	Intercept	1	0.459	0.300	1.531	0.126	Intercept	1	-1.480	0.182	-8.146	**<0.001****
	NTMR	1	-0.059	0.427	-0.138	0.890	NTMR	1	0.127	0.267	0.473	0.637
	Coral area	1	-0.208	0.222	-0.933	0.351	Coral area	1	-0.225	0.143	-1.573	0.117
	Seagrass area	1	-0.609	0.258	-2.361	0.018	Seagrass area	1	0.016	0.179	0.089	0.929
	Mangrove	1	0.298	0.275	1.079	0.281	Mangrove	1.824	Intermediate trough		1.905	0.152
	Depth	3.207	Intermediate peak		17.49	**<0.001****	Depth	1	0.510	0.082	6.161	**<0.001****
	Sand	1	-0.100	0.180	-0.556	0.578	Sand	1	0.038	0.079	0.485	0.628
	Rock	1	0.134	0.148	0.906	0.365	Rock	1	0.267	0.088	3.037	**0.003***
	CBCT	2.644	Negative		12.72	**0.004***	CBCT	1	-0.122	0.168	-0.728	0.467

Table 5.6 (continued)

	Bernoulli model: presence/absence						**Gamma model: biomass**					
	Effect	**df**	**Estimate**	**SE**	**z**	***p***	**Effect**	**df**	**Estimate**	**SE**	**z**	***p***
Rabbitfish that use non-reef habitats	Intercept	1	-0.283	0.338	-0.838	0.402	Intercept	1	-1.471	0.184	-7.981	**<0.001****
	NTMR	1	0.718	0.536	1.341	0.180	NTMR	1	0.955	0.270	3.539	**<0.001****
	Coral area	1	0.009	0.286	0.030	0.976	Coral area	3.330	Intermediate peak		4.267	**0.005***
	Seagrass area	1	0.825	0.391	2.109	0.035	Seagrass area	1	0.025	0.145	0.169	0.866
	Mangrove	3.330	Complex		12.24	**0.009***	Mangrove	1	0.081	0.157	0.513	0.608
	CMCE	1	0.264	0.156	1.686	0.092	CMCE	1	0.445	0.114	3.907	**<0.001****
	Sand	1	-0.282	0.143	-1.981	0.048	Sand	1	0.303	0.124	2.443	0.016
	Macroalgae	1	0.733	0.191	3.848	**<0.001****	Macroalgae	1	-0.253	0.116	-2.185	0.030
Snapper that only use reef habitats	Intercept	1	-1.310	0.213	-6.137	**<0.001****	Intercept	1	-1.455	0.259	-5.625	**<0.001****
	NTMR	1	1.836	0.325	5.658	**<0.001****	NTMR	1	1.236	0.302	4.099	**<0.001****
	Coral area	1	0.279	0.164	1.699	0.089	Coral area	1	-0.130	0.164	-0.793	0.429
	Seagrass area	1	-0.200	0.200	-0.997	0.319	Seagrass area	1	-0.261	0.237	-1.103	0.272
	Mangrove	1	-0.451	0.177	-2.550	0.011	Mangrove	2.799	Intermediate trough		2.961	0.039
	Depth	1	0.471	0.155	3.049	**0.002***	Depth	1	0.700	0.126	5.545	**<0.001****
	Sand	1	-0.234	0.145	-1.611	0.107	Sand	1	0.103	0.127	0.813	0.418
	Macroalgae	1	-0.844	0.279	-3.027	**0.002***	Macroalgae	1	-0.303	0.308	-0.982	0.328
Snapper that use non-reef habitats	Intercept	1	-3.249	0.459	-7.085	**<0.001****	Intercept	1	-1.475	0.371	-3.975	**<0.001****
	NTMR	1	2.252	0.549	4.102	**<0.001****	NTMR	1	1.792	0.399	4.486	**<0.001****
	Coral area	1	-0.102	0.246	-0.414	0.679	Coral area	1	0.043	0.156	0.274	0.785
	Seagrass area	1	-0.272	0.376	-0.725	0.468	Seagrass area	1	-0.084	0.249	-0.338	0.737
	Mangrove	1	0.062	0.308	0.201	0.840	Mangrove	1	0.279	0.174	1.604	0.115
	Sand	1	0.325	0.166	1.955	0.051	Sand	1	0.740	0.133	5.575	**<0.001****
	Depth	1	0.210	0.171	1.226	0.220	Depth	2.664	Intermediate peak		6.593	**0.001***
	CMCE	1	0.678	0.194	3.500	**<0.001****	CMCE	1	0.427	0.160	2.671	0.010

Table 5.6 (continued)

	Bernoulli model: presence/absence						Gamma model: biomass					
	Effect	**df**	**Estimate**	**SE**	**z**	***p***	**Effect**	**df**	**Estimate**	**SE**	**z**	***p***
Grouper that only use reef habitats	Intercept	1	-0.895	0.269	-3.333	**<0.001****	Intercept	1	-1.553	0.299	-5.201	**<0.001****
	NTMR	1	1.160	0.391	2.964	**0.003***	NTMR	1	1.365	0.391	3.491	**<0.001****
	Coral area	1	0.325	0.196	1.656	0.098	Coral area	1	-0.216	0.196	-1.102	0.272
	Seagrass area	1	-0.427	0.258	-1.656	0.098	Seagrass area	1	0.022	0.289	0.078	0.938
	Mangrove	1	-0.254	0.251	-1.013	0.311	Mangrove	1	-0.257	0.250	-1.025	0.307
	Depth	2.443	Intermediate peak		36.56	**<0.001****	Depth	1	0.419	0.118	3.553	**<0.001****
	CMCE	1	0.503	0.159	3.162	**0.002***	CMCE	1.512	Intermediate peak		1.385	0.238

5.5. Discussion

This study provides the first empirical evidence that traditional metrics of coral reef habitat suitability or "quality", such as depth and percent cover of key benthic variables, are overwhelmingly better predictors of the presence and biomass of foodfish than are measures of habitat extent and connectedness. The presence and biomass of all six foodfish groups explored in this study were consistently and significantly associated with group-specific measures of habitat suitability or "quality", and often with no-take marine reserve (NTMR) protection as well. Measures of habitat extent and connectedness (coral reef area, seagrass bed area, and a mangrove connectivity index) were rarely significant drivers of the presence or biomass of the reef fish groups investigated here (Table 5.6, Fig. 5.4). These results indicate that extrapolation of fish presence and biomass estimates, whether for fisheries or conservation purposes, must be informed by *in situ* assessments of benthic habitat condition.

In addition, this work highlights the importance and the effectiveness of NTMRs in this region. NTMR protection was a significant driver of foodfish biomass for five of six fish groups presented here (Table 5.6, Fig. 5.3B, and Fig. 5.3D), which is a typical benefit of marine reserves to fishery targeted species (Lester et al. 2009, Molloy et al. 2009, Russ and Alcala 2010). Surprisingly, NTMR protection was also a significant driver of fish presence for three of the six groups presented here (Table 5.6, Fig. 5.3A, and Fig. 5.3C). The three fish groups are those often most favoured by local artisanal fishers: groupers and both groups of snapper (Russ and Alcala 2003, 2010). This indicates that fishing pressure on snappers and groupers outside NTMRs in this region is so intense (Alcala and Russ 2002) that they are often completely absent from fished areas. Local eradication of foodfish groups representing a total of 24 different species

(Table 5.2) is highly concerning, and indicates an immediate need to reduce fishing pressure on these taxa.

Implementation of further NTMR areas is one of several possible conservation and fisheries management strategies in the region (McClanahan et al. 2006, McClanahan and Cinner 2008, Cinner et al. 2009). The results of this study highlight the value of NTMR protection to most of the taxa studied here, and also elucidate the habitat characteristics necessary to promote the presence and biomass of these fish groups. Together, these outcomes serve to inform coastal resource managers on some of the most important characteristics of future NTMRs: habitat condition is more important than habitat extent. This statement has two major implications. First, that decisions on the placement of future NTMRs should include *in situ* assessment of habitat condition, and keep in mind the habitat preferences or aversions of taxa of interest (e.g. percent cover of different types of live coral, rubble, macroalgae), in addition to underlying factors such as larval connectivity (Almany et al. 2009, McCook et al. 2009). Second, that regional management strategies should include policies that promote the health of reef and reef-associated habitats. These include improving water quality, preventing destructive fishing, and managing for a changing climate (McCook 1999, McLeod et al. 2010, Pratchett et al. 2011, Brodie et al. 2012, Burke et al. 2012, Groves et al. 2012). Although the effects of habitat degradation on coral reef fishes are relatively well understood (Jones and Syms 1998, Feary et al. 2007, Wilson et al. 2008), the current study adds to the story by clarifying that the presence and biomass of several coral reef fish groups are primarily influenced by the condition or suitability of their habitats.

The overwhelming non-significance of measures of habitat extent and connectedness in the current study is in stark contrast to recent and ongoing research into the pre-eminence of habitat connectedness (a.k.a. “seascape connectivity” or "habitat connectivity") in coral reef systems (e.g. Dorenbosch et al. 2007, Unsworth et al. 2008, Berkström et al. 2012, Olds et al. 2012a, 2012b, Martin et al. 2015). It is clear from the literature that many coral reef associated fishes use both reef and non-reef habitats (e.g. seagrass, mangrove, Unsworth et al. 2007, Berkström et al. 2012, Honda et al. 2013) and that many of these species are more abundant when reef and non-reef habitats are close to each other in space (Olds et al. 2012a, 2012b, 2013, Martin et al. 2015). Much of this research is from the Indo-Pacific, and even from within the Coral Triangle (e.g. Unsworth et al. 2007, 2008, Honda et al. 2013), and so is directly comparable to this study system.

I postulate that the weak influence of measures of habitat extent and connectedness identified in the current study result from three main factors. Firstly, that extreme fishing pressure in this region, and in shallow coastal habitats in particular (Alcala and Russ 2002, Green et al. 2004, Newton et al. 2007), could be masking the effects of other drivers, such as habitat extent and connectedness. Fishing pressure in the central Philippines is far more intense than that encountered on the Great Barrier Reef, where much of the research on the effects of habitat connectedness has been carried out (Olds et al. 2012a, 2012b, Martin et al. 2015). Secondly, mangrove habitats in the Philippines have experienced extensive deforestation over the past 100 years, and are now severely fragmented and extremely reduced relative to their historical levels (Primavera 2000, Walters 2003, Green et al. 2004). They are therefore unlikely to provide the same ecological services as extensive and relatively pristine mangrove habitats that form the basis of much of the research on habitat connectedness (Olds et al. 2012a, 2012b, Martin et al. 2015). In addition, the ecological services provided by mangroves (e.g. nurseries) are likely to be even greater in regions such as the Caribbean, where mangrove stands are subtidal and therefore always accessible to coral reef fishes (e.g. Mumby et al. 2004), than in the Indo-Pacific, where mangrove stands are intertidal (Nagelkerken et al. 2008). Thirdly, the current study differs from many others in that it explored both traditional measures of benthic habitat condition and more modern estimates of habitat extent and connectedness, which is uncommon in this field. With the exception of Olds et al. (2012a) and Martin et al. (2015), studies in this field commonly assess spatial variables alone (e.g. extent, proximity), and would therefore not capture the importance of benthic habitat condition that we identified in our study. Furthermore, the selection of benthic habitat variables in the hurdle models for each fish group represented a combination of influential variables unique to that group, rather than a broad and coarse single variable such as “coral cover” or “rugosity.” It is possible that including relevant benthic habitat variables in spatially explicit models that assess the presence, biomass, or density of key fish groups would modify their outcomes, such that species-specific measures of benthic condition or suitability would generally outperform the influence of spatial metrics such as habitat extent or connectedness.

It is unlikely that the pre-eminence of measures of benthic habitat variables over spatial habitat characteristics in this study is due to the mismatch of scales between the transects on which fish abundance and benthic habitat characteristics were collected, and the satellite imagery of the habitat spatial extent and connectedness. This is because the mismatch of scales is limited, as benthic surveys were extensive, covering between 2,400 and 4,200 m^2 at each site (12 to 21 transects of 200 m^2 each), while the remotely-sensed data on habitat extent and connectedness at each site was deliberately constrained to site-level habitat assessments, with the combined coral reef and seagrass area at each site ranging from 5,000 to 49,000 m^2 (0.5 to 49 ha). Thus, benthic surveys covered on average 24% of the coral and seagrass area at each study site. I therefore consider the results of the statistical analyses to be a true and accurate indication that all six reef fish groups in the study were more strongly influenced by measures of benthic habitat condition and suitability than by measures of habitat spatial extent and connectedness.

The significance of key benthic habitat variables in the hurdle models for each fish group was consistent with the literature on the habitat preferences of each group. For example, goatfish are commonly associated with sandy, rubbly, and rocky reef areas (Allen and Erdmann 2012, Russ et al. 2015a). Macroalgae is an important food source for rabbitfish that use non-reef habitats (Table 5.2, Table 5.6) (Allen and Erdmann 2012), while many snapper forage near sandy substrata (Table 5.2, Table 5.6) (Hiatt and Strasburg 1960). Given that cover of massive and encrusting corals was extremely collinear with rugosity (thus rugosity was omitted from analyses), the regular significance of massive and encrusting coral cover in the hurdle models (Table 5.6) should be interpreted with caution, as the fish groups may be responding to the coral itself, or to the habitat complexity produced by the coral. Benthic rugosity or habitat complexity are well-established major drivers of fish assemblages and abundance (Graham and Nash 2013, Emslie et al. 2014). Thus, the generally positive effect of massive and encrusting coral cover on non-reef snapper and reef grouper (Table 5.6) may in fact be a proxy for the more complex, rugose environment these predators prefer (Gratwicke and Speight 2005, Emslie et al. 2014). The same may be true of the positive effect of massive and encrusting coral cover on reef-using goatfish and non-reef using rabbitfish (Table 5.6), especially as the biomass of rabbitfish that use non-reef habitats at some point in their lives was dominated at some sites by large-bodied species such as *S. guttatus* and *S. lineatus*, which are both associated with highly rugose areas such as gullies and ledges (Allen and Erdmann 2012). Depth frequently recurred as a significant influence on fish presence and biomass (Table 5.6). This could be a reflection of the generally greater availability of coral habitat on the reef crest and slope compared to the reef flat (Done 1983), or possibly to ontogenetic movement of large individuals towards deeper reef environments. However, the significant and generally positive effect of depth may also be an indication of fishing pressure, with fishes in shallow reef areas more vulnerable to the intense human extractive activities in this region (Alcala and Russ 2002, Newton et al. 2007).

Although measures of habitat extent and connectedness were not as strong drivers of coral reef fish in this system as has been found in other studies (e.g. Mumby et al. 2004, Olds et al. 2012a, 2012b, 2013, Martin et al. 2015), they must not be dismissed out of hand, as extensive ecological data is available to validate the importance of non-reef habitats to many coral reef fish taxa (e.g. Ogden and Quinn 1984, Nagelkerken et al. 2000, Unsworth et al. 2008). Several of the fish taxa assessed in this study were selected for monitoring based on known multiple-habitat uses, such as *S. vermiculatus,* and *S. corallinus'* ontogenetic shift from seagrass beds as juveniles to coral reefs as adults (Lieske and Myers 2001, Allen and Erdmann 2012), while others are known to use non-reef habitats throughout their lives (e.g. *S. canaliculatus*, Table 5.2). In addition, significant spatial habitat effects were observed in some cases, such as the peak in biomass of rabbitfish that use non-reef habitats at intermediate levels of coral reef area, and the negative influence of large areas of seagrass on the biomass of goatfish that only use reef habitats (Table 5.6). This study's inability to detect consistent and significant effects of these non-reef habitats does not preclude their importance to coral reef fishes, and may be in part a result of the use of biomass rather than abundance as a measure of fish response, as juveniles have a much smaller biomass than adult fishes. In addition, I reiterate the concern that the long-term degradation of mangrove habitats (Primavera 2000, Walters 2003), in conjunction with the intense fishing pressure in inshore habitats in this region (Alcala and Russ 2002, Green et al. 2004, Newton et al. 2007), could make the NTMR effect dominate in this system and potentially mask or reduce the influence of habitat spatial extent and connectedness.

Overall, these results suggest that NTMR status and *in situ* measures of benthic habitat condition provide the best prediction of the presence and biomass of six different foodfish groups, and that habitat spatial extent and connectedness were rarely significant drivers in this system. I recommend that future research on this topic include similar measures of habitat suitability or condition, as relevant to their study taxa, and I encourage reef managers to appreciate the value of NTMRs in this system, and to use these results to prioritise management for reef health.

Chapter 6: General Discussion

Quantifying the habitat characteristics that determine coral reef fish abundance, species richness, growth rates, and assemblage structure is essential both to inform placement of no-take marine reserves (NTMRs), and to identify potential stressors that may require more complex management strategies. The work reported in this thesis provides this type of information for coastal resource managers in the central Philippines, using a standardised survey and sampling design that can be replicated in many other regions and for many other taxa. This series of studies elucidated both known and novel habitat associations of the iconic *Chaetodon* butterflyfish, and used these associations to provide a metric of disturbance and recovery of coral reefs through time. The work was then extended to taxa with more complex habitat associations, and of more interest to local fisheries, to determine that habitat spatial extent and connectedness are far less important in this system than are taxon-specific measures of habitat condition, such as percent cover of massive and encrusting coral, and percent cover of rubble.

6.1. Identifying and quantifying the extent to which habitat condition drives the abundance and species richness of *Chaetodon* butterflyfish

Some of the habitat associations of *Chaetodon* butterflyfish are particularly well-known, such as the strong relationship between live hard coral cover and the abundance of obligate corallivorous *Chaetodon* (Reese 1981, Harmelin-Vivien and Bouchon-Navaro 1983, Bell et al. 1985, Bozec et al. 2005, Pratchett et al. 2006). This relationship is extremely predictable, such that *Chaetodon* butterflyfish abundance has often been promoted for use as an indicator of coral reef health (Reese 1981, Bozec et al. 2005). However, the habitat associations of generalist *Chaetodon* are less well-known, even though they can sometimes dominate local *Chaetodon* assemblages both numerically (Pratchett et al. 2013, this thesis) and in terms of species richness (this thesis). In addition, most research on *Chaetodon* habitat associations fails to take into account a key trophic relationship for this taxon: that they are potential prey for a wide number of predators on coral reefs, particularly as juveniles.

The work presented in **Chapter 2** of this thesis explicitly tested the influence of a wide range of habitat characteristics on the abundance of corallivorous and generalist *Chaetodon,* and overall *Chaetodon* species richness. This research reinforced certain well-established associations between *Chaetodon* butterflyfish and their habitats, such as increased abundance of obligate corallivores with increased availability of branching and tabular live hard coral and with increasing benthic rugosity (Fig. 2.3), but also elucidated and quantified several less-known influences on *Chaetodon* abundance and diversity. One of these is that the negative effect of macroalgal cover on *Chaetodon* abundance and species richness is stronger and more directly influential than has previously been reported in the literature (Done 1992, Lecchini et al. 2013). Another key point of interest is that *Chaetodon* were not affected by the density of large predators (Table 2.4), but corallivorous *Chaetodon* were negatively influenced by the density of small predators (mesopredators), which are most likely targeting new recruits and juveniles (Holmes and McCormick 2010, Feeney et al. 2012). These results encourage the management of coral reefs to limit macroalgal growth (e.g. improved water quality and reduced fishing pressure on herbivores) and to control the abundance of mesopredators.

6.2. Identifying and quantifying the extent to which habitat condition drives spatial variation in post-settlement growth of a *Chaetodon* butterflyfish

Habitat characteristics can influence not only the presence and abundance of a species, but also its physiology and development (Tupper and Boutilier 1997, Suthers 1998). In the context of coral reef fishes, resource availability is tightly linked with growth rates and body condition (Kerrigan 1994, Suthers 1998), while exposure to predation can have variable effects on juvenile growth rates (Gagliano and McCormick 2007, Gagliano et al. 2007). Given the extremely high mortality rate in young reef fishes (Doherty et al. 2004, McCormick and Hoey 2004, Almany and Webster 2006), the outcomes of even minor differences in growth and development rates may well have implications for the survival and reproduction of reef fishes (Jones and McCormick 2002). Therefore, while population connectivity studies in coral reef systems generally focus on parent-offspring connections and larval settlement patterns (Almany et al. 2007, Cowen and Sponaugle 2009, Abesamis 2011, Berumen et al. 2012a, Harrison et al. 2012), there is no guarantee that predicted or observed patterns of larval settlement equate to true patterns of survival, growth, and eventually reproduction.

The research presented in **Chapter 3** of this thesis indicated that the growth rate of juveniles of a common generalist butterflyfish, *Chaetodon vagabundus*, varied significantly at spatial scales of just 1-5km and was associated with several key habitat characteristics. Because these differences in early post-settlement growth rates may have consequences for survival and later reproduction of individuals, it adds important detail to our understanding of population connectivity patterns beyond predicted or observed patterns of larval settlement.

Some of the variation in early post-settlement growth rates could be explained by the known habitat preferences of juvenile *C. vagabundus*, such as the high growth rates seen when rock cover is high and rugosity is low (Table 3.3), which is typical of the rocky reef flats this species recruits to (Harmelin-Vivien 1989, Pratchett et al. 2008b, Clark and Russ 2012). However, other habitat associations were unexpected, such as a strongly negative influence of macroalgal cover on the growth rates of newly-settled *C. vagabundus* (Table 3.3, Fig 3.7). The significant negative influence of macroalgal cover in this region again emphasises the importance of management to control macroalgae, such as by improving water quality and reducing fishing pressure on herbivores.

6.3. Identifying and quantifying rates and degrees of decline and recovery of benthic habitats and *Chaetodon* butterflyfish

The strong association between corallivorous *Chaetodon* butterflyfish and the live branching and tabular corals on which they feed and in which they shelter is well-established (Bell et al. 1985, Bozec et al. 2005, Pratchett et al. 2006), and recent information has added important detail regarding the strength of the relationship and other key habitat characteristics that influence *Chaetodon* abundance and species richness, such as macroalgal cover and rock cover (**Chapter 2**, this thesis). Given that coral reefs are exposed to a number of both natural and anthropogenic environmental disturbances, some of which can be extremely destructive (Wilson et al. 2006, Emslie et al. 2014), it is important to monitor both coral reef benthic habitats and their fish communities through time to quantify expectations of the rates and degrees of their declines and recoveries.

The work presented in **Chapter 4** of this thesis relied on data collected by G.R. Russ during 31 years of almost annual monitoring of coral reef benthic communities and fish assemblages at four offshore sites (two NTMRs and two fished sites) in the central Philippines. Four of the major *Chaetodon*-habitat associations identified at inshore reefs in this region in **Chapter 2** persisted throughout the 31 years of monitoring offshore reefs: a strong positive relationship between corallivorous *Chaetodon* abundance and branching and tabular live coral cover, and a generally positive relationship between habitat complexity and the abundance of corallivorous *Chaetodon,* the abundance of generalist *Chaetodon,* and overall *Chaetodon* species richness. The negative relationship between macroalgae and *Chaetodon* abundance identified in **Chapter 2** could not be investigated further in this chapter as macroalgae was not observed at any of the offshore reefs. Instead, the abundance of generalist *Chaetodon* and *Chaetodon* species richness both exhibited an equivalently strong negative association with sand and rubble cover (Fig. 4.2). The uniquely long and consistent monitoring created the opportunity to quantify the effects of several major disturbance events and recovery periods, which saw environmental disturbances reduce branching and tabular coral cover and the abundance of corallivorous *Chaetodon* on average by half in just 1-2 years, while recovery periods saw branching and tabular coral cover and abundance of corallivorous *Chaetodon* on average double in 11-12 years. The order of magnitude difference in the rate of recovery as compared to the rate of decline is an important concern for reef managers and users. Furthermore, the NTMR status of some of the study sites did not significantly affect benthic cover or *Chaetodon* abundance, species richness, or assemblage structure (Fig. 4.3 and Fig. 4.7), which serves as an important reminder that NTMR designation is not a panacea for coral reefs subjected to increasing rates and severity of environmental disturbances (Wilson et al. 2010, Graham et al. 2015).

6.4. Identifying and quantifying the relative effects of habitat condition, extent, and connectedness at driving the biomass of fishery-targeted coral reef fishes

Many so-called “coral reef fishes” use a range of reef and non-reef habitats at different periods in their lives (Unsworth et al. 2007, Krumme 2009, Nagelkerken 2009), and recent research into optimising NTMR placement has sought to incorporate this usage of multiple habitats (Mumby 2006, Olds et al. 2013). In particular, the spatial extent (i.e. area) of key habitats, and their proximity to each other (i.e. connectedness) have been identified as significant drivers of the abundance and species richness of certain coral reef fish taxa (Olds et al. 2012a, Martin et al. 2015). However, to date, only Olds et al. (2012a) and Martin et al. (2015) have explicitly tested both the effect of spatial variables such as habitat extent and proximity *and* the effect of traditional metrics of habitat suitability to their focal taxa. Furthermore, both Olds et al. (2012a) and Martin et al. (2015) were limited to generic metrics of habitat suitability such as benthic rugosity and total live coral cover.

The work presented in **Chapter 5** of this thesis combined extensive *in situ* collection of traditional habitat condition metrics, such as depth and percent cover of massive and encrusting corals, with spatially extensive, high precision, field calibrated remotely-sensed imagery that quantified the spatial extent and connectedness of major habitat types (coral reef, seagrass beds, mangrove stands), to determine which variables most strongly influenced the presence/absence and biomass of several major fishery taxa. Study taxa included both heavily and lightly targeted species groups in order to provide directly relevant information to coastal resource managers in this region. A heretofore unique combination of remote sensing, spatial analysis, *in situ* surveys of the benthic and fish assemblages, and advanced statistical modelling allowed me to determine that NTMR protection and taxon-specific measures of habitat condition (e.g. percent rubble cover for goatfish) were consistently strong predictors of species presence and biomass, while measures of habitat extent and connectedness were only occasionally significant drivers in this system (Tables 5.5). These results encourage the management of coastal resources to promote habitat health, and the placement of NTMRs in areas of high habitat quality rather than in marginal habitats in order to maximize their benefits to local fisheries.

6.5. Implications for management

The research topics explored in this thesis highlight three novel pieces of information for local coastal resource managers, in addition to providing evidence in support of six well-known management concerns. The novel information was:

1) Delivery of benthic habitat map spatial shapefiles to the Coral Triangle Atlas open-access online database, as well as to the Department of Environment and Natural Resources of Negros Oriental, Dumaguete City, Philippines.
2) Evidence that *Chaetodon* assemblages at four offshore sites were unique and distinct over the course of 31 years of disturbances and recovery, suggesting that population connectivity among these sites is low. Spatially extensive parentage analysis and hydrodynamic modelling could elucidate whether these sites are population sources or sinks, and where their larval immigrants originate from in order to inform protection measures for source areas.

3) Evidence that early post-settlement growth rates of a model coral reef fish, *C. vagabundus*, can vary at scales of 1-5 km due to differences in habitat suitability, suggesting that any patterns in larval settlement are acted upon by post-settlement forces that have the potential to significantly alter post-settlement patterns of survival, and eventually reproduction of individuals.

Results from this thesis that support existing knowledge of the management issues facing coral reefs are:

1) The importance of controlling macroalgal growth, as it has strong negative effects on the abundance, species richness, and growth rates of *Chaetodon* butterflyfishes. This should include improving water quality (McManus and Polsenberg 2004, Pandolfi et al. 2005, Brodie et al. 2012) and allowing stocks of herbivores to recover (Bellwood et al. 2004, McManus and Polsenberg 2004, Mumby et al. 2006, Hughes et al. 2007).
2) The importance of monitoring mesopredator abundance, as they are important predators of juvenile reef fishes, and significantly affect the abundance and species richness of corallivorous *Chaetodon* butterflyfishes. Mesopredator release has been observed in other systems (Baum and Worm 2009, Prugh et al. 2009), and local resource managers should be aware of this possibility, and manage for it by allowing stocks of large piscivores and top predators to recover (Baum and Worm 2009, Prugh et al. 2009) either by implementing NTMRs or using other measures to reduce fishing mortality.
3) The value of collecting and using locally-derived life history data to calibrate ecological models such as larval dispersal models, as key characteristics such as pelagic larval duration can vary strongly across a species' range (Wellington and Victor 1992, Bay et al. 2006).

4) The order-of-magnitude difference in the rate of recovery (11-12 years) versus the rate of decline (1-2 years) of coral reef benthic communities and butterflyfish assemblages means that coral reef management must operate on long-term, multi-decadal, multi-generational timescales, which is frequently beyond the scope of many funding cycles and political priorities (Russ and Alcala 2004, Christie 2005, Christie et al. 2005, Young et al. 2007, Russ and Alcala 2010).
5) The importance of conducting *in situ* assessments of fish assemblages and benthic communities, rather than extrapolating measures of fish presence and biomass over entire reef areas, which may vary strongly in their condition and suitability to the fish taxa of interest.
6) The importance of placing NTMRs in high quality, good condition locations to maximise their benefits to conservation and fisheries, rather than in marginal or degraded areas. The expansion of protected areas is often a result of the designation of remote and highly degraded areas as no-take or protected (Pressey and Tully 1994, Edgar et al. 2014, Di Minin and Toivonen 2015). These areas will clearly not produce the same fisheries or conservation benefits as NTMRs placed at high quality sites.

6.6. Future research directions and opportunities for improvement

The intersection of ecology, remote sensing, and statistical modelling represents an exciting new avenue of continued research, with the potential to produce powerful, practical information for direct use in the management of coral reef systems. For example, the use of remotely-sensed data in ecological research on coral reef systems has enormous potential to produce high-precision, high-accuracy maps of shallow-water habitats for use by coastal resource managers in managing fisheries and in achieving conservation goals (Spalding et al. 2001, Hamel and Andréfouët 2010, Goodman et al. 2013). In this thesis, classification accuracy for most habitat types was relatively high, with the notable exception of deep-water (>5 m) coral reefs, which had large levels of commission error, i.e. a large number of non-reef areas incorrectly designated as reef (Table 5.4). The classification accuracy for this class of benthos, and for all other classes, would likely improve significantly if training and validation field data could be collected in areas that were inaccessible during prior fieldwork due to inclement weather and local political ill will. In addition, classification accuracy may be further improved by the implementation of computationally intensive classification algorithms such as Support Vector Machine (Szuster et al. 2011), rather than the traditional Maximum Likelihood approach used in this thesis.

Furthermore, remotely-sensed habitat data are not limited to qualitative thematic mapping (e.g. coral reef area, seagrass bed area), and can actually be used to provide spatially-explicit, pixel-scale quantitative assessment of percent benthic cover, of the type that is traditionally generated by geolocated *in situ* surveys. A truly quantitative spatial product would provide resource managers with measures of both coral reef spatial extent *and* percent cover of live coral on the reef area (or seagrass bed spatial extent *and* percent cover of seagrass in the seagrass area). However, generating this type of quantitative product requires collection of extremely high-precision calibration data, collected via labour-intensive in-water photo transects of the benthos (Joyce et al. 2013), and is therefore not yet a financially viable alternative to *in situ* benthic habitat surveys.

In addition, continued research into the key variables determining the presence/absence and biomass of coral reef taxa of interest to fisheries or conservation presents an exciting opportunity to produce ecological models for direct use by resource managers. “Top-down” algorithms based on empirical data could allow users to specify a desired biomass of a fish taxon of interest, and would output the habitat conditions required to achieve it. Conversely, “bottom-up” algorithms based on empirical data could allow users to input the habitat characteristics of their study site, and would output the fish taxa and biomass that could theoretically be achieved under those habitat conditions.

Less technical avenues of continued research include expanding the work on early growth history of *C. vagabundus*, described in **Chapter 3**, to determine whether spatial differences in growth rates continue into adulthood, and whether these differences are actually associated with greater survivorship, and therefore reproductive potential. Extending the sampling design to collect similar information for a fishery-targeted species would also indicate whether fishing pressure itself affects growth rates of coral reef fishes at different life stages, as has been found in coral trout on the Great Barrier Reef (Russ et al. 1995). Such samples would also serve to elucidate whether the PLD of other species is reduced in the central Philippines relative to elsewhere in their range, and therefore whether NTMR network design in the region should take into account reduced dispersal distances in this region.

In addition, the surprisingly strong negative effect of macroalgal cover on the abundance of *Chaetodon, Chaetodon* species richness, and early post-settlement growth rates of *C. vagabundus* identified in **Chapter 2** and **Chapter 3** warrants further exploration. A negative relationship between macroalgae and reef fish abundance has generally been interpreted as a consequence of decreased live coral cover, without a direct cause-and-effect relationship between macroalgae and reef fish abundance (Done 1992, Mumby et al. 2006). However, the results of both chapters point to a considerable, and possibly more direct, negative algal effect on *Chaetodon* butterflyfishes, rather than simply a side effect of the loss of live coral cover. In those chapters, I hypothesise that the strong negative effect of macroalgal cover could be the result of reduced availability of coral prey (Pratchett et al. 2006), reduced availability of non-coral invertebrate prey (Stella et al. 2011), or repulsive olfactory cues for *Chaetodon* larvae (Lecchini et al. 2013). Recent work has determined that both generalist and obligate corallivorous adult *Chaetodon* are deterred by the presence of macroalgae, as a result of both visual and olfactory cues (Brooker et al. 2016). This is an exciting finding that encourages further investigation into the topic in order to better understand this important driver of coral reef fish abundance, species richness, and growth.

6.7. Concluding remarks

The research reported in this thesis has produced several outcomes that further our ecological understanding of coral reef systems in general, and of coral reefs in the central Philippines in particular, and that are directly informative to reef managers in the region. The results of each chapter consistently corroborate the literature on many fundamental points of species biology and ecology, while also providing new insights into the relationship between several coral reef fish taxa and benthic habitat characteristics. Overwhelmingly, species-specific measures of habitat condition proved to be the best predictors of the abundance, species richness, assemblage structure, and growth of several taxa of coral reef fishes. Continued investigation into the benthos-fish relationship will likely produce ever more exiting and practical ecological data to better understand and manage coral reef ecosystems.

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