

EFFECTS OF SEAWEED FARMING ON
TROPICAL SHALLOW CORAL ECOSYSTEMS

by

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Abstract

Seascapes are being transformed by human activities through a variety of spatially extensive extractive uses. This industrialization has the potential to radically alter the ecology of our oceans. Through focused ecosystem-based management of already degraded systems, it may be possible to create novel ecosystems that maximize benefits for humans, while increasing the diversity and abundance of dependent communities. In this thesis I examine seaweed farming on degraded coral reef ecosystems in order to examine 1) the relationship between seaweed farms and rabbitfish production globally, 2) the relationship between seaweed farms established on shallow coral reef ecosystems and fish assemblage composition, and 3) the diet composition of herbivorous fish in relation to the presence of seaweed farms. I found a correlation between seaweed farming and catches of rabbitfish (family Siganidae), implying farms may drive herbivorous fish catch in Southeast Asia. However, within regions, I found little evidence of increased abundance, biomass, and size of rabbitfish in areas with farms relative to those without. Therefore, the addition of farmed seaweeds was unlikely to subsidize rabbitfish diets, but replaced wild seaweeds removed by farmers. Investigation of seaweed farming activities on coral reef fish assemblages found farms negatively impacted diversity, abundance, and total biomass even in locations subject to blast fishing. These results have significant implications for the management of shallow coral ecosystems. Traditionally, areas of human use within seascapes are divided into distinct categories of use vs. wilderness. Increasingly seascapes have become patchworks of human use, and their impacts may result in different ecological functions. The designation of an area for restoration, protection, or a particular use must be based on several factors including the potential for the activity to alter ecosystem function as well as its ecological context. A novel ecosystems approach to degraded shallow coral reef ecosystems would dictate further human activities within radically altered systems account for both the current ecological function and the entire range of options for further use rather than only focusing on use and impacts solely in terms of traditional restoration.

Preface

This thesis represents my own work, some of which has been published elsewhere. Three of the chapters in this thesis have been published in peer-reviewed journals (Chapter 2) and others are being prepared for submission (Chapters 3 and 4). I am (or will be) the lead author on all published papers. I was primarily responsible for conceptualization, experimental design, collecting information (with help from volunteers), data management, data analysis, and writing in each of the manuscripts. However, my co-authors have made significant contributions and improved manuscripts substantially. I list my co-authors and outline their contributions below.

A version of Chapter 2 has been published Plos One as, “A global analysis of the relationship between farmed seaweed production and herbivorous fish catch” by E. J. Hehre and J. J. Meeuwig. Initial conceptualization and funding for this chapter was provided by Professor Jessica Meeuwig, who gave feedback on the design and implementation of surveys, and provided edits throughout the analysis and writing.

A version of Chapter 3 is under review as, “All flesh is grass: farmed seaweed in the diet of a rabbitfish and implications for fisheries” by E. James Hehre, Daniel Pauly, and J. J. Meeuwig. Initial conceptualization for this chapter was provided by Professor Jessica Meeuwig who helped conceptualize the study, and gave feedback on the design and implementation of surveys, and with Prof. Daniel Pauly provided edits throughout the analysis and writing.

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Animal Ethics

Animals were cared for in accordance with the Guide to the Care and Use of Experimental Animals (Vol. 1, 2nd ed. , 1993, and Vol. 2, 1984). All data were collected in accordance with the University of British Columbia (UBC) Policy # 91 (Research and Teaching Involving Animals) and has the approval of the UBC Committee on Animal Care (approval # A10-0158). Permissions for UVC protocols were not required per Philippine Bureau of Fisheries and Aquatic Resources (BFAR) and field studies did not involve endangered or protected species.

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Dedication

To my beautiful and patient wife Tammy and my amazing daughter Danica. Thank you for all of the sacrifices, which have allowed me to pursue this dream

vincimus per patientiam

CHAPTER 1

General Introduction

Seascapes globally are being transformed by human activities (Halpern et al. 2008) creating mosaics of spatially extensive extractive uses such as fishing among dwindling residual areas of marine wilderness (Pauly et al. 2002, McCauley et al. 2015). The ecological consequences of changes, both negative and positive, are difficult to understand or predict despite the general recognition of the importance of regional change (Spaling and Smit 1993). Marine conservation efforts have traditionally focused on native habitat or fragments, largely ignoring species distributions in human dominated areas (Ricketts et al. 2001, Ricketts and Imhoff 2003, Tscharnkte et al. 2005). However, the continuing and unprecedented transformation of landscapes globally necessitates thinking about both resource management and conservation in new ways (Lindenmayer et al. 2008).

The intensity of human activities drives a range of ecosystem changes including establishment of invasive species (Folke et al. 1996, Robinson 2008), habitat homogenization (Smart et al. 2006, White and Kerr 2007), and declines in diversity (Sala and Knowlton 2006, Hobbs et al. 2009). Human activities also have the potential to create novel systems, which are increasingly recognized by ecologists as those whose characteristics are novel in both their species combinations and in their human agency and which occur as consequences of both inadvertent or deliberate human interventions in natural ecosystems (Hobbs et al. 2006, Hobbs et al. 2009). Novel ecosystems (also referred to as “emerging”; e.g. Milton 2003) are identified where large differences are present between its physiochemical and biological characteristics and those of the original ecosystem generating essentially new anthropogenic landscapes with potentially divergent function (Doley et al. 2012). As human populations grow over time, impacts will continue to increase, insuring novel ecosystems will become more extensive over large areas of the world (Hobbs et al. 2009). Through focused ecosystem-based management of already degraded systems, it may however be possible to create novel ecosystems that maximize benefits for humans, while at the same time increase

the diversity and abundance of dependent constituent communities (Saunders et al. 2005, Hobbs et al. 2006).

Industrialization has the potential to radically alter the ecology of our oceans particularly through increased rates of defaunation which in turn can lead to imperiled food security, increased social conflict, decreased storm protection, and reduced flows of ecosystem services (McCauley et al. 2015). Much of this global industrialization occurs in shallow, near-shore ecosystems (Halpern et al. 2008, Carpenter et al. 2008, Burke and Spalding 2011). One such example of this industrialization can be observed in the global expansion of seaweed farming, which in the last 50 years has grown into a US\$ 7.4 billion dollar industry (Mathiesen 2012), with most of the expansion occurring in degraded near-shore shallow ecosystems. The potential for agriculture to create novel ecosystems within industrialized landscapes has been evaluated to some degree (Cramer et al. 2008). However, while a limited number of marine ecosystems impacted by human activities have been evaluated in the context of novel ecosystems and their resulting ecological function (e.g., kelp forests; Hobbs 2009), the implementation of marine agriculture (mariculture) in areas already impacted by human activities is yet to be explored. The focus of this thesis is to understand how farming seaweed on degraded shallow ecosystems affects ecological function in the context of the creation of a novel ecosystem.

1.1 Degraded Shallow Coral Reefs

Degraded shallow coral reefs are an example of a circumtropical marine ecosystem that has been heavily degraded by anthropogenic activities. This degradation is likely to have resulted in the creation of novel ecosystems given major changes in ecosystem function such as loss of functionally important species (McClanahan and Shafir 1990, Hughes 1994, Dulvy et al. 2004b), or fundamental changes to habitat structure (Wilson et al. 2010). Worldwide, the continued decline of coral reefs affects the millions of people in the tropics that depend on the goods and services provided by reefs (Wilson et al. 2010). Indeed, the majority of the world's coral reefs are found in developing countries with high rates of population growth (Polunin and Roberts 1996). Social inequalities also mean that many people turn to fishing as an occupation of last resort, placing significant pressures on tropical marine fisheries (Pauly

1994, Jennings and Polunin 1996, Polunin and Roberts 1996, McManus 1997), which are an important source of both revenue and protein for millions of people globally (Jennings and Polunin 1996, Allison and Ellis 2001, Badjeck et al. 2010).

As part of its 2012 Reefs at Risk initiative, the World Resources Institute classified more than 60% of the world's coral reefs as threatened from local stressors including overfishing, pollution, and coastal development (Burke and Spalding 2011). In the Coral Triangle, which includes the countries of Indonesia, Malaysia, Papua New Guinea, the Philippines, Solomon Islands, and Timor-Leste, that number is much higher with 85% of reefs listed as threatened and 45% listed as threatened at high or very high levels. When large-scale climate effects are included, such as the effects of thermal stress and bleaching, the global percentage of reefs at risk climbs to 75%, and within the Coral Triangle, it is estimated to be as high as 90% (Burke and Spalding 2011).

Coral reef degradation as the result of anthropogenic impacts from overfishing, pollution, and coastal development has been present for at least the last two centuries (Hughes 2003). However, as human populations have increased, the scale of human impacts on reefs has grown exponentially (Hughes 2003). This trend is compounded by the globalization of markets: where once reef resources were harvested for local consumption, they are now exploited to satisfy a global market. Of particular concern is the expansion of Malthusian overfishing where poor fishers, faced with declining catches, pursue wholesale resource destruction in their effort to maintain their incomes (Pauly 1988). This destruction, in many cases through the use of damaging gears and dynamite fishing, radically reduces diversity and has major effects on not only target species, but major indirect effects on other species and assemblage structure as a whole (Pauly 1988, Roberts 1995). Furthermore coral reefs can be very slow to recover from the effects of both blast and other destructive fishing practices (Fox and Caldwell 2006) and therefore the resulting homogenization of coral reef habitat can result in longterm changes to coral reef communities. By as early as 1988, more than 40 countries had reported blast fishing and 15 others had reported the use of poisons that indiscriminately kill fish and their coral habitat (Jennings and Polunin 1996). As reef fish are closely associated with reef structure (Choat and Clements 1989) and species can be highly dependent on both the biotic (Karlson and Hurd 1993, Stachowicz 2001) and physical

structure (Hewitt et al. 2005, Thrush et al. 2006) of reefs, the continued loss of reef habitat, combined with the effects of overfishing will have a severe impact on coral reef fish assemblages (Wilson et al. 2010) and food security (Ehrlich et al. 1993).

Shallow coral reef ecosystems are important biologically. They are centres for biological diversity, productivity, and provide protective barriers for coastlines. In addition, shallow coral reefs have ecological and functional linkages to other marine habitats like seagrass meadows and mangrove forests. These habitats exchange energy, nutrients, species, and physical benefits, with species within these habitats, connected through a large and complex food chain (Carpenter et al. 2008, Burke and Spalding 2011). Impacts to biodiversity can include loss of functional trophic resilience and species resilience (Folke et al. 2002), which in turn may lead to the creation of novel ecosystems (Hobbs et al. 2009).

1.2 Seaweed Farms Create Novel Ecosystems

Seaweed farming is a major transformational activity in shallow coral ecosystems. The commercial harvest of farmed seaweeds now takes place in approximately 35 countries around the world and provides a variety of products that, in 2012, had a total annual value of US\$7.5 billion (Mathiesen 2012). Although seaweed farming occurs globally from tropical to temperate waters, the vast majority of seaweed farming (98.9%, 18.9 million tonnes) is concentrated in China and Southeast Asia. In Southeast Asia, small subsistence farms (<1 ha) predominate, and their proliferation is in large part governed by both access to useable habitats and proximity to markets (Sievanen et al. 2005).

The anthropogenic impacts of seaweed farms on shallow coral reefs have significant implications for fish as the structure of fish assemblages is strongly correlated to habitat (Friedlander and Parrish 1998, McClanahan et al. 2001, Vlach et al. 2005, Sievanen et al. 2005, Pusey 1977). Introducing new activities, like seaweed farms into coral reef ecosystems may dramatically alter fish assemblages. However, the degree to which those activities affect fish will be related to the nature of both the habitat and the activities. In coral reef ecosystems that are in relatively good condition, seaweed farming may decrease coral cover (Sievanen et al. 2005). Conversely, in highly disturbed areas subject to, for instance, blast fishing, the influence of any additional human disturbance may be undetectable. Moreover it is

conceivable that in some cases new human activities may benefit disturbed habitats by reducing some of the most destructive activities, like blast and cyanide fishing, and replacing them with less destructive activities such as seaweed farming (Sievanen et al. 2005).

Seaweed farming has been identified as an alternative occupation for artisanal fishers in Southeast Asia capable of leading to a reduction in the number of people exploiting declining fisheries (Crawford 2002, Sievanen et al. 2005, Hill et al. 2011). However, there is little evidence that seaweed farming reduces fisher numbers. As an artisanal livelihood, seaweed farming is attractive because it requires relatively low entry costs, and very little equipment or technical expertise is required (Ask et al. 2003, Hill et al. 2011). Analysis of the practicality of seaweed farming focuses on the potential for return on investment and the relatively higher income it can generate compared to fishing (Hill et al. 2011, Hurtado-Ponce and Agbayani 2002, Hurtado-Ponce 2003, Samonte et al. 2007). However, the reality is that the relationship between the two activities is complicated. While some fishers may have given up fishing for seaweed farming, many have been reported as continuing to fish at the same levels in addition to engaging in seaweed farming (Sievanen et al. 2005). This may be in part because the revenue streams from fishing and seaweed farming are fundamentally different in that fishing provides a more immediate return while the profits from seaweed farming may be deferred for months between planting and harvest (Hill et al. 2011).

Secondly, women and children can tend seaweed farms while men are out fishing, placing few constraints on fishing, which is typically male-dominated (Crawford 2002; Sievanen et al. 2005). Lastly, seaweed farming has undergone boom and bust cycles in many sites due to disease and price fluctuations, causing even those that did stop fishing to revert to this activity (Hill 2012).

Previous research on seaweed farms focused on individual facets of affected ecosystems like water quality, erosion, and nutrient depletion, primarily within seagrass beds (Sievanen et al. 2005). However, little information exists on the impacts of seaweed production on shallow coral reef ecosystems (Sievanen et al. 2005). Many artisanal seaweed farms are located on shallow coral ecosystems because of access, lower investment (no requirement for a boat), and proximity to sites suitable for drying and to markets (Green et al. 2004). These farms

have the potential to place further pressure on shallow coral reef ecosystems through increased siltation, trampling, shading, and impairment of recruitment ability (Sievanen et al. 2005). However, it is possible that seaweed farms may benefit these systems. Seaweed farms add physical structure in the form of agricultural matrices onto otherwise homogenized seascapes, providing shelter for marine organisms and potentially an additional food source for fish. Additionally, seaweed farm boundaries create social structures that may serve to exclude destructive fishing practices within their boundaries. In this context, seaweed farms situated on degraded coral ecosystems may represent a novel ecosystem, which is functionally distinct from wild, healthy shallow coral ecosystems.

1.3 Seaweed Farming on Danajon Bank as a Model System

Danajon Bank lies in the heart of the Coral Triangle (Figure 1.1), an area that straddles two biogeographic regions (the Indonesia-Philippines and the Southwestern Pacific regions) and is widely considered to be the global epicenter of marine biodiversity (Allen 2007). Located off the northern shore of Bohol Island, Danajon Bank is the only double barrier reef in the Philippines and one of only three in the Indo-Pacific region (Pinchon 1977). The overall area of the reef is 2,353 square kilometers comprising 40 islands with over 700 kilometers of aggregate coastline; represents 1% of the total coral cover out of 27,000 km² in the Philippines. This rare double barrier reef system was once one of the most productive and highly diverse reef systems in the world but is now considered one of the most seriously threatened and degraded (Wilkinson 2004). In many areas within the inner bank, coral mortality has already exceeded 80% (Marcus et al. 2007). Seaweed farming on Danajon Bank began in the 1960s and quickly spread as it proved to be a profitable supplementary activity to traditional fishing (Trono 1990). By the late 1970s, it was estimated that 5 km² of the available reef had been transformed into seaweed farms, with over 8,500 people fully or partially engaged in seaweed farming. (Trono 1990). Danajon Bank has seen significant expansion of seaweed farming activity since the 1970s, fuelled largely by improving connectivity to markets and ambient environmental factors such as optimum water temperature and constant water exchange. Government actively started promoting seaweed farming within fishing communities on Danajon Bank in the mid-1990s with assistance primarily provided in the form of financial and technical assistance via People's

Organisations that are a focal point within villages for community-based coastal resource management activities (Hill, 2011).

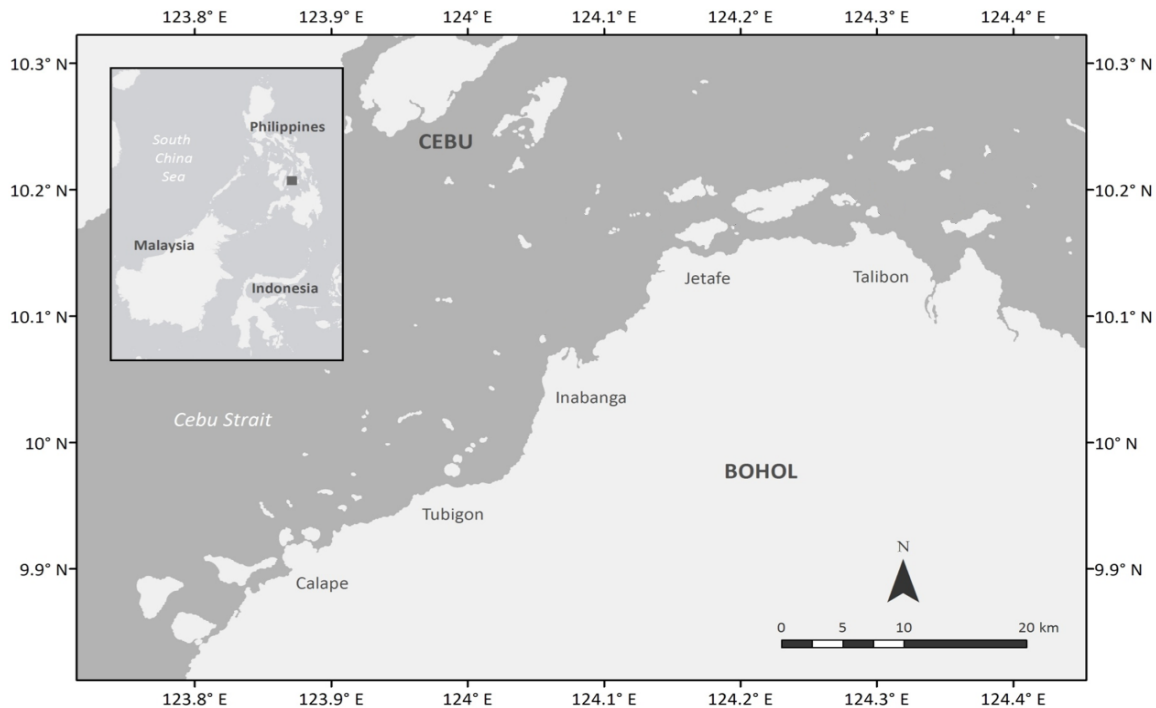


Figure 1.1. Map of northern Bohol Province, Central Philippines including the Danajon Bank.

Individuals or households claim areas of the reef for seaweed farming. These areas vary in size depending on the resources of the individual or household and their ability to farm that area. Seaweed farmers are required to register farm plots (up to 1 ha per household) with the municipal agricultural officer, and pay a license fee for their use. Sometimes, the municipal agricultural officer will then formalise the boundaries, normally by visiting the site and recording the location of the boundaries on a handheld global positioning system device. Not all seaweed farmers register their areas, but registration is becoming increasingly widespread. Relatively wealthy and politically well-connected households often have access to the largest and most convenient areas and will often hire laborers for their seaweed farms (Hill 2011). Even for those households that work their own seaweed farms, labour may be hired in or out depending on farm requirements and availability. Payment for such labour is normally based

on the quantity of work undertaken in terms of the number of monolines planted or harvested. Men, women, and children undertake the intensive labor of seaweed farming (Hill 2011).

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Most seaweed farmers on Danajon Bank cultivate *Eucheuma spinosum*, (spiny Eucheuma) and *Kappaphycus alvarezii*, (Elkhorn moss). Currently, most seaweed farming is practised artisanally and is labour intensive, requiring only very basic technology and minimal investment. There are also a limited number of large-scale industrial farms operated by Taiwanese and South Korean interests. While several different farming techniques are employed on Danajon Bank, *E. spinosum* is produced primarily through a broadcast method whereby seedlings are simply cast out onto the shallow coral reef and harvested at a later date. In contrast, *K. alvarezii*, the more valuable of the two species, is primarily farmed by attaching seedlings to nylon monolines anchored with a series of mangrove stakes on the coral reefs.

The islands of Danajon Bank contain seventeen municipalities, which in turn belong to four provinces and two regions. Located within one of the most impoverished areas in the country, Danajon Bank attracts a significant population of fishers and other marine dependent stakeholders competing for increasingly scarce marine resources (Calumpong et al. 1997, Armada et al. 2009). The majority of people in the region live along the coast, and it is estimated that 43% are directly involved in fishing. However, at least 50% of the inhabitants of northern Bohol are directly involved in fishing, and only 5% of the inhabitants own land dedicated to agriculture (Calumpong et al. 1997).

Conservation of marine resources on Danajon Bank is particularly critical since the many people involved in municipal fisheries fall below the poverty line. In Bohol, this number approaches 50% and, as these families are the most dependent on fish as a source of inexpensive protein, they are dependent on the quality of marine resources for their income and health (Green et al. 2004). As a result, Danajon Bank is increasingly threatened from the over-extraction of resources, and habitat destruction (Christie et al. 2006). The continued

degradation of the coral reef ecosystem has serious implications for those who rely on its resources for their survival.

Blast fishing is still common in some communities on Danajon Bank (author's pers. obs.) and local oral histories date the genesis of blast fishing to the late 1950s or early 1960s. This aligns with the consensus of experts in the Philippines Bureau of Fisheries and Aquatic Resources (BFAR) as well as several regional NGOs: blast fishing in this area has been prevalent over a long period of time. The presence of cratering indicates that blast fishing has contributed to the extensive observed rubble fields. My own estimates, based on the advanced weathering of the rubble, places some of the damage to be several decades old and as witnesses, the practice continues to date. Regardless of the time frame, extensive blast fishing is most likely the cause of the general homogenization of habitat within some locations, and may potentially impede coral reef recovery for decades if not centuries (Fox et al. 2003, Fox and Caldwell 2006).

Understanding the ecological role of seaweed farming on degraded coral reef ecosystems is a pressing issue as seaweed farming is likely to remain on Danajon Bank for three reasons. First, it is an important contributor to family incomes in a region of poverty and limited employment options. While seaweed farming is unlikely to replace fishing because of a combination of both social (i.e., fishing traditions) and economic factors (i.e., the price volatility for *Eucheuma*, (Crawford 2002)), it remains a significant economic activity. Second, both the provincial and national governments are promoting seaweed farming as an alternative/supplemental economic activity (Hill et al. 2011). This latter factor coincides with the third issue, which is a large influx of investment from foreign investors to develop large-scale seaweed production on Danajon Bank (Sievanen et al. 2005). While the environmental and economic viability of large-scale seaweed farms on Danajon Bank remains to be demonstrated, it does represent a shift towards commercially implemented and managed operations from the existing model of small family-operated subsistence farms. This shift has significant implications for local farmers who rely on the profits from seaweed to supplement declining returns from fishing. As more area is placed into commercial seaweed production, income from selling seaweed independently to local brokers would be replaced by low hourly wages from working on large farms owned by corporations.

Seaweed farming provides a useful case study for the creation of novel ecosystems not only because of its global scale and ubiquity, but because the introduction of farms onto degraded coral reef systems has the potential to significantly change the biotic composition and function when compared to wild, healthy shallow coral systems, noting that these wild systems have already transitioned to heavily degraded ecosystems. As in terrestrial systems, the proximate change in the management regime of these marine systems has the potential to result in changes in: 1) community composition, 2) plant/animal interactions, 3) biogeochemistry, and 4) disturbance frequencies (Hobbs et al. 2006). Understanding the function of these systems is critical then, particularly when trying to assess the allocation of conservation resources. If these farms do indeed represent novel ecosystems, how do they compare functionally to wild, healthy systems and do they in fact provide ecological benefits in their current state relative to their otherwise heavily degraded state. Only when this is determined can managers decide whether these systems require 1) a significant investment of resources in order to prevent them from changing further into a new and less desirable form or 2) whether the novel ecosystems created by seaweed farms can be better managed by accepting them for whatever benefits they may provide.

1.4 Thesis Objectives

The overall aim of this thesis is to evaluate the function of seaweed farms on degraded corals in the context of novel ecosystems, both globally and locally. In particular this thesis will determine the ecological impacts of seaweed farms on reef fish assemblages as well as the potential benefits to an herbivorous rabbitfish (*Siganus canaliculatus*). This will be achieved by addressing the following specific objectives:

- Chapter 2) Investigate the relationship between seaweed farms and rabbitfish production globally;
- Chapter 3) Investigate the diet composition of herbivorous fish in relation to the presence of seaweed farms on shallow coral reef ecosystems; and

Chapter 4) Establish foundational knowledge on the relationship between seaweed farms established on shallow coral reef ecosystems and fish assemblage composition.

1.5 Thesis Outline

Globally, farmed seaweed production is expanding rapidly in shallow marine habitats, and while it provides artisanal income to millions of farmers, it can negatively impact shallow coral reef and seagrass habitats. Despite the potential for negative impacts, seaweed farming may also subsidise herbivorous reef fish such as the Siganidae, which are a valuable target fish family, thereby resulting in increased fisheries catches.

In Chapter 2, based on fisheries data from a seaweed farming hotspot in the central Philippines, I examine the link between increasing farmed seaweed production and siganid catch against reef fish catch. The generality of this regional pattern is then further tested by analysing seaweed production, siganid catch, and reef fish catch for six major seaweed-producing countries in the tropics where increased seaweed production will correspond with increased production of siganids relative to other reef fish species.

Seaweed farming potentially provides economic benefits to artisanal farmers and subsidizes reef fish populations by providing an additional food source for herbivorous fish. However, the role of farmed seaweed in herbivorous fish diets remains unclear. In Chapter 3, using gut content and stable isotope analyses, I examine the contribution of farmed seaweed in the central Philippines to the diet of an obligate herbivorous rabbitfish, the white-spotted spinefoot *Siganus canaliculatus* (Family Siganidae). I hypothesise that rabbitfish consumption of farmed seaweed will increase with increased farm density, and seaweed farms can potentially lead to increased rabbitfish abundance and biomass.

Although demand for seaweed-derived products is driving the expansion of seaweed farming onto shallow coral reef ecosystems, the effects of farms on fish assemblages remain largely unexplored. Shallow coral reef ecosystems provide food and shelter for highly diverse fish assemblages but are increasingly modified by anthropogenic activities. In Chapter 4, I hypothesize that the introduction of seaweed farms into degraded shallow coral reefs has the

potential to generate ecological benefits for fish by adding structural complexity and a possible food source and that these benefits will be manifested in the fish assemblages as increased diversity, biomass, and abundance.

Finally, I synthesise the main findings of my thesis in Chapter 5 and discuss how the findings can be applied to evaluating the function of seaweed farms on degraded shallow coral reefs. Additionally, I evaluate the benefits of using a novel ecosystems approach to assessing the ecological function of seaweed farms and discuss how the insights gained can be applied for better management of critical shallow coral habitat.

CHAPTER 2

A Global Analysis of the Relationship between Farmed Seaweed Production and Herbivorous Fish Catch

2.1 Summary

Globally, farmed seaweed production is expanding rapidly in shallow marine habitats. While seaweed farming provides vital income to millions of artisanal farmers, it can negatively impact shallow coral reef and seagrass habitats. However, seaweed farming may also potentially provide food subsidies for herbivorous reef fish such as the Siganidae, a valuable target family, resulting in increased catch. Comparisons of reef fish landings across the central Philippines revealed that the catch of siganids was positively correlated to farmed seaweed production whilst negatively correlated to total reef fish catch over the same period of time. We tested the generality of this pattern by analysing seaweed production, siganid catch, and reef fish catch for six major seaweed-producing countries in the tropics. We hypothesized that increased seaweed production would correspond with increased catch of siganids but not other reef fish species. Analysis of the global data showed a positive correlation between farmed seaweeds and siganids in Southeast Asia (Indonesia, Malaysia, and the Philippines) but not Africa (Tanzania and Zanzibar), or the Western Pacific (Fiji). In Southeast Asia, siganid catch increased disproportionately faster with seaweed production than did reef fish catch. Low continuity, sporadic production and smaller volumes of seaweed farming may explain the differences.

2.2 Introduction

The commercial cultivation of seaweeds occurs in approximately 35 countries around the world and provides a variety of products that, in 2011, produced 21 million tonnes with a total annual value of US\$7.35 billion (FAO (Food and Agriculture Organization of the United Nations) Fisheries and Aquaculture Department 2012). Of that total, food products contributed almost US\$ 5 billion (FAO (Food and Agriculture Organization of the United Nations) Fisheries and Aquaculture Department 2012). Seaweed cultivation continues to expand rapidly as demand for seaweed products such as carrageenan has outstripped supply from wild resources. Although seaweed farming occurs globally, the vast majority of seaweed farming (98.9%, 18.9 million tonnes) is concentrated in China (60%) and Southeast Asia, including Indonesia (21%), the Philippines (9%), and Malaysia (1%). Throughout Southeast Asia, small subsistence farms (<1 ha) predominate, and their proliferation is in large part governed by both accessibility to useable habitats and proximity to markets (Sievanen et al. 2005). Rising demand for seaweed products and the need for impoverished communities to develop alternative livelihoods are driving seaweed farms to expand into new locations, including onto coral reefs (Sievanen et al. 2005, Graham et al. 2006).

The majority of the world's coral reefs are found in developing countries with high rates of population growth (Munro 1996). Combined with social inequality, population growth has significantly increased pressures on tropical marine fisheries (Pauly 1994, Jennings & Polunin 1996, Polunin & Roberts 1996, McManus 1997, Sievanen et al. 2005), which are an important source of revenue and protein for millions of people globally (Jennings & Polunin 1996, Allison & Ellis 2001, Badjeck et al. 2010). The ecological impacts of coastal population growth primarily derive from both the system loading effects of pollution and siltation and the extractive and degrading effects of resource overexploitation (Hughes 1994, Knowlton 2001, Jackson 2001, Hughes 2003). In many places, this is exacerbated by the use of destructive practices like blast and cyanide fishing. In many places, these impacts are exacerbated by the use of destructive practices like blast and cyanide fishing. Once damaged, the capacity of a reef to recover depends on several factors, including its fundamental starting condition and the degree to which the causes of reef decline have been removed. While a growing number of studies indicate that reef recovery is possible with effective

implementation of coastal management and alternative livelihood programs (Rasher et al. 2013, Graham et al. 2015, MacNeil et al. 2015), progress will be constrained unless human population growth rates slow and poverty is alleviated.

The benefits of seaweed farming are unclear despite the practice being advocated as a way to improve reef health through poverty alleviation and reduced fisheries exploitation (Sievanen et al. 2005). Recent studies have shown that the introduction of seaweed farming does little to mitigate the effects of fisheries overexploitation, and that rather than replacing fishing, it is utilized as an additional source of income (Hill et al. 2011). However, seaweed farms also tend to be located in easily accessible, shallow and sheltered habitats situated in close proximity to markets. As such, many of the areas in which farms are located have already been degraded by overfishing and habitat loss (Juanich 1988, Burke & Spalding 2011) and thus may not cause additional habitat degradation. However, the direct ecological impacts of seaweed farming are still debated as empirical studies have typically produced different and conflicting results. For instance, in Indonesia, Blankenhorn (2007) found that where seagrass was not cleared as part of farm establishment, seaweed farming itself had no negative effect on seagrass beds (Blankenhorn 2007). By contrast, Ekloff (2006) recommended that seaweed farming in shallow seagrass areas should be avoided and that damage to seagrass beds was mitigated only by the small scale of farms and the recovery periods dictated by generally low market prices (Eklöf et al. 2006).

Hehre and Meeuwig (2015) also showed that seaweed farming on degraded shallow coral reefs corresponded with lower species richness, abundance, and biomass of associated fish assemblages, despite initial speculation that farms may benefit fish assemblages by adding physical complexity and shelter, and a potential food source for herbivores (Orth et al. 1984, Bergman et al. 2001, Sievanen et al. 2005, Eklöf et al. 2006, Hehre & Meeuwig 2015). These results are consistent with other studies that have shown both lower fish abundances and species richness in macroalgal-dominated versus coral-dominated habitats (Wilson et al. 2010, Williamson et al. 2014). Furthermore it has been demonstrated experimentally that herbivorous fishes will avoid areas of high macroalgal biomass (Hoey & Bellwood 2011). However, despite these findings, it is still possible seaweed farms increase rabbitfish productivity rather than standing biomass (Allen 1971, Beddington & Cooke 1983,

Christensen & Pauly 1995). While the Underwater Visual Census methods used in Hehre & Meeuwig 2015 give us a measure of abundance, abundance may not necessarily reflect productivity (Myers & Worm 2003, Maunder et al. 2006). Increases in siganid productivity relative to farming could be masked by the concentration of fishing effort within the farms.

Though they may provide benefits in terms of both recruitment and food, specific fisheries benefits derived from seaweed farms also remain unclear. Herbivorous fish such as siganids forage on a broad range of algae (Fox et al. 2009, Hoey et al. 2013) (Lam 1974, Ogden & Lobel 1978, Fox & Bellwood 2008, Soliman et al. 2008, FAO (Food and Agriculture Organization of the United Nations) Fisheries and Aquaculture Department 2012). Field studies have demonstrated that siganids play an important role as consumers of naturally-occurring macroalgae on coral reefs, and Sargassum in particular (McCook 1997, Mantyka & Bellwood 2007, Fox & Bellwood 2008). Additionally, siganid foraging on macroalgae has been blamed for wide-scale damage to seaweed crops throughout Southeast Asia (Juanich 1988).

Moreover, Hehre and Meeuwig (in review) found that although siganids feed on farmed seaweeds, these likely function as a replacement for wild seaweeds rather than an actual subsidy to catches, given animals were smaller and less abundant within farmed areas than in areas not associated with farms. There is evidence that some species of siganids such as *Siganus canaliculatus*, *Siganus fuscescens* and *Siganus spinus* settle directly to macroalgal beds despite most siganids settling to coral-dominated habitats (Wilson et al. 2010, Hoey et al. 2013). Many of the species that settle to macroalgal beds are also those that are frequently targeted by fishers, as is the case in the Philippines for *S. canaliculatus*. However, the potential of seaweed farms to enhance fisheries requires further investigation. In the context of declining fish returns and the potential for critical income for poor people, seaweed farms may be beneficial to reef fish by adding both structure to habitats homogenized by human presence and a potential food source to the environment. Additionally, in those areas already subjected to a high degree of disturbance, where the majority of substrate has already been negatively affected, the presence of any additional human disturbance may not be detectable. Indeed, it is possible that the addition of further human activities may in fact serve to benefit the underlying reef by reducing some of the most destructive activities like blast and cyanide

fishing, and replacing them with less destructive ones. Limiting the structural degradation of reefs caused by destructive practices is particularly important in light of the link between coral reef decline and losses in fisheries productivity (Rogers et al. 2014).

Here, we test the hypothesis that increased seaweed production is correlated with higher catches of herbivorous fishes (the Siganidae) and whether siganid catches increase proportionately more quickly with seaweed production than associated reef fish catches. We use regional data from a major centre of seaweed farming in the Philippines on seaweed production and catches of the siganid, *S. canaliculatus*, to determine if a localised relationship exists and how this corresponds to reef fish catches more generally. We then collated global data on farmed seaweed and fisheries catches as reported to the FAO (Sievanen et al. 2005, FAO (Food and Agriculture Organization of the United Nations) Fisheries and Aquaculture Department 2012). We focused on six tropical countries from three regions that both produce seaweeds and report siganid catches: Southeast Asia including Indonesia, Malaysia, and the Philippines; Africa including Tanzania, and Zanzibar; and the Western Pacific which was represented by Fiji. Combined, these regions account for 35% of global farmed seaweed production in 2011. We also extracted FAO catch data for non-herbivorous reef fish to determine whether siganid catches increased more quickly with increasing seaweed production, than general reef fish catches. These data allow us to understand how the large-scale implementation of seaweed farming throughout the tropics may influence catches of herbivores like siganids.

2.3 Methods

2.3.1 Local Data

Bohol, a province located in the central Philippines, is a populous region with a substantial degree of poverty (Sievanen et al. 2005, Graham et al. 2006, Hill et al. 2011). Residents of Bohol, particularly in the northern region of Danajon Bank, are highly dependent on both fishing and seaweed farming since few alternative income-generating opportunities exist (Munro 1996, Green et al. 2004, Christie et al. 2006, Armada et al. 2009, Hill et al. 2011). Indeed, Danajon Bank is a major producer of farmed seaweed in the Philippines (Pauly 1994, Jennings & Polunin 1996, Polunin & Roberts 1996, McManus 1997, Sievanen et al. 2005,

Armada et al. 2009). The majority of farming here is conducted on an artisanal scale: households are able to claim an area of up to 1 ha for farming on the reef which they are required to register with municipal agricultural officer (Jennings & Polunin 1996, Allison & Ellis 2001, Badjeck et al. 2010, Hill et al. 2011). Local subsistence fisheries are multispecies with a wide range of targets exploited for either direct consumption or sale, with siganids a key target for both purposes. Continued unsustainable levels of fishing effort combined with the use of illegal and destructive fishing methods, such as dynamite and cyanide, have led to declining catches further compounding poverty (Green et al. 2000, 2004; Christie et al. 2006; Armada et al. 2009). Additionally the continued degradation of the reef structure from anthropogenic activities has led Danajon bank to be classified as one of the most degraded reef systems in the world (Hughes 1994, Knowlton 2001, Jackson 2001, Hughes 2003, Marcus et al. 2007).

Seaweed production, and siganid and reef fish catch data for Bohol were extracted from the database of the Philippine Bureau of Agricultural Statistics (PBAS; (Jennings & Polunin 1996)). The PBAS generates basic data on fisheries production and socioeconomic data related to agriculture and fisheries. Fisheries landings of reef fishes (in tonnes per year) were monitored for the years 2002-2012 as part of a government project designed to evaluate artisanal catch returns, and centered mainly on Danajon Bank (Sievanen et al. 2005).

2.3.2 Regional Data

Regional data on seaweed production and catches of herbivorous siganids and common reef fish species (in tonnes per year) have been compiled by the FAO since 1950 in varying levels of detail. We extracted these data for six countries in three regions: Southeast Asia (Indonesia, Malaysia, and the Philippines); Africa (Tanzania, and Zanzibar); and Western Pacific (Fiji) (Figure 2.1). A range of reef-associated taxa was selected (excluding siganids) as a control for trends in siganid catches, as effort data is unavailable. The inclusion of as many reef-associated species as possible was important in order to integrate the effects of changes in effort across a variety of reef fisheries independent of the gear used for extraction, which can vary within and among regions.

Combined, these countries account for 35% of the world's seaweed production, and 58.4% when China is excluded. These countries were included in the analysis because concurrent records were available for seaweed production, siganid catches and reef fish catches for at least 15 years (FAO world fisheries and aquaculture 2012). Data were extracted from the Food and Agriculture Organisation of the United Nations (FAO) database using the Fishstat J software (<http://www.fao.org/fishery/statistics/software/fishstatj/en>). These statistics mainly represent commercial operations as artisanal, subsistence, and recreational fisheries are not typically reported (Norberg 1977, Harper et al. 2011, Hill et al. 2011). As such production levels may underestimate total landings, depending on the scale of non-commercial activities.

Our analysis of commercially farmed seaweeds included all carrageenophytes, the marine plants commonly known as red seaweeds (Rhodophyceae). The carrageenan produced by these algae is a polysaccharide used as a hydrocolloid for the manufacture of many food, pharmaceutical and industrial products. Carrageenophytes comprise nearly 50% of global landings and receive the highest prices. The carrageenophytes in the FAO database are classified as “*Eucheuma* seaweeds nei” (where nei is “not elsewhere identified”) and “Spiny eucheuma” (interpreted as *Eucheuma spinosum*), *Gracilaria* red seaweeds (*Gracilaria* spp.), and elkhorn moss (*Kappaphycus alvarezii*).

Catch data were compiled for the siganids, a group of herbivores reported to FAO as “spinefeet”. Fisheries catches can increase simply due to increased effort through time independent of total abundance (Juanich 1988, Swartz et al. 2010, Burke & Spalding 2011, Anticamara et al. 2011, Worm & Branch 2012). However, no effort data are available in the FAO database against which changes in catch could be controlled. As a surrogate control for effort, we also extracted the catch data for a range of reef fish species (excluding siganids) representing a total of 35 different families [Table 2.2] to allow us to determine whether there was a disproportionate increase in siganid catches relative to catches of other reef fish, likely subject to similar levels of fishing effort and gears.



Figure 2.1. Countries from the three regions (Southeast Asia, Africa, and the Western Pacific) included in the global analysis of seaweed production.

2.3.3 Modelling

We used regression analysis to examine the relationship between siganid catches and seaweed production, and between siganid catches and reef fish catches. For each variable, we calculated the percentage of the maximum value (PMV) for each year as the fraction of the highest value observed over the time series. This was done for both fish catches and seaweed production in order to generate a general trend independent of volume (Worm et al. 2006, Blankenhorn 2007). Specifically, this then allows a comparison of a standardised change in siganid catch or reef fish catch as a function of a unit change in seaweed production. Data were checked to ensure that the assumptions of linear regression in terms of distribution and homogeneity (Zar 2010). Regressions included only years where commercial seaweed farming began consistently so that initial low years prior to wide scale commercial production did not confound the results. Outliers, defined as data points diverging more than three standard deviations from the mean, were also removed from the analysis. Slopes of the regression line were interpreted as a rate of increase relative to seaweed production in order to compare the relationship between siganid catch and seaweed production against other reef

fish (excluding siganids) and seaweed production, which acted as a de facto control for increased fishing pressure across all reef fish. Differences between slopes were tested using a t test (Eklöf et al. 2006, Zar 2010).

2.4 Results

2.4.1 Local Analysis

Reports from the province of Bohol to the PBAS revealed that widescale farmed seaweed production for both elkhorn (*K. alvarezzi*) and eucheuma (*E. spinosum*) began in 1995. Over a twelve-year time period, production increased steadily from 74,755 tonnes per annum in 2002 to 126,551 in 2011, with the exception of 2008 where mean annual production declined to 84,924 tonnes (Fig. 2). A local survey of reef fish including siganids conducted by the Bohol office of the PBAS recorded landings for the same time period peaked at 825.8 tonnes in 2011, which coincided with the maximum production in seaweeds (Figure 2.2).

Reef fish landings for the same time frame were highest in 2004 at 80170 tonnes (Figure 2.2). The relationship between siganid catch and seaweed production was significant and positive ($p=2.77 \times 10^{-6}$, $R^2= 0.89$, $n=12$), however there was no significant relationship between reef fish catch and seaweed production ($p=0.10$, $R^2= 0.50$, $n=12$): reef fish catches initially decreased relative to seaweed production and in general were steady or declining with rising seaweed production (Table 2.1; Figure 2.3). We did not compare the slopes given the non-significant relationship for reef fish catch and seaweed production (Table 2.1; Figure 2.3).

2.4.2 Global Analyses

Fishbase lists 23 species of Siganid for Southeast Asia, Africa, and the Western Pacific (Table 2.1). Nine species are common to Southeast Asia and the Western Pacific, while only two: *Siganus argenteus* and *Siganus stellatus* are confirmed between Southeast Asia and Africa, with another three species, *Siganus guttatus*, *Siganus rivulatus* and *Siganus sutor* listed as possibly shared but unconfirmed.

Siganid catch was significantly correlated with seaweed production in Southeast Asia (Indonesia, Malaysia and the Philippines) (Table 2.1; Figure 2.5). Further, siganid landings in those locations increased at a faster rate relative to seaweed production than did reef fish landings as a proportion of the maximum value (PMV). The other regions showed no consistent patterns.

Table 2.1. Regression statistics for siganid and reef fish catches as a function of seaweed production respectively, including the estimated slope, intercept (int.), coefficient of determination (R²) and p values. Where both relationships are positive and significant (p<0.05), slopes were compared with a t test with corresponding t-values (t), degrees of freedom (df) and p values presented. NT indicates no test. Results are presented for the regional analysis (Bohol) and for the three regions: Southeast Asia (Indonesia, Malaysia, and the Philippines); Africa (Mainland Tanzania and Zanzibar); and the Western Pacific (Fiji).

Country/ Province	Siganids				Reef Fish				Slope Comparison		
	Slope	int.	R ²	p	Slope	int	R ²	p	t	df	p
Bohol	2.06	1.05	0.89	2.77 E-06	2.77 E-06	1.22	0.50	0.10			NT
Indonesia	0.80	0.26	0.78	0.004	0.004	0.59	0.53	0.006	3.97	12	<0.001
Malaysia	0.33	0.68	0.55	0.01	0.01	0.45	0.72	0.002	6.36	16	<0.001
Philippines	0.44	0.43	0.65	5.5 E-06	5.5 E-06	0.42	0.82	1.0 E-06	3.20	40	<0.002
Mainland	-0.41	0.82	0.40	0.001	0.001	0.38	0.18	0.04			NT
Zanzibar	-0.01	0.70	0.00	0.58	0.58	0.74	0.41	0.03			NT
Fiji	0.37	0.25	0.37	0.09	0.09	0.19	0.11	0.008			NT

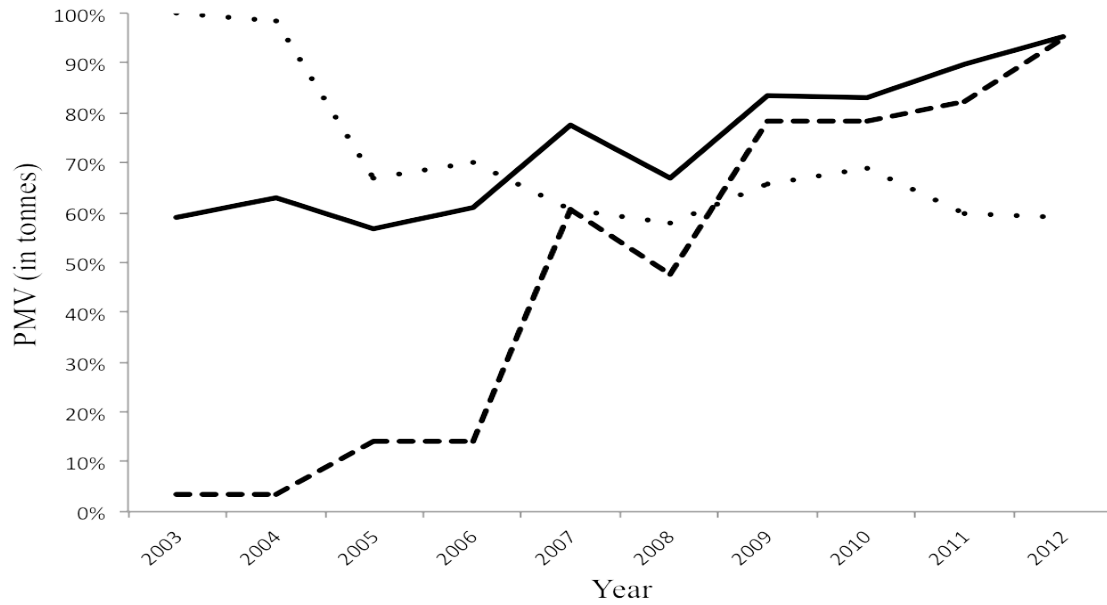


Figure 2.2. Temporal trends in seaweed production (solid line), siganid catch (dashed line) and reef fish catch (dotted line) as a percentage of maximum value (PMV) for the Bohol Province, Philippines.

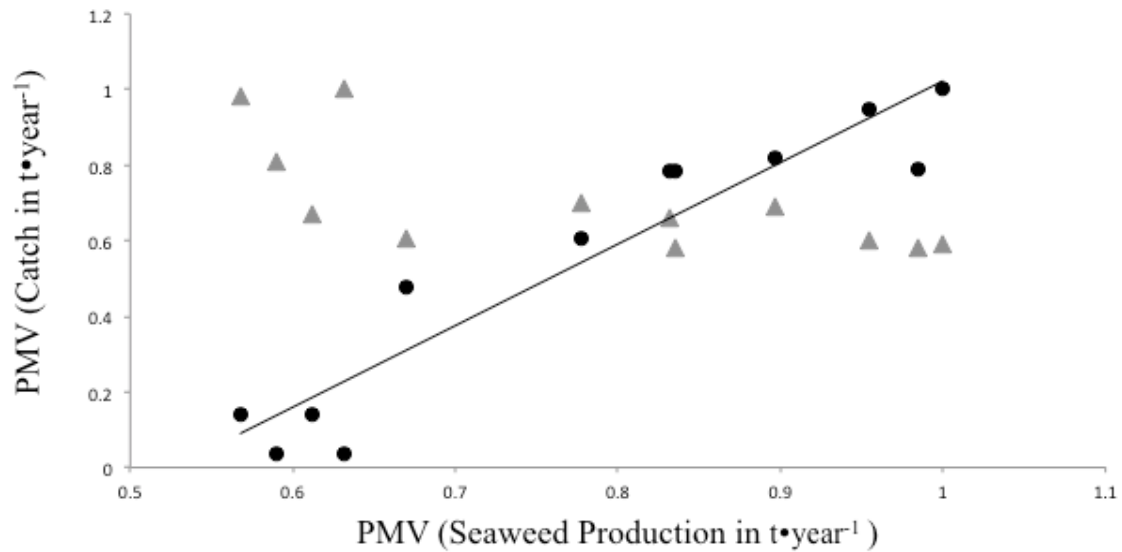


Figure 2.3. Comparison of the relationships between siganid catch (circles) and reef fish catch (triangles) vs. seaweed production, with all values calculated as a percentage of the maximum value (PMV) in tonnes for Bohol Province, Philippines over the period 2002-2012.

2.4.3 Southeast Asia

In Indonesia, reports to the FAO were initiated in 1950 under the category of “red algae” (Figure 2.4). In 2000, this category was made redundant and production was instead allocated to “*Eucheuma nei*” and “*Gracilaria spp*”. *Eucheuma nei* was dominant and accounted for 92% of total red algae production on average (range: 86%-97%), with *Gracilaria spp.* tending to become more important through time. Given the long time series available for the combined production of *Eucheuma nei* and *Gracilaria spp.*, we summed the two between 2000 and 2011 for a combined value comparable to that reported from 1950 to 1999. Seaweed production varied from approximately 10 tonnes in 1950 to 5,170,201 tonnes in 2011, exhibiting a sharp increase onward of the 1990s (Figure 2.4). Reporting of reef fish generally commenced in 1950, but siganid landings were only reported from 2004 to 2011, showing an annual rate of catch increase of 8% per annum, with some suggestion of a decline in the last two years (Figure 2.4). Mean landings of reef fish in terms of PMV increased steadily at 2% per annum from 1975 (Figure 2.4). There were significant positive relationships between siganid catch and farmed seaweed ($p=0.004$; $R^2=0.78$, $n=8$) (Table 2.1; Figure 2.5), as well as between reef fish catch and farmed seaweed ($p=0.0006$; $R^2=0.88$, $n=8$), (Table 2.1; Figure 2.5). Comparison of the slopes showed siganid catch increased more quickly relative to seaweed production than did reef fish catch ($t=3.97$; $p<0.001$) (Table 2.1; Figure 2.5).

In Malaysia, reports to the FAO began in 2001 for both Spiny *Eucheuma* and Elkhorn with the latter accounting for about 96% of the production over this period. Annual production varied from approximately 863 and 18,000 tonnes in 2001 to a peak of 7,892 (2010) and 239,450 (2011) for Spiny *Eucheuma* and Elkhorn respectively (Figure 2.4). Both taxa showed rapid increases in production averaging approximately 9-10% per annum over this period. Reporting of reef fish generally commenced in 1950, and siganid landings were reported from 1982 to 2011 during which period there was an approximate 1% increase per annum in siganid landings. Mean catch of other reef fish increased steadily at 1.7% per annum from 1975 (Figure 2.4). There was a significant positive relationship between siganid catch and seaweed production ($p=0.01$; $R^2=0.55$; $n=10$) (Table 2.1; Figure 2.5) and between reef fish catch and seaweed production, ($p=0.002$; $R^2=0.72$; $n=10$). (Table 2.1; Figure 2.5).

Comparison of the slopes showed siganid catch increased more quickly relative to seaweed production than did reef fish catch ($t=6.61$; $p<0.001$)(Table 2.1; Figure 2.5).

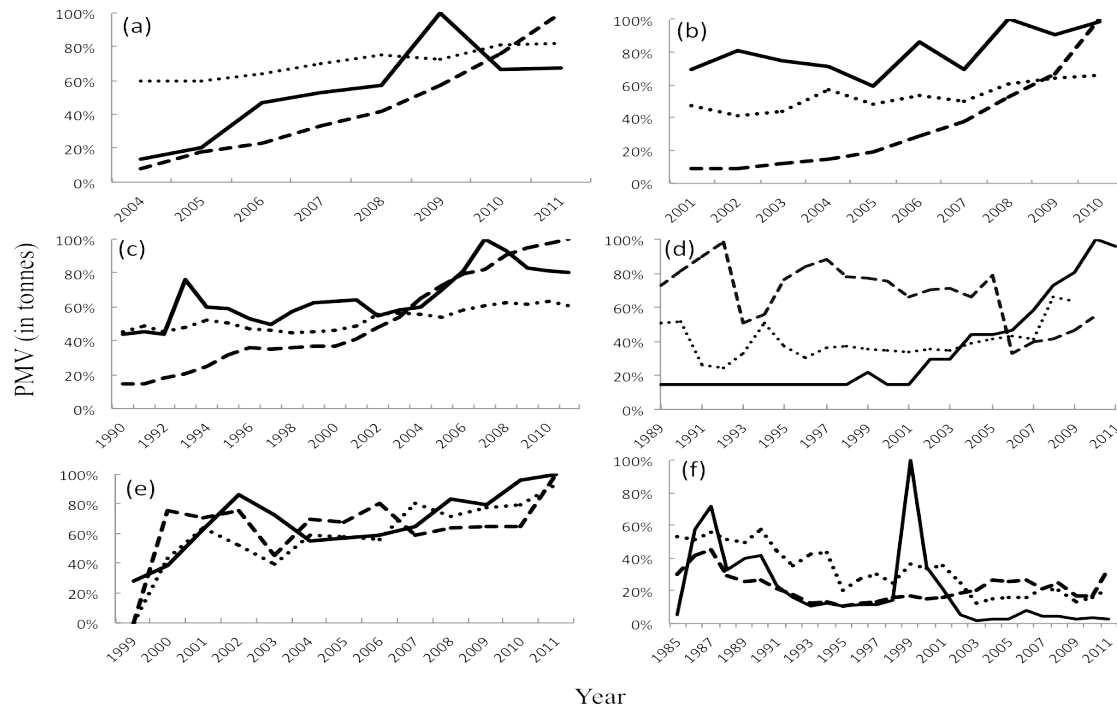


Figure 2.4. Temporal trends in seaweed production (solid line), siganid catch (dashed line) and reef fish catch (dotted line) as a percentage of maximum value (PMV) for the focal countries in each of the three regions: Southeast Asia (a) Indonesia, (b) Malaysia, (c) the Philippines; Africa (d) Mainland Tanzania and (e) Zanzibar; and the Western Pacific (f) Fiji.

In the Philippines, reports to the FAO began in 1965 for Elkhorn, 1974 for Spiny Eucheuma, in 2002 for Gracilaria. Gracilaria is reported at very low levels, accounting for typically less than 0.1% of the combined production of the three seaweeds. Production of Elkhorn varied from 1,000 tonnes to 1,697,682 tonnes while Spiny Eucheuma ranged from 3,000 tonnes to 136,183 tonnes per annum, and Gracilaria from 389 to 2479 (Figure 2.4). Elkhorn showed a steady rise from 1980 with two distinct peaks in 1980 and 1996. Spiny Eucheuma showed a sharp increase in production from 2000 at a rate of approximately 5% per annum. Reporting of reef fish generally commenced in 1950, with siganid catches reported from 1963 to 2011, during which period there was an approximate 2% increase per annum (Figure 2.4). Mean landings of other reef fish increased steadily at less than 1% per annum over the same period

(Fig. 4). There were strong significant positive relationships between siganid catch and farmed seaweed production, and between reef fish catch and seaweed production ($p=5.50 \text{ E-}6$; $R^2=0.65$; $n=22$, and $p=1.0 \text{ E-}06$; $R^2=0.81$; $n=22$, respectively) (Table 2.1; Figure 2.5). Comparison of the slopes showed siganid catch increased more quickly relative to seaweed production than did reef fish catch ($t=3.20$; $p<0.002$) (Table 2.1; Figure 2.5)

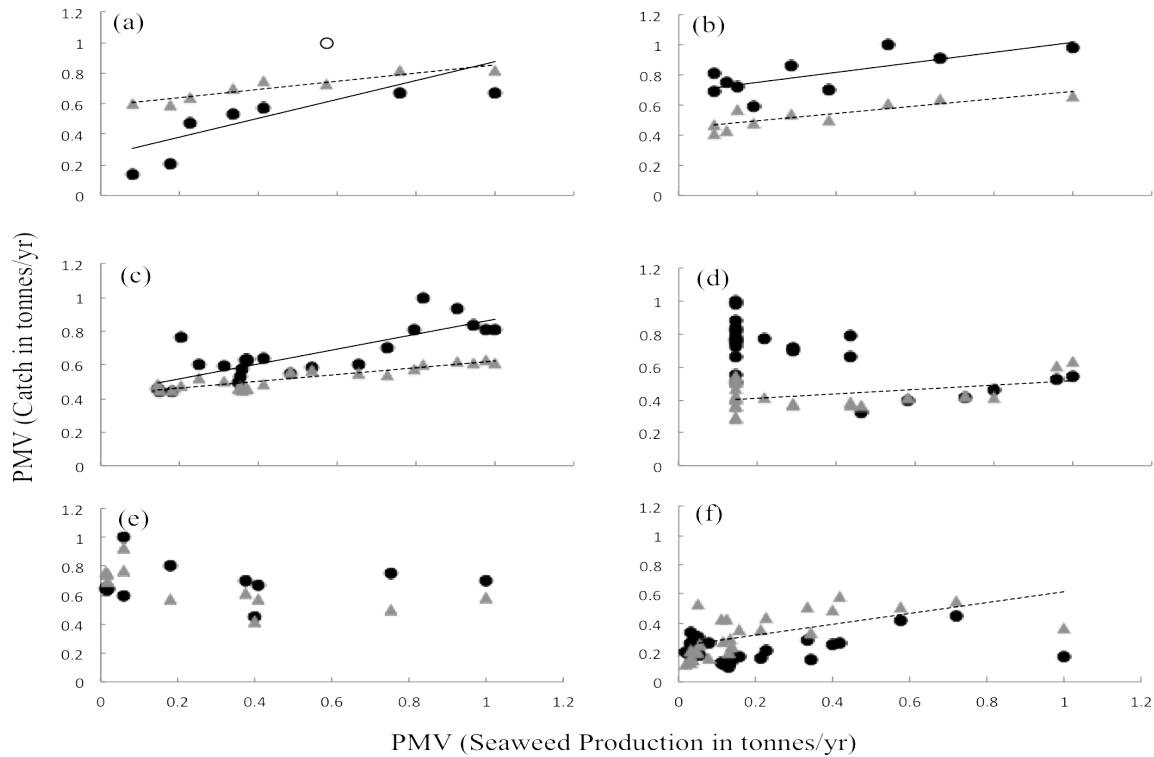


Figure 2.5. Comparison of the relationships between siganid catch and seaweed (circles) and reef fish catch (triangles) vs. seaweed production, with all values calculated as a percentage of maximum value (PMV) for three regions : (Southeast Asia, Africa, and the Western Pacific) (a) Indonesia, (b) Malaysia, (c) the Philippines (d) Mainland Tanzania (e) Zanzibar; and (f) Fiji.

2.4.4 Africa

In Mainland Tanzania, reports to the FAO began in 1989 under the heading of “*Eucheuma species nei*” (Figure 2.4). Production varied from approximately 1,000 tonnes per annum in 1989 to 6,885 t•year⁻¹ in 2010, exhibiting a sharp increase in production of approximately 8% per annum from 2001 (Figure 2.4). Reporting of reef fish generally commenced in 1973

with a large increase in siganid landings between 1989 and 2005, after which landings decreased substantially (Figure 2.4). There was a significant but negative correlation between siganid catch and farmed seaweed production ($p=0.0001$, $R^2=0.40$; $n=23$) while reef fish catch was significantly and positively correlated to seaweed production ($p=0.04$; $R^2=0.18$; $n=23$; Table 2.1; Figure 2.5).

In Zanzibar, reports to the FAO began in 1990 under the heading of “Spiny Eucheuma” (Figure 2.4). Production varied from 8,080 t•year⁻¹ in 1990 to 129,779 t•year⁻¹ in 2011, exhibiting a general steady increase of approximately 4% per annum (Figure 2.4). Reporting of reef fish commenced in 2000 with no clear trends in siganid landings: catches ranged from 710 t•year⁻¹ in 2003 to 1573 t•year⁻¹ in 2011 with a mean of 1096 t•year⁻¹ (± 207 SD) and no trends through time. Mean landings of other reef fish generally increased between 2000 and 2011 at a rate of 4% per annum (Figure 2.4). There was no significant relationship between siganid catch and farmed seaweed production ($p=0.58$; $R^2=0.005$; $n=12$), and reef fish catch and seaweed production though significant, were negatively correlated ($p=0.03$; $R^2=0.41$; $n=12$) (Table 2.1; Figure 2.5).

2.4.5 Western Pacific

In Fiji, reports to the FAO on farmed seaweed production began in 1985 under the heading of “Eucheuma nei” (Figure 2.4). Production varied from 250 tonnes per annum in 2003 to 15,090 t•year⁻¹ in 1999. There was a strong boom-and-bust cycle with two major peaks in 1987 and 1999. Annual production was highly variable until 1989, when it declined to, and stabilised at a mean value of approximately 590 t•year⁻¹ (± 260 SD). Reported landings of siganids ranged between 62 and 595 t•year⁻¹, reaching a general plateau from 1991 to 2011 of 112 t•year⁻¹ (± 34.9 SD). Siganid landings peaked in 1980, six years prior to the first peak in farmed Eucheuma. Mean landings of other reef fish generally declined from the 1980s onwards. There were no significant relationships between siganid catch and farmed Eucheuma production ($p=0.09$, $R^2=0.11$, $n=27$) although there was a significant positive relationship between reef fish catch and seaweed production ($p=0.008$, $R^2=0.37$, $n=27$) over the period that Eucheuma production was reported (1985-2011) (Table 2.1; Figure 2.5).

2.5 Discussion

At the regional level in Bohol, our study documented a positive relationship between siganid catch and the production of farmed seaweed relative and one where siganid catches increased more rapidly than reef fish catches relative to seaweed production. This lends empirical support to the idea that more abundant food supplies may increase production of some herbivorous reef fish (Orth et al. 1984, Chopin et al. 2001, Bergman et al. 2001, Sievanen et al. 2005, Eklöf et al. 2006, Allen et al. 2012, Hehre & Meeuwig 2015). Such a derived benefit appears to have occurred despite the elevated levels of habitat fragmentation driven by the rapid expansion of the seaweed farming industry (Lam 1974, Ogden & Lobel 1978, Bergman et al. 2001, Sievanen et al. 2005, Eklöf et al. 2006, Soliman et al. 2008, FAO (Food and Agriculture Organization of the United Nations) Fisheries and Aquaculture Department 2012) and within the context of a complex mosaic of anthropogenic use in the generally degraded seascapes of Danajon Bank region (Juanich 1988, Christie et al. 2006). Reefs in the area were already highly degraded from a host of anthropogenic activities before the addition of seaweed farming. However, clearing associated with the establishment of farms would serve to remove the living coral and rubble alike, along with constituent seaweeds, in order to reduce entanglement of the monolines used in farms (Christie et al. 2006, Graham 2014). However, in spite of the additional homogenisation of the substrate associated with farms, they would also serve to introduce a food source for the herbivorous rabbitfish and it is therefore possible that in this context, the establishment of seaweed farms fosters increased rabbitfish catch.

Fishing effort is a spatially and temporally heterogeneous process that generally increases as a function of human population size (Swartz et al. 2010, Anticamara et al. 2011, Worm & Branch 2012). Therefore it was necessary to establish a control for inherent differences in fishing effort. The interpretation of the positive correlation between siganid catch and seaweed production as evidence of a seaweed-derived benefit to siganids, is based on the use of the reef fish /seaweed production relationship as a proxy for fishing effort. In Bohol, the relationship between reef fish and seaweed production is flat, relative to the doubling of siganid catch per unit increase in seaweed production. In context, within the same region, fisheries catch per unit effort is declining () due to a declining resource base. The reef fish

comparison may be inappropriate if the set of species used in the comparison are unrepresentative of general fishing effort, but care was taken to incorporate species subject to similar fishing techniques and found on similar habitats. It may also be inappropriate if there has been a shift in effort towards siganids over this period. This is unlikely as there is a long history of siganid extraction in the region (), particularly in light of the region's depleted state since the 1970s. The comparison does suggest that siganid catches are increasing disproportionately quickly relative to reef fish catches that are in decline, which provides confidence in the use of reef fish catch as a control.

We observed similar patterns globally in Southeast Asia, where strong correlations were found between siganid catch and seaweed production, and where these relationships showed more rapid rates of increase than those based on reef fish and seaweed production. The strongest correlations between siganids and farmed red seaweeds were observed in Southeast Asia. Given the Philippines and Indonesia are respectively ranked 2nd and 3rd for global production of carrageenophytes, and Malaysia 7th, (FAO (Food and Agriculture Organization of the United Nations) Fisheries and Aquaculture Department 2012), this suggests a pattern of global significance. Such patterns were not, however, apparent in either Africa or the Western Pacific. Differences between seaweed production in Africa and the Western Pacific, as opposed to Southeast Asia, lie both in the duration and continuity of farming, which could have significant implications for the establishment of farmed seaweed as a food source for reef fish. In Fiji, for instance, the recurrent destruction of farming operations by typhoons has discouraged farmers from investing in infrastructure (Armada et al. 2009, Lal & Vuki 2010), and as a result, seaweed farming has been re-introduced on at least three occasions since the 1970s, typically on a small scale. Furthermore, fluctuating world market prices, high transportation costs to remote farming sites and an absence of local processing infrastructure all make seaweed farming less attractive than traditional fishing to many Fijians (Armada et al. 2009, Lal & Vuki 2010).

Similarly, in Africa, commercial seaweed farming has been both slow to establish and inconsistent in its application due to several factors, including (a) the failure of an economically valuable species of carrageenophyte, *K. alvarezii* (Elkhorn moss), and (b) societal and cultural changes associated with increased farming activities (Fröcklin et al.

2011). For example, *K. alvarezii*, the most profitable seaweed species, is now failing to grow in areas where it was previously cultivated due to changes in environmental conditions. These changes include warmer seas, epiphytism, and fouling (Kite-Powell et al. 2005, Msuya et al. 2007). Additionally, while initially promoted as a tool for coastal development particularly for women in Africa, further studies have shown that many women were abandoning seaweed farm because of health concerns (Bryceson 2002, la Torre-Castro & Lindström 2009, Fröcklin et al. 2011) as well as in response to negative perceptions of the benefits of farming compared to the additional workload (Bryceson 2002), and pressure over the associated cultural and societal changes brought by increased farming activities (Pettersson-Löfquist 1995, Fröcklin et al. 2011).

The scale of commercial seaweed farming may be another contributing factor to differences between Southeast Asia and Africa and the Western Pacific. Africa and the Western Pacific make relatively small contributions to worldwide production (< 1%) (FAO (Food and Agriculture Organization of the United Nations) Fisheries and Aquaculture Department 2012). In Fiji, seaweed farming has occurred on a fairly small scale, with the maximum export occurring close to the inception of commercial production in 1987 and with a peak export of only 10,850 tonnes (FAO (Food and Agriculture Organization of the United Nations) Fisheries and Aquaculture Department 2012). Further, in the 26 years since the commencement of commercial seaweed farming in Fiji, there has only been one increase in total production in six years (in 2000), and the overall trend has been one of general decline (FAO (Food and Agriculture Organization of the United Nations) Fisheries and Aquaculture Department 2012). In both Tanzania and Zanzibar, maximum seaweed production was 129,000 and just over 100,000 tonnes respectively. These levels are orders of magnitude lower seaweed production levels in Southeast Asia. It is important to recognise that the scale of seaweed farming is to some degree a function of available habitat for farms. There is much less reef in Tanzania, Zanzibar and Fiji than in the Southeast Asian countries, 28% vs 4.8% of world's reefs (FAO (Food and Agriculture Organization of the United Nations) Fisheries and Aquaculture Department 2012). Where seaweed farming occurs in Southeast Asia, it tends to be concentrated: seaweed production for Indonesia, Malaysia and the Philippines exceeds 101 t x km², 72 t x km⁻², and 70 t x km⁻², based on total reef area by nation (Spalding et al. 2001), and regions such as Bohol support intense production (). In Africa and the

Western Pacific seaweed production for Tanzania and Fiji was only 2 t x km⁻² (Spalding et al. 2001), with farming occurring in low volumes compared to the scale possible based on available reefs. It may be that under these conditions, seaweed production does not increase to a threshold sufficient to support increased siganid catches. The exception is Zanzibar, which has relatively high seaweed production relative to reef area (Spalding et al. 2001). However, the comparison is inappropriate for Zanzibar as most seaweed production here occurs on sand flat flats and not shallow coral reefs. The implication is that in locations with low areal coverage, reef fish would be much less likely to encounter and subsequently benefit from farmed seaweed.

Differences in the relationships between siganids, reef fish, and seaweed production in Southeast Asia and Africa may also reflect differences in the ecology and feeding strategies of the siganids found in these regions (Borsa et al. 2007, Fox et al. 2009, Brandl & Bellwood 2013, Hoey et al. 2013, Brandl et al. 2014, Woodland). For example, in Bohol, *S. canaliculatus* is the major siganid targeted by fisheries. It tends to settle directly on algal beds rather than coral reefs and consumes macroalgae (Hoey et al. 2013), (Hehre and Meeuwig in review) and therefore may be particularly well adapted to taking advantage of the implementation of seaweed farming. In contrast, *Siganus sutor*, common in the Indian Ocean Region and east Africa, while known to settle in algal beds like *S. canaliculatus*, exhibits a dietary preference for turf algae (Robinson et al. 2007, Mcclanahan et al. 2007, Vincent et al. 2011, Samoilys et al. 2013), suggesting that seaweed farms would not provide the same dietary benefits for *S. sutor* as they would for *S. canaliculatus*. In the absence of taxonomic resolution within the FAO global database, regional studies will help elucidate the relative importance of seaweed farming in terms of the provision of shelter vs. the provision of additional food sources.

The differences in feeding ecology of the main targeted species between the two regions may also underpin the lack of relationship between siganid catches and seaweed production in the Eastern Indian Ocean. Siganid fisheries for *S. sutor* in the Indian Ocean appear to be enhanced by the presence of algal dominated degraded reefs (Robinson et al. 2007, Mcclanahan et al. 2007, Vincent et al. 2011, Samoilys et al. 2013), reflecting *S. sutor*'s dietary preference for turf algae within these systems. As seaweed farms result in the clearing

of turf algae, seaweed farming may present a dietary penalty for *S. sutor* rather than a benefit as it does for *S. canaliculatus*. Such a scenario would imply that the effects of seaweed farming may vary depending on location and species, and highlights the need for further investigation into both the ecological and dietary strategies of affected fish assemblages.

Another possibility is that siganid catch may not be a direct result of seaweed farming itself, but an effect of algal domination as a result of coral reef degradation present where seaweed farming tends to occur, but initiated before commercial seaweed farming. Coral reefs in Southeast Asia show significantly higher levels of human impact from a variety of activities than either Fiji or Africa (Burke & Spalding 2011), and degraded reefs tend to be dominated by macroalgae (Bellwood et al. 2004). As was the case in the central Philippines where the consumption of farmed red seaweeds by siganids initially appeared as a direct food subsidy (Hehre & Meeuwig in review), farms in Southeast Asia tend to be situated across wide expanses of algal dominated reefs that have subsequently been cleared for farms, leaving farmed seaweed as a replacement for areas that would have otherwise contain wild food items. Following such a system shift from algal dominated coral reefs to seaweed farms, farmed seaweed may affect fish populations in two ways. Farms may provide a replacement food source where farms have been established by clearing reefs. In this case seaweed farms, while increasing siganid catches do so only because other seaweeds have been cleared as a result of their implementation thereby resulting in either increases or maintenance of herbivorous fish. Second, farms may serve to physically concentrate populations of dependent fish, which in turn may facilitate their capture. FAO data alone do not encapsulate this information nor does it allow us to disentangle these two processes without additional surveys. It is therefore difficult to confirm whether seaweed farming provides a true subsidy to fish or whether the benefits derived from the implementation of commercial seaweed production come as a result of a decrease in other available food items.

In the face of declining returns from fisheries depleted by over-extraction, destructive fishing practices, and habitat degradation over an extended period of time (Armada et al. 2009), the potential for an expanding seaweed farming industry to enhance the productivity of a valuable food fish, the siganid, is potentially important to both artisanal fishers and seaweed farmers alike. Over the last two decades, seaweed farming has grown worldwide and become

an important commodity on the world market that generates significant socio-economic benefits for marginalized coastal communities in developing countries. Higher continuity, less sporadic production and higher volumes of seaweed production may explain why siganid catch increased disproportionately faster than reef fish catches in Southeast Asia when compared to Africa and the South Pacific, and therefore, this correlative study demonstrates the potential for seaweed farming to increase siganid catch.

Table 2.2. Common names of demersal fish and the corresponding family names from Bohol Province and six countries included in the analyses; Fiji, Indonesia (Indo.), Malaysia (Mal.), Philippines (Phil.), Mainland Tanzania (Tanz.), and Zanzibar (Zanz.), as retrieved from the FAO database.

FAO (common name)	Family	Bohol	Fiji	Indo.	Mal.	Phil.	Tanz.	Zanz.
Anchovies	Engraulidae	x						
Batfishes	Ephippidae					x		
Bigeyes	Priacanthidae			x	x			
Bombay-duck	Synodontidae			x	x			
Cardinalfishes	Apogonidae		x					
Chocolate hind	Serranidae			x				
Conger eels	Congridae					x		
Croakers, drums	Sciaenidae			x	x			
Daggertooth	Muraenesocidae				x			
Eeltail catfishes	Plotosidae				x			
Emperors	Lethrinidae		x	x	x		x	x
Flatfishes	Paralichthyidae			x	x	x		
Flatheads	Platycephalidae				x			
Fusiliers	Caesionidae	x		x	x	x		
Glassfishes	Gerridae					x		
Goatfishes	Mullidae	x	x	x	x	x		x
Gobies	Gobiidae					x		
Groupers	Serranidae	x	x		x	x	x	x
Grunts, sweetlips	Lethrinidae			x	x			
Hairtails, scabbardfishes	Trichiuridae	x		x	x	x		
Indian halibut	Psettodidae			x			x	
Indo-Pacific mackerel	Scombridae	x						

FAO (common name)	Family	Bohol	Fiji	Indo.	Mal.	Phil.	Tanz.	Zanz.
Indo-Pacific tarpon	Megalopidae				x	x		
Largeeye breams	Lethrinidae		x					
Lizardfishes	Synodontidae			x	x	x		
Mangrove red snapper	Lutjanidae				x			
Mojarras, silver biddies	Gerridae		x		x	x		
Monocle breams	Nemipteridae				x			
Moonfish	Lampridae					x		
Mulletts	Mugilidae	x	x	x	x	x	x	x
Parrotfishes	Scaridae	x			x			x
Ponyfishes, Slipmouths	Leiognathidae	x	x	x		x		
Porgies, seabreams	Lethrinidae	x				x		
Big-eyed scad	Carangidae	x						
Sardines	Clupeidae	x						
Scats	Scatophagidae					x		
Sea catfishes	Plotosidae			x	x	x	x	
Sillago-whittings	Sillaginidae				x	x		
Snappers	Lutjanidae	x	x	x	x	x		x
Spinefeet, rabbitfish	Siganidae	x	x		x	x		x
Spotted sicklefish	Drepaneidae				x	x		
Surgeonfishes	Acanthuridae		x			x		
Threadfin breams	Nemipteridae	x		x	x	x	x	
Threadfins, tasselfishes	Polynemidae				x	x		
Tonguefishes	Cynoglossidae				x			
Triggerfishes, durgons	Balistidae		x		x			
Wrasses, hogfishes	Labridae		x		x	x	x	

CHAPTER 3

All Flesh is Grass: Farmed Seaweed in the Diet of a Rabbitfish and Implications for Fisheries

3.1 Summary

Seaweed farming may provide economic benefits to artisanal farmers and food for herbivorous fish. However, the role of farmed seaweed in herbivorous fish diets remains unclear. Using gut content and stable isotope analyses we examined the contribution of farmed seaweed to the diet of an herbivorous rabbitfish, *Siganus canaliculatus*. We hypothesised that rabbitfish consumption of farmed seaweed would increase with farm density leading to increased abundance and biomass. We found farmed seaweeds comprised a higher proportion of rabbitfish diet in areas with high farm densities compared to low farm densities, and both proportions were higher than reference sites. Wild brown turf algae still comprised a large proportion of rabbitfish diet in high farm densities. Situating seaweed farms in shallow coral ecosystems changed the movement and behaviour of rabbitfish. Abundance, biomass, and size of rabbitfish were highest in sites without farms and consuming farmed seaweed did not lead to increases. We concluded farmed seaweed was not a subsidy, but a replacement for wild seaweeds. Therefore farms may not provide benefits to herbivorous fish and their fisheries.

3.2 Introduction

Demand for seaweed extracts, which are used in a wide variety of commercial products, has increased over the past four decades such that by 2011, well over 20 million tonnes of seaweed valued at US \$7.35 billion were utilized by industry (FAO (Food and Agriculture Organization of the United Nations) Fisheries and Aquaculture Department 2012). The

increased demand for seaweed-derived products has resulted in a rapid expansion of seaweed cultivation, which has seen consistent growth in production since 1970, with an average annual increase in excess of 7 percent. Commercial seaweed harvesting now occurs in approximately tropical 35 countries under a variety of environmental conditions, including farms located in seagrass and shallow coral reef habitats (FAO (Food and Agriculture Organization of the United Nations) Fisheries and Aquaculture Department 2012).

Seaweed farming may have several positive consequences. For example, seaweed farming has been proposed as an alternative livelihood to fishing and thus a mechanism to reduce pressure on overexploited reef fish populations in developing countries (Salayo et al. 2008). In particular, in highly degraded marine habitats, the introduction of an agricultural matrix (the seaweed farm) creates a novel ecosystem (*sensu* Hobbs et al. 2009), adding physical complexity to the environment in the form of support structures and lines, seaweed mass as a food source for herbivores, and potential shelter from predation (Orth et al. 1984). Food subsidies provided to herbivorous fish populations may increase herbivore abundance, biomass, and size leading to indirect effects on other elements within ecosystems (Polis et al. 1997, Baxter et al. 2004, Allen et al. 2012). Also, from an ecosystem-based fisheries management perspective, the ecological effects of seaweed farming in habitats already degraded by overfishing, destructive fishing practices such as blasting and the use of cyanide, and pollution, may indirectly benefit fisheries by increasing fish catches (Pollnac et al. 1997).

However, seaweed farming has also been shown to have direct negative effects on corals through increased siltation, mechanical damage, removal, and impairment of recruitment ability (Sievanen et al. 2005) and negative or at best neutral impacts on fish assemblages (Hehre and Meeuwig 2015). Despite providing additional income to relatively impoverished households, seaweed farming has also had little effect on reducing overall fishing pressure, as the tendency is for families to incorporate additional sources of income rather than replacing one with another (Hill et al. 2011). The effects on herbivorous species that are theoretically well positioned to benefit from seaweed farming have not, however, been assessed.

Siganids, commonly known as rabbitfish, are a family of fishes that may directly benefit from seaweed farms by consumption of cultivated seaweeds. Some rabbitfish are considered true

herbivores, eating a wide range of algae (Lam 1974, Ogden and Lobel 1978, Soliman et al. 2008). Indeed, seaweed farmers throughout Southeast Asia have blamed rabbitfish for wide scale grazing damage to seaweed crops (Juanich 1988), with some estimates of crop loss from rabbitfish consumption exceeding 30% (Bindu and Levine 2010). As such, it is possible that the productivity of rabbitfish populations has increased with the expansion of seaweed farms, potentially benefitting commercial and artisanal fisheries that target these animals. Such a scenario could serve to balance concern with respect to the role of rabbitfish as pests, since increased numbers of rabbitfish could increase yields of an important artisanal food source (Chopin et al. 2001, Allen et al. 2012). However, little is known about the feeding ecology of rabbitfish in environments that include seaweed farms.

Stable isotope analysis is a powerful technique to evaluate the relative contributions of different food sources to diets and quantify trophic positions of fish (Lochman and Phillips 1996, Gu et al. 1996, Gamboa-Delgado et al. 2008). Because the isotopic composition of consumer tissues reflects the isotopic composition of its food, measurements of tissue $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ provide information on the sources of assimilated carbon and nitrogen (Chen et al. 2012). While fish diets are often studied using gut contents, gut content data are representative only of the food ingested just prior to the time of sampling (Pinnegar and Polunin 1999). Conversely, the analysis of the stable isotope signatures of prey and predators provides information about the food-web structure and energy flow over longer time periods (Pinnegar and Polunin 1999, Phillips and Gregg 2003, Carassou et al. 2008). As they are complementary methods, the combined analysis of gut contents and stable isotopes can provide a valuable tool for quantifying diet for a range of marine reef fish species (Peterson and Fry 1987, Michener and Kaufman 2008).

Determining the degree to which rabbitfish feed on farmed seaweed is essential to understanding the role of these herbivorous fish in modified shallow reef ecosystems, but this is insufficient for identifying whether rabbitfish production is subsidised by seaweed farming. Catch per unit effort (CPUE) data are a more direct measure of stock abundance and are relevant to determine whether seaweed farming leads to increases in fisheries productivity (Harley et al. 2001, Maunder et al. 2006), but these data are often unavailable, particularly for remote, artisanal fisheries (Harper et al. 2011). As an alternative, underwater visual

census (UVC) has been used to determine the status of exploited populations (Buxton and Smale 1989, Dulvy et al. 2004, Robbins et al. 2006), generating estimates of relative abundance (Samoilys and Carlos 2000, Edgar et al. 2004, Salayo et al. 2008, Kulbicki et al. 2010), biomass (Jennings and Polunin 1995), and individual size (Zeller and Russ 2000). An important caveat lies in recognising that the relationships between such population attributes and CPUE are not always linear (Harley et al. 2001, Maunder et al. 2006).

Here, we used gut content and stable isotope analysis to examine the contribution of farmed seaweed to the overall diet of a valuable food fish, the white-spotted rabbitfish *Siganus canaliculatus* (Park, 1797). We further quantified how the density of farming affected its abundance, biomass, and size. This herbivorous rabbitfish is ubiquitous throughout the shallow, coral reef ecosystems of the Danjon Bank region of the central Philippines (Polis et al. 1997, Parkyn et al. 2001, Mantel et al. 2004, Baxter et al. 2004, Layman et al. 2005, Allen et al. 2012), a region that has been undergoing a rapid expansion of seaweed farming (Sievanen et al. 2005). It is also highly valued by subsistence, artisanal, and commercial fishers both regionally (Sievanen et al. 2005), and globally (FAO (Food and Agriculture Organization of the United Nations) Fisheries and Aquaculture Department 2012). We hypothesised that where present, farmed seaweed would comprise a significant proportion of the diet of this rabbitfish, and that this proportion would increase with the density of farming in a region. We also hypothesised that seaweed farming would subsidise rabbitfish production in highly degraded, shallow coral ecosystems, as evidenced by increasing abundance, biomass, and size of rabbitfish with increasing density of seaweed farms.

3.3 Methods

3.3.1 Study Area

This study was conducted on Danajon Bank of the Central Philippines (Figure 1). Located off the northern shore of Bohol Island, Danajon Bank is one of only three double barrier reefs in the Indo-Pacific region (Pinchon 1977). The reef itself has an area of 2353 km² and consists of 40 islands. Located within one of the most impoverished regions in the country, Danajon Bank possesses a significant population of fishers and other marine-dependent residents accessing increasingly scarce resources (Calumpong et al. 1997, Christie et al. 2006, Armada

et al. 2009, Bindu and Levine 2010). The majority of people in the Bohol region live along the coast and in Danajon Bank region of northern Bohol. At least 50% of the inhabitants are directly involved in fishing, and only 5% of the inhabitants possess land dedicated to agriculture (Armada et al. 2009). Seaweed farming is rapidly expanding in the region at a time when reef fisheries are in decline due to several co-incident factors including open-access regimes, excess fishing effort, destructive fishing practices, a high dependence on fishing, and an overall lack of integrated planning and management of coastal resources (Christie et al. 2006). Catch data from Bohol indicate that current fisheries landings are less than one-tenth of those recorded in the 1960s (Armada et al. 2009).

3.3.2 Sampling

We sampled six sites that represented three different levels of seaweed farming on the inner Danajon Bank, with levels based on percent coverage of the available shallow coral habitat by seaweed farms. The sites comprised: two high farm density sites (HD; 100% of reef habitat covered by farms), two low farm density sites (LD; < 10% of reef habitat covered by farms) and two reference area sites (RA; no seaweed farms within a 2 km radius). Seaweed farms varied in size (600 m² to 2025 m²) and time since farms were established (approximately 10- 15 years), but nearly all were located within shallow coral reef ecosystems on the inner Danajon Bank (Figure 1). At each site, we collected rabbitfish for gut content and stable isotope analyses, and we gathered quantitative data on the fish assemblages. We were not able to collect gut content, length measurements and fish assemblage data at one HD site as the field team was requested to leave by armed guards despite having the necessary permissions. Consequently, this site was not included in the dietary and length analyses, but was included in the isotopic analysis.

Free divers collected 25 rabbitfish from each of the six sites between March 1 and April 30, 2013. Individual fish were captured by spearfishing within two hours either side of midnight (22:00 to 02:00) to minimize error associated with variable rates of gut content evacuation (Waddington and Bellchambers 2008). Fish were returned to the boat immediately after capture, euthanized, and their guts removed and preserved in 10% buffered formalin solution to halt digestion. Formalin was replaced after a period of two weeks with 70% technical

grade ethanol (Kelsch and Shields 1996). Tissue samples for isotope analysis were preserved with salt (Xu et al. 2011) given the lack of adequate refrigeration in this remote region. We also collected samples of potential diet items including naturally occurring “wild” macrophytic seaweeds (brown, green), epiphytes and seagrass found in the region, as well as locally farmed red seaweeds. Seaweed samples were preserved according to the same salt drying protocols used for rabbitfish tissue samples.

3.3.3 Gut Contents

Intact stomachs were removed by cutting above the cardiac sphincter (esophagus) and below the pyloric sphincter (large intestine). An incision was made along the longitudinal axis of the stomach, and the contents were removed and weighed. After removing the gut contents, the foregut membrane was then reweighed (Bowen 1996). Gut contents were rinsed into a petri dish and contents identified by type (farmed red algae, wild brown algae (including turf algae and *Sargassum spp.*), wild green algae, red epiphytes, seagrass) using a dissecting microscope (6.4-40x magnification). Due to the breakdown of diet items in the gut, it was not always possible to identify contents.

3.3.4 Stable Isotopes

Salt dried samples from potential diet items and rabbitfish muscle tissue were used for stable isotope analysis. All samples were soaked in de-ionized water for eight hours to remove salt, placed in an oven at 60 °C until dry, then ground to a fine powder using a ball mill grinder. Samples were analysed for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ by continuous-flow isotope ratio mass spectrometry using a Delta V Plus mass spectrometer coupled to a Thermo Flash 1112 elemental analyzer via a Conflo IV (Thermo-Finnigan/Germany). Samples were analyzed in dual isotope mode, allowing $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ to be measured on the same sample. Multi-point normalization was applied (based on international reference materials obtained from the International Atomic Energy Agency: $\delta^{13}\text{C}$ - NBS22, USGS24, NBS19, LSVEC; and for $\delta^{15}\text{N}$ —IAEA-N1, IAEA-N2, IAEA-NO-3 and laboratory standards) in order to convert δ -values to the international VPDB and AIR scales (Skrzypek et al. 2010). Analytical uncertainty was 0.10‰ (one sigma) for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$.

3.3.5 Underwater Visual Census

Fish assemblages were sampled using underwater visual census (UVC) (English 1997). At each of the five selected sampling sites, five transects of 20 m x 5 m were laid parallel to the reef crest to control for depth. Starting point coordinates were assigned using a random number generator with transects separated by a minimum of 5 m. Ten minutes after transects were laid, the fish survey was conducted. Passes along transects were timed to ensure that durations were uniform. If large numbers of fish were present, the survey was conducted in two passes, the first to identify more mobile species and the second to identify more sedentary species (English 1997, Kulbicki et al. 2010). Individual fish within the transect were identified to species and total lengths were estimated (Sale 1991). The same investigator (EJH) conducted all fish transects.

3.3.6 Statistical Analysis

A nested two factor permutational ANOVA (PERMANOVA) was used to test whether location and/or the level of farming coverage (HD, LD, and RA) influenced the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of potential diet items and the isotopic signatures of rabbitfish. Variation in each isotopic signature was analysed in a nested two factor ANOVA (Anderson 2001), where location was nested with the level of farming density present with a Euclidean distance matrix calculated (Zar 1999).

Table 3.1. Results of gut content and stable isotope analyses for *S. canaliculatus* by farm density where HD are high density farm sites, LD are low density farm sites, and RA are reference area sites, showing sample length, gut content weight, primary seaweed type found in guts, and mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of tissue samples.

Location	Farm Density	Mean Length \pm SE (n =25)	Mean Content Wt \pm SE (n =8)	Primary Seaweed Type in Gut	Mean $\delta^{13}\text{C}$	Mean $\delta^{15}\text{N}$
Alumar (AL)	HD	14.38 \pm 0.45	0.63 \pm 0.25	Farmed	-18.19	6.58
Cataban (CT)	LD	12.23 \pm 19	0.62 \pm 0.16	Brown/Farmed	-15.03	5.77
Pandanon (PN)	LD	13.00 \pm 0.35	0.82 \pm 0.23	Brown/Farmed	-14.50	6.46
Bilangbilangan (BB)	RA	12.26 \pm 0.29	0.44 \pm 0.13	Brown	-13.97	6.09
Cabal-an (CB)	RA	12.68 \pm 0.32	0.40 \pm 0.19	Brown	-14.32	6.37

The $\delta^{13}\text{C}$ data were also analysed using the mixing model software Isosource (Phillips and Gregg 2003) to estimate the potential contributions of four types of seaweed food sources at each level of farm density. Source increments were specified from 0-100% and the mass balance tolerance was specified at 1.5% of the observed signature. Histograms were produced to show the distribution of feasible contributions from each source to rabbitfish diet. Values were calculated for 1-99 percentile ranges for their distributions. We assumed no trophic-level effect for $\delta^{13}\text{C}$ (Post 2002).

Abundance, biomass, and size of rabbitfish were compared across the three levels of seaweed farm density. While abundance and size (estimated as mean length) were estimated directly in the field, rabbitfish biomass was derived by summing the weights of individual fish that were calculated from the *in situ* length estimates and the fork length (FL in cm) -weight (Wt in g) relationship for this species $Wt(L) = 0.01148FL^{2.99}$. Total abundance and total biomass of all fish species per site were estimated by summing abundance and biomass across transects at each site, with species specific length-weight relationships applied. Mean size of rabbitfish per site was estimated by calculating the length of individual fish for each transect and then averaging lengths per site. Finally, as the total abundance and biomass of the fish assemblage also varied across sites, we calculated the percent abundance and percent biomass of rabbitfish relative to the entire fish assemblage.

3.4 Results

A total of 100 rabbitfish were collected from five sites (Figure 3.1). Fish specimens ranged in total length from 10.0 cm to 18.0 cm and in dry weight from 22.2 g to 129.4 g. Sites did not vary in mean total length of sampled fish or in the weight of gut contents (Table 3.1).

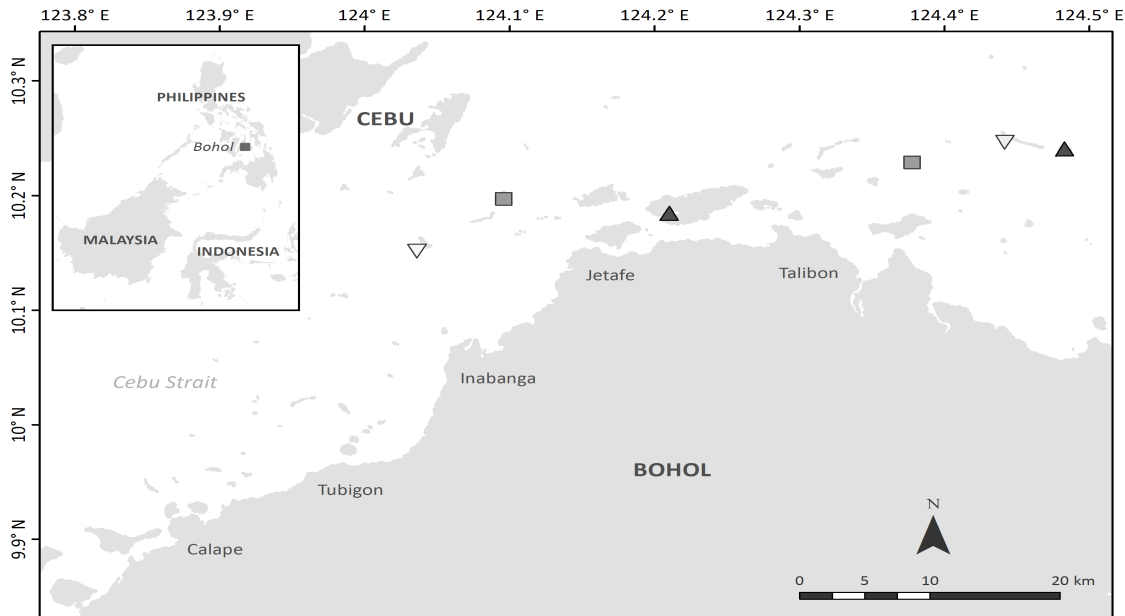


Figure 3.1. Study area in northwest Bohol Province, Philippines, with focal sites where circles, triangles, and squares are high farm density sites (HD), low farm density sites (LD), and reference area sites (RA) respectively.

Table 3.2 Diet analysis of *S. canaliculatus* based on differences for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. Seaweed samples containing exclusively red (farmed), brown (wild), and mixed (both farmed and wild) areas for three levels of farm density: high farm density sites (HD), low farm density sites (LD), and reference area sites (RA).

Farming Density	Seaweed Type (origin)		
	Red (farmed)	Brown (wild)	Mixed (farmed and wild)
HD (n=1 site)	7	1	0
LD (n=2 sites)	0	4	12
RA (n=2 sites)	0	0	16

The $\delta^{13}\text{C}$ values of potential dietary seaweeds for rabbitfish had a mean value of -17.33 ± 0.93 SE (range: -20.03 to -14.83) (Figure 3.2), and the values of each type of diet item differed significantly ($p < .001$). Specifically, farmed seaweed returned isotopic values that were more negative than those of wild brown or green seaweed. The $\delta^{15}\text{N}$ values of potential dietary items had a mean value of 2.49 ± 0.76 SE (range 0.94 to 3.65 ; Figure 3.2), and were not significantly different across diet items ($p = 0.21$).

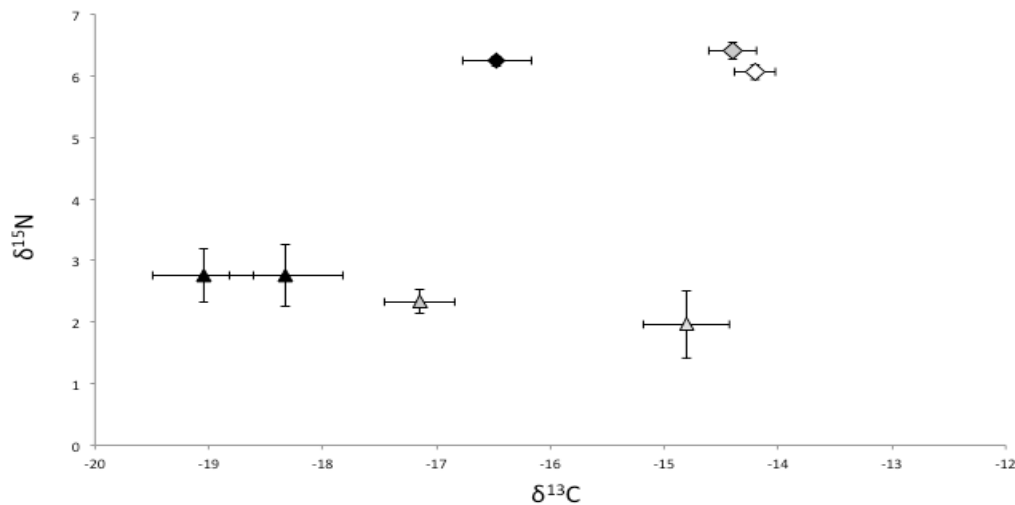


Figure 3.2. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopes for both fish tissue and seaweed samples where black, grey, and white diamonds are tissue samples from high farm density sites (HD), low farm density sites (LD) and reference area sites (RA) respectively, and grey and black triangles are samples from wild brown and farmed red seaweeds respectively.

Gut contents were analysed for a subsample of eight of the 20 fish collected at each of the five sites. This was the minimum number of guts available at each site given some guts were empty or had been damaged in transport, and were thus discarded. Mean gut content weight was 0.58 g (± 0.09 SE; range 0.01 g to 2.11 g). The gut contents of fish collected in HD sites were mainly farmed seaweed with 87.5% of the fish having contents exclusively consisting of farmed red seaweed (Table 3.2). Gut contents of fish collected in LD sites were exclusively wild brown seaweed (75%) or a mix of farmed red seaweed and wild brown algae (25%) or (Table 3.2). All gut contents of fish collected in unfarmed RA sites consisted exclusively of wild brown seaweed (Table 3.2).

The $\delta^{13}\text{C}$ of fish tissue samples from six sites had a mean value of -15.94 ± 0.23 SE (range: -21.78 to -11.21). Farm density marginally affected $\delta^{13}\text{C}$ values ($p = .066$; Table 3.3), however differences among locations were significant ($p = 0.009$; Table 3.3). High variance within locations in LD and RA sites may account for the lack of significance for $\delta^{13}\text{C}$. However, an MDA plot by farming density shows clear separation among HD sites and both LD and RA sites (Figure 3.2) with the mean density of $\delta^{13}\text{C}$ signatures for HD sites of -19.14 ± 0.15 SE, while LD and RA sites had mean $\delta^{13}\text{C}$ signatures of -14.76 ± 0.16 SE and -13.92 ± 0.14 SE respectively.

Table 3.2. Nested PERMANOVA testing the concentration differences in tissue samples for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for three levels of seaweed farming by farm density where Location (Loc) is nested in Density (Den) and where HD are high density farm sites, LD are low density farm sites, and RA are reference area sites.

Source	P(perm)	df	SS	MS	Pseudo-F
$\delta^{15}\text{N}$					
Den	0.851	2	0.5288	0.2644	0.0699
Loc(Den)	0.001	3	12.7960	4.2655	8.2155
$\delta^{13}\text{C}$					
Den	0.0658	2	628.9300	314.4600	93.2910
Loc(Den)	0.0085	3	10.1120	3.3708	4.0998

The $\delta^{15}\text{N}$ signatures for fish tissue samples had a mean value of 6.15 ± 0.06 SE (range: from 4.57 to 8.70). There was no significant effect of farm density on $\delta^{15}\text{N}$ ($p = 0.851$; Table 3.3) though there were significant differences among locations ($p = 0.851$; Table 3.3).

Mixing model analysis of dietary contributions based on farm density revealed that at the HD site, the highest percent frequencies of feasible contributions to rabbitfish diet were nearly equal proportions of *K. alvarezii* and brown turf algae with minimal contributions from *Sargassum* spp. or *E. spinosum* (Figure 3.3). In both LD and RA sites, the mixing model suggested a diet consisting almost exclusively of brown turf algae with relatively minor contributions from farmed *E. spinosum* and *K. alvarezii*, or wild *Sargassum* spp. (Figure 3.3).

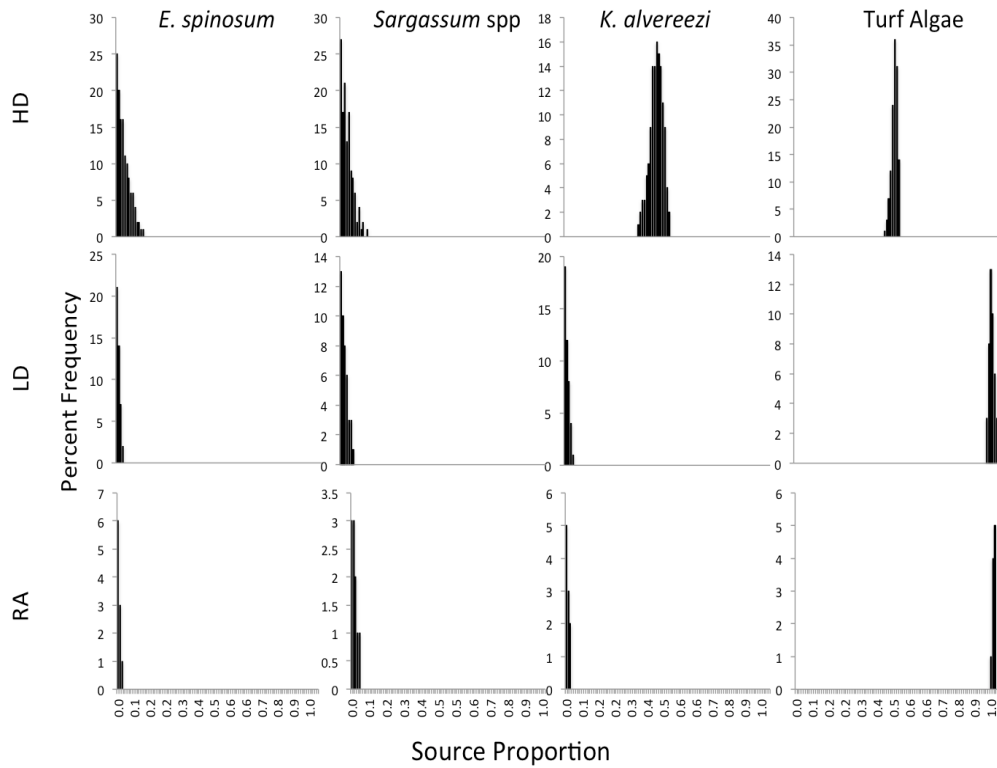


Figure 3.3. Frequency distribution of the contributions of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopes for each of four diet sources for high farm density sites (HD), low farm density sites (LD), and reference area sites (RA).

At the five sites sampled as part of the larger 2011 program (Hehre and Meeuwig 2015.), 3260 fish were counted representing 138 species and 31 families. Densities of rabbitfish ranged from 0.0 m^{-2} to 13.0 m^{-2} , and the species comprised between 0.0% and 14.0% of the fish assemblage by abundance. Biomass of rabbitfish per square meter of ranged from 0.0 $\text{kg}\cdot\text{m}^{-2}$ to 4.4 $\text{kg}\cdot\text{m}^{-2}$, and comprised between 0.0% and 32.0% of the total fish biomass. Mean size varied from 6 to 14 cm with an average of 7.1 cm (± 3.48 SE). There was no effect of farm density on the mean abundance, percent abundance, biomass, percent biomass, or mean size of rabbitfish ($p = 0.20, 0.29, 0.16, 0.33,$ and 0.15 respectively). However, there were consistent directional trends for abundance, biomass, percent biomass and mean size, all of which were greater in RA sites when compared to the LD and HD sites (Figure 3.4).

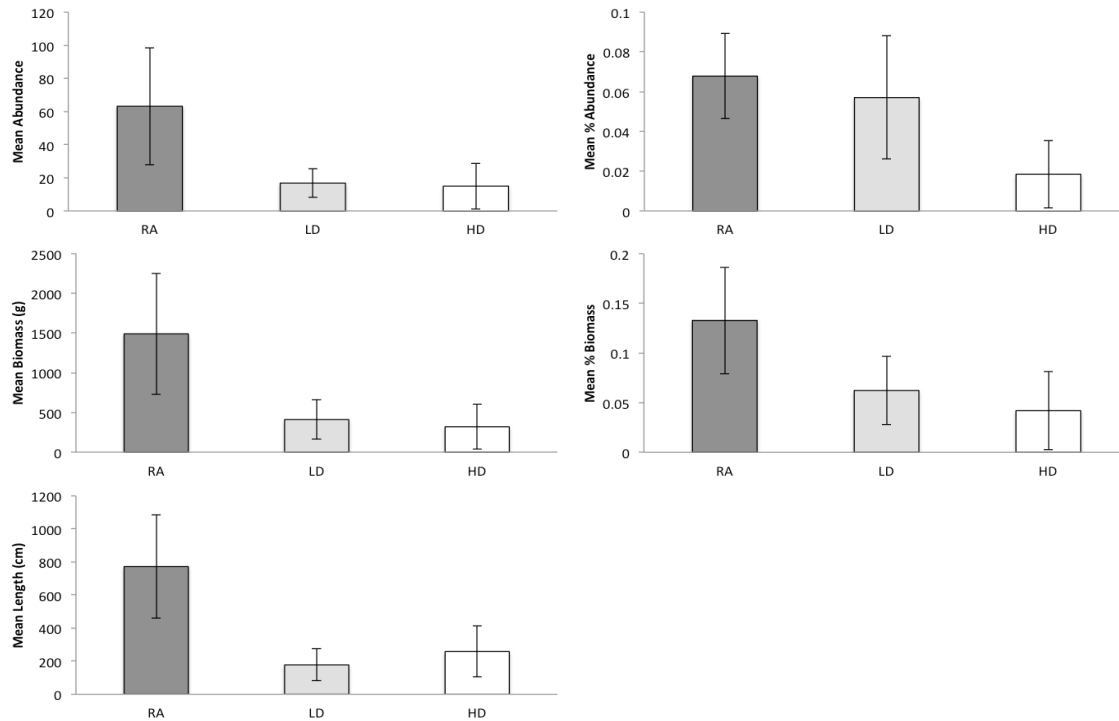


Figure 3.4. Mean abundance, mean % abundance, mean biomass (g), mean % biomass, and mean length (cm) of rabbitfish in fish assemblages by farming density for high farm density sites (HD), low farm density farm sites (LD), and reference area sites (RA).

3.5 Discussion

Our objectives were to understand how seaweed farming influences the diet of rabbitfish and to determine whether farming led to differences in abundance, biomass, and size of rabbitfish which could potentially generate ecosystem-based fisheries benefits from this important food source. We hypothesised that seaweed farms could generate ecological benefits by creating habitat and providing a food source for rabbitfish in otherwise degraded seascapes. We predicted that where seaweed farms were present, farmed seaweed would make up a significant portion of the diet, and that the presence of seaweed farming on Danajon Bank would lead to higher abundance, greater biomass, and larger size of individuals.

Both gut content and stable isotope analysis confirmed that rabbitfish eat farmed seaweed. Both analyses were qualitatively similar in that the amount of farmed seaweed increased in diets with increasing farm density. However, the results of the isotopic analyses in the HD

site indicated that, while farmed seaweed covered 100% of the area, it only comprised 50% of the total diet. The remaining diet consisted of wild brown turf algae in contrast to gut contents that consisted almost exclusively of farmed red algae. Similarly, in LD sites, isotopic analyses reflected a diet dominated by brown turf algae despite the presence of farmed seaweeds while gut contents results indicated a mixture of both farmed and wild brown seaweeds in diets. Analyses of fish from RA sites were in closer agreement, with both indicating that diets consisted exclusively of wild brown seaweeds. Differences in the relative amounts of wild and farmed seaweeds in gut content and isotope samples are consistent with the nature of the methods, which reflect dietary choices over different time scales (Davis et al. 2012). Farms at HD and LD sites almost exclusively contained farmed red seaweed regardless of the overall coverage of farms. As gut contents reflect the composition of recently ingested food (Hyslop 1980, Salayo et al. 2008, Davis et al. 2012), it is not surprising that “in-farm” collected animals had guts dominated by farmed seaweed. In contrast, one of the primary strengths of isotopic analysis is that it tends to reflect longer term dietary choices (Davis et al. 2012), thus the lower proportions of farmed seaweeds in the isotope samples suggests that through time, a wider variety of diet items are consumed even where seaweed farms dominate the seascape.

The presence of turf algae in diets from fish taken in the HD site raises questions about whether food availability or selectivity drives the dietary choices of the animals (*sensu* Schoener 1971 and Senft 1989) given the nearly exclusive cover of farmed seaweeds. Herbivorous fish have been typically shown to feed selectively (Paul and Hay 1986, Ireland and Horn 1991, Zoufal and Taborsky 1991, Ojeda and Munoz 1999, Pillans et al. 2004). A study conducted in Danajon Bank in the 1970s found that rabbitfish consumed brown turf algae more frequently than farmed algae, and that farmed reds were hardly ever eaten (Westernhagen 1974). Subsequent reef degradation over the ensuing 40 years has led to macro-algal dominance within Danajon Bank (Christie et al. 2006, Marcus et al. 2007), but this has not necessarily led to more food choices for rabbitfish. Degraded reefs tend to be dominated by macroalgae (Bellwood et al. 2004), which potentially provide a greater amount of food to herbivores. However, those same reefs tend to be dominated by a few algal types, typically consisting mostly of erect brown algae (Hoey and Bellwood 2009). Additionally,

extensive clearing of substrate within heavily farmed areas may further reduce dietary choices for rabbitfish.

While we had initially hypothesized that the density of seaweed farms would drive the proportion of farmed seaweed in rabbitfish diets, our results showed the differences among farming density was not significant. The lack of ordination in our results relative to farming density suggests that rabbitfish are not feeding in proportion to the relative availability of food items. In fact, over the longer term, farmed seaweed constituted at best half of rabbitfish diet even in the HD site where seaweed farms covered the entire area, suggesting turf algae is being consumed disproportionately to its availability. Furthermore, in RA sites with no seaweed farms and where degraded reefs are dominated by *Sargassum* spp. and brown turf algae, brown turf algae still overwhelmingly dominated rabbitfish diet despite *Sargassum* spp. comprising a significant portion of rabbitfish diet in other locations (Fox and Bellwood 2008, Fox 2012). While *Sargassum* spp. and farmed seaweed represent potential diet items in our study sites, rabbitfish appear to demonstrate a preference for brown turf algae, which implies some diet selectivity.

Diet selectivity can reflect a range of drivers (Brooker et al. 2012) and may relate to nutritional content (defined as energy, nitrogen concentration, carbon, carbohydrate, and ash-free dry mass (Hyslop 1980, Stein et al. 1984, Pillans et al. 2004), morphological characteristics which include size, shape, and relative toughness (Watson and Norton 1985, McShane et al. 1994, Pillans et al. 2004), or toxicity from defensive chemicals (Steinberg 1986, Targett et al. 1986, Ireland and Horn 1991, Pillans et al. 2004). The energetic content of farmed seaweeds (e.g., *Eucheuma* spp.) is higher than wild brown seaweeds with the former having higher protein and carbohydrate content than the latter (Villaluz 1953, Westernhagen 1974), suggesting this would be a preferred diet item. However, previous studies have shown that the relationship between herbivorous fish food choices and macrophyte nutrient content is rarely supported (Neighbors and Horn 1991, Sturm and Horn 1998). The selection of particular algae as a diet item for rabbitfish, and indeed the lower caloric value of consumed brown algae, suggest that diet composition is not related to the diet item's caloric and/or macronutrient value (Horn and Neighbors 1984, Neighbors and Horn 1991, Sturm and Horn 1998, Pillans et al. 2004). It remains unclear the extent to which

morphological differences between farmed seaweeds and wild brown seaweeds are a factor in diet selection for rabbitfish, since gut contents indicated that both are consumed frequently. While farmed carrageenophytes do contain secondary metabolites, as with morphological differences, it is unclear the extent to which they may discourage rabbitfish from consuming farmed seaweeds.

Acquisition risk has also been proposed as a driver of both diet selectivity (Brown 2003) and foraging behaviour (Pettersson and Bronmark 1993). In this study, rabbitfish appear to have traveled considerably farther than expected compared to other congeners in order to acquire wild brown seaweeds, a behaviour that may increase risk of predation (Brown 2003). Typical home ranges for siganids and other herbivores are on the scale of hectares, yet isotope data from the HD site indicated farmed seaweed comprised a maximum of 50% of rabbitfish diet, indicating movements in some instances of at least 2 kilometers distance across fairly deep channels, despite predation risk associated with such movements. However, it is important to note that rabbitfish also face the risk of being caught by fishers in seaweed farms, particularly at night. Thus the net trade-off of moving away from seaweed farms to consume brown seaweeds may be positive. While it is possible that the wild brown algae signature corresponds to another diet item within farms not included in this study, this is unlikely since farms were generally cleared of all substrate and algae. Moreover, in order to contribute such a high percentage to the diet of rabbitfish, an item would have to be relatively abundant, and thus unlikely to go unnoticed.

Disturbance associated with seaweed farming activities may also affect rabbitfish by altering diel foraging patterns (Karlson and Hurd 1993). Such disturbances include farmers maintaining lines or harvesting product. The potential for increased daytime activities to change endogenous rhythms in rabbitfish raises the question as to whether rabbitfish in our study area have always exhibited nocturnal feeding patterns. Previous to the implementation of wide-scale seaweed farming, rabbitfish on Danajon Bank were typically targeted in the afternoon when they could be found feeding on the shallow reefs (pers. comm. from local fishers). Critical then is to determine to what degree any decrease in foraging efficiency (due to nocturnal feeding conditions driven by disturbance) are compensated for by a decreased energetic costs of nocturnal feeding (MacArthur and Pianka 1966). Nocturnal feeding, while

not common in rabbitfish, has been previously documented in *Siganus lineatus* in the context of an interspecific shift in diel activity rhythm (Fox 2012). Flexibility in rabbitfish feeding patterns may represent the effect of external stimuli such as targeted fishing within seaweed farms encouraging animals to forage more widely or daytime disturbance encouraging animals to forage at night. If *S. canaliculatus* has indeed altered its diel feeding behavior, it may have the potential to provide further insight into biological rhythm plasticity (see Fox and Bellwood 2011).

We saw no evidence in this study that seaweed farms increased the abundance or biomass of rabbitfish, or that rabbitfish consumed large amounts of it when available. Placing seaweed farms on already degraded shallow reefs, typically dominated by algae, does not appear to represent an additional subsidy for herbivorous fish. The shift from coral to algal dominated rubble on Danajon Bank occurred before the introduction of seaweed farming and is most likely associated with the prevalence of destructive fishing practices and increased levels of pollution (Sievanen et al. 2005, Alcala and Russ 2006). Ostensibly, algal overgrowth of the reef creates more opportunities for herbivorous fish relative to other reef fish. But the current clearing of coral substrate associated with implementing seaweed farms removes wild seaweeds and replaces them with farmed. Subsequently, the introduction of farmed seaweed onto algae dominated reefs does not necessarily constitute the creation of an additional food source, but rather the replacement one food source with another.

The overall mean size of rabbitfish in our study was 7-11cm, which represents a 10% reduction from the mean of those observed 20 years previously in the same vicinity (Westernhagen and Rosenthal 1976). Such a reduction in overall mean size is characteristic of growth overfishing (Pauly 1988, Armada et al. 2009) and is indicative of the long term effects of unconstrained fishing effort within Danajon Bank (Christie et al. 2006, Armada et al. 2009, Hill et al. 2011). In areas with no fishing, such as no-take MPAs, animals may accumulate leading to higher abundance, biomass, and size (Roberts 2001, Halpern and Warner 2002, Harmelin-Vivien et al. 2008, Watson et al. 2009). Thus, it is likely that the patterns we see in our results are consistent with an MPA effect, where species richness and biomass are highest inside protected areas and then decrease with distance (Mcclanahan and Kaunda-Arara 1996, Russ et al. 2003, Alcala and Russ 2006, Stobart et al. 2009), since the

RA sites were in fact associated with MPAs. In this case, the lower species richness and biomass detected within farms reflects the spatial location of farmed sites were located farthest from RA sites (MPA effect), and therefore unrelated to the effect of the farms themselves.

The presence of seaweed farms may still lead to increased rabbitfish productivity, without biomass increase (Allen 1971, Beddington and Cooke 1983, Christensen and Pauly 1995). While UVC methods used for the fish assemblage data can give us a measure of relative abundance for rabbitfish among areas, abundance may not be indicative of productivity (as measured by sustained CPUE), particularly since the two are seldom proportional over both catch history and geographic range (Myers and Worm 2003, Maunder et al. 2006). As a result, any increases in rabbitfish productivity from increased farming may in fact be masked by the concentration of fishing effort within the farms necessitating quantifying CPUE within farms as a means to determine actual yield. However these data would need to be considered with caution as seaweed farms, like other human made structures, may also serve to aggregate rabbitfish populations (Bohnsack and Sutherland 1985, Bohnsack 1989, Pickering et al. 1999, Collins et al. 2002) and as a result CPUE data may exhibit hyperstability (Erisman et al. 2011).

Our study demonstrates that rabbitfish exhibit dietary selectivity, implying both movement and behavior were influenced by the wide scale introduction of seaweed farming. However, the presence of seaweed farms does not appear to increase rabbitfish productivity despite their potential to supplement rabbitfish diets. While we were only able to comprehensively sample five sites for dietary information, only one of which was an HD site due to restricted access, our study raises important questions about the impact of changing seascapes on herbivorous reef fish diet selectivity and behaviour.

The results of our study have implications for the management of shallow coral ecosystems. First, our study shows that rabbitfish consume farmed seaweeds but the high proportion of wild brown seaweed even in a high farm density site suggests that there is some selectivity towards non-farmed diet items, whether that is due to displacement or quality is unclear. The low abundance, biomass, and size of rabbitfish in both HD and LD sites relative to RA sites

suggests that farms are not increasing rabbitfish productivity in terms of standing biomass. Previous research suggests that there is a neutral or net negative effect of seaweed farms on fish assemblages despite the already degraded nature of these shallow coral reef ecosystems (Hehre and Meeuwig 2015). From the perspective of ecosystem-based fisheries management, particularly in the face of declining returns from fisheries depleted by over-extraction, destructive fishing practices, and habitat degradation over an extended period of time (Armada et al. 2009), the potential for the expansion of seaweed farming to provide increases in rabbitfish biomass has been of interest. However we see little evidence of increased abundance, biomass, and size. Therefore, the addition of farmed seaweeds is unlikely to function as a subsidy to rabbitfish diets, rather it acts as a replacement for the seaweeds removed in the implementation seaweed farms.

CHAPTER 4

Differential Response of fish Assemblages to Coral Reef-Based Seaweed Farming

4.1 Summary

As the global demand for seaweed-derived products drives the expansion of seaweed farming onto more shallow coral ecosystems, the effects of farms on fish assemblages remain largely unexplored. Shallow coral reefs provide food and shelter for highly diverse fish assemblages but are increasingly modified by anthropogenic activities. We hypothesized that the introduction of seaweed farms into degraded shallow coral reefs had potential to generate ecological benefits for fish by adding structural complexity and a possible food source. We conducted 210 transects at 14 locations, with sampling stratified across seaweed farms and sites adjacent to and distant from farms. At a seascape scale locations were classified by the level of their exposure to human disturbance. We compared sites where (1) marine protected areas (MPAs) were established, (2) neither MPAs nor blast fishing was present (hence “unprotected”), and (3) blast fishing occurred. We observed 80,186 fish representing 148 species from 38 families. The negative effects of seaweed farms on fish assemblages appeared stronger in the absence of blast fishing and were strongest when MPAs were present, likely reflecting the positive influence of the MPAs on fish within them. Species differentiating fish assemblages with respect to seaweed farming and disturbance were typically small but also included two key target species. The propensity for seaweed farms to increase fish diversity, abundance, and biomass is limited and may reduce MPA benefits. We suggest that careful consideration be given to the placement of seaweed farms relative to MPAs.

4.2 Introduction

Seascapes are being transformed on a global scale (Halpern et al. 2008) with human activities creating mosaics of modified habitat. This is particularly true for spatially extensive extractive activities like fishing, which result in dwindling residual areas of marine wilderness (Pauly et al. 2002, Graham and Mcclanahan 2013). While it is generally recognized that changes in activities will lead to impacts, the nature of these impacts on the regional ecology remain difficult to predict (Spaling and Smit 1993). Until recently, most studies have largely ignored species distributions within human dominated areas, focusing instead on the last remnants of wild nature in order to preserve them (Ricketts et al. 2001, Tschardt et al. 2005). For instance, recent research has documented the connection between the intensity of human activity and subsequent changes in ecosystems, including declines in diversity (Folke et al. 1996, Chapin et al. 1998, Bergman et al. 2001, Sievanen et al. 2005, Eklöf et al. 2006), occurrence of invasive species (Robinson 2008, Hulme 2009, Burke and Spalding 2011), or habitat homogenization (Sievanen et al. 2005, McKinney 2006, Smart et al. 2006, White and Kerr 2007, Armada et al. 2009). This suggests that modified ecosystems are increasingly extensive over large areas of the world (Allen 2008, Hobbs et al. 2009).

The transformation of seascapes has significant implications for fish communities since fish assemblage structure is strongly correlated to habitat (Friedlander and Parrish 1998, McClanahan et al. 2001, Vlach et al. 2005, Pusey 1977). The introduction of new human activities that alter fishing mortality or habitat can lead to changes in species diversity (Folke et al. 1996, Chapin et al. 1998, Bergman et al. 2001, Sievanen et al. 2005, Eklöf et al. 2006), abundance (Hughes et al. 1998, DeMartini et al. 2008), and biomass (McClanahan et al. 2007), as well as changes in community composition (Micheli and Halpern 2005), size structure (Dulvy et al. 2004a), and distribution (Dulvy et al. 2004b) of fish assemblages. The degree to which these anthropogenic activities affect fish will be related to the nature of both the habitat and the activities. For instance, in less impacted shallow coral reef ecosystems, where the percentage of living coral is relatively high compared to dead coral or rubble, coral cover decreases with increasing human presence through the combined effects of trampling, shading, siltation, and mechanical damage (Sievanen et al. 2005). Conversely, in highly

disturbed areas where the majority of coral is already dead, the impacts/influence of any additional human disturbance may not be detectable. In fact, it is conceivable that human presence may serve to benefit underlying benthos in some cases by reducing some of the most destructive activities, like blast and cyanide fishing, and replacing them with less destructive ones (Sievanen et al. 2005).

Seaweed farming provides a useful case study for the addition of new, potentially less destructive human activities within already degraded environments because of both its scale and ubiquity in tropical regions. Commercial harvesting occurs in approximately 35 countries around the world in waters ranging from cold temperate to tropical, providing a variety of products that, in 2008, had a total annual value of US\$7.35 billion (Fisheries 2010). In the Indo-Pacific region, seaweed farming consists mostly of small subsistence farms ($> 1 \text{ ha}^2$), and their proliferation is in large part governed by both accessibility to useable habitats and proximity to markets (Sievanen et al. 2005). As demand for seaweed derived products increases, farms once primarily located on shallow seagrass beds (Bergman et al. 2001, Crawford 2002, Eklöf et al. 2005, 2006, Lyimo et al. 2006) are now expanding into new locations that consist almost exclusively of shallow coral reefs (Crawford 2002). In addition, foreign corporations are converting large areas of patchy small community farms into extensive industrial-scale ventures (Armada et al. 2009). The potential ecosystem impacts of this expansion include loss of coral cover through increased siltation, trampling, shading, and impairment of recruitment ability (Sievanen et al. 2005). The subsequent impacts on fish communities, as well as the potential for direct disturbance, may cause further declines in fish diversity and abundance, with important implications for food security.

Little information currently exists on the ecological impacts of seaweed production on shallow coral reef ecosystems or the fish assemblages they support. Indeed, previous research has solely focused on single facets of farm impacts such as shading, siltation, and mechanical damage, and has been conducted primarily within seagrass beds, typically at the level of individual farms (Bergman et al. 2001, Sievanen et al. 2005, Eklöf et al. 2006). However, shallow coral reef ecosystems are important biologically and socioeconomically; they are hotspots of diversity and productivity, maintain protective barriers for coastlines, and provide

a source of livelihood and sustenance to over a million small-scale fishers (Burke and Spalding 2011).

Here, we investigated the impact of seaweed farming on fish assemblages in a rare shallow double barrier reef ecosystem, Danajon Bank of the Philippines. The Philippines is the third greatest producer of farmed seaweeds internationally (Mathiesen 2012), and farming on Danajon Bank is a growing industry that is expanding rapidly across the entire system (Sievanen et al. 2005, Armada et al. 2009). We hypothesized that in degraded coral ecosystems, seaweed farming would have a positive effect on the species richness, abundance, and overall biomass of fish assemblages as it adds structural complexity and food to the habitat (Sievanen et al. 2005). As seaweed farms may also be located near marine protected areas (MPAs) and/or be exposed to blast fishing, we were additionally interested in the effects that the level of nearby protection/disturbance may have on the relationship between seaweed farms and fish assemblages. Specifically, we tested whether locations with well-enforced MPAs (where disturbance was relatively low), would have higher diversity, abundance, and biomass due to both benefits from the seaweed farms and spillover effects from the MPAs. In locations subject to blast fishing (and thereby more highly disturbed), seaweed farms may function as *de facto* MPAs, augmenting fish diversity, abundance, and biomass.

4.3 Methods

4.3.1 Study Area

The Philippines is located in the heart of the Coral Triangle, an area that encompasses the Indonesia-Philippines and the Southwestern Pacific biogeographic regions, and is widely considered to be the global epicenter of marine biodiversity (Allen 2008). Situated off the northern shore of Bohol Island, Danajon Bank is the only double barrier reef in the Philippines and one of only three such reefs in the Indo-Pacific region (Pinchon 1977). The reef stretches over a total area of 2,353 km² comprising 40 islands and represents 1% of the 27,000 km² of estimated total coral reef cover in the Philippines.

Most seaweed farming on Danajon Bank is of *Eucheuma spinosum* and *Kappaphycus alvarezii* and is practiced on an artisanal scale, although Taiwanese and South Korean interests operate a number of large-scale industrial farms. While several different farming techniques are employed on Danajon Bank, *E. spinosum* is produced primarily through a broadcast method whereby seedlings are simply cast out onto the shallow coral and harvested at a later date. In contrast, *K. alvarezii* is primarily farmed by attaching seedlings to nylon monolines anchored with a series of mangrove stakes on coral substrate which were generally laid parallel to the reef situated in shallow water between the reef drop off and the shoreline. These two methods were the only ones encountered and co-occurred at each of the study sites. As monoline farms are clearly delineated by stakes, they were the focus of our study. The depth of these farms varied between a few centimeters to 1 m at mean low tide to ensure propagules were not exposed during low water.

Blast fishing is still common in some communities on Danajon Bank (author's pers. obs.), although its exact history within the study area is difficult to determine. Local oral histories date the genesis of blast fishing to the late 1950s or early 1960s. This aligns with the consensus of experts in the Philippines Bureau of Fisheries and Aquatic Resources (BFAR) as well as several regional NGOs that blast fishing in this area has been chronic over a long period of time. The presence of cratering indicates that blast fishing has contributed to the extensive rubble fields observed. Our own estimates, based on the advanced weathering of the rubble, places some of the damage to be several decades old and as witnessed, the practice continues to this day. Regardless of the time frame, extensive blast fishing is most likely the cause of the general homogenization of habitat within some locations, and may potentially impede coral recovery for decades if not centuries (Fox et al. 2003; Fox and Caldwell 2006).

4.3.2 Sampling

Fish assemblages were first sampled at Handumon between mid June and the end of July in 2010. Following this pilot work, the remaining 13 locations were sampled from mid June to mid-September, 2011. All sampling was done using standard underwater visual fish census (UVC) methods (English 1997). We identified 14 locations (~2.3 km² each) across Danajon

Bank, where seaweed farms were present (Figure 4.1; Table 4.1). At each location, sampling sites (<2500 m² each) were established (1) within the seaweed farm (SF), (2) adjacent (ADJ) to the farm (but no further than 5 m from the farm edge) and (3) at a distance from the farm (FAR) (at least 100 m from the farm edge and in an area that had never been farmed). These three classifications represent an ordinal ranking of potential impacts, with the latter acting as a reference/control category. Adjacent sites were chosen to be as close as possible to farm sites without necessarily being in immediate contact with them due to the placement of impediments like netting and poles. FAR sites were a minimum of 100 m to ensure maximum separation from SF and ADJ sites. Additionally, because of the varying layout of the monolines within farms, farm size was estimated from the location of the mangrove stakes that demarcated their perimeters. Five transects were completed within each site, each measuring 20 m x 5 m due to local visibility conditions. Transects were laid parallel to the reef to control for depth which ranged from 0.0m at mean low tide to 2.0m at mean high tide.

Locations were classified with respect to the presence (MP) or absence (“unprotected”, UP) of MPAs and/or blast fishing (BL) with additional information compiled on farm size, distance to market, island area, and population (Table 4.1). Information on the history of MPAs was obtained from local community members, government representatives, and NGO databases. The occurrence of blast fishing was initially based on fisher reports, which were later confirmed by visual evidence (blast craters or directly witnessing the blast fishing itself); it did not include the use of small blasting caps employed by farmers to drive rabbitfish from farms as this practice neither destroys habitat nor kills the fish.

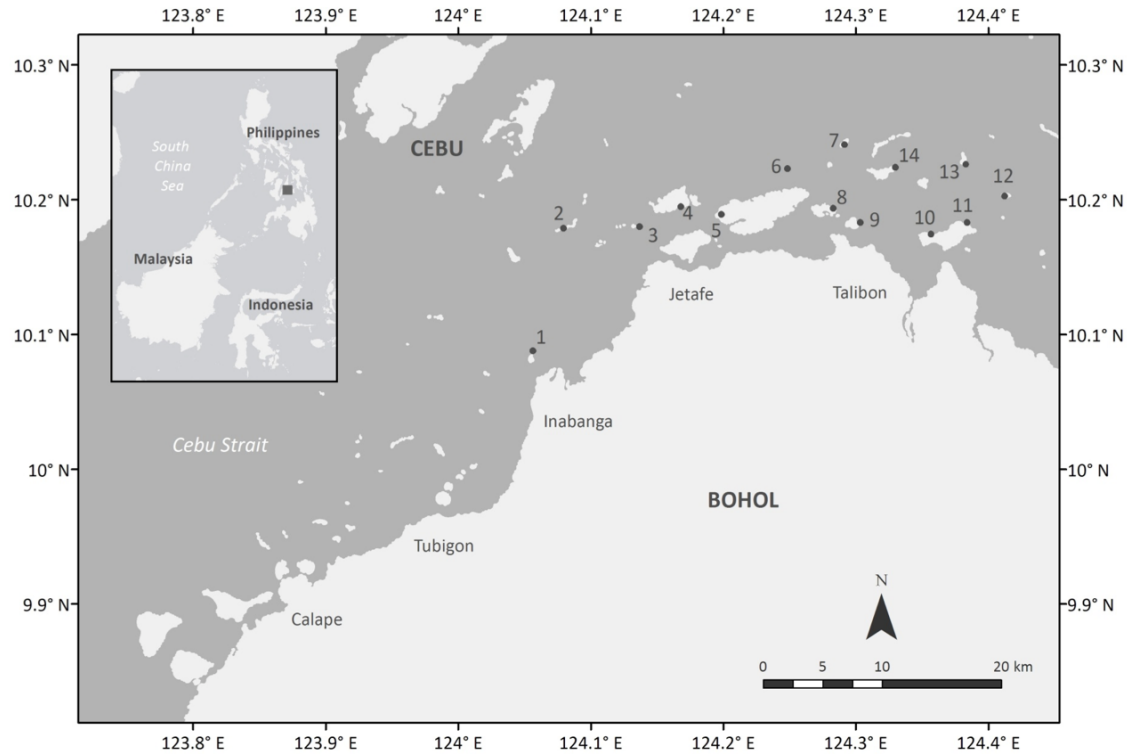


Figure 4.1. Map of the study area, showing the location of sampling sites. (1) Pandao, (2) Pandanon, (3) Jandayan Sur. (4) Jandayan Norte, (5) Handumon, (6) Tahong Tahong, (7) Guindacpan, (8) Tambo, (9) Banbanon, (10) Busili-an, (11) Pinamgo, (12) Cataban, (13) Saag, (14) Bansa.

Three locations were classified as having well-enforced no-take MPAs, and as they were the only unfarmed areas within the location, served as our FAR sites. Four locations had extensive levels of blast fishing (both historical and current), and a further seven had neither effective MPAs nor blast fishing. Transect starting point coordinates were assigned using a random number generator and transects were separated by a minimum of 5 m. Transects were only conducted if visibility allowed for clear sight of at least 5 meters forward and 5 meters wide. We used free diving techniques to maximize time underwater without requiring SCUBA apparatus, which presented a risk of diver entanglement within seaweed farms. Fish surveys were conducted ten minutes after the line was laid, and passes along transects were timed to maximise consistency. Surveys were generally undertaken in the first pass along transects (Bellwood 1988, English 1997), unless large numbers of fish were detected. In these cases, two passes were performed: the first to identify more mobile species, the second

focusing on the more sessile/cryptic ones. Individual fish within the belt transect were identified to species level and body lengths were estimated based on training sessions with metal cut outs near sample sites prior to the census (Sale 1998). The same investigator conducted all fish transects.

Table 4.1. Summary of sampling locations, in increasing order of farm size. Attributes include the presence/absence of marine protected areas (MPAs), the date of MPA establishment (where applicable), the presence/absence of blast fishing, the size of the seaweed farm and its distance to the nearest port, and the size of, and number of residents on, the associated island (Pop. size).

Location	Farm size (m ²)	Blast	MPA established*	Enforced MPA	Distance to port (km)	Islandsize (ha)	Pop.size
Busili-an	500		2007	✓	4.93	4.28	1654
Pinamgo	500	✓	2002		4.93	4.28	1654
Pandao	600		2002		3.88	0.01	0
Guindacpan	625	✓	1996		9.39	0.13	2204
Tahongtahong	700	✓	N/A		13.4	0.01	200
Saag	750		1997		6.54	0.36	640
Pandanon	900	✓	1996		10.5	0.29	2062
Cataban	1050		1996	✓	6.58	0.7	1251
Bansaan	1050		1994		7.17	1.17	1500
Banbanon	1225		2002		6.62	0.6	0
Jandayan Sur	1300		2002		0.85	4.52	2481
Jandayan Norte	1450		2002		1.88	4.52	2481
Handumon	1500		1995	✓	3.5	4.52	2481
Tambo	2025		N/A		4	1.25	150

* Source: <http://acc coast.bmb.gov.ph/database/mpa-database>

4.3.3 Analysis

Univariate attributes of the fish assemblage included the number of species, total fish abundance, and total fish biomass. While species numbers and total abundance were estimated directly, biomass values were derived from species-specific length-weight relationships whereby the weights of individual fish (or a similarly sized congener or

confamilial, where unavailable) were calculated from *in situ* estimates of lengths and then summed (Froese and Pauly 2014). Mean values of species richness, total abundance, total biomass, and individual species' abundances per transect were then averaged at the site level (SF, ADJ, FAR) for each location (henceforth referred to as transect-1).

We tested for the effects of farming (SF, ADJ, FAR) and disturbance (MP, UP, BL) on univariate and multivariate attributes of the fish assemblages using permutational techniques (Clarke 2006, Anderson et al. 2010). Given the sampling occurred during the summer period of two consecutive years at 1 and 13 locations respectively, we reran all analyses without Handumon to test for the potential of this location to influence the results, either because of its innate differences or because of the earlier sampling period. Because the effects of blast fishing and MPAs are likely to occur at the scale of locations (~2.3 km²) rather than sites (<2500 m²), the analysis was conducted at the former spatial scale. Specifically, Russ (2003) clearly demonstrated spill-overs from effective MPAs and Fox (2003) and Fox and Caldwell (2006) have documented the spatially extensive impacts of blast fishing. A two-way fixed effects PERMANOVA was used to test the effects of seaweed farming and disturbance on species richness, abundance, and biomass, based on a Euclidean distance matrix with no variable transformation (Anderson 2011). We chose a design where location (LOC) a random factor with 14 levels, and the degree of seaweed farming present (FARM) a fixed factor with three levels, were nested in the amount of human disturbance present (DIS), also a fixed factor with three levels (Quinn and Keough 2002). Additionally, where results for PERMANOVA were significant, pairwise tests among levels of FARM were conducted (Fujii et al. 2014). A test of variance using PERMDISP indicated no effect or dispersion ($p>0.05$). We square root transformed the multivariate data on species abundances to reduce the influence of relatively abundant species and then calculated the Bray Curtis dissimilarity matrix. PERMANOVA was then used to test for the effect of farming and disturbance on species composition. Additionally, an unconstrained principal coordinate analysis (PCO) was also run using the distances among centroids to visualize both the relative size of the effects and the interactions contained in the model. Similarity percentage (SIMPER) analyses were conducted to identify the key species distinguishing assemblages as a function of farming and disturbance. Specifically, we identified the top five species that most contributed to

dissimilarity between all pairwise combinations of significant factors. All analyses were run in software PRIMER v6.0 (Clarke 2006, Anderson et al. 2010).

4.4 Results

We sampled 210 transects at 42 sites within the 14 locations, capturing data on 80,186 individual fish representing 143 species from 38 families. Fish lengths varied from 1 cm to 40 cm, and small, reef-associated individuals/species generally dominated the assemblage.

Table 4.2. Univariate permutational analysis of variance (PERMANOVA) of the effects of seaweed farming (FARM) and human disturbance (DIS) on fish species richness, abundance and biomass. Sampling locations were either subject to blast fishing (BL), unprotected (UP) or protected (MPA). Within these locations, three types of sites were examined: seaweed farm sites (SF), adjacent sites (ADJ) and far sites (FAR). Location (LOC) is a random factor nested in both FARM and Disturbance, which are fixed factors, reporting degrees of freedom (df), sums of squares (SS), mean squares (MS), F values and p. All Pairwise tests significant at $p < 0.001$.

	Source	P(perm)	df	SS	MS	Pseudo-F
Species richness	DIS	NS	2	218.61	109.30	3.11
	FARM(DIS)	NS	6	137.94	22.99	0.90
	LOC(DIS)	1.00E-05	11	384.64	34.97	6.99
	FARM(DIS)xLOC(DIS)	1.00E-05	21	540.20	25.72	5.14
	Residuals		169	845.8	5.0047	
Abundance	DIS	NS	2	714.49	357.25	0.16
	FARM(DIS)	NS	6	15833.00	2638.80	1.34
	LOC(DIS)	0.002	11	24953.00	2268.40	3.27
	FARM(DIS)xLOC(DIS)	0.001	21	41476.00	1975.00	2.85
	Residuals		169	1.17E+05	693.41	
Biomass	DIS	0.02	2	3.73E+06	1.86E+06	6.07E+00
	FARM(DIS)	0.0034	6	5.41E+06	9.01E+05	4.69E+00
	LOC(DIS)	0.005	11	3.36E+06	3.05E+05	2.54E+00
	FARM(DIS)xLOC(DIS)	0.05	21	4.05E+06	1.93E+05	1.61E+00
	Residuals		169	2.03E+07	1.20E+05	

4.4.1 Species Richness, Abundance and Biomass

Species richness, averaged by site, varied from 5.1 to 11.3 transect-1 across the 14 locations, with a mean of 8.19 (SE = 1.82). Total abundance and biomass ranged from 17.2 to 96.9 transect-1 and 93.1 to 916.6 g transect-1 respectively, with means of 35.1 transect-1 (SE = 20.71) and 441 g site-1 (SE = 230). Biomass generally declined with proximity to seaweed farms regardless of the level of disturbance (Table 4.2) but abundance and species richness did not. For biomass, pairwise tests among levels of FARM showed between (p=0.022) and MPA sites (Figure 4.3). There was clear directionality in species richness as a function of farming in locations where MPAs were present, with the highest species richness in FAR sites and the lowest in SF sites (Figure 4.2). We found the same directionality for total abundance in locations subject to blast fishing, with highest abundances occurring in FAR sites and the lowest abundances in SF sites. No differences were detectable in locations that were unprotected or where MPAs were present (Table 4.2; Figure 4.2). Biomass increased with distance from seaweed farms (Figure 4.2) in the presence of an MPA but was indistinguishable when comparing sites at unprotected and blast locations. There was no change to the significance of tests when the Handumon location was excluded from the analysis.

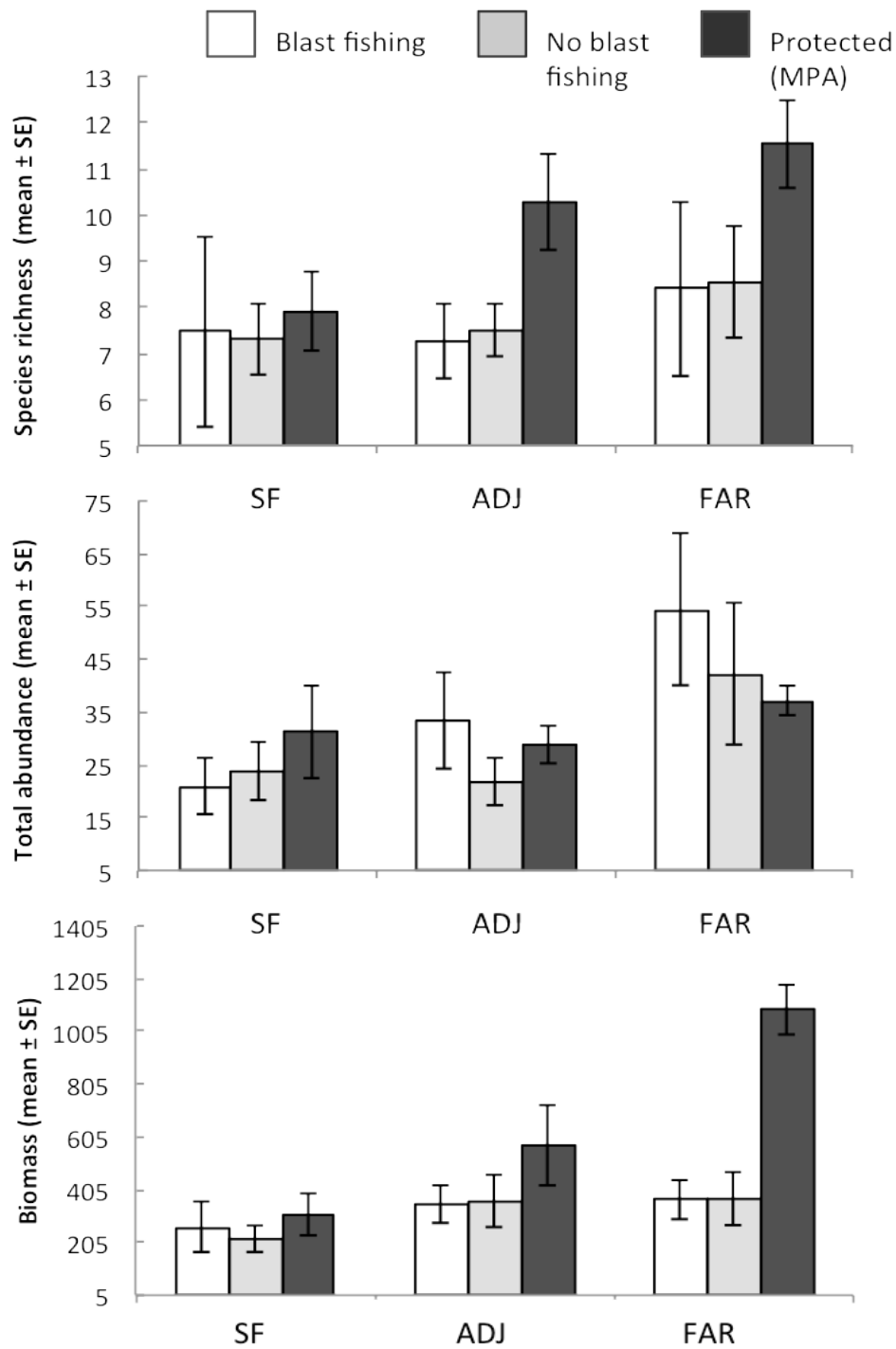


Figure 4.2. Impacts of human disturbance on the abundance, biomass and diversity of reef-associated fish in Danajon Bank. SF indicate sites where seaweed farming occurs, ADJ and FAR are adjacent and far sites, respectively. Values represent site-specific averages.

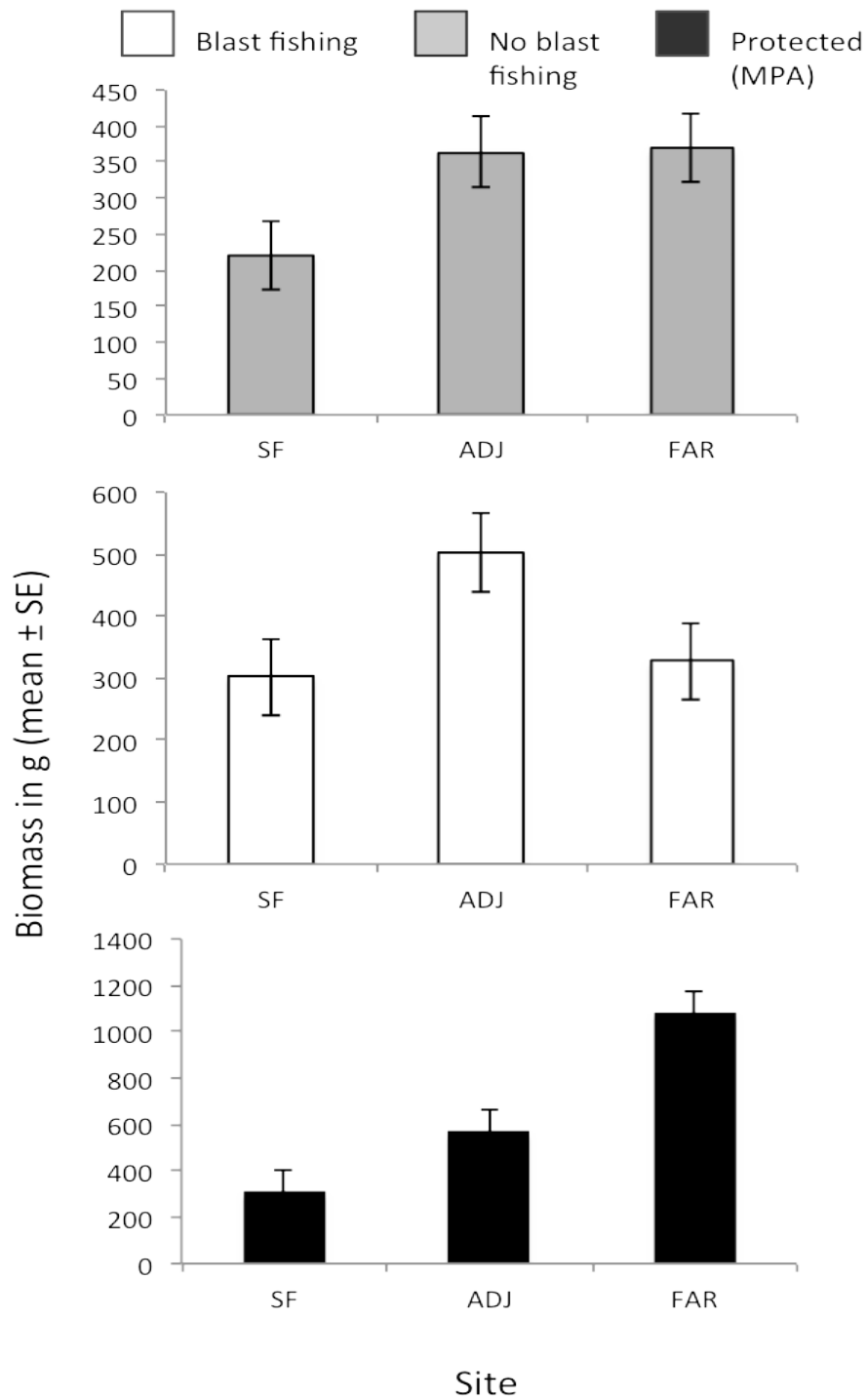


Figure 4.3. Impacts of human disturbance on the abundance, biomass and diversity of reef-associated fish in Danajon Bank. SF indicate sites where seaweed farming occurs, ADJ and FAR are adjacent and far sites, respectively. Values represent site-specific averages.

4.4.2 Species Assemblage Composition

Species assemblage composition varied significantly the level of disturbance (MP, UP and BL) among islands ($p = 0.0001$) and there was a significant interaction between the level of farming which was present (SF, ADJ, FAR) and the location as a function of the level of disturbance ($p = 0.0001$; Table 4.3). The greatest differences in assemblage structure within locations were for those locations with MPAs, where a directional gradient from seaweed farms to sites distant from the farms could be observed (Figure 4.4). Locations without MPAs, whether subject to blast fishing or not, had clear differences in their assemblages between the effects of seaweed farms, but lacked clear directionality (Figure 4.4).

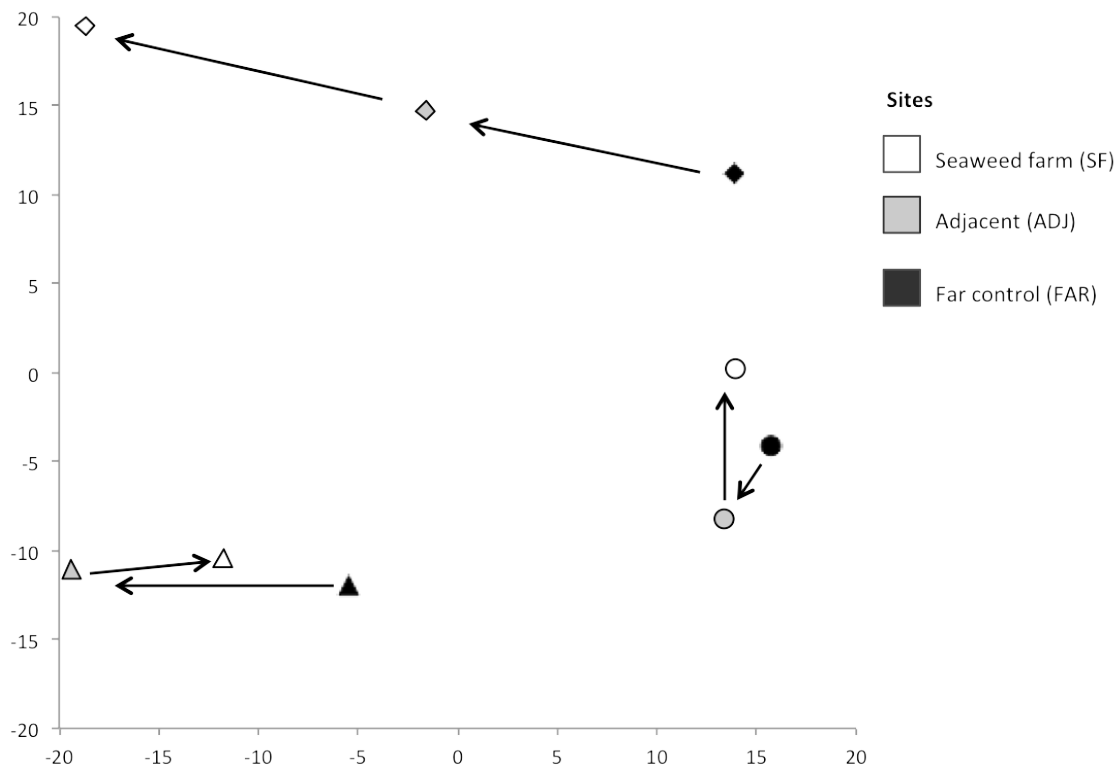


Figure 4.4. Principal coordinates analysis (PCO) showing the centroids for Location (MPA = diamond; and UP = circle; BL = triangle; and FARM levels (SF = black; ADJ = grey; and FAR = white).

Table 4.3. Multivariate permutational analysis of variance (PERMANOVA) of the effects of seaweed farming (FARM) and human disturbance (DIS) on fish species richness, abundance and biomass. Sampling locations were either subject to blast fishing (BL), unprotected (UP) or protected (MPA). Within these locations, three types of sites were examined: seaweed farm sites (SF), adjacent sites (ADJ) and far sites (FAR). Location (LOC) is a random factor nested in both FARM and Disturbance which are fixed factors, reporting degrees of freedom (df), sums of squares (SS), mean squares (MS), F values and p. All Pairwise tests significant at $p < 0.001$.

	Source	P(perm)	df	SS	MS	Pseudo-F
Assemblage	DIS	0.16	6	34079	5679.8	1.182
	FARM(DIS)	0.25	2	50086	25043	1.1734
	IS(DIS)	0.0001	11	2.33E+05	21215	11.052
	FARM(DIS)xIS(DIS)	0.0001	21	1.01E+05	4824.6	2.5134
	Residuals		173	3.24E+05	1919.6	

We identified eight species that corresponded to the effects of farming and disturbance. These included small species such as the damselfishes *Amblypomacentrus breviceps*, *Dascyllus aruanus*, *Pomacentrus chrysurus* and *Pomacentrus opisthostigma*, the cardinal fish *Apogon magaritiphorus*, a small wrasse *Halichores scapularis*, and medium grazers such as the parrotfish *Scarus ghobban* and the rabbitfish *Siganus canaliculatus*, both of which are also important target species. Distinct differences were evident in the abundance of these indicator species, separating the locations with blast fishing from those without. In locations where blast fishing was present, the assemblage was dominated by *D. aruanus*, which feeds on plants and invertebrates and tends to inhabit isolated coral heads in small groups (Froese and Pauly 2014); its numbers systematically declined with proximity to seaweed farms. Additionally, *A. magaritiphorus*, a small omnivorous cardinal fish (Froese and Pauly 2014) was also present in blast fishing locations but was also more common in seaweed farms. *Amblypomacentrus breviceps*, known to frequent rubble in sand or silty areas (Froese and Pauly 2014), was also common in seaweed farms regardless of the presence or absence of blasting (Figure 4.5). Of the two medium sized species, *S. canaliculatus*, an obligate herbivore, was present only in farmed sites in locations subject to blast fishing, while *S. ghobban*, a grazer known to feed on both detritus and plants (Froese and Pauly 2014), was most common in locations with MPAs and more common in the near controls of locations subject to blast fishing or unprotected (Figure 4.5).

4.5 Discussion

Our objective was to understand how seaweed farms influence shallow coral fish assemblages, given the increasing fragmentation of seascapes driven by this rapidly growing sector. The expansion of seaweed farms on Danajon Bank is also occurring in the context of MPA establishment and ongoing destructive practices such as blast fishing, which result in a complex and constantly evolving matrix of human use. We hypothesized that seaweed farms may generate ecological benefits by creating habitat and providing a food source for other fishes (Sievanen et al. 2005) in otherwise generally degraded seascapes (Christie et al. 2006). Specifically, because seaweed farms potentially added both habitat structure and a food source, we predicted that the fish assemblages would exhibit greater diversity, abundance, and biomass in closer proximity to seaweed farms.

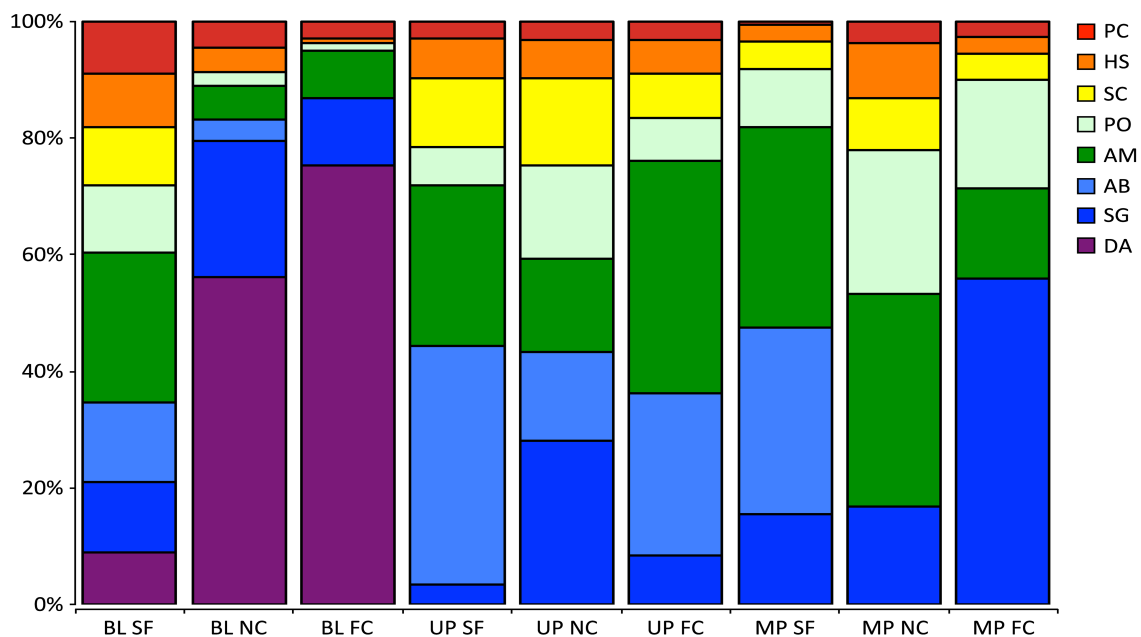


Figure 4.5. Similarity Percentage Analysis (SIMPER) of total abundance for top eight species present at each of 14 locations : *Amblypomacentrus breviceps* (AB), *Apogon margaritophorus* (AM), *Dascyllus aruanus* (DA), *Halichoeres scapularis* (HS), *Pomacentrus chrysurus* (PC), *Pomacentrus opisthostigma* (PO), *Siganus canaliculatus* (SC), and *Scarus ghobban* (SG), where locations were ranked along a gradient of disturbance from: blast fishing with no protected area present (BL), no blast fishing but no protection (UP), and no blast fishing with a protected area present (MP).

Our results generally suggested the opposite, with species richness and total biomass tending to decline with proximity to seaweed farms, regardless of whether blast fishing or an MPA was present, and with total abundance showing few systematic differences. These results were consistent with previous studies on seaweed farms established on seagrass communities (Bergman et al. 2001, Eklöf et al. 2006) and with patterns observed in other regions where habitat homogenisation occurred (Hewitt et al. 2005, Thrush et al. 2006, Airolidi et al. 2008, Graham and McClanahan 2013). Specifically, seaweed farms located in seagrass habitats negatively alter macrofaunal community composition as well as large invertebrate epifauna and fish communities (Bergman et al. 2001, Eklöf et al. 2006). In homogenized habitats, the further loss of ecological function can actually be proportionally greater than expected from simply an overall decline in species richness, possibly due to the fact that those species that are lost tend to be non-randomly distributed among functional and ecological categories, but tend to include larger specialist species and therefore have a disproportionately large effect on the physical and biological environment (Dobson et al. 2006, Thrush et al. 2006, Airolidi et al. 2008). The fact that FAR sites typically had greater biomass than seaweed farms and their adjacent areas may indicate that the latter lack suitable habitat/cover for these animals and/or that the level of human activity within and adjacent to the farms is sufficiently disruptive to drive fish away. Reported impacts of seaweed farms on coral habitat include trampling, shading and siltation (Sievanen et al. 2005). Such disturbances could potentially have a range of effects including the fragmentation, degradation or loss of preferred habitat (Julian Caley et al. 2001). As many reef associated fishes display specific habitat requirements, such as food sources, recruitment habitat (Graham et al. 2006), or topographical complexity (e.g. holes, crevices, or occupying caves) (McCormick 1994), seaweed farms have the potential to negatively affect both the biological and physical structure of shallow coral reefs, which in turn may result in a loss of diversity, and decreases in abundance and biomass (Thrush et al. 2006).

The effect of farming was greatest in those locations with effective MPAs. These locations tended to have higher biomass within the MPA (FAR sites) relative to the associated seaweed farms and adjacent sites, with species richness, and abundance showing less clear patterns. Such patterns are consistent with those typically reported for MPAs, where species richness,

and biomass are highest inside, but then decline with increasing distance from the MPA (Alcala and Russ 2006, Stobart et al. 2009, Barrett et al. 2009). Moreover, the scale of the relative differences between MP sites and seaweed farms was also consistent with previous MPA studies: species richness was approximately 30% greater in the MPAs relative to typical reports of 20-30% increases and biomass was 300% higher relative to unprotected areas (Halpern 2003). It is therefore likely that the observed increases in total biomass with distance from the seaweed farms were due to the beneficial effects of the MPAs rather than a negative effect of the seaweed farms at these locations. Moreover, there is no evidence that the seaweed farms are generating benefits to the fish assemblages. Unprotected locations and those with blast fishing had lower diversity and biomass than did locations with MPAs, and indeed, were relatively indistinguishable (Dobson et al. 2006, Fox and Caldwell 2006, Thrush et al. 2006, Airolidi et al. 2008). The exception to this pattern appeared in FAR and ADJ sites where total abundance was higher in both unprotected and blasting locations. This was due to their respective assemblages being dominated by numerous, small-bodied fish like *A. magaritaphorous*, which was commonly found among patches of rubble and debris (Author's pers. obs.).

Abundance showed similar patterns to species richness and biomass at locations without MPAs. In these locations, abundance was on average 1.8 and 2.6 times greater in FAR sites than in seaweed farms in unprotected and blast fishing locations respectively. This was an unexpected result because the habitats in locations subject to blast fishing or unprotected were generally severely degraded (author's pers. obs.). The driver of high abundance at FAR sites at blast locations was the small damselfish *D. aruanus*, which has an affinity for live branching coral and a dislike of disturbed reef habitat (Sale 1972, Sweatman 1983). However, based on observations in the field, it was notable that the *D. aruanus* was exclusively observed in high numbers on the last remaining pieces of branching coral in these locations. This may be due in part to several coinciding factors including that once seaweed farms are in place, blast fishers avoid the farms and their general vicinity due to social constraints (Sievanen et al. 2005). This was evident in communities on Danajon Bank where blasting was prevalent, but considerable care was taken to avoid damaging neighbouring seaweed farms (author's pers. obs.). In locations with blast fishing, seaweed farms also

tended to be heavily cleared and the coral rubble piled outside the perimeter of the seaweed farm. In these locations, the displaced coral rubble was frequented by large numbers of small fish such as *A. margaritaphorous*, which find themselves sandwiched between two structurally degraded environments, one the result of blast fishing (Fox and Caldwell 2006) and the other the result of intentional clearing.

Univariate and multivariate analysis were in good agreement, and showed that species composition varied most with level of disturbance, as evidenced by the strong separation of locations between those with MPAs, those that are unprotected and those subject to blast fishing. In locations with MPAs, the shift in fish assemblage from small species such as *A. margaritaphorus* in the seaweed farms to larger target species such as the parrotfish *S. ghobban* in the MPAs is consistent with effective protection of target species and increase in mean size (Halpern 2003, Stobart et al. 2009). The lack of directional differences in the assemblages of unprotected and blast locations may reflect the relatively depauperate composition of these locations, such that differences between sites as a function of distance from seaweed farms are difficult to discern (Hughes 2012). Fish assemblages within Danajon Bank are under continual disturbance from a variety of anthropogenic sources including destructive fishing practices, clearing, trampling, and exposure to pollution (Sievanen et al. 2005, Alcala and Russ 2006). These locations may simply have reached a resultant level of habitat degradation where the only constituent members of the fish community to fill this niche are the few species that can tolerate high levels of anthropogenic disturbance (Thrush et al. 2006, Airolidi et al. 2008).

We identified a set of eight indicator species that distinguished sites on the basis of seaweed farming and the presence/absence of blast fishing and MPAs, out of the 143 species recorded. That only eight species accounted for the vast majority of differences between locations potentially reflects the already relatively species-reduced nature of the region (Christie et al. 2006). Locations subject to blast fishing were characterised by very small species such as *D. aruanus*, *A. margaritaphorous*, *P. bifasciatus* and *P. opisthostigma*. This pattern is consistent with other studies that document the role of blast fishing in decreasing structural complexity of coral reefs, thereby favouring dominance by small, disturbance-tolerant species (Hughes 1994, Fox et al. 2003, Fox and Caldwell 2006). Two of our indicator species, *S. ghobban* and

S. canaliculatus, are relatively large bodied herbivores that are highly sought as food fish on Danajon Bank (Soliman et al. 2008), and were more common at MPA sites. Of particular interest was *S. canaliculatus*, as seaweed farmers report that this rabbitfish forages heavily on farmed seaweeds, likely due to their reported obligate herbivory (Sale 1991). Accordingly, we had expected to see increased numbers associated with seaweed farms, however this was not reflected in the data. The lack of rabbitfish in the seaweed farms may reflect both the use of small blasting caps to drive away this perceived crop pest and pressure ensuing from targeted spearfishing (Hehre, pers. obs.). It may be that fishing pressure is sufficient to maintain low numbers of rabbitfish even within seaweed farms despite their potential as a supplementary food source.

These results have significant implications for seascape management. First, we found no evidence to suggest that seaweed farms have the potential to generate benefits with respect to fish assemblages. Moreover, abundance and biomass decreased with proximity to seaweed farms even in locations subject to blast fishing or that are otherwise unprotected. This suggests that there may be a net negative effect of seaweed farms on fish assemblages despite the already generally degraded nature of these shallow coral reef ecosystems. Second, our study confirmed the importance of MPAs for fish in shallow coral habitats since the presence of MPAs was the most influential determinant of species richness and biomass. Both points are particularly important because seaweed farms currently bound no-take MPAs and there have been proposals to include seaweed farms within no-take MPAs, rendering them multiple-use MPAs. Specifically, some of these proposals involve using seaweed farms as physical buffers against destructive fishing practices as well as integrating seaweed farming within the boundaries of MPAs in order to potentially gain political consensus for the expansion of protected areas. Seaweed farming has typically been perceived as “ecologically friendly”, with minimal negative effects on fish or benthos in already degraded ecosystems with the added benefit that the presence of farm workers can act as a means of MPA enforcement. We argue that seaweed farms can have a negative impact on fish assemblages and that fish within MPAs, as currently enforced, are more diverse, abundant and larger than those observed in farms. To this end, the placement of seaweed farms should be carefully and

cautiously considered, with particular attention being drawn to farm sites adjacent to, or located within, MPAs.

The regional scale of our study allowed us to test the effects of seaweed farms on fish assemblages against existing practices that include the over-exploitation of fisheries resources and the presence of destructive fishing (Armada et al. 2009), as well as the positive introduction of MPAs. Seaweed farming has become an important source of income to families dependent on increasingly sparse catch returns (Hill et al. 2011). However, in spite of the initial promotion of seaweed farming as an alternative livelihood, there remains little evidence that farming mitigates fishing pressure (Hill et al. 2011), or provides benefits for constituent shallow coral fish assemblages. At present few environmental conditions are considered in either the number of permits issued for seaweed farms, or in their location on shallow coral ecosystems. In this context, our results have significant implications for managers who need to both address the need for alternative livelihoods given unsustainable fishing practices and find ways of maximizing the positive benefits of MPAs whilst minimizing the negative effects of seaweed farms.

CHAPTER 5

General Discussion

Seascapes are being transformed globally by a variety of anthropogenic impacts including climate change, pollution, and overfishing, all manifestations of a growing human population. Coral reef ecosystems are important ecologically, biologically and socioeconomically since they are centres of biological diversity, productivity, and are protective barriers for coastlines. Shallow coral reef ecosystems are particularly at risk because they lie in the land water interface making them highly accessible and vulnerable to impacts of human activities (Carpenter et al. 2008, Burke and Spalding 2011). In addition, continuing pressure from different human activities on ecosystems creates matrices of different uses within landscapes (Pauly et al. 2002, Halpern et al. 2008).

Seaweed farming is frequently promoted by governments and non-governmental organisations (NGOs) alike as a means of reducing the number of people dependent on overexploited fisheries (Hill et al. 2011). Combined with social inequality, population growth has significantly increased pressures on tropical marine fisheries (Pauly 1994, Jennings and Polunin 1996, Polunin and Roberts 1996, McManus 1997), which are an important source of revenue and protein for millions of people globally (Jennings and Polunin 1996, Allison and Ellis 2001, Badjeck et al. 2010). Most tropical reefs occur in the poorest countries and in the face of declining fisheries returns there is pressure to seek alternative livelihoods as a means of support. Seaweed farming is one such alternative yet there is little evidence that seaweed farming as an alternative livelihood actually reduces fisher numbers (Crawford 2002, Sievanen et al. 2005, Hill 2011) and the ecological implications have been unclear.

5.1 Ecological Implications of Seaweed Farming in Degraded Environments

Globally, the continued degradation of shallow coral reefs as a result of anthropogenic disturbances has resulted in widescale habitat homogenization. The initial hypothesis of this thesis was that seaweed farms had the potential to change ecosystem function in degraded shallow coral reef ecosystems through addition of structure. Specifically, the agricultural matrices associated with seaweed farms would add structural complexity to homogenized seascapes. Since physical complexity is strongly correlated with both diversity and abundance (Bell and Galzin 1984, Friedlander and Parrish 1998, Wilson et al. 2010, Graham 2014), this would subsequently equate to differences in diversity, abundance, and biomass of reef fish assemblages. Additionally, since both *K. alvarezzi* (Elkhorn moss) and *E. spinosum* (Spiny Eucheuma), the two most commonly cultivated types of colloidal seaweed, are consumed by herbivorous reef fish, I hypothesized that increased seaweed biomass on shallow coral reefs may also create an additional food source. On a global scale, there seems to be evidence that seaweed farms may in fact bolster production of herbivorous fish (Chapter 2). In the face of declining returns from fisheries depleted by over-extraction, destructive fishing practices, and habitat degradation over an extended period of time (Armada et al. 2009), the potential for an expanding seaweed farming industry to promote the productivity of food fish would be important. Siganid production was strongly related to seaweed production in Southeast Asia, relative to reef fish production, although this pattern was not present in locations in East Africa or the Pacific, and may be due to the scale and duration of farming. This implies that seaweed farms may need to achieve a critical density before providing a detectable benefit to herbivorous reef fish. Irrespective of the impacts of farming itself on reef fish assemblages, the placement of seaweed farms on degraded coral reefs may therefore drive herbivorous fish catch.

From the perspective of ecosystem-based fisheries management, particularly in the face of declining returns from fisheries the potential for the expansion of seaweed farming to provide increases in rabbitfish biomass is important. Contrary to the results of the global study for Southeast Asia, while rabbitfish consumed farmed seaweeds, the high proportion of wild brown seaweed even in a high farm density site suggests some selectivity towards

non-farmed diet items (Chapter 3). Whether the exhibited selectivity was a result of the animals' displacement in response to farm activities, targeted fishing within the farms, or qualities of the seaweed itself remains unclear. However, we also saw little evidence of increased abundance, biomass, and size of rabbitfish in areas with farms relative to those without (Chapter 4). Therefore, the addition of farmed seaweeds is unlikely to function as a subsidy to rabbitfish diets leading to increased biomass, but as a replacement for the seaweeds removed in the implementation of seaweed farms.

In Chapter 2, increased seaweed production in Southeast Asia was correlated with increased siganid catch; however, in Chapter 3 farmed seaweed was shown to be more likely a replacement than a subsidy of siganid diets. The difference may be that Chapter 2 captures the correlation between seaweed production and siganid catch as it is manifested in catches which may not be as obvious in terms of underwater visual census (UVC) as used in Chapter 3. Further, while the system driver may be the increase of algae, in Chapter 3 it is not clear whether this is due the presence of farms or greater algal domination of coral reefs resulting from higher levels of coral reef degradation. In Chapter 3, farmed seaweeds may have simply replaced wild ones as more farms were implemented. To this end, the results of Chapter 2 need to be considered with caution.

Further investigation into the impact of seaweed farming on reef fish assemblages (Chapter 4) found that farms had a negative impact on diversity, abundance, and total biomass. Moreover, species richness and biomass decreased with proximity to seaweed farms even in locations subject to blast fishing or that were otherwise unprotected. This suggests that there may be a net negative effect of seaweed farms on fish assemblages despite the already generally degraded nature of these shallow coral reef ecosystems. Moreover, the study supported the importance of MPAs for fish in shallow coral reef habitats since the presence of MPAs was the most influential determinant of species richness and biomass.

5.2 Management Implications

Seaweed farms continue to provide economic benefits to millions of artisanal farmers globally and the sector is expanding. Most farming activities occur in the shallows where

they are easily accessible from land. These important areas have important linkages to others and support a host of other human activities, making them critical both ecologically and socio-economically. Their management then is a balance between the increasing number of human activities within these areas to generate necessary sources of income in the context of a burgeoning human population, and the need to preserve ecosystem functions on which many of these same people rely. Seaweed farming is socioeconomically important because in most cases it is practiced artisanally, meaning the income it generates directly benefits the families who engage in it instead of less directly through hourly wages. In many cases these farmers are also women who may otherwise find themselves socioeconomically disenfranchised.

Globally there was evidence that rabbitfish productivity increased with seaweed farming in Southeast Asia, which would translate into benefits to artisanal reef fisheries. This is of particular importance since artisanal and commercial fisheries comparatively catch the same amount of fish for human consumption (30 million tons) each year, yet artisanal fisheries employ 25 times the number of fishers (over 12 million people) and annually use an eighth of the amount of fuel compared to industrial fisheries. In addition, more than 90% of these fisheries operate in developing countries (Béné et al. 2010). Overexploitation continues to be a problem in artisanal fisheries, particularly in those with access to cash markets (Huber 1994). Human population density, technological efficiency and market pressure have been cited as probable causes of overfishing (Cinner and McClanahan 2006), in addition to socioeconomic factors (Cinner et al. 2009). In essence, any boost in fisheries productivity as a result of seaweed farms would seem a benefit. However, those same benefits to herbivores may come at the expense of the rest of the assemblage in terms of diversity, biomass, and abundance (Chapters 3 and 4) since the implementation of seaweed farms frequently involves removing habitat.

Of primary concern to management is that in many places virtually no ecological consideration is given to the location of seaweed farms on shallow coral reef ecosystems. In both the Philippines and Indonesia, permission for seaweed farms is granted locally by community leaders whose decisions tend to be based on individual needs, perceived economic benefits, and politics, rather than ecological considerations. Allocation of shallow

ecosystem resources are often driven by the impetus to create additional livelihoods in order to offset continued losses from declining fisheries returns which result from the deleterious effects of continued unsustainable fishing practices.

When the ecological implications are considered, it has been in the context that seaweed farming may play a role in providing *de facto* protection to reef habitats by physically restricting access or as a deterrent to destructive behaviours such as blast fishing through increased human presence. Seaweed farming has been marketed as “ecologically friendly” with minimal potential for negative effects on fish or benthos in already degraded shallow ecosystems with the added benefit that the presence of farm workers can act as a means of MPA enforcement. This is particularly relevant in Danajon Bank where this study was conducted because seaweed farms currently bound virtually all no-take MPAs and there are current proposals to include seaweed farms within them to create multiple-use MPAs. The genesis of this strategy is born of the belief that seaweed farms can serve as physical buffers against destructive fishing practices as well as integrating seaweed farming within the boundaries of MPAs in order to gain political consensus for the expansion of protected areas. However, in light of the negative ecological effects evident even in the presence of other destructive practices, the location of seaweed farms on degraded shallow coral reefs generally and in or near MPAs specifically needs to be given careful consideration.

5.3 Novel Ecosystems Approach

Seascapes are increasingly composed of altered ecosystems (McCauley et al. 2015). Traditionally, areas of human use within seascapes, as with their terrestrial counterparts, tend to be divided into distinct categories of use vs. wilderness (Hobbs et al. 2014). Increasingly seascapes, largely as a result of growing human population, have become patchworks of human use. This is particularly the case with shallow coral reef ecosystems because of their physical proximity to human populations. Because different human activities, or in many cases, combinations of activities will have different impacts, they may result in the different ecological functioning of these modified systems when compared to a wild state. Therefore, the designation of an area for restoration, protection, or a particular use(s) must necessarily

be based on several factors including the potential for the individual activity to alter ecosystem function as well as its ecological context.

A novel ecosystems approach to degraded shallow coral reef ecosystems would dictate that any further human activities within these radically altered systems would take into account both the current ecological function and the entire range of options for further use rather than simply focusing on use and impacts solely in terms of traditional restoration (Hobbs et al. 2009, Hobbs et al. 2014). Seaweed farming has been practiced in Danajon Bank at least since the 1960s but did not expand much until the late 1980s. By that time, degradation of the reef due to population pressure, destructive fishing practices and overfishing was well advanced (Christie et al. 2006, Armada et al. 2009). Therefore, despite the ecological impacts of seaweed farming on undisturbed coral (trampling, siltation, mechanical damage) being well documented, the ecological function of a seaweed farm placed on highly degraded shallow coral reef has been largely unknown (Chapters 3 and 4). However, by 2006, coral mortality in the region was as high as 70% (Marcus et al. 2007) and this figure is independent of whether the area was farmed or not. Approaching wide-scale seaweed farming on degraded shallow coral reefs from a traditional restoration standpoint, as with terrestrial systems, would require at least the attempt to return these systems to an original (or at least an approximation of an original) state (Hobbs et al. 2014). A novel ecosystems approach on the other hand involves discriminating “patches” of varying states of modification (e.g., seaweed farms, MPAs, gleaning areas) and evaluating them in terms of their existing function, both in terms of their delivery of different combinations of ecological goods and services, and their interactions with broader scale processes.

The concept of novel ecosystems as a management tool is not without controversy. In their critique of Hobbs (2014), Murcia et al. 2014 makes the point that novel ecosystems may act as a “Trojan horse” in that “the argument that attempting to restore an ecosystem is futile despite the fact that it is demonstrably often wrong and that novel ecosystems can serve our purposes better can only lead policy-makers to be more willing to allow environmentally damaging projects”. However, novel ecosystems have formed as a result of human population, and as populations continue to grow, the combined effects of agriculture, urbanization, and climate change will only bring about more novel ecosystems, some of

which may in fact provide valuable good and services. There can be little doubt that introducing seaweed farms onto degraded coral reef systems significantly changes both the biotic composition and function when compared to wild, healthy shallow coral systems. Understanding their function is particularly important when trying to assess the allocation of conservation resources. In this context, the concept of novel ecosystems can provide a more extensive and robust toolkit for managers to better evaluate current ecological states within ecosystems, and to better allocate resources. If seaweed farms actually represent the creation of novel ecosystems, how do they compare functionally to wild, healthy systems and do they in fact provide ecological benefits in their current state? How does this compare to the function of the heavily degraded systems they are situated on? Only when the answers to these questions are answered can managers decide whether these systems will benefit from the further investment of significant resources in order to prevent further degradation and loss of function or whether in fact, the novel ecosystems created by seaweed farms are better managed by the acceptance of their current state for whatever benefits they may provide.

5.4 Future Directions

The research presented here demonstrates that while the introduction of seaweed farms globally may provide benefits for herbivorous fish, on a local scale, herbivores still demonstrated dietary selectivity for wild brown algae. Further, despite the possibility for the agricultural matrix associated with farms to provide both structure and food, farms had a negative effect on coral reef fish assemblages. Applying the analyses used here to regions in both the South Pacific and Africa would demonstrate whether dietary selectivity and seaweed farm impacts on fish assemblages are shared across multiple regions.

The global analyses used in this thesis in Chapter 2 demonstrated a relationship between seaweed farming areas in Southeast Asia and rabbitfish production. However, while it did identify a difference between regions, it did not identify the cause(s) of the difference between Southeast Asia, Africa and the Pacific. Identifying the cause(s) of this difference would be informative in order to identify seaweed farming drivers of herbivorous fish production.

Chapter 3 suggested that herbivorous rabbitfish might be traveling substantial distances to consume wild brown algae beyond home ranges typically reported. This raises the question of whether the home ranges of rabbitfish are affected by seaweed farming and its associated activities, or whether the home range of *S. canaliculatus* as observed is typical of this species. Chapter 4 found that the negative effects of seaweed farms on fish assemblages appeared stronger in the absence of blast fishing and were strongest when MPAs were present which was likely a reflection of the positive influence of the MPAs on fish within them. Chapter 4 also found that the seaweed farms had a very limited potential to increase fish diversity, abundance, and biomass and may reduce MPA benefits. One of the main difficulties with Chapter 4 was that it relied on an unbalanced design, which could be greatly simplified if it could be conducted in an area where seaweed farming on corals was still nascent or at least less prolific.

5.5 Concluding Remarks

Shallow coral reef ecosystems are important ecologically since they are centres for biological diversity, productivity, and function as protective barriers for coastlines with critical connections to other ecosystems. Shallow coral reef ecosystems already experience significant degradation and increasing pressure from anthropogenic disturbance since they lie at the interface between the land and the open ocean. However, seaweed farms situated on these shallow coral reefs provide a livelihood option for impoverished artisanal fishers and farmers. Novel ecosystems that challenge conventional conservation and restoration are a present reality. Despite concern that embracing novel ecosystems as a concept may lead to the erosion of progress in creating networks of protected areas or lead to management trade-offs (Hobbs et al. 2014), recognizing these systems as “novel” allows for them to be managed within a more flexible framework without compromising the larger landscape conservation goals. This thesis represents the first step in evaluating the ecological function of seaweed farms situated on degraded shallow coral reefs in terms of their function as they currently exist and their potential to provide ecological benefits to both coral reef fish assemblages and to humans.

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