

**FISHING PRESSURE
AND BENTHIC ASSOCIATIONS:
HERBIVOROUS FISHES ON
REEF FLATS IN FIJI**

by

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This thesis is dedicated
to my parents

Jackie Tanny Fa'anunu
and
Haniteli 'Ofa Fa'anunu

for instilling in me my love for the ocean,
...and the islands.

'OFA LAHI ATU

ABSTRACT

Herbivory by marine fishes is a fundamental ecosystem process that contributes to structuring reef communities. The removal of herbivores through fishing results in the overgrowth of macroalgae which in turn greatly reduce space occupied by framework-building corals through direct and indirect mortality and reduced coral recruitment. This study sought to determine the effect of fishing on herbivorous fish biomass by comparing data between protected (*tabu*) and fished (*tara*) sites on the reef flat at six locations in the Fiji Islands. It also explored the relationship between fish biomass and a metric of fishing pressure as well as macroalgae biomass, and benthic community composition. Average total fish biomass was lower in all *tara* than in *tabu* sites and significantly so for half of the locations. *Tabu* effects were greatest where fishing pressure was highest. The functional groups “scrapers/small excavators” and “farmers” were significantly less prominent in *tara* than in *tabu* areas. These two functional groups together make up over 90% of total herbivore biomass on the reef flat and were significantly correlated with benthic community composition. Farmers were positively correlated with turf algae cover, a relationship driven mainly by the damselfish *Stegastes nigricans*, the pomacentrid species with the highest average biomass. Scrapers/small excavators were positively correlated with coral and calcareous coralline algae (CCA) cover, and negatively with macroalgae biomass, with greatest effects attributable to the parrotfishes, *H. longiceps* and *S. ghobban*. PCA results show levels of herbivory is a possible driver for the opposing relationship between herbivorous fish functional group biomass and fleshy algae biomass and also identifies possible biogeographical influences on fish community structure. These results support the generalization that herbivorous fish biomass is critical to the health and resilience of shallow coral reef habitats.

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TABLE OF CONTENTS

Dedication	iii
Abstract	iv
Acknowledgements	v
Table of Contents	viii
List of Tables	x
List of Figures	xi
1. Introduction	1
1.1 General Introduction	1
1.2 Herbivory and Coral-Macroalgae Phase Shifts	1
1.3 Fiji Situation.....	6
1.4 Research Objectives.....	8
2. Methods	10
2.1 Site Description.....	10
2.2 Experimental Design	11
2.2.1 Study Species	12
2.2.2 Fish Data	14
2.2.3 Benthic Data	14
2.2.4 Metric of Fishing Pressure	15
2.3 Data Analysis	16

3. Results.....	18
3.1 Effect of fishing.....	18
3.1.1 Tabu vs. tara at study locations.....	18
3.1.2 Functional Groups.....	21
3.1.3 Species Assemblage.....	24
3.2 Benthic Associations.....	26
3.2.1 Functional Groups and Benthic Variables.....	26
3.2.2 Scrapers/small excavators size classes.....	28
3.2.3 Dominant Species.....	29
4. Discussion.....	30
4.1 Effect of fishing	30
4.2 Note on species composition and spatial variability.....	33
4.3 Benthic Associations: Scrapers/small excavators and farmers	35
5. Implications	38
Literature Cited	42
Appendix I: Site Descriptions	50
Appendix II: Research Protocol	56
Appendix III: Study species	59

LIST OF TABLES

Table 1. Summary of research locations.....	11
Table 2. Student's t test results.....	19
Table 3. Wilcoxon Rank Sum test results.....	22
Table 4. Top ten herbivorous fish species.....	25
Table 5. Spearman's Rank correlations of fish functional groups	28

LIST OF FIGURES

Figure 1. Map of research locations	10
Figure 2. Fish biomass in <i>tabu</i> vs. <i>tara</i> at research locations	19
Figure 3. Biomass ratios at research locations.....	20
Figure 4. Relationship between fish biomass ratio and fishing pressure	20
Figure 5. Herbivorous fish functional group biomass.....	22
Figure 6. Biomass ratios of herbivorous fish functional groups	23
Figure 7. PCA of fish functional groups benthic variables.....	27

INTRODUCTION

1.1 General Introduction

This research characterizes the herbivorous fish community on the reef flat in Fiji to investigate the possible effects of fishing pressure on resilience of this reef zone to macroalgal phase shifts. The Fiji Islands is an archipelago situated in the tropical Central Pacific covering over 320 islands and approximately 10,000 square kilometers of coral reefs. It is a country facing the pressures of globalization and population growth and the resulting degradation of inshore reefs and marine resources. The popular existence of traditionally managed marine protected areas on the fringing reefs sets up a natural experiment to assess the effect of fishing on the herbivorous fish community, and to make inferences about the impact of fishing on the benthic community. This study was supported by Conservation International's Marine Managed Area Science program (CI-MMAS) and is in line with their goal of identifying the best ways to use marine management areas to sustain ocean and human health.

1.2 Herbivory and Coral-Macroalgal Phase Shifts

The concept of phase shifts is garnering attention as coral reefs are succumbing to human impacts and undergo shifts to less desirable ecological states, usually an alternate assemblage dominated by fleshy macroalgae. Left to grow unchecked, macroalgae can hinder coral growth and recruitment through both direct and indirect effects (Littler and Littler 1999, Vermeig and Lindberg 2000, Smith et al 2006). Furthermore, this shift is accompanied by a hysteresis or

resistance to the restoration of hard coral cover, thus decreasing coral reef resilience (cite references). The magnitude of the consequences of this change is enormous considering the tens of millions of people worldwide that depend on healthy marine systems for the goods and services they provide (Moberg and Folke 1999, Sadovy 2005).

Human-induced disturbances, the main drivers behind this ecological phase shift, are progressively becoming more widespread and persistent. Overfishing, pollution, sedimentation, warmer waters and the spread of diseases can act independently to cause recoverable phase shifts, but when applied synergistically and continually, they can result in irreversible changes to an alternate state (Nystrom et al 2000, Bellwood et al 2004). The most well studied example of this phenomenon is the mass die-off throughout the Caribbean in 1983 of its dominant herbivore, the sea urchin *Diadema antillarum*. It has been inferred that intensive fishing led to the dominance of the urchins acting as the main herbivore on these reefs (Hay 1984). Consequently when the epizoid die-off occurred followed by a hurricane, macroalgae took over the reefs, persisted over time (Hughes 1994, McClanahan et al 2001) and were particularly prolific in the more heavily fished regions where herbivorous fish abundances were low (Koslow et al 1994 in Williams and Polunin 2001).

Evidence abounds that herbivory, particularly by herbivorous fishes, is a fundamental ecosystem process that structures reef communities. High rates of algal production on intact coral reef systems are balanced by high consumption rates of herbivores removing up to 100% of the net daily production of algae (Hay 1991). Herbivores suppress dominance by algae by restricting spread and succession to later, more frondose species (Diaz-Pulido and McCook 2003). These

later successional stages can directly outcompete corals and coralline algae for space and light, and prevent coral recruitment (Littler and Littler 1984, Belliveau and Paul 2002). They trap sediments that increase turbidity that allow for further algal expansion (Littler and Littler 1999), and discourage the settlement of the crustose coralline algae that coral rely on for cues to settle to a reef (Fabricious and De'ath 2001). Fleshy algae can also indirectly cause coral mortality by enhancing microbial activity that may lead to conditions of hypoxia on coral surfaces (Smith et. al. 2006).

Overfishing is said to be the largest anthropogenic cause of ecological endangerment and extinction in the marine environment (Jackson et al 2001). On coral reefs, top down effects combined with direct take can lead to depletion of herbivorous fishes (Jennings and Polunin 1996). Such declines of herbivorous fish are found to be associated with increasing macroalgal dominance (Hughes et al 2007, Bellwood et al 2004, Smith et al 2001, Sluka and Miller 2001, Hay 1997, Hay et al 1983). Small scale experiments (McClanahan et al 2003, Hughes et al 2007) and regional studies (Bellwood et al 2004, Burkepile and Hay 2006) have demonstrated how the overfishing of herbivorous fishes compromises the resilience of coral reefs through the mechanisms mentioned above. One such study was conducted in Fiji by Littler and Littler (1997) on two reefs exposed to two different levels of fishing pressure, to assess the effect of herbivorous fish in initiating recovery of the beneficial crustose coralline algae after a bacterial infestation known as the coralline lethal orange disease (CLOD). Their surveys and experiment showed that the highly fished Nacalevu Reef underwent a phase shift from coral to turf algal domination from which it did not recover. Alternatively, on Butoko Reef, intact assemblages of

large herbivores were observed to feed on the increased growth of turf and as a result opened up space for *Acropora* coral recruits to colonize.

Through a variety of studies that have confirmed the inverse relationship between different characteristics of herbivorous fish and macroalgae cover (Williams and Polunin 2001, Mumby et al 2006, Fox and Bellwood 2007, Friedlander et al 2007), the metric of fish biomass has been identified as one of the best indicators of this relationship (Green and Bellwood, 2009). The idea that the largest sized fishes –those that have the largest biomass- exert the greatest impact on the substratum has been demonstrated experimentally. Exclusion of large herbivores causes dramatic algal growth in experimental cages (Hughes et al 2007), and feeding studies found that larger herbivores graze larger areas (Fox and Bellwood 2007). The inverse relationship between large herbivore biomass and algal cover is especially true of parrotfishes where the volume of epilithic algal matrix per kilogram removed by larger individuals is much larger than that of the same mass of small individuals (Bonaldo and Bellwood 2008). Large parrotfishes, especially those over 1kg, are considered to have the most significant role in the maintenance of the benthic structure and prevention of phase shifts (Green and Bellwood 2009). This role will obviously be highly influenced by selective harvesting of the larger size classes through fishing.

In addition to biomass, the representation of functional groups in an assemblage is thought to be critical to a reef's resilience (Green and Bellwood 2009). Whereas the herbivorous fish guilds span a broad taxonomic range, they have regularly been lumped together in the past based on the common ecosystem function they play as primary consumers (Blondel 2003, Burkepile and Hay 2008). However, this group of fishes encompasses a large amount of within-group biological and

functional diversity than is usually acknowledged. Study of the morphology, feeding selectivity and behavior of herbivorous fish families and species (Adey et al 1977, Bellwood and Choat 1990, Wainwright and Bellwood 2002, Choat et al 2004, Bellwood et al 2004, Rice and Westneat 2005, Hoey and Bellwood 2008, Green and Bellwood 2009) have catalogued the diversity of functions within this guild and defined finer groupings. Excavators/Bioeroders open up hard reef matrix that corals and calcareous coralline algae can settle on. Scrapers/Small Excavators scour epilithic algal turf leaving behind exposed substratum. Grazers/Detrivores intensely graze on epilithic algal turfs eliminating macroalgae before they become established. Browsers bite off macroalgae and their associated epiphytes, reducing their biomass and diminishing shading and overgrowth. Farmers promote turf algae in their territories, keeping the algal community at early stages of succession and preventing dominance by opportunistic species (Ferreira et al 1998). They also keep coral predators at bay (Gochfield 2010).

Usually within a functional group species or ‘driver’ species assume a dominant role because of certain behavioral, biological or ecological traits or because of their density, biomass or productivity (Kulbicki et al 2004). The dominance of species in a functional group can change spatially and also temporally and while the function will ideally be maintained, the diversity of the group and the rank of species in the group may change according to regional or local factors (Peterson et al 1998 in Kulbicki et al 2004).

The high biological diversity within the herbivorous fish guild enhances the resilience of the coral reef ecosystem by providing a variety of functions that can respond to stabilize the system after major disturbances (Elmqvist et al 2003). Termed as ‘response diversity’ or ‘functional

redundancy,' this attribute effectively ensures that if a species is lost, another species that can play the same role will replace it thereby preserving its ecosystem function. Thus, a diverse representation of functional groups and species within those functional groups will better ensure greater resistance against a variety of environmental stressors.

The diversity of responses that an ecosystem may have to disturbance that is detectable through the relative differences in population characteristics and behavior of individuals or groups of herbivores is the underlying theme of continued research today. Information on the function of herbivores is provided through continuing research efforts, such as the notable study on the Great Barrier Reef in Australia that documented the influence of a single species of batfish (Ephippidae) previously regarded as an invertivore, which consumed most *Sargassum* seaweed in an experimentally-induced phase shift (Bellwood et al 2006). Subsequent studies have added a rabbitfish and a nasine surgeonfish to the list of *Sargassum*-eating browsers as well as identifying some species of parrotfish that switched to browsing *Sargassum* in the face of a major disturbance (Fox and Bellwood 2008, Bonaldo and Bellwood 2008, Hoey and Bellwood 2009). Evidently it is essential to maintain intact assemblages of herbivorous fishes in order to ensure coral reef resilience.

1.3 The Fiji Situation

As coral reefs worldwide are increasingly coming under the pressure of human induced disturbances, the small, relatively remote oceanic islands of the Central Pacific are also beginning to face similar issues. In Fiji noticeable changes have taken place in the last few

decades with rural communities now suffering from declines of fisheries in their coastal waters attributed to decreasing sizes and abundances of living marine resources (Veitayaki 1998). This is especially true for areas near urban development and concentrated agricultural use (Comely et al 2003, Sykes and Morris 2007, Lovell and Sykes 2008, Grober et al 2007). Many factors have contributed to the current degraded habitats and low productivity levels, namely overfishing, use of destructive fishing methods such as gill netting and fish poisoning, pollution by untreated sewerage, runoff from poultry and pig farms, sedimentation from poor farming practices and logging, littering, limestone harvesting, boat traffic and global, the spread of the destructive crown of thorns, and climate change effects such as bleaching and the spread of disease (Tamata and Lovell 1996, Mosely and Aalsbersberg 2001, Comely et al 2003, Department of Fisheries 2007).

The general decline of the marine environment is a real problem because the majority of the Fijian population depends on its resources for a portion of their consumption and income. Over 800 of Fiji's villages scattered across the country totaled a population of over 827, 900 in 2007 (Fiji Island Bureau of Statistics 2008). More than 80% of this population lives by the coast (Department of Fisheries 2007) with the majority leading subsistence-based livelihoods, communally relying on land and marine resources. Annual artisanal and subsistence catches are made up of over 17,000 estimated tons of reef-associated finfish, invertebrates and marine plants (Starkhouse 2009, Gillett 2009).

The reef flat of a Fijian coral reef is the zone that bears the brunt of the aforementioned threats. This is the most accessible part of a reef system due to its close proximity to the coast and its

shallow nature. It is therefore the most intensively utilized and impacted zone by local communities and land-based activities. Ecologically, this marine environment provides shelter for juvenile fish and a feeding ground for herbivores (Russ 1984). Scarids and acanthurids are among the larger diurnal herbivorous species that travel the short distance from deeper nocturnal reef cover to these shallow grazing grounds during the day (Randall 1965 in Parrish 1989).

As a result there are noticeable effects of degradation particularly the increase of macroalgae on the reef flat in some areas (Grober et al 2008). The spread of macroalgae, especially along the coast of the main island of Viti Levu where population is highest, is now a concern for coastal communities who believe that their reefs are being smothered to death by the presence of large amounts of *Sargassum* and *Turbinaria* (Fiji Times July 2008, pers. comm. S. Meo Sept 2008). While certain references have been made to the probable causes of runoff from sewerage and piggeries, and the overfishing of herbivorous fish (Tamata and Lovell 1996, Mosely and Aalbersberg 2003), there is a lack of studies dedicated to the understanding of the underlying ecological linkages at play.

1.4 Research Objectives

As changes are taking place on the intensively harvested reef flat zones worldwide, there is a need to document the condition of this important ecosystem to better understand the linkages between man, fish and algae. Many studies have been conducted in deeper, calmer regions of coral reefs, but the body of knowledge that exists for the shallow reef flats still remain limited. In

the Central Pacific, information on the herbivorous fish guild - especially with regards to their biomass - remains largely undocumented.

This study sought to fill this gap by documenting reef flat conditions to determine: 1) the effects of fishing (and fishing pressure) on the biomass of herbivorous functional groups and species; and 2) the relationship between herbivorous fish biomass and environmental factors of fishing pressure, macroalgae biomass, and percent cover of benthic categories. To this end, comparisons between protected (*tabu*) and fished (*tara*) sites were expected to answer questions of to what degree fishing is asserting its top down effect on coral reef communities and how effective *tabu* areas are in protecting assemblages of herbivorous against fishing. Categorizing the reef flat herbivore community into functional groups and characterizing their associations with the benthic community can also generate insight into the role of herbivorous fishes in structuring the benthic community on the reef flat.

2. METHODS

2.1 SITE DESCRIPTION

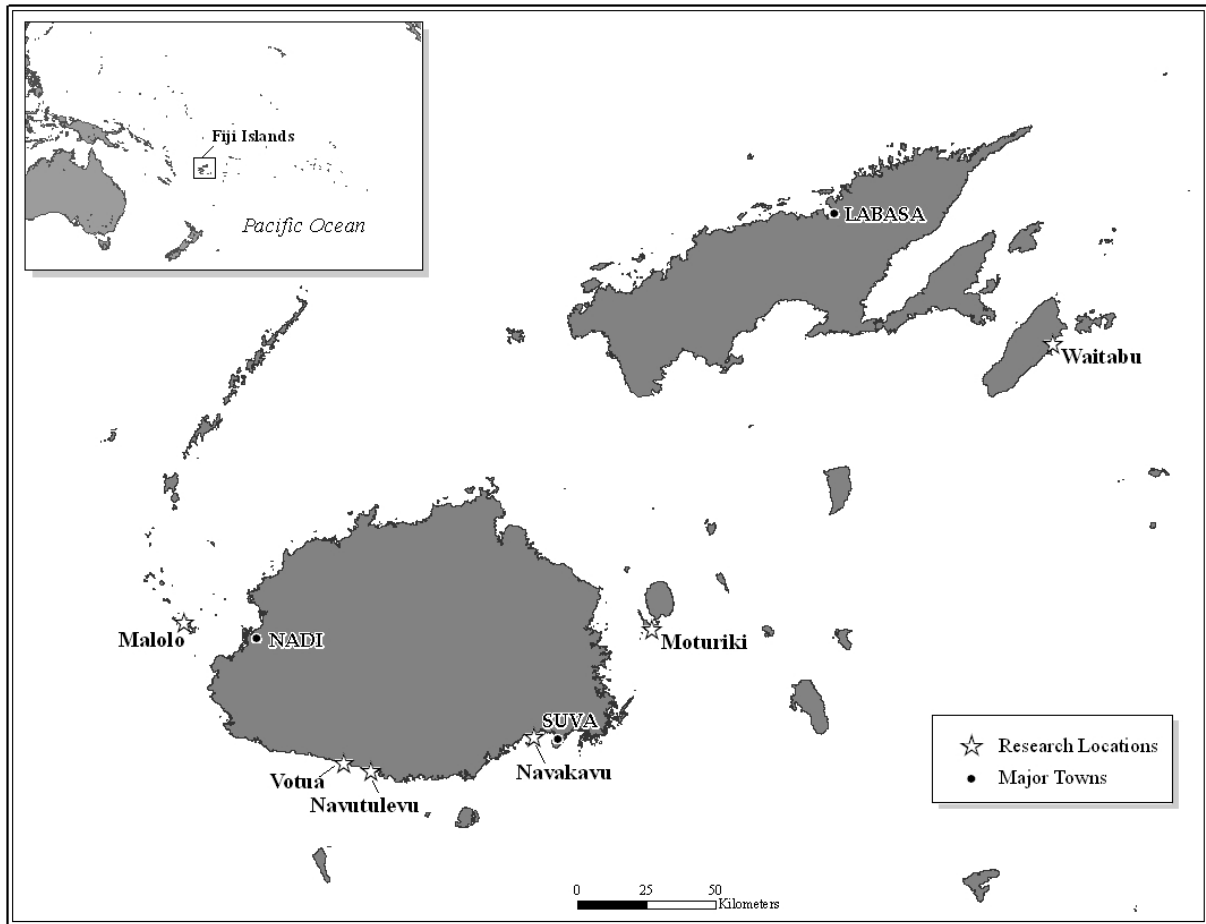


Figure 1. Map of Fiji Islands and research locations.

Six locations in Fiji were chosen for study, three on the largest main island of Viti Levu and three on smaller offshore islands (Figure 1) (see APPENDIX I for individual site maps and descriptions). Criteria for choosing these sites are: (1) inclusion in this study's sponsor Conservation International-Marine Managed Areas Science Program's (CI-MMAS) sites, (2)

presence of a known protected area (*tabu*), (3) presence of a partner organization to work with and gain access to the village, (4) ease of reef access, availability of survey resources, and (5) representation of different locations throughout Fiji (see APPENDIX II for a description of research protocol in Fiji). A summary of the six survey locations is provided in Table 1.

Table 1. Summary of research locations. Partner acronyms stand for: PCDF: Partners in Community Development Fiji; MES: Mamanuca Environmental Society; CI: Conservation International; IAS: Institute of Applied Science (University of the South Pacific); FLMMA: Fiji Local Marine Managed Area Network.

Site	Region	Pop	Protected Area (<i>Tabu</i>)		Partner Organization
			Year Est.	Area (km ²)	
Moturiki	Lomaiviti	909	2000	5.78	PCDF, Blue Ventures
Malolo	Malolo	1404	resort est.	1.43	MES, CI
Navakavu	Navakavu	5263	2001	2.93	IAS, FLMMA, CI
Navutulevu	Coral Coast	862	2004	0.63	Fisheries Dept.
Votua	Coral Coast	1342	2002	0.55	IAS, FLMMA
Waitabu	Taveuni	1481	1998	0.77	FLMMA, Resort Support, CI

2.2 EXPERIMENTAL DESIGN

Each of the six study locations were divided into sites of fully-protected areas (*Tabu*) and fished areas (*Tara*) to make a total of twelve sites. Belt transects for sampling fish and benthic categories were placed haphazardly, parallel to the reef crest, on reefs that were observed to be composed of at least 50% hard substratum. The numbers of transects per site varied from 13 to 21, dependent on the amount of hard substratum available to survey without pseudo-replication. Each transect was marked on a GPS which ensured that they were located at least 20 meters away from each other. Field surveys were carried out between February and May 2009.

2.2.1 Study Species

A total of five functional groups of herbivores were identified for this study: Large excavators/bioeroders, scrapers/small excavators, grazers/detritivores, browsers and farmers. The first four groups encompass all observed members of the 6 fish families Acanthuridae, Ephippidae, Kyphosidae, Pomacanthidae, Labridae (Tribe Scarini) and Siganidae. These herbivore guilds are recognized by Green and Bellwood (2009) as critical to coral reef resilience through the combined impacts that they have on the substratum. Green and Bellwood (2009) have excluded other herbivorous fish families such as blennies, gobies, damselfishes, filefish, triggerfish and wrasses for reasons such as being too small, cryptic, encompassing too wide of a diet range or not having had their trophic status confirmed.

For the purpose of this study, damselfishes were included as a fifth functional group: Farmers. Their impact on the substratum differs because of selective feeding and weeding that only extends as far as the central portion of their serial territories. Roving herbivores, in contrast, cover a much wider ranging area, often travel in schools, and exclusively remove algae (rather than also cultivating it), thus having a greater ability to prevent phase shift through numbers and biomass. In an experimental study on an inshore Australian reef with low roving herbivore densities and relatively low coral cover (similar to many sub-tidal reef flats in Fiji), farmers were found to be the most important player, preventing a 30% increase in macroalgal cover (Ceccarelli 2004). This observation suggests that there may be situations where farmers can play an important role in *preventing* increases of macroalgal cover, especially if they occur in large numbers. This is the opposite of the effect normally ascribed to farmer fishes, but is consistent

with the hypothesis that they can favor coral growth beyond the perimeters of the farm (Kaufman 1977).

Using the above fish families as a guide, a list of study species was generated by narrowing the species list down to those listed in a study at the Navakavu location by Thaman et al (2008).

Thaman et al (2008) conducted a detailed study at this site with the main purpose of identifying and recording all existing species of fishes. Subsequent lists were then cross-referenced with the IUCN Handbook (Green and Bellwood, 2009) and assigned to functional groups. For the group farmers, Fishbase (www.fishbase.org) and Randall (2005) were used to determine damselfishes known to have benthic algae as a significant part of their diet. A total of 87 species of herbivorous fish were identified for this study and 60 were observed in the field (see APPENDIX III for the complete list of species observed).

To determine macroalgae study species, macroalgae harvested in the field were identified to the lowest possible taxonomic level using Skelton and South (2000) as a guide. They were then lumped into three predominate genera, *Sargassum*, *Turbinaria*, and *Halimeda*. All other species that were not observed consistently were lumped as 'Other.' Additionally, all benthic life forms were recorded as percent cover in the field. For the purpose of this study, the five main categories of coral, fleshy algae, calcareous algae, calcareous coralline algae, and turf were used.

2.2.2 Fish Data

The fish sampling protocol was adapted to conform to Conservation International's Marine Managed Areas Science Program (CI-MMAS) protocol. Belt transects were used to record fish species by name, abundance and length visually within a 20 X 4m belt transect. Each transect started from a point haphazardly chosen on at least 50% hard substrate and placed roughly parallel to the reef crest within the depth range of 0.5 to 3.0m. Large, roving herbivores were recorded on the first swim while laying the transect line. Smaller, sedentary species were recorded on the returning pass.

Fish length was estimated by total length (TL). This was later converted to fork length (FL) for species with forked tails (Acanthurids, Siganids and Kyphosids) since these are the values used for the standard length-weight (L-W) formula $W = aL^b$ for calculating fish biomass described in Kulbicki et al (2005). Length estimates were grouped into 5-cm size classes, 0-5cm, 6-10cm, 11-15cm, 16-20cm, 21-25cm. Fishes larger than 25cm were estimated to the nearest cm. The mid-point of each size class was then used for calculating fish biomass. Training for fish length and transect width estimation included trials in the field and also the author's participation in the Coral Reef Initiative for the Pacific (CRISP) Coral Reef Ecology & Survey Methods workshop held 12th – 19th September 2008 in Suva, Fiji.

2.2.3 Benthic Data

Macroalgae biomass and benthic taxa percent cover were surveyed along the same belt transect used for recording fish. Once divers reached the end of the second pass of the fish transect, the

first diver swam back along the transect placing a 0.25m² quadrat at 6 randomly selected points on the right-hand side of the transect line and recorded benthic percent cover. The second diver followed the first diver and harvested all macroalgae within each quadrat, placing them into plastic bags. The macroalgae were later separated and identified to the lowest possible taxonomic level, wet-weighed on a scale to the nearest 0.1 gram and pooled per transect.

2.2.4 Metric of fishing pressure

A proxy for fishing pressure was adapted from Kronen et al (2003) who determined fishing pressure as a function of population divided by fished reef surface areas at rural coastal communities in Tonga and Fiji. The authors found that fishing pressure was most positively significantly correlated with lagoon and reef finfish catch density and negatively with low resource status, a relationship they termed ‘resource degradation.’ Of the 8 fish families recorded, 3 were from the herbivorous fish families (Scaridae, Acanthuridae and Siganidae). Their study found that most fish groups were negatively associated with ‘resource degradation.’

The same formula was used in this study to characterize fishing pressure since it had been tested in Fiji and was a relatively straightforward method to use for this thesis. Population numbers were obtained from the Fiji Census Bureau from their 2007 Census except for the Moturiki location which was received from Partners for Community Development Fiji (PCDF) via Blue Ventures NGO for the year 2008. Total reef surface area was measured using the area tool in Google Earth. Boundaries were drawn from the shore to the reef crest and according to boundaries established by customary tenure (*qoliqoli*), resorts, natural barriers such as channels or bays or distances further than 10km.

2.3 DATA ANALYSIS

To determine the effect of fishing on fish biomass, pooled t-tests were conducted using the statistical software JMP 9 (SAS Institute, North Carolina, USA). To establish associations between fish biomass, benthic characteristics and fishing pressure multivariate Spearman's Rank Correlations were used. Multivariate tests (MDS, ANOSIM, PCA) were conducted using the statistical software PRIMER-E v. 6.0.2 (Plymouth Marine Laboratory, Plymouth, England). Pooled t-tests were conducted to determine the average biomass difference between *tabu* and *tara* at each of the six study locations, and within the four functional groups. All data were tested for normality (Shapiro-Wilk) and equal variances (Bartlett's test). For variables that did not pass assumption tests, data were natural log (ln) transformed.

An ordination procedure was used to determine if species assemblages could be meaningfully grouped based on similarities of their biomass density. First, biomass data was fourth root transformed to reduce the right-skewing effects that schooling fish have on assemblage biomass data relative to non-schooling species. Data was then converted into a Bray-Curtis similarity matrix and multidimensional scaling (MDS) applied to the matrix. This technique plots the similarity among samples based on their distance from each other in multivariate space. Test statistics that determine the potential differences in the assemblage structure were then generated by running a one way Analysis of Similarity (ANOSIM) on the same Bray-Curtis similarity matrix.

Principle Component Analysis (PCA) and Spearman's Rank Correlations were used to explore correlations among fish biomass, fishing pressure and benthic characteristics of macroalgae biomass and substrate category cover. All data were square root transformed and normalized prior to analysis.

For the correlations tests, scrapers/small excavator's biomass was divided into three categories according to size class. This was to determine the relative importance of size class in affecting the relationship between parrotfish and environmental factors as proposed by Bonaldo and Bellwood (2008). Their study found that in the case of the species *Scarus rivulatus*, smaller size classes had a markedly different type of impact on the substratum than large size classes. The smaller size classes crop the algal surface thereby controlling algal height, whereas large size classes remove the epilithic algal matrix along with fragments of the underlying reef, thereby opening up beneficial calcareous surfaces.

This study followed the size class categorization of Fox and Bellwood (2007) for its basic division of small (0-10cm), medium (11-25cm), and large (>25cm) size classes. Also, significant differences in substratum impact had been found previously between these size classes for the common parrotfish species: *S. rivulatus*. Fox and Bellwood (2007) found that bites by large individuals removed more than double the area of material than those of medium-sized individuals, who in turn remove over nine times more area than those of small-sized individuals.

3. RESULTS

3.1 EFFECT OF FISHING

3.1.1 *Tabu* vs. *Tara* at study locations

Mean herbivorous fish biomass were consistently higher in reserve areas, *tabu*, compared to fished areas, *tara* with three of these areas showing highly significant differences (all $p < 0.001$) (Table 2, Figure 2). These three locations, Navakavu, Navutulevu and Votua, are all located off the main island of Viti Levu. The three remaining locations with non-significant differences are situated off smaller outer islands. The distinction between main island and outer island locations was further highlighted by the ratio of mean herbivorous fish biomass inside *tabu* versus *tara* (Figure 3). The largest biomass ratios occurred at main island sites while the lowest ratios occurred at outer island sites. The positive relationship between biomass ratios and fishing pressure suggested that fishing pressure was a possible cause for the ratios seen at the locations (Figure 4). Although not significant, the relationship indicated that locations with the highest fishing pressure were the main island locations which also had the highest differences of biomass between *tabu* and *tara*.

Table 2. Results of comparisons of mean herbivorous fish biomass (kg ha^{-1}) between *tabu* and *tara* at six research locations. ** denotes a significance of $p < 0.01$ after a sequential Bonferroni adjustment ($p_i \leq \alpha/(k)$) is applied to the table of p-values ranked from smallest (p_i) to largest (p_k). This was applied to test for significance at the group-wide α level and control for type-I error (Rice 1989).

	Mean Biomass kg ha ⁻¹ (SE)				%Diff	T	p	
	Tabu		Tara					
Navakavu	823.99	(80.05)	253.14	(29.5)	226	3.02	<0.001	**
Navutulevu	406.8	(47.62)	158.71	(25.35)	156	0.59	<0.001	**
Votua	274.24	(27.13)	108.61	(11.13)	152	1.81	<0.001	**
Moturiki	435.47	(48.57)	332.16	(35.95)	31	2.63	0.048	
Waitabu	440.22	(214.00)	197.29	(43.20)	123	-0.85	0.228	
Malolo	504.07	(110.38)	331.37	(43.84)	52	2.52	0.400	

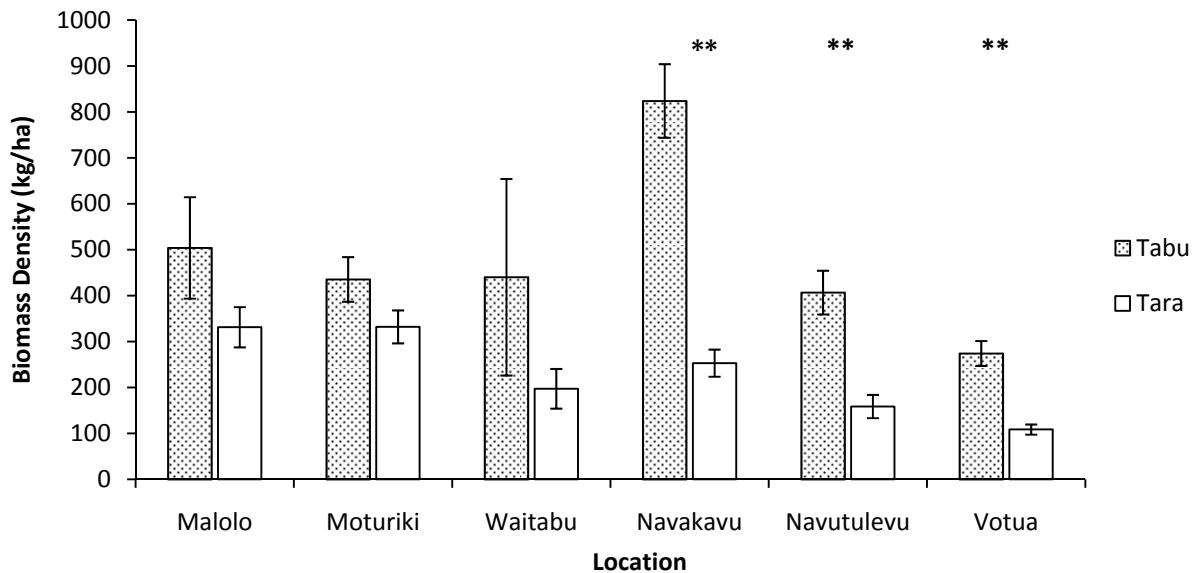


Figure 2. Comparisons of mean herbivorous fish biomass (kg ha^{-1}) between *tabu* and *tara* at the six research locations. Error bars indicate one standard error above and below the mean. ** denotes locations of significant difference as found by the student's t-test (Table 2).

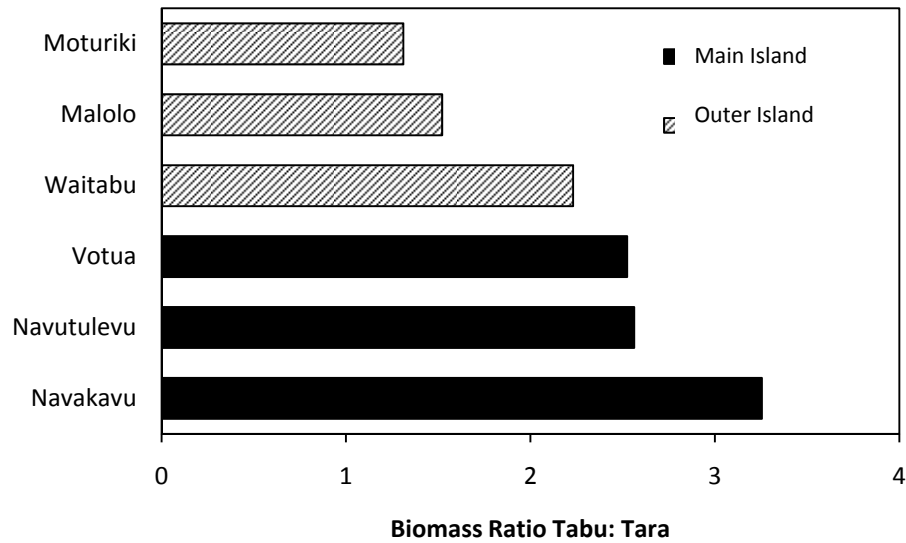


Figure 3. Ratio of mean biomass in *tabu* vs. *tara* among the six study locations.

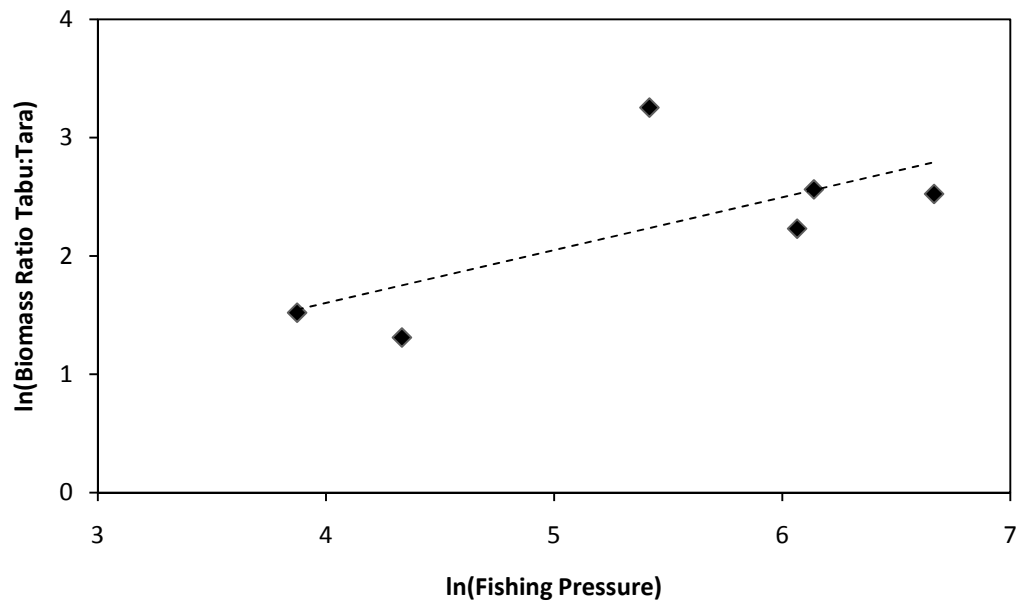


Figure 4. Relationship between biomass ratio of *tabu* vs. *tara*, and fishing pressure (population/fished area). Value are natural log (ln) transformed.

3.1.2 Functional Groups

The relative contribution of functional groups to total average biomass across all locations in order of highest to lowest were: scrapers/small excavators (55%), farmers (38%), grazers (5%) and browsers (2%). Scrapers/small excavators and browsers had a higher relative contribution to total biomass inside *tabu* (57%, 4%) compared to *tara* (53%, 1%). These values were higher in outer island *tabus* (66%, 6%), than main island *tabus* (47%, 2%) suggesting their dominance in these locations relative to other functional groups. Their biomass in *tara* were comparable across management regimes and geographic regions.

All four functional groups observed in this study had higher biomass in *tabu* compared to *tara*. This difference was highly significant for scrapers/small excavators ($p < 0.01$) and farmers ($p < 0.01$) (Table 3). Browsers were not commonly observed and thus have very low biomass values. However, relatively large biomass values in *tabu* at outer island locations Malolo and Waitabu (Figure 5) contributed to make browser biomass in *tabu* areas over four times greater than that in *tara* areas (Table 3). In all, these results suggest strong negative effects of fishing pressure on three of the four functional groups.

For scrapers/small excavators and farmers, the negative effects of fishing appeared strongest at the main island locations Navakavu, Navutulevu, and Votua where the differences in biomass between *tabu* and *tara* are consistently positive (Figure 5). Additionally, at the location Waitabu, the difference for scrapers/small excavators was the highest of all locations with a biomass ratio approximately four times that of the location with the lowest ratio, Moturiki (Figure 6).

Table 3. Wilcoxon (Rank Sum) test comparisons of mean biomass (kg ha⁻¹) between *tabu* and *tara* areas of four herbivorous functional groups. ** denotes a significance of $p < 0.01$ after a sequential Bonferroni adjustment ($p_i \leq \alpha/(k)$) is applied to the table of p-values ranked from smallest (p_i) to largest (p_k). This is to test for significance at the group-wide α level and control for type-I error (Rice 1989).

	Mean Biomass kg ha ⁻¹ (SE)				%Diff	Z	p	
	Tabu		Tara					
Farmers	154.18	(13.52)	78.04	(6.63)	98	5.34	<0.001	**
Scraper/Small Excavator	224.70	(29.14)	107.44	(11.13)	109	3.76	<0.001	**
Browsers	13.14	(4.64)	2.36	(0.8)	457	1.48	0.14	
Grazers/Detritivores	70.90	(12.16)	43.13	(5.7)	64	1.22	0.22	

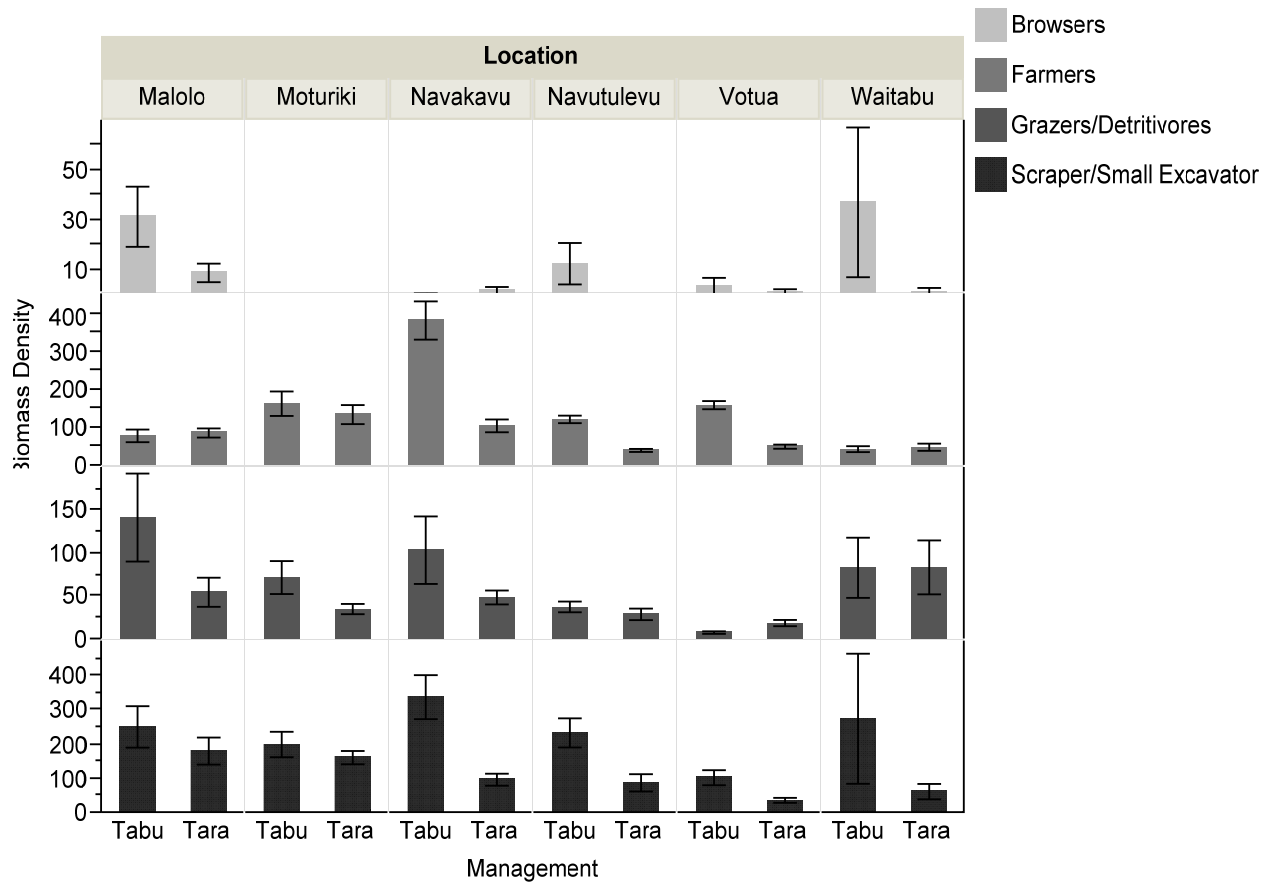


Figure 5. Comparisons between *tabu* and *tara* areas for each functional group at each of the six study locations. Error bars are one standard error from the mean.

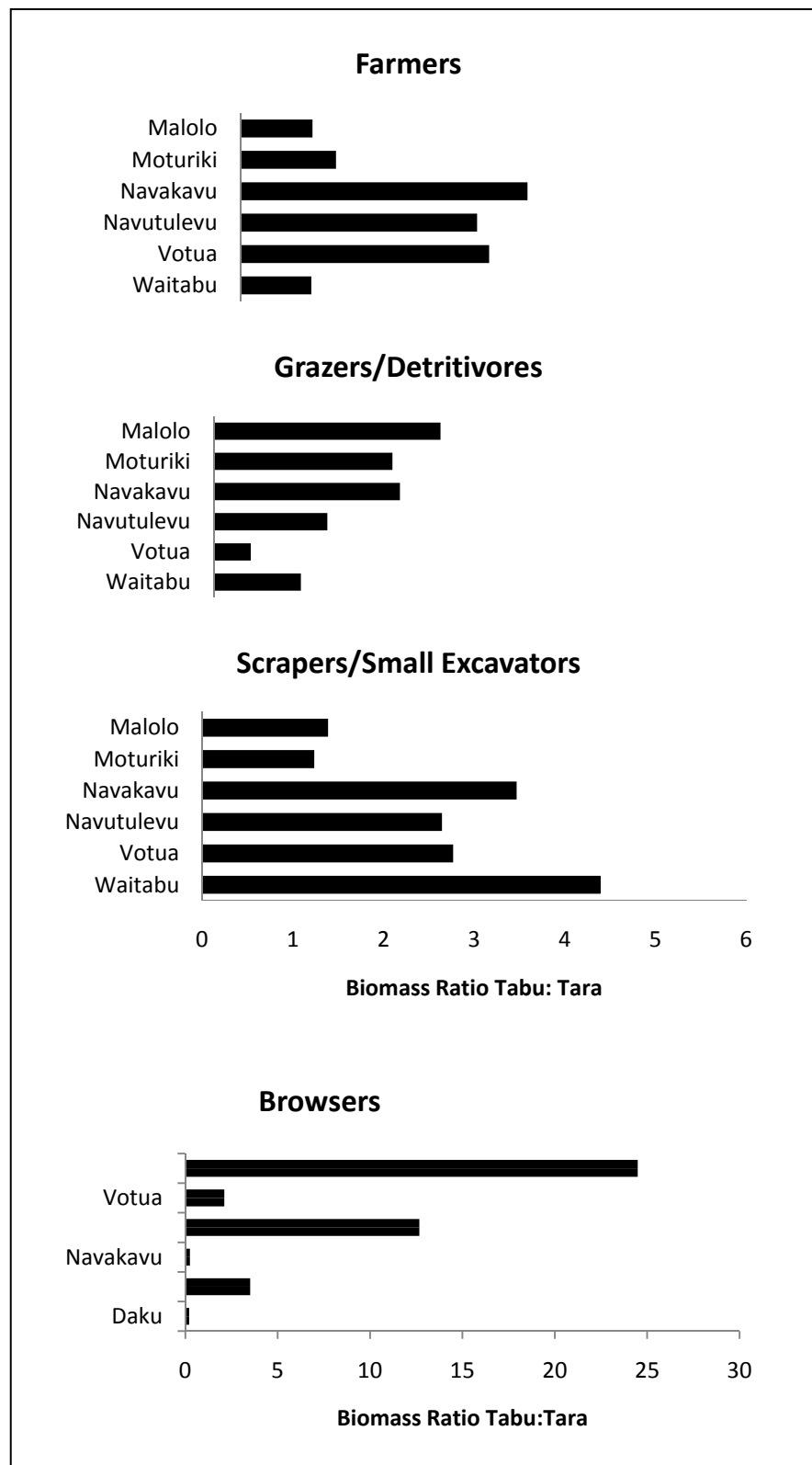


Figure 6. Ratio of mean biomass of four herbivorous fish functional groups in *tabu* vs. *tara* among the six study locations. Due to very low biomass values, Browsers biomass ratios are shown on a separate axis.

3.1.3 Species assemblage

The similarity matrix of the biomass density (kg ha^{-1}) of the 60 herbivorous fish species observed in this study showed no strong separation in ordination space between *tabu* and *tara* ($R = 0.026$, $p = 0.32$). The separation between main island locations and outer island locations was also not significant ($R = 0.204$, $p = 0.065$).

The ten species with the highest average biomass values in *tabu* areas in order of highest to lowest are: *Stegates nigricans*, *Chlorurus sordidus*, *Scarus rivulatus*, *Stegates punctatus*, *Chlorurus microrhinos*, *Hipposcarus longiceps*, *Acanthurus auranticavus*, *Chlorurus bleekeri*, *Scarus ghobban* and *Acanthurus triostegus* (Table 4). Collectively these ten species make up over two thirds (68%) of the total average biomass in tabus, of all sixty species of herbivorous fish observed in this study.

The top ten species come from three of the four observed functional groups. Scrapers/small excavators dominate the list while browsers are not present at all. *S. nigricans*, and secondarily *C. sordidus*, are both the two dominant species with the highest average biomass as well as abundance. Together they make up a third of the total biomass and numbers of all 60 species. Some species such as *C. microrhinos*, *H. longiceps*, and *S. ghobban* occur at very low abundances (<1% of all species) but have high biomass indicating their presence as large individuals. In contrast, the parrotfishes *C. sordidus*, *S. rivulatus*, and *C. bleekeri* occurred in relatively high numbers and were thus generally observed as smaller individuals. (Author's Note: At initial phase, small to medium sizes (< 20cm), *S. rivulatus*, *S. globiceps* and *S. psittacus* were

hard to distinguish from each other in murky conditions. This confounding factor should be noted when assessing the rank of *S. rivulatus* in the top ten species list.)

Table 4. Top ten species with the highest average biomass in *tabu* showing average biomass and abundance figures as well a percent contribution to the total average value in *tabus*.

	Biomass (kg ha ⁻¹) (SE)					Abundance (# ha ⁻¹) (SE)				
	<i>Tabu</i>		<i>Tara</i>		%	<i>Tabu</i>		<i>Tara</i>		%
<i>S. nigricans</i>	95.67	(32.85)	38.43	(16.25)	20	3875.77	(944.84)	1658.63	(591.72)	22
<i>C. sordidus</i>	59.69	(14.70)	29.82	(8.75)	12	1675.53	(373.18)	1115.97	(339.65)	10
<i>S. rivulatus</i>	39.31	(12.34)	15.68	(8.63)	8	532.10	(132.60)	773.61	(319.17)	3
<i>S. punctatus</i>	28.03	(19.47)	5.35	(2.91)	6	1110.76	(571.43)	254.17	(125.36)	6
<i>C. microrhinos</i>	20.35	(20.35)	0.06	(0.05)	4	15.46	(14.25)	5.06	(3.27)	<1
<i>H. longiceps</i>	19.02	(10.56)	1.84	(1.69)	4	67.01	(29.97)	5.41	(2.90)	<1
<i>A. auranticavus</i>	17.86	(11.62)	4.68	(2.61)	4	273.56	(136.45)	95.83	(43.60)	2
<i>C. bleekeri</i>	17.08	(9.53)	8.23	(4.11)	4	715.93	(618.75)	372.47	(361.25)	4
<i>S. ghobban</i>	15.98	(9.22)	5.01	(2.89)	3	59.07	(20.84)	38.24	(17.94)	<1
<i>A. triostegus</i>	13.39	(4.05)	3.41	(1.23)	3	1011.32	(308.82)	261.95	(89.74)	6

3.2 ASSOCIATIONS WITH ENVIRONMENTAL FACTORS

3.2.1 Functional groups and benthic variables

The first principle component (PC1-x axis) makes up 46% of the data's variability and is interpreted as a gradient in levels of herbivory. The twelve study sites fall along this axis as relative distances between CCA/coral dominated, and algae dominated reef community conditions. There were significant associations of herbivore functional groups (scrapers/small excavators (loading: -0.338), grazers/detritivores (loading: -0.392), and farmers (loading: -0.406)), with CCA (loading: -0.341), coral (loading: -0.372), and turf (loading: -0.375). Fleshy algae biomass (loading: 0.390) occurred at the opposite end leading to the interpretation that the gradient is influenced by the top down effects of fish herbivory. The twelve sites fall out as generally *tabu* sites at the end of high herbivory levels to *tara* sites at the end of low herbivory levels suggesting that level of herbivory is possibly influenced by management/fishing pressure.

The second principle component (PC2-y axis) describes an additional 25% of the data's variability and is interpreted as an axis representing a spectrum of coral reef habitat diversity. The axis is characterised by groupings of fish functional groups. One end had significant loadings of browsers (loading: 0.616), and scrapers/small excavators (loading: 0.330), and the opposite end had significant loadings of farmers (loading: -0.310) and grazers/detritivores (loading: -0.322). Coincidentally outer island sites occur at the browsers and scrapers/small excavators end and main island sites tend towards the farmers and grazers/detritivores end. This separation is assumed to be based on roving herbivores preferring outer island sites where an array of habitat types (ie, reef dropoffs, sand channels, sea grass, patch reefs) were more

commonly observed nearby. More sedentary groups of fishes were characteristic of the main island sites where a more homogenous collection of habitat types along with a larger component of riverine input were observed.

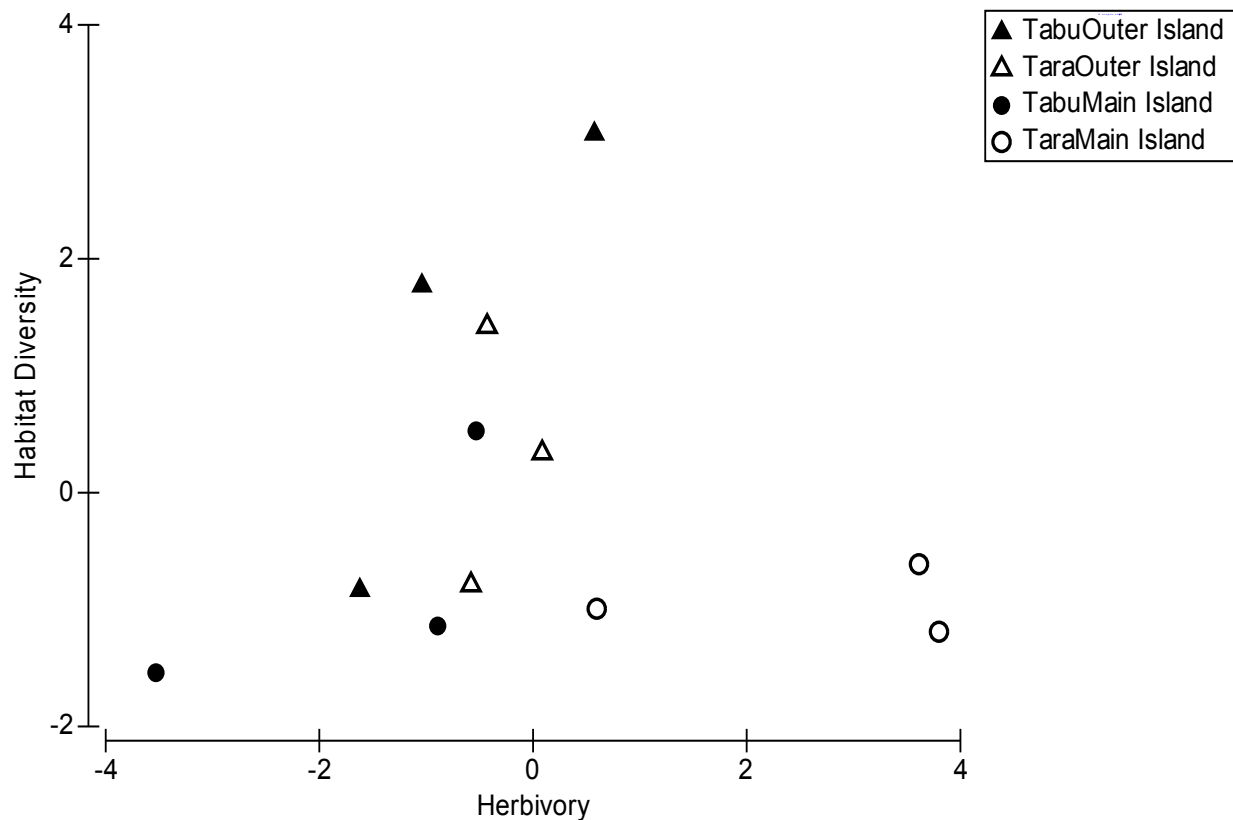


Figure 7. Principal Component Analysis (PCA) of four herbivorous fish functional groups percent cover of coral, crustose coralline algae (CCA), and turf algae, and biomass of fleshy and calcareous algae.

3.2.2 Scrapers/Small Excavators Size Classes

Scrapers/small excavators may play an important role in structuring the benthic community.

Spearman rank correlations among small, medium and large size classes show that the majority of the significant relationships with benthic categories occur under the medium (11-25cm) to large (>25cm) size classes (Table 5). The opposing relationship between scrapers/small excavators and fleshy algae cover and biomass driving PC1 was found by Spearman's rank correlations to be significant for large size classes (% fleshy algae cover: $R=-0.718$, $p=0.009$) (fleshy algae biomass: $R=-0.81$, $p=0.001$) (Table 5). In addition, positive significant correlations were found between large size classes and percent coral cover ($R=0.585$, $p=0.046$), and between medium size classes and percent CCA cover ($R=0.692$, $p=0.013$).

Table 5. Spearman's rank correlation results between functional groups and environmental factors. Scrapers/small excavators are divided into three size classes. Benthic percent cover of fleshy algae and fleshy algae biomass were correlated and are shown separately. Significant correlations ($p \leq 0.05$) are in bold. CA: Calcareous algae, CCA: Crustose Coralline Algae.

	Browsers	Farmers	Grazers/ Detritivores	Scrapers/Small Excavators		
				Small	Medium	Large
% Cover CA	0.175	-0.273	-0.273	0.399	-0.147	0.387
% Cover CCA	0.315	0.301	0.301	0.000	0.692	0.401
% Cover Coral	-0.091	0.329	0.329	0.343	0.140	0.585
% Cover Fleshy Algae	-0.308	-0.308	-0.308	0.063	-0.378	-0.718
% Cover Turf	-0.280	0.783	0.783	0.322	0.364	0.176
Biomass Halimeda sp	0.021	-0.084	-0.084	0.266	0.014	-0.430
Biomass Other Spp	-0.511	-0.161	-0.161	0.224	-0.294	-0.507
Biomass Sargassum sp	-0.183	-0.134	-0.134	-0.120	-0.289	-0.731
Biomass T. ornata	-0.063	-0.035	-0.035	-0.238	0.147	-0.225
Fishing Pressure	0.212	-0.353	-0.353	-0.424	-0.438	-0.384

3.2.3 Dominant Species

Spearman rank correlations results demonstrate a significant negative correlation between fishing pressure and *A. auranticavus* ($R=-0.749$, $p = 0.005$). Furthermore, *H. longiceps* was positively correlated with percent coral cover ($R=0.705$, $p=0.011$) and negatively correlated with fleshy algae cover ($R=-0.691$, $p=0.013$), and fleshy algae biomass ($R=-0.644$, $p=0.024$). *S. ghobban* was also significantly negatively correlated with fleshy algae biomass ($R=-0.692$, $p=0.013$).

4. DISCUSSION

4.1 EFFECT OF FISHING

Findings from this study indicated that fishing negatively impacts the mean total biomass of herbivorous fishes on reef flats in Fiji. Herbivore biomass values were always higher inside reserves (*tabu*) compared to fished (*tara*) areas. In particular, this difference was significant at the three study locations situated in coastal regions of the main island of Viti Levu. This indicated that while fishing impacts the herbivorous fish community everywhere, the geographical location may determine just how intense this impact may be.

Analysis using the metric for fishing pressure (population divided by fished surface areas) found that high values of fishing pressure is coincident with main island sites where biomass in fished areas are lowest and where the ratio of fish biomass between protected and fished sites are greatest. This result corroborates findings by Kronen et al (2005) who developed this proxy for fishing pressure, and who found it to be highly significantly correlated with finfish catch density at rural coastal communities throughout Pacific Island Countries and Territories (PICTs) including Fiji. Graham et al (2005) also found their similar metric for fishing intensity (population/reef front) to have a negative relationship with fish size, with larger size classes exhibiting the biggest response to exploitation. Because the metric used in this study was a function of the population number at the study locations, the findings indicate a direct negative influence of human population size through fishing on the herbivorous fish community.

All four functional groups observed in this study were negatively affected by fishing, with lower biomass values in *tara* areas than in *tabus*. In the case of the three functional groups scrapers/small excavators, grazers/detritivores and browsers, this trend was most likely due to the extraction of a range of fish sizes (as small as less than 10cm) for subsistence (Rawlinson et al 1992, Kronen et al 2003). Large scarids, *N. unicornis*, other acanthurids, and siganids are also highly targeted fishes in Fiji for commercial sale (Gillet and Moy 2006).

The finding of significantly higher biomass of farmers in reserves was contrary to the expected outcome of higher biomass values in fished areas. Higher biomass in fished areas was anticipated given its undesirability as a food fish combined with as an expected reduction of competition with other herbivores through fishing. A study in Australia found increases in damselfish abundance in exclusion areas that were constructed to simulate overfishing and the loss of large herbivores (their competitors) from coral reefs (Ceccarelli et al 2006). Additionally, farmers are not listed as a targeted group species for fishing (although it has been recorded in catches for subsistence use on fringing reefs along the Viti Levu coast (Rawlinson et al 1992)) and so protection was not expected to have a significant influence.

This result may in fact be due to the combination of territorial behavior of the farmers and differences of habitat between reserve and fished areas rather than the effect of fishing on this group. The two most dominant farmers in reserve areas, *Stegastes nigricans* and *S. punctatus* (a.k.a. *S. lividus*), are the most aggressively territorial of the common Fijian reef pomacentrids (Ceccarelli 2004) and can effectively exclude other herbivores from their territories. Competition with roving herbivores may not have been that great an issue for them. Additionally, *Stegastes*

colonies are highly associated with corals, particularly *Acropora* sp, which they utilize for habitat and protection (Allen and Emery 1985 in Zemke-White and Beatson 2005). This relationship is a possible explanation for the significant high biomass in reserves, since coral cover was also found to be significantly higher in reserves than in fished areas. What may be most interesting is that elevated densities of predators in reserves did not result in depressed populations of pomacentrids. The presence of a habitat effect and absence of a strong predator effect due to habitat availability, mirror the results of Precht et al (2010) in the Caribbean.

Grazers/detritivores showed a weak response to fishing compared to the functional groups scrapers/small excavators and farmers. This finding is consistent with studies by Russ and Alcala (1998), Kronen et al (2003) and MacKay (2001), who found acanthurids, particularly siganids, to be marginally affected by fishing. An explanation for this result could be that popularly fished siganids, especially *S. spinus*, have a high capacity to tolerate fishing pressure due to small size, short life span, early reproduction maturity & rapid initial growth (Kulbicki 1992 in Kronen et al 2003). This study found higher biomass of *S. spinus* in fished areas, an indication of either the resilience of this species against current levels of fishing, or its affinity to the type of habitat found in fished areas, or a combination of both.

The browsers functional group, characteristically observed in outer island reserves, were not significantly higher in reserves than fished areas in terms of biomass nor did they make the top ten species that make up two thirds of the total biomass of fish observed in this study. These findings, however, do not necessarily downplay their vulnerability to fishing or their critical role in the reef flat ecosystem. In fact, large *Naso unicornis* are one of most targeted species by

spearfishing in Fiji (Gillet & Moy 2006). When it comes to browsers, species composition, rather than biomass, may be a better indicator of how this group functionally influences the ecosystem. This can especially be true for some species of nasine acanthurids that become predominantly zooplanktivorous as they attain sizes larger than 20cm (Randall 2005, Green and Bellwood 2009) and therefore larger biomass for these species may not necessarily be good indicators of their impacts on the reef substratum.

An additional factor contributing to the low observations of the browsers functional group was that the sampling methods did not take into account their behavior. The feeding behavior of *Naso unicornis*, the most commonly observed browser in this study, has been linked to surf and lunar periodicity. Large sized individuals of this species aggregate around current lines during heavy surf to feed on brown algae torn away from the reef, and at night when there is a bright moon (pers. comm. Gerry Davis, April, 2011). Other nocturnal movements have also been recorded (Meyer and Holland 2005). Additionally, *Kyphosus* spp. and *Platax* spp. may not have been observed because they prefer channels or surf swept outer reefs (Fishbase.org) to the nearshore reef flats where the majority of surveys were conducted. To better characterize this functional group, surveys must take into consideration these spatial and temporal conditions.

4.2 NOTE ON SPECIES COMPOSITION AND SPATIAL VARIABILITY

Clearly, geography plays a large role in determining fish community composition at any specific site, but fishing is an important contributor and the two interact. For example, the moderate separation of functional groups by main vs. outer island may be tied to reduced fishing pressure

(of browsers and scrapers/small excavators) associated with the geographical remoteness of outer islands (Williams et al 2008, Gillett and Cartwright 2010). Habitat diversity (Parrish 1989), structural complexity (Friedlander & Parish 1998), underwater topography (Meyer and Holland 2005), and hydrodynamics (Fulton et al 2005, Floeter et al 2007) are some biophysical factors known to influence the spatial distribution of fish. At this study's outer island sites, a higher variation in habitat types (ie, reef dropoffs, sand channels, sea grass, lagoons, patch reefs), topography and exposure to ocean flushing were observed adjacent to the reef flat. These are possible explanations for the abundance of browsers and scrapers/small excavators at these sites since large individuals of these roving herbivores are quite mobile, strong swimmers that are capable of moving large distances and between habitat types or depths for feeding, cover at night or spawning (Lieske and Myers 1994). CCA was also characteristic of these sites either as a function of the presence of scrapers, or because of a comparatively larger oceanic influence here (Floeter et al 2007), or both.

In contrast, grazers/detritivores, farmers and turf algae were characteristic of main island sites, where habitats were observed to be more contiguous and greatly influenced by terrigenous inputs from the larger rivers nearby. Compared to browsers and scrapers/small excavators, farmers and some grazers/detritivores are smaller, more site attached (Bell and Kramer 2000 in Meyer and Holland 2005), are positively correlated with increasing terrestrial influence (Letourneur et al 1998), and graze algal growth promoted by fresh water runoff (Kuitert and Tono-zuka 2001). They are well adapted to the varied water conditions of the fringing reef at main island sites.

4.3 BENTHIC ASSOCIATIONS: SCRAPERS/SMALL EXCAVATORS AND FARMERS.

The functional group scrapers/small excavators is an important group of fishes not only because they are an essential source of protein/food (Jennings et al 1999) but also because of their high abundance across regions in Fiji (Jennings and Polunin 1996, Sykes and Morris 2007). Because they are known for their diverse roles in structuring healthy reef communities, the widespread occurrence of parrotfishes and their strong positive response to protection as shown in this study gives a promising outlook for the ability of this functional group to maintain healthy reefs if fishing pressure is managed properly. The fact that 6 out of the top 10 species that make up two thirds of the biomass in protected areas are parrotfishes points to the possible advantages that high within-group parrotfish diversity can bring to the system. Studies in Australia (Wismer et al 2009) and findings of an experiment in Florida (Burkepile and Hay 2008) investigating consumer diversity found mixed herbivorous fish treatments to lower macroalgae abundance by up to 76%, enhance CCA cover by up to 64%, and increase coral cover by 22%.

Large size classes of scrapers/small excavators play important structuring roles on coral reefs but are highly targeted by fishing activities. In Fiji, they have exhibited the greatest response to exploitation (Mackay et al 2005) with some species such as *B. muricatum*, and *S. ghobban* reportedly becoming increasingly scarce over the years (Dulvy and Polunin 2004, Kuster et al 2005). Interestingly, this study found medium size classes of parrotfishes (11-25cm) to be the size class that significantly responded to protection against fishing. This is good news considering that this size class removes over 9 times more volume of the epilithic matrix than that of the small size class (1-10cm) (Bonaldo and Bellwood 2008), and in the case of species

from the *Chlorurus* genus, have bite rates that increase markedly above sizes of 15-20cm (Lokrantz et al 2008).

Large size classes of parrotfishes (>25cm) were observed a lot less frequently in this study and bioeroders/large excavators (>35cm) were not observed at all. Part of this is certainly due to rarity as a result of overexploitation, but it could also be due in large part to their ability to swim away quickly and undetected as divers were approaching during surveys. This issue highlights a need to expand the sampling methodology to account for the roving nature of these larger individuals that cross various reef zones and water depths.

Nevertheless, the large size classes of scrapers/small excavators was the size class that significantly correlated with the most number of benthic categories. Correlations were especially strong with coral, coralline algae and fleshy algae, the main factors involved in a reef's resilience against phase shifts. This result is consistent with much of what the literature puts forward about the importance of large herbivores in contributing to a reef's resilience against phase shifts. The fact that the results also indicate a strong negative relationship of its larger parrotfishes such as *C. microrhinos* and *H. longiceps* with fishing pressure warrants careful protective measures for species that attain this size class in order to preserve their important reef structuring abilities.

Besides scrapers/small excavators, farmers also significantly benefited from protection within most reserves. One key farmer species was identified as the species attaining the highest average biomass values of all the herbivores in this study. *S. nigricans* (and secondarily *S. punctatus/lividus*) was dominant on the reef flat in terms of biomass and was strongly positively

correlated with turf algae. This is a well studied taxon in Fiji and worldwide, with authors (Hixson and Bernstorff 1983, Ceccarelli et al 2005, Axline-Minotti 2003) referring to members of this genus as a keystone species for their effectiveness at preventing turf succession to unpalatable macroalgae (Ferreira et al 1998, Hata et al 2002, Gobler et al 2006), supporting nutrient regeneration on the reef flat because of extensive cover of territories (Klumpp and Polunin 1989, Lison de Loma et al 2010), decreasing sediment cover (Ceccarelli et al 2005), and increasing diversity and density of corals inside its territories post disturbance (Done et al 1991) and through time through defense against heavy predation of recruits by corallivores (Gochfield 2010) . The study by Gobler et al (2006) conducted on a shallow fringing reef in Fiji which found significant increases in brown macroalgae in herbivore exclusion (and nutrient treatment) plots, is strong evidence of the advantage of the presence of this genus on Fijian reefs.

Based on these studies, it can be assumed that the significant presence of this genus on reef flats at study sites in Fiji has a positive effect on the benthic community through the different mechanisms mentioned above. It is therefore possible to speculate that the effects of the genus are comparable to or even more important than other herbivorous fish in particular areas on the inner reef zone where other herbivore abundance and sizes might be low (Russ 1984) and where *Stegastes* and other algal-gardening pomacentrids can be the dominant herbivores present (Ceccarelli 2004).

5. IMPLICATIONS

This study found a diversity of herbivorous species present on the reef flat that varied in size and abundance depending on both management regime and location. The functional groups scrapers/ small excavators and farmers were well represented and were significantly protected at locations on the main island of Viti Levu where fished areas are reportedly more vulnerable to fishing pressure and habitat degradation (Mosely and Aalbersberg 2003, Lovell and Sykes 2008).

The successes of the three main island reserves in harboring herbivores and benthic communities that are significantly ‘healthier’ than adjacent fished areas is a precedent for the setting up of more, and more effective protected areas around Viti Levu. The Navakavu *tabu* is an excellent example of how a *tabu* can be effectively managed and sustain relative high biomass of herbivores even when situated next to the country’s largest urban center and source of fishing pressure. This is evidence for the efficacy of *tabus* that are well enforced and properly situated to encompass ideal habitat. and maximise ecosystem productivity.

An important finding of this study is the considerable presence of farmers on the reef flat and their potential role of keeping algae at early successional stages. The notion of a positive effect of farmers on coral community health is controversial given that they sometimes kill coral to initiate the algal garden, but it draws support from several lines of recent evidence. This functional group faces little threat from fishing but instead may suffer from general habitat degradation and loss of the appropriate coral habitat for their territories. This was obvious at main island sites where *Stegastes* biomass was significantly lower in fished sites and where the

reef was observed to be relatively degraded and dominated by *Sargassum*. A correlated decrease in *Stegastes* numbers with increased eutrophication, as tested in an experiment on Dravuni, Fiji (Gobler et al 2006), could possibly lead to a phase shift to macroalgal dominance at main island sites where anthropogenic inputs of nutrients along coastal areas are an increasing threat (Mosely and Aalbersberg 2003). Farmers would most benefit from the protection of their habitat through *tabu*, as well as control of land-based sources of pollution.

It can be assumed through its dominance in biomass and numbers, that the functional group scrapers/small excavators is the leading group of herbivores impacting and structuring the reef flat. Their effect is thought to be twofold through scraping of the epilithic algal matrix by abundant smaller species such as *C. sordidus*, *S. rivulatus* and *C. bleekeri*, and through small-scale excavating by large size classes of the species *C. microrhinos*, *H. longiceps* and *S. ghobban*. The larger sized individuals warrant special attention because of their high association and beneficial relationship with coral and crustose coralline algae.

In Fiji these larger individuals are increasingly targeted with the advent of modern fishing technology such as the use of spear guns, SCUBA, and motorized boats that allow fisherman to catch more per trip, travel further and poach more easily (Gillet and Moy 2006, Kuster et al 2005). The use of fishing bans as a form of management is a common and proven effective method at the village level, though more typically applied to reef flat invertebrate food sources. Such bans can be placed on those larger herbivores reported to be decreasing such as *S. ghobban* and the very favored and highly spearfished species, *N. unicornis* (Kuster et al 2005). Other

suggested methods of management are government controls on spearfishing gear and practice, as well penalties on the sale of illegal species (Gillet and Moy 2006) and sizes.

Furthermore, there is a need for *tabu* to extend to and encompass the complete home range of these larger, more mobile species. While these species visit the reef flat during the day, they also move to deeper areas and channels to take cover at night and to spawn (Randall 1965 in Parrish 1989). These areas are often where harvesting occurs so *tabus* must ensure that they include these vulnerable areas. While Fiji has strong-community buy-in to establishing small *tabus* (Govan 2009, Jupiter and Egli 2009), they are, however, often situated on shallow reef flat so it is essential to expand the average *tabu* to explicitly include deeper areas and channels, either through the establishment of larger areas covering multiple reef habitats, or through a network of smaller, closely spaced *tabus*. Such systems will likely be more effective than the traditional, single reef-flat tabu area in sustaining a resilient assemblage of large herbivores exhibiting a diversity of functions.

This strategy might benefit browsers, in particular, since alarmingly low numbers were observed on the reef flat. Further study needs to be conducted on this functional group and their role in the reef ecosystem in Fiji because members of this group have exhibited the capacity to play a key role in the reversal of macroalgal shifts, once they have occurred. It would be beneficial to conduct feeding behavior studies on a number of different herbivores such as those conducted on the Great Barrier Reef (Bellwood and Choat 1990, Fox and Bellwood 2007, Mantyka and Bellwood 2007) to identify those that have the potential to function as browsers. While most herbivores prefer to feed on epilithic algae it is thought that their food preferences can adapt to

changes on a reef, such as the increased availability of macroalgae that disturbance might bring about. In such conditions scarids and siganids, who normally play a different function, have been observed to browse on calcified algae and fleshy brown algae such as *Sargassum* (Mantyka and Bellwood 2007), and in the Caribbean, this is the habit of particular species (mostly of the genus *Sparisoma*) (Adey et al. 1977). To ensure that these nascent functionalities are retained, as well as to promote functional diversity *and* redundancy, management must ensure that an intact, diverse assemblage of species and functional groups are protected. In this regard, the traditional *tabu* system affords a strong beginning, but one that needs to be well enforced and expanded beyond the reef flat in the face of mounting human pressures.

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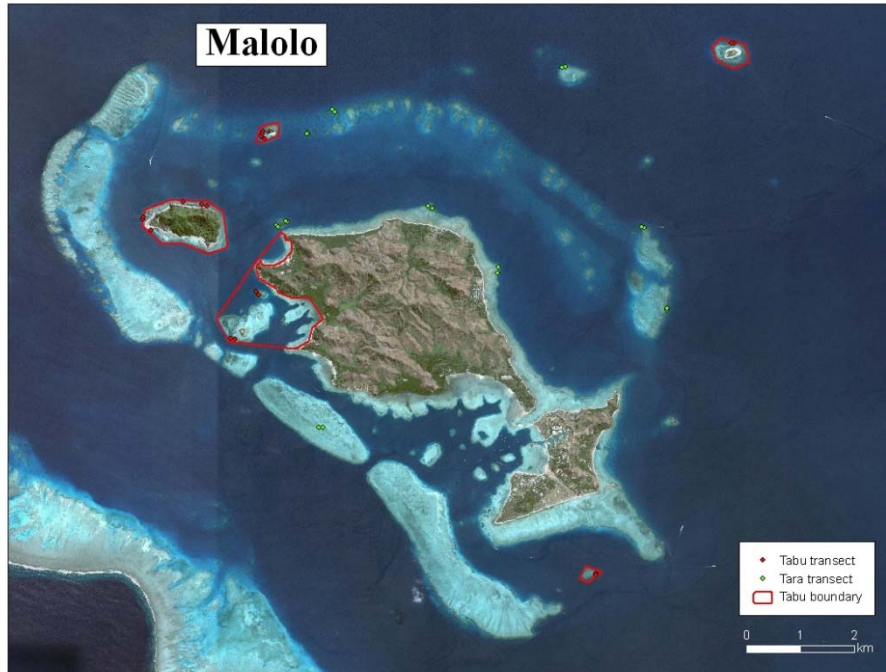
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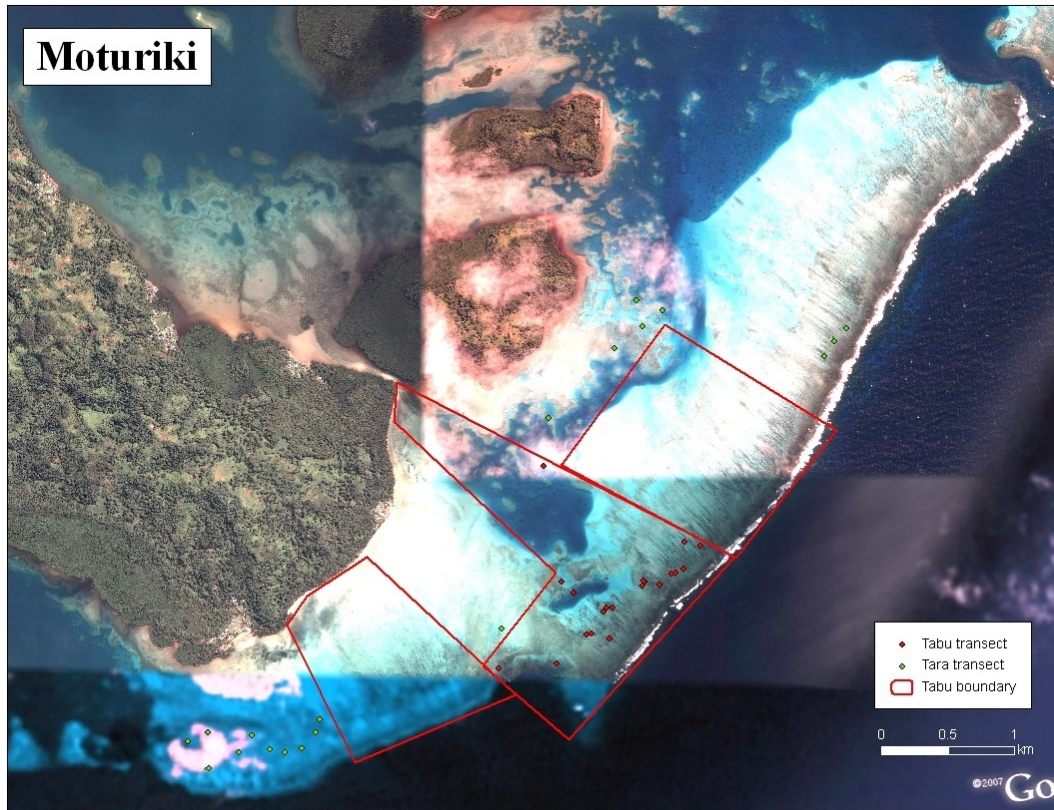
APPENDIX I : Site Descriptions

1. Malolo



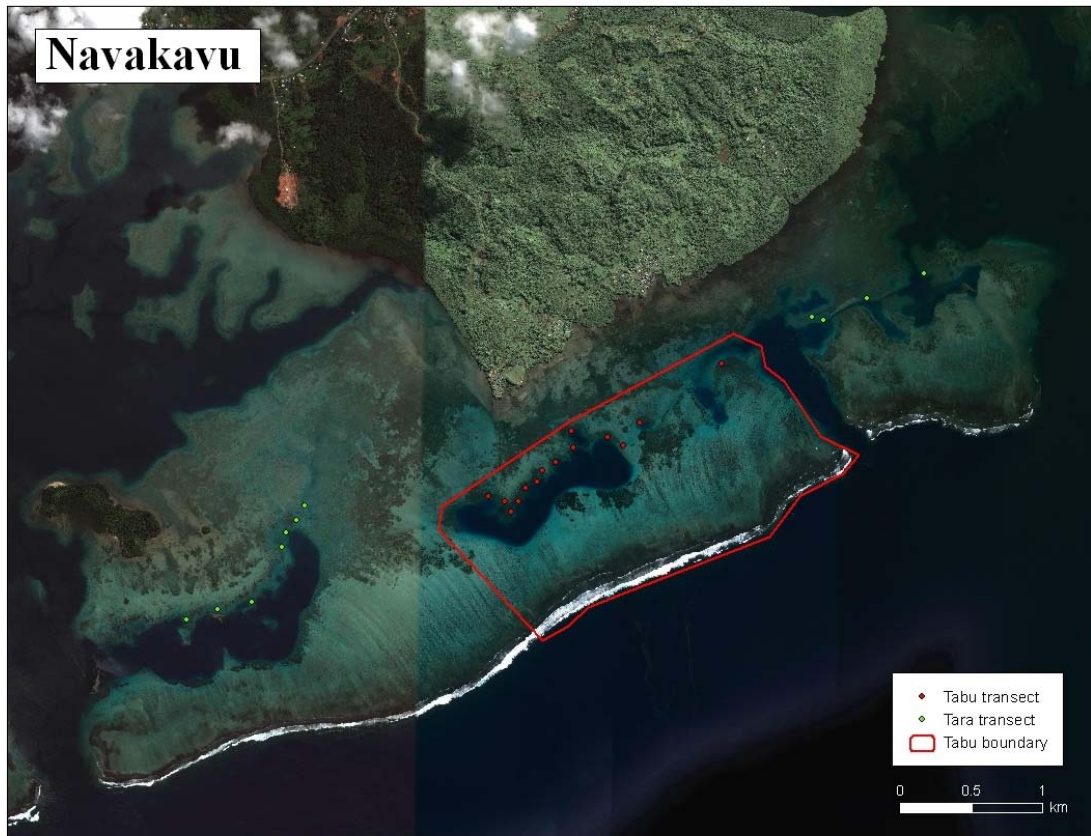
Malolo is located on the western, leeward side of the main island of Viti Levu in the Mamanuca Island Group. This study site is composed of the main volcanic island Malolo and the immediate surrounding smaller limestone islands. This group of island is protected from large southerly swell by the Malolo Barrier Reefs that lie to the south west. Closer in and surrounding the island group almost completely is a second system of protected barrier reefs. Each island also has a narrow band of fringing reefs surrounding them. Sampling was conducted on the fringing as well as the immediate barrier reef. Malolo and its islands are generally dry as is characteristic of Fiji leeward locations, but there are intermittent streams that flow from the highest peak of 723ft. Mangroves occur on the western and southern edges of Malolo, opposite from the two village communities of Yaro and Solevu. These two villages have in the past designated *tabu* areas on the eastern reefs but they have been opened since (Meo & Comely pers. comm.). Areas that are now prohibited from fishing are designated by the resorts in areas adjacent to the resorts and mainly around the smaller islands of Waidiqi, Qalito, Mociu and Navini. The Mamanuca Environmental Society (MES) is an NGO that has worked closely with resorts on the management and monitoring of the reefs in the Mamanucas since 2003. The two villages on Malolo belong to the Vanua Malolo which has a customary fishing area that extends much further northward to include two more villages on other islands. Thus only four villages have fishing rights to a large area of reefs although many resorts also have contracts to take guests out on fishing trips. Numerous fishermen from the Nadi urban area also fish around these islands. Most fishing of herbivorous fish species is done by spearfishing.

2. Moturiki



This study site is located off the island of Moturiki in the Lomaiviti Island Group off the eastern side of the large main island, Viti Levu. Moturiki is an oblong volcanic island approximately 6 miles long and about 436ft high at its highest point. Mangroves surround most of the island except for the southeastern end exposed to the trade winds. Here sandy shores extend out to a broad stretch of reef composed of shallow inter-tidal reef flats, seagrass beds, lagoons, patch reefs, deep channels and ending at a well developed back reef and crest. Five small streams empty onto the study area. Sampling was conducted along this expanse of reef on patch reef on the western and central parts and back reef on the eastern, seaward end. A large component of this reef stretch is designated as three *tabu* areas by the three closest villages: Daku, Uluibau and Niubasaga, which have population numbers of 85, 275, and 42 respectively. Each *tabu* is about 1km² on average and were initiated in 2000 with the help of the non-governmental organization Partners in Community Development Fiji (PCDF). All residents of Moturiki and surrounding small islands (approx 1,000 total) belong to the Vanua (ownership unit) Moturiki, who have customary rights to all reefs surrounding the island. However, most of the fishing in the area is done by members of the nearest villages with regular visits from other Moturiki villages and outside fishermen from nearby islands and poachers from the urban areas of Viti Levu. Fish extraction is conducted using nets, spear and line. Herbivorous fish from the families Acanthuridae, Siganidae and Scaridae are mainly caught by spear (Tunidau pers. comm.). Siganids and Acanthurids are also targeted by lay net fishing in the intertidal areas.

3. Navakavu



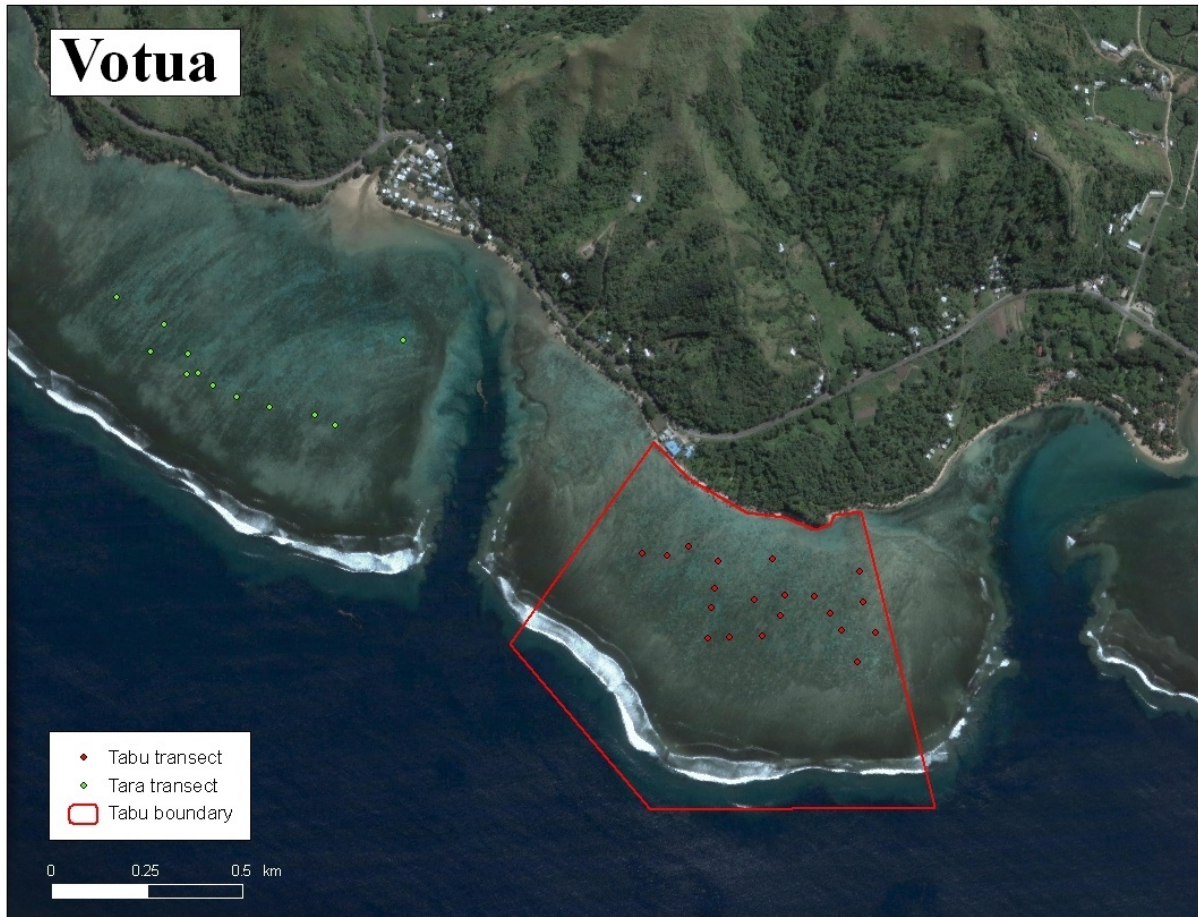
The Navakavu site is the closest location to an urban area, which is Suva, the capital of Fiji and the most populated town in the country. It lies just adjacent to three village communities and two settlements Muaivuso, Nabaka, Waiqanake, Namakala and Ucuinamomo. These communities make up of approx. 600 people who belong to the Yavusa (traditionally linked unit or clan) Navakavu and who fish as their primary source of income (Beukering et al 2007). Their customary fish rights cover most of the Cakauwaidroka Reef, which is a wide fringing reef that includes mudflats, seagrass beds, blue holes or deep channels, submerged coral heads and a shallow subtidal reef crest. Sampling was conducted along the blue holes and back reefs. A couple of rivers flow into the reef system as well as numerous streams. Its location on the windward side of Viti Levu exposes this site to the swells from the south, the southeast trade winds and regular rainfall. The Navakavu *tabu* is centrally located within the customary fishing grounds and around a blue hole. It was set up by the villagers in 2001 with the help of the University of the South Pacific (USP). It is now a member of the Fiji Locally Marine Managed Network (FLMMA). Enforcement is high for the *tabu*, but the *tara* areas are heavily fished by Navakavu members, nearby villagers and poachers from the urban fish markets in Suva. Lay nets and line fishing are the most common methods of fishing (pers. obs.) though night spearfishing by poachers with SCUBA gear and fast boats may account for a large amount of fish removed (Thaman et al 2008).

4. Navutulevu



The Navutulevu site lies on the central southern coast of Viti Levu on the Coral Coast in the District of Serua. This site comprises of a narrow fringing reef that extends just east of the Namatakula passage east to the Somosomo Passage. The reef is mainly subtidal with a deeper reef flat in the middle that extends to a shallow intertidal reef crest. Sampling was conducted on this middle reef flat. A deep channel cuts across the reef from where the Navutulevu Creek empties and out through the Navutulevu Pass. Only the eastern end in Somosomo Bay has mangroves but seagrass grows further west of this on Tabati Reef. The two villages Navutulevu and Naboutini have customary fishing rights to this stretch of reef where net fishing, line fishing and gleaning are heavily practiced. Night spearfishing and poaching of the *tabu* area occurs regularly (fish warden pers. comm.). The *tabu* area was initiated by the Navutulevu village in 2004 with the help of the Government Department of Fisheries (pers. comm. William Saladrau).

5. Votua



Votua is located further west of Navutulevu along the Coral Coast in the Nadroga District. The reef here is almost identical to the Navutulevu site with a deep channel originating from a stream adjacent to the village and flowing out between the designated *tabu* area and *tara* area. However, there are no mangroves or sea grass beds nearby. Reef flats are subtidal and wave exposure and currents are high. Sampling was conducted on the reef flat. Votua lies within the Vanua Davutukia *qoliqoli* which extends much further westward although reef usage is mostly restricted to the nearby adjacent village of Votua and the Votua Housing, Vatukulelima, and Vuniwai Settlements. The *tabu* was initiated in 2003 with the help of USP and is now a FLMMA site. It is also run by the village as a tourism attraction with snorkeling tours available to tourists from nearby resorts. The *tabu* is also a popular research site and the village regularly cater to local and international researchers. Fishing methods by the community are similar to those of Navutulevu although marine resources are not considered their primary source of livelihood (FLMMA 2006).

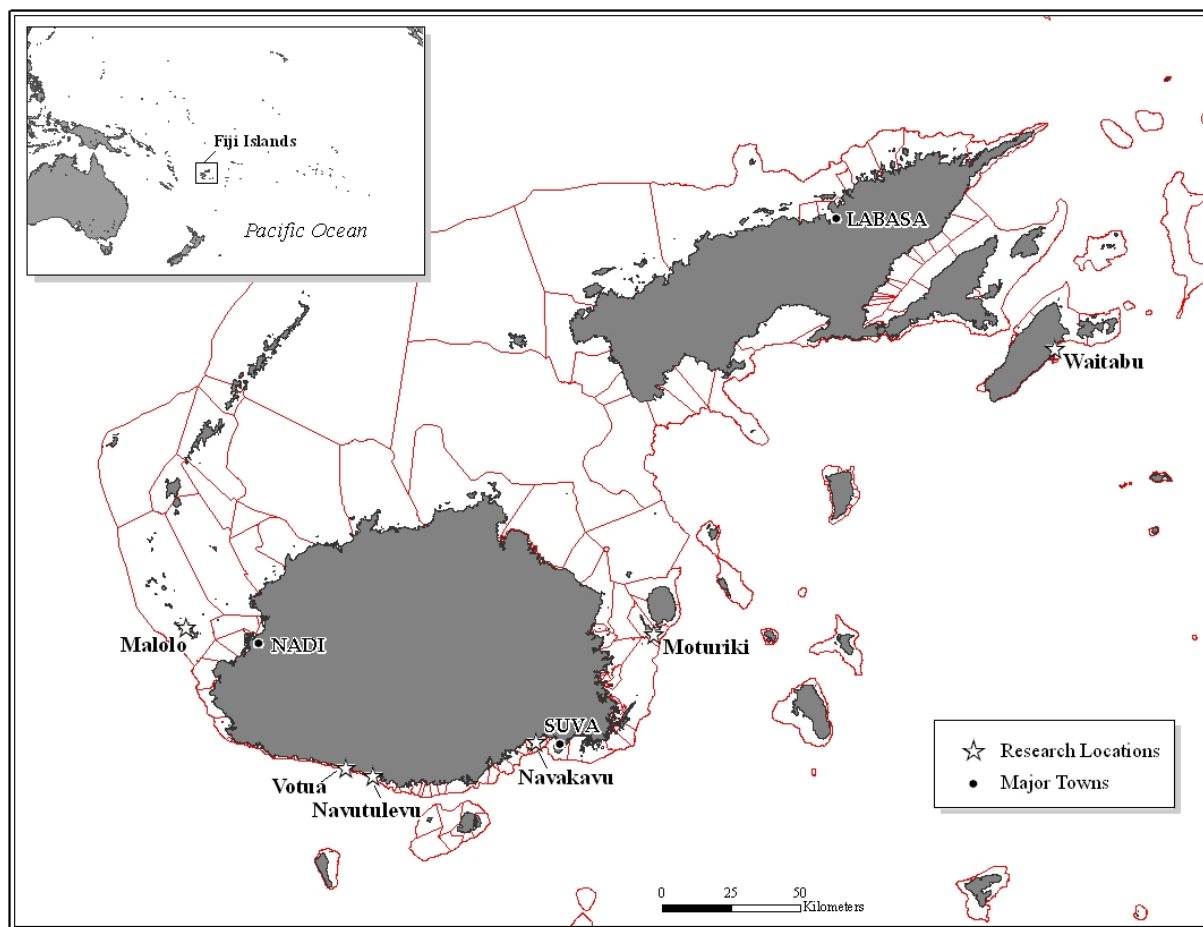
6. Waitabu



Waitabu is the third of the outer island sites. It is located on the fringing reefs off the eastern, windward coast of Taveuni Island, which lies east of the large island Vanua Levu. Taveuni itself is a large volcanic island that is approx 25 miles long and 3,911 ft at its highest peak, thus large enough to create an orographical effect on the island. The reef here is an even shelf of sand, rubble, submerged corals and soft corals that stretches from sandy beaches to the edge of the reef. In some places this shelf is very narrow. The site is on the windward side of the island so it can be surgy across the reef when there is swell. Sampling was done on the back reef. The *qoliqoli* stretches much further north from the study site though the most regular users are Waitabu, Vidawa and Korovou Villages and Navaka, Wai and Wunimakita Settlements. Two *tabu* are present at this study site, Waitabu Tabu and Korovou Tabu. The Waitabu Tabu was set up in 1998 with the help of NZAID and is now run as a tourist attraction to resorts and cruise ship visitors with tours and overnight camping available (www.waitabu.org). This site is a member of FLMMA.

APPENDIX II: Research protocol in Fiji

There are approximately 246 actively marine managed areas or tabu in Fiji. Each tabu is managed by the local community residing nearby and who have customary rights to the land and the adjacent reef system. These reef systems are known as *qoliqoli* or traditional fishing grounds (410 total, see figure). The majority of the *tabus* (217 total) are members of the Fiji Locally Marine Managed Area Network (FLMMA, www.LMMAnetwork.org), a supporting organization composed of local experts and stakeholders who work with communities in setting up areas for protection, creating management plans and conducting monitoring. The few *tabus* that are not part of FLMMA are usually supported by a partnership between the communities and the government or other non-governmental entities.



To conduct research in Fiji it is critical to go through the appropriate protocols to gain access to sites. It is important to establish a working relationship with partner organizations as they are the representatives to the communities and act in their best interest to ensure that researchers go through the respectful and culturally appropriate way of introduction, fieldwork and acknowledgement of communities' property. Of the six locations chosen for study, Navakavu, Votua and Waitabu are FLMMA members. Of the remaining three, Malolo *tabus* are managed

by resorts with support from the Mamanuca Environmental Society, Moturiki is partnered with the Pacific Community Development Foundation (PCDF) and Blue Ventures, and Navutulevu is supported by the Fisheries Department.

The FLMMA Network has a formal and structured system to gain access for researchers. A researcher must establish a Memorandum of Understanding between its sponsoring institution and the Network. This includes a submission of a research proposal to be reviewed by the FLMMA Biological Working Group and Executive Committee. Upon approval, the researcher must then agree to and sign a Letter of Agreement which outlines rules of conduct for the researcher to follow while staying at and conducting research at research sites. Special emphasis is placed on the introduction process whereby the researcher must ensure that the community at large is aware of and understands the process and purpose of the research and any value that comes out of it. Proper follow-up is also important to ensure that the communities gain access to the research findings.

This study's research proposal was created in consultation with the CI-MMAS chief scientist and his doctorate student, both faculty at Boston University. Additional review was provided by faculty from IAS-USP who sit on the FLMMA Biological Working Group. The proposal was submitted to FLMMA and approved under the CI-MMAS Memorandum of Understanding for their larger Fiji project.

When visiting the research site for the first time it is essential to present a *sevusevu*, which is a small offering of kava. This is the culturally appropriate form of introduction and sign of respect to the community. The *sevusevu* is presented to the traditional head of the village or the *Turanganikoro* (and any elders that may be available) with a speech in Fijian by a member of the partner organization who has accompanied the researcher for this very reason. Typically the village would have been contacted ahead of time to set up a good time for the researcher to be in the village, and for a family to prepare to host the researcher. The speech then is a formality but is an essential formal introduction that addresses and respectfully acknowledges the elders and the community and their property, formally asks for permission to enter and conduct research. It introduces the researcher and describes where they are from and what type of work they want to do. The researcher is also asked to formally say a few words about themselves while the accompanying partner member translates. The *Turanga ni koro* (Fijian word all in italics? then says a speech in reply, accepting the *sevusevu* and welcoming the visitors. Afterward, the kava bowl, *tanoa*, is brought out, the kava pounded into powder and mixed with water, and served to all present. With the formalities over, this is the time for casual conversation and getting to know to each other before the researcher is taken to their host family.

For this study, all fieldwork entailed a homestay at all sites except for the Navakavu site in Suva, where the researcher's family's home is situated. Staying with the community is a very pleasant experience and a highlight of fieldwork. It is an opportunity for the visitor to experience village life first hand, and an intimate way to get to know the people behind the resource upon which the study is based. The researcher can join in most communal functions from kava drinking in the evenings to attending church on Sundays. Sunday is a rest day for all with no work allowed including fieldwork.

All six communities provided research assistance in some way, whether it was through diving assistants, and/or a boat and boat driver. A total of 10 community members helped out with in-

water fieldwork at all sites. They were a mix of people from the teenager daughter of the host family to the village fish warden. They were very competent in the water, quickly grasped the concept of fieldwork and were a big help in identifying appropriate reef for surveying and pointing out tabu boundaries.

It is also customary that at the end of a homestay, just before leaving, that a kava ceremony take place either informally or with another *sevusevu* to conclude the work done and thank the community for their support. It is here that a modest money gift is presented to the relevant leader as payment for the homestay and for fieldwork assistance. In the case of the first two site visits, where research was conducted as part of a larger team of marine surveyors from CI-MMAS, IAS-USP and Fisheries Department (FLMMA), the farewell kava ceremony was a festive affair. It took half of a day with a whole community gathering, copious amounts of kava passed around, much singing and dancing, and the sprinkling of talcum powder on each other's heads as a celebratory way of demonstrating appreciation between the two parties. A visitor is hardly ever forgotten after having stayed in the village and after that initial visit, is always welcomed back. To honor that bond, the researcher is obliged to share the results or benefits of their study with the community.

APPENDIX III: Study Species

Functional Group	Family Name	Scientific Name	Common Name	Vernacular Name
Browsers	Kyphosidae	<i>Kyphosus vaigiensis</i>	long-finned drummer	guru ni cakau
	Acanthuridae	<i>Naso lituratus</i>	orangespined unicornfish	ta masimasi
		<i>Naso unicornis</i>	bluespine unicornfish	ta
Farmers	Pomacanthidae	<i>Centropyge bicolor</i>	bicolor angelfish	nn
		<i>Centropyge bispinosa</i>	twospined angelfish	nn
		<i>Centropyge flavissima</i>	lemonpeel angelfish	nn
		<i>Pomacanthus imperator</i>	emperor angelfish	lati ni daveta
		<i>Pomacanthus semicirculatus</i>	semi-circle angelfish	lati ni daveta
	Pomacentridae	<i>Chrysiptera biocellata</i>	two-spot damselfish	guru
		<i>Chrysiptera brownriggi</i>	surge damselfish	guru
		<i>Chrysiptera unimaculata</i>	onespot demoiselle	guru
		<i>Neoglyphidodon carlsoni</i>	Carlson's damselfish	guru
		<i>Plectroglyphidodon dickii</i>	blackbar devil	guru
		<i>Plectroglyphidodon lacrymatus</i>	whitespotted devil	guru
		<i>Pomacentrus bankanensis</i>	speckled damsel	guru
		<i>Pomacentrus brachialis</i>	charcoal damsel	guru
		<i>Pomacentrus coelestis</i>	neon damsel	nn
		<i>Pomacentrus moluccensis</i>	lemon damsel	guru
		<i>Pomacentrus spilotoceps</i>	threespot damsel	guru
		<i>Pomacentrus vaiuli</i>	princess damsel	guru
		<i>Stegastes albifasciatus</i>	whitebar gregory	guru ni veilase
		<i>Stegastes nigricans</i>	dusky gregory	guru ni veilase
		<i>Stegastes punctatus</i>	bluntsnout gregory	guru ni veilase
		<i>Abudefduf sordidus</i>	blackspot sergeant	
Grazers/detritivores	Acanthuridae	<i>Acanthurus auranticavus</i>	orange-socket surgeonfish	balagi
		<i>Acanthurus blochii</i>	ringtail surgeonfish	balagi
		<i>Acanthurus lineatus</i>	striped surgeonfish	dridri oriori
		<i>Acanthurus nigrofasciatus</i>	brown surgeonfish	dridri
		<i>Acanthurus olivaceus</i>	orangeband surgeonfish	dridri
		<i>Acanthurus pyroferus</i>	mimic surgeonfish	dridri
		<i>Acanthurus triostegus</i>	convict surgeonfish	tabace
		<i>Zebrasoma scopas</i>	brushtail tang	via

		<i>Zebrasoma veliferum</i>	sailfin tang	via
	Siganidae	<i>Siganus argenteus</i>	forktail rabbitfish	nuqa roro
		<i>Siganus doliatus</i>	barred rabbitfish	nuqa roro
		<i>Siganus punctatus</i>	goldspotted rabbitfish	nuqa ni cakau
		<i>Siganus spinus</i>	spiny rabbitfish	nuqanuqa
		<i>Siganus uspi</i>	USP rabbitfish	nuqa roro
		<i>Siganus vermiculatus</i>	vermiculate rabbitfish	nuqa, nuqa ni vei dogo
Scrapers/small excavators	Scaridae	<i>Calostomas spinidens</i>	raggedtooth parrotfish	ilava vucesa
		<i>Cetoscarus bicolor</i>	bicolor parrotfish	soqo - IP, lawi - TP
		<i>Chlorurus bleekeri</i>	Bleeker's parrotfish	bubute - IP, kakarawa - TP
		<i>Chlorurus japonensis</i>	redtail parrotfish	bubute, soqo - IP, kakarawa - TP
		<i>Chlorurus microrhinos</i>	steephead parrotfish	ulurua
		<i>Chlorurus sordidus</i>	bullethead parrotfish	bubute - IP, kakarawa - TP
		<i>Hipposcarus longiceps</i>	Pacific longnose parrotfish	ulavi - IP, TP
		<i>Scarus altipinnis</i>	minifin parrotfish	soqo - IP, lawi - TP
		<i>Scarus chameleon</i>	chameleon parrotfish	bubute - IP, kakarawa - TP
		<i>Scarus dimidiatus</i>	yellowbarred parrotfish	maqwa - IP, kakarawa - TP
		<i>Scarus flavipectoralis</i>	yellowfin parrotfish	bubute - IP, kakarawa - TP
		<i>Scarus frenatus</i>	bridled parrotfish	soqo - IP, kakarawa - TP
		<i>Scarus ghobban</i>	bluebarred parrotfish	ulavi - IP, TP
		<i>Scarus globiceps</i>	globehead parrotfish	bubute - IP, kakarawa - TP
		<i>Scarus niger</i>	swarthy parrotfish	soqo - IP, TP
		<i>Scarus oviceps</i>	egghead parrotfish	maqwa - IP, kakarawa - TP
		<i>Scarus psittacus</i>	palenose parrotfish	bubute - IP, kakarawa - TP
		<i>Scarus rivulatus</i>	surf parrotfish	bubute - IP, kakarawa - TP
		<i>Scarus rubroviolaceus</i>	ember parrotfish	soqo, bubute - IP, kakarawa - TP
		<i>Scarus schlegeli</i>	Schlegel's parrotfish	bubute - IP, kakarawa - TP
		<i>Scarus spinus</i>	greensnout parrotfish	bubute - IP, kakarawa - TP