The ecological effectiveness of locally managed marine areas on reef fish in Rarotonga, Cook Islands

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Abstract

Marine protected areas (MPAs) have been widely adopted as a principal tool to counteract the growing threats to coral reefs. However, many MPAs remain as 'paper parks' and only 15% of coral MPAs are adequately managed. Locally managed marine areas (LMMAs) are an alternative to government-run MPAs and are collaboratively managed by governments and local communities. This study evaluates the effectiveness of LMMAs on reef fish in Rarotonga, Cook Islands. Five LMMAs and open-access areas were surveyed by underwater visual census, using fish biomass and density as metrics of effectiveness. Univariate analysis was performed on total, family and targeted species biomass and density. Multivariate generalised linear models (GLMs) were used to determine the factors driving biomass and density of two targeted families, Acanthuridae and Mullidae. Total biomass and density was higher in the majority of LMMAs compared with corresponding controls, but these differences were rarely significant. Of 22 families recorded, eight had significant differences between LMMAs and controls, with most families exhibiting increases in LMMAs. Targeted species generally exhibited a positive response to protection, with significantly greater biomass and densities in two LMMAs; Edgewater (p<0.0001, p<0.0001) and Akapuao (p<0.02). GLMs revealed that protection was only significantly related to Acanthurids and Mullids at the hotel-managed LMMAs (Edgewater and Aroa). This is probably due to better enforcement and compliance at these sites. Instead, environmental/physical variables (e.g. structural complexity) were more influential and these results correlate with Acanthuridae and Mullidae ecology. Although this study provides some evidence for LMMA effectiveness there are several key recommendations to increase both Rarotonga's LMMA effectiveness and study robustness. Most importantly, it is recommended that quantitative information regarding compliance and degree of fishing in adjacent areas is collected.

Introduction

Coral reefs are biologically, physically and economically essential environments (Gleason et al., 2010). Reefs provide abundant goods and services, supporting 275 million people living within 30km of them (Burke et al., 2011). Despite this enormous importance, 60% of reefs are threatened globally by unsustainable human activity (Bridge et al., 2013). Habitat destruction and overexploitation are considered amongst the most pervasive threats (Hughes et al., 2011). To counteract the threats to reefs, marine protected areas (MPAs) have been widely adopted as a principal tool (Graham et al., 2011; Ault et al., 2013). Worldwide, MPAs cover 8.3 million km^2 of the ocean and encompass 27% of reefs (Spalding et al., 2013). Irrespective of size, MPAs have a number of potential ecological benefits (Lester et al., 2009). Prohibiting fishing enables regeneration of coral reefs and reduces stress, which increases resilience and recovery trajectories when additional disturbance occurs (Anticamara et al., 2010; Carassou et al., 2013).

Reef fish have responded well to protection worldwide and targeted species often demonstrate the most notable changes (Halpern, 2003; Noble et al., 2013). Responses include increased biomass (Roberts et al., 2001), body-size (Fenberg et al., 2012) and density (Bartholomew et al., 2007). These responses occur due to improved habitat complexity/quality by removal of destructive fishing methods and direct release of fishing pressure (Harborne et al., 2012). Further, MPAs can replenish adjacent areas through spillover of exploitable species/individuals and increase recruitment by protecting spawning stock (Roberts et al., 2005).

However, despite their popularity, these centralised government-controlled MPAs often fail, existing as 'paper parks'[1] (Agardy et al., 2011). Recent estimates suggest worldwide only 15% of reef MPAs are effectively managed (Burke et al., 2011). Failures have been attributed to inadequate funding, management and enforcement (Rife et al., 2013). Additionally, many MPAs, particularly those in community-driven countries, do not address social concerns or involve communities in decision-making (Christie, 2004). These MPAs suffer a lack of compliance, which further leads to MPA breakdown (Campbell et al., 2012). As a result, countless MPAs seldom achieve any positive ecological differences in fish communities compared with open-access areas (e.g. McClanahan et al., 2006).

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[1] A paper park is defined as *'an area where protection only occurs in theory'* (Mora et al., 2006; Guidetti et al., 2008).

The inadequacies of top-down, centralised MPAs coupled with growing realisation of the importance of community involvement (e.g. for traditional knowledge) are driving local communities to adopt some responsibility for managing their marine resources and environments (Drew, 2005; Rocliffe et al., in press). One alternative to traditional MPAs are decentralised 'locally managed marine areas' (LMMAs), a *"collaborative MPA management system between local communities and governments"* (Govan, 2009). The latest review identified 655 LMMAs within the Indo-Pacific (Rocliffe and Peabody, 2013) and their involvement and empowerment of communities generally results in enhanced acceptance of regulations (Pollnac et al., 2001).

Rarotonga, Cook Islands is one example where LMMAs have been established. Rarotonga's six lagoonal LMMAs, known locally as *Ra'ui*, began being re-implemented in 1998[2] (Churcher-Hoffman, 2002). This was in response to community recognition of declining fish populations (Pinca et al., 2009), degraded lagoon health (May, 2003) and ciguatera outbreaks in the early 1990s (Churcher-Hoffman, 2002). Overfishing of Rarotonga's lagoonal fish was first recorded in 1955 and the adoption of spearfishing in the 1980s accelerated lagoonal fishing (Pinca et al., 2009). Although fishing pressure is not enormous in Rarotonga compared with other Pacific nations, several fish families are exploited commercially or for subsistence and in 2011, 52% of Rarotongan people undertook lagoonal reef-fisheries (Cook Islands Statistics, 2011). These *Ra'ui* aim to safeguard Rarotonga's heavily impacted marine resources and cover 14% of Rarotonga's lagoons (Miller et al., 2011). They have occasionally been opened for short periods of harvesting since establishment (Miller et al., 2011). However, when closed, all extraction within their boundaries is prohibited (Egerton, 2005). *Ra'ui* have no legal basis and instead are traditionally-run, policed by social pressures and local residents respect of *mana,* the power of their chiefs (Miller, 2009). They are declared by community leaders and are managed by these leaders and the government (Raumea et al., 2000).

Previous studies have indicated that Rarotonga's LMMAs are ecologically effective, recording increased fish densities and biomass in comparison with open-access areas (May, 2003). Protecting Rarotonga's fish is important to local communities to safeguard subsistence livelihoods and for attracting tourism, which contributes approximately 90% to annual GDP (Rocliffe, S. pers comm. 2013).

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[2] The *Ra'ui* were first implemented in the 1888 after European missionaries arrived in Rarotonga to control cash crop harvest and export (Churcher-Hoffman, 2002).

Research may offer key insights into LMMA effectiveness and assist in future establishment. This study investigates the effectiveness of Rarotonga's LMMAs (*Ra'ui* herein) on fish assemblages. It is hypothesised that these *Ra'ui* will perform similarly to effective MPAs worldwide containing healthier fish assemblages compared with unprotected areas. To investigate *Ra'ui* effectiveness, several research questions were examined:

1. Do the *Ra'ui* contain greater density and/or biomass:

      i.   overall

     ii.   between families

    iii.   and/or targeted species compared with unprotected areas?

2. What biological, physical and management factors influence biomass and density?

Methods

Study Sites

All research was conducted in shallow lagoons surrounding Rarotonga, Cook Islands between 2nd July-15th August 2013 (Fig.1). Rarotonga is a high volcanic island surrounded by $2.6km^2$ of almost continuous fringing reef that encloses $8km^2$ of lagoon (Ponia, 2000). It is the most developed, largest ($67.1km^2$) and capital of the 15 Cook Islands (Churcher-Hoffman, 2002).
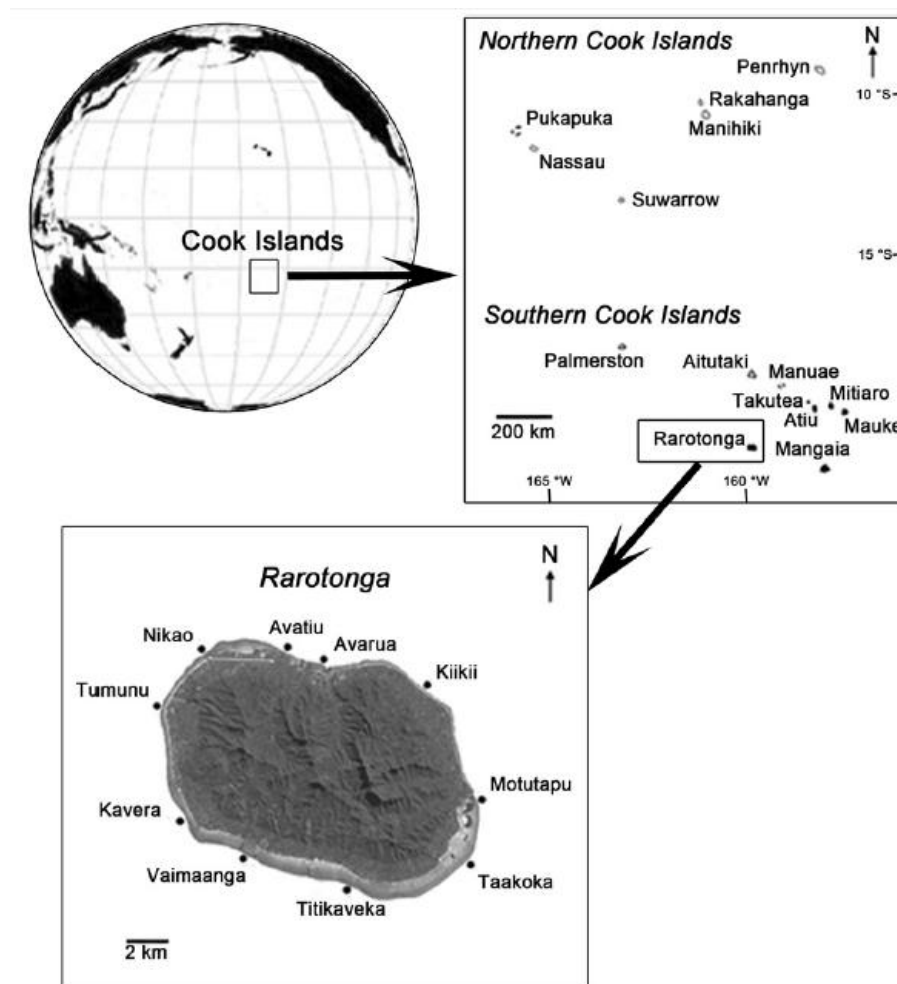

Fig.1. Map of Rarotonga's districts and location (21° 12'S, 159° 46'W) in the Cook Islands and in the Pacific Ocean.
Source: Rongo and Woesik (2013).

Five of the six *Ra'ui* were surveyed (Fig.2; Table.1). Pou'ara was not surveyed due to insufficient lagoon depth (<0.3m)[3] and insufficient area for appropriate transect replication. Each *Ra'ui* was paired with a control site of similar habitat, depth and substrate for accurate comparisons. Controls were located a minimum of 200m from *Ra'ui* boundaries to ensure clear distinction between protected and open-access areas (Walmsley and White, 2003). Each control and *Ra'ui* were divided into two zones; inner (shore to mid-reef) and outer (mid-reef to reef-crest).

Fig.2. Map of the study sites (*Ra'ui* and controls) in Rarotonga, Cook Islands. Pou'ara *Ra'ui* is indicated for reference although it was not surveyed during this study due to inadequate depth and survey area.
Image Credit: Steve Rocliffe.

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[3] This low depth has been attributed to the five cyclones that hit Rarotonga in 2005 and displaced rocks and uplifted sand, creating a sandbar which covers the area, prohibiting incoming water and fish (MMR. pers comm., 2013; Rocliffe, S., pers. comm., 2013).

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Table.1. Characteristics of the six *Ra'ui* in order of establishment around Rarotonga, Cook Islands. One asterisk (*) denotes a *Ra'ui* managed/established by a local hotel and the community, with higher levels of enforcement and two asterisks (**) indicates the *Ra'ui* (Pou'ara) not chosen for the study due to inadequate water depth and survey area (see text).
Source: Churcher-Hoffman (2002); Miller et al. (2011); MMR, pers. comm. (2013); Rocliffe, S. pers. comm. (2013).

Ra'ui Name	Rarotonga District	Area Protected (ha)	Date Established	Protection Duration (years since last opened)	History
Aroko	Ngatangiia	71.1	February 1998	13	Opened 16th February-2nd March 2000 for 14 days
Tikioki	Titkaveka	40.2	February 1998	13	Opened 1st February 2000 for 24 hours. Permanently closed since
Akapuao	Titkaveka	101.1	February 2000	13	May have been opened, date unknown
Aroa*	Arorangi	32.5	May 2000	10	Opened for trochus harvest in 2001 for two weeks. Opened again for trochus harvest June-August 2003
Edgewater*	Arorangi	5.4	2008	5	Not lifted since established
Pou'ara**	Matavera	4.8	February 1998	11	One third of the *Ra'ui* opened for one day on February 2nd 2000. Opened for three days in 2002

Survey Techniques

Initial Procedures

Prior to commencing surveys, training procedures were undertaken to eliminate inter-observer bias and/or variability. An in-water exercise to confirm that all observers could estimate fish lengths accurately was undertaken. This involved observers estimating varying lengths of pipe (3-47cm) until a non-significant ($p > 0.05$) result was achieved using paired t-tests (Bell et al., 1985).

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The optimum number of transect replicates was determined by performing 16 transects (50m x 5m) recording fish count data. A bootstrapping procedure was used to randomly select 1000 estimates of mean density for different levels of transect replication (Efron and Tibshirani, 1993). Plotting the coefficient of variation (Bros and Cowell, 1987) identified eight transects as the minimum acceptable replication level.

Underwater Visual Census

This study employed the underwater visual census technique, which is the dominant and most effective tool used in reef ecology studies (Bozec et al., 2011; Dickens et al., 2011). Eight haphazardly located belt-transects (50m x 5m) were sampled in the inner and outer-zone of each *Ra'ui* and control (total: 160 transects). Each census day's starting point was determined using the random number generator in Excel. For consistency and to avoid diurnal-nocturnal fish changeover, surveying was performed 2.5 hours either side of high tide and between 08:00-16.30 (English et al., 1997). To avoid inaccurate results, sites with fish feeding (Tikioki, Edgewater) were surveyed at least 30 minutes after feeding.

To minimise disturbance and tape presence, a five-minute acclimation period occurred before each census (Irigoyen et al., 2013). Environmental variables (depth, cloud cover, visibility, sea-temperature) were recorded at the beginning of each transect. Following this, one surveyor[4] swam along the transect at a constant speed (10-12min/transect) recording non-cryptic, diurnal fish counts to species-level and total length to nearest centimetre. On the second pass, estimates of mean structural complexity on a five-point scale were recorded every 10m (Table.2) (Graham et al., 2003; Hawkins et al., 2006). Although this is a semi-quantitative method, it provides a useful rapid assessment of complexity (Hawkins and Roberts, 2004). A second surveyor recorded the presence of live coral and algae if it occurred directly under the point at 50cm intervals[5] (as per: Campbell et al., 2012).

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[4] All surveys were undertaken snorkelling apart from at Tikioki where surveys were SCUBA dived due to greater lagoonal water depths.

Table.2. Five-point scale used to semi-quantitatively estimate mean structural complexity of reefs assessed on 50m x 5m transects in *Ra'ui* and control sites of Rarotonga's lagoons. Structural complexity was estimated every 10m along the transect and a total mean of the five values was calculated.
Method and scale adapted from: Graham et al. (2003); Hawkins et al. (2006).

Scale Number	Complexity Scale Description
1	Smooth – no holes or irregularities in substrate
2	Some complexity to the surfaces but generally little
3	Generally complex surface structure
4	Strong complexity in surface structure, with cracks, spaces, holes, etc.
5	Very complex surfaces with lots of spaces, nooks, crannies, under-hangs and caves

Data Analysis

Means for fish biomass and density (both overall and family-level), structural complexity and percentage algal and coral cover were calculated for each *Ra'ui* and control. Biomass was determined by estimating body mass of each individual fish using length-weight relationships ($W=aL^{b}$). Constants (a, b) were obtained from Fishbase (www.fishbase.org; Noble et al., 2013).

Each site was analysed separately due to different characteristics and levels of protection and enforcement between the *Ra'ui* (Table.1). For univariate analysis, data were checked prior to analysis for homogeneity of variance (Fligner-Kileen test) and normality (Shapiro-Wilk test) (Crawley, 2007). One-way analysis of variance (ANOVA) was performed when assumptions were met (Dytham, 2011). When assumptions were not met Wilcoxon tests, the non-parametric alternative, were used (Crawley, 2007). Analysis was performed per control and *Ra'ui* pair for total, each family and targeted non-ciguatoxic species biomass and density. Investigating targeted species enables the influence of protection on exploited species to be examined (Table.3). Ciguatoxic species according to Rongo and Woesik (2013) were removed to enable accurate analysis of targeted species.

Finally, multivariate generalised linear models (GLMs) were performed per site to investigate the influence of physical, biological and management parameters on two frequently recorded targeted families; Acanthuridae and Mullidae (Friedlander et al., 2003). Ciguatoxic species were removed to ensure only targeted species were analysed (Table.3). These two families were analysed to ensure consistency and because both had adequate sample sizes for analysis (Miller, 2009). Density and biomass per family were response variables. Depth, visibility, structural complexity, protection status, zone, mean percentage algal and coral cover were predictor variables. The variables were checked for normality and heteroscedasticity prior to analysis using Shapiro-Wilk tests and were transformed as necessary (Table.4) (Crawley, 2007). Gaussian error and identity-link functions were applied (Harmelin-Vivien et al., 2008) and independence of variables was established prior to analysis (Hawkins et al., 2006). Backward-forward stepwise selection obtained minimum adequate models based on the Akaike Information Criterion (Zuur et al., 2010). All analysis was undertaken using R (Version 3.0.0).

Table.3. List of the targeted reef fish of Rarotonga, Cook Islands. Species with an [a] indicates that they are targeted for the aquarium fishery and [c] indicates a species that is considered highly ciguatoxic (i.e. very unlikely to be fished at the present time).
Sources: Pinca et al. (2009); FAO (2010); Rocliffe, S. pers. comm. (2013); Rongo and Woesik (2013).

Family	Scientific Name	Common Name
Acanthuridae	Acanthurus guttatus	Whitespotted surgeonfish
	Acanthurus leucopareius	Whitebar surgeonfish
	Acanthurus triostegus	Convict surgeonfish
	Acanthurus xanthopterus	Yellowfin surgeonfish
	Ctenochaetus striatus	Striped bristletooth
	Naso lituratus	Orangespine unicornfish
	Naso unicornis	Bluespine unicornfish
	Zebrasoma scopas	Brushtail tang
Carangidae	Caranx melampygus[c]	Bluefin trevally
	Caranx sexfasciatus	Bigeye trevally
	Selar crumenophthalmus	Bigeye scad
Diodontidae	*Diodon hystrix*	Spot-fin porcupinefish
Holocentridae	*Sargocentron spiniferum*	Sabre squirrelfish
Kyphosidae	*Kyphosus bigibbus*	Brown chub
	Kyphosus cinerascens	Topsail drummer
Lethrinidae	*Gnathodentex aureolineatus*	Striped large-eye bream
	Lethrinus xanthochilus	Yellowlip emperor
	Monotaxis grandoculis	Bigeye emperor
Lutjanidae	*Lutjanus bohar*	Red snapper
	Lutjanus fulvus[c]	Flametail snapper
	Lutjanus monostigma	Onespot snapper
Mugilidae	*Neomyxus leuciscus*	Acute-jawed mullet
Mullidae	*Mulloidichthys flavolineatus*[c]	Yellowstripe goatfish
	Mulloidichthys vanicolensis	Yellowfin goatfish
	Parupeneus multifasciatus	Multibar goatfish
Pomacanthidae	*Centropyge flavissima*[a]	Lemonpeel angel
	Centropyge loricula[a]	Flame angel
Scaridae	*Chlorurus frontalis*[c]	Tan-faced parrotfish
	Clorurus sordidus	Daisy parrotfish
	Scarus altipinnis	Filament-finned parrotfish
	Hipposcarus longiceps	Pacific longnose parrotfish
	Scarus psittacus	Common parrotfish
Serrandiae	*Cephalopholis argus*[c]	Peacock grouper
	Epinephelus fasciatus	Blacktip grouper
	Epinephelus hexagonatus	Hexagon grouper
	Epinephelus merra	Dwarf spotted grouper
	Epinephelus tauvina[c]	Greasy grouper
	Variola louti	Lyretail grouper
Siginidae	*Sifanus argenteus*	Forktail rabbitfish
	Siganus spinus	Scribbled rabbitfish

Table.4. List of the necessary transformations applied to variables for each site in order to meet assumptions of normality and heteroscedasticity of multivariate generalised linear model analysis on Acanthuridae and Mullidae families at the five study sites in Rarotonga.

Site	Transformation		
	Log	**Square-Root**	**Square**
Akapuao	Acanthuridae biomass Mullidae biomass Mullidae density Depth	Coral cover	
Aroa	Acanthuridae biomass Structural complexity	Mullidae biomass Depth Visibility	
Edgewater	Acanthuridae biomass Acanthuridae density	Mullidae biomass Mullidae density Visibility	Depth
Tikioki	Acanthuridae biomass Acanthuridae density Structural complexity Visibility	Mullidae biomass Mullidae density	Depth

Results

Overall, 108 species, from 22 families of fish were recorded (Table.5). The ten most common species recorded accounted for 72% of the total number of recorded individuals (Table.6).

Table.5. The number of reef fish species and individuals recorded per family in five sites in Rarotonga's lagoons using underwater visual census methodology (2nd July-15th August 2013).

	Reef Fish Family	Total Number of Species Recorded	Total Number of Individuals Recorded
	Acanthuridae	10	5095
	Balistidae	4	244
	Belonidae	1	95
	Carangidae	1	13
	Chaetodontidae	17	530
	Diodontidae	1	4
	Fistulariidae	1	17
	Holocentridae	5	33
	Kyphosidae	2	15
	Labridae	14	1852
	Lethrinidae	3	260
	Lutjanidae	3	14
	Mugilidae	1	4
	Mullidae	6	226
	Ostraciidae	2	19
	Pomacanthidae	2	91
	Pomacentridae	15	3352
	Scaridae	8	445
	Serranidae	5	61
	Siganidae	2	104
	Tetraodontidae	4	301
	Zanclidae	1	27
Total	**22**	**108**	**12,802**

Table.6. The ten most commonly recorded reef fish species in five sites in Rarotonga's lagoons using underwater visual census methodology (2nd July-15th August 2013). Their total frequency and mean frequency per transect (individuals/250m ± SE) for each transect is given.

Rank	Reef Fish Family	Scientific Name	Common Name	Total Frequency Recorded (No. of Individuals)	Mean Frequency per Transect (individuals/250m ± SE)
1	Acanthuridae	*Ctenochaetus striatus*	Striped bristletooth	2919	182 ± 47.83
2	Acanthuridae	*Acanthurus triostegus*	Convict surgeonfish	1950	121 ± 38.19
3	Pomacentridae	*Stegastes fasciolatus*	Pacific gregory	1028	64.25 ± 17.34
4	Labridae	*Halichoeres trimaculatus*	Threespot wrasse	750	46.88 ± 12.59
5	Pomacentridae	*Dascyllus aruanus*	Humbug dascyllus	620	38.75 ± 17.01
6	Pomacentridae	*Chrysiptera glauca*	Grey demoiselle	433	27.06 ± 7.45
7	Labridae	*Thalassoma lutescens*	Sunset wrasse	423	26.44 ± 7,09
8	Pomacentridae	*Chromis viridis*	Blue green damselfish	409	25.56 ± 17.5
9	Scaridae	*Scarus psittacus*	Palenose/common parrotfish	291	18.19 ±5.33
10	Tetraodontidae	*Canthigaster solandri*	Spotted sharpnose	288	18 ± 5.22
	Total			**9111**	

Univariate Analysis

Density

Total mean density was higher in all *Ra'ui* (12-34% higher) excluding Tikioki where density was 13% higher in the control than its paired *Ra'ui* (Fig.3; Table.7). Aroa *Ra'ui* and control recorded the highest mean densities (59.6 and 52.45 individuals/100m^2 respectively) of all sites and Aroko control the lowest (17.7 individuals/100m^2). Despite higher densities in most *Ra'ui* compared with controls, analysis revealed these differences were not significant (Table.7).

Three sites (Akapuao, Aroa and Edgewater) had higher mean density of targeted, non-ciguatoxic species in their *Ra'ui* relative to corresponding controls (Fig.4). This difference was significant at Akapuao (24.75% higher) and Edgewater (64.84% higher) (Table.7).
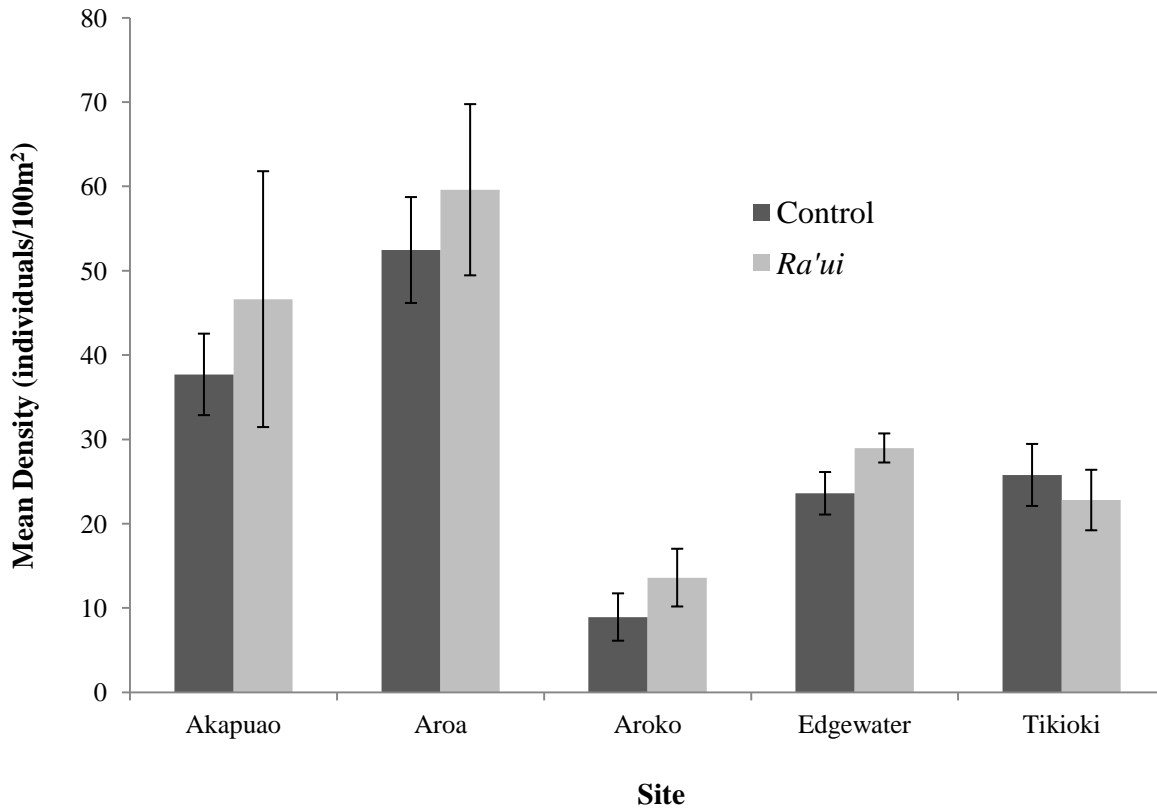

Fig.3. Mean total density (individuals/100m^2) for five *Ra'ui* and paired control sites in Rarotonga, Cook Islands (± SE, N=32 per site).

Table.7. Results of one-way ANOVA (F, *d.f.* = degrees of freedom for source and residual) or Wilcoxon test (W) for total reef fish density (individuals/100m^2) per site (*Ra'ui* Vs. control) and overall density for targeted, non-ciguatoxic reef fish (*Ra'ui* Vs. control). Beside each significant result "+" represents a positive trend and "-" represents a negative trend. The percentage difference between each sites *Ra'ui* and corresponding control is provided. A positive percentage represents higher density in the *Ra'ui* and a negative percentage represents higher density in the control. Targeted species information obtained from Pinca et al. (2009); Rocliffe., S. pers. comm. (2013) and ciguatoxic species information obtained from Rongo and Woesik (2011); Rongo and Woesik (2013).

Site	Test Statistics	P		Percentage Difference Between *Ra'ui* and Controls
Total				
Akapuao	W=147.5	NS		19.14
Aroa	W=105	NS		12.00
Aroko	W=96	NS		34.34
Edgewater	*d.f*= 1,30 F= 3.09	NS		18.55
Tikioki	W=144	NS		-13.05
Targeted, Non-Ciguatoxic				
Akapuao[+]	W=64	0.02	*	24.75
Aroa	*d.f.* =1,30 F= 1.99	NS		39.10
Aroko	W=144	NS		-76.39
Edgewater[+]	W=21	<0.0001	***	64.84
Tikioki	W=157	NS		-22.06

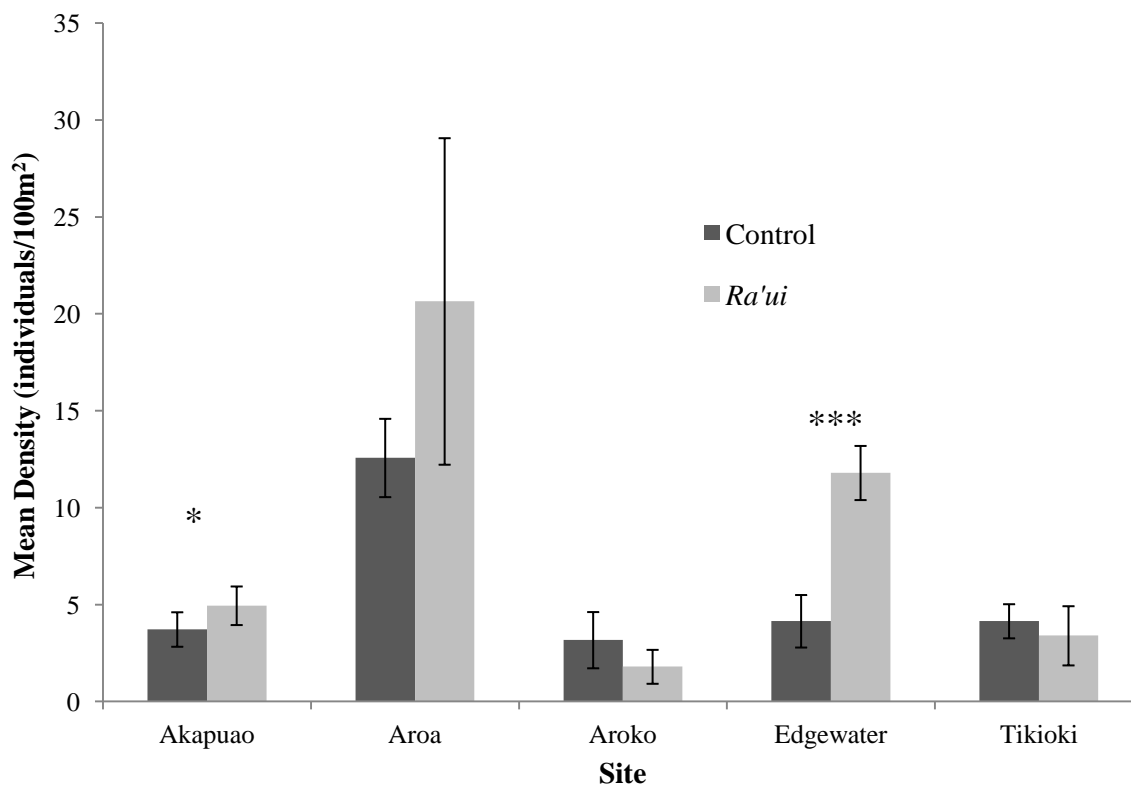NS not significant, * significant at p<0.05, ** significant at p<0.01 and *** significant at p<0.001

Fig.4. Mean total density (individuals/100m^2) of targeted, non-ciguatoxic reef fish species for five *Ra'ui* and paired control sites in Rarotonga, Cook Islands (± SE, N=32 per site). An asterisk (*) denotes a significant difference between *Ra'ui* and control, refer to Table 7 for detailed statistical analysis results.
Targeted species information obtained from Pinca et al. (2009); FAO (2010); Rocliffe., S. pers. comm. (2013) and ciguatoxic species information obtained from Rongo and Woesik (2011); Rongo and Woesik (2013).

Analysis of family density between *Ra'ui* and controls revealed of 22 families recorded, just eight families' density was significantly different (Table.8). Density was significantly greater in Akapuao control for three families relative to Akapuao *Ra'ui*. For Edgewater, two families had significantly greater density in the *Ra'ui*. Balistidae, Acanthuridae and Tetraodontidae exhibited the most significant differences between protected and open-access areas (p<0.0001). Trends varied amongst species and between sites. Labridae density was statistically significant in both Aroko and Akapuao, however exhibited a positive and negative trend to protection respectively. Similarly, Balistidae were significantly different at two sites, exhibiting a negative trend in Akapuao and positive in Aroa.

Table.8. Significant (p<0.05) results of one-way ANOVA or Wilcoxon test (W) for density (individuals/100m^2) per site, per reef fish family (*Ra'ui* Vs. control). Besides each family "+" represents a positive trend and "-" represents a negative trend.

Site	Family	Test Statistics	P	
Akapuao	Balistidae$^-$	W=210	<0.0001	***
	Labridae$^-$	W=196.5	0.010	**
	Mullidae$^-$	W=185	0.014	*
Aroa	Balistidae$^+$	W=45.5	0.002	**
Aroko	Labridae$^+$	W=72	0.03	*
Edgewater	Acanthuridae$^+$	W=39	<0.0001	***
	Pomacanthidae$^-$	*d.f.* =1,30 F=4.37	0.045	*
	Scaridae$^+$	W=72.5	0.014	*
Tikioki	Lethrinidae$^+$	W=180	0.014	*
	Tetraodontidae$^-$		<0.0001	***

NS not significant, * significant at p<0.05, ** significant at p<0.01 and *** significant at p<0.001

Biomass

The results were similar to density analysis. All *Ra'uis* displayed higher total mean biomass relative to controls, apart from Tikioki where biomass was 10% greater in the control (Fig.5; Table.9). Aroa had the highest total mean biomass of all pairings (121,4603g/100m^2 *Ra'ui* and 794,441g/100m^2 control). Aroko control site recorded the lowest biomass (218,887g/100m^2). Edgewater was the only site with significant difference in total mean biomass between the *Ra'ui* and control (p<0.0001), with 49.83% higher biomass in the *Ra'ui* (Table.9).

Analysis of targeted, non-ciguatoxic species revealed that biomass was higher in all *Ra'ui*, excluding Aroko where biomass was 130% greater in the control (Fig.6). Edgewater had 77.91% higher biomass in the *Ra'ui* and was the only site with a significant difference (p<0.0001) (Table.9).
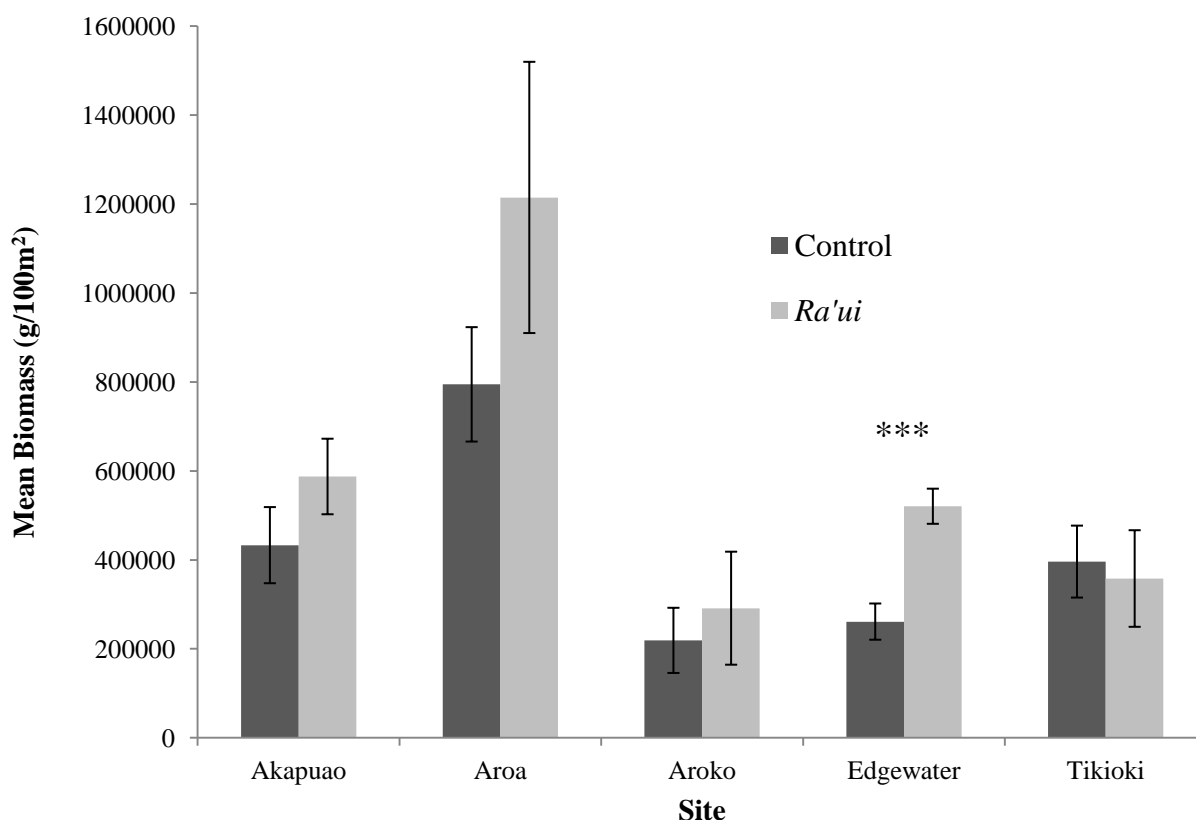

Fig.5. Mean total biomass (g/100m^2) for five *Ra'ui* and paired control sites in Rarotonga, Cook Islands (± SE, N=32 per site). An asterisk (*) denotes a significant difference between *Ra'ui* and control, refer to Table 9 for detailed statistical analysis results.
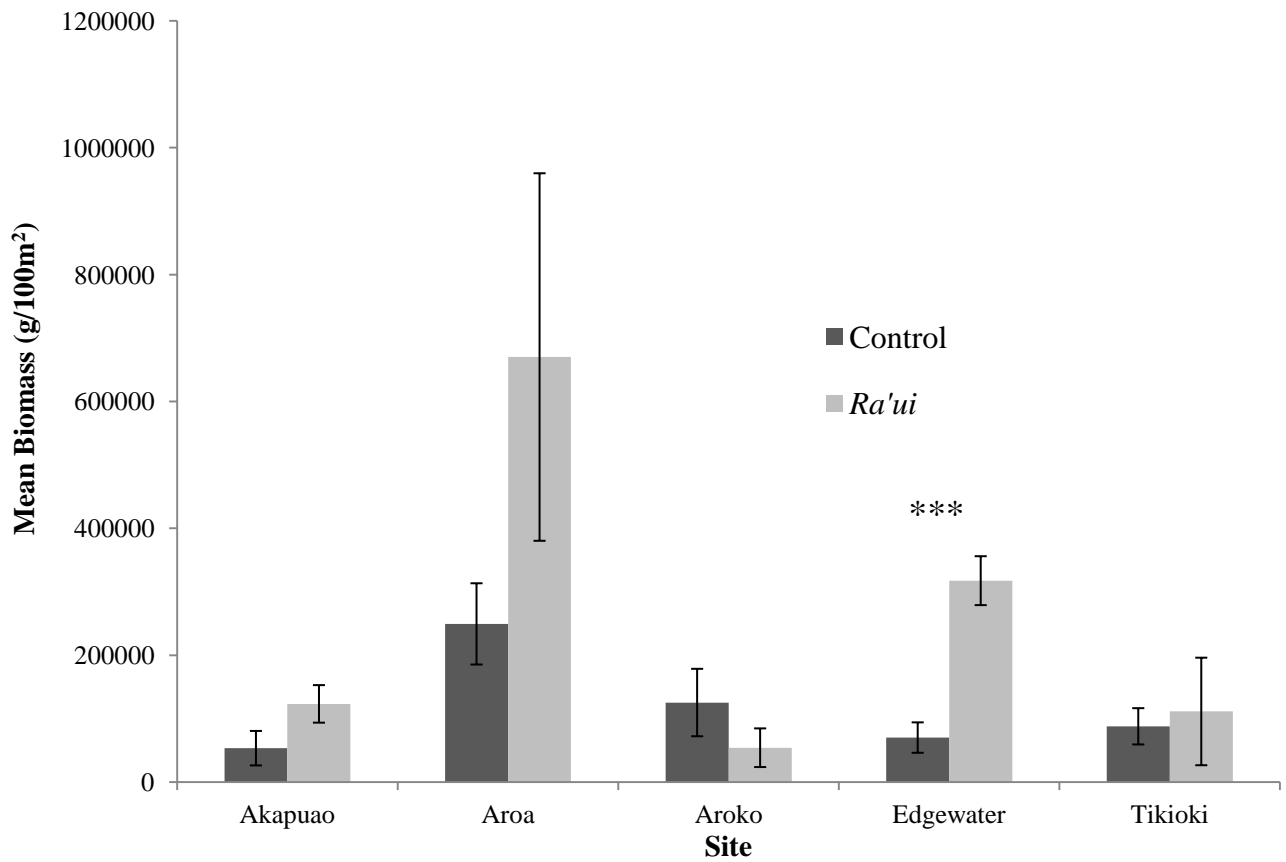
Fig.6. Mean total biomass (g/100m^2) of targeted, non-ciguatoxic reef fish species for five *Ra'ui* and paired control sites in Rarotonga, Cook Islands (± SE, N=32 per site). An asterisk (*) denotes a significant difference between *Ra'ui* and control, refer to Table 9 for detailed statistical analysis results.

Targeted species information obtained from Pinca et al. (2009); FAO (2010); Rocliffe., S. pers. comm. (2013) and ciguatoxic species information obtained from Rongo and Woesik (2011); Rongo and Woesik (2013).

Table.9. Results of one-way ANOVA (F, *d.f.* = degrees of freedom for source and residual) or Wilcoxon test (W) for total reef fish biomass (g/100m^2) per site (*Ra'ui* Vs. control) and overall biomass for targeted, non-ciguatoxic species (*Ra'ui* Vs. control). Besides each significant result "+" represents a positive trend and "-" represents a negative trend. The percentage difference between each sites *Ra'ui* and corresponding control is provided. A positive percentage represents higher biomass in the *Ra'ui* and a negative percentage represents higher biomass in the control. Targeted species information obtained from Pinca et al. (2009); Rocliffe., S. pers. comm. (2013) and ciguatoxic species information obtained from Rongo and Woesik (2011); Rongo and Woesik (2013).

Site	Test Statistics	P		Percentage Difference Between *Ra'ui* and Controls
Total				
Akapuao	*d.f.* =1,30 F=1.64	NS		26.29
Aroa	W=105	NS		34.60
Aroko	W=111	NS		24.84
Edgewater$^+$	*d.f*= 1,30 F= 20.91	<0.0001	***	49.83
Tikioki	W=147	NS		-10.62
Targeted, Non-Ciguatoxic				
Akapuao	W=104	0.02		56.65
Aroa	W=147	NS		62.79
Aroko	W=140.5	NS		-131.56
Edgewater$^+$	W=30.5	<0.0001	***	77.91
Tikioki	W=169.5	NS		21.04

NS not significant, * significant at p<0.05, ** significant at p<0.01 and *** significant at p<0.001

For eight families, biomass was significantly different between *Ra'ui*s and corresponding controls (Table.10). Families with significantly greater biomass in *Ra'ui*s (e.g. Acanthuridae) exhibited similar responses found in density analysis. Families at Edgewater exhibited the greatest difference in biomass, with increased biomass in the *Ra'ui*. At Akapuao, Balistidae, Labridae and Mullidae had significantly greater biomass in the control site. Families at Aroko recorded no significant differences between biomass in the control and *Ra'ui*. Acanthuridae (Edgewater; higher biomass in *Ra'ui*) and Tetraodontidae (Tikioki; higher biomass in control) exhibited the most significant difference between protected and open-access areas (p<0.0001).

Table.10. Significant (p<0.05) results of one-way ANOVA (F, *d.f.* = degrees of freedom for source and residual) or Wilcoxon test (W) for biomass (g/100m^2) per site, per reef fish family (*Ra'ui* Vs. control). Besides each family "+" represents a positive trend and "-" represents a negative trend. "—" indicates site where no significant results occurred.

Site	Family	Test Statistics	P	
Akapuao	Balistidae⁻	W=193	0.01	**
	Labridae⁻	W=194	0.01	**
	Mullidae⁻	W=181.5	0.02	*
Aroa	Balistidae⁺	W=55.5	0.006	**
	Mullidae⁺	W=73	0.03	*
Aroko	—	—	—	
Edgewater	Acanthuridae⁺	W=20	<0.0001	***
	Scaridae⁺	W=72	0.014	*
	Zanclidae⁺	W=96	0.039	*
Tikioki	Lethrinidae⁺	W=180	0.014	*
	Tetraodontidae⁻	W=225.5	<0.0001	***

NS not significant, * significant at p<0.05, ** significant at p<0.01 and *** significant at p<0.001

Substrate

Figure 7 and table 11 illustrate differences in substrate between sites and protection status. Structural complexity was higher in *Ra'ui* in three of the five pairs (Akapuao, Aroko, Edgewater). Mean complexity ranged from 0.93 in Aroko control to 2.3 in Akapuao *Ra'ui*. Differences between complexity in *Ra'ui* and controls were only significant in Aroko and Tikioki, with greater complexity in Aroko *Ra'ui* and Tikioki control. Average coral cover was higher in all *Ra'uis* and this difference was significant at Aroko and Edgewater. Coral cover was highest in Tikioki *Ra'ui* (7.78%) and lowest in Aroko control (0.44%). Mean algal cover was higher in all controls compared with corresponding *Ra'uis* but these differences were only significant in Aroa (p<0.0001). This excludes Tikioki where algal cover was almost equal between control and *Ra'ui*. Overall, algal cover was highest at Edgewater site (63.5% *Ra'ui*, 71.75% control) and lowest in Aroa *Ra'ui* (16.5%). Generally, algal cover displayed an opposite trend to coral cover, where sites with high coral have lower algal cover.
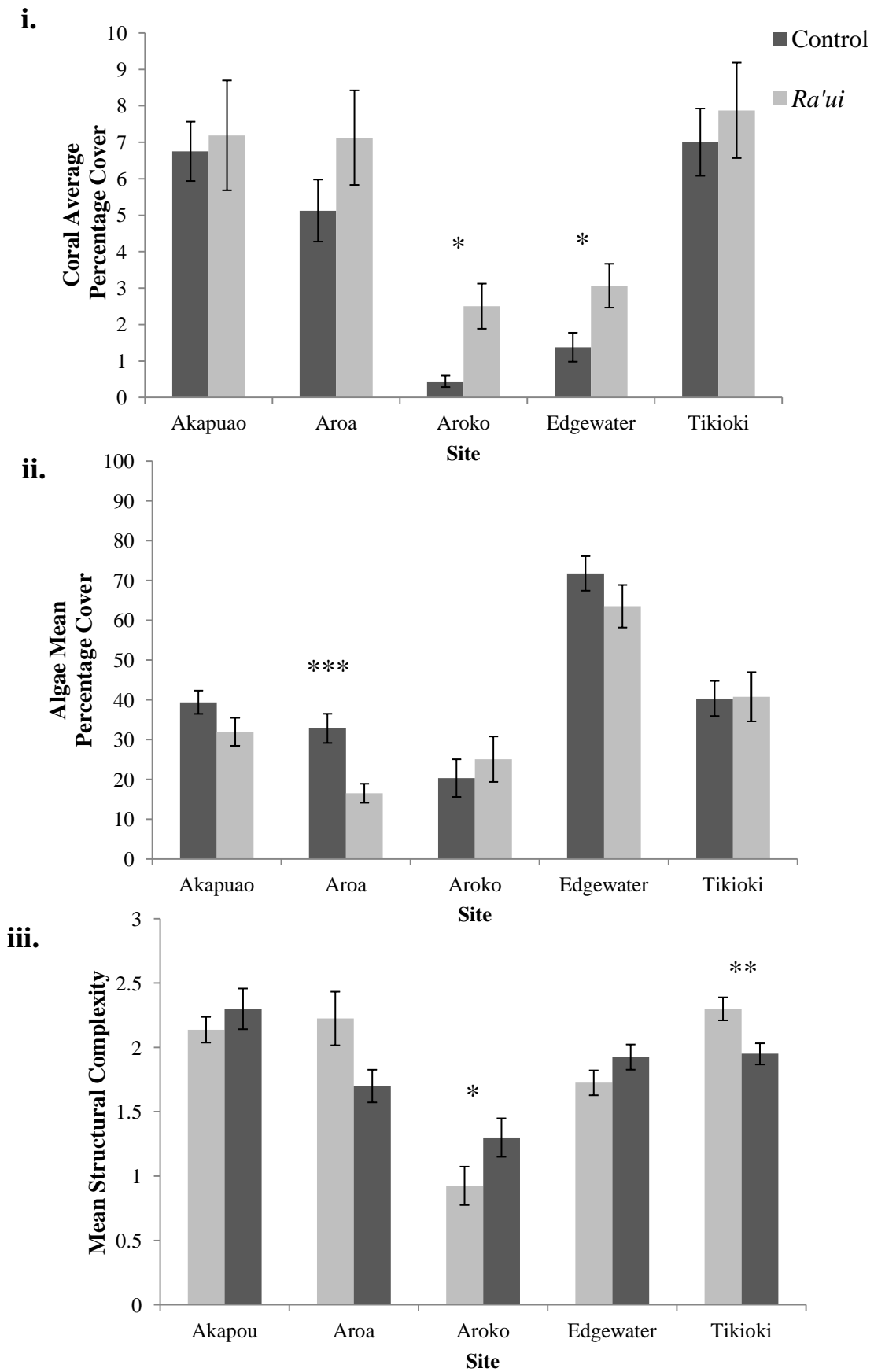
i.

ii.

iii.

Fig.7. Mean values of cover of algae (i) and scleractinian coral (ii) (%) and mean structural complexity (iii) for five *Ra'ui* and paired control sites in Rarotonga, Cook Islands (± SE, N=32 per site). See methods for complexity scale. An asterisk (*) denotes a significant difference between *Ra'ui* and control, refer to Table 11 for detailed statistical analysis results.

Table.11. Significant (p<0.05) results of one-way ANOVAs (F, *d.f.* = degrees of freedom for source and residual) or Wilcoxon test (W) for mean coral cover, mean algal cover and mean structural complexity per site (*Ra'ui* Vs. control). Besides each significant site "+" represents a positive trend and "-" represents a negative trend. See methods for complexity scale.

Site	Test Statistics	P	
Coral Cover			
Akapuao	W=138	NS	
Aroa	*df*= 1,30	NS	
	F=1.66		
Aroko+	W=67.5	0.02	*
Edgewater+	W=70	0.03	*
Tikioki	*df*=1,30	NS	
	F=0.30		
Algal Cover			
Akapuao	*df*= 1,30	NS	
	F=2.7		
Aroa-	*df*= 1,30	<0.0001	***
	F=13.96		
Aroko	W=111	NS	
Edgewater	*df*= 1,30	NS	
	F= 1.43		
Tikioki	*df*= 1,30	NS	
	F= 0.003		
Structural Complexity			
Akapuao	*d.f.* =1,30	NS	
Aroa	F=0.756		
	W=177.5	NS	
Aroko+	W=72.5	0.04	*
Edgewater	*d.f*= 1,30	NS	
	F= 2.115		
Tikioki-	W=196	0.009	**

NS not significant, * significant at p<0.05, ** significant at p<0.01 and *** significant at p<0.001

Multivariate Analysis

Targeted Acanthuridae and Mullidae families were frequently recorded at all sites (Fig.8). Stepwise GLMs revealed that a range of variables influenced their density and biomass (Table.12). Acanthurids were related to a wider variety of variables compared with Mullids, who were only related to variables at Aroa and Edgewater. This highlights the differences between sites. Structural complexity and protection were identified as most frequently influencing biomass and density. Depth, temperature and visibility were not related to fish density or biomass.

Protection was a significant predictor for Acanthurids and Mullids at Edgewater and Aroa respectively. Protection was most highly significantly influential at Edgewater (P=0.0002) for Acanthurids and has probably heavily contributed to significant results identified in univariate analysis. Structural complexity was identified as a significant positive predictor of density and biomass for both families at Akapuao, Aroa and Tikioki. This corresponds with their high mean structural complexity. Coral and algal cover were positive predictors of Acanthuridae biomass and/or density at Aroko and Aroa. Zone was negatively related to Acanthuridae biomass at Akapuao and Aroko, and Mullidae density at Aroko, with higher biomass and densities occurring in the outer-reef.
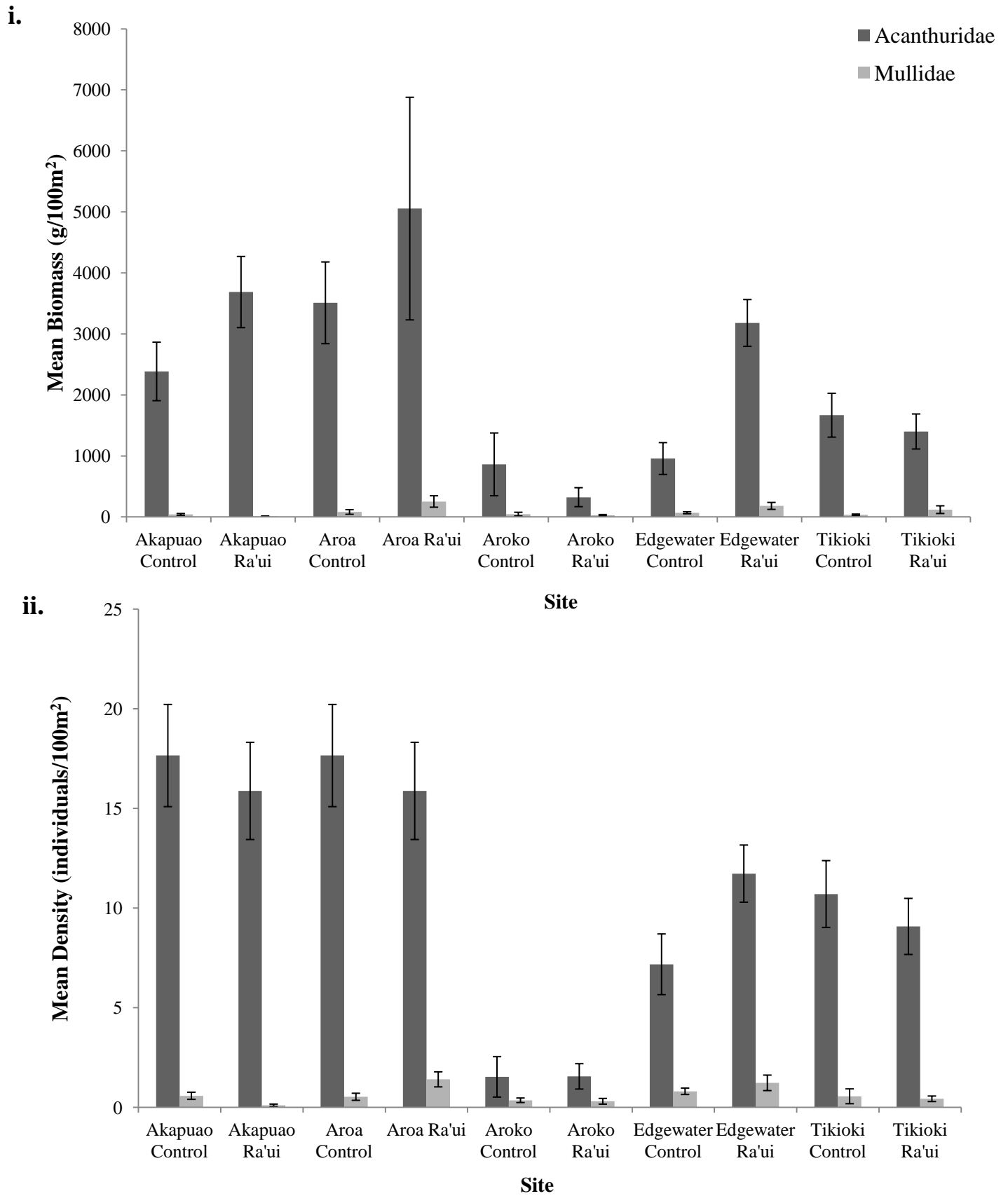
i.

ii.

Fig.8. The mean total biomass (i) (g/100m^2) and density (ii) (individuals/100m^2) of the two most frequently recorded targeted reef fish families; Acanthuridae and Mullidae in five study sites (*Ra'ui* and control) in Rarotonga, Cook Islands (± SE, N=32 per site).

Table.12. Significant predictor variables and test statistics obtained from multivariate stepwise GLMs of Acanthuridae and Mullidae biomass (g/100m^2) and density (individuals/100m^2) (response variables) and physical, biological and management predictor variables (temperature, depth, visibility, coral and algal percentage cover, structural complexity, zone (inner, outer) and protection status (control, reserve) at five sites in Rarotonga, Cook Islands at the 95% level (where p<0.05). The %D represents percentage deviance explained (100 x [1- residual deviance/ null deviance] and the Akaike Information Criterion (AIC) are per reduced model. Besides each variable "+" represents a positive trend and "-" represents a negative trend. A dash "—" indicates site where no significant predictor variables occurred. See methods (Table.4) for transformations and Appendix.1 for list of all the predictor variables remaining in reduced models following backward-forward stepwise selection.

Family and Response Variable	Site	Significant Variable(s)	P	Test Statistics	
				AIC	**% D**
Acanthuridae Biomass	Akapuao	Zone$^-$	0.003	11.72	69.37
		SC$^+$	0.006		
	Aroa	—	—	—	—
	Aroko	Zone$^-$	0.014	144.05	33.62
		Algae$^+$	0.05		
	Edgewater	Protection$^+$	0.0002	29.21	38.18
	Tikioki	SC$^+$	0.024	37.58	28.93
Acanthuridae Density	Akapuao	—	—	—	—
	Aroko	Algae$^+$	0.007	35.86	23.79
	Aroa	Coral$^+$	0.04	299.26	26.30
	Edgewater	Protection$^+$	0.003	11.10	39.95
	Tikioki	SC$^+$	0.0004	0.28	59.71
Mullidae Biomass	Akapuao	—	—	—	—
	Aroa	Protection$^+$	0.037	380.11	13.71
	Aroko	—	—	—	—
	Edgewater	—	—	—	—
	Tikioki	—	—	—	—
Mullidae Density	Akapuao	—	—	—	—
	Aroa	Protection$^+$	0.004	51.35	35.27
		SC$^+$	0.002		
	Aroko	—	—	—	—
	Edgewater	Zone$^-$	0.008	45.36	21.74
	Tikioki	—	—	—	—

Discussion

Total Biomass and Density

Total biomass and density were higher in the majority of *Ra'uis* compared with control sites. This finding correlates with other studies (e.g. Papua New Guinea LMMA; Cinner et al., 2005) and displays the build-up of fish communities within the *Ra'uis*. This trend occurs because fish migrate into protected areas to take advantage of their increased resources and improved habitat quality (Maliao et al., 2009). Increases in biomass and density translate into increased reproductive potential and success, predominantly as larger individuals are more fecund (Clements et al., 2012).

There was a lack of statistical significance, but the study methods used were highly robust. Therefore, high error variation within pairs may have masked statistical differences (Friedlander et al., 2003). It is also probable that variable compliance and enforcement between sites has contributed to the lack of statistical significance of density and biomass between *Ra'uis* and corresponding controls. The *Ra'ui* do experience minor illegal fishing, and this was witnessed on two occasions during surveying, but the *Ra'ui* are still considered safe refuges for fish (Miller, 2009).

Edgewater *Ra'ui* stood out as the LMMA having the greatest positive ecological effect on fish. This *Ra'ui* is unique in that it has been established and run by a Rarotongan hotel in collaboration with the local community. As a result, illegal fishing is non-existent due to permanent monitoring. A study of hotel-run Whale Island Reserve, Vietnam, demonstrated similar results (Svensson et al., 2009). Their study found average fish density and size were higher within the reserve compared with unprotected sites.

Increasingly hotels are recognising the potential of marine protection for financial security and tourism revenue (Bottema and Bush, 2012). Hotel management often succeeds due to lower start-up costs because of existing infrastructure and no time lag of information/fund transfer between governments and local levels (Teh et al., 2008). Maintaining tourist interest and revenue provide hotels with an added incentive for effective management and enforcement (Svensson et al., 2009). This study has demonstrated that the Edgewater *Ra'ui* is a prime example of the potential success of hotel management (Bottema and Bush, 2012). Aroa *Ra'ui* is also hotel-run, however unlike Edgewater, there was no significant difference between the *Ra'ui* and control for total biomass or density. The reason for this remains

unclear, although the huge variation between the *Ra'ui* and control is the most likely explanation.

One complication of this result at Edgewater is the presence of fish feeding which may have confounded the ecological effectiveness of protection. Fish feeding can alter natural behavioural patterns and population distributions (Millazzo et al., 2006). It also artificially aggregates species, particularly generalist feeders and predators (Ilarri et al., 2008). An increase in large-bodied predators can result in decreased prey population densities (Millazzo et al., 2005). This would explain the observed pattern at Edgewater *Ra'ui* where biomass was significantly higher but density was not. Conversely, several quantitative studies have argued that there is still no conclusive evidence that recreational fish feeding has a negative impact on fish communities and ecology (Hémery and McClanahan, 2005). Fish feeding is therefore a key research area to determine its ecological effects in Rarotonga.

Tikioki was the only site with higher total density and biomass in its control. Correlating with an earlier study where Miller (2009) identified Tikioki *Ra'ui* as the least effective at enhancing fish density. This *Ra'ui* is amongst the most popular sites in Rarotonga, with large numbers of tourists participating in watersport activities, particularly snorkelling. High levels of watersports can have a damaging effect on coral reefs and disturb their fish assemblages (Thurstan et al., 2012). The low maximum depth of Tikioki *Ra'ui* (2.6m) combined with its high-use makes it subject to substantial substrate damage (Claudet et al., 2010). This could reduce fish biomass and density by degrading habitats and resources, thus explaining the higher biomass and density in the control (Camp and Fraser, 2012). Degradation of coral and complexity is important as both variables proved to be significant predictors of Acanthuridae and Mullidae density and/or biomass in the study sites. Finally, despite high visitor numbers that should increase vigilance, compliance has been reported lowest at Tikioki *Ra'ui* (Egerton, 2005) and illegal gillnetting was observed at dusk once during surveying. Illegal fishing will slow the build-up of fish populations in this *Ra'ui.*

Family Density and Biomass

Families exhibited varying responses across the five sites. These differences in density and biomass were also inconsistent. This suggests that environmental conditions were influential and that protection efficacy varies (Egerton, 2005). Multivariate analysis largely confirmed this.

In Tikioki, where total biomass and density were higher in the control, Lethrinidae were the only family to display a significant increase in the *Ra'ui*. The reasons are unclear but Lethrinidae may have responded well to protection as they are commercially exploited with vulnerable life-histories (Bartlett et al., 2009). Thus, removal of fishing pressure may have enabled their populations to increase.

Balistidae were another family exhibiting interesting patterns. In Aroa, biomass and density were greater in the *Ra'ui* and in Akapuao, the opposite trend occurred. This pattern may be in response to prey distribution (e.g. dominant prey *Echinometra mathaei*) (Johansson et al., 2013). Data collected on Rarotonga's invertebrates alongside this study identified almost double the density of *E. mathaei* in Aroa *Ra'ui* compared with its control. In Akapuao *E. mathaei* density was over five-fold higher in the control than Aroa *Ra'ui*. It could be inferred that Balistidae species are following the prey density in the relevant sites. This is consistent with the Johansson et al. (2013) study in Ningaloo Reef, Australia. Further, Mullidae and Labridae were also significantly higher in Akapuao control. This might be explained by its more sheltered location as high exposure has been shown to negatively affect fish assemblages (Friedlander et al., 2003).

Targeted Fish

Ciguatera outbreaks have reduced fishing pressure in Rarotonga's lagoons (Pinca et al., 2009). However, because cases of ciguatera are declining it is likely that reef fishing pressure will increase in the near future (Rongo and Woesik, 2013). This highlights the importance of evaluating the effectiveness of the *Ra'ui* for targeted families and will provide an insight into their protection if fishing increases.

Density and biomass of targeted fish were higher in the majority of *Ra'ui*. Differences between *Ra'ui* and controls were significant in Edgewater for density and biomass and for density at Akapuao. These results suggest that releasing targeted species from fishing pressure has enabled them to increase in number and/or size (Russ and Alcala, 2004). The significantly higher biomass and density of targeted fish in Edgewater *Ra'ui* is likely due to greater enforcement/compliance. Akapuao's significant result is also indicative of higher compliance, probably due to its location adjacent to a hotel that helps police the area (Rocliffe, S. pers. comm. 2013). A lack of significant differences at the other sites could be explained by the caveat of ciguatera poisoning and its limited research. This makes assessing the response of targeted species difficult. Further, most other studies find biomass of

exploited families more significant than density because fisheries typically target large-bodied individuals (Friedlander et al., 2003). The greater number of significant differences in density observed in this study is probably due to larger-bodied species being more ciguatoxic, which prevents their exploitation (Rongo and Woesik, 2011). Instead, high abundances of smaller sized families are targeted and hence densities respond more noticeably.

Multivariate analysis on two highly targeted families revealed that protection, zone, structural complexity, percentage coral and algal cover were important predictors of their biomass and density. Acanthurids and Mullids were only significantly related to protection at the two hotel-managed sites, which again is indicative of greater effectiveness and enforcement/compliance. Acanthurids exhibited a positive relationship with protection at Edgewater. This infers that protection at Edgewater *Ra'ui* is adequate due to aforementioned reasons. Acanthurids have also been highlighted amongst families with the greatest positive response to protection elsewhere, for example at Apo Island, Philippines (Abesamis and Russ, 2005). In Apo Island, associated spillover was also high and due to significantly greater Acanthurid biomass and density in Edgewater *Ra'ui,* it is possible that spillover is also occurring. This would have positive benefits as compliance increases when local fishers derive direct benefits from a protected area (Jameson et al., 2002). Eight species of Acanthurids are targeted in Rarotonga, enhancing the probability of compliance and thus effectiveness of Edgewater *Ra'ui* (FAO, 2010).

Mullids are also a highly targeted family and their biomass and density were positively related to protection at Aroa. This finding corresponds with an earlier study that identified significantly higher Mullidae biomass and density in Aroa *Ra'ui* relative to open-access areas (Miller, 2009). This significant relationship is probably due to Aroa *Ra'ui's* large size (32.5ha) which enhances both its ability to provide refuge to the large schools formed by Mullids and the probability of encompassing their daily home-ranges (Uiblein, 2007; Pavlov et al., 2013). Meyer et al. (2007) also observed a positive response of Mullids to protection in Hawaii's Waikiki MPA because they actively avoided areas with high spearfishing. Spearfishing is one of the major fishing methods in Rarotonga so a similar response may be occurring (Kronen et al., 2010). This is increasingly likely as spearfishing was commonly observed adjacent to Aroa *Ra'ui* (pers.obs). Finally, due to the *Ra'ui's* hotel-front location and vigilant staff there are no reports of illegal fishing.

Protection was only occasionally the significant predictor of biomass and density, instead biological and physical variables appear more influential. Structural complexity was identified as an important significant positive predictor of both Acanthuridae (Akapuao, Tikioki) and Mullidae (Aroa) assemblages. This correlates with the highest average complexity of the five sites recorded at Tikioki, Akapuao and Aroa. Complexity has previously been recognised as a key determinant in structuring fish assemblage (e.g. Johansson et al., 2012). A highly complex habitat provides refuges and microhabitats for foraging and nesting (Graham and Nash, 2013). Shelter and refuge reduce predation risk and lower competition through enhanced niche availability (Vergés et al., 2011). This ultimately increases an individual's survival rate and an area's carrying capacity (Harborne et al., 2012).

Generally, as complexity increases algal cover declines and coral cover increases (Lemoine and Valentine, 2012). This pattern was largely observed in Rarotonga. Coral provides food and microhabitats for fish and reductions in coral cover impact fish community structure (Harborne et al., 2012). In Rarotonga, the majority of lagoon fishing is undertaken on foot either by walking nets through the lagoons, or by spearfishing (Kronen et al., 2010). These fishing methods have been shown to damage corals and degrade reef complexity in Rarotonga through physical breaking or smothering by sediment re-suspension (Drumm, 2004; Hardman et al., 2013). Interestingly at Aroa, Acanthuridae density was significantly influenced by coral cover and not by complexity. Possibly explained by the *Ra'ui*'s low average complexity but very high coral cover. This suggests that Acanthurids favour any form of highly heterogeneous habitat (Marshell et al., 2011). Similar preferences were identified for Mullids at Aroa and Edgewater.

Acanthurid and Mullid biomass and density were higher in the outer zones of the lagoons at Akapuao, Aroko and Edgewater. This is also probably related to the higher rugosity of the outer reef, particularly at Aroko where the inner zone was comprised predominantly of sand (pers.obs). Higher complexity and coral cover have often been shown to increase with protection (Graham and Nash, 2013). It is difficult in this study to conclude this due to a lack of quantitative fishing and enforcement information. Although, it is likely that if *Ra'ui* enforcement was greatly improved, both complexity and coral cover would increase and subsequently result in increased fish biomass and density (Messmer et al., 2011).

Recommendations and Conclusion

Rarotonga's *Ra'ui* have received little attention and as a result there is limited baseline information available to make accurate conclusions. It would be beneficial to repeat this study again in the future to enable temporal comparisons of *Ra'ui* effectiveness. This information would be invaluable to mangers/community leaders and could assist in future *Ra'ui* establishment and decisions (i.e. lifting bans). Research on the influences of fish feeding and ciguatera are necessary to investigate their impacts on these results.

Although non-compliance seems minimal, one caveat of this study is the lack of specific, quantitative information regarding compliance within each *Ra'ui* and the degree of fishing in adjacent areas. This indicates a key area for research in Rarotonga and results could be used in future assessments of *Ra'ui* effectiveness. There are several potential methods to improve compliance and awareness of the *Ra'ui*, which will increase their ecological effectiveness. Education and awareness of their boundaries, aims and locations through marker buoys, information signs and/or outreach events are low-cost and effective methods. Such improvements have been successful in other small MPAs worldwide (e.g. Philippines; Walmsley and White, 2003).

This study found fish biomass and density were greater in the majority of *Ra'ui* compared with corresponding control sites. These differences were most commonly related to environmental characteristics, such as reef complexity. This finding is important as this information could be used to ensure future LMMAs are located in suitable areas to enhance fish biomass and density. The two hotel-run *Ra'ui*, Edgewater and Aroa, were identified as the most ecologically effective LMMAs in Rarotonga. Edgewater *Ra'ui* was particularly effective, exhibiting significant increases in total, family and targeted species biomass and density. Two of the most heavily targeted families also exhibited positive relationships with protection at these sites. This is encouraging because it indicates that moving towards local hotel and community collaborative MPA management could be a good alternative to MPAs ineffectively run by the government. These two *Ra'ui* could act as templates for the less effective *Ra'ui* to ensure long-term sustainability and conservation of Rarotonga's economically and biologically important reef fish.

Word Count: 5000

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Appendices

Appendix 1: Full models and reduced minimum adequate models used in multivariate analysis.

Appendix 1. Full and reduced minimum adequate models from stepwise GLM analysis using Gaussian error function of Acanthuridae and Mullidae families' biomass (g/100m^2) and density (individuals/100m^2). SC = structural complexity. See results section for significant predictor variables and methods section for transformations. 'None' indicates a GLM analysis whereby no minimum adequate model was found.

Family	Site	Full Model	Reduced Minimum Adequate Model
Acanthuridae Biomass	Akapaou	Biomass, protection, zone, coral, algae, SC	Biomass, zone, SC
	Aroa	Biomass, protection, temperature, depth, visibility, coral, algae, SC	Biomass, visibility, SC
	Aroko	Biomass, protection, zone, temperature, visibility, coral, algae, SC	Biomass, zone, temperature, visibility, algae
	Edgewater	Biomass, protection, zone, temperature, depth, visibility, algae, coral, SC	Biomass, protection
	Tikioki	Biomass, protection, zone, coral, algae, SC	Biomass, zone, SC
Acanthuridae Density	Akapaou	Density, protection, zone, depth, coral, algae	Density, protection, zone, coral, SC
	Aroa	Density, temperature, visibility, coral, SC	Density, coral, SC
	Aroko	Density, protection, zone, temperature, coral, algae, SC	Density, zone, algae
	Edgewater	Density, protection, zone, depth, visibility, coral, algae, SC	Density, protection, SC
	Tikioki	Density, protection, coral, algae, visibility, SC	Density, protection, coral, algae, SC
Mullidae Biomass	Akapaou	Biomass, depth, protection, zone, visibility, coral, algae, SC	Biomass, depth, coral
	Aroa	Biomass, protection, zone, depth, visibility, coral, algae, SC	Biomass, protection
	Aroko	Density, protection, zone, visibility, SC, coral, algae, temperature	None
	Edgewater	Biomass, protection, zone, depth, coral, algae, SC	Biomass, zone, coral, algae
	Tikioki	Biomass, protection, zone, coral, algae, SC	Biomass, algae
Mullidae Density	Akapaou	Density, protection, zone, visibility, coral, algae, SC	None
	Aroa	Density, protection, zone, depth, visibility, coral, algae, SC	Density, protection, zone, SC
	Aroko	Density, protection, zone, depth, SC, coral, algae	None
	Edgewater	Density, protection, zone, depth, coral, SC	Density, zone, depth
	Tikioki	Density, protection, zone, depth, coral, algae, SC	None