

Effects of a single intensive harvest event on fish populations inside a customary marine closure

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Abstract In September 2008, the villagers of Kia Island, Fiji, opened their customary managed closure (Cakaulevu tabu) to fishing for a fundraiser that lasted for 5 weeks. We report on opportunistic before-after-control-impact surveys describing changes to coral reef communities both 4 weeks into the harvest and 1 year later compared with pre-harvest conditions. Prior to the harvest, there was a gradient in mean fish abundance and biomass per transect, with highest levels in the north of the closure (250 fish transect⁻¹, 8,145.8 kg ha⁻¹), intermediate levels in the south of the closure (159 fish transect⁻¹, 4,672.1 kg ha⁻¹) and lowest levels in the control area open to fishing (109 fish transect⁻¹, 594.0 kg ha⁻¹). During the harvest, there were extensive depletions in large-bodied, primary targeted fish species, with significant loss in biomass of Acanthuridae and Carangidae in the north and Lutjanidae and Serranidae in the south. We also observed significant increases in Acanthuridae, Lethrinidae and Scaridae in the control, suggesting a “bail-out” effect whereby fish left the closure in response to a rapid increase in fishing pressure. These

changes were coupled with a large increase in turf algal cover at all survey areas, despite a large numerical increase in small, roving acanthurids (e.g., *Ctenochaetus striatus*) and scarids (e.g., *Chlorurus sordidus*). By 1 year later, fish biomass was significantly lower within the closure than before the harvest, while values in the control returned to pre-harvest levels, suggesting non-compliance with the reinstated fishing ban. We use the lessons learned from this event to suggest recommendations for promoting effective management of periodically harvested customary closures that are a common feature across much of Oceania.

Keywords Marine protected areas · Customary management · Tabu areas · Coral reef fisheries · Periodic harvest · Fiji

Introduction

Attempts to reduce threats to the marine environment in Oceania, particularly from overfishing, have increasingly focused on ecosystem-based approaches to conservation, including the designation of marine protected areas (MPAs) (Jupiter and Egli 2011; Aswani et al. 2012). There is strong evidence that permanent, no-take areas provide fisheries benefits in terms of increased numerical abundance and biomass (Mumby and Steneck 2008; Lester et al. 2009) and growing evidence to support density-dependent adult spill-over and larval exchange supported by increased egg production from larger fish (Abesamis and Russ 2005; McCook et al. 2010). However, in many Pacific islands, there are strong cultural and legislative barriers to placing permanent restrictions on access to traditional fishing grounds (Foale and Manele 2004; Ruddle and Hickey 2008; Clarke and Jupiter 2010). Conservation organizations and practitioners

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working in this region, such as partners within the Locally Managed Marine Area (LMMA) network, typically advocate an integration of traditional management practices and scientific knowledge. The LMMA network is composed of government and non-government organizations working together with communities to share knowledge and best practice for coastal and marine resource management to achieve local objectives (Govan et al. 2009). Such approaches have resulted in management systems that comprise a multitude of different strategies including no-take closures, temporary closures, size limits, seasonal or species bans and gear restrictions (Ban et al. 2011). Of these, periodically harvested marine closures are the most common form of spatial management (Govan et al. 2009).

The relative effectiveness of permanent no-take MPAs versus other management strategies has been the subject of much debate in the literature. There is some evidence that periodically harvested closures can promote short-term recovery of fish abundance and biomass (Cinner et al. 2005; Bartlett et al. 2009a), and compliance may be stronger under these customary management systems compared with western-style permanent no-take areas (Cinner et al. 2006). Yet, positive perceptions by locals of their effectiveness are not always validated by ecological surveys, particularly for fish biomass (Bartlett et al. 2009b). Furthermore, long-term ecological studies and meta-analyses suggest that MPAs must be no-take and permanently closed to achieve sustained fisheries benefits (Russ and Alcala 2004; Di Franco et al. 2009; Lester et al. 2009; Maliao et al. 2009). This is often due to focused fishing efforts within MPA boundaries when they are opened. Permitted periodic harvests within traditional MPAs have been observed to remove marine resources with “alarming efficiency” (Foale and Manele 2004), and fisheries benefits from protection (e.g., increased fish size, abundance and spillover potential) have been rapidly removed where no-take status has been revoked (Alcala et al. 2005; Williams et al. 2006).

It is clear that while MPAs other than permanent no-take closures can contribute towards achieving objectives for sustainable resource use and conservation, different management strategies are not equally effective (Mills et al. 2011). The effectiveness of a management strategy will vary across species and habitats and in response to the objective being measured. Given that periodically harvested closures are the only feasible management option throughout much of the Pacific, science-based guidelines for the frequency and intensity with which such MPAs can be sustainably harvested are urgently required. Attempts to develop such guidelines have been constrained by a lack of empirical evidence for the impact of periodic harvests on fish populations. Here, we report on an opportunistic pre-, during and post-harvest (1 year later) survey of a

customary closure (*tabu* area) in Fiji. We investigate the direct and indirect effects of the harvest event on coral reef fish biomass and abundance, potential fish behavioural responses and reef benthos. Based on these analyses, we provide recommendations to improve the sustainability of local coastal resource management strategies.

Methods

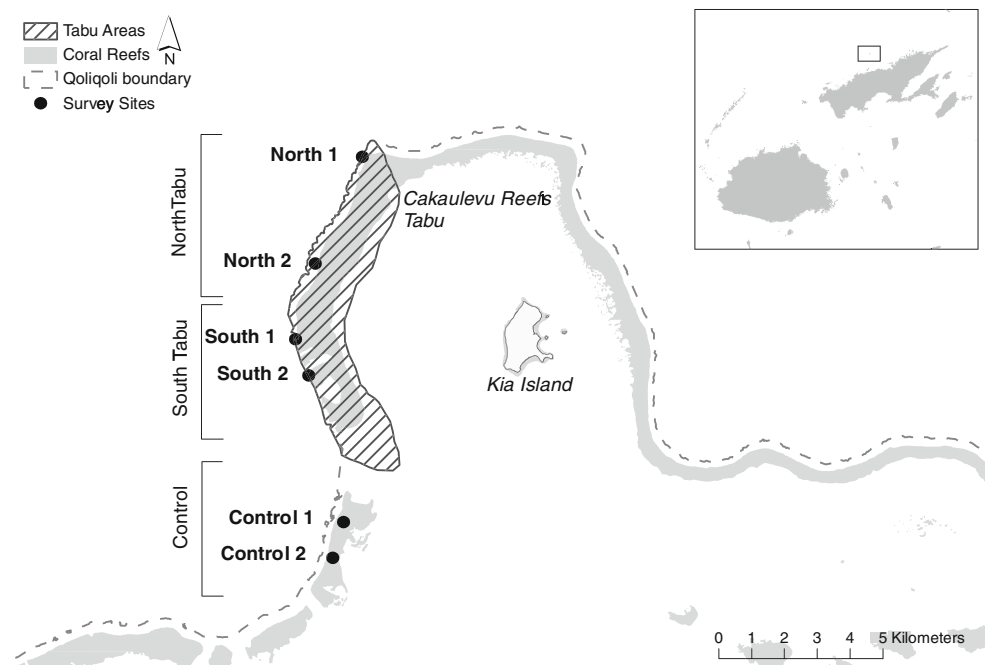
Study site

The Cakaulevu *tabu* area (15.5 km²) is located on the exposed outer barrier reef west of Kia Island, Macuata Province, on the island of Vanua Levu in Fiji (Fig. 1). In 2005, the high chief of Macuata, together with the Cokovata Qolioli Management Committee, endorsed the establishment of a network of nine community-managed *tabu* areas, including the Cakaulevu *tabu*. The MPA network was established with the assistance of conservation partners, led by the WWF South Pacific Programme, with the objectives to protect reef fish stocks for the future and to conserve marine biodiversity. Prior to 2005, the Cakaulevu *tabu* was informally protected and may have been opened periodically for subsistence use, but to our knowledge was never previously harvested for commercial extraction.

The residents of the three villages on Kia Island have traditional fishing rights within their customary fishing ground (*qoliqoli*) and are heavily dependent upon marine resources for their livelihoods, as the small, steep-sloped island contains little arable land. In September 2008, the communities collectively decided to harvest the Cakaulevu *tabu* to raise funds to support school, church and provincial fees for island residents. Initially, the goal was to raise FJD\$12,000 (USD\$7,492 based on exchange rates from 22 September 2008, the first day of the harvest) from the sale of invertebrates (predominantly *bêche-de-mer*) and fish. This goal was exceeded on the first day, and upon realizing the potential for profit, community members extended the harvest period for 5 weeks. Residents and traditional fishing rights owners living outside of Kia Island who returned for the event fished in shifts over 24 h periods from Mondays through Saturdays. Based on daily amounts paid out by middlemen from three seafood export companies (reported to A. Cakacaka), we estimated a total revenue to community members of over FJD\$200,000 (USD\$124,871). The majority of the catch was caught with spearguns, Hawaiian slings, and hook and line (S. Jupiter and A. Cakacaka, pers. obs.).

Researchers from the Wildlife Conservation Society (WCS) surveyed reefs inside and outside the Cakaulevu *tabu* in September 2008 as part of a larger project to assess

Fig. 1 Map of Kia Island and the Cakaulevu tabu area showing the locations of survey sites inside and outside the MPA. The *inset* shows the location of the study region in Macuata Province on the island of Vanua Levu, Fiji



the effectiveness of networks of community MPAs to increase food fish biomass (Jupiter and Egli 2011). Three days after the start of the survey, the communities informed WCS of their decision to open the tabu area. The WCS team then returned to survey the same sites 4 weeks into the harvest (October 2008) to determine the effects of the harvest event on fish populations, and 1 year later (October 2009) to look for evidence of recovery.

Fish and benthic surveys

Underwater visual census surveys of fish and benthic substrate were conducted on forereef sites inside ($n = 4$) and outside ($n = 2$) of the Cakaulevu tabu area (Fig. 1) using the methods described in Jupiter and Egli (2011). Due to notable differences in reef geomorphology (S. Jupiter, pers. obs.) that initially supported distinct fish communities, the survey sites within the tabu area were divided into two regions for analysis. The northern tabu sites are characterized by high current and steep reef slopes/vertical walls, and the southern tabu sites are characterized by less current and a gradual slope with variable topography and channels to 20 m. The control sites, located on a reef to the south of the Cakaulevu tabu, share similar reef geomorphology to the southern tabu sites. The location and replication of survey sites were constrained by the opportunistic nature of the study and are admittedly not ideal for this purpose. Nevertheless, these data permit a before-after-control-impact (BACI) analysis of the effects of opening a customary marine closure.

At each site, trained fish observers from WCS estimated fish size (2–5 cm, then 5 cm classes to 40 cm, and size to the nearest cm above 40 cm) and abundance at ten replicate 5 m × 50 m belt transects at shallow (5–8 m; $n = 5$) and deep (12–15 m; $n = 5$) depths. They recorded fish from the following families: Acanthuridae, Balistidae, Carangidae, Carcharhinidae, Chaetodontidae, Chanidae, Ephippidae, Haemulidae, Kyphosidae, Labridae, Lethrinidae, Lutjanidae, Mullidae, Pomacanthidae, Scaridae, Scombridae, Serranidae (subfamily Epinephelinae only), Siganidae, Sphyrnaeidae and Zanclidae. We calculated biomass from size class estimates of length (L) and existing published values from FishBase (Froese and Pauly 2009) used in the standard length–weight (L – W) expression $W = aL^b$, where a and b parameter values were preferentially selected from sites closest to Fiji (Jupiter and Egli 2011). As many of the L – W conversions required fork length (FL), a length–length (L – L) conversion factor was obtained from FishBase where necessary to convert from total length (TL) recorded during the surveys to FL before biomass estimation. Because the biomass conversion formula resulted in some grossly overestimated weights for fishes that substantially change morphology as they age, maximum published weights were used for certain species when these fish were sighted above threshold sizes, as per Jupiter and Egli (2011). We additionally assessed which species were most likely to be primary targets based on: market value information from the Fiji Department of Fisheries divisional office in Labasa; maximum length from FishBase; and position typically found in the water column (fish high in the water column are more easily targeted by spearfishers).

To determine associations between fish communities and benthos both before and following the harvest, separate observers recorded benthic life-form categories along the same 50 m transects surveyed for fish assemblages at 0.5 m intervals using the point-intercept method. We combined life-form categories into 6 functional strata: fleshy algae/cyanobacteria, including cyanobacteria, algal assemblages and fleshy macroalgae >2 cm height; live hard coral, including *Millepora* and *Tubipora*; other soft substrate, including soft corals, sponges, ascidians, anemones and zooanthids; reef matrix, including dead coral, reef pavement and coralline algae; turf algae, defined as algae ≤ 2 cm height on reef matrix or dead coral; and unconsolidated substrate, comprised of rubble, sand or silt.

Statistical analyses

To assess how the harvest affected reef fish populations within and outside of the Cakaulevu tabu, we conducted permutational multivariate analysis of variance (PERMANOVA) analyses with 4,999 permutations using log₁₀ Modified Gower resemblance matrices (Anderson 2001; McArdle and Anderson 2001) of fish abundance and biomass summed at the transect level for total fish and for the following major food fish families: Acanthuridae; Carangidae; Lethrinidae; Lutjanidae; Scaridae; and Serranidae. We first tested the main effects models with three levels of fixed factors: sampling period, area and site nested within area. Samples were pooled across depths for each site. Where a significant interaction term was found between sampling period and area, we conducted separate post hoc pair-wise comparisons within sampling period between each area and within area between each sampling period (Anderson et al. 2008). Total and scarid biomass PERMANOVA analyses were conducted with and without *Bolbometopon muricatum* records, as the presence of these large fish that tend to occur in groups may mask other impacts from fishing. To assess potential differences in benthic structure that may influence fish community assemblages, we performed the same PERMANOVA model design on a Euclidean distance similarity matrix of percent benthic strata cover for each transect and then conducted post hoc pair-wise comparisons within sampling period between each area and within area between each sampling period. We performed these analyses using PRIMER version 6 software with PERMANOVA extension.

We assessed differences in reef fish community composition through time using canonical analysis of principal coordinates (CAP) performed on a Bray–Curtis dissimilarity matrix of species presence–absence data using R software. CAP is a constrained ordination procedure that initially calculates unconstrained principal coordinate (PCO) axes, followed by canonical discriminant analysis on the principal coordinates to maximize separation

between groups (Anderson and Willis 2003). We selected the number of principal coordinate axes (m) that provided the best distinction between groups, following the method described in Anderson and Willis (2003). The CAP procedure provides misclassification errors using a “leave-one-out” method, whereby each observation is removed from the analysis and then placed in the canonical space determined by the rest of the observations (Anderson and Willis 2003). The percentage of correct classifications provides a measure of the goodness of fit. Species’ correlations with the first two CAP axes were plotted to identify those that had greatest influence on site groupings.

Results

Total fish abundance and biomass

Under pre-harvest conditions, we observed a strong gradient of mean fish abundance with the highest values in the north (250 fish transect⁻¹), followed by the south (159 fish transect⁻¹) and control (109 fish transect⁻¹) (Fig. 2). There was significant variability in abundance by sampling period, area, and the interactions between sampling period and area, as well as sampling period and site (Table 1a). Each area was significantly different from the others (Table 2a). Mean fish biomass followed the same general pattern (north: 8,145.8 kg ha⁻¹; south: 4,672.1 kg ha⁻¹; control: 594.0 kg ha⁻¹), with significant variation across all factors (Table 1b). When *Bolbometopon muricatum* biomass was excluded, each area was significantly different from the others, but only the north and south were significantly different from the control with *B. muricatum* (Table 2b, c). Four weeks into the harvest, mean fish abundance significantly increased in the north and control (Fig. 2a). In contrast, mean fish biomass declined in the north and south but significantly increased in the control area (Fig. 2b). Fish abundance was significantly higher in the north (354 fish transect⁻¹) than south (188 fish transect⁻¹), but not higher than the control (256 fish transect⁻¹) (Table 2a). Fish biomass was significantly greater in the north (4,763.6 kg ha⁻¹) than the south (2,246.2 kg ha⁻¹) and control (4,582.6 kg ha⁻¹), which were not significantly different from each other (Table 2b). By 1 year later, fish biomass was significantly lower than pre-harvest levels in the north and south of the tabu, while the control was not significantly different from pre-harvest conditions (Fig. 2b). Although fish abundance was significantly higher in the north (211 fish transect⁻¹) than the control (153 fish transect⁻¹), fish biomass was significantly lower in the north (987.4 kg ha⁻¹) than in the control (1,544.8 kg ha⁻¹). Exclusion of *B. muricatum* biomass records from the pair-wise comparisons of within-sampling period analyses only changed the outcome of the pre-harvest

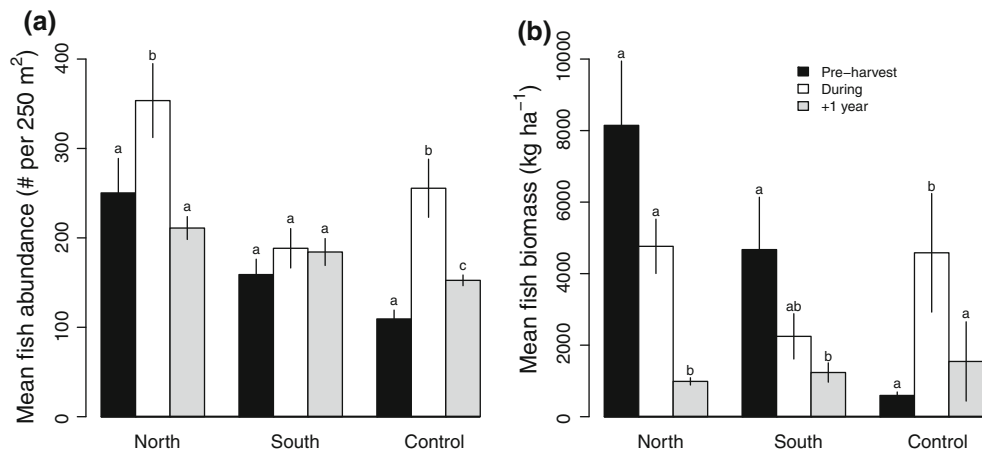


Fig. 2 Total mean abundance (# per 250 m²) (a) and biomass (kg ha⁻¹) (b) per transect of reef fish at sites inside (north and south) and outside (control) the Cakaulevu tabu area before (black bars), during (white bars) and 1 year after (grey bars) a 5-week intensive harvest event. Adjacent different letters indicate that a significant

difference exists between sampling periods (e.g., “a b a” indicates that pre-harvest is significantly different from during harvest but not from 1 year later, and “a ab b” indicates that pre-harvest is not significantly different from during harvest but is significantly different from 1 year later). Error bars indicate one standard error

Table 1 PERMANOVA main effects results of differences in mean fish (a) abundance per transect (# per 250 m²), (b) biomass (kg ha⁻¹) and (c) biomass (kg ha⁻¹) with *Bolbometopon muricatum* records excluded

Sources	df	SS	MS	Pseudo-F	P(perm)	Permutations
<i>(a) Total fish abundance</i>						
Sampling	2	1.176	0.588	16.359	0.0002	4,988
Area	2	1.344	0.672	18.694	0.0002	4,988
Site (area)	3	0.173	0.058	1.601	0.1910	4,989
Sampling × area	4	0.506	0.126	3.520	0.0074	4,987
Sampling × site (area)	6	0.783	0.130	3.631	0.0022	4,986
Residual	162	5.821	0.036			
Total	179	9.802				
<i>(b) Total fish biomass</i>						
Sampling	2	6.820	3.410	25.290	0.0002	4,985
Area	2	7.107	3.554	26.354	0.0002	4,986
Site (area)	3	7.509	2.503	18.562	0.0002	4,982
Sampling × area	4	4.580	1.145	8.492	0.0002	4,987
Sampling × site (area)	6	5.765	0.961	7.126	0.0002	4,986
Residual	162	21.844	0.135			
Total	179	53.625				
<i>(c) Total fish biomass (no B. muricatum)</i>						
Sampling	2	5.719	2.859	28.373	0.0002	4,988
Area	2	9.851	4.926	48.876	0.0002	4,989
Site (area)	3	7.626	2.542	25.225	0.0002	4,988
Sampling × area	4	2.805	0.701	6.957	0.0002	4,988
Sampling × site (area)	6	4.699	0.783	7.771	0.0002	4,984
Residual	162	16.326	0.101			
Total	179	47.025				

Significant P(perm) values are indicated in bold

north–south comparison described above (Table 2c). Exclusion of *B. muricatum* biomass records from between-sampling period analyses only changed the outcome

of the comparison between pre-harvest and during harvest conditions in the south, which became significantly different.

Table 2 PERMANOVA pair-wise comparisons within sampling period between each area for mean fish (a) abundance per transect (# per 250 m²), (b) biomass (kg ha⁻¹) and (c) biomass (kg ha⁻¹) with *Bolbometopon muricatum* records excluded

	(a) Abundance			(b) Biomass			(c) Biomass (no <i>B. muricatum</i>)		
	Level	<i>t</i>	<i>P</i> (perm)	Level	<i>t</i>	<i>P</i> (perm)	Level	<i>t</i>	<i>P</i> (perm)
<i>Pre-harvest</i>									
North–south	*	2.3099	0.0262	NS	1.7506	0.0912	*	2.3365	0.0296
North–control	***	4.8354	0.0002	***	8.4888	0.0002	***	8.4319	0.0002
South–control	*	2.3664	0.0234	***	5.2251	0.0002	***	4.5654	0.0002
<i>Post-harvest</i>									
North–south	**	4.1252	0.0010	***	4.5592	0.0006	***	4.5592	0.0004
North–control	NS	1.9563	0.0566	*	2.2941	0.0252	***	5.2354	0.0002
South–control	NS	1.8283	0.0734	NS	1.0254	0.3118	NS	0.4823	0.6374
<i>1-year later</i>									
North–south	NS	1.5589	0.1348	NS	0.0731	0.9406	NS	0.0731	0.9382
North–control	***	4.1997	0.0002	*	2.4548	0.0126	***	5.3798	0.0002
South–control	NS	1.2805	0.2046	*	2.2189	0.0254	***	4.2777	0.0002

Significance levels denoted as: NS not significant, * *P*(perm) < 0.05, ** *P*(perm) < 0.01, *** *P*(perm) < 0.0010

Fish community composition

The CAP analysis showed significant shifts in species composition between sampling periods as primary target fish disappeared from the assemblages during the harvest and further by 1 year later (Fig. 3). The first eight PCO axes explained 83.1% of the variability in the dissimilarity matrix, and 94.4% of observations were classified correctly using the leave-one-out procedure (*p* = 0.005). Species' correlations with the first two CAP axes are shown in Fig. 3. Species negatively correlated with axis 1 are associated with sites pre-harvest and during the harvest.

There was significant variability in both fish abundance and biomass at the family level that varied slightly by taxonomic group (Electronic Supplemental Material, ESM Table S1). While the interaction between sampling period and area was always significant for fish biomass across all fish families analysed, it was not significant for fish abundance of acanthurids, serranids or scarids when *B. muricatum* numbers were excluded (ESM Table S1a, k, m). Pre-harvest biomass in the north was dominated by acanthurids and carangids, which was significantly higher than in the control (ESM Table S2a, b; Fig. 4). Pre-harvest biomass in the south was dominated by lutjanids and scarids, which was significantly higher than in the control (ESM Table S2d, e; Fig. 4).

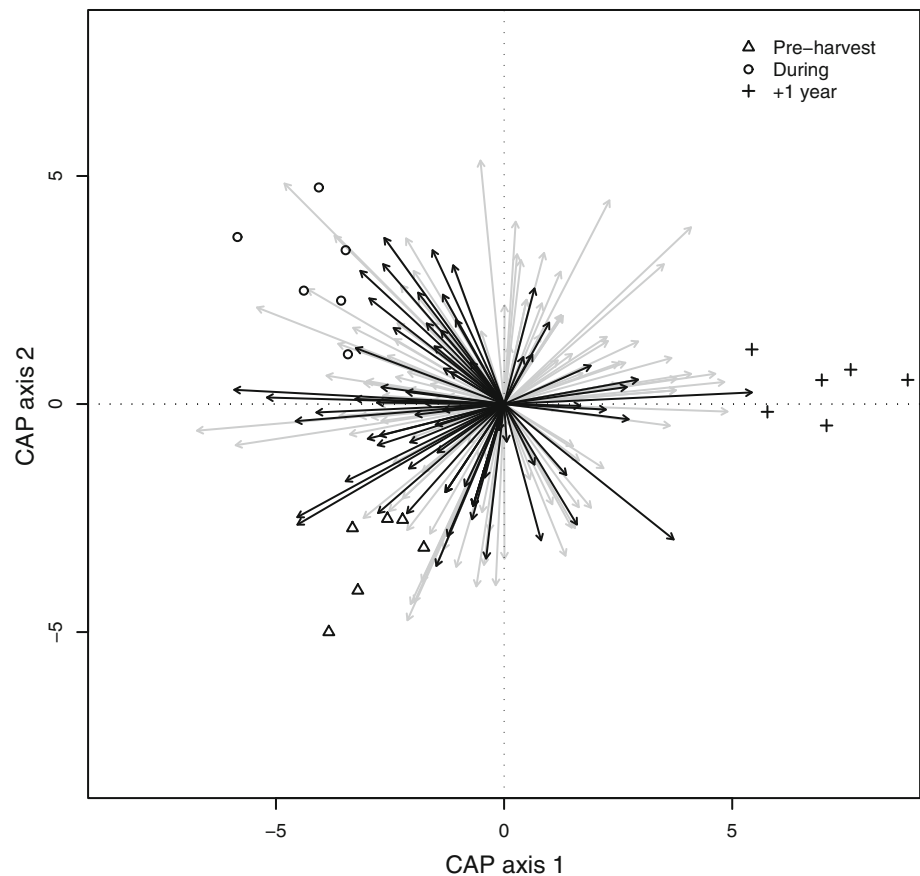
With respect to changes in fish biomass at the family level, by 4 weeks into the harvest, there were significant decreases inside the Cakaulevu tabu of acanthurids (north), carangids (north), lutjanids (south) and serranids (south), coupled with significant increases in acanthurids, lethrins and scarids in the control (Fig. 4). These decreases in biomass inside the tabu occurred despite numerical increase in

acanthurids and scarids that increased in abundance everywhere (though only significantly for scarids in the south and control; Fig. 5). Excluding *B. muricatum* biomass from the scarid within-sampling and between-sampling analyses did not substantially affect the outcomes (ESM Table S2f). Within acanthurids and carangids, the large-bodied species of *Naso unicornis*, *N. tonganus*, *N. caesi*, *Acanthurus fowleri*, *A. auranticavus*, *Caranx melampygus* and *C. papuensis* were severely depleted during the harvest, with large increases in the highly mobile *N. caesi* and *A. auranticavus* in the control (Table 3). Within lutjanids and scarids, there was a significant decrease in biomass during the harvest due to losses of *Macolor macularis*, *Lutjanus bohar*, *L. gibbus*, *L. fulviflamma*, *B. muricatum* and *Cetoscarus bicolor*, of which *L. gibbus*, *B. muricatum* and *C. bicolor* increased in the control (Table 3). Biomass of *Chlorurus bleekeri*, *C. sordidus*, *Ctenochaetus striatus*, *Melichthys vidua* and *Scarus schlegeli* increased across all survey areas during the harvest (Table 3). By 1 year later, the biomass of carangids and serranids was nearly negligible everywhere, and biomass of acanthurids (north only), carangids (north and south), lutjanids (south only) and serranids (south only) was significantly lower than pre-harvest values, even though numbers of acanthurids (north and south), lutjanids (south) and serranids (south) remained nearly equivalent to pre-harvest levels (Figs. 4, 5).

Benthic composition

There were significant differences in benthic composition, and these differences varied by sampling period, area, site and the interactions between sampling period and area and

Fig. 3 CAP ordination plot of reef fish presence–absence data from survey sites inside and outside the Cakaulevu tabu area at three different times of sampling. *Arrows* indicate species' correlations with the first two CAP axes, with primary target species shown in *black*



sampling periods and site (Table 4). Prior to the harvest, the cover of benthic strata in the north was not significantly different from the south or the control, though the south was significantly different from the control which had less live coral and higher cover of reef matrix, turf algae and other soft substrate (Table 4). During the harvest, benthic cover in the north changed significantly, with mean cover of turf algae increasing from 13.2 to 24.2% and reef matrix declining from 21.9 to 11.8%. Benthic strata cover changed significantly in the south during the harvest and was significantly different from the north and control due to relatively larger increases in turf algae (14.7% to 44.0%) and reductions in live coral (49.7% to 33.3%). Benthic cover also changed significantly in the control, with substantial increase in turf algae (17.6% to 37.4%) and consequent reduction in reef matrix (26.6 to 11.5%). By 1 year later, benthic strata cover in the north, south and control was not significantly different from pre-harvest conditions as turf algal cover returned to pre-harvest levels everywhere. Overall benthic community composition was not significantly different between the north and the south or between the south and the control, although the north was again significantly different from the control (Table 4).

Discussion

Our study demonstrates that a single intensive harvest event can quickly remove almost all positive effects of protection on fish biomass and subsequent reproductive output in a marine protected area. Our results echo other findings, suggesting that substantial benefits to fisheries from closures can be removed in a very short time period through focused fishing efforts (Russ and Alcala 2003; Williams et al. 2006).

The main impact of the Cakaulevu tabu harvest was seen in loss of large-bodied fish, whose depletion differed between the north and south and reflected initial differences in community composition and catchability. The high currents and steep walls of the north part of the tabu supported initial high densities of planktivorous and predatory fish, which would have built up during the preceding years of informal and formal protection. The largest losses from the north unsurprisingly were from acanthurids, especially *Naso unicornis*, *N. tonganus*, *N. caesioides*, *Acanthurus fowleri* and *A. auranticavus*, and from carangids, particularly *Caranx melampygus*, *C. papuensis* and *Carangoides oblongus* (Table 3). Of these, all except *A. auranticavus* inhabit mid-to high position in the water column near the reef, making

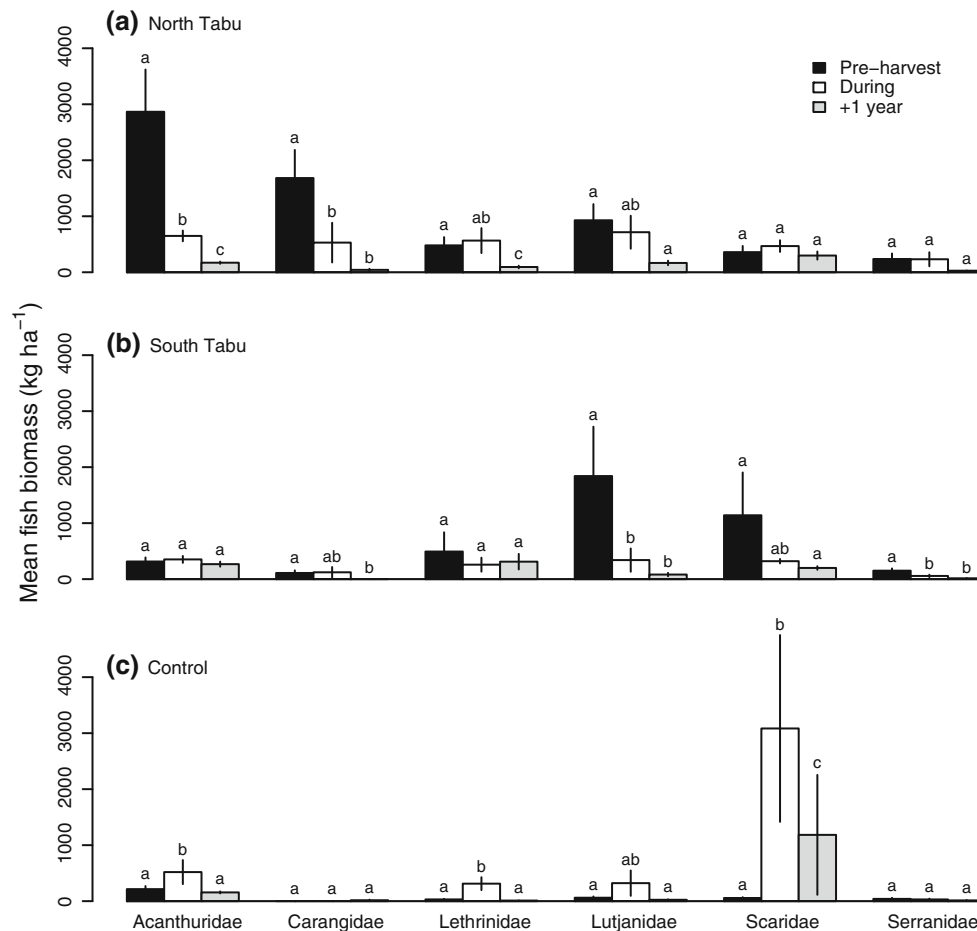


Fig. 4 Mean biomass (kg ha^{-1}) of targeted food fish families at sites inside (a and b) and outside (c) the Cakaulevu tabu area, before (black bars), during (white bars) and 1 year after (grey bars) a 5-week intensive harvest event. Adjacent different letters indicate that a significant difference exists between sampling periods within each

family group (e.g., “a b a” indicates that pre-harvest is significantly different from during harvest but not from 1 year later, and “a ab b” indicates that pre-harvest is not significantly different from during harvest but is significantly different from 1 year later). Error bars indicate one standard error

them easy targets for spearfishers. By contrast, the largest loss of biomass in the south was principally from large lutjanids, such as *Lutjanus bohar* and *L. gibbus*, plus *Macolor macularis* and *M. niger*, which are also easily caught due to their high position in the water column. Large scarids, such as *Chlorurus microrhinos*, *C. bleekeri* and *Cetoscarus bicolor*, in addition to *Bolbometopon muricatum*, were also reduced, likely because they are easy targets for spearfishers at night when they rest on the reef (e.g., Aswani and Hamilton 2004).

During the harvest, fish communities in the Cakaulevu tabu were dominated by acanthurids and scarids, which became more numerically abundant. Similar effects have been seen in previous studies, where scarids increased in abundance following fishing (Russ and Alcalá 1998) or where acanthurid and siganid numbers increased with linear distance away from a no-take zone (Ashworth and Ormond 2005). We have also observed this pattern elsewhere in Fiji, where fish communities on reefs under heavy

fishing pressure are dominated by *Ctenochaetus striatus*, *Chlorurus sordidus*, *Scarus schlegeli* and other non-targeted species (Jupiter and Egli 2011). The prevalence of high numbers of small herbivores and detritivores could possibly be a consequence of a decline in territorial aggression from the removal of large species (Vine 1974; Robertson et al. 1979; Choat and Bellwood 1985) or a combination of various ecological processes.

Regardless of the mechanism, although absolute numbers increased inside the tabu during the harvest, mean biomass of these predominantly herbivorous acanthurids and scarids declined. These large declines, coupled with large increases in turf algae, suggest that by 4 weeks into the harvest grazing capacity may have been reduced. The interpretation is supported by herbivore exclusion manipulations on the Great Barrier Reef that demonstrate the strong role herbivores play in shaping spatial variation in algal turfs (Bonaldo and Bellwood 2011). We are not aware of any other study that documents a turf algal bloom

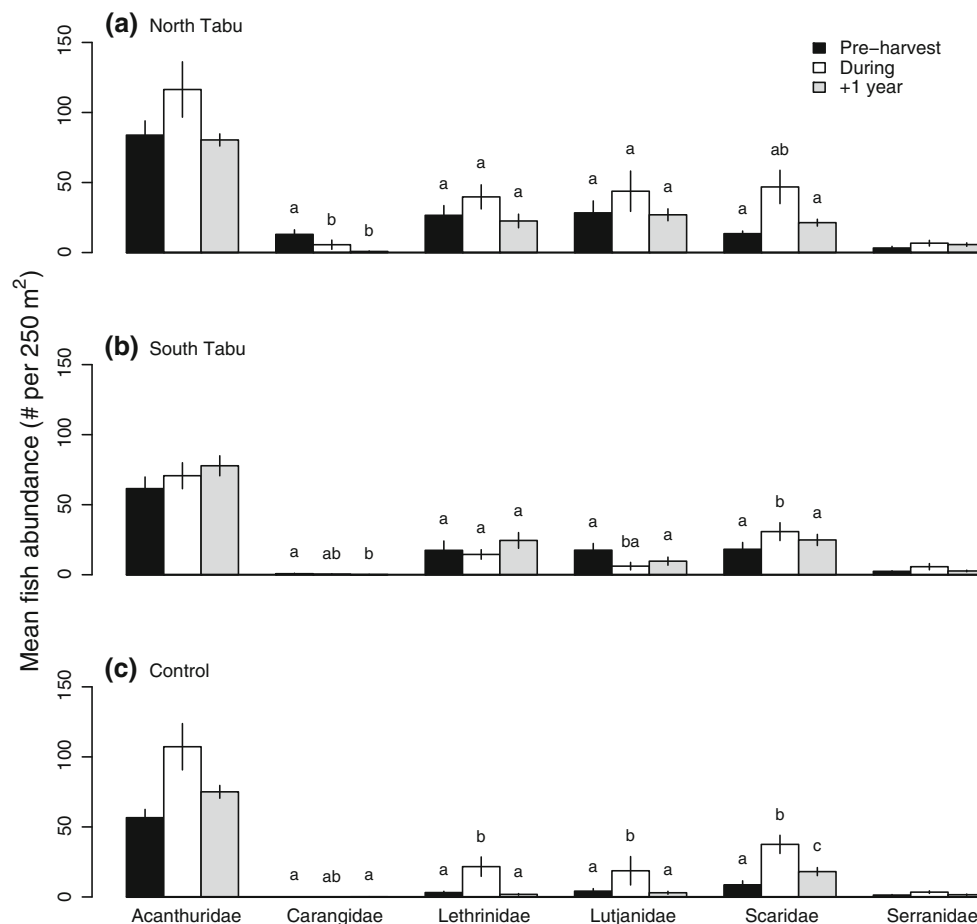


Fig. 5 Mean abundance (# per 250 m²) of targeted food fish families at sites inside (a and b) and outside (c) the Cakaulevu tabu area, before (black bars), during (white bars) and 1 year after (grey bars) a 5-week intensive harvest event. Adjacent *different letters* indicate that a significant difference exists between sampling periods within each

family group (e.g., “a b a” indicates that pre-harvest is significantly different from during harvest but not from 1 year later, and “a ab b” indicates that pre-harvest is not significantly different from during harvest but is significantly different from 1 year later). *Error bars* indicate one standard error

associated with a massive fish harvest, likely because there are few opportunities to conduct BACI surveys so soon following the start of an intensive fishing event. However, because there were also equivalent increases in turf algae in the control area and considerable variability in benthic cover at the site level, we cannot unequivocally attribute the change in benthic cover to fishing alone and we cannot discount that the results may partially be attributed to the placement of transects in different locations when we conducted surveys during the harvest and 1 year later.

Our results further suggest that surveys using fish abundance data alone, without size estimates or complementary benthic composition data, need to be interpreted with caution. In our study, reliance solely on abundance data for interpretation could have led to the quite different conclusion that harvesting a protected area can be beneficial, as mean fish abundance in the north during the harvest was significantly greater than pre-harvest levels. This observation is important as partner organizations within the

Fiji LMMA network generally only train community monitors to record fish abundance (e.g., Tawake et al. 2004). Significant increases in surgeonfish abundances recorded over time by Fijian communities (Seidel 2009) may thus reflect increased abundance of small opportunistic species (e.g., *C. striatus*) responding to indirect effects of fishing pressure rather than positive fishery gains from management.

During the harvest, we observed significant increases in both fish abundance and biomass (with and without *B. muricatum*) in the control area, suggesting a possible behaviourally driven “bail-out” effect of fish moving from the tabu area to the adjacent control in response to the reversal in patterns of fishing effort. This is also supported by the breakdown of the north–south–control biomass gradient during the fishing event and the levelling off in the following year. Short-term behavioural responses of exploited species to fishing (e.g., Gotanda et al. 2009) can potentially magnify the perceived effectiveness of

Table 3 Fish species that exhibited large changes in biomass following 4 weeks of intensive harvest listed with feeding guild, position most often found in the water column, group size and likelihood to move in response to fishing pressure

Species	North	South	Control	Feeding	Water column	Group size	Mobility
<i>(a) Large depletion in tabu, no increase in control</i>							
<i>Naso unicornis</i>	-1,303.3 (-15.7)	-2.4 (-1.5)	0.0 (0.0)	Planktivore	High	Small groups	Low
<i>Caranx melampygus</i>	-1,014.4 (-14.3)	-36.7 (-1.5)	0.0 (0.0)	Predator	Mid	Solitary/small groups	High
<i>Acanthurus fowleri</i>	-425.9 (-17.8)	-36.2 (-6.8)	0.0 (0.0)	Grazer	Mid	Solitary	Low
<i>Naso tonganus</i>	-315.5 (-8.5)	0.0 (0.0)	0.0 (0.0)	Planktivore	High	Small groups	Low
<i>Lethrinus olivaceus</i>	-209.0 (-8.8)	-63.8 (-12.0)	0.0 (0.0)	Predator	Mid	Solitary	Moderate
<i>Caranx papuensis</i>	-187.7 (7.0)	0.0 (0.0)	0.0 (0.0)	Predator	Mid	Solitary/small groups	High
<i>Macolor macularis</i>	-105.1 (-1.7)	-681.9 (-8.1)	-23.3 (0.2)	Predator	Mid	Small groups	Moderate
<i>Scolopsis trilineatus</i>	-62.5 (-38.0)	0.0 (0.0)	0.0 (0.0)	Invertivore	Benthic-assoc.	Solitary	Low
<i>Cheilinus undulatus</i>	-45.1 (-0.4)	-27.6 (0.0)	0.0 (0.0)	Invertivore	Mid	Solitary	Moderate
<i>Lutjanus fulviflamma</i>	-44.8 (-31.5)	-19.4 (-3.3)	0.0 (0.0)	Predator	Mid	Small groups	Moderate
<i>Carangoides oblongus</i>	-44.7 (-8.0)	0.0 (0.0)	0.0 (0.0)	Predator	High	Solitary	High
<i>Chanos chanos</i>	-42.9 (-2.0)	0.0 (0.0)	0.0 (0.0)	Predator	Mid-High	Schooling	High
<i>Caesio caeruleaura</i>	-42.4 (-35.6)	-11.5 (-25.7)	0.0 (0.0)	Planktivore	High	Schooling	High
<i>Platax teira</i>	-19.4 (-1.5)	-106.5 (-0.5)	0.0 (0.0)	Generalist	High	Schooling	Low
<i>(b) Large depletion in tabu, slight increase in control</i>							
<i>Lutjanus bolus</i>	-323.1 (-4.1)	-458.1 (-6.7)	9.1 (1.0)	Predator	Mid	Small groups	High
<i>Epinephelus malabaricus</i>	-26.7 (0.0)	-45.2 (-1.0)	1.3 (1.0)	Predator	Benthic-assoc.	Solitary	Low
<i>Epinephelus polyphekadion</i>	-11.6 (-3.0)	-28.3 (-0.8)	0.7 (1.0)	Predator	Benthic-assoc.	Solitary	Low
<i>Parupeneus crassilabris</i>	-102.4 (-4.4)	0.0 (0.0)	2.2 (3.5)	Generalist	Benthic-assoc.	Small groups	Moderate
<i>(c) Large depletion in tabu, large increase in control</i>							
<i>Naso caesius</i>	-399.6 (-8.8)	0.7 (4.0)	64.4 (-4.3)	Planktivore	High	Small groups	High
<i>Bolbometopon muricatum</i>	-63.9 (-2.0)	-868.6 (-5.3)	2,801.3 (21.7)	Excavator	Mid	Schooling	High
<i>Acanthurus auranticavus</i>	-55.1 (-13.5)	-41.4 (-4.1)	104.0 (38.5)	Grazer/Deitritivore	Mid	Schooling	High
<i>Balistoides viridescens</i>	-8.1 (-0.3)	-110.5 (-0.8)	42.6 (0.2)	Invertivore	Mid	Solitary	Low
<i>Lutjanus gibbus</i>	178.3 (15.4)	-99.6 (-6.9)	239.6 (20.3)	Predator	Mid	Schooling	High
<i>Monotaxis grandoculis</i>	234.8 (3.6)	-221.4 (-3.5)	259.1 (8.3)	Invertivore	Mid	Schooling	Low
<i>Cetoscarus bicolor</i>	34.1 (1.4)	-44.5 (-3.7)	26.0 (0.6)	Excavator	Benthic-assoc.	Solitary	Moderate
<i>(d) Large increase everywhere</i>							
<i>Chlorurus bleekeri</i>	60.6 (6.5)	47.4 (0.8)	59.6 (3.6)	Scrapper/small excavator	Benthic-assoc.	Solitary	High
<i>Chlorurus sordidus</i>	89.2 (5.6)	57.1 (2.0)	58.4 (2.2)	Scrapper/small excavator	Benthic-assoc.	Solitary	High
<i>Ctenochaetus striatus</i>	126.6 (11.1)	64.1 (7.0)	78.8 (8.3)	Deitritivore	Benthic-assoc.	Small groups	High
<i>Melichthys vidua</i>	88.4 (1.9)	18.7 (0.4)	26.4 (0.3)	Omnivore	Mid	Small groups	Low
<i>Scarus schlegelii</i>	49.5 (6.8)	26.1 (1.9)	22.5 (2.6)	Scrapper/small excavator	Benthic-assoc.	Small groups	High

Values for north, south and control indicate change in mean kg ha⁻¹ biomass from 4 weeks into the harvest compared with pre-harvest surveys. Values in parenthesis indicate mean change in abundance (# per 250 m²)

protected areas. For example, open areas with high intensity of fishing pressure can cause “spill-in” of exploited species into reserves (Eggleston and Parsons 2008). Consequently, the reverse pattern is likely to occur when periodic closures are opened to fishing, resulting in a “bail-out” of targeted species. A small portion of this trend observed from the Kia Island data may be simply due to instantaneous variation in fish community assemblages (McClanahan et al. 2007a), especially from schooling species. This may explain, for example, why the sum of the mean increase in lethrinid biomass during the harvest in the control (+281.4 kg ha⁻¹) and the north (+85.5 kg ha⁻¹) was in fact slightly more than the mean decrease from the south (-234.4 kg ha⁻¹). However, the consistent pattern of loss of large-bodied acanthurids, carangids, lethrinids, lutjanids and scarids in the tabu during the harvest, coupled with a corresponding increase in numbers and biomass of most of these taxa in the control, suggests that many of the targeted fish that did not get caught moved. Some of the larger individuals of vulnerable species in the Cakaulevu tabu may have escaped predation by swimming deeper (S. Jupiter and A. Cakacaka, pers. obs.), as has been observed in other studies of Fijian reef fish communities from fished locations (Goetze et al. 2011). Others that are capable of moving large distances may have fled away from the focus of predation (Table 3), which is supported by the work of Januchowski-Hartley et al. (2011) who demonstrate that body size is a strong factor associated with flight initiation distance at higher levels of fishing pressure.

One year after the harvest event, total fish biomass had not recovered inside the Cakaulevu tabu, and the biomass of piscivores such as carangids and serranids was nearly exhausted everywhere. As there were no significant differences in benthic composition inside the tabu compared with pre-harvest conditions, it is likely that the fish communities were still impacted by ongoing fishing. Theoretical and empirical studies suggest that even light levels of fishing can prevent any potential recovery to fish populations and eliminate any benefits to surrounding areas (Westera et al. 2003; Denny and Babcock 2004; Byers and Noonburg 2007). Although the residents of Kia Island claimed to have reinstated the ban on fishing after 5 weeks of harvesting in 2008, several community members stated that they regularly saw boats fishing in the tabu area (S. Jupiter, pers. comm.). Once the communities established contacts with middlemen from local seafood companies during the harvest, the ease of market access may have eroded compliance with local management rules (Cinner et al. 2007; Clarke and Jupiter 2010). Additionally, if outsiders perceive that the tabu is no longer enforced and they will not be detected, they may be more likely to poach (Sutinen and Kuperan 1999), particularly given the light penalties for non-compliance under the Fiji *Fisheries Act* (Clarke and Jupiter 2010).

Studies from elsewhere in Fiji and from across Oceania demonstrate that customary management can effectively conserve marine resources under certain conditions (e.g., Cinner et al. 2005; McClanahan et al. 2006; Jupiter and Egli 2011). These conditions include secure community fishing rights or customary marine tenure, respect for the management authority from within and outside the community, broad awareness of management rules and boundaries, and limits on the duration and intensity with which managed areas may be harvested (Aswani and Hamilton 2004; Bartlett et al. 2009a; Clarke and Jupiter 2010). Indeed, the highly significant differences in fish abundance and biomass inside versus outside of the Cakaulevu tabu prior to the harvest confirm anecdotal reports of strong compliance with customary management rules since 2005. These conditions are additionally aided by the placement of customary fishing closures in naturally productive locations (Jupiter and Egli 2011). Customary management is less likely to succeed in areas with high population density and commercialization of marine resources (Cinner and Aswani 2007). Given that hundreds of periodically harvested closures have already been established in Oceania and that the practice is rapidly expanding (Bartlett et al. 2009b), we offer the following recommendations to improve knowledge and planning for management success:

1. To maintain sustainable fisheries benefits for the future, harvests must be controlled. Control measures can include restrictions on effort, gear, duration of opening, access and size of catch. Moreover, during a harvest, the amount extracted from a closure has to be lower than the amount of build-up since initiation of protection, and in many cases, substantial build-up may take years to decades to occur (McClanahan and Graham 2005; Babcock et al. 2010). Given that different species have very different catchability and recovery rates (e.g., McClanahan et al. 2007b; Babcock et al. 2010), species- or guild-specific take guidelines may need to be developed (Cohen and Foale 2011).
2. Catch should be monitored to ensure that some breeding stocks remain to provide for local replenishment as well as replenishment of adjacent fishing grounds and neighbouring closures. Larger reef fish generally have greater egg production and tend to produce larger eggs, which may be more viable (e.g., Evans et al. 2008).
3. Managers should undertake broad consultation to reach consensus for a verbal or written plan that details the process by which openings are authorized and the frequency, location, duration and gear type with which they can occur. This has been done for certain areas in Fiji (e.g., Kubulau District; WCS 2009), and generally results in fewer uncontrolled harvests. Because the Kia

Table 4 (a) Mean percent cover of each benthic strata. (b) PERMANOVA main effects results of differences in mean benthic cover. (c) PERMANOVA pair-wise comparisons of differences in benthic cover within sampling period between each area. (d) PERMANOVA pair-wise comparisons of differences in benthic cover within area between each sampling period

	FAC	LC	OT	RM	TA	US	
<i>(a) Benthic cover</i>							
<i>Pre-harvest</i>							
North	0.8	46.6	6.0	21.9	13.3	10.2	
South	0.4	49.7	7.4	20.9	14.7	6.8	
Control	0.8	36.0	10.8	26.6	17.6	8.0	
<i>During harvest</i>							
North	0.6	47.9	5.7	11.8	24.3	9.8	
South	0.5	33.3	5.8	6.3	44.0	10.2	
Control	1.1	36.9	8.2	11.5	37.4	5.1	
<i>1 year later</i>							
North	3.3	48.2	4.4	29.3	9.5	5.4	
South	2.5	43.2	5.6	26.2	14.5	8.2	
Control	3.0	40.2	5.5	27.0	17.3	7.2	
Source	<i>df</i>	SS	MS	Pseudo-F	P(perm)	Permutations	
<i>(b) PERMANOVA main effects</i>							
Sampling	2	28,779.0	14,390.0	29.2	0.0002	4,978	
Area	2	6,739.9	3,369.9	6.8	0.0002	4,987	
Site (area)	3	24,431.0	8,143.6	16.5	0.0002	4,986	
Sampling × area	4	4,864.2	1,216.1	2.5	0.0064	4,979	
Sampling × site (area)	6	14,630.0	2,438.3	4.9	0.0002	4,977	
Residual	162	79,948.0	493.5				
Total	179	159,390.0					
Pair-wise comparisons	(c) Between area			(d) Between sampling			
	Level	<i>t</i>	<i>P</i> (perm)	Level	<i>t</i>	<i>P</i> (perm)	
<i>Pre-harvest</i>							
North–south	NS	0.628	0.7458	North			
North–control	NS	1.425	0.1248	Pre-During	**	2.120	0.0074
South–control	*	1.767	0.0392	Pre-1 year	NS	1.254	0.1944
<i>During harvest</i>							
North–south	***	5.472	0.0002	During-1 year	***	3.815	0.0002
North–control	***	3.420	0.0002	South			
South–control	**	2.102	0.0040	Pre-During	***	6.045	0.0002
<i>1 year later</i>							
North–south	NS	1.213	0.2130	Pre-1 year	NS	1.304	0.1616
North–control	*	1.672	0.0440	During-1 year	***	6.726	0.0002
South–control	NS	0.666	0.7072	Control			
				Pre-During	***	3.099	0.0008
				Pre-1 year	NS	0.846	0.4796
				During-1 year	***	4.207	0.0002

Significant *P*(perm) values are indicated in bold

FAC, fleshy algae/cyanobacteria; LC, live coral; OT, other soft substrate; RM, reef matrix; TA, turf algae; US, unconsolidated substrate

For (c) and (d), significance level denoted as: NS not significant, * *P*(perm) < 0.05, ** *P*(perm) < 0.01, *** *P*(perm) < 0.001

communities did not have a well-developed management plan, there was no impediment to extending their harvest until resources were exhausted.

4. Finally, management success from the perspective of Pacific communities is most often related to achieving

objectives of providing for immediate food or income to meet cultural or social obligations (Foale et al. 2011). Conservation practitioners and resource managers need to realize this difference in objectives and work with fishers to raise awareness of the risk of stock collapse of

vulnerable species if openings are too frequent or harvests are too intense. If not regulated, even a single opening may cause a highly significant decline in fish biomass, requiring a long period for recovery.

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