

Abstract—Does adult spillover (movement out of marine protected areas [MPAs]) of fish create a net export of fish biomass from MPAs to adjacent fished reefs? Biomass of five commercial reef fish species was estimated by visual census within and outside three MPAs in Guam, Micronesia. For most species and sites, biomass was significantly higher within the MPAs than in adjacent fished sites. Movement of fishes into and out of the MPAs was determined by mark-recapture experiments, in which fishes were tagged both inside and outside of MPAs. Four out of five species studied showed little or no net movement out of MPAs. However, the orangespine surgeonfish (*Naso lituratus*) showed a net spillover of biomass from all three MPAs; 21.5% of tagged individuals and 29% of the tagged biomass emigrated from MPAs. Patterns of spillover were strongly influenced by physical habitat barriers, such as channels, headlands, or other topographic features. MPAs that are physically connected by contiguous reef structures will likely provide more spillover to adjacent fished sites than those that are separated by habitat barriers. This study demonstrates that MPAs can enhance export of fish biomass to fished areas, but spillover is species-specific and depends on factors such as species size and mobility.

Spillover of commercially valuable reef fishes from marine protected areas in Guam, Micronesia

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Over the past two decades, marine protected areas (MPAs) have been increasingly adopted as an important fisheries management tool. The primary goals for MPAs are to protect critical habitat and biodiversity, to sustain or enhance fisheries by preventing spawning stock collapse, and to provide recruitment to fished areas (Gell and Roberts, 2003; Halpern, 2003). Enhancement of fished areas may occur through transport of larvae from spawning stock within the MPA (Gerber et al., 2005) or by a net emigration of adult fish to adjacent fished areas—a movement that is commonly known as “spillover” (e.g., Alcala et al., 2005; Abesamis et al., 2006; Goni et al., 2006).

The role of spillover in determining MPA effectiveness has been addressed in both theoretical modeling studies (e.g., DeMartini, 1993; Kramer and Chapman, 1999; Gerber et al., 2005) and in empirical studies. The latter involve indirect documentation of spillover inferred from increases in fish biomass or catch per unit of effort (CPUE) in adjacent fished areas (e.g., Russ and Alcala, 1996; Roberts et al., 2001; Tupper and Rudd, 2002; Alcala et al., 2005), and direct documentation of fish movement through mark-recapture or sonic tracking experiments (e.g., Chapman and Kramer, 2000; Meyer et al., 2000; Kaunda-Arara and Rose, 2004; Meyer and Holland, 2005). There are a number of ways in which movement across MPA boundaries may occur; these

include random movements of fish during their routine activities (sometimes referred to as diffusion), emigration in response to density dependence (e.g., Tupper and Juanes, 1999; Abesamis and Russ, 2005), directed dispersal due to migration, and ontogenetic habitat shifts (Gerber et al., 2005). In order for spillover to effectively enhance adjacent fisheries, the net direction of these movements, and the number and size of fishes moving, must result in a net flow of biomass out of the MPA. Measuring the movement of biomass into the MPA should therefore be equally important to measuring outward movements. However, few studies have measured immigration, and therefore net spillover, and those that do address bidirectional movements have reported conflicting results, depending on the species or life history stage, the habitat, and the size and placement of the MPA (e.g., Kelly and MacDiarmid, 2003; Zeller et al., 2003; Tremain et al., 2004; Goni et al., 2006).

The degree of spillover from MPAs depends on the rate of fish migration across MPA boundaries (DeMartini, 1993; Gerber et al., 2005). Larger or more mobile species with large home ranges may spend too much time outside of the MPAs to be effectively protected, whereas smaller, more sedentary species with small home ranges may not cross MPA boundaries in sufficient numbers to enhance adjacent fisheries by spillover (DeMartini, 1993; Tupper and Rudd, 2002). If the

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goal of a MPA is to enhance local fisheries by spillover in addition to conserving spawning biomass, then it must be designed and situated so that net movement of fishes from the MPA to fished areas can take place. In most tropical island nations, enhancement of local fisheries by adult spillover may be critical for continued support of the preserve system by the local fishing community (Russ and Alcala, 1999; Galal et al., 2002). In general, arguments for larval spillover carry little weight with fishermen because dispersal may not occur on spatiotemporal or "visual" scales that are meaningful to them (Russ and Alcala, 1996; Russ, 2002; Abesamis et al., 2006). This situation is doubtless the case in Guam, where little is known about the movement of fishes on coral reefs.

One characteristic of heavily exploited reefs is the very low abundance (in some cases virtual absence) of large carnivorous fishes, particularly groupers (Serranidae) and snappers (Lutjanidae) (Russ, 1991, 2002; Medley et al., 1993). In Guam, grouper biomass is noticeably lower than at the less heavily populated islands in Micronesia (e.g., Palau). Much research has therefore been directed at determining the effects of implementing MPAs on populations of large predatory fishes (e.g., Russ and Alcala, 1996, 2004). In Micronesia, however, herbivorous fishes, particularly surgeonfishes and unicornfishes (Acanthuridae) and parrotfishes (Scaridae) are equally important to local fisheries, and in many areas they have dominated the catch (Amesbury et al., 1986). Thus, it is important to understand the effects of MPAs on herbivorous and carnivorous fishes.

To address whether MPAs in Guam can increase fish biomass and provide spillover to adjacent reef areas, biomass of five important reef fish species inside three MPAs in Guam and on adjacent exploited reefs was determined by using underwater visual census. Net movements of both herbivorous and carnivorous reef fish across MPA boundaries were determined by using mark-recapture experiments.

Materials and methods

Study sites

In May of 1997, the Guam Department of Aquatic and Wildlife Resources (DAWR) established a network of five MPAs, termed "marine preserves," around the island, which accounted for 11.8% of Guam's shoreline and 15.3% of Guam's reef area. Fishing within these MPAs is restricted to shore-based cast netting and hook-and-line fishing for select reef species, except for the Piti Bomb Holes Marine Preserve, where no reef fishing (i.e., fishing from the shore to the reef margin) is allowed. Trolling seaward of the reef margin for pelagic fish is allowed in all preserves. Despite being implemented in 1997, the marine preserves did not become enforced until October 1999. Even then, only warnings were issued until January 2001, at which time the regulations became fully enforced, and all violators were subject to

any or all penalties applicable under the law. This study was conducted in 2003–04 at three MPA sites (Achang Reef Flat Marine Preserve, Piti Bomb Holes Marine Preserve, and Tumon Bay Marine Preserve—hereafter referred to as Achang, Piti, and Tumon, respectively) on the western and southern coasts of Guam, Micronesia (Fig. 1). All three sites consist of shallow reef flats that lead seaward to a reef crest and then drop off to a reef slope. The two remaining marine preserves, Sasa Bay and Pati Point, were not surveyed. Sasa Bay is a mangrove swamp with no coral reefs within its boundaries, and Pati Point is located within a restricted military area (Anderson Air Force Base).

The Achang preserve is the largest of the three preserves (4.8 km²). It includes a wide variety of habitats: mangroves, seagrass, sand, coral, and three channels that cut through the fringing reef from the outer reef slope to the reef flat. The largest of these, Manell Channel, separates Achang reef flat from Cocos Lagoon, to the west of Achang Reef Flat. To the west, the reef flat narrows and is interrupted by a rocky headland. Reference fished sites for the Achang Preserve were located in Cocos Lagoon. Seasonal traditional fishing is permitted in the Achang Preserve for juvenile streamlined spinefoot (*Siganus argenteus*), juvenile fusiliers (*Pterocaesio tile*), and big eye scad (*Selar crumenophthalmus*) under special permit.

The Piti preserve covers 3.6 km² and consists of a broad reef flat (1.4 km²) in Piti Bay bordered by Tepungan Channel to the west. The fringing reef is continuous from Piti Bay eastward to the fished sites at Asan Bay. The reef flat includes unique features known as "bomb holes," which provide sheltered areas of deeper water. The deepest of these sinkholes were 9–10 m deep and were densely populated by a variety of hard and soft coral species. They host rich soft coral communities and fish and invertebrate assemblages not often found within the reef margin. The main sinkhole is occupied by an 11-m in diameter underwater observatory that was completed in 1996. It is also frequented by commercial scuba divers during diving tours (up to 200 divers a day). Fish feeding is a common practice around the observatory; therefore, our survey sites were located away from the sinkholes in order to minimize possible confounding effects of fish feeding and diver presence.

The Tumon preserve lies adjacent to the central tourist district on Guam. It is 4.5 km² in total area and consists of extensive reef flats (2.7 km²), a gently sloping fore reef slope, and a broad shelf habitat. The reef flat is dominated by coral patch reefs. The Tumon MPA is bordered by headlands to the east and west, which interrupt the reef flat, although there is contiguous fringing reef which links Tumon with Tanguisson to the east. However, there is a sewage outfall at Tanguisson which may reduce movement of fish to the east. Because of the distance from the reef flat at the western boundary of the Tumon MPA to the reef flat at East Agana Bay (approximately 3 km), Tanguisson was the location chosen for the fished sites. Limited traditional fishing with hook-and-line or cast net from shore is allowed in

the Tumon Bay preserve for four types of fish: convict surgeonfish (*Acanthurus triostegus*), spinefeet (*Siganus* spp., known regionally as rabbitfish), juvenile jacks and trevallies (*Caranx* spp.), and juvenile goatfishes (Mullidae). Cast nets are sometimes used for convict surgeonfish and spinefeet along the reef margin.

At each site, visual census and tagging were performed as near to the geometric center of the MPA as possible. The closest distance to the MPA boundary was measured, and census sites on adjacent fished reefs were chosen at this same distance outside the MPA. All transects were surveyed and tagging was conducted in habitats as similar as possible, generally on the seaward edge of the reef flat at a 2–3 m depth, where the substrate typically consisted of sand, rubble, and scattered patch reefs (mainly *Porites* spp.), and where seagrass beds are nearer to shore (except in Tumon, where seagrass is scarce). This experimental design served to minimize bias due to among-site variation in distance from the reserve boundary and habitat type.

Estimation of biomass in MPAs and adjacent fished areas

Underwater visual census was used to estimate biomass of five exploited reef fishes at three MPAs and adjacent fished sites. These included three herbivores: convict surgeonfish (*Acanthurus triostegus*), orangespine unicornfish (*Naso lituratus*), and little spinefoot (*Siganus spinus*), and two carnivores: yellowstripe goatfish (*Mulloidichthys flavolineatus*), and honeycomb grouper (*Epinephelus merra*). These five species were chosen because of their great abundance and prevalence in the Guam nearshore reef fishery and because they are relatively easy to capture and tag. At each study site, four 50 m × 5 m transects were laid haphazardly. Divers swam each transect slowly, counting all commercially important species and estimating their lengths to the nearest cm. All divers were trained in fish size estimation for one month before this study. Biomass estimates were conducted biweekly from May through August 2003. In total, 32 transects were completed at each MPA and adjacent reference sites (8 census days × 4 transects at each site). Biomass was estimated by substituting the length of each fish on the transect into length-weight regressions for that species. The total weight of all fish by species was then used as an estimate of biomass.

Mark-recapture study

The five study species were collected from three preserves and from surrounding areas of reference sites. Within each preserve, six permanent quadrats, each



Figure 1

Map of Guam showing the locations of the three marine protected areas (MPAs) and three reference sites. MPAs (hatched areas) are Achang Reef Flat Marine Preserve, Piti Bomb Holes Marine Preserve, and Tumon Bay Marine Preserve. Reference sites are Cocos Lagoon, Asan Bay, and Tanguisson. Inset shows the location of Guam within the Western Pacific region.

20 × 20 m in planar area, were located at a distance of 800 m from the boundary of the MPA and reference site. The perimeter of each study site was marked at 1-m intervals by tying flagging tape to a dead coral. Another six quadrats were marked on fished reefs at the reference site, also at a distance of 800 m from the MPA boundary. This distance was chosen because it allowed the location of the study sites to fall into appropriate and similar habitats at all MPAs and fish sites. This distance also ensured that all tagged fish had an equal distance to move in order to enter or leave the MPA. It also represented sufficient distance from the MPAs to encompass a large area of fished reef. A square area was chosen for the mark-recapture study because it was easier to deploy surround nets

and to quantify fishing effort in a large square than in a typical narrow rectangle used for belt transects. Within each permanent quadrat, fish were captured by squirting an anesthetic (10% solution of Quinaldine sulfate in seawater) into the water where the fish were hiding and by casting a surround net (for smaller and more sedentary fishes) around corals heads or small patch reefs. For each species, an attempt was made to tag the same number of individuals at each MPA and reference site. Because target species density was generally lower at the fished sites (see "Results" section), fish were captured and tagged first at the fished sites by exhaustively fishing each 20×20 m quadrat. The same numbers of fish were then tagged in quadrats within the MPAs. This procedure ensured that tagging effort was equal across all sites, although fishing effort was often lower in the MPAs because sufficient fish could be captured in a shorter time. For recaptures of tagged fish, all permanent quadrats were fished exhaustively and all tagged individuals were recorded.

Tagging took place biweekly from May through July 2003 and from January through March 2004. Recaptured fish were collected weekly from May through August 2003 and January through April 2004 ($n=32$ total recapture attempts per site), allowing 1 week to 6 months between tagging and recapture. Captured fish were identified, measured, and tagged with visible implant elastomer (VIE) tags (Northwest Marine Technologies, Inc., Shaw Island, WA), and immediately released at the site of capture. The VIE tag was implanted under a fish's skin and thus would not become entangled, scraped off, or fouled with algae. Tag loss can lead to underestimates of recapture rates if a fish is recaptured after losing its tag. Past studies with several reef fish families (Labridae, Scaridae, Acanthuridae, and Serranidae) showed high (>90%) retention of elastomer implants, particularly for individuals greater than 150 mm standard length (Tupper, 2007). The effective life of the VIE tag in most reef fish is about 6 months, after which the tissue surrounding the tag generally has overgrown and obscured the tag (Tupper, 2007). The use of surround nets allowed for capture of resighted tagged fish. This approach enabled much higher recapture rates than those in more conventional studies where external tags and nonselective gears (such as traps) are solely used.

Analysis of data

To calculate spillover (S) for a given species, the numbers and biomass of tagged fish emigrating or immigrating across an MPA boundary were estimated. Spillover was calculated as the number (or biomass) of emigrants minus the number (or biomass) of immigrants. Percent spillover was calculated as the proportion of tagged fish (numbers and biomass) exported to adjacent fished areas minus the proportion of tagged biomass imported to the MPA:

$$S = (B_e/B_p - B_i/B_R) \times 100,$$

where S = percent spillover;
 B_e = biomass emigrating from the preserve;
 B_p = biomass remaining in the preserve;
 B_i = biomass immigrating into the preserve;
 and
 B_R = biomass remaining in the reference site.

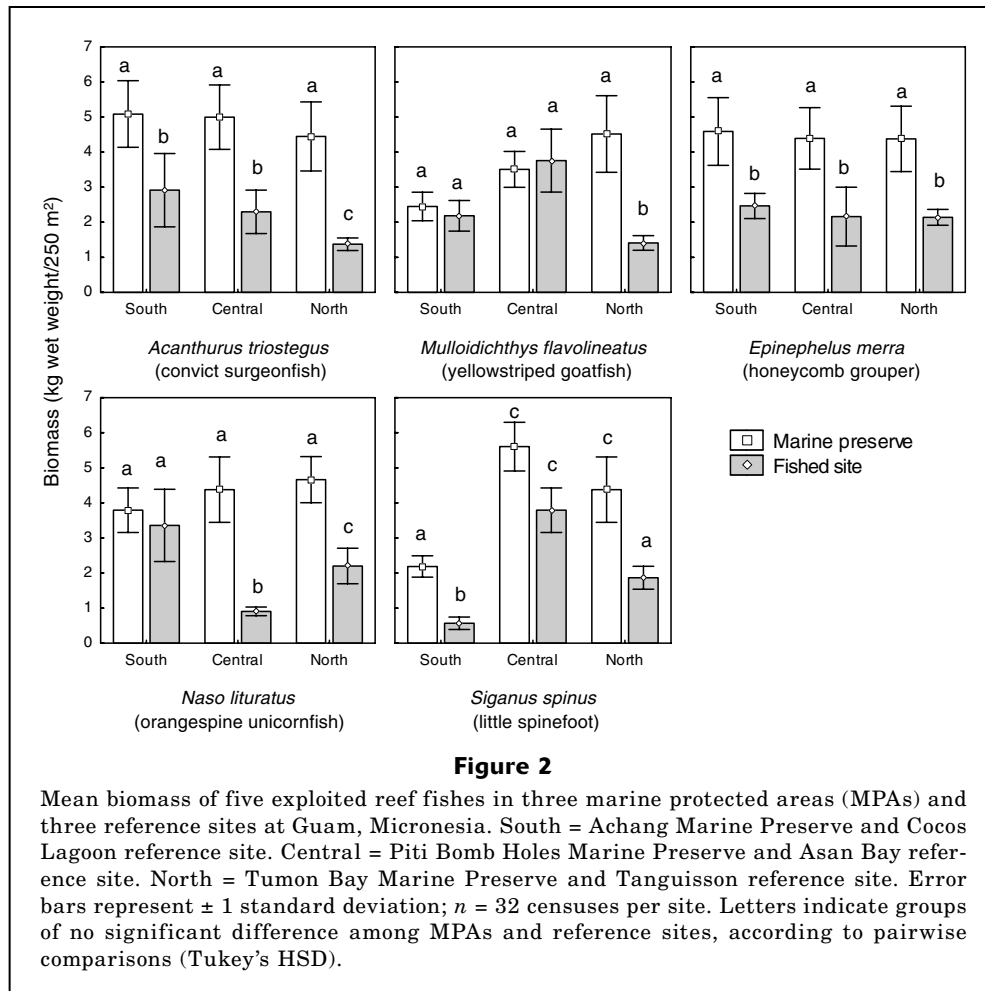
A positive value would indicate net spillover; a negative value would indicate net influx of biomass to the MPA. Thus, a positive value indicates that the MPA is a source of biomass for adjacent fished areas, where a negative value indicates that the MPA is a biomass sink and perhaps better suited to conserving biomass of a given species than to enhancing local fisheries.

Before analysis, all raw data were tested for normality by using the Shapiro-Wilk W test and for homogeneity of variance by using Levene's test (Sokal and Rohlf, 1995). Because raw density and raw spillover data did not initially meet these assumptions, they were square-root transformed. Percent spillover data were arc-sin transformed. All transformed data met the assumptions of parametric analysis of variance (ANOVA). Variation in mean fish biomass between locations and between MPAs and fish sites was determined with 2-way ANOVA. For this analysis, each MPA was paired with its adjacent fished site and this grouping resulted in three pairs: North (Tumon and Tanguisson), central (Piti and Asan Bay), and south (Achang and Cocos Lagoon). The ANOVA design was crossed, with location (north vs. central vs. south) as one factor and protection status (MPA vs. fished site) as a second factor. Variation in mean spillover between locations and between species was also analyzed by using 2-way ANOVA. Tukey's honestly significant difference (HSD) was used as a *post hoc* comparison test to determine pairwise differences in mean biomass and mean spillover in MPAs and reference sites. Linear regression was used to explore the relationship between density (expressed as biomass) of fish within the MPAs and the spillover rate from the MPAs.

Results

Biomass estimates

Mean biomass of the three herbivorous species was higher in MPAs than in the fished sites (Fig. 2). Mean biomass of convict surgeonfish did not differ between locations (i.e., between south, central, and north, 2-way ANOVA, $F=0.79$, $P=0.46$) but was significantly higher in MPAs than in fished sites at all locations ($F=13.47$, $P<0.001$; Tukey's HSD, $P<0.05$ for all paired comparisons). There was no significant interaction between location and protective status. Mean biomass of orange-spine unicornfish also did not differ between locations (2-way ANOVA, $F=0.90$, $P=0.42$) but was significantly higher in MPAs than in fished sites ($F=12.02$, $P<0.0001$). There was a significant interaction ($F=9.4$, $P<0.01$) between location and protective status because biomass



of orangespine unicornfish was significantly higher in the Piti and Tumon MPAs than in adjacent fished sites (Tukey's HSD, $P < 0.05$), but there was no significant difference in biomass between Achang and Cocos Lagoon (Tukey's HSD, $P < 0.05$). Mean biomass of little spinefoot differed significantly between locations (2-way ANOVA, $F = 15.02$, $P < 0.0001$) and was significantly higher in the north and central locations than in the south (Tukey's HSD, $P < 0.05$). Mean biomass of little spinefoot was also significantly higher on protected reefs ($F = 16.01$, $P < 0.0001$) at all locations (Tukey's HSD, $P < 0.05$ for all paired comparisons).

For carnivorous species, mean biomass of yellowstripe goatfish (Fig. 2) did not differ between locations (2-way ANOVA, $F = 1.76$, $P = 0.18$). There was a nonsignificant higher abundance in MPAs than in reference sites ($F = 3.30$, $P = 0.076$). There was a significant interaction between location and protective status ($F = 3.32$, $P < 0.05$), which occurred because biomass of yellowstripe goatfish was higher in the Tumon MPA than at Tanguisson, but did not differ between MPAs and reference sites at the central and south locations. Mean biomass of honeycomb grouper (Fig. 2) did not differ between locations (2-way ANOVA, $F = 0.07$, $P = 0.93$) but was significantly higher

in MPAs than at fished sites ($F = 11.33$, $P = 0.002$) at all locations.

Spillover

A total of 2674 fishes were tagged; of these 935 (35%) were recaptured (Table 1). The species with the highest recapture rate (78%) was the honeycomb grouper; a solitary, benthic predator. Mobile, schooling species such as yellowstripe goatfish and little spinefoot had lower recapture rates (25–35%) but were abundant enough to allow relatively large numbers of returns.

Most recaptured fish did not cross the MPA boundaries. The overall grand mean spillover (i.e., over all species at all sites) was 5.9% of individuals and 8.0% of biomass from the MPAs. Table 2 shows biomass and mean number of tagged fish remaining within each MPA and fished site, immigrating to each MPA, and emigrating to each fished site. The difference between emigration and immigration is shown in Table 2 as the net flux in biomass and as the net flux in numbers. Spillover (the proportion of tagged fish exported to adjacent fished areas minus the proportion of tagged fish imported to the MPA) is also presented as spillover in

Table 1

Number of fish tagged and recaptured at three marine protected areas (MPAs) and three fished sites in Guam, Micronesia. Study species were convict surgeonfish (*Acanthurus triostegus*), honeycomb grouper (*Epinephelus merra*), yellowstripe goatfish (*Mulloidichthys flavolineatus*), orangespine unicornfish (*Naso lituratus*), and little spinefoot (*Siganus spinus*).

Species	Achang MPA	Cocos Lagoon	Piti MPA	Asan Bay	Tumon MPA	Tanguisson	Total	Recaptures	% Recaptured
Convict surgeonfish	135	134	135	130	132	130	796	247	31.0
Orangespine unicornfish	50	47	48	45	50	44	284	112	39.4
Yellowstrip goatfish	65	62	65	65	70	63	390	137	35.1
Honeycomb grouper	40	40	41	40	40	39	240	188	78.3
Little spinefoot	162	157	165	158	164	158	964	251	26.0
Total	452	440	454	438	456	434	2674	935	35.0

biomass and in numbers. For both net flux and spillover, a positive value indicates net movement out of the MPA; a negative value indicates net movement into the MPA. For the combination of all species, overall spillover was lowest at the Tumon MPA, where only 1.7% of all tagged biomass was exported (two-way ANOVA, $F=17.12$, $P<0.01$, Tukey's HSD, $P<0.05$). Spillover did not differ between the other two MPAs (20.3% at Piti and 16.7% at Achang, Tukey's HSD, $P<0.05$).

A significant interaction between species and location (two-way ANOVA, $F=7.73$, $P<0.0001$) warranted a closer inspection of fish movements at each location. Orangespine unicornfish was the only species exported from all three MPAs. The overall mean spillover for orangespine unicornfish was 29.4% of biomass (Table 2) and 21.5% of individuals (Table 2). This was significantly higher than the other four species (2-way ANOVA, $F=6.27$, $P<0.0001$). There was no significant difference in spillover of orangespine unicornfish between MPAs (2-way ANOVA, $F=2.71$, $P=0.34$). Although yellowstripe goatfish showed low overall mean spillover (1.1% of individuals imported to MPAs but 16.4% of biomass exported), it was actually very mobile; 34% of its tagged biomass moved into the Achang MPA, and 31% of its tagged biomass moved out of the Piti MPA. These net inward and outward movements at different locations cancelled each other in the calculation of overall mean spillover for this species. No movement of this species occurred across the Tumon MPA boundaries. In contrast, net export of convict surgeonfish occurred at Achang and Piti MPAs, but there was a net import of surgeonfish biomass to the Tumon MPA (Table 2). Spillover of convict surgeonfish did not differ between the Achang and Piti MPAs (Tukey's HSD, $P>0.05$). Honeycomb grouper showed an overall mean outward movement of 3.3% of tagged biomass (Table 2). However, there was no net movement of individuals across MPA boundaries at all sites (Table 2); this result indicated that primarily larger individuals moved out of the MPAs.

In general, for most species, the percentage of biomass exported from the MPAs was greater than the percentage of individuals exported. The exception was

that of yellowstripe goatfish at the Achang MPA, which showed a net outward movement of 15.6% of individuals (Table 2) but a net inward movement that was 34.2% of biomass (Table 2), indicating that the fish moving into Achang MPA were much larger than the fish moving out. In contrast, at Piti there was a net outward movement of 15.6% of individuals and 30.8% of the biomass for yellowstripe goatfish, indicating that larger fish were primarily exported. The effect of resident biomass on spillover of each species was examined by plotting spillover (in biomass) against the biomass ratio of each species at each MPA, measured as biomass inside the MPA divided by the biomass at the fished site. The variation in density between censuses rendered it impossible to create separate regressions for each species or MPA. Thus, the overall mean biomass ratio and mean spillover were pooled for all species and MPAs into a single regression. No relationship was found between the biomass ratio and mean spillover ($r^2=0.1$, $P=0.34$; Fig. 3).

Discussion

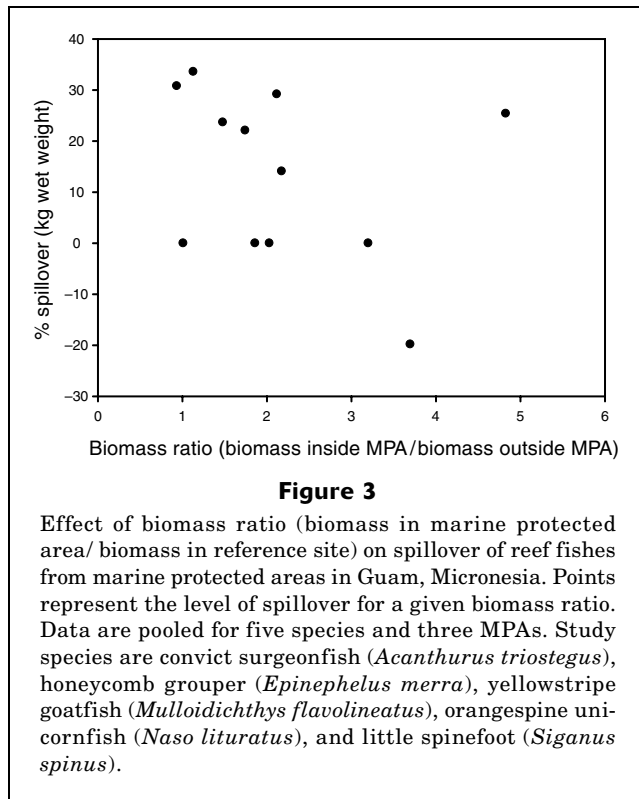
One of the primary effects of protection from fishing is an increase in size and abundance of fishes, and therefore in biomass, in MPAs (Russ, 2002; Halpern, 2003). Biomass of reef fish was greater in marine reserve areas than in fished areas after about six years of effective no-take protection at Sumilon and Apo Islands in the Philippines (Alcala et al., 2005). Moreover, these differences became larger with increased duration of protection up to 19 years. Russ and Alcala (2004) concluded that the time required for full recovery of reef fish populations at the Sumilon and Apo Island MPAs would be 15 and 40 years, respectively. Biomass of leopard coral grouper (*Plectropomus leopardus*) and spotted coral grouper (*P. maculatus*), two large roving grouper species, was five times higher in no-fishing zones than in fished zones of the Great Barrier Reef Marine Park, after 14 years of protection (Evans and Russ, 2004). Numerous other studies had found no difference in biomass of *Plectro-*

Table 2

Summary of mean numbers and biomass of recaptured fish that remained resident in the marine protected areas (MPAs) and fished sites, or that moved into or out of the MPAs. Spillover is the difference between emigration from and immigration to the MPAs. Percent spillover is the proportion of tagged fish emigrating from the MPAs minus the proportion of tagged fish immigrating to the MPAs. Data are presented as biomass of fish and number of fish. All data are means ± 1 standard deviation; $n = 32$ recapture events for each site. Superscripts (^{a,b}) indicate significant differences among MPAs according to pairwise comparisons (Tukey's honestly significant difference [HSD] test). Fished sites for Achang, Piti, and Tumon were Cocos Lagoon, Asan Bay, and Tanguisson, respectively (see Fig. 1). Study species were convict surgeonfish (*Acanthurus triostegus*), honeycomb grouper (*Epinephelus merra*), yellowstripe goatfish (*Mulloidichthys flavolineatus*), orangespine unicornfish (*Naso lituratus*), and little spinefoot (*Siganus spinus*).

		Biomass of fish					
Species	Location	Fish biomass (MPA) 250 m ²	Fish biomass (fished site) g wet wt/ 250 m ²	Biomass immigrants g wet wt/ 250 m ²	Biomass emigrants g wet wt/ 250 m ²	Spillover (biomass) g wet wt/ 250 m ²	Spillover (%)
Convict surgeonfish	Achang	2207 \pm 408	2742 \pm 777	407 \pm 316	1232 \pm 658	825 \pm 742	22.1 \pm 19.8 ^a
	Piti	4051 \pm 1684	4806 \pm 1376	1137 \pm 666	1848 \pm 791	711 \pm 1055	14.1 \pm 15.9 ^a
	Tumon	2720 \pm 1757	2969 \pm 1841	2018 \pm 682	1109 \pm 326	-910 \pm 564	-19.8 \pm 18.0 ^b
Honeycomb grouper	Achang	3206 \pm 863	3206 \pm 862	141 \pm 283	184 \pm 367	42 \pm 85	1.4 \pm 2.7
	Piti	1886 \pm 304	1716 \pm 463	530 \pm 398	749 \pm 59	220 \pm 358	7.5 \pm 12.4
	Tumon	2494 \pm 362	2588 \pm 285	141 \pm 283	168 \pm 336	27 \pm 53	0.9 \pm 1.9
Yellowstripe goatfish	Achang	2514 \pm 759	2524 \pm 791	1647 \pm 551	523 \pm 1045	-1125 \pm 561	-34.2 \pm 19.7 ^a
	Piti	2005 \pm 986	2752 \pm 1517	209 \pm 246	1227 \pm 472	1016 \pm 720	30.8 \pm 31.4 ^b
	Tumon	2267 \pm 396	2267 \pm 396	0	0	0	0 ^b
Orangespine unicornfish	Achang	1872 \pm 1248	2932 \pm 1682	291 \pm 346	1351 \pm 379	1060 \pm 450	33.6 \pm 5.2
	Piti	4546 \pm 689	6459 \pm 592	1321 \pm 995	3234 \pm 1139	1914 \pm 630	25.4 \pm 9.3
	Tumon	2563 \pm 1353	4046 \pm 2543	341 \pm 404	1824 \pm 1437	1483 \pm 1614	29.2 \pm 35.5
Little spinefoot	Achang	4097 \pm 1434	3824 \pm 1599	1476 \pm 334	1203 \pm 417	-272 \pm 311	-6.2 \pm 5.6 ^a
	Piti	2629 \pm 994	4357 \pm 1624	547 \pm 271	2275 \pm 405	1728 \pm 639	23.7 \pm 6.3 ^b
	Tumon	3524 \pm 1530	3169 \pm 1526	806 \pm 678	451 \pm 302	-644 \pm 228	-8.6 \pm 19.5 ^a

		Number of fish					
Species	Location	Number of fish (MPA)	Number of fish (reference site)	Number of immigrants	Number of emigrants	Spillover (numbers)	Spillover (%)
Convict surgeonfish	Achang	6.5 \pm 0.58	7.8 \pm 0.96	1.0 \pm 0.82	2.3 \pm 0.96	1.3 \pm 0.96	13.9 \pm 10.6 ^a
	Piti	9.3 \pm 3.30	9.8 \pm 1.71	2.8 \pm 1.50	3.3 \pm 1.50	0.5 \pm 1.73	6.0 \pm 13.1 ^a
	Tumon	7.8 \pm 1.89	6.8 \pm 3.20	3.3 \pm 0.96	1.5 \pm 0.58	-1.8 \pm 0.96	-20.0 \pm 20.2 ^b
Honeycomb grouper	Achang	5.0 \pm 1.41	5.0 \pm 1.41	0.3 \pm 0.50	0.3 \pm 0.50	0	0
	Piti	3.0 \pm 0.82	3.0 \pm 0.82	1.0 \pm 0.82	1.0 \pm 0.00	0.0 \pm 0.82	0.0 \pm 16.3
	Tumon	4.5 \pm 0.58	4.5 \pm 0.58	0.3 \pm 0.50	0.3 \pm 0.50	0	0
Yellowstripe goatfish	Achang	4.8 \pm 1.50	4.8 \pm 2.06	3.0 \pm 0.82	1.3 \pm 2.50	-1.8 \pm 1.89	1.5 \pm 5.8
	Piti	4.5 \pm 1.73	5.0 \pm 2.71	0.5 \pm 0.58	1.5 \pm 0.58	1.0 \pm 1.15	15.6 \pm 19.4
	Tumon	4.5 \pm 0.58	4.5 \pm 0.58	0	0	0	0
Orangespine unicornfish	Achang	3.5 \pm 1.73	4.8 \pm 2.22	0.5 \pm 0.58	1.8 \pm 0.50	1.3 \pm 0.50	23.8 \pm 2.5
	Piti	9.0 \pm 4.08	9.5 \pm 1.73	1.8 \pm 1.26	3.8 \pm 1.71	2.0 \pm 0.82	17.2 \pm 6.5
	Tumon	4.0 \pm 1.63	5.8 \pm 3.10	0.5 \pm 0.58	2.3 \pm 1.71	1.8 \pm 2.06	23.4 \pm 33.4
Little spinefoot	Achang	9.8 \pm 2.22	9.3 \pm 2.99	2.8 \pm 0.50	2.3 \pm 1.26	-0.5 \pm 1.00	-5.8 \pm 8.3 ^a
	Piti	6.8 \pm 2.22	9.5 \pm 3.32	1.3 \pm 0.50	4.0 \pm 0.82	2.8 \pm 1.26	24.5 \pm 7.7 ^b
	Tumon	7.8 \pm 1.50	7.0 \pm 2.58	1.8 \pm 1.71	0.8 \pm 0.50	-1.0 \pm 1.63	-11.6 \pm 20.5 ^a



pomus spp. after <10 years of protection (reviewed in Evans and Russ, 2004). In Kenyan MPAs, complete recovery of fish populations was estimated to take 22 years (McClanahan and Graham, 2005). Other studies have reported more rapid buildup of biomass. Biomass of five commercially exploited fish families tripled within three years of implementation of the Soufriere Marine Management Area in St. Lucia (Roberts et al., 2001). Biomass of reef fish in another MPA in St. Lucia, Anse Chastanet Reserve, doubled within two years of effective protection (Roberts and Hawkins, 1997) and a similar, rapid buildup of biomass was observed in a small MPA in Saba (Roberts, 1995). Rates of biomass buildup inside MPAs should generally be consistent with life history characteristics of the fish (Russ and Alcalá, 1996; Mosquera et al., 2000; Alcalá et al., 2005). Large predators (e.g., epinepheline serranids [large groupers], Lutjanidae, Lethrinidae, and Carangidae) and many Acanthuridae (surgeonfish) are long-lived, often with low rates of natural mortality and recruitment. Such characteristics would indicate that recovery rates would be gradual, as observed by Evans and Russ (2004) and Alcalá et al. (2005).

In this study, it was not possible to determine the rate of biomass buildup because data were not collected at the initial implementation of the MPAs or at the initiation of full enforcement. After approximately 2.5 years of protection, biomass of all five study species of reef fish was higher within the MPAs than in fished sites, although the difference was not statistically sig-

nificant at the 95% confidence level for yellowstripe goatfish. A longer period of protection may result in greater biomass differentials between the marine preserves and fished sites. Biomass of all three species of herbivores was significantly higher within the MPAs, indicating that fishing pressure on herbivores in Guam is sufficient to show a biomass increase within no-fishing zones. Thus, increasing herbivore biomass on exploited reefs through spillover from MPAs may have the potential to reduce algal overgrowth, at least within a limited area adjacent to the MPA.

Given rapid population turnover, coupled with high fishing effort in the reference areas, significantly higher biomass in the MPAs may be evident after only 2–3 years of protection. All the species in this study are small to medium-size fishes with rapid growth and maturation rates (Choat and Robertson, 2002). What is somewhat surprising is that the densities of convict surgeonfish, yellowstripe goatfish, and little spinefoot were all significantly higher in the Tumon MPA than at the adjacent fished site, given that these species were legally targeted by subsistence fishermen within the MPA. However, the regulations stipulate that fishing with hook-and-line or cast net only and from shore or the exposed reef margin only. Moreover, fishermen in Tumon would have to contend with large numbers of tourists in the immediate vicinity, and fishing effort appeared low throughout the course of this study.

Several studies indicate that MPAs connected to fished areas by continuous reef will have higher rates of spillover (e.g., Kaunda-Arara and Rose, 2004). In this study, the highest overall spillover to surrounding fished reefs occurred from Piti, where the MPA and fished site are connected by a continuous reef flat. This was the only site at which no net inward movement of any species occurred. Fishermen were often seen along the boundary of the marine preserve, no doubt “fishing the line” in hopes of catching larger fish emigrating from the Piti MPA. When species were combined, the lowest rate of net flux occurred at Tumon. The fished site to the east of Tumon was at Tanguisson. These two bays are divided by a high, rocky headland (Punta Dos Amantes) with no reef flat. A sewage outfall just north of Punta Dos Amantes also separates the MPA and fished site. However, three of the five study species appeared to move freely between Tumon and Tanguisson—only yellowstripe goatfish and honeycomb grouper did not. Thus, the low overall rate of net flux was caused by the net import of convict surgeonfish and little spinefoot that balanced the net export of orangespine unicornfish. The overall spillover from Achang to Cocos Lagoon was also low, perhaps partly because these areas are separated by a wide tidal channel to the west of the Achang reef flat. However, the low mean spillover from Achang occurred because of the large number of adult yellowstripe goatfish moving into the MPA. These results demonstrate the importance of determining spillover at the species level. Because different species can vary in their market value, the mean spillover of all fishes from an MPA may not be

indicative of the net value of fish moving from MPAs to fished reefs.

The results of this study demonstrate that large, mobile herbivores like orangespine unicornfish may be exported from MPAs. The high rates of spillover for this species may result in part from its larger size in relation to the other species. In general larger fish have larger home ranges (Kramer and Chapman, 1999). In this study, the percentage of biomass exported from a given MPA tended to be higher than the percentage of individuals exported, indicating that spillover was primarily accomplished by larger fish. However, some acanthurids are known to be very site attached (e.g. Bell and Kramer, 2000; Meyer and Holland, 2005). For example, the larger congener (*N. unicornis*) is very site attached, and Meyer and Holland (2005) found little evidence for spillover of this species from a small (0.34 km²) no-take marine reserve in Waikiki, Hawaii. Movements of adult *N. vlamingii* across the boundaries of Apo Island marine reserve are rare, but density-dependent interactions within the reserve are sufficient to displace smaller fish from the reserve (Abesamis and Russ, 2005). In a separate study, no cross-boundary migration was found for three other acanthurids: *Acanthurus nigricans*, *Ctenochaetus striatus*, and *N. unicornis* (M. Tupper, unpubl. data). Convict surgeonfish showed notable spillover (14–22% of tagged biomass) at Achang and Piti, but showed a net import of 20% of tagged biomass into Tumon. Similarly, yellowstripe goatfish showed net import to Achang and net spillover from Piti. These species tended to form large, mobile foraging schools at all locations. The spatial variation in movement of these two species may be a function of foraging or spawning movements constrained or modified by natural physical barriers (channels or headlands) and possibly anthropogenic barriers (e.g., the sewer outfall south of Tanguisson). For example, net inward movement of yellowstripe goatfish to Achang may be related to a spawning aggregation of this species located in Asgadoo Channel, in the center of the Achang MPA (M. Tupper, unpubl. data). Alternatively, the disparity in direction of net movement at different sites may be simply explained by large ranging schools that happened to be tagged inside but recaptured outside the MPA at one location and vice versa at another. As might be expected, the honeycomb grouper, a small, sedentary, ambush predator, showed very low rates of spillover; no net movement in either direction was found at any of the study sites.

Movement across MPA boundaries may occur as a result of random dispersal of fish during their routine activities, directed dispersal due to migration or ontogenetic habitat shifts (Gerber et al., 2005), or emigration in response to density dependence. High densities of conspecifics in MPAs may lead to increased juvenile mortality (Goeden, 1979; Tupper and Juanes, 1999), decreased growth (Béné and Tewfik, 2003; Tewfik and Béné, 2003), or increased emigration, or to a combination of all three (Tupper and Juanes, 1999; Abesamis and Russ, 2005). In this study, there was no relation

between density and spillover of reef fish. This may have been due to fact that the density of fish in Guam's MPAs has not yet reached carrying capacity, i.e., the biomass within the MPAs is not yet representative of virgin, unfished stocks. It should be noted that pooled species and locations were used in the regression analysis. More data on individual species and locations would result in a more powerful test.

In conclusion, rates of adult import or export from MPAs appear to result from a combination of foraging behavior, potential spawning movements, and random daily movements across MPA boundaries. These movements were influenced by reef topography. Spillover was highest in areas joined by continuous fringing reef systems and lowest where reefs were separated by a headland barrier. Knowledge of fish movement patterns with respect to reef topography may be useful for choosing MPA boundaries in order to maximize the spillover of target species. The herbivorous orangespine unicornfish showed the highest rate of spillover from MPAs, which indicates that MPAs have the potential to provide herbivore biomass to adjacent fished areas which may be suffering from algal overgrowth due to fishing of herbivores and from nutrient input due to agricultural activities. However, given the declines in density of exploited fishes at the fished sites since the implementation of the MPAs (Gutierrez¹), it is evident that overall spillover has not yet been sufficient to increase fish biomass on adjacent reefs. This is not surprising, given the relatively short time since the implementation of these MPAs and the displacement of fishing effort from the MPAs to adjacent fished areas. Although spillover rates of four out of five study species were quite low, adult migration is only one process that may benefit fisheries. Further research is needed to determine the role of MPAs in enhancing larval supply and the transport of recruits from Guam's MPAs to adjacent fished areas.

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¹ Gutierrez, J. 2004. Personal commun. Division of Aquatic and Wildlife Resources, 163 Dairy Road, Mangilao, Guam 96910.

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