Research

Periodic Closures as Adaptive Coral Reef Management in the Indo-Pacific

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ABSTRACT. This study explores the social, economic, and ecological context within which communities in Papua New Guinea and Indonesia use adaptive coral reef management. We tested whether periodic closures had positive effects on reef resources, and found that both the biomass and the average size of fishes commonly caught in Indo-Pacific subsistence fisheries were greater inside areas subject to periodic closures compared to sites with year-round open access. Surprisingly, both long-lived and short-lived species benefited from periodic closures. Our study sites were remote communities that shared many socioeconomic characteristics; these may be crucial to the effectiveness of adaptive management of reef resources through periodic closures. Some of these factors include exclusive tenure over marine resources, a body of traditional ecological knowledge that allows for the rapid assessment of resource conditions, social customs that facilitate compliance with closures, relatively small human populations, negligible migration, and a relatively low dependence on fisheries. This dynamic adaptive management system, in which communities manage their resources among multiple social and ecological baselines, contrasts with western fisheries management practices, centered on maintaining exploited populations at stable levels in which net production is maximized.

Key Words: *adaptive management; coral reefs; socioeconomic; periodic closures; traditional management; social-ecological systems*

INTRODUCTION

Coral reefs are one of the most productive and biologically diverse environments on Earth (Paulay 1997, Reaka-Kudla 1997). Most reefs occur in developing nations in which they are often heavily relied upon as a source of food and, in many cases, economic development. Growing coastal populations and increased resource extraction rates have put coral reefs at a high risk of catastrophic biodiversity loss, which would likely have severe consequences for the productivity of these systems and the human populations that depend upon them (Wilkinson 2002, Hughes et al. 2003, Hooper et al. 2005). As a result, developing effective management strategies for coral reefs has become one of the foremost challenges confronting conservation scientists and managers.

One of the primary extractive activities on reefs is fishing. Two general categories of management strategies have been implemented or proposed for coral reef fisheries (Polunin and Roberts 1996). First, borrowing from conventional fisheries management common in developed nations, various combinations of gear restrictions, size limits, catch quotas, temporal restrictions during vulnerable life stages, e.g. spawning aggregations, and other methods of effort reduction, e.g., permitting, alternative income projects, etc., have been attempted or suggested as solutions. However, such complex measures are difficult to administer or enforce in developing nations and; therefore, they frequently prove to be of limited utility (Russ 2002). As an alternative, a second management strategy has been proposed by a number of scientists and conservation practitioners, establishing networks of fully protected marine reserves within which extractive activities are prohibited (Hall 1998, Fogarty 1999). Efforts to establish reserves in developing nations have faced a variety of problems. For example, closed areas often displace or marginalize subsistence fishers, resulting in increased conflict over marine resources (Christie

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2004). As a result, the use of fully closed reserves as fishery management in developing countries has, at present, achieved limited success (McClanahan 1999, Pollnac et al. 2001).

At first glance, conventional techniques and marine reserves appear to differ considerably in their approach to fisheries management, but both are based on a similar principle, i.e., harvesting "surplus" production (Guénette et al. 1998, Caddy 1999). Caddy (1999) has argued that surplus production theory arose in the 1930s and has formed the basis for the overriding concept in conventional management, maximum sustainable yield (MSY). Generally, regulations seek to control fishing effort or catch characteristics, e.g., fish size, such that population size/biomass is maintained at a predetermined level that produces the greatest surplus of harvestable biomass and; therefore, provides the greatest benefit to the fishery. Marine reserves function similarly, for they allow population size and biomass to increase to, and be maintained at, the natural carrying capacity of the reserve habitat (Guénette et al. 1998). Excess production from the reserve population, whether in the form of adult spillover or export of larvae, can theoretically be harvested by adjacent fisheries (Russ 2002). Although the goals are different, both management approaches assume, or seek to achieve, a stable population equilibrium, a concept that has created considerable discussion (Earn and Rohani 1999, Lloyd and May 1999).

One potential alternative is a dynamic cycle of prohibiting and allowing harvesting within prescribed areas. Such periodic closures of tropical marine resources are well documented in traditional societies (Johannes 1982, Hviding 1996, Ruttan 1998, Colding and Folke 2000, 2001, Aswani and Weiant 2004), but the ecological consequences of these practices on coral reef ecosystems are not well understood. As a result, periodic closures are rarely used in conventional coral reef management, and we know little about the ability of such techniques to manage reef fisheries, conserve reef resources, or protect biodiversity.

Our recent research has integrated social and biological sciences to explore resource use and customary management in Melanesia in the modern conservation context (Cinner et al. 2005*ab*, Cinner and McClanahan, *in press*). In this paper, we attempt to build upon these studies by presenting two case studies of the ecological and socioeconomic context in which traditional periodic closures operate: one from a village in the Madang Province of Papua New Guinea, and another from a village in North Sulawesi, Indonesia. Our goals were: (1) to examine whether and how periodic closures influence reef resources; (2) to examine how these systems may differ from conventional fisheries management and conservation models; and (3) to identify the social, economic, and cultural mechanisms that may influence the ability of communities to successfully manage their resources through periodic closures.

BACKGROUND AND STUDY SITES

Cultural context of resource governance

Some communities in the Indo-Pacific use customary marine tenure to prevent "outsiders" from exploiting resources (Malinowski 1922, 1935, Hviding 1983, Polunin 1984, Wright 1985, Carrier 1987, Hviding 1996, Mantjoro 1996, Ruttan 1998, Aswani 1999, Aswani 2002, Johannes 2002*a*). Additionally, some communities have certain practices, beliefs, and dietary restrictions that limit their own resource use. Together, these practices have been variously termed "traditional management," "taboos," "folk management," and "local management" (Dyer and McGoodwin 1994, Pollnac and Johnson 2005), and can take a variety of forms: banning a particular type of harvesting gear (Hviding 1996, Johannes 1981, 2002*b*), temporal or seasonal harvesting restrictions (Hviding 1996, Johannes 1978), gear-restricted areas that are occasionally harvested (Cinner et al. 2005*a*), and periodic closures (Hviding 1983, Polunin 1984, Wright 1985). A considerable amount of ethnographic work has focused on describing the historical and cultural mechanisms that have led to these practices. Our goal was to build on this previous work by exploring these issues using a different approach: synchronic socioeconomic and ecological research.

Due to the high cost of providing Self Contained Underwater Breathing Apparatus (SCUBA) support for ecological research in remote locations, we were restricted to 10 d of data collection at each of our two field sites. A key limitation of this time-restricted approach is that some important historical and cultural processes that may take ethnographers years to unravel, e.g., genealogies, could not be explored. We acknowledge that synchronic

research does have limitations in this type of study, but hope that the insights gained by simultaneously investigating socioeconomic and ecological data outweigh the costs of our inability to incorporate the diachronic research typically used in sociocultural studies of traditional management.

Kakarotan, Sangihe-Talaud Archipelago, North Sulawesi, Indonesia

Kakarotan Island, in the northernmost reaches of the Sangihe-Talaud archipelago, is a small coral cay with a population of approximately 730 people in 144 households (Fig. 1). A system of periodic reef closures called *mane'e* is practiced; each year, one of nine reef areas is closed for a period, and then opened to harvest fish for a traditional ceremony. The *mane´e* practice starts with a taboo on all fishing activities within one area (Fig. 1). The taboo generally lasts for six months, although this can vary with social and ecological concerns. Site selection and duration of the taboo are decided during a meeting of the community's traditional leaders. There appeared to be no systematic method for selecting which area would be closed, although the location of the closure was said to frequently switch between sites from year to year. In recent years, one the largest *mane'e* areas, (~ 50 ha) had been closed several times. The boundaries of this largest area ranged from the shoreline to the bottom of the reef slope. During the lowest tide of a specified month, the community collectively harvests the closed area to provide fish for a large feast.

The origin of this practice and the original purpose of the feast were unclear, and community leaders and elders cited tradition as the dominant factor (this is not uncommon, see Berkes et al. 2000, Pollnac and Johnson 2005). Observing the annual harvest and participating in the feast has recently become an attraction for Indonesians from the Sulawesi mainland, and attracting these tourists was cited as a secondary reason for the closure. Sanctions exist for violations of the taboo; a warning is given on the first offense and a fine on the second. Most *mane'e* areas are clearly visible from the community, and fishers tended to fish in groups of 10-20 canoes, thereby making it difficult for individuals to break community rules and increasing the chance of their detection and reporting. At the time of our study, the closure was not in effect and extractive activities were permitted in the *mane'e* area. Our research in Kakarotan occurred over 10 d in September 2002.

## Muluk Village, Karkar Island, Madang Province, Papua New Guinea (PNG)

The Muluk community, on the eastern side of Karkar Island, consisted of approximately 330 people in 50 households (Fig. 1). Muluk claims exclusive-use rights over reefs along the entire coastline adjacent to their village and the neighboring village of Wadau. In Muluk, management consists of closing approximately 58 ha of reef adjacent to the village for 1-2 yr, whenever the village chiefs notice that the fish catch is declining. Chiefs cited their own fishing experience, their observations of low catches at landing sites by other fishers, and reports by fishers that fish were remaining "too far away" as ways that they "noticed" declining catches. The explicitly stated reason for periodic closures was that fish "would become easier to catch" after some period of closure, particularly while spearfishing. Resource users explained that when heavily fished, reef fishes altered their behavior such that they remained farther away from fishers, and were therefore more difficult to catch. By periodically closing the resource to extractive activities, it was thought that reef fishes would become more "tame," thereby allowing fishers to catch fish more effectively. The decision to close reefs is reached through a consensus between the three clan-chiefs. The reef closure in Muluk generally occurred 2-3 times within a 10-yr span. At the time of our study, the area had been closed for approximately 6 mo. Key informants were unclear as to when this periodic closure system began, but could confirm its presence for at least 60 yr. Our research in Muluk occurred over 10 d in December 2001.

METHODS

Assessment of reef resources

To test for effects of periodic closures on biological resources, we compared three randomly-selected sites within the managed area to three control sites outside the managed area at Kakarotan, and five managed sites and five control sites at Muluk. At both Kakarotan and Muluk, control sites were within 1.5 km of the managed area boundary. We used timed swims to estimate fish species richness, and we conducted line transects to obtain quantitative information on fish biomass, fish size, fish abundance, substratum composition, e.g., hard coral cover, etc., coral recruitment, abundance of

Fig. 1. Map of study sites and periodic closures areas.
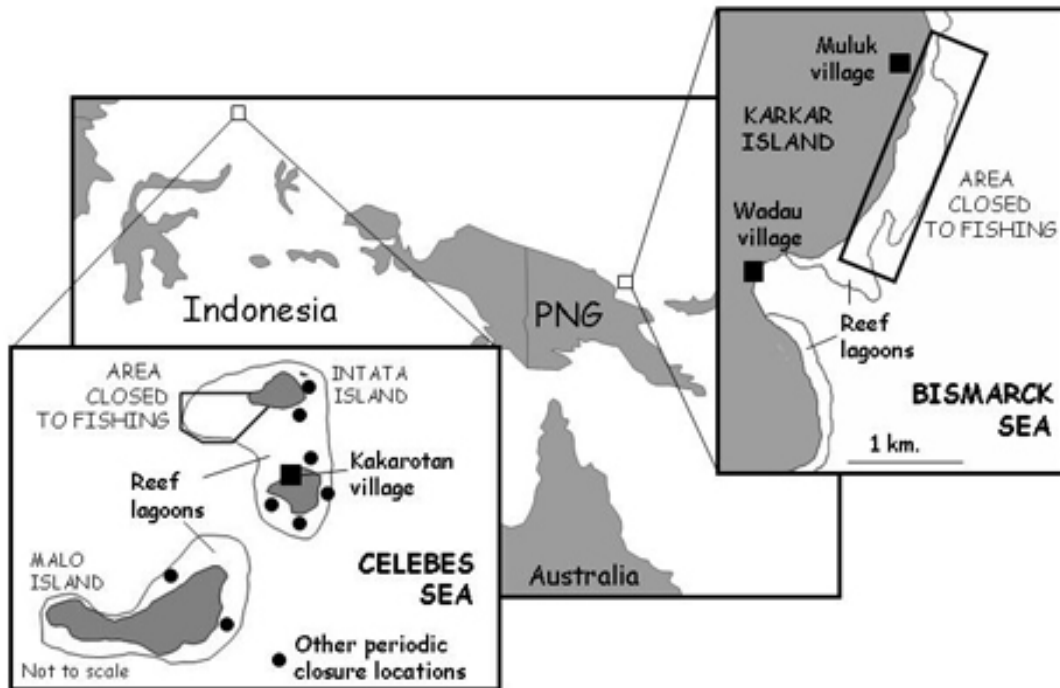
giant clams (*Tridacna* spp.), recent damage to coral from human activities, and the amount of discarded fishing gear. Giant clams were a focus of study because they are heavily exploited in this region, and a few species have been reduced to near extinction levels (Villanoy et al. 1988, Green and Craig 1999). Due to the limited time at each site, we were not able to study the seasonal patterns of fish or fish catch, but other more detailed studies have found that tropical benthic or reef fisheries exhibit low seasonality (McClanahan and Mangi 2000, Pet-Soede 2000).

To estimate total fish species richness, we randomly selected one starting point within the managed area and one starting point outside the managed area, and we recorded all noncryptic fish species encountered during a 1-hr swim on SCUBA. Cryptic fishes from four families, Apogonidae (cardinalfishes), Blenniidae (combtooth blennies), Gobiidae (gobies) and Tripterygiidae (threefin blennies) were excluded from our analyses. The path of the timed swim followed a haphazard, zigzag pattern on the reef to include all reef habitats from the shallow reef flat to the deeper reef base. Total survey area both within and outside the managed area was approximately 3.5 ha. We identified species based on descriptions and nomenclature of Allen and Swainston (1993), Randall et al. (1997), Myers (1999), and The International Center for Living Aquatic Resources

Management: ICLARM Fishbase 2000 (Froese and Pauly 2000), and used the coral fish diversity index (CFDI) (Allen and Werner 2002) to quantify species richness.

At each of the six survey sites at Karkarotan and the 10 survey sites at Muluk, we recorded densities of all noncryptic species along three 50 m belt transects, placed haphazardly at two depths, i.e., 3 m and 7 m. On each transect, we surveyed sedentary damselfish (Pomacentridae) within a 2 m-wide belt, and the remaining families within a 5 m-wide belt. We used discrete group sampling (DGS) to record fish abundance (Greene and Alevizon 1989); four passes were made over each transect, and during each pass we noted the abundance of fish from particular groups: Group 1: Pomacentridae, Group 2: Labridae (wrasse), Group 3: Acanthuridae (surgeonfishes), Scaridae (parrotfishes) and Siganidae (rabbitfishes), and Group 4: Balistidae (triggerfishes), Caesionidae (fusiliers), Chaetodontidae (butterflyfishes), Haemulidae (grunts), Lethrinidae (emperors), Lutjanidae (snapper), Nempteridae (threadfin breams), Pomacanthidae (angelfishes), and Serranidae (sea basses). We only recorded those fish that had a total length (TL) of >3 cm to reduce the difficulties associated with sampling small juveniles, and the influence of sporadic recruitment episodes on abundance estimates. Surveys at 3 m depths were conducted while snorkeling, whereas surveys at 7 m were conducted using SCUBA. We used species-specific values from FishBase 2000 (Froese and Pauly 2000) to calculate mean trophic levels.

We examined the size structure of fish populations from the four groups along each 50 m transect during two passes along each transect. On the first pass, we recorded all fishes ≥ 10 cm total length (TL) within a 5 m-wide belt. On the second pass, we recorded all fishes ≤ 10 cm TL within a 2 m-wide belt. We identified and pooled all reef fishes and reef-associated fishes into family-level groupings, with relatively uncommon families grouped into a single "other" category. Each individual was assigned to one of five size categories: 3-5 cm, 5-10 cm, 10-20 cm, 20-30 cm, and 30-40 cm. Size estimates of fish > 40 cm and fish of unusual shape, e.g., trumpetfish (Aulostomidae), were recorded to the nearest 1 cm to allow for more precise biomass conversions. For each family, we used representative length-weight conversions, obtained from FishBase 2000 (Froese and Pauly 2000) to convert size-frequency data into biomass data. For fish in the five size classes, we

used the midpoint of the size class in biomass calculations. Whenever available, we used species-specific formulas to calculate biomass for fish > 40 cm TL and fish of unusual shape.

We validated the accuracy and precision of underwater size estimates every 2-3 d by testing the ability of observers to correctly estimate the length of sections of PVC pipe. At each new site, 10 sections of numbered PVC pipe were placed underwater on a length of rope with attached weights. Observers estimated the length of each section and recorded its number from a distance of 5 m, and we compared estimates to actual lengths. Estimates were generally within 10% of the actual lengths.

We estimated benthic cover composition at each site along 18 standard line-intercept transects (McClanahan and Shafir 1990), each of which had a length of 10 m. We placed all transects parallel to the reef crest, with three transects laid flat along the reef two meters shoreward of the crest, three transects along the crest, and three transects on the reef slope at a depth of 2-3 m. A further nine transects, three at each depth, were surveyed on the reef slope at 6 m, 7 m, and 8 m. We recorded the type of benthic cover and linear distance occupied by each cover category along each transect. Benthic cover categories were as follows: hard coral, soft coral (alcyonaceans), sponges, sea grasses, gorgonians (gorgonaceans), zooanthids, anemones, ascidians, bryozoans, fleshy algae, turf algae, encrusting red algae, coralline algae, and sand. We identified hard corals, including the octocorals *Heliopora*, *Millepora* and *Tubipora* spp., to genus based on descriptions and the nomenclature of Veron (2000), and fleshy algae to species based on Allen and Steene (1994). To estimate coral diversity at each site, we used data on the cover of hard coral genera along line-intercept transects to calculate a Simpson's diversity index where diversity, *D*, is calculated as:

$$D = 1 - \sum (n_i/N_t)^2$$

Where n_i is the cover of the individual genera and N_t is the total coral cover (Magurran 2004).

We recorded the abundance of giant clams (*Tridacna* spp.) along four 1 m x 100 m belt transects at each site, each laid flat along the reef, approximately 20 m shoreward of the reef crest. We used 0.0625 m^2 quadrats to examine the density of

coral recruits, defined as colonies between 0.5-5 cm in diameter, per unit area. To assess the effect of fishing activities on reefs, we recorded the presence of discarded fishing gear, including nets, fishing lines, and spears, along the same transects that were used for benthic cover and giant clam surveys. We also recorded recent coral damage, defined as pieces of coral broken off the main colony, but still alive, and recently upturned corals along these transects. There had been no recent storm activity in either of the study areas, so we assumed that coral damage was due to human activities. We noted corals damaged by fishes, e.g., humphead parrotfish (*Bolbometapon muricatum*), and excluded them from analyses.

To aid in comparisons with other studies, we converted ecological data into standard units such as ha or m^2. Measures of variability were based on these converted units and not on the original units of measure. We used MANOVA to compare managed areas and control areas. When variables did not meet the assumptions of normality, we used a nonparametric Mann Whitney U-test (Siegel and Castellan 1988).

Assessment of catch composition

To determine the types of fishes targeted by fishermen and the types of gear used for their collection, we examined catch composition at Kakarotan over 10 d. We observed a total of 1405 reef-associated fishes and used a digital camera (Sony DSC P-1, 3.3 megapixel) to record catch composition for use in species determination (Cinner and McClanahan, *in press*). We were unable to collect similar data at Muluk, because fishers were targeting a seasonal abundance of non reef-associated fishes (flyingfishes [Exocoetidae]) during our observation period and, thus, harvesting from the reef was minimal. Fishers suggested that fishing activities would regain focus on reef fishes once the abundance of flying fish had declined.

Assessment of socioeconomic factors

We used a combination of household surveys, key informant interviews, oral histories, and participant observation in resource use activities to gather information on fishing pressure, occupational diversity, immigration, governance of coastal resources, and awareness of and compliance with closures. We used the methods described by Henry (1990) to systematically sample 59 of the 144 households in Kakarotan, and we opportunistically sampled 41 of the 50 households in Muluk.

Questions in household surveys were directed toward the head of the household, i.e., male, female, or both depending on who was present at the time of the interview. We determined participation in fishing, agriculture, and other occupations by asking respondents to rank the occupations of their household from most to least important (Pollnac and Crawford 2000). We estimated fishing pressure by asking respondents how many days per week, on average, did each member of the household engage in specific fishing activities. We attempted to account for potential variation in seasonality of resource use activities by asking respondents about their activities in both the high and low fishing seasons, asking key informants about the average duration of the each season and averaging the total number of days for both seasons based on season length. We extrapolated these data to estimate the total fishing pressure on reef resources for each community. We used a finite population correction factor, which adjusts for error based on the proportion of the community surveyed (Scheaffer et al. 1996), to calculate errors for quantitative socioeconomic variables.

Depending upon the needs of a study, migration status can be defined in a variety of ways, including whether a person was born in another village or province, or belonged to a different language group, etc. Since use rights to marine resources in Papua New Guinea are often primarily delineated at the village level, we defined immigrants as individuals born in other villages.

We assessed awareness of closures by asking the fishers in our sample if there were places in which people were not supposed to fish. Fishers were asked to provide descriptive details of any places they mentioned. For the purposes of this question, we considered respondents fishers if they ranked fishing among their household's four most important occupations or livelihood strategies. To assess compliance with closures, we then asked fishers if people still fished in the closure area. We grouped their response to the compliance question into four ordinal categories: (1) nobody fishes there, (2) a few people fish there, (3) many people fish there, and (4) almost everybody fishes there.

We used participant observations, oral histories, and five key informant interviews at each site, including fishers, traditional leaders, and elected officials to verify the accuracy of household survey responses and to gain a better understanding of the context of coastal resource use and management. We selected key informants using nonprobability sampling techniques, including convenience sampling, e.g., a respondent was approached when observed returning from fishing, or snowball sampling, i.e., community members suggest appropriate respondents. Resource user key informants were individually interviewed, although community leaders and elders were usually interviewed in the presence of others. Oral histories and key informant interviews consisted of open-ended questions used to probe respondents about specific fishing practices, why and how the closures were implemented, and the origin of the closure practice.

Size of fishing grounds

We calculated the areas of shallow-water fishing grounds, i.e. reef, sand, and seagrass, in Muluk by digitally tracing the edges of the reef, corresponding approximately to the 10 m depth contour, on a 1:100,000 aerial photograph, and calculating the area with the UTHSCSA Image Tool 2.0 (University of Texas Health and Science Center, San Antonio, USA). For Kakarotan, we estimated the area of the fishing grounds using a nautical chart, because we were unable to obtain aerial photographs or satellite images.

RESULTS

Reef resources

At both Muluk and Kakarotan, the biomass and the average lengths of targeted fishes were greater inside the managed area compared to control sites (Table 1). At Muluk, both fish biomass and average size were 25% greater, and families with greater biomass included Lutjanidae (snappers), Lethrinidae (emperors), Acanthuridae (surgeonfishes), Serranidae (sea basses) and Siganidae (rabbitfishes) (Table 2). At Kakarotan, fish biomass was 37% greater, average size was 17% greater, and families with greater biomass included Scaridae (parrotfishes), Pomacanthidae (damselfishes), Serranidae, Haemulidae (sweetlips), Nemipteridae (threadfin breams) and

Balistidae (triggerfishes) (Table 3). Families responding positively to closures have a range of life histories and included a substantial number of relatively long-lived species with low population doubling times (Tables 2 and 3, Appendices 1 and 2).

The mean trophic level of fish communities was greater inside the managed area at Muluk relative to control sites, but did not differ at Kakarotan (Table 1). At Muluk, the abundance of giant clams was significantly greater within the managed area, whereas coral recruitment and the amount of recent damage to corals were both lower within the managed area. No significant differences in any other ecological variables were detected between managed and control sites at either Muluk or Kakarotan (Table 1).

Catch composition

Spear guns, nets, and lines caught 84%, 14%, and 2%, respectively, of the 1405 fish captured by fishers at Kakarotan during our survey period. Although 28 fish families were represented in the catch, two families dominated, i.e., Acanthuridae, 50% of the catch, and Scaridae, 31% of the catch. Balistidae and Serranidae accounted for 3.4% and 2% of the catch, respectively (Table 4).

Socioeconomic factors

Livelihood strategies at both Kakarotan and Muluk were similar (Fig. 2). In both communities, households engaged in a range of livelihood activities. Kakarotan averaged 3.9 (3.7,4.1) occupations per household (mean ± 95% CI), and Muluk averaged 3.3 (3.2, 3.4). Over 85% of households in both communities engaged in some fishing activity, but few households ranked fishing as their primary livelihood strategy. Agriculture was the primary occupation for most households in both communities, and in Kakarotan, over 80% of the households engaged in informal economic activities, such as weaving mats or owning a small shop.

Immigration to both communities was low: 7.5% of the respondents had immigrated to Muluk and 2.1% had immigrated to Kakarotan. Community participation and interaction was high: 96% of the Kakarotan households and 62% of the Muluk

Table 1. Comparison of ecological variables inside and outside periodic closure areas.

	Muluk						Kakarotan					
	Inside	SE	**Outside**	SE	*F*	*P*	**Inside**	SE	**Outside**	SE	*F*	*P*
Target fish spp. average size (cm total length)	11.1	0.2	8.9	0.3	28.8	**0.001**	10.3	0.3	8.9	0.2	13.8	**0.02**
Average fish trophic level (by weight)	2.7	0	2.5	0	3.3	**0.001**	2.4	0	2.3	0.1	4.2	NS
Coral recruits (density per m^2)	4.7	0.4	7.6	0.7	12.7	**0.007**	1.1	0.4	0.4	0.1	2.6	NS
Target fish spp. biomass (kg/ha)	377.6	12.2	301.1	28.4	6.1	**0.038**	139.1	4.6	101.3	10.4	11.1	**0.03**
Discarded fishing gears (density/ha)	11.1	11.1	44.4	11.1	4.5	0.07	2.9	2.9	79.8	43.7		**<0.05**^{U}
Giant clams (density/ ha)	410	288	0	0		**0.01**^{U}	316.7	120.2	450	104.1	0.7	NS
Recently damaged coral (% of live coral cover x 10^{-3})	0	0	1.1	0.2		**0.01**^{U}	8.6	6.1	0	0		NS^U
Dominant coral genera	Acropora		Porites			NA	Porites		Porites			NA
Dominant coral genera (% of total hard coral cover)	29.6	2	31.4	4.5		NA	53.6	4.3	44.4	14.6		NA
Maximum # of coral genera	47		51			NA	37		35			NA
Target fish abundance (density/ ha)	3065.3	507.4	3004	395.4	0.1	NS	1971.1	112.8	2026.7	358.2	0.1	NS
Fish species richness per site (CFDI)	79.4	8	82.2	6.5	0.1	NS	82.3	3.78	87.3	5.2	0.6	NS
Hard coral % cover	35.3	4.2	40.8	4.5	0.8	NS	5.2	0.3	4	2.1	0.1	NS
Coral diversity (D)	0.8	0	0.8	0	0.9	NS	0.6	0.1	0.7	0.1	0.5	NS

households were involved in some type of community group, and 69% and 83% of households, respectively, were involved in community decision making.

Spear guns and line fishing comprised the majority of the fishing activity in both communities (Fig. 3).

There was approximately four times more gross fishing effort in Kakarotan (827 ± 197 fishing trips/ wk) as in Muluk (198 ± 24 fishing trips/wk). This difference was largely due to the higher population of Kakarotan, but there was also slightly higher fishing effort per household in Kakarotan (5.4 ± 1.3 fishing trips per household/wk) compared to Muluk

Table 2. Muluk: Results of the one-way ANOVAs for comparisons of biomass, inside vs. outside closures, and a summary of life histories and resilience to overfishing. Adapted from Froese and Pauly (1995) for families commonly caught in subsistence Indo-Pacific fisheries.

Family	*F*	*p**	Population doubling time	Resilience to overfishing
Lutjanidae	17.67	<0.01	Long	Low
Lethrinidae	11.40	<0.01	Long	Low
Acanthuridae	10.14	<0.01	Short-Long	Medium
Serranidae	-	<0.01[U]	Intermediate	Low
Siganidae	6.36	<0.05	Short- Intermediate	Medium -high
Balistidae	2.29	NS	Intermediate	Medium
Chaetodontidae	1.67	NS	Short	High
Labridae	0.92	NS	Intermediate -Long	Low- Medium
Nemipteridae	0.74	NS	Intermediate	Medium
Pomacanthidae	0.37	NS	Intermediate	Medium
Scaridae	0.11	NS	Intermediate-long	Intermediate-Low
Mullidae	-	NS[U]	Intermediate	Medium
Haemulidae	-	NS[U]	Long	Low

* In all cases, significant results indicate higher fish biomass inside managed areas than outside.
[U]data did not meet assumptions of ANOVA and were analyzed using Mann-Whitney U tests.
Population doubling time: Short = <15 mo, Intermediate = 1.4-4.4 yr, Long = 4.5-14 yr.

(4.0 ± 0.5). Kakarotan had access to 265 ha of fishing ground compared to 92 ha at Muluk. Therefore, fishing pressure relative to fishing ground area was relatively low in both communities with 3.1 trips/ha/wk in Karkarotan and 2.1 trips/ha/wk in Muluk.

Key informants in both communities noted that customary marine tenure institutions provided village leaders with the legal or *de facto* authority to prohibit outsiders from extracting resources from fishing grounds surrounding the villages and to prohibit everybody from extractive activities within periodic closure areas. Village leaders had the authority and autonomy to develop and adapt rules to change the location and duration of the closure to reflect ecological or social conditions. In considering where, when, and how long to implement periodic closures, decision makers appeared to use their understanding of social-ecological systems to interpret threshold levels of social and ecological indicators, commonly referred to as traditional ecological knowledge. For example, in Muluk, decision makers identified the key indicator as the distance a fisher could approach a targeted fish before the fish fled. When village chiefs perceived that this distance was large, i.e., fish did not allow a close approach, they placed a taboo on the reef for an undetermined period. When they perceived that this distance was acceptably small and fish were easier to catch, the taboo was lifted. In Kakarotan, more rigid social factors influenced where and when a taboo was placed. The occurrence of an annual feast largely determined the amount of time an area was closed, and other social

Table 3. Kakarotan: Results of the one-way ANOVAs for comparisons of biomass, inside vs. outside closures, life histories, and a summary of life histories and resilience to overfishing. Adapted from Froese and Pauly (1995) for families commonly caught in subsistence Indo-Pacific fisheries.

Family	F	p*	Population doubling time	Resilience to overfishing
Scaridae	46.49	<0.01	Short-long	Low-high
Pomacanthidae	9.28	<0.05	Short-Intermediate	Medium-High
Serranidae	-	<0.05[U]	Intermediate-Long	Low-Medium
Haemulidae	-	<0.05[U]	Long	Low
Nemipteridae	-	<0.05[U]	Short-Intermediate	Medium-High
Balistidae	-	<0.05[U]	Intermediate	Medium
Lutjanidae	1.31	NS	Intermediate	Medium
Lethrinidae	-	NS[U]	Long	Low
Acanthuridae	1.59	NS	Short-Long	Low-High
Siganidae	1.00	NS	Short	High
Chaetodontidae	2.13	NS	Short-Intermediate	Medium-High
Labridae	6.69	NS	Intermediate-Long	Low-Medium
Mullidae	2.09	NS	Intermediate	Intermediate

* In all cases, significant results indicate higher fish biomass inside managed areas than outside.
[U]data did not meet assumptions of ANOVA and were analyzed using Mann-Whitney U tests.
Population doubling time: Shor<15 mo, Intermediate = 1.4-4.4 yr, Long = 4.5-14. yr

factors such as whether government officials were expected to attend the feast, influenced which area was selected for closure. However, environmental conditions also influenced Kakarotan's taboo, as the traditional leader kept the area closed for an entire yr during 1998-1999, coinciding with a severe El Niño bleaching event.

Initiation ceremonies and village feasts help to remind people of the rules and embed the closures within the culture. For example, in Muluk, individuals were required to undergo an initiation ceremony before participating in the flying fish fishery. During the initiation ceremony, which we witnessed, elders recited the rules and discussed appropriate fisher behavior. In Kakarotan, the closure area was harvested to provide fish for an annual feast, which was said to be an important cultural event garnering extensive community participation. Consequently, awareness of reef closures in both communities was high; approximately 98% of fishers in Kakarotan and 79% of fishers in Muluk reported awareness of traditional spatial restrictions in their fishing activities. Reported and observed compliance with reef closures was reasonably high, particularly considering there were no active enforcement patrols. Almost 91% of Kakarotan fishers reported that few or no people violated closure rules. Reported compliance at Muluk was lower, with 52% of fishers reporting that few or no people violated closure rules. However, the lower incidence of discarded fishing gears inside managed areas at both Kakarotan and Muluk suggests that closures did reduce fishing effort (Table 1).

Table 4. Fish families caught in Kakarotan fishing activities.

Family	All gear	Speargun	Net	Line
Acanthuridae	50.4	48.6	65.8	15.4
Balistidae	3.3	3.6	1.0	7.7
Belonidae	0.1	0	0	3.8
Bothidae	0.1	0.1	0	0
Carangidae	0.4	0.2	0	11.5
Chaetodontidae	0.4	0.3	1.0	0
Diodontidae	0.3	0.3	0	0
Fistulariidae	0.1	0.1	0	0
Hemulidae	0.1	0.1	0	0
Holocentridae	1.9	2.1	0	3.8
Kyphosidae	0.9	1.0	0.5	0
Labridae	2.2	2.2	2.0	3.8
Lethrinidae	2.1	2.4	0.5	0
Lutjanidae	1.0	1.1	0	3.8
Monocanthidae	0.3	0.3	0	0
Mullidae	0.2	0.1	0	7.7
Nemipteridae	0.6	0.6	0	7.7
Ostraciidae	0.2	0.1	1.0	0
Pempheridae	0.1	0.1	0	0
Pomacentridae	0.4	0.2	1.5	0
Priacanthidae	0.1	0.1	0	0
Scaridae	31.4	33.0	26.1	0
Scombridae	0.2	0	0	11.5
Serranidae	2.0	1.9	0	23.1
Siganidae	0.5	0.5	0.5	0
Zanclidae	1.0	1.2	0	0
N	1405	1180	199	26

Fig. 2. Distribution of occupations in Muluk and Kakarotan, highlighting the proportion engaged as a primary occupation.
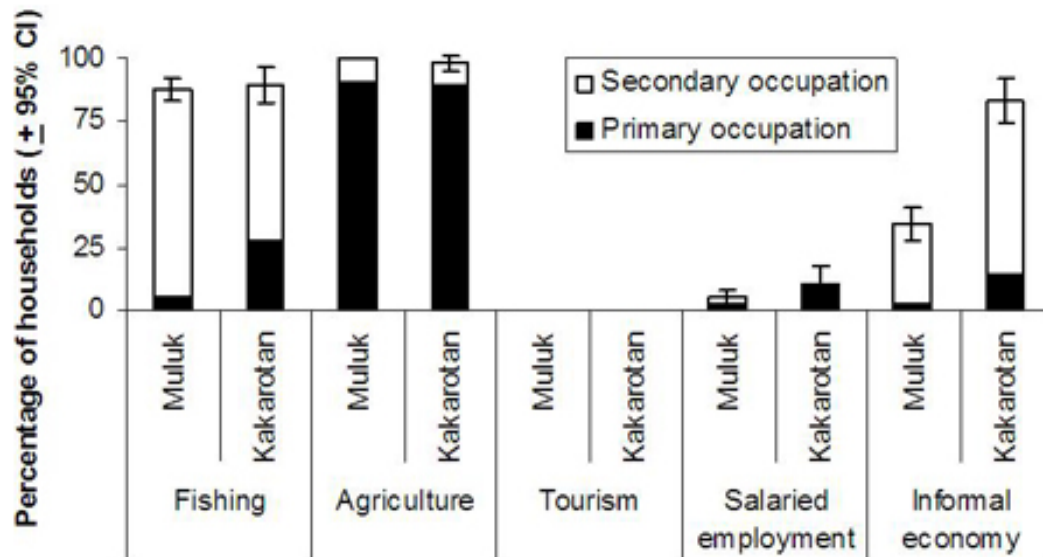

DISCUSSION

At both Muluk, Papua New Guinea, and Kakarotan, Indonesia, we found that the biomass and the average size of fishes commonly caught in Indo-Pacific subsistence fisheries were greater inside areas subject to periodic closures compared to sites with year-round open access. Surprisingly, both long and short-lived species benefited from periodic closures. Our study sites were remote communities that shared many socioeconomic characteristics; these may be crucial to the effectiveness of adaptive management of reef resources through periodic closures. Some of these factors include exclusive tenure over marine resources, a body of traditional ecological knowledge that allows for the rapid assessment of reef resources, social customs to bolster compliance with closures, a relatively low human population size, negligible migration, and a relatively low dependence on fisheries. This dynamic adaptive management system contrasts strongly with western fisheries management practices, centered on maintaining exploited populations at stable and high surplus production levels.

Fig. 3. Fishing trips/wk by gear type for Muluk and Kakarotan.
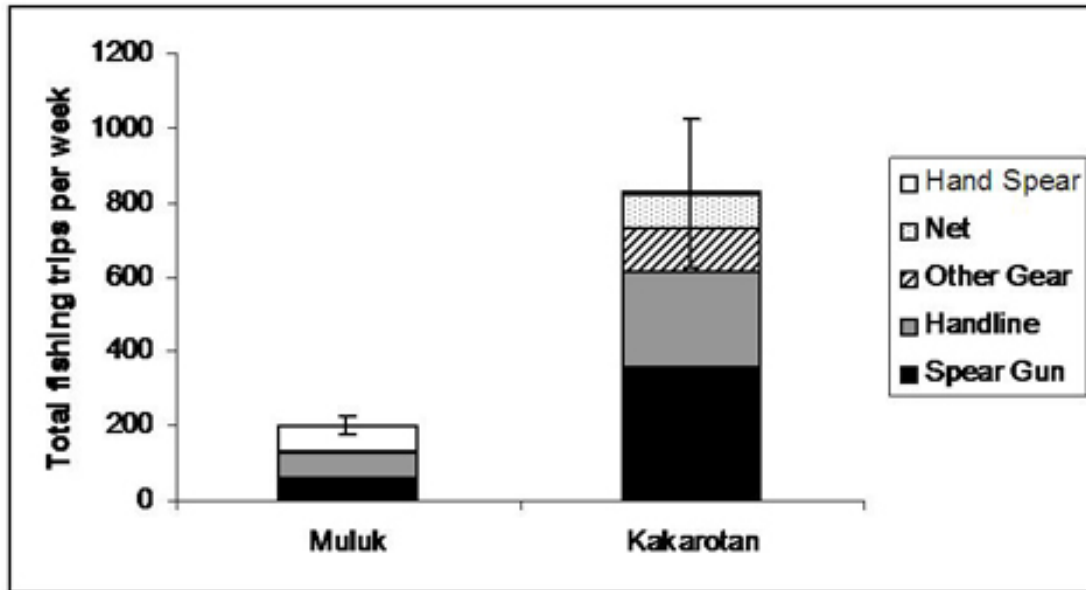
Effects of periodic closures on reef resources

This study suggests that periodic closures can have significant positive benefits for coral reef fisheries. In both Indonesia and Papua New Guinea, we found that fish biomass and average fish size were greater inside the managed areas relative to the openly-fished control sites. We did not detect any differences in abundance between managed and control sites. However, fish density was extremely variable among sites, a trend reported in a number of other studies (Russ and Alcala 1998*a*, Dulvy et al. 2004). Such variability in abundance among sites could make detecting any differences in abundance between managed and control sites difficult. Studies

of closed areas on coral reefs that have been opened to fishing show that fish biomass can be depleted rapidly, often within a few months (Russ and Alcala 1998*b*, McClanahan and Mangi 2000). In contrast, recovery to pre-exploitation levels can take years to decades (McClanahan 2000, Russ and Alcala 2004, McClanahan and Graham 2005), especially for species possessing life history characteristics that make them especially susceptible to fishing, including long-lived and slow-growing species with slow population growth rates. As a result, we predicted that periodic closures would most benefit species resilient to exploitation, i.e., short-lived and fast-growing species with fast population growth rates. Contrary to our expectations, we found that

both biomass and average size was greater inside managed areas for several families characterized by high longevity, low natural mortality, and low somatic and population growth.

Although this result demonstrates that the effects of periodic closures were long lasting, it does not explain why such species would benefit from this type of management. One likely explanation is that periodic closures reduce overall fishing pressure inside managed areas, and as a result, long-lived, slow-growing species suffer lower mortality and; therefore, persist longer inside managed areas relative to openly fished sites. The critical assumption here is that fishing pressure inside a managed area opened to fishing is similar to that in areas that are always open to fishing. Our observations of fishing activities at Kakarotan support this assumption, although more intensive research on foraging practices would be required to determine the spatial distribution of fishing effort (Aswani 1998). Consistent with this hypothesis, in Kakarotan, species of Scaridae were heavily exploited; they ranked second in importance and included more than 30% of the catch we observed, but they had significantly greater biomass inside the managed area. Although our sampling was inadequate to characterize the annual fish catch, our results of the families that are exploited with the gears used in Kakarotan are consistent with other studies examining gear selectivity (Pet-Soede 2000, McClanahan and Mangi 2004, Cinner and McClanahan, *in press*). Furthermore, the higher abundance of discarded fishing gear in fully fished areas at both locations suggests lower fishing pressure inside managed areas. In situations in which fishing pressure within a previously closed area is as great or greater than it is in fully opened fished areas, periodic closures would not likely benefit fisheries (Russ and Alcala 2003). Alternatively, long-lived, slow-growing species may only be targeted in fully opened sites, yet avoided in managed areas. However, our qualitative observations of fish catches in Kakarotan do not support this suggestion. Additionally, although long-lived species made up only a minor portion of the catches in Kakarotan, suggesting they are not heavily targeted, this cannot explain why biomass of these families was greater inside the managed area. Therefore, we suggest that the positive effects of periodic closures were likely caused by an overall reduction in fishing pressure inside the managed area.

In addition to fish biomass and average fish size, periodic closures had a relatively minor effect on other ecological variables. At Muluk, average trophic level of fishes, human-induced coral damage, and abundance of giant clams were greater within the managed area, although the density of coral recruits was greater in fully open control sites. At Kakarotan, there was no difference between managed and control sites. The absence of a strong effect on other key ecological variables such as species richness, is not surprising given the relatively low levels of exploitation, relative to other parts of Southeast Asia, at Muluk and Kakarotan, and small differences between managed and unmanaged sites.

Comparisons with conventional fisheries management strategies

The adaptive management practices we present in this paper are based on a different conceptual framework than conventional sustainable yield and full closed area models. Here, we develop a conceptual model to highlight some of the ways that these systems differ. Conventional fisheries management techniques, whether they rely on methods of fishing effort reduction or the full closure of defined areas such as marine reserves, manage resources to maintain relatively stable population sizes of harvested organisms and extract surplus production (Fig. 4*a,b*). In contrast, periodic closures seek to build a surplus of natural resources that can then be harvested. The adaptive cases we studied at Muluk and Kakarotan managed resources between two dynamic baselines or thresholds: a low baseline that signals community leaders to place a taboo ceasing resource extraction and a high baseline that signals community leaders to lift the taboo and resume extraction (Fig. 4*c*).

Whereas yield-based fisheries and marine reserve theories attempt to consistently maximize economic and ecosystem benefits, periodic closures aim to meet the cyclical needs of coastal communities. Any conservation effects are potentially only by-products of other activities, in this case, community needs, a term referred to as epiphenomenal conservation (see Ruttan and Borgerhoff Mulder 1999). This cyclical system of prohibiting resource use then receiving direct benefits from the closure can lead to very different expectations between communities and conservationists on the purpose and duration of reef closures. Foale and Manele

Fig. 4. Comparison of models (a) sustainable fisheries management, (b) closed areas, and (c) adaptive management using periodic closures.
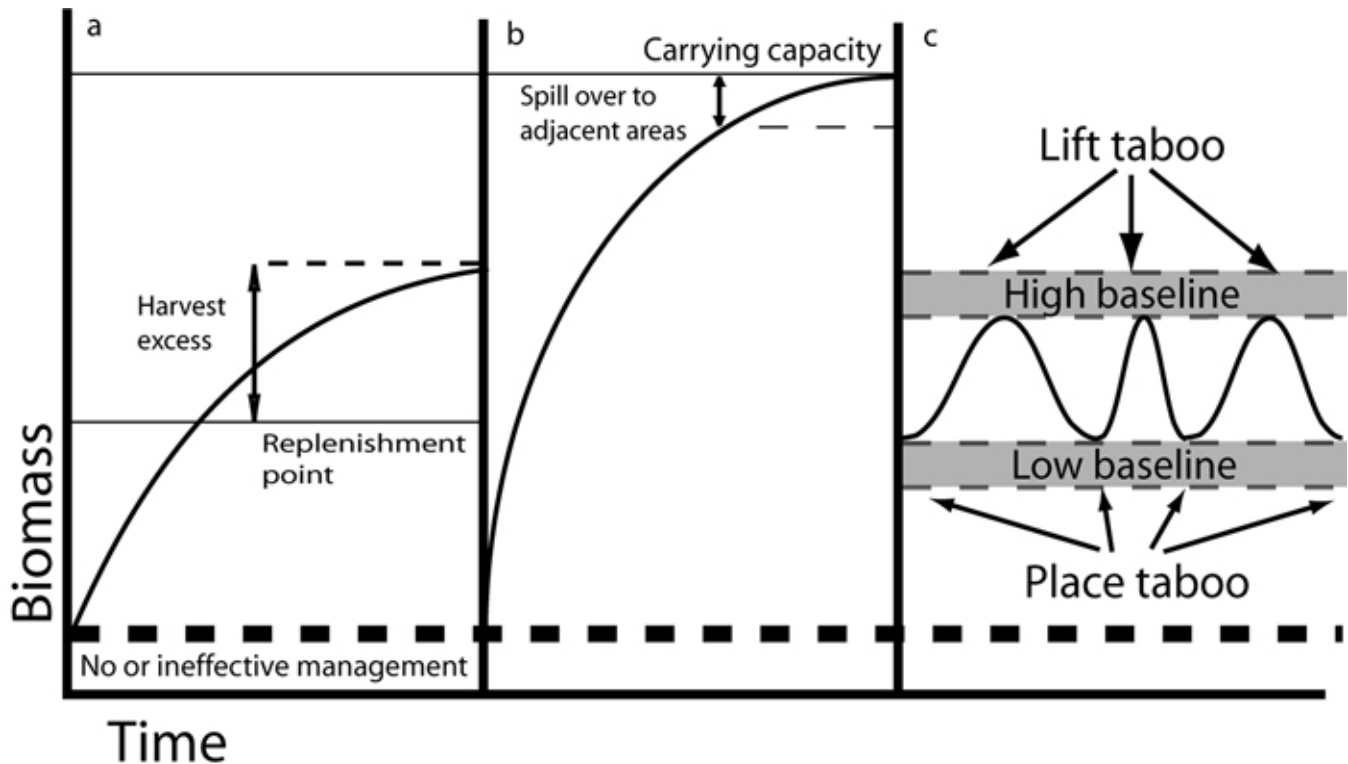
(2004) note that the customary model is akin to saving money then spending it all, and the western model is akin to keeping money in the bank and living off of the interest. Highlighting these differences is important because the practices, expectations, and enabling mechanisms associated with these periodic closures contrast strongly with those associated with western conservation and management.

Socioeconomic factors associated with periodic closures

Socioeconomic factors, or their lack of consideration in resource management planning, can cause marine conservation efforts to fail (Christie et al. 2003). This is because social, economic, and cultural factors influence whether individuals and communities create incentives to overexploit common-property resources or,

alternatively, cooperate to successfully manage them (Ostrom 1990, Pretty 2003). Recent literature has highlighted the importance of social dimensions such as social capital, knowledge, and flexibility in adaptive management of social-ecological systems (Olsson et al. 2004, Folke et al. 2005). Here we build upon this framework by speculating on how these and other mechanisms may enable these communities to make use of periodic closures. These factors may be best explored in our study by breaking down the adaptive management cycle into four phases, i.e., placing the taboo, observing the taboo, lifting the taboo/harvesting resources within managed areas, and evaluating the condition of the resource, then investigating the social, economic, and cultural factors that may influence each phase (Fig. 5).

The first component, placement of the taboo, may have been facilitated by flexibility in the resource governance structure (Gunderson 1999, Dietz et al.

Fig. 5. Conceptual model of adaptive management phases. Each phase, i.e., placing, observing, and lifting the taboo, and evaluating the social-ecological system is facilitated by specific social, economic, and cultural factors.
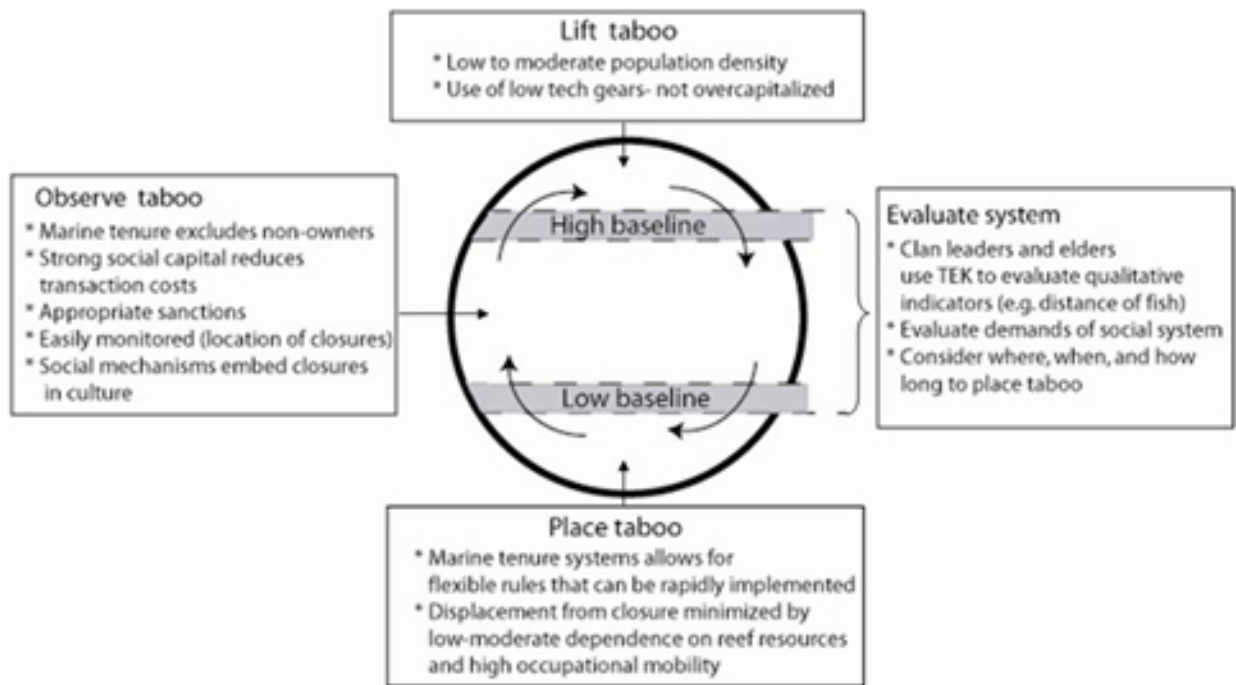
2003, Folke et al. 2005), the small human population size, and a moderate to low dependence on the resource. Highly decentralized customary marine tenure regimes nested within national or provincial authorities provided community leaders with the authority to develop and implement locally appropriate rules and sanctions virtually at will and with minimal bureaucracy (Hviding 1998). The relatively low dependence on fisheries and high degree of occupational multiplicity allows community members to switch to other occupations when restrictions are in place. This diversity of livelihood options minimizes economic displacement from the closures and allows the communities the added livelihood security of replenishing natural resources within closures. In communities in which dependence on marine resources is higher and there are fewer available livelihood options, periodic or permanent closures, covering large proportions of fishing areas, may create significant economic displacement and disadvantages and may; therefore, be met with resistance.

The second component, compliance with the taboo, was likely facilitated by several socioeconomic factors. These include the exclusion of outsiders and

high social capital, as indicated by low migration (Curran and Agardy 2002), and a high degree of group interaction (Ostrom 1990), including membership in community groups, social mechanisms that embed the closures in the culture, appropriate and graduated sanctions, and the ease of monitoring the closures. Flexibility in governance is coupled with the legitimate, or *de facto*, ability to exclude outsiders from accessing marine resources, which can be an important factor in the governance of common resources (Dietz et al. 2003). The communities we studied are relatively small, so the transaction costs of cooperation and collective action such as developing, monitoring, and enforcing rules, are relatively low (Ostrom 1990, Anderies et al. 2004). Low migration into these communities, a single religious institution in each community, and high incidences of daily interaction and cooperation provided culturally and religiously homogenous populations with high social capital, as measured by social bonds and norms (Scheffer et al. 2002, Pretty 2003), and shared world views (Berkes et al. 2000).

The low migration in these communities is not necessarily common in coastal communities in the region (Cinner 2005, Kramer et al. 2002, Koczberski and Curry 2004), and may have important implications for the integrity of their respective resource governance institutions. Both communities also had extremely strong traditional leadership and social mechanisms that embedded the closures into local traditions and customs. For example, traditional ceremonies were regularly held after the taboo was lifted. Cultural internalization of traditional management regimes can help to reinforce awareness of, and justification for, such practices (Berkes et al. 2000, Aswani and Hamilton 2004). This perceived legitimacy of both the practices and the traditional authorities may help to promote compliance with fisheries management regulations resulting in low enforcement and monitoring costs (Sutinen and Kuperan 1999, Anderies et al. 2004). Periodic closure areas were also placed close to the communities and were therefore easily monitored by community members (Crawford et al. 2004). Sanctions were locally appropriate and graduated and repeat offenses carried a higher penalty (Ostrom 1990, Dietz et al. 2003). Importantly, the communities both perceived and received direct benefits from closures in the form of fish for significant cultural events and increased fish yield during periods when the area is open to fishing.

The third component, opening access to closed reefs, has resulted in massive exploitation of reef resources in the highly capitalized, high human population density, and open-access fisheries such as those studied in the Philippines (Russ and Alcala 1998*b*). However, we found periodic closures, even when opened to exploitation, had a significantly higher fish biomass than reefs continually open to fishing activity. Relatively low fishing pressure, the use of low-tech boats and gears, and the ability to exclude outsiders from accessing resources in the communities we studied, suggests that recently opened areas may not be subjected to disproportionately intense exploitation. Also, because reefs are not open-access, there is little incentive for individuals to preemptively overexploit resources (Hardin 1968).

The final component of the management cycle, evaluation, occurred continually throughout the adaptive cycle, i.e., after the taboo was placed and resources were rebuilding, and after lifting the taboo as resources declined due to exploitation. Evaluation of the social-ecological system appeared crucial in informing community leaders as to when, where, and how long to place closures. These communities relied on traditional ecological knowledge (TEK) to make sense of, and react to, changes in their social-ecological systems (Johannes 1982, Berkes et al. 2000, Gadgil et al. 2000, Huntington 2000, Drew 2005). Traditional cultural mechanisms such as initiation rights for certain fishing practices, which involve the passing of knowledge, appeared to reinforce and maintain a base of TEK (Berkes et al. 2000).

CONCLUSIONS

Adaptive strategies are an important component of holistic ecosystem management (Holling 2001), but few examples exist of such management in coral reef fisheries (McManus et al. 1988). This is, in part, because the ability to practice adaptive management may rely on the presence of specific social mechanisms. In particular, institutions must have the capacity to interpret, and respond to, changing resource conditions, and both resource use practices and governance regimes must be flexible enough to allow for rapid decision making (Gunderson 1999).

The adaptive periodic closures we studied were practiced explicitly to meet social goals, including providing food resources at a time of social

significance, rather than to fulfill western notions of conservation or resource management. As a result, it is unlikely that these periodic closures can conserve all of the resources and biological processes conserved by large and full protected reserves, i.e., those that are permanently closed to all extractive activities (McClanahan and Graham 2005, McClanahan et al., *in press*). However, the unfortunate reality in many developing countries is that, despite massive funding efforts by NGOs and development agencies, such fully closed reserves often suffer from low levels of enforcement, monitoring, and compliance (McClanahan 1999, Pollnac et al. 2001) and are thus, in many cases, ineffective at either conserving marine resources or enhancing fisheries. In contrast, we found that adaptive periodic closures increased fish biomass and average fish size, albeit well below the levels that might be expected for unexploited ecosystems (McClanahan and Graham 2005). Furthermore, this strategy achieved high levels of community support and compliance without external financial assistance. We do not suggest that this type of management can replace large fully closed marine reserves and other management strategies, or that the reimplementation of these systems could occur without funding. Instead, we aim to highlight adaptive periodic closures as one of many potential tools in the effort to conserve resources and enhance fisheries.

The applicability of periodic closures is likely limited to situations characterized by a suite of specific social and economic factors, including low human population density, decentralized and flexible control of marine resources, people that adhere to traditions, and low reliance on the resource. However, we suggest that such conditions are present in the coastal communities of many developing nations around the Indo-Pacific, an area of high biodiversity and conservation value. When the proper socioeconomic factors are found, and large, permanently-closed reserves are unrealistic or have repeatedly failed, adaptive periodic closures may be a more viable conservation strategy.

Responses to this article can be read online at:
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APPENDIX 1. List of species comprising each family in Muluk and their associated life history and resilience to overfishing

FAMILY	SPECIES	Population doubling time	Resilience to overfishing
Acanthuridae	*Acanthurus lineatus*	1.4-4.4 years	Medium
Acanthuridae	*Acanthurus nigricans*	4.5-14 years	Low
Acanthuridae	*Acanthurus nigrofuscus*	1.4-4.4 years	Medium
Acanthuridae	*Acanthurus pyroferus*	1.4-4.4 years	Medium
Acanthuridae	*Ctenochaetus binotatus*	1.4-4.4 years	Medium
Acanthuridae	*Ctenochaetus striatus*	< 15 months	High
Acanthuridae	*Ctenochaetus strigosus*	< 15 months	High
Acanthuridae	*Naso lituratus*	1.4-4.4 years	Medium
Acanthuridae	*Naso vlamingi*	4.5-14 years	Low
Acanthuridae	*Zebrasoma scopas*	4.5-14 years	Medium
Balistidae	*Balistapus undulatus*	1.4-4.4 years	Medium
Chaetodontidae	*Chaetodon baronessa*	< 15 months	High
Chaetodontidae	*Chaetodon citrinellus*	< 15 months	High
Chaetodontidae	*Chaetodon kleinii*	< 15 months	High
Chaetodontidae	*Chaetodon ornatissimus*	< 15 months	High
Chaetodontidae	*Chaetodon oxycephala*	< 15 months	High
Chaetodontidae	*Chaetodon pelewensis*	< 15 months	High
Chaetodontidae	*Chaetodon semion*	< 15 months	High
Chaetodontidae	*Chaetodon trifascialis*	1.4-4.4 years	Medium
Chaetodontidae	*Chaetodon trifasciatus*	< 15 months	High
Chaetodontidae	*Chaetodon vagabundas*	< 15 months	High
Chaetodontidae	*Forcipiger longirostris*	< 15 months	High
Chaetodontidae	*Hemitaurichthys polylepis*	< 15 months	High
Chaetodontidae	*Heniochus chrysostomus*	< 15 months	High
Chaetodontidae	*Heniochus varius*	< 15 months	High
Haemulidae	*Plectorhinchus chaetodonoides*	4.5-14 years	Low

(con'd)

Haemulidae	*Plectorhinchus orientalis*	4.5-14 years	Low
Labridae	*Anampses neoguinicus*	1.4-4.4 years	Medium
Labridae	*Bodianus diana*	1.4-4.4 years	Medium
Labridae	*Bodianus mesothorax*	1.4-4.4 years	Medium
Labridae	*Cheilinus chlorurus*	4.5-14 years	Low
Labridae	*Cheilinus diagramma*	NA	NA
Labridae	*Cheilinus fasciatus*	NA	NA
Labridae	*Cheilinus oxycephalis*	1.4-4.4 years	Medium
Labridae	*Chelio inermis*	4.5-14 years	Low
Labridae	*Cheorodon anchorago*	NA	NA
Labridae	*Epibulus insidiator*	4.5-14 years	Low
Labridae	*Gomphosus varius*	4.5-14 years	Low
Labridae	*Halichoeres hortulanus*	1.4-4.4 years	Medium
Labridae	*Halichoeres leucurus*	1.4-4.4 years	Medium
Labridae	*Halichoeres marginatus*	1.4-4.4 years	Medium
Labridae	*Halichoeres melanurus*	1.4-4.4 years	Medium
Labridae	*Hemigymnus melapterus*	4.5-14 years	Low
Labridae	*Hemigymnus fasciatus*	4.5-14 years	Low
Labridae	*Labrichthyes unilineatus*	1.4-4.4 years	Medium
Labridae	*Labroides dimidiatus*	1.4-4.4 years	Medium
Labridae	*Macropharyngodon meleagris*	1.4-4.4 years	Medium
Labridae	*Pseudochelinus hexataenia*	< 15 months	High
Labridae	*Stethojulis bandanensis*	1.4-4.4 years	Medium
Labridae	*Thalasoma amblycephalum*	1.4-4.4 years	Medium
Labridae	*Thalasoma hardwicki*	< 15 months	High
Lethrinidae	*Gnathodentex aurolineatus*	1.4-4.4 years	Medium
Lethrinidae	*Lethrinus erythricanthus*	4.5-14 years	Low
Lethrinidae	*Monotaxis grandulosus*	4.5-14 years	Low
Lutjanidae	*Aphareus rutilans*	4.5-14 years	Low

(con'd)

Lutjanidae	*Macolor macularis*	4.5-14 years	Low
Lutjanidae	*Macolor niger*	4.5-14 years	Low
Mullidae	*Parupenus multifasciatus*	1.4-4.4 years	Medium
Mullidae	*Parupenus cyclostomus*	1.4-4.4 years	Medium
Nemipteridae	*Scolopsis bilineata*	1.4-4.4 years	Medium
Pomacanthidae	*Centropyge vroliki*	1.4-4.4 years	Medium
Pomacanthidae	*Pygoplites diacanthus*	1.4-4.4 years	Medium
Scaridae	*Bolbometapon muricatum*	4.5-14 years	Low
Scaridae	*Calatomus carolinus*	NA	NA
Scaridae	*Cetoscarus bicolor*	1.4-4.4 years	Medium
Scaridae	*Chlororus microrhinos*	NA	NA
Scaridae	*Chlorurus bleekeri*	1.4-4.4 years	Medium
Scaridae	*Chlorurus pyrhurus*	1.4-4.4 years	Medium
Scaridae	*Chlorurus sordidus*	1.4-4.4 years	Medium
Scaridae	*Scarus chameleon*	1.4-4.4 years	Medium
Scaridae	*Scarus dimidiatus*	1.4-4.4 years	Medium
Scaridae	*Scarus flavipectoralis*	1.4-4.4 years	Medium
Scaridae	*Scarus niger*	1.4-4.4 years	Medium
Scaridae	*Scarus spinus*	1.4-4.4 years	Medium
Serranidae	*Cephalopholis urodeta*	1.4-4.4 years	Medium
Serranidae	*Epinephalus fuscoguttatus*	1.4-4.4 years	Medium
Serranidae	*Epinephalus spilotoceps*	1.4-4.4 years	Medium
Siganidae	*Siganus coralinus*	< 15 months	High
Siganidae	*Siganus doliatus*	< 15 months	High
Siganidae	*Siganus puellus*	1.4-4.4 years	Medium

Biomass and average size of families in bold were significantly higher inside periodic closures

APPENDIX 2. List of species comprising each family in Muluk and their associated life history and resilience to overfishing

FAMILY	SPECIES	Population doubling time	Resilience
Acanthuridae	*Acanthurus nigricans*	4.5-14 years	Low
Acanthuridae	*Acanthurus nigrofuscus*	1.4-4.4 years	Medium
Acanthuridae	*Acanthurus pyroferus*	1.4-4.4 years	Medium
Acanthuridae	*Acanthurus thompsoni*	1.4-4.4 years	Medium
Acanthuridae	*Ctenochaetus striatus*	< 15 months	High
Acanthuridae	*Naso lituratus*	1.4-4.4 years	Medium
Acanthuridae	*Naso vlamingi*	4.5-14 years	Low
Acanthuridae	*Zebrasoma scopas*	4.5-14 years	Medium
Balistidae	*Balistapus undulatus*	1.4-4.4 years	Medium
Balistidae	*Melichthyes vidua*	1.4-4.4 years	Medium
Balistidae	*Sufflamen fraenatus*	1.4-4.4 years	Medium
Chaetodontidae	*Chaetodon auriga*	< 15 months	High
Chaetodontidae	*Chaetodon citrinellus*	< 15 months	High
Chaetodontidae	*Chaetodon ephippium*	1.4-4.4 years	Medium
Chaetodontidae	*Chaetodon kleinii*	< 15 months	High
Chaetodontidae	*Chaetodon rafflesi*	< 15 months	High
Chaetodontidae	*Chaetodon reticulatus*	< 15 months	High
Chaetodontidae	*Chaetodon trifasciatus*	1.4-4.4 years	Medium
Chaetodontidae	*Chaetodon ulietensis*	< 15 months	High
Chaetodontidae	*Chaetodon unimaculatus*	< 15 months	High
Chaetodontidae	*Chaetodon vagabundas*	< 15 months	High
Chaetodontidae	*Forcipiger longirostris*	< 15 months	High
Chaetodontidae	*Hemitaurichthys polylepis*	< 15 months	High
Chaetodontidae	*Heniochus chrysostomus*	< 15 months	High
Chaetodontidae	*Heniochus varius*	< 15 months	High
Haemulidae	*Plectorhinchus chaetodonoides*	4.5-14 years	Low

(con'd)

Haemulidae	*Plectorhinchus lineatus*	4.5-14 years	Low
Labridae	*Anampses caerulopunctatus*	4.5-14 years	Low
Labridae	*Anampses meleagrides*	4.5-14 years	Low
Labridae	*Anampses twistii*	4.5-14 years	Low
Labridae	*Cheilinus celebicus*	NA	NA
Labridae	*Cheilinus chlorurus*	4.5-14 years	Low
Labridae	*Cheilinus diagramma*	NA	NA
Labridae	*Cheilinus oxycephalis*	1.4-4.4 years	Medium
Labridae	*Cheilinus unifasciatus*	NA	NA
Labridae	*Cirrhilabrus cyanopleura*	1.4-4.4 years	Medium
Labridae	*Cirrhilabrus punctatus*	1.4-4.4 years	Medium
Labridae	*Coris gaimardi*	4.5-14 years	Low
Labridae	*Coris shroederi*	NA	NA
Labridae	*Epibulus insidiator*	4.5-14 years	Low
Labridae	*Gomphosus varius*	4.5-14 years	Low
Labridae	*Halichoeres podostigma*	1.4-4.4 years	Medium
Labridae	*Halichoeres biocellatus*	1.4-4.4 years	Medium
Labridae	*Halichoeres hortulanus*	1.4-4.4 years	Medium
Labridae	*Halichoeres leucurus*	1.4-4.4 years	Medium
Labridae	*Halichoeres marginatus*	1.4-4.4 years	Medium
Labridae	*Halichoeres melanurus*	1.4-4.4 years	Medium
Labridae	*Halichoeres scapularis*	1.4-4.4 years	Medium
Labridae	*Hemigymnus melapterus*	4.5-14 years	Low
Labridae	*Hemigymus fasciatus*	4.5-14 years	Low
Labridae	*Hologymnosus annulatus*	4.5-14 years	Low
Labridae	*Labrichthyes unilineatus*	1.4-4.4 years	Medium
Labridae	*Labroides bicolor*	1.4-4.4 years	Medium
Labridae	*Labroides dimidiatus*	1.4-4.4 years	Medium
Labridae	*Labroides pectoralis*	1.4-4.4 years	Medium

(con'd)

Labridae	*Macropharyngodon meleagris*	1.4-4.4 years	Medium
Labridae	*Oxycheilinus bimaculatus*	1.4-4.4 years	Medium
Labridae	*Pseudochelinus hexataenia*	< 15 months	High
Labridae	*Pseudochelinus octotaenia*	1.4-4.4 years	Medium
Labridae	*Stethojulis bandanensis*	1.4-4.4 years	Medium
Labridae	*Thallasoma amblycephalum*	1.4-4.4 years	Medium
Labridae	*Thallasoma hardwicki*	< 15 months	High
Labridae	*Thallasoma lunare*	1.4-4.4 years	Medium
Labridae	*Thallasoma quinquivitatum*	1.4-4.4 years	Medium
Lethrinidae	*Lethrinus erythricanthus*	4.5-14 years	Low
Lethrinidae	*Monotaxis grandoculis*	4.5-14 years	Low
Lutjanidae	*Labroides pectoralis*	1.4-4.4 years	Medium
Mullidae	*Parapaeneus bifasciatus*	1.4-4.4 years	Medium
Mullidae	*Parupenus multifasciatus*	1.4-4.4 years	Medium
Nemipteridae	*Scolopsis bilineata*	1.4-4.4 years	Medium
Nemipteridae	*Scolopsis lineatus*	< 15 months	High
Nemipteridae	*Scolopsis margaritifera*	< 15 months	High
Pomacanthidae	*Centropyge bispinosus*	< 15 months	High
Pomacanthidae	*Centropyge vroliki*	1.4-4.4 years	Medium
Pomacanthidae	*Pygoplites diacanthus*	1.4-4.4 years	Medium
Scaridae	*Calatomus carolinus*	NA	NA
Scaridae	*Chlororus microrhinos*	NA	NA
Scaridae	*Chlorurus bleekeri*	1.4-4.4 years	Medium
Scaridae	*Chlorurus pyrhurus*	1.4-4.4 years	Medium
Scaridae	*Chlorurus sordidus*	1.4-4.4 years	Medium
Scaridae	*Scarus chameleon*	1.4-4.4 years	Medium
Scaridae	*Scarus dimidiatus*	1.4-4.4 years	Medium
Scaridae	*Scarus flavipectoralis*	1.4-4.4 years	Medium
Scaridae	*Scarus forsteni*	4.5-14 years	Low

(con'd)

Scaridae	*Scarus niger*	1.4-4.4 years	Medium
Scaridae	*Scarus oviceps*	1.4-4.4 years	Medium
Scaridae	*Scarus psittacus*	< 15 months	High
Scaridae	*Scarus quoyi*	1.4-4.4 years	Medium
Scaridae	*Scarus schleigeli*	1.4-4.4 years	Medium
Scaridae	*Scarus spinus*	1.4-4.4 years	Medium
Serranidae	*Cephalopholis argus*	4.5-14 years	Low
Serranidae	*Cephalopholis urodeta*	1.4-4.4 years	Medium
Serranidae	*Epinephalus merra*	1.4-4.4 years	Medium
Serranidae	*Plectropomus leopardus*	1.4-4.4 years	Medium
Siganidae	*Siganus vulpinus*	< 15 months	High

Biomass and average size of families in bold were significantly higher inside periodic closures