

Identification and assessment of reproductively active squaretail coral grouper (*Plectropomus areolatus*) (Rüppell, 1830) movement and fishery vulnerability for conservation planning and management

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Abstract

Using conventional spaghetti-type Floy tags, 647 squaretail coralgroupers, *Plectropomus areolatus*, were tagged within the Kehpara Marine Sanctuary (KMS) between January and May 2005, including 22 males and 21 females implanted with Vemco V16[®] acoustic tags. Over 17 months, 59 conventionally tagged fish (9.1% of the total) were recaptured. Forty-five of those (76.3%) were taken within the spawning season (January-May), including 20 fish recaptured within KMS. Of all fish taken outside KMS (n=39), five were from unreported locations, while 87% were captured within 10-12 km of the site, including 25 of 39 fish taken at or proximate to channels adjacent to KMS. Recaptured fish remained at liberty for 71 ± 79 d, with a maximum reported distance of 27 km. Inter-annual and inter-monthly FSA site fidelity was shown for 22 of 43 acoustically tagged fish. Similarly, 20 Floy-tagged fish were recaptured at KMS within 1-5 months of tagging. Combined capture and movement patterns suggest that individual FSA represent a sub-set of the spawning population and that no aggregation contains the entire reproductive population for the species at that site. As such, estimates of the reproductive population size (and changes therein) cannot rely solely on counts taken within individual months of the reproductive season. In addition, a number of individuals demonstrated patterns of movement that suggest a common reproductive migratory pathway (RMP). Results further suggest that many individuals spawning at KMS reside temporarily or permanently within a relatively small area (10-12 km linear distance from the site) proximate to KMS, at least during the reproductive period. The combined results suggest a high level of fishing vulnerability for squaretail coralgroupers at the FSA site and along the RMP where fish concentrate during the reproductive season. Ripe males were taken from KMS site ≤ 9 d and gravid females ≤ 5 d before full moon, with a male-to-female capture ratio of 4:1. The sex-specific size distribution was largely non-overlapping, with females occupying smaller size classes and males larger size classes, similar to other protogynous serranids. Sex-specific reproductive behavioral differences may catalyze sexual selection by the fishery to reduce reproductive output. The data highlight the effectiveness of KMS to protect reproductively active squaretail coralgroupers within the FSA and the need for improved management that includes a combined sale and catch ban during the entire spawning season and an expansion of the KMS to include RMP.

Introduction

Among commercially important coral reef fishes, perhaps the most vulnerable to overexploitation are the medium- and large-bodied serranids that form (fish) spawning aggregations (FSA) (Johannes et al. 1999; Rhodes and Sadovy 2002). Because FSA often number in the 100s to 1,000s of individuals and form predictably in time and space, they are favored and frequent targets of artisanal and commercial fisheries, including the Southeast Asia-based live reef food fish trade (LRFFT). Unfortunately, individuals are generally taken from, or in route to, aggregations prior to egg release (Sadovy and Vincent 2002; Rhodes and Tupper *unpublished manuscript*), which often occurs during the final day(s) of the aggregation. Since spawning during these periods may represent 100% of the species' annual reproductive output (Shapiro et al. 1993) and locally spawned larvae may be contributing substantially to local populations (Jones et al. 1999; Swearer et al. 1999; Rhodes et al. 2003), aggregation fishing is unsustainable, particularly when intensive. Reproductive output may also be affected if, like other serranids, the sexual pattern is hermaphroditic (Shapiro 1987) and fishing results in size or sexual selection within or outside the spawning population to alter sex ratio (Koenig et al. 1996). Since overfishing has been implicated in grouper aggregations loss (Sadovy 1994) and spawning aggregation site-based marine protected areas (MPAs) are being widely touted as a management tool, an investigation into existing FSA-based MPA effectiveness, particularly the vulnerability of fishes outside the MPA within the reproductive season, is needed.

Past reports have shown that a number of aggregation spawners, particularly serranids, have the capacity to move over long distances to reach FSA sites (Carter et al. 1994; Luckhurst 1998; Bolden 2000; The Nature Conservancy *unpublished data*). Some more recent studies, however, suggests that long distance movement to reach FSA sites may be more of an exception than the rule (e.g. Zeller 1998) and that all or some members of the FSA may utilize common reproductive migratory pathways (RMP) to reach spawning sites, thereby enhancing their vulnerability to exploitation if these pathways remain unprotected (Starr R, *personal communication*¹).

¹ Starr, R. Moss Landing Marine Laboratories, Moss Landing, CA, *personal communication*, November 2005.

Within the tropical Pacific, only Palau and Pohnpei have developed management protocols specifically to protect commercially important serranids (squaretail coral grouper, *Plectropomus areolatus*, brown-marbled grouper, *Epinephelus fuscoguttatus*, and camouflage grouper, *E. polyphkadion*) during reproductive periods (Johannes et al. 1999; Rhodes and Sadovy 2002). These management protocols include the implementation of FSA-based MPAs and a seasonal sales ban during periods of peak aggregation abundance. These protections fall short of protecting all spawning grouper, since many sites unknown to managers are being fished and because sales bans do not effectively cover entire spawning seasons for fishes targeted for protection by management. Additionally, key RMP to spawning sites have not been incorporated into existing FSA-based MPAs, thereby leaving spawning individuals vulnerable to exploitation. To address these shortfalls in management, investigations of fish movement around existing MPAs and fishing effects on reproductively active individuals during spawning periods are urgently needed.

Methods

The proposed study was conducted at a known, protected FSA site in Pohnpei, Federated States of Micronesia [Kehpara Marine Sanctuary (KMS)] where *Plectropomus areolatus*, *Epinephelus polyphkadion* and *E. fuscoguttatus* aggregate and spawn seasonally (Figure 1) (Rhodes and Sadovy 2002; Rhodes et al. 2005). The squaretail coral grouper aggregation forms seaward along approximately 0.5 km stretch of the barrier reef in 10-30 m of water. Using live bait on hook-and-line and mask and snorkel, fishers targeted squaretail coral grouper (*Plectropomus areolatus*) daily during 5 d in January and 7 days in February through May, prior to and including full moon periods when the species aggregates. Soak times and catch volumes were recorded daily to gauge the impacts of aggregation fishing according to catch-per-unit-effort (CPUE). At the time of collection, fish were brought onboard and placed for 3-5 min in anesthesia (0.75 g l⁻¹ MS-222) in an aerated tank filled with fresh seawater. To assess aggregation sex ratio, possible gear selectivity, estimate the morphometric parameters of the spawning population and investigate reproductive pattern and fecundity for the species, all individuals were weighed (nearest g body weight), measured (nearest cm total and standard length) and

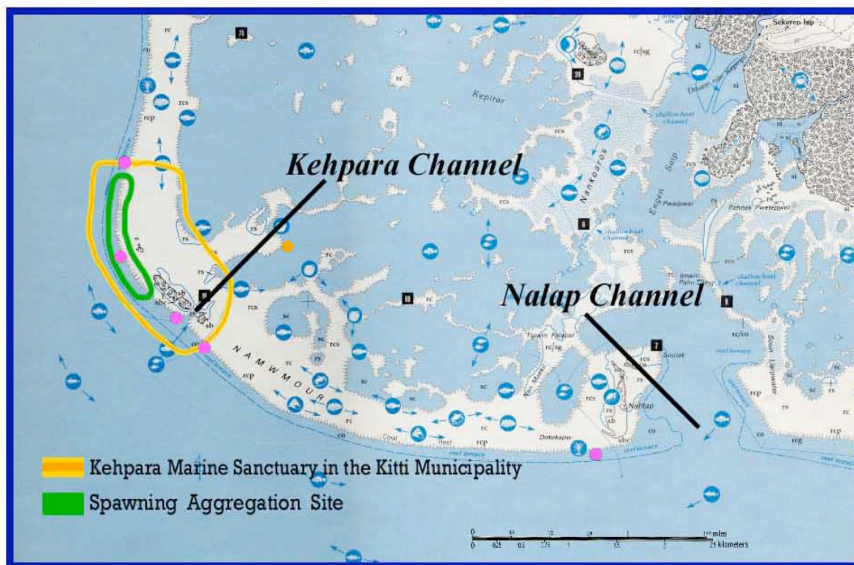
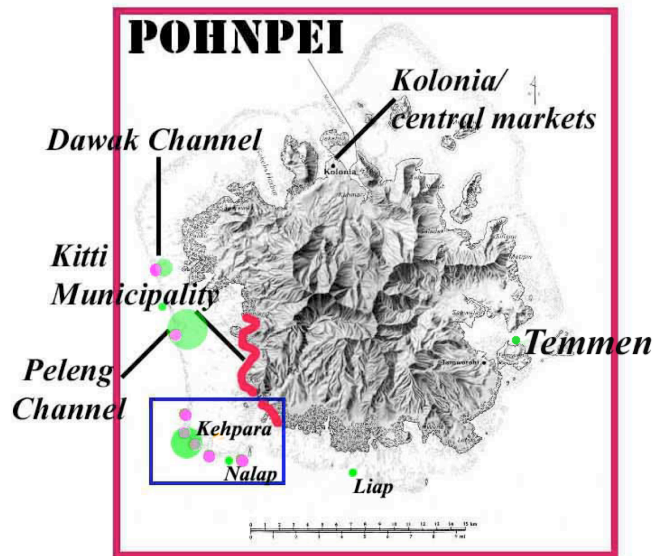


Figure 1: Top map shows the receiver locations (pink) and catch location for recaptured individuals (green). Dot sizes for recaptures are relative in size to the numbers of tagged fish re-captured for each locale. The red line indicates the locations of most Kitti Municipality fisher communities. The KMS MPA is highlighted in the lower figure.

sexed (using a 1-mm bore cannula) according to established methods (Rhodes and Sadovy 2002) prior to air bladder deflation and implantation of a coded Vemco VR16[®] acoustic transmitter and/or Floy FT-68B spaghetti tag. To determine potential distance of movement, times at liberty and catch location, all fish received a uniquely numbered Floy

tag that provided contact and reward information following re-capture. Individuals were also injected with a solution of 50 mg kg⁻¹ body weight oxytetracycline (OTC) for otolith marking for a subsequent age and growth analysis. Inclusive, 40 fish were surgically implanted with Vemco V16[®] acoustic transmitters that included 20 males tagged in January and 20 females implanted in February. One additional female was tagged in April following recapture and tag loss from a February-tagged female and two additional males were tagged with recovered tags in February following the captured of two acoustically tagged males in January. To implant the tags, incisions (~3.5 cm) were made with a surgical scalpel through the abdominal wall just prior to the vent. Following insertion, incisions were closed using ConMed Reflex One[®] 35 Wide surgical skin staples with care not to damage internal organs and then coated in topical antibiotic (Tupper and Able 2000). All tagged fish were allowed to recover in an aerated fresh seawater bath for 10-20 min prior to release in shallow water and observed on snorkel to follow initial recovery.

To track fish acoustically for distance and direction of movement as well as determine residency times within the aggregation, seven moored Vemco VR2[®] receivers were placed within and around the FSA site: one central to the aggregation, one at north and south KMS boundaries, one at the KMS-enclosed reef channel (Kehpara Channel) and one channels adjacent to and north (~8 km) of the KMS (Peleng Channel). Two additional receivers were deployed along the outer barrier reef: one just north of Peleng Channel (seaward of Dawak Island) and one just north of Nalap Channel (Figure 1). Receivers were deployed during the first month of the survey (Jan 2005) and remained in place through the end of the spawning season in May 2006.

To recover tagged fishes, a reward scheme was proposed and announced three times weekly through local radio address and by posting flyers around the island. The announcements included a general background and study objectives. At the time of return, fishers were interviewed for general and specific catch location, gear and contact information and given US \$5 in addition to the price of the fish. All fish were again weighed and measured, with gonads and otoliths extracted and preserved for subsequent life history analysis.

Results

Between 21 January and 21 May 2005, a total of 647 squaretail coralgroupers were collected and tagged at Kehpara Marine Sanctuary that included 511 males, 129 females and 7 individuals of undetermined (unknown) sex (post-spawn or juvenile) (Table 1). This total was taken in just 100 hrs of fishing over 25 days for an average of 3.1 ± 0.9 hrs d^{-1} and a catch-per-unit-effort of 3.83 fish hr^{-12}). Within the reproductive period, the

	Jan		Feb		Mar		Apr		May		Total
	n	fdc	n	fdc	n	fdc	n	fdc	n	fdc	
Male	71	4	125	4	96	6	130	9	89	8	511
Female	0	***	32	3	38	5	37	5	22	5	129
Unknown	4	3	0	***	0	***	0	***	3	8	7
M:F ratio			3.9:1		2.5:1		3.5:1		4:1		4:1

Table 1: Summary table of sex-specific catch of squaretail coralgroupers at the KMS site. n=total number of individuals collected; fdc=first day of catch relative to (prior to) the full moon.

fishery-dependent sex ratio varied from 2.5:1 (Mar) to 4:1 (May) male-to-female; no females were taken in January. Males appeared in catch up to 9 d prior to the full moon, whereas females were never taken greater than 5 d prior to full moon. Although gravid females were captured and frequently observed from 1-3 d prior to full moon, no spawning was observed. Size frequency varied from 318-469 mm SL for mature females (mean= 389.4 ± 29.5 mm SL), while mature males were distributed from 390-570 mm SL (mean= 462.1 ± 28.1 mm SL) (Figure 2), with males exclusively occupying the larger size classes and females exclusive to smaller size classes. Individuals of undetermined sex were 480-575 mm SL (mean= 446.7 ± 31.7 mm SL). A general decrease in the mean size of mature males was observed over the five months of capture, while mature female mean size simultaneously increased (Figure 3).

² CPUE findings represent a sub-sample of the total number of days fished and excludes catch and effort from January when data was not collected. Catch records also exclude fish lost to sharks.

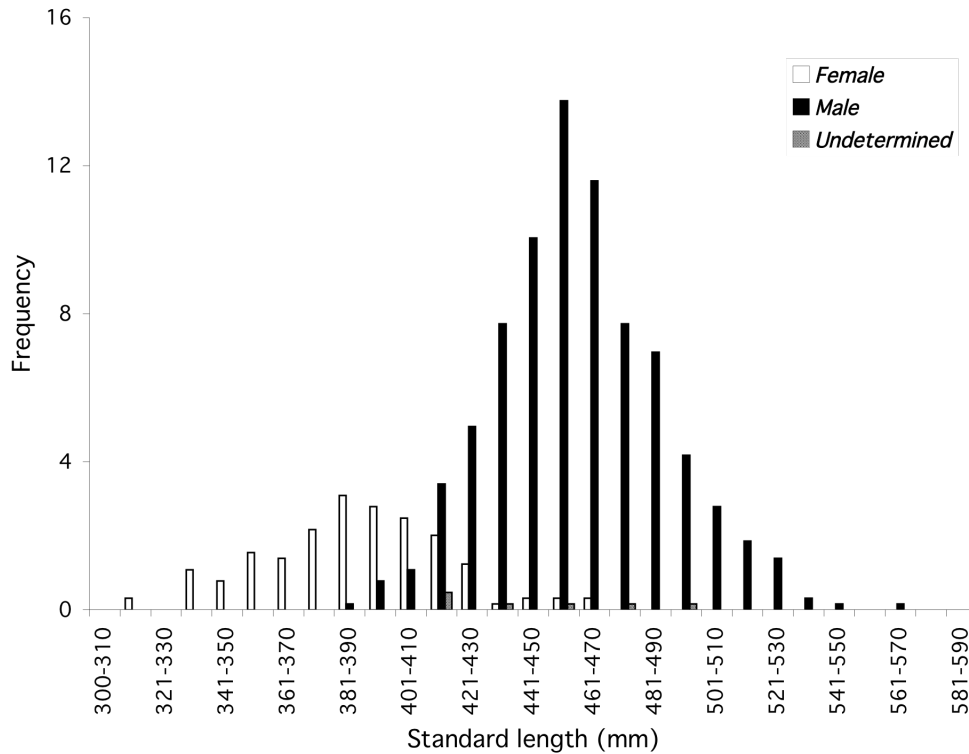


Figure 2: Size frequency distribution of the 647 squaretail coralgroupers extracted from the Kehpara Marine Sanctuary for tagging in 2005.

Conventional tagging

Of the 647 individuals tagged between 21 January and 21 May 2005, 59 tagged fish (9.1% of the total) were recaptured either at the FSA by researchers or by the fishery (Table 2). The average number of days at liberty (DAL) was 71 ± 79 d and ranged from 1-328 d. For fish recaptured at the KMS site, the average DAL was 51 ± 28 d and for those captured outside KMS 81 ± 94 DAL³. Maximum distance traveled by a tagged fish was 27 km (Table 3). Time at liberty did not correspond with distance of movement. All tagged individuals (n=20) recaptured by researchers (January-May) inside the KMS were male and one individual was recapture twice during two separate months. Of the tags returned by the fishery, macroscopic sex determination revealed one sexually unidentified, 8 females and 27 males within the catch. One individual was returned with an illegible tag, one tag was returned and lost by the market and a third capture reported, but with no fish

³ No fishing was conducted at KMS after 21 May, so that the maximum DAL for recaptures inside KMS is 120 d.

or tag returned—all of unknown sex. No microscopic histological examinations have been undertaken to date to confirm sexual identification or sexual pattern. TConventionally tagged fish were commonly observed during 2005-2006 dives at KMS.

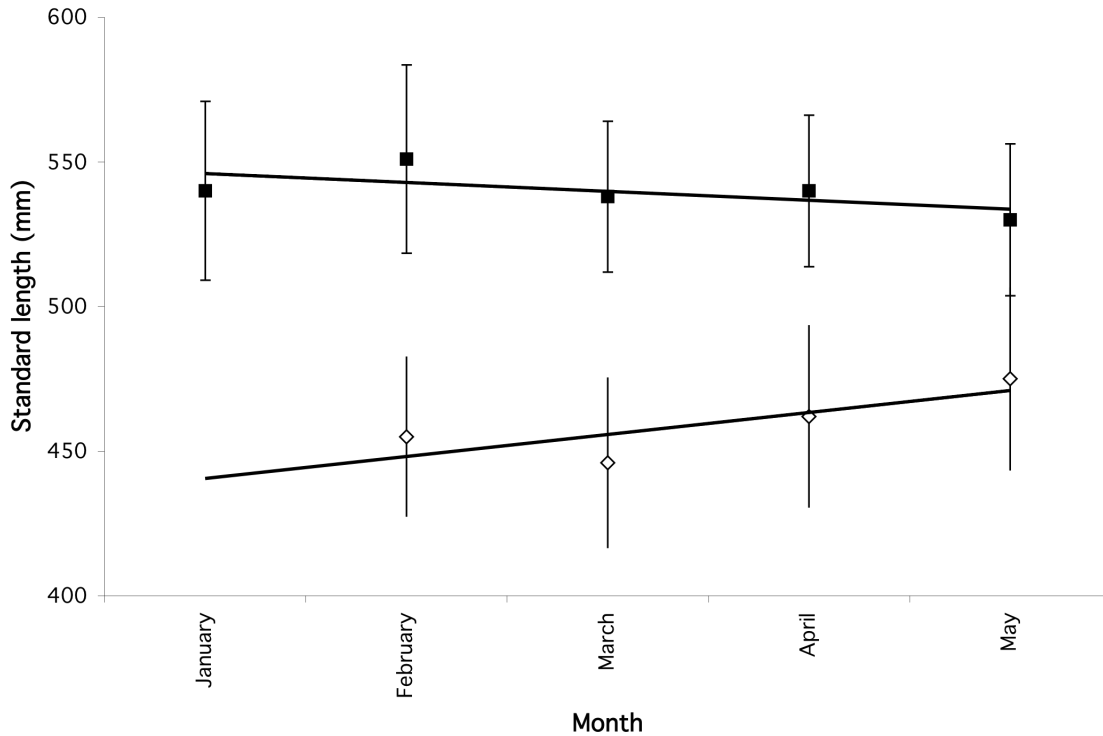


Figure 3: Trends in mean (\pm SD) size distribution of catch of squaretail coral grouper at the Kehpara Marine Sanctuary in 2005. Males are represented by solid black squares; white diamonds represents females.

	J	F	M	A	M	J	J	A	S	O	N	D	J	F
Fishers (F)	1	5	7	3	8	3	0	0	1	1	6	0	2	2
Taggers (T)	0	2	6	5	7	0	0	0	0	0	0	0	0	0

Table 2: Results of the conventional tag-recapture component of the program. Numbers represent individual recaptures taken away from the site (fishers) and within the sanctuary (researchers). The shaded area represents the sales ban period. Months are abbreviated in the upper column.

SITE	Sex			~ Distance from FSA (km)
	M	F	Unknown	
KMS	20	0	0	0.0
Nalap	0	1	0	3.5
Liap	1	0	0	7.0
Peleng	18	7	0	8.0
Dawak	5	0	0	12.0
Penieu	1	0	0	12.0
Temmen	0	0	1	27.0
Unknown	3	0	2	***
Totals	48	8	3	

Table 3: Summary table of approximate distances for recaptured fish by sex as reported by fishers. Sites listings are relative to the location and distance away from and on either side of the Kehpara FSA. M=male; F=female.

As shown, 25.6% of the total catch by fishers was taken during the March-April sales ban period and 58.9% during the reproductive season⁴, The combined percentage of fish taken by researchers and fishers during the reproductive period is 72.9% of the total, demonstrating the high vulnerability experienced by fish during this period. Most individuals taken by the fishery (82%) were captured inside the lagoon within ~10-12 km of the FSA site, with the majority captured just inside the Peleng and Dawak channels. Only four of 59 recaptures were from locations south of KMS (Liap, Nalap and Penieu) (Table 3 and Figure 1).

Acoustic tagging

A total of 20 male and 20 female squaretail coralgroupers were tagged at the Kehpara Marine Sanctuary using Vemco V16[®] acoustic tags in January and February 2005, respectively. One additional female tag was deployed in April 2005, following the loss of an acoustic tag from a recaptured female and two additional male coralgroupers were tagged in February following the return of two tagged males by the fishery in January. Of the 42 tags deployed, signals were received at or away from the tagging site for 13 of 22 males and 10 of 21 females. No signals were received from 7 males and 7 females and signals were received only during the first month for 2 males and 4 females. Table 4

⁴ Fishers were permitted to provide tagged fish to the program during the sales ban period for grouper by Pohnpei State.

gives temporal and location data for tagged individuals. Data from 4 females and 8 males suggests an RMP between the KMS spawning site from Peleng Channel or points north, with receiver times confirming travel direction and location sequence. Travel times for one female and two males between the KMS and Peleng were less than or slightly longer than 1 d and one made the ~8-km journey in just less than 4 hr on two separate occasions. The receiver located south of the KMS boundary picked up only one individual through the project period.

Results from the 17 months of acoustic monitoring suggest that each of five monthly (2 weeks mo^{-1}) squaretail coralgroupers spawning aggregations (FSA) within the reproductive period (January-May) is composed of a sub-population of the total adult population. In other words, varying proportions of the potential reproductive population participated in each monthly spawning bout; the entire adult population appears to never be present at the site during a single month. For example, of the 20 males acoustically tagged in January 2005, only 30% (7 individuals) were present at the FSA site in February. This number was reduced to 25% (5 individuals) in March and 15% (3 individuals) in April and May, although monitoring data has shown the aggregation size to increase annually between January and April (Rhodes et al. 2005). We assume that individuals that never returned were lost to tag mortality, to the fishery or have yet returned to spawn. At least one male (2256) left the site after tagging in March 2005 and did not appear again at the FSA or on any other receiver location until March 2006. Two males (2258, 2268) and one female (2281) returned to the site or resided at the site in one or more months outside the spawning season and no clear differences were noted in frequency of movement to the site between sexes. In contrast, males generally appeared to demonstrate higher activity patterns during diurnal periods, with movement largely between 6 a.m.- 6 p.m. and limited or no movement during nocturnal periods. Alternatively, females showed more moderate activity levels throughout the day, with relatively higher nocturnal activity than males. Although females did not show up in catch less than 5 d prior to full moon, receiver data shows that female presence overlapped with males and, for some individuals, remained at the FSA through much of the month.

Year		2005												2006				
Tag	Sex	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May
2250-A	M																	
2250-B	M	4,5	4,5	44,7	4	4												
2251	M	4	4															
2252	M	4	4															
2253	M																	
2254	M	4																
2255	M	4	4,5,6	4														
2256	M	4	4,5,6	4,5												4,5,6, 4,5,6,7		
2257	M	4,6	4,5,6	4,5,6														
2258	M	4	4	4	4	4	4	4	4	4	4		4	4		4	4	4
2259	M	4,5																
2260-A	M																	
2260-B	M																	
2261	M	4,5,6	4															
2262	M																	
2263	M	4	4,6	1,4,5,6	5													
2264	M	4	4															
2265	M	2,3,4	3,4	4														
2266	M																	
2267	M	4																
2268	M	4	4		4	4	4	4	4,5	4	4	3,4,5						
2269	M	4,5																
2244	F				4,6,7													
2270	F		2,4	4														
2271	F		2	2,3,4														
2272	F																	
2273	F		4,6	6			4											
2274	F																	
2275	F		4															
2276	F				4													
2277	F																	
2278	F																	
2279	F		4															
2280	F		4	2,4														
2281	F		4	2,4		4	4	4						4	4	4	4	4
2282	F																	
2283	F		4															
2284	F			2														
2285	F																	
2286	F		4,5	5	5,7			5										
2287	F		4,5	4														
2288	F																	
2289	F		4,5															

Table 4: Summary table of acoustically tagged fish location by date. Tag numbers 2250-A and 2260-A were replaced by 2250-B and 2260-B following the capture of two January-tagged males. Tag 2244 was first tagged in April 2005. Numbers correspond to receiver locations from south to north: 1=Nalap; 2=south KMS boundary; 3=Kehpara Channel; 4=center of KMS squaretail coral grouper FSA; 5=north KMS boundary; 6=south apron Peleng Channel; 7=outer reef Dawak Island, north of Peleng Channel.

Additionally, acoustic data (supported by catch data, *below*) suggest the aggregation that formed during the initial month of the ‘reproductive’ season (January) was composed entirely, or nearly so, of males, such that the aggregation was not actually a spawning aggregation. Additional work is needed to confirm this finding and determine if all-male aggregations are common during the first month of the reproductive season.

Discussion

The results of the conventional and acoustic tagging project clearly highlight the vulnerability of squaretail coral grouper to fishing within the reproductive season, both at and away from the spawning site and demonstrate the effectiveness of the KMS in protecting spawners at the FSA site. The data also provide evidence to suggest a common reproductive migratory pathway (RMP) for the species and demonstrate both the ease in which FSA can be extirpated over a short timeframe when fishing pressure is intense and the need to incorporate RMP into FSA-based MPAs. Specifically, in just over 100 hr of fishing, 2-3 fishers removed (and released) 647 squaretail coral grouper from the KMS FSA site. By increasing the number of fishers and soak time several-fold, as common to FSA fishing elsewhere, thousands of individuals could be easily removed, as shown for the congeneric camouflage grouper (*Epinephelus polyphekadion*) in Pohnpei prior to its inclusion into the KMS in 1999 (Rhodes 1999). Clear effects of intense FSA fishing have been shown elsewhere in the form of FSA extirpation and reduced reproductive output from changes in sex ratio and loss of genetic diversity (e.g. Koenig et al. 1996; Beets and Friedlander 1998; Chapman et al. 1999; Sala et al. 2001; Hamilton and Kama 2004; Hamilton et al. 2005). Indeed, assuming the survey catch data presented here can be used as a baseline, the loss of FSA over a 2-3 yr timeframe is easily foreseeable under intense fishing pressure, such as that reported from the commercial live reef food fish trade (e.g. Johannes et al. 1999; Hamilton and Kama 2004).

In the case of Pohnpei, reproductively active and mature, resting squaretail coral grouper appear to maintain a presence at or proximate to the FSA site. This proximity includes nearby Peleng Channel 10 km north of KMS—a preferred fishing site for Kitti (Municipality) fishers throughout the year (Rhodes and Tupper *unpublished data*). Indeed, 87% of individuals taken by the fishery were captured 10-12 km from the KMS both within and outside the spawning season. For squaretail coral grouper, this data seems to suggest limited movement by the KMS spawning population and also highlights the potential for localized extinction and associated impacts to fish community structure and fisheries through the loss of the KMS FSA from overfishing. The data also provides additional support to the notion that long distance movement by at least some FSA-forming serranids may be an exception rather than a rule. Indeed, previous reports of

movement in other species in relation to FSA also suggest that long distance movement may be rare and that many participants are resident to areas proximate to the FSA site: leopard coral grouper, *Plectropomus leopardus* (Zeller 1997, 1998), Nassau grouper, *Epinephelus striatus* (Starr R, *personal communication*) and black grouper, *Mycteroperca bonaci* (The Nature Conservancy *unpublished data*). If limited movement from FSA or residency with areas proximate to FSA is common, large permanent area closures that encompass FSA and RMP may provide near-total protection to what appear to be localized spawning stocks. Alternatively, small-scale FSA-based MPAs or seasonal sales bans (such as those currently used in Palau and Pohnpei) and temporal area closures may be limited in protecting adult populations. This is reflected in both the amount of fish taken by the fisheries within the March–April sales ban period (25.6%) and the number taken outside the KMS MPA within the reproductive period (66.7%). Based on these results, the KMS should be expanded from its current location to include all outer reef areas between Kehpara and Peleng Channels and, at a minimum, inner reef and lagoon areas proximate to the FSA and the inner channel boundaries. In addition, a sales *and* catch ban should be implemented that covers the entire reproductive period (January–May) to protect other FSA sites in the area⁵. A more detailed assessment of the spatial requirements could be achieved through active tracking of acoustically tagged individuals throughout the year, but particularly during the reproductive season.

Acoustic data clearly show that at least some reproductively active individuals move seaward along the outer barrier reef to reach KMS and Peleng and, in fact, may utilize the main channels north of the site (Peleng and Dawak Channels) to access the lagoon (Figure 1 and Tables 3 and 4). Interestingly, few tagged individuals were either captured or appeared on receivers placed to the south of KMS (i.e. Nalap) and none were observed to moved into the lagoon through Kehpara Channel, even though anecdotal reports indicated large-scale movement of squaretail coral grouper through the channel prior to 1995 within the reproductive season⁶. However, intensive net fishing just inside the Kehpara Channel through the late 1980s and early 1990s resulted in increasingly

⁵ The latter option—a sales and catch ban—is currently being considered by the Pohnpei State Legislature, along with a seasonal spearfishing ban during the reproductive season.

⁶ Paul D. *Personal communication*. 1997. Landowner, Black Coral Resort and Pohnpei Division of Marine Resources and Development conservation officer,.

smaller numbers of squaretail coralgroupers until fish became commercially extinct and netting stopped as a result. Findings from this survey suggest that a separate, but now extirpated squaretail coralgroupers FSA may have existed proximate to the current KMS FSA that no longer forms. Combined findings and local accounts strongly suggest that local artisanal fishing can impact FSA to promote extirpation similar to commercial activities when fishing is intense, as shown in Melanesia (Hamilton and Kama 2004).

From both the acoustic and conventional tagging data, squaretail coralgroupers appear to move to and from FSA repeatedly throughout the spawning season, suggesting repeat spawning by at least some individuals within the year (Table 1). In addition, the combined tagging data suggest that each of the monthly FSA is actually a sub-component of the entire reproductive population. This notion is supported by mature, resting (KMS-tagged) individuals being captured outside the FSA during the reproductive period (e.g. at Peleng) and also by the absence of acoustically tagged and active individuals at the FSA site during some reproductive months (Table 4). For example, although most males that returned repeatedly during the spawning season did so frequently, only one individual returned in all months of the spawning season and, in fact, appears to be resident. Conversely, females were rarely present during more than two consecutive months of the spawning season and none was present in all reproductive months. While these numbers may indicate tag-induced mortality, several individuals provide suggestive evidence that the reproductive population is substantially larger than that observed during any single spawning month, including the peak month of April that has been detailed through monitoring activities from 2002-2006 (Rhodes et al. 2005). Results may also indicate that the female population is substantially larger, since most acoustically tagged individuals did not return during the peak month of spawning (April) and no conventionally tagged females were recaptured at the KMS following initial tagging. Zeller (1998) provides some support for this by showing that among 35 leopard coralgroupers tracked during spawning periods between 1993 and 1995, only 31% participated in spawning aggregation activities. Therefore, mature coralgroupers and possibly other serranids may not reproduce over regular intervals within or even among reproductive seasons. Unfortunately, an accurate portrait of how aggregations are composed both numerically and sexually in relation to the adult population was not obtainable during this project and

this information is still needed to understand how fisheries impact populations, how MPA act to protect individuals and how species such as squaretail coralgroupers replenish populations in time.

Sexual differences in abundance and behavior were apparent throughout the project. Firstly, in January, catch at KMS during tagging activities was composed entirely of males. While it is possible that females were at the FSA during this period, none were captured even though fishing was conducted when females were otherwise present, i.e. 0-4 d prior to full moon. For example, an average of 32 females mo^{-1} was caught February-May at a 3.5: 1 mean male: female sex ratio. This strongly suggests that the January FSA was not reproductive. Secondly, more than 50% of males acoustically tagged in January remained at the site through the following full moon period (February), with nearly all individuals⁷ abandoning the site following spawning during subsequent reproductive months (confirmed by dive observations). The relevance of the male behavior observed in at KMS in January is unknown, but similar observations have been recorded for the species in the Solomon Islands (Hamilton RJ, *personal communication*). While this may merely reflect a behavioral phenomenon, such as the establishment of territory prior to spawning, it may also indicate an absence of available females during the early part of the reproductive season through fishing mortality or undocumented sex-specific variances in reproductive behavior. From a fisheries management perspective, FSA fishing during these pre-spawn, all-male periods would be sexually selective and likely impact reproductive success in subsequent spawning periods. Thirdly, males demonstrated daily behavior patterns somewhat different from females in that males were highly active during diurnal periods (6 a.m.-6 p.m.), but were otherwise limited, particularly nocturnally. Conversely, those few females that did remain at the site showed a somewhat greater propensity for nocturnal activity. These observations may suggest differences in foraging activity by females that are otherwise harassed during daylight hours by males to spawn. Fourthly, sex-specific variations in size were observed throughout the project with the mean size of males larger during the initial months of the survey and decreasing through the spawning season. Females demonstrated the opposite pattern. Larger males are known to maintain larger territories and may have better

⁷ Residency is suggested for two individuals.

reproductive success (i.e. fertilize a larger number of females) as a result. However, larger, more fecund females were present at a time when the mean size of males was at its nadir. Larger females have also recently been shown to have better eggs and more viable larvae (Berkeley et al. 2004). From an evolutionary standpoint, it would seem that larger males would improve the success of their progeny by fertilizing larger females later in the reproductive season. A similar phenomenon has been suggested for mutton snapper (*Lutjanus analis*) in Belize whereby size variation occurs through the spawning season and suggests that the phenomenon may be common to seasonal spawners. The evolutionary benefit of employing such a strategy deserves further investigation. Fifthly, the sex ratio was noticeably skewed toward males. In Palau, sex ratio imbalance was shown to result in harassment of females by males to the point that females did not spawn (Johannes et al. 1999). In the western Atlantic, gag grouper were selectively fished to the point of highly reduced reproductive output through sperm limitation (Koenig et al. 1996). While the operational sex ratio and spawning method is unknown for squaretail coral grouper, further investigation is warranted to determine whether reproductive success and output are affected by the observed imbalance, assuming it is not merely a effect of gear. However, the fisheries ratio for recaptured individuals was 3.4:1, with 27 of 30 of the interviewed fishers using spear, suggesting that the female population may indeed be reduced relative to that of males. Finally, although catch composition suggests that females arrive at the FSA beginning 5 d prior to the full moon versus 9 d prior to full moon for males, no evidence from tagging was given to support variability in arrival or residency times between sexes. Although the samples size of acoustically tagged females was considered too small to specifically detail variations in residency or arrival-departure times in the species, at least some females arrived at approximately the same time as males and frequented the site between spawning periods (i.e. during last quarter and new moons). If there is indeed no difference in male-female residency times at FSA, issues of vulnerability and sexual selection would lie entirely with gear use. For example, spearfishing would allow both sexes to be taken in relatively equal proportions in comparison to hook-and-line fishing, which is shown through this survey to act on females over shorter timeframes (relative to spawning) than for males. These variations should be taken into account when deciding on management strategies for the species.

In summary, the effectiveness of the no-take year-round KMS to protect squaretail coral grouper (and adjacent FSA of brown-marbled, *Epinephelus fuscoguttatus*, and camouflage, *E. polyphekadion*, grouper) is evident. Without this protection, hundreds and perhaps thousands of groupers could be easily removed during all months of the spawning season. However, it is also evident that many reproductively active individuals never reach the spawning site and are taken along RMP or in areas adjacent to the KMS, thereby reducing overall annual reproductive output for the spawning population. This reduction comes in the form of direct removal of gravid individuals prior to spawning, direct removal of resting individuals otherwise destined to spawn in a subsequent spawning event within the year, or an alteration in sex ratio through selective fishing. To improve management in Pohnpei, a recommended course of action for the state is to (1) expand KMS to include the squaretail coral grouper RMP, (2) place a ban on catch as well as sale of squaretail coral grouper during the spawning season and (3) include all reproductive months in the ban. Additional consideration should be given to banning nighttime spearfishing either seasonally during the January-May reproductive season (that also includes numerous other locally important species) or banning the practice outright, as done elsewhere following periods of overfishing (Rhodes and Tupper *unpublished data*).⁸ These measures would not only protect squaretail coral grouper at KMS, but may also effectively protect reproductively active squaretail coral grouper at other sites within the area, assuming spawning times are similar. It is our hope that the information presented here fills some of the critical information gaps for MPA development and provides a greater understanding of the reproductive behavior and life history of aggregating serranids for conservation planning and management.

⁸ These recommendations are currently being considered in Pohnpei by local and state marine resource agencies and non-government agencies to improve conservation of reef fishes in the state, as a direct consequence of this and a 2006 NOAA-sponsored reef fish market survey.

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