The vulnerability of reproductively active squaretail coralgrouper (*Plectropomus areolatus*) to fishing

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Abstract—Squaretail coralgrouper (*Plectropomus areolatus*) were captured and tagged at a fish spawning aggregation (FSA) site with conventional and acoustic tags to assess their vulnerability to fishing and spatial dynamics during reproductive periods. Males outnumbered females in catch and, on average, were larger than females. Findings revealed a high vulnerability to fishing, particularly during reproductive periods, and most fish were recaptured within the 5-month spawning season and within 10–12 km of the aggregation site. Individual and sex-specific variability in movement to, and residency times at, the FSA site indicates that individual monthly spawning aggregations represent subsets of the total reproductive population. Some individuals appeared to move along a common migratory corridor to reach the FSA site. Sex-specific behavioral differences, particularly longer residency times, appear to increase the vulnerability of reproductively active males to fishing, particularly within a FSA, which could reduce reproductive output. Both fishery-dependent and fishery-independent data indicate that only males were present within the first month of aggregation. The combined results indicate that reproductively active *P. areolatus* are highly vulnerable to fishing and that FSAs and migratory corridors of reproductively active fish should be incorporated into marine protected areas. The capture of *P. areolatus* during reproductive periods should be restricted as part of a comprehensive management strategy.

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Epinepheline serranids (groupers, hinds, lyretails) that form fish spawning aggregations (FSAs) are among the most vulnerable coral reef fishes to overexploitation (Coleman et al., 2000; Sadovy and Domeier, 2005). Indeed, 20 of 162 epinepheline serranids (hereafter, serranids), including species that form FSAs, are now considered vulnerable or endangered according to IUCN Red List criteria. Among those listed as vulnerable is the squaretail coralgrouper (*Plectropomus areolatus*) (Rüppell, 1830) that forms temporally and spatially predictable FSAs, often numbering in the 100s to 1000s of individuals. These traits contribute to the targeting of *P. areolatus* by local and foreign commercial fisheries, including the Southeast Asia-based live reef food fish fishery (Sadovy et al., 2003). When both FSAs and reproductively active individuals are targeted enroute to spawning sites, reproductive populations may experience population-level changes that affect reproductive output, including skewed aggregation sex ratios following sexual selection (e.g., Koenig et al., 1996), size reductions (e.g., Beets and Friedlander, 1998), changes in genetic diversity (Chapman et al., 1999), and loss or decline in FSA (e.g., Sadovy and Domeier, 2005). With few exceptions, FSA fishing is unsustainable under anything more than light fishing pressure, such as that characteristic of limited subsistence-level fishing (Sadovy and Domeier, 2005). Reports of grouper FSA loss continue to increase worldwide (e.g., Matos-Caraballo et al., 2006; Aguilar-Perera, 2007) and increased fishing mortality at FSAs is implicated in local fishery declines (Sadovy and Domeier, 2005). Among measures recently touted to protect FSAs and reproductive populations from overfishing are marine protected areas (MPAs). However, few reports show the effectiveness of MPAs in limiting or preventing FSA loss, or in improving population-level abundance (Nemeth, 2005). Moreover, most existing FSA-based MPAs are small and likely leave reproductively active individuals vulnerable to fishing, such as some reproductively active serranids that appear to use common migratory corridors to reach FSAs, where they can be fished before they spawn (Nemeth et al., 2007; Starr et al., 2007). Migratory corridors and the dangers of overexploitation when corridors are left unprotected are recorded for a number of fishes, such as gadids (e.g., Rose, 1993). To design effective management for reproductive populations of serranids such as squaretail coralgrouper, areas of high fishing vulnerability must be identified, including FSA sites, migratory corridors, and other areas where fish may concentrate during reproductive periods.

Within the tropical Pacific, only Palau and Pohnpei have developed long-term management protocols at the national level specifically to protect commercially important serranids (*P. areolatus*, *Epinephelus fuscoguttatus* [brown-marbled grouper], and *E. polyphekadion* [camouflage grouper]) during reproductive periods (Rhodes and Sadovy, 2002). Temporary community-based MPAs are used elsewhere, such as at the Solomon Islands and Papua New Guinea, whereby fishing is allowed at FSAs after periods of build-up within the aggregating population. For Pohnpei, where the current study was focused, management protocols include a small-scale MPA that protects *P. areolatus*, *E. polyphekadion,* and *E. fuscoguttatus* at a common FSA site (Kehpara Marine Sanctuary [KMS]) and a seasonal serranid sales ban that coincides with peak reproductive periods for these species (March–April). However, these measures fall short of fully protecting these and other FSA-forming serranids because 1) some unprotected FSAs continue to be fished (e.g., at nearby Ant Atoll and Palikir Pass); 2) sales bans do not cover entire spawning seasons for the aforementioned species; and 3) some serranids appear to reproduce outside the sales ban period (Rhodes and Tupper, 2007). Migratory corridors have not been investigated locally, including around the KMS, and thus reproductively active individuals possibly exist outside current MPA boundaries and are, therefore, vulnerable to exploitation. Finally, subsistence catch for aggregating serranids, shown to lead to overexploitation elsewhere (e.g., Olsen and LaPlace, 1979), remains open year round, including during the sales ban period.

In Pohnpei, *P. areolatus* is a favored target of local subsistence fishermen and small-scale commercial fishermen, representing approximately 12% of the combined-gear commercial coral reef grouper fishery that includes 24 species (Rhodes and Tupper, 2007). The species is taken year-round largely as juveniles and small adults from inner reef areas during nighttime spearfishing activities, but is also known to be targeted at FSA sites, including at least three known unprotected FSA sites. Anecdotal evidence indicates that one local *P. areolatus* FSA may have been extirpated in the 1990s after continued targeting of an annual reproductive migration that ceased to form around 1995. Gravid *P. areolatus* are commonly found in markets during reproductive months outside the March–April serranid sales ban period, occasionally in the hundreds of individuals, and there is concern that reproductively active *P. areolatus* from the KMS may be targeted along migratory corridors or other areas where fish congregate (i.e., staging areas) for noncommercial use during sales-ban periods.

Using both conventional and acoustic tag-recapture techniques, we examined the vulnerability of squaretail coralgrouper to fishing by examining spatial and temporal trends of tagged individuals at a single protected spawning aggregation site. The study objectives were 1) to determine potential sexual differences in behavior (within reproductive periods) that may facilitate capture and impact reproduction; 2) to examine the potential catchment area(s) (determined from recaptures) from which reproductive populations of *P. areolatus* at KMS may be drawn; 3) to assess the direction and distance of movement of fish in relation to the FSA to improve MPA design; 4) to identify potential migratory corridors of spawners in relation to KMS where fishermen may concentrate fishing activities; 5) to determine if the existing MPA at KMS adequately protects reproductively active individuals; and 6) to assess whether current fisheries management could be improved to reduce the capture of reproductive fishes during spawning periods, particularly at the FSA site. Estimates of overall fishing mortality and fisheries sustainability for squaretail coralgrouper in Pohnpei are outside the scope of the current study because information on stock characteristics and the fishery (particularly subsistence) remain incomplete and, therefore, statements concerning these indices would be premature.

Material and methods

Site description

The tagging study was conducted at the Kehpara Marine Sanctuary, a known protected FSA site in Pohnpei, Federated States of Micronesia (6°55′N, 158°15′E), where *P. areolatus, E. polyphekadion,* and *E. fuscoguttatus* aggregate seasonally to spawn (Fig. 1). *Plectropomus areolatus* forms aggregations annually from ca. January–May at KMS, seaward of the barrier reef along approximately 0.5 km of the reef flat and wall at ~10–30 m depth (first author, unpubl. data). During the aggregation period, individuals seek shelter and remain in relatively close proximity (<5 m) to the low-relief coral that covers much of the site. During daytime, individuals can be observed meandering among large high-relief stands of coral in shallower portions of the reef flat and over the intermittent sand patches and rubble piles that are found throughout the area. Although *P. areolatus* aggregations have been monitored at the site over a 7-yr period, spawning has never been observed within aggregation months. Histological analyses of gonads have recently confirmed a seasonal and lunar periodicity of spawning for this species (first author, unpubl. data).

Fish capture, catch per unit of effort, and tagging

To capture fish for tagging, two locally hired fishermen used live bait (*Myripristis* sp.), hook-and-line, and mask and snorkel to target *P. areolatus* from the surface within the FSA site. Fishing was conducted daily over 5 days in January and 7 days monthly from February through May just before and including the full moon, for a total of 33 fishing days. Target depths for fishing ranged from ~15–30 m where fish aggregate within the FSA site. To estimate catch-per-unit-of-effort (CPUE), daily soak times and catch volumes were recorded from February to May. No CPUE estimates were made in January, although fishing methods and times were similar among months. Following capture and before processing, fish were brought onboard and anesthetized in a 0.75 g/L

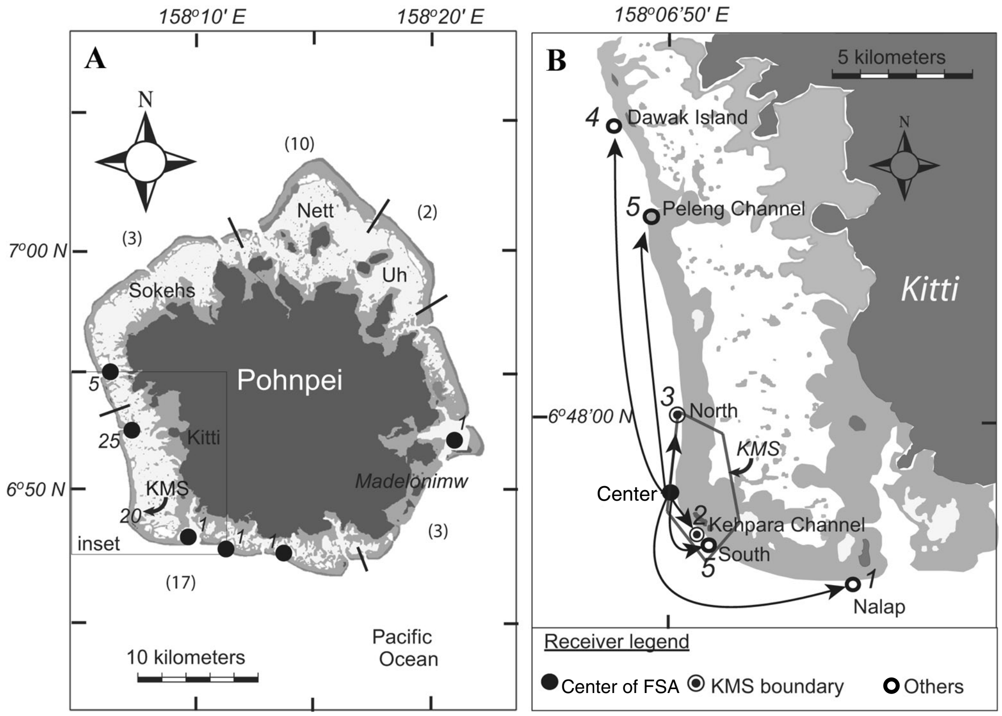

Figure 1

(**A**) Map of the Pohnpei Island showing the general catch locales (circles) and number (italics) of recaptured conventionally tagged squaretail coralgrouper (*Plectropomus areolatus*). Catch locales are (counterclockwise from left) Dawak, Peleng Channel, Nalap, Liap, Penieu, and Temmen. Catch probabilities (in parentheses), or the number of recaptures anticipated within a municipal reef area, are based on the total number of recaptures from this study (January 2005–February 2006) divided by the percent fishing effort allocated to a municipal reef area. Effort estimates were derived from a 2006 market survey that included interviews of 1123 commercial reef fishermen (Rhodes et al., 2007). Estimates of catch probability exclude recaptures with unreported catch locales (n=5) and fish captured by researchers inside the Kehpara Marine Sanctuary (KMS) (n=20). Municipalities (Nett, Sokehs, Kitti, Madelonimw, Uh) are separated by black diagonal lines. (**B**) Inset map shows the direction of movement and number of individuals detected by Vemco VR2 acoustic receivers outside the KMS during the study period. The Kehpara Marine Sanctuary is represented by the area outlined in gray. FSA=fish spawning aggregation. Others=other receivers.

tricane methanesulfonate-seawater solution until fish lost equilibrium (~3–5 minutes). Following anesthesia and air bladder deflation, all individuals were weighed (nearest g body weight), measured (nearest mm total length [TL] and standard length [SL]), and sex was determined macroscopically by using a 1-mm bore nylon cannula (Rhodes and Sadovy, 2002).

To determine the potential distance of movement, times at liberty and catchment areas (defined as the area from which spawning individuals are drawn [Sadovy and Domeier, 2005]), all captured fish were tagged with a uniquely numbered Floy FT-1-94 conventional tag (Floy Tag, Seattle, WA) that provided contact and reward information. Of these Floy-tagged specimens, 40 fish (20 males and 20 females) were surgically implanted with Vemco V16 acoustic transmitters (Vemco AMIRIX Systems, Halifax, Nova Scotia) in January and February. For tag implantation, abdominal incisions (~3.5 cm) were made just anterior to the vent and were closed with ConMed Reflex One® 35 Wide surgical skin staples (ConMed Endosurgery, Utica, NY) (Tupper and Able, 2000). After surgery, fish were allowed to recover 10–20 min onboard in fresh aerated seawater before release into shallow (2–5 m) water near the reef crest. Most acoustic-tagged and some Floy-tagged fish were observed from the surface by snorkel divers to follow initial recovery and to monitor potential predation.

Acoustic tracking and tag recovery

For acoustic tracking of fish distance and direction of movement, and to determine residency times within the FSA, a total of 7 Vemco VR2 receivers were moored in January 2005 at the following locations: center of the FSA, at north and south KMS boundaries, within the Kehpara and Peleng channels adjacent to the FSA, and seaward of Dawak and Nalap islands that are north and south, respectively, of channels adjacent to the FSA

Table 1

Summary table of sex-specific catch of squaretail coralgrouper (*Plectropomus areolatus*) at the aggregation site during tagging in 2005. *N* = total number of individuals collected during the reproductive season; *n*=monthly sample size; FDC = first day of catch before the full moon; na = data not available.

		Month									
		January		February		March		April		May	
Sex	*n*	FDC	*n*	FDC	*n*	FDC	*n*	FDC	*n*	FDC	*N*
Male	71	4	125	4	96	6	130	9	89	8	511
Female	0	na	32	3	38	5	37	5	22	5	129
Unknown	4	3	0	na	0	na	0	na	3	8	7
Total	75		157		134		167		114		647

(Fig. 1). All receivers were tethered above the barrier reef at 10–25 m depth at seaward-facing promontories to maximize detection range. All receivers were removed after 17 months that covered two full consecutive spawning seasons. Prior range testing in Palau under similar physical and oceanographic conditions was performed for 13 receivers along four cardinal directions with a line-attached transmitter. The transmitter was towed behind the boat and away from the receivers, and times and distances from the receiver were recorded by GPS. Distance and times were later matched to receiver-logged transmissions to determine minimum and maximum detection distances. Testing confirmed an average maximum detection distance of 442 m along the reef parallel to the barrier reef crest and 975 m from the receiver seaward. Within the channel (here, Ulong Channel), the receiver detected tags at an average of 746 m parallel to the channel, while distance perpendicular to the channel was constrained by the channel width, similar to the constraints for detection distances from the receiver to the reef crest (perpendicular to the barrier reef).

To enhance the potential for tag recovery, a reward scheme (US$5 plus fish market value) was broadcast island-wide on local AM radio and by flyer postings. Records for catch location and gear type were taken from local fishermen at the time of reward. Recaptured fish were reweighed and measured, and gonads and otoliths were extracted for subsequent life history analyses.

Analysis of catch probability

A separate creel survey was conducted in 2006 to determine the distribution of fishing effort within Pohnpei's small-scale commercial coral reef fishery (Rhodes et al., 2007). The 2006 effort data were used to estimate the number of likely recaptures for *P. areolatus* under a random distribution (postspawning dispersal) scenario (chi-square analysis, after a square-root transformation) for each municipality. For this analysis, those fish captured by researchers inside the KMS were excluded, as were an additional five individuals for which there was no recorded recapture location.

Results

Initial capture numbers, CPUE, and size distribution of fish

Between January and May 2005, 647 *P. areolatus* were captured and tagged at the Kehpara Marine Sanctuary over 33 fishing days and 170 fishing hours, with an estimated CPUE of 3.8 fish per hour per fisherman, to highlight the vulnerability of reproductive *P. areolatus* to hook-and-line fishing at the aggregation site. Catch included 511 males, 129 females, and 7 individuals that could not be identified to sex with macroscopic methods. Males typically preceded females in catch by 1–4 days, except in January when no females were taken (Table 1). The average sex ratio for catch (February–May) was 3.4 males:1 female, indicating either an absence of females within the January FSA or highly variable sex-specific differences in catch between January and other months. Late-stage vitellogenic oocytes were observed in all cannulated females, and no females were captured with hydrated oocytes (to indicate imminent spawning), although subsequent histological examination of gonads from recaptured individuals confirmed evidence of spawning activity. All males were ripe at the time of capture during all months of tagging.

Males captured at the FSA were, on average, larger than females. The size frequency range was 378–542 mm TL for mature females (mean ±standard error [SE]=458.0 ±2.8 mm TL], and 450–660 mm TL for mature males (mean=541.4 ±1.3 mm TL) (Fig. 2). Only males were present in size classes above 550 mm TL, and only females were observed in size classes below 440 mm TL. Individuals of undetermined sex ranged from 480 to 575 mm TL (mean=523.3 ±14.6 mm TL) and thus overlapped in size with mature males. The mean size of captured males declined slightly during the survey, while captured female mean size increased. During tagging, similar behavior, including courtship and territorial displays, was observed between tagged and untagged fish to indicate minimal or no effects from tagging on at least some behavior commonly associated with reproduction.

Conventional tagging

The majority of conventional tag recaptures occurred within the January–May spawning season and thus indicated that *P. areolatus* are most vulnerable during reproductive periods, whereas the potential for sexual selection to reduce reproductive output was reflected in the male-dominated capture and recapture sex ratio and the high spawning-site fidelity shown by males within the reproductive season. Of the 647 *P. areolatus* tagged, 59 individuals (9.1% of the total) were recaptured (Table 2), including 39 individuals recaptured by commercial fishermen and 20 individuals recaptured at the KMS by researchers during tagging. All individuals recaptured at the KMS were males. Among the males recaptured at KMS, 50% were taken one month after tagging, 15% were taken after two months, 20% after three months, and 5% after 4 months. At the KMS, one male was recaptured twice in the same month and another male was taken three times over three separate months—a finding that demonstrates that at least some individuals return repeatedly within the spawning season. Outside the KMS, fishermen recaptured 27 males, eight females, and one fish of unknown sex (at the time of tagging). Three additional recaptures by the fishery could not be identified either to sex (owing to illegibility of the information on the tag) or to recapture location (which was unreported) or both sex and recapture location were not identified. The fishery recapture sex ratio (individuals of known sex taken outside the KMS) was 3.4:1 male:female, which matched the sex ratio of fish captured during initial tagging within the KMS (Table 1). Recaptured fish remained at liberty from 1 to 328 days, averaging 71 days for those taken by the fishery and 51 days for fish retaken within the KMS by researchers. The maximum straight-line distance traveled by a recaptured fish was ~27 km between the KMS and Temmen (Fig. 1A).

Squaretail coralgrouper appear highly vulnerable to fishing within and in areas immediately near the FSA site. A total of 97.1% of all fish were recaptured within 12 km of the FSA site during the 17-month survey period, and 88% of the recaptures with reported locations were taken from areas north of the FSA. The fishery made 61.5% of all recaptures within the 5-month spawning season, and 25.6% of all recaptures occurred during the March–April sales ban period, which demonstrates the ineffectiveness of the ban in protecting reproductively active fish (Table 2). Reported recaptures by the fishery were primarily recaptured fish from the inner reef, including a substantial number from areas immediately adjacent to Peleng Channel (42% of all individuals) that included 88% of all females and 64% of male recaptured. The distribution of fishery recaptures significantly deviated from expectations (χ^2=10.911, 0.25<P<0.05) based on known catch records and area-specific effort data taken from 2006 creel surveys of the commercial reef fish fishery (Fig. 1). Only 3 of 59 recaptured fish were from locations south of KMS (Liap, Nalap, and Penieu), and only one individual was recaptured from the eastern side of the island (Fig. 1).

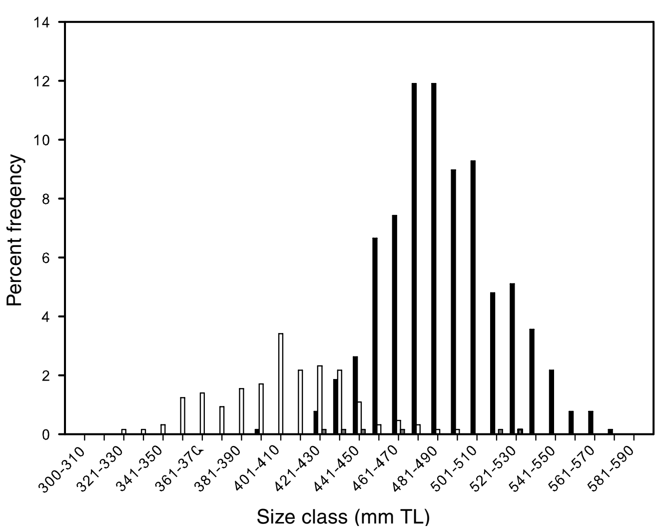

Figure 2

Size frequency distribution (mm total length, TL) of squaretail coralgrouper (*Plectropomus areolatus*, n=647) taken by hook and line from the Kehpara Marine Sanctuary during the initial tagging exercise in 2005. White bars=females; black bars=males.

Acoustic tagging

Of the 40 acoustically tagged fish, three individuals (7.5%) were recaptured by the fishery (January 2005: 2 males; March 2005: 1 female). Immediately after recapture, three replacement tags were deployed (February 2005: 2 males; April 2005: 1 female). Of the 43 total tag deployments, signals following initial detections were received from 13 of 22 males and 10 of 21 females (54% overall) to indicate high tag-induced mortality immediately after tagging or a rapid post-tag departure of individuals from the FSA without subsequent return. No predation was observed at KMS during snorkel or dive operations after the release of tagged individuals.

For those acoustically tagged individuals returning to the FSA, patterns of movement (seasonal and annual site visitation) were highly variable both within and among individuals (Table 3), although some individuals appeared to move along a common migratory corridor to reach the FSA where fishermen could potentially concentrate efforts and substantially impact reproductive populations. Data from four females and eight males provided point-to-point directional data to show a predominantly northward movement away from the FSA (i.e., north of the KMS southern MPA boundary) after spawning (Fig. 1B)— a movement that is reinforced by recapture data from conventional tagging (Fig. 1A).

Table 2

Temporal distribution of recaptured squaretail coralgrouper (*Plectropomus areolatus*) taken outside (by the fishery) and inside (by researchers) the Kehpara Marine Sanctuary (KMS). The entire shaded area represents the reproductive season and the sales ban period is darkly shaded. Months are abbreviated. CP, total = cumulative percent of total catch by month; CP, ban = cumulative percent contribution of the total recaptures within the sales ban period, including those by fishermen and researchers. All = the combined recaptures by the fishery (outside the KMS) and by researchers (within the KMS); *n* = sample size of recaptures within the study period; CP sample size (*n*) is that used to calculate cumulative percents; a = Peleng Channel or proximity; b = Dawak Channel or proximity; c = Nalap or vicinity; d = unknown locale; e = Liap; f = Penieu; g = Temmen.

		Year														
		2005												2006		
		Months												Months		
		J	F	M	A	M	J	J	A	S	O	N	D	J	F	*n*
Fishery	Recaptures	1[a]	5[a,d]	7[a,c]	3[a,b]	8[a,b,c]	3[a,b]	0	0	1[e]	1[a]	6[a,d,f]	0	2[a,g]	2[a]	39
	CP, total	3	15	33	41	62	69	69	69	72	74	90	90	95	100	39
	CP, ban	—	—	18	26	—										10
KMS	Recaptures	0	2	6	5	7										20
	CP, total	0	10	40	65	100										20
	CP, ban	—	—	30	55	—										11
All	CP, total	2	14	34	49	75	80	80	80	81	83	93	93	97	100	59
	CP, ban	—	—	22	36	—										21

Table 3

Presence (●) of acoustically tagged squaretail coralgrouper (*Plectropomus areolatus*) to show the observed variability in residency times (as site visitations) at the Kehpara Marine Sanctuary fish spawning aggregation (FSA) site over a 17-month period (January 2005–May 2006). The study period encompasses two complete reproductive seasons (~January–May). The table represents only individuals present at the FSA for one month or more after initial tagging.

	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M
Males	●	●	●	●	●												
	●	●															
	●	●	●														
	●	●	●												●	●	
	●	●	●														
	●	●	●	●	●	●	●	●	●	●		●	●		●	●	
	●	●	●	●													
	●	●		●	●	●	●	●	●	●	●						
Females		●	●		●	●	●						●	●	●	●	●
		●	●														
		●				●											
				●													
		●	●	●				●									

Travel speed for three fish that moved between Peleng Channel and the KMS (=8 km) was 2.1 km/h (1 female, 2 males), and all fish made the trip in ≤1 day. Although several acoustically tagged individuals moved southward to the KMS boundary, only one appeared to travel as far as Nalap. The apparent limited movement southward from the KMS is also reflected in the low number of conventional tag recaptures (n=4) from areas south or east of KMS. No movement was detected directly within Kehpara Channel, in contrast to previous anecdotal reports of post-spawning migrations through the channel. Some individuals were detected seaward of the channel.

Residence times at the FSA were sex-specific, thus creating a potential to promote sexual selection and negatively impact reproductive output when fishing was concentrated on the FSA. From acoustic results, we determined that males remained at the KMS over longer periods both within the reproductive season (2.2± 0.3 SE mo., males; 1.6 ±0.2 mo., females) and during the 17-mo. survey period (3.0 ±0.7 mo., males; 1.9 ±0.4 mo., females) (Table 3). Conversely, according to the acoustic data, males and females appeared to overlap entirely within a reproductive month. This overlap was not reflected in fisheries-dependent data because no females were captured ≥5 days before a full moon, whereas males were taken as early as 8–9 days before a full moon, indicating sex-specific variations in feeding or catchability.

Virtually all males acoustically tagged in January remained at the aggregation site until spawning was concluded in February, further enhancing the potential for sexual selection before actual spawning within the aggregation period. Few females appeared to remain at the FSA site after spawning during subsequent months. Only three individuals were present in all possible spawning months, and two males and three females returned to or resided at the KMS during nonreproductive periods (Table 3).

Discussion

The vulnerability of FSAs to overfishing is widely recognized (Sadovy and Domeier, 2005) and the present study shows the conditions under which FSA loss and possible population decline can occur. For example, under a hyperstable fishing scenario (no CPUE reduction in relation to abundance) and using CPUE estimates from this study (3.83 fish per hr per fisherman) and peak FSA abundance estimates for squaretail coralgrouper at KMS, only 250 fishing days at 6 h of fishing per day would be required to deplete the entire FSA, equivalent to only 36 fishermen fishing over 7 days. Such a scenario was borne out in 1998 when an estimated 4000 reproductively active fish were taken from the adjacent camouflage grouper FSA in just over 7 days (Rhodes and Sadovy, 2002). During that event, up to 20 boats with 2–3 fishermen/boat fished the aggregation daily with no observed change in CPUE, before the aggregation was included into the KMS by executive order in 1999. Underwater visual census (UVC) counts in later years showed that only several hundred camouflage grouper remained at the camouflage grouper FSA site and that only minor increases in abundance were apparent after 7 years of monitoring (2001–07). Similarly heavy aggregation fishing has resulted in either loss, near-extirpation, or a substantial reduction in FSA abundance elsewhere (e.g., Craig, 1969; Sadovy and Eklund, 1999; Sala et al., 2001).

Migratory corridors used by reproductive fish increase the vulnerability of *P. areolatus* (and other fishes) to overfishing by concentrating reproductively active or resting fish within confined areas similar to the FSA in our study. Although it is not clear whether all *P. areolatus* (at KMS or elsewhere) use these migratory corridors, several small groups of squaretail coralgrouper (5–10 individuals, presumably males) were observed moving southward along the reef between Peleng Channel and KMS and groups of up to 100 females (identification based on size and color) were observed moving in deeper water (20–30 m) toward the FSA during the spawning season. Groups of roving female squaretail coralgrouper have also been reported near FSA in the Solomon Islands during reproductive periods. Other serranids reported or suggested to use migratory corridors to reach FSAs include *Epinephelus guttatus* (red hind) in the U.S. Virgin Islands (Nemeth, 2005), *P. areolatus* in Palau, and *Epinephelus striatus* (Nassau grouper) in Belize (Starr et al., 2007). In each case, fishermen apparently target the unprotected areas where fish congregate, thereby reducing the effectiveness of existing MPAs to protect reproductive individuals, as observed in Pohnpei. The apparent targeting of these migratory corridors and the ease by which fishermen can remove individuals from these and other areas where fish congregate highlights the need to identify and incorporate those areas into MPAs.

The observed sex-specific differences in the behavior of *P. areolatus* within the reproductive season have the potential to promote selective fishing and to impact the spawning sex ratio and reproductive output (e.g., Beets and Friedlander, 1998). In Pohnpei, sex-specific behavioral differences were manifested as 1) a greater abundance of males in FSA-catch both seasonal and monthly, particularly in January when no females were captured; 2) the persistence of males at the FSA over several weeks during the initial aggregation period (January–February); and 3) longer male residency times at the FSA seasonally. Similar to the current study, previous studies of FSA-forming serranids have also shown that males often precede females to the FSA and, therefore, have longer residency times (Samoilys, 1997; Rhodes and Sadovy, 2002; Starr et al., 2007). For squaretail coralgrouper, longer residency times appear to increase the catchability of males. Alternatively, males may outnumber females at the FSA site in all months and be reflected in the catch sex ratio. Further fisheries-independent assessments of aggregation (and population) sex ratio are needed to confirm whether males indeed outnumber females. Acoustic data also indicate that in addition to taking bait over more days than females, male squaretail coralgrouper frequent the FSA over more months—a finding that is similar to those from acoustic surveys of Nassau grouper in Belize (Starr et al., 2007) and UVC monitoring of freeze-brand tagged leopard coralgrouper (*P. leopardus*) along the Great Barrier Reef (Zeller, 1998). Fisheries-dependent size data from FSA catch have also indicated protracted residency times for male red hind in the U.S. Virgin Islands (Nemeth, 2005). Protracted male residency time may increase the potential for sexual selection, leading to adverse affects on reproduction, such as sperm limitation (Coleman et al., 1999). Similarly, the removal of larger individuals (males in protogynous species) may lead to reductions in the mean size of both males and females (from compensated sex change) to reduce overall fecundity (Vincent and Sadovy, 1998) and, in the case of extreme operational sex ratios, may adversely affect reproductive behavior. At the KMS FSA, males appeared to be more vulnerable to line fishing than were females, comprising 79% of the catch during tagging operations and representing all recaptures within the KMS. Males also dominated recaptures by the fishery among spear-caught individuals. Interestingly, females and juvenile squaretail coralgrouper dominated marketed catch of squaretail coralgrouper overall, and 97% of the marketed catch in 2006 was smaller than the mean size of sexually mature males (Rhodes and Tupper, 2007). Thus, in Pohnpei, the potential currently exists for both growth overfishing and recruitment overfishing and there is an urgent need for a thorough examination of island-wide stock levels and sustainability within the squaretail coralgrouper fishery, as well as the sustainability of both the subsistence and other fisheries targeting FSAs. One possible explanation for the paucity of females in catch is that recaptured females went unreported or that fishermen targeted larger individuals (i.e., males) to benefit from the combined higher fish value and reward. An improvement to our study would be to perform real-time observations of the fishery at heavily fished locations, such as Peleng Channel, to verify the sex ratio of the catch.

Among acoustically tagged individuals, the data showed a high degree of variation in the seasonal pattern and duration of stay for individuals that frequent the FSA site. Although these results could be explained in part by mortality (natural, fishing, and tag-induced, particularly acoustic) or a failure of receivers to detect all fish present, similar variability has been shown elsewhere for serranids with the use of these and other tagging methods (e.g., Zeller, 1998; Starr et al., 2007). In Pohnpei, a gradual reduction in the number of acoustically tagged individuals returning to the FSA was observed within a reproductive year; only 50% of tagged individuals returned in the month after initial tagging. Similar findings were found for acoustically tagged Nassau grouper in Belize, where no more than 50% of tagged *E. striatus* males and 52% of tagged females were present during any reproductive month following tagging (Starr et al., 2007). Nassau grouper returning to the FSA after having been tagged showed a similar sequential decrease in numbers. On the Great Barrier Reef, only 31% of tagged mature leopard coralgrouper participated in spawning aggregation activities within a reproductive year; this percentage may indicate that individuals do not spawn annually (Zeller, 1998). Although Zeller (1998) suggested that tagged individuals may reproduce outside FSAs, spawning outside aggregations for FSA-forming species has not been shown. Likewise, high site fidelity has been shown for a number of serranids, with individuals observed moving past an active conspecific FSA to return to the site where they previously spawned. Sequential reductions in the number of conventionally tagged red hind have also been shown in the U.S. Virgin Islands (Nemeth et al., 2007). Although it is possible that the observed findings could be explained by natural or fisheries-related mortality, it seems more likely that some adults do not participate in all potential spawning months within the reproductive season and that some may not spawn in consecutive years. Although more investigations are needed, if these implications are correct, individual (monthly) FSAs represent subsets of the reproductive population, and these subsets complicate monitoring programs that solely use FSAs to estimate reproductive population abundance and changes therein. Regardless, these results indicate that the relationship between a FSA and the adult population is complex and additional work is needed on serranid reproductive dynamics for designing effective monitoring and management strategies for adult populations and in understanding impacts on these populations through FSA-targeted fishing.

The assessment of catchment areas for aggregating serranids by using tagging methods is relatively new, yet necessary to complete our understanding of reproductive population dynamics and to determine sustainability when fishing efforts are unevenly distributed. In Pohnpei, support for a catchment area of ~200–300 km^2 for the KMS-based squaretail coralgrouper FSA is provided from recapture data that indicates short-scale (10–12 km) movement of individuals in relation to the FSA after spawning. The observed recapture patterns do not appear to be strictly tied to area-specific fishing effort because Kitti municipality receives only 50% of fishing efforts statewide, yet >95% of recaptures occurred within a relatively small area of the municipality (Rhodes et al., 2007). Although it is possible that fishing effort during spawning months (and full moon periods) is more concentrated in Kitti than at other municipalities, such a pattern was not borne out from over 1000 interviews (2006) of fishermen participating in commercial fishing activities. Thus, for squaretail coralgrouper in Pohnpei, the reproductive population in relation to the KMS spawning aggregation appears to be highly localized and thus management could be applied to individual aggregations, in addition to combined aggregations within Pohnpei. Similar to sex-specific residency patterns, other studies of FSA-forming serranids also indicate that adults are concentrated within relatively small areas in relation to their respective FSA. For example, evidence exists for confined catchment areas for red hind determined from two FSAs in the U.S. Virgin Islands: 1) 500 km^2 for the St. Thomas FSA and 2) 90 km^2 for the St. Croix site FSA (Nemeth et al., 2007). The catchment area for Nassau grouper at the Glover's Reef Atoll FSA (Belize) appears to be no more than 384 km^2 (Starr et al., 2007). For *P. leopardus* along the Great Barrier Reef, Zeller (1998) estimated a catchment (migration) area of ca. 80 km^2. For these species, data clearly indicate limited movement by (most) individuals after spawning and highlight the potential for localized extinction and associated impacts to fish community structure and fisheries from FSA fishing (or unsustainable fishing of individuals at earlier life history stages). The data also provide additional support to suggest that, while possible, long distance movement by reproductively active serranids may be more rare than previously assumed and that many aggregating grouper are resident to areas near the spawning site.

The effectiveness of the no-take year-round KMS to protect *P. areolatus* FSAs is evident, because without this protection, thousands of groupers could be removed within the spawning season and there would be the potential for rapid FSA loss and localized population extinctions. Regardless of the effectiveness of the KMS in protecting spawners at the spawning site, the potential for the fishery to impact the reproductive individuals still exists. Spawners are being taken along migratory corridors or other areas where fish congregate outside the KMS, with the potential to meet or exceed the level of fishing mortality experienced under aggregation fishing. In Pohnpei, problems with the existing sales-ban strategy are now evident. Firstly, 36% of all recaptured fish are taken during serranid sales ban months. Secondly, the serranid sales ban was recently shown to place added pressure on other equally vulnerable commercial species not currently managed, such as scarids (Rhodes et al., 2007). The increase in catch volume of scarids, for example, implies that fishermen have greater concern for maintaining catch volume than for the survival of individual species and indicates that efforts should be concentrated on measures to reduce overall catch volume. Similar reductions may be needed in catch volume of juveniles and small adults to stem potential recruitment overfishing. Thus, effective protection of reproductively active serranids will require innovative solutions that provide protection for both reproductive and nonreproductive individuals, while alleviating the potential negative effects of individual species management. The results from this and related studies highlight the complexities of reproductive population dynamics for aggregating serranids and support total protection through no-take bans during reproductive periods and no-take areas that support aggregations and associated areas where reproductive individuals congregate. Future studies should be designed to fill the gaps in our current understanding of serranid stocks in Pohnpei to enable a determination of sustainable harvest levels. Numerous examples globally indicate that the current harvest of reproductive adults and targeting of juveniles is currently unsustainable and that population declines and aggregation losses are imminent without a rapid move toward improved management.

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Literature cited

Aguilar-Perera, A.
2007. Disappearance of a Nassau grouper spawning aggregation off the southern Mexican coast. Mar. Ecol. Prog. Ser. 327:289–296.

Beets, J., and A. Friedlander.
1998. Evaluation of a conservation strategy: a spawning aggregation closure for red hind, *Epinephelus guttatus,* in the U.S. Virgin Islands. Environ. Biol. Fishes 55:91–98.

Chapman, R. W., G. R. Sedberry, C. C. Koenig, and B. E. Eleby.
1999. Stock identification of gag, *Mycteroperca microlepis*, along the southeast coast of the United States. Mar. Biotechnol. 1:137–146.

Coleman, F. C., C. C. Koenig, A.-M. Eklund, and C. B. Grimes.
1999. Management and conservation of temperate reef fishes in the grouper-snapper complex of the southeastern United States. *In* Life in the fast lane: ecology and conservation of long-lived marine animals (J. A. Musick, ed.), p. 233–242. Am. Fish. Soc., Bethesda, MD.

Coleman, F. C., C. C. Koenig, G. R. Huntsman, J. A. Musick, A. M. Eklund, J. C. McGovern, R. W. Chapman, G. R. Sedberry, and C. B. Grimes.
2000. Long-lived reef fishes: the grouper-snapper complex. Fisheries 25:14–20.

Craig, A. K.
1969. The grouper fishery of Cay Glory, British Honduras. Ann. Assoc. Am. Geogr. 59:252–263.

Matos-Caraballo, D., J. M. Posada, and B. E. Luckhurst.
2006. Fishery-dependent evaluation of a spawning aggregation of tiger grouper (*Mycteroperca tigris*) at Vieques Island, Puerto Rico. Bull. Mar. Sci. 79(1):1–16.

Nemeth, R.
2005. Population characteristics of a recovering US Virgin Islands red hind spawning aggregation following protection. Mar. Ecol. Prog. Ser. 286:81–97.

Nemeth, R. S., J. Blondeau, S. Herzlieb, and E. Kadison.
2007. Spatial and temporal patterns of movement and migration at spawning aggregations of red hind, *Epinephelus guttatus*, in the U.S. Virgin Islands. Environ. Biol. Fishes 78:365–381.

Olsen, D. A., and J. A. LaPlace.
1979. A study of a Virgin Islands grouper fishery based on a breeding aggregation. Proc. Gulf Caribb. Fish. Inst. 31:130–144.

Rhodes, K. L., and Y. Sadovy.
2002. Temporal and spatial trends in spawning aggregations of camouflage grouper, *Epinephelus polyphekadion* (Bleeker 1849) in Pohnpei, Micronesia. Environ. Biol. Fishes 63:27–39.

Rhodes, K. L., and M. H. Tupper.
2007. A preliminary market-based analysis of the Pohnpei, Micronesia, grouper (Serranidae: Epinepheline) fishery reveals unsustainable fishing practices. Coral Reefs 26:335–344.

Rhodes, K. L., M. H. Tupper and C. B. Wichilmel.
2007. Characterization and management of the com-

mercial sector of the Pohnpei coral reef fishery, Micronesia. Coral Reefs, DOI (digital object identifier) 10.1007/x00338-007-0331.

Rose, G. A.
1993. Cod spawning on a migration highway in the northwest Atlantic. Nature 366:458–461.

Sadovy, Y. J., and M. Domeier.
2005. Are aggregation-fisheries sustainable? Reef fish fisheries as a case study. Coral Reefs 24:254–262.

Sadovy, Y., and A. M. Eklund.
1999. Synopsis of biological data on the Nassau grouper, *Epinephelus striatus* (Bloch, 1792), and the jewfish, *E. itajara* (Lichtenstein, 1822). NOAA Tech. Rep. NMFS 146, 68 p.

Sadovy, Y. J., T. J. Donaldson, T. R. Graham, F. McGilvray, G. J. Muldoon, M. J. Phillips, M. A. Rimmer, A. Smith, and B. Yeeting.
2003. While stocks last: the live reef food fish trade, 147 p. Asian Development Bank Publs., Manila, Philippines.

Sala, E., E. Ballasteros, and R. M. Starr.
2001. Rapid decline of Nassau grouper spawning aggregations in Belize: Fishery management and conservation needs. Fisheries 26:23–30.

Samoilys, M. A.
1997. Movement in a large predatory fish: coral trout, *Plectropomus leopardus* (Pisces: Serranidae), on Heron Reef, Australia. Coral Reefs 16:151–159.

Starr, R. M., E. Sala, E. Ballesteros, and M. Zabala.
2007. Spatial dynamics of the Nassau grouper *Epinephelus striatus* in a Caribbean atoll. Mar. Ecol. Prog. Ser. 343:239–249.

Tupper, M., and K. Able.
2000. Habitat use, movements, and food habits of striped bass (*Morone saxatilis*) in Delaware Bay (USA): comparisons between a restored and a reference salt marsh. Mar. Biol. 137:1049–1058.

Vincent, A. C. J., and Y. Sadovy.
1998. Reproductive ecology in the conservation and management of fishes. *In* Behavioural ecology and conservation biology (T. Caro, ed.), p. 209–245. Oxford Univ. Press, New York, NY.

Zeller, D. C.
1998. Spawning aggregations: patterns of movement of the coral trout *Plectropomus leopardus* (Serranidae) as determined by ultrasonic telemetry. Mar. Ecol. Prog. Ser. 162:253–26.