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Goldspotted spinefoot *Siganus punctatus* (Siganidae) age-based reproductive life history and fisheries vulnerability

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RUNNING HEAD: *SIGANUS PUNCTATUS* AGE-BASED LIFE HISTORY

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Between February 2015 and 2016, samples of the Indo-Pacific goldspotted spinefoot *Siganus punctatus* were taken from local fish markets, feeding sites and nursery grounds on the main island of Pohnpei, Micronesia, to ascertain sexual pattern, reproductive seasonality, age, growth and mortality. Microscopic examinations of gonads identified two seasonal peaks in reproduction: February to May and September to December, with evidence of some spawning activity in most months. Ripe females were observed four days on either side of the new moon. Females first matured at *c.* 180 mm fork length (L_F) and 1 year of age, which coincides with their entry into the fishery. Ninety five per cent of individuals were less than 3 years and the oldest fish were 8 years. To examine the species vulnerability to fishing, a tag-and-recapture study was conducted over four months in 2015 in a locally managed marine area and at an unprotected site. Findings suggest high residency and high vulnerability to fishing at shallow-water feeding sites and restricted migration overall. The placement of marine protected areas within critical habitat appears to be an effective conservation strategy for this species, particularly when combined with gear and seasonal market restrictions during vulnerable life-history phases.

Key words: fishery; herbivory; marine protected areas; Micronesia; rabbitfish; Siganidae.

INTRODUCTION

Rabbitfish and spinefoot (Siganidae) are herbivorous species that are key components of coral-reef fish and coastal fisheries communities throughout their ranges. As browsers and grazers of macroscopic algae, rabbitfish play important roles in ecosystem function by helping to limit algal growth, maintaining coral-reef community structure (Thacker *et al*., 2001; Folke *et al.*, 2004; Fox *et al.*, 2009; Bennett & Bellwood, 2011) and improving conditions for coral recruitment, recovery and persistence (Hughes *et al*., 2007). Rabbitfish are also of great interest to aquaculture throughout the world because of their general life histories, in particular, high fecundity, frequent spawning, fast growth and maturation and lower trophic requirements. While rabbitfish life histories are characteristic of fishes generally resilient to overfishing, they have nonetheless been overexploited in some areas (Mehanna & Abdallah, 2002; Grandcourt *et al*., 2007; Soliman *et al*., 2008).

Rabbitfish have been variously categorized based on diet (*e.g.* Hoey *et al.*, 2013) and general morphological characteristics, such as snout length and body proportions, [*i.e.* fusiform: *e.g. Siganus fuscecens* (Houttuyn 1782), *Siganus sutor* (Valenciennes 1835), *Siganus canaliculatus* (Park 1797) and deep-bodied: *e.g. Siganus puellus* (Schlegel 1852), *Siganus punctatus* (Schneider & Forster 1801), *Siganus doliatus* Guérin-Méneville 1829-38] (Woodland, 1990), which has generally been supported by molecular phylogenies (Borsa *et al*., 2007). Rabbitfish are also dichotomized by their non-reproductive associations with other conspecifics, either as schooling or pairing, although there have been observations within species of both types of associations [*e.g. Siganus javus* (L. 1766), *Siganus woodlandi* Randall & Kulbicki, 2005. These non-reproductive associations may not be reflective of their spawning patterns (*i.e.* non-reproductive pairing species spawning in aggregations), which need to be considered during assessments of their vulnerabilities to fisheries and management planning (Fox *et al.*, 2015). Most research to date has been conducted on schooling species, particularly for aquaculture purposes [*e.g. S. canaliculatus* (Sabapathy & Teo, 1993); *Siganus lineatus* (Valencinnes 1835) (Soto, 1995); *Siganus rivulatus* Forsskål & Neibuhr 1775 El-Dakar *et al*., 2007; *Siganus guttatus* (Bloch 1787) (Harvey *et al.* 1985; Duray & Kohno, 1988)], but little has been done until recently on the reproductive aspects of pairing species in the wild (Park *et al.*, 2006; Fox *et al*., 2015 for *S. doliatus*).

Within the Siganidae, many species have been evaluated for age, growth and reproductive life history (Ntiba & Jaccarini, 1988; Al-Marzouqi *et al*., 2011; Taylor *et al*., 2016) and some have been examined for movement, home range and residency to understand area and habitat requirements (Bellwood *et al*., 2016; Weeks *et al*., 2016), but few have combined these types of assessments (Fox & Bellwood, 2011; Bijoux *et al*., 2013). Overall, most siganid research has been conducted in captive conditions for aquaculture purposes (Lam, 1974; Hara & Kohno, 1986; Duray, 1998; Takemura *et al.*, 2004). For most species, there has been little life-history research in the wild, particularly age-based research. Among species with a paucity of life-history information is the gold-spotted spinefoot *S. punctatus*, which pair as adults. Apart from examinations of feeding and anecdotal reports of spawning sites and times (Johannes, 1981) the species' life history has heretofore not been fully investigated even though it is common to catches throughout its distributional range and has the potential to be affected from overfishing and habitat loss from man-made and natural disturbances.

Where data exists for the tropical Pacific Ocean, rabbitfish are shown to be important components of local small-scale fisheries (Rhodes *et al*., 2008; Taylor *et al*., 2016; J. Cuetos-Bueno & D. Hernandez, unpubl. data; K. Rhodes & D. Hernandez, unpubl. data). In the Solomon Islands, 14 species of rabbitfishes are currently represented in commercial catches, including *S. punctatus* (K. Rhodes, unpubl. data). In Chuuk (Federated States of Micronesia; FSM), seven species of rabbitfish were identified in markets, representing 5.7% of commercial biomass in 2014 (J. Cuetos-Bueno & D. Hernandez, unpubl. data). In Palau, six species of rabbitfishes are preferred or opportunistic targets, including *S. punctatus* (Bejarano *et al*., 2014). In 2005, market surveys in Pohnpei, FSM, identified *S. punctatus* as the eighth most common species in speared (51% of all catches examined) and netted (26% of all catches examined) catches (Rhodes *et al*., 2008), while a later survey found *S. punctatus* present in 98.8% of catches that included herbivorous species (Bejarano *et al*., 2013). Volumetric contributions by siganids in Pohnpei in 2005 were 6.4% of total catch, but had increased to 8.0% by 2015 (K. Rhodes & D. Hernandez, unpubl. data), suggesting that rabbitfish may require some management to prevent overfishing. These observations and the general lack of biological information for siganids also suggest the need for improving understanding of rabbitfish life histories, including habitat use, to develop the most appropriate management strategies.

In Pohnpei, a partnership between the local Conservation Society of Pohnpei (CSP; www.serehd.org) and the Nan Wap (Madelonimw Municipality) communities of Dolopwail, Lukop, Aparahk and Metipw enabled the designation of a locally managed marine area (LMMA) in 2010 that incorporates nearshore coral-reef habitat, including healthy seagrass beds where rabbitfish are known to feed. To examine the functionality of this small-scale LMMA for rabbitfish protection, a tag–recapture programme was conducted in 2015 within the LMMA and at a second, more distant and unprotected control site in 2016, with the objective of examining rabbitfish movement and fishing vulnerability, including for *S. punctatus* (local name: palapal). In addition, a 10 year follow-up fish-market survey was conducted in 2015 to gauge potential changes in catch and size composition within the small-scale fishery, thereby allowing samples of *S. punctatus* to be collected for life-history analyses. These parallel surveys were done to inform management and identify potential changes to existing management that may benefit these and other rabbitfish species.

MATERIALS AND METHODS

REPRODUCTION

The study was conducted throughout the main island of Pohnpei, one of the four FSM island states in the Caroline Islands chain in the western Pacific Ocean (Fig. 1). Samples for reproductive, age, growth and mortality analyses were collected from 21 fish markets around the island (19 February 2015 to 11 February 2016), with supplemental samples collected during a 4 month tag–recapture exercise within the Nan Wap (Madelonimw Municipality) LMMA (06^{o} 522 N; 158^{o} 202 E) (16 February - 20 March 2015) and in Enipein, Kitti Municipality (06^{o} 462N; 158^{o} 132E to 06^{o} 472N; 158^{o} 102E) (8–9 March 2016). Fish < 150 mm fork length (L_F) that had not been recruited to the fishery were collected opportunistically by spear to provides samples for the growth curve and identify early gonad maturation. Following sampling, fish were measured (nearest mm L_F) and weighed (total mass, M_T, nearest 1.0 g) before removing gonads. Sampled gonads were weighed wet (M_G, nearest 0.1 g) and stored in 10% formalin prior to transfer to 70% ethanol.

For assessment of gonad development stage and sex, a small (*c.* 4 mm^2) section of larger gonads (gonads *c.* >1.0 g) or the whole gonad (gonads *c.* < 1.0 g) was taken from each sample, stained (eosin and haemotoxylin), processed (Leica TP1050 tissue processor; www.leica.com) and sectioned transversely (0.7 µm) (University of Davis Department of Pathobiological Sciences, Davis, CA, U.S.A.). Gonad staging used criteria previously developed for the gonochoristic camouflage grouper *Epinphelus polyphekadion* (Bleeker 1849) (Rhodes *et al*., 2011; (Supporting Information Table SI). Sectioned gonads were examined microscopically under (x10– x200) magnification. Females were considered mature if they had vitellogenic or late-stage, hydrated oocytes, or had signs of prior spawning that included a thickened tunica, post-ovulatory follicles and muscle bundles. Although five stages of male development were identified, none were definitively classified as immature owing to the difficulty in differentiating between early maturation-stage males and resting, mature males. Once development stages were ascertained, individuals were assessed by fish length for size and age at sexual maturity and grouped by development stage and month to identify reproductive seasonality. Determinations of sexual pattern followed criteria outlined by Sadovy de Mitcheson & Liu (2008). The gonado-somatic index (I_G) was used to aid in identifying seasonal reproductive activity at a monthly resolution, where $I_G = 100M_GM_T^{-1}$. Spawning times, with respect to the lunar cycle, were examined using mature, ripe and spent females.

AGE, GROWTH AND MORTALITY

For age, growth and mortality assessments, a random sub-sample of fish taken throughout the year and from each size class was used. For each individual, one sagittal otolith was weighed and sectioned using a GEMMASTA GFL8 faceting machine (Shall-Lap Supplies Ltd; www.shell-lap.com.au). Thin transverse sections of 150 µm were taken through the core, by mounting sagittae on a clear glass slide using thermoplastic glue (Crystalbond 509, Agar Scientific; www.agarscientific.com) and grinding each side to the primordium using a 1600 grit diamond lap. Otoliths were examined on three separate occasions by a single reader and assigned an age (Supporting Information Fig. S1) when two or more readings matched, which occurred for every specimen. Juvenile fish with no annuli were polished further using 9, 3 and 0.3 µm lapping film, until clarity of daily growth increments was optimized. As before, daily growth increments were interpreted on three separate occasions. Final ages were estimated as the mean of the three separate counts provided all counts were within 10% of the median. Length-at-age data was fitted to the von Bertalanffy growth function (VBGF) using non-linear least-squares procedures to estimate sex-specific growth parameters. The VBGF is represented by: $L_t = L \; [1 - e^{-K(t - t0)}]$, where L_t is the L_F of a fish at age t, L is the mean asymptotic L_F, K is the growth coefficient which describes the rate at which fish grow towards L, t is the age of the fish and t_0 is the theoretical age at which L_F is equal to zero, as described by the growth rate. The t_0 was fixed at 0 to adequately describe early growth trajectories from hatching in the absence of large numbers of young (< 1 year) fish. These parameters were compared between sexes using bivariate 95% confidence ellipses surrounding the *K* and *L* estimates (Kimura, 1980). Total mortality (*Z*) was estimated from sex-specific age structures using age-based catch curves. The natural logarithm of the number of fish in each age class was plotted against its corresponding age and *Z* was estimated as the absolute value of the slope from a fitted line. The equation of Hoenig (1983) was used to derive an estimate of natural mortality (*M*) based on maximum observed age (t_{max}), under the assumption that maximum observed age reflects the true life span and therefore $Z = M$, where $Z = e^{[1.46 - 1.01\ln(t_{max})]}$.

TAG–RECAPTURE AND FISHERIES VULNERABILITY

For fish vulnerability and movement, several rabbitfish species, including *S. punctatus* were sampled using 30.5 m (1002) monofilament gillnets with 5 cm (22) net mesh from inner reef areas within the Nan Wap LMMA (tag recapture: 16–18 February and 18–20 March 2015; recapture only: 17–18 April and 17–18 May 2015; new moon 18 February, 20 March, 18 April and 18 May) and the unprotected Enipein site (tag recapture: 8–9 March 2016; new moon 9 March). The two sites differ in that the Nan Wap LMMA (3.05 km^2) contains abundant, healthy seagrass beds on broad reef flats, while Enipein is open to fishing and characterized by mechanically degraded reefs from fishing (*i.e.* dead and damaged corals) with little remaining seagrass. Numerous channels surround both sites and connect mangrove, lagoon and outer reef habitats. Tagging at all sites and times used identical methods and gears, although sample sizes, as net sets, were conducted at Enipein over only 2 days in 1 month. At each site, nets were extended across the target area, with rabbitfish driven into the nets by a team of fishers before encircling the targeted fish. All effort was at or following sunrise during outgoing low tide over 3 (Nan Wap) or 2 (Enipein) days just before and including new moon. Fishing for tagging at each site continued until the tidal level was too shallow to fish (*c.* < 30 cm). Captured fish were removed from the net and held in seawater in a round holding container (3 m diameter by 1 m depth), individually removed for tagging, identified to species, measured to the nearest mm L_F and tagged without anaesthesia between the dorsal pterigiophores with a uniquely numbered T-bar type spaghetti tag (Floy Tag; www.floytag.com) prior to release at the point of capture. All tags were printed with unique identification numbers, a telephone contact number and REWARD in local language. To expand participation, announcements about the programme and reward were repeatedly made during the project *via* local public radio. Rewards for recaptured fish were made through to May 2016, with the general or specific locations of all returned tags recorded and mapped. The mark–recapture surveys were conducted to examine potential distance of movement (as reported recapture locations), site use (as repeated recaptured by individuals at the tagging site) and fisheries vulnerability (as the per cent of tagged fish recaptured outside the LMMA), with an understanding that some recaptures may have been unreported, reported using false location information or that some tags may have dropped off fish prior to capture. Fishing vulnerability was measured as the percentage of fish recaptured relative to the number tagged, whether within the LMMA study area or outside.

RESULTS

REPRODUCTION

From 19 February 2015 and 11 February 2016, 368 *S. punctatus* gonads were collected primarily from markets, with supplemental samples taken during tagging or through spearing. Sizes of all individuals ranged from 61 to 263 mm L_F (mean ± S.E. = 214.2 ± 1.5 mm L_F).

Microscopic gonad analyses were conducted on a sub-sample of 281 fish ranging in size from 77 to 273 mm L_F (mean ± S.E. = 214.3 ± 1.8 mm L_F). Immature females (n = 67) ranged from 162 to 252 mm L_F (mean ± S.E. = 199.9 ± 2.8 mm L_F), while mature females (n = 99) were 228.9 ± 2.0 mm L_F. Mature males (n = 109) ranged from 143 to 272 mm L_F (mean ± S.E. = 2142.6 mm L_F), with no significant difference in size between males and females (Student's t-test: $\alpha = 0.05$, $P > 0.05$; d.f. = 2).

Based on microscopic gonad analysis, the species is gonochoristic, with no indication of sex change observed. Reproductive seasonality from I_G analysis suggests a February–

June spawning season with some activity in November, but microscopy revealed spawning activity, as hydrated and spent oocytes, from February to May and September to December (Fig. 2). Although the sample size in October was relatively robust, no reproductively active females were observed. In contrast, vitellogenic eggs indicating potential reproductive activity were observed in all but 3 months of the year, which included July, with only six samples. The combined data suggest a primary spawning period from February–May and a secondary period from September–December, with reproductively mature gonads observed in most months portending possible monthly reproduction.

For lunar periodicity, 23 ripe and three spent females were used to estimate spawning times relative to the new moon. Females with hydrated oocytes were observed from four days prior to 4 days after new moon, while spent females were observed only on days 3 and 4 after new moon.

AGE, GROWTH AND MORTALITY

For age, growth and mortality estimates, a random sub-sample of 116 individuals was examined following removal of one or both sagittae. Samples for age analysis included 64 females, 44 males and 4 individuals with undifferentiated tissue. The smallest individuals in the fishery were all mature, with individuals less than 160 mm L_F taken outside the fishery specifically for the purpose of life-history assessment [Fig. 3(a)]. The smallest mature female was 183 mm L_F and 1 year of age, while the oldest female was 8 years old. The estimated instantaneous rate of Z = 0.46 [Fig. 3(b)] and M = 0.53 yr^{-1}, which is actually below that estimated for Z from the age-based catch curve, suggesting that the estimate of Z may be low as a response to a sampling or selection bias. Among females sampled for age, 71.9% ranged between 1 and 2 years old. For females, the size at 50% sexual maturity was reached at 214 mm L_F [Fig. 4(a)], while 50% age at sexual maturity occurred at 1.5 years [Fig. 4(b)]. Growth trajectories and associated growth parameters of males and females were virtually identical (Fig. 5). The VBGF parameters for *S. punctatus* (collectively across sexes) were L = 241 mm L_F and K = 1.66 yr^{-1}.

TAG-RECEPATURE AND FISHERIES VULNERABILITY

In 2015, 864 *S. punctatus* ranging in size from 165 to 267 mm L_F (mean ± S.E. = 222.0 ± 0.5 mm L_F) were captured and tagged in the protected Nan Wap LMMA. An additional 81 and 31 rabbitfish were captured and examined for tags in April and May 2015, respectively, at Nan Wap. A total of 53 *S. punctatus* were recaptured within the Nan Wap LMMA during tagging surveys (6.1% of the total), with an additional five tags taken outside the LMMA by the fishery (0.6%) (Fig. 1). Recaptured fish during Nan Wap tagging were taken in the same month as initial tagging or 1 or 2 months post-tagging to show site fidelity to feeding locations. Nan Wap tagged fish were at liberty for a mean ± S.E. of 35.7 ± 2.6 days, while those recaptured by the fishery remained at liberty 35.8 ± 7.0 days.

In contrast, only 7 *S. punctatus* ranging from 176 to 235 mm FL (mean ± S.E. = 208.4 ± 7.1 L_F) were captured and tagged in Enipein during March 2016 sampling. At Enipein, only one of seven tagged fish was recaptured (14.3% of the total), with a time at liberty of 41 days (Fig. 1). For both sites, recaptures ranged from 1 to 89 days at liberty varied by month, however most tagged fish (80%) were recaptured in the month immediately following tagging, with 20% recaptured after 1 month.

DISCUSSION

Similar to other *Siganus* spp. examined for life history, *S. punctatus*, was shown to be an early maturing, fast-growing and short-lived species, with seasonally defined reproduction and a gonochoristic sexual pattern. Although some evidence (*e.g.* vitellogenic oocytes) suggests possible monthly spawning, two definitive reproductive periods were identified through mature, ripe and spent ovaries: a primary period from February–May and a secondary period from September–December. Secondary reproductive periods have been reported for only a few *Siganus* spp. (Ntiba & Jaccarini, 1990; Takemura *et al*., 2004; Park *et al*., 2006; Agembe, 2012; Taylor *et al*., 2016). For

S. punctatus, the primary spawning season coincided with seasonal low sea surface temperatures, similar to that reported regionally for Forktail spinefoot *Siganus argenteus* (Quoy & Gaimard 1825) in the Commonwealth of the Northern Mariana Islands and a number of other regional aggregating coral-reef fishes, including some unicornfish [*e.g.* bluespine unicornfish *Naso unicornis* (Forsskål 1775)] (Taylor *et al*., 2014) and epinephelid groupers [*e.g.* squaretail coralgrouper *Plectropomus areolatus* (Rüppell 1830) and brown-marbled grouper *Epinephelus fuscoguttatus* (Forsskål 1775)] (Rhodes *et al*., 2014). In addition to water temperature, Park *et al*. (2006) also noted the seasonal onset of reproduction for little spinefoot *Siganus spinus* (L. 1758) and *S. argenteus* in Chuuk (FSM) in concert with increasing photoperiod. For *S. punctatus*, confirmation of spawning, as spent ovaries, were observed 3 and 4 days past new moon, but ripe ovaries were present from 4 days prior to 4 days after new moon, suggesting a protracted spawning period. The latter generally corresponds to accounts by Johannes (1981) who first reported *S. punctatus* spawning in Pohnpei at new moon and for several days thereafter, based on anecdotal accounts from fishers.

Although the actual spawning site was not identified during the current study, recapture data suggest *S. punctatus* spawn within the boundaries of the LMMA, based on the limited number of recaptures by the fishery. Some additional recaptures without tag returns were anecdotally reported, however the recapture locations and species identification and tag numbers of these fish remain unknown. Past studies for other species (*e.g. S. sutor*, *S. doliatus*) suggest that at least some *Siganus* spp. migrate over relatively long distances (*e.g.* 3 km) along common reproductive migratory corridors to reach spawning sites (Bijoux *et al*., 2013; Samoilys *et al*., 2013; Fox *et al*., 2015), which may increase their vulnerability to fishing and affect overall reproductive output. For the current study, recorded recaptures primarily occurred during subsequent sampling during tagging exercises and occurred within the LMMA. Those tags returned by the fishery were reportedly taken from nearby channel sites proximate to or within the Nan Wap LMMA. Anecdotal reports from Pohnpeian and Palauan fishers identified spawning sites near or in outer reef passages (Johannes, 1981). The combined tag-recapture data suggest limited movement away from the tagging site, *i.e*. high residency and supports the value of small-scale marine protected areas encompassing critical habitat in protecting populations of *S. punctatus*. In contrast, tag-recapture data from unprotected areas of Enipein, which are characterized as receiving high levels of fishing pressure, identified the need for protected areas in other areas of Pohnpei where critical habitat for this species exists.

As noted in an earlier account of *S. argenteus*, there are few age-based reproductive studies of siganids (Taylor *et al*., 2016). Instead, life-history information is dispersed in various age and growth studies and a few others focused on reproductive life history. Interestingly, few specifically list age and size at sexual maturity in combination. For those species that have been studied, *S. punctatus* life history is similar in age, growth and maturity and in having a seasonal reproductive pattern linked to specific lunar cycles. Similar to *S. punctatus*, *S. canaliculatus*, in United Arab Emirates was reported as having a maturation schedule around 1 year of age in the southern coast of the Arabian Gulf and a longevity of 8 years (Grandcourt *et al*., 2007; Al-Marzouqi *et al*., 2011), which accords with earlier suggestions of maturation schedules by Ghais (1993). Similarly, Shakman *et al*. (2008) showed marbled spinefoot *S. rivulatus* ranging in age from 1 to 6 years, with dusky spinefoot *Siganus luridus* (Rüppell 1829), ranging in age from 1 to 7 years. A maximum age of 5 years was reported for *S. rivulatus* from the Egyptian sector of the Red Sea (Mehanna & Abdallah, 2002). None of these authors, including Bariche (2005), have reported age at sexual maturity for these species. Azzurro *et al*. (2007) reported first size at sexual maturity for *S. luridus* at 16.5 cm L_T in the Mediterranean Sea. For *S. argenteus,* maturity was slightly older than 1 year (1.3 yr) and longevity was reported as 7 years (Taylor *et al*., 2016). For shoemaker spinefoot *S. sutor*, the size at 50% female maturity of 1 year was reported as 28.2 cm L_T, however no age was given (Agembe, 2012).

Based on the available evidence and recent findings (K. Rhodes unpubl. data) *Siganus* spp. are increasingly targeted by the Pohnpei fishery. Specifically, in 2015, siganids represented 17.3% of examined catch numerically among more than 690 catches examined. Volumes of siganids increased from 6.3% of the total commercial catch in 2005 to 8.0% in 2015. Although it is currently unclear whether *S. punctatus* or siganids in general require specific management in Pohnpei, the paucity of *Siganus* spp. in Enipein catches suggests the species could benefit from additional management measures, particularly those focused on critical habitat and life-history stages. Protection of this and other *Siganus* spp. could also benefit from additional studies that examine migration patterns, which could influence the size and placement of future area-based measures focused on *Siganus* spp. conservation.

While the fishery currently comprises *S. punctatus* that have reached the size and age of maturity, mortality schedules are high for younger individuals, with 1 and 2 year olds dominating the catch. This latter finding may be unsurprising given that the species reached maximum size within the first 2 years, nonetheless 95% of sampled individuals were < 3 years old. While size limits are not generally conducive to smaller species that reach asymptotic growth at young ages, Pohnpei could institute other forms of protection for *Siganus* spp. by including, for example, a September–December catch and sales ban to overlap with the secondary spawning period. A 1 March–30 April grouper sales closure (Epinephelidae) exists during part of the main reproductive season and has good compliance among fishers and markets, suggesting additional non-overlapping seasonal bans may have some utility in protecting *Siganus* spp. and other species during vulnerable spawning times. Other siganids in Pohnpei [*e.g. S. doliatus*, *S. puellus* and *Siganus randalli* (Woodland 1990)] show similar reproductive schedules, suggesting that a seasonal ban would potentially benefit a number of siganids. The addition of community-based LMMAs or MPAs within other areas identified as critical habitat may also improve *Siganus* spp. populations. Of the 864 individuals taken from the LMMA (35 fish per set), 56 individuals recaptures, while at the unprotected site only seven fish were captured and tagged (0.4 fish per set), supporting both a high level of site fidelity and residency and the need for protected areas from fishing. It seems apparent that the southernmost reefs around Kitti Municipality could benefit from area protection both to protect *Siganus* spp. during critical life-history events, but also to help restore degraded coral and seagrass beds. Based on information of movement of other siganids, Weeks *et al*. (2016) suggest that protected areas for *S. punctatus* should be *c.* 3.2 km in linear distance, which roughly accords with that of the Nan Wap LMMA. This and other *Siganus* spp. would benefit further by identifying other critical habitats, such as spawning sites and migratory pathways and including them in future sites identified as important to *Siganus* spp. persistence utilizing a similar area and design to the Nan Wap LMMA.

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Supporting Information

Supporting information may be found in the online version of this paper.

Table SI. Criteria used in macroscopic and microscopic evaluation of maturation stages of gold-spotted rabbitfish *Siganus punctatus*.

Fig. S1. Photomicrograph of a 6 year old *S. punctatus*. Bars reflect annual growth increments .

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