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RESEARCH ARTICLE

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Aligning fisheries management with life history in two commercially important groupers in Chuuk, Federated States of Micronesia

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Abstract

1. Camouflage grouper, *Epinephelus polyphekadion* (Bleeker, 1849), and squaretail coralgrouper, *Plectropomus areolatus* (Rüppell, 1830), are commercially important medium-bodied groupers that aggregate at specific sites and times to spawn and are highly vulnerable to fishing during these events. Populations of both species are in decline globally, such that management specifically targeting these species is warranted.
2. A 12-month fish market survey in Chuuk, Federated States of Micronesia, provided an opportunity to examine age-based reproductive life history of these two groupers and assess whether current management acts to conserve them. Life history characteristics of both *E. polyphekadion* and *P. areolatus* include a functionally gonochoristic sexual pattern and rapid growth particularly during early life history.
3. *P. areolatus* demonstrated early maturity (2.8 years) and a relatively brief lifespan (10 years), while delayed maturity (4.5 years) and higher longevity (25 years) was shown for *E. polyphekadion*. The spawning seasons for *E. polyphekadion* and *P. areolatus* were 2 and 3 months, respectively, which fall entirely within the January–April grouper sales, catch, and export ban period for Chuuk. Marketed catch included 22% *E. polyphekadion* and 15% *P. areolatus* juveniles, suggesting that size limits may aid in the conservation of these species.
4. Findings from this and recent grouper life history studies suggest that the current 4-month ban in Chuuk be applied only to grouper species known to reproduce during these months to minimize economic impacts to fishers and market owners, and prevent shifts in fishing pressure to more vulnerable species, such as those with low population turnover times, slow growth, or late maturity. Size limits for catch, sale and export are also warranted as an additional management option.

KEYWORDS

age and growth, Epinephelidae, *Epinephelus polyphekadion*, fisheries management, Micronesia, *Plectropomus areolatus*

1 | INTRODUCTION

Camouflage grouper (*Epinephelus polyphekadion*) and squaretail coralgrouper (*Plectropomus areolatus*) are two widely distributed tropical Indo-Pacific groupers (Epinephelidae) that are primary targets of both subsistence and small- and large-scale commercial fisheries (e.g. Rhodes, 2012; Rhodes & Sadovy de Mitcheson, 2012), including the south-east Asia-based live reef food fish trade (Sadovy et al., 2003). Both species commonly form small (100s of individuals) (e.g. Hamilton, Ginigele, Aswani, & Ecohard, 2012; Hughes, 2017) to large (1000s–10,000s of individuals) (e.g. Mourier et al., 2016; Rhodes, Nemeth, Kadison, & Joseph, 2014) (fish) spawning aggregations (FSA, hereafter) to reproduce, where they are particularly vulnerable to fishing (Rhodes, Taylor, & McIlwain, 2011; Robinson, Graham, Cinner, Almany, & Waldie, 2014). As a direct result of the temporal and spatial predictability of these aggregations, fishers target them, often with devastating impacts to the FSA and the populations forming them (e.g. Aguilar-Perera, 2006; Coleman, Koenig, & Collins, 1996; Hughes, Hamilton, Choat, & Rhodes, 2020; Rhodes et al., 2011; Rhodes et al., 2014). FSA fishing has contributed to the decline and extirpation of aggregations for both species in their respective distributional ranges and both species are now listed as Vulnerable (VU A4d) on the IUCN Redlist (Rhodes, Choat et al., 2018; Rhodes, Sadovy, & Samoilys, 2018). For *P. areolatus*, FSA often occur in shallow water, with fish dormant during night-time, thereby providing an easy target for the night-time spearfisheries that operate widely across the Indo-Pacific (Hamilton, Matawai, & Potuku, 2004). In contrast, *E. polyphekadion* is highly aggressive toward bait while aggregating and is thus highly vulnerable to hook-and-line fishing (Robinson et al., 2014). For these reasons and because these species are important to local and regional fisheries, there is a need to better understand these species' life histories at the site level to achieve the best management outcomes.

Previous research has examined the life histories of both *E. polyphekadion* and *P. areolatus*, including age-based reproductive life history (Hughes, 2017; Rhodes et al., 2011, 2013), spawning seasonality (e.g. Hamilton et al., 2012; Hughes et al., 2020; Rhodes & Sadovy, 2002), and the spatial and temporal dynamics of FSA formation (Hamilton et al., 2012; Hughes, 2017; Hughes et al., 2020; Rhodes et al., 2013, 2014; Rhodes & Sadovy, 2002). Based on the available data, both *E. polyphekadion* and *P. areolatus* are functionally gonochoristic species with the potential for sexual transition (Hughes, 2017; Rhodes et al., 2011, 2013). Earlier studies identified these species as protogynous hermaphrodites: for *E. polyphekadion* (e.g. Buslé-Sicard, Debas, Fourcault, & Fuchs, 1992 (as *Epinephelus microdon*) through hormone injections in a laboratory setting; Williams, Currey, Begg, Murchie, & Balagh, 2008, for wild-caught *P. areolatus*, based on sex-specific differences in age and growth). Neither produced sufficient histological evidence in support of sexual transition, namely the co-existence of mature male and female gametes in wild-caught specimens. A more recent report misdiagnosed the sexual pattern for *E. polyphekadion* by mistaking immature bisexual juveniles as transitional individuals (Ohta, Akita, Uehara, & Ebisawa, 2017). Some evidence in support of sex change in *P. areolatus* has been reported previously (Rhodes et al., 2013), including the absence of males in the smallest size and age classes, suggesting some males may transition from functional females to functional males. Similar to other studies, however, no transitional individuals were identified among the 330 samples examined.

Regional life history studies have been conducted on both species (Hughes, 2017; Rhodes et al., 2011, 2013). Prior studies identified a maximum age of 12 years for *P. areolatus* in Pohnpei (Federated States of Micronesia, hereafter FSM) and Solomon Islands (Hughes, 2017; Rhodes et al., 2013), and 14 years in the eastern Torres Strait (Williams et al., 2008), with first maturity at 2 years old or younger. By contrast, *E. polyphekadion* has a longevity of at least 25 years and matures starting at *ca*. 4 years old (Rhodes et al., 2011). Grandcourt (2005) identified longevity in *E. polyphekadion* of 31 years in Seychelles, while Mapleston et al. (2009) have reported ages up to 44 years in the Great Barrier Reef. Both the current and past studies have been primarily conducted to identify demographic differences and understand how to better manage and conserve local populations, including spawning aggregations.

In Chuuk, these two species are both major targets of a small-scale yet substantial commercial fishery that provides fish for local sale as well as for export to Guam, which heavily relies on reef-fish imports from Chuuk (Cuetos-Bueno, Hernandez-Ortiz, Graham, & Houk, 2018). The volumetric contribution of these two species (out of *ca*. 150 landed reef fish species) represented *ca*. 18% of the total catch biomass during a 2014 market survey of coral reef fishes in Chuuk (Cuetos-Bueno et al., 2018), thereby supporting the need for gathering baseline data on the life history of these fish, particularly reproductive life history that includes size-at-sexual maturity and reproductive seasonality. Following confirmation of anecdotal reports from fishers regarding location and timing of FSAs and of targeting of those species during migration to and away from FSAs (Cuetos-Bueno et al., 2018; The Nature Conservancy, 2003) the Chuuk State Legislature passed a total ban on catch, sales, and export of these and other grouper species in 2016 from January to April (Chuuk State Law No. 13-16-16, Act No. 13-21, Section 14). These bans are enforced at markets and ports by the Chuuk Department of Marine Resources. Reef areas are controlled and monitored by private landowners through marine tenure, with the state restricted from enforcement in these areas unless a request by the landowner is made. At the time of the legislation's passage, no detailed information on the species' maturity schedule or spawning seasonality existed to allow for further management decision-making or to evaluate the effectiveness or impacts of the existing ban.

The objectives of the current study were to evaluate the life history of these two species, particularly reproductive life history, to determine whether existing management measures are appropriate. Currently, no limited size- or gear-based restrictions exist in Chuuk, except for bans on the use of chemicals and explosives, the latter which is still used to stun fish in areas where monitoring is lax. Both species are also primary targets of the local commercial and export trade and of interest to the south-east Asia-based live reef food fish trade. Although the trade is currently banned in Chuuk, illegal fishing in remote locations, i.e. outer atolls and areas outside of regular monitoring, is common. It is therefore paramount that investigations of their life histories and vulnerabilities be assessed. Demographic differences are known for these species relative to spawning times, age, growth (Hughes, 2017), and possibly sexual pattern, such that additional life history examinations are warranted to ensure that appropriate management is applied at the country or even site level.

2 | METHODS

2.1 | Reproduction

Between 18 January and 14 December 2014, local coral reef fish markets were sampled daily in Weno, Chuuk, FSM (Figure 1) for *E. polyphekadion* and *P. areolatus*, during a broader investigation of the small-scale commercial fishery (Cuetos-Bueno et al., 2018). Fish were purchased opportunistically. Individuals of both species are available throughout the year. Following capture, fish are typically stored on ice and transported the same day to market, where they are kept on ice for up to 3 days before discard. Sampling for the current study targeted individuals across the available size range, with additional (although unsuccessful) efforts made to sample 0-age fish in order to anchor the growth curve. Samples in each month were taken during all lunar phases (i.e. full and new moons and first and third quarters). Once purchased, fish were weighed (to the nearest 10 g) and measured (nearest 1 mm total length, L_T, hereafter) before removing gonads and otoliths. Gonads were weighed to the nearest 0.1 g and preserved in a 10% formalin solution. Gonads were subsequently transferred to a 70% ethanol solution prior to histological processing. Otoliths were removed, dried, and stored, and weighed to the nearest 0.001 g prior to sectioning. Gonad and fish weights were used to determine reproductive seasonality through the gonadosomatic index (I_G) using the following formula:

$$I_G = (\text{Gonad weight}/\text{fish weight}) \times 100.$$

For gonad analysis, a small portion of larger gonads (*ca.* > 1.0 g) or whole gonads (*ca.* < 1 g) was removed from each sample, stained (eosin, haematoxylin), processed (Leica TP1050 tissue processor; www.leica.com) and transverse sectioned (7 μm; University of California, Davis, Department of Pathobiological Sciences, Davis, CA, USA) for assessment of development stage and sex. Staging used previously developed criteria for both *E. polyphekadion* and *P. areolatus* (Rhodes et al., 2011, 2013) (Table 1). Once development stages were ascertained, individuals were assessed by fish length (and age) for size and age at sexual maturity and binned by development stage and month to identify reproductive seasonality. Owing to difficulties in differentiating among males undergoing early development and male development post-spawning, all males were considered mature, regardless of size, and classified as M1 (Table 1).

2.2 | Sexual pattern

The determination of sexual pattern in both species followed the criteria established by Sadovy de Mitcheson and Liu (2008). Under these strict criteria, evidence of sexual transition (as protogyny) is defined as the presence of mature male reproductive tissues coexisting in a gonad that contains mature female reproductive tissue (ripe or spent oocytes) or other firm evidence of prior female reproductive activity (i.e. muscle bundles together with atretic late stage oocytes or post-ovulatory follicles).

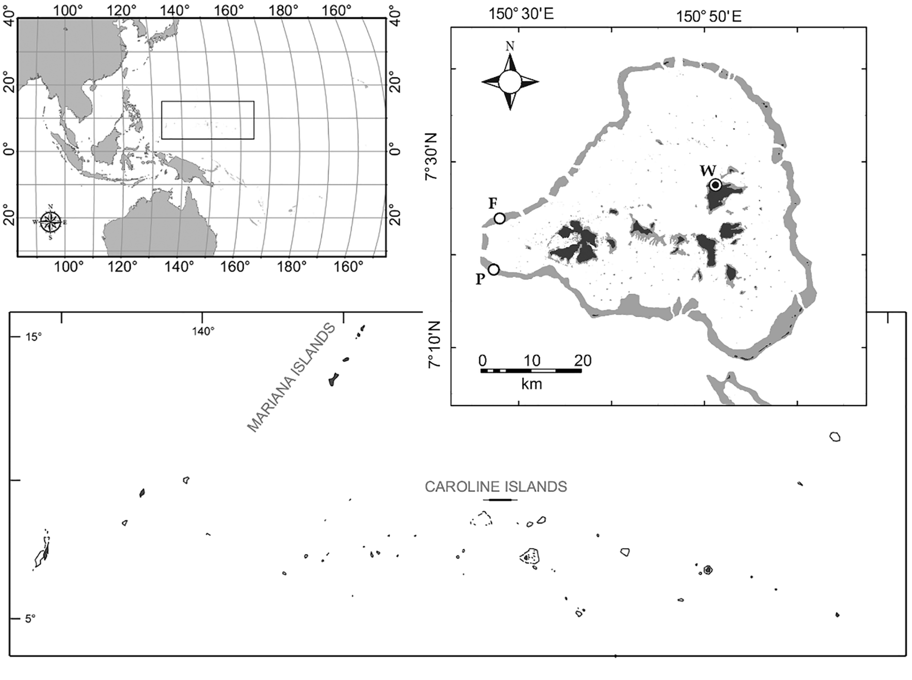

FIGURE 1 Map of Chuuk, Federated States of Micronesia (top right) highlighting Weno (W) where fish markets and export facilities are centralized, and Pianu (P) and Fenufon (F) where fish in later stages of reproductive development were sampled. The location is shown relative to a global (top left) and regional scale (bottom)

TABLE 1 Macroscopic and microscopic criteria for gonad development stages

Maturity stage	Macroscopic	Microscopic
Ovaries		
F1 (immature/bipotential)	Small, strand-like tissue, compact, pink or cream; oocytes indiscernible; indistinguishable from M1 males	Gonad wall thin; tightly packed previtellogenic Stage 1 (nucleolar) and 2 (perinucleolar) oocytes and gonia; no large muscle bundles present
F2 (developing; mature resting)	Relatively small but rounded, greyish with thickened gonad wall; oocytes indiscernible and small (<0.4 mm); indistinguishable from M2 prior to cortical alveolus stage when oocytes become discernible	Stages 1 and 2 and cortical alveolus stage oocytes present; represents individuals that are recovering from spawning as indicated by distinct muscle bundles, thick gonad wall, and an absence of post-ovulatory follicles; includes developing (maturing) and inactive females with actively advancing oocytes
F3 (mature, active)	Large and greyish with transparent gonad wall; large vitellogenic oocytes becoming clearly visible and tightly packed	Mainly vitellogenic (Stage 3) oocytes; gonad wall stretched and thin; Stage 1 and 2 oocytes relatively few; no large-scale atresia or post-ovulatory follicles
F4 (mature, ripe)	Ovary large, clear, hydrated oocytes visible through wall; typical of individuals just prior to spawning; egg release possible with application of light abdominal pressure	All stages of oocyte development, but dominated by Stage 4 (hydrated) and late Stage 3; yolk fusion and hydration are extensive
F5 (post-spawn)	Ovary flaccid with obvious capillaries; few oocytes visible	Post-ovulatory follicles numerous and large prominent muscle bundles scattered throughout the gonad; the gonad wall is thickened; few Stage 3 and/or 4 oocytes may be present and undergoing atresia
Testes		
M1 (immature/inactive)	Indistinguishable from F1 females (see the description of F1)	Gonad filled with varying amounts of stroma, usually the dominant feature; 1° and 2° spermatocytes, and spermatids largely absent (< 1%); sperm sinus may be present; large, vacuous central cavity often present; gonial lobules and brown bodies may be evident; some Stage 1 previtellogenic oocytes present in varying amounts, but not the dominant feature; signs of previous reproductive activity, such as muscle bundles, often evident
M2 (developing)	Gonad greyish in appearance and flaccid; M2 individuals are indistinguishable from F2 until milt becomes evident in the sperm sinus	Gonad largely filled with stroma; 1° and 2° spermatocytes, and spermatids in minor proportions, usually < 10% of the volume; sperm sinus present or not; central cavity small or absent; gonia-filled seminiferous tubules a major feature; gonial lobules and brown bodies may be evident; some Stage 1 previtellogenic oocytes possible in varying amounts, but not the dominant feature; past evidence of spawning, such as thick tunica and sperm sinus present
M3 (mature)	Gonad expanding and becoming rounded, large and greyish; milt may run from macroscopically sectioned gonad and some pockets of milt visible through the tunica	1° and 2° spermatocytes and early sperm formation, sperm crypts and seminiferous tubules; sperm/spermatids and 2° spermatocytes represent 10–50% of the volume; sperm sinus present with thick or thickening tunica; Stage 1 and 2 oocytes a minor component

TABLE 1 (Continued)

Maturity stage	Macroscopic	Microscopic
M4 (mature, active)	Testes large and white with sperm visible in sinuses; milt release with light abdominal pressure	Seminiferous tubules extensive and filled with sperm; gonad volume > 50% sperm/spermatids and few gonia
M5 (post-spawn)	Testes flaccid and bloody; sperm release still possible on application of abdominal pressure	Sperm sinuses and seminiferous tubules largely empty with little, no or atretic sperm; muscle bundles abundant and gonad empty of early stages of spermatogenic tissue; thick tunica and some signs of early atresia of remaining sperm/spermatocytes

Note: Adapted from Rhodes and Sadovy (2002).

2.3 | Age and growth

For otoliths, one sagittal otolith from each otolith pair was weighed to the nearest 0.001 g. The sagitta was affixed by thermoplastic glue to a clear glass slide and sanded along the longitudinal axis to the primordium using a 600-grit diamond lapidary wheel with constant water flow. The otolith was then removed and affixed to a clean slide with the flat surface down and then sanded until a thin transverse section (~200 μm) was obtained through the core. Otoliths were examined on a minimum of two separate occasions when ages agreed and three times when the first two reads differed. Reads were conducted by a single experienced reader and assigned an age (Russ, Lou, Higgs, & Ferreira, 1998). Once final reads were done, length-at-age data were fitted to the von Bertalanffy growth function (VBGF) using non-linear least-squares procedures to estimate sex specific growth parameters. To anchor the growth curve, the current study set the size at settlement at 2.5 cm and used a modified VBGF, which replaces t_0 (x-intercept; theoretical age when length equals zero) with L_0 (y-intercept; length at age zero). The VBGF is herein represented by: $L_t = L_\infty - (L_\infty - L_0)e^{-Kt}$, where L_t is the L_T of a fish at age t, L_∞ is the mean asymptotic L_T, K is the growth coefficient, which describes the rate at which fish grow towards L_∞, t is the age of the fish and L_0 is the L_T at settlement. Differences in lengths and ages between sexes in mature individuals were tested using Mann–Whitney *U* tests (Mann & Whitney, 1947), as data were non-normal and sample sizes were unequal. Individuals classified in the F1 stage (immature, bipotential individuals) were excluded from these analyses as their potential sex was unknown.

Annual instantaneous mortality rates (*Z*) were estimated for both species from age distributions using Beverton and Holt's age-based catch curves: $Z = \frac{1}{t - t'}$, where t is the mean age of all fish aged t′ and older, and t′ is the age at which fish are fully recruited to the fishery (Sparre & Venema, 1998).

Sizes (SSM_{50}) and ages (ASM_{50}) at 50% sexual maturity were calculated for both species using reproductive data for combined sexes and separately for females only, thus providing managers an option when setting size limits. Binomial generalized linear models (GLM) were used to generate logistic curves, and lengths and ages at which 50% of the individuals were mature was calculated as the quotient of the coefficients of the models (−a/b). Logistic curves were plotted over the proportion of mature individuals by size and age for females only.

Owing to a paucity of early stage animals in the samples and in order to anchor the length-at-age curves, the current study utilized young-of-the-year samples of *P. areolatus* taken from Manus, Papua New Guinea (Almany et al., 2013) similar to previous age-and-growth examination for the species in Pohnpei (Micronesia) (Rhodes et al., 2013). Data analyses and visualization were conducted using R (R Core Team, 2019) and the tidyverse package (Wickham, 2017).

2.4 | Environmental monitoring

To compare reproductive periods to environmental parameters, monthly mean, maximum and minimum sea surface temperature measurements were derived from the Weno Municipal Offices, Sea Temperature (https://www.seatemperature.org/australia-pacific/micronesia/weno-municipal-offices.htm). Data from these periods was downloaded and plotted as a monthly mean against mean monthly GSI and proportional gonad development stages.

3 | RESULTS

A total of 281 *Plectropomus areolatus* and 277 *Epinephelus polyphekadion* were sampled from Chuuk reef fish markets between 19 January and 22 December 2014 (Table 1). Of these, histological gonad processing was performed on random selections of 166 *P. areolatus* and 148 *E. polyphekadion*, with otolith analysis conducted on random selections of 152 *P. areolatus* and 167 *E. polyphekadion*.

3.1 | Reproduction

3.1.1 | *Epinephelus polyphekadion*

In total, 148 *E. polyphekadion* (53% of all sampled fish) were examined for reproductive development. Samples included 37 immature individuals (F1; range = 184–357 mm L_T; mean ± SE = 260.5 ± 7.4 mm L_T), 69 mature females (F2–F5; range = 259–546 mm L_T; mean ± SE = 343.4 ± 7.2 mm L_T), and 42 males (M1–M5; range = 157–454 mm L_T; mean ± SE = 364.1 ± 10.3 mm L_T; Figure 2a).

Few sampled individuals showed signs of late stage reproductive development (F3–F5) or spawning activity for robust confirmation of reproductive seasonality. Among samples, only five females were at or beyond the vitellogenic stages of oocyte development (F3: n = 3; F4: n = 2), while eight males were mature (n = 2), ripe (n = 1), or spent (n = 5; Figure 3a). Among these individuals, most were captured at or near an anecdotally reported spawning aggregation site (Figure 1). Mature, active (F3) and ripe (F4) females were observed in February and March, with GSI values of 3.8 and 3.2, respectively (Figure 3a). No mature females were sampled in January and no spent females were sampled during the study period. Based on the available data, the reproductive season appears to be limited to a 2-month spawning season in February and March, which coincides with the brief 2-month spawning season observed for the species in the region, and which falls within the seasonal grouper catch and sales ban period for Chuuk. The 2 months of elevated GSI for *E. polyphekadion* in Chuuk coincides with the nadir and subsequent seasonal increase in sea surface water temperature (Figure 3a), an environmental characteristic also observed in Pohnpei. For females, the minimum size of maturity was 259.0 mm L_T, while 50% size-at-sexual maturity (SSM$_{50}$) was 286.5 mm L_T (model coefficients: a = −12.936, b = 0.045; Figure 4a). For all individuals combined, the SSM$_{50}$ was 276.6 mm L_T, (a = −11.090, b = 0.040) with 22% of marketed fish below the combined SSM$_{50}$. Mean male and female lengths were significantly different (Mann–Whitney *U* test, P = 0.023).

3.1.2 | *Plectropomus areolatus*

For *P. areolatus*, of the 282 fish taken from markets, 166 individuals were sampled for gonad processing (59% of the total). Among those, 62 were immature (F1) individuals (range = 204–405 mm L_T; mean ± SE = 309.2 ± 6.4 mm L_T), 85 were developing or mature (F2–F4) females (range = 146–567 mm L_T; mean ± SE = 351.9 ± 6.1 mm L_T) and 17 were males (M1–M5; range = 350–580 mm L_T; mean ± SE = 397.7 ± 17.5 mm L_T; Figure 2b). Among mature females, few were in late stages of oocyte development, with five mature females in vitellogenesis (F3) and one mature, ripe (F4) female with hydrated oocytes. No spent females were observed. For mature males in late stages of spermatogenesis (M3-M4), only one individual was observed, while three spent (M5) males were found among samples. Based on this limited dataset and increases in GSI, the spawning season for *P. areolatus* appears minimally to be January to March (Figure 3b). Indications that some reproductive activity may occur earlier is found in an increase in GSI in December; however, additional data are required to confirm actual spawning times. Similar to other regional locales investigated, the presumed spawning season overlaps with *E. polyphekadion* and coincides with annual lows in SST. The presumed spawning season for *P. areolatus* thus falls within the sales, catch, and export ban period for groupers in Chuuk. For *P. areolatus*, the smallest mature female was 146 mm L_T, SSM$_{50}$ for all fish was 299.1 mm L_T (a = −7.546, b = 0.025) and SSM$_{50}$ for females was 301.7 mm L_T (a = −7.350, b = 0.024; Figure 4b). Based on these estimates, *ca.* 15% of marketed *P. areolatus* were taken below the combined sex 50% size-at-sexual maturity. Mean male and female lengths were not significantly different (Mann–Whitney *U* test: P = 0.50).

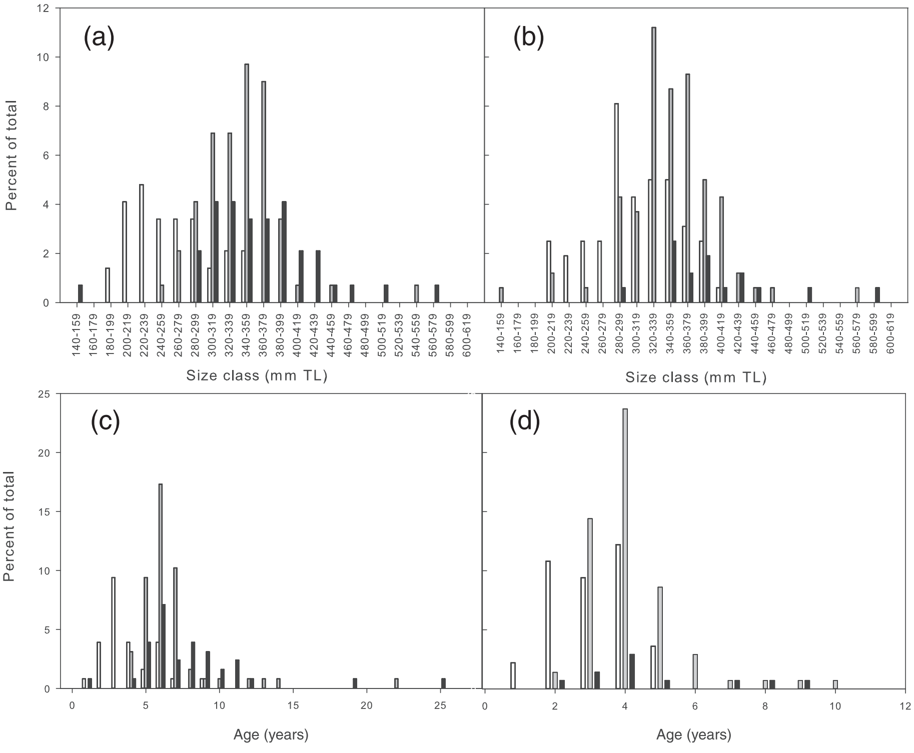

FIGURE 2 Sex- and age-specific size distribution of sampled groupers taken from Chuuk fish markets between 18 January and 14 December 2014. (a) Size frequency distribution of *Epinephelus polyphekadion*; (b) size frequency distribution of *Plectropomus areolatus*; (c) age-frequency distribution of *E. polyphekadion*, and (d) age-frequency distribution of *P. areolatus*. White bars = immature; grey bars = females; black bars = males; TL = total length

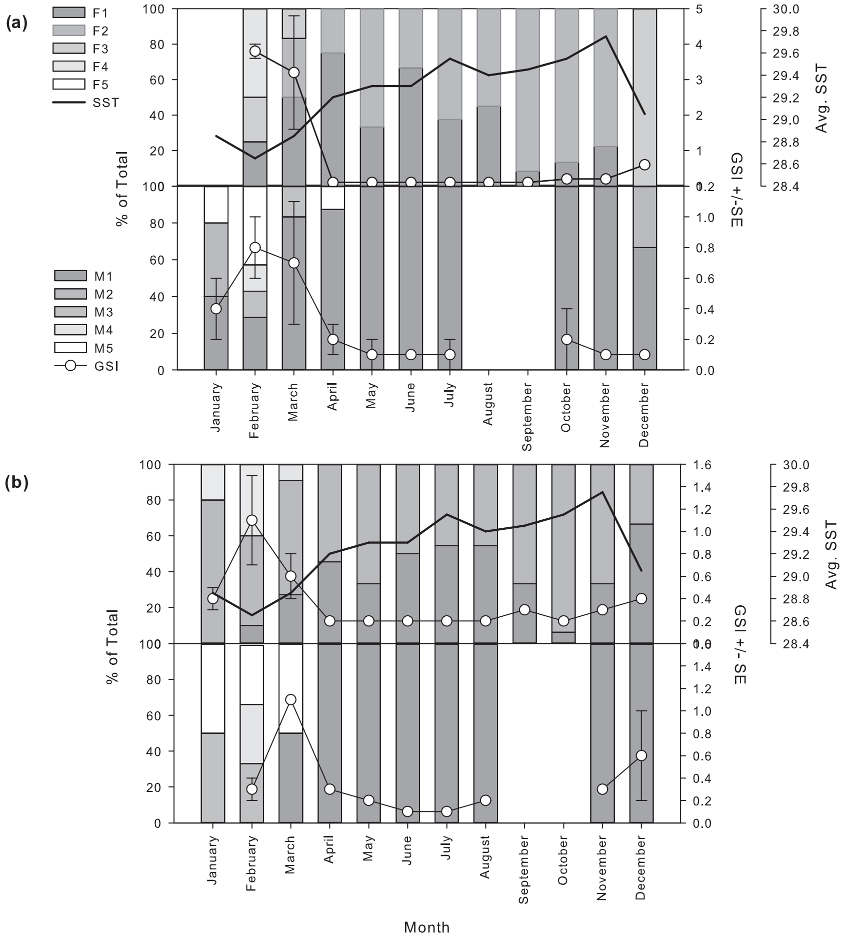

FIGURE 3 Monthly distribution of gonad development stages for groupers taken from Chuuk fish markets in 2014. (a) *Epinephelus polyphekadion* females (top) and males (bottom) and (b) *Plectropomus areolatus* females (top) and males (bottom). Gonadosomatic indices (GSI: open circles) and sea surface temperatures (SST; ° C) are plotted against gonad development stages to show increased GSI during periods of the lowest sea surface temperature. GSI values indicate a March–April reproductive season for camouflage grouper and January–March for squaretail coralgrouper in Chuuk

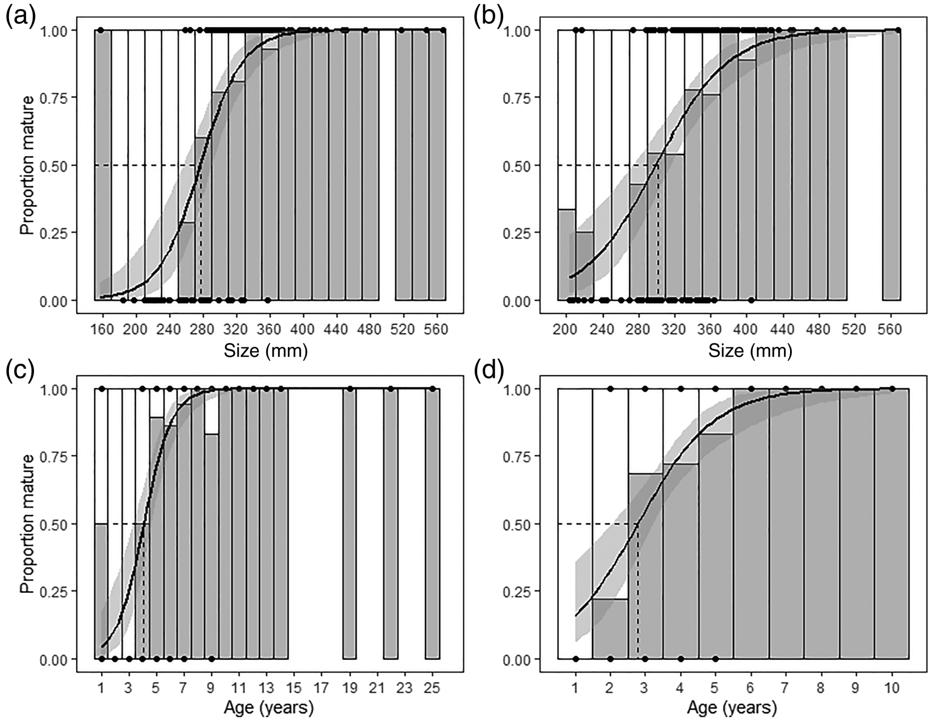

FIGURE 4 Size-at-50% sexual maturity (SSM$_{50}$; top) and age-at-50% sexual maturity (ASM$_{50}$; bottom) curves for groupers taken from the Chuuk fish market in 2014. (a) SSM$_{50}$ for *Epinephelus polyphekadion*; (b) SSM$_{50}$ for *Plectropomus areolatus*; (c) ASM$_{50}$ for *E. polyphekadion*, and (d) ASM$_{50}$ for *P. areolatus*. Dots at the top and bottom of the graph represent the presence of mature and immature fish, respectively

3.1.3 | Sexual pattern

For both species, no transitional individuals were found among the samples examined for reproductive development. Significant sex-specific size (and age, below) differences were observed for *E. polyphekadion*, but not for *P. areolatus*. Using the criteria of Sadovy de Mitcheson and Liu (2008), *E. polyphekadion* and *P. areolatus* in Chuuk are characterized as functionally gonochoristic with the potential for sexual transition, similar to other locations where rigour has been applied.

3.2 | Age and growth

3.2.1 | *Epinephelus polyphekadion*

For *E. polyphekadion*, ages of the 167 individuals examined ranged from 1 to 25 years. Immature individuals ranged from 1–9 years (mean ± SE = 3.8 ± 0.3 year), mature females ranged from 4–22 years (mean ± SE = 6.7 ± 0.4 year) and males were 1–25 years old (mean ± SE = 8.1 ± 0.7 year; Figure 2c). Mean male and female ages were significantly different (Mann–Whitney *U* test, $P = 0.038$). For *E. polyphekadion* females, 50% age-at-sexual maturity (ASM_{50}) was 4.49 years (model coefficients: a = −4.832, b = 1.076), while ASM_{50} for all individuals combined was 4.09 years (a = −4.095, b = 0.999; Figure 4c). Estimates of growth parameters for all fish were $L_\infty = 467.7$ for both sexes combined, $K = 0.20$ (Figure 5a) and differences in the growth curves were not significantly different (likelihood ratio, $P > 0.10$): for females, $L_\infty = 529.3$ and $K = 0.11$; for all individuals, $Z = 0.57$. Otolith weight was significantly correlated with fish age (ANOVA: F-stat = 2657, df = 157, $P << 0.001$). Marketed fish were as young as 1 year and averaged 6.4 ± 0.3 years.

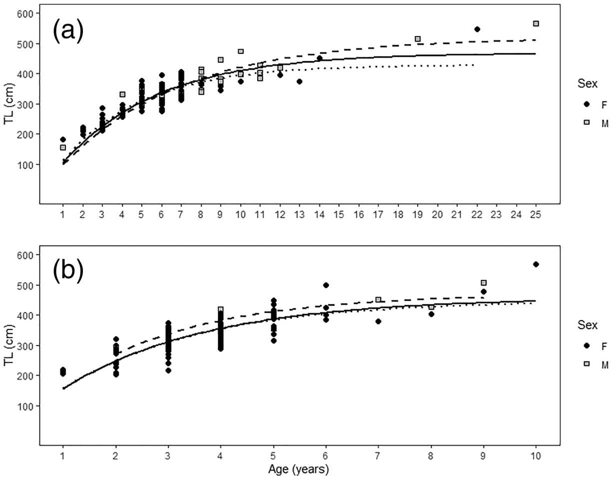

FIGURE 5 The von Bertalanffy growth curves for grouper taken from fish markets in Weno, Chuuk. (a) *Epinephelus polyphekadion* and (b) *Plectropomus areolatus*. The combined data are represented by the solid line. Males (dotted line) are shown to have a smaller size at age than females (dashed line), which may reflect the low sample size of males taken during the survey. TL = total length

3.2.2 | *Plectropomus areolatus*

The age of *P. areolatus* ranged from 1 to 10 years ($n = 152$ individuals). Immature fish ranged from 1 to 5 years (mean ± SE = 3.1 ± 1.2 years), females from 2 to 10 years (mean ± SE = 4.2 ± 0.2 years) and males from 2 to 9 years (mean ± SE = 4.8 ± 0.7; Figure 2d). Mean male and female ages and lengths were not significantly different (Mann–Whitney *U* test: $P = 0.087$, $P = 0.50$, respectively). Similar to *E. polyphekadion*, otolith weight was significantly correlated with fish age (ANOVA: F-stat = 2657, df = 157, $P << 0.001$). For *P. areolatus*, the ASM_{50} was 2.8 years (a = −2.588, b = 0.928; Figure 4d), while 50% of females matured at 2.9 years (a = −2.768, b = 0.948). Estimates of growth parameters for all fish were $L_\infty = 456.9$ mm TL for both sexes combined, $K = 0.36$ (Figure 5d), and growth curves were not significantly different by sex (likelihood ratio, $P > 0.10$). For females, $L_\infty = 447.8$, $K = 0.36$ and $Z = 1.49$ overall. Fish taken from the market were as young as 1 year and averaged 3.8 ± 0.1 years.

4 | DISCUSSION

4.1 | Reproduction and regional differences in reproductive seasonality

Microscopic gonad assessments confirmed reproductive activity for *E. polyphekadion* in February and March, while *P. areolatus* reproduces from January to March. For both species, reproductive seasonality was determined based on a small number of female oocytes in late stages of development, indicative of imminent spawning, and elevated gonado-somatic indices. For *E. polyphekadion*, a 2-month spawning season was indicated by elevated GSI values in February and March and the presence of late-stage oocytes in a few females. For *E. polyphekadion*, the duration of this brief peak spawning period conforms to other central and western Pacific sites (Ohta et al., 2017), the western Indian Ocean (Bijoux et al., 2013; Robinson et al., 2014) and Melanesia (Hamilton et al., 2012; Hughes et al., 2020; Waldie, 2016). For each of these locales, the overall reproductive season may extend from 3 to 5 months, with the formation of smaller FSA on either side of the peak (Table 2).

In contrast to other regional studies, reproductive activity for *P. areolatus* in Chuuk appears to be confined to a 3-month period, which would represent the briefest reproductive season thus far reported for the species (Table 2). Although Williams et al. (2008) reported a 2-month (July–August) peak for the Torres Strait, some potential reproductive activity was identified during October and November to indicate a lengthier spawning season. In other locales, substantially longer spawning seasons of five months or longer have been reported (e.g. Johannes, Squire, Graham, Sadovy, & Renguul, 1999; Rhodes et al., 2013; Wilson, Rhodes, & Rotinsulu, 2010). In some parts of Melanesia (Hamilton et al., 2012; Hughes, 2017; Hughes et al., 2020) and Indonesia (Pet, Mous, Muljadi, Sadovy, & Squire, 2005), *P. areolatus* FSA form monthly, with peaks in FSA abundance (i.e. reproduction) typically 2–5 months. These

TABLE 2 Summary table of known reproductive parameters of *Plectropomus areolatus* and *Epinephelus polyphekadion*

Species/Location	*n*	Size range (mm)	Size diff	L_{50} (L_T)	Month (All)	Month (Peak)	Lunar cycle	Sex Pattern	Valid	References
P. areolatus										
Chuuk	166	146–580	N	299.1	Jan–Mar		FM	G_F	Y	Current study
Pohnpei	330	244–670	Y	366.0	Jan–May	Mar–Apr	FM	G_F	Y	Rhodes et al., 2013
Torres Strait	448	300–640			Jun–Nov	Jul–Aug		P	N	Williams et al., 2008
Solomon I.										
Roviana					Jan–Dec	Jan–Feb	NM			Hamilton et al., 2012
Gizo	425	170–552	Y	321.6_f	Jan–Dec	Mar–Jun	NM	G_F	Y	Hughes et al., 2020
Parara	202	155–560	N	338.0_f	Jan–Dec	Mar–Apr	NM	G_F	Y	Hughes, 2017
PNG					Jan–Dec	Oct–Mar	NM			Waldie, 2016
Palau	45	300–557	Y		Jan–Dec	May–Aug	NM			Johannes et al., 1999
Indonesia										
Komodo					Sep–Feb		FM			Pet et al., 2005
Ayau					Sep–Jan		NM			Wilson et al., 2010
Fiji					Jun–Nov	V				Fox, Naisilisili, Batibasaga, & Jupiter, 2012
Red Sea	135	240–560	Y					P	N	DesRosiers, 2011
E. polyphekadion										
Chuuk	148	157–546	Y	276.6	Feb–Mar	Feb–Mar	FM	G_F	Y	Current study
Pohnpei	465		Y	327.0	Feb–Apr	V (2)	FM	G_F	Y	Rhodes et al., 2011
Solomon I										
Roviana					Feb–Mar	V (1)	NM			Hamilton et al., 2012
Gizo					Mar–Aug	Mar–May	NM			Hughes, 2017
Great Barrier Reef	343	220–691			Oct–Dec					Mapleston et al., 2009
French Polynesia					Jun–Jul		FM			Mourier et al., 2019
Seychelles	85	444–684	Y		Dec–Feb	V (2)	NM			Robinson et al., 2008
PNG (Dyaul 1)	402	100–534	333_f		Apr–Aug	May–Jun	NM			Waldie, 2016
PNG (Dyaul 2)					Jul–Oct	Jul–Aug	NM			Hamilton et al., 2011
Okinawa, Japan	143	207–618	Y	358	Mar–Jun	Apr–May	FM	P	N	Ohta et al., 2017
Palau		239–500	Y		Jun–Aug	V (1)	NM	P	Y	Johannes et al., 1999
Fiji					Jun–Oct	V				Fox et al., 2012

Abbreviations: $_f$, only L_{50} for females reported; FM, full moon; G_F, functional gonochore; L_{50} (L_T), length at 50% sexual maturity, as total length (mm); Month, months of aggregation formation; *n*, samples size; NM, new moon; Size diff, significant sex-specific size differences found; N, no; P, protogynous hermaphrodite; PNG, Papau New Guinea; V, variable, with the number of potential monthly shifts of peak abundance in parentheses; Valid, confirmation of sexual pattern using criteria of Sadovy de Mitcheson and Liu (2008) or tagging studies (Johannes et al., 1999); Y, yes.

examples highlight the widespread regional diversity in spawning times for these species and suggest additional sampling may be needed in Chuuk to further define the reproductive season.

4.2 | Age and growth

Throughout its range, *E. polyphekadion* is characterized as a late maturing fish with a relatively long life span (Table 3). In Chuuk, the oldest fish was 25 years old, represented by a single specimen. This maximum age generally falls within the range reported elsewhere, with maximum ages ranging from 22 to 36 years (Grandcourt, 2005; Mapleston et al., 2009; Ohta et al., 2017; Pears, 2005; Rhodes et al., 2011; Waldie, 2016).

Sex-specific growth was significantly different and conforms to other studies where mean size in males is typically larger than females (e.g. Ohta et al., 2017; Rhodes et al., 2011; Waldie, 2016) (Table 3). In both Chuuk and Okinawa (Ohta et al., 2017), sex-specific age differences were also identified, which varied with findings for Pohnpei where sample sizes were larger and more balanced between sexes.

In contrast to *E. polyphekadion*, *P. areolatus* matured at a much younger age in Chuuk (SSM_{50} = 2.8 years) and had a longevity of only 10 years among individuals sampled. This is among the shortest recorded lifespan for the species to date (Table 3). Maximum reported age estimates vary widely within the Pacific, ranging from 8 years in Marovo lagoon (Solomon Islands) to 12 years in Pohnpei (Rhodes et al., 2013), the Torres Strait, Roviana Lagoon (Solomon Islands) and the Red Sea (Hughes, 2017). Williams et al. (2008) earlier reported a maximum age of 14 years for the species from Torres Strait.

4.3 | Sexual pattern and male development pathway

Sex-specific size and age for mature fish overlapped for both species in Chuuk, but were significantly different for *E. polyphekadion* only. Although size and age differences alone have been used to suggest hermaphroditism in fish in earlier studies, the current study used a more conservative approach that requires confirmation of prior female function in mature males (Sadovy de Mitcheson & Liu, 2008). As no individuals undergoing sexual transition were identified for either species, *E. polyphekadion* and *P. areolatus* are herein considered functionally gonochoristic with the potential for sexual transition, similar to other regional findings where rigour has been applied (Rhodes et al., 2011, 2013; Rhodes & Sadovy, 2002) (Table 2). In combination with this study, at least 1,948 individuals of *E. polyphekadion* and more than 1,521 *P. areolatus* have been examined microscopically across the size

TABLE 3 Summary table of key age and growth parameters for *Epinephelus polyphekadion* and *Plectropomus areolatus*

Species/location	*n*	Age range	Mean age	*K*	*Z*	L_∞ (L_T)	References
P. areolatus							
Chuuk	152	1–10	2.8	0.36	1.49		Current study
Pohnpei	263	2–12		0.64	0.43		Rhodes et al., 2013
Torres Strait	409	1–12	5.0	0.66	0.39	541	Hughes, 2017
Torres Strait	417	2–14		0.09	0.3	764	Williams et al., 2008
Solomon Islands							
Roviana	78	2–12	4.5	0.47	0.37		Hughes, 2017
Marovo	187	1–8	3.3	0.48	0.99		Hughes, 2017
Gizo	431	0.6–10	4.2	0.42	0.61		Hughes, 2017
Parara	199	0.6–12	4.9	0.42	0.38		Hughes, 2017
Rowley Shoals	255	2.11	5.3	0.41	0.75		Hughes, 2017
Red Sea	101	1–12	3–7	0.50	0.53		Hughes, 2017
Red Sea	135	0.5–9	3.0				DesRosiers, 2011
E. polyphekadion							
Chuuk	167	1–25	8.1	0.20	0.57		Current study
Pohnpei	551	4–22	6.4	0.25	0.23	447.1	Rhodes et al., 2011
Great Barrier Reef	201	4–33	10.7	0.20		537.0	Pears, Choat, Mapstone, and Begg, 2006
Great Barrier Reef	330	2–44		0.19		562.3	Mapleston et al., 2009
Seychelles	101	4–36	6.1	0.21		582.4	Pears et al., 2006
Seychelles	77	5–31		0.18		579.0	Grandcourt, 2005
Papua New Guinea	483	5–22		0.23		438.4	Waldie, 2016
Okinawa, Japan	106	3–26	6.9	0.14		565.8	Ohta et al., 2017

Note: K is the growth coefficient, which describes the rate at which fish grow towards L_∞ is the rate at which fish grow toward *Z* (asymptotic average length). *n* = samples size.

spectrum. Among those, only one *P. areolatus* and two *E. polyphekadion* individuals have been definitively identified as transitional. The latter evidence was from a tagging study by Johannes et al. (1999) whereby two tagged females were recaptured as males. No photomicrographs were provided to confirm the finding. Similarly, the lone *P. areolatus* transitional suggests sexual transition may be a rare phenomenon for both species and uncharacteristic of the broader sexual pattern. Thus, while sexual transition is clearly possible for both species, it does not appear to be the primary pattern of male development in these species.

The youngest female for both species was slightly younger than the SSM_{50} for both sexes combined, while males were found at Age 1 in *E. polyphekadion* and Age 2 for *P. areolatus*. These data suggest that males are derived from immature sexually bipotential individuals (F1) similar to previous descriptions of epinepheline male development for both functional gonochores (e.g. Erisman, Rosales-Casián, & Hastings, 2007; Rhodes et al., 2011, 2013; Sadovy & Colin, 1995) and diandric hermaphrodites (e.g. Liu & Sadovy de Mitcheson, 2009; Palma et al., 2019).

4.4 | Temperature, lunar periodicity, and predicting spawning times

For both *E. polyphekadion* and *P. areolatus*, reproduction in Chuuk is correlated with low to increasing sea surface temperatures, similar to Pohnpei (Rhodes et al., 2014). In other regional locales, however, temperature profiles during reproductive periods vary. For example, in the Solomon Islands, reproductive peaks for these two species tend to occur during seasonal highs (Hamilton et al., 2012; Hughes et al., 2020), while in Palau the reproductive peaks for *E. polyphekadion* and *P. areolatus* occur weeks prior to seasonal increases in sea surface temperature (Johannes et al., 1999). These two examples suggest that while some regional similarities exist, temperature profiles cannot be used reliably as an indicator of spawning in these species.

In Chuuk, reproductive activity was closely aligned to the full moon (Table 2). While full moon spawning is typical of most Northern Hemisphere FSA for these species, in the Southern Hemisphere FSA formation typically occurs at the new moon. Exceptions occur in both hemispheres; however, spawning times for both species during new and full moons may suggest a linkage to associated high tidal variation and flow to enhance dispersal or retention (e.g. Almany et al., 2013). Thus, similar to temperature, specific lunar periodicity lacks dependability as an indicator of spawning times and demonstrates the variability within the species for reproduction relative to lunar periodicity. Without discarding the possibility that these two environmental parameters play a role in reproductive periodicity in these species, they do not appear to be the primary drivers.

4.5 | Fisheries and management

Groupers provide the basis for a billion dollar fishing industry that is increasing annually in catch volume (Sadovy de Mitcheson et al., 2013, 2020). In the central Pacific, the Chuuk commercial coral reef fishery represents one of the largest in the region and is highly reliant on groupers for domestic sale and export. Export values and volumes averaged US$1.5 million $year^{-1}$ and 148 mt $year^{-1}$ from 2003 to 2014, with 18% of the total fishery being represented by the two groupers examined herein (Cuetos-Bueno & Houk, 2018). Although few reproductively active fish were sampled during the year, monthly exports of fish from Chuuk to Guam have historically increased during February, March, and April (2007–2017), which corresponds to the reproductive season of *E. polyphekadion* and *P. areolatus* (also *Epinephelus maculatus* (Bloch, 1790) (Rhodes, Taylor, Cuetos-Bueno, & Hernandez-Ortiz, 2016)). During this period, exports were 24.5 ± 5.9% SE higher than other months of the year (Cuetos-Bueno & Houk, 2018). In many fisheries, such increases are often linked to spawning aggregation fishing (e.g. Erisman et al., 2012; Sadovy de Mitcheson, 2016; Sadovy de Mitcheson & Erisman, 2012; Sadovy & Eklund, 1999). In Chuuk, the increase is due in part to higher fish demand during lent, a 40-day period observed by Catholics during the run up to Easter when the consumption of other meats is discouraged (Cuetos-Bueno & Houk, 2018). Within these months, fish catch was sufficiently excessive to cause spoilage and waste at markets, which eventually helped to catalyse the Chuuk government to institute the current ban. Although the ban was not directly instituted to protect fish spawning aggregations, it indirectly acts to diminish FSA fishing where it may occur and, thereby, reduces impacts to grouper populations during the reproductive season. The ban also blocks commercial avenues to markets and exporters, which are monitored closely by the Department of Marine Resources.

In spite of Chuuk's current grouper ban, FSAs of these two species and other aggregating fishes remain vulnerable to fishing, with the outcomes often dire (e.g. Aguilar-Perera, 2006; Beets & Friedlander, 1995; Mangubhai et al., 2011; Rhodes et al., 2014; Sadovy de Mitcheson et al., 2013; Sadovy de Mitcheson & Erisman, 2012; Sadovy & Eklund, 1999). As such, there has been an urgent call for management of these events to contribute to better conservation (e.g. Sadovy de Mitcheson et al., 2013, 2020). While a number of management options have been used over the years to protect aggregating groupers, single management options including both marine protected areas and sales, catch, and export bans, often have had less success in achieving population increases (Russell, Luckhurst, & Lindeman, 2012). For example, in Fakarava, French Polynesia, area protection of the largest known *E. polyphekadion* FSA, combined with restrictions on trap fishing during known spawning times has not stopped perceived declines, suggesting additional measures, such as a seasonal closure during the 2-month reproductive season is needed. In Palau, where marine protected areas have been combined with an April to September sales and catch ban, increases in FSA density and abundance at some sites have been recorded after long-term declines (Y. Sadovy, personal communication, May 2020). At Dyaul Island, Papua New Guinea, area protection through a locally managed marine area formed in 2004 has allowed a restoration of FSA from low density levels following years of fishing by the south-east Asia live reef fish food trade (Hamilton, Potuku, & Montambault, 2011). In Solomon Islands, an October to February sales and catch ban is currently in effect; however, due to the country's wide geographic extent and highly variable reproductive seasonality, many FSAs remain unprotected, with significant declines shown for the species at known sites (Hughes, 2017; Hughes et al., 2020). Since all known FSAs of these species in Solomon Islands form between full and new moons, it has been suggested that a more effective management strategy would be to combine locally managed marine areas with full-to-new moon sales closures each month of the year (Hughes et al., 2020).

In Pohnpei, marine resources are managed under an open access system that allows fishers access to any reef area. This arrangement, together with night-time spearfishing, has contributed to widespread declines in coastal marine resources (Rhodes et al., 2015). In spite of overall declines, a few private landowners and communities have made some progress towards conserving resources in localized areas. For example, FSA densities of co-aggregating *E. polyphekadion*, *P. areolatus*, and *E. fuscoguttatus* (Forsskål, 1775) had remained steady or had increased under a well enforced locally managed marine area (2001–2005) until enforcement was handed to the state and yearly declines ensued (Rhodes et al., 2014). Similar declines were observed at a multi-species grouper FSA at nearby Ant Atoll until a private landowner took over from state monitoring and enforcement, with FSA and populations of non-aggregating fishes now anecdotally increasing (W. Hawley, personal communication, June 2019). Similarly, increases in rabbitfish (Siganidae) abundances occurred at a multi-species FSA after placing the area under local community control. These examples provide strong evidence that a rights-based management approach may be more effective in Pohnpei than state-sponsored open access and enforcement.

In Chuuk, marine tenureship is enshrined in the state constitution, thus establishing a rights-based fishing scenario. By law, fisheries protections fall under the national, state and municipal governments, as well as private landowners. The state government controls commerce (marketing and exports) and aids private landowners in enforcement at tenured reef areas when requested. The state is otherwise without enforcement power in privately held reef areas; nor can they implement marine protected areas without owner support. Thus, FSAs are being indirectly protected from fishing through the January–April ban and directly through marine tenureship. Since these events serve as a bellwether of population status, their identification and monitoring is warranted to help gauge the impact of current management protocols.

4.6 | Aligning management to life history and the consequences of mis-management

In Pohnpei, a 1 March to 30 April grouper sales ban was implemented in 1985 (since extended to May and including a catch ban). Similar to Chuuk, the Pohnpei fishery targets more than 20 grouper species (Rhodes, Tupper, & Wilchilmel, 2008; Rhodes, Sadovy, et al., 2018), few of which are known to form FSA. For those that do, FSA form from January to May, with peaks during March and April (Rhodes et al., 2014), including for *E. polyphekadion* and *P. areolatus* (Table 2). Owing to the lengthy spawning season, the ban allowed FSA fishing in non-ban periods of FSA formation, resulting in a market glut in groupers, massive spoilage and continued declines in FSA abundance. Impacts to other fish families were also observed, since fishers shifted away from groupers during the ban period toward parrotfish (Scaridae), snappers (Lutjanidae), and other herbivores (e.g. rabbitfish and surgeonfish (Acanthuridae) (Rhodes et al., 2008). A similar shift in target species has been documented in Palau (Bejarano Chavarro, Mumby, & Golbuu, 2013), with additional pressure placed on undersized herbivores during ban periods. These findings highlight the unintended ecological and economic consequences of blanket bans on fishes without a complete understanding of the fishery and fish life history.

In Chuuk, current and recent research have identified only four grouper species (*E. fuscoguttatus*, *E. polyphekadion*, *E. maculatus*, and *P. areolatus*) that aggregate to spawn during the grouper ban period. Similar to Pohnpei and Palau, Chuukese fishers are likely to be shifting effort to other species or else suffering the economic burdens imposed by the loss of catch volume. Based on findings herein, Chuuk (and Pohnpei) could limit the current ban to known FSA-forming species (similar to Palau) and, in doing so: (i) achieve its goal of protecting groupers during perceived aggregation periods; (ii) reduce the ecological impacts from shifting effort to other, perhaps more vulnerable or ecologically important species (e.g. herbivores, corallivores or fish with late maturation, longevity and low population turnover rates); and, (iii) provide greater ecological and economic balance to its management strategy. Likewise, the state could utilize the size-at-maturity data from this and recent (Rhodes et al., 2016) research to implement size limits and reduce or eliminate undersized catch of these species in markets year-round.

As highlighted by these various fishing and management scenarios, for conservation to be successful, there is a need to align management policy with local political, biological, and cultural characteristics, and identify science-supported measures that can be community-sponsored and effectively enforced. The demographic differences shown in Table 2 and Table 3 reinforce the need to continue to perform examinations of these and other commercially important species at the country and perhaps even site level to identify conservation measures that properly align with life history traits. Similarly, it is also integral to conduct socio-economic assessments of the fishery to anticipate possible responses to whatever management measure may be applied. Finally, although FSA in Chuuk are indirectly protected via the grouper ban, it remains critical to identify and assess them to establish baselines for reproductive populations and record changes that may result from management actions.

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