

**RAPID REPRODUCTIVE ANALYSIS AND WEIGHT-LENGTH RELATION
OF THE HUMPNOSE BIG-EYE BREEM, *MONOTAXIS GRANDOCULIS*
(ACTINOPTERYGII: PERCIFORMES: LETHRINIDAE), FROM MICRONESIA
WITH IMPLICATIONS FOR FISHERIES**

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Abstract. We present a weight–length relation and use rapid and low-cost histological methods to generate preliminary reproductive parameters for *Monotaxis grandoculis* (Forsskål, 1775), based on specimens collected in Guam and Pohnpei [$W = 0.033(FL)^{2.91}$]. We estimated female L_{50} at 30.0 cm FL and male L_{50} at 35.4 cm FL. The species is gonochoric. Overall and operational sex ratios were not significantly different from 1:1; however, among mature individuals, the proportion of females was an inverse function of length with no females > 33.5 cm FL but males to 44.5 cm FL. Batch fecundity was an exponential function of length but, because females were absent in the largest size classes, the highest per capita egg production was by individuals at 31.7 cm FL, only 71.2% of maximum observed specimen length. Boat-based creel surveys in Guam showed that the mean length of *M. grandoculis* in the catch decreased below both female and male L_{50} from 2010 to 2019, suggesting a significant decline in spawning stock biomass.

Keywords: maturation, sex ratio, fecundity, Pohnpei, Guam

INTRODUCTION

The humpnose big-eye bream, *Monotaxis grandoculis* (Forsskål, 1775), occurs from the east coast of Africa to Hawaii and south-eastern Oceania; and from southern Japan to northern Australia (Carpenter and Allen 1989). This species is also reported from Turkey as a probable Lessepsian migrant to the eastern Mediterranean (Bilecenoglu 2007). In its native range, it has been frequently found fresh in fish markets (Carpenter and Allen 1989). A market-based survey of the Pohnpei coral-reef fishery (Rhodes et al. 2008) indicated that *M. grandoculis* was very common, ranking 9th by frequency of occurrence. A market-based survey on Kosrae, Federated States of Micronesia (FSM), found that the species ranked 14th in annual reef-fish landings (Houk et al. 2017). On a

broader scale, *M. grandoculis* was considered one of six species accounting for a consistently high proportion of the biomass landed across four Micronesian jurisdictions (Commonwealth of the Northern Mariana Islands, Guam, Yap, and Pohnpei) (Houk et al. 2012).

Due to its importance in Micronesian reef fisheries and because reproductive information appears to be lacking for this species, the objective of this study was to provide preliminary histology-based estimates of reproductive parameters for the Micronesian region. Our approach also permitted production of a weight–length relation. Furthermore, we compared the mean length of *Monotaxis grandoculis* in creel surveys of boat-based catch to our size-at-maturity length estimates. The mean length in the exploited phase of a stock can provide an ecological

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indicator of fishing impacts on exploited populations and, in relation to the size-at-maturity, reflects the status of the spawning stock biomass of the population (Ault et al. 2014, 2019). Larger female fish tend to produce relatively more eggs than smaller females (Barneche et al. 2018) which has led to fisheries guidance not to target large reef fishes to retain spawning stock biomass in the form of “big old fat fecund female fish (BOFFFFS)” (Hixon et al. 2014). We examined the size-specific sex-ratio to determine the relative contribution of length classes to reproductive output and evaluate the applicability of the BOFFFFS concept for *M. grandoculis*. The comparison of the mean length in the catch to the length-at-maturity and the size-specific sex ratio analysis coupled to fecundity-at-size provide biologically-relevant indicators that could inform fisheries management of this highly exploited, yet data-limited coral-reef fish in Micronesia.

MATERIAL AND METHODS

A total 127 specimens of *Monotaxis grandoculis* were collected from Pohnpei, FSM, between 20 July and 6 August 2016 and from Guam, United States of America, between 21 March and 20 June 2017. Sampling time and duration were dictated by funding and travel logistics in both locations. Thirty-eight specimens were obtained in FSM; 35 specimens were purchased from fish markets on Pohnpei, the remaining three specimens were speared at nearby Ant Atoll. On Guam, 89 specimens were purchased from fish markets.

Rapid, histology-based methods from Longenecker et al. (2017) were used to obtain lengths and weights, to describe the sexual pattern, and to estimate size-at-maturity, sex-ratios, and a length-batch fecundity relation. Briefly, for each specimen fork length (FL) was measured to the nearest mm, and whole body weight was estimated with a hanging spring-scale. Gonads were excised and weighed to 0.001 g on a portable jeweler’s scale. For each ovary that appeared to be at or nearing maturity, an approximately 1-cm thick transverse section was removed from one lobe, weighed to 0.001 g, and transferred to approximately 15 mL Gilson’s fluid (Pohnpei) or frozen (Guam) in a skirted 50-mL centrifuge tube for later batch fecundity analysis (below). For all gonads (regardless of sex or reproductive status) an approximately 3 mm × 3 mm × 3 mm subsample was fixed in Dietrich’s solution for at least 24 h. The fixed subsample was trimmed to approximately 8-mm³ then embedded in plastic (JB4, Electron Microscopy Sciences) and serially sectioned. At least five tissue sections were mounted on a microscope slide, stained with hematoxylin and eosin (Pohnpei) or toluidine blue (Guam). Ovary sections were examined at 100× and testis sections at 400× for evidence of reproductive maturity. Ovaries were classified according to Wallace and Sellman (1981) and testes according to Nagahama (1983). Females were considered mature with the onset of vitellogenesis (appearance of yolk protein in the oocytes), and males were considered mature when the testes contained visible spermatozoa.

To estimate batch fecundity on Pohnpei, methods modified from Agger et al. (1974) were used; ovarian

samples preserved in Gilson’s fluid were vigorously hand shaken at least once per day for 14 days to liberate oocytes from the stroma. On Guam, methods modified from Marteinsdottir and Begg (2002) were used to reduce processing time and to eliminate the use of the marine pollutant, mercuric chloride; ovarian samples were thawed, to each was added 6 mL of buffered enzyme solution (0.1 M Tris/5 mM CaCl₂, pH 7.6) and 6 mg collagenase (Type 4, Worthington Biochemical Corporation), connective tissue was digested for 2 h at ambient temperature with gentle hand shaking every 20 min, then 2.5 mL Dietrich’s solution were added to fix the liberated oocytes. Estimates of the oocyte number were generated for ovarian samples that, based on the histological examination above, had reached at least late vitellogenesis (≥ stage 3b). The samples were diluted with water to a total volume of 400 mL, stirred to distribute oocytes, and a Stempel pipette was used to obtain ten 1-mL subsamples. Counts of oocytes in the largest size-class in each subsample were recorded, and batch fecundity (BF) was estimated with the following equation

$$BF = (N_o \cdot V)(W_o \cdot W_s^{-1})$$

where N_o is the mean number of mature oocytes per mL, V is the total dilution volume in mL, W_o is the total ovary weight, W_s is the sample weight.

Data were analyzed as follows. A series of weight-length relations (WLRs) were constructed by linear regression of log-transformed data and any data point with a residual > 0.1 was considered to be an outlier. Analysis of covariance (ANCOVA) was used to test for differences in site-specific and sex-specific WLRs. Logistic regression analysis of the dependent variable, percent mature individuals, and the independent variable, the mean length of individuals within each 2.5-cm size class for females and 5.0-cm size class for males, was used to produce a maturation curve. The regression model was

$$\%F = 100 \cdot \left(1 + e^{(-\ln(19))((L - L_{50})(L_{95} - L_{50})^{-1})} \right)^{-1}$$

where %F is the predicted percentage of mature individuals at a given length, L , L_{50} is the length comprising 50% mature individuals, and L_{95} is the length comprising 95% mature individuals (Williams et al. 2008). Sex-specific L_{50} values are reported as estimates of size-at-maturity. Chi-square (χ^2) analysis was used to test whether overall and operational sex ratios differed from 1 : 1. Size-specific sex ratios were examined by determining the percentage of mature females (of total mature individuals) in each size class and then plotting the proportion of mature females as a function of the mean length within each size class. Exploratory regression analysis was used to evaluate whether the likelihood of a mature individual being female varied predictably with length. Linear regression analysis of log-transformed data was used to test for relations between length and batch fecundity. Identification of

the part of a population responsible for the majority of egg production was done by first multiplying the result of the length–fecundity relation at a given length by the likelihood that an individual at that length is female. The product was then plotted as a function of length. For comparative purposes, the likelihood of an individual being female was assumed to be constant across all lengths (using the overall sex ratio) and the product was plotted as a function of length. Thus, both curves were standardized to represent per capita batch fecundity versus length. The trend in the mean length of *Monotaxis grandoculis* catch was evaluated from annual boat-based creel surveys for Guam from 2010–2019 using ordinary linear regression plotted against the size-at-maturity estimates. Non-confidential creel survey data were provided by the Western Pacific Fisheries Information Network of the NOAA Fisheries Pacific Islands Fisheries Science Center via data request PICDR-112964.

RESULTS

Island-specific WLRs were $0.039FL^{2.86}$ for Pohnpei and $0.030FL^{2.94}$ for Guam. However, ANCOVA did not detect a significant location-based difference in the WLR for this data set ($F = 2.01$, $DF = 1$, $P = 0.159$), we, therefore, treated all data as a single statistical population. Total body weight (W) in g can be estimated from fork length (FL) in cm: $W = 0.033FL^{2.91}$. The 95% CI of regression parameters a and b are 0.028–0.039 and 2.87–2.96, respectively ($r^2 = 0.992$, $n = 127$, FL range: 16.2–44.5 cm, W range: 110–2100 g). ANCOVA did not detect a significant sex-based difference in the WLR for the 100 histologically sexed individuals in this population ($F = 0.03$, $DF = 1$, $P = 0.862$). Figure 1 shows that the WLR from the presently reported study is visually indistinguishable from previously published WLRs from Pohnpei ($W = 0.039FL^{2.86}$; Longenecker and Langston 2016), and Guam ($W = 0.043FL^{2.84}$; Kamikawa et al. 2015). Further, the WLR from the presently reported study is nearly indistinguishable from WLRs published for American Samoa ($W = 0.031FL^{2.93}$; Matthews et al. 2019) and New Caledonia ($W = 0.023FL^{3.02}$; Kulbicki et al. 2015). However, specimens from the presently reported study may weigh slightly more per unit length than those from Yap, FSM ($W = 0.036FL^{2.85}$; Smith and Dalzell 1993); we cannot be certain because Smith and Dalzell (1993) did not specify whether their WLR was for TL or FL, and they apparently used curvilinear regression analysis to construct their WLR. Finally, specimens from the presently reported study weighed slightly less per unit length than those from the Philippines ($W = 0.036SL^{3.03}$, $FL = 0.046 + 1.145(SL)$; Bos et al. 2017).

We histologically examined gonads of 43 male and 57 female specimens. Figure 2 shows examples of immature and mature testes and ovaries. Ovaries of mature females exhibited group-synchronous oocyte development. The smallest female with vitellogenic oocytes was 18.1 cm FL. We estimated female L_{50} at 27.9 cm FL for Pohnpei and 30.9 cm FL for Guam. We then tested whether island-specific estimates were significantly different; using bootstrap methods (Manly 1997), we constructed

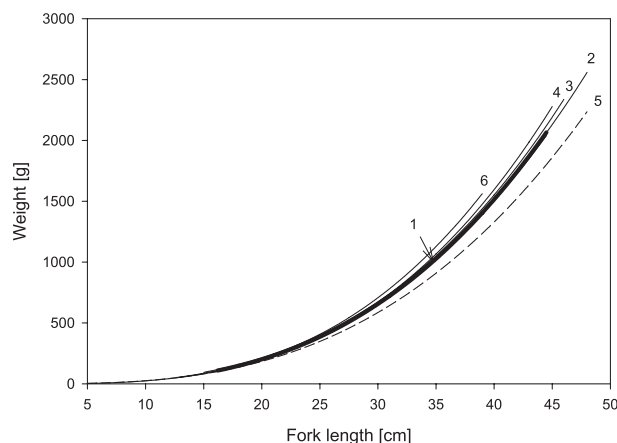


Fig. 1. A comparison of WLRs from the presently reported study (bold) and other published studies: (1) Pohnpei, FSM (Longenecker and Langston 2016); (2) Guam, USA (Kamikawa et al. 2015); (3) American Samoa, USA (Matthews et al. 2019); (4) New Caledonia, France (Kulbicki et al. 2005); (5) Republic of the Philippines (Bos et al. 2017); (6) Yap, FSM, authors do not explain whether TL or FL was used (Smith and Dalzell 1993); solid curves represent WLRs with parameters estimated from linear regression of log-transformed length and weight data, with known minimum and maximum lengths; dashed curve represents an apparent curvilinear regression, with unstated minimum and maximum lengths, the curve may represent extrapolations at small and large lengths

empirical distributions of L_{50} estimates by resampling 1,000 times with replacement the length and maturity data for female fish for each island and calculating size-at-maturity. We then used random pairs of L_{50} estimates to generate a distribution of between-island differences in female L_{50} . We then compared the difference between the initial island-specific L_{50} estimates with the 95% confidence intervals for the distribution of between-island differences in L_{50} for females using empirically-derived values for the 0.025 and 0.975 quantiles. We found that the between-island difference in female L_{50} estimates (3 cm FL) was not statistically significant (95% CI = 0.5–8.7 cm FL). We, therefore, pooled the data from both islands to generate an overall female L_{50} of 30.0 cm FL (Fig. 3A). The smallest male with spermiated testes was 19.5 cm FL. We had too few immature male specimens from Pohnpei to estimate a male L_{50} for that island and therefore could not test for a statistically significant between-island difference in male L_{50} values. We estimated male L_{50} at 41.1 cm FL for Guam. Using pooled data, we estimated male L_{50} at 35.4 cm FL (this estimate ignored the smallest size class, represented by a single, mature individual; Fig. 3A).

DISCUSSION

Because we analyzed the minimum number of specimens necessary to generate estimates of reproductive parameters, and because our specimen collections represented only

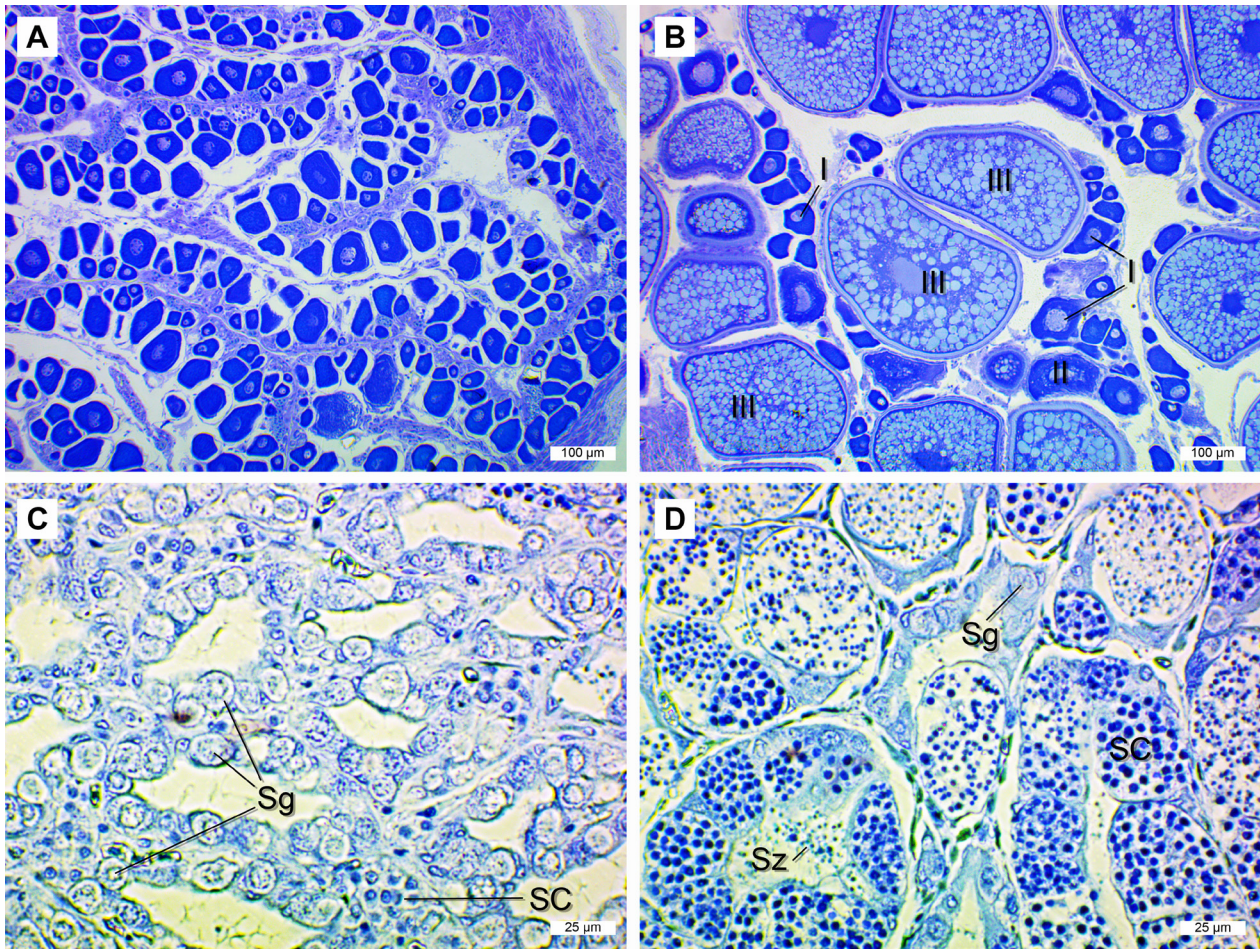


Fig. 2. Photomicrographs of *Monotaxis grandoculis* gonads from the Micronesian region: (A) ovary of a 22.0 cm FL immature female from Guam with primary-growth oocytes, 100 \times ; (B) ovary of a 30.7 cm FL mature female from Guam with primary-growth (I), cortical vesicle (II), and vitellogenic (III) oocytes, 100 \times ; (C) testis of a 28.6 cm FL immature male from Pohnpei with spermatogenic cysts (SC) and spermatogonia (Sg), 400 \times ; (D) testis of a 20.4 cm FL mature male from Pohnpei with spermatogenic cysts (SC), spermatogonia (Sg), and tailed spermatozoa (Sz), 400 \times

about one-quarter of the months in a year, the results should be considered preliminary. Despite these limitations, our emphasis on microscopic examination of gametes yields a more-reliable evaluation of individual reproductive status than gross (i.e., macroscopic) examination. In the presently reported study, macroscopic evaluation of gonads led to incorrect assignment of sex and/or reproductive status in 55.0% of *Monotaxis grandoculis* specimens. Of the assignment errors, 43% were incorrect sex, 50% were incorrect reproductive status, and 7% were incorrect for sex and reproductive status. Similar errors have been reported for other species (Vitale et al. 2006, Grandcourt et al. 2011, Longenecker et al. 2013a, 2013b, 2017). This degree of error indicates a decoupling between the physiognomy and cellular processes of gonads, which can have profound impacts on estimates of reproductive parameters. For *M. grandoculis*, macroscopic analysis leads to a 0.8 cm overestimate of female L_{50} , and a 6.3 cm underestimate of male L_{50} . These estimates are 2.7% higher and 17.8% lower than the histologically determined values for females and males, respectively. The latter error suggests that *M. grandoculis* testes outwardly appear to be mature well before they produce sperm.

A t-test for unequal variances indicated the female mean length of 26.4 cm FL was significantly shorter than the male mean length of 31.4 cm FL ($t = -4.06$, $df = 59$, $P < 0.000$), which is suggestive of protogyny. However, we did not see diagnostic evidence of sex change. For example, we did not observe a central membrane-lined lumen in testes, or any gonad containing a mixture of ovarian and spermatogenic tissue. Lethrinids are generally considered to be hermaphroditic. This sexual pattern is particularly well-demonstrated for *Lethrinus* species, which may exhibit functional protogyny or prematurational sex change (Ebisawa 1997, 2006, Trianni 2011, Currey et al. 2013, Taylor et al. 2017). A sex-based bimodal size distribution for this population of *Monotaxis grandoculis* is suggestive of protogyny. However, because we did not see structural or germinal evidence of sex change, we classify *M. grandoculis* as a gonochoric species.

Overall sex ratio was 1 : 0.88 (M : F) on Pohnpei and 1 : 1.59 on Guam. Neither overall sex ratio was significantly different from 1 : 1, nor were island-specific ratios significantly different (Fisher's exact test, $P = 0.192$). We therefore pooled data for an overall sex ratio of 1 :

1.33, which was not significantly different from 1 : 1 ($\chi^2 = 1.960$, $DF = 1$, $P = 0.162$). The operational sex ratio was 1 : 0.46 (M : F) on Pohnpei and 1 : 1.60 on Guam. Neither operational sex ratio was significantly different from 1 : 1, nor were island-specific ratios significantly different (Fisher's exact test, $P = 0.149$). We therefore pooled data for an operational sex ratio of 1 : 0.89, which was not significantly different from 1 : 1 ($\chi^2 = 0.188$, $DF = 1$, $P = 0.732$). As was demonstrated for L_{50} estimates, histological and macroscopic results differed. The latter suggest that overall sex ratio is significantly female biased ($\chi^2 = 4.445$, $DF = 1$, $P = 0.035$), in contrast to the 1 : 1 ratio of histological analysis. These differences can have profound impacts on length-based fishery management strategies for this species.

Despite the parity of overall and operational sex ratios, the likelihood of a mature individual being female varied with length (Fig. 3B); the smallest individuals were more likely to be male, individuals 23.1–33.5 cm FL were more likely to be female, and larger individuals were more likely to be male. All specimens ≥ 33.6 cm FL were males. However, a curvilinear regression equation (Gaussian, 3-parameter peak function) suggested that less than 10% of individuals ≥ 38.9 cm FL would be females and that about 1% of individuals ≥ 42.7 cm FL would be females ($r^2 = 0.72$).

Length and batch fecundity values were not significantly related on Pohnpei ($P = 0.54$) or Guam ($P = 0.33$) or for pooled data ($P = 0.19$); however, we report the latter to illustrate the impact of sex ratio on per capita egg production, below. A poorly descriptive regression equation suggested that batch fecundity (BF) can be estimated from female fork length (FL_{\square}) in cm (Fig. 3C): $BF = 0.008FL_{\square}^{4.46}$. The 95% CI of regression parameters a and b were $4.94 \cdot 10^{-13}$ – $1.37 \cdot 10^8$ and -2.52 – 11.4 , respectively ($r^2 = 0.214$, $n = 10$, FL_{\square} range: 23.8–33.0, BF range: 4022–84 496).

The curves in Fig. 3D illustrates the impact of sex ratio on the relation between FL and per capita egg production per spawning event. If operational sex ratio was considered invariant, expected per capita batch fecundity was greatest at maximum size (Fig. 3D, dashed curve). However, when the variable likelihood of a mature individual being female was considered, the decreasing chance of large individuals being female eventually overwhelms length-specific increases in batch fecundity such that egg production per spawning event peaks at 31.7 cm FL, well below maximum observed length (Fig. 3D, solid curve). Females ≤ 37.7 cm FL are collectively responsible for 90% of egg production per spawning event.

The mean length of *Monotaxis grandoculis* in the catch from boat-based creel surveys significantly declined from 2010 to 2019 ($n = 55$ specimens, $F_{1,54} = 6.33$, $P = 0.015$). The downward trend in the mean length of catch relative to the male and female L_{50} estimates can provide an ecological indicator of the potentially declining status of the spawning stock biomass of this population (Fig. 4). Of concern, is that mean catch lengths represent the size classes of females collectively responsible for 92.4% of

per capita egg production per spawning event, and that mean catch lengths in three of the five most recent survey years were well below both male and female L_{50} estimates. These results should be interpreted cautiously given the preliminary nature of the reproductive analysis and relatively low number of specimens in the creel surveys but the strength of the trend, and given the frequency that this species is found in fish markets (Rhodes et al. 2008, Houk et al. 2012, 2017), warrants further examination of the status of *M. grandoculis* in Micronesia, and Guam, in particular.

The size-specific sex ratios reported here, where females become increasingly rare, or absent, with increasing length, are commonly reported for lethriniids (Ebisawa 1997, 2006, Trianni 2011, Currey et al. 2013). However, the impact of this pattern on impressions of which size classes are responsible for the majority of population-level egg production is currently under-recognized (but see Longenecker et al. 2014, 2017). Failing to account for the negligible chance of large *Monotaxis grandoculis* individuals being female would lead to an overestimate of 93 136 eggs per spawning event of per capita egg production by the largest individuals in this population. Per capita egg production per spawning event peaks just 1.7 cm larger than female L_{50} and 12.8 cm smaller than the maximum observed size in this population. Given the lack of conspicuous sexual dimorphism in *M. grandoculis*, the general guidance to protect BOFFFFS in the population could be practically interpreted as leave all big fish in the population, not just females. The implications of these results to fishery management cannot be overstated; targeting fish in the largest size classes may have little impact on the overall reproductive output for the population. Furthermore, protecting the largest fish by imposing slot limits, for example, would direct fishing pressure to the size classes that are collectively responsible for the majority of population-level egg production per spawning event contrary to guidance provided by the BOFFFFS concept.

On the basis of statistical tests for differences between island-specific WLR, L_{50} , and length-batch fecundity relations, we pooled data from Pohnpei and Guam. Thus, we assumed the two populations have statistically similar life history traits. However, the preliminary nature of our results may lead to the assumption being overturned by future work. Nevertheless, the presently reported results are important because one of the fundamental challenges for the assessment of tropical fish species is an accurate understanding of the reproductive dynamics of managed stocks. The sheer diversity of coral-reef fishes and the supposed cost associated with the detailed reproductive analysis of each species are often cited as barriers to obtaining important baseline life-history information (Roberts and Polunin 1993, Johannes 1998, Froese and Binohlan 2000). We demonstrate that rapid reproductive analysis can be used to generate estimates of size-at-maturity, fecundity-at-size, and size-specific sex ratios as critical biological parameters for ecological indicators of the status of data-limited coral reef fish stocks. Because

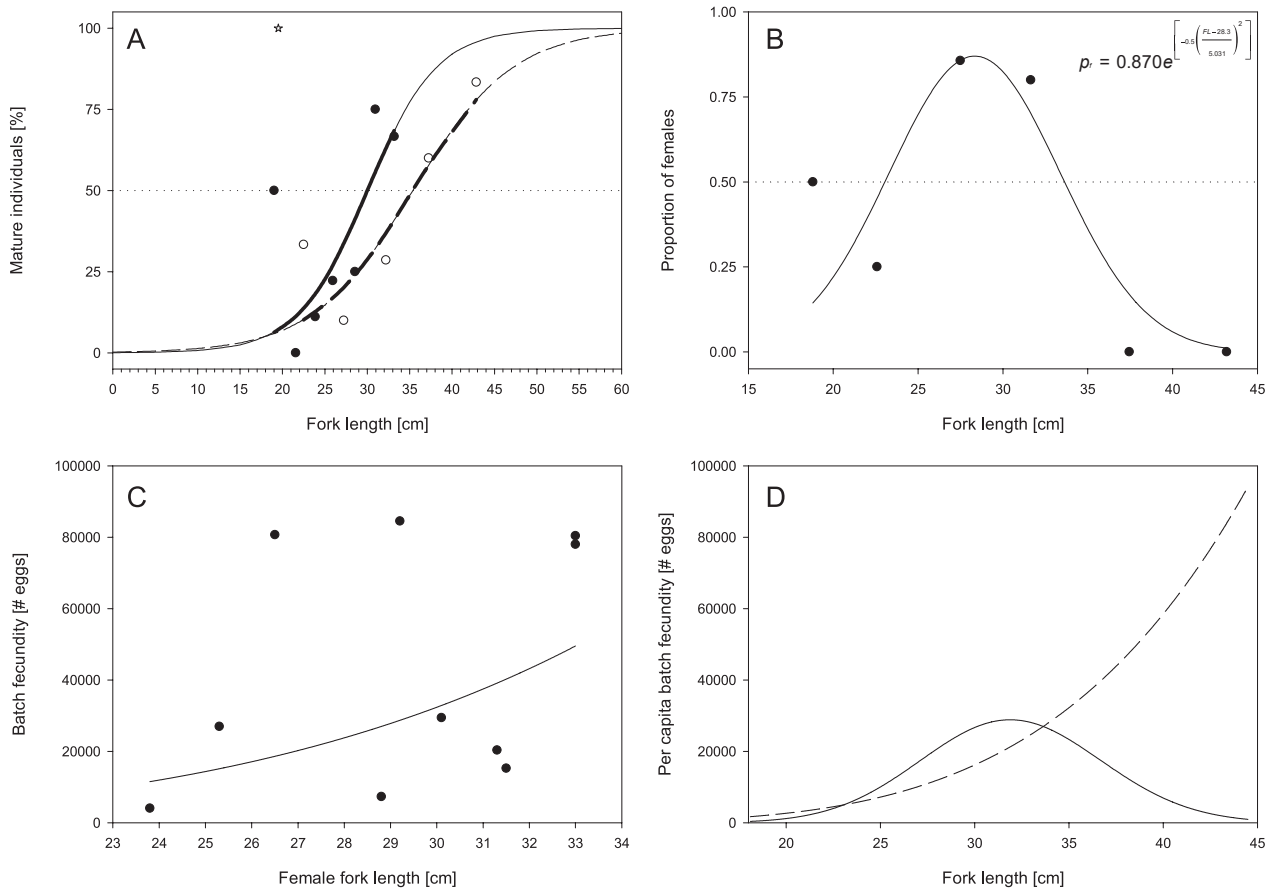


Fig. 3. Estimates of reproductive parameters for *Monotaxis grandoculis* from the Micronesian region: (A) size-at-maturity for females (solid circles, solid curve) and males (open circles, dashed curve), the male curve ignores the smallest size class, represented by a single, mature individual (star), the bolded portion of each curve represents the range for which data were collected with model extrapolations plotted in light grey; (B) proportion of females (p_f) versus length; (C) length-batch fecundity relation; (D) per capita batch fecundity versus length accounting for the size-specific likelihood that a mature individual is female (solid curve) and assuming operational sex ratios are invariant across sizes (dashed curve)

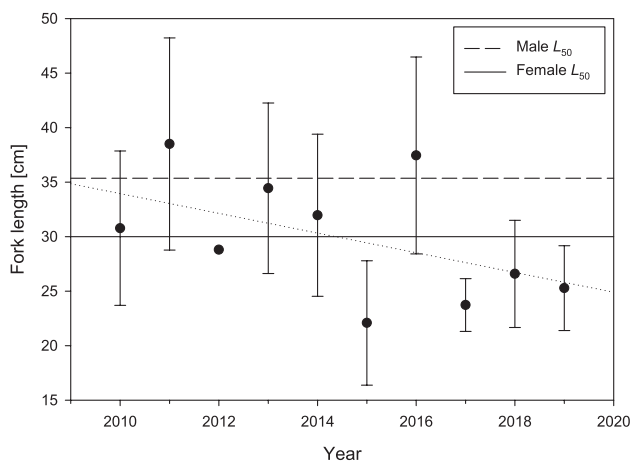


Fig. 4. Time series of mean fork length (\pm standard deviation) of *Monotaxis grandoculis* catch from annual boat-based creel surveys for Guam from 2010 to 2019. Dotted line is a trend in mean lengths from ordinary linear regression. For comparison, solid horizontal line represents female L_{50} estimate and dashed horizontal line male L_{50} estimate

reproductive size is unknown for ~83% of exploited fishes worldwide (Froese and Binohlan 2000), the rapid analysis approach has the potential to vastly improve the understanding of coral-reef fisheries biology and increase the capacity for these studies in tropical ecosystems worldwide.

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