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Life-history, exploitation and extinction risk of the data-poor Baraka's whipray (*Maculabatis ambigua*) in small-scale tropical fisheries

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Abstract

The Baraka's whipray (*Maculabatis ambigua*) is a major constituent of small-scale fisheries catch in the south-western Indian Ocean. Despite this, little is known of its life-history or exploitation status. We provide the first estimates of crucial life-history parameters and the maximum intrinsic population growth rate r_{max}, using specimens collected from small-scale fisheries landings in Kenya, Zanzibar and Madagascar (with northern Madagascar representing a range extension for this species). We assess the relative risk of overexploitation by combining r_{max} with estimates of total Z, fishing F, and natural M mortality, and an estimate of the exploitation ratio E. The data indicate that Baraka's whipray is a medium-sized, fast-growing, early maturing species, with a relatively long lifespan. This results in a high r_{max} relative to many other elasmobranchs, which when combined with estimates of F suggests that the species is not at imminent risk of extinction. Yet, estimates of exploitation ratio E indicate likely overfishing for the species, with full recruitment to the fishery being post-maturation and exploitation occurring across a broad range of age and size classes. Thus, Baraka's whipray is unlikely to be biologically sustainable in the face of current fisheries pressures. This paper makes an important contribution to filling the gap in available data and is a step towards developing evidence-based fisheries management for this species. Further, it demonstrates a simple and widely applicable framework for assessment of data-poor elasmobranch exploitation status and extinction risk.

KEYWORDS
Bland–Altman, elasmobranch, life-history, r_{max}, Indian Ocean

1 | INTRODUCTION

Elasmobranchs (sharks and rays) generally display slow growth, late maturity and low fecundity (Compagno, 1990). These life-history traits mean elasmobranchs are intrinsically sensitive to non-natural mortalities and limits their recovery potential (Dulvy *et al*., 2014a). However, there is considerable variation in the life-history traits both among (Jacobsen & Bennett, 2011; Stevens & McLoughlin, 1991) and within (Jacobsen & Bennett, 2010; Lombardi-Carlson *et al*., 2003; O'Shea *et al*., 2013) species. Fisheries are the most prominent source of non-natural mortalities for elasmobranchs at the global level (Dulvy *et al*., 2014a; Worm *et al*., 2013). Understanding species and stockspecific life-history traits is important when assessing the sustainability of fisheries exploitation, conducting stock assessment, producing demographics models and predicting rebound potential (Cailliet & Goldman, 2004; Frisk *et al*., 2001; Smith *et al*., 2008). Thus, species and population-specific life-history traits are pivotal in the formulation of evidence-based fisheries management (Barnett *et al*., 2019).

Without species-specific life-history and fisheries exploitation data, the management of data-poor fisheries may be ineffective or even detrimental to the long-term sustainability of elasmobranchs. Efforts to manage shark resources have been initiated throughout the southwestern Indian Ocean (SWIO) region (Kenya, Tanzania including Zanzibar, Mozambique, Seychelles, Comoros, Mayotte, Madagascar, La Réunion and Mauritius), *e.g*. development of National Plans of Action (Temple *et al*., 2018). Yet, our understanding of the scale and composition of elasmobranch exploitation in SWIO fisheries is extremely poor. Recent vulnerability assessments based on small-scale fisheries landings suggest that several coastal rays, primarily whiptail stingrays (Family Dasyatidae), may be at risk across the SWIO (Temple *et al*., 2019). Many of these species have either limited or no regional life-history data available. Rays contribute nearly half of SWIO small-scale fisheries landed elasmobranch catch (by weight and number) and originate from many of the same fisheries as sharks (Temple *et al*., 2019). Despite this, rays have received little consideration in SWIO elasmobranch management formulation.

Although only recently described (Last *et al*., 2016b), Baraka's whipray (*Maculabatis ambigua*) is the most common ray in Kenyan small-scale fisheries catch and a common constituent of small-scale fisheries catch in Zanzibar. Baraka's whipray are primarily caught in bottom-set gillnets (Barrowclift *et al*., 2017; Temple *et al*., 2019) and are regularly bycatch in trawl fisheries elsewhere within their range (Last *et al*., 2016b). Baraka's whipray was originally thought to be distributed from Zanzibar to the Red Sea and possibly further into the northern Indian Ocean (Last *et al*., 2016b). Little is known of the life history of this species.

Here, we investigate key life-history parameters of Baraka's whipray through the production of disc width–weight relationships, age-structured growth models, and maturation and longevity estimates. Subsequently, we estimate maximum intrinsic population growth rate, which is combined with estimates of female fisheries and natural mortalities and female exploitation ratio to assess relative extinction and overexploitation risk of this data-poor species.

2 | MATERIALS AND METHODS

2.1 | Sample collection

Baraka's whipray specimens (n = 48) from small-scale fisheries landings were sampled with the consent of fishers and/or merchants at the village of Mkokotoni and the Darajani Market, Stone Town in Zanzibar between 28 July 2015 and 19 August 2015 (Figure 1). Where possible, we recorded the disc width (cm), weight (kg) and sex of each specimen. Male maturity status (immature or mature) was recorded based on calcification of claspers (Walker, 2005), with only those specimens exhibiting complete calcification considered mature. Maturity status could not be recorded for females because fishers and merchants did not consent to examination of the reproductive tract. Vertebrae were extracted from the mid-disc of 47 specimens to be used for aging and stored at −20°C. Supplementary data for Baraka's whipray (n = 155) were recorded by trained fisheries observers across Kenya, Zanzibar and northern Madagascar during a 12-month landings monitoring programme between June 2016 and June 2017 (Temple *et al*., 2019) (Figure 1). Disc width, weight, sex and male maturity status were recorded. Observers also opportunistically recorded female maturity, with only those observed with fertilized eggs considered as mature. Both sets of specimens were caught across a range of gear types (bottom-set gillnets = 78, drift gillnets = 38, handlines = 8, longlines = 6, beach seine = 2, ringnet = 2, and unknown = 69).

Where relevant, samples were collected under a research permit from the Office of Chief Government Statistician Zanzibar (No. 0697), exported under the provision of the then Ministry of Livestock and Fisheries Zanzibar and imported to the UK under IMP/GEN/2014/06.

We assume that all catches originate from the same population or stock. Specimens where disc width was not recorded (n = 29) were disregarded from all analyses. Data analyses and visualizations were carried out and produced using R statistical software, version x64 3.6.0 (R Core Team, 2019).

2.2 | Disc width–weight relationship

Disc width and weight data of all specimens that had not been gutted (n = 100) were natural log (ln) transformed and their relationship described using linear models. Cook's distance (4/n) was used to identify data points exerting undue influence on linear models, likely resulting from measurement and/or data entry errors; these points were removed (n = 5) and the models subsequently re-run. The sex of specimens was included as an interaction variable and compared to the null model using ANOVA to determine whether the effect of sex was significant. The 95% confidence interval (95%CI) of the linear models was derived using bootstrapping with replacement for 10,000 iterations.

2.3 | Age estimation

Two vertebrae from each sampled specimen were cleaned of excess muscle and connective tissue, and both neural and haemal arches were removed. Subsequently, vertebrae were immersed in a 5% sodium hydrochloride solution for 10–30 min, dependent on the vertebrae size and quantity of remaining tissues. Samples were washed, then towel and air dried. Cleaned vertebrae were embedded in clear epoxy resin (Buehler EpoxiCure; Lake Bluff, Illinois, United States). A single sagittal-plane section was taken from each vertebra using a slow-speed precision saw with a diamond wafering blade (Buehler IsoMet Low Speed Precision Cutter). Several section widths were trialled (600, 450, 300, 200 and 150 μm), with 200 μm producing the highest readability. Sections were mounted permanently onto glass

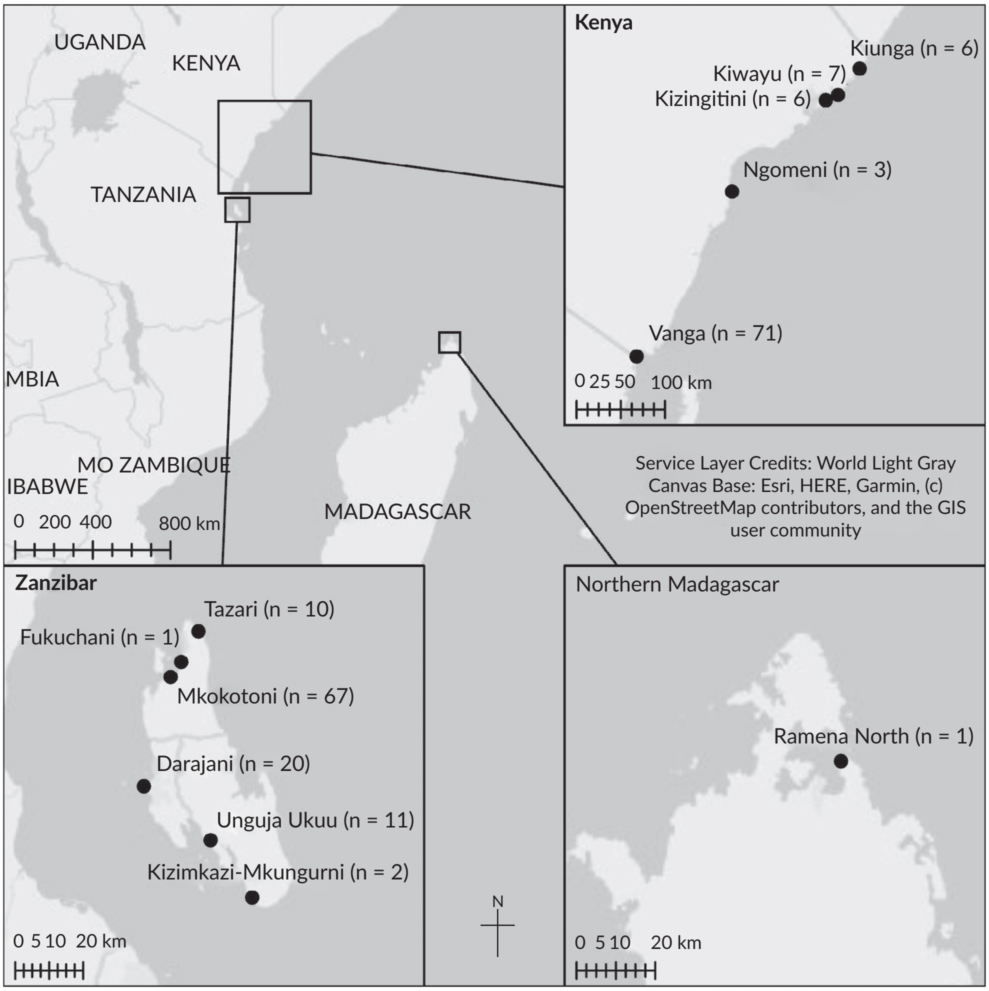

FIGURE 1 Locations of landing sites and markets in the south-western Indian Ocean where Baraka's whipray *Maculabatis ambigua* were sampled between July 2015 and June 2017. Sample sizes for individuals recorded by fisheries observers are displayed

slides (Fisher Chemical DPX Phthalate Free Mounting Media; Hampton, New Hampshire, United States) and photographed using a digital macro-lens camera (Nikon SLR D7200; Tokyo, Japan). Image enhancement for growth band reading was carried out in Adobe Photoshop CS3 (San Jose, California, United States) (Campana, 2014).

The age (to the nearest 0.5 years) for each individual specimen was determined by examination of paired opaque and translucent banding in the vertebral *corpus calcareum*. The birth band was distinct but did not show a clear change in angle on the *corpus calcareum* (Figure 2). Age was estimated from the independent examination of both sagittal sections (images were randomized before reading) by two independent readers. Mean age estimates for each specimen were generated for each reader and compared. Where reader mean estimates differed by <1 year the mean was taken as the best estimate. This allowable difference was more conservative than in other studies in light of the restricted sample size (Jacobsen & Bennett, 2011; Smith *et al*., 2008). If differences in mean age estimates between readers were >1 year, ages were re-estimated with both readers present. If readers could not agree (*n* = 0) samples would have been discarded (Goldman, 2005).

Commonly, measures of agreement, precision and bias in age reads are given as percentage agreement (PA), PA ±1 year, the coefficient of variation (CV) and the average percentage error (APE) (Beamish & Fournier, 1981; Chang, 1982). These measures are presented but are commonly recognized as imperfect (Cailliet *et al*., 2006;

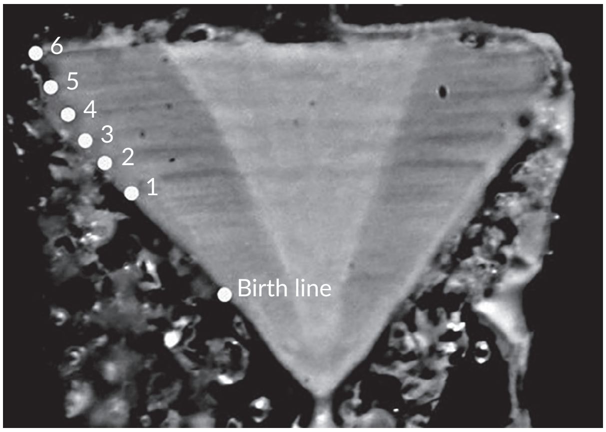

FIGURE 2 Photograph of sectioned vertebrae, with birth line and annuli marked, taken from a 63 cm disc-width male Baraka's whipray *Maculabatis ambigua* captured in a bottom-set gillnet in August 2015. This individual was aged 6 years

Goldman, 2005). We suggest that the Bland–Altman approach, designed for method comparison, provides improved quantification and visualization of agreement, precision and bias among reads and readers compared to the standard methods used in aging studies (Bland & Altman, 1999, 2003). Bias in the relationship between reads (within and among readers) is assessed through linear modelling of the mean age read for each specimen against the difference between reads for each specimen. Precision in age reads (within and among readers) is described by the limits of agreement (LOA) defined by the 95% mean confidence interval of the difference between reads. We display the results of the Bland–Altman method as the primary measure of agreement, precision and bias.

Validation of growth band periodicity was not possible within this study. The short temporal period within which samples were collected and the restricted sample size meant that both marginal incremental analysis and edge analysis, which are the most common validation methods for elasmobranchs (Cailliet *et al*., 2006), were not possible to conduct. Furthermore, mark-recapture of chemically marked or captive reared individuals was not feasible within the constraints of this study.

2.4 | Growth modelling

Age and disc width data were fit to three growth models using nonlinear regression (package *nls*). Reasonable starting values for growth model parameters were estimated using self-starter functions (packages *FSAtools* and *stats*) before fitting. Models were run for males and females both separately and combined. Model selection was made through comparison of Akaike's information criterion corrected for small sample size (AICc). Kimura's likelihood ratio test was used to determine whether sex had a significant effect on the growth model (Haddon, 2010). The 95%CI for growth curves and growth curve coefficients were derived *via* bootstrapping with replacement for 10,000 iterations. The growth models fit were:

the three-parameter von Bertalanffy growth function (Von Bertalanffy 1938),

$$DW_t = DW_\infty - \left((DW_\infty - DW_0) e^{(-kt)} \right) \tag{1}$$

the three-parameter Gompertz growth function (Ricker 1975),

$$DW_t = DW_\infty e^{e^{-k(t-\alpha)}} \tag{2}$$

and the logistic growth function (Ricker, 1979),

$$DW_t = \frac{DW_\infty}{1 + e^{-k(t-\alpha)}} \tag{3}$$

where DW_t is the disc width at age t, DW_∞ is the asymptotic disc width, DW_0 is disc width at age zero, k is a growth constant and α is the inflection point.

2.5 | Estimation of the maximum intrinsic population growth rate

The maximum intrinsic population growth rate r_{max} for female Baraka's whipray, as it is females that constrain population growth, was estimated using the simplified Euler–Loktka equation, accounting for juvenile mortality (Cortés, 2016; Pardo *et al*., 2016b):

$$l_{t_{mat}} b = e^{r_{max} t_{mat}} - e^{-M} \left(e^{r_{max}} \right)^{t_{mat}-1} \tag{4}$$

where $l_{t_{mat}}$ is survival to maturity, b is the annual reproductive output of female offspring, t_{mat} is age at maturity and $M$is the instantaneous rate of natural mortality. We calculate $l_{t_{mat}}$ as:

$$l_{t_{mat}} = \left(e^{-M} \right)^{t_{mat}} \tag{5}$$

There are no data for the annual reproductive output of Baraka's whipray, thus we provided a plausible estimate of b from related species, as has been done for other data-poor species (D'Alberto *et al*., 2019; Pardo *et al*., 2016a). Whitespotted whipray (*Maculabatis gerradi*) and blackspotted whipray (*Maculabatis astra*) litters are reported as 1–4 and 1–3 pups, respectively (Last *et al*., 2016a; White *et al*., 2006). We assume reproduction is annual and that the sex ratio is 1:1. Hence, 0.5–2 female pups per year was considered a plausible range for b for the purpose of estimating r_{max}.

We cannot directly estimate t_{mat} for female Baraka's whipray because the infrequent observations of female maturity (n = 2) were both opportunistic and reliant upon the presence of fertilized eggs. However, other studies of whiptail stingrays suggest that males and females mature at a similar size (Da Silva *et al*., 2018; Jacobsen & Bennett, 2010, 2011; White, 2007). As such, we assume female size at maturity matches that of males. Disc width at which 50% of males reach maturity (White, 2007) was estimated from logistic regression and bootstrapping with replacement for 10,000 iterations used to define 95%CI. This male size at maturity range was then converted into age using the disc width and age relationship from the relevant selected growth model, providing a range estimate for female t_{mat}.

Lastly, in order to estimate M we first need to estimate longevity t_{max}. Estimates for t_{max} were bound by the theoretical age at which female Baraka's whipray reached 95% DW_∞ and 99% DW_∞ (Fabens, 1965; Ricker, 1979). 95% DW_∞ is calculated as $5\ln(2)k^{-1}$ and 99% DW_∞ calculated as $7\ln(2)k^{-1}$. Subsequently, M was calculated as:

$$M = \left(\frac{t_{max} + t_{mat}}{2} \right)^{-1} \tag{6}$$

The simplified Euler–Loktka equation, solving for r_{max}, was then optimized using the nlminb function (package *stats*). We made 1,000,000 draws from the estimated ranges of b, t_{mat} and M, assuming a uniform probability distribution within these ranges in order to explore the full range of potential estimates for r_{max}, particularly given the uncertainty in these parameters (Dulvy *et al*., 2014b).

2.6 | Estimating total mortality, fisheries mortality and the exploitation ratio

To draw direct comparisons with r_{max} estimates, we estimate the following parameters for female Baraka's whipray only. To estimate female instantaneous fisheries mortality F for Baraka's whipray, we first estimated total female instantaneous mortality Z (±95%CI) using an age-frequency approach, the Chapman–Robson catch curve method (R package *FSA*). In using this approach, we treat all small-scale fisheries monitored in this study as if they were one fishery, assuming that age classes beyond that of full recruitment to the fishery are equally vulnerable to the fishery, M is constant across age/size classes, the fishery has reached equilibrium and exploitation occurs from within a closed population. Equal vulnerability to the fishery

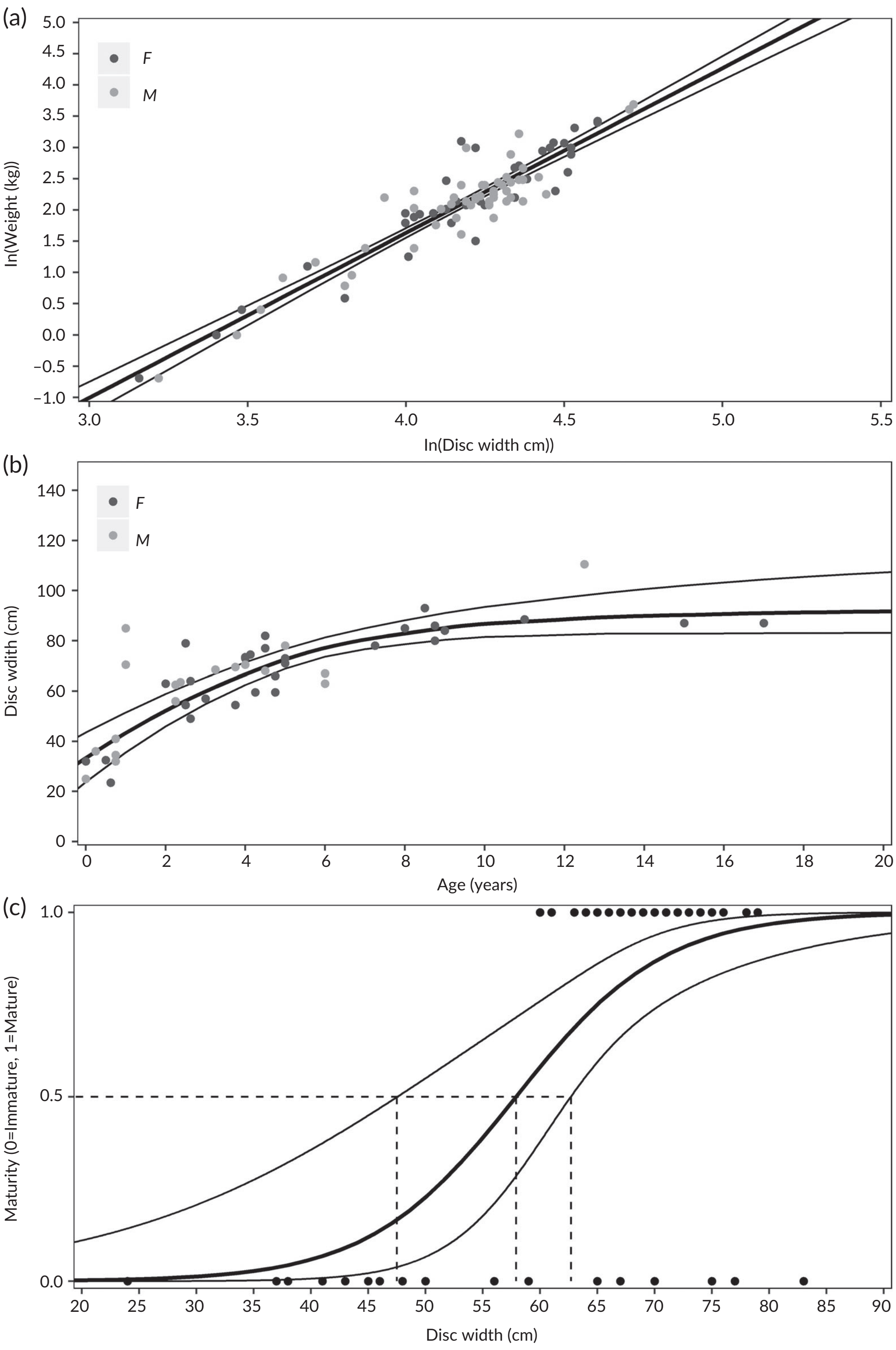

FIGURE 3 (a) Linear relationship with bootstrapped 95% confidence intervals between the natural log transformed disc width (cm) and weight (kg) for combined female and male Baraka's whipray *Maculabatis ambigua*, ln(weight) = 2.64 × ln(disc width) – 8.92. (●) F. (●) M. (b) Three-parameter von Bertalanffy growth curve with bootstrapped 95% confidence intervals describing the disc width and age relationship for both male and female Baraka's whipray combined, k = 0.241 (95%CI 0.119, 0.382), DW_{∞} = 93.4 cm (95%CI 82.9, 113.4) and DW_0 = 33.4 cm (95%CI 25.4, 42.6). (●) F. (●) M. (c) Logistic regression with bootstrapped 95% confidence intervals describing the relationship between disc width and maturity status (immature or mature) for male Baraka's whipray, disc width at 50% maturity is displayed

beyond age of full recruitment is reasonable given that the samples are drawn from a range of gear types across a large area and are thus unlikely to be strongly size selective. Similarly, the fishery is likely to have reached equilibrium given that the coastal elasmobranch fisheries of this region are well established (Temple *et al*., 2018). However, predation pressures on this species are unknown. Species which continue to grow substantially after age at full recruitment may show nonconstant M across ages as they outgrow some of their predators (Lorenzen, 2000). Additionally, nothing is known of the population structure of this species. Thus, it is possible that all assumptions of the catch curve may not be fully met with potential resultant biases on Z estimates. The Chapman–Robson method was selected as the regression estimator because traditional catch curves may show negative bias in mortality estimation (Smith *et al*., 2012).

Age was estimated, using the best fitting growth model, for all recorded catches with disc width data (n = 127) from the 12-month landings monitoring programme. Age of full recruitment to the fishery was assumed as the age class at peak abundance and Z was estimated from 1 year after the age of peak abundance (Smith *et al*., 2012). We made 1,000,000 draws from the estimated ranges of M and Z, assuming uniform and normal probability distributions, respectively. Ranges for M were subtracted from those of Z to estimate F, which was subsequently compared to $r_{\max}$ and the female exploitation rate E. We drew inference on the likely biological sustainability status of Baraka's whipray by comparing F/Z to an optimum value of 0.5 (Gulland, 1971; Pauly, 1983).

2.7 | Ethical statement

All samples in this study were derived from specimens originating from fisheries catches. The study did not provide inducements (financial or otherwise) for the provision of specimens. As such, there were no relevant animal welfare implications.

3 | RESULTS

3.1 | Disc width–weight relationship

There was no difference in the disc width–weight relationship between males and females (ANOVA, $F_{1,2}$ = 0.1673, P = 0.532). Thus, the disc width–weight relationship was modelled with males and females combined (R^2 = 0.872, F = 600.9, P < 0.001) (Figure 3a).

3.2 | Age estimation

Age was successfully estimated for all 47 specimens. Bland–Altman analyses showed no evidence of bias within reader 1 (R^2 = 0.038, F = 1.78, P = 0.189; Figure 4a,b) or reader 2 (R^2 = 0.001, F = 0.049, P = 0.825, Figure 4c,d). However, evidence of significant bias between readers was found (R^2 = 0.118, F = 6.04, P = 0.018, Figure 4e,f), with reader 1 producing higher estimates than reader 2 for older specimens. LOAs are presented alongside standard precision metrics (Table 1). Variability in age band counts was not considered to be unusually high when compared to other studies (Baje *et al*., 2018; Gutteridge *et al*., 2013; Jacobsen & Bennett, 2010). Consensus was reached between readers for all specimens with initial disparities >1 year, suggesting that the significant bias identified by the Bland–Altman approach was likely to have been overcome. Furthermore, the Bland–Altman approach demonstrated no evidence for an increase or decrease in discrepancies between age-reads with increasing age, indicating consistency in the variability within and among readers, and thus increasing confidence in the validity of band reads across age-spectra. Agreement between readers was likely influenced, in part, by the substantial subannuli banding prominent in young specimens. We recommend that future aging studies consider the use of this method when presenting the results of reader agreement, precision and bias in banding counts.

3.3 | Growth modelling

Age estimates for specimens ranged from 0 to 12.5 years for males and 0 to 17 years for females. Of the growth models tested, the three-parameter von Bertalanffy yielded the best fit for females, males and combined sex data. Kimura's likelihood ratio test indicated no significant effect of sex on the von Bertalanffy growth model fit (χ^2 = 3.76, P = 0.288) and so the combined fit for both sexes was selected and used for all subsequent analyses (Figure 3b). The von Bertalanffy growth parameter estimates for combined sexes were k = 0.241 (95%CI 0.119, 0.382), DW_∞ = 93.4 cm (95%CI 82.9, 113.4) and DW_0 = 33.4 cm (95%CI 25.4, 42.6).

3.4 | Estimating maximum intrinsic population growth rate

Disc width at which 50% of males reach maturity was estimated to be 57.9 cm (95%CI 47.5, 62.7) (Figure 3c). These estimates equate to half of males reaching maturity at 2.18 years old (95%CI 1.12, 2.79). The smallest of the female specimens classified as mature had a disc width of 62 cm, equivalent to an age of 2.7 years. For the purpose of estimating $r_{\max}$ we assume female t_{mat} to range uniformly from 1.12 to 2.79 years. Estimates for $t_{\max}$ were calculated based on age at 95% DW_∞ (Ricker, 1979) and at 99% DW_∞ (Fabens, 1965), yielding 14.4 years and 20.2 years, respectively. However, the maximum age directly observed during this study was 17 years. Thus, for the purpose of estimating $r_{\max}$ we assume $t_{\max}$ to range uniformly from 17 to 20.2 years. Using the drawn-down estimates of $t_{\max}$ and t_{mat}, we calculate median M to be 0.097 (95th percentiles 0.089, 0.107). Using the distributions of b, $t_{\max}$, t_{mat} and M, we calculate the median $r_{\max}$ for Baraka's whipray to be 0.446 (95th percentiles 0.220, 0.781; Figure 5a).

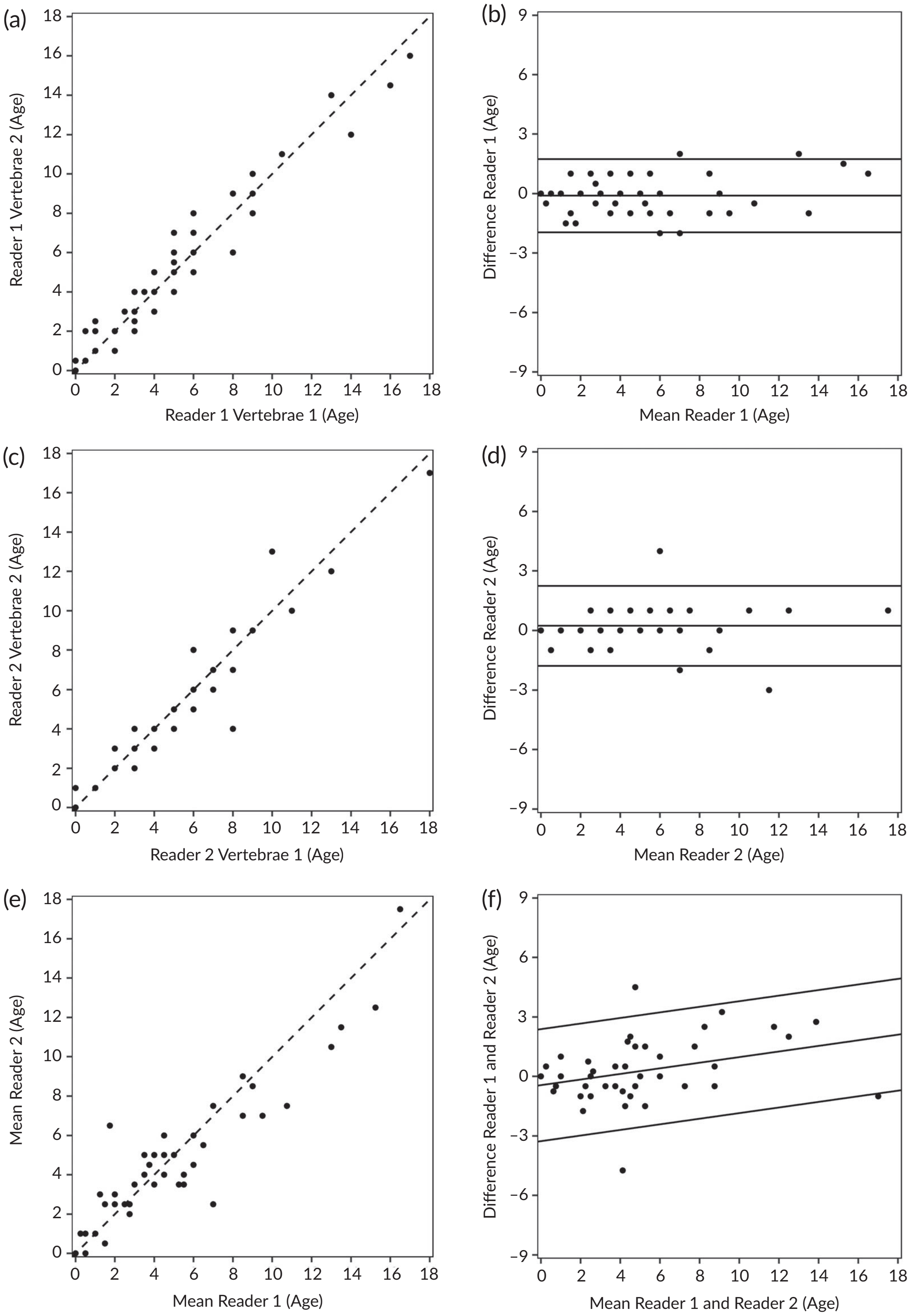

FIGURE 4 Bland–Altman assessments of agreement, precision and bias in age estimates (year ± 0.5) for Baraka's whipray *Maculabatis ambigua* within and between readers. (a) Relationship between vertebrae age band counts for reader 1. (b) Bland–Altman plot displaying bias and precision between vertebrae age band counts for reader 1. (c) Relationship between vertebrae age band counts for reader 2. (d) Bland–Altman plot displaying bias and precision between vertebrae age band counts for reader 2. (e) Relationship between mean vertebrae age band counts from reader 1 and reader 2. (f) Bland–Altman plot displaying bias and precision between mean vertebrae age band counts from reader 1 and reader 2

TABLE 1 Precision values for comparisons of age estimates for Baraka's whipray (*Maculabatis ambigua*) within and between readers; percentage agreement (PA), percentage agreement ±1 year, coefficient of variation (CV), average percentage error (APE) and Bland–Altman limits of agreement (LOA)

Comparison	PA (%)	PA ± 1 year (%)	CV (%)	APE (%)	LOA (years)
Within reader 1	34.04	85.11	15.38	10.87	±1.85
Within reader 2	46.81	93.61	12.87	9.10	±2.01
Between reader 1 and reader 2	12.77	68.09	24.14	17.07	±2.82

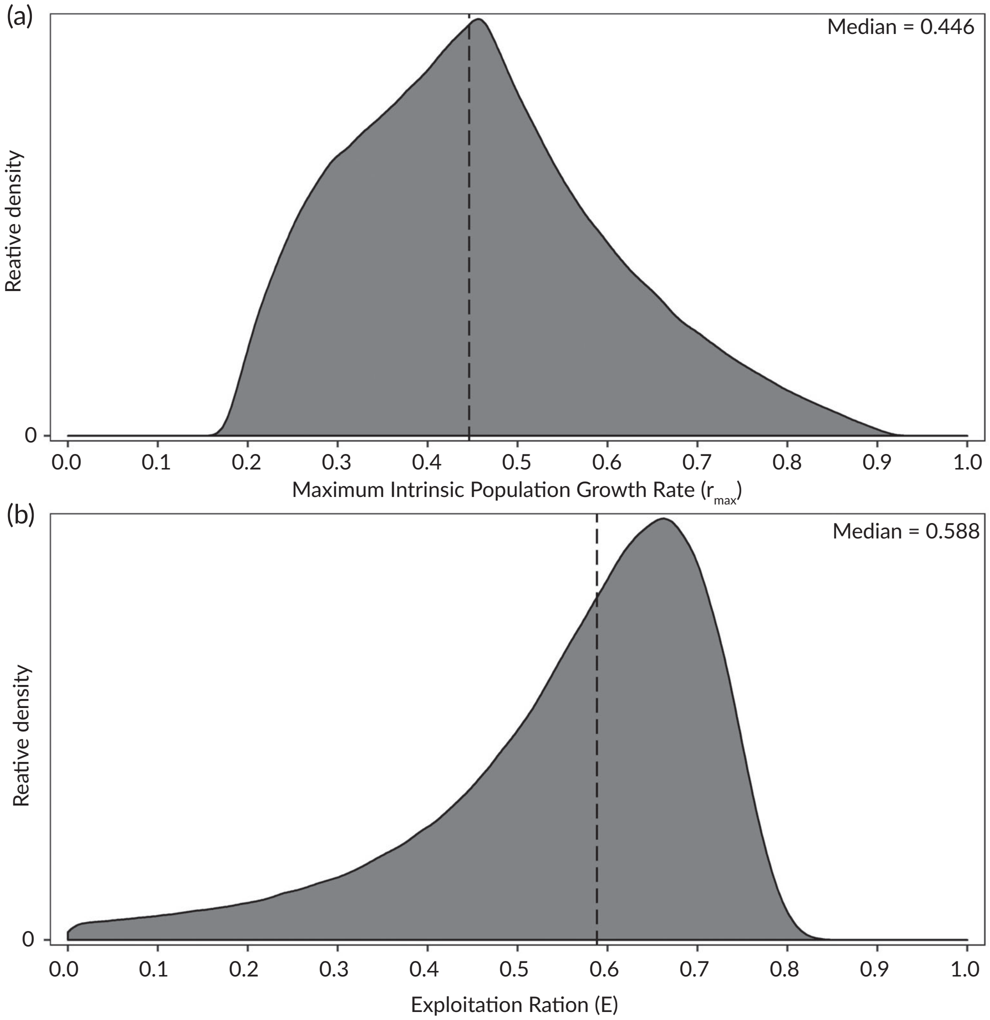

FIGURE 5 (a) Estimated distribution of the maximum intrinsic population growth rate (*E*) with median displayed for Baraka's whipray *Maculabatis ambigua*. (b) The estimated distribution for the exploitation ratio (r_{max}) with median displayed for Baraka's whipray in south-western Indian Ocean small-scale fisheries

3.5 | Estimating total mortality, fisheries mortality and the exploitation ratio

Age at full female recruitment to the fishery was estimated as 3 years (Figure 6), yielding an estimate for *Z* of 0.237 (95%CI 0.175, 0.298), equivalent to an annual mortality rate of 21.1% (95%CI 16.1, 25.8). Given this and the estimate for *M*, we estimate median *F* to be 0.139 (95th percentiles –0.029, 0.307), considerably lower than estimates for r_{max}. Median *E* is estimated from *F* and *Z* at 0.588 (95th percentiles –0.349, 0.764). The proportion of the estimated distribution of *E* greater than the optimal value of *E* = 0.5 is 68.7%, hence there is a reasonably high likelihood of overfishing for Baraka's whipray (Figure 5b).

4 | DISCUSSION

We provide the first estimates for key life-history parameters, extinction risk and exploitation status of the recently described and widely fished Baraka's whipray. Baraka's whipray is a medium-sized, relatively fast-growing and early maturing species of whiptail stingray that exhibits a moderately long lifespan. These life-history traits mean that Baraka's whipray is potentially more resilient to fisheries pressure than many other widely exploited elasmobranchs, reflected in our relatively high estimate for r_{max}. The disparity between r_{max} and female *F* estimates suggest that Baraka's whipray should not currently be considered at high extinction risk. Yet, the plausible distribution of the

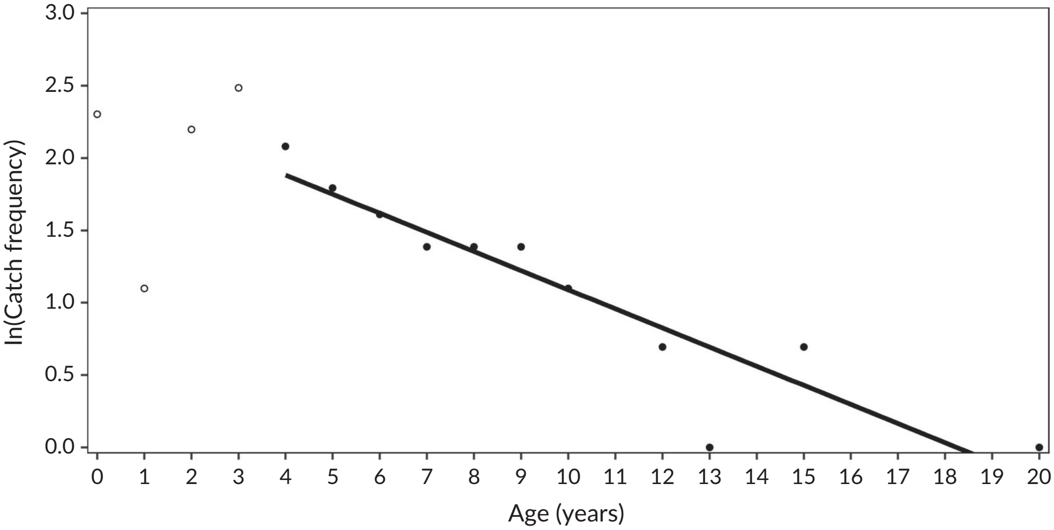

FIGURE 6 Chapman-Robson catch curve for female Baraka's whipray *Maculabatis ambigua* across south-western Indian Ocean small-scale fisheries, displaying age class of full recruitment to the fishery (age class 3) and catch curve regression line from age class 4 to 16, total mortality Z is estimated at 0.237 (95%CI 0.175, 0.298)

female exploitation ratio E suggests a reasonably high likelihood (68.7%) of overfishing in this unmanaged species. However, given the relatively robust life-history traits displayed by Baraka's whipray, if managed effectively there is potential for this species to become one of the biologically sustainable elasmobranch fisheries (Simpfendorfer & Dulvy, 2017). Our study also reveals a larger maximum size (recorded disc width of 112 cm) and wider geographic distribution than previously known (Last *et al*., 2016b), as evidenced by catches of Baraka's whipray in northern Madagascar. In the following sections we consider (a) the life-history traits of Baraka's whipray relative to other whiprays and (b) the priority data gaps for future research.

Growth models from this study indicate that Baraka's whipray is a fast-growing species with early maturation relative to other similarly sized whiptail stingrays. For example, blackspotted whipray (male: $k = 0.03$, female: $k = 0.03$), blue stingray (*Dasyatis chrysonota*) (male: $k = 0.175$, female: $k = 0.07$) and diamond stingray (*Hypanus* (formerly *Dasyatis*) *dipterura*) (male: $k = 0.1$, female: $k = 0.05$) (Cowley, 1997; Jacobsen & Bennett, 2011; Smith *et al*., 2007). However, it must be considered that k may exhibit considerable variability, a product of the constraints of both the study (*e.g*., sample size and representation of size classes) and the growth-models used (Cailliet & Goldman, 2004; Smith *et al*., 2007). This may result in wide variability of k even within species, as demonstrated in Kuhl's maskray (*Neotrygon kuhlii*), where k ranges between 0.08 and 0.38 (Jacobsen & Bennett, 2010; O'Shea *et al*., 2013), which may reflect locally varying life histories or species complexes. The rapid growth of Baraka's whipray is consistent with the early maturation observed in males and females.

Whiptail stingrays, and Baraka's whipray in particular, display earlier maturation relative to both longevity and size compared to other elasmobranchs (Frisk *et al*., 2001). Our estimates indicate that male Baraka's whipray mature faster (~11–13% t_{max}) and at a similar relative size (~62% DW_∞) to other whiptail stingrays. For example, Kuhl's maskray (3.95 years, ~19% t_{max}, ~65% DW_∞), blackspotted whipray (7.32 years, ~41% t_{max}, ~65% DW_∞), speckled maskray *N. picta* (~64% DW_∞) and common stingray (*Dasyatis pastinaca*) (~52% DW_∞) (Jacobsen & Bennett, 2010, 2011; Pierce & Bennett, 2010; Yigin & Ismen, 2012). Unfortunately, female maturation could not be assessed directly in this study. Working on the assumption that males and females mature at similar size classes (Da Silva *et al*., 2018; Jacobsen & Bennett, 2010, 2011; White, 2007), estimates suggest they also mature relatively early. Given the importance of female maturity in understanding fish population dynamics, verification of the estimates provided here is a clear priority.

Relatively fast growth rates ($k > 0.1$) and early maturation are generally associated with higher potential rates of population increase and thus higher rebound potentials (Branstetter, 1990; Frisk *et al*., 2001; Musick, 1999). However, species with fewer than five female offspring per year tend to have very low estimates of r_{max} (Pardo *et al*., 2016b). The early maturation of Baraka's whipray, combined with a moderately long lifespan relative to other whiptail stingrays, likely off-sets the apparently low number of female offspring per year and results in a high r_{max} estimate relative to those of many threatened elasmobranchs (Dulvy *et al*., 2014b). However, uncertainty remains around the fecundity (litter size and inter-birth interval) of this species. The smallest specimens measured in this study and DW_0 values estimated from the joint male and female growth model (23.5 and 33.4 cm disc width, respectively) are large relative to DW_∞ estimates, suggesting high maternal investment in offspring and thus likely few offspring per litter. Verifying our assumptions for sex ratio, inter-birth interval and annual fecundity is a clear priority for future exploitation assessments of Baraka's whipray and other exploited elasmobranchs in both SWIO and global fisheries.

Despite the potentially robust life-history traits of Baraka's whipray, our distributional estimates of E suggest likely overfishing of the species. Thus, management interventions are required, particularly given that the degree of overfishing is likely to increase with rising regional fisheries pressure (Temple *et al*., 2018). In addition to probable overfishing, the age and size class selectivity of the fisheries is of further concern. Restricting elasmobranch fisheries to catches of non-adult age classes can be an effective management strategy for these taxa (Prince, 2002; Simpfendorfer, 1999) but may result in prohibativly low yields. Protection of subadults is likely optimal for maximizing the future reproductive potential of the stock (Kindsvater *et al*., 2016). Assuming the size-at-maturity estimates presented here are approximately representative, our data suggest that full recruitment to the fishery occurs primarily in young adults. Furthermore, exploitation continues across a broad range of adult age and size classes, indicative of a nonselective fishery. Whilst the nonselective nature of catches is not unexpected given the multigear, multispecies nature of SWIO small-scale fisheries, patterns of pressure across post-maturity life-stages is of great concern for the biological sustainability of both Baraka's whipray and numerous other elasmobranch species caught in these fisheries (Kiszka & van der Elst, 2015; Temple *et al*., 2019).

Lastly, we must note that our analyses assume that vertebral banding observed in Baraka's whipray are consistent, annual and continual. Such assumptions may lead to misclassification of age in elasmobranchs if violated (Harry, 2018; Kinney *et al*., 2016; Natanson & Cailliet, 1990), if there is difficulty in counting increasingly small bands in older animals, or if there is variability in band formation among vertebrae within individuals (Natanson *et al*., 2018). Whilst violation of annual banding assumptions have been seen in elasmobranchs, they have thus far been most common in large and longer-lived species. Furthermore, annual band deposition has been validated in several other whiptail stingrays (Cowley, 1997; Jacobsen & Bennett, 2010; Pierce & Bennett, 2010; Smith *et al*., 2007). Thus, we consider our assumption to be reasonable but encourage continued vigilance for and research focus on banding periodicity in this and other elasmobranch species.

The life-history, $r_{\max}$, exploitation and mortality data information presented here for the recently described Baraka's whipray represent an important step towards improving evidence-based fisheries management in the region. However, the limitations of the study also outline the priority next steps required for the sustainable exploitation of this species. Improving our understanding of female maturation and fecundity is crucial in estimation of exploitation resilience. Furthermore, life-history traits may vary significantly between stocks, yet nothing is known of the structure of Baraka's whipray stocks within its range. Stock structure is key for defining management units for fisheries (Pita *et al*., 2016) and meeting the assumptions of stock assessment approaches, with differing life histories between stocks having implications for their resilience to fisheries exploitation and subsequent management needs. Given the prominence and likely economic importance of elasmobranchs, including Baraka's whipray, in SWIO small-scale fisheries (Temple *et al*., 2019), understanding stock structure and population dynamics are important in supporting and tailoring accurate and effective fisheries management actions at regional, national and local levels.

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CONTRIBUTIONS

This study was conceived by A.J.T, P.B, S.M.S. and N.K.D. Specimens were collected by N.J, N.W, A.J.T and P.B. Data extraction was conducted by A.J.T and E.B. Data analyses were conducted by A.J.T. Manuscript preparation and editing were conducted by A.J.T, P.B, S. M.S., N.K.D, N.J, N.W and E.B. Funding for the study was generated by A.J.T, P.B, S.M.S., N.J and N.W.

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