Chapter 6

Growth, maturity, and diet of the pearl whipray (*Fontitrygon margaritella*) from the Bijagós Archipelago, Guinea-Bissau

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Abstract

The pearl whipray *Fontitrygon margaritella* (Compagno and Roberts 1984) is a common elasmobranch in coastal western African waters. However, knowledge of their life history and trophic ecology remains limited. Therefore, we aimed to determine the growth, maturity and diet of *F. margaritella* from the Bijagós Archipelago in Guinea-Bissau. Growth was modeled using von Bertalanffy, Gompertz and logistic functions. Model selection revealed that no model significantly outperformed another. The sampled age ranged from less than one year to seven years (1.8 ± 1.9 cm, mean ± standard deviation), and size (disc width) ranged from 12.2 cm to 30.6 cm (18.7 ± 5.2 cm). Size-at-maturity was estimated at 20.3 cm (95% CI: 18.8-21.8 cm) for males and 24.3 cm for females (95% CI: 21.9-26.5 cm), corresponding to ages of 2.2 and 3.9 years. The diet differed significantly among young-of-the-year (YOY), juveniles and adults (p = 0.001). Diet of all life stages consisted mainly of crustaceans (27.4%, 28.5%, 33.3%) and polychaetes (12.5%, 26.7%, 20.3%), for YOY, juveniles and adults, respectively. This study shows that *F. margaritella* is relatively fast-growing, matures early and experiences ontogenetic diet shifts. These results contribute to status assessments and conservation efforts of *F. margaritella* and closely related species.

Introduction

The abundance of sharks and rays (i.e., elasmobranchs) is often considered an indicator of healthy marine ecosystems, as these species have important ecological roles as top and mesopredators. Their population trends may indicate overexploitation of these species, which can potentially alter ecosystem functioning (Barría et al. 2015, Flowers et al. 2021, Navia et al. 2007, Vaudo and Heithaus, 2011). Determining such population trends requires information about the life history of a species, such as the age-at-maturity, maximum age and growth coefficients (Meiía-Falla et al. 2014). A lack of knowledge of life-history parameters can impair the status assessment of elasmobranch species, hampering effective management of these K-selected species (i.e., late maturity, low fecundity and slow growth) (Ismen 2003, O'Shea et al. 2013). Furthermore, understanding the trophic ecology of a species is required to determine a species' ecological role within an ecosystem (Vaudo and Heithaus 2011). The trophic ecology of a species can help determine the structuring roles, energy flow, and bioaccumulation of ecological contaminants within an ecosystem (Bowes and Thorp 2015, MacNeil et al. 2005). Thus, understanding the life history and trophic ecology of individual species is an essential step in preserving ecosystem functions and services (Coll et al. 2013).

Elasmobranch species off the West African coast remain largely unstudied, with the necessary data for population trend analysis and conservation status often missing. This is especially the case for endemic species in the region, like *F. margaritella*. Although this species is one of the most common species in coastal fisheries throughout the region, its life-history characteristics and trophic ecology remain poorly understood (Moore *et al.* 2019). This species ranges from Mauritania to Angola, and it can be found in shallow marine and estuarine soft-bottom habitats (Marshall and Cronin 2016). The maximum attained size is thought to be around 34 cm, and females can have up to 3 pups per litter (Moore *et al.* 2019). Understanding the life history and trophic ecology of *F. margaritella* may also provide broader insights into the biology of other *Fontitrygon*-species, which mostly occur in data-deficient regions off West Africa and the northern coast of South America. Here, we aim to fill a critical knowledge gap surrounding this species by determining the growth, size- and age-at-maturity, and diet of *F. margaritella* from the Bijagós Archipelago in Guinea-Bissau.

Methods

The Bijagós Archipelago comprises 88 islands and islets and is located off the coast of Guinea-Bissau. The archipelago is listed as a UNESCO Biosphere Reserve and RAMSAR site. The coastal zone of the archipelago consists of mangrove forests, soft-bottom intertidal flats, gullies and deep channels. We collected ray specimens between October and December 2019 from artisanal fishers and were caught around Urok (11.4833° N, 15.9667° W), Bubaque (11.2448° N, 15.8701° W), Soga (11.3500° N, 15.8667° W) and Orango (11.2494° N, 162212° W) or from an unknown location within the Bijagós Archipelago (Figure 6.1). All rays were stored in a field freezer (-10°C) until processing. To rule out any misidentification of this species with the related daisy whipray (*Fontitrygon margarita*), we sequenced tissue samples of the pelvic fins for species identification. This was done using the ASNM and ChimeraF primer ("AAGGACTACTTTGATAGAGT" a variant of ILEM) adapted from Naylor *et al.* (2012).



Figure 6.1 Overview of the study sites in the Bijagós Archipelago, Guinea-Bissau. The colors indicate the different sampling regions and their respective sample sizes (purple = Urok, orange = Soga, gray = Bubaque, and green = Orango). Specimens for which the origin within the archipelago could not be confirmed were labeled as 'location unknown'.

Ethical statement

For this study, we collaborated with the local fishing communities within the Bijagós Archipelago. All rays were obtained from catches by local fishers and were solely captured for consumption. After collecting the required samples, all rays were returned to the local communities for consumption. All rays were deceased at the time of sampling. All research and use of animals was conducted with permission and per the regulations of the Instituto da Biodiversidade e das Áreas Protegidas (IBAP), the responsible national institute in Guinea-Bissau (reference number: 396/IBAP/2019 and 393/IBAP/2019).

Age and Growth

For each individual that was sampled, we recorded sex, body size as disc width (DW)and total length (TL) and weight. In addition, five to ten anterior vertebrae were stored in 70% ethanol for each individual. In the laboratory, vertebrae were cleaned by removing excess tissue, after which one vertebra per individual was fixated in clear epoxy resin (Poly-Pox THX 500 resin and Poly-Pox 155 hardener) following the instructions of Campana (2014). A centered sagittal cross-section with a thickness of 500 µm was cut for each vertebra to create a typical 'bowtie' cross-section, which was fixed to a microscope slide and used for aging (see Campana, 2014). Each crosssection was photographed using a compound light trinocular microscope (Zeiss) at 5x10 magnification. As growth band deposition in other dasyatid rays like the blue stingray (Dasyatis chrysonota), the brown stingray (Dasyatis lata) and the diamond stingray (Dasyatis dipterura) is annual. We assumed deposition in F. margaritella also to be annual (Cowley 1997, Dale and Holland 2012, Smith and Merriner 2007). Age was determined independently by two researchers by counting growth bands. All age readings that differed were taken out of the analysis. Previously, using a multimodel approach for growth studies has been advocated to incorporate candidate models with alternative characteristics (Smart et al. 2016). Hence, the following three growth functions were fitted:

A logistic growth function, adapted from MacKendrick and Kesava (1911):

$$DW_{age} = \frac{DW_{inf}}{1 + \left(\frac{DW_{inf} - DW_{birth}}{DW_{birth}}\right)e^{-k \times age}}$$
(1)

A Gompertz growth function, adapted from Ricker (1975):

$$DW_{age} = DW_{birth} \times exp \left(ln \ln \left(\frac{DW_{inf}}{DW_{birth}} \right) \left(1 - exp \exp \left(-k \times age \right) \right) \right)$$
(2)

A von Bertalanffy growth function, adapted from von Bertalanffy (1938):

$$DW_{age} = DW_{birth} + \left(\left(DW_{birth} - DW_{inf} \right) \times \left(1 - exp \ exp \ \left(-k \times age \right) \right) \right)$$
(3)

These growth functions describe the relationship between age and body size (disc width; DW), with the asymptotic disc width DW_{inf} , the size at birth DW_{Birth} , the growth coefficient k, the estimated age based on vertebrae growth band counts (*age*), and the predicted size-at-age DW_{age} . Parameters were estimated using Bayesian MCMC models (Bürkner 2017, 2018).

The prior values for size at birth (10 cm) and maximum disc width (34 cm) are based on data recorded by Moore *et al.* (2019) and given a lognormal prior as these were positive parameters. Hence, for the size at birth (DW_{Birth}) prior, a lognormal distribution of 10 and a standard deviation of 1 was used. For the maximum disc width prior, a lognormal distribution of 34 and a standard deviation of 1 was used for the maximum disc width prior. Lastly, for the growth coefficient (k), a prior with a normal distribution of -1 and a standard deviation of 1 was used. For each model, four chains were run with 3500 iterations each, including 1000 discarded warm-up iterations, so a total of 10000 iterations were sampled for each model. Effective sample sizes for each model parameter exceeded 1000. Convergence and mixing of chains were monitored with trace plots and R-hat statistics. Model performance was compared using the leave-one-out cross-validation using the 'loo' R-package (Vehtari *et al.* 2017, Yao *et al.* 2018).

Sex		Immature	Mature
Female	Ovaries	Not distinguishable	Distinguishable
	Follicles	Underdeveloped or in groups with different sizes	Well-developed or atretic and vitellogenic
	Uteri	Between tubular and wide in shape with developed walls	Tubular to wide in shape, developed walls, possibly with embryos
	Epigonal organ	Predominant	Present
Male	Testis	Lobulated, low blood supply	High volume, lobulated, increased blood supply
	Ductus deferens	Barely or not undulated	Strongly undulated
	Epigonal organ	Present	Limitedly present

Table 6.1 Developmental stages of reproductive organs used to assess maturity stage (immature
or mature). Adapted from Osaer <i>et al.</i> (2015).

Maturity

We determined the maturity stage as either 'immature' or 'mature'. Females are regarded as mature when epigonal organs are present, ovaries contain well-developed

follicles of similar sizes or are atretic and vitellogenic in groups or singular, and uteri are tubular to wide in shape, with developed walls or with distinguishable embryos. Lastly, males are regarded as mature when a little epigonal organ is present, testis have a high volume, are fully lobulated with increased blood supply or pale and decreased in size, and ductus deferens is strongly undulated. Individuals were regarded as immature if their reproductive organs were less developed than described above. Table 6.1 provides short descriptions used to determine the maturity stage. To calculate the median disc width at maturity (DW_{50}) for both sexes combined and separated, we used the following logistic maturity formula (Mollet *et al.* 2000):

$$Y = (1 + e^{-(a+bX)})^{-1}$$
(4)

Median size at maturity is calculated using Equation (5) similarly, for this model, 3,500 iterations and 1000 warm-up iterations were used. The priors used were uninformative, namely 10 following a normal distribution with a standard deviation of 5 for both a and b, as this could not be based on previous values.

$$DW_{50} = -a/b \tag{5}$$

Diet

The stomachs of sampled specimens were removed and weighed before determining stomach contents. Excess moisture was removed from stomach contents using paper towels to remove weight bias by stomach fluids. Stomach contents were sorted into one of six categories: crustaceans, polychaetes, bivalves, other mollusks, teleosts or unidentified (unrecognizable prey items). Appendix 6.1 provides a representative photo of each taxa encountered in stomach contents. These taxa categories were not defined prior to data collection but based on prey items encountered due to the lack of description for benthic species from our study area. We recorded the number of prey items and mass for each group to the nearest centigram. To prevent bias of large prey items, we calculated the diet composition using the index of importance (*IOI*) as proposed by Gray *et al.* (1997). First, the percentage of each prey group relative to the body weight of the individual ($%W_a$) was calculated as:

$$\% W_a = (100 \times W_a) / W_{body} \tag{6}$$

where W_a is the sum weight of prey group a (Gray *et al.* 1997).

Secondly, the frequency of occurrence for prey group a $(\% F_a)$ was calculated as:

$$\%F_a = (100 \times S_a)/S \tag{7}$$

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where S_a is the number of stomachs containing for a given prey group, and S denotes the total number of stomachs containing food (Hyslop, 1980).

Lastly, the index of importance for each prey group (IOI_a) was calculated as:

$$IOI_a = 100 \times HI_a / \sum_{a=1}^{n} \blacksquare HI$$
(8)

with:

$$HI_a = \%F_a + \%W_a \tag{9}$$

Diet composition was analyzed for three different life stages: YOY (individuals < 1 year of age), juveniles (individuals >= 1 year, but have not reached DW_{50}) and adults (mature individuals, > DW_{50}). Raw data is provided in Appendix 6.2. We performed a PERMANOVA (R-package 'vegan') (Oksanen *et al.* 2020) and a pairwise Adonis function (Martinez Arbizu, 2016) to determine which life stages differ in their diet composition.

Results

A total of 75 individual *F. margaritella* were sampled, consisting of 38 males and 37 females (0.5:0.5 m:f ratio) ranging from 12.2 to 30.6 cm DW and body mass ranging from 59 to 1,208 g.

Age and growth

71 Individuals (m = 38, f = 33) were used for size-at-age analysis. Measured disc widths ranged from 12.2 cm to 30.6 cm (18.7 \pm 5.1 cm), and age ranged from less than one to seven years (1.8 \pm 1.9 years). All three growth functions estimated similar values for disc width size-at-birth: 13.87, 14.01 and 14.01 cm (von Bertalanffy, Gompertz and Logistic growth functions, respectively). Maximum disc width estimates varied between the three growth functions. The logistic growth function estimated a maximum disc width of 34.46 cm, close to the observed maximum size of 34 cm, recorded by Moore *et al.* (2019), whereas the von Bertalanffy function estimated 44.70 cm and the Gompertz function 38.09 cm (Table 6.2). Model selection showed that no model outperformed any of the others based on LOO information criterion (LOOIC) (Table 2). However, there is likely little reliable difference in the predictive capability between these models, as the difference in LOOIC values was less than two between all models. When considering the maximum reported size by Moore *et al.* (2019) to be 34 cm as the maximum disc width, *F. margaritella* individuals seem to reach their maximum size between 10 and 12 years (Figure 6.2). Additionally, *F.*

margaritella seems to attain between 40.3% and 64.7% of their maximum disc width within their first year, based on the largest and smallest rays of one year old.

Table 6.2 Model and model selection estimates for the von Bertalanffy, Gompertz and the logistic growth function. (n) sample size for size at age analysis. (LOOIC) LOO information criterion. (SE) standard error of the LOOIC values. (DW_a) asymptotic disc width. (DW_{Birth}) disc width at birth. (K) growth rate. (95% CI) credible interval.

Model	n	LOOIC	SE	DW (cm)	95% CI DW	DW _{BIRTH} (cm)	95% CI DW _{BIRTH}	K (year) ⁻¹	95% CI K
Von Bertalanffy function	71	278.7	14.2	44.7	33.1 - 75.2	13.9	13.3 - 14.4	0.1	0.04 - 0.2
Gompertz function	71	279.4	14.8	38.1	30.9 - 55.1	14.0	13.3- 14.6	0.2	0.1- 0.3
Logistic function	71	280.1	15.1	34.5	29.4 - 44.2	14.0	13.5 - 15.0	0.3	0.2 - 0.4



Figure 6.2 Growth functions fitted to size-at-age data of *F. margaritella* (Gompertz curve in green, von Bertalanffy curve in blue and the logistic growth curve in red). The horizontal dashed line represents the maximum reported disc width of 34 cm (Moore *et al.* 2019). The median disc width at which males reach maturity (DW_{50}) is shown in orange (DW = 20.3 cm, age = 2.2 years old) and magenta for females (DW = 24.3 cm, age = 3.9 years old).

Maturity

We determined the maturity stage of 69 individuals (m = 35, f = 34). Of six individuals, the reproductive state was unclear due to fishery-related damages or (partial) decomposition of organs. The disc width of the largest sampled immature male was 23.7 cm, and the largest immature female had a disc width of 30.6 cm. Based on the binomial logistic regression, median size-at-maturity is reached at 20.3 cm DW (CI 95% 18.8-21.8 cm) for males and 24.3 cm DW (CI 95% 21.9-26.5 cm) for females (Table 6.3). Based on the von Bertalanffy growth function, this size-at-maturity corresponds with an age-at-maturity of 2.2 and 3.9 years for males and females, respectively.

Table 6.3 Summary of size-at-maturity parameter estimates and 95% credible interval (CI)values for males, females, and both sexes combined.

Sex	а	95% CI	b	95% CI	DW ₅₀	95% CI
Male	-9.05	-13.91 – -4.94	0.45	0.24 - 0.70	20.1	18.8 - 21.8
Female	-8.29	-13.07 – -4.82	0.36	0.21 – 0.57	23.0	21.9 - 26.5
Combined	-9.01	-12.99 – -5.95	0.43	0.28 - 0.61	21.0	19.7 – 22.3





Figure 6.3 Index of Importance (IOI) for each prey taxa for youngof-the-year (YOY), juvenile and adult *Fontitrygon margaritella*. Colors indicate the prey group taxa. Crustaceans (red). Polychaetes (orange). Bivalves (yellow). Other Molluscs (green). Teleost fishes (blue). Unidentified (brown). Raw data is provided in Appendix 6.2.

Diet

For diet analysis, we used a total of 65 stomachs sampled (1.19 \pm 1.25 g). We identified 22 individuals as young-of-the-year (YOY; <1 year of age), 19 as juvenile (>= 1 year of age and smaller than DW₅₀) and 24 as adults (>= DW₅₀). Based on the Index of Importance, the same prey species made up the majority of *F. margaritella's* diet across all life stages: crustaceans: 27.4%-33.3%, polychaetes: 12.5%-26.7%, Bivalves: 12.5-20.3, other mollusks: 0%-7.2%, Teleosts: 0%-4.3%, and unidentified prey: 30.4%-55.0% (Figure 6.3). Besides unidentified prey, crustaceans and Polychaetes were the most common prey items for all age classes in terms of mass and number of individual prey (Table 6.4).

Diet composition differed significantly between life stages (PERMANOVA DF = 2, sum of squares = 2.3, F = 22.6, R² = 0.27 p = 0.001), and a post-hoc test revealed that all life stages have a significantly different diet composition (YOY-Juveniles: F = 7.8, R² = 0.1, p = 0.002) (YOY-Adults: F = 17.2, R² = 0.28, p = 0.001) (Juveniles-Adults: F = 6.0, R-squared = 0.1, p = 0.001.

	YOY	Juvenile	Adult
Crustaceans mass (g)	0.8	3.5	17.5
Crustaceans count (n)	224	270	331
Nr. stomachs (%)	50	84.2	95.8
Polychaetes mass (g)	1.0	1.4	5.5
Polychaetes count (n)	68	99	331
Nr. stomachs (%)	22.7	78.9	58.3

Table 6.4 Summary of the total mass (grams), total count (n) and percentage of stomachs that contained crustaceans and polychaetes for young-of-the-year (YOY), juveniles and adults.

Discussion

Elasmobranchs are still subject to fisheries in the coastal waters of West Africa despite their vulnerability to fishing (Moore *et al.* 2019). Understanding the life history and trophic ecology of elasmobranch species is essential for the risk assessment of both these species and the ecosystems in which they often play a key role. This study is the first to present detailed data about the growth, median size-at-maturity and diet of the poorly studied *F. margaritella* in the Bijagós Archipelago, Guinea-Bissau.

Based on the growth curves of *F. margaritella*, it seems to achieve the maximum recorded disc width size of 34 cm between 10 and 12 years. Surprisingly, the maximum age of our sampled specimens was only 7 years (n=1). One-year-old *F. margaritella*

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are between 40.3% and 64.7% of their maximum disc width, comparable to the fastgrowing Roger's stingray (*Urotrygon rogersi*) (Mejía-Falla *et al.* 2014). In addition, a slow-growing batoid species (*Dasyatis fluviorum*) has been observed to have a growth coefficient of around 0.03 year⁻¹ (Pierce and Bennett 2010), which is around a third of the growth coefficient observed for *F. margaritella* of 0.10 year⁻¹. The growth rate that we found is comparable to other fast-growing species, such as Roger's stingray (*Urotrygon rogersi*), Kuhl's maskray (*Neotrygon kuhlii*) and the Diamond stingray, which is between 0.1 and 0.24 year⁻¹ (Mejía-Falla *et al.* 2014, Temple *et al.* 2020).

Our study indicates that in the Bijagós Archipelago, male *F. margaritella* mature earlier than females. This has also been confirmed in other ray species, such as the brown stingray (Dasyatis lata) and the common stingray (Dasyatis pastinaca; Ismen 2003, Dale and Holland 2012). This sex difference in size at maturity can have several possible causes. For instance, this could be related to male biting behavior during reproduction, which is common in many elasmobranch species (Kajiura et al. 2000). Unlike males, large females of Haller's round ray (Urolophus halleri) have been observed to obtain a relatively thicker disc with increased disc width, which may help minimize damage from male reproductive biting behavior (Nordell 1994). Alternatively, larger females are thought to produce larger litters and, therefore, have a greater reproductive output (Lyons et al. 2017), which could be a reason female F. margaritella mature later and at a larger body size. Perhaps a more likely explanation may be that size-at-maturity may also vary based on the increased energetic expenditure during the gestation period (Goodwin et al. 2002). Females of F. margaritella reach maturity at around 32.5% of their lifespan, and males reach maturity at around 18.3% (considering a maximum age of 12 years). This is similar to other species, such as the Kuhl's maskray (Neotrygon kuhlii) and the blackspotted whipray (Maculabatis gerradi), which mature between 19-41% of their lifespan (Temple et al. 2020). However, whether size-atmaturity differs in other areas remains unknown. Our estimates of male and female median size-at-maturity should be interpreted cautiously due to low sample sizes. However, a study on Baraka's whiprays (*Maculabatis ambigua*) by Temple *et al.* (2020) provided an accurate estimate for size-at-maturity for males based on a low sample size. Furthermore, the approximation of male maturity by Last et al. (2016) (~21 cm DW) differs only 7 mm (0.3%) from our estimation and is within the range of our 95% credible interval (18.8-21.8 cm), supporting our median size-at-maturity estimations for male F. margaritella.

Additionally, the gestation period and frequency need verification to assess the reproductive rate of *F. margaritella*, as this is thought to vary within the family of

Dasyatidae (Carlson *et al.* 2020, Notarbartolo di Sciara *et al.* 2015). Hence, a wellrounded comprehension of the life history of *F. margaritella* gestation period and frequency should also be studied.

We found that the diet of *F. margaritella* within the Bijagós Archipelago consisted mostly of crustaceans and polychaetes. This indicates that F. margaritella acts as a small, low trophic-level meso-predator that links benthic communities with top predators in the Bijagós Archipelago. The presence of teleost items in the stomach contents of *F. margaritella* suggests that the species occasionally consumes teleost prey, as observed in other batoid species (Lim et al. 2019, Farias et al. 2006). Whereas other studies show that batoids ontogenetically include more teleost prey (Gray et al. 1997, Lim et al. 2019, Farias et al. 2006), in our study one YOY was observed to have consumed small teleost prey. The high proportion of unidentified prey encountered likely results from soft-bodied prey (e.g., polychaetes and small crustaceans), which may digest faster (Farias et al. 2006). The unidentified prey items could also be inorganic matter, sediment and plant matter ingested during prey consumption (Ajemian and Powers., 2011). DNA metabarcoding on stomach contents could improve estimates of prey abundance and, combined with environmental DNA analysis of benthos, may highlight prey preference (Harms-Tuohy et al. 2016). We found that F. margaritella undergoes an ontogenetic diet shift, and adults seem to incorporate more diverse prey into their diet, such as teleosts and a higher abundance of crustaceans, possibly giving older individuals a slightly higher trophic level. Ontogenetic diet shifts could result from changes in teeth morphology, jaw teeth strength, body size and sensory sensitivity of the peripheral (Smith and Merriner 1985, Nordell 1994, Kempster et al. 2013, Lim et al. 2019). Ontogenetic diet shifts may also result from different energetic needs and local prey availability coinciding with ontogenetic differences in distribution (Lim et al. 2019). Regardless, ontogenetic diet shifts could suggest that different life stages fulfill different trophic roles and affect food webs differently.

Comprehensive knowledge of the life history and ecology of a species is necessary to establish adequate conservation efforts (Ismen 2003, O'Shea *et al.* 2013). With many elasmobranch populations declining globally, the need for insight into their life history and trophic ecology for conservation increases. This study presents one of the first known estimates for growth, median size-at-maturity, and diet composition of *F. margaritella*. Compared to other ray species, *F. margaritella* seems to be a fast-growing and early-maturing species. The diet description presented in this paper may provide preliminary insights into their trophic role in the coastal ecosystems of West Africa. Additionally, fishing intensity, natural mortality rate and recruitment

rate of *F. margaritella* require study to assess fishing vulnerability (Le Quesne and Jennings 2012). This study contributes to the knowledge of *F. margaritella*, a commonly exploited elasmobranch species in the West African region, and may help conservation efforts of similar species.

Conclusions

F. margaritella is a small, fast-growing ray species, reaching maturity after 2.2 and 3.9 years for males and females, respectively. The diet of this species within the Bijagós Archipelago consists primarily of polychaetes, but the contribution of harder prey species (e.g., crustaceans) increases ontogenetically. This study presents the first description of the growth, median size-at-maturity and diet of *F. margaritella*, which is needed for science-based management of coastal fisheries and ecosystems. These results fill an important knowledge gap on the life history and trophic ecology of this species and this data-deficient genus of whiprays.

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Life History of the Pearl Whipray