



# Growth, reproduction, and age at maturity of Lessa's butterfly ray *Gymnura lessae* in the northern Gulf of Mexico

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**Abstract** In the northern Gulf of Mexico, batoids are caught as bycatch in the shrimp trawl fishery and targeted by recreational bowfishers. The vulnerability of these batoid species to overexploitation is primarily dictated by their life history strategies. Lessa's butterfly ray, *Gymnura lessae*, is a sexually dimorphic piscivorous batoid ranging from the northern Caribbean Sea to Massachusetts. Species in the family Gymnuridae have small, poorly mineralized centra; as a result, age and growth has only been described in one species, *G. altavela*. In this study, we examined size at maturity, reproduction, sex-specific growth

(using Electronic Length Frequency Analysis), instantaneous natural mortality, and age at maturity of *G. lessae* in the northern Gulf of Mexico. Overall, 552 *G. lessae* were sampled from 2016 to 2018, of which 322 were male and 230 were female. Estimated disc width at 50% maturity was 340.0 mm and 461.4 mm for males and females, respectively. Sex-specific von Bertalanffy growth parameter estimates were  $DW_{\infty}=427.1$  mm,  $k=1.34$  year<sup>-1</sup>, and  $t_0=-0.35$  years for males, and  $DW_{\infty}=882.2$  mm,  $k=0.40$  year<sup>-1</sup>, and  $t_0=-0.56$  years for females. Instantaneous natural mortality was higher for males (1.48) than females (0.48). Most age-0 males (93.8%,  $n=16$ ) and 30.7% of age-0 females ( $n=13$ ) appeared to mature fast enough to mate just 1 year after birth. Our results indicate that *G. lessae* is fast growing, quick maturing, and relatively fecund in the northern Gulf of Mexico and is thus at low risk of overexploitation.

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## Introduction

Batoids (Chondrichthyes: Batoidea) are a large group of cartilaginous fishes, currently comprising more than 600 described species (Last et al. 2016). Unfortunately, many batoid populations have declined in abundance, as over a third of batoids are considered

to be “threatened with extinction” by the International Union for the Conservation of Nature (IUCN; Dulvy et al. 2021b). Nevertheless, most coastal ecosystems support a suite of batoid species, many of which occupy distinct ecological niches (Vaudo and Heithaus 2011; Humphries et al. 2016). The estuaries of the northern Gulf of Mexico are no exception, sustaining a diverse assemblage of batoids known to fulfill vital ecosystem roles through predator–prey interactions (Strong et al. 1990). For instance, the foraging activities of these batoids can disturb sediments and create feeding pits, which free trapped organic particles for benthic invertebrates (Thrush et al. 1991; O’Shea et al. 2012).

Life history studies for batoids are limited in the northern Gulf of Mexico, and growth parameter estimates are nonexistent for most of these species (Neer and Thompson 2005; Henningsen and Leaf 2010). This lack of life history data makes it difficult to evaluate the sensitivity of many batoid species to over-exploitation (Dulvy et al. 2014). Although batoids caught as bycatch in the northern Gulf of Mexico are generally discarded (annual US commercial landings of batoids have been below 50 metric tons in the Gulf of Mexico since 1994 (<http://www.st.nmfs.noaa.gov/commercial-fisheries/commercial-landings/annual-landings/index>)), post-release mortality and capture-induced abortion represent potential threats to batoid populations (Adams et al. 2018). In the Mexican portion of the southern Gulf of Mexico, a few thousand tons of batoids are harvested annually via targeted commercial batoid fisheries (DOF 2022), though it is unknown whether these fisheries impact batoid populations in the northern Gulf of Mexico. Similar to the US commercial sector, batoids are rarely targeted by US recreational rod and reel fishers; however, batoids are one of the primary targets of recreational bowfishers, a fishery that has been growing in the USA during recent years (Scarnecchia and Schooley 2020). Since most of these coastal batoids are unregulated, and the number of freelance bow hunters is unknown, the impacts of bowfishers on coastal U.S. Gulf of Mexico batoid populations are largely unassessed (Lahn 2018).

One common coastal batoid in the northern Gulf of Mexico is Lessa’s butterfly ray, *Gymnura lessae*, a sexually dimorphic medium-sized batoid ranging from the northern Caribbean Sea to Massachusetts (Yokota and de Carvalho 2017). *Gymnura lessae*

was formerly part of the *G. micrura* species complex; however, the complex was redescribed by Yokota and de Carvalho (2017), who separated *G. micrura* in the Western Atlantic into South American (*G. micrura*) and North American (*G. lessae*) species. As a teleost-specialized predator that feeds predominantly on medium-sized forage fishes, *G. lessae* occupies a higher trophic level than most other batoids (Jargowsky et al. 2020). While the species is classified as Least Concern by the IUCN Red List (Dulvy et al. 2021a), the existing data on the reproductive biology of *G. lessae* are highly variable in the Gulf of Mexico and there is no information with regard to age and growth (Cu-Salazar et al. 2014; Parsons 2017). The lack of age and growth data is unsurprising, as species in the family Gymnuridae have small, poorly mineralized centra, preventing them from being aged through traditional means (Ridewood 1921; Parsons et al. 2018). In addition, most Gymnurids do poorly in captivity, which inhibits captive study (Henningsen 1996). Age and growth have only been reported for the largest Gymnurid (*G. altavela*, Parsons et al. 2018), and this required the use of high-resolution X-ray computed tomography to examine vertebral centra. Given these challenges, our ability to study growth in smaller Gymnurids is limited.

In the absence of viable hard parts for aging, an alternative method for estimating growth parameters is fitting growth functions over length-frequency data sequentially arranged in time (Pauly and David 1981). While this method, which is known as electronic length frequency analysis (ELEFAN), does not allow for the estimation of maximum age, the growth parameter estimates obtained from the ELEFAN method can be crucial for the proper management of data poor stocks (Pauly 1980), especially for short- and medium-lived species (Wang et al. 2021). For Gymnurids and other difficult to age batoids that do poor in captivity, this may be the only way to estimate growth parameters without using more complex and expensive methods like bomb radiocarbon dating or high-resolution X-ray computed tomography (Kalish 1993; Parsons et al. 2018). To help inform fisheries managers of the sensitivity of *G. lessae* to overexploitation, we investigated size at maturity, reproduction, sex-specific growth, and age at maturity of male and female *G. lessae* in the northern Gulf of Mexico.

## Methods

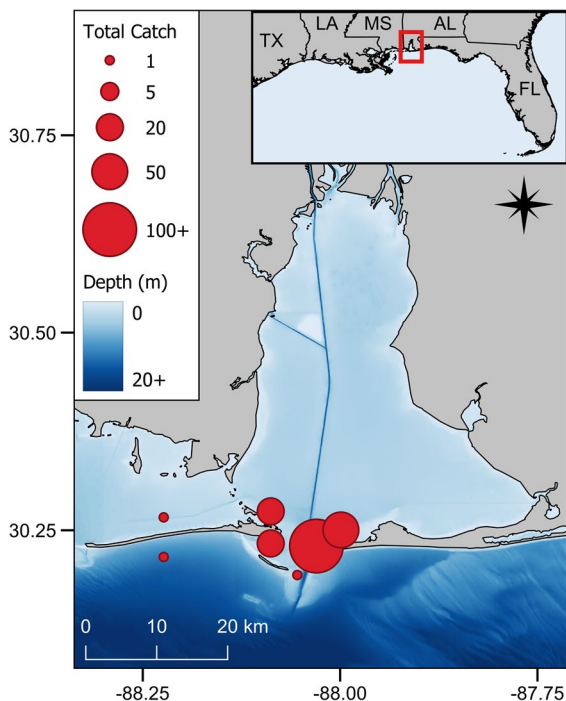
### Study area and sample collection

*Gymnura lessae* were opportunistically sampled from non-scientific fishery-independent bottom trawls performed in and around Mobile Bay, Alabama, from February 2016 to May 2018 (Fig. 1). Trawls were conducted during daylight hours using a 7.6 m otter trawl towed for approximately 30 min in 5 to 10 m of water at approximately 4.6 km h<sup>-1</sup> (a small subset of trawls, 3.7%, used a 4.9 m otter trawl). Hydrographic data was obtained from Alabama's Real-Time Coastal Observing System (ARCOS; [arcos.disl.org](http://arcos.disl.org)); specifically, the Dauphin Island Station. Water temperatures were warmest in the month of July, with an average of 30.4 °C, and coldest in January, with an average of 13.0 °C. Salinities were quite variable depending on river discharge, ranging from 0 to 32.8 ppt, with a median value of 18.4 ppt. However, it should be noted that *G. lessae* were sampled at depths greater than the ARCOS measurement depths. Site-specific bottom

temperatures were likely lower, and salinities higher, than those represented by ARCOS.

For all captured *G. lessae*, general catch locations were recorded and measurements were taken for disc width (DW; mm), weight (kg), and sex. For males, claspers were examined for calcification, categorized as uncalcified, partially calcified, or fully calcified; and for elongation, categorized as unelongated, partially elongated, or fully elongated. Internal reproductive organs were collected from all mature and maturing *G. lessae*; while some of these organs were extracted immediately after capture, in most cases (92%), the entire specimen was frozen at -29 °C until it could be processed at a later date. For males, each testis was measured for length and width (mm) and then a modified gonadosomatic index (GSI) was created by multiplying testis length by width and dividing by the DW (cm). For females, uterus widths (mm), oviducal gland width (mm), and the largest follicle diameter (LFD; mm) were measured. Uterine eggs were noted when present but were generally not quantifiable as they degraded during the freezing and thawing process. Embryos were counted, sexed, and measured (DW), and any external coloration was noted. Like the uterine eggs, the sizes of smaller embryos were difficult to quantify due to deterioration that occurred during the freezing process. As a result, uterine eggs and degraded embryos were assigned a DW of 0 mm for comparison purposes.

For maturity status, individuals were placed into one of three categories: juvenile, subadult, or adult (only adults were considered mature). Males were assigned maturity following criteria outlined in Conrath (2005), where specimens were categorized as juveniles if they had non-calcified, unelongated claspers, and undeveloped testes, subadults if they had partially calcified/elongated claspers and partially developed testes, and adults if they had fully calcified/elongated claspers and fully developed testes. Females were assigned maturity following criteria modified from both Conrath (2005) and Burgos-Vázquez et al. (2019). Specifically, females were categorized as juveniles if they had an undeveloped ovary, undeveloped oviducal glands, and thread-like uteri. Females were categorized as subadults if the ovary lacked follicles greater than 4 mm in diameter, the oviducts were not fully differentiated, and the uterine villi were either short or absent. Lastly, females were categorized as adults if they had fully differentiated and enlarged oviducts and long uterine villi.



**Fig. 1** Map showing the locations where *Gymnura lessae* were sampled during the study (2016 to 2018) via an otter trawl. Circle size corresponds to sample size, with larger circles indicating greater numbers of samples

## Data analysis

Size differences between males and females were analyzed using randomization tests and the sex ratio was tested for significance using a binomial test ( $\alpha=0.05$ ) in the software program R (v. 4.1.1; R Core Team 2021). Disc width at 50% maturity ( $DW_{50}$ ) was estimated with a logistic regression fit to binomial maturity data using the packages “FSA” (Ogle et al. 2021) and “car” (Fox and Weisberg 2019) in R (v. 4.1.1; R Core Team 2021). To explore the reproductive seasonality and synchronicity of *G. lessae* in the northern Gulf of Mexico, box plots displaying modified GSI, LFD, and embryo size (DW) by month were created. Differences in these values by month were investigated with randomization tests. Left versus right uterine fecundity and embryo sex ratio were also investigated using binomial tests and a linear model was fit to examine differences in uterine fecundity by female DW ( $\alpha=0.05$ ).

Sex-specific growth was examined through the ELEFAN method, which obtains growth parameter estimates from length-frequency data, using the “TropFishR” package (Mildenberger et al. 2017) in R (v. 4.1.1; R Core Team 2021). For each sex, bin size was calculated based on recommendations from Wang et al. (2020) and the moving average was set according to the approximate number of bins spanning the smallest (i.e., youngest) cohort width. A von Bertalanffy growth function (VBGF) was then fit to sex-specific length-frequency data, which was pooled by month, using a simulated annealing algorithm (Xiang et al. 2013):

$$DW_t = DW_{\infty} \left[ 1 - e^{-k(t-t_0)} \right], \quad (1)$$

where  $DW_t$  is mean disc width at time  $t$  (years),  $DW_{\infty}$  is asymptotic disc width (mm),  $k$  is the growth coefficient ( $\text{year}^{-1}$ ),  $t$  is time (years), and  $t_0$  is the hypothetical age (years) at which length equals zero (von Bertalanffy 1938). However, since time of year was used in this case rather than true age,  $t_0$  was replaced by  $t_{\text{anchor}}$ :

$$DW_t = DW_{\infty} \left[ 1 - e^{-k(t-t_{\text{anchor}})} \right], \quad (2)$$

where  $t_{\text{anchor}}$  is the fraction of the year where yearly repeating growth curves cross length equal to zero. Then, to obtain an estimate of  $t_0$  from  $t_{\text{anchor}}$ , the following formula was used:

$$t_0 = t_{\text{anchor}} - t_{\text{birth}}, \quad (3)$$

where  $t_{\text{birth}}$  is the birthdate calculated as a fraction of the year. Lastly, instantaneous natural mortality rate ( $M$ ) was calculated for each sex using Pauly's (1980) nonlinear least-squares estimator, omitting temperature (Pauly<sub>nlst</sub>; Then et al. 2015), in the package FSA (Ogle et al. 2021) in R (v. 4.1.1; R Core Team 2021):

$$M = 4.118k^{0.73}DW_{\infty}^{-0.333} \quad (4)$$

## Results

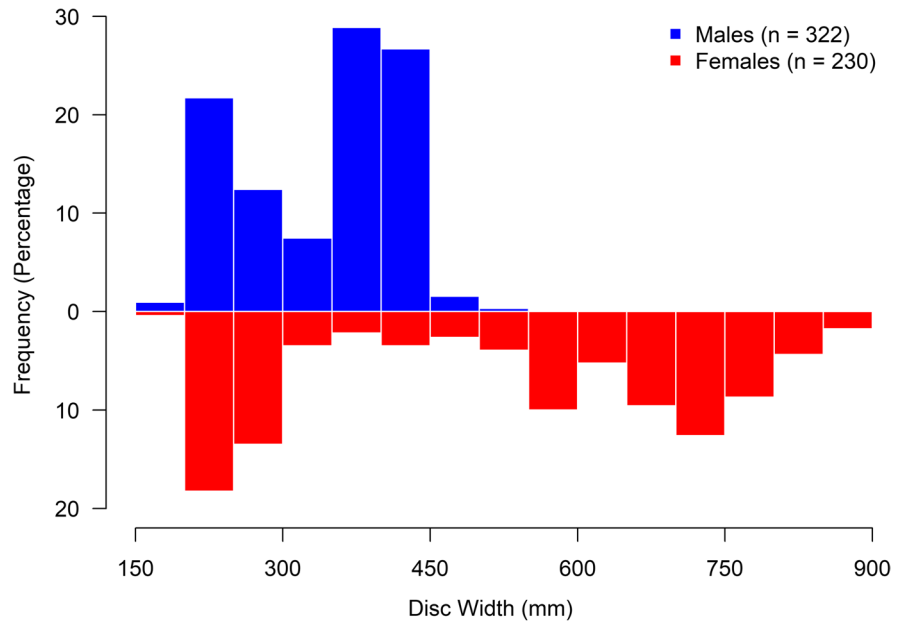
### Catch trends

From February 2016 to May 2018, 552 *G. lessae* were sampled from 458 bottom trawls performed in and around Mobile Bay, Alabama. Males ( $n=322$ ) were caught more frequently than females ( $n=230$ ;  $p<0.001$ ), and females (189–890 mm DW) were significantly larger than males (190–501 mm DW;  $p<0.001$ ; Fig. 2). Sampling was conducted across all months of the calendar year; however, there was no positive catch in January, August, or December due to low sampling effort during those months (Fig. 3). Catch-per-unit-effort was lowest for *G. lessae* from November to March, indicating that individuals likely moved out of our sampling area when water temperatures declined.

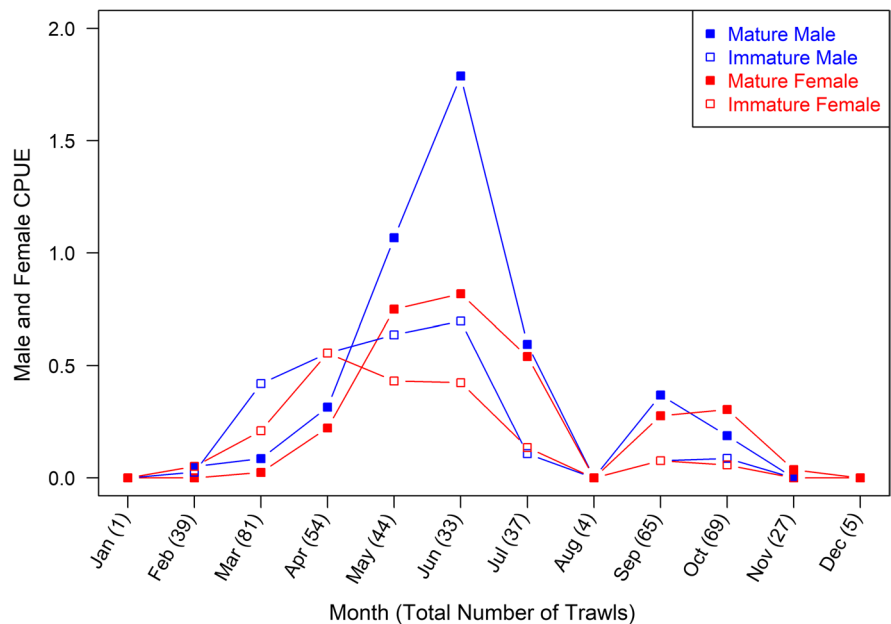
### Size at maturity and reproduction

Disc width at 50% maturity was 340.1 mm (95% CI 334.8–345.3 mm) and 461.4 mm (95% CI 430.1–493.8 mm) for males and females, respectively (Fig. 4). The largest immature male and female were 377 mm and 502 mm, respectively. The smallest mature male and female were 335 mm and 429 mm, respectively. Modified GSI values increased throughout the year and differed significantly by month ( $p<0.001$ ; Fig. 5a). Modified GSI was highest in October, and the October value was significantly different from the months February through May ( $p<0.05$ ). Both testes were functional. Sperm was noted in one specimen caught in late October, one caught in February, and four caught in March, though the sperm in the February and March

**Fig. 2** Length-frequency distributions for male and female *Gymnura lessae* sampled in the northern Gulf of Mexico



**Fig. 3** Catch-per-unit-effort (CPUE; *Gymnura lessae* caught per trawl) by month for mature and immature male and female *Gymnura lessae*, as well as the total number of trawls performed by month

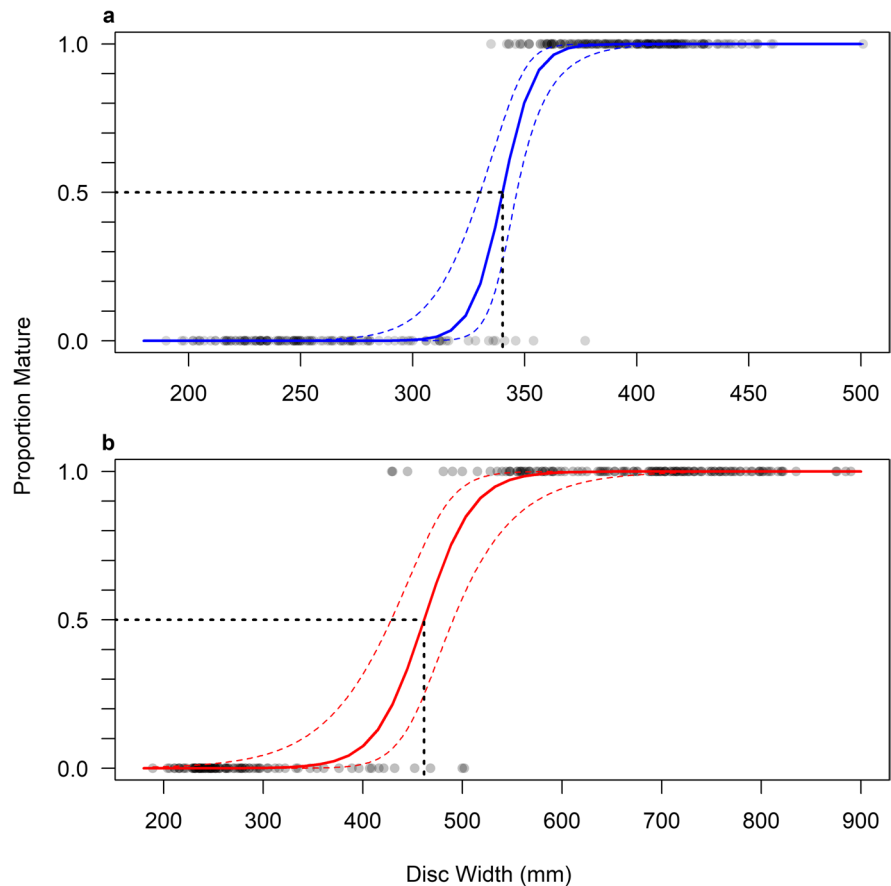


specimens appeared to be residual based on testis size. In females, like in all other Gymnurids, only the left ovary was functional. Largest follicle diameter by month was unimodal and significantly different across month ( $p < 0.001$ ; Fig. 5b). Specifically, both the March and October values were significantly different from the months May through July ( $p < 0.05$ ). The largest measured follicle in the study was 16.9 mm in

diameter, which was from a specimen that was collected in mid-October.

Embryo size was significantly different across months ( $p < 0.001$ ), with DW greatest in September and October; these values were significantly different from all other months ( $p < 0.05$ ; Fig. 5c). Embryos from June and July were generally semi-translucent and pink in color, whereas embryos from September

**Fig. 4** Logistic regression, with 95% confidence intervals, fit to **a** male ( $n=322$ ) and **b** female ( $n=230$ ) sex-specific *Gymnura les-sae* binomial maturity data. Disc width at 50% maturity is denoted with black dashed lines on each plot. Darker points represent more fish in a given size class

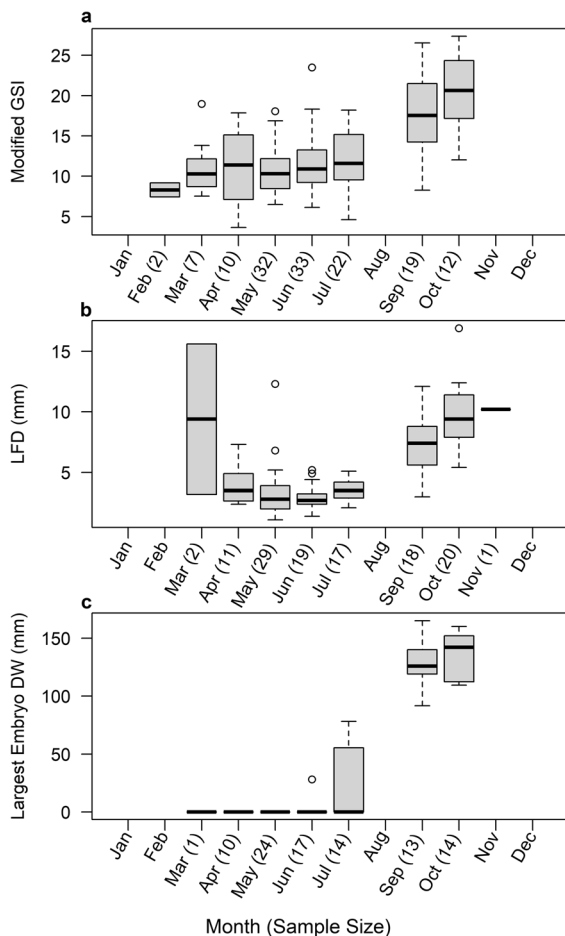


were generally a tan color, which darkened to brown in October (Fig. 6). Unfortunately, due to a lack of mature females captured after October, we were unable to document further changes in the embryos prior to parturition. However, based on the largest embryo DW (165 mm) and the smallest free-swimming juvenile DW (189 mm), mean size at birth is likely somewhere between those two values.

Mean uterine fecundity was 8.3 (2–14). Of the 34 gravid females with quantifiable embryos, 23.5% had at least one deformed, non-viable embryo (these were not included in uterine fecundity estimates). Embryos often varied in size within a gravid female, with an average difference in DW between the smallest and largest embryos of 20.7 mm. The smallest gravid female was 490 mm DW. Neither the left versus right uterine fecundity ( $p=0.47$ ) nor the embryo sex ratio ( $p=0.74$ ) was significantly different. However, uterine fecundity was strongly correlated with female disc width ( $y=0.033x-15.834$ ,  $R^2=0.726$ ,  $p<0.001$ ; Fig. 7).

Female reproduction was determined to be annual, rather than biennial. All gravid females captured in October ( $n=14$ ) had vitellogenic follicles measuring  $\geq 7.0$  mm and near full-term embryos (Fig. 6e). In addition, 123 of 134 mature females (91.8%) sampled during this project were either gravid ( $n=103$ ), had evidence of capture-induced abortion ( $n=7$ ), or never pupped ( $n=13$ ). Neither parturition nor evidence of mating was observed during the study due to a lack of mature specimens from November to February, but trends in male and female reproductive analyses indicate that parturition likely occurs around December to January, with mating occurring immediately thereafter. Ovulation and fertilization likely happen in March. Of the two mature females captured in March, one had uterine eggs but no vitellogenic follicles, and the other had no uterine eggs, but several vitellogenic follicles and the second highest LFD measured in the study. In April, 9 of the 10 mature females had uterine eggs, and the one that did not show evidence





**Fig. 5** Box plots for **a** modified gonadosomatic index (GSI; left testis length, multiplied by testis width, divided by disc width), **b** largest follicle diameter (LFD), and **c** largest embryo disc width (DW) for *Gymnura lessae* by month, as well as the sample size for each month. The line in the box is the median, the box is the interquartile range, the whiskers are 1.5 times the interquartile range, and dots are values that exceed 1.5 times the interquartile range

of capture-induced abortion; thus, gestation is likely about 10 to 12 months long.

### Growth

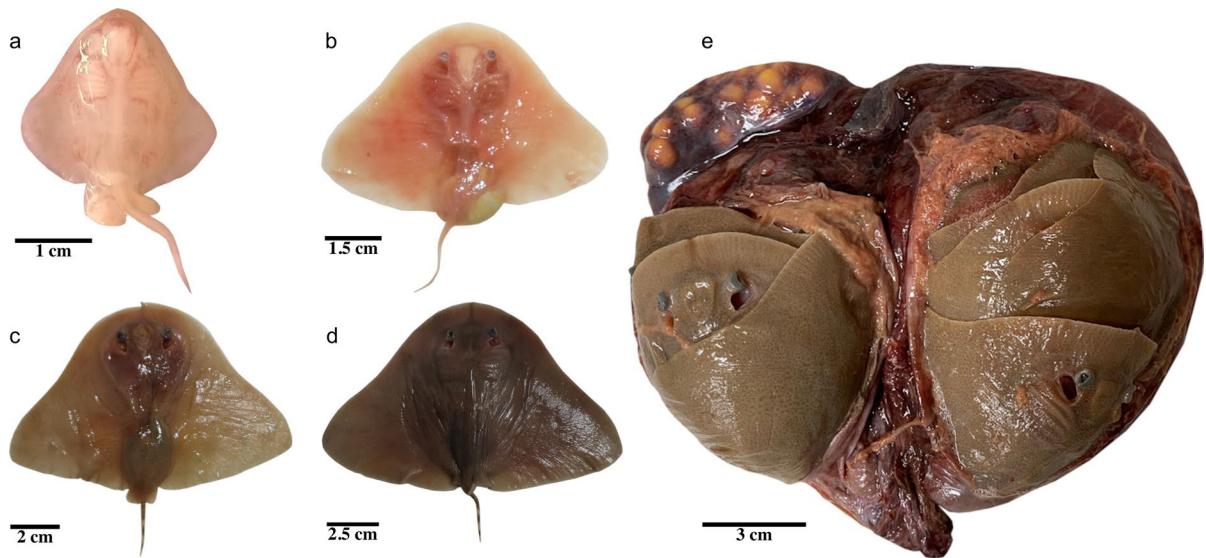
The ELEFAN method enabled the estimation of growth parameters for *G. lessae*. Since parturition for *G. lessae* was estimated to occur in December and January, a January 1 birthdate was assigned to the species; as such, the parameters  $t_{\text{anchor}}$  and  $t_0$  were functionally identical. The growth models demonstrated rapid growth for both males ( $n=304$ ) and

females ( $n=217$ ), von Bertalanffy growth parameter estimates of  $DW_{\infty}=427.1$  mm,  $k=1.34$  year<sup>-1</sup>,  $t_0=-0.35$  years, and  $DW_{\infty}=882.2$  mm,  $k=0.40$  year<sup>-1</sup>,  $t_0=-0.56$  years for males and females, respectively (Fig. 8). Growth curves tracked well with the male and female age-0 cohorts, which were distinct from other cohorts; however, this distinction between cohorts became less evident over time (Fig. 8). Although a greater sample size may have enabled us to track each cohort for a longer duration, individual cohort length ranges typically start to overlap once growth begins to plateau, making it difficult to differentiate between cohorts regardless of sample size. The estimated instantaneous natural mortality rate was higher for males at 1.48 than females at 0.48. Growth parameter estimates were used to project DW out to 1 year after birth (i.e., to January, when mature *G. lessae* likely mate). These projections indicated males (projected to 357.1 mm) would surpass  $DW_{50}$  (340.1 mm), but suggested females (projected to 409.5 mm) would not reach  $DW_{50}$  (461.4 mm) until an estimated age of 1.3 years.

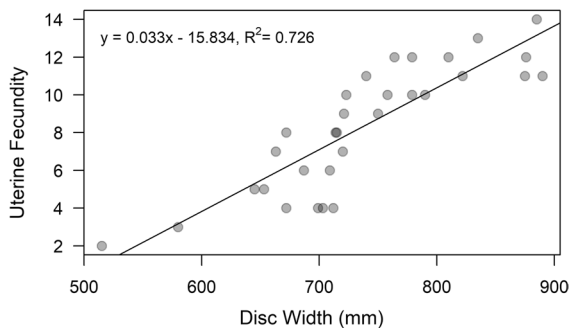
### Age at maturity

The results of the length-frequency analysis were used to identify age-0 individuals caught in September and October (i.e., approximately 9 to 10 months old) to estimate the percentage of age-0 individuals likely to reach maturity and mate around January (i.e., 1 year after birth). All males caught in September and October that measured 377 mm DW (the largest transitional male) or smaller ( $n=16$ ) were considered to be age-0. Of these 16 males, 5 were classified as adults, 10 as subadults, and 1 as juvenile (Table 1). All ten of the subadults had claspers that were fully elongated but only partially calcified; however, each had testes that appeared fully developed and enlarged. Thus, 15 of the 16 age-0 males examined (93.8%) would have likely attempted to mate around January. In addition, only one immature male greater than 300 mm DW was captured between January and June (i.e., age-1 or older), and this individual was partially deformed, missing a left clasper (Table 1).

Of the females measuring less than 500 mm DW (i.e., age-0) and caught in September and October ( $n=13$ ), four were classified as adults, four as subadults, and five as juveniles (Table 1). Based on the LFDs of the adult age-0 females (all  $\geq 4.5$  mm), it was



**Fig. 6** *Gymnura lessae* embryos from specimens captured in **a** June, **b** July, **c** September, and **d** October, as well as **e** a partially dissected uterus from a specimen captured in October, alongside an ovary containing vitellogenic follicles



**Fig. 7** Uterine fecundity of *Gymnura lessae* compared to disc width, with a linear regression fit to the data

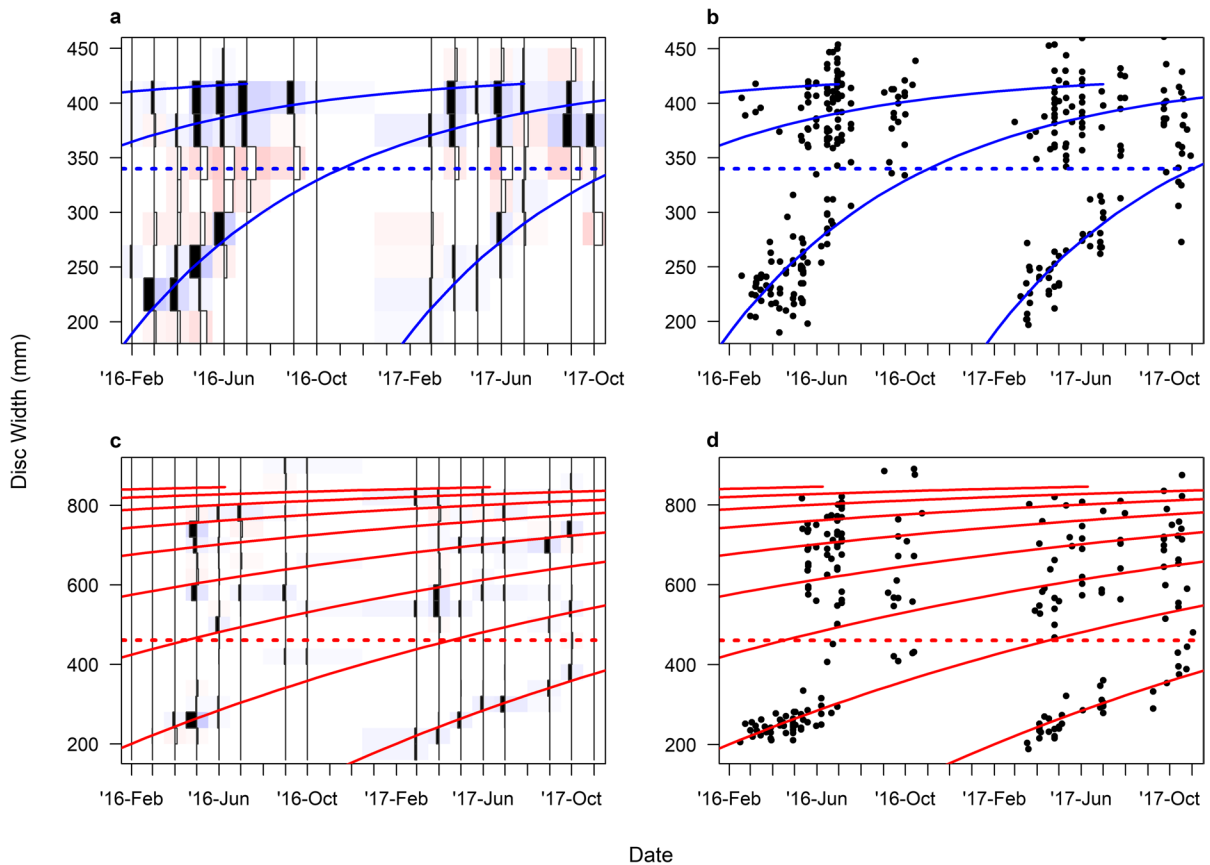
assumed that all four would have attempted to mate around January (Table 1). However, unlike with the subadult males caught during September and October, the probability that the four subadult females would mature and mate in January was difficult to confidently estimate. Therefore, we attempted to estimate the percentage of age-1 females that likely mated 1 year after birth. Females greater than 400 mm DW but less than 550 mm DW, caught between January and July, were assumed to be age-1 ( $n=13$ ). Similarly, females greater than 500 mm DW but less than 650 mm DW, caught between August and December, were also assumed to be age-1 ( $n=12$ ). Of these 25 age-1 females, 10 (40%) were determined to be

reproductively active during age-1 (Table 1). Most of these age-1 females were categorized as adults ( $n=19$ ; 76%); however, four (16%) were classified as subadults and one (4%), caught in May, was classified as a juvenile (Table 1).

## Discussion

The results of this study provide novel insight into the growth and reproduction of *G. lessae* in the northern Gulf of Mexico. Our study was the first to produce a precise size at maturity estimate for male *G. lessae* in the Gulf of Mexico, as previous studies lacked adequate sample sizes to do so. Our  $DW_{50}$  estimate (340.0 mm) is smaller than reported for male *G. lessae* in the Atlantic; however, this is unsurprising as not only are *G. lessae* in the Atlantic larger, but *G. lessae* in the Gulf of Mexico are potentially a separate, undescribed species of *Gymnura* (Parsons 2017). For females, this study's  $DW_{50}$  estimate (461.4 mm) was similar to that reported by Parsons (2017) for northern Gulf of Mexico *G. lessae* specimens (448 mm) but smaller than that reported by Cu-Salazar et al. (2014) for *G. lessae* in the southern Gulf of Mexico (568 mm). However, this difference is driven primarily by variations in maturity criteria, as when we match our criteria to those of Cu-Salazar





**Fig. 8** A von Bertalanffy growth function (VBGF) fit using a simulated annealing algorithm to length-frequency data for male *Gymnura lessae* ( $DW_{\infty}=427.1$  mm,  $k=1.34$  year<sup>-1</sup>,  $t_0=-0.35$  years) plotted over **a** the binned and restructured data used to fit the VBGF and **b** a scatter plot of individual disc widths plotted by date of capture; and female *Gymnura*

*lessae* ( $DW_{\infty}=882.2$  mm,  $k=0.40$  year<sup>-1</sup>,  $t_0=-0.56$  years) plotted over **c** the binned and restructured data used to fit the VBGF and **d** a scatter plot of individual disc widths plotted by date of capture. Disc width at 50% maturity is denoted with a dashed horizontal line on each plot

**Table 1** Maturity stages of age-0 *Gymnura lessae* sampled in September and October and age-1 (or older for males) *Gymnura lessae* sampled throughout the year, as well as the percentage of those specimens that were estimated to mate 1 year after birth

	Male		Female	
	Age-0	Age-1 +	Age-0	Age-1
Juvenile	1	1	4	1
Subadult	10	0	4	4
Adult	5	185	5	19
Percentage to mate at 1 year	93.8%	NA	30.7%	40.0%

et al. (2014) (i.e., females must either be gravid or have recently given birth to be considered mature), our  $DW_{50}$  estimate increases to 596 mm. Given the differences in latitude, we would expect *G. lessae* to mature at a slightly smaller size in the southern Gulf of Mexico (Fisher et al. 2010). This difference is nonetheless important to note due to potential management implications (Araújo et al. 2016). Compared to other Gymnurids, our male and female  $DW_{50}$  estimates were larger than those reported for *G. micrura* (Yokota et al. 2012), similar to those reported for *G. australis* (Jacobsen et al. 2009), and smaller than those reported for *G. lessae* in the Atlantic (potentially a different species than Gulf of Mexico *G. lessae*; Parsons 2017), *G. zonura* (White and Dharmadi

2007), *G. altavela* (Alkusaity et al. 2014), *G. marmorata* (Burgos-Vázquez et al. 2019), and *G. poecilura* (Menon et al. 2020).

The mean and maximum uterine fecundity reported for *G. lessae* in this study are the highest reported for the species (Daiber and Booth 1960; Cu-Salazar et al. 2014; Parsons 2017) and are some of the highest reported for the genus, second to only *G. marmorata* (Burgos-Vázquez et al. 2019). However, capture-induced abortion is reportedly common for *Gymnura*; thus, mean fecundity estimates for most *Gymnurids* are likely underestimated to some extent (Bizzarro 2005; Parsons 2017). Considering that most previous *Gymnura* studies obtained their specimens via fishery-dependent means, whereas all specimens collected during this study were captured in fishery-independent trawls, it is possible that capture-induced abortion rates in this study were lower than in others. Therefore, differences in mean fecundity estimates between this study (8.3) and those reported in other studies, such as for *G. lessae* in the southern Gulf of Mexico (4.3; Cu-Salazar et al. 2014), could be due in part to differences in sampling design rather than biology.

The reproductive cycle described in this study was similar to that reported for *G. lessae* in the southern Gulf of Mexico (Cu-Salazar et al. 2014). Both populations exhibited an annual, synchronous reproductive pattern, with gestations of approximately 10 to 12 months and mating occurring immediately following parturition. Although we were unable to determine the exact time of parturition, it likely occurs about a month earlier here than in the southern Gulf of Mexico (February) based on the monthly follicle and embryo sizes reported in this study and those reported by Cu-Salazar et al. (2014). Like with size at maturity, this variation is also probably driven by latitudinal differences.

Our growth parameter estimates, which are the first for any *Gymnurid* except *G. altavela* (Parsons et al. 2018), indicated that although both sexes are fast growing, males grow faster than females. However, females were significantly larger than males based on both the maximum sizes observed in this study and the  $DW_{\infty}$  estimates, wherein the female estimate was more than twice the male estimate. While other methods for estimating growth, such as hard part analysis or captive study, are considered more accurate and precise, the ELEFAN method proved to be

useful in this case since *G. lessae* have poorly mineralized centra and poor survival in captivity. Nonetheless, future studies using alternative techniques, such as tag-recapture, are necessary for validating the growth parameters estimated in this study, as well as estimating the lifespan of the species. Scatter plots show a relatively wide distribution of DWs for age-0 individuals from February through May, which was presumably due to differences in size at birth, rather than a protracted parturition period (Fig. 8b, 8d). This spread also explains why the simulated annealing algorithm used to generate the female growth curves appeared to slightly underestimate  $k$  relative to the raw data (Fig. 8d). While we were unable to estimate the maximum age for the species, it is likely that females grow older than males based on estimates of  $M$  (Pauly 1980). This makes sense from a reproductive perspective, as an age-4 male is likely only marginally more reproductively fit than an age-2 male, whereas an age-4 female is estimated to have triple the uterine fecundity (8.4) of an age-2 female (2.7).

When the growth estimates are coupled with the reproductive data, it is clear that almost all males and a large portion of females mate just 1 year after birth. While an elasmobranch reaching maturity in just 1 year appears to be quite rare, it has been previously reported in batoids (*Urotrygon rogersi*, Mejía-Falla et al. 2014) and sharks (*Rhizoprionodon taylori*, Simpfendorfer 1993). For females, whether or not to mate at this time depends on the prioritization of short-term versus long-term fecundity early in life. A female that mates just 1 year after birth has an increased likelihood of having at least one set of offspring prior to death (scenario A). However, since uterine fecundity is highly correlated with DW, a female that prioritizes growth over reproduction and lives at least 3 years will presumably have a greater per-year fecundity throughout its life (scenario B). The scenario employed by a given female is likely dependent upon mortality rate. In this way, individuals living in a population with high mortality are more likely to apply scenario A, whereas individuals living in a population with low mortality are more likely to apply scenario B. However, this theory would be difficult to prove given it would require intensive sampling across multiple populations with variable, but known, fishing mortality.

The reproduction, growth, and age at maturity of *G. lessae* are different from those of most other

common coastal batoids in the northern Gulf of Mexico. Although the uterine fecundity of *G. lessae* is similar to that of *Narcine bancroftii* (Rudloe 1989), it is greater than that of the three species of *Hypanus* (*H. americanus*, *H. sabinus*, *H. sayi*; Snelson et al. 1988; Snelson et al. 1989; Ramírez-Mosqueda et al. 2012) and *Rhinoptera bonasus* (Neer and Thompson 2005). In addition, *G. lessae* is the only species in which parturition occurs exclusively in the late fall or winter. Estimates of growth parameters are limited to *R. bonasus* (Neer and Thompson 2005) and captive *H. americanus* (Henningsen and Leaf 2010), both of which were found to grow larger and slower than *G. lessae*. Similarly, both species were found to mature slower than *G. lessae*, with *R. bonasus* maturing in 4–5 years and *H. americanus* maturing in 3–4 years and 5–6 years for males and females, respectively (Neer and Thompson 2005; Henningsen and Leaf 2010). Age at maturity has been estimated for *N. bancroftii* in the northern Gulf of Mexico based on length-frequency data, which indicated that the species has the potential to produce offspring at 24 months of age (Rudloe 1989). Thus, life history characteristics indicate that *G. lessae* and *N. bancroftii* are likely more resilient to exploitation than other coastal batoids found in the northern Gulf of Mexico.

Overall, *G. lessae* appear to be fast growing, quick maturing, and relatively fecund compared to most other batoids in the northern Gulf of Mexico. These traits likely increase the resilience of *G. lessae* to a variety of anthropogenic impacts, including fishing mortality and habitat alterations (Carlson et al. 2017). However, since *G. lessae* in the Atlantic are larger and potentially a different species than those in the Gulf of Mexico, our conclusions may not apply to both populations, particularly with regard to age at maturity. While *G. lessae* is categorized as “Least Concern” by the IUCN Red List, a status supported by our results, 9 of the other 11 species of *Gymnura* are currently classified as “Near Threatened” or in a threatened category (IUCN Red List 2021). Therefore, given the difficulties of estimating growth for Gymnurids through traditional methods, we recommend that future studies explore the use of length-frequency analysis to estimate growth parameters for other Gymnurids that exhibit synchronous reproductive cycles to better understand their sensitivities to anthropogenic impacts.

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**Author contribution** All authors contributed to the study conception and design. Material preparation, data collection, and analysis were performed by MBJ and BLH-B. The first draft of the manuscript was written by MBJ, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

**Data availability** The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

## Declarations

**Ethics approval** The care and use of experimental animals complied with Alabama state animal welfare laws, guidelines, and policies as approved by the University of South Alabama under the IACUC protocols (IACUC Board Reference Number 974304). All efforts were taken to reduce animal suffering during handling.

**Competing interests** The authors declare no competing interests.

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