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Size at sexual maturity, seasonal variation by maturity stages, and fecundity of the spotted round ray (*Urobatis maculatus*) and the thorny stingray (*Urotrygon rogersi*) from the northern tropical eastern Pacific

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Abstract

Round rays (family: Urotrygonidae) are commonly caught as by-catch by shrimp trawl fisheries in the tropical eastern Pacific (TEP). However, little information on their life history and catch species composition exists for most round ray species, preventing the evaluation of the impact of fishing on their populations. The mean size at sexual maturity (DW_{50}), seasonal variation by maturity stages, and fecundity for two round ray species caught during shrimp trawl research cruises in the south-eastern Gulf of California (northern TEP) were estimated using a multi-model approach and inference for the first time, to determine the part of the population of each species that is being affected by shrimp trawling. Disc width (*DW*) ranged from 7.0 to 30.9 cm for the spotted round ray (*Urobatis maculatus*), and 7.2–33.5 cm for the thorny stingray (*Urotrygon rogersi*), with females reaching larger sizes than males in both species. The DW_{50} was estimated at 12.8 and 11.8 cm *DW* for the males and females of *U. maculatus*, respectively, whereas for *U.rogersi*, it was 15.0 and 18.4 cm *DW* for males and females, respectively. Embryos were found in females ≥14.5 cm *DW* in both species. The maximum fecundity was five embryos for *U. maculatus* (mean = 3.1 ± 0.2 S.E., mode = 4), and six embryos for *U. rogersi* (mean = 3.0 ± 0.3 S.E., mode = 2). Fecundity and embryo size did not vary with maternal size. Male and female immature and mature individuals for both species, including pregnant females, were found in the catches in all seasons of the year. Our results can help determine the vulnerability of the studied species populations to fishing pressure from shrimp trawling in the northern TEP and guide the development of future monitoring strategies and conservation actions for these species, if necessary.

KEYWORDS
Batoidea, by-catch, endangered species, Mexican Pacific, reproduction, shrimp fishery

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1 | INTRODUCTION

Elasmobranchs are principally threatened by overexploitation through targeted fisheries and incidental catches (by-catch) (Cronin et al., 2022; Dulvy et al., 2021; Pacoureau et al., 2021). For example, in the Gulf of Mexico, shrimp trawl fisheries are responsible for the decline in the abundance of small coastal elasmobranchs (Shepherd & Myers, 2005), whereas in the tropical eastern Pacific (TEP) this fishery commonly catches round rays of the family Urotrygonidae as by-catch (Morales-Saldaña et al., 2022). Specifically, in the northern TEP, which corresponds to the Gulf of California (GC) and the North Pacific coast of Mexico, the shrimp trawl fisheries represent a considerable source of additional fishing mortality for rays caught as by-catch (Bizzarro et al., 2007, 2009; Morales-Azpeitia et al., 2013), which include a high proportion of juvenile and adult round rays of the genus *Urobatis* spp. and *Urotrygon* spp. (Alvarez-Fuentes et al., 2023; Garcés-García et al., 2020; López-Martínez et al., 2010; Nava-Nava, 2013; Rábago-Quiroz et al., 2012). However, the real impact of shrimp trawling fishery on the abundance of round rays remains unknown in this area (Garcés-García et al., 2020). The shrimp fishery is the most important industry in Mexico in terms of income and employment and represents nearly 40% of the total national fish production value (Arreguín-Sánchez et al., 2017; Lluch-Cota et al., 2007), which means that the effect of the shrimp trawl fishery on the abundance of these taxa might be high.

The spotted round ray *Urobatis maculatus* Garman 1913 and the thorny stingray *Urotrygon rogersi* are species with no commercial value in Mexico but are commonly caught as by-catch by the shrimp trawl fisheries (Garcés-García et al., 2020; Herrera-Valdivia et al., 2016; López-Martínez et al., 2010; Rábago-Quiroz et al., 2012). According to the IUCN's Red List, *U. maculatus* is classified as a "Least Concern" species due to its small size, reaching sexual maturity at a smaller length and early age, and being relatively productive (Pollom et al., 2020). In contrast, *U. rogersi* is classified as "Near Threatened" by the IUCN Red List, because this species is subject to intense and largely unmanaged fishing pressure throughout its range. According to the IUCN, a population reduction of 20%–29% has occurred over the past three generations (15 years) (Kyne et al., 2020; Morales-Saldaña et al., 2022). However, information on abundance and the life history (e.g., age and size at maturity, number, and size of offspring, growth patterns) of both species is scarce or nonexistent in the GC and the north Pacific coast of Mexico, and therefore the real impact of the shrimp trawl fisheries on their populations is unknown.

Biological information and species-specific data collection are important to improve assessments of commercially exploited or by-catch species and propose conservation, management, and monitoring strategies (Clarke et al., 2018; Oliver et al., 2015; White et al., 2019), which have been recommended to prevent declines and extinctions of the TEP round ray populations (Morales-Saldaña et al., 2022). Particularly, size at sexual maturity and fecundity are key reproductive parameters, essential for the assessment and management of exploited populations, allowing the estimation of the vulnerability of the elasmobranch populations to fishing pressure by incorporating it into ecological risk or demographic assessment analyses (Barnett et al., 2013; Cortés et al., 2010; Santana et al., 2020), which is also useful for assessing the health of their populations and making inferences and predictions of their populations (Morales-Saldaña et al., 2022). In addition, these reproductive parameters could be used to establish a minimum catch size for exploited species (Aragón-Noriega, 2015; Caddy & Mahon, 1995; Mendivil-Mendoza et al., 2018), mainly if these are low fecundity species (Croll et al., 2016; Marshall et al., 2023; NOM-029-PESC-2006, DOF, 2007; Salomón-Aguilar, 2015), or other management measures.

Fishery-independent surveys can provide important information on the abundance and life-history parameters of elasmobranchs (Rago, 2005; Runcie et al., 2016; Talwar et al., 2020), being useful when little data are available from commercial fisheries (Dennis et al., 2015; Kacev et al., 2017). Furthermore, fishery-independent surveys in several parts of the world have shown that elasmobranchs such as dogfishes (Squaliformes), angel sharks (Squatiniformes), and rays (batoids), caught as by-catch by demersal trawls, have suffered marked declines in abundance (Walker, 2005a). Using data from fishery-independent shrimp trawl surveys, we assessed the size at sexual maturity and the seasonal variation by maturity stages of *U. maculatus* and *U. rogersi* to determine which parts of the population are being caught as by-catch by shrimp trawling operating in the studied area. We also estimate the fecundity and determine if a relationship between maternal size and the number and size of the embryos exists. The working hypothesis is that by-catch from shrimp trawling affects individuals at different stages of maturity for both species in the studied area. The information obtained in the present study integrated into ecological risk or demographic assessment analyses will be useful to determine the vulnerability of the studied species populations to fishing pressure from shrimp trawling and propose conservation actions, if necessary.

2 | MATERIALS AND METHODS

2.1 | Ethics statement

The Mexican Institute for Research in Sustainable Fisheries and Aquaculture (IMIPAS) conducted fishery-independent shrimp trawl surveys under three permits issued by the corresponding Mexican authorities (National Commission for Fisheries and Aquaculture of Mexico, CONAPESCA, https://www.gob.mx/conapesca): PPF/DGOPA-238/13, PPF/DGOPA-052/14, and PPF/DGOPA-002/18. These surveys aim to evaluate the shrimp populations and species caught as by-catch. The majority of collected individuals were dead on deck, whereas individuals still alive were killed immediately by destruction of the brain and severance of the spinal cord using a knife (Holmes et al., 2022; O'Shea et al., 2013).

2.2 | Study area and data collection

All the analysed round rays were caught during 1117 tows carried out from February 2012 to January 2020, on board the R.V. INAPESCA I

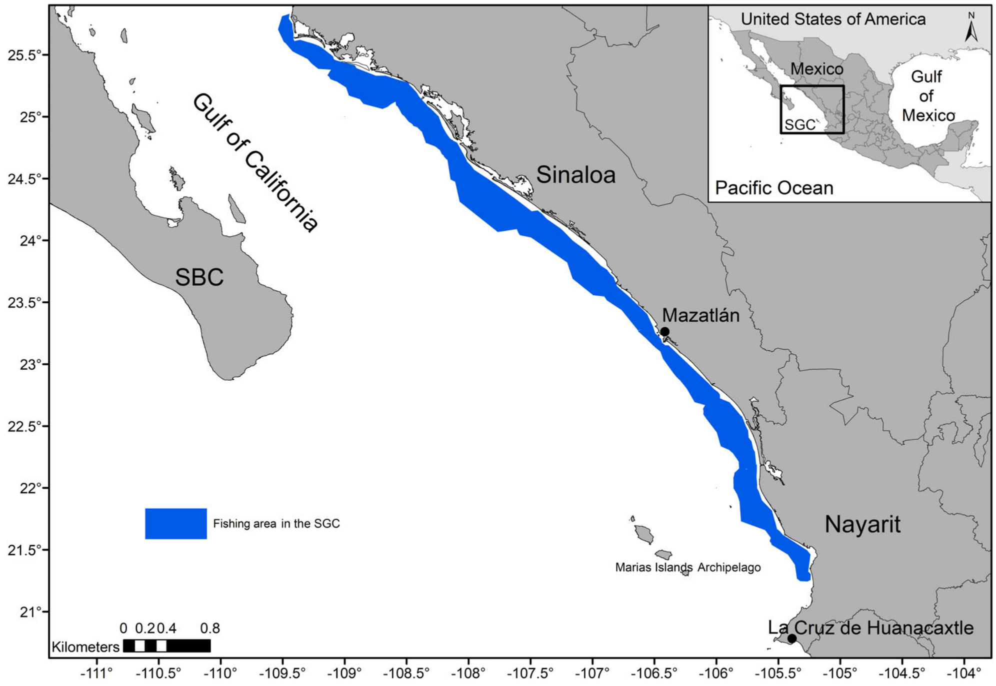


FIGURE 1 Fishing area in the continental shelf of the south-eastern Gulf of California (northern tropical eastern Pacific), established for shrimp trawl research cruises undertaken by the National Fisheries and Aquaculture Institute of Mexico (INAPESCA), Mexico. SBC, South Baja California.

and R.V. BIP XII. The dates when the cruises occurred varied each year, but samples from all seasons and months were obtained during the studied period, so the individuals for each month and season were obtained from the sum of those particular periods. The trawls were carried out on the southeastern coast of the GC and Mexican Pacific, in the fishing area where commercial shrimp vessels operate (NOM-002-SAG/PESC-2013-DOF, 2013). In such areas, INAPESCA carries out studies of shrimp populations (Liedo-Galindo & González-Ania, 2005) (Figure 1). The typical double nets (33 m in length, mesh-size of 51 mm in the square, belly, and wings, and 38 mm in the cod end) used in the industrial demersal shrimp trawl fishery were employed to undertake the trawls, at depths of 9–64 m with a towing speed of 2 knots for 1 h. The surveys were carried out throughout the year, including the closed fishing period for shrimp fishery (early April to early September), when shrimp trawling is prohibited to commercial vessels, but is allowed to government research vessels (NOM-002-SAG/PESC-2013-DOF, 2013), and information from commercial catches is not available.

Round rays from all observed cohorts were collected randomly (without prioritizing the collection of any particular cohort) in each tow once the nets were discharged over the deck, and frozen on board. At the laboratory, all individuals were identified to the species level using various taxonomic keys (e.g., Castro-Aguirre & Espinosa-Pérez, 1996; Corro-Espinosa & Ramos-Carrillo, 2004; McEachran & Notarbartolo-Di Sciara, 1995; Robertson & Allen, 2015). The unique traits of both species were identified based on morphology, and a follow-up study in the south-eastern Gulf of California utilized molecular techniques (genomic DNA) (Alvarado-Marín, 2023) to confirm the accuracy of the identification of the individuals analysed for this study. All individuals were sexed by identifying the presence or absence of claspers (Carrier et al., 2004), and the disc width (DW) was measured to the nearest centimeter at the widest part of the disc.

2.3 | Size at sexual maturity (DW_{50})

The maturity stage was assigned to each individual based on the macroscopic inspection of the reproductive structures: primarily ovary development confirmed by the uterus and oviducal gland condition for the females; and clasper rigidity stage confirmed by testis development for males (Garcés-García et al., 2020; Walker, 2005b) (Table 1). The size at sexual maturity (disc width at which 50% of the individuals in the population are sexually mature, DW_{50}) was estimated for each sex from the proportion of immature and mature individuals at each class interval, using the Gompertz model (asymmetric and non-logistic curve) and the Brouwer and Griffiths model (symmetric logistic curve), avoiding the use of redundant models (Burnham & Anderson, 2002; García-Rodríguez et al., 2020; Katsanevakis, 2006). Class intervals (bandwidth) were determined using the Sheather-Jones selection procedure (Muro-Torres et al., 2023; Sheather & Jones, 1991) in RStudio 2022.12.0 + 353.

Model 1 (Gompertz, 1825)

$$P_i = Exp^{-Exp^{-\theta\left(DW_i - \widehat{DW}_{50}\right)}}$$

Model 2 (Brouwer & Griffiths, 2005)

$$P_i = \frac{1}{1 + Exp^{-\left(DW_i - \widehat{DW}_{50}\right)/\alpha}}$$

where P_i is the proportion of mature individuals in size class i, θ is the rate at which sexual maturity is attained, DW_i is the disc width within each size class i, $\widehat{DW}_{50}$ is the disc width at which 50% of the

TABLE 1 Maturity stages assigned based on the development of reproductive structures (adapted from Garcés-García et al., 2020; Walker, 2005b).

Maturity stages	Females			Males	
	Ovary	**Oviducal gland**	**Uterus**	**Testis**	**Clasper**
Immature	Not differentiated from the epigonal organ, without visible oocytes	Indistinct from the oviduct.	Indistinct from the oviduct.	Not differentiated from the epigonal organ.	Pliable, short with no calcification.
Maturing	Differentiated from the epigonal organ, with whitish oocytes of diameter <3 mm.	Differentiated from the oviduct, larger than wider.	Uniformly enlarged tubular structure.	Differentiated from the epigonal organ, not lobed or vascularized	Enlarged, partly calcified.
Mature	Differentiated from the epigonal organ, with yellowish oocytes of diameter ≥3 mm.	Heart shape well differentiated from the oviduct.	Enlarged tubular structure distended, with or without the presence of eggs or embryos.	Enlarged, lobed, and vascularized	Enlarged, rigid, and fully calcified.

individuals in the population are sexually mature, and α is the width of the maturity ogive.

Each model was adjusted by minimizing the objective likelihood function with the direct search algorithm of Newton (Kutner et al., 2004), according to the following equation that assumes a binomial distribution (Jacob-Cervantes & Aguirre-Villaseñor, 2014):

$$-LnL=-\sum_{i=1}^{n}\left[m_i*Ln\left(\frac{P_i}{1-P_i}\right)+n_i*Ln(1-P_i)+Ln\binom{n_i}{m_i}\right]$$

$$\text{Binomial coefficient}:\binom{n_i}{m_i}=\frac{n_i!}{((n_i-m_i)!*m_i!)}$$

where P_i is the proportion of mature individuals in size class i, n_i is the total number of individuals within each size class i, and m_i is the number of sexually mature individuals in each size class i.

The 95% confidence intervals ($CI_{95\%}$) of the DW_{50} were estimated with 3000 bootstrap replicates using the percentile confidence intervals method (Haddon, 2011). The models were compared using a multi-model approach with the corrected AIC_c, the difference of Akaike (Δ_i), and the weight of Akaike (w_i) (Akaike, 1973; Burnham & Anderson, 2002; Hurvich & Tsai, 1989).

In case Akaike's weight displayed no "clear winner" ($\%w_i > 90\%$; Katsanevakis, 2006; Katsanevakis & Maravelias, 2008) the DW_{50} of the average model was estimated using a multi-model inference (Burnham & Anderson, 2002; Katsanevakis & Maravelias, 2008; Luquin-Covarrubias et al., 2016).

2.4 | Variation by maturity stages

The frequency by maturity stages for both sexes was determined monthly (sum of individuals caught for each particular month during 2012–2020) and seasonally (sum of individuals caught for each group of months in each particular season during 2012–2020). The seasons were divided as follows: dry cool season (DCS, from December 1 to March 31), dry warm season (DWS, from April 1 to June 30), and humid warm season (HWS, from July 1 to November 30) (Alvarez-Fuentes et al., 2023).

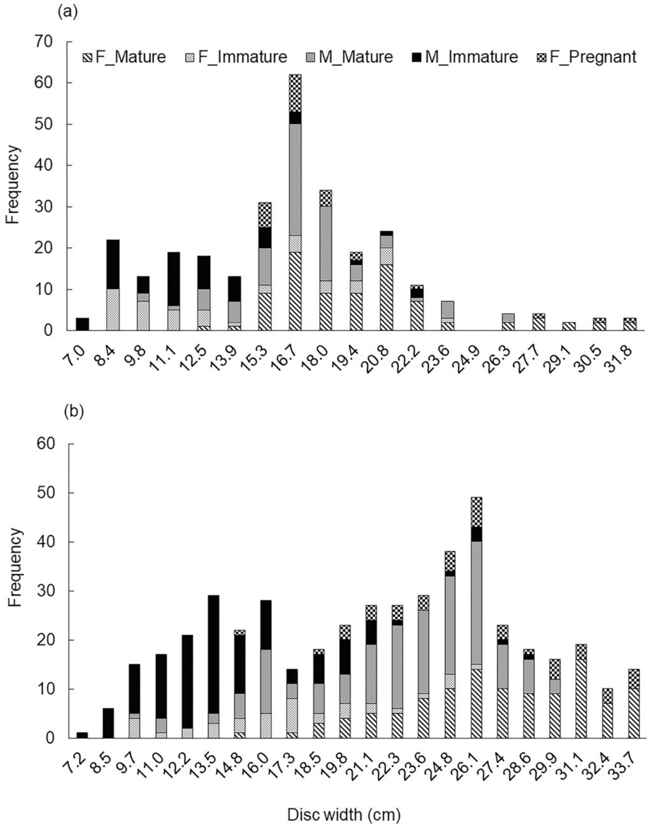


FIGURE 2 Size-frequency distribution by stage of sexual maturity for (a) *Urobatis maculatus* (*n*: sample size = 267, class interval or bandwidth = 1.38 cm) and (b) *Urotrygon rogersi* (*n* = 422, class interval or bandwidth = 1.26 cm) from shrimp trawl by-catch in the south-eastern Gulf of California, Mexico. F_Immature, immature females; F_Mature, mature females; F_Pregnant, pregnant females; M_Immature, immature males; M_Mature, mature males.

TABLE 2 The size at sexual maturity (DW_{50}) estimated for males and females of *Urobatis maculatus* and *Urotrygon rogersi* in the south-eastern Gulf of California (Mexico) using two sigmoidal models.

Species	Model	Parameter	Males	$CI_{95\%}$	Females	$CI_{95\%}$
Urobatis maculatus	Gompertz	DW_{50}	12.3	11.0–13.4	11.1	8.0–13.0
		Θ	0.32	0.22–0.49	0.21	0.12–0.34
		AIC_c	50.4		34.5	
		Δi	0		0	
		$\%w_i$	67.6		51.0	
	Brouwer and Griffiths	DW_{50}	13.8	12.6–14.7	12.5	9.6–14.3
		α	2.31	1.39–3.80	4.43	3.06–6.84
		AIC_c	51.9		34.6	
		Δi	1.5		0.08	
		$\%w_i$	32.4		49.0	
	MMI	$\overline{DW}_{50}$	12.8	11.5–13.8	11.8	8.8–13.6
Urotrygon rogersi	Gompertz	DW_{50}	15.0	13.8–16.2	17.7	13.8–21.4
		Θ	0.21	0.17–0.27	0.33	0.27–0.57
		AIC_c	62.5		29.6	
		Δi	0		0	
		$\%w_i$	99.3		50.5	
	Brouwer and Griffiths	DW_{50}	17.8	16.7–18.7	19.1	15.7–20.9
		α	2.97	2.31–3.81	2.48	0.92–4.28
		AIC_c	72.4		29.5	
		Δi	9.9		0.04	
		$\%w_i$	0.7		49.5	
	MMI	$\overline{DW}_{50}$	-		18.4	14.7–21.1

Abbreviations: θ and α, parameters of the models; Δi, Akaike's difference; $\%w_i$, percentage weight of Akaike; *AICc*, corrected Akaike Information Criterion; $CI_{95\%}$, confidence intervals; $\overline{DW}_{50}$, the size at sexual maturity of the average model; MMI, multi-model inference.

2.5 | Embryos and the effect of maternal size on litter size and size of embryos

Embryos were counted, sexed, and measured. The sex ratio of embryos was tested for a significant difference from the expected 1:1 using the χ^2 test modified by Yates (Yates, 1934; Zar, 2010). To determine whether there was an effect of maternal size on fecundity (litter size) and size of embryos both were plotted against female *DW*, and the relationships were examined using linear regression analysis (Mejía-Falla et al., 2012).

3 | RESULTS

3.1 | Size at sexual maturity (DW_{50})

A total of 267 individuals of *U. maculatus* (139 males, 128 females), and 422 of *U. rogersi* (272 males, 150 females) were analysed. *U. maculatus* ranged in size from 7.0 to 30.9 cm *DW*. Females ranged in size from 7.4 to 30.9 cm *DW*, whereas males ranged in size from 7.0 to 25.8 cm *DW*. For *U. maculatus*' males, 58 (41.7%) were immature with sizes of 7.0–21.5 cm *DW*, whereas 81 (58.3%) were mature with sizes of 8.9–25.8 cm *DW* (Figure 2a). Regarding the females, 44 (34.4%) were immature with sizes of 7.4–23 cm *DW*, and 84 (65.6%) were mature with sizes of 11.4–30.9 cm *DW*; of the latter 25 were pregnant females (14.5–30.9 cm *DW*) (Figure 2a). The two models compared appear to fit the data of males and females of *U. maculatus* well ($\Delta_i \leq 2$, Table 2; Figure 3a,b). Therefore, the size at sexual maturity (DW_{50}) of the average model was estimated for both sexes, with the DW_{50} of females being smaller than that of males (Table 2, Figure 3a,b).

U. rogersi ranged in size from 7.2 to 33.5 cm *DW*. Females ranged in size from 8.5 to 33.5 cm *DW*, whereas males in size ranged from 7.2 to 29.5 cm *DW*. Out of the 272 *U. rogersi's* males, 123 (45.2%) were immature with sizes of 7.2–27.5 cm *DW*, whereas 149 (54.8%) were mature with sizes of 9.7–29.5 cm *DW* (Figure 2b). Regarding the females, 38 (25.3%) were immature with sizes of 8.5–25.8 cm *DW*, and 112 (74.7%) were mature with sizes of 14.7–33.5 cm *DW*; of the latter 42 were pregnant females (14.7–33.5 cm *DW*) (Figure 2b). *U. rogersi's* males adjusted better with the Gompertz model for the data according to the AIC_c and Akaike's difference ($\Delta_i \leq 2$); thus it was not necessary to estimate the average model (Table 2; Figure 3c). In contrast, the DW_{50} of the average model was estimated for females because both models fit the data ($\Delta_i \leq 2$, Table 2), with a DW_{50} of females larger than that of males (Table 2; Figure 3c,d).

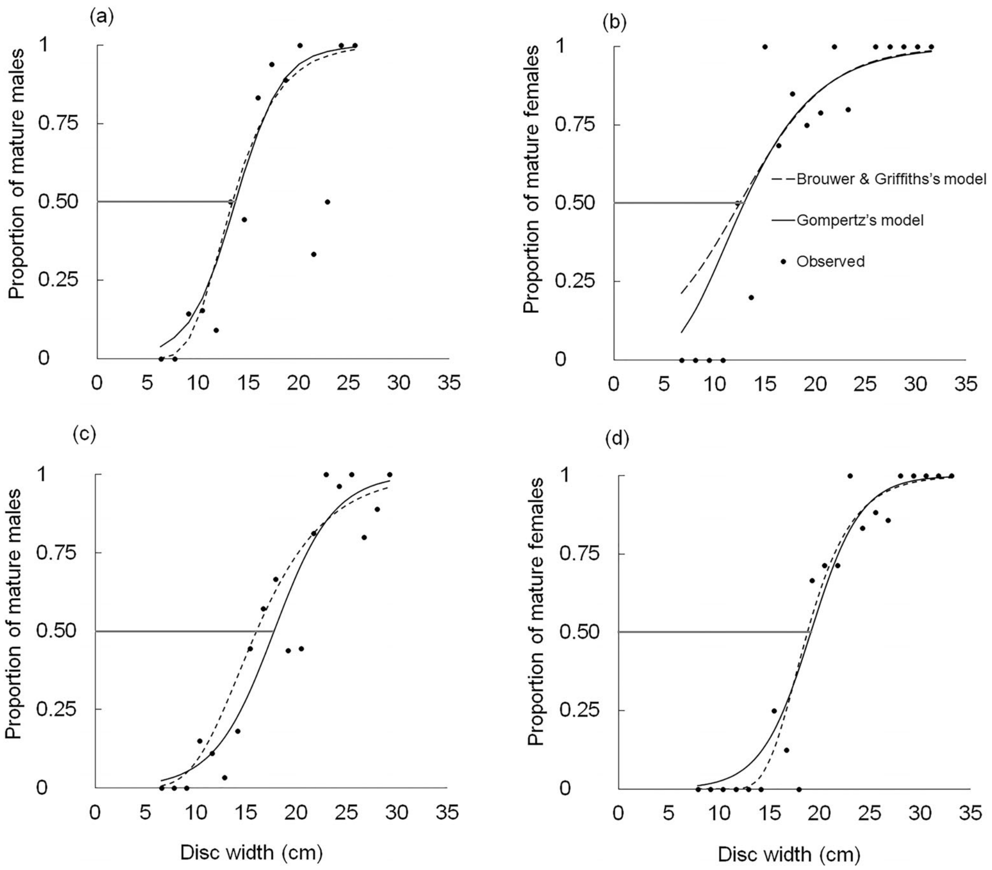


FIGURE 3 Maturity curves of (a) males and (b) females of *Urobatis maculatus*, and (c) males and (d) females of *Urotrygon rogersi* in the southeastern Gulf of California, Mexico, estimated with two sigmoidal models.

3.2 | Variation by maturity stages

The highest numbers of immature individuals for males of *U. maculatus* were captured in January (DCS), August, and September (HWS). In contrast, immature individuals of females were more frequent during January (DCS), June (DWS), and September (HWS) (Table 3; Figure 4a,b). Mature males of *U. maculatus* were frequently observed during January and February (DCS), whereas mature females were more abundant during February to March (DCS), and September (HWS) (Table 3; Figure 4a,b). Pregnant females were observed in the catches during March (DCS), August, and September (HWS), with a higher abundance in September (Table 3). The largest numbers of immature individuals for both sexes of *U. rogersi* were caught during August and September (HWS) (Table 3; Figure 4c,d). Mature males of *U. rogersi* were frequent during July August, and September (HWS), whereas mature females were more abundant during January (DCS), June (DWS), and August (HWS) (Table 3; Figure 4c,d). Pregnant females were observed in the catches during most of the year and in all seasons, except for March and October, being more abundant during August (Table 3, HWS).

3.3 | Embryos and the effect of maternal size on litter size and size of embryos

A total of 66 intra-uterine embryos (37 males, 25 females, and 4 undetermined) of *U. maculatus* were found, with sizes from 2.3 to 11.1 cm *DW* (mean ± S.E., 7.3 ± 0.6 cm *DW*). Fecundity varied between one and five embryos (mean ± S.E., 3.1 ± 0.2, mode = 4). The sex ratio of the embryos (0.66F:1M) did not differ from the 1:1 ratio ($\chi^2 = 1.952$, $df = 1$, $p = 0.162$). Maternal *DW* did not show any relationship with litter size ($R = 0.029$, $R^2 = 0.0008$, $F_{1,19} = 0.016$, $p = 0.901$) or with embryo *DW* ($R = 0.377$, $R^2 = 0.142$, $F_{1,17} = 2.809$, $p = 0.112$) (Figure 5a,b).

A total of 140 intra-uterine embryos (62 males, 64 females, and 14 undetermined) of *U. rogersi* were found, with sizes from 3.0 to 11.0 cm *DW* (mean ± S.E., 6.3 ± 0.3 cm *DW*). Fecundity varied between one and six embryos (mean ± S.E., 3.0 ± 0.3, mode = 2). The sex ratio of the embryos (1.03F:1M) did not differ from the 1:1 ratio ($\chi^2 = 0.008$, $df = 1$, $p = 0.929$). Maternal *DW* did not show any relationship with litter size ($R = 0.158$, $R^2 = 0.025$, $F_{1,35} = 0.901$, $p = 0.349$) or with embryo *DW* ($R = 0.128$, $R^2 = 0.016$, $F_{1,57} = 0.945$, $p = 0.335$) (Figure 5c,d).

4 | DISCUSSION

Both *U. maculatus* and *U. rogersi* are important components of the demersal ecosystem in the northern TEP, as they occupy intermediate positions within the food webs like other rays, thus linking the primary producers to the top levels of the food chain (Cortés et al., 2008). However, very little is known about their life history, especially in the studied area (Last et al., 2016), which limits the assessment of their population trends.

TABLE 3 Number of individuals caught by maturity stage per month (sum of individuals caught for each particular month during 2012–2020), season (sum of individuals caught for each group of months in each particular season during 2012–2020), and year for *Urobatis maculatus* and *Urotrygon rogersi* from fishery-independent shrimp trawl surveys in the south-eastern Gulf of California (Mexico).

	U. maculatus						***U. rogersi***					
	Females			**Males**			**Females**			**Males**		
	Immature	**Mature**	**Pregnant**	**Immature**	**Mature**	**Total**	**Immature**	**Mature**	**Pregnant**	**Immature**	**Mature**	**Total**
Month												
January	8	2	-	11	24	45	3	10	2	8	9	32
February	2	12	-	6	26	46	1	3	1	-	2	7
March	-	16	1	2	2	21	-	1	-	3	6	10
April	1	-	-	-	-	1	-	5	2	-	6	13
May	-	2	-	-	1	3	-	9	1	-	4	14
June	5	9	-	2	2	18	2	11	2	2	14	31
July	3	1	-	3	2	9	1	3	1	4	23	32
August	3	7	5	12	3	30	10	40	14	30	40	134
September	4	15	14	11	1	45	10	3	3	67	18	101
October	-	-	-	-	-	0	-	-	-	-	-	0
November	-	-	-	-	-	0	1	3	3	5	10	22
December	4	-	-	-	4	8	-	4	3	3	9	19
Season												
Dry cool season	14	30	1	19	56	120	4	18	6	14	26	68
Dry warm season	6	11	0	2	3	22	2	25	5	2	24	58
Humid warm season	10	23	19	26	6	84	22	49	21	106	91	289
Year												
2012	-	-	-	-	1	1	1	8	3	-	6	18
2013	-	-	-	-	1	1	1	-	-	1	12	14
2014	5	20	1	11	32	69	1	14	3	3	25	46
2015	-	-	-	-	-	0	1	2	1	2	6	12
2016	6	20	1	3	10	40	1	6	3	13	15	38
2017	17	8	2	28	7	62	18	31	15	84	60	208
2018	4	15	1	-	3	23	1	13	2	1	9	26
2019	3	19	19	5	3	49	5	23	9	12	5	54
2020	9	1	-	11	24	45	7	11	3	8	10	39

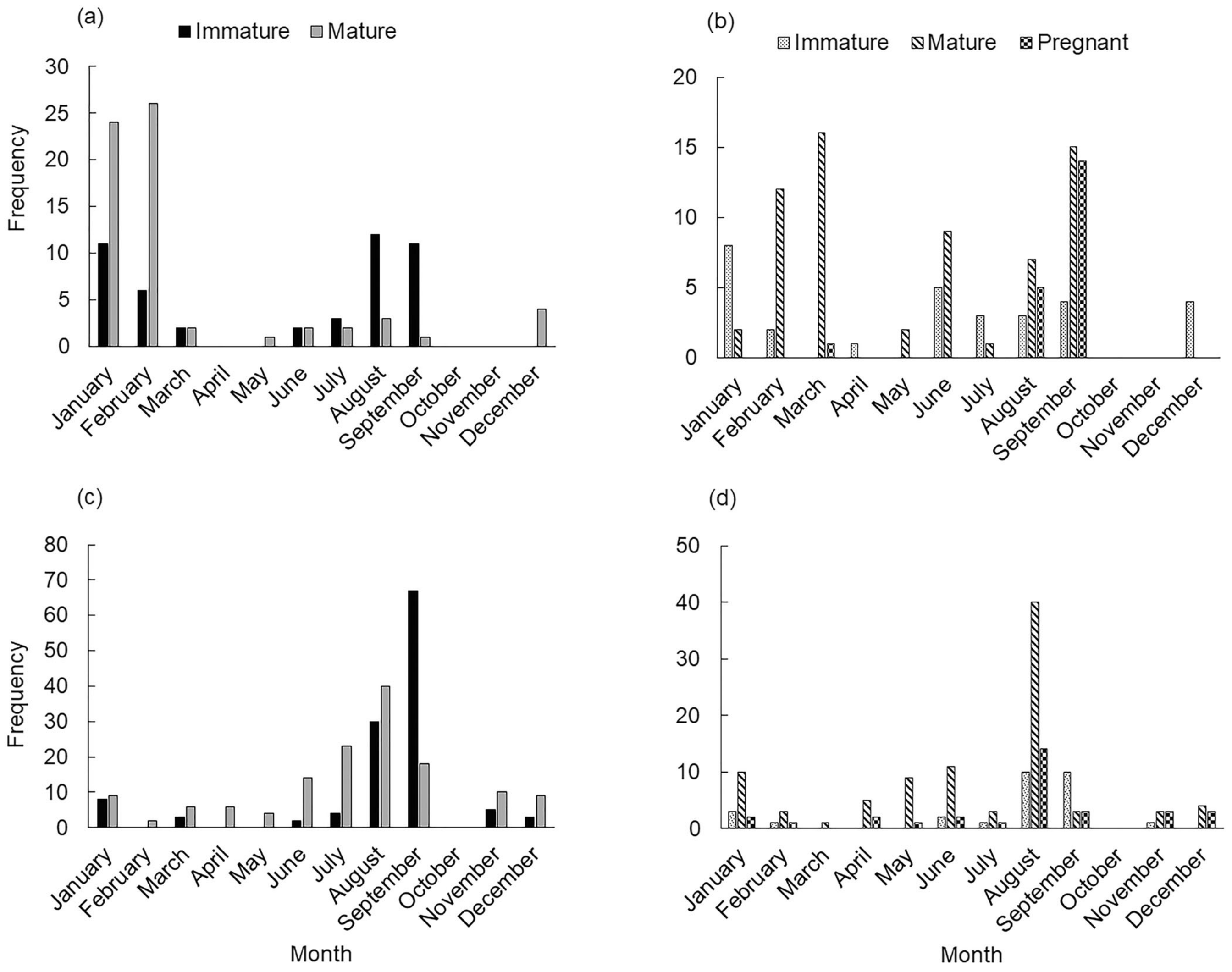


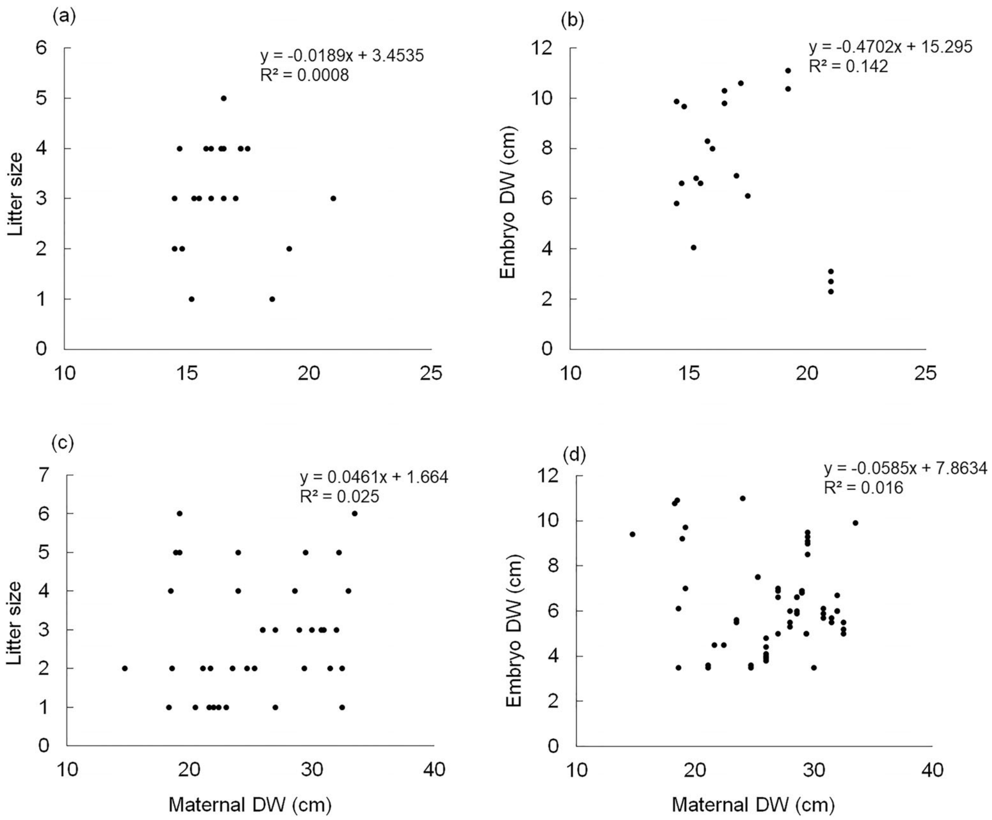
FIGURE 4 Seasonal variation (sum of individuals caught for each particular month during 2012–2020) by maturity stages of (a, $n = 112$) males and (b, $n= 94$) females of *Urobatis maculatus*, and (c, $n = 263$) males and (d, $n = 120$) females of *Urotrygon rogersi* in the southeastern Gulf of California, Mexico.

Fishery-independent shrimp trawl surveys carried out during the closed fishing period for shrimp (March to September) and elasmobranch fisheries (May to July) provided higher availability of data to estimate the reproductive parameters of the analysed round rays. Accurate estimates of abundance and life-history parameters of elasmobranchs are important to propose and implement appropriate management, monitoring, and conservation strategies (Clarke et al., 2018; Harry, 2018; Oliver et al., 2015; White et al., 2019).

In both species, females had a larger maximum *DW* than males, suggesting size sexual dimorphism (Ebert et al., 2008a, 2008b). Similar observations have been made for similar species in the Gulf of California (*U. rogersi*) (Ehemann et al., 2022), in the Gulf of Tehuantepec (southern Pacific coast of Mexico) (Medina-Bautista, 2011), and in the Colombian Pacific (Mejía-Falla et al., 2012; Mejía-Mercado, 2007). Similar information is not available for *U. maculatus* from the few previous studies available (De La Cruz-Agüero et al., 2018; González-González et al., 2020; Ontiveros-Granillo, 2009), where the maximum and minimum sizes of this species in catches are reported without differentiating by sex. However, size sexual dimorphism is common in elasmobranchs (Cortés, 2000; Da Silva et al., 2018; Kyne et al., 2016; Walker, 2005b).

Information on the DW_{50} for *U. maculatus* is presented here for the first time, with the estimated DW_{50} for females being smaller than that of males. In contrast, the DW_{50} of the females of *U. rogersi* was larger than that of males, which coincides with reports from Mejía-Falla et al. (2012). This pattern in many species of elasmobranchs may be in part explained by the need for females to attain a larger size to support pups (Cortés, 2000, 2004; Leung et al., 2023). However, this pattern was not evidenced in *U. maculatus*, probably due to the small size of this species (Pollom et al., 2020), which has also been suggested for some species of rays like the zipper sand skate *Psammobatis extenta* (Garman 1913) and the Venezuela round stingray *Urotrygon*

FIGURE 5 (a) Relationship of maternal disc width (maternal DW) with litter size (number of embryos) for *Urobatis maculatus* (*n* = 21). (b) Relationship of maternal DW with embryo's disc width (embryo DW) for *Urobatis maculatus* (*n* = 19). (c) Relationship of maternal DW with litter size for *Urotrygon rogersi* (*n* = 37). (d) Relationship of maternal DW with embryo DW for *Urotrygon rogersi* (*n*= 59).



venezuelae Schultz 1949 (Acevedo et al., 2015; Braccini & Chiaramonte, 2002).

U. maculatus was also found to mature at a smaller size and present a lower DW_{50}-maximum observed *DW* ratio in comparison to other round rays (Table 4), suggesting an earlier maturation, which could allow it to be productive enough to withstand fishing pressure compared to other species (Pollom et al., 2020; Walker & Heessen, 1996). Larger-bodied and late maturing ray species are more susceptible to overfishing than smaller-bodied, early-maturing ones (Dulvy & Reynolds, 2002; Sguotti et al., 2016; Walker & Hislop, 1998).

In comparison with other studies, both females and males of *U. rogersi* in the present study (fishery-independent shrimp trawl surveys) from the northern TEP matured at larger *DW* than those from the Colombian Pacific (Mejía-Falla et al., 2012) (Table 4). The likely reason for this observation was that in that study the individuals of *U. rogersi* come from artisanal shrimp trawls in shallow waters (≤10 m depth), whereas in the present study, the individuals of this specie were caught at depths of 9–64 m; thus such differences may result in different cohorts of these populations being caught (e.g., Bustamante & Bennett, 2013; Nakano & Seki, 2003). However, other factors could have also influenced these observed differences in the DW_{50} between regions, for example, the sample size (Bellodi et al., 2016; Da Silva et al., 2018), the structure of the data concerning the proportion of mature individuals in each size class (Chen & Paloheimo, 1994; Molina & Cazorla, 2015; Trippel & Harvey, 1991), the criteria for assigning maturity, mainly when performing macroscopic observation of reproductive structures (Martin & Cailliet, 1988; Oviedo-Pérez et al., 2014; Tagliafico et al., 2016) or selectivity of the fishing gear (Estalles et al., 2017; Martins et al., 2018; Tagliafico et al., 2012). The differences could also be related to the existence of subpopulations with different natural variability in maturity (Alkusairy & Saad, 2017; Araújo et al., 2016; Da Silva et al., 2018; Snelson Jr. et al., 2008), caused by different oceanographic and environmental conditions (Girard & Du Buit, 1999; Saadaoui et al., 2015; Yamaguchi et al., 2000), or even fishing pressure (Aranha et al., 2009; Fahmi et al., 2009; Serra-Pereira et al., 2015).

The use of a multi-model approach and inference assures that the observed results are more reliable than those obtained in previous studies (Alvarez-Fuentes et al., 2023; García-Rodríguez et al., 2020; Katsanevakis, 2014). In some species of elasmobranchs, such as Atlantic sharpnose shark *Rhizoprionodon terraenovae* (Richardson, 1836), bat eagle ray *Myliobatis californica* Gill 1865, giant electric ray *Narcine entemedor* Jordan & Starks, 1895, and blotched stingray *Urotrygon chilensis* (Günther, 1872), the multi-model approach and inference have also been used to estimate size at sexual maturity (Alvarez-Fuentes et al., 2023; García-Rodríguez et al., 2020; Oviedo-Pérez et al., 2014; Pérez-Palafox et al., 2022).

U. maculatus and *U. rogersi* mainly showed a higher frequency of mature females and pregnant females during the DCS or the HWS. The same pattern has been reported for other round rays such as Haller's round ray *Urobatis halleri* (Cooper, 1863), dwarf stingray *Urotrygon nana* Miyake & McEachran 1988, and *U. chilensis* in the Gulf of California (Alvarez-Fuentes et al., 2023; Morales-Azpeitia et al., 2011; Nava-Nava, 2013; Rubio-Lozano, 2009; Serrano-Acevedo, 2007).

TABLE 4 Size at sexual maturity of several species of round rays (Urotrygonidae).

Species	*DWfm* (cm)		$DW_{50\%}$ (cm)		*DWmobs* (cm)		$DW_{50\%}$-*DWmobs* ratio (%)		Sampling zone	References
	Females	Males	Females	Males	Females	Males	Females	Males		
Urobatis halleri	14.5	14.5	15	15	31	25	48.4	60	Ventura and San Diego, California	Babel (1967)
U. halleri	17	13	17.9	17.03	26	22	68.8	77.4	Guaymas, Sonora, northern GC	Serrano-Acevedo (2007)
Urobatis maculatus	11.4	8.9	11.8	12.8	30.9	25.8	38.1	49.6	South-eastern GC, Mexico	The present study
Urobatis jamaicensis	-	-	15	15.4	24.1	21.6	62.2	71.3	South-east Florida	Schieber et al. (2023)
Urotrygon chilensis	11.8	13	14.6	15.2	25.5	21.5	57.3	70.7	Teacapán, southeast of the GC	Rubio-Lozano (2009)
U. chilensis	16.5	16	-	-	25.2	28.5	-	-	San Felipe, Puerto Peñasco, Matanchen Bay, northern and southern GC	De la Rosa-Meza (2010)
Urotrygon rogersi	10.5	10.5	12.3	11.8	19.9	17	61.8	69.4	Central-south Pacific coast of Colombia	Mejía-Falla et al. (2012)
U. rogersi	14.7	9.7	18.4	15	33.5	29.5	54.9	50.8	South-eastern GC, Mexico	The present study
Urotrygon aspidura	18	17	-	-	25.2	28.5	-	-	San Felipe, Puerto Peñasco, Matanchen Bay, northern and southern GC	De la Rosa-Meza (2010)
U. aspidura	15	-	-	-	26.5	-	-	-	Pacific coast of Colombia	Torres-Palacios et al. (2019)

Abbreviations: *DW*, disk width; *DWfm*, size at first maturity; $DW_{50\%}$, size at 50% of sexual maturity; *DWmobs*, maximum observed disk width; GC, Gulf of California.

However, to determine the reproductive cycle of analysed species, other analyses are also necessary (e.g., monthly and seasonal variations in the gonadosomatic and hepatosomatic indices, ovulation time, embryonic growth, and parturition dates) (Alvarez-Fuentes et al., 2023; Mejía-Falla et al., 2012), which will be analysed in other studies.

An annual reproductive cycle has been reported for *Urobatis halleri* in California (Babel, 1967; Mull et al., 2010), whereas a biannual reproductive cycle, with ovulation coinciding with parturition, has been described for the yellow stingray *Urobatis jamaicensis* (Cuvier, 1816) in south-east Florida (Schieber et al., 2023). Furthermore, a triannual reproductive cycle, with overlapping ovarian and uterine cycles, has been reported for *U. rogersi* in Colombia (Mejía-Falla et al., 2012), whereas two reproductive periods (a major one during the HWS and the other one during the DCS) has been proposed for *U. chilensis* in the south-eastern Gulf of California (Alvarez-Fuentes et al., 2023), showing the diversity of strategies in these species.

The abundance and distribution patterns of elasmobranchs can be affected by interannual changes in water temperature associated with climatic anomalies such as El Niño Southern Oscillation (ENSO) and its variations between warm (El Niño) and cold (La Niña) conditions (Arnés-Urgellés et al., 2021; Osgood et al., 2021; Ruiz-Barreiro et al., 2019). Further studies are necessary to analyse the impact of these climatic anomalies on the distribution of analysed round rays by maturity stages in the Gulf of California.

In several round rays such as *U. halleri*, *U. jamaicensis*, the small-eyed round stingray *Urotrygon microphthalmum* Delsman 194, *U. chilensis*, and even *U. rogersi* the female size seems to be related to the litter size or the size of the pups (Babel, 1967; Fahy et al., 2007; Mejía-Falla et al., 2012; Rubio-Lozano, 2009; Santander-Neto et al., 2016; Serrano-Acevedo, 2007). However, these relationships were not found for *U. rogersi* and *U. maculatus* in the present study. Aborted embryos of both species were observed in the catches, which could have affected the relationship between the variables analysed.

Both analysed species showed low fecundities, probably related to the aborted embryos observed of both species in the catches (e.g., Mejía-Falla et al., 2012). However, these fecundities were consistent with the range reported for several species of the family Urotrygonidae (one to six embryos) (Acevedo et al., 2015; Alvarez-Fuentes et al., 2023; Babel, 1967; Ehemann et al., 2022; Last et al., 2016). The maximum observed fecundity for *U. rogersi* in the present study was higher than that reported by Mejía-Falla et al. (2012) in Colombia (three embryos). Mejía-Falla et al. (2012) considered 113 embryos aborted, which could have underestimated their fecundity estimates.

Pup abortion has also been reported for this species in La Paz Bay, Baja California Sur, Gulf of California (Ehemann et al., 2022).

Pup abortion or premature birth is common in ray species caught as by-catch, particularly during trawling (Adams et al., 2018; Wosnick et al., 2018a, 2018b). This process of capture-induced parturition causes recruit mortality and reduces maternal survival in elasmobranchs, even if the mature female survives the capture event (Adams et al., 2018; Wosnick et al., 2018a, 2018b). In addition, capture stress suffered by pregnant rays such as southern fiddler ray *Trygonorrhina dumerilii* (Castelnau, 1873) could alter traits and survival (e.g., smaller size, reduced growth, altered burying behavior, reduced boldness, altered swimming behavior) of neonates (Finotto et al., 2021). Therefore, these issues could be investigated in future studies for the analysed species.

Several breeding and nursery areas (e.g., Playa Sur Mazatlan, lagoon complex Santa Maria Bay-Altata, and Teacapan in Sinaloa) in the south-eastern Gulf of California have been reported for some round rays like *U. halleri*, *U. chilensis*, and *U. nana* (Nava-Nava, 2013; Salomón-Aguilar, 2015). Nevertheless, other spatiotemporal analyses are necessary to determine the specific breeding and nursery areas for *U. maculatus* and *U. rogersi* in the studied zone (e.g., Carlisle et al., 2007; Heupel et al., 2007).

A lower abundance of immature individuals in the catches is important to prevent growth overfishing (Akhilesh et al., 2020; Pauly, 1988; Raje & Joshi, 2003). However, the high catch of mature individuals (including pregnant females) could lead to recruitment overfishing (Allen et al., 2013; Walters & Martell, 2004; Woodhams & Harte, 2018), which affects the abundance of elasmobranchs (D'Alberto et al., 2022; Di Lorenzo et al., 2022; Musick et al., 2000). In particular, bottom-trawl fisheries have caused marked declines in the abundance of several ray species (Coll et al., 2013; Dulvy et al., 2014; Dureuil et al., 2018; Winter & Arkhipkin, 2023), including *U. rogersi* (Kyne et al., 2020).

Considering that all stages of maturity were found in the catches from fishery-independent shrimp trawl surveys, ecological risk or demographic assessment analyses are needed to characterize the vulnerability and responses of studied round ray populations to fishing mortality (Barnett et al., 2013; Gallagher et al., 2012; Santana et al., 2020). Other analyses, such as the seasonality of catches, the spatiotemporal distribution, and the reproductive cycle (e.g., seasonal variations in the gonadosomatic and hepatosomatic indices, ovulation time, embryonic growth) of analysed species are needed too. In addition, in future studies it would be important to obtain data from the commercial shrimp fishery to determine its effect on round ray populations, considering the potential advantages of the closed fishing period for the shrimp trawl fishery in the GC (early April to early September) as an indirect protection measure for analysed round rays. Future analyses could also use multiple data sets (both fishery-independent and fishery-dependent data) to improve the estimation of life-history and fishery parameters (Dennis et al., 2015; Kacev et al., 2017).

5 | CONCLUSIONS

Differences in DW_{50} between sexes and between species were found depending on the model used, highlighting the convenience of using a multi-model approach and inference.

Differences in the DW_{50} of *U. rogersi* with previous studies could be due to the existence of subpopulations related to the environmental conditions or fishing pressure, though other factors could be influencing such estimations, such as sampling size, selectivity, depth of capture, as well as the criteria to determine maturity stages. Both analysed species showed low fecundities. However, the early maturity of *U. maculatus* in comparison to other species in the family Urotrygonidae suggests that this species could be less affected than other round rays by fishing pressure.

Future analysis of the depth and seasons influencing the by-catch of round rays is needed. In addition, other studies are needed to determine the abundance of the species in the by-catch from commercial shrimp trawling, and how it may affect the populations of these species over time. Furthermore, it is necessary to determine if the non-fishing period established for the shrimp fishery (early April to early September) could be beneficial for the population of these species.

Our results can help in the development of future management and conservation strategies for the studied species. The estimated DW_{50} for *U. maculatus* and *U. rogersi* presented here could be used as a reference point to establish a minimum size of capture for these species. Although they are not targeted species, round rays are commonly used for bait, fish meal, local consumption (meat), or for sale in local markets, as well as their increasing importance in the aquarium trade (Morales-Saldaña et al., 2022).

AUTHOR CONTRIBUTIONS

Alain García-Rodríguez, Javier Tovar-Ávila, and Felipe Amezcua conceived the research idea. Javier Tovar-Ávila and Felipe Amezcua supervised the research activity. A. Hiromi Arellano-Cuenca and David Rivas-Landa carried out the laboratory work, and together with Darío A. Chávez-Arrenquín, performed fieldwork and data collection. Alain García-Rodríguez and Felipe Amezcua processed and analysed the data. Alain García-Rodríguez wrote the manuscript with input from all co-authors.

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