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Reproductive ecology of the Argus brief squid *Lolliguncula argus* in the coast off Oaxaca, southern Mexican Pacific

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Abstract

Lolliguncula argus is a squid species endemic to the Tropical Eastern Pacific and caught incidentally by the artisanal fishery around Puerto Angel, Oaxaca (Mexico). Due to the low abundance of Argus brief squid, basic aspects of the species' reproductive biology have not been adequately studied. Therefore, in this study, we assess size at maturity (L_{50}), gonad maturation, ovarian development and spawning pattern by means of both histological and oocyte size–frequency analyses. Our results are based on 581 squid specimens: 534 females (11.9–82.4 mm dorsal mantle length, DML) and 47 males (16.0–68.2 mm DML) caught by artisanal fishery from May 2017 to April 2018. The L_{50} was 58.0 mm DML for females and 55.4 mm DML for males. The ovulation pattern in *L. argus* is asynchronous, with multiple-batch spawning in a relatively short period of time (intermittent spawning). *Lolliguncula argus* breed in the coastal waters off Puerto Angel, in the western margin of the Gulf of Tehuantepec, and exhibit gregarious behaviour during spawning events, which is associated with the regional oceanographic conditions. Based on these results, we determine that the opportunistic reproductive strategy of *L. argus* occurs in response to suitable regional environmental conditions.

Introduction

Worldwide squid populations are characterized by individuals living fast and dying young (Rodhouse *et al*., 2014). This life pattern implies short life cycles, high metabolic rates, rapid growth in response to phenotypic plasticity, and marked sensitivity to changing environmental conditions (Jackson & Domeier, 2003; Pecl & Jackson, 2008). In addition, squid and other taxa of cephalopods display different ovulation patterns (Rocha *et al*., 2001) employing highly flexible spawning strategies, determined by the environmental seasonality of each region throughout their distribution range (e.g. Pecl & Jackson, 2008; Lin *et al*., 2018; Golikov *et al*., 2019).

Therefore, the knowledge on the abundance and distribution dynamics has implications in the studies on the ecosystem structure and in squid fishery management (Rodhouse *et al*., 2014; Doubleday & Connell, 2018). Loliginidae (offshore squids) contribute to a significant part (529,000 tonnes) of worldwide squid catches (FAO, 2022). Three loliginid squids are the most frequently caught by artisanal fisheries in the Mexican Pacific: *Lolliguncula diomedeae* Hoyle, 1904, *L. panamensis* Berry, 1911, and *L. argus* Brakoniecki & Roper, 1985 (Jereb *et al*., 2010). However, only *L. diomedeae* and *L. panamensis* are abundant in the bycatch of the artisanal shrimp trawl fleet (Alejo-Plata *et al*., 2001; Arizmendi-Rodríguez *et al*., 2012*a*; Guzmán-Intzin *et al*., 2020). In consequence, these two squid species have been the subject of several biological studies (Sánchez, 2003; Arizmendi-Rodríguez *et al*., 2012*a*; Guzmán-Intzin *et al*., 2020; León-Guzmán *et al*., 2020).

On the other hand, the Argus brief squid (*L. argus*), a squid species endemic to the eastern Pacific (Jereb *et al*., 2010) has been studied mainly in regard to its taxonomy and biogeography, due to its lower abundance in catches (Granados *et al*., 2013; Alejo-Plata *et al*., 2016; Costa *et al*., 2021). Currently, there are no studies addressing the reproductive biology of *L. argus* throughout its distribution range (Supplementary Table S1).

The marked increase in the abundance of *L. argus* from May 2017 to April 2018 in the Puerto Angel, Oaxaca region (southern Mexican Pacific) allowed studies on the reproductive biology of this species to be carried out.

Artisanal fishery is an important commercial activity on the Puerto Angel coast, and is based mostly on trolling lines, surface longlines, driftnets and surface gill nets. In particular, the local cephalopod fishery mostly targets *Octopus hubbsorum* (Alejo-Plata *et al*., 2016), while loliginid squid catch serves for local consumption or is used as bait for sharks and other pelagic fisheries, in conjunction with spoon-fishing nets locally known as 'chacalmata'. This study aims to provide data on the reproductive ecology of *L. argus*, with a focus on ovarian development and spawning patterns by means of both histological and oocyte size–frequency analyses.

Materials and methods

Study area

Puerto Angel lies on the coast of Oaxaca, in the western margin of the Gulf of Tehuantepec (Mexican Pacific). The continental shelf width varies from 106.8 km at the gulf to 17.8 km at Puerto Angel (Figure 1). The climate is characterized by a rainy season from May–October, and a dry season from November–April. During the dry season, strong winds known as 'Tehuanos' that originate in the Gulf of Mexico blow across the Isthmus of Tehuantepec, causing upwellings that increase biological productivity in this area (Trasviña & Barton, 2008), while to the west of Puerto Angel, westerly surface winds are dominant (Reyes-Hernández *et al.*, 2019).

Satellite images clearly show the oceanographic conditions prevalent in the Gulf of Tehuantepec, with high chlorophyll *a* (Chl-a, a proxy of primary production) concentrations and a relatively low sea surface temperature (SST) due to strong vertical and entrainment mixing (Trasviña *et al.*, 1995).

Data on sea surface temperature (SST, 1988–2019; NOAA ER SST V3b, https://psl.noaa.gov/thredds/catalog/Datasets/noaa.ersst/catalog.html), sea surface salinity (SSS, 2011–2015; NASA EOSDIS PO.DAAC, https://podaac.jpl.nasa.gov) and Chl-a concentration (https://marine.copernicus.eu/newsflash/oc-323-153 oceancolour_glo_chl_l4_nrt_observations_009_033) (Supplementary Figure S1) for *L. argus* bycatch were obtained by delimiting polygons around the fishing zone, using MATLAB® version 2006.

Sampling and processing

The squid samples were obtained from artisanal fishing activities carried out from May 2017 to April 2018. However, not all months were sampled due to adverse weather conditions that prevented fishing activities or due to an absence of squid coincident with two hurricanes and one earthquake that occurred in September 2017 in the Gulf of Tehuantepec area. Consequently, our results exclude samples from July–September (Table 1). We captured squid at about 5 km from the coast, using a spoon-fishing net. All the specimens were preserved in ice for transportation to the laboratory, identifying a total of 581 *L. argus* specimens, following the criteria of Brakoniecki & Roper (1985).

The dorsal mantle length (DML) and total weight (W) were measured with a 0.01 mm precision digital calliper and weighing scales to the nearest 0.1 g, respectively. We determined sex by macroscopic observation of the gonads, which we removed and weighted to the nearest 0.01 g. Prior mating was confirmed by the presence of implanted spermatangia on the inner lining of immature female mantle cavity. Maturity stages were determined according to the scale proposed by Juanico (1983), who classifies the squid as follows. Females: (I) Immature with presence of nidamental glands and a small translucent ovary; (II) Maturing with small nidamental glands and a translucent ovary containing small oocytes; (III) Mature with larger nidamental glands, an opaque-yellow ovary, presence of oocytes, and a visible oviduct; (IV) Spawning with presence of swollen and firm nidamental glands, an ovary full of oocytes (occupying half of the posterior mantle cavity), and a full oviduct; and (V) Post-spawning with flaccid or reduced nidamental glands, a flaccid ovary and oviduct with some immature oocytes, and remaining tissue.

The maturation stages for males were as follows. (I) Immature with absence of spermatophores in the spermatophoric sac; (II) Maturing with small, scarce spermatophores and visually distinguishable testis; and (III) Mature with abundant presence of well-developed spermatophores, and larger testis. Because squid males produce spermatangias continuously, it was difficult to discriminate them from spent individuals, thus in the framework of the present study spawning and spent males were pooled together and assigned maturity stage III.

To analyse gonad development, a section of each ovary was fixed in 10% formalin, dehydrated and cleared with citriSol™, and embedded in paraplast, to cut them in serial sections 7 µm thick using a Leica RM2145® manual rotary microtome (Leica Biosystems). Each section was stained following the haematoxylin-eosin procedure (Bancroft *et al.*, 1996). The gonads were examined based on the oogenesis process outlined by Melo & Sauer (1999); an evidence of

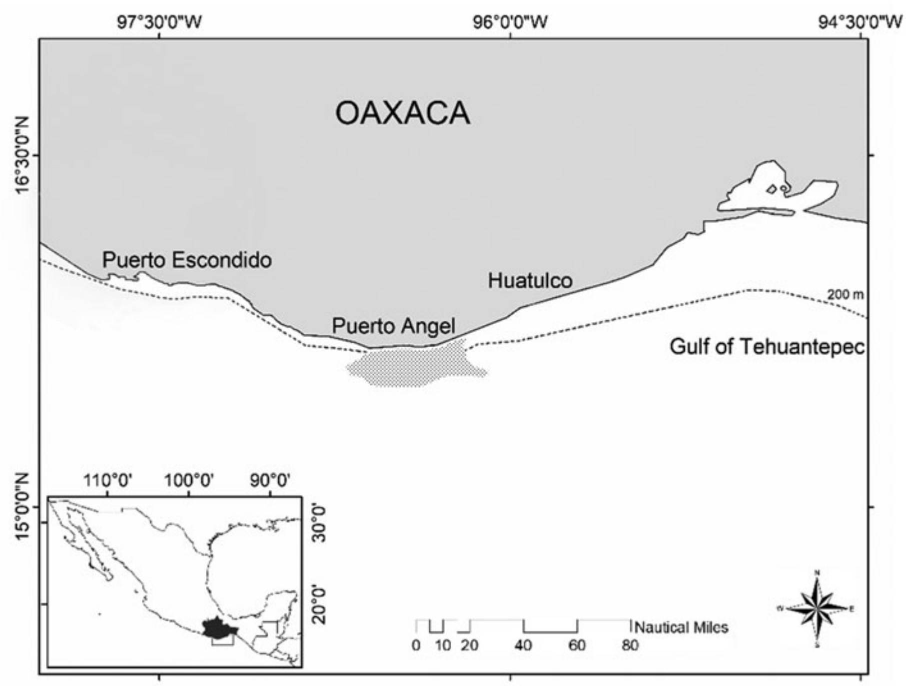

Fig. 1. Study area. Dotted polygon represents artisanal fishing area in Puerto Angel Oaxaca, southern Mexican Pacific.

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Table 1. Number of females and males of *Lolliguncula argus* by month caught in Puerto Angel, Oaxaca, Mexico

Year	Month	Frequency		Sex-ratio	
		Females	Males	(F:M)	χ^2
2017	May	202	25	8:1	$P < 0.05$
	June	19	12	1.6:1	$P > 0.05$
	July	[a]–	[a]	–	–
	August	[b]	[b]	–	–
	September	[b]	[b]	–	–
	October	126	10	12.6:1	$P < 0.05$
	November	76	–	–	–
	December	24	–	–	–
2018	January	[a]	[a]	–	–
	February	12	–	–	–
	March	13	–	–	–
	April	62	–	–	–
	Total	534	47		

[a]Samplings with no catches.
[b]Artisanal fishing activities were very limited.

ovulation was verified by observing the integrity of the surrounding follicles (Melo & Sauer, 2007).

Ovaries and oviducts were removed from 20 female specimens at different maturity stages (III, IV and V). Oocytes were isolated and counted in the three ovary subsamples (each weighing 0.05–0.07 g, measured to the nearest 0.01 mg), damaged oocytes were discarded. The larger diameter of each oocyte was recorded using a Zeiss® stereo microscope equipped with a digital camera and software for image analysis (Zen 2.3). The major axis length was recorded.

Data analysis

A χ^2 test ($P = 0.05$) with Yates's correction was used to determine whether the sex ratio by month deviated from 1:1 (Zar, 1999). The gonadosomatic index (GSI) was estimated following the equation $GSI = Wg/W \times 100$, where Wg is the weight of the gonad and W the total weight of the squid. Data were tested for normality with the Shapiro–Wilk test. Since the data did not satisfy the normality assumption, the monthly variations were analysed using the non-parametric Kruskal–Wallis test (Zar, 1999).

The length at which 50% of all specimens were sexually mature (L_{50}) was estimated for males and females separately using a logistic function and applying maximum likelihood (Haddon, 2001). The DML – (W) relationship was used to convert L_{50} to W_{50}. All statistical analyses were carried out using the software Statistica v.7.0.

Results

Maturation and reproduction

A total of 581 *L. argus* individuals were collected during the nine months of sampling: 534 females (11.9–82.4 mm DML) and 47 males (16.0–68.2 mm DML). Females were clearly predominant ($P < 0.05$), the sex ratio was lower in June (1.5F: 1M, $\chi^2 = 1.16$, $P > 0.05$) (Table 1).

A total of 50.5% of examined females were at mature (III) and spawning (IV) stages, and 28.1% were post-spawning (V) (Table 2, Figure 2). The monthly proportions of maturity stages showed high reproductive activity from April–June and from October–December (Figure 2), coinciding with higher GSI values (Figure 3A, B); 70.2% of mature females showed spermatangia attached to the inner wall of the mantle cavity. Spawning females were present throughout the entire sampling period, with peaks of spawning activity in February and March, and from October–December; post-spawning females (V) were found throughout the entire sampling period (Figure 3A).

The sexual maturity stage of females was not determined by specimen size. Nonetheless, females larger than 46.0 mm DML were starting to become sexually mature, while those at 50.0 mm DML had mature oocytes.

GSI differed significantly between squids at different stages of maturity ($F(4, 815) = 248.6$, $P < 0.05$). The monthly GSI values of females also exhibited significant differences ($H(8, 581) = 410.67$, $P < 0.01$) (Figure 3B).

Table 2. Body size in females *Lolliguncula argus* off Puerto Angel, Oaxaca, Mexico

Maturity stages	N	Mantle length (ML, mm)	Mean ± SD	Body weight (W, g)	Mean ± SD
I	42	11.91–34.57	25.86 ± 10.72	1.0–3.0	1.3 ± 0.46
II	72	16–49	39.03 ± 18.99	1.0–5.0	2.7 ± 1.15
III	216	30–78.4	57.23 ± 11.35	1.9–16.0	6.9 ± 3.18
IV	54	46.5–82.4	69.23 ± 30.30	5.0–16.7	11.5 ± 2.87
V	150	31.8–72.3	62.04 ± 29.12	4.8–17.1	9.6 ± 1.46

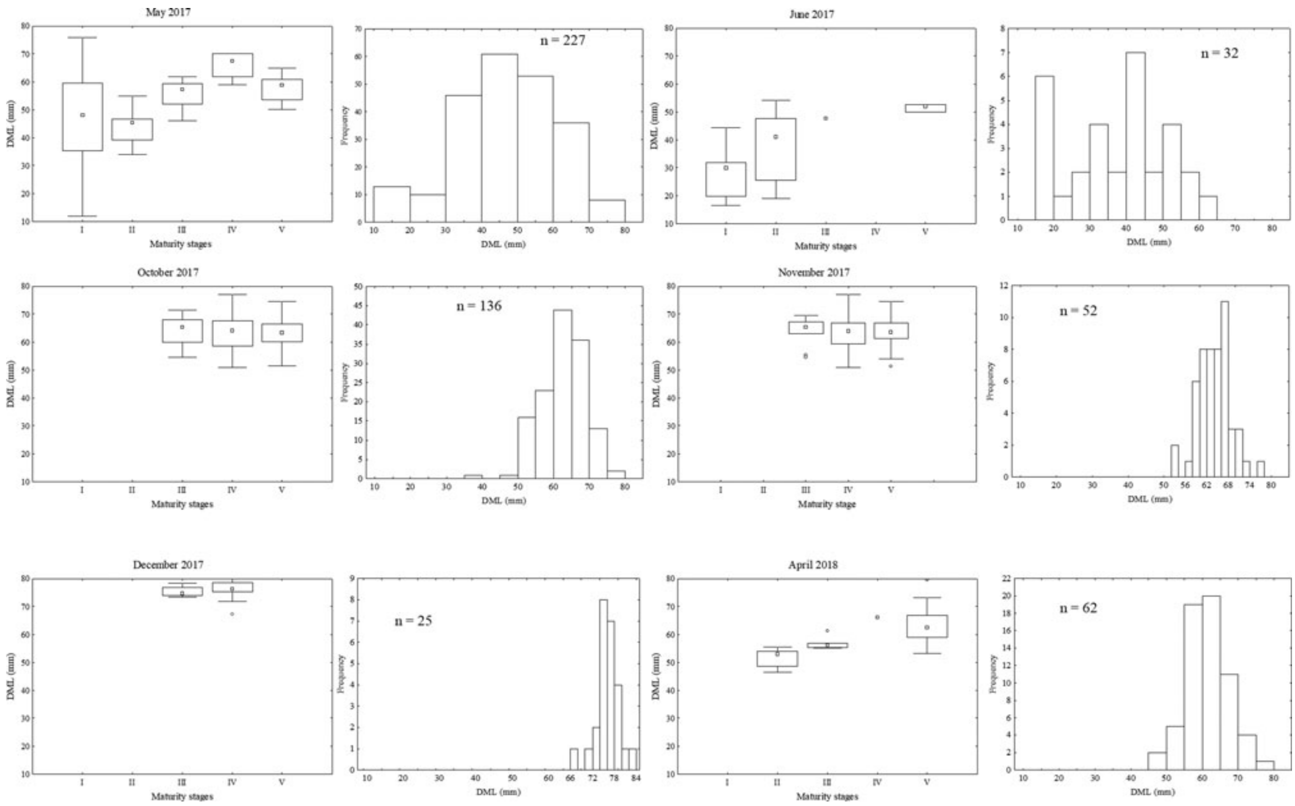

Fig. 2. Length-frequencies by month (right) and maturity stages (left) for females *Lolliguncula argus* sampled from the Puerto Angel, Oaxaca, May 2017 to April 2018.

Immature males (8.5%) were present in May and June, with a GSI value of 3.3–5.0. The monthly proportions of maturity stages showed high spawning activity in May and June (68.2%) and October (23.3%), with GSI values of 4.0–10 and 3.5–7.8, respectively.

The estimated size at sexual maturity (L_{50}) was 58.0 mm DML (95% confidence interval, CI) for females and 55.4 mm DML (95% CI) for males. The estimated W_{50} was 7.12 g for females and 5.46 g for males (Figure 4). Females mature at lengths ranging from 46.0–70.0 mm DML, and males mature at 50.0–65.0 mm DML. Two peaks of spawning were observed from May to June and in October (Figures 2 and 3).

Oocyte development and spawning

As oocyte maturation progresses, the ovary continues producing new primary oocytes (Figure 5A, B). In maturity stages IV and V, oogonia (0.08 mm), previtellogenic oocytes (1.2–1.55 mm), vitellogenic oocytes (1.55–2.9 mm), postvitellogenic oocytes (2.9–3.6 mm in diameter), and postovulatory follicles were found (Figure 5C–E). During these ovarian phases, oocytes between 2.9 and 3.6 mm in diameter fill the oviducts, indicating the presence of pre-spawning females.

Gonad maturation was determined to show a pattern of group-synchronous ovulation, due to the predominance of small oocytes in maturity stages III and IV and the clear presence of batches (Figure 6). Morphologically and quantitatively (diameter) differentiated oocytes were observed in the ovary of *L. argus* at intermittent spawning events coincident with low temperature values (Figure 3A).

Discussion

The seasonal distribution of the data collected over nine sampling months is the result of a higher proportion of mature squids in

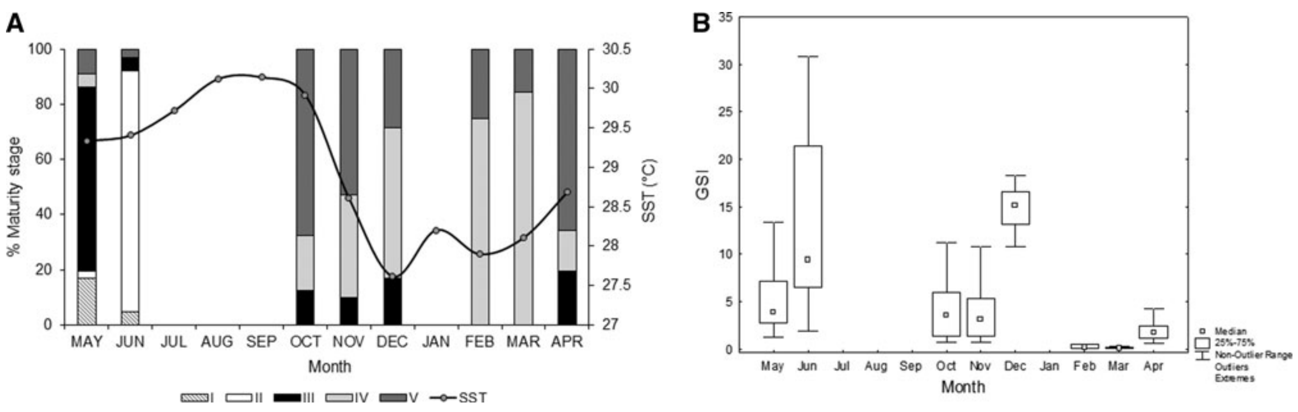

Fig. 3. (A) Maturity classification of female *Lolliguncula argus* and sea surface temperature (SST) in geographic locations where *L. argus* specimens were caught; (B) Box plots of gonadosomatic indices (GSI). (I) immature, (II) maturing, (III) mature, (IV) spawning and (V) post-spawning.

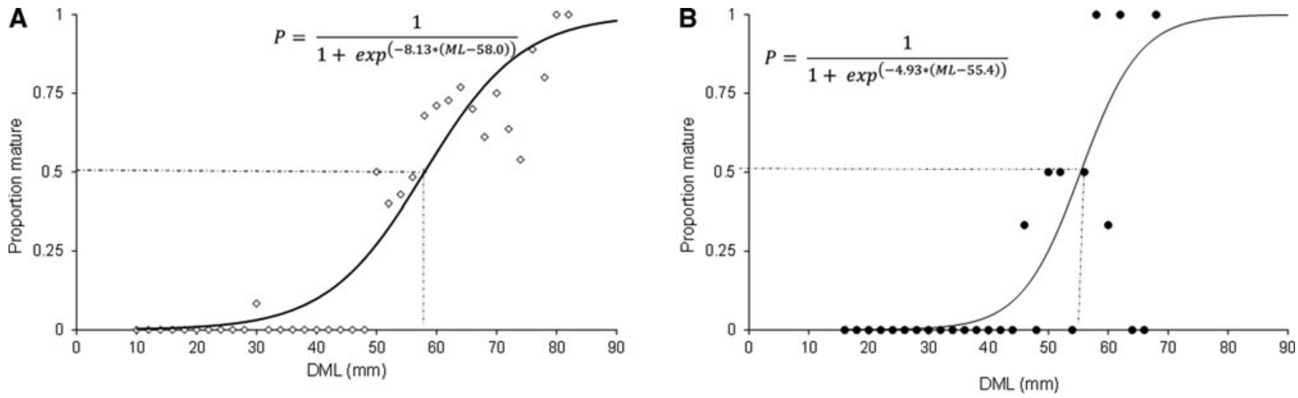

Fig. 4. *Lolliguncula argus* sampled from the Puerto Angel, Oaxaca. Proportion of mature specimens by length. (A) females, (B) males. Fitted curve illustrates the optima logistic maturation ogive fitted by maximum likelihood.

May–June and October; meanwhile the presence of small and immature squids from May–June suggests a first pulse of recruitment. The absence of juveniles (<10.0 mm DML) in the samples can be interpreted as a result of a low abundance of this size group; however, it is also likely to be due to the selectivity of the fishing gear used. One additional factor may be logistical limitations in analysing incidental catches of non-target species.

The maximum mantle length values for *L. argus* females (82 mm DML) and males (68.0 mm DML) reported here are larger than those of the squid species from the Gulf of California (females 39 mm DML and males 30 mm DML) (Jereb *et al.*, 2010). These differences could be explained by the low number of individuals previously recorded, as well as the fishing gear and depth of the catch; indeed, size and maturity of loliginids varies according to depth, temperature and dissolved oxygen (Rodrigues & Gasalla, 2008; Arizmendi-Rodríguez *et al.*, 2012*b*; Guzmán-Intzin *et al.*, 2020; León-Guzmán *et al.*, 2020).

Sexual size dimorphism is well known in loliginids (Rodrigues & Gasalla, 2008). Males of *Loligo* spp. exhibit larger sizes than females (Perez *et al.*, 2002; Olyott *et al.*, 2006; Moreno *et al.*, 2007; Rodrigues & Gasalla, 2008), while females of *L. argus* (this study) and the other species of the genus *Lolliguncula* show larger maximum sizes than males, *L. brevis* (Martins & Perez, 2007), *L. panamensis* (Arizmendi-Rodríguez *et al.*, 2012*b*; Guzmán-Intzin *et al.*, 2020) and *L. diomedeae* (León-Guzmán *et al.*, 2020).

According to Pecl & Jackson (2008), coastal loliginid squids, such as *L. argus*, can tolerate and even thrive in warm sea temperatures, increasing their body sizes, and various species do show increased growth rates in warm waters. However, as evident here, populations of the same species show greater growth rates in tropical waters than in temperate waters.

During recent decades, the catch of squid as well as other cephalopods has increased globally, perhaps in response to fish stock depletion and environmental changes (Doubleday *et al.*, 2016). This could explain the marked increase in abundance of *L. argus* during the most recent sampling events (two years) un the Puerto Ángel coast.

Loliginid squids are characterized by inshore spawning migrations (Sauer *et al.*, 1992; Hanlon & Messenger, 1996). The predominance of Argus brief squid females during the sampling period ($P < 0.05$) showed a close relationship with their reproductive behaviour. The low abundance of males has been associated with a natural death process after mating (Hanlon & Messenger, 1996). Therefore, the presence of mature males could indicate aggregations for mating. Various studies have demonstrated a close relationship between loliginid spawning aggregations and a male-biased sex ratio (Jackson & Forsythe, 2002; Perez *et al.*, 2002; Arizmendi-Rodríguez *et al.*, 2012*a*), whereas other loliginids (e.g. *L. vulgaris*) aggregate by sex in the vicinity of spawning areas (Sauer *et al.*, 1992). Due to the limited number of male specimens in this study, the size differences reported here need to be corroborated by studies with a larger sample size.

The presence of spermatangium patches within the mantle cavity in immature females indicates mating at early stages, possibly for ensure sufficient availability of sperm, as mating encounters between the sexes may be limited. Similar behaviour has been reported for other cephalopods such as *Loligo plei* (Rodrigues & Gasalla, 2008), *Heteroteuthis dispar* (Hoving *et al.*, 2008), *Bathyteuthis berryi* (Bush *et al.*, 2012), *Octopus vulgaris* (Cuccu *et al.*, 2013), *O. hubbsorum* (Alejo-Plata & Gómez-Márquez, 2015) and *Argonauta nouryi* (Alejo-Plata & Martínez, 2020). In these species, the spermatangia is retained in the mantle cavity until the spawning event.

To obtain higher precision in size-at-maturity evaluations, the results presented here were validated by means of a histological review of the ovaries, reducing the possibility of including immature and post-spawning females (e.g. DeMartini *et al.*, 2000). The histological identification of the most advanced group of oocytes is an accurate indicator of the temporal and spatial spawning patterns of females (Melo & Sauer, 1999). Some immature Argus brief squid females exhibited sizes as large as fully mature female specimens, suggesting maturation events at different times and body sizes, while also indicating a bimodal distribution of adult size frequencies during the maturation phase.

The results of our study suggest that spawning and post-spawning stages in the Argus brief squid are characterized by oocyte growth in batches that include the presence of postovulatory follicles (POF) and atretic follicles, in addition to previtellogenic and vitellogenic oocytes. Meanwhile, the ovaries of mature females contained a range of oocyte sizes with a predominance of small oocytes throughout sexual maturation. The fact that some mature oocytes were found in mature and spawning females suggests that *L. argus* spawned in several batches within a relatively short period of time (intermittent spawning), as defined by Rocha *et al.* (2001).

The presence of different types of oocytes in the ovary of *L. argus* suggests that this species exhibits synchronous oocyte development by groups. This spawning pattern is common to other loliginid species with tropical distribution such as *Loligo reynaudii* (Sauer *et al.*, 2000), *L. gahi* (Laptikhovsky & Arkhipkin, 2001), *L. panamensis* (Arizmendi-Rodríguez *et al.*, 2012*a*), *L. brevis* (Perez & Zaleski, 2013) and *L. diomedeae* (León-Guzmán *et al.*, 2020). The results reported here suggest that the occurrence of spawning and post-spawning squids may be related to low SST conditions occurring from October–March in the coast off Puerto Angel,

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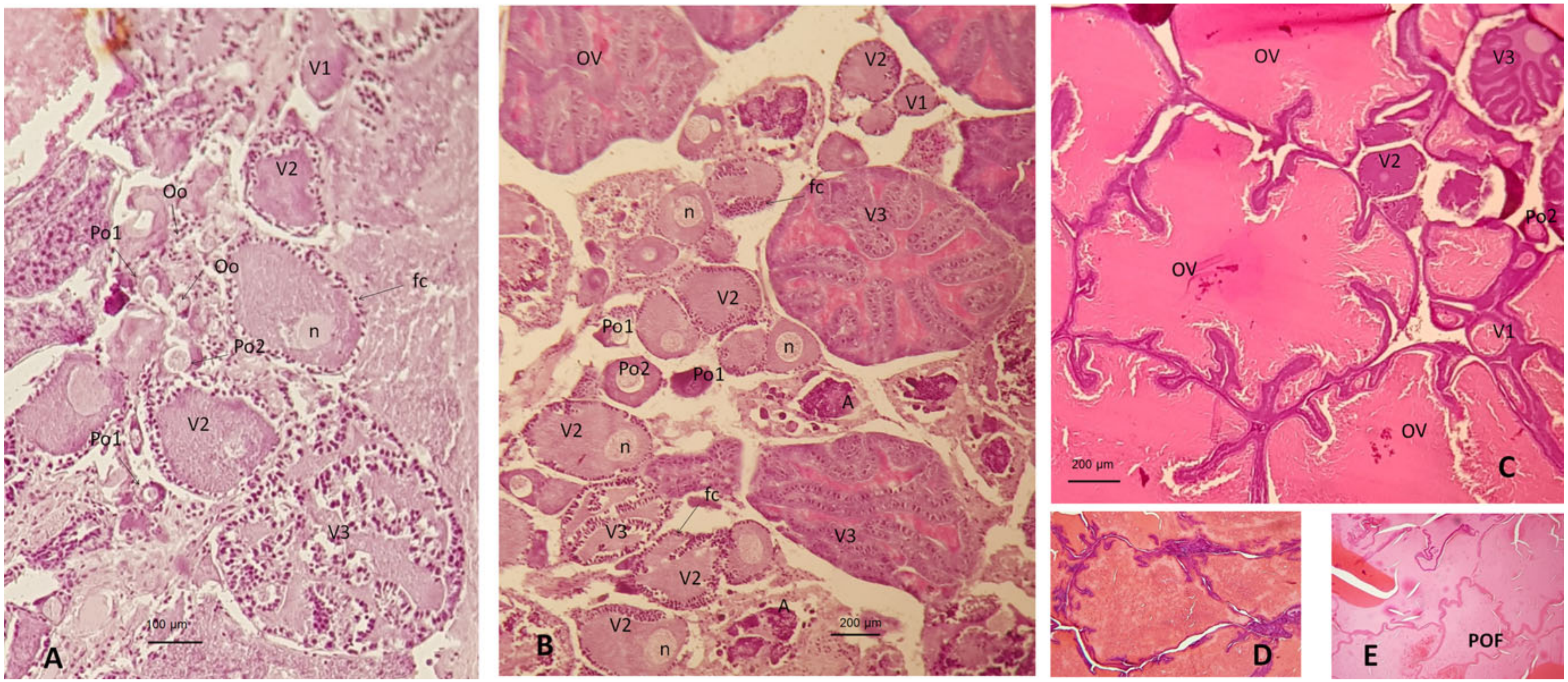

Fig. 5. Gonad development in female *Lolliguncula argus* sampled from the Puerto Angel, Oaxaca. (A) Primary growth (Previtellogenesis), Oo, oogonia; previtellogenic oocytes, Po1, Po2; (B) Secondary growth (Vitellogenesis), early vitellogenic oocytes, V1; late vitellogenic oocytes, V2 and V3; (C) Tertiary growth (Postvitellogenesis), ovulate oocytes, OV; (D) Early stage expulsion of follicle; (E) Postspawned, postovulatory follicle POF. A, atresia, fc, follicle cell, n, nucleus. Paraffin sections 7 µm, haematoxylin and eosin stain.

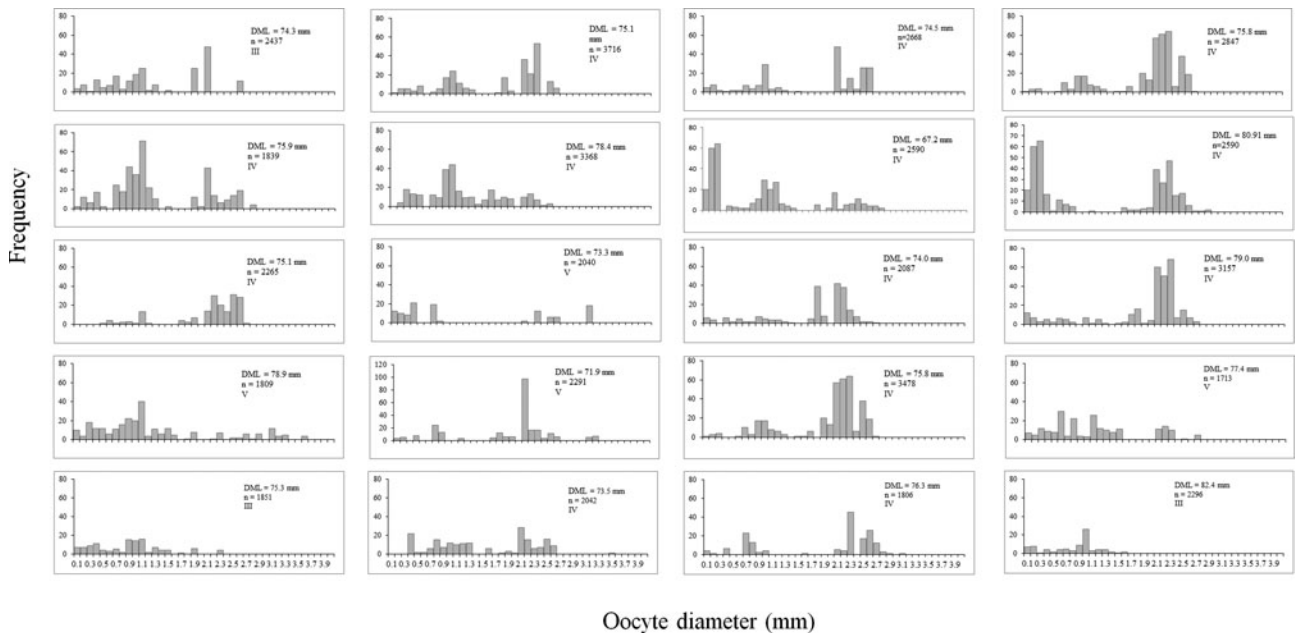

Fig. 6. *Lolliguncula argus* females. Size-frequency distribution of whole oocytes in ovaries of 20 females (Stages III, IV and V).

when coastal currents are mainly south-eastward (Reyes-Hernández *et al*., 2019). Squid are highly sensitive to temperature and therefore can be viewed 'probably as climate change indicators' (Pecl & Jackson, 2008). To advance knowledge about *L. argus* and other tropical squid species, longer and simultaneous physical and biological time series collections are required.

Squid sampled directly from the catches of artisanal fisheries were exceptionally useful for establishing an understanding of several key aspects of the reproductive biology of *L. argus*, including important information about their spawning patterns. The presence of mature and spawning females suggests that this species extensively uses the coast of Puerto Angel as a reproductive area, exhibiting gregarious behaviour during spawning activity. Based on these results, the spawning behaviour of *L. argus* may constitute an opportunistic reproductive strategy in which individuals spawn at different times when the environment provides suitable conditions for doing so. The reproductive strategy reported here may be a response to suitable regional oceanographic conditions.

Supplementary material. The supplementary material for this article can be found at https://doi.org/10.1017/S0025315422000984

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