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Research Article

First record and biological data of juvenile *Dosidicus gigas* in the Gulf of Tehuantepec, eastern Central Pacific Ocean

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ABSTRACT. The Humboldt squid, *Dosidicus gigas* D'Orbigny, 1835, is endemic to the eastern Pacific. Knowledge of its biology is largely limited to commercial-sized adults, leaving juveniles scarcely documented. This study provides the first reference on the distribution, sex ratio, and feeding of juvenile *D. gigas* in the Gulf of Tehuantepec (GT). The study was based on 403 juveniles collected in April 2022 aboard the RV Dr. Jorge Carranza Fraser (IMIPAS). The field sampling consisted of 50 fishing hauls, 12 of which were positive for juveniles of *D. gigas*. We identified three size classes: I (11.0-29.9 mm mantle length, ML, undifferentiated); II (30-59.9 mm); and III (60-99.9 mm). Females >60 mm showed positive allometric growth. Individuals of both sexes and across size classes II and III consumed all four prey groups, with planktonic crustaceans dominating their diet. Fish consumption increased in size-class III. Significant differences in prey frequency of occurrence among the three size classes indicate an ontogenetic dietary shift, with prey selection changing significantly as size increases. Our results also indicate that juvenile *D. gigas* are widely distributed in the oceanic zone west of the GT, where they feed mainly on euphausiids, mesopelagic fishes, and small squid. Therefore, productivity pulses associated with the Tehuano winds (mainly from November to April) and the formation of mesoscale eddies in the GT may provide favorable environmental conditions for juvenile *D. gigas*. The occurrence reported here may be related to this upwelling. Despite limitations due to the lack of year-round data, this study provides new insights into the biology of juvenile *D. gigas* in the GT.

Keywords: jumbo squid; squid ecology; life history; feeding; Gulf of Tehuantepec; Mexico

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INTRODUCTION

The Humboldt (jumbo) squid, *Dosidicus gigas*, is a cephalopod species endemic to the eastern Pacific Ocean (Jereb et al. 2010), which occurs with high abundance in the most productive areas of the California and Peru Current Systems (Nigmatullin et al. 2001), and the Costa Rica Dome (Ichii et al. 2002, Waluda & Rodhouse 2006, Liu et al. 2010). Through these current systems, *D. gigas* makes long migrations from the Gulf of Alaska to Chile (Jereb et al. 2010), as well as diel vertical migrations into deep waters with minimum dissolved oxygen conditions (Gilly et al. 2006), and is a part-time resident of the permanent oxygen minimum zone (OMZ) in the eastern tropical Pacific (Trübenbach et al. 2013).

D. gigas is a short-lived species that exhibits high growth rates, high fertility, as well as a variable sex ratio (Tafur et al. 2010, Liu et al. 2013, Chen et al. 2014). Moreover, *D. gigas* plays a dual ecological role as prey and predator, exhibiting high voracity and a broad-spectrum diet (Bazzino et al. 2010). In addition, because of its high economic value, this species is an important fishing target in the waters of Peru, Chile, Ecuador, and the Gulf of California, and it serves as prey for larger pelagic fishes (Ibáñez et al. 2008, Keyl et al. 2008, Csirke et al. 2015).

Because *D. gigas* is highly sensitive to environmental factors, fluctuations in habitat conditions can rapidly shift its population density and spatial distribution (Waluda et al. 2006, Liu et al. 2010). During the juvenile phase, temperature influences *D. gigas* development in two ways: early maturation (small-medium specimens) or late maturation (large specimens) (Arkhipkin et al. 2015), possibly in response to the oceanographic variability that characterizes the eastern Pacific (Sánchez et al. 2016). In addition, juvenile squid appear to respond to the environmental impact caused by the El Niño Southern Oscillation (ENSO) with an alternative life path in which the gigantism commonly observed in coastal habitats of the continental shelf changes to small-sized forms due to an accelerated reproductive behavior in an offshore environment (Hoving et al. 2013).

Currently, information on the biology and population dynamics of *D. gigas* is mainly focused on commercial-sized adult specimens (e.g. Keyl et al. 2008, Markaida et al. 2008, Chen et al. 2014, Csirke et al. 2015). Still, it is scarcely documented for juvenile specimens <100 mm mantle length (ML). Most of this information refers to its condition as prey for juvenile fishes (including small tuna and mahi-mahi), other squid species, and sea birds (Nigmatullin et al. 2001). Juvenile *D. gigas* also exhibit complex population dynamics and adapt to fluctuating environmental conditions, reflected in patterns of sexual segregation in feeding habits (Gong et al. 2018). These highlights underscore the importance of studying this phase of *Dosidicus* development.

Information on their distribution patterns and life-history traits remains poorly known. Therefore, to supplement existing knowledge, this study presents the first records of juvenile *D. gigas* along the Gulf of Tehuantepec (GT), based on acoustic-trawl surveys conducted in spring 2022. It provides data on biological parameters (length, weight, and sex), diet, and mantle length-weight relationship (MLWR). We hypothesized that juvenile *D. gigas* in the GT are driven by the region's high primary productivity and thermal structure, which provide an optimal habitat for rapid growth and opportunistic feeding on local prey assemblages.

MATERIALS AND METHODS

Study area

The GT is located in the Mexican South Pacific (13°30'-16°30'N, 92°30'-96°00'W; Fig. 1), in a coastal region characterized by a continental shelf that is wider to the east and narrower to the west (Barton et al. 2009). The climate includes a rainy season from May to October, characterized by tropical storm and hurricane formation, and a dry season from November to April. During the dry season, upwelling and entrainment occur due to strong jets of wind called "Tehuanos" that come from the Gulf of Mexico and blow across the Isthmus of Tehuantepec (Trasviña & Barton 2008).

The GT is a highly productive area, with seasonal changes in primary and secondary productivity driven by the region's climatic and oceanographic conditions (Lara-Lara et al. 1998). Climate varies during the rainy and "Tehuanos" seasons, generating mesoscale processes that affect biological productivity and marine biodiversity (Gallegos-García & Barberán-Falcón 1998). In addition to changes due to the occurrence of climatic events such as northerly winds, tropical storms, and ENSO, as well as the circulation of large-scale currents influenced by the trade wind system and the intertropical convergence zone, which also impact the GT region (Gallegos-García & Barberán-Falcón 1998, Monreal-Gómez & Salas de León 1998).

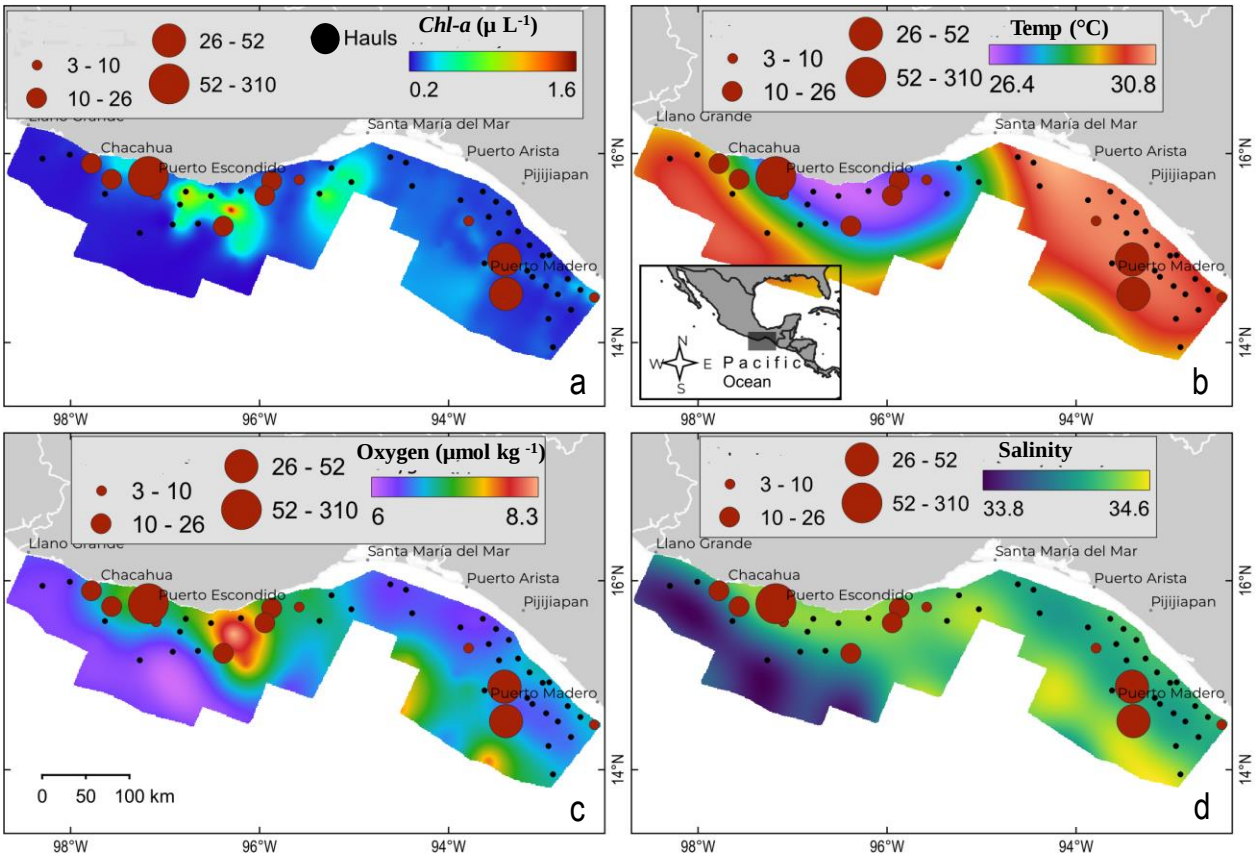


Figure 1. Study area along the Gulf of Tehuantepec. Fishing hauls (black circles) and abundance of *Dosidicus gigas* (red circles). The background shading represents *in situ* environmental conditions at 100 m depth. a) Fluorescence, b) temperature, c) dissolved oxygen, and d) salinity. Oceanographic conditions previously described for the study area by Alejo-Plata et al. (2023) and Vallarta-Zárate et al. (2023).

Sampling and processing

Acoustic, biological, and oceanographic data were collected during one research survey conducted by IMIPAS in April 2022 to identify the presence of fishing resources in the GT that could be potentially usable (Fishing Permit No. PPF/DGOPA-0004/22) (Table S1). Acoustic-trawl sampling was performed along parallel transects spaced 15 nm apart in the Oaxaca region and 10 nm apart along the coast of Chiapas, aboard the Mexican research vessel Dr. Jorge Carranza Fraser (Fig. 1). The survey area was further expanded offshore when additional small pelagic fish (SPF) target species were detected. We collected acoustic data using a calibrated EK60 multi-frequency echosounder (SIMRAD, Kongsberg Maritime AS, Horten, Norway), equipped with five split-beam transducers (18, 38, 70, 120 and 200 kHz).

Field sampling consisted of 50 fishing hauls with a midwater net composed of four equal caps (top and bottom footrope length: 48.17 m [158 ft]). A 25/25 design wing trawl with decreasing mesh sizes toward the wingspan, starting from 160 to 5 cm, made of multifilament nylon and ultra-high molecular weight polyethylene. The net uses a flake or bag provided inside, made of 17 mm knotless Raschel-type nylon fabric. The net was towed at an average speed of 6.5 km h^{-1} (3.5 kn) for 45 min, at an average depth of 20 m.

Twelve fishing hauls were positive for juveniles of *D. gigas*. The specimens were mainly collected in the GT's oceanic zone at 20 m depth. According to the oceanographic conditions previously described for the study area by Alejo-Plata et al. (2023) and Vallarta-Zárate et al. (2023), the sampling stations were located within the mixed layer, with dissolved oxygen concentrations varying between 200 and 237 µmol kg^{-1}, with a maximum chlorophyll-*a* of 5.5 µg L^{-1} (Fig. 1).

Once the catch was deposited on the ship's deck, the juvenile specimens of *D. gigas* were placed in plastic

bags to keep them frozen and transport them to the laboratory. Key anatomical features used for identification include a pair of internal and ocular photophores. Additionally, the type of union of the cartilaginous clasps is a key feature (Okutani 1974, Jereb & Roper 2010), which is fitted/fused in this species and does not tear. All squid specimens were measured for dorsal ML (to the nearest 0.1 mm) and weighed (TW, to the nearest 0.01 g), and squids were sexed by macroscopic examination of fresh gonads, following the description of Lipínski & Underhill (1995). Immature females exhibited small, transparent, band-like nidamental glands, while other structures were not visible to the naked eye. Immature males had thin, translucent testes and a developing spermatophoric complex without visible spermatophores.

Size-classes and mantle length-weight relationship (MLWR)

Juvenile *D. gigas* were grouped into three size classes based on ML following Nigmatullin et al. (2001): class I (11.0-29.9 mm ML), class II (30.0-59.9 mm ML), and class III (60.0-99.9 mm ML). We estimated the MLWR by sex and size class using the potential equation $W = aML^b$, where a is the intercept of the regression model, and b is the allometric coefficient (Ricker 1973). We tested the estimated value of parameter b using a t-Student test to determine whether growth was isometric or allometric (Zar 1999).

Feeding

A total of 365 stomachs were examined using the visual stomach fullness index (FI), as follows: (0) empty, (1) scarce remains, (2) half full, (3) almost full, and (4) full (Breiby & Jobling 1985). Stomach contents were filtered through a 500 µm mesh sieve to retain prey remains of juvenile *D. gigas*. We identified food items to the maximum taxonomic level, then sorted and counted them by taxon. Crustaceans were recognized by exoskeletons, appendages and eyes; fish by the presence of scales, otoliths, vertebrae, spines and jaw bones; and cephalopods by the presence of beaks, gladius, lenses, suckers, statolith and arm pieces (e.g. Clarke 1986, Hendrickx 1995, Harvey et al. 2000). The relative frequency of occurrence (%FO) of the prey items was calculated as the percentage of squids that fed on a given prey, relative to all squid stomachs examined (Cailliet 1977). Cannibalism was determined following Ibarra-Garcia et al. (2014) and based on its %FO. Stomach content weight (SCW) and fullness weight index [FWI = (SCW × 100) / (W - SCW)] were also calculated (Rasero et al. 1996).

Data analysis

We assessed differences in ML between groups using a Kruskal-Wallis test, followed by Dunn's *post-hoc* test for pairwise comparisons. We set statistical significance at $P < 0.05$. We used a chi-squared (X^2) test to determine whether the sex ratio by size group deviated from 1:1.

Differences in FWI between size classes were determined by applying a nonparametric Kruskal-Wallis ANOVA (Zar 1999). We compared FO of common prey items between sizes using a contingency table and by estimating G statistics (Crow 1981). This statistic has an X^2 distribution.

$$G = 2 \sum_i O_{ij} \; ln \; \frac{O_i}{E_i}$$

where Oij is the FO of prey of the I category ingested by j squid category, Oi is the FO of prey of the i category ingested by all squids, Ei is the expected value. Statistical analyses were conducted using the Statistica 6.0 software package (StatSoft).

A voucher sample of *D. gigas* specimens used in this study was housed in the Mexican Pacific Collection of Cephalopods (MHNUMAR-CEPHA 5102-505) of the Universidad del Mar (UMAR), Puerto Ángel, Oaxaca, Mexico.

RESULTS

Size classes, sex ratio, and mantle length-weight relationship (MLWR)

Four hundred and four juvenile individuals were examined, consisting of 13 undifferentiated individuals (20-25.0 mm ML), 167 females (30 to 93 mm ML), and 223 males (26-97 mm ML). Squid larger than 30 mm ML were the most abundant in the total catch (Fig. 2). The squids were grouped into three different size-classes: class I (11.0-29.9 mm ML; undifferentiated); class II (30.0-59.9 mm ML) with a sex ratio of 1F:1.3M ($P > 0.05$), and class III (60.0-99.9 mm ML) with a sex-ratio of 1F:1.4M ($P < 0.05$) (Table 1). A Kruskal-Wallis test showed a significant difference between groups, $H(2) = 37.64$, $P < 0.01$. *Post-hoc* comparisons using Dunn's test with Bonferroni correction showed no significant difference between females and males ($P > 0.05$), while the undifferentiated group differed significantly from both sexes ($P < 0.05$). The notched box plot indicates that, with 95% confidence, the median of the undifferentiated group differs significantly from both the male and female groups. At the same time, no significant difference exists between males and females (Fig. 3).

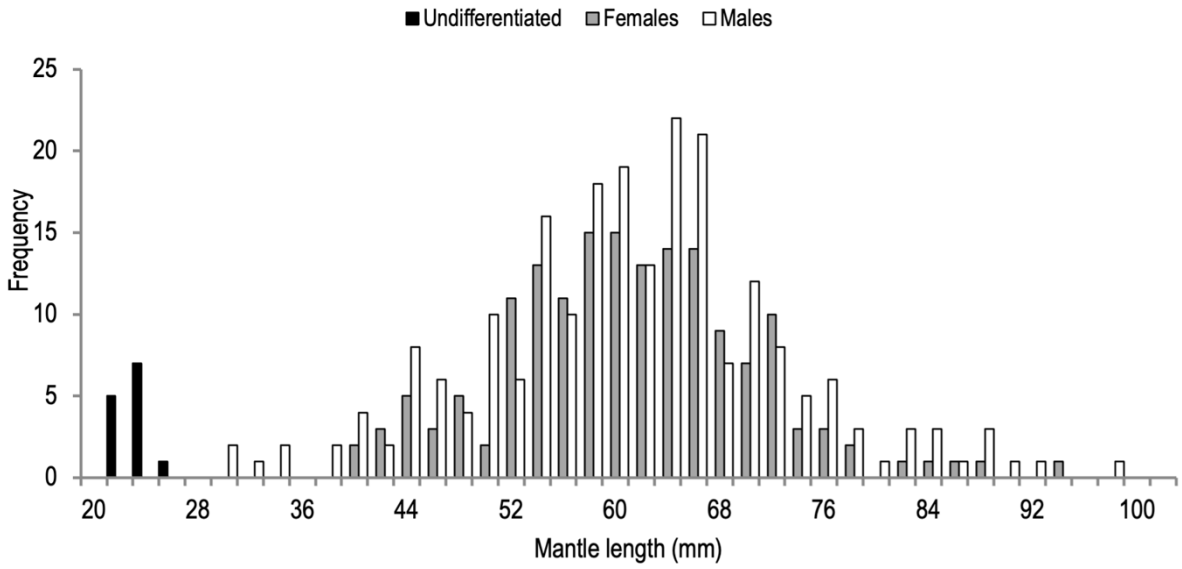


Figure 2. Size structure of *Dosidicus gigas* juveniles from the Gulf of Tehuantepec, April 2022. The arrows indicate the modes of the size classes: class I (11.0-29.9 mm mantle length, ML), class II (30.0-59.9 mm ML), and class III (60.0-99.9 mm ML).

Table 1. Size classes of mantle length for juvenile *Dosidicus gigas* by sex. ML: mantle length.

Size-class (mm ML)	I 11.0-29.9	II 30-59.9	III 60-99.9
Undifferentiated	13		
Females		82	85
Males		103	120
Total	13	185	205

The *b* values of the MLWR reported in this study showed negative or positive allometric growth. They ranged from 2.1731 to 3.3185, depending on the size-class and sex of squid. For undifferentiated squids of size-class I, $b = 2.1731$ (Fig. 4). The MLWR was significant for size-classes II and III ($R^2 > 0.6$) in both males and females. In size-class II, the coefficient *b* indicated negative allometric growth ($b < 3.0$, $P < 0.05$). In size class III, males showed negative allometric growth ($b < 3.0$, $P < 0.05$), while females showed positive allometric growth ($b > 3.0$, $P < 0.05$) (Fig. 4, Table 2).

Diet composition

A total of 46% of the examined stomachs were empty (Fig. 5a), while 54% (197 stomachs) contained food. Stomach FWI increased significantly with size in females (Fig. 4b), but decreased significantly in class III males, $H(2) = 49.96$, $P < 0.01$. Most stomachs in size-class I contained scarce food remains, with only one being full, whereas the number of stomachs containing food items increased in size-class II. Similarly, in size-class III, there was an increase in the number of stomachs with scarce, half-full, and full contents (Figs. 5b-c).

Individuals of both sexes and across size-classes II and III consumed all four prey groups, with planktonic crustaceans dominating the diet. While fish consumption increased in size-class III, the %FO of squid and crustaceans remained similar between classes II and III. Notably, fish and squid consumption increased in individuals >60 mm ML. Significant differences in prey frequency of occurrence among the three size-classes (G-test = 22.22, df = 6, $P < 0.01$) indicate an ontogenetic dietary shift, with prey selection changing significantly as size increases.

Based on the %FO, the main prey consumed by juvenile *D. gigas* were planktonic crustaceans represented by euphausiids, cephalopods of the genera *Abraliopsis* Pfeffer, 1884 and *Leachia* Jean Victoire Audouin**,** 1826; fishes mostly composed of lightfishes *Vinciguerria lucetia* Garman, 1899. Cannibalism was recorded in individual size-class III (21.5% FO).

DISCUSSION

Size-classes, sex ratio and growth

The results indicate that males are more abundant than females; Gong et al. (2018) noted that male *D. gigas* undergo earlier gonadal development, allowing them to mature at smaller sizes than females (Chen et al. 2014).

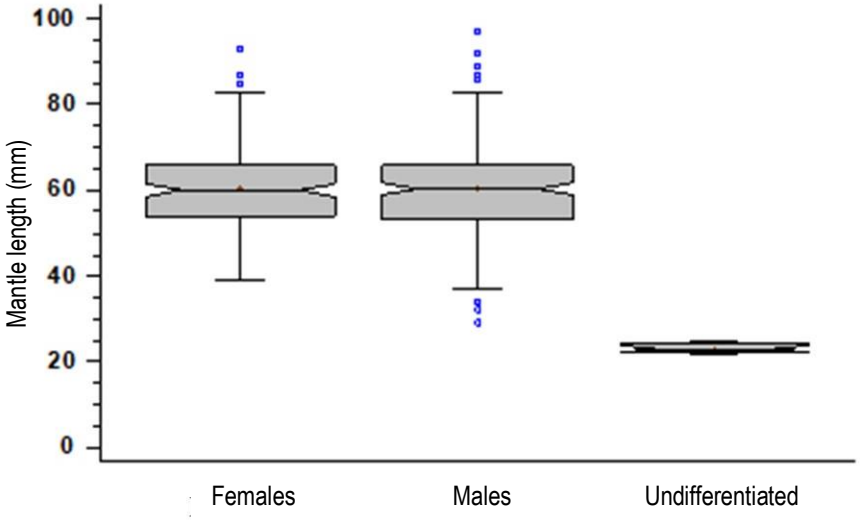


Figure 3. Comparison of the median across undifferentiated, male, and female groups. The notched box plot indicates that medians differ significantly between the undifferentiated juvenile and both males and females (95% confidence). No significant difference is observed between males and females.

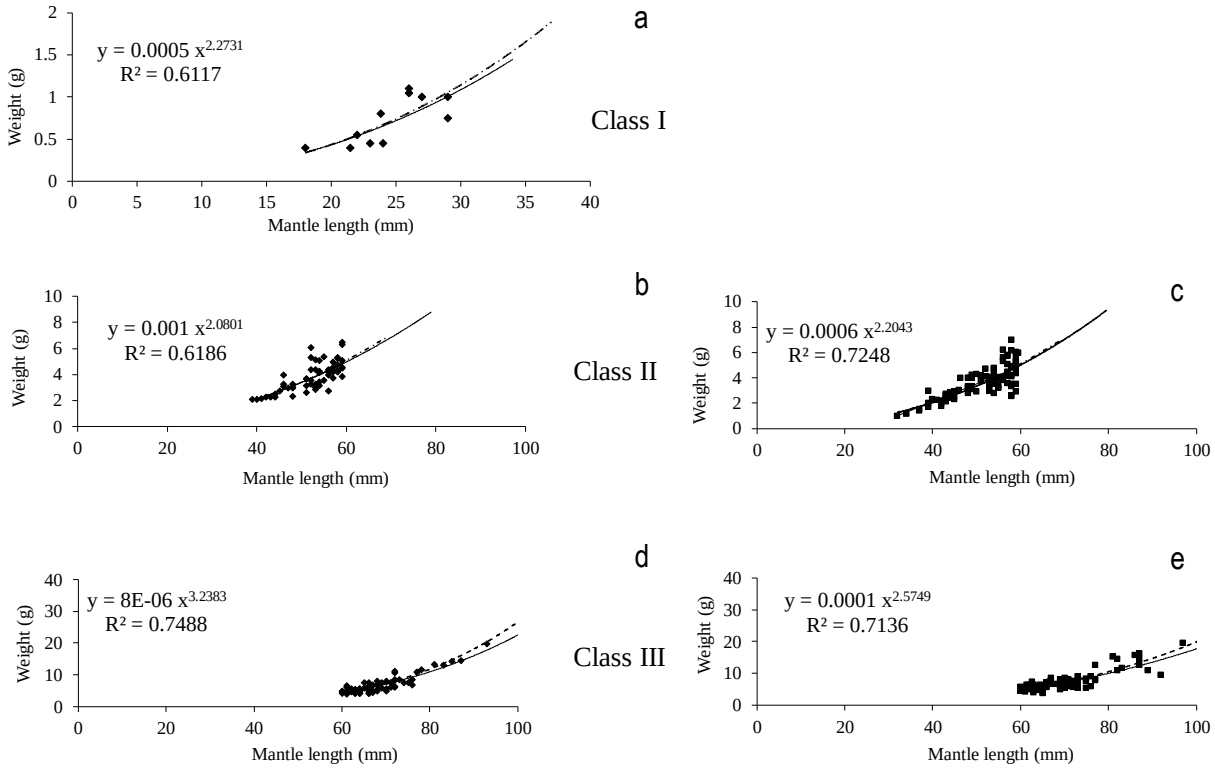


Figure 4. Juvenile *Dosidicus gigas.* Mantle length-weight relationships (MLWR). a) Undifferentiated (class I); b) females and c) males, class II; d) females and e) males, class III. − Potential (Y), ---- Potential (prediction for Y).

In contrast, adult's populations are dominated by large mature females, likely due to reproductive behavior and the selectivity of the fishing gear used (Markaida 2006).

The MLWR is a crucial biological parameter for understanding individual growth, morphological changes, and condition factor (Froese 2006). To our knowledge, this study is the first to report MLWR relationships for

Table 2. Parameters of mantle length-weight relationships (MLWR) for juvenile *Dosidicus gigas* caught in the Gulf of Tehuantepec. *A*: intercept, *b*: slope, R^2: coefficient of determination, CI: confidence interval, G: growth type, A: allometric, and I: isometric.

Size-Class	Group	n	Mantle length (mm)		Total weight (g)		Relationships constants			
			Min-Max	Mean	Min-Max	Mean	*a*	*b* ± CI 95%	R^2	G
Class I	Undifferentiated	13	18-29.9	24.48	0.4-1.1	0.72	0.0005	2.270 ± 0.1054	0.612	A-
Class II	Females	82	39-59.0	52.34	2.1-6.5	3.85	0.001	2.080 ± 0.182	0.612	A-
	Males	103	32-60.0	50.87	1.0-7.0	3.63	0.0006	2.200 ± 0.162	0.725	A-
Class III	Females	85	60-93.0	68.07	4.1-19.7	6.83	0.0001	2.575 ± 0.356	0.714	A+
	Males	120	60-97.0	69.29	3.8-19.6	7.21	0.000008	3.228 ± 0.436	0.749	A-

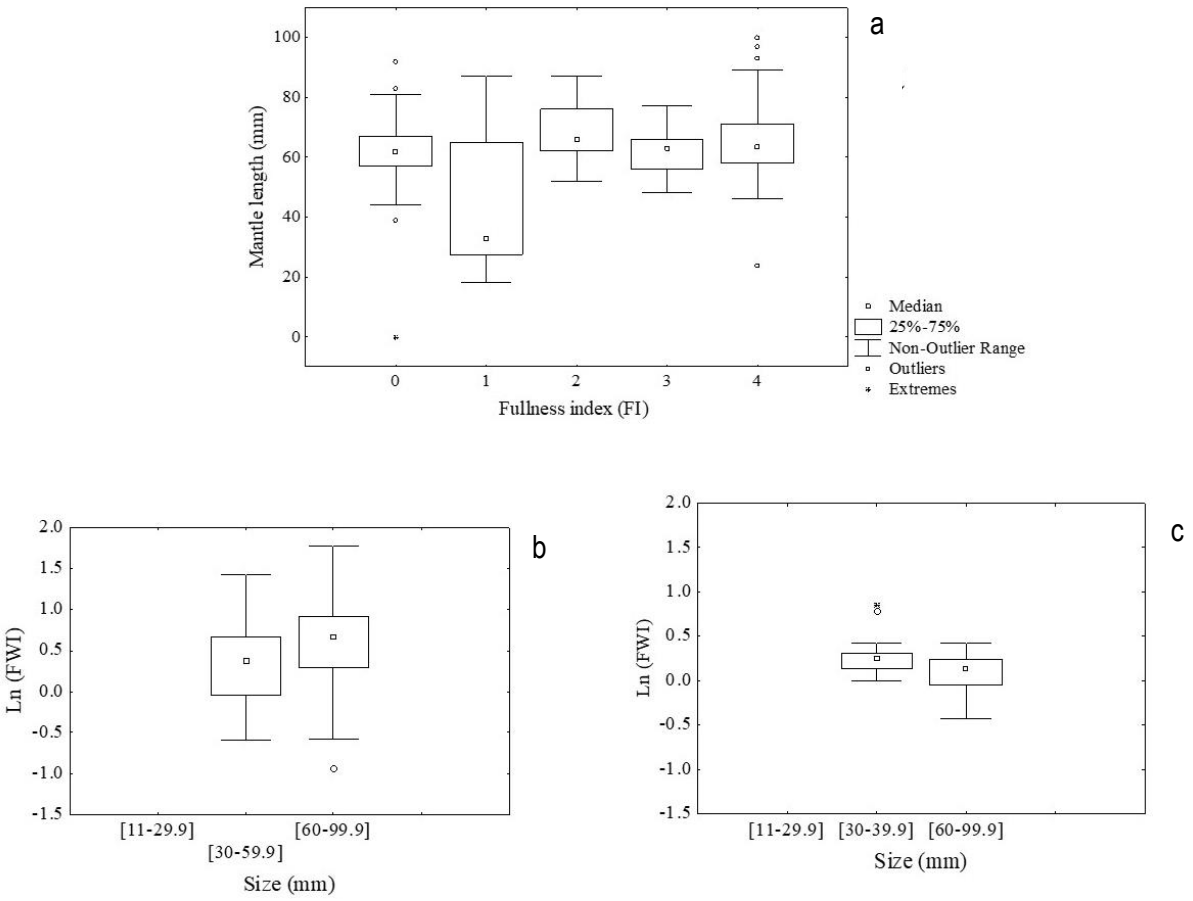


Figure 5. Stomach fullness relationship with mantle length of *D. gigas* by size-classes: (0) empty, (1) scarce remains, (2) half full, (3) almost full, (4) full. Distribution of the natural logarithm of the fullness weight index [Ln (FW1)] according to size-class. a) Overall, b) females, and c) males.

juvenile *D. gigas* in relation to size-class and sex. Previous studies on juveniles from Peru reported a *b* value of 2.956, with the MLWR obtained for combined sexes within a 15-144 mm ML size range (Goicochea et al. 2018).

D. gigas juveniles in this study showed values ranging from 2.1731 to 3.3185, indicating varied allometric growth by size and sex. Specifically, size-classes I and II showed negative allometric growth ($b < 3.0$, $P < 0.05$) for both sexes. In contrast, females in size class III exhibited positive allometric growth in relation to ovary and nidamental gland development, which aligns with the range of *b* values reported by Bazzino (2014) for adult females of this squid species.

Therefore, knowing the MLWR across life history stages to assess allometric shifts contributes to improving the accuracy of estimation models for population assessments (De Robertis & Williams 2008) and will aid further fisheries research for the management of *D. gigas* in this region.

Diet composition

Juvenile *D. gigas* preyed mainly on planktonic crustaceans, with euphausiids being the primary food source. The distribution of euphausiid (krill) swarms in the GT is strongly related to the prevailing oceanographic conditions of the area. Biological production begins in winter and accumulates, resulting in massive concentrations of zooplankton and euphausiids in March and April, before waters become too warm in summer (Färber-Lorda et al. 1994). The abundance and availability of euphausiids to juvenile *D. gigas* is exploited by the squid's opportunistic feeding on available resources. Furthermore, for small juveniles (size classes I and II), krill is the primary prey because its size makes it easy to capture with their tentacles.

Although *D. gigas* in size classes II and III consumed larger prey (fish and squid), krill remained the primary food source, confirming that *D. gigas* is an opportunistic predator in its juvenile stage, with a variable diet determined by prey availability. The significant dietary shift may occur after 90 mm, when myctophid fish and squid replace euphausiids as the main prey. According to Portner et al. (2020), consuming large amounts of relatively small, high-calorie prey, as with *V. lucetia*, contributes to faster growth and larger body sizes before sexual maturity (Rosas-Luis et al. 2011).

The significant differences in FO among the three size classes (G-test = 22.22, df = 6, $P < 0.01$) likely reflect variability in the development of feeding capacity, increasing swimming ability, and metabolic demand as squid grow. These factors may reduce intraspecific competition to improve survival. Thus, feeding strategies change throughout ontogeny according to size-specific abilities and requirements, as suggested by Gong et al. (2018).

While cannibalism is common in *D. gigas* adults (Markaida & Sosa-Nishizaki 2003, Ibañez et al. 2008) and typically occurs when large individuals prey on smaller ones in response to their high abundance (Ibáñez & Keyl 2010), a recent study on trophic niches suggests spatial and food resource segregation among different size groups (Gong et al. 2018). In this context, our results indicate that cannibalistic behavior in *D. gigas* begins during the juvenile stage at sizes exceeding 60 mm ML. The high abundance of euphausiids, small squid (*Abraliopsis* and *Leachia* spp.), and the mesopelagic fish *V. lucetia* in the diet of *D. gigas* supports the hypothesis that it opportunistically feeds on local prey. Consequently, food availability primarily determines the distribution of juvenile *D. gigas* in the water column. This high degree of trophic plasticity highlights the species' capacity to thrive in fluctuating marine environments by efficiently exploiting local resources.

Our results indicate that juvenile *D. gigas* are widely distributed in the oceanic zone west of the GT, where they feed mainly on euphausiids, mesopelagic fishes, and small squid. Therefore, according to the literature, productivity pulses associated with the Tehuano winds -mainly from November to April (Trasviña & Barton 2008)- and the formation of mesoscale eddies in the GT (Flores-Vidal et al. 2011) likely sustain the high availability of these prey items, providing favorable environmental conditions for this species. The occurrence reported in this work could be linked to this upwelling event, which fuels the local trophic web. Despite limitations stemming from the lack of year-round data, this study provides new insights into the biology of juvenile *D. gigas* in the GT.

Credit author contribution

M.C. Alejo-Plata: conceptualization, investigation, formal analysis, formal analysis supervision, visualization, writing-original draft, review and editing; R.S. Rojas-González: formal analysis, visualization, review and editing; J.R Vallarta-Zárate: formal analysis, methodology, review and editing; A.F. González-Acosta: formal analysis, methodology, review and editing; C. Chapa-Balcorta: formal analysis, review and editing; V.H. Martínez-Magaña: formal analysis, methodology.

Conflict of interest

The authors declare no conflict of interest.

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