



# Reproductive traits of the deep-sea shrimp *Plesionika williamsi* (decapoda: Pandalidae) from the eastern-central atlantic

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## ARTICLE INFO

### Keywords:

Sex-ratio  
Brood size  
Maturity  
Depth-size distribution  
Pandalidae

## ABSTRACT

The reproductive aspects of all *Plesionika* species are relatively well known worldwide, except for the deepest species of the genus, *Plesionika williamsi*, for which little information is available throughout its range. The ovarian maturity, sex ratio, brood size, and size-depth distribution of the deep-sea shrimp *Plesionika williamsi* (Pandalidae) in the Canary Islands (eastern-central Atlantic) were analysed. Ovigerous females were observed all year round, with the highest number of ovigerous females recorded between July and October. The presence of a greater number of ovigerous females during the summer may reflect a high local availability of food or the optimal abiotic conditions, which are factors with a strong influence on reproduction. The presence of non-ovigerous mature females throughout the year indicates that their resting period in the reproductive cycle occurs asynchronously. The physiological size at first sexual maturity was 19.24 mm in carapace length (CL) and the length at first sexual maturity was estimated at 23.15 mm CL. Estimates of size at first sexual maturity based on ovigerous females describe the result of the reproduction process, whereas size at first sexual maturity based on ovarian maturity deals with physiological preparation for reproduction. The modal size class of egg production was 24–30 mm CL, which yielded 83.22% of the population egg production. *Plesionika williamsi* is an iteroparous species that can produce small eggs during egg extrusion. The mean number of external embryos carried by females was 3048 and can be considered a true approximation of the number of larvae released in each batch, which depend on the conditions existing in each system. The shallower individuals are associated with a depth stratum that represents the boundary between two water masses present in the Canary Islands. The increase in size with depth is related to the presence of submarine volcanic canyons, which constitutes a flow channel of surface organic matter to depth.

## 1. Introduction

In marine ecosystems, decapods are one of the most important taxonomic groups in ecological roles and species richness, inhabiting between the intertidal zone and the hadal area (Bianchi et al., 2022; Capezuto et al., 2023). Species living in deep-sea habitats have life histories and reproductive cycles adapted to the twilight and aphotic zone, with composition patterns and amounts of organic matter being different from those found in shallow waters (Carbonell and Abelló, 1998; Triay-Portella et al., 2017). The genus *Plesionika* consists of decapods that are distributed around the world, occurring in tropical and subtropical waters over the shelf and slope bottoms (Medeiros-Leal

et al., 2022; Sreelakshmy and Chakraborty, 2023). The genus contains only marine species, most of which are deep-water species. Deep-water caridean shrimps show clear differences in size and weight between sexes, with females being larger and heavier than males (González et al., 2016; Triay-Portella et al., 2017; Medeiros-Leal et al., 2022). They also show stratification among shrimp species in their distribution in relation to depth and the size distribution among individuals of the same species, with larger individuals being concentrated in deeper waters than juveniles (Thessalou-Legaki et al., 1989; González et al., 2016; Triay-Portella et al., 2017, 2023). The sex ratio in caridean shrimps is usually skewed in favour of females, and specimens in ovigerous conditions are observed throughout the year, indicating several peaks of reproductive

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<https://doi.org/10.1016/j.dsr.2024.104320>

Received 27 October 2023; Received in revised form 14 April 2024; Accepted 3 May 2024

Available online 10 May 2024

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activity (Thessalou-Legaki, 1992; Company and Sardà, 1997; Maiorano et al., 2002; Posenti et al., 2007; Koçak et al., 2012; Sousa et al., 2014; Anastasopoulou et al., 2018).

*Plesionika williamsi* Forest, 1964 is widely distributed in tropical and subtropical seas around the world's oceans. However, there is no biological information on this species, except for the estimation of size at first sexual maturity based on the absence/presence of thoracic teeth (Triay-Portella et al., 2018). It inhabits muddy and rocky substrates at depths between 230 and 1140 m (e.g., Holthuis, 1980; González and Santana, 1996; Komai et al., 2005; Triay-Portella et al., 2023). In the Canary Islands, several studies have been conducted to evaluate the potential of deep-sea resources and to obtain basic information on *Plesionika* species (e.g., Triay-Portella et al., 2017, 2018, 2023; Pajuelo et al., 2018). The Canaries are in the Canary Current System, which is one of the Large Marine Ecosystems in the world (Sherman and Hempel, 2009). The Canary Islands are characterized by their bathymetry and hydrography due to the presence of three water masses in the first 1000 m of depth (Hernández-Guerra et al., 2002).

In the Canary Islands, fishing with semi-floating shrimp-traps takes place between 100 and 500 m, where *P. williamsi* represents only 0.25% of the pandalid species (Pajuelo et al., 2018), with *Plesionika edwardsii* representing approximately 59%, *Heterocarpus ensifer* 18%, *Plesionika ensis* 12% and *Plesionika narval* 9%. However, the highest abundances of *P. williamsi* are located between 400 and 800 m depth, outside the main fishing activity, where it is one of the characteristic species of the system (Pajuelo et al., 2015). In the Canary Islands, as in many other parts of the world, the overexploitation of coastal resources is leading to the exploitation of deeper and deeper species (Jenings et al., 2001) such as *P. williamsi*, a trend that will continue in the Canary Islands in the coming years in the absence of measures (Pajuelo et al., 2010). This underscores the need for an urgent understanding of the basic/primary biological characteristics of this species. Such knowledge is crucial to establish necessary measures ensuring the sustainability of this living resource before its intensive exploitation begins.

In this study, the reproductive traits of *P. williamsi* in the Canary Islands were analysed, specifically the sex ratio, ovarian development and maturity, size-depth distribution and spawning in addition to fecundity, size at first maturity, and length-weight relationship. The scarcity of information on this species limits the implementation of conservation measures for this resource, which should be based on a more complete knowledge of its life cycle and ecology.

## 2. Materials and methods

Samples of *Plesionika williamsi* were obtained based on catches from cruises around the Canary archipelago in December 2014, January to March 2017, April-June-July 2016, August and September 2018, April and October–November 2022. The study areas were randomly sampled from a depth interval of 300–1000 m. The sampled locations varied from trip to trip, and the sampling effort across the bathymetric range was equally distributed at 100 m intervals. Specimens of *P. williamsi* were collected using experimental bottom traps. A ground line with 10 traps was used, spaced 100 m apart, and deployed on the seabed. This fishing gear is a rectangular base tronco pyramidal trap, with a bottom base of  $1.15 \times 0.80$  m, a top base of  $1.15 \times 0.70$  m, and 0.50 m height, covered with  $15 \times 15$ -mm<sup>2</sup> metallic mesh. Each trap has a truncated cone aperture of 19 cm inner diameter with Atlantic chub mackerel (*Somber colias*) used as bait. All fishing operations were conducted over approximately 24 h (Pajuelo et al., 2015).

Carapace length (CL) (calculated in mm) was measured from the posterior edge of the eye socket to the mid-dorsal rear edge of the carapace with a digital calliper, with an error of 0.01 mm. The total weight (TW) (measured in g) was recorded from fresh shrimp, with an error of 0.01 g. Sex was recorded based on the presence of the male appendix on the endopod of the second pleopod and the inspection of the shape of the endopod of the first pair of pleopods (King and Moffitt,

1984; Triay-Portella et al., 2017). The ovigerous condition of females was recorded based on the presence of eggs in the abdomen (King and Moffitt, 1984; Triay-Portella et al., 2017). Females were dissected to remove the ovary, which extended anteriorly to the orbital margin; then, ovaries (n = 189) were fixed and preserved in 4% buffered formaldehyde and subsequently processed histologically to assign maturity condition and stage. Tissues were dehydrated in ethanol solutions, cleared in isoparaffin H, and embedded in paraffin (Triay-Portella et al., 2014). Sections (n = 189) were sliced (5 µm each) and stained using Harris' haematoxylin followed by an eosin counterstain (Triay-Portella et al., 2017). The oocyte morphology and ovary stage were histologically described according to the scale defined by ICES (2010).

The differences in carapace length and total weight between males and females were analysed using Student's *t*-test and the Kolmogorov–Smirnov Z-test, as well as the non-ovigerous and ovigerous status of females (Sokal and Rohlf, 2012). The relationship between CL–TW for both sexes was calculated using a potential function. Statistical differences were tested using the *t*-test (Sachs, 1982). In all cases, the normal distribution of the variables analysed were previously checked.

The sex ratio was calculated, and a Pearson's chi-square test was estimated to test the equality of males' and females' frequencies (Sokal and Rohlf, 2012).

The number of eggs (embryos in stage IV) by CL class was analysed from 33 females following Triay-Portella et al. (2017). For each brood, 3 subsamples of 0.1 g were taken, and the number of eggs were counted. Fecundity was obtained for each female, and the fecundity-CL relationship was obtained by fitting a linear function ( $NE = b + a \cdot CL$ ) to logarithmically transformed data of the number of eggs (NE) versus CL using linear regression adjusted by the least squares method (González et al., 2016; Triay-Portella et al., 2017). To evaluate the reproductive period and estimate the length at first maturity, the relative proportion of ovigerous females per month was determined. The months with the highest percentage of ovigerous females (between July and October) were chosen to estimate the size at first sexual maturity. The relative reproductive potential (RRP) was estimated according to Bischoff et al. (2015). The RRP estimates the size class of spawning females that makes the greatest contribution to egg production in a population.

The size at first sexual maturity ( $CL_{50}$ ), which is defined as the carapace length where 50% of females are in ovigerous condition, was calculated from the relationship between the percentage of females in ovigerous condition and CL. The size at first physiological maturity ( $CL_{f50}$ ) was estimated as the percentage at which 50% of the ovaries were mature and defined as the relationship between the percentage of females with mature ovaries and CL. The frequency (in percentage) of females in ovigerous condition (Foc) or females with mature ovaries (Fmo) per size was fitted to a logistic equation:  $F = 100 / (1 + \exp(-\alpha \cdot (CL - L_{50})))$  using a nonlinear regression by means of Levenberg–Marquardt algorithm, where  $\alpha$  is a model parameter and  $L_{50}$  is the length at sexual maturity  $CL_{50}$  or the size at first physiological maturity  $CL_{f50}$  (González et al., 2016; Triay-Portella et al., 2017). The relative size at onset of maturity (RSOM) was calculated using the equation  $RSOM = CL_{50} / CL_{max}$ , where  $CL_{max}$  is the maximum size recorded by the species (Charnov, 1990).

The depth trends of the carapace length were explored as functions of depth with generalized additive models (GAMs) (Hastie and Tibshirani, 1990). Models were tested using smoothing splines of depth (as a continuous variable) as explanatory variables. GAM models were used to explore curvilinear relationships with depth. Models were tested with Gaussian, Poisson, and negative binomial errors, and their adequacy was gauged according to the percentage of the total deviance explained by the model (%DE) and the Akaike information criterion (AIC) (Akaike, 1970) and after inspection of the diagnostic plots. These procedures were performed with R version 4.2.1 (R Core Team, 2022) and the specialized package mgcv (Wood, 2006).

### 3. Results

A total of 832 shrimp of *Plesionika williamsi* were analysed. Females were larger and heavier than males of the species (Table 1, Fig. 1). Differences between sexes were 3.4 mm (9.13%) in size (CL) and 7.4 g (25.87%) in weight. Student's *t*-test ( $t > 8.57$ ,  $p < 0.0001$ ) showed significant differences in mean carapace length (CL) and total weight (TW) between males (CL,  $22.82 \pm 4.21$  mm; TW,  $7.97 \pm 4.01$  g) and females (CL,  $25.45 \pm 4.59$  mm; TW,  $11.38 \pm 5.81$  g). Student's *t*-test ( $t > 2.81$ ,  $p < 0.005$ ) found significant differences in the mean CL and mean TW between ovigerous (CL,  $26.54 \pm 4.73$  mm; TW,  $12.60 \pm 6.02$  g) and non-ovigerous females (CL,  $24.92 \pm 4.44$  mm; TW,  $10.78 \pm 5.62$  g). The ranges of CL and TW differed significantly between males and females (K-S test, CL,  $Z = 3.42$ ,  $p < 0.0001$ ; TW,  $Z = 3.72$ ,  $p < 0.0001$ ) and between ovigerous and non-ovigerous females (K-S test, CL,  $Z = 1.71$ ,  $p = 0.005$ ; TW,  $Z = 1.53$ ,  $p = 0.018$ ).

The parameters of the CL-TW relationship are presented in Table 2. The CL-TW relationship was allometrically negative for males and all individuals but isometric for females (Table 2).

Males were dominant in *P. williamsi* (1:0.84). The Pearson chi-square test revealed that the null hypothesis (equality sex frequencies) must be rejected ( $\chi^2 = 6.58$ ;  $p = 0.010$ ). However, females were significantly more abundant than males (1:1.42) for CLs higher than 26 mm ( $\chi^2 > 10.60$ ;  $p < 0.001$ ) (Fig. 2).

Immature females (stage 1) were characterized by the presence of oogonia, early previtellogenic oocytes, and a few late previtellogenic oocytes. Developing/recovering females (stage 2) had disorganized ovaries, with abundant connective tissue, while the germinal zone stayed well defined, and oogonia, early previtellogenic oocytes, and late previtellogenic oocytes were present (Fig. 3). Maturing female (stage 3) ovaries had two distinct zones: the germinal zone in the centre of the ovary and the growth zone around the germinal zone. The germinal zone was characterized by oogonia, early previtellogenic oocytes, and late previtellogenic oocytes, and the growth zone contained late previtellogenic oocytes, early vitellogenic oocytes, and late vitellogenic oocytes surrounded by follicular cells (Fig. 3). Mature female (stage 4) ovaries had a small, constricted germinal zone circled by advanced late vitellogenic oocytes. The oocytes attained their maximum size at this stage. Germinal vesicle ruptured oocytes and atretic oocytes could also be observed (Fig. 3). Females in spent (stage 5) were characterized by the presence of late atretic oocytes, abundant connective tissue, and follicular cells (Fig. 3).

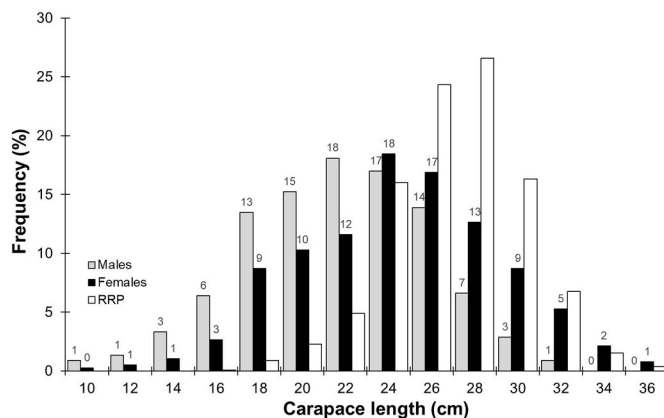
The number of eggs increased linearly significantly with size (ANOVA  $F = 22,003$ ,  $p < 0.0001$ ) (Fig. 4). The mean number of eggs was  $3048 \pm 2134$ , ranging from 571 eggs (19.9 mm CL) to 8475 eggs (35.2 mm CL) (Fig. 4).

Ovigerous females were observed year-round (Fig. 5). The highest number of ovigerous females was recorded between July and October (Fig. 5). The length at first sexual maturity was estimated at 23.15 mm CL, and the length at first physiological maturity was estimated at 19.24 mm CL (Fig. 6). Relative size at onset of maturity is  $RSOM = 53\%$ .

The modal size class of egg production was 24–30 mm CL (56.73% of females), which yielded 83.22% of the population's egg production (Fig. 1); females smaller than 24 mm CL comprised 35.09% of the population and produced only 8.13% of the eggs.

**Table 1**  
Number of analysed individuals, carapace length, and total weight of *Plesionika williamsi* from the Canary Islands.

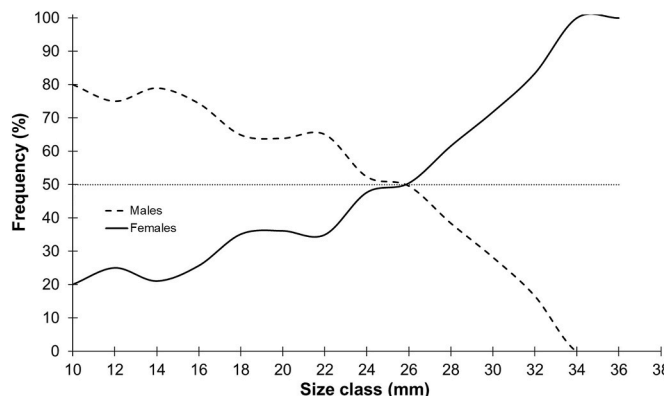
	Number	Carapace length min-max (mm)	Total weight min-max (g)
Total	832	11.1–37.2	0.9–28.6
Males	453	11.1–33.8	0.9–21.2
Females	379	11.9–37.2	1.0–28.6
Ovigerous females	132	14.5–37.2	1.9–28.5



**Fig. 1.** Frequency-size distribution for males and females of *Plesionika williamsi* from the Canary Islands and their relative reproductive potential (RRP). Numbers above bars indicate cases.

**Table 2**  
Parameters of CL-TW ( $TW = a \cdot CL^b$ ) for males, females, and all individuals of *Plesionika williamsi* from the Canary Islands. a, intercept; b, allometric coefficient; S.E., standard error;  $r^2$ , determination coefficient; t, *t*-test value; \*, significance at 0.05 level.

	a	b	S.E.(b)	$r^2$	t
Males	0.000829	2.902	0.027	0.963	3.629*
Females	0.000698	2.967	0.032	0.959	1.031
All specimens	0.000716	2.954	0.020	0.964	2.190*

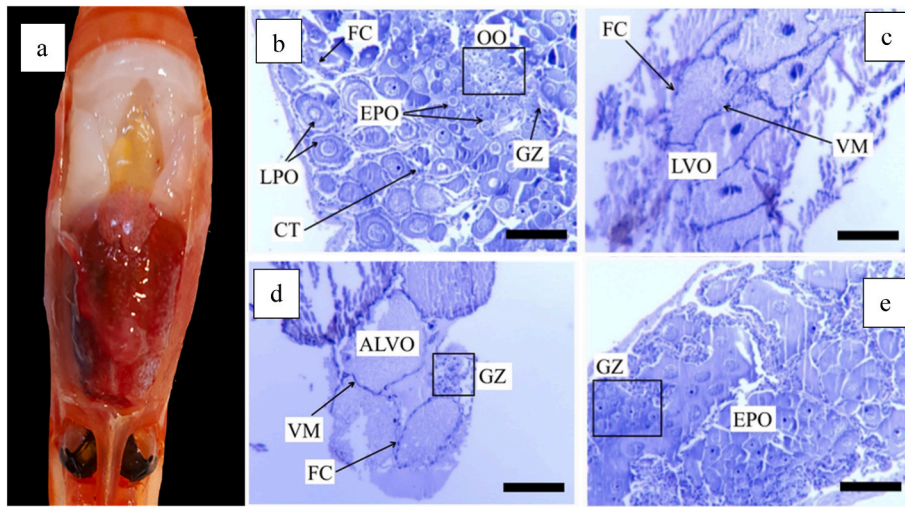


**Fig. 2.** Frequency of males and females by size classes of *Plesionika williamsi* from the Canary Islands.

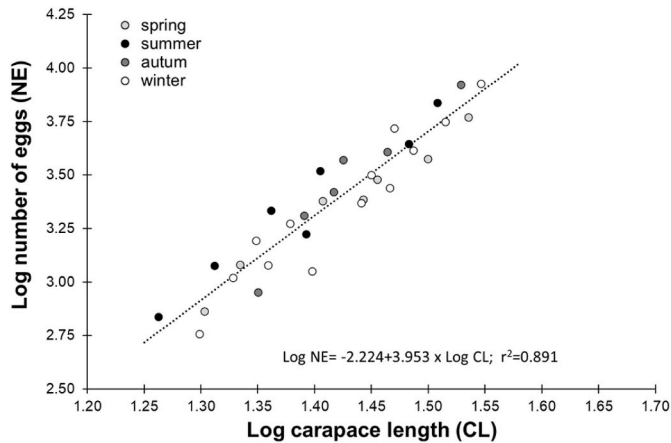
The Gaussian model was also used to evaluate the relationship between carapace length and depth for males, ovigerous females, and non-ovigerous females (Table 3). The present results indicated that CL increases with depth for males and females (Fig. 7). ANOVA of the carapace length (CL) among different depth strata showed significant differences for males ( $F = 37.58$ ;  $p < 0.0001$ ), ovigerous females ( $F = 14.35$ ;  $p < 0.0001$ ), and non-ovigerous females ( $F = 22.65$ ;  $p < 0.0001$ ). ANOVA of the CL of ovigerous and non-ovigerous females among different depth strata did not show significant differences ( $F = 0.322$ ,  $p = 0.899$ ). ANOVA of CL by sex among different depth strata did not show significant differences ( $F = 0.243$ ,  $p = 0.943$ ).

### 4. Discussion

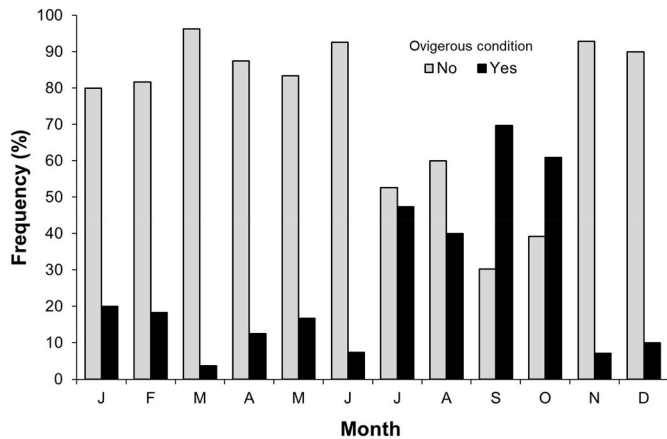
The life history pattern of *Plesionika williamsi* is similar to that of the other *Plesionika* species, which were characterized by differences in size



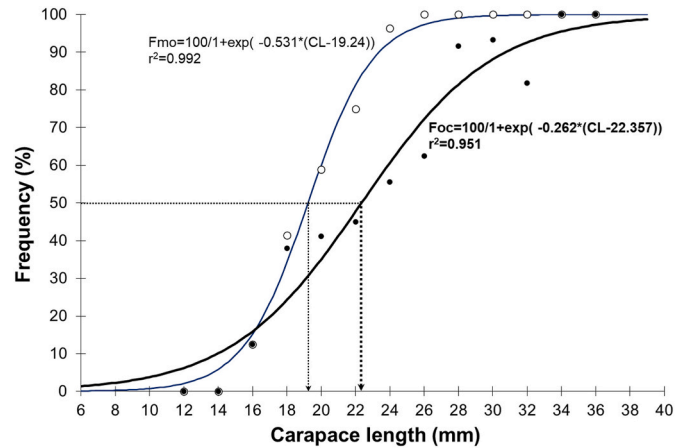
**Fig. 3.** Histological sections of *Plesionika williamsi* from the Canary Islands. a) Macroscopic observation of a gonad in developing stage; b) Stage 2, oocytes in early (EPO) and late (LPO) previtellogenic oocytes surrounded by some follicular cells (FC) and connective tissue (CT), germinal zone (GZ), and oogonia (OO); c) Stage 3, late vitellogenic oocyte (LVO) surrounded by connective tissue and follicular cells; d) Stage 4, late vitellogenic oocytes advanced (ALVO) surrounded by the vitelline membrane (VM), follicular cells, and remains of germinal zone; e) Stage 5, germinal zone with some early previtellogenic oocytes. Scale bar represents 200 μm.



**Fig. 4.** Brood size estimates in logarithmic number of eggs (NE) by logarithmic carapace length (CL) for *Plesionika williamsi* from the Canary Islands, where NE is the number of eggs in logarithm and  $r^2$  is the determination coefficient. Fitted line correspond to logarithmically transformed linear model estimate.



**Fig. 5.** Temporal variation of percentage of ovigerous and nonovigerous females of *Plesionika williamsi* from the Canary Islands.



**Fig. 6.** Sexual maturity ogive (Foc), maturity ogive (Fmo), size at first sexual and physiological maturity of *Plesionika williamsi* from the Canary Islands.

and weight between sexes, with females being larger and heavier than males, and the presence of ovigerous females in many months throughout the year, with some peaks of reproductive activity (Colloca, 2002; Maiorano et al., 2002; Posenti et al., 2007; Koçak et al., 2012; Sousa et al., 2014; González et al., 2016; Triay-Portella et al., 2017).

The skewed sex ratio toward males has been observed in this species caught simultaneously using different fishing systems in the same area (unpublished data). In addition, a skewed sex ratio toward females has also been observed for larger sizes, which rules out a more exploratory behaviour by males and, thus a higher vulnerability to the fishing system. The observed pattern of females reaching a larger size and weight than males is common when males do not show aggressive competition for copulation or do not exhibit defensive behaviour toward females (Briones-Fourzán et al., 2010; González et al., 2016; Triay-Portella et al., 2017). The predominance of females in large sizes has also been observed in all research developed on species of the genus *Plesionika* (King, 1986; Company and Sardà, 1997; Colloca, 2002; Maiorano et al., 2002; Sousa et al., 2014, 2019), suggesting that this dominance is a biological characteristic of the genus.

*Plesionika williamsi* is an iteroparous species that can produce thousands of small eggs during egg extrusion. Brood size estimates can be

**Table 3**

Results of the (a) Gaussian generalized additive model for the carapace length of males, ovigerous females, and non-ovigerous females of *Plesionika williamsi* on depth (m). Values of the parametric coefficient and the corresponding Wald tests ( $t = \text{estimate}/\text{standard error}$ ) and p-value and smoothed term as the equivalent degrees of freedom as well as an F test and its associated p-values. DE (%) deviance explained. AIC, Akaike information criterion.

Gam (Carapace length ~ s (Depth))							
<b>Males</b>							
<b>Parametric coefficients</b>	<b>Estimate</b>	<b>t</b>	<b>Pr(&gt;  t )</b>	<b>Smoothed terms</b>	<b>EDF</b>	<b>F</b>	<b>p-value</b>
Intercept	22.82	139.3	<0.0001	s (depth)	5.35	6.47	<0.0001
DE (%) = 32.2 AIC = 58.2							
<b>Ovigerous females</b>							
<b>Parametric coefficients</b>	<b>Estimate</b>	<b>t</b>	<b>Pr(&gt;  t )</b>	<b>Smoothed terms</b>	<b>EDF</b>	<b>F</b>	<b>p-value</b>
Intercept	26.68	86.01	<0.0001	s (depth)	1.78	38.89	<0.0001
DE (%) = 40.4 AIC = 67.9							
<b>Non-ovigerous females</b>							
<b>Parametric coefficients</b>	<b>Estimate</b>	<b>t</b>	<b>Pr(&gt;  t )</b>	<b>Smoothed terms</b>	<b>EDF</b>	<b>F</b>	<b>p-value</b>
Intercept	24.78	107.9	<0.0001	s (depth)	3.07	34.28	<0.0001
DE (%) = 35.5 AIC = 61.3							

considered congruent with values obtained from other populations of *Plesionika* species, such as *P. narval* (Thessalou-Legaki, 1992), *P. edwardsii* (Company and Sardà, 1997; Posenti et al., 2007; González et al., 2016; Triay-Portella et al., 2017), *P. semilaevis* (Ohtomi, 1997), *P. heterocarpus* (Company and Sardà, 1997), and *P. martia* (Company and Sardà, 1997; Maiorano et al., 2002; Chilari et al., 2005). The number of carried eggs is limited by the space available in the female abdomen. In turn, the total number of eggs can vary depending on the shape and size of the eggs, as well as the body size of the animal (Reid and Corey, 1991; Triay-Portella et al., 2017). The variability found in brood size among females may be due to fecundity data coming from different reproductive periods, which may add to variability in female size and embryo loss during the incubation period, as has been observed in other *Plesionika* species (Ohtomi, 1997; Maiorano et al., 2002; Ahamed and Ohtomi, 2011; Triay-Portella et al., 2017). This reduction can be due to parasites, mechanical friction, predators, and the increase in egg volume during its development (Ahamed and Ohtomi, 2011; Triay-Portella et al., 2017). A lower embryo production in winter than in summer may be explained by the need for higher yolk content in eggs in winter-spring (colder waters) to provide sufficient internal energy supplies for survival during incubation than in warmer waters in summer (González et al., 2016). Females with higher yolk content in eggs (larger) have less space available for egg attachment to pleopods and lower fecundity than females of the same size with reproduction during summer (González et al., 2016). The brood estimation based only on stage I individuals or only on advanced eggs (as in our case, only those of stage IV) has advantages and disadvantages. Stage I eggs provide a true estimate of biological ability to produce eggs and allow comparisons between populations to identify patterns or latitudinal changes, excluding system-specific conditions (i. e., González et al., 2016). Overall, the reduction in egg extrusion to larval release is significant due to various factors specific to the system. These factors include an increase in egg size during development, which, for instance, doubles in size in the case of *P. edwardsii* (Triay-Portella et al., 2017). Other factors contributing to the reduction include the presence of predators or parasites and loss due to friction. In the case of *P. edwardsii*, this reduction varies between 14% and 18% depending on size (González et al., 2016; Triay-Portella et al., 2017). Therefore, estimating brood capacity based on the later stages of development provides a more accurate assessment of the species' ability to produce offspring that complete the biological cycle and contribute to the adult population. This estimation is made under conditions where no parasites or predators are observed to affect the species, and individuals are captured in traps to prevent egg loss caused by mechanical friction, as seen in trawl fisheries (Triay-Portella et al., 2017).

The presence of non-ovigerous mature females throughout the year indicates that the resting period in their reproductive cycle occurs asynchronously. This asynchronous interruption of the reproductive process is related to the moulting process (Triay-Portella et al., 2017), as females are receptive only for a brief period after ecdysis, and ovarian

maturation necessarily occurs earlier so that fertilization can occur after moulting (Triay-Portella et al., 2017). The presence of ovigerous females year-round is a biological characteristic of deep sea pandalids, which present long reproductive periods, including ovarian maturation, egg extrusion, and egg development (Chilari et al., 2005; González et al., 2016; Triay-Portella et al., 2017).

A reproductive strategy of continuous embryo hatching is observed in several deep-sea species, such as *P. izumiae* (Ahamed and Ohtomi, 2011), *P. martia* (Maiorano et al., 2002), *P. edwardsii* (Colloca, 2002; García-Rodríguez et al., 2000; González et al., 2016; Triay-Portella et al., 2017) and *P. semilaevis* (Ohtomi, 1997). These species exhibit the ability for females to reproduce multiple times within a reproductive period, which appears to be a biological characteristic of the genus *Plesionika*. Multiple spawning during the reproductive season can be inferred, as suggested by Bauer (2023) by recording a synchronous evolution of ovarian maturation stage and developmental stage in embryos in the same female as has been observed in *P. williamsi*.

The repetitive output of thousands of small eggs by females and the high variability in egg number among females reflect a reproductive strategy to compensate for high larval mortality (Marshall et al., 2008; Crean and Marshall, 2009; Briones-Fourzán et al., 2010; Triay-Portella et al., 2017). *Plesionika* species have prolonged planktotrophic larval development with high mortality rates (King and Butler, 1985; Company and Sardà, 1997; Bauer, 2004; Landeira et al., 2009).

Both the size at first sexual maturity based on ovarian maturation (physiological maturity) and the size based on ovigerous condition are equally valuable and reliable in assessing reproductive aspects. The size based on ovigerous females represents the result of the reproductive process, while the size based on ovary maturity reflects the physiological preparation for reproduction. The estimation of size at first physiological maturity is highly correlated with that obtained by Triay-Portella et al. (2018) in the same population of *P. williamsi* based on thoracic teeth, with a difference lower than 0.5 mm in CL, confirming that determination of sexual maturity through thoracic teeth represents a faster and economic alternative to the classical histological analysis. Sexual maturity is reached at the same relative size, which represents a specific percentage of the maximum body size (Triay-Portella et al., 2017) described according to the rule proposed by Charnov (1990). The estimated relative size at onset of maturity (53%) is similar to values observed in other pandalids, ranging from 53% to 58% in different localities, sexual typologies, latitudes, or reproductive strategies. The low variation in the relative physiological size at first sexual maturity reflects genotypic characteristics linked to plasticity in the size of the species of the genus *Plesionika* under different environmental conditions (Hirose et al., 2013; Triay-Portella et al., 2017).

In deep ecosystems, patterns of decreasing and increasing body size with depth have been observed in several taxonomic groups, with decreasing food availability with increasing depth being the main factor involved (Ramirez-Llodra et al., 2010; Priede et al., 2013). This makes

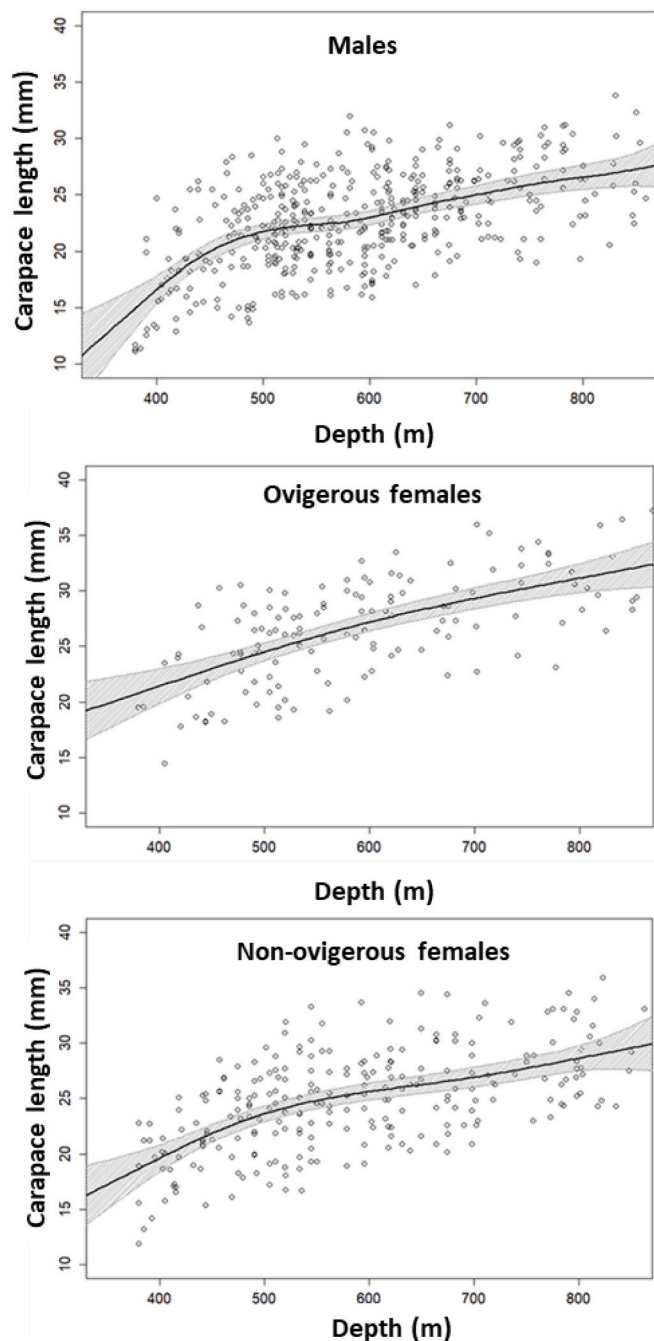


Fig. 7. Generalized Additive Model (GAM) of the mean carapace length with depth for males, ovigerous, and nonovigerous females of *Plesionika williamsi* from the Canary Islands.

the reduction in body size with depth the result of a trade-off between reproductive efficiency and metabolic rate and may lead to increased abundance of individuals and increased offspring production capacity (Ramirez-Llodra et al., 2010). However, regional variations in the efficiency of the transfer of surface-derived particulate organic matter to deeper areas may change this pattern (Dell'Anno et al., 2013; van der Grient and Rogers, 2015). In the Canary Islands, the presence of submarine volcanic canyons constitutes a flow channel of surface organic matter to depth (Pajuelo et al., 2015) that can explain the increase in size with depth. The presence of smaller individuals in shallower areas may reflect an ecological opportunity (van der Grient and Rogers, 2015). These shallower individuals are associated with a depth stratum that represents the boundary between two water masses present in the

Canary Islands (Pajuelo et al., 2015).

*P. williamsi* is caught together with other larger and more abundant pandalids in its deep distribution, such as *Heterocarpus grimaldi* and *Heterocarpus laevigatus*, so some simple conservation measures can be applied, such as increasing the mesh size of traps, providing escape areas for smaller specimens in traps, or avoiding extraction activities during the months when ovigerous females are more abundant.

#### CRedit authorship contribution statement

**A. Bautista:** Data curation, Formal analysis, Investigation, Methodology. **J.G. Pajuelo:** Conceptualization, Formal analysis, Investigation, Supervision, Writing – original draft, Writing – review & editing. **J.A. González:** Funding acquisition, Investigation, Project administration. **J. M. Lorenzo:** Investigation, Project administration. **R. Triay-Portella:** Conceptualization, Investigation, Methodology, Writing – original draft.

#### Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

#### Data availability

Data will be made available on request.

#### Acknowledgments

Financial support was received from the ERDF of the EU in the framework of the Transnational Cooperation Programme MAC (Madeira-Açores-Canarias) projects MACAROFood (MAC/2.3 d/015) and MARISCOMAC (MAC/2.3 d/097).

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