

Unraveling distributional patterns and life-history traits of a deep-water shrimp *Plesionika edwardsii* (Decapoda, Pandalidae) under unexploited virgin conditions: a benchmark for fisheries management

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ABSTRACT

Plesionika edwardsii (J.F. Brandt in von Middendorf, 1851) is a cosmopolitan species that inhabits cold temperate and subarctic waters between 50 and 680 m. In the Azorean region, this is the second most abundant shrimp species and populations remain unexploited. To provide insights into a pristine state that can be useful for comparisons across regions and serve as a benchmark for a potential fishery in the future, we analyzed data collected during shrimp trap surveys in the Azores between 1999 and 2000. *Plesionika edwardsii* were caught between 100 and 600 m depth, with the biggest catches between 200 and 400 m. Sizes varied from 8.3 to 31.3 mm cephalothorax length (CL). Females were bigger and more abundant than males and predominated at depths up to 300 m. Ovigerous females were caught throughout most of the year, with a peak of abundance during the winter. The size at 50 % maturity was 25 mm CL. High variability in distributional patterns and life-history traits has been observed in our study and when compared with literature from other regions, it is difficult to distinguish which differences are potentially fishing-induced. Future studies should investigate the oceanographic processes associated with *P. edwardsii* ecology and commercial fisheries should be made on a precautionary basis.

KEYWORDS

Azores, Pandalid shrimp, population structure, soldier striped shrimp, sustainable exploitation

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INTRODUCTION

The soldier striped shrimp *Plesionika edwardsii* (J.F. Brandt in von Middendorf, 1851) is a cosmopolitan pandalid species that inhabits cold temperate and subarctic waters between 50 and 680 m deep (Chan and Yu, 1991). It is known from the Western Atlantic (South Carolina and North Bahamas to the Gulf of Mexico), Eastern Atlantic (North-West Spain to Sierra Leone, including the archipelagos of Azores, Madeira, Canaries, and Cape Verde and most of the Mediterranean Sea), and Indo-Pacific (around Seychelles and Réunion Island, Indonesia, Philippines, Taiwan, New Britain, New Caledonia, Vanuatu, Fiji, and French Polynesia) (Chan and Yu, 1991; Martins and Hargreaves, 1991; González et al., 2001).

Plesionika edwardsii is included in the Food and Agriculture Organization of the United Nations (FAO) species catalogue of interest to fisheries (Holthuis, 1980). Since 1984, this species has been caught in the Western Mediterranean (the east coast of Spain, Balearic Islands, Corsica, Sardinia, and Sicily) with multiple shrimp traps (Santana et al., 1997; Vafidis et al., 2005). This fishery has expanded to the NE Atlantic archipelagos (Canary and Madeira) since 1997, where a small-scale fishery operates targeting pandalid species (González et al., 1997). Although the soldier striped shrimp is trapped in the Mediterranean and Atlantic, landing records are scarce or absent. Catches for the western Mediterranean landed in Spain (Santa Pola, Alicante) are available between 1984 and 1991, with values around 60 and 100 t year⁻¹ (González et al., 1992).

Despite being the second most abundant shrimp species, and probably the one with the highest fishing potential (Martins and Hargreaves, 1991; Pinho et al., 2001), there is currently no commercial trap fisheries targeting *P. edwardsii* in the mid-North Atlantic (Azorean region, ICES Subdivision 10a2). This resource can be considered virgin, since besides not being directly exploited, there is no incidental catch by other fisheries in this area. Small-scale fisheries using highly selective gear (pole-and-line for tuna and handline or longline for demersal/deep-water fish species) are the most important fisheries in the Azorean region (Silva and Pinho, 2007; Santos et al., 2019a; 2020). Trawling in this area is difficult due to

the steep, rocky and irregular seafloor (Menezes et al., 2006), which is avoided by trawlers so as not to damage nets. Moreover, the Azores has banned bottom trawling fisheries in its waters since 2004 aiming to protect deep-sea ecosystems such as cold-water corals (Council Regulation (EC) no. 1811/2004).

Studies of unexploited virgin populations can provide managers with benchmarks against which the effects of fishing or management regimes and actions can be measured (Hilborn and Walters, 1992). In this context, the present study has the objective of providing baseline information on abundance, size composition, depth distribution, growth, sex ratio and reproductive aspects of *P. edwardsii* populations under unexploited virgin conditions in the mid-North Atlantic Ocean (Azores archipelago). Besides that, this is the first study to describe population aspects of soldier striped shrimp inhabiting the remote outer region of the Azores, and this scientific knowledge is crucial before the development of any sustainable fishery; in accordance with the “precautionary approach” principle.

MATERIAL AND METHODS

Sampling area and data collection

Shrimps were caught around the central group of the Azores archipelago (mid-North Atlantic; Fig. 1). A total of 26 research cruises (65 fishing operations or sets; Tab. S1) were seasonally conducted from the summer (March) of 1999 to spring (June) of 2000. The study area was stratified into depth strata with 100 m intervals from a depth of 100 to 600 m, which corresponds to the main range of *Plesionika* species distribution in the Azores (Pinho et al., 2001). Sampling effort across the bathymetric range was equally distributed at 100 m intervals (stratified sampling design). Within each stratum, sets were randomly allocated along different areas within the Azorean central group guaranteeing a minimum of two sets per stratum.

Shrimps were collected using multiple semi-cylindrical traps deployed at approximately five meters above the seafloor, with a 67 × 46 cm base length and 37 cm height, covered with a 20 × 20 mm cotton net. Each trap had a single entrance funnel at the top

that had an inner diameter of 19 cm. Each gear set consisted of 8–10 traps equally spaced (50 m) along a rope. Atlantic chub mackerel *Scomber colias* Gmelin, 1789 was used as bait, and immersion time was 24 h.

Cephalothorax length (CL, from the postorbital eye socket to the posterior median edge of the cephalothorax) of each shrimp collected was measured to the nearest 0.1 mm, and the wet weight (WW) was measured to the nearest 0.01 g. The shrimp biomass was estimated using catch per unit effort (CPUE) data (g trap⁻¹). Sex was determined under a stereomicroscope based on the presence or absence of the appendix masculina on the endopod of the second pleopod (King

and Moffitt, 1984). Ovigerous condition of females was determined based on the presence or absence of eggs on the pleopods (King and Moffitt, 1984).

Data analysis

Abundance (CPUE) and CL data (dependent variables) were analyzed across seasons, depth strata and sexes (explanatory variables; Tab. 1). The effects of the explanatory variables on abundance and size composition were analyzed using Generalized Linear Models (GLM) with Gamma distribution (Zuur and Ieno, 2016). The general formulation used in the present study was expressed by the following equation:

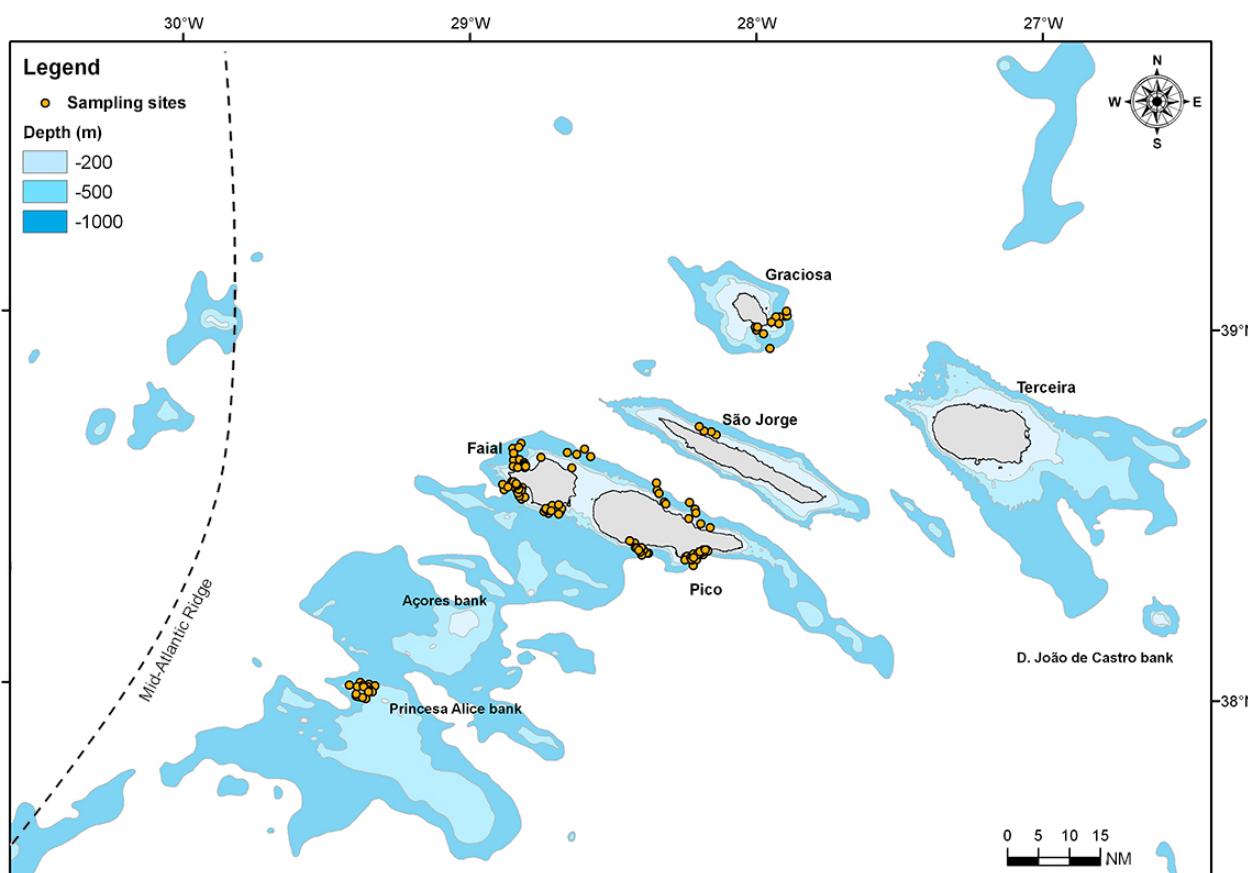


Figure 1. Sampling areas of *Plesionika edwardsii* in the mid-North Atlantic Ocean, Azorean region (ICES Subdivision 10a2) between 1999 and 2000. Orange dots represent each site sampled by a trap.

Table 1. Explanatory variables hypothesized to affect catch rate and size composition of *Plesionika edwardsii* in the Azorean region during the period 1999–2000.

Explanatory variable	Type	Levels	Description
Season	Categorical	4	Spring, Summer, Autumn, Winter
Depth	Categorical	6	100, 200, 300, 400, 500, 600
Sex	Categorical	3	Males, Non-ovigerous females, Ovigerous females

$$g(\text{CPUE or CL}) = \text{Season} + \text{Depth} + \text{Sex} + \text{Season} \times \text{Depth} + \text{Season} \times \text{Sex} + \text{Depth} \times \text{Sex} + \text{Season} \times \text{Depth} \times \text{Sex}$$

where $g()$ is the log link function.

The Akaike information criterion was used for model selection (Tab. S2). When the best model was fitted, explanatory variables that contributed significantly to the explained deviance were identified using P -values based on chi-squared distribution < 0.05 and the percentage of explained deviance $\geq 5\%$. Post-hoc Tukey's test was employed to locate the source of significant differences.

The relationship between CL and WW ($W = a \text{CL}^b$) was estimated for males, non-ovigerous and ovigerous females and combined sexes. The parameters a (intercept) and b (allometric coefficient) were estimated by simple linear regression (least squares method) of the log-transformed CL and WW after residual analysis. Statistical differences ($P < 0.05$) between CL-WW relationships were verified by likelihood-ratio test (LRT).

Sex ratio was estimated for depth stratum and size class. Equality of frequencies between sexes was

checked using Pearson chi-square goodness-of-fit test at 0.05 significance level. Size at which 50 % of the individuals are mature (L_{50}) was estimated by Bayesian regression approach fitting a logistic curve to the proportion of ovigerous females grouped by size class (1 mm CL) using *sizeMat* package in R (Torrejon-Magallanes, 2019). The logistic function used was $P_{CS} = 1/[1 + e^{-(\beta_0 + \beta_1 CL)}]$ where P_{CS} is the probability of an individual being mature at a determinate CL carapace length, β_0 (intercept) and β_1 (slope) are estimated parameters.

RESULTS

Abundance and distribution

A total of 2,418 individuals (22.9 kg) of *P. edwardsii* were caught between 100 and 600 m depth. The highest catches were obtained during the autumn-winter period (Fig. 2; Tabs. 2, 3; Tabs. S3, S4). Shrimp biomass was concentrated between 200 and 400 m deep (Tabs. 2, 3; Tabs. S3, S4). Non-ovigerous and ovigerous females were more abundant than males during the autumn and winter period, respectively (Fig. 2; Tabs. 2, 3; Tabs. S3, S4).

Table 2. Catch per unit effort (CPUE) of *Plesionika edwardsii* by season, depth and sex in the Azorean region during the period 1999–2000. CI: 0.95 confidence interval.

CPUE (g trap ⁻¹)	Season				Depth stratum						Sex				Combined sexes	
	Spring	Summer	Autumn	Winter	100	200	300	400	500	600	Male	Female				
												Ovigerous	Non-ovigerous	Total		
Mean	7.76	19.05	40.10	54.40	10.98	43.07	58.61	17.86	13.56	1.16	10.34	17.23	15.54	27.60	36.46	
± CI	2.21	6.60	4.53	7.34	4.10	7.44	6.18	3.46	2.65	0.26	0.93	2.30	1.88	2.64	3.30	

Table 3. Results from Generalized Linear Models (GLMs) for effects of season (spring, summer, autumn, winter), depth stratum (100, 200, 300, 400, 500, 600 m) and sex (male, ovigerous female, non-ovigerous female) on abundance and size composition of *Plesionika edwardsii* in the Azorean region during the period 1999–2000. Detailed model selection procedure is in Tab. S2.

Model	Abundance				Size composition			
	d.f.	Res. Dev.	% of Dev. exp.	P	d.f.	Res. Dev.	% of Dev. exp.	P
Null		269.3				95.134		
Season	3	238.4	24.3	< 0.001	3	93.264	5.9	< 0.001
Depth	5	196.3	33.1	< 0.001	5	87.526	18.1	< 0.001
Sex	2	194.1	1.8	0.304	2	74.113	42.2	< 0.001
Season × Depth		nonEst	nonEst	nonEst	11	71.03	9.7	< 0.001
Season × Sex	6	149.8	34.8	< 0.001	6	66.582	14	< 0.001
Depth × Sex		nonEst	nonEst	nonEst	9	65.165	4.5	< 0.001
Season × Depth × Sex		nonEst	nonEst	nonEst	16	63.373	5.6	< 0.001

Note: d.f.: degrees of freedom; Res. Dev.: residual deviance; % of Dev. exp.: percent of deviance explained.

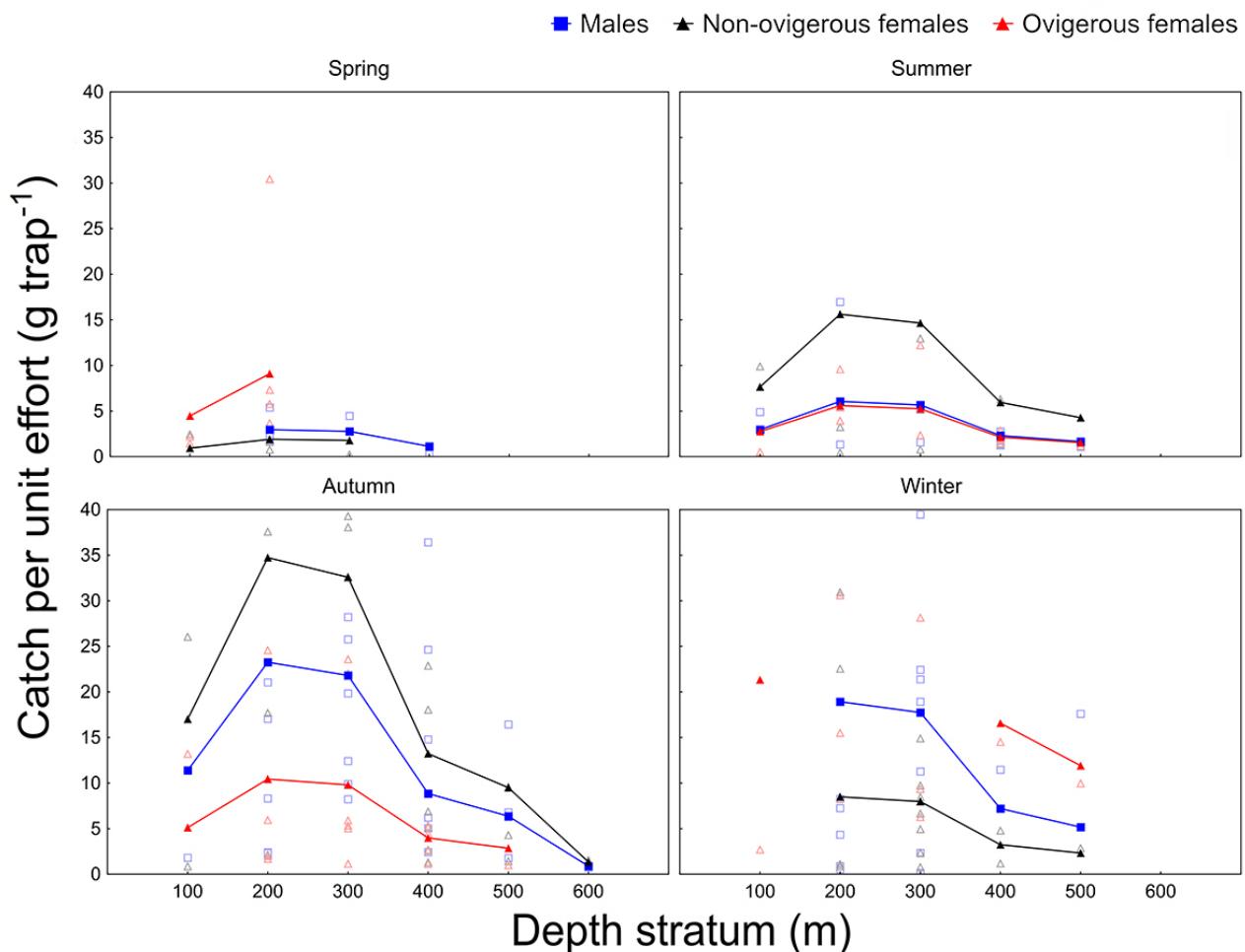


Figure 2. Seasonal predicted mean catch per unit effort (CPUE, g trap^{-1}) by depth stratum for males, non-ovigerous and ovigerous females of *Plesionika edwardsii* in the Azorean region for the period 1999–2000. Light-colored symbols represent raw data. Detailed parameter estimates are in Tab. S4.

Size structure

Length frequency distribution was bimodal for both males and females (Fig. 3). Ovigerous females attained significantly larger sizes than non-ovigerous females and males (Tab. 3; Tabs. S3, S4). Males ranged from 9.2 to 29.8 mm CL and non-ovigerous and ovigerous females ranged from 8.3 to 29.3 mm CL and 13.9 to 31.3 mm CL, respectively (Tab. S5). Mean CL was significantly smaller during the spring for both non-ovigerous females and males (Tab. 3; Tabs. S3, S4; Fig. 4). A bigger-deeper trend was observed for all sexes up to 400 m deep (Tab. 3; Tabs. S3, S4; Fig. 4).

CL-WW relationship

The allometric coefficient (b) of CL-WW relationship indicated the existence of a negative

allometry for all sexes (i.e., $b < 3$; Tab. 4). In all cases, the coefficient of determination (R^2) was high, indicating strong correlation between CL and WW. LRT results showed significant differences ($P < 0.001$) between all CL-WW relationships calculated for males, non-ovigerous and ovigerous females and combined sexes (Tab. 4).

Sex ratio

The sex ratio showed females dominating significantly ($\chi^2 \geq 41.8$, $P < 0.001$) up to 400 m deep (Fig. 5). Males were significantly more abundant than females between 400 and 500 m ($\chi^2 \geq 4.2$, $P < 0.05$). Regarding the differences in sex ratio by size class, females were significantly more abundant in CLs larger than 20 mm ($\chi^2 \geq 3.9$, $P < 0.05$; Fig. 6).

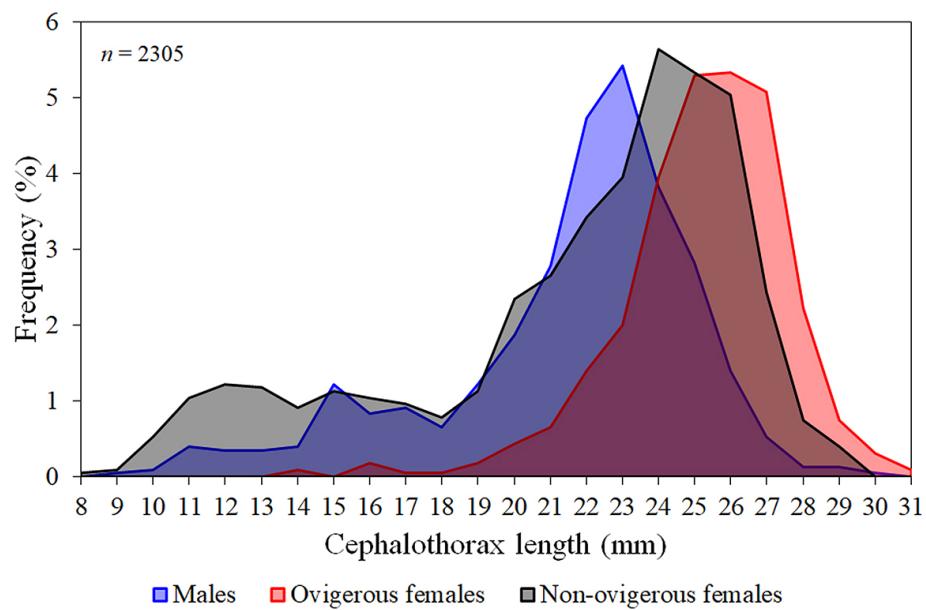


Figure 3. Size frequency distribution of males, non-ovigerous and ovigerous females *Plesionika edwardsii* in the Azorean region during the period 1999–2000.

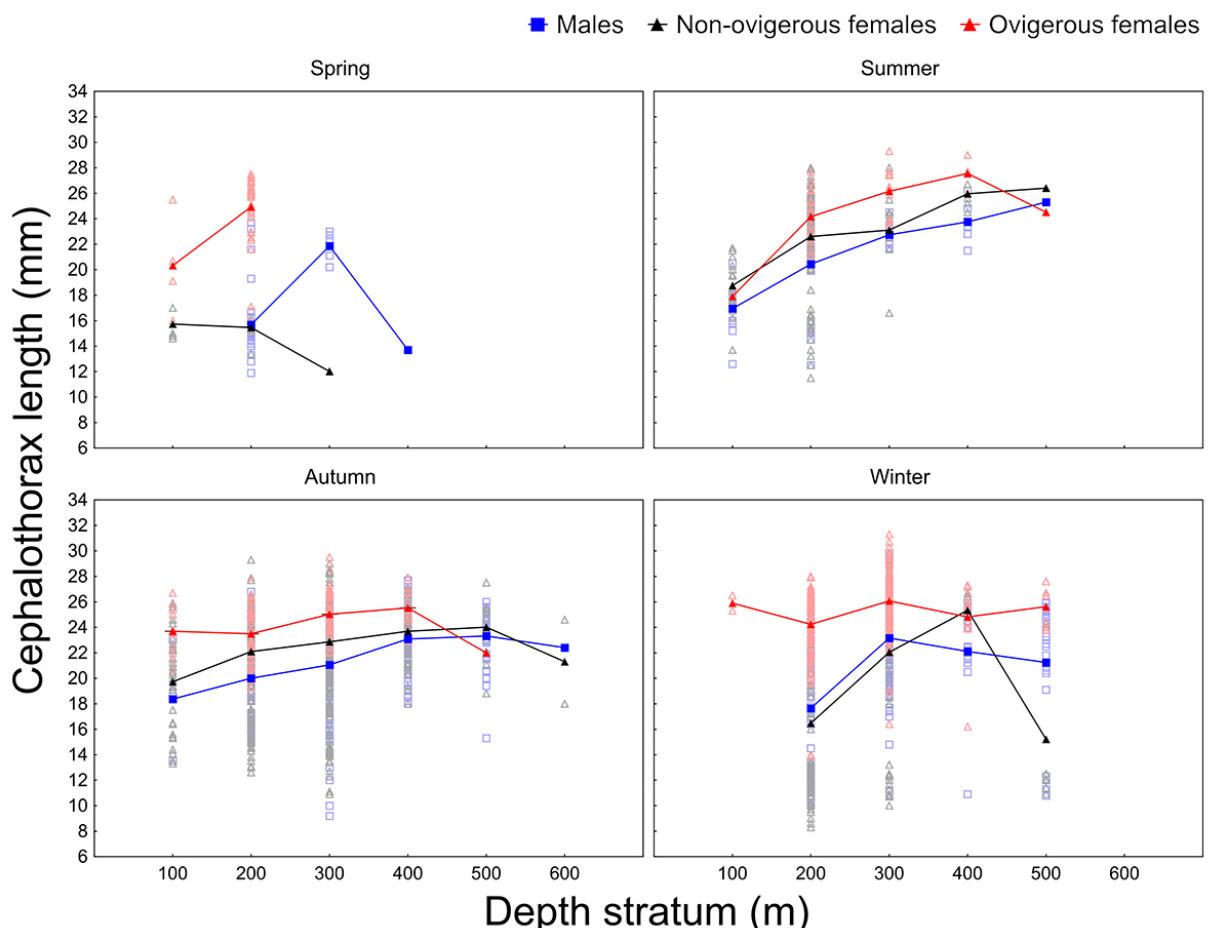


Figure 4. Seasonal predicted mean cephalothorax length (CL) by depth stratum for males, non-ovigerous and ovigerous females of *Plesionika edwardsii* in the Azorean region for the period 1999–2000. Light-colored symbols represent raw data. Detailed parameter estimates are in Tab. S4.

Table 4. Parameters of CL-WW relationship ($W = a \text{CL}^b$) for males, females and all shrimps of *Plesionika edwardsii* caught during the period 1999–2000. a : intercept, b : regression coefficient (allometric coefficient), SE: standard error, P -value: likelihood ratio test p value; R^2 : determination coefficient; n : number of individuals.

Sex	a	b	SE (a)	SE (b)	P -value	R^2	n
Males	0.0041	2.44	0.0005	0.041	<0.001	0.9117	693
Females	0.0046	2.43	0.0004	0.032	<0.001	0.9283	1610
Ovigerous females	0.0140	2.09	0.0020	0.060	<0.001	0.6099	644
Non-ovigerous females	0.0058	2.34	0.0006	0.034	<0.001	0.9491	966
Total	0.0031	2.55	0.0020	0.026	<0.001	0.9238	2303

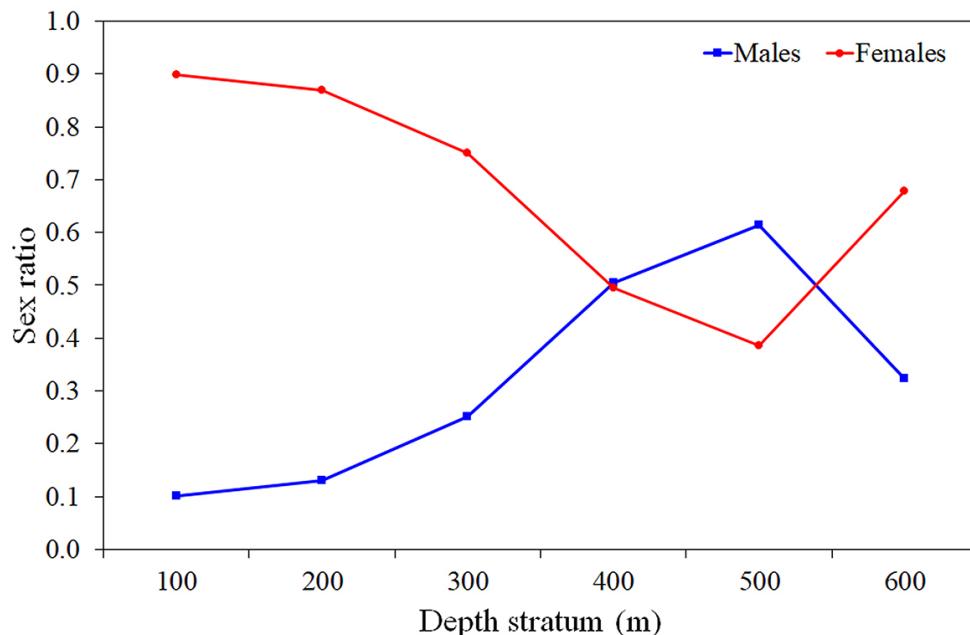


Figure 5. Sex ratio of *Plesionika edwardsii* by depth stratum in the Azorean region during the period 1999–2000.

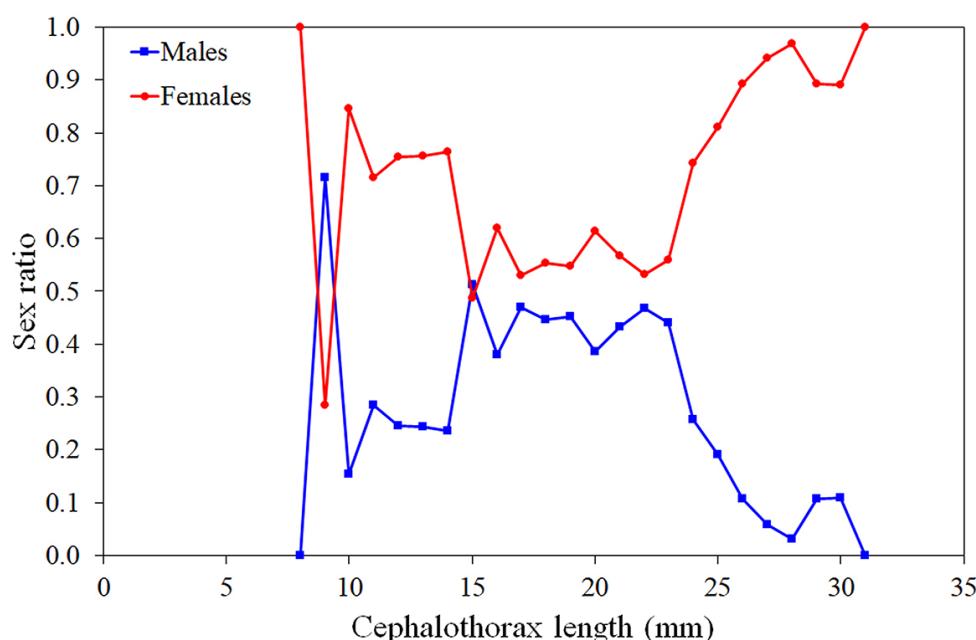


Figure 6. Sex ratio of *Plesionika edwardsii* by size class in the Azorean region during the period 1999–2000.

Reproduction

Females carrying eggs on pleopods were observed throughout the year, with a peak in biomass during the winter (Tabs. 3, 4; Fig. 2). CPUE data showed significant segregation in habitat use by sex and reproductive condition (Tabs. 3, 4; Fig. 2). Non-

ovigerous females were more abundant in shallower waters up to 200 m deep. Ovigerous females mainly occupied intermediate depth strata between 200 and 300 m. Males were mainly taken from depths ranging between 400 and 500 m (Fig. 2). The L_{50} in ovigerous samples was estimated at 25.0 mm CL (Fig. 7).

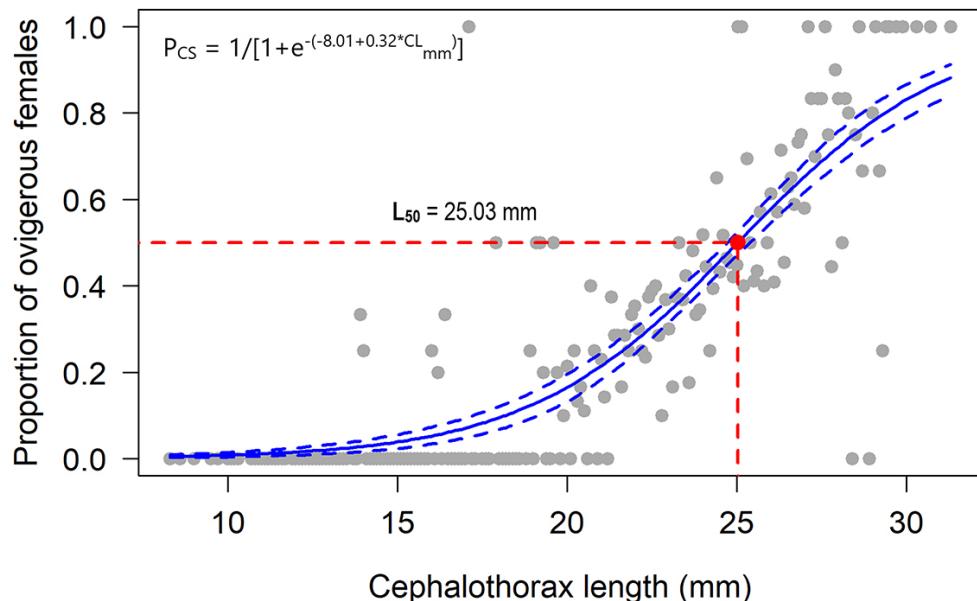


Figure 7. Size at which 50 % of the shrimps are mature (L_{50}) estimated for *Plesionika edwardsii* in the Azorean region fitting a logistic curve to the proportion of ovigerous females. Logistic curve was estimated combining all data obtained during the period 1999–2000.

DISCUSSION

Several studies on distribution, abundance and population biology of *P. edwardsii* have been carried out in the North Atlantic Ocean and Mediterranean Sea (e.g. Santana *et al.*, 1997; Colloca, 2002; Fanelli *et al.*, 2004; Possenti *et al.*, 2007; González *et al.*, 2016). However, this is the first work that reveals the population biology and dynamics in unexploited, virgin fishing grounds allowing comparisons with literature from other areas characterized by different fishing pressures.

In the mid-North Atlantic (Azorean region), unexploited virgin *P. edwardsii* populations mainly occurred from 200 to 400 m, which is suggested by Chan and Yu (1991) as the main occurrence range of the species. In other regions of the world, the depth range where the greatest abundances are observed varies from 100 to 150 m in Cape Verde (González *et al.*,

2016), 150 to 200 m in Madeira (González *et al.*, 2016), 150 to 300 m in the Canaries (Santana *et al.*, 1997), 300 to 500 m in North Africa (Crosnier and Foster, 1973), 250 to 550 m in the Mediterranean Sea (Holthuis, 1987, Company and Sardà, 1997; Carbonell and Abelló, 1998; Fanelli *et al.*, 2004), and is around 230 m in Martinique (Paulmier and Gervain, 1994), and 275 m in Fiji (King and Butler, 1985). *Plesionika edwardsii* inhabiting unexploited fishing grounds in the Azorean region are therefore found at the same depth as in the regions of Madeira, Canaries, Martinique and Fiji, and at a deeper depth than in the Mediterranean Sea and North Africa. These results did not suggest a straightforward relationship between depth distribution pattern and different levels of fishing pressure. Like other species from the genus, *P. edwardsii* is a benthic species with moderate locomotor capacity, showing no daily

migration behavior in the water column (Company and Sardà, 2000). However, environmental specificity of hydrodynamic conditions, topography and food availability are factors that can considerably drive their spatial distribution along its occurrence areas (Cartes, 1993; Puig *et al.*, 2001; Carbonell *et al.*, 2003; Fanelli and Cartes, 2004).

Seasonality also seems to influence the distribution of this pandalid species. It is known that *P. edwardsii* tends to concentrate in deeper waters during the winter, moves shallower during the spring, reaching its shallowest depths in the summer and then returns to deeper water again in the autumn (Santana *et al.*, 1997; Oliveira *et al.*, 2014). The depth movement in response to seasonal changes has also been reported for *Plesionika narval* (Fabricius, 1787) off the Canaries (González *et al.*, 1997) and in the Eastern Mediterranean (Thessalou-Legaki *et al.*, 1989) and may explain the higher autumn-winter catches in the deep-zone sampled (between 100 and 600 m) during the present study.

The observed CL range of *P. edwardsii* in the Azores (8.3 to 31.3 mm CL) is approximately equal to the observations made by other authors in Martinique

(11.0 to 28.0 mm; Paulmier and Gervain, 1994), Cape Verde (11.0 to 29.0 mm; González *et al.*, 2016), the western and central Mediterranean (9.9 to 29.1 mm and 7.0 to 30.0 mm CL, respectively; García-Rodríguez *et al.*, 2000; Colloca, 2002), Canaries (11.0 to 30.0 mm; González *et al.*, 2016) and Madeira (12.0 to 33.0 mm; González *et al.*, 2016). These results did not indicate a clear change in CL distribution toward smaller individuals caused by size-selective harvesting in exploited fishing grounds; as already reported for other pandalid shrimps (Charnov, 1981; Hannah, 1991). However, the maximum CL of these populations highlights a latitudinal pattern, with bigger shrimps found at higher latitudes (Azores) and smaller ones at lower latitudes (Martinique). This pattern confirms the hypothesis of size increases with latitude due to different thermal exposures — Bergmann's rule — (Bergmann, 1847) previously reported for *P. edwardsii* (González *et al.*, 2016) and other marine decapod crustaceans (Steele, 1988).

Sexual size dimorphism with females larger than males and ovigerous females larger than non-ovigerous females has been described for *P. edwardsii* populations inhabiting the central and western Mediterranean

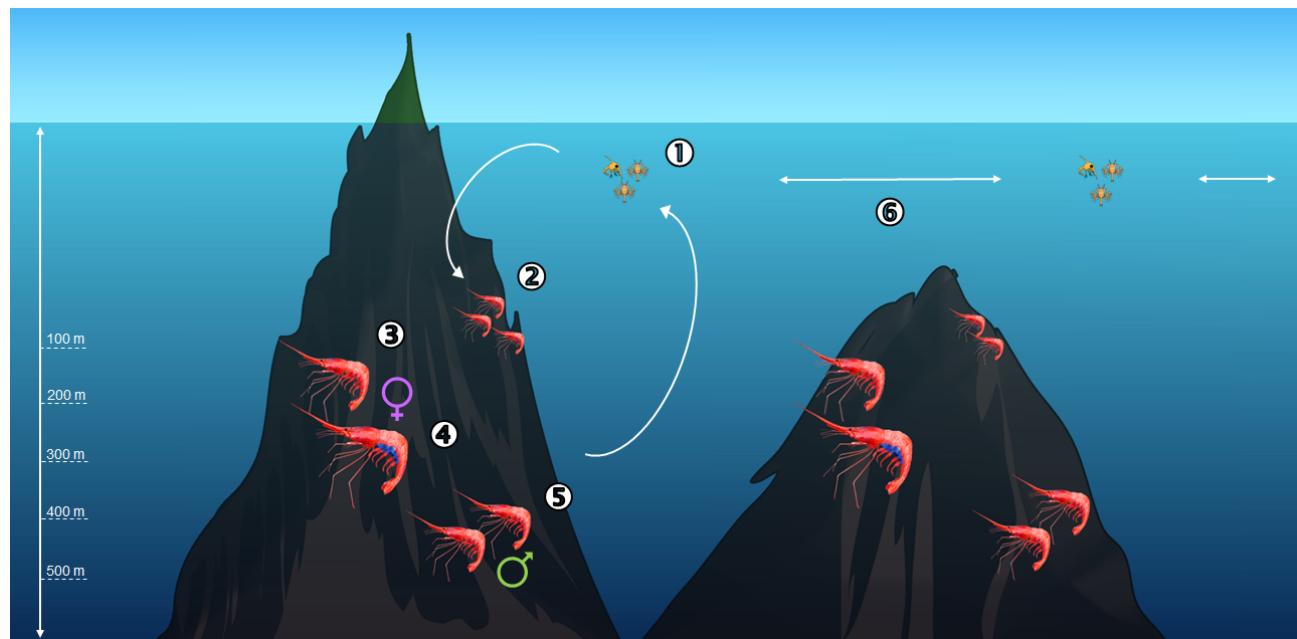


Figure 8. Hypothesized life cycle of *Plesionika edwardsii* in the Azorean region. After the incubation period of shrimp eggs, (1) larvae are released into the water column and (2) juveniles develop in shallow waters. Mature females and males are distributed up to 600 m with a sexual segregation by depth: (3) non-ovigerous females are mainly found up to 200 m, (4) ovigerous females between 200 and 300 m, and (5) males from 400 to 500 m deep. Females are bigger than males, and ovigerous females are bigger than non-ovigerous females. A bigger-deeper trend is observed up to 400 m. (6) Long larval stages of *P. edwardsii* increases its potential for dispersal (Landeira *et al.*, 2009), favoring connectivity and stock homogeneity between adjacent areas.

(García-Rodríguez *et al.*, 2000; Colloca 2002), Cape Verde (González *et al.*, 2016), Canaries (Santana *et al.*, 1997), Madeira (González *et al.*, 2016), and Martinique (Paulmier and Gervain, 1994). The dominance of females in the largest sizes could be due to differences in growth or in their differential mortality (Santana *et al.*, 1997). In fact, females seem to have higher growth rates than males (*e.g.*, Santana *et al.*, 1997; García-Rodríguez *et al.*, 2000; González *et al.*, 2016), which accounts for the observed patterns of sizes and sex ratios.

A bigger-deeper trend was observed for both sexes up to 400 m deep. This result was similar to that obtained in the Mediterranean Sea (Company and Sardà, 1997; Carbonell and Abelló, 1998) and NE Atlantic (González *et al.*, 2016). Bathymetric segregation by reproductive condition (ovigerous and non-ovigerous) was first reported in this study and suggests a gradual downward movement of females as they reach an ovigerous condition (Fig. 8). Such depth segregations seem to be in accordance with a distribution pattern which is supposed to reduce interspecific competition for space and available food resources (Cartes, 1993; 1998; Santos *et al.*, 2019b).

Negative allometry was observed in the CL-WW relationships for males, ovigerous and non-ovigerous females and combined sexes. These results agree with the allometric coefficient (b) reported for *P. edwardsii* in other North Atlantic and Mediterranean regions (Santana *et al.*, 1997; García-Rodríguez *et al.*, 2000; Colloca, 2002; González *et al.*, 2016). Although *P. edwardsii* is a nektobenthic crustacean, and therefore tends to increase weight isometrically with length (Company and Sardà, 1997), it is a specialized active predator that feeds mainly on macro-planktonic prey (Cartes, 1993). Therefore, the negative allometry observed suggest greater mobility, which may be advantageous during predation in deep-sea open-ocean areas characterized by narrow and steep shelves and rugged bottoms, such as in the Azores.

Ovigerous females of *P. edwardsii* were observed throughout most of the year. A broad spawning season also characterizes *P. edwardsii* in other marine systems (Poupin *et al.*, 1990; Santana *et al.*, 1997, Colloca, 2002), where a peak of spawning activity has been registered during the spring and summer. In the Azorean region, a peak of ovigerous female abundance

during the winter may indicate strong spawning activity during the subsequent warmer seasons in this North Atlantic area. This interpretation is in line with the seasonal pattern of phytoplankton sedimentation in the region (Martins *et al.*, 2007), which would favor larval growth, survival and recruitment (match-mismatch hypothesis; Cushing, 1990). However, more detailed investigations are recommended to clearly define this spawning time and related environmental driving forces.

The estimated L_{50} for mid-Atlantic *P. edwardsii* populations (25.0 mm CL) is longer than that obtained in the Mediterranean Sea (16.3 mm CL; Carbonell *et al.*, 2003). The fact that females in the Azorean region are mature at larger sizes than in the Mediterranean may reflect the absence of fishing targeting *P. edwardsii* in this mid-North Atlantic region, as opposed to the Mediterranean. Reductions in the size at maturity can be caused by phenotypic alterations and/or genetic adaptations (Law, 2000; Pukk *et al.*, 2013) and changes toward a smaller maturation size, due to high selective fishing pressure, have been widely detected in other species (Enberg *et al.*, 2012; Lappalainen *et al.*, 2016).

However, this relationship between intensive selective fishing and size at maturity does not seem to be as straightforward as it seems. CL at sexual maturity in ovigerous samples was estimated at 20.7 mm in Madeira, 19.7 mm in Canaries and 16.9 mm in Cape Verde (González *et al.*, 2016). Contrary to what is observed, similarity is expected in the observed size at maturity in the Macaronesia region for two main reasons: (1) shrimp fisheries in this region do not exist (Azores) or are developed on a highly artisanal basis (Madeira, Canary Islands and Cape Verde), and (2) preliminary studies on genetic diversity indicate these populations probably belong to a single stock (Manent *et al.*, 2013). This stock connectivity should be favored by the long larval stages of *P. edwardsii* (see Landeira *et al.*, 2009) which increase its potential for dispersal (Fig. 8). In this sense, size at maturity should also be correlated with latitude, as demonstrated for the CL distribution pattern. This may be because, as latitude increases, selection should favor increased size at maturity to maximize adult fitness (Fischer and Fiedler, 2002; González *et al.*, 2016).

Plesionika edwardsii shrimp appear to have the potential for a small artisanal fishery using semi-

pelagic traps, that can be used as an alternative to transferring fishing effort from intensively exploited demersal fisheries. However, primary fishing areas (*i.e.*, areas with depths between 200 and 400 m in which this species showed highest abundances) are very limited in the Azores (see Fig. 1). Besides that, we observed this species showed a high variability in distributional patterns and life-history traits and because of this, exploratory studies on the economic viability of this fishery should be conducted before starting any commercial fishing activity. Given the observed seasonal and spatial variability in its abundance, it was difficult to distinguish what differences were caused by fishing effect and what were not. Therefore, a directed fishery should be done on a precautionary basis, and should start with a very limited number of artisanal vessels, and their activity should be scientifically monitored so that the sustainability of the resource is assessed annually.

The present study provides valuable insights into a pristine state of the *P. edwardsii* population that can be useful for comparisons across regions and serve as a benchmark for a potential fishery in the future. The latter is much needed information that is often lacking, as collection and time series data typically begin after the onset of a fishery. Finally, we recommend further studies in order to better understand the oceanographic processes involved in biological and ecological patterns exhibited by this shrimp species (*e.g.*, oceanic circulation and mixing of stocks, assessment of the effects of temperature changes and ocean acidification on individuals).

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SUPPLEMENTARY MATERIAL

Table S1. Summary of total number of sets and traps by season and depth stratum employed to catch *Plesionika edwardsii* in the Azorean region during the period 1999–2000.

Table S2. Model selection results from Generalized Linear Models (GLMs) for effects of season (spring, summer, autumn, winter), depth stratum (100, 200, 300, 400, 500, 600 m) and sex (male, ovigerous female, non-ovigerous female) on abundance (catch per unit effort - CPUE) and size composition (cephalothorax length - CL) of *Plesionika edwardsii* in the Azorean region during the period 1999–2000. Detailed parameter estimates from fitting GLMs to abundance and CL are in Tab. S4.

Table S3. Tukey-adjusted post-hoc comparisons for Generalized Linear Models (GLMs) results. GLMs tested the effects of season (spring, summer, autumn, winter), depth stratum (100, 200, 300, 400, 500, 600 m) and sex (M: males, FO: ovigerous females, FN: non-ovigerous females) on abundances and size composition of *Plesionika edwardsii* in the Azorean region during the period 1999–2000. SE: standard error, LCL: lower 0.95 confidence limit, UCL: upper 0.95 confidence limit. Groups sharing a letter are not significantly different at the alpha = 0.05 level. Results are given on the log (not the response) scale.

Table S4. Parameter estimates from fitting Generalized Linear Models (GLMs) to abundance and size composition of *Plesionika edwardsii* in the Azorean region during the period 1999–2000. Variables: Season (spring, summer, autumn, winter), depth stratum (100, 200, 300, 400, 500, 600 m) and sex (M: male, FO: ovigerous female, FN: non-ovigerous female). SE: standard error.

Table S5. Summary of size statistics for males, non-ovigerous and ovigerous females *Plesionika edwardsii* in the Azorean region during the period 1999–2000. CL: cephalothorax length, WW: wet weight, n: number of individuals, CI: 0.95 confidence interval.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ETHICS STATEMENT

No specific authorization was required for any of the activities undertaken during this work at any of the sites visited. The study was conducted in the waters of the Azorean Exclusive Economic Zone. Threatened or

protected species have not been involved in any part of the field studies. Shrimp samples were collected randomly from scientific surveys and commercial landings. No approval was required from the Portuguese official veterinary department, and this study was performed in accordance with relevant institutional and national guidelines and regulations.

AUTHOR CONTRIBUTIONS

RS wrote the manuscript with support from WS, AN-P and OM. RS designed and performed the analysis and interpretation of data. MP, EI and OM helped conceive and revise the manuscript.

CONFLICT OF INTEREST

Authors have no conflict of interest.

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