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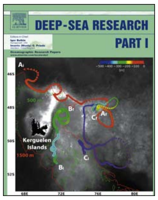

Latitudinal patterns in the life-history traits of three isolated Atlantic populations of the deep-water shrimp *Plesionika edwardsii* (Decapoda, Pandalidae)

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ABSTRACT

Patterns in the life-history traits of the pandalid shrimp *Plesionika edwardsii* are studied for the first time in three isolated Atlantic populations (Madeira, Canaries and Cape Verde Islands) to gain an understanding of their latitudinal variations. The maximum carapace size of the populations studied, as well as the maximum weight, showed clear latitudinal patterns. The patterns observed may be a consequence of the temperature experienced by shrimps during development, 1.37 °C higher in the Canaries and 5.96 °C higher in the Cape Verde Islands than in Madeira. These temperature differences among populations may have induced phenotypic plasticity because the observed final body size decreased as the temperature increased. A latitudinal north-south pattern was also observed in the maximum size of ovigerous females, with larger sizes found in the Madeira area and lower sizes observed in the Cape Verde Islands. A similar pattern was observed in the brood size and maximum egg size. Females of *P. edwardsii* produced smaller eggs in the Cape Verde Islands than did those at the higher latitude in Madeira. *P. edwardsii* was larger at sexual maturity in Madeira than in the Cape Verde Islands. The relative size at sexual maturity is not affected by latitude or environmental factors and is the same in the three areas studied, varying slightly between 0.568 and 0.585. *P. edwardsii* had a long reproductive season with ovigerous females observed all year round, although latitudinal variations were observed. Seasonally, there were more ovigerous females in spring and summer in Madeira and from winter to summer in the Cape Verde Islands. *P. edwardsii* showed a latitudinal pattern in size, with asymptotic size and growth rate showing a latitudinal compensation gradient as a result of an increased growth performance in the Madeira population compared to that of the Cape Verde Islands.

1. Introduction

A species can adjust its life-history traits to environmental conditions through plasticity or genetic variations, thereby giving the species the ability to have a wide geographical distribution (Cardoso and Defeo, 2004; Marshall et al., 2008). In this regard, the fitness of a species plays an important role in its distribution and abundance; the reproductive and growth components of fitness are two of the most important processes because they require the greatest energy inputs in the life cycle of an organism (Sastry, 1983; Sexton et al., 2009). Among the reproductive components, egg production is an important evolutionary and ecological trait that reflects the maternal energy investment and influences the offspring and maternal fitness (Briones-Fourzán et al., 2010). Other aspects, such as moult cycles, synchronization between reproduction and moulting, and size-related growth rate, are the main biological processes regulating growth in crustaceans. These biological processes are linked to external abiotic factors, such as temperature, hours of daylight, and food availability, which can stimulate or inhibit growth processes (Company and Sardà, 2000). All of these aspects are important because the accumulation of small fitness differences throughout the life cycle results in important differences in overall fitness, which affects the ability of distribution and abundance of the species (Sexton et al., 2009).

In species occurring along broad latitudinal gradients, such as the deep-water shrimp species of the genus *Plesionika* Bate, 1888,

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local phenotypic plasticity or genetic variations in environmental conditions may be observed as differences in growth and reproductive features among populations (Wehrtmann and Lardies, 1999; Marshall et al., 2008; Briones-Fourzán et al., 2010). Species of the genus *Plesionika* play an important ecological role in benthic ecosystems, and the life-history traits of species living in these habitats, such as *Plesionika edwardsii* (Brandt, 1851), may need to adapt to deep environmental features (Carbonell and Abelló, 1998; Vafidis et al., 2005).

P. edwardsii inhabits the eastern Atlantic, from the southwest of Spain to Angola, including Madeira, Canary and Cape Verde Islands (González et al., 2001). These three archipelagos are located in the Canary Current System, which is one of the Large Marine Ecosystems of the World and Linked Watersheds (LMEs) across global oceans (Sherman and Hempel, 2009). They are characterized by their singular bathymetry, hydrography and productivity, as well as their ability to support marine populations that have adapted their feeding, reproductive and growth strategies (Hernández-León et al., 2007). The region of Madeira is dominated by the Canary Current system, which induces a southward net transport (Caldeira and Sangrà, 2012). The presence of a seamount at the southeast end of Madeira produces a localized island upwelling of cold nutrient-rich waters around the coasts (Caldeira et al., 2002). The Canary Islands are characterized by the presence of the first 500 m of depth of Eastern North Atlantic Central Water (Hernández-Guerra et al., 2002). Meanwhile, the sea waters off the Cape Verde Islands are under the influence of the North Equatorial Counter-Current and the Canary Current. The seasonal circulation patterns of this Counter-Current mainly show their influence in the south-eastern part of the archipelago (Marques et al., 2009).

In this work, latitudinal variations in the life-history traits of *P. edwardsii*, including depth distributions and demography, are analysed as indicators of biogeographic trends along a latitudinal gradient in the three island regions. This comparison can reveal how this species responds to geographic environmental variations with regard to their life-history traits, providing more information for a better understanding of the relationship between variation in fitness and environment and between fitness and abundance (Sexton et al., 2009). A thorough understanding of their ecology, mainly the reproductive, growth and brood size strategies, and their latitudinal differences would be of great interest considering that deep-water species are especially vulnerable to exploitation (Polidoro et al., 2008).

2. Materials and methods

2.1. Sampling and data collection

Shrimp caught around the Madeira (MA), Canary (CIS) and Cape Verde (CVS) archipelagos (Fig. 1) during 22 research cruises conducted between 2006 and 2012 were studied. Shrimp were captured with multiple semi-floating shrimp traps deployed at approximately 2.5 m above the sea floor, with a 56 × 57 cm base length and a 57 cm height, covered with a 15 × 20-mm plastic mesh. Each trap had one troncoconical opening that had an inner diameter of 19 cm. The fishing gear consisted of 75 traps on a fishing rope separated from each other by 15 m. Atlantic chub mackerel (*Scomber colias*) was used as bait, and immersion times ranged from 20 to 24 h. For each cruise, salinity and temperature data were obtained along the water column using a CTD sensor..

The study areas were randomly sampled from a depth of 50–500 m. The sampled locations varied from trip to trip, and the sampling effort across the bathymetric range was equally distributed at 50 m intervals, with eight strata prospected: 100–149, 150–199, 200–249, 250–299, 300–349, 350–399, 400–449, and 450–500 m. During each cruise, an average of 225 traps for each depth stratum were deployed over the sea ground, covering sandy, muddy, and rocky bottoms, with a total of 1800 traps used. The standardized mean biomass (in weight per trap) of each stratum was analysed and tested for differences among the strata using ANOVA. Additionally, the standardized mean biomass (in weight per trap) of the strata of highest abundance were compared for differences among archipelagos using ANOVA.

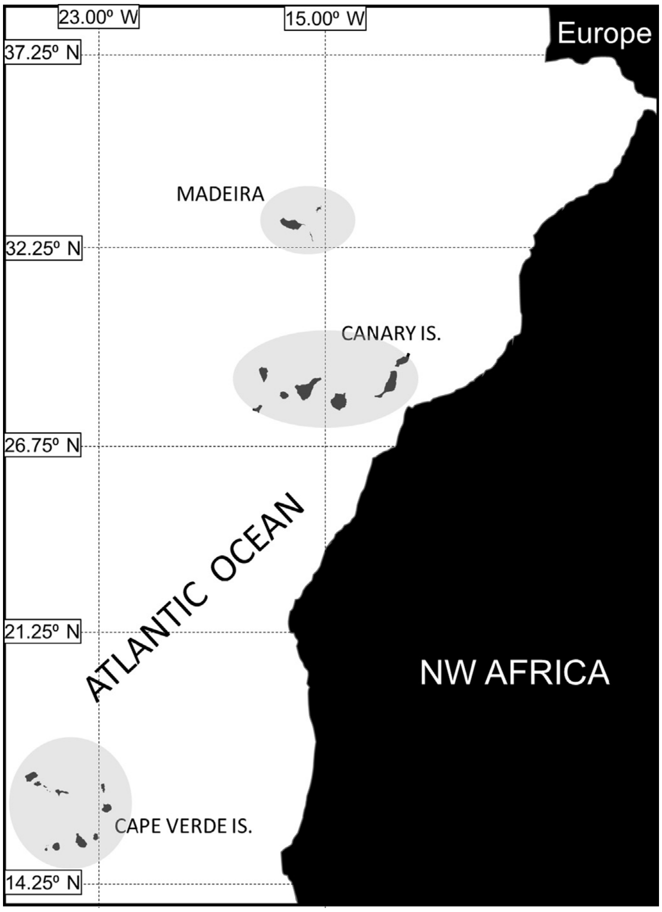

Fig. 1. Geographical location of the study areas of Madeira, Canaries, and Cape Verde Islands..

Five traits from each shrimp were measured: carapace length, weight, maturity stage, egg number, and egg volume. Further, five traits of each population were estimated, namely, length at maturity, fecundity, reproductive output, growth rate and maximum length.

Carapace length (CL, from the posterior edge of the eye socket to the mid-dorsal rear edge of the carapace) was measured with a digital calliper to the nearest 0.01 mm, and the total weight (TW) was measured to the nearest 0.01 g. Shrimp were sexed under a binocular microscope based on the presence or absence of the appendix masculina on the endopod of the second pleopod, together with the examination of the shape of the endopod of the first pleopod (King and Moffitt, 1984). The ovigerous condition of females was also recorded based on the presence of external or remaining eggs on the pleopods (King and Moffitt, 1984).

2.2. Relationships between main variables and sex ratio

The CL–TW relationship was estimated for males and females using a power equation. The equality of the two CL–TW regressions estimated by sexes was assessed using an *F*-test (Sachs, 1982). Differences between the expected value from the isometric growth ($b=3$) in the CL–TW relationship and values of the regression coefficient (*b)* were compared using a *t*-test (Sachs, 1982).

The sex ratio was estimated for the total sample and each size interval. The Pearson chi-square goodness-of-fit test was used to evaluate the equality of frequencies between sexes. The equality in CL and in TW between males and females among areas was analysed using two-way ANOVA. The equality in CL among depth strata was compared using ANOVA. Once the null hypothesis was rejected, Dunnett's *T3* post hoc test was applied to determine which strata differed. The post hoc test identified homogeneous subsets where means did not differ within each subset (Sokal and Rohlf, 2012). For all statistical tests, the significance level was $\alpha=0.05$.

2.3. Spawning period and maturity

To assess the reproductive period, the relative proportion of females of *P. edwardsii* in the ovigerous condition by season was determined. For seasonal analysis, winter includes samples from January to March, spring includes samples from April to June, summer includes samples from July to September, and autumn includes samples from October to December. The percentage of ovigerous females for each 1 mm CL class was examined using the samples collected during the main reproductive period ($>70\%$ of the females in ovigerous condition). Size at sexual maturity (CL_{50}) (the carapace length at which 50% of females are ovigerous) was determined from the relationship between the percentage of ovigerous females and the CL class. The percentage of ovigerous females (P) by size class was fitted to a logistic equation $P=100/(1+\exp(-c^*(CL–CL_{50})$ using non-linear regression, where c is the model parameter and CL_{50} is the size at sexual maturity.

The relative reproductive potential (RRP) was estimated for *P. edwardsii* according to Biscoito 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 of the appendix masculina was measured (Ahamedi and Ohtomi, 2014) and then estimated as a percentage of the size of the appendix interna (King and Moffitt, 1984) in a subsample of 150 males. This relative length of the appendix masculina with CL was estimated as an indicator of morphological maturity when increasing in size with shrimp growth, suggesting that male characteristics were developing and that those individuals with reduced appendix masculina were immature males (King and Moffitt, 1984). A power equation was fitted to the data using non-linear regression for the values in which the data could be separated into two groups. The size at which allometric growth changed, as an indicator of morphometric maturity, was iteratively searched using increments of 0.1 mm CL (Ahamedi and Ohtomi, 2014). An *F*-test based on the difference between the residual sums of squares was estimated for assessing the equality of the sums of squares of the two subsets and of the simple model (Somerton, 1980). An *F*-test was also calculated to test differences between the two regressions, corresponding to the sexually immature and mature growth phases (Sachs, 1982). The relative growth patterns of the appendix masculina with the size of the second pleopods, in both sexually immature and mature growth phases, were analysed using a *t*-test for assessing the equality of the regression coefficient (Sachs, 1982).

To compare the results among the populations studied, the relative size at onset of maturity (R_{SOM}) was calculated using the equation $R_{SOM}=CL_{50}/CL_{\infty}$, where CL_{∞} is the asymptotic maximum size attained by shrimp (Charnov, 1990; Hirose et al., 2013).

2.4. Fecundity and egg morphology

For ovigerous females, egg morphology was classified in four stages as follows: Stage I, eggs are blue with their embryos lacking eye pigmentation and yolk filling most of the embryo volume; Stage II, eggs are pale blue with eyespot pigmentation present in the embryos and appendage rudiments, and the nerve ganglia appear as a thickening of the blastoderm; Stage III, eggs are light brown with eye pigmentation clearly visible in the embryos, and there is a large cephalothorax, extending abdomen, and complete segmentation; Stage IV, eggs are ready to hatch or the remains of hatched eggs are observed on female pleopods.

Ovigerous females from all size classes were used for the morphological study of eggs and then used to estimate fecundity. Pleopods with attached eggs were removed from females, and then egg masses were placed on a 100 μm mesh, washed and isolated from pleopods. For each developmental stage of embryos, 15 females of each size class were selected to estimate the egg volume (mm^3). From each ovigerous female, the maximum and minimum diameters of 30–35 randomly selected eggs were measured. Egg volume (mm^3) was calculated as $EV=(4/3\pi a2c)$, where "*a*" and "*c*" represent the maximum and minimum egg diameter, respectively. The equality in egg volume between males and females among areas was analysed using two-way ANOVA.

The total number of eggs in stage III attached to the pleopods was counted directly under a binocular microscope in 60 females from all size classes (Triay-Portella et al., 2014). A linear function was fitted to number of eggs versus CL.

2.5. Growth

The carapace length frequency distributions (in 0.5 mm intervals) were estimated seasonally for males and females. Growth was studied using seasonal length-frequency distributions by sex according to the Petersen method (Sparre et al., 1989). The CL-frequency distributions of each sex and season were separated using model progression analysis (Bhattacharya's method) with FiSAT II software (Gayanilo et al., 2005). Bhattacharya's method identifies normal distributions of the polymodal CL length-frequency distributions. Separation indices between different cohorts with values of less than 2 indicate a large overlap between cohorts and were considered statistically unacceptable (Sparre et al., 1989). The routine NORMSEP (normal distribution separator) in the FiSAT II software was used for the decomposition of mixtures of normal distributions on the basis of Hasselblad's maximum likelihood method (Hasselblad, 1966). The normal distribution of each component was assumed to represent an age group in the shrimp population. Growth was modeled using the von Bertalanffy growth function (VBGF). A preliminary estimation of L_{∞} was obtained separately for males and females using the Gulland and Holt (1959) method, and the k value was obtained by ELEFAN I using the FiSAT II software (Gayanilo et al., 2005). The growth parameters of the VBGF were estimated from the growth increment data, which were estimated from linking of the mean lengths. A routine analysis of length-at-age data were used for the non-linear estimation of the growth parameters. The growth performance index φ' ($\varphi'=2^*\log L_{\infty}+\log k$) was used to compare the growth rates between sexes and among areas (Pauly and Munro, 1984).

3. Results

3.1. Size structure

A total of 197,031 individuals of *P. edwardsii* were collected (30,458 in MA, 109,689 in CIS, and 56,884 in CVS) (Table 1). In all areas, females were larger and heavier than males (Table 1). In MA, differences between sexes were 2.43 mm (7.30%) in maximum size

Table 1
Carapace length (CL in mm) and total weight (TW in g) for males and females of *P. edwardsii*. *Min*, minimum; *Max*, maximum; *Mean*, mean value; s.d. standard deviation; *n*, number of specimens.

Area/Sex	CL			TW			
	Min	Max	Mean ± s.d.	Min	Max	Mean ± s.d.	n
Madeira							
Males	12.05	30.85	23.88 ± 2.62	1.07	19.22	9.60 ± 2.55	13879
Females	12.06	33.28	25.68 ± 2.88	1.06	24.21	12.96 ± 3.69	16582
Canaries							
Males	7.94	28.29	21.98 ± 2.66	0.71	15.20	7.57 ± 2.26	46622
Females	7.06	30.45	23.16 ± 2.93	0.55	20.60	9.47 ± 3.06	63067
Cape Verde Is.							
Males	10.95	26.86	18.20 ± 2.03	0.75	14.40	4.18 ± 1.31	24292
Females	10.60	29.10	18.98 ± 2.24	0.80	19.36	5.28 ± 1.87	32592

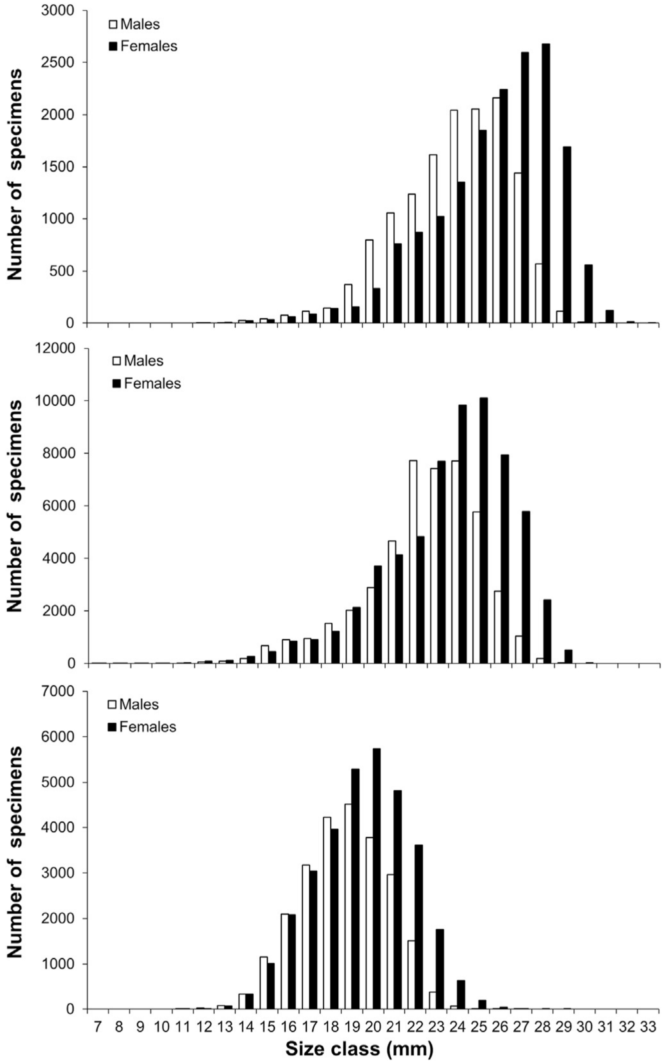

Fig. 2. Number of male and female specimens of *Plesionika edwardsii* in Madeira (top), Canaries (middle) and Cape Verde Islands (bottom).

(CL) and 4.99 g (20.61%) in weight (TW). In CIS, these differences were 2.16 mm (7.09%) in CL and 5.40 g (26.21%) in TW. In CVS, these differences were 2.24 mm (7.69%) in CL and 4.96 g (25.61%) in TW. The highest values of length and weight were recorded in MA, while the lowest were in CVS. (Fig. 2). Two-way ANOVA comparing the differences in CL and TW between males and females among areas showed significant differences for the factors of sex ($F_{1,>1000} > 6433$, $p < 0.0001$) and area ($F_{2,>1000} > 4191$, $p < 0.0001$), as well as for the interaction effect ($F_{2,>1000} > 290.17$, $p < 0.0001$)..

The *F*-test for the CL–TW relationship between sexes in all of the archipelagos showed statistically significant differences between the two regressions estimated (all areas: $F_{1,>1000} \geq 7.51$, $p = 0.0063$). The regression coefficient was highest in CVS and lowest in MA, and a *t*-test with the null hypothesis of equality in the regression coefficient (H_0: b=3) was rejected in all archipelagos for all groups (negative allometric growth) (Table 2). The *F*-test for the CL–TW relationship of males and females among areas showed significant differences between males and females for the three regions studied (males $F_{2,>1000} = 5.92$, $p = 0.0028$; females $F_{2,>1000} = 5.33$, $p = 0.0050$).

3.2. Sex ratio

The sex ratio showed a predominance of females in all areas (MA 1:1.20, CIS 1:1.35, CVS 1:1.34), and the Pearson chi-square goodness-of-fit test indicated that the null hypothesis of equality sex frequencies was rejected (all areas $\chi^2_1 \geq 240.4$, $p < 0.0001$). Males were significantly more abundant than females in the 17- to 25-mm CL size classes in MA ($\chi^2_1 \geq 4.0$, $p = 0.0455$) (Fig. 3). However, females were significantly more abundant in size classes larger than 25 mm CL ($\chi^2_1 = 119.03$, $p < 0.0001$). In CIS, females were dominant in the 23-mm CL size class ($\chi^2_1 = 5.11$, $p = 0.0238$),

Table 2
Parameters of CL–TW relationship ($TW = a{*}CL^b$) for males, females and all shrimps of *P. edwardsii*. *a*, intercept; *b*, regression coefficient (allometric coefficient); s.d., standard deviation; r^2, determination coefficient; *n*, number of specimens; *t*, *t*-test value;

Sex	a	b	s.d. (b)	r^2	n	*t*
Madeira						
Males	0.005266	2.360	0.008785	0.869	13879	72.8[a]
Females	0.003494	2.525	0.009228	0.862	16582	51.4[a]
Ovigerous	0.005869	2.372	0.011431	0.804	12541	54.9[a]
Non ovigerous	0.001065	2.525	0.013429	0.921	4041	35.3[a]
All shrimps	0.001907	2.697	0.007076	0.860	30458	42.8[a]
Canaries						
Males	0.002442	2.592	0.003697	0.935	46622	110.3[a]
Females	0.001821	2.712	0.003789	0.919	63067	76.0[a]
Ovigerous	0.002301	2.651	0.003735	0.907	29420	93.4[a]
Non ovigerous	0.002158	2.643	0.003846	0.952	33647	92.8[a]
All shrimps	0.002796	2.590	0.005735	0.889	109689	71.4[a]
Cape Verde Is.						
Males	0.001373	2.754	0.008933	0.894	24292	27.5[a]
Females	0.000881	2.942	0.007070	0.922	32592	8.20[a]
Ovigerous	0.001146	2.858	0.008383	0.903	25732	16.9[a]
Non ovigerous	0.001065	2.854	0.013960	0.911	6860	10.4[a]
All shrimps	0.000751	2.981	0.006019	0.901	56884	2.5[a]

[a] null hypothesis of isometric growth rejected.

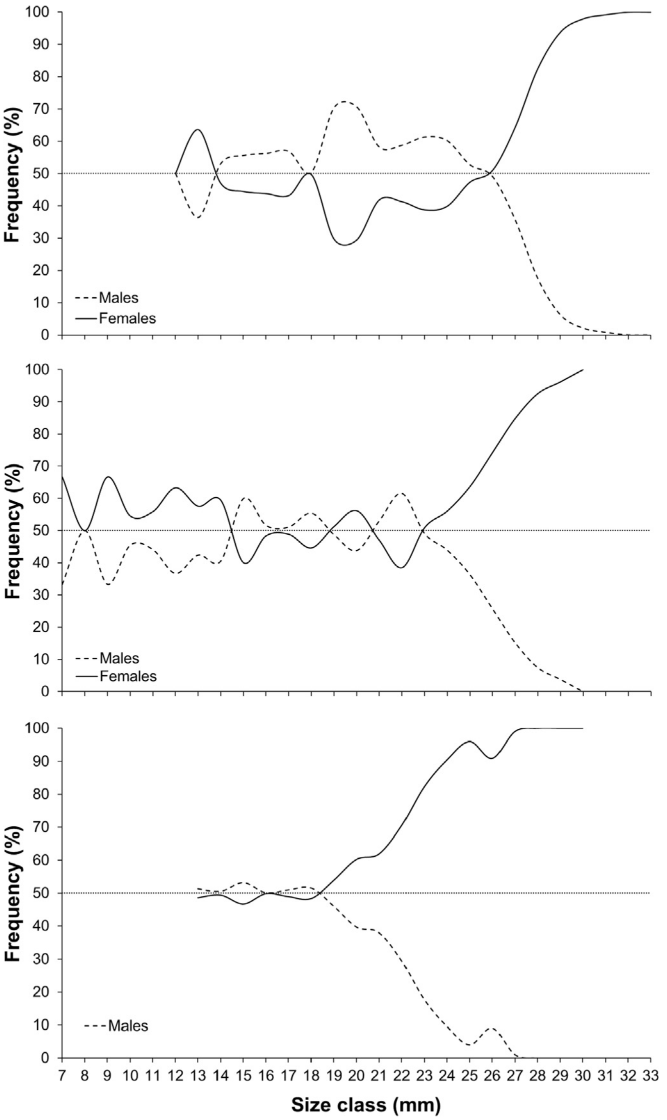

Fig. 3. Frequency of males and females by size classes of *Plesionika edwardsii* in Madeira (top), Canaries (middle) and Cape Verde Islands (bottom).

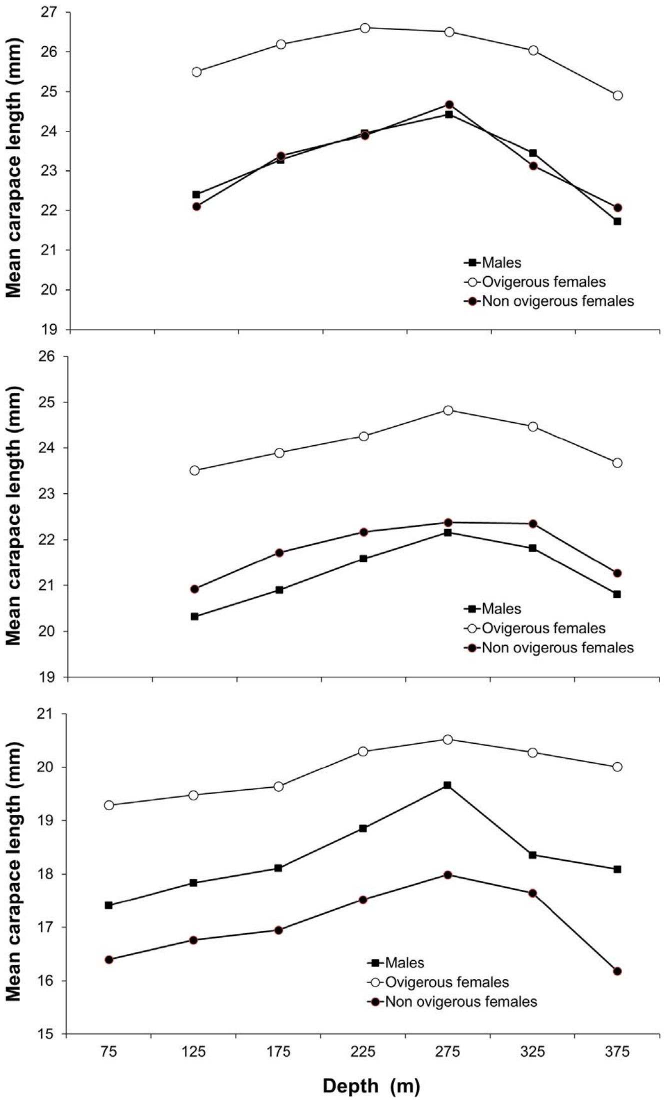

Fig. 4. Variation of the mean carapace length with depth for males, non-ovigerous and ovigerous females of *Plesionika edwardsii* in Madeira (top), Canaries (middle) and Cape Verde Islands (bottom).

and a similar pattern was observed in females in the 18-mm CL size class in CVS ($\chi^2_1=4.32$, $p=0.0377$) (Fig. 3), indicating a north-south pattern. The relative magnitude of sex-ratio biases was different among areas, 69.29% in MA, 67.27% in CIS and 55.90% in CVS, with a maximum difference of 13.38% between areas, showing the highest relative difference in MA and the lowest in CVS..

3.3. Depth distribution

A similar pattern was observed for males and females in all areas, with the mean CL increasing until reaching the 225 to 275 m depth stratum (Fig. 4). However, the mean size observed in each stratum showed a north-south pattern, with the highest values in MA and the lowest in CVS. Student's *t*-test indicated that the null hypothesis for equality in the mean CL in each stratum between consecutive areas was rejected for males and females (in all cases: $t_{>1000} \geq 2.76$, $p=0.0058$). ANOVA determining the differences between CL and sex among different depth strata showed significant differences in the three areas (all areas: males $F_{5,>1000} \geq 157.95$, $p<0.0001$, females $F_{5,>1000} \geq 45.65$, $p<0.0001$). Dunnett's *T3* post hoc test showed significant differences in CL among all strata in all areas ($p<0.05$). The standardized biomass showed a decreasing pattern at depths below the thermocline in the three areas (Fig. 5). The maximum value of standardized biomass with depth was located immediately below the thermocline in the three areas and was found at depths of 100–150 m in CVS 17.01–22.30° C), 200–250 m in CIS 16.10–17.71° C) and 150–200 m in MA 15.48–16.34° C) (Fig. 5). Both temperature at the maximum abundance depth and at the depth range distribution showed a decreasing pattern with latitude. ANOVA of the standardized biomass among different depth strata showed significant differences in the three areas (MA $F_{6,>50}=5.54$, $p=0.0002$; CIS $F_{7,>200}=4.62$, $p<0.0001$; CVS $F_{7,>100}=4.86$, $p<0.0001$). ANOVA indicated significant differences in the standardized biomass at the maximum abundance stratum among areas ($F_{2,>120}=9.95$, $p=0.0001$). Dunnett's *T3* post hoc test showed significant differences in the mean standardized biomass among all areas ($p<0.05$)...

3.4. Spawning period

Ovigerous females represented 75.63% of the total females in MA, 46.64% in CIS, and 79.58% in CVS. Ovigerous females were observed in all seasons in the three areas (Fig. 6). Of the total

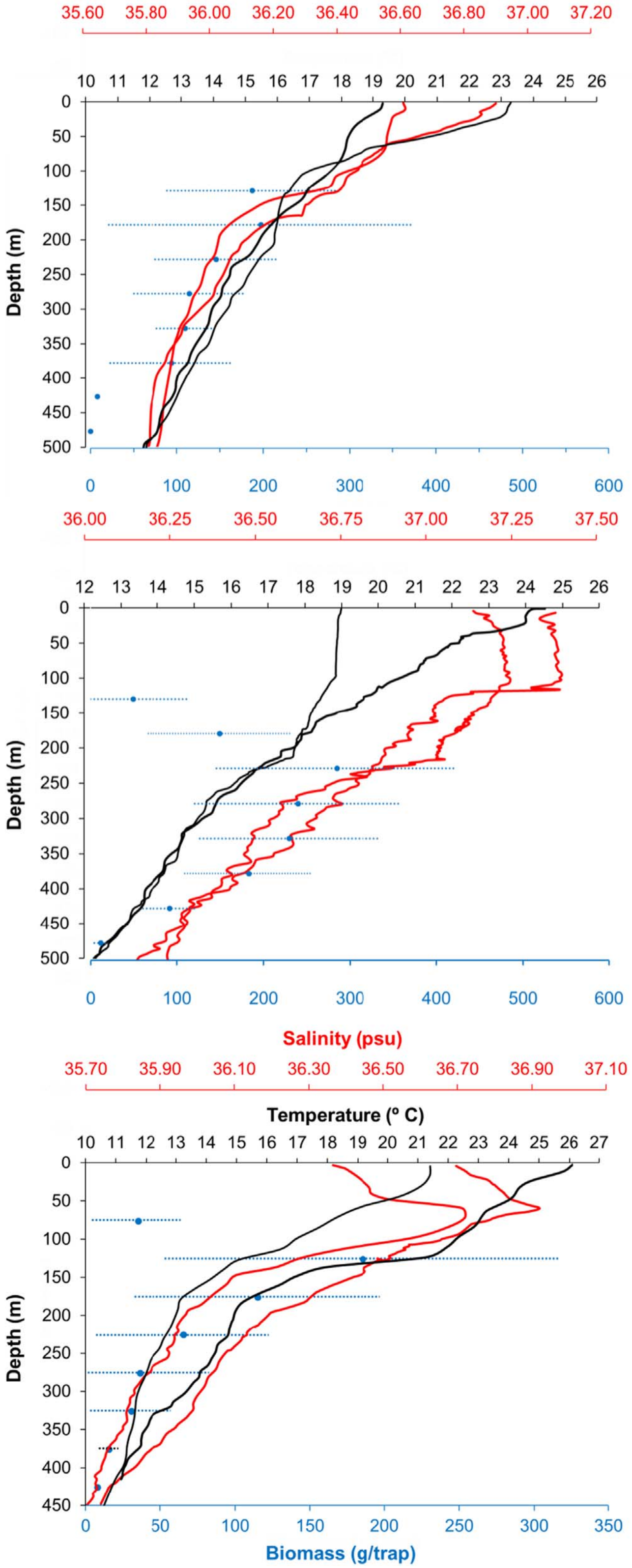

Fig. 5. Changes in both salinity and temperature with depth corresponding to the extreme values observed for seasons and areas and standardized *Plesionika edwardsii* biomass (horizontal lines mean ± sd) by depth stratum of 50 m in Madeira (top), Canaries (middle) and Cape Verde Islands (bottom).

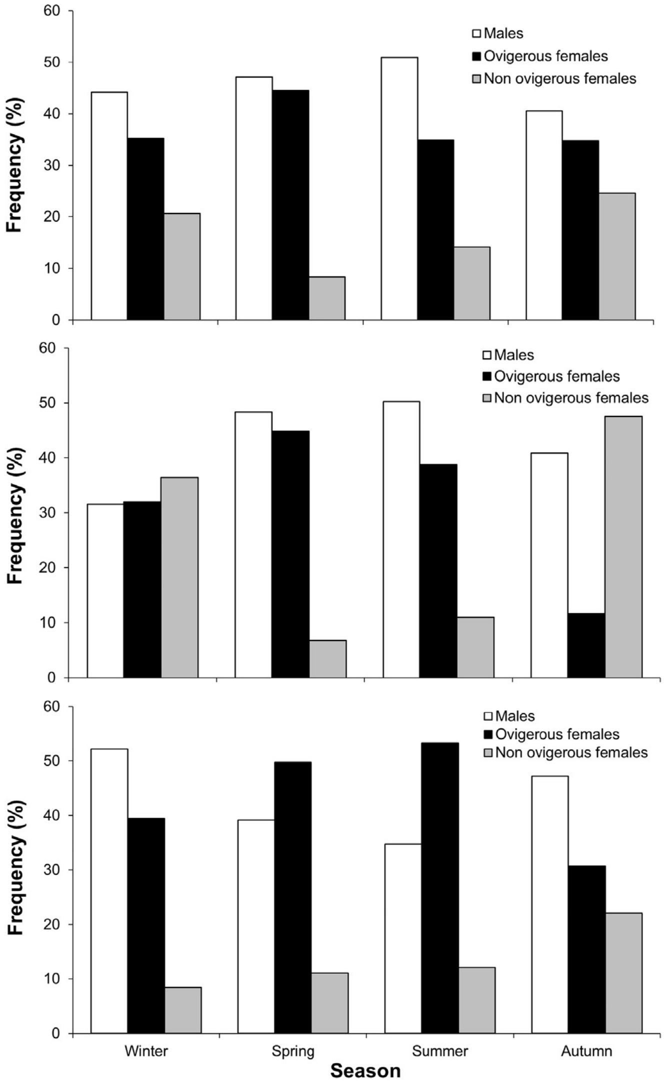

Fig. 6. Seasonal frequency of males, non-ovigerous and ovigerous females of *Plesionika edwardsii* in Madeira (top), Canaries (middle) and Cape Verde Islands (bottom).

females, the ovigerous ones were dominant (> 70% of females) in spring and summer in both MA and CIS and from winter to summer in CVS. Eggs in stage I were found in high proportions in females carrying eggs year-round in all areas and seasons (Fig. 7). Eggs in stages II and III were observed in proportions lower than 24.84% and 20.13% of females carrying eggs, respectively, in all areas and seasons (Fig. 7). Eggs in stage IV were found in proportions higher than 5% of berried females in spring and summer in MA, from spring to autumn in CIS, and in all seasons in CVS (Fig. 7)...

3.5. *Sexual maturity of females*

Student's *t*-test showed significant differences in mean CL between ovigerous and non-ovigerous females for the three areas (all cases, $t_{>1000} \geq 47.71$, $p < 0.0001$) (Table 3). Likewise, Student's *t*-test showed significant differences in the mean CL between ovigerous (all cases $t_{>1000} \geq 3.28$, $p=0.0011$) and non-ovigerous females (all cases $t_{>1000} \geq 2.71$, $p=0.0068$) of consecutive areas. The length at sexual maturity in ovigerous samples was estimated at 20.72 mm CL in MA, 19.65 mm CL in CIS, and 16.89 mm CL in CVS (Table 3), showing a north-south size pattern at sexual maturity.

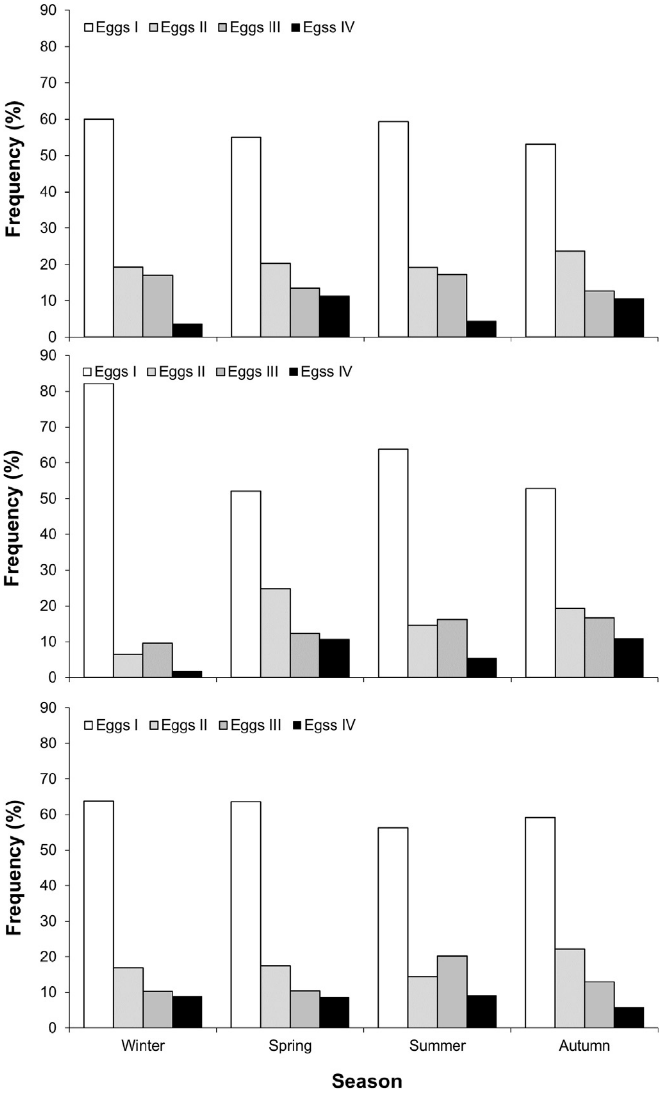

Fig. 7. Seasonal frequency of eggs developmental stage (I-IV) of *Plesionika edwardsii* in Madeira (top), Canaries (middle) and Cape Verde Islands (bottom)..

Table 3
Carapace length (CL in mm) for ovigerous and non-ovigerous females of *P. edwardsii. Min*, minimum; *Max*, maximum; *Mean*, mean value; s.d., standard deviation; *n*, number of specimens. c, parameter of the logistic equation of maturity; CL_{50}, size at sexual maturity; r^2 coefficient of determination..

Area/Sex	CL (mm)			c	CL_{50}	r^2	n
	Min	Max	Mean ± s.d.				
Madeira							
Ovigerous	12.45	33.28	26.36 ± 2.27	0.5194	20.72	0.982	13879
Non ovigerous	12.06	33.28	23.58 ± 3.58				16582
Canaries							
Ovigerous	12.01	30.45	24.18 ± 2.05	0.7357	19.65	0.966	46622
Non ovigerous	7.06	30.45	22.26 ± 3.27				63067
Cape Verde Is.							
Ovigerous	10.63	29.60	21.57 ± 1.90	0.7449	18.29	0.984	24292
Non ovigerous	10.60	29.10	19.84 ± 2.11				32592

3.6. Sexual maturity of males

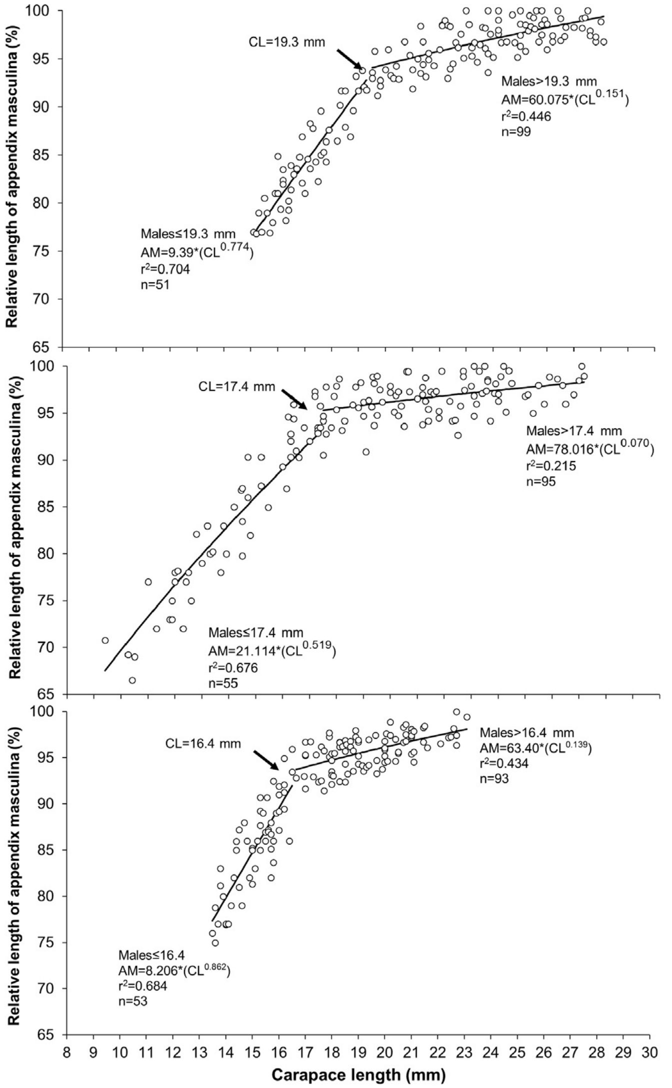

Fig. 8. Relative length of the appendix masculina by carapace length for males of *Plesionika edwardsii* in Madeira (top), Canaries (middle) and Cape Verde Islands (bottom), where n is the number of shrimp and r^2 is the determination coefficient. Fitted lines correspond to each potential model estimate. Arrows indicate the size at which allometric growth changes, as an indicator of morphological maturity.

The ratio of the appendix masculina was plotted against CL, revealing changes in relative growth associated with maturity (Fig. 8). The relative growth of the appendix masculina showed changes related to ontogeny. Allometric growth changes occurred at a size of 19.3 mm CL in Madeira, 17.4 mm CL in the Canaries, and 16.4 mm CL in the Cape Verde Islands ($F_{2,>50} \geq 5.01$, $p=0.0104$), showing the largest size in MA and the smallest in CVS. An *F*-test showed significant differences between the two regressions (the pre- and post-maturity growth phases) in all cases ($F_{1,>40} \geq 8.56$, $p=0.0056$). A *t*-test on the growth of the appendix masculina showed significant differences in the regression coefficient between the subsets considered ($t_{>50}=3.95$, $p=0.0003$). Allometry in the growth of the appendix masculina was always observed irrespective of subset (pre- or post-maturity phase) or area..

R_{SOM} was very similar for males and females from Madeira (0.582 and 0.573 for males and females, respectively), with a difference of 1.42% between sexes. In the Canaries, the difference in R_{SOM} between sexes was 0.71% (0.578 males, 0.574 females). In the Cape Verde Islands, R_{SOM} was very similar (0.585 males, 0.568 females), with a difference of 2.98% between sexes. Differences were smaller than 1.13% in males and 1.16% in females when comparing each sex among populations.

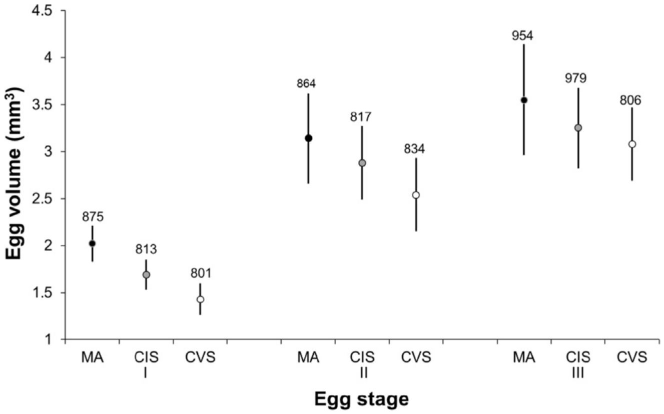

Fig. 9. Mean egg volume (mm^3) and standard deviation of *Plesionika edwardsii* by area and egg development stage. The number indicates the number of eggs counted.

3.7. *Egg volume and number of eggs*

The mean egg volume increased from stage I to stage III in all areas (Fig. 9), showing the highest volume in MA and the lowest in CVS. A two-way ANOVA on egg volume by egg developmental stage among areas showed significant differences for factors stage and area (stage, $F_{4,>1000}=1567.4$, $p<0.0001$; area, $F_{4,>1000}=340.9$, $p<0.0001$), as well as for the interaction effect ($F_{4,>1000}=48.75$, $p<0.0001$)..

The number of eggs increased significantly with female size in the three areas, showing a north-south pattern. The linear equations of the three regression were significantly different (ANCOVA, $F_{2,177}=17.13$, $p<0.0001$) (Fig. 10). The number of external eggs carried by females in stage III ranged from 2382 to 10859 eggs in MA (Table 4), from 1856 to 8032 eggs in CIS, and from 1278 to 7094 eggs in CVS, with females having the lowest limits of this range (Table 4). The number of eggs among archipelagos for the whole body size ranges of each area showed significant differences (ANOVA, $F_{2,177}=57.21$, $p<0.0001$). For the common range of body size of the three archipelagos (19.4–23.5 mm) the number of eggs among areas also showed significant differences (ANOVA, $F_{2,88}=5.43$, $p<0.006$), with mean number of eggs of 3616 in CVS, 4059 in CIS, and 4407 in MA..

The modal size class of egg production showed the largest size in MA and the smallest in CVS, with a north-south pattern. The modal size class of egg production in Madeira was 24–29 mm CL (74.78% of females), which yielded 83.75% of the population egg production (Fig. 11); females smaller than 24 mm CL comprised 21.02% of the population and produced only 8.66% of the eggs. In the Canaries, the modal size class was 23-27 mm CL (60.55% of females), which yielded 66.07% of total egg production; females smaller than 23 mm CL comprised 25.34% of the population and produced only 9.45% of the eggs (Fig. 11). Finally, in the Cape Verde Islands the modal size class of egg production was 19–22 mm CL (59.68% of females), which yielded 70.71% of the population egg production (Fig. 11); females smaller than 19 mm CL comprised 32.23% of the population and produced only 9.65% of the eggs..

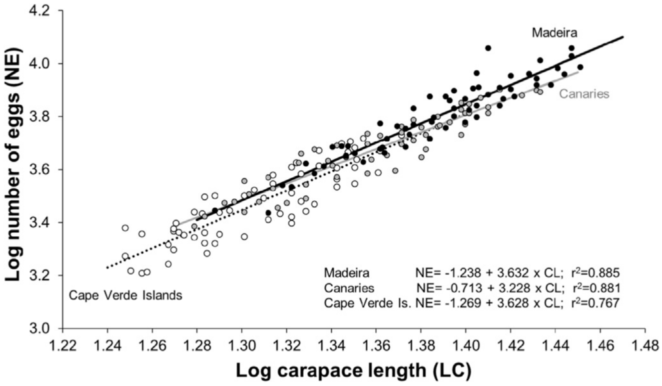

Fig. 10. Brood size estimates in logarithmic number of eggs (NE) by logarithmic carapace length (CL) for *Plesionika edwardsii* females in Madeira, Canaries and Cape Verde Islands, where n is the number of females and r^2 is the determination coefficient. Fitted lines correspond to each logarithmically transformed linear model estimate.

3.8. *Growth*

The analysis of modal progression showed that males attained a smaller asymptotic length and growth rate than females in the three archipelagos (Table 5). The asymptotic length and the growth rate for males and females increased according to a south-north pattern from the Cape Verde to Madeira Islands. The growth performance index (φ‘) was highest in MA and lowest in CVS, varying between 2.60 and 2.77 for males and from 2.73 to 2.88 for females. The highest relative age estimated by means of the growth increment data converted in length at relative age was 3.81 years in MA, 3.85 years in CIS, and 3.88 years in CVS.

4. Discussion

In the studied areas, the populations of *P. edwardsii* showed clear variations in their life-history traits. These changes could be due to variations linked to changes in environmental factors along latitudinal gradients, as in the case of temperature, or could occur as a consequence of the species being distributed among geographic breaks in the form of isolated islands with different environmental conditions (Barria et al., 2014). In the present study, latitude could be more important than breaks in the phenotypic variations for the majority of these fitness-related traits because the influence of geographic breaks depends on the larval dispersal ability of each species; species with low dispersal ability and short larval stages are highly affected by breaks (Barria et al., 2014). In this regard, Landeira et al. (2009) described a series of long larval stages for *P. edwardsii* that increases their potential for dispersal ability and reduces the influence of geographic breaks in the form of isolated islands. In any case, *P. edwardsii*, as an ectotherm species, has minimized the fitness costs associated with exposure to variations in temperature in the studied areas through local phenotypic plasticity or genetic variations. Both mechanisms could be evolving together, and it is difficult to determine the contribution of each (Yampolsky et al., 2014).

The maximum carapace size of the populations studied, as well as the maximum weight showed a clear latitudinal pattern, with larger shrimps observed at higher latitudes (Madeira) and smaller shrimps at lower latitudes (Cape Verde Islands). This increase in body size with latitude is known as Bergmann's rule and has been described in other decapod crustaceans (Hirose et al., 2013). The mechanisms underlying Bergmann's rule are related to different thermal exposures that could result in different physiological costs at the cellular level (Stillman and Somero, 2000; Hirose et al., 2013). This agrees with the range of temperatures of the maximum abundance of the species, which is 1.37° C higher in the Canaries and 5.96° C in the Cape Verde Islands than in Madeira. The clear latitudinal gradients found in body size are consistent with the trends observed in morphological characteristics, showing higher asymptotic size, physiological and morphometric length at maturity, modal class size egg production, and growth rate in Madeira compared to the Cape Verde Islands.

The size at sexual maturity also showed a correlated increase

Table 4
Maximum, minimum and mean number of eggs, with standard deviation (±sd), and the corresponding carapace length (CL), total weight (TW) and CL range analysed of females of *P. edwardsii*. n, number of specimens. *Min*, minimum; *Max*, maximum; *Mean*, mean value; s.d., standard deviation; *n*, number of specimens.

Area	Eggs number			CL (mm)		TW (g)		CL range (mm)		n
	Min	Max	Mean ± s.d.	Min	Max	Min	Max	Min	Max	
Madeira	2739	11455	5998 ± 1823	20.5	28.00	6.15	14.43	19.4	28.3	60
Canaries	2436	7998	4482 ± 1947	19.1	25.10	5.48	10.54	19.0	27.1	60
Cape Verde Is.	1621	6183	3209 ± 1495	17.7	22.30	3.94	6.91	17.7	23.5	60

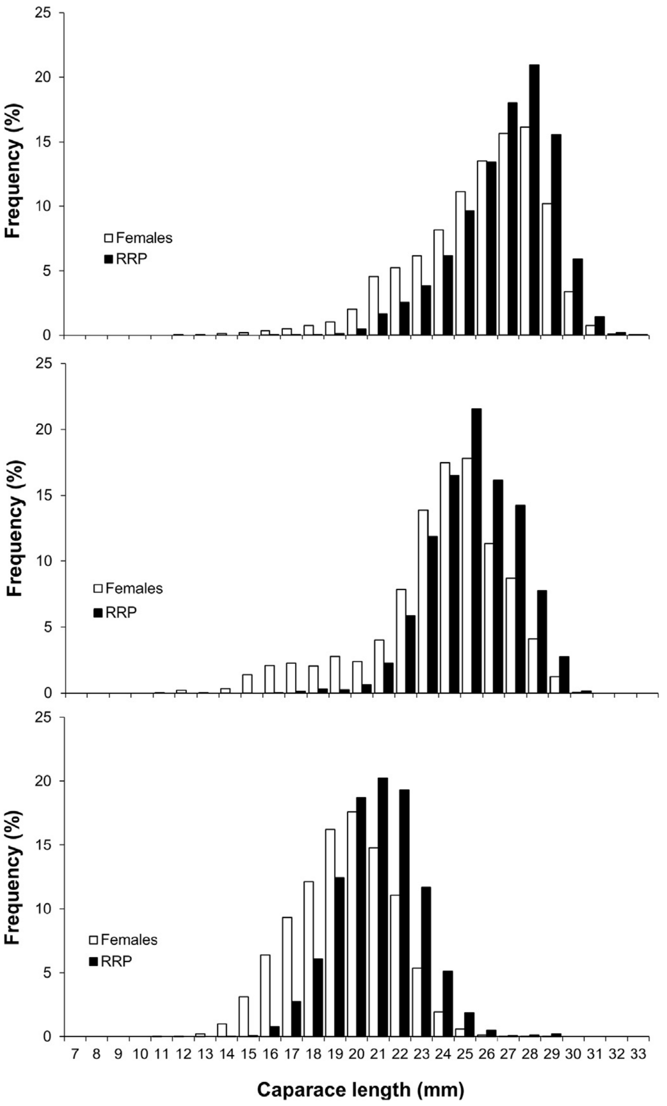

Fig. 11. Frequency-size distribution of *Plesionika edwardsii* females in Madeira (top), Canaries (middle) and Cape Verde Islands (bottom) and its relative reproductive potential (RRP).

Table 5
von Bertalanffy growth parameters (±standard deviation) of *P. edwardsii* and growth performance index (φ‘) ($\varphi' = 2*\log L_\infty + \log k$), where L_∞, is the asymptotic length; k, the growth rate; t_0, the relative age at 0 length.

Area/Sex	L_∞ (mm)	k (year^{-1})	t_0 (year)	φ‘
Madeira				
Males	33.13 ± 1.335	0.54 ± 0.052	0.12 ± 0.070	2.77
Females	36.08 ± 1.608	0.59 ± 0.060	0.03 ± 0.058	2.88
Canaries				
Males	30.06 ± 0.511	0.52 ± 0.028	0.03 ± 0.044	2.67
Females	34.19 ± 1.871	0.57 ± 0.078	−0.18 ± 0.073	2.82
Cape Verdes Is.				
Males	28.01 ± 1.390	0.51 ± 0.090	0.09 ± 0.143	2.60
Females	32.20 ± 0.165	0.53 ± 0.009	−0.01 ± 0.010	2.73

with latitude. This may be because as the latitude increases, selection should favor an increase in size at maturity to maximize adult fitness (Fischer and Fiedler, 2002). This pattern of maturity, beginning at smaller sizes in the Cape Verdean population with warmer habitats, compared to those in colder habitats and in higher latitudes, such as Madeira, has been described in other decapods (Hines, 1989; Lardies and Castilla, 2001; Lardies and Wehrtmann, 2001; Terossi et al., 2010a, b). The relative morphometric and physiological size at sexual maturity is not affected by latitude or environmental factors and occurs at the same size in the three areas studied, varying only slightly between 0.568 and 0.585. Similar results have been observed for other pandalids, with values oscillating between 0.53 and 0.58 in different localities irrespective of species, sexual typology, latitude or strategy of reproduction (Charnov, 1990; Briones-Fourzán et al., 2010; Hirose et al., 2013). The absence of intraspecific variation in the relative size at sexual maturity can reflect a genotypic character that is linked to the large plasticity in size of *P. edwardsii* under different environmental conditions.

The sex ratio as a function of size showed that females reached a larger size than males. This pattern is common when males do not show a defensive behavior towards females or do not exhibit aggressive male-male competition for copulation (Briones-Fourzán et al., 2010). The sex ratio, as a function of relative size, showed that the size at which sex-ratios diverged is strongly affected by latitude or environmental factors.

P. edwardsii, similar to other deep-water pandalids, usually had long reproductive seasons (Ohtomi, 1997; Company and Sardá, 1997), with ovigerous females observed year-round, although with latitudinal variations. Seasonally, there were more ovigerous females in spring and summer at higher latitudes, but more in winter to summer at lower latitudes. These changes in spawning activity may reflect differences in the local availability of food or the optimal thermal environmental conditions, which are limiting factors for reproductive activity (Tyler, 1988; Barradas-Ortiz et al., 2003). A latitudinal north-south pattern was also observed in fecundity and maximum egg size. In the Cape Verde Islands, the developed strategy involves a lower production of embryos and a smaller size of eggs than those at the higher latitude in Madeira. These results are in agreement with the latitudinal differences in egg production and size observed for other decapods (Lonsdale and Levinton, 1985a; Wehrtmann and Kattner, 1998; Lardies and Castilla, 2001; Lardies and Wehrtmann, 2001; Terossi et al., 2010a, b). This pattern may be explained by the necessity of a higher yolk content in eggs in colder regions to provide sufficient internal energy provisions for survival during longer periods of incubation than in warmer areas as an adaptation to protect the embryo against low temperatures (Wehrtmann and Kattner, 1998; Lardies and Castilla, 2001; Terossi et al., 2010a, 2010b; Viegas et al., 2012).

The latitudinal egg size increment observed was likely related to the maternal body size (Rollinson and Hutchings, 2011). Females with larger embryos have less available space for egg attachment on pleopods and lower fecundity than females of the same size from different populations with small eggs (Terossi et al., 2010a, b). Therefore, the higher maximum size reached for females in Madeira compensates for the reduction in the available space for egg attachment on pleopods with the higher eggs size, which is advantageous for more offspring production (Briones-Fourzán et al., 2010; Terossi et al., 2010a, b).

The asymptotic size and growth rate, like other components of the life-history traits studied, showed a latitudinal pattern in *P. edwardsii*. Theoretically, a latitudinal increment in temperature and growing season generate a latitudinal increment of the growth rate and asymptotic size in the populations at lower latitudes. This was observed in the Cape Verde Islands, with individuals experiencing a higher temperature during longer seasons than those of higher latitudes, such as Madeira, where environments would theoretically reduce growth (Yamahira et al., 2007; Chavarie et al., 2010). To avoid this reduction of the growth rate body size in Madeira, latitudinal compensatory growth has been observed in the present study. Adaptations to higher latitudes through latitudinal compensation in growth is common among ectotherms (Yamahira et al., 2007; Yamahira and Takeshi, 2008). This compensation mechanism may be due to a maximization of growth rate, named thermal adaptation, suggesting that individuals from Madeira have a thermal reaction norm for better growth rates at lower temperatures than individuals from the Cape Verde Islands (Levinton, 1983; Lonsdale and Levinton, 1985b; Chavarie et al., 2010). In this case, populations differ in the temperatures at which lesser and maximal growth are possible and not in temperatures the maximal growth rate that can be reached, meaning that the growth rate can be maximized in each environmental condition (Yamahira and Conover, 2002).

Latitudinal compensation in growth could also be a consequence of latitudinal differences in the length of the growing season as indicated by Conover and Present (1990) and Yamahira et al. (2007). The annual temperature cycle in Madeira involves favorable periods that permit growth, and periods when growth ceases, and energy reserves are utilized for metabolism. As the length of the growing season declines with the increase of latitude, the Madeiran population may compensate for the shorter growing season by evolving a higher overall capacity for growth through temperature adaptation. In this situation, the growth of individuals may occur over the same temperature range in all areas, but the reaction norms of growth with temperature, named countergradient variation, may differ in intensity (Conover and Present, 1990; Conover, 1992; Yamahira and Conover, 2002; Chavarie et al., 2010). Although a local temperature adaptation has been described for crustaceans (Lonsdale and Levinton, 1985b; Yamahira and Conover, 2002), the growth strategy of *P. edwardsii* may be the result of a mixture of both forms of latitudinal compensation by adapting to differences in the temperature and length of growing season.

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