



Considerations on the Biology of *Plesionika narval* (Fabricius, 1787) in the Northeastern Atlantic

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Abstract

Life history traits of *Plesionika narval* were studied in the Northeastern Atlantic, Madeira archipelago including growth, age, sexual maturity, recruitment pattern and mortality. A total of 28,262 specimens were sampled over a period of 8 years comprising two time series from 1991 to 1995 and 2004 to 2008. The relative growth pattern showed a negative allometric nature of growth for combined sexes, males, females, non ovigerous and ovigerous females. Estimated asymptotic carapace length (CL_{∞}) and growth coefficient (K) showed higher values in females ($CL_{\infty}=30.21$ mm, $K=0.450$ year⁻¹) comparatively to males ($CL_{\infty}=28.61$ mm, $K=0.430$ year⁻¹), resulting in better overall growth performance in females. The maximum life span (t_{max}) was estimated at 6.81 years for combined sexes, 6.97 for males and 6.66 for females, however 99.95% of the individuals were younger than 3 years. Although a seasonal spawning season was evident from late summer to late autumn, reproduction may be prolonged throughout the year since ovigerous females are present in all months and achieving sexual maturity at 14.61 mm. The recruitment pattern was continuous throughout the year with a major peak occurring in spring. The total mortality (Z) and fishing mortality (F) were higher in females than in males while natural mortality (M) was similar between groups.

Keywords: Pandalid shrimps, growth, reproduction, recruitment, mortality.

Introduction

Plesionika is a widely distributed genus of deep water shrimps that occurs in tropical and sub-tropical regions along the continental shelf and slope (Cartes *et al.*, 1993; Carbonell and Abelló, 1998; Vafidis *et al.*, 2005). They are nektobenthic species which feed on pelagic and benthic resources playing an important ecological role in benthic assemblages. Furthermore, they constitute an important prey of demersal fishes and cephalopods (Cartes *et al.*, 1993; Cartes, 1998; Cartes *et al.*, 2002; Fanelli and Cartes 2004; Vafidis *et al.*, 2005; Fanelli *et al.*, 2007).

Plesionika narval (Fabricius, 1787) is a cosmopolitan species occurring from the surface down to 910 m of depth in a large variety of habitats including muddy, sand-muddy, rocky bottoms and submarine caves (Biscoito, 1993; Holthuis, 1987; Thessalou-Legaki, 1989). It can be found in the Eastern Atlantic Ocean, from the southwest Iberian Peninsula to Angola, the Mediterranean Sea, the Red Sea and Indo-West Pacific from Madagascar to French Polynesia (Crosnier and Forest, 1973; Holthuis, 1980; Chan and Crosnier, 1991; Martins and

Hargreaves, 1991; González *et al.*, 1997; Li, 2006; Li and Davie, 2006).

The shrimp *P. narval* is recognized by FAO as a species of interest to fisheries (Holthuis, 1980) since it occurs in great abundance, is easily captured in bottom trawls and traps (Lagardère, 1981; Holthuis, 1987; Biscoito, 1993) and is exploited in a small scale artisanal fisheries in Madeira (Biscoito, 1993), the Canary Islands (González *et al.*, 1997) and the Mediterranean Sea (Arculeo *et al.*, 2002).

Life history traits such as growth, reproductive strategy and mortality are dependent on a complex combination of selective forces (Stearns, 1992; King, 1995) and are important in understanding the distribution and abundance of a species (Begon *et al.*, 1996). Furthermore, from a fisheries point of view, knowledge on the biology of a species is essential to its sustainable exploitation (Rodríguez and Bahamonde, 1986; King, 1995; Amin *et al.*, 2009).

The life history traits of several *Plesionika* species have been fairly well studied (Vafidis *et al.*, 2005), however only González *et al.* (1997) and Arculeo and Lo Brutto (2011) have focused on the biology of *P. narval* in the Canary Islands and the

Southeastern Tyrrhenian Sea respectively. This work aims to describe growth, age structure, reproduction, sexual maturity, recruitment and mortality rate of *P. narval* from experimental trap catches in the Madeira archipelago providing additional information for this species.

Materials and Methods

The material examined in this study was obtained from 311 fishing sets carried out on the insular shelves and slopes off Madeira (Figure 1) at depths ranging from 50 to 1300 m in research surveys using bottom and floating traps, over a period of 8 years, comprising two time series from 1991 to 1995 and from 2004 to 2008. The data from the two time series was tested for the homogeneity of variance using Levene's test (Zar, 1996). The survey's design and sampling procedures are described in Biscoito *et al.* (1992) and Carvalho *et al.* (2007).

Data Collection

The carapace length (CL) was measured to the nearest 0.01 mm from the posterior margin of the orbit to the posterior dorsal margin of the carapace using electronic digital calipers. The individual weight (W) was recorded using an electronic digital scale, with an accuracy of 0.01 g. Sex was determined by the presence or absence of masculine appendages in the second pair of pleopods, by dissection under a stereoscopic microscope (Zariquiey-Alvarez, 1968; King and Moffitt, 1984; Thessalou-Legaki, 1989). Females were examined for presence of external eggs, and the stage of egg maturation was assigned according to Company and Sardà (1997).

Data Analysis

Relative Growth

The relationship between W and CL were determined, adjusting the data to a potential relationship as $W = aCL^b$, where W is the wet weight in g, CL is the carapace length in mm, and a and b the constants. Regressions were calculated separately for combined sexes, males and females (nonovigerous, ovigerous and total females).

Nature of growth was tested using Student t-test in order to determine if the b coefficient was different from 3 with a significance level of 0.05. The differences in the slopes of the growth curves between groups were tested using general linear models.

Absolute Growth and Age

Absolute growth was studied using monthly length-frequency (CL) distributions for combined sexes, males and females. Identification of modes in the polymodal length-frequency was performed using Bhattacharya's method, included in the package FISAT (Fish Stock Assessment Tools - FAO-ICLARM), VER 1.2.0 (Gayanilo *et al.*, 2005). All the identified size-age groups were derived from at least three consecutive points and selection of the best results was based on the values of the separation index (>2) for the different age groups and the number of individuals per age group (Sparre and Venema, 1992). NORMSEP by Hasselblad and Tomlinson (1971) was used to decompose the mixtures of normal distributions based on Hasselblad's maximum likelihood method (Hasselblad, 1966).

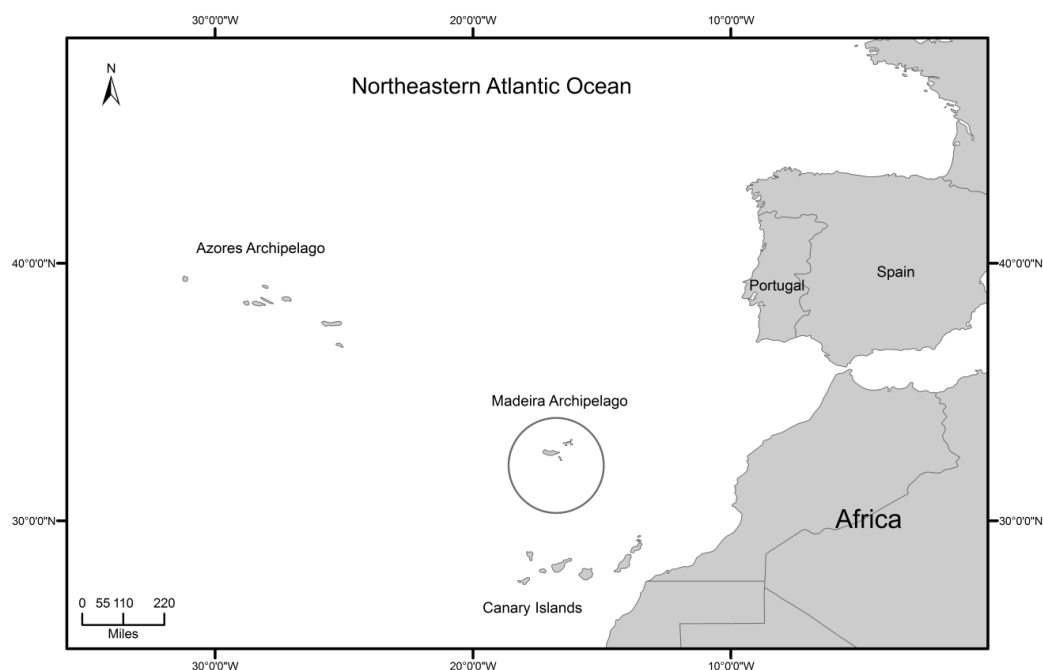


Figure 1. Geographic location of the study area, Madeira Archipelago, Northeastern Atlantic.

The von Bertalanffy Growth Functions (VBGF) parameters were estimated applying the Gulland and Holt method (Gulland and Holt, 1959) in the routine ELEFAN I available in FISAT (Gayanilo and Pauly, 1997) for all groups, according to

$$CL_t = CL_\infty \{1 - \exp[-k(t - t_0)]\}$$

(Gulland and Holt, 1959) where CL_t is the mean carapace length at age t (mm), CL_∞ is the asymptotic carapace length (mm), K the growth coefficient (year^{-1}), t the age of *P. narval* (years) and t_0 is the hypothetical age at which the length is zero (years).

As the growth parameters CL_∞ and K are inversely correlated the growth performance index

$$(\phi'), \phi' = \log_{10}(k) + 2 \log_{10} CL_\infty$$

(Pauly and Munro, 1984) was employed to compare growth rates between groups and fishing areas in the Northeastern Atlantic.

The age at length was determined using the inverse von Bertalanffy growth equation and the potential longevity ($A_{0.95}$) was estimated from:

$$A_{0.95} = t_0 + 2.996/K \text{ (Taylor, 1958).}$$

Reproduction and Recruitment

The proportion of mature females per month was plotted in order to estimate the spawning season. Kruskal-Wallis statistic test was used to test the proportions of mature individuals along the year (Zar, 1996).

Size at sexual maturity (CL_{m50}) (the size at which 50% of all females in a stock of crustaceans are mature) was estimated from the relationship between the proportion of ovigerous females and carapace length CL , described by the logistic equation:

$$P = 1 / (1 + \exp^{-(a+b \cdot CL)}) \text{ (Sparre and Venema, 1997)}$$

where P is the balanced probability, a and b were the equation parameters estimated by the linear least square method using the logarithmic transformation. The mean size at maturity was defined as the size at which 50% of the population is mature, when $P = 0.5$ then $CL_{m50} = -a/b$ (King, 1995).

The recruitment pattern was estimated by projecting the length-frequency data backwards on the time axis using the growth parameters (Moreau and Cuende, 1991) and normal distribution of this pattern was obtained by NORMSEP (Pauly and Caddy, 1985) in FISAT.

Mortality

Total mortality (Z) was estimated using the length converted catch curve method. Natural mortality rate (M) was estimated using Pauly's

empirical model:

$$\log_{10} M = -0.0066 - 0.279 (\log_{10} CL_\infty) + 0.6543 (\log_{10} K) + 0.4634 (\log_{10} T) \text{ (Pauly, 1980)}$$

where, CL_∞ the asymptotic carapace length (mm), K the growth coefficient (year^{-1}) and T the annual mean habitat temperature ($^{\circ}\text{C}$), 14.5°C in the habitat of the species in the study area. Fishing mortality (F) was obtained by subtracting M from Z .

Results

Size Composition

A total of 28262 specimens were sampled including 8580 (30.36%) males and 19682 (69.64%) females. The sizes of *P. narval* ranged from a minimum size of 2.45 mm to a maximum of 28.61 mm carapace length (CL), with a mean of 13.56 mm. The males varied from a minimum of 2.45 mm to a maximum of 27.72 mm CL , with a mean of 12.39 ± 3.01 mm CL . In the case of the females, the minimum size was 6.72 mm and the maximum 28.61 mm CL , while the mean was 14.07 ± 2.90 mm (Figure 2). The monthly CL frequency for males and females is presented in Figure 3 and Figure 4. The mean carapace length was significantly different between sexes ($t = -44.190$; $P < 0.05$). Carapace length had homogenous variance between the two considered time series ($W = 3.019$; $P > 0.05$).

Life History Traits

Relative Growth

Carapace length–weight relationships for the different groups are presented in Table 1. In all the examined groups, the b coefficient returned values inferior to 3 and the difference was highly significant ($P < 0.001$), indicating negative allometry. Size-weight relationships differed significantly between sexes ($F = 390.107$; $P < 0.05$) and according to the ovigerous condition in females ($F = 41.064$; $P < 0.05$).

Absolute Growth and Age

The estimates of von Bertalanffy growth parameters are presented in Table 2. Estimated asymptotic carapace length (CL_∞) and growth coefficient (K) showed higher values in females ($CL_\infty = 30.21$ mm, $K = 0.450 \text{ year}^{-1}$) comparatively to males ($CL_\infty = 28.61$ mm, $K = 0.430 \text{ year}^{-1}$), resulting in better overall growth performance in females.

The species *P. narval* showed a predominance of specimens aged between 1 and 2 years for combined sexes (73.00%), males (65.05%) and females (76.87%). The maximum life span (t_{max}) was estimated at 6.81 years for combined sexes, 6.97 for males and 6.66 for females, however 99.95% of the

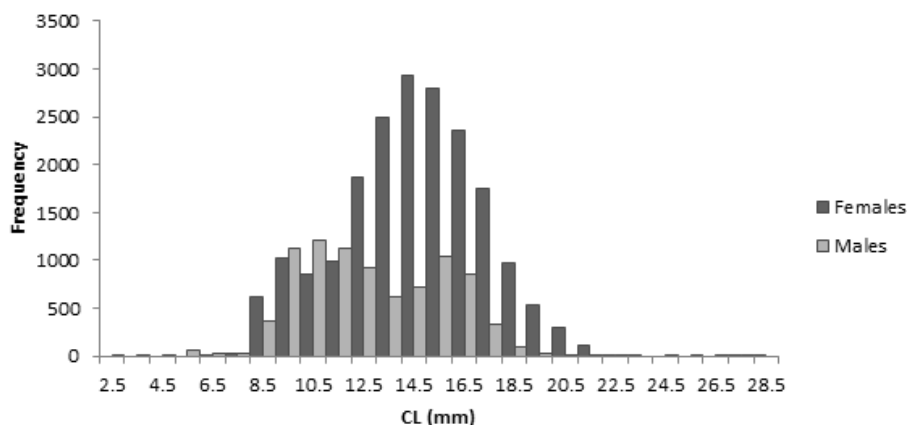


Figure 2. Length frequency distribution of *Plesionika narval* per sex caught in Madeira Archipelago, northeastern Atlantic.

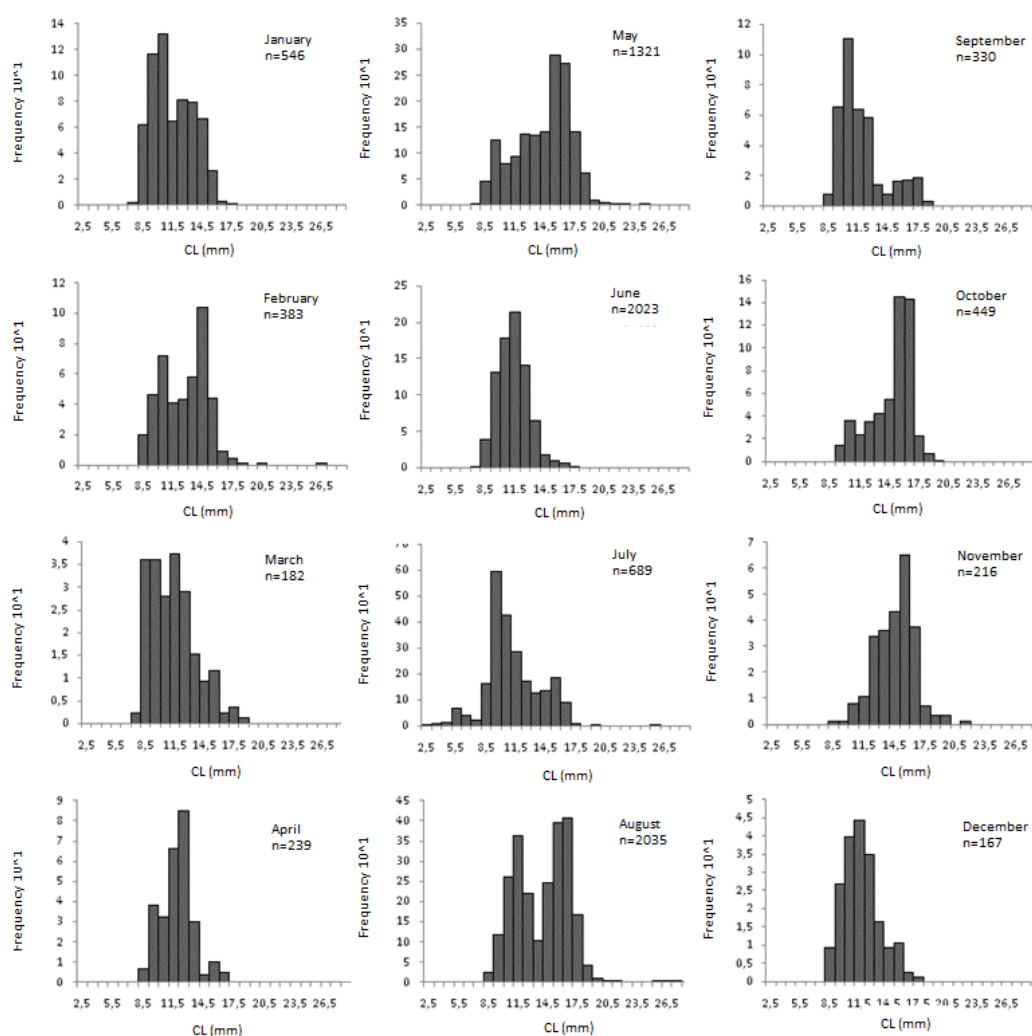


Figure 3. Monthly length-frequency distributions for males of *Plesionika narval* caught in Madeira Archipelago, northeastern Atlantic.

individuals were younger than 3 years (Figure 5).

Reproduction and Recruitment

Ovigerous females were present all year round

with a spawning season starting in late summer until late autumn. The proportion of ovigerous females was significantly different throughout the year ($\chi^2=3209.006$; $P<0.05$) with the highest proportion in August (86.18%) and the lowest (16.92%) in January

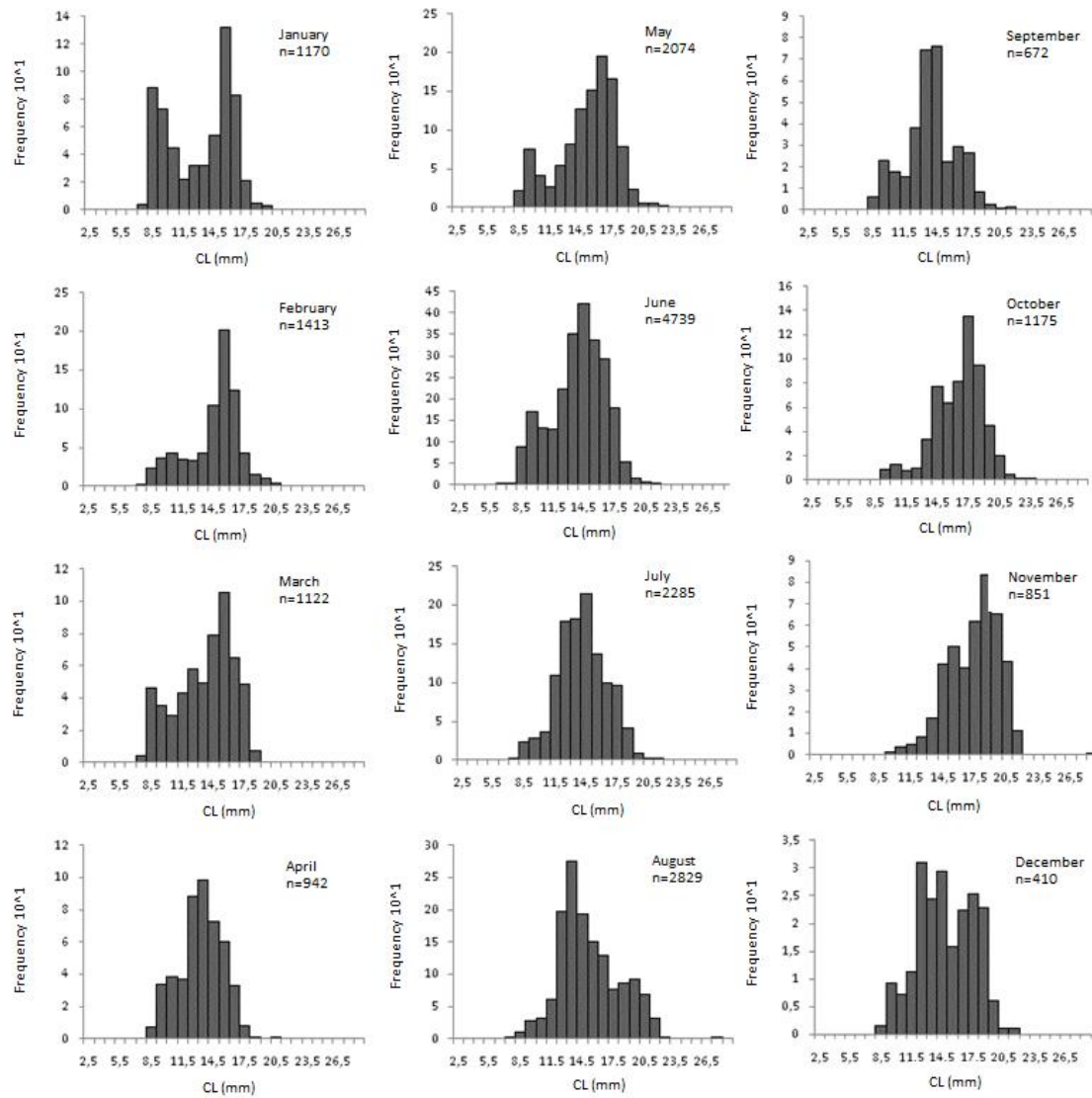


Figure 4. Monthly length-frequency distributions for females of *Plesionika narval* caught in Madeira Archipelago, northeastern Atlantic.

Table 1. Parameters of CL-W relationship for combined sexes, males and females (total, nonovigerous, and ovigerous) of *P. narval* in Madeira archipelago, Northeastern Atlantic

Group	n	a	b	r ²	nature of growth	S
Combined sexes	28236	0.002	2.649	0.848	A ⁻	***
Males	8569	0.008	2.087	0.688	A ⁻	***
Females	19667	0.001	2.883	0.923	A ⁻	***
Nonovigerous females	7446	0.001	2.843	0.935	A ⁻	***
Ovigerous females	12221	0.004	2.438	0.814	A ⁻	***

n: sample size; a and b = parameters of equation $W = aL^b$; r²: coefficient of determination; nature of growth: A⁻ negative allometry; S: significance level *** P<0.001.

(Figure 6).

The smallest and largest female bearing eggs had a carapace length of 6.72 mm and 28.61 mm respectively. The size at first maturity was 14.61 mm, corresponding to 1.47 years old specimens (Figure 7). This species shows a continuous recruitment pattern throughout the year with a major peak occurring in

spring (Figure 8) considering recruits the smallest caught specimens which in this study was 2.45mm of CL.

Mortality

Total and fishing mortalities were higher in

Table 2. Summary of the von Bertalanffy growth parameters (L_{∞} - asymptotic length, K – growth coefficient), growth performance index (ϕ') and potential longevity ($A_{0.95}$) estimated for species of *Plesionika* from different areas. M - males, F - females and I – indeterminate

Species	Area	Sex	L_{∞} (mm)	K (year ⁻¹)	ϕ'	$A_{0.95}^{**}$
<i>P. narval</i>	Madeira archipelago (Present study)	M+F	30.51	0.440	2.61	6.81
		M	28.61	0.430	2.55	6.97
		F	30.21	0.450	2.61	6.66
	Canary archipelago (González et al., 1997)	M	29.50	0.540	2.67*	5.55
		F	31.90	0.660	2.84*	4.54
		Southern Tyrrhenian Sea (Arculeo and Lo Brutto, 2011)	M	27.40	0.650	2.62
<i>P. martia</i>	Eastern-central Mediterranean (Maiorano et al., 2002)	F	17.8	0.710	2.28	4.22
		M	28.00	0.500	2.59	5.99
	Northwestern Mediterranean (Company and Sardà, 2000)	F	30.50	0.440	2.61	6.81
		I+M+F	30.10	0.500	2.66*	5.99
		M	27.50	0.540	2.61*	5.55
	Eastern Ionian sea (Chilari et al., 2005)	F	30.40	0.390	2.56*	7.68
M		28.20	0.530	2.62	5.65	
<i>P. edwardsii</i>	Canary archipelago (Santana et al., 1997)	F	30.60	0.310	2.46	9.66
		M	28.28	0.690	2.74	4.34
	Central Mediterranean Sea (Colloca, 2002)	F	25.75	0.550	2.56	5.45
		M	26.41	0.840	2.76	3.57
	Northwestern Mediterranean (Company and Sardà, 2000)	F	29.33	0.690	2.77	4.34
		I+M+F	31.00	0.700	2.83*	4.28
		M	32.00	0.800	2.91*	3.75
	Spanish W. Mediterranean Sea (García-Rodríguez et al., 2000)	F	31.00	0.650	2.80*	4.61
		M	26.00	0.800	2.73	3.75
	Pacific ocean (King, 1986)	F	31.00	0.800	2.89	3.75
<i>P. acanthonotus</i>	Northwestern Mediterranean (Company and Sardà, 2000)	M+F	29.50	0.660	2.76	4.54
		I+M+F	19.00	0.550	2.30*	5.45
		M	18.40	0.500	2.23*	5.99
<i>P. giglioli</i>	Northwestern Mediterranean (Company and Sardà, 2000)	F	19.00	0.550	2.30*	5.45
		I+M+F	21.00	0.750	2.52*	3.99
		M	20.00	0.550	2.34*	5.45
<i>P. heterocarpus</i>	Northwestern Mediterranean (Company and Sardà, 2000)	F	20.50	0.750	2.50*	3.99
		I+M+F	22.70	0.900	2.67*	3.33
		M	22.40	1.000	2.70*	3.00
		F	23.00	0.900	2.68*	3.33

* calculated as: $\phi' = \log_{10}(K) + 2 \log_{10}(L_{\infty})$ (Pauly and Munro, 1984)

** calculated as: $A_{0.95} = t_0 + 2,996/K$ (Taylor, 1958) assuming $t_0 = 0$

females than in males while natural mortality was similar between groups (Table 3).

Discussion

The size distribution in *P. narval* in the present study is in accordance with those reported for this species in the Canary Islands (Caldentey et al., 1990; Lozano et al., 1990; González et al., 1997), the Azores (Graça, 2008), the Southern Tyrrhenian Sea (Arculeo and Lo Brutto, 2011) and other pandalid shrimps (Sanz, 1986; Company and Sardà, 2000; Maiorano et al., 2002; Tuset et al., 2009) with female size consistently exceeding that of males as a result of differential morphological development, reproductive investment and distinct habitat preference (King, 1995).

The present data suggest that weight increases with negative allometry for all groups, the b coefficient varies from 2.087 to 2.883 and is supported by high values of correlation indicating an elevated predictability between carapace length and weight of the shrimps. The negative allometry of

growth observed for *P. narval* in the Madeira archipelago is consistent with the results obtained for this species in the Azores (Martins and Hargreaves, 1991), the Canary Islands (González et al., 1997) and the Southern Tyrrhenian Sea (Arculeo and Lo Brutto, 2011). The same pattern has been reported for *Plesionika edwardsii* (Brandt, 1851), *Plesionika antigai* Zariquiey-Alvarez, 1955, *Plesionika giglioli* (Senna, 1903), *Plesionika heterocarpus* (A. Costa, 1871) and *Plesionika martia* (A. Milne-Edwards, 1883) (Santana et al., 1997; Company and Sardà, 2000; Maiorano et al., 2002; Chilari et al., 2005; Vafidis et al., 2008). This pattern may result in higher mobility providing an advantage in predation since *P. narval* as well as *P. edwardsii* and *P. martia* are highly specialized active predators of macroplanktonic species (Cartes, 1993). Another explanation could be related to the low availability of preys in oligotrophic waters as reported for *P. martia* by Chilari et al. (2005) in the Eastern Ionian Sea. The negative allometry was less evident in females of *P. narval* probably as a result of differences in feeding and breeding behavior and greater capacity of

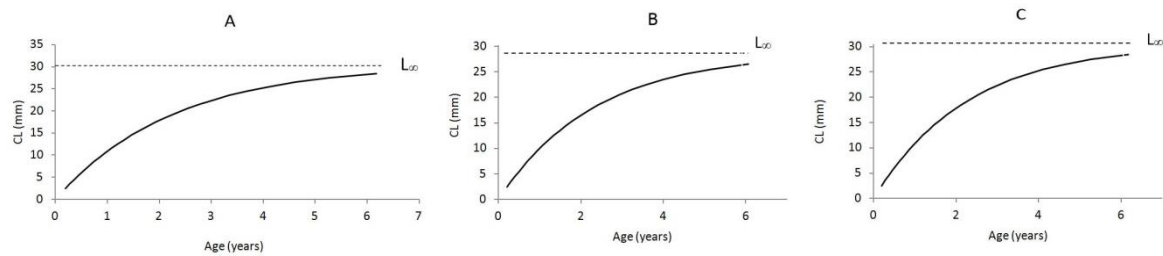


Figure 5. Von Bertalanffy growth curve of *Plesionika narval* for combined sexes (A), males (B) and females (C).

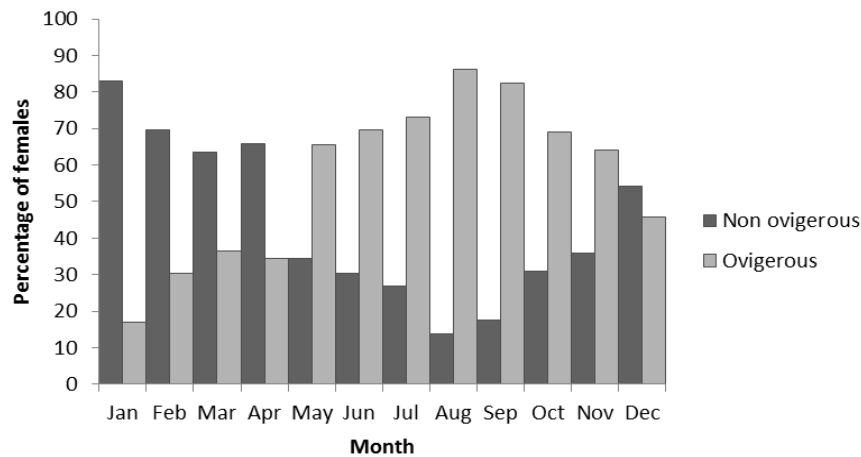


Figure 6. Proportion of ovigerous and non ovigerous females of *Plesionika narval* from Madeira archipelago by month.

obtaining, converting and storing energy.

In crustaceans, food availability and water temperature play an important role in growth dynamics. In habitats with more available food and higher temperatures crustaceans tend to have higher growth rates (Hartnoll, 1983).

In general, the life history pattern obtained in Madeira archipelago for *P. narval* was similar to that found in other caridean shrimps. A comparison of von Bertalanffy growth parameters is presented in table 2. (King and Butler, 1985; King, 1987; González *et al.*, 1997; Santana *et al.*, 1997; Company and Sardà, 2000; García-Rodríguez *et al.*, 2000; Colloca, 2002; Maiorano *et al.*, 2002; Chilari *et al.*, 2005). The asymptotic carapace length of males was smaller than that of females and congruent with the maximum captured length of both sexes. This is a common pattern in pandalid shrimps and has been reported for various species (Dailey and Ralston, 1986). In addition, males had a lower growth coefficient in comparison to females. A similar pattern was also reported for *P. narval* in the Canary Islands by González *et al.* (1997), but with higher values, suggesting that in the Canary Islands this species reaches the asymptotic carapace length more rapidly. The situation in the archipelago of Madeira may be explained because of the presence of very steep and rugged slopes (Biscoito, 1993), the oligotrophic nature of their waters Caldeira *et al.* (2002) and warmer sea water temperature (Aristegui *et al.*, 2006), the influence of sea water temperature on growth rates

was also referred for *Pandalus borealis* Krøyer, 1838 by Hansen and Aschan (2001) which found that lower sea water temperature decreases growth rates in this species.

The growth performance index has been shown to be remarkably constant between different species of the genus *Plesionika* (Company and Sardà, 2000) which is in agreement with Sparre *et al.* (1989) that state that in similar taxa this index is relatively constant. Nonetheless in *P. narval* in Madeira archipelago the growth performance index was slightly lower than the one reported for this species in the Canary Islands by (González *et al.*, 1997), which is in accordance with Clarke *et al.* (2004) which state that the growth performance index decreases with the increase of latitude.

Shrimps in areas influenced by cold water show slower growth, delayed maturity and increased longevity (Allen, 1959; Nilssen and Hopkins, 1991). Longevity of *P. narval* was higher in the archipelago of Madeira than in the Canary Islands and Southern Tyrrhenian Sea probably as a result of the oligotrophic nature of sea water in Madeira (Caldeira *et al.*, 2002) which induces slower growth rates and higher longevity, in addition higher sea water temperature in the Canary Islands and its larger continental slope (Aristegui *et al.*, 2006) contribute to higher growth rates (Berrigan and Charnov, 1994).

The presence of ovigerous females throughout the year suggests a continuous reproductive activity all year round. The same pattern has been described

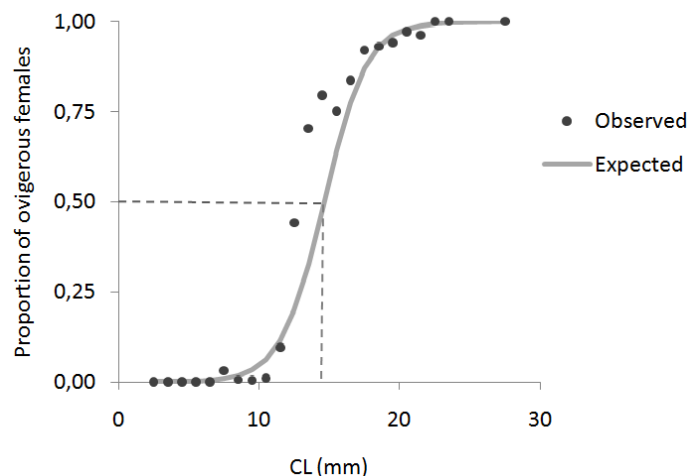


Figure 7. Expected and observed proportion by size of ovigerous female shrimps, with size at first maturity (CL_{m50}) with a determination coefficient of 0.87.

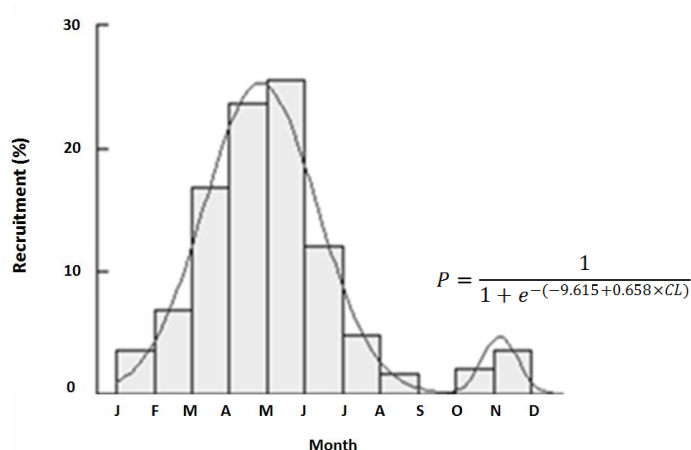


Figure 8. Recruitment pattern of *Plesionika narval* of Madeira Island in the northeastern Atlantic.

Table 3. Mortality rates (Z – total mortality; M – natural mortality; F – fishing mortality) of *P. narval* in Madeira archipelago, Northeastern Atlantic

Group	Z (year ⁻¹)	M (year ⁻¹)	F (year ⁻¹)
Combined sexes	1.83	0.77	1.06
Males	1.70	0.77	0.93
Females	2.13	0.78	1.35

for *P. narval* in the Canary Islands (González *et al.*, 1997) and *P. edwardsii* (Company and Sardà, 2000) and *P. martia* (Maiorano *et al.*, 2002) in the Mediterranean Sea. Nonetheless, an increase in percentage of ovigerous females, from late summer to late autumn suggests some degree of seasonality, due to variation of environmental conditions leading to an increased spawning activity in late summer/autumn as reported by Company *et al.* (2003) for other pandalid shrimps.

In general, size at first maturity in pandalid shrimps is correlated to the asymptotic carapace length of the species, with larger species achieving

sexual maturity at a larger length than smaller species (Company and Sardà, 1997; González *et al.*, 1997; Colloca, 2002; Maiorano *et al.*, 2002; Carbonell *et al.*, 2003 and Chilari *et al.*, 2005). The estimated value of carapace length at first maturity of *P. narval* in the archipelago of Madeira was higher than that reported for the Canary Islands by González *et al.* (1997), this might be explained by the existence of different abiotic conditions in the two archipelagos. Berrigan and Charnov (1994) stated that a decrease in growth rate can be related to the decrease in temperature and results in a later sexual maturation at larger sizes. The same pattern was observed for the pandalid

Heterocarpus ensifer A. Milne-Edwards, 1881 from Madeira and the Canary Islands by Tuset *et al.* (2009) and *P. borealis* from Svalbard (Hansen and Aschan, 2000).

The recruitment pattern was continuous throughout the year as indicated by the presence of ovigerous females all year round, which allows the entrance of new recruits in the adult population to occur outside the main recruitment season which was estimated to occur during spring. A similar behaviour has been reported for *P. martia* in the Eastern Ionian Sea (Chilari *et al.*, 2005).

Total and fishing mortalities in *P. narval* were higher in females than in males contrary to natural mortality which was similar between groups. This pattern indicates that fishing exerts higher pressure on females due to their larger size which renders them more susceptible to fishing traps. The relatively high total mortality and slow growth rate suggests that in this species biomass is maximized at an early age which is in agreement with King (1986).

Conclusions

Life history traits of *P. narval* in the archipelago of Madeira exhibited similar characteristics and behaviour to those described for other pandalid shrimps. The found differences are probably explained by specific environmental and anthropogenic conditions such as oligotrophy, sea water temperature and fishing pressure.

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References

- Allen, J.A. 1959. On the biology of *Pandalus borealis* Krøyer, with reference to a population off the Northumberland coast. *Journal of the Marine Biological Association of the United Kingdom*, 38: 189-220. doi: 10.1017/S002531540001568X;
- Amin, S.M.N., Arshad, A., Bujang, J.S., Siraj, S.S. and Goddard, S. 2009. Reproductive Biology of the Sergestid Shrimp *Acetes indicus* (Decapoda: Sergestidae) in Coastal Waters of Malacca, Peninsular Malaysia. *Zoological Studies*, 48(6): 753-760.
- Arculeo, M. and Lo Brutto, S. 2011. Growth and reproduction data of *Plesionika narval* (decapoda, caridea, pandalidae) off the island of Ustica (southern Tyrrhenian sea). *Crustaceana*, 84(11): 1367-1375. doi: 10.1163/156854011X596955;
- Arculeo, M., Mazzola, A. and Riggio, S. 2002. Catture sperimentali con le nasse di *Plesionika narval* (Fabr.) (Crustacea Decapoda) nell'isola di Ustica (Tirreno Meridionale). *Naturalista Siciliano*, IV-26(1-2): 13-20.
- Aristegui, J., Álvarez-Salgado, X.A., Barton, E.D., Figueiras, F.G., Hernández-León, S., Roy, C. and Santos, A.M.P. 2006. Oceanography and fisheries of the Canary current/iberian region of the Eastern North Atlantic. In: A.R. Robinson and K.H. Brink (Eds.), *The Sea. The Global Coastal Ocean: Interdisciplinary Regional Studies and Syntheses*, Harvard University Press, Cambridge: 14: 879-934.
- Begon, M., Harper, J.L. and Townsend, C.R. 1996. *Ecology: Individuals, Populations and Communities*. Blackwell Scientific Publications, Oxford, 945 pp.
- Berrigan, D. and Charnov, E.L. 1994. Reaction norms for age and size at maturity in response to temperature: A puzzle for life historians. *Oikos*, 70: 474-478.
- Biscoito, M.J. 1993. An account of the shrimps of the family Pandalidae (Crustacea, Decapoda, Caridea) in Madeiran waters. *Courier Forschungsinstitut Senckenberg*, 159: 321-325.
- Biscoito, M.J., Pinto, A.R., Maul, G.E., Faria, G.T. and Amorim, A.B. 1992. Estudo ecológico e biológico das comunidades de peixes e crustáceos decápodes bentónicos da vertente continental da Madeira. *Relatório de Progresso do Projecto PMCT/C/Mar/985/90. MMF and DSIP*, 59 pp.
- Caldeira, R.M.A., Groom, S., Miller, P., Pilgrim, D. and Nezhlin, N.P. 2002. Sea-surface signatures of the island mass effect phenomena around Madeira Island, Northeast Atlantic. *Remote Sensing of Environment*, 80: 336-360.
- Caldentey, M.A., González, J.A., Lozano, I.J. and Santana, J.I. 1990. Aproximación a la talla de primera madurez sexual de pandálidos en las Islas Canarias. *Vieraea*, 19: 201-208.
- Carbonell, A. and Abelló, P. 1998. Distribution characteristics of pandalid shrimps (Decapoda: Caridea: Pandalidae) along the western Mediterranean Sea. *Journal of Natural History*, 32: 1463-1474. doi: 10.1080/00222939800771001;
- Carbonell, A., Palmer, M., Abelló, P., Torres, P., Alemany, R. and Sola, L.G. 2003. Mesoscale geographical patterns in the distribution of pandalid shrimps *Plesionika* spp. in the western Mediterranean. *Marine Ecology Progress Series*, 247: 151-158. doi: 10.3354/meps247151;
- Cartes, J.E. 1993. Diets of deep-water pandalid shrimps on the western Mediterranean slope. *Marine Ecology Progress Series*, 96: 49-61.
- Cartes, J.E. 1998. Feeding strategies and partition of food resources in deep-water decapod crustaceans (400-2300 m). *Journal of the Marine Biological Association of the United Kingdom*, 78: 509-524. doi: 10.1017/S002531540004159X;
- Cartes, J.E., Abelló, P., Lloris, D., Carbonell, A., Torres, P., Maynou, F. and Sola, L.G. 2002. Feeding guilds of western Mediterranean demersal fish and crustaceans: an analysis based on a spring survey. *Scientia Marina*, 66(2): 209-220.
- Cartes, J., Sardà, F. and Abelló, P. 1993. Decapod crustaceans collected by deep-water trawls (between 1000 and 2200 m) in the Catalan area (North-Western Mediterranean). *Bios (Thessaloniki) - Scientific Annals of the School of Biology*, 1: 207-213.
- Carvalho, D., Delgado, J., Biscoito, M., Freitas, M., González, J.A., Santana, J.I., Tuset, V.M., Isidro, E. and Pinho, M.R., Consórcio PESCOPROF 2007.

- Recursos Pesqueiros de Águas Profundas do Atlântico Centro-Oriental: Alternativas à Pesca na Macaronésia. Relatório técnico-científico final do Projecto PESCOPROF-2 (03MAC/4.2/M8). Funchal, 156 pp.
- Chan, T. and Crosnier, A. 1991. Crustacea Decapoda: studies of the *Plesionika narval* (Fabricius, 1787) group (Pandalidae) with description of six new species. In: A. Crosnier (Ed.), Résultats des Campagnes MUSORSTOM, 9. Mémoires du Muséum National d'Histoire Naturelle, Paris: 413-461.
- Chilari, A., Thessalou-Legaki, M. and Petrakis, G. 2005. Population structure and reproduction of the deep-water shrimp *Plesionika martia* (Decapoda: Pandalidae) from the eastern Ionian Sea. *Journal of Crustacean Biology*, 25: 233-241. doi:10.1651/C-2513
- Clarke, A., Prothero-Thomas, E., Beaumont, J.C., Chapman, A.L. and Brey, T. 2004. Growth in the limpet *Nacella concinna* from contrasting sites in Antarctica. *Polar Biology*, 28: 62-71. doi: 10.1007/s00300-004-0647-8
- Colloca, F. 2002. Life cycle of the deep-water pandalid shrimp *Plesionika edwardsii* (Decapoda, Caridea) in the Central Mediterranean Sea. *Journal of Crustacean Biology*, 22: 775-783. doi: 10.1651/0278-0372(2002)022[0775:LCOTDW]2.0.CO;2
- Company, J.B., Puig, P., Cartes, J.E. and Palanques, A. 2003. Duration and timing of reproduction in decapods crustaceans of the NW Mediterranean continental margin: is there a general pattern?. *Scientia Marina*, 261: 201-216. doi: 10.3354/meps 261201.
- Company, J.B. and Sardà, F. 1997. Reproductive patterns and population characteristics in five deep-water pandalid shrimps in the western Mediterranean along a depth gradient (150-1100 m). *Marine Ecology Progress Series*, 148: 49-58. doi: 10.3354/meps148049
- Company, J.B. and Sardà, F. 2000. Growth parameters of deep-water decapod crustaceans in the northwestern Mediterranean Sea: a comparative approach. *Marine Biology*, 136(1): 79-90. doi: 10.1007/s002270050011
- Crosnier, A. and Forest, J. 1973. Les crevettes profondes de l'Atlantique Oriental tropical. *Faune Tropicale*, 19: 1-409.
- Dailey, M.D. and Ralston, S. 1986. Aspects of the reproductive biology, spatial distribution, growth and mortality of the deepwater caridean shrimp *Heterocarpus laevigatus* in Hawaii. *Fishery Bulletin*, 84: 915-925.
- Fanelli, E. and Cartes, J.E. 2004. Feeding habits of pandalid shrimps from the Alboran Sea (SW Mediterranean): influence of biological and environmental factors. *Marine Ecology Progress Series*, 280: 27-238.
- Fanelli, E., Colloca, F. and Ardizzone, G. 2007. Decapod crustacean assemblages off the West coast of central Italy (western Mediterranean). *Scientia Marina*, 71: 19-28.
- García-Rodríguez, M., Esteban, A. and Perez Gil, J.L. 2000. Consideration on the biology of *Plesionika edwardsii* (Brandt, 1851) (Decapoda, Caridea, Pandalidae) from experimental trap catches in the Spanish western Mediterranean Sea. *Scientia Marina*, 64(4): 369-379.
- Gayanilo, F.C.Jr. and Pauly, D. 1997. The FAO-ICLARM Stock Assessment Tool (FISAT). Reference Manual. FAO Computerized Information Series (Fisheries), 8: 1-262.
- Gayanilo, F.C.Jr., Sparre, P. and Pauly, D. 2005. The FAO-ICLARM Stock Assessment Tools (FISAT II). Revised version. User's Guide. FAO Computerized Information Series (Fisheries), 8: 1-168.
- González, J.A., Tuset, V.M., Lozano, I.J. and Santana, J.I. 1997. Biology of *Plesionika narval* (Crustacea, Decapoda, Pandalidae) around the Canary Islands (eastern central Atlantic). *Estuarine, Coastal and Shelf Science*, 44: 339-350.
- Graça, G.N.S.N. 2008. Aspectos da biologia do Camarão *Plesionika narval* (Fabricius, 1787) nos Açores. MSc. thesis. Algarve: Universidade do Algarve.
- Gulland, J.A. and Holt, S.J. 1959. Estimation of growth parameters for data at unequal time intervals. *Journal du Conseil - Conseil International pour l'Exploration de la Mer*, 25(1): 47-49. doi: 10.1093/icesjms/25.1.47;
- Hansen, H.O. and Aschan, M. 2000. Growth, Size- and age at maturity of shrimp, *Pandalus borealis*, at Svalbard related to environmental parameters. *Journal of Northwest Atlantic Fishery Science*, 27: 83-91.
- Hartnoll, R.G., 1983. Growth. In: D.E. Bliss (Ed.), *The Biology of Crustacea* (vol. 8). Academic Press, New York: 214-282.
- Hasselblad, V. 1966. Estimation of parameters for a mixture of normal distributions. *Technometrics*, 8: 431-444. doi: 10.1080/00401706.1966.10490375;
- Hasselblad, V. and Tomlinson, P.K. 1971. NORMSEP. Normal distribution separator. In: N.J. Abramson (Ed.), *Computer Programs for Fish Stock Assessment*. FAO Fisheries Technical Paper, Rome: 101:11(1)2.1-11(1)2.10.
- Holthuis, L.B. 1980. FAO Species Catalogue. Shrimps and Prawns of the World. An Annotated Catalogue of Species of Interest to Fisheries. FAO Fisheries Circular, 125(1): 1-271.
- Holthuis, L.B. 1987. Crevettes. In: W. Fischer, M. Schneider and M.-L. Bauchot (Eds.), *Fiches FAO d'identification des espèces pour les besoins de la pêche méditerranée et mer noire. zone de pêche 37 (revision 1), 1, végétaux et invertébrés*, Food and Agriculture Organization of the United Nations, Rome: 189-292.
- King, M. 1987. Distribution and ecology of deep-water caridean shrimps (Crustacea; Natantia) near tropical Pacific islands. *Bulletin of Marine Science*, 41(2): 192-203.
- King, M. 1995. Fisheries biology assessment and management. Fishing News Books, London, 341 pp.
- King, M.G. 1986. The fishery resources of Pacific islands countries. Part I. Deep-water shrimps. FAO Fisheries Technical Paper, 272(1): 1-45.
- King, M.G. and Butler, A.J. 1985. Relationship of life-history patterns to depth in deep-water caridean shrimps (Crustacea: Natantia). *Marine biology*, 86: 129-203. doi: 10.1007/BF00399018;
- King, M.G. and Moffitt, R.B. 1984. The sexuality of tropical deepwater shrimps (Decapoda: Pandalidae). *Journal of Crustacean Biology*, 4: 567-571.
- Lagardère, J.P. 1981. Shrimps and prawns. In: W. Fischer, G. Bianchi and W.B. Scott (Eds.), *Fiches FAO Species Identification Sheets for Fishery Purposes. Eastern Central Atlantic- Fishing Areas 34, 47 (in part) (vol. 6)*. Food and Agriculture Organization of the United Nations, Ottawa: 1-304.
- Li, X. 2006. Additional pandaloid shrimps from the South China Sea (Crustacea: Decapoda: Caridea), with description of one new species. *The Raffles Bulletin of Zoology*, 54(2): 361-372.

- Li, X. and Davie, P.J.F. 2006. An account of the pandaloid shrimps (Crustacea: Decapoda: Caridea) in the collections of the Queensland Museum. *Memoires of the Queensland Museum*, 52(1): 151-170.
- Lozano, G., Carrillo, J., Caldentey, M., Santana, J., Lozano, I., González, J., Jiménez, S., Lozano, F., Brito, A., Fanlo, M. and Hernández, C. 1990. Distribución estacional y batimétrica de Pandalidos en el talud de Gran Canaria. In: L. Gallego-Castejon (Ed.), *Bentos VI*. Edit. Bilbilis, Palma de Mallorca: 213-221.
- Maiorano, P., D'Onghia, G., Capezzuto, F. and Sion, L. 2002. Life-history traits of *Plesionika martia* (Milne Edwards, 1883) (Decapoda: Caridea) from the eastern-central Mediterranean Sea. *Marine Biology*, 141: 527-539. doi: 10.1007/s00227-002-0851-4;
- Martins, H. and Hargreaves, P. 1991. Shrimps of the Families Pandalidae and Hippolytidae (Crustacea: Decapoda) caught in benthic traps off the Azores. *Arquipélago Life Earth Science*, 9: 47-61.
- Moreau, J. and Cuende, F.X. 1991. On improving the resolution of the recruitment patterns of fishes. *ICLARM Fishbyte*, 9: 45-46.
- Nilssen, E.M. and Hopkins, C.C.E. 1991. Population parameters and life histories of the deep-water prawn, *Pandalus borealis* from different regions. *ICES CM* 1991/K:2
- Pauly, D. 1980. On the interrelation between natural mortality, growth parameters and mean environmental temperature in 175 fish stocks. *Journal du Conseil - Conseil International pour l'Exploration de la Mer*, 39(2): 175-192.
- Pauly, D. and Caddy, J.F. 1985. A modification of Bhattacharya's method for the analysis of mixtures of normal distributions. *FAO Fisheries Circular*, Rome, 781: 1-16.
- Pauly, D. and Munro, J.L. 1984. Once more on the comparison of growth in fish and invertebrates. *ICLARM Fishbyte*, 2(1): 21.
- Rodríguez, L. and Bahamonde, R. 1986. Estimación del crecimiento y mortalidad natural en *Munida subrugosa* del Estrecho de Magallanes. *Investigación Pesquera*, 33: 25-32.
- Santana, J.I., González, J.A., Lozano, I.J. and Tuset, V.M. 1997. Life history of *Plesionika edwardsii* (Crustacea, Decapoda, Pandalidae) around the Canary Islands, eastern central Atlantic. *South African Journal of Marine Science*, 18: 39-48.
- Sanz, A. 1986. Observaciones sobre la biología de *Plesionika heterocarpus* (Costa, 1871) (Crustacea: Decapoda: Pandalidae) en el Mediterráneo Oeste. *Actas de las VII Jornadas de la Asociación Española de Entomología*, Sevilla, Spain: 175-179.
- Sparre, P., Ursin, E. and Venema, S.C. 1989. Introduction to tropical fish stock assessment, Part 1 Manual. *FAO Fisheries Technical Paper*, 306/1, Rome, 337 pp.
- Sparre, P. and Venema, S.C. 1992. Introduction to tropical fish stock assessment, Part 1 Manual. *FAO Fisheries Technical Paper*, 306/1, Rev. 1, Rome, 376 pp.
- Sparre, P. and Venema, S.C. 1997. Introduction to tropical fish stock assessment, Part 1 Manual. *FAO Fisheries Technical Paper*, 306/1 Rev. 2, Rome, 392 pp.
- Stearns, S.C. 1992. *The evolution of life histories*. Oxford University Press, Oxford, 248 pp.
- Taylor, C.C. 1958. Cod growth and temperature. *Journal du Conseil - Conseil International pour l'Exploration de la Mer*, 23(3): 366-370.
- Thessalou-Legaki, M. 1989. Allometric growth of male secondary sexual characters and dioecy in *Parapandalus narval* (Decapoda: Pandalidae). *Journal of Crustacean Biology*, 9: 595-600.
- Tuset, V.M., Pérez-Penálvo, J.A., Delgado, J., Pinho, M.R., Santana, J.I., Biscoito, M., González, J.A. and Carvalho, D. 2009. Biology of the deep-water shrimp *Heterocarpus ensifer* (Caridea: Pandalidae) off the Canary, Madeira and the Azores islands (Northeastern Atlantic). *Journal of Crustacean Biology*, 29(4): 507-515. doi: 10.1651/08-3070.1;
- Vafidis, D., Leontarakis, P.K., Dailianis, T. and Kallianiotis, A. 2008. Population characteristics of four deep-water pandalid shrimps (Decapoda: Caridea) in the northern Aegean Sea (NE Mediterranean). *Journal of Natural History*, 42(31): 2079-2093. doi: 10.1080/00222930802254672;
- Vafidis, D., Politou, C.-Y., Carbonell, A. and Company, J.B. 2005. A review on the biology and fisheries of the genus *Plesionika* Bate, 1888 in European Waters: distribution, ecology, biology and fishing. *Crustaceana*, 78: 335-352.
- Zar, J.H. 1996. *Biostatistical analysis*. Prentice-Hall International Editions, New Jersey, 662 pp.
- Zariquiey-Alvarez, R. 1968. Crustáceos Decápodos Ibéricos. *Investigación Pesquera*, 32: 1-510.