



Pasiphaeid shrimps in the western Mediterranean: geographical variability in distribution and population patterns

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Summary: This work aimed to analyse the main characteristics of the bathymetric and geographic distribution, population size structure and size at maturity of the continental slope caridean shrimps *Pasiphaea sivado* and *Pasiphaea multidentata* in the western Mediterranean, as well as to try to relate the patterns obtained with geomorphologic and hydrographic characteristics. The study area encompassed the Mediterranean coast of the Iberian Peninsula. In both species, marked differences in depth distribution, density, and population size structure were found between Algerian basin populations, particularly in the Alboran Sea, and those in the Catalano-Balearic basin. Both shrimps showed a shallower bathymetric range in the westernmost region of the Algerian basin than in the rest of geographic sectors, linked to the occurrence of upwelling areas on the northwestern edges of the Alboran Sea. Populations of *P. sivado* reached larger densities, sizes and maturity size in the Algerian basin. No recruitment of *P. multidentata* was detected in the Algerian basin, whereas it was present in the Catalano-Balearic basin. In both species, the window range of bottom temperature and salinity was larger in juveniles than in adults. These different distribution and population dynamics imply that ecological functioning of these species differs between the two geomorphological basins of the western Mediterranean Sea.

Keywords: *Pasiphaea*; density; biomass; recruitment; maturity size; population dynamics; size structure.

Camarones pasiféidos del Mediterráneo occidental: variabilidad geográfica en distribución y patrones poblacionales

Resumen: Este trabajo se enfocó en el estudio de las principales características de la distribución batimétrica y geográfica, estructura de tallas y talla de madurez de los camarones carideos *Pasiphaea sivado* y *Pasiphaea multidentata*, habitantes del talud continental, en el Mediterráneo occidental. También se analizan las pautas observadas en función de las características geomorfológicas e hidrográficas del área de estudio, las costas mediterráneas de la Península Ibérica. En ambas especies se hallaron importantes diferencias en su distribución batimétrica, densidad y estructura de tallas poblacional entre las poblaciones presentes en la Cuenca Argelina, particularmente en el mar de Alborán, respecto a las habitantes de la Cuenca Catalano-Balear. Ambas especies presentaron un rango batimétrico comprendiendo aguas más someras en la región más occidental de la Cuenca Argelina respecto al resto de sectores geográficos estudiados, en relación con la presencia de zonas de afloramiento en los límites noroccidentales del mar de Alborán. Las poblaciones de *P. sivado* presentaron mayores densidades, tallas y talla de madurez en la Cuenca Argelina. No se detectó reclutamiento de *P. multidentata* en la Cuenca Catalano-Balear. En ambas especies, el rango de temperatura y salinidad en el fondo asociado a su presencia fue superior en juveniles que en adultos. Las diferencias halladas en las pautas de distribución y dinámica poblacional en ambas especies implican un distinto funcionamiento ecológico entre las dos cuencas geomorfológicas del Mediterráneo occidental.

Palabras clave: *Pasiphaea*; densidad; biomasa; reclutamiento; talla de madurez; dinámica poblacional; estructura de tallas.

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INTRODUCTION

Benthopelagic shrimps have a widespread geographic and bathymetric distribution from high latitudes in both hemispheres to intertropical waters (Crosnier and Forest 1973, Casanova and Judkins 1976, Serejo et al. 2007). Many continental slope shrimps show cyclic movements associated with the photoperiod, as shown in some pasiphaeid and sergestid shrimps (Frogliia and Giannini 1982, Cartes 1993a, Aguzzi et al. 2007). This vertical daily migration behaviour shown by some of these species provides them with an important role in the transfer of matter and energy from the upper primary productive layers of the ocean, where these species tend to feed during the night, down to the epibenthic community of the continental slope, where they dwell during the day (Cartes 1993b, Herring and Roe 1988, Naylor 2010). Benthopelagic shrimps are thus a fundamental food item for fish, other crustaceans and cephalopods with nektobenthic habits on the continental slope and deep sea (Garrison and Link 2000, Fanelli and Cartes 2008). Moreover, some of these species play an important ecological role and have potential for exploitation as commercial target species, as is the case of *Pasiphaea japonica* (Nanjo and Ohtomi 2009). Studies of the biology and ecology of pasiphaeid shrimps have been conducted in a few regions, such as the Japan Sea (Nanjo 2007, Nanjo and Ohtomi 2009), the Mediterranean Sea (Orsi-Relini and Relini 1990, Company et al. 2001), and the northeastern and southeastern Atlantic Ocean (Matthews and Pinnoi 1973, Gibbons et al. 1994, Kensley and Schotte 2006).

The family Pasiphaeidae has a worldwide distribution, and over 90 species are known to date (Hayashi 1999, Tavares and Cardoso 2006, De Grave and Fransen 2011). In the northeast Atlantic up to 18 Pasiphaeidae species are known to occur, eight of them belonging to the genus *Pasiphaea* (Casanova and Judkins 1977, d'Udekem d'Acoz 1999, Koukouras 2000), but only two species of Pasiphaeidae are present in the Mediterranean Sea, namely *Pasiphaea sivado* (Risso, 1816) and *Pasiphaea multidentata* (Esmark, 1866).

Pasiphaea sivado is a benthopelagic caridean shrimp commonly captured as a by-catch by demersal trawling on the upper slope across the eastern Atlantic and the Mediterranean Sea (González-Gurriarán and Olaso 1987, Abelló et al. 2002) down to a maximum depth of around 800 m (Abelló et al. 1988, 2002). Biological studies on this species have been mainly performed in the western Mediterranean, where it has been reported to reproduce continuously throughout the year, although peaking in autumn-winter, and a longevity of up to two years has been estimated (Company et al. 2001, 2003). The species has been shown to predate mainly on euphausiids, calanoid copepods, and epibenthic peracarid crustaceans (Lagardère 1972, Cartes 1993b).

Pasiphaea multidentata inhabits benthic boundary layers on the middle and lower slope down to 2000 m depth (Cartes 1993c, Abelló et al. 2002, Tecchio et al. 2011), with juveniles inhabiting shallower waters than adults (Company et al. 2001). It also performs

vertical migrations into upper water layers during the night, mainly but not exclusively restricted to juveniles (Cartes 1993a, Aguzzi et al. 2007, Simão et al. 2014). In the northwestern Mediterranean the species shows a marked seasonality in reproduction, with ovigerous females being only present from September to February, and it reaches an estimated longevity of around 3.5 years (Company et al. 2001, Ramirez-Llodra et al. 2007). It is an active nocturnal feeder on benthopelagic crustaceans such as *Gennadas elegans*, *P. sivado*, *P. multidentata*, sergestid shrimps and small mesopelagic fish such as myctophids and *Cyclothone* spp. (Cartes 1993a).

The main objectives of this paper are to analyse the main characteristics of the bathymetric and geographic distribution, population size structure and some reproduction-related characteristics of both *P. sivado* and *P. multidentata* in the western Mediterranean, as well as to relate the patterns obtained with geomorphologic and hydrographic characteristics.

MATERIALS AND METHODS

Study area and oceanographic context

The study area encompassed the continental shelf, upper and middle slope down to a depth of 800 m along the Iberian Peninsula Mediterranean coasts from Gibraltar in the SW to Cape Creus in the NE (Fig. 1). Overall, the continental shelf is very narrow in the Alboran Sea and Vera Gulf, south of Cape Palos, and widens to the north, reaching a maximum width of up to 70 km in the Ebro Delta-Columbretes Islands area. North of Barcelona, the continental shelf is heavily indented by several submarine canyons.

The western Mediterranean is influenced by the inflow of Atlantic water through the Strait of Gibraltar (Hopkins 1985, Millot 2005), where lighter Atlantic water inflows towards the Mediterranean on surface waters, and higher density Mediterranean water outflows towards the Atlantic Ocean at depth. This surface inflow of Atlantic waters generates two anticyclonic gyres between the Strait of Gibraltar and Cape Gata, and adjacent upwelling cells in the vicinity of the Strait (Vargas-Yáñez and Sabatés 2007). The main current of inflowing Atlantic waters is directed from Cape Gata towards the North African coast, generating the Almeria-Oran front (AOF). From there the current continues its inflow along the North African coasts towards the central and eastern Mediterranean. The AOF is a strong thermohaline front confined to the upper layers of the water column and shows great seasonal and interannual variability in strength (Tintoré et al. 1988). The Atlantic water also flows northeastwardly, due to the detachment of anticyclonic gyres which reach the Balearic Islands and generate a second thermohaline front along the northeastern part of the archipelago, associated with the NE flowing Balearic Current (Tintoré et al. 1988, López-Jurado et al. 2008, Monserrat et al. 2008). The interaction between the strong Northern Current, flowing southwestwards along the continental slope from the Gulf of Lions, and the Balearic Current

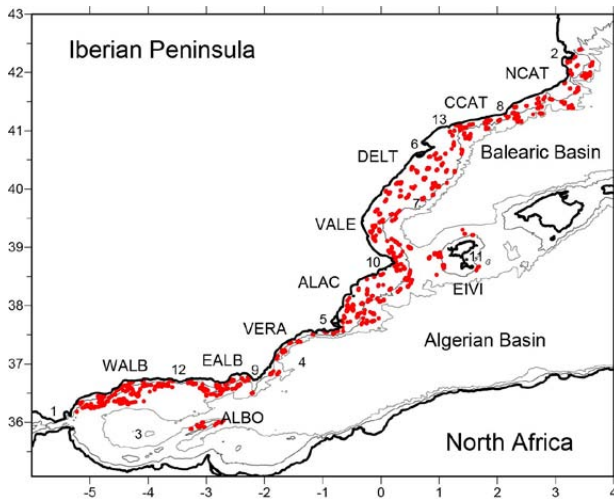


Fig. 1. – Iberian Peninsula Mediterranean coast showing position of the sampling hauls in the study regions: western Alboran (WALB); eastern Alboran (EALB); Alboran Island (ALBO); Vera Gulf (VERA); Alacant (ALAC); Eivissa Island (EIVI); Valencia (VALE); Ebro Delta region (DELT); central Catalonia (CCAT) and northern Catalonia (NCAT). 200 m and 1000 m isobaths are shown. 1, Gibraltar; 2, Cape Creus; 3, Alboran Sea; 4, Vera Gulf; 5, Cape Palos; 6, Ebro Delta; 7, Columbretes Islands; 8, Barcelona; 9, Cape Gata; 10, Cape La Nao; 11, Eivissa; 12, Cape Sacratif; 13, Cape Salou/Tarragona.

in the Eivissa Channel region (between Cape La Nao and the island of Eivissa) generates a cyclonic gyre over the Balearic basin enclosing the oldest resident waters in its centre (Salat 1995, Sabatés et al. 2007).

Sampling and analysis

The material studied in the present work was obtained from the Spanish Mediterranean International Trawl Surveys (MEDITS_ES) performed in spring from 1994 to 2008. The aim of this project is to obtain density, biomass and recruitment indices of the main target species exploited by the demersal fishery throughout the European Union and adjacent Mediterranean countries, based on a common sampling protocol (Bertrand et al. 2002). The Spanish surveys were performed on board the R/V *Cornide de Saave-*

dra. These cruises took place in spring, centred in the month of May, and had a mean duration of 28.9 valid workdays (range: 21-37), with an average of 4.0 hauls per day. The survey always started in the Alboran Sea and ended in the Gulf of Lions. All hauls were performed during day-time. Overall, samples were taken at depths ranging from 25 m down to 800 m based on a randomly stratified sampling design according to the FAO General Fisheries Commission for the Mediterranean (GFCM) geographic subareas and depth strata (Bertrand et al 2002). Because of the large amount and spread of samples taken throughout this area and depths, in the present analysis it was possible to further subdivide the area into ten geographic sectors, established according to their geomorphology and previous biogeographic studies (Abelló et al. 2002, Rufino et al. 2005): the western Alboran (WALB) from Gibraltar to Cape Sacratif; the eastern Alboran (EALB) from Cape Sacratif to Cape Gata; Alboran Island (ALBO); Vera Gulf (VERA) from Cape Gata to Cape Palos; Alacant (ALAC) from Cape Palos to Cape La Nao; Eivissa Island (EIVI); Valencia (VALE) from Cape La Nao to the Columbretes Islands; the Ebro Delta region (DELT) from the Columbretes Islands to Cape Salou/Tarragona; central Catalonia (CCAT) from Cape Salou/Tarragona to Barcelona, and northern Catalonia (NCAT), from Barcelona to Cape Creus. The sectors WALB to EIVI were considered to belong to the Algerian basin, while those from VALE to NCAT were considered to belong to the Catalano-Balearic basin. The sampling design also allowed finer 50 m range depth strata to be delimited.

The bottom trawl used was a GOC-73 model (Fiorentini et al. 1999). The mouth of the net had a 3 m vertical opening allowing the capture of epibenthic and benthopelagic fish and crustaceans, and a codend stretched mesh size of 20 mm. The hauls were performed at a speed of 3 knots with a duration of one hour, except for the hauls performed shallower than 200 m, which had a duration of 30 minutes. A total of 1741 valid hauls were performed during the study period (Table 1).

Table 1. – Number of hauls taken by depth stratum and geographic sector (1994-2008). Western Alboran (WALB); eastern Alboran (EALB); Alboran Island (ALBO); Vera Gulf (VERA); Alacant (ALAC); Eivissa Island (EIVI); Valencia (VALE); Ebro Delta region (DELT); Central Catalonia (CCAT); northern Catalonia (NCAT).

Depth stratum (m)	WALB	EALB	ALBO	VERA	ALAC	EIVI	VALE	DELT	CCAT	NCAT	Total
0-50	22	15	-	8	31	-	13	43	26	6	164
51-100	47	35	2	23	86	-	76	172	62	33	536
101-150	23	11	3	5	46	6	35	44	24	49	246
151-200	9	10	-	18	23	-	5	5	4	7	81
201-250	10	11	-	-	7	5	-	-	10	6	49
251-300	7	6	-	20	20	8	6	1	3	9	80
301-350	21	10	2	6	12	4	10	1	5	15	86
351-400	14	5	5	1	4	2	2	1	5	3	42
401-450	16	14	-	8	14	1	-	2	6	10	71
451-500	1	3	1	2	19	11	-	-	3	11	51
501-550	21	14	4	9	18	4	-	-	6	11	87
551-600	13	10	3	3	19	10	3	-	6	5	72
601-650	22	15	2	1	5	-	2	-	5	11	63
651-700	12	1	2	3	1	11	-	-	6	8	44
701-750	15	1	1	7	-	2	10	-	2	2	40
751-800	13	7	3	-	-	-	5	-	1	-	28
Total	266	168	28	114	305	64	167	269	174	186	1741

Table 2. – Mean density (ind. km⁻²) of *Pasiphaea sivado* and *Pasiphaea multidentata* within each depth stratum and geographic sector along the Iberian Peninsula Mediterranean coast. Mean density per geographic sector corresponds to densities within the 350-500 m depth strata for *P. sivado* and >500 m for *P. multidentata* (i.e. those with the overall highest frequency of occurrence).

Depth stratum (m)	WALB	EALB	ALBO	VERA	ALAC	EIVI	VALE	DELT	CCAT	NCAT	Total
<i>Pasiphaea sivado</i>											
0-50	0	0	-	0	0	-	0	0	0	0	0
50-100	0	0	0	0	0	-	0	0	0	0	0
100-150	1	0	0	0	3	0	0	0	0	0	1
150-200	411	0	-	3	0	-	4	0	0	0	47
200-250	3347	0	-	-	9	0	-	-	11	0	687
250-300	7146	1048	-	750	3145	0	295	3167	61	56	1748
300-350	8663	3453	0	119	4288	0	1027	176	3328	2400	3857
350-400	9200	2847	81	2350	426	1588	458	436	18358	2483	5983
400-450	13614	7387	-	187	1782	0	-	108	6879	8916	6737
450-500	5867	110	588	296	442	26368	-	-	299	987	6227
500-550	494	55	0	158	110	3	-	-	61	380	220
550-600	156	0	0	0	0	3	0	-	23	40	33
600-650	17	4	0	657	0	-	5	-	0	7	19
650-700	10	0	0	18	0	0	-	-	128	0	21
700-750	2	0	0	0	-	0	0	-	44	44	5
750-800	3	0	0	-	-	-	0	-	0	-	1
Number of samples (350-500 m)	31	22	6	11	37	14	2	3	14	24	164
Mean density (350-500 m)	9560	3448	335	944	883	9319	458	272	8512	4129	6316
<i>Pasiphaea multidentata</i>											
0-50	0	0	-	0	0	-	0	0	0	0	0
50-100	0	0	0	0	0	-	0	0	0	0	0
100-150	0	0	0	0	0	0	0	0	0	0	0
150-200	0	0	-	0	0	-	0	0	0	0	0
200-250	0	0	-	-	0	0	-	-	0	0	0
250-300	74	0	-	0	0	0	0	11	0	0	7
300-350	0	0	0	0	11	0	25	0	0	0	4
350-400	0	2	0	0	0	0	0	0	0	0	0
400-450	4	22	-	56	117	0	-	199	141	80	63
450-500	0	80	0	50	97	18	-	-	142	379	137
500-550	28	42	92	281	124	94	-	-	199	11	92
550-600	34	37	28	59	281	502	58	-	127	263	190
600-650	124	38	70	213	178	-	102	-	16	46	85
650-700	24	48	99	1029	439	295	-	-	21	85	185
700-750	87	0	66	101	-	95	93	-	158	138	95
750-800	36	35	37	-	-	-	186	-	154	-	67
Number of samples (>500 m)	96	48	15	23	43	27	20	0	26	37	335
Mean density (>500 m)	56	33	65	337	256	247	110	-	113	109	119

Once on board, the total catch was separated by species, weighed and counted. When species abundances were too high, a random subsample in weight was taken to estimate the number of individuals, according to the programme protocol (Bertrand et al. 2002). Density and biomass were then standardized by swept area to obtain the number of individuals and weight (in g) per square kilometre. The swept area was calculated taking into account the horizontal opening of the trawl, measured with Scanmar devices, and the distance from the starting point of the haul (net on the bottom) to the end of the effective haul (net off the bottom), measured from GPS latitude and longitude readings. Density, biomass and size structure were analysed in terms of bathymetric and geographic distribution of the two species. The number of samples taken within each combination of geographic sectors and depth intervals (and totals) is given in Table 2. Mean density and biomass values were calculated by averaging the obtained density values over the total number of hauls made within each combination of geographic sector and depth interval, including zero values. For both species, and for the whole study area, one-way analysis of variance was used to test for significant interannual differences in density (natural logarithmic transformation), after testing for normality of data and

homogeneity of variances (Guijarro et al. 2008, 2009). If no significant interannual differences were detected, a two-way ANOVA was then used considering geographical sectors and 100-m depth strata as factors to test for significant differences.

From 1998, all individuals, or a subsample of up to 60 individuals, of each species, *P. sivado* and/or *P. multidentata*, for each haul were sexed and measured (carapace length, CL) with an accuracy of 0.1 mm. Ovigerous females, and females with developed ovaries (oocytes being visible through the carapace) were considered as mature and noted down. Size frequency distributions (SFD), weighted by the density of the corresponding sample, were obtained for each combination of geographic sector and depth stratum. SFD based on <15 individuals per cell have not been presented in the obtained figures. Normal-distributed components were identified in SFD using the Bhattacharya method implemented in Fisat II. Mean sizes identified with this method for each depth stratum were pooled in a frequency distribution of significant components by geographic sector. This provides greater precision in the actual number of cohorts present in each geographic sector and in their average size (Abelló 1986, Yamasaki 1988, Queiroga 1993). Size at sexual maturity by geographic sector was estimated by fitting a logistic

Table 3. – Mean biomass (g km^{-2}) of *Pasiphaea sivado* and *Pasiphaea multidentata* within each depth stratum and geographic sector along the Iberian Peninsula Mediterranean coast. Mean biomass per geographic sector corresponds to values within the 350-500 m depth strata for *P. sivado* and >500 m for *P. multidentata* (i.e. those with the overall highest frequency of occurrence).

Depth stratum (m)	WALB	EALB	ALBO	VERA	ALAC	EIVI	VALE	DELT	CCAT	NCAT	Total
<i>Pasiphaea sivado</i>											
0-50	0	0	-	0	0	-	0	0	0	0	0
50-100	0	0	0	0	0	-	0	0	0	0	0
100-150	1	0	0	0	4	0	0	0	0	0	1
150-200	150	0	-	4	0	-	4	0	0	0	18
200-250	3979	0	-	-	17	0	-	-	18	0	818
250-300	9174	1020	-	524	2656	0	155	4642	29	32	1749
300-350	13853	2961	0	139	4023	0	1423	301	3146	2811	5140
350-400	12988	4967	131	1224	490	2299	664	185	25558	2739	8396
400-450	22070	7192	-	287	2021	0	-	155	5306	9323	8588
450-500	15496	178	1098	477	568	35611	-	-	436	1159	8523
500-550	1141	91	0	266	184	3	-	-	94	650	444
550-600	343	0	0	0	0	2	0	-	29	54	68
600-650	34	6	0	1137	0	-	11	-	0	6	33
650-700	22	0	0	25	0	0	-	-	72	0	17
700-750	3	0	0	0	-	0	0	-	67	44	7
750-800	6	0	0	-	-	-	0	-	0	-	3
Number of samples (350-500 m)	31	22	6	11	37	14	2	3	14	24	164
Mean biomass (350-500 m)	16851	4112	614	663	1026	12637	664	170	10433	4407	8502
<i>Pasiphaea multidentata</i>											
0-50	0	0	-	0	0	-	0	0	0	0	0
50-100	0	0	0	0	0	-	0	0	0	0	0
100-150	0	0	0	0	0	0	0	0	0	0	0
150-200	0	0	-	0	0	-	0	0	0	0	0
200-250	0	0	-	-	0	0	-	-	0	0	0
250-300	88	0	-	2	0	0	0	22	0	0	8
300-350	0	0	0	0	33	0	145	0	0	0	21
350-400	0	14	0	0	0	0	0	0	0	0	2
400-450	26	130	-	361	693	0	-	945	370	102	281
450-500	0	501	0	317	466	88	-	-	266	209	295
500-550	167	198	577	2009	575	449	-	-	773	59	507
550-600	230	252	165	386	1551	2823	338	-	726	1351	1069
600-650	696	256	413	1314	999	-	577	-	114	271	492
650-700	165	402	577	7568	2718	1779	-	-	118	351	1183
700-750	672	0	485	584	-	587	656	-	917	944	653
750-800	245	281	861	-	-	-	1064	-	1121	-	437
Number of samples taken (>500 m)	96	48	15	23	43	27	20	0	26	37	335
Mean biomass (>500 m)	362	231	513	2372	1461	1410	659	-	628	595	723

function to the proportion of mature females by 1 mm CL size. Logistic fittings were compared among them using a generalized linear model analysis with geographical sectors as factors. A post-hoc test was used to compare size at 50% maturity (L_{50}) among sectors. Analysis was restricted to the sectors with the highest number of sampled females (WALB, EALB, ALAC, CCAT, NCAT).

Information on mean temperature and salinity on the bottom during each trawl was recorded with a CTD SBE-37 placed at the float-line of the net. Data from the 2001-2006 cruises were used to calculate mean temperature and salinity by depth stratum for each geographic sector. In order to assess the optimal temperature and salinity window for each species, the range, 25 and 75 percentiles were calculated. For each species each sample was additionally categorized as juvenile or adult depending on its mean CL: for *P. sivado*, samples with mean $CL \leq 16$ mm were considered as juvenile samples, and those with $CL > 16$ mm as adult (Company et al 2001, Simão 2013); for *P. multidentata*, an evident size break at 20 mm CL was present in our SFD in agreement with the size at maturity observed by Company et al. (2001) (see also below, and Simão 2013).

RESULTS

Pasiphaea sivado

Density and biomass

The overall depth distribution of *P. sivado* in the study area ranged between 141 and 765 m. Densities of *P. sivado* per haul ranged between 8 and 186109 ind. km^{-2} . No significant differences were found concerning interannual variability in densities (ANOVA, $F_{14,340}=0.731$, $p=0.743$). The interaction between depth and geographical sector was not significant ($F_{5,277}=1.275$, $p=0.218$). Two-way ANOVA showed that densities across both geographical sectors ($F_{5,277}=4.331$, $p=0.001$) and depth strata ($F_{3,277}=20.400$, $p=0.000$) differed significantly. The highest mean density values were found at depths between 250 and 500 m, i.e. within the preferential occurrence depth strata for the species (350-500 m) (Table 2). The WALB population showed the widest depth distribution range for the whole sampled Iberian coast populations. Sizeable densities were found in this sector at depths between 150 and 600 m. In the rest of sampled sectors, densities rose sharply only from 250 m downwards

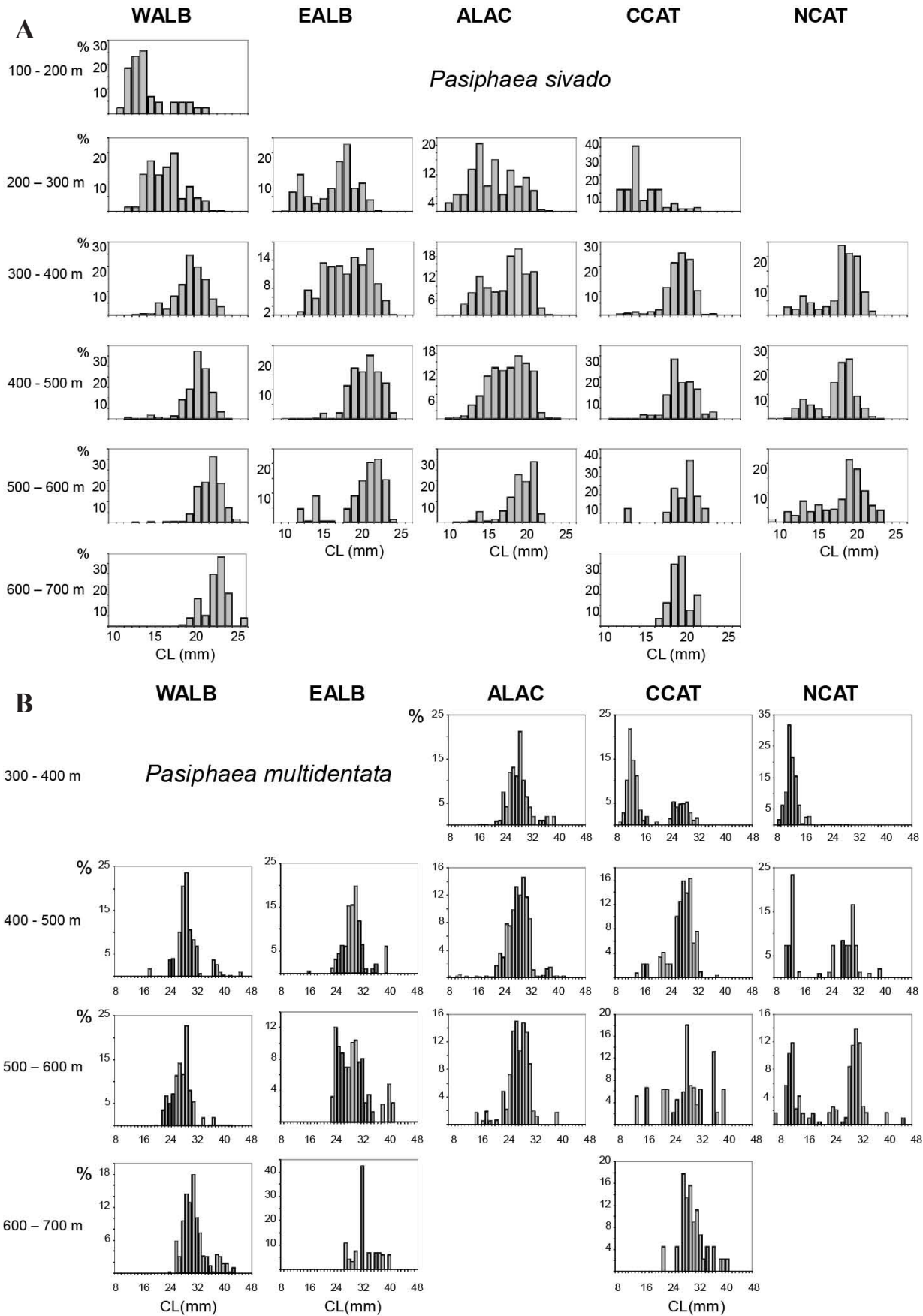


Fig. 2. – A, size frequency distributions of *Pasiphaea sivado* per depth interval in the five best sampled geographic sectors. Total N: WALB=1502; EALB=592; ALAC=999; CCAT=653; NCAT=462). B, size frequency distributions of *Pasiphaea multidentata* per depth interval in the five best sampled geographic sectors. Total N: WALB=337; EALB=118; ALAC=668; CCAT=225; NCAT=205).

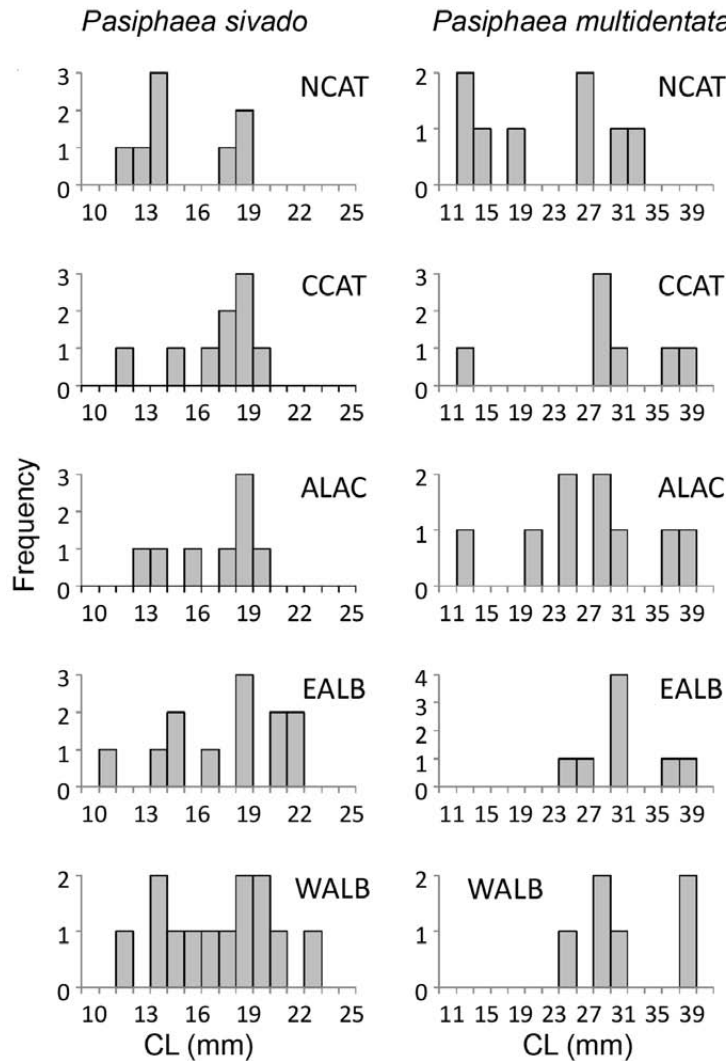


Fig. 3. – Frequency distribution of normally-distributed identified components in the size frequency distributions of *Pasiphaea sivado* and *P. multidentata* by geographic sector (NCAT, northern Catalonia; CCAT, central Catalonia; ALAC, Alacant; EALB, eastern Alboran; WALB, western Alboran). Size class intervals of 1 mm in *P. sivado* and 2 mm in *P. multidentata*.

to around 500-600 m. Overall, the areas with highest mean density values were the WALB and the EALB and CCAT and NCAT. Eivissa also showed very high mean densities, but the relatively low sample size and the large variability in densities in this area makes it difficult to make any definitive statement about this area. Both density and biomass (Tables 2 and 3) followed a similar bathymetric and geographic pattern throughout the studied geographic area.

Size structure and size at maturity

Overall, sizes of *P. sivado* ranged from 9.2 to 26.1 mm CL. SFD per 100 m depth strata and geographic sector (Fig. 2A) revealed that the WALB population showed a clear size-increasing trend with depth, with juvenile individuals being restricted to the upper 100-300 m; the largest individuals were recorded in the two deepest strata (500-700 m). Populations along the Catalan coast did not show such a marked increasing trend, but rather showed a similar size structure with depth, except for the relatively high abundance

of juveniles in the upper depth occurrence stratum (200-300 m).

Based on the analysis of significant normally-distributed cohorts in the several SFD by depth stratum using the Bhattacharya method, the frequency distribution of the mean sizes of the normally-distributed identified components per sector (Fig. 3) showed that most populations were structured in two main cohorts, broadly corresponding to juvenile (placed around 14 mm CL) and adult individuals (placed around 19 mm CL); the populations in the Alboran Sea also showed additional significant cohorts around 22 mm CL, which were not identified in the rest of the sampled sectors.

Geographic sectors were shown to be a significant factor for the analysis of maturity size (GLM, $p < 0.01$) (Fig. 4). L_{50} ranged from 20.62 mm CL in the WALB to 22.98 mm CL in ALAC. A post-hoc test showed that L_{50} was significantly smaller ($p < 0.05$) in the WALB than in the other sectors studied, whereas there were no significant differences between the other sectors (Table 4).

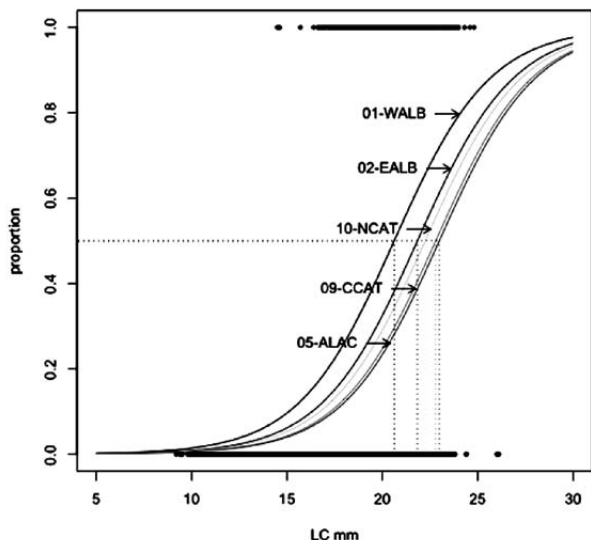


Fig. 4. – Logistic functions adjusted to the proportion of mature female *Pasiphaea sivado* by size by geographic sector.

Temperature and salinity

Throughout the study area, bottom temperatures ranged between 12.80 and 16.56°C, while salinities ranged between 37.14 and 38.54. Occurrences of *P. sivado*. took place at bottom temperatures between 12.98 and 13.42°C and salinities between 38.18 and 38.54. The temperature-salinity window was narrower for adults than for juveniles; in particular, adults occurred (percentiles 25-75) at temperatures between 13.17 and 13.27°C and salinities between 38.43 and 38.51, while juveniles occurred at temperatures between 13.04 and 13.28°C and salinities between 38.36 and 38.48.

Pasiphaea multidentata

Density and biomass

The overall depth distribution of *P. multidentata* in the study area ranged between 265 and 799 m. Density values of *P. multidentata* ranged between 7.5 and 3696 ind. km⁻². No significant differences in densities were found between years (ANOVA, $F_{14,321}=1.266$, $p=0.227$). Densities differed significantly between areas ($F_{6,295}=7.489$, $p=0.000$) but not between depth strata ($F_3=0.5484$, $p=0.650$). Significant interaction was detected ($p=0.006$). The highest mean densities were

Table 4. – Post-hoc test among geographic sectors concerning the estimated size at 50% maturity (L_{50}) in *Pasiphaea sivado* identified by fitting a logistic function to the proportion of mature females by size (Fig. 4) ($p<0.05$).

L_{50} (mm)	Geographic sector				
	WALB	EALB	ALAC	CCAT	NCAT
20.62	WALB	—	—	—	—
21.83	EALB	EALB<WALB	—	—	—
22.98	ALAC	ALAC<WALB	ns	—	—
22.79	CCAT	CCAT<WALB	ns	ns	—
22.24	NCAT	NCAT<WALB	ns	ns	ns

generally found deeper than 500 m in the Algerian basin (from WALB to Eivissa), whereas in the northernmost sectors the highest mean densities were found slightly shallower (400-500 m) (Table 2). Overall, the highest mean densities were found in the intermediate sectors, from the Gulf of Vera to Eivissa Channel. Densities were also high in the northernmost sectors (central and northern Catalonia), while the lowest density values were detected in the Alboran Sea. Biomass showed a slightly different pattern (Table 3), since the depth of the highest values was below 500 m in all sampled sectors (except the EALB), including those in the Balearic basin. This finding is related to the different size structure found in the two basins, with a higher occurrence of juveniles, occurring in shallower waters, in the northern sectors than in the rest of the sampled sectors (see below).

Size structure

Sizes of *P. multidentata* ranged between 7.7 and 47.9 mm CL. The most noteworthy feature of SFD per depth and sector (Fig. 2A) is that the occurrence of juveniles was practically restricted to the sectors of the Catalano-Balearic basin (CCAT and NCAT), where the population size structure was clearly bimodal, with the juvenile cohort ranging from 8 to 16 mm CL and adults from 24 to 32 mm CL. In these northern sectors, very few individuals with sizes around or larger than 40 mm CL were found. In contrast, in the populations from the Alboran Sea and Alacant, the sectors belonging to the Algerian basin, very few or hardly any juveniles were found. In these sectors, most of the population was comprised of adult individuals ranging between 24 and 32 mm CL, but a third, larger, cohort was also discernible at sizes of around 40 mm in most samples.

The frequency distribution of the mean sizes of the cohorts identified in the SFD by depth strata (Fig. 3) showed that most populations were structured in 2-3 main cohorts, broadly corresponding to juvenile (placed around 13-19 mm CL) and adult individuals, with two main cohorts, one around 30 mm CL and one around 38 mm CL, the latter not present in NCAT. Juvenile cohorts were only identified in the NCAT, CCAT and ALAC.

Temperature and salinity

P. multidentata occurred at bottom temperatures between 12.91°C and 13.43°C and salinities between 38.20 and 38.54. The temperature window was narrower for juveniles than for adults, while the salinity range for juveniles was slightly broader. In particular, adults occurred (percentiles 25-75) at temperatures between 13.10 and 13.25°C and salinities of 38.44 and 38.50, while juveniles occurred at temperatures between 13.25 and 13.30°C and salinities between 38.42 and 38.50.

DISCUSSION

The information obtained during the studied series of trawl surveys was used to analyse the distribution

patterns of density and biomass of the two species of the genus *Pasiphaea* present in the western Mediterranean throughout the southern and eastern coasts of the Iberian Peninsula down to depths of around 800 m. Furthermore, their population size structure was also described. While the overall depth range distribution of both *P. sivado* and *P. multidentata* found in the present study falls within the ranges described in the literature for these species (Cartes 1993c, Koukouras et al. 2000, Fanelli et al. 2007), several patterns were studied in detail given the broad geographic range of the surveys (Bertrand et al. 2002).

Most of the previously available information on distribution patterns, size structure and other population characteristics of the two species was restricted to the northernmost sampled area: the Catalan coasts (Abelló et al. 1988, 2002, Cartes 1993a,b,c, Company et al. 2001, 2003, Aguzzi et al. 2007, Ramirez-Llodra et al. 2007). Orsi-Relini and Pinca (1990) and Orsi-Relini and Relini (1990), respectively, provided information on reproduction and trophic interactions in the Ligurian Sea (NE of the western Mediterranean basin). No biological or population information are available from other areas within the distribution range of the two species. Our results have shown the occurrence of marked differences in both distribution and population characteristics between the southwestern areas of the Alboran Sea, located in the Algerian basin of the western Mediterranean, and the northeastern area, the Catalan Sea in the Catalano-Balearic basin.

Thus, the geographic distribution of densities of *P. sivado* has first shown a heterogeneous distribution pattern with two main nuclei: one in the Alboran Sea, especially in its western area, and one along the Catalan coasts in the northeast. Additionally, the bathymetric distribution in the WALB sector was markedly different from that in the other geographic sectors. In this area, the species occurred in both much shallower and deeper waters, reaching markedly higher densities at depths between 100 and 250 m, where it is largely absent in the remaining sectors. The bathymetric distribution of *P. multidentata* extended to shallower waters in the WALB sector. This pattern was especially evident in *P. sivado*, and is in agreement with the occurrence of temporal upwellings located along the northwesternmost region of the Alboran Sea, in the area around Malaga (Vargas-Yáñez and Sabatés 2007). These upwellings are responsible for the occurrence of high primary production cells which have been shown to provide plankton blooms followed by high epibenthic shrimp secondary production (Fanelli and Cartes 2004). The occurrence of these upwelling cells close to the coast is caused by the interaction of the permanent strong eastward inflow of Atlantic water into the Mediterranean through the nearby Strait of Gibraltar. Inside the Mediterranean Sea, the inflow is influenced by the steep continental slope of the southern Iberian continental margin, and intense local westerly winds (Millot, 2005, Vargas-Yáñez and Sabatés 2007), which contribute to offshore displacement of the surface water, allowing the inflow of deeper, cooler and nutrient-rich waters to shallower areas.

Within the sampled depth ranges, densities of *P. sivado* have been shown to be much higher than those of *P. multidentata*, in agreement with Company et al. (2001), who suggested that the greater fecundity output of *P. sivado* would support its higher population densities when compared with *P. multidentata*. Both juvenile and adult *P. sivado* are known to perform upward vertical migrations at night, while remaining on the bottom or close to it (epibenthic layer) during the day (Cartes 1993a, Aguzzi et al. 2007). In this way they can be considered benthopelagic species. Night-time migrations into the water column have also been reported for *P. multidentata*, but mainly restricted to juveniles, with the apparent exception of the adults (CL>30 mm), which were assumed to perform bathymetric displacements along the seabed (Cartes 1993a, Cartes et al. 1993, Aguzzi et al. 2007). However, recent research has shown that adult *P. multidentata* are also able to migrate vertically in the water column (Simão et al. 2014). The day-time sampling schedule of the present trawl surveys would accordingly be suitable for sampling both juveniles and adults of the two species.

The relationship between mean density and percentage occurrence by depth stratum was used to delimit depth strata showing high figures of both density and occurrence, which could be assumed to be the optimal depth ranges for the species. These were clearly located between 300 and 500 m in *P. sivado*, and deeper than 500 m (down to the deepest sampled depth, 800 m) in *P. multidentata*. It must be emphasized that the sampling schedule clearly encompassed the whole bathymetric distribution range of *P. sivado* in the study area (Abelló et al. 1988, 2002, Cartes et al. 1994), whereas in *P. multidentata* it did not reach the deepest distribution of the species, which has been reported to occur down to 2261 m depth (Cartes 1993c) in the Mediterranean.

Both species increased in size with depth, as shown in Company et al. (2001), with juveniles being found in much shallower waters than adults. In *P. sivado*, populations in the Alboran Sea reached larger sizes than those in the northwestern Mediterranean and in intermediate sectors. This implies that the population dynamics in these areas are different, and probably linked to the high productivity of the Alboran Sea (Fanelli and Cartes 2004). Recruitment in *P. sivado* was detected throughout the study area, in agreement with the main autumn-winter reproductive season of the species observed in the Catalan Sea (Company et al. 2001), and was mainly located at depths shallower than 300-400 m. By contrast, recruitment in *P. multidentata* was not present in the Algerian basin sectors (Alboran Sea and Alacant regions), while it was marked in the Catalano-Balearic basin. The reproductive season in *P. multidentata*, from studies made in the Catalan Sea (Company et al. 2001, Ramirez-Llodra et al. 2007), is centred in late autumn-winter. The absence of recruitment in spring in the geographic sectors belonging to the Algerian basin may imply that seasonality of reproduction in this species significantly differs between the populations inhabiting the two basins.

The analysis of the available environmental information clearly detected differences between the two species

with respect to temperature and salinity on the bottom, as well as between juveniles and adults of the two species. Temperature and salinity windows (25-75 percentiles) of adults of the two species clearly overlapped, but the salinity range of *P. multidentata* was narrower than that of *P. sivado*, and much narrower than that of juveniles of the species, while the temperature range was contiguous but non-overlapping at a limiting temperature of 13.25°C. By contrast, the temperature-salinity window of *P. sivado* juveniles was much larger, and more widely overlapping, than that of the adults, which were associated with higher salinities. This finding clearly showed that in both species, but particularly in *P. sivado*, juveniles had a wider thermohaline window, indicating they are able to cope with a wider variability in temperature and salinity conditions. A close dependence on a restricted salinity range has also been shown in deep-sea and continental slope crustaceans, such as *Parapenaeus antennatus* and *Aristeus antennatus* (Guijarro et al. 2008, 2009), while species displacements related to movements of water masses have also been found to occur at wide temporal and geographical scales (Cartes et al 2009, 2011), linked to relatively small density changes in seawater masses.

The differential distribution pattern between juveniles and adults of both *P. sivado* and *P. multidentata* (Company et al. 2001) could be related, as in other caridean shrimps inhabiting the continental slope (Company and Sardá 1997, Carbonell and Abelló 1998), to trophic resource partitioning between the two ontogenetic phases, which would allow a lesser degree of intraspecific competition. The dietary overlap between these species has been shown to be low due to the different size spectra of their respective prey items (Cartes 1993b). Adults of *P. sivado* and juvenile *P. multidentata* share a similar body size range, and are both important food items for *P. multidentata* adults (Cartes 1993b). Thus, size segregation would also be helpful to avoid intraspecific predation.

The present study has shown that in both *P. sivado* and *P. multidentata*, the populations inhabiting the Alboran Sea were clearly differentiated from those in the Catalano-Balearic basin concerning their bathymetric distribution, density, maturity size, and population size structure. The populations in the intermediate Alacant sector showed more affinities with the Alboran Sea populations than with the northern populations, especially in *P. multidentata*, which is consistent with their general affinity for the Algerian basin.

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