Short spatio-temporal variations in the population dynamics and biology of the deep-water rose shrimp *Parapenaeus longirostris* (Decapoda: Crustacea) in the western Mediterranean

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SUMMARY: The deep-water rose shrimp *Parapenaeus longirostris* is a demersal decapod crustacean that is commercially exploited by trawl fleets. The present work compares its population dynamics, biology and condition in two locations (southern and north-western Mallorca in the Balearic Islands, western Mediterranean, separated by a distance of 120 km) with different environmental conditions and explores the relationships between the species and certain environmental factors. Six multidisciplinary bimonthly surveys were carried out during 2003 and 2004 in these two locations (between 150 and 750 m depth) in order to collect data on the demersal species with bottom trawl, the hydrography (temperature and salinity) with CTD casts, and trophic resources (zooplankton in the water column and suprabenthos with Bongo net and Macer-GIROQ sledge respectively) and sediments with a Shipeck dredge. The trawl fleets from both locations were monitored by monthly on board sampling and daily landings obtained from sales bills. Additional data was obtained from other trawl surveys. Temporal differences were detected both annually, with a decreasing trend over the last years in species abundance, and seasonally, in the biological indexes analysed. Bathymetric differences were also found in abundance, mean length, sex-ratio and condition of females. There were clear differences between the two locations studied, with higher abundance, condition and mean length and a lower length at first maturity for females in the north-western location. Trophic conditions could act as a link between geo-physical and biological changes. These short spatio-temporal differences could be due to the higher productivity found at this location, with higher density of preferred prey for the studied species together with adequate sea-floor topography, sediment composition and hydrographical characteristics.

Keywords: *Parapenaeus longirostris*, reproduction, fishery, spatio-temporal variations, hydrography, bottom characteristics, prey availability.

RESUMEN: VARIACIONES ESPACIO-TEMPORALES A PEQUEÑA ESCALA EN LA DINÁMICA POBLACIONAL Y BIOLOGÍA DE LA GAMBA BLANCA *PARAPENAEUS LONGIROSTRIS* (CRUSTACEA: DECAPODA) EN EL MEDITERRÁNEO OCCIDENTAL. – La gamba blanca *Parapenaeus longirostris* es un crustáceo decápodo demersal explotado comercialmente por la flota de arrastre. Este trabajo tiene como objetivo comparar su dinámica poblacional, biología y condición en dos localidades (situadas al sur y al noroeste de Mallorca en las Islas Baleares, Mediterráneo occidental, separadas por 120 km de distancia) con diferentes condiciones ambientales y explorar las relaciones entre la especie y algunos factores ambientales. Se realizaron seis campañas multidisciplinares bimensuales durante 2003 y 2004 en estas dos localidades (entre 150 y 750 m de profundidad) para obtener datos de las especies demersales con arrastre de fondo, de la hidrografía (temperatura y salinidad) con registros de CTD, de los recursos tróficos (zooplancton de la columna de agua y suprabentos, con una red Bongo y un patín Macer-GIROQ respectivamente) y de sedimentos con una draga Shipeck. El seguimiento de las flotas de arrastre que operan en ambas localidades se realizó con muestreos mensuales a bordo y desembarcos diarios obtenidos de hojas de venta. Se usaron datos adicionales de otras campañas de arrastre. Se han detectado diferencias anuales, con una tendencia decreciente de la abundancia en los últimos años, y estacionalmente, en los índices biológicos analizados. También se han encontrado diferencias batimétricas en la abundancia, talla media, proporción de sexos y condición de las hembras. Se han visto claras diferencias entre las dos localidades estudiadas, con mayor abundancia, condición y talla media y una menor talla de primera madurez para hembras en la localidad situada al noroeste. Las condiciones tróficas podrían actuar como conexión entre los cambios geofísicos y biológicos, ya que la mayor productividad detectada en esta localidad, con una mayor densidad de presas preferidas para la

especie estudiada junto a una topografía del fondo marino, composición de sedimentos y características hidrográficas adecuadas podrían determinar estas diferencias espacio-temporales a pequeña escala.

Palabras clave: *Parapenaeus longirostris*, reproducción, pesquería, variaciones espacio-temporales, hidrografía, características del fondo, disponibilidad de presas.

INTRODUCTION

The deep-water rose shrimp, *Parapenaeus longirostris* (Lucas, 1846), is a demersal decapod crustacean with a wide geographic distribution, which covers the entire Mediterranean and eastern Atlantic, from the north of the Iberian Peninsula to the south of Angola (Sobrino *et al.*, 2005). It is broadly distributed both in the Mediterranean and Atlantic between 20 m and 750 m (Tom *et al.*, 1988), while its maximum abundance has been observed between 100 and 400 m depth (Lembo *et al.*, 1999). Although it presents a clear size increment with depth (Froglia, 1982), some authors suggest that adults move during the spawning period to shallower waters, where the occurrence of larvae has been detected (Dos Santos, 1998). It is a species of commercial interest for the trawl fishery throughout its distribution range (Ribeiro-Cascalho and Arrobas, 1987; Levi *et al.*, 1995). In the Balearic Islands (western Mediterranean), where deep-water decapod crustaceans represent around 20 and 50% of trawl landings in terms of weight and economic value respectively (unpublished data), the deep-water rose shrimp is the third species both in weight, after the red shrimp *Aristeus antennatus* (Risso, 1816) and a mixed category of Pandalidae, and earnings, after the red shrimp and the Norway lobster *Nephrops norvegicus* (L.).

In the Mediterranean, the most abundant information on deep-water rose shrimp comes from the eastern and central basins, where the species is more abundant than in the western basin (Abelló *et al.*, 2002). Thus, in the eastern and central Mediterranean, there is information available on its distribution (e.g. Bombace, 1975; Lembo *et al.*, 2000), biology (e.g. Mori *et al.*, 2000; Bayhan *et al.*, 2005), diet (Kapiris, 2004), fishery (Sbrana *et al.*, 2006), including stock assessment (Levi *et al.*, 1995; Lembo *et al.*, 1999), and trawl selectivity (Deval *et al.*, 2006b; Ragonese and Bianchini, 2006). In the western Mediterranean, the available studies have only focused on its distribution (Abelló *et al.*, 2002), diet (Cartes, 1995), energy content (Company and Sardà, 1998) and morphology (Sardà *et al.*, 2005) on the Iberian coast, and on its distribution (Nouar and Maurin, 2001) on the Algerian coast.

The role the environment plays in the abundance of deep-water rose shrimp has not been studied in depth, although the possible relation between the species and some environmental factors has been discussed. Its abundance has been suggested to be related to bottom characteristics (Ribeiro-Cascalho and Arrobas, 1987; Tom *et al.*, 1988; Nouar and Maurin, 2001), benthic communities such as octocorallians (Nouar and Maurin, 2001) or crinoid beds (Colloca *et al.*, 2004) and the presence of certain water masses (Bombace, 1975). Prey availability is also an important factor that conditions the distribution of decapod crustaceans in deep-water Mediterranean environments in which food is considered a limiting factor (Cartes, 1993; Cartes and Carrassón, 2004). In this area, the deep-water rose shrimp has a diet based on infauna and suprabenthos (Cartes, 1995). Apart from this, the role of other factors has not been tested and not even a joint analysis of the deep-water rose shrimp's abundance and the environmental variables has been previously performed.

The objectives of the present work were (i) to study the population dynamics, biology and condition of the deep-water rose shrimp off the Balearic Islands, (ii) to compare these parameters in two locations with different environmental conditions and similar fishing exploitation rates, sited in the south and northwest areas off Mallorca, and (ii) to explore the relationships between the species and some environmental parameters (hydrography, sediment characteristics and potential trophic resources).

MATERIALS AND METHODS

Study area

The Balearic Islands delimit two sub-basins in the western Mediterranean, the Balearic sub-basin (BsB) in the north and the Algerian sub-basin (AsB) in the south (Fig. 1). The shelf in the Balearic archipelago is narrow and steep on the northern side, and wider and gentler in the south. There is not much terrigenous-muddy sediment due to the absence of river discharges. Sandy-muddy and detrital sediments occur at the shelf-slope break, whereas muddy

bottoms of biogenic origin dominate the deeper areas (Acosta *et al.*, 2002). The hydrographic conditions of the Islands have been studied widely (e.g. Pinot *et al.*, 2002; López-Jurado *et al.*, 2008), with the Balearic channels described as important passages for the exchange between the cooler, more saline waters of the BsB and the warmer, fresher waters of the AsB. The temporal variability in hydrodynamic conditions of the area is mainly conditioned by the Northern Current (NC), which carries waters formed during winter in the Gulf of Lions (Western Mediterranean Intermediate Waters, WIW) southwards along the continental slope, and reaches the channel between the Iberian coast and the Islands. The main branch proceeds southward, while the minor one re-circulates cyclonically and returns to the northeast to form the Balearic Current (BC), which flows along the insular slope. After cold winters, greater amounts of WIW (characterised by a minimum temperature in the water column, 12.5-13.0°C) are formed, the NC is partially blocked at the channels and reinforces the BC (Pinot *et al.*, 2002; Monserrat *et al.*, 2008). Within the general oligotrophic environment of the Mediterranean, the waters around the Balearic archipelago, where there is no supply of nutrients from land runoff, show more pronounced

oligotrophy than the adjacent waters off the Iberian coast and the Gulf of Lions (Estrada, 1996; Bosc *et al.*, 2004). Frontal meso-scale events between Mediterranean waters and waters of Atlantic origin (Pinot *et al.*, 1995) and input of cold northern water into the channels (Fernández de Puelles *et al.*, 2004) act as external fertilisation mechanisms which enhance productivity off the Balearic Islands.

Sampling and biological data

Seasonal sampling was carried out during six multidisciplinary surveys (seasonal IDEA surveys, SIS), at two different locations off Mallorca, Cabrera (CA) in the AsB and Sóller (SO) in the BsB (Fig. 1), between August 2003 and June 2004. These locations, separated by a maximum of 120 km, are traditional trawl fishing grounds in which similar effort is exerted on deep-water rose shrimp (Moranta *et al.*, 2008).

During these surveys, 72 bottom trawls were carried out on board F/V *Moralti Nou*, six for each survey and location, covering a large bathymetric range (150, 250, 350, 550, 650 and 750 m depth), using a commercial net with a cod-end of 20 mm stretched mesh size. Each haul was tracked with a
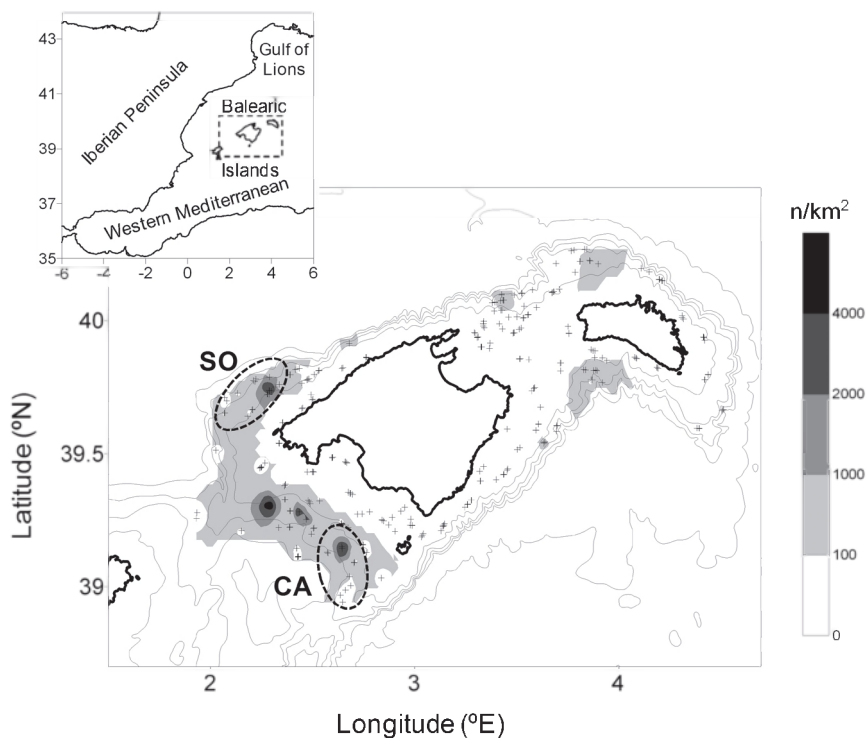

FIG. 1. – Map showing the Balearic Islands, with the two locations studied (CA: Cabrera; SO: Sóller) during the seasonal IDEA surveys and the spatial distribution of *Parapenaeus longirostris* from annual BALAR surveys (ABS). The contour map was estimated from data collected during ABS (crosses indicate sampling stations), by applying the squared distance gridding method (n/km^2 per haul). The 200, 600, 800, 1000 and 2000 m isobaths are also shown.

GPS and the opening of the net was controlled using a SCANMAR system. Mean horizontal and vertical net openings were 25 m and 2.5 m respectively. The mean towing speed was 2.7 knots and the trawling time 60 minutes.

All deep-water rose shrimps caught were counted, weighed and measured (carapace length: mm CL) for both sexes separately. Standardised abundance (n/km^2) and biomass (g/km^2) were calculated according to survey and location for the total population as well as for small and large individuals. These size classes correspond to individuals up to and over 25 mm CL, which is approximately juveniles and adults respectively.

Length frequency distributions per haul were calculated for the whole population from the 11484 specimens caught. For those hauls with more than 15 individuals, a mean length was calculated. Sex-ratio, as a percentage of females, was calculated for each haul and also according to length.

For the biological sampling, all the individuals (for hauls with <50 individuals) or a sub-sample of at least 50 individuals (for hauls with >50 individuals) were collected and analysed at the laboratory. A total of 919 specimens were measured, weighed and sexed. Maturity was determined by macroscopic observation of the gonads. Four stages were used for females (I: immature/spent/post-spawned ovaries; II: developing ovaries; III: advanced ovaries; IV: ripe ovaries; Mori *et al.*, 2000) and two for males (I: immature; II mature). For females, gonad weight was also taken and two biological indexes were estimated for each female sampled: (i) gonadosomatic index (GSI), as the percentage of gonad weight over total weight, and (ii) relative condition index (Kn; Le Cren, 1951), as observed weight over expected weight, estimated from a length-weight relationship, considering all data. The percentage of each maturity stage was estimated for each survey and location. The percentage of mature specimens (stages III-IV) according to size was also calculated, and the length at first maturity was modelled using only data from those months when the reproductive activity of the stock was at its maximum. Kn was also calculated for males.

In addition, trawl fishery daily landings of deep-water rose shrimp for the period 2001-2007 were obtained from sales bills. The trawl fleet usually carries out a single trip per day in the study area, so the sales bills allowed us to calculate the monthly and annual standardised catch per unit effort (CPUE) for the trawl fleet operating off Mallorca. The presence of the species in the daily sales bills was the criterion for selecting the days used, considering boat and day as units of effort. From September 2003 to September 2004, the commercial fleet which operates in CA and SO was also monitored by on board sampling (seasonal IDEA fleet monitoring, SIF). Data was obtained for deep-water rose shrimp catches, length frequency distributions and sex-ratio for each season and location. Sex-ratio was also estimated according to length. In addition, data obtained from other experimental bottom trawl fishing surveys, carried out annually around the Balearic Islands down to 800 m depth, were also used (annual BALAR surveys, ABS, Massutí and Reñones, 2005). This information was related to abundance, biomass, sex-ratio and length frequency in deep-water rose shrimp catches for the period 2001-2007. A mean length was obtained for those hauls with more than 15 individuals.

Environmental parameters

During the SIS, water temperature and salinity above the bottom during each trawl were recorded with a CTD SBE-37 situated at the float-line of the net.

Other oceanographic data were also collected during the SIS on board R/V *Francisco de Paula Navarro*. Samples of sediments, zooplankton in the water column and suprabenthos were obtained in both locations (CA and SO) with a Shipeck grab, Bongo net and Macer-GIROQ suprabenthic sledge respectively, at around 150, 350, 675 and 775 m depth. Further information of hydrological and trophic sampling during the SIS can be found in Cartes *et al.* (2008) and López-Jurado *et al.* (2008).

Sediments were stored on board at –20ºC for later laboratory analyses, which comprised mineralogical composition and grain size, and organic matter analyses. The granulometric analysis was carried out using two different techniques: the particle sizes of both the coarsest (mainly sand) and the finest samples were determined by dry sieving and using a Coulter LS particle size analyser (Tucker, 1988) respectively. The fraction (%) of gravel (2-64 mm), sand (0.0625-2 mm), silt (2-62.5 μm) and clay (0.06-2) was estimated (Blott and Pye, 2001) at each station. The grain size distribution of each sample was summarised by logarithmically transforming its median into Φ values ($\Phi = -\log_2 d$, where d is the grain diameter in mm), as well as its sorting coeffi-

cient IGSD (Inclusive Graphic Standard Deviation) (Gray, 1981; Blott and Pye, 2001):

$$\sigma = \frac{\phi_{84} - \phi_{16}}{4} + \frac{\phi_{95} - \phi_5}{6.6}.$$

The mineralogical composition was analysed by means of X-ray diffraction which was performed on a Siemens D-5000 device (Tucker, 1988; Gingele and Leipe, 1997). The organic matter content was obtained by calcination for two hours at 550°C.

Several groups collected by the suprabenthic sledge, both from the infauna (Polychaeta, Bivalvia) and suprabenthos (Amphipoda Gammaridea), were considered to be potential trophic resources for deep-water rose shrimp, which was deduced from previous papers on diet (Cartes, 1995; Kapiris, 2004). The data for polychaetes and bivalves have only a comparative value within our sampling (between locations and seasons), and not in terms of absolute values.

Data analysis

One-way analysis of variance (ANOVA) was used to test seasonal differences for the standardised abundance and biomass from the SIS and mean length and sex-ratio from the SIS and SIF, after testing for normality of data and homogeneity of variances. When no differences were detected, a two-way ANOVA was used, considering location and depth as factors. When seasonal differences were expected for the biological indexes GSI and Kn, a one-way ANOVA was used to reject spatial differences, and a two-way ANOVA, considering season and depth as factors, was used after testing for normality of data and homogeneity of variances. A chi-squared test was applied to evaluate the predominance of each sex in relation to size class and depth.

Cluster analysis was used to analyse length frequency distributions, grouped into 5 mm intervals, from SIS and SIF. Similarity percentage analysis was also applied to estimate the dissimilarity between these groups and the contribution of the main size classes to this similarity.

The parameters of the size-weight relationship and the Von Bertalanffy growth function (VBGF) were determined for sex, location and for sexes and locations combined. These were calculated using a relationship in the form of: $W = a \, CL^b$; where W was the total weight in grams, CL the carapace length in millimetres and a and b the parameters to be estimated, with b as the allometric coefficient. The VBGF parameters were estimated from the analysis of length frequency distributions, grouped into 2 mm size classes, with the LFDA 5.0 software (Kirkwood *et al.*, 2001), following the equation: $CL_t = CL_\infty (1-e^{-k(t-t_0)})$; where CL_∞ was the theoretical maximum length, CL_t the length at age t, k the growth coefficient and t_0 the age at which the size is 0. The Growth Performance Index (ϕ'; Munro and Pauly, 1983) was also calculated for each sex, location and their combinations.

Redundancy Analysis (RDA) was used to detect possible variations in the environmental variables between surveys and locations. The RDA was used because it links the species composition (response) matrix directly with the environmental (explanatory) matrix. The environmental matrix was composed of one continuous variable (depth) and three categorical variables (location, stratum and survey).

Joint analysis of density values (abundance and biomass) and environmental parameters was performed by multiple regressions, considering the total population and both size classes (juveniles and adults) separately. The environmental variables used were mean, minimum and maximum temperature and salinity above the bottom, percentage of organic matter, sands, silts and clays from the sediments and the total prey biomass.

RESULTS

The three datasets (SIS, SIF and ABS), with maximum abundance values between 300 and 450 m depth (polynomial curve fitted to abundances from ABS, $R^2 = 0.6$) showed that the bathymetric distribution of the deep-water rose shrimp in the Balearic Islands ranges between 130 and 650 m depth. The distribution presented spatial differences, as the shrimp was more abundant in the fishing grounds sited in the south and northwest of Mallorca (Fig. 1). Both CPUE from the commercial fleet (Fig. 2a) and abundances from the ABS (Fig. 2b) showed maximum values in 2001-2002, with a clear decreasing trend since then. When seasonality was considered (Fig. 2c), the highest values for the commercial CPUE were detected during spring and minimum values during autumn. The abundance and biomass of juveniles, adults and the total population did not show significant seasonal differences between SIS (Table 1). Therefore, a second ANOVA was performed with location and depth as factors. Depth and the
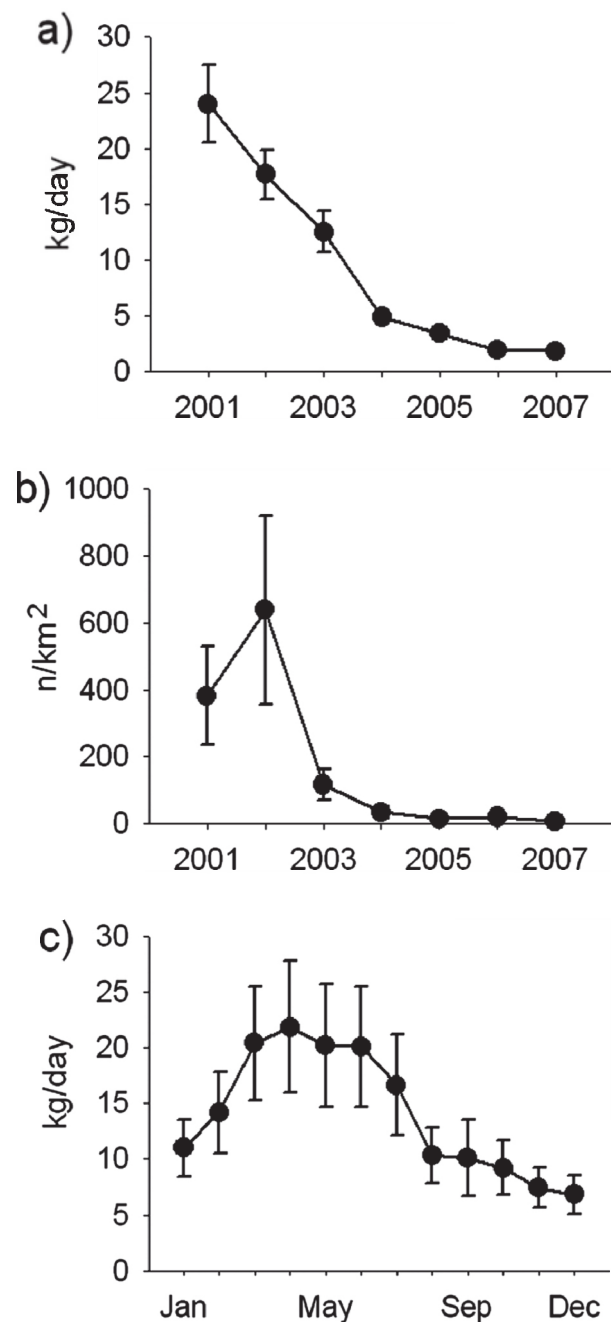
FIG. 2. – Catch per unit effort (CPUE) of *Parapenaeus longirostris* off the Balearic Islands: a) annual CPUE from the Mallorca trawl fleet (kg/boat/day); b) CPUE from annual BALAR surveys (n/km²); c) seasonal CPUE from the Mallorca trawl fleet (kg/boat/day). Error lines are standard errors.
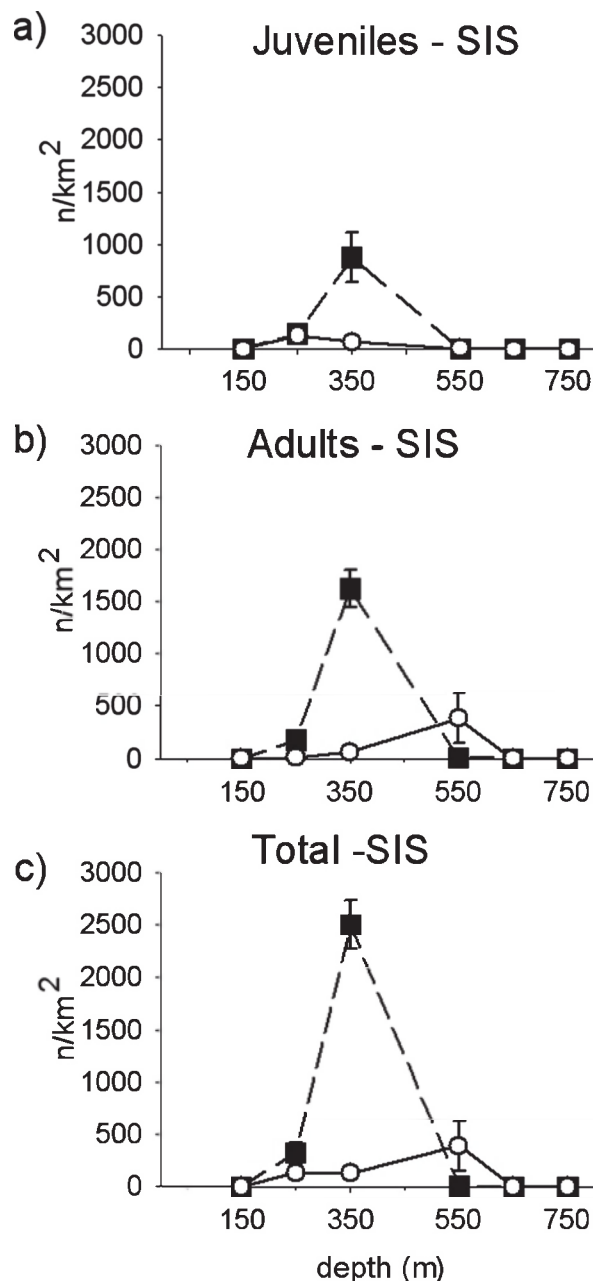

FIG. 3. – *Parapenaeus longirostris* abundance (n/km²) estimated in relation to depth, for juveniles, adults and total population, from the seasonal IDEA surveys (SIS) at each location studied (Cabrera: white circles and solid lines; Sóller: black squares and dashed line). Error lines are standard errors.

interaction depth-location were significant ($p < 0.05$) for juveniles, adults and the total population (both in n/km² and g/km²), while location was only significant for adults (n/km²). The post-hoc tests suggested that the highest values are found in SO at 350 m depth in all cases, while CA showed different bathymetric trends, with the highest values for juveniles at 250 m and for adults at 550 m (Fig. 3).

Cluster results from the length-frequency analysis, when the whole population was considered, showed three different groups (Fig. 4) for both the SIS and SIF. In both cases, the first group was composed by the shallower hauls from CA, formed by small individuals; the second one was formed by medium depths from CA and shallower to medium from SO; the third one was composed of larger individuals, with deeper hauls from CA and intermediate from
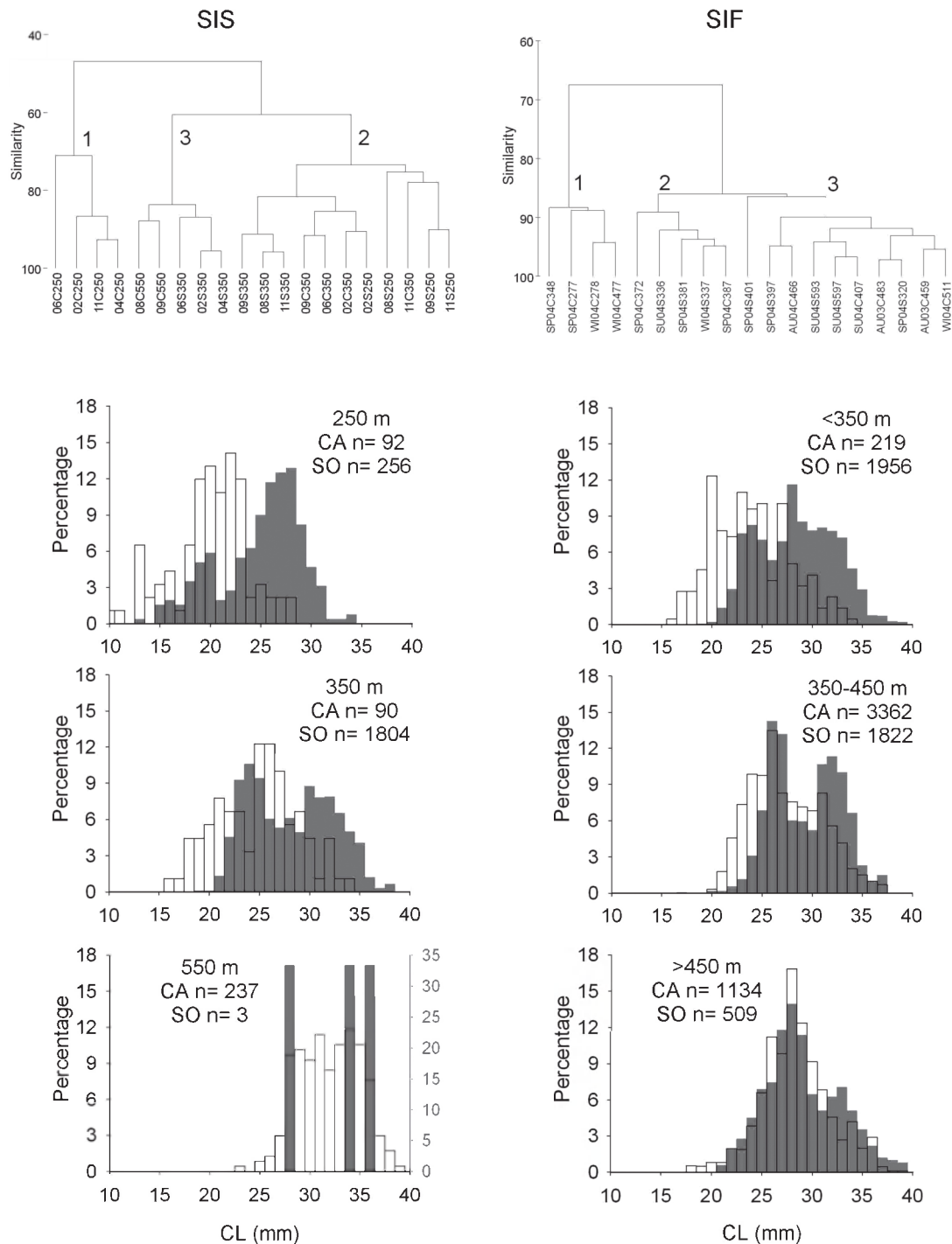
FIG. 4 – *Parapenaeus longirostris* length frequency distributions, according to depth and location (CA: white bars; SO: grey bars), obtained from the seasonal IDEA surveys (SIS) and the seasonal IDEA fleet monitoring (SIF), and results of the cluster analysis. Sample labels indicate survey/season (08: Aug'03; 09: Sep'03; 11: Nov'03; 02: Feb'04; 04: Apr'04; 06: Jun'04; SP04: AU03: autumn'03; WI04: winter'04; SP04: spring'04; SU04: summer'04; AU04: autumn'04), location (C: Cabrera; S: Sóller) and mean depth (in m); n: number of specimens measured.

SO. These differences between the two locations in the bathymetric distribution of the different length classes were also reflected in the size frequency distributions when depth and area were considered as factors, with a higher proportion of large individuals between 250 and 450 m depth at SO (Fig. 4). The analysis of the mean length, according to location and depth, confirmed these significant differences between locations, for two datasets (SIS and SIF, Table 1), with higher values at SO. A general trend

TABLE 1. – Summary of the results of the analysis of variance (ANOVA) and post hoc Tuckey's Honest Significant Difference (HSD) test for all the indexes analysed, showing the significance of the factors: survey (S), depth (D), location (L) and their interactions (D x L: depth-location; S x L: season-location). CA: Cabrera; SO: Sóller; ns: not significant. D1: <350 m; D2: 350-450 m; D3: >450 m.

Seasonal IDEA surveys (SIS)

		one-way ANOVA S		two-way ANOVA L	D	LxD	HSD
Abundance	Juveniles	ns		ns	<0.001	<0.001	250=350>550
	Adults	ns		<0.05	<0.001	<0.001	350>250=550; SO>CA
	Total	ns		ns	<0.001	<0.001	250=350>550
Biomass	Juveniles	ns		ns	<0.001	<0.001	250=350>550
	Adults	ns		ns	<0.001	<0.001	350>250=550
	Total	ns		ns	<0.001	<0.001	250=350>550
Mean length		ns		<0.001	<0.001	ns	550>350>250; SO>CA
Sex ratio		ns		ns	<0.05	ns	250>350

		L		S	D	SxD	
GSI		ns		<0.01	<0.001	ns	350>250
Kn	Females	<0.001	CA	<0.01	<0.01	<0.05	250>350>550
		(SO>CA)	SO	<0.001	ns	<0.05	
	Males	<0.001	CA	ns	ns	ns	
		(SO>CA)	SO	ns	ns	ns	

Seasonal IDEA fleet monitoring (SIF)

	one-way ANOVA S	two-way ANOVA L	D	LxD	HSD
Mean length	ns	<0.001	<0.05	ns	D3>D2>D1; SO>CA
Sex ratio	ns	ns	<0.01	ns	D1=D2>D3

TABLE 2. – Relative (size-weight relationship: $W = a \cdot CL^b$) and absolute growth (CL_∞: theoretical maximum length, in mm; k: growth coefficient, in years^{-1}; t_0: age at which the size is 0; ϕ': Growth Performance Index), according to sex and for the total population of *Parapenaeus longirostris*, for each location (CA: Cabrera; SO: Sóller) and for the two areas together (CA-SO), estimated from IDEA sampling.

Relative growth — Seasonal IDEA surveys (SIS)

	Females a	b	r^2	n	Males a	b	r^2	n	Females+Males a	b	r^2	n
CA	0.0027	2.4880	0.9838	159	0.0029	2.4688	0.9133	69	0.0027	2.4854	0.9838	228
SO	0.0027	2.5066	0.9563	434	0.0025	2.5160	0.9133	145	0.0022	2.5587	0.9673	579
CA-SO	0.0022	2.5626	0.9808	593	0.0024	2.5335	0.9776	214	0.0022	2.5682	0.9825	807

Absolute growth — Seasonal IDEA surveys (SIS)

	Females CL_∞	k	t_0	score	ϕ'	Males CL_∞	k	t_0	score	ϕ'	Females+Males CL_∞	k	t_0	score	ϕ'
CA	41.0	0.65	-0.16	0.295	6.996	33.5	0.97	-0.10	0.486	6.993	40.9	0.69	-0.07	0.309	7.051
SO	45.0	0.66	-0.24	0.379	7.198	30.1	0.99	-0.79	0.706	6.799	40.0	0.85	-0.60	0.456	7.215
CA-SO	44.0	0.67	-0.21	0.445	7.168	31.3	1.00	-0.49	0.646	6.887	40.0	0.84	-0.49	0.447	7.203

Absolute growth — Seasonal IDEA fleet monitoring (SIF)

	Females CL_∞	k	t_0	score	ϕ'	Males CL_∞	k	t_0	score	ϕ'	Females+Males CL_∞	k	t_0	score	ϕ'
CA	44.0	0.73	-0.92	0.326	7.254	30.9	0.99	-0.01	0.536	6.851	40.0	0.73	-0.99	0.348	7.063
SO	41.0	0.85	-0.27	0.433	7.265	31.5	0.90	-0.60	0.569	6.795	40.0	0.69	-0.23	0.315	7.007
CA-SO	44.0	0.85	-0.27	0.433	7.406	30.0	0.80	-0.10	0.701	6.579	40.0	0.89	-0.60	0.210	7.261

of increasing size with depth was detected, which was consistent in both locations (Table 1; lineal fit for ABS, $R^2= 0.8$).

The results obtained for the size-weight relationships for females, males and total population are shown in Table 2. In all cases, values for the allometric coefficients were lower than 3. These values were similar for females and males; however, non-significant differences were found between SO and CA, and slightly higher values in SO compared to CA. The VBGF parameters showed high k values, especially for males. L_∞ was always higher for females (Table 2).

The overall sex-ratio for the species was 73% females. There were no significant differences in the sex-ratio in relation to survey, season or loca-
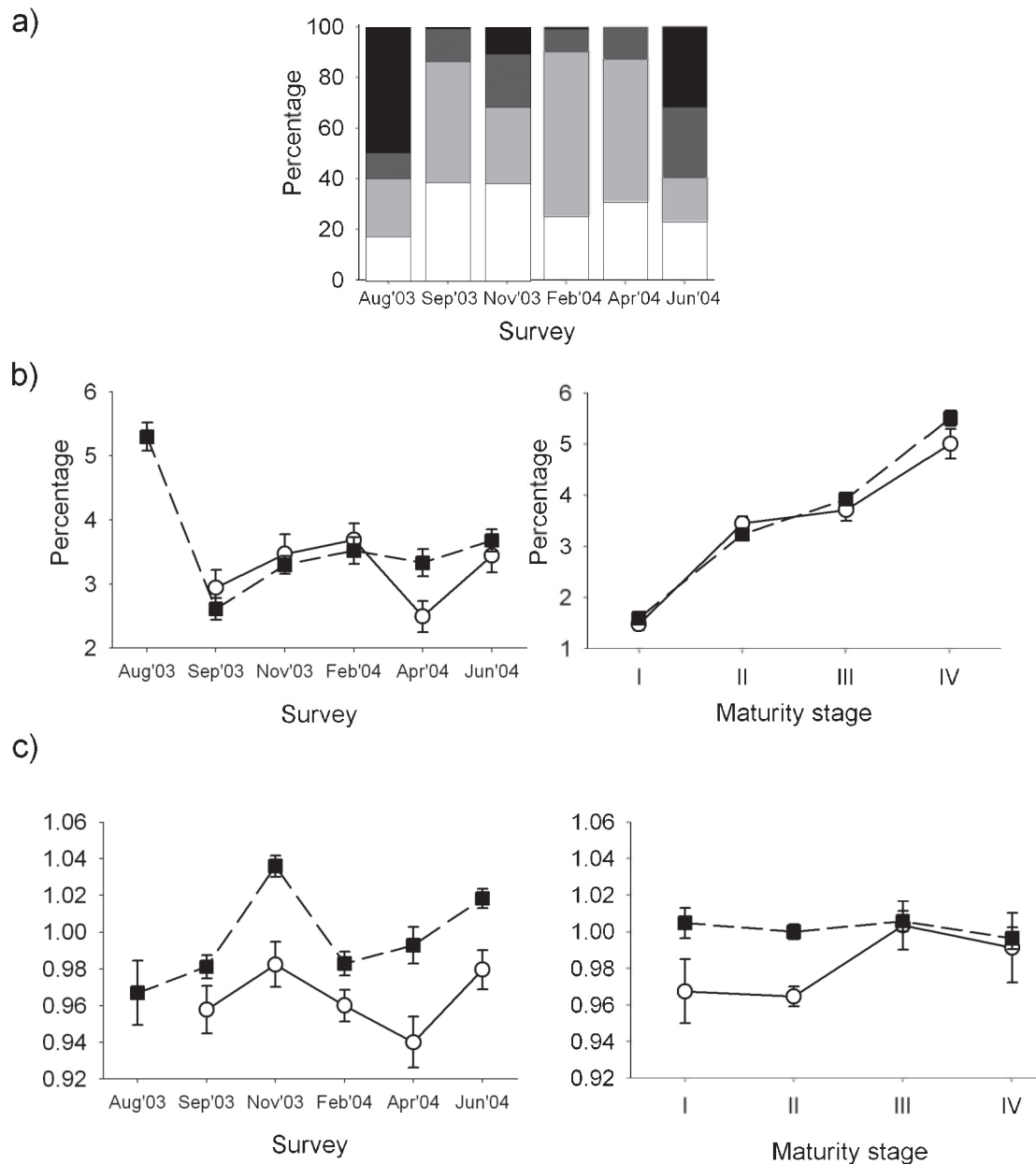
FIG. 5. – Percentage of each maturity stage (a; I: white; II: light grey; III: dark grey; IV: black; mature specimens correspond to stages III and IV), gonadosomatic index (b, GSI) and condition index (c, Kn) according to survey and location, and maturity stage and location, for females of *Parapenaeus longirostris* sampled in the seasonal IDEA surveys. Cabrera: white circles and solid lines; Sóller: black squares and dashed line. Error lines are standard errors.

tion, either for SIS or SIF (Table 1). However, there was a significant decreasing trend in the percentage of females with depth (Table 1; lineal fit for ABS, $R^2 = 0.5$). Females were always more abundant than males in the SIS data; however, males were more abundant than females in the deepest hauls of SIF. Sex-ratio according to length showed an increment in the percentage of females in relation to length, i.e. males were more abundant in the smallest size classes and females predominated at sizes >28-30 mm CL.

Length at first maturity for females was estimated at 29.5, 27.0 and 28.5 mm CL for CA, SO and the combination of both locations respectively. All males sampled were mature, so length at first maturity could not be calculated. Although maturing females were found all year round (maturity stages III and IV), two peaks were detected, one in Nov'03 and a larger one in Aug'03 and Jun'04 (Fig. 5a). There were no spatial differences in the GSI for females, but it showed significant differences between surveys, with the highest values in Aug'03

TABLE 3. – Summary values of the hydrographic variables (T and S) and sediment characteristics (OM, Φ, σ and percentage of gravel, sand, silt and clay; see Material and Methods), obtained in each survey at the two locations studied (CA: Cabrera; SO: Sóller), and the results of the redundancy analysis (RDA). The full RDA model contains all the variables included in the model: Depth (D), Location (L), Survey (S) and the Interaction Location-Survey (LxS). The explained variance (EV) for the full model and each variable after extracting the effect of the co-variables is also indicated. Note that the sum of the variance explained for each variable is greater than 100% due to the shared variance. T: temperature; S: salinity; OM: organic matter; Φ: median; σ: inclusive graphic standard deviation.

		T (°C)	S (psu)	OM (%)	Φ	σ	Gravel (%)	Sand (%)	Silt (%)	Clay (%)
CA	Aug'03	13.11±0.05	38.42±0.10	4.98±1.71	4.83±1.65	2.32±0.31	1.77	40.78	49.22	8.23
	Sep'03	13.13±0.05	38.43±0.09	4.70±2.13	4.35±1.83	2.16±0.35	3.52	41.47	47.47	7.54
	Nov'03	13.14±0.05	38.44±0.09	4.19±2.13	4.81±1.83	2.45±0.35	2.53	38.12	50.24	9.12
	Feb'04	13.19±0.14	38.43±0.12	4.13±1.43	4.98±2.51	2.04±0.36	2.03	34.43	52.30	11.25
	Apr'04	13.16±0.09	38.44±0.10	5.75±1.93	4.94±2.65	1.99±0.36	2.53	39.16	49.28	9.04
	Jun'04	13.11±0.06	38.45±0.10	5.97±1.97	4.37±2.36	2.11±0.36	2.38	44.58	45.56	7.49
SO	Aug'03	13.07±0.08	38.39±0.13	5.35±2.51	4.62±3.24	1.84±0.33	13.03	22.43	54.78	9.76
	Sep'03	13.14±0.10	38.42±0.11	5.51±1.90	4.12±2.43	2.23±0.27	8.18	38.97	46.62	6.23
	Nov'03	13.12±0.13	38.43±0.09	4.08±2.42	3.89±2.87	2.12±0.27	14.94	30.89	47.26	6.91
	Feb'04	13.15±0.18	38.40±0.12	4.25±2.42	4.88±3.10	2.12±0.29	9.58	23.85	55.95	10.63
	Apr'04	13.07±0.14	38.41±0.11	5.95±1.34	4.40±2.60	2.17±0.29	8.18	32.45	51.36	8.02
	Jun'04	13.09±0.08	38.46±0.09	6.91±2.02	4.47±2.94	1.97±0.31	10.85	26.30	54.24	8.61

RDA results	Effect	Covariance	Trace	EV	F-ratio	P
	Full model		0.78		10.50	0.0001
	D	L,S	0.73	93.59	127.10	0.0001
	L	D,S	0.03	3.72	5.12	0.007
	S	D,L	0.01	1.79	0.50	0.90
	LxS	D,L,S	0.01	1.54	0.37	0.96

(Fig. 5b; Table 1). Significant differences were also obtained for this index in relation to depth, with the highest values at 350 m depth (Table 1). There was also an increasing trend with the maturity stage (Fig. 5b). However, Kn showed significant differences between the two locations (Fig. 5c; Table 1), with higher values in SO than in CA for both sexes. For females, differences in Kn were also found per survey, with two peaks, one in Nov'03 and the other in Jun'04, and a decreasing trend with depth. Kn values also increased according to maturity stage in CA, and remained practically constant in SO (Fig. 5c).

The summary values and statistics of the physical environmental parameters analysed are presented in Table 3. Significant differences were obtained in relation to depth (p=0.0001), and this variable accounted for the highest proportion of the explained variance (93.6%). Temperature values and the percentages of gravels and sands were higher at shallower depths, while the rest of the variables increased with depth (Fig. 6). Significant differences were also detected between locations, but with a low proportion of the explained variance (3.7%). The differences were mainly due to the sediment granulometry, as gravel was predominant at SO at shallow depths. These differences in the sediment characteristics between locations were also clear when the percentage of silt and clays in relation to depth was considered (Fig. 7a), with lower values in SO than CA in shallower waters and the opposite occurring between 300 m
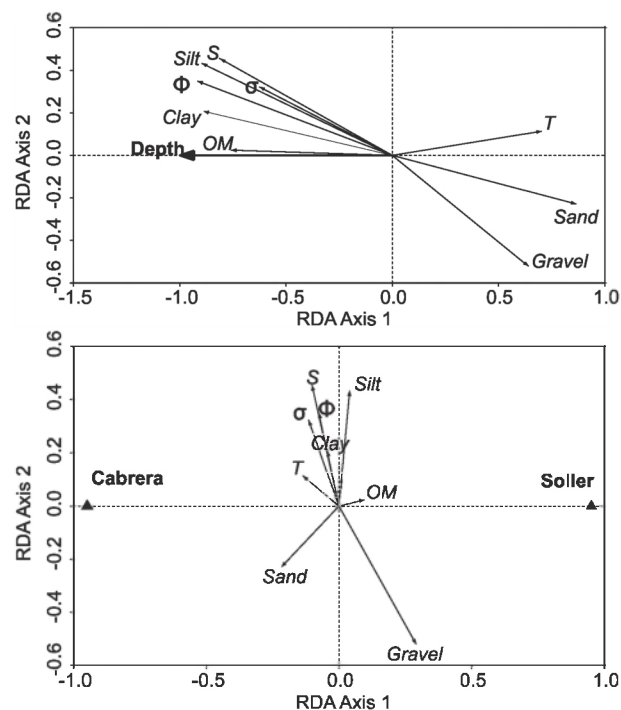

FIG. 6. – Results of the Redundancy Analysis (RDA) for the environmental variables matrix (T: temperature, S: salinity, OM: organic matter, Φ: median, σ: inclusive graphic standard deviation; sediment composition, as a percentage of granule, sand, silt and clay). In the top model the variable location (Cabrera and Sóller) has been considered as co-variable, while in the bottom model the co-variable is depth.

and 700 m depth. The dynamics of the main prey biomass at the 350 m station, which coincided with the maximum abundance of the deep-water rose shrimp, showed higher values off SO (Fig. 7b), which were
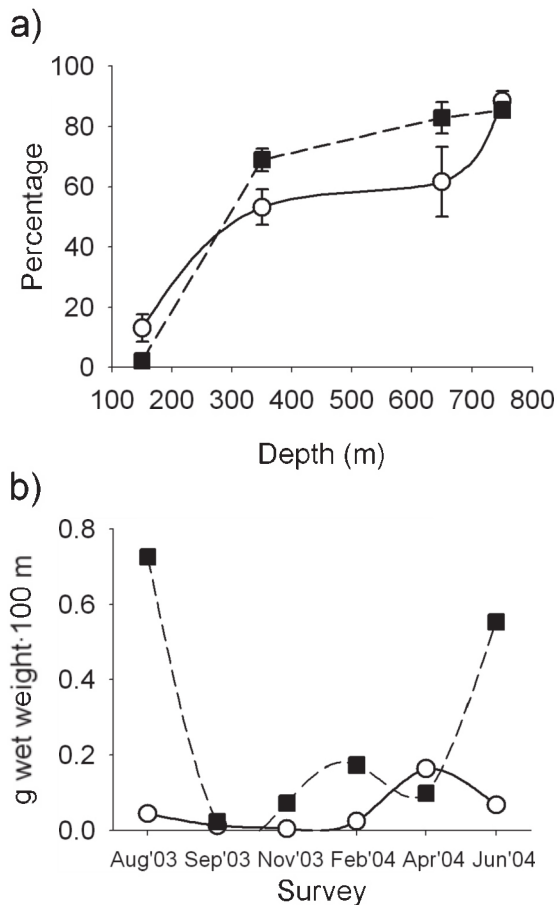
a)

b)

FIG. 7. – Percentage of silts and clays in sediments according to depth (a) and potential trophic resources for *Parapenaeus longirostris* in relation to season (b), at each location (Cabrera: white circles and solid lines; Sóller: black squares and dashed line). Error lines are standard errors.

TABLE 4. – Summary results of the multiple linear regression of the standardised abundance (n/km^2) and biomass (g/km^2) of juveniles, adults and total population of *Parapenaeus longirostris* obtained from the data from the seasonal IDEA surveys, showing the response of the abundance and biomass to significant environmental variables. Variance explained in each model in brackets.

		Variable	Coefficient	p
Juveniles	n/km^2 (0.91)	Silt	5.300	0.003
		Mean salinity	-1.478	0.006
		Sand	6.852	0.004
		Clay	1.721	0.033
		Preys	0.400	0.130
		Organic matter	-0.411	0.078
	g/km^2 (0.87)	Silt	4.949	0.009
		Mean salinity	-1.586	0.011
		Sand	6.644	0.012
		Clay	1.807	0.056
		Preys	0.477	0.140
		Organic matter	-0.333	0.207
Adults	n/km^2 (0.16)	Mean temperature	-0.395	0.204
	g/km^2 (0.16)	Mean temperature	-0.383	0.219
Total	n/km^2 (0.38)	Mean salinity	-0.6801	0.043
		Preys	0.360	0.245
	g/km^2 (0.15)	Mean temperature	-0.384	0.218

and 15% of variance for the abundance and biomass respectively.

DISCUSSION

The population dynamics of the deep-water rose shrimp in the Balearic Islands shows significant temporal differences both annually, concerning its abundance, and seasonally, concerning the biological and condition indexes analysed. Bathymetric differences were also detected in the abundance and in some biological parameters, such as the mean length and sex-ratio, as well as in the condition of females. Spatial differences were also found between the two locations studied; adults were more abundant in the north-western location (SO), where the condition index of both sexes and mean length were higher, while the length at first maturity for females showed the opposite trend, as it showed small values in this location. The bottom sediment and characteristics of the water masses, as well as the availability of potential trophic resources also seem to be important factors affecting the abundance of the deep-water rose shrimp and could determine the differences found between the locations studied. Previous studies have suggested that the characteristics of water masses and substrate are factors that influence this species

marginally significant (T-test, p=0.06) with maximum values in Aug'03 and Jun'04. Minimal values were found in Sep'03 and Nov'03.

The results of the multiple linear regression showed that the environmental factors analysed influenced the juveniles more than the adults of deep-water rose shrimp (Table 4). The most important factors were the bottom sediment characteristics and mean water salinity near the bottom, together with the abundance of potential prey. Juveniles were positively correlated to the percentage of silts, sands and clays and to the abundance of prey, while they were negatively correlated to the mean salinity near the bottom. These variables represented up to 91% of the variance explained. For adults, the significance of the models only explained 16% of variance, and was negatively correlated to the mean temperature near the bottom. The total population was negatively correlated to mean salinity and temperature and positively correlated to the prey, which explained 38%

(Bombace, 1975; Ribeiro-Cascalho and Arrobas, 1987; Tom *et al.*, 1988; Nouar and Maurin, 2001).

The nearly complete absence of deep-water rose shrimp on the Balearic shelf can be explained by the sediment characteristics at the bottom, as the lack of terrigenous muddy bottoms that originate from river run-off, means that this species is not distributed in as shallow depths as in other areas (20 m minimum depth; Sobrino *et al.*, 2005); 135 m was the minimum depth at which the shrimp was found in our study area. Similar results were obtained by Abad *et al.* (2007) in the Alboran Sea (south-western Mediterranean), where rose shrimp was captured by the bottom trawl fleet between 150 and 350 m depth. However, this is not a general rule for the Mediterranean, as standardised experimental MEDITS surveys reported the presence of this species from 50 m depth (Abelló *et al.*, 2002). According to these authors, it is in these shallow waters that juveniles and larvae are usually found, while larger individuals are distributed in deeper waters, which is also reflected in our study by the increase in the mean length with depth. On a local scale, the high hydrographical variability between locations and differences in the geomorphology and sediments marked the variations found in the deep-water rose shrimp between CA and SO, southern and north-western Mallorca respectively. The slope in SO is steeper than in CA, where it is necessary to reach deeper bottoms in order to find the same sediment composition as in SO. This area is influenced more by the slope fronts, which transport WIW from the Gulf of Lions, one of the most productive areas in the Mediterranean owing to a number of oceanographic features, including a wide shelf, presence of submarine canons, river runoff, strong vertical mixing in winter and occasional coastal upwellings (Champalbert, 1996; Estrada, 1996; Bosc *et al.*, 2004; Canals *et al.*, 2006). These water masses, with low temperature (<13°C) and salinity values, are mainly detected during late spring and summer in the Balearic Islands (López-Jurado *et al.*, 2008; Monserrat *et al.*, 2008; Fig. 8). Their presence increases the primary production in the area (Estrada, 1996), with the consequent enrichment of the trophic chain (Fernández de Puelles *et al.*, 2004). Cartes *et al.* (2008) reported higher abundance of suprabenthos and zooplankton in SO than in CA, mainly in late spring-early summer when the WIW arrives to the Islands. Our results suggest that infauna and suprabenthos have a similar response to its dynamics at 350 m depth, with maximum bio-
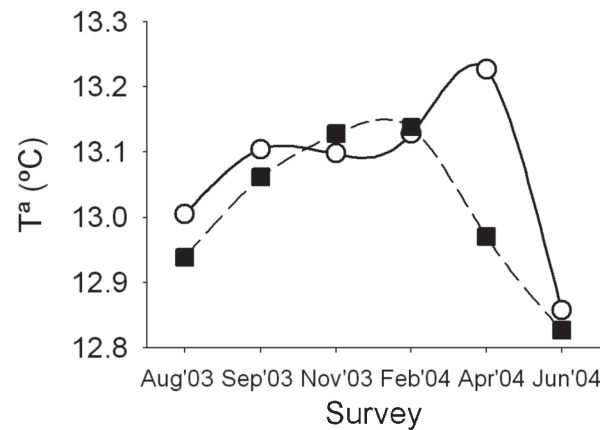

FIG. 8. – Minimum temperature in the water column, estimated from CTD SBE-911+ casts according to survey and location (Cabrera: white circles and solid lines; Sóller: black squares and dashed line), which indicates the presence of Western Mediterranean Intermediate Waters.

mass in spring-summer. The highest CPUE values from the commercial trawl fleet for deep-water rose shrimp were also obtained in spring. Therefore, the presence of muddy and more or less sandy sediments at depths with the highest productivity, which is reflected in high availability of potential prey, marks the highest abundances for both juveniles and adults of the deep-water rose shrimp in the north-western location. However, in the southern, less productive location, juveniles and adults show different depths of maximum abundance (250 and 550 m respectively) and a deeper distribution in order to find appropriate sediment characteristics, which are also probably favoured by the gentler slope at this location.

Both females and males were in a better condition in SO, the more productive location studied. Better condition in some fishes, modelled by lipid reserves, has been related to high productivity areas (Lloret *et al.*, 2002, Lloret *et al.*, 2005). This better condition is reflected not only in the condition index, but also in the allometric growth parameter. In the case of females, although seasonal differences in condition related to reproduction were detected, the higher values in SO were found all year round and for all the maturity stages. Previous studies in the area showed a better condition in SO than in CA for the red shrimp *A. antennatus* (Guijarro *et al.*, 2008) and European hake *Merluccius merluccius* (L.) recruits (Hidalgo *et al.*, 2008), which confirms that the north-western location is a more highly productive area than the southern location.

The better condition of deep-water rose shrimp in SO could be the reason for the smaller length at first maturity found for females there, as energetic condi-

tion has a positive effect on the probability of maturing (Baulier *et al.*, 2006). The values of length at first maturity estimated in our study are higher than those previously reported both in the Mediterranean (Levi *et al.*, 1995; Mori *et al.*, 2000; Ben Meriem *et al.*, 2001) and Atlantic (Ribeiro-Cascalho and Arrobas, 1987; Sobrino and García, 1994, 2007), and are similar to those reported by Spedicato *et al.* (1996), in the central Mediterranean. However, comparisons of the first maturity size must be viewed with caution, as these values may be greatly influenced by sample size and composition (Mori *et al.*, 2000), especially if there is an absence of smaller lengths in the samples (Ben Meriem *et al.*, 2001). The differences between locations observed in our study cannot be attributed to any of these factors, because both areas show similar length frequency distributions, even with smaller specimens in CA than in SO.

The absence of a seasonal pattern in the abundance of juveniles reflects the continuous spawning found for this species in our study. Although high abundance of juveniles has been found for a certain season in some studies (for instance, during autumn in the central Mediterranean, Lembo *et al.*, 1999), continuous spawning is common both in the Mediterranean (Nouar, 1985; Tom *et al.*, 1988; Spedicato *et al.*, 1996; Mori *et al.*, 2000; Ben Meriem *et al.*, 2001; Bayhan *et al.*, 2005) and the Atlantic (Dos Santos, 1998; Ribeiro-Cascalho and Arrobas, 1987; Sobrino and García, 1994), with peaks of reproductive activity varying between areas without a clear trend. Our peaks of maximum spawning are reflected differentially in the biological indexes. Hence, maximum GSI values were detected in summer, while maximum Kn values were found in late spring and especially in autumn. This suggests that the spring-summer spawning period (especially summer) is more important than the autumn one, as the values of GSI are higher and the shrimp's condition is at its minimum in summer. As *P. longirostris* is iterouparous the resource availability (higher in summer) may favour higher fecundity (GSI) in summer. According to Bayhan *et al.* (2005), the negative relationship between GSI and Kn is more pronounced during the period of most intense spawning. This lack of homogeneity in the seasonal behaviour of both parameters could be explained by the fact that larger mature females mainly spawn in spring-summer, whereas smaller adult females spawn in autumn (Sobrino and García, 2007), and the number of oocytes in the ovary increases significantly with length (Mori *et al.*, 2000). Thus, a higher number of oocytes in the mature ovaries of large females during summer is reflected in the highest GSI values, which also correspond to low Kn values. However, during the autumn spawning Kn presents high values, but the GSI is not as high as in summer.

The size-weight relationships suggest a negative allometry both for females and males, which has also been found in other studies both in the Mediterranean (Levi *et al.*, 1995) and the Atlantic (Ribeiro-Cascalho and Arrobas, 1987; Sobrino and García, 1994).Our results for the absolute growth agree with previous studies (see Sobrino *et al.*, 2005), which characterised the deep-water rose shrimp as a fast-growth species, with a life span of 2 to 3 years. Males grow faster than females and reach lower maximum lengths. Recent estimations of growth parameters, performed by quantification of the age-pigment lipofuscin in the brains of this species (Vila, 2005), reported similar values to those found with more classical methods, which confirms the fast growth of deep-water rose shrimp.

The highest CPUE values found for the species during spring in our study area agree with the season of maximum values observed by the commercial trawl fleet in the central Mediterranean (Sbrana *et al.*, 2006). Moreover, the decreasing trend found in the CPUE over the last years, which was confirmed by the annual surveys, has also been found in other areas in the western and central Mediterranean, such as the Iberian coast (GFCM, 2006) and the northern Tyrrhenian Sea (Sbrana *et al.*, 2006). This trend, however, differs from that found in the eastern Mediterranean (e.g. Sea of Marmara, Deval *et al.*, 2006a). The large fluctuations observed in Italian waters may be due not only to environmental conditions that greatly affect this short life span and fast growing species, but also to the different exploitation rates over the years (Sbrana *et al.*, 2006). In the Balearic Islands, where the trawl fishing effort has not significantly changed over the last years, the environmental conditions should be considered as the main factor affecting this species. The influence of environmental conditions (sediment, water masses and availability of prey), observed in our study in a short spatio-temporal range, should also be taken into account when long-term trends are analysed. The importance of large-scale factors on the population dynamics of deep-water crustaceans has already been suggested (Relini and Orsi Relini, 1987; Carbonell *et al.*, 1999; Anderson, 2000; Lloret *et al.*,

2001; Wieland, 2004; Koeller et al., 2007; Maynou, 2008). In our study area two oceanographic scenarios, associated with macro and meso-scale climate regimes, could influence the population dynamics of European hake and red shrimp (Massutí et al., 2008). Although the annual data series available for the deep-water rose shrimp is too short to analyse this matter further, it should be analysed in the future in order to obtain a wider view of the influence the environment has on this species.

The occurrence of adequate environmental characteristics, such as appropriate seafloor topography, sediment composition, hydrographical characteristics and prey availability seem to mark the short spatial and temporal differences found in the abundance, bathymetric distribution, biology and condition of the deep-water rose shrimp in the Balearic Islands. This reflects the importance of the north-western location as a high productivity area in the Archipelago, with trophic conditions acting as a link between geo-physical and biological changes.

ACKNOWLEDGEMENTS

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