

Seasonality of planktonic crustacean decapod larvae in the subtropical waters of Gran Canaria Island, NE Atlantic

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Summary: A monitoring programme was established to collect plankton samples and information of environmental variables over the shelf off the island of Gran Canaria during 2005 and 2006. It produced a detailed snapshot of the composition and seasonal assemblages of the decapod larvae community in this locality, in the subtropical waters of the Canary Islands (NE Atlantic), where information about crustacean phenology has been poorly studied. The larval community was mainly composed of benthic taxa, but the contribution of pelagic taxa was also significant. Infraorders Anomura (33.4%) and Caridea (32.8%) accounted for more than half the total collected larvae. High diversity, relatively low larval abundance throughout the year and weak seasonality characterized the annual cycle. However, in relation to the temporal dynamics of temperature, two distinct larval assemblages (cold and warm) were identified that correspond to periods of mixing and stratification of the water column. The results also indicate that larval release times and durations in the subtropical waters are earlier and longer than at other higher latitudes in the NE Atlantic. We detected the presence of larvae of six species that have not yet been reported from the Canary Islands (*Pandalina brevivrostris*, *Processa edulis*, *Necallianasa truncata*, *Parapenaeus longirostris*, *Crangon crangon*, *Nematopagurus longicornis*). Finally, this study provides a baseline for future comparisons with respect to fishery pressure and climate variability in this subtropical region.

Keywords: decapod larvae; phenology; assemblages; temperature; subtropical waters; Canary Islands.

Estacionalidad de las larvas de crustáceos decápodos en las aguas subtropicales de la isla de Gran Canaria, Atlántico NE

Resumen: Durante 2005 y 2006 se estableció un monitoreo para recolectar muestras de plancton e información de las variables ambientales sobre la plataforma insular de Gran Canaria. Esto produjo una instantánea detallada de la composición y estacionalidad de las asociaciones de la comunidad de larvas de decápodos en las aguas subtropicales de esta localidad de las Islas Canarias (Atlántico NE), donde la información sobre la fenología de crustáceos está pobremente estudiada. La comunidad de larvas estuvo principalmente compuesta por taxones bentónicos, pero con una contribución significativa de taxones pelágicos. Los infraórdenes Anomura (33.4%) y Caridea (32.8%) representaron más de la mitad del total de las larvas recolectadas. Alta diversidad, relativamente baja abundancia de larvas a lo largo de todo el año, y débil estacionalidad caracterizaron el ciclo anual. Sin embargo, y relacionado con la dinámica temporal de la temperatura, dos asociaciones larvianas distintas (fría y cálida) fueron identificadas que correspondieron con periodos de mezcla y estratificación de la columna de agua. Los resultados también indican que la duración y periodos de liberación de larvas en las aguas subtropicales son más tempranos y largos en el tiempo en comparación con otras latitudes más altas en el Atlántico NE. Además, se detecta la presencia de larvas de seis especies que no han sido citadas con anterioridad para las Islas Canarias (*Pandalina brevivrostris*, *Processa edulis*, *Necallianasa truncata*, *Parapenaeus longirostris*, *Crangon crangon*, *Nematopagurus longicornis*). Finalmente, este estudio supone un punto de referencia para futuras comparaciones en relación con la presión pesquera y la variabilidad climática en esta región subtropical.

Palabras clave: larvas de decápodos; fenología; temperatura; diversidad; aguas subtropicales; Islas Canarias.

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INTRODUCTION

A key component for ecosystem and fishery management is an understanding of the reproductive strategies adopted by crustacean decapods in response to physical and biological processes. Most decapods have complex life cycles in which they release larvae into the water column where, as plankton, they develop through larval stages and may be transported far from their parental populations or retained near them by specific oceanographic features and larval behaviour (Shanks 1995, Queiroga and Blanton 2005, Jones et al. 2007). Therefore, the seasonal occurrence of larvae in the plankton usually provides valuable insight into the phenology of decapods. Further, the planktonic stage is a critical phase and larval pool mortality can exceed 90%, constituting a bottleneck that limits the population size (White et al. 2014). Laboratory and field studies have shown that larval mortality is determined by predation, competition for food and space, disease, and environmental stresses such as temperature, salinity, low oxygen concentrations, pollution, and ultraviolet irradiation (Shanks 1995, Eckman 1996). Thus, many species have evolved elaborate behavioural and life history strategies that exploit favourable periods of the year (those best matching optimal niche requirements) for growth, and minimize exposure of sensitive larval stages to stressful conditions (Ji et al. 2010). Physical and biological cues seem to be involved that trigger larval release, such as temperature increase (Shirley and Shirley 1989), phytoplankton blooms (Starr et al. 1990), daylight duration and tidal amplitude (Morgan and Anastasia 2008). In general, the annual cycle of decapod larvae in temperate waters of NE Atlantic is related to the temperature regime, and seems to be linked to phytoplankton blooms (Kirby et al. 2008), with two main abundance peaks during spring and summer (Highfield et al. 2010, Pan et al. 2011). However, comparatively little is known about the seasonality of decapod larvae in tropical and subtropical regions (Epifanio and Dittel 1984, Reyns and Spoungle 1999). It is expected that the higher and more stable temperature throughout the year in lower latitudes favours continuous reproduction (Bauer 1992), leading to a weaker seasonality of decapod larvae in the plankton.

In the subtropical waters of the Canary Islands, decapod crustacean fauna is relatively well studied. Currently, around 300 species have been reported (González and Quiles 2003, Moro et al. 2014, González 2016), yet knowledge of distribution, population dynamics and reproductive biology is limited to a few key species found in seagrass meadow ecosystems (García-Sanz et al. 2014) and to some deep-water species with commercial interest for small-scale local fisheries (Tuset et al. 2009, González et al. 2016a, Triay-Portella et al. 2017). Similarly, little is known about the larval biology of decapods in the area, although significant efforts have recently been focused on the larval development of species whose larval morphology is still unknown (e.g. Landeira and Cuesta 2012, Landeira et al. 2014,

2015). Accurate taxonomic descriptions have aided the identification of larvae in the plankton and the study of transport processes in the Canary-African Coastal Transition Zone. The spatial distribution of larvae over the shelf of the island of Gran Canaria shows a clear pattern, in which larval abundances are much higher in the weak flow area around the stagnation point upstream of the island and the warm lee region downstream, where less intense winds occur (Landeira et al. 2009, 2013). In open waters, the larval abundance is usually very low, but there is a clear physical/biological coupling between mesoscale oceanographic activity and decapod larvae distribution. Eddies generated downstream of the archipelago when the Canary Current impinges upon the island topography (Hernández-Guerra et al. 1993, Sangrà et al. 2007) act as oceanic retention zones for larvae of neritic species (Landeira et al. 2010, 2012, 2017). Furthermore, it has been observed that filaments of upwelled waters originating over the continental shelf transport larvae from the African coast towards the ocean, indicating that they provide a conduit to the islands that connects populations (Brochier et al. 2011, Landeira et al. 2012, 2017).

In the context of climate change, several studies have described pronounced responses by marine ecosystems to global warming. Currently, a shift of the biogeographical distribution and phenological patterns is being observed in response to increasing temperature trends (Parmesan 2006). In the North Sea, long-term time series from continuous plankton recorders have revealed earlier temporal occurrences of several species of crustacean decapods (Lindley et al. 1993), increased abundances of decapod larvae (Kirby et al. 2008, Kirby and Beaugrand 2009) and increasing spatial extents of warm-water species, as well as the arrival of new species (Lindley et al. 2010). At lower latitudes, the effects of this warming are expected to include increased disturbances in crustacean decapods dynamics, but with as yet unknown consequences. It is therefore important to study the current state of decapod larvae assemblages in order to predict and/or detect changes in their population dynamics due to a future warming scenario in the tropics and subtropics. For this reason, using an intensive sampling monitoring off Gran Canaria, we describe here for the first time the seasonal assemblage of the decapod larvae community and associated environmental variables at the Canary Islands. Our primary aim was to test whether the larval community in the subtropical waters of the Canary Islands shows a lesser seasonality than that at other northern latitudes in the eastern Atlantic. Moreover, we report the first record of several species based on the presence of their larval stages in plankton samples.

MATERIALS AND METHODS

Sampling and laboratory analysis

In the framework of the ConAfrica project, weekly sampling was carried out from January 2005 to December 2006 (n=76 samples) during daylight hours

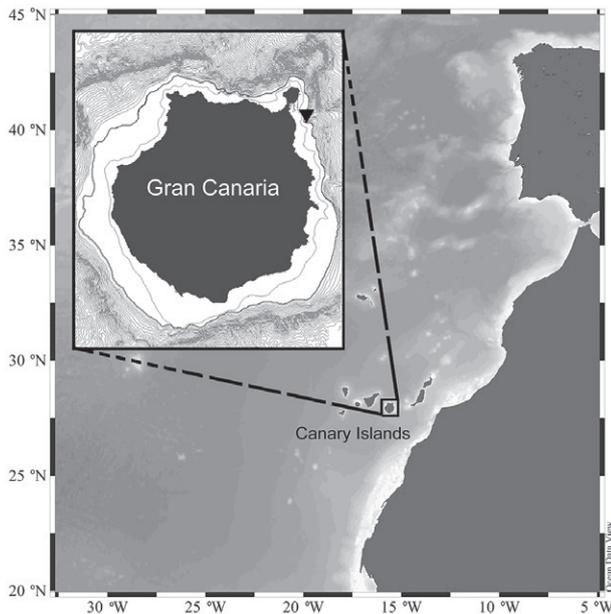


Fig. 1. – Study area in the NE Atlantic, showing the location of the sampling station (black triangle) near the island of Gran Canaria.

aboard the R/V *Solana II*. This study focuses on station 1 (28°04.00'N 15°21.62'W), located over the 100 m isobath in an area of weak flow associated with the stagnation point upstream of the island (Moyano and Hernández-León 2011, Landeira et al. 2013, Fig. 1). Zooplankton were collected using a Bongo net of 40 cm mouth diameter fitted with nets of 200 µm mesh size. The net was towed obliquely from 90 m to the surface at 2 knots (1 m s⁻¹) and a wire speed of 0.5 m s⁻¹, and it was attempted to maintain a wire angle of approximately 45°. Flow rate was estimated using calibrated flowmeters (General Oceanics), and the mean volume of water filtered was 27.84 m³. For taxonomic identification, one of the samples was immediately fixed in a 4% solution of formalin in seawater. Prior to zooplankton sampling, vertical profiles of temperature, salinity and fluorescence were recorded using a CTD SBE25 (Sea-Bird Electronics, Inc., Bellevue, WA, USA). Phytoplankton chlorophyll *a* was derived from water samples taken in the mixed layer at a depth of 15 m with a Niskin bottle.

In the laboratory, decapod larvae were sorted and quantified. For holoplanktonic pelagic shrimps which are planktonic during their whole lives (e.g. *Lucifer typus*), only larval stages were analysed. Following Anger (2001) and Martin et al. (2014), the transition from planktonic to benthic stages such as the decapodite stage in Caridea or megalopae in Brachyura were considered as last larval stages, whereas postlarval stages were not considered in this study. Larvae were identified using the guides given by dos Santos and Lindley (2001) and dos Santos and González-Gordillo (2004), and using the specific taxonomic descriptions recommended in the checklist of González-Gordillo et al. (2001). General taxonomical nomenclature follows De Grave et al. (2009). The catches were standardized by number of decapod larvae per 100 m³.

Data analysis

The Shannon–Wiener diversity index (H'),

$$H' = - \sum_{i=1}^S p_i \ln p_i$$

(where S is the number of species and p_i is the proportion of individuals in species i), was used to analyse changes in temporal and spatial diversity in the decapod larvae community. The parametric statistical method (Student t test, $p > 0.05$) was used to evaluate interannual differences in larval abundance and diversity (previously tested for homogeneity of variances using Levene's test). Multivariate analysis was used to identify larval assemblages with distinct community structure. Only species present in both 2005 and 2006 were used in the analysis in order to eliminate the effect of rare and multispecies groups (e.g. *Sergestidae* spp., *Pagurus* spp.). A total of 49 species were left from the initial 105.

In a first step, to examine temporal differences between months, within years and between years, an analysis of similarities (two-way nested ANOSIM) was performed on the species resemblance matrix using the log-transformed abundance data from all the samples in a Bray–Curtis similarity matrix. After this analysis, using the same Bray–Curtis similarity matrix, a non-metric multidimensional scaling (MDS) was performed to obtain a graphical ordination of the samples (Clarke and Warwick 2001). It was assumed that stress coefficients greater than 0.15 indicate a good representation of data (Clarke and Gorley 2006).

Due to the absence of any temporal structure in the decapod larvae community (see Results), forced by the elevated number of taxa and the weak seasonality of decapod larvae in subtropical waters (Reyns and Spoungle 1999), a month-averaged larval abundance data was used in a second step of the analysis (removing the factor year). In this second step, in order to divide the 12 months into distinct periods of larval assemblages, a cluster analysis and similarity profile routine (SIMPROF; $p < 0.01$; 999 permutations) were performed using the log-transformed abundance data in a Bray–Curtis similarity matrix. SIMPROF is a permutation test that objectively determines whether any significant group structure exists within a set of samples (Clarke and Gorley 2006).

After this analysis, using the same Bray–Curtis similarity matrix, a non-metric MDS was performed. The significant results of the SIMPROF test were entered into the MDS plot to assess the level of agreement between the two techniques. Complementarily, the RELATE procedure, employing Spearman rank correlation coefficients (r), was used to determine whether the series of sequential points for mean monthly samples on MDS ordination plots approximated a circle and, if so, the extent to which the distribution of those points was correlated with a true circle (Clarke and Warwick 2001). The groups of months detected were used as factors to test significant differences in temporal larval assemblages of decapod species using a one-way similarity analysis (ANOSIM).

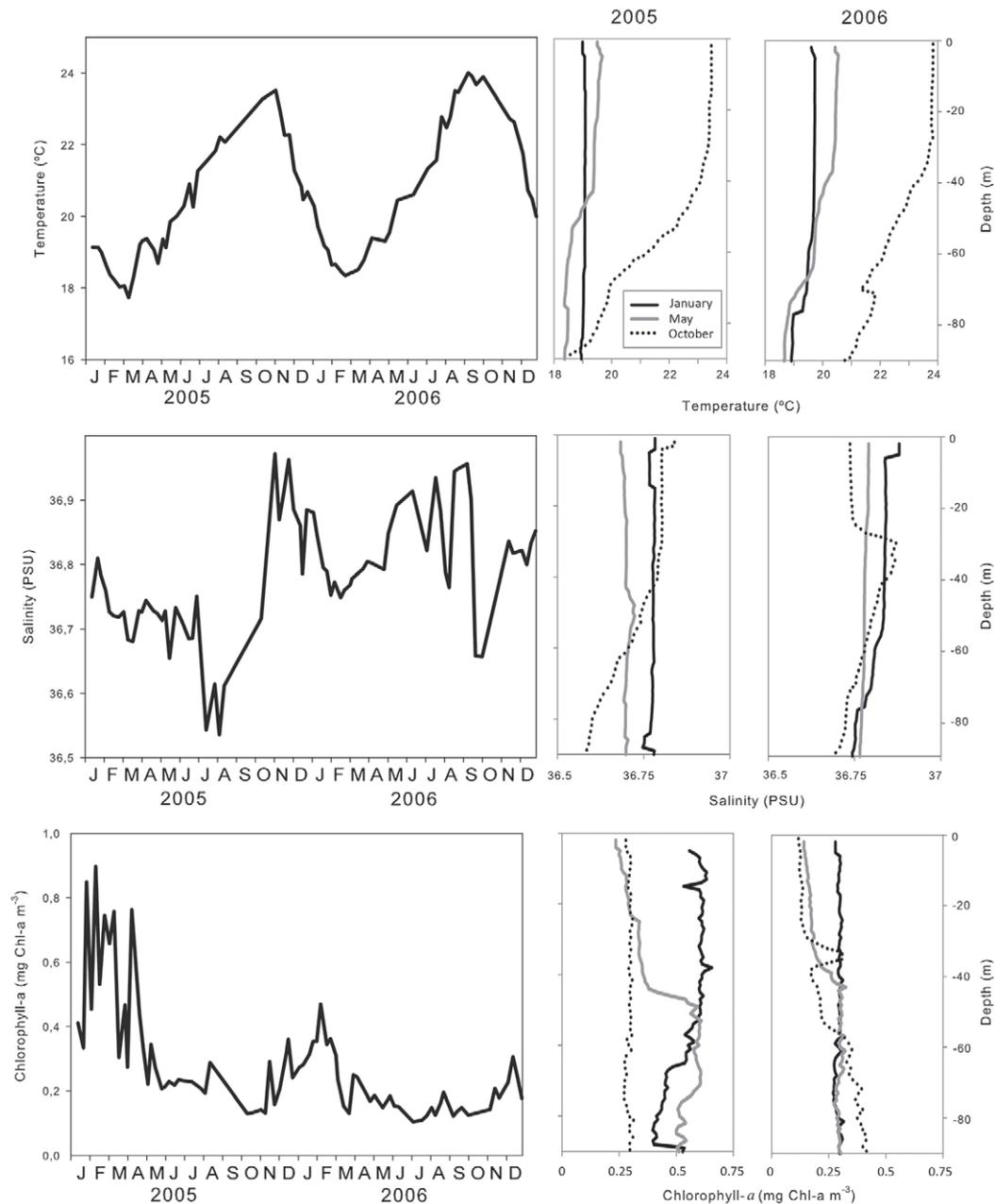


Fig. 2. – Temporal distribution of temperature (°C), salinity (practical salinity unit, PSU) at 2 m depth, and average chlorophyll *a* (15–75 m) (mg Chl-*a* m⁻³) from January 2005 to December 2006. Vertical profiles of temperature, salinity and chlorophyll *a* are averaged values for January, May and October.

A similarity percentages (SIMPER) test was then used to determine which species contributed most to characterization of each period of distinct larval assemblage (Clarke and Warwick 2001, Clarke and Gorley 2006). The non-parametric Spearman rank correlation was used to explore the relationship between sea surface temperature, salinity and chlorophyll *a*, and decapod larvae variables (total abundance and diversity). Finally, an MDS plot was represented by superimposing bubbles of increasing size related to significantly correlated variables in order to visualize the link with larval assemblages. Statistical analyses were carried out using PRIMER v.6.1 and SPSS 15.0.

RESULTS

Hydrographic conditions

Temperature showed a consistent seasonal trend in which the heating due to strong insolation led to maximum values in the mixed layer at 20–30 m (22.9°C in 2005 and 24.1°C in 2006) from August to October. The cooling of the water column started in November and finished around March–April, showing minimum values of 17.7°C in 2015 and 18.3°C in 2016 (Fig. 2). Salinity did not show a seasonal pattern and ranged from 36.54 to 36.97 (Fig. 2). The temporal distribution of chlorophyll *a* was negatively correlated with

Table 1. – Matrix showing the Spearman correlation coefficients for decapod larvae variables (abundance, n° larvae/100 m³; diversity, Shannon diversity index values) and environmental variables (temperature, °C; salinity; chlorophyll *a*, mg Chl-*a* m⁻³) at the surface (2 m depth); * $p < 0.05$; ** $p < 0.01$.

	Abundance	Diversity	Temperature	Salinity
Abundance				
Diversity	0.84**			
Temperature	0.43**	0.33**		
Salinity	0.25	0.12	0.37**	
Chlorophyll <i>a</i>	-0.27*	-0.24**	-0.73**	-0.41**

temperature (Spearman rank correlation: $r = -0.73$, $p < 0.01$) and showed the typical seasonality of the Canary Island waters (Table 1, Fig. 2). The quasi-permanent thermocline, which promotes oligotrophic conditions during most of the year and limits phytoplankton production in the Canary Islands (Aristegui et al. 2001), led to standing stocks of chlorophyll *a* lower than 0.2 mg m⁻³ during the summer (Fig. 2). This situation changed in winter, when the temperature dropped below 19°C and the cooling of the surface eroded the thermocline, promoting the development of a major phytoplankton bloom in February-March, followed by another smaller peak around April known as the late winter bloom. Interannual differences were observed. The highest chlorophyll *a* values (0.9 mg m⁻³) occurred during the bloom of 2005, with a mean standing stock of 0.7 ± 0.16 mg m⁻³. In 2006 the peak occurred during the same period but was weaker, with

a mean standing stock of 0.36 ± 0.05 mg m⁻³ and maximum values of 0.47 mg m⁻³. The temporal evolution of temperature suggested different durations of the mixing period. In January 2006 the temperature was still above 19°C, preventing deep convection. In May the heating of the surface waters was already visible, especially in 2006, when the temperature was above 20°C at the beginning of the month. This situation led to a shorter mixing period in 2006 that promoted a lesser phytoplankton bloom.

Decapod larvae community

A total of 6967 larvae belonging to 105 different taxa were identified during the two-year study. Gathered in different suborders, the Pleocyemata and Dendrobranchiata were represented by 85 and 20 taxa, respectively. Within the Pleocyemata, the infraorders with the highest number of taxa were Brachyura (36 taxa) and Caridea (31 taxa). Average species diversity was relatively high (2.40 ± 0.59), with the highest values (>3) in June-August of both years and the lowest (0.60) in January 2005 (Fig. 3). A significant positive correlation with temperature (Spearman rank correlation: $r = 0.33$, $p < 0.01$) was also evidenced this tendency (Table 1). Differences in diversity between years were also significant (Student *t* test, $df = 74$, $t = -2.982$, $p = 0.004$), with 2005 showing a lower mean value (2.19 ± 0.86) than 2006 (2.57 ± 0.44).

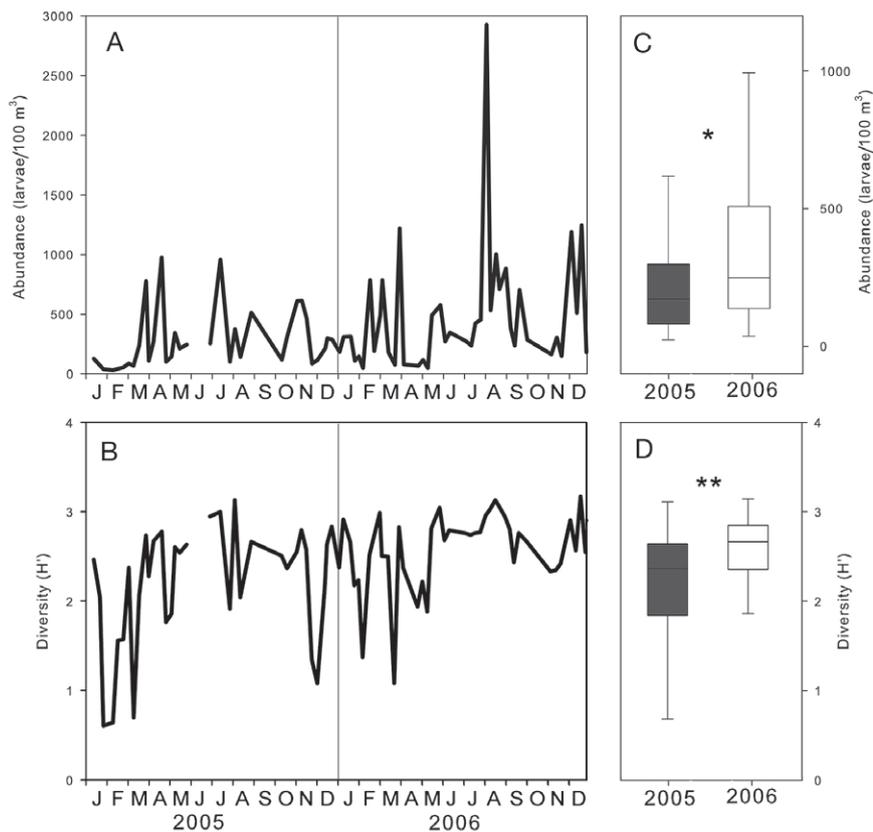


Fig. 3. – Temporal variation of the abundance (larvae/100 m³) (a) and Shannon–Wiener diversity index (H') (b) of decapod larvae. Boxplots show yearly comparisons of abundance (c) and diversity (d). In each boxplot, the median (solid line) is indicated in the centre of the box and the edges of the box are the 25th and 75th percentiles; whiskers extend to the most extreme data points that were not considered to be outliers. Results from the Student *t* test are highlighted as follow: * $p < 0.05$, ** $p < 0.01$.

Table 2. – Taxonomic list of decapod larvae collected in Gran Canaria, showing the monthly presence/absence.

	J	F	M	A	M	JN	JL	A	S	O	N	D
DENDROBRANCHIATA												
<i>Benthescyrmus</i> sp.	X	X										
<i>Gennadas</i> sp.	X		X		X	X	X	X	X		X	X
<i>Parapenaeus longirostris</i> (Lucas, 1846)		X				X	X					X
<i>Funchalia</i> spp.	X											
<i>Solenocera membranacea</i> (Risso, 1816)	X											
<i>Lucifer typus</i> H. Milne-Edwards, 1837	X	X	X	X	X	X	X	X	X	X	X	X
<i>Petalidium</i> spp.	X	X	X									
<i>Allosergestes pectinatus</i> (Sund, 1920)	X	X	X	X	X	X	X	X	X		X	X
<i>Allosergestes sargassi</i> (Ortmann, 1893)						X	X	X		X	X	
<i>Deosergestes curvatus</i> (Crosnier & Forest, 1973)	X				X	X	X				X	X
<i>Deosergestes henseni</i> (Ortmann, 1893)					X	X	X	X	X		X	
<i>Parasergestes armatus</i> (Krøyer, 1855)			X									
<i>Parasergestes diapontius</i> (Bate, 1881)							X	X		X	X	
<i>Parasergestes vigilax</i> (Stimpson, 1860)	X	X			X	X	X	X	X		X	X
<i>Sergestes atlanticus</i> Milne-Edwards, 1830	X	X	X	X		X	X			X	X	X
<i>Sergestes cornutus</i> Krøyer, 1855	X	X	X		X						X	X
<i>Sergia robusta</i> (Smith, 1882)	X	X	X		X	X	X	X	X		X	X
<i>Sergia splendens</i> (Sund, 1920)	X				X		X	X	X		X	X
<i>Sergia tenuiremis</i> (Krøyer, 1855)							X					
<i>Sergestidae</i> spp.	X		X								X	X
PLEOCYEMATA												
CARIDEA												
<i>Acanthephyra</i> spp.	X	X	X		X						X	X
<i>Oplophoridae</i> spp.	X					X		X				X
<i>Nematocarcinus</i> spp.					X			X			X	
<i>Cinetorhynchus rigens</i> (Gordon, 1936)	X	X	X	X	X		X			X		X
<i>Brachycarpus biunguiculatus</i> (Lucas, 1846)					X		X	X	X			
<i>Pontonia pinnophylax</i> (Otto, 1821)					X							
<i>Pontonia</i> spp.	X		X				X	X			X	X
<i>Periclimenes</i> sp.	X	X	X	X	X	X	X	X	X	X	X	X
<i>Athanas nitescens</i> (Leach, 1813)	X	X	X	X	X	X	X	X	X	X	X	X
<i>Alpheus glaber</i> (Olivi, 1792)	X	X	X	X	X	X	X	X	X	X	X	X
<i>Alpheus macrocheles</i> (Hailstone, 1835)	X	X	X	X	X	X	X	X	X		X	X
<i>Alpheus</i> spp.	X		X		X			X	X		X	X
<i>Alpheidae</i> spp.	X	X	X	X	X						X	X
<i>Eualus occultus</i> (Lebour, 1936)	X		X	X	X	X	X	X	X		X	X
<i>Eualus pusiolus</i> (Krøyer, 1841)			X									
<i>Hippolyte</i> sp.	X		X			X	X	X	X		X	X
<i>Latreutes fucorum</i> (Fabricius, 1798)	X	X	X	X	X	X	X	X	X	X	X	X
<i>Lysmata seticaudata</i> (Risso, 1816)	X		X		X	X	X	X	X		X	X
<i>Lysmata</i> sp.			X			X						
<i>Processa edulis</i> (Risso, 1816)			X		X		X	X	X		X	
<i>Processa modica</i> Williamson & Rochanaburanon, 1979		X	X	X	X	X		X	X	X	X	X
<i>Processa noveli</i> Al-Adhub & Williamson, 1975	X	X	X	X	X	X	X	X	X	X	X	X
<i>Processa</i> spp.	X	X	X	X	X	X	X	X	X		X	X
<i>Pandalina brevirostris</i> (Rathke, 1843)	X	X	X	X	X	X	X	X	X		X	X
<i>Pandalidae</i> spp.	X	X	X	X	X	X	X	X	X	X	X	X
<i>Aegaeon cataphractus</i> (Olivi, 1792)			X		X			X			X	
<i>Philocheras bispinosus</i> (Hailstone, 1835)	X		X	X	X		X	X			X	X
<i>Philocheras sculptus</i> (Bell, 1847)	X	X	X	X	X	X	X	X			X	X
<i>Philocheras trispinosus</i> (Hailstone, 1835)								X				
<i>Crangon crangon</i> (Linnaeus, 1758)	X											
AXIIDEA												
<i>Necallianassa truncata</i> (Giard & Bonnier, 1890)			X		X	X	X	X	X		X	
<i>Pestarella candida</i> (Olivi, 1792)							X					
<i>Callianasidae</i> SL16					X	X	X	X				
GEBIIDEA												
<i>Upogebia</i> sp.	X		X	X		X	X	X	X	X	X	X
STENOPODIDEA												
<i>Stenopus spinosus</i> Risso, 1827												X
<i>Stenopidae</i> sp1.											X	
ACHELATA												
<i>Scyllarus</i> spp.	X			X	X	X	X	X	X	X	X	X
ANOMURA												
<i>Galathea intermedia</i> Lilljeborg, 1851	X	X	X	X	X	X	X	X	X	X	X	X
<i>Munida</i> spp.	X	X	X	X	X	X	X	X	X	X	X	X
<i>Clibanarius aequabilis</i> (Dana, 1851)		X	X	X	X	X	X	X	X	X	X	X
<i>Dardanus arrosor</i> (Herbst, 1796)					X	X		X	X		X	X
<i>Calcinus tubularis</i> (Linnaeus, 1767)		X	X		X	X	X	X	X	X	X	X
<i>Pagurus</i> spp.	X	X	X	X	X	X	X	X	X	X	X	X
<i>Nematopagurus longicornis</i> A. Milne-Edwards & Bouvier, 1892	X		X		X	X	X					X
<i>Porcellana platycheles</i> (Pennant, 1777)			X									
<i>Albunea carabus</i> (Linnaeus, 1758)								X	X			
BRACHYURA												
<i>Dromia personata</i> (Linnaeus, 1758)		X										
<i>Ethusa mascarone</i> (Linnaeus, 1758)					X	X						

	J	F	M	A	M	JN	JL	A	S	O	N	D
<i>Ebalia tumefacta</i> (Montagu, 1808)			X	X	X	X	X	X	X	X	X	X
<i>Ebalia</i> spp.	X	X	X	X	X	X						X
<i>Ilia nucleus</i> (Linnaeus, 1758)	X	X	X	X	X	X	X	X	X	X	X	X
<i>Maja brachydactyla</i> Balss, 1922					X							X
<i>Maja</i> spp.							X	X	X	X		
<i>Acanthonyx lunulatus</i> (Risso, 1816)	X					X		X			X	
<i>Pisa tetraodon</i> (Pennant, 1777)	X	X	X	X	X	X	X	X	X	X	X	X
<i>Stenorhynchus lanceolatus</i> (Brullé, 1837)				X			X	X	X			X
<i>Inachus</i> spp.				X		X	X					
<i>Herbstia condyliata</i> (Fabricius, 1787)						X						
<i>Macropodia</i> sp.												X
<i>Eurynome</i> spp.	X		X									X
<i>Majidae</i> spp.		X	X	X	X	X	X	X	X	X	X	X
<i>Xantho hydrophilus</i> (Herbst, 1790)	X	X	X	X	X	X	X	X			X	X
<i>Xantho</i> spp.	X	X	X	X	X	X	X	X	X		X	X
<i>Pilumnus</i> spp.				X								
<i>Monodaeus couchii</i> (Couch, 1851)			X	X				X				
<i>Nanocassiope melanodactyla</i> (A. Milne-Edwards, 1867)	X	X	X	X	X	X	X	X	X	X	X	X
<i>Liocarcinus</i> spp.	X		X	X		X		X	X		X	X
<i>Macropius</i> spp.	X											
<i>Atelecyclus</i> spp.	X	X	X	X	X	X	X	X	X		X	X
<i>Parthenope</i> spp.	X	X	X	X	X	X	X	X	X	X	X	X
<i>Distolambrus maltzami</i> (Miers, 1881)					X		X					
<i>Goneplax rhomboides</i> (Linnaeus, 1758)	X		X	X							X	X
<i>Geryonidae</i> spp.			X				X	X	X			
<i>Grapsus adscensionis</i> (Osbeck, 1765)	X	X	X	X	X	X	X	X	X			
<i>Pachygrapsus</i> spp.	X			X	X	X	X	X	X	X	X	
<i>Planes minutus</i> (Linnaeus, 1758)					X	X						
<i>Percnon gibbesi</i> (H. Milne-Edwards, 1853)	X		X	X	X	X	X	X	X	X	X	X
<i>Plagusia depressa</i> (Fabricius, 1775)	X	X	X	X	X	X	X	X	X		X	X
<i>Calappa granulata</i> (Linnaeus, 1758)					X	X		X	X		X	X
<i>Grapsidae</i> spp.			X			X						

In terms of relative abundance, the infraorders Anomura and Caridea accounted for 33.4% and 32.8% of the total decapod larvae catches, respectively. Other less abundant taxonomic groups were Brachyura (17.5%), Dendrobranchiata (17.5%), Axiidea and Gebiidea (6%). Achelata and Stenopodidea did not show abundance greater than 5%, while Polychelida, Astacidea, and Glypheidea (this infraorder has not been recorded in the Canary Islands) were not observed in the samples (Table 2). The remaining infraorders are not present in the Canary Islands. The most abundant families within Anomura were Galatheidae (12.2%), Diogenidae (9.2%), and Paguridae (11.8%) due to the main contribution of *Galathea intermedia*, *Calcinus tubularis* and *Pagurus* spp. (Table 2). In Caridea, the families Apheidae, Hippolytidae and Processidae had abundances of around 7% of the total sample, with *Processa nouveli* and *Latreutes fucorum* as the most abundant species. The families Brachyura, Majidae, Xanthidae and Grapsidae accounted for around 3% of total abundance. The average abundances of *Upogebia* spp. (3.8%) and *Pandalina brevis* (3.1%) were also noteworthy. Regarding adult habitat, larvae of benthic species (86.1%) were more abundant than larvae of pelagic species (13.9%) (Table 2). Larvae in the first stage of development, zoea I, accounted for 37.8±13.4% of the total decapod larvae, whereas larvae in the last stage of development always accounted for less than 5% of the total larvae.

Total abundances ranged from a minimum value of 30.2 larvae/100 m³ recorded in February 2005 to the maximum value of 2925 larvae/100 m³ in 12 August 2006. The mean abundance in 2005 (281.02±86.35 larvae/100 m³) was significantly lower (Student *t* test,

df=74, *t*=-2.07, *p*=0.021) than in 2006 (478.14±116.13 larvae/100 m³). Decapod larvae were present in the plankton all year round, making it difficult to observe, a priori, any seasonal/interannual patterns (Fig. 3). A two-way ANOSIM test revealed a slight significant difference among months (Global R=0.372, *p*=0.03) but not among years (Global R=0.133, *p*=0.4). This result was supported by the MDS plot, which showed a poor spatial ordination of the samples based on their decapod larvae composition (Fig. 4).

However, when the factor year was removed and month-averaged larval abundance data were used, the multivariate statistical analysis revealed seasonality in decapod larvae community (Fig. 5). Two significantly different groups of months (*p*<0.001) were distinguished using SIMPROF at a 58% level of similarity.

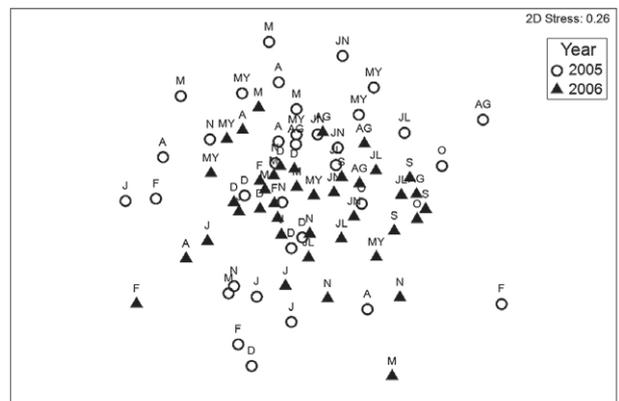


Fig. 4. – Non-metric multidimensional scaling ordination based on the Bray-Curtis similarity matrix of decapod larval abundance, using all samples collected in 2005 and 2006.

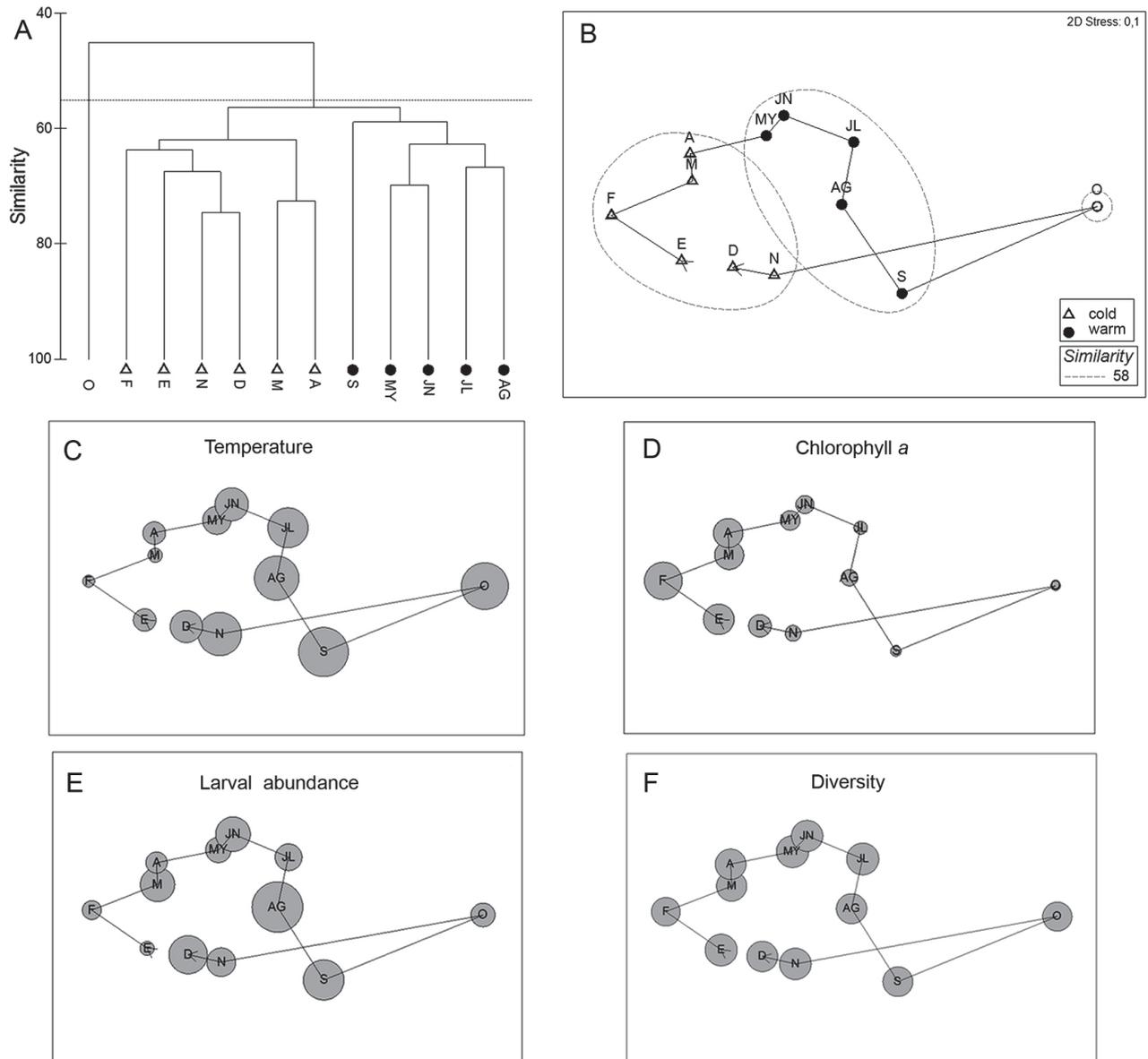


Fig. 5. – Dendrogram showing the classification of months from the Bray-Curtis similarity matrix of monthly averages of decapod larval abundance (A) Non-metric multidimensional scaling (MDS) ordination based on the same similarity matrix. (B) Average temperature, chlorophyll *a*, larval abundance and species diversity for each month is superimposed as proportional bubbles over the MDS plot (C-F). Dotted lines separate larval assemblages at the 58% similarity threshold.

An MDS plot (2D stress, 0.14) with a superimposed significant cluster shows the separation of the two distinct larval assemblages. A “warm” cluster includes May-September, while the other “cold” cluster includes November-April, and October appears as a transition between the two seasons (Fig. 5). In this ordination, the months tend to undergo a clockwise cyclical spatial distribution (Fig. 5), and RELATE confirmed that the cyclicity was consistent with that of a circle ($p=0.001$), with a rank correlation coefficient of 0.485. Moreover, the ANOSIM routine revealed that cold and warm larval assemblages were significantly different (Global $R=0.489$, $p=0.002$). The average abundance of decapod larvae, temperature, and chlorophyll *a* are superimposed as proportional bubbles over the MDS plot to visualize the relationship of these variables with

the assemblages (Fig. 5), showing that during the warm period the larval abundance is also higher, in agreement with the positive correlation (Spearman rank correlation: $r=0.43$, $p<0.01$) between these two variables (Table 1). Conversely, as mention above, chlorophyll *a* was higher during colder months and therefore negatively correlated (Spearman rank correlation: $r=-0.27$, $p<0.05$) with decapod larva abundance.

This larval assemblage was difficult to visualize in the temporal distribution plot of abundant species, since they were collected in almost every single sampling event, indicating year-round spawning (Figs 6, 7). However, the SIMPER routine revealed that changes in composition and/or abundance were characteristic of the warm and cold assemblages (Table 3). Warm assemblages were found in species that spawn in sum-

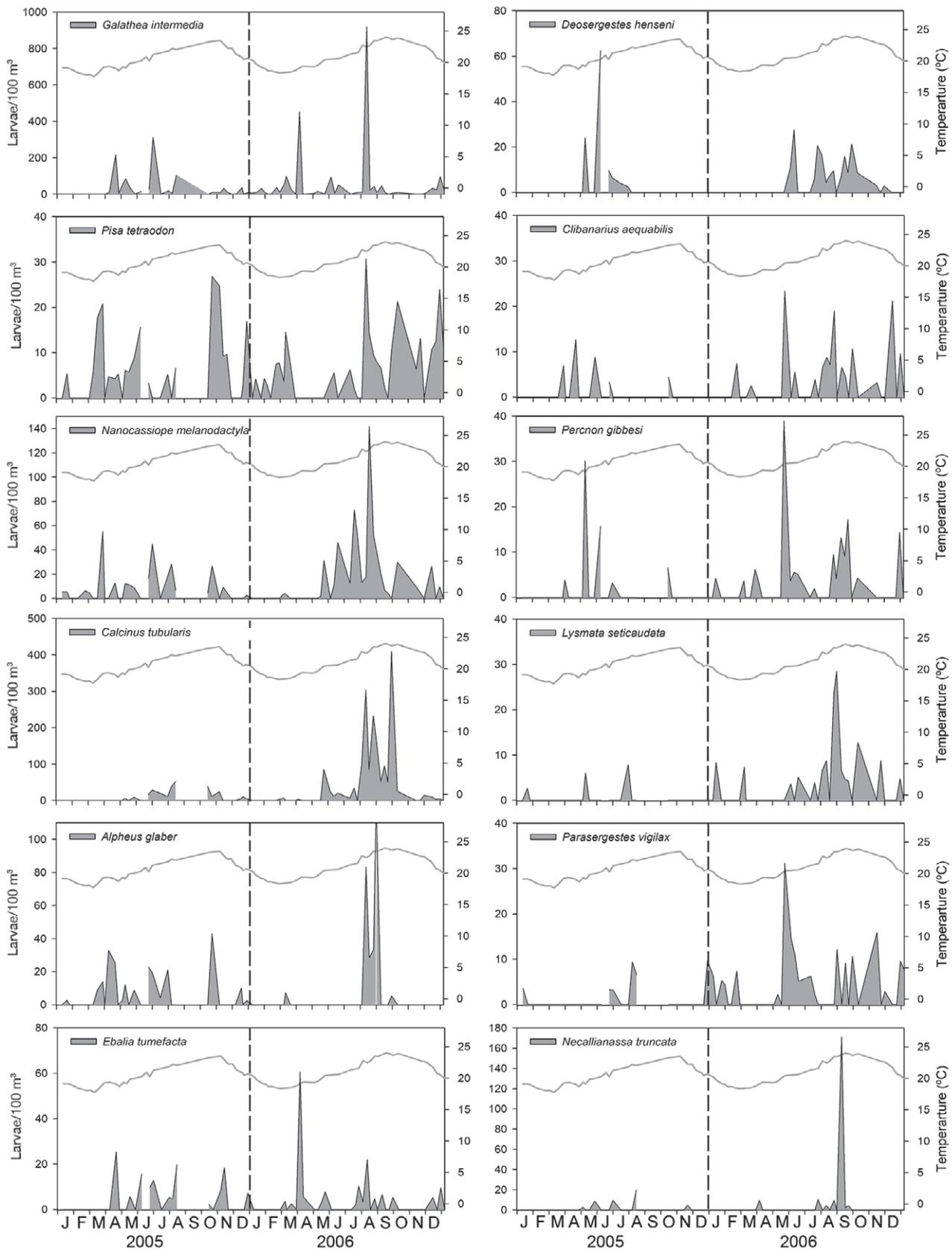


Fig. 6. – Temporal distribution of decapod larval abundance (larvae/100 m³) of typical species of “warm assemblage” during the years 2005 and 2006. Temporal distribution of temperature (°C) at the surface (2 m depth) is also shown. Note that left y-axis scales differ among species.

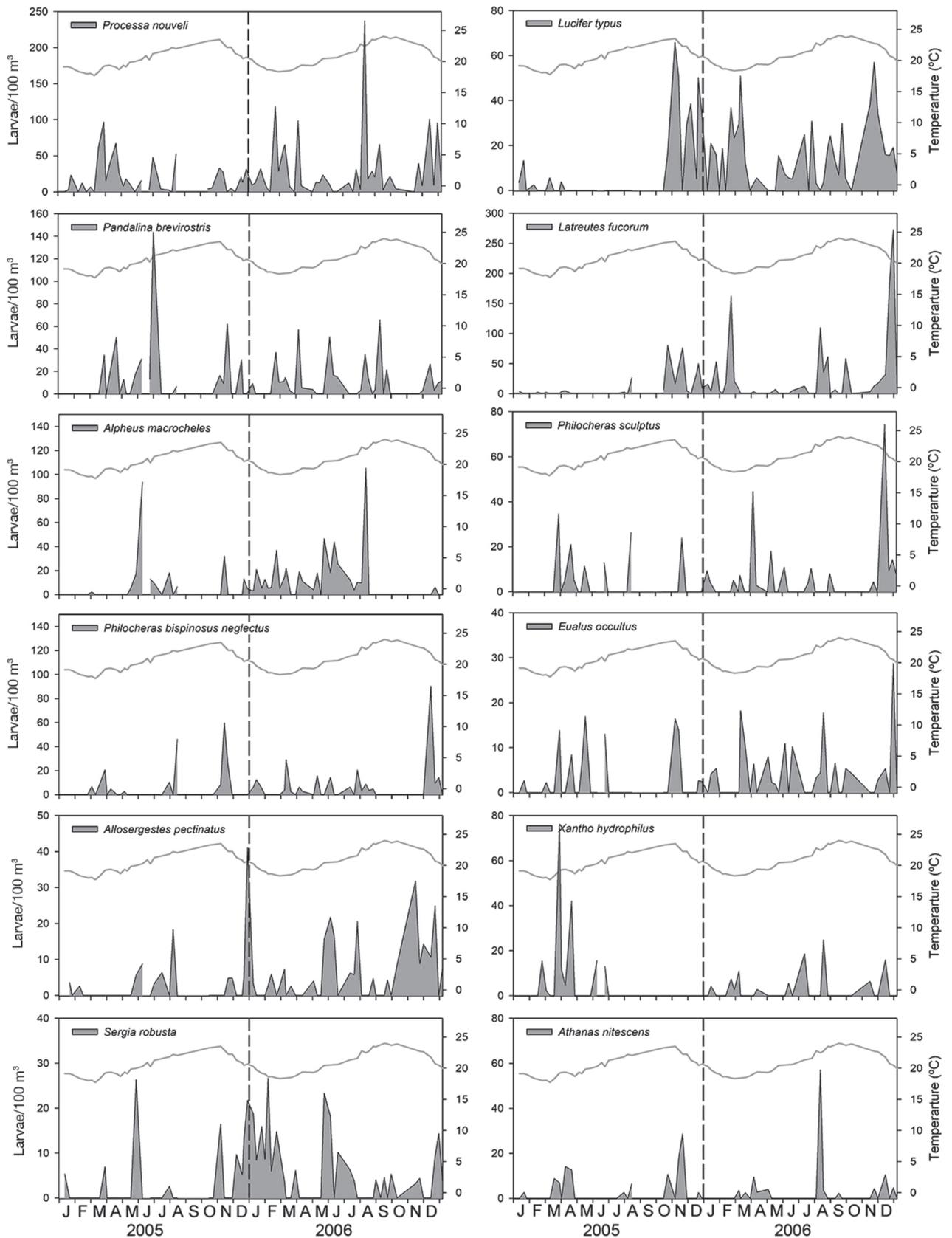


Fig. 7. – Temporal distribution of decapod larval abundance (larvae/100 m³) of typical species of “cold assemblage” during the years 2005 and 2006. Temporal distribution of temperature (°C) at the surface (2 m depth) is also shown. Note that left y-axis scales differ among species.

Table 3. – Values correspond to the percentage of similarity (SIMPER analysis) of the species that contributed to 80% of average similarity for each assemblage.

	Cold assemblage	Warm assemblage
<i>Processa nouveli</i>	12.01	8.11
<i>Galathea intermedia</i>	9.52	9.37
<i>Lucifer typus</i>	7.84	4.56
<i>Pandalina brevirostris</i>	6.8	3.02
<i>Latreutes fucorum</i>	6.4	4.03
<i>Pisa tetraodon</i>	5.39	4.48
<i>Alpheus macrocheles</i>	5.26	2.98
<i>Nanocassiope melanodactyla</i>	4.39	8.44
<i>Philocheras sculptus</i>	4.52	
<i>Philocheras bispinosus</i>	3.59	
<i>Eualus occultus</i>	3.22	
<i>Allosergestes pectinatus</i>	3.2	
<i>Xantho hydrophilus</i>	3.16	
<i>Sergia robusta</i>	3.08	
<i>Athanas nitescens</i>	2.07	
<i>Calcinus tubularis</i>		11.82
<i>Alpheus glaber</i>		4.63
<i>Ebalia tumefacta</i>		3.36
<i>Deosergestes henseni</i>		3.11
<i>Clibanarius aequabilis</i>		3.05
<i>Percnon gibbesi</i>		2.87
<i>Lysmata seticaudata</i>		2.22
<i>Parasergestes vigilax</i>		2.16
<i>Necallianassa truncata</i>		1.7

mer, such as *Calcinus tubularis* larvae primarily collected in summer (54.1 ± 23.8 larvae/100 m³) and *Nanocassiope melanodactyla* that was abundant during this period (19.4 ± 11.2 larvae/100 m³) (Fig. 6). In the case of the pelagic species *Deosergestes henseni*, the larvae were collected exclusively in summer and showed a peak around June (19.9 ± 8.8 larvae/100 m³), and *Parasergestes vigilax* was especially abundant during the summer and autumn of 2006 (Fig. 6). *Pachygrapus* spp. larvae showed a clear peak (May–October) in 2006 that was not evident in 2005. Other species, such as *Alpheus glaber*, *Clibanarius aequabilis*, *Percnon gibbesi* and *Lysmata seticaudata*, helped typify the warm assemblage but with lower (<4) similarity percentages (Fig. 6, Table 3). The cold assemblage was characterized by species that exhibited winter–autumn peaks, but their presence in the plankton was not always restricted to cold months. This is the case of *Latreutes fucorum* (peaks in late summer), and of *Eualus occultus*, *Pandalina brevirostris*, and *Philocheras bispinosus* (peaks in spring–summer) (Fig. 7). Other species that had elevated larval abundance throughout the year (e.g. *Processa nouveli*, *Galathea intermedia*, or *Lucifer typus*) contributed strongly to the cold assemblage but were also important for the warm assemblage (Table 3).

New records

We report, for the first time in the Canary Islands waters, the presence of larvae of the species *Pandalina brevirostris*, *Processa edulis*, *Necallianassa truncata*, *Parapenaeus longirostris*, *Crangon crangon* and *Nematopagurus longicornis*. All larval stages of *P. brevirostris* were found and, as mentioned above, it is an abundant species (mean abundance of 12.21 larvae/100 m³) characterizing the cold assemblage (Fig. 6, Table 3). *Processa edulis* (zoea I–III stages) was caught

in March, May, June–September and November, when it peaked with a mean abundance of 10.18 larvae/100 m³ (Table 2). Larvae of mud shrimp *N. truncata* (zoea I–III stages) were frequently collected in the plankton, especially in summer, when they achieved significant concentrations in September (mean abundance of 44.46 larvae/100 m³). *N. longicornis* zoeae III and zoeae IV were observed in March (maximum value of 13.85 larvae/100 m³), July and December 2005 and in January and May 2006. *P. longirostris* larvae in protozoea III stage of development were observed sporadically in June (3.19 larvae/100 m³) and July (2.61 larvae/100 m³) 2005, and in February and December 2006 (around 7 larvae/100 m³). Only one larva (zoea IV) of *C. crangon* was caught in January 2006.

DISCUSSION

Composition and larval assemblages

This description of the entire larval community of Gran Canaria provides valuable information about the composition and potential spawning season for the most abundant species, which have been largely under-studied. Broadly, the decapod larvae community in Gran Canaria is characterized by contracted larval hatching periods, significant contributions from pelagic species, and weaker seasonality in comparison with higher latitudes, but has two distinct larval assemblages.

The year-round occurrence of decapod larvae in the plankton indicates that crustacean decapods can reproduce throughout the year. The temporal distribution of decapod larvae suggests a contracted larval hatching period for many species, but with abundance peaks associated with seasonality. This characteristic pattern observed in the subtropical waters of Gran Canaria contrasts with what happens at higher latitudes of the NE Atlantic. For example, in Svalbard, in the Arctic Ocean, decapod larvae occurred in the plankton during short periods from May to August, with a peak in mid-June (Stübner et al. 2016). In the North Sea, the presence of a marked seasonality characterized by the virtual absence of larvae from December to February and by the presence of two main abundance peaks in spring and summer and extending into autumn is well documented (Highfield et al. 2010, Pan et al. 2011). This larval seasonality is also visible, but the presence of larvae in the plankton is year-round at lower latitudes of the Mediterranean Sea (Bourdillon-Casanova 1960, Fusté 1982), the Atlantic coasts of Portugal (dos Santos 1999) and southern Spain (González-Gordillo and Rodríguez 2003). In temperate regions, increases in water temperature trigger breeding events in which reproduction intensifies. However, in the tropics and subtropics the higher and less variable temperatures favour continuous reproduction (Bauer 1992). For instance, xanthid larvae are found in the water column all year round at the Canary Islands, with settlement peaks in spring and autumn (García-Sanz et al. 2014), whereas in the southern Iberian Peninsula, xanthid larvae are only present in the plankton in spring (González-Gordillo and Rodríguez 2003), or from April to September

(Paula 1987), with a restricted settlement period in July-October (Flores et al. 2002). The less variable annual temperature regime in the Canary Islands (18–24°C, Barton et al. 1998) leads to a protracted breeding season coupled with multiple peaks of zoeae I, which may indicate non-synchronous release and the presence of multiple cohorts.

In addition, in coincidence with the results of Moyano and Hernández-León (2011) for fish larvae, we identified two distinct seasonal larval assemblages, “cold” and “warm”, in which temperature seemed to play a key role in structuring the temporal variability of the decapod larvae community. The cold assemblage (November–April) occurred during the mixing period, when low temperatures and surface cooling erode the thermocline, allowing diffusion of nutrients that promotes elevated production of phytoplankton and zooplankton (Arístegui et al. 2001, Moyano and Hernández-León 2011). Species that were more abundant in winter-spring, such as *P. nouveli*, *L. typus*, *Philocheras sculptus* and *G. intermedia*, were typical of the cold assemblage. Little is known about their reproductive strategies, although results from settlement experiments conducted in seagrass meadows and macroalgal beds off Gran Canaria (García-Sanz et al. 2014) have provided valuable information that is in agreement with that observed in the present study, suggesting pelagic/benthic coupling. Thus, *Galathea* spp. (including *G. intermedia*) and *Pagurus* spp. had two settlement periods, but the main peak (April–May) is related to the highest larval abundance observed in the plankton in winter. During the warm assemblage period (May–September), the surface heating stratifies the water column. This leads to reformation of the main thermocline, which then limits vertical nutrient fluxes and phytoplankton production (Arístegui et al. 2001, Moyano and Hernández-León 2011). High abundances of *N. melanodactyla*, *D. henseni*, *C. tubularis* and *C. aequabilis* are characteristic of this assemblage. The settlement of *C. tubularis* and grapsid crabs (including *Pachygrapsus* spp.) occurred from October to December (García-Sanz et al. 2014), just after the summer plankton peak. Larval abundance in summer of the pelagic shrimp *D. henseni* is also characteristic of this assemblage. This species is one of the most abundant of the mesopelagic community in Canary Island waters (Ariza et al. 2015), although its larval stages have also been collected in September (FAX99 cruise, Landeira et al. 2017), and October–November (CANARIAS 9110 cruise, Landeira et al. 2009), suggesting a longer spawning season than that observed in the present study.

The contribution of pelagic shrimps to the larval community is significantly higher than that reported from other Atlantic regions (e.g. from Portugal by dos Santos 1999 and from southern Spain by González-Gordillo and Rodríguez 2003), indicating considerable oceanic influence on the coastal region of the Canary Islands (Arístegui et al. 2001). It seems that this is a common pattern, since relatively high larval densities of pelagic species over the island shelf have been reported in other archipelagos, such as the Balearic

Islands in the western Mediterranean (Torres et al. 2014) and Saint Paul’s Rock in the equatorial Atlantic (Brandão et al. 2012).

Several deep-water shrimp pandalids, particularly *Plesionika narval* (Fabricius, 1787) but also *P. edwardsii* (Brandt, 1851) and *Heterocarpus ensifer* A. Milne-Edwards, 1881, are targeted by local small-scale fisheries operating with bottom traps at some island localities (González 1995). Oviparous females occur year-round but a mass spawning peak occurs in the Canary Islands in spring and summer (Tuset et al. 2009, González et al. 2016a, Triay-Portella et al. 2017). In the present study, larvae of *Heterocarpus* spp. and *Plesionika* spp. were included in *Pandalidae* spp., because it is still impossible to distinguish these two genera using morphological characters in view of their remarkable similarity. Despite this limitation, larvae of *Pandalidae* spp. were present in the plankton throughout the year and peaked in September, supporting the spawning period reported.

According to González (2016), intertidal crab species such as *Plagusia depressa*, *Xantho* spp., *Grapsus adscensionis*, *Pachygrapsus* spp. and *Percnon gibbesi* are intensively harvested, mainly by hand, to be used for human consumption and/or as bait by small-scale fisheries. Harvesting pressure is frequently high and, in some regions, there are clear symptoms of overexploitation. This author recommended an urgent study of basic biological parameters such as population status for the implementation of conservation measures (González 2016). The presence of these larvae in the plankton can be interpreted as an indicator of the breeding season of these species. Abundance of *P. depressa* and *Pachygrapsus* spp. peaked during summer, whereas *P. gibbesi* and *G. adscensionis* seem to have two peaks, in spring and summer, respectively.

Equally notable in our results is the absence of larvae from taxa that are common in our sampling region as adults. This was the case of the shrimp *Palaemon elegans* Rathke, 1837 and the crab *Eriphia verrucosa* (Forskål, 1775), which inhabit intertidal ponds and shallow water rocky shores (González 1995, d’Udekem d’Acoz 1999). The fact that we did not find these taxa is difficult to explain with the available data.

New records

Plankton surveys have proved useful for the assessment of diversity in marine ecosystems. This brings us the possibility of sampling, at the same time, larvae of both pelagic and benthic species inhabiting shallow, deep-water and/or cryptic habitats, which are sometimes difficult to collect as adults. For example, similar samplings have facilitated the detection of non-indigenous species such as a new unreported pinotherid crab in the Gulf of Cádiz (Marco-Herrero et al. 2017). In the western Mediterranean Sea, the study of plankton samples has also led to the detection of larvae of the invasive shrimp *Palaemon macrodactylus* Rathbun, 1902 (Torres et al. 2012), but it also has provided valuable information on deep-water species of interest for conservation and fishing exploitation,

such as *Aristeus antennatus* (Risso, 1816), *Parapanaeus longirostris* and *Scyllarides latus* (Latreille, 1803) (Torres et al. 2013).

In the present study, we identified larvae of species that have not yet been reported from the Canary Islands. For example, the high abundance and temporally stable occurrence of *P. brevis*, *P. edulis*, and *N. truncata* larvae suggest that these species may not only be present in the study region, but also relatively common. If the presence of adult populations is confirmed, the geographical distribution of these four species would extend to the south (d'Udekem D'Acoz 1999).

We also report the occurrence of larval forms of unknown crustacean adults. This is the case of *Stenopidae* sp1 that were collected in November 2006. In the Canary Islands, *Stenopus spinosus* was the only member of Stenopodidea until the recent record of *Spongiocaris koehleri* (Caullery, 1896) observed by González et al. (2016b). However, *S. koehleri* larvae cannot be found in the plankton since they have direct development (Kemp 1910). This finding suggests that another stenopodid species may be present in the Canary Islands. Another example is the larval form of *Callianasidae* SL16, which was relatively abundant from May to August. This larval form was described by dos Santos (1999) from plankton specimens collected south of Portugal in July. It has also been observed in the NW African upwelling, where it was transported towards the ocean during a strong filament event in August-September 1999 (Landeira et al. 2017). The only callianassid species reported for the Canary Islands are *Pestarella tyrrhena* (Petagna, 1792) (González and Quiles 2003) and *Pestarella candida* (Moro et al. 2014), which are also present off NW Africa and Portugal (d'Udekem D'Acoz 1999). However, their larval morphology is clearly different, since *Callianasidae* SL16 has spines on the entire ventral margin of carapace, and in the other two species the spines are present only on the anteroventral margin (for details see the original descriptions listed in González-Gordillo et al. 2001). Therefore, it is reasonable to think that another callianassid species is present in the study area.

The hermit crab *N. longicornis* is distributed at a depth of 70-800 m along the NE Atlantic coast, including Madeira, the Azores, Morocco, and Cape Verde Islands (d'Udekem d'Acoz 1999, d'Udekem d'Acoz and Wirtz 2002). The Canary Islands is the only archipelago in the area without records, so it seems that González (1995) was right when he suggested that this species could also be present in the Canary Islands. *Crangon crangon* is widely distributed along the NE Atlantic coasts from the White Sea and Iceland down to Morocco, in the Baltic Sea, the Mediterranean Sea, and also the Black Sea (d'Udekem d'Acoz 1999). If this species was present in the Canary Islands, it would constitute the southernmost population. However, in our opinion it is unlikely that find adult populations will be found there since there is no evidence for its occurrence in other northern Macaronesian archipelagos, such as the Selvagen Islands, Madeira and the Azores (d'Udekem d'Acoz 1999). Moreover, *C. crangon* is an epibenthic shrimp that preferably inhabits soft-sediment in estua-

rine habitats (Holthuis 1980) that do not exist in the Canary Islands. It is possible that this larva reached the Gran Canaria coast transported by upwelling filaments from Africa, as has been suggested by Landeira et al. (2017), but with the available data it is not possible to support this hypothesis.

P. longirostris is one of the most important commercial shrimps found in the Mediterranean Sea and the NE Atlantic, from Galicia to Angola (d'Udekem d'Acoz 1999, Holthuis 1980). *P. longirostris* larvae have already been observed offshore, south of the Canary Islands in association with an African upwelling filament but, until now, these larvae have never been sampled over the island shelf (Landeira et al. 2009). The presence of extensive adult populations is unlikely but the recent observations of single specimens of *P. longirostris* (Forskål, 1775) by different scuba divers in muddy-sandy habitats of Lanzarote, Gran Canaria and Tenerife islands (Moro et al. 2014) make the occurrence of *P. longirostris* more probable in the Canary Islands.

Future prospects

This study provides accurate information about the composition and assemblage of decapod larvae in the Canary Islands region. Furthermore, the data collected during this study provide a baseline for future comparisons with respect to fishery pressure and climate variability. Despite the less evident seasonality displayed by most of the species examined, we identify two distinct temporal assemblages of decapod larvae for the subtropical waters of the Canary Islands. Despite significant inter-year differences in diversity and larval abundance, there were no evident changes in the larval assemblages. The detection of such changes in the community requires a multiyear dataset obtained in long-term monitoring programmes (Lindley et al. 2010). This may be important, because the temporal distribution of spawning of different species is likely to vary under climate change.

Since 1997 the sea surface temperature has undergone a warming trend of 0.25°C decade⁻¹ in the Canary Islands region (Vélez-Belchí et al. 2015), but little is known about subsequent alterations in breeding success and distribution of crustacean species. However, there is already clear evidence of a tropicalization in the Canary Islands ecosystems. For instance, many of the new records of fish (Brito et al. 2005), decapod crustaceans (González et al. 2017), other invertebrates (Brito 2008) and algae (Afonso-Carrillo et al. 2006, 2007) are tropical species. Also, the warming during recent decades has enabled species with tropical affinities to spread quickly across the archipelago (e.g. ephemeral benthic algae, Sangil et al. 2012), or to increase their populations significantly due to more favourable and longer recruitment events (e.g. echinoid *Diadema africana* Rodríguez, Hernández and Clemente, 2010, Hernández et al. 2010). The successful establishment of the tropical hydrocoral *Millepora* sp. (Clemente et al. 2011) is also noteworthy, as it suggests profound future changes in benthic communities if warming trends

continue. We consider the establishment of long-term plankton sampling programmes in tropical-subtropical regions of the NE Atlantic to track these interannual alterations in phenology and non-native crustacean species occurrence, which are already visible in temperate regions (Kirby and Beaugrand 2009, Lindley et al. 2010), to be of paramount importance.

To detect northward distribution shifts of tropical species in relation to current and future conditions in the subtropical and temperate Atlantic, more accurate larval descriptions are needed. According to González (2016), at least 23 brachyuran benthic species occurring in the Canary Islands have their northern limit of distribution at this archipelago. However, from these species only the larval morphology of *Stenorhynchus lanceolatus* (which actually occurs also in Madeira) and *Microcassiope minor* (Dana, 1852) (which is present also in the Azores islands) are known, and are described by Paula and Cartaxana (1991) and Clark et al. (2004), respectively. We therefore encourage the scientific community to continue to improve the taxonomic description of the larval morphology of decapod crustaceans following the current standards, especially of tropical species that are presently less studied.

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