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DOCTORAL THESIS
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DECAPOD CRUSTACEAN LARVAE INHABITING OFFSHORE BALEARIC SEA WATERS (WESTERN MEDITERRANEAN): TAXONOMY AND ECOLOGY

Asvin Pérez Torres

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Director:Enric Massutí
Directora:Patricia Reglero

Tutora:Nona Sheila Agawin

Doctor by the Universitat de les Illes Balears

List of manuscripts

Lead author's works that nurtured this thesis as a compendium of articles, which have been possible by the efforts of all my co-authors, are the following:

- Torres AP, Dos Santos A, Alemany F and Massutí E - 2013. Larval stages of crustacean key species of interest for conservation and fishing exploitation in the western Mediterranean. *Scientia Marina*, 77 – 1, pp. 149 - 160.
  doi: 10.3989/scimar.03749.26D. (Chapter 2)
  JCR index in "Marine & Freshwater Biology": Q3
- Torres AP, Palero F, Dos Santos A, Abelló P, Blanco E, Bone A and Guerao G - 2014. Larval stages of the deep-sea lobster *Polycheles typhlops* (Decapoda, Polychelida) identified by DNA analysis: morphology, systematic, distribution and ecology. *Helgoland Marine Research*, 68, pp. 379 -397.
  DOI 10.1007/s10152-014-0397-0 (Chapter 3)
  JCR index in "Marine & Freshwater Biology": Q3
- Torres AP, Dos Santos A, Cuesta J A, Carbonell A, Massutí E, Alemany F and Reglero P - 2012. First record of *Palaemon macrodactylus* Rathbun, 1902 (Decapoda, Palaemonidae) in the Mediterranean Sea. *Mediterranean Marine Science*, 13 (2): pp. 278 - 282. DOI: 10.12681/mms.309 (Chapter 4)
  JCR index in "Marine & Freshwater Biology": Q2
- Torres AP, Dos Santos A, Balbín R, Alemany F, Massutí E and Reglero P – 2014. Decapod crustacean larval communities in the Balearic Sea (western Mediterranean): seasonal composition, horizontal and vertical distribution patterns. *Journal of Marine Systems*, 138, pp. 112-126. http://dx.doi.org/10.1016/j.jmarsys.2013.11.017 (Chapter 5)
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- Torres AP, Reglero P, Hidalgo M, Abelló P, Simão D, Alemany F, Massutí E and Dos Santos A. Vertical distribution of decapod crustaceans: seasonality and diel migration patterns over ontogeny off Balearic Islands (Western Mediterranean Sea) *Marine Ecology Progress Series*, Submitted (Chapter 6)
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The phD candidate has participated in two papers directly related to the line of research of this thesis.which have not been included in this thesis:

Marco-Herrero E, Torres AP, Cuesta JA, Guerao G, Palero F and Abelló P – 2013. The systematic position of Ergasticus (Decapoda, Brachyura) and allied genera, a molecular and morphological approach. *Zoologica Scripta*, 42(4):427-439

Simão DS, Torres AP, Olivar MP and Abelló P – 2014. Vertical and temporal distribution of pelagic decapod crustaceans over the shelf-break and middle slope in two contrasting zones around Mallorca (western Mediterranean Sea). *Journal of Marine Systems*, 138:139-149

A mis padres, a Sam y a Ramón

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Chapter 4. Invasive species. “First record of *Palaemon macrodactylus* Rathbun, 1902 (Decapoda, Palaemonidae) in the western Mediterranean“

Chapter 5. W Mediterranean decapod larval community. “Decapod crustacean larval communities in the Balearic Sea (Western Mediterranean): seasonal composition, horizontal and vertical distribution patterns”

Chapter 6. Ontogenetic decapod vertical distribution. “Vertical distribution of decapod crustaceans: seasonality and diel migration patterns over ontogeny off Balearic Islands (western Mediterranean Sea)”

Abbreviations and acronyms

A	adult group (DGS 5 and DGS 6)
A (cluster)	late Autumn cluster
AD	average densities
Ah	Adult habitat
AICc	Akaike Information Criterion, corrected
Asshelf	late Autumn Souternh shelf break cluster
AW	Atlantic water
BeT	beam trawl
BIC	Bayesian Information Criterion
BoT	commercial bottom trawl
C1	first mid dorsal carapace column
C2	posterior mid dorsal carapace column
CL	carapace length
CW	carapace maximum width
D	decapodid
DCM	deep chlorophyll maximum
DSG	developmental stage groups
DT-MADT	Delay Time data gridded into a Map of Absolute Dynamic Topography
DVM	diel vertical migrations
ea	*Eusergestes arcticus*(Krøyer 1855)
fluo	Fluorescence
ge	*Gennadas elegans* (Smith 1882)
GLM	Generalized linear models
IDEADOS	Structure and dynamics of the benthopelagic slope ecosystem in two oligotrophic zones of the western Mediterranean: a multidisciplinary approach at different temporal scales in the Balearic Islands
IKMT	Isaaks-Kidd Midwater Trawl
K2P	Kimura 2-Parameter
L	larval group= DSG 1, DSG 2, DSG 3 and DSG 4
LIW	Levantine Intermediate Water
MAPs	Marine Protected Areas
MDS	Multidimensional scaling ordination
MEDAR	Mediterranean Data Archeology and Rescue

MII	second mysis
ML	HYDRO-BIOS multi-net
MLD	mixing layer depth
MLD	mixing layer depth
MOCNESS (MC)	multiple opening closing net and environmental sensing system
nc	no captures for 3-h interval
NW	north-western
OAMMS-04	Observation, analysis and modelling of the Mediterranenan Sea
OVD	ontogenetic vertical distribution
PAR	photosynthetically active radiation
PII	second protozoea
PT	Pelagic Trawl net
pv	*Parasergestes vigilax* (Stimpson 1860)
R	rostral spine
RDL	rostro-dorsal length = TL zoea of Brachyura
S	south
S (cluster)	Summer cluster
sal	salinity
SEM	scanning electron microscopy
sr	*Sergia robusta* (Smith 1882)
Ssslope	Summer Southern mid slope cluster
t1	first pereiopod
t2	second pereiopod
temp	temperature
TL	total length
VM	vertical migration
WIW	Western Intermediate Water
WIW	Western Mediterranean Intermediate Water
WMD	weighted mean depths
WMDW	Western Mediterranean Deep Water
ZI	first zoea
ZII	second zoea
ZIII	third zoea

Summary

Comprehending evolution, distribution and ecology of marine animals require information on reproductive biology and developmental patterns, as early life stages (larvae) constitute, for several taxa, critical periods within the life cycle in which abundance and distribution of populations are largely determined.

Considering the importance of the decapod crustaceans on Mediterranean marine ecosystems and fisheries and the lack of information regarding their ecology, especially that on their early life stages, present thesis address the analysis of the decapod planktonic larval communities, specially of the deep and offshore species. The first section of the thesis relates to the issues arising from the accurate and precise taxonomic identification of the specimens, which constitute the fundamental prerequisite for any further study of the entire community, as well those related to the ecology of individual species. Subsequently, this further allowed to elaborate detailed descriptions of previously unknown larval stages, contributing in overcoming the actual limitations of the available literature, still incomplete for many families, as well as to expand on the knowledge of the biology and ecology of some species, as a result of the new information gathered on their larval stages. The second section includes further studies on communities' structure and species vertical distribution, as well their variations along ontogenetic development, exploring their ecological implications.

The data collection took place around the Mallorca Island in the Balearic archipelago (Western Mediterranean). Specifically, decapod larvae were obtained from meso-zooplankton depth-stratified samples, whereas juveniles and adults were captured with different gears. Sampling was carried out at two stations located on the continental shelf break and middle slope, northwest and south of Mallorca in late autumn 2009 and summer 2010. The first analysis consisted in a detailed taxonomic study, focusing on previously poorly studied or unknown larval stages. As a result of these analyses, the first larval stage of *Scyllarides latus* and the second mysis stage of *Aristeus antennatus* were found and described for the first time. Larval stages of other species of fishing or conservation interest not previously recorded in the area,

as the larvae of *Parapenaeus longirostris* and the larva of *Maja squinado*, were also identified. Moreover, molecular and morphological analysis permitted to assign certain larval morphotipes previpusly misclassified in the available literature to *Polycheles typhlops*. In addition, larvae of an invasive species previously not observed in the Mediterranean, the oriental shrimp *Palaemon macrodactylus*, were discovered. The establishment of this species in the Mediterranean was subsequently confirmed through the finding of adult populations.

The vertical distributions and their seasonal, circadian and ontogenetic changes were analyzed in detail in four predominant species within the decapod communities: *Gennadas elegans, Eusergestes arcticus, Sergia robusta* and *Parasergestes vigilax*. The accurate information on larval vertical distributions of these species, which play an important role in energetic dynamics of continental slope and bathyal ecosystems, could be incorporated in a circulation model to understand their adult's distributions.

Summing up, this work consolidates a recently initiated line of research focused on the study of decapod crustacean larval communities in the Balearic Sea, tackling for the first time the analysis of their vertical structure and its ecological implications.

Resumen

Entender la evolución, la distribución y la ecología de los animales marinos requiere de información previa sobre la biología reproductiva y los patrones de desarrollo, puesto que los estadios tempranos de vida (larvas), constituyen en muchos taxones periodos críticos del ciclo vital, en el que se determinan en gran medida las abundancias y distribuciones de las poblaciones.

Teniendo en cuenta la importancia de los crustáceos decápodos en los ecosistemas marinos y pesquerías del Mediterráneo y a la poca información existente sobre su ecología, especialmente en lo que respecta a sus estados tempranos de desarrollo, esta tesis se centra en el análisis de la comunidad de larvas de decápodos, especialmente de especies que habitan en zonas profundas y aguas abiertas. La primera sección de la tesis se refiere a las cuestiones que surgen de la precisa identificación taxonómica de los individuos, que constituye el prerrequisito fundamental para ulteriores estudios de toda la comunidad, así como a las relacionadas con la ecología de cada especie considerada individualmente. Posteriormente, estas identificaciones permitieron tanto elaborar descripciones morfológicas detalladas de estadios larvarios hasta ahora desconocidos, contribuyendo a superar las limitaciones de la bibliografía existente hasta la fecha, incompleta para algunas familias, como ampliar el conocimiento de la biología y ecología de algunas especies como resultado de la nueva información aportada sobre sus fases larvarias. La segunda parte de la tesis incluye estudios innovadores sobre la estructura de la comunidad larvaria y la distribución vertical de las especies, así como sobre sus variaciones a lo largo del desarrollo ontogenético y sus implicaciones ecológicas.

La recolección de datos para esta tesis se llevó a cabo alrededor de la isla de Mallorca, en el archipiélago Balear (Mediterráneo Occidental). En concreto, las larvas de decápodos se obtuvieron de muestras de meso-zooplancton tomadas en diferentes estratos de profundidad, mientras que juveniles y adultos fueron capturados con diferentes artes. El muestreo se llevó a cabo sobre dos estaciones situadas respectivamente sobre el límite de la plataforma continental y el talud medio, en el noroeste y sur de Mallorca, durante finales de otoño de 2009 y el

verano de 2010. Los primeros análisis consistieron en un estudio taxonómico detallado de todas las larvas de decápodos presentes en dichas muestras, prestando especial atención a estados de desarrollo poco es estudiados o desconocidos. Como resultado de estos análisis se encontraron y describieron el primer estado de vida libre de *Scyllarides latus* y la segunda mysis de *Aristeus antennatus*. Se identificaron asimismo estadíos larvarios de otras especies, de interés para la pesca o cuestiones de conservación, como son las de *Parapenaeus longirostris* y la larva de *Maja squinado*. Además, análisis moleculares y morfológicos permitieron reasignar morfotipos larvarios previamente mal clasificados en la literatura disponible a *Polycheles typhlops*. Finalmente, se descubrieron larvas de una especie invasora desconocida hasta la fecha en el Mediterráneo, *Palaemon macrodactylus*. La presencia de esta especie se ha confirmado con el reciente hallazgo de poblaciones adultas en el área.

Concretamente, las distribuciones verticales y sus cambios estacionales, circadianos y ontogenéticos, fueron analizadas para cuatro de las especies dominantes en la comunidad: *Gennadas elegans, Eusergestes arcticus, Sergia robusta* y *Parasergestes vigilax*. La información precisa sobre la distribución larvaria en la vertical de estas especies, que juegan un importante papel en la dinámica de transferencia energética en los ecosistemas batiales y del talud continental, podría incorporarse en un modelo de circulación hidrodinámico, lo que ayudaría a la compresión de la distribución de sus adultos.

En resumen, este trabajo consolida una línea de investigación recientemente iniciada centrada en el estudio de las comunidades larvarias de los decápodos del Mar Balear, abordando por primera vez el análisis de la estructuración vertical de las mismas y sus implicaciones ecológicas.

Resum

Entendre l'evolució, la distribució i l'ecologia dels animals marins requereix informació prèvia sobre la biologia reproductiva i els patrons de desenvolupament, ja que els estadis primerencs de vida (larves), constitueixen en molts taxons períodes crítics del cicle vital, en els quals l'abundància i la distribució de les poblacions queda en gran mesura determinada.

Atesa la importància dels crustacis decàpodes en els ecosistemes marins i les pesqueries de la Mediterrània, i la poca informació que existeix sobre la seva ecologia, especialment pel que fa a les primeres etapes de desenvolupament, aquesta tesi se centra en l'anàlisi de la comunitat de larves de decàpodes, especialment d'espècies que habiten en zones de gran fondària i en aigües obertes. La primera secció de la tesi es refereix a les qüestions que sorgeixen de la identificació taxonòmica precisa dels individus, que constitueix el prerequisist fonamental per dur a terme nous estudis de tota la comunitat, així com a les relacionades amb l'ecologia de cada espècie considerada individualment. Posteriorment, aquestes identificacions varen permetre tant l'elaboració de descripcions morfològiques d'estadis larvaris que fins ara eren desconeguts, contribuint a superar les limitacions que afecten a la bibliografia existent , incompleta per a algunes famílies, com ampliar el coneixement de la biologia i ecologia d'algunes espècies, com a resultat de la nova informació aportada sobre les seves fases larvàries. La segona part de l'estudi inclou estudis innovadors sobre l'estructura de la comunitat larvària i la distribució vertical de les espècies, així com les variacions al llarg del seu desenvolupament ontogenètic i les implicacions ecològiques.

La recollida de dades per a aquesta tesi es va dur a terme al voltant de l'illa de Mallorca, a l'arxipèlag Balear (Mediterrània Occidental). Concretament, les larves de decàpodes es van obtenir de mostres de meso-zooplàncton preses en diferents estrats de profunditat, mentre que juvenils i adults van ser capturats amb diferents arts. El mostreig es va dur a terme sobre dues estacions situades al límit de la plataforma continental i al talús mig, al nord-oest i al sud de Mallorca, a finals de la tardor de 2009 i l'estiu de 2010. Les primeres anàlisis van consistir en un estudi

taxonòmic detallat de totes les larves de decàpodes presents en aquestes mostres, prestant especial atenció a estats de desenvolupament poc estudiats o desconeguts. Com a resultat d'aquestes anàlisis es varen trobar i descriure el primer estat de vida lliure de *Scyllarides latus* i la segona mysis de *Aristeus antennatus*. Es van identificar així mateix estadis larvaris d'altres espècies, d'interès per a la pesca o qüestions de conservació, com són les larves de *Parapenaeus longirostris* i la de *Maja squinado*. A més, anàlisis moleculars i morfològics varen permetre reassignar morfotipus larvaris prèviament mal classificats en la literatura disponible a *Polycheles typhlops* identificats erròniament en la literatura disponible. Finalment, es van descobrir larves de una espècie invasora desconeguda fins ara a la Mediterrània, *Palaemon macrodactylus*. La presència d'aquesta espècie s'ha confirmat amb la recent troballa de poblacions adultes en l'àrea.

Concretament, les distribucions verticals durant el dia i la nit i els seus canvis estacionals, circadians i ontogenètics durant l'estiu i la tardor, van ser analitzades per a quatre de les espècies dominants en la comunitat: *Gennadas elegans, Eusergestes arcticus, Sergia robusta* i *Parasergestes vigilax*. La informació precisa sobre la distribució larvària en la vertical d'aquestes espècies, que juguen un important paper en la dinàmica de transferència energètica en els ecosistemes batials i del talús continental, podria incorporar-se en un model de circulació hidrodinàmic, el que ajudaria a la comprensió de la distribució dels adults.

En resum, aquest treball consolida una línia d'investigació, recentment iniciada, centrada en l'estudi de les comunitats larvàries dels decàpodes del Mar Balear, que aborda per primera vegada l'anàlisi de la seva estructuració vertical i les implicacions ecològiques.

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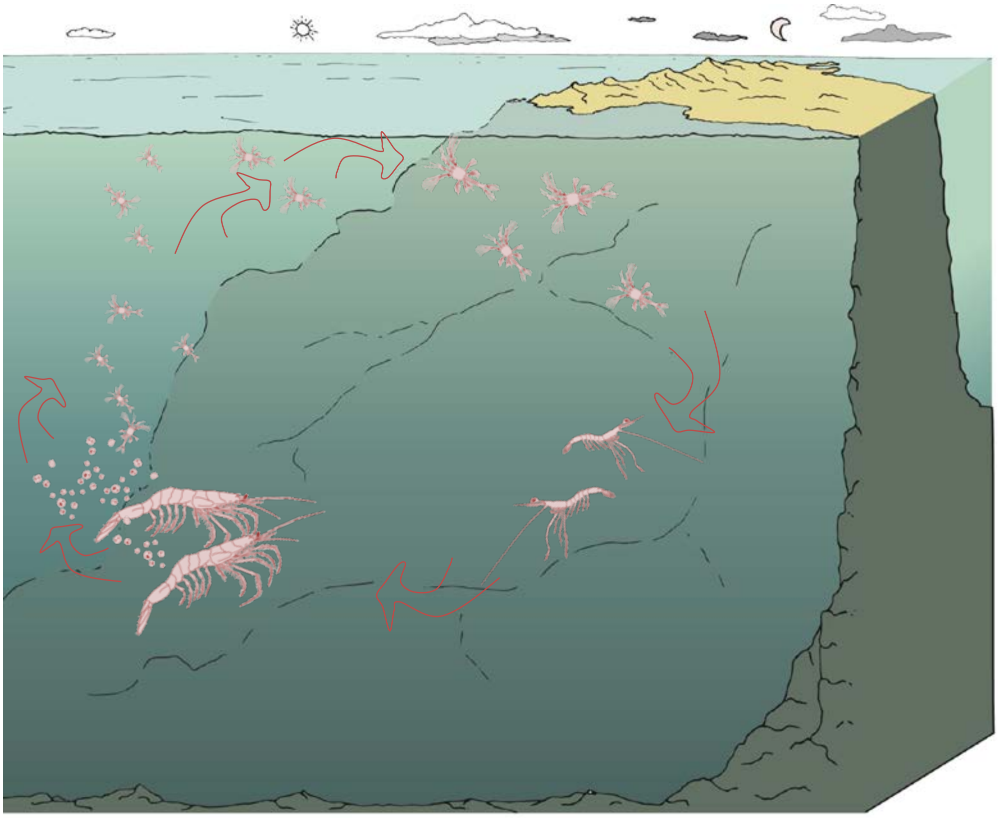
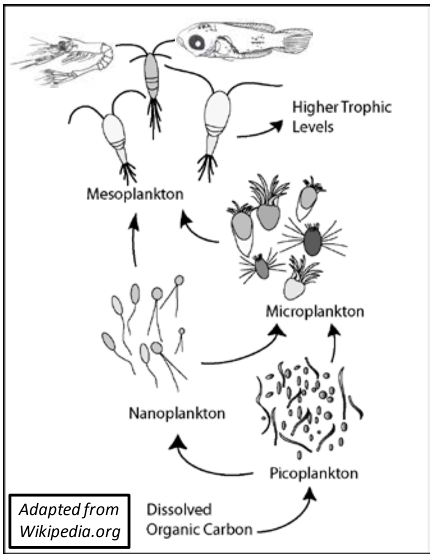
Chapter 1

Introduction and objectives



1.1. General background and larval study interest

The knowledge of reproductive biology and developmental patterns is a key issue in order to undestand evolution, distribution and ecology of marine animals. Marine organisms display numerous reproductive strategies, from asexual to sexual. Animals with sexual strategy produce eggs which can be deposited in nests or directly on the bottom, kept attached to the parents, or be released as free moving particles to the pelagic environment. These eggs hatch as several types of larval forms, whose duration is very variable among and within taxonomic groups, from hours to months, even years. In most cases, the larvae become part of planktonic communities, constituting, besides the aforementioned pelagic eggs, the so called meroplankton. Meroplankton is a temporary component of zooplankton primarily made up from the early life stages of different organisms with sizes between 0.2 – 2 mm, whose later developmental stages are not planktonic. The lack of information about these planktonic phases should impede to get a complete view of the biology of the species. In addition, understanding the whole planktonic community dynamics is imperative for marine ecosystems. As holoplankton (organisms spending their whole life cycle in the plankton), meroplankton is an important component of the pelagic food webs, contributing to the transfer of the organic energy produced by phytoplankton or bacterial loops to higher trophic levels (e.g. Azam et al. 1983, Sommer and Sommer 2006).

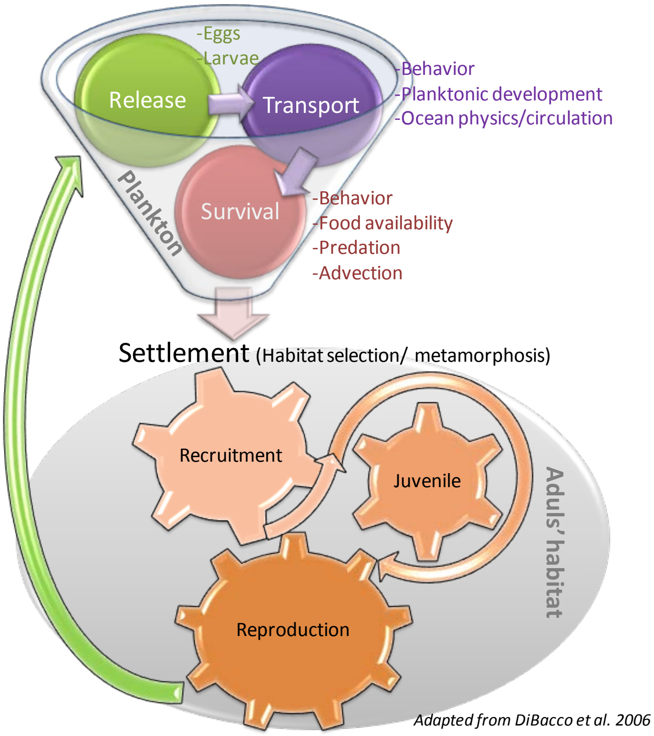


Adapted from Wikipedia.org

From the single species point of view, despite meroplanktonic stages represent a relatively short period within the entire life cycle, they are crucial as they may determine the recruitment spatial dynamics and strength, and hence the whole dynamics of many marine species populations. Due to the existence of these planktonic early life stages, the majority of marine populations are considered demographically open, as they may be highly ‘connected’ through their larval dispersive phase (Becker et al. 2007, Cowen and Sponaugle 2009). Changes in dispersion patterns induced by differences in hydrodynamic scenarios can result in important variations in the number of recruits arriving to a given area. Recruitment variability has fisheries implications, since it partly explains some of the interannual population abundance fluctuations at local scales observed in some species (e.g. spiny lobster Kough et al. 2013). On the other hand, interannual recruitment variability is also the result of larval survival rates along the planktonic phase resulting from the environmental factors affecting larval mortality rates. Such factors include not only trophic interactions, both preys availability and predators pressure, but a suite of complex physical and biological processes (Bailey and Houde 1989, Houde 2008). Since small variations in such daily larval mortality rates can lead to high fluctuations in the number of recruits, meroplanktonic phases have been defined as a ‘critical period’ (May 1974) (Fig 1.1).

The existence of large fluctuations in the biomass of exploited marine populations is well documented (Cushing et al. 1996). Partly, these fluctuations are directly attributable to fishing activity, and there is the urgent need to reduce the intense pressure on the world’s fisheries exerted by modern fishing fleets, developing fishing practices highly destructive for marine ecosystems (e.g. FAO 2002, Hilborn et al. 2003). However, as mentioned above, important variations in recruitment intensity induced by causes other than fishing and mainly related to processes affecting early live stages also occur, which highlight the necessity of supporting further studies on the early life history stages (Cowen 2002).

The first to link such fluctuations with factors affecting larval stages was Johan Hjort, in the early 20th century (Hjort 1914, Hjort 1926). Hjort hypothesized that the spatial overlap with the adequate preys at the moment of mouth opening was determinant for cod larvae survival, and hence it was the main factor driving cod population biomass. Many hypotheses explaining the mechanisms through which environmental factors affect larval survival have subsequently been proposed ('match-mismatch' by Cushing 1990; 'member/vagrant' by Sinclair 1988 and Sinclair and Iles 1989; 'stable-ocean' by Lasker 1981; 'ocean triads' by Bakun 1998). Most of these hypotheses were focused on fish larvae studies, but also for marine benthic invertebrates the importance of larval supply in determining the abundance and spatial distribution of adult populations is well established (Gaines et al 1985, Minchinton and Scheibling 1991). Thus, the impact of climatic changes on zooplankton can also influence the recruitment success of many invertebrate populations, as have been demonstrated to occur in pelagic fish stocks (Alheit and Niquen 2004).



Adapted from DiBacco et al. 2006

Figure 1.1. Connectivity steps from early life stages released into the plankton until their return to adults' habitat.

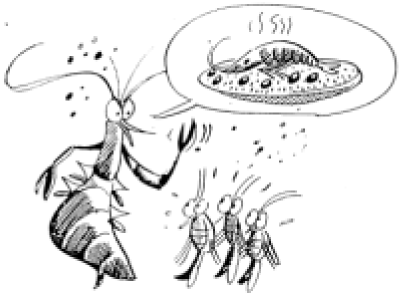
Larval development plays an important role in ecology, biogeography, and evolution of marine organisms (Jablonski and Lutz 1983). Consequently, it can be expected that spawning strategies and larval development, both from the morphological and ecological point of view, have evolved to maximize the survival of the offspring and hence that of the populations. Many species of deep-sea invertebrates reproduce continuously in hydrothermal vent habitats while others spawn seasonally, coinciding with potentially favorable conditions for their larvae, such as presence of organic matter or phytoplankton blooms (Eckelbarger and Watling 1995).

Two broad types of pelagic larvae are known to be released by invertebrate populations inhabiting the sea bottom or pelagic waters: a) short living and b) long living larvae. Within those with a short pelagic life, two larval strategies exist: the planktotropic larvae, constituted by the larvae that feed and grow in the plankton and the lecithotrophic, non-feeding free-swimming larvae with yolk reservations. The majority of benthic and pelagic marine invertebrates produce long-lived-planktotrophic larvae ("b" type), which typically do not feed in earliest stages of development while feeding organs form. This strategy has persisted in many clades for hundreds of millions of years (Wray 1995).

Among marine invertebrates, it may be expected that the decapod crustaceans, considering the relatively long duration of their planktotrophic larval stages during which they feed mainly phytoplankton and micro-zooplankton, be especially sensitive to any environmental factor affecting larval dispersion and survival. In fact, some studies demonstrating that pre-settlement processes affect directly the survival of post-larvae and juveniles in decapods have been already published (Giménez 2010).

Marine organisms, including their larval stages, are not only influenced by natural variations of environmental variables, they also suffer direct anthropogenic impacts. At present, the elevated CO_2 in the marine environment has the potential to impact the health, function and activity of many benthic invertebrates across a range of taxonomic groups (Metzger et al. 2007, Pane and Barry 2007, Spicer et al. 2007), as well as crustacean growth (e.g. Wickens 1984, Kurihara et al. 2008). Another factor, as demonstrated recently in Mediterranean, is the effect of seismic and marine noise on decapod larvae (Pearson et al. 1994) as well as adult crab development (Christian et al. 2003, Wale et al. 2013).

It is recognized that marine decapods abundance and diversity in coastal ecosystems, due to their roles in food webs throughout their life cycles, are highly important issues in the study of the dynamics of marine coastal ecosystems (Squires 1990). Moreover, in the Mediterranean area they constitute very important fishing resources, and are even targeted by some semi-industrial slope bottom trawl fisheries (such as red and rose shrimps or Norway lobster e.g. Sardà et al. 2004, Cartes et al. 2008, Guijarro et al. 2008, 2009, Moranta et al. 2008) and artisanal fleets (European lobster by Ceccaldi and Latrouite 1994).



Pierre Y. Noel 1992

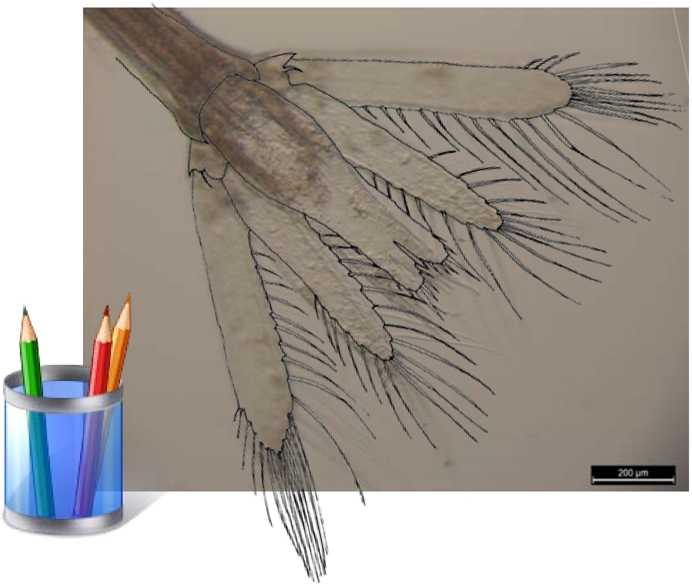
More specifically, the present thesis focuses on determining with the maximum precision and accuracy the taxonomic composition of decapods larval assemblages in the Balearic Sea. Innovatively, it describes also the vertical distributions of the most abundant species in offshore areas and explores the implications of resulting data in the ecology of decapod crustacean communities. The importance of taxonomic studies and that of the knowledge on vertical distribution of decapod larvae and their diel and ontogenic variations is detailed in the following sub-sections of this introduction.

1.2 Taxonomy: importance in biodiversity conservation and management

In 1992 the Rio de Janeiro Convention on Biological Diversity agreed that human beings are leading species to extinction and habitats to destruction, and that some measures had to be taken. Then become evident that the taxonomy was in crisis (Guerra-García et al. 2008) and was an almost extinct discipline (Boero 2001, Boero et al. 2005) at least as regards the classical taxonomic works based on morphological descriptions. This maybe occur because identification using morphological characteristics alone, especially in small organisms, and even more if they are analyzed during larval period, when changes are continuous, is not an easy task, and always time consuming.

Alike most studies of any taxonomic group in a previously non-studied area, which generally follow three consecutive phases, it is determining their composition, structure and dynamics (Juniper and Tunnicliffe 1997), and this study uses the same approach. Extensive knowledge of taxonomy, time and experience are required to achieve reliable identifications. Due to the lack of expertise, many research teams are unable to identify, to species level and accurately, most of the organisms present in a plankton sample. As a result, many of the errors or wrong conclusions stem from misidentifications at species level, which in some taxonomic groups can be as high as 90 % (Vecchione et al. 2000).

Improvements of available morphological descriptions, based on rearing and laboratory experiments in last decades, have facilitated the taxonomical identification of the plankton samples (e.g. Bartilotti et al. 2008, 2009, 2012). However, many species are difficult to cultivate and hence biological material from field sampling, whose identification is often inaccurate, is necessary to elaborate their larval morphological descriptions. In addition to classical morphological descriptions, molecular techniques, as barcoding, have been successfully applied, allowing for an increased number of biodiversity studies in some seas (Heimeier et al. 2010). Morphological descriptions can still be the basis of conventional taxonomic studies, but further genetic analysis or other sophisticated bio-investigations can give us a more reliable and complete view on their taxonomical place and evolution (phylogeny). The classification system used today is still based on Linnaean taxonomy (binomial nomenclature), but most of species have been re-classified due to new discoveries and scientific progress, especially with the development of phylogenetic systematics and genomics. Thus, accurate taxonomic meroplankton identification is a challenging task, constituting the basis for ecological studies on diversity and distribution.



Despite the problems affecting taxonomy as a research discipline, at present, the biodiversity of the oceans is of great concern. Compared with terrestrial habitats the pelagic system, the largest on the earth, is composed of taxa with vast ranges of distribution inhabiting different environmental conditions, to which animals are adapted through genetic diversity (Ormond et al. 1997). The applications of the information generated by the taxonomic studies of meroplanktonic communities are diverse. For example, the meroplankton diversity may be an indicator of climate change (Kirby et al. 2007, 2008), since global distributions of species and communities composition are expected to shift due to climate change. Accurate taxonomical information is also essential for the different agencies responsible for managing and controlling Invasive Alien Species (Meyerson and Mooney 2007). Alien species are one of the major detriments to biodiversity worldwide. In the Mediterranean, more than 986 marine alien species have been detected until 2012 (Zenetos et al. 2012). According to this increased sampling efforts, as well as long-term monitoring programs directed to determine the taxonomic composition of biocenosis, mainly in poorly known ecosystems, are required (Coll et al. 2010).

Increased knowledge on biodiversity of larval communities' will improve the management of ecosystems from a conservation point of view. In addition, it has proved to be useful for fisheries management. Thus, studies on meroplanktonic communities provide information for spatial management, defining spawning and nursery areas. Meroplanktonnic studies allow also determining the abundance of marine species that are or can constitute fishery resources, benthic or pelagic, since quantitative data on eggs or larval abundances constitute the basis for applying several indirect and direct assessment methods (e.g. Priede and Watson 1993, Scott et al. 1993).

In conclusion, taxonomic studies providing accurate morphological descriptions and genetic characterization are indispensable for carrying out further accurate studies of species biology and ecology. A proper classification at species level of field sampled organisms is crucial for development and testing most of ecological hypothesis related to recruitment processes and for measuring biodiversity in the marine pelagic ecosystems. More taxonomic research is needed to address gaps in knowledge in spatial and temporal regional and global patterns of different species, as well as in genetic responses to environmental change, in order to better understand populations' structure and thus allow for development of reliable ecological models.

1.3 State of the art of decapod larvae taxonomic studies: gaps and difficulties

Scientific studies of decapod taxonomy date back to the 1960s. There are a number of reviews on available literature published in the last decades: Ingle 1992, 1998, Williams et al. 1993, Williamson 1982, Anger 2001, González-Gordillo et al. 2001, Dos Santos and González-Gordillo 2004. However, descriptions of many decapod larval species are still unavailable, and hence the complete larval development is known for only a relatively small number of species (Harvey et al 2002). In addition, part of available literature on decapod larval taxonomy is incomplete and inaccurate, since some of the larval species already classified and described have been recently ascribed to other taxa.

Traditionally, larval descriptions come from spawning of coastal or shelf species reared under laboratory conditions (Shanks 2001). There is very little information for species from offshore or cold-water environments such as the deep-sea, characterized by slow rates of development. Even if a given larval form has already been described, many researchers studying decapod larvae as a mean to get insights into the knowledge of adults populations are not taxonomy experts, and they have usually great difficulties for recognizing through visual observation the family or the larval stage in a plankton sample taken from the wild (Fig. 1.2). These difficulties are enhanced by the fact that the great majority of crustacean decapods have a complex life history, producing pelagic larvae that may largely differ in morphology and habits from their adults (Anger 2001). Significant changes in morphology (e.g. new abdominal segment and appendage), function (e.g. appendages), size, behavior, feeding, ecology and physiology occur between nauplia, protozoea, zoea, decapodid and juvenile phases, named “metamorphosis” by a number of authors, occur during ontogenic development. Emerging molecular phylogenetic studies together with closer scrutinies of internal and external morphological characteristics, have improved the taxonomic classification of Decapoda (Fig. 1.3). However, studies of taxonomy, systematics and phylogeny of Crustacea have been and are even at present supported in most of cases only by larval morphology traits (Martin and Davis 2001).

It is important to note that larvae show a wide range of adaptations to the pelagic environment and many aspects of larval biology are similar to other plankton groups (Hall and Wake 1999). Furthermore, “Evolutionary developmental Biology” (Evo-Devo), based on Haeckel’s idea of “ontogeny recapitulate phylogeny” in combination with the analysis of larval features representing secondary adaptations to larval habitat, have proven important in the last decade (e.g. Scholtz 2003). As a result of this revived interest on larval taxonomy, during the last ten years (2003-2013) there has been more than one hundred studies published relating to decapod larvae descriptions (webofknowledge.com). The experience acquired within the framework of this thesis in relation to the field of larval taxonomy recommends the use of improved optical analytical tools, as latest generation microscopes integrated in IAS (Image Analysis Systems). In addition molecular techniques should also be considered in decapod larval taxonomy to clarify doubts and correct errors in the last century’s identifications.

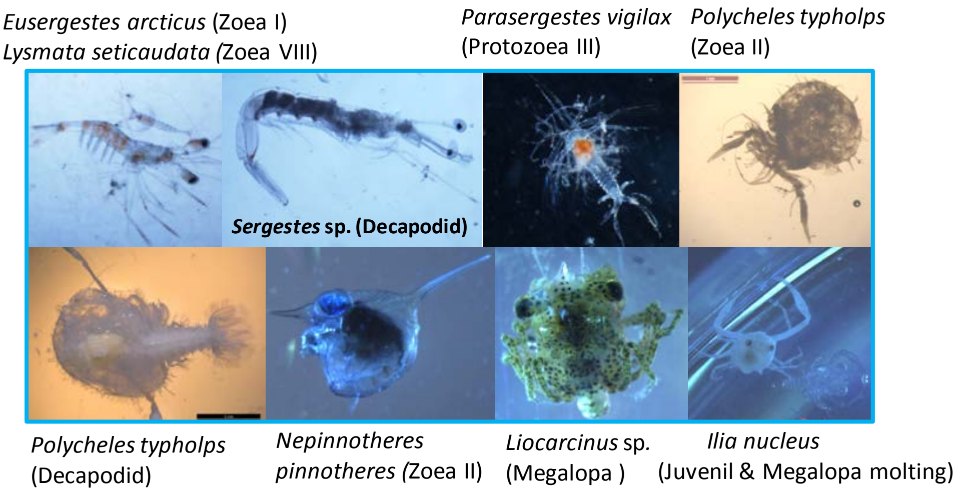


Figure 1.2 Example of decapod crustaceans morphological diversity among species and developmental larval stages (in brackets) off Balearic waters.

CLASSIFICATION OF CRUSTACEA (Martin & Davis, 2001)
Subphylum **Crustacea** Brünnich, 1772
Class **Malacostraca** Latreille, 1802
Subclass **Eumalacostraca** Grobben, 1892
Superorder **Eucarida** Calman, 1904
Order **Decapoda** Latreille, 1802

		Species level
Suborder **Dendrobranchiata** Bate, 1888	Superfamily **Penaeoidea** Rafinesque, 1815	*Aristeus antennatus* *Parapenaeus longirostris* *Gennadas elegans*
	Superfamily **Sergestoidea** Dana, 1852	*Eusergestes arcticus* *Sergia robusta* *Parasergestes vigilax*
Suborder **Pleocyemata** Burkenroad, 1963	Infraorder **Stenopodidea** Claus, 1872	
	Infraorder **Caridea** Dana, 1852	*Palaemon macrodactylus*
	Infraorder **Astacidea** Latreille, 1802	
	Infraorder **Thalassinidea** Latreille, 1831	
	Infraorder **Palinura** Latreille, 1802	*Polycheles typhlops* *Scyllarides latus*
	Infraorder **Anomura** MacLeay, 1838	
	Infraorder **Brachyura** Latreille, 1802	*Maja squinado* *Ergasticus clouei*

Figure 1.3 Decapod crustacean taxon Tree (adapted from Martin and Davis 2001) and species used to produce single works in this thesis on the right. Species in purple take part of taxonomic part and the blue ones from ecological results, specifically for vertical distribution models.

Most species of decapod crustacean larvae inhabiting the Balearic waters according to the literature have been identified in this study (García and Massutí 1987), this could give an idea of the potential of this line of research, supported by new techniques noted above. Taxonomic analyses have allowed also the identification of zoeas of an invasive species whose presence in the Mediterranean was hitherto unknown, *Palaemon macrodactylus*. After publishing this larval presence adult populations were immediately found in North Adriatic lagoons (Cuesta et al. 2014, Cavraro et al. 2014).

1.3.1 Vertical migrations: importance for understanding larval ecology and recruitment processes

Once highlighted the importance and intrinsic value of the larval communities' taxonomic study, the next step is to apply this information to expand the knowledge of the different species ecology. Research on all the phases of the life cycles of marine organisms is imperative. Due to their complexity it is the only way to understand how organisms cope with biotic and abiotic environmental factors, such as tides, currents, temperature, light, stratification and others influencing them. There are a relatively high number of studies on the factors influencing adult populations (e.g. Hill et al. 1982, Guijarro et al. 2008). However, those dealing with larval dispersal and survival are very few. Within the field, an important line of research lacking is that on larval dispersal and populations' connectivity. The majority of large-scale dispersal by planktonic marine organisms it was believed primarily passive, driven by the major currents, despite that this idea it is changing taking account the larval behavior (Chiswell and Booth 2008). In fact, it is also modulated by active movements of zooplankters, for example migrations within the water column (Rundle et al. 2007).

One type of management tool that has been widely proposed within the framework of an ecosystem approach for which the plankton dispersion processes are of outmost importance are the Marine Protected Areas (MPAs). Eggs and larvae that drift out of a MPA may serve to repopulate other zones, thus eventually benefiting the fisheries out of the protected areas. Phylogeographic studies suggested that in order to develop successful MAPs identification of the sites with greater larval retention and self-recruitment is necessary (Small and Wares 2010). Thus, larval export from reserves has a potential of enhance recruitment over large regions. However, its success will depend upon many factors difficult to predict. Spillover effects occur relatively close to MPAs (from 1-10 up to 100 km), but larval dispersal, depending on vertical positions of planktonic eggs and larvae, may be significant further away, from 10 to 100km for invertebrates (Palumbi 2004).

It has been demonstrated that the natal origin is one of the main factors to take into account in order to understand population dynamics and connectivity processes (Cowen et al. 2007). The larval duration (Shanks 2009) and vertical position of the larvae also influence the offshore dispersal (Dos Santos et al. 2008). Larval dispersion depends on series of physical and biological factors influencing their passive transport but also of larval behavior, for example when and where metamorphosis has to take place. Thus, orientated larval movements are also a key element in the recruitment process (Staaterman et al. 2012), having demographic consequences. Regrettably, most of studies of larval transport consider only horizontal spatial dimension, whereas the vertical axis is ignored despite the fact that when swimming vertically larvae can modify their horizontal distribution, encountering different currents.

Russell (1927) described the changes in vertical distribution with age such as ‘ontogenetic vertical distribution’ (OVD), which involved changes in mean depths and range’s limits taking also into account the time of the year (Pearre 1979). Ontogenetic vertical migration plays an important role in decapod population spatial dynamics. Pelagic larvae are good swimmers (Jeffs and Holland 2000) that feed in upper layers and return to the adult habitat to settle (organic matter exportation), conditioning directly the distribution of adult population (Shanks 1995). Diel vertical migrations (DVM) condition long distance larval transport andare related to strategies improving efficient utilization of resources or predation avoidance (Gliwicz 1986). Once the larvae are in search of food in the photic zone the risk of being preyed at shallow depths by visual predators is increased. The adaptability of the larvae to poor food conditions seems, nevertheless, to be greater than hitherto believed (Thorson 1950). However, in oligotrophic regions, such as the study area (western Mediterranean), diel migrations occur throughout the year, even though some species stop diel migrations during summer when primary production is low.

In summary, information regarding vertical movements, both ontogenetic and diel vertical migrations is necessary for more accurate sampling within the first 100 meters from the surface, in order to better understanding larval dispersion and population connectivity (Pineda et al. 2007).

1.3.2 State of the art of decapod larval ecology studies, with special attention to issues related to vertical distribution: gaps and difficulties

Physiological changes along successive life-history stages in estuarine decapods are due to variations in the conditions of their particular environments (Simith et al. 2014, Anger 2001). The understanding of decapods egg production and recruitment processes is very scarce (Botsford 1991). In fact, till last decade the ecology of decapod larvae and especially for offshore waters was almost unexplored (e.g. Dos Santos et al. 2008, Landeira et al 2009).

Fisheries and adult population data date back to 1850, whereas larval records, an indirect method of assessment, have been recorded for just 25 years (Koettker and Freire 2006). The paucity of knowledge on crustacean decapod larval ecology is partly a result of the aforementioned difficulties inherent to their study, derived from their small size and fragility, and also from the great morphological variations among species and developmental phases (Fig 1.2) (Dos Santos and González-Gordillo 2004). As a result, first studies from field catches, focused on morphology and diversity, were performed in as late as the 80’s (Williamson 1982). Further lack of knowledge about the larval ecology of species inhabiting offshore waters could be explained by the level of difficulty to the meroplankton studies carried out in these waters. In oceanic waters the zooplankton composition is generally characterized by the relatively lower proportion of meroplankton, especially in terms of biodiversity, and the presence of vertical migrators (Ormond et al. 1997). Alike, for this thesis, in order to get representative samples it was necessary to analyze the whole samples. Laboratory work is based on identifying and separating the decapod larvae from the much larger amount of other planktonic taxa. Following laborious sorting tasks, all the decapods larvae of different species were identified to the lowest taxonomic level, overcoming the difficulties associated to decapod larvae taxonomic studies described in the previous section, which permitted to carry out studies at community level. Such community studies are still rare for most places around the world especially in offshore waters (e.g. Brandão et al. 2013, Landeira et al. 2013).

Meroplanktonic larvae can actively control their vertical positions in phase with diel cycle, which not only determines horizontal transport trajectories but also affects their physiology. Initially, it was thought that the movement of planktonic decapod crustaceans' larvae to deeper waters was a great disadvantage, as colder temperatures reduce metabolic rates, resulting in prolonged development time and reduced growth (González-Ortegón and Giménez 2014). Therefore, the decrease in depth was proposed that was not a strategy for optimizing growth, but a trade-off between food availability and predator avoidance (Stich and Lampert 1981). However, despite the importance, currently few authors have addressed the issue of the vertical distribution of decapod larvae in offshore waters (Koettker et al. 2010, Pochelon et al. 2014), where larvae of pelagic decapods, whose diversity is much lower than that of benthic decapod species, dominate. Among pelagic decapods the most abundant are the pelagic shrimps of the suborder Dendrobranchiata.

Pelagics shrimps are members' of nektonic and micronektonic communities of open oceans. Their fertilization is external, their eggs hatch as free-swimming nauplii and only have free living stages, every larval development consist of different stages within each phase (Martin et al. 2014). Mediterranean mesopelagic shrimps have not been thoroughly studied and information on the adult distribution is poor (Casanova 1977, Koukouras 2000, Koukouras et al. 2000). In other areas it has been demonstrated that in terms of abundance, they are an important component of pelagic communities (e.g. *Gennadas elegans* in Pacific by Heffernan and Hopkins 1981). In our study area the importance of mesopelagic shrimp has been highlighted recently (Simão et al. 2014). It has been proposed that their larvae could constitute a link between pelagic primary producers and the higher trophic levels (Drake and Arias 1993). Spawning activity in pelagic shrimps is difficult to assess from the maturity state in the adults since they are rarely caught with gonads. Thus, the larval captures reported in this thesis constitute novel information regarding the spawning of many Mediterranean decapods. Following the description of decapod larval communities in different seasons and vertical strata, carried out within the framework of this thesis, a study on summer decapods larvae community inhabiting epipelagic waters of Balearic sea has been published (Carbonell et al. 2014). In both studies pelagic shrimps dominate the offshore decapods larval community, locally.

In order to fill some of the existing gaps regarding the ecological implications of decapod larval vertical distribution and the ontogenetic and diel variations, our study focused on the most abundant decapod species in offshore Western Mediterranean waters, *Gennadas elegans, Eusergestes arcticus, Sergia robusta* and *Parasergestes vigilax,* also being the most abundant species in our samples. In pelagic shrimps several adaptations to plaktonic existence are observed, as enormously developed spines in carapace of protozoeal and zoeal Sergestidae and heavily setose antennules and antenna in *Gennadas* genera (Omori 1974). Gurney (1924, 1942) and Heldt (1938) described the protozoea and mysis of *G. elegans*. Larval development stages of *E. arcticus* had been described by different authors (e.g. Williamson 1915, Hansen and Coutière 1922, Gurney and Lebour 1940). For *S. robusta,* larvae were firstly described by Williamson (1915) and Hansen and Coutière (1922). In the case of *P. vigilax* studies by Hansen and Coutière (1922) and Gurney (1924) described their larval stages for the first time. Within our study, Dendrobranchiata larvae were identified based on the information provided by the study of Dos Santos and Lindley (2001).

1.4 The framework project and study area

The current research on populations and aquatic ecosystems, especially those subjected to human impact, involves a high degree of complexity and requires a multidisciplinary approach to study the overall functioning of the ecosystems. Within this framework, one of the aims was to assess which are the most important interactions among the ecosystem components and the factors and processes driving them (Browman and Stergiou 2004, Pikitch et al. 2004). Our research is centered on Mediterranean, a sea with a biological productivity known to be among the lowest in the world, despite supporting fishing activities for centuries (Estrada et al. 1985). Crustacean decapods are the key target of the deepwater bottom trawl fishery carried out in the western Mediterranean (Sardà 1993, GFCM 2004). It is currently accepted that the management of crustacean resources must include fishery records, adult biology, larval transport and recruitment studies (Fehlauer and Freire 2002). In Mediterranean, summer season, when deep chlorophyll maximum (DCM) is temporally found (Estrada et al. 1993), is the least productive because the stratification of the water reduces the transfer of nutrients from deeper layers.

In the Balearic Sea (Western Mediterranean, thesis study area) some studies on mero-plankton have been carried out, but most of them focusing on ichthyoplanktonic fraction (Alemany et al. 2006, Torres et al. 2011, Rodríguez et al. 2013, Olivar et al. 2014). However, despite their importance, little is known about the larval developmental stages of most of the exploited decapod species (Carbonell et al. 2010) as well as decapod crustaceans with interest for conservation (Mallol et al. 2014). This worldwide gap of knowledge (Fig. 1.4) is especially important in the case of populations inhabiting Balearic Sea, since up to the decapod community work Torres et al. (2014), which conforms chapter 5, no single study providing data on decapod larval communities has been published. This thesis is the first one on decapod crustacean larvae in the Mediterranean.

The present thesis forms part of the project entitled “Structure and dynamics of the benthopelagic slope ecosystem in two oligotrophic zones of the western Mediterranean: a multidisciplinary approach at different temporal scales in the Balearic Islands”, acronym IDEADOS. The overall objective of the framework project

IDEADOS consists of determining the relationships between environmental conditions and the nektobenthic slope communities at two oligotrophic areas of the western Mediterranean, northern and southern Balearic Islands, in the Balearic and Algerian sub-basins, respectively, with different geomorphologic and hydrodynamic characteristics (Fig. 1.5).

Vertical distributions have not yet taken into account in dispersive models performed currently for Mediterranean (Rossi et al. 2014). The position of the larvae in the water column may be influenced by hydrography, which determines their horizontal dispersion driven by the currents and therefore, the connectivity between populations (Fig. 1.6). This project provides an excellent frame to compare how different environmental scenarios shape the interactions between the benthic and the pelagic communities (micro-, meso- and macrozooplankton, micro- and macronekton), by applying different and complementary techniques (Fig. 1.7). In this context, this thesis aids in understanding of the role of vertical migrators on the secondary production of deep-sea, taking advantage of the different sampling techniques used in IDEADOS project, since they allowed sampling decapod along their different stages of development along water column.

Framework project emphasizes the study of the trophic coupling of the nektobenthic organisms and the populations of the meso- and bathypelagic domain, as potential preys, through different temporal scales and different levels of organization (population, community and ecosystem). Decapod larvae importance as a prey of fish (Rice 1963) and paralarvae (Roura et al. 2012) has been verified. Adult stages can be also preyed by other decapods (Cartes et al. 2008), elasmobanchs (Valls et al. 2011) and fish (Roger 1994).

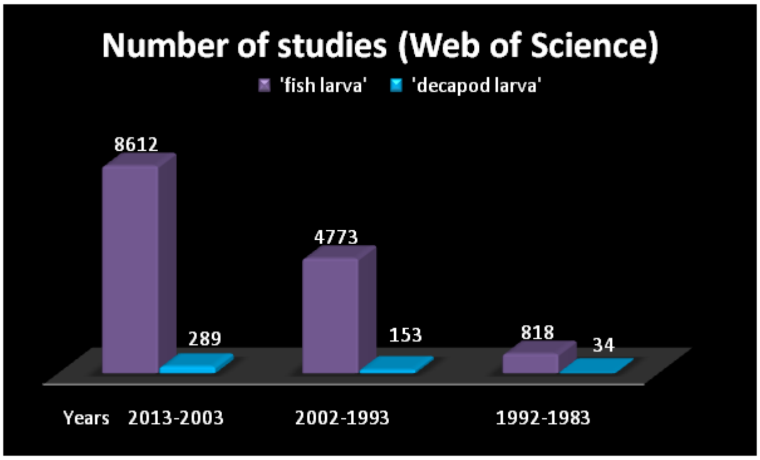


Figure 1.4 Number of works containing the words 'fish larva' or 'decapod larva' as a topic according to Web of Science during last thirty years.

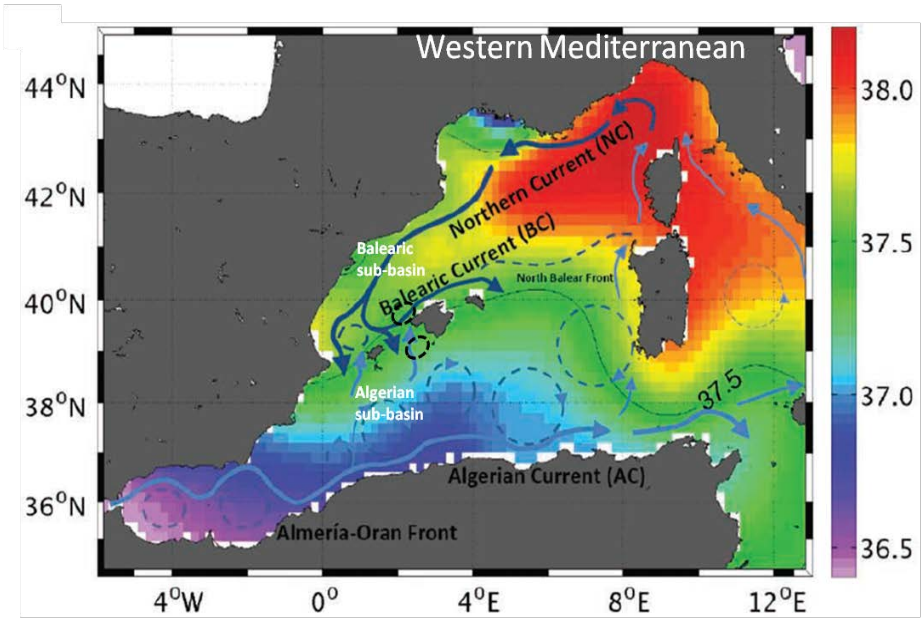


Figure 1.5 Western Mediterranean with the study area identify by black dashed circles. Main hydrographic features and data for salinity (right exe) obtained from MEDAR Group were averaged for July.

Figure 1.6 Population connectivity of pelagic (blue narrow) and benthic organisms (green narrow) occurs during plankton larval phases when individuals return to settle to their natal location. During the larval critical period the vertical position influence the dispersal, is in this vertical distribution focused this phD Thesis (Animals images from http://ian.umces.edu/symbols/)

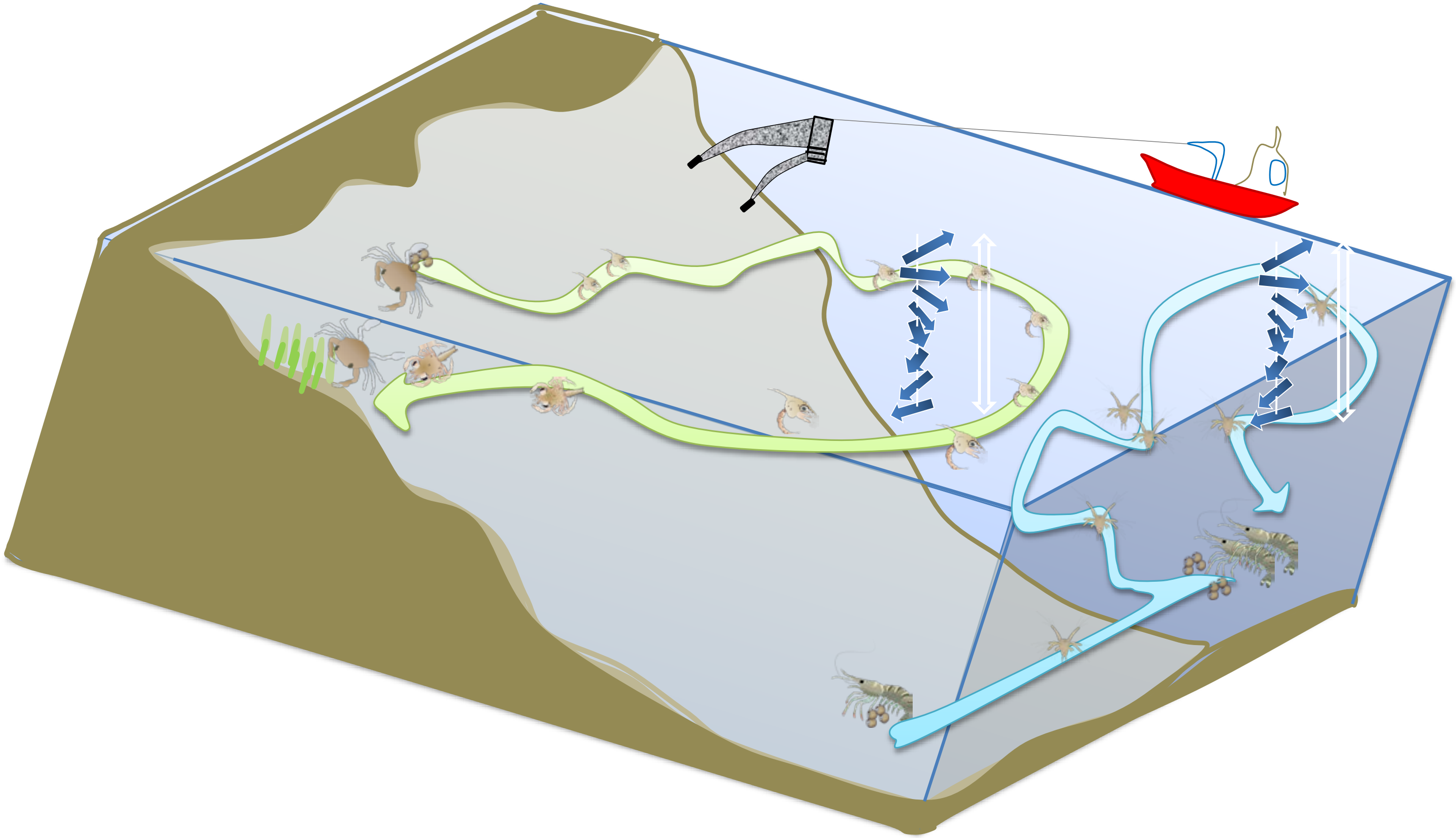


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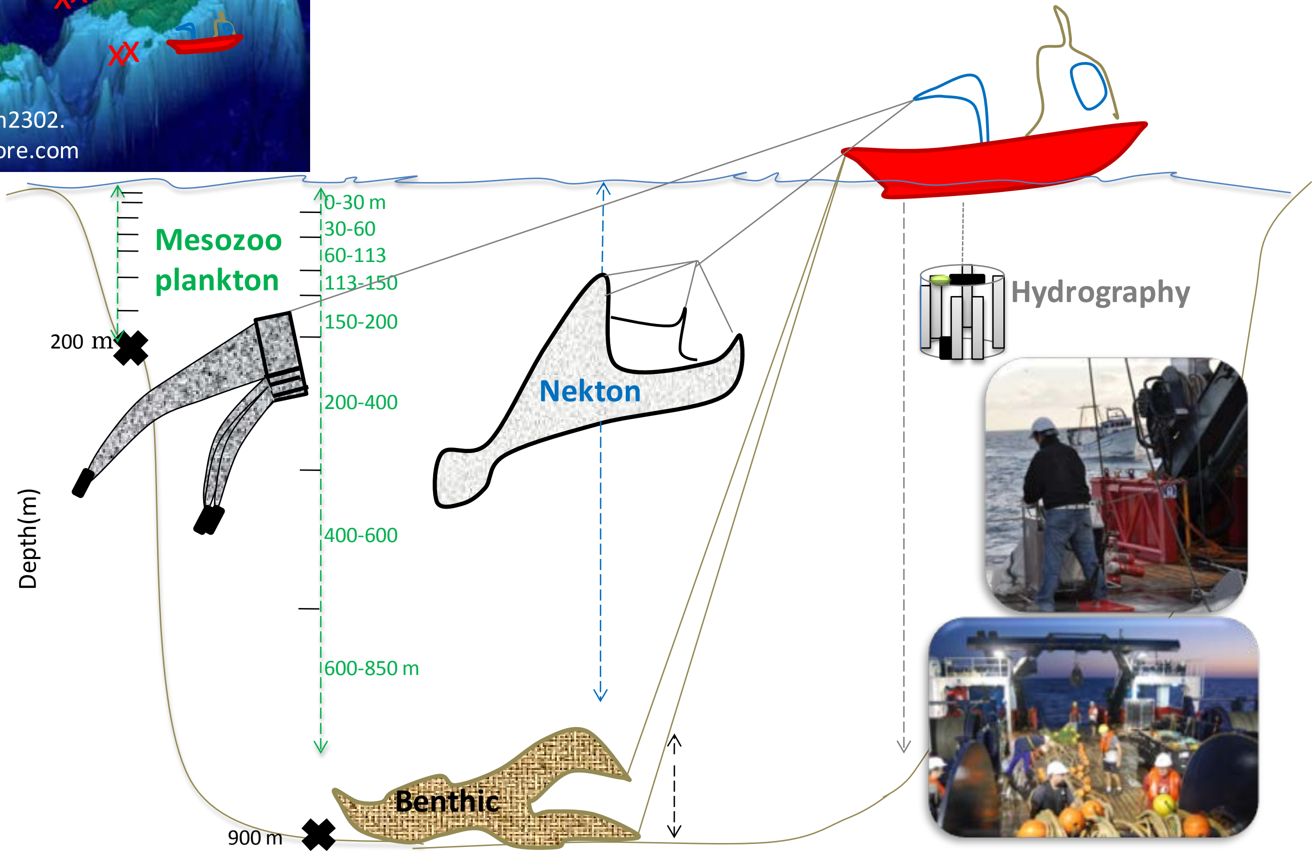
Figure 1.7 Study area with four stations located over shelf break and middle slope off the north-west area and south of Mallorca Island. Scheme of different and complementary techniques used in this thesis (see Methodologies).



1.5. Objectives and structure of the thesis

The aim of this thesis is to provide the scientific community with relevant information on the decapod larval community inhabiting Western Mediterranean waters as starting point for studies of larval drift and survival that could affect recruitment processes and hence the dynamics of decapod crustaceans adult populations. In order to achieve this strategic objective, the immediate objectives are:

i) to make available an accurate characterization of the decapods larval community taxonomic structure, including morphological descriptions of unknown larval stages, and

ii) determining the vertical distribution of different taxa along ontogeny and diel cycles and their seasonal variations, relating it with environmental scenarios and exploring their ecological implications in selected key species, as pelagic shimps.

The thesis is based on the analysis of the decapod larval community structure and distribution throughout the water column in two seasons and areas with contrasting environmental conditions, to date largely unknown. Specifics goals are detailed in each chapter, the first being this introduction. Following chapters focused on single species taxonomic works and morphologic descriptions (Chapter 2 to 4), decapod larval community characterization (Chapter 5) and analysis of vertical distributions of pelagic shrimps larvae and adults and their ecological implications (Chapter 6), finishing with a conclusions chapter (Chapter 7). See general framework thesis questions (Fig. 1.8).

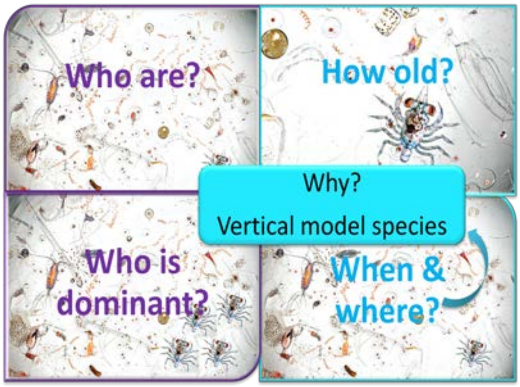


Figure 1.8 General framework thesis questions scheme. Purple boxes represent the objectives of taxonomy and the blue ones of communities and ecology (Background image adapted from Christopher Jobson).

More specifically, the first chapters in the PhD deal with the identification of decapod larvae, including detailed taxonomic descriptions of the development stages of larvae from wild plankton samples reported in the area for the first time (chapter 2 and 3) and rare decapods larvae from species of special interest for conservation and fishing exploitation (chapter 2). The larvae of the group of decapods named anciently “Reptantia” (composed by Suborder Pleocyemata), which contains the vast majority of decapods including the most familiar and emblematic of Crustaceans, have been studied in this thesis through the description of lobsters (Palinura: chapter 2 & 3) and crabs (Brachyura: in collaboration Marco-Herrero et al. 2013) larvae (see Fig. 1.3). Through both classifications based on morphology and molecular techniques some taxonomic uncertainties have been resolved, assigning morphotypes previously missasigned to deep species, as *Polycheles typhlops* (chapter 3). Our study aided to resolve systematic positions among some crabs genera such as the case of study of *Ergasticus clouei* (Marco-Herrero et al. 2013). Within the whole decapod larval community was detected even a new species in the Mediterranean, the oriental shrimp, *Palaemon macrodactylus*. It was hypothesizing that the presence of these larvae, detected for the first time in the Mediterranean, could imply that there were settled adult populations which were reproducing in this Sea (chapter 4). The accurate charachterization of decapod crustacean larval community to species level, in relation to the first objective (i), is presented within the first part of the community study (see chapter 5).

Regarding objective ii, the ecological approach to the analysis of decapods larvae vertical distribution needs to take into account that the water column was stratified in summer, showing strong gradients in the upper 100 meters, whereas in late autumn, conditions were more homogeneous down to the mixing layer depth (MLD). In relation to this objective, the specific vertical and seasonal patterns in offshore Western Mediterranean larval decapod assemblages are presented in the second part of chapter 5. Also in relation to this objective, in order to understand the early and late life biology of offshore species with mesopelagic or epipelagic lifecycle in offshore habitats, a series of studies were performed using the most abundant decapod species in offshore Western Mediterranean decapod during the larval phases (four Dendrobranchiata) and adult phases (Simão et al. 2014) as a model. The results of such studies, which allowed characterizing their vertical movements along day and night in two different seasons showing contrasting environmental scenarios, are explained in chapter 6. The vertical distribution of the different developmental stages and their migrations along day and night were analized from the point of view of adult's spatial spawning strategies, comparing the vertical distribution of the adults and those of the first larval stages. The relation between vertical distribution patterns and the processes that may allow a trade-off between prey-predator were also explored. In addition, the influence of these vertical patterns on the dispersion of the organisms and the connectivity among populations, as well their influences in the flows of energy along the water column or the coupling between pelagic and benthic domains are also discussed within chapter 6.

The specific information on larval vertical distribution at species level and stage of development provided by this thesis is outstanding to develop predictive models that estimate population connectivity through larval dispersal, since vertical distributions have not yet taken into account in dispersive models performed currently for Mediterranean (Rossi et al. 2014). Understanding patterns of connectivity in the future for decapods species will improve the actual management and will help to design new measures for the spatial management of these resources. The main thesis' conclusions are summarized in chapter 7.

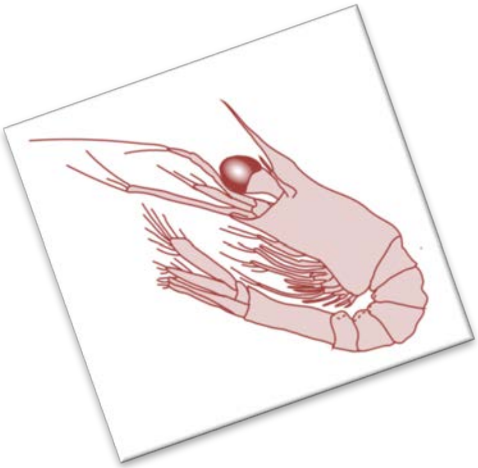
Chapter 2

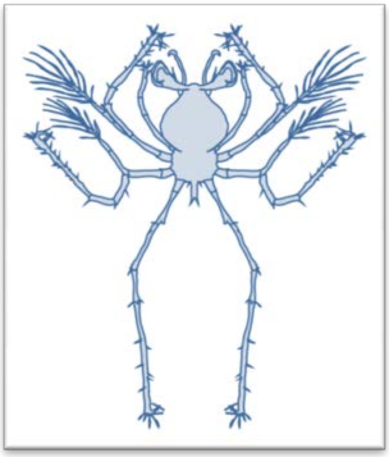
Species of interest for conservation and fishing exploitation

Torres AP, Dos Santos A, Alemany F and Massutí E- 2013 Larval stages of crustacean key species of interest for conservation and fishing exploitation in the western Mediterranean. Scientia Marina, 77 - 1, pp. 149 - 160.

2.1 Abstract

Decapod crustaceans are the main target species of deep water bottom trawl fisheries in the western Mediterranean. Despite their importance for fisheries and conservation, little is known about their larval development, especially in the case of deep water species. In this chapter we present new information on the occurrence and morphology of larval stages for some species of commercial interest based on samples collected off the Balearic Islands. Mesozooplankton sampling was carried out using depth-stratified sampling devices at two stations located on the continental shelf break and mid slope, in the northwest and south of Mallorca in late autumn 2009 and summer 2010. We describe in detail the second mysis stage of the red shrimp *Aristeus antennatus*, not previously known, and the first larval stage of the slipper lobster *Scyllarides latus*, poorly described almost a hundred years ago. We also report the second finding of larvae of the spider crab *Maja squinado* and the first capture from the field of larval stages of the rose shrimp *Parapenaeus longirostris* and slipper lobster in the Mediterranean.





2.2 Introduction

Decapod crustaceans such as *Nephrops norvegicus* and some Dendrobranchiata shrimps (*Aristeus antennatus*, *Aristeomorpha foliacea* and *Parapenaeus longirostris*) are the main target species of the deep water bottom trawl fishery carried out in the western Mediterranean (Sardà 1998, Sardà et al. 2004, Moranta et al. 2008). Other decapod crustaceans, such as lobsters, spiny and slipper lobsters, and spider crabs, are also species of interest for the small-scale fisheries (Goñi and Latrouite 2005), although during the last few decades some of these taxa have almost disappeared in catches (Bannister 1993, Spanier and Lavalli 1998).

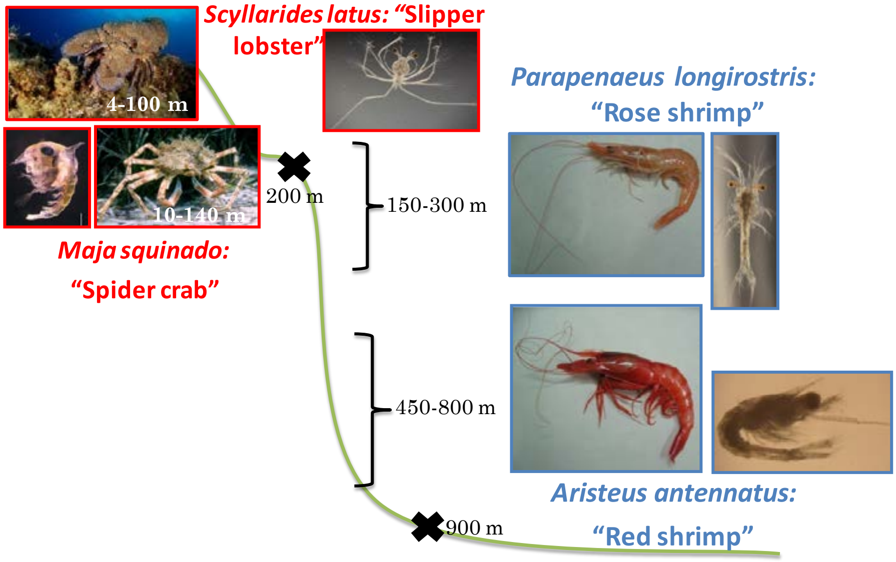
It is currently accepted that, for the management of sustainable crustacean fisheries, information on the biology of the species, their larval ecology and recruitment characteristics should be integrated (Fehlauer and Freire 2002). While long-term information is usually available on the fisheries and adult populations for most commercially important species, larval records are much scarcer or even completely lacking. The study of planktonic stages and the larval transport modeling of deep-sea benthic invertebrates is one of the most efficient and economical ways to acquire this kind of information, especially because studies on adult benthic populations require a greater investment (Yearsley and Sigwart 2011). However, with larval development known for only a small number of species (Harvey et al. 2002), there is a need for more research on these developmental stages.

In the western Mediterranean, some studies have provided larval morphological descriptions for continental shelf species (e.g. Guerao and Abelló 1997, 1999, Guerao et al. 2006) and information on decapod larval communities (e.g. Fusté 1982, 1987, Olivar et al. 1998, González-Gordillo and Rodríguez 2003), whereas others have presented data on their vertical distribution and the meso-scale horizontal patterns of larval distribution in the neuston layer (e.g. Abelló and Guerao 1999). However, we still have poor knowledge concerning the morphology of larval stages of most continental slope species. This is largely due to the relative scarcity of these species in standard plankton samples and the lack of expertise for their correct identification and recognition in the samples. Most of all, difficulties in the capture of adult specimens alive and their reproduction and survival under laboratory conditions have prevented the description of the complete larval series for *Aristeus antennatus* and *Scyllarides latus* leading to a point when any information on their morphology and distribution is valuable to better understand their ecological traits.

In the western Mediterranean, the shrimps *P. longirostris* (Lucas 1846) and *A. antennatus* (Risso 1816) are exploited by bottom trawlers on the upper and mid continental slope bottoms, respectively. They are well known in terms of their biology and fishery (e.g. Sardà et al. 2004, Cartes et al. 2008, Guijarro et al. 2008, 2009, Moranta et al. 2008 and references therein). However, their larvae have been proving difficult to find and only a few references on their occurrence and morphology are available to date (Heldt 1938, 1954, 1955, Seridji 1971, Dos Santos 1998, Carbonell et al. 2010, Landeira 2010). *Scyllarides latus* (Latreille 1803) and *Maja squinado* (Herbst 1788) represent smaller-scale fisheries resources that are currently included in the list of species whose exploitation is regulated under Annex III of the Barcelona Convention Protocol (1976). While the slipper lobster *S. latus* has been fished intensively, only some larval stages have been captured and described (stage I by Santucci 1925, 1928; stage VIII by Maigret 1978; stage XI by Martins 1985). The crab *M. squinado,* whose larval stages were described by Bourdillon-Casanova (1960) and Guerao et al. (2008), was considered commercially extinct. As a consequence, the regional government of the Balearic Islands has been developing a programme for restocking in the archipelago since 2006 (http://dgpesca.caib.es).

The aim of the present study is to provide new information on the occurrence and morphology of larval stages of the red shrimp *Aristeus antennatus*, the rose shrimp *Parapenaeus longirostris*, the slipper lobster *Scyllarides latus* and the Mediterranean spider crab *Maja squinado,* all species that are important for fisheries management and conservation purposes.

"New findings on larval stages of crustacean decapods of interest for **conservation** and **fishing** exploitation in the Western Mediterranean"



2.3 Materials and methods

Two multidisciplinary research surveys were conducted off the Balearic Archipelago (western Mediterranean; Fig. 2.1) during late autumn (29 November to 18 December 2009) and summer (11 to 30 July 2010). The main objectives of the surveys were to determine the taxonomic composition, abundance, structure and vertical distribution of the meroplanktonic community at two stations located over 200 m and 900 m depth (shelf break and mid slope, respectively), off the northwest and south of Mallorca Island (Balearic and Algerian sub-basin, respectively), each site representing different environmental conditions (Pinot et al. 2002, López-Jurado et al. 2008).

To determine vertical distribution of decapods larvae during the daily cycle, series of oblique hauls were performed at four stations for 36 h at each site. During the course of the study a total of 218 depth-stratified mesozooplankton samples were selected to study decapod larvae, which were integrated in 34 hauls. From these, 18 were collected using HYDRO-BIOS multi-net in 2009 and 16 with a multiple opening closing net and environmental sensing system (MOCNESS) in 2010 (Olivar et al. 2012). During each oblique haul along the whole column, generally performed down to 200 m depth on the shelf break and 500 m (in summer) or 850 m (in late autumn) on the mid slope, seven and five depth strata were fished in summer and late autumn, respectively.

The thicknesses of these strata depended on bathymetry and season. In late autumn the strata were 200-120, 120-90, 90-60, 60-30 and 30 m from the surface on the shelf and 850-600, 600-350, 350-200, 200-60 and 60 m from the surface on the slope. In summer the strata were 200-150, 150-125, 125-100, 100-75, 75-50, 50-25 and 25 m from the surface on the shelf and 500–400, 400–200, 200-125, 125-75, 75-50, 50-25 and 25 m from the surface on the slope. The net mouth openings were 0.25 and 1 m^2, respectively, and mesh size was 333 µm for both net types. Both devices were towed at ~2 knots. Immediately after collection, all samples were preserved in ~4% borax-buffered formaldehyde prepared using seawater. In the laboratory, samples were subsequently sorted for decapod crustacean larvae and identified to species and developmental stage, whenever possible, using identification keys (Dos Santos and Lindley 2001, Dos Santos and González-Gordillo 2004) and the following available descriptions for species: Heldt (1955) for *Aristeus antennatus*, Heldt (1938) for *Parapenaeus longirostris*, Guerao et al. (2008) for *Maja squinado* and Santucci (1928) for *Scyllarides latus*.

Drawings and measurements were made with a camera lucida on a binocular Leica M205C stereo microscope. Setal observations and their drawings were made using a Zeiss compound microscope with a camera lucida. The preparation of slides was temporary. Larval description followed the standards described by Clark et al. (1998) and the setal terminology used was that established by Ingle (1993) and Garm (2004). Whenever necessary, the long plumose setae on distal exopod segments were drawn truncated and setulation on appendages is absent. Setal counts are presented in a proximal to distal sequence.

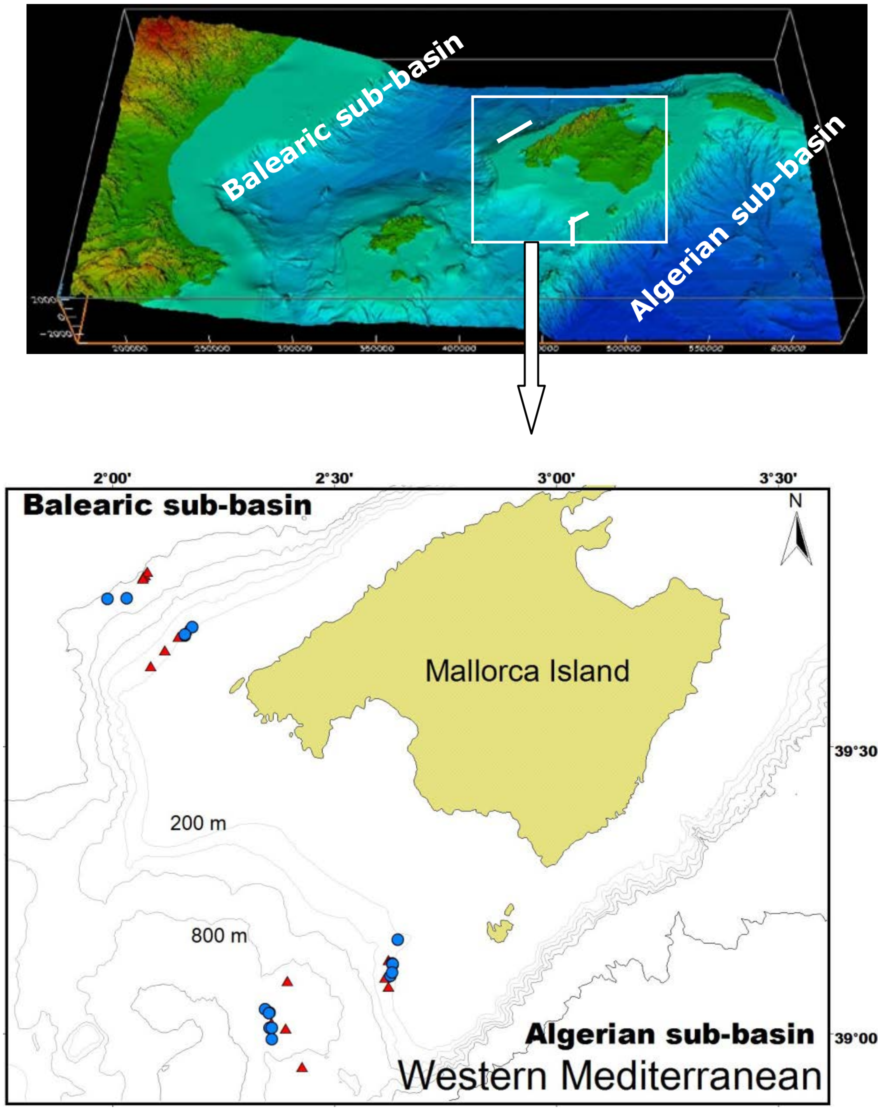


Figure 2.1 Study area in the Western Mediterranean Sea, identifying plankton stations sampled (blue dots = late autumn; red triangles = summer), at four stations located over shelf break (200 isobath) and mid slope (900 isobath) off the northwest and south of Mallorca Island (Balearic and Algerian sub-basin, respectively).

The following measurements were taken: total length (TL), between the tip of the rostrum and the posterior end of the telson; rostro-dorsal length of brachyuran zoea (RDL), between the tips of the dorsal and rostral spines; and carapace length (CL), from the tip of the rostrum to the posterior margin of the carapace. For *Scyllarides latus* and *Maja squinado*, carapace maximum width (CW) was also measured.

All studied specimens are deposited at the Centre Oceanogràfic de les Balears, with the following catalogue numbers: for *P. longirostris* one second protozoea from late autumn, ID2_1209_C1.2.N4 and one from summer, ID2_0710_E11N7; for *A. antennatus* one second protozoea, ID2_0710_E6N7, another second protozoea, ID2_0710_E24N8, and a second mysis dissected, ID2_0710_E18N8; for *S. latus* a first zoea dissected, ID2_0710_E19N8; and for *M. squinado* a second zoea, ID2_0710_E18N8.

2.4 Results

2.4.1 Occurrence and abundance of larval stages

A total of 7448 decapod larvae belonging to 120 different taxa were identified to the lowest recognizable taxonomic level. Among these, we identified and measured a total of seven specimens of species that are of high interest for conservation and fishing exploitation in the western Mediterranean. Three larvae of *A. antennatus* were captured in summer, of which two corresponded to the second protozoea (PII) and one to the second mysis stage (MII). Two specimens of the second protozoea (PII) larval stage of *P. longirostris* were also found in the samples in both seasons. Also, the first larval stage (ZI) of *S. latus* and the second zoea (ZII) of *M. squinado* were captured in summer. Relevant information about these specimens and the hauls in which they were found, such as size, density, date, geographic point, time of day, water depth stratum and bottom depth, is shown in Table 2.1.

2.4.2 Morphological description of mysis II of *Aristeus antennatus* (Figs 2.2 & 2.3)

Size: 4.1 mm TL and 1.6 mm CL.

Pereion (Fig. 2.2A): with gastro-frontal and gastro-orbital carinas, rostrum slender and slightly upward-pointing, extending to end of second segment of antennular peduncle, with 4 very small simple setae (Fig. 2.2B); supraorbital spines and prominent pterigostomial spines present; eyes reaching posterior end of antennular peduncle.

Antennule (Fig. 2.2D): peduncle 3-segmented, proximal segment with 8 plumose setae distributed along inner margin, 3 small plumose setae on stylocerite, 1 simple spine positioned at mid-length of segment and 6 plumose setae distally; second segment with 2 plumose setae along inner margin, 1 sparsely plumose seta on outer margin and 2 plumose and 1 simple setae distally on outer margin; distal segment with 2 plumose setae along inner margin and 4 long plumose setae, 4 short plumose setae and 1 simple small seta distally. Inner flagellum unsegmented, with 1 small simple seta on distal margin. Outer flagellum unsegmented, with 2 aesthetascs placed sub-terminally and 4 aesthetascs and 1 simple seta distally.

Antenna (Fig. 2.2E): protopod without setae; scaphocerite with 13 plumose setae sparsely distributed along inner margin and 5 plumose setae on distal outer margin; flagellum composed of 11 segments, with 1 small simple seta on distal margin of the fifth segment and 1 small plumose seta on distal margin of the ninth segment and 3 more on the posterior end of the distal segment.

Mandible (Fig. 2.2F): armature of incisor and molar processes as illustrated, incisive part with numerous teeth; palp unsegmented, with 1 long plumose distal seta.

Maxillule (Fig. 2.2G): coxal endite with 8 serrulate, papposerrate and simple seta; basial endite with 10 strong cuspidate and 4 sparsely plumose setae; endopod 2-segmented with 2 sparsely plumose setae on the proximal segment and 2, 2+2 sparsely plumose setae on distal segment.

Maxilla (Fig. 2.2H): coxal endite bilobed with 6+12 long plumose setae; basial endite bilobed with 7+4 plumose setae; endopod 4-segmented bearing 2+2+2+2 long plumose setae and 1 small simple seta on distal segment plus an additional endite at its base with 2 plumose setae; scaphognathite with 22 marginal plumose setae.

First maxilliped (Fig. 2.3A): protopod slightly bilobed, proximal coxal portion with 12 papposerrate setae; distal basial portion with 14 papposerrate setae along margin and 1 small papposerrate seta on distal end between exopod and endopod; endopod 4-segmented with 3, 2, 2, 4+1 papposerrate setae; exopod unsegmented with 6 long plumose setae on distal margin; epipod bilobed.

Table 2.1. Information on number (N), total length (TL), TL zoea of Brachyura (RDL), carapace length (CL), carapace maximum width (CW), densities, date, geographical location, time of day, captured depth stratum and bottom depth for captured larvae of *Aristeus antennatus*, *Parapenaeus longirostris*, *Scyllarides latus* and *Maja squinado*. Development stages: PII, second protozoea stage; ZI, first zoeal stage; ZII, second zoeal stage; MII, second mysid stage.

Speciesand stage	N	LT (mm)	CL,CW (mm)	Density (N/1000m^3)	Date	Latitude (N)	Longitude (E)	Time (GMT)	Captured strata (m)	Bottom depth (m)
A. antennatus MII	1	4.06 LT	1.65 CL	9.3	24/07/2010	39°51.00’	2°14.40’	10:30	0-25	979
A. antennatus PII	1	1.59 LT	0.73 CL	4.4	26/07/2010	39°40.98’	2°12.30’	8:33	0-25	222
	1	1.63 LT	0.83 CL	3.9	15/07/2010	39°00.96’	2°24.72’	12:30	25-50	900
P. longirostris PII	1	2.35 LT	0.90 CL	17.8	17/07/2010	39°01.92’	2°41.70’	13:29	25-50	248
	1	2.86 LT	1.32 CL	11.1	02/12/2009	39°05.52’	2°42.42’	13:30	30-60	234
S. latus ZI	1	1.95 LT	1.15CL 1.06CW	7.1	24/07/2010	39°49.08’	2°09.06’	0:10	0-25	974
M. squinado ZII	1	0.36RDL	1.32CL 1.12CW	9.3	24/07/2010	39°51.00’	2°14.40’	10:30	0-25	979

Second maxilliped (Fig. 2.3B): coxa without setae; basis with 1+2+1+1 papposerrate setae; endopod 5-segmented with 3+1, 2+1, 0, 2+1, 2+2 papposerrate setae and 1 additional simple seta on distal segment; exopod unsegmented, with 5 long plumose setae on distal end.

Third maxilliped (Fig. 2.3C): coxa without setae; basis with 2 papposerrate and 1 simple seta; endopod 5-segmented, with 2, 1, 1+1, 2+1, 4 papposerrate and 1 simple setae; exopod 3-segmented, with 2, 2, 2 plumose setae distally.

First pereiopod (Fig. 2.3D): coxa without setae; basis with 2 papposerrate setae; endopod 4-segmented, first segment with 1 simple seta and 1, 2 papposerrate setae on last two segments; exopod 2-segmented, with 2+2, 2 long plumose setae.

Second pereiopod (Fig. 2.3E): coxal endite without setae; basis with 1 simple seta; endopod 3-segmented, with 0, 1, 1+2 papposerrate setae; exopod 2-segmented, with 2+2, 2 long plumose setae distally.

Third pereiopod (Fig. 2.3F): coxa and basis without setae; endopod 2-segmented, with 1 simple seta on first segment and 1+2 papposerrate setae on terminal segment; exopod damaged.

Fourth pereiopod (Fig. 2.3G): coxal endite with 2 small simple setae on posterior margin; basis unarmed; endopod unsegmented, with 1+2 papposerrate setae; exopod unsegmented, with 2+2+2 long plumose setae distally.

Fifth pereiopod (Fig. 2.3H): coxa and basis partially segmented and without setae; endopod unsegmented, with 1 simple seta terminally; exopod unsegmented, with 2+2 long plumose setae.

Pleon (Figs, 2.2A, 2.2C): first to fifth pleomere unarmed; sixth pleomere with one pair of lateral spines and 1 small ventral spine.

Pleopods (Fig. 2.2C): developed as small uniramous buds.

Uropods (Fig. 2.2I): protopod with a strong median carina ending as a very strong curved spine; endopod with 19 plumose setae along margin; exopod longer than endopod with 22 and 23 plumose setae along inner and posterior margins and without outer spine.

Telson (Fig. 2.2I): long, slender and biramous posteriorly, each branch with 4 spines on the inner side, two small ones on the outer side and 1 strong spine terminally; a pair of small lateral spines in the on the posterior margin of telson.

2.4.3 Morphological description of zoea I of *Scyllarides latus* (Fig. 2.4)

Size: 2.0 mm TL and 1.1 mm CL.

Pereion (Fig. 2.4A): extremely flattened dorso-ventrally; cephalic shield pear shaped, about as long as wide. Eyes (Fig. 2.4B) stalked, longer than wide, slightly longer than antennules, peduncle cone shaped.

Antennule (Fig. 2.4C): unsegmented and uniramous, with 3 aesthetascs, 2 simple setae and 1 small spine at distal margin, and small denticle located at two thirds of its length on inner margin.

Antenna (Fig. 2.4C): unsegmented and biramous; endopod 2-segmented, with 4 terminal setae; exopod unsegmented, with 2 terminals spine-like setae.

Labrum (Fig. 2.4D_1): superior portion simple, inferior portion bifid.

Mandibles: symmetrical (Fig. 2.4D_3).

Maxillule (Fig. 2.4D_4): biramous and unsegmented; coxal endite with 1 strong cuspidate and 2 shorter setae; basial endite with 2 strong terminal cuspidate and 2 simple spine setae sub-terminally.

Maxilla (Fig. 2.4D_5): Uniramous, 2-segmented, longer proximal segment with 1+2 simple setae, shorter distal segmented with 4 plumose setae.

First maxilliped: absent.

Second maxilliped (Fig. 2.4F): uniramous, 5-segmented, with 1 (simple), 1 (simple), 1 (simple), 5 (2 serrate and 3 papposerrate), 4 (simple) + 1 (stout and simple) setae.

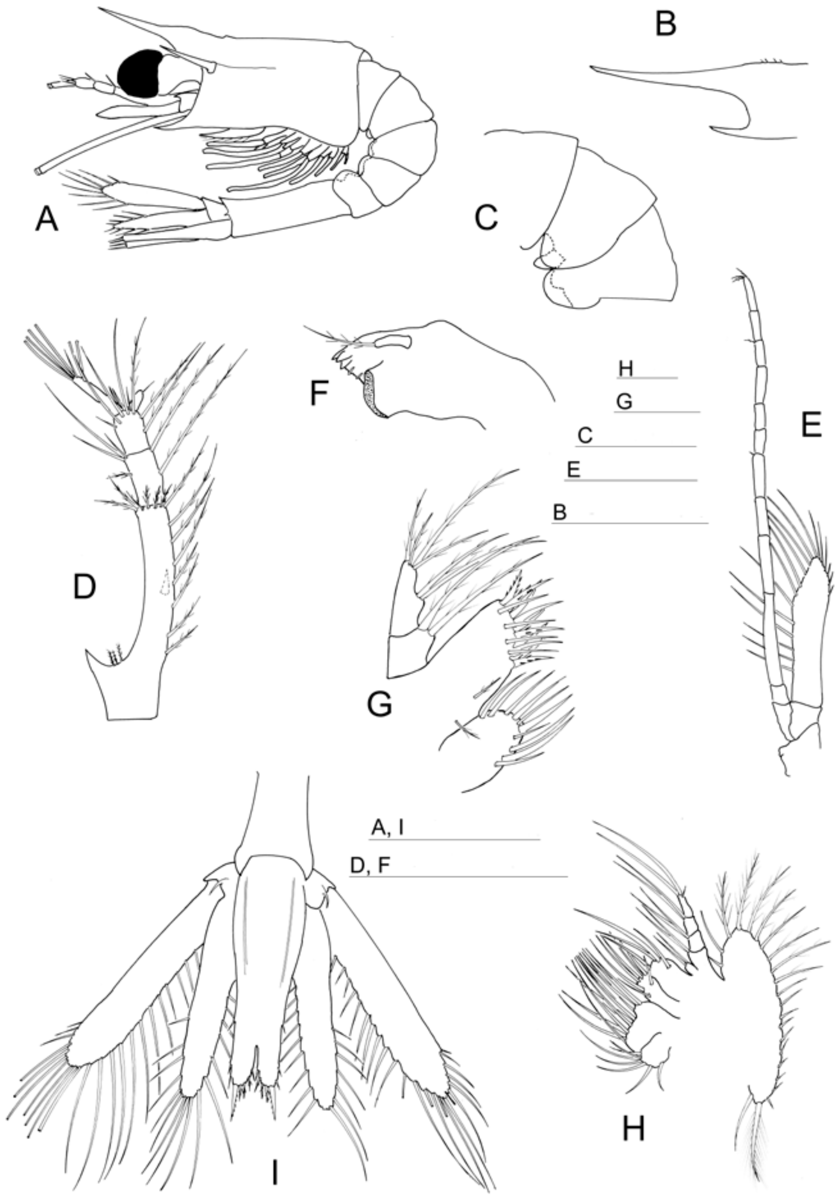


Figure 2.2. Mysis II of the red shrimp *Aristeus antennatus* (Risso, 1816). (A) Lateral view; (B) rostrum; (C) detail of pleon and pleopods of somites 1-3; (D) antennule; (E) antenna; (F) right mandible; (G) maxillule; (H) maxilla; (I) uropods and telson. Scale bar: 1 mm.

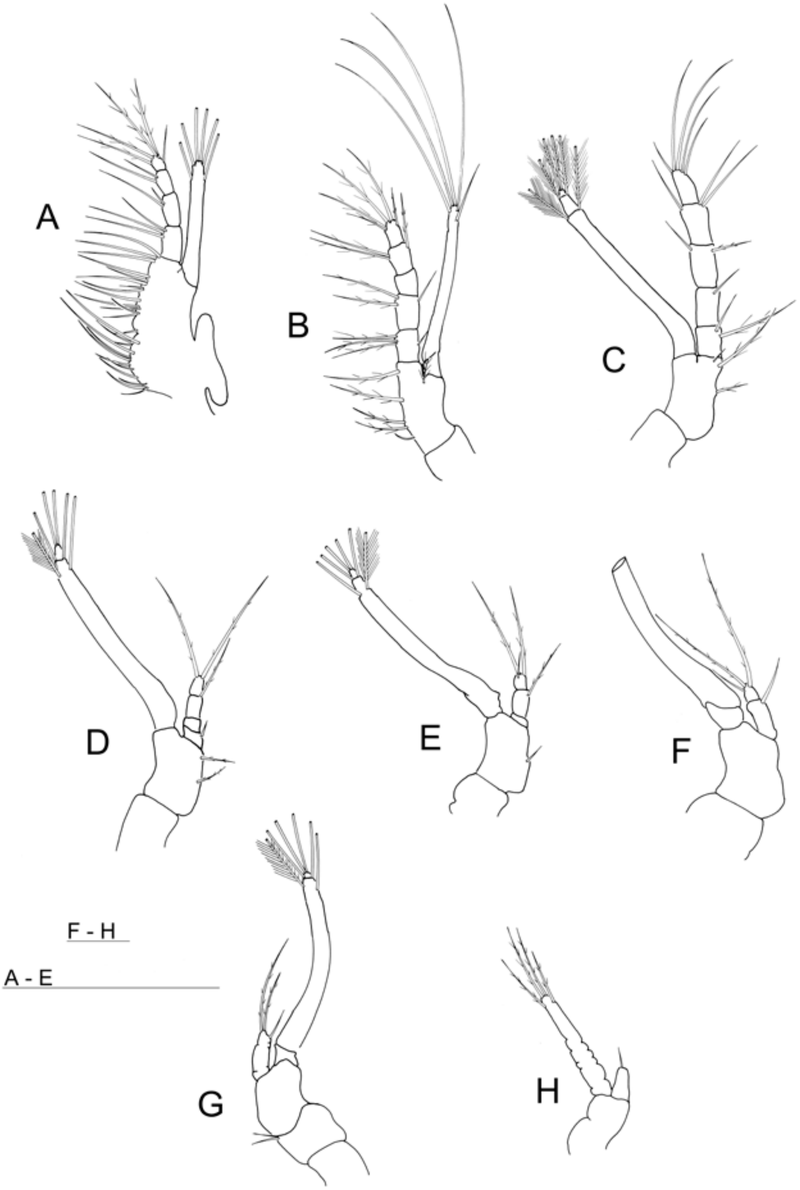


Figure 2.3. Appendages of Mysis II of red shrimp *Aristeus antennatus* (Risso, 1816). (A) first maxilliped; (B) second maxilliped; (C) third maxilliped; (D) first pereiopod; (E) second pereiopod; (F) third pereiopod; (G) fourth pereiopod; (H) fifth pereiopod. Scale bars: 1 mm.

Third maxilliped (Fig. 2.4A, 2.4E): uniramous, 5-segmented; first segment with 2 short simple setae; second segment with 1 simple seta located mid-length; third segment with 2 simple seta at distal margin; fourth segment has 2 stout serrated spines sub-terminally and 2 on distal margin and 4 short papposerrate setae; fifth segment with 3 papposerrate and 1 simple seta.

First pereiopod (Fig. 2.4A): biramous; coxa with 1 distinct coxal spine, basis unarmed; endopod 4-segmented, first segment with 1 small spine at mid-length and 1+1 spines terminally, second segment with 1+1 serrate setae on distal margin, third segment, the longest, with inner margin serrated and several plumodenticulate and serrate setae placed as shown; distal segment with 4 simple setae, 1 small spine and 1 stout simple setae terminally; exopod 6-segmented with 0, 2, 2, 2, 2 and 2 long plumose setae, respectively.

Second pereiopod (Fig. 2.4A): biramous; with 1 coxal spine and basis unarmed; endopod 4-segmented and serrated on inner margin, first segment with 1 spine at mid-length and 2+1 serrate spines terminally, second segment with 2+1 serrate setae on distal margin, third segment, the longest, several plumodenticulate and serrate setae placed as shown; distal segment with 4 simple setae and 1 stout seta terminally; exopod 6-segmented with 0, 2, 2, 2, 2 and 2 long plumose setae.

Third pereiopod (Fig. 2.4A, 2.4A$_1$): about 1.3 times the length of first and second pereiopods; coxa and basis unarmed; endopod 4-segmented, first segment with 1 simple seta proximally, 3 small setae along the margin and 2+1 serrate spines terminally, second segment with 2+1 serrate setae on distal margin, third segment, the longest, with several plumodenticulate and serrate setae placed as shown; short distal segment with 3 simple setae and 1 stout seta terminally; exopod present as a small bud.

Fourth and fifth pereiopods: absent.

Pleon (Fig. 2.4A, 2.4G): unsegmented, longer than wide, slightly rounded posteriorly.

Pleopods: absent.

Uropods: absent.

Telson (Fig. 2.4G): bilobed, not completely separated from the pleon from the ventral side, with 3 setae on each side, 2 setose and 1 simple.

2.5 Discussion

The nekto-benthic behaviour and deep water dwelling of the adults of some decapod crustaceans often makes obtaining and rearing such species in laboratory conditions very difficult. This fact is one of the reasons for our scant knowledge on the morphology and duration of larval phases of these species. This is especially problematic in Penaeoidea, which release their fertilized eggs freely into the water column, hatching as nauplius larvae. In other decapods, the eggs remain attached to the female pleopods for incubation and the larvae hatch in a more advanced zoeal developmental stage. Therefore, any information about larval morphologies of these species obtained from plankton sampling in the wild is valuable, even though it is based on few specimens and hence the variability in the development of some characters among individuals cannot be fully recorded. The way in which we identified the larvae of the considered species and the importance of our findings for improving knowledge on their larval development and ecology are discussed below.

2.5.1 Second mysis of *Aristeus antennatus*

Laboratory rearing of Penaeideans is not easy and for a number of them the description of several larval stages is still lacking. Therefore, descriptions from plankton samples are still required, since they are necessary to carry out quantitative studies of larval abundance and distribution, and to obtain a broad knowledge of the larval ecology of these species for sustainable management under an ecosystem approach. In this regard, Heldt (1955) described some larval stages of *A. antennatus* from plankton samples taken in the Balearic Sea in the summer of 1954 by means of horizontal hauls at the surface. Using some larvae captured alive, this author undertook some rearing experiments, allowing her to follow and document the progression from second protozoea to the first mysis stage, and thus establish a developmental sequence that she attributed to this species.

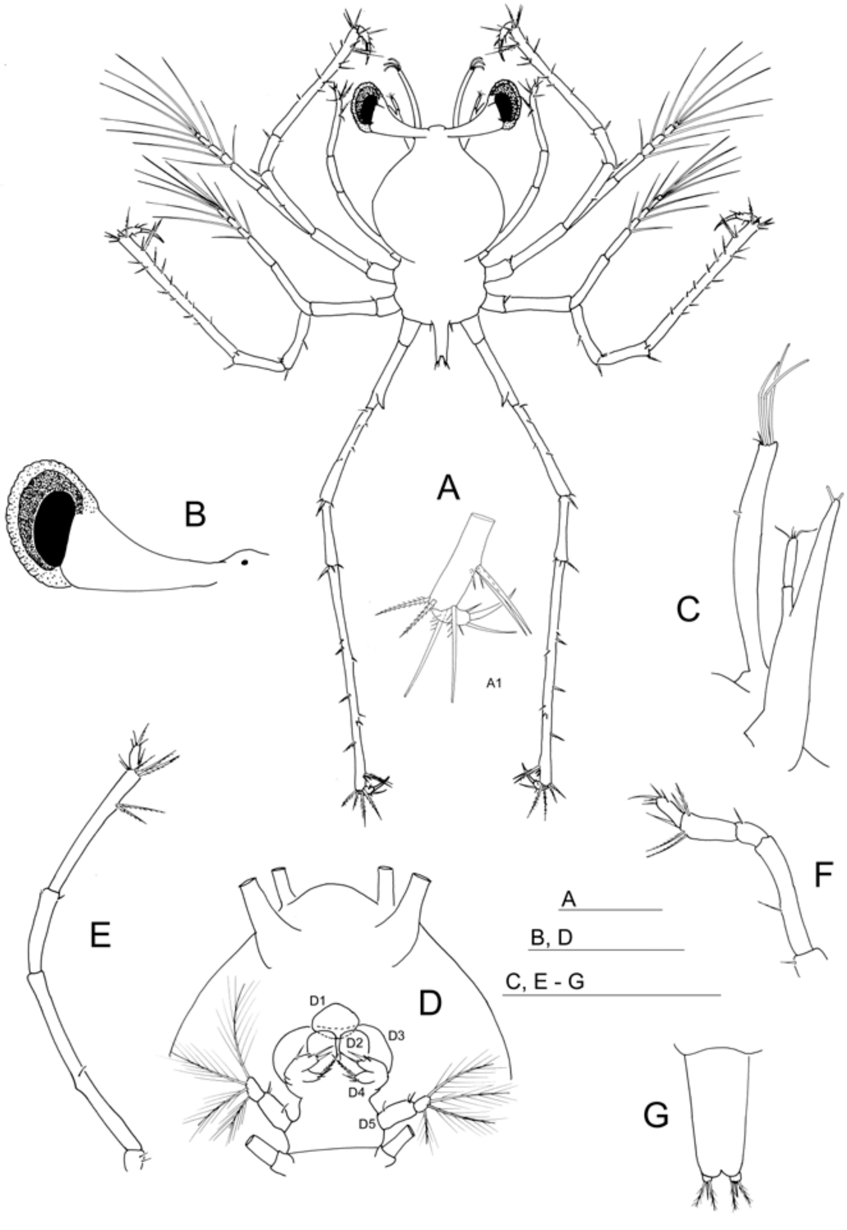


Figure 2.4. Zoea I (phyllosoma) of Mediterranean slipper lobster *Scyllarides latus* (Latreille, 1803).(A) dorsal view; (A_1) detail of the dactyl of the third pereiopod; (B) right eye; (C) antennule and antenna; (D) masticatory apparatus; (D_1); dorsal view of labrum; (D_2) paragnaths; (D_3) mandible; (D_4) maxillule; (D_5) maxilla; (E) third maxilliped; (F) second maxilliped; (G) pleon and telson. Scale bar: 1 mm.

Heldt (1955) also described for the first time the larval stages of *Aristaeomorpha foliacea*. Since both descriptions were made from wild plankton samples, and therefore the larvae were of unknown parentage, she deduced their identity as follows: 1) the known Penaeoidea species for the western Mediterranean at the time were *Gennadas elegans, Aristaeomorpha foliacea, Aristeus antennatus, Solenocera membranacea, Funchalia woodwardi, P. longirostris, Melicertus kerathurus and Sicyonia carinata*; 2) *P. longirostris, M. kerathurus* and *S. carinata* could be eliminated as candidates as she obtained the juvenile form from larvae cultured in laboratory; 3) she established the identity of larvae of *S. membranacea* and *G. elegans* by laboratory studies using live Protozoea I and Protozoea II, respectively; 4) for *F. woodwardi* the decapodid and several mysis stages were already described from plankton samples; 5) by exclusion she attributed the two Penaeoidea larval series obtained to the remaining two species with unknown larvae, *Aristaeomorpha foliacea, Aristeus antennatus*; and 6) further evidence was that the larval series were found within the main fishery areas and during the reproductive period known for the latter two species.

Finally, the assignment of these two larval series to each of the two remaining species was based on size evidence and pigmentation. Noting size differences in larvae, Heldt attributed the series with bigger larvae to *A. foliacea*, since the adults of this species are bigger than those of *A. antennatus.* However, aware that small larvae do not always correspond to small adults, e.g. *S. membranacea* has big larvae and small adults, she also considered pigmentation. Adults of *A. foliacea* are readily distinguishable from any other species by their strong red colour and she was able to observe that specimens of one of the larval series, the one with bigger larvae, possessed the strong red pigment that was distinctive from the metanauplius stage onward. Therefore, the larval series with smaller larvae and light red pigmentation was attributed to *A. antennatus*.

We based our identification of the second mysis stage on the morphological features distinguishing the first mysis of *A. antennatus* and *A. foliacea*: according to Heldt (1955), the first mysis stage of *A. antennatus* can be distinguished from the same stage of *A. foliacea* by the presence of long pterigostomian spines in the former species and the presence of dorsal spines and postrostral carina on the carapace in the latter species. In addition, the antennal endopod is longer than the exopod in *A. foliacea*. Finally, the telson in *A. antennatus* is composed of two cylindrical rami, as in typical Penaeoidea larvae, but in *A. foliacea* the median cleft on the telson is not so clearly distinguished (see plates XVI and VIII Fig. a, respectively, in Heldt 1955).

The second mysis stage described in the present study possesses strong pterigostomian spines and the rostrum does not have dorsal spines or a carina, and we can still recognize the two cylindrical rami on the posterior end of the telson. This therefore places it in the larval sequence of *A. antennatus* described by Heldt (1955). The main reasons for assigning the larva described here to the second mysis stage are: (i) the specimen possesses pleopod buds, absent from the previous stage; (ii) the 4th pereiopod, which was rudimentary in mysis I, is now functional; (iii) the 5th pereiopod has an endopod and exopod, the latter with setae, which in the previous stage is just a simple bud; and (iv) the endopod of the antenna is two times longer than the scaphocerite, which in the previous stage was about the same length.

2.5.2 First zoea of *Scyllarides latus*

The species-specific identity of scyllarid larvae has been confirmed only for a few species in the world (Webber and Booth 2001; Holthuis 2002), which makes systematic comparative studies almost impractical. Santucci (1925) described the first stage of *S. latus* from Mediterranean samples taken in the wild, confirming identification after comparison with individuals obtained from rearing experiments (Santucci, 1928). This author stated that both groups of specimens corresponded to the first developmental stage of *S. latus*. Santucci (1928) also compared these *S. latus* larvae with older larvae described previously by Stephensen (1923) as *S. latus*. He concluded that the larvae described by Stephensen (1923) were in fact the fourth zoeal stage of *Scyllarus arctus*.

Considering that the larva described here possesses all the characteristics described by Santucci (1928), we assigned it to the first larval stage of *S. latus*. The present description adds more detailed morphological information, not mentioned previously by Santucci (1925, 1928). The new information refers to the number and type of setae on the antennules, maxillule, maxilla, maxillipeds and telson, and we also give more details on the ornamentation of the three pereiopods (see Table 2.2 for details). We also give more details on the morphology of the pleon and telson. This should not only improve the identification of this species but also be useful in comparisons with other species of the genus and family.

2.5.3 Occurrence and abundance of larval stages

Although occurrences of the target species were rare among all the collected material, our findings of *A. antennatus* larvae are in agreement with previous reports in the Balearic Islands (Heldt 1955; Carbonell et al. 2010) and with the known spawning season of this species for the area, from May to September, with a maximum in June-August (Carbonell 2005, Guijarro et al. 2008). The occurrence of *A. antennatus* larvae in near-surface layers of the water column is also in accordance with previous records and with the reproductive model proposed for this species, in which newly hatched larvae perform an ontogenetic migration through the water column to euphotic waters (Carbonell et al. 2010). The finding of the second mysis stage at surface layers agrees with the hypothesis of Sardà et al. (2004), in which all larval stages develop in these more productive waters until the decapodid stage, which moves to deeper waters to reach the benthic habitat of adults. Of the three captured larvae, two were caught off northwestern Mallorca, an area where the highest concentrations of mature females were detected in summer (Guijarro et al. 2008). However, the distribution of *A. antennatus* larvae in the study area depends not only on the location of spawners but also on circulation of water masses and topographic features around the Balearic Archipelago (Carbonell et al. 2010).

The two larvae of *P. longirostris* reported in the present study were captured in surface waters over the shelf break, corresponding to the upper limit of distribution of the adults. This larval presence in shallower areas than those where the highest abundance of adults has been found, i.e. at circa 350 m depth (Guijarro et al. 2009), supports the probability of displacement of adults during the spawning period to lower depths (Dos Santos 1998). These larvae were found during two different periods (July and December), which coincide with the spawning period of the species in the area. Although maturing females have been found all year round, two peaks have been detected in June-August and November (Guijarro et al. 2009).

Table 2.2. List of differences between the present study and Santucci (1925, 1928) for first larval stage of *Scyllarides latus*.

	Number and type of setae on:					Ornamentation
	Antennule	Maxillule	Maxilla	Maxillipeds	Telson	Pereiopods
Santucci (1925, 1928)	4 setae	No description	Eccentric and elongated, with 4 distal setae	No description	2 long spines	No description
Present work	3 aesthetascs, 2 simple setae and 1 small spine at distal margin.	coxal endite: 1 cuspidate and 2 short setae; basial endite: 2 cuspidate terminal and 2 simple sub-terminally spines.	2-segmented: proximal segment with 1+2 simple setae; distal segmented with 4 plumose setae.	1st maxilliped: absent. 2nd maxilliped uniramous, 5-segmented with 1, 1, 1, 5, 4 + 1 setae. 3rd maxilliped: uniramous, 5-segmented with 2, 1, 1, 2+2+4, 3+ 1 setae.	with 3 setae on each side, 2 plumose and 1 simple.	First pereiopod: biramous, coxa with 1 spine, basis unarmed, endopod 4-segmented: 1+1+1, 1+1, 0, 4+1+1 setae, exopod 6-segmented with 0,2,2,2,2,2 long setae. Second pereiopod: biramous, coxa with 1 spine, basis unarmed, endopod 4-segmented: 1+2+1, 2+1, 0, 4+1 setae, exopod 6-segmented with 0,2,2,2,2,2 setae. Third pereiopod: about 1.3 the length of 1st and 2nd pereiopod, biramous, coxa and basis unarmed, endopod 4-segmented: 1+3+ 2+1, 2+1, 0, 3+1 setae, exopod as a small bud.

Although the duration of larval stages of species of *Scyllarides* cannot be accurately estimated, complete larval development should require several months, perhaps nine to eleven (Robertson 1969, Martins 1985). In the Gulf of Mexico, phyllosoma larvae of *Scyllarides nodifer* have been shown to have the ability to remain in the area for 8-9 months, with a circulation system that supports local recruitment (Lyons 1970). Taking into account the early stage of the larva of *S. latus* found in surface waters in July, one month after the maximum peak of the spawning of this species in the Balearic Islands (Reñones et al*.* 2010), and the current velocities around the archipelago (Pinot et al*.* 2002), it is highly likely that this larva originated from an adult population dwelling in the same area.

Stevcic (1967) reported three broods for *Maja squinado* per year in the Adriatic Sea, between March and August. Similarly, laboratory experiments have shown that this species spawns between March and July (Durán et al. 2011) and that, at a water temperature of 18ºC, it takes 4-5 days post-hatch to reach the zoea II stage, 9-10 days to reach the megalopa stage and 16-17 days after hatching to reach the first crab instar (Durán et al. 2012). The last zoeal stage reported in our study was captured in surface waters in July 2010. The presence of larvae in the area, in addition to some sporadic catches of adult specimens reported since 2009, could be an indication of the success of the restocking program of this species, carried out at Mallorca Island, where juveniles hatched and reared in captivity have been released in the sea since 2008.

In summary, our study is an important contribution to knowledge on the distribution and abundance of rare larval stages of benthic invertebrates and provides new information about larvae of species of interest for fishing and conservation. We describe in detail, for the first time, the second mysis stage of *Aristeus antennatus* and the first larval stage of *Scyllarides latus*, poorly known since its first report dates back almost one century. We also report the occurrence of the larval stages of *A. antennatus*, *Parapenaeus longirostris. S. latus* and *Maja squinado* in the plankton of the western Mediterranean, which represent the sixth, the third, the fourth and the second worldwide finding of these species, respectively. In the case of *P. longirostris* and *S. latus* it represents the first captures from the field of larval stages for these species in the Mediterranean.

Although the scarcity of data indicates the need for further studies to obtain a global understanding of the larval development of these decapod crustaceans, these new descriptions will facilitate the identification of larval stages of species of interest for a wider community of researchers and hence the generation of new information about the larval ecology and the recruitment, which will be useful for improving the management of these species.

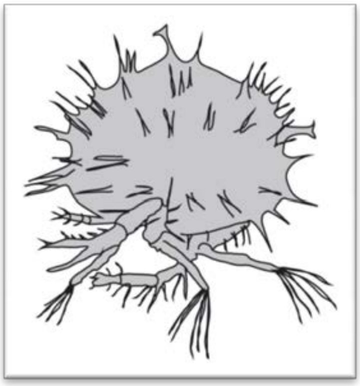
Chapter 3

Morphology and classification of deep-sea larvae

Torres AP, Palero F, Dos Santos A, Abelló P, Blanco E, Bone A and Guerao G- 2014. Larval stages of the deep-sea lobster Polycheles typhlops (Decapoda, Polychelida) identified by DNA analysis: morphology, systematic, distribution and ecology. Helgoland Marine Research, 68, pp. 379 -397.

3.1 Abstract

A total of 25 specimens of *Eryoneicus* larvae were collected near the Balearic Archipelago (western Western Mediterranean Sea) in 2009 and 2010. Detailed morphological examination indicated that the smallest individual corresponded with the first zoea (ZI) stage of *Polycheles typhlops* hatched from a berried female by Guerao and Abelló (J Nat Hist 30(8):1179–1184, 1996). Only two species of deep-sea polychelid lobster, namely *P. typhlops* and *Stereomastis sculpta*, are known to occur in the Mediterranean. Genetic distance comparisons and phylogenetic analysis of the mitochondrial 16S rDNA and Cox I genes of this early larva together with adults from several *Polycheles* and *Stereomastis* species allowed us to assign it to *P. typhlops*. This is the first wild-caught larval stage of a polychelid lobster being identified using molecular techniques. The remaining specimens were attributed to zoeal stages II - III and decapodid stage based on morphological comparison. The arrangement of spines along the anterior part of the mid dorsal line (R, 1, 1, 1, 2, C1), characteristic of the former species *E. puritanii*, discriminates these larvae from other *Eryoneicus* found in the Mediterranean. The clear presence of epipods on the third maxilliped and pereiopods of the decapodid stage gives further support to the identification of *E. puritanii* as the larval stages of *P. typhlops*. Additionally, information on the ecology of these larvae, their abundances during different seasons, as well as their bathymetric distribution is reported.



3.2 Introduction

Mediterranean deep-sea benthos is dominated by fishes and decapod crustaceans, but the biology of several key groups is still largely unknown (Cartes and Abelló 1992). Polychelid lobsters are often referred to as ”deep-sea blind lobsters” because all extant forms live in deep water and have reduced eyes. These lobsters can be easily distinguished from other reptantia decapods by the presence of well-developed chelae on pereiopods 1-4 (Galil 2000, Ahyong 2009). The Polychelidae now includes over 40 extant and fossil species, but the systematics of the family is still under debate, especially at the genus level (Ahyong and Brown 2002, Ahyong and Chan 2004, Ahyong and Galil 2006). Despite several taxonomic uncertainties have been clarified within this family in recent years (Ahyong 2009, Chan 2010), studies concerning the biology of polychelids are still lacking. There is some information available on the trophic role of these lobsters (Cartes 1993, 1998, Maynou and Cartes 1998, Cartes et al. 2007, Gastoni et al. 2010), but sampling difficulties have prevented scientists from understanding the ecology of polychelids in detail. Knowledge of the reproductive biology of deep-sea species is also scarce and mostly confined to a few species from deep continental slopes and hydrothermal vent habitats (Wenner 1979, Abelló and Cartes 1992, Mullineaux et al. 1995, Maiorano et al. 1998, Company and Sardà 1998, Company et al. 2003, Follesa et al. 2007, Cabiddu et al. 2008). Similarly, the links that have been established to date between deep-sea benthic adults and pelagic larval forms are uncertain.

Only two species of polychelid lobsters, namely *Polycheles typhlops* (Heller 1862) and *Stereomastis sculpta* (Smith 1880), are known to occur in deep-sea muddy sand bottoms of the Mediterranean Sea (Zariquiey-Alvarez 1968). Previous studies carried out in NW Mediterranean have reported *P. typhlops* at depths between 300 and 2,000 m and *S. sculpta* between 1,196 and 2,261 m (Abelló and Cartes 1992, Cartes et al. 1993, Company and Sardà 2000, Company et al. 2003, 2004, Follesa et al. 2007). Females of both species can be found in shallower depths than males, suggesting a relationship with reproductive behaviour (Abelló and Cartes 1992). In both *P. typhlops* and *S. sculpta*, females attain larger sizes than males, with the largest females being more likely to be found gravid than smaller females. Ovigerous females of *P. typhlops* have been captured throughout the year in the Western

Mediterranean (Abelló and Valladares 1988, Maiorano et al. 1998, Company et al. 2003, Follesa et al. 2007). Gravid females of *Stereomastis nana* from the western North Atlantic were also caught throughout the year and presented a size-distribution pattern similar to local populations of *P. typhlops* (Wenner 1979). Spawning-related movements to locate the optimal depth range for hatching may explain the large proportion of ovigerous females at the shallowest depths of the species distribution, as found in other bathyal species (Wigley et al. 1975, Somerton 1981, Abelló and Macpherson 1991). Knowledge on larval morphology, vertical distribution and ecology of many decapod species is still scarce in the Western Mediterranean (Torres et al. 2013, 2014) and particularly for deep-sea species. This is largely due to the relative scarcity of plankton samples covering the entire water column and the lack of expertise for their correct identification. Moreover, the capture of living deep-sea lobsters and their larval-rearing under laboratory conditions presents serious difficulties.

Several planktonic specimens collected from Mediterranean or nearby Atlantic waters, and originally described under the generic name *Eryoneicus*, have been claimed to correspond to the larval stages of Polychelidae (Bernard 1953, Fredj and Laubier 1985). The first description for the genus *Eryoneicus,* a specimen “half an inch” long captured around 3,000 m depth in the Canary Islands, was reported as *Eryoneicus caecus* by Bate (1888) and later as *Eryoneicus faxoni* by Bouvier (1905). Several smaller specimens, ranging from 5 to 10 mm in total length, were caught in the Gulf of Napoli and described as *Eryoneicus puritanii* by Lo Bianco (1903). Another specimen captured around 3,000 m depth in Azores waters was named *Eryoneicus spinoculatus* by Bouvier (1905, 1917) and then Selbie (1914) described three new species, namely *E. hibernicus*, *E. scharffi* and *E. kempi*, based on late-stage larvae collected from north Atlantic waters. According to Fredj and Laubier (1985), out of the four different *Eryoneicus* species that can be found in deep Mediterranean Sea waters, one type (*E. puritanii*) could be assigned to *P. typhlops*, whereas the other three (*E. faxoni, E. kempi* and *E. spinoculatus*) could not be accepted as larval stages of *S. sculpta* and perhaps belong to adult species that still have to be discovered (Fredj and Laubier 1985). All of these late-stage *Eryoneicus* show a very inflated carapace with numerous spines and functional natatory pleopods (Bernard 1953).

Despite the *Eryoneicus* name was suppressed by the International Commission on Zoological Nomenclature (1965) (see also Holthuis 1962), the different larvae are still named referring to the old nomenclature given that no study has conclusively proved the assignment of any *Eryoneicus* to the corresponding adult species. Indeed, no information on polychelid larvae hatching in captivity was available until Guerao and Abelló (1996) described a first larval stage of *P. typhlops*. The larvae hatched by Guerao and Abelló (1996) had not yet extruded or only partially extruded the natatory setae of the cephalothoracic appendages, so the description may not reflect the actual morphology of the larvae when hatching under natural conditions. The smallest *Eryoneicus* sampled from the wild so far, with a carapace length (CL) of 2 mm, was attributed to the third larval stage of *E. connus* by Bernard (1953). Selbie (1914) also caught a "juvenile" stage of *Eryonicus* sp. which corresponds to an advanced zoeal stage (TL = 7 mm; Plate IV) with undeveloped pleopods. Later stages of *Eryoneicus* larvae have well-developed pleopods and fit the definition of megalopa in this respect (Williamson 1969). The concepts "post-larva", "decapodid" and "megalopa" have been interchangeably used in many decapod larval descriptions to refer to the transition phase between pelagic larvae and benthic phases (Gurney 1942, Kaestner 1970; Felder et al. 1985, Anger 2001). In the present study, the general name "decapodid" is used to denote the final larval phase preceding the moult to the first juvenile stage, and characterized by the existence of functional pleopods and uropods with long plumose natatory setae (Kaestner 1970).

The aim of this study is to provide new evidence on the occurrence, distribution and morphology of larval stages of *P. typhlops.* Complete morphological descriptions are provided for three zoeal and one decapodid stages, while identification of the first larval stage of *P. typhlops* is confirmed through DNA analyses. In addition, a comparison of our plankton-collected specimens with previous descriptions of the larval stages of other Polychelidae is included. Finally, information on the ecology of these larvae, their abundances during different seasons, as well as their bathymetric distribution in the aphotic layers of the water column is reported.

3.3 Materials and methods

3.3.1 Sampling

Two multidisciplinary research surveys were conducted off the Balearic Islands (western Mediterranean) during late autumn (29 November to 18 December 2009) and summer (11-30 July 2010). The main objective of the surveys was to determine the taxonomic composition, abundance, structure and vertical distribution of the mero-planktonic community at two stations located off the northwest and south of Mallorca (Balearic and Algerian sub-basin, respectively). The sampling sites were located over 200 and 900 m depth (shelf break and middle slope, respectively) and present different environmental conditions (Pinot et al. 2002, López-Jurado et al. 2008). At the southern station off Mallorca the upper slope is irregular, with numerous small canyons, while it is smooth in the northern station (Acosta et al. 2002). Two additional polychelid zoeal stages were captured between 300 and 400 m depth over the slope of Blanes canyon (NW Mediterranean) during 2004 under the “Observation, analysis and modelling of the Mediterranenan Sea” (OAMMS-04) survey, and were also used for photographic record.

A total of 218 depth-stratified meso-zooplankton samples, which were integrated in 34 hauls, were used to analyse decapod larvae composition. From these, 18 samples were collected using a multi-net (HYDRO-BIOS) in 2009 and 16 samples using a multiple opening-closing net and environmental sensing system (MOCNESS) in 2010 (Olivar et al. 2012). In order to determine the vertical distribution of decapod larvae, a series of oblique hauls were performed at four stations for 36 h at each site during the surveys in 2009 and 2010. Each oblique haul was performed down to 200 m depth on the shelf break and 500 m (in summer) or 850 m (in late autumn) on the middle slope, and seven or five depth strata were sampled depending on the season (summer and late autumn, respectively). The thickness of these strata changed with bathymetry and season (sampling protocols as in Torres et al. 2014). Supra-benthos samples were collected with a rectangular net rigged in a beam-trawl and used to catch mega-benthic fauna within 0.6 m above the bottom, with a cod-end mesh size of 500 µm in late autumn and 1,000 µm during summer. The catch speed was three knots and the effective tow duration was 30 min. Supra-benthic samples were preserved in ethanol 96% immediately after collection (sampling protocols as in Herrera et al. 2014). Once in the laboratory, decapod crustacean larvae were sorted and identified to species level and developmental stage whenever possible, using available descriptions and keys (Dos Santos and González-Gordillo 2004). Information on the stations where polychelid larvae were found is presented in Table 3.1. The zoeal stages and decapodid have been deposited at the Biological Collections of Reference of the Institut de Ciències del Mar (CSIC) in Barcelona under accession numbers ICMD000049-56.

In order to obtain reference DNA sequences for larval identification, several adult specimens for both *P. typhlops* and *S. sculpta* were sampled from Mediterranean deep sea waters. *P. typhlops* was sampled from the region under the MEDITS2011 research cruise and *S. sculpta* was sampled in July 2010 from the Catalano-Balearic basin, between Barcelona and Mallorca. DNA sequences for specimens from Atlantic waters were obtained from GenBank (Table 3.2).

3.3.2 DNA analyses

Total genomic DNA extraction from the first zoea specimen captured during supra-benthos sampling south of the Balearic Sea (Station: 39.067N – 2.675E; Table 3.1) and the adult specimens from Mediterranean waters was performed using the Chelex-resin method (Palero et al. 2010). The standard universal primers for DNA barcoding (Folmer et al. 1994) were used for PCR amplification; given that they had been previously tested in *Polycheles* with positive results (see Palero et al. 2009). Amplifications were carried out with ~30 ng of genomic DNA in a reaction containing 1 U of Taq polymerase (Amersham), 1× buffer (Amersham), 0.2 mM of each primer and 0.12 mM dNTPs. The PCR thermal profile used was 94ºC for 4 min for initial denaturation, followed by 30 cycles of 94ºC for 30 s, 50ºC for 30 s, 72ºC for 30 s and a final extension at 72ºC for 4 min. Amplified PCR products were purified with QIAGEN-QIAquick PCR Purification Kit (QIAGEN Inc) prior to direct sequencing of the product. The sequences were obtained using the Big-Dye Ready-Reaction kit v3.1 (Applied Biosystems) on an ABI Prism 3770 automated sequencer from the Scientific and Technical Services of the Center for Public Health Research (Valencia, Spain).

Table 3.1. Information on the stage of development, number (N), densities, date of capture, geographical location, time of day, capture depth and bottom depth for larvae of *Polycheles typhlops* during late autumn (2009) and summer (2010) surveys.

Season (net)	Stage of developement	*N*	Densities (*N*/1,000m^3)	Date	Latitude (N)	Longitude (E)	Time GMT	Capture Depth (m)	Bottom depth (m)
Late autumn (HYDRO-BIOS)	zoea I	1	1.2	04/12/2009	39.003	2.419	23:54	350-600	907
	zoea I	1	0.8	04/12/2009	39.003	2.419	23:54	200-350	907
Summer (Beam-trawl)	zoea I	1	2.5	19/07/2010	39.067	2.675	17:40	358	359
Summer (MOCNESS)	zoea I	5	6.1	15/07/2010	38.904	2.496	2:01	400-500	668
	zoea I	1	1.1	15/07/2010	39.060	2.461	16:42	400-500	853
	zoea I	6	2.8	15/07/2010	39.053	2.453	16:56	200-400	858
	zoea I	1	0.5	23/07/2010	39.813	2.151	4:16	200-400	957
	zoea I	3	2.1	24/07/2010	39.804	2.136	23:45	200-400	966
	zoea II	1	0.5	14/07/2010	38.974	2.457	7:11	200-400	893
	zoea II	2	0.9	15/07/2010	39.053	2.453	16:56	200-400	858
	zoea II	1	0.5	23/07/2010	39.813	2.151	4:16	200-400	957
	zoea III	1	0.4	15/07/2010	38.959	2.435	21:02	200-400	905
	decapodid	1	0.6	24/07/2010	39.804	2.137	5:54	600-800	964

Table 3.2 Samples included for phylogenetic analyses in the present study.

Species	Voucher	Genbank acc	Locality
Polycheles typhlops	JSDUKdeep 58	JQ305984.1	57.30 N 9.00 W (Scotland, SW St Kilda)
Polycheles typhlops	JSDPX15-15	JQ306172.1	37.36 N 9.17 W (Portugal)
Polycheles typhlops	M11L031-1	KJ825708	Western Mediterranean
Polycheles typhlops	M11L031-2	KJ825709	Western Mediterranean
Polycheles typhlops	Eryoneicus_Majorca	KJ825710	Western Mediterranean
Polycheles enthrix	MNHN:IU200814828	HQ241553.1	France, Nouvelle-Calédonie (South)
Stereomastis nana	JSDUKdeep-41	JQ305991.1	58.29 N 9.00 W (Scotland, SW St Kilda)
Stereomastis nana	JSDUKdeep-43	JQ305992.1	58.29 N 9.00 W (Scotland, SW St Kilda)
Stereomastis sculpta	AI-101	KJ825706	Western Mediterranean
Stereomastis sculpta	AI-102	KJ825707	Western Mediterranean
Stereomastis sculpta	PSCU-2	EU377741.1	Sardinia, Italy
Sagmariasus verreauxii	KC3212	FJ174952.1	Australia

The DNA sequence alignment was conducted using the program MUSCLE v3.6 (Edgar 2004) with default parameters and then checked by eye. Before carrying out the likelihood-based analysis, model selection of nucleotide substitution was performed with MEGA5 (Tamura et al. 2011) according to BIC scores (Bayesian Information Criterion) and AICc value (Akaike Information Criterion, corrected). The aligned dataset was then used to estimate maximum likelihood (ML) phylogenies under the selected DNA substitution model using MEGA5 (Tamura et al. 2011). Bootstrap branch support values were calculated with 500 ML replicates. The aligned dataset was also used in MEGA5 (Tamura et al. 2011) to estimate Kimura 2-Parameter (K2P) distances among DNA sequences of the larval specimen and adults from different polychelid species.

3.3.3 Morphological descriptions

Dissection and measurements were taken with a Nikon SMZ800 stereo microscope equipped with an image analysing system (AnalySIS, SIS, Münster, Germany). An Olympus BH-2 microscope was used in the observation of the features of the appendages. The following measurements were taken: carapace length (CL) was measured as the distance from the frontal margin to the posterior margin of the carapace; carapace width (CW) as the greatest distance across the carapace; total length (TL) was measured as the distance from the frontal margin of the carapace to the posterior tip of the telson. The number of individuals examined per stage varied between 1 and 4.

For scanning electron microscopy (SEM), two first zoeal stages were sonicated for 2-3 min for removal of surface debris and dehydrated in a graded ethanol series (70%, 90% and 100%). After critical-point-drying, individuals were mounted on SEM stubs with self-adhesive carbon stickers and were coated in gold. Dried specimens were observed with a Hitachi H-4100 FE SEM.

The long plumose setae on the distal exopod of the maxillipeds and pereiopods are drawn truncated for clarity. Larval descriptions follow the basic malacostracan body pattern from anterior to posterior, and setal armature on appendages is described from proximal to distal subdivisions and from endopod to exopod (Clark et al. 1998, Haug et al. 2013). The setal terminology used was established by Ingle (1993).

3.4 Results

3.4.1 Phylogenetic analyses

The new sequences for the *Eryoneicus* larva (Station: 39.067°N – 2.675°E; Table 3.1) and the adult samples used for molecular analyses have been deposited in GenBank with Accession numbers as shown in Table 3.2. The length of the aligned dataset for the COI gene was 679bp and showed an excess for AT content (~60%), as commonly found in mtDNA gene sequences. The TN93+I DNA substitution model gave the lowest score under both the AICc (3,602.16) and the BIC (3,800.37), and therefore it was used for subsequent maximum likelihood searches. The phylogenetic tree obtained clearly showed the species-level assignment of the larvae, with the clade formed by the *Eryoneicus* specimen and the available *P. typhlops* adult specimens providing a 100 bootstrap support (Fig. 3.1). The K2P distance values observed when comparing the zoea collected from the plankton with either *S. nana* (21.7 %) or *S. sculpta* (24.8 %) fall within divergence levels observed among different genera, whereas the comparison with *P. typhlops* (0.17 %) is within the standard intra-specific distances observed in decapod crustaceans (see "**3.5** Discussion").

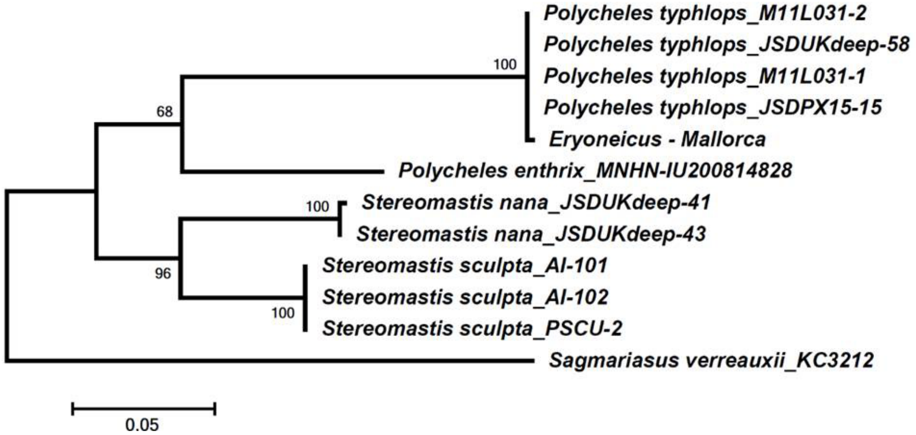


Figure 3.1. Maximum-likelihood phylogenetic tree estimated from the COI sequence data, showing the position of the *Eryoneicus* specimen genetically analysed in the present study.

3.4.2 Morphological descriptions

The first zoeal stage and the decapodid stage are described in detail. For the zoeal stages II and III, only the main differences from the first zoea are presented.

Zoea I

Size: TL= 1.8-2.0 mm; CL= 1.4-1.6 mm; CW= 1.3-1.5 mm.

Carapace (Figs. 3.2a, b, 3.3a, b). Globose, almost spherical, much wider than the pleon, with numerous (55-60) ramified spines and long plumose setae. Two robust processes (column) are placed along the mid dorsal line, one is at mid dorsal carapace (C1, Fig. 3.2b, c) and the other is at the posterior part (C2, Fig. 3.2b, d, e). The arrangement of spines on mid dorsal line is R, 1, 1, 1, 2, C1, 2 C2 (see Fig. 3.3b). Frontal margin with a rostral spine (Figs. 3.3c, f), long and ramified (Fig. 3.2e). Vestigial eyes-stalk present. Details of the first spine of dorsal carina and antennal spine are shown in Fig. 3.2g, h.

Antennule (Fig. 3.3d). Not subdivided and conical, with 2 aesthetascs and 3 setae distally. Inner flagellum bud present.

Antenna (Fig. 3.3e). Biramous, not subdivided and without setae.

Mandible (Fig. 3.3f). Well-developed, showing no distinction between molar and incisor portions, with eight teeth. Not subdivided palp bud present.

Maxillule (Fig. 3.3g). Coxal endite with five plumo-denticulate setae (four terminal + one long setae in the inner margin). Basipodal endite with eight setae (three cuspidate + five plumo-denticulate).

Maxilla (Fig. 3.3h). A single lobe present with two simple setae. Exopod (scaphognathite) with 26-28 marginal plumose setae.

First maxilliped (Fig. 3.4a). Biramous. Protopod with four setae on the inner margin. Endopod not subdivided with 4 terminal plumose setae and one subterminal simple setae. Exopod not subdivided with four lateral and four long terminal plumose setae.

Second maxilliped (Fig. 3.4b). Biramous. Protopod with six setae in the inner margin. Endopod 3-subdivided with 2, 6, 5 setae. Exopod long (around three times longer than the endopod) with four long terminal plumose setae.

Third maxilliped (Fig. 3.4c). Biramous. Protopod with two setae. Endopod 5-subdivided with 1, 4, 4, 7, 5 setae. Exopod with 6 long terminal plumose setae.

First pereiopod (Fig. 3.4d). Biramous. Coxa with three setae. Basis with five setae. Endopod 4-subdivided and cheliform; ischio-merus (ischium and merus not separated) with four strong ramified spines and with a long plumose seta adjacent to each spine; carpus with two strong ramified spines and two distal simple small spines, and with a long plumose seta adjacent to each spine; propodus longer than the ischio-merus and with about 14 setae, including small setae on fixed finger; dactylus half the length of the propodus, apically curved with about ten setae randomly distributed on both margins. Exopod with six long plumose setae.

Second pereiopod (Fig. 3.4e). Biramous. The coxa was lost. Basis with four setae. Endopod four-subdivided and cheliform, shorter than the first pereiopod; ischio-merus with five strong ramified spines and with a long plumose seta adjacent to each spine; carpus half the length of the ischio-meurs with two strong ramified spines and five simple minute spines, with a long plumose seta adjacent to each spine; propodus longer than carpus with several minute setae randomly distributed; dactylus 2/5 times the length of the propodus with several minute setae distributed as figured. Exopod with six long plumose setae.

Third pereiopod. Present as bud (not figured).

Fourth and fith pereiopods: absent.

Pleon (Fig. 3.4f). Small and six-segmented. With a pair of postero-dorsal long sparsely setose setae on pleonites 3-6.

Minute pleopod buds are present on pleonites 2-6.

Telson: triangular, with two posterior minute processes on each side of the small concave posterior margin.

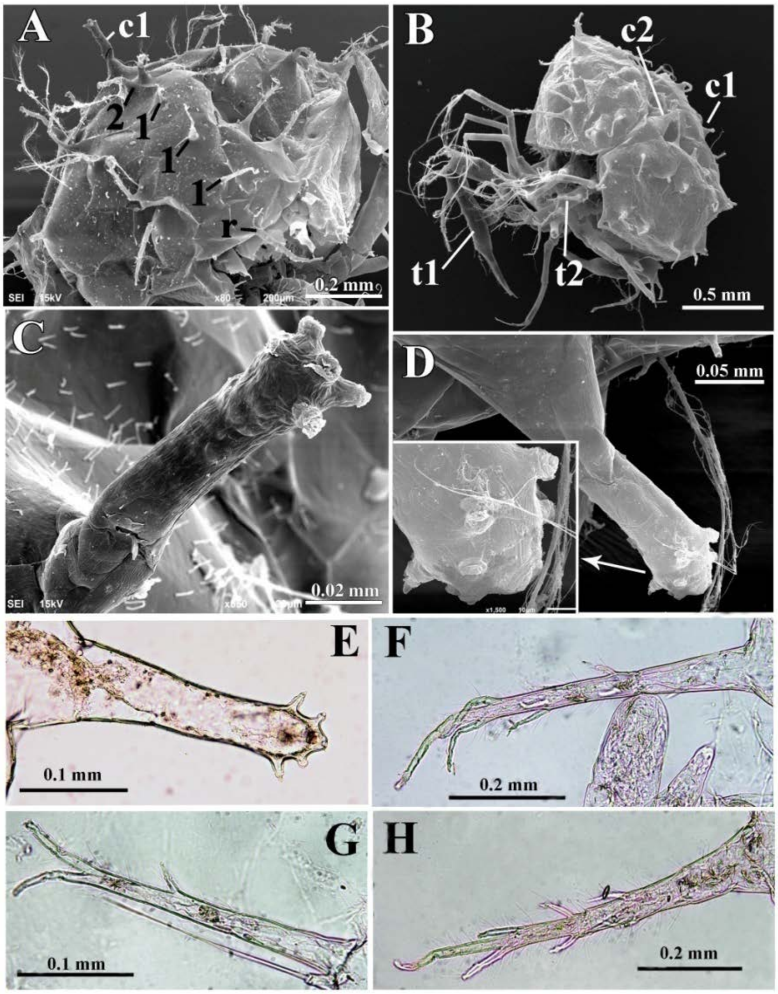


Figure 3.2. *Polycheles typhlops*. First larval stage (ZI). a carapace, frontal view, indicating spines on mid dorsal line; b total animal, posterior view; c anterior column; d, e posterior column; f rostral spine; g first spine of dorsal carina; h antennal spine. **r** rostral spine; *c1* anterior column; *c2* posterior column; *t1* first pereiopod; *t2* second pereiopod.

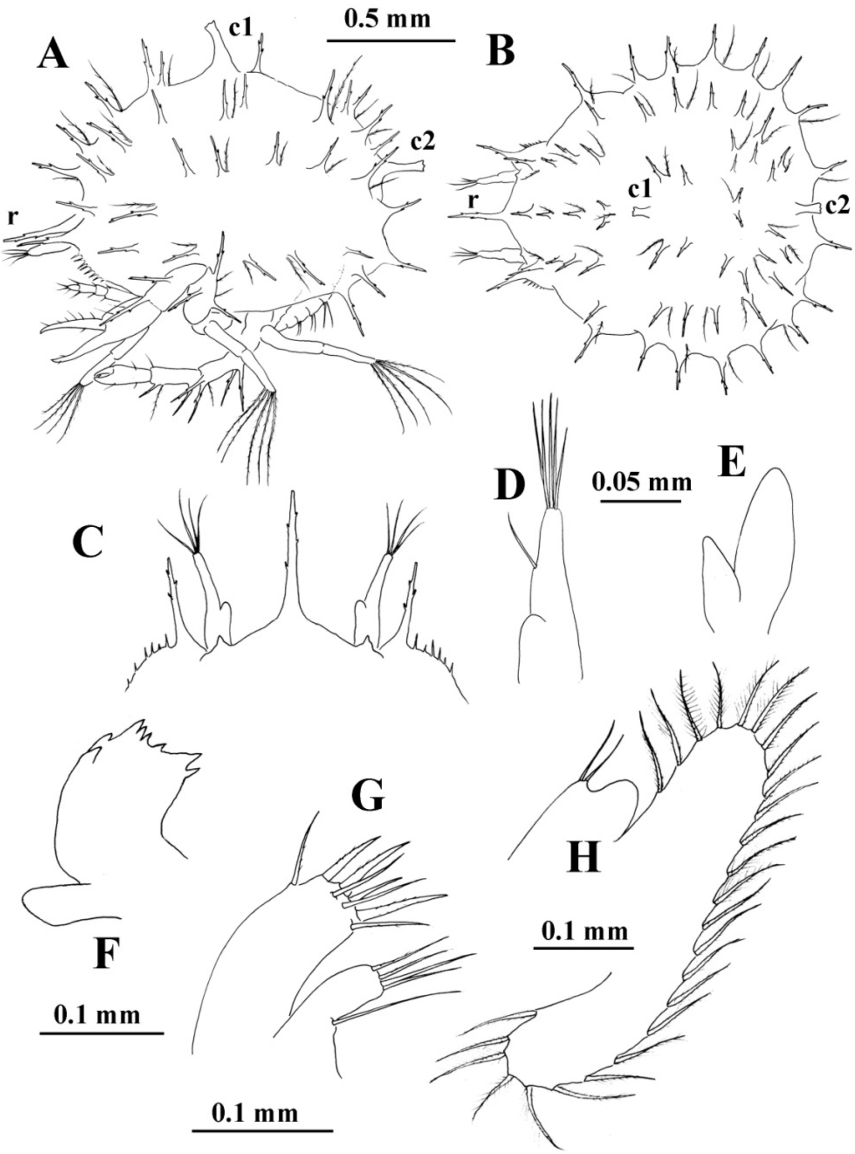


Figure 3.3. *Polycheles typhlops*. First larval stage (ZI). a Total animal, lateral view; b total animal, dorsal view; c frontal margin, dorsal view; d antennule; e antenna; f mandible; g maxillule; h maxilla. Abbreviations: *c1* column anterior; *c2* column posterior; *r* rostral spine.

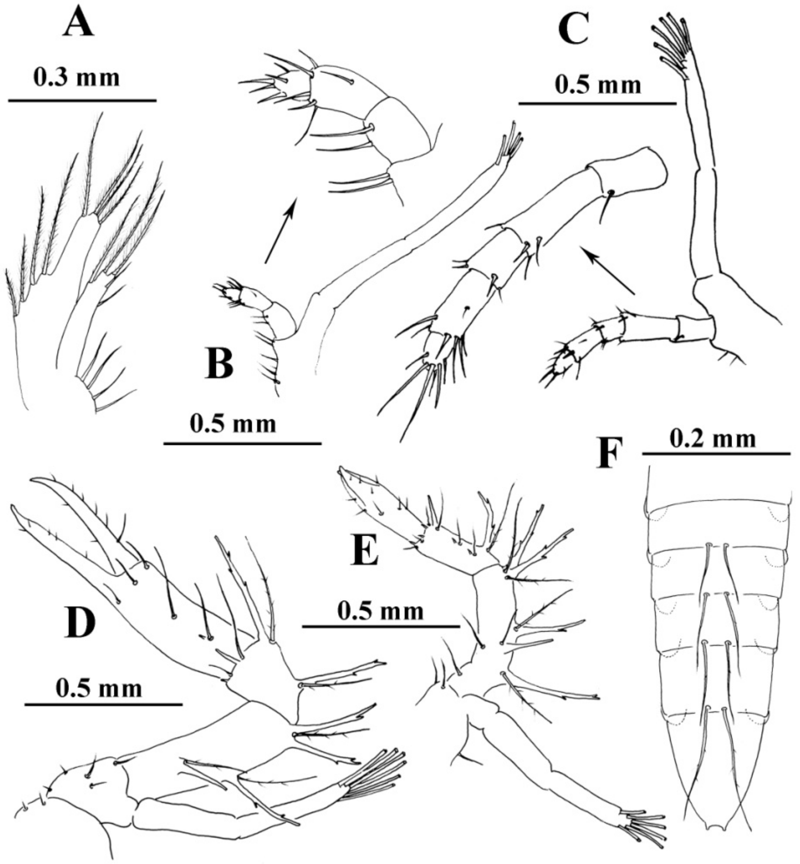


Figure 3.4. *Polycheles typhlops*. First larval stage (ZI). a first maxilliped; b second maxilliped; c thrid maxilliped; d first pereiopod; e second pereiopod; f pleon, dorsal view.

Zoea II

Size: TL= 3.3 mm; CL= 2.3 mm; CW= 2.2 mm.

Carapace (Figs. 3.5a, 3.6a, b). Frontal region with rostrum and a pairs of long (shorter than rostrum) ramified spines. The arrangement of spines on mid dorsal line is R, 1, 1, 1, 2, C_1, 2, 2, C_2, 2.

Antennule (Fig. 3.6c). Outer flagellum 2-subdivided, with 2 sub-terminal aesthetascs and 3 terminal setae on distal subdivision. Inner flagellum longer than previous stage.

Antenna (Fig. 3.6d). Incipiently subdivided. Renal bud process present.

Mandible (Fig. 3.6e). Now with ten teeth.

Maxilla. Exopod (scaphognathite) with 33 marginal plumose setae.

Second maxilliped. Protopod with 7 setae in the inner margin. Endopod three-subdivided with 3, 6, 5 setae.

Third maxilliped. Endopod five-subdivided with 2, 6, 4, 7, 5 setae.

Second pereiopod. Ischio-merus with one additional simple spine in the inner margin. Carpus with one additional minute distal spine.

Third pereiopod. Biramous, not subdivided and unarmed.

Pereiopods 4 and 5. Uniramous, present as a bud.

Pleon (Fig. 3.6f-h). Pleonites completely differentiated.

Pleopods (Fig. 3.6g) Biramous buds on pleonites 2-5. Pleonite six with biramous uropod buds.

Telson (Fig. 3.6h). Unarmed, 2 times longer than wide, posterior end 1/3 length of anterior part.

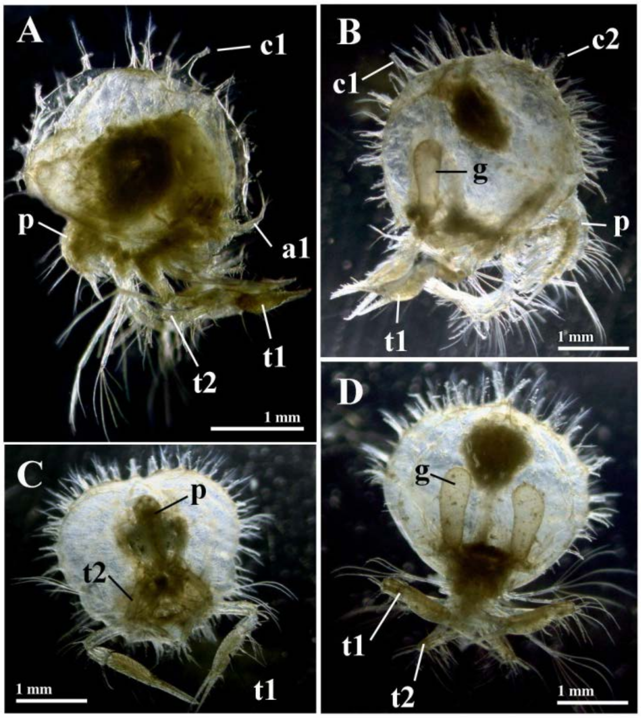


Figure 3.5. *Polycheles typhlops*. Second zoeal stage (ZII). a, lateral view. Third zoeal stage b, lateral view; c, ventral view; d, frontal view. Abbreviations: a1, antennule; c1, anterior column; c2, posterior column; g, antennal gland; p, pleon; t1, first pereiopod; t2, second pereiopod. (material from OAMMS-04 surveys).

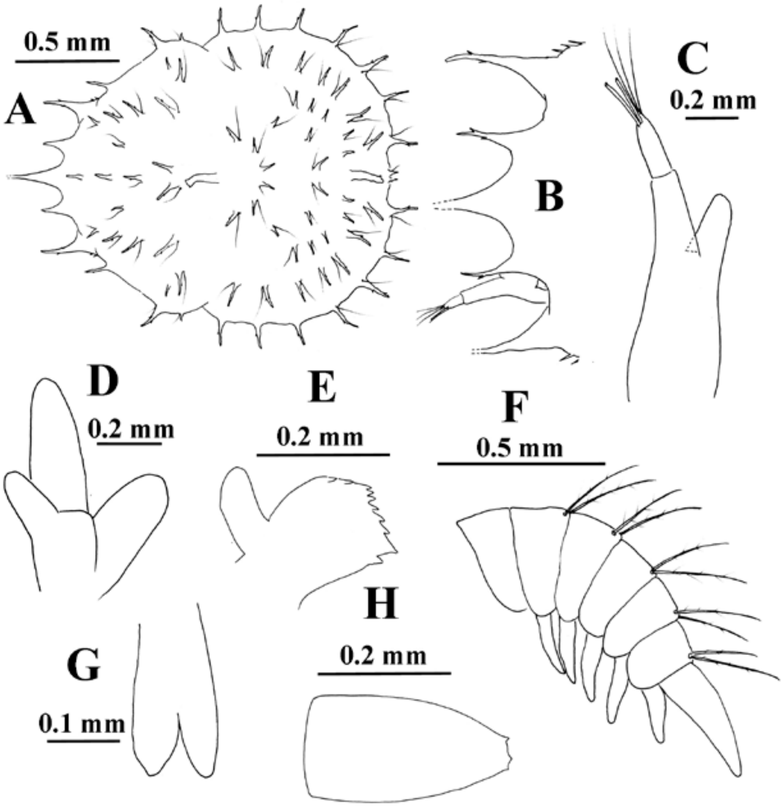


Figure 3.6. *Polycheles typhlops*. Second zoeal stage (ZII).

a cefalothorax, dorsal view; b frontal margin, dorsal view; c antennule; d antenna; e mandible; f pleon; g first pleopod; h telson.

Zoea III

Size: TL= 4.7 mm; CL= 3.3 mm; CW= 3.4 mm.

Carapace (Figs. 3.5b-d, 3.7a, b). Cervical groove and branchial carinae incipiently developed. The number of the spines increases, many scattered between carinae.

Antennule (Fig. 3.7c). Biramous. Statolith present in the peduncle, with two short spines. Inner flagellum incipiently three-subdivided with 0, 2, 2 aesthetascs and 0, 0, 3 setae. Outer flagellum not subdivided with 3 terminal setae.

Antenna (Fig. 3.7d). Biramous. Exopod incipiently subdivided, without setae; endopod not subdivided, shorter than renal process and with one terminal setae.

Mandible (Fig. 3.7e). Now with 10 teeth. Palp 2-subdivided with a simple seta on distal subdivision.

Maxilla (Fig. 3.7f). Two endites with 3 and 2 setae, respectively. Scaphognathite with 50-54 plumose marginal setae (not figured).

First maxilliped. Protopod with 5 setae on the inner side. Exopod not subdivided with 8 plumose setae.

Second maxilliped. Protopod with nine setae. Endopod three-subdivided with 6, 8, 5 setae.

Third maxilliped. Protopod with six setae. Endopod five-subdivided with 4, 12, 6, 10, 5 setae.

First pereiopod (Fig. 3.7g). Ischio-merus with four strong ramified spines; carpus with five spines (2 strong ramified + 3 simple); propodus with seven simple spines. Setation as shown.

Second pereiopod (Fig. 3.7h). Ischio-merus with nine spines (five strong ramified + four simple); carpus with eight spines (two strong ramified + six simple). Setation as shown.

Pereiopods 3–5. Short and not subdivided.

Pleon (Fig. 3.7i-k). Small. First pleonite with one dorsal simple setae; second pelonite with a small postero-dorsal process and two long plumose setae; pleonites 3-5 each with one long postero-dorsal process, two long plumose setae and two simple setae; pleonite sixth with one long postero-dorsal process, two long and two small setae; all pleonites with rounded pleura, except the sixth that ends with a small process. Pleopods (Fig. 3.7i, k). Without setae, propod incipiently separated from the ramus; endopod presenting a small *appendix interna*.

Telson (Fig. 3.7i, j). Triangular shape in dorsal view, ending in a sharp median point, with one long antero-dorsal spine and two small simple setae on dorsal margin, lateral margins with 7-8 spines on each side.

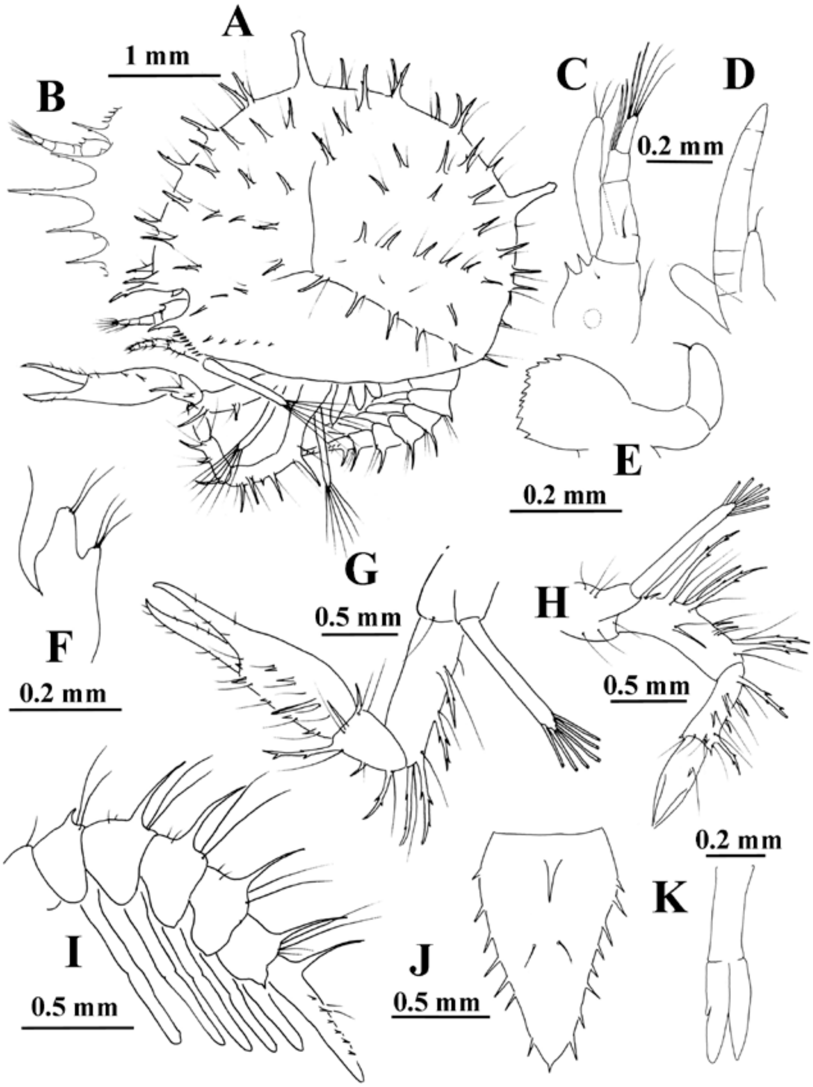


Figure 3.7. *Polycheles typhlops*. Third zoeal stage (ZIII). a total animal, lateral view; b frontal margin, dorsal view; c antennule; d antenna; e mandible; f maxilla, endites; g first pereiopod; h second pereiopod; i pleon; j telson; k first pleopod.

Decapodid

Size: TL= 16.3 mm; CL= 8.5 mm; CW= 7.7 mm.

Carapace (Figs. 3.8a-c). Longer than wider, pear-shaped in dorsal view. Frontal margin with rostral spine simple, shorter than antennular peduncle. Orbital sinus well defined, internal angle of orbital sinus sparsely setose ending in a pointed process. Surface with more than 180 spines and long plumose setae, some in rows and carinae but many scattered between them. The arrangement of spines on median carina, between the rostral spine and the posterior margin is R, 1, 1, 1, 2, C_1, 2, 2, C_2, 2 (see Fig. 3.8a, b). Brachial region with four carinae; branchial upper carina with 11-13 spines; lateral carina with about 25 spines, including the antennal spine; longitudinal brachial carina with six spines in the posterior half of the carapace and about 24 minute spines in the anterior half of the carapace. Branchial lower carina with 17 small spines in the posterior half of the carapace; this carina does not reach the anterior part of the carapace. Eyestalks with a spine.

Antennule (Fig. 3.8d). Peduncle 3-subdivided, basal subdivision flattened and enlarged with two distal long simple setae, the inner margin extends in the form of a long ridge triangular whose outer margin has about six long spines; posterior subdivisions unarmed. Outer flagellum approximately three times shorter than inner flagellum with 9-10 subdivisions, inner flagellum with 27 subdivisions.

Antenna (Fig. 3.8e). Renal process long, oblique, distally dilated. Scaphocerite short, lingulate, with 23-25 plumose setae. Flagellum of the endopod with 30 subdivisions.

Mandible (Fig. 3.8f). Similar to the zoeae with 14-15 triangular teeth, no show distinction between molar and incisor portions. Palp two-subdivided with 20-24 and more than 30 setae, respectively.

Maxillule (Fig. 3.8g). Coxal and basipodal endite with about 15 and 23 setae, respectively; without endopod.

Maxilla (Fig. 3.8h). Biramous, two maxillar lobes present, the smaller one with 3 distal simple setae and the longer one with 13 marginal simple setae. Scaphognathite large with numerous marginal plumose setae.

First maxilliped (Fig. 3.9a). Endopod slender; exopodal lobe membraneous, reniform, extending further back than scaphognathite, exopod anteriorly divided into two lobes enclosing efferent passage.

Second maxilliped (Fig. 3.9b). Endopod four-subdivided densely setose.

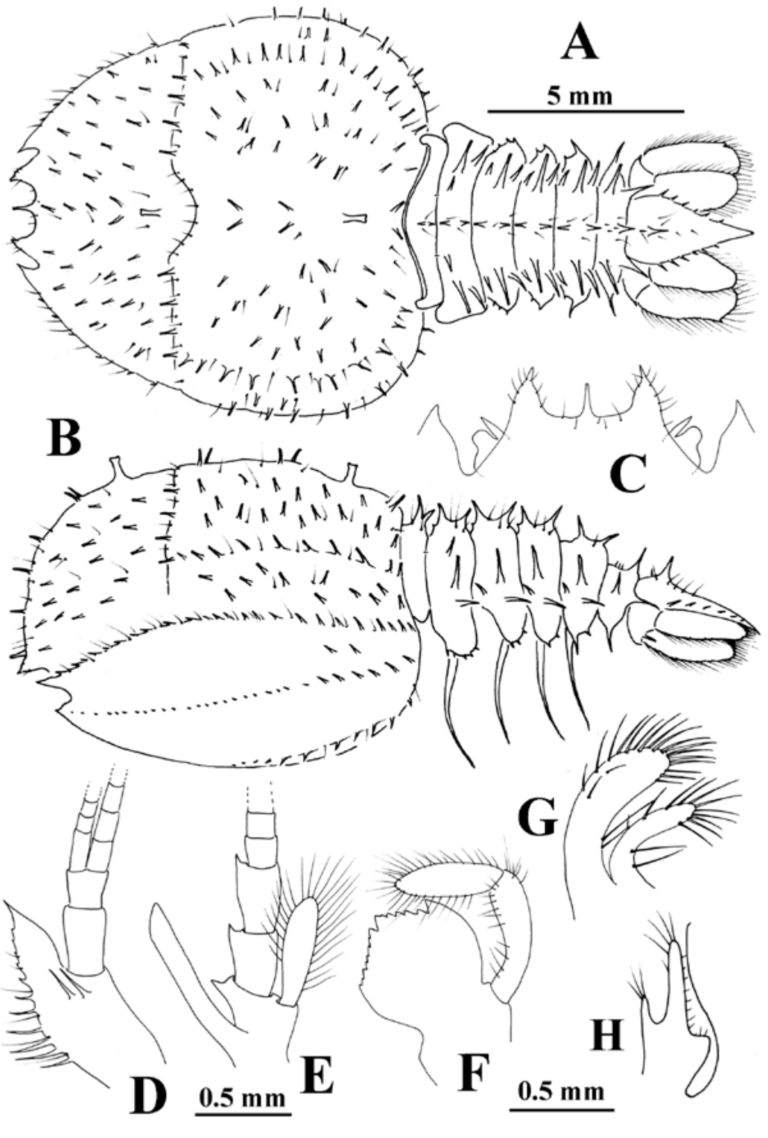


Figure 3.8. *Polycheles typhlops*. Decapodid stage. a Total animal, dorsal view; b total animal, lateral view; c frontal region, dorsal view; d antennule; e antenna; f mandible; g maxillule; h maxilla, endopod and endites.

Third maxilliped (Fig. 3.9c). Endopod five-subdivided densely setose, with vestigial epipod.

First pereiopod (Fig. 3.9d). First pereiopod very long, more robust than P2-5, ischium and merus now separated; spination as shown. Podobranch, epipod and two arthrobranch present.

Pereiopods 2-5 (Fig. 3.9 e-h). Successively shorter posteriorly. Pereiopods 2-4 cheliform. Long spines present in ischio-merus and carpus of the second pereiopod

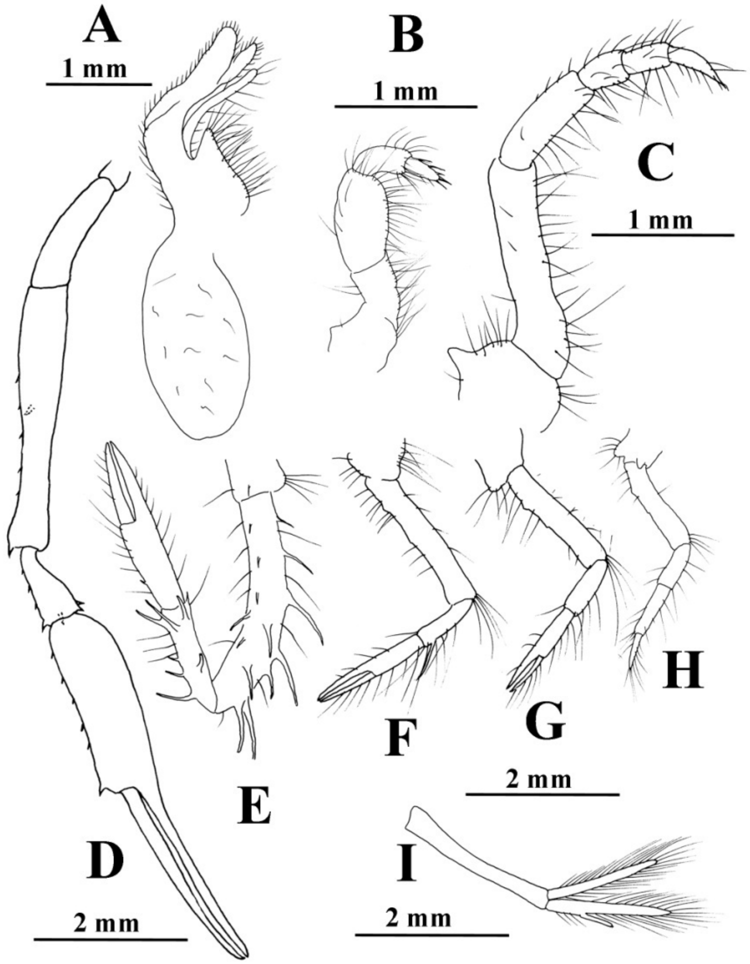


Figure 3.9. *Polycheles typhlops*. Decapodid stage. a, first maxilliped; b, Second maxilliped; c, third maxilliped; d-h, pereiopods 1-5; i, first pleopod.

(Fig. 3.9e). Third pereiopod with a distal long spine on carpus. Pereiopods 2-4 with podobranch, epipod, 2 arthrobranch and one pleurobranch present. Pereiopod five with one pleurobranch.

Pleon (Figs. 3.8a, b). Well-developed, spinulation indicated in Table 3.3; pleura of pleonites 1-2 rounded; pleura of pleonites 3-6 ending in a short sharp spine on the third and fourth but long and pointed on the fifth and sixth.

Table 3.3. *Polycheles typhlops*, decapodid. Number of spines of the pleonites (1-6). A, present study; B, Bouvier (1917) bi, bifurcated; in, inferior; me, median; su, superior.

Spines	Pleonites											
	1		2		3		4		5		6	
Dorsal	A	B	A	B	A	B	A	B	A	B	A	B
Anterior small	0	0	1	1	1	1	1	1	0	0	0	0
Median small	0	0	0	0	0	0	0	0	0	0	3	0
Anterior strong	0	0	1	1	1	1	1	1	1	1	0	0
Posterior strong	1bi	1	1	1	1	1	1	1	1	1	1	1
Lateral												
Posterior small	1	0	0	0	0	0	0	0	0	0	0	0
Pleural strong (su)	0	0	1	1	0	0	0	0	0	0	0	0
Pleural strong (me)	0	0	1	1	2	1	2	1	2	1	1	1
Pleural strong (in)	0	0	1	1	1	1	1	1	1	1	1	1

Pleopods (Fig. 3.9i). Biramous and functional; endopod with 30-32 plumose setae and bears an *appendix interna* with 10 coupling hooks; exopod with 34-36 plumose setae. Uropods functional, with numerous long plumose setae (endopod and exopod with more than 50 and 65 respectively).

Telson (Figs. 3.8a, b). Lanceolate in dorsal view, dorsal surface with one small and one strong spine placed anteriorly and several short simple setae randomly distributed. Each lateral margin with 6-9 spines.

3.4.3 Spatial and vertical distribution of Polycheles typhlops larvae

Twenty-five specimens of *P. typhlops* larvae were identified from samples taken in the Balearic Sea (Fig. 2.1, see chapter 2). The larvae were captured mainly during the summer season (2010) but also in late autumn (2009). Relevant information about sampling details, such as location of sampling sites, density of larvae, date, time of sampling, water depth stratum and bottom depth are shown in Table 3.1. All zoea larvae and decapodid stages were found below the 200 m depth (Table 3.1; Fig. 3.10). Additionally, one first zoea stage was captured in the upper slope, near the bottom in the supra-benthos compartment (Table 3.1). Regarding their vertical distribution, the first zoeal stage could be found from 200 to 600 m depth, but mean abundances were higher in the layer between 300 and 500 m depth (Fig. 3.10) and in the southern study area. The last two zoeal stages were captured in a shallower layer (200–450 m depth), while the decapodid stage was collected near the bottom, between 600 and 800 m depth, in the northwest area. The vertical profiles of fluorescence during the late autumn survey were homogeneously distributed in the south and the northwest, ranging between 0.1 – 0.3 mg/m^3 (Fig. 3.10A). Higher values were observed during the summer, with values ranging between 0.05 and 1.03 mg/m^3 (Fig. 3.10B) and the presence of clines.

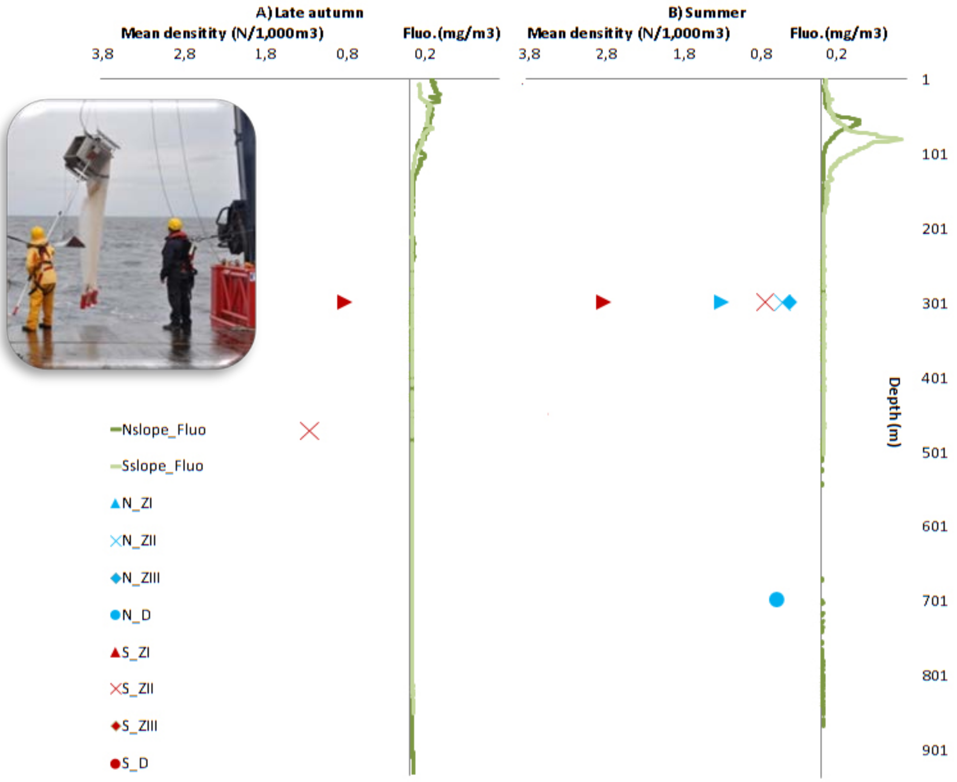


Figure 3.10. Seasonal fluorescence vertical profiles at northwest in dark green (Nslope_Fluo) and south middle slope in light green (Sslope_Fluo) from surface down to maximum sampled depth, adapted from Torres et al. (2014). Mean seasonal densities ontogenetic distributions of *Polycheles typhlops* larvae in the water column (depth mean) during the late autumn (A) and summer (B) cruises, at northwest (N, blue) and south (S, red) over middle slope. (ZI: first larval stage; ZII: second larval stage; ZIII: third larval stage; D: decapodid).

3.5 Discussion

3.5.1 Phylogenetic and morphology of *Polycheles typhlops* larvae

Accurate identification of marine larvae has traditionally required the rearing of larval stages in aquaria, but the development of species-specific markers (DNA barcoding) facilitates now the assignment of wild-caught planktonic larvae (Palero et al. 2008, Marco-Herrero et al. 2013). Matzen da Silva et al. (2011) have recently shown that the standard DNA barcoding COI gene region resolves relationships among decapod crustaceans. In their study, the observed mean Kimura 2-Parameter (K2P) distance values did range from 0.29 to 1.38% within species, 6.38-20.92% within genus and 11.39-25.62% within family. The K2P distance values found here when comparing our smallest zoea specimen (Station: 39.067°N – 2.675°E; Table 3.1) with either *S. nana* (21.7%) or *S. sculpta* (24.8%) fall within divergence levels observed among different genera, whereas the comparison with *P. typhlops* (0.17%) is well within the K2P distance observed inside species. The molecular phylogeny also showed significant statistical support for the clustering of the larval sequence with DNA sequences obtained from adult specimens of *P. typhlops*. Therefore, the genetic results obtained in the present study, together with the fact that *Stereomastis* and *Polycheles* are the only polychelid genera known to occur in the Mediterranean, indicate that the first zoea larva collected from western Mediterranean waters corresponds to *P. typhlops*. The larval development of *P. typhlops* is found to include at least three zoeal and one decapodid stages. Despite no molecular confirmation was made for the identity of ZII-ZIII and decapodid stages, species identification is inferred on morphological evidence (spination on the anterior part of mid dorsal line along the larval development and presence of epipodites on the decapodid stage). Following Ahyong (2009), the presence of epipodites on maxilliped 3 and pereiopods is used as one of the key features that allow for discrimination between the genera *Stereomastis* and *Polycheles.*

The smaller larvae of *P. typhlops* presented in this study were assigned to the ZI stage because they showed similar size (~1mm CL) and the same degree of development as the first zoeal stage described from material reared in the laboratory (Guerao and Abelló 1996). The first zoea of *P. typhlops* had in both cases well-developed first and second pereiopods (biramous) and rudimentary pleopods. However, the description by Guerao and Abelló (1996) may not reflect the actual morphology of the larvae when hatching under natural conditions, given that many spines and setae on the carapace and appendages were not yet extruded. The degree of development indicates that the two later zoeae described here may correspond to the second (ZII) and third (ZIII) zoeal stages. These stages have well-developed inter-orbital spines, which are tiny in the first stage, pereiopods 4-5 present as buds and biramous pleopods. In the third zoeal stage, the pleopods are much more developed, even though the number of functional pereiopods does not increase. The main features that separate stages ZII and ZIII are the presence of appendix interna on the pleopods (but ramus without setae) in the third zoea, antennal exopod incipiently subdivided, telson triangular and setal development. From our observations, the zoea of Polychelidae are characterized by the presence of natatory exopods on the appendages of the pereion (maxillipeds and pereiopods), rostrum projecting and the absence of functional pleopods (see also Bernard 1953, Williamson 1983). The morphology and size of the most advanced zoea and the decapodid indicate that intermediate larval stages should exist between these two. In fact, the carapace of the decapodid is ~150% longer than the zoea III carapace while the increasing progression in size of the carapace among the zoeal stages does not exceed 44%. The morphology of *Eryoneicus* larvae appears to change gradually and no true metamorphosis has been observed between different stages (Bernard 1953, Williamson 1983). The most dramatic change that occurs between ZIII and the decapodid, besides the change in relative size of the pleon, is the appearance of well-developed and uniramous pereiopods.

Early stages of *Eryoneicus* species are seldom captured and the complete zoeal development of a polychelid lobster is still unknown (e.g. Balss 1925; Stephensen 1935, Bernard 1953). The first description of a zoeal stage was reported by Selbie (1914) as a “juvenile” *Eryonicus* sp. from NW Atlantic waters. According to Selbie (1914): “This very interesting specimen was taken by the midwater otter trawl off the south-west coast ; at the same station a small *E. Faxoni* was taken, and it is possible that the present specimen belongs to the same species”. Indeed, the zoea described by Selbie (1914) presented an arrangement of spines on the anterior part of the mid dorsal line (R, 1, 2, C_1) clearly different from that found in our zoeal and decapodid stages (R, 1, 1, 1, 2, C_1) and belongs probably to another species. Other early-stage *Eryoneicus* larvae described by Balss (1925) from Valdivia (SE Atlantic) and from the Arctic by Stephensen (1935) do not correspond to the zoeae of *P. typhlops*. Nevertheless, the decapodid described in the present study agrees very well with the description of *E. puritanii* given by Bouvier (1917). Only small differences were noted compared with Bouvier's account (Table 3.3), such as the branchial lower carina not ending at the longitudinal carina, no pre-cervical grooves present, and minor differences in the spinulation pattern (see Table 3.3, Figs. 3.8a, b). In our decapodid stage the dorsal spine of the first pleonite is forked at the base, there are two median pleural spines in pleonites 3-5 and pleonite six bears three minute spines dorsally. These small differences could be attributed to the fact that the decapodid phase may include various stages, of which the latter would be neotenic forms with secondary sexual characteristics (see Williamson 1983).

Descriptions of *E. puritanii* specimens by Lo Bianco (1903), Bouvier (1917) and Bernard (1953) have been previously attributed to *P. typhlops* (Bouvier 1940, Kotthaus 1966). Lo Bianco (1903) samples were captured in the Gulf of Napoli (Western Mediterranean Sea), but several specimens attributed to *E. puritanii* have also been captured along the eastern Atlantic Ocean (Bernard 1953, Kotthaus 1966, Hernández and Tiefenbacher 1999, Hernández et al. 2007). *E. puritanii* larvae described by Bernard (1953) were ascribed to *P. typhlops* by Bouvier (1940) and Kotthaus (1966). Despite Bernard's description (1953, Fig. 21) does not fit present standards, it seems to correspond to our second zoeal stage. Regarding the comparison of our decapodid with Lo Bianco's original description, a different telson was figured (with a terminal spine) and therefore his description may not correspond to a decapodid stage of *P. typhlops* (Lo Bianco 1903, see Fig. 25 plate 8). Recall here that the decapodid (megalopa, see Anger 2001) denotes the final larval phase preceding moulting to the first juvenile stage and it is characterized by the existence of functional pleopods and uropods, subdivided and with long plumose natatory setae. Apart from *E. puritanii* catches by Lo Bianco (1903), other *Eryoneicus* forms were captured in the Mediterranean, namely the *E. faxoni* and *E. kempi* forms (Williamson 1983). The descriptions for *E. kempi* (Selbie 1914) and *E. puritanii*

(Bouvier 1917) are similar, sharing the spine formula on the mid dorsal line (Bernard 1953). However, several differences can be observed between both species, such as the long spines and basal subdivision of the antennules or the cheliform 5th pereiopod.

3.5.2 Spatial and vertical distribution of Polycheles typhlops larvae

Although occurrences of adult polychelid lobsters on the epibenthos of the middle slope are common in the study area (Ramón et al. 2014), *P. typhlops* larvae were rare among all the collected material and were found exclusively in aphotic layers, corresponding to the lowest fluorescence values (Olivar et al. 2012, Torres et al. 2014). The highest peak of *P. typhlops* larval abundances during the summer agrees with the highest frequency of ovigerous females in the Mediterranean (Follesa et al. 2007), and the bi-seasonal presence of larvae is in agreement with the fact that *P. typhlops* males are sexually active during the whole year (Cabiddu et al. 2008, Gastoni et al. 2010). The occurrence of *P. typhlops* larvae in deep plankton just above the adult populations is also in accordance with previous larval records. Bernard (1953) had already noted that all the *Eryoneicus* forms were captured below the euphotic zone, and pointed towards the possibility of vertical ontogenetic migrations. The present study confirmed that *P. typhlops* larvae inhabit waters below the euphotic layer and that the decapodid stage is to be found in the deepest layers. This pattern further supports the idea that the larvae descend into deeper waters throughout their development, approaching the bottom at the end of the last larval stage in order to search for a suitable place to settle (Marta-Almeida et al. 2008, Shanks 2009). The lack of accounts for zoeal stages of *P. typhlops* in the previous literature is probably related with the low frequency of plankton sampling on deep waters, given that plankton studies usually focus on the photic layer. The larvae included in this study were captured at depths (between 200 and 800 m) where the photosynthetically active radiation (PAR) does not penetrate (e.g. Crise et al. 1998) and where local hydrographic currents are weaker than in shallower layers (Pinot et al. 1996, Amores et al. 2013). By staying within this depth range, and through depth-keeping mechanisms (Shanks and Brink 2005), *P. typhlops* larvae might avoid the passive transportation suffered by other deep species spreading their larvae to the surface layers (Marta-Almeida et al. 2008).

The highest early-zoea larval densities were observed in the south slope during the summer season, coinciding with the maximum values of surface fluorescence and organic matter fluxes. Organic matter mean content of settling material, opal and $CaCO_3$ fluxes to the necto-benthic communities estimated during the same oceanographic surveys show that the major inputs of marine organic matter (phytoplankton blooms) took place during summer in the south, being lithogenic fraction higher in the north area (Pasqual et al. 2014). On the north-west study area, where the shelf is narrower and the slope is quite pronounced, the currents over the shelf create mixed conditions (Torres et al. 2014). Laboratory studies on captured bathyal echinoids indicate that an increase in gonad size in response to food enhancement could increase spawning production (Eckelbarger and Watling 1995), and a similar response could also explain the highest *P. typhlops* larval abundance in the southern slope. Stomach contents for *E. puritanii* taken between 500 and 2,500 meters depth showed that they are able to feed on cnidaria, cyanophyceae, diatoms or coccolithophores (Bernard 1953), and support the classical view of deep-sea organisms being nourished by a “rain” of organic detritus coming from surface waters (Agassiz 1888). The capacity of decapod larvae to feed on microorganisms (Anger 2001) would be crucial in aphotic layers, where most C and N is sequestered in prokaryotes and bacterial biomass is dominant over phytoplankton biomass (Cho and Azam 1990, Lasternas et al. 2010). These facts give light in understanding the presence of polychelid *Eryoneicus* in dark oligotrophic waters where the larvae could take advantages of faecal pellets of herbivorous organisms covered with bacteria (Marshall 1954).

3.6 Conclusions

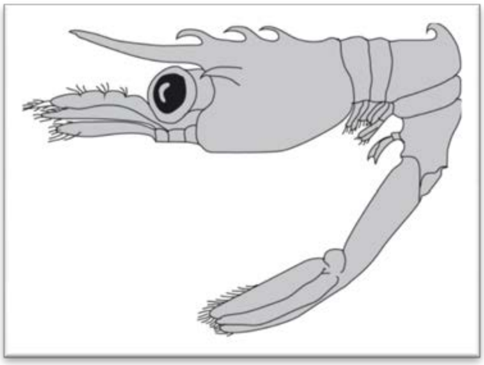
Detailed morphological examination, analysis of DNA sequences and comparison with previous studies provide evidence to support the assignment of the ancient species *E. puritanii* to the larval stages of *P. typhlops.* The larvae of *P. typhlops* are found to possess functional cheliform pereiopods and undeveloped eyes from the early zoeal stages. Besides the arrangement of spines on the anterior part of the mid dorsal line and the results from the DNA analysis on the ZI stage, the clear presence of an epipodite on maxilliped 3 and the periopods provides further support to the connection between *E. puritanii*, our decapodid specimen and *P. typhlops*. The results obtained in this study provide new information on the distribution and abundance of larval stages for one of the key groups of deep-sea fauna. The scarcity of conclusive data in the previous literature indicates the need for further descriptions in conjunction with the use of molecular techniques. An improvement of our knowledge about the larval ecology and recruitment of deep-sea species will be of utmost importance for the management of bathyal fauna.

Chapter 4
Invasive species

Torres AP, Dos Santos A, Cuesta J A, Carbonell A, Massutí E, Alemany F and Reglero P- 2012. First record of Palaemon macrodactylus Rathbun, 1902 (Decapoda, Palaemonidae) in the Mediterranean Sea. Mediterranean Marine Science, 13 (2): pp. 278 - 282.

4.1 Abstract

The Mediterranean Sea is one of the world's hotspots for marine bio-invasions. Most invasions are first documented based on an initial record of occasional adult captures. However, reports of larval stages could indicate that there is an adult population that is reproducing and therefore well established in the area. The spread of the oriental shrimp, *Palaemon macrodactylus,* from its native estuarine waters of southeast Asia to new regions worldwide is well documented. We report the first record of this species in the Mediterranean based on the presence of its larval stages in plankton samples. Decapod larvae were collected in five offshore plankton surveys performed off the Balearic Islands (western Mediterranean), and zoeae III and VI of the oriental shrimp were found among them. Taking into account the duration of the successive developmental stages, and the hydrodynamic characteristics of the study area, these larvae were most probably spawned by adult populations not yet documented. The larvae were found in marine waters despite the fact that adults usually inhabit brackish waters. Our study is a good example of how plankton studies can help to detect larval stages of invasive species before the adult populations are detected.



4.2 Introduction

Most benthic marine invertebrates have planktonic larval stages that spend from hours to months in the pelagic environment before settling to the bottom. It is during these early life stages that there is the highest dispersal, which determines the connectivity among populations (Cowen and Sponaugle 2009). Larval transport can occur by natural means, through currents, as well as through anthropogenic pathways and vectors. One of the main introduction vectors of marine alien species worldwide is ship ballast water (Galil 2009), in which a species can reach areas far from its native distribution range and could become an invasive species in the newly colonized area.

Palaemon macrodactylus Rathbun, 1902 is an estuarine shrimp native to the western Pacific that has been described in waters around Japan (Rathbun 1902), China and Korea (Newman 1963). Little is known about its early life history stages; however, its adult biology and its expansion and colonization period in different estuaries around the world are well described in the literature. In marine waters, well-established populations have only been reported in the port of Mar de Plata (Argentina) (Vázquez et al. 2012).

In 1957, *P. macrodactylus* adults were reported for the first time in the eastern Pacific, which was the first finding of this species outside its native habitat (Newman 1963). Adult specimens have been reported in the eastern Atlantic, on estuarine coasts of Europe, where they extended from the south to the north in one decade, and later in the western Atlantic, and in 2009 they were recorded in the Black Sea (Lavesque et al. 2010, and references therein). The chronology and geographic distribution with all the records are shown in Figure 4.1.

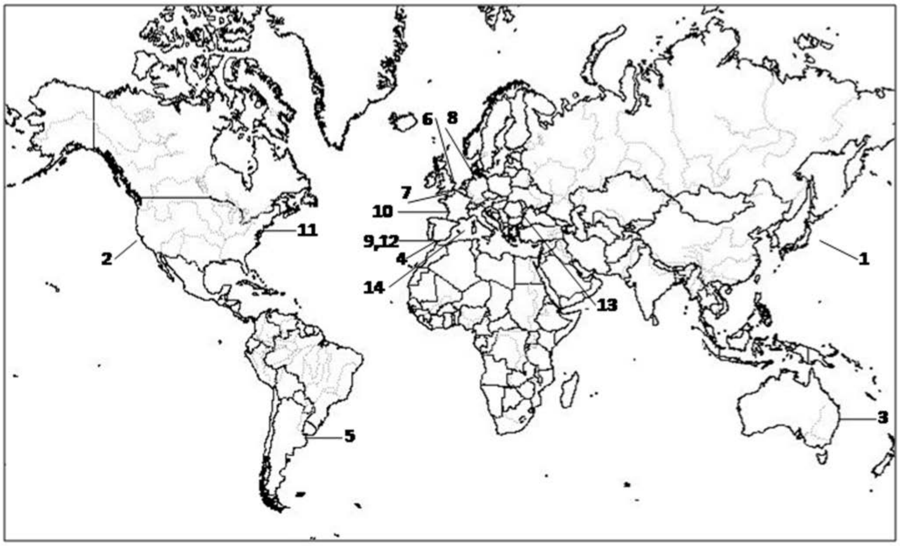


Figure 4.1 Chronology of the appearance of *P. macrodactylus* around the world, showing the distribution of worldwide points (updated from González-Ortegón et al. 2007, and the references therein). *1(O/E)* north coast of China, Korea and Japan. *2(A/E)* Pacific coast of North America. *3(A/E)* southwestern Australia. *4(A+L/E)* Gulf of Cádiz, Spain. *5 (A/M)* Mar del Plata harbour, Argentina. *6(A/E)* Suffolk, U.K. *7(A/E)* North Sea (Belgium, Netherlands and north France). *8(A/E)* Mouth of the Geeste River and Hooksiel, Germany. *9(L/E)* Guadiana River, Spain (Cuesta and González-Ortegón unpublished data). *10(A/E)* Gironde estuary, France. *11(A/E)* New York estuary, North America. *12(A/E)* Guadiana River, Spain. *13(A/M+E)* Constana harbour and Varna Lake, Black Sea. *14(L/M)* Present work in Balearic Islands. *(O:* origin area; *A:* adult phase; *L:* larval phase, *E:* estuarine habitat; *M:* marine habitat)

Unfortunately, there are still large gaps in the current information on the larval ecology of *P. macrodactylus*. Estuarine species follow two main life cycle strategies (Strathmann 1982): one strategy involves the adaptation of all life cycle stages to the estuarine conditions; and the other strategy involves exporting larval stages to adjacent offshore marine areas. In laboratory conditions, the oriental shrimp needs around 15-20 days (6-7 zoeal stages) after hatching before it metamorphoses into a first juvenile (Little 1969). *P. macrodactylus* larvae are easily identified by the presence of a dorsal hooked spine on the third abdominal segment (Fig. 4.2, Fig. 4.3a, b), which is not present in any other known European palaemonid larvae

(González-Ortegón and Cuesta 2006). The larvae are planktonic and are very abundant in the plankton of delta areas during summer (Siegfried 1980).

Figure 4.2 *Palaemon macrodactylus,* Zoea VI, captured in the Balearic Sea in 2005.

P. macrodactylus larvae were collected in two of five intensive multidisciplinary surveys conducted around the Balearic Islands (western Mediterranean). These samples are the first record of this species in the Mediterranean Sea. Information on the larval developmental stages and oceanic situation off the Balearic Islands is given and discussed. This study aims to inform the scientific community of the presence of a new invasive species and lay the foundations for assessing the possible interaction between the exotic shrimp and native carideans in future works. We report the presence of oriental shrimp larvae, which have been detected before the adult population.

Figure 4.3 *Palaemon macrodactylus,* Zoea III captured in the Balearic Sea in 2010, general view (a) whole lateral view, (b) abdominal dorsal spine detail, (c) rostral dorsal spines and (d) telson.

4.3 Material and methods

Five multidisciplinary oceanographic cruises were conducted off the Balearic Islands during the summers of 2001, 2004, 2005 and 2010, and in the winter of 2009 (western Mediterranean; Fig. 4.4). The first three cruises (2001, 2004 and 2005) focused on the horizontal distribution of meroplankton. About 196 stations were sampled using a 60-cm Bongo net towed at ~2 knots on oblique hauls from 70 m depth to the surface (Alemany et al. 2010). The 2009 and 2010 cruises were aimed at studying the vertical distribution of the meroplankton in two areas of western and southern Mallorca, among other objectives. A total of 218 depth-stratified mesozooplankton samples were collected with the Hydrobios multinet in 2009 and a multiple opening/closing net and environmental sensing system (MOCNESS; Olivar et al. 2012) in 2010. The mouth openings of these nets were 0.25 m^2 in 2009 and 1 m^2

in 2010, and the mesh size was 333 µm. Both devices were towed at ~2 knots, performing oblique stratified sampling from the near bottom to the surface at the 200 m and 900 m isobaths.

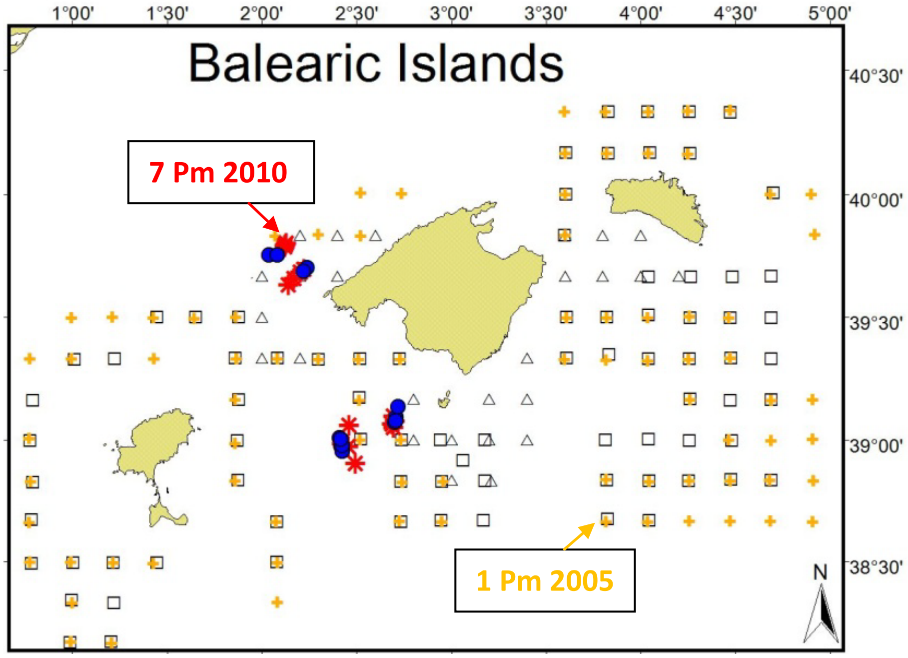


Figure 4.4 Study area (Balearic Islands point 14_Fig.4.1), showing sampling stations (black triangles 2001; black squares 2004; orange crosses 2005; blue dots 2009; red asterisks 2010). *Palaemon macrodactylus* capture points (Pm) and numbers for 2005 (orange) and 2010 (red).

Immediately after sampling, all samples were preserved in ~4% borax-buffered formaldehyde, prepared using seawater. Once in the laboratory, samples were sorted for decapod larvae. Decapod zoeae were identified to species level and developmental stage, using the identification key developed by Dos Santos and González-Gordillo (2004). The larvae of *Palaemon macrodactylus* larvae were confirmed using the description by Little (1969). Total length (TL) (from the tip of the rostrum to the posterior end of the telson) and carapace length (CL) (from the tip of the rostrum to the posterior dorsal end of the carapace) were measured for all specimens.

All specimens have been deposited at the Centre Oceanogràfic de les Balears, in Palma de Mallorca (Spain), with catalogue numbers Tunibal05_E1517Or215 and ID2_0710_E18N8.

4.4 Results

A total of eight *Palaemon macrodactylus* larvae were found in the summer samples. In 2005, one zoeal stage VI, with developed pleopods but without setae (Fig. 4.2) and measuring 4.8 mm TL and 1.5 mm CL, was found in the upper 70 m of the water column off southeastern Mallorca (Balearic Islands; 38°40.20’ N and 3°49.20’ E), at a sampling station situated over the 2000 m isobath (Fig. 4.4). In 2010, another seven specimens were found over the 900 m isobath off western Mallorca (39°51.00’ N and 2°14.40’ E; Fig. 4.4), all at the same sampling station and in the same depth layer (0-25 m). The 2010 larvae were zoeae in stage III: they had two dorsal spines on the carapace (Fig. 4.3c) and had not yet developed pleopods (Fig. 4.3a). In addition, in these larvae the sixth somite of the pleon was separated from the telson and uropods, consisting of rudimentary uro-endopods and setose uro-exopods (Fig. 4.3d). The seven specimens measured on average 2.55 mm TL (±0.11 SD) and 0.73 mm CL (±0.05 SD).

4.5 Discussion

We report the presence of *P. macrodactylus* larvae off the Balearic Islands, which is the first record of this species in the Mediterranean. Several hypotheses could be considered to explain the presence of these larvae. One would be that these larvae come directly from ballast water discharges, since previous studies have demonstrated that larvae remain viable in ship tanks (Chu et al. 1997). In fact, the first report of oriental shrimp larvae in the Guadalquivir estuary, the nearest place to our study area where this species has been recorded, proposed that ballast water was the vector of transport (Cuesta et al. 2004). However, this hypothesis is very unlikely considering that the larvae we found were very young, the sampling site is far from the main commercial shipping routes, and the larvae appeared in different years, forming a relatively dense patch in the last year. A second hypothesis would be that the larvae are transported by currents to our study area in the Balearic Sea from the nearest known settled adult population, since surface Atlantic water entering the Mediterranean from the Gulf of Cadiz, part of which later reaches the Balearic archipelago, would facilitate the spread of larvae to this sea. Taking into account the estimated age of the larvae collected in our samples, 4-5 days old (zoea III) and 13-15 days old (zoea VI), and the current velocities (Pinot et al. 2002), it is highly improbable that there is a connection between the Atlantic adult population and the larvae collected off the Balearic Islands. Finally, the third hypothesis would be that undetected adult populations have colonized nearby Mediterranean estuarine areas on the Spanish Mediterranean Levantine coast or in the Balearic archipelago. Therefore, the larvae found in 2010 northwest of Mallorca Island could have originated in any of the estuaries in this area, e.g. the Ebro Delta (Spain). Mainland coastal areas are mainly connected with the Balearic Sea through the Northern Current, which flows southwards along the continental margin and forms the Balearic Current, which flows along the northern margin of the Balearic Islands (Pinot et al. 2002, López-Jurado et al. 2008). However, it seems unrealistic that the larvae found in 2005 southeast of Mallorca could reach this area of the Balearic Islands from the Spanish coast in such a short time, given the predominant currents. It is much more probable that these larvae, and even those found in 2010, come from adult populations settled in the Balearic Islands. This archipelago does not have large estuaries, but there are several small areas of saline brackish waters as well as shallow marine areas with extensive seagrass beds (Del Hoyo 1992) that this species could inhabit. The dominant currents around the Balearic Islands explain why fish larvae from adults reproducing in coastal areas are found in open marine waters (Torres et al. 2011), and could also explain the presence of oriental shrimp larvae in these open marine waters.

The fact that the hypothetical *Palaemon macrodactylus* populations that have colonized some areas of the western Mediterranean have not yet been detected could be attributed to the fact that adult forms of some decapods are difficult to catch, for example *Jaxea nocturna*, for which the larvae were also found before the adults (Fitzgerald 1951). Another possibility is that, due to their morphological similarity, *P. macrodactylus* could be confused with the native *Palaemon serratus* and *Palaemon elegans*, which occupy the same habitats (González-Ortegón and Cuesta 2006). This often occurs within the framework of field sampling surveys not directed specifically at detecting allocthonous species, because if the analysis is not carried out by specialized taxonomists, individuals of non-native species can be attributed to similar congeneric native species.

In any case, the presence of these larvae in open marine waters, where have not been previously found, suggests that the life cycle strategies of this estuarine species could include exporting the larval stages to offshore marine areas, increasing their dispersal capacity in relation to estuarine species that spend their entire life cycle in brackish waters. This capacity to spread increases the possibilities of the oriental shrimp becoming an invasive species, and thus a potential problem for native carideans populations. It is possible that *P. macrodactylus* could compete successfully with these indigenous species for food and habitat, as Ashelby et al. (2004) suggested. Like many Mediterranean carideans, *P. macrodactylus* is largely carnivorous (Siegfried 1982), such as *Gnathophyllum elegans*, *Palaemon* spp., *Periclimenes* spp., *Pontophilus spinosus*, *Crangon crangon* and *Philocheras* spp. Interactions between *P. macrodactylus* and *Palaemon* spp. or *Crangon* spp., its congeneric genres in the Mediterranean, have been detected in several parts of the world (González-Ortegón et al. 2010). Since an invasive species can only be eradicated if it is detected in time, monitoring of all larval phases is crucial for minimizing the impact of bioinvasions, as suggested by González-Ortegón and Cuesta (2006).

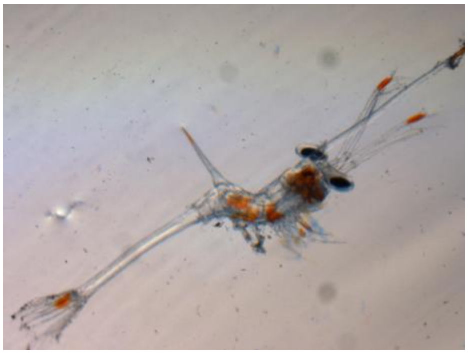
Summing up, this work proves that collecting early life history stages in the plankton can help to detect invasive species earlier and hopefully prevent their negative impacts.

Chapter 5
W Mediterranean decapod larval community

Torres AP, Dos Santos A, Balbín R, Alemany F, Massutí E and Reglero P-2014 Decapod crustacean larval communities in the Balearic Sea (western Mediterranean): seasonal composition, horizontal and vertical distribution patterns. Journal of Marine Systems, 138, pp. 112-126.

5.1 Abstract

Decapod crustaceans are the main target species of deep water bottom trawl fisheries in the Balearic Sea but little is known about their larval stages. This chapter focuses on the species composition of the decapod larval community, describing the main spatio-temporal assemblages and assessing their vertical distribution. Mesozooplankton sampling was carried out using depth-stratified sampling devices at two stations located over the shelf break and the mid slope, in the north-western and southern of Mallorca in late autumn 2009 and summer 2010. Differences among decapod larvae communities, in terms of composition, adult's habitat such as pelagic or benthic, and distribution patterns were observed between seasons, areas and station. Results showed that for both seasons most species and developmental stages aggregated within the upper water column (above 75 m depth) and showed higher biodiversity in summer compared to late autumn. Most abundant species were pelagic prawns (e.g. Sergestidae) occurring in both seasons and areas. The larval assemblages' distributions were different between seasonal hydrographic scenarios and during situations of stratified and no-stratified water column. The vertical distributions patterns of different larval developmental stages in respect to the adult's habitat were analyzed in relation to environmental variables. Fluorescence had the highest explanatory power. Four clearly different vertical patterns were identified: two corresponding to late autumn, which were common for all the main larval groups and other two in summer, one corresponding to larvae of coastal benthic and the second to pelagic species larvae.



5.2 Introduction

Most species of decapod crustaceans produce planktotrophic pelagic larvae that in some areas and seasons can constitute a dominant group of the meroplankton (Beaugrand 2005, Highfield et al. 2010). During their planktonic life they pass through many larval stages whose complexity varies among species, spending from hours to months in the pelagic environment before joining the parental population. Descriptions of decapod larvae communities are still rare for most places around the world (e.g. Brandão et al. 2013, Landeira et al. 2013). When available, they usually describe the nearshore communities (e.g. Fusté 1982, 1987, Paula 1987) because studies focusing on the spatial and temporal distribution of decapod larvae on estuarine or coastal waters are more accessible and hence monitoring less costly. Besides, there has been a worldwide interest to explain variations in larval supply rates in productive shelf areas, where physical processes such as seasonal upwelling can drive large larval mass to settle (e.g. Queiroga et al. 2007).

Decapod species associated with the continental shelf and slope tend to have a wide spatial offshore distribution, while those of coastal and nearshore species are usually found much closer to the coast (e.g. Dos Santos et al. 2008, Miller and Morgan 2013). The temporal spawning patterns tend to vary among species with some species reproducing in cold, some in warm months and others all year around (e.g. González-Gordillo and Rodríguez 2003, Pessani 1993).

Decapod larvae feed on phytoplankton, detritus and other zooplankton (Anger 2001). Therefore, we may expect rich communities of decapod larvae associated to areas of high primary productivity e.g. in coastal upwelling (Fusté and Gili 1991) or in eddies around oceanic islands (Landeira et al. 2009, 2010). Surface fronts and mesoscale eddies may act as spatial hotspots of larval densities since these structures may increase the availability of trophic resources to biological organisms (Bakun and Weeks 2006). Furthermore, protozoeal stages of the Dendrobranchiata are capable of retaining particles such as microorganisms, which can be crucial in oligotrophic waters where bacteria biomass is dominant over phytoplankton biomass and most carbon and nitrogen occur sequestered in bacteria (Cho and Azam 1990).

Within the general oligotrophic environment of the western Mediterranean, the waters around the Balearic Islands show an even more pronounced oligotrophy (Bosc et al. 2004, Fernández de Puelles et al. 2007). However, the biological production around the Balearic Sea during summer is partly associated to mesoscale oceanographic features, fronts and eddies which may result in punctual productive zones (Alcaraz et al. 2007, Estrada et al. 1993, Jansà et al. 1998). This could explain the relatively high abundances of other meroplanktonic groups, as fish larvae, aggregating in the area, especially during summer (Alemany et al. 2006, Torres et al. 2011). Therefore, we may expect the presence of high abundances of decapod crustacean larvae as well. In the western Mediterranean, most surveys targeting meroplankton have been conducted during summer, when the water column is stratified with a well defined thermocline. Below the thermocline a deep chlorophyll maximum (DCM) is temporally found (Estrada et al. 1993, Jansà et al. 1998), coinciding with the maximum concentration of zooplankton (Alcaraz et al. 2007, Saiz et al. 2007). In Mediterranean waters few studies address together all groups that constitute the meroplankton concluding that their abundance in general decreases in autumn (e.g. Vives 1966, Olivar et al. 2010). In the Balearic Islands, the mesozooplankton community shows a clear seasonal pattern with highest abundances during summer and lowest numbers during winter. However, significant peaks can be recorded in autumn, mainly due to an increase in copepod abundances (Fernández de Puelles et al. 2003).

Some macro-zooplankton crustacean species are believed to be capable of utilizing dominant currents and maintain their vertical position in the water column to avoid food limitation in the general oligotrophic environment (Andersen et al. 2004). Vertical ontogenetic migration has been shown to play an important role in larvae of benthic species since they are hatched from eggs carried by bottom-dwelling females, after release into the water column they tend to feed in the upper layers and return to the adult habitat to settle. In the case of benthic species, an ontogenetic final migration from upper layers of the water column to settle in the bottom near adults' habitats is also well established (see review Queiroga and Blanton 2004). Vertical migration behavior has been described for larvae that develop in estuarine, shelf, and oceanic waters (Queiroga and Blanton 2004) and is considered to be mainly performed by the need to feed and, at the same time, avoid predation (Pearre 2003).

In the western Mediterranean Sea some studies have considered the annual distribution of decapod larvae (e.g. Fusté 1982, 1987, Pessani 1993). Other studies have focused primarily on the summer season (Olivar et al. 1998). In an important area for crustacean fisheries, such as Balearic Islands, studies thus far have only focused on individual single species (Carbonell et al. 2010, Marco-Herrero et al. 2013, Torres et al. 2012, Torres et al. 2013).

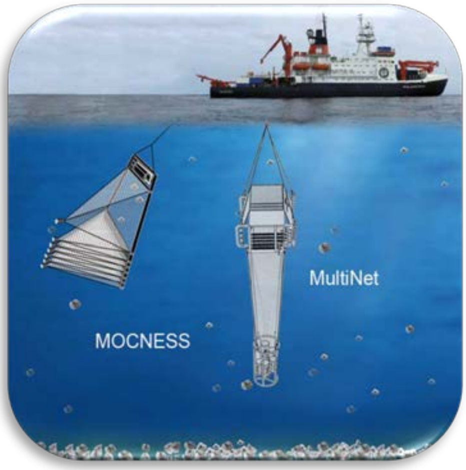
The southern part of Balearic Islands, that forms part of the Algerian sub-basin, during summer, receives new lower salinity surface water from the Atlantic (AW) and the hydrodynamics of this area are thus strongly influenced by this density gradient. To the northern, the Balearic sub-basin consists of colder and more saline Atlantic surface waters that has remained longer in the Mediterranean (resident AW), and its dynamics is affected by notable atmospheric forcing, mainly wind. The Western Intermediate Water (WIW) is a modification of the Atlantic waters, formed only during winter in the Gulf of Lion and the northern continental shelves of the north-western Mediterranean (from the Ligurian Sea to the Catalan coast), and is not a consistent feature found every year around at the Balearic channels (Monserrat et al. 2008, Vargas-Yáñez et al. 2012). As a consequence, there are significant differences between the general hydrodynamic conditions that affect the north and the south of the islands.

The present study is the first specific research on the decapod larval community off the Balearic archipelago. Our aim is to describe seasonal patterns in the composition of the decapod larvae community and assess differences between the shelf break and the slope regions and between Balearic and Argelian sub-basins. We characterize these communities according to their adult habitats i.e. if the adult stages have a pelagic or benthic life mode, their taxonomic group and their larval development stage. Our hypothesis is that decapod larvae communities will be different for the two seasons and that both will be characterized mainly by larvae of pelagic species. In addition, the northern study area where the shelf is narrower and the slope is quite pronounced, the currents over the shelf created mixed conditions. In this case we expect to have an important component of larvae from coastal species in the northern stations, at least during warm season. Taking into account the resources availability for the oligotrophic Mediterranean Sea we analyze and discuss environmental variables vertical distribution and their effect on the larval vertical distribution from pelagic or benthic adult's habitat in relation with the main oceanographic features of the area.

5.3 Material and methods

5.3.1 Sampling methodology

Two multidisciplinary research surveys were conducted off the Balearic archipelago (western Mediterranean; Fig. 5.1) during late autumn (29th November to 18th December 2009) and summer (11 to 30th July 2010) on board the R/V *Sarmiento de Gamboa*. We sampled a total of 4 stations during each cruise. One station was located over the shelf break (250 m depth) and the other over the mid slope (900 m depth) off the north-western (N), in Balearic sub-basin. The other two stations were also located in the shelf break and the mid slope but in the southern (S) of the Mallorca Island, in Algerian sub-basin. In each station we conducted repeated stratified hauls continuously during 36 hours. A total of 34 hauls resulting in 218 depth-stratified samples were sampled for decapod larvae. The hauls were distributed as: 5 hauls in the northern during late autumn, 13 hauls in the southern during late autumn, 8 hauls in the northern during summer and 8 hauls in the southern during summer (Fig. 5.1).



Graphics: Erika Mackay, photo of Polarstern: Peter Wiebe, WHOI

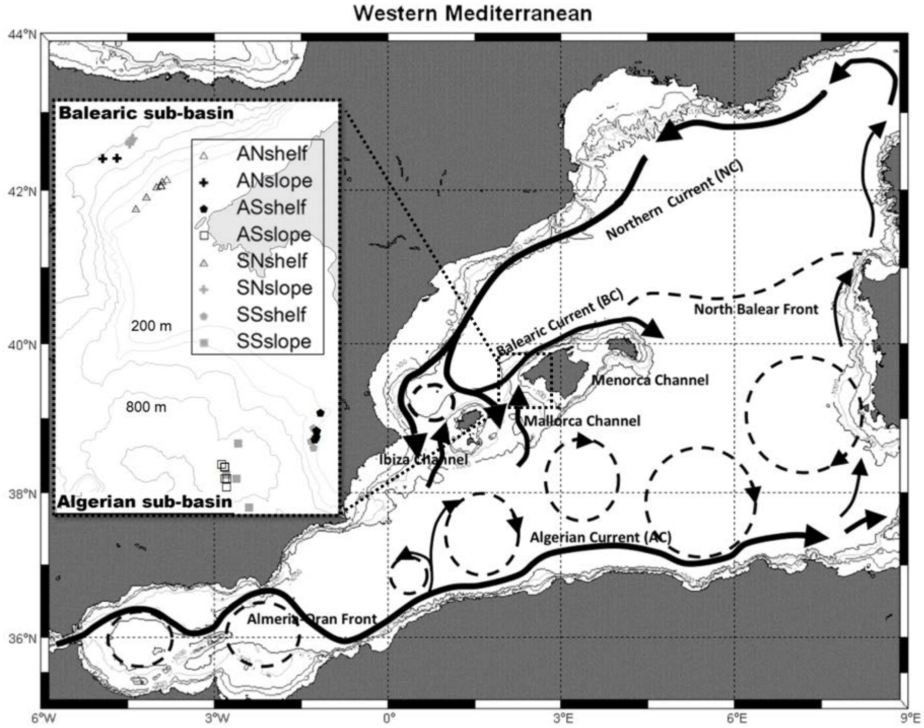


Figure 5.1. The study area and main hydrographic features. The Mallorca and Ibiza channels, the Northern and Balearic Currents, and the Algerian Gyres are indicated. Study area (framed and dotted) with haul's position during late autumn (A) 2009 (black) and summer (S) 2010 (grey), at four plankton stations located over shelf break (250 isobath) and mid slope (900 isobath) off the northwest (N) (Balearic sub-basin) and southern (S)(Algerian sub-basin) of Mallorca Island. Grey lines indicate isobaths (200, 400, 600, 800 and 1000 m).Seasonal stations symbols: (Δ) Northern shelf break; (+) Northern mid slope; (♦) Southern shelf break; (□) Southern mid slope.

The samples were collected in late autumn using an HYDRO-BIOS MultiNet sampling five depth strata and in summer with a Multiple Opening-Closing Net and Environmental Sensing System (MOCNESS) sampling seven depth strata (Olivar et al. 2012). The net mouth openings were 0.25 and 1 m^2, respectively, and the mesh size was 333 µm for both nets. Both devices were towed at ~2 knots. The volume of water filtered in each layer varied from 44 to 2414 m^3, depending on the depth range of the layer sampled. The whole water column from a given depth relatively close to the bottom was sampled and the thickness of each layer varied depending on the bathymetry and the season (Table 5.1). Immediately after collection all samples were preserved in ~5 % borax-buffered formaldehyde, prepared using seawater. Once in the laboratory, samples were subsequently sorted for crustacean decapod larvae, which were identified to species level and developmental stage, whenever possible, using available descriptions (Dos Santos and Lindley 2001, Dos Santos and González-Gordillo 2004).

Late autumn (2009)		Summer (2010)	
Shelf break (m)	Mid slope (m)	Shelf break (m)	Mid slope (m)
0-30	0-60	0-25	0-25
30-60	60-200	25-50	25-50
60-90	200-350	50-75	50-75
90-120	350-600	75-100	75-125
120-200	600-850	100-125	125-200
		125-150	200-400
		150-200	400-500

Table 5.1. Depth strata level with the thickness of each layer in meters during the late autumn and summer surveys over the shelf break and the mid slope stations.

Geostrophic velocities at surface were obtained for both seasons from satellite altimetry data (Fig. 5.2a and 5.2b), which were downloaded from MyOcean (Bahurel et al. 2009). Delay Time data gridded into a Map of Absolute Dynamic Topography (DT-MADT) was used (Aviso 2012). Hydrographic measurements were recorded using a CTD (SBE911) at the four plankton stations (Fig. 5.3a-5.3h). A salinity value of < 37.0 is the criterion used to identify the fresher Atlantic water (AW), and that of > 37.5 was used to identify resident AW. We refer to water with intermediate salinity values between 37.0 – 37.5 as mixed AW.

Vertical profiles of potential temperature, salinity and fluorescence were averaged at 1 m intervals to depict the vertical structure of the 200 first meters of water column and also θ − S diagrams were performed, based on potential temperature and salinity, to describe the water masses. The fluorescence concentration at the different depths was used as a proxy for food availability. Temperature values were used to describe the position of the thermocline and the thermal characteristics of the water column. Salinity was used to identify different water masses.

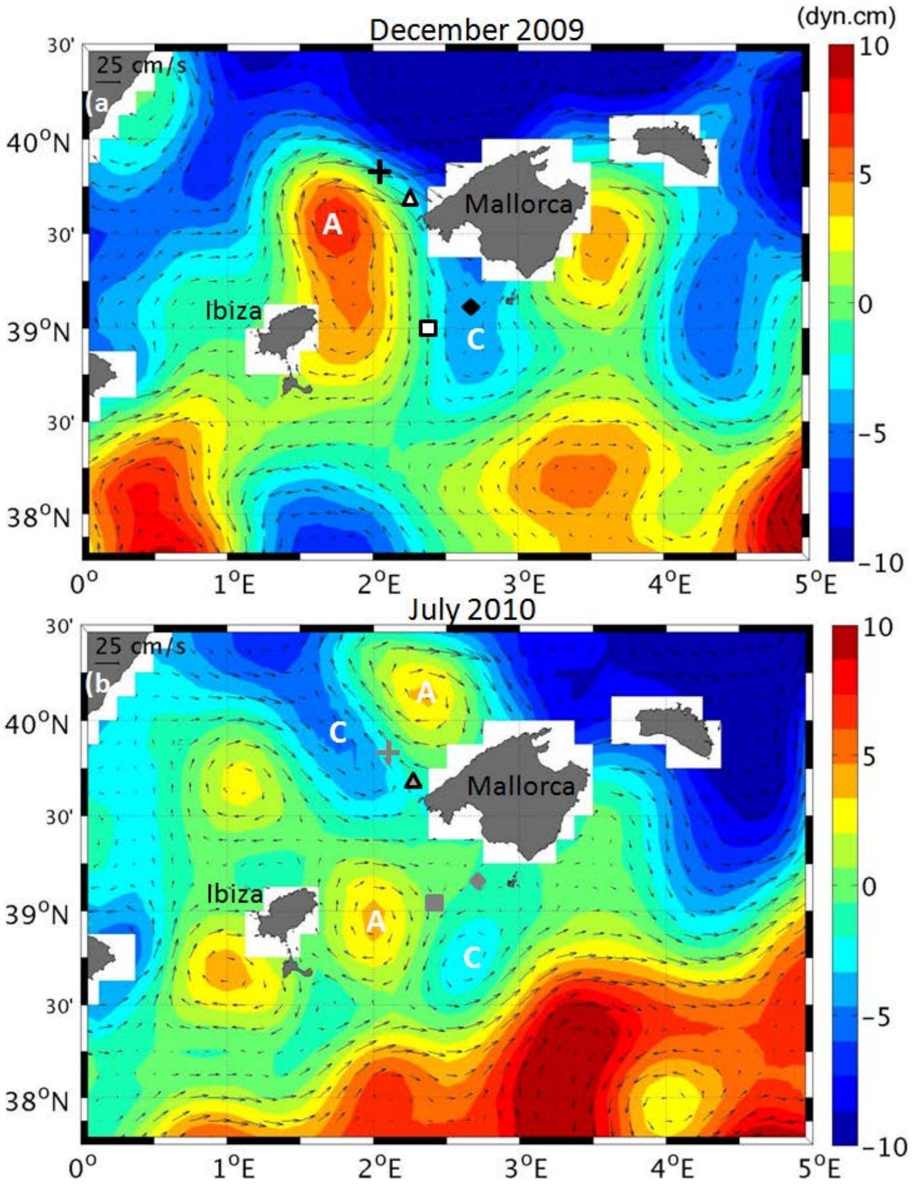


Figure 5.2. Map of absolute dynamic topography and surface derived geostrophic currents at study area during late autumn in 2009 (a) and summer in 2010 (b) with hydrographic stations and structures (A: Anticyclonic eddie; C: Cyclonic eddie) Stations symbols: (Δ) Northern shelf break; (+) Northern mid slope; (♦) Southern shelf break; (☐) Southern mid slope

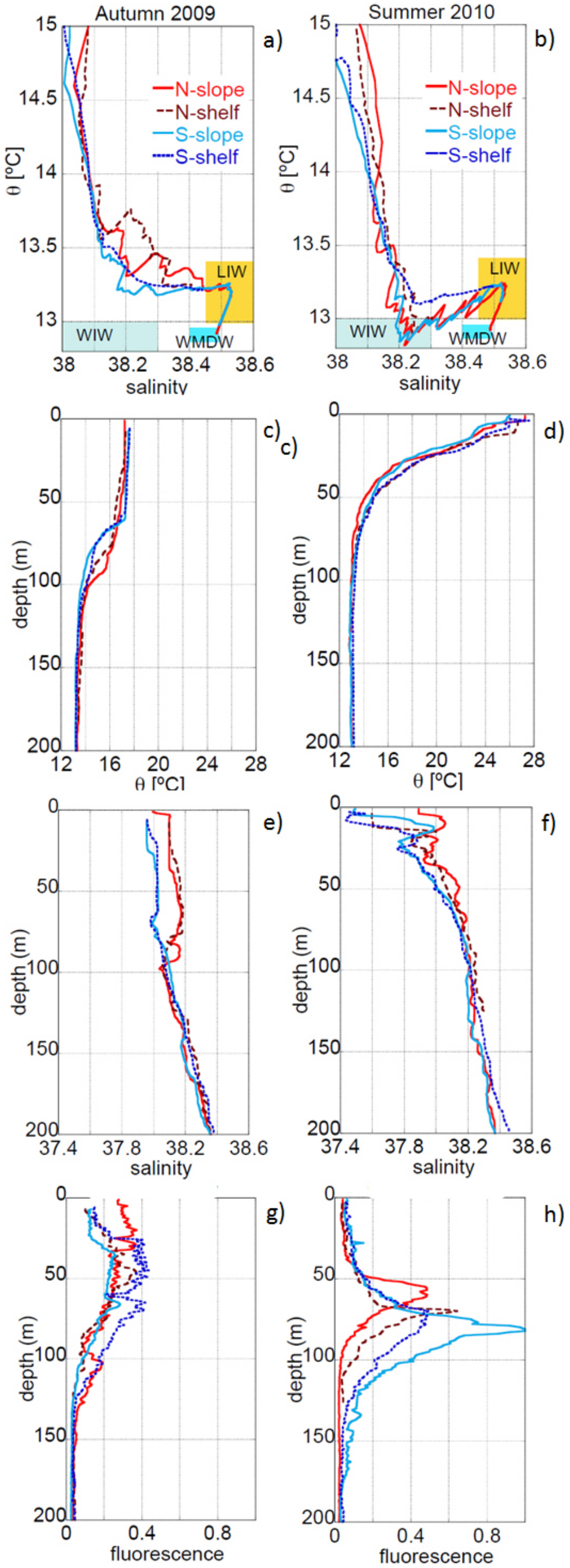


Figure 5.3. Seasonal θ – S diagram with colour boxes indicating the different water masses (a, b), potential temperature (c, d), salinity (e, f) and fluorescence (g, h) vertical profiles at four stations. For TS profiles below 50 m to bottom were plotted and the rest of variables from surface down to 200 m.

Stations lines: red: Northern mid slope; dark red dotted: Northern shelf break; blue: Southern mid slope; dark blue dotted: Southern shelf break

Water masses: Levantine Intermediate Water (LIW), Western Mediterranean Intermediate Water (WIW) and Western Mediterranean Deep Water (WMDW)

5.3.2 Spatial and seasonal larval distribution analysis

The species richness has been analyzed by means of dominance plots usually used to evaluate ecosystem status. Cumulative dominance percentage of species were calculated as the proportion of total hauls, by season, areas and sampling stations, where a species was present.

Density estimates of the organisms at each depth stratified sample were standardized to number of individuals per 100 m^3 at lowest taxonomic level identified, for each area and season. The frequency of occurrence of each taxonomic level was calculated. The species were grouped by their taxa group and their adult habitat to analyze their contributions to the larval community. Regarding their corresponding taxa group the decapod larval species were grouped in 7 categories as presented in Table 5.2 under the taxa column. According to their adult's habitat the larvae were assigned to 11 groups as presented in the column Adults Habitat in Table 5.2. To assess the vertical distribution of the larvae, besides the adult habitat classification we separated the larvae by ontogenetic developmental stage.

Differences in the composition of the assemblages of the larval community in the first 200 m, during late autumn and summer and at the four stations per season, were analyzed using nonparametric multivariate analysis applied to densities of the larvae (Clarke 1993). Prior to the analysis, data were squared root transformed in order to prevent the dominant larval species from masking the responses of those with low densities (Clarke and Warwick 2001). The Bray–Curtis similarity index was chosen as the similarity coefficient and the group average was used as the clustering algorithm (Clarke and Warwick 2001). Cluster analysis and their corresponding two-dimensional representations by Multidimensional scaling ordination (MDS) were used to identify larval assemblages during both seasons. Stress coefficients with values <0.15 indicate that the data are portrayed well (Clarke and Gorley 2006). We calculated the percentage contribution of average densities of the dominants groups by adult's habitat for main larval assemblage described by Cluster (SIMPER analysis).

Decapod larvae pass through several developmental stages that were merged in 2 groups to analyze their vertical distribution. A first group named stage 1 included the first zoeal stages (Z) and a second group named stage 2 included the advanced zoeal stages. The second developmental group (stage 2) never included megalopal or decapodite stages.

5.3.3 Vertical larval distribution analysis

The seasonal vertical distribution patterns for the main larval taxa belonging to the more representative adults' origin (coastal epibenthic, coastal nektobenthic, epipelagic and mesopelagic) were analyzed within the first 200 meters of the water column, where most decapod larvae were found (up to 90.7 % and 93.7 % of the total density in autumn and summer, respectively). General Linear Models (GLMs) were used to analyze the environmental variables that could drive the larval vertical distributions. Temperature, salinity and fluorescence were used as continuous co-variables and larval density as the independent variable. Area (northern and southern) and station (shelf break and mid slope) were included in the model as factors.

5.4 Results

5.4.1 Hydrographic conditions

In the upper layers, during late autumn, a well defined anticyclonic gyre at the north of Ibiza deflected Northern Current waters (Fig 5.2a). The southern area was mainly under the influence of a cyclonic gyre formed by resident Atlantic waters (AW) re-circulated from the Balearic sub-basin and flowing from coastal areas at the east of Mallorca (Fig. 5.2a). During summer, we observed an anticyclonic gyre in the northern area, but situated slightly northwards and affecting mostly the slope and a cyclonic meander to the south-western. In contrast, the southern area was mostly occupied by an anticyclonic gyre of recent Atlantic Waters, detached from the main current of recent Atlantic Waters flowing in SW-NE direction at the south of the archipelago, trapped at the east of Ibiza Island (Fig. 5.2b). The geostrophic currents during late autumn reached higher values than during summer (Fig. 5.2a and b).

Therefore, there were contrasting hydrographic conditions between the late autumn and summer seasons (Fig. 5.2 and 5.3) due to (a) the income of new AW in the upper layers in summer, (b) the seasonal differences in the presence / absence of Western Intermediate Waters (WIW) and (c) the stratification of the water column (Fig. 5.3).

The water masses found at the surface during both surveys were different. Thus, during late autumn we could find only resident surface Atlantic Waters in both areas (Fig. 5.3a) whereas in summer we also observed mixed Atlantic waters in the southern (Fig. 5.3b).The seasonal differences in WIW are clearly observed in the θ – S diagrams, indicating absence of WIW (Fig. 5.3a) during autumn, whereas during summer three of the stations showed the presence of WIW (Fig. 5.3b).

The water column was stratified in summer whereas in late autumn conditions were of mixed layer without clear clines. More specifically, the temperature in the upper layers was colder in late autumn, around 17ºC, whereas in summer temperatures up to 26ºC and 27ºC were recorded (Fig. 5.3c and d). In late autumn the surface waters were saltier (~38) than during summer, when the income of recent AW resulted in the presence of less saline waters (37.5 – 37.9) (Fig. 5.3e and f). Regarding surface fluorescence values, in autumn (range between 0.1 – 0.3; Fig. 5.3g) were higher than in summer (~0.05; Fig. 5.3h). The vertical profiles of the environmental variables during the late autumn survey were homogeneously distributed down to the mixing layer depth (MLD), located at 60 and 80 m depth in the southern and the northern, respectively (Fig.5.3c, e and g).

In summer, environmental variables showed strong gradients in the upper 100 meters. A shallow MLD of around 10-13 m and a thermocline located between 10 to 50 m depth was observed in the summer, in both areas (Fig. 5.3d). During late autumn no halocline was detected and in summer halocline was located between 5 to 25 m depth, when surface waters were influence by wind (Fig. 5.3e and f). Deep fluorescence maximums with values between 0.4 and 1 were found below the MLD between 50 and 80 m depth in summer (Fig. 5.3h). The maximum fluorescence peak was located over slope in the southern study area, at 80 m depth, and the minimum in northern area also over the slope, at 55 m depth, which in addition represented the shallowest registered depth of such fluorescence peak.

5.4.2 Assemblage composition, seasonal and horizontal larval distribution

The list of all taxa identified in the samples with total individuals identified for each season and the mean densities for same season and in the same area are given in

Table 5.2. From the total of 121 taxa found, 19 were identified at family level (or higher), 27 at genus level and 75 at species level. Most of them appeared only in summer (63), whereas only 7 were exclusively present in late autumn. In terms of the main decapod taxa groups, the most abundant in the samples were shrimps (Dendrobranchiata) larvae that accounted for 63 % of the total decapod larvae sampled during late autumn and 52 % in summer, followed by crabs species (Brachyura) for late autumn, with 18 %, and in summer by caridean shrimps, with 32 %. The minor groups during both seasons were, in order of abundance, hermit crabs, squat lobsters, slipper lobster and ghost shrimps. Regarding the origin of the larvae, they were mainly constituted by species from mesopelagic and epipelagic habitats, comprising around 57 % of the total captures.

Shrimps larvae during autumn were mainly *Gennadas elegans*, whereas in summer *Parasergestes vigilax* and *Eusergestes arcticus* were the most abundant ones. Mean densities of *G. elegans* during late autumn were about 14.5 ind. per 100 m^3 (±8.7) in northern stations to 6.1 ind. per 100 m^3 (±3.8) in southern stations (Table 5.2). The crab species *Goneplax rhomboides*, second in order of abundance during the fall season, appeared only in the southern, with mean abundances of 2.9 ind. per 100 m^3 (±4.3). *E. arcticus* and *Plesionika* spp. registered important abundances as well in this season. The summer's most abundant species was *P. vigilax,* showing densities from 1.8 ind. per 100 m^3 (±2.6) in the northern area to 2.2 ind. per 100 m^3 (±3.4) in the southern. Three crab taxa exclusively found in summer and relatively abundant were *Parthenope* spp., *Ebalia* spp. and *Xantho* spp., followed by hermit crabs such as *Calcinus tubularis*.

Table 5.2. The seasonal number of decapods larvae (N), their seasonal and area (northern and southern stations) frequency of occurrence (F) and the average density (ρ) over the water column (number of larvae/100 m^3 ± SD) of the different taxa identified, during late autumn (2009) and summer (2010). A classification of the different taxa according to their adult habitats is provided. (^)Exclusively autumn appearance and (*) exclusively summer appearance

		Late autumn					Summer				
			Northern		Southern			Northern		Southern	
Taxa	Adults Habitat	N	F (%)	ρ ± SD	F (%)	ρ ± SD	N	F (%)	ρ ± SD	F (%)	ρ ± SD
SHRIMPS (Dendrobranchiata)											
**Allosergestes sargassi*	mesopelagic						7	50.00	0.02 ± 0.02	50.00	0.01 ± 0.02
**Aristeus antennatus*	oceanic epibenthic						3	25.00	0.01 ± 0.02	25.00	0.01 ± 0.01
^Dendrobranchiata n. id.	-	1	20.00	0.02 ± 0.05							
Deosergestes corniculum	epipelagic	2			15.38	0.02 ± 0.05	70	100.00	0.14 ± 0.11	75.00	0.12 ± 0.22
Deosergestes henseni	mesopelagic	2	20.00	0.02 ± 0.05	7.69	0.01 ± 0.05	162	87.50	0.26 ± 0.25	100.00	0.48 ± 0.55
Eusergestes arcticus	mesopelagic	256	100.00	3.92 ± 2.98	61.54	0.46 ± 0.51	616	100.00	1.94 ± 2.61	100.00	0.97 ± 0.87
Gennadas elegans	mesopelagic	1445	100.00	14.53 ± 8.73	100.00	6.05 ± 3.81	132	75.00	0.10 ± 0.11	100.00	0.57 ± 0.50
**Lucifer typus*	epipelagic						1	12.50	0.01 ± 0.01		
Parapenaeus longirostris	oceanic epibenthic	1	0.00		7.69	0.01 ± 0.05	1			12.50	0.01 ± 0.02
Parasergestes vigilax	epipelagic	4	20.00	0.04 ± 0.08	23.08	0.03 ± 0.06	887	100.00	1.77 ± 2.67	100.00	2.21 ± 3.43
Sergestes atlanticus	epipelagic	12	20.00	0.28 ± 0.64	23.08	0.04 ± 0.09	23	62.50	0.05 ± 0.06	62.50	0.04 ± 0.04
Sergestes spp.	epipelagic	12	40.00	0.05 ± 0.06	46.15	0.13 ± 0.18	277	100.00	0.72 ± 0.33	87.50	0.49 ± 0.48
Sergestidae n.id.	-	116	100.00	1.83 ± 0.68	53.85	0.29 ± 0.39	97	87.50	0.23 ± 0.37	100.00	0.26 ± 0.17
Sergia robusta	mesopelagic	140	80.00	2.35 ± 3.03	69.23	0.47 ± 0.47	160	87.50	0.49 ± 0.54	87.50	0.20 ± 0.20
**Sergia splendens*	mesopelagic						2	12.50	0.01 ± 0.03		
Sergia spp.	mesopelagic	22	80.00	0.44 ± 0.48	23.08	0.03 ± 0.06	1	12.50	0.01 ± 0.01		
Solenocera membranacea	coastal nektobenthic	28	20.00	0.05 ± 0.11	69.23	0.32 ± 0.37	126	100.00	0.52 ± 0.66	50.00	0.24 ± 0.28
CARIDEAN SHRIMPS (Caridea)											
Acanthephyra spp.	meso/bathypelagic	27	80.00	0.32 ± 0.36	76.92	0.17 ± 0.17	102	87.50	0.36 ± 0.22	75.00	0.05 ± 0.06
**Aegaeon spp.*	cosmopolite epibenthic						22	62.50	0.12 ± 0.15	25.00	0.02 ± 0.04
Alpheus glaber	cosmopolite nektobenthic	32	40.00	0.05 ± 0.08	53.85	0.44 ± 0.63	144	87.50	0.54 ± 0.46	75.00	0.22 ± 0.24
Alpheus spp.	cosmopolite nektobenthic	10			30.77	0.13 ± 0.35	185	100.00	0.61 ± 0.96	50.00	0.05 ± 0.11
Athanas nitescens	coastal epibenthic	7	20.00	0.01 ± 0.03	30.77	0.11 ± 0.17	24	75.00	0.09 ± 0.15	25.00	0.04 ± 0.07
^Brachycarpus biunguiculatus	coastal epibenthic	1			7.69	0.02 ± 0.07					

Table 5.2 (continued)		Late autumn					Summer				
			Northern		Southern			Northern		Southern	
Taxa	Adults Habitat	N	F (%)	ρ ± SD	F (%)	ρ ± SD	N	F (%)	ρ ± SD	F (%)	ρ ± SD
Caridea n. id.	-	12			23.08	0.08 ± 0.17	5	12.5	0.01 ± 0.02	37.5	0.02 ± 0.04
*_Caridion steveni_	coastal epibenthic						1			12.5	0.01 ± 0.02
*_Chlorotocus crassicornis_	oceanic epibenthic						1	12.5	0.01 ± 0.02		
Eualus cranchii	coastal epibenthic	3			23.08	0.05 ± 0.1	45	75	0.17 ± 0.32	37.5	0.11 ± 0.16
*_Eualus occultus_	coastal epibenthic						7	25	0.04 ± 0.1	12.5	0.01 ± 0.02
Eualus spp.	coastal epibenthic	1			7.69	0.02 ± 0.08	28	75	0.05 ± 0.04	50	0.11 ± 0.18
Hippolytidae n.id.	coastal epibenthic	8	20	0.02 ± 0.1	46.15	0.08 ± 0.11	24	75	0.1 ± 0.13	62.5	0.05 ± 0.06
*_Lysmata seticaudata_	intertidal nektobenthic						1	12.5	0.01 ± 0.01		
*_Lysmata spp._	intertidal nektobenthic						20	75	0.08 ± 0.07	12.5	0.01 ± 0.01
*_Palaemon elegans_	intertidal nektobenthic						1	12.5	0.01 ± 0.02		
*_Palaemon macrodactylus_	intertidal nektobenthic						7	12.5	0.02 ± 0.06		
*_Palaemon spp._	intertidal nektobenthic						1	12.5	0.01 ± 0.01		
*Palaemonidae n.id	intertidal nektobenthic						1	12.5	0.01 ± 0.02		
Pandalidae n.id.	-	9			38.46	0.09 ± 0.19	44	87.5	0.12 ± 0.12	75	0.14 ± 0.18
Pandalina brevirostris	coastal nektobenthic	8			46.15	0.09 ± 0.12	78	62.5	0.35 ± 0.47	87.5	0.15 ± 0.13
*_Pasiphaea sivado_	cosmopolite epibenthic						3	25	0.01 ± 0.02	12.5	0.01 ± 0.02
^_Philocheras echinulatus_	oceanic epibenthic	6	20	0.04 ± 0.1	30.77	0.09 ± 0.17					
*_Philocheras fasciatus_	intertidal epibenthic						2	25	0.01 ± 0.02		
Philocheras sculptus	coastal epibenthic	5			38.46	0.09 ± 0.12	3	12.5	0.01 ± 0.04	12.5	0.01 ± 0.02
^_Philocheras spp._	oceanic epibenthic	2			7.69	0.04 ± 0.16					
Philocheras trispinosus	intertidal epibenthic	2			15.38	0.03 ± 0.08	1	12.5	0.01 ± 0.02		
*Pleocyemata n. id.	-						1			12.5	0.01 ± 0.02
Plesionika spp.	coastal nektobenthic	103	60	0.11 ± 0.1	100	1.54 ± 1.85	370	100	1.32 ± 1.33	100	0.85 ± 1.03
*_Pontonia spp._	coastal epibenthic						3	12.5	0.01 ± 0.01	12.5	0.01 ± 0.02
*Pontoniinae n.id.	coastal epibenthic						14	50	0.04 ± 0.06	50	0.02 ± 0.03
Processa canaliculata	oceanic epibenthic	6	40	0.04 ± 0.1	23.08	0.06 ± 0.13	42	62.5	0.29 ± 0.4	12.5	0.01 ± 0.02
Processa edulis edulis	intertidal epibenthic	13			53.85	0.2 ± 0.24	51	100	0.25 ± 0.23	50	0.03 ± 0.05
*_Processa macrodactyla_	coastal epibenthic						5	25	0.04 ± 0.08		
*_Processa modica caroli_	coastal epibenthic						8	25	0.04 ± 0.08	12.5	0.01 ± 0.01
Processa modica modica	coastal epibenthic	1	20	0.02 ± 0.1			1	12.5	0.01 ± 0.01		

Table 5.2 (continued)		Late autumn					Summer				
			Northern		Southern			Northern		Southern	
Taxa	Adults Habitat	N	F (%)	ρ ± SD	F (%)	ρ ± SD	N	F (%)	ρ ± SD	F (%)	ρ ± SD
Processa nouveli	coastal epibenthic	3			23.08	0.05 ± 0.1	27	87.5	0.12 ± 0.13	50	0.03 ± 0.03
Processa spp.	oceanic epibenthic	35	20	0.07 ± 0.2	61.54	0.5 ± 0.57	78	87.5	0.4 ± 0.53	87.5	0.11 ± 0.11
Processa elegantula	coastal epibenthic	3			15.38	0.06 ± 0.16	7	37.5	0.04 ± 0.07		
**Stenopus spinosus*	cosmopolite epibenthic						4	37.5	0.02 ± 0.02		
HERMIT CRABS (Paguridae and Diogenidae)											
Anapagurus spp.	cosmopolite epibenthic	25	20	0.01 ± 0	38.46	0.42 ± 0.71	20	50	0.02 ± 0.02	50	0.1 ± 0.12
**Calcinus tubularis*	intertidal epibenthic						144	87.5	0.44 ± 0.89	12.5	0.01 ± 0.02
**Clibanarius erythropus*	intertidal epibenthic						2	12.5	0.01 ± 0.02		
**Dardanus arrosor*	coastal epibenthic						7	37.5	0.02 ± 0.03	12.5	0.01 ± 0.02
**Diogenes pugilator*	intertidal epibenthic						6	37.5	0.03 ± 0.05		
**Nematopagurus longicornis*	oceanic epibenthic						8	12.5	0.01 ± 0.02	37.5	0.05 ± 0.07
**Pagurus cuanensis*	coastal epibenthic						1	12.5	0.01 ± 0.02		
Pagurus spp.	cosmopolite epibenthic	16	20	0.04 ± 0.1	53.85	0.24 ± 0.27	11	50	0.03 ± 0.04	25	0.01 ± 0.02
GHOST SHRIMPS (Axiidea and Gebiidea)											
**Callianassa subterranea*	endobenthic						1	12.5	0.01 ± 0.01		
Callianassidae n.id.	endobenthic	1			7.69	0.01 ± 0.03	6	50	0.04 ± 0.05		
**Necallianassa truncata*	endobenthic						7			37.5	0.05 ± 0.08
**Upogebia deltaura*	endobenthic						2	12.5	0.01 ± 0.04		
**Upogebia pusilla*	endobenthic						1	12.5	0 ± 0.01		
**Upogebia spp.*	endobenthic						1	12.5	0.01 ± 0.01		
SLIPPER LOBSTER (Scyllaridae)											
**Scyllarides latus*	coastal epibenthic						1	12.5	0.01 ± 0.01		
**Scyllarus arctus*	coastal epibenthic						2	12.5	0.01 ± 0.04		
**Scyllarus pygmaeus*	coastal epibenthic						1	12.5	0.01 ± 0.01		
Scyllarus spp.	coastal epibenthic	1			7.69	0.01 ± 0.05	8	12.5	0.02 ± 0.06	37.5	0.02 ± 0.04
SQUAT LOBSTERS (Galatheidae, Porcellanidae and Polychelidae)											
Galathea dispersa	coastal epibenthic	1			7.69	0.02 ± 0.06	5			37.5	0.02 ± 0.03
Galathea FSL21	-	1			7.69	0.01 ± 0.05	19	50	0.09 ± 0.16	37.5	0.04 ± 0.07
Galathea intermedia	coastal epibenthic	9			46.15	0.13 ± 0.19	2	25	0.01 ± 0.03		
Galathea n.id.	coastal epibenthic	2				0.03 ± 0.07	2	25	0.01 ± 0.02		
Galathea S22	-	1	20	0.04 ± 0.1			24	87.5	0.15 ± 0.21		

Table 5.2 (continued)

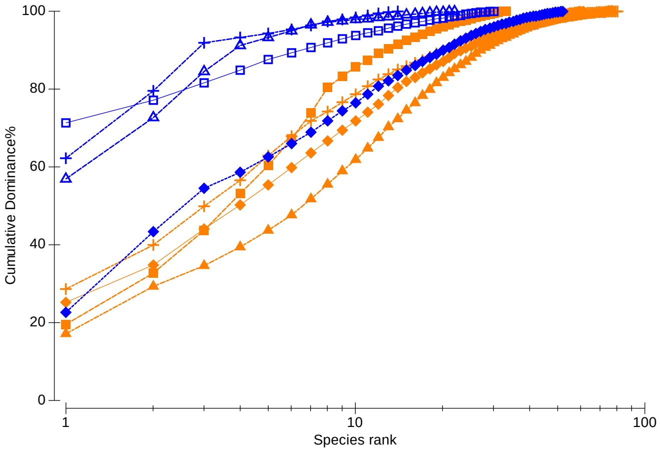
		Late autumn					Summer				
			Northern		Southern			Northern		Southern	
Taxa	Adults Habitat	N	F (%)	ρ ± SD	F (%)	ρ ± SD	N	F (%)	ρ ± SD	F (%)	ρ ± SD
Polychelidae n. id.	oceanic epibenthic	2			7.69	0.01 ± 0.02	21	25	0.02 ± 0.03	50	0.04 ± 0.07
CRABS (Brachyura)											
*_Acanthonyx lunulatus_	coastal epibenthic						5	12.5	0.02 ± 0.04		
^_Achaeus cranchii_	coastal epibenthic	1			7.69	0.01 ± 0.05					
*_Atelecyclus rotundatus_	coastal epibenthic						4	25	0.01 ± 0.02	12.5	0.01 ± 0.02
*_Atelecyclus sp._	coastal epibenthic						1			12.5	0.01 ± 0.02
^_Achaeus cranchii_	coastal epibenthic	1			7.69	0.01 ± 0.05					
*_Atelecyclus rotundatus_	coastal epibenthic						4	25	0.01 ± 0.02	12.5	0.01 ± 0.02
*_Atelecyclus sp._	coastal epibenthic						1			12.5	0.01 ± 0.02
Bathynectes spp.	coastal nektobenthic	6	20	0.04 ± 0.1	30.77	0.08 ± 0.15	1			12.5	0.01 ± 0.02
Brachyura n.id.	-	4	20	0.04 ± 0.1	15.38	0.04 ± 0.1	6	25	0.02 ± 0.06	25	0.01 ± 0.02
*_Calappa granulata_	oceanic epibenthic						41	62.5	0.13 ± 0.2	25	0.01 ± 0.02
*_Carcinus aestuarii_	intertidal epibenthic						1			12.5	0.01 ± 0.02
*_Corystes cassivelaunus_	coastal epibenthic						1	12.5	0.01 ± 0.02		
*_Distolambrus maltzami_	oceanic epibenthic						1	12.5	0.01 ± 0.02		
*_Dorhynchus thomsoni_	oceanic epibenthic						1	12.5	0.01 ± 0.01		
Ebalia spp.	oceanic epibenthic	26	20	0.15 ± 0.3	53.85	0.34 ± 0.54	78	100	0.32 ± 0.23	87.5	0.07 ± 0.05
*_Ergasticus clouei_	oceanic epibenthic						5			25	0.03 ± 0.06
*_Eriphia verrucosa_	intertidal epibenthic						1	12.5	0.01 ± 0.01		
*_Ethusa mascarone_	coastal epibenthic						4	25	0.02 ± 0.04		
^_Eurynome spp._	coastal epibenthic	3			23.08	0.05 ± 0.09					
Goneplax rhomboides	coastal epibenthic	172			76.92	2.94 ± 4.32	37	62.5	0.22 ± 0.25	37.5	0.01 ± 0.02
*Heterotremata	-						1	12.5	0.01 ± 0.01		
*_Homola barbata_	cosmopolite epibenthic						4	25	0.01 ± 0.01	25	0.01 ± 0.03
*_Ilia nucleus_	coastal epibenthic						5			50	0.03 ± 0.04
^_Liocarcinus depurator_	intertidal epibenthic	2			7.69	0.04 ± 0.16					
Liocarcinus spp.	intertidal epibenthic	33			69.23	0.51 ± 0.8	23	87.5	0.07 ± 0.05	37.5	0.04 ± 0.06
*_Macropodia sp._	coastal epibenthic						1	12.5	0.01 ± 0.02		
*_Maja sp._	coastal epibenthic						2	12.5	0.01 ± 0.02		
*_Maja squinado_	coastal epibenthic						1	12.5	0.01 ± 0.01		
Majidae n.id.	coastal epibenthic	2	20	0.04 ± 0.1	7.69	0.02 ± 0.08	7	12.5	0.01 ± 0.01	25	0.04 ± 0.07

Table 5.2 (continued)		Late autumn					Summer				
			Northern		Southern			Northern		Southern	
Taxa	Adults Habitat	N	F (%)	ρ ± SD	F (%)	ρ ± SD	N	F (%)	ρ ± SD	F (%)	ρ ± SD
**Monodaeus couchii*	oceanic epibenthic						50	87.5	0.27 ± 0.33	12.5	0.01 ± 0.02
**Nepinnotheres pinnotheres*	coastal epibenthic						9	37.5	0.03 ± 0.05		
**Pachygrapsus marmoratus*	intertidal epibenthic						2			25	0.01 ± 0.02
**Pachygrapsus spp.*	intertidal epibenthic						15	37.5	0.05 ± 0.1	25	0.01 ± 0.02
Parthenope spp.	cosmopolite epibenthic	11			38.46	0.13 ± 0.22	81	100	0.33 ± 0.2	62.5	0.06 ± 0.09
Pilumnus spp.	coastal epibenthic	2			7.69	0.04 ± 0.16	12	50	0.04 ± 0.05		
**Pirimela denticulata*	coastal epibenthic						1	12.5	0.01 ± 0.02		
*Plagusiidae n.id.	coastal epibenthic						8	12.5	0.03 ± 0.07		
Polybiidae n.id.	coastal nektobenthic	19	20	0.04 ± 0.1	30.77	0.35 ± 1.08	2	25	0.01 ± 0.02		
*Porcellanidae n.id.	coastal epibenthic						1	12.5	0.01 ± 0.01		
*Portunidae n.id.	-						23	12.5	0.01 ± 0.02	50	0.15 ± 0.19
**Thia scutellata*	coastal epibenthic						3	25	0.02 ± 0.04		
Xantho spp.	coastal epibenthic	1			7.69	0.01 ± 0.05	102	100	0.33 ± 0.64	25	0.01 ± 0.02
*Xanthoidea n. id.	-						1	12.5	0.01 ± 0.01		
Total		2679		24.6 ± 14		17.3 ± 12.1	4769		14.5 ± 6.85		8.53 ± 7.43

The species rank plots showed that the decapods larval community was most diverse during summer, especially in the northern area, and higher species dominance were registered in late autumn (Fig. 5.4). In late autumn, the southern area showed the highest diversity, having the "southern shelf break" station similar species richness, as the ones found at summer stations.

Figure 5. 4. Multiple k-dominance curves with cumulative dominance percentage of species described at four plankton stations during late autumn (blue) and summer (orange).

Seasonal stations symbols: (Δ) Northern shelf break; (+) Northern mid slope; (♦) Southern shelf break; (□) Southern mid slope.



The analysis of the horizontal distribution of larvae grouped considering the adult's habitats showed no clear pattern between areas. During late autumn the larvae were mainly from mesopelagic species, which dominated in the northern area, whereas in the southern a mixed assemblage was observed, with high percentage of larvae from coastal epibentic species (Table 5.3). In summer, at the northern area the assemblage was mixed, with larvae from all types of species, whereas in the southern area the community was mainly constituted by larvae belonging to pelagic, coastal necktobenthic and oceanic epibenthic species (Table 5.3). Moreover, significant differences between seasons, areas and station for the second group of development stage were detected for larvae from coastal epibenthic and nektobenthic adult's, which are summarized in Table 5.4. Furthermore, for the first group of development stage differences between area and station were significant for late autumn for pelagic and for pelagic and coastal species at summer (Table 5.5).

Table 5.3. Similarities among cluster assemblages regarding taxa composition grouped by their adult habitat. Only the groups that represent more than 50% of the cumulative contribution to explain the variability of each seasonal Cluster group (SIMPER) are included.

Adult habitat	Cluster A	Cluster ASshelf	Cluster S	Cluster SSslope
Mesopelagic	74.78%	22.55%	18.83%	48.78%
Epipelagic			16.10%	16.62%
Coastal necktobenthic		17.73%	16.46%	
Coastal epibenthic		18.86%		

(A:late Autumn; ASshelf:late Autumn Souternh shelf break; S: Summer; SSslope: Summer Southern mid slope)

Table 5.4. Effect of fluorescence (fluo), temperature (temp) and salinity (sal) on the density of late zoeas/protozoeas (stage 2) over the water column as estimated from a generalized linear model. Area and station (shelf break or mid slope) are included in the model as factors. Results are shown for late autumn and summer for the larvae classified by their adult habitat. The asterisks *** indicate significant effects (p<0.001)

		Factor		Variables		
Season	Adult habitat	area	station	fluo	temp	sal
Late autumn	Mesopelagic & epipelagic	***	ns	***	***	ns
	Coastal epibenthic & nektobenthic	***	***	***	ns	ns
Summer	Mesopelagic & epipelagic	ns	ns	***	ns	***
	Coastal epibenthic & nektobenthic	***	***	***	***	***

No significance "ns"= p>0.001

Table 5.5. Effect of fluorescence (fluo), temperature (temp) and salinity (sal) on the density of early zoeas/protozoeas (stage 1) estimated from a generalized linear model. Area and station (shelf break or mid slope) are included in the model as factors. Results are shown for late autumn and summer for the larvae classified by their adult habitat. The asterisks *** indicate significant effects (p<0.001)

		Factor		Variables		
Season	Functional group	area	station	Fluo	temp	sal
Autumn	Mesopelagic & epipelagic	***	***	Ns	***	***
	Coastal epibenthic & nektobenthic	***	ns	***	ns	ns
Summer	Mesopelagic & epipelagic	***	***	***	***	ns
	Coastal epibenthic & nektobenthic	***	***	***	ns	***

No significance "ns"= p>0.001

The inter-relationships by season, determined by means of the cluster analysis considering the available data from the hauls carried out at different depth ranges between 0 and 200 m, are presented in Fig. 5.5a and c. The SIMPER analysis was used to identify those adults habitats, used as a proxy for the origin of the larvae, primarily responsible for the differences among larval assemblages. The adult habitats explained more than 50 % of the analyzed cluster variability. In both seasons, larvae from mesopelagic species were the dominant group, despite the larvae of epipelagic species were also important in summer (Table 5.3). The "late Autumn Southern shelf break" cluster group (ASshelf; Fig. 5.5a, b) was the most diverse, with a predominance of coastal benthic species (epibenthic plus necktobenthic) and with an important contribution of mesopelagic species. Nevertheless, the rest of the hauls in "late Autumn" (A; Fig. 5.5a, 5b) were clearly dominated by larvae of mesopelagic species. At "Summer the Southern slope" Cluster assemblage (SSslope; Fig. 5.5c, d) grouped hauls from southern slope, whereas the rest of summery hauls were grouped in the "Summer" cluster assemblage (S; Fig. 5.5c, d). The similarity analysis for summer season revealed that about 50 % of the variability was explained by larvae from coastal benthic species (coastal epibenthic and necktobenthic), grouped in summer cluster assemblage "S", except in the "Summer Southern slope" cluster assemblage "SSslope“, which was exclusively formed by larvae of mesopelagic and epipelagic species.

5.4.3 Vertical larval distribution

A general vertical distribution pattern, characterized by the aggregation of individuals within the upper 75 m of water column, was followed by all taxa and larval stages. However, two different vertical distribution patterns were identified in each season for the main larval groups according to the adult's habitat and the larval developmental stage.

For late autumn, the non-stratified season, the general pattern (pattern 1) shows that the larvae were mainly concentrated at depths between the 25 and 75 m. It happened in both zoeal groups (pattern 1a, see Fig. 5.6a, c and pattern 1b, see Fig. 5.7c), being fluorescence the variable that explained most of the vertical distribution

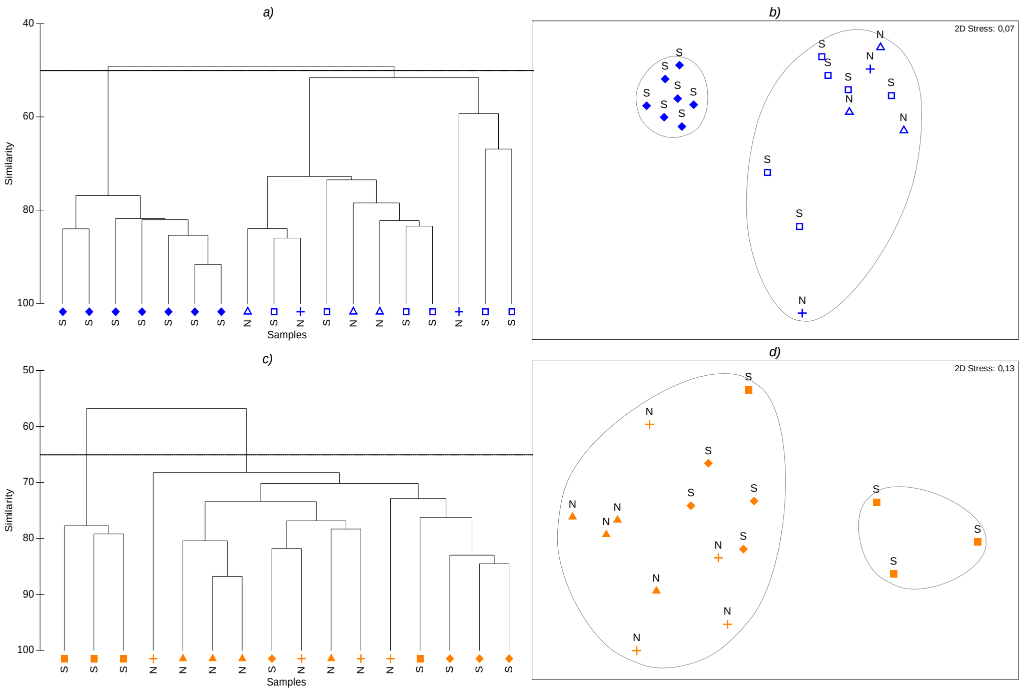


Figure 5.5. Seasonal cluster analysis (on the left) and Multidimensional scaling (MDS) of BrayCurtis similarities (on the right) of hauls based on adults habitat densities and their assemblages at 50 % similarity during late autumnin blue (a and b) and 65 % during summerin orange (c and d). Clusters groups in bubbles, two during late autumn (AS shelf: late Autumn Southern over shelf break; A: Autumn rest of the samples) and other two during summer (S: Summer rest of the samples; SS slope: Summer Southern over mid slope). Samples legends N: Northern stations and S: Southern stations.

Seasonal stations symbols: (Δ) Northern shelf break; (+) Northern mid slope; (♦) Southern shelf break; (□) Southern mid slope.

variability (Fig. 5.6b,d, 5.7d). However, during late autumn this pattern differed for stage 1 (early protozoeae) by larvae belonging to pelagic species, which were mainly found between 60 and 200 m depth (pattern 2 see Fig. 5.7a) and showed a strong relation to temperature and salinity (Fig. 5.7b).

In addition, during fall season in southern area the highest densities of early zoeae of coastal benthic species were situated over shelf break (Fig. 5.7c). At this station (southern shelf break) the temperature and fluorescence presented the highest values during the season (Fig. 5.3d, f) coinciding with the depth of densities' peak of larvae (around 25-75m). At this point we found the highest abundances of developmental larval group 1 from coastal epibenthic and nektobenthic taxa, composed mainly by *G.rhomboides* and *Plesionika* spp*.,* respectively.

During summer, when the water column was stratified, showing a marked thermocline, halocline and fluorescence peak, two different patterns were identified also. All larval stages of coastal epibenthic and nektobenthic species presented a decreasing density from surface down to 75 m (pattern 3, see Fig. 5.6f, 5.7g). Temperature, salinity and fluorescence explained the stage 2 (late zoeae) distribution pattern (Fig. 5.6g). For the stage 1 group, fluorescence and salinity were the main variables explaining the vertical distribution of the larvae (Fig.5.7h), corresponding to the minimum observed values, recorded at surface, to the maximum larval abundance.

The larvae of the mesopelagic and epipelagic species showed two clear peaks in summer (pattern 4), one at the surface layers, from 0 m to 25 m depth, and the other from 50 m to 75 m depth (Fig. 5.6e, 5.7e). The surface peak was mainly attributable to *P. vigilax*, and was best explained by temperature, suggesting that these larvae preferred warm waters above the thermocline. On the other hand, fluorescence was the environmental variable that best explained the deep peak, where the main abundances were of *E. arcticus*, suggesting that these larvae concentrate at the maximum fluorescence peak (Fig. 5.7f).

The highest larval abundances in late autumn were registered at the southern shelf break station. The highest values of temperature and fluorescence during late autumn at this station (17.6 ºC and 0.43, Fig. 5.3c, g) agree well with the depth in which the highest densities of larvae were found (around 25-75 m, Fig. 5.6 and 5.7). The highest abundances in summer were found at the surface layers of the northern mid slope station (Fig. 5.6 and 5.7). The highest values of temperature during warm season (27 ºC; Fig. 5.3d) at this station agree with the depth in which the highest densities of larvae were registered.

Fig. 5.6 (next pag.). Scatterplots of observed (a, c, e, f) and predicted (b, d, g) larval densities (n/m^3) with explanatory variables, of adult habitat epipelagic (Ah_7), mesopelagic (Ah_8), coastal epibenthic (Ah_3) and coastal nektobenthic (Ah_4) of late development stage group (stage 2), at four plankton stations during autumn and summer. Environmental variables fluorescence (fluo), temperature (temp) and salinity (sal). Stations symbols: (Δ) Northern shelf break; (+) Northern mid slope; (♦) Southern shelf break; (□) Southern mid slope. nd= not enough data

Fig. 5.7 (next pag.). Scatterplots of observed (a, c, e, g) and predicted (b, d, f, h) larval densities (n/m^3) with explanatory variables, of functional groups epipelagic (Ah_7), mesopelagic (Ah_8), coastal epibenthic (Ah_3) and coastal nektobenthic (Ah_4) of group 1 of early stages (stage 1), at four plankton stations during autumn and summer. Environmental variables fluorescence (fluo), temperature (temp) and salinity (sal). Stations symbols: (Δ) Northern shelf break; (+) Northern mid slope; (♦) Southern shelf break; (□) Southern mid slope

Fig. 5.6

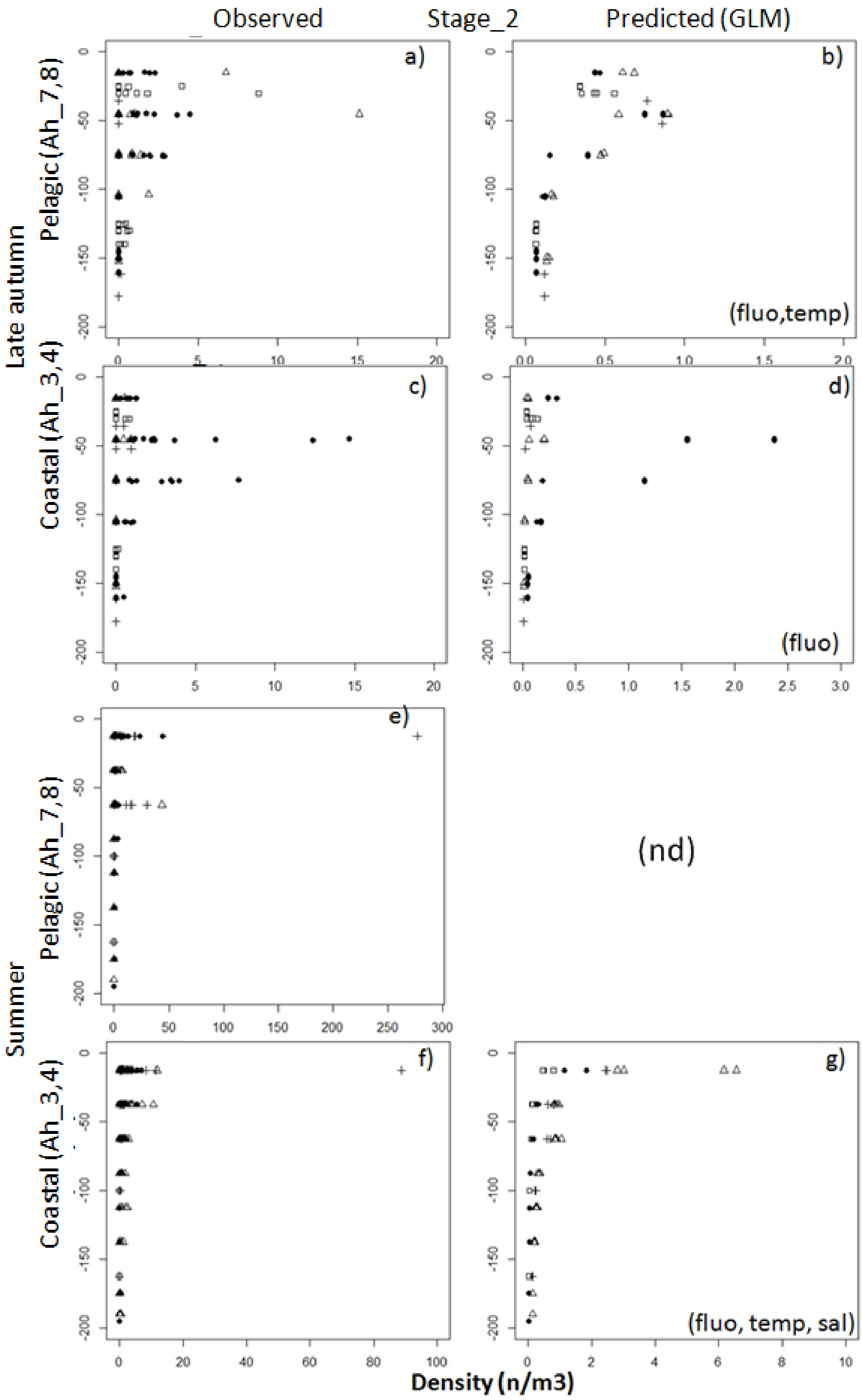
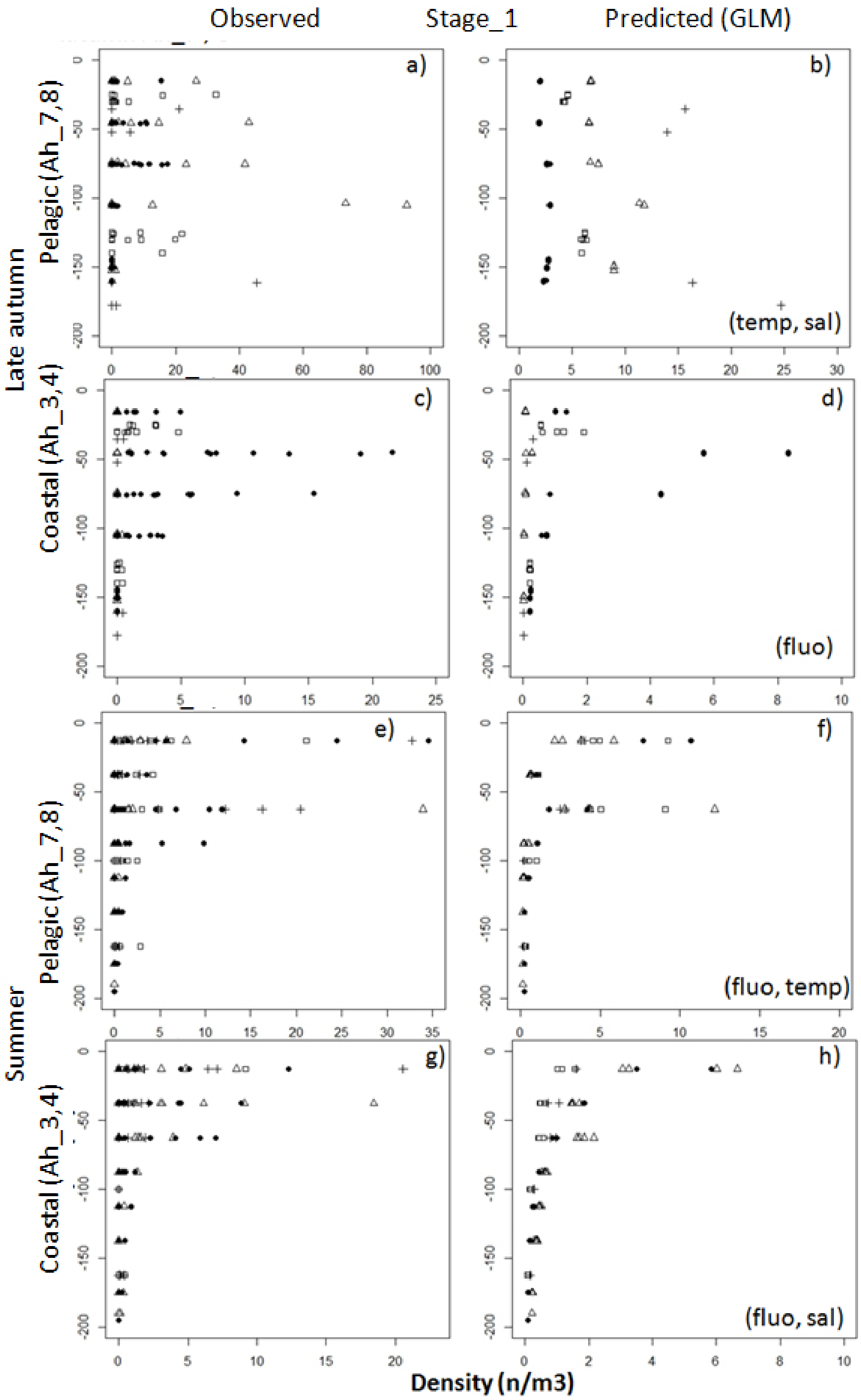

Observed
Stage_2
Predicted (GLM)
Late autumn
Pelagic (Ah_7,8)
Coastal (Ah_3,4)
Summer
Pelagic (Ah_7,8)
Coastal (Ah_3,4)
a)
b)
(fluo,temp)
c)
d)
(fluo)
e)
(nd)
f)
g)
(fluo, temp, sal)
0
-50
-100
-150
-200
0
5
10
15
20
0.0
0.5
1.0
1.5
2.0
2.5
3.0
0
50
100
150
200
250
300
0
20
40
60
80
100
0
2
4
6
8
10
Density (n/m3)

Fig. 5.7


Observed
Stage_1
Predicted (GLM)
Late autumn
Summer
Pelagic (Ah_7,8)
Coastal (Ah_3,4)
a)
b)
c)
d)
e)
f)
g)
h)
(temp, sal)
(fluo)
(fluo, temp)
(fluo, sal)
0
-50
-100
-150
-200
0
20
40
60
80
100
0
5
10
15
20
25
30
0
5
10
15
20
25
0
2
4
6
8
10
0
5
10
15
20
25
30
35
0
5
10
15
20
0
5
10
15
20
0
2
4
6
8
10
Density (n/m3)

5.5 Discussion

5.5.1 Seasonal and horizontal larval distribution

We found decapod larval densities around 100 times lower than those reported for productive upwelling nearby coastal Atlantic areas (e.g. Dos Santos et al. 2008, Fusté and Gili 1991). This agrees well with the oligothrophic characteristics of the Mediterranean Sea nevertheless the sampled area of the present study is located on the shelf break where recurrent mesoscale eddy activity is observed. However, late autumn larval densities were similar to those found off Canary Islands (23.7 ind. per 100 m^3 ± 22.9; Landeira et al. 2010). This could be related to the ”island mass effect” (Doty and Oguri 1956), which cause and enhancement of primary productivity around islands in relation to open ocean waters (Gilmartin and Revelante 1974, Hernández-León 1991), increasing preys availability and, in consequence, we could expect higher abundances of decapod larvae. Mesoscale oceanographic features such as fronts and eddies are key mechanisms to enhance the biological productivity in specific areas (Alcaraz et al. 2007, Estrada 1996). The Balearic Sea, due to the interaction among different water masses and of those with the island’s topography, is a hydrodinamically complex area (López-Jurado et al. 1995, 1996, Pinot et al. 2002). Moreover, we found the maximum peak of larval density during summer in the northern area, associated to strong geostrophic currents and an anticyclonic eddy. The continuous current system that runs from the mainland to the Balearic archipelago in some years could result, in local enrichment processes derived from the more productive area linked to the Spanish mainland rivers (López-Jurado et al. 2008, Pinot et al. 2002).

The dominance of shrimps (Dendrobranchiata species) in our assemblages is in agreement with those observed for offshore waters around oceanic islands (e.g. Brandão et al. 2013 off Saint Paul’s Rocks, Southwest Atlantic Ocean; Landeira et al. 2009 off Canary Islands). On the contrary, crab larvae usually dominate decapod larvae assemblages from continental shelf areas (e.g. Dos Santos et al. 2008) or neritic areas around Atlantic islands (Koettker and Freire 2006).

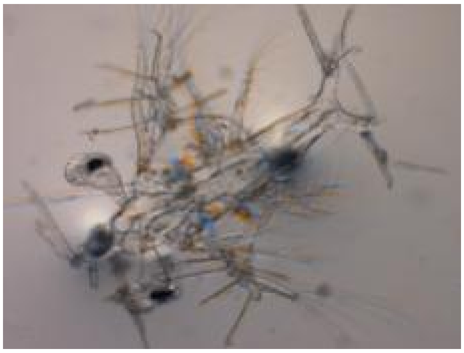
In our study, crabs were the second most abundant group during late autumn and the third in summer, suggesting some degree of mixing between typical offshore, such as mesopelagics, and nearshore, such as coastal-benthic species. Specifically, information on the casual occurrence and morphology of larval stages of the red shrimp *Aristeus antennatus*, the rose shrimp *Parapenaeus longirostris*, the slipper lobster *Scyllarides latus* and the Mediterranean spider crab *Maja squinado*, species that are important for fisheries management and conservation purposes have been published recently (Torres et al. 2013).

The most abundant taxon in our samples at late autumn, *G. elegans* (Dendrobranchiata), presented its highest densities at the northern of the Balearic Islands (14.5 ind. per 100 m^3 ± 8.7) coinciding with the highest velocity currents. This high density in Balearic oligotrophic waters could be explained by the capacity of Dendrobranchiata early life stages to retain picoplankton which tend to dominant over phytoplankton biomass. Thus picoplankton could act as source for carbon and nitrogen (Cho and Azam 1990). It must be pointed out that in autumn the maxima of dissolved organic carbon are found in surface waters, where it is continuously removed from surface waters by diffusive processes during the stratified period in north-western Mediterranean (Copin-Montégut and Avril 1993).

A review of the relevant literature shows that Mediterranean pelagic shrimps have not been thoroughly studied and information on their adult distribution is poor (e.g. Casanova 1977, Koukouras 2000, Koukouras et al. 2000). Within this context, the present study allows us to reveal some ecological traits for these pelagic species that currently are of no commercial interest to the fishing industry and for which no previous information of this type exists for the western Mediterranean (Simão et al. 2014).

According to Champalbert (1996) zooplankton communities in the western Mediterranean present low diversity at inshore waters, especially when the continental shelf is narrow. Contrastingly, in our case decapod larval k-dominance curves showed different behavior, in the northern shelf in summer, since our highest diversity and density values were registered there, despite the shelf is narrower than in the southern area. The larvae of coastal nektobenthic and epibenthic species dominated the decapod larvae community in this area and season, showing the maximum values of biodiversity registered for Mediterranean Sea (Fusté 1987, García-Comas et al. 2011, Pessani 1975). In late autumn larvae of these groups dominated also the communities over the shelf break in the southern part of the Balearic Islands. However, overall the larvae of pelagic species dominated in the majority of our samples, comprising 57 % of total decapod larvae.

Our data revealed the highest densities and biodiversity of decapod larvae in summer, coinciding with the major reproductive season for most decapods species in the western Mediterranean (García Raso 1982, Zariquiey 1968). The seasonal pattern described for pelagic shrimps (Dendrobranchiata and Caridea) larvae agrees with the seasonality in species composition of the neighboring Ligurian Sea, where the species maximums were registered in June and the minimum in autumn-winter (Pessani 1993). As mentioned above, in our samples taken off the Balearic Islands, the most abundant species were the mesopelagic shrimp *G. elegans*. In a study carried out on the shelf of Catalonian coast all the year round, *G. elegans* larvae showed their maximum abundance during February, and the minimum in October, but no larvae were found in December and July (Fusté 1987). On the contrary, we registered the presence of *G. elegans* larvae in both months, being present in abundance in December. Therefore we can conclude that this species reproduces during all year in the western Mediterranean, and that late autumn–winter potentially being their most important reproductive season.



5.5.2 Hydrographic effect on larval assemblages

Larval densities during the autumn season differed between the two study zones (northern and southern). The highest densities were observed in the southern shelf break and the lowest at the northern slope stations. The larval assemblages were mainly constituted by larvae of mesopelagic species, except for the southern shelf break station, where coastal benthic species larvae dominated. The observed differences were probably related with the currents registered in the area.

There was a strong north-south flowing current during late autumn, originated in offshore areas of Balearic sub-basin and associated to a front perpendicular to the shelf located in the northern sampling area, which swept both northern area and southern slope stations (Balbín et al. 2012). This current could explain why the majority of decapod larvae at the northern and in the outer southern stations (autumn cluster group) belonged to mesopelagic species. The larvae of coastal benthic species were concentrated over the southern shelf break station (Autumn Southern shelf cluster group) where a cyclonic gyre could promote its retention. Species richness and also larval densities were highest at this southern shelf break station. This fact could also be a consequence of the aforementioned gyre; it not only would retain larvae, but would produce the mixing of larvae of more coastal and deeper upper slope species, increasing the diversity of such mixed larval assemblage.

In summer, both the northern stations and the southern shelf break station with a high similarity, showed a mixed larval assemblage, and composed by mesopelagic, epipelagic and coastal necktobenthic species, without any clear dominance of one group over the others. On the contrary, almost only larvae from pelagic species were found at the southern slope station coinciding with an anticyclonic input of lower salinity Atlantic, since up to 80 % of specimens were *P. vigilax* early protozoeae (stage 1). Most of the late protozoeae of this species were caught over the northern slope, in the front side of an anticyclonic eddy.

Currents in summer were in general less intense than in late autumn, which could allow spatial retention of larvae close to the area of their release. However, in the northern area, the cyclonic gyre located over the shelf break sampling station should promote the advection of coastal larvae to the nearby offshore stations, favoring the existence of the mixed assemblage with the highest biodiversity. In fact, in the north of Mallorca where the shelf is narrower and the slope is quite pronounced, the currents over the shelf created mixed conditions, that could explain the important component of larvae from coastal species. Specifically, over the northern shelf break the highest larval densities of *Plesionika* spp. and *Xantho* spp. swept from coastal benthic zones were caught. In the northern slope station, the only with surface resident AW, had been influenced by a heavy anticyclonic feature which would also favour the mixing of larvae. The highest larval density value was registered, corresponding mainly to larvae of epipelagic adults (e.g. Sergestidae), as those of *P. vigilax* mentioned above.

Mesoscale advective processes (surface fronts and eddies) affect planktonic communities and may offer opportunities for exceptional local productivity and growth of species. Owing to the complex hydrodynamic situation and topographic features in the study area, mesopelagic species were also relatively abundant in stations located over the shelf break, being found together with larvae of neritic species.

The general structure of decapod larvae community found off the Balearic Islands is similar to that reported in nearby Spanish continental coast by Fusté (1987), with pelagic taxa being more dominant. The mesopelagic species dominance during both seasons in our study area was expected as all sampling stations were not located close to the shore, the shelf in this area is relatively narrow and hence the distance between shelf break and slope stations is short, and also because the existence of mesoscale features as eddies favor the advection of offshore species larvae to shelf.

5.5.3 Environmental effect on vertical larval distribution

Most decapod larvae were distributed between the 0-75m and followed well the vertical pattern in fluorescence during both seasons. The early and late protozoeae are mostly phytotrophic and they can adapt their movements in the water column to stay by the fluorescence peak and optimize their feeding. Increasing food abundance enhances feeding rates and resulting developmental rates in decapod larvae (Dawirs 1985). Therefore, observed larval distribution may reflect an optimization of their behavior in the water column to favor the encounter of food. Decapod larvae show positive phototaxis in the laboratory (e.g. Sulkin 1975), which is supported by the finding of the current study that found mainly larvae within the euphotic layer (0–200 m).

The earliest stages of the pelagic species (mesopelagic and epipelagic) in late autumn were distributed between 60 and 200 meters. These developmental stages could have been caught during their first ontogenetic migration upwards from the deepest layers were they were probably born since the adults of these species, e.g. *G. elegans,* are mostly located in the mid slope within the Deep Scattering and the Benthic Boundary Layers around 400 m depth close to the bottom (Ramón et al. 2014, Simão et al. 2014). Another example is the case of *E. arcticus*. The adults inhabit the mesopelagic waters whereas the larvae were located mostly between 50 and 75 m depth. For the epipelagic shrimp *P. vigilax* most larvae were located in the first 25 m of the water column.

Crustacean larvae are able to swim across environmental gradients in the water column such as the thermocline (Dos Santos et al. 2008, Lindley et al. 1994). They can perform diel vertical migrations though patterns can vary among the successive developmental stages and species (e.g. Andersen et al. 2004, Dos Santos et al. 2008, Lindley et al. 1994). We have observed larvae above the thermocline during the summer supporting these previous findings. Though some of the larvae were found at the highest temperatures, most larvae were not located in the warmest layers. The occurrence of the larvae of the same species across temperatures ranges of 13-27 ºC reinforces the conclusion that temperature is not a main variable defining the vertical distribution of the early life stages of decapod crustaceans.

Migratory behavior in crustacean larvae has been related to predator-avoidance, hunger and adaptations to optimize dispersal by currents (Queiroga and Blanton 2004, Landeira 2009, Pearre 2003). At surface, potential predators such as fish larvae (Olivar et al. 2014) coexist with crustacean larvae. On the other hand, late stages can predate on zooplankton while earlier stages prey mostly on phytoplankton. The vertical position of the crustacean larvae may reflect strategies considering a trade-off between the optimization of food availability and survival. Further research on the overlap in the water column of crustacean and fish larvae can help to describe such trade-offs.

5.6. Conclusions and perspectives

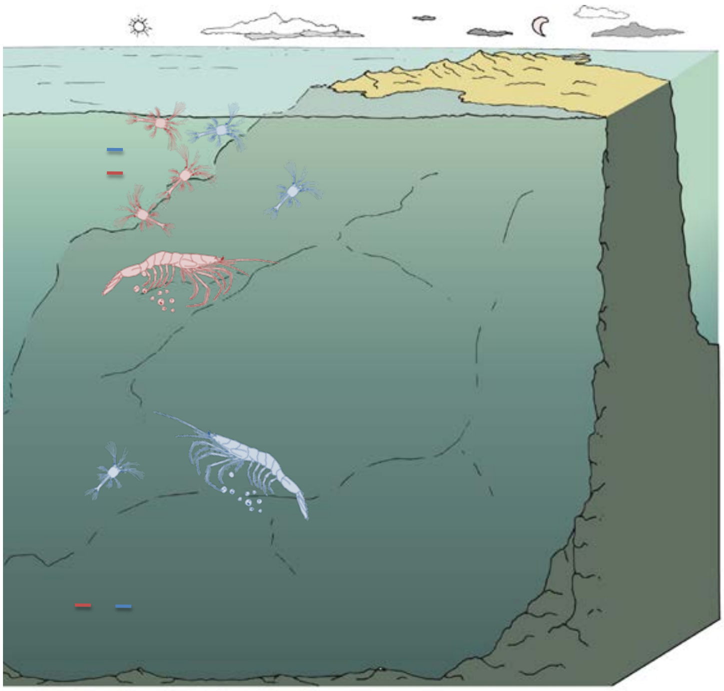
Our study provides for the first time an accurate analysis of the decapod larvae structure and vertical distribution over shelf break and mid slope in two seasons at two areas off the Balearic Islands. The community of decapod larvae in the study area is composed mainly of larvae of mesopelagic shrimp species (Dendrobranchiata). Our results show also that the complex surface water circulation patterns around the Balearic Archipelago, characterized by the presence of mesoescale structures as fronts and eddies, can lead to local larval retention over the adult populations. The oceanography causes the mixing of coastal and mesopelagic species larvae in the area.

The analyses of the vertical distribution of larvae show most larvae concentrate in the first 75 m of the water column thought differences are observed among species mostly related to the vertical distribution of different ontogenetic developmental stages. The main factor explaining the observed vertical distributions is food availability. The larvae are concentrated in the depth ranges of the water column where the fluorescence values confirm higher concentration of potential preys, considering that decapod larvae feed on picoplankton and phytoplankton. Within this context, the vertical position of the crustacean larvae may reflect strategies considering a trade-off between the optimization of food availability and survival. However, further improvements on the knowledge of ecology and vertical distribution of autotrophic and heterotrophic plankton, communities are deemed necessary in the area to achieve a better understanding of the biological processes affecting decapod larvae survival.

The positioning of the larvae along the water column could be related to species specific strategies developed to optimize recruitment processes, since transport of decapod larvae throughout their pelagic larval stages is a key determinant of adult population dynamics. The larval vertical migration behaviors may couple with vertically stratified flows to retain larvae nearshore. Thus, by varying their vertical position in relation to mesoescale hydrological structures, they could control in a certain way their transport from spawning to nursery areas. In order to identify better their effect on life history traits our results underline the need for further detailed studies, with new data taken concurrently on both physical and biological parameters. These kinds of studies would allow developing biophysical models which require not only accurate 3D hydrodynamic models but reliable information on larval distribution, ecology and behavior. Thus, the knowledge on larval assemblage's structure, distribution and ecology will be essential in improving our understanding of population's dynamics and population connectivity aspects that will be important to inform management strategies.

Chapter 6
Ontogenetic decapod vertical distribution

Torres AP, Reglero P, Hidalgo M, Abelló P, Simão D, Alemany F, Massutí E and Dos Santos A. Vertical distribution of decapod crustaceans: seasonality and diel migration patterns over ontogeny off Balearic Islands (Western Mediterranean Sea) Marine Ecology Progress Series, Submitted



6.1 Abstract

The most important migration in marine ecosystems in terms of biomass displacement is that associated to vertical movements of different types of organisms up and down in the water column. In this chapter, vertical migration (VM) for decapod crustaceans is documented and comparatively assessed in western Mediterranean water column through ontogeny, combining information of larvae, juvenile and adult stages. Decapod larvae were obtained from meso-zooplankton depth-stratified samples, whereas juveniles and adults (nekton and micronekton) were captured with different pelagic, epibenthic and demersal gears. Specifically, vertical distributions in day-night time and their ontogenetic changes, in two seasons representing stratified and non-stratified hydrographic conditions, were analyzed in four predominant species from decapod community off Balearic Islands (western Mediterranean Sea). These target species were pelagic shrimps, three mesopelagic ones: *Gennadas elegans, Eusergestes arcticus* and *Sergia robusta* and the epipelagic *Parasergestes vigilax*, from which larvae were caught, only during summer, in the study area. Contrary to the common pattern generally described for shelf and coastal decapod larvae, which ascent to surface during the night, offshore decapod crustaceans' larvae from these mesopelagic adults considered in the study followed a reverse VM. Adults' diel vertical migration (DVM) patterns were similar between seasons but different among species. Seasonal and life history effect on larval vertical distribution and survival, as well its potential effect on the distribution of adult populations, are discussed. DVM of planktonic and adult stages are argued as evolutionary trade-off between predator avoidance and food availability.

6.2 Introduction

A challenging question in marine ecology is to identify what are the factors that determine the larval and adult depth distributions. During the larval stage, changes in the vertical position may affect the dispersion-retention patterns which may determine the settlement areas (Marta-Almeida et al. 2006, Fiksen et al. 2007). In order to guarantee the success of the offspring spawners can follow diverse strategies to reduce the temporal and spatial matching of eggs and their potential predators.These strategies include seasonal and moon phase’s preferences for spawning within the year and daytime or tidal period within seasons. In pelagic species the initial position in the water column of the eggs and larvae is tighly connected to the adult depth distribution. Adults select to spawn in depths that optimize larval survival and drift trajectories to the nursery areas (e.g. Kitagawa et al. 2010). Thus, the larval vertical distribution may be connected with their different post-settlement habitat requirements (Leis et al. 2009).

The diel vertical migration of zooplankton (DVM) and the movements of micronektonic and nektonic organisms represent some of the most important displacements in the marine ecosystems, with an impact in all trophic levels. This behavior has been commonly interpreted as a strategy to balance feeding-predation risk trade-offs in planktonic, micronekton and nektonic organisms, e.g. Irigoien et al. 2004, Olivar et al. 2014, Bernal et al. 2013. The most common pattern of DVM is a night-time ascent and descent of zooplankters at the first hours of dawn, probably to reduce overlap with their visual predators (Forward 1988, Pearre 2003). A second pattern is the reverse or diurnal DVM, which could be adopted by zooplankton grazers to exploit the higher phytoplankton abundances of the upper layers during the day, descending to deeper layers at night (Hutchinson 1967, Irigoien et al. 2004). A third pattern, the twilight DVM, is characterized by an ascent to the surface in early morning followed by descent at sunrise or, followed by an ascent at sunset and a final descent to deeper water around midnight (Cohen and Forward, 2005).

The amplitude of the diel vertical distributions may differ between species and ontogenetic stages in response to biotic and abiotic factors (George 1983). Changes in the vertical distribution with age are refered as ‘ontogenetic vertical distribution’ (OVD, first described by Russell 1927). OVD involves variations in the mean depth and spatial range distribution over the life cycle as the morphology and feeding needs of the organisms change (Pearre 1979).

Decapods’ ability of microscopic larvae and adults to regulate their movements and DVM in a dynamic environment with different depth-stratified conditions has been confirmed (e.g. for larvae Dos Santos et al. 2008, Kunze et al. 2013, for adults Donaldson 1975).Larvae of estuarine and continental shelf decapods show marked OVD and DVM behaviours that range from few meters in estuaries to several tens of meters in the shelf (e.g. Queiroga and Blanton, 2004, Dos Santos et al. 2008) These movements have been related to to the physical processes and biotic variables as a strategy to avoid predation and optimize dispersion or retention (Shanks 1995, Queiroga and Blanton 2004). However, there is little knowledge on the OVD and DVM patterns of decapod species that inhabit offshore waters, including benthic decapods and pelagic shrimps that spread larvae to the euphotic zones (Pochelon et al. 2014, Koettker et al. 2010).

The few studies on offshore benthic decapods larvae suggest some species follow a nocturnal or common DVM (e.g. Lindley et al. 1994) as observed also in pelagic adults linked to predator-prey trade-offs (Foxton 1970, Foxton and Roe 1974, Andersen et al. 2004). However, no descriptions have been provided on OVD patterns regarding spawning strategies and further offspring survival in pelagic decapods. Predictions using larval transport models carried out on crabs reveal that changes in the time and location of spawning events can result in large variations in retention and settlement, due to seasonal variations of the physical flow field (Tilburg et al. 2011).

Pelagic shrimps have only free living stages throughout the life cycle. They have external fertilization and eggs are generally released directly into the water column hatching as free-swimming nauplii after a few hours. Every larval development consist of different stages within each phase, 5-8 stages during the nauplius phase, 3 protozoeae and 2-5 mysis during the zoea phase and, uncertain number of stages during the decapodid phase. The earliest stage nauplii is rare to find in plankton and do not feed, the consecutive larval phases feed mainly on phytoplankton and micro-zooplankton (e.g. Ewald 1965), until the last phase (decapodid) that precedes the metamorphosis to the juvenile stage (Dendrobranchiata’s details in Martin et al.

2014 and references therein). Thus, it is important to take into account the developmental stage to understand patterns in the OVD and DVM in relation to the different spawning strategies estimated from the adult's vertical distributions.

Four Dendrobranchiata species, here after called pelagic shrimps, are predominant in the offshore western Mediterranean communities, both as larvae and adult (Torres et al. 2014, Casanova 1977, Simão et al. 2014). *Parasergestes vigilax* 'pv' (Stimpson 1860) is an epipelagic species as adult, distributed above 200 m depth. The other three are the mesopelagic species *Gennadas elegans* 'ge' (Smith 1882), *Sergia robusta* 'sr' (Smith 1882) and *Eusergestes arcticus* 'ea' (Krøyer 1855) which inhabit depths greater than 200 m as adults.

Taking as reference the aforementioned decapod pelagic species we build up a comparative model to achieve a better understanding of the vertical distribution and DVM patterns in pelagic shrimps. The present study is the first specific research on pelagic shrimp's vertical distribution combining several ontogenetic stages along day and night and in different oceanographic scenarios. The first objective was to characterize the spawning strategies and the seasonal distribution of adult's populations in western Mediterranean. Secondly, we wanted to compare and analyze the vertical distribution of the four most abundant species different developmental stages in two contrasting seasonal scenarios (stratificated and non-stratificated water column). Finally, we hypothesize that mesopelagic and epipelagic species have different patterns of vertical distributions according to their ontogenetic behavior.

6.3 Material and methods

6.3.1. Field work

Two multidisciplinary research surveys were conducted off the Balearic archipelago (western Mediterranean, Fig. 6.1) during late autumn (29th November to 18th December 2009) and summer (11th to 30th July 2010). Each survey was carried out with two vessels: *R/V Sarmiento de Gamboa,* which was used to collect samples in the water column, and the *F/V Punta des Vent* (commercial bottom trawler), that obtained samples from the epibenthic and demersal habitats (Massutí et al. 2014). To be able to obtain pelagic decapods in all developmental stages we sampled 2 seasons from surface waters to bottom layers by different devices with several mesh sizes (Table 6.1). Two areas were studied, one located in the north-west (N), in Balearic sub-basin, and the other in the south (S) of the Majorca Island, in the Algerian sub-basin (Massutí et al. 2014). Decapod larvae were collected by means of depth-stratified meso-zooplankton hauls, from depths near seabed to the surface. In late autumn five depth-intervals within the water column were sampled using HYDRO-BIOS multi-net (ML), whereas during summer seven depth-intervals were sampled using a Multiple Opening-Closing Net and Environmental Sensing System (MOCNESS: MC).

Nektonic and micronektonic pelagic decapod adults and juveniles (usually 2-20 cm in length) were sampled by two different pelagic gears with different mouth openings and cod-end mesh sizes: a Pelagic Trawl net (PT) and an Isaaks-Kidd Midwater Trawl (IKMT) (Table 6.1). Mesozooplankton and pelagic nekton hauls were performed continuously during 36 h, collecting samples at 3-h intervals, more details on sampling protocols are found in Olivar et al. (2012), Torres et al. (2014) and Simão et al. (2014). Additionally, adults and juveniles were sampled during day time with two deep bottom devices (Table 6.1): a commercial bottom trawl (BoT) which collected nekto-benthic species and a beam trawl (BeT) that captured epi-benthic species at the superficial layer of the bottom seabed (Rueda et al. 2014, Ramón et al. 2014).

6.3.2. Sample processing

The target species for the study was the most abundant decapods species in all phases (larvae to adults) are: *Gennadas elegans*, *Eusergestes arcticus*, *Sergia robusta* and *Parasergestes vigilax*, see Table 6.2. The species chosen have different life histories, inhabiting different habitat as adults and depth range.

All meso-zooplankton and micronekton samples were preserved immediately after collection in ~5% borax-buffered formaldehyde prepared using seawater. Once in the laboratory, samples were subsequently sorted for decapod larvae, which were identified to species level and developmental stage, whenever possible, using available descriptions (Dos Santos and Lindley 2001, Dos Santos and González-Gordillo 2004). Adult and juveniles pelagic decapod crustaceans were sorted out and identified to species level (Zariquiey 1968).

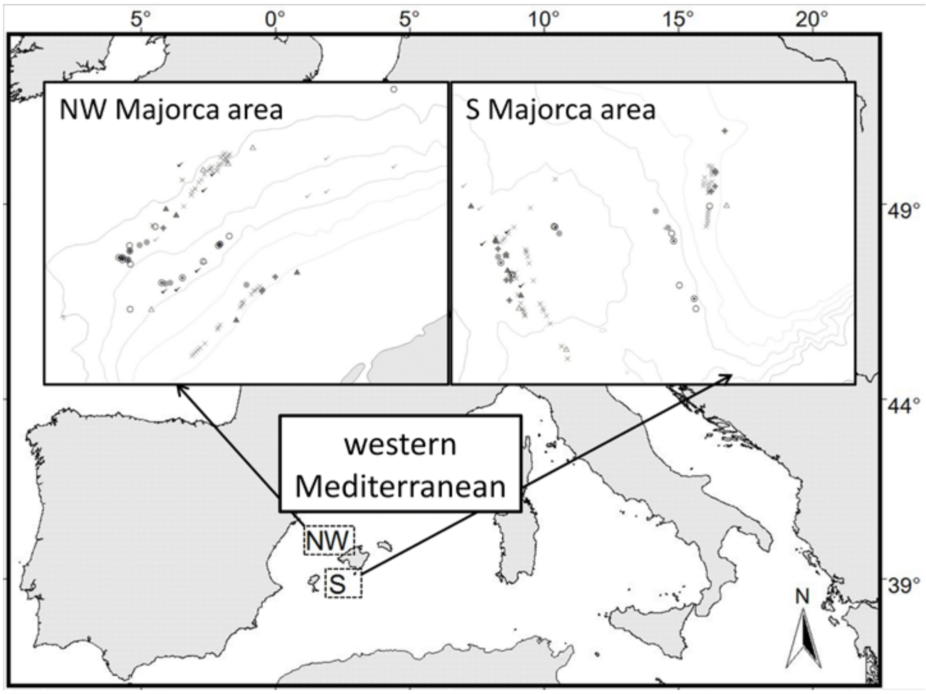


Fig. 6.1 Study area with haul's position during late autumn 2009 (grey symbols) and summer 2010 (black symbols) at four stations located over shelf break (250 isobath) and middle slope (900 isobath) off the north-west (NW) area and south (S) of Mallorca Island. Grey lines indicate isobaths (200, 400, 600, 800 and 1,000 m).

Symbols code: Crosses: HYDRO-BIOS multi-net and MOCNESS; Triangle: Isaaks-Kidd Midwater Trawl; Stick: Mid-water pelagic Trawl net; Circles: Beam trawl; Circle with dot inside: Commercial bottom trawl

6.3.3. Data analysis

Seasonal and ontogenic vertical distribution

The seasonal variability in the abundance and vertical distribution of the four species and their different developmental stages, larval and adult, were estimated separately by gear. Prior to the analyses, captures from ML, MC, IKMT and PT, here onwards named as the “pelagic” gears, were standardized to number of individuals per 100 m^3. Separately, juvenile and adults captured using the BoT and the BeT, here onwards named as the “benthic” gears, and were standardized to number of individuals per m^2.

The analyzed specimens were grouped into 6 developmental stage groups (DSG 1-6) in order to simplify and gain strength for the statistical analysis. The first group (DSG 1) included the first protozoeal (Pz) stages (Pz I + Pz II). The second group (DSG 2) included the third Pz and Mysis (Pz III + Mysis I + Mysis II). The third group (DSG 3) was exclusive for *G. elegans* and included Mysis III and Mysis IV. The fourth group (DSG 4) consisted of decapodids. The fifth group (DSG 5) included juveniles, whereas the sixth group (DSG 6) included the adults.

To obtain an index of seasonal and ontogenetic variation of the average vertical distribution, the seasonal weighted mean depth for each species by DSG ($WMD_{sp,DSG}$) was calculated as follows:

Where A is the abundance for a given species (sp) of a given developmental stage group (DSG) at a given depth-interval (i) and D is the depth in meters calculated for each depth-interval as the mean depth of the interval (i). Depth-interval ranges from i=1 to m for each species and DSG. The estimated WMD were compared between species and DSG, considering separately pelagic and benthic gears, by means of ANOVA. The accepted level of significance of p-value throughout our study was less than 0.05.

Table 6.1. Habitats, communities, gears, sampled characteristics needed to obtain decapods in all developmental stages during each cruise (late autumn or summer) and during day and/or night.

Larval (L) and adult stages (A)

Habitat	**Community**	**Gear**	**Depth sampled**	**Mean mouth**	**Mesh size**	**Developmental stages**	**Season**	**Day & Night**
Pelagic	Mesozooplankton	HYDRO-BIOS multi-net (ML)	0 - 850 m	0.25 m^2	333 µm	L + A	Late autumn	√
	Mesozooplankton	MOCNESS (MC)	0 - 500 m	1 m^2	333 µm	L + A	Summer	√
	Macrozooplankton & Micronekton	Isaaks-Kidd Midwater Trawl (IKMT)	0 - 600 m	3 m^2	3 mm	A	both	√
	Nekton	Mid-water pelagic Trawl net	0 - 600 m	196 m^2	10 mm cod-end	A	both	√
Benthic	Epibenthos	Beam trawl (BeT)	250/650/850m	0.6 m (vertical)	10 mm cod-end	A	both	day
	Benthos	Commercial bottom trawl (BoT)	250/650/850m	2 m (vertical)	20 mm cod-end	A	both	day

Diel vertical distribution along ontogeny

Diel vertical distributions were only investigated on captures obtained from the pelagic gears, which were the only ones conducted both during day and night. Larval daily vertical distributions were described joining the four developmental stage groups DSG 1, DSG 2, DSG 3 and DSG 4 together (larval group, L), whereas juveniles and adults were grouped in the Adults group (A), because there were few juveniles captures (see Table 6.2).

Generalized linear models (GLMs, McCullagh and Nelder 1989) programmed in R software (R Development Core Team 2005) were used to analyze changes in the vertical distributions of decapods along the day. In all cases the dependent variable in the model was the number of individuals captured at a given depth interval and at a given time interval. Larvae (L) and adults (A) were considered separately for each season and species. We did not model quantitatively but we compared qualitatively larval captures between seasons because no significant avoidance to mesozooplankton nets is considered in these sizes (Skjoldal et al. 2013). The covariates included in the model were the average depth in each sampling depth-interval (log-transformed, log10), stage of development (DSG1-6), the time of day (3-h interval) included as factor and the interaction between depth and time of the day. The volume of water filtered (m^3) or the area sampled (m^2) were included as an offset (after natural log transformation) for the Larval and the Adult models respectively, to account the effort put into sample capture. The typically patchy nature of plankton was accounted for by using an over-dispersed Poisson distribution to model larval decapod data.

Our aim was to model the interaction between depth and time (3-h interval) in order to understand how animals change their position along water column during day and night. To present the diel variation of the vertical distribution for each developmental group (L or A) and species, we plotted the estimated depth-interval slope for each time of the day (i.e. interaction between depth and time in GLM). We then contrasted these diel patterns between seasons, developmental stages and species. The slope values indicate the strength of the depth effect (i.e. vertical distribution) in the response, which is the log-transformed density. Thus, positive slope values would indicate higher individuals' densities in deeper strata, whereas negative values mean shallower distributions. However, in order to facilitate interpretation of the graphics the values of the slopes were multiplied by – 1, thus predominant surface positions at a given time interval take positive values, while deep positions take negative values.

For interpretation purposes, slopes' plots are presented combined with information on average densities for each 3-h intervals integrating the whole water column, positioning it at depth where the maximum densities were captured.

6.4 Results

6.4.1 Seasonal pelagic shrimp's distribution and spawning strategies

Adults of the four species were caught during both seasons with all the gears. The most abundant species were *Gennadas elegans* and *Eusergestes arcticus*, being *G. elegans* the dominant species in autumn and *E. arcticus* in summer (Table 6.2). *Parasergestes vigilax* larvae were only caught in summer while larvae of the other three species were caught in both seasons (Table 6.2).

The age structure of *G. elegans* larvae during autumn was contrary to the summer since only 10 % of larvae were DSG 1 and around 80% DSG 3 (Mysis IV) in summer whereas in autumn DSG 1 dominated but older stages were scarce (Fig. 6.2). Regarding their spatial distribution no clear spatial pattern was identified but Mysis IV (DSG 3) aggregated in the south during summer. The adults accounted for 50% of the total captures in the northern area during autumn when also 50% of DSG 1 and 10% of DSG 2 were caught and later larval stages and juveniles were absent.

Captures of *E. arcticus* DSG 1 were similar between seasons and Pz I dominated during autumn but only few Pz II were caught (Table 6.2). *E. arcticus* decapodids and juveniles were only caught in summer. Furthermore, the highest abundances of DSG 2 of *E. arcticus occured*in summer whereas only one Mysis I was representing the larval stages of this species during autumn. *S. robusta* early larvae (DSG 1) counts were similar between seasonsbut more advanced mysis and decapodids, as well as juveniles, were only captured in summer. Abundnaces of early larval stages (DSG 1) of *E. arcticus* and *S. robusta* were similar between seasons. The adults of *S. robusta* represented 80% of the total abundances obtained during the summer survey (Fig. 6.2). No spatial pattern was identified betweenseasons though *E. arcticus* adults were more abundant at northern stations where decapodids also concentrate. Despite *P. vigilax* larvae only appeared in summer, their adults were captured in Balearic Sea in both seasons (Table 6.2 and Fig. 6.2). *P. vigilax* adults were captured in both study areas being their earlier larval stages (DSG 1) more abundant in the southern part than DSG 2, which dominated in the north area and consistedexclusively of decapodids.

6.4.2 Ontogenetic vertical distribution (OVD)

Adult's shrimps were captured by the six different gears used though differences in species composition and abundances were observed (Table 6.1 and Fig. 6.3). Adults of the four species were caught by nekton and micronekton gears (PT and IKMT) whilethe trawling "benthic" gears also caught juveniles. Juveniles of G. elegans were caught by PT gears during autumn. While during summer PT were able to capture juveniles of *G. elegans* and *E. arcticus*. Some adults of *S. robusta* were fortuitously captured also by plankton nets (Fig. 6.3). The epipelagic species *P. vigilax* was captured by the “pelagic” devices and hardly ever by the "benthic" ones. However, the major proportion of *S. robusta* was sorted from “benthic” samples and particularly by bottom trawl (Fig. 6.3).

Weighted mean depths (WMD) differed between the larval stage and juvenile-adult regardless of species or season (Fig. 6.4). The larval stages of the four species were distributed shallower in the water column compared to their juveniles and adults (Figs. 6.4a-d; ANOVA $p<0.001$). Most larvae were caught in the upper 100 meters whereas adults were distributed down to 200 meters depth for (*P. vigilax*,Fig.6.4d) or to 300-450 meters (*G. elegans*,Fig. 6.4a and *S. robusta*,Fig. 6.4c). Larvae and adults of *P. vigilax* showed the shallowest distribution of all species (Fig. 6.4d). *E. arcticus*, WMD of adults and larvae were similar in summer (ANOVA $p>0.05$) but not in autumn, when adults were caught 400 m deeper than larvae (ANOVA $p<0.001$; Fig. 6.4b).

As for the larvae, the WMD of the juveniles were shallower than those of adults (Fig. 6.5). *G. elegans* and *E. arcticus* juveniles were only caught with pelagic nets. Juveniles of *S. robusta* were captured by the benthic gears and showed a shallower WMD than their adults (Fig. 6.5). *E. arcticus* had the widest range of distribution, from 72 m to 745 m depth. Juveniles of *S. robusta* showed the narrowest range of distribution and also the deepest, from 417 m to 835 m depth. Most species, except *S. robusta*, showed seasonal WMD variability between their ranges of depth distribution. *P. vigilax* adults captured by pelagic devices had close WMD between seasons. However, *G. elegans* and *E. arcticus* adults showed a wide distance between seasonal WMD, for both pelagic and benthic communities. Adults of *G. elegans* and *E. arcticus* had narrow autumn ranges of distribution between water column and seafloor, whereas during summer their dispersion was wider.

6.4.3 Diel vertical distribution

Decapod larvae performed vertical migrations along day-night hours in autumn, showing a general pattern of ascension towards the surface during day-light hours (Table 6.3, Fig. 6.6). In contrast, no clear migratory behavior was registered during summer (Fig. 6.6). However, differences in depth ranges and migration timings were observed among the four species. The larval vertical migrations along day-night patterns of *Gennadas elegans* were different between seasons. In autumn, most of larvae which were Pz I and Pz II (see Table 6.2) descended down to 500 m depth (21-24 h), rising to the surface during daytime (Fig. 6.6a), while narrower movements that occurs on first 150 m existed should not be neglected. Such migratory behavior of *G. elegans* was not observed during summer, when most larvae were distributed in the upper 100 m where differences along day-night seems to took place (Fig. 6.6b). Seasonal vertical migrations along day-night patterns for *Eusergestes arcticus* were similar *to G. elegans* (Figs. 6.6a, d), but their larvae were even shallower distributed at 9-12 h during summer (Fig. 6.6d). This summer surface peak in the morning was also observed for the larvae of *Parasergestex vigilax* (Fig. 6.6e). Signs of DVM are observed in all these data, where larval records positions along water column indicate diel movements, primarily focused on the first 100 m depth. No vertical migrations along day-night patterns were observed for the larvae of *Sergia robusta* in both seasons, being captured in the upper 150 m overall day (Figs. 6.6f, g). However, despite no larvae were captured between 21-00 hours in any season, the model suggested a mean descent *of S. robusta* larvae to deeper layers in autumn at night (Fig. 6.6f).

			Autumn		Summer		
Species	**DSG**	**DS**	**North**	**South**	**North**	**South**	**Total**
Gennadas elegans (ge)							3034
Larvae	ge_1						1428
		Pz I	*472*	*178*	*9*	*19*	
		Pz II	*172*	*523*	-	*55*	
Larvae	ge_2						135
		Pz III	*15*	*73*	*1*	*29*	
		M I	-	*8*	-	*2*	
		M II	-	-	*7*	-	
Larvae	ge_3	M IV	-	1	2	7	10
Juvenile	ge_5	Juvenil	-	1	12	13	26
Adult	ge_6	Adult	699	110	338	288	1435
Eusergestes arcticus (ea)							2199
Larvae	ea_1						632
		Pz I	*175*	*71*	*100*	*120*	
		Pz II	*9*	-	*94*	*63*	
Larvae	ea_2						233
		Pz III	-	-	*115*	*4*	
		M I	*1*	-	*41*	-	
		M II	-	-	*70*	*2*	
Larvae	ea_4	Decapodid	-	-	7	-	7
Juvenile	ea_5	Juvenil	-	-	10	2	12
Adult	ea_6	Adult	522	130	454	209	1315
Sergia robusta (sr)							818
Larvae	sr_1						173
		Pz I	*8*	*16*	*2*	*7*	
		Pz II	*45*	*27*	*43*	*25*	
Larvae	sr_2						114
		Pz III	*37*	*6*	*27*	*2*	
		M I	-	-	*28*	-	
		M II	*1*	-	*13*	-	
Larvae	sr_4	Decapodid	-	-	11	2	13
Juvenile	sr_5	Juvenil	-	-	-	-	
Adult	sr_6	Adult	102	13	265	132	512
Parasergestes vigilax (pv)							967
Larvae	pv_1						261
		Pz I	-	-	*3*	*58*	
		Pz II	-	-	*58*	*140*	
Larvae	pv_2						614
		Pz III	-	-	*251*	*50*	
		Z I	-	-	*141*	*20*	
		Z II	-	-	*52*	*24*	
Larvae	pv_4	Decapodid	-	-	16	-	16
Juvenile	pv_5	Juvenil	-	-	-	-	
Adult	pv_6	Adult	13	29	18	16	76

Table 6.2 Target species caught from late autumn survey (2009) and summer survey (2010) at northern and southern stations. The number of decapods are divided in larvae with their different developmental stage group (DSG from 1 to 4) third group (DSG 3) is exclusive for G. elegans, juvenile (DSG 5) and adults (DSG 6). All larval stages were captured by a HYDRO-BIOS multi-net (dark gray) in autumn and by MOCNESS (light gray) in summer. And adults (DSG 6) off Balearic Sea captured by all the gears (see Fig. 6.3)

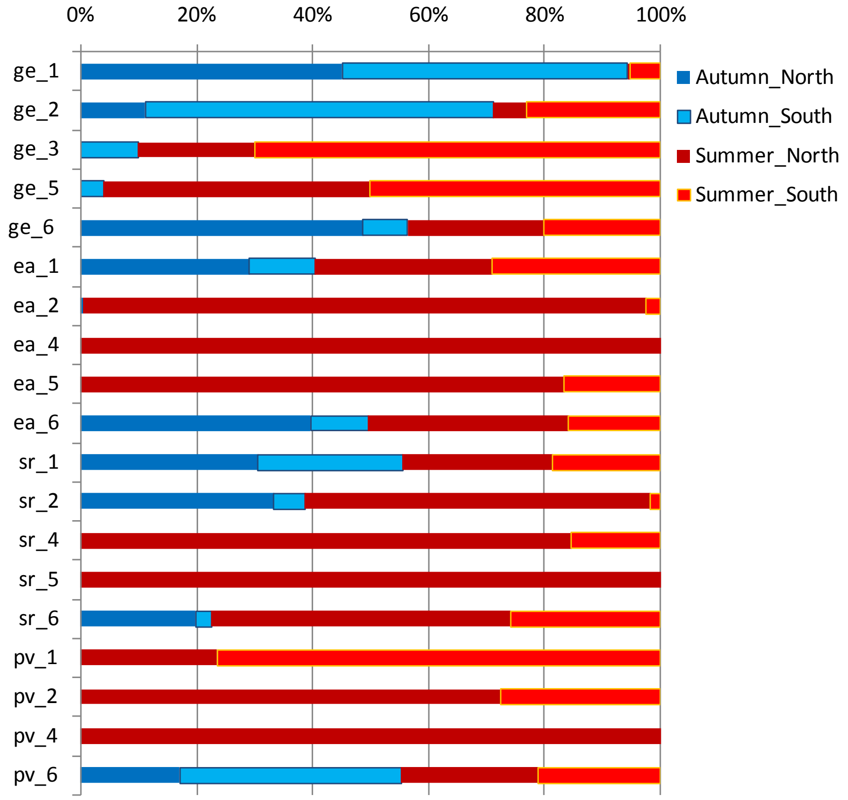


Figure 6.2 Percentage of total N of the four species *Gennadas elegans* (ge), *Eusergestes arcticus* (ea), *Sergia robusta* (sr) and *Parasergestes vigilax* (pv) by developmental stage groups (DSG) and season/area combination.Larval stages grouped in developmental stages groups (DSG1-4) 1: Pz I + Pz II; 2: Pz III + Mysis I + Mysis II; 3: Mysis III + Mysis IV; 4: Decapodids; Juvenile-adult stages (DSG5-6) 5: juveniles; 6: adults

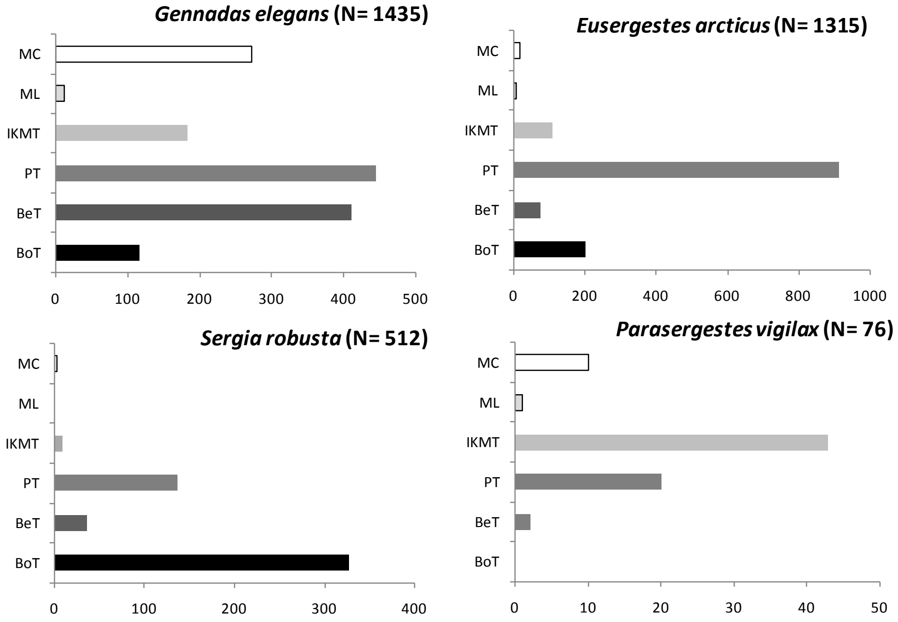


Figure 6.3 Total number of individuals (both juvenile and adult) caught (N) by the different sampling devices used.
BoT: bottom trawl; Bet: beam trawl; PT: Pelagic Trawl net; IKMT: Isaaks-Kidd Midwater Trawl; ML: HYDRO-BIOS multi-net; MC: MOCNESS

Adults' vertical migrations along day-night patterns were similar between seasons while contrasting between species (Table 6.3, Fig. 6.7). In autumn, adults of *G. elegans* showed the same pattern of the larval stages, descending down to 500 m depth progressively during nighttime and rising to the surface during daytime (Fig. 6.7a). In summer, adults were also found in the deeper layers at night (800 m depth) while displaying a strong migratory behavior towards the surface during sunrise and sunset (Fig. 6.7b). Contrary to their larvae, adults of *E. arcticus* did not perform strong migrations and were generally captured in the upper 300 m during both seasons (Figs. 6.7c, d). Data were very scarce in autumn for *S. robusta* and *P. vigilax* adults and no pattern was modeled (Table 6.3). In summer, *P. vigilax* adults performed a progressive ascent to the surface during nighttime (Fig. 6.7e), whereas *S. robusta* reached the surface at sunrise (Fig. 6.7f). These two adults’ species were found at the deepest position around-after midday while not wide displacements were recorded for their larvae. The shallowest position of adult of deeper species, *G. elegans* and *S. robusta,* took place between 6 h to 9h, whereas for the other two species arise surface around 3 h to 6h GMT.

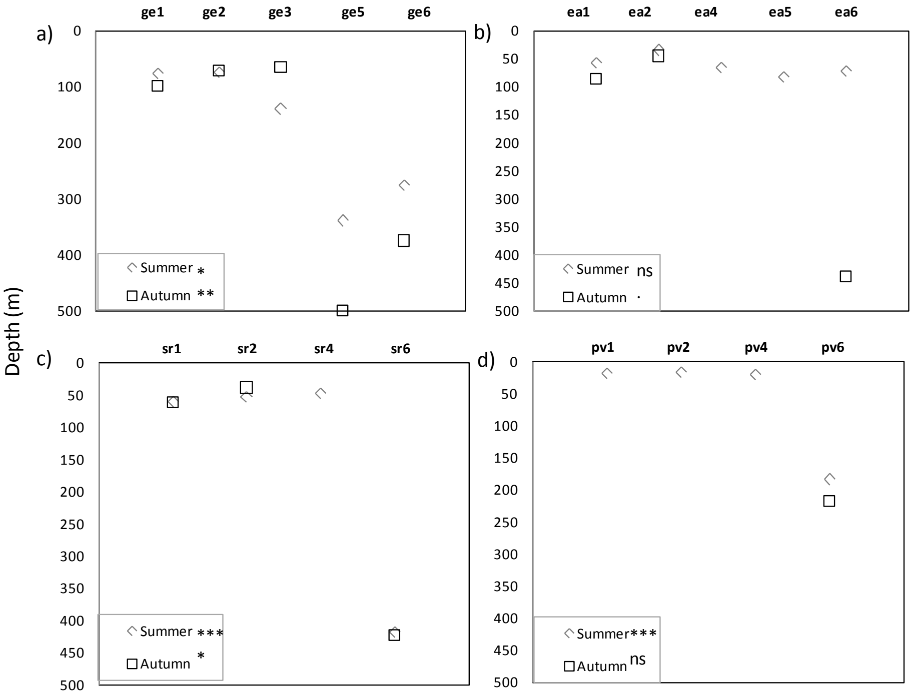


Figure 6.4 Four species (a-d) average development stages group (DSG) mean weighted depth during summer in grey and late autumn in black, captured by pelagic gears. Depth is in meters. Species statistic significance of WMD between Larval or juvenil-Adult stages with asteriscus (p-value < 0.005 ***; ns: no significative)

Larval stages grouped in developmental stages groups (DSG1-4) 1: Pz I + Pz II; 2: Pz III + Mysis I + Mysis II; 3: Mysis III + Mysis IV; 4: Decapodids; Juvenile-adult stages (DSG5-6) 5: juveniles; 6: adults

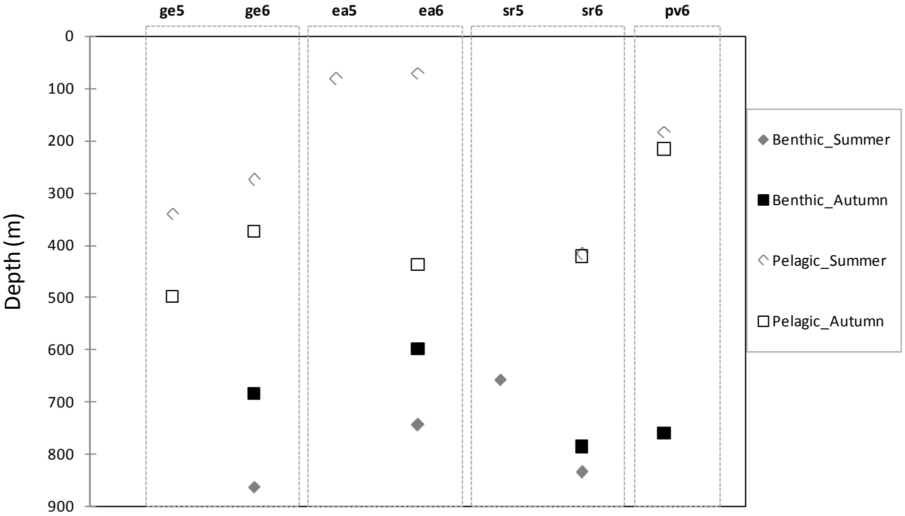
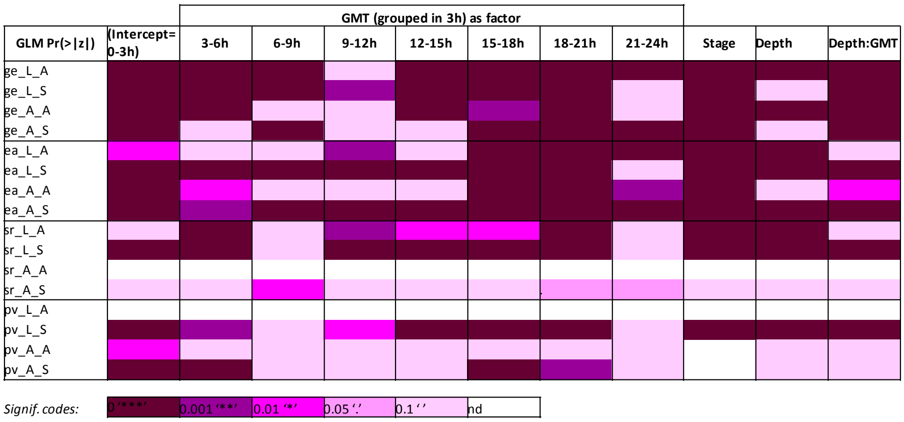


Figure 6.5 Four species average juveniles (DSG 5) and adults (DSG 6) mean weighted depth during summer in grey and late autumn in black, captured by pelagic (P; symbol unfilled) gears and by benthics ones (B; symbol filled). Depth is in meters. Species statistic significance of WMD between gears with asteriscus (p-value < 0.005 ***) ge ***; ea ***; sr***; pv ***

Table 6.3 GLM results significance. Predicted larval and adults densities interaction between depth distribution along the day and night (GMT h), stage of development, depth distribution and between depth distribution and time hour interaction.

(Dispersion parameter for poisson family taken to be 1)



		GMT (grouped in 3h) as factor									
GLM Pr(>|z|)	**(Intercept= 0-3h)**	**3-6h**	**6-9h**	**9-12h**	**12-15h**	**15-18h**	**18-21h**	**21-24h**	**Stage**	**Depth**	**Depth:GMT**
ge_L_A	***	***	***	‘ ’	***	***	***	***	***	***	***
ge_L_S	***	***	***	**	***	***	***	‘ ’	***	‘ ’	***
ge_A_A	***	***	‘ ’	‘ ’	***	**	***	‘ ’	***	***	***
ge_A_S	***	‘ ’	***	‘ ’	‘ ’	***	***	***	***	‘ ’	***
ea_L_A	*	‘ ’	‘ ’	**	‘ ’	***	***	***	***	***	‘ ’
ea_L_S	***	***	***	***	***	***	***	‘ ’	***	***	***
ea_A_A	***	*	‘ ’	‘ ’	‘ ’	***	***	**	***	‘ ’	*
ea_A_S	***	**	***	***	***	***	***	***	***	***	***
sr_L_A	‘ ’	***	‘ ’	**	*	*	***	‘ ’	***	***	‘ ’
sr_L_S	***	***	‘ ’	***	***	***	***	‘ ’	***	***	***
sr_A_A											
sr_A_S	‘ ’	‘ ’	*	‘ ’	‘ ’	‘ ’	.	.	‘ ’	‘ ’	‘ ’
pv_L_A											
pv_L_S	***	**	‘ ’	*	***	***	***	‘ ’	***	***	***
pv_A_A	*	‘ ’	‘ ’	‘ ’	‘ ’	‘ ’	‘ ’	‘ ’		‘ ’	‘ ’
pv_A_S	***	***	‘ ’	‘ ’	‘ ’	***	**	‘ ’		‘ ’	‘ ’

Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ nd

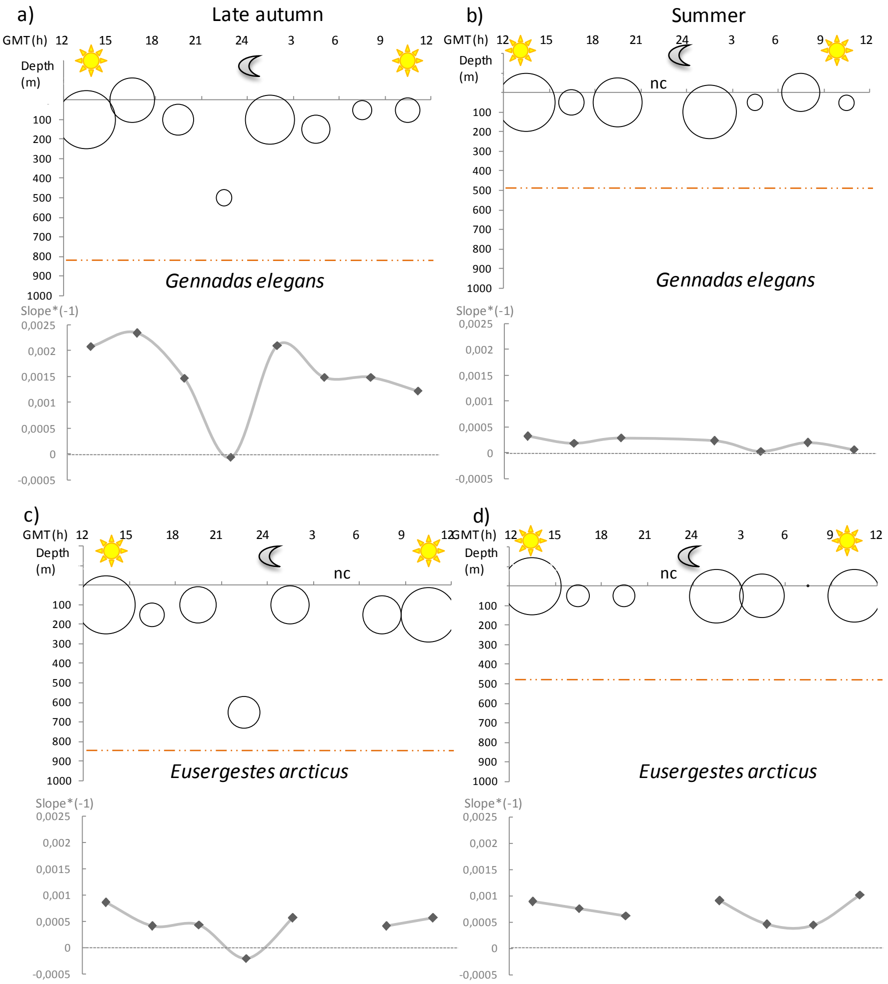


Figure 6.6 The larval average density was estimated for each of the 3 hours intervals integrating the whole water column. Seasonal larvae of the four target species (a-g) average densities (AD) observed along day hours captured by pelagic gears (bubbles, on the top). The AD by each 3-h interval was plotted at depth where the maximum density was recorded in that time level. The bubble sizes are in proportion in each figure, according to the maximum density recorded for each species during larval period by season. Red dotted line indicate the deepest layer larval sampled by season (850 m in autumn and 500 in summer). The slopes of the modeled densities are plotted by dots (on the bottom) and were joined by lines.

NOTE: When there is not enough data to model there is not grey dot.

Remember: In order to facilitate interpretation of the graphs the values of the slopes were multiplied by – 1.

nc: no captures for 3-h interval

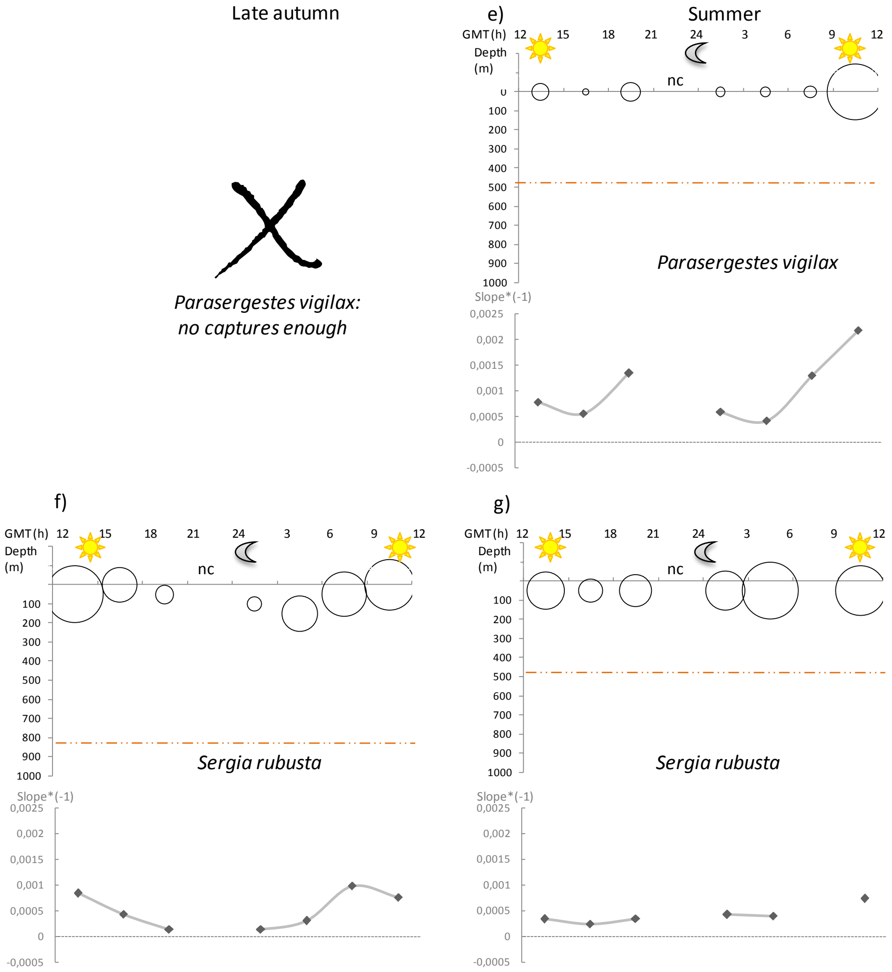


Figure 6.6 (continued)

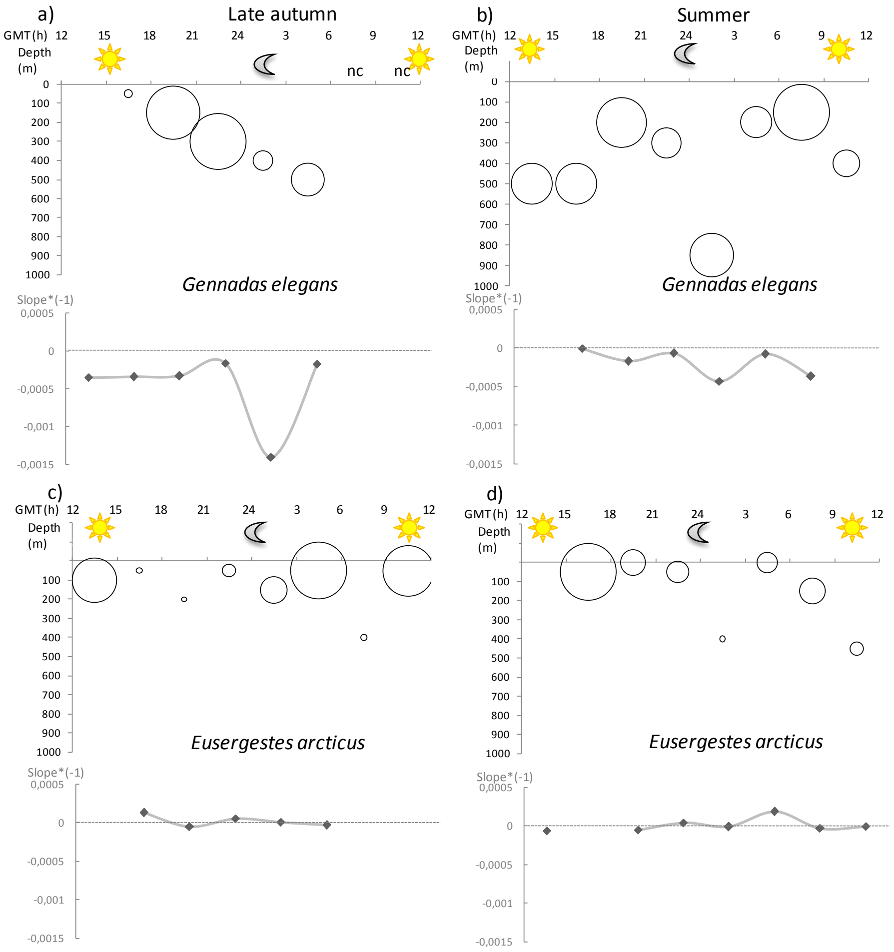


Figure 6.7 The adults average density was estimated for each of the 3 hours intervals integrating the whole water column. Seasonal adults of the four target species (a-f) average densities (AD) observed along day hours captured by pelagic gears (bubbles, on the top). The AD by each 3-h interval was plotted at depth where the maximum density was recorded in that time level. The bubble sizes are in proportion in each figure, according to the maximum density recorded for each species during adult period by season. The slopes of the modeled densities are plotted by dots (on the bottom) and were joined by lines.

NOTE: When there is not enough data to model there is not grey dot.

Remember: In order to facilitate interpretation of the graphs the values of the slopes were multiplied by – 1.

nc: no captures for 3-h interval

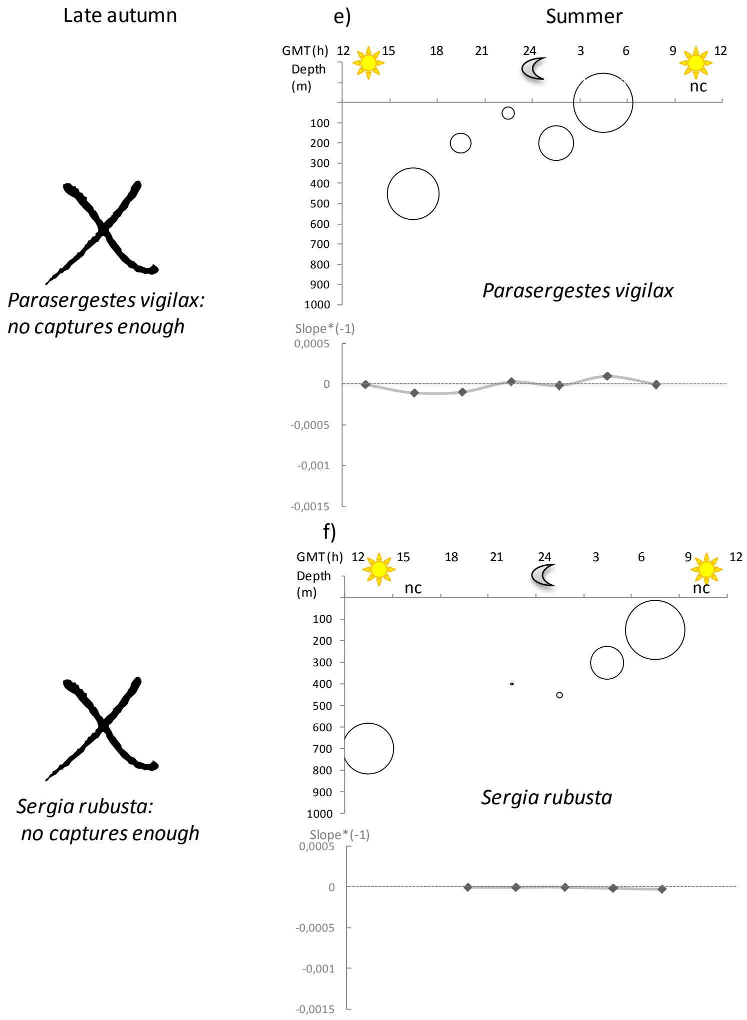


Figure 6.7 (continued)

6.5 Discussion

This study describes the spawning strategies for pelagic shrimps focusing on the analyses of the different stages in the life cycle of decapods. Patterns in the vertical distribution of the different developmental stages suggest a marked ontogenetic migration behavior. The most novel result is that larvae of some species ascended towards the surface during day-light in autumn supporting the hypothesis of reverse DVM as suggested for offshore species (e.g. Pochelon et al. 2014).

Our results demonstrate seasonal and ontogenetic differences in diel migration patterns. Thus, larvae of the three mesopelagic species seem to show a reverse DVM with non-stratified conditions, reaching the deepest position between 21h and 00h. During summer no DVM behavior was observed. On the contrary, only *G. elegans* adults showed a reverse migration pattern that was not observed in adults of the other species.

6.5.1 Seasonal distribution and spawning strategies of decapods

Spawning activity in pelagic shrimps is difficult to assess in adults since they are rarely caught with mature gonads. In addition, the duration of the larval period is not accurately estimated since adults are difficult to obtain alive to rear in laboratory conditions. In our study the first larval group considered (Protozoeae I and II) were caught in both seasons. According to these results, we suggest that mesopelagic species could spawn at least from July to December or alternatively could have an iteroparous reproductive strategy with two spawning periods, in summer and late autumn. A bimodal reproductive strategy has already been described in shallower species from shelf waters, such as Caridean shrimps (Boddeke 1982). In any case, spawning should have a longer duration in the mesopelagic species than in the epipelagic species *P. vigilax*, whose larvae were only captured in summer.

Most late larval stages were caught in summer suggesting recruitment to the area mostly occurs during the stratified environmental season. Food-limited conditions and lower temperatures characterize the area in late autumn and could affects survival and enlarge the duration of development as suggested from laboratory studies in other decapod species (González-Ortegón and Giménez 2014).

The natal origin of the species and the vertical position of the larvae to disperse offshore (Dos Santos et al. 2008) are main factors to understand population dynamics and connectivity (Cowen et al. 2007). We have deduced the spatial spawning strategies comparing the vertical distribution in the water column of the adult and that of their first larval stages (Fig. 6.8). Regardless of the season, adults were usually distributed throughout the water column with maximum densities around the Deep Scattering Layers located at 400 m depth (Simão et al. 2014). Some of the early larval stages were found at similar depths though the range of depth distribution could vary across species and seasons. The autumnal spawning of *G. elegans* and *E. arcticus* should occur down to 650 m depth, while in summer *G. elegans* early larval stages were found above 150 m depth.

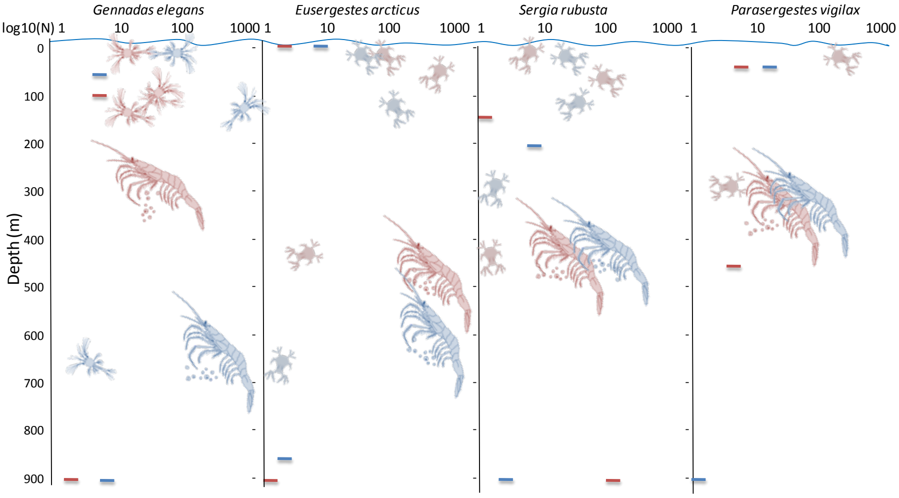


Figure 6.8 Scheme spawning strategies. Seasonal (autumn and summer) vertical distributions of adults and larval in first developmental stage group (Protozoeae I + II) and maximums captured (log 10 (N)) with pelagics and benthics gears. Speculative season and approximate depth of spawning are indicated with free eggs. Larvae and adults distributions were plotted in blue for late autumn and in red for summer, the shallowest and the deepest adults' distributions are represented with a line. Note: sampling conducted down to 900 m depth.

The ecological approach to the analysis of larvae vertical distribution needs to take into account that the water column was stratified in summer, showing strong gradients in the upper 100 meters, whereas in late autumn, conditions were more homogeneous down to the mixing layer depth (MLD). As a consecuence, because during summer the spawning is shifted to shallower layers, larval distribution could be different between seasons with implications in transport (Dellatorre et al. 2014). For epipelagic Sergestidae, the peaks of larval abundance were observed in the epipelagic habitats, increasing in abundance in shallowlayers and peaking at surface (Torres et al. 2014).

6.5.2 Ontogenetic vertical distribution (OVD)

Short time after spawning, nauplii become protozoea (the first larval stages caught in this study) and perform their first ontogenetic migration moving upwards. The larvae further develop in the upper layers of the water column (Pz III, Mysis I and II) and later move down to deeper positions (Mysis III and IV). This is the observed pattern for mesopelagic species in summerwhen the third larval group is found deeper close to the adults' dwell. The biggest larval displacement, at least 400 m, are performed by larvae belonged to *S. robusta,* a demersal species. Whereas, larvae of *P. vigilax* (epipelagic)*,* presenting shallower distribution around 200 m depth.

Nutritional requirements vary along the life cycle and can influence the vertical distribution. Naupliar phases do not feed because yolk reservations, protozoeae feed mainly on phytoplankton and mysis and decapodid stages ingest microalgae and zooplankton (e.g. Ewald 1965). Vertical distribution could be explained to find food because during the first 24-48 h molting to next larval stages is able if optimal feed conditions envelop them (Calado et al. 2007, Giménez 2002, Rotllant et al. 2010). Though little is known about potential predators of decapods over their successive life stages, predators may be specific for each developmental stage. It has been described that paralarvae feed on decapods larvae (Roura et al. 2012) whereas other decapods and elasmobranchs may prey on pelagic decapod adults in study area (Cartes et al. 2008, Valls et al. 2011). There is also information on the teleostean fish preying on decapods (e.g. Roger 1994).

6.5.3 Diel vertical distribution

Decapods can vary their position between day-night in relation to a predator-prey trade-off, both larvae (Sulkin et al. 1988) and adults (Foxton 1970), constituting a link between pelagic primary producers and the higher trophic levels (Macquart-Moulin and Patriti 1993). As a contrasting feature with other groups of meroplankton, decapod larvae are able to cross easily hydrographic clines, such as the thermocline (Dos Santos et al. 2008, Lindley et al. 1994). Early protozoeae of *G. elegans* and *E. arcticus,* who are phytoplankter feeders, dominated the autumn larval assemblage and seem to show reverse or diurnal pattern in our study area. Different seasonal DVM pattern is a behavior already describe for benthic crab larvae and this reverse DVM pattern is already describe for offshore benthic crab larvae (Dellatorre et al. 2014, Pochelon et al. 2014). During stratified season, a deep chlorophyll maximum (DCM) is temporally found (Estrada et al. 1993), while in autumn feeding conditions are homogenous through water column. Seasonal changes in vertical migration patterns have been described in deep plankton and related to the differences in light hours following the rhythm of local sunrise and sunset (van Haren and Compton 2013). In the study area, *P. vigilax* larvae are located in the surface layers. This larval behavior is best explained by temperature in the models whereas larvae of mesopelagic species dominate in the deeper layers close to the temporally DCM (Torres et al. 2014, Hidalgo et al. 2014). *P. vigilax distributed in the upper layers* may ensure their encounter with prey feeding oncopepod nauplii or even smaller prey such as cyanobacteria, prochlorophytes or nanociliates that are usually found in large densities above the DCM in NW Mediterranean waters (Andersen et al. 2001, Vidussi et al. 2000, Pérez et al. 2000).

The reverse DVM behavior found in this study for mesopelagic early larvae has been described for a variety of other phytoplankters and zooplankters such as copepoda, and appendicularians (Pearre 2003, Tester et al. 2004, Irigoien et al. 2004). Reverse DVM has been described in a recent study for brachyuran crabs larvae during winter in offshore Atlantic waters (Pochelon et al. 2014). In their work, reverse DVM behavior is discussed by larvae being more vulnerable to visual predators during day hours at the surface.Besides, *Calanus* spp also undergo reverse migrations that allow them to avoid predators that follow the common DVM pattern, such as chaetognaths (Irigoien et al. 2004). These last examples of reverse behavior in conjunction with our results support the theory that in open waters reverse DVM could be a strategy to escape from tactile stimuli predators allowing decapod larvae to be in surface waters in hours of light exposure.

Contrary to other studies, that show how Sergestidae females from offshore areas release their eggs near surface (Koettker et al. 2010), our results support the hypothesis, already described for Penaeids, that spawning occurs in the deeper layers (Dall et al. 1990). First larval stages will afterwards migrate to the euphotic layer. Early larval stages were observed in deeper layers at night hours in our study supporting spawning occurs at night. Our intensive sampling in the water column provides detailed vertical distribution patterns that could be incorporated into hydrodynamic circulation models (i.e. Regional Ocean Model System; Shchepetkin and McWilliams 2005) to predict larval transport. Larval trajectories are necessary to understand connectivity across populations, to increase our knowledge of the metapopulation dynamics and biogeography and to improve current management of natural resources. The organisms performing large vertical migrations play a mayor role on the secondary production of deep-sea (Klages et al. 2001). In our area, pelagic shrimps, target species of this work must be taken into account to describe the energetic dynamics of the continental slope and bathyal ecosystems.

Chapter 7
General conclusions

1. Considering the 121 different taxa: 19 to family level, 27 to genus and 75 to species level, identified among the more than 7,000 larvae that have been examined within this study, it can be concluded that the plankton community integrates species whose adults occupy a wide range of niches, from benthic to pelagic species, and hence larval studies constitute a good method for characterizing the decapods crustacean community in a given region.

2. The following larval records can be qualified as worldwide interesting:

i) The sixth report of capture of *Aristeus antennatus* larvae worldwide that represents the fourth report of capture in the Mediterranean; ii) The third finding of *Parapenaeus longirostris* larvae worldwide which is the second in the Mediterranean; iii) The fourth finding of *Scyllarides latus* larvae worldwide, which is the first capture of larvae of this species in the Mediterranean; iv) The second report of capture of spider crab *Maja squinado* larvae in the Mediterranean since its description in the same sea in the sixties. This finding suggests the restocking program for this species carried out in the Balearic Islands since 2008 may be successful.

3. Hence, this study describes for first time the second mysis of *Aristeus antennatus* and improves previous descriptions of the morphology of the first zoea of *Scyllarides latus.* These new descriptions enable their identification in future field samplings and contribute to a better understanding of their ecology. For species of commercial interest or threatened species such knowledge is relevant because of its potential application to improve the management of these resources.

4. The application of molecular techniques, such is the case of the first identification, confirmed by genetic analysis, of *Polycheles typhlops* zoea and morphological links to the successive stages until the last planktonic state named decapodid, have allowed almost closing the life cycle of this species. Extensive larval morphological analyses have confirmed that the old assignments of those morphotypes to *Eryoneicus puritanii* were erroneous, since they in fact correspond to the dispersive stages of *Polycheles typhlops*. It must be pointed out that in deep-sea species, morphological descriptions from plankton samples have a high added value, given the difficulty of catching and keeping adults alive in laboratory conditions for reproduction.

5. *Palaemon macrodactylus* larval discovery has allowed to confirm that this species reproduces and is fully settled and adapted in the Mediterranean Sea. The publication of this finding alerted the scientific community in further designs of adults sampling strategies, which immediately resulted in the finding of *P. macrodactylus* adults' populations in the North Adriatic lagoons.

6. Early larval stages belonging to deep-sea adults living in close relationship with the substrate, such as *Aristeus antennatus*, *Parapenaeus longirostris*, *Ergasticus clouei, Calappa grannulata* or *Polycheles typhlops,* have been collected in the first 50 meters depth of the water column, which allow rejecting the hypothesis that such larval stages remain close to the bottom, sharing the adult's habitat.

7. Mean larval densities reported in this study were low, a general pattern in oligotrophic regions, around 100 times lower than those reported for nearby coastal Atlantic productive upwelling areas. Occasionally, high larval densities were recorded, which were attributable to the oceanographic and hydrodynamic scenario found in the Balearic Sea.

8. Mesoscale structures influence larval spatial patterns, favoring the retention of larvae of different species in the study area. Therefore, the oceanography and processes such as the "island-mass effect", that can improve the biological productivity at the regional scale and thus larval survival, can explain the existence of mixed larval communities in the Balearic Sea composed of neritic and oceanic larval species.

9. Among the 121 taxa identified, the majority, 63, appeared only in summer, while 7 were exclusively captured in autumn, allowing concluding that in the Balearic Sea the diversity of the decapod larval community is higher during summer.

10. This study confirms a longer spawning period for meso-pelagic than for epi-pelagic species, such as *Parasergestes vigilax*, whose larvae have been captured only in summer.

11. During summer, larvae belonging to epi-pelagic species such as *Parasergestes vigilax* are the most abundant, with average densities of 2.2 larvae per 100 m^3 in the south of the islands. These larvae are mainly concentrated in the first 25 meters of the water column. Meso-pelagic species dominate the larval community in late autumn being *Gennadas elegans* the most abundant species with average densities of 14.5 larvae per 100 m^3 in the northern stations.

12. Fluorescence, as an indicator of chlorophyll, has been one of the environmental factors that best explained the vertical distribution of decapod larvae. In summer, during the stratification period, larvae would aggregate close to thermocline where they can find large patches of prey. Maximum densities of *Parasergestes vigilax* were located within the first 25 meters but a second peak of larval abundance was identified associated to the maximum chlorophyll depth, mainly attributable to *Eusergestes arcticus* larvae. In contrast, during autumn when the clines are breaking, larvae are distributed in a wider range of depths, such as *Gennadas elegans,* in relation to the wider vertical dispersion of their prey. This would be an adaptive strategy to maximize the chances of encountering prey.

13. The most abundant decapods in the water column are: *Gennadas elegans, Eusergestes arcticus, Sergia robusta* and *Parasergestes vigilax*. Their distribution could be explained by the vertical migration of the early life stages from the deeper habitats where adults are settled, to the shallower areas where larval food resources are more abundant. The ontogenetic migrations of these species show that intermediate stages are distributed in the surface layers whereas later stages (megalopa or decapodids) are mostly found in the deep layers.

Palinurus elephas phyllosoma, from Ernst Haeckel's Kunstformen der Natur

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Annex I
Conclusiones generales

1. Teniendo en cuenta que hasta 121 taxones diferentes: 19 a nivel de familia, 27 a nivel de género y 75 a nivel de especie, fueron identificandas entre las mas de las 7000 larvas examinadas en este estudio, se puede concluir que la misma comunidad planctónica integra las larvas de especies cuyos adultos ocupan nichos muy diferentes, desde especies pelágicas a bentónicas. Los resultados muestran que los estudios meroplanctónicos, permiten caracterizar las biocenosis en una región determinada de forma relativamente sencilla. Así, al contrario de lo que sucede en los estudios basados en formas adultas, en el marco de un único estudio y aplicando sólo un tipo de metodología de muestreo de plancton es posible identificar casi todas las especies de decápodos de un área determinada.

2. Las siguientes citas pueden ser calificadas de relevantes a nivel internacional:

i) Sexto registro de captura de larvas de *Aristeus antennatus* a nivel mundial, que representa la cuarta cita en el Mediterráneo; ii) Tercera cita mundial de larvas de *Parapenaeus longirostris*, segunda en el Mediterráneo; iii) Cuarta cita mundial de larvas de *Scyllarides latus*, lo que supone la primera captura de larvas de esta especie en el Mediterráneo; iv) Segunda captura de larvas de centolla, *Maja squinado*, en el Mediterráneo, desde su descripción en los años sesenta a partir de ejemplares provenientes de aguas del mismo mar. Este hallazgo podría sugerir el posible éxito de un programa de repoblación de esta especie llevado a cabo en las Islas Baleares desde el 2008.

3. Se estudió describe por vez primera la segunda mysis de *Aristeus antennatus* y mejora las descripciones anteriores de la morfología de la primera zoea de *Scyllarides latus*. Estas nuevas descripciones permitirán su futura identificación a partir de muestras capturadas en el mar y contribuyen a una mejor comprensión de su ecología. Para especies de interés comercial o especies en su día amenazadas, dicho conocimiento es relevante por su potencial aplicación a la mejora de la gestión de esos recursos.

4. La aplicación de técnicas moleculares, como el caso de la primera identificación, confirmada por análisis genéticos, de la zoea de *Polycheles typhlops*, y su vinculación morfológica a los sucesivos estados de desarrollo hasta llegar al último estado planctónico de decapodito. Los exhaustivos análisis morfológicos de dichas larvas han permitido confirmar que las antiguas asignaciones de esos morfotipos a *Eryoneicus puritanii* eran erróneas, ya que en realidad corresponden a las fases dispersivas de *Polycheles typhlops*. Hay que señalar que en especies de aguas profundidas, las descripciones morfológicas a partir de muestras de plancton presentan un gran valor añadido, dada la dificultad de capturar adultos y mantenerlos vivos en el laboratorio para su reproducción.

5. El descubrimiento de *Palaemon macrodactylus* ha permitido confirmar que esta especie se reproduce y está totalmente asentada y adaptada en el Mar Mediterráneo. La publicación de este hallazgo alertó a la comunidad científica, impulsando muestreos específicos dirigidos a adultos esta especie, que se tradujeron en el inmediato hallazgo de las poblaciones adultas de *P. macrodactylus* en las lagunas del Adriático Norte.

6. Los estadíos larvarios tempranos pertenecientes a adultos de grandes profundidades que viven en estrecha relación con el sustrato, como *Aristeus antennatus, Parapenaeus longirostris, Ergasticus clouei, Calappa grannulata* o *Polycheles typhlops*, han sido recolectados en los 50 primeros metros de la columna de agua, lo que permite descartar la hipótesis de que los estados larvarios de estas especies permanecen en zonas cercanas al fondo compartiendo el hábitat de los adultos.

7. Los valores medios de densidad larvaria registrados fueron bajos, como es característico de zonas oligotróficas, en torno a cien veces menores que las registradas en zonas costeras del Atlántico próximas de surgencias o “upwellings”. Ocasionalmente, altas densidades larvarias se han registrado atribuibles a la oceanografía y a escenarios hidrodinámicos del Mar Balear.

8. Estructuras de mesoescala condicionan también los patrones de distribución larvaria, los que favorecen la concentración de larvas de distintas especies. Siendo la hidrografía y procesos tales como el “efecto masa-isla” que pueden mejorar la productividad biológica a escala regional y por ello la supervivencia larvaria, la causa de la existencia de comunidades larvarias mixtas en el Mar Balear, compuestas por larvas de especies neríticas y oceánicas.

9. Entre los 121 taxones identificados, la mayoría, 63, aparecieron exclusivamente en verano, mientras que 7 fueron exclusivamente otoñales, lo qu ayuda a concluir que la diversidad de la comunidad larvaria de crustáceos decápodos en el Mar Balear es mayor durante el verano.

10. Este estudio confirma una mayor duración de la puesta en las especies meso-pelágicas respecto a las epi-pelágicas, como es el caso por ejemplo de *Parasergestes vigilax*, cuyas larvas se han encontrado sólo en verano.

11. En verano, dominan larvas de especies epi-pelágicas, como *Parasergestesvigilax* que es la más abundante en la zona, con densidades medias 2.2 larvas por 100 m^3 en el sur de las islas. Estas larvas se concentran mayoritariamente en los primeros 25 metros de la columna de agua. A finales de otoño, en cambio, dominan la comunidad larvas de especies meso-pelágicas, siendo la más abundante *Gennadas elegans*, con densidades medias 14.5 larvas por 100 m^3 en las estaciones norteñas.

12. .La fluorescencia, como un indicador de la clorofila, ha sido uno de los factores ambientales analizados que mejor explica la distribución vertical de las larvas de decápodos. En verano, durante la época de estratificación, las larvas se concentrarían en zonas próximas a la termoclina donde pueden concentrarse las presas. Densidades máximas de *Parasergestes vigilax* se encuentran dentro de los primeros 25 metros, detectándose un segundo pico de abundancia, en este caso atribuible a larvas de *Eusergestes arcticus*, asociado al máximo profundo de clorofila. Por el contrario en otoño, cuando se quiebran las clinas, las larvas se distribuyen en un rango más amplio de profundidades, como es el caso de las larvas de *Gennadas elegans*, como resultado de la mayor dispersión vertical de las presas. Esta podría ser una estrategia para maximizar las oportunidades de encontrar presas.

13. Los decápodos más abundantes en la columna de agua son: *Gennadas elegans, Eusergestes arcticus, Sergia robusta* y *Parasergestes vigilax.* Su distribución se podría explicar por la migración vertical de los estadios larvarios tempranos desde los hábitats de los adultos más profundos, hacia las zonas más superficiales donde se concentran los recursos tróficos. Las migraciones ontogenéticas de dichas especies muestran que los estadios intermedios se distribuyen en capas superficiales, mientras que los estadios tardíos (megalopas o decapoditos) se encuentran en las capas más profundas.

Palinurus elephas phyllosoma, from Ernst Haeckel's Kunstformen der Natur