Small-scale distribution characteristics of *Munida* spp. populations (Decapoda: Anomura) off the Catalan coasts (western Mediterranean)

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Abstract

The small-scale distribution characteristics of three species of the anomuran genus *Munida*, namely *Munida rutllanti, Munida intermedia* and *Munida tenuimana*, have been studied on the lower shelf and upper-middle continental slope near the coasts of Tarragona and the Ebro delta region in the western Mediterranean. The differential bathymetric distribution showed that a fair degree of overlap exists between *M. rutllanti* and *M. intermedia*, with the former being mainly found at shallower depths. The size population structure of the three species showed that polymodality, as indicative of a longer life-span and of a higher degree of population structuring was more evident in the deeper-living species, whereas unimodality, as an indication of a recruitment dependent population, was more evident in the shallowest-occurring species. Geostatistics have been applied to determine the degree of spatial variability occurring in *M. intermedia* abundance, the better-sampled species. The Mantel test has been used to assess the significance of the overlap between the three species distributions as well as the relation between certain population parameters. A discussion on the population characteristics of *M. rutllanti* is made in relation with its expansion along the western Mediterranean in the last decades.
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1. Introduction

Five species of the squat lobster genus *Munida* are known in the western Mediterranean (Zariquiey Álvarez, 1968; D'Udekem d'Acoz, 1999), three of which are usually found on soft-bottom areas: *Munida rutllanti* Zariquiey Álvarez, 1952, *Munida intermedia* A. Milne Edwards and Bouvier, 1899 and *Munida tenuimana* G.O. Sars, 1882. The shallower-occurring species *M. rutllanti*, mostly concentrates on the shelf and upper slope, *M. intermedia* is mainly distributed

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from the shelf-break to the middle slope, whereas *M. tenuimana* mostly occurs on the middle and lower slope, with its distribution extending down to over 2000 m depth (Abelló et al., 1988, 2002; Cartes, 1993a). The biology and ecology of the different species of the genus *Munida* in the Mediterranean and NE Atlantic waters have been studied by various authors, among whom Hartnoll et al. (1992), Freire et al. (1992), Gramitto and Froglia (1998), Sanz-Brau et al. (1998), and Company et al. (2003). The presence of several congeneric species over a depth gradient suggests the occurrence of a certain degree of ecological exclusion or habitat partitioning among them.

Geostatistical analysis has been applied in ecology to the study of the spatial organisation of populations or environmental variables (Cressie, 1991; Rossi et al., 1992; Webster and Oliver, 2001). It allows an accurate analysis of the spatial distribution of geo-referenced variables, such as density, size structure or any other biological variables, producing distribution maps of the variable under study (Maynou et al., 1996). Within this context, this work was designed to study the small-scale distribution and population size structure of *M. rutllanti*, *M. intermedia* and *M. tenuimana* using spatial correlation tests to detect any possible interspecies and intraspecies interactions. Geostatistical analysis was applied only to *M. intermedia* data since this was the best-sampled species, with the aim to detect small-scale spatial structures. The population variables were also investigated in relation to physical and ecological parameters that could explain the differential distribution of the three *Munida* species in the study area.

2. Material and methods

2.1. Study area

The geomorphology of the study area is characterised by a wide continental shelf off the Ebro delta, with a steeper slope in the southern sector than in the northeast. Two canyons are also found indenting the shelf (Fig. 1). The sediments in the area were studied by Maynou and Sardà (1997), showing three distinct areas based on redox potential, organic matter, sediment temperature, grain size and distribution, and carbonate content characteristics. They presented a high carbonate content and the texture ranged between mud and muddy-sands with various sorting levels, from well sorted areas to poorly sorted areas corresponding to the Ebro river outflow influence area.

The hydrography of the study area is characterised by the rich Ebro river outflow and by a permanent south-westward slope current that flows over the continental shelf (Font et al., 1988). The water column can be divided into three layers: a superficial water mass down to ca. 200 m that has considerable seasonal temperature and salinity fluctuations (Hopkins, 1985; Font et al., 1988), the Levantine intermediate water between 200 and 600 m, which shows little seasonal variation, and the Mediterranean deep water below 600 m with almost constant temperature (12.8 °C) and salinity (38.4 PSU).

2.2. Survey

A trawl survey (GEODELTA) was conducted over muddy bottoms off the Tarragona and Ebro delta continental shelf and slope (Fig. 1) (Maynou and Sardà, 1997). A regular grid 1 by 2 nautical miles was set parallel to the coast and a start location for each tow was randomly selected within each cell. The sampling was conducted between 7 and 15 April 1994 and a total of 72 stations were sampled. The depth of the sampling locations varied from 83 to 713 m.

The experimental sampling gear was a specially designed single-warp otter trawl ('Maireta System Trawl'; Sardà et al., 1998). The codend stretched mesh was 12 mm so as to retain small individuals not normally available to the commercial fishing gear. The actual opening of the trawl was measured using an acoustic system (SCANMAR) and stabilised at 13.4 m width by 2.0 m height. During the survey, tows were made parallel to the depth contours. The duration of each tow was set to exactly 15 min (time of effective trawling). The towing speed varied between 2.3 and 2.7 knots (mean 2.5 knots). Start and end locations for each tow were taken by GPS. The actual surface covered by each tow was computed from the GPS and the SCANMAR readings.

The total catch of the three species of *Munida* was counted, weighed, sexed and measured. In juvenile individuals and in individuals infested by rhizocephalan parasites, sex was determined by the position of
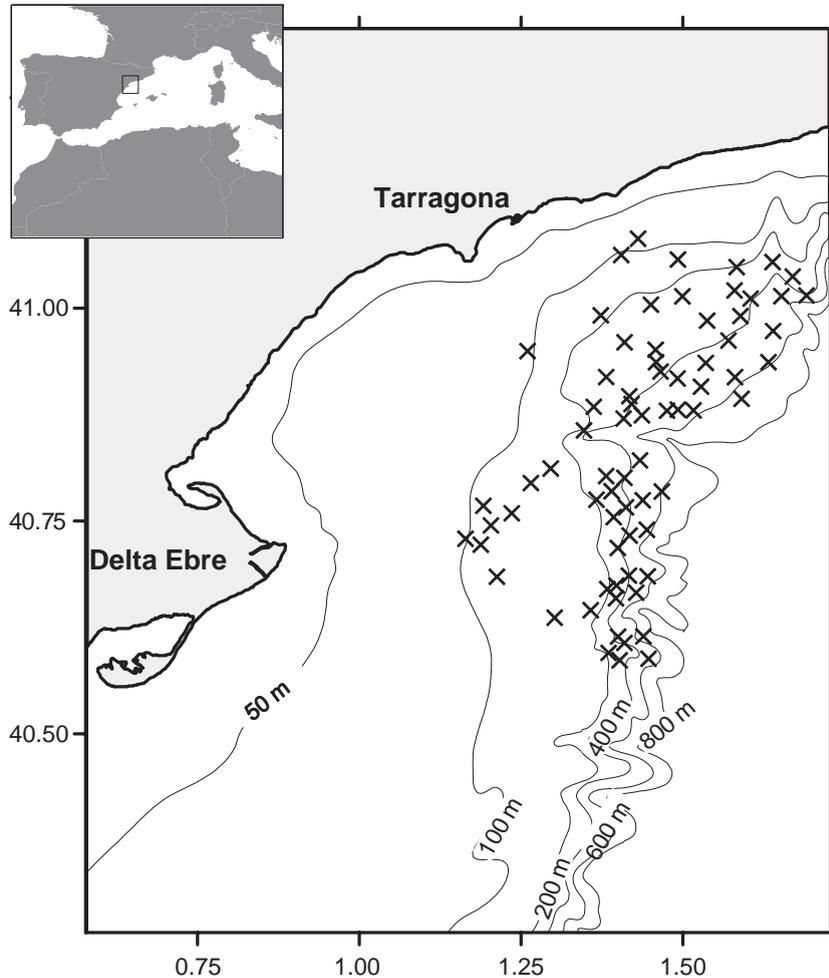
Fig. 1. Map of the study area with locations of trawl hauls.

the gonopores; otherwise, males were recognised by their first and second modified pleopods, and females by the occurrence of well-developed pleopods in all abdominal segments. The density of each species was computed as number of individuals ha^{-1} from the total surface covered by each tow. The distribution of the *Munida* species with depth was calculated as the mean number of individuals ha^{-1} by 50 m depth intervals.

Carapace length (CL) was measured in mm from the posterior margin of the right-hand side orbit to the posterior border of the carapace. Sizes of individuals of the three different *Munida* species were grouped in 1 mm classes and were plotted separately for males and females. Polymodality in size frequency distribu-

tions was assessed by determining the normal components of the distribution with the subroutine NORMSEP, fed with the results of the previously applied Bhattacharya's method, included in the software package FiSat II available from the FAO website.

The presence of a rhyzocephalan parasite was noted for *M. intermedia* to assess the rates of infection in this species and the spatial structuring of the infection.

2.3. Geostatistics

The fundamentals of geostatistics, with emphasis on the methods employed here, can be found

elsewhere (e.g. Cressie, 1991; Maynou, 1998; Webster and Oliver, 2001). Basically, the density of each *Munida* species can be considered as the random variable $Z(\mathbf{x_i})$: Number of individuals Ha^{-1} at location $\mathbf{x_i}$, whose properties are relatively constant over the area at the spatial and temporal scales of study. These assumptions can be verified in practice by an exploratory data analysis previous to geostatistical analysis (Webster and Oliver, 2001).

Under these conditions, the structure of spatial variability of *Munida* species abundance can be studied by computing an appropriate structure function, for instance a variogram (Cressie, 1991). The shape of the variogram gives clues to the spatial structure of the variable under study.

Modelisation of the unevenness in spatial correlation along and accross depth contours was attempted by means of anisotropic semivariograms (i.e. correlation functions that take into account the direction in addition to the geographical location) across the depth contours (angle 120°) and along the depth contours (angle 30°) but no meaningful structure could be recovered, due probably to the low (37) number of samples. General, isotropic variograms were used for all three categories (males, females, total).

Another aspect of geostatistics is the possibility of estimating the density of the variable of interest at points not sampled or over areas where a global estimate is needed (Cressie, 1991). This is known as *kriging* and can be regarded as spatial prediction or estimation. In order to proceed with kriging, the experimental variogram has to be fitted to a theoretical variogram model (some models are given in Cressie, 1991 and Webster and Oliver, 2001). When the experimental variogram has been computed correctly and there exists a clear underlying spatial structure, it is often easy to choose and fit a theoretical model. When there is no obvious pattern in the variogram, it is always possible to consider other geostatistical models or assume that there is no spatial structure in the variable at the scale of study.

The behaviour of the variogram near the origin requires a detailed study. A variogram may show a discontinuity near the origin, called the nugget effect (Cressie, 1991), which can be attributed to measurement error, micro-scale variability or small-scale spatial structure. For instance, below ca. 1 km, little can be said from our data set, since this is the average tow length in our study. A nugget component is usually included in most theoretical
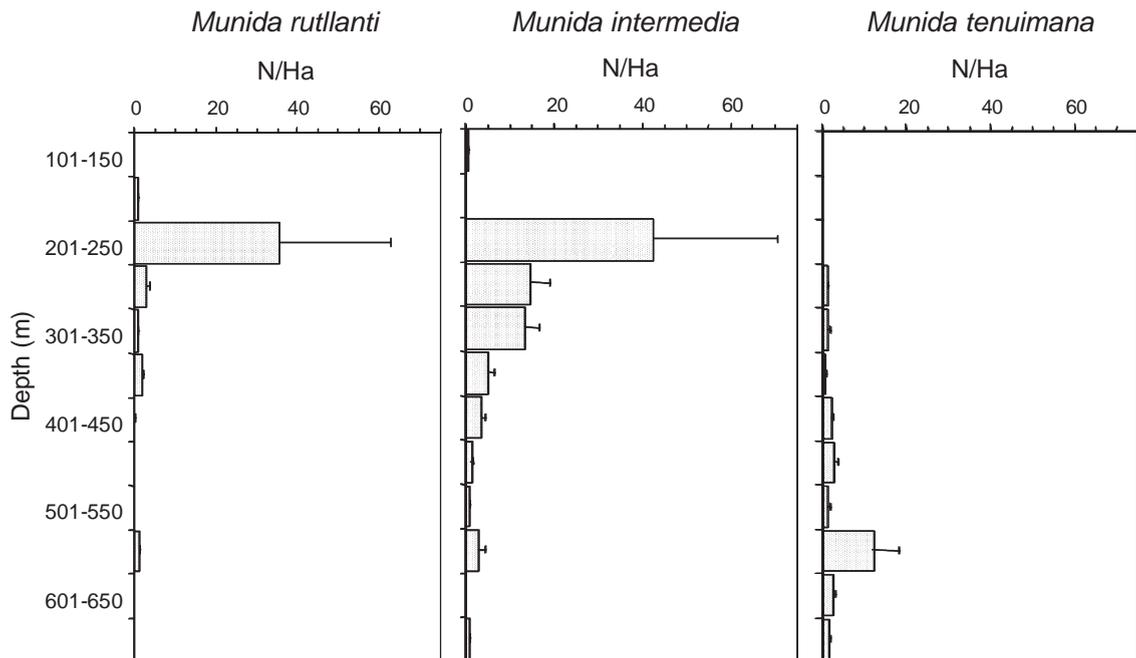
Fig. 2. Mean density (n ha^{-1}) plus standard error of the mean, of the three *Munida* species sampled.

variogram models. Sill corresponds to the data variance accounted for by the model.

2.4. Mantel test

Mantel's normalised *r* statistic (Mantel, 1967) was used to determine the degree of correlation between a matrix **A** of geographic distances and a matrix **B** of biological distances, or dissimilarities. We used the Euclidean coefficients to construct the matrix of geographic distance and the Manhattan coefficient for the matrix of biological distance (Legendre and Legendre, 1984). Mantel's *r* statistic was tested by a permutation procedure with 1000 randomisations of the **A** matrix, following the procedure detailed in Manly (1985), to contrast the null hypothesis of

absence of correlation between matrix **A** and **B**. Additionally, Mantel's test was also used to estimate the degree of overlap between two biological matrices, **B** and **C**, representing the dissimilarities between two biological data sets, e.g. density of *M. intermedia* and *M. tenuimana*, or two different sexes of each *Munida* species.

3. Results

3.1. Differential bathymetric distribution

The distribution of densities with depth in the three species studied (Fig. 2) shows that the populations studied are differentially depth-structured, with *M.*
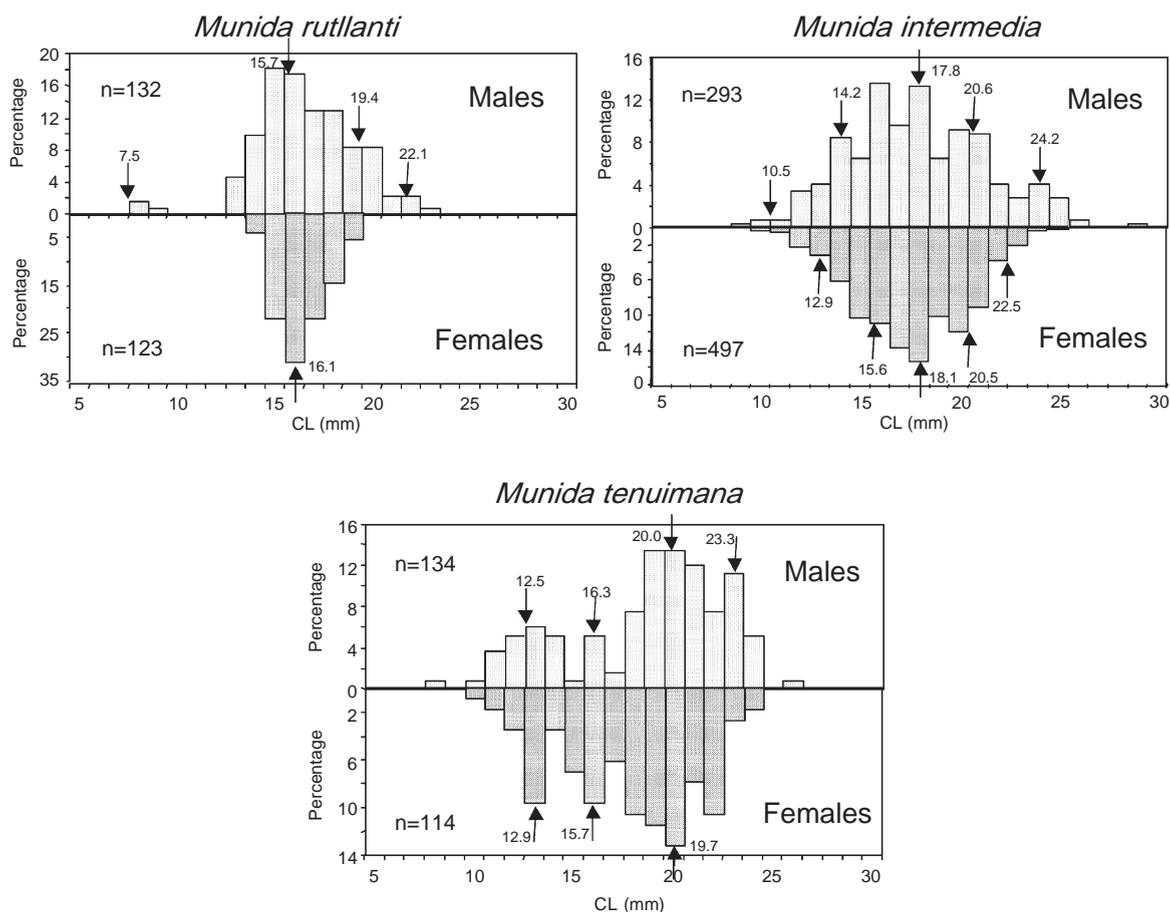
Fig. 3. Size frequency distributions by sex of the three *Munida* species sampled. The mean sizes (in cm) of the modal components identified by the NORMSEP method are indicated by arrows.

rutllanti and *M. intermedia* sharing the upper continental slope. Peak densities of *M. rutllanti* were mainly located within a narrow stripe on the upper slope, especially within the 201–250 m depth interval. Densities of *M. intermedia* also peaked at 201–250 m, widely overlapping with those of *M. rutllanti,* but were also relatively high down to 450 m. Densities of *M. tenuimana* peaked in the middle continental slope, especially in the 551–600 m depth interval.

3.2. Size structure

The overall population structure of the three species of *Munida* considered (Fig. 3) shows that, in all species, males reached larger sizes than females. In addition, several modes, attributed to different moult/age classes, were identified in all three species. Polimodality was lower in *M. rutllanti*, the only species in which a clear recruitment peak could be identified; three normal components were identified in adult males; however, only one single normal peak could be identified in females. In both *M. intermedia* and *M. tenuimana*, polimodality appeared to be higher, since five normal components were identified in *M. intermedia*, and four and three for male and female *M. tenuimana*, respectively. Reliability of the analysis is higher in the case of *M. intermedia*, since the sampling encompassed the whole bathymetric range of the species and the number of individuals sampled was higher, whereas *M. rutllanti* is known to occur shallower, and the sampling only encompassed the shallower range of the deep-sea *M. tenuimana*.

3.3. Geostatistical analysis

Geostatistical analysis was only applied to *M. intermedia* data since the other *Munida* species in the area did not occur in a sufficient number of samples for this type of analysis to be performed properly. The best-fitting variogram in our study was found to follow the exponential model (Fig. 4). Three maps, one for male densities, one for females and another for the whole population (Figs. 5, 6 and 7) were produced for the sampled population of *M. intermedia*.

Males of *M. intermedia* had a range of spatial correlation of 18 km, with a sill of 35 and a nugget of
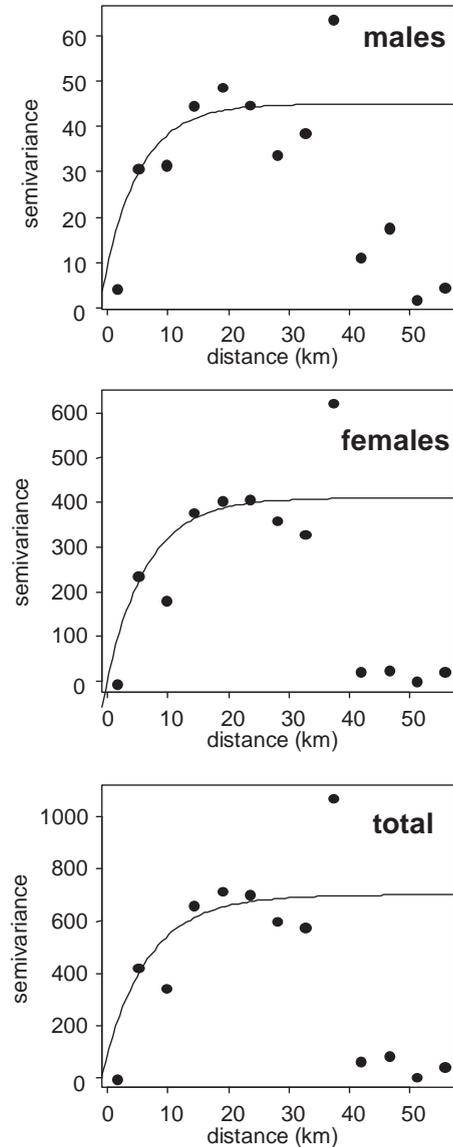
Fig. 4. Experimental (circles) and fitted exponential models (line) for each biological category of *Munida intermedia*. Nugget is the data variance not accounted for by the model, while sill is the data variance accounted for by the model. Nugget + sill correspond to the total data variance.

10. The range for females was 20 km, the sill was 350 and the nugget 10, while for both sexes combined the range was 22 km, with a sill of 600 and a nugget of 100 (Fig. 4).

Males and females showed similar geographical distribution patterns but densities of females were higher than those of males (Figs. 5 and 6). Both
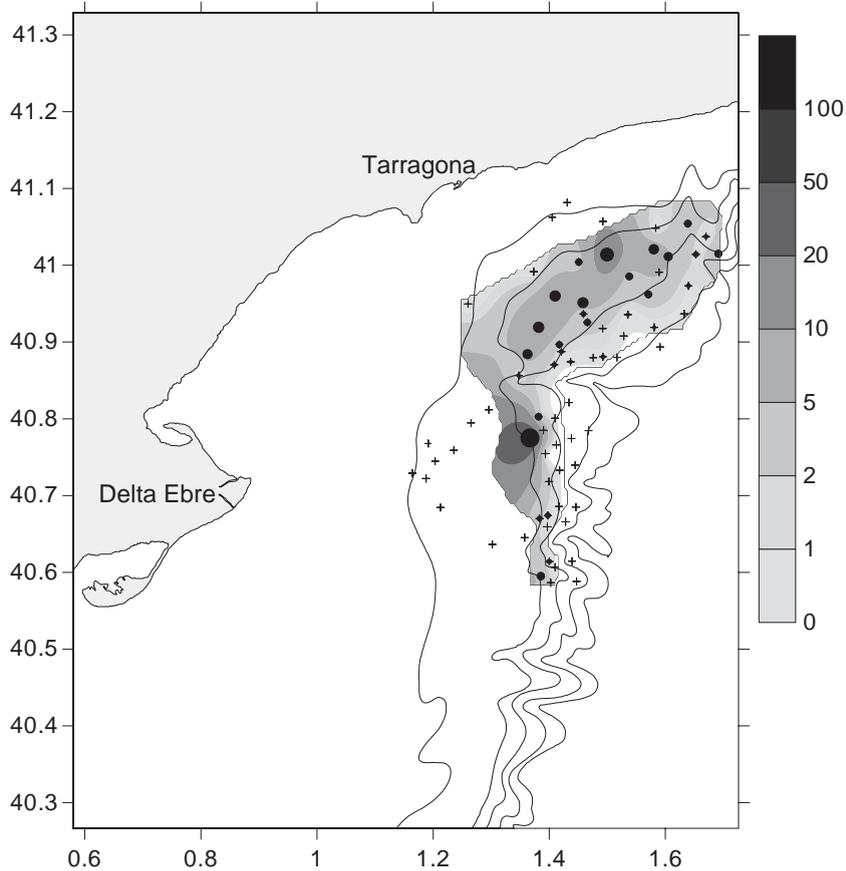
Fig. 5. Contour density map of *Munida intermedia* males (n ha^{-1}) with plot of actual values, proportional to circle size or zero values (crosses).

sexes were present in all the samples where *M. intermedia* was present, but the total number of females sampled (497) accounted for 63% of the population while males (293) only accounted for 37%. Data also showed that this species was closely associated with a depth range, since over 90% of the population was found between the 200 and 400 m isobaths (Fig. 7). The bathymetric distribution spread below 400 m only on the northern part of the sampling area, which is the one with the less steep continental slope.

3.4. Mantel test

The results of the Mantel test for autocorrelation (Table 1) show that, for *M. rutllanti*, size was not significantly correlated with space for neither males, females nor total, indicating that there is no size-

dependent spatial structuring in this species. The Mantel test for overlap between males and females showed that the density of males was positively correlated with the density of females (r=0.9986, p<0.001), indicating that there is no sex segregation in *M. rutllanti*.

Densities of males and females of *M. intermedia* showed significant spatial autocorrelation as detected by the Mantel test (Table 1: r=0.9298, p<0.001); this can also be visually assessed when Figs. 4 and 5 are compared. Size was not significantly correlated with space, neither for males nor females. The presence of the rhyzocephalan parasite (males infected: 29.7%, females infected: 25.4%) was not spatially autocorrelated, neither in males nor in females, indicating that there were no defined patches of infected individuals. However, males and females infected with the parasite were
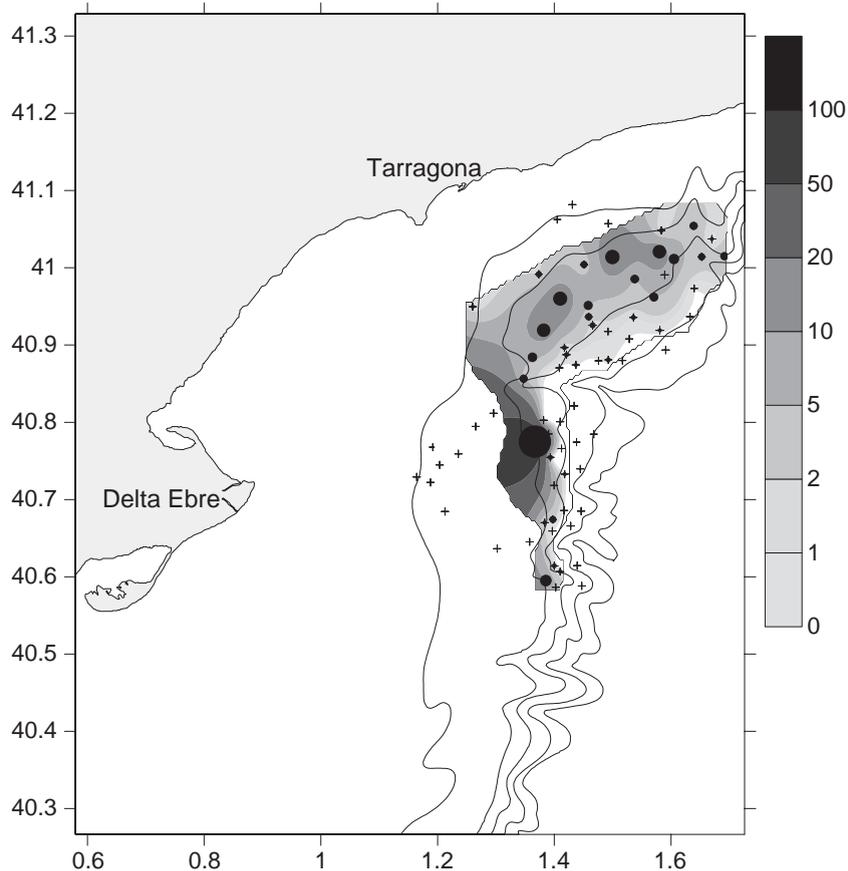
Fig. 6. Contour density map of *Munida intermedia* females (n ha^{-1}) with plot of actual values, proportional to circle size or zero values (crosses).

spatially correlated (r=0.6341, p<0.001), suggesting that the parasite does not act differentially on males and females.

For *M. tenuimana*, sizes of males and females did not to vary spatially, but 'total size' (males and females pooled) was significantly, although weakly, autocorrelated (r=0.2576, p<0.035), suggesting that, at the level of the entire population, there may be some size-dependent structuring. As for the other two *Munida* species, males and females significantly overlapped (r=0.9789, p<0.001), but no spatial structure was found by sex.

Table 1 also shows the results of the Mantel test for overlap between species pairs. The two shallow-dwelling species, *M. intermedia* and *M. rutllanti*, significantly overlapped (r=0.9609, p=0.004), while neither species overlapped with *M. tenuimana*.

4. Discussion

For the three *Munida* species here studied, depth appeared as an important factor determining their distribution characteristics. The presence of several congeneric species co-occurring over a depth gradient suggests the existence of a certain degree of ecological overlap among them, which may be minimised by factors such as different food habits (e.g. Cartes, 1993b, 2002 on *Plesionika* species) or differential behaviour (e.g. Abelló et al., 1991 on *Liocarcinus*). Although this study concentrates on the bathymetric and horizontal variations in distribution character-istics, there is no doubt that temporal changes should also be taken into account when investigating the patterns of distribution and population structure of species and communities (Demestre et al., 2000).
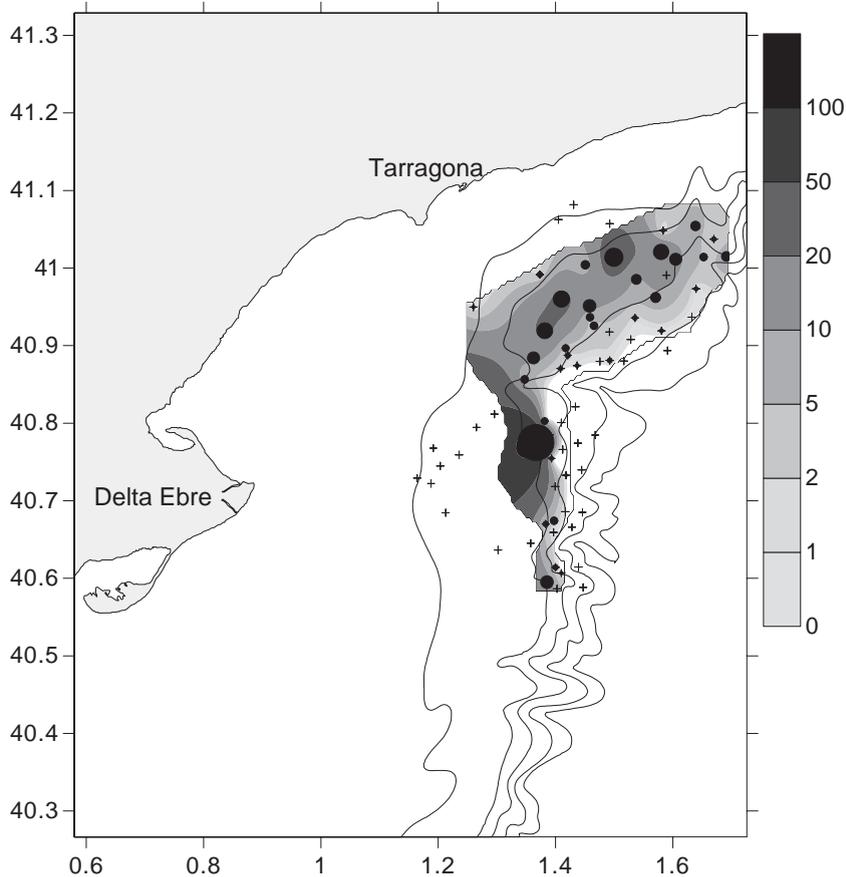
Fig. 7. Contour density map of total (males + females) *Munida intermedia* (n ha^{-1}) with plot of actual values, proportional to circle size or zero values (crosses).

Depth-related distributions are essential to describe the marine community and help us to understand the ecology of the marine environments. Some studies show that many decapod species present marked zonation patterns with depth: e.g. Hargreaves (1984), Fariña et al. (1997) and Attrill et al. (1990) in the North Atlantic, and Maynou et al. (1996), Cartes et al. (1994) and Abelló et al. (2002) in the Mediterranean. Depth in itself may not cause zonation, but there is a range of physical and geomorphological factors that vary with depth, and species therefore need to develop physiological adaptations to increasing depth. Thus, temperature, light, pressure, oxygen content, food availability, bottom slope and sediment characteristics etc., have been put forward to explain species distributions given the marked vertical gradients that most of them present with depth (Puig et al., 2001).

Increase in pressure has long been considered one of the main factors controlling species depth distributions (Somero, 1990). Frontal currents on the slope have also been found to account for the distribution patterns observed for some deep-water continental slope species, since they may be affected by the increased turbulence or inflow of Organic Matter (Puig et al., 2001). Nonetheless, explanations as to the causes of why the fauna changes with depth are still highly conjectural, and seem to depend on the local characteristics of the area studied. González-Gurriarán and Olaso (1987) suggested that the difference in zoning between the two overlapping species of *Munida*, *M. intermedia* and *M. sarsi* off Galicia might be a result of their temperature preferences, *M. sarsi* being characteristic of cold temperate waters, and *M. intermedia* of warm temperate waters.

Table 1
Results of the Mantel tests of spatial autocorrelarion (r) between a biological distance matrix and a geographical distance matrix, or between two biological distance matrices

	Variables tested	r	p
Munida rutllanti	CL males	0.035	0.305
	CL females	−0.020	0.420
	CL total	0.378	0.085
	N males:N females	0.999	<0.001
	CL males:CL females	−0.102	0.403
Munida intermedia	CL males	0.135	0.102
	CL females	−0.019	0.463
	N parasitised Males /Ha	−0.086	0.856
	N parasitised Females /Ha	−0.068	0.643
	CL total	0.014	0.403
	N parasitised Total /Ha	−0.737	0.825
	N males:N females	0.930	<0.001
	CL males:CL females	−0.093	0.764
	Parasitised males: parasitised females	0.634	<0.001
Munida tenuimana	CL males	−0.035	0.505
	CL females	0.058	0.215
	CL total	0.258	0.035
	N males:N females	0.979	<0.001
	CL males:CL females	−0.075	0.651
All *Munida* spp.	*M. intermedia: M. rutllanti*	0.961	0.004
	M. intermedia: M. tenuimana	−0.037	0.517
	M. rutllanti: M. tenuimana	−0.028	0.416

Probabilities (p) were computed by 1000 permutations.

Although our results at small spatial scale from 1994 do not show a clear depth segregation between *M. rutllanti* and *M. intermedia*, current evidence of the bathymetric distribution of these species at a larger spatial scale (Abelló et al., 2002) along the western Mediterranean indicates that *M. rutllanti* has been found distributed between 40 and 587 m (preferentially between 150 and 400 m), while *M. intermedia* is found between 118 and 641 m (preferentially between 200 and 500 m). The ability to adapt to the unstable shelf environment could be determinant for the bathymetric segregation. In this way, *M. rutllanti* would be the species most resilient to changes of temperature and salinity which seasonally affect the area down to around 200 m. This hypothesis is backed by the apparent easiness with which this eastern Atlantic warm-water species has been spreading northwards and eastwards into the Mediterranean over the last decades from its original tropical and subtropical habitat off northwest Africa. Thus, Zariquiey Álvarez (1968) recorded the occurrence of this species only on the southern Mediterranean coasts of North Africa, near the Straits of Gibraltar, with no records of the species on Mediterranean coasts of the Iberian peninsula. Later on, the species was scarcely recorded along the western Mediterranean coasts (Sardà and Palomera, 1981; García-Raso, 1985; Abelló et al., 1988; Garcia Socias and Gracia, 1988), whereas presently it constitutes well-established populations in the western Mediterranean (Sanz-Brau et al., 1998; Abelló et al., 2002). Pérès (1985) remarked that this species occurred in deep waters along the North African Mediterranean coast from Gibraltar to Tunisia, being considered a species of Atlantic origin. This pattern of distribution is in accordance with the main surface currents of Atlantic origin entering the Mediterranean through the Gibraltar straits (Font et al., 1998). *M. rutllanti* probably shows a higher degree of resistance and adaptability to environmental changes than the other species, thus allowing colonisation of new areas, favoured by the slow, but constant, temperature increase of Mediterranean waters, both in shallow (Pascual et al., 1997) and deep areas (Bethoux et al., 1990). Given the high degree of overlap between the bathymetric and spatial distributions of *M. rutllanti* and *M. intermedia* found in the present study, a possible displacement of *M. intermedia* populations may be taking place towards deeper areas, or limiting the upper bathymetric distribution limit. Long-term temporal series are needed to properly clarify this aspect.

M. intermedia would be less resistant to environmental changes than *M. rutllanti*, whereas *M. tenuimana* would show less tolerance to changes in temperature and salinity and be adapted to higher pressure regimes and low nutrient availability, since it is the only species never occurring on the continental shelf. In fact, no significant overlap was detected between the distribution of *M. tenuimana* and that of either of the other two species. Overlap was, however, significant between the distributions of *M. rutllanti* and *M. intermedia*. Overlap between these species also can be inferred from the data presented by Abelló et al. (2002). In the deepest parts of its bathymetric range, overlap was also reported by Sanz-Brau et al. (1998). The difference in life strategies also supports this idea; while *M. rutllanti* appears to be a species with a short life span, with populations highly dependent on recruitment, as suggested by its population size

structure (see also Sanz-Brau et al., 1998), the other *Munida* species have longer life spans and more structured populations (Gramitto and Froglia, 1998; Hartnoll et al., 1992; Company and Sardà, 2000). In a similar way, Hartnoll et al. (1992) observed that *M. tenuimana* in the North Atlantic was found much deeper than, and with little overlap with, *M. sarsi*, a characteristic species of the upper slope that may be considered the ecological equivalent in the North Atlantic of *M. intermedia* in the Mediterranean.

Sediment grain and composition can also affect the distribution of benthic and epibenthic species, especially in those with burrowing and burying habits (Somers, 1987; Atkinson and Taylor, 1988). The study area presented little variation in its sediment composition throughout the upper and middle slope (Maynou and Sardà, 1997). Even though sediment characteristics certainly could determine *Munida* distribution at a larger scale, it did not account, within the ranges sampled, for the small (18–22 km) patches found in our study. Some species of the genus *Munida*, such as *M. tenuimana*, have been reported to be burrowers (Hartnoll et al., 1992) and therefore show territorial behaviour (Attrill et al., 1990) which could result in competition. This is, however, a still controversial aspect, since Gramitto and Froglia (1998), using underwater television surveys, reported that *M. intermedia* does not burrow, although it can partially hide, in the soft sediment. These authors also reported that catch rates were higher in night-time hauls and attributed this to an increased vulnerability to the trawl gear probably due to a greater activity at night. This pattern is shown by typical burrow builders such as *Nephrops norvegicus* or *Squilla mantis* (Atkinson and Naylor, 1976; Froglia and Giannini, 1989; Aguzzi et al., 2003) but also by species that bury in the sediment (Al-Adhub and Naylor, 1975; Froglia and Gramitto, 1987). However, Aguzzi et al. (2003), in samplings performed in the same study area as the present study, did not report significant day-night variations in catchability for *Munida* species.

Cartes et al. (1994) stressed the importance of submarine canyons for the distribution of certain species. Similar to the present findings, these authors detected that *M. intermedia* was scarcely found within canyons. These authors also found a seasonal difference in species abundance, with lowest densities of *M.*

intermedia being recorded in spring and highest in autumn. Since the present sampling was carried out in spring, we can assume that the occurrence of *M. intermedia* within canyons was at its lowest level.

However, the distribution of species is not only affected by environmental factors; biological interactions are also very important. Species within the same genus present similar morphological, behavioural and ecological characteristics and therefore increased competition (Soto, 1991). Studies in other areas also show depth segregation of *Munida* species. For example, the differential species occurrence in the North Atlantic varies with depth from the shallower *M. rugosa* (shallower than 300 m), through *M. sarsi* (most abundant between 250–815 m), to the deeper-living *M. tenuimana* (740–1400 m) (Hartnoll et al., 1992). Note that *M. tenuimana* may occur in shallower waters in the Mediterranean than in the Atlantic (e.g. Abelló et al., 1988, 2002; Maynou and Cartes, 2000).

Most species of the genus *Munida* present benthic habits, with a few showing benthopelagic habits (Wenner, 1982; Zeldis, 1985; Company and Sardà, 1998). Feeding studies have delimited this group of anomurans as carnivorous, scavengers and opportunists, feeding on fish remains and slow-moving benthic organisms (Garm and Høeg, 2000; Cartes, 1993c). Active predation on euphausiids has, however, recently been reported (Hudson and Wigham, 2003). The different species of the genus found in the Mediterranean region do not show important differences in their diets (J.E. Cartes, pers. comm., 2001); therefore, if they have similar diets, they are bound to occupy different physical or temporal spaces in order to minimise competition. Cartes et al. (1994) found that, while species preying on endobenthic resources predominate in canyons, benthic scavengers and epibenthic predators such as *Munida* species were scarcer. The species of the genus *Munida* present such a wide diet spectrum (Garm and Høeg, 2000; J.E. Cartes, pers. comm., 2001) that exclusion due to competition for food cannot be an important factor in determining the distribution in patches.

Our results indicate that *M. intermedia* is a species showing spatial structures with high density patches. This species does not show differential segregation by size or sex, as verified by geostatistics for other crustaceans (eg. Comeau et al., 1998). The other two

species analysed, *M. rutllanti* and *M. tenuimana,* did not present sufficient data to conduct a proper geostatistical analysis, but the Mantel test for spatial correlation indicated that *M. rutllanti* does not present significant size or sex structuring, while, in agreement with Sardà and Cartes (1993), *M. tenuimana* may show some degree of structuring by size, but not by sex. The distribution of *M. intermedia* was specifically studied by Freire et al. (1992) on the Galician shelf, showing patches of 16–25 km diameter along the continental shelf. The patch size found in our study was 18–22 km, which falls within the range found by Freire et al. (1992).

Size structure is a valuable indicator of the age composition and growth rate of a population. While *M. intermedia* and *M. tenuimana* have a deeper overall distribution (Abelló et al., 1988, 2002) and similar life cycles, both of them with a reproductive season centred in winter (Gramitto and Froglia, 1998; Company et al., 2003), the reproductive period of *M. rutllanti* takes place in the summer months (Sanz-Brau et al., 1998). This could reduce the inter-specific competition between *M. rutllanti* and *M. intermedia*, which are the ones that show a greater depth overlap. Dietary needs in relation with gonad maturation may differ seasonally between the two species, thus allowing a higher degree of geographical distribution overlap (Company et al., 2003). In the case of *M. rutllanti*, a new recruitment cohort could be observed in males, in accordance with the seasonality reported by Sanz-Brau et al. (1998), whereas *M. intermedia* and *M. tenuimana* did not show recruitment peaks, since the sampling probably took place too early in the season to allow detection of the new recruits hatched in winter, and, in the case of *M. tenuimana* because the full depth distribution range of the species was not sampled. The lower number of normal components identified in the size frequency distributions of *M. rutllanti* is indicative of a probable lower life-span of this species when compared with the deeper-dwelling *M. intermedia* and *M. tenuimana*.

We conclude that minor variations on environmental parameters coupled with the differential life history characteristics of *Munida* species contribute to explain the differential distribution of the three species in the study area. Since they have similar diets, their population structure, adaptability and life strategies are determinant in reducing competition for resources.

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