

Small-scale non-linear geostatistical analysis of *Liocarcinus depurator* (Crustacea: Brachyura) abundance and size structure in a western Mediterranean population

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ABSTRACT: The small-scale spatial distribution of density and biomass of the crab *Liocarcinus depurator* off the Ebro delta was analysed using universal kriging (non-linear geostatistics), considering depth as an external trend. In order to understand the spatial distribution of crab size, a third variable was created from the residuals of the non-linear regression between biomass and density. Variogram analysis of crab density and residuals of the biomass/density relationship presented a quadratic relationship with depth, while biomass showed a linear relationship with depth. All experimental variograms were fitted to spherical models. The patch size (range) found was 10.64 km for density, 14.53 km for biomass and 20.49 km for the residual variables. The spatial distribution of 8 sediment variables (temperature, redox potential at 1 and 6 cm depth [R1 and R6], carbonate content [CO₃], median grain size [ϕ], sediment sorting [IGSD: inclusive graphic standard deviation] and organic matter content [OM]) was studied. The maps obtained were compared with those calculated for the biological variables of *L. depurator* using Mantel and partial Mantel tests. Distribution characteristics of this species were significantly affected by most sediment variables considered, particularly by temperature, organic matter content and redox potential, although overall the correlation level was low, coinciding with the generalist ecological role and opportunistic behaviour of the species. Density and biomass, as well as residuals, presented a negative correlation with the sorting coefficient (IGSD) and with carbonates. In relation to IGSD, high densities of *L. depurator* were found in homogeneous sediments. Residuals (size structure of the population) were significantly correlated with grain size (ϕ), with larger individuals occurring in finer sediments, while juveniles were preferably found in areas with very fine sand sediments. Both density and biomass presented significant positive correlations with the redox potential, indicating that the species favoured well-oxygenated sediments with a low organic content.

KEY WORDS: Geostatistics · Sediment variables · *Liocarcinus depurator* · Portunidae · Kriging · Mantel test · Temperature · Granulometry · Spatial distribution

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INTRODUCTION

Patchy distributions of individuals in marine benthic systems can be related to local environmental conditions as well as to biotic factors such as competition and predation (Whittaker & Levin 1977, Palmer 1988). For example, predators may more readily locate prey

items in some habitats than others and hence reduce prey abundance differentially between habitats (Southern & Lowe 1968). Additionally, the physical environment, for example temperature, salinity and sediment characteristics, has been shown to determine small-scale distribution in benthic crabs (e.g. Vernberg & Vernberg 1983). Sediment grain size, which is deter-

mined by hydrodynamic sorting mechanisms, and organic content are considered the 2 most influential characteristics determining occupancy by marine benthos (Gray 1981).

Surveys designed to assess the density of benthic organisms often do not take into account the spatial heterogeneity of the habitats or try to account for it by implementing differential habitat sampling, often referred to as stratified random sampling (Petitgas 1996). However, empirical evidence suggests that the existence of structure at different spatial scales does induce autocorrelation between pairs of samples, producing biases in density estimates (Petitgas 1996). Further, there is interest in ecology to quantify the structure of spatial dependence among samples in order to gain knowledge on the spatial structure of benthic organisms and the factors determining such structure. In this context, the use of geostatistics has been advocated by several authors as a useful tool to describe and model spatial dependence in benthic organisms (e.g. Sullivan 1991, Petitgas 1993, 1994, 1996, Maynou et al. 1996, Maynou 1998, Fernandes & Rivoirard 1999, Rivoirard et al. 2000). Conan (1985) first introduced geostatistical techniques to marine biology, using kriging to produce unbiased biomass estimates and mapping isodensity contours of the scallop *Placopecten magellanicus*.

Most applications of geostatistics to marine organisms and fisheries are focused on fish species and were recently reviewed by Petitgas (1993, 2001). However, the application of geostatistics to crustacean populations is still limited (Freire et al. 1991b, 1992, Simard et al. 1992, González-Gurriarán et al. 1993, Maynou et al. 1996, 1998, Maynou 1998). Additionally, most applications in geostatistics are restricted to linear geostatistics and ordinary kriging, without taking into account possible data transformation or correlation with environmental variables to improve parameter estimates and reduce variance. Furthermore, when the variable under study is not stationary, non-linear geostatistics are clearly more appropriate (Cressie 1991).

Differences in spatial distribution according to biological categories, such as number of juveniles, females, males, berried females, etc., has been widely reported in the crustacean literature (e.g. Abelló et al. 1990, 1997, Ardizzone et al. 1990, Rossi & Costantini 2000), although it has received less research effort within the field of geostatistics (Comeau et al. 1998, Maynou et al. 1998, Lembo et al. 2000a). However, some studies suggest that different scales of spatial structuring (e.g. by geographic sectors, latitude or depth) may exist for a given species, as shown for the snow crab *Chionoecetes opilio*, for which an important spatial segregation was detected by sex and size in the

Gulf of Saint Lawrence using geostatistics (Comeau et al. 1998). The spatial structure of the shrimps *Parape-naeus longirostris* and *Aristeus antennatus* was studied by Lembo et al. (1999, 2000a,b) in the Tyrrhenian Sea from stratified, random, bottom-trawl data. These authors applied cross-variograms and co-kriging to the data, considering depth as an auxiliary variable, which allowed a density estimation closer to the known pattern for this species, thus overcoming the limitations presented by ordinary kriging. These analyses were able to detect 3 zones with higher densities within the sampling area, which persisted in the same localities from 1995 to 1997 (Lembo et al. 1999). The procedure significantly increased the fit of the models, and decreased the standard error of the estimates. In the case of *A. antennatus*, Lembo et al. (2000a,b) also analysed the variable 'percentage of females larger than median length', and in *P. longirostris* the 'number of recruits km⁻²' through disjunctive kriging techniques.

Liocarcinus depurator is the most common and abundant brachyuran crab on trawlable muddy bottoms of the continental shelf in the western Mediterranean (Mori & Zunino 1987, Abelló et al. 1988, 2002, Abelló 1993, González-Gurriarán et al. 1993). Given its abundance and the fact that it is a predator of mobile benthic and epibenthic organisms, it may prove to be a 'keystone' species in the community (Abelló & Cartes 1987, Mori & Manconi 1989). *L. depurator* is distributed along the eastern Atlantic coasts from Mauritania to Norway and throughout the Mediterranean (Zariquiey-Álvarez 1968, d'Udekem d'Acoz 1999), with a wide bathymetric range (continental shelf and upper slope). It occurs on several types of substrata, especially on muddy and sandy-mud bottoms (Minervini et al. 1982). Abelló (1993) showed a trend for crab sizes of both sexes to increase with increasing depth in a population off the Catalan coast. Recruitment took place mainly on the shallow continental shelf (25 to 50 m), although the bathymetric range where recruitment could take place was wider. For *L. depurator*, geostatistical analyses have been applied by Freire et al. (1991a) and González-Gurriarán et al. (1993) off the Atlantic Iberian coasts and by Ungaro et al. (1999) in the SW Adriatic Sea. Both studies reported that *L. depurator* aggregates spatially in patches, both on the Galician continental shelf and in the Adriatic Sea. Depth, bottom steepness and sediment characteristics have been shown in these studies as factors affecting the spatial structure of *L. depurator*.

The objectives of the present work were to analyse the spatial distribution of *Liocarcinus depurator* in a population located off the Ebro delta in the western Mediterranean, and to relate the distribution patterns to observed environmental parameters in order to try

to understand the spatial variability presented by the populations of this species, under the hypothesis that sediment characteristics significantly affect distribution parameters. Furthermore, this study aimed at illustrating the use of non-linear geostatistics and how this technique could be more widely applied to study spatial patterns of benthic species.

MATERIALS AND METHODS

Survey. A trawl survey (GEODELTA) was conducted over muddy bottoms off the Ebro delta continental shelf and slope (40° 20' N to 41° 00' N, NE Spain, Fig. 1) with the RV 'García del Cid'. A regular grid, 1 × 2 nautical miles, was set parallel to the coast and a start location for each tow was randomly selected within each cell; 1 area in the southern region was not sampled due to the presence of oil-rig platforms. Sampling was conducted between 7 and 15 April 1994 with a total of 72 stations. The water depth varied from 83 to 713 m across the sampling sites. The northern part of the study area is characterised by a narrow shelf (8 to 10 km wide) with a gentle slope seawards that is cut by deep submarine canyons. South of ~40° 50' N, the shelf becomes progressively wider (38 to 40 km) and the slope steeper, with fewer submarine canyons. The sampling gear was a modified otter trawl drawn by a single warp (Maireta System Trawl; Sardà et al. 1994).

The cod-end stretched-mesh width was 12 mm in order to retain small individuals not normally caught by commercial fishing gear. The working dimensions of the trawl mouth were measured acoustically (SCANMAR) and averaged 13.4 × 2.0 m. The effective trawling time was 15 min and trawls were always run parallel to the depth contours. Towing speed varied between 2.3 and 2.7 knots (mean 2.5 knots). The start and end locations for each tow were recorded by GPS. The actual surface covered by each tow was computed from the GPS and SCANMAR readings. The total *Lio-carcinus depurator* catch was counted and weighed, and the carapace length of each crab was measured. Density was computed from the total surface covered by each tow as number of individuals ha⁻¹ and biomass as g ha⁻¹. We considered 3 biological variables: density, biomass, and the residuals of the non-linear relationship between biomass and density, as an indicator of the relative size of individuals (see Fig. 2). This latter variable was used to overcome the problem of the small number of individuals caught in some samples, which did not allow the study of the spatial structure of further biological categories such as mean carapace size, number of females or number of males.

Sediment samples were collected using a Van Veen grab (Gray 1981) every second trawl haul, except in the continental shelf area at depths shallower than 200 m, where sediment heterogeneity was presumably higher and 1 sediment sample was collected per tow. Sediment samples were analysed following the methodology of Maynou & Sardà (1997) and Alonso et al. (1999). The surface sediment temperature (T , °C) and the redox potential at 1 and 6 cm from the sediment surface (R1 and R6, mV) were measured on-board ship using a double-joint, multimeter electrode (Orion Research Model 250A) immediately after sample collection. Sediment samples were stored at -20°C for later laboratory analyses. The redox potential for marine sediments is usually negative, with higher negative values for more reduced sediments generally indicating sediments containing large amounts of organic matter. Normally, undisturbed marine sediments are structured in layers, and redox potential measurements in the deeper levels (6 cm in our case) show higher negative values than those near the surface (1 cm in our case). Grain-size analysis was carried out on the sediment samples using a SEDIGRAPH 5000D for the fine-grained fraction (<50 µm) and sedimentation-tube analysis for the coarse-grained fraction. For each sample, the proportions of sand (62.5 to 1000 µm), silt (2 to 62.5 µm) and clay (0.06 to 2 µm) were determined. The grain-size distribution of each sample was summarised also by its median, $\phi = -\log_2$ (median grain size in mm) (Gray 1981), and its sorting coefficient IGSD (inclusive graphic standard deviation; Gray

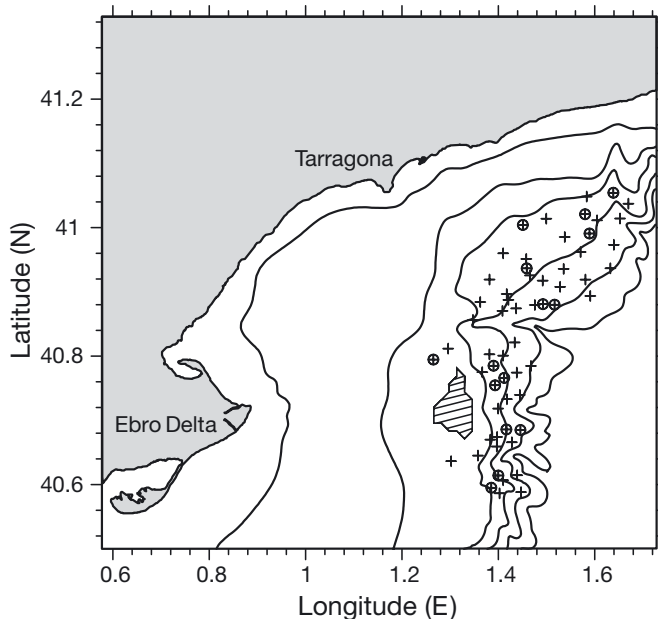


Fig. 1. Study area showing locations of sampling stations (+) and sites where sediment samples were also taken (⊕). Contour lines represent depth isolines (left to right: coast line, 50, 100, 200, 400, 600 and 800 m depth). Hatching: non-trawlable bottom in vicinity of oil-rig platform

1981). Low IGSD values indicate well-sorted sediments and high values poorly sorted sediments (Maynou & Sardá 1997). The carbonate content (% of CO₃ by volume) of each sediment sample was determined using a Bernard calcimeter, following the methodology of Vatan (1967).

Statistical methods. Mantel's normalised r -statistic (Mantel 1967) can be used to determine the degree of correlation between 2 distance matrices, A and B, using any of the distance coefficients available in the ecological literature (Legendre & Legendre 1998). Mantel's r -statistic was used as an additional test for the existence of spatial autocorrelation, by constructing a matrix, A, of geographical distances (using Euclidean distance) and a matrix, B, of biological distances (using the Manhattan coefficient of dissimilarity). The partial Mantel test was used to analyse the residual correlation between 2 matrices, A and B, by extracting the correlation due to a distance matrix, C, which may represent a common environmental factor structuring Matrices A and B: in this case depth. The significance of both the Mantel and partial Mantel coefficients were tested by permutation (Manly 1985, Legendre 2000). The Mantel test was performed using the library 'vegan' of the software package R, and the partial Mantel test was programmed by one of the authors (F. M.) in R following the methods outlined in Legendre (2000). The correlation coefficient used in the Mantel test was Kendall's (Sokal & Rohlf 1995).

The fundamentals of geostatistics, with emphasis on the non-linear methods employed here, have been explained in several publications (e.g. Cressie 1991, Diggle et al. 2003). Linear geostatistics were not used in this work because of 'non-stationarity' in the data (see e.g. Cressie 1991 on the assumptions and limitations of linear geostatistics). Considering the variable Z_i observed at x_i spatial locations, where $i = 1, \dots, n$, as the realisation of a spatial process $S(x)$, the expectation of $\mu(x)$ is:

$$\mu(x) = \sum_{k=1}^p f_k(x)\beta_k + S(x) \quad (1)$$

where $\mu(x)$ is an appropriate transformation of Z_i to ensure normality, $f_k(x)$ is a set of spatially-referenced p explanatory variables, and β_k are the coefficients of these explanatory variables. This can be viewed as a generalised linear model (McCullagh & Nelder 1983) in a spatial context (Diggle et al. 2003) or as a generalisation of universal kriging to non-Gaussian data (Cressie 1991). The procedure applied to fit this method was to find a suitable transformation of the raw data to ensure normality and then model the autocorrelation function $\gamma(h)$ of the spatial process $S(x)$ taking into account the explanatory variables $f(x)$. The range of the semivariogram can be interpreted as the dis-

tance beyond which no effects of spatial covariance among the samples exist (Maynou et al. 1998). In the absence of spatial autocorrelation, the mathematical expectation of the semivariograms, the sample variance and the semivariogram appears flat (pure nugget effect (Maynou et al. 1998). The term 'range' indicates the size of the patches in which the population is structured (Sokal & Oden 1978).

We used, as dependent Z_i variables, 2 measures of *Liocarcinus depurator* abundance (ind. ha⁻¹ and g ha⁻¹) and the residuals of the non-linear regression between ind. ha⁻¹ and g ha⁻¹ as an index of crab size. As explanatory variables, $f_k(x)$, we used a linear trend in x , a quadratic trend in x , a linear trend with depth, and a quadratic trend with depth. The general Box-Cox set of transformations was used. The autocorrelation function $\gamma(h)$ of the spatial process $S(x)$ was fitted by weighted least-squares (as recommended by Cressie 1991 for Gaussian random processes). The analyses were conducted using the software package R (Ihaka & Gentleman 1996) and the library 'geoR' (Ribeiro & Diggle 1999).

The degree of correlation between the sediment and the biological variables was analysed between the kriging estimates with the Mantel test (Mantel 1967) and the partial Mantel test (Smouse et al. 1986). Additionally, Mantel's spatial correlograms were calculated to estimate the degree of spatial correlation in relation to the scale (distance) between abundance and each environmental variable (Legendre & Legendre 1998). This statistic was calculated with the use of the 'ncf' package (R language [Ihaka & Gentleman 1996]), with 10 000 permutations.

RESULTS

Density and biomass of *Liocarcinus depurator* were significantly correlated (biomass = 5.69 × abundance^{1.31}, $r^2 = 0.9074$, $df = 69$, $p < 0.0001$) by non-linear regression (Fig. 2). Despite the low number of samples, the exponent $b = 1.31$ of the fitted relationship biomass = $a \times \text{density}^b$ is similar to that found in previous studies (approximately 4/3: Burton 1998) and therefore the relationship fitted in this study can be considered to be within the usual estimated ranges, thus validating the variable residual. The residuals were not normal (tested using the Box-Cox methodology [Sokal & Rohlf 1995]), neither were any of the variables. No empirical transformation improved the quality of the data and we used universal kriging as a particular case of the general model given in Eq. (1), because kriging is robust to departures from normality (Cressie 1991).

The results of the Mantel and partial (removing the effect of depth) Mantel tests (Table 1) indicated that

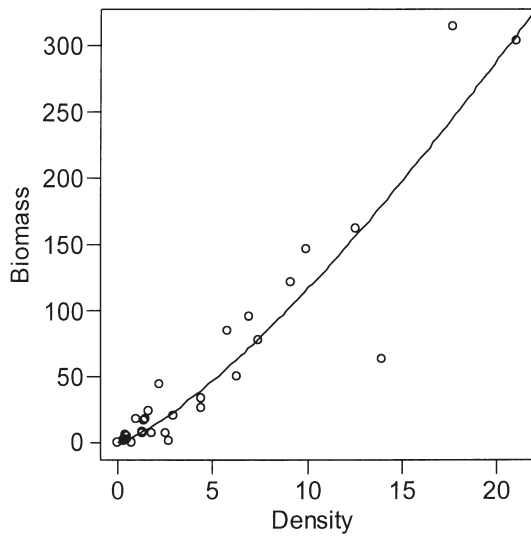


Fig. 2. *Liocarcinus depurator*. Non-linear regression between abundance and biomass with fitted regression line (biomass = $5.69 \times \text{abundance}^{1.31}$, $r^2 = 0.9074$)

Table 1. *Liocarcinus depurator*. Results of Mantel test and partial Mantel (removing effect of depth) using Kendall's correlation index. Significant spatial correlations ($0.95 < p < 0.05$) are in bold, negative correlation in italics. Temp.: temperature; R1R6: vertical difference between between R1 and R6 (redox potential); CO₃: carbonate content; φ: median grain size; ISGD: sorting coefficient (inclusive graphic standard deviation); OM: organic matter

Variable	Simple		Partial	
	r	p	r	p
Abundance	0.166	<0.001	0.139	0.007
Biomass	0.137	0.015	0.117	0.022
Residuals	0.142	0.007	0.121	0.019
Temp.	0.0670	0.0509	0.0306	0.1859
R1	0.0260	0.2421	0.0304	0.2161
R6	0.0596	0.0779	0.0632	0.0751
R1R6	-0.0333	0.7680	-0.0303	0.7423
CO ₃	0.1441	0.0021	0.1275	0.0036
φ	0.0522	0.1348	0.0229	0.2914
IGSD	0.2154	0.0001	0.2006	0.0000
OM	-0.0519	0.9109	-0.0679	0.9697

density, biomass, residuals, carbonates and the sorting index (IGSD) were spatially structured. By removing the effect of depth (partial Mantel test), spatial structure was still present, although there was a general decrease in spatial correlation (*r*), indicating that the spatial structure found did not depend solely on depth.

The parameters of the different fitted semi-variogram models (spherical, Gaussian and exponential) (Table 2) indicated that the spherical model was the most statistically appropriate when considering an automatic model selection, since the minimising function always presented the lowest values. Density and residuals showed a quadratic relationship with depth, while the relationship of biomass with depth was linear. The patch size (range) was 10.64 km for density, 14.53 km for biomass and 20.49 km for the residuals.

The variation in the range obtained with each model (no trend, 1st with depth and 2nd with depth) for all variables (Table 2) indicated the possible values of the patch size, allowing comparison with previous studies which used only linear geostatistics with no trend (Freire et al. 1993, González-Gurriarán et al. 1993, Ungaro et al. 1999). The degree of spatial dependence (Robertson & Freckmann 1995) was high and varied between 82 and 100%, indicating that most of the total variance could be explained by the variogram models. Fig. 3

Table 2. *Liocarcinus depurator*. Models fitted with weighted least-squares to experimental semivariograms produced for each biological variable. Sp. d.: spatial departure indicating % of variance explained by the model: $(1 - \text{nugget/sill}) \times 100$; 1st depth indicates linear trend with depth, 2nd depth quadratic trend; sph: spherical; gau: Gaussian; exp: exponential; Min. funct.: value of the minimising function. Model selected for kriging is in bold

Factor	Nugget	Sill	Sp. d.	Range	Min. funct.
Abundance					
No trend					
sph	2.13	16.69	87	21.88	12967
gau	4.64	14.16	67	10.66	13364
exp	0.00	21.20	100	10.25	13576
1st depth					
sph	2.39	10.28	77	14.80	7368
gau	4.20	8.51	51	7.50	7418
2nd depth					
sph	1.88	10.52	82	14.53	6335
gau	3.80	8.66	56	7.43	6396
Biomass					
No trend					
sph	73.66	3282.38	98	14.49	376640297
exp	0.00	3531.88	100	6.16	418281717
1st depth					
sph	0.00	2661.70	100	10.64	298068268
2nd depth					
sph	0.00	2626.25	100	10.78	318271642
Residuals					
No trend					
sph	39.92	296.21	87	20.18	16653572
exp	0.00	359.57	100	8.25	17172209
1st depth					
sph	39.84	296.14	87	20.16	16579790
2nd depth					
sph	43.18	291.86	85	20.49	15649224

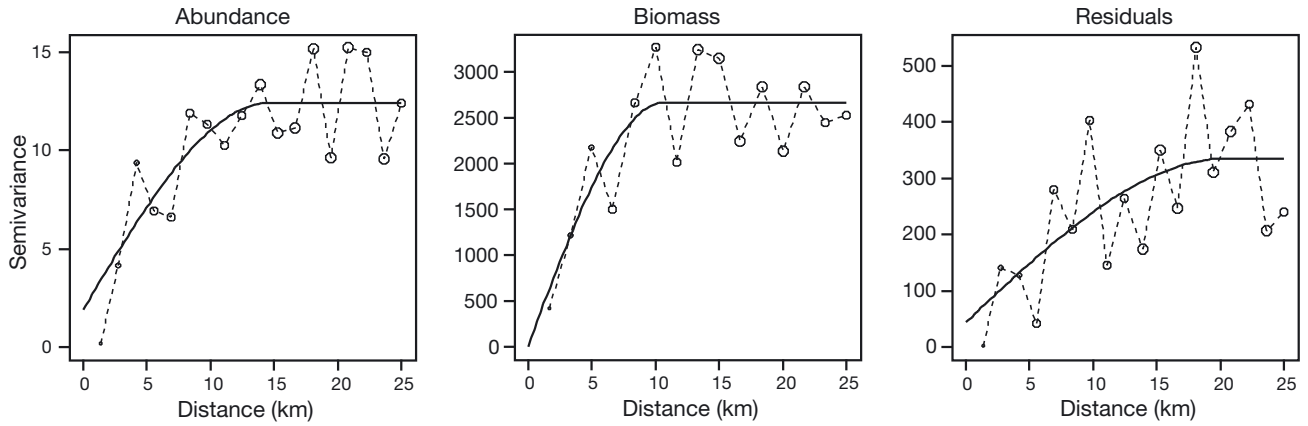


Fig. 3. *Liocarcinus depurator*. Experimental semivariogram and respective spherical model fitted with weighted least-squares (size of the markers is proportional to number of pairs divided by median pair number)

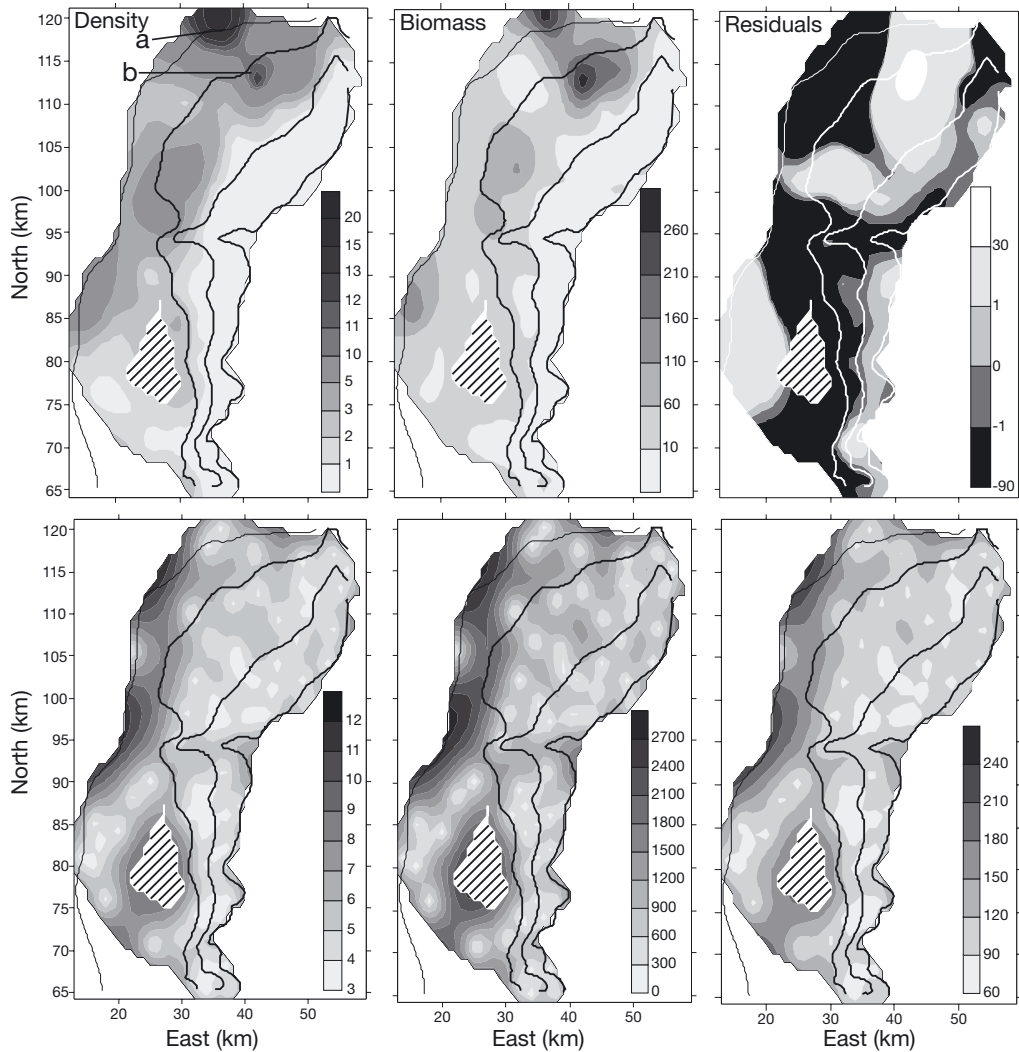


Fig. 4. *Liocarcinus depurator*. Maps of the biological variables (density [ind. ha⁻¹], biomass [g ha⁻¹] and residuals), produced by kriging with external trend (top graphs), and estimation variances (bottom graphs); the graphs of residuals and variances are dimensionless. Contour depth lines from left to right: 100, 200, 400 and 600 m. Hatched area corresponds to oil-rig platform. a,b: 2 patches with greatest densities. See Table 2 for model values

presents the experimental semivariograms with their selected model fits.

Kriging maps with external trend predictions and estimation variances are presented in Fig. 4 for the 3 biological variables studied. Sparse distribution of the variances of the kriging estimates can be observed for all variables. In the north of the study area, 2 main patches of distribution were found in both density and biomass around the 100 and 200 m depth contours (patches a and b, respectively, in Fig. 4). A central area (around 200 m depth) of high density and biomass was also observed close to the main submarine canyon. Overall, *Liocarcinus depurator* showed greater density and biomass in shallow than in deeper waters within the sampling area. The residuals map shows that, especially in the northern area with highest density and biomass, greater concentrations of small individuals were present at shallower depths (patch a; Fig. 5), while larger individuals were found in the deeper area (patch b; Fig. 5). For depths greater than 400 m, the residuals map should be interpreted with care, since density was lower, and the residuals obtained may not be completely representative.

A hierarchical procedure similar to that used for the biological variables was used to determine the most appropriate spatial model for the sediment variables. For brevity, only the best model is presented in Table 3. Depth, temperature, carbonates and IGSD were fitted to a linear semivariogram model. Organic matter and R1 showed a spherical semivariogram model whereas ϕ presented a Gaussian model, all of them with a quadratic trend with depth. Note that the actual range of a Gaussian model is $\text{range} \times \sqrt{3}$ (Cressie 1991). For both R1 and ϕ , kriging with external drift was calculated, while for the remaining variables ordinary kriging was performed (Fig. 6). Sediment temperature showed a trend with depth, with higher temperatures at greater depths within the range represented (12.2 to 13.6°C), due to the effect of water salinity on density, since slightly warmer but more saline waters were found at

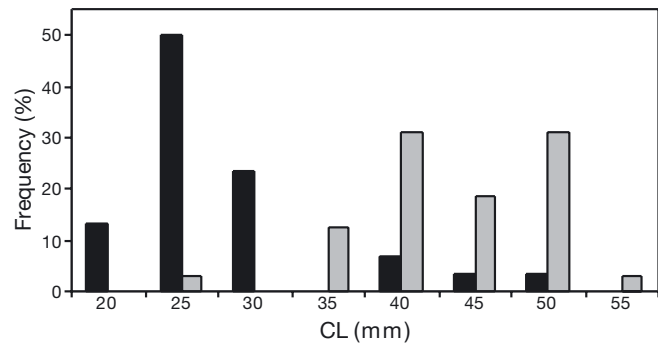


Fig. 5. *Liocarcinus depurator*. Relative frequency of carapace length (CL) in 2 trawls from which a similar number of crabs was measured from patches a (black bars, 30 crabs) and b (grey bars, 32 crabs), in the kriged density map (Fig. 4). Note differences in size distributions between the 2 trawls

greater depths. The redox potential at 1 cm depth (R1) showed maximum values (R1 from -8 to -310 mV) close to the canyon area and in the southernmost area, although the overall distribution was rather patchy. R6 also showed a patchy distribution (maximum R6 was -105 mV and minimum was -370 mV). Carbonates and IGSD showed a similar pattern of distribution, with lower values in the north (carbonate content range: 23.0 to 41.1%; IGSD range: 1.7 to 3.5) and higher values in the south. The organic matter content of the sediment showed a positive trend with increasing depth, and was particularly high around the deep canyon in the study area. Even though temperature, R1, R6 and ϕ did not present a significant spatial autocorrelation when using both Mantel tests ($p > 0.05$), the analysis of the semivariograms of R1 and ϕ clearly showed spatial structure (Table 3).

The Mantel test using Kendall's correlation index showed that all sediment variables were significantly correlated with at least 1 biological variable, but the degree of overlap (r) varied greatly (Table 4). The spa-

Table 3. Models fitted with weighted least-squares to experimental semivariograms produced for each sediment variable. Sp. d.: spatial departure, indicating % of variance explained by the model: $(1 - \text{nugget/sill}) \times 100$; 1st depth indicates linear trend with the covariate depth, 2nd depth quadratic trend. Range/slope indicates slope in linear (lin) models, and range in the other models. Further abbreviations as in Tables 1 & 2

Variable	Model	Covariate	Nugget	Sill	Sp. d.	Range/slope	Min. funct.
Depth	lin	No trend	372.361			1999.519	1.74×10^{12}
Temp.	lin	No trend	0.041			0.005	0
R1	sph	2nd depth	0.000	3253.730	100	5.950	316937573
R6	lin	No trend	2140.783			1.000	144683791
R1R6	lin	No trend	1555.870			1.000	65579879
CO ₃	lin	No trend	15.910			0.540	11218
ϕ	gau	2nd depth	0.000	2.005	100	7.534	110
IGSD	lin	No trend	0.124			0.012	2
OM	sph	2nd depth	0.994	1.989	100	20.113	131.6

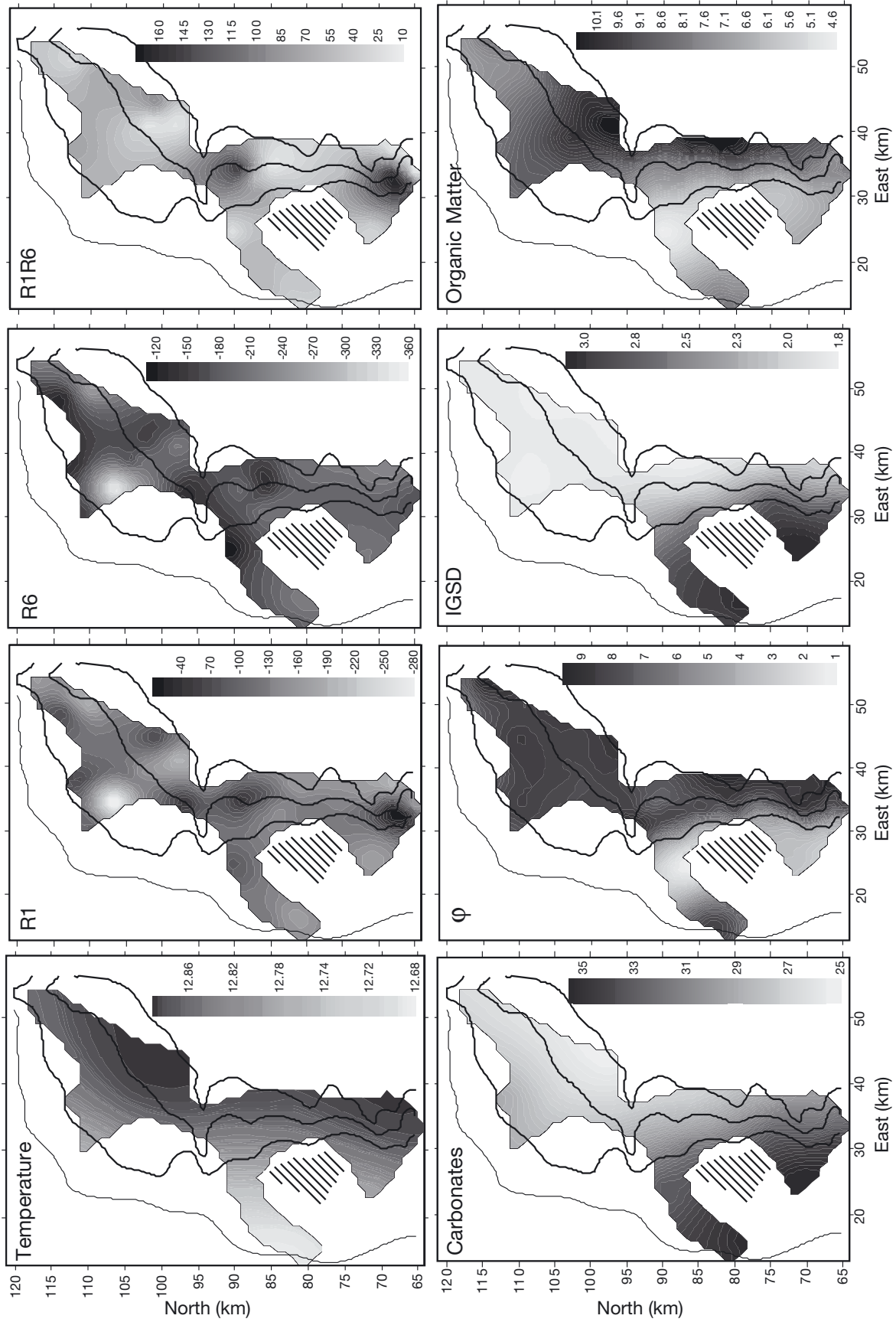


Fig. 6. Maps of sediment variables. Temperature ($^{\circ}\text{C}$), ϕ and organic matter (%) were produced by kriging with external drift, while maps of R1 (mV), R6 (mV), carbonates (%) and IGSD were produced by ordinary kriging (see Table 3 for values of semivariogram models and Table 1 for abbreviations). Contour depth lines from left to right: 100, 200, 400 and 600 m

tial overlaps of R1R6 (vertical difference in the redox potential between 1 and 6 cm) and IGSD with density, carbonates with biomass and carbonates and IGSD with residuals were not significantly correlated using the Mantel test, but when extracting the effect of depth (partial Mantel test) these correlations became significant. The opposite occurred between carbonates and ϕ with density, in which the correlation was due only to the spurious effect of depth, since when depth was extracted from the relationship the overlap became non-significant (Table 4). These results reinforce the importance of the incorporation of depth into the analysis, in particular when using the partial Mantel test.

The partial Mantel test results indicated that temperature, redox potential (R1 and R6) and organic matter were positively correlated with both density and biomass of *Liocarcinus depurator*, while the sorting coeffi-

Table 4. *Liocarcinus depurator*. Mantel and partial Mantel correlations of estimated kriging values (limited to sampling area) between abundance (ind. ha⁻¹), biomass (g ha⁻¹) and residuals with sediment variables (temperature, R1, R6, R1R6, carbonates, ϕ , IGSD) and with each other. $p < 0.05$ indicates significant overlapping. Significant spatial correlation ($0.95 < p < 0.05$) is in bold, negative correlation in italics. Abbreviations as in Table 1

Sediment variable	Mantel		Partial Mantel	
	r	p	r	p
Abundance				
Temp.	0.3826	0.0000	0.1885	0.0011
R1	0.2875	0.0000	0.1567	0.0032
R6	0.4105	0.0000	0.2729	0.0000
R1R6	-0.0700	0.9070	<i>-0.1047</i>	<i>0.9814</i>
CO ₃	0.0581	0.0479	-0.0474	0.9269
ϕ	0.1050	0.0226	-0.0484	0.8116
IGSD	-0.0178	0.6448	<i>-0.1231</i>	<i>0.9968</i>
OM	0.3673	0.0000	0.1619	0.0002
Biomass				
Temp.	0.3059	0.0000	0.1363	0.0070
R1	0.2392	0.0001	0.1246	0.0106
R6	0.4017	0.0000	0.2874	0.0000
R1R6	<i>-0.1068</i>	<i>0.9824</i>	<i>-0.1344</i>	<i>0.9972</i>
CO ₃	0.0198	0.2463	<i>-0.0657</i>	<i>0.9794</i>
ϕ	0.0639	0.1052	-0.0592	0.8681
IGSD	<i>-0.0728</i>	<i>0.9505</i>	<i>-0.1574</i>	<i>0.9998</i>
OM	0.3067	0.0000	0.1334	0.0003
Residuals				
Temperature	0.3619	0.0000	0.2307	0.0000
R1	0.1946	0.0009	0.0895	0.0508
R6	0.2438	0.0001	0.1177	0.0162
R1R6	0.0024	0.4619	-0.0074	0.5340
CO ₃	0.0143	0.2998	<i>-0.0579</i>	<i>0.9623</i>
ϕ	0.2036	0.0000	0.1188	0.0132
IGSD	-0.0333	0.7642	<i>-0.0982</i>	<i>0.9798</i>
OM	0.3180	0.0000	0.1747	0.0000

Table 5. *Liocarcinus depurator*. Kendall's correlation index (r_k) of partial Mantel test of estimated kriging values (limited to sampling area) between abundance (ind. ha⁻¹), biomass (g ha⁻¹) and residuals with sediment variables (temperature, R1, R6, R1R6, carbonates, ϕ , IGSD and OM). Only significant correlations are indicated. Positive values indicate significant overlap, negative values (italics) significant exclusion.

Abbreviations as in Table 1

	Abundance	Biomass	Residuals
Temp.	0.19	0.14	0.23
R1	0.16	0.12	
R6	0.27	0.29	0.12
R1R6	<i>-0.10</i>	<i>-0.13</i>	
CO ₃		<i>-0.07</i>	<i>-0.06</i>
ϕ			0.12
IGSD	<i>-0.12</i>	<i>-0.16</i>	<i>-0.10</i>
OM	0.16	0.13	0.17

cient IGSD and the variable R1R6 were negatively correlated with them, thus indicating that these sediment variables are determinant for *L. depurator* distribution (Fig. 7, Table 5). Residuals, the indirect index of size structure, were significantly correlated with all sediment variables except for R1 and R1R6; grain size ϕ was only significantly correlated with residuals, thus indicating that it only affected the differential distribution of adults and juveniles, but not that of biomass or density (Table 4).

Fig. 8 shows the spatial Mantel correlogram between the environmental variables and distance. Significant correlations were observed only for shorter distances in all cases, except with the redox potential (R1, R6 and R1R6), which was correlated at larger distances, and depth, which showed significant correlation for both shorter and larger distances. Temperature, carbonates and IGSD showed significant correlations with larger distances (15 to 20 km).

DISCUSSION

Simple and partial Mantel tests were able to detect the occurrence of spatial structure in density and biomass of *Liocarcinus depurator*, as well as in density/biomass residuals and in sediment variables, even when the effect of depth was eliminated from the relationship. However, the performance of a Mantel test to check the occurrence of a significant spatial structure was non-conclusive for all variables, since some sediment variables (R1 and ϕ) were not significantly spatially correlated according to this test, but presented clearly structured semivariograms. The inability to detect spatial correlation in these cases may be due to the lower number of samples (36 samples) or may point to the low statistical power of the Mantel test.

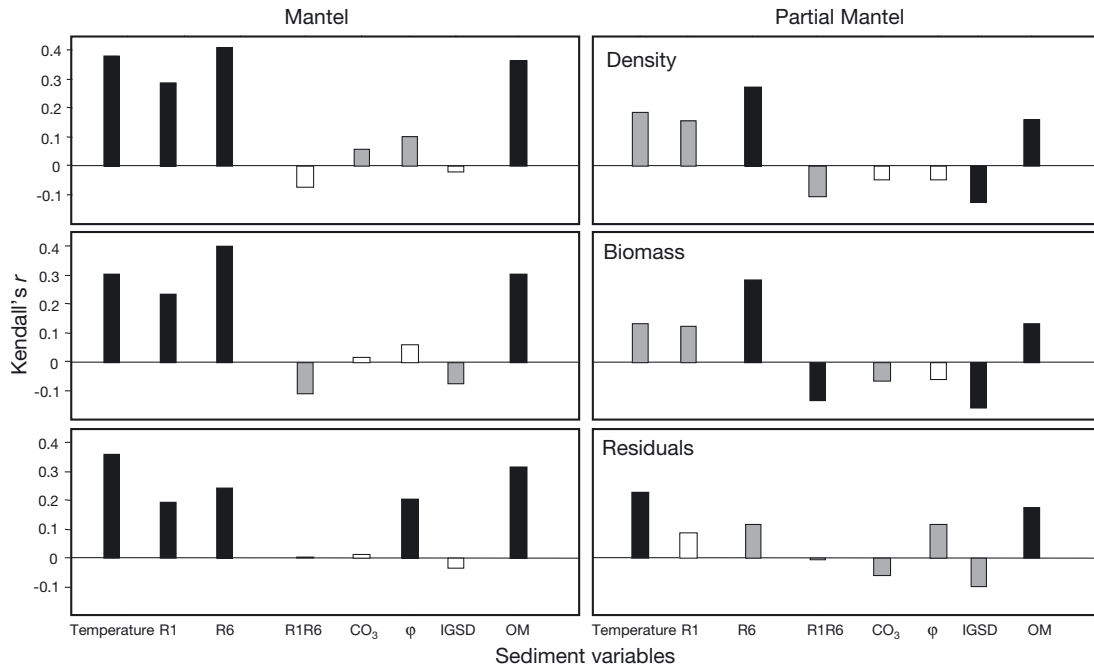


Fig. 7. *Liocarcinus depurator*. Significant spatial correlations of biological variables with sediment variables (black bars: abundance; grey bars: biomass; white bars: residuals). Abbreviations as in Table 1

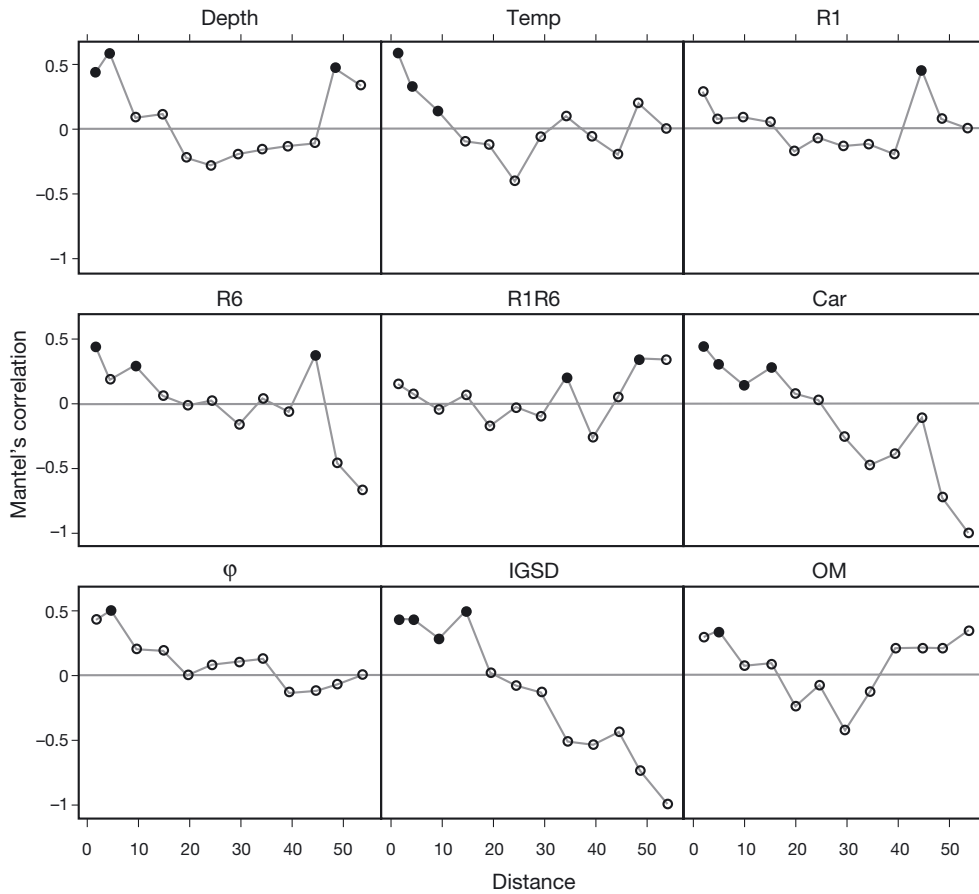


Fig. 8. *Liocarcinus depurator*. Mantel spatial correlogram between crab density and environmental variables. ●: significant correlations (10 000 permutations, $p \leq 0.05$); ○: not significant; Car: carbonates. Other abbreviations as in Table 1

Automatic, semiautomatic or manual semivariogram model selection has been the subject of discussion in the literature (Cressie 1991, Petitgas 1996, Rivoirard et al. 2000). In this study, it was observed that the minimising function from weighted least-squares allowed the selection of the most appropriate spatial model, although previous information on the ecology of the species was also fundamental.

Depth is known to play a key role in structuring *Liocarcinus depurator* populations, in regard to both density and size structure (Mori & Zunino 1987, Abelló et al. 1988, Abelló 1993). González-Gurriarán et al. (1993) reported that although depth may be the major large-scale physical factor affecting distribution patterns, it did not appear to be determinant within their study area (the Galician coast). This was not the case in our study, where depth played a major role in the spatial distribution of the crab. González-Gurriarán et al. (1993) concluded that sediment and oceanographic conditions were also important variables affecting the spatial distribution of the species. Previous geostatistical studies with other species also showed depth to be an important covariant in geostatistical fisheries studies (Sullivan 1991, Simard et al. 1992). When comparing the different spatial models fitted to the calculated semivariograms for the biological variables studied, the best model (that with the smallest minimising function) was the spherical model, a result obtained in previous crustacean studies (Freire et al. 1991b, González-Gurriarán et al. 1993, Maynou et al. 1998). Taking a depth trend into account clearly increased the precision of the model.

Previous studies of *Liocarcinus depurator* spatial structure in the Atlantic continental shelf (Galicia) detected patch sizes between 14 and 22 km (González-Gurriarán et al. 1993), which is in accordance with present results (21.88 km). Still, also in Galicia, a range of 3 km was estimated inside the Ria de Ferrol (Freire et al. 1993), a much smaller range than that observed in the adjacent Galician continental shelf by González-Gurriarán et al. (1993) and in the present study. These differences may be related to the fact that the Ria de Ferrol sampling area was approximately 15×2 km, and the maximum semivariogram distance was 8 km; it would therefore not have been possible to detect a greater patch size in that study (Freire et al. 1993). Results from a geostatistical study in the SW Adriatic Sea by Ungaro et al. (1999) detected a patch size (effective range) of 160 km ($0.48^\circ \times 60 \text{ min} \times 1.852 \text{ km} = 53.34 \text{ km}$, which for the exponential model used in that study would mean an effective range of $3 \times \text{range}$ [Cressie 1991] = $53.34 \text{ km} \times 3 = 160 \text{ km}$) in an autumn survey and 69.67 km ($0.209^\circ \times 60 \text{ min} \times 1.852 \text{ km} \times 3 = 69.67 \text{ km}$) in a spring survey. This is much larger than the patch size observed either in our study or in the

Galician study (González-Gurriarán et al. 1993). However, Ungaro et al. (1999) did not publish sufficient details to allow interpretation of these large values.

Within the present study area, both density and biomass of *Liocarcinus depurator* were higher in the northern than in the southern area. The northern part is characterised by a narrow shelf (8 to 10 km width) and a gentle slope cut by deep submarine canyons, in contrast to the southern part where the shelf becomes progressively wider (38 to 40 km) and the slope steeper. Submarine canyons tend to have high macrofaunal and meiofaunal biomass, in accordance with the higher rates of production and sedimentation from the shelf (Cartes et al. 1994, Maynou et al. 1996). The higher densities of *L. depurator* in the northern area may accordingly be related to increased prey resources, given the vicinity of the submarine canyons.

The creation of the residual variables (as an index of mean size of the individuals in a sample), extracted from the non-linear relationship between biomass and density, proved to be a useful and powerful tool for data analysis, and its application could be expanded to the field of fisheries, where the size of many non-target species is often not measured but data on species density and biomass per haul is available. This method is also valuable when the low number of specimens captured does not allow a valid size-frequency analysis. The present results indicate that the use of this variable was successful in discriminating between areas with different population-size structures, possible recruitment areas and overall spatial size-segregation trends. Thus, in areas with large densities, the smaller crabs clearly occupied shallower depths and larger individuals were concentrated in deeper areas. There is data in the literature on size relationships as a function of depth in many taxa, with patterns often difficult to generalise (Stefanescu et al. 1992, Carbonell et al. 2003). Previous studies on the distribution characteristics of *L. depurator* have also detected strong geographic variability in densities (Abelló 1986, 1993), as well as the key role of depth in structuring populations in regard to both density and size structure (Mori & Zunino 1987, Abelló et al. 1988, Abelló 1993), with a tendency for small sizes to be found in shallower waters.

Sediment characteristics have been found to strongly influence occurrence and distribution of many benthic decapod crustaceans, especially of those with burrowing and burying habits (Atkinson & Taylor 1988, Pinheiro et al. 1996, Comeau et al. 1998). In this study, the use of geostatistical procedures was fundamental in identifying which sediment variables may influence the distribution of *Liocarcinus depurator*. Distribution characteristics of this species were significantly affected by most sediment variables considered, particu-

larly by temperature, organic matter content and redox potential, although overall the correlation level was low, thus emphasising the ecological strength and opportunistic behaviour of the species. Density and biomass, as well as residuals, presented a negative correlation with the sorting coefficient (IGSD) and with carbonates. In relation to IGSD, high densities of *L. depurator* were found in homogeneous sediments corresponding to low-energy areas. Residuals (e.g. size structure of the population) were significantly correlated with grain size (ϕ), with larger individuals occurring in finer sediments, while juveniles were preferentially found in areas with very fine sand sediments. Minervini et al. (1982) showed that the distribution of *L. depurator* was mainly related to muddy sediments, in contrast with the congeneric species *L. vernalis* which was mainly found in sandy sediments. In the present study, both density and biomass displayed significant positive correlations with the redox potential, indicating that the species favours well-oxygenated sediments with low organic content.

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