

Spatial structure and seasonality of decapod crustacean populations on the northwestern Mediterranean slope

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Abstract

Two trawl surveys designed for geostatistical analysis were made in spring and fall 1991 on *Nephrops norvegicus* fishing grounds off Barcelona, Spain. High-resolution geostatistical techniques—a new tool for analyzing species assemblages—were used to map and assess species abundances. Of the 43 decapod crustacean species collected, the spatial structures of the nine most abundant were analyzed and mapped by kriging. The maps of abundance drawn by kriging showed that the populations within the depth range of a species were not spread uniformly but were segregated in areas of high density. The locations of high concentration patches were generally mutually exclusive between pairs of species. The depth-related zonation of the megafaunal assemblage studied was complemented by a strong alongshore spatial heterogeneity. The spatial structure revealed by the geostatistical analysis, namely local dominance by one or a few species and a spatial pattern of high-density patches, made it difficult to predict the relative species composition at a given place, thus challenging the concept of a community of ecologically interacting decapod crustaceans over the continental slope. Local factors, such as canyon-mediated hydrographic processes and sediment resuspension, helped account for the horizontal heterogeneity in the spatial distribution of decapod crustaceans.

Marine species assemblages have traditionally been analyzed by multivariate statistical techniques primarily designed for automated classification. As a result, the deep-sea megafaunas have been conceptualized as a series of species assemblages whose composition is largely related to depth or as belts extending along the depth contours where species composition would be more or less uniform (Menzies et al. 1973; Haedrich et al. 1980; Carney et al. 1983). This approach has sustained the concept of discrete sets of species assemblages forming a community fitting a particular type of environment or biotope (*see* Mills 1969). Depth-related zonation of dominant megafaunal groups (fish, crustaceans, echinoderms) has been described for many deep-sea areas (Haedrich et al. 1980; Hecker 1990; Cartes and Sardà 1992), although depth as such is not likely to be the direct causative factor (Hecker 1990). Horizontal segregation of species assemblages is less well documented, although it might originate from horizontal heterogeneities in the physical environment

such as sediment types and hydrological processes (Marle and Musick 1974; Hecker 1990).

Decapod crustaceans and fish are the dominant megafauna in the benthic communities on the northwestern Mediterranean slope (Pérès 1985; Cartes and Sardà 1992). In the area studied, the species assemblages of decapod crustaceans have been described by Abelló et al. (1988), who used multivariate analysis to sort species abundance indices obtained from commercial bottom trawls pooled over a 2-yr period from shelf, upper, and middle slope depths (3–871 m) off the Catalan coast.

We used new navigation gear and statistical techniques to design, conduct, and analyze two experimental surveys over lower shelf to middle slope depths (145–705 m) off Barcelona, Spain. The advent of the Global Positioning System (GPS), of acoustic remote sensing of gear performance (SCANMAR), and of spatial analysis tools (Geostatistics) allows us to precisely visualize the spatial distribution of marine species. Our objectives are twofold: to illustrate the applicability of geostatistical techniques in a biological oceanographic context and to draw inferences on the spatial distribution of decapod crustacean species in the deep sea. Geostatistics (Matheron 1971; Journal and Huijbregts 1978) is a methodology used in the earth sciences to analyze, model, estimate, and map the spatial distribution of natural resources through an analysis of their spatial autocorrelation. It was introduced in biological oceanography by G. Y. Conan in an ICES report (ICES C.M. 1985/K:30).

Acknowledgments

The research work of F. Maynou was supported by a graduate research fellowship from the Dirección General de Investigación Científica y Técnica (DGICYT) of the Ministerio de Educación y Ciencia (Spain). The work of G. Y. Conan in Spain was sponsored by a personal award from the DGICYT.

We thank Sharon McGladdery for comments during the preparation of the manuscript and two anonymous reviewers for many helpful comments on the manuscript.

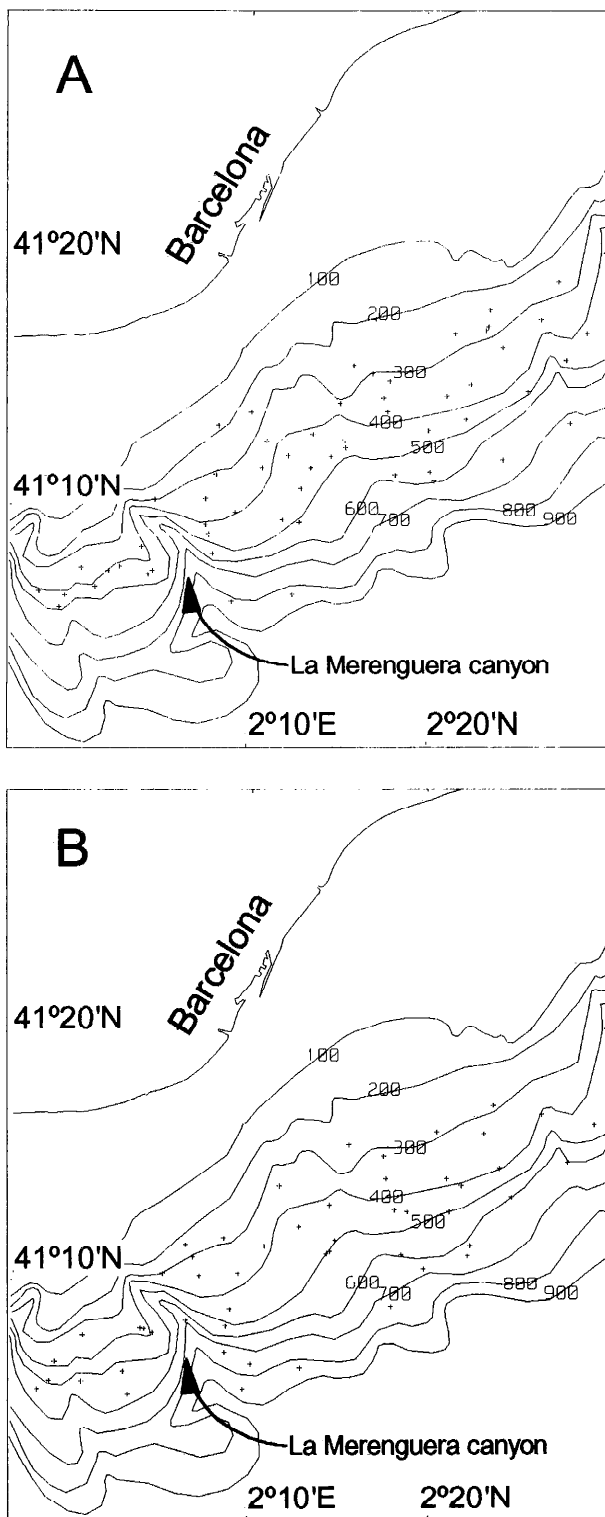


Fig. 1. Bathymetry (depth contours in meters) and position of stations. A. Spring survey. B. Fall survey.

The geostatistical model we built for decapod crustacean species allowed for a high-resolution representation of the actual two-dimensional distribution of each species over the study area. The analysis and comparison of den-

sity maps of selected species showed a spatial arrangement of the decapod crustacean populations in patches of high and low density. Furthermore, the high-density patches did not overlap extensively for any two species.

We conclude that the extent of horizontal variability in the spatial distribution of deep-sea benthic megafauna is of the same order as the vertical (depth-related) variability. We visualize the composition of deep-sea megafaunal communities as two-dimensional intergrading patches of locally dominant species bounded vertically by depth and horizontally by canyons or other topographically mediated factors.

Material and methods

Sea sampling—Fifty-three trawl hauls were taken in spring 1991 (GEOESC-1, 27 April–5 May 1991) and 45 in the fall (GEOESC-2, 29 November–7 December 1991) at depths ranging from 146 to 705 m on the Catalan Sea slope off Barcelona (Fig. 1). The stations were set on a regular grid (1.852×3.704 km) comprehensively covering the area surveyed ($41^{\circ}00'–41^{\circ}25'N$, $1^{\circ}57'–2^{\circ}30'E$). Within each cell, a start point for a haul was placed at random. This sampling scheme was used to minimize the variance for global kriging estimates, while optimizing information for estimating semivariograms (ICES C.M. 1988/K:10, 1992/K:22). The slope of the study area is cut by several submarine canyons, the most important of which is La Merenguera (Fig. 1).

The sampling gear used—a Maireta system single-warp bottom trawl (MST)—was built specifically for our surveys. The design is derived from the semiballoon otter trawl (OTSB-14, Merrett and Marshall 1981)—a type of bottom trawl widely used in deep-sea sampling. The cod-end stretched mesh was 12 mm.

Tows were limited to 15 min to avoid subsampling the catch and to keep the approximation of point sampling as realistic as possible (ICES C.M. 1988/K:10, 1992/K:22). Satellite positioning (GPS) was used to locate and measure the length of the tows, which varied from 0.574 to 2.376 km, based on ship positions. GPS precision was 200–300 m. SCANMAR sensors were used to measure the aperture of the fishing gear, which varied from 12 to 15 m (stabilized at 13.4 m). The use of GPS and SCANMAR combined provided a precise estimate of the area swept by the trawl at each station (from 7,691.6 to 31,838.4 m²). Sampling was carried out between 0700 and 1900 hours to avoid any bias related to day–night behavior of the decapod crustacean species encountered in the area (Cartes et al. 1993). Samples were sorted and the species identified, counted, and weighed on the ship or at the laboratory.

Statistical analysis—A geostatistical model was built to analyze the density [No. individuals/unit area, denoted $Z(x)$] for selected species and the diversity index (H' , Shannon and Weaver 1963) for the spring and fall surveys. $Z(x)$ represents the density of a species indexed over x , the coordinates of the sampling units on the plane.

Geostatistics is a two-step technique which uses geo-

graphically positioned data. First, the structure of spatial variability of $Z(x)$ is assessed by an experimental covariance function (semivariogram, covariogram, or correlogram, called structure functions in the geostatistical literature). These functions are analogous to the spatial autocorrelation functions used in spatial ecology (Sokal and Oden 1978).

Following earlier work (ICES C.M. 1992/K:22), we used the semivariogram, rather than the covariogram or correlogram, as a spatial descriptor. The semivariogram is a plot of the semivariance of population densities $[Z(x_i) - Z(x_j)]^2$ at locations x_i, x_j set a distance h apart. In the absence of spatial autocorrelation among samples, the mathematical expectation of the semivariance is the variance of $Z(x)$, and it is independent of the spatial position of the samples. A monotonous increase in the semivariance value as h increases reveals the presence of (positive) spatial autocorrelation. The experimental semivariogram, as given by Matheron (1971), is

$$\hat{\gamma}(h) = \frac{1}{2N(h)} \sum_{N(h)} [Z(x_i) - Z(x_j)]^2. \quad (1)$$

In our semivariograms, the semivariance increased monotonously with h up to a distance a (called the range of the semivariogram), where the semivariance stabilized around the population variance (sill of the semivariogram, denoted c' in geostatistics). The range can be interpreted in ecology as the distance beyond which the effects of spatial autocorrelation are negligible. Thus, the range defines a zone within which the densities $Z(x)$ are correlated and likely to be similar in value, defining a patch. Sokal and Oden (1978, referring to the correlogram) further suggest that the range of the semivariogram can be related to the size of the patches in which the populations structure themselves.

Our semivariograms also showed a discontinuity at the origin, called the nugget effect in geostatistics (denoted c_0). The nugget effect corresponds to the concept of between-replicate variability and indicates a certain microscale variability, a spatial structure at a scale smaller than the tow length (~ 1 km in the present study), or variability resulting from the differences in area swept by different tows, or measurement error. It is often difficult to ascertain the exact underlying process generating the nugget effect, although spatial processes at scales < 1 km and, to a lesser extent, differences in swept area among tows were probably significant in this study.

The computation of local average and variance within a moving window in the area defined by the sampling points showed a linear relationship between the average and the standard deviation for most species studied. This effect is well known in ecology as Taylor's power law (Taylor 1961). In geostatistics, this has been termed the proportional effect (David 1977) and would preclude the use of the experimental semivariogram given by Eq. 1. The use of a relative semivariogram is recommended in such cases. The relative semivariogram is computed by dividing the experimental semivariogram at lag h by the square of the mean of the values $Z(x)$ used in the computation of the experimental semivariogram at lag h , de-

Table 1. Crustacean decapod species selected for geostatistical study. Percentages represent relative abundance (numbers and biomass). N—Nektobenthic species; B-E—benthic-endo-benthic species; M—mesopelagic species (from Cartes and Sardà 1992, table 1).

	Hab-its	GEOESC-1		GEOESC-2	
		% No.	% Wt.	% No.	% Wt.
<i>Aristeus antennatus</i>	N	6.7	13.6	8.1	35.9
<i>Solenocera membranacea</i>	B-E	2.1	3.5	6.5	4.7
<i>Sergestes arcticus</i>	M	19.3	0.4	35.0	3.4
<i>Pasiphaea sivado</i>	M	27.6	17.5	2.9	0.7
<i>Processa nouveli</i>	B-E	9.0	2.7	10.1	1.2
<i>Plesionika heterocarpus</i>	N	6.8	12.0	2.6	2.5
<i>Plesionika martia</i>	N	5.5	4.0	0.6	6.2
<i>Nephrops norvegicus</i>	B-E	2.3	31.9	2.6	19.3
<i>Calocaris macandreae</i>	E	9.0	2.4	3.0	0.3
All other species		11.7	12.0	28.6	25.8

noted $m(h)$. The relative semivariogram is defined as (David 1977)

$$\hat{\gamma}_R(h) = \frac{\hat{\gamma}(h)}{\hat{m}(h)^2}. \quad (2)$$

The experimental semivariograms were modeled by a theoretical semivariance function (Matheron 1971; Journel and Huijbregts 1978). The spherical model adequately fitted our experimental semivariograms in most cases. In this model, three parameters need to be estimated from the experimental semivariogram: nugget (c_0), range (a), and sill (c'). The spherical model is given by

$$\gamma(h) = \begin{cases} c_0 + c' \left(\frac{3h}{2a} - \frac{1}{2} \left(\frac{h}{a} \right)^3 \right) & h < a \\ c_0 + c' & h \geq a \end{cases}. \quad (3)$$

To obtain high-resolution cartography of $Z(x)$, we proceeded to the second stage in the geostatistical modeling—kriging (Matheron 1971; Journel and Huijbregts 1978). Point kriging was used to estimate the value of $Z(x)$ at the nodes of an arbitrarily fine mesh grid over a polygon defined by depth contours and the sampling points (between 200 and 700 m, and from 1°57' to 2°30'E, ICES C.M. 1992/K:22). The mesh used in this study comprised $\sim 200 \times 200$ nodes. The internodal distance was of the same order as the precision of the positioning system.

The kriging estimate of $Z(x)$ at each node was obtained by a linear combination of the samples, each weighted by a factor (w_i) which depends on the relative position of the sampling points, the theoretical semivariogram, and the $Z(x)$ values at the sampling points. The weights were obtained by solving a linear system of equations (Matheron 1971; Journel and Huijbregts 1978) at each node. Intuitively, the weight assigned to sampling points closer to the node to be estimated was higher than the weight assigned to faraway locations. The estimated density values at each node x_0 of the grid were given by

$$Z^*(x_0) = \sum_i w_i Z(x_i). \quad (4)$$

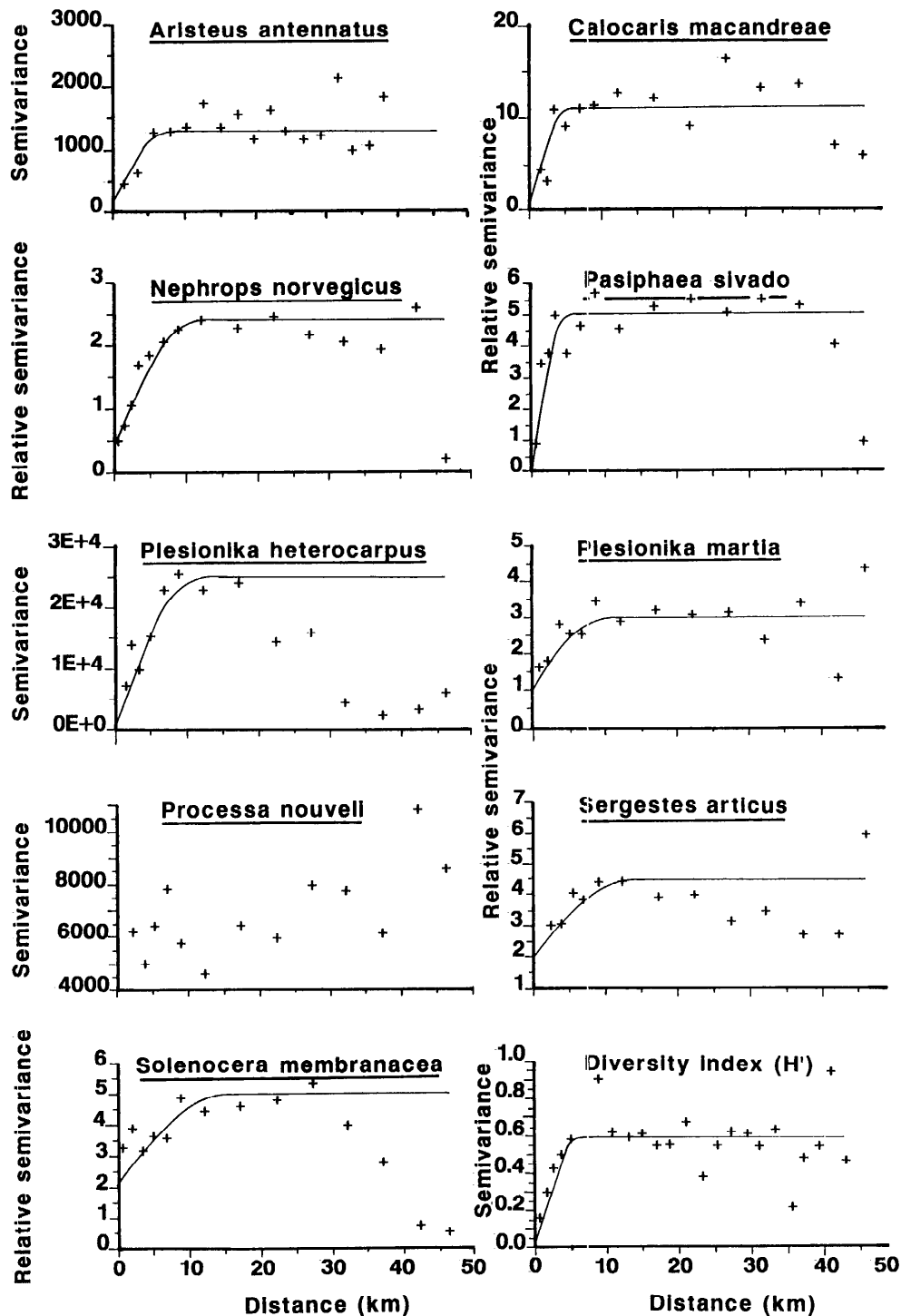


Fig. 2. Spherical models fitted to experimental semivariograms, spring. Relative semivariograms were computed when a local variance-local mean relationship biased the computation of the semivariograms (ICES C.M. 1992/K:22).

A variant of the point-kriging technique—block kriging—allowed us to estimate the unbiased mean density of each species over the area restricted by the polygon. The kriging variance obtained when computing block estimates (Matheron 1971) was used here to assign confi-

dence intervals to the estimates. The mapping by point kriging and the global estimates by block kriging within an irregular contour were produced by a numerical algorithm developed by G. Y. Conan run on a PC 486-DX 66 Mhz.

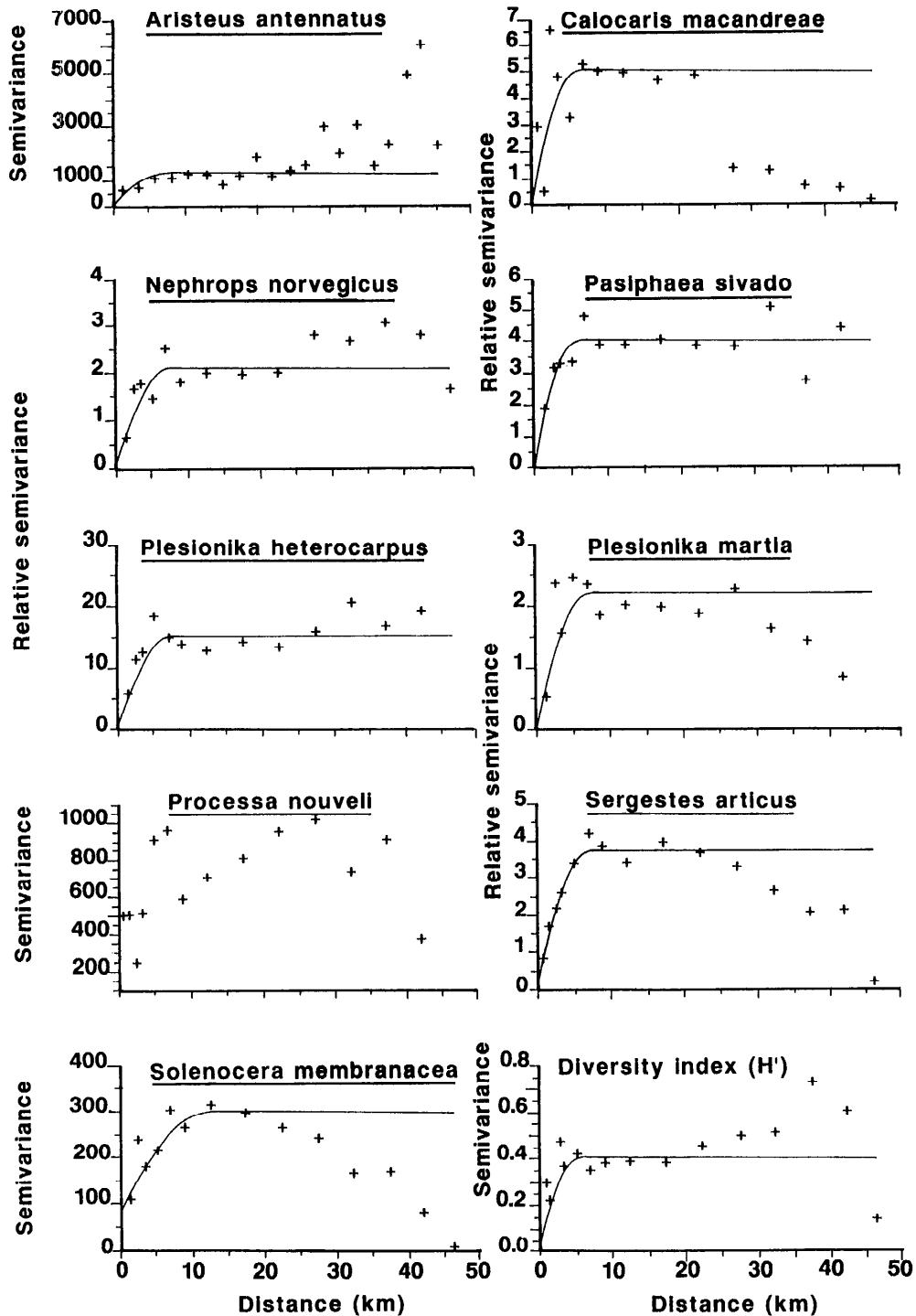


Fig. 3. Spherical models fitted to experimental semivariograms, fall.

The density maps obtained by kriging are not conventionally tested for significance in geostatistics, nor is there a test to compare the similarity between two maps. The methods of map comparison based on developments from the field of quantitative geography (Berry and Marble 1968) are of little use for data sets in which there is strong autocorrelation among points.

We investigated the applicability of Mantel's correlation test g (Mantel 1967; Manly 1985) to the problem of comparing the overall similarity between maps of any two species. For two distance matrices A and B, the test checks whether the spatial pattern (zones of high and low density) in matrix A overlaps the spatial pattern of matrix B and to what extent. The distance coefficient used here

Table 2. Parameters of spherical model fitted to experimental semivariograms of selected species. Type indicates absolute (A) or relative (R).

	Spring			Fall			Type
	Range (km)	Nugget	Sill	Range (km)	Nugget	Sill	
<i>Aristeus antennatus</i>	7.5	100	1,200	7.5	0	1,300	A
<i>Calocaris macandreae</i>	6.0	0	11	6.0	0	5	R
<i>Nephrops norvegicus</i>	12.0	0.4	2	7.5	0	2.1	R
<i>Pasiphaea sivado</i>	5.5	0	5	5.5	0	4	R
<i>Plesionika heterocarpus</i>	12.0	0	25,000	7.5	0	15	A-R
<i>Plesionika martia</i>	10.0	1	2	7.0	0	2.2	R
<i>Processa nouveli</i>	—	—	—	—	—	—	—
<i>Sergestes arcticus</i>	13.5	2	2.5	7.0	0	3.7	R
<i>Solenocera membranacea</i>	16.0	3	2	12.0	80	220	R-A
Diversity index (H')	6.0	0	0.6	5.5	0	0.4	A

was the absolute difference in density between points x_i , x_j divided by the maximum density of the species for each matrix. The correlation statistic g is large and positive when the two matrices are positively correlated (i.e. they show lows and highs at corresponding locations). The correlation statistic is large and negative when the two matrices are negatively correlated and the high-density locations in matrix A correspond to low density locations in matrix B and vice versa. When there is no clear pattern of correlation, g is near 0.

The g statistic can be tested for significance either by a normal approximation or by a permutation test (Manly 1985). We implemented the Mantel's test program given by Manly (1985) through 500 permutations.

Results

We encountered 43 species of decapod crustaceans in the two surveys, most belonging to the suborder Dendrobranchiata and the infraorder Caridea. As noted by others (Abelló et al. 1988), the brachyuran fauna becomes less important below shelf depths. The dominant species in abundance or biomass are also economically important in the area studied and were selected for geostatistical analysis. They were *Aristeus antennatus*, *Solenocera membranacea*, *Sergestes arcticus*, *Pasiphaea sivado*, *Processa nouveli*, *Plesionika heterocarpus*, *Plesionika martia*, *Nephrops norvegicus*, and *Calocaris macandreae* (Table 1).

Spatial and temporal structure—An experimental semivariogram was computed for spring and fall for each of the species retained for geostatistical study and for the diversity index. Most of the experimental semivariograms satisfactorily fit a spherical model (Figs. 2, 3). The parameters of range, nugget, and sill for each semivariogram are shown in Table 2. A spherical model did not fit *P. nouveli* data. This species may structure itself spatially at scales smaller than those surveyed.

Most species are spatially autocorrelated at distances that vary from 5.5 to 16 km (Figs. 2 and 3, Table 2). No

clear relationship between habits of the species (Table 1) and range (Table 2) could be discerned. The range of the semivariogram remained fairly constant between spring and fall for *A. antennatus*, *P. sivado*, and *C. macandreae*; it decreased for *S. membranacea*, *S. arcticus*, *P. heterocarpus*, *P. martia*, and *N. norvegicus* (Table 2). The range of the semivariogram can be interpreted as a mean patch size (Sokal and Oden 1978). The populations of the species spatially modeled by means of the spherical semivariogram were structured roughly in circular patches with radii defined by the range of the semivariogram, as a first approximation (anisotropy could not be demonstrated for any of the species). The diversity index showed spatial autocorrelation with a range of 5.5–6.0 km (Figs. 2 and 3, Table 2).

There was a decrease in semivariance below the sill value at large distances for some species (particularly *P. martia* and *S. membranacea* in Fig. 2 and *C. macandreae*, *P. martia*, and *S. membranacea* in Fig. 3). For each species, this effect was due to the comparison of low values of $Z(x)$ at the extremes of the study area in the computation of $[Z(x_i) - Z(x_j)]^2$ in Eq. 1.

Mapping and assessment—The density maps drawn for the species to which a spherical semivariogram could be fitted are shown in Figs. 4 and 5. Visual comparison of the different maps for each survey showed that populations of different species aggregate in high-density patches. These patches only marginally overlap for most pairs of species, giving a mosaic of transition zones (both vertically and horizontally) where species diversity is higher (Fig. 6). The spring map of H' (Fig. 6A) showed its lowest values in the shallow upper slope, following patches where *P. heterocarpus* was dominant. The low-diversity patches of the fall map (Fig. 6B) were mainly due to dominance of *S. arcticus* in the shallow upper slope and *Aristeus antennatus* in sectors of the middle slope. Most areas on the slope showed higher H' in the fall survey than in the spring survey.

Visual inspection of Figs. 4 and 5 showed that *A. antennatus* and *C. macandreae* tended to occupy the deeper

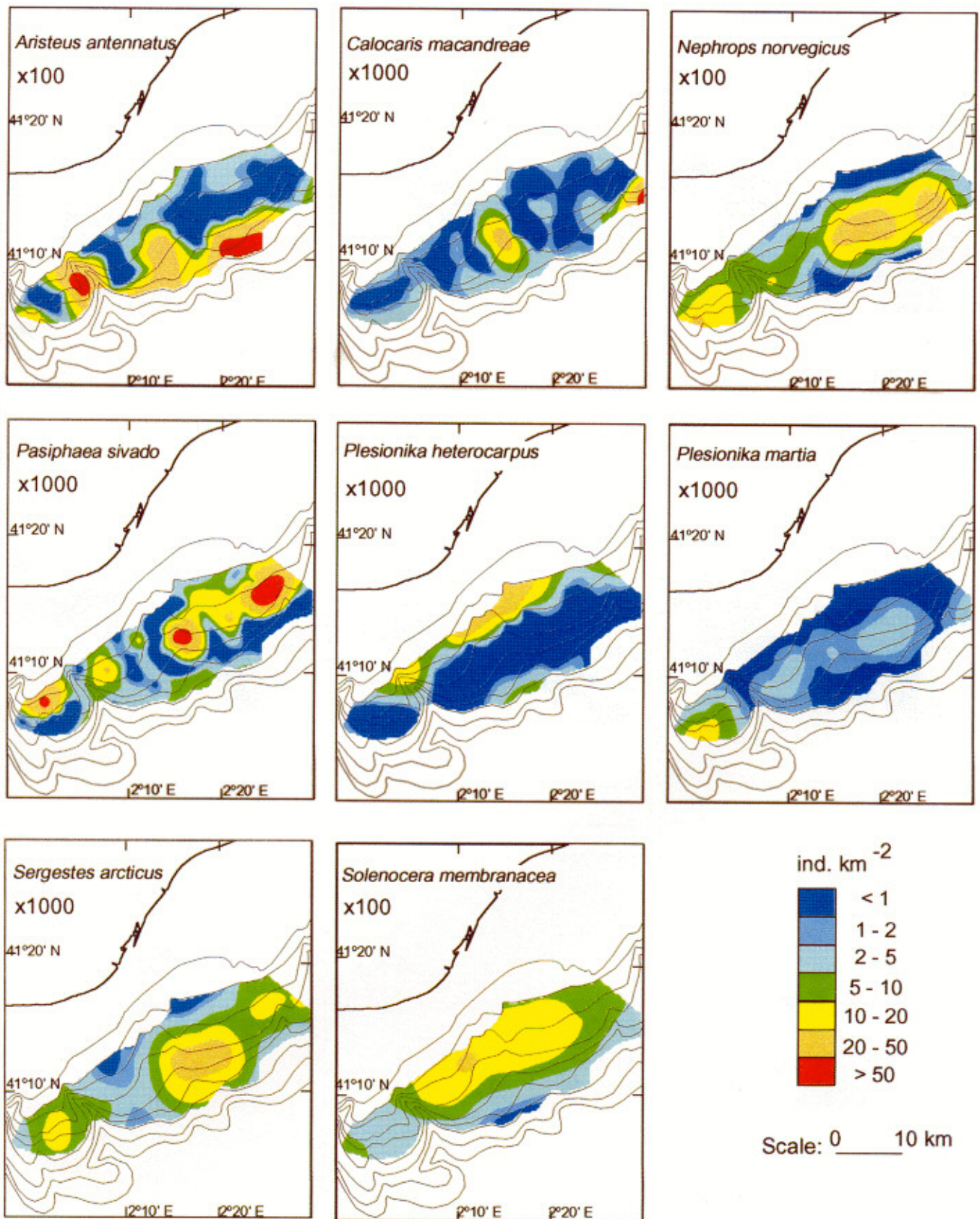


Fig. 4. Density maps generated by point kriging, spring.

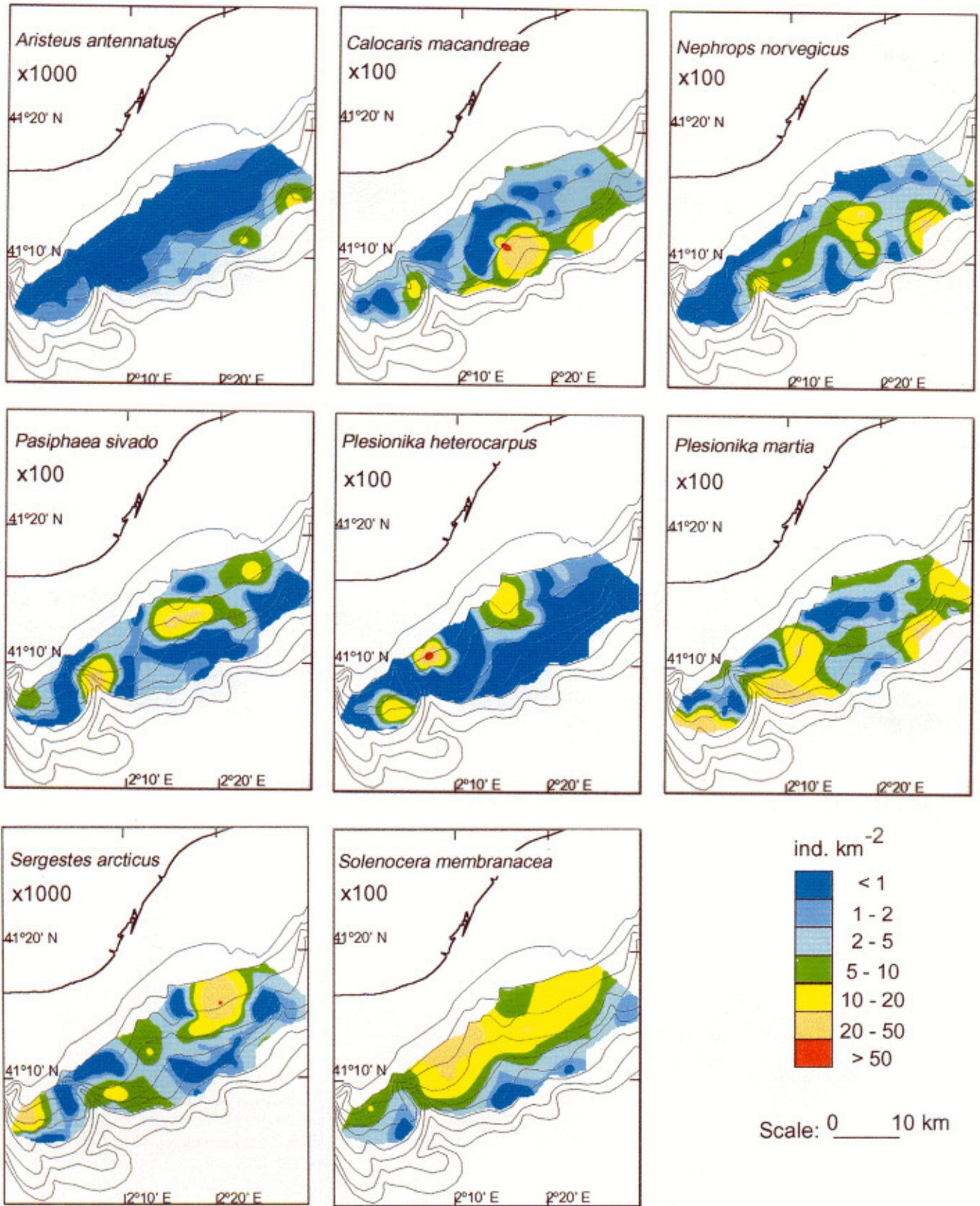


Fig. 5. Density maps generated by point kriging, fall.

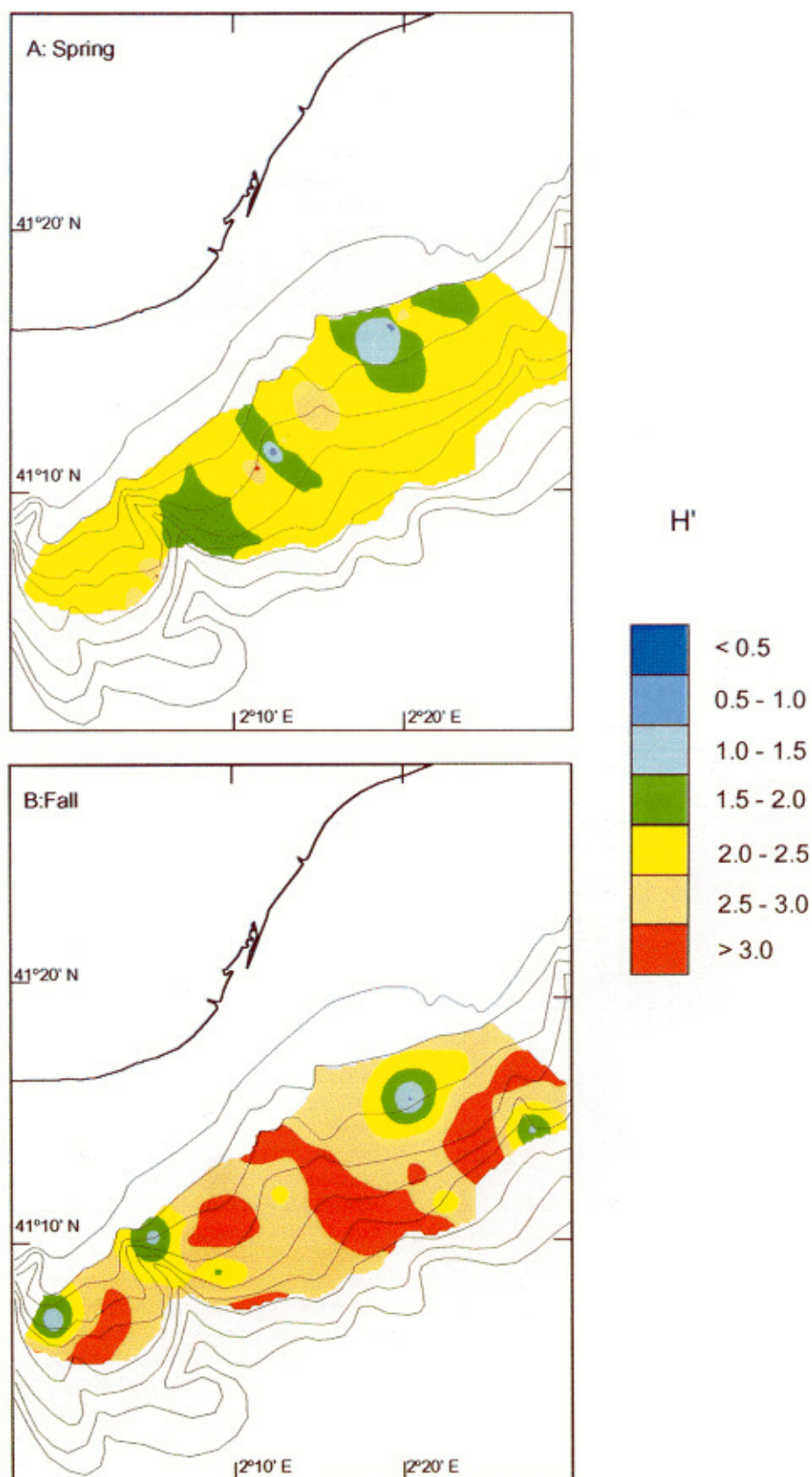


Fig. 6. Diversity index maps generated by point kriging.

Table 3. Pairwise comparison of maps in Figs. 4 and 5 by means of Mantel's test. Spring survey below main diagonal; fall survey above main diagonal. Positive g indicates spatial overlapping, negative g indicates spatial avoidance. $P(g)$ significant near 0 and near 1, respectively. Results significant at the 5% level are shown bold face.

	<i>A. antennatus</i>	<i>C. macandreae</i>	<i>N. norvegicus</i>	<i>P. sivado</i>	<i>P. heterocarpus</i>	<i>P. martia</i>	<i>S. arcticus</i>	<i>S. membranacea</i>
<i>Aristeus antennatus</i>	—	2.251 g	-0.712 $P(g)$	-0.723 $P(g)$	0.548 g	1.243 g	-0.701 g	-0.632 $P(g)$
<i>Calocaris macandreae</i>	-0.282 $P(g)$	—	-0.265 $P(g)$	-0.762 $P(g)$	0.705 $P(g)$	0.107 $P(g)$	0.758 $P(g)$	0.736 $P(g)$
<i>Nephrops norvegicus</i>	0.623 g	0.392 g	0.603 $P(g)$	0.224 $P(g)$	0.684 $P(g)$	0.192 $P(g)$	0.663 $P(g)$	0.824 $P(g)$
<i>Pasiphaea sivado</i>	-1.154 $P(g)$	0.875 $P(g)$	3.584 $P(g)$	0.001 $P(g)$	-0.185 g	0.498 g	-0.400 g	2.842 $P(g)$
<i>Plesionika heterocarpus</i>	0.864 $P(g)$	0.348 g	1.313 $P(g)$	—	0.002 g	-0.702 g	0.345 $P(g)$	0.002 $P(g)$
<i>Plesionika martia</i>	0.863 $P(g)$	-0.633 $P(g)$	0.095 g	-0.723 $P(g)$	0.772 $P(g)$	0.758 $P(g)$	1.522 g	3.551 $P(g)$
<i>Sergestes arcticus</i>	0.805 $P(g)$	-0.564 g	-0.784 g	0.764 $P(g)$	—	-0.692 g	-0.201 g	0.001 $P(g)$
<i>Solenocera membranacea</i>	-0.574 $P(g)$	0.645 g	0.782 $P(g)$	0.842 g	-0.724 g	0.755 $P(g)$	0.579 $P(g)$	0.405 $P(g)$
	-1.153 $P(g)$	0.261 $P(g)$	2.554 g	-0.800 $P(g)$	0.764 g	—	-0.042 g	-1.273 $P(g)$
	0.875 $P(g)$	-0.636 g	4.143 g	1.874 g	0.764 g	1.278 g	0.516 $P(g)$	0.898 $P(g)$
	-0.914 g	0.736 $P(g)$	< 0.001 $P(g)$	0.031 $P(g)$	-0.764 g	0.102 g	—	1.502 $P(g)$
	0.819 $P(g)$	-0.538 g	0.560 $P(g)$	0.121 $P(g)$	-0.743 g	0.345 g	-0.364 g	0.067 $P(g)$
		0.702 $P(g)$			0.770 $P(g)$	0.633 $P(g)$	0.641 $P(g)$	

parts of the area studied, while *P. heterocarpus*, *P. sivado*, and to a lesser extent *S. membranacea* were more abundant in the shelf-break to upper slope area. *N. norvegicus*, *P. martia*, and *S. arcticus* ranged over the upper slope. This pattern coincided broadly with the species assemblages reported by Abelló et al. (1988). The species assemblages were defined by Abelló et al. as shelf assemblage (<200 m), upper slope assemblage (200–400 m), and deep slope (>400 m). Detailed examination of each of the maps in Figs. 4 and 5, however, shows the difficulty in assigning a discrete depth-range to each species. The species assemblages were less clear-cut than the original categories suggest.

For a given depth range, the dominant species were not spread uniformly. Instead, there was considerable horizontal (along depth contour) heterogeneity. The high-density patches of any given species were bounded vertically (across depth contours) by depth but also horizontally by factors other than depth. Examination of Figs. 4 and 5 shows that horizontal heterogeneity was as important as vertical heterogeneity.

The effect of horizontal heterogeneity was most marked in the vicinity of the main canyon area. Further, the slope regions west and east of the main canyon support high-density patches belonging to different species. Only *P. martia* was present in high concentrations on the slope west of the canyon, where species concentrated primarily on the slope east of the canyon (*S. arcticus*, *P. sivado*, and *N. norvegicus*) were less abundant. Other species, such as *S. membranacea*, *P. heterocarpus*, and *C. macandreae*, were present in high densities only on the slope east of the canyon.

The results of the Mantel's correlation test are shown in Table 3. The test was carried out between pairs of species for each survey; a comparison between spring and fall surveys was not attempted because the sampling points were set at different locations.

In the spring survey, the test was significant (at the 5% level) in three instances, which demonstrated extensive overlapping of high-density patches between *N. norvegicus* and *P. martia*, between *N. norvegicus* and *S. arcticus*, and between *S. arcticus* and *P. sivado*. Pairs of species that segregated extensively (for instance, *A. antennatus* from *P. sivado* and from *S. arcticus*) did not yield significant negative values of g at the 5% level, although g was consistently large and negative, coinciding with the visual analysis of Figs. 4 and 5. The test is only effective for detecting pairs of species that segregate extensively, where high-density patches of one species coincide exactly with locations of low-density patches for the other species.

In the fall survey, the test was significant in four cases. It showed positive correlation between the maps of *A. antennatus* and *C. macandreae*, between *N. norvegicus* and *P. sivado*, between *N. norvegicus* and *S. membranacea*, and between *P. sivado* and *S. membranacea*.

The average density of each species was estimated by global kriging over the area of study (Table 4). The density of *P. sivado*, *P. heterocarpus*, and *C. macandreae* decreased in the fall survey. The densities reported here should be considered unbiased abundance indices, even

Table 4. Global kriging estimates for average density (No. ind. km⁻²). Standard deviation of estimate in parentheses.

	Spring	Fall
<i>Aristeus antennatus</i>	1,551.3 (393.9)	1,407.6 (368.7)
<i>Calocaris macandreae</i>	2,655.4 (1,269.7)	470.6 (149.4)
<i>Nephrops norvegicus</i>	742.2 (162.2)	329.8 (65.5)
<i>Pasiphaea sivado</i>	9,060.2 (3,004.5)	396.9 (115.3)
<i>Plesionika heterocarpus</i>	6,829.0 (1,383.9)	223.5 (118.6)
<i>Plesionika martia</i>	1,550.3 (431.1)	919.4 (188.4)
<i>Sergestes arcticus</i>	6,851.7 (2,419.2)	5,449.4 (1,447.9)
<i>Solenocera membranacea</i>	772.2 (274.6)	860.3 (198.3)

allowing for the absence of full catchability of certain species due to the mesopelagic habits of *Pasiphaea* spp. and *S. arcticus* and the burrowing habits of *C. macandreae* and *N. norvegicus*. A comparison with density values reported in the literature for the same species is limited by the different gear used and by the units in which those values are commonly reported (ind. h⁻¹ or kg h⁻¹, most frequently).

The precision of our estimates of mean density, as given by the kriging standard deviation (Table 4), was higher than that typically reported in the literature. Cartes and Sardà (1992) for instance, used stratified random sampling and reported standard errors of the same magnitude or higher than the mean (i.e. the precision of their estimates was lower than ours).

Discussion

The availability of new navigation and gear technology (GPS, SCANMAR) concomitant with spatial statistical tools allowed us to visualize the spatial distribution of benthic decapod crustaceans and to compute precise and unbiased regionalized abundance estimates.

The analysis of point samples revealed spatial structures at the scale studied (10⁰–10² km) for most of the decapod crustacean species selected. These spatial structures appeared as species-specific, high-density patches of 5.5–16-km radius approximated by the semivariogram range in the absence of anisotropy. These structures have been partially masked in the past by integrating lengthy (several kilometers) trawl hauls along the depth contours, imprecise positioning, and the use of standard multivariate classifications. The absence of alongshore anisotropy (higher autocorrelation among samples along rather than across the isobaths) for any of the species further helped obscure the notion of horizontal continuity beyond a local scale.

Geostatistical analysis revealed that the species considered were not strongly spatially associated, but shared a common environment by segregating into patches that tended to be species-specific. Similarly, Haedrich and Merrett (1990) found that individual species of fish in the Atlantic were rarely associated with any other individual species.

Although there is some limitation to drawing conclu-

sions on the seasonality of the species studied with only two data sets available, some degree of temporal variability of decapod crustaceans at an annual scale has been detected by other workers in the same area (Tobar and Sardà 1992; Sardà et al. 1994). Their findings helped us partially account for the differences in the spatial structure observed between spring and fall, namely that the patch size of some species, but not of all, remained constant between spring and fall (as revealed by the range of the fitted semivariograms) and that the location of high-density patches shifted for some species between spring and fall. The oceanographic conditions at the depths surveyed have been reported to be stable throughout the year (Hopkins 1985; Salat and Cruzado 1981) and do not readily explain the spatial structures observed nor their possible seasonality.

The canyon area revealed the most important shifts in species composition and abundance, both in time and space. Canyons are dynamic environments, funneling coastal terrigenous sediments and serving as conduits for deep-water upwelling (Shepard et al. 1974; Houston and Haedrich 1984) and showing seasonal variability (Gardner 1989). Also, a high spatial variability of the sediment resuspension at small scales has been demonstrated by Crassous et al. (1991) over a lower slope area in the NW Mediterranean. Cartes and Sardà (1992) suggested that the vertical faunal zonation in the Mediterranean deep sea might be caused, at least partially, by resuspension of sediments associated with canyons and the steeper parts of the slope and by impoverishment of organic matter in the bottom sediments with increasing depth. A topographically mediated food gradient also has been invoked to account for the spatial distribution of megafaunal assemblages in the NW Atlantic (Hecker 1990). These phenomena may account for the horizontal heterogeneity in the spatial distribution of decapods observed here, though intra- and interspecific biotic processes should also be considered.

The diversity index also was found to be structured in high-value patches. Although the low diversity of certain areas may be related to local high dominance by a few species (mainly over muddy sand bottoms near the shelf-break or in zones of high density of *A. antennatus*), the areas of high diversity seemed to reflect transition zones between high-density patches of different species. Locally, relatively higher values of *H'* were found when compared

to the results reported by Cartes and Sardà (1992), probably due to the higher catchability of mesopelagic species by the MST sampling compared to the OTSB-14 used by Cartes and Sardà.

We conclude that the depth-related zonation of decapod crustacean species in the NW Mediterranean reported earlier (Abelló et al. 1988) is complemented by an important horizontal component that reflects a strong two-dimensional spatial heterogeneity. The distribution of species can be as discontinuous and diverse horizontally as it is along the depth gradients. It is the juxtaposition of these patches which generates apparent species assemblages. The extent of spatial heterogeneity at the scale of study (10^0 – 10^2 km) also supplements the strong spatial heterogeneity demonstrated by others at smaller scales (de Bovée et al. 1990 for meiobenthos; Jumars 1978 for macrobenthos; Grassle et al. 1975 for megabenthos), which is one of the factors advanced to account for the high diversity observed in deep-sea faunas (Grassle 1991).

Although the species inventory was very similar in all the sampling stations, the local dominance of one or a few species over restricted areas and the strong spatial heterogeneity in the distribution of decapod species make it difficult to predict the relative species composition at a given place. This challenges the concept of a community of ecologically interacting decapod crustaceans, in the sense of Mills (1969). We agree with Haedrich and Merrett (1990) that those aspects of traditional benthic community theory (developed for coastal and shallow waters; Glémarec 1973; Mills 1969) that are related to species constancy and species co-occurrence may be of little relevance in the deep sea, at least for megafaunal assemblages (fish, decapod crustaceans).

The two-dimensional spatial heterogeneity of megafaunal species is often masked by the use of standard multivariate techniques accompanied by less precise positioning or pooling of the sampling locations over predetermined depth strata. Spatial statistical techniques may overcome some of these limitations and optimize the use of the important but often neglected exact spatial positions of the sampling units.

The strength of the geostatistical methodology compared to autocorrelation analyses more often used in ecology is the possibility of going beyond the simple description of the autocorrelation structure to provide an accurate depiction of the actual spatial distribution of the species. The shortcomings of the methodology used here were mainly related to the restriction of performing univariate analysis on multivariate data and the difficulty of map comparison. Although the use of geostatistics has been extended to the bivariate case (cross-semivariograms, cokriging: Journal and Huijbregts 1978), its applicability in population biology is limited by the often nonlinear relationships encountered between densities of any two species. Analytical procedures for map comparison have not been developed, but the use of Mantel's correlation statistic proved useful for defining a measure of overall similarity between density maps of different species.

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Submitted: 19 July 1994

Accepted: 5 August 1995

Amended: 17 October 1995