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Spatial structure and ecological variation of meroplankton on the French-Belgian coast of the North Sea

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ABSTRACT: The spatial pattern of specific populations or communities plays an important role in ecological theories such as species diversity, community succession and stability. A method based on canonical correspondence ordination (CCA) and constrained ordination was used to partition the variation observed in the species abundance data matrix into 4 independent components: spatial, environmental, spatial + environmental, undetermined. Mantel and partial Mantel test results were in accordance with CCA results.

KEY WORDS: North Sea · Meroplankton Community structure · Canonical correspondence analysis (CCA) · Constrained ordination · Monte Carlo permutation test · Mantel statistics

INTRODUCTION

Meroplankton species and hydrological monitoring data were collected along a transect in the Southern Bight of the North Sea. The coastal locations studied are characterized by the presence of a benthic community continuum dominated by the bivalve *Abra alba*, which is subjected to seasonal and yearly fluctuations (Dewarumez et al. 1991). Most of the benthic species have a pelagic phase during their life cycle, with the meroplanktonic larvae dispersed over a period of time which varies from 1 wk to 1 mo. The complexities involved in the interpretation of the effects of localised wind-driven advection transport on the intensity of water mass movements in relation to the changes in the distribution and abundance of meroplankton and zooplankton in this area have been discussed by many authors (Colebrook 1978, Colebrook & Taylor 1984, Belgrano et al. 1990, Dewarumez et al. 1991). The aim of this study was to assess the spatial hetereogeneity of the meroplankton community structure in relation to hydrodynamic and environmental processes, in order to understand the mechanisms involved in the larval dispersion and the complex biological fluxes existing in the coastal waters between the English Channel and the Southern Bight of the North Sea (Luczak et al. 1993).

Multivariate analysis techniques such as classification, clustering and ordination are commonly used to describe marine ecological data. Classification can be regarded as a hierarchical assignment of objects into groups and is either agglomerative or divisive. Clustering permits combination into groups of species, times, and locations. The results are presented in the forms of dendrograms for hierarchical methods and by partition for non-hierarchical methods. Ordination techniques reduce the dimensionality of the data sets and the variance is expressed by few component axes. The majority of the ordination techniques are based on 2 types of response models: a linear or monotonous and a unimodal Gaussian. Unfortunately, no specific techniques are available when the response curve is bimodal and for this reason new approaches and new methods for analysing ecological data are necessary. An awareness of these limitations is therefore important in choosing and correctly using the most appropiate statistical methods to test hypotheses and explore field results.

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The development of multivariate statistical techniques (ter Braak 1988a) allows the application of partially constrained ordinations, where by means of multiple linear regression it is possible to remove the signal and effects of covariables such as environmental parameters or spatial constraints. The method proposed by Borcard et al. (1992) was based on canonical correspondence analysis (CCA). This technique allows measurement of the amount of variation as a sum of canonical eigenvalues for the species matrix which can be explained by environmental variables. In most cases environmental variables alone are not able to fully explain the amount of variation observed in the species community structure. The need to compare sets of biotic and abiotic data with spatial coordinates or distance between the samples as suggested by ter Braak (1987) is extremely important for further understanding the concept of spatial hetereogeneity, which can be regarded as functional in ecosystems.

The spatial component of the community structure can be isolated from the species-environment component to detect if the environmental control model can explain the variation observed (May 1984). The application of this method to marine ecological data sets is presented here by considering the associated statistical problem of spatial autocorrelation across geographic space. The spatial autocorrelation of plankton communities can be used to quantify community dissimilarities (Mackas 1984). In this case space was used as an explanatory variable (Legendre & Fortin 1989). The results obtained by applying CCA and the Mantel and partial Mantel tests are reported here. These methods are suitable for extracting the relationship of species with the environment, taking into account the spatial component present in the data (Borcard & Legendre 1994).

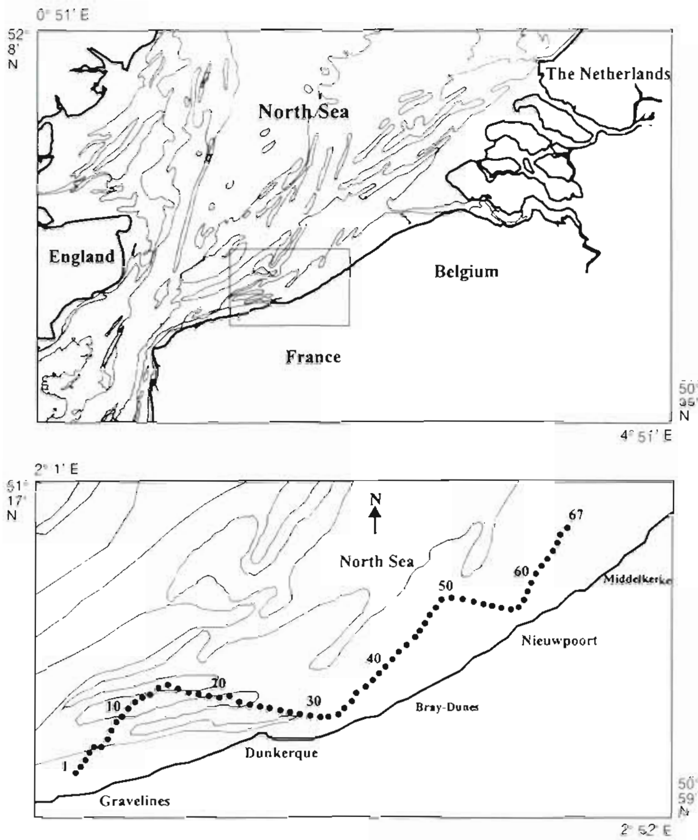

Fig. 1. Schematic map of the study area. Sampling transect along the coastline is presented by a dotted line

METHODS

Data. The sampling cruises were conducted on 10 and 21 June 1989 along a transect from Gravelines (France) to Middelkerke (Belgium), 35 nautical miles into the Southern Bight of the North Sea (Fig. 1) in connection with the research program RENORA founded by the PNDR (Programme National sur le Déterminisme du Recrutement, France). Temperature, salinity and water density were measured at 20 s intervals by a hydrological probe. Depth and corrected depth were measured on board by the Color Echo Sounder system (model Raytheon V800). For meroplankton, 64 and 67 samples, respectively, were collected during the 2 cruises at 3 m depth by a volumetric pump (PCM Moineau, 200 l min^{-1}). Each sample corresponded to 5 min continuous pumping. Samples were filtered on board using a 80 µm mesh size plankton net attached to the pumping system. Meroplankton samples were counted according to the method proposed by Frontier (1969, 1972). A list of environmental variables and names of taxonomic groups are reported in Table 1. The wind direction and velocity data were obtained from the meteorological station at Dunkerque (France).

Table 1. Taxonomic groups and environmental variables

Taxonomic group	Environmental variables
Lanice conchilega	Salinity (ppt)
Pectinaria koreni	Temperature (°C)
Magelona mirabilis	Density (kg m^{-3})
Polydora spp.	Corrected depth (m)
Nephtys spp.	Tidal height (m)
Ampharetidae	
Bivalves	
Echinoids	

Table 2. Each step of the 4 canonical correspondence analyses (CCA); • indicates the data matrix input, – indicates no input. Covariables were used in Steps (3) & (4)

CCA input	Species matrix	Covariables matrix	Environmental matrix	Spatial matrix
Step (1)	•	–	•	–
Step (2)	•	–	–	•
Step (3)	•	Spatial matrix	•	–
Step (4)	•	Environmental matrix	–	•

Numerical analysis. The data for the CCA were divided into 3 matrices: (1) species densities, (2) environmental variables and (3) geographic locations of the samples (spatial component). Following Legendre (1990), and Borcard et al. (1992), the geographic coordinates of the sampling locations were used to perform a cubic trend surface regression to ensure the extraction of more complex structures, such as patches, and not only the linear gradient pattern in the species matrix. The 3 data sets were analysed using CCA, with the spatial and the environmental matrices as covariables, alternatively (Table 2). Running 2 canonical ordinations constrained by a set of explanatory variables (covariables) allowed us to measure the impact on the species data of the effects of environmental conditions and of the spatial structure. With the awareness that in some cases the species and the environmental variables share the same spatial structure, the degree of variation in the species data owing to the spatial structure was partialled out by the use of covariables. The 4 steps in Table 2 represent the 4 fractions of the variations as suggested by Borcard et al. (1992). The p-values for each analysis were determined by a Monte Carlo permutation test. A Mantel test as proposed by Mantel (1967) and partial Mantel tests (Smouse et al. 1986) were computed to correlate and link the ecological structure with the spatial gradient present in the environment (Legendre & Troussellier 1988, Legendre & Fortin 1989). The 3 data matrices were transformed into distance matrices prior to these tests; euclidean distances among sampling locations were used to form the spatial distance matrix. The CANOCO program of ter Braak (1988b) was used for the CCA in conjunction with the Monte Carlo permutation test. The Mantel and partial Mantel tests were performed with the programs of the the R Package for Multivariate Data Analysis by Legendre & Vaudor (1991).

RESULTS

Spatial variation of the physical and biological data

The transport of water masses coming from the English Channel and entering the North Sea at Calais is greatly influenced by meteorological factors; the mean transport velocity can change from an estimate of 1 km d^{-1} for the English Channel to 5 km d^{-1} for the Dover-Calais strait (Pingree et al. 1975, Pingree & Maddock 1977, Prandle 1978). The general circulation pattern tends to be in the northeast direction, but the wind can change and reverse this general trend (Djenidi et al. 1986, Dewarumez et al. 1991). The first cruise on 10 June was characterized by a southwest wind with a mean wind velocity of 3.9 m s^{-1}. Wind conditions were reversed during the second cruise on 21 June with a northeast wind of mean velocity 5.3 m s^{-1}. The temperature distribution in Fig. 2A shows a clear input of warm water for the first cruise (18.70°C) at Stn 4, concomitant with Gravelines Power Station. The mean temperature value was 15.20°C. Under the influence of the southwest wind the colder water masses coming from the Dover-Calais strait can reach the Belgian coast as far as Middelkerke. The second

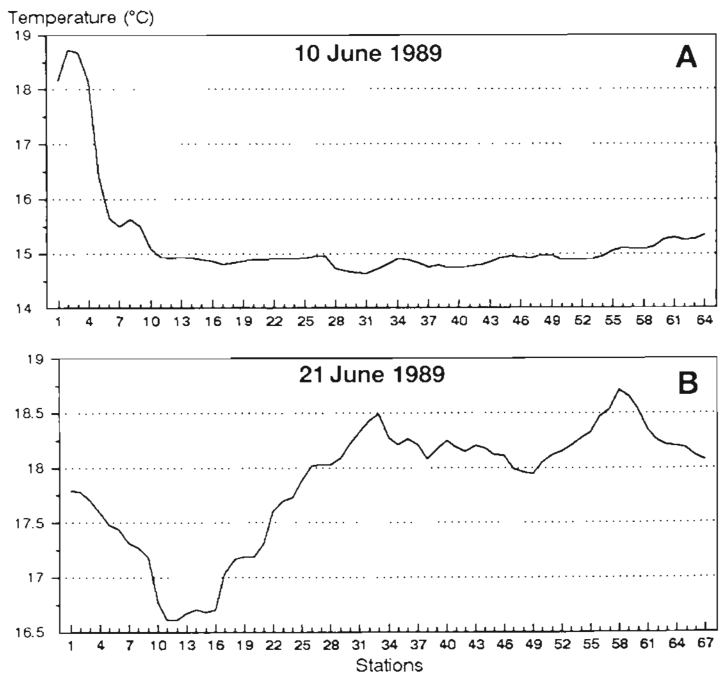

Fig. 2. (A) Temperature distribution for the first cruise shows an increase in temperature at Stn 4 (Gravelines Power Station), and the general lower temperature values coming from the Calais-Dover strait under the influence of the southwest wind. (B) Temperature distribution for the second cruise shows warmer water coming from the Belgian coast (Stn 67) reaching the coastal location (Stn 16) along the French coast under the influence of the northeast wind

cruise on 21 June (Fig. 2B) showed the effect of the northeast wind on temperature distribution; warmer water from the Belgian coast was transported southward, thus reaching the French coast. The mean temperature value was 17.85°C, decreasing to a minimum value of 16.65°C at Stn 11. The salinity distribution in Fig. 3A shows for the 10 June cruise the presence of 3 salinity fronts: one between Stns 2 & 7 of 0.6 ppt, which can be regarded as an anomaly due to the presence of the Gravelines Power Station; one between Stns 30 & 40 of 1.2 ppt; and one between Stns 52 & 60 of 1.4 ppt. The mean salinity value was 32.85 ppt. For the second cruise on 21 June (Fig. 3B), the salinity distribution showed the presence of 2 fronts: one from Stns 34 to 40 of 0.8 ppt, and one from Stns 48 to 52 of 0.5 ppt. The mean salinity value was 32.69 ppt. As an example of the spatial distribution of one of the meroplankton taxa, the density values of *Polydora* spp. are presented together with the temperature and salinity distribution. The adults of *Polydora* spp. were present in the macrobenthos as a distinct population, one characterizing the French coast (Souplet & Dewarumez 1980, Souplet et al. 1980), and one the Belgian coast (Daro & Polk 1973). The larval dispersion of these polychaetes under different wind conditions can bring changes in the spatial distibution and spatial structure of the population. The highest density values of *Polydora* spp. were found on 10 June (Fig. 4A) at Stn 4, with 160 ind. m^{-3}, concomitant with the highest temperature value of 18.7°C, and also at Stn 55, with 110 ind. m^{-3}. The larvae distribution in relation to salinity (Fig 5A) showed that higher densities were located before and after the salinity front (Stns 3, 4, 43, 55). For 21 June (Figs. 4B & 5B), the highest density value was found at Stn 58 with 2080 ind. m^{-3}, concomitant with high temperature values (18.6°C), and located after the salinity front. During this cruise the effect of the wind was apparent in that more larvae of *Polydora* spp. were transported south along the Belgian coast (Stns 67 to 50), reaching the French coast as far as Stn 25.

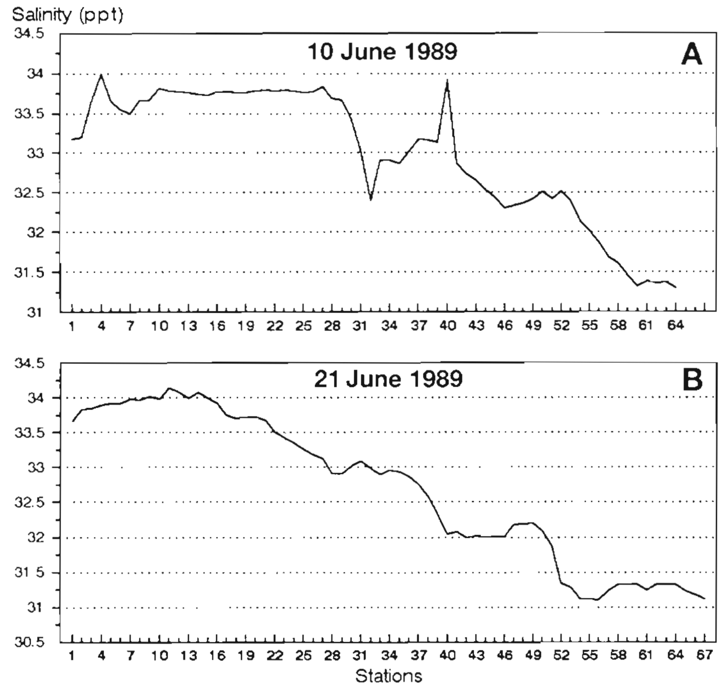

Fig. 3. (A) Salinity distribution for the first cruise shows the presence of salinity fronts between Stns 2 & 7 (Gravelines Power Station), 30 & 40, 52 & 60. (B) Salinity distribution for the second cruise shows the presence of 2 salinity fronts between Stns 34 & 40, 48 & 52; the effect of the northeast wind enhances the transport of less saline water coming from the Scheldt estuary and reaching the French coast

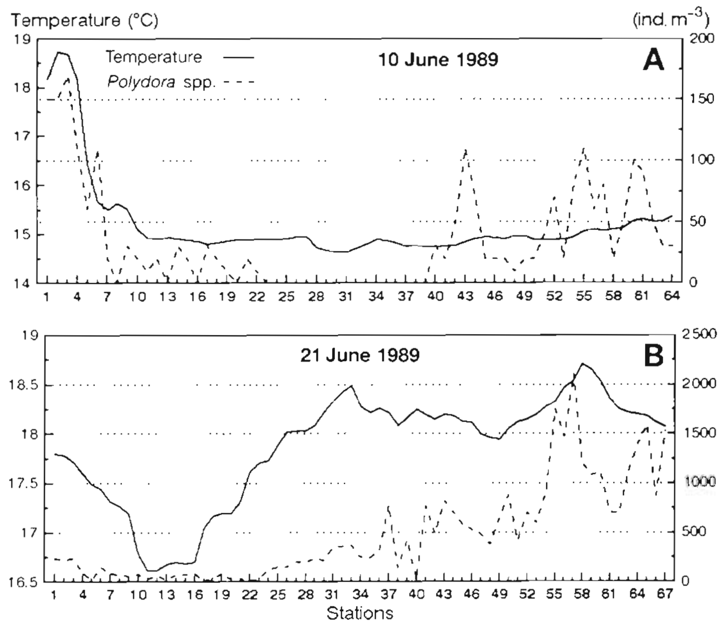

Fig. 4. *Polydora* spp. density distribution and temperature for (A) the first cruise shows 2 distinct populations, one from Stns 1 to 23 (French coast) and one from Stns 39 to 64 (French-Belgian coast), (B) the second cruise; due to the northeast wind more larvae are transported southward

Canonical correspondence analyses

The results of the 4 CCAs for each cruise are presented in Table 3. The percentage of the total variation of the species matrix accounted

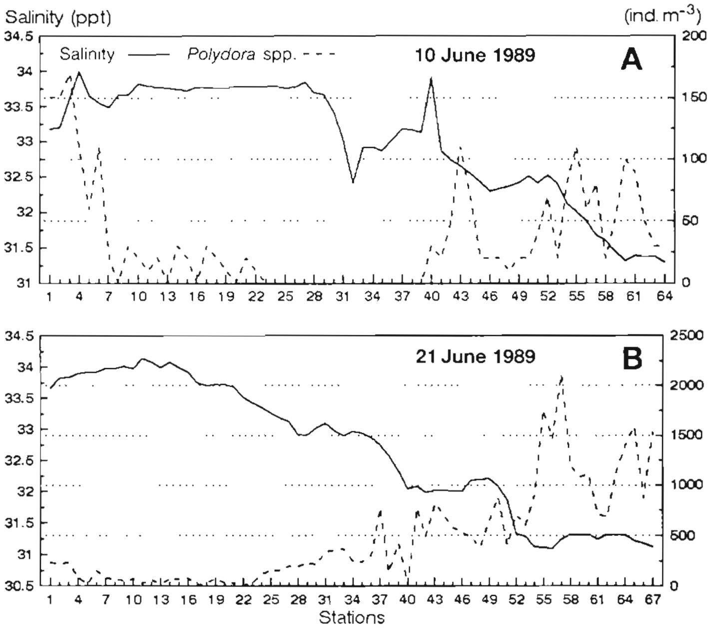

Fig. 5. *Polydora* spp. density distribution and salinity for (A) the first cruise, (B) the second cruise. Higher densities of larvae are found before or after a salinity front

for by each step of the analysis was obtained as suggested by Borcard et al. (1992) and Borcard & Legendre (1994). For the 10 June cruise (Fig. 6A), the whole variation of the species matrix was 67.3% and was explained in the following fractions: Fraction (a) representing the nonspatial environmental variation, accounted for 9.6% of the total variation; Fraction (b), which can be regarded as the spatially structured environmental variation, accounted for 42.6%; Fraction (c), representing the spatial species variation not shared by the environmental variables, accounted for 15.1% of the total variation, and Fraction (d), which can be regarded as the expression of the unexplained variation and the possible stochastic fluctuations, was equal to 32.7% of the total variation. Results for 21 June are presented in Fig. 6B.

The Monte Carlo permutation tests on the trace statistics for both sets of analyses were significant at a Bonferroni-corrected α' probability level of 0.05/4 = 0.0125. During the first cruise, the effect of the southwest wind maintained the general water circulation pattern along the coastal locations sampled, and mixing with water masses coming from the Scheldt estuary did not occur. During the second cruise, northeast wind conditions reversed the general trend of the water circulation pattern, inducing more mixing with the water masses coming from the Scheldt estuary. The change in environmental conditions resulted in an increase of Fractions (a) and (b) on 21 June. The variation in the species matrix due to the influence of the environment was 1.5% higher, and the influence of the environment together with the spatial component was 5.5% higher. The amount of the strictly spatial variation in Fraction (c) that remains unexplained by environmental variables was higher during the first cruise, suggesting that under the southwest wind condition the space component is stronger. In the reversed wind condition, Fraction (c) was reduced from 15.1% to 8.5%, showing the greater importance of changes in the environmental conditions rather than the purely spatial. The undetermined variation, Fraction (d), was very similar for both cruises, suggesting that this amount of variation can be regarded as the effect of local effects, such as short-term tidally induced variability and mesoscale changes in the residual current pattern. It is however very important that the results identify and quantify this information.

Table 3. Results of the canonical correspondence analyses (CCA) are reported as the amount of canonical inertia explained by the SE (species-environment matrices), SS (species-space matrices), SE/S (species-environment matrices constrained by the space matrix) and SS/E (species-space matrices constrained by the environment matrix). Total inertia indicates the sum of all unconstrained eigenvalues. The overall amount of explained variation as a percentage of the total variation of the species matrix for 10 June 1989 was 67.3%, obtained by summing Steps (1) & (4), or Steps (2) & (3), and partitioned as: (a) nonspatial environmental variation (Step 3): 9.6%; (b) spatially structured environmental variation (Steps 1 to 3 or Steps 2 to 4): 42.6%; (c) spatial species variation not shared by the environmental variables (Step 4): 15.1%; (d) unexplained variation and stochastic fluctuations: 100 − 67.3 = 32.7%. For 21 June 1989 the total explained variation was 67.7% and partitioned as: (a) 11.1%, (b) 48.1%, (c) 8.5%, (d) 32.3%

Date	SE	SS	SE/S	SS/E	Total inertia
10 June 1989	0.152	0.168	0.028	0.044	0.291
21 June 1989	0.634	0.607	0.119	0.091	1.07

Percentage of the variation

CCA 10 June 1989	CCA 21 June 1989
Step (1): 0.152 × 100/0.291 = 52.2%	Step (1): 0.634 × 100/1.07 = 59.2%
Step (2): 0.168 × 100/0.291 = 57.7%	Step (2): 0.607 × 100/1.07 = 56.7%
Step (3): 0.028 × 100/0.291 = 9.6%	Step (3): 0.119 × 100/1.07 = 11.1%
Step (4): 0.044 × 100/0.291 = 15.1%	Step (4): 0.091 × 100/1.07 = 8.5%
Total explained variation = 67.3%	Total explained variation = 67.7%

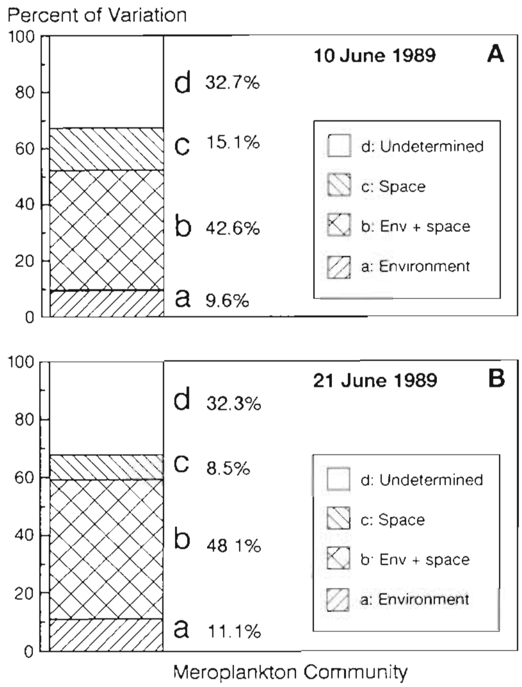

Fig. 6. (A) Variation partitioning of the meroplankton community data matrix for the first cruise. The whole variation of the species matrix is partitioned into 4 fractions: (a) nonspatial environmental, (b) spatially structured environmental variation, (c) spatial species variation not shared by the environmental variable, (d) undetermined variation and stochastic fluctuations. (B) Variation partitioning of the meroplankton community data matrix for the second cruise

Mantel and partial Mantel tests

The Mantel test among the 3 matrices considered (1) geographic distance, (2) environmental variables and (3) species for the 2 sampling dates, with the following correlations:

10 June 1989: $R_{1,2} = 0.498$ ($p < 0.001$)
$R_{1,3} = 0.389$ ($p < 0.001$)
$R_{2,3} = 0.512$ ($p < 0.001$)

21 June 1989: $R_{1,2} = 0.560$ ($p < 0.001$)
$R_{1,3} = 0.315$ ($p < 0.001$)
$R_{2,3} = 0.589$ ($p < 0.001$)

For both sets of calculations the null hypothesis (H_0) that the multivariate data are not autocorrelated as a gradient was rejected at the 1% significance level according to the test of significance in Mantel statistics (Mantel 1967, Legendre & Fortin 1989).

The partial Mantel tests for the 2 cruises gave the following correlations:

10 June 1989: $R_{1,2} = 0.377$ ($p < 0.001$)*
$R_{1,3} = 0.179$ ($p = 0.04592$) ns
$R_{2,3} = 0.398$ ($p < 0.001$)*

21 June 1989: $R_{1,2} = 0.488$ ($p < 0.001$)*
$R_{1,3} = -0.022$ ($p = 0.05612$) ns
$R_{2,3} = 0.524$ ($p < 0.001$)*

The partial Mantel tests for the 2 transects show that the computed partial correlation between the geography (space) matrix and the species (meroplankton) matrix ($R_{1,3}$) was non-significant (ns). The correlations between the geography (space) matrix and the environment ($R_{1,2}$), and between the environment and the species (meroplankton, $R_{2,3}$) were highly significant (*) at a Bonferroni-corrected α' probability level of 0.05/4 = 0.0125. This result shows that the structure in the meroplankton distribution comes from the structuring of the environmental variable. If we compare the 2 sampling cruises, the Mantel statistic describing the influence of the environment on the meroplankton community structure for the 10 June cruise is reduced from 0.512 to 0.398 when controlling for the effect of space, but remains very highly significant. The specific influence of the environment is therefore 0.398, while the difference of 0.254 ($0.498 \times 0.512 = 0.254$) can be regarded as the influence of the spatial structure imbedded in the environment on the species distribution. For 21 June, the Mantel statistic describing the influence of the environment on meroplankton was reduced from 0.589 to 0.524 when controlling for the effect of space. The influence of the environment of 0.524, and the difference of 0.329 ($0.589 \times 0.560 = 0.329$), correspond to the influence on the species distribution exerted by the spatial structure present in the environment. The Mantel and partial Mantel tests were in accordance with the results of the CCAs. The spatial gradient present in the environment can partly explain the variation we observed in the distribution patterns of *Polydora* spp. This shows that changes in the spatial structure of the environment do influence the meroplankton community structure. A more important point as proposed by Legendre & Troussellier (1988) is to interpret Mantel and partial Mantel tests in a causal framework. Following their models, the results above indicate that the environmental matrix has a significant effect on the species matrix, but there remains some significant yet unexplained spatial variation in the species data.

DISCUSSION AND CONCLUSION

The meroplankton community composition changes because of changes in ecological descriptors with reference to the environmental control model. Hudon & Lamarche (1989) suggested the importance of considering the physiographic characteristics of the study area in order to test the effects of climatic and hydrographic factors on the advection and survival of planktonic crustacean larvae. The effects of wind-driven water mass exchange on the distribution of pelagic organisms was tested by Christopher et al. (1987).

The results presented in this paper suggest the importance of considering *a priori* the presence of spatial autocorrelation in the data and to regard this as a departure point for any ecological research. As suggested by Mackas (1984), it is important to determine to what extent samples in different locations are dependent on their separation. The use of CCA offered the possibility to factor out the covariables, in this case environmental variables and the geographic distance between samples, in a partial ordination (ter Braak 1987), and to test the variation occurring between samples along a successional pattern (Palmer 1993). The inclusion of space in the form of a spatial distance matrix allowed quantification of the amount of variability associated with a precise spatial structure. This variability, expressed by the Fraction (c), can either be explained or not explained by the environmental variables considered, and can also suggest the importance of using other environmental variables to explain spatial variability. Species variability is not always related and controlled directly by the set of environmental variables chosen, but by other effects such as meteorological events or top-down ecological processes (Legendre 1990). The CCA associated with the Monte Carlo permutation test and the method proposed by Borcard et al. (1992) were found to be adequate for representing species environmental relationships, taking into account the spatial component, and for testing the significance on the environmental variables. In this canonical ordination technique the linear combination of the environmental variables that can account for the dispersion of the species score is more strongly expressed by the first axis. This method also performs well in the presence of skewed species distributions (Palmer 1993), and the arch effect present in other multivariate techniques is generally avoided (Økland 1986, Michin 1987).

The utility of CCA in respect to other ordination methods have been extensively discussed by several authors (ter Braak & Prentice 1988, Palmer 1993). In this study the use of the covariables and associated significance tests further extends the validity of this ordination technique. The concept of homogeneity in ecological communities on the basis of locations sampled can be explored by using CCA and the selected set of environmental variables as covariables. The use of Mantel and partial Mantel tests provided further useful information on the significance of spatial autocorrelation. The Mantel test for matrix correlation measured to what extent the variation in distance matrix A corresponded to the variation in distance matrix B. The partial Mantel test measured the level of correlation between matrices A and B, while controlling for the effects exerted by matrix C. The partial Mantel statistic can be regarded as causal modelling (Smouse et al. 1986, Legendre & Troussellier 1988), and used to predict, as in the present work, the possible effects of the environmental variables on the meroplankton community structure compared to the effect of space.

The presence of a spatial structure shared by the species community and the environment may, as suggested by Legendre & Troussellier (1988), overestimate the interaction occurring at different degrees of intensity between the species and the set of environmental variables measured. The method used, however, allowed us to quantify this kind of association and to give useful information in a more classical modelling approach. The Mantel and partial Mantel tests were used to remove the influence of environmental variables from classification in biological space, and to point out the importance of spatial and environmental structures within the system studied. The changes in wind conditions explained the possible transport of meroplankton in the opposite direction to the prevailing northeasterly residual tidal current (Belgrano et al. 1990), allowing for a southwesterly dispersal (Luczack et al. 1993). Monitoring the dispersal of meroplankton species at a pelagic level can be extremely useful as a biological tracer of water masses and as a quantifier of the availability of larvae to the adult benthic community in relation to recruitment processes.

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