

# Multivariate Approach to Study Species Assemblages at Large Spatiotemporal Scales: The Community Structure of the Epibenthic Fauna of the Estuary and Gulf of St. Lawrence<sup>1</sup>

P.-L. Ardisson and E. Bourget

*GIROQ, Département de biologie, Université Laval, Québec (Qué.) G1K 7P4 Canada*

and P. Legendre

*Département de sciences biologiques, Université de Montréal, C.P. 6128, Succursale A, Montréal (Qué.) H3C 3J7 Canada*

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We investigated hierarchical organization and spatiotemporal discontinuities in species abundances in the epibenthic community of the Estuary and Gulf of St. Lawrence. Quantitative samples were obtained from 1975 to 1984, on 161 collectors (navigation buoys) moored yearly from May through November. Maximum biomass values of the dominant species, common to all regions studied, were used to assess epibenthic community structure. Numerical methods were used to characterize spatial structure and temporal variability of the dominant assemblage. Spatially constrained clustering and ordination techniques revealed six broad biogeographic zones whose limits vary yearly. However, spatially unconstrained clustering and ordination techniques showed two major sets of non-contiguous localities, each characterized by a singular biotic structure. Further, spatial autocorrelation analyses showed a significant relationship between biomass and geographic distance. The resulting spatial structure of biomass was dependent on the species considered. The multidimensional Mantel technique showed an 8-yr period of variation in community structure at large (whole system, Gulf) and intermediate (North Shore plus Lower North Shore) spatial scales. The amplitude and asymmetry of this temporal cycle increased as the spatial scale decreased. In spite of the observed discontinuous spatial patterns, the temporal oscillations in community structure detected at different spatial scales suggest that the Estuary-Gulf system responds to the external input of auxiliary energy as an integrated system.

Une étude fut réalisée pour mettre en évidence l'organisation hiérarchique et les discontinuités spatiotemporelles dans les abondances d'espèces de la communauté épibenthique de l'estuaire et du golfe du Saint-Laurent. Des échantillons quantitatifs furent obtenus de 1975 à 1984 sur 161 collecteurs, mouillés de mai à novembre de chaque année. La biomasse maximale des espèces dominantes, communes à toutes les régions étudiées, fut utilisée pour évaluer la structure de la communauté épibenthique. Des méthodes numériques furent utilisées pour caractériser la structure spatiale et la variabilité temporelle de l'assemblage dominant. Des analyses de groupement et d'ordination avec contrainte spatiale ont montré six zones biogéographiques majeures dont les limites varient d'une année à l'autre. Cependant, des analyses de groupement et d'ordination sans contrainte spatiale révélèrent deux groupes majeurs de localités non contiguës, chacun caractérisé par une structure biotique singulière. Par ailleurs, des analyses d'autocorrelation spatiale ont montré une relation significative entre la biomasse et la distance géographique. Le type de structure spatiale qui en résulte dépend de l'espèce considérée. Le test multidimensionnel de Mantel a mis en évidence une période de variations de 8 ans dans la structure de la communauté, et cela à différentes échelles spatiales (système Estuaire-Golfe, Golfe, et Côte Nord-Basse Côte Nord). L'amplitude et l'asymétrie de ce cycle temporel varient inversement avec l'échelle d'observation. En dépit des discontinuités observées dans les patrons spatiaux, l'oscillation temporelle dans la structure de la communauté observée à différentes échelles spatiales suggère que le système Estuaire-Golfe répond aux apports externes d'énergie auxiliaire comme un système intégré.

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**O**ne aim of community ecology is to explain the patterns of natural assemblages of organisms. Patterns can be detected by making comparisons among features of natural communities, or between natural systems and logical or theoretical models of community structure (Wiens 1984). When

the first of these two approaches is considered, multivariate statistical methods allow us to analyse patterns in biotic data (species attributes/sites/times) and to relate biotic patterns to spatiotemporal environmental patterns (Field et al. 1987). In this context, understanding environmental variability and related population effects in a wide array of spatiotemporal scales has become a central point in community studies (Allen and Starr 1982; Brown 1984; Wiens 1984; Morris 1987). The spatial and temporal scales at which ecological systems are

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examined influence the patterns observed, the processes accounting for them as well as our perception of their stability (Legendre and Demers 1984; Brown and Maurer 1987; DeAngelis and Waterhouse 1987; Bourget 1988).

A scale-oriented approach to community structure follows logically from the hierarchical paradigm of complex ecological systems (Platt et al. 1981; Allen and Starr 1982; Ulanowicz and Platt 1985). According to this view, biotic structures are seen as a series of nested and non-nested mosaics in time and space where complexity comes from the nonlinearity and asymmetry of the interactions between biological entities and their environment. Kolasa (1989) suggests that species abundances reflect the relative size as well as the degree of fragmentation of the habitat used by a given species. In this hierarchical view, habitat fragmentation appears to increase as a function of increasing resolution. As a consequence, in hierarchical theories, processes occurring within each level of the hierarchy are considered to pertain to a higher holistic level that integrates the summary outcomes of many simultaneous processes (Ulanowicz and Platt 1985; Kolasa 1989).

Here, in order to determine the driving processes controlling the spatial and temporal patterns of variability of the marine epibenthic invertebrate community of the Estuary and Gulf of St. Lawrence, we analyse the structure of the benthic assemblages at several levels of resolution in time and space. We examine whether different levels of organization do exist in these benthic assemblages and if the entire system behaves as a continuous and stable entity. An effort was made to determine spatial patterns for single species as well as for assemblages of species. In addition to revealing spatio-temporal patterns, the complementary use of different numerical methods allowed an assessment of the appropriateness of the individual techniques used as well as the robustness of the structures revealed by each method. Patterns are interpreted in the light of the dynamics of dominant species and hydrodynamic processes. The yearly spatial structure was studied at a large scale (Estuary and Gulf). The temporal variability of the spatial structures was analysed at large and intermediate (regional) spatial scales during 10 yr, from 1975 to 1984. At these spatial and temporal scales, changes in the biomass structure of the dominant assemblage is used as the key element. Through these changes, the existence of significant discontinuities in community structure between localities and over time was revealed and consequently, biogeographic patterns were found.

## Materials and Methods

### Data

The spatio-temporal variations in structure of the dominant epibenthic assemblage of the Estuary and Gulf of St. Lawrence were studied from 1975 to 1984 (except in 1978 and 1979), on 161 collectors (navigation buoys) moored by Transport Canada from May through November of each year (Fig. 1). Abundance data are biomasses of the five dominant species, those common to all regions in the study. This assemblage is composed of the following sessile species: the hydroid *Obelia longissima* (Pallas), the bivalves *Hiattella arctica* (L.) and *Mytilus edulis* (L.), and the cirripedes *Semibalanus balanoides* (L.) and *Balanus crenatus* (Bruguière). Since the buoys are moored and retrieved in a short lapse of time (about 2 wk) each year, their use allowed us to obtain samples on a large spatial scale without introducing seasonal differences in the abundances of species

among the regions considered. For a more detailed description of the advantages of navigation buoys as collectors, see Fradette and Bourget (1980, 1981).

### Field and Laboratory Procedures

After retrieval of the buoys in November, the organisms attached to their surface were preserved due to the freezing air temperature. Shortly after the buoys arrived in the port of Québec, the attached invertebrate fauna was sampled following the methods of Fradette and Bourget (1980). Quantitative samples of 0.01 m<sup>2</sup> were obtained from the area of maximum biomass on each buoy, for each one of the five dominant species. The sites of maximum biomass were determined by visual inspection. Since the species distributions on the buoys are most often patchy, sampling the community in the areas of maximum biomass is the easiest way of obtaining data that are comparable among buoys. The only alternative would have been to randomly select a large number of quadrats on each buoy, which would have generated an unmanageable number of samples. Biomass was used as an indicator of abundance because, as stated by Field et al. (1982), colonial animals cannot meaningfully be counted, whereas all organisms can be expressed in units of mass.

All specimens were sorted, identified, and fixed in formalin (4%). The wet weight of each species was obtained after a 5-min drying period on blotting paper. The dry weights were calculated using the wet weight to dry decalcified weight conversion indices estimated by Fradette and Bourget (1980): *O. longissima* 0.18, *H. arctica* 0.17, *M. edulis* 0.09, *S. balanoides* 0.07, and *B. crenatus* 0.06.

### Numerical Analyses

In order to identify the spatial structure of the community yearly, each year's biomass data were assembled into a multivariate data matrix (locations × species) which excluded sampling stations with zero biomass values for all species. Departures from normality were tested for each biomass variable by means of the non parametric Kolmogorov-Smirnov test, using corrected critical values calculated by Lilliefors (1967). Normality of data was achieved using the Box-Cox method (Sokal and Rohlf 1981). The asymmetric form of the Gower (1971) coefficient of similarity (S19 in Legendre and Legendre 1984) was then used to compute pairwise similarities among all stations. In addition to excluding joint absences, this similarity measure weighs all species equally in the analysis, irrespective of their absolute range of variation in the samples. From these resemblance matrices, spatially unconstrained clustering and scaling (ordination) techniques were used in conjunction with spatially constrained ones, after testing for the presence of spatial autocorrelation in the data.

### Spatial autocorrelation analyses

Ecological systems are structured in space, either by forcing environmental variables or by the biological activity itself. These departures from randomness in the spatial distribution of ecological values are called spatial autocorrelation. The presence of spatial autocorrelation in data can be statistically assessed using, for instance, the Mantel test, and the shape of the spatial autocorrelation structure can be described by structure functions such as the Moran correlogram (Legendre and Fortin 1989).

We tested for the presence of spatial autocorrelation in the multivariate data by means of the Mantel test (Mantel 1967;

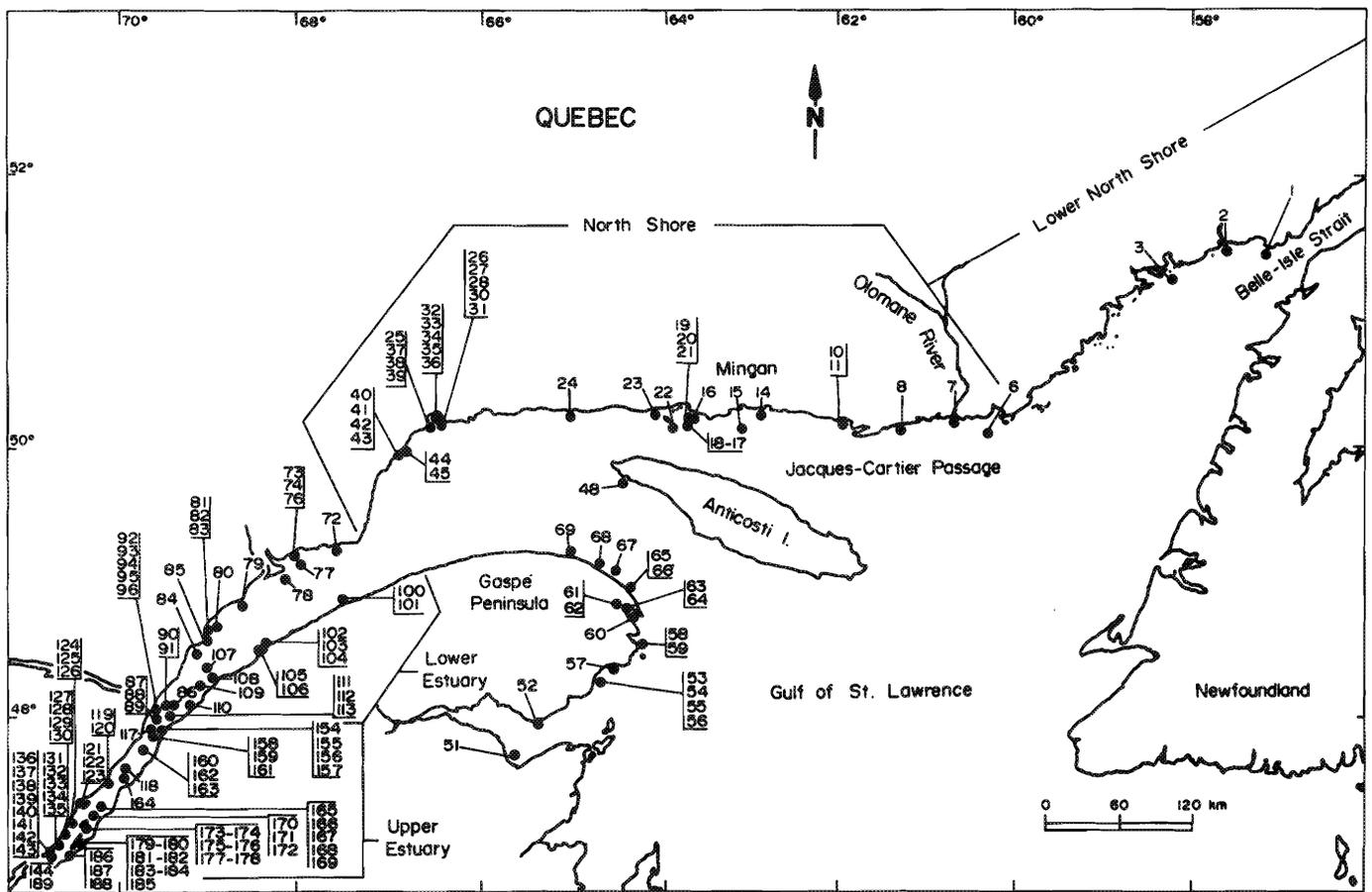


FIG. 1. Position of the sampling stations in the Estuary and Gulf of St. Lawrence.

Sokal and Thomson 1987; Legendre and Fortin 1989). Mantel tests were carried out between (1) the matrix of geographic distances among stations (buoys) and (2) matrices of similarity (converted into distances  $D = 1 - S$ ) among stations based on the species biomass data, as described above. The null hypothesis was that of independence of the distances in the two matrices. In each yearly test, the normalized Mantel statistic  $r$  was tested by randomization. In order to study the persistence of a spatial ecological structure through time, the results of the simple Mantel tests, computed on a yearly basis during the period 1975–84, were assembled in a single graph of Mantel statistics  $r$  vs. time. The overall significance of these values were tested using the Bonferroni method of correcting for multiple tests (Cooper 1968; Miller 1977).

Spatial autocorrelagrams (Sokal and Oden 1978; Sokal and Thomson 1987; Legendre and Fortin 1989) were computed to demonstrate the presence of spatial patterns in the dominant species taken one by one. Moran's  $I$  coefficient was used to describe the spatial autocorrelation of the species biomass as a function of distance. Geographic distances among buoys were divided into classes for this analysis. Individual spatial autocorrelation coefficients were tested in the conventional manner, using standard errors based on the expectations of their moments (Cliff and Ord 1981). The graph of Moran's  $I$  coefficients against distances is called a correlogram. Its overall significance was tested by the Bonferroni technique (Oden 1984). Spatial autocorrelation was analyzed for each of the five dominant species, both on a yearly basis and on average values representing the overall period 1975–84. Two spatial scales

were considered: the whole system, and the Estuary and Gulf regions taken separately.

#### Clustering and scaling analyses

UPGMA clustering (Rohlf 1963) was used to group localities with similar biotic structures. UPGMA was preferred to other agglomerative hierarchical methods because it gave the highest correlation between the original similarities and the cophenetic matrix (similarities implied by the dendrogram). Only the groups with similarities greater than 0.50 were retained for study. The matrix of Gower's distances among samples was also subjected to a principal coordinates analysis (Gower 1966). The principal coordinates method was chosen as the scaling (ordination) method instead of principal component analysis because of the existence of many zeros in the matrix entries. To determine the species contributing most to the formation of the reduced space, Kendall correlations were computed to relate the first two principal coordinate axes with the biomass of each of the dominant species in turn. The UPGMA-clustering results were plotted in the space of the first two principal coordinates to help interpret relationships among groups. Clustering and scaling analyses were carried out on a yearly basis at the large geographic scale (whole system).

The chronological clustering technique of Legendre et al. (1985) was used to identify significant discontinuities in structure in the multivariate spatial series of the dominant assemblage. Although the chronological clustering method was originally conceived as a time-constrained method, it can be used as a space-constrained method as well, provided that the spatial data form a one dimensional series (Galzin and Legendre 1987).

Space constraint, in this context, means that only those samples that are contiguous along the spatial series are allowed to cluster (see Discussion: Biogeographic Patterns). The level of connectedness of the proportional-link linkage algorithm was set to 75%. In this method, a randomization test procedure is used at each clustering step to determine whether or not two objects or groups should be allowed to cluster; the statistical criterion for rejection of the null hypothesis was relaxed progressively in three steps ( $\alpha = 0.15, 0.20, 0.25$ ) to test for successively less significant clusters. These connectedness and significance levels provided the best representation of the biotic structure at the large and intermediate spatial scales.

Because of the difficulty of establishing a sequential series of stations in two diverging directions, that would have included the Estuary and Gulf regions in the same analysis, only the spatial series of data from sampling collectors moored along the Gulf of St. Lawrence shores, ordered counter-clockwise, were submitted to this analysis. Since the sampling stations were not ordered along a real transect, but were positioned irregularly alongshore (Fig. 1), the counter-clockwise sequence was of interest at large and intermediate spatial scales but irrelevant at a scale of tens of kilometres. The theoretical model of succession upon which this spatial clustering analysis is based involves larval dispersal of benthic species, parallel to the coast, following the circulation patterns of the surface layer of the Estuary and Gulf of St. Lawrence (El-Sabh and Johannessen 1972; El-Sabh 1976). This form of clustering was applied both on a yearly basis within the period 1975–84, and on average values throughout years.

A complementary approach used to confirm the importance of the discontinuities in community structure was to perform a constrained ordination on the resemblance data matrix. Geographic information was used to constrain the output of an unconstrained scaling program, using the method proposed by Legendre (1987). The question to be answered by such a method is the following: when forced to obey the geographic contiguity constraint, do the community data still produce a gradient? In other words, is the underlying biological structure continuous, when considering the geographic arrangement of stations? This was done by computing  $C = A + wB$ , when  $A$  and  $B$  were, respectively, an ecological and a geographic distance matrix among stations,  $w$  was a scalar weight (ranging between 0 and 1) and  $C$  was the new spatially constrained distance matrix. A nonmetric multidimensional scaling analysis (Shepard 1962, 1966; Kruskal and Wish 1978) was then performed in the conventional manner for different values of  $w$ , and the result was selected which had the smallest value of  $w$  and in which all clusters were still internally contiguous ( $w = 0.01$ ). This method could also be used to obtain constrained clusters from unconstrained clustering programs. Because this algebraic operation on the resemblance matrix does not change the Euclidean property of the distance matrix, principal coordinates analysis could have been used to obtain a constrained ordination. However, nonmetric multidimensional scaling (NMDS) was preferred here because, according to Gower (1966), when distances are Euclidean, NMDS permits summarization of distances in a smaller number of dimensions than principal coordinates analysis.

Once the spatial discontinuities in community structure were established, the Kruskal–Wallis one-way analysis of variance was used to test the heterogeneity of means among biogeographic zones for each of the dominant species. Since the species had been used to delineate the biogeographic zones, sig-

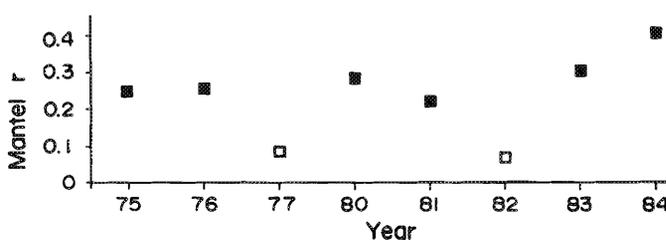


FIG. 2. Mantel statistics across years, for spatial variation patterns between two distance matrices (geographic and ecological) referring to the same collectors. The abscissa shows time in years. Ordinate: normalized Mantel's statistic  $r$ . Solid squares: Mantel tests significant at the Bonferroni-corrected probability level of  $(0.05/8 = 0.00625)$  for an overall significance level of 0.05 over 8 simultaneous tests. Open squares: non-significant values.

nificant Kruskal–Wallis results have to be interpreted as measures of species contribution, and not as strict significance tests.

### Temporal variability analysis

The spatial methods described above could, as a last resort, also reveal the temporal variability trends because the spatial structure was analyzed year by year. This would, however, produce a rather rough picture. A simpler and more elegant way to describe temporal variability is to compare pairs of similarity matrices by means of the Mantel test, where each matrix represents the structure of the dominant assemblage for a particular year. The null hypothesis tested here is the independence of the elements in the two matrices. When the output of pairwise computations among all possible combinations of resemblance matrices from different years are summarized in a square matrix form, two different analyses are then possible: (1) examination of community evolution from year to year, selecting the values on the subdiagonal that correspond to consecutive years (e.g. 1975–76, 1976–77, and so forth); or (2) examination of the overall variability structure from the period 1975 to 1984 by considering the  $r$  values of the whole matrix. Both of these avenues were investigated. (1) Single  $r$  values for consecutive years were assembled in a single graph of Mantel's statistics against time. The overall significance of these values was tested using the Bonferroni technique. (2) On the other hand, the overall matrix of Mantel statistics values, tested for overall significance using the Bonferroni technique, was subjected to a principal coordinate analysis in order to represent the yearly variability in a two-dimensional space, and to a UPGMA clustering analysis in order to show the similarity relationships among years. Temporal variability analyses were carried out at large and intermediate (regional) scales.

## Results

### Spatial Autocorrelation in Data

Results of the Mantel tests (Fig. 2) showed positive and highly significant correlations between ecologic and geographic distance matrices for all years, except in 1977 and 1982. Positive correlations for particular years mean that similarity in biomass structure among sampling stations decreases as geographic distance among these same sampling stations increases, i.e. that there is a significant spatial dependency of biotic resemblance with distance.

The yearly spatial patterns of single species (not shown) were, however, highly variable and hard to characterize. Since

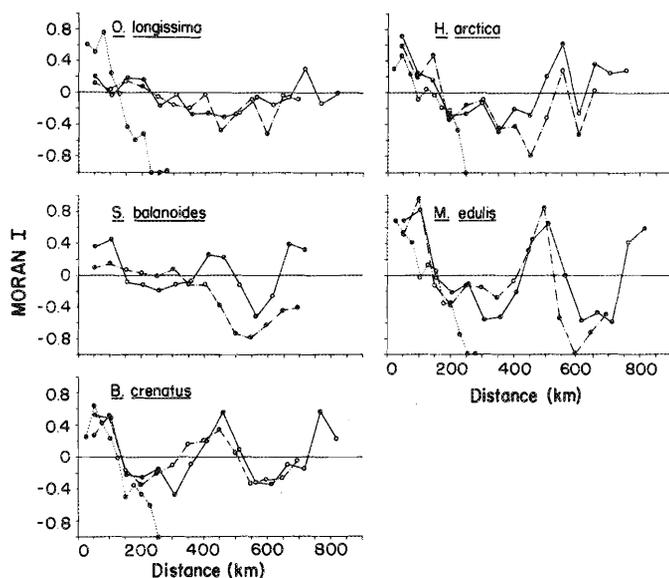


FIG. 3. Correlograms of geographic variation patterns of biomass of the five dominant epibenthic species of the Estuary and Gulf of St. Lawrence. Abscissa: distance in km. Ordinate: Moran's autocorrelation coefficient  $I$ . — whole system (Gulf and Estuary); - - - Gulf; ..... Estuary. Significant autocorrelation coefficients ( $P \leq 0.05$ ) are indicated by solid circles. All correlograms shown are significant at the overall significance level  $P = 0.05$ .

no definite trends across years were observed, the spatial patterns of single species were summarized by computing correlograms on average values representing the entire period of study (Fig. 3). Rules for interpreting spatial correlograms are provided by Sokal (1979) and by Legendre and Fortin (1989). The correlogram for *Obelia longissima* (Fig. 3) showed, at the whole system scale, a weak gradient. This spatial pattern displays only the irregular decline from positive autocorrelation at 50 km to negative autocorrelation at 450 km. Likewise at the Gulf scale, only this irregular decline from positive to negative autocorrelation values was found. The correlograms for *Hiatella arctica*, *Semibalanus balanoides*, *Mytilus edulis*, and *Balanus crenatus* (Fig. 3), on the other hand, were characterized by a patchy structure both at the whole system and at the Gulf scales. Distances between patch centers are given by the distance where the second positive peak in  $I$  values occurs, as demonstrated by Legendre and Fortin (1989). Although not quite constant, that distance was approximately 400–500 km for these species. Because of the limited spatial distribution and lower abundance in the Estuary of the species that are normally dominant, only the 1983 correlograms (except for *S. balanoides*) are shown in Fig. 3 for that region. All these species showed a well-established cline from significant positive autocorrelation at 25–100 km to significant negative autocorrelation at 150–250 km. Although this method of analysis cannot show the directionality of the spatial variation pattern (for a directional spatial autocorrelation method see Oden and Sokal 1986), because of the particular configuration of the study area, the autocorrelation values for greater distances necessarily corresponds to sites located near the tips of a diagonal axis oriented northeast–southwest (see Fig. 1).

#### Spatial Discontinuities in Community Structure

The yearly UPGMA clusters obtained at similarity values ( $S$ )  $\geq 0.57$  are represented in Fig. 4. Although the scatter dia-

grams of stations in the reduced space formed by the first two principal coordinate axes were highly variable on a temporal basis, no trends in dispersal patterns for individual years were found. Two major groups of stations can be identified based on spatial discontinuities in the yearly biotic data. The first group (Fig. 4, A-1 to H-1), formed at  $S = 0.57$ – $0.77$ , consisted mostly of stations from the Lower North Shore, the Eastern North Shore (stations 6–14), the Mingan Islands region, the Anticosti Island (one station) and the Lower and Upper Estuary. The second group (Fig. 4, A-2 to H-2) formed at  $S = 0.60$ – $0.74$ , consisted mostly of stations from the Western North Shore (stations 24–45) and the Gasp  Peninsula. Except for the stations from the Lower North Shore that always grouped into the first cluster (A-1 to H-1), stations from other regions could not be entirely associated to a particular cluster during the overall period of study. Analysis of secondary clusters formed at higher similarity levels did not improve the structure outlined above. When clustering envelopes are ignored and more attention is paid to the overall dispersal of stations in the reduced space, it can be seen that stations formed a gradient along axis I whose sequence from negative to positive values was: (1) Gasp  Peninsula, (2) Western North Shore, (3) Eastern North Shore, (4) Lower Estuary, Mingan Islands region and Lower North Shore in a variable order and (5) Upper Estuary. However, only the stations from the Lower North Shore could clearly be discriminated along axis II when viewed from positive to negative values. Furthermore, during the whole period of study, the first principal axis was strongly and negatively correlated with *M. edulis* and *B. crenatus*, while the second principal axis was strongly and negatively (except in 1981, 1983, and 1984) correlated with *O. longissima* (Table 1). These correlation coefficients cannot be tested for significance because the principal coordinates are derived from these five species abundance data.

The annual spatially constrained clusters for the period 1975–84 are shown in Fig. 5. The most fundamental breaks occur at the probabilistic clustering criterion value  $\alpha = 0.15$ . Relaxation of the probability level from  $\alpha = 0.15$ – $0.25$  has a magnification effect that may allow finer structures to emerge. At  $\alpha = 0.20$  some homogeneous clusters were split into lesser ones. For example, the cluster formed by stations 3–45 which emerged at  $\alpha = 0.15$  in Fig. 5C, was partitioned in four smaller clusters when viewed at  $\alpha = 0.20$ . However, not all of these new clusters are of ecological interest. Clusters like 25–30, 31–41, and 42–45 in Fig. 5C were formed at a very small spatial scale whereas stations were not ordered in a real spatial sequence. Varying the clustering criterion from  $\alpha = 0.20$ – $0.25$  (not shown) essentially yielded the same clusters. At this last probability level, the singleton character of station 7 was confirmed in 1983, as well as for station 24 during 1981, 1983, and the whole period 1975–84. Group expansion tests (GET) (Legendre et al. 1985) showed that the clustering structures observed are actually a continuum that could grow in many of its parts by incorporating spatially adjacent stations. Three fundamental breaks persisted, however, throughout the years. These break points occurred between stations 23 and 25 (24 is a singleton), 45 and 69, and in 1984 between 58 and 57 (Fig. 5H). The *a posteriori* tests (Legendre et al. 1985) showed groups that would have merged in a single cluster if the spatial constraint had not existed. On the other hand, the precise location of the break points was highly variable across years (see Fig. 5, A–H). Nevertheless, the most distinct groups from these year-by-year analyses are the following: stations 1–7 (from the Belle-Isle Strait to the mouth of the Olomane river), stations 1–14 (Lower

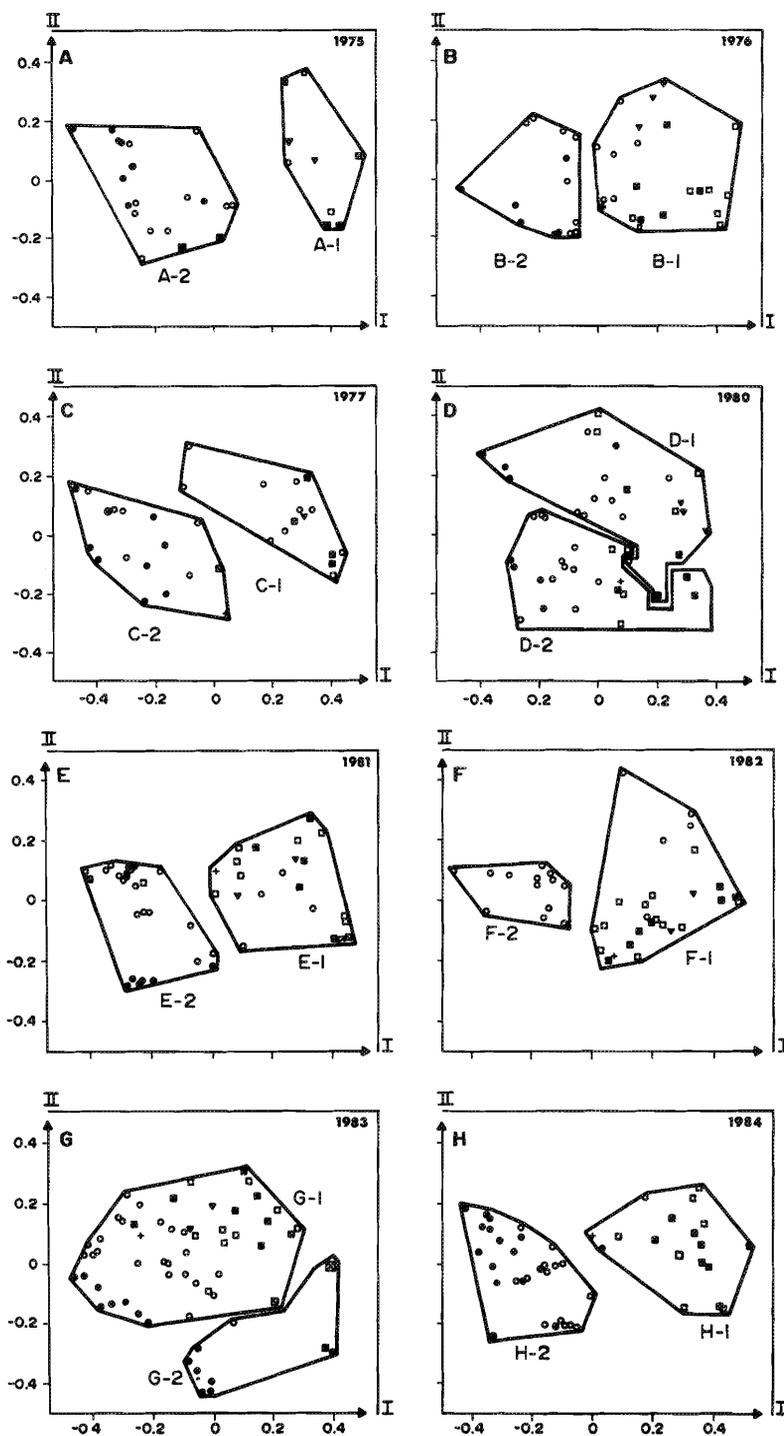


FIG. 4. Scatter diagrams of sampling sites in the reduced space formed by the first two principal coordinates of each analysis. Envelopes represent groups obtained by UPGMA clustering at  $S \geq 0.57$ . A to H are yearly analyses from 1975 to 1984 (except 1978 and 1979). Symbols represent collectors from the different sampling regions;  $\nabla$ , Lower North Shore;  $\circ$ , North Shore;  $\blacksquare$ , Mingan Islands;  $\bullet$ , Gaspé Peninsula;  $+$ , Anticosti Island;  $\square$ , Lower Estuary (north coast);  $\square$ , Lower Estuary (south coast);  $\square$ , Upper Estuary.

North Shore plus Eastern North Shore), stations 1–23 (from the Lower North Shore to the Mingan Islands region), stations 1–45 (Lower North Shore plus North Shore), stations 69–58 (the Northeastern Gaspé Peninsula, coalesced with stations from the Western North Shore in 1976, 1980, and 1981), and stations 57–52 (the Southeastern Gaspé Peninsula, coalesced with remaining stations of the Gaspé Peninsula in 1976–77). This

picture shows a fluctuating structure that expands or shrinks by incorporating or dropping spatially-adjacent stations from one year to the next. Figure 5I, computed from average values, summarizes the representative structure for the entire period. Five major clusters are revealed: (1) stations 1–14 (Lower North Shore plus Eastern North Shore), (2) stations 15–23 (Mingan Islands region), (3) stations 25–45 (Western North Shore),

TABLE 1. Kendall correlation values between biomass of single dominant species and principal coordinate axes I and II.

Year	Species									
	<i>O. longissima</i>		<i>H. arctica</i>		<i>S. balanoides</i>		<i>M. edulis</i>		<i>B. crenatus</i>	
	I	II	I	II	I	II	I	II	I	II
1975	0.39	-0.77	-0.28	-0.04	-0.26	0.05	-0.77	-0.01	-0.54	0.03
1976	0.32	-0.94	-0.32	-0.13	-0.33	0.33	-0.93	-0.27	-0.84	0.21
1977	0.01	-0.56	-0.58	0.00	-0.52	0.37	-0.90	-0.02	-0.56	0.36
1980	-0.01	-0.85	-0.40	-0.17	0.14	-0.01	-0.93	-0.03	-0.40	0.39
1981	-0.41	0.63	-0.56	-0.01	-0.19	0.11	-0.82	-0.04	-0.34	-0.22
1982	-0.78	-0.19	-0.63	0.21	-0.47	0.33	-0.58	0.34	-0.44	0.56
1983	-0.68	0.32	-0.55	0.10	-0.34	0.19	-0.65	-0.36	-0.65	-0.22
1984	-0.28	0.80	-0.16	0.16	-0.14	-0.21	-0.92	0.02	-0.35	-0.02

(4) stations 69–65 (Northeastern Gaspé Peninsula and, (5) stations 63–52 (Southeastern Gaspé Peninsula). According to the Group Expansion Test (GET), when the structure created by the chronological clustering procedure is destroyed and each one of the previous groups formed are allowed, in turn, to expand, the first two clusters (1 and 2) and the last two (4 and 5) could, respectively, be merged together, reducing in this way the spatial structure to three sharply different regions representing clearly differentiated and non-overlapping subseries. Therefore, these reduced clusters are (1) stations 1–23 (Lower North shore up to the Mingan Islands), (2) stations 25–45 (Western North Shore) and (3) stations 69–52 (Gaspé Peninsula).

Spatially constrained nonmetric scaling analyses (Fig. 6) were performed in two dimensions, with a resulting stress varying between 0.043 and 0.125, depending on years. The scalar weight  $w$  chosen to constrain the starting matrix for the scaling analysis was sufficiently small ( $w=0.01$ ) that the geographic data did not receive an undue weight in the matrix operation  $C = A + wB$ ; it was just large enough to allow neighbouring stations to be together in the ordination. The NMDS technique, unlike spatially constrained clustering, was performed on a resemblance matrix containing all sampling stations, including the Estuary and Anticosti stations (Fig. 6, A–H). The NMDS results are in keeping with those of the spatially constrained clustering analysis. There is, however, a fundamental difference between these two techniques that may obscure the results. In the clustering analysis, the spatial constraint concerns immediate neighbours only, while in the scaling analysis the geographic constraint implies all pairwise distance relationships among stations. For that reason, drawing the constrained clusters in the constrained NMDS space would not be useful to the interpretation of relationships among clusters.

Synthesizing the constrained clustering results on average values (Fig. 5 I) and those of the constrained scaling (Fig. 6, A–H) shows that the spatial epibenthic structure during the entire period of study is characterized by six major "biogeographic zones" (Fig. 7). These are: (1) Lower North Shore plus Eastern North Shore (stations 1–14), (2) Mingan Islands (stations 15–23), (3) Western North Shore (stations 25–45), (4) Northeastern Gaspé Peninsula (stations 69–65), (5) Southeastern Gaspé Peninsula (Stations 63–52) and, (6) Lower Estuary plus Upper Estuary, from Pointe-des-Monts (station 72) to the south of Ile aux Coudres (station 171). No secondary subseries could be discriminated in the Estuary region. The Kruskal–Wallis analysis of variance showed very highly significant ( $P<0.001$ ) heterogeneity of means among these "biogeographic zones", both for total biomass and for biomass of each of the dominant species (Table 2). This test must be read simply as an indication of the strength of the observed differences, since it is obviously improper to test a classification criterion (here: the six regions) against the very data that gave rise to it by clustering. Even with an independent classification criterion dividing the study area into regions, spatial autocorrelation in the species abundance data could have led to significant results in the analysis of variance, even in the absence of discontinuities in the data (Legendre et al. 1990).

Temporal Variability

The analyses of temporal variability of the dominant epibenthic assemblage were carried out on a set of matrices similar to the one represented in Fig. 8. These matrices were computed for each of the spatial scales examined. The graphs of Mantel statistic values across years, at large and intermediate (regional) spatial scales, are shown in Fig. 9. Mantel tests showed positive and highly significant correlations between the epibenthic biomass structure of consecutive years during the period 1975–84, at all three spatial scales considered. The degree of resemblance between consecutive years, however, was not constant throughout the period of study. Changes in resemblance seem to obey a periodic fluctuation of about 8 yr, whose amplitude increases as the spatial scale decreases. The period of study, however, was not long enough to determine the extent of the cycle of variation more precisely. The total variability of the Mantel matrices, corresponding to the same three spatial scales, is represented in Fig. 10. The dispersion pattern of years in the reduced space of the first two principal coordinate axes confirms the existence of a cycle of variation in biomass structure during this period at all three spatial scales. Dendrograms in this same figure illustrate the finer relationships of similarity among years. These results are in conformity with those of the dispersion diagrams (same figure) as well as the Mantel results in Fig. 9.

#### Temporal Variability

Discussion

Spatial Structure of Biomass

Overall, the spatial autocorrelation analyses (Fig. 2 and 3) showed a significant relationship between biomass and space. In the multivariate mode, the spatial affinity in community structure decreased with increasing geographic distance. A change from a coarse to a finer scale of examination resulted in a more complex picture of the spatial distribution of biomass,

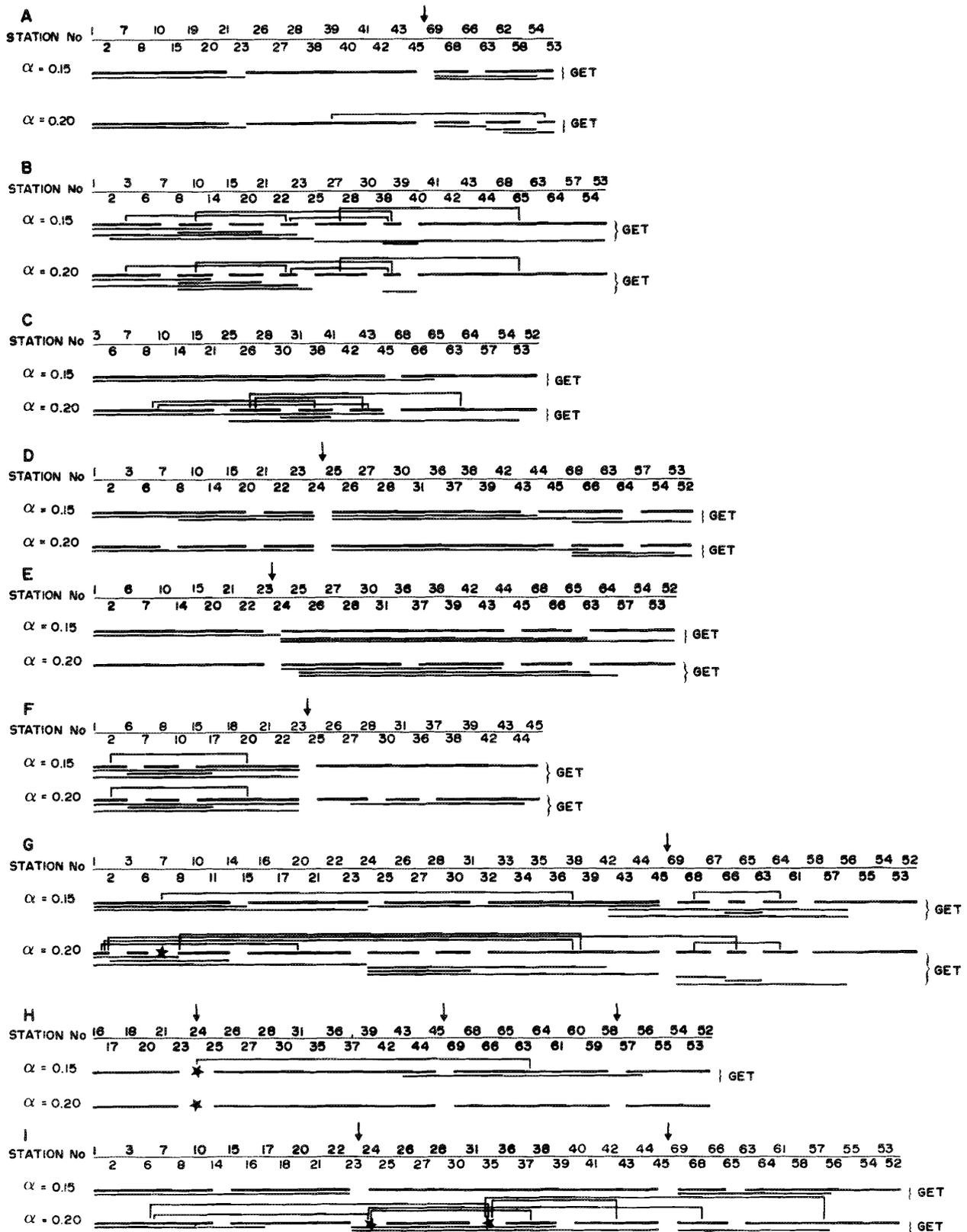


FIG. 5. Spatially constrained clustering of buoys based on the biomass data of species. Abbreviations and symbols: A to H, yearly clustering diagrams from 1975 to 1984 (except 1978 and 1979); I, clustering diagram on average biomass values for the entire period of study; heavy horizontal lines, clusters of biomass data from contiguous stations; GET, group expansion tests; horizontal brackets, *a posteriori* tests with probability of fusion greater than  $\alpha$ ; vertical arrows, most important breakpoints in the data series; stars, singletons; stations 1-3, the Lower North Shore; stations 6-45, the North Shore; stations 15-23, the Mingan island region; stations 69-52, the Gasp  Peninsula.

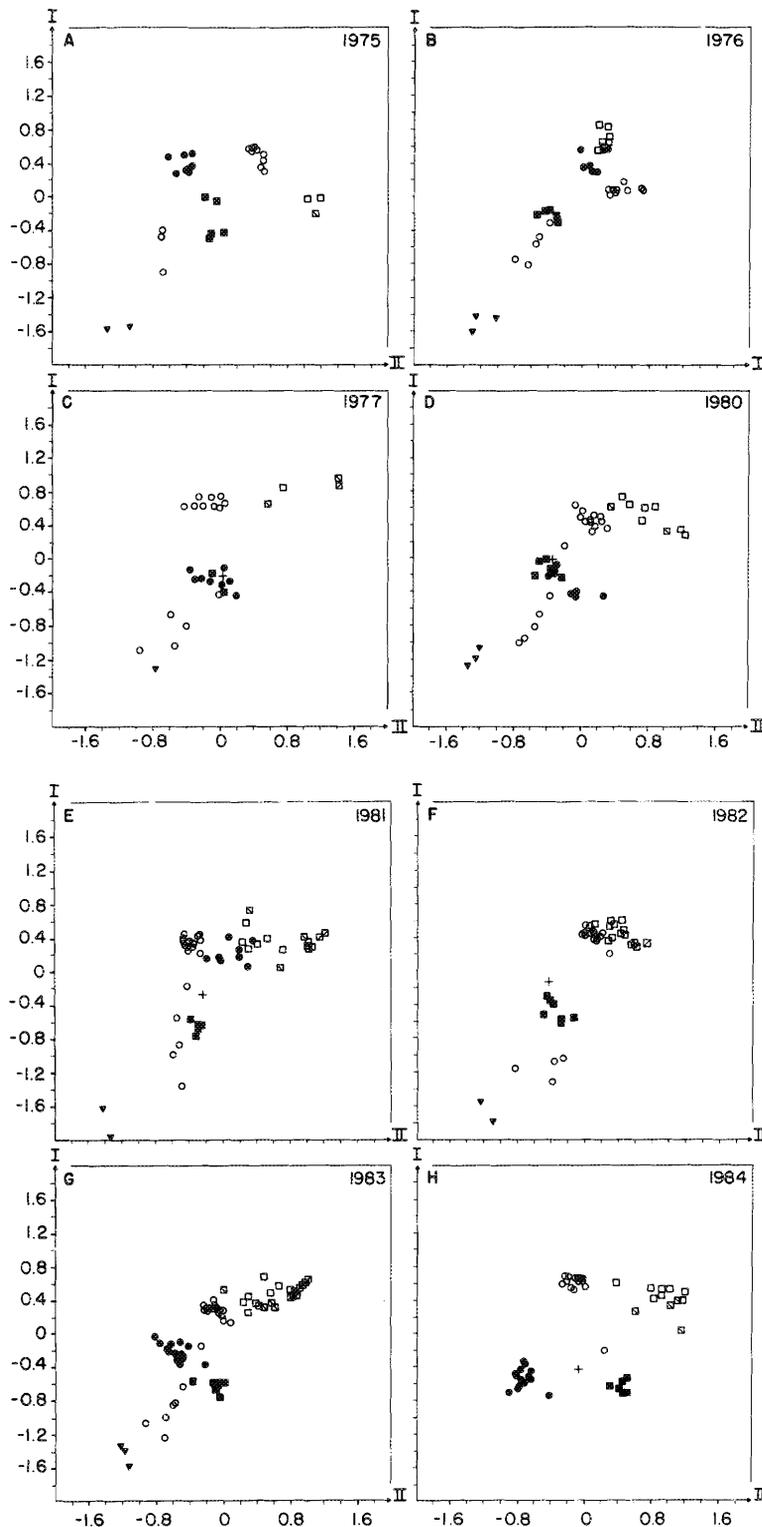


FIG. 6. Two-dimensional nonmetric multidimensional scaling of biomass data of stations. Scaling was performed on a spatially constrained resemblance matrix (Gower's index of similarity). A to H are yearly dispersal analyses from 1975 to 1984 (except 1978 and 1979). Symbols represent collectors from the different sampling regions:  $\blacktriangledown$ , Lower North Shore;  $\circ$ , North Shore;  $\blacksquare$ , Mingan Islands;  $\bullet$ , Gaspé Peninsula;  $+$ , Anticosti island;  $\square$ , Lower Estuary (north coast);  $\blacksquare$ , Lower Estuary (south coast);  $\boxplus$ , Upper Estuary.

the spatial patterns depending on species (see below). This is supported by the results of the one-way analysis of variance of means among "biogeographic zones" (Fig. 7) which indicates

a significantly heterogeneous distribution of biomass throughout the study area. The existence of spatial inhomogeneities is now recognized as a more realistic

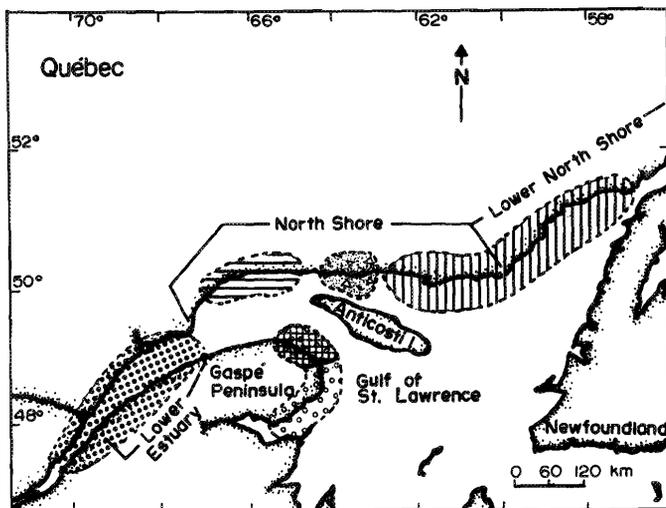


FIG. 7. Biogeographic zones during the period 1975–84 for the epibenthic fauna of the Estuary and Gulf of St. Lawrence.

ecological characteristic of species than regular or random distributions (Taylor 1984; Vance 1984; Fahrig and Paloheimo 1988a, b; Nagylaki 1988).

Trying to explain the spatial structure observed is difficult because studies of dispersal and survival of benthic larvae in the study area are lacking. Most of the quantitative studies concerning larval settlement, growth, biotic interactions, and seasonal variations of epibenthic populations in the St. Lawrence system (e.g. Archambault and Bourget 1983; Hudon et al. 1983; Brault and Bourget 1985) have been carried out at small spatio-temporal scales and did not take into account local recruitment vs. immigration–emigration processes. Hence, the crucial questions concerning larval population dynamics remain to a large extent unanswered. Certainly the presence and abundance of settling larvae is not the only factor controlling patterns. Biotic events occurring during and after settlement, such as biotic interactions among both dominant and rare epibenthic species, are also important (Buss 1980; Grosberg 1981; Brault and Bourget (1985). On the other hand, and as suggested by Sokal and Thomson (1987), the spatial patterns of biomass observed for single species may also reflect the spatial patterning of resources or other environmental factors affecting the populations. The evidence accumulated on the primary productivity and physical oceanography of the Estuary and Gulf of St. Lawrence (e.g. Lauzier et al. 1957; Steven 1974; El-Sabh 1976, 1979; Benoit et al. 1985; Therriault and

Levasseur 1985; Legendre and Demers 1985) shows the physical environment to be spatially heterogeneous, resembling a mosaic of nested habitats, each one characterized by different physical and biological attributes. This suggests that the causes of patchiness are not the same from region to region and that the environmental factors are themselves patterned in space, constituting in this way a major structural force for epibenthic populations. Changes in autocorrelation values of biomass with increasing horizontal distance may then reflect the biological response of particular species to the carrying capacity of the surface layer of neighbouring localities within the limits of the study area.

As mentioned earlier, correlograms had different shapes depending on species. Two fundamental patterns emerged from them: a cline and a patchy pattern. The spatial structure of *O. longissima* at the whole system and the Gulf scales, and those of all species but *S. balanoides* at the Estuary scale, correspond to the former pattern. In contrast, the spatial structures of *H. arctica*, *M. edulis*, *S. balanoides*, and *B. crenatus* at the whole system and the Gulf scales were patchy. Correlograms also describe the change in correlation strength with increasing distance. In the Estuary area, correlation values diminished markedly in a relatively short distance (from 25–250 km). In light of the work of Therriault and Levasseur (1985), the strong slope of correlograms in the Estuary should be interpreted as resulting from a high spatial heterogeneity in carrying capacity of the environment within a relatively small area. On the basis of the spatial patterns of phytoplankton production, these authors divided the Lower Estuary into four regions, each one characterized by different values of temperature, salinity, turbidity, and nutrients. They concluded that each of these four regions was dominated by different hydrodynamic processes which have a different influence on the stability conditions of the water column. This suggests that, in this area, events occurring during and after settlement may also influence the structure of the assemblage as measured by biomass. This is quite obvious in *S. balanoides* which, although present in the Lower Estuary, was poorly represented and did not show significant spatial patterns at the time of sampling. Increasingly harsh conditions farther up the Estuary (e.g. increasing turbidity, lower salinity, highly variable nutrient content) probably reduced the growth of this species. The patchiness of *H. arctica*, *M. edulis*, *S. balanoides*, and *B. crenatus*, at the whole system and at the Gulf scales, is characterized by a patch diameter smaller than the interpatch distance. The patchiness of the biomass structure of these species could be the result of alternation of favorable and unfavorable conditions in space,

TABLE 2. Maximum average biomass values ( $g \cdot 0.01 m^{-2}$ ) of dominant epibenthic species during the period 1975–84. Values in parentheses are standard deviations;  $n^*$ , number of samples per biogeographic zone.

Species	Biogeographic zone					
	Lower North Shore plus Eastern North Shore $n = 8$	Mingan island region $n = 6$	Western North Shore $n = 16$	Northeastern Gasp� Peninsula $n = 4$	Southeastern Gasp� Peninsula $n = 7$	Lower Estuary to Ile aux Coudres $n = 13$
<i>O. longissima</i>	0.37 (0.41)	1.86 (2.53)	3.35 (4.75)	5.42 (7.83)	0.60 (0.95)	1.51 (1.75)
<i>H. arctica</i>	0.03 (0.08)	0.08 (0.21)	0.51 (1.15)	0.12 (0.22)	0.09 (0.15)	0.10 (0.67)
<i>M. edulis</i>	0.95 (2.14)	0.18 (0.29)	3.30 (2.02)	9.81 (5.67)	8.91 (5.18)	0.48 (1.14)
<i>S. balanoides</i>	1.20 (2.61)	0.14 (0.34)	0.39 (0.67)	0.36 (0.71)	0.24 (0.86)	0.01 (0.06)
<i>B. crenatus</i>	0.79 (1.29)	0.10 (0.12)	1.14 (1.20)	0.75 (0.98)	1.68 (1.91)	0.19 (0.64)
Total biomass	3.63 (4.54)	2.34 (2.91)	8.90 (5.73)	17.4 (11.2)	11.7 (6.71)	2.27 (3.00)

\*Samples obtained from collectors moored during most of the period of study (occasional buoys were discarded).

	75	76	77	80	81	82	83	84
75	1.000	0.603	0.297	0.343	0.529	0.390	0.473	0.770
76	0.603	1.000	0.434	0.499	0.411	0.320	0.403	0.461
77	0.297	0.434	1.000	0.373	0.265	0.142	0.358	0.320
80	0.343	0.499	0.373	1.000	0.396	0.387	0.432	0.428
81	0.529	0.411	0.265	0.396	1.000	0.524	0.542	0.518
82	0.390	0.320	0.142	0.387	0.524	1.000	0.578	0.506
83	0.473	0.403	0.358	0.432	0.542	0.578	1.000	0.477
84	0.770	0.461	0.320	0.428	0.518	0.506	0.477	1.000

FIG. 8. Matrix of biotic resemblance among yearly biomass structures in the Estuary and Gulf of St. Lawrence during the period 1975–84. Each value in the matrix is a Mantel statistic  $r$  computed between two similarity matrices comparing different years. The subdiagonal values correspond to the comparisons of consecutive years. The entire matrix is significant at the overall significance level  $P < 0.01$ .

probably reflecting the patchiness of the physical environment itself.

#### Biogeographic Patterns

Clustering and scaling data on the basis of a resemblance matrix is another way of making inferences concerning community structure. Available methods, however, have different levels of model rigidity (Legendre et al. 1987). While unconstrained clustering and scaling techniques delineate spatial structures on the exclusive basis of the similarity among objects for the variables under study, regardless of the causal processes that generated them, constrained methods (e.g. time or space), by restricting the set of possible solutions to those that make sense in terms of these same constraints, delimit homogeneous regions that are more probably controlled by the same type of causal processes (Legendre 1987).

In light of the previous discussion, the spatial structures derived from unconstrained clustering and ordination analyses (Fig. 4) summarize the yearly spatial variability of biomass resulting from different but converging generating processes. The sampling sites scattered in the reduced space of the two principal coordinate axes throughout the period of study were highly variable. Yet these sites could not be entirely associated to particular clusters nor clearly discriminated along these same axes. However, when considering the main trends of variability, the clustering results, in conformity with the scaling results, showed that the stations from the Western North Shore were associated with those of the Gasp  Peninsula, both located on the left side of the first principal axis. Likewise, the collectors from the Lower North Shore, the Eastern North Shore, the Mingan Islands, Anticosti Island, and the Lower and Upper Estuary were associated to each other, and positioned on the right side of these graphs. This spatial structure, excluding the Eastern North Shore, is in keeping with the one obtained by Fradette and Bourget (1981) for the period 1975–76. In their study, these authors related the objects from the Eastern North Shore to those of the Western North Shore and the Gasp  Peninsula, even though objects 6 and 7 (4 and 5 in their study) were considered as belonging to the Lower North Shore. According to Fradette and Bourget (1981), the geographic gradient of summer surface water temperature is the factor that best explains

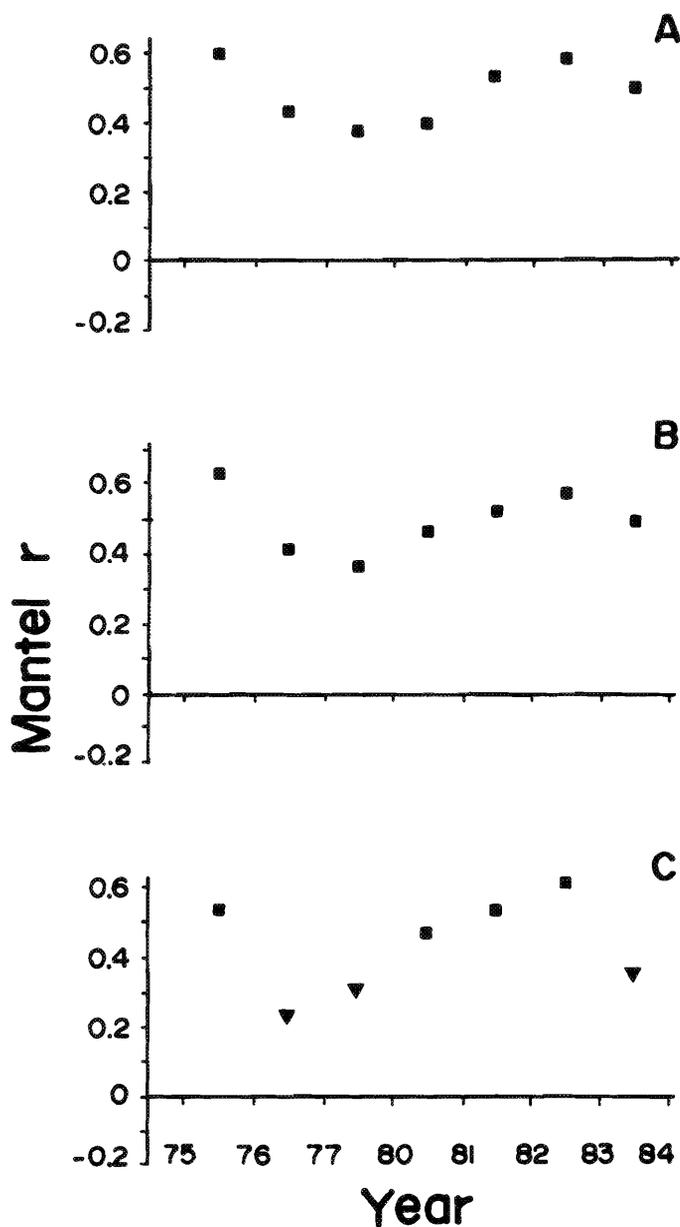


FIG. 9. Mantel statistics across years, for biotic resemblance between biomass structure of epibenthic assemblages of consecutive years during the period 1975–84 (except 1978–79), at different spatial scales. A, whole system (Gulf and Estuary); B, Gulf; C, Lower North Shore together with the North Shore. Abscissa: years. Ordinate: normalized Mantel statistic  $r$ . Black squares, coefficients significant at  $P < 0.001$ . Black triangles, coefficients significant at  $P \leq 0.024$ . The entire graphs are significant at the overall significance level  $P < 0.01$ .

the observed clusters. Thus, the stations located on the left side of the first principal axis, those of the North Shore (the Mingan Islands region excluded) and the Gasp  Peninsula localities, correspond to the areas of warmer summer surface water (9–16°C). Similarly, the samples located at the right of the first principal axis, those of the Lower North Shore, the Mingan Islands and the Lower Estuary localities, correspond to areas of colder summer surface water (4–14°C). These clusters are formed of similar sites coming from a set of heterogeneous localities influenced by different hydrodynamic processes (see El-Sabh 1976, 1979; Tang 1980; Dickie and Trites 1983; Bah and Legendre 1985). Two regions, the Mingan Islands and the Lower Estuary, are characterized by a common trait that

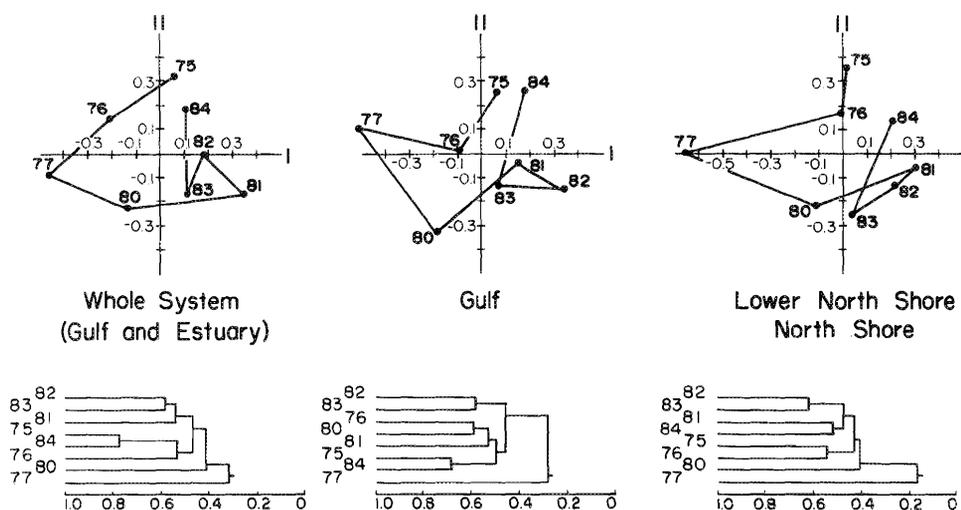


FIG. 10. UPGMA clustering and principal coordinate analysis of the normalized Mantel statistics  $r$ , representing the temporal variability in biomass structure of yearly epibenthic assemblages in the Estuary and Gulf of St. Lawrence during the period 1975–84 at different spatial scales. Line segments between years outline the chronological sequence. A, whole system (Gulf and Estuary); B, Gulf; C, Lower North Shore together with the North Shore. Black circles represent years in the reduced space of the first two principal axes. Dendrograms represent similarity relationships in biomass structure among years.

accounts for their similarity: the upwelling of colder, deeper waters during the summer months (Lauzier et al. 1957; Forrester 1974; Steven 1974). According to Fradette and Bourget (1980, 1981) this factor, in conjunction with other local characteristics, would be involved in the reduction of larval recruitment that is observed there. Thus, whereas in the Mingan Island region the surface dilution of larvae by upwelled waters and their subsequent offshore dispersal may be responsible for the reduced abundance of most of the species, in the Lower Estuary this effect would be obtained by the combined action of the surface dilution of larvae by upwelled waters, the loss of larvae by the downstream residual circulation, and the gradually increasing severity of the physicochemical conditions (e.g. temperature, salinity, turbidity). Moreover, the westward drift of cold water, originating partly from the Labrador current and from the episodic nearshore wind-forced upwellings in the Lower North Shore area influencing the Jacques-Cartier passage (Huntsman et al. 1954; Lauzier et al. 1957; El-Sabh 1976; Rose and Leggett 1988), can explain the affinity of the Eastern North Shore with the Lower North Shore and their inclusion into the cluster located on the right side of the first principal axis. In addition, the correlations between the two principal coordinate axes and the biomass of single species indicate that *M. edulis*, *B. crenatus* and *O. longissima* were the species that most contributed to the formation of the reduced space, showing in this way their preponderant role as structuring agents of the dominant assemblage.

In the presence of spatially autocorrelated data, spatially constrained clustering and scaling methods lead to a more realistic representation of the variability of biomass (Legendre et al. 1987; Legendre 1987). These analyses showed the most conspicuous discontinuities in community structure between contiguous localities. The six homogeneous “biogeographic zones” thus established (Fig. 7) characterize the average variability trends of a very resilient oscillating yearly structure. In the present study, the expression “biogeographic zone” is used only as a working concept intended to identify homogeneous

areas with distinct assemblage structure of the dominant species, and not to imply differences in geographic range and species composition with increasing distance. In order to illustrate these biogeographic zones, the average biomass structure of the dominant assemblage of each zone is represented in Fig. 11. Except for the species assemblages from the Mingan Islands and the Lower and Upper Estuary which were similar both in structure and in total biomass, the species assemblages of each of the other biogeographic zones showed a singular biomass structure. The highest total biomass values of the Estuary–Gulf system during this period came from the Western North Shore and the Gaspé Peninsula zones. These results are in agreement with Steven (1974), who described this area as the region of maximum primary production in the Estuary–Gulf system. The dominant oceanographic features accounting for the nutrient richness of the surface layer of this area (Steven 1974; El-Sabh 1976) are a stationary counter-clockwise gyre, and the Gaspé Current flowing seaward along the entire length of the Gaspé coast.

#### Temporal Fluctuation in Biotic Resemblance

It has been shown that the yearly community structure was significantly autocorrelated during the period 1975–84, and that the strength of the correlation between years is not constant, varying in a cyclic way. What is the significance of this period of variation, and how can it be explained? At large and intermediate spatial scales, the temporal fluctuation in biotic resemblance between neighbouring years was gradual and apparently stable. Such an oscillating pattern, reflecting the change in similarity structure from one year to the next, suggests that singular biological or physical events (e.g. low density of recruiting competent larvae, or cold and strongly mixed summer surface water layer) may have a long-lasting influence on the community structure of subsequent years. However, the specific causal processes (physical and biotic) forcing the yearly community structure remain to be elucidated. From the thermo-

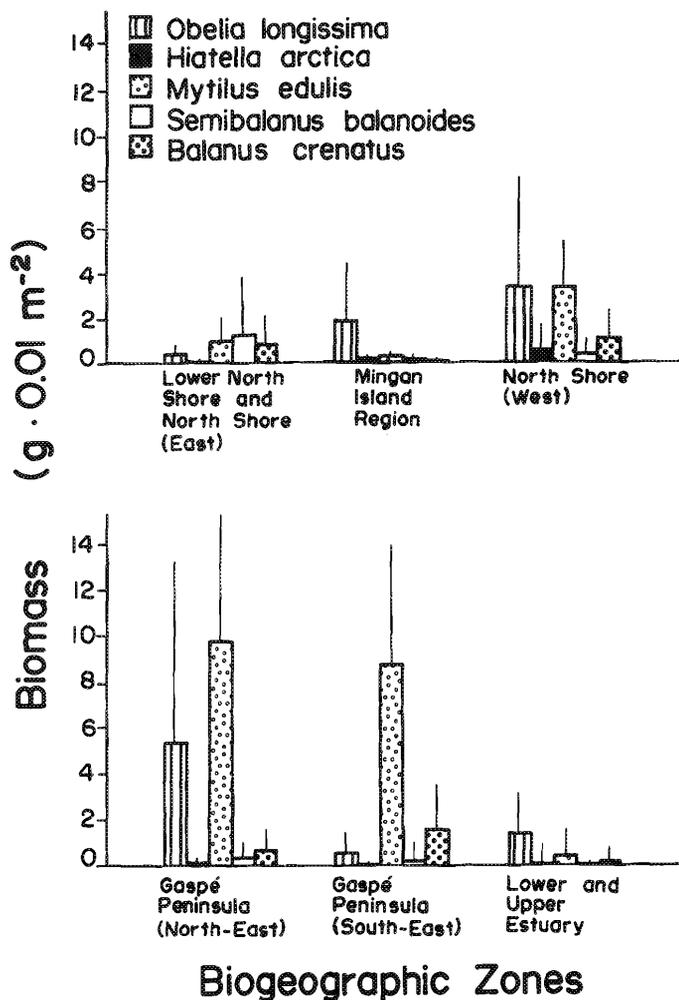


FIG. 11. Structure of the dominant epibenthic assemblage in the different biogeographic zones of the Estuary and Gulf of St. Lawrence, during the period 1975–84. Vertical bars: one standard deviation.

dynamic point of view, periodic fluctuations need an external input of energy. On continental shelves and in estuarine areas, the main sources of energy input are freshwater runoff, winds, and tides (Legendre and Demers 1985). These sources of auxiliary energy have varying periodicities and, spatially, their effects on stability and community organization are not exerted homogeneously (Platt and Denman 1975; Margalef 1979; Ulanowicz and Platt 1985). The relative weights of these driving forces at different spatio-temporal scales remain to be assessed, as well as the physical and biological mechanisms by which the variability in the energy input is transmitted to the epibenthic community inhabiting the surface water layer.

In previous sections we have emphasized the complementary use of different numerical techniques in order to reveal the spatial structure and temporal variability of observational data. This approach allowed us to overcome the shortcomings of single methods while taking advantage of the implicit and/or explicit hypotheses concerning the causal relationships among variables in each one of them. The use of different spatio-temporal scales of observation made complex patterns in community structure emerge. From this point of view the biogeographic zones thus obtained should be considered only as an abstraction helping to visualize the average structure throughout the period of study, while the year-by-year analyses represent a more realistic picture of community structure. On a yearly basis, spatial patterns

resulted in a set of nested subseries that expands or shrinks from one year to the next, probably reflecting the larval population dynamics and the patterning of the environment itself. A proposal worth considering is that, in spite of these spatial discontinuities, the temporal oscillations in community structure observed at intermediate and large spatial scales suggest that the Estuary–Gulf system responds to external inputs of auxiliary energy as an integrated system. More intensive and simultaneous surveys of both biotic and physical rate processes are needed to elucidate the dynamics of the structures revealed in this study.

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### References

- ALLEN, T. F. H., AND T. B. STARR. 1982. Hierarchy: perspectives for ecological complexity. University of Chicago Press, Chicago, IL. 310 p.
- ARCHAMBAULT, D., AND E. BOURGET. 1983. Importance du régime de dénudation sur la structure et la succession des communautés intertidales de substrat rocheux en milieu subarctique. *Can. J. Fish. Aquat. Sci.* 40: 1278–1292.
- BAH, A., AND L. LEGENDRE. 1985. Biomasse phytoplanctonique et mélange de marée dans l'estuaire moyen du Saint-Laurent. *Naturaliste Can.* 112: 39–49.
- BENOIT, J., M. I. EL-SABH, AND C. L. TANG. 1985. Structure and seasonal characteristics of the Gaspé current. *J. Geophys. Res.* 90: 3225–3236.
- BOURGET, E. 1988. Barnacle larval settlement: the perception of cues at different spatial scales, p. 153–172. *In* G. Chelazzi and M. Vannini [ed.] Behavioral adaptation to intertidal life. NATO ASI Series, Vol. A151. Plenum, New York, NY.
- BRAULT, S., AND E. BOURGET. 1985. Structural changes in an estuarine subtidal epibenthic community: biotic and physical causes. *Mar. Ecol. Prog. Ser.* 21: 63–73.
- BROWN, J. H. 1984. On the relationship between abundance and distribution of species. *Am. Nat.* 124: 255–279.
- BROWN, J. H., AND B. A. MAURER. 1987. Evolution of species assemblages: effects of energetic constraints and species dynamics on the diversification of the North American avifauna. *Am. Nat.* 130: 1–17.
- BUSS, L. W. 1980. Bryozoan overgrowth interactions: the interdependence of competition for space and food. *Nature (Lond.)* 281: 475–477.
- CLIFF, A. D., AND J. K. ORD. 1981. Spatial processes: Models and applications. Pion Limited, London, UK.
- COOPER, D. W. 1968. The significance level in multiple tests made simultaneously. *Heredity* 23: 614–617.
- DEANGELIS, D. L., AND J. C. WATERHOUSE. 1987. Equilibrium and nonequilibrium concepts in ecological models. *Ecol. Monogr.* 57: 1–21.
- DICKIE, L. M., AND R. W. TRITES. 1983. The Gulf of St. Lawrence, p. 403–425. *In* B. H. Ketchum [ed.] Estuaries and enclosed seas. Elsevier, Amsterdam, The Netherlands.
- EL-SABH, M. I. 1976. Surface circulation pattern in the Gulf of St. Lawrence. *J. Fish. Res. Board Can.* 33: 124–138.
1979. The Lower St. Lawrence Estuary as a physical oceanographic system. *Naturaliste Can.* 106: 55–73.
- EL-SABH, M. I., AND O. M. JOHANNESSEN. 1972. Winter geostrophic circulation in the Gulf of St. Lawrence. *J. Fish. Res. Board Can.* 29: 595–598.
- FAHRIG, L., AND J. PALOHEIMO. 1988a. Determinants of local population size in patchy habitats. *Theor. Popul. Biol.* 34: 194–213.
- 1988b. Effect of spatial arrangement of habitat patches on local population size. *Ecology* 69: 468–475.
- FIELD, J. G., K. R. CLARKE, AND R. M. WARWICK. 1982. A practical strategy for analysing multispecies distribution patterns. *Mar. Ecol. Prog. Ser.* 8: 37–52.

- FIELD, J. G., R. H. GREEN, F. A. DE L. ANDRADE, E. FRESI, P. GROS, B. H. MCARDLE, M. SCARDI, AND D. WARTENBERG. 1987. Numerical ecology: developments for studying the benthos, p. 485-494. *In* P. and L. Legendre [ed.] Developments in numerical ecology. NATO ASI series, Vol. G14. Springer-Verlag, Berlin.
- FORRESTER, W. D. 1974. Internal tides in St. Lawrence Estuary. *J. Mar. Res.* 32: 55-66.
- FRADETTE, P., AND E. BOURGET 1980. Ecology of benthic epifauna of the Estuary and Gulf of St. Lawrence: factors influencing their distribution and abundance on buoys. *Can. J. Fish. Aquat. Sci.* 37: 979-999.
1981. Groupement et ordination appliqués à l'étude de la répartition de l'épifaune benthique de l'estuaire maritime et du golfe du Saint-Laurent. *J. Exp. Mar. Biol. Ecol.* 50: 133-152.
- GALZIN, R., AND P. LEGENDRE. 1987. The fish communities of a coral reef transect. *Pacific Sci.* 41: 158-165.
- GOWER, J. C. 1966. Some distance properties of latent root and vector methods used in multivariate analysis. *Biometrika* 53: 325-338.
1971. A general coefficient of similarity and some of its properties. *Biometrics* 27: 857-871.
- GROSBERG, R. K. 1981. Competitive ability influences habitat choice in marine invertebrates. *Nature (Lond.)* 290: 700-702.
- HUDON, C., E. BOURGET, AND P. LEGENDRE. 1983. An integrated study of the factors influencing the choice of the settling site of *Balanus crenatus* cyprid larvae. *Can. J. Fish. Aquat. Sci.* 40: 1186-1194.
- HUNTSMAN, A. G., W. B. BAILEY, AND H. B. HACHEY. 1954. The general oceanography of the Strait of Belle Isle. *J. Fish. Res. Board Can.* 11: 198-260.
- KOLASA, J. 1989. Ecological systems in hierarchical perspective: breaks in community structure and other consequences. *Ecology* 70: 36-47.
- KRUSKAL, J. B., AND M. WISH. 1978. Multidimensional scaling. Sage Publications, Beverly Hills, CA 93 p.
- LAUZIER, L., R. W. TRITES, AND H. B. HACHEY. 1957. Some features of the surface layer of the Gulf of St. Lawrence. *Bull. Fish. Res. Board Can.* 111: 195-212.
- LEGENDRE, L., C. D. COLLINS, C. M. YENTSCH, J. C. BEZDEK, J. W. CAMPBELL, Y. ESCOUFIER, M. ESTRADA, AND F. IBANEZ. 1987. Numerical ecology: developments for biological oceanography and limnology, p. 521-527. *In* P. and L. Legendre [ed.] Developments in numerical ecology. NATO ASI series. Vol. G14. Springer-Verlag, Berlin.
- LEGENDRE, L., AND P. LEGENDRE. 1984. Ecologie numérique, T.2. La structure des données écologiques. 2<sup>e</sup> édition. Collection d'écologie 13, Masson, Paris et les Presses de l'Université du Québec, P.Q. 335 p.
- LEGENDRE, L., AND S. DEMERS. 1984. Towards dynamic biological oceanography and limnology. *Can. J. Fish. Aquat. Sci.* 41: 2-19.
1985. Auxiliary energy, ergoclines and aquatic biological production. *Naturaliste Can.* 112: 5-14.
- LEGENDRE, P. 1987. Constrained clustering, p. 289-307. *In* P. and L. Legendre [ed.] Developments in numerical ecology. NATO ASI series, Vol. G14. Springer-Verlag, Berlin.
- LEGENDRE, P., S. DALLOT, AND L. LEGENDRE. 1985. Succession of species within a community: chronological clustering, with applications to marine and freshwater zooplankton. *Am. Nat.* 125: 257-288.
- LEGENDRE, P. AND M.-J. FORTIN. 1989. Spatial pattern and ecological analysis. *Vegetation* 80: 107-138.
- LEGENDRE, P., N. L. ODEN, R. R. SOKAL, A. VAUDOR, AND J. KIM. 1990. Approximate analysis of variance of spatially autocorrelated regional data. *J. Class.* 7: 53-75.
- LILLIEFORS, H. W. 1967. The Kolmogorov-Smirnov test for normality with mean and variance unknown. *J. Am. Stat. Assoc.* 62: 399-402.
- MANTEL, N. 1967. The detection of disease clustering and a generalized regression approach. *Cancer Res.* 27: 209-220.
- MARGALEF, R. 1979. The organization of space. *Oikos* 33: 152-159.
- MILLER, R. G., JR. 1977. Developments in multiple comparisons. *J. Am. Stat. Assoc.* 72: 779-788.
- MORRIS, D. W. 1987. Ecological scale and habitat use. *Ecology* 68: 362-369.
- NAGYLAKI, T. 1988. The influence of spatial inhomogeneities on neutral models of geographical variation. *Theor. Popul. Biol.* 33: 291-310.
- ODEN, N. L. 1984. Assessing the significance of a spatial correlogram. *Geogr. Anal.* 16: 1-16.
- ODEN, N. L., AND R. R. SOKAL. 1986. Directional autocorrelation: an extension of spatial correlograms to two dimensions. *Syst. Zool.* 35: 608-617.
- PLAITT, T., AND K. L. DENMAN. 1975. Spectral analysis in ecology. *Annu. Rev. Ecol. Syst.* 6: 189-210.
- PLATT, T., K. H. MANN, AND R. E. ULANOWICZ. 1981. Mathematical models in biological oceanography. Monographs on oceanographic methodology 7, UNESCO Press, Paris, France, 157 p.
- ROHLF, F. J. 1963. Classification of *Aedes* by numerical taxonomic methods (Diptera: Culicidae). *Ann. Entomol. Soc. Am.* 56: 798-804.
- ROSE, G. A., AND W. C. LEGGETT. 1988. Atmosphere-ocean coupling in the northern Gulf of St. Lawrence: frequency-dependent wind-forced variations in nearshore sea temperatures and currents. *Can. J. Fish. Aquat. Sci.* 45: 1222-1233.
- SHEPARD, R. N. 1962. The analysis of proximities: multidimensional scaling with an unknown distance function. *Psychometrika*. 27: 125-139, 219-246.
1966. Metric structures in ordinal data. *J. Math. Psychol.* 3: 287-315.
- SOKAL, R. R. 1979. Ecological parameters inferred from spatial correlograms, p. 167-196. *In* G. P. Patil and M. L. Rosenzweig, [ed.] contemporary quantitative ecology and related ecometrics. Statistical Ecology Series, Vol. 12. International Co-operative Pub. House, Fairland, MD.
- SOKAL, R. R., AND N. L. ODEN. 1978. Spatial autocorrelation in biology. 1. Methodology. *Biol. J. Linn. Soc.* 10: 199-228.
- SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry. The principles and practice of statistics in biological research. 2nd ed. W. H. Freeman and Co., San Francisco, CA. 859 p.
- SOKAL, R. R., AND J. D. THOMSON. 1987. Applications of spatial autocorrelation in ecology, p. 431-466. *In* P. and L. Legendre [ed.] Developments in numerical ecology. NATO ASI series, Vol. G14. Springer-Verlag, Berlin.
- STEVEN, D. M. 1974. Primary and secondary production in the Gulf of St. Lawrence. *McGill Univ., Mar. Sci. Centre MS Rep.* 26. 116 p.
- TANG, C. L. 1980. Mixing and circulation in the Northwestern Gulf of St. Lawrence: a study of a buoyancy-driven current system. *J. Geophys. Res.* 85: 2787-2796.
- TAYLOR, L. R. 1984. Assessing and interpreting the spatial distributions of insect populations. *Annu. Rev. Entomol.* 29: 321-357.
- TERRIAULT, J.-C., AND M. LEVASSEUR. 1985. Control of phytoplankton production in the lower St. Lawrence estuary: light and freshwater runoff. *Naturaliste Can.* 112: 77-96.
- ULANOWICZ, R. E., AND T. PLATT [ED.]. 1985. Ecosystem theory for biological oceanography. *Can. Bull. Fish. Aquat. Sci.* 213: 260 p.
- VANCE, R. R. 1984. The effect of dispersal on population stability in one-species, discrete-space population growth models. *Am. Nat.* 123: 230-254.
- WIENS, J. A. 1984. On understanding a non-equilibrium world: myth and reality in community patterns and processes, p. 439-457. *In* D. R. Strong et al. [ed.] Ecological Communities: conceptual issues and the evidence. Princeton Univ. Press, Princeton, NJ.