Journal of Plankton Research Vol.20 no.7 pp.1387–1401, 1998

Spatio-temporal structure of tidally mixed coastal waters: variability and heterogeneity

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Abstract. In the tidally mixed coastal waters of the eastern English Channel, the vertical properties of temperature, salinity, *in vivo* fluorescence, turbidity and light were investigated along an inshore–offshore transect, sampled in different tidal conditions. The vertical distribution of these parameters was then characterized in terms of mean value, variability (i.e. standard deviation) and heterogeneity (i.e. fractal dimension), regarded as a quantitative characterization of the structure of the vertical variability of both physical and biological parameters. These different estimates were then subjected to multivariate spatio-temporal analysis and showed a very specific spatio-temporal structure suggesting a differential control of the vertical properties of water masses associated with both inshore–offshore gradient and tidal advection. In particular, the fractal dimension (i.e. heterogeneity) of *in vivo* fluorescence is higher during ebb for offshore waters, suggesting a density dependence of the phytoplankton biomass structure. In contrast, the vertical variability of fluorescence is higher during flood for inshore waters, leading to an inverse relationship between variability and heterogeneity of the vertical distribution of phytoplankton biomass.

Introduction

The general importance of recognizing the causes and consequences of heterogeneity has frequently been emphasized both in marine and terrestrial ecology (Hutchinson, 1953; Levin and Paine, 1974; Wiens, 1976; Roughgarden, 1977; Southwood, 1977, 1988; Kolasa and Rollo, 1991; Levin, 1992). However, there is great confusion in the scientific literature about the relative meaning of 'variability' and 'heterogeneity', depending essentially on a choice of approach (Downing, 1991; Naeem and Colwell, 1991; Shachak and Brand, 1991). General measures of heterogeneity are sometimes not widely known (Kolasa and Rollo, 1991) and are usually associated with traditional descriptors, such as the variance-to-mean ratio (Taylor, 1961; Frontier, 1972; Downing *et al.*, 1987), or the variance associated with a mean abundance estimation, regarded as a primary measure to examine heterogeneity changes across scales (Greig-Smith, 1952; Kershaw, 1957; Goodall, 1974; Ripley, 1987). In this paper, 'variability' indicates changes in the values of a given quantitative or qualitative descriptor (Kolasa and Rollo, 1991), whereas 'heterogeneity' refers to the structure of its variability, estimated using the concept of fractal dimension. Initially introduced to describe the structure of patterns so irregular and fragmented that they present not simply a higher degree but an altogether different level of complexity, as compared with Euclidean approximations (Mandelbrot, 1977, 1983), the concept of fractal more generally characterizes patterns exhibiting structure at all scales. Fractal dimension then appears as a useful measure of spatial heterogeneity, offering the advantage of describing variability as a continuous function of scale (Palmer, 1988). Low and high fractal dimensions characterize heterogeneous and homogeneous patterns exhibiting strong and weak spatial dependence, respectively. Since the fractal dimension increases with an increase in complexity of a geometrical object, the fractal geometry therefore provides a method of gaining new insights into spatial patterns and heterogeneity. The applicability of these concepts to planktonology has recently been demonstrated (Seuront and Lagadeuc, 1997).

In the eastern English Channel, characterized by its megatidal regime, the fluvial supplies, distributed from the Bay of Seine to Cape Griz-Nez, generate a coastal water mass drifting nearshore, separated from the open sea by a frontal area (Brylinski and Lagadeuc, 1990; Lagadeuc *et al.*, 1997). This coastal flow ('fleuve côtier'; Brylinski *et al.*, 1991) is characterized by its freshness, turbidity (Dupont *et al.*, 1991) and phytoplankton richness (Brylinski *et al.*, 1984; Quisthoudt, 1987). Moreover, the dissipation of tidal energy is basically regarded to be responsible for the vertical homogenization of inshore and offshore water masses (50 m maximum depth). However, recent investigations have shown that the variability perceived in temperature and phytoplankton biomass fluctuations can be wholly characterized in terms of heterogeneity over a wide range of scales (Seuront *et al.*, 1996a,b; Seuront, 1997) and that this heterogeneity cannot be neglected. Indeed, considering the vertical and temporal heterogeneity of photosynthetic parameters, estimates of primary production are increased from 40 to 100% (Lizon *et al.*, 1995; Lizon, 1997; Lizon and Lagadeuc, 1998). The goal of the present paper is to focus on changes through time and space of the vertical patterns of both physical and biological parameters characterized in terms of variability and heterogeneity using a multivariate approach similar to the spatio-temporal analysis initially introduced by Ibanez (1973). Our main findings are: (i) that the variability perceived in vertical patterns of well-mixed waters can be quantitatively characterized as structurally homogeneous using the concept of fractal dimension; (ii) that there is a very specific structure in space and time of variability and heterogeneity associated with both inshore–offshore gradient and tidal forcing; (iii) that a multivariate spatio-temporal analysis, used in conjunction with fractal analyses, provides an appreciation of the nature and magnitude of the sources of variability, and appears to be critical for understanding the underlying biological and physical processes, and also for designing sampling strategies.

Method

Study area and sampling

Sampling was carried out in April 1993 during spring tide in the Dover straight (eastern English Channel), along a transect perpendicular to the coast and to the general drift of waters. The transect consisted of 15 equidistant stations (0.3 nautical mile) and was sampled four times from inshore to offshore waters (50°54'35N, 1°37'15E to 50°57'28N, 1°32'35E), leading to equivalent sampling of inshore and offshore water masses (Figure 1). It takes ~2.5 h to sample each transect, which was separated from the one after by ~30 min. At each station, measurements of physical parameters [temperature, salinity, transmission and photosynthetically active radiation (PAR)] and *in vivo* fluorescence (i.e. an index of phytoplankton biomass) were taken from the surface to bottom with an SBE 25 Sealogger CTD and a Sea Tech fluorometer, respectively.

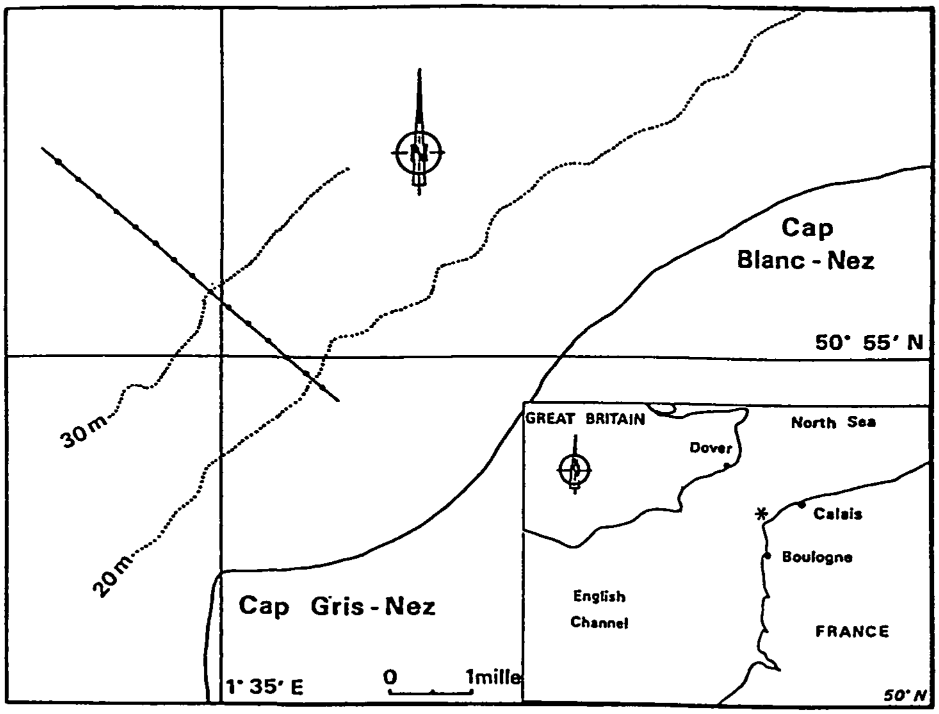


Fig. 1. Position of the stations along the transect, in the eastern English Channel in the Dover Strait.

Data analysis

Fractal dimensions were estimated using a method (Burrough, 1981, 1983) based on geostatistics and regionalized variables (RV) theory (Matheron, 1971; Journel and Huijbregts, 1978). Patterns of variation in RV can then be expressed by their semivariance $\gamma(h)$, defined as:

$$\gamma(h) = \frac{1}{2N(h)} \sum_{i=1}^{N(h)} [Z_{x+h} - Z_x]^2 \tag{1}$$

where $N(h)$ is the number of pairs of data separated by the distance, or lag h, and Z_x and Z_{x+h} are the observed values of a given variable at point x and $x + h$. The fractal dimension D was estimated from the slope m of a log–log plot of the semivariogram (Burrough, 1981, 1983):

$$D = (4 - m)/2 \tag{2}$$

It can be noticed that if the $\gamma(h)$ values estimated between two near samples are no more or less different than between two distant samples, the slope of the semivariogram will be 0, corresponding to a fractal dimension of 2. The slope of the semivariogram m (and therefore the fractal dimension D), indicating the rate of change from one scale to another, can then be regarded as an index of the degree of spatial dependence of a given parameter. Only scales less than half of the total length of the data set are considered, because greater distances are more affected by low sample sizes and spurious properties of the data (Journel and Huijbregts, 1978).

Since our aim was to look for the spatio-temporal properties of our sampling, we applied a method similar to the spatio-temporal analysis developed by Ibanez (1973) to characterize sampling processes in plankton ecology. We selected variables related to the space–time scales of our sampling experiment and a principal component analysis (PCA) was performed on the observations (i.e. stations along each transect, Q mode) and the variables (R mode, *sensu* Legendre and Legendre, 1984). These variables are latitude, longitude, depth, sun elevation and tidal current direction. We take as an arbitrary origin for latitude and longitude a point located at the intersect between the transect extension and the coastline. Depth is expressed in metres, sun elevation reaches its maximum value around solar midday, and decreases before and after the solar midday at the same rate, and current direction is expressed as an alternance between northerly and southerly drifts during flood and ebb tides, respectively. Furthermore, the identification of the components of the multivariate analyses was carried out using the factor loadings of the variable in the R mode of PCA analysis since the factor loading of a given factor could be related to the variance explained by such a factor (Legendre and Legendre, 1984). Because a criterion is needed for deciding upon appropriate observations to group in the data space, a cluster analysis based on an unweighted centroid algorithm (Sokal and Michener, 1958) has been carried out on a (Euclidean) distance matrix calculated from the first two principal components of the multivariate analysis. Afterwards, we introduced additional variables related to both mean, variability and heterogeneity (i.e. mean, standard deviation and fractal dimension) of temperature, salinity, light transmission, PAR and *in vivo* fluorescence in order to characterize their organization in the spatio-temporal space associated with the sampling experiment. Wind speed and direction were also introduced as indicators of external physical forcing.

Results

Fractal dimensions were estimated for *in vivo* fluorescence, temperature and salinity which exhibited a scaling behaviour over the whole range of studied scales, for inshore as well as for offshore stations (Figure 2). Their linearity over the whole range of spatial scales illustrates spatial dependence, suggesting that the same process can be regarded as the source of physical and biological patterns. Indeed, the mean fractal dimensions of temperature, salinity and *in vivo* fluorescence, estimated for the whole data set as 1.495 (± 0.020 SE), 1.510 (± 0.017 SE) and 1.485 (± 0.019 SE), respectively, were not significantly different (Kruskal–Wallis test, $P > 0.05$). However, the mean fractal dimensions (Table I) and their spatial distribution along each transect (Figure 3) lead to further

Table I. The mean fractal dimensions of temperature (D_T), salinity (D_S) and *in vivo* fluorescence (D_F) for the four sampled transects, shown together with their standard error

Transect	Fractal dimension D		
	D_T	D_S	D_F
1	1.488 (0.032)	1.520 (0.024)	1.502 (0.044)
2	1.626 (0.025)	1.544 (0.034)	1.472 (0.030)
3	1.545 (0.016)	1.597 (0.018)	1.432 (0.034)
4	1.399 (0.032)	1.367 (0.048)	1.545 (0.040)

conclusions. First, except in the case of *in vivo* fluorescence, mean fractal dimensions were significantly different between transects (Kruskal–Wallis test, $P < 0.05$). Furthermore, except in the case of the first transect, mean fractal dimensions of fluorescence, salinity and temperature are significantly different for each transect (Kruskal–Wallis test, $P < 0.05$), the salinity and temperature fractal dimension being not significantly different (Dunn test, $P > 0.05$; Siegel and Castellan, 1988). Second, *in vivo* fluorescence fractal dimensions exhibit a significant tendency to increase for each transect (estimated by calculating the Kendall coefficient of rank correlation τ between the series and the x axis values; Kendall and Stuart, 1966), whereas temperature and salinity exhibit tendencies to increase for the first and fourth transects, and tendencies to decrease for the second transect. Furthermore, PAR and transmission did not exhibit even a partial scaling behaviour (i.e. their variability is independent of scale), and therefore were not subjected to fractal analysis (data not shown).

The results of PCA showed that two components explained 95.20% of the total variance. The first component (PC-1), which explained 58.95% of the variance, was significantly correlated to latitude, longitude and depth (Figure 4a; Table II). This component can then be considered representative of the transect from inshore to offshore waters. The second component (PC-2), which explained 35.25% of the variance, was significantly correlated to tidal current direction and sun elevation (Figure 4a; Table II). The significance of the latter component is essentially linked to the alternance of tidal current directions, the significant inverse correlation of this axis to sun elevation being associated with the solar midday occurrence during flood tide. The projections of the observations in a bidimensional plane defined by the first two components showed two distinct parts. The upper and lower parts characterize stations sampled during ebb and flood tides, respectively (Figure 4b). Furthermore, the unweighted centroid clustering showed four groups of observations (Table III; Figure 4b), which confirmed and specified the previous results. The nature of these clusters in the environmental space was related to the temporal and spatial discrimination shown by the PCA, highlighting both flood tide–ebb tide and inshore–offshore differences associated with the gradients shown by the two principal axes.

The additional variables (Table IV), shown in the space of the two first principal components, have been plotted considering their correlation with these axes

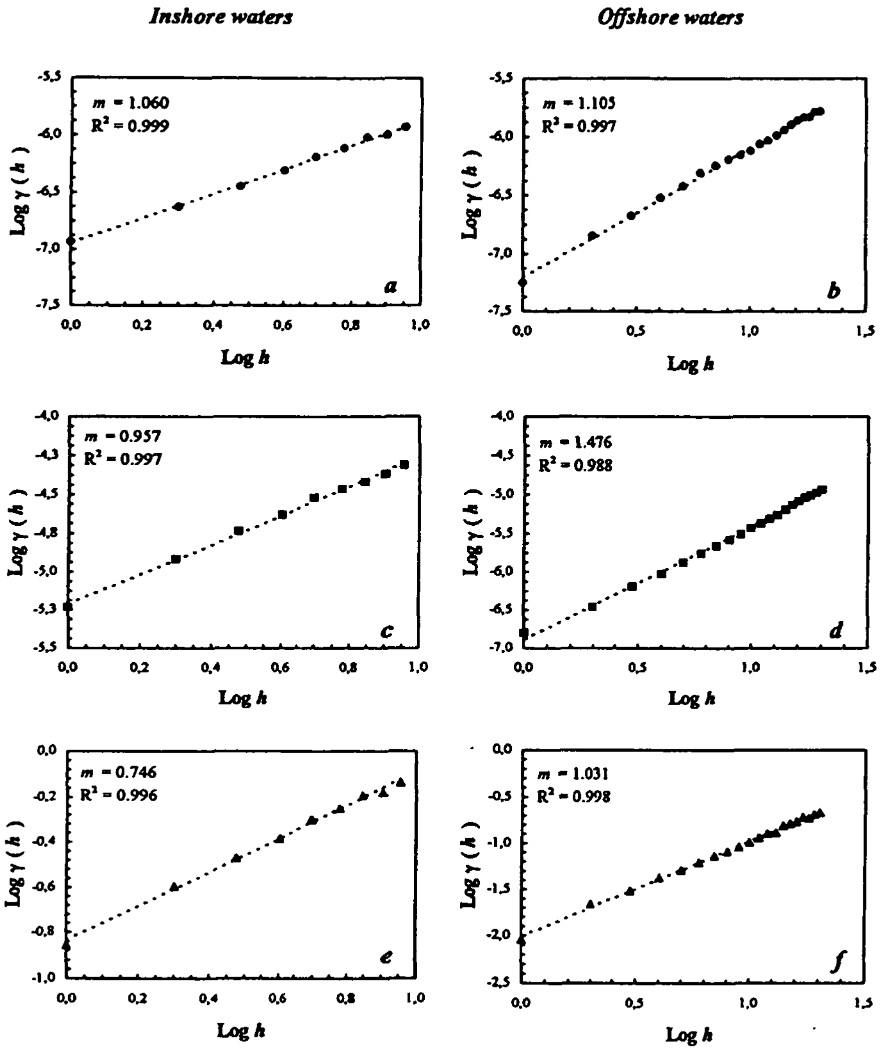


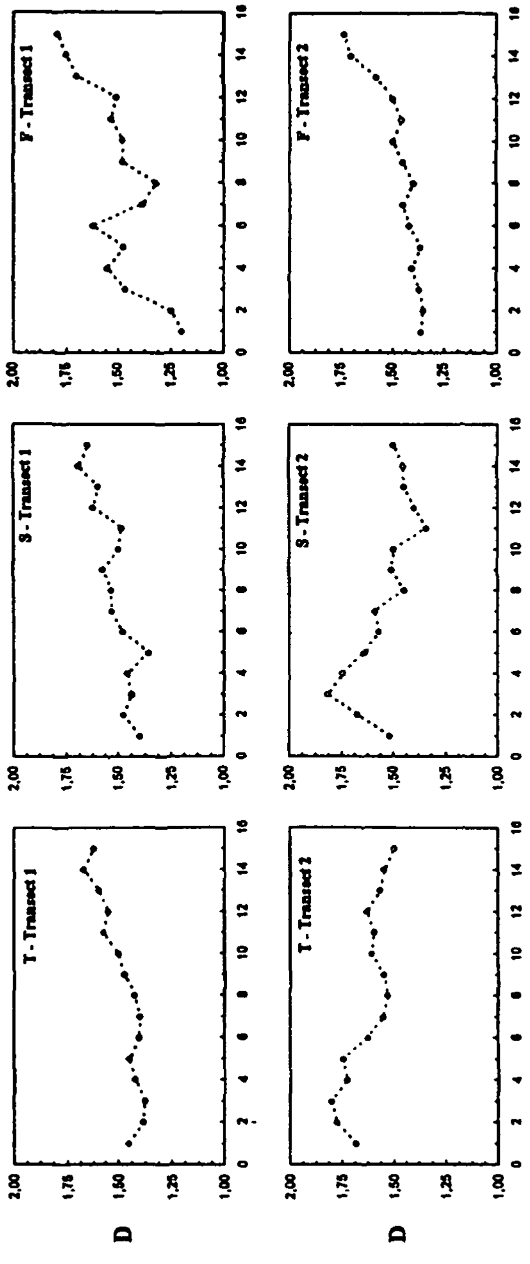
Fig. 2. Double logarithmic semivariograms of temperature, salinity and *in vivo* fluorescence (from top to bottom) for inshore (a, c and e) and offshore (b, d and f) stations of the first transect, shown together with their best fitting line. m is the slope of the empirical semivariance $\gamma(h)$ versus the lag h, in a log–log plot.

as coordinates; a central square indicates the 95% confidence limits (Figure 5). The coordinates of the initial five spatio-temporal variables were also plotted considering the values of their corresponding eigen vectors. The observed means, standard deviations and fractal dimensions exhibited very specific behaviours (Table IV). The behaviour of observed means can be divided into two different groups. First, the means of salinity, transmission and PAR showed a tendency to increase from inshore to offshore waters, whereas temperature and *in vivo* fluorescence showed an inverse tendency. These results, in agreement with our previous clustering observations (cf. Figure 4b and Table III), can be related to the very specific hydrological structure observed in the eastern English Channel, characterized by an inshore–offshore gradient in terms of salinity, temperature, turbidity, phytoplankton and zooplankton biomass (Brylinski and Lagadeuc, 1990; Brylinski *et al.*, 1991).

The distribution of standard deviations (SD) and fractal dimensions (D) on the PCA plot leads to further conclusions. The standard deviations of temperature and salinity exhibit very similar behaviours, showing a higher vertical variability for inshore waters where mixing processes associated with tidal drift are more developed. On the contrary, the vertical variability of *in vivo* fluorescence and transmission is higher during flood and ebb tides, respectively, but is also slightly higher for inshore than offshore waters. These observations suggest a differential alteration of the mean vertical properties of water masses associated with both inshore–offshore gradient and tidal advection. Therefore, in the case of purely passive scalars (such as temperature and salinity), fluctuations are directly linked with tidal mixing processes, whereas in the case of transmission and fluorescence, other processes—related to physical and chemical properties of particulate matters or the species composition and physiological state of phytoplankton cells—get into action and should be taken into account very carefully. Only the fractal dimensions estimated for *in vivo* fluorescence are significantly correlated with the two first principal components in the case of fluorescence (Figure 5; Table IV). This last observation confirms the absence of systematic variations observed in the spatial distribution of temperature and salinity fractal dimensions, and the tendency to increase of fluorescence fractal dimensions along each transect (cf. Figure 3). *In vivo* fluorescence fractal dimension is then higher for offshore stations and during ebb tide.

Discussion

The empirical fractal dimensions, estimated over the whole range of considered scales for offshore and inshore stations, suggest that the scales of spatial dependence are very similar for *in vivo* fluorescence, salinity and temperature, indicating similar sources of physical and biological patterns. However, as shown by the spatio-temporal analysis, fractal dimensions of salinity and temperature are tidally and geographically independent, in opposition to fluorescence fractal dimensions, obviously higher in offshore waters (cf. Figure 5 and Table IV). The vertical structure of *in vivo* fluorescence is then more homogeneous, or less structured, in offshore locations where the mean observed values of fluorescence are low, suggesting a link between the structure and the strength of the fluorescence signal (i.e. phytoplankton biomass). Indeed, considering the absence of photoinhibition (i.e. a clear decrease of *in vivo* fluorescence around solar midday; Falkowski and Kiefer, 1985), phytoplankton biomass distribution in the eastern English Channel might then be strongly density dependent, whereas Prairie and Duarte (1996) found a weak density dependence in a set of various marine and freshwater phytoplankton populations. In that way, because of the strong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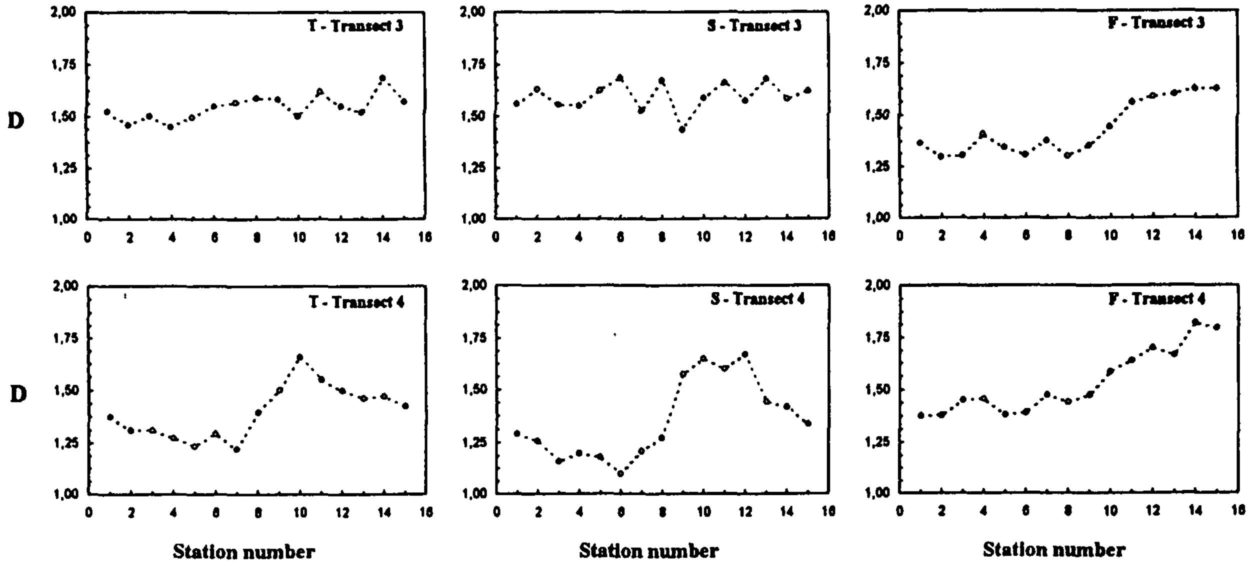

Fig. 3. Evolution of the fractal dimension D of temperature, salinity and *in vivo* fluorescence (from left to right) for each transect (from top to bottom), along the inshore–offshore transect.

Table II. The first two spatio-temporal eigen vectors (standardized after multiplication by the square root of the eigen vectors' corresponding eigen values) associated with the five spatio-temporal variables

	PC-1	PC-2
Latitude	–0.979	0.160
Longitude	0.981	–0.161
Depth	–0.977	–0.058
Sun elevation	–0.271	–0.906
Current direction	0.013	0.941

PC-1, first principal component; PC-2, second principal component.

Table III. Clusters of stations using the first two components of the PCA. Cluster analysis has been carried out on a Euclidean distance matrix calculated from the two first principal components of the PAC

C-I	C-II	C-III	C-IV
T_{1-1}–T_{1-10}	T_{1-11}–T_{1-15}	T_{2-14}–T_{2-15}	T_{3-1}–T_{3-7}
T_{2-1}–T_{2-7}	T_{2-10}–T_{2-13}	T_{3-8}–T_{3-15}	T_{4-1}–T_{4-6}
T_{4-7}–T_{4-8}	T_{4-9}–T_{4-15}		

C, cluster; T_{i-j}, transect number (*i*) and station number (*j*).

hydrodynamic conditions occurring in the eastern English Channel, the observed density dependence could be a consequence of the aggregation processes of phytoplankton cells, mainly driven by phytoplankton density and hydrodynamics (Riebesell, 1991a,b; Kiørboe, 1997). Fractal dimension of fluorescence also exhibits a tidal dependence, leading to an inverse relationship between fractal dimension and standard deviation of fluorescence (cf. Figure 5). Fractal dimension and standard deviation are then higher during ebb and flood, respectively. However, even if precise phenomenological arguments are still lacking to explain these differences, it can be suggested that horizontal advection processes associated with the semidiurnal M2 tidal component can be responsible for the advection of different water masses through the entire water column, and modify the biological structure of the water column, leading to a differential tidal control in terms of biological variability and heterogeneity between inshore and offshore waters. Whatever that may be, we showed that in tidally mixed coastal waters the vertical variability of both physical and biological parameters could be wholly characterized in terms of heterogeneity on small scales (i.e. the scale of the water column). Moreover, the vertical variability and its related heterogeneity present very specific patterns in time and/or in space on larger scales (i.e. scales related to the tidal cycle and to the inshore–offshore hydrological gradient).

Previous studies on the dynamics of plankton populations have generally underscored the importance of both temporal and spatial variability of biomass and population structure (e.g. Haury *et al.*, 1978). Our results indicate that the variability—in so far as it describes the amplitude of fluctuations around a mean value—is an insufficient parameter to characterize the structure of a given

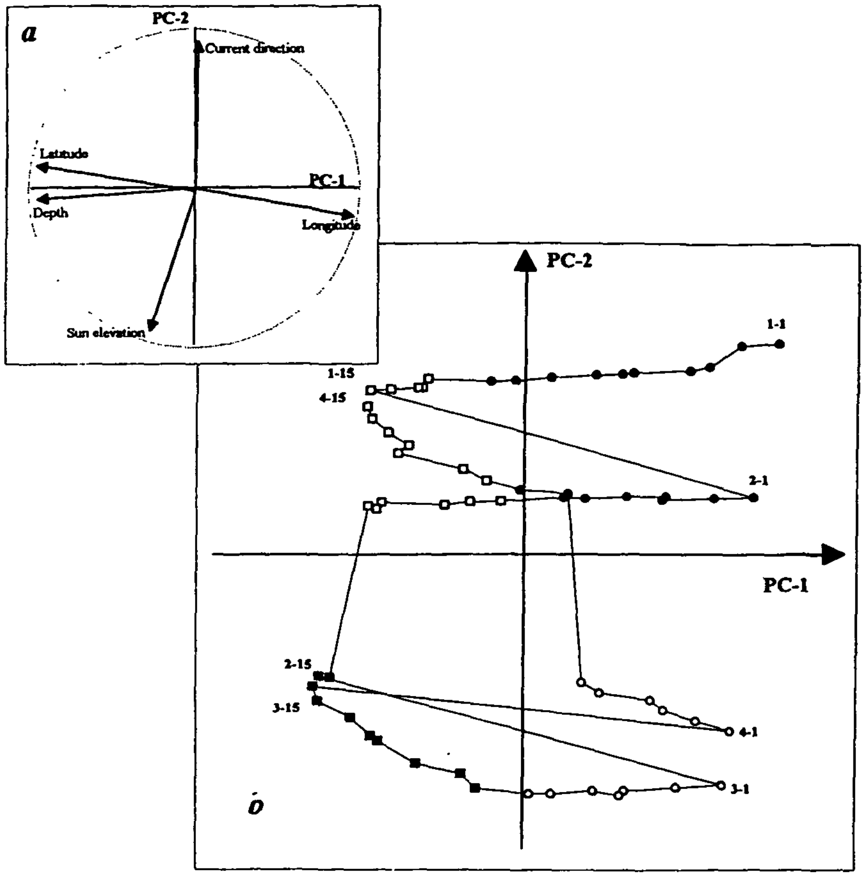

Fig. 4. Correlation circle showing (a) the position of the initial variables and (b) the position of the stations in the bidimensional space of the principal axes PC-1 and PC-2. Clusters are shown by dark circles (C-I), open squares (C-II), dark squares (C-III) and open circles (C-IV).

process. Describing and characterizing this variability is, however, a main problem in plankton ecology, especially given recent developments in methods for continuously recording at high spatial and temporal resolution (Dickey, 1988, 1991). In that way, the main contribution of semivariogram analysis and fractal dimensions is then to identify and to characterize the scales of spatial dependence—as well as the scales of temporal dependence (e.g. Seuront and Lagadeuc, 1997)—which are of main interest to appreciate the nature and magnitude of sources of variability, critical for understanding the underlying biological and physical processes. Moreover, quantitative characterization of patterns, as realized in the framework of fractal dimensions, provides a basis for comparing models to data, and biological to environmental fluctuations. Such an approach also has considerable implications for the design and evaluation of sampling schemes in coastal as well as in open ocean. Indeed, the accuracy of a regional

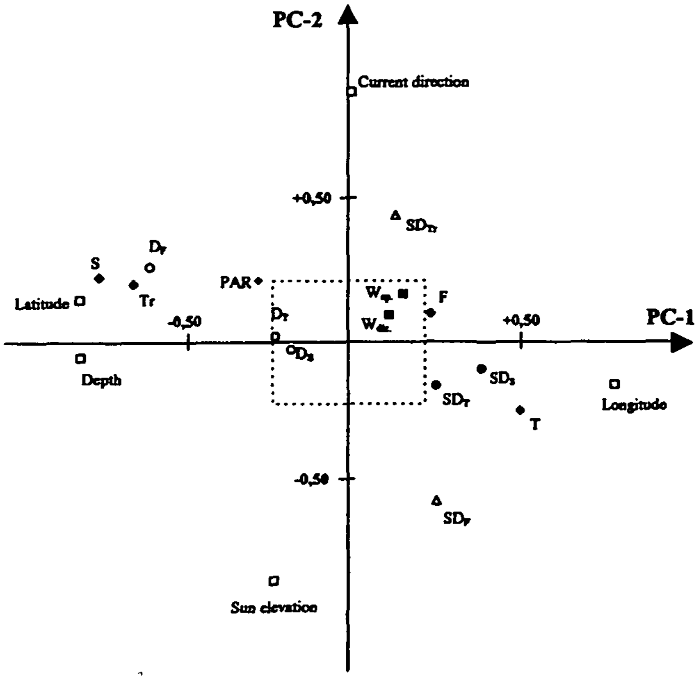

Fig. 5. Position of the 14 factors (for codes, see Table IV) in the bidimensional space of PC-1 and PC-2. The coordinates are the correlation coefficients with these axes. The five initial coordinates (no abbreviations) are placed with the corresponding elements of the eigen vectors (standardized after multiplication by the square root of the corresponding eigen values). Factors significantly correlated with PC-1 and/or PC-2 are located outside the central square, corresponding to the 95% confidence interval.

estimate of a spatially dependent parameter (i.e. temperature, salinity and *in vivo* fluorescence) will depend on both fractal dimension estimates and the scale at which measurements are taken. In contrast, the accuracy of a regional estimate of a spatially independent (e.g. transmission) parameter will depend only on the number of observations.

This paper has presented evidence for the potential of spatio-temporal analysis, used in conjunction with semivariogram and fractal analyses, to become an important descriptive tool in plankton ecology. Furthermore, distinguishing between variability and heterogeneity, such an approach provides new insights into the spatial and temporal structure of highly fluctuating patterns and processes, the understanding of which is actually a major issue in marine ecology. Indeed, both physical and biological small-scale variability experienced by planktonic organisms have been shown to have important implications for foraging, growth and population dynamics (Goldman, 1988; Costello *et al.*, 1990; Marrasé *et al.*, 1990; Davis *et al.*, 1991; Rothschild, 1992), while heterogeneity (i.e. a structured variability in space and/or in time) is increasingly regarded as an intrinsic property of ecosystems (Levin, 1976; Chesson, 1986; Chesson and Case, 1986; Naeem and Colwell, 1991). Future studies investigating the magnitude of key

Table IV. Names and codes of the 14 additional variables used in the PCA, together with their correlation with the two first components of the PCA. The codes are used on the graphs

Additional data	Code	PC-1	PC-2
Mean value			
Temperature	T	0.628	–0.259
Salinity	S	–0.912	0.244
Fluorescence	F	0.300	0.107
Transmission	Tr	–0.789	0.219
PAR	PAR	–0.327	0.232
Standard deviation			
Temperature	SD_T	0.320	–0.165
Salinity	SD_S	0.484	–0.102
Fluorescence	SD_F	0.320	–0.559
Transmission	SD_{Tr}	0.171	0.419
Fractal dimension			
Temperature	D_T	–0.267	0.022
Salinity	D_S	–0.205	–0.029
Fluorescence	D_F	–0.729	0.282
Wind speed	*Wsp.*	0.200	0.180
Wind direction	*Wdir.*	0.150	0.100

PC-1, first principal component; PC-2, second principal component.

fluxes (e.g. carbon or nitrogen cycles) in marine systems should then take advantage to focus on the ecological consequences of the spatio-temporal structure of variability and heterogeneity in order to provide the most precise understanding of a given system, critical to obtain robust estimates of stocks and fluxes (Platt *et al.*, 1989).

Acknowledgements

We would like to thank Bert Klein and one anonymous reviewer for their comments on an earlier version of the manuscript, and Fabrice Lizon for fruitful discussions. Thanks are also extended to the captain and crew of the N/O 'Sepia II' for their assistance during the cruise.

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Received on December 30, 1997; accepted on March 17, 1998