Relationships between Benthic Communities and Physical Environment in a Lagoon Ecosystem

Bertrand Millet† and Olivier Guelorget‡

†Centre d'Océanologie de
  Marseille
Université d'Aix-Marseille II
Campus de Luminy
F-13288 Marseille, France

‡Laboratoire d'Hydrobiologie
  Marine
Université de Montpellier II
Place Eugène Bataillon
F-34095 Montpellier, France

ABSTRACT ∎

MILLET, B. and GUELORGET, O., 1993. Relationships between benthic communities and physical environment in a lagoon ecosystem. *Journal of Coastal Research*, 9(2), 378–389. Fort Lauderdale (Florida), ISSN 0749-0208.

The Thau lagoon differs from other mediterranean lagoon sites in the apparent complexity of its benthic community structures, which seem to result from the relative complexity of its physical environment.

A statistical analysis of the relationship between the abundances and biomasses of benthic taxa and the lagoonal hydrodynamic characteristics was carried out. An ACE-type statistical algorithm is used to expose the non-linear relationships in multiple regressions. Polychaete and crustacean biomasses along with mollusc densities at 15 sampling stations are considered as dependent variables. The granulometric fraction of the sediment below 40 μ as well as hydrodynamic descriptors such as kinetic energy and the exchange term H$\cdot$V , resulting from a numerical modeling of circulation forced by stochastic winds, are considered as predictors.

The results demonstrate that the exchanges resulting from the hydrodynamic conditions within the watermass have a dominant beneficial influence on the development of each of the zoological groups considered. In addition, the importance of the sedimentary substrate is confirmed, but gives an interesting non-linear result, with a threshold between 3 and 6% of the fraction of fine particles below 40 μ. Apart from the quantification of this sedimentological indicator it appears that the dominant influence of the hydrodynamic exchange processes throughout the lagoon on the development of the benthic biological structures, quite independently of any bathymetric considerations, could give a new insight into the spatial organization of benthic communities in lagoonal ecosystems.

ADDITIONAL INDEX WORDS: *Coastal zone, benthos ecology, granulometry, hydrodynamic model, statistical analysis.*

INTRODUCTION

The Thau lagoon is unlike most other mediterranean lagoons, where observations typically show a biological organization along a very marked confinement gradient relative to the sea. On the contrary, benthic communities within the Thau lagoon look randomly distributed without any gradient clearly defined between sea inlets and the inner lagoon.

From a bionomic point of view, the Thau lagoon presents no unusual features, and for the most part of its surface area seems to be composed of only one biotope. This vast biotope should be classed under zones II and III of the paralic realm as defined by GUELORGET and PERTHUISOT (1983, 1992).

This lack of strict biological structuring normally found throughout the coastal systems and

shallow water bodies studied by GUELORGET *et al.* (1986, 1987, 1989, 1990), and by NICOLAIDOU *et al.* (1988), may be connected with a certain heterogeneity of the environment. This heterogeneity is linked in particular to the unusually diffuse nature of its contacts with the sea (two true channels, and percolation through the sand-bar), the complexity of an exceptionally variable bathymetry (alternating shallows and canyons of up to 10 meters deep), the presence of under-water freshwater springs, and finally the fixed shell-fish breeding structures occupying one-third of its surface.

Given the unusual character of the Thau lagoon, it seems logical to set aside the concept of a limited ecosystem organization around a strictly bi-polar gradient of the confinement between the sea and the continental shelves, to take a new and wider view, encompassing a possible simultaneous spatial distribution of several confinement gradients.

DATA AND METHODS

Area

The Thau lagoon is a French mediterranean brackish ecosystem (25 km long, 5 km wide and 10 m at its maximum depth) situated close to Sète Harbour (3°32'–3°42'E; 43°20'–43°28'N). A small catchment area (300 km²) provides irregular fresh water supply according to a sharply contrasted mediterranean climatic rate, while a permanent communication with the sea through Sète Harbour channels efficiently controls the water renewal (Figure 1).

Sampling Design

The study of the benthic communities and sediment was carried out as part of the integrated research program on fundamental ecology in the lagoonal environment (Ecothau program) whose scope and objectives are presented in AMANIEU *et al.* (1989).

The granulometric sediment analysis and the benthic macrofauna study were carried out using samples from 15 stations situated all over the lagoon. Sampling (4 samples of 0.1 m² per station) was carried out by divers using an Ekman dredger than sieved through a 1 mm² mesh.

Specific richness has been determined at each station, and quantitative data considered in the statistical analysis are density and biomass, which represent respectively the number of individuals found per m², and the weight per m² of decalcified dry organic matter.

Sediment Features

Figure 2 shows the spatial distribution of upper sediment granulometry resulting from the above-mentioned sampling. The sedimentology evolution of the Thau lagoon comprises successions of fairly similar granulometric zones, generally with a low rate of the less than 40 μ category. However, three zones of siltation must be noted:

(1) The shallow area "la Crique de l'Angle" which receives terrigenous inputs from the lagoon's principal tributary and where siltation is maximal.

(2) The central zone of the lagoon where the shell-fish breeding structures are fixed.

(3) Elsewhere, sampling showed the presence of variably coloured sandy or muddy-sand substrates. The sediments filling the basin are in general either: rough around the edges, in the south well graded by wave action, but of mixed size in the north owing to the terrigenous inputs, or finer in all the central part of the basin, independently of depth.

Hydrodynamic Modeling

A two-dimensional numerical model of the horizontal vertical-averaged circulation is applied to the Thau lagoon and is first presented in MILLET (1989). The model computes the wind-induced fields of flow and elevation values, according to the lagoon bathymetry, wind stress and bottom friction. The Coriolis force (weak) is considered and the non-linear advection terms are taken into account because of the steep bathymetric gradients, and the small size of the numerical grid (250 m). Horizontal turbulent viscosity is neglected and vertical turbulent viscosity is treated globally by the use of the terms of surface wind-shear and bottom friction. The two-dimensional conception of the model seems justified by the shallowness of the lagoon, and no thermal or saline stratification was observed. The basic equations of shallow water dynamics used are the following:

$$\delta U/\delta t + U\delta U/\delta x + V\delta U/\delta y - fV + g\delta\zeta/\delta x$$
$$- \tau_{sx}/\rho H + \tau_{bx}/\rho H = 0$$
$$\delta V/\delta t + U\delta V/\delta x + V\delta V/\delta y + fU + g\delta\zeta/\delta y$$
$$- \tau_{sy}/\rho H + \tau_{by}/\rho H = 0$$
$$\delta\zeta/\delta t + \delta(HU)/\delta x + \delta(HV)/\delta y = 0$$

where:

τ_{sx} and τ_{sy}: the components according to the horizontal directions of wind stress.

$\tau_{sx} = C_d\rho_a \cdot W^2 \cdot \sin \alpha$ and $\tau_{sy} = C_d\rho_a \cdot W^2 \cdot \cos \alpha$ (DRONKERS, 1964; CSANADY, 1982)

τ_{bx} and τ_{by}: the components according to the horizontal directions of bottom stress

$\tau_{bx} = [\rho g U(U^2 + V^2)^{1/2}]/C^2$ and $\tau_{by} = [\rho g V(U^2 + V^2)^{1/2}]/C^2$

U and V: the velocity components according to the two horizontal directions

f: $2 \cdot \omega \cdot \sin \lambda$: the Coriolis term

ω: angular speed of earth's rotation

λ: latitude

ζ: elevation of the basin compared with the original level at rest

H: total depth of the water column

ρ: density of the water considered constant

g: acceleration of gravity

C_d: wind-drag coefficient

ρ_a: air-density

α: wind-direction, constant over the entire area

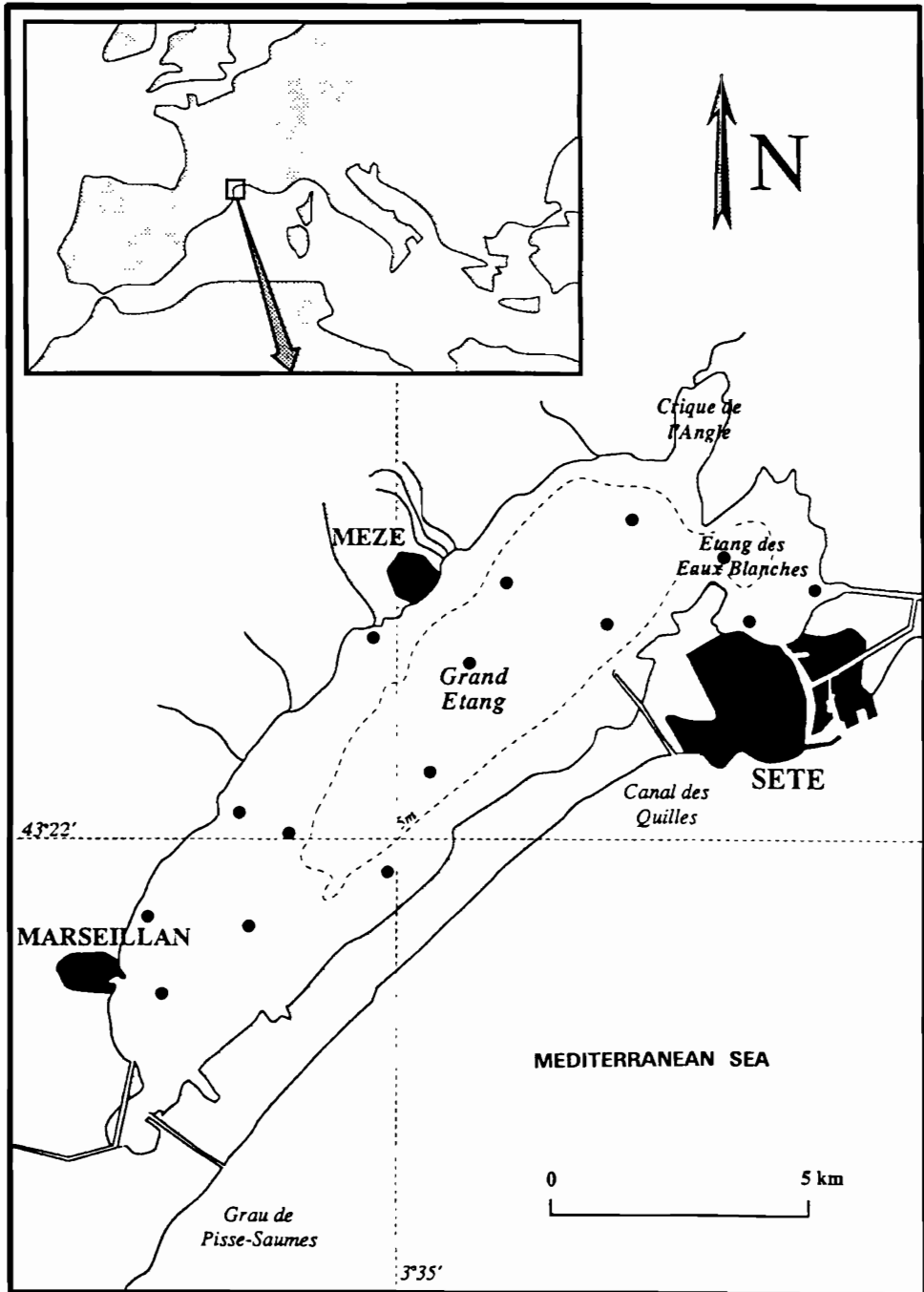W: wind velocity

C: Chézy coefficient

Figure 1.   General layout of the Thau lagoon showing the positions of the sampling stations.
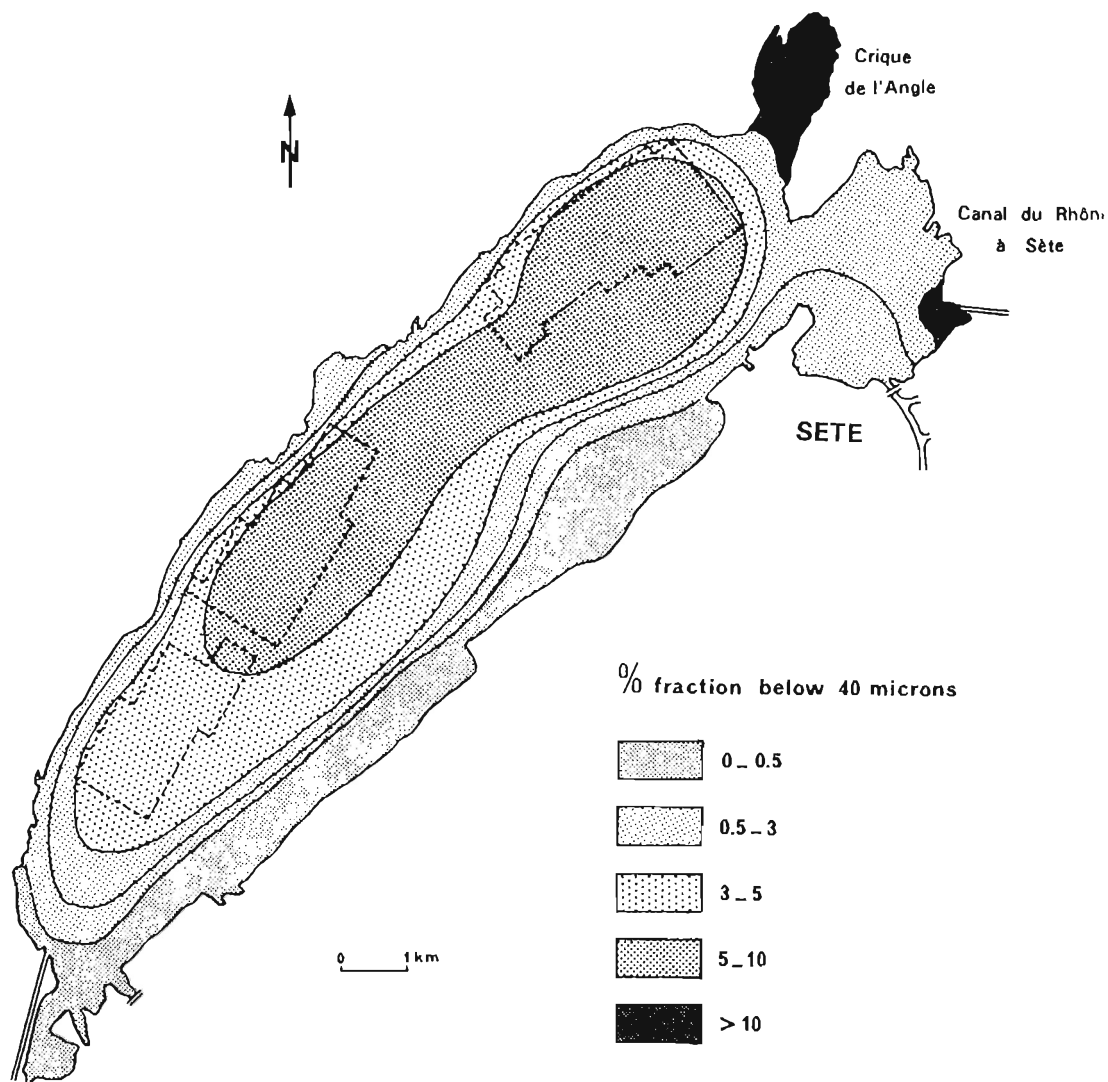
Figure 2.   Granulometry of the sediment layer (fraction below 40 μ).

The equations are solved in finite difference form with a classical ADI (Alternating Direction Implicit) numerical scheme (LEENDERTSE *et al.*, 1971; LEENDERTSE, 1984). Figure 3A presents the bathymetry of the lagoon and Figures 3B to E present the interannual typology of hydrodynamic motions within the lagoon computed from the typology of the local wind regime, corresponding to constant wind direction and intensity over periods of 24 hours at least, and describing respectively four dominant situations NW-325° (8 m·s⁻¹), W-290° (8 m·sec⁻¹), NE-45° (5 m·sec⁻¹) and SE-110° (8 m·sec⁻¹). These four stationary wind situations are statistically representative of the local climatic regime and represent respectively 25%, 18%, 15% and 9% of the annual time, consistently with the 25-yr climatic stochastic analysis. A 48-hr simulation is performed for each typical climatic situation previously described, using a 250-meter mesh and a 1-minute time-step,
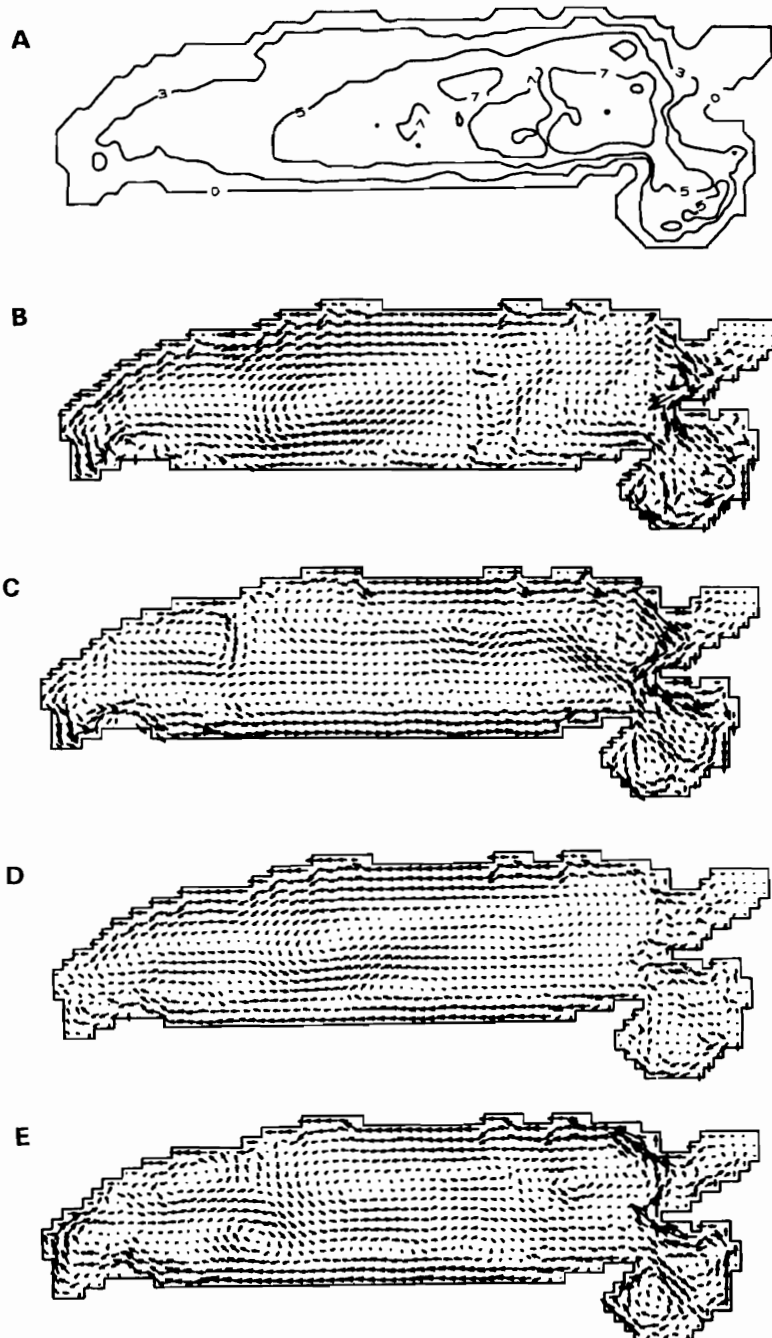
Figure 3. (A) Bathymetry of the Thau lagoon (3 m, 5 m and 7 m-isolines). Velocity fields within the Thau lagoon, in relation to the local wind stochastic range, and computed at steady state from the 2-D numerical model (current scale: 3 mm = 15 cm·s⁻¹). (B) NW-325°—8 m·sec⁻¹ (25%); (C) W-290°—8 m·sec⁻¹ (18%); (D) NE-45°—5 m·sec⁻¹ (15%) and (E) SE-110°—8 m·sec⁻¹ (9%).

with constant wind direction and intensity in order to reach a steady state for computed elevations and velocities.

The hydrodynamic information computed from each simulation, corresponding to each climatic situation, is then synthesized through three types of physical descriptors, as the kinetic energy $\rho V^2/2$, the bottom stress $\rho g V^2/C^2$, and the global term H^2V^2, computed at each mesh-location of the model from velocities and elevations. We did not consider the term $\rho HV^2/2$ because of redundant results with the kinetic term $\rho V^2/2$. Chézy coefficient C is depth-dependent and computed from a constant Manning coefficient k with the formula $C = kH^{1/6}$. A spatial range is obtained for Chézy coefficient between C = 45 and C = 64 Sl, using the fixed value k = 45 Sl for each simulation. The local kinetic energy is related to the extent of vertical diffusive exchange through the water column. The magnitude of bottom stress reflects the likelihood of sediment disturbance. The descriptor H^2V^2 gives a measure of the vertical and horizontal diffusive exchange rate through the whole water mass, and can be used as an effective coefficient of horizontal diffusion by vertical-shear effect (SAFFMAN, 1962; BOWDEN, 1965).

These physical descriptors are then considered on an interannual scale, and a single weighted average value is then computed for each of them, taking into account simultaneously the relative weights of the typical wind frequencies previously described: NW-325 (0.35), W-290 (0.28), NE-45 (0.23) and SE-110 (0.14).

Figure 4A shows the bottom stress isolines averaged on an interannual scale. This map suggests a spatial variation of potential sediment erosion throughout the lagoon, which seems consistent with the upper sediment granulometry (Figure 2). This similarity between the mapping of substrate characteristics and the computed erosive potential distribution in the lagoon emphasizes the influence of hydrodynamics in the ecological functioning of the lagoon, and confirms the ability of the model to express the spatial distribution of physical energies.

Figure 4B shows the spatial structure of H^2V^2 term isolines averaged on an interannual scale. A distinction may be observed between the eastern and western parts of the lagoon, along a diagonal line running north-south as described in MILLET (1989). Experiments showed that the H^2V^2 isolines were homogeneously distributed all over the lagoon area for the low range values below 0.1 Sl,

but strictly gathered in the eastern part of the lagoon for the high range values between 0.1 and 0.5 Sl.

The eastern part of the lagoon featured by a high rate of longitudinal dispersion by shearing (high H^2V^2 range), associated with hydrodynamic heterogeneity and gyratory structures (Figure 3), may be considered as a zone of vertical and horizontal exchanges throughout the water masses, and characterized by high ecological receptivity.

In contrast, the western part of the lagoon, showing rapid and homogeneous fluxes of large water masses (Figure 3), associated with a lack of longitudinal dispersion by shearing (low H^2V^2 range only), may be considered as an energy distribution zone with low ecological receptivity.

Statistical Method

We use an Alternating Conditional Expectation (ACE) iterative algorithm, developed by BREIMAN and FRIEDMAN (1985), which empirically computes optimal transformations for multiple regressions of ecological parameters. The dependent Y variable and all predictor variables $X_1 \ldots X_p$ are replaced by functions $T_1(Y), T_2(X_1), \ldots, T_{p+1}(X_p)$ to maximize the correlation coefficient in the following linear model: $T_1(Y) = T_2(X_1) +, \ldots, + T_{p+1}(X_p)$. The main advantage of this method is that the algorithm converges each time toward an optimal and single solution that is empirically defined without any previous assumption concerning patterns of distribution. The results are then expressed by simply plotting the transformed values against the original data for each variable considered in the model. The stability of the transformed function, the range of the transformed values, and the regression coefficient are retained as the most explicit criteria to identify accurate relationships. MENDELSSOHN and CURY (1987), CURY and ROY (1989), MILLET and CECCHI (1992) have previously used this procedure to emphasize the ecological importance of the wind stress variability in fish recruitment, and phytoplankton dynamics. This method will be tested here, in lagoon field, to deal with the non linear relationship assumed between the benthic communities, the granulometry of the upper sediment and the wind-induced hydrodynamic features within the water mass.

RESULTS

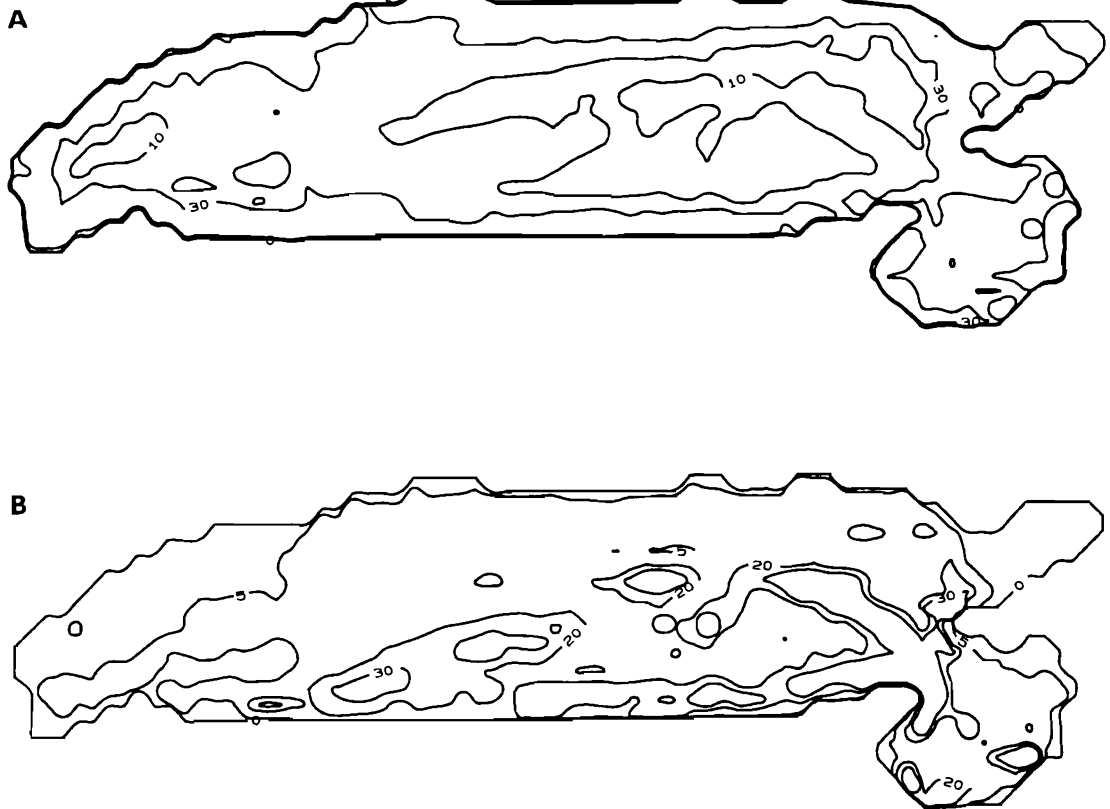The polychaete and crustacean biomass and the mollusc density sampled at the 15 stations pre-

Figure 4. Spatial and stochastic features on an interannual time scale of: (A) bottom stress isolines: 10 and 30·10 $^{-4}$ SI. (B) diffusive exchange term H^2V^2 isolines: 5, 20 and 30·10 $^{-2}$ SI.

viously described are successively considered as the dependent variable in the ACE algorithm. The granulometry (fraction of fine particles below 40μ) regressed on the kinetic energy, and the kinetic energy regressed on the interannual averaged H^2V^2 term gave respective correlation coefficients $r = -0.54$ and $r = 0.35$, revealing high dependences between these predictors which are considered separately in the ACE computations. Inversely, the granulometry and the H^2V^2 term are simultaneously considered in the ACE computations, despite the low dependence between these predictors ($r = 0.16$), to test the stability of the information obtained from the single-predictor computations.

Several attempts showed that the most meaningful information was given by the spatial average of the hydrodynamic terms over sets of four meshes, corresponding to a surface area of 500 meters square, which is a spatial scale quite consistent with the complex hydrodynamic structures of the eastern part of the lagoon (Figure 3).

The ACE computation is first applied to the crustacean biomass with only one predictor and gave the best results with the kinetic energy predictor ($r^2 = 0.68$ on Figure 5) and also good results with the granulometry predictor ($r^2 = 0.57$ on Figure 6). The results obtained with the H^2V^2 predictor alone are not shown and only explained 23% of the variance with a small range of transformed values. Transformation of the crustacean biomass is in both cases quite linear with a positive slope (Figures 5A and 6A). Transformation of the kinetic energy is almost linear with a positive slope (Figure 5B), which suggests a beneficial effect of the rate of physical energy within the water column on the crustacean activity. Transformation of the granulometry presents two dif-
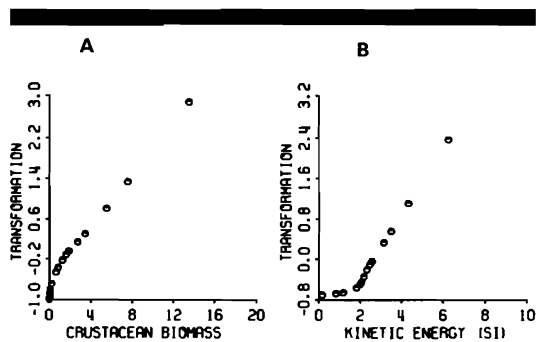
Figure 5. ACE optimal transformations for the crustacean bio-mass (A) and the kinetic energy predictor (B).

Figure 6. ACE optimal transformations for the crustacean bio-mass (A) and the granulometry predictor (B).

ferent negative slopes with a discontinuity for fractions of fine particle around 3% (Figure 6B), which suggests a beneficial effect of the coarse granulometry on the crustacean biomass, and especially for fractions below 3% of fine particles. A good fit is obtained by simultaneously computing crustacean biomass with the granulometry and the H^2V^2 predictors, less dependent on the granulometry than the kinetic energy (Figure 7), and the transformation of the crustacean biomass shows a positive linear relationship that accounted for 64% of the variance. Nevertheless Figure 7 shows redundant information with previous computations which used single predictors, and remains, despite two predictors, less significant than the kinetic energy computation (Figure 5). This latter test confirms the major contribution of the high rate of kinetic energy within the water column to develop crustacean biomass. This result confirms that crustaceans fit in with an environment characterized by rough sediments and relatively high energetic water bodies, associated with a rapid renewal of food particles.

The computation is then applied to the poly-chaete biomass with the same sets of predictors, and gave good results with the kinetic energy predictor ($r^2 = 0.57$ on Figure 8) and so significant with the granulometry predictor ($r^2 = 0.53$ on Figure 9). The results obtained with the H^2V^2 predictor alone are not shown and only explained 29% of the variance with again a small range of transformed values. Transformation of the poly-chaete biomass is in both cases slightly curved with a positive slope (Figures 8A and 9A). Transformation of the kinetic energy presents a linear positive relationship (Figure 8B), which suggests a beneficial effect of the rate of physical energy
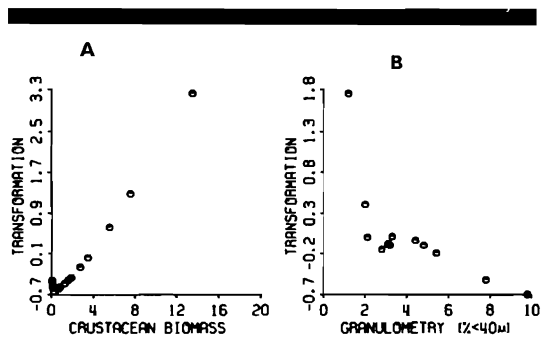
within the water column on the polychaete activity. Transformation of the granulometry is slightly curved with a negative slope which remains steep until the fraction of the fine particles reaches a value around 5%, and then becomes slightly positive for finest sediments (Figure 9B). This result indicates that the polychaete development is enhanced by rough granulometry below the fraction of 5% of fine particles, but seems no longer concerned by a finer sedimentary environment. Furthermore, the best fit is obtained by simultaneously computing polychaete biomass with the granulometry and the H^2V^2 predictors (Figure 10), where the transformation of the poly-chaete biomass shows a positive linear relationship that accounted for 78% of the variance. The results on Figure 10 are consistent with results previously described using single predictors, and confirms, more clearly than in the crustacean case, the large contribution of both the high rate of physical energy within the water mass and also the sediment feature to explain polychaete development.

The computation is then applied to the mollusc density with the same sets of predictors, but the best results are obtained by computing mollusc density with the diffusive exchange term H^2V^2 ($r^2 = 0.72$ on Figure 11) and insufficient results are obtained with the granulometry predictor ($r^2 = 0.33$ on Figure 12). The results obtained with the kinetic energy predictor alone are not shown and only explained 41% of the variance. Transformation of the mollusc density is curved with the H^2V^2 predictor (Figure 11A) and almost linear with the granulometry predictor (Figure 12A), with in both cases a positive slope for densities higher than 50. Transformation of the H^2V^2 term is curved
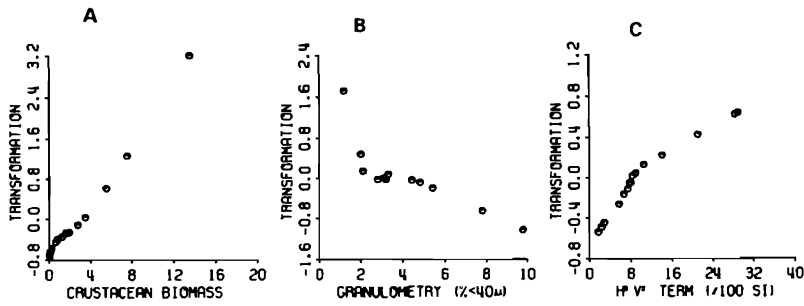
Figure 7.   ACE optimal transformations for the crustacean biomass (A), the granulometry (B), and the H²V² hydrodynamic predictors (C).

with a positive slope for values higher than 0.08 Sl (Figure 11B), which suggests a beneficial effect of the rate of the diffusive exchange processes throughout the water mass on the mollusc activity. Transformation of the granulometry is dome-shaped and shows a steep negative slope for fractions below 3% of the fine particles, and then a positive relationship for higher fractions corresponding to the finest sediments (Figure 12B). This result indicates a beneficial effect of both a rough sediment (below 3% of fine particles) and also a fine sediment (beyond 6% of fine particles) to the mollusc settlement, with a detrimental effect of a granulometry around 4–5% of fine particles. Furthermore, the best fit is obtained by simultaneously computing mollusc density with the granulometry and the H²V² predictors (Figure 13), where the transformation of the mollusc density shows a positive relationship that accounted for 80% of the variance. The results on Figure 13 are quite consistent with results previously de-scribed using single predictors, and reinforce the important role of the sediment feature to control mollusc development. The results suggest a detrimental effect of a threshold granulometry around 4–5% of fine particles, and a beneficial effect of both coarser and finer fractions.

DISCUSSION

The results obtained from the ACE computations previously described give a new insight into the variations of three benthic communities (polychaetes, molluscs and crustaceans) according to the physical environment in the lagoon. It appears that this physical environment may be significantly described using two descriptors: a sedimentological descriptor quantifying the fine fraction of sediment below 40 μ, and a hydrodynamic descriptor resulting from a numerical model with stochastic value, quantifying the rate of kinetic energy within the water column, or the capacity for diffusive exchange throughout the water mass.
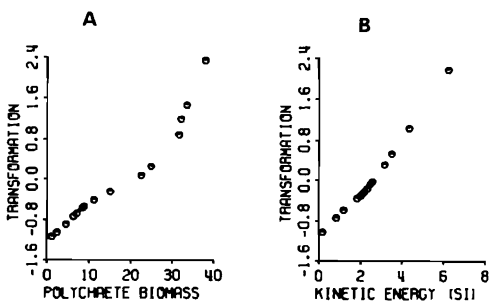

Figure 8.   ACE optimal transformations for the polychaete biomass (A) and the kinetic energy predictor (B).
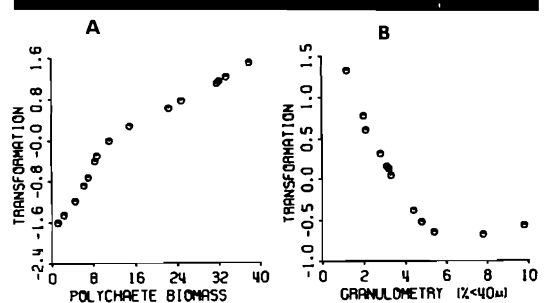

Figure 9.   ACE optimal transformations for the polychaete biomass (A) and the granulometry predictor (B).
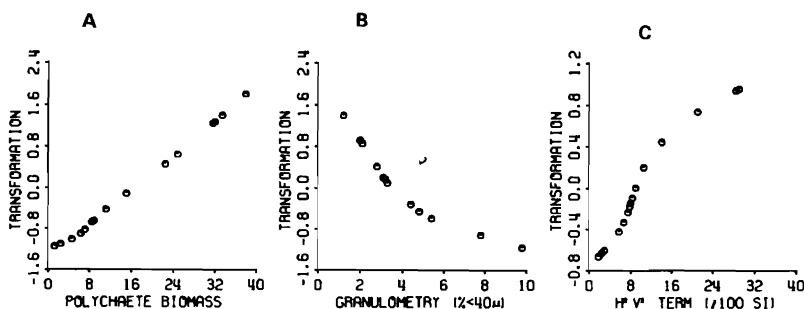
Figure 10. ACE optimal transformations for the polychaete biomass (A), the granulometry (B), and the H^2V^2 hydrodynamic predictors (C).

The high correlation coefficient values obtained in all these computations express the high explanatory level of the descriptors considered with regard to the variations of mollusc densities and polychaete and crustacean biomasses in the lagoon.

If similar results are obtained for the three biological communities, biomass is considered for the crustaceans and polychaetes, and density for the molluscs. This distinction is not the result of an "*a priori*" choice, but corresponds to the best results given by the exploratory ACE statistical computations. Moreover, this distinction reflects the optimal experimental conditions for counting molluscs that leads to more accurate density than biomass.

Granulometry, expressed through the fine fraction of upper sediment fraction below 40 μ appears to be a determinant ecological descriptor as regards the spatial organization and dynamics of the benthic macrofauna, and more clearly for crustaceans and polychaetes than for molluscs,

but with non-linear results showing specificities for each zoological group (Figures 6, 9 and 12). The negative effect on the crustacean and polychaete communities of an increase in fine sedimentary particles (Figures 6B and 9B) may be explained by their nectobenthic position, their relative independence in relation to the substrate and the recognized beneficial effect of a coarser sediment on the establishment and proliferation of the principal lagoonal species. The pole corresponding to coarse sediments on Figure 9B may coincide with the abundance of muddy-sand living species such as the polychaetes *Glycera convoluta, Nephtys hombergii,* and the fine sediment pole may coincide with the presence of mud-living species such as the *Capitellidae.* The results obtained for the molluscs (Figure 12B) reveal two poles corresponding to two positive effects situated at the extremes of the granulometric scale used. The pole corresponding to coarse sediments may coincide with the abundance of species such as *Venerupis aurea, Venerupis decussata* and
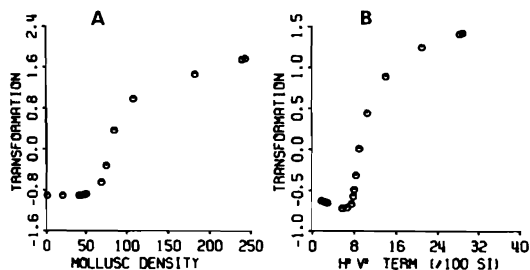

Figure 11. ACE optimal transformations for the mollusc density (A) and the H^2V^2 hydrodynamic predictor (B).
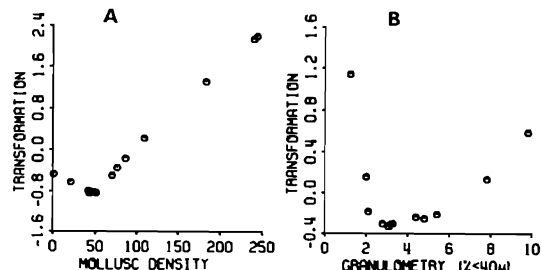

Figure 12. ACE optimal transformations for the mollusc density (A) and the granulometry predictor (B).
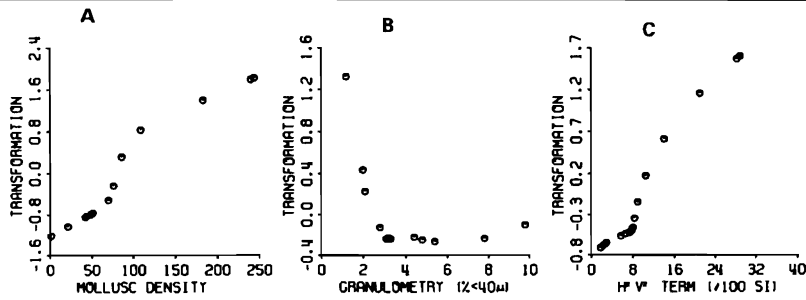
Figure 13.   ACE optimal transformations for the mollusc density (A), the granulometry (B), and the H^2V^2 hydrodynamic predictors (C).

Loripes lacteus, and at the other end of the scale, mud-living species such as *Abra ovata* and *Cerastoderma glaucum.* For each of these groups, transformation functions of the granulometry present slope discontinuities which correspond to different fraction values: 3% for crustaceans, 5% for polychaetes and a threshold between 3 and 6% for molluscs (Figures 6B, 9B and 12B). These threshold values cannot yet be accepted as an absolute quantification, and require validation in other coastal environments. However, this pattern may already be related to the limit which marks the passage from the marine domain (zone III) to the paralic domain proper (zone IV), as defined by GUELORGET and PERTHUISOT (1983, 1992) in coastal systems. Indeed, zone III is simply a transition zone classed as "mixed", since it supports species found both in sea and in lagoon, while zone IV alone is colonized by strictly paralic species.

The hydrodynamic descriptor appears indispensable to obtaining meaningful information from all the ACE computations.

The kinetic energy acts as a dominant descriptor with a positive curve and best correlation coefficients regarding the crustaceans (Figure 5B), and as an equivalent descriptor to the granulometry regarding the polychaetes (Figure 8B). This result presented by crustaceans and polychaetes might be related to a great sensitivity to energetic physical conditions within the water column immediately above. Figure 8 shows the higher transformation values (T(Y)max = 3.0 and T(X)max = 2.4) corresponding to higher values for both crustacean biomass and kinetic energy. This correspondence emphasizes the beneficial influence of high energetic sites for crustacean develop-

ment, and can be related in this study to a local abundance of a sand living species *Uppogebia littoralis* collected in the southern part of the lagoon which is characterized by shallow depths, coarse sediments and a high kinetic energy level (Figures 2 and 3).

The best fit is obtained in computing the mollusc density with the diffusive term H^2V^2. This result might be related to the great sensitivity of the filters to the rate of vertical and horizontal diffusive exchange throughout the water masses. Furthermore, this result leads to the hypothesis that the gradient of confinement relative to the sea (related to the sea-water renewal) could be physically incorporated in this hydrodynamic descriptor. Now this descriptor brings out the potentialities of vertical diffusive exchange, which is important, but even more so horizontally, which puts it in the forefront as an aid to understanding the organization of the lagoon's energetic and trophic systems. This descriptor would also be invaluable for expressing the exchange potentiality at any point in the lagoon, and thus its diffusive exchange capacity with neighbouring water masses, and, by degrees, with an exterior marine environment.

This analysis is based on both a classic survey of the principal ecological structures functioning together in a lagoon ecosystem (granulometry and benthic communities), and on a generalized timescale numerical computation of spatial distribution conditions of the energies within the water masses (hydrodynamic modeling). This dual approach is reinforced by the use of a powerful statistical algorithm which gives a new insight into the hierarchical description of the dominant environmental factors involved in the functional or-

ganization of the lagoon ecosystem. This case study of the seemingly most unusual Thau lagoon reinforces the major role of hydrodynamic conditions within the water masses together with the classic sedimentological characteristics of the lagoon in a better understanding of the benthic communities spatial patterns. Crustaceans and polychaetes benefit from a high level of kinetic energy within the water column; and molluscs from a high rate of diffusive exchange throughout the water masses. The beneficial impact of the coarse sediment (related to high energetic conditions) is also emphasized for the three groups considered.

The classic concept of depth gives way, here, to hydrodynamic concepts which seem to open up new fields of investigation concerning a dynamic approach to such a complex lagoonal ecosystem.

LITERATURE CITED

AMANIEU, M.; LEGENDRE, P.; TROUSSELLIER, M., and FRISONI, G.F., 1989. Le programme "Ecothau": théorie écologique et base de la modélisation. *Oceanologica Acta*, 12, 189–199.

BOWDEN, K.F., 1965. Horizontal mixing in the sea due to a shearing current. *Journal of Fluid Mechanic*, 21, 83–95.

BREIMAN, L. and FRIEDMAN, J.H., 1985. Estimating optimal transformations for multiple regression and correlation. *Journal of American Statistical Association*, 80, 580–619.

CSANADY, G.T., 1982. *Circulation in the Coastal Ocean*. Dordrecht: Reidel.

CURY, P. and ROY, C., 1989. Optimal environmental window and pelagic fish recruitment success in upwelling areas. *Canadian Journal of Fisheries and Aquatic Sciences*, 46, 670–680.

DRONKERS, J.J., 1964. *Tidal Computations in Rivers and Coastal Waters*. Amsterdam: North Holland, 517p.

GUELORGET, O. and PERTHUISOT, J.P., 1983. *Le Domaine Paralique: Expressions Géologiques, Biologiques et Economiques du Confinement*. Paris: Travaux du Laboratoire de Géologie, Ecole Normale Supérieure, 136p.

GUELORGET, O. and PERTHUISOT, J.P., 1992. Paralic eco-systems. Biological organization and functioning. *Vie et Milieu*, 42(2), 215–251.

GUELORGET, O.; FRISONI, G.F.; MONTI, D., and PERTHUISOT, J.P., 1986. Contribution à l'étude écologique des lagunes septentrionales de la baie d'Amvrakia (Grèce). *Oceanologica Acta*, 9, 1, 9–17.

GUELORGET, O.; PERTHUISOT, J.P.; FRISONI, G.F., and MONTI, D., 1987. Le rôle du confinement dans l'organisation biogéologique de la lagune de Nador (Maroc). *Oceanologica Acta*, 10(4), 435–444.

GUELORGET, O.; FRISONI, G.F.; XIMENES, M.C., and PERTHUISOT, J.P., 1989. Expressions biogéologiques du confinement dans le Lac Melah (Algérie). *Revue d'Hydrobiologie Tropicale*, 22(2), 87–99.

GUELORGET, O.; GAUJOUS, D.; LOUIS, M., and PERTHUISOT, J.P., 1990. Macrobenthofauna of lagoons in Guadeloupean mangroves: Role and expression of the confinement. *Journal of Coastal Research*, 6(3), 611–626.

LEENDERTSE, J.J., 1984. *Verification of a Model of the Eastern Scheldt*. Santa Monica, California: Rand Corporation, R-3108-NETH, 127p.

LEENDERTSE, J.J. and GRITTON, E.C., 1971. *A Water Quality Simulation Model for Well-mixed Estuaries and Coastal Seas: Computation Procedures*. Santa Monica, California: Rand Corporation, R-708-NYC, 53p.

MENDELSSOHN, R. and CURY, P., 1987. Fluctuations of a fortnightly abundance index of the ivoirian coastal pelagic species and associated environmental conditions. *Canadian Journal of Fisheries and Aquatic Sciences*, 44, 408–421.

MILLET, B., 1989. Fonctionnement hydrodynamique du Bassin de Thau. Validation écologique d'un modèle numérique de circulation. *Oceanologica Acta*, 12(1), 37–46.

MILLET, B. and CECCHI, P., 1992. Wind-induced hydrodynamic control of phytoplankton biomass in a lagoon ecosystem. *Limnology and Oceanography*, 37(1), 140–146.

NICOLAIDOU, A.; BOURGOUTZANI, F.; ZENETOS, A.; GUELORGET, O., and PERTHUISOT, J.P., 1988. Distribution of molluscs and polychaetes in coastal lagoon in Greece. *Estuarine, Coastal and Shelf Sciences*, 26, 337–350.

SAFFMAN, P.G., 1962. The effect of wind shear on horizontal spread from an instantaneous ground source. *Quarterly Journal of the Royal Meteorological Society*, 88, 382–393.