

Spatial and seasonal variability in the relationships between benthic communities and physical environment in a lagoon ecosystem

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ABSTRACT: Hydrodynamic processes within a shallow Mediterranean lagoon, the Etang du Prévoist in southwestern France, are essentially controlled by the combined effects of tide and wind, which induce both horizontal advection and vertical turbulent diffusion. The spatial distribution of macrobenthic organisms within this lagoon varies seasonally, according to variability in the hierarchy of the forcing environmental conditions. A 2-dimensional numerical model is used to compute spatial distributions in the lagoon of the tide- and wind-induced hydrodynamic kinetic energy under typical environmental conditions. An Alternating Conditional Expectation (ACE) algorithm is used to demonstrate non-linear spatial and seasonal relationships in multiple regression between benthic communities and physical environment. Mollusc and crustacean biomasses at 8 sampling stations are considered as dependent variables in the ACE analyses, while the distance of each sampling station from the sea inlet, the granulometry of the upper sediment (fraction of fine particles below 40 μm), and the computed tide- or wind-induced kinetic energy are considered successively as predictors. Results provide insight into the relationships between benthic macrofauna and sediment or hydrodynamic features, and especially into the spatial and seasonal variability of these relationships. Spatially, results emphasize the distinction between the optimal development of molluscs, associated with the energetic physical environment prevailing at seaward locations, and that of crustaceans associated with the more confined environment prevailing landwards. In addition, a distance of 1.6 km from the sea inlet is computed and proposed as the maximum spatial extension in the inner lagoon of a specific marine influence. Temporally, the major contributions of distance from the sea inlet, granulometry and tide-induced hydrodynamics, in regressions from January to May, confirm the central role of sediment features and tidal impact in explaining the seasonal variability of benthic macrofauna from winter to spring, related to the recruitment dynamics of marine larvae. Also seasonally, the increasing efficiency as a predictor of tide-induced kinetic energy from May to October supports a beneficial impact of marine water circulation on benthic macrofauna in preventing, at seaward locations, the anoxia which prevails in the inner lagoon in summer.

KEY WORDS: Lagoon · Mollusc · Crustacean · Granulometry · Kinetic energy · Statistical analysis · Hydrodynamic model

INTRODUCTION

Hydrodynamic processes in lagoons are essentially controlled by external energy inputs from tide or wind stresses, which induce both horizontal advective dispersion and turbulent vertical exchanges within the water masses (Kullenberg 1978). However the spatial

pattern, seasonal dynamics and biological efficiency of horizontal and vertical physical processes are quite different according to whether the dominant forcing function is the wind or the tide.

Previous studies have clearly demonstrated the central role of tide- and wind-induced physical processes in the control of phytoplankton dynamics (Levasseur et

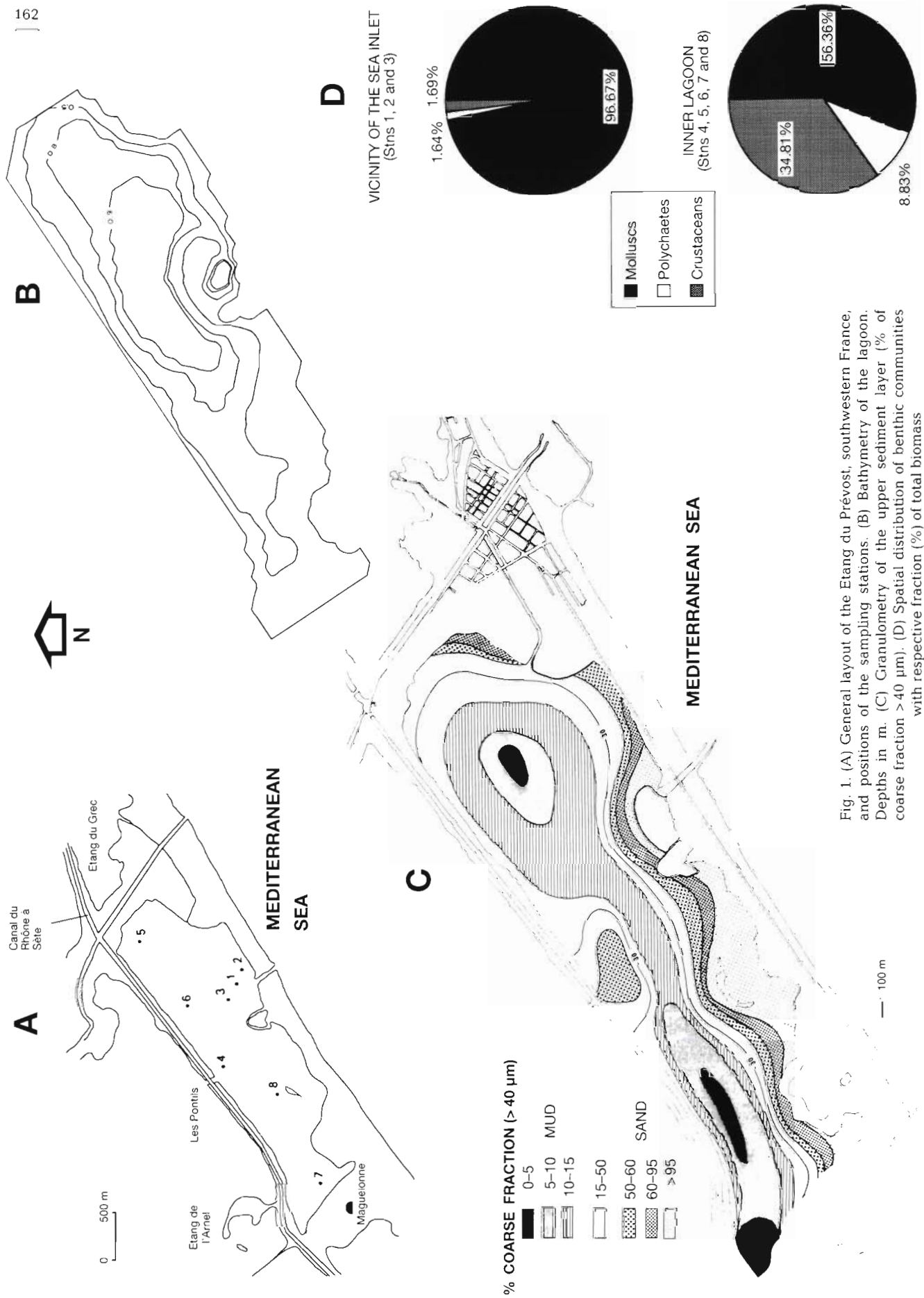


Fig. 1. (A) General layout of the Etang du Prévost, southwestern France, and positions of the sampling stations. (B) Bathymetry of the lagoon. Depths in m. (C) Granulometry of the upper sediment layer (% of coarse fraction > 40 μ m). (D) Spatial distribution of benthic communities with respective fraction (%) of total biomass

al. 1983, 1984), and non-linear relationships, especially between plankton biomass and wind-induced circulation, have been demonstrated in the Mediterranean lagoon of Thau (Millet & Cecchi 1992). In parallel, the major role of tide- and wind-induced processes in the control of the time-space dynamics of benthic communities was confirmed (Emerson 1990, Hamerlynck & Mees 1991), and non-linear relationships between benthic biomass and wind-induced horizontal dispersion have recently been suggested, also for the Thau lagoon (Millet & Guelorget 1993).

Multidisciplinary studies in various Mediterranean lagoons have provided evidence of an organizational and functional pattern in these coastal systems, corresponding to the optimal reaction of benthic organisms to fit in with their physical environment. As a result, there is one feature in common as regards the spatial distribution of macrobenthic communities in all Mediterranean lagoon systems, whether these are very shallow, very deep, brackish or very salty, namely that there is a succession of benthic species determined by distance from the sea (Guelorget & Perthuisot 1983, 1992).

This concept of isolation from the sea emphasizes the ecological relevance of the relationships between spatial distribution of organisms and movements of marine water within the system. Therefore, it is of interest to obtain further insight into the ecological impact of the major hydrodynamic processes involved in the circulation of water masses from the sea inlet to the inner lagoon (marine water renewal).

The present study was performed in the lagoon of Etang du Prévost, located near the lagoon of Thau previously mentioned, but differing by being very shallow, which is likely to reinforce barotropic tidal velocities (inversely proportional to the volumes of water involved), as opposed to vertically sheared wind-induced motions (independent of volume). The benthic communities were previously described (Guelorget & Michel 1979a, b, Amanieu et al. 1980), but a new approach, focusing on the space-time variability of biomass in relation to both tide- and wind-induced physical processes, provides a closer insight into the relative significance of tide- or wind-forced dynamics.

A numerical model was therefore necessary to compute the main hydrodynamic features spatially over the whole area, while allowing a clear distinction between tidal input or wind-stress forcing. Using an Alternating Conditional Expectations (ACE) statistical algorithm, seasonal changes in biomasses of molluscs and crustaceans recorded during 3 surveys carried out in October 1973 and January and May 1974 are regressed against several observed physical descriptors (distance from the sea inlet, granulometry), or computed hydrodynamic predictors (kinetic energy),

including a comparison of forcing by only tide and only typical wind condition.

DATA AND METHODS

Study area. The Etang du Prévost is a shallow lagoon near Montpellier in southwestern France, measuring 3.5 km in length and 800 m in width, with an area of about 380 ha, a permanent sea inlet and a small channel, Les Pontils, connecting with the adjacent lagoon, Etang de l'Arnel (Fig. 1A). Depths in the lagoon range from 0.30 m on the periphery to 1.50 m in the middle (Fig. 1B).

Sampling design. Analysis of the benthic communities was carried out at 8 stations across the lagoon (Fig. 1A). At each sampling survey (October 1973, January and May 1974) and at each of 8 stations, 5 samples of 0.1 m² each were collected with an Ekman grab sampler. After sieving on a 2 mm² mesh vacuum sieve, the sieve residue was treated and fixed with 10 % neutral formaline. Biomass, after drying in an oven, corresponds to dry weights of organic matter in mg m⁻².

Sediment features. The substratum consists essentially of shelly mud, with a variable sand content, and the fine fraction < 40 µm ranging from 60 to 80 %. The distribution of bed sediments measured by content of particles > 40 µm is shown in Fig. 1C. There is a band of sandy mud in the northern half, a band of silty sand in the southern half, a higher sand content in the vicinity of the sea inlet and of the channel between the lagoons, and a higher mud content in low energy areas, in the middle and at the eastern and western ends.

Benthic communities. The spatial structure of the benthic communities is presented in Fig. 1D. One pattern is defined in the vicinity of the sea inlet featuring a large dominance of molluscs, with biomasses averaged yearly from 12 samples (1 sample collected each month) at Stns 1, 2 & 3 (Fig. 1A). A second pattern is defined in the inner lagoon, featuring a larger fraction of crustacean biomass, with averaged values collected at Stns 4, 5, 6, 7 & 8. Near the sea inlet, mollusc communities are dominated by *Ruditapes aureus*, *R. decussatus*, *Scrobicularia plana*, and *Loripes lacteus*, and *Donax trunculus*, *D. semistriatus*, *Tellina tenuis*, *Mactra glauca*, *Venus gallina*, *V. verrucosa*, and *Acanthocardia echinata* are also present. In the inner lagoon, molluscs are exclusively represented by *Cerastoderma glaucum* and *Abra ovata*, whereas crustaceans are represented by typical lagoonal species as *Gammarus insensibilis*, *G. aequicauda*, *Corophium insidiosum*, *Idotea baltica*, *Sphaeroma hookeri* and *Carcinus mediterraneus*.

Hydrodynamic model. A 2-dimensional numerical model of the vertically averaged circulation was

applied to the lagoon. The model computes wind-induced and tide-induced currents and elevations, according to lagoon bathymetry, wind stress, tidal input and bottom friction. The Coriolis force (weak), and the non-linear advection terms are both taken into account. The advection terms are used in preference to the terms of horizontal turbulent viscosity, and the vertical turbulent viscosity is treated globally by the use of the terms of surface wind shear and bottom friction. The use of a 2-dimensional model is justified by the shallowness of the lagoon, and by the absence of thermal or saline stratification. The equations of the model are as follows:

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

where:

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

$$\tau_{sx} = C_d \rho_a W^2 \sin \alpha \quad \text{and} \quad \tau_{sy} = C_d \rho_a W^2 \cos \alpha$$

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

$$\begin{aligned}\tau_{bx} &= [\rho g U(U^2 + V^2)^{1/2}]/C^2 \quad \text{and} \\ \tau_{by} &= [\rho g V(U^2 + V^2)^{1/2}]/C^2\end{aligned}$$

U and V are the velocity components according to the horizontal directions

$f = 2\omega \sin \lambda$ is the Coriolis parameter

ω is angular speed of earth's rotation

λ is latitude

ζ is elevation of the water level

H is depth of the water column

ρ is water density (constant)

g is acceleration due to gravity

C_d is wind-drag coefficient

ρ_a is air density

α is wind-direction (constant)

W is wind velocity

C is Chézy bottom stress coefficient

The equations are solved in finite difference form with a classical ADI (Alternating Direction Implicit) numerical scheme using a 50 m grid and a 10 s time-step (Leendertse 1984, Millet 1989). The tide-induced and wind-induced hydrodynamic movements are computed separately, to distinguish between ecological features of each forcing function.

Statistical analysis. An ACE iterative algorithm, developed by Breiman & Friedman (1985), was used to compute optimal transformations for multiple regressions. The dependent Y variable and every predictor variable X_1, \dots, X_p are replaced by functions $\theta(Y)$, $f_1(X_1), \dots, f_p(X_p)$ to maximize the correlation coefficient in the following linear model: $\theta(Y) = f_1(X_1) + \dots + f_p(X_p)$.

The ACE algorithm can be considered as a non-parametric method that operates on the joint distribution of a dependent variable Y and predictors X_1, \dots, X_p , but in generalizing classical additive models in including a transformation of the response Y . There is a close similarity between ACE and canonical correlation analysis. However, the canonical correlation finds the linear combination of the X_p that is maximally correlated with Y , while ACE generalizes this by finding the linear combination of transformed X_p that is maximally correlated with a transformation of Y . This is the reason ACE remains more suitable for investigating non-linear relationships between variables. The ACE procedure computes the 'optimal transformation for regression' that is the unique set of functions $\theta(Y)$ and $f_i(X_i)$ quantified by minimizing the squared error loss: $E\{[\theta(Y) - \sum_i f_i(X_i)]^2\}$.

The alternating estimation procedure first initializes $\theta(Y) = (Y - E(Y))/\text{var}(Y)^{1/2}$, then computes, for fixed $\theta(Y)$ and for each predictor k considered, the minimizing functions $f_k(X_k) = E\{\theta(Y) - \sum_{i \neq k} f_i(X_i) | X_k\}$, and then computes from previous values $f_i(X_i)$ the minimizing $\theta(Y) = E\{\sum_i f_i(X_i) | Y\}/\text{var}(\sum_i f_i(X_i) | Y)^{1/2}$. The computation continues alternating between these 2 steps until the squared error loss $E\{[\theta(Y) - \sum_i f_i(X_i)]^2\}$ does not change.

Unlike the traditional approaches, ACE does not require any assumption of an underlying model relating Y to X_1, \dots, X_p , and the algorithm converges each time to an optimal and single solution, empirically defined without any previous speculation on a given known family of distributions, and computed without ambiguity. In addition, the algorithm converges quite rapidly. Results are expressed by plotting the transformed values versus the original data for each variable considered in the model, enabling direct coincidence between some particular shapes of the transformed functions and the correspondent observations to be shown, and sometimes establishing threshold values. In addition, this representation allows the selection of the predictors to which the dependent variable at each seasonal sampling fits the best. The most explicit criteria considered to identify accurate relationships are not limited to the R^2 results, but extended for each predictor to the shape of the smoothed transformations, the stability of these shapes after several attempts and the range between the highest and lowest transformation values. Cury & Roy (1989), Millet & Cecchi (1992), and Millet & Guelorget (1993) have previously used this procedure to emphasize the ecological impact of environmental discontinuities for pelagic fish recruitment or phytoplankton and benthos dynamics in different coastal systems.

In the present study, the ACE method was tested in the Etang du Prévost lagoon to determine the assumed non-linear and seasonal relationships be-

tween the benthic communities, the granulometry of the upper sediment and tide or wind-induced hydrodynamic features. The mollusc and crustacean biomasses sampled at the 8 stations previously described (Fig. 1) were successively considered as dependent variables in the ACE computations. The hydrodynamic information was summarized by the wind and tide-induced kinetic energy computed at each mesh-location (10^{-1} N m^{-2}). Physical descriptors related to the level of vertical turbulent diffusion, locally induced through the water column, were considered as independent variables in the ACE computations. The granulometry of the upper sediment (fraction of fine particles $< 40 \mu\text{m}$) and the distance of each sampling station from the sea inlet (km) were also considered as predictors in the ACE computations. The distances from the sea inlet were measured by following, between the inlet and the position of each station, the flood-tide trajectories drawn from the current field computed by the numerical model under both tide and wind forcing (see Fig. 3C).

These predictors are not independent of each other and the corresponding correlations were checked on the complete sample (8 values) with the following results:

Tide-ind. kinetic energy/granulometry: $r = -0.829$

Tide-ind. kinetic energy/dist. from sea inlet: $r = -0.657$

Wind-induced kinetic energy/granulometry: $r = -0.874$

Wind-ind. kinetic energy/dist. from sea inlet: $r = -0.698$

The correlations computed with kinetic energy versus granulometry are quite significant following z tests at the confidence level $p = 0.05$, whereas correlations computed versus the distance from sea inlet lie just below the limit of significance, that is $r = 0.707$. However, kinetic energy and distance from sea inlet have been considered as variables too closely correlated to be introduced simultaneously in an ACE additive model. Therefore, we only used ACE procedures for

estimating single predictor models (granulometry or distance or kinetic energy).

Nevertheless, ACE frequently presents artefacts in low-correlation settings ($R^2 = 30$ to 40%), that lead to the computation of especially well-smoothed parabolic or dome-shaped transformations in samples where no dominant trend can be clearly defined, or in samples with disjoint clusters, either for additive model or single predictor. These artefacts are reinforced in cases of small samples ($n < 20$) with low-correlated variables, and experience showed that it seems better in these cases to rather consider ACE as a correlation than a regression tool (Tibshirani 1988). In the present study, although the sample considered is very small ($n = 8$), the relevance of the ACE algorithm is reinforced by the high correlations computed (R^2 values) and slightly curved transformations without dome-shaped artefacts. In addition, we limited the ACE interpretations to the meaning of the seasonal variations of correlation intensities and slope directions in the non-linear monotonous transformed functions. The whole data set considered is reported in Table 1.

RESULTS

Hydrodynamic modelling

First, a simulation of the tide-induced circulation was run for a 24 h period. The tidal input was a typical signal recorded in 1988 in the neighbouring harbour of Sète during a period of stability, when the average level was consistent with the mean interannual sea level, and of a range (34 cm) equal to the mean interannual tidal range for the same station (Fig. 2A). In parallel, a simulation of the wind-induced circulation was run for a 24 h period. The forcing input was a stationary wind stress of NW (293°) and 8 m s^{-1} (Fig. 2B), which corresponded to the prevailing wind observed during the sampling period, accounting for 20 % of the

Table 1. Benthos data and environmental predictors considered in ACE computations. k.e.: kinetic energy

Stn	Biomass (mg m^{-2} dry organic matter)						Environmental predictors			
	Mollusc ($\times 10^3$)			Crustacean ($\times 10^2$)			Granulometry fraction $< 40 \mu\text{m}$	Distance from sea inlet (km)	Wind-ind. k.e. ($\times 10^{-1} \text{ N m}^{-2}$)	Tide-ind. k.e. ($\times 10^{-1} \text{ N m}^{-2}$)
	Jan	May	Oct	Jan	May	Oct				
1	410.9	502.1	117.8	17.03	0.13	1.97	4.21	0.22	172.8	229.1
2	23.8	73.4	77.3	5.46	4.35	4.61	25.2	0.16	113.6	115.3
3	37.1	34.2	23.1	22.5	12.1	7.22	33.8	0.35	108.6	36.2
4	5.29	26.4	0.89	44.9	0.86	1.38	27.5	1.63	40.5	4.93
5	4.47	8.89	3.39	28.4	68.3	0.42	61.4	2.19	52.5	0.05
6	16.5	22.7	13.4	101.2	22.2	29.6	68.0	0.85	1.50	1.04
7	19.5	13.6	7.64	104.0	76.9	0.91	61.3	3.06	18.3	0.27
8	8.39	12.0	21.5	21.4	32.4	8.48	62.0	1.78	34.8	4.07

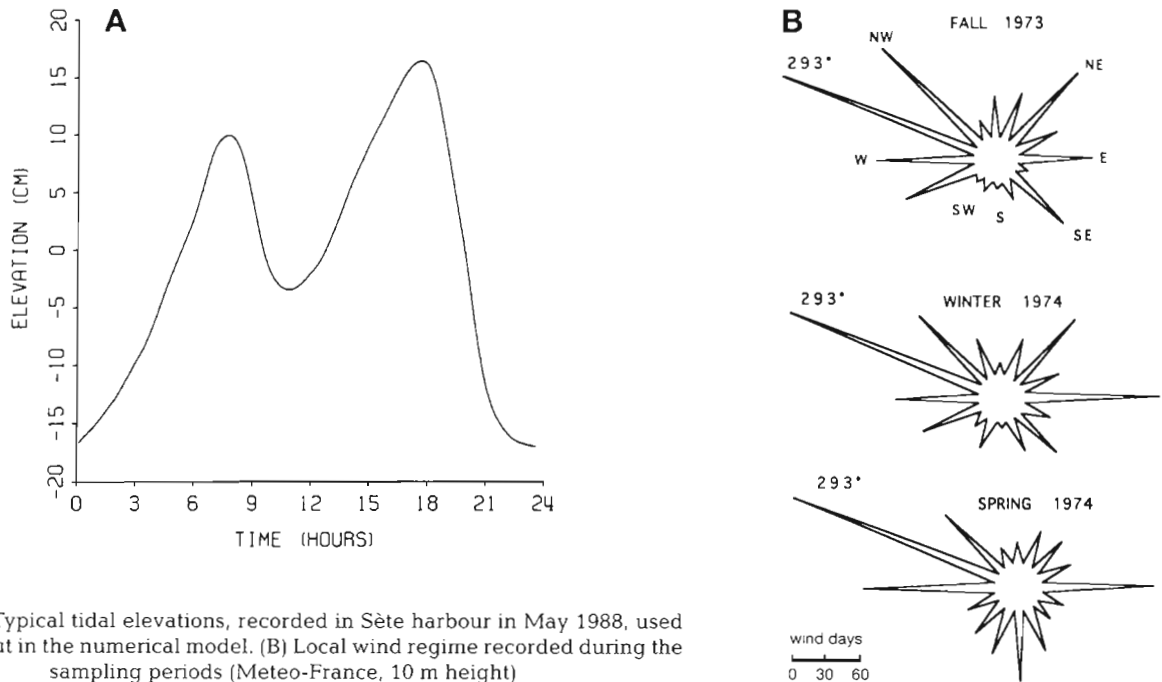


Fig. 2. (A) Typical tidal elevations, recorded in Sète harbour in May 1988, used as tidal input in the numerical model. (B) Local wind regime recorded during the sampling periods (Meteo-France, 10 m height)

time between October 1973 and May 1974. In addition, this observed wind pattern was consistent with the interannual statistical wind regime (1951 to 1980) established for the region by the national office Meteo-France: NW (290°) accounting for 18% of the time.

Computed results for tide- and wind-induced current fields are each shown after a 24 h period of simulation in Fig. 3A & B, according to the strongest flood tide currents (Fig. 3A) and the dominant situation in the local wind regime (Fig. 3B). Results of a third simulation corresponding to both the tide and wind typical forcings previously described, but acting simultaneously during a 24 h period, are presented in Fig. 3C. The corresponding isolines of kinetic energies computed with tide-only or wind-only forcing are presented in Fig. 4A & B respectively.

Statistical analysis

In all the ACE computations, transformations obtained for the dependent variables (biomass) are plotted on the first diagrams of each figure against the original data. Transformations of mollusc (Figs. 5, 7 & 9) and crustacean (Figs. 6, 8 & 10) biomasses were in all cases curved with a positive slope, spread over a fairly wide range of values, with good stability from one analysis to another, which means that a good interpretation of the transformations can be obtained with the predictors considered.

January

The ACE algorithm was first applied to the mollusc biomass sampled in January 1974 with the environmental (distance and granulometry) and hydrodynamic (kinetic energy) predictors previously described, and the main results are presented in Fig. 5.

First, transformation of environmental predictors such as the distance from the sea inlet (Fig. 5A) and the granulometry (Fig. 5B) showed in both cases negative curved relationships that respectively explained 54% and 55% of the variance. In addition, the negative slope of the transformation of the distance from the sea inlet (Fig. 5A) was steeper below a threshold value of 1.6 km than for greater distances. These results underline the importance of the spatial position according to the tidal circulation and the granulometry in the development of the mollusc biomass, which benefits from the proximity of the sea inlet, associated with the coarse fraction of the sediment.

Second, transformations of hydrodynamic predictors such as the tide-induced (Fig. 5C) and wind-induced kinetic energy (Fig. 5D) showed positive relationships that respectively accounted for 85% and 83% of the variance. These results indicate that the mollusc biomass benefits from an increase in kinetic energy throughout the water column, in a way that is linear for high values (above 3 N m^{-2}), and that the behaviour of kinetic energy with regard to mollusc biomass does not appear meaningful for weak values below this limit nor

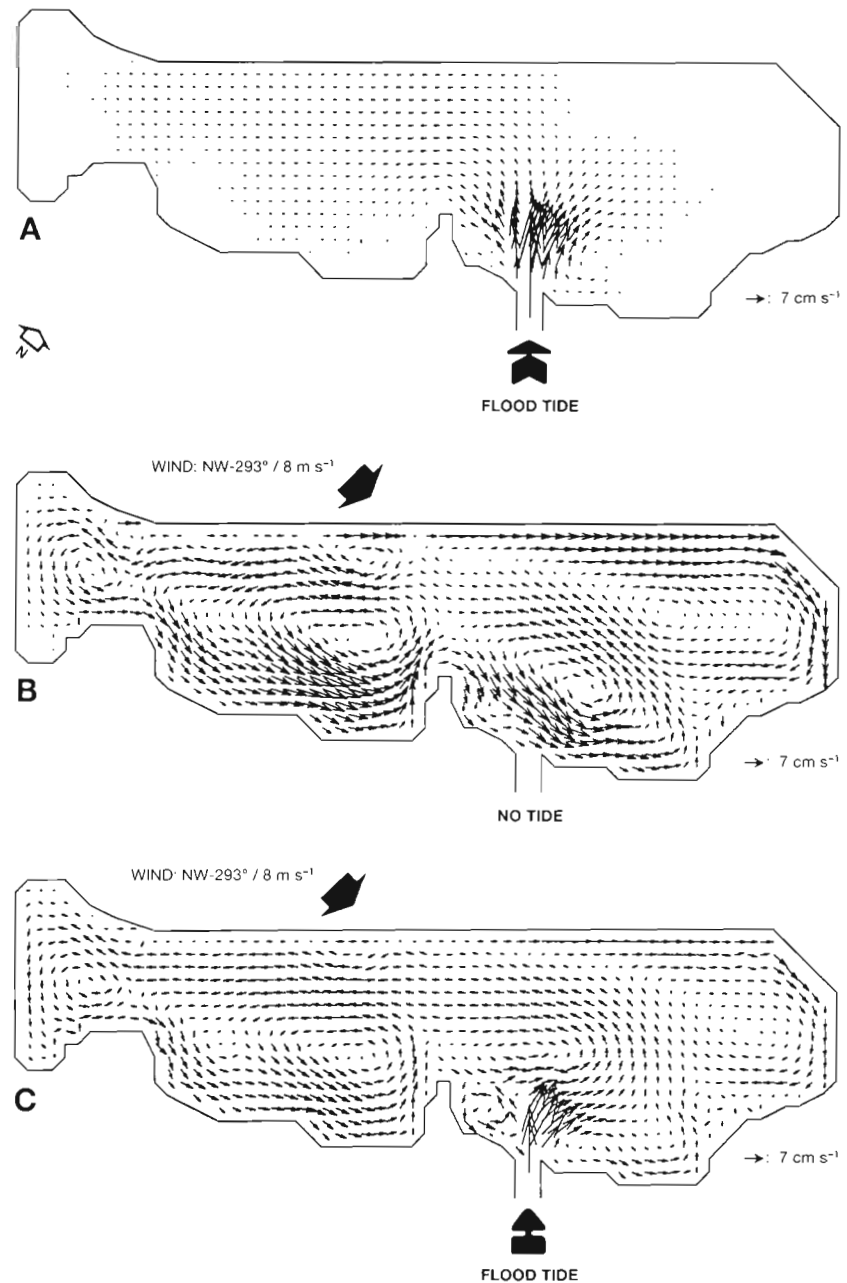


Fig. 3. (A) Computed tide-induced vertically averaged current field, corresponding to the maximum of typical flood-tide. (B) Computed wind-induced vertically averaged current field, corresponding to a typical NW (293°) and 8 m s^{-1} stationary wind. (C) Computed current field, corresponding to both tide and wind forcings previously described acting simultaneously

for both tide and wind forcings that correspond to the landward areas of the lagoon (Fig. 3).

The ACE algorithm was then applied to the crustacean biomass sampled in January 1974 with the environmental and hydrodynamic predictors previously described (Fig. 6).

First, transformation of environmental predictors such as distance from the sea inlet (Fig. 6A) and granulometry (Fig. 6B) showed in both cases positive relationships that respectively explained 44 % and 42 % of the variance. Transformation of the granulometry remained linear for the whole range of values consid-

ered, but the transformation of the distance from the sea inlet (Fig. 6A) showed a non-linear relationship with a steeper slope below a threshold value of 1.6 km than for increasing distances. These results indicate the importance of the spatial position according to the tidal circulation and the granulometry in the development of the crustacean biomass, which benefits from landward locations far from the sea inlet, associated with the finest fraction of the sediment.

Second, transformations of hydrodynamic predictors such as the tide-induced (Fig. 6C) and wind-induced kinetic energy (Fig. 6D) showed negative curved rela-

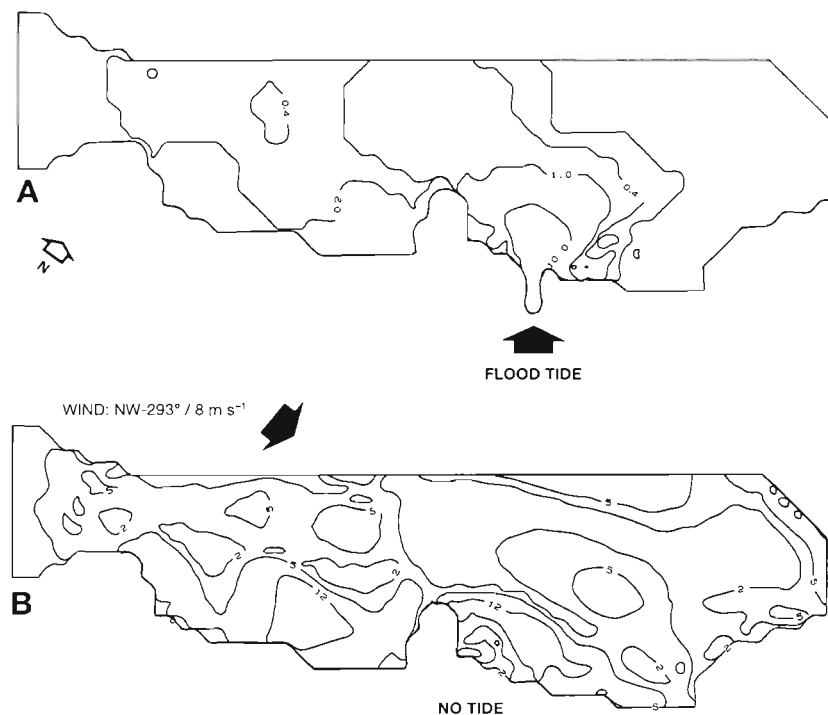


Fig. 4. (A) Spatial features of tide-induced kinetic energy isolines: 0.2, 0.4, 1 and 10 N m^{-2} . (B) Spatial features of wind-induced (NW, 293°; 8 m s^{-1}) kinetic energy isolines: 2, 5 and 12 N m^{-2} .

tionships that respectively accounted for 54 % and 80 % of the variance. These results indicate that the crustacean biomass benefits from weak kinetic energy in the water column, and especially for low values below 3 N m^{-2} , and the detrimental effect on crustacean biomass of higher range of turbulent energy beyond this limit is emphasized for both tide and wind forcings. In addition, the wind-induced kinetic energy appears in January as the most meaningful predictor to describe crustacean biomass pattern within the lagoon.

May

The ACE algorithm was applied to the mollusc biomass sampled in May 1974 with the same environmental and hydrodynamic predictors previously considered, and the main results are presented in Fig. 7.

First, transformation of environmental predictors such as distance from the sea inlet (Fig. 7A) and granulometry (Fig. 7B) showed again in both cases negative linear relationships that respectively explained 68 % and 78 % of the variance. These results reinforce the beneficial effect on the mollusc development of the proximity of the sea inlet, associated with the coarse fraction of the sediment, but no distinction here can be clearly suggested between the positions below or above the limit of 1.6 km from the sea inlet, which was seen for the January sample. In addition, the impact of

the granulometry on the mollusc biomass considerably increases in May, compared with the results obtained for the January sample (only 55 % of variance explained).

Second, transformations of hydrodynamic predictors such as the tide-induced (Fig. 7C) and wind-induced kinetic energy (Fig. 7D), showed positive relationships that respectively accounted for 89 % and 81 % of the variance. These results remain quite similar to and as significant as those obtained for mollusc biomass of the January sample.

The ACE algorithm was applied to the crustacean biomass sampled in May 1974 with the same environmental and hydrodynamic predictors, and the main results are presented in Fig. 8.

First, transformation of environmental predictors such as the distance from the sea inlet (Fig. 8A) and the granulometry (Fig. 8B) showed in both cases positive linear relationships that respectively explained 80 % and 75 % of the variance. These results considerably reinforce the pertinence of the environmental predictors to explain in May the crustacean development, compared with results previously obtained for the January sample in which only 44 % and 42 % of variance were explained respectively for distance and granulometry (Fig. 6A, B). In addition, the results confirm the beneficial effect on the crustacean biomass of landward locations associated with fine granulometry, but without the threshold effect of the limit value (1.6 km from the sea inlet) in the January sample.

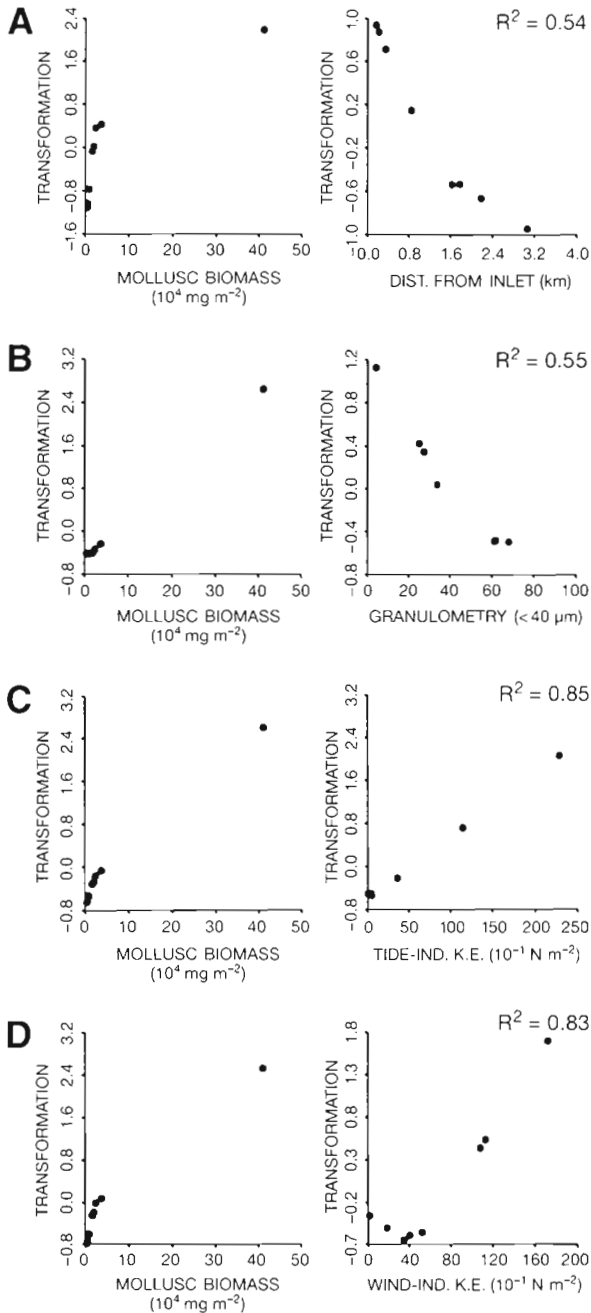


Fig. 5. ACE optimal transformations of mollusc biomass and environmental predictors (A, Distance from inlet; B, Granulometry; C, Tide-induced kinetic energy; D, Wind-induced kinetic energy) for January 1974 sampling

Second, transformations of the tide-induced (Fig. 8C) and wind-induced kinetic energy (Fig. 8D) showed negative curved relationships that respectively accounted for 73 % and 40 % of the variance. These results confirm that the crustacean biomass benefits from weak kinetic energy, as previously shown for the January sample (Fig. 6C, D). In addition, it is worth noting that the im-

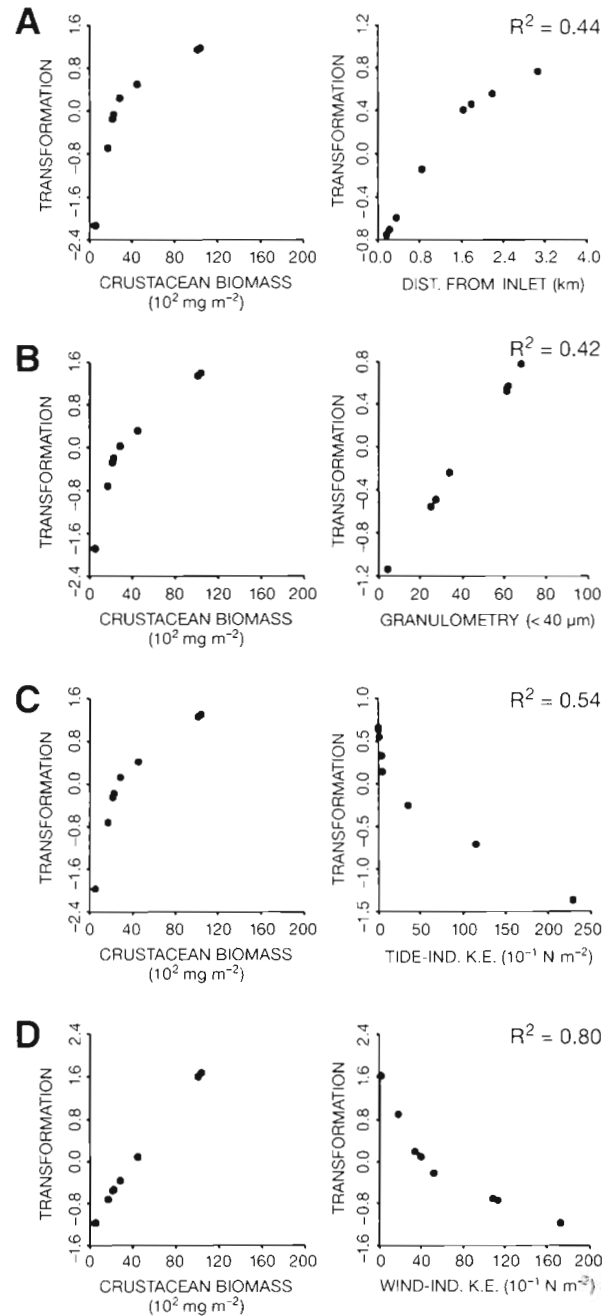


Fig. 6. ACE optimal transformations of crustacean biomass and environmental predictors (A, Distance from inlet; B, Granulometry; C, Tide-induced kinetic energy; D, Wind-induced kinetic energy) for January 1974 sampling

part of the tide-induced kinetic energy increases here considerably in relation to the previously described January sample (only 54 % of variance explained in January) whereas the impact of the wind-induced kinetic energy broadly decreases (80 % of variance explained in January). The tide-induced kinetic energy appears in May as the most pertinent hydrodynamic predictor for

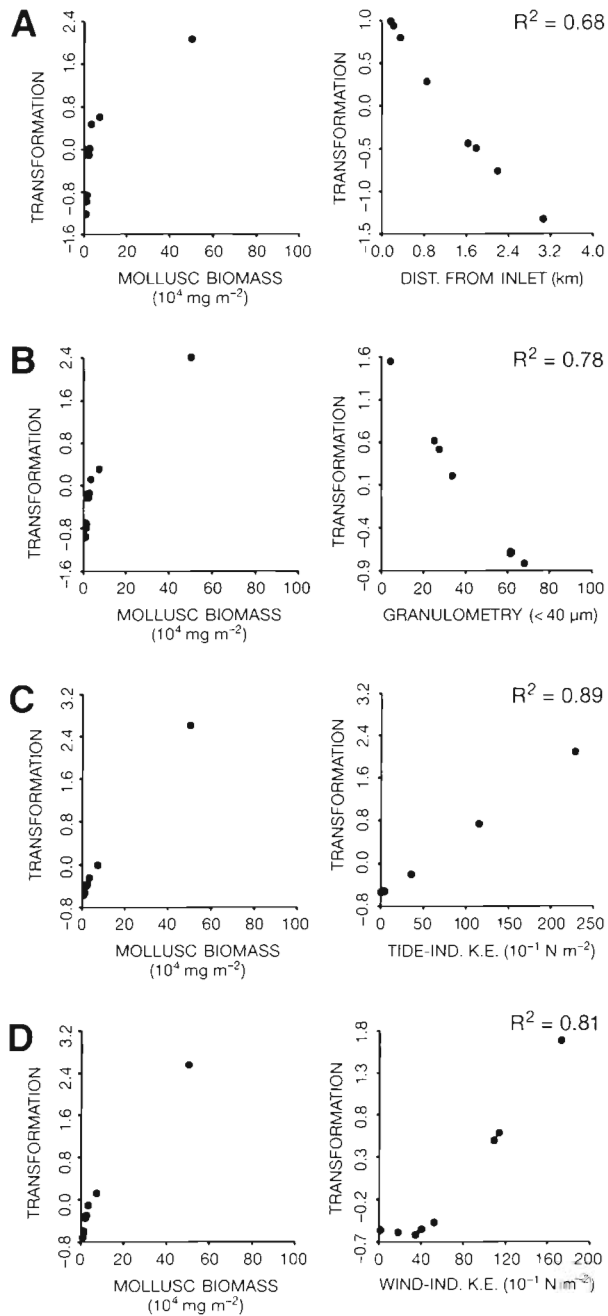


Fig. 7 ACE optimal transformations for mollusc biomass and environmental predictors (A, Distance from inlet; B, Granulometry; C, Tide-induced kinetic energy; D, Wind-induced kinetic energy) for May 1974 sampling

crustacean biomass enhancement, in contrast to the results obtained in January.

October

The ACE algorithm was also applied to the mollusc biomass sampled in October 1973 with the same pre-

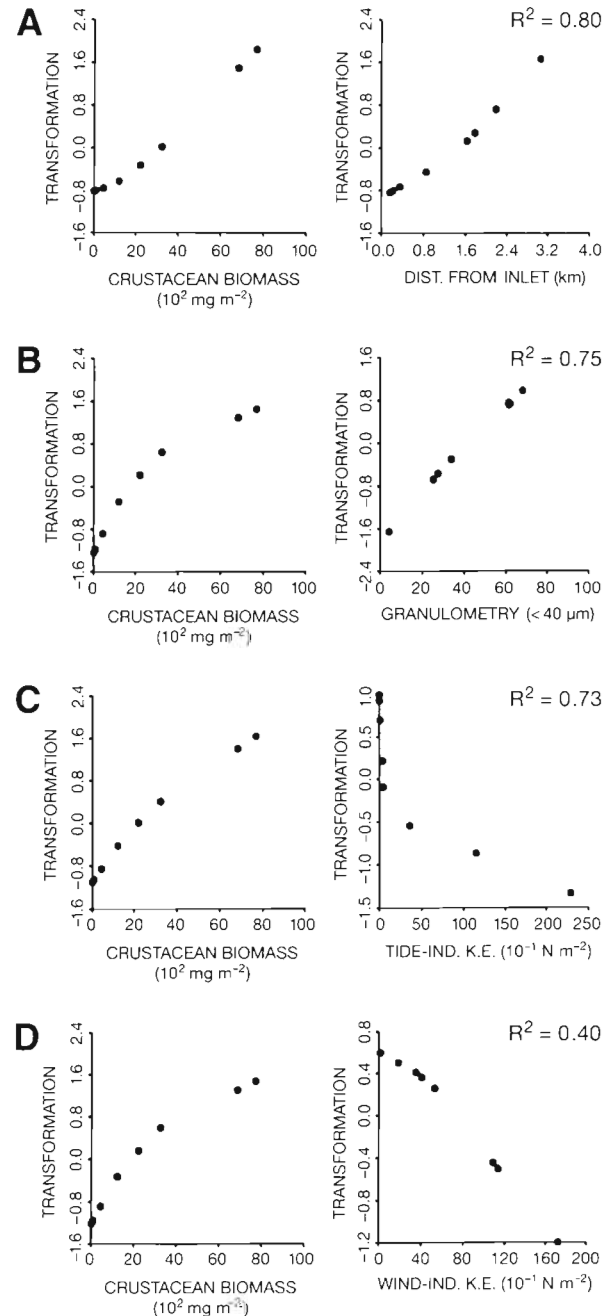


Fig. 8 ACE optimal transformations for crustacean biomass and environmental predictors (A, Distance from inlet; B, Granulometry; C, Tide-induced kinetic energy; D, Wind-induced kinetic energy) for May 1974 sampling

dictors previously considered, and the main results are presented in Fig. 9.

First, transformation of environmental predictors such as the distance from the sea inlet (Fig. 9A) and the granulometry (Fig. 9B) still showed in both cases negative and slightly curved relationships that respectively explained 67 % and 69 % of the variance. These results

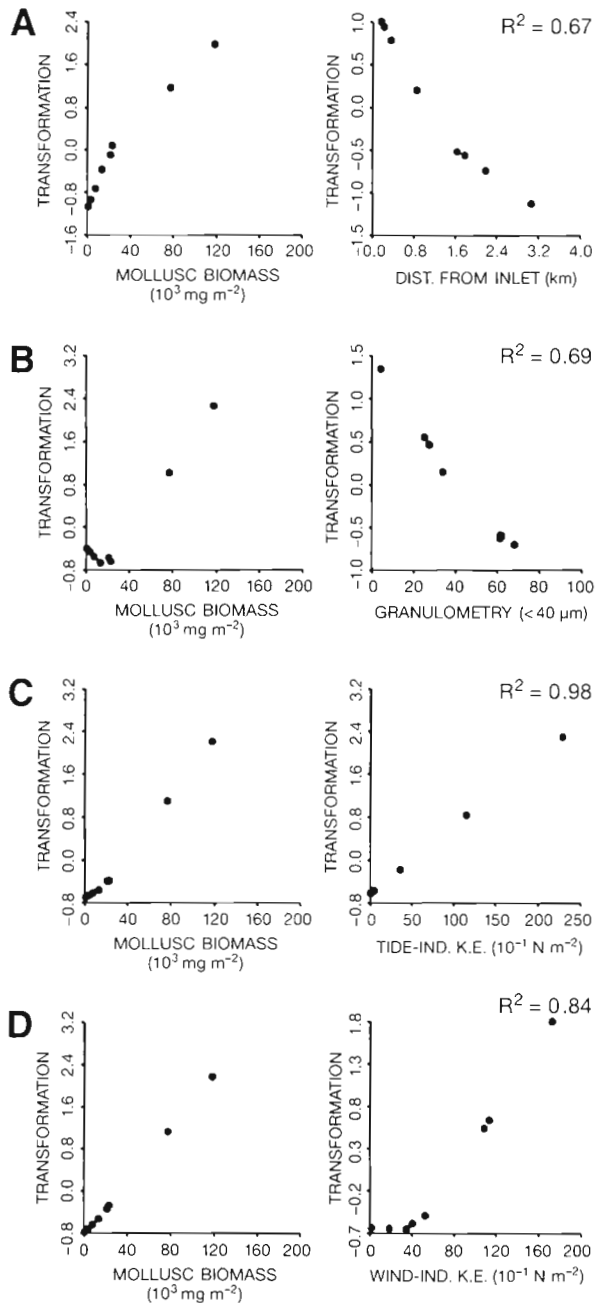


Fig. 9. ACE optimal transformations for mollusc biomass and environmental predictors (A, Distance from inlet; B, Granulometry; C, Tide-induced kinetic energy; D, Wind-induced kinetic energy) for October 1973 sampling

confirm in October the beneficial effect on the mollusc development of the proximity of the sea inlet, associated with the coarse fraction of the sediment, and a slight impact of the limit of 1.6 km from the sea inlet reappears here more clearly than for the May sample.

Second, transformations of the tide-induced (Fig. 9C) and wind-induced kinetic energy (Fig. 9D) showed pos-

itive relationships that respectively accounted for 98 % and 84 % of the variance, with quite similar shapes to those previously described for the May sample, reinforcing in October the major role of the physical energy of the water column for mollusc development.

The ACE algorithm was applied to the crustacean biomass sampled in October 1973 with the same predictors, and the main results are presented in Fig. 10.

Transformation of the distance from the sea inlet (Fig. 10A) showed here a negative curved relationship that explained 40 % of the variance. The slope presented here again a slight break corresponding to the distance of 1.6 km from the inlet, and became steeper in the landward direction than for seaward areas. It is noteworthy that this transformation function was negative in October whereas it appeared symmetrically positive in January (Fig. 7A), with a similar break at 1.6 km from the inlet, but an increasing slope in seaward direction.

Transformation of the granulometry presented here a weak positive relationship (Fig. 10B) with only 38 % of the variance explained, and a non-interpretable minimum in the transformation for the dependent biomass.

It was important to note a considerable decline in information for this October sample, and that the only information obtained, with very weak fit, came from the distance from the sea inlet previously described (Fig. 10A), whereas the granulometry (Fig. 10B) and, in a similar way, none of the kinetic energy predictors (not shown) gave any interpretable result relating to the crustacean biomass.

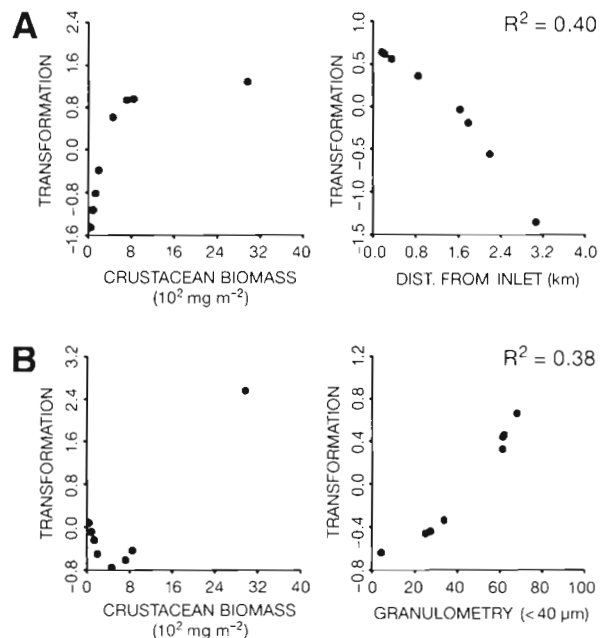


Fig. 10. ACE optimal transformations for crustacean biomass and environmental predictors (A, Distance from inlet; B, Granulometry) for October 1973 sampling

DISCUSSION

The results confirm the high degree of sensitivity of benthic organisms to the environmental conditions prevailing in the shallow lagoon. This study is likely to provide a closer insight into the relationships between benthic macrofauna and sediment or hydrodynamic features, but more particularly into the spatial and seasonal variability of these relationships.

The ACE method emphasizes non-linear shapes within regressions, that clearly appear for the relationships between biomass and the distance of each station from the sea inlet (limit value: 1.6 km). In addition, comparisons between similar analyses performed on each seasonal sample (January, May, October), suggest several hypotheses relating to a hierarchical succession of each environmental predictor involved in the control of the dynamics of benthos patterns for each season.

First, from a spatial point of view, the treatments of the January and May samples show a clear distinction between the partitioning of biomass between molluscs and crustaceans, in relation to specific physical conditions which differ within the lagoon, for both winter and spring periods, according to the seaward or landward positions of the sampling stations. It appears that optimal development of molluscs (highest biomasses) benefits from a high level of both tide and wind-induced kinetic energy, associated with locations at the vicinity of the sea inlet and dominance of coarse sediment (Figs. 5 & 7). On the other hand, it appears that optimal development of crustaceans benefits from a low level of kinetic energy, associated with landward positions within the lagoon and dominance of fine sediment (Figs. 6 & 8).

Settlement of marine pelecypod molluscs *Ruditapes aureus*, *R. decussatus*, *Loripes lacteus* and *Scrobicularia plana* occurs exclusively on the sandy sediment near the inlet. These species strongly benefit from the high energetic conditions prevailing at the seaward locations in the lagoon, associated with enhanced fluxes required to promote the development of suspension feeders (Dorey et al. 1973). In the inner lagoon, the 2 typical lagoonal species *Cerastoderma glaucum* and *Abra ovata* occur exclusively on the muddy substrate prevailing in low-energy and enriched areas.

In contrast, settlement of crustaceans *Carcinus mediterraneus*, *Corophium insidiosum*, *Gammarus insensibilis*, *G. aequicauda* and *Idotea baltica* occurs exclusively on fine sediment enriched with organic matter, according to the diet of these detritivorous species. In addition, at the beginning of the spring season, these mobile organisms are able to avoid detrimental environmental conditions by moving seawards to new locations influenced by marine water near the inlet (Fresi et al. 1985).

The coherent contribution of the well-correlated predictors kinetic energy (high or low level), and granulometry (coarse or fine fraction), is not surprising and consistent with the results of both numerical modelling (Figs. 3 & 4) and field observations (Fig. 1C). In addition, the high correlation between the tide- and wind-induced kinetic energy (high or low level) and the distance from the sea inlet (seaward or landward location), are quite consistent with the barotropic nature of the computed tidal circulation, and the shallowness of the inlet. Therefore, the environmental optimum found for molluscs in the vicinity of the sea inlet might be explained mainly by the coarse sediment prevailing in this energetic area influenced by strong tide- and wind-induced currents.

In addition, the location of this optimum close to the sea inlet can also reveal a specific dependence to a marine influence, and this hypothesis is consistent with previous investigations in different coastal lagoons (Nicolaidou et al. 1988, Guelorget et al. 1990). Thus, the direct hydrochemical influence of marine water might contribute to the biological organization of lagoons, in controlling the degree of restriction of inner areas with respect to the sea, which is inversely proportional to marine element fluxes at a given point (Guelorget & Perthuisot 1992). This concept seems consistent with the 'embayment degree' proposed for coastal ecosystems in Japan (Miyadi et al. 1944, Horikoshi 1988).

An interesting result gained by using the ACE algorithm also consists in the computation of the limit distance of 1.6 km from the sea inlet, a spatial discontinuity between the landward and seaward poles within the lagoon. This discontinuity might correspond with the maximum spatial extension of a specific marine influence inside the lagoon, according to the local hydrodynamic conditions for flood tide circulation.

Second, from a temporal point of view, the results show the seasonal variability of the relative efficiency of each predictor in the ACE computations which differs from January to May samples.

Granulometry appears as a major predictor for both molluscs and crustaceans in May with respectively 78% and 75% of the variance (Figs. 7B & 8B), but only represents 55% and 42% of the variance in January (Figs. 5B & 6B). This increasing efficiency of granulometry suggests that this environmental predictor is important in spring as hydrodynamic predictor, and confirms the major role of sediment features in explaining the seasonal variability of benthic biomass from winter to spring. This result might be related to the spring development of macrofauna for both molluscs and crustaceans, which strongly depends on the occurrence of appropriate substratum.

In addition, tide-induced kinetic energy appears as the dominant hydrodynamic predictor for crustaceans in May, with 73 % of the variance (Fig. 8C), whereas this predictor only represents 54 % of the variance in January (Fig. 6C). In contrast, wind-induced kinetic energy only explained 40 % of the variance in May (Fig. 8D), instead of 80 % in January (Fig. 6D). This increasing efficiency of tidal impact in explaining the seasonal development of crustacean biomass from winter to spring, and the decreasing efficiency of wind impact between the same periods, might be also related to recruitment processes of marine larvae, whose success strongly depends on the tidal movement of marine water within the lagoon. This hypothesis is reinforced by the similar increasing relevance of distance from the sea inlet, which in May describes 80 % of the variance for crustacean biomass (Fig. 8A), instead of 44 % in January (Fig. 6A), confirming the beneficial effect of landward locations to crustacean biomass enhancement (positive slope), and the attenuation of the discontinuity near 1.6 km from inlet. Although mollusc development from January to May does not seem sensitive to hydrodynamic predictors (Figs. 5C, D & 7C, D), crustacean seasonal development reveals an interesting dependence on tidal motions, associated with the low energetic range localized in landward areas.

These results suggest in May an increasing ecological influence of marine waters which might promote, in spring, the recruitment success of crustacean larvae, spatially according to the presence of fine granulometry and the trajectory of the flood-tide in the inner lagoon. Thus, the benthic structure in May might reflect the reorganization of mobile crustacean organisms which migrate during the winter period from landward locations where drastic conditions prevail, toward warmer and enriched marine water masses where they temporarily could find better environmental conditions. In parallel, the simultaneous development of mollusc communities appears more strongly dependent, in the vicinity of the sea inlet, to coarse granulometry and high energetic range in the water column, but regardless whether tide or wind act as forcing processes.

Third, the results demonstrate a seasonal change of predictor impacts in ACE computations from May to October samples.

The decreasing mollusc biomasses in October do not show a notable change in the correspondence to the relative impacts of each environmental and hydrodynamic predictors, as compared to May, except for the further increasing efficiency of tide-induced kinetic energy which explains 98 % of the variance in October (Fig. 9C), instead of 89 % in May (Fig. 7C).

On the other hand, the drastic decrease in crustacean biomass from spring to fall can only be associated with the distance from the sea inlet, the last predictor to be considered relevant in ACE computations, with 40 % of variance explained (Fig. 10A). In addition, it is of interest to note that transformation of distance is in October symmetrically shaped in comparison with May, with here a negative slope that shows the new beneficial effect of seaward positions on crustacean communities, whereas only landward locations appeared as efficient in January and May.

These results suggest in October a further increasing impact of marine water circulation which might enhance locally, in the proximity of the sea inlet, the chances for benthic organisms to survive during the anoxic crises that prevail in the inner lagoon in summer. The specific impact of tidal circulation in water renewal in the vicinity of the sea inlet during summer appears more restrictive for crustaceans, which preferentially develop in landward positions, than for molluscs whose environmental optimum is localized in seaward positions.

The relative impacts of dystrophic crises on benthic macrofauna seem to depend on the adaptative strategy of each zoological group considered: to burrow into the sediment or to migrate within water masses. Results obtained on this small lagoonal ecosystem illustrate the rapid reaction of benthic populations to contrasting seasonal dynamics of the physical environment. Therefore, sedentary infauna like molluscs is strongly affected by summer anoxic conditions, whereas mobile organisms like crustaceans remain able to migrate within the lagoon and find a better fit with the variability of the ecosystem (Amanieu et al. 1975, Josefson & Jensen 1992).

CONCLUSION

These results require validation in other comparable environments, but they open the way to further investigations on spatial and temporal non-linear relationships between larval phases of benthic species and physical environment.

The first use of the present approach might be to analyse seasonal variability in typical and non-temporal physical descriptors of the lagoon environment in the hierarchy of their contributions to regressions with benthos spatial and seasonal development. Several hypotheses are therefore suggested to interpret this time-space variability in benthos-physics relationships and this hierarchical pattern of physical descriptors in relation to the ecological sensitivity and seasonal phases of each benthic species considered.

These hypotheses, and it might be here the second interest of the present study, emphasize the central role of marine water influence, associated with the tidal excursion of water masses in the inner lagoon, from the inlet to landward positions, both to promote juveniles recruitment in spring (in landward areas) and to prevent organisms from experiencing anoxic crises in summer (in seaward areas).

These biological and trophic impacts of marine waters in a Mediterranean lagoon, despite the weak amplitude of the local tide, may be related to the shallowness of the Etang du Prévost, with 1.5 m maximum depth, which reinforces the barotropic tidal propagation throughout the whole area. This specific feature of shallow ecosystems can be compared with results previously obtained concerning benthos-physics relationships in a deep neighbouring lagoon with 10 m maximum depth, the Bassin de Thau, where wind-induced horizontal dispersion (Millet & Guelorget 1993) substitutes for vertical turbulent kinetic energy, and wind-induced stochastic recruitment (Borsa & Millet 1992) substitutes for tide-induced seasonal input.

In addition, any research that leads to recognition of the spatial distribution of water masses not affected by dystrophic crises, by simply considering the level of kinetic energy reached within the water masses, would make a valuable contribution to decisions concerning optimal shellfish farming in shallow embayments.

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