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Empirical modelling of the growth of *Ruditapes philippinarum* by means of non linear regression on factorial coordinates

Philippe Goulletquer and Cédric Bacher

IFREMER, Station de La Tremblade, Mus de Loup, BP n° 133, 17390 La Tremblade (France).

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Abstract

In order to highlight the main factors accounting for the growth of clams in Marennes-Oléron Bay, three locations were investigated in 1984-85. First, factor analysis provided information on fluctuations of the environment. Second, principal components analysis was used to study ecological phenomena. The main axes explained the growth rate, which was included in an allometric model. Its properties were then studied by means of sensitivity analysis.

Keywords : Trophic relationships, *Ruditapes philippinarum*, principal components analysis, non-linear model, sensitivity analysis.

Modelisation empirique de la croissance de Ruditapes phillipinarum : *utilisation de la régression non linéaire sur coordonnées factorielles.*

Résumé

Afin de dégager les principaux facteurs responsables de la croissance de *Ruditapes philippinarum* dans le bassin de Marennes-Oléron, trois populations d'élevage ont été suivies en 1984-85. Dans un premier temps, l'analyse factorielle permet d'étudier les fluctuations des paramètres environnementaux. L'analyse en composantes principales est utilisée pour représenter les phénomènes écologiques. Les axes principaux expliquent le taux de croissance qui est introduit dans un modèle allométrique. Ses propriétés sont étudiées au moyen de l'analyse de sensibilité.

Mots-clés : Relations trophiques, *Ruditapes philippinarum*, analyse en composantes principales, modèle non linéaire, analyse de sensibilité.

INTRODUCTION

Trophic characteristics of bivalves have been studied by many authors, investigating the relationships between growth and environmental descriptors. For example, Wildish and Kristmanson (1985) related body weight fluctuations to the flow of particulate organic matter (POM X current speed), and Fréchette and Bourget (1985) related growth in length to particulate organic matter concentration (POM as indicated by chlorophyll *a* and phaeopigments) for *Mytilus edulis.*

Wallace and Reinsnes (1985) explained differences in growth of *Chlamys islandica* as the result of differences in nutritional conditions for the scallops, defined by the relationship between particulate organic and inorganic matter in the water column. Besides, shell biometric data are often used (Kautsky, 1982; Page and Hubbard, 1987), but winter emaciation, or seasonal variations affecting condition have been scarcely treated. This study aims are to describe the relationship between seasonal variations in the weight of *Ruditapes philippinarum* and environmental descriptors (represented by hydrological and sedimentary temporal series, over a two years' period).

MATERIALS AND METHODS

The use of statistical methods has recently made it possible to describe trophic relationships (for a review, *see* Héral, 1987). Variability between species and the use of different computation methods may explain divergent results. Non-parametric methods, establishing rank-correlations, have presented the most divergent results (Soniat and Ray, 1985; Beninger and Lucas, 1984). More informative results are obtained when statistical methods are applied to rank the descriptors in order of importance (Bodoy and Plante-Cuny, 1984; Plante-Cuny and Bodoy, 1987; Héral *et al.*, 1984; Page and Hubbard, 1987). Since linear regression is the most common method used, these results are only reliable as far as the relationships are consistent with the hypothesis of linearity. Our paper applies non-linear statistical analysis and the idea of classification to evaluate relationships between environmental descriptors and bivalve growth. The property of prediction should be improved, and the regression model is expected to be more general. It enables to classify the descriptors according to their effect on growth and to compare spatially separated areas. Moreover, the study of the properties of the model allows discrimination of the effects of environmental variability on growth among areas and among years.

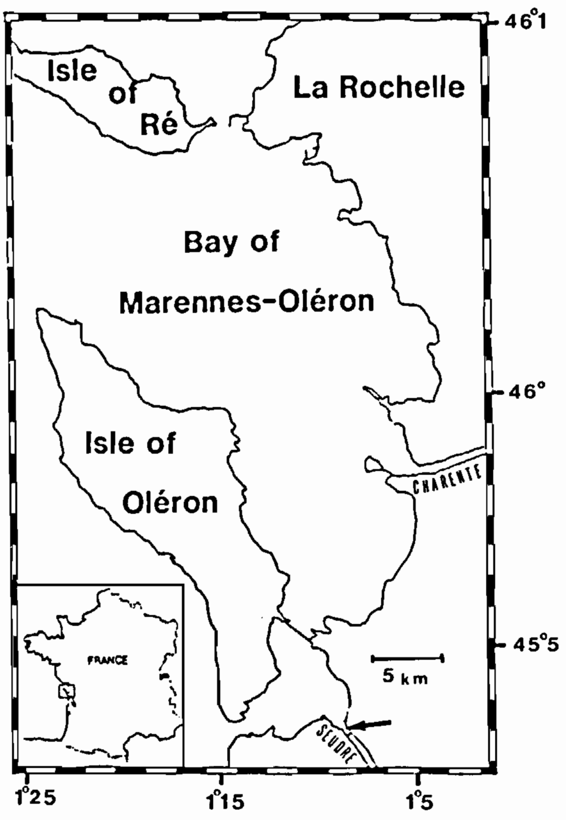

Figure 1. — Geographical location and sample area.

The study was conducted in the Seudre river estuary in the bay of Marennes-Oléron (*fig.* 1). The experimental design involved the survey of three areas defined by their intertidal level of exposure called low, medium, high level (12, 19, 46% emersion respectively). Substratum was a soft bottom (65% silt). Experimental populations of *Manila clams* in each area were sown in March 1984, with an average length (28.4 ± 0.04 mm), total weight (5.15 ± 0.01 g) and soft tissue weight (123.4 ± 6.2 mg) at a density of 200 individuals.m^{-2}.

MULTIVARIATE ANALYSIS OF ENVIRONMENTAL DESCRIPTORS

Sampling

Since benthic pigments constitute a part of the clam diet (Bodoy and Plante-Cuny, 1984; Plante-Cuny and Bodoy, 1987), the sediment was sampled using sediment cores twice a month. The six following descriptors were surveyed in the upper centimetre of cores: particulate organic matter (POM), carbohydrates, proteins, lipids, chlorophyll *a* and phaeopigments.

The amount of organic matter in the upper centimetre of the cores was measured by weight difference on ignition at 450°C for 24 hours. Carbohydrate analysis was performed using the method of Dubois *et al.* (1956) and analysis of proteins using the method of Lowry (1956). After extraction (Bligh and Dyer, 1959), lipids were dosed by the Marsh and Weinstein method (1966). Chlorophyll *a* and phaeopigments, extracted with 90% acetone, were measured by spectrophotometry (Lorenzen, 1967).

Data were averaged to filter short-term variability (*i.e.* less than a month). Thereby monthly growth could be related to the mean values of the descriptors during the month elapsed. According to Héral *et al.* (1987), the variability of hydrological characteristics results from four sources: stratification between surface and bottom; tidal fluctuation (daily cycle); fortnightly period (spring and neap tides); seasonal trends.

The sampling strategy aimed at estimating an unbiased mean of each variable, averaged over the water column and over a month. Samples were collected at the surface and the bottom of the water column and averaged. Data were collected twice a month on spring and neap tides. The times of sampling was dependent on the low tide hour and chosen to estimate the tidal mean. Nine descriptors were surveyed: temperature, POM, particulate inorganic matter (PIM), chlorophyll *a*, phaeopigments, proteins, lipids, carbohydrates, dissolved oxygen (O_2P).

The temperature was measured *in situ* and dissolved oxygen was estimated by the Winckler method (Strickland and Parsons, 1972). To analyse the biochemical composition of particulate organic matter, water samples were pre-filtered through a 250 µm, previously heated to 450°C for 1 hour. POM and PIM, were measured by weighing after ignition at 450°C (1 hour). Chlorophyll *a* and phaeopigments were measured by fluorometry (Yentsch and Menzel, 1963) after extraction in acetone 90%. Proteins, lipids and carbohydrates were analysed using the methods described earlier.

Data analysis

For each descriptor of the sediment and water column, 48 observations were available on the three areas together. Using STATITCF software package, Principal Components Analysis (PCA) was performed on the correlation matrix of water column and sediment descriptors and yielded an ordination of ten independent principal axes ordered according to descreasing variance. Denoting $X(48, 15)$ the matrix of normalized observations, X' the transpose of X and U_α the eigenvector associated to the αth eigenvalue λ_α of the correlation matrix $C=X'X$, the coordinate of the *i*th observation on axis α, $Y_{\alpha(i)}$ is equal to the *i*th element of the vector XU_α. Thus the vector Y_α represents the coordinates of observations on axis α, and $Y=(Y_1 \ldots Y_{10})$ is the new matrix of observations in the space generated by the eigenvectors (Volle, 1981).

GROWTH MODEL

Sampling

The growth of clams is described by changes of dry tissue weight, estimated from monthly sampling of 20 individuals from each area. Dry tissue weight was measured after lyophilisation (24 hours). The variations in length or whole weight are not so informative: these two parameters did not show any noticeable decrease during winter. Two periods of growth were considered: from March 1984 until July 1984 (class 1), from September 1984 until July 1985 (class 2). Data collected during the spawning season (weight loss due to the release of gametes) were not included in the treatment.

Equation

Both W and G are known to integrate past events. In general, W or G are expressed as a function of the environment and of the initial weight. Accordingly the model is written:

$$\frac{dW}{dt}=GW^b \qquad (1)$$

The parameters G and *b* are supposed to be dependent on the environment and the species respectively (Sebens, 1982).

Provided $b \neq 1$ and G is constant between t_1 and t_2, integration yields:

$$W=[W_0^c+G.c(t_2-t_1)]^{1/c}, \qquad c=1-b \qquad (2)$$

In order to take into account the time of exposure in the explanation of the growth, the time elapsed between two samples is corrected by a multiplicative factor defined as the fraction of daily immersion time. Thus:

$$W_{t+1}=[W_t^c+(G.\Delta t.c)]^{1/c} \qquad (3)$$

Where Δt is corrected for immersion time.

The growth rate G may be related to the principal axes Y_i extracted from the factor analysis; the relationship is written:

$$G=\sum_i a_i.Y_i+a_0 \qquad (4)$$

Parameter estimation

The model is an extension of the orthogonal regression (Tomassone *et al.*, 1983) to the nonlinear case. The simplex algorithm (Nelder and Mead, 1965; Schnute, 1982) was applied to estimate the parameters b, a_0, a_i. It is a direct search method which minimizes the residual sum of squares (RSS):

$$RSS=\sum_i (W_{obs}-W_{cal})^2$$

The calculations are kept on running until any modification of the parameters have no more noticeable effect on the value of the RSS.

The Fisher test allows to compare it with the total sum of squares SYY:

$$SYY=\sum_i (W_{obs}-\bar{W})^2$$

in order to check the goodness of fit of the model. Since all the axes are independent, any axis X_i explains a part of the variability (contribution) of G: $c_i=a_i^2\lambda_i$ (λ_i is the ith eigen-value). The computation of c_i allows one to rank the axes according to their importance in the explanation of the growth rate. Eventually, a new optimisation may be performed once axes of lesser contribution are excluded. The new criterion RSS_2 may be compared to the former one with the Fisher test:

$$\frac{(RSS_2-RSS_1)/(n_2-n_1)}{RSS_1/n_1}$$

(n_1, n_2 = degrees of freedom).

Unless the loss of information is significant (at the level of 5×10^{-2}) the trials are continued. Similar to a linear stepwise descendant regression process, this method decreases the number of variables to select the more significant ones. Derived from PCA, they may contribute to the explanation of G because of

Table 1. – Correlation matrix between the 15 descriptors. Hydrology PHEO: phaeopigment, CHLA: chlorophyll *a*, TEMP: temperature, O_2P: dissolved oxygen, PROT: protein, LIP: lipid, CARB: carbohydrate, PIM: particulate inorganic matter, POM: particulate organic matter. Sediment PHEO: phaeopigment, CHLA: chlorophyll *a*, PROT: protein, LIP: lipid, CARB: carbohydrate, POM: particulate organic matter.

	Water									Sediment					
	PROT	LIP	CARB	PIM	POM	CHLA	PHEO	TEMP	O_2P	POM	CHLA	PHEO	PROT	LIP	CARB
Water:															
PROT	1.000														
LIP	0.154	1.000													
CARB	0.601	0.010	1.000												
PIM	0.133	0.062	0.702	1.000											
POM	−0.073	0.490	0.289	0.554	1.000										
CHLA	0.391	−0.009	0.265	−0.136	−0.026	1.000									
PHEO	0.271	−0.014	0.054	−0.316	−0.202	0.767	1.000								
TEMP	−0.133	0.074	−0.480	−0.270	−0.063	0.245	0.460	1.000							
O_2P	0.117	0.284	0.258	−0.158	0.086	0.432	0.577	−0.247	1.000						
Sediment															
POM	0.147	−0.119	0.086	−0.054	−0.218	0.060	0.025	−0.142	0.029	1.000					
CHLA	−0.058	−0.022	0.024	−0.123	−0.160	−0.042	−0.075	−0.168	0.028	0.357	1.000				
PHEO	−0.036	0.008	0.054	−0.014	−0.127	0.039	0.004	0.007	−0.041	0.726	0.658	1.000			
PROT	0.174	−0.068	0.161	−0.090	0.115	0.309	0.159	−0.032	0.082	0.146	0.254	0.148	1.000		
LIP	0.196	−0.042	0.113	−0.064	0.011	−0.065	−0.198	−0.238	−0.045	0.531	0.182	0.394	0.464	1.000	
CARB	−0.127	−0.175	0.117	0.081	−0.056	−0.129	−0.143	−0.316	0.100	0.657	0.352	0.575	0.436	0.614	1.000

the high score of the coefficient a_i or the eigenvalue λ_i. Thereby the secondary axes in the analysis of the environmental descriptors (characterized by low value of λ_i) cannot be removed because of their potential impact on growth.

Sensitivity analysis

Once the parameters of the model are determined, the influence of the environmental descriptors on the expected weight may be estimated through a sensitivity analysis. A random fluctuation T of the one parameter a_i around its true value leads to a final weight different from the one expected for each area and for each class. Given a normal distribution $\mathcal{N}(0, \sigma)$ for T, the final weight will also follow a normal distribution whose standard deviation σ_i may be estimated by running *n* simulations with *n* values of T; the ratio σ_i/σ highlights the sensitivity of the model with respect to parameter a_i for each site and class. From an ecological point of view, the sensitivity of growth to natural fluctuations taken into account in principal axes equations, is outlined. In this study, values of $n(50)$ and $\sigma(0.01)$ were chosen to remain in the validity domain of the model.

The model is then applied to compare sites or years at equal initial weights or times of exposure. Simultations are run with other initial conditions and the final weight expresses the growth potential in these cases.

RESULTS

Principal Components Analysis (PCA) was performed on hydrological and sediment descriptors. The examination of the partial correlations matrix showed that these 2 groups were independent (*table* 1). This result obviously led to perform separate analyses for each set without altering the basic principle of global independence. Both analyses provided ten principal axes which explained 95% of the variability.

The growth model

The ten axes derived from the PCA were included in the growth model. After sorting, 5 were finally input into the growth equation (*table* 2). The simulations and observations are displayed on *figure* 2. Since the F test is greater than the F(37, 7) given by tables at a level of 0.05, the goodness of fit of the model is probably to be correct.

Table 2. – Percentage of variance explained by the 5 axes finally entered into the model; regression coefficient of each axis; $a_0 = 1.40$ and $b = 0.61$ (*see* text).

	Axis	% variance	a_i
Water	Y_1	67.9	−1.37
	Y_3	18.3	0.94
	Y_4	6.4	0.64
	Y_2	6.3	0.42
Sediment	Y_8	1.1	0.30

RSS = 13.5, SYY = 170, $n = 35$, $p = 7$, F(7,35) = 58.

Sensitivity analysis provides more information on the influence of each axis. From *table* 3 the percentage of total sensitivity accounted for by each axis was calculated for each area and class. The axes extracted

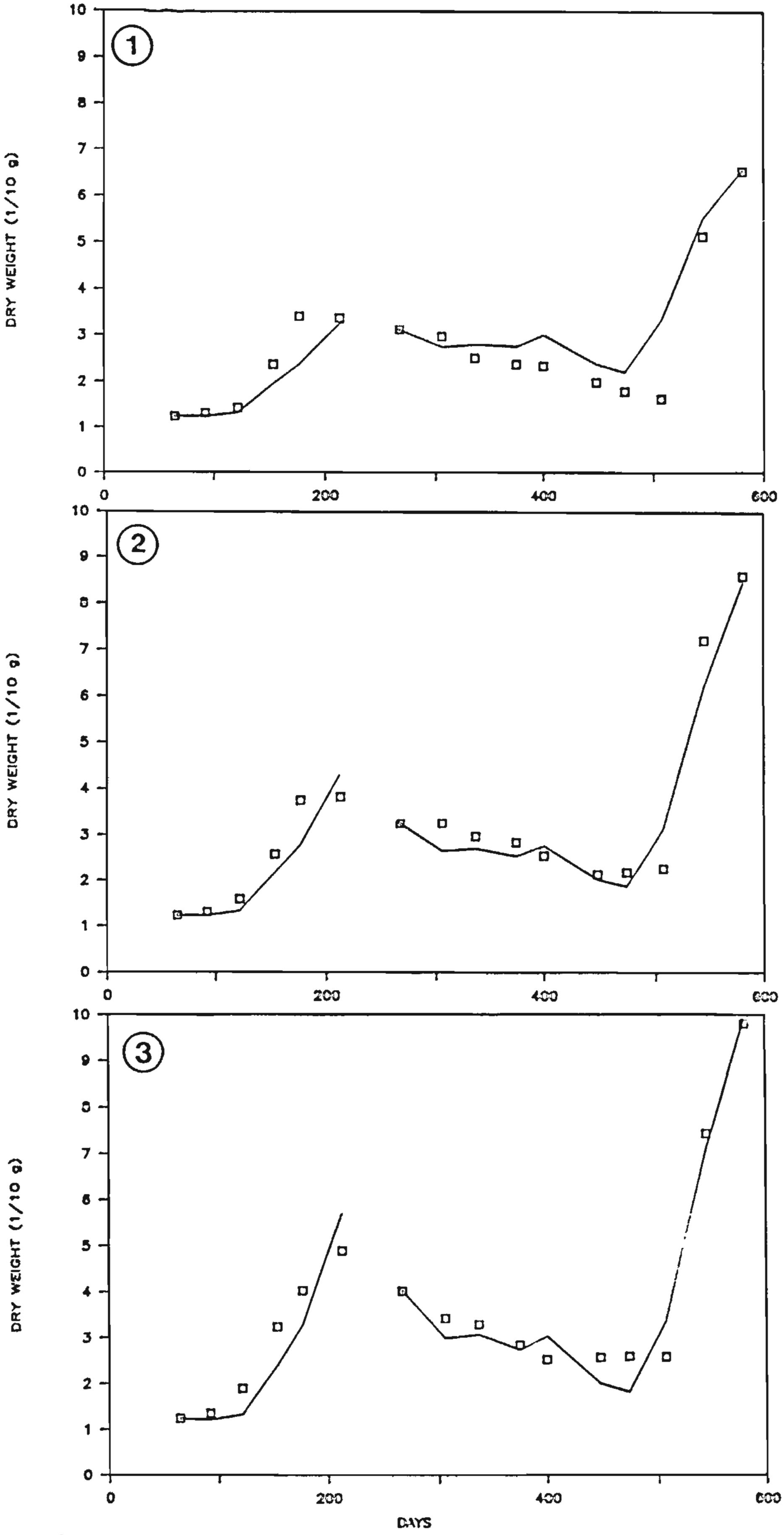

Figure 2. – Growth model (continuous line) and observations (squares): (1) high level area (46% emersion) and classes 1 and 2. (2) medium level area (19% emersion) and classes 1 and 2. (3) low level area (12% emersion) and classes 1 and 2.

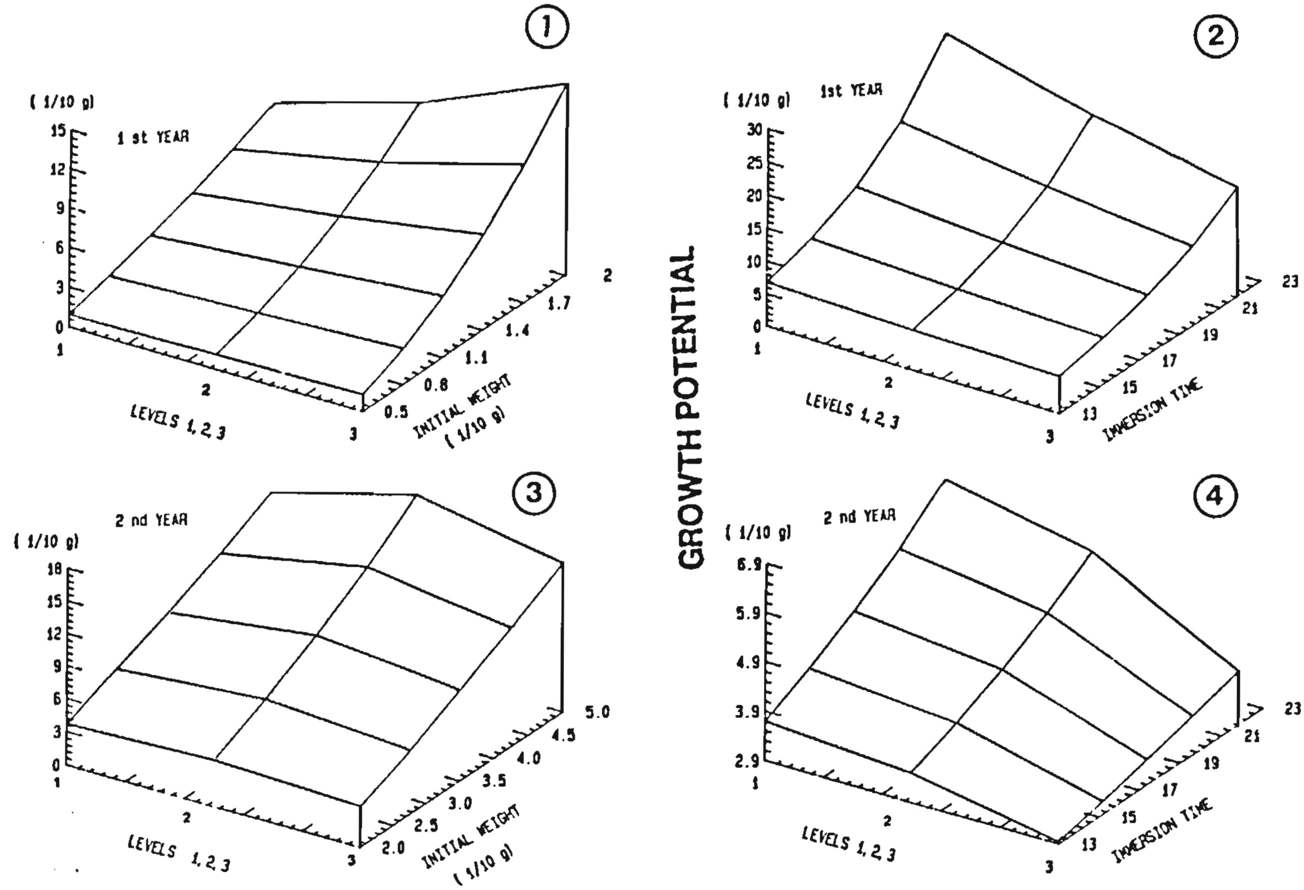

Figure 3. — Simulation of growth potential (1/10 g) for the three areas corresponding to high (1), medium (2) and low (3) levels of emersion. (1) first class and different initial weights (1/10 g). (2) first class and different immersion times (hours/day). (3) second class and different initial weights (1/10 g). (4) second class and different immersion times (hours/day).

Table 3. — Sensitivity of the final weight to the regression coefficients of the five axes retained. Percentages of sensitivity are given in parenthesis (*see* text for further explanation).

	1st class			2nd class		
Level Axis	1 (high)	2 (medium)	3 (low)	1 (high)	2 (medium)	3 (low)
Y_1	1.27	2.49	4.49	3.16	5.88	9.08
	(57)	(63)	(61)	(52)	(56)	(55)
Y_2	0.11	0.22	0.40	0.14	0.26	0.40
	(5)	(6)	(5)	(2)	(2)	(2)
Y_3	0.01	0.03	0.05	0.19	0.36	0.56
	(0)	(0)	(0)	(3)	(3)	(3)
Y_4	0.56	1.09	1.96	1.48	2.75	4.25
	(25)	(28)	(26)	(24)	(26)	(26)
Y_8	0.28	0.12	0.54	1.10	1.27	2.26
	(12)	(3)	(7)	(18)	(12)	(14)

from the sedimentary analysis were responsible for 7 and 14% of the sensitivity according to the class considered (respectively first and second one). The first class is more sensitive to hydrological conditions than the second one.

Although the low level area carried out the highest weight during the survey, simulation and sensitivity analysis enable one to compare the growth performance of the two classes. *Figure* 3(1) shows the highest growth potential of the low level area whatever the initial weight. Since hydrological characteristics are the same for the three areas, such differences may be attributed to the sedimentary characteristics or to the immersion time. The low sensitivity to sedimentary disturbances (7%) and the computations of growth potential related to immersion time [*fig.* 3(2)] intend to show that high immersion time is mainly responsible for growth of the first class. However the sensitivity to the sediment is greater than that expected from the computation of contribution (*tables* 2, 3). This difference must be attributed to the non-linearity of the model.

Because of the differences in initial weights of clams in the second class, no direct information may be derived from the observations. However, the simulations of growth potential versus initial weight [*fig.* 3(3)] for each area show the high score of the medium level area compared to the low level one. The effect of immersion time is also important [*see* simulations with different immersion times on *figure* 3(4)] and growth would be still better with longer immersion time in the high and medium areas. The impact of sedimentary conditions is more consistent for the second class than for the first one and inverts the classification of areas.

We can return to the original descriptors by identifying factor axes with ecological descriptors. Analyses of the projections of descriptors and observations highlighted the annual fluctuations, and the variability between years and between areas.

Hydrological analysis

Since hydrological parameters were the same for all three areas, a single analysis was carried out and the different areas were not discriminated.

The first three axes account for 72% of the total variability among the nine variables (*table* 4). By comparing the projections of variables (correlations) and of observations, periodical and single fluctuations may be identified. Points close to the center of the graph are insufficiently represented and are not taken into account in the analysis. Five axes were extracted by the analysis, but only the first three were plotted; axes 4 and 5 may be investigated from the *table* 5*a*.

Table 4. — Eigenvalues and percentage of variance explained by the principal axes of PCA of hydrological and sedimentary descriptors.

PCA	Water		Sediment	
Axis	Eigenvalue	%	Eigenvalue	%
Y_1	2.56	28	3.24	54
Y_2	2.51	28	1.12	19
Y_3	1.45	16	0.83	14
Y_4	1.09	12	0.36	6
Y_5	0.80	9	0.27	5

The first axis is correlated with 3 variables [*fig.* 4(1)]: chlorophyll *a*+phaeopigments, dissolved oxygen, proteins and appears to be characteristic of the bloom period (June 1984, May 1985) [*fig.* 5(1)]. In contrast, earlier and later periods (March and April, October and November) are related to poorer waters and are projected on the other side of the first axis [*fig.* 5(1)].

The second axis discriminates temperature and seston linked to carbohydrates which show a peak in winter.

The different origins of nutrients appear on the first plane [*fig.* 4(1), 5(1)]: bloom in May and June, detritus in winter and show a one month lag between 1984 and 1985. The time scale does not allow to investigate the true lag within oscillations with a period less than 2 months.

The third axis is related to the concentration of lipids [*fig.* 4(2), 5(2)]. A peak is noticed in February 1985 in contrast with January, December and March. This strenghthens the assessment of short term fluctuations.

Dissolved oxygen and temperature are opposed on the 4th axis which defines a second component of both variables related to January and August 1985. The fifth axis shows another component of protein fluctuations. As shown by the qualities of representation (*table* 5*b*), this component corresponds to March, May and July 1984; it disappears in 1985.

Finally, axes 3 and 5 describe short term fluctuations related to specific amounts of nutrients. Axis 4 is only related to physical parameters.

Table 5a. — Correlations between hydrological variables and principal axes.

Axis	Y_1	Y_2	Y_3	Y_4	Y_5
PROT	0.35	0.11	0.10	0.05	0.36
LIP	0.03	0.07	0.62	0.03	0.22
CARB	0.21	0.64	0.10	0.01	0.00
PIM	0.00	0.72	0.00	0.13	0.07
POM	0.00	0.38	0.44	0.02	0.05
CHLA	0.74	0.03	0.00	0.04	0.03
PHEO	0.72	0.18	0.00	0.01	0.03
TEMP	0.01	0.38	0.16	0.41	0.00
O_2P	0.49	0.00	0.03	0.40	0.04

Table 5b. — Qualities of representation of observations on axes Y_4 and Y_5 extracted from the PCA of hydrology.

Date	Axis Y_4	Axis Y_5
March 1984	0.212	0.343
April 1984	0.002	0.215
May 1984	0.110	0.366
June 1984	0.034	0.106
July 1984	0.236	0.331
August 1984	0.017	0.044
October 1984	0.213	0.005
November 1984	0.020	0.039
December 1984	0.061	0.050
Janvier 1985	0.423	0.001
February 1985	0.196	0.000
March 1985	0.041	0.039
April 1985	0.077	0.145
May 1985	0.063	0.005
June 1985	0.010	0.005
July 1985	0.340	0.095

Sedimentary analysis

54% of variability is explained by the first axis. The 5 axes of the analysis account for 98% of the original variability (*table* 4). Principal and secondary fluctuations are present.

Chlorophyll *a*, phaeopigment and POM may be seen on the first axis [*fig.* 4(3), 4(4)]. The first two

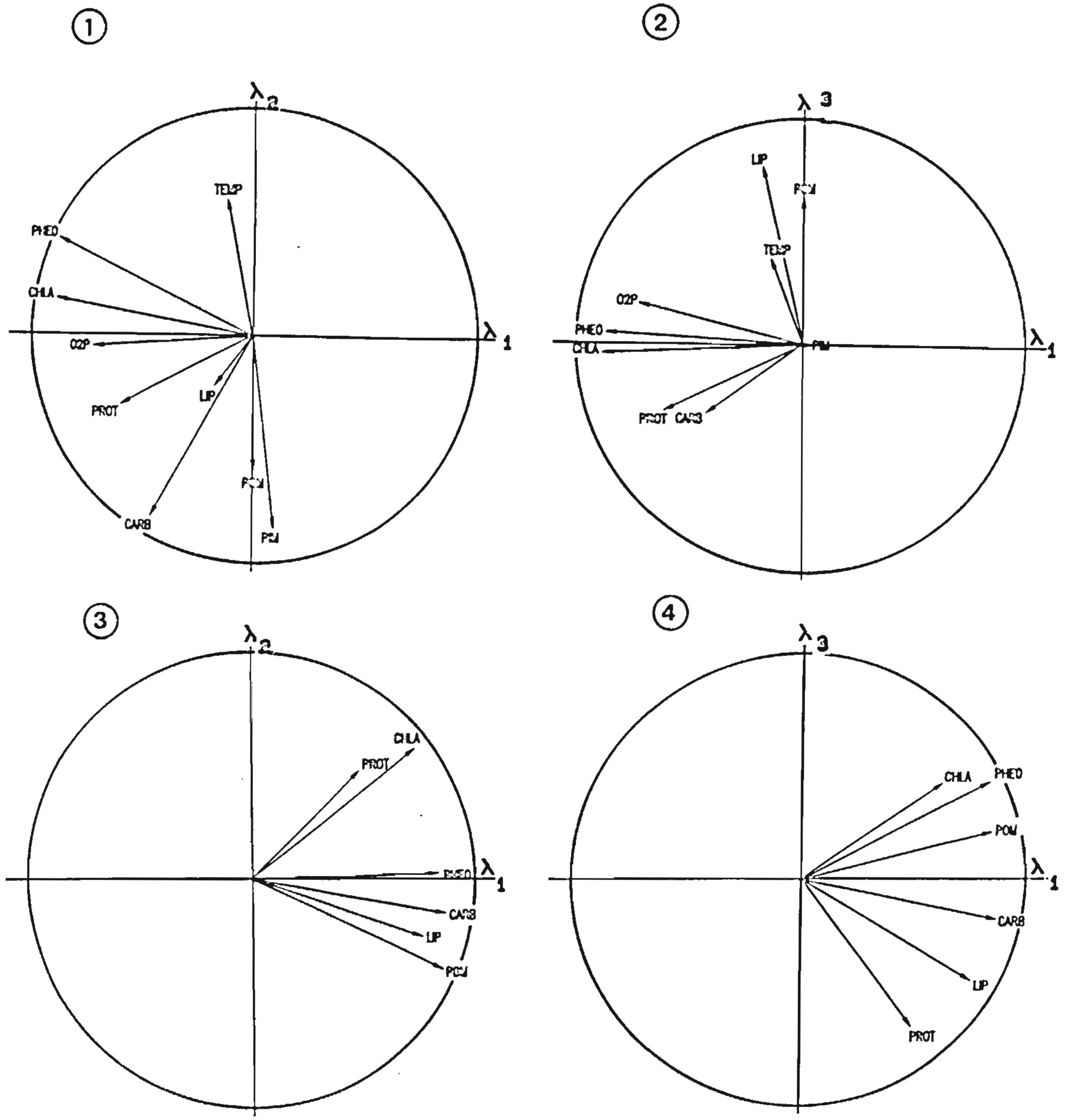

Figure 4. — Correlations between descriptors and principal axes. (1) axes 1, 2 extracted from the PCA of hydrology. (2) axees 1, 3 extracted from the PCA of hydrology. (3) axes 1, 2 extracted from the PCA of sediment. (4) axes 1, 3 extracted from the PCA of sediment.

variables are of major influence. The proteins are associated with the second axis, and are independent of the former set. The comparison with the results of hydrological analysis shows the impact on the axes of ending bloom periods (August, 1985; October, 1984; November, 1984). From April to June, high levels of proteins, lipids, carbohydrates are noticed. In contrast, the summer periods correspond to low levels of proteins lipids, carbohydrates (July 1984, August 1984, 1985).

As already indicated in the hydrological analysis, higher order axes may be analysed as secondary seasonal components (*table* 6). Only chlorophyll *a*, lipids and carbohydrates are concerned. The same peak of lipids appears in water and sediment in February. Lipid and carbohydrate peaks occur mainly in winter.

The differences between areas are easily visible in the plane of axes 1, 2 which shows a decreasing con-

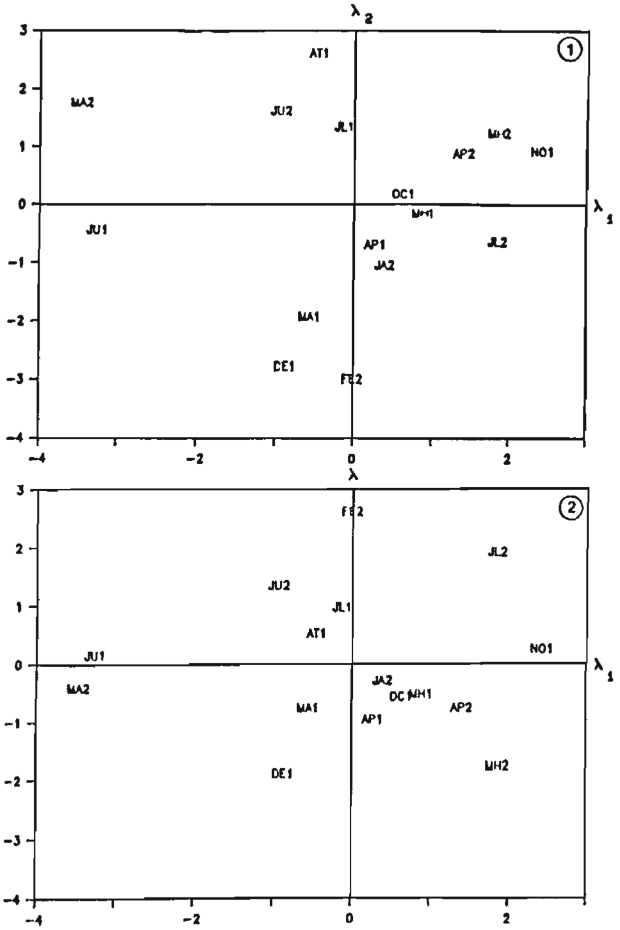

Figure 5. — Principal components analysis of hydrology. (1) Projections of observations on the plane (1,2). (2) Projections of observations on the plane (1,3). First class: MH 1: March, AP 1: April, MA 1: May, JU 1: June, JL 1: July, AT 1: August 1984. Second class: OC 1: October, NO 1: November, DE 1: December 1984, JA 2: January, FE 2: February, MH 2: March, AP 2: April, MA 2: May, JU 2: June, JL 2: July 1985

Table 6. — Correlations between sedimentary variables and principal axes.

Axis	Y_1	Y_2	Y_3	Y_4	Y_5
POM	0.67	0.04	0.09	0.01	0.07
CHLA	0.39	0.19	0.36	0.02	0.02
PHEO	0.69	0.20	0.00	0.00	0.01
PROT	0.24	0.45	0.24	0.01	0.05
LIP	0.53	0.21	0.06	0.20	0.01
CARB	0.72	0.03	0.02	0.12	0.01

centration gradient from the high level to the low level area, highly correlated with the first axis [*fig.* 6(4)].

Low level area

Four well defined periods appear on the first plane [*fig.* 6(3)]:

— April, May, June with high concentrations in proteins, lipids and carbohydrates;

— July, August with low levels of POM;

— October, November considered as a post bloom period (chlorophyll *a*, phaeopigment);

— Winter, a season with average concentrations.

A slight time-lag discriminates the 2 years projected on the same plane. The plane 1-3 brings little information, since the *y*-coordinate of all the observations but one is negative [*fig.* 6(6)].

On the first bisector, the months of October and November coincide with a peak of lipids. The third axis also discriminates the 2 years according to detritic materials. As a consequence, more nutrients were available for food all over 1984 compared to 1985.

Medium level area

This area differs from the others by both stability and low levels of nutrients no matter the organic compartment considered [*fig.* 6(2), 6(5)]. Bloom periods are not very intense and are shown in the plane 1-3 [*fig.* 6(5)].

High level area

When first analysing the plane 1-2 organic matter flows occurred mainly in June 1984 [*fig.* 6(1)]. One can notice greater oscillations in 1985 with two main peaks of nutrients in June and March corresponding to chlorophyll *a*, phaeopigments and proteins, lipids and carbohydrates. A rapid succession of seston peaks occurs in June and is an indicator of a great sensitivity of sediment to environmental fluctuations. In contrast with the low level area, the third axis is far from being stable. For instance positive coordinates are observed in April, May 1984, in winter and June 1985 so that chlorophyll *a* and proteins vary rapidly [*fig.* 6(4)].

DISCUSSION

Combining correlations and the classification, the following descriptors are demonstrated to be of decreasing importance: chlorophyll *a* + phaeopigments (axis 1), temperature (axes 2+4), lipids (axis 3), sediment organic matter (axis 8).

Data on trophic relationships have been compiled in *table* 7. Kautsky (1982) on *Mytilus edulis*, Héral *et al.* (1984) on *Crassostrea gigas* obtained such correlations *in situ*. The influence of temperature on bivalve physiology was demonstrated by many authors. For example, an effect of temperature on growth, excretion and gametogenesis of *Ruditapes philippinarum* has been shown by Mann and Glomb (1978) and Mann (1979). Ventilation rate (Bernard, 1983) and respiration rate were also modified by temperature (Bernard, 1983; Laing *et al.*, 1987). Laing *et al.* (1987) showed that growth efficiency depended on temperature and phytoplankton nutritional value. The contents in polyunsaturated fatty acids (PUFA) were underlined by Waldock and Holland (1984). The quantity and quality of lipids appear to be important to the growth of *R. philippinarum*, as suggested by

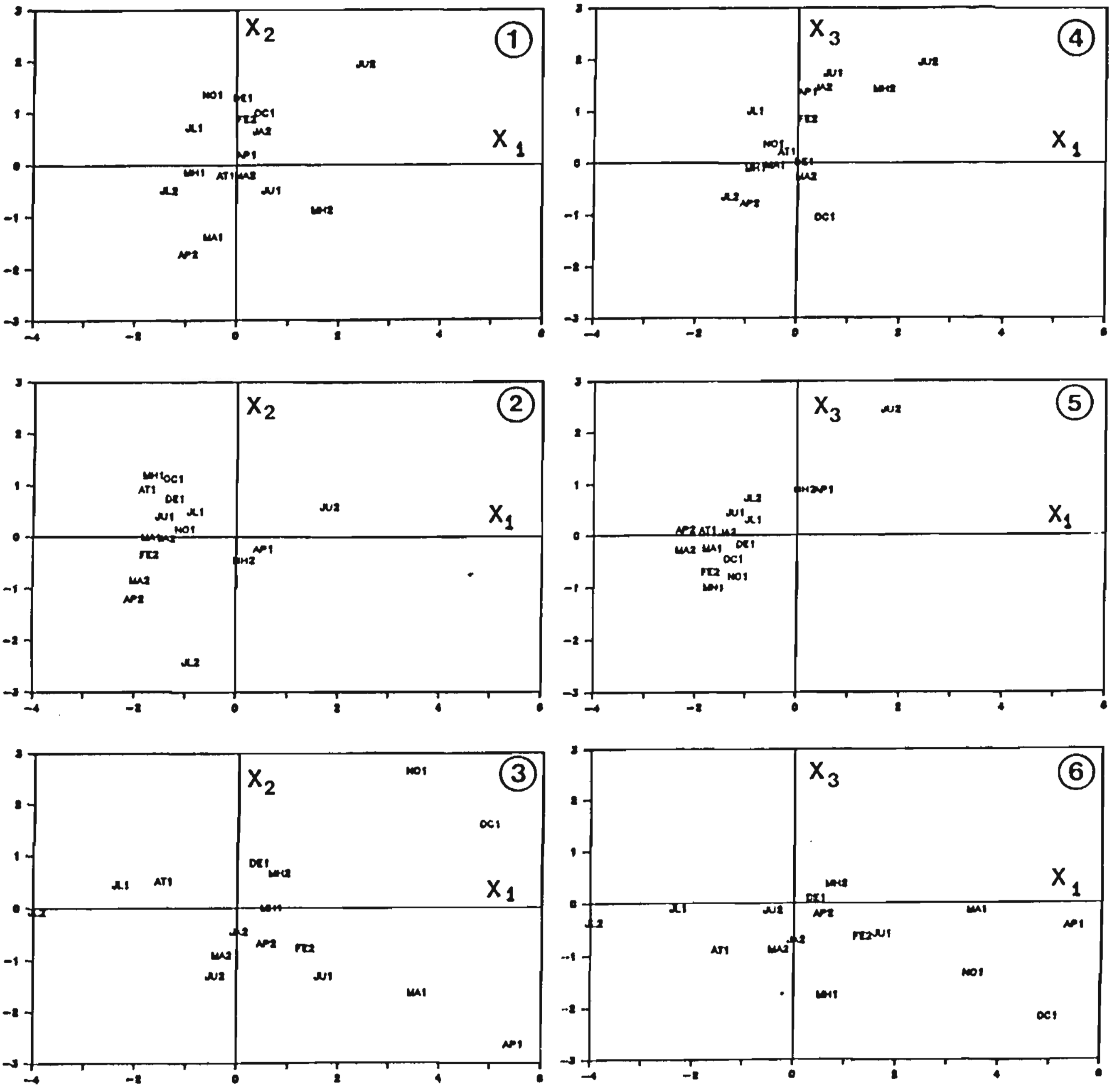

Figure 6. — Projections of observations on principal axes extracted from the PCA of sediment. Axes 1,2: (1) high level, (2) medium level, (3) low level. Axes 1,3: (4) high level, (5) medium level, (6) low level.

the sensitivity of the model to this factor. Although no strong correlations were found between the meat production and the detritic organic matter in estuarine areas, growth in weight was correlated with chlorophyll *a* concentration. Similar results have been found with *C. gigas* (Héral *et al.*, 1984). The correlations observed between growth, water column and the interface between water and sediment, need to be confirmed by animal field studies to assess the influence of each variable, and to avoid any casual correlation (Héral *et al.*, 1984). The results of the present study show significant correlations for two classes at different tidal exposures, during two years. Even though explanatory variables are identical, the sensitivity varied between the 2 years, as demonstrated by the stronger sediment effect in 1985. However the winter conditions in 1985, which caused a more frequent resuspension of superficial sediment, could

Table 7. – Review of factors and methods used for the study of trophic relationships.

Authors	Species	Dependent Variable	Positive factors	Negative factors	Calculation used to establish correlation
Hargrave and Peer (1973)	Benthic biomass	Biomass	Clorophyll *a*	–	No
Lelong and Riva (1976)	*Ruditapes philippinarum*	Length	Phytoplankton, T°, salinity	–	No
Vahl (1980)	*Chlamys islandica*	Dry weight	–	PIM	No
Héral *et al.* (1983)	*Crassostrea gigas* (adult)	Dry weight	–	PIM	No
Deslous-Paoli and Héral (1984)	*Crassostrea gigas*	Dry weight	–	PIM	No
Fréchette and Bourget (1985)	*Mytilus edulis*	Length Dry weight	POM	–	No
Wallace and Reinsnes (1985)	*Chlamys islandica*	Dry weight	Food quantity, PIM, % POM.	–	No
Wildish and Kristmanson (1979)	Biomass	Biomass	ATP current speed, POM	–	No
Wildish and Kristmanson (1984)	*Mytilus edulis*	Biomass	ATP current speed, POM	–	No
Wildish and Kristmanson (1985)	*Mytilus edulis*	Wet weight	POM current speed	–	No
Beninger and Lucas (1984)	*Ruditapes philippinarum*, *Ruditapes decussatus*	Dry weight	No correlation with: temperature salinity	–	Non parametric tests
Soniat *et al.* (1985)	*Crassostrea virginica*	Dry weight gonad	Proteins, Lipids, Carbohydrates	Temperature	Non parametric tests
Wildish *et al.* (1981)	*Molluscs*	Biomass	Log ATP current speed	Erosion sediment	Linear regression
Kautsky (1982)	*Mytilus edulis*	Length	T°, chlorophyll *a*	–	Linear regression
Deslous-Paoli *et al.* (1982)	*Crassostrea gigas*	Biochemical composition	Chlorophyll *a*, carbohydr.	PIM	Factor analysis
Héral *et al.* (1984)	*Crassostrea gigas*	Dry weight	T°, chlorophyll *a*, pheopigment dissolved orga. (sediment and water)	Bacteria	Multiple linear regression
Bodoy and Plante-Cuny (1984)	*Ruditapes decussatus*	Length	Chlorophyll *a*, primary production (water + sediment)	–	Multiple linear regression
Plante-Cuny and Bodoy (1987)	*Donax trunculus*				
Page and Hubbard (1987)	*Mytilus edulis*	Length	Chlorophyll *a* (T°, No significant)	–	Multiple linear regression
Parache and Massé (1986)	*Mytilus galloprovincialis*	Length	Pheopigment proteins	–	Stepwise regression
Parache and Massé (1987)	*Mytilus galloprovincialis* (adults, juveniles)	Dry weight	Lipids, carbohydrates, T°, proteins	–	Stepwise regression

explain the difference in model sensitivity. Furthermore, the dominant phytobenthic species on muddy bottom are generally large diatoms (Rincé, 1978). These species could represent a more easily available food for the older clams.

The daily submersion time represents the more important factor in determining growth differences between intertidal levels, such as demonstrated by the growth model. These differences can be attributed to the difference of food availability. Tidal level has long been recognized as an important factor in controlling growth [e. g. Glock and Chew, 1979 on *R. philippinarum*, Griffiths (1981) on *Choromytilus meridionalis*, Gillmor (1982), Craeyermeersh *et al.* (1986) on *Mytilus edulis*].

Many authors have suggested that food depletion can occur, due to the activity of suspension feeders during tidal cycles. Fréchette and Bourget (1985) show that depletion of organic particles limits the growth of *M. edulis*. In the same way, Cloern (1982) and Cohen *et al.* (1984) suggested that benthic organisms were present in quantities large enough to reduce the phytoplanktonic biomass. Peterson and Black (1987) demonstrated that potential food depletion in the water column is a "priority" effect of suspension feeders in intertidal shore. Héral *et al.* (1983) and Deslous-Paoli and Héral (1984) found that *C. gigas* retained between 0.1 and 0.5% of the water column energy, at a density of 200 g/m^2 in the bay of Marennes-Oléron, while the current speed varied between 0.5 $m.s^{-1}$ and 1.5 $m.s^{-1}$. The retention rate of *R. philippinarum* was 0.8 times the retention rate of *C. gigas*, with particles retained of nearly the same size (Deslous-Paoli *et al.*, 1987). For these reasons, the depletion of POM due to 40 g/m^2 biomass of clams remains usually lower than 1% and does not account for growth limitation. However, at a major scale, depletion rates are related to residual currents, water residence time and biomass levels in the bay (Héral, 1987; Bacher, 1987).

Since submersion time is the most important factor which explains growth differences between sites, the filtration time is not the only factor affected by submersion. Any increase in tidal exposure will have physiological effects (Bayne *et al.*, 1976; Griffiths, 1981; Fang, 1982). A sensitivity of growth to the sediment organic content has been shown. These results agree with those obtained by Plante-Cuny and Bodoy (1987), who observed a positive correlation between primary production in sediment and growth of *R. decussatus*. A significant positive correlation between phytobenthic primary production, chlorophyll *a* concentrations and level of exposure was also found by Cadée and Hegeman (1977). These results are supported by the work of Admiral and Peletier (1980) and Colijn and de Yonge (1984) in estuarine areas. The high primary production resulted mainly from a longer lighting at high elevation. Sediment organic content is correlated to the level of exposure. Thus the quality or quantity of available food in the higher levels of sediment may counteract the growth deficit due to increasing tidal exposure. Simulations of the growth model were performed with equal immersion time or weight. The larger weight obtained at high or medium levels supported this phenomenon.

The value of the exponent $b=0.6$ shows that the model is really non linear. Consequently, our model shoud be more precise than a linear one and the comparisons more reliable. Theoretically, estimation of the parameters requires cross combinations of the factors. This should have led to study the growth of different cohorts, since initial weight is partly taken into account. On the contrary, interdependent estimators of the parameters results from the correlations between some factors (e. g. initial weight and level of immersion). Results do not allow generalization in that case, even though computed values are consistent with observations. In this study, the experimental design encompasses some heterogeneity since the spawning at the end of the first year leads to initial weight variability between the areas. However, the whole data set does not support exactly the cross effects hypothesis and the model parameters should not be applied to other sites without due precautions.

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