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Association of two complementary mathematical methods : correspondence analysis and rank-frequency diagrams in the study of the organization and structure of benthic mediterranean populations.

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Abstract : This study showed the process of recolonization of a defaunated substrate by a "muddy sands in sheltered area" (SVMC) population. Twenty four experimental boxes were placed at 5 m depth, in Lazaret Bay, Toulon during an annual cycle.

To compare natural and experimental conditions, a few meters apart from the experimental site, autochtonous sediments were also monthly sampled. The structure and degree of organization of populations were followed by means of Correspondence Analysis, a multivariate method of ordination in reduced space, and Rank-Frequency Diagrams. Correspondence Analysis were applied to 140 taxa of benthic organisms.

Both technics were complementary, showing the evolution of the experimental population towards a state resembling the natural surrounding population. After one year, almost the same diversity and lists of species were found, nevertheless the organization (*i.e.* relative proportions of species) appeared to be different.

Résumé : Cette étude montre le processus de recolonisation par une communauté des "Sables Vaseux de Mode Calme" (S.V.M.C.), d'un substrat dépourvu de faune.

24 modules expérimentaux ont été placés, par 5 m de profondeur, dans la baie du Lazaret, Toulon, pendant un cycle annuel. Afin de comparer le milieu naturel et les conditions expérimentales, des prélèvements mensuels de sédiment autochtone ont été simultanément réalisés.

La structure et le degré d'organisation des populations ont été suivis au moyen de diverses techniques statistiques et notamment une technique multivariée d'ordination (Analyse Factorielle des Correspondances) et des Diagrammes Rangs-Fréquences. L'Analyse des correspondances a été appliquée aux données obtenues à partir de 140 taxons benthiques. Ces deux techniques sont complémentaires, montrant l'évolution des populations expérimentales vers un état voisin du naturel environnant. Après une année, on trouve presque la même diversité et des listes d'espèces similaires. Néanmoins, l'organisation, c'est-à-dire les proportions relatives des espèces, apparaît être quelque peu différente.

Introduction

In recent years, the study of spatio-temporal evolution of benthic assemblages has become one of the most important preoccupations in the field of marine ecology. Several are the reasons to choose the benthos as subject of study ; between these, the role it plays in nutrient recycling (Valiela, 1984).

Investigations have been made to study the processes and sequences of benthic colonization and recolonization (Girin & Flasch, 1972 ; Sarnthein & Richter, 1974 ; Mc Call, 1977 ; Arntz & Rumohr, 1978 ; Desbruyères *et al.*, 1980 ; Santos & Simon, 1980 ; Bhaud, 1981 ; Stora, 1982 ; Dauvin, 1984 ; Diaz-Castañeda, 1989 ; Diaz-Castañeda *et al.*, 1989). Different authors consider and develop several methodologies in order to compare the evolution of populations in the natural environment with those observed in experimental boxes containing similar populations. They try to state accurately the way adults and juveniles colonize the substratum, the interspecific competition and the ecological succession of different benthic populations. A strategy in the study of the development of populations consists in observing the recolonization of a previously defaunated sediment. This methodology gives information not only on the individual post-larval growth but also on the dynamics of the various populations.

This paper presents the results of a one-year study on the shallow benthic community at the Lazaret's bay (Toulon). The aim is to provide further information on the processes and sequences of recolonization of a soft bottom community and to examine the spatial and temporal variations in relation to the environmental conditions, with the help of Factorial of Analysis Correspondences (FAC) and Rank-Frequency Diagrams (RFD).

MATERIALS AND METHODS

Area studied

Sediments were taken from a littoral brackish lagoon, the Berre Lagoon, located 40 km north-west of Marseille, France (Fig. 1). These sediments had been devoided from macrofauna due to lack of oxygen and the presence of hydrogen sulphide. We transplanted the entire samples to a less disturbed biotope, 100 km away, the Lazaret Bay, inside the "rade abri", near Toulon were water and sediment quality seemed to be better, hence allowing the study of recolonization in a more stable biotope, after the intensive pollution has been partially released.

The populations able to colonize the sediments of Berre Lagoon an Lazaret Bay if not too polluted belong to the "Muddy Sand in Sheltered Area" (in French "Sables vaseux de mode calme" or SVMC, Peres & Picard, 1964). These calm environments are propicious to *in situ* experimentation.

Granulometric characteristics (stated by Pr Arnoux, Laboratoire d'Hydrologie et de Molysmologie Aquatique from the University of Aix-Marseille II), are rather different (Table I), particularly with a less important conchiferous fraction in the Berre Lagoon. Nevertheless the macrobenthic potential communities are similar (Bourcier & *al.*, 1979).

TABLE I

Grain size analysis of sediments from Berre Lagoon and Lazaret Bay

Grain size	Berre	Lazaret
> 2 mm	3,1 %	27,8 %
63 µ to 2 mm	21,5 %	36,5 %
< 63 µ	75,4 %	35,7 %

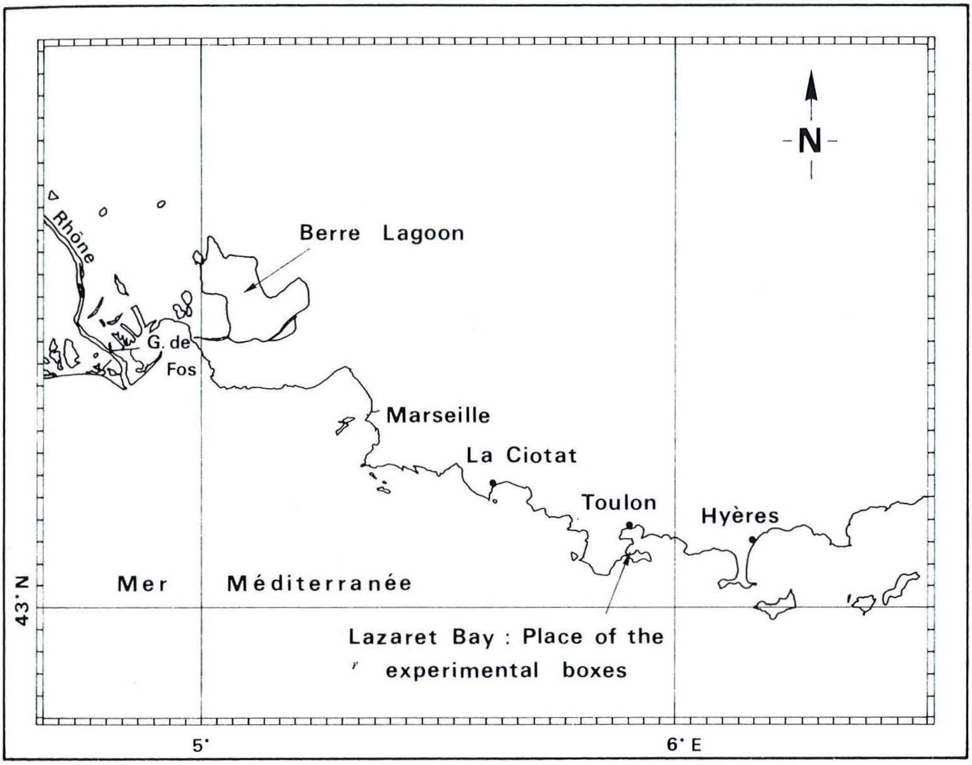

Fig. 1 : Geographic location of Berre lagoon, Toulon (experimental site) and neighbouring Mediterranean coast.

Another reason for choosing this site was the relatively weak hydrodynamism, avoiding disturbance in the experimental boxes, and also the possibility of leaving the experimental installation without any supervision because of the isolated character of the place.

Sampling technique

The recolonization study of soft sediments was made at 5 m depth in the Lazaret Bay. The SVMC sediment was taken from the Berre Lagoon with an Orange-Peel grab taking about 5 dm^3 over a 0.12 m^2 surface. The absence of any alive macrobenthic organisms was first ascertained, then the samples were put into experimental boxes.

These boxes were square plastic recipients of 26 cm side and 11 cm height. They were choosen for their maniability while diving, and because the volume and surface of sediment they hold were not very different from those of the grab samples, namely 0.065 m^2 and about 5.2 dm^3 if filled up until 8 cm heigh. The empty containers were previously submerged during various days into flowing sea water to eliminate as much as possible the chemical substances absorbed by the plastic and able to be released at the contact of water and of influencing the recolonization processes.

Then the boxes were submerged. To avoid any disturbance or loss of sediment when the containers were positioned by diving, they were covered with a plastic sheet kept in place by an elastic. The 24 containers were arranged in parallel lines on the sea floor ; plastic sheets were perforated to allow progressive entrance of sea water without washing of sediments ; the plastic sheets were then removed. To avoid any displacement, each container was fixed to the bottom with two wooden sticks. The sediment surface was approximately 8 cm above the sea floor.

The procedure was the same, but inversed, for the recovery of the experimental boxes, avoiding disturbances or loss of organisms. The recovery was done also by scuba diving.

24 experimental boxes were prepared to study the annual cycle with its seasonal variations, removing two boxes each month during one year, one to be used for the chemical analyses of pollutants and the other for the faunistical analysis. The experiment began on 8 March 1982 and finished on 11 March 1983.

To compare natural and experimental conditions, a few meters apart from the experimental site, 10 l of autochthonous sediment were also monthly sampled with an orange-peel grab, *i.e.* 5 l for the faunistical analysis and 5 l for the chemical one. Also one week before placing the containers, some grab samples were taken in order to have a state of reference (Table II, sample 1*).

The monthly sampling was, as far as possible observed when removing the boxes for examination. Dates of sampling for experimental and natural populations are given in Table II.

TABLE II

Sampling dates

N° Sample	Date	
1*	02.03.82	grab
	08.03.82	Placement of experimental boxes
2	01.04.82	2 boxes + grab
3	03.05.82	"
4	01.06.82	"
5	28.06.82	"
6	30.07.82	"
7	08.09.82	"
8	12.10.82	"
9	15.11.82	"
10	22.12.82	"
11	24.01.83	"
12	11.03.83	"

* In this paper, only the faunistical data were analysed. The analysis of pollutants was performed by Pr Arnoux Laboratoire d'Hydrologie et Molysmologie Aquatique, Faculté de Pharmacie, Université d'Aix-Marseille II.

After recovering the experimental boxes, shifting of sediments was done at the laboratory. The less conchiferous fraction of the sediment used here did facilitate the extraction of the macrofauna. The sediment was first washed on a sieve with 1 mm diagonal mesh and the last shiftings of each sample were made on a 0,5 mm mesh in order to preserve as far as possible the juvenile macrofauna. The remaining contents were fixed in 10 % neutralized formalin ; later mollusks, echinoderms and crustaceans were transfered into 70 % alcohol.

Species were determined and the individuals were counted (per species or per taxon).

Data analysis

Two numerical treatments of the data were combined here : a Correspondence Factorial Analysis (FAC) on the contingency table crossing samples and species or taxa (Benzecri *et al.*, 1973 ; Legendre & Legendre, 1979, 1984 ; Leprêtre, 1988) and Rank-Frequency Diagrams (RFD) (Frontier, 1976, 1985, Volle, 1985).

Correspondence Analysis

Analysis of parameters considered separately often gives a partial idea of the studied phenomenon. This is the reason why we performed numerical analyses to get a synthetical vision to understand the community structure and its functioning. Factorial analyses show the contribution of both different species and different samples to the explanation of a global phenomenon. These methods are rather diversified and are nowadays of a great use in ecology (Legendre & Legendre, 1979 ; Lebart *et al.*, 1982 ; Lagarde, 1983).

FAC analyses a contingency table such as each line and column sums have sense, and are homogeneous, namely both represent a number of individuals (per species or per sample). In fact, the table shares a total quantity, namely the total number of counted organisms, into lines and columns. The FAC leads to compare the profile of lines and columns and to perform a correspondence between the classification of lines (samples) and the classification of columns (taxa). Finally the relevant information, or inertia, contained in the table can be summarized into a space of few dimensions, for example 2 or 3. In this representation in reduced space, resemblances between samples and taxa can be represented by the proximity between the representative vectors of lines and columns, given by a "barycentric transformation".

Nevertheless an analysis can't be made in one step and mechanically. After a first analysis of the complete contingency table, it can be seen that a few number of lines and/or columns play a strong role, and the few first axis or planes interprete only the variations of these samples and/or taxa, crushing the role and the significance of the others. These principal axes are not uninteresting, but on the contrary are too obvious and borrow the remaining information ; in such case, FAC should be performed on the table of the remaining lines and columns after removing the obvious parameters. The samples and/or taxa to be removed are seen as they account for a too high proportion of the inertia of one of the axes. That occurs when one species is either sporadic and abundant in one sample, or rare. In that case, the species and the correspondent few samples account for 85 % of the inertia of an axis for example, which explains only that correspondence. Eliminating that species, and the evident correspondence with few samples, leads to a better description of the remaining structure.

Rank-Frequency Diagrams

This method consists in representing the frequency distribution of species in a community or sample as a retrocumulated distribution, putting in abscissa the rank of each species in a decreasing order of abundance (the first species being the most abundant, the second following the first and so on) ; and in ordinate, the abundancy or the frequency of the species in the sample. This diagram is equivalent to a retrocumulated frequency curve because assuming that the r^{th} species, from a total number S, has the frequence F_r is equivalent to assume that a proportion r/S of the species has a frequency $\geq F_r$.

A number of species distributions have been described in the past, Preston log-normal distribution, Mac Arthur or broken stick distribution, etc. No fitting to any model is intented here, diagrams are only given for a descriptive aim and, following Frontier (1976, 1983, 1985). Ranks and frequencies of species are plotted in a logarithmic scale.

The shape of the curve obtained is usually characteristic of the structure and the evolution stage of the community. During natural evolution of a planktonic ecosystem, Frontier (op. cit.) recognizes three principal stages, and an intermediary stage between the first two stages :

Stage 1 : the curve is "S" shaped and indicates the development of a pioneer community with predominance of one or few species. This kind of curve is observed in conditions of enriching of biogenous elements, or in overexploitation, or chronic pollution. It characterizes a juvenile population.

Stage 2 : it approachs to Mac Arthur's "broken stick" model, diversity increases and reachs maximum values in the ecological succession. It indicates the apparition of a more and more complex network of interactions as new species, which demands previous changes of the ecosystem, appear.

Stage 3 : it indicates some decrease of the diversity. It is a readjustment of diversity which was too high to permit a long term stability of the ecosystem. Rank-Frequency Diagrams become rectilinear, at least over a part of the curve. Frontier (1985) suggests some different interpretations for this last kind of curve, as well as of curves with "steps" which ought to correspond to intermediary stages of the ecological succession (transitory stages), or to aleatory fluctuations of abundance, or to a bad sampling method which mixes several communities.

The importance of these diagrams resides in the fact that they give a supplementary information : the maturity degree of population is more easier to estimate from the curve shape than by a merely numerical index, which depends on the number of species.

Rare species constitute, in every frequency distribution of species, a tail of distribution not easily interpreted, that had been removed from the diagrams.

RESULTS

Correspondence analysis

The samples from the natural sediment surrounding the experimental boxes were called "grab" (G) and the samples from the boxes are called "experimental" (E).

Analysis of the complete data table (Fig. 2a, b)

A FAC on the total set of data, from a table of 110 species x 23 samples (namely 12 G and 11 E) was done first. The big number of species, of which only a few strongly contributed to the three first inertia axis, led us to practice a second analysis, following the methodology explained above, retaining only 32 species responsible for the greatest part of the inertia of the three first axes and eliminating the too sporadic ones. The three first axes explained respectively 24.9, 13.9 and 13.5 % of the total inertia. For species abbreviations, see Table III.

TABLE III

Species abbreviations used in Correspondence Analyses and Rank-Frequency Diagrams.

AA	*Abra alba*
AC	*Armandia cirrosa*
AF	*Aricia fœtida*
AO	*Aonides oxycephala*
AP	*Acanthocardia paucicostata*
C	Cirratulidae
CC	Cirratulidae sp 1
CCa	*Capitella capitata*
CE	*Cardium exiguum*
CF	*Cirrophorus* cf. *furcatus*
CG	*Corbula gibba*
CH	*Chone* sp.
CHi	*Chiton*
CI sp	Cirratulidae sp 2
CR	*Corophium runcicorne*
C sp	*Caprella sp.*
Cr	Crangonidae
Co	*Corophium sp.*
DS	*Dexamine spinosa*
EP	*Erichthonius punctatus*
GA	*Gammarus aequicauda*
GI	*Gammarus insensibilis*
GE	*Golfingia elongata*
GM	*Gouldia minima*
HF	*Heteromastus filiformis*
LL	*Leptomysis lingura*
LLa	*Lumbrinereis latreilli*
LP	*Leucothoë pachycera*
Mi	*Microdeutopus sp.*
MB	*Microdeutopus bifidus*
ME	*Mercierella enigmatica*
MG	*Maera grossimana*
M sp	*Macropipus sp.*
N	Nereïdae
NC	*Nereis caudata*
Ne	Nematodes
NL	*Notomastus latericerus*
NV	*Nicolea venustula*
OP	*Ophryotrocha puerilis*
PA	*Pectinaria auricoma*
PC	*Pista cristata*

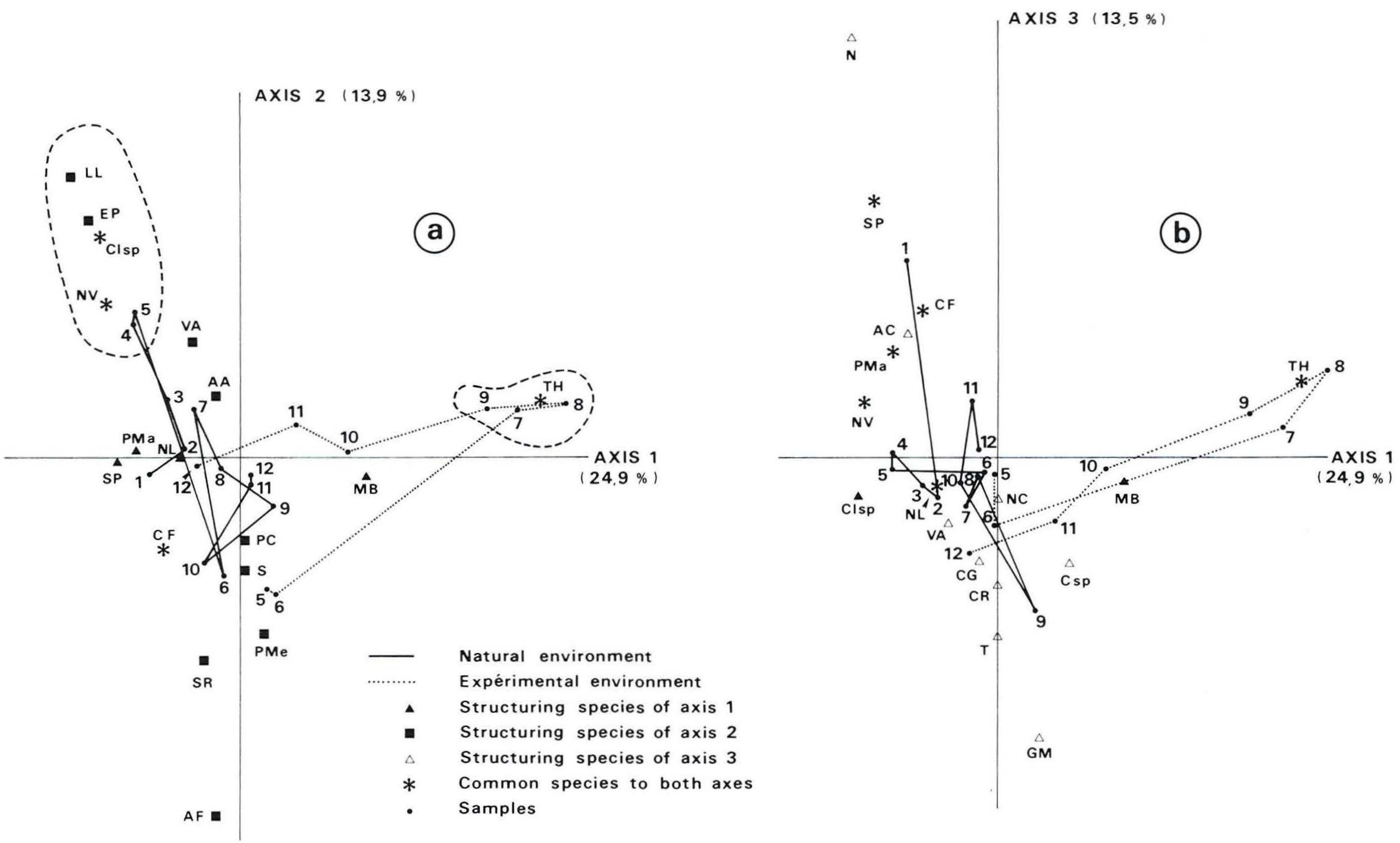

Fig. 2 : Ordination of samples and species on Axes 1-2 (a) and 1-3 (b), derived from Correspondence Analysis. Natural and experimental environments.

PM	*Phtisica marina*
PMa	*Prionospio malmgreni*
PMe	*Polycirrus medusae*
S	Spionidae
Sa	Sabellidae
SE	*Stylarioïdes eruca*
SH	*Syllis hyalina*
SM	*Stenothoë monoculoides*
SP	*Syllis prolifera*
SR	*Staurocephalus rudolphii*
SaR	*Scrupocellaria reptans*
S sp	*Spio decoratus*
T	Terebellidae
TH	*Tharyx* cf. *marioni*
TS	*Tellina serrata*
UG	*Upogebia* cf. *graciliceps*
VA	*Venerupis aurea*

It could be noted that the "samples" points and the 32 "species" points retained in the second analysis, as projected in the three first axes, were almost superimposed with those of the first analysis using 110 species. This result justified our method of species selection.

The results of the analysis, namely the ordination of samples and species in the space of the three first axes, are given in Fig. 2.

The evolution throughout the year appeared when joining the projections of different samples following a chronological order, separately for the grab samples and for the experimental boxes. The two sets were obviously disjoined : grab samples (linked by a continous line) were grouped together in the planes of axes 1-2 (Fig. 2a) and 1-3 (Fig. 2b) in only one side of axe 1, with little oscillations respectively parallel to axes 2 and 3, and not far from the origin. On the other hand, "boxes" (samples bound by a dotted line) showed an accentuated evolution, mainly parallel to axe 1.

In the plane of axes 1 and 2 (Fig. 2) an evolution of the experimental environment could be seen on the side of axis 1 opposed to the group of "grab" points excepted for the last sample (12). It moved away at first along axis 1, and then returned afterwards near "grab" sample 8. "Experimental boxes" points 5 and 6 were opposed to the others according to their projection on axis 2. In the plane of axes 1 and 3, an evolution of the experimental environment was observed. Boxes 5 and 6 were near the origin, then the experimental samples evolved along axis 1 as seen above. From box 8 (October) the "box" points progressively approached the "grab" samples. In both planes, evolution in natural and experimental environments was described by two approximative perpendicular trajectories.

These results of FAC confirmed those of dendrograms performed with Sanders and Sörensen indexes and given elsewhere (Diaz-Castaneda, 1984). They showed two obvious groups, the natural bottom samples (G) and the experimental samples (E). Species composition and population evolution were distinct in both kind of environments.

Contrarily, ordination of species was not very clear and only evoke two groups of characteristic species in the plane of axes 1 and 2 (Fig. 2a : two stripped contours). The reason was that all or almost all species participated to the ordination of both set of samples, but this participation could not be discerned by the analysis. The first group was made of the Crustaceans *Leptomysis lingura*, *Erichtonius punctatus*, the Polychaetes : Cirratulidae *sp.* 2 and *Nicolea venustula*, characteristic of grab samples 4 and 5. In the second group the Polychaete *Tharyx* sp. *marioni* was found strongly linked with experimental boxes 7, 8 and 9. This last genus has been described as very abundant in zones submitted to pollution or perturbation (Bellan, 1967 ; Fauchald & Jumars, 1979).

Analysis of the experimental boxes (Fig. 3a, b)

FAC was performed from a table of 83 species x 8 experimental samples. As a matter of fact, data from the first three months of the experiment were withdrawn due to the small number of organisms at the beginning of the colonizating sequence. The three first axes extracted respectively 29, 23.4 and 14.5 % of the total inertia. Temporal evolution appeared from June (Box 5). This annual evolution was described first by a displacement along axis 2 : projections 5 to 9. A strong individualisation of samples 7, 8 and 9 was observed, mainly characterized by the presence of the polychaete *Tharyx* cf. *marioni* (TH) ; then an horizontal displacement towards the left side of axis 1 (Fig. 3a : boxes 10, 11 and 12) was obvious. Therefore axis 2 seemed to oppose the two first experimental boxes to the next ones, and axis 1 opposed last boxes to intermediary ones 7, 8 and 9. In the inertia plane 2-3 (Fig. 3b), firstly an evolution along axis 3 was observed. Axis 2 separated boxes 5 and 6 from others. Then, axis 3 separated boxes 5 and 6, each of them representing a group of structuring species*.

The principal species (structuring species) were distributed in the inertia planes in relation with the structure of the set of samples. As shown in Fig. 3, there were three groups of species in the plane (1, 2) and only two in the (1.3). Axis 1 opposed two groups of species. One at the right in relation with box 5 (corresponding to early summer) made of *Gammarus aequicauda* (Ga), *Gammarus insensibilis* (GI), *Staurocephalus rudolphii* (SR), *Spio sp.* (Ssp), *Lumbrinereis latreilli* (Lla), *Polycirrus medusa* (PMe), Cirratulidae (C), *Aricia foetida* (AF), *Golfingia elongata* (GE) and Nematodes (Ne). The other group also joined several species around the two last experimental boxes (January and March 1983). Some taxa such as *Corbula gibba*, *Corophium runcicorne*, *Notomastus latericeus*, Spionidae and Terebellidae were very abundant at the end of the experiment, which showed that they found propitious conditions for their development in the experimental boxes. Intermediary boxes 7, 8 and 9 were closely linked to the polychaete *Tharyx* cf. *marioni*, which reached in this period an abundance oscillating between 48 and 90 individuals per box.

The representation of the similarity Sanders matrix supported the results of the FAC where samples 7, 8 and 9 were also found with affinity levels varying between 56 and 67 %. Besides, we found two groups formed by boxes 5-6 and 11-12 with respectively 45 and 43 % of affinity. Finally, axis 3 clearly set apart from boxes 7 to 12, boxes 5 and 6 cor-

* "Structuring species" : species with a strong contribution (at least 20 %) to the inertia of at least one axis (strong correlation).

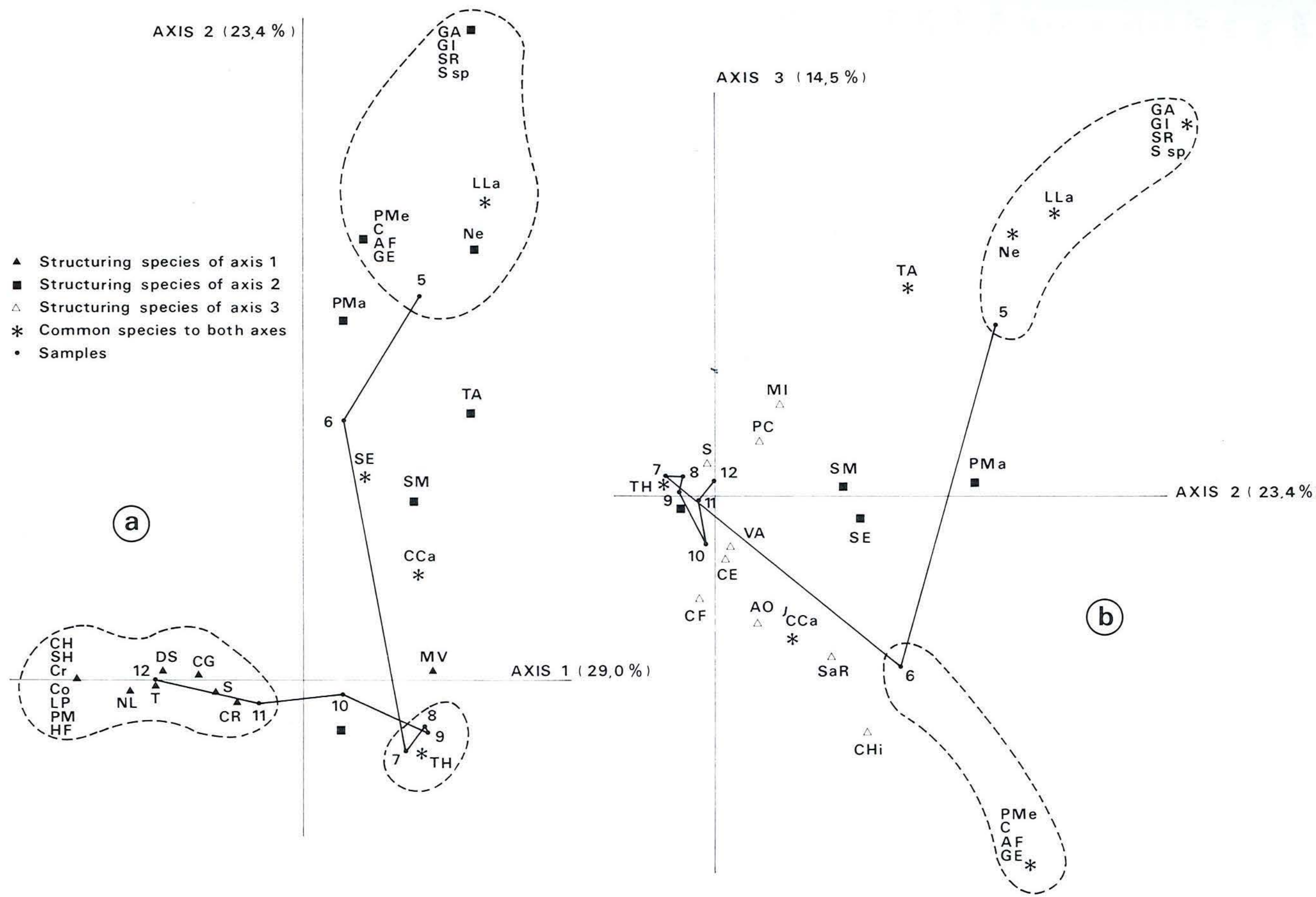

Fig. 3 : Ordination of samples and species on the plane of Axes 1-2 (a) and 2-3 (b) in the experimental environment.

responding to June an July. Thus it could be observed in the right superior side of Fig. 3b a group of taxa bound to box 5 : *Gammarus aequicauda* (GA), *Gammarus insensibilis* (GI), *Staurocephalus rudolphii* (SR), *Spio sp.* (Ssp), *Lumbrinereis latreilli* (Lla) and Nematodes (Ne). At the opposite side there was a group of four taxa linked to box 6 : *Polycirrus medusae* (PMe), *Aricia foetida* (AF), Cirratulidae (C), just as the Sipunculid *Golfingia elongata* (GE). Moreover, *Tharyx* cf. *marioni* (TH) was closely linked to boxes 7, 8 and 9, as previously observed.

Analysis of the grab samples (Fig. 4a, b)

The three first axes explained 18.8, 16.3, and 13 % of the total inertia respectively.

Temporal evolution seemed more obvious than in the analysis of the complete data table. Except samples 7 and 9, decentralized for particular reasons (September and November storms), the annual evolution was described by a displacement along axis 1 : projections near the origin (samples 1 and 2), followed by an evolution towards the left extremity of the axis (samples 3, 4, 5), finally towards the right extremity (6 and 8 to 12). Axis 2 seemed to only oppose samples 1 and 9.

The principal species were distributed with respect to this structure of samples.

Axis 1 showed a group of species of which certain were found especially in spring-time (March to June) : *Erichtonius punctatus* (EP), Cirratulidae *sp.* 2 (CIsp), *Nicolea venustula* (NV), *Leptomysis linguura* (LL), *Venerupis aurea* (VA) and *Abra alba* (AA). Axis 2 separated two groups of species, the first (at the first month of the experience : 82-3-2 was formed by *Caprella sp.* (Csp), *Prionospio malmgreni* (PMa), Cirratulidae *sp.* 1 (CC), *Pista cristata* (PC), *Cirrophorus* cf. *furcatus* (CF), *Armandia cirrosa* (AC) and Nereidae (N). Contrarily, November had the next species : *Gouldia minima* (GM) *Macropipus sp.* (Msp), *Ophryotrocha puerilis* (OP) and Terebellidae (T). Finally, axis 3 showed near July, October and November an association of muddy tolerant species as *Polycirrus medusae* (PMe), and pollution or disturbance indicators as *Staurocephalus rudolphii* (SR). *Phtisica marina* (PM) and some members of the Cirratulidae family (C) (Fig. 4b).

Study of temporal evolution of population structure by Rank-Frequency Diagrams.

Rank-Frequency Diagrams in natural environment

First, it could be noted that the population presented a rather stable structure. Superimposing all the curves (Fig. 5) showed a rather homogeneous set, with small aleatory fluctuations. Only sample 7, September, was different from the others by giving a more straight curve ; the population of this sample showed a perturbation, already put in relation with the storm of early September, which affected the natural bottom much more than the population of experimental boxes.

It was possible to state precisely the storm influence by comparing samples 6, 7, 8 and 9 (Fig. 5b) : in 7, species richness decreased from 30 species in the presvious month to 15 ; at the same time the rank-frequency curve became more vertical (diminution of the evenness). Consequently, the Shannon diversity index decreased from 3,67 to 3,00. These variations showed obviously the destructurating effect of the storm. In samples 8 and 9, diversity rose

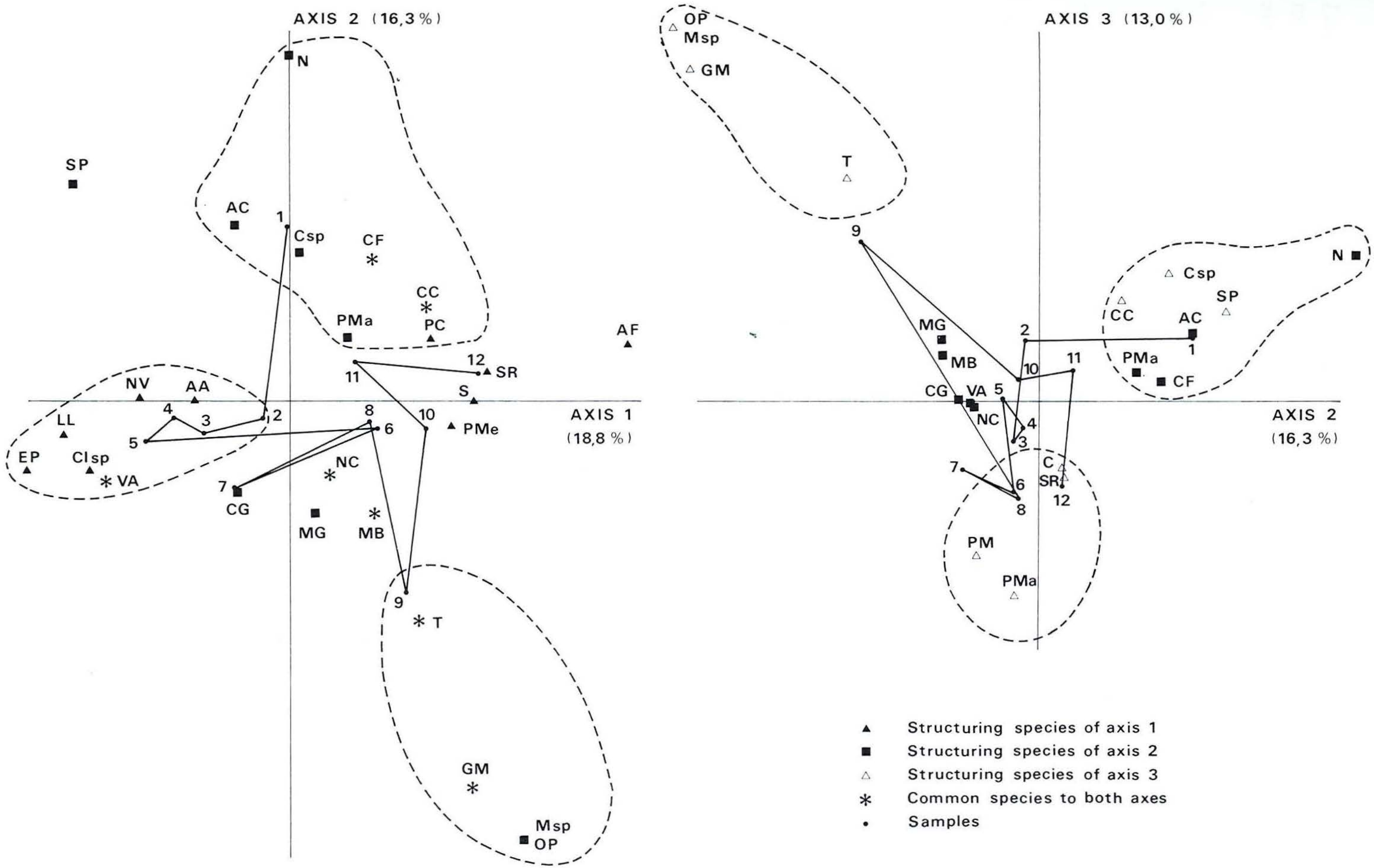

Fig. 4 : Ordination of samples and species on Axes 1-2 (a) and 2-3 (b) in the natural environment (grab samples).

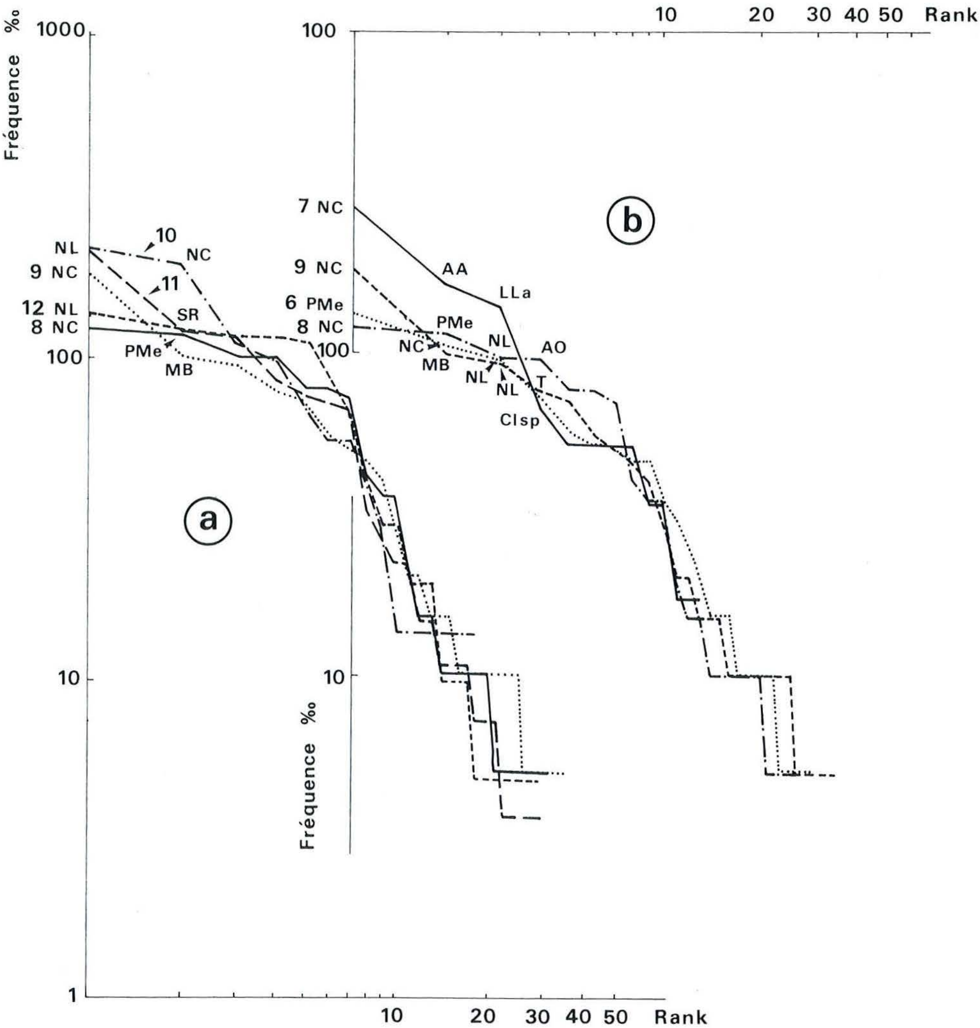

Fig. 5 : Rank-Frequency Diagrams in natural environment :
a) samples 6 to 9 (July to November 1982)
b) samples 8 to 12 (October 1982 to March 1983).

again to 3.5. Diversity indexes were calculated without taking into consideration the very rare species (Frontier, 1983).

Sample 10 (December) gave a low diversity (2.76) still unexplained. Next diversity values were 3.5 and 3.4. Diagrams 8 to 11 (Fig. 5a) showed a progressive straightening of the curves, evoking an evolution towards stage 3. However, the curve 12 showed an obvious shape of a "stage 2", evoking that there was perhaps, not only an evolution from stage 2 towards stage 3, but also some oscillations just as it was recently verified in plankton (Adiwigala, 1983).

At the end of summer (September) dominant taxa were : *Nereis caudata, Abra alba, Lumbrinereis latreilli* and Cirratulidae *sp.* 2. Some very abundant species in the previous months, such as the Polychaetes *Notomastus latericeus* and *Polycirrus medusae*, were absent here (Fig. 5b).

RFD from the last three months of the experiment, January to March 1983, showed species with high frequency : *Notomastus latericeus, Cirrophorus* cf. *furcatus* and *Staurocephalus rudolphii* (Fig. 5a).

Diversity index generally presented higher values than in experimental environment, oscillating between 2,76 and 4,03. The highest values corresponded to spring-time. This period was linked to an important recruitment of post-larvae.

Rank-Frequency Diagrams evolution in the experimental population.

Contrarily to natural environment, experimental boxes populations showed a marked evolution of the rank-frequency distribution (Fig. 6a, b, c). At the beginning of colonization (boxes 5 and 6), population was poor and presented not very regular curves (Fig. 6a). In fact, graphs were roughly stretched along a line of slope — 1, they didn't show any concavity and they were very different from next diagrams. Evenness was high (0.900 to 0.907). Most abundant species at this stage, which could be called "pioneers species", were *Polycirrus medusae, Microdeutopus bifidus, Prionospio malmgreni, Capitella capitata, Venerupis aurea* and *Abra alba.*

Afterwards, we observed the arrival of new species which colonized the experimental boxes. Next three samples (boxes 7, 8, 9 : Fig. 6b) showed a stage 1, particularly marked in box 8 corresponding to October (evenness : 0,573). Dominant species was the Polychaete *Tharyx* cf. *marioni* (90 individuals) which belongs to the surface deposit-feeders.

In October, we noted a rH increase in experimental sediments, whereas ammonium concentration decreased from 30.6 to 18.2 μatg l^{-1}. In respect to heavy metals, zinc decreased considerabily while copper increased from 4,3 to 6,9 $\mu g l^{-1}$. Perhaps these variations of the pollutant load can explain the shape of the curve and the low diversity index (1.82).

For the last three boxes (December to March 1983) stages 2 or 3 could be recognized (Fig. 6c), similar to diagrams observed in natural environment. The most abundant species, by decreasing order, were : *Notomastus latericeus, Tharyx sp., Abra alba, Microdeutopus bifidus, Corbula gibba, Nereis caudata* and *Upogebia* cf. *graciliceps.* The Shannon diversity index rose rapidly in the whole series, reaching the same orders of magnitude than those found in the natural environment.

DISCUSSION

Conclusion of correspondence analysis

1 - Both environments had different structures (quantitative relations between species) and evolutions. On one hand we had an "open", relatively stable, environment (natural bottom) and on the other hand, a "confined" environment following a strong evolution (experimental environment).

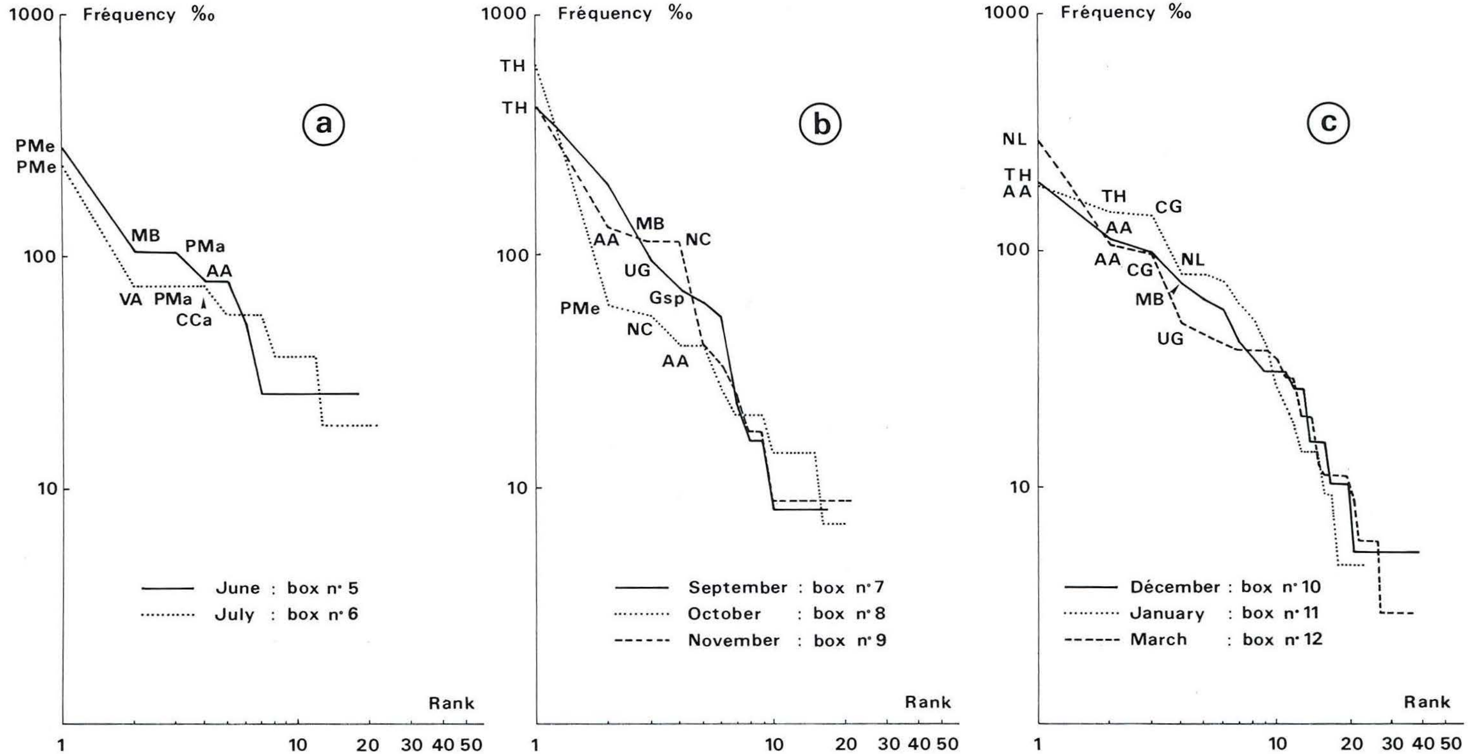

Fig. 6 : Evolution of Rank-Frequency Diagrams in experimental boxes 5 to 12 (June 1982 to March 1983).
a) Boxes 5 and 6
b) Boxes 7, 8 and 9
c) Boxes 10, 11 and 12.

At the end of this survey (one year) almost the same species and the same diversity values in both environments were observed. Nevertheless, the organization seemed to be different concerning the relative abundance of species in the two cases.

2 - The evolution of the natural environment described an annual cycle as seen in the rotation of "grab" points around the origin, with some aberrant points marking particular phenomena (7, 9 : storms). Sample 5 seemed also individualized, but for an unknown reason.

3 - Experimental environment seemed to evolve in four phases :

- Boxes 2, 3 and 4 (beginning of the experiment) were almost defaunated ; they had been excluded from the analyses.

- Boxes 5 and 6 corresponded to the beginning of colonization, with the rapid arrival of some pioneer species.

- Boxes 7, 8 and 9 corresponded to an intermediary state, which persisted about three months.

- The last boxes 10, 11 and 12 showed an evolution towards a final population resembling to the natural exterior population.

Conclusions of the Rank-Frequency Diagrams : effects of pollution and evolution of the population structure.

Frontier (1983, 1985) assumes that under a chronic pollution the structure community turns out to recover a shape similar to the stage 1. In fact, few species are able to maintain themselves in such conditions of stress and in this way, competition decreases, allowing remaining species to multiply quickly.

Gray (1981), Hily (1983), Pearson and Rosenberg (1978) assume that the diversity index in lowered by severe pollution stress, therefore it appears to be a relatively sensible tool for measuring pollution effects. Pearson and Rosenberg (1978) check a sequence of changes. Firstly the most sensitive species are lost. Then, as the redox potential discontinuity layer ("RPDL") approaches the surface, limiting the distribution of the aerobic species and when pollution becomes more severe, the community is progressively simplified to only a few tolerant species such as *Capitella capitata* and *Nereis caudata*.

Under the effects of a chronic pollution the rank-frequency diagrams become more and more vertical.

In a natural succession, stage 1 shows little evolution of the population ; it can correspond, either to the beginning of the colonization, or a population whose structure and organization are deeply affected by disturbances (Diaz-Castañeda, 1989).

In the present experiment a depollution process was rather noted, as a partial release of pollutants outside experimental sediments, with a progressive recolonization by a population which evolved towards a mature balanced stage. The diagrams performed showed the juvenile stage of experimental populations at the beginning of colonization, evolving towards a stage 2 that might be compared to that observed in the natural environment.

In addition, curves with steps, in some cases, could indicate a transitory stage (Fig. 6c). It could be thought of an intermediary stage between stages 1 and 2 of the ecological succession. As for the natural population (Bay of Lazaret, Toulon), it seemed rather stable in spite of the non negligible pollutants concentration.

As a conclusion, the study of experimental population dynamics compared to natural "*in situ*" population showed a tendency of the first one towards the acquisition of :

- a species diversity similar to that of the natural environment,
- the same lists of species,
- Rank-frequency diagrams of the same shape,
- nevertheless, the order of species in the RFD were different in both cases.

While time passed, new species and particularly Polychaetes colonized this environment in a different way than in the exterior environment (Diaz-Castañeda & Safran, 1988). Each population seemed to "balance itself" in its own way according to the *confined* or *open* character of the biotope. After one year of evolution, the experimental boxes population was not the same that the natural surrounding population ; the quantitative equilibrium between species was realized in a different way.

Comparison between AFC and RFD

Figure 7 shows a synthetic sketch joining the results of the factorial analyses (grab + experimental together) in the plane of axes 1-3, and rank-frequency diagrams (RFD) at the different recolonization stages of the boxes and of the natural bottom. To each characteristic phase of recolonization, corresponded a typical form of RFD.

In the natural environment, it could be observed that population presented a rather stable structure (Fig. 7 see G = all samples). However, samples 7 and 9 seemed apart from the others in the FAC and their rank-frequency diagrams were more vertical. The RFD corresponding to samples 8 to 11 showed a progressive straightening of curves evoking an evolution towards stage 3.

Experimental boxes 5 and 6 (June, July) corresponded to a latency phase, before any structuration of the experimental population and without any competition among too scarce individuals. It was a stage anterior to stage 1, characterized by the polychaete *Polycirrus medusae* in first rank. This "latency phase", preceding the settlement of any pioneer stage or DRF type 1, was recently observed in very perturbated benthos by several authors (Prygiel, 1983 ; Hily, 1984). It evokes a passive recolonization from the exterior environment, sporadic and still without established relations of competition : it is not yet a real "community". The RFD is enough stroken but follows a general slope close to — 1.

Then, we remark than the FAC showed a displacement along axis 1, isolating boxes 7, 8, 9 (September to November), this period presented more evolved DRF, especially at stages 1 and 1', evoking already the existence of competitive relations. Among the best represented species were : *Tharyx cf. marioni, Polycirrus medusae, Microdeutopus bifidus* and *Abra alba*. RFD showed a slope close to — 2.

The group of experimental boxes 10, 11 and 12 was characterized by RFD corresponding to a more evolved stage 2 or 3. More abundant species were *Notomastus latericeus*. *Tharyx* cf. *marioni* and *Abra alba*. The evolution checked in the FAC graphs was in this way intersected by a parallel evolution of the RFD. According to the FAC, the group for-

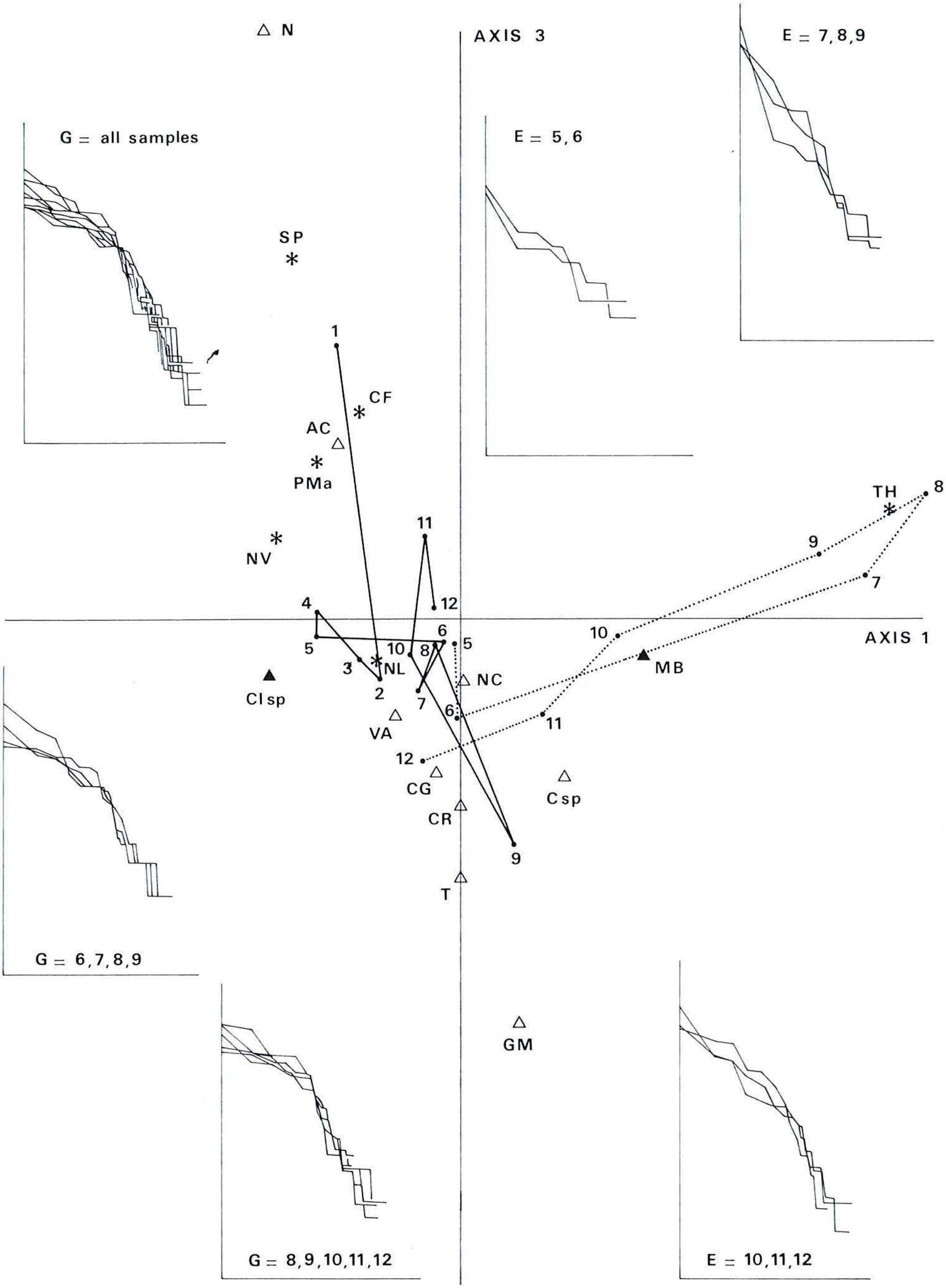

Fig. 7 : Synthetic sketch joining the results of FAC (grab + experimental) in the plane of Axes 1 and 3 and RFD at the different recolonization stages of the boxes and of the natural bottom.
———— : RFD Natural environment (G)
- - - - - - - - : RFD Experimental environment (E).

med by the three last boxes of the experiment brought the experimental population close to the natural community, and this was found also with the RFD which showed a shape not very different in both environments at that time. Nevertheless, the experimental community showed always a steeper RFD.

Finally, the comparison of results obtained with the help of these two mathematical methods showed that FAC and RFD were complementary, allowing a better global vision of the organization and structure of these populations.

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