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Macrozoobenthic recolonization after dredging in a sandy mud area of the Bay of Brest enriched by organic matter

Recolonization
Benthos
Dredging
Ecological succession
Melinna palmata

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ABSTRACT

The recolonization was followed for 3 years from the end of dredging. The species, abundance, biomass curves, and the rank-frequency distributions showed the progressive structuration of the community. The numeral and ponderal cycle of main species and the correspondance analysis explained the main phases of ecological succession : 1) reorganisation of the microbiological processes ; 2) constitution of a pioneer community characterized by a peak of opportunistic species (*Chaetozone setosa*) ; 3) establisment of a young and robust community with a high diversity and production ; 4) maturation of the community with high interspecific competition ; 5) negative evolution caused by high dominance of *Melinna palmata*. The definition of the stability of such community is discussed.

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RÉSUMÉ

Dynamique de la recolonisation par la macrofaune d'un substrat dragué à proximité du port de Brest

La recolonisation de la zone draguée par la macrofaune benthique a été étudiée mensuellement pendant trois années après l'arrêt des dragages. L'analyse des fluctuations : espèces-abondance, biomasses et des distributions rang-fréquence, montre un parallélisme avec la reconstitution des caractéristiques physico-chimiques du sédiment. L'étude des cycles numérique et pondéraux des principales espèces ainsi que l'analyse des correspondances, permettent d'expliquer la succession écologique observée : 1) période de réorganisation des processus microbiologiques ; 2) peuplement pionnier dominé par les espèces opportunistes ; 3) peuplement jeune et robuste à forte densité et production ; 4) maturation du peuplement. Forte compétition interspécifique ; 5) recul de la structure provoqué par le déséquilibre apporté par une très forte dominance de *Melinna p.* La succession écologique montre une stabilité de trajectoire aboutissant en trois ans à un peuplement à forte résilience.

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INTRODUCTION

The study of recolonisation processes in zoobenthos has recently provided much information about benthic communities dynamics. Succession following abatment of organic pollution in many different areas (Leppäkoski, 1975 ; Rosenberg, 1975 ; Pearson, Rosenberg, 1978) and recovery after dredging (Cronin, 1970 ; Kaplan *et al.*, 1975 ; Bondsdorff, 1980) appears to follow the same pattern. In the present study the recolonisation of a dredged sediment by the benthic fauna in the neighbourhood of the harbour of Brest was followed for three years from the end of dredging in August 1978. Changes in the parameters of community composition : richness, density, biomass, in the structural parameters of the community : rank frequencies distribution, diversity, and fluctuations in the trophic and ecological group of species, have been assessed in detail during the recovery period.

THE INVESTIGATED AREA (Fig. 1)

In a previous study (Hily, 1983 *a*) the effect of varying organic inputs on the benthic macrofauna in this part of the Bay of Brest were defined. The dredged area is situated between the polluted zone of the harbour and a transitional zone where the communities were unbalanced. 8,5 millions t of sediments were dredged and used for land reclamations. Dredgings began in September 1977 and finished in August 1978. Sampling began in May 1978.

MATERIAL AND METHODS

To sample macrobenthos a Smith Mac Intyre grab was used, 8 samples of 0,1 m^2 were taken each month and sieved on a 1 mm mesh in the same station (in a circle approxim 100 m ∅). The mean total organic matter of the sediment was obtained by calcination (600 °C-10 hours ; Byers *et al.*, 1978).

The evolution of chemical and microbiological conditions in the sediment had great importance for the macrobenthic recolonisation. The values of the redox potential of the sediments were used to characterize these conditions. The U test of Mann and Whitney (*in* Sokal, Rohlf, 1981) was used to compare abundance and number of species. Biomass was determined as dry weight measured with an accurancy of 0,001 mg after decalcification, tubes of polychaetes were excluded.

The correspondance analysis, method developed by Cordier (1965) was used to order the community changes observed with time (data processing : programme written by Ménesguen, Centre Océanologique de Bretagne, with HP 9845).

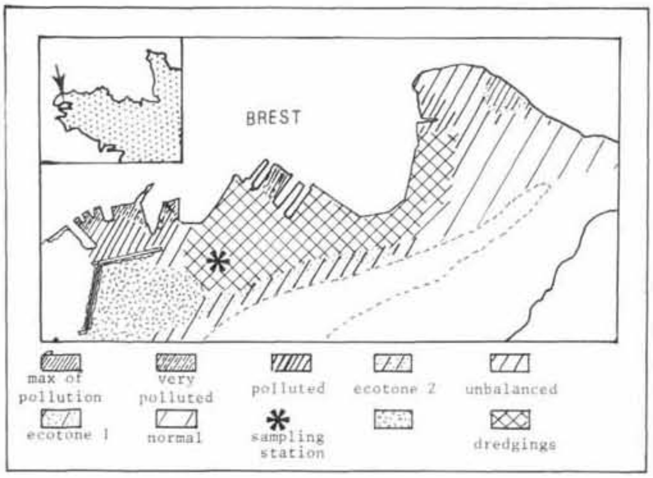


Figure 1

Localisation of the studied area (position of the star) in the disturbed environment of the Bay of Brest (the different phases of degradation of this area were defined in *Hily, 1983* a*).*

Position de la station dans la rade de Brest (les étapes de la dégradation des peuplements ont été définies dans Hily, 1983 *a*).

RESULTS

Water characteristics

Salinity and temperature were measured in the near bottom water. Maximal salinity variations were between 35 ‰ in autumn and 32 ‰ in March and April. Maximal temperature variations between 7.7 °C in January and February and 17.7 °C in August and September. These variations are not limiting factor for the development of the normal infauna of the littoral waters.

Sediments characteristics

In this part of the Bay of Brest the sediments are primarly of sandy mud ; the pelitic fraction (% < 63 µm) increased over the three years of the study : from 47 % in May 1978, 60 % in May 1980, to 70 % in May 1981.

This increase in the fine fraction can be attributed to the redeposition of fine particles of sediment after the end of dredging, followed by an increased natural sedimentation caused by the modification of the tidal currents by the construction of banks and docks.

The mean total organic matter of the sediment was 8.7 % at the sediment surface. This is a high value compared with those of similar sediments in a non perturbed zone of the Bay of Brest which may be attributed to the effect of the organic effluents discharged to the area from the town of Brest. Fluctuations in the rate of organic matter input showed only small seasonal variations and no significant change was noticed over the three years studied.

Every month 2 redox potential values were measured each centimeter in the upper ten centimeters ; Figure 2 shows the changes in redox potential in the third centimeter, this depth is sufficient to escape the heterogeneity of the sediment surface, and the chemical and microbiological conditions in the upper three centimeters seems to be determinant to the development of many species. Fenchel and Riedl (1970) and Witfield (1969) described the relation-ships between the redox potential and the physicochemical conditions in the sediment. The ecological succession is related to the chemical conditions of the sediment (Pearson, Stanley, 1979). In the area the sediment was reduced until winter 1979 and stayed oxidized from January 1979. This progressive amelioration of the microbiological and chemical conditions of the sediment are correlated with a progressive recolonisation by the infauna species.

Fluctuations of the mean number of species (Fig. 3)

At the end of dredging (August 1978) there were only a mean of 2-3 species per sample, the community had fewer species than during winter 1978-1979. The following year (1979) spring and autumn recruitments increased the number of species. However, many juveniles of various species which settled were not able to survive in a reduced sediment and by the end of the winter 1979-1980 only seven new species were fully established. In 1980, there were also two periods

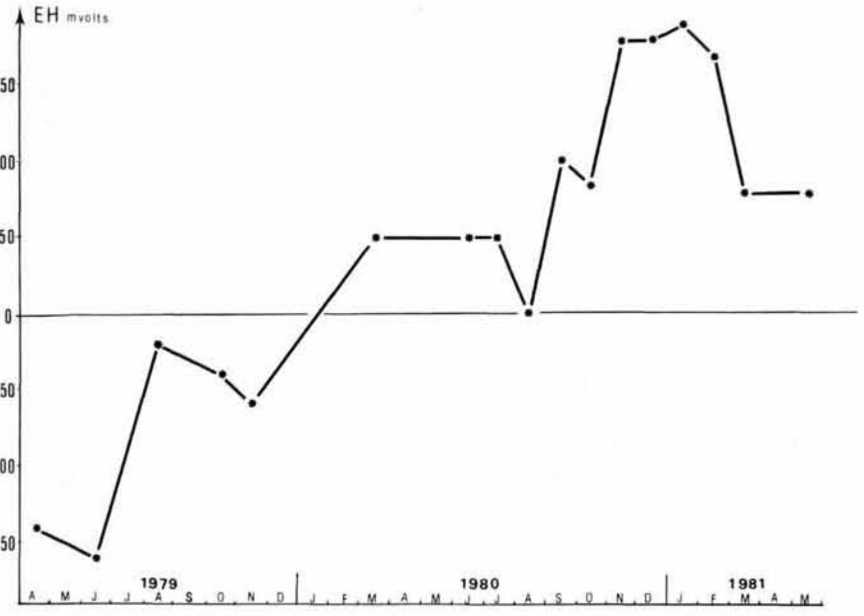


Figure 2

Evolution of the redox potential in the 3rd centimetre in the sediment (each point is the mean of two measures).

Évolution du potentiel d'oxydo-réduction dans le 3e centimètre du sédiment (chaque point est la moyenne de deux valeurs mesurées).

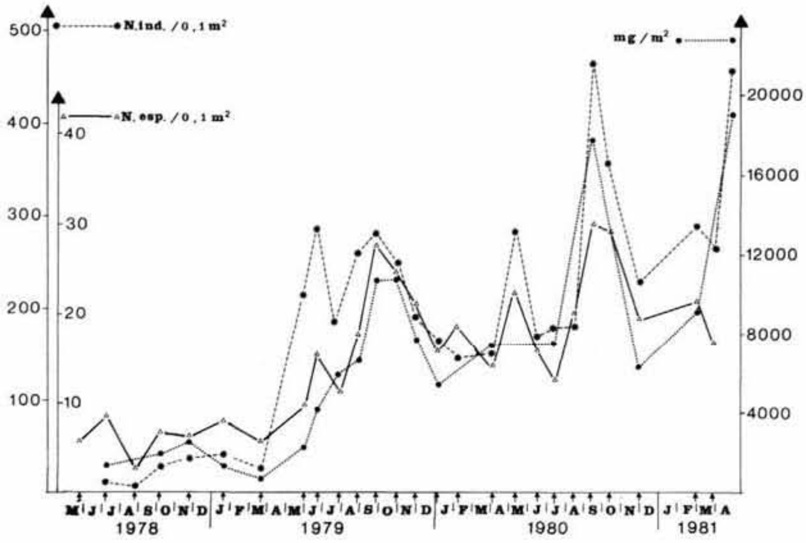


Figure 3

Species : 1) abundance ; 2) biomass ; 3) curves during the recolonization of the dredged area.

Courbes du nombre d'espèces : *a*) de l'abondance totale d'individus ; *b*) des biomasses totales ; *c*) pendant la recolonisation de la zone draguée.

of settlement of new species, and in the third winter (1980-1981) the community comprised twenty species.

In view of the further increase in the number of species in spring 1981 it can be assumed that the recolonisation was not finished at this date.

Fluctuations of the mean number of individuals (Fig. 3)

There is quite a long delay (7-8 months) before a significant increase in the number of individuals (U test < 0). Then after the spring and autumn recruitments in 1979 the number of individual was multiplicated by thirty.

The spring recruitments were always lower than the autumn recruitments in the Bay of Brest. The statistical U test of Mann and Whitney showed that in spring there was generally recruitment of many species but few individuals (*Cultellus pellucidus*, *Phyllodoce* sp., *Notomastus latericeus*, *Stylarioides* sp., *Scalibregma inflatum*, *Lumbrinereis latreilli*...) : test U was < 0 for the number of species and > 0 for abundance and in autumn there were big recruitments of some well adapted species (*Ampharete grubei*, *Nephthys hombergii*, *Polydora antennata*, *Chaetozone setosa*, *Melinna palmata*) : test U < 0 for the number of species and > 0 for the number of individuals. From May 1980 the succession became a quantitative succession (variations in the ranks of species), most of the species were potentially present in the sediment.

Evolution of the total biomass (Fig. 3)

The total biomass followed a more regular increasing curve than the species and abundance curves. Indeed the mortality after the spring recruitments was balanced by the growth of surviving individuals, but in winter the combination of the stoppage of growth and mortality induced a severe decrease in the total biomass. Such seasonal variations in biomass are a sign of instability in the community structure, but also indicative of high productivity, most of the species have young populations which have high growth rate joined with high mortality.

COMMUNITY STRUCTURE (Fig. 4)

Parricularly in the perturbed environments, the rank-frequencies diagramms give a better expression of the community structure than the diversity indices (H. Shannon) and the equitability. In such diagramms, species are ranked by decreasing order of abundance : for a species A the log of dominance (*) is plotted against the log rank A. Frontier (1976) used this method to describe the phases of an ecological succession in plankton. The evolution of the curves for three successive months of September is characteristic of the evolution of the community structure (Fig. 4) :

— *September* 1978 : small number of species and individuals. A straight curve is a sign of an unstructured community in which no species is dominant and the relations of competition and predation between species and individuals are low.

— *September* 1979 : numbers of species and individuals increase. Several species are dominant which give a convex curve. It should be a sign of « relative maturity » of the community in which the interconnections between species are high. But it is an unstable structure because in

— *September* 1980 : the species *Melinna palmata* is largely dominant, the other species have dominant frequencies between 5 and 10 % and all the others have a very low frequency which give a curve shape corresponding according to Frontier (1977) to « an ageing » of the community. The interelations between species are limited by the large dominance of *Melinna palmata*.

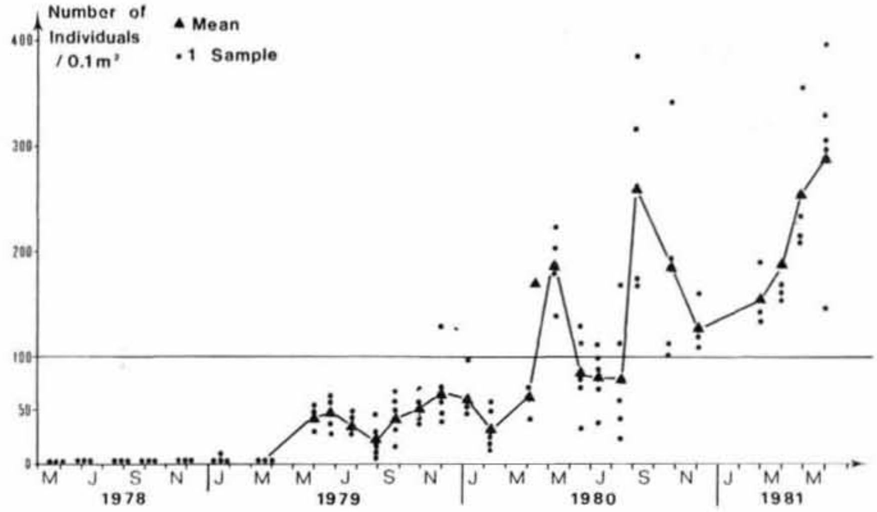
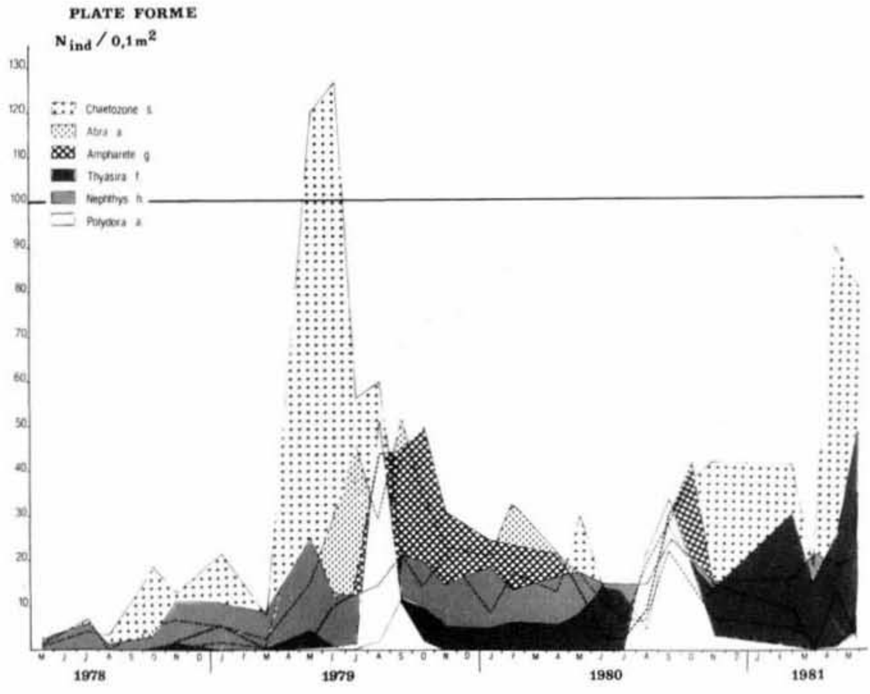


Figure 4

Rank frequencies diagrams (relative frequencies of species ranked by decreasing order). Smooted curves of samples of September on which the relative frequencies of 5 main species are located.

Diagrammes rang-fréquences (fréquences relatives des espèces en ordonnées), rangées par ordre décroissant (en abscisse ; échelles log-log). La position des cinq premières espèces est située sur les courbes lissées.



(*) $\frac{\log Na \times 100}{\log Nt}$

Na = mean number of individuals of the A species
Nt = mean number of individuals of all the species.

Fluctuations in the abundances of the main species in the succession (Fig. 5)

The dominant species were essentially polychaetes : *Nephthys hombergii* a motile omnivorous predator, the cirratulid *Chaetozone setosa*, a subsurface deposit feeder, living free in the sediment ; three species of sessile, tubicolous surface deposit feeders : two ampharetidae *Melinna palmata* and *Ampharete acutifrons* (= *grubei*) and a spionidae : *Polydora antennata* (var : *pulchra*) together with two bivalve molluscs surface deposit feeders : *Abra alba* and *Thyasira flexuosa*.

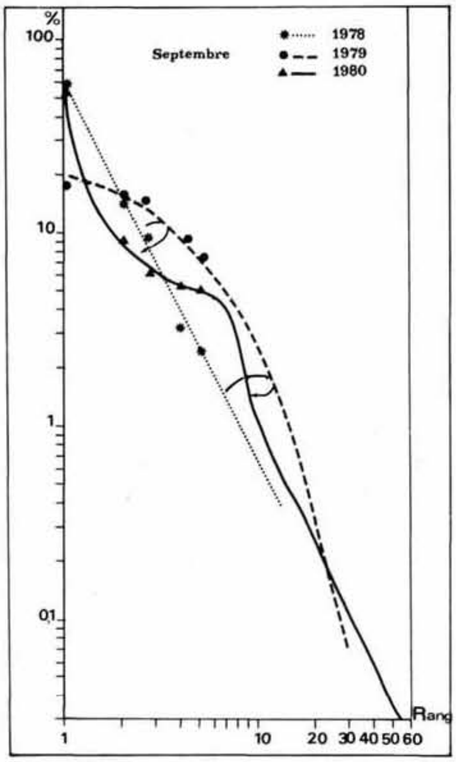


Figure 5

Main species densities during recolonisation.

Évolution des densités des espèces principales :

A) *Melinna palmata ;*
B) *Chaetozone seosa, Abra alba, Thyasira flexuosa, Nephthys hombergii, Polydora antennata.*

At the beginning of the succession, the dominant species were *Abra alba* and *Nephthys hombergii* which still survived after the dredgings or which were able to migrate actively into the area from other undisturbed areas *Chaetozone setosa* settled rapidly and had a short demographic explosion 9 months after dredgings ; *Chaetozone setosa* is an opportunistic species with a short biological cycle (< 1 year) resistant in anoxic sediment. This species is dominant in the polluted sediment in the harbour of Brest (Hily, 1983 *a*).

In autumn 1979, all the species had a good recruitment ; this phase of the succession give the community structure described by the corresponding curve in Figure 4. During the two following years, *Melinna palmata* became more and more dominant and recruitment of other species was limited.

Changes in biomass of the main species

The *Abra alba* population was dominant in terms of biomass for the first 20 months after dredging and was then replaced by *Melinna palmata*, *Nephthys hombergii*, as it have be previously observed became dominant during the period of rapid modifications in the hierarchy of main species (transitional periods).

Correspondance analysis (Fig. 6)

In such analysis the species (= variables) which have similar fluctuations are regrouped in the same part of the plane and the observations which have a similar structure are also regrouped in the same way (Legendre, Legendre, 1979). Densities of 14 species from 27 sampling dates (= observations) in the station were used for the analysis. Figure 6 shows the projection of the observations and the variable-points.

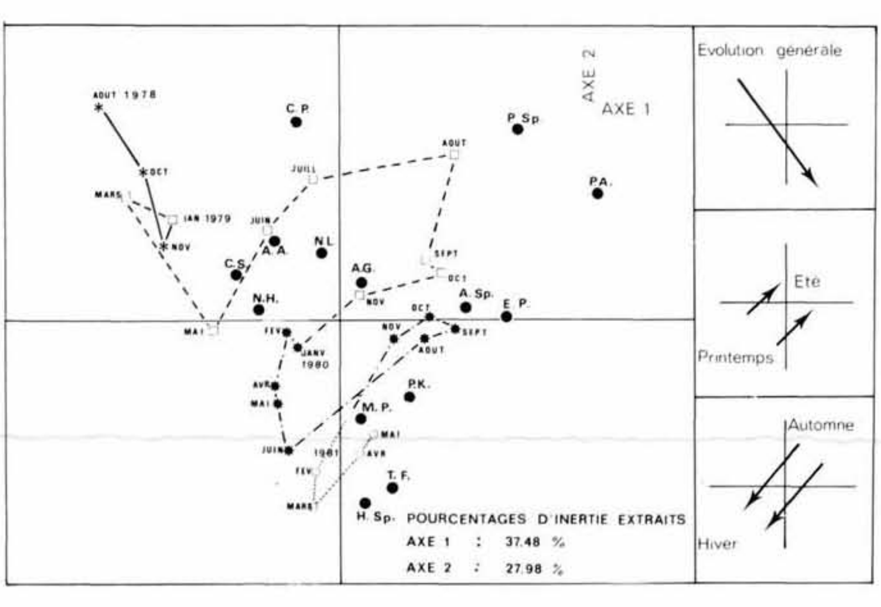


Figure 6

Correspondance analysis : — projection of observations (dates of sampling) and variables (species) in the plane of axis 1 and 2 ; — stars : 1978 observations ;— squares : 1979 observations ; — asterisks : 1980 observations ; — white circles : 1981 observations ; lack circles : position of variables (species).

C.S. : Chaetozone setosa ; *N.H.* : Nephthys hombergii ; *A.A.* : Abra alba ; *C.P.* : Cultellus pellucidus ; *N.L.* : Notomastus latericeus ; *P.sp.* : Phyllodoce *sp.* ; *P.A.* : Polydora antennata ; *A.G.* : Ampharete grubei ; *A.sp.* : Ampelisca *sp.* ; *E.P.* : Eumida parva ; *M.P.* : Melinna palmata ; *H.sp.* : Halcampa *sp.* ; *T.F.* : Thyasira flexuosa ; *P.K.* : Pectinaria koreni.

Interpretation :

A) *General direction of the succession.*
B) *Seasonal oscillations : spring summer.*
C) *Seasonal oscillations : autumn winter.*

Analyse des correspondances : projection des observations (dates de prélèvement) et des variables (espèces). Plan des axes 1 et 2.

Projection of observation-points

According to their order in time, they give a good expression of the general features of the dynamics of the colonisation processes. The interpretation of the results is given in three appendix of Figure 5.

A) There is a migration of the community on an axis which represents the resultant of the evolution of the community in the succession. Indeed the three observations of winter (January 1979 — January 1980 — February 1981) are situated on this axis which consequently represents the evolution of the winter « base-line » of the community.

B and C) On both sides of this general community evolution axis, the analysis shows seasonal fluctuations : autumnal ones were always larger than spring ones, furthermore, the projection of spring and autumn observations are nearer to the general evolution axis in the course of time. This decreasing amplitude in seasonal fluctuations should be a sign of an increasing stability of the system.

Projection of variable-points

Nearer is the position of a species to the position of a date of sampling, (observation) more is this species important in the community at that time. As different authors have already noticed (Leppäkoski, 1975 ; Rosenberg, 1976; Bonsdorff, 1980) the succession of species approaches a succession along a decreasing gradient of organic enrichment : *Chaetozone setosa*, *Nephthys hombergii*, *Abra alba*, *Notomastus latericeus* which can live in reduced sediments, are associated with the first period of recolonisation. Then *Cultellus pellucidus* (a small bivalve) and *Phyllodoce* sp. (carnivorous polychaete), which are free living sediment species are characteristic of the following period ; *Polydora antennata* an opportunistic species, is the first tubicolous species of this succession before *Ampharete grubei* and *Melinna palmata*.

DISCUSSION AND CONCLUSION

The recolonisation of the sediment was not a succession of species but a succession of phases in the community structure : there was not qualitative substitutions of species, since all the species sampled in 1978 stayed in the community after that year ; no species sampled in May 1979 dissapeared after ; among the 44 species sampled in the area between August 1978 and May 1980 for the same period, 36 were present in the samples of a reference station whithout the same sediment characteristics but localized in a non perturbated area (Hily, 1983 *b*). It was quantitative modifications in the relative dominance of species which induced a succession of ecological phases corresponding with different levels of organisation of the community. This succession of phases had already been shown by different authors (Heatwole, Levins, 1972 ; Kaplan *et al*., 1975 ; Bondsdorff, 1980). These phases are plotted in Figure 7 :

— At the end of dredging the balance of the sediment was destroyed and macrofauna had almost disappeared, only some individuals of *Abra* and *Nephthys* still survived (August 1978).

— The first phase of the succession is a period of reorganisation of the chemical and microbiological processes. The sediment surface is reduced and only some opportunistic species were able to settle. Some motile predators (*Nephthys hombergii*) immigrated (autumn 1978-winter 1978-1979).

— The second phase is the establishment of a pionneer community characterized by an opportunist's peak (*Chaetozone setosa*). It can be assumed that the development of many individuals (*Abra*, *Chaetozone*) living in the upper two centimeters of the sediment in spring 1979, induced an intense bioturbation which contributed importantly to the subsidence of the redox potential discontinuity. Indeed the Eh value increased from ($\simeq +25$ mV) on the end of spring to $+200$ mV at the end of autumn. This amelioration of microbio-

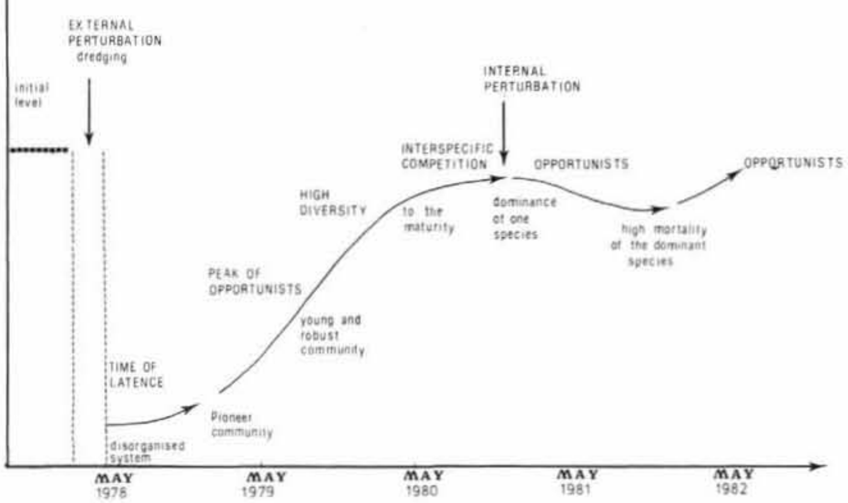


Figure 7

Schematic evolution of the structure of the studied community during recolonization.

Évolution schématique de la structure du peuplement étudié au cours de la recolonisation.

logical and chemical conditions of the upper centimeters of the sediments should favour the settlement of juveniles of species more sensitive to anoxic sediments (Hylleberg, Henriksen, 1980) and so, start the third phase.

— The third phase was the establishment of a young and robust community : many species tolerant to instability and characteristic of semi polluted areas or transition zones developed new populations. The opportunists regressed (increase of competition). The community was dominated by surface deposit feeders. Many tubicolous species settled. The rapid growth of lots of juveniles which were dominant in the demographic structure of the populations, joined with their high mortality, induced a high production on this period.

The forth phase is the « organisation period » with the establishment of a hierarchy between species which should be the result of high interspecific competition. The dominance became very different from one species to an other (*see* Fig. 4). The number of species in each trophic group is increasing. Productivity decrease (ageing of the populations) biological cycles are longer and growth rates of *Melinna palmata* (Guillou, Hily, 1982), *Abra alba* (Hily, Le Bris, 1983), *Nephthys hombergii* is decreasing.

The big long living species of bivalves (*Lutraria*, *Mya*) crustaceans (*Calianassa*, *Eupagurus*) and echinoderms (*Ophiura*, *Asterias*, *Marthasterias*, *Cucumaria*) are recruited only in the 5th phase. These big species were not disturbed by the increasing dominance of *Melinna palmata* but many species in the equivalent class size were apparently inhibited by the relative abundance of this species.

The ordinate of Figure 7 which is the schematic representation of the main phases of the succession, represents a theorical level of structure (or organisation) of the community, this organisation is a function of the number of possible interactions (competition, predation...) between species which is not far from of the definition of the « connectance » (Da Silva Viera, 1979). This organisation should be optimum when the gradient of relative dominance between species should be strong, associated with an high number of species.

This optimum should be an hypothetic climax which is not reached here. The phase of organisation (phase IV) which drives to the maturity of the community is stopped by the excessive domination of *Melinna palmata*. This proliferation of one species should induced an unbalance and stopped the increasing complexity of the system. The following year (1981-1982) it has been observed two others phases of the succession : a high mortality of *Melinna palmata* population followed by a new peak of opportunistic species (*Polydora antennata*). Thus, each unbalance of the community is corresponding with a proliferation of one opportunistic species.

Why did the community not reach a level of balance after four years ? The studies of different authors on recolonisation of marine sediments generally found that a period of 2 years was sufficient to achieve a level of maturity (Harrison *et al.*, 1964 ; Heatwole, Levins, 1972 ; Kaplan *et al.*, 1975 ; Simon, Dauer, 1977). A juvenile ecosystem is dependant on the external contributions (Odum, 1969 ; Frontier, 1977) like nutrient supply, larvae and immigrants. When the ecosystem is mature, it is more independant of external sources. When such a mature community is enriched artificially with additional nutrients, it returns to a juvenile phase. The dominance of *Melinna palmata* and its later decline coinciding with the increase in *Polydora antennata* are indicative of continuing instability in the community structure. This evidence suggests that « maturity » in this system would not be reached for some years, if at all. It is probable that the community might oscillate about an immature, or unstable phase because of continual disturbance or stress caused by sediment instability or pollution.

This is also suggested by a comparison with the neighbouring communities which were not dredged but which were influenced by the same environmental conditions. These have unbalanced populations and transitory communities between the polluted zone of the harbour and the normal zone of the bay of Brest (Hily, 1983 *a*). It can be assumed that rapid fluctuations and rotation in populations are the normal dynamics of the communities situated in such areas, indeed these communities are dominated by « r » strategies species (Hily, 1983 *b*). That community dynamics is a kind of stability which can be named « Resiliency » defined like : the capacity of the community to react actively against the anthropogenic disturbances.

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