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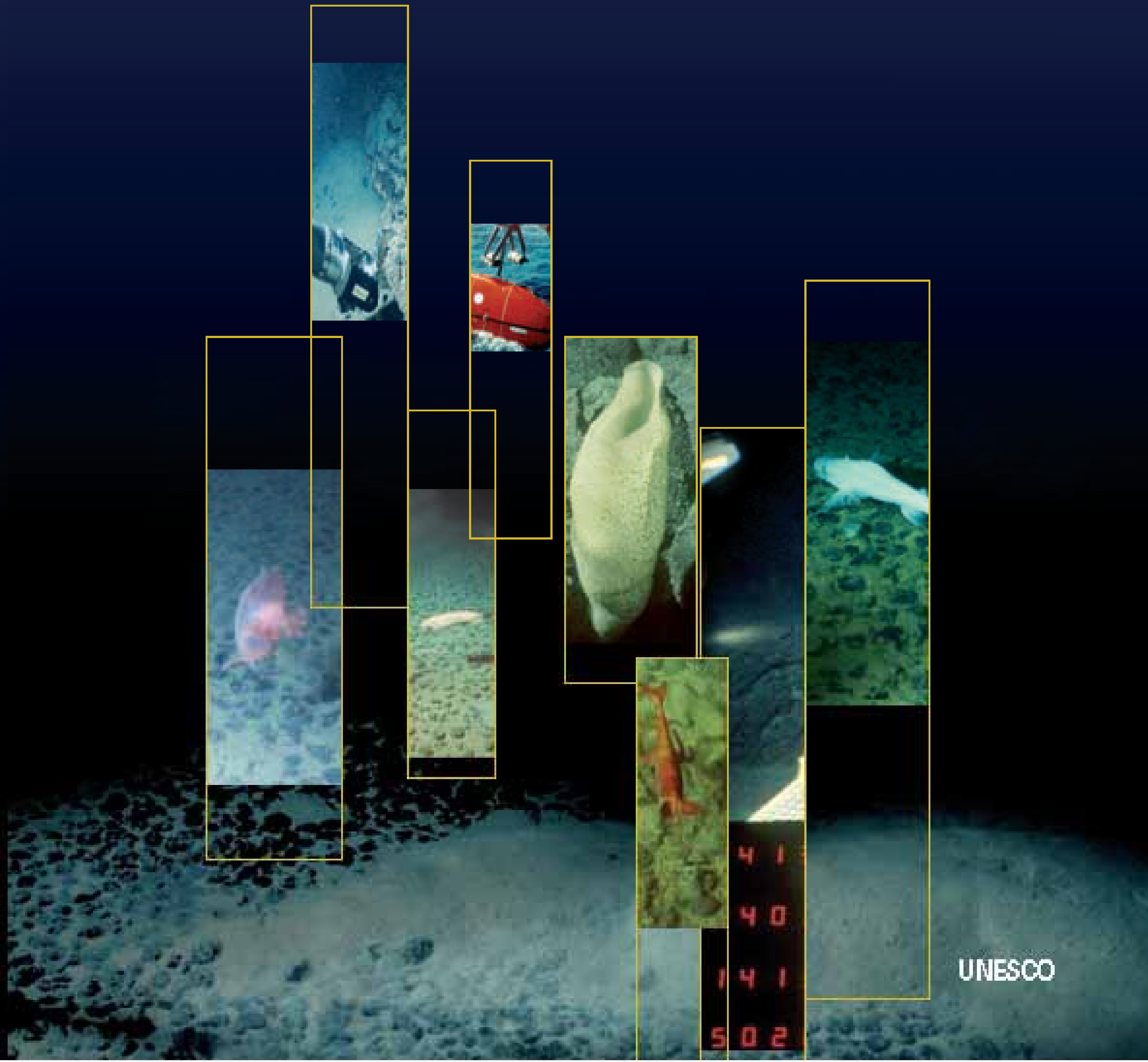
Technical Series 69

Biodiversity
and distribution of the megafauna

Vol.1 The polymetallic nodule ecosystem of the Eastern Equatorial Pacific Ocean



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Biodiversity and distribution of the megafauna :

Vol.1 The polymetallic nodule ecosystem of the Eastern Equatorial Pacific Ocean

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Preface

At the bottom of the ocean, lying at an average depth of 3 to 4 kilometres, abyssal plains cover 60% of the planet's surface. Despite significant efforts involving research expeditions, our knowledge of megafaunal diversity in this huge and important domain is still severely limited. It is estimated that less than 1% of the abyssal plains have been sampled. Because of the low densities of the suprabenthic megafauna on the abyssal sea floor, only a small number of species have been described taxonomically. In a polymetallic nodule environment, the task is even more difficult due to grinding effects during trawling or to the high cost of submarine expeditions enabling to collect specimens *in situ*. Thus the few specimens collected within the large equatorial nodule belt can hardly describe the biodiversity and distribution of suprabenthic populations.

I have the pleasure to present this Technical Report which displays a unique comprehensive reference baseline of a polymetallic nodule ecosystem located in the abyssal tropical east Pacific Ocean between the Clarion and Clipperton fracture zone. On the basis of more than 200 000 photographs and 55 hours of video taken during several French and American oceanographic cruises, the structure of suprabenthic megafaunal populations has been described on both qualitative (taxonomic identification, taxonomic richness, ethology) and quantitative levels (taxonomic abundance, correlations to specific habitats..). This study contains comparisons of data collected by different means and strategies of photographic and video exploration in an international effort to investigate different sites within the nodule belt of the Clarion-Clipperton fracture zone. The roles of limiting factors and biotic factors in the dynamics of suprabenthic assemblages are also addressed.

Sampling the different size fractions of the benthos on the abyssal plains has always proved to be a major challenge. No single methodology is free of bias and can secure high quantitative precision. Given the available technological tools, photographic exploration of megabenthic communities represents a cost-effective way of evaluating the diversity and distribution of megabenthic communities in large expanses of the ocean. Knowledge of the taxonomy of deep-sea animals is still patchy, especially for the megabenthos which is too sparse and too mobile to be sampled adequately at a regional level in any other way than by imagery. A system that combines video and photography has proved to be efficient for rapid assessment and impact monitoring of large survey areas in a reasonable time.

The careful description of the megafauna within the polymetallic nodule ecosystem will serve as basis for drawing recommendations for the strategy of deep seabed mining and conservation of the diversity. This study is a valuable contribution to the work carried out by the International Seabed Authority in this area. I am extremely pleased that the Intergovernmental Oceanographic Commission through the generous support of the Government of Flanders (Kingdom of Belgium) has been able to support the work of Dr Virginie Tilot.

Patricio A. Bernal
Executive Secretary IOC
Assistant Director General of UNESCO

Acknowledgements

We are very grateful to the Government of Flanders and especially Dr Rudy Herman of the Science and Innovation Administration of the ministry of Flanders for his enthusiasm in bringing to fruition a project in the field of the abyssal environment, in anticipation of the future exploitation of polymetallic nodules. Our gratitude is also due to the Intergovernmental Oceanographic Commission of UNESCO and its Executive Secretary, Mr Patricio Bernal, for agreeing to co-ordinate this project with his team, among whom we acknowledge Dr Ümit Ünlüata for initiating this publication and Dr Alexei Suzyumov for his excellent advice during its production.

This document would not have been possible without the support of the "Institut Français de Recherche pour l'Exploitation de la Mer" (Ifremer) which made available its facilities, data and expertise, notably teams from the departments of Deep ocean ecosystems and Marine geosciences. I thank also Mr Michel Stahlberger from the legal and logistic affairs department of Ifremer as well as the Communication Service, in particular Michel Gouillou and his team.

I thank my collaborators, Mr Jean Pierre Lenoble, former president of the "Association Française pour la Recherche et l'Exploitation des NODules polymétalliques" (AFERNOD) for writing the section on the nodule-facies and Mr Elie Jarmache, jurist responsible for Law of the Sea at the department of Programmes and Strategy at Ifremer, for developing a section on the legal context of mining permits. Mr Philippe Saget, geologist, has always given valuable assistance. He is the fountain of knowledge on all matters concerning nodules, having participated in almost all the work undertaken by France since 1975, and is in charge of the analytic, photographic and bibliographic database coupled to a Geographic Information System.

This work would not have been possible without a considerable exchange of correspondence with the many specialists whose names are given in an appendix and who kindly brought their advice and knowledge to bear on my hypotheses of animal identification. I also thank Mr Lucien Laubier, Director of the oceanographic Institute in Paris for reviewing the manuscript. I acknowledge the valuable help of Mrs Anne-Marie Damiano and her team at the library of the oceanographic Museum of Monaco for bibliographic research.

It has also been an honour to have as a collaborator Professor Vanreusel of the University of Ghent. My considerable thanks go to Dr Helen Fortune-Hopkins for the translation and to Madame Caroline d'Espeuilles for editing the drafts and to Miss Marianne Cassaigne for digitizing the photographs and figures.

Summary

The biodiversity and distribution of abyssal megafaunal assemblages in a region of polymetallic nodules of the Eastern Equatorial Pacific Ocean, within the Clarion-Clipperton fracture zone, is analysed at several levels in this study.

On a qualitative level, the identification, ethology, taxonomic richness and faunal composition classified by functional groups, are described over the whole area, to provide a baseline reference. An annotated photographic atlas is produced with the participation of worldwide specialists for each phylum. Inventories based on a collection of about 200 000 photographs of the ocean floor and some 55 hours of film show a taxonomic diversity of 240 taxa, of which 46 are echinoderms. Cnidaria is the most diverse phylum in the Clarion-Clipperton fracture zone encompassing 59 different taxa. Suspension feeders are the best represented trophic group in the zone.

On a quantitative level, the particularly well described site, NIXO 45 (130°00'W/130°10'W, 13°56'N/14°08'N) at a mean depth of 4 950 m, was chosen to evaluate faunal relative abundance and composition, classified by phyla and by trophic and functional groups, for different edaphic conditions. Results show that whatever the edaphic facies, suspension feeders are more abundant than detritus feeders, carnivores and scavengers. The highest total faunal abundance is on nodule-facies C+10 % and nodule-facies C+ with slope > 15°. The greatest density of suspension feeders is observed on nodule-facies O (no nodules) on ancient sediments, dating from the Oligocene to the middle Miocene, and on nodule-facies C+ with slope > 15°, while detritus feeders are more abundant on nodule-facies C+10 %.

Similarities among taxa and among some types of environment and substratum were emphasized by a factor analysis of Reciprocal Averaging, allowing discrimination of preferential habitats and 'faunal facies', ranked according to an edaphic gradient. Quantitative analysis was also undertaken at species level to study spatial heterogeneity in the distribution of populations. Comparisons are made with data from other means of *in situ* observation. The 'Nautile' explored one of the facies at the NIXO 45 site, the 'R.A.I.E' was used for three nodule-facies at the NIXO 41 site and the 'Deep Tow Instrumentation System' for the three nodule-facies ECHO 1 site. An estimate of megafaunal biomass by trophic group is discussed for the three sites studied. These are then compared with estimates of biomass for the megafauna, macrofauna and meiofauna sampled at the DOMES C site. The role of limiting factors (edaphic heterogeneity, currents) and biotic factors in the structure of suprabenthic assemblages is discussed.

1. Introduction

This study was undertaken within the framework of a project inaugurated in 2004 under the auspices of the Government of Flanders and the Intergovernmental Oceanographic Commission of UNESCO entitled 'The study of the biodiversity and distribution of megafaunal assemblages in a region of polymetallic nodules of the Eastern Equatorial Pacific: management of the impact of mineral exploitation'.

The objectives of this study are to evaluate the biodiversity and distribution of benthic megafaunal assemblages within an ecosystem of polymetallic nodules in the Eastern Equatorial Pacific Ocean. This forms an environmental and faunistic reference base, built on a synthesis and update of work undertaken by the author (Tilot, 1992c).

The study of environmental and edaphic conditions aids a better understanding of the biodiversity and heterogeneity of suprabenthic populations. Likewise, the associations that may exist between some functional assemblages and particular biotopes, especially within the different 'nodule-facies' (facies with different morphological types of nodules) are factors operating in these population dynamics.

The role of limiting factors in the structure of suprabenthic assemblages, such as environmental heterogeneity, currents and biotic factors, can then be discussed in the light of this knowledge. This information is essential for environmental impact studies, since it enables predictions to be made on the functional dynamics of suprabenthic assemblages within their biotopes in response to the disturbance caused by the collection of polymetallic nodules. This knowledge would enable compensatory measures to be taken, to mitigate the impact on the benthos of any future exploitation. Understanding the functional dynamics of the abyssal ecosystem could also aid in understanding the role of the fauna in the presence, formation and maintenance of nodule deposits on the seafloor.

The megafauna is defined as organisms (> 1-4 cm) that are visible in photographs of the ocean floor (Grassle *et al*, 1975; Gage & Tyler, 1991; Smith *et al*, 1997). It is only relatively recently that the importance of the megafauna in the functioning of deep ocean environments has become evident (Rex, 1981; Smith & Hamilton, 1983; Sibuet, 1987; Pawson, 1988a). This faunal category comprises a significant fraction (17-50 %) of benthic abyssal biomass (Haedrich & Rowe, 1977; Sibuet & Lawrence, 1981; Sibuet *et al*, 1984) and the study of its abundance, composition and distribution is essential to an understanding of the functioning of the ecology of the abyssal suprabenthos. In the case of a nodule substratum, the megafauna can be used as an indicator of recolonisation after impact of the substratum (Bluhm, 1997) or of the variation in flux of particulate organic carbon (Smith *et al*, 1997). The megafauna is also one of the principal agents of bioturbation of the deep sea benthos (Mauviel & Sibuet, 1985; Levin *et al*, 1986) and so can influence many other biological and geochemical components of the ocean depths (Sharma & Rao, 1992).

Because of its scattered distribution, the study of the megafauna requires the sampling of large areas, as already commented on by Rice *et al* (1982). Studies of the megafauna are often limited to particular zoological groups such as echinoderms (Haedrich *et al*, 1980; Sibuet & Lawrence, 1981; Rice *et al*, 1982; Pawson, 1983; Briggs *et al*, 1996; Copley *et al*, 1996; Piepenburg *et al*, 1996; Bluhm & Gebruk, 1999) or even holothurians (Matsui *et al*, 1997).

Some quantitative studies of the megafauna are based on specimens collected by trawling (Okutani, 1969; Dahl *et al*, 1977; Carney & Carey, 1976, 1982; Laubier

& Sibuet, 1979; Pearcy *et al*, 1982; Sibuet *et al*, 1984; Richardson *et al*, 1987).

Quantitative analysis of the epibenthos and records of animal behaviour are based on photographic and video data taken by towed or fixed devices and manned submersibles (Owen *et al*, 1967; Rowe, 1971; Grassle *et al*, 1975; Lemche *et al*, 1976; Cohen & Pawson, 1977; Patil *et al*, 1980; Wigley & Theroux, 1981; Mauviel, 1982; Ohta, 1985; Laubier *et al*, 1985; Foell, 1988; Pawson, 1988a, b; Tilot *et al*, 1988; Foell & Pawson, 1989; Kaufmann *et al*, 1989; Wheatcroft *et al*, 1989; Bluhm, 1991; Thiel *et al*, 1991; Sharma & Rao, 1991; Christiansen & Thiel, 1992; Smith *et al*, 1992; Christiansen, 1993; Bluhm, 1994; Bluhm & Thiel, 1996; Lauerman *et al*, 1996; Radziejewska, 1997; Piepenburg & Schmid, 1997; Hughes & Atkinson, 1997; Fukushima & Imajima, 1997; Kaufmann & Smith, 1997; Kotlinski & Tkatchenko, 1997; Matsui *et al*, 1997; Tkatchenko & Radziejewska, 1998; Radziejewska & Kotlinski, 2002).

Some studies have compared two systems of sampling, such as trawls and photographic probes (Haedrich & Rowe, 1977; Aldred *et al*, 1979; Rice *et al*, 1979; Dyer *et al*, 1982; Wakefield & Smithey, 1989; Nybakken *et al*, 1999), sometimes in combination with a manned submersible (Uzmann *et al*, 1977). According to Haedrich *et al* (1975), abundances calculated from trawl data are underestimated by an order of magnitude or more, whereas Young *et al* (1985) considered that photographic data result in underestimates. Ohta (1983) concluded that photographic studies give more precise estimates than those based on specimens collected by trawls, even if they are supplemented by an odometer. However, since these analyses have been made over a great range of depths, at different sites, under variable environmental conditions, and using different means and strategies of sampling, it is difficult to compare their results.

The two systems of sampling involving either the collection of specimens or images are in fact complementary (Chave & Jones, 1991; Christiansen & Thiel, 1992; Pipenburg & Schmid, 1997). Studies of suprabenthic communities need descriptions and exact taxonomic identifications of organisms (Rice *et al* 1982; Briggs *et al*, 1996; Copley *et al*, 1996; Piepenburg *et al*, 1996). They also require accurate and rapid estimates of faunal abundance at least possible cost, which involves photographing large areas as well as providing information on habitats and faunal behaviour, especially at the substratum interface (Ohta, 1985; Kaufmann *et al*, 1989; Hughes & Atkinson 1997; Nybakken *et al*, 1999; Foell *et al* 1992, Bluhm 1994, Bluhm *et al* 1995; Schriever 1995, Schriever *et al* 1997). Radziejewska & Stoyanova (2000) opted for photographs supplemented by video footage as providing the most accurate data at least cost for rapid environmental assessment, before and after the impact of a benthic plume causing resedimentation. This would simulate the effects of the exploitation of polymetallic nodules and the recolonisation by benthic communities of the resedimented nodule zones of the eastern Pacific Ocean.

Most of the megafauna in the abyssal area of the Clarion-Clipperton fracture zone within the tropical north-east Pacific is still unknown to science (Belyaev, 1989), since it has been little sampled and rarely observed before the recent intensification of effort. For just over 100 years, this zone of the Pacific has only been sporadically sampled, as during the voyages of the *Challenger* in 1873-75 and the *l'Albatross*s in 1904-1905 (Menzies *et al*, 1973). But since the 1950s, the discovery of significant deposits of polymetallic nodules and the economic interest that they have aroused have lead to an international exploratory effort. Prospection of the deposits in this zone has collected a large quantity of data on the distribution, abundance and composition of the polymetallic nodules and their geological, physico-chemical and biological environment. Lastly, the cruise by the French submarine 'the Nautile', which collected numerous images and specimens (NODINAUT, 2004), has permitted, amongst other things, the identification of large numbers of specimens.

Hecker & Paul (1977), Paul *et al* (1978), du Castel (1982), Thorndike *et al* (1982), Foell (1988), Pawson (1985, 1988 a, 1988 b), Foell & Pawson (1985), Pawson & Foell (1983, 1984, 1986), Foell *et al* (1986), Tilot *et al* (1988) and Morgan (1991) have all identified new taxa at generic and specific level, and analysed the megafauna of the nodule region in the Clarion-Clipperton fracture zone qualitatively and semi-quantitatively. These authors have also estimated abundance and faunal diversity in relation to the percentage coverage of nodules.

The collection of video and photographic data on the suprabenthos of this nodule zone can shed light on the identity, behaviour and preferential habitats of the megabenthos, as well as on the composition and spatial variability of populations on different substrata. In addition, photographic documents help enable *in situ* identification of the sampled animals, which are sometimes difficult to identify after preservation. The analysis of the suprabenthic megafauna presented here is based on about 200 000 photographs and 55 hours of film taken since 1975 by various submarine devices, including towed apparatuses such as the 'Remorquage Abyssal d'Instruments par l'Exploration' or 'R.A.I.E.', 'Deep Tow Instrument System', and a 'troika' (Tilot, 1992b) and by autonomous devices such as cameras coupled to free samplers 'E.D.1', the 'Épaulard' and lastly the manned submarine 'the Nautile'.

2. General Context

The most economically important deposits of polymetallic nodules are found within the Clarion-Clipperton fracture zone in the central northern Pacific Ocean (figure 1).

2.1 THE CLARION-CLIPPERTON FRACTURE ZONE

The oceanic meteorological environment

In the Clarion-Clipperton fracture zone, the surface water is swept by trade winds of mean force 4 in a north/north-easterly direction, creating stable conditions. Waves have a significant height, of 1 to 2 m. The surface currents have a maximum depth of 500 m and form part of the North Equatorial current directed towards the West, the North Equatorial countercur-

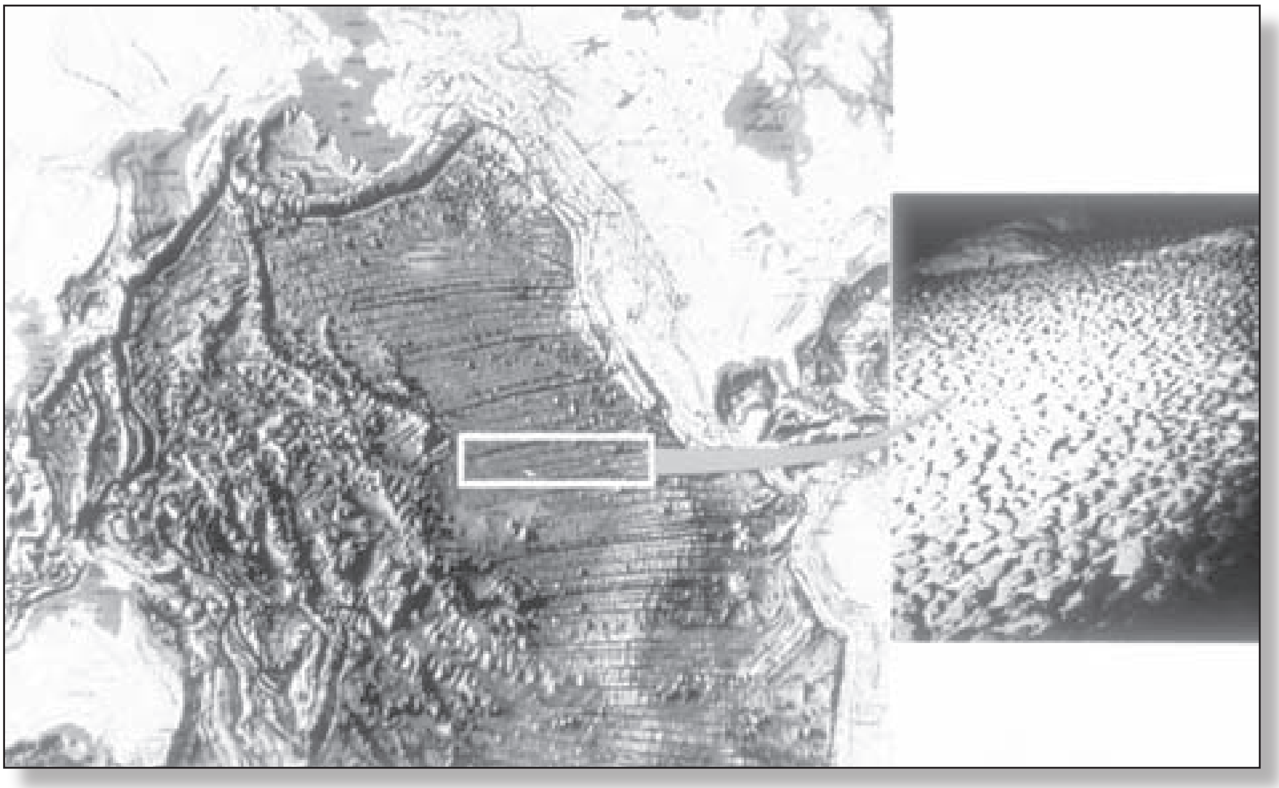


Fig. 1. Location of polymetallic nodule deposits in the Clarion-Clipperton fracture zone on a map of the topography of the seabed of the northern central Pacific Ocean (© Ifremer/GEMONOD). (See colour appendix 1, p. 127).

rent towards the East, and the Southern Equatorial current towards the West. They have a mean speed of 20 cm/s (0.4 knots) at a depth of 20 m, decreasing to 12 cm/s (0.2 knots) at 300 m (NOAA, 1981), and are very variable in direction. In winter, from November to May, stronger winds (30 to 40 knots) are occasionally observed during storms, and from June to October, tropical cyclones can be encountered (winds > 100 knots). At intermediate depths (300-4800 m), the currents are weak (mean 0.08 knots) and variable in direction.

The general scheme of deep oceanic circulation (from 1 to 10 cm/s) in the Pacific Ocean is related to the movement of Antarctic waters, originating near the Ross Sea, and which descend along the Australian coast and emerge at the edge of the Samoan Islands. The water masses then move northwards, giving rise to two currents, one along the coast of the Philippines and Japan in the western Pacific, and the other directed towards the north-east Pacific Ocean. Crossing the region of the Line Islands, the latter ends up in the Clarion-Clipperton fracture zone (figure 2). Here, deep ocean currents are probably influenced by the topography of the ocean floor and vary between 0.1 and 0.15 knots in a predominantly south-easterly direction. Near the ocean floor, they are directed southwards by the orientation of the topography. Measurements by NOAA (1981) show deep ocean current speeds of 2.1 cm/s to 24 cm/s at 6 m above the ocean floor.

Physico-chemical characteristics of the water column and biological productivity

The circulation of water masses in the Pacific Ocean has undergone important changes over the course of time. These variations have led to fluctuations in biogenic productivity (figure 3) that have especially affected the extent of the zone of high equatorial productivity, as well as alterations in physico-chemical parameters (van Andel & Heath, 1973; Cook, 1975; Berger *et al.*, 1987; Pujos, 1987). According to analyses of percentages of CaCO3 in sediments, the circulation has been fairly stable since the end of the Miocene (10 Ma).

Calm tropical zones extend on either side of the equator and over about 3/4 of the tropical Pacific, contrasting with the equatorial zone which is subject to the upwelling of deep cold water, rich in nutritive salts and giving rise to very high planktonic productivity.

Comparative data from the surface and the water column were obtained by NOAA (1981) in the DOMES study area (5°-20°N and 128°-155°W) within the Clarion-Clipperton fracture zone. The thermocline is at 150 m depth in summer and at 130 m in winter. A thermal frontier is thus established, oriented east-west, and underlying the divergence zone between the North Equatorial current and countercurrent. The salinity of the surface water is 34 in 1000 throughout the year. The distribution of dissolved oxygen and nutrients is strongly linked to the thermal characteristics at the surface down to 200 m depth (Anderson, 1979). The thermocline inhibits the vertical transport of nutrients. Zones of minimal oxygen content occur at 300 m and 500 m. The level of particles in suspension is maximal at the surface, to a depth of 300 m, then generally lower (7-12 mg/l) throughout the water column, increasing again near the ocean floor (10-14 mg/l). This causes the presence of a weak cloudy layer and deep ocean currents that are strong enough to put particles back into suspension (Ozturgut *et al.*, 1978). Concentrations of nickel and copper in solution increase on the ocean floor at 4800 m, whereas manganese in solution reaches its maximum at the surface and in the zone of minimal dissolved oxygen (Baker & Feely, 1979).

Fig. 2. Map on the present-day pattern of deep ocean circulation in the Pacific Ocean (Demidova, 1999).

Values for annual primary production are variable in the Clarion-Clipperton fracture zone and can be described as oligotrophic (with production of 15-35 gC/m^2/an) to mesotrophic (150 gC/m^2/an) in the most westerly regions (Koblentz-Mishke *et al.*, 1970; Longhurst *et al.*, 1995; Berger *et al.*, 1987). Analyses of chlorophyll A in the oligotrophic zones show mean concentrations of 0.063 mg/m^3 in summer and 0.12 mg/m^3 in winter. That represents a low mean value for daily primary productivity of 1.5 mgC/m^3/j in summer and 2.7mgC/m^3/j in winter when compared with a level of primary production in the euphotic zone of 43.8 gC/m^2/an in summer and 52.5 gC/m^2/an in winter (El-Sayed & Taguchi, 1979). The micronekton, zooplankton and neuston vary between 3 and 8 g/m^3, with a maximum in winter due to greater insolation (16 % more than in summer according to Franceschini, 1979). The greatest

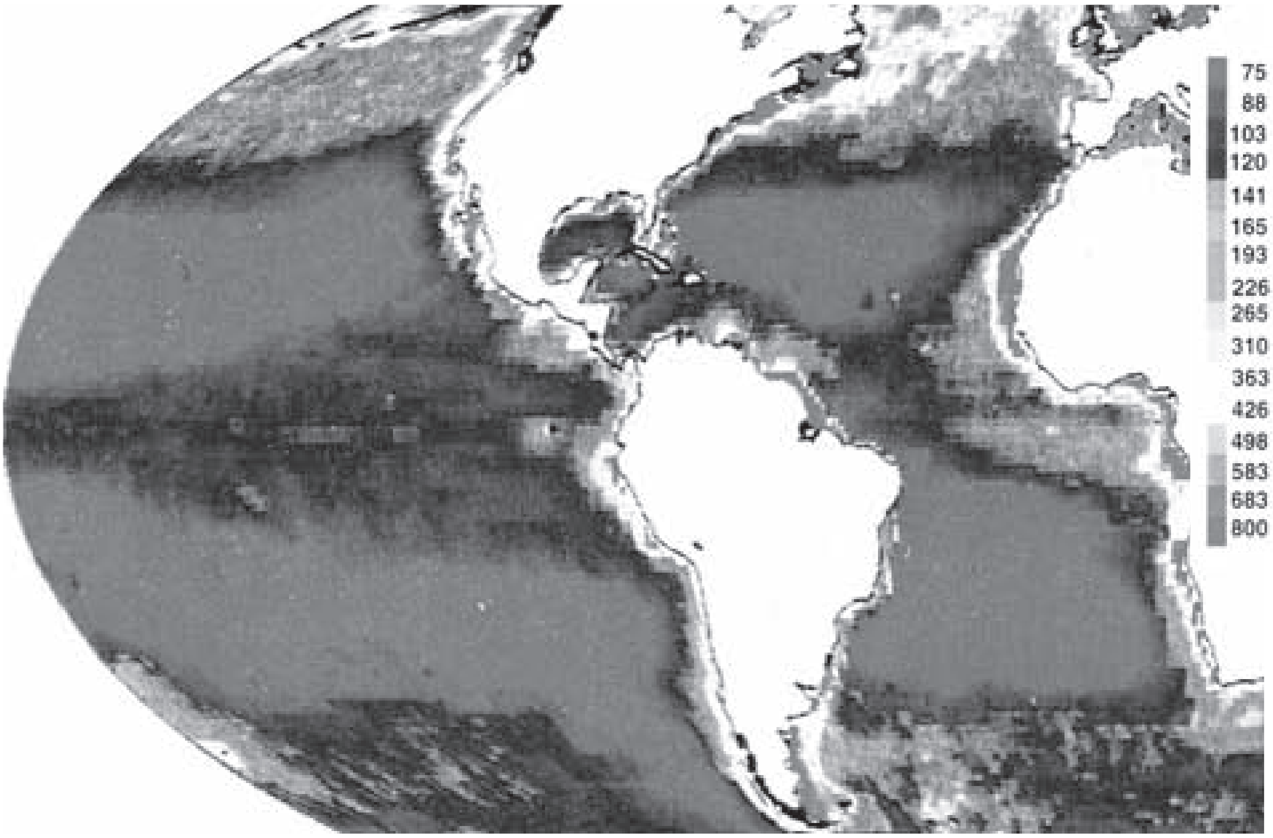


Fig. 3. Map on the geographical distribution on a world scale of mean annual primary productivity (mg C/m^2/an) calculated from data on C14. (Longhurst et al., 1995). (See colour appendix 1, p. 127).

concentrations of macroplankton are found in the first 150 m of the water column while the lowest concentrations are found at around 200 m depth and below 900 m. Maximum bacterial activity is found at the surface and in the zone of minimal dissolved oxygen (200 m).

The salinity in the lowest layer of the water column, to 300 m from the ocean floor, is uniform with a mean value of 34.7 per 1000. Dissolved oxygen content is from 359 mg atm/l in the west and 332 mg atm/l in the east in the Clarion-Clipperton fracture zone. Concentrations of nutrients increase close to the ocean floor. At 400 m above the floor, levels of particles in suspension increase, indicating the presence of a weak cloudy layer. The temperature on the ocean floor is close to 1°C.

The abyssal suprabenthic fauna

The abyssal fauna, living on or close to the ocean floor, and especially the macrofauna which has been much studied in the literature, is characterised by great diversity and low population density (36 to 268 individuals per m^2). It is dominated (62 % of the total fauna) by the meiofauna (animals retained by a mesh of 40 mm) whose biomass is composed mostly of detritus feeders, and which represents 81 % of the total for the macrofauna (animals retained by a mesh of 250 mm) (Hecker & Paul, 1979). This fauna is characterised in general by its small size, a low metabolic rate, great longevity, slow maturation, low reproductive potential, and low rates of colonisation (Thorson, 1957; Mills, 1983; Rex, 1983). These characteristics are adaptations to extreme environmental conditions of great temporal stability, with temperatures of 1 to 3°C, pressures around 500 atm and *a priori* very low input of nutrients from the surface arriving on the ocean floor (oligotrophic environment). Consequently the abyssal environment is considered as having great ecological stability (Rex, 1983).

However, current data from research in the abyssal environment, and especially in the Clarion-Clipperton fracture zone, demonstrate variability in biotic and abiotic conditions in space and time, thus revolutionising our previous ideas of great environmental stability that were based on a model of unchanging environmental conditions (Tyler, 1995; Radziejewska & Stoyanova, 2000). Natural biotic and abiotic disturbances may also maintain these suprabenthic communities in equilibrium. A seasonal cycle exists with considerable variation in the vertical flow of detritus particles (Smith *et al.*, 1997; Lauerman *et al.*, 1997; Drazen *et al.*, 1998; Thurston *et al.*, 1998) related to variation in the flux of particulate organic carbon (Smith & al., 1997; Scharek *et al.*, 1999). This is controlled principally by the periodic deposition of planktonic debris that originates in the eutrophic zone

(Thiel *et al.*, 1988/1999; Gehlen *et al.*, 1997; Smith *et al.*, 1997; Khripounoff *et al.*, 1998; Scharek *et al.*, 1999). These results were confirmed by Smith *et al.* (1994) in experiments with a remote camera positioned on the ocean floor for 386 days. Similarly, Ruhl & Smith (2004) observed a significant change in the structure of the dominant suprabenthic megafaunal community in the north-eastern Pacific Ocean following an *el Nino*/la *Nina* climatic change between 1997 and 1999.

Other disturbances may be produced in the zone, such as changes in deep ocean currents, as well as 'benthic storms' phenomena that have been observed during long term *in situ* measurements (Kontar & Sokov, 1994; Aller, 1997).

Geological environment

Three principal structural elements delimit the Clarion-Clipperton fracture zone (figure 4):

- To the north and south, the Clarion-Clipperton fractures form part of major oceanic structures which carve the Pacific abyssal plain into large parallel strips, oriented E-W for more than 5 000 km and reaching 5 500 m depth.
- To the west, the chain of the Line Islands runs in a NW-SE direction and separates the Clarion-Clipperton fracture zone from the region of seamounts and subduction of the West Pacific basin.
- To the east are the contours of the fossil ridge of Mathematicians, which rises to depths of 3 000-3 500 m. Further east, the East Pacific accretion ridge forms the boundary between the Pacific, Cocos and Nazca plates in the north equatorial Pacific Ocean.

The nature and distribution of sediments on the ocean floor are a function of numerous processes closely connected with the geographic locality of deposition sites. The Pacific ocean extends over a very considerable area between latitudes 70°N (Bering Sea) and 70°S (Amundsen Sea), and a great variety of sediments are found over its floor.

The main features of the depositional history of the Clarion-Clipperton fracture zone were initially retraced by the bores of the "Deep Sea Drilling Project" along a transect close to the East Pacific ridge near Hawaii (Tracey *et al.*, 1971; van Andel & Heath, 1973; Cook, 1975).

The general appearance of the Clarion-Clipperton fracture zone is one of abyssal hills, elongated in a

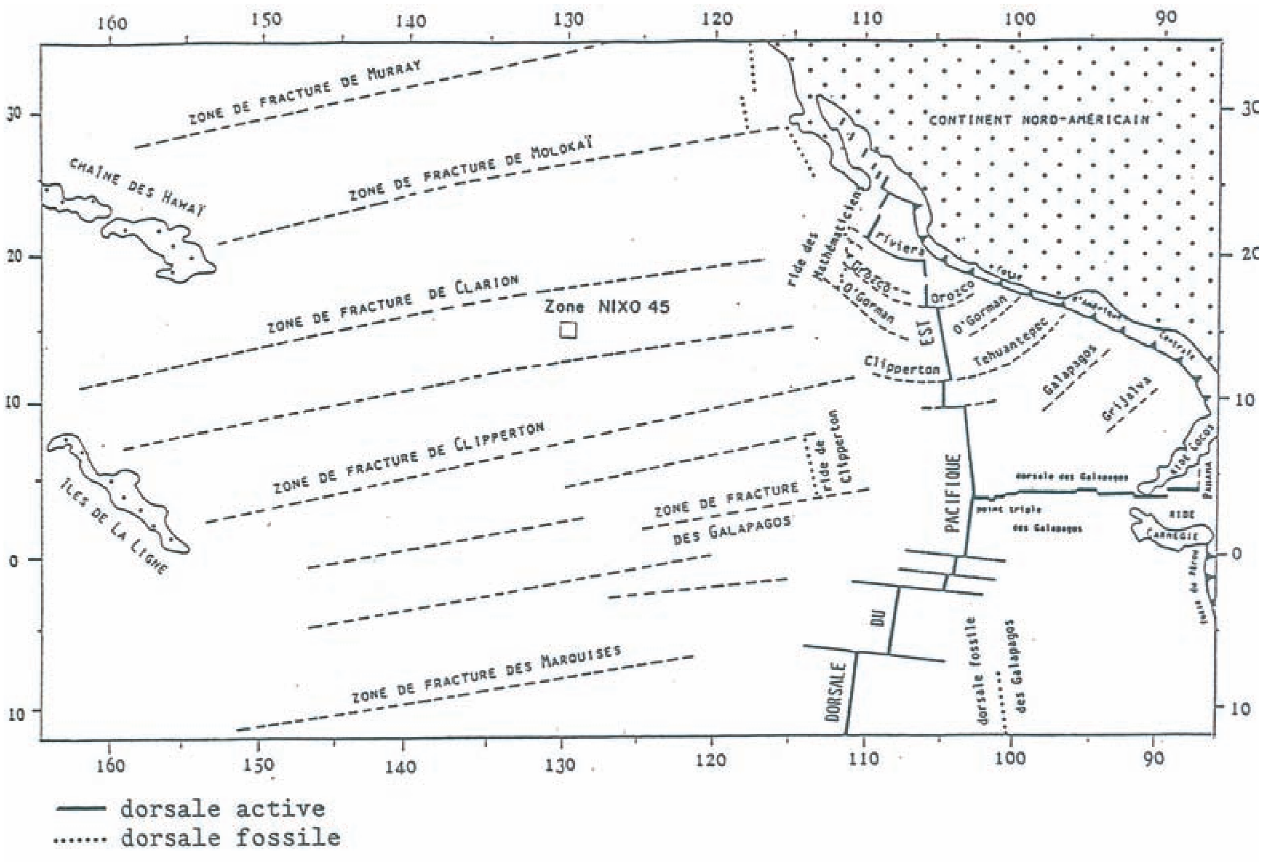


Fig. 4. Map on the regional geological setting of the Clarion and Clipperton fracture zone (van Andel & Heath, 1973).

north-south direction, parallel with one another and accompanied by escarpments (cliffs). These abyssal hills are somewhat elongated with irregular, elliptically domed summits and steep sides, and are the result of tectonic extension occurring on the dorsal flanks (Menard, 1964). In the Eastern Equatorial Pacific Ocean, the sediment coverage is about 20 % thicker in morphological depressions than on the ridges and, under the influence of sedimentary processes, the contours tend to soften (Shor, 1959). This embankment of sediments must have been caused by the lateral transport of particles in suspension by weak currents.

The basaltic substratum dates from 78 Ma at the site furthest east (161°W) and from 23 Ma at the furthest west (159°W). It originates from the functioning of the Farallon ridge. It was then subject to the following events: fracturing by faults parallel to the ridge, a shift towards the west and north, an increase in depth due to the recooling of the oceanic crust, and finally, 10 million years ago, intensive refracturing accompanying a fall in the East Pacific ridge. This last process created a final episode of faulting producing escarpments that are now partially exposed, or when weaker, a local increase in the slope corresponding to the edge of a fissure. The basaltic platform presents a very rough microtopography of the seabed where it outcrops (Menard, 1964).

The whole sedimentary covering in the Clarion-Clipperton region is 100 to 300 m thick. A transition is seen in the sedimentary facies depending on latitude and longitude. The relatively narrow depth of the sediments is witness to the slow rate of sedimentation together with the dissolving of carbonates from about 15 Ma and possibly to hiatuses in deposition, during which the polymetallic nodules developed. The presence of ancient fossils in the present-day sediments is proof of the ever-present phenomenon of erosion. Stratigraphic reconstruction of the different sedimentary formations is as follows:

The Line Islands formation is at the base of the lithostratigraphic column, deposited on the basaltic platform and consisting of semi-hardened brown silts rich in radiolarians. These silts are rich in iron oxides and manganese but also contain calcareous nannofossils, as well as siliceous inclusions of chemical or biochemical origin (cherts). This formation dates from the Eocene (40 Ma) and does not occur in the study zone. It is developed further west, towards 130°-140°W, and increases westwards, to a thickness of about 150 m at 140°/150°W.

The Marquesas Islands formation is stratigraphically discordant over the preceding one, and corresponds to a period of sedimentation from 35 to about 20 Ma. It is composed of white calcareous silts with nannofossils that are very soluble in sea water. Foraminifera are very abundant as well as a siliceous fraction composed of radiolarians. The CaCO3 content is generally above 80-95 %. The lowest part of the formation has a chalky nature and contains siliceous concretions. The range of colours runs from white to orange differentiating layers 25 to 250 cm thick. This formation reaches a thickness of 300 m near the Clipperton fracture. In the region studied, its thickness is limited to 90 m.

The Clipperton formation is the most recent, dating from the middle Miocene to the present. It is formed of pelagic sediments, varying in thickness from 30 to 50 m. These sediments are composed principally of brown radiolarian silts with a very high level of silica. At the base is a transition, with alternating levels of carbonates and siliceous clay, limited to a few metres thick in the study area (Du Castel, 1985). The calcium carbonate content and the homogeneous chemical composition of these silts are comparable with those that characterise the Marquesas Islands formation. The transition between these two latter formations is marked by cyclical variations (from which comes

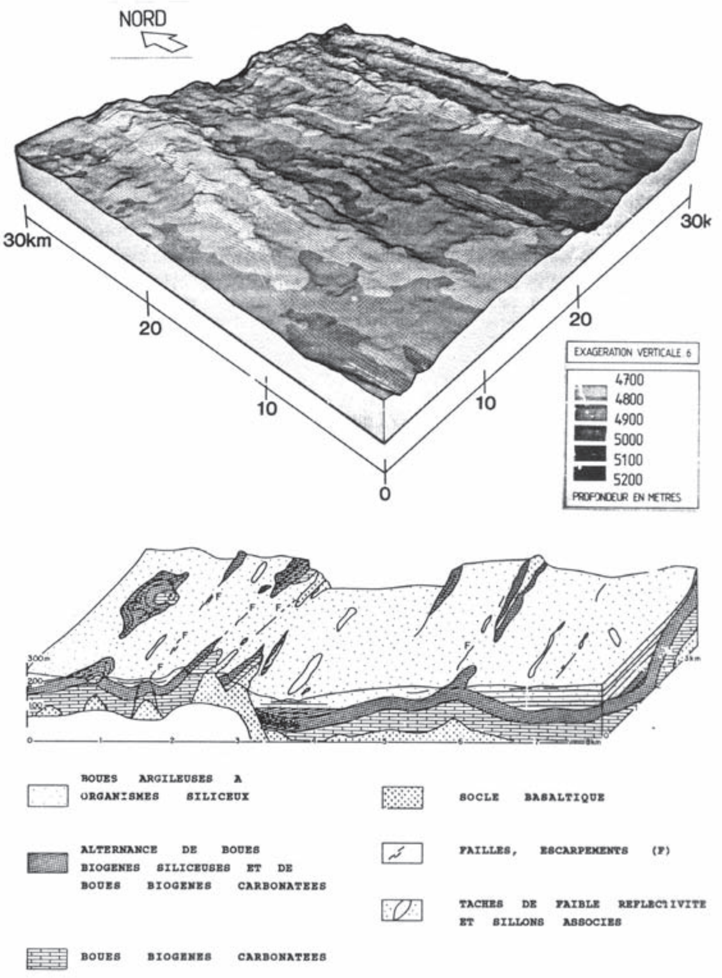


Fig. 5. Block diagram showing the geological formations of the environment of the polymetallic nodules in the Clarion-Clipperton Zone. (© Ifremer)

the definition of 'cyclical series') of sedimentary processes, rather than by the chemical composition of the sediments. This cyclical series is the result of temporal variation in the biological productivity of the surface waters, and stratification and circulation of water, which causes changes in the depth of the CCD (carbonate compensation depth). Figure 5 shows the different geological formations in the Clarion-Clipperton fracture zone.

2.2 POLYMETALLIC NODULES

In a geological sense, a nodule refers to a relatively small mineral assemblage, 5 to 10 cm diameter, consisting predominantly of Mn-Fe and often irregular and rounded in shape. Polymetallic nodules were first discovered in the Kara sea in the Russian Arctic in 1868, and subsequently sampled from the depths of the Atlantic by scientists on the British expedition on the *H.M.S. Challenger* in 1873. Since then they have been found in numerous marine and fresh water environments, and they appear to be ubiquitous on the ocean floor wherever the rate of sedimentation is extremely low (Halbach, 1980). It was only in the 1950s that these nodules assumed importance because of their richness in economically important minerals. Not only do they contain oxides and hydroxides of iron and manganese, but also of copper, nickel and cobalt (Goldberg, 1954).

Since the beginning of the 1970s, these nodules have been the subject of numerous studies involving sampling, dredging, selective photography, photographic transects, continuous videos and manipulation *in situ* by manned submersibles. This work has been financed by industrial and governmental organisations in order to estimate the richness of submarine deposits, since their exploitation could reduce, if not remove, the dependence of some industrialized countries on other countries. The discovery of nodule deposits has given rise to numerous investigations of their origin, growth and distribution, as well as studies of possible correlations with their physico-chemical environment and substratum.

Polymetallic nodules generally lie on the sediment, forming a more or less well developed superficial covering. However, nodules are also buried to several metres depth within the sediments (Friedrich & Plüger, 1974; Friedrich, 1979). The superficial covering of nodules depends principally on their size and abundance on the ocean floor and is sometimes accompanied by a change in chemical composition (Friedrich & Plüger, 1974). Changes in nodule abundance per unit area can be rapid although difficult to quantify. Some studies have attempted to demonstrate a relationship between geochemical and mineralogical characteristics and the geological environment of the nodules (Crerar & Barnes, 1974; Usui, 1979; Pautot & Melguen, 1979), but the diversity of these parameters does not allow the extrapolation of this type of analysis to a global oceanic scale. In regions of abyssal hills, the shape of the nodules is principally hummocky. In more active zones with fractures and ancient volcanic structures, one finds polynodules made of several concretions adjacent to one another, with a smooth surface (Friedrich & Plueger, 1974; Halbach & Özkara, 1979b). The distribution of nodules seems to be more influenced by the degree of slope than by variation in factors such as longitude, latitude and depth. Distribution varies exponentially with degree of slope, and when the slope is less than 5°, the correlation between terrain and nodule abundance is positive, whereas on greater slopes, nodules are much less abundant (Wang *et al.*, 2001).

Nodule composition

Mineral components contained in the oceans originate from the leaching of the continental crusts, the weathering of submarine volcanic rocks, from submarine, aerial eruptions and continental winds. These components are all transported in the form of solutions, colloids or suspensions. After marine transport by various currents, they are incorporated directly into sediments by gravitational deposition, chemical precipitation or by the action of living organisms which ingest them (figure 6). Substances fixed throughout skeletons and tissues can be up to 100 000 times more concentrated in organic matter than in sea water. After the decomposition of dead organisms on the ocean floor, a chemical and biological chain may form a closed system that recycles some elements (Schneider, 1981).

Polymetallic nodules are composed of irregular concentric envelopes of oxides and hydroxides of iron and manganese, giving them a stromatolite-like structure. The successive layers of growth are a function of the variation in intensity and mode of physico-chemical exchange with the environment. Layers rich in iron are the least crystallised and contain cobalt as a minor element, while the layers of manganese are better crystallised and richer in copper and nickel. Associated with these metallic deposits are epibionts, organic particles (various tests) and minerals of detritic origin. The incrustations of manganese also contain silica, whose quantity is variable but can reach 10 % (Halbach & Puteanus, 1984). The mean composition of metals in a nodule can vary considerably. The order of magnitude of concentrations is as follows: manganese = 20-30 % ; iron = 5-7 % ; copper = 1 % ; nickel = 1 % ; cobalt = 0.2 %. The wet density of a nodule is 2g/m^3, its water composition is 30 % and its porosity 50 %.

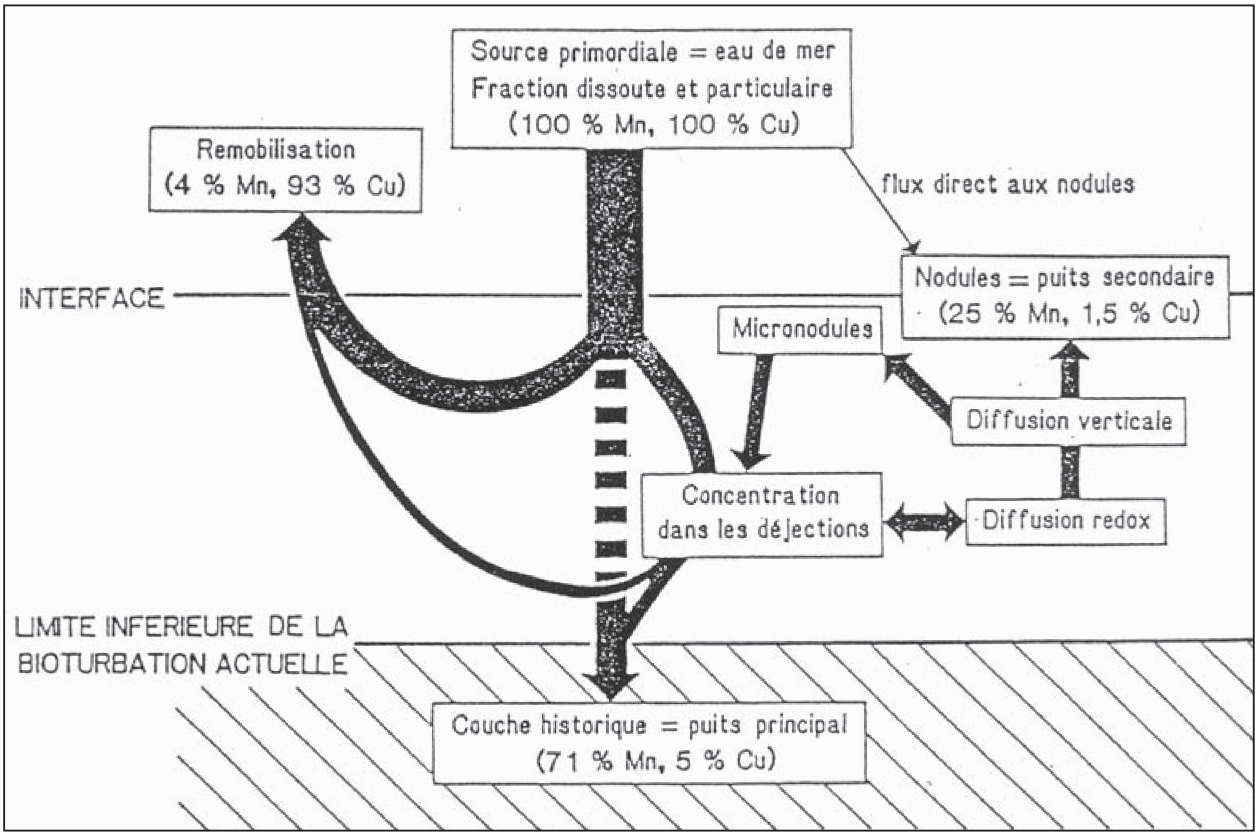


Fig. 6. Schematic representation of the various processes found in a system of inflow, deposition and biological recycling of minerals in an oceanic system (Saguez, 1985).

Formation and growth of nodules

The formation and growth of nodules has not yet been clearly explained. However, numerous hypotheses have been put forward based on observations of the ocean floor. According to von Stackelberg & Beiersdorf (1990), two conditions determine the growth of nodules: the degree of proximity of the CCD and exposure to currents. These conditions also determine the local depositional history, and consequently an interaction between the historical sedimentary context and the local growth of nodules occurs. Liang (1993) put forward a theory of a formational relationship, involving a model of kinetic-static-progressive development in relation to the characteristics of the nodule's internal structure and the space-time relationship between its formation and the associated sediments. In the central Pacific Ocean, nodule formation can be classified in relation to the history of sedimentation by the structure of the layers into three phases of growth with two hiatuses. Qian & Wang (1999) concluded from their work on geochronological methods that their formation was closely linked to the layer of deep oceanic water from the Antarctic or Antarctic Bottom Water (ABW). Thus the polymetallic nodules of the eastern Pacific Ocean have been formed gradually since the Oligocene with the main stages of formation at the beginning of the Miocene, the middle of the Miocene and the end of the Pliocene.

Nodules are found preferentially on ocean floors that have gentle topography and are rich in fine sediments (silts, clay). They grow from coarser elements such as otoliths or the vertebrae of marine mammals, sharks' teeth, mineral debris, or from fragments of shells, older nodules or volcanic rocks. The growth of nodules is linked to the migration of manganese across the sediments, then its precipitation and accumulation in the form of concentric layers by oxidation close to the water-sediment interface. A hypothesis of animal participation in their growth has been put forward in which foraminifers, xenophyophores, polychaetes and microorganisms all contribute to this chemical process (Wendt, 1974; Greenslate *et al.*, 1974; Ehrlich, 1978; Thiel, 1978).

Certain microorganisms that live on the surface of concretions and crusts of manganese are capable of using the chemical oxidizing potential of ions (Mn^{2+}, Fe^{3+}, Mn^{4+}) in sea water to extract the energy necessary for their metabolism, and thus causing the precipitation of metallic oxides and hydroxides. Such hypotheses are supported by observations made by the scanning microscope (Larock & Ehrlich, 1978; Ghiorse, 1980), which have shown microorganisms sheltering in the numerous cavities in the cortex of the nodules (Wendt, 1974; Thiel, 1978); their food would be supplied by sea water. Biological activity could thus play a significant role in the growth of nodules. This hypothesis has also been proposed by von Stackelberg (1979, 1982) based on a study of the internal growth-structure of nodules.

The water-sediment interface is an important habitat for nodule growth. In the first few centimetres to several decimetres of sediment, organic substances are decomposed and mineralised by various members of the food chain. Detritus feeders ingest sediments and assimilate and decompose organic substances. So there exists a zone of weak oxidation-reduction potential in the sediment, in which the metals liberated from mineralised organic substances, tests, skeletons and micronodules can dissolve. It has been observed that increased levels of heavy metals are correlated with levels of organic carbon (Hartmann *et al.*, 1975; Hartmann, 1979; Gundlach *et al.*, 1979). Once mobilised, metals (Mn, Cu, Ni, Co) can migrate to the sediment surface from the beginning of depositional diagenesis and contribute to the growth of nodules.

Several processes of nodule formation have thus been proposed (Halbach & Özkara, 1979b), by hydrogenesis (precipitation from sea water), by precocious diagenesis or by a combination of the two. As far as hydrogenesis is concerned, the nodule grows at its summital pole from metal precipitates originating from the water around the suprabenthos, while precocious diagenesis enables the nodule to grow at its lower pole, from metals originating in water percolating in the sediment from zones of reduction. A hypothesis of growth of an oxic type has also been proposed (Callender & Bowser, 1980; Klinkhammer, 1980) to explain the partial remobilisation of metals in the superficial part of the oxidising sediments that makes the lower surface of the nodules grow. Dymond *et al.* (1984) defined oxic growth as a process comprising the oxidation of organic matter and the dissolving of organisms.

The rate of growth of nodules in the abyssal environment must be extremely slow. It has been estimated by radiochronological methods at several millimetres (4-9 mm) per million years (Heye, 1988; Harada & Nishida, 1976, 1979; Krihnaswami *et al.*, 1982). This phenomenon is thus much slower that the average rate of sedimentation on the ocean floor (1 millimetre per thousand years). Wu *et al.* (1999) compared the rate of growth of four nodules, one from the central part of the north Pacific Ocean and three from the Clarion-Clipperton fracture zone (CCFZ) with the aid of a super-accelerated mass spectrometer (10)Be. The rates of growth were respectively 7.5, 2.7, 9.6 and 1.5 mm per million years and are in line with values given in the literature.

The growth of nodules is not regular, and its discontinuity has been demonstrated by Heye (1988). This theory was challenged by von Stackelberg & Beiersdorf (1991) who advanced a hypothesis by which buried nodules would still be immature. Once buried, nodules cease growth. It is only under the pressure of upward growth that they take on the appearance of the nodules at the sediment surface. Consequently it is clear that a very low rate of sedimentation would be favourable to their growth.

According to von Stackelberg (1982), a hiatus (or absence of sedimentation) occurred in the Clarion-Clipperton region between the beginning of the Miocene and the end of the Pliocene (13 to 16 Ma) and consequently this period would have been the most favourable for the start of nodule development. In the middle Miocene (19 Ma) the circulation of the oceans was revolutionised by the closure of the Tethys and the upthrust of Central America, after which Antarctic waters were able to pour into the Pacific basin. This drove the phenomena of erosion and reduction in the rate of sedimentation, linked to the dissolving of carbonates and silica, which are favourable conditions for nodule formation. Von Stackelberg (1990) also assumed that some nodules were able to start growing while calcareous sedimentation at the beginning of the Miocene still prevailed. He attributed the presence of a hiatus in the lower Miocene to the action of strong currents caused by the outpouring of Antarctic waters into the basin of the Central Pacific Ocean.

The nodules of the Clarion-Clipperton region started their growth from potential nuclei such as particles torn off by erosion, fragments removed from beds of hardened sediments (pelagic sediments), volcanic ash or fragments of chert. Fragments of rocks such as basalt (von Stackelberg & Marchig, 1987) were able to act as nuclei in the regions of abyssal hills where turbidity currents were significant. Finally fragments of nodules produced by autofragmentation also served as kernels. This autofragmentation occurred during the ageing of primary precipitates by dehydration due to the appearance of radial and concentric fissures (Halbach & Özkara, 1979b). The nodular debris that served as kernels is evidence of a more ancient generation of nodules (19 to 20 Ma according to Beiersdorf, 1987).

Sustention of nodule deposits on the seafloor

The phenomena that allow nodules to remain on the seafloor have not yet been fully elucidated by observations from towed cameras and still photographs. The role of bioturbation or biological activity has been proposed, as has that of currents. However, measurements of present-day deep ocean currents show speeds between 2 and 25 cm/sec (Amos *et al.*, 1977). This speed is sufficient to transport fine particles and thus, in places, reduce the real rate of sedimentation, and it is too low to cause the erosion of even lightly consolidated sediments.

According to Schneider (1981), another trophic category belonging to the megafauna, could be implicated in the maintenance of nodules at the sediment surface: detritus feeders such as echiurians, sipunculids, sessile polychaetes, isopods, peracarids, molluscs, asteroids, echinoids, holothurians and hemichordates. These animals ingest the film of sediment at the water-sediment interface and sometimes push nodules out of the way when they pass. Some echiurians construct remarkable mounds reaching more than 2 m in length by 80 cm wide and about 50 cm high (Tilot, 1991, 1992a). In photographs and videos, one can see the evidence of biological activity (mounds, tracks, dark trails and alignment of nodules) which appears intense in some cases (Hartmann *et al.*, 1975; Hartmann, 1979; Schneider, 1981; von Stackelberg, 1984). These tracks could have been created some tens if not hundreds of years ago by animals which disappeared long ago. The probability that a nodule would be turned over has been estimated at once in every 103-104 years for small nodules (Huh, 1982). Moreover, these traces of burrowing activity represent a particular biotope capable of altering the environment by modifying the chemical conditions of the sediment, as well as the current at the water-sediment interface, by increasing turbulence and inducing an exchange with the interstitial water in the galleries (Ray & Aller, 1985).

Improving our knowledge of the nodule ecosystem and suprabenthic assemblages allows a better understanding of relationships between certain animal groups and environmental conditions and habitats, and in this way will help us to elucidate the role of biological activity at the depositional interface.

2.3. THE COMMON HERITAGE OF MANKIND AND PIONEER INVESTORS

The United Nations Convention on the Law of the Sea is at the origin of a redefinition of marine areas to a extent that is not equalled elsewhere in international law. The allocation of sovereign rights to each coastal state has a collective equivalent or ‘commonwealth’, with the advent of the common heritage of humanity. The Zone is defined as the space situated outside the limits of national jurisdiction, which comprises the marine depths and their substratum (article 1.1 of the Convention). The Zone and its resources are placed outside all national claims; they are the common heritage of mankind (article 136). These resources are precisely defined: they comprise all *in situ* solid, liquid or gaseous mineral resources that are found in the marine depths or in their substrata, including polymetallic nodules (article 133). The final text of the Convention on the Law of the Sea was adopted on the 30 April 1982 by 130 votes in favour, 4 against (Federal Republic of Germany, Australia, United States, and the United Kingdom) and 17 abstentions. The United Nations Convention on the Law of the Sea came into effect in November 1994.

From the beginning, France was one of the small group of states claiming the status of ‘pioneer investor’ for the exploration of polymetallic nodules, along with India, Japan and Russia. Private industrial groups (consortia) with American and British status or under various sponsorships have also shown an interest in the mineral resources of the deep ocean. On the 1st July 1981, following the example of American, German and English companies, the ‘Centre National pour l’Exploitation des Océans’ (CNEXO) deposited before the French government, on behalf of the ‘Association Française pour l’Exploration et la Recherche des NOdules’ (AFERNOD), a request for a permit of exploration covering a sector of 455 000 km^2. This permit request was modified on the 12th July 1982 by reducing the area to 300 000 km^2, to conform to the regulations of the United Nations Convention on the Law of the Sea.

On 10th December 1982, when the Convention on the Law of the Sea was signed in Jamaica by 119 delegates, France had reservations about the applicability of the part relating to the deep sea and Federal Republic of Germany, the United States and the United Kingdom refused to sign. An interim legal system to protect preliminary investments in the deep ocean was put in place internationally by the Conference which had drawn up the Convention on the Law of the Sea. This system was managed by a Preparatory Commission of the International Seabed Authority and the International Tribunal for the Law of the Sea, and was responsible for setting up a permanent system.

A series of modifications to the French permit request were made in order to take account of various agreements that had the purpose of resolving conflicts of overlap with American consortia in 1983, and then with American and Japanese consortia in 1984. The French request was thus reduced to 219 000 km^2 of which 94 500 km^2 were retained from the request in July 1982. On the 3rd August 1984, France deposited before the UN Secretary General its request for permits of exploration and its registration as a pioneer investor on behalf of AFERNOD and signed a provisional arrangement with seven other countries (Federal Germany, Belgium, United States, United Kingdom, Italy, Japan, and the Netherlands), ratifying the results of negotiations conducted between the consortia.

On 5th September 1986 in New York, the Preparatory Commission ratified an agreement under whose terms conflicts between claimants could be settled and registration would operate. The central condition of this agreement was the commitment of each claimant to contribute to the setting-up of a site of 52 300 km² in the Pacific Ocean which would revert to the international Authority. Each claimant was allocated a site of its choosing of the same area, and could add to this site up to 75 000 km².

On the 17 December 1987, and at the same time as Japan and Russia, France deposited before the Secretary General of the United Nations a claim as a 'pioneer investor' for an area of 75 000 km² in three parts, of which 43 960 km² resulted from the claim made by AFERNOD in July 1981. Since that date, these three countries have been in possession of mining permits, that of France being in three zones, represented in blue in figure 7.

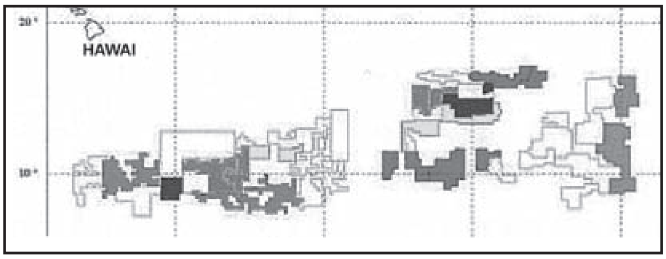


Fig. 7. Location of the zones of mining permits for the exploitation of polymetallic nodules in the eastern tropical Pacific Ocean. (See colour appendix 1, p. 129).

COMRA (China Ocean Mineral Resources Research Development Association) of the Peoples Republic of China was registered on the 5 March 1992 as a pioneer investor and was allocated a sector of 150 000 km² in the western part of the Clarion-Clipperton fracture zone. On the 21 August 1992, Interocean Metal, a consortium of companies from Bulgaria, Cuba, Poland, Czech Republic, Slovakia and the Soviet Union received investor status, with a sector of 150 000 km² in the eastern part of the Clarion-Clipperton fracture zone. In total 2 316 418 km² was thus covered by mining titles, of which 887 768 km² was reserved to the International Authority, 675 000 km² allocated by the Preparatory Commission and 615 350 km² claimed by governments which had not signed the Convention on the Law of the Sea.

As for France, AFERNOD was registered with Ifremer as its moral representative. The hazards or difficulties of progressing to a more active phase in the management of this dossier, and the lasting absence of economic and commercial prospects, have recently brought about the demise of AFERNOD. The legal title thus reverts directly to Ifremer on behalf of the state, without any modification or other consequences. The legal part of this agreement envisages two stages: the registration of pioneer investors and contractualisation.

Registration occurs under an interim regime required by the states themselves and concerned with preserving their investments and their precedence for access to resources. This question is regulated by Resolution II of the Final Act of the 3rd United Nations Conference on the Law of the Sea. This stage was reached on 17 December 1987 and France, following the example of other claimants, registered for the sectors claimed in the Pacific as soon as she had satisfied the various conditions in Resolution II and the negotiations which followed its adoption, to make it compatible with the activities of the pioneers.

Contracts were drawn up well before becoming a legal reality and were linked with the coming onto force of the Convention, at the end of the negotiations to modify Part XI. This established, in Kingston (Jamaica), international regulations for the deep sea, as well as the International Seabed Authority, a new international body responsible for overseeing the common heritage of mankind.

On the 28 July 1994, negotiations undertaken on the initiative of the Secretary General of the United Nations between signatories and non-signatories of the Convention resulted in the adoption of resolution 48/263 of the United Nations, known as the 'Agreement relating to the Implementation of Part XI of the UN Convention on the Law of the Sea'. This text, which was nevertheless part of the Convention, made certain modifications to the measures previously taken. Thus an obligation to transfer technology was added, along with arrangements relating to the limitation of production and financial clauses connected to the creation of an international body and to contracts of exploration and exploitation of resources.

The International Seabed Authority was officially created and inaugurated in November 1994, and consists of the following bodies:

- The General Assembly, at which not only the countries that have ratified or adhere to the Convention and to the Accord participate, but also those provisional member countries which have agreed to comply with the Accord while waiting for their final adhesion to the Convention. France ratified the Convention on 11 April 1996,

- A Council of 36 members elected by the Assembly,

- Two expert commissions: the Legal and Technical Commission and the Finance Committee.

From 1995 to 2000, the Authority set in place various bodies and approved plans of work deposited by the pioneer investors. In July 2000, it adopted the rules relating to prospection and exploration for polymetallic nodules in the zone, a type of mining code restricted to exploration. The General Secretariat progressively arranged the human and material foundation, and was able to envisage transition to a new phase, which transformed the status of pioneer investors into contractors with the Authority. This phase was all the more important and necessary as the initial number of pioneer investors increased and the newcomers had an active presence, trying to align themselves with the countries that had been part of the system from the beginning.

The operators whose plan of work was approved in August 1997, had, in 2001, to lodge with the Authority a contract of exploration based on the arrangements adopted in the Mining Code. These plans of work foresaw only general exploration during the first five years, and intended to move to detailed exploration, feasibility studies and mineral testing only when economic conditions allowed them to envisage commercial exploitation.

In June 2001, Ifremer signed a contract with the International Seabed Authority on behalf of France. This was a standard contract for 15 years, divided into three periods of five years each, to allow evaluation of its implementation. It is part of France's obligations, as defined by the International Seabed Authority, to undertake some work which seeks to improve our knowledge of suprabenthic ecosystems in the presence of nodules and to evaluate the risks of future mineral exploitation. Within the scope of the first five year phase, up to 2006, Ifremer is engaged in a major programme of cruises at the French site, including the NODINAUT cruise which took place from the 17 May to 28 June 2004 with an international team onboard and in association with the Kaplan programme coordinated by the University of Hawaii. The objectives of this programme are to evaluate biodiversity and species distributions in order to predict and manage the impact of the exploitation of polymetallic nodules.

The International Authority, which manages the common heritage was delighted with the implementation of the Kalpan programme when its administrative and scientific worth was strengthened by diffusion of its scientific results. Recommendations proposed in this programme on the impact of future exploitation of mineral resources and the conservation of biodiversity will assist the International Authority in drawing up and implementing rules and regulations and a strategy to protect the marine environment, in particular biodiversity and genetic resources.

Thus the stakes go beyond the great stages of deep sea statutes; the challenges are great for the scientific and industrial communities as well as for lawyers and diplomats.

Actions taken by France concerning deposits of polymetallic nodules in the East Equatorial Pacific Ocean

The first French exploratory cruises for polymetallic nodules in the Clarion-Clipperton fracture zone commenced in 1975. They were carried out by the 'Centre National pour l'Exploitation des Océans' (CNEXO), which in 1984 became the 'Institut Français de Recherche pour l'Exploitation de la MER' (Ifremer), and on behalf of the 'Association Française pour la Recherche et l'Exploitation des NODules polymétalliques' (AFERNOD). The objective of the first intensive missions was to identify areas of nodule deposits and evaluate their economic potential. A systematic survey over about 2 500 000 km^2 was based on sampling every 93 km. The Noria (NOdule RIches et Abondants) zone of about 450 000 km^2 was then delimited and surveyed using a more concentrated grid with a station every 2.4 km, in order to determine the structural, bathymetric and sedimentary environment of the nodules, using seismic and bathymetric readings, photographs and samples.

The objectives of the exploratory phase, from 1979 to 1981, were to characterize potential deposits, gain detailed knowledge of the topography of the ocean floor and the spatial limits of the mineral resources, and to identify any major obstacles. CNEXO decided to employ two simultaneous methods to achieve these aims:

- to map the deep ocean floor using a multibeam sounder (Seabeam) which is sufficiently precise to reconstruct the distribution of abyssal hills and planes with minimum error,

- to observe the nodule covering and obstacles, which range from a few metres to tens of metres, by means of a trawled device or 'R.A.I.E.', or a remote device, the 'Épaulard', which were equipped with cameras, pressure gauges, and sediment samplers. Their photographs enabled estimates to be made of the importance and nature of any obstacles, and the abundance and quality of nodules.

During the following exploratory phase, AFERNOD characterized the potential deposits at the sites delimited during the previous phases. The aim of this phase was to acquire the knowledge necessary to define a strategy of exploitation. The programme of technological study for the development of the nodule deposits was started in 1980, and required data and samples that would enable engineers to carry out their work. Since 1982, two cruises have led to:

- the building up of a collection of 25 tonnes of wet nodules resulting from 49 dredges divided between 12 different localities, all situated in the zone that was the object of the exclusive research permit requested in July 1981.

- the detailed study of a test site designated NIXO 45 by PLA 2-6000. This site was chosen on the basis of available information for its relatively uniform relief and the presence of areas both with and without nodules. It has been explored by a tight grid layout performed by the 'Épaulard' and 'R.A.I.E.' and numerous samples have been taken using the Kullenberg and TAAF corers.

After the construction of the 'Système Acoustique Remorqué' (SAR, towed acoustic system), this apparatus and the N/O *Jean Charcot* were available again for the exploration of the nodule zones only in 1986. During two cruises, three regions were explored using the SAR and the 'Épaulard'. Sediment samples were also taken using Kullenberg and TAAF corers. Physico-chemical analysis of the mineral potential and numerous tests on methods of metallurgical treatment and collection (such as crushing and pumping) were carried out on 25 tonnes of nodule samples. The geotechnical data from the sediment cores enabled a better choice of equipment for deep ocean locomotion (caterpillars). Observations from the lateral sonar (SAR) confirmed ideas on the frequency and distribution of obstacles and contributed to the establishment of a dredging strategy.

Although the tests by the PLA 2-6000 collector had not taken place at the NIXO 45 site with this intention, detailed exploration brought about fundamental changes in thought, which lead to the redirection of international discussions towards a specific objective, that of obtaining a clearly delimited minimum zone of about 45 000 km^2 in the eastern sector. This was finally attained despite a multitude of overlapping demands by other pioneers. The study of NIXO 45 also allowed the analysis of suprabenthic faunal assemblages in relation to different environmental parameters and nodule substrata.

Finally, in December 1988, a cruise by the manned submersible 'Nautile', was able to make 16 dives which allowed geologists and engineers to explore the ocean floor at 5 000 m depth and to carry out a series of experiments. The sites chosen for the dives by the 'Nautile' were based on maps of obstacles made in 1986 by the SAR. These dives confirmed the preceding syntheses based on a number of former data and served to establish the reconstruction of the submarine landscape of nodule deposits. Measurements of soil mechanics were made *in situ* from the 'Nautile' by means of a field vane tester. Observations and measurements were also made on nodule resistance and conditions of collection.

The activities relating to polymetallic nodules and performed by Ifremer, formed part of France's contractual obligations to the International Seabed Authority following its signature in June 2001. The obligations were to 'pursue a certain number of projects with the aim of improving our knowledge of suprabenthic ecosystems based around the subject "Nodule", and to evaluate the risks of future exploitation by mining'. It was in this context that the NODINAUT cruise with the submarine 'Nautile' took place from 17 May to 28 June 2004.

The work presented in this document and submitted to the International Authority, has similar objectives to the Kaplan programme but focuses on the megafauna. A referential state of megafaunal assemblages is discussed in relation to various environmental parameters and nodule coverage. The analysis was based on the examination of photographic and video data collected by France from the beginning of its exploration of nodule deposits in the Clarion-Clipperton Fracture Zone (Tilot, 1992c). On basis of this referential state, recommendations regarding conservation of the biodiversity and strategy of monitoring with a view to minimizing the impact of the proposed exploitation of polymetallic nodules are proposed. The megafauna is a faunal group still relatively poorly studied, especially at population level within the Clarion-Clipperton fracture zone. The Kaplan programme lead by the University of Hawaii looked essentially at the macro- and meiofaunas. However, the recent cruise by Ifremer permitted notably the photography and sampling of the megafauna, the study of fauna attached to nodules and the making of a few video transects over three nodule-facies. These data are currently being analyzed and would augment our reference base on benthic assemblages, verifying the estimates and hypotheses of functional structure presented here. In spite of the small amount of sampling, preliminary results on the two nodule-facies analyzed on NIXO 45 site appear to confirm our identifications and faunal assessments.

2.4. ECONOMIC PERSPECTIVES OF MINERAL EXPLOITATION

There are no exploited terrestrial deposits that contain the four metals present in polymetallic nodules. However, one can compare the manganese in nodules with deposits of Mn exploited in Africa and South America, and nickel and cobalt with low grade deposits of lateritic nickel. When there are new requirements for Ni, a choice will have to be made between the exploitation of nickel-bearing laterites or nodules. Economics would envisage profitability of nodule exploitation when the progressive exhaustion of the richest nickel deposits leads to tension in the market for this metal and a sustained increase in its price. Some economists estimate that the exploitation of nodules will not be profitable until the price of metals returns to that of the 1970s. Others recognise the necessity

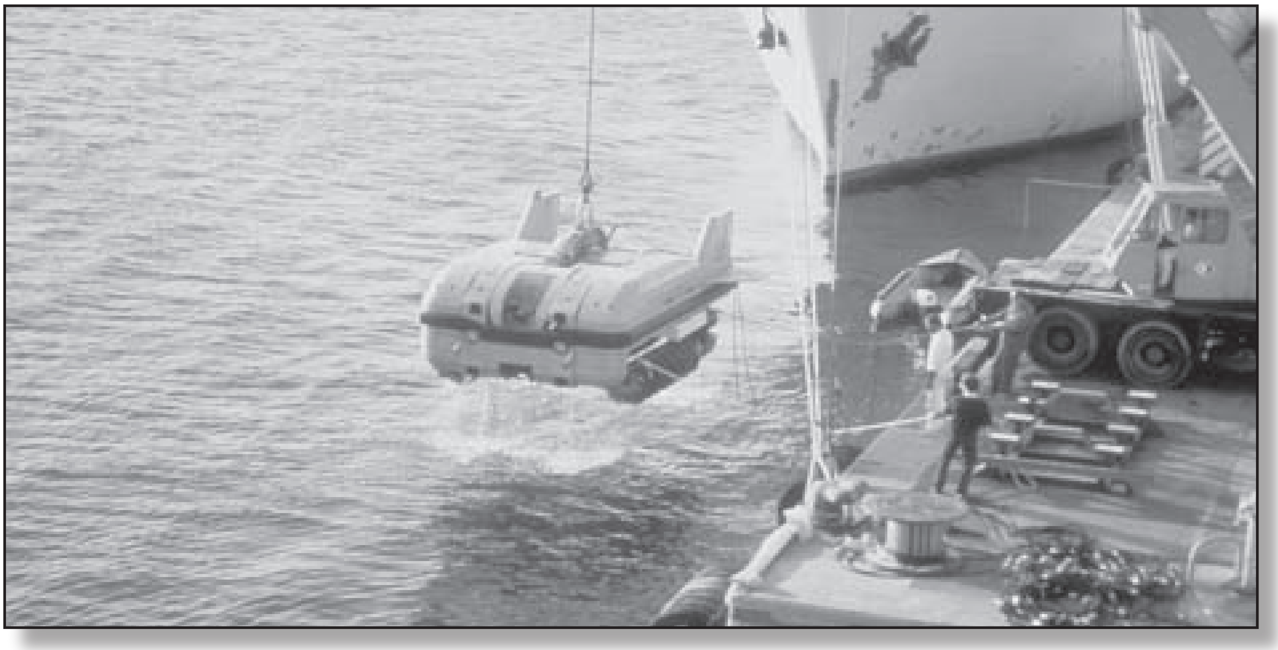


Fig. 8. Photograph of an autonomous sampling device developed by Ifremer for the collection of polymetallic nodules. © Ifremer (See colour appendix 1, p. 128).

of in-depth study of the market for the compounds present in polymetallic nodules. The choice between nickel-bearing laterites and nodules could be made sooner than anticipated, by taking into consideration the manganese component. Some governments, for example in Japan, China, Korea and India, continue to support research and development of a technology for operating in the deep ocean that will be applicable to the exploitation of nodule deposits, in order to give to their industry the possibility of such a choice.

An investigation by the study group for the development of means necessary for the exploitation of nodules ('Groupement d'Etude pour la mise au point des MOyens nécessaires à l'exploitation des NODules' or GEMONOD, which comprises the CEA and Ifremer) shows that nodule exploitation is economically comparable with that of terrestrial mineral deposits that contain the same metals. Nevertheless, the "nodule" project is undoubtedly innovative and involves a technological risk, which should attenuate at a level economically comparable to that of other risks, and in particular political ones, which would remain in the countries where the lateritic deposits are found.

In conclusion, commencement of exploitation will start when the economic conditions allow. In the meantime, new technologies of exploration and exploitation will have been conceived, and it is by means of these and the development of our knowledge of the ecosystems of the nodule deposits that strategies of conservation and exploitation will have to be formulated.

2.5. DEFINITION OF THE 'NODULE-FACIES'

Most of the studies concerning concretions refer to classifications based principally on their morphological and geochemical characteristics (Meyer, 1973; Halbach & Özkara, 1979b; Saguez, 1985). The great variability of conditions in the geological environment (topography, erosion by deep ocean currents and the model of regional deposition) has lead to differentiation of nodule beds and the recognition of 'nodule-facies'. The classification by AFERNOD (Hein & Voisset, 1978) was based on a photographic study of the ocean depths associated with samples and morphological and geochemical measurements of the types of facies. However, as seen in photographs, these facies were established by geologists to facilitate mining prospection and are not based on origin or nodule composition, but on population, size, morphology and environmental conditions. These latter parameters are suitable for ecologists in their studies of the substrata on which the fauna subsists. A subjective classification of eight nodule-facies made during the study of photographic transects covered by towed and autonomous devices and the 'Nautile' appears to be well adapted to the regional scale. These eight different nodule-facies are described as follows:

- Nodule-facies C is composed of large nodules (6-15 cm diameter or sometimes more), sunk well into the surface sediments if not completely (60-100 %), hummocky on the surface and heterogeneous (sometimes granular) and elliptical (figures 11, 13). An equatorial thickening can easily be seen because of the distribution of sediment which partially covers the nodule. It is generally set deep in the surface sediments and fracture fissures are often readily seen. Attached organisms are frequent. The superficial texture is smooth to rough and the dominant structure is botryoidal. The nodules are never coherent. The concentration diminishes (2 to 10 kg/m^2) with increasing nodule size. They cover only 15 to 20 % of the ocean floor and their abundance is limited to 8 kg/m^2. The higher values found in some samples can be explained by the complete burial of some of the nodules. The factor of slope > 15 % has been studied on nodule-facies C 30 %. These nodules are always present in the southern part of the AFERNOD zone but further north coexist with nodule-facies B. The underlying silts are less clayey and richer in radiolarians. They have a high water content and very weak cohesion for the first few centimetres, forming a semi-liquid layer. These nodules are rich in manganese (30 %, with a ratio to iron of 6), nickel (1.4 %) and copper (1.2 %). The concentric layers of hydroxides of manganese are well crystallised.

- Nodule-facies Cp is a variant of C with a granular surface.

- Nodule-facies C+ has slightly smaller nodules (7.5 cm diameter), less sunken into the silt (30-60 %), homogeneous in size, with a hummocky surface, a predominantly mottled-dendritic internal structure and found at concentrations of 8 to 20 kg/m^2. The superficial texture is smooth to rough and nodules are not coherent.

- Nodule-facies C+m (m = mixed) is a variant of nodule-facies C, composed of nodules with the same degree of burial and the same mean diameter but they are more heterogeneous in size and present at greater density on the ocean floor.

- Nodule-facies B is composed of isolated nodules (never coherent) that are ovoid and flattened with a scarcely developed equatorial thickening (figure 10). Their diameter varies from 4 to 7 cm and their concentration from 5 to 20 kg/m^2. Their surface is hummocky and rough except at the summit where it is smooth or sometimes granular. Some of these nodules are apparently fragments of older nodules, a clear sign of displacement after fragmentation, while others show lines of fragmentation. The degree of burial is 30 to 60 %. These nodules are the most important economically as they have high levels of manganese (29 %, with a ratio to iron of 5), nickel (1-4 %) and copper (1-4 %), and low levels of iron and cobalt. The hydroxides are well crystallised and the structure is speckled-dendritic. The concentric layers are thicker and more regular, and formed of well crystallised hydroxides with micro-tunnels (10A°-manganate, buserite, todorokite). These nodules form vast beds lying on the sediment, with a coverage of 30 to 50 % and concentration greater than 10 kg/m^2. They are found in the northern part of the AFERNOD zone and are associated with clayey radiolarian silts.

- Nodule-facies B′ is a variant of facies B. It differs by having nodules with a smoother surface, a mean diameter less than 3 to 4 cm and a scarcely differentiated equatorial rim. This nodule-facies is characterised by the presence of a significant quantity of cohering nodules of identical fragility to those of nodule-facies A.

- Nodule-facies BP consists of flattened ovoid nodules, very frequently cohering and 2.5 to 4 cm in diameter. Their concentration varies from 4 to 10 kg/m^2. Polynodules and ancient fragments are very frequent. The surface appears smooth, their degree of burial is from 0 to 30 %, and their structure is porous, microgranular on the upper and lower surfaces, and finely concentrically laminar in the interior. The kernel is sometimes a fragment of an older nodule. These nodules are generally close to rock outcrops.

- Nodule-facies A groups together very numerous small nodules (3 to 6 kg/m^2) with smooth surfaces that are 20 to 30 mm in diameter and irregular, often multilobed, in shape (figure 9). Polynodules and older fragments are frequent, and they rest on the sediment, scarcely buried. They border encrustations, plates (EP) and rock outcrops, covering about 50 % of the substratum in large homogeneous deposits, sometimes in facies mixed with larger nodules or plates (figure 14). In origin, the kernel is volcanic or sedimentary with a high level of silica. Geologists have suggested that they have been disturbed during their growth by environmental changes such volcanic events, more or less associated with weak tectonic movements, changes in the pattern of currents, depositional disturbances at the base of cliffs, and falls of particles or even blocks. These nodules are relatively rich in iron (9-10 %) and cobalt, with a ratio of manganese-iron of 2.5, and relatively poor in nickel and copper. The layers of hydroxides are irregular and poorly crystallised and their structure is finely and concentrically laminar. These are the nodules principally associated with red clay formations in the northern part of the Clarion-Clipperton fracture zone. They are sometimes orientated in bands marking outcrops of harder sediments.

In the Clarion-Clipperton fracture zone, nodules are generally flattened because their growth is greatest in a horizontal plane (cruise NIXONAUT-GEMONOD, 1988), and they are not all of the same age. The aging of unstable hydroxides is accompanied by an increase in their crystallization. Fissures running across the nodules are filled with clayey sediments. Some fissures cause autofragmentation and the fragments then grow themselves. The oldest nodules contain kernels of ancient fragments (nodule-facies BP and A), dating from the lower Miocene (Saguez, 1985).

Two other nodule-facies are seen, EP, with plates and encrustations, and O, without visible nodules :

- Nodule-facies EP is formed of encrustations and plates of irregular shape, associated or not with angular plates 5 to 15+ cm across (figure 16). Nodules are sometimes present, generally of type A, sometimes B, but never C. Sediment can partially cover the plates. Sometimes large blocks of stratified sediment or blocks of pillow rock, which are outcrops of basaltic lava, occur close to outcrops of hard sediments. In the AFERNOD zone, this facies is only found close to uneven topography. Encrustations appear frequently towards the upper edge of cliffs, forming a more or less continuous level, following abundant nodules of facies B or A. Geologists sometimes interpret this as a distinct stratigraphic level underlying the nodule-bearing sediment. They are seen also on small terraces which mark the upper levels of cliffs composed of scarcely hardened beige silts that contain carbonates from coccoliths and discoasters, stratified into banks 0.2 to 1 m. The plates, blocks and debris of irregular shape are found at the base of escarpments in continuity with zones called facies "zero". Some of these blocks preserve the stratification visible in the cliffs and have evidently fallen from them. Fissures can be seen, 0.5 to 1 m wide and several tens of metres long at the summit of the cliffs and several metres back from the edge, corresponding to sections in the course of becoming detached. It is also at the base of escarpments that outcrops of cushion basalt are found.

- Nodule-facies O has no nodules at the surface nor any plates or encrustations (figure 12). It is possible that these are completely buried and that this facies is an ultimate form of nodule-facies C completely covered over. That is not the case for facies O at the foot of cliffs, steps and escarpments (figure 15). The substratum is composed either of ancient sediments (Oligocene to Miocene) or more recent sediments (Plio-Quaternary). During the NIXONAUT cruise, this facies was found in three places:

- in a band several tens of metres wide between deposits of nodule-facies B or C and at the base of escarpments,

- close to hard outcrops of carbonated silts which form small steps,

- in vast deposits situated in low regions (valleys) where they appear as grey features in images obtained by the lateral towed sonar (SAR) close to the ocean floor.

In this study, video and photographic transects were analysed over the following nodule-facies: A30 %, C5 %, C10 %, C15 %, C20 %, C30 %, C40 %, B40 %, B50 %, BP35 %, BP50 %, O old sediments, O recent sediments.

The current classification established by Hoffert & Saget (2004) reorganised the eight nodule-facies into five principal nodule-facies (table 1). This classification simplifies the description of the nodules and puts it in line with those proposed by other consortia. It is based on the simple observation of polymetallic nodules.

Caractéristiques		Faciès 0	Faciès Encroûtement et plaques (EP)	Faciès A	Faciès B	Faciès C
Morphologie						
Morphologie régulière	Sphère			++		
	Ellipse				++	+++
	Disque				+	
Morphologie irrégulière	Polylobé			caractéristique	+	
	Plaques		caractéristique			
	Fragment de Nodules				fréquent	+
	Quelconque				possible	
Taille	> 15cm Très gros nodules		+			++
	10 à 15 cm Gros nodules		+++		+	+++
	5 à 10 cm Taille moyenne		+	++	+++	+
	2,5 à 5 cm Petits nodules			+++	+	+
	< 2,5 cm Très petits nodules			++		
Aspect de la face supérieure						
	Lisse			+++	++	++
	Granulaire				+	++
	Botryoïdal (mamelonné)					+++
Aspect de la surface extérieure						
Ceinture équatoriale				Non	rare	+++
Indications de tendance à la fracturation				Non	+++	+++
Degré d'enfouissement			Nul ou faible	faible	faible	+++
Sédiment posé sur une partie de la face supérieure			+	Non	+	+++
Organismes fixés				+	observable	+++
Remarques		Parfois sédiment induré	Possibilité de traces de volcanisme			

Tableau. 1. Summary of the 5 types of nodule-facies based on visual observations and photographs of the seabed (Hoffert & Saget, 2004). © Ifremer

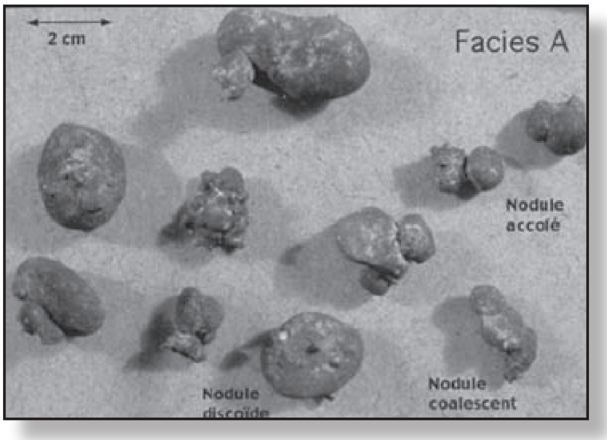


Fig. 9. Photograph of nodule-facies A, with small irregular nodules (Hoffert & Saget, 2004). © Ifremer

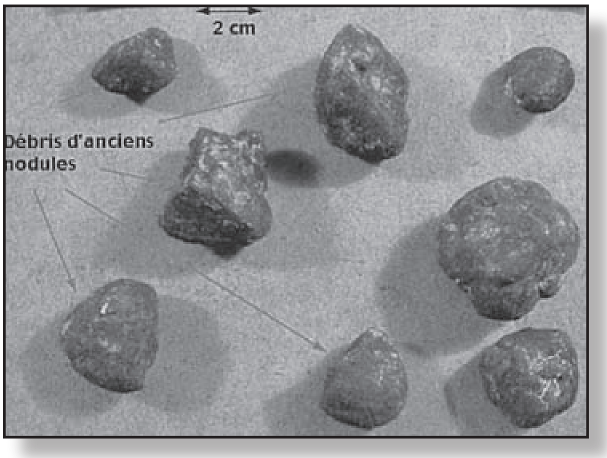


Fig. 10. Photograph of nodule -facies B, regularly shaped nodules with numerous pieces of debris from old nodules (Hoffert & Saget, 2004). © Ifremer

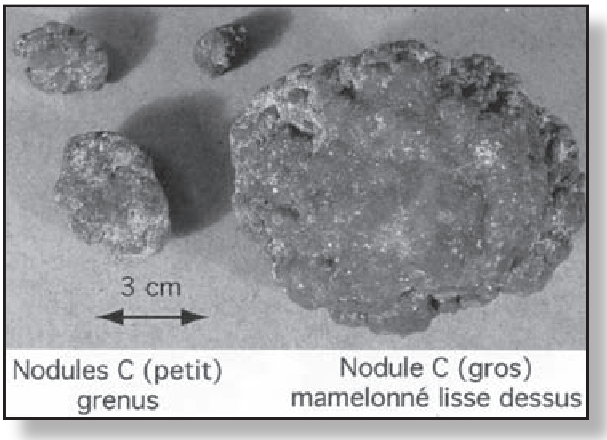


Fig. 11. Photograph of nodule -facies C, hummocky nodules with an equatorial thickening (Hoffert & Saget, 2004). © Ifremer

Fig. 12. Photograph of nodule -facies O seen from the 'Nautile' during the NIXONAUT cruise. © Ifremer

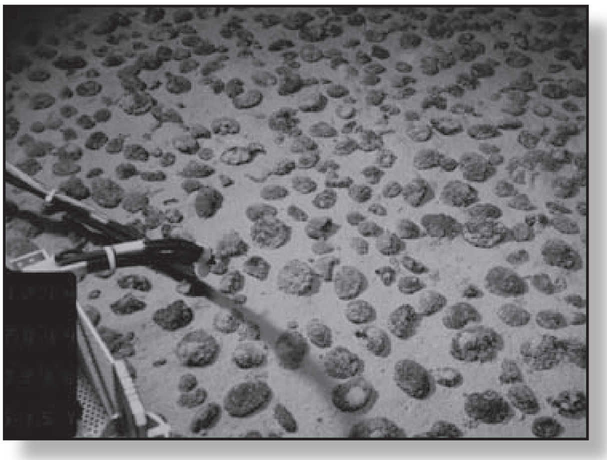


Fig. 13. Photograph of nodule -facies C seen from the 'Nautile' during the NIXONAUT cruise. © Ifremer (See colour appendix 1, p. 130).

Fig. 14. Photograph of nodule -facies B and C mixed, seen from the 'Nautile' during the NIXONAUT cruise. © Ifremer

Fig. 15. Photograph of steps in an outcrop of hardened carbonaceous silt, seen from the 'Nautile' during the NIXONAUT cruise, (PL 15). © Ifremer (See colour appendix 1, p. 130).

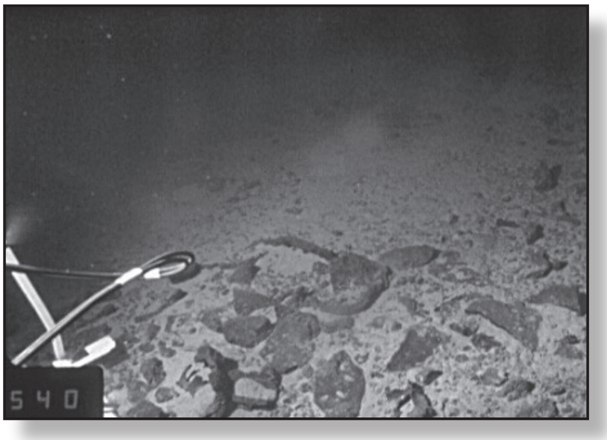


Fig. 16. Photograph of nodule -facies A, associated with small plates (facies-EP), NIXONAUT cruise, zone 48, (PL 15). © Ifremer

2.6 THE NIXO 45 SITE

From 1979 onwards, the deployment of the multibeam sounder (Seabeam) and systems of continuous photography of the ocean floor ('Épaulard', 'R.A.I.E.') enabled a more precise study of relationships between relief and the distribution of nodules and sediments. From the perspective of testing dredging systems, the NIXO 45 site was selected for its relatively flat topography and its richness of polymetallic nodules. This site extends for 360 km^2 between the Clarion fracture to the north and the Clipperton fracture to the south (130°00'W/130°10'W, 13°56'N/14°08'N) in a region of abyssal hills, whose substratum can be dated from about 40 Ma (Herron, 1972).

Structural and morphological features

Du Castel (1985) presented the geological setting of the NIXO 45 area in the first geological map at 1/20 000, describing morphological features such as basins, valleys, hills and plateaux, and within which the various nodule-facies are distributed (figure 17). Large morphological features of the region are a central depression of maximum depth 5 150 m, bordered by two hills to the west and east, which rise to a depth of about 4750 m. Numerous tectonic events define the minor structures such as plateaux, hills and secondary valleys. The whole morphological structure has a principal north-south orientation, parallel to the ancient axis of accretion. Although the major part of the relief is undulating, there are flatter areas known as "plateaux" (du Castel, 1985), whose origin is uncertain but could be structural (due to variation in the rate of accretion or large out-flowings on the flanks of the ridges). Their origin could also be dynamic, due to the abrasion of contours and accumulation of sediments. This latter explanation supposes the existence of significant deep ocean currents during the geological history of this region.

Escarpments are relatively numerous and play an active part in the geomorphological landscape of the NIXO 45 site. They are generally cut into more or less regular successive steps with subvertical walls. The analysis of photographic data shows that these undulations are very largely still active. This suggests the existence of tectonic readjustments, closely linked to plate movements, which involve the formation of slopes and cones of scree. The most marked slopes are observed on the sides of hills. They rarely exceed 7° though can reach 15° locally.

In 1986, use of the bathymetric multibeam sounder 'Seabeam' and high resolution lateral sonar 'SAR' (Système Acoustique Remorqué or towed acoustic system), coupled with sonar profiles at 3.5 kHz and cores from superficial sediments, enabled precise understanding of the geological environment in the nodule area. In addition, 'SAR' was able to detect the effects of tectonic activity and recent erosion by the existence of outcrops of the basaltic platform, eroded by the deep ocean currents, and the thickening of the sedimentary series which, with the presence of drag folds, suggested the refaulting of the platform (Le Suavé *et al.*, 1987). In 1988, during the NIXONAUT cruise, the 'Nautile' enabled the exploration of this area in particular and the *in situ* verification of the distribution of nodules, sediments and submarine relief. Similarly, the geotechnical characteristics of the sediments were evaluated in advance of having to support the collection devices, as well as carrying out tests of crushing and nodule collection. The analysis of samples and films enabled the geological history of the region to be clarified.

Although the present-day morphology has been fashioned by tectonic and major paleo-oceanographic events, detailed topography owes more to quaternary climatic events. New hypotheses (Hoffert *et al.*, 1992) redefine the sedimentary environment which has embedded the nodules and show the determining role of the Plio-Quaternary period in their distribution and in their morphological, chemical and mineralogical modification. The present distribution of nodules would thus be the consequence of the dynamics of deep ocean currents due to climatic variations in the Quaternary. According to this hypothesis, the sight of nodule deposits on the seabed is due entirely to the existence of present-day erosion (less than 210 000 years) which once interrupted, causes rapid nodule burial. Lonsdale & Southard (1974) also showed that in identical conditions nodule-bearing sediments are more sensitive to erosion created by lower current speeds than are sediments without nodules.

The superficial layer of sediments

The sedimentary coverage outcropping in the NIXO 45 region consists of deposits from the middle Oligocene (30 Ma) to the present (figure 18). The oldest sediments (pre-Miocene) were deposited above the CCD in the form of calcareous silts formed of coccoliths. One study referring more precisely to the NIXO 45 area (Ricou, 1990) defines the "Bedded Series based on acoustic characters which express considerable stratification. These deeper sediments outcrop at cliffs dissected by fracturing and landslides.

The upper formation is discordant with the underlying "Bedded Series". Laying below the CCD, it is formed of clay and siliceous sediments. This sedimentation dates from the end of the Miocene to the present. Its acoustic characteristics designates it as "Transparent Series" (Piper *et al.*, 1979). Two facies, "red clays" and "contemporary siliceous silts" can be distinguished. The second constitutes almost all of it and contains deposits of iron oxyhydroxide and zeolites. The "siliceous silt" facies outcrops over almost the whole of the NIXO 45 site and forms the substratum on which

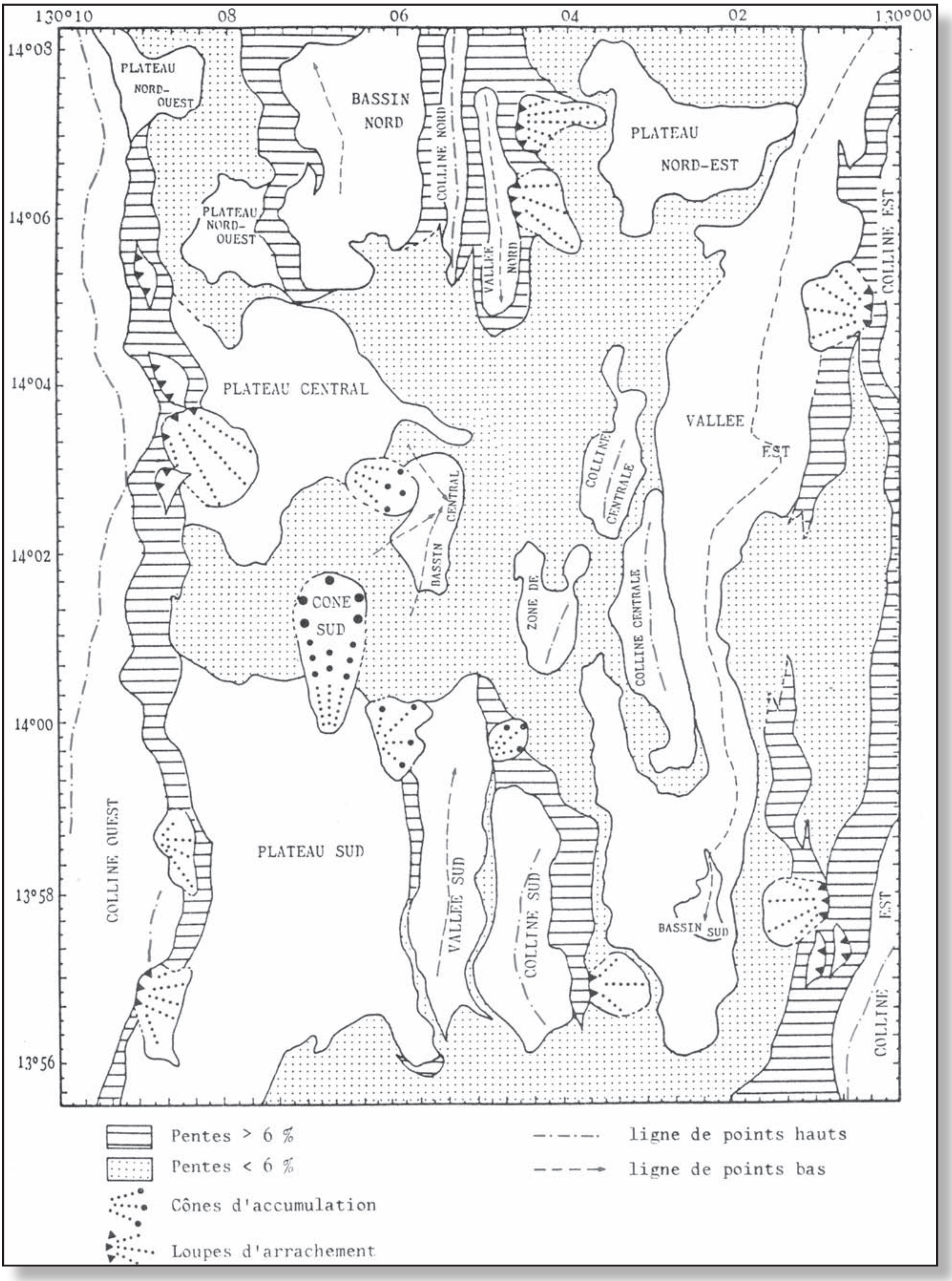


Fig. 17. Map of the major morphological structures found on the NIXO 45 site (du Castel, 1985).

the nodules grow. It only forms a superficial covering, a few metres thick and consists of animals from the recent Quaternary, almost always in association with older fauna. The model for deposition of contemporary sediments in the region of NIXO 45 involves disturbance by deep ocean currents, whose speed does not exceed 17 cm/s and which are associated with water of Antarctic origin. They carry sediment particles for a thickness of about 400 m, in cold water rich in oxygen. This site forms part of the northern border of the zone of high planktonic productivity of the equatorial Pacific Ocean. The phenomenon of particle settling or pelagic sedimentation is predominantly at these great depths.

The mechanical resistance of the ocean floor at the NIXO 45 site has been estimated from cores of recent clayey silt and analysis by a field vane tester (NIXONAUT-GEMONOD cruise, 1988). The cohesion is weak for recent silt; it rises from 1-2 kPa in the interface layer to 3-5 kPa at several tens of centimetres depth. In contrast, it is clearly stronger in older floor, reaching 20-80 kPa.

Distribution of the nodule-facies

The work of du Castel (1985) demonstrated transitions in facies within the NIXO 45 site and well marked relationships with the regional environment (figure 19). The probability of lateral movement from one nodule-facies to another was calculated by a Markov analysis, which gave high values for transition between nodule-facies EP, BP and A, indicating the possible development of nodule-facies BP into A. High values of transition between nodule-facies C and O might indicate growth of these nodules in the sediment (du Castel, 1985). Frequently at NIXO 45, progressive passage between the following pairs of nodule-facies has been noted: B and BP, B and C+, C+ and O. In contrast, sharp transitions have been observed between C+ and Cp, B and BP, and BP and areas of outcropping EP.

Taken together, the geological observations made at NIXO 45 have allowed the precise description of the distribution of nodule-facies, as well as establishing the principal correlations between the geological data (from cores and photographs) and the geophysics of the beds of superficial sediments in the region (Hein & Voisset, 1978; du Castel, 1985; Saguez, 1985).

The principal correlations that have been established are:

- Polymetallic nodules are preferentially associated with radiolarian silt belonging in part to the recent Quaternary.

- The influence of topography is seen by the lack of surface nodules in the central part of the NIXO 45 region, where there is an increase in depth (> 5 000 m) and ancient deposits dating from the lower Quaternary to the Oligocene. A thickening of the sedimentary coverage on top of the series could be the cause of the concealment of the nodules.

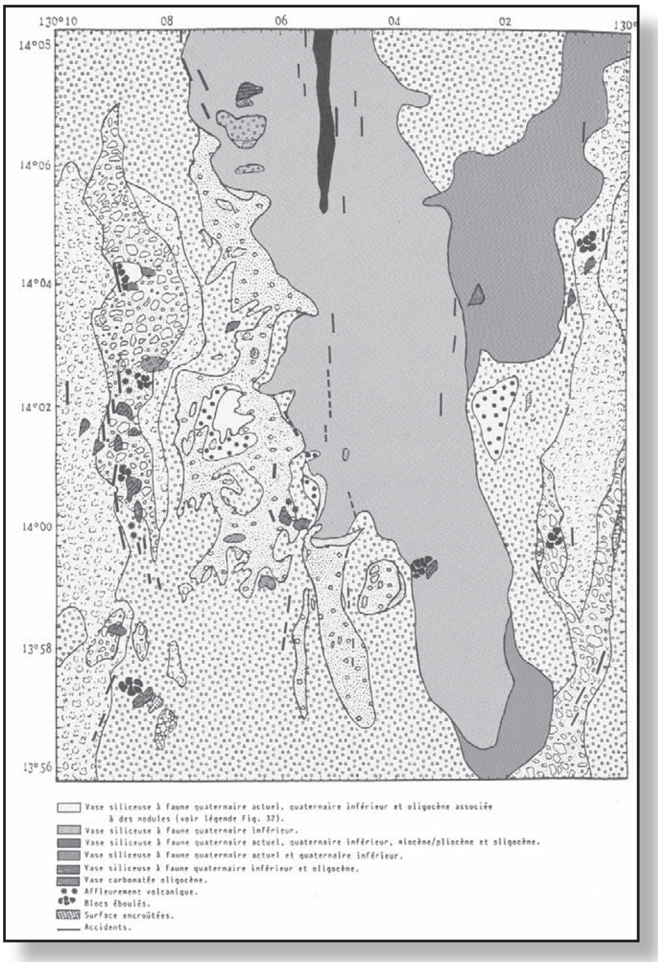


Fig. 18. Map of the superficial sediments in the NIXO 45 site (du Castel, 1985).

- The development of channels without nodules (fissures), several hundreds of metres long and some tens of metres wide, in valley bottoms, which according to Hoffert *et al.* (1992), correspond to the thickening of recent sedimentary deposits. These date from the Pliocene, according to cores taken during the NIXONAUT cruise in 1988. The presence of these channels correlates with beds of large, rich and abundant nodules. The channels are known as “grey features” because of their weak reflectivity (transparent facies) in sonar images. The well-defined edges of these “grey features” consist of very recent Quaternary sediments (less than 210 000 years, fide Hoffert *et al.*, 1992) associated with nodules. According to these authors, the grey marks are the consequence of acceleration by masses of deep ocean water during the Plio-Quaternary and may now be covered by a current that is sufficiently strong to prevent the deposition of sediment particles.

- On steep slopes nodules are generally smaller or absent (nodule-facies BP).

- Areas of unstable terrain (15-20 %) due to gravitational landslides do not allow the retention of nodules at the water-sediment interface.

- The development of nodules could take place within sedimentary layers, by dendritic growth.

The geographic distribution of nodules, whether at the scale of the NIXO 45 site (Hein & Voisset, 1978) or the Pacific Ocean (Halbach, 1980), suggests that the physico-chemical and biological mechanisms that are responsible for the genesis and growth of polymetallic nodules are not stable, either in space or time. The geochemical characteristics of nodules reflect variation in content and supply of oceanic minerals during the course of their growth. These relationships change very rapidly and can be linked to geological events that are considered instantaneous (such as volcanic eruptions) or ultra-rapid (climatic fluctuations). Organisms have played an essential role in the development of nodules. Some, such as thuramminids and other Foraminifera, are systematically associated with nodules (Saguez, 1985), while possible relationships exist between chemical and biological activity around some concretions are not yet well established.

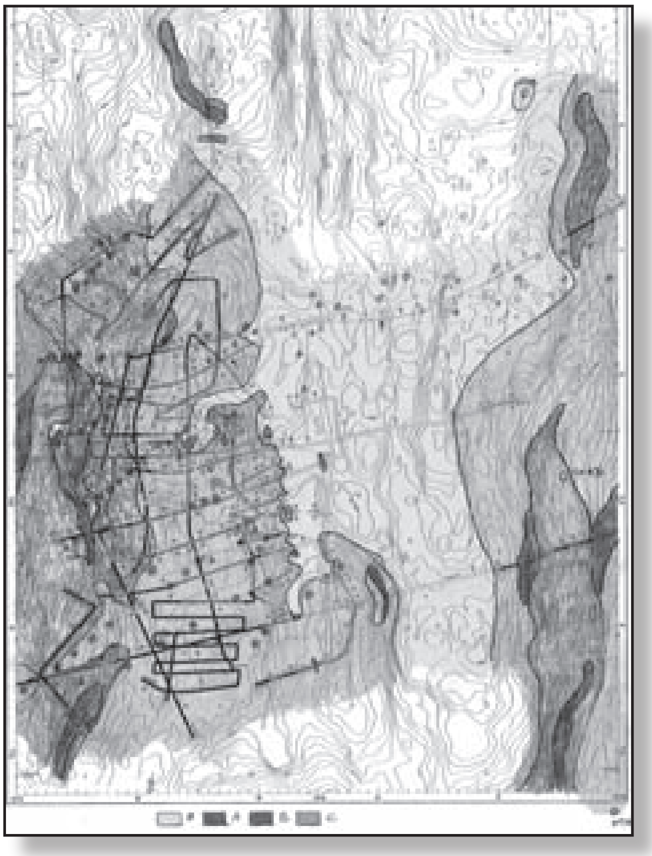


Fig. 19. Map of the distribution of the principal nodule-facies with the location of transects of the 'Épaulard' and 'R.A.I.E.' in the NIXO 45 site (Saget pers. comm., 2004).

3. Materials and Methods

3.1. METHODS OF OBSERVATION

Towed devices

The **'R.A.I.E.'** (Remorquage Abyssal d'Instruments pour l'Exploration) was developed for Ifremer to investigate polymetallic deposits on the seabed (figures 20 and 21). This device, weighing 2300 kg, can dispense with ballast. Its metal frame 4.6 x 1.2 x 1.2 m carries photographic equipment consisting of two Benthos 377 cameras (28 mm and 16 mm) which are able to take 3 800 shots and a Benthos 387 flash (4 lights of 1500 J). It is also equipped with 40 Ah batteries, an acoustic Benthos altimeter (frequency 100 kHz, resolution 0.1 m), a depthmeter (teledyne Taber T 2000 with precision of 20 m and resolution of 0.1 m), a magnetic recorder (Sea Data 610 with capacity 11 Mbits), a high resolution temperature probe and a real-time vertical positioner (Pinger Suber). The angle of view is subvertical, inclined at 10°, to avoid recording the ballast in the photographic field. It has a maximum tow speed of 1.5 knots, maximum immersion of 6 000 m and a range of 32 to 60 hours.

The swimming altitude of the 'R.A.I.E." in relation to the ocean floor is controlled in real time from the surface, by means of the reception of emissions from the pinger. For an altitude of 3 m, for example, the surface that is photographed is 7 m^2. The interval between shots in the version of 'R.A.I.E.' used in the nodule zones is of 16 seconds.

Close to 76 200 photographs, relating to a total distance of 1 447 km, were taken by the 'R.A..I.E.' in the NIXO 45 zone. These photographs form the major part of the visual data from the ocean floor which were used in the present study.

The **'Deep Tow Instrumentation System'**, developed for the Scripps Institute of oceanography in the USA, is a metal chassis towed near the seabed, equipped with a 35 mm video camera and two Benthos cameras with 50 mm (wide angle) and 70 mm (telephoto) objective lenses (figures 22 and 23). It also has equipment for collecting biological samples (nets) and water samples, flashes, a lateral sonar, a depthmeter, a magnetic recorder and acoustic altimeter, a temperature probe and a vertical positioning system (Spiess & Lonsdale, 1982). During the ECHO I cruise in June 1983, the height of the camera above the floor was 10 m. As this was often too high for the recognition of the fauna, the 70 mm telephoto objective was used to reveal greater detail. Figure 23 represents the route of 'Deep Tow' during this cruise and the localities of the photographic transects and cores. During the ECHO I expedition 'Deep Tow' made 11 photographic transects and collected about 5 500 photographs of the ocean floor which were analysed in this present study.

A **'troika'** is a towed submarine suprabenthic camera sleigh, 2.5 x 1 x 1.6 m, developed by commander J.Y. Cousteau (figure 24). This device is equipped with two Benthos 372 cameras, a Hydroproducts SDA video camera, an Edgerton 382 flash, and a 200 W spotlight. The towing speed is 3 knots in calm water and 1 knot in turbid water. The area covered by photographs is from 1 to 2.5 m^2 and the definition allows identification of objects greater than 5 cm. This system was used at sites A and B of the COPANO cruise in 1979 (Pautot & Hoffert, 1984) in the Clarion-Clipperton fracture zone (site A: 132°44'W-16°34'N; site B: 133°20'W-14°30'N). The interval between shots was 6 seconds.

A total of 2 400 photographs taken by a ‘troika’ at these two sites were analysed in this study. Figure 25 depicts an exceptional photograph of a swimming holothurian *Peniagone leander*.

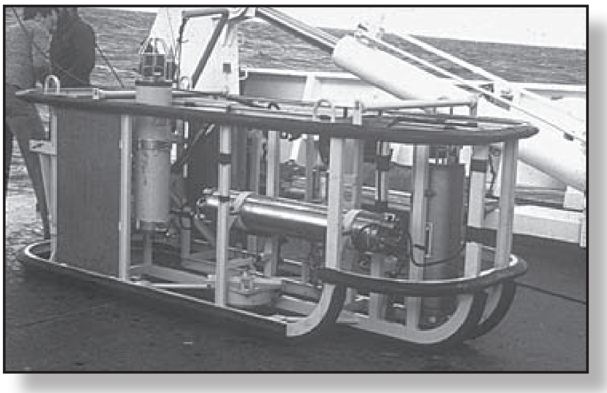


Fig. 20. Photograph of the towed device ‘R.A.I.E’ (Remorquage Abyssal d’Instruments pour l’Exploration). © Ifremer

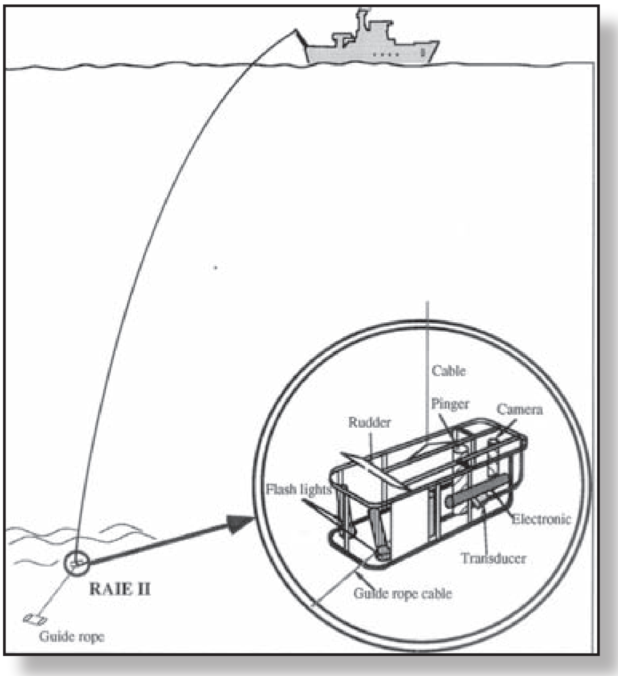


Fig. 21. Diagram of the of the towed device ‘R.A.I.E’. © Ifremer

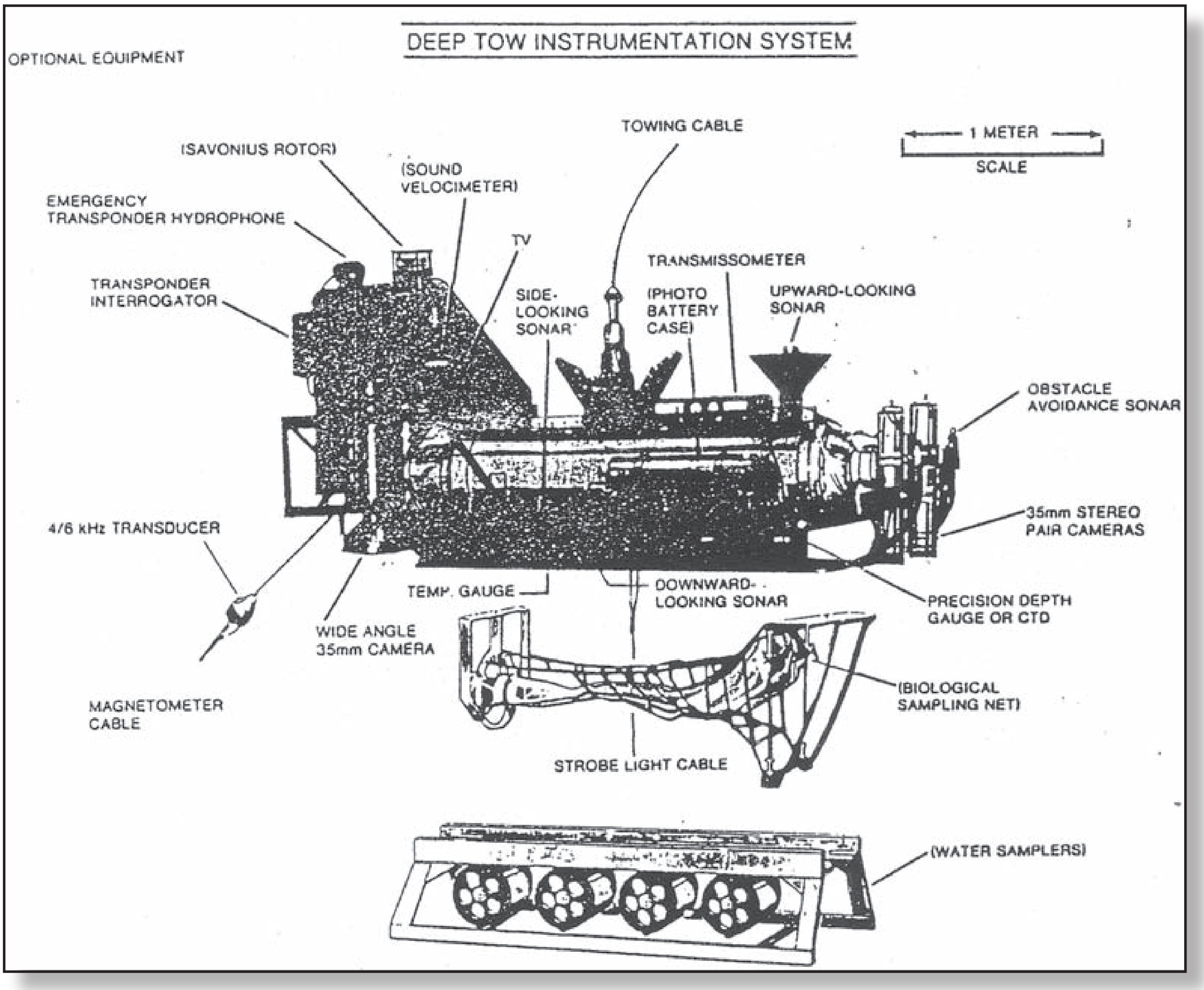


Fig. 22. Diagram of the ‘Deep Tow Instrumentation System’ used during the ECHO I cruise. © Ifremer

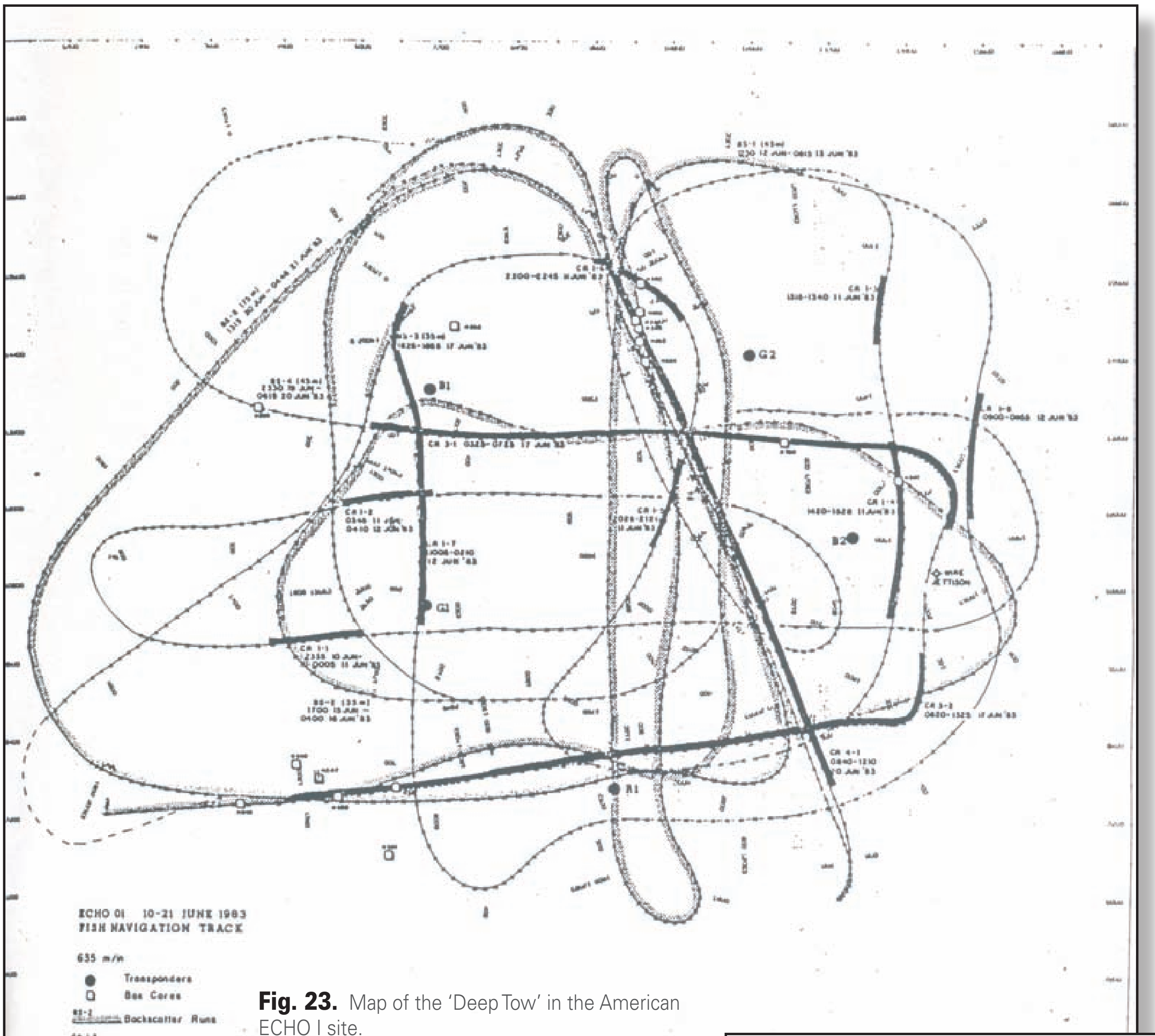


Fig. 23. Map of the 'Deep Tow' in the American ECHO I site.

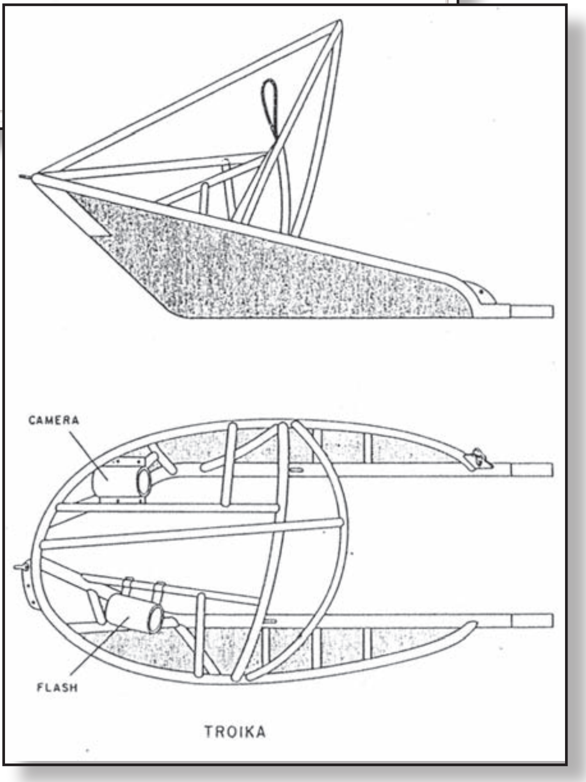


Fig. 24. Diagram of the towed supra-benthic camera sleigh or 'troika'.

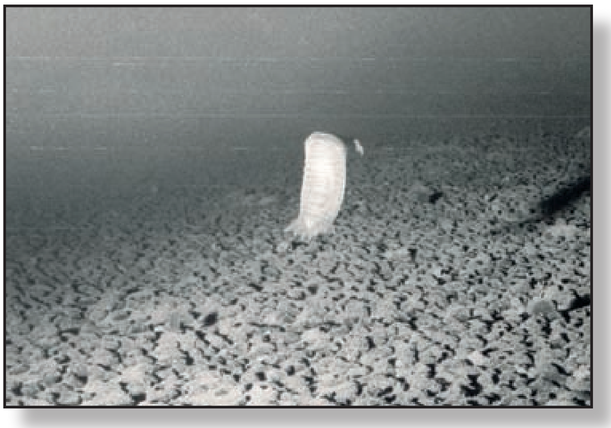


Fig. 25. Photograph of a holothurian swimming over a bed of nodules taken by a 'troika'. © Ifremer

Remote controlled devices

The free sampler 'ED1' (a camera coupled to a sampling device) was conceived by the EGMO company (figure 26). It is equipped with a camera that allows a slightly oblique angle of shot in relation to the vertical, photographing an area of about a square metre. During the first years of prospecting in the nodule zones, this apparatus was used intensively in a very accurate manner (rate of loss close to 1 %). A total of 3 213 stations (or photographs) were taken in the Clarion-Clipperton fracture zone from 1975 onwards and these photographs were examined for this study.

The 'Épaulard' is an autonomous unmanned submersible developed by Ifremer. This submersible is 4 x 2 x 1.1 m and is piloted from the surface by acoustic controls to a depth of 6 000 m (figures 27, 28). It moves at a speed of 1 m per second between 5 and 10 m above the seabed, with a maximum range of 7 hours. Its altitude stays constant due to a guide-rope, and in the case of prospecting in the Pacific Ocean, the 'Épaulard' was maintained at about 5 m from the ocean floor, allowing contiguous fields of view with shots taken at 5 second intervals. This submersible is equipped with a 200 joule flash and a Benthos 377 camera capable of taking 5 000 photographs at a rate of one every 5 to 10 seconds. Figure 31 illustrates the type of photograph that this apparatus can take. In addition, 'Épaulard' possesses a magnetic recorder which gives the time, distance, altitude, depth and temperature, and two echo-sounders, a magnetic compass and an acoustic transducer for sending and receiving. The 'Épaulard' is a valuable tool for detailed work and for providing photographic faunistic data for quantitative analyses.

Figure 29 illustrates the topographic 'Seabeam' chart and the trajectories of the 'Épaulard' and the 'R.A.I.E.', showing details of the different nodule-facies and their populations on the ocean floor. Each photograph covers an area of about 25 m^2 at an elevation of 5 m. Figure 31 shows a photograph taken at an exceptional angle caused by the presence of a cliff, which broke an even course at a fixed elevation. The present study has examined in detail a total of 84 937 photographs taken since 1975 along 227 km of profiles in the Clarion-Clipperton fracture zone.

The 'Nautile' is an autonomous manned submersible, 8 x 2.7 x 3.45 m, developed by Ifremer and the D.T.C.N.. It is capable of descending to 6 000 m and moving at a maximum speed of 2.5 knots with range of 13 hours (figure 30). The 'Nautile' is equipped with two arms, one capable of manipulation and the other of grasping, as well as a panoramic sonar, a TV camera, two photographic cameras, six searchlights (3 000 W) and a sediment sounder. The cameras of the 'Nautile' can be oriented so that they have an oblique view down to the ocean floor, which is useful for faunal identification compared with the vertical shots from the 'Épaulard' and the subvertical ones from the 'R.A.I.E.'. The width of the field of view is estimated to be about 2 m by adapting the Canadian grid perspectives of Wakefield & Genin (1987).

During the NIXONAUT cruise in 1988, the 'Nautile' was able to make 16 dives over the nodule zones, resulting in a total of 55 hours of video footage and 2 090 photographs of the seabed in the Clarion-Clipperton fracture zone that were examined in this study. It is from the 'Nautile', that the first images in colour appeared. Figure 32 shows the localization of the

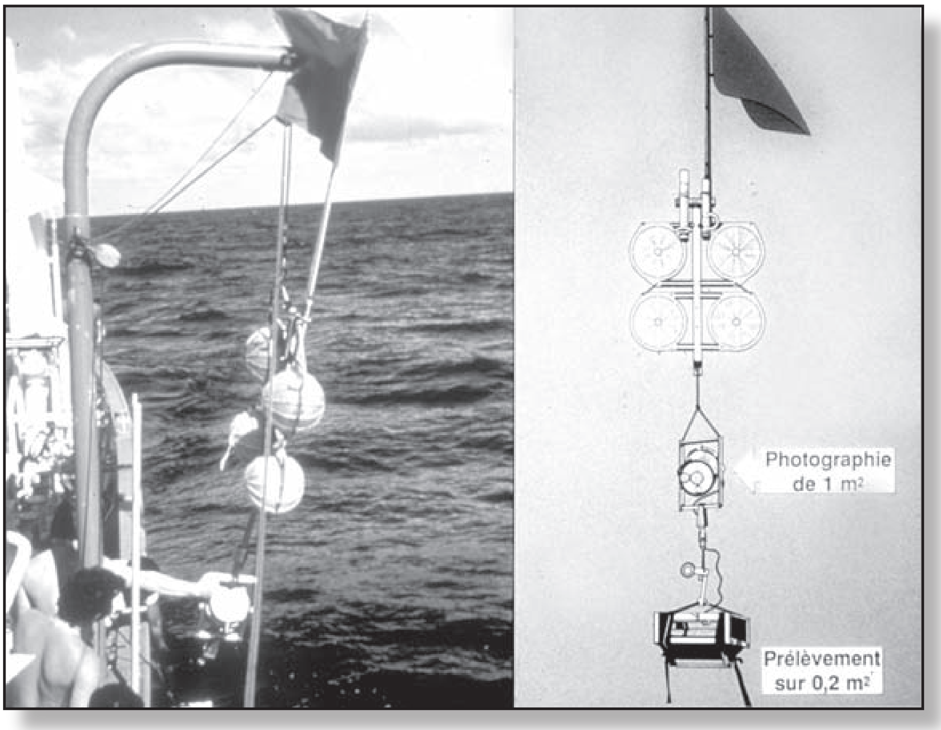


Fig. 26. Diagram and photograph of the remote device 'ED1' (camera coupled to a sampling device). © Ifremer (See colour appendix 1, p. 128).

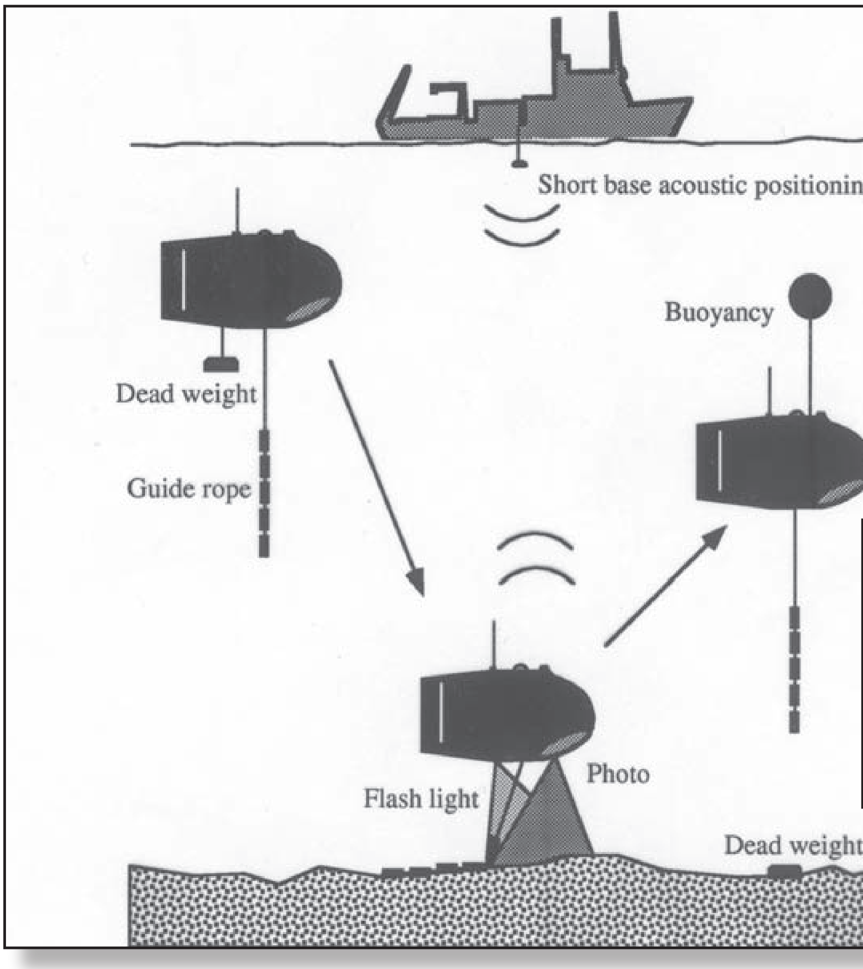


Fig. 27. Diagram of the autonomous submersible the 'Épaulard'. © Ifremer

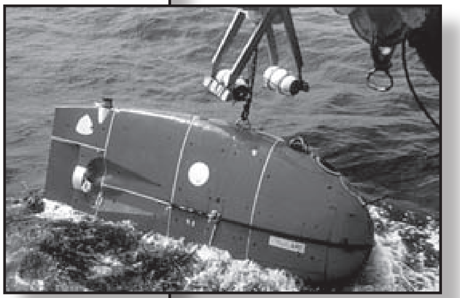


Fig. 28. Photograph of the autonomous submersible the 'Épaulard'. © Ifremer (See colour appendix 1, p. 128).

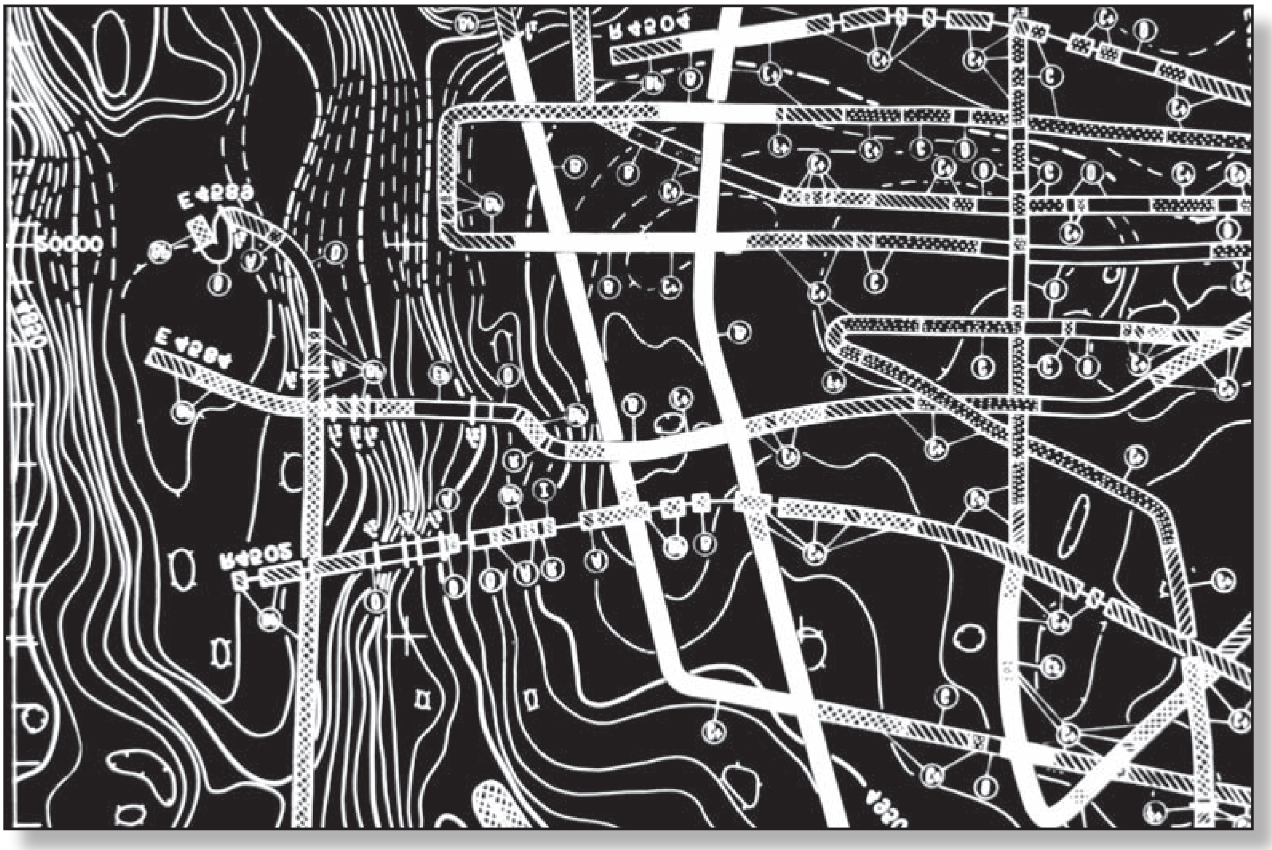


Fig. 29. Seabeam bathymetric map, showing the transects of the 'Épaulard' and 'R.A.I.E.', indicating the various nodule-facies and density of nodules. © Ifremer

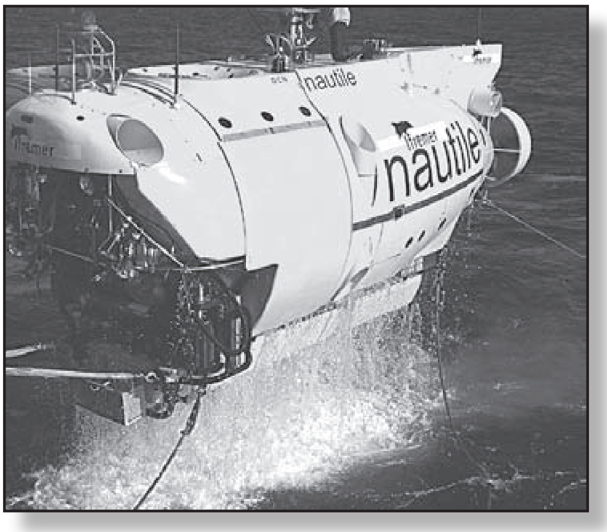


Fig. 30. Photograph of the autonomous manned submersible the 'Nautile'. © Ifremer (See colour appendix 1, p. 128).

Fig. 31. Photograph of a crinoid *Ptilocrinus sp.* on a cliff, taken by the 'Épaulard'. © Ifremer

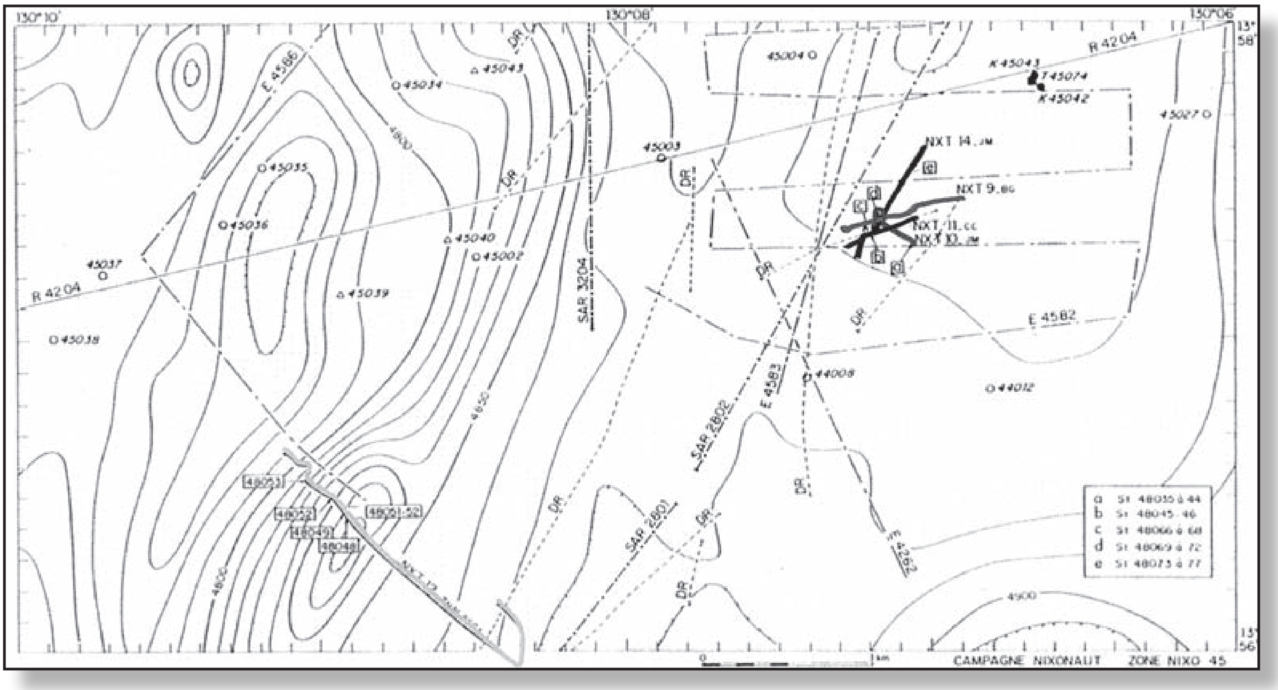


Fig. 32. Locations of dives made by the 'Nautile' during the NIXONAUT cruise. © Ifremer

Fig. 33. Photograph of ophidioid fish and a sponge taken by "the Nautile" during the NIXONAUT cruise. © Ifremer

dives made during this cruise, and figure 33 is a photograph of megafauna on nodule-facies C taken during NIXONAUT cruise.

3.2. Strategies of data analysis

Strategy applied to the qualitative analysis

The faunal organisms observed in the films and photographs were designated as taxa since none of the specimens photographed in this study were collected. Moreover, a taxon is defined as an assemblage of organisms of any taxonomic rank that are sufficiently distinct to merit being assigned to a definite category. Among the different types of arrangement, a synthetic Linnean classification has been adopted for the most recognisable forms. Nevertheless, the problem of equivalence of taxa is judged to be insoluble for the present, in view of the current absence of common criteria between different groups.

For each taxon, a maximum of information was gleaned from a collection of about 200 000 photographs and 55 hours of film for the qualitative analysis. The size, tracks, behaviour and habitats (different substrata) permitted the compilation of an exhaustive database. Comparisons were made with the fauna from the Peruvian Basin in the southern Pacific Ocean, analysed from the German DISCOL cruise (Tilot, 1989), to find possible organisms in common between the two regions (tropical north-eastern and south-eastern Pacific), and thus obtain information on the distribution of taxa which have been collected elsewhere. Films from the oceanographic cruises lead by Ifremer in the Atlantic Ocean, such as Biogas, Cymor, Cyaporc, and Abyplaine, were viewed with a similar objective. Literature describing species collected in the region or close to it, and bearing similarities to the organisms observed, has also been used. Finally this analysis benefited from the help of an international network of taxonomists listed in Appendix 3. They proposed hypotheses of identification based on information from images and the literature. Appendix 2 lists the codes used.

Strategy applied to the quantitative analysis

The three sites which were selected within the Clarion-Clipperton fracture zone for quantitative analysis of suprabenthic assemblages were the French sites NIXO 45 and NIXO 41 (to the south of NIXO 45) and the American site ECHO 1 (to the east of NIXO 45), which is partially within the "Preservational Reference Area" (PRA) (figure 34).

The NIXO 45 site

The NIXO 45 site (130°00'W/130°10'W-13°56'N/14°08'N) was selected for the quantitative analysis of suprabenthic faunal assemblages because it has been particularly well explored and sampled within Ifremer's marine geosciences programmes.

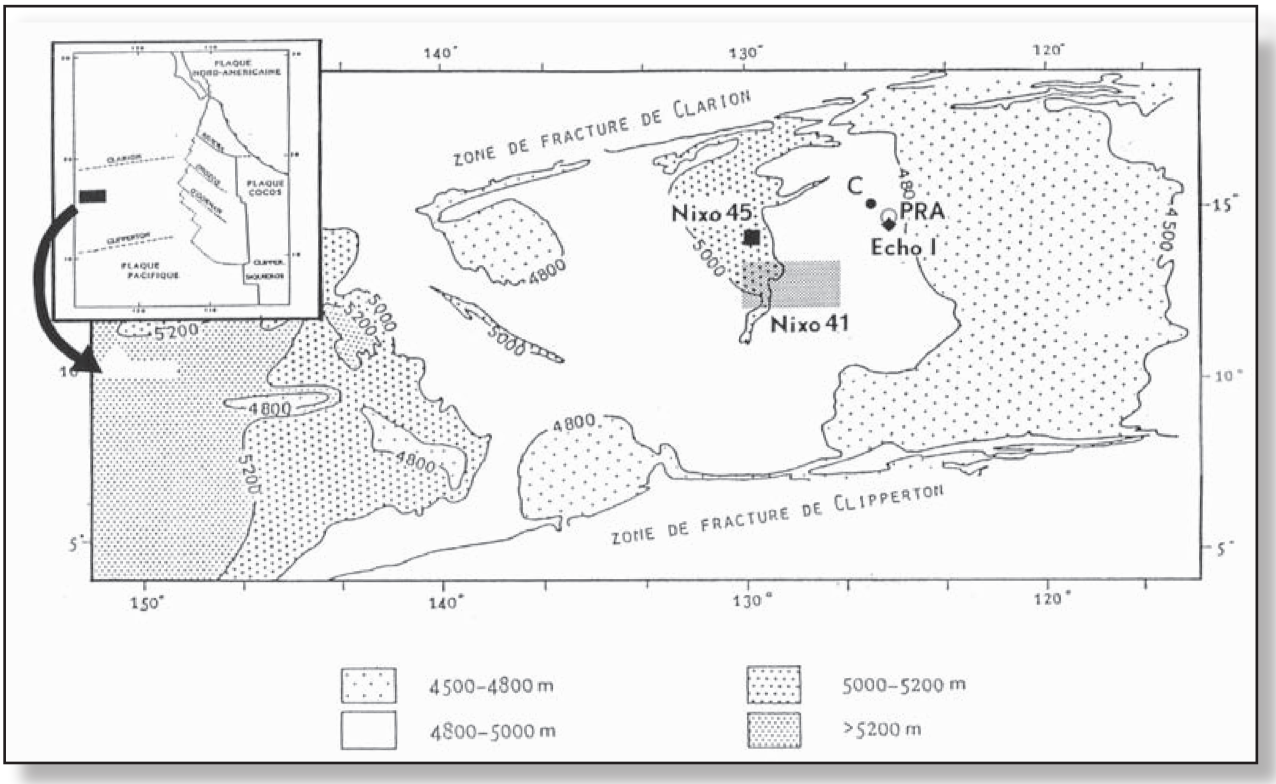


Fig. 34. Bathymetric map showing the location of the 3 sites where fauna was studied quantitatively (Mammerick & Smith, 1981). © Ifremer

Analysis of photographic data from the ‘Épaulard’

A total of 48 100 photographs along 75 km of transects performed by the ‘Epaulard’ and 17 km by the ‘R.A.I.E.’ has been analyzed in this study of the referential state of a nodule ecosystem in the CCFZ. The photographic areas representative of each nodule-facies were selected along the route of the ‘Épaulard’ by reference to the morphological structure of the NIXO 45 site (figure 17) and the distribution of different facies of nodules and sediments (figures 18 and 19). Selection was made in such a way as to equalize the respective areas of the various nodule-facies, to avoid bias towards certain microfacies. Segments that were as dispersed as possible within the same facies were chosen in order to demonstrate the true heterogeneity of the area. To account for the influence of environmental factors on the fauna, the effects of slope (> 15 %) and nodule coverage (2 % to 50 %) were tested. The effect of sedimentary substratum type was also analysed for facies O (without nodules), by comparing four beds of ancient sediments (Oligocene to Miocene), selected because of their importance in the region, and a bed of young sediments (Plio-Quaternary).

A random selection of 48 100 photographs, covering an area of about 76 000 m^2, collected by the ‘Epaulard’ and the R.A.I.E. have been analyzed by units of 200 photographs of about 3 800 m^2 in the following way:

Nodule-facies O	1 set of 200 photographs / sediments Plio-Quaternary;
	4 sets of 200 photographs / sediments Oligocene to Miocene;
Nodule-facies C+	1 set of 200 photographs / sediments Plio-Quaternary / nodule coverage 2-5 %;
	1 set of 200 photographs / sediments Plio-Quaternary / nodule coverage 10 %;
	1 set of 200 photographs / sediments Plio-Quaternary / nodule coverage 15 %;
	1 set of 200 photographs / sediments Plio-Quaternary / nodule coverage 20 %;
	1 set of 200 photographs / sediments Plio-Quaternary / nodule coverage 30 %;
	2 setsof 200 photographs / sediments Plio-Quaternary / nodule coverage 40 %;
	1 set of 200 photographs / sediments Plio-Quaternary / nodule coverage 20-40 % and 15 % slope;
Nodule-facies B	3 sets of 200 photographs / sediments Plio-Quaternary / nodule coverage 40 %;
	1 set de 200 photographs / sediments Plio-Quaternary / nodule coverage 50 %;
Nodule-facies BP	1 set of 200 photographs / sediments Plio-Quaternary / nodule coverage 35 %;
	1 set of 200 photographs / sediments Plio-Quaternary / nodule coverage 50 %.
Rocky outcrops (AR)	1 set of 28 photographs.

Analysis of photographic data from the ‘Nautile’

In order to compare the different means of photographic exploration from the ‘Nautile’ and the ‘Épaulard’, a 1250 m route, covered by the ‘Nautile’ at an even speed and altitude of about 5 m, was selected. This transect was of significant length and passed over nodule-facies B’ medium with 40 % nodule coverage, in which the nodules have a roundness of 0.7 and are of smaller diameter (2 to 4 cm) than those of nodule-facies B.

The NIXO 41 site

This site was explored during the SEANOD 2 cruise in December and January 1980-1981. It was situated at 127°W/130°W, 12°10’N/13°35’N, at an overall depth of 5000 m and a depth of 4 700 m in its central basin and in the western and eastern parts. Its general topography consists of lines of abyssal hills, oriented N 350° to N 005°, low in height (100 to 150 m) and of variable wavelength. This hilly landscape is dissected in its eastern part by two wide valleys with flattish bottoms: that to the east is 6 km wide with a slightly rounded bottom and a difference in height of 350 to 450 m, while the other to the west is 4 km wide with a height difference of 200 to 300 m. This site was chosen in order to explore a nodule-facies previously unknown faunistically, facies A, as the latter is scarcely represented at the NIXO 45 site. The purpose was to compare faunistic data from here with photographs recorded by the ‘R.A.I.E.’ from a nodule-bearing environment at comparable depth, and so data from nodule-facies B 35 % and C+ 30 % at the NIXO 41 site were analysed. For this, the camera was at a mean elevation of 5 m with an interval between shots of 32 seconds. A total area of 18 000 photographs along 274 km of transects performed by the R.A.I.E enabled to analyze 34.2 ha of the deep seabed. The total area analysed quantitatively was estimated at about 8 400 m^2.

The ECHO I Site

This site was chosen to compare photographic information collected by another type of exploratory device, 'Deep Tow', over beds of polymetallic nodules similar to those analysed at the NIXO 45 site. The site 'ECHO I' is at 14°40'N-125°25'W near DOMES C, at a depth of 4 500 m in a landscape of abyssal hills interrupted by groups of seamounts and small escarpments, and has been well studied (Spiess *et al.*, 1987). These abyssal hills are 10 to 15 m high and aligned parallel to the axis of accretion which found more than 200 km to the east. The transect travelled by 'Deep Tow' and the positions of the sedimentary samples are east and north of latitude 14°34'N and longitude 125°30'W (figure 23). The oldest sediments date from the Oligocene (25 Ma) while the upper layers date from the Miocene (Heath, 1981).

At this site, faunistic data was analysed from three types of nodule-facies, similar to some already studied at NIXO 45: facies O, facies B 45 % and facies C 40 %, over a total surface area of about 12 400 m^2. These nodule-facies differ, however, by the fact that at NIXO 45, facies C and B are situated on recent sediments dating from the Plio-Quaternary, while at ECHO I, they are associated with more ancient sediments, from the Miocene.

Two types of camera objectives were used: a 70 mm telephoto a 50 mm wide angle, thus giving complementary data for each photograph. The elevation of the shots varied between 7.3 and 9.8 m and was generally too high for distinguishing small animals, although it did allow censusing of larger shapes and evidence of bioturbation on the ocean floor, such as mounds. The telephoto enabled the megafauna to be distinguished on the smallest surfaces. Photographs were taken at regular intervals varying between 7 and 26 seconds.

3.3 QUANTITATIVE ANALYSIS OF PHOTOGRAPHS FROM THE 'ÉPAULARD', 'R.A.I.E.' AND 'DEEP TOW'

The surface areas photographed by the 'Épaulard' and 'R.A.I.E' were similar. Data was analysed using a programme developed by Ifremer for studying the spatial distribution of megafauna photographed *in situ* (Sibuet, 1987). This computer program adds by successive increments the surface area of each photograph calculated from the elevation of the camera. A multivariate analysis of relationships was then performed with a CYBER 992-31 calculator using SPAD. N software.

4. Qualitative Analysis

4.1 COMPILATION OF AN ANNOTATED TAXONOMIC REFERENCE BASE

The description of suprabenthic assemblages begins with the compilation of a reference base, in this case an annotated taxonomic atlas containing observations and ideas on the morphology, ethology and feeding behaviour of each taxon identified in the photographs. Information on the geographic and bathymetric distribution of these taxa was compiled from data from abyssal regions outside the Clarion-Clipperton fracture zone, especially other regions of the Pacific and the Atlantic Oceans. The literature was consulted in order to gather all available information on specimens collected and identified in the Clarion-Clipperton fracture zone and neighbouring regions. Hypotheses of identification for the taxa in this study were collated on the advice of international specialists (see Appendix 3), and those accepted are presented and commented in an annotated photographic atlas, which forms Volume 2 of this publication. The list of codes used for identifying the taxa is presented in appendix 2, and follows the classification of Parker (1982).

Part of this annotated reference base is presented in a separate document 'Annotated photographic atlas of the echinoderms of the Clarion-Clipperton fracture zone'. A photographic panorama of the rest of the megafauna is displayed as appendix 1 of this document.

Echinoderms were chosen because they are particularly well suited to photographic analysis. They are generally of a size that is easily visible and the shapes are clearly recognisable. In addition, echinoderms are known to be one of the best represented groups in the abyssal domain (Zenkevitch & Birstein, 1956; Hansen, 1967, 1975; Belyaev, 1972; Sibuet, 1977, 1984, 1987; Laubier & Sibuet, 1979) and the best studied (Pawson, 1976, 1977, 1983; Gage *et al.*, 1984; Lampitt & Billett, 1984; Pawson & Foell, 1984; Harvey & Gage; 1988, Morgan, 1991). The importance of this phylum is well illustrated by its abundance and diversity (Alton, 1966; Sibuet, 1974, 1984; Bluhm & Gebruk, 1999) and biomass (Zenkevitch, 1963; Filatova, 1969). Echinoderms appear to be well adapted to the abyssal domain (Haedrich *et al.*, 1980; Sibuet & Lawrence, 1981; Ohta, 1983; Sibuet, 1984, 1987; Billet *et al.*, 1988).

The echinoderm phylum is generally represented by the dominant class of holothurians (Carney & Carey, 1982; Sibuet, 1987; Matsui *et al.*, 1997). A fraction of these is adapted to a mesopelagic life (Barnes *et al.*, 1976; Pawson, 1976, 1985; Sibuet, 1987; Billett *et al.*, 1985; Ohta, 1985; Pawson & Foell, 1986; Miller, 1988; Miller & Pawson, 1990) as confirmed by the observations of this study, both on the species described in the literature as mesopelagic and on others that have previously been considered as entirely benthic.

4.2 TAXONOMIC RICHNESS OF THE FAUNA OF THE CLARION-CLIPPERTON FRACTURE ZONE

The term taxonomic richness is used here rather than species richness because unfortunately no specimens could be collected and consequently no precise faunal identifications could be made at a specific level. Although most of the suprabenthic megafauna in the Clarion-Clipperton fracture zone has not been sampled (Belyaev, 1989), the taxa observed have been arranged according to the families (and genera when possible) to which they are most likely to belong, in agreement with specialists, in order to evaluate the taxonomic richness of the study area.

A total of 240 distinct taxa in 13 phyla have been enumerated, some of which are at the limit of the definition for megafauna (that is visible in photographs, according to the definitions of Haedrich *et al.*, 1975, 1980 and Grassle *et al.*, 1975). If one excludes those that are difficult to distinguish and retains only those generally found in photographic analyses of the megafauna, the total is of 159 taxa. This figure is relatively high compared with the results from other photographic explorations made between the Clarion and Clipperton factures zones (Foell *et al.*, 1986; Pawson, 1988; Foell *et al.*, 1990).

Some studies of the taxonomic diversity of suprabenthic megafauna have proposed that maximum species richness occurs at depths between 2 000 m and 4 000 m. These values are equivalent to those that characterize tropical coastal habitats (Vinagradova, 1962; Sanders, 1968; Sanders & Hessler, 1969; Rex, 1976; Sibuet, 1977; Haedrich *et al.*, 1980; Paterson *et al.*, 1985). The macrofauna similarly reaches its maximum species richness between 2 000 m and 4 000 m (Hecker & Paul, 1979; Rex, 1981, 1983), although studies in the central northern Pacific Ocean indicate a peak of macrofaunal diversity between 5 000 m and 6 000 m (Hessler & Jumars, 1974).

The results of our analysis show that some phyla have quite significant taxonomic richness, such as (in order of importance) cnidarians (59 taxa), echinoderms (46 taxa), sponges (38 taxa) and chordates (27 taxa). Figure 35 shows a histogram of the variability of taxonomic richness within the different phyla.

In order to remove all imprecision on the degree of taxonomic identification, taxinomic richness has been assessed according to the number of families within each phylum as displayed in Figure 36. Cnidarians are again dominant, with 32 families, while echinoderms and chordates are only represented by 18 families each, arthropods by 12, and molluscs and sponges by 10 families.

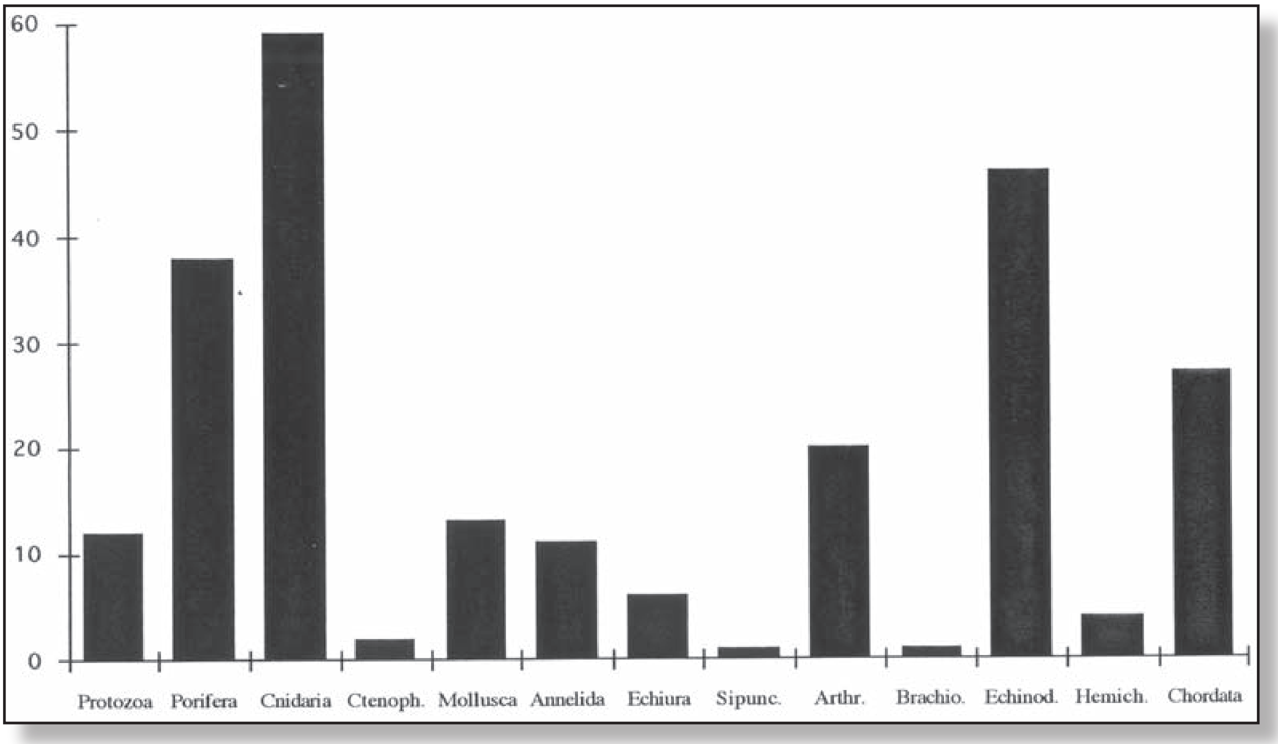


Fig. 35. Histogram of the number of taxa in each phylum for the megafauna of the Clarion-Clipperton fracture zone.

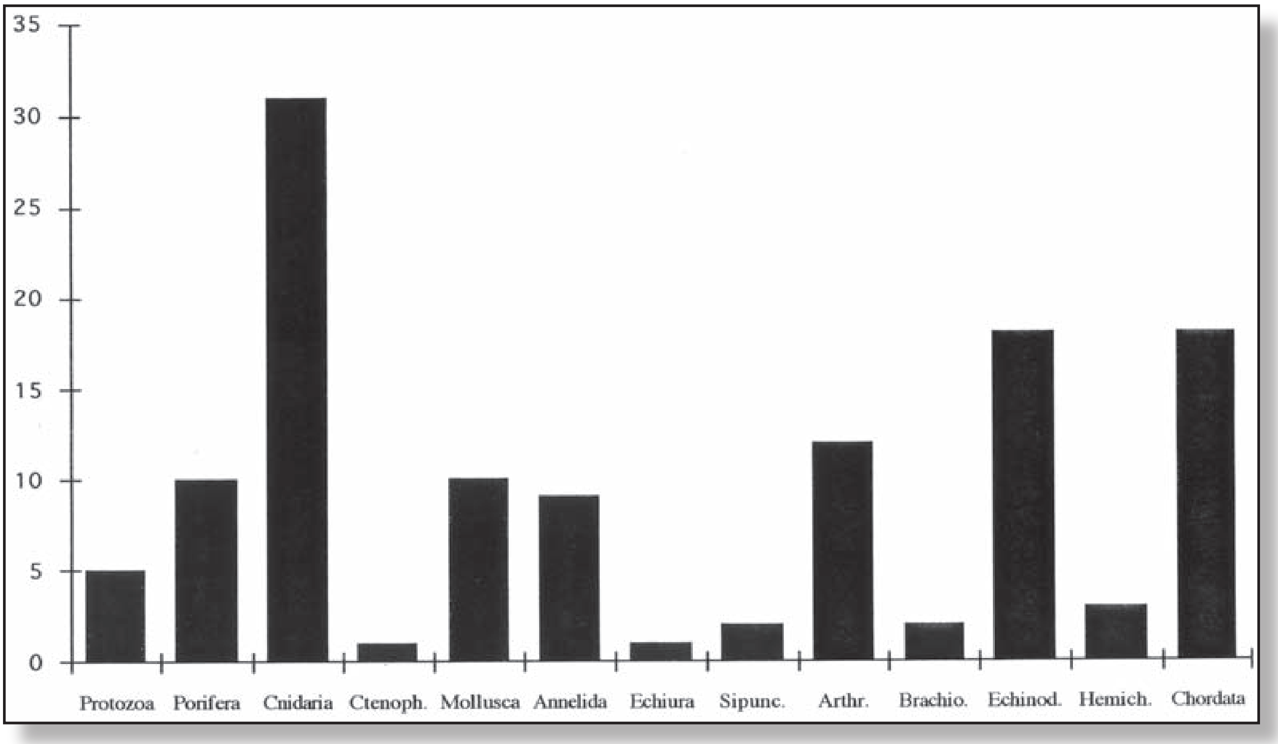


Fig. 36. Histogram of the number of families in each phylum for the megafauna of the Clarion-Clipperton fracture zone.

Comparison of figures 35 and 36 shows that in contrast to the apparently more cosmopolitan cnidarians, echinoderms are only represented by a small number of families containing relatively more taxa observed in the study area. Some members of these families are entirely abyssal (Madsen, 1961; Pawson, 1967, 1983; Hansen, 1975; Sibuet, 1976, 1977, 1980; Bisol *et al.*, 1984).

This predominance of cnidarians, both in taxonomic richness and the number of families represented, contradicts the results of Foell *et al.* (1986) in the study zone and of Alton (1966), Sibuet (1984) and Rex (1981) in some parts of the abyssal Atlantic Ocean. In the case of Foell *et al.* (1986), it may be that the sampling strategy forced these authors to dismiss detailed analysis of the very numerous so-called "white spots", which are reflections of light from the flashes. According to these authors, they are sponges and cnidarians, such as small actinids. In addition, their study was based on a collection of only 2 149 photographs of the ocean floor with taxonomic identification carried as far as possible only for the echinoderms, while our study was based on a total of about 200 000 photographs and involved the same degree of effort for taxonomic identification for each phylum. However, the high values of taxonomic richness observed here for echinoderms (45 taxa of which 31 holothurians) are comparable to those of Foell et al., (1986) who recorded 30 echinoderms including 20 holothurians.

The values presented here for echinoderm diversity are similar to the maximum diversity in the northern Atlantic Ocean between 1380 m and 1874 m, based on collected specimens (Haedrich *et al.*, 1980). But at equivalent depths to those in the study area (4 000-5 000 m), these authors only found nine echinoderms and six fish (compared with 17 taxonomically distinct types of fish in this study). In contrast, the diversity of the holothurians in the Clarion-Clipperton study area appears to be of the same order of magnitude as in the Bay of Biscay at 3 000 m depth (Sibuet, 1977).

In order to standardize the values of taxonomic richness observed in this study, a census of the total number of families listed for the abyssal domain at depth intervals between 3 000 m and 6 000 m was made from literature sources. Since no complete inventory of this subject had ever been made, it was necessary to find data concerning each phylum and especially to analyse data on the species richness of the hadal and abyssal faunas from numerous Russian cruises (Zenkevitch, 1966; Belyaev, 1985).

In the study zone, we found about the same percentage (70 %) of families compared with the total number known from the abyssal domain, for cnidarians (32/44), sponges (10/14) and chordates (18/26), while echinoderms (18/45) only represented 40 % of the families that inhabit the abyssal regions of the oceans.

However, it must be noted that phyla are not sampled in an equal manner in the deep ocean, and some could be studied more, and consequently sampled more, than appeared to be the case for echinoderms (Pawson 1976; Gage *et al.* 1984; Lampitt & Billett, 1984; Pawson & Foell, 1984; Harvey & Gage, 1988; Matsui *et al.*, 1997). In addition, the means and strategies of sampling are very variable and this without doubt also contributes to the variation in values for taxonomic richness. It is interesting also that among the echiurians and hemichordates, all the families so far recorded in the abyssal domain are represented in the study area.

4.3. TAXONOMIC RICHNESS BY TROPHIC AND FUNCTIONAL GROUPS

To understand the structure of faunal assemblages and how suprabenthic ecosystems in the study zone func tion, one must apprehend the feeding and functional behaviour of their taxonomic components. The megafauna of the Clarion-Clipperton fracture zone can be classified into six trophic and functional groups that are corroborated by an exhaustive review of the literature: sessile suspension feeders, mobile suspension feeders, sessile detritus feeders, mobile detritus feeders and mobile carnivores/scavengers.

Moreover, cases of ambivalent feeding behaviour, such as suspension/detritus/carnivorous feeding and scavenging occur in the abyssal domain, as seen in some actinids in families Actinostolidae and Actinoscyphiidae. These ambivalent behaviours suggest opportunistic feeding which could be an adaptation to the meagre nutritional supplies characterizing the abyssal domain. These opportunist behaviours can be adopted by numerous members of the suprabenthos according to analyses of intestinal contents (Sokolova, 1957; Allen & Sanders, 1966; Carey, 1972; Hansen, 1975; Monniot & Monniot, 1975; Fauchald & Jumars, 1979; Sibuet, 1980; Taghon *et al.*, 1980; Dauer *et al.*, 1984). Such opportunism could be a means of exploiting ecotones between two regions dominated by a particular trophic group and related to variation in the flow of particulate carbon (Taghon *et al.*, 1980; Tyler, 1988; Smith *et al.*, 1994; Rowe, 1996; Smith *et al.*, 1997; Radziejewska & Stoyanova, 2000; Ruhl & Smith, 2004).

In terms of taxonomic richness, sessile suspension feeders (84 sessile taxa and 10 mobile taxa) dominate over carnivores/scavengers (72 taxa) and detritus feeders, which consist essentially of mobile taxa (61 taxa). The taxonomic richness of suspension feeders is principally represented by the cnidarians (35 taxa) and by all the sponges observed in the study zone (38 taxa). As for detritus feeders, their taxonomic richness is principally due to holothurians (31 taxa).

The results of this study underline the predominant taxonomic diversity of suspension feeders. This contradicts the findings of Sanders & Hessler (1969), Menzies *et al.* (1973), Hessler & Jumars (1974) and Sibuet (1984), who demonstrate that the diversity and abundance of detritus feeders made them the dominant fraction of the abyssal epibenthos. However, one result in the study area verifies previous results, i.e. that holothurians are the most abundant members of the detritus feeders, as shown by Hansen (1967, 1975), Belyaev (1972), Sibuet (1984, 1987) and Laubier & Sibuet (1979).

Figure 37 displays values for taxonomic richness within trophic and functional groups in the form of histograms.

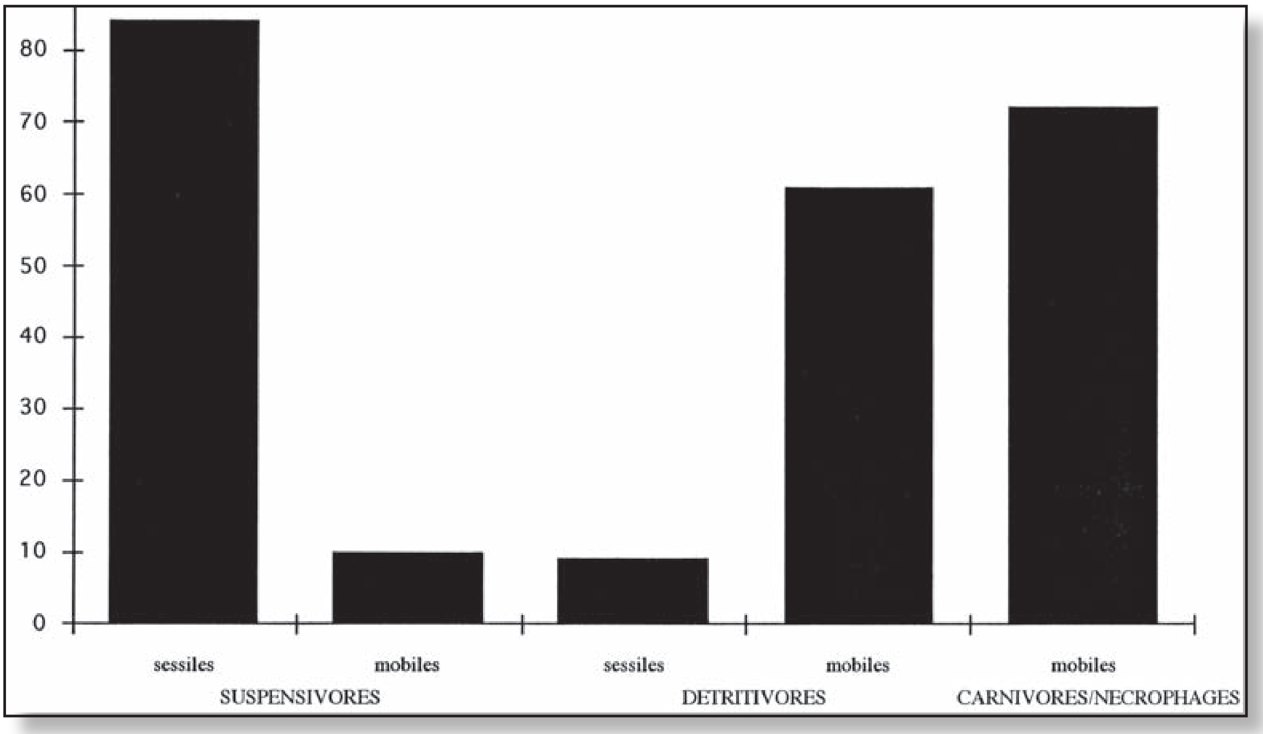


Fig. 37. Histogram of the taxonomic richness within trophic and functional groups for the megafauna of the Clarion-Clipperton fracture zone.

5. Quantitative Analysis

In-depth quantitative analysis of the suprabenthic faunal assemblages of the Clarion-Clipperton fracture zone was conducted for the NIXO 45 site and in complementary and comparative fashions at the NIXO 41 and ECHO 1 sites. Analysis was carried out at three levels of observation: at a general level over the whole study area, at the level of nodule-facies, and at a specific level with taxa as the units. As in the qualitative analysis, quantitative data on faunal categories which are at the limit of megafauna, and which belong to the macrofauna according to the definitions of Sanders *et al.* (1965), are given here for information only.

5.1 THE NIXO 45 SITE

Abundance and faunal composition by phylum

The results show that among the dominant phyla over the whole of the NIXO 45 site, a majority of cnidarians (258 taxa/ha) is found, outnumbering echinoderms (180 taxa/ha) and sponges (56 taxa/ha) (figure 38). Figure 39 gives details of the composition of different phyla over the whole of the NIXO 45 area. Within the cnidarians, actinids dominate (135 ind/ha) over octocoralliarids (105 ind/ha), medusas belonging to classes Scyphozoa and Hydrozoa (12 ind/ha), antipatharids (5 ind/ha), siphonophores and ceriantharids (1 ind/ha). Among the echinoderms observed, the majority are holothurians (64 ind/ha) and crinoids (61 ind/ha), plus echinoids (36 ind/ha), ophiuroids (13 ind/ha) and asteroids (6 ind/ha). For arthropods, isopods are found principally on nodule-facies C+ 2-5 % with 11 ind/ha and swimming and creeping decapods on facies with a large covering of nodules BP 50 % and B 50 % (5 ind/ha). Among molluscs, cephalopods are only seen on nodule-facies C+ 20 % and nudibranchs only on nodule-facies BP 50 %, at low density (3 ind/ha). For chordates, fish are the most abundant (29 ind/ha) on facies O with recent sediments and tunicates are only observed on nodule-facies BP 50 % at a density of 3 ind/ha.

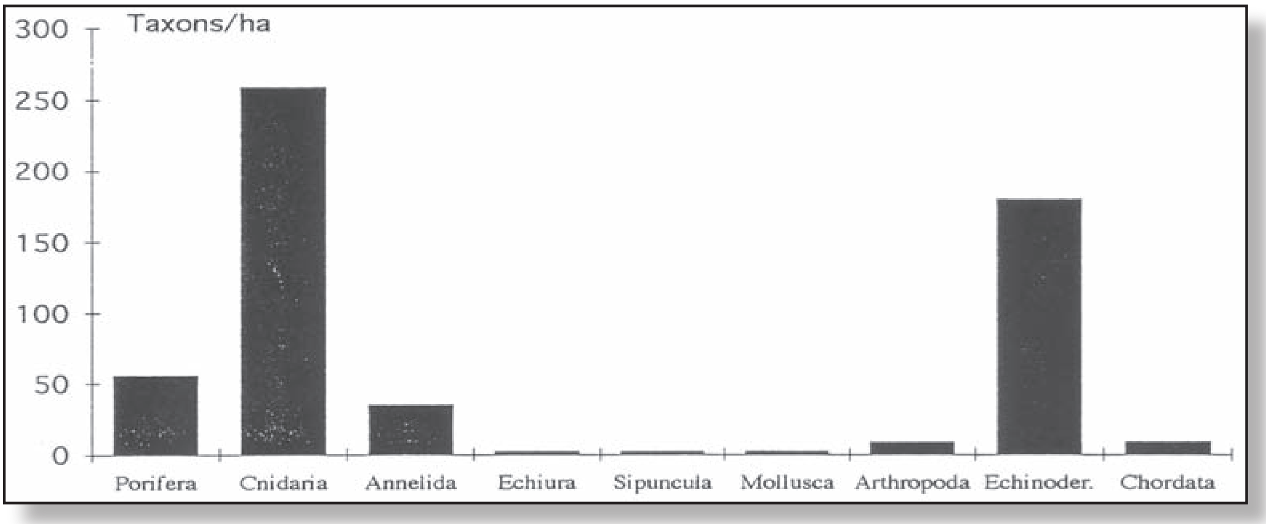


Fig. 38. Histogram of abundance within each phylum at the NIXO 45 site.

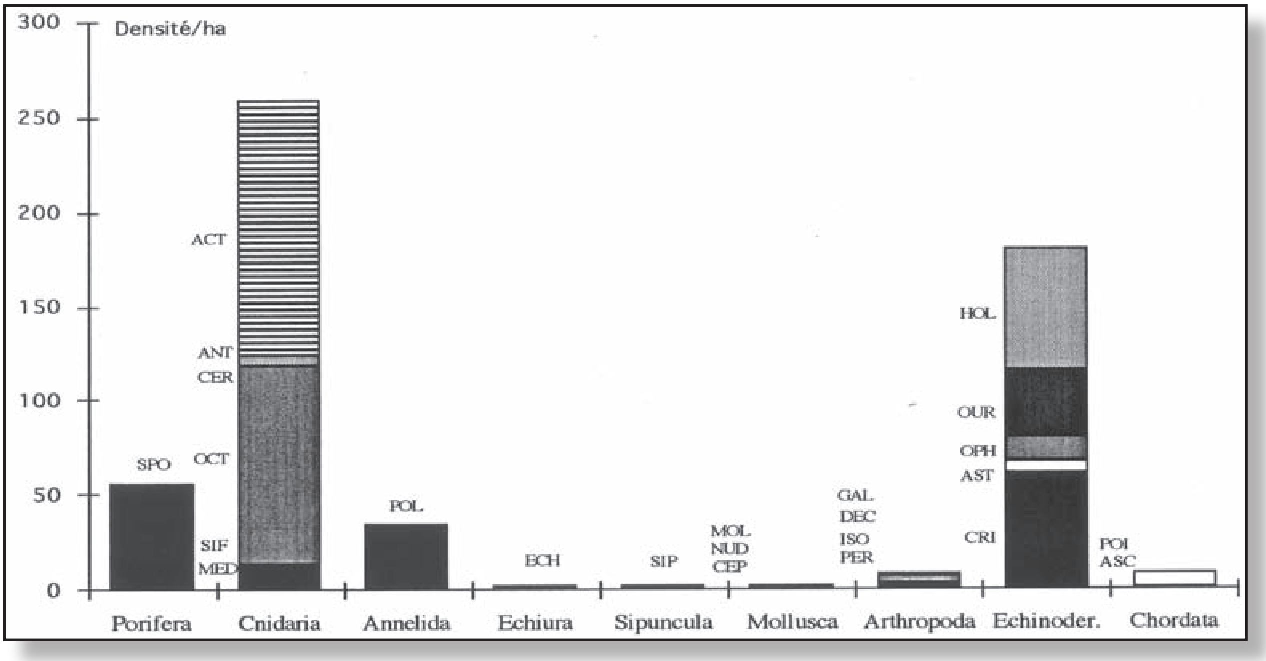


Fig. 39. Histogram of the partitioned abundance within each phylum at the NIXO 45.

Abundance and faunal composition for the two dominant phyla

Variation in the composition of the two dominant phyla, cnidarians and echinoderms, for each type of nodule-facies is shown in figures 40 a, b, c.

Among the cnidarians, actinids are the principal representatives on all facies with nodules, and are most abundant (215 ind/ha) on nodule-facies C+ 15 %. Octocoralliarids are predominant members of the cnidarians on the site and preferentially abundant on nodule-facies O on recent sediments (313 ind/ha), and more abundant (194 ind/ha) than actinids on sloping facies (C+ 20 to 40 %) and rock outcrops, with densities of 175 ind/ha and 23 ind/400m^2 respectively. Medusas belonging to the classes Scyphozoa and Hydrozoa are most abundant (61 ind/ha) on nodule-facies C+ with a low covering of nodule (10 %). Antipatharids are observed on all facies except facies O on ancient sediments, nodule-facies C+ 30 %, nodule-facies BP 50 % and rock outcrops, and reach their most significant density (11 ind/ha) on nodule-facies C+ 10 %.

Among the echinoderms, echinoids predominate on facies O on recent sediments and nodule-facies C+ 2-20%; they show a peak of abundance (190 ind/ha) on nodule-facies C+ 10 %. Crinoids are predominant on sloping nodule-facies (C+ 20–40 %) and are at their highest density (122 ind/ha) on nodule-facies C+ 10 %. Holothurians are most abundant on facies O on ancient sediments and on all nodule-covered facies B and BP, as well as on other facies with dense nodules (facies C+ 30-40 %). Holothurians are most abundant (101 ind/ha) on facies BP 50 %, ophiuroids on facies BP 35 % (68 ind/ha) and asteroids on the two most extreme facies from the point of view of nodule covering, facies O on recent sediments and B 50 % (16 ind/ha).

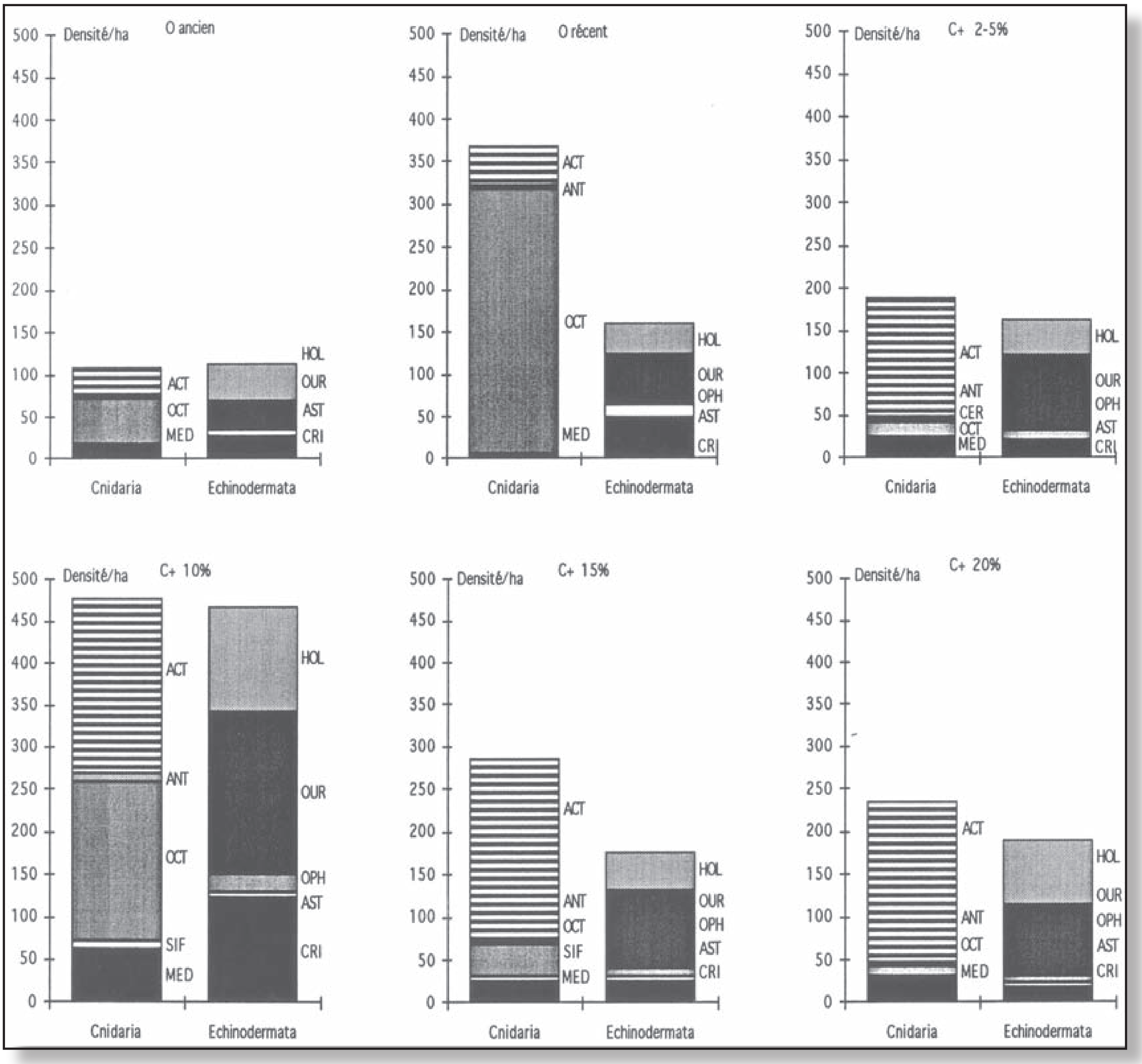


Fig. 40a. Histograms of the partitioned abundance on each nodule-facies for the two dominant phyla at the NIXO 45 site.

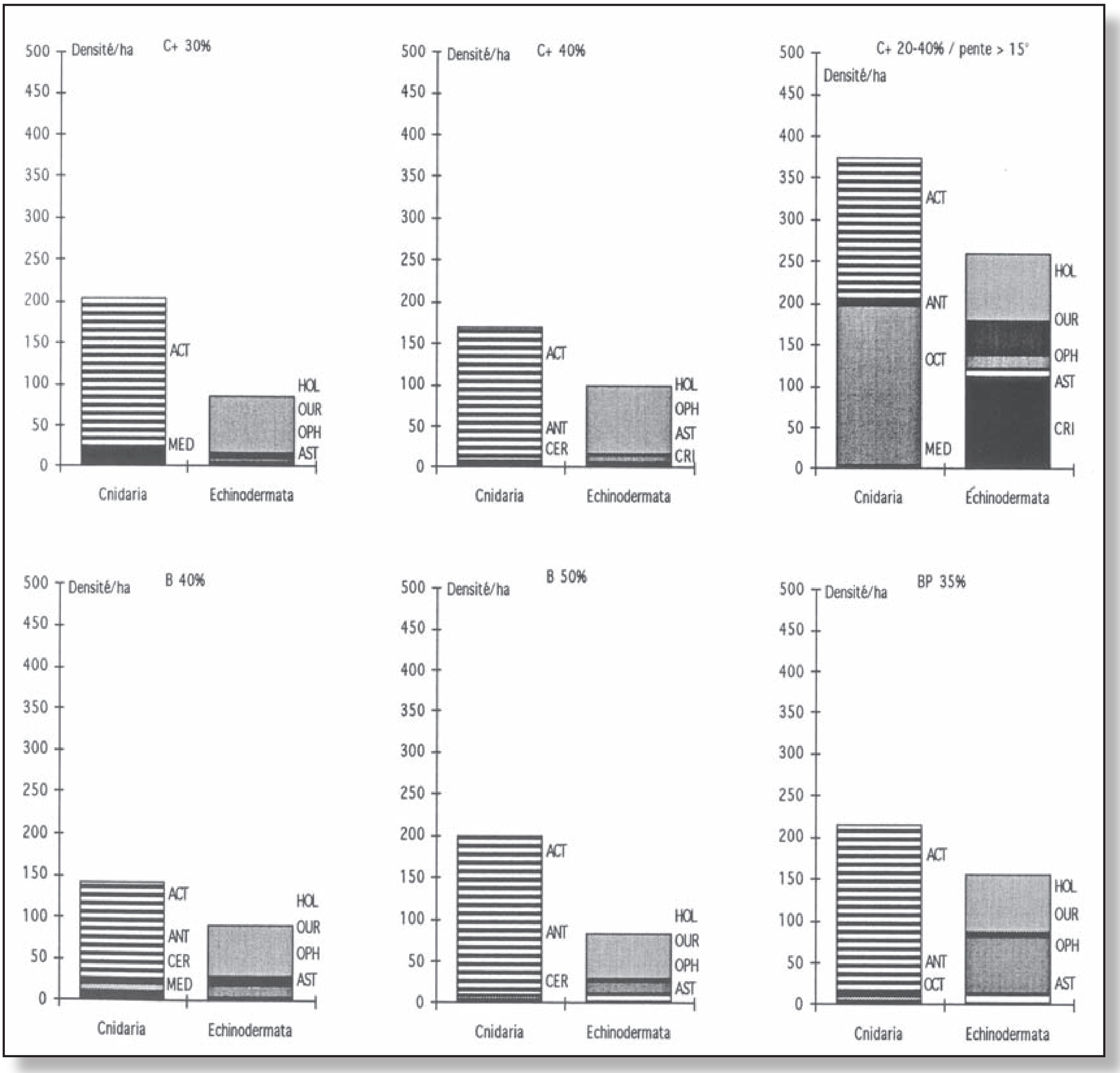


Fig. 40b. Histograms of the partitioned abundance on each nodule-facies for the two dominant phyla at the NIXO 45 site.

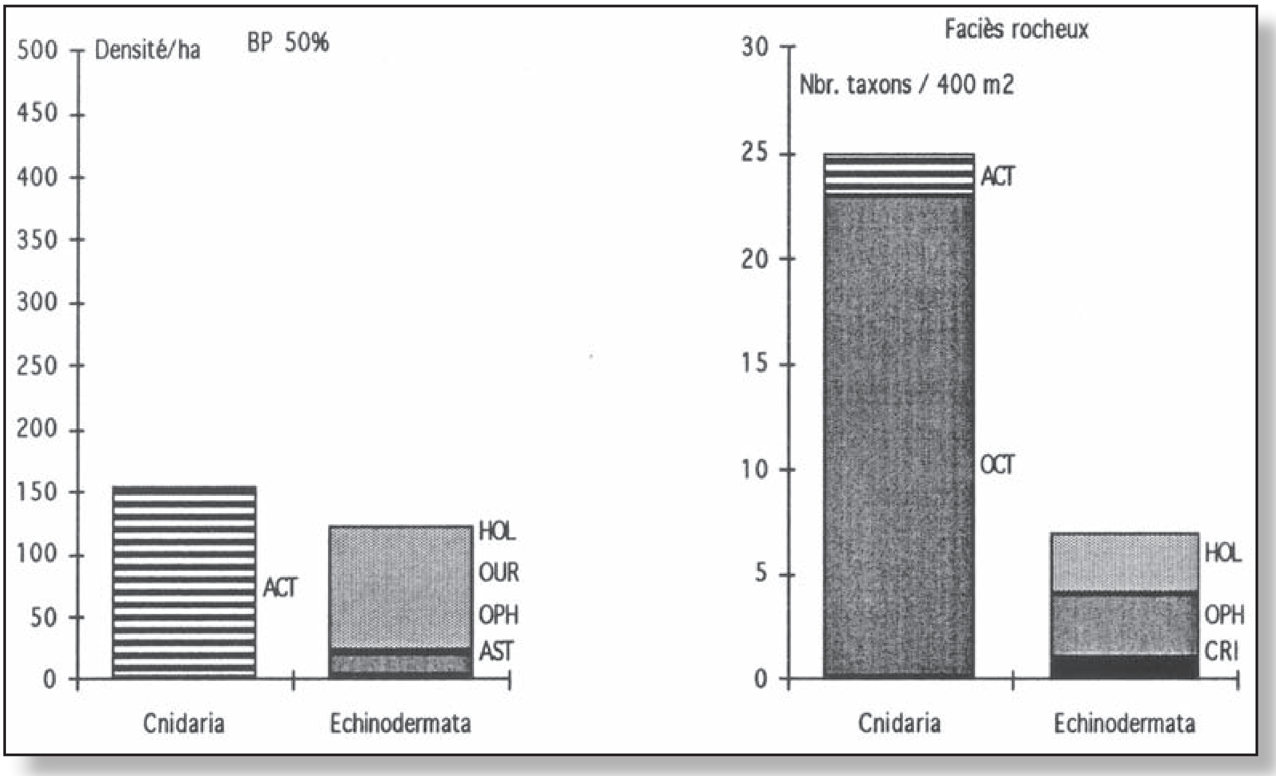


Fig. 40c. Histograms of the partitioned abundance on each nodule-facies for the two dominant phyla at the NIXO 45 site.

Abundance and faunal composition by nodule-facies

Because of substratum heterogeneity, demonstrated by the existence of different facies at the site (figure 19), variation in abundance and faunal composition in relation to nodule-facies was investigated. Results display a greater abundance of fauna on facies C+ with large nodules (6-10 cm diameter) at low density (10 %) or higher density (20 % to 40 % on a slope of 15°) on recent sediments composed of siliceous clays, dating from the Plio-Quaternary (figure 41). It shows that cnidarians, echinoderms, sponges and sipunculids are the most abundant (478 ind/ha, 467 ind/ha, 116 ind/ha and 14 ind/ha respectively) on the facies with large scattered nodules C+ (10 % coverage), while annelids and chordates predominate on facies O composed of recent sediments (92 ind/ha and 29 ind/ha respectively), arthropods (21 ind/ha) on facies C+ with slope > 15° and nodule-covering of 20 to 40 %, molluscs (14 ind/ha) on facies C+ 15 % and echiurians (10 ind/ha) on facies BP 35 %.

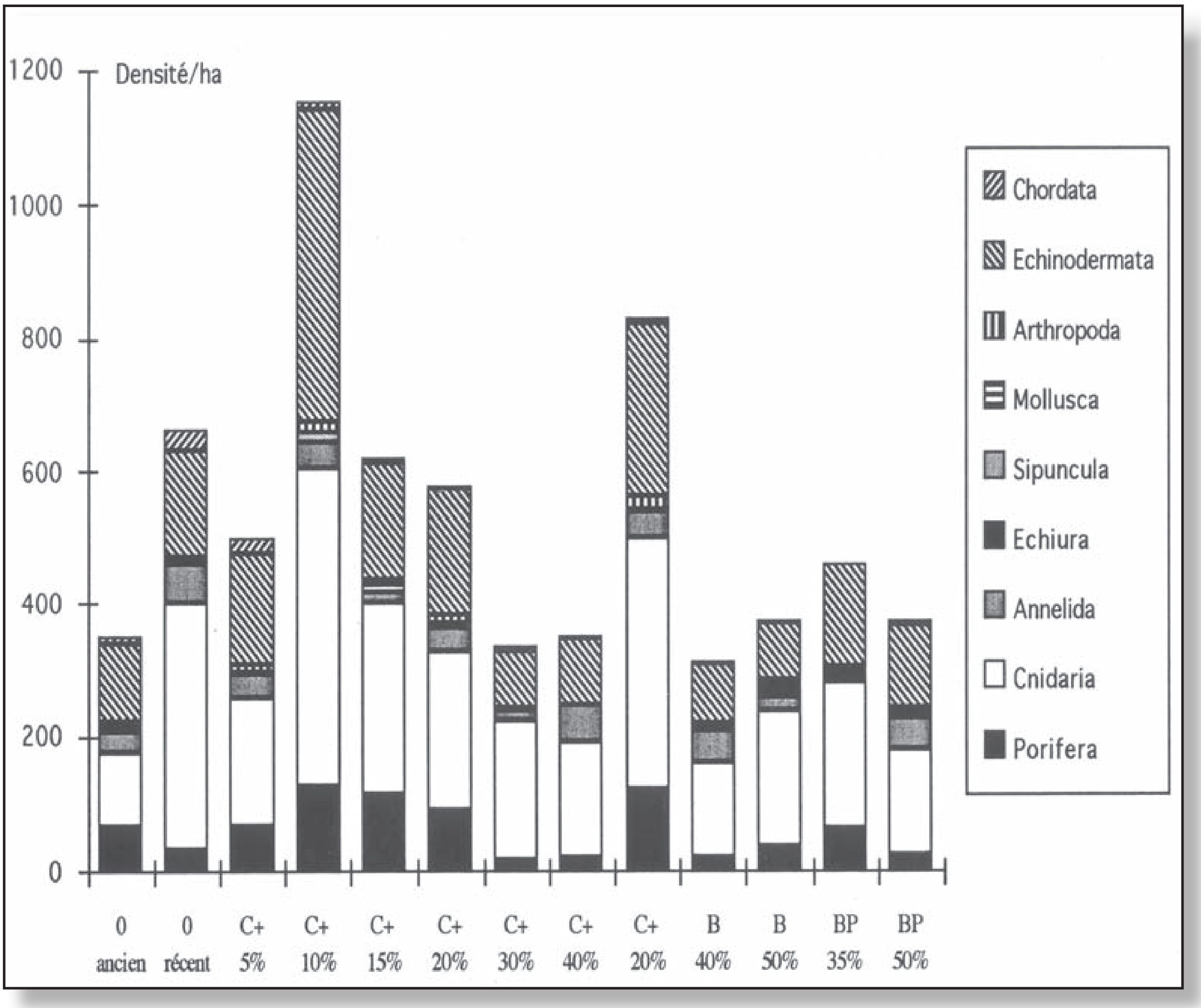


Fig. 41. Histogram of the partitioned faunal abundance on each nodule-facies at the NIXO 45 site.

Faunal composition by trophic and functional groups

Distribution of the megafauna by functional group over the whole of the NIXO 45 site is represented in figure 42. The faunal composition of each functional category is represented by the cumulative partitioning of each histogram. One can thus see a majority of sessile suspension feeders (361 ind/ha) in comparison with motile detritus feeders (109 ind/ha) and motile carnivores/scavengers (53 ind/ha), motile suspension feeders (29 ind/ha) and sessile detritus feeders (5 ind/ha).

Among sessile suspension feeders, actinids are more numerous (123 ind/ha) than octocoralliarids (105 ind/ha), crinoids (61 ind/ha), sponges (56 ind/ha), sedentary polychaetes (12 ind/ha), antipatharids (5 ind/ha) and tunicates (1 ind/ha).

In terms of density among the motile detritus feeders, holothurians (64 ind/ha) outnumber echinoids (36 ind/ha), and asteroids and peracarids (3 ind/ha). Motile carnivores and scavengers are dominated by swimming polychaetes (23 ind/ha), hydromedusas and scyphomedusas (12 ind/ha), fish (9 ind/ha), decapods (5 ind/ha), molluscs (2 ind/ha), siphonophores and ceriantharids (1 ind/ha).

Motile suspension feeders are dominated essentially by ophiuroids (13 ind/ha), corallimorpharids (12 ind/ha), brisingids (3 ind/ha), molluscs and free crinoids (1 ind/ha). Sessile detritus feeders are weakly represented, by sipunculids (2 ind/ha) and echiurians, as well as some sedentary polychaetes (2 ind/ha).

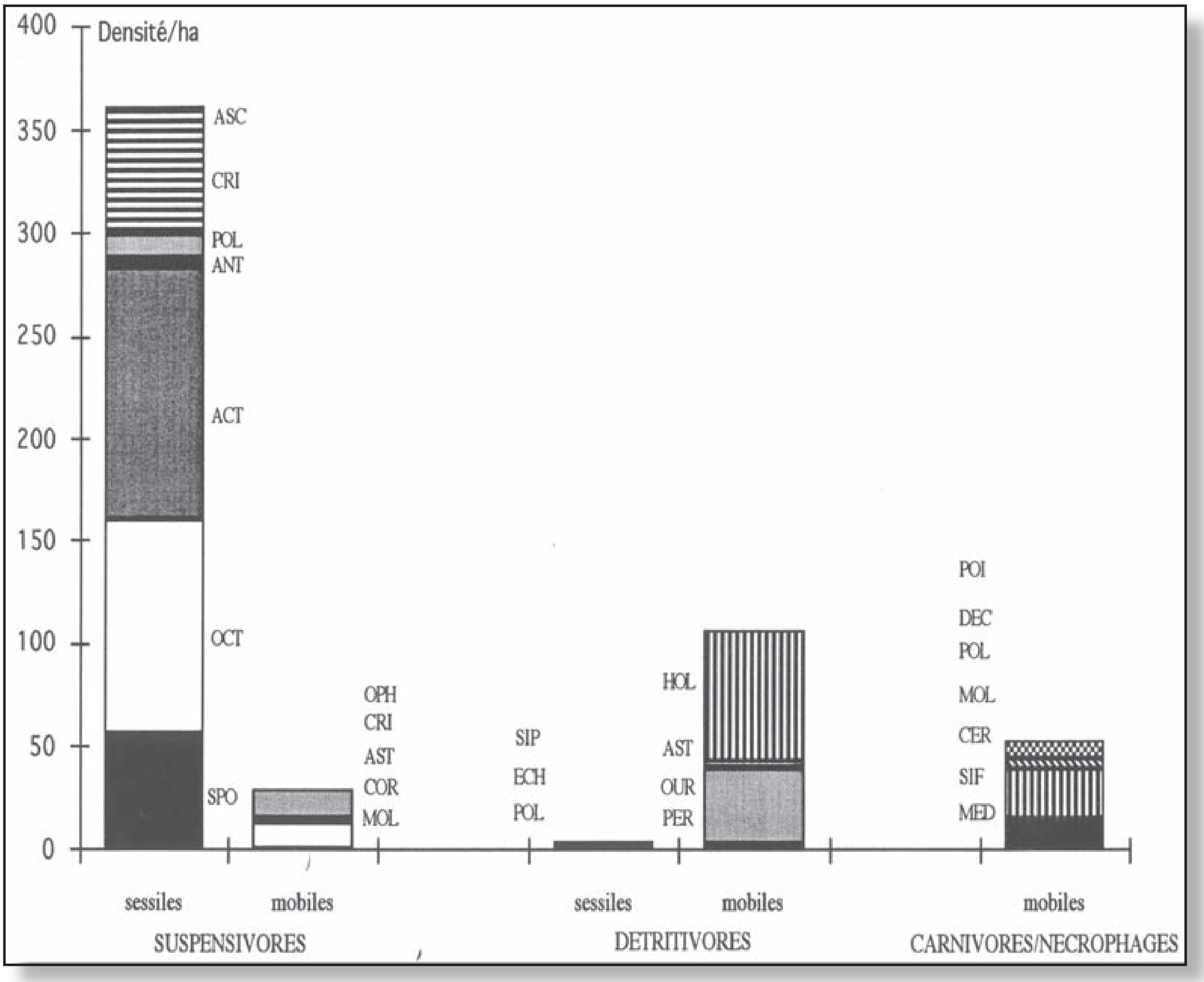


Fig. 42. Histogram of the partitioned faunal abundance within trophic and functional groups over the whole of the NIXO 45 site.

Faunal composition in relation to edaphic gradient

Densities and major trophic trends within these faunal assemblages are shown in figures 43 A and B in relation to edaphic gradient. When trophic composition on each facies is shown in terms of percentages, the order of dominance of trophic groups is homogeneous, irrespective of the edaphic conditions.

Thus the order of dominance, of suspension feeders over detritus feeders and lastly over carnivores, is verified on all facies. In descending order of faunal abundance, the nodule-facies are: facies C+ 10 %, facies on slopes > 15°, facies O on recent sediments, facies C+ 15 %, facies C+ 20 %, facies BP 35 %, facies C+ 2-5 %, facies B 50 %, facies BP 50 %, facies O old sediment, facies C+ 40 %, facies C+ 30 % and facies B 40 %. Figure 43 B demonstrates that in general, the same proportions of different phyla are present on all nodule-facies.

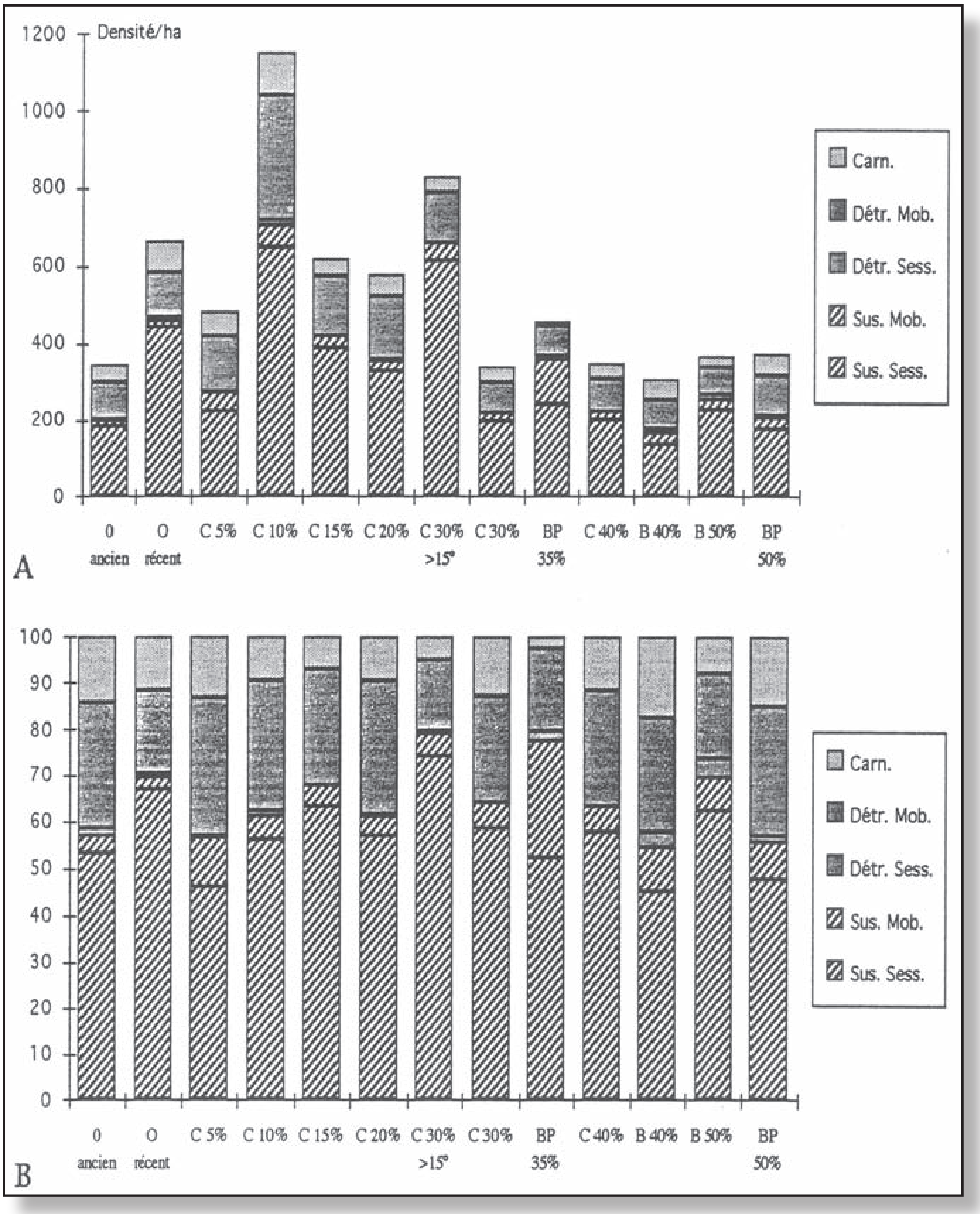


Fig. 43.
A) Histogram of the partitioned trophic and functional groups in relation to edaphic gradient at the NIXO 45 site.
B) Histogram of the partitioned trophic and functional composition of the fauna at the NIXO 45 site in percentage terms.

Faunal composition within each nodule-facies

The densities of the different components of these trophic and functional groups on each nodule-facies is represented in figures 44 a, b and c, by the cumulative partitioning of each functional category. Overall for the NIXO 45 site, the order of trophic and functional dominance on each nodule-facies is the same, with the exception of the special case of rock outcrops, where only sessile suspension feeders are widely abundant.

Within the dominant trophic group of sessile suspension feeders are octocoralliarids, actinids, antipatharids and crinoids. Among the other members of this trophic group, sponges are predominant with a density of 126 ind/ha on nodule-facies C+ 10 %, and sedentary polychaetes exploit all facies and are particularly abundant (28 ind/ha) on nodule-facies C+ 20 %.

Two classes predominate among the motile detritus feeders, echinoids and holothurians, which appear to share habitats. Peracarids are only observed on facies O on both recent and ancient sediments, and on nodule-facies C+ independent of the percentage of nodule coverage. Isopods in particular are more abundant (11 ind/ha) on nodule-facies C+ (2-5 %). Carnivores and scavengers are only dominated by swimming polychaetes on facies O with recent sediments, nodule-facies C+ 20 %, C+ 40 %, B 40 %, B 50 %, BP 50 % and rock outcrops are particularly abundant (42 ind/ha) on nodule-facies B 40 %. Fish, which are cosmopolitan, are at high density (29 ind/ha) on facies O with recent sediments. Scyphomedusas, hydromedusas and siphonophores, which are usually part of the zooplankton, are mentioned here for information only. Medusas are observed on almost all facies but they are at their highest density (16 ind/ha) on facies O with ancient sediments, while siphonophores are relatively abundant (11 ind/ha) on nodule-facies C+10 %. The largest quantity of decapods (14 ind/ha) is found on nodule-facies C+10 %. Gastropods are most abundant (14 ind/ha) on nodule-facies C+ 15 % and cephalopods are only observed on facies nodule-C+ 20 % at a density of 3 ind/ha. Ceriantharids are present at equal densities (3 ind/ha) on nodule-facies C+ 2-5 %, C+ 40 %, B 40 % and B 50 %.

Among the mobile suspension feeders, a predominance of corallimorpharids are observed on facies O with ancient sediments (where they are the only representatives of this functional group), facies O with recent sediments, and nodule-facies C+ 2-5 % to 30 %, with a maximum density of 39 ind/ha on nodule-facies C+ 2-5 %. Brisingids are present on nearly all facies with recent sediments and most abundant (10 ind/ha) on nodule-facies C+ 20-40 % on slopes. Ophiuroids are observed on all nodule-facies and especially on nodule-BP 35 % at a density of 68 ind/ha, and they are the only mobile suspension feeders on rock outcrops. Free crinoids are only seen on nodule-facies C+ 20 % at low density (3 ind/ha).

The sessile detritus feeders consist entirely of echiurians which prevail on nodule-facies B 40%, B 50% (16 ind/ha), BP 35%, BP 50%. Sipunculids are the main detritus feeders on facies O and on facies with a low density of large nodules (C+ 2-5 % to 20 %), reaching a maximum density of 15 ind/ha on facies C+ 10 %.

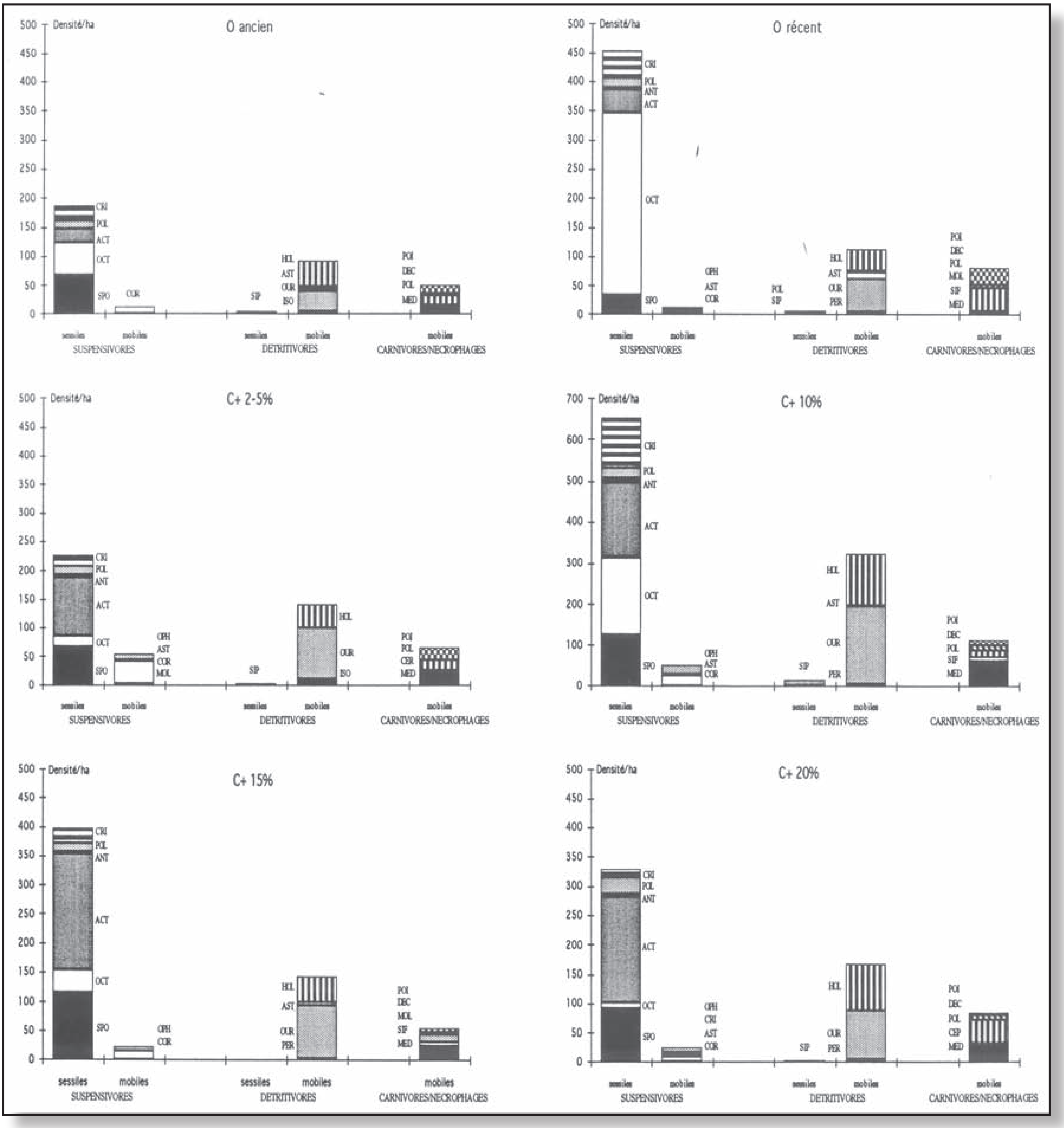


Fig. 44a. Histograms of faunal abundance partitioned and classed by trophic and functional group for each facies.

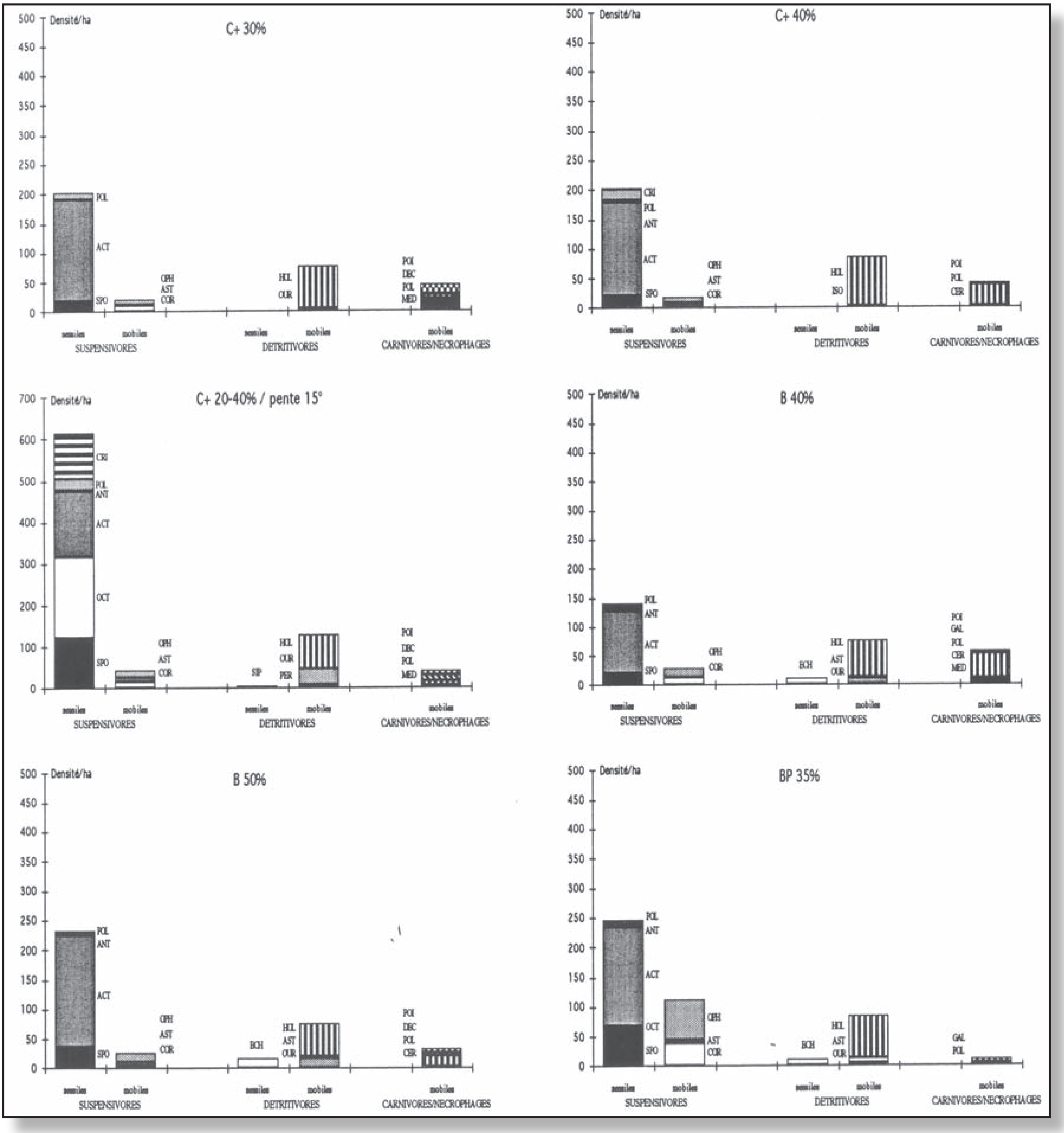


Fig. 44b. Histograms of faunal abundance partitioned and classed by trophic and functional group for each facies.

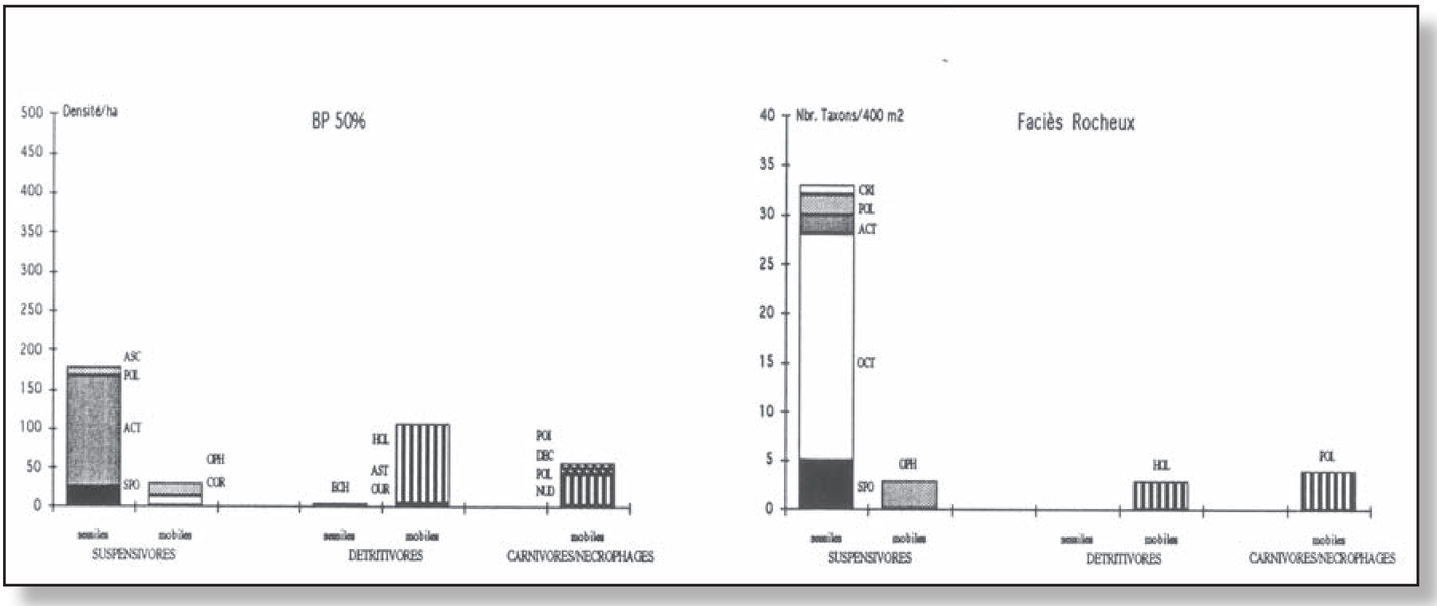


Fig. 44c. Histograms of faunal abundance partitioned and classed by trophic and functional group for each facies.

Quantitative analysis at the level of taxa

Densities of the most abundant 20 taxa at the NIXO 45 site are shown in figure 45. Among these taxa we find the same order of dominance of suspension feeders over detritus feeders and over carnivores and scavengers. Based on the hypotheses of identification proposed from the qualitative analysis of faunal assemblages, the most frequently observed suspension feeders belong to the phyla Cnidaria, Echinodermata, sponges and Annelida. Cnidarians comprise actinids, belonging to the families Actinostolidae and Actinernidae, corallimorpharids, plus gorgonians of the families Callozostrinae, Primnoidae or Isididae. The most abundant suspension-feeding echinoderms are fixed crinoids of the families Bathycrinidae and Hyocrinidae and ophiuroids of the family Ophiuridae. The most frequent sponges are from the families Hyalonematidae and Pachastrellidae. Suspension-feeding annelids here are *Incertae sedis* living in contorted tubes about 40 cm long which, according to Zibrowius (pers. comm.), resemble very large *Protula sp.* that live at lesser depth.

The most frequent detritus feeders are echinoids and holothurians. The echinoids are *Plesiodiadema globulosum* in family Aspidodiadematidae. In order of importance, the holothurians are the Aspidochirotids*:* *Pseudotichopus mollis, Synallactes aenigma* and *Synallactes profundi* and the Elasipodids*: Benthodytes incerta* and *Peniagone leander*. Carnivores are also represented in low proportion by polychaetes, belong to the families Polynoidae, Aphroditidae, Tomopteridae and Hesionidae, and medusas, belonging to the scyphomedusas and hydromedusas.

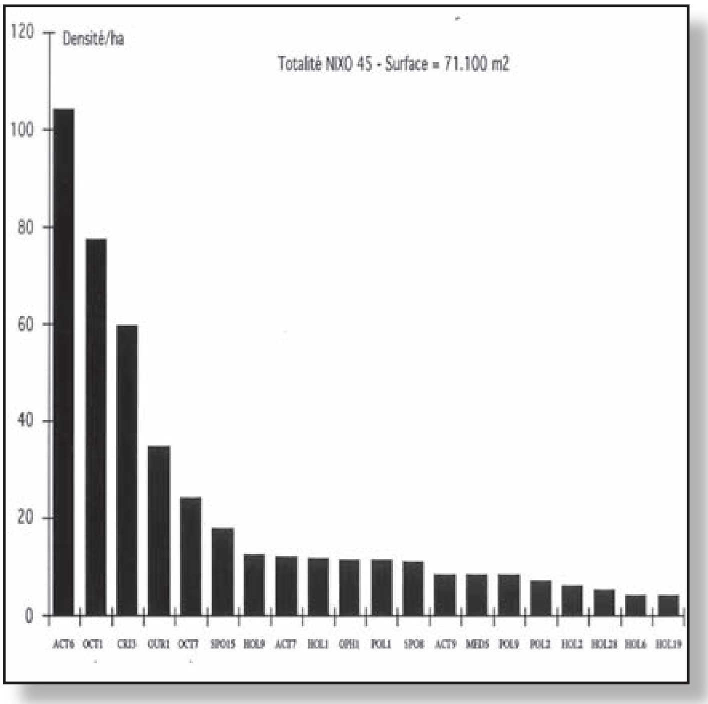


Fig. 45. Histogram of the density of the most abundant taxa at the NIXO 45 site.

Distribution of taxa in three dominant faunal groups

Variation in the distribution of taxa within the three dominant faunal groups at the NIXO 45 site, viz. sponges, actinids/corallimorpharids and holothurians, gives an indication of possible preferential habitats on different facies.

Distribution of actinids and corallimorpharids on different facies

Sincyonis tuberculata have a relatively high abundance on all the facies studied, though its maximum density of 166 ind/ha is on facies B 50 %, which has a dense covering of small nodules. This does not appear to be the case for other actinids and corallimorpharids, and the majority of these organisms prefer a low covering of nodules (2–15 %) or a facies without nodules, as is the case for *Amphianthus bathybium* which reach a density peak on facies O with ancient sediments. The corallimorpharids *Nectatis singularis* display a higher density (37 ind/ha) on nodule-facies C+ 2 to 5 % and the actinids *Actinernus verrill*, *Bolocera sp.* and *Liponema sp.* have their maximum abundance on nodule-facies C+ 10 to 15 %.

Distribution of holothurians on different facies

The following results were found for the most abundant holothurians: *Mesothuria murrayi* are preferentially present on nodule-facies C+ 10 % with a density of 40 ind/ha, *Benthodytes incerta* and *Synallactes profundi* are most abundant on nodule-facies BP 35-50 % with a density of 25 ind/ha, *Enypniastes eximia* on nodule-facies C+ 10 % with a density of 25 ind/ha, *Synallactes aenigma* on facies O with ancient sediments at a density of 21 ind/ha, and *Benthodytes sp.* on nodule-facies C+ 20-40 % with a slope > 15° at a density of 13 ind/ha. Specific habitat partitioning at the level of taxonomic units is thus observed.

Distribution of sponges on different facies

Maximum densities for sponges highlight certain habitat preferences, as for the hexactinellids *Hyalonema sp.* on nodule-facies C+ 10 % with a density of 57 ind/ha, *Caulophacus sp.* on nodule-facies C+ 15 % with a density of 51 ind/ha and *Pheronema sp.* on facies O on ancient sediments with 18 ind/ha, while the demosponge *Poecillasta sp.* appears to prefer nodule-facies C+ 2-5 % (density 16 ind/ha). Hexactinellids in the form of rings are most abundant on facies O with ancient sediments, but if the rings are two-horned, this taxon is most abundant on nodule-facies BP 35 %. The hexactinellids *Cornucopia sp.* are often present on nodule-facies C+ 20-40 % and on slopes and rock outcrops. Among the demosponges, *Cladorhiza sp.* are most abundant on facies O with ancient sediments and *Poecillastra sp.* on nodule-facies BP 35 % and C+ 40 %, while *Phakellia sp.* and *Esperiopsis sp.* are most abundant on nodule-facies C+ 10 %.

These quantitative data on the preferences of substratum displayed by different populations of actinids, holothurians and sponges raise the possibility that correlations exist between certain taxa and certain environmental factors such as slope and nodule coverage. A multivariate analysis could better demonstrate which factors govern the spatial heterogeneity of animal populations and thus help to identify possible ecological niches.

Multivariate analysis of benthic assemblages

Quantitative data on the fauna observed (144 taxa) and the nodule-facies and sediments (38 variables) of the NIXO 45 zone were subjected to a multi-dimensional scaling in order to demonstrate the internal structure of the data; from this, a series of hypotheses on the spatial heterogeneity of populations can be posed. The analysis expresses the organisation of the dispersion of a group of points according to a certain number of principal axes of inertia or "factors", by arranging them into a hierarchy. The degree of similarity of the different variables is shown graphically in two dimensions by the distance between taxa (figure 46) and between the different nodule-facies (figure 47). The first factor, the axis of maximum elongation or maximum variance between each pair of points, was selected. The degrees of similarity between the different variables are represented in figures 46 and 47.

In figures 46 and 47, the parabolic shape of the distribution of the points indicates a Guttman effect. This effect is frequently produced when one of the variables is naturally ordered. However, in figure 46, the taxa are arranged in a parabola with a break in continuity due to the isolation of some octocoralliarids (OCT 1, OCT 7), fish in families Ophidiidae and Ipnopnidae, asteroids in families Pterasteridae and Porcellenaste ridae, holothurians *Benthodytes sp.*, polychaetes in families Terebellidae and Cirratulidae, and sipunculids. The Guttman effect is most pronounced in figure 46 where the parabola relates to three groups of facies, the first containing all of facies O (with a clearly distinct subgroup on facies with ancient sediments), the second comprising facies with low nodule covering (C+ 2 to 20 % but with the exception of one of the facies C+ 40 %) and the third consisting of facies with a dense covering of nodules (C+ 30 %, 40 %; B 40 %, 50 % ; BP 35 %, BP 50 %). The group for facies O is clearly distinct from the two groups of facies with nodules and forms an oblique continuum following a gradient.

The significance of axis 1 appears to be the factor of nodule coverage, and this naturally ordered factor is the cause of the Guttman effect. But it is not the only reason for it because the continuum of nodule-bearing facies is not parallel to axis 1, and its obliqueness indicates a contribution by axis 2. It is also apparent that intra-facies heterogeneity is very low compared with inter-facies heterogeneity. Thus the identity of the selected facies has been preserved during sampling and the analysis of relationships enables discrimination between these facies. Examination of the absolute contributions reveals that the facies contributing most to the structure are the two facies O and particularly facies O with recent sediments, which contributes the most to axis 2.

One finds among the taxa that make the greatest contribution to plane 1-2 the list of the most frequently observed taxa (figure 42). The actinid *Syncionis tuberculata* is only significant for plane 1 by providing the greatest contributions, both absolute (16.5 %) and relative (0.79 %), to axis 1 and no contribution (0 %) to axis 2. In contrast, the echinoid *Pleisiodiadema globulosum* is responsible for the greatest contribution (8.6 %) to axis 2 as well as a considerable contribution (11.4 %) to axis 1.

It is by the multidimensional positioning of taxa and facies given by the indexes of similarity that one can obtain the ordination of taxa along "niche-dimensions" from the indexes of effective overlap provided by the multidimensional scaling. By superposing figures 46 and 47, one can discover certain faunistic and edaphic affinities that can be called "preferential habitats".

Faunal affinities in relation to edaphic gradient

The "niche-dimensions", by which faunal assemblages

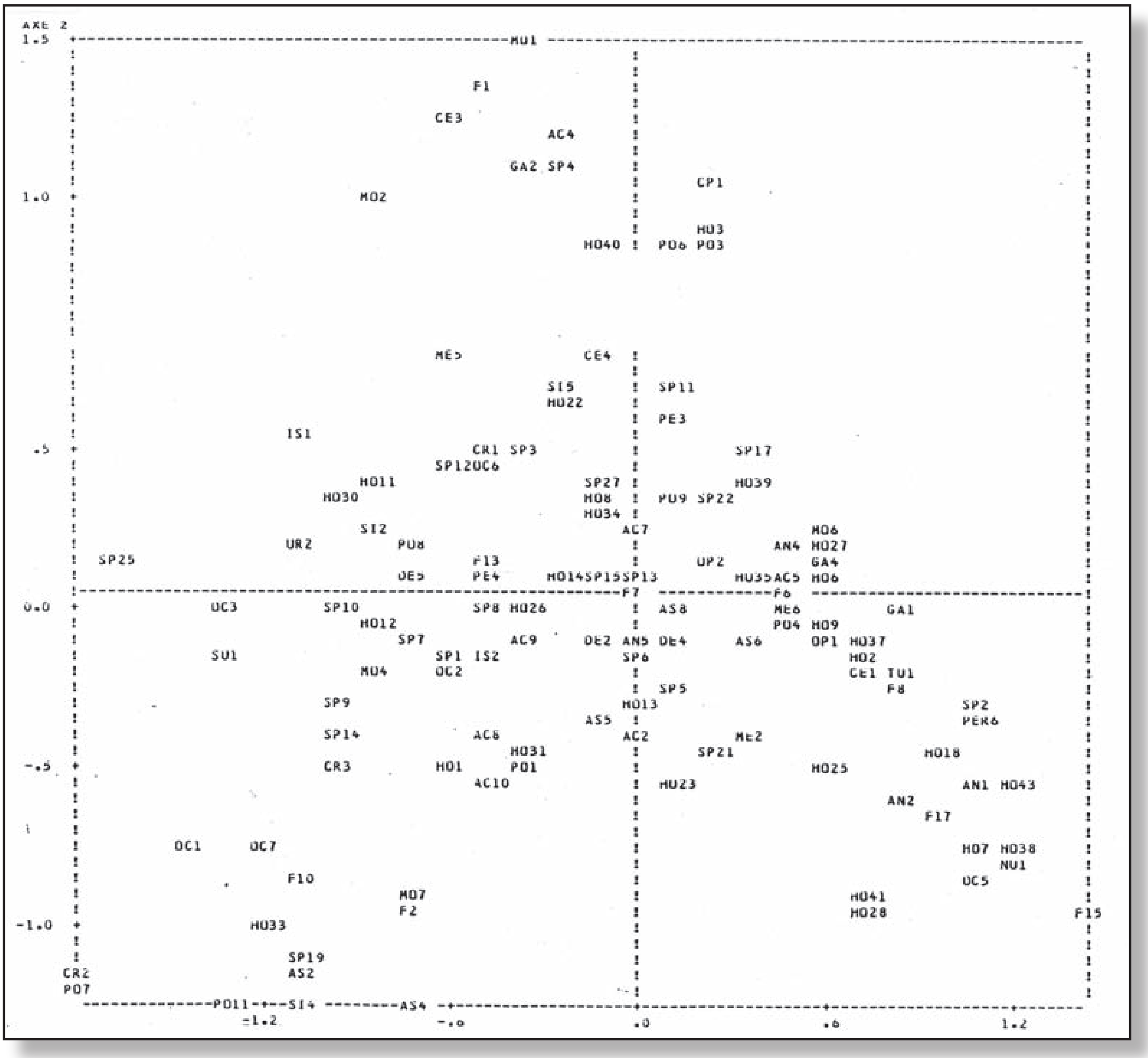


Fig. 46. Degree of similarity of the different taxa seen in the NIXO 45 site; Representation based on a multi-dimensional scaling.

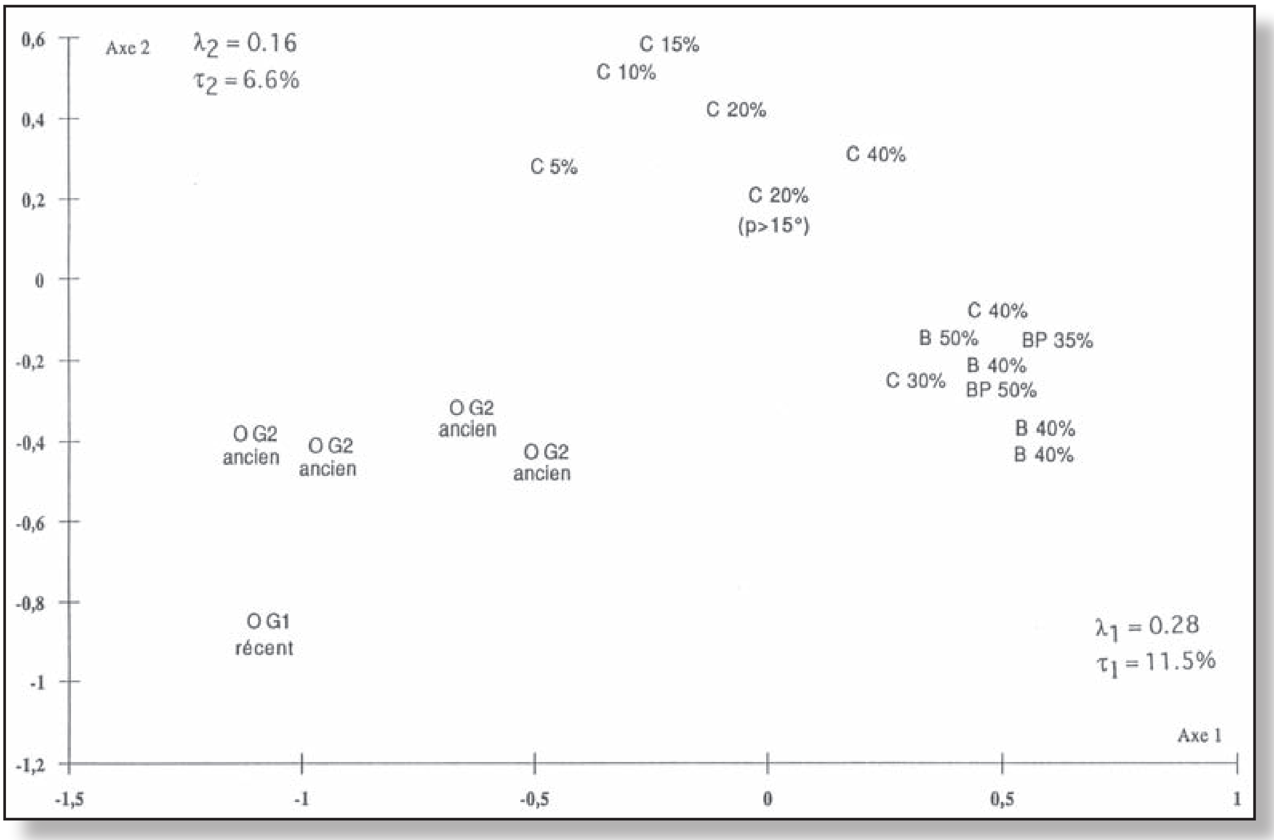


Fig. 47. Degree of similarity of the different nodule-facies of the NIXO 45 site; Representation based on a multi-dimensional scaling.

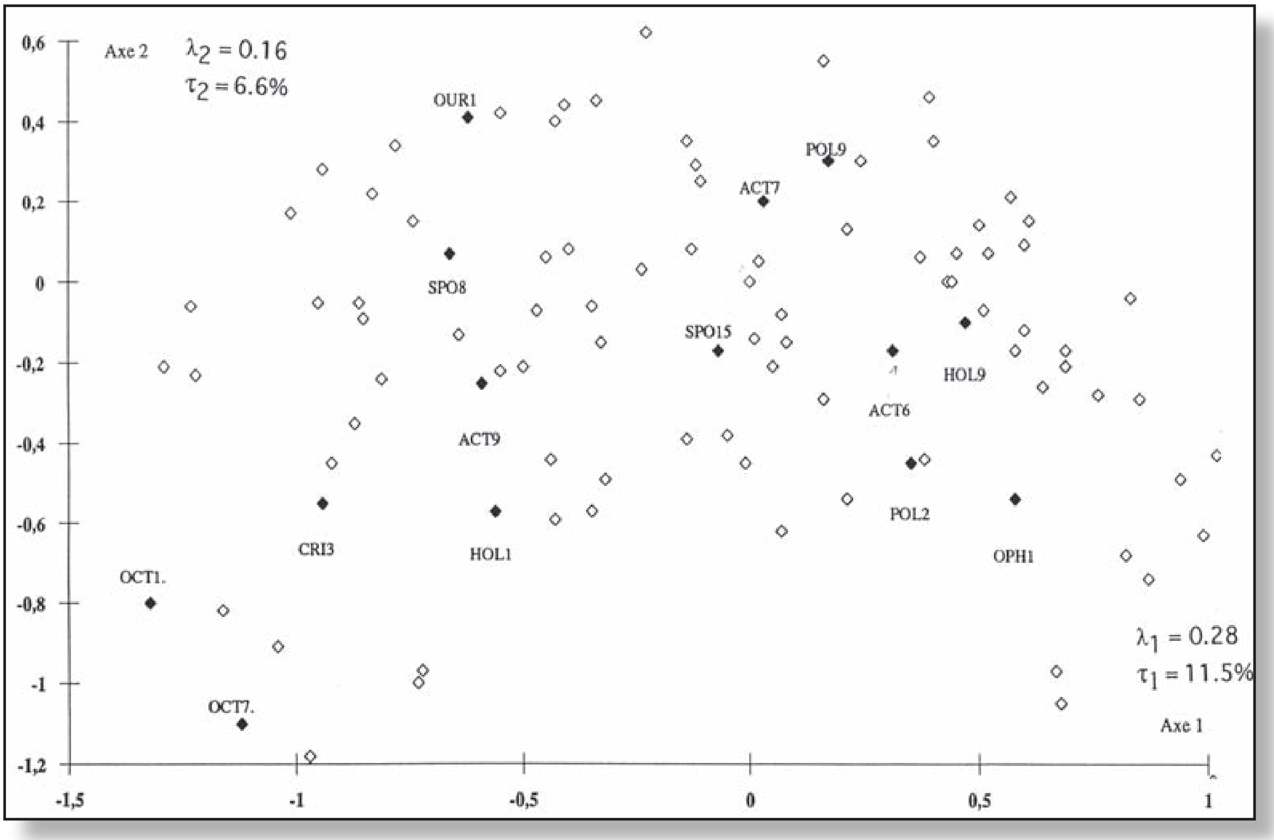


Fig. 48. Degree of similarity of the most abundant taxa at the NIXO 45 site; Representation based on a multi-dimensional scaling.

are organised, are extrapolated from the multivariate analysis of data. The multidimensional scaling shows that the principal factor that differentiates the "faunistic facies" is the effect of nodule coverage.

The most abundant taxa within the spread of points (figure 46) are shown in figure 45. Their abundance profiles in relation to different edaphic characteristics reveal habitat preferences and the existence of exclusive species. The order of abundance of the 16 taxa that are most frequently observed over the whole area (about 71 100 m^2 at the NIXO 45 site) is not followed here (figure 42). A heterogeneity of densities is apparent within the different nodule-facies, and certain peaks or plateaux exceed, at the scale of facies (about 3 750 m^2), the total densities for the whole study site. The results show that:

- Fixed crinoids of the family Hyocrinidae are abundant especially on facies O on ancient sediments, nodule-facies C+ 2 to 15 % and on nodule-facies with slope > 15° C+ 20-40 %. Their maximum density is 400 ind/ha on a facies O on ancient sediments.

- Octocoralliarids (OCT 7) of family Primnoidae are clearly most dense (221 ind/ha) on facies O with ancient sediments while other octocoralliarids (OCT 1), from family Isididae, have a higher density (342 ind/ha) on facies O with ancient sediments and on nodule-facies C+ 15 %. A peak of abundance of 109 ind/ha occurs on sloping facies.

- Echinoids (OUR 1) *Plesiodiadema globulosum* display a higher density on nodule-facies C+ 2 to 30 % with a peak of 187 ind/ha on nodule-facies C+ 10 %. Their density rises again on nodule-facies C+ with slope > 15°.

- Ophiuroids (OPH 1) *Ophiomusium armatum* are principally abundant on nodule-facies BP 35 % with a maximum density of 68 ind/ha.

The results also show more complex and varying peaks of density, with well marked peaks of abundance on nodule-facies C+ 2-20 % and peaks of lesser importance on sloping facies. From the details of the analyses, the following variations are observed:

- Scyphomedusas and hydromedusas are characterized by a small nodule coverage clearly more abundant on facies (C+ 2 -30 %), with a density of 61 ind/ha.

- Actinids of the family Actinerniidae display a peak of abundance of 51 ind/ha on nodule-facies C+ 15 %.

- Corallimorpharids have two peaks of abundance, the principal one of 37 ind/ha on nodule-facies C+ 2-5 % and the second of 23 ind/ha on nodule-facies BP 35 %.

- Sponges (SPO 15), belonging to the Hyalonematidae display two peaks of abundance, the first of 57 ind/ha on nodule-facies C+ 10 % and the second of 46 ind/ha on sloping facies. Sponges (SPO 8), in family Pachastrellidae, are abundant on facies O and facies with low nodule coverage (C+ 2-30 %), with an increase in density on nodule-facies BP 50 %, and a maximum density of 25 ind/ha on nodule-facies C+ 20 %.

- Holothurians (HOL 1) *Synallactes aenigma* are abundant on facies O (with a maximum density of 29 ind/ha), nodule-facies C+ 30 % and nodule-facies BP 50 %. Holothurians, (HOL 9) *Mesothuria murrayi*, display two peaks of abundance, the more pronounced one (39 ind/ha) on nodule-facies C+ 10 % and the second (24 ind/ha) on facies BP 35 %.

- Polynoids (POL 1 and POL 2) are abundant on facies O with ancient and recent sediments (with a peak of 34 ind/ha for POL 1) and on facies with high nodule coverage, B 40 % to 50 % and C+ 40 %. The polychaete worms (POL 9), *Incertae sedis*, living in contorted tubes about 40 cm long, are abundant especially on nodule-facies C+ and most particularly on sloping facies (26 ind/ha).

In general, suspension feeders show a great number of peaks of faunal abundance on facies O with ancient sediments and on sloping nodule-facies C+ 20 to 40 % and an essentially detritus feeding fauna is seen on nodule-facies C+ 10 %. Facies O with ancient sediments and nodule-facies C+ 15 % accommodate the most exclusive taxa.

The different faunal assemblages that characterize each facies are the following:

- **Nodule-facies O on recent sediments** is distinguished by the abundance of a mobile fauna, mainly detritus feeders and carnivores, and composed of isopods of the family Munnopsidae, asteroids of the family Porcellenasteridae, and Ophidioid and Ipnopid fish. Suspension feeders on this facies are sedentary polychaete worms responsible for a particular form of disturbance known in the literature as "witches rings" which sometimes encircle a central mound (Heezen & Hollister, 1971). Taxa exclusive to this facies are sedentary polychaetes of the family Cirratulidae, the holothurians *Psychropotes longicauda* from family Psychropotidae and the siphonophores *Physonectes*.

- **Nodule-facies O on ancient sediments** is characterised by a majority of suspension feeders, notably octocoralliarids belonging to the families Primnoidae and Isididae, Hyocrinidae, and actinids of the families Hormathiidae and Actinoscyphiidae. Detritus feeders are represented by Pterasteridae, holothurians such as *Synallactes aenigma* and *Benthodytes lingua*, and by peracarids, probably of the order Cumacea. Taxa unique to this facies are suspension feeders such as Demospongia of the family Cladorhizidae and sedentary polychaetes which form characteristic rounded mounds. Detritus feeders exclusive to this facies are the asteroids *Hymenaster violaceus* and the holothurians *Benthodytes lingua*, and exclusive carnivores such as gastropods of the family Pterotracheidae and Liparid fish.

- **Nodule-facies C+ 2-5 %** has especially a fixed fauna with a predominance of suspension feeders such as alveolate hexactinellid sponges, which are unique to this facies, octocoralliarids belonging to the families Isididae and Umbellulidae and corallimorpharids of the family Sideractiidae. The most abundant detritus feeders are Munnopsid isopods and the holothurians *Peniagone gracilis*. Ophidioid fish are the most abundant carnivores. Taxa exclusive to this facies are bivalves belonging to the Vesicomyidae.

- **Nodule-facies C+ 10 %** accommodates in great abundance a fauna that is largely mobile and detritus feeding such as the sipunculids *Nephasoma elisae*, the echinoids *Plesiodiadema globulosum* and the holothurians *Mesothuria murrayi, Paelopatides sp.* and *Pannychia moseleyi*. The most abundant suspension feeders of this facies are Hexactinellid sponges of the Hyalonematidae and the octocoralliarids Primnoidae. Carnivores are medusas of the family Trachynemidae and decapods of the genus *Plesiopenaeus*, which are exclusive to this facies, as are demospongian sponges of the genus *Phakellia*.

- **Nodule-facies C+ 15 %** is distinguished by an essentially mobile and largely suspension-feeding fauna such as the actinids *Liponema* and *Actinoscyphia sp.* and polychaete members of the Sabellidae. The most abundant detritus feeders are echinoids of the family Aeropsidae, which leave a characteristic sinuous trail, and the holothurians *Peniagone vitrea*. Abundant carnivores on this facies are archaeogastropods and siphonophores of the family Rhodaliidae. Taxa exclusive to this facies are, for the most part, carnivores such as a Physonectes siphonophores, neogastropod members of the Turridae, polychaetes in families Polynoidae or Aphroditidae and fish *Coryphaenoides yaquinae*. Suspension feeders unique to the facies are sponges of the family Caulophacidae.

- **Nodule-facies C+ 20 %** is characterised by mobile organisms, mostly suspension feeders such as sponges of the genus *Poecillastra* and free crinoids belonging to the family Antedonidae. Detritus feeders are peracarids of the order Cumacea and the holothurian *Meseres macdonaldi*. Taxa unique to this facies are sponges of the genus *Hyalonema*, Chiroteuthid cephalopods and Galatheids with a rounded rostrum.

- **Nodule-facies C+ 30 %** has an abundant mobile fauna which is largely carnivorous, such as cephalopods of the genus *Benthesicymus* (unique to this facies), and medusas of the family Nausithoidae. The common detritus feeders on this facies are the swimming holothurians *Enypniastes eximia*.

- **Nodule-facies C+ 20 to 40 % on slopes > 15°** is differentiated by a fixed fauna mostly of suspension feeders represented by Hexactinellid sponges in the form of a ring, others in the shape of a dish, or members of the Rossellidae, Euretidae and Demospongia of the family Cladorhizidae, as well as sedentary polychaetes in contorted tubes about 40 cm long. The most abundant detritus feeders on this sloping facies are echinoderms such as Brisingidae with 10 arms and holothurians of the genus *Benthodytes*. Carnivores are decapods of the genus *Nematocarcinus* and Bythitidae fish of the genus *Typhlonus*. A taxon exclusive to this facies is a peracarid of the order Tanaidacea.

- **Nodule-facies C+ 40 %** has a fauna in the main consisting of carnivorous polychaetes from the families Hesionidae and Aphroditidae and swimming polychaetes *Incertae sedis* about 10 cm and dark in colour. Abundant detritus feeders on this facies are holothurians *Peniagone intermedia* while suspension feeders are sponges of the genus *Euplectella* and dark ophiuroids belonging to the genus *Ophiomusium*. Taxa unique to this facies are the holothurians *Orphnurgus* and *Amperima naresi* and ascidians about 30 cm diameter and apparently free-living.

- **Nodule-facies B 40 %** is distinguished by a predominance of mobile detritus feeders such as the holothurians *Psychronaetes hanseni* and *Benthodytes typica* and asteroids of the genus *Hymenaster*. Suspension feeders are the antipatharids *Bathypates patula* and *Bathypates lyra* as well as Brisingidae of the genus *Freyella*. Taxa unique to this facies are mostly detritus feeders such as peracarid amphipods and holothurians belonging to the family Elpidiidae and the Deimatidae such as *Deima validum*. A suspension feeder unique to this facies is an octocoralliarid of the family Umbellulidae.

- **Nodule-facies B 50 %** has only one abundant suspension feeder, the actinid *Sincyonis tuberculata* and one carnivore, a swimming aphroditid polychaete. A unique taxon is the antipatharid *Schizopathes crassa*.
- **Nodule-facies BP 35 %** is characterised by a fauna of fixed suspension feeders including vase-shaped sponges of the genus *Poecillastra*, actinids of the genera *Bolocera* and *Actinoscyphia* as well as ophiuroids identified as *Ophiomusium armatum*. A two-horned ring-shaped Hexactinellid sponge is exclusive to this facies.
- **Nodule-facies BP 50 %** has a fauna comprised mostly of quite abundant detritivorous holothurians such as *Synallactes aenigma, Synallactes profundi* and *Peniagone leanderas* well as a member of the genus *Benthodytes*. A carnivorous polynoid polychaete also proliferates on this facies, and a nudibranch (NUD1) is exclusive to it.

Spatial heterogeneity at a nodule-facies level

The intra-facies spatial distribution of some of the most frequently observed taxa in the study area is analysed here. A more or less aggregated spatial distribution can also be indicative of the functional relationships that some organisms maintain with their substratum. The heterogeneity in space and time of some populations can create, by bioturbation (Tilot, 1991), a microheterogeneity of habitats. According to the equilibrium theory of Sanders (1968), this would lead to mechanisms of partitioning trophic resources, and is one of the hypotheses explaining the great taxonomic richness found in the abyssal environment.

An analysis was made of the distribution of two of the most abundant taxa at the study site which belong to the best represented phyla and functional groups: the actinids, *Sincyonis tuberculata* and the holothurians, *Mesothuria murrayi*. The aim was to identify the level of spatial heterogeneity of their populations within nodule-facies O, C+, B and BP, in order to compare the observed distributions with certain types of theoretical distribution that are commonly seen in nature, such as: random distribution corresponding to a Poisson curve, regular distribution corresponding to a normal curve and aggregated distribution corresponding principally to a negative binomial curve.

Four total sampling areas were considered: facies O and nodule-facies B covering surface areas of 15 300 m^2 and 15 400 m^2 respectively, 28 700 m^2 for nodule-facies C+ and nodule-facies BP with a surface area of 7 900 m^2 .

The spatial distribution of taxa was estimated by means of relationships which combined the mean X and the variance σ^2 for the following different unit areas (or quadrats): 50 m^2, 100 m^2, 200 m^2, 400 m^2, 800 m^2, 1 600 m^2, 3 200 m^2, 6 400 m^2 (12 800 m^2 and 25 600 m^2 for nodule-facies C+). Following the recommendations of Elliot (1971), the following distribution indexes were calculated:

Fisher coefficient: $d=\frac{s2}{\overline{X}}$

Lexis index = $\frac{s2}{\sqrt{\overline{X}}}$,

David & Moore index = $\frac{s2}{\overline{X}}-1$

and Morisita index: $I\delta = n\,\frac{S(x2)-Sx}{(Sx)2-Sx}$

The size of the sampling areas or quadrats is essential to the analysis of distribution of a taxon. An aggregated distribution can only be detected when the area of the quadrat is greater than that occupied by one or rather several aggregations of taxa.

The results show that:

- **on nodule-facies C+** the distribution of *Sincyonis tuberculata* is aggregated above 1600 m^2 according to the Levis, David & Moore indexes and Fisher's coefficient, and random at 400 m^2 and 800 m^2.
- **on nodule-facies O** the distribution is random at 1 600 m^2 while at 800 m^2, it is aggregated. However, it may be that in an area of 1600 m^2 the population of *Sincyonis tuberculata* is distributed in small aggregations that are arranged in a random fashion according to Poisson's law.

Table 2 presents changes in the ratios of Morisita indexes for quadrat areas within the four facies studied. A distinct peak occurs at 32 q suggesting that the size of aggregations of *Sincyonis tuberculata* on facies O is 1600 m^2. Distributions on the three other facies follow similar trends, i.e. slightly aggregated at quadrat sizes of 100 m^2 up to 400 m^2 on nodule-facies C+ then random. Above 6 400 m^2 they all decline, indicating that sampling areas are large enough to encompass possible aggregations of actinids.

The analysis of types of distribution pattern for the most abundant holothurians at the study site, *Mesothuria murrayi*, has been made by changes in the ratio of Morisita indices (table 3). The distribution and sizes of aggregations of populations of *Mesothuria murrayi* vary according to nodule-facies :

- on nodule-facies B, the distribution becomes random between 200 m^2 and 800 m^2,
- on nodule-facies C+, the distribution is aggregated at 100 m^2 and 400 m^2, and random between 800 m^2 and 1 600 m^2,
- on nodule-facies BP, the distribution is aggregated with a peak at 800 m^2 and another lesser peak at 200 m^2,
- on nodule-facies O, no holothurians belonging to *Mesothuria murrayi* are observed.

The peak of aggregation at 400 m^2 agrees with the results of an analysis of spatial heterogeneity of the holothurians *Mesothuria sp.* and *Benthogone rosea sp.* in the Atlantic Ocean (Sibuet, 1987). As for populations of *Sincyonis tuberculata*, the curves of change in ratio for the Morisita indexes on nodule-facies B and C+ tend towards a maximum spread above 2 800 m^2.

$\frac{I\delta}{I\delta}$	$\frac{50}{100}$	$\frac{100}{200}$	$\frac{200}{400}$	$\frac{400}{800}$	$\frac{800}{1600}$	$\frac{1600}{3200}$	$\frac{3200}{6400}$	$\frac{6400}{12800}$	$\frac{12800}{25600}$
Faciès C^+	1,1	1,1	1,1	1	0,9	0,9	0,9	0,86	0,75
Faciès O	1,2	1	1,2	0,9	1,7	1,2	0,9	0,75	
Faciès B	1,1	0,9	1	1	0,9	0,9	0,8	0,75	

Table 2. Summary of the variation of the ratios of Morisita indexes, defining the distributions adopted by populations of actinids *Sincyonis tuberculata* with increasing quadrat size on three different nodule-facies in the NIXO 45 site.

$\frac{I\delta}{I\delta}$	$\frac{50}{100}$	$\frac{100}{200}$	$\frac{200}{400}$	$\frac{400}{800}$	$\frac{800}{1600}$	$\frac{1600}{3200}$	$\frac{3200}{6400}$	$\frac{6400}{12800}$	$\frac{12800}{25600}$
Faciès C^+	2,3	1,7	1,9	1,4	1,2	0,8	1,2	0,8	0,7
Faciès B	1	1,5	1,1	1,3	0,8	0,8	0,9	0,7	
Faciès BP	0,6	1,4	1,1	2,2	0,5	0,9	0,9		

Table 3. Summary of the variation of the ratios of Morisita indexes, defining the distributions adopted by populations of holothurians *Mesothuria murrayi* with increasing quadrat size on three different nodule-facies in the NIXO 45 site.

Comparison of faunal data from the 'Nautile' and the 'Épaulard'

To compare two different methods of photographic exploration, the 'Épaulard', equipped with a photographic camera, and the manned submersible 'Nautile', with its video camera, data were analysed from a transect 1 250 m long filmed by the 'Nautile'. This was the only transect of the NIXONAUT cruise (1988) which travelled at a steady speed in a straight line, at an altitude of about 5 m and was thus comparable to a photographic transect made by the 'Épaulard'. This transect passed over a nodule-facies B mean 40 % in the NIXO 45 zone.

Figure 49 shows the abundance of various taxa classified by phylum. It is immediately evident that densities in all faunal categories are generally higher (1.4 to 1.7 times for the dominant phyla) in the video data from the 'Nautile' than in the data from the 'Épaulard'. The total density of the megafauna was estimated from the 'Nautile' as 508 ind/ha whereas it was only 312 ind/ha in the photographic transects from the 'Épaulard'. This may be due to the fact that the area explored along the trajectory of the 'Nautile' was less (2 500 m^2) than that for the 'Épaulard' (3 850 m^2).

These results contradict the suggestion that one would find a smaller number of taxa in the transects viewed by the 'Nautile' because of its oblique descending view and its scrolling, rather than fixed, images. However, a greater number of fish was observed along the transect of the 'Nautile' (20 ind/ha, i.e. 12 times more than in the images from the 'Épaulard'). Fish appear to be attracted by the activities of the submersible and the cloud of benthic sediments that is caused by the movement of water close to the ocean floor.

The fauna recorded on the images taken by the 'Nautile' displays in general the same taxonomic proportions as those observed by the 'Épaulard', with cnidarians (228 ind/ha of which 93 % actinids) and echinoderms (132 ind/ha of which 67 % holothurians). However, the density of echiurians is greater (48 ind/ha, against 11 ind/ha in the 'Épaulard' data). Their mounds, about 210 cm long by 65 cm wide, are more easily detected in the videos from the 'Nautile'. In contrast, wandering polychaetes are more easily detected in the 'Épaulard' images, where they are abundant, having a density of 44 ind/ha (1.6 times greater than in video images from the 'Nautile'), but their presence could also be interpreted as a seasonal phenomenon linked to changes in environmental conditions and flux in particulate matter. Sipunculids and gastropod molluscs, at the limit of the megafauna, were detected in the transect filmed by the 'Nautile', while no members of these groups were observed along the transect sampled by the 'Épaulard'. However, for the 'Nautile', taxa could not be identified as precisely as they could in the photographs taken by the 'Épaulard' and the level of identification could not be extended beyond taxonomic order.

Figure 50 shows the trophic and functional composition of the fauna observed on nodule-facies B 40 % from the 'Épaulard' and 'Nautile'. The proportions of different faunal groups and the order of their relative abundance are similar, although suspension feeders and detritus feeders are about 0.5 times as many in the transect from the 'Nautile', and carnivores and scavengers have more or less the same total density. The abundance of polynoids in images from the 'Épaulard' balances out the greater number of fish in films taken by the 'Nautile'.

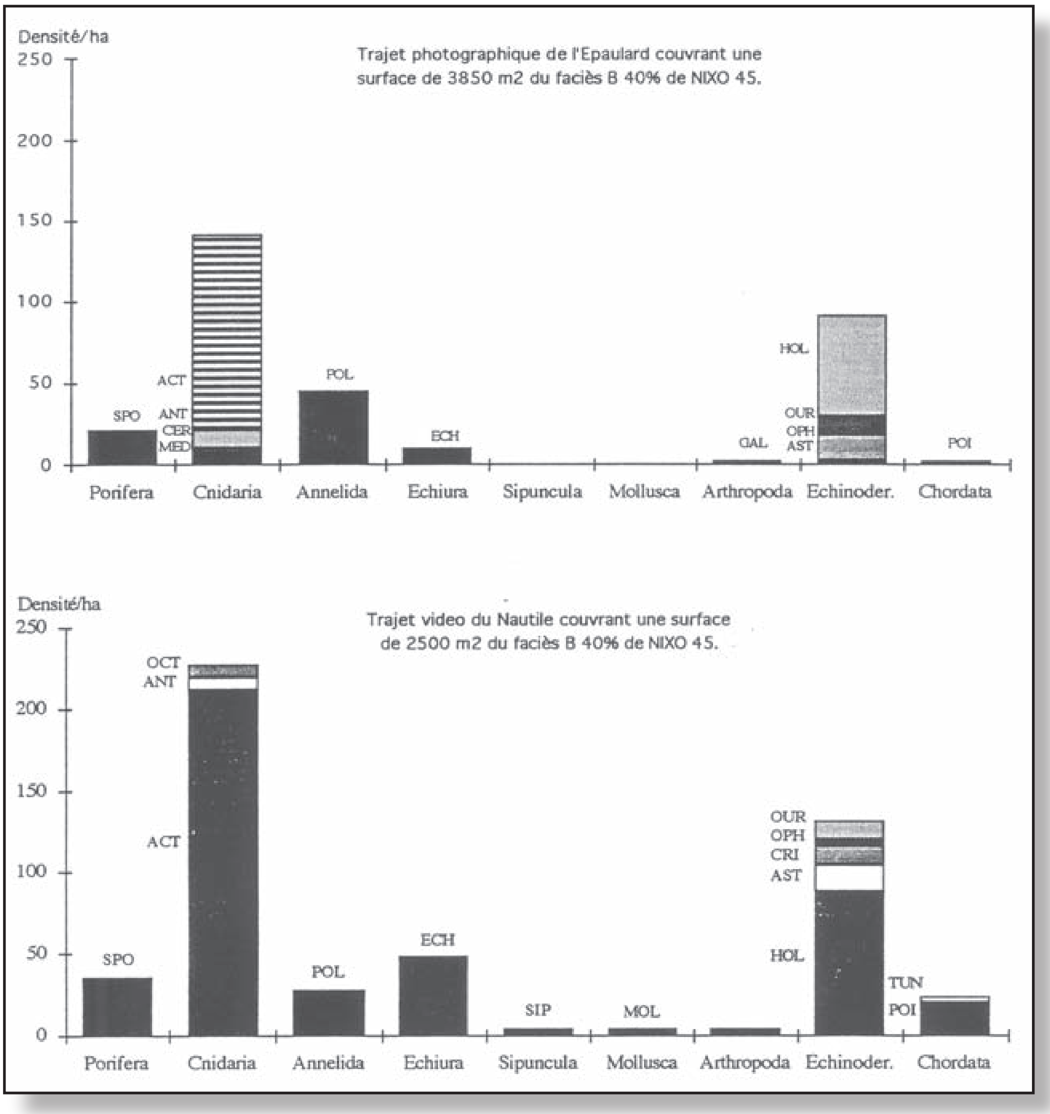


Fig. 49. Histograms of the partitioned abundance of taxa, arranged by phylum, filmed by the 'Nautile' on a transect over nodule-facies B 40 %, during the NIXONAUT cruise.

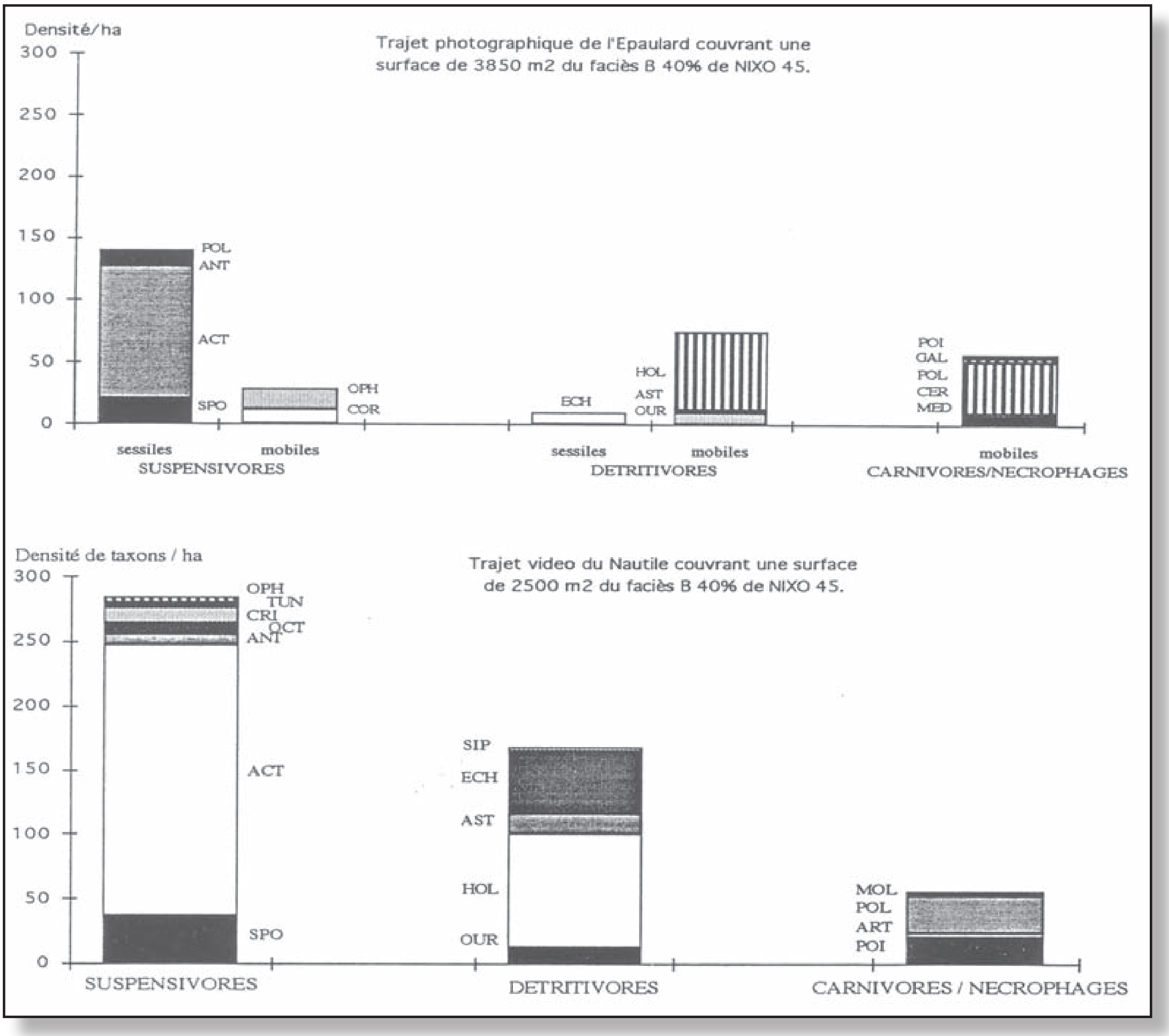


Fig. 50. Histograms of the partitioned abundance of taxa, arranged by trophic and functional group, filmed by the 'Nautile' on a transect over nodule-facies B 40 %, during the NIXONAUT cruise.

5.2. THE NIXO 41 SITE

Faunal abundance composition by phylum

In order to make comparisons, faunal data from three nodule-facies at the NIXO 41 site were analysed, nodule-facies A 30 %, C+ 30 % and B 35 %. Since nodule-facies A (covered with small smooth nodules 20 to 30 mm diameter) was too under-represented at the NIXO 45 site to be used in quantitative analyses, it was investigated at the NIXO 41 site even though fewer photographs were collected than for the NIXO 45 site. This facies had a nodule covering of 30 % at the NIXO 41 site.

Nodule-facies C+ 30 % and B 35 % were compared with homologous facies at the NIXO 45 site. At NIXO 45 the area analysed for each facies was estimated at about 3 850 m^2, but usable data was more limited at NIXO 41 and the areas analysed were smaller, with nodule-facies A 30 % covering only 2 950 m^2, nodule-facies C+ 30 % 3 100 m^2 and nodule-facies B 35 %, 2 300 m^2.

The means of exploration at the NIXO 41 site also differed from those used at NIXO 45, by using the towed 'R.A.I.E', which took photographs every 32 seconds at an elevation of approximately 5 m. The strategy of sampling also differed: at NIXO 45 the transects covered by the 'Épaulard' were more meandering and sampled facies in more detail (figure 19) while at the NIXO 41 site, the 'R.A.I.E.' had a long rectilinear route. The extent of the areas photographed were similar to those recorded by the 'Épaulard' with the same objective lenses and shot vertically; however, fewer photographs were taken at sufficient height (5 m) for both qualitative and quantitative analysis.

Figure 51 summarizes the faunistic composition classified by phylum of the three nodule-facies studied at the NIXO 41 site:

- Overall, echinoderms (622 ind/ha) are the most abundant group and outnumber cnidarians (459 ind/ha).

- On nodule-facies C+ 30 %, the densities of the two phyla are much higher than on the same facies at the NIXO 45 site (where their densities are 86 ind/ha and 204 ind/ha respectively). At the NIXO 41 site, the most abundant echinoderms are ophiuroids (156 ind/ha) while at NIXO 45, the dominant members of this phylum are holothurians and crinoids on sloping nodule-facies C. In addition, the density of actinids (456 ind/ha) on nodule-facies C+ 30 % is 2.5 times greater. Sponges number 65 ind/ha, while their density at the NIXO 45 site is only 18 ind/ha. Densities for polychaetes and echinoids are respectively 3.2 and 2.6 times greater at the NIXO 41 site, and only holothurians have similar mean densities (9 ind/ha) at both sites.

- On nodule-facies A 30 %, echinoderms (247 ind/ha) are again more numerous than cnidarians (135 ind/ha) but to a lesser degree. The density of cnidarians is similar to that (141 ind/ha) on nodule-facies B 40 % at NIXO 45, while the greater density of echinoderms approaches that seen on sloping nodule-facies C+ 20 to 40 % at the NIXO 45 site. Nodule-facies A 30 % is characterised by a relatively high density (30 ind/ha) of echiurians, which is twice

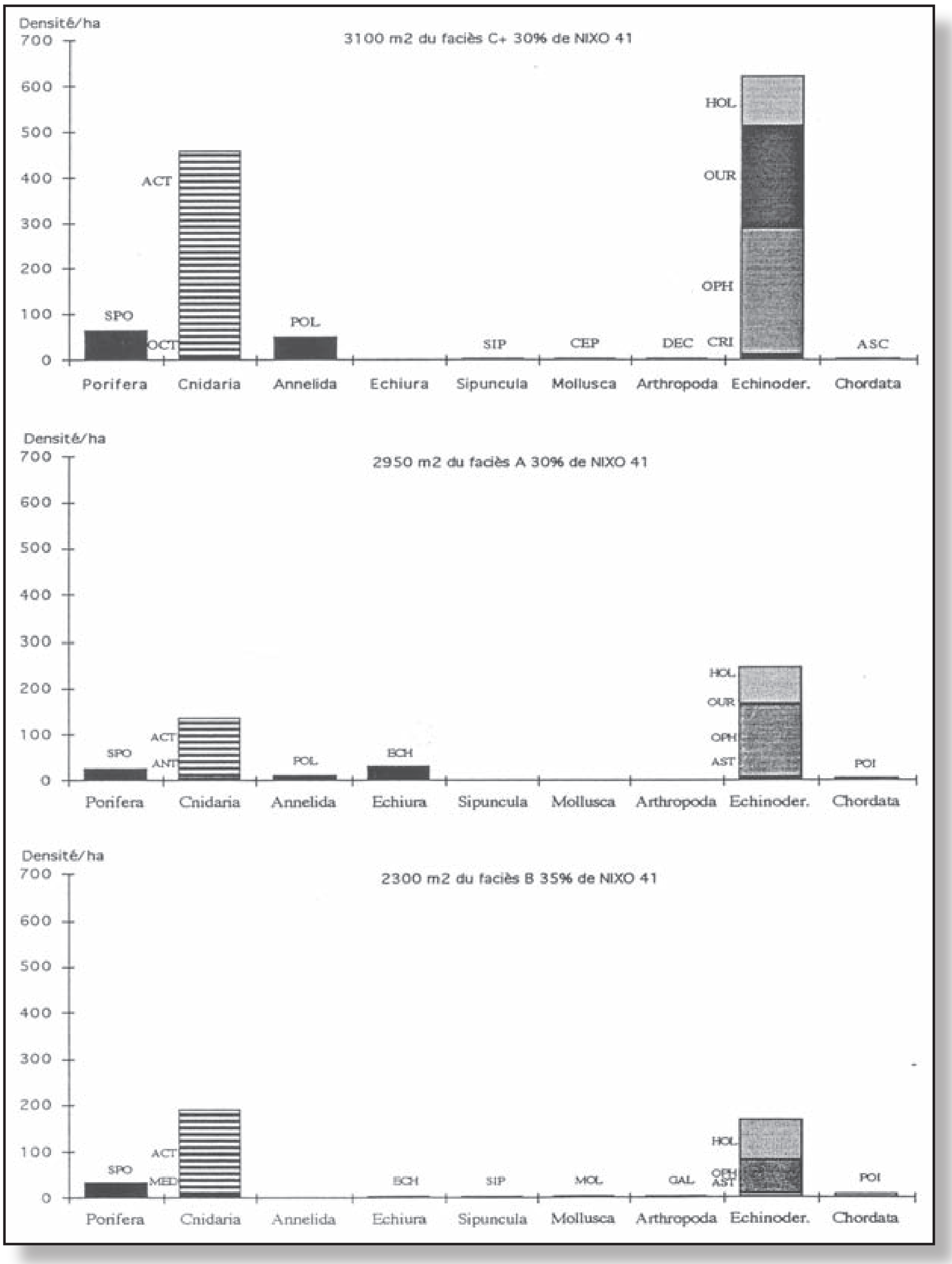


Fig. 51. Histograms of the partitioned abundance of taxa, arranged by phylum, observed by the 'R.A.I.E.' on three nodule-facies in the NIXO 41 site.

their greatest abundance (16 ind/ha) recorded at the NIXO 45 site on nodule-facies B 50 %.

- The faunal composition of nodule-facies B 35 % resembles that found at NIXO 45. Cnidarians (190 ind/ha) predominate slightly over echinoderms (168 ind/ha), as on nodule-facies B 40 % at NIXO 45, although densities there are lower (141 ind/ha and 91 ind/ha respectively).

Faunal composition by trophic and functional groups

For the NIXO 41 site, taxa were classified by trophic and functional group to determine whether the greater abundance of echinoderms in relation to cnidarians on nodule-facies C+ 30 % and A 30 % was reflected in the composition of the faunal assemblages by a greater proportion of detritus feeders than suspension feeders. On nodule-facies B 35 % at NIXO 41 and on all nodule-facies at NIXO 45, suspension feeders are more numerous.

However, figure 52 shows clearly that suspension feeders predominate over detritus feeders because ophiuroids, which are the dominant group of echinoderms at NIXO 41, are principally suspension feeders. Thus the trophic groups have the same order of abundance as at the NIXO 45 site.

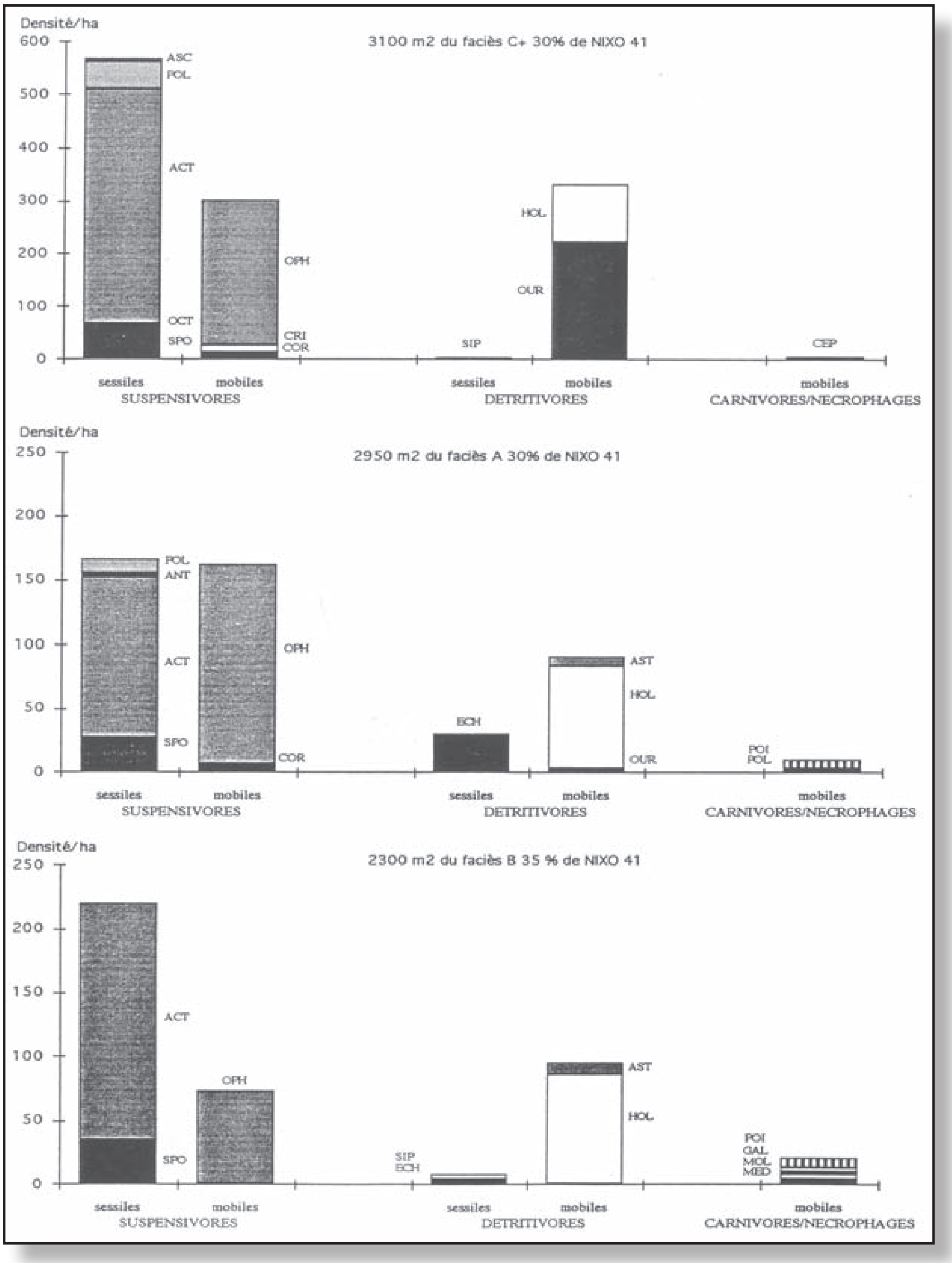


Fig. 52. Histograms of the partitioned abundance of taxa, arranged by trophic and functional group, observed by the 'R.A.I.E.' on three nodule-facies in the NIXO 41 site.

Sessile suspension feeders on nodule-facies C+ 30 % reach densities comparable to those observed on sloping nodule-facies C+ 20 to 40 % at NIXO 45. The relatively high density of mobile detritus feeders is close to that on nodule-facies C+ 10 % at NIXO 45.

Nodule-facies A, because of its large population of ophiuroids, is remarkable for having almost equal densities of mobile and sessile suspension feeders, while the relatively large proportion of sessile detritus feeders is due to echiurians.

Mobile suspension feeders, which are mostly ophiuroids, are in relatively low abundance (73 ind/ha) on nodule-facies B 35 % but nevertheless, their density is close to that of the holothurians, which are the principal mobile detritus feeders.

Quantitative analysis at the level of taxa

The most abundant 20 taxa over the whole of the NIXO 41 site are shown in figure 53. It is noticeable that most of the taxa are the same as those identified at the NIXO 45 site (figure 45). Densities for the most abundant taxa, in decreasing order, are 232 ind/ha for the actinids *Sincyonis tuberculata* (ACT 6), 174 ind/ha for the brittle stars *Ophiomusium armatum* (OPH 1) (their density at this site is unique), 83 ind/ha for sea urchins *Plesiodiadema globulosum* (OUR 1), 25 ind/ha for holothurians *Psychronaetes hanseni* (HOL 21), 23 ind/ha for actinids *Actinernus verrill* (ACT 7) and 23 ind/ha for polychaete worms *Incertae sedis* living in contorted tubes 40 cm long (POL 9). Abundances distinctive to this zone are those of free crinoids *Fariometra parvula* (CRI 1), brittle stars *Ophiomusium armatum* (OPH 1) including a dark form of *Ophiomusium armatum* (OPH 2), holothurians *Psychronaetes hanseni* (HOL 21) and *Paelopatides sp.* (HOL 22), echiurians *Jacobia birsteini* (ECH 1), sponges of the genus *Pheronema* (SPO 14) and hexactinellids *Incertae sedis* with an alveoliform disc (SPO 3).

Distribution of various holothurians on different facies

Analyses demonstrate that certain holothurians have affinities with particular edaphic conditions at the NIXO 41 site:

- Holothurians *Synallactes aenigma* (HOL 1) prefer nodule-facies C+ 30 % and B 35 % where their density is 16 ind/ha. This value is close to that observed on nodule-facies C+ 30 % at the NIXO 45 site (18 ind/ha) but much higher than the low densities (3 ind/ha) recorded on nodule-facies B 40 % at NIXO 45. Because of insufficient data, it was not possible to determine whether these holothurians are more abundant on facies O on ancient sediments, as it is at the NIXO 45 site where the density reaches 21 ind/ha.

- Holothurians *Synallactes profundi* (HOL 2) are recorded on all three nodule-facies at NIXO 41, but especially on nodule-facies C+ 30 % where their abundance is 29 ind/ha. On the homologous facies at NIXO 45, they are only observed at a density of 5 ind/ha. In contrast, this taxon is present at a comparable density (25 ind/ha) on nodule-facies BP 50 %.

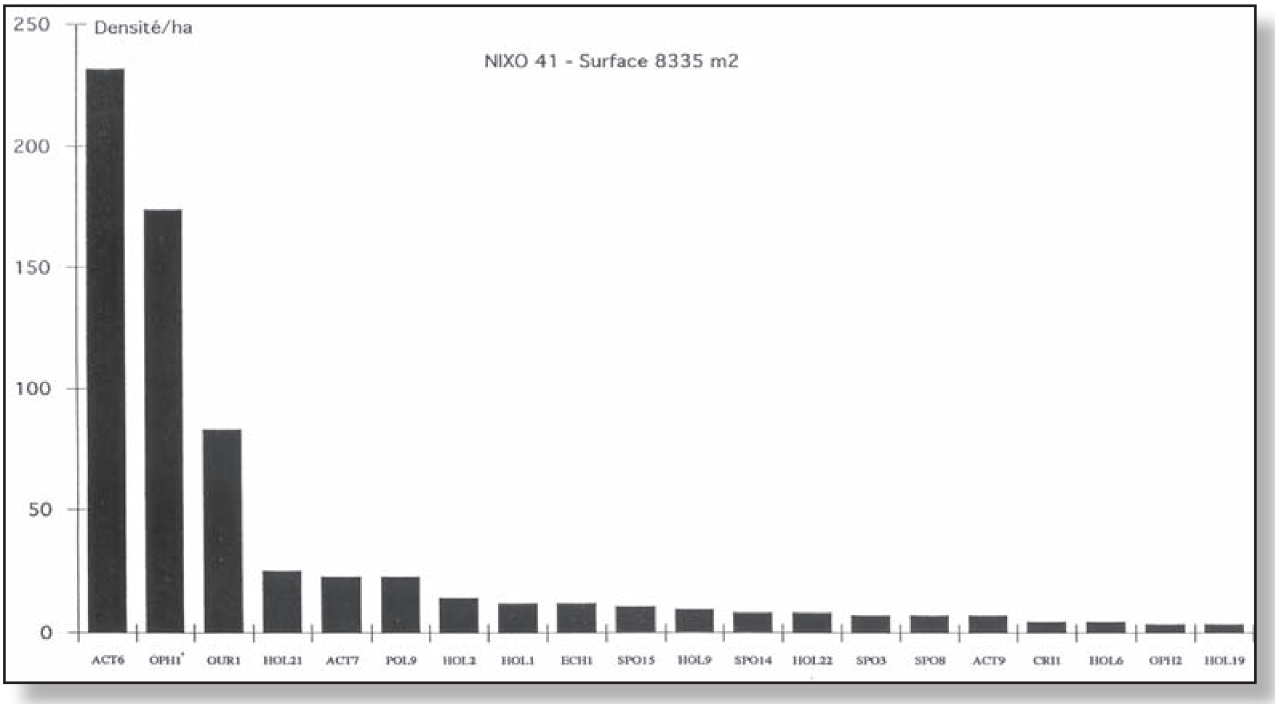


Fig. 53. Histogram of the density of the 20 most abundant taxons in the NIXO 41 site.

- Holothurians *Deima validum* (HOL 5) are only identified on nodule-facies A 30 % at low density (3 ind/ha). This result is similar to that observed on nodule-facies B 40 % at the NIXO 45 site.

- Holothurians *Benthodytes sp.* (HOL 6) are observed on nodule-facies A 30 % and especially on nodule-facies C+ 30 %, with a density of 10 ind/ha. At the NIXO 45 site these taxa prefer (16 ind/ha) sloping nodule-facies C+ 20 to 40 %.

- Holothurians *Mesothuria murrayi* (HOL 9) are especially abundant on nodule-facies A 30 % with a density of 14 ind/ha. At the NIXO 45 site, these holothurians prefer nodule-facies C+ 10 % (40 ind/ha).

- Holothurians *Peniagone vitrea* (HOL 11) and Amperima rosea (HOL13) are only observed on nodule-facies A 30 % at low density (3 ind/ha). *Peniagone vitrea* occur on nodule-facies C+ 15 % at NIXO 45 at this same low density while *Amperima rosea* prefer nodule-facies C+ 2 to 5 % with a density of 5 ind/ha.

- Holothurians *Peniagone intermedia* (HOL 14) are only found on nodule-facies B 35 % at a density of 4 ind/ha. The taxon is not recorded on nodule-facies B 40 % at NIXO 45 but is present on nodule-facies C+ 40 %, where it is at a similar density of 6 ind/ha.

- Holothurians *Peniagone leander* (HOL 19) prefer nodule-facies C+ 30 % and A 30 % where their abundance is 7 ind/ha. These results confirm those observed at NIXO 45 (C+ 30 %).

- Holothurians *Enypniastes eximia* (HOL 18) prefer nodule-facies C+ 30 % with a density of 7 ind/ha. Their density on the same facies is similar (6 ind/ha) at the NIXO 45 site, where they are especially abundant on nodule-facies C+ 10 % with a density of 25 ind/ha.

- Holothurians *Psychronaetes hanseni* (HOL 21) are abundant on all nodule-facies and especially B 35 % where their density is relatively high (47 ind/ha). On the homologous facies at the NIXO 45 site it has a much lower density (10 ind/ha).

- Holothurians of the genus *Paelopatides* (HOL 22) are most frequent on nodule-facies B 35 % at a density of 4 ind/ha, the same density at which they are found on nodule-facies C+ 10 % at the NIXO 45 site.

In conclusion, the data from similar depths in regions of polymetallic nodules are comparable despite different methods of exploration and sampling strategies. No taxon is found to be exclusive to the NIXO 41 site, and all the taxa observed here have already been identified from NIXO 45. Faunal composition and levels of abundance on nodule-facies B 35 % are similar to those of the same facies at the NIXO 45 site.

In contrast, nodule-facies C+ 30 % is distinguished from that at NIXO 45 by its greater faunal abundance and by a reversal in the usual order of dominance observed at sites in the present study. Echinoderms are the most abundant group, with a high density of ophiuroids whose suspension-feeding behaviour maintains the predominance of suspension feeders over detritus feeders. Nodule-facies A 30 % resembles nodule-facies B 40 % in its population of cnidarians, and resembles sloping nodule-facies C+ 20 to 40 % in having a majority of echinoderms. This facies is also characterised by a relatively high density of sessile detritus feeding echiurians.

In taking the example of holothurians, it is noticeable that some have the same preferential habitats and abundances as their homologues at NIXO 45, such as *Synallactes aenigma, Benthodytes sp., Psychronaetes hanseni* and the swimming holothurians *Peniagone leander* and *Enypniastes eximia*.

5.3. THE ECHO 1 SITE

Abundance and faunal composition by phylum

The "Deep Tow Instrumentation System" was used for photographic exploration at the "ECHO 1" site, which is situated at a lesser depth (mean 4 500 m) to the east of the NIXO 45 and 41 sites (figure 34). The three nodule-facies O, B 45 % and C+ 40 % have homologues at the NIXO 45 site with the exception of the sedimentary context for nodule-facies B 45 % and C+ 40 %, which dates from the Oligocene for the older layers, instead of the Plio-Quaternary. The sampling strategy was different, with the interval between shots varying between 7 and 26 seconds. The two scales of observation determined by the two objective lenses, 50 mm and 70 mm (telephoto), gave complementary data for each photograph. The telephoto lens had the drawback that its elevation (mean of 8.5 m) was generally too high for faunal identification. The total area analysed was 12 400 m^2 with the 50 mm objective and 8 300 m^2 for the photographs taken through the telephoto lens.

Figure 54 shows the overall faunal composition and abundance for the two zones analysed. The results from using the telephoto lens show a greater abundance of sponges (71 ind/ha) compared with echinoderms (59 ind/ha) and cnidarians (52 ind/ha), while the areas seen through the 50 mm objective are abundant in echinoderms (123 ind/ha) due to large numbers of echinoids (65 ind/ha). The elevation of the camera did not allow organisms of small size and complex shapes to be identified, and this explains the lower abundance of sponges and octocoralliarids in photographs taken with the 50 mm objective. In addition, the surface areas studied were different and estimates of abundance of some animals may be a function of the spatial heterogeneity of their populations as indicated by the population densities of sponges (1.5 times more abundant with the telephoto), octocoralliarids (5 times more abundant with the telephoto), echinoids (3 times more abundant with the 50 mm lens), holothurians (2 times greater with the 50 mm), sipunculids (2.3 times greater with the 50 mm) and echiurians (4.3 time greater with the 50 mm). In contrast, medusas, actinids (almost 9 ind/ha), crinoids (almost 7 ind/ha), asteroids (almost 2 ind/ha), ophiuroids, polychaetes, molluscs, arthropods, ascidians and fish maintain the same densities irrespective of which of the two methods of photographic exploration is used.

As the two series of surface areas analysed differ by a factor of 1.5, only the densities seen with a 50 mm objective lens were used for comparison with data from NIXO 45 for similar nodule-facies.

The predominance overall of echinoderms in photographs taken with a 50 mm lens distinguishes these results from those at the NIXO 45 site but recalls those observed on nodule-facies A 30 % and C+ 30 % at the NIXO 41 site. This preponderance of echinoderms is not due to an overabundance of ophiuroids as at NIXO 41 but by large numbers of holothurians and echinoids, whose respective densities vary according to the nodule-facies. Considerable populations of sipunculids (50 ind/ha) and echiurians were also detected because of the particular form of their bioturbation.

Figure 55 illustrates variation in faunal composition, observed with a 50 mm objective, for nodule-facies O, B 45 % and C 40 %. On all three nodule-facies the same predominance of echinoderms is seen, with a majority of echinoids on facies O and of holothurians on the two other facies.

Nodule-facies O with ancient sediments is characterised by a high density of echinoderms (204 ind/ha), the majority of which are echinoids, whose preferred habitat it is (151 ind/ha), as well as a relatively large population of sipunculids (122 ind/ha) and fish (16 ind/ha). The homologous facies O at the

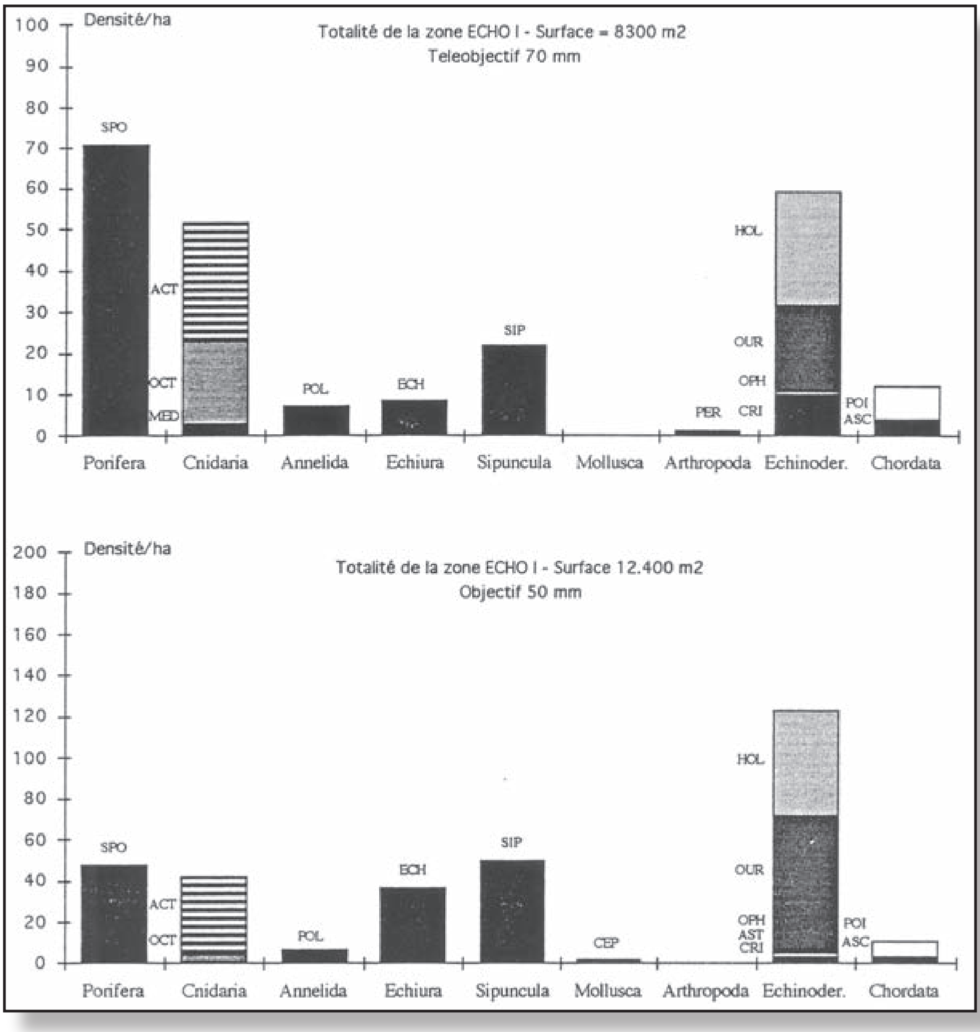


Fig. 54. Histograms of the partitioned abundance of taxa, arranged by phylum, observed by the 'Deep Tow' over the whole of the ECHO 1 site using two types of lens (70 and 50 mm).

NIXO 45 site has a lower density of echinoderms (114 ind/ha) composed in almost equal parts of echinoids (34 ind/ha), holothurians (45 ind/ha) and crinoids (26 ind/ha). In contrast, the population of echiurians (0 ind/ha) at the two sites is similar, as are those of holothurians, molluscs and fish (about 2 ind/ha).

Nodule-facies B 45 % on ancient sediments consists principally of echinoderms (72 ind/ha) with a majority of holothurians (61 ind/ha), cnidarians (56 ind/ha of which 48 ind/ha are actinids), echiurians (42 ind/ha) and sponges (40 ind/ha). This facies has similar populations of asteroids, holothurians, sipunculids, ascidians, cephalopods and echinoids (about 3 ind/ha) to the homologous facies with recent sediments at the NIXO 45 site. Nodule-facies B 45 % with ancient sediments has approximately the same density of sponges as nodule-facies B 50 % with recent sediments at the NIXO 45 site and nodule-facies B 35 % at the NIXO 41 site.

Nodule-facies C 40 % on ancient sediments supports principally echinoderms (96 ind/ha) of which the majority are holothurians (56 ind/ha). This facies is the preferential habitat of echiurians (77 ind/ha), sponges (72 ind/ha), actinids (64 ind/ha), ascidians (8 ind/ha) and polychaetes (11 ind/ha). The population densities of crinoids, asteroids, sipunculids and molluscs are similar at about 3 ind/ha and close to those on the homologous facies C+ 40 % at NIXO 45.

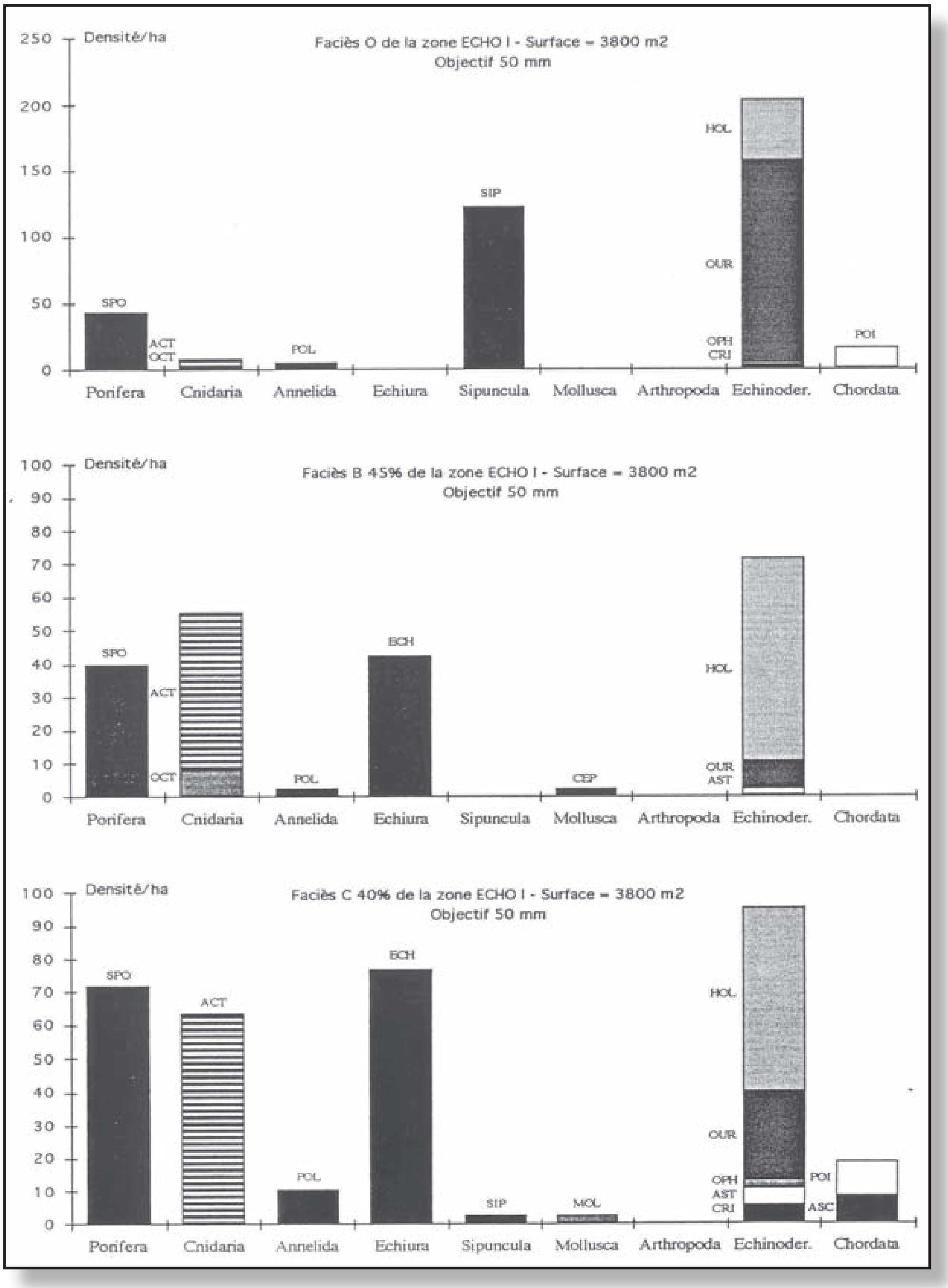


Fig. 55. Histograms of the partitioned abundance of taxa, arranged by phylum, observed by the 'Deep Tow' for three nodule-facies in the ECHO 1 site, using a 50 mm lens.

The faunal composition classified by trophic and functional groups for the three nodule-facies studied at the ECHO I site is represented in figure 56. Detritus feeders, as indicated by the abundance of sipunculids, echinoids and echiurians, are predominant on all facies. This trophic group is particularly abundant on facies O with ancient sediments (326 ind/ha). Suspension feeders are most numerous on nodule-facies C+ 40 %. These results differ from those observed on the two homologous nodule-facies at NIXO 45 and 41 (figures 42, 44 and 52).

The results from the photographs taken with the 70 mm telephoto lens were examined (figure 57) in order to determine the effects of scale of observation on the estimates of faunal composition for the same transect.

The order of abundance changes in favour of sponges with preferential habitats on nodule-facies C+ 40 % with ancient sediments and facies O where densities reach 96 ind/ha and 92 ind/ha respectively. Octocoralliarids are also abundant (44 ind/ha) on facies O and echinoderms have similar densities (96 ind/ha) to sponges on their preferred habitat, facies C+ 40 %. Actinids were only observed on two nodule-facies and especially on facies B 45 %.

Comparison of figures 55 and 57, which relate to the two different objective lenses, shows that the faunal composition on each facies appears different depending on which lens is used. The faunal characteristics on each facies are as follows:

- Nodule-facies O with ancient sediments observed through a telephoto lens supports a clear majority of sponges (96 ind/ha) and sipunculids (64 ind/ha) while the population of Cnidaria is equal to that of octocoralliarids (44 ind/ha). The same facies sampled through a 50 mm objective has a reversed order of abundance, with echinoderms being dominant, of which 73 % are echinoids. These organisms are almost 10 times more numerous that their homologues when sampled with the telephoto lens. Nevertheless, sedentary polychaetes and sipunculids maintain the same population densities independent of the scale of observation, and the latter are preferentially abundant on this facies.

- Nodule-facies B 45 % with ancient sediments sampled through a telephoto lens shows a dominance of cnidarians (64 ind/ha) over echinoderms (44 ind/ha) and sponges (36 ind/ha). The homologous nodule-facies examined with a 50 mm lens shows the same density of actinids but densities for sponges and all echinoderms including holothurians are approximately double. Echiurians are 3.5 times more abundant.

- Nodule-facies C+ 40 % with ancient sediments seen through the telephoto lens is characterised by almost equal abundances of echinoderms (about 4 ind/ha) and sponges (96 ind/ha). This facies examined by a 50 mm lens supports the same population density of echinoderms at about 4 ind/ha while densities of actinids are 1.2 times higher, chordates 2.3 times higher, and echiurians up to 4.8 times higher and for which this is the preferred habitat.

Thus preferential habitats independent of the scale of observation are as follows:

- Nodule-facies C+ 40 % for sponges, echiurians and crinoids.

- Nodule-facies O for sipunculids and fish.

These results agree with the major faunistic trends on homologous facies at the NIXO 45 study site.

Faunal composition by trophic and functional groups

We investigated if the dominance order of trophic and functional behaviours displays also a reversed order when assessing the abundance of the main phyla on photographs taken with the telephoto lens.

Figure 58 illustrates well this inversion when comparing with analysis from photographs taken with a 50mm lens. Suspension feeders prevail on detritus feeders whatever the nodule-facies. The preferential habitat of suspension feeders is the nodule-facies C+40% with a density of 168 ind/ha while motile detritus feeders and sessile detritus feeders display respectively densities of 80 ind/ha and 68 ind/ha.

These results are consistent with those from similar nodule-facies of Nixo45 apart from a greater abundance of motile detritus-feeders on facies-nodule O. Also the analysis of photographs taken with a 50 mm lens display the same preferential habitats for the suspension feeders, sessile detritus feeders and the carnivores and scavengers while mobile detritus feeders prefer facies 0 as habitat.

Quantitative analysis at the level of taxa

Faunal composition was examined at the scale of taxa by seeking to find the most abundant taxa at each of the two levels of observation (50 mm and 70 mm). Figure 59 shows that apart from the actinid *Sincyonis tuberculata* (ACT 6), the taxa which predominate in each case are not the same or do not follow the same order of abundance.

Areas analysed with the aid of the 50 mm lens have abundant forms of bioturbation left by burrowing detritus feeders such as irregular echinoids belonging to the family Aeropsidae (OUR 2), sipunculids of the

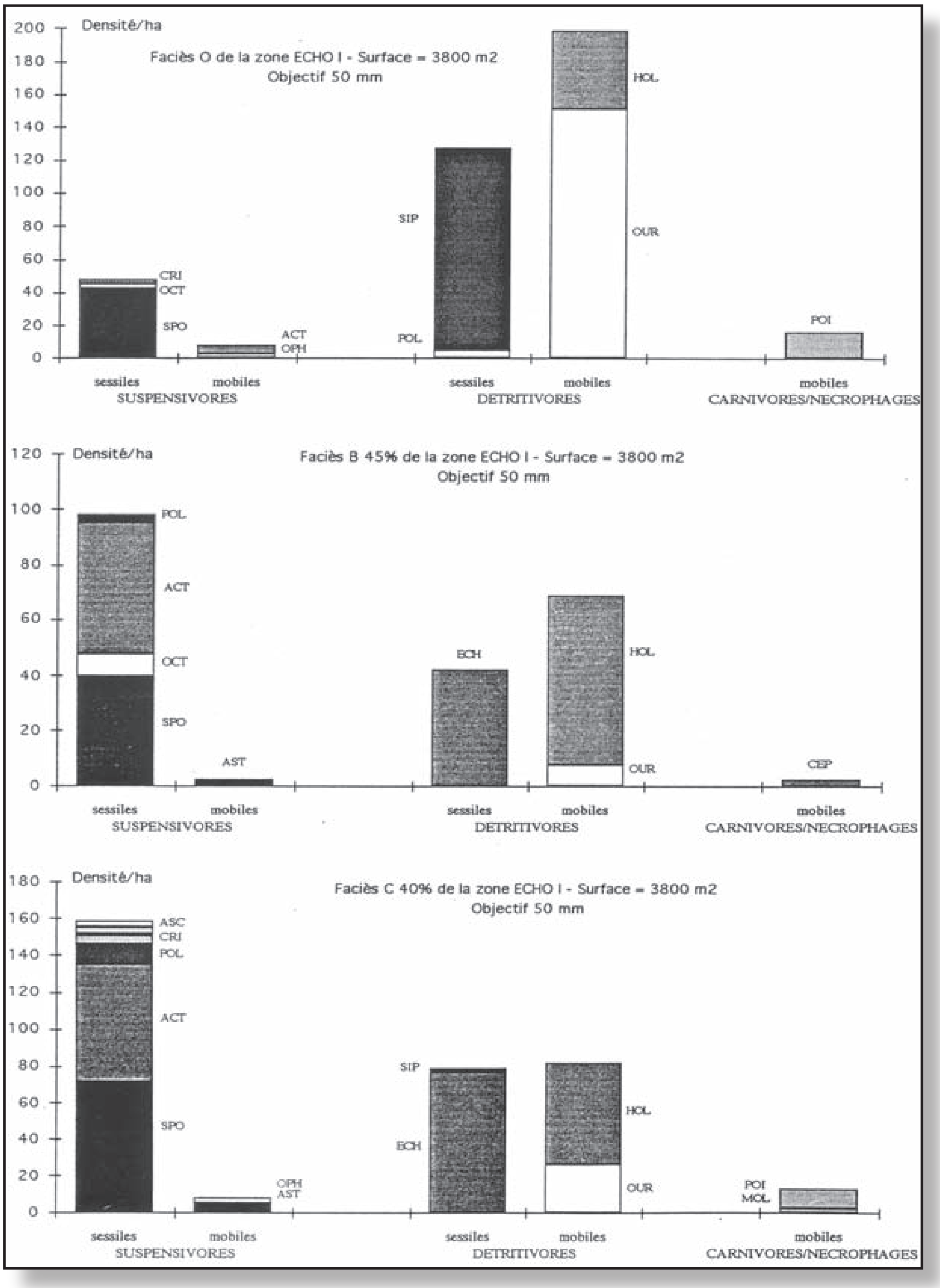


Fig. 56. Histograms of the partitioned abundance of taxa, arranged by phylum, observed by the 'Deep Tow' for three nodule-facies in the ECHO 1 site, using a 50 mm lens.

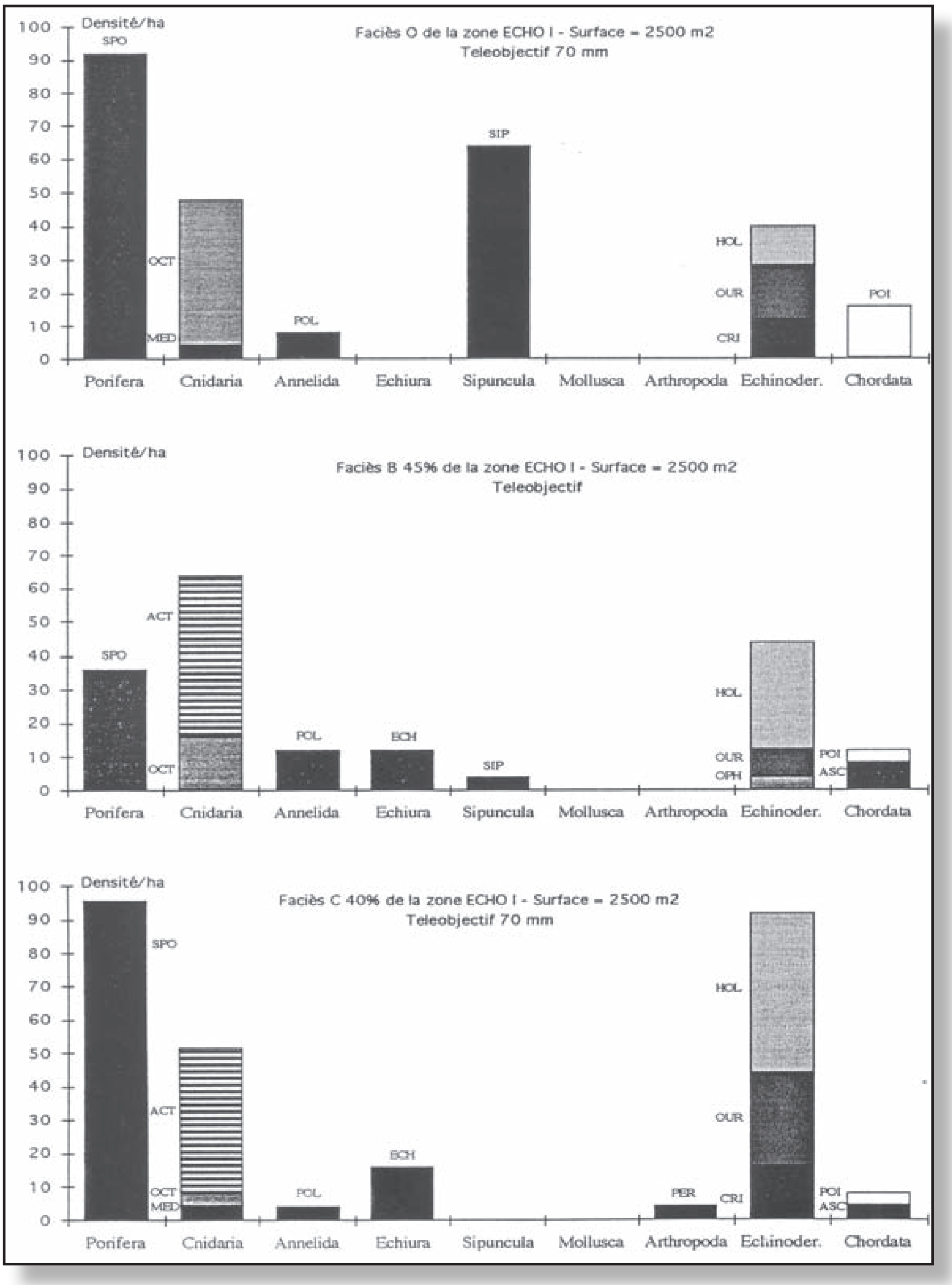


Fig. 57. Histograms of the partitioned abundance and faunal composition of taxa, arranged by trophic and functional group, observed by the 'Deep Tow' for three nodule-facies in the ECHO 1 site, using a 70 mm telephoto lens.

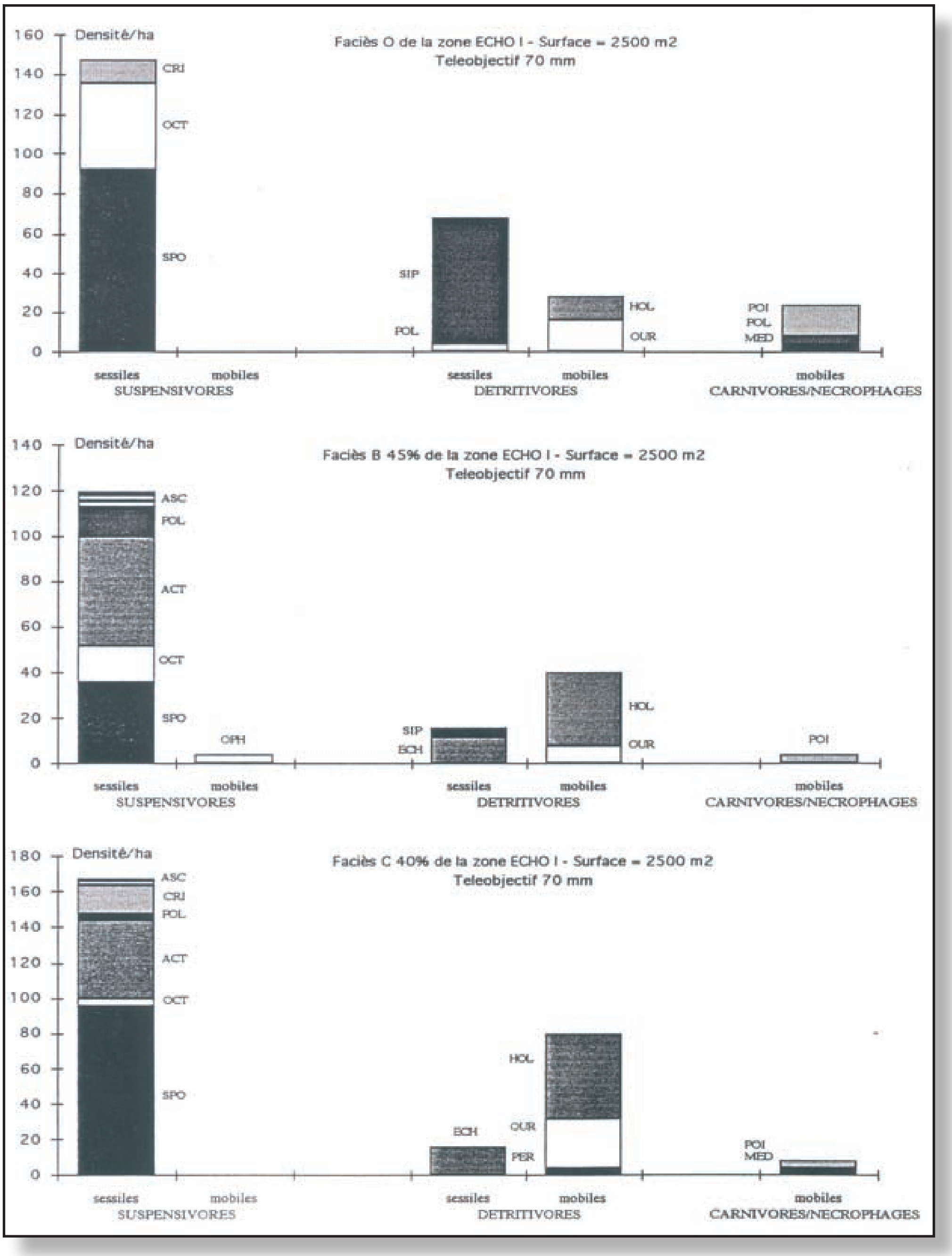


Fig. 58. Histograms of the partitioned abundance and faunal composition of taxa, arranged by trophic and functional group, observed by the 'Deep Tow' for the three nodule-facies in the ECHO 1 site, using a 70 mm telephoto lens.

family Sipunculidae or Golfingiidae (SIP 1) and by echiurians of the family Bonellidae (ECH 1).

At the sediment surface, faunal assemblages are seen where the predominant organisms are the sessile suspension-feeding actinids *Sincyonis tuberculata* (ACT 6), Hexactinellid sponges *Incertae sedis* in the form of a ring (SPO 1), Hexactinellids of the family Hyalonematidae (SPO 14), Polymastiidae (SPO 27), Euretidae *Eurete erectum* (SPO 11), Hyalonematidae of the genus *Hyalonema* (SPO 15), octocoralliarids of the family Plumularidae (OCT 1) and the polychaete worms *Incertae sedis* with long contorted tubes (POL 9).

Detritus feeding echinoderms are the echinoids *Plesiodiadema globulosum* (OUR 1) and the holothurians Synallactidae, *Synallactes profundi* (HOL 2), *Meseres macdonaldi* (HOL 8), *Mesothuria murrayi* (HOL 9), *Synallactes aenigma* (HOL 1), and members of the Elpidiidae, *Peniagone gracilis* (HOL 12), *Amperima rosea* (HOL 13) and the Deimatidae of the genus *Orphnurgus* (HOL 3). The only mobile carnivores are Ophidioid fish (POI 2).

The following taxa are among the 20 most abundant taxa at the NIXO 45 site (figure 42): actinids *Sincyonis tuberculata* (ACT 6), octocoralliarids of the family Plumularidae (OCT 1), sponges of the genus *Hyalonema* (SPO 15), sea urchins *Plesiodiadema globulosum* (OUR 1), holothurians *Mesothuria murrayi* (HOL 9) and polychaete worms *Incertae sedis* with long contorted tubes (POL 9).

Some other taxa are also among the most abundant at NIXO 41 such as: actinids *Sincyonis tuberculata* (ACT 6), echiurians *Jacobia birsteini* (ECH 1), sponges *Pheronema sp.* (SPO 14) and *Hyalonema* sp. (SPO 15), echinoids *Plesiodiadema globulosum* (OUR 1), polychaete worms *Incertae sedis* with long contorted tubes (POL 9) and holothurians Synallactes aenigma (HOL 1), *Synallactes profundi* (HOL 2) and *Mesothuria murrayi* (HOL 9).

In areas sampled by the telephoto lens most of the taxa observed with a 50 mm lens are found but in a different order of abundance. Predominant ones are: sponges of the family Polymastiidae (SPO 27), actinids *Sincyonis tuberculata* (ACT 6), sipunculids of the family Sipunculidae or Golfingiidae (SIP 1), octocoralliarids of the family Plumularidae (OCT 1), burrowing detritus feeders such as irregular echinoids belonging to the family Aeropsidae (OUR 2) and holothurians Deimatidae *Orphnurgus sp.* (HOL 3).

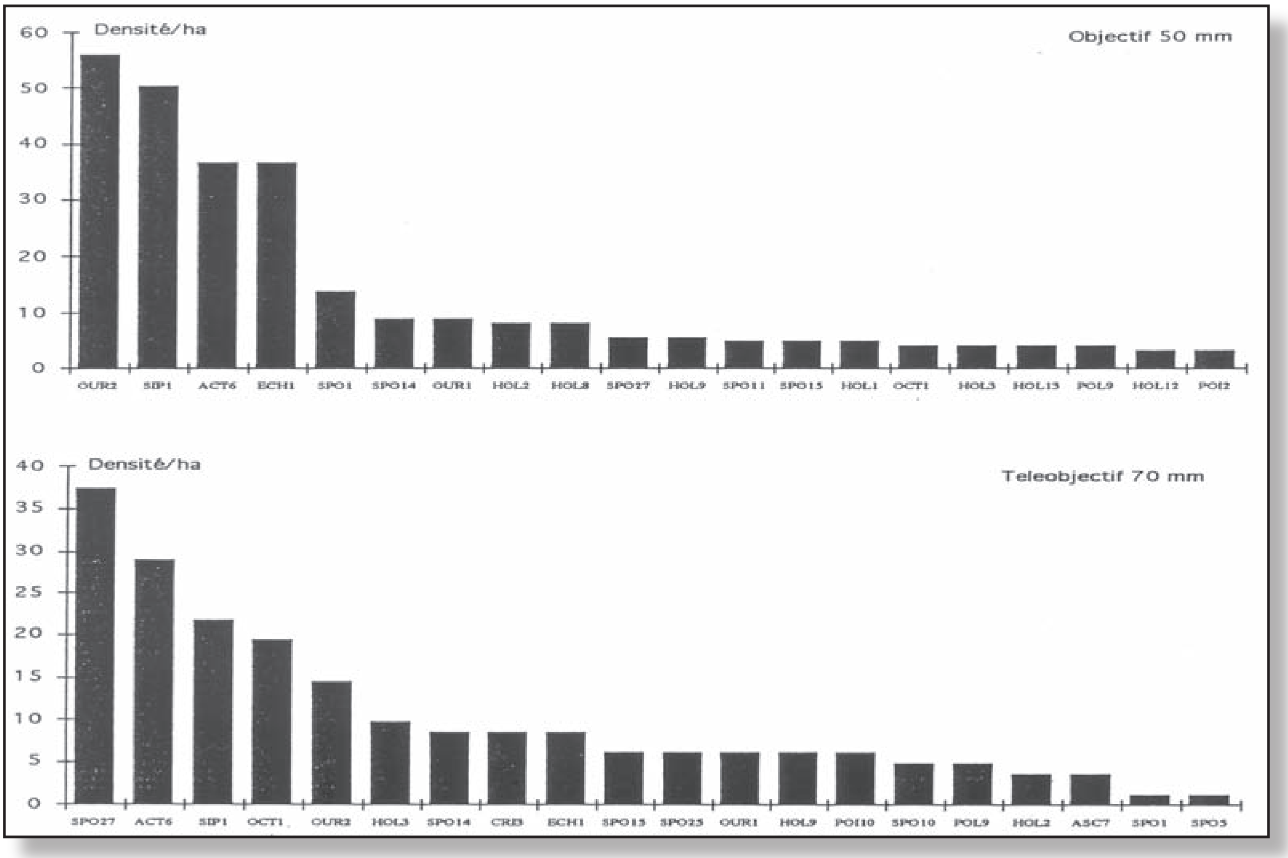


Fig. 59. Histograms of the most abundant taxa observed at the ECHO 1 site, as recorded through a 50 mm lens and a 70 mm telephoto lens.

Taxa that are present exclusively at the scale of the telephoto lens are sessile suspension-feeders, such as fixed crinoids of the genus *Ptilocrinus* (CRI 3), which also belong to the 20 most abundant taxa at the NIXO 45 site, fish of the genus *Ipnops* (POI 10), Demosponges of the genus *Chondrocladia* (SPO 10), Hexactinellids of the family Rossellidae (SPO 5) and the composite ascidians *Incertae sedis* (ASC 7). These taxa are generally difficult to make out on a nodule substratum with a 50 mm.

Distribution of holothurians on different facies

In order to detect variation in distributions at a taxonomic scale and the possibility of preferential habitats on nodule-facies O, B 45 % and C+ 40 % with ancient sediments, the distribution of various holothurians observed at the ECHO 1 site was investigated at the two scales of observation (50 mm and telephoto).

Nodule-facies O with ancient sediments, independent of the scale of observation, preferentially supports holothurians Synallactidae *Meseres murrayi* (HOL 8) at a density of 19 ind/ha seen through the 50 mm lens and 4 ind/ha with the telephoto. Two taxa appear to be exclusive to this facies: the holothurians Deimatidae *Deima validum* (HOL 5) seen with the 50 mm lens and *Psychropotes verrucosa* (HOL 23) seen with the telephoto. Preferences for this nodule-facies do not agree with those from photographic data from the NIXO 45 site where they are as follows: *Psychropotes verrucosa* are more abundant on nodule-facies C+ 10 % (a facies which is not represented in photographic data from ECHO 1), *Meseres murrayi* on nodule-facies C+ 20 % and *Deima validum* on nodule-facies B 40 %. Neither do these results confirm those from the NIXO 41 site where these taxa have not been recorded, except for *Deima validum*, which was one of the taxa exclusive to nodule-facies A 30 %.

Nodule-facies B 45 % on ancient sediments, independent of the scale of observation, preferentially supports holothurians in the families Laetmogonidae *Psychronaetes hanseni* (HOL 21), Psychropotidae *Psychropotes longicauda* (HOL 17) and Synallactidae *Mesothuria murrayi* (HOL 9). Holothurians *Synallactes profundi* (HOL 2) are especially abundant on this nodule-facies as examined with a 50 mm objective, with a density of 13 ind/ha, similar to *Orphnurgus* (HOL 3) with 11ind/ha, *Benthodytes sp.* (HOL 6). Some holothurians seem exclusive to this type of nodule-facies such as *Paelopatides sp.* (HOL 22). These observations are not in agreement with those from the NIXO 45 site, but they do confirm those from NIXO 41 for *Psychronaetes hanseni* and *Paelopatides sp.*

Nodule-facies C+ 40 % on ancient sediments, independent of the scale of observation, preferentially supports the holothurians *Peniagone gracilis* (HOL 12), which are exclusive to this nodule-facies. Other holothurians, mostly members of the family Elpidiidae, are unique to this nodule-facies as examined by a 50 mm lens, such as *Peniagone papillata* (HOL 10) and with a telephoto lens, such as *Amperima rosea* (HOL 13), *Peniagone gracilis* (HOL 12) and *Benthodytes sp.* (HOL 6). The highest abundances are seen with *Synallactes aenigma* (HOL 1), showing a density of 11 ind/ha in photographs taken by 50 mm lens, and *Synallactes profundi* (HOL 2) with 11 ind/ha and *Orphnurgus* (HOL 3) with 20 ind/ha in photographs taken by telephoto. These observations are confirmed at the NIXO 45 site for the exclusive taxon *Orphnurgus sp.* and for holothurians of the genus *Benthodytes*. In contrast, none of these results were observed at the NIXO 41 site.

5.4. ESTIMATES OF BIOMASS AT THE STUDY SITES

Biomasses of the megafauna at the three study sites (NIXO 45, NIXO 41 and ECHO 1) were estimated from values of mean fresh weight per unit. By referring to the data of Vinogradov (1953) and Salonen *et al.* (1976), these fresh weights were transformed into weight of organic matter using data on the water content of each organism, the weight of organic carbon being considered as equivalent to 51.8 % of the weight of dry organic matter. Evaluation of biomass (mgC/m^2) is a function of the density of the different taxa and their individual mean weight in mgC. Since only faunal assemblages in the same dimensional categories are compared here, the fish are omitted. Estimates of biomass have been calculated from values of density and individual mean weight.

The results show that total biomass for invertebrate megabenthic assemblages varies according to the different sites studied. The total biomass for the megafauna at NIXO 45 is 1.8 times less than that at NIXO 41 which is itself 6.2 times greater than at ECHO 1 (using a telephoto). Analysis of the contributions of the various faunistic components to the total also provides information on differences in biomass between the study sites. These biomass data, organised by trophic group, are shown as percentages in figures 60 and 61.

Estimates of megafaunal biomass at the NIXO 45 and NIXO 41 sites

Figure 60 shows that the order of dominance for biomass of the three trophic groups follows that for estimates of density. The biomass of suspension feeders is greater than that for detritus feeders, which is itself greater than that of carnivores. The biomass of suspension feeders at the NIXO 45 site (351 mgC/m^2) is about 11 times that for detritus feeders (32 mgC/m^2) which is 16 times greater than that for carnivores and scavengers (2 mgC/m^2). Fish have an estimated biomass of 119 mgC/m^2.

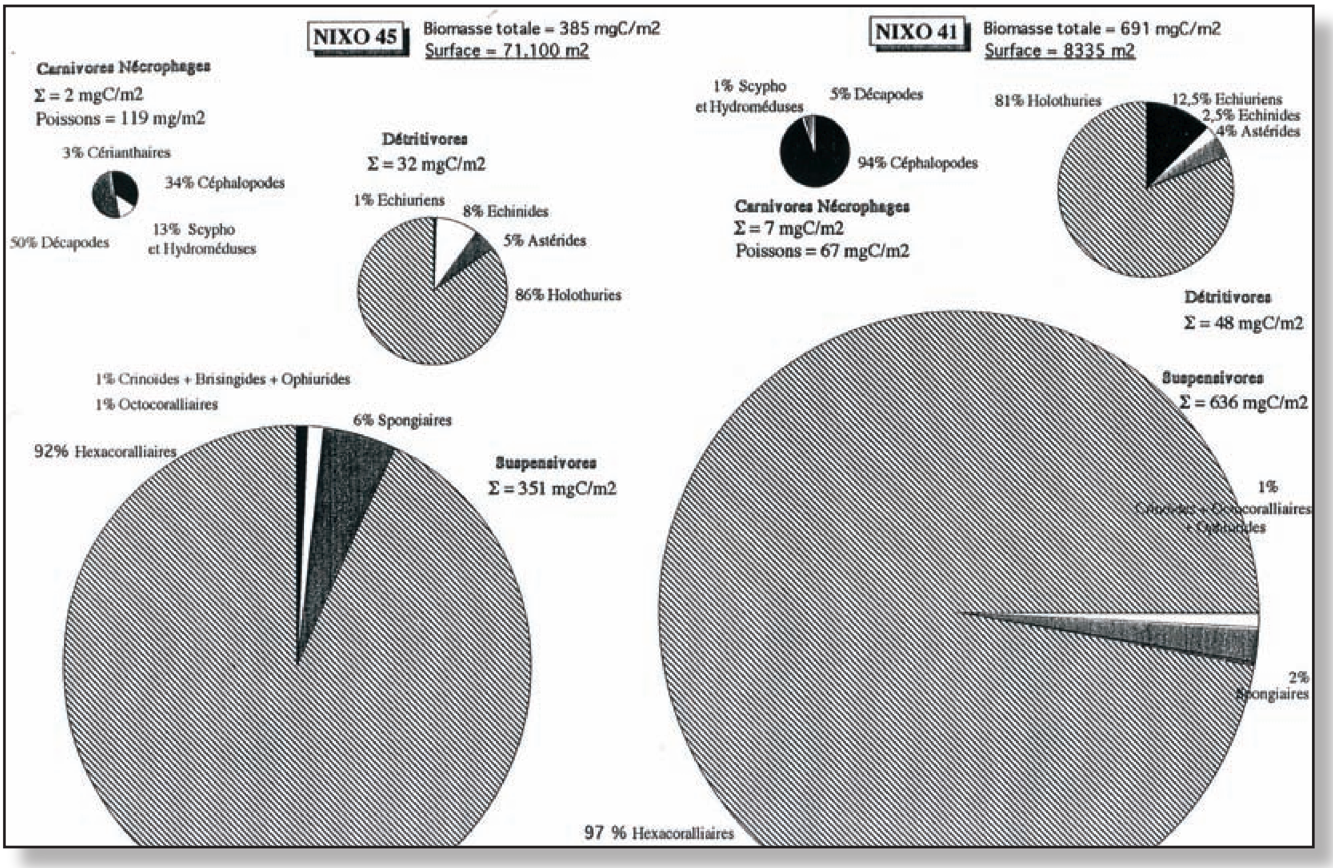


Fig. 60. Diagramatic representation of partitioned estimates of megafaunal biomass, arranged by trophic groups, for the NIXO 45 and 41 study sites.

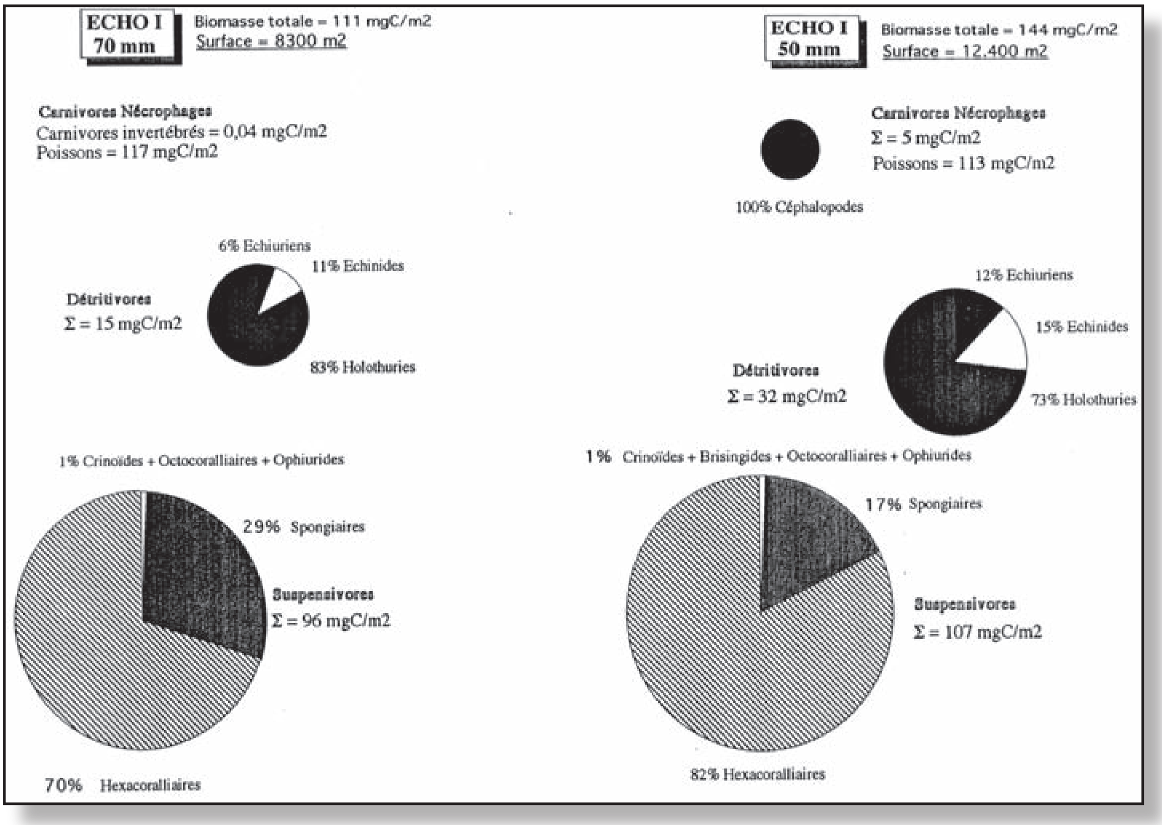


Fig. 61. Diagramatic representation of partitioned estimates of megafaunal biomass, arranged by trophic groups, at the ECHO 1 study site, recorded through 50 and 70 mm lenses.

Comparison of these data with those from the NIXO 41 site shows that the total biomass is almost twice as great as at NIXO 45. The biomasses of suspension feeders, detritus feeders and carnivores are respectively about 2, 1.5 and 3.5 times greater at the NIXO 41 site.

However, even if estimates of biomass are given per hectare, it must be recognised that abundances were estimated from different surface areas (the total area surveyed at NIXO 45 is 8.5 times greater than that at NIXO 41) and consequently not all the nodule-facies studied at NIXO 45 are represented at NIXO 41. Comparisons can only be made for homologous facies at each of the sites. Thus at NIXO 45, biomasses on the three homologous nodule-facies at NIXO 41 are estimated at 1 225 mgC/m^2 with 90.3 % hexacoralliarids (in taking nodule-facies B 40 % as homologous with nodule-facies A 30 %, whose representation was too low at NIXO 45). This biomass is 1.7 times greater than that observed at NIXO 41.

Nevertheless the proportions of the different trophic groups at NIXO 41 reveal a certain homogeneity of trophic assemblages on similar nodule-facies. At the NIXO 41 site, these proportions are slightly different from those over the whole of the NIXO 45 site. The biomass of suspension feeders (636 mgC/m^2) is 13 times greater than that of detritus feeders (48 mgC/m^2), which is 7 times greater than that for carnivores and scavengers (7 mgC/m^2). The biomass of fish is almost half that estimated over the whole of the NIXO 45 site where they appear to be associated with entirely sedimentary substratum or nodule-facies with low nodule coverage. If only homologous facies are considered at the NIXO 45 and NIXO 41 sites, the proportions are very different, with the biomass of suspension feeders (1 133 mgC/m^2) being about seven times greater than for detritus feeders (173 mgC/m^2), whose biomass is four times greater than that of carnivores (43 mgC/m^2).

By examining the proportions of different faunal components in the estimate of biomass for each trophic group for the whole of the NIXO 45 and NIXO 41 sites, one finds that:

- The biomass of suspension feeders is composed in both cases of about the same mean percentage of hexacoralliarids (95 %), sponges (4 %) and crinoids, brisingids, octocoralliarids and ophiuroids (1 %). This dominant contribution of hexacoralliarids is confirmed at the same depth in the Cape Verde Basin in the Atlantic Ocean (Sibuet, 1980).
- The biomass of holothurians consists of 83.5 % of that for detritus feeders over the two sites. Nevertheless, holothurians represent only a small percentage (7 %) of the total biomass for the megafauna at the two NIXO sites, whereas this group represents nearly 20 % of the total biomass at the station in the Bay of Biscay at comparable depths (Sibuet, 1987). Asteroids maintain the same mean percentage of 4.5 % while echiurians and echinoids vary in biomass according to the site studied. The biomass of echinoids is only 2.5 % of that for detritus feeders at NIXO 41 while at NIXO 45, this group represents 8 % of detritus feeding biomass. Conversely the biomass of echiurians is only 1 % of that for detritus feeders at the NIXO 45 site, contrasting with 12.5 % at NIXO 41. This is because echiurians preferentially inhabit facies with high nodule coverage, such as those selected at the NIXO 41 site, while echinoids are abundant on facies without nodules or with a low nodule coverage, which are well represented at the NIXO 45 site.
- The biomass of invertebrate carnivores and scavengers also varies according to the site studied. At NIXO 45, decapods represent 50 % of these trophic groups while they contribute only 5 % at NIXO 41. In contrast, the biomass of cephalopods is much greater (94 %) at the NIXO 41 site than at NIXO 45 (34 %).

When considering only the three nodule-facies at the NIXO 45 site that are homologous with those at NIXO 41, hexacoralliarids represent 98 % and sponges 2 % of suspension feeders, and similar percentages are observed at the NIXO 41 site. For detritus feeders, echinoids only represent 1 % of the biomass, which is composed largely of holothurians (46 %), though these contribute only 6 % to the total biomass. Carnivore biomass is dominated by medusas (86 %), in contrast to the results seen at NIXO 41.

Estimates of megafaunal biomass at the ECHO 1 site

For the fauna at the ECHO 1 site, trophic groups show the same order of dominance as at the NIXO 41 and NIXO 45 sites (figure 61). Considering the homologous facies at the NIXO 45 site as those studied at ECHO 1, the total biomass is 1 024 mgC/m^2 divided into 963.3 mgC/m^2 for suspension feeders (9 times greater than at ECHO 1), 97.42 mgC/m^2 for detritus feeders (3 times greater than at ECHO 1) and 40.28 mgC/m^2 for invertebrate carnivores (8 times greater than at ECHO 1).

The 50 mm and 70 mm (telephoto) lenses provide two complementary scales of observation that compensate for the disadvantage of the 50 mm lens, which takes pictures from an elevation that is generally too high to enable identification with the same degree of precision as that carried out at the NIXO 45 and 41 sites.

According to the data from the 50 mm lens, the biomass of suspension feeders is much lower (107 mgC/

m²) at the ECHO 1 site and is only three times greater than of detritus feeders (32 mgC/m²), which is itself seven times greater than that for carnivores and scavengers (4.5 mgC/m²). In contrast, the biomass of fish is relatively high (113 mgC/m²) and close to that estimated overall for the NIXO 45 site. The same is true for estimates of biomass of detritus feeders and carnivores, which are approximately equivalent to those at NIXO 45 for these trophic groups.

Percentages of biomass for faunal components within each trophic group are slightly different from those observed at the NIXO 41 and 45 sites. The biomass of suspension feeders at ECHO 1 comprises a greater proportion of sponges (17 % instead of 6 % on the homologous facies at NIXO 45) to the detriment of hexacoralliarids, which are reduced to about 12 % in this trophic group at NIXO 45. The biomass of detritus feeders at NIXO 41 site is composed of a larger proportion of holothurians (73 %) than at the NIXO 45 site. Echiurians form a similar percentage (12 %) to that observed at the NIXO 41site. The biomass of carnivores is entirely represented by cephalopods at NIXO 45, as at NIXO 41.

Estimates of biomass resulting from the analysis of data from ECHO 1 with the telephoto lens (70 mm) over an area approximately equivalent to that at the NIXO 41 site are lower (111 mgC/m²) than those estimated with the 50 mm lens (144 mgC/m²). The biomass of detritus feeders appears to be about half, while that of invertebrate carnivores is zero. Only the biomasses of suspension feeders and the category of fish are close to the values observed using the 50 mm objective lens. Values for biomass from the analysis of data seen through the telephoto lens are clearly lower than those from the NIXO 45 and 41 sites, except for fish. When considering the different percentages of faunal components contributing to the trophic groups, the same trends are seen as those from the data with a 50 mm lens, although sponges form a greater proportion (12 %) to the detriment of hexacoralliarids, and for detritus feeders, holothurians form a greater proportion at the expense of echiurians. This proportion of holothurians (83 %) resembles that observed at the NIXO 45 and 41 sites.

Estimates of macrofaunal and meiofaunal biomass

To compare the trophic structure of different faunal categories, estimates given in the literature (Paul & Hecker, 1977; Hecker & Paul, 1979; Radziejewska, 1997; Trueblood & Ozturgut, 1997; Radziejewska & Modlitba, 1999; Stoyanova, 2001; Radziejewska, 2002; Radziejewska *et al.*, 2003) for the macrofauna and meiofauna of the Clarion-Clipperton fracture zone were examined. Paul & Hecker (1977) and Hecker & Paul (1979) sampled the macrofauna (metazoans retained by a 250 mm sieve) and the meiofauna (metazoans retained by a 40 mm mesh) at three study sites, DOMES A, B and C. Cited here for comparison are results from the analysis of 38 USNEL corers of 0.25 m² from the site closest to our study, the DOMES C site, situated at 16 ° N and 126 ° W, beneath the North Equatorial Current (figure 31).

Data on the macrofauna and meiofauna analysed by Hecker & Paul (1979) and their classification into trophic categories demonstrate a predominance (3.5 times greater) of limivores or detritus feeders over suspension feeders. In order of importance, the limivores consist largely of annelids, arthropods and molluscs. At the DOMES C site, Hecker & Paul (1979) found a density of 268 ind/m² which is greater than that observed at DOMES A and B.

This density is comparable with that of 238 ind/m² given by Paul & Jumars (1976) but clearly lower than the estimate of 356 ind/m² given by Wilson & Hessler (in Mullineaux, 1989) for the DOMES C site. This density lies in between estimates for two regions of the Pacific Ocean at equal depths since it is about twice as high as the macrofauna (115/m²) of the central oligotrophic Pacific Ocean (Hessler & Jumars, 1974) and almost three times less than that of about 750/m² from near the Equator at 3°N. The mean density observed at the mining site in the Indian Basin is 365.5 ind/m² (Ingole *et al.*, 1999). The density of the macrofauna at DOMES C is also 2.5 times greater than that observed, at similar depth and with the same method of sampling, in the Cape Verde Basin in the Atlantic Ocean (Sibuet, 1980) and 1.2 times greater than that measured on the Vema fault (Khripounoff *et al.*, 1980).

The macrofauna at the DOMES C site comprises 53 % suspension feeders. It includes small-sized individuals and juveniles of the megafauna (sponges, actinids, brachiopods, ophiuroids, crinoids and cirripedes) that Hecker & Paul (1979) discovered in their cores and which are too small to be detected in photographs of the megafauna. If one excludes these juveniles, the biomass of suspension feeders is 4.6 mgC/m², composed largely of 17 % polychaetes, 16 % bivalves and 1 % tunicates. Detritus feeding polychaetes, according to the definitions of trophic behaviour in Jumars & Fauchald (1977), comprise 38 % of the limivore biomass at DOMES C. The estimates of Paul & Jumars (1976) are slightly different as regards the contribution of cnidarians at the DOMES C site, where this faunal group is dominant, and forms 55 % of the total macrofaunal biomass. This considerable biomass of cnidarians appears to be unique to DOMES C site, given their lesser importance in the central Pacific Ocean (Hessler & Jumars, 1974).

The biomass of the limivore macrofauna of the Pacific Ocean is dominated by annelids (38 %), mostly polychaetes, with 7 % arthropods, such as tanaidaceans, isopods, pycnogonids, cumaceans and amphipods. The importance of polychaetes as dominant components of the macrofauna at DOMES C recalls the results of Paul & Jumars (1976) who found 30.6 % polychaetes at the DOMES C site, while Hessler & Jumars (1974) found 55.1 % at a site in the central Pacific Ocean. These results also concur with those of Ingole *et al.* (1999, 2001) for the site in the Indian Ocean sampled during the INDEX programme. The proportions they found are respectively 55 % polychaetes, 12 % tanaidaceans, 8 % isopods for the most abundant categories which were concentrated in the upper 2 cm of superficial sediments. These figures are also comparable to those of Sibuet (1980) who found that polychaetes contribute to 52% of the total of the macrofauna in the Cape Verde Basin.

The meiobenthos of the DOMES C site is characterised by high biodiversity of two large groups, ostracods and nematodes. Estimates for biomass of the polychaetes at this site demonstrate more ostracods (87,61 %) than nematodes (12.38 %). However, these proportions were not confirmed by Renaud-Mornant & Gourbault (1990) at 17 locations situated to the west of NIXO 45, between 130°54W-130°41W and 14°06N-14°33N at depths between 4 960 m and 5 154 m. These authors found biomasses of 0.2 to 3.2 mgC/m^2, composed largely of nematodes (84-100 %) and harpacticoid copepods (0-10 %), and they interpreted these low biomass values as the result of numerous juveniles and nanism of adult forms (60-80 %) whose presence might be an adaptation to low nutritional resources. Abundant and diverse nematodes were also observed by Paul & Jumars (1976) at comparable depths at the DOMES C site, and similar proportions were confirmed more recently by various authors, such as Trueblood & Ozturgut (1997) at the BIE site of NOAA, Radziejewska & Modlitba (1999), Radziejewska & Stoyanova (2001), Radziejewska (2002) and Radziejewska *et al.* (2003) over a band within the nearby IOM site (10°10'N-13°10'N and 119°25'W,-120°40'W).

Similarly, at the INDEX EIA site in the Indian Basin, proportions are similar with a majority of nematodes (60 %) and harpacticoid copepods (21 %) concentrated in the first 5 cm thickness (Ingole *et al.*, 1999). These findings were also confirmed by Rachor (1975) off Portugal, by Dinet & Vivier (1977) in the Bay of Biscay, by Dinet (1973) in the south-east Atlantic Ocean and by Pfannkuche (1985) in the north-east Atlantic. Likewise, Hessler & Jumars (1974) obtained high percentages for nematodes (56-85 %) in samples from the central Pacific in similar bathymetric and hydrographic conditions.

Measurements by Hecker & Paul (1979) at the three sites, DOMES A, B and C, showed that the greatest abundances and biomasses were found at the DOMES C site. These authors also found a more marked presence of suspension feeders than in our study. Similarly, Radziejewska & Modlitba (1999) and Radziejewska *et al.* (2001) demonstrated significant differences in abundance and faunal composition in relation to substratum heterogeneity, notably in relation to sediment properties, also confirming results for the megafauna of our study.

Estimates of flux in particulate organic carbon

In seeking to explain the origin of this faunistic abundance, the energetic contribution arriving on the benthos should be considered. Since no measurements of particulate organic flux have been obtained from particle traps at the study sites, values of primary production at the surface were taken from the literature in order to calculate the flux in particulate organic carbon originating at the surface, using the equation proposed by Berger *et al.* (1987):

$$J = (9 \times PP) / Z + (0.7 \times PP) / Z^{0.5}$$

- J is the flux in particulate organic carbon expressed as gC/m^2/y
- PP is the primary production estimated at the surface of the study zone in gC/m^3/y
- Z is the mean depth of the site in m

The primary production at the surface of the DOMES C site is relatively high, reaching about 125 gC/m^2/y (compared with 90 gC/m^2/y at the DOMES A and B sites) according to the calculations of Berger *et al.* (1987), based on information for latitude, distribution of phosphates and distances from the coast.

These estimates confirm those of Koblentz-Mishke *et al.* (1970) based on measurements of C_{14} but contrast with those given by El-Sayed & Satoru (1979) based on measurements of the vertical distribution of chlorophyll A at the DOMES A, B and C sites. Indeed site C, the closest of the study sites, has the greatest primary production of the three sites, with 148.6 ± 57 mgC/m^3/day or 54.23 ± 20.8 gC/m^3/y, a value clearly lower than those cited previously. These authors were able to show a seasonal variation in primary production with minima between August and October and maxima in February to March. When examined more closely, the positions of their stations are further north than the DOMES C site (where primary production is about 125 gC/m^3/y according to Berger *et al.*, 1987) and in a zone of lower productivity, which, according to the estimates of Berger *et al.* (1987), has a primary productivity of about 90 gC/m^2/y. Similarly, based on Berger *et al.* (1987), the meiofaunal study sites of Renaud-Mornant & Gourbault (1990) fall within a zone of primary productivity of 125 gC/m^2/y.

Consequently, for the more southerly study sites of NIXO 45 and 41, an estimated mean value for primary production of 150 $gC/m^2/y$ has been adopted. This value, with that of 5 000 m mean depth for the NIXO 45 site, has been integrated into the equation of Berger *et al.* (1987):

$$J = (9 \times 150) / 5\,000 + (0{,}7 \times 150) / 5\,000^{0.5}$$

The particulate flux (J) was thus calculated as 1.75 $gC/m^2/y$ or 4.79 $mgC/m^2/day$. This value of particulate flux is greater than of 0.2 $mgCm^2/day$ measured at 5 800 m depth in the central circulation (gyre) of the oligotrophic zone to the north of the Hawaiian Islands (Smith *et al.*, 1989). A comparable value of 3.29 $mgC/m^2/day$ was found for the site at 4 900 m depth near Cape Verde (Sibuet, 1987).

Thus the present data from research in the abyssal environment and especially in the Clarion-Clipperton fracture zone underlines the variation in biotic and abiotic conditions in space and time which have revolutionized previous notions of great stability based on unchanging environmental conditions (Tyler, 1995; Radziejewska & Stoyanova, 2000). Natural disturbances of biotic and abiotic origin can also maintain suprabenthic communities in equilibrium. A seasonal cycle exists with considerable variation in the vertical flux of detritic particles (Smith *et al.*, 1997; Lauerman *et al.*,1997; Drazen *et al.*, 1998; Thurston *et al.*, 1998) related to variation in particulate organic carbon (Smith al., 1997; Scharek *et al.*, 1999) and controlled principally by the periodic deposition of planktonic debris originating in the euphotic zone (Thiel *et al.*, 1988/1999; Gehlen *et al.*, 1997; Smith *et al.*, 1997; Khripounoff *et al.*, 1998; Scharek *et al.*, 1999). These results were confirmed by Smith *et al.* (1994) in their experiments with a remotely operated camera positioned on the ocean floor for a period of 386 days.

The results of Hecker & Paul (1979) highlighted an east-west gradient in the density, biomass, and percentage of suspension feeders, with greater values at DOMES C, the site further east. This gradient appears to be a reflection of primary production at the surface, according to the estimates of Berger *et al.* (1987). The results confirm the fact that the control of faunal abundance in the abyssal epibenthos is related to the energy contributed by the sedimentation of particulate organic matter generated in the photic layer (Rowe, 1971; Sokolova, 1972; Menzies *et al.*, 1973; Steele, 1974; Thiel, 1975; 1979; Rowe & Staresnic, 1979; Khripounoff, 1979; Hinga *et al.*, 1979; Wangersky & Wangersky, 1981; Stockton & Delaca, 1982; Rowe, 1983; Vinogradova & Tseitlin, 1983).

This gradient could also be interpreted as resulting from the degree of proximity of the system to the lateral flow of organic particulate material. The DOMES C site is directly downstream of the highly productive Californian Current and in the eastern part of the system of equatorial Pacific currents. The abundance of suspension feeders is correlated with the abundance of particles in suspension, and measurements of currents at an elevation of 6 m reach mean values of 2 to 5 cm/sec, with maximum values of 24 cm/sec, creating local erosion and redeposition of the sediments (NOAA, 1981).

If the biomass for each faunal category is divided by the value of flux in particulate organic carbon, one finds that the ratios are not similar. At the NIXO 45 site, the ratio for the megafauna is 80.4. That for NIXO 41 is 329, taking into account its higher primary production of 180 $gC/m^2/y$, while at the ECHO 1 site, the ratio is 35, taking into account its lower primary production of 125 $gC/m^2/y$. The ratio for total macrofaunal biomass over flux in particulate organic carbon is 11 for the DOMES C site. Finally, for the meiofauna, the ratio is 0.3 for the DOMES C site.

6. Discussion

6.1. COMPARAISON OF DIFFERENT *IN SITU* OBSERVATION DEVICES

The manned submersible "the Nautile" enables the morphologies of organisms at the study sites to be seen from an oblique view point, which is different from the vertical view of the 'Epaulard'. The impression in colour and the scrolling of images in photographs and films of the 'Nautile' adds information on taxa behaviour and to the images taken by the other devices. In this way it has been possible to film the complex swimming movements of some holothurians (Tilot, 1990). Nevertheless, the images taken at the study site by the 'Nautile' are not sufficient in quantity and quality to form a photographic reference base for a taxonomic atlas of a geographical region such as the Clarion-Clipperton fracture zone. It is due to the impressive quantity of photographs taken by the 'Épaulard', the 'R.A.I.E.', the 'troika' and the 'ED1' that we are able to build up such a data reference base. The quantity, detail, angle of view and generally lower elevation of the still images from these apparatuses enable taxonomic identification to be taken further. Video images are a good complement for a reference base that is already well documented. Thus by knowing the taxa well, one can recognise at first glance shapes that would otherwise be difficult to identify.

Data from video sampling by the 'Nautile' indicates that the abundances of suspension feeders and detritus feeders at the NIXO 45 site are over estimated by 1.4 and 1.7 times respectively in comparison with the values recorded by the 'Épaulard'. The density of carnivores is more or less the same due to the fact that the abundance of wandering polychaetes in photographs from the 'Épaulard' balances out the greater density of fish in images from the 'Nautile'. These results are surprising given the low level of precision in the oblique shots on heterogeneous nodule deposits on the seabed, the scrolling of images and the fact that the approach of the 'Nautile' might cause animals to flee. As suggested by the quantitative analysis, this "overstimation" of densities could be because the surface area explored by the 'Nautile' was 2 500 m^2, and consequently less than the 3 850 m^2 sampled by the 'Épaulard', and because fish seem attracted by the presence of the 'Nautile' and its activities, as well as by the plume of sediment produced by its passage. However, comparison of the results shows that faunal composition is proportional except for four times as many echiurian burrows in images from the 'Nautile'. These particular forms of bioturbation created by echiurians are mounds 210 cm long by 65 cm wide and are without doubt more readily detected in the plunging and wider field of view of the 'Nautile'.

The 'R.A.I.E.' is equipped with the same camera as the 'Épaulard' and consequently takes similar photographs. Differences between the data from the two devices are due to differences in the sampling strategies and the fact that the 'R.A.I.E.' was more difficult to manoeuvre and keep at a constant elevation, as it was subject to oscillations from the cable which tows it. Nevertheless, it has an advantage over the 'Épaulard' by being able to explore more broken terrain. Thus sets of photographs at an "acceptable" elevation for quantitative analysis (5 m maximum) were selected along a transect. The sampling strategies at the NIXO 41 and NIXO 45 sites differed notably in the interval between shots, which was 32 seconds for NIXO 41 and 5 seconds for those taken by the 'Épaulard' at NIXO 45. In consequence, the areas photographed are not contiguous at the NIXO 41 site whereas they are at NIXO 45. The towed 'R.A.I.E.' apparatus is well adapted for exploration over long distances with heterogeneous surface conditions, and is able to make organisms cleary visible from higher elevation or to detect particular forms of bioturbation, such as mounds built by echiurians.

We cannot draw conclusions on the relative performance of the different observational devices from the fact that estimates of abundance are different for homologous facies since several factors are involved, notably the geographical difference between the sites and the different surface areas sampled (1.3 times less at the NIXO 41 site). Greater abundances at the NIXO 41 site might be explained by the fact that this site is more southerly than NIXO 45 and in a zone of higher primary productivity, of between 150 and 250 gC/m^2/y (Berger *et al.*, 1987). Only the faunal composition of facies B 35 % is the same as that of the homologous nodule facies B 40 % at the NIXO 45 site, where cnidarians are slightly more dominant than echinoderms. The sharpness of the photographs allows us to state that the taxa seen at NIXO 41 had already been observed in photographs from NIXO 45. Nevertheless, we can conclude nothing from the absence of unique taxa at the NIXO 41 site because the surface area explored was 8.5 times smaller than that at NIXO 45.

The 'Deep Tow' has the same drawbacks as the towed apparatus 'R.A.I.E.', but they are more pronounced since its oscillations are greater and most of the photographs taken through a 50 mm lens were taken from too high an elevation to develop the taxonomic identifications to the same level as with the photographs taken by the 'Épaulard' or 'R.A.I.E.', at an elevation of 5 m. In addition, the interval between shots varied between 7 and 26 seconds and the areas photographed were illuminated in a non-uniform manner by the flashes. Thus estimates of surface areas have been adapted so that only the uniformly illuminated areas have been counted, i.e. those within a circle whose size varied according to the elevation. The telephoto lens enabled greater precision in identifying organisms on smaller surface areas (and thus more dependent on the spatial distributions of the species). The images taken at higher elevation allowed only large animals to be detected, along with significant evidence of biological activity, such as the mounds created by echiurians.

As with the 'R.A.I.E', differences in quantitative data do not allow us to compare the different *in situ* observational devices. The clear dominance of echinoderms, represented especially by echinoids on facies O on ancient sediments and holothurians on nodule facies B 45 % and C 40 %, seems distinctive of the ECHO 1 site, close to DOMES C, and confirms the data of Paul & Jumars (1976), Morgan (1991a) and Radziejewska & Stoyanova (2000).

The data presented here and in the literature lead to the conclusion that the quality of the images depends on the optical characteristics of the cameras and the construction of the observation system. Foell *et al.* (1986), Pawson (1988), Foell (1992), Morgan *et al.* (1993), Bluhm (1994) and the scientists of the German geological expeditions used vertical cameras. Hecker (1990) and Radziejewska & Stoyanova (2000) preferred a horizontal system involving a towed device with an obliquely inclined camera. This last system may be better for taxonomic identification while the vertical system is a good choice for estimating size and density.

6.2. COMPARAISON OF SUPRA-BENTHIC ASSEMBLAGES AT THE STUDY SITES

Taxonomic richness

The figure for taxonomic richness at the NIXO 45 site is 122 different taxa of which 37 are echinoderms (represented principally by 26 holothurians) and 27 cnidarians. The figure for the whole of the Clarion-Clipperton fracture zone is 240 taxa (or 159 if the taxa which traditionally come under the macrofauna and zooplankton are excluded) of which 46 are echinoderms (including 31 holothurians). However, not all of these were observed principally because the surface areas sampled vary by a factor of about 50. The phylum Echinodermata was noted in a preliminary study (Tilot *et al.*, 1988) as the most diverse at the NIXO 45 site, but it is not in fact the most taxonomically diverse group when considering the fauna of the entire Clarion-Clipperton fracture zone. This is the Cnidaria, with 59 different taxa, and which thus outnumbers the echinoderms, which nevertheless have quite a high number (46) of different taxa (figure 35). The sampled surface areas, the edaphic situation, currents, biotic variables and values for primary production all influence greatly the expression of diversity of this phylum, as will be discussed below.

The total of 122 taxa observed at the NIXO 45 site is greater than that proposed by Du Castel (1982) for the same site. This author distinguished only 14 taxa, including 6 holothurians. This significant difference in taxonomic diversity could be due in part to the difference in size of the areas studied, as du Castel (1982) sampled a total area of 17 280 m^2 while the present study is based on an area of 71 070 m^2. Values of taxonomic diversity found by the present study agree instead with those of Foell & Pawson (1986) for a region near the DOMES C site, north-west of NIXO 45. They listed more than 80 taxa of which 38 were echinoderms, including 24 holothurians, 10 were fish and only 12 were sessile taxa. Pawson (1988b) found that the phylum Echinodermata presented the greatest taxonomic diversity at a site to the south-west of NIXO 45 that was sampled photographically. Echinoderms were also the most diverse group according to Morgan (1991), who explored sites of different longitude in the Clarion-Clipperton fracture zone and listed a total of 50 invertebrates and seven fish.

These levels of taxonomic richness can be compared with 90 species, including 35 echinoderms, observed in the north-east Atlantic Ocean by Haedrich *et al.* (1980) at 2 504-3 113 m depth. However, these authors only listed 25 species at equivalent depths (3 879-4986 m) to the sites analyzed here. A decrease in diversity with increasing depth (Rex, 1983) was thus verified by the results of Haedrich *et al.* (1980) but not in the present study, where high diversity was prevalent in the abyssal depths. Our results agree instead with those of Sibuet (1977) and Gage *et al.* (1984), who observed a considerable diversity of echinoderms at bathyal and abyssal depths (2 740-3 540 m).

In his comparison of the megafauna of the North Pacific Ocean (the IOM site in the CCFZ, Kotlinski *et al.*, 1996) and the South Pacific Ocean (DEA sites in the Peruvian Basin) based on photographic and video data, Bluhm (1994) recorded taxonomic richness of 80 and 110 taxa respectively, of which 53 were common to both regions. On the whole, the most abundant categories were sponges, cnidarians, crustacea, bryozoans and holothurians.

Faunal abundance

The total density of the megafauna at the NIXO 45 site is estimated at 498 ind/ha. This value is lower than the 538/ha proposed by Du Castel (1982) for the same site, but as mentioned previously, the area sampled by Du Castel was four times smaller and may explain in part the overestimates of density per hectare. In addition, the facies sampled in her study do not reflect the true heterogeneity of the NIXO 45 site and some of the microfacies were overrepresented in relation to others.

The total density of 498 ind/ha for the NIXO 45 site estimated here is, in contrast, greater than the 360 ind/ha proposed by Morgan *et al.* (1993) and the 310 ind/ha estimated by Ozturgut *et al.* (1978) for the DOMES C site, which is considered to be the most faunistically abundant of the three DOMES sites. However, not only was the area photographed by these authors 2.6 times smaller, but this site is found under a zone where primary production is 2.5 times less than above the NIXO 45 site (as described previously in the estimations of biomass for the study sites). Similar values of abundance for sites close to DOMES C have been proposed by other authors. Hecker & Paul (1977) gave a density of 305 ind/ha for a surface area of 27 183 m^2 near DOMES C. Foell (1988) estimated a total density of 363 ind/ha based on a surface area of 9 260 km^2 situated 15°N-126°W near DOMES C and 361 ind/ha for an area of 1 087 542 m^2 filmed at a site south-west of NIXO 45. Foell *et al.* (1986) and Pawson (1988) obtained a similar result of 356 ind/ha, and Paul & Jumars (1976) found a comparable density of 341 ind/ha for a region of 81 355 m^2 at the DOMES C site. The total density of 356 ind/ha estimated by Pawson (1988b) at the same site most closely approaches the estimate proposed here, despite the fact that the surface area studied was only 31 196 m^2.

In contrast, the estimates of Morgan (1991) at a site neighbouring NIXO 45 and covering 11 068 m^2 are greater (938 ind/ha) than those proposed here. Similarly the estimates of Bluhm (1993) for two sites to the west and east, at the pioneering IOM site, were 3 081 ind/ha and 4 165 ind/ha respectively. Densities reported for the DISCOL site in the Peruvian region of the south Pacific were of the order of 1 404 ind/ha and 1 631 ind/ha, and 5 190 ind/ha for the SOPAC site (Bluhm, 1994). But according to this author, these values could be over estimates since the size and number of photographic and video samples were not representative of the site, the surface area of each image was too small (0.25 m^2) and the counts included many non-identified taxa, often belonging to the macrofauna.

Estimates of densities for stations at the same depths in the Atlantic Ocean are generally lower than those presented here. Low densities of 300 ind/ha have been observed in the Cape Verde Basin at 4 950 m depth by Sibuet *et al.* (1982), based on a relatively small area of 2 217 m^2. This value is nevertheless greater than the 123 ind/ha measured by trawling an area of 28 750 m^2 at the same station. Another site, at 4 440 m in the Demerara abyssal plain in the equatorial Atlantic Ocean had a megafaunal density of 106 ind/ha, which is low compared with that of 246 ind/ha for site at 4 840 m and subject to an unusual flow 1.6 times greater (Sibuet *et al.*, 1984). Finally, a similar density to that measured at the NIXO 45 site was observed at a station in the Bay of Biscay at 4 440 m depth (Sibuet *et al.*, 1980). These latter estimates of density do not agree with the general trend underlined by Smith & Hamilton (1983) of a decrease in density correlating with increasing depth.

Faunal composition

The megafauna over the whole of the NIXO 45 site is characterised by a dominance of cnidarians (258 ind/ha) over echinoderms (180 ind/ha) and sponges (56 taxa/ha) (figure 38). Cnidaria consist principally of actinids (135 ind/ha) and octocoralliarids (105 ind/ha) while echinoderms are represented mostly by holothurians (64 ind/ha) and crinoids (61 ind/ha). The relative abundance of actinids (52 %) and echinoderms (36 %) agree with the estimates of Morgan *et al.* (1993), which were 54 % and 32 % respectively for a study site further west, as well as with the results of Radziejewska & Stoyanova (2000) at the IOM site in the Clarion-Clipperton fracture zone. These results are not similar to those proposed by Du Castel (1982) for the NIXO 45 site, in which echinoderms (351 ind/ha) predominated over cnidarians (113 ind/ha). According to this author, the principal representatives of these two predominant phyla are holothurians (178 ind/ha) and actinids, whose density of 106 ind/ha is relatively large. Octocoralliarids were not recorded in the counts, thus distorting comparisons with the results presented in this document.

Morgan *et al.* (1993), in contrast, recorded a greater abundance of echinoderms (42 %) in relation to actinids (34-38 %) at two other sites further east. At the DOMES C site, Hecker & Paul (1977) found echinoderms had a relative abundance of 69 % compared with 16 % for actinids, while Foell *et al.* (1986) and Foell (1988) reported values of 51.5 % for echinoderms and 23 % for actinids.

At the DEA and SOPAC sites in the South Pacific Ocean (Bluhm, 1994), echinoderms have a relative abundance of 34 % and 27 % and sponges have similar abundances of 25 % and 31 %, but data for actinids were not presented in the analysis.

Echinoderms also have the highest relative abundance at most of the abyssal sites sampled in the North Atlantic Ocean, such as those at 3 244 m to 3 740 m, where they were recorded as composing 88 % of the megafaunal density, due to the super abundance of two species of ophiuroids. This percentage of ophiuroids decreased by 17 % from 3 879 m to 4 986 m depth (Haedrich *et al.*, 1980). Grassle *et al.* (1975) showed that at 1 778-1 830 m the megafauna is dominated by ophiuroids and echinoids, and thus the importance of this phylum varies according to depth. Rice *et al.* (1982) observed a super abundance of pennatulids at 980 m, replaced by one of echinoderms at 1 400 m.

The density of holothurians at NIXO 45 is 64 ind/ha. This value is close to the maximum abundance of 53 ind/ha observed at a series of depths between 3 992 m and 4 252 m in the Bay of Biscay and sampled by trawling (Sibuet *et al.*, 1980). A similar estimate of 50 ind/ha was observed in the Porcupine basin (Rice *et al.*, 1982) but this is much less than the values of 160 to 4 230 ind/ha measured in the Norwegian Sea between 2 000 m and 3 000 m (Dahl *et al.*, 1977). In comparison, the densities of holothurians reported in the Atlantic Ocean for depths similar to those of the present study are very low at 30 ind/ha for a site at 4 950 m in the Cape Verde Basin (Sibuet *et al.*, 1982).

The phylum Cnidaria is predominant in the faunal composition of sites at longitudes from 135.8° W to 126°20 W between the Clarion and Clipperton fracture zone at the same depths as in the present study. The site closest to NIXO 45, described by Morgan (1991), has a majority of actinids, which reach a density of 360 ind/ha. Similarly, at a site south-west of NIXO 45, Pawson (1988) found a majority of actinids (186 ind/ha), which were present at twice the density of ophiuroids and sponges, and associated with significant nodule-coverage. At a site in the Bay of Biscay in the Atlantic Ocean that was subject to currents of 10 cm/sec, the population of actinids was of comparable density to that at NIXO 45 (Sibuet *et al.*, 1980), while in the Cape Verde Basin, octocoralliarids predominated (139 ind/ha) (Sibuet *et al.*, 1982).

Estimates of relative abundance for sponges (11 %) in the present study are similar to those of Morgan *et al.* (1993) for his site further west (7 %) and to values proposed by Foell *et al.* (1986), Foell (1992) and Pawson (1988) of 11 %. These abundances are also comparable to those proposed for the DEA and SOPAC sites in the South Pacific Ocean (Bluhm, 1994). In contrast, Radziejewska & Stoyanova (2000) found that among suspension feeders, sponges and not actinids are dominant (40 %) on nodule substrata, as in the present study at NIXO 45.

However, since the estimates given in the literature are based on different methods and sampling strategies that represent substrata and faunal populations to different degrees, comparisons can only be made for interest, after analysis of the different methodologies.

Trophic structure of suprabenthic assemblages

At the NIXO 45 site, suspension feeders (374 ind/ha) outnumber detritus feeders (114 ind/ha) over the whole site as well as on each facies (figures 42, 43 and 44), and these results have been confirmed by recent studies (Morgan, 1991; Radziejewska & Stoyanova, 2000). According to Du Castel (1982), the dominance of suspension feeders is small (258 ind/ha) compared with 252 ind/ha for detritus feeders, while Pawson (1988a) showed that it is greater (75 %), at a site south-west of NIXO 45. However, Ozturgut *et al.* (1978) found that at the DOMES C site, detritus feeders were slightly more numerous (50 %) than suspension feeders (43 %). The density of detritus feeders at the NIXO 45 site is comparable with a figure of 90 ind/

ha at 4950 m in the Cape Verde Basin (Sibuet, 1980), and the density of carnivores (53 ind/ha) at the NIXO 45 site is comparable with 40 ind/ha observed at 3 000 m in the Bay of Biscay (Sibuet, 1977).

A majority of suspension feeders has also been observed at some abyssal sites in the Atlantic Ocean, such as at 4840 m on the Demerara abyssal plane, in the equatorial Atlantic, where this trophic group is represented by 106 ind/ha (Sibuet *et al.*, 1984). These authors were able to demonstrate correlations between flow and the dominant trophic group, and thus at the base of the Amazon cone, at 4 440 m depth, detritus feeders dominate where the flow is 1.6 times greater than at the station at 4 840 m.

The assertion that suspension feeders predominate in the oligotrophic zone (Sokolova, 1968) is supported by results from the Demerara site (Sibuet *et al.*, 1984), but not from the present study. Within the Clarion-Clipperton fracture zone, one might expect to see more suspension feeders at sites which have the lowest primary production at the surface, and thus there would be a gradient from west to east, with more suspension feeders at the more western oligotrophic sites of DOMES A and B compared with site C. In the same way, site C would have lower primary production than NIXO 45 and NIXO 41 located in the mesotrophic zone (with values of primary production between 150 and 250 gC/m^2/yr according to Berger *et al.*, 1987), and ought therefore to have more suspension feeders. But differences in values for primary production are not the only factors which influence the structure suprabenthic assemblages. There is also a horizontal contribution of nutritive sediment particles when currents originate in the west, in zones of high primary production, with the abundance of particles in suspension decreasing progressively eastwards. So the DOMES C site is characterised by a majority of echinoderms (Paul & Jumars, 1976), and especially echinoids (Morgan, 1991). These authors demonstrated a gradient of dominance of actinids to the west (close to NIXO 45) and echinoids to the east, at 126°20W-13°07N (close to ECHO 1), accompanied by a general increase in abundance. The same gradient of dominance was observed in the present study at the NIXO 45 and 41 sites. Actinids are adapted to lower energetic resources.

Combining these observations and those at sites further west, an increase in suspension feeders (7 % to 49 %) has been observed, with lower levels at the DOMES A site and higher ones at DOMES C (Hecker & Paul, 1977). Similarly, to the south of DOMES C, suspension feeders are more abundant at the sites NIXO 45 and NIXO 41, as shown in the present study by the importance of ophiuroids. This abundance can not be explained here as an adaptation to lower resource levels nor to oligotrophic conditions (Sokolova, 1968) since the sites are in the mesotrophic zone, but instead by their particular edaphic and hydrological conditions, as previously shown.

Preferential habitats and their faunal assemblages

At the NIXO 45 and NIXO 41 sites, the same order of dominance and proportionality of suspension feeders over detritus feeders and carnivores is observed what ever the facies (figure 43), with only the faunal components of the tropic groups differing. But abundance varies according to nodule coverage and abiotic factors such as the effect of slope. A greater total abundance is seen on nodule-facies C+ 10 % and nodule-facies C+ with slope > 15° at NIXO 45 (figure 41). Cnidaria (mostly octocoralliarids) are the main components of the faunal assemblages belonging to each facies (figures 40 a, b, c).

To avoid repeating the descriptions of the faunal assemblages on each facies that have already been described in detail in the chapter on quantitative analysis, only elements of comparison with the literature are discussed here.

The greatest abundance of suspension feeders was observed on facies O with ancient sediments and on sloping facies C+ 20 to 40 %, whereas detritus feeders were abundant especially nodule-facies C+10%, facies O on ancient sediments and nodule-facies C+15%. These data confirm in detail those ofTilot *et al.* (1988). Similarly, Du Castel (1982) also discovered an abundance of fixed suspension feeders and surface disturbances on nodule-facies C+ and B. She considered this abundance was due to the geomorphology and hydrodynamic conditions of the site. Similarly, she found the same order of faunistic abundance by facies as that observed in the present study, i.e. in order of importance: nodule-facies C+, O, B and A. A majority of octocoralliarids was observed on nodule-facies O as in this study on the homologous facies composed of recent sediments, while actinids predominated on nodule-facies C+ and B. The preferential habitats noted by Du Castel (1982) were only confirmed in the present study as regards a greater abundance of motile animals on nodule-facies C+ and BP.

Recent studies (Morgan, 1991; Radziejewska, 1997; Radziejewska & Stoyanova, 2000) demonstrate a clearly marked faunal abundance on nodular substrata, with a dominance of suspension feeders, compared with substrata without nodules, thus confirming our results. However, among the suspension feeders, these authors found that sponges were dominant while our results underlined the dominance of cnidarians. Similarly, among detritus feeders, these authors found that ophiuroids were dominant, while here, it is the holothurians and crinoids. But details of percentage coverage and size of nodules were not taken into account by these authors, nor was the influence of other environmental variables, let alone the large contribution of particulate flow over the substratum, which may be a major contributing factor in faunal abundance according to Smith *et al.* (1997), Drazen *et al.* (1998) and Thurston *et al.* (1998). The results of Radziejewska & Stoyanova (2000) showed a predominance of mobile megafauna over suspension feeders on substrata without nodules, confirming the results of the present study at NIXO 45 for facies O on ancient sediments. In contrast, the faunal characteristics of the facies investigated by Pawson (1988a) to the south-west of NIXO 45 were not confirmed here. Ophiuroids and regular echinoids are not found preferentially on facies O at the NIXO 45 site, but prefer instead nodule-facies BP 35 % and C+ 2-5 %. In addition, this author found no sponges and actinids on facies O whereas Pachastrellidae were abundant at 69 ind/ha and Hormathiidae numbered 13 ind/ha on facies O at the NIXO 45 site. Nevertheless, in agreement with our results, the highest total densities were observed on medium nodule-coverage, the lowest densities were associated with rather dense coverage (and not with facies O) and the density of actinids varied as a function of nodule-coverage.

The present study demonstrates results in common with studies undertaken by Foell *et al.* (1986) at a site further east of NIXO 45, where echiniods *Plesiodiadema globulosum* were more abundant on facies with low nodule-coverage and where fixed crinoids were especially associated with facies with 20 to 40 % nodule-coverage.

Moving to the level of taxa, one might suggest that the Clarion-Clipperton study area is a zoogeographic sub-region according to definitions used by Hansen (1975), in view of the new species which are unique to it, such as *Peniagone leander* (Pawson & Foell, 1986) and *Psychronaetes hanseni* (Pawson, 1983), and from the characteristics of its faunal assemblages. At the NIXO 45 site, the most frequently observed suspension feeders belong to the Cnidaria and represent the families Actinostolidae, Actinernidae, Primnoidae and Isididae, while the most frequent detritus feeders are the Bathycrinidae and Ophiuridae. The most frequently observed sponges are Hyalonematidae and Pachastrellidae. The highest number of exclusive taxa is seen on facies O on ancient sediments and nodule-facies C +15 %. The most abundant taxa at the three sites of NIXO 45, 41 and ECHO 1 were actinids *Sincyonis tuberculata*, sponges of the genus *Hyalonema*, holothurians *Mesothuria murrayi*, polychaetes *Incertae sedis* living in contorted tubes 40 cm long and echinoids *Plesiodiadema globulosum*.

6.3. LIMITING FACTORS: CURRENTS, GEOMORPHOLOGY, EDAPHIC HETEROGENEITY AND ADAPTATIONS OF THE FAUNAL ASSEMBLAGES

The currents over the seabed at the DOMES C site were measured over six months by a chain of current-metres (Hayes, 1979). The current speed measured at 6 m above the ocean floor was 0 to 12 cm/sec and varied according to an almost symmetrical rhythm of tidal currents, with a slight resultant mean towards the north-west, as indicated in some photographs by the presence of a uniform deposit of fluffy sediments around the edges of the nodules. The current speed was greatest at 30 m above the ocean floor. These data on currents agree with previous work at neighbouring sites (Harvey & Patzert, 1976). Temperature profiles indicate weak stratification in the first 200 m above the seabed, and the absence of mixing in the layers adjacent to the sea floor. So the gradient in velocity over a nodule-field is influenced by the speed of currents above the bottom layer and the topography of the ocean floor. Abiotic disturbance in the study area can be produced by variation in the currents at depth and the phenomenon of benthic storms, which have been observed during long term *in situ* measurements (Kontar & Sokov, 1994; Aller, 1997).

The morphology of the NIXO 45 site comprises horsts and grabens, which favour the acceleration of currents and the creation of slopes (figure 17). Nodule-facies B and C+, localised on the hill to the west and between the plateaux to the south and centre, appear to be where currents circulate according to the abundance of sessile suspension feeders and their orientation (Du Castel, 1982). The fixed fauna can thus serve as markers for seabed currents (Heezen & Hollister, 1971; Kennett, 1982). Facies O on recent sediments are, in the deepest parts, in the axis of a graben, while nodule-facies BP are on the slopes and summits of horsts. To the north-east of the plateaux (Du Castel, 1985), ridges and furrows 10 to 20 cm wide and about 1m long are observed on the ledges of the steps. These structures recall the ‘furrows’ described by Hollister *et al.* (1984) and Kennett (1982) and are associated with a strong local current (10 to 15 cm/sec). The “furrows” are oriented N40 to N50 and would have been caused by a current in a parallel direction and which was thus at an identical orientation to the present current. The orientation of the present current can be seen at about 100 m from the steps from the orientation of fixed organisms (Du Castel, 1982).

Currents, observed *in situ* at the DOMES C site by a system of cameras joined to currentmeters and nephelometers submerged for 1000 days, were not strong enough to cause erosion but sufficient to prevent the deposition of particles (Gardner *et al.*, 1984). These authors also concluded that biological activity is not sufficient to keep the nodules at the surface but it is the only cause of change in the nodules' environment. According to their observations, decomposition of holothurian excrement occurs in one month and the mucous film of a hemichordate in 12 days. In addition, animals were observed creeping and "nibbling" the film covering the surface of the nodules. But these observations on one very small area of the ocean floor, though lasting a long time biologically, are of too short a duration to measure a geological phenomenon, even a recent one. According to Hoffert *et al.* (1992), the present distribution of nodules is the consequence of dynamic deep-ocean currents due to Quaternary changes in climate; the maintenance of nodule deposits on the sediment surface is due only to present-day erosion (less than 210 000 years), and if interrupted, rapid burial of the nodules results. In addition, the microtopography of the nodules' environment is sufficiently heterogeneous to create turbulence because the sediments with nodules are more sensitive to erosion created by weaker currents than are the sediments without nodules.

Using the pattern of hydrodynamic flow over the nodules to predict *a priori* the distribution of suprabenthic organisms is a means of determining the relative importance of physical processes on biological ones in the structure of abyssal communities. Two factors which give structure to suprabenthic communities are the pattern of bottom water flow and the availability of particular food. Mullineaux (1989) found a vertical stratification of epifauna on nodules at the DOMES C site. Thus the suspension feeders live preferentially at the summit of nodules with smooth texture and higher levels of contact, while detritus feeders colonised the base of nodules with rougher surfaces, weak cohesion, weak particle contact and a higher rate of deposition.

Suspension feeders are often situated in places with significant particle flow (Ebling *et al.*, 1948; Pequegnat, 1964; Riedl, 1971; Hughes, 1975; Genin *et al.*, 1986). The impact of currents on the suprabenthic fauna was evaluated by Jumars & Nowell (1984) and Butman (1987). Its effect on populations of suspension feeders was studied by La Barbera (1984), Merz (1984), Sebens & Koehl (1984), Holland *et al.* (1986) and Muschenheim (1987) and on detritus feeders by Taghon *et al.* (1980) and Miller & Jumars (1986). The efficiency of suspension feeders depends on the speed of flow of particles in suspension, which in turn is determined by the speed of the current, on the concentration of material in suspension and on the efficiency of the collection system (Leonard *et al.*, 1988). When currents exceed about 7 cm/sec at 1 m above the benthos, detritus from the ocean floor can be put back into suspension (Lampitt & Paterson, 1987) and thus mixed actively and rapidly, in a logarithmic fashion, throughout the layer of water adjacent to the sediment interface (Cacchione *et al.*, 1988; Jumars & Gallagher, 1982; Hollister *et al.*, 1984; Jumars & Nowell, 1984). As elevation above the ocean floor increases, the efficiency of the feeding by suspension feeders decreases, because concentrations of particles put back into suspension are lower.

Thus many passive suspension feeders are large in size and elevate their filters sufficiently high to collect more food where the current is stronger (Rice *et al.*, 1979; Jumars & Gallagher, 1982; Fujita *et al.*, 1987). Consequently the currents affect populations of suspension feeders by influencing their nutritional resources (Sebens, 1984; Leonard *et al.*, 1988), the dispersion of larvae and the transport of sediments (Cacchione *et al.*, 1988). Local increases in suspension feeders have been correlated with variations in currents (Peguegnat, 1964; Sebens, 1984; Sibuet & Segonzac, 1985).

At the NIXO 45 site, the considerable abundance and diversity of suspension feeders has been confirmed by recent studies (Morgan, 1991; Radziejewska & Stoyanova, 2000). As shown in the qualitative analysis, observations of specialists, together with information from the literature, classify the following organisms as suspension feeders: sponges, alcyonarids, cerianthbarids, actiniarids, corallimorpharids, antipatharids, archaeogastropods, sedentary polychaetes, cirripedes, brachiopods, crinoids, ophiuroids, brisingids and ascidians. Octocoralliarids and crinoids predominate on sloping facies that favour the acceleration of currents (Du Castel, 1982). Evidence of currents commonly seen at the study sites are the crinoids leaning in the direction of the current, comatulids with their "feeding-net" turned towards the current, and hydroids *Branchiocerianthus imperator* and ceriantharids pointing in the direction of current. Ophiuroids are frequently observed on the long stalks of sponges of the genus *Hyalonema* where they can capture particles in suspension better, and this behaviour has also been observed by Fujita & Ohta (1988) in the case of the ophiuroid *Asteronyx loveni*. A marked dominance by actinids, comparable to that observed at the NIXO 45 site, associated with currents of 10 cm/sec has been observed at a site at 4 440 m depth in the Bay of Biscay (Sibuet *et al.*, 1980).

Besides suspension feeders, some detritus feeders are adapted to a pelagic life. Numerous "swimming holothurians" have been identified from the Clarion-Clipperton fracture zone and their behaviour was described in the qualitative analysis of suprabenthic assemblages. Some such as *Enypniastes eximia*, *Peniagone leander* and *Peniagone diaphana* are "true swimmers" according to the definitions of Miller & Pawson (1990), spending most of their time in the water column. However, according to these authors, examination of their gastric contents indicates that they are not suspension feeders but they live in a meso-pelagic fashion, feeding from detritus particles put in suspension by their beating/swimming movements if not by currents. This unusual behaviour could be an intermediate stage in the adaptive evolution of an essentially meso-pelagic life style, similar to that lead by *Pelagothuria natatrix* which has only ever been observed in the water column (Ludwig, 1894; Chun, 1900). But the position most frequently adopted by *Enypniastes eximia* at the study sites is that adopted in the case of currents, according to Ohta (1985), where by it sets its velum like a sail, opposed to the direction of the current, and uses its ventro-lateral podia as brakes.

In the present study, these holothurians have been observed at more than 5 m elevation but this gives no indication of the maximum or "cruising" elevation that these organisms can reach. In fact, a *Peniagone leander* was seen at about 250 m elevation and some *Enypniastes eximia* at 50 m from the ocean floor (Pawson, 1976, 1982) and some juvenile forms have been reported from up to 3000 m (Billett *et al.*, 1985). This positioning at different elevations indicates the presence and intensity of currents and flow of particles. Various causes might give rise to such behaviour, such as fleeing from a predator (or an observation device) or from any danger, such as turbidity currents (Ohta, 1983). It could also be to escape from the turbulence of the Ekman layer adjacent to the ocean floor or simply a means of displacement by letting itself float at least energetic cost while searching for the most rapid currents. Another reason might be dispersion related to a viviparous mode of reproduction, as is the case of *Enypniastes eximia* (Ohta, 1983), or for physiological reasons, in order to increase gaseous exchange by beating it sails and podia, and so compensating for the lack of specialised respiratory organs, or to enhance the efficiency of parenteral assimilation by movements by increasing the surface area of the body (Miller & Pawson, 1990). Holothurians that are "facultative swimmers" according to the definition of Miller & Pawson (1990), found in the study zone are: *Psychropotes verrucosa*, *Psychropotes semperiana*, *Psychropotes longicauda* and *Benthodytes valdiviae*. Those whose morphology is adapted to swimming are: *Pannychia moseleyi* and *Benthodytes typica*.

6.4. BIOTIC AND ABIOTIC STRUCTURING FACTORS

The relatively great taxonomic richness that characterizes faunal assemblages in the Clarion-Clipperton fracture zone can be considered as the consequence of processes on two temporal scales. The first, in the long term, relates to an evolutive diversity at the origin of speciation and the geographical distribution of taxa assembled into suprabenthic communities that are in a state of equilibrium. The second, in the short term, occurs in an ecological context involving mechanisms of disequilibrium such as competitive exclusion, predation, and stochastic variation, which could lead to local species extinction. Two theories seek to explain the maintenance of taxonomic richness in a state of equilibrium in the abyssal domain, which is generally poor in nutritional resources.

On the one hand, according to the theory of temporal stability or "equilibrium" proposed by Sanders (1968), diversity can be explained by stable physical conditions that enable the development of adaptive evolutionary strategies which would minimize competition. According to Valentine (1973), the taxonomic richness of animal communities in a state of equilibrium is due to the partitioning of meagre nutritional resources by the increasing specialisation of feeding regimes. On an evolutionary scale, taxonomic diversity can be explained by the low chances of extinction of rare species over the vast expanses of the abyssal domain (Abele & Walters, 1979) and very diverse faunal assemblages would form part of a mature ecosystem with a highly predictable structure (Margalef, 1963). By considering the marked trend towards trophic opportunism in faunal assemblages in the study zone, habitat heterogeneity may be proposed instead as being the factor at the origin of resource partitioning and taxonomic diversity. This second interpretation of Sanders' theory of stability has also been advocated by Jumars (1976), Thistle (1981), Jumars & Gallagher (1982) and Jumars & Eckman (1983) at the scale of the individual ambit (sphere of influence) of suprabenthic organisms. In this way, the heterogeneity of edaphic conditions at the study sites, with nodules and sediments, would explain the relatively high taxonomic richness of the suprabenthic assemblages through partitioning into preferential habitats along an edaphic gradient (as demonstrated in the present study by the multivariate analysis of benthic assemblages of Nixo 45 site).

The second explanation for the taxonomic diversity observed in the study zone follows from theories of "disequilibrium", that is control of terrestrial and intertidal communities by predation (Paine, 1966; Paine & Vadas, 1969; Harper, 1969; Connell, 1970; Dayton & Hessler, 1972). But a mechanism which maintains faunal diversity in the short term by "disequilibrium" can not explain taxonomic richness on a biogeographic scale, which implies instead long term evolutionary mechanisms. Instead one could propose a hypothesis of intermediary biological disturbances which would maintain the spatio-temporal heterogeneity of populations. These disturbances would minimize by predation competitive interactions and thus permit the coexistence of species and the partitioning of the same nutritional resources (Connell, 1978). This process would favour generalist feeding behaviour and the overlapping of feeding regimes on a large scale, as appears to be the case in the present study.

However, this "generalist" feeding may well only be a reflection of the shortage of nutritional resources in the abyssal world (Hessler & Jumars, 1974; Jumars & Gallagher, 1982). Intermediary biological disturbances create microenvironments that are susceptible to colonisation by the lateral immigration of mobile suprabenthic species or the establishment of larval propagules. Biologically disturbed microenvironments can trap the flow of organic particles and consequently cause a local increase in nutritional resources. This enrichment initiates greater biological activity as well as a higher rate of decomposition (Aller & Aller, 1986) attracting opportunistic colonisers (Grassle & Sanders, 1973). As these microenvironments are not created simultaneously, a mosaic of disturbed microenvironments at different stages of colonisation can be observed, and this mosaic maintains a permanent state of "disequilibrium" (Bernstein *et al.*, 1978; Thistle, 1981; Rex, 1981).

Biotic activity can maintain in equilibrium communities with different trophic behaviours (Probert, 1984) such as the suprabenthic assemblages of the Clarion-Clipperton fracture zone. This bioturbation, if too extensive, could also create a disequilibrium of trophic communities. One can cite in support of this the study by Thayer (1979), which explained a net decline in the population of sessile suspension feeders living on Phanerozoic substrata by increasing disturbance caused by detritus feeders. This same phenomenon is produced in present day marine environments (Rhoads, 1974; Peterson, 1977).

Current data from research in the abyssal environment and especially in the Clarion-Clipperton fracture zone demonstrate a variability in biotic and abiotic conditions in space and time that revolutionizes the preconceived notion of a very stable environment moulded by an unchanging environmental context (Tyler, 1995; Radziejewska & Stoyanova, 2000). Natural disturbances of biotic and abiotic origin could also maintain suprabenthic communities in equilibrium. A seasonal cycle exists, and great variation in the vertical flow of detritus particles (Smith *et al.*, 1997; Drazen *et al.*, 1998; Thurston *et al.*, 1998) causing variation in the flux of particulate organic carbon (Smith al., 1997; Scharek *et al.*, 1999). This is controlled principally by the periodic deposition of planktonic debris that originates in the euphotic zone and its accompanying phenomena (Thiel *et al.*, 1988/1989; Gehlen *et al.*, 1997; Smith *et al.*, 1997; Khripounoff *et al.*, 1998; Scharek *et al.*, 1999). Photosynthetic pigments with natural 234Th radionuclides in the vertical flow of principally phyto-detritus particles affect the mobile suprabenthic megafauna, and especially the holothurians, stimulating their movement (Smith *et al.*, 1994/1997; Lauerman *et al.*, 1997). But relationships between this flux and suprabenthic assemblages are not yet well understood (Sibuet *et al.*, 1982).

Other disturbances may occur in this zone, such as variation in deep ocean currents and the phenomenon of 'benthic storms' that have been observed *in situ* (Kontar & Sokov, 1994; Aller, 1997).

Bibliographic References

ABELE L. G. and K. WALTERS, 1979. Marine benthic diversity : A critique and alternative parameters, J. *Biogeogr.*, **6**: 115-126.

AGASSIZ A., 1872a. Revision of the Echini. *Illustrated Catalogue of the Museum of Comparative Zoology at Harvard University*, **7(1)**: 1-242.

AGASSIZ A., 1872b. Revision of the Echini. *Illustrated Catalogue of the Museum of Comparative Zoology at Harvard University*, **7(3)**: 381-629.

AGASSIZ A., 1879. Preliminary report on the Echini. of the exploring expedition of *H.M.S. "Challenger". Proceedings of the American Academy of Arts and Sciences,* **14**: 190-212.

AGASSIZ A., 1881. Report on the Echinoidea dredged by *H.M.S. Challenger* during the years 1873-1876. *Report of the Scientific Results of the Voyage of H.M.S. "Challenger" 1873-76*, **3(9)**: 1-321.

AGASSIZ A., 1890. Notice of *Calamocrinus diomedeae*, a new stalked crinoid from the Galapagos, dredged by the U.S. Fish Comission steamer "Albatross", Lieut. Commander Z.L. Tanner, U.S.N., commanding. *Bulletin of the Museum of Comparative Zoology at Harvard University*, **20(6)**: 165-167.

AGASSIZ A., 1898. Reports on the dredging operations off the west coast of Central America, Mexico and the Gulf of California, by the U.S.S. "Albatross" during 1891. Preliminary report on the Echini. *Bulletin of the Museum of Comparative Zoology at Harvard University,* **32(5):** 71-86.

AGASSIZ A., 1904. The Panamic Deep Sea Echini. Report XXXII on an exploration off the west coasts of Mexico, Central and South America, and off the Galapagos Islands. *Memoirs of the Museum of Comparative Zoology at Harvard College*, **31**: 1-243.

AGASSIZ A. and H.L. CLARK, 1907. Hawaiian and other Echini. The Cnidaridae. *Memoirs of the Museum of Comparative Zoology at Harvard College*, **34(1)**: 1-43.

AGATEP C.P., 1967. Some elasipodid holothurians of Antarctic and Subantarctic seas. *Antarctic Res. Ser.*, **11** : 49-71.

ALDRED R.G., M. NIXON and J. YOUNG, 1978. The blind octopus *Cirrothauma sp.. Nature*, **275**: 547-549.

ALDRED R.G., K. RIEMANN-ZURNECK, H. THIEL and A.L. RICE, 1979. Ecological observations on the deep-sea anemone *Actinoscyphia aurelia. Oceanologica acta,* **2** : 389-396.

ALDRED R.G., M. NIXON and J. YOUNG, 1983. *Cirrothauma murrayi chun*, a finned octoped. *Philosophical Transactions of the Royal Society of London*, **B 301** : 1-54.

ALEKSEEV D.O., 1989. New data on squid fauna in the South Pacific (in russian). *Fisheries research : contemporary problems*, 1989, pp. 17-29.

ALLEN J.A., 1983. The ecology of deep-sea molluscs. In : *The Mollusca*, **6**, Ecology. W.D Russel-Hunter Ed., Academic Press, New-York: 29-75.

ALLEN J.A.and H.L. SANDERS, 1966. Adaptations to abyssal life as shown by the bivalve *Abra profundorum* (Smith). *Deep-Sea Research*, **13**: 1175-1184.

ALLEN J. R. L., 1982. Sedimentary structures, their character and physical basis, 643 p., Elsevier, Amsterdam.

ALLER R.C., 1977. The influence of macrobenthos on chemical diagenesis of marine sediments, Thesis, Number of 600 p., Yale University, New Haven.

ALLER R.C., 1984. The importance of relict burrow structures and burrow irrigation in controlling solute distributions, *Geochim. Cosmochim*. Acta, **48**: 1929-1934.

ALLER R., 1997. Benthic community response to temporal and spatial gradients in physical disturbance within a deep-sea western boundary region, *Deep-Sea Res*. I, **44**, 39-69.

ALLER J.Y. and R. C. ALLER, 1986. Evidence for localized enhancement of biological activity associated with tube and burrow structures in deep-sea sediments at the HEBBLE site, western North Atlantic, *Deep-Sea Res.*, **33** : 755-790.

ALTON M., 1966. Bathymetric distribution of the sea stars off the Northern Oregon coast. *Journal of the Fisheries Research Board of Canada*, **23**: 1673-1714.

AMOS A.F., O. A. ROELS, C. GARSIDE, T.C. MALONE and A. PAUL, 1977. Environmental aspects of nodule mining. in *Marine Manganese Deposits*, G.P. Glasby Eds., Elsevier Publication Compagny, Amsterdam, Oxford, New York, 391-437.

ANDERSON J., 1979. Nutrient chemistry in the tropical north Pacific : DOMES sites A, B and C. In : *Marine Geology and Oceanography of the Pacific Manganese Nodule Province*, J.L. Bishoff and D.Z. Piper Eds., Plenum Press, New York, 113-161.

ANON, 1984. Deep Seabed Stable Reference Areas, *Nat. Acad. Press*, Washington, 74 pp.

BACKER E.T. and R.A. FEELY, 1979. Chemical composition, size distribution and particle morphology of suspensed particulate matter at DOMES sites A, B and C : Relationships with local sediment composition. In : *Marine Geology and Oceanography of the Pacific Manganese Nodule Province*, J.L. Bishoff and D.Z. Piper Eds., Plenum Press, New York, 163-201.

BÄCKER H. and MILL, J.B., 1984. Deep-sea mineral deposits : The present state of knowledge and new developments. *Mem.Soc.Geol.It.* **27**, 73-84.

BAILEY-BROCK J. and P. KNIGHT-JONES, 1976. Spirorbidae (Polychaeta) collected by R.V. Vitjos from abyssal depths of the Pacific ocean. *J. Zool. London*, **181** : 315-321.

BAMBER R.N., 2000. Pycnogonida: pycnogonids from French cruises to new Caledonia, Fiji, Tahiti and Marquesas. New records and new species. Résultats des campagnes MUSORSTOM, *Mémoires du Muséum National d'Histoire Naturelle*, **21 (184)**, pp. 611-625.

BAMBER R.N., 2004. Pycnogonides (Arthropoda: Pycnogonida) de Nouvelle-Calédonie, de Fidji and de Tonga : nouvelles occurrences and nouvelles espèces. *Mémoires du Muséum National d'Histoire Naturelle*, n° 191, pp. 73-84.

BARHAM E.G., N.J. AYER Jr and R.E. BOYCE, 1967. Macrobenthos of the San Diego trough : Photographic census and observations from bathyscaphe, Trieste. *Deep-Sea Research*, **14**: 773-784.

BARNES R.D., 1968. Invertebrate Zoology, 2nd Edition, W.B. Saunders Company.

BARNES A.T., L.B. QUENTIN, J.J. CHILDRESS and D.L. PAWSON, 1976. Deep-sea macroplanktonic sea cucumbers : suspended sediment feeders captured from deep submergence vehicle. *Science*, **194**: 1083-1085.

BARTSCH I., 1983. Ophiuroidea (Echinodermata) from the northwestern Atlantic deep-sea "Meteor", *Forsch. Ergebnisse, Reihe D*, **36**: 13-20.

BEIERSDORF H., 1987. Interpretation of seafloor relief and acoustic facies in the Clarion-Clipperton block southeast of Hawaii in terms of depositional diagenetic and tectonic processes. *Geologisches Jahrbuch*, **D87**: 27-69.

BELYAEV G.M., 1971. Deep water holothurians of the genus *Elpidia*. In : *Fauna of the Kurile-Kamchatka Trench and its environment*, **92**., Vyeniamin Grigor'yevich Bogorov Ed., Trudy Instituta Okeanologii, P.P. Shirshova, 326-367 (In Russian).

BELYAEV G.M., 1972. Hadal bottom fauna of the World Ocean. *Publ. for the Smithsonian Institution. Washington by the Israel Progr. of Sci. Translat*. Jerusalem, 199 p.

BELYAEV G.M., 1985. Abyssal starfishes of the genera *Eremicaster* and *Abyssaster* (Porcellanasteridae): Composition and distribution, *Revue Zoologique*, **LXIV (6)**.

BELYAEV G.M., 1989. Deep-sea oceanic trenches and their fauna, *Nauka*, Moskva, 255pp (en Russe).

BELYAEV G.M. and N.G. VINOGRADOVA, 1961. *Etude des faunes des fosses profondes*. **Tome 1**: 125-132.

BERGER W. H., A. A. EKDALE and P. P. BRYANT, 1979. Selective preservation of burrows in deep-sea carbonates, *Mar. Geol*., **32**: 205-230.

BERGER W.H., K. FISHER, C. LAI and G. WU. 1987. Ocean productivity and organic carbon flux. Overview and map of primary production and export production. *University of San Diego*. SID ref. 87-30.

BERGQUIST F., 1978. Sponges. Hutchinson of London.

BERNSTEIN B. B., R. R. HESSLER, R. SMITH and P. A. JUMARS, 1978. Spatial distribution of benthic Foraminifera in the central North Pacific, *Limnol. Oceanogr.*, **23**: 401-416.

BETT B.J. and RICE A.L., 1993. The feeding behaviour of an abyssal echiuran revealed by *in situ* time-lapse photography. *Deep-Sea Research I*, **40** : 1767-1779.

BETT B.J., RICE A.L. and THURSTON M.H., 1995. A quantitative photographic survey of "spoke-burrow" type Lebensspuren on the cape Verde Abyssal plain. *Internationale revue der gesamten Hydrobiologie*, **80** : 153-170.

BILLETT D.S.M., 1991. Deep-Sea holothurians. *Oceanog. Mar. Biol. Annual Review*, **29**: 259-317.

BILLETT D.S.M. and Q.J. HUGGETT, 1987. Echinodermata. In : H.S.J.Roe (Ed.), Great Meteor East: a biological characterisation. *Inst. Oceanogr. Sci. Report*, 248. Institute of Oceanographic Sciences, Wormley : 109-118.

BILLETT D.S.M., R.S. LAMPITT, A.L. RICE and R.F.C. MANTOURA, 1983. Seasonal sedimentation of phytoplankton to the deep-sea benthos. *Nature* **302** : 502-522.

BILLETT D.S.M., B. HANSEN and Q.J. HUGGETT, 1985. Pelagic Holothurioidea (Echinodermata) of the northeast Atlantic. *Proceedings of the fifth international conference*, Galway, 24-29 September 1984: 399-411.

BILLETT D.S.M., C. LLEWELLYN and J. WATSON, 1988. Are deep-sea holothurian selective feeders? In : Echinoderm Biology. Burke *and al.* Eds., Balkema/Rotterdam, 421-429.

BISOL P.M., R. COSTA and M. SIBUET, 1984. Ecological and genetical survey on two deep-sea holothurians : *Benthogone rosea* and *Benthodytes typica*. *Marine Ecology - Progress Series*, **15**: 275-281.

BLUHM H., 1991. Megafauna analysis of photographs from the DISCOL experimental area (tropical southeastern Pacific Ocean). *6th Deep sea Biology Symposium 30 juin-5 juillet 1991*, (Copenhagen), p17.

BLUHM H., 1993. Effects of deep-sea mining for managanse nodules on the abyssal megabenthic community. In : *Proc. 25th Annu. Offshore Technol. Conf. Houston, Texas (May 3-6, 1993) OTC Paper* **7134** : 521-529.

BLUHM H., 1994. Monitoring megabenthic communities in abyssal manganese nodule sites of the East Pacific Ocean in association with commercial deep-sea mining. *Aquatic conservation : marine and freshwater ecosystems*, **4** : 187-201.

BLUHM H., 1997. Megafauna as indicators for the recolonisation of abyssal areas impacted by physical disturbances. *International Symposium on Environmental Studies for Deep-Sea Mining* (Tokyo, Japan), 49-63.

BLUHM H., 2001. Re-establishment of an abyssal megabenthic community after experimental physical disturbance of the seafloor. *Deep-Sea Research II*, **48** : 3427-3431.

BLUHM H. and H. THIEL, 1996. Photographic and video surveys for large scale animal and seafloor surface charting aiming at ecological characterization of habitats and communities. *International seminar of deep seabed mining technology*, 15-23 October, 1996, Beijing, China.

BLUHM H. and A. GEBRUK, 1999. Holothuroidea (Echinodermata) of the Peru basin-Ecological and Taxonomic Remarks Based on Underwater Images. *Marine Ecology*, **20 (2)** : 167-195.

BLUHM H., SCHRIEVER G. and H. THIEL, 1993. International Megafauna Atlas System. Institut fûr Hydrobiologie und Fischereiwissenschaft Universität Hamburg. *Internet site*: http://www.biologie.uni-hamburg.de

BLUHM H., SCHRIEVER G. and H. THIEL, 1995. Megabenthic recolonization in a experimentally disturbed abyssal manganese nodule area. *Marine Georesources and Geotechnology*, **13** : 393-416.

BOONE L., 1933. Scientific results of cruises yachts "Eagle" and "Ara", 1921-1928. Coelenterata, Echinodermata, and Mollusca. *Bulletin of the Vanderbilt Marine Museum*, **4** : 1-217.

BOROWSKI C., 1995. New records of Longosomatidae (*Heterospioperuana sp.n.*) (Annelida, Polychaeta) from the abyssal Southeast Pacific with the description of *Heterospioperuana sp.* N. and general remarks on the family. Zur zoogeographie und systematik insbesondere der polychaeten und ostracoden, 1995, pp. 129-144, *Mitt. Hamb. Zool. Mus. Inst. (ERG. BD.)*, **92 :** 129-144.

BOSS K., 1982. Mollusca. In : *Synopsis and Classification of Living Organisms*, Mc Graw-Hill, pp 945-1166.

BOUCHET P. and A. WAREN, 1979. The abyssal molluscan fauna of the Norvegian Sea and its relation to other faunas. *Sarsia*, **64**: 211-43.

BOUCHET P. and A. WAREN, 1980. Revision of the North-Easth Atlantic bathyal and abyssal Turridae (Mollusca, Gastropoda). *The Journal of Molluscan Studies*, **8**: 1-120.

BOUCHET P. and A. WAREN, 1985. Mollusca Gastropoda: taxonomical notes on tropical deep water Buccinidae with descriptions of new taxa. *Mem. Mus. Nat. Hist. Natur. Ser. A. Zool.*, **133**: 457-499.

BOURGOIN A., M. GUILLOU and C. MORVAN, 1985. Etude préliminaire de l'épifaune des sédiments meubles de la rade de Brest (Finistère, France) à l'aide d'une caméra vidéo sous-marine. *Annales de l'Institut Océanographique*, **61 (1)**: 39-50.

BOURNE D. and B. HEEZEN, 1965. A wandering enteropneust from the Abyssal Pacific and the distribution of Spiral Tracks on the Sea Floor. *Science*, **150**: 60-62.

BRACONNOT J.C., 1970. Mises au point à l'usage des étudiants d'océanographie biologique. Fasc. 1. Salpides and Doliolides. Groupement des océanographes de l'université Paris VI. Station zoologique Villefranche sur mer.

BRIGGS K.B., RICHARDSON M.D. and YOUNG D.K., 1996. The classification and structure of megafaunal assemblages in the Venezuela Basin, Caribbean sea, *J. Mar. Res.*, **54 :** 705-730.

BRIEN P., C. LEVI, M. SARA, O. TUZAT and J. VACELET, 1973. Spongiaires zoologie III, Fasc. I. P.P. *Grassé Masson and Cie*. Ed. Paris: 1-716.

BRUUN A.F., 1953. Problems of life in the deepest deep-sea. *Nat. Geogr. Mag.*, **26(5)**: 247-262.

BRUUN A.F., 1956a. The abyssal fauna: its ecology, distribution and origin. *Nature*, **177**: 1105-1108.

BRUUN A.F., 1956b. Animal life of the deep-sea bottom. *The Galathes deep-sea expedition 1950-1952*. Vol. I, Allen & Unwin Ltd: 149-195.

BUCKLAND S.T., D.R. ANDERSON, K.BURNHAM and LAAKE, 1993. Distance sampling : estmating abundance of biological populatons. Chapman and Hall, New York, 446pp.

BUTMAN C.A., 1987. Larval settlement of soft-sediment invertebrates: the spatial scales of pattern explained by active habitat selection and the emerging role of hydronimical processes. *Oceaonogr. Mar. Biol. Ann. Rev.*, **25**: 113-165.

CACCHIONE D.A., W.C. SCHWAB, M. NOBLE and G. TATE, 1988. Internal tides and sediment movement on horizon Guyot Mid-Pacific mountains. *Geo. Marine Letters*, **8**: 11-17.

CALLENDER E. and C. BOWSER, 1980. Manganese and coper geochemistry of interstitial fluids from manganese nodule-rich pelagic sediments of the north eastern equatorial Pacific ocean. *American Journal of Science*, **280**: 1063-1096.

CAREY A.G. Jr., 1972. Food sources of sublittoral, bathyal and abyssal asteroids in the Northeast Pacific Ocean. *Ophelia*, **10**: 35-47.

CARLGREEN O., 1956. Actinaria from depths exceeding 6000m. *Galathea report*, **2**: 9-16.

CARNEY R. and A. CAREY, 1976. Distribution pattern of holothurians on the northeastern Pacific (Oregon, USA) continental self, slope, and abyssal plain. *Thalassia Jugoslavica*, **12**: 67-74.

CARNEY R. and A. CAREY, 1982. Distribution and diversity of holothuroids (Echinodermata) on Cascadia Basin and Tufts Abyssal Plain. *Deep-Sea Research*, **29(5A)** : 597-607.

CARPENTER P.H., 1884. *Challenger* scientific results, *Zoology 11*.

CARPENTER P.H., 1888. Chalenger scientific results, *Zoology 20*.

CHAVE E.H. and JONES A.T., 1991. Deep-water megafauna of the Kohala and Haleakala slopes, Alenuihaha Channel, Hawaii, *Deep-Sea Res.*, **38** : 781-803.

CHERBONNIER G., 1964. *Myriotrochus bruuni* (Hansen), holothurie apode récoltée en 1962 par le bathyscaphe « Archimède » dans la fosse du Japon. *Vie and milieu*, **17**: 169-172.

CHERBONNIER G. and M. SIBUET, 1972. Résultats scientifiques de la campagne Noratlante: Astérides and Ophiurides. *Bulletin du Museum national d'Histoire Naturelle*, 3ème Série, **102**.

CHILD C.A.., 2002. Pycnogonida of the southeast Pacific *Biological Oceanographic Project*. 48 pp.

CHILD C.A. and M. SEGONZAC, 1996. *Sericosura heteroscela* and *S. cyrtoma*, new species, and other Pycnogonida from Atlantic and Pacific hydrothermal vents, with notes on habitat and environment. *Proceedings of the Biological Socierty of Washington*, **109(4)**, 664-676.

CHRISTIANSEN B., 1993. A television and photographic survey of megafaunal abundance in central Sognefjorden, Western Norway, *Sarsia*, **78** :1-8

CHRISTIANSEN B. and THIEL H., 1992. Deep-sea epibenthic megafauna of the Northeast Atlantic: abundance and biomass at three mid-oceanic locations estimated from photographic transects, In : *Deep-sea food chains and the global carbon cycle*, Rowe G.T., Pariente V. (eds), Kluwer Academic Publishers, Amsterdam, pp 125-138.

CHUN C., 1900. Aus den Tiefen des Weltmeeres, Jena, Gustav Fisher, p 549.

CLARK A.H., 1907. Descriptions of new species of recent unstalked Crinoids from the North Pacific Ocean. *Proceedings of the United States National Museum*, **33 (1559)**: 69-84.

CLARK A.H., 1908. Notice of some crinoids in the collection of the Museum of comparative Zoology. *Bulletin of the Museum of Comparative Zoology at Harvard University*, **51(8)**: 233-248.

CLARK A.H., 1920. A new name for *Heliaster multiradiatus* (Gray). *Proceedings of the Biological Society of Washington*, **33**: 183.

CLARKE A.H., 1960. A giant ultra-abyssal Cocculina (*C. Superba N.p.*) from the Argentina Basin. *Natur. Hist. Pap. Nat. Mus. Canada*, **7**: 1-4.

CLARKE A.H., 1961. Abyssal molluscs from the South Atlantic Ocean. *Bull. Mus. Comp. Zool.*, **125(12)**: 345-387.

CLARKE A.H., 1962a. Annotated list and bibliography of the abyssal marine molluscs of the world. *Bull. Nat. Mus. Canada*, **181**: 1-114.

CLARKE A.H., 1962b. On the composition, zoogeography, origin and age of the deep-sea mollusc fauna. *Deep-sea Research*, **9**: 291-306.

CLARKE A.H., 1968. Burrow frequency in abyssal sediments. *Deep-Sea Research*, **15**: 379-400.

CLARK A.H. and A.M. CLARK, 1967. A Monograph of the Existing Crinoids. Suborders Oligophreata (concluded) and Macrophreata. U.*S. National Museum Bulletin N° 82*, **1(5)**: 1-860.

CLARK A.M., 1981. Notes on Atlantic and other Asteroidea. 3. The families Ganeriidae and Asterinidae, with description of a new Asterinid genus. *Bulletin of the British Museum (Natural History) Zoology*, **45(7):** 359-380.

CLARK H.L., 1901a. Echinoderms from Puget Sound. Observations made on the echinoderms collected by the parties from Columbia University in Puget Sound in 1896 and 1897. *Proceedings of the Boston Society of Natural History*, **29**: 323-337.

CLARK H.L., 1901b. Holothurians of the Pacific Coast of North America. *Zoologischer Anzeiger*, **24**: 162-171.

CLARK H.L., 1907. The Apodous Holothurians. *Smithsonian Contributions to Knowledge*, **35**: 1-206.

CLARK H.L., 1910. The Echinoderms of Peru. *Bulletin of the Museum of Comparative Zoology at Harvard University*, **52 (17)**: 321-358.

CLARK H.L., 1911. North Pacific Ophiurans in the collection of the United States National Museum. *U.S. National Museum Bulletin*, **75**: 1-302.

CLARK H.L., 1913. Echinoderms from Lower California, with descriptions of new species. *Bulletin of the American Museum of Natural History*, **32**: 185-236..

CLARK H.L., 1915. Catalogue of recent Ophiurans based on the collection of the Museum of Comparative Zoology. *Memoirs of the Museum of Comparative Zoology at Harvard College*, **25(4)**: 165-376.

CLARK H.L., 1917a. Ophiuroidea. Report XVIII and XXX on the scientific results of the expedition of the "Albatross" to the tropical Pacific, 1899-1900 and 1904-1905. *Bulletin of the Museum of Comparative Zoology at Harvard University*, **1(12)**: 429-453.

CLARK H.L., 1917b. Hawaiian and other Pacific Echini. The Echinoneidae, Nucleolitidae, Urechinidae, Echinocorythidae, Calymnidae, Pourtalesiidae, Palaeostomatidae, Aeropsidae, Palaeopneustidae, Hemiasteridae and Spatangidae. *Memoirs of the Museum of Comparative Zoology at Harvard College*, **46(2)** : 85-283.

CLARK H.L., 1920a. Asteroidea. Report XXXII on the scientific results of the expedition of the "Albatross" to the tropical Pacific, 1904-1905. *Memoirs of the Museum of comparative Zoology at Harvard College*, **39 (3)**: 69-114.

CLARK H.L., 1920b. Holothuroidea. Report XXXIII on the scientific results of the expedition of the "Albatross" to the tropical Pacific, 1899-1900. *Memoirs of the Museum of comparative Zoology at Harvard College*, **39(4)** : 121-154.

CLARK H.L., 1923. Echinoderms from Lower California with descriptions of new species: supplementary report. *Bulletin of the American Museum of Natural History*, **48(6)**: 147-163.

CLARK H.L., 1924. The Holothurians of the Museum of Comparative Zoology. The Synaptinae. *Bulletin of the Museum of Comparative Zoology at Harvard University*, **65(13)**: 459-501.

COHEN D. M. and D.L. PAWSON, 1977. Observations from the DSRV Alvin on populations of benthic fishes and selected larger invertebrates in and near DWD-106. *NOAA. Baseline report of environmental conditions in deepwater dumpsite 106*.

CONNELL J.H., 1970. A predator-prey system in the marine intertidal region. 1. *Balanus glandula* and several predatory species of *Thais, Ecol. Monogr.*, **40** : 49-78.

CONNELL J.H., 1978. Diversity in tropical rain forests and coral reefs, *Science*, **199**: 1302-1310.

COOK H.E., 1975. North american stratigraphic principles as applied to deep sea sediments. *American Association of Petroleum and Geologists Bulletin*, **59** : 817-837.

COPLEY J.T.P., TYLER P.A., SHEADER M., MURTON B.J. and GERMAN C.R., 1996. Megafauna from sublittoral to abyssal depths along the Mid-Atlantic Ridge south of Iceland, *Oceanol. Acta*, **19**, 549-559.

CRERAR D.A. and H.L. BARNES, 1974. Deposition of deep-sea manganese nodules. *Geochimica and Cosmochimica Acta*, **38**: 279-300.

CUENOT L., 1948. Les Echinodermes, *Traité de zoologie*, **XI**, Masson and Cie, 1-363.

CUTLER E.B. and N.J. CUTLER, 1980. Sipuncula collected by the R/V Vema. *J. Zool. London*, **190**: 193-209.

DAHL E., L. LAUBIER, M. SIBUET and J.O. STROMBERG, 1977. Some quantitative results on benthic communities of the deep Norvegian sea. *Astarte*, **5**: 61-79.

DATTAGUPTA A.K, 1977. A new genus and a new species of bonnelid Echiura from the Caribbean deep-sea. *Proc. Zool. Soc.*, **30**: 17-23.

DATTAGUPTA A.K, 1981. Atlantic echiurans. Part I. Report on twenty-two species of deep-sea echiurans of the North and South Atlantic Ocean. *Bulletin du Museum National d'Histoire Naturelle de Paris*, **3**: 353-378.

DAUER D.M., C.A. MAYBURY and R.M. EWING, 1959. Feeding behaviour and general ecology of several spionid polychaetes from the Chesapeake Bay, *J. Exp. Mar. Biol. Ecol.*, **54**: 21-38.

DAVID B. and M. SIBUET, 1985. Distribution and diversité des échinides. *Peuplements profonds du Golfe de Gascogne. Campagne Biogas*. L. Laubier and C. Monniot Eds, Ifremer: 509-534.

DAVIES T. A. and D. S. GORSLINE, 1976. Oceanic sediments and sedimentary processes. In : *Chemical Oceanography*, J.P.R. Chester and R. Chester Eds., Academic Press : 1-80.

DAWYDOFF C., 1959. Classe des Echiuriens. *Traité de zoologie*. Tome **V(1)**: 855-907.

DAYTON P.K., 1989. Competition, disturbance and community organization : The provision and subsequent utilization of space in a rocky intertidal community, *Ecol. Monogr.* **41**: 351-389.

DAYTON P.K. and R.R. HESSLER, 1972. Role of biological disturbance in maintaining diversity in the deep-sea. *Deep-Sea Research*, **19**: 199-208.

DEICHMANN E., 1930. The holothurians of the western part of the Atlantic ocean. *Bull. Mus. Comp. Zool. Harvard*, **71**: 41-226.

DEICHMANN E., 1940. Report on the holothurians collected by the Harvard-Havana Expedition 1938 and 1939, with a revision of the Molpadonia of the Atlantic Ocean. *Mem. Soc. Cub. Hist. Nat. "Felipe Poey",* **14**: 183-240.

DEICHMANN E., 1954. The holothurians of the gulf of Mexico. *Fishery Bulletin, Fish Wilde Service U.S.*, **55** : 381-410.

DEMIDOVA T.A., 1999. The physical environment in nodule provinces of the deep sea. Deep seabed polymetallic nodule exploration : development of environmantal guidelines (Sanya, Chine), *Ed. International Seabed Authority*, *1-5 juin 1998*: 79-116.

DEMING J. W., 1985. Distribution and activity of bacterial populations in abyssal sediments. In : *Peuplements profonds du golfe de Gascogne*, edited by L. Laubier and C. Monniot: 177-182, Brest.

DE RIDDER C. and J.M. LAWRENCE, 1982. Food and feeding mechanisms: Echinoidea. In: *Echinoderm nutrition*. M.Jangoux and J.M. Lawrence Eds, A.A. Balkema Publishers, Rotterdam: 57-115.

DESBRUYERES D., 1980. Sphaerodoridae (Annélides polychètes) profonds du Nord-Est Atlantique. *Bull. Mus. Hist. Nat. Paris*, 4ème Série, **2 (1)**: 109-128.

DESBRUYERES D., F. GAILL, L. LAUBIER and Y. FOUQUET, 1985. Polychaetons annelides from hydrothermal vent ecosystems: An ecological overview. *Biol. Soc. Wash. Bull.*, **16**: 103-116.

DESBRUYERES D., J.Y. BERVAS and A. KHRIPOUNOFF, 1980. Un cas de colonisation rapide d'un sédiment profond, *Oceanol. Acta*, **3** : 285-291.

DE VAUGELAS J., 1989. Deep-sea lebensspuren: remarks on some echiuran traces in the Porcupine Seabight, northeast Atlantic, *Deep-Sea Reearch.*, **36**: 975-982.

DICK R.E. and E.J. FOELL, 1985. Analysis of SIO deep tow photographs of mining device tracks, "ECHO I" cruise, mining test site. *Unpublished report number MS-200-151 of deep sea ventures, INC.* 1-28.

DINET A., 1973. Distribution quantitative du méiobenthos profond dans la région de la dorsale de Walvis (Sud-Ouest Africain). *Marine Biologie*, **20**: 20-26.

DINET A. and M.H. VIVIER, 1977. Le meiobenthos abyssal du golfe de Gascogne. I. Considérations sur les données quantitatives. *Cahiers de Biologie Marine*, **18**: 85-97.

DODERLEIN L., 1921. Die Asteriden der Siboga-Expedition. II. Porcellanasteridae, Astropectinidae, Benthopectinidae. *Siboga-Expeditie 46 b*: 1-47.

DOUMENC D.A. and M. VAN PRAET, 1987. Ordre des Actiniaires des Ptychodactiniaires, des Grallimorphaires. *Traité de zoologie*, (**3**), publié sous la direction de P.P. Grassé: 257-401.

DRAZEN J.C., R.J. BALDWIN and K.L. SMITH Jr, 1998. Sediment community response to a temporally varying food supply at an abyssal station in the NE pacific. *Deep-Sea Research Pt II* **45** : 893-913.

DU BUIT M.H., 1978. Alimentation de quelques poissons téléostéens de profondeur dans la zone du seuil de Wyville Thomson. *Oceanologica acta*, **1**: 129-134.

DU CASTEL V., 1982. Relation faune-substrat dans les faciès abyssaux à nodules polymétalliques de l'océan Pacifique est équatorial. *DEA*, Université de Bretagne Occidentale, 30 p.

DU CASTEL V., 1985. Etablissement d'une carte géologique au 1/20.000e d'un domaine océanique profond dans une zone riche en nodules polymétalliques du Pacifique Nord (zone Clarion-Clipperton). *Thèse de Doctorat, Université de Bretagne Occidentale,* 211 p.

DYER M.F., W.G. FRY, P.D. FRY and G.J. CRANMER, 1982. A series of north sea benthos surveys with trawl and headline camera. *J. Mar. Biol. Ass. U.K.*, **62**: 297-313.

DYMOND J., M. LYLE, B. FINNEY, D. Z. PIPER, K. MURPHY, R. CONARD and N. PISIOS, 1984. Ferromanganese nodules from Manop sites H, S and R. Control of mineralogical and chemical composition by multiple accretionary processes. *Geochimica and Cosmochimica Acta*, **48**: 931-949.

EBLING F.J., A. KITCHING, R.D. PURCHON and R. BOSSINDALE, 1948. The ecology of the Lough Ine rapids with special reference to water currents. 2. The fauna of the Saccorhiza canopy. *J. Anim. Ecol.*, **17** : 223-244.

EDWARDS C.L., 1907. The holothurians of the north Pacific coast of North America. *Proc. U.S. Nat. Mus.*, **33** : 49-68.

EHRLICH H.L., 1978. Conditions for bacterial participation in the initiation of manganese deposition around marine sediment particles. In : *Methods, Metals and Assessment*, W. E. Krumbein Eds., Ann Arbor Science, Michigan: 839-845.

EKDALE A. A., 1985. Paleoecology of the marine endobenthos, *Paleogeograph. Paleoclimat. Paleoecol.*, **50** : 63-81.

EKDALE A.A. and W.H. BERGER, 1978. Deep-sea ichnofaciès : Modern organism traces on and in pelagic carbonates of the western equatorial Pacific. *Paleogeograph. Paleoclimat. Paleoecol.*, **23**: 263-278.

EKMAN S., 1926. Systematisch phylogenetisch studien über Elasipoden und Aspidochiroten. Zoologische Jahrbucher, Abteiluns für.

ELLIOTT J.M., 1971. Some methods for the statistical analysis of samples of benthic invertebrates. *Freshwater biological association*, Scientific publication n°25.

EL-SAYED S.Z. and T. SATORU, 1979. Phytoplankton standing crop and primary productivity in the tropical Pacific. In : *Marine Geology and Oceanography of the Pacific Manganese Nodule Province*, J.L. Bishoff and D.Z. Piper Eds., Plenum Press, New York : 241-285.

ETTER R.J. and GRASSLE J.F., 1992. Patterns of species diversity in the deep sea as a function of sediment particle size diversity. *Nature*: **360**, 576-8.

EWING M. and R.A. DAVIES, 1967. Lebensspuren photographed on the ocean floor. In : *Johns Hopkins Oceanographic Studies N°3*: 259-294.

FARRELL J. W. and W. L. PRELL, 1989. Climatic change and $CaCO_3$ preservation : An 800 000 years bathymetric reconstruction from the central equatorial Pacific ocean. *Paleoceanography*, **4**: 447-466.

FAUCHALD K., 1977. Some nereid polychaetes from deep water. Essays polychaetous annelids. *Mem. Dr. Olga Hartman*. Los Angeles: 157-171.

FAUCHALD K. and P.A. JUMARS, 1979. The diet of worms: a study of polychaete feeding guilds. *Marine Biology Annual Review*, **17**: 193-284.

FELL F.J., 1982. Echinodermata. In : *Synopsis and classification of living organisms*, McGraw Hill : 785-818.

FILATOVA Z.A., 1958. Au sujet de quelques nouvelles espèces de mollusques Bivalvia du Nord-Ouest de l'Océan Pacifique. *Tr. IN-TA Océanologie AN URSS*, **27**: 208-218.

FILATOVA Z.A., 1969. The quantitative distribution of the deep-sea bottom fauna. In : *The Pacific Ocean. Vol. 7. Biology of the Pacific Ocean. Book 2: The deep sea bottom fauna.* V.G. Kurt Ed., Moscou: 202-216.

FISHER W.K., 1905. New starfishes from the deep water off California and Alaska. *Bulletin of the U.S. Bureau of Fisheries*, **4**: 291-320.

FISHER W.K., 1907. The Holothurians of the Hawaiian Islands. *Proceedings of the United States National Museum,* **32**: 637-744.

FISHER W.K., 1910. Nex starfishes from the North Pacific. *Zoologisher Anzeiger*, **35**: 545-553.

FISHER W.K., 1911. Asteroidea of the North Pacific and adjacent waters. Part 1. Phanerozonia and Spinulosa. *U.S. National Museum Bulletin*, **76**: 1-419.

FISHER W.K., 1928-1930. Asteroidea of the North Pacific and adjacent waters. Part 2 & 3. Forcipulata. U.*S. National Museum Bulletin*, **76**: 1-245 ; 1-356.

FOELL E.J., 1988. Videotape and photograph imagery-based analysis of abyssal megafauna near DOMES site C in the eastern tropical Pacific. *5th Deep-Sea Biology Symposium*, Brest: 87.

FOELL E.J., 1992. Abyssal megabenthos and Microtopographic Features of the Cruise 92P Area of the North-eastern Tropical Pacific Ocean near DOMES Site C, *Report under NOAA Contract 40-AANC-8-00964, NOAA*, Washington D.C.: 1-38.

FOELL E. and D. PAWSON, 1985. Photographic atlas of abyssal megafauna from the Clarion-Clipperton fracture zone, north-eastern equatorial Pacific. *4th International Deep Sea Biology Symposium (Hamburg).*

FOELL E. and D. PAWSON 1986. Photographs of Invertebrate megafauna from abyssal depths of the N. Eastern équatorial Pacific Ocean. *The Ohio Journal of Science*, **86 (3)** : 61-68.

FOELL E. and D. PAWSON, 1989. Assessment of abyssal benthic megafauna on a ferro-manganese nodule deposit using videotaped television survey data. *Offshore Technology Conference, Houston, Texas*: 313-320.

FOELL E., R. DICK and D. PAWSON, 1986. Occurrence, distribution and populations of benthic megafauna near DOMES Site C as discerned from videotape recordings and bottom photographs. *Final Report to NOAA/OME* under contract N° 50 DGNC-5-00133: 1-82.

FOELL E., H. HENNIGAR and D. PAWSON, 1989. Assesment of abyssal benthic megafauna on a ferromanganese nodule deposit using videotaped television survey data. *Offshore Technology Conference*, May 1-4, Texas : 313-320.

FOELL E., H. THIEL and G. SCHRIEVER, 1990. DISCOL : A Long-Term, Large-Scale, Disturbance-Recolonization Experiment in the Abyssal eastern Tropical South Pacific Ocean. *Offshore Technology conference*, OTC 632 : 497-503.

FOELL E., G. SCHRIEVER, H. BLUHM, C. BUSSAU and H. THIEL, 1992. Disturbance and recolonization experiment in the Abyssal South Pacific Ocean (DISCOL) : an update. In : Proc. *22nd Annu. Offshore Technol. Conf. Houston, Texas, May 7-10, 1990* ; OTC 632: 497-503.

FRANCESCHINI G.A., 1979. The solar radiation environment in the eastern tropical north Pacific. In : *Marine Geology and Oceanography of the Pacific Manganese Nodule Province,* J.L. Bishoff and D.Z. Piper Eds., Plenum Press, New York: 1-41.

FRIEDRICH G., 1979. Manganese nodules - A contribution to the BMFT/DFG special program. *Komm. Geowiss. Gemeisch*., **VIII**: 29-49.

FRIEDRICH G. and W. PLÜGER, 1974. The distribution of manganese, iron, cobalt, nickel, copper and zinc in manganese nodules in various fields. *Meerestechnik*, **6**: 203-206.

FUKUSHIMA T and M. IMAJIMA, 1997. A study of a macrobenthos community in a resedimentation area. *Proceedings of International Symposium on Environmental Studies for Deep-Sea Mining*, Tokyo, Japan, November 20-21: 331-335.

FUJITA T., 1988. Ecology of deep-sea ophiuroids. *Benthos research*, **33/34**: 61-73.

FUJITA T. and S. OHTA, 1988. Photographic observations of the life style of a deep-sea ophiuroid *Asteronyx loveni* (Echinodermata). *Deep Sea Research*, **35**: 2029-2043.

FUJITA T., S. OHTA and T. OJI, 1987. Photographic observations of the stalked crinoid *Metacrinus rotundus* Carpenter in the Suruga Bay, Central Japan. *Journal of Oceanographical Soc. of Japan*, **43**: 333-343.

GAGE J. D., 1978. Animals in deep-sea sediments, *Proc. R. Soc. Edinburgh*, **76B**: 77-93.

GAGE J.D. and P.A. TYLER, 1991. Deep-sea biology. A natural history of organisms at the deep-sea floor. Cambridge University Press, Cambridge.

GAGE J.B., M. PEARSON, D.S.M. BILLETT, A.M. CLARK, M. JENSEN, G.L.J. PATERSON and TYLER, 1984. Echinoderm zonation in the Rockall Trough (NE Atlantic). *Proceedings of the 5th International Echinoderm Conference*, 24-29 Septembre 1984.

GAGE J.B., D.S.M. BILLETT, M. JENSEN and P.A. TYLER, 1985. Echinoderms of the Rockall Trough and adjacent areas, 2: Echinoidea and Holothurioidea. *Bulletin of the British Museum of Natural History (Zoology),* **48(4)** : 173-213.

GARDNER W.D., L.G. SULLIVAN and E.M. THORNDIKE, 1984. Long-term photographic, current, and nephelometer observations of manganese nodule environments in the Pacific, *Earth Planet. Sci. Lett.*, **70**: 95-109.

GEBRUK A.V., 1986. Deep-sea Holothurians of the family Elpidiidae. *Nauka*, Moscow : 160 pp.

GEBRUK A.V., 1989. Revision of the family Pelagothuriidae (Holothurioidea, Elasipoda) with a review of swimming holothurians. Part I. Revision Pelagothuriidae. *Zool. Zhur.,* **68(12) :** 57-66.

GEBRUK A.V., 1990. Revision of the family Pelagothuriidae (Holothurioidea, Elasipoda) with a review of swimming holothurians. Part II. Review of swimming holothurians and their origin. *Zool. Zhur.*, **69(3) :** 60-68.

GEHLEN M., C. RABOUILLE, U. EZAT and L. GUIDI-GUILVARD, 1997. Drastic changes in deep-sea sediment porewater composition induced by episodic input of organic matter, *Limnol. Oceanogr.*, **42** : 980-986.

GEISTDOERFER P., 1978. Ecologie alimentaire des Macrouridae. *Revue des travaux de l'Institut des Pêches Maritimes*, **42**: 177-260.

GEISTDOERFER P., 1986. Nouvelles captures and redescription d'un poisson Zoarcidae (Pisces, Perciformes, Zoarcoidei) des sites hydrothermaux de la ride du Pacifique oriental. *Bulletin du Museum National d'Histoire Naturelle (FRANCE) (4eme SER.) (A. ZOOL. BIOL. ECOL. ANIM.),* **8(4)** : 969-980.

GEISTDOERFER P., 1991. Ichtyofaune associée à l'hydrothermalisme océanique and description de *Thermobiotes mytilogeiton*, nouveau genre and nouvelle espèce de Synaphobranchidae (Pisces, Anguilliformes) de l'Océan Pacifique. C.R. ACAD.SCI. (PARIS), Ser. III., **312 (3)**: 91-97.

GENIN A., P. K. DAYTON, P. F. LONSDALE and F. N. SPIESS, 1986. Corals on seamounts peaks provide evidence of current acceleration over deep-sea topography. *Earth Planet. Sci. Lett.*, **322**: 59-61.

GHIORSE W.C., 1980. Electron microscope analysis of metal-depositing microorganisms in surface layers of basaltic sea ferromanganese concretions. Biogeochemistry of ancient and modern environments, Canberra, Australia: 345-354.

GILSEN T., 1940. Investigations on the ecology of *Echiurus*, *Acta Universitatis Linden*, **36**: 3-35.

GINSBERG R. N. and H. A. LOWENSTAM, 1958. The influence of marine bottom communities on the depositional environment of sediments, *J. Geol.*, **66**: 310-318.

GLASBY G.P., 2000. Lessons learned from deep-sea mining, *Science*, **289**, (5479): 551-553.

GOLBERG E., 1954. Marine Chemistry. 1. Chemical scavengers of the sea. *Journal of Geology*, **62** : 249-265.

GONZALEZ A.F., A. GUERRA, S. PASCUAL and P. BRIAND, 1998. *Vulcanoctopus hydrothermalis* gen. and sp. nov. (Mollusca, Cephalopoda): an octopod from a deep-sea hydrothermal vent site. *Cahiers de Biologie Marine*. **39(2)**: 169-184.

GOY J., 1979. Méduses. *Campagne de la Calypso au large des côtes atlantiques de l'Amérique du Sud*, **35**: 263-296.

GRASSLE J.F., 1989. Species diversity in deep-sea communities. *Trends in Ecology and Evolution*, **4**: 12-15.

GRASSLE J.F., 1991. Deep sea benthic biodiversity, the ocean bottom supports communities that may be as diverse as those of any habitat on Earth. *Bioscience*, **41(7)**: 464-469.

GRASSLE J.F. and H.L. SANDERS, 1973. Life histories and the role of disturbance. *Deep-Sea Research*, **20** : 643-659.

GRASSLE J.F. and W. SMITH, 1976. A similarity measure sensitive to the contribution of rare species and its use in investigation of variation in marine benthic communities. *Oecologia*, **25**: 13-22.

GRASSLE J.F. and N.J. MACIOLEK, 1992. Deep-sea species richness: regional and local diversity estimates from quantitaive bottom samples. *American Naturalist*, **139**: 313-341.

GRASSLE J.F., H.L. SANDERS, R.R. HESSLER, G.T. ROWE and T. McLELLAN, 1975. Pattern and zonation: A study of the bathyal megafauna using the research submersible Alvin. *Deep-Sea Research*, **22**: 457-481.

GRAY J.E., 1851. Description of some new genera and species of Spatangidae in the Bristish Museum. *Annals and Magazine of Natural History*, Serie 2, 7: 130-134.

GRAY J.E., 1855. An arrangement of the families of Echinida, with descriptions of some new genera and species. *Proceedings of the Zoological Society of London* : 35-39.

GRAY J.S., 1981. The ecology of marine sediments. An introduction to the structure and function of benthic communities, 185 p., Cambridge University Press, Cambridge.

GREENSLATE J., 1974. Microorganims participate in the construction of manganese nodules. *Nature*, **249**: 181-185.

GREENSLATE J., R.R. HESSLER and H. THIEL, 1974. Manganese nodules are alive and well on the sea floor. *10th Anniversary Conference*: 171-181.

GREIG J.A., 1921. Echinodermata. Rep. Scient. *Results "Michad Sars" N. Atl. deep sea Exped.* **3(2)**: 1-47.

GUNDLACH H., V. MARCHIG and C. SCHNIES, 1979. What is the origin of the metals in the manganese nodules? In : *Marine Row materials and Sea Technique*, P. Halbach Eds., Verlag Geneckauf, Essen, 46-82.

HAEDRICH R.L. and N.R. HENDERSON, 1974. Pelagic food of *Coryphaenoides armatus*, a deep benthic rattail. *Deep-Sea Research*, **21**: 739-744.

HAEDRICH R.L. and G.T. ROWE, 1977. Megafaunal biomass in the deep sea. *Nature*, **269**: 141-142.

HAEDRICH R.L., G.T. ROWE and P.T. POLLONI, 1975. Zonation and faunal composition of epibenthic populations on the continental slope south of New England. *J. Mar. Res.*, **33**: 191-212.

HAEDRICH R.L., G.T. ROWE and P.T. POLLONI, 1980. The megabenthic fauna in the deep sea south of New England, USA. *Mar. Biol.*, **57**: 165-179.

HALBACH P., 1980. The metallic Minerals of the Pacific seafloor. *Geol. J.*, **45**: 407-422.

HALBACH P. and M. OZKARA, 1979a. Morphological and geochemical classification of deep-sea ferromanganese nodules and its genetical interpretation. *Colloques Internationaux du CNRS*, Gif-sur-Yvette: 77-88.

HALBACH P. and M. OZKARA, 1979b. Pelagic manganese nodule types and their growth conditions. *Marine Raw Materials and Sea Technology*, Essen: 83-101.

HALBACH P. and D. PUTEANUS, 1984. The influence of the carbonate dissolution rate on the growth and composition of Co-rich ferromanganese crusts from Central Pacific seamount areas. *Earth And Planetary Science Letters*, **68**: 73-87.

HALBACH P., G. FRIEDRICH and U. Von STACKELBERG, 1988. The managanese nodule belt of the Pacific Ocean. Geological Environment, Nodule Formation and Mining Aspects. F. Enke Verlag, Stuttgart: 1-254.

HALPERN J.A., 1968. Biological investigations of the deeps sea. 38. A new western Atlantic *Dipsacaster* (Echinodermata, Asteroida) with the distribution of known species. *Proceedings of the Biological Society of Washington*, **81**: 231-240.

HANSEN B., 1956. Holothurioridea from depths exceeding 6000 meters. *Galathea Report. Scientifc Results of the Danish deep-Sea expedition round the World* 1950-52, **2**: 33-54.

HANSEN B., 1967. The taxonomy and zoogeography of the deep-sea holothurians in their evolutionary aspects. *Studies in Tropical Oceanography (Miami)*, **5** : 480-501.

HANSEN B., 1972. Photographic evidence of a unique type of walking in deep-sea holothurians. *Deep-Sea Research*, **19**: 401-462.

HANSEN B., 1975. Systematics and biology of the deep-sea holothurians. Pt. I Elasipoda. *Galathea Report. Scientific Results of the Danish Deep-Sea Expedition Round the World 1950-52*, **13**: 5-262.

HARADA K. and S. NISHIDA, 1976. Biostratigraphy of some marine manganese nodules. *Nature*, **260**: 770-771.

HARADA K. and S. NISHIDA, 1979. Biochronology of some Pacific manganese nodules and their growth mechanism. *Colloques Internationaux du CNRS*, Gif-sur-Yvette: 25-30.

HARPER J.L., 1969. The role of predation in vegetational diversity, Brookhaven symp. Biol., **22**: 48-62.

HARTMANN M., 1979. Evidence for early diagenetic mobilization of trace metals from dislocation of pelagic sediments. *Chemical Geology*, **26**: 277-293.

HARTMAN W.D., 1982. Porifera. In: *Synopsis and classification of living organisms*. S.P. PARKER Ed, Mc-Graw Hill Corp., Tome 1: 641-666.

HARTMANN M., P. KOEGLER, P. MUELLER and E. SUESS, 1975. Results of research on manganese nodules. In : *Geoscientific research in the area of manganese nodule research*, G. Friedrich Eds., Federal Ministry on Research and Technology, Bohn: 60-113.

HARVEY R.R. and W.C. PATZERT, 1976. Deep current measurements suggest long waves in the eastern equatorial Pacific. *Science*, **193**: 883-885.

HARVEY R. and J.D. GAGE, 1988. Echinoderm distributions in the rockall trough and adjacent areas. *5th Deep-Sea Biology Symposium*, Juin-Juillet.

HAYES S., 1979. Benthic current observations at DOMES sites A, B, C in the tropical central North Pacific ocean, in *Marine Geology and Oceanography of the Pacific Manganese Nodule Province*, edited by J.L. Bischoff and D.Z. Piper, Plenum Press: 83-112.

HEATH G.R., 1981. Ferromanaganese nodules of the deep sea. *Economic Geology*, 75th Anniv, vol.1905/1980 : 736-765.

HECKER B., 1988. Variation in megafaunal assemblages on the continental margin south of New England. *Deep-Sea Research*, 37A: 37-57.

HECKER B. and A.Z. PAUL, 1977. Benthic baseline survey of the DOMES area. *DOMES final report under NOAA contract 03-6-022-35141*: 1-115.

HECKER B. and A. PAUL, 1979. Abyssal community structure of the benthic infauna of the eastern equatorial Pacific: DOMES sites A, B and C. In : *Marine Geology and Oceanography of the Pacific Manganese Nodule Province*, J.L. Bishoff and D.Z. Piper Eds., Plenum Press, New York: 287-307.

HEDING S.G., 1928. Synaptidae. N° 46 in "Papers from Dr. Th. Mortensen's Pacific Expedition, 1914-16." *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening*, **85**: 105-323.

HEDING S.G., 1931. On the classification of the Molpadids. *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening*, **92**: 275-284.

HEDING S.G., 1935. Holothurioidea I. Apoda, Molpadioidea, Gephyrothurioidea. *Danish Ingolf Expedition*, **4** : 1-84.

HEDING S.G., 1940. Die holothurien der deutschen Tiefsee expedition. II. Aspidochirote und Elasipode Formenwies. *Ergebn. Dt. Tiefsee Exped*. "Valdivia", **24**: 317-375.

HEDING S.G., 1942. Holothuriodea. II. Aspidochirotida, Elasipoda, Dendrochirota. *Dan. Ingolf. Expedit*. **4** (13) : 1-39.

HEEZEN B. and C. HOLLISTER, 1971. The face of the deep. Oxford University Prsee, New York: 1-659.

HEIN P. and M. VOISSET, 1978. Les nodules polymétalliques de la zone Clarion Clipperton: Faciès and géochimie, *Rapport Interne*, Centre National pour l'Expoitation des Océans.

HENDLER G., 1982. The feeding biology of *Ophioderma brevispinum*. *J. Internat. Echinod. Conf., Tampa Bay*, J.M. Laurence ed. A.A. Balkema, Rotterdam.

HEROUARD E., 1899. Troisième note préliminaire sur les Holothuries provenant des dragages du yacht "Princesse Alice". Révision de la sous-famille des Elpidiinae and description de nouvelles espèces. *Bull. Soc. Zool. de France*, **24**: 170-175.

HEROUARD E., 1902. Holothuries provenant des campagnes de la "Princesse Alice" (1892-1897). *Résultats Camp. Scientif. Prince Albert I*, **21**: 1-61.

HEROUARD E., 1923. Holothuries provenant des campagnes des yachts "Princesse Alice" and "Hirondelle II" (1898-1915). *Résultats Camp. Scientif. Prince Albert I*, **66**: 1-163.

HERRING P.J., 1974. New observations on the bioluminescence of echinoderms. *J. Zool. London*, **172**: 401-418.

HERRON E. M., 1972. Sea-Floor Spreading and the Cenozoic History of the East-Central Pacific. *Geological Society of America Bulletin*, **83**: 1671-1692.

HERROUIN G., LENOBLE J.P., CHARLES C., MAUVIEL F., BERNARD J. and TAINE B., 1989. A manganese nodule industrial venture would be profitable. Summary of a 4-year study in France. *OTC* 5597: 321-332

HESSLER R.R., 1974. The structure of deep benthic communities from central oceanic waters. *Conference 33. Annual Biology Colloquium*, Corvallis, OR (USA), 21 Apr. 1972.

HESSLER R.R. and P.A. JUMARS, 1974. Abyssal community analysis from replicate box cores in the central North Pacific. *Deep-Sea Research*, **21**: 185-209.

HESSLER R.R., J.D. ISAACS and E.L. MILLS, 1972. Giant amphipod from the abyssal Pacific ocean, *Science*, 175 : 636-637.

HESSLER R.R., G. WILSON and D. THISTLE, 1979. The deep-sea isopods : A biogeographic and phylogenetic overview. *Sarsia*, **64 (1-2)**: 67-75.

HEYE D., 1988. The internal microstructure of manganese nodules and their relationship to the growth rate. *Marine Geology*, **26**: 59-66.

HINGA K.J., N. McSIEBURTH and G.R. HEATH, 1979. The supply and use of organic material by the deep-sea benthos. *Journal of Marine Research*, **37**: 557-579.

HOFFERT M. and P. SAGET, 2004. Manuel d'identification des « faciès-nodules » pour la zone de plongées NIXO-45. *Rapport interne Ifremer*: 1-26, mai 2004.

HOFFERT M., A.M. KARPOFF, A. SCHAAF and G. PAUTOT, 1978. The sedimentary deposits of the Tiki Basin South East Pacific, passage from carbonate oozes to "metalliferous sediments", *Colloques Internationaux du CNRS, La Génèse des Nodules de Manganèse*, Gif-sur-Yvette.

HOFFERT M., R. LE SUAVE, G. PAUTOT, A. SCHAAF, P. COCHONAT, Y. MOREL and P. LARQUE, 1992. Caractérisation, par observations directes à l'aide du submersible « Nautile », de structures érosives actuelles des zones à nodules polymétalliques du Pacifique Nord équatorial: les "taches grises". *Compte rendu à l'Académie des Sciences*.

HOLLAND N.D., J.R. STRICKLEV and A.B. LEONARD, 1986. Particle interception, transport and rejection by the feather star *Oligometra serripinna* (Echinodermata: Crinoidea) studied by frame analyses of video tapes. *Marine Biology*, **93**: 11-126.

HOLLISTER C.D., B.C. HEEZEN and K.E. NAFE, 1975. Animal traces on the deep-sea floor, In : *The Study of Trace Fossils,* edited by R.W. Frey, Springer Verlag, Berlin: 493-510.

HOLLISTER C.D., A.R. M. NOWELL and P.A. JUMARS, 1984. The dynamic abyss, *Sci. Amer.*, **250**: 42-53.

HONJO S., 1980. Material fluxes and modes of sedimentation in the mesopelagic and bathypelagic zones. *J. Mar. Res.*, **38**: 53-97.

HUGGET Q.J., 1987. Mapping of hemipelagic versus turbiditic muds by feeding traces observed in deep-sea photographs. In : *Geology and Geochemistry of Abyssal Plains*, P.P.E. Wearer and Thomson Eds. *Geol. Soc. Spec. Publ.* **31**: 105-112.

HUGHES R.G., 1975. The distribution of epizoites on the hydroid *Nemertesia antennina. J. Mar. Biol. Assoc. U.K.*, **55**: 275-294.

HUGHES D.J. and ATKINSON R.J.A., 1997. A towed video survey of megafaunal bioturbation in the North-Eastern Irish sea, *J. Mar. Biol. Ass. U.K.*, **77**: 635-653.

HUH C.A., 1982. Radiochemical and chemical studies of manganese nodules from three sedimentary regions in the north Pacific. Ph.D. Thesis, University of Southern California, Los Angeles: 1-305.

HURLBERT S.H., 1971. The nonconcept of species diversity : a critique and alternative parameters. *Ecology* **52** : 577-586.

IFREMER, 1988. Actes du colloque "les sources hydrothermales de la ride du Pacifique oriental. Biologie and écologie, Paris, 4-7 Novembre 1985. *Oceanologica acta*, **vol. HS**, N°8, Gauthiers-villars, Montrouge cedex (France).

INGOLE B.S., Z.A. ANSARI, P. MATONDKAR and N. RODRIGUES, 1999. Immediate response of Meio and Macrobenthos to disturbance caused by a benthic disturber. *Proceedings of the Third (1999) Ocean Mining Symposium India, November 8-10, 1999*: 191-197.

INGOLE B.S., Z.A. ANSARI, V. RATHOD and N. RODRIGUES, 2001. Response of deep-sea macrobenthos to a small-scale environmental disturbance. *Deep-Sea Research II*, **48**: 3401-3410.

INGRAM C.L and R.R. HESSLER, 1983. Distribution and behavior of scavenging amphipods from the central North Pacific. *Deep-sea Research*, **30**: 683-706.

INGRAM C.L. and R.R. HESSLER, 1987. Population biology of the deep-sea amphipod *Eurythenes gryllus*: inferences from instar analyses, *Deep-sea Research*, **34** : 1889-1910.

JAIN S.C., and E.E. FISCHER, 1980. Scour around bridge piers at high flow velocities, *J. Hydraul. Dir. Am. Soc. Civ. Engrs.*, **106**: 1827-1842.

JANGOUX M., 1982. Food and feeding mechanisms: Asteroidea. In: *Echinoderm nutrition*. M.Jangoux and J.M. Lawrence Eds, A.A. Balkema Publishers, Rotterdam: 117-159.

JONES N.S., 1969. The systematics and distribution of Cumacea from depth exceeding 200 meters. *Galathea Report*, **10**: 99-177.

JORGENSEN C.B., 1966. The biology of suspension feeding. Pergamon Press, New York.

JUMARS P.A., 1974. A generic revision of the Dorvilleidae (Polychaeta), with six new species from the Deep North Pacific. *Zool. J. Lin. Soc.*, **54 (2):** 101-135.

JUMARS P.A., 1976. Deep-sea species diversity: Does it have a characteristic scale? *J. Mar. Res.*, **34**: 217-246.

JUMARS P.A., 1981. Limits in predicting and detecting benthic community responses to manganese nodule mining., *Mar.Mining,* **3**: 213-229.

JUMARS P. and K. FAUCHALD, 1977. Between community contrasts in successful polychaete feeding strategies. *Ecology of marine benthos*, B.C. Coull Ed, University of S. Coroling Press, Colombia: 1-20.

JUMARS P. A. and E.D. GALLAGHER, 1982. Deep-sea community structure : three plays on the benthic proscenium. In : *The Environment of the Deep Sea*, edited by W.G. Ernst and J.G. Morin, Prentice-Hall, Englewood Cliffs, New Jersey: 217-255.

JUMARS P.A. and J. ECKMAN, 1983. Spatial structure within deep-sea benthic communities. In : *The Sea*, edited by G.T. Rowe, Wiley-Interscience, New York: 399-451.

JUMARS P.A. and A.R.M. NOWELL, 1984. Fluid and sediment dynamic effects on marine benthic community structure. *Ann. Zool.*, **24**: 45-55.

KAUFMANN R.S. and K.L. SMITH Jr, 1997. Activity patterns of mobile epibenthic megafauna at an abyssal site in the eastern North Pacific: Results from a 17-month time-lapse photography study. *Deep-sea Research* (Part I), **44 (4)**: 559-579.

KAUFMANN R.S., W. W. WAKEFIELD and A. GENIN, 1989. Distribution of epibenthic megafauna and lebensspuren on two central North Pacific seamounts. *Deep-Sea Research*, **36**: 1863-1896.

KENNETT J.P., 1982. Marine Geology. Prentice Hall Inc, Englewood Cliffs: 1-815.

KENSLEY B., 1982. Deep-water Atlantic Anthuridea (Crustacea: Isopoda). *Smithsonian Contributions to Zoology*, **346**: 1-60.

KHRIPOUNOFF A., 1979. Nutrition des invertébrés benthiques abyssaux: exemple des holothuries and des isopodes. In: *Relations trophiques dans l'Ecosystème benthique abyssal: descriptions and bilan énergétique*. Thèse de Doctorat de 3ème cycle. Université P. and M. Curie, Paris.

KHRIPOUNOFF A. and M. SIBUET, 1980. La nutrition d'échinodermes abyssaux. I. Alimentation des holothuries. *Marine Biology*, **60**: 17-26.

KHRIPOUNOFF A., D. DESBRUYERES and P. CHARDY, 1980. Les peuplements benthiques de la faille de Vema : Données quantitatives and bilan d'énergie en milieu abyssal. *Oceanologica Acta*, **3**: 187-198.

KHRIPOUNOFF A., P. CRASSOUS, D. DESBRUYERES and J. LECOZ, 1985. *Peuplements profonds du golfe de Gascogne*. Laubier and Monniot Eds.: 101-118.

KHRIPOUNOFF A., A. VANGRIESHEIM and P. CRASSOUS, 1998. Vertical and temporal variations of particle fluxes in the deep tropical atlantic, *Deep-Sea Res. I*, **45**: 293-316.

KIRKEGAARD J.B., 1956. Benthic Polychaeta from depths exceeding 6000 meters. *Ibid.*, **2**: 63-78.

KITCHELL J.A. and D.L. CLARK, 1979. A multivariate approach to biofaciès analysis of deep-sea traces from the central arctic, *Journal of Paleontology*, **53**: 1045-1067.

KITCHELL J.A., J.F. KITCHELL, G.L. JOHNSON and K.L. HUNKINS, 1978. Abyssal traces and megafauna : Comparison of productivity, diversity and density in the Arctic and Antarctic, *Paleobiology*, **4**: 171-180.

KLINKHAMMER G.P., 1980. Early diagenesis in sediments from the eastern equatorial Pacific, II - Pore water metal results. *Earth and Planetary Science Letters*, **49**: 81-101.

KNUDSEN J., 1964. Scaphopoda and Gastropoda form depths exceeding 6000 m. *Galathea Report*, **7**: 125-136.

KNUDSEN J., 1970. The systematics and biology of abyssal and hadal Bivalvia. *Galathea Report*, **11**: 7-241.

KNUDSEN J., 1979, IX. Deep-sea bivalve. In : *Pathways in malacology*, S.V.D, Spoel and A.C.V. Bruggen Eds., J. Leverde - Scheltema L Holkema, Utrecht, 195-224.

KOBLENTZ-MISHKE O.J., V.V. VOLKOVISINKY and J.G. KABANOVA, 1970. Plankton primary production of the world ocean. In: *Scientific Exploration of the South Pacific*, Wooster, W.S. (ed.), N.A.S., Washington, D.C. : 183-193.

KOEHLER R., 1909. Echinodermes provenant des campagnes du yacht Princesse-Alice (Astérides, Ophiures, Echinides and Crinoides). *Res. Camp. Sci. Prince de Monaco*, Tome 34: 1-317.

KOEHLER R., 1914. Echinodermata of the Indian Museum, Echinoidea, **1**: 18.

KOEHLER R. and C. VANEY, 1905. Echinodermata of the Indian Museum. Holothuroidea. Indian Museum Calcutta : 1-22.

KOLMER D.W., 1985. Acrocirridae (annélides polychètes) abyssaux : Golfe de Gascogne and Méditerranée. In : *Peuplements profonds du Golfe de Gascogne*, Ifremer : 355-364.

KONTAR E.A. and SOKOV A.V., 1994. A benthic storm in the northeastern tropical Pacific over the fields of manganese nodules, *Deep-Sea Research*, **41**: 1069-1089.

KOTLINSKI, R., 1996. Morphogenetic types of polymetallic nodules in the Clarion-Clipperton ore field. *International seminar on deep sea-bed mining technology, 18-20 October, 1996*, Beijing, China : 1-12.

KOTLINSKI R. and G. TKATCHENKO, 1997. Preliminary results of IOM Environmental research (Poland). *Proceedings of International Symposium on Environmental Studies for Deep-Sea Mining*, Tokyo, Japan, November 20-21: 35-44.

KOTLINSKI R. and STOYANOVA, 1998. Physical, chemical and geological changes of marine environment caused by the Benthic Impact Experiment at the IOM BIE site. In : *Proceedings 8th ISOPE Conf.*, **Vol. II**, Chung J.S., Frederking R.M.W., Saeki H., Moshagen H. (eds.), Montreal : 277-281.

KOTLINSKI R., V. STOYANOVA and G. TKATCHENKO, 1996. Environmental studies on a reference transect in the IOM pioneer area. In : *Proc. 6th ISOPE Conf.*, **Vol I**, Chung J.S, Das B., Roesset J. (eds), Los Angeles: 54-57.

KRAMP P.L., 1956. Hydroids from depths exceeding 6000 meters. *Galathea Report*, **2**: 17-20.

KRAMP P.L., 1959. *Stephanoscyphus* (Scyphozoa). *Galathea Report*, **1**: 173-188.

KRISHNASWAMI S., A. MANGINI, T. H. THOMAS, P. SHARMA, J. K. COCHRAN, K. K. TUREKIAN and P. D. PARKER, 1982. 10Be and Th isotopes in manganese nodules and adjacent sediments : Nodule growth histories and nuclide behavior. *Earth and Planetary Science Letters*, **59** : 217-234.

LA BARBERA M., 1984. Feeding currents and particle capture mechanisms in suspension feeding animals. *Ann. Zool.*, **24**: 71-84.

LALOU C., L. KUT, E. BRICHET, G. POUPEAU and P. ROMARY, 1979. Techno encrustation part I : Radiometric studies. Colloques Internationnaux du CNRS, *La Génèse des Nodules de Manganèse*, **289**: 261-269.

LAMBSHEAD J.D. and G. BOUCHER, 2003. Marine nematode deep-sea biodiversity-hyperdiverse or hype? *Journal of Biogeography*, **30**: 475-485.

LAMPITT R.S. and D.S.M. BILLETT, 1984. Deep-sea echinodermes : A time and motion study. *Proceedings of the 5th International Echinoderm Conference, Galway, 24-29 Sept.*

LAMPITT R.S. and G.L.J. PATERSON, 1987. The feeding behaviour of an abyssal sea anemone from *in situ* time lapse photographs and trawl samples. *Oceanologica acta*, **10**: 455-461.

LAROCK P. A. and H. L. EHRLICH, 1979. Observations of bacterial microcolonies on the surface of ferro-manganese nodules from Blake plateau by scanning electron microscopy. *Microbial Ecology*, **2**: 84-96.

LAUBIER L. and M. SIBUET, 1979. Ecology of the benthic communities of the deep North-East Atlantic. *Ambio*, **6**: 37-42.

LAUBIER L., D. REYSS and M. SIBUET, 1985. L'utilisation des sous-marins habités pour l'étude de l'écosystème abyssal. Le cas particulier des sources hydrothermales. *Bulletin de l'Institut Oceanographique de Monaco*, **4**: 107-129.

LAUERMAN L.M., R.S. KAUFMANN and K.L. SMITH, 1996. Distribution and abundance of epibenthic megafauna at a long time-series station in the abyssal North-East Pacific. *Deep-Sea Res.* I, **43 (7)** : 1075-1103.

LAUERMAN L.M., J.M., SMOAK, T.J. SHAW, W.S. MOORE and K.L. SMITH, 1997. 234_{th} and 210_{th} evidence from rapid ingestion of settling particles by mobile epibenthic megafauna in the abyssal NE Pacific. *Limnol. Oceanogr.*, **42(3**): 589-595.

LEMCHE H., B. HANSEN, F.J. MADSEN, O.S. TENDAL and T. WOLFF, 1976. Hadal life as analyzed from photographs. *Vid. medd. Dan. naturhist. foren.*, **139**: 263-336.

LENOBLE J.P., 1989. The French Research Programme for Deep Seabed Mining of the polymetallic nodule deposits. Institut Français de Recherche pour l'Exploration de la Mer (Ifremer): 1-9.

LEONARD A.B., J.R. STRICKLER and N.D. HOLLAND, 1988. Effects of current speed on filtration during suspension feeding in *Oligonetra serripinna* (Echinodermata : Crinoidea). *Marine Biology*, **97** : 111-125.

LE SUAVE R., M. VOISSET, J.F. BOURILLET, P. COCHONAT, J. GUILLAUME, E. DREZEN, Y. MOREL, G. OLLIER, S. REY, S. RICOU and P. SAGET, 1987. Mise en évidence de phénomènes tectoniques and érosifs récents en domaine intraplaque profond, à l'aide du « S.A.R. » (Système Acoustique Remorqué). Exemple du Pacifique

Nord équatorial. *Comptes Rendus de l'Académie des Sciences de Paris* Série II, **305**: 1211-1216.

LEVENSTEIN R.A., 1971. A new polychaete species of the genus *Macellicephaloides* from the Aleutian Trench. *J. Fish. Res. Board Canada*, **28 (10)**: 1429-1431.

LEVI C., 1964. Spongiaires des zones bathyale, abyssale and hadale. *Galathea Report*, **7**: 63-112.

LEVI C., 1972-1973. *Galathea Report*, **7**.

LEVIN L.A. and C.L. THOMAS, 1989. The influence of hydrodynamic regime on infaunal assemblages inhabiting carbonate sediments on central Pacific seamounts. *Deep-Sea Research*, **36**: 1897-1915.

LEVIN L.A., D.J. DEMASTER, L.D. MCCANN and C.L.THOMAS, 1986. Effects of giant protozoans (class Xenophyophorea) on deep-seamount benthos. *Marine Ecology Progress Series*, **29**: 99-104.

LEWIS J.B., 1982. Feeding behaviour and feeding ecology of the Octocorallia (Coelenterata: Anthozoa). *Journal Zoological of London*, **196**: 371-384.

LIANG D., 1993. Formation patterns and preservation condition of polymetallic nodule. *Marine geology and Quaternary geology*, **13(4)**: 1-14.

LITVINOVA N.M. and M.N. SOKOLOVA, 1971. Feeding of deep-sea ophiuroids of the genus *Amphiophiura. Okeanologiya*, **11**: 240-247.

LONGHURST A., S. SATHYENDRANATH, T. PLATT and C. CAVERHILL, 1995. An estimate of global primary product in the ocean from satellite radiometer data. *Journal of Plankton Research*, **17**: 1245-1271.

LOUBERE P., 1998. The impact of seasonality on the benthos as reflected in the assemblages of deep-sea foraminifera. *Deep-Sea Research*, **45**: 409-432.

LUDWIG H., 1894. Reports on an exploration off the west coasts of Mexico, Central and South America, and off the Galapagos Islands, in charge of Alexander Agassiz, by the U.S. Fish Commission steamer "Albatross", during 1891, Lieut. Commander Z.L. Tanner, U.S.N., commanding. XII. The Holothurioidea. *Memoirs of the Museum of Comparative Zoology at Harvard College*, **17(3)**: 1-183.

LUDWIG H., 1905. Asteroidea. Reports on an exploration off the west coasts of Mexico, Central and South America, and off the Galapagos Islands during 1891 by the "Albatross", A. Agassiz XXXV ; Reports on the scientific results of the espedition to the Tropical Pacific in charge of A. Agassiz aboard the "Albatross", from Aug. 1899 to Mar 1900. *Memoirs of the Museum of Comparative Zoology at Havard College*, **32** : 1-292.

LUKE S.R., 1982. Catalog of the Benthic Invertebrate Collections, Echinodermata. Scripps Institution of Oceanography Reference Series, University of California, n° 82-5 : 1-66.

LUTKEN C.F. and T. MORTENSEN, 1899. Reports on an exploration off the west coasts of Mexico, Central and South America, and off the Galapagos Islands. In : charge of A. Agassiz, during 1891 on the "Albatros". *Memoirs of the Museum of Comparative Zoology at Harvard University*, **23(2)**: 93-208.

LYMAN T., 1878. Ophiuridae and Astrophytidae of the "*Challenger*" expedition, 1. *Bulletin of the Museum of Comparative Zoology at Harvard University*, **5**: 65-163.

LYMAN T., 1879. Ophiuridae and Astrophytidae of the "*Challenger*" expedition, 2. *Bulletin of the Museum of Comparative Zoology at Harvard University*, **6 (2)** : 17-83.

LYMAN T., 1882. Report on the Ophiuroidea dredged by HMS "*Challenger*" during the years 1873-6. *Report of the scientific results of the voyage of HMS "Challenger", 1873-1976*, **5 (14)**: 1-386.

MACGINITIE G. E. and N. MACGINITIE, 1968. Echiuroidea.In : *Natural History of Marine Animals*, McGraw-Hill, New York, 184-193.

MACURDA D. and D. MEYER, 1976. The identification and interpretation of stalked crinoids (Echinodermata) from deep-water photographs. *Bulletin of Marine Science*, **26 (2)**: 205-215.

MADSEN J., 1947-1948. Holothurioidea. *Reports of the Swedish Deep-Sea Expedition*, **Vol. II (12)**.

MADSEN F.J., 1951. Ophiuroidea. *Report of the Swedish Deep-Sea Expedition 1947-1948*, **2(9)**: 108-117.

MADSEN F.J., 1953. Holothurioidea. *Report of the Swedish Deep-Sea Expedition 1947-1948*, **2 (12)**: 151-173.

MADSEN F.J., 1956. Echinoidea, Asteroidea and Ophiuroidea from depths exceeding 6000 meters. *Ibid.*, **2**: 23-32.

MADSEN F.J., 1961a. The Porcellenasteridae. A monographic revision of an abyssal group of sea-stars. *Galathea Report*, **4**: 33-174.

MADSEN F.J., 1961b. On the zoogeography and origin of the abyssal fauna in view of the knowledge of the Porcellanasteridae. *Galathea Report*, **4**: 177-218.

MADSEN F.J., 1977. The Ophioleucidae (Ophiuroidea). *Galathea Report. Scientific Results of the Danish Deep-Sea Expedition Round the World 1950-52*, **14**: 109-122.

MAHAUT M.L., 1991. Modélisation à l'état stable du cycle du carbone dans le réseau trophique profond de la Terrasse de Meriadzek (golfe de Gascogne). Thèse de Doctorat, Université de Paris VI.

MALUF L., 1988. Composition and distribution of the Central East pacific Echinoderms. *Techn. Report Nat. Hist. Mus. Los Angeles County*, **2**: 2-42.

MARGALEF R., 1963. On certain unifying principles in ecology, *Amer. Nat.*, **97**: 357-374.

MASSIN C., 1982. Effects of feeding on the environment : Holuthuroidea. In: *Echinoderm nutrition*, M. Jangoux and J. Lawrence Eds, A.A. Balkema Publishers, Rotterdam: 493-497.

MATSUI T, K. OCAWA and T. FUKUSHIMA, 1997. Distribution of megafauna two years after a deep sea impact. *Proceedings of International Symposium on environmental Studies for Deep-Sea Mining*, Tokyo, Japan, November 20-21: 337-343.

MAUCHLINE J. and J.D.M. GORDON, 1985. Trophic diversity in deep-sea fish. *Fish. Biol.*, **26**: 527-535.

MAUVIEL A., 1982. La bioturbation actuelle dans le milieu abyssal de l'Océan Atlantique Nord, Thèse de 3ème Cycle, Université de Bretagne Occidentale, Brest: 1-103.

MAUVIEL A. and M. SIBUET, 1985. Répartition des traces animales and importance de la bioturbation. In: *Peuplements profonds du Golfe de Gascogne. Campagne Biogas*. L. Laubier and C. Monniot Eds, Ifremer.

MAUVIEL F., 1988. Synthèse des documents disponibles sur les courants de surface. Ifremer. *Rapport Interne*.

MCLENDON, J.F., 1909. The ophiurans of the San Diego region. *University of California Publications in Zoology*, **6**: 33-64.

MEADOWS P.S., 1986. Biological activity and seabed sediment structure, *Nature*, **323**: 207.

MENARD H.W., 1964. Geology of the Pacific Ocean, McGraw-Hill Inc., New York, 1-271.

MENZIES R.J., 1962. On the food and feeding habits of abyssal organisms as exemplified by the Isopoda. *Int. Revue ges Hydrobiol.*, **47**: 339-358.

MENZIES R.J., R.Y. GEORGE and G.T. ROWE, 1973. Abyssal environment and ecology of the World Oceans. John Wiley & Sons Wiley, **XXIII**: 1-488.

MERZ R.A., 1984. Self-generated versus environmentally produced feeding currents : A comparison for the Sabellid polychete *Eudistcylia vancouveri*. *Biol. Bull.*, **167** : 200-209.

MEYER D.L., 1982. Food and feeding mechanisms: Crinozoa. In: *Echinoderm nutrition*. M. Jangoux and J.M. Lawrence Eds, A.A. Balkema Publishers, Rotterdam : 25-42.

MEYER K., 1973. Surface and manganese nodule facies, encountered on the R/V Valdivia cruise 1972/73. *The Origin and Distribution of Manganese Nodules in the Pacific and Prospects for Exploration*, Honolulu: 125-130.

MILLAR R.H., 1959. Ascidiacea. *Galathea Report*, **1**: 189-210.

MILLER D.C. and P.A. JUMARS, 1986. Pellet accumulation, sediment supply and chowding as determinants of surface deposit-feeding rate in *Pseudopolydora Kempi japonica* Imajima Hartman (Polycheta: Spionidae). *J. Exp. Mar. Biol. Ecol.*, **99**: 1-17.

MILLER J., 1988. Analysis of swimming behaviour in four species of bathyal holothurians. *5th Deep-Sea Biology Symposium*, 26 Juin-1 Juillet 1988.

MILLER J. and D. PAWSON, 1990. Swimming sea Cucumbers (Echinodermata: Holothuroidea): a survey with analysis of swimming behavior in Four Bathyal Species. *Smithsonian Contributions to the Marine Sciences*, **35** : 1-16.

MILLS E., 1983. Problems of deep-sea biology : An historical perspective. In : *The Sea*, G.T. Rowe Eds. : 1-79.

MINITCHEV C., 1969. Nudibranchiata, mollusques (gastropodes, Opisthobranchia). Biologie de l'Océan Pacifique. *Science*, **2**: 42-44.

MITSUKURI K., 1912. Studies on actinopodons holothurioidea. *J. Coll. Sci. Imp. Univ. Tokyo*, **29(2)**: 1-238.

MONNIOT C., 1984. Les invertébrés suspensivores: adaptations à un régime carnivore chez les tuniciers. *Oceanis*, **10**: 605-621.

MONNIOT C. and F. MONNIOT, 1975. Abyssal tunicates : an ecological paradox. *Annales de l'Institut Océanographique*, **51**: 100-129.

MONNIOT C. and F. MONNIOT, 1977. Tuniciers benthiques profonds du Nord-Est Atlantique. Résultats des campagnes Biogas. *Bulletin du Museum National d'Histoire Naturelle*, **466**: 696-722.

MONNIOT C. and F. MONNIOT, 1978. Recent work on the deep-sea tunicates. *Oceanogr. Mar. Biology Ann. Rev.*, **16**: 181-228.

MOORE H.M. and D. ROBERTS, 1994. Feeding strategies in abyssal holothurians. In : B.DAVID, A. GUILE, J.P. FERAL and ROUX (Eds), *Echinoderms through time*. Balkema, Rotterdam : 531-537.

MORGAN C., 1991a. Geographical distributions of benthic megafauna in the Clarion-Clipperton zone. *NOAA report 1991*.

MORGAN C., 1991b. Opportunistic collection of environmental data in the northeastern Pacific Ocean. *NOAA report 1991.*

MORGAN C., NICHOLS J.A., SELK B.W., TOTH J.R. and WALLIN C., 1993. Preliminary analysis of exploration data from Pacific deposits of manganese nodules, *Marine Georesources and Geotechnology*, **11** : 1-25.

MOROSITA M., 1959. Measuring the dispersion of individuals and analysis of the distributional patterns. *Mem. Fac. Sci. Kyushu Univ.*, Serie E, **2**: 215-235.

MORTENSEN T., 1938. On the vegetarian diet of some deep-sea Echinoids, *Annot Zool. Japon*, **17(3,4)**: 225-230.

MORTENSEN T., 1940. A Monograph of the Echinoidea. III. 1, Aulodonta. C.A. Reitzel, Copenhagen: 1-370.

MORTENSEN T., 1950. A Monograph of the Echinoidea, Spatangoida 1. C.A. Reitzel, Copenhagen, Tome 1 : 1-432.

MORTENSEN T., 1951a. A Monograph of the Echinoidea Spatangoida 2 C.A. Reitzel, Copenhagen, Tome 2 : 1-593.

MORTENSEN T., 1951b. Echinoidea. *Report of the Swedish Deep-Sea Expedition 1947-1948*, **2(3)**: 45-48.

MULLER P.J. and E. SUESS, 1979. Productivity, sedimentation rate and sedimentary organic matter in the oceans. 1. Organic carbon preservation. *Deep-Sea Research*, **26** : 1347-1362.

MULLINEAUX L.S., 1987. Organisms living on manganese nodules and crusts: distribution and abundance at three North Pacific sites. *Deep Sea Research*. **34** : 165-184.

MULLINEAUX L.S., 1989. Vertical distributions of the epifauna on manganese nodules : Implications for settlement and feeding. *Limnology and Oceanography*, **34**: 1247-1262.

MURINA V., 1976. New abyssal species of Echiurans from the Pacific and Atlantic Oceans, *Zool. Zh.*, 55 : 837-843.

MUSCHENHEIM D.K., 1987. The role of hydrodynamic sorting of seston in the nutrition of benthic suspension feeder, *Spio setosa* (Polychaeta: Spionidae). *Biol. Oceanograph.*, **4**: 265-288.

NESIS K.N., 1978. Comparison of cephalopod faunas along the coasts of Central America. *Acad. Sci., Inst. Oceanol., Moscow, USSR, M. Starobogatov, Y.A.*. In : *Molluscs:*

their systematics, evolution and significance. Likharev, Malacol. Rev., (EDS), **11 (1-2)**: 127-128.

NICKERSON C.R., 1978. Consolidation and permeability characteristics of the deep sea sediments : North Central Pacific ocean, M.Sc. Thesis, Worcester Polytechnic Institute, Worcester: 1-212.

NIELSEN J.G., 1964. Fishes from depths exceeding 6000 meters. *Galathea Report*, **7**: 113-124.

NIELSEN J., 1966a. On the genera *Acanthonus* and *Typhlonus* (Pisces, Brotulidae), *Galathea Report*, **8**: 33-47.

NIELSEN J., 1966b. Synopsis of the Ipnopidae (Pisces, Iniomi). The description of two new abyssal species *Galathea Report*, **8**: 49-75.

NIXON M., 1986. The diets of Cephalopods. In: *Cephalopod life cycles*, Volume 2, P. Boyle Ed, Academic Press, London.

N.O.A.A., 1981. Deep Seabed Mining. Final Programmatic Environmental Impact Statement. NOAA. *Technical Report*. Vol.I: 1-295.

NYBAKKEN J., C. SMITH, L. SMITH-BEASLEY, G. MORENO, A. SUMMERS and L. WEETMAN, 1999. Distribution, density and relative abundance of benthic invertebrate megafauna from three sites at the base of the continental slope off central California as determined by camera sled and beam trawl, *Deep-Sea Res. II*, **45**: 1753-1780.

OEBIUS H., H. BECKER, S. ROLINSKI and J. JANKOWSKI, 2001. Parametrization and evaluation of marine environmental impacts produced by deep-sea manganese nodule mining. *Deep-Sea Research II*, **48** : 3453-3467.

OHTA S., 1983. Photographic census of large-sized benthic organisms in the bathyal zone of Suruga Bay, Central Japan. *Bull. Oceano. Res. Inst. Univ. Tokyo*, **15**: 1-244.

OHTA S., 1984. Star-shaped feeding trace produced by Echiuran worms on the deep-sea floor of the Bay of Bengal. *Deep-Sea Research*, **31 (12)**: 1415-1432.

OHTA S., 1985. Photographic observations of the swimming behavior of the deep-sea Pelagothuriid Holothurian *Enypiastes* (Elasipoda, Holothuroidea). *Journal of the Oceanographical Society of Japan*, **41(1**) : 121-133.

OKADA H., S. OHTA and N. NIITSUMA, 1980. Lebensspuren photographed on the deep-sea floor of Sugura Bay, Central Japan, *Geoscience Reports of Shizuoka University*, **7**: 31-36.

OKUTANI T., 1969. Synopsis of bathyal and abyssal megalo-invertebrates from Sagami Bay and south Boso Peninsula trawled by R/S Soyo-Maru. *Bulletin of the Tokai Regional Fisheries Research Laboratory*, **57**: 1-61.

OKUTANI T., 1974. Review and new records of abyssal and hadal molluscan fauna in Japanese and adjacent waters. *Venus*, **33(1)**: 23-39.

OKUTANI T., 1982. Characteristics and distribution of abyssal megalobenthos fauna around the proposed dumpling site st. B in the Northwest Pacific Basin. Surv. Rep. on Mar. biota and background in connection with ocean dumping of low-level radioactive wastes (1977-1980). Plankton and Benthos. *Tokai Reg. Fish. Res. Lab.* : 1-20.

OMORI M. and W. VERVOORT, 1986. Observations and living specimen of the giant hydroid *Brandrioce riantus imperator. Zoologische mededelingen Rijksmuseum Historie te Teiden*, **60(16)**.

OSHIMA H., 1916-1919. Northwestern Pacific holothurians collected by the "Albatross". *Zool. Mag. Tokyo*, articles from Volumes 28-31.

OUBINTSIEV G.B., 1972. Géomorphologie and tectonique des fonds de l'Océan Pacifique. *Sciences*: 394.

OUCHAKOV P.V., 1952. Etude des faunes d'eaux profondes. *Origine*, **6**: 100-102.

OUCHAKOV P.V., 1975. Famille des Phyllodocidae des eaux profondes (polychètes, Phyllodocidae) de la fosse Sud-Sandwich. *Tr. IN-TA Océanologie AN URSS*, Tome 103 : 143-150.

OWEN J.M., H.L. SANDERS and R.R. HESSLER, 1967. Bottom photography as a tool for estimating benthic populations. In : *Deep-Sea Photography*, J. B. Hershey Eds., Johns Hopkins Press, Baltimore: 229-234.

OZTURGUT E., G. ANDERSON, R.E. BURNS, J.W. LAVELLE and S.A. SWIFT, 1978. Deep ocean mining of manganese nodules in the North Pacific : Preliminary environmental conditions and anticipated mining effects. NOAA Tech. *Memorandum ERL Mesa-33*: 1-133.

OZTURGUT E., J.W. LAVELLE, O. STEFFIN and S.A. SWIFT, 1980. Environmental investigations during manganese nodule mining tests in the north equatorial Pacific in November 1978. NOAA. *Technical Memorandum*. ERL MESA-48: 1-50.

PAINE R.T., 1966. Food-web complexity and species diversity, *Americain Naturalist*, **100**: 65-75.

PAINE R.T. and R.L. VADAS, 1969. The effects of grazing by sea urchins, *Strongylocentrotus spp.*, on benthic algal populations, *Limnol. Oceanogr.*, **14**: 710-719.

PARKER S., 1982. Synopsis and classification of living organisms, McGraw Hill: 1-1232.

PASTERNAK F.A., 1964. The deep-sea pennatularians and antipatharians obtained by R/S Vityaz in the Indian Ocean. *Trudy Instituta Okeanologii*, AN SSSR, 69.

PASTERNAK F.A., 1975. *Umbellula* des eaux profondes de la mer des Caraïbes and du chenal de Porto Rico, Tome 100: 160-173.

PASTERNAK F.A., 1976. Nouvelles données dans la composition and la propagation de Zoantharia (Hexacorallia *Antipatharia*) dans les eaux profondes des océans Pacifique, Indien and Atlantique, Tome 99: 45-58.

PATERSON G.L.J., 1985. The deep-sea Ophiuroidea of the North Atlantic Ocean. *Bull. Brit. Mus. (Natur. Hist.). Ser. Zool.*, **49 (1)**: 1-162.

PATERSON G.L.J., P.Y.D. LAMBSHEAD and M. SIBUET, 1985. The Ophiuroidea fauna of the Bay of Biscay: its distribution and diversity. In: *Peuplements profonds du Golfe de Gascogne. Campagne Biogas*. L. Laubier and C. Monniot Eds, Ifremer: 491-507.

PATIL G.P., C. TAILLIE and R.L. WIGLEY, 1980. Transect sampling methods and their applications to the deep-sea red crab. In : *Advanced concepts in Ocean measurements for marine biology*, F.P. Diemer, F.J. Vernberg and D.Z. Mirkes, editors, University of south Carolina Press: 493-520.

PAUL A.Z., 1976. Deep-sea bottom photographs show that benthic organisms remove sediment cover from manganese nodules, *Nature*, **263**: 50-51.

PAUL A. and B. HECKER, 1977. Benthic base-line survey of the DOMES area. *NOAA/ERL(DOMES)*, 14: 1-122.

PAUL A. and P. JUMARS, 1976. Preliminary report on the benthos of the North equatorial Pacific ocean. *Progress Report.*

PAUL A.Z., E.M.THORNDIKE, L.G. SULLIVAN, B.C. HEEZEN and R.D. GERARD, 1978. Observations of the deep-sea floor from 202 days of time-lapse photography. *Nature*, **272**: 812-814.

PAUTOT G. and M. MELGUEN, 1979. Influence of deep water circulation and sea-floor morphology on the abundance and grade of central south Pacific manganese nodules. In : *Marine Geology and Oceanography of the Pacific Manganese Nodule Province*, J.L. Bishoff and D.Z. Piper Eds., Plenum Press, New York : 621-649.

PAUTOT G. and M. HOFFERT, 1984. Les nodules du Pacifique Central dans leur environnement géologique : Campagne COPANO 1979. *Résultats des Campagnes à la Mer*, CNEXO, 28: 1-202.

PAWSON D., 1967. Elasipod Holothurians of Antarctica I Genus *Amperina. Bull. Southern Calif. Acad. Sc. Los Angeles*, **66(1)**: 54-58.

PAWSON D., 1976. Some aspects of the biology of deep-sea echinoderms. *Thallossia Jugoslavica*, **12 (1)**: 287-293.

PAWSON D., 1982. Deep-Sea Echinoderms in the tongue of the ocean, Bahamas islands : a survey using the research submersible Alvin. *Australian Museum Memoir*, **16**: 129-145.

PAWSON D., 1983. *Psychronaetes hanseni*, a new genus and species of Elasipodan sea cucumber from the eastern central Pacific (Echinodermata: Holothuroidea). *Proceedings of the Biological Society of Washington*, **96(1)**: 154-159.

PAWSON D., 1985. *Psychropotes hyalinus*, new species. A swimming elasipod sea cucumber (Echinodermata : Holothuroidea) from the North Central Pacific Ocean. *Proc. Biology Soc. Wash*, **98 (2)**: 523-525.

PAWSON D., 1988a. Analysis of some Omco seafloor photographs from cruises GR 7901, 8005 and 8102: Megafauna and manganese nodule data. PART I. Text, *Final report under NOAA Contract 40-AANC-602101*, NOAA, Washington D.C.: 1-81.

PAWSON D., 1988b. Preliminary analysis of megafauna in seafloor photographs from the Clarion-Clipperton fracture zone, Eastern Pacific ocean. *5th Deep Sea Biology Symposium*, Brest: 1-16.

PAWSON D. and E. FOELL, 1983. Atlas of photographs of megafauna from the study area. *Report n° MS-200-146 of Deep-sea Ventures Inc.*, Gloucester Point, Virginia: 1-120.

PAWSON D. and E. FOELL, 1984. An annotated atlas of abyssal echinoderms from the Clarion-Clipperton Fracture Zone, equatorial Eastern North Pacific. *Proceedings of the 5th International Echinoderm Conference*, Galway, 24-29 Sept: 1-168.

PAWSON D. and E. FOELL, 1986. *Peniagone leander* new species, an abyssal benthopelagic sea cucumber (Echinodermata: Holothuroidea) from the Eastern Central Pacific Ocean. *Bulletin of Marine Science*, **38 (2)**: 293-299.

PAX F., M. VAN PRAET and D. DOUMENC, 1987. Les Antipathaires. Traité de zoologie, Tome III, fasc. 3. In : *Cnidaires*, publié sous la direction de P.P. Grassé.

PEARCY W.G., D.L. STEIN and R.S. CARNEY, 1982. The deep-sea benthic fish fauna of the northeastern Pacific ocean on Cascadia and Tufts Abyssal Plains and adjoining continental slopes. *Biological Oceanography*, **1**: 375-428.

PEARSON M. and J.D. GAGE, 1984. Diets of some deep-sea brittle stars in the Rockall Trough. *Marine Biology*, **82**: 247-258.

PEQUEGNAT W.E., 1964. The epifauna of a California siltstone reef. *Ecology*, **45**: 272-283.

PERÈS J. M., 1982. Major benthic assemblages, Wiley, Chichester: 1-642.

PERRIER R., 1896. Sur les Elasipodes recueillis par le "Travailleur" and le "Talisman". *Comptes rendus Hebdomadaires des Séances de l'Académie des Sciences*, Série D, **123**: 900-903.

PERRIER R. and REMY, 1902. Holothuries. *Exp. Scientif. Travailleur Talisman*: 273-554.

PETERSON C.H., 1977. Competitive organization of the soft-bottom macrobenthic communities of the southern California lagoons, *Mar. Biol.*, **43**: 343-359.

PFANNKUCHE O., 1985. The deep-sea meiofauna of the Porcupine seabight and abyssal plain (NE Atlantic). Population, structure, distribution, standing stocks. *Oceanologica Acta*, **8**: 343-354.

PIEPENBURG D., and M.K. SCHMID, 1997. A photographic survey of the epibenthic megafauna of the Artic Laptev Sea shelf: distribution, abundance and estimates of biomass and organic carbon demand, *Mar.Ecol.progr. Ser.*, **147**: 63-75.

PIEPENBURG D., CHERNOVA N.V., DORRIEN C.F. VON GUTT J., NEYELOV A.V., RACHOR E., SALDANHA L. and SCHMID M.K., 1996. Megabenthic communities in the waters around Svalbard, *Polar Biol.*, **16**, 431-446.

PIPER D.Z. and B. FOWLER, 1980. New constraint on the maintenance of Mn nodules at the sediment surface, *Nature*, **286**: 880-883.

PIPER D.Z., H.E. COOK and C. T. GARDNER, 1979. Lithic and acoustic stratigraphy of the equatorial north Pacific : DOMES sites A, B and C. in *Marine Geology and Oceanography of the Pacific Manganese Nodule Province*, J.L. Bishoff and D.Z. Piper Eds., Plenum Press, New York: 309-347.

PROBERT P.K., 1984. Disturbance, sediment stability, and trophic structure of soft-bottom communities, J. *Mar. Res.*, **42**: 893-921.

PUJOS A., 1987. Mise en place de la circulation au Pacific central équatorial and des assemblages de nannofossiles calcaires au Néogène (Leg DSDP 85). Influence de la glaciation antarctique entre 15 and 7 Ma au Néogène. *Bulletin de la Société Géologique de France*, **8**: 431-439.

QIAN J. and WANG X., 1999. The study on the formation ages and the growth rates of the polymetallic nodules in the East Pacific Ocean. *Oceanologia and limologia sinica*, **17(3):** 39-45.

RAAB W., 1972. Physical and chemical features of Pacific deep-sea manganese nodules and their implications to the genesis of nodules. In : *Ferromanganese Deposits on the Ocean-Floor*, edited by D.R. Horn, National Science Foundation, Washington D.C : 31-49.

RAAS T.S., V.A. GRIGORASH, V.D. SPANOVSKAYA and YUN SHCHERBACHEV, 1975. Deep-sea demersal fishes collected during the 14th cruise of the Akademik Kurchatov (in russian). *Multiple investigation of the Caribbean Sea, Gulf of Mexico and adjacent waters (Tr. Inst. Okeanol.),* **100**.

RACHOR E., 1975. Quantitative untersuchungen über meiobenthos der Nordostlantischen tiefsee. *Meteor Forschung Ergebnisse*, Ser. D, **21**: 1-10.

RADZIEJEWSKA T., 1997. Immediate responses of benthic meio- and megafauna to disturbance caused by polymetallic nodule miner simulator. *Proceedings of the International Symposium on Environmental Studies for Deep-Sea Mining,* Tokyo, Japan (November 20-21): 223-235.

RADZIEJEWSKA T., 2002. Responses of Deep-Sea Meiobenthic Communities to Sediment Disturbance Simulating Effects of Polymetallic Nodule Mining. *Internt. Rev. Hydrobiol.*, **87(4)**: 457-465.

RADZIEJEWSKA T. and I. MODLITBA, 1999. Vertical distribution of meiobenthos in relation to geotechnical properties of deep-sea sediment in the IOM pioneer area (Clarion-Clipperton Fracture Zone, NE Pacific). *Proceedings of the Third (1999) Ocean Mining Symposium, Goa, India, November 8-10*: 126-184.

RADZIEJEWSKA T. and V. STOYANOVA, 2000. Abyssal epibenthic megafauna of the Clarion-Clipperton area (NE Pacific): changes in time and space versus anthropogenic environmental disturbance, *Oceanological Studies*, **24(2):** 83-101.

RADZIEJEWSKA T. and R. KOTLINSKI, 2002. Acquiring marine life data while experimentally assessing environmental impact of simulated mining in the deep sea. *ICES Council Meeting Documents*.

RADZIEJEWSKA T., K. SZAMALEK and R. KOTLINSKI, 2003. Marine Environment in the IOM Area (Clarion-Clipperton Region, Subtropical Pacific) : Current knowledge and future needs. *Proceedings of the Fifth (2003) Ocean Mining Symposium, Tsukuba, Japan, September 15-19 :* 188-193.

RAY A.J. and R.C. ALLER, 1985. Physical irrigation of relict burrows : Implication for sediment chemistry. *Marine Geology* : 371-379.

RENAUD-MORNANT J. and GOURBAULT N., 1990. Evaluation of abyssal meiobenthos in the Eastern Central Pacific (CCFZ). *Progress in Oceanography*, **24**: 317-329.

REX A., 1976. Biological accomodation in the deep-sea benthos : Comparative evidence on the importance of predation and productivity. *Deep-Sea Research*, **23** : 975-987.

REX M., 1981. Community structure in the deep-sea benthos. *Ann. Rev. Ecol. Syst.*, **12**: 331-353.

REX M.A., 1983. Geographic patterns of species diversity in the deep-sea benthos. In : *Deep Sea Biology*, G.T. Rowe Eds., John Wiley & Sons, New York: 453-472.

REX M. A., C.T. STUART, R.R HESSLER, J.A. ALLEN, H.L SANDERS and G.D.F. WILSON, 1993. Global-scale latitudinal patterns of species diversity in the deep-sea benthos. *Nature*, **365**: 636-639.

RHOADS D. C., 1974. Organism-sediment relations on the muddy sea floor, *Oceanogr. Mar. Biol. Ann. Rev.*, **12**: 263-300.

RICE A.L., R.G. ALDRED, D.S.M. BILLETT and M.H. THURSTON, 1979. The combine use of an epibenthic sledge and a deep-sea camera to give quantitative relevance to macro-benthos samples. *Ambio Special Report*, **6** : 59-63.

RICE A., R. ALDRED, E. DARLINGTON and R. WILD, 1982. The quantitative estimation of the deep sea megabenthos : a new approach to an old problem. *Oceanol. Acta*, **5**: 1.

RICHARDSON M. D., K. B. BRIGGS and D. K. YOUNG, 1985. Effects of biological activity by abyssal benthic macroinvetebrates on a sedimentary structure in the Venezuela Basin, *Mar. Geol.*, **68**: 243-267.

RICOU A., 1990. La dynamique sédimentaire en milieu intraplaque océanique dans les zones riches en nodules polymétalliques (Zone Clarion-Clipperton, Pacifique Nord-est). Thèse de Doctorat, Université des Sciences de la Vie and de la Terre, Strasbourg: 1-184.

RIEDL R., 1971. Water movement. In : *Marine Geology*, O. Kinne Ed., Vol. I, Part 2: 1123-1156.

RIEMANN F., 1983. Biological aspects of deep-sea manganese nodule formation. *Oceanologica Acta*, **6**: 303-311.

RIEMANN-ZURNECK K., 1979. Two disc-shaped deep-sea Anthozoa from the gulf of Biscay, with a survey of adaptation types in the Actiniaria. *Zoomorphologie*, **93**: 227-243.

RISK M. J., 1973. Silurian echiuroids : Possible feeding traces in the Thorold sandstone, *Science*, **180**: 1285-1287.

ROBSON G.C., 1930. Cephalopoda. I. Octopoda. *"Discovery" Report*, **2**: 371-402.

RODRIGUES N., SHARMA R. and NATH BN, 2001. Impact of benthic disturbance on megafauna in Central Indian Basin. *Deep Sea Research II,* vol. **48**(16) : 3401-3411.

ROMERO-WETZEL, 1987. Sipunculans as inhabitants of very deep narrow burrows in deep-sea sediments. *Marine Biol.*, **96**: 87-91.

ROMERO-WETZEL, 1989. Branched burrows systems of the Enteropneust *Steredsalanus canadensis* (Spengel) in deep-sea sediments of the Vöring plateau, Norwegian Sea. *Sarsta*, **74**: 85-89.

ROPER C.F.E. and W.L. BRUNDAGE Jr, 1972. Cirrate Octopods with associated Deep-Sea Organisms: New Biological Data Based on Deep Benthic Photographs (Cephalopoda). *Smithsonian Contributions to Zoology*, **121**: 1-46.

ROUX M., 1980. Les Crinoïdes pédonculés (Echinodermes) photographiés sur les dorsales océaniques de l'Atlantique and du Pacifique. Implications biogéographiques. *Comptes Rendus de l'Académie des Sciences de Paris*, Série D, **291**: 901-904.

ROUX M., 1985. Les crinoïdes pédonculés (Echinodermes) de l'Atlantique N.E.: inventaire, écologie and biogéographie. In : *Peuplements profonds du Golfe de Gascogne. Campagne Biogas.* L. Laubier and C. Monniot Eds., Ifremer: 479-489.

ROUX M., 2004. New Hyocrinid Crinoids (Echinodermata) from Submersible Investigations in the Pacific Ocean. *Pacific Science*, October 2004, **58(4)** : 597-613.

ROWE G.T., 1968. Distribution patterns in populations of large deep-sea benthic invertebrates off North Carolina. Ph.D. Thesis. Duke University, Durham, N.C.: 1-296.

ROWE G.T., 1971. Benthic biomass and surface productivity. In: *Fertility of the sea*. J.D. Costlow, Gordon & Bread Eds.: 441-454.

ROWE G.T., 1983. Biomass and production of the deep-sea macrobenthos. In: *The Sea,* Vol. 8, ed. G.T. Rowe. New York: Wiley-Interscience: 97-121.

ROWE G.T., 1996. The cycling of organic matter in food-limited environments. Deep-sea and extreme shallow water habitats : affinities and adaptations. *Biosystematics and Ecology Series* **11**: 233-260.

ROWE G.T. and R.J. MENZIES, 1969. Zonation of large benthic invertebrates in the deep sea off the Carolinas. *Deep-Sea Research*, **16**: 531-537.

ROWE G.T. and N. STARESIMIC, 1979. Sources of organic matter to the deep-sea benthos. In : *The Deep Sea Ecology and Exploitation. Ambio Special Report*, **6** : 19-24.

ROY K., D. JABLONSKI and J.W. VALENTINE, 1994. Eastern Pacific molluscan provinces and latitudinal diversity gradient: No evidence for "Rapoport's rule". *Proceedings of the National Academy of Sciences, USA*, **91**: 8871-8874.

RUHL H.A. and K.L. SMITH Jr, 2004. Shifts in Deep-Sea Community Structure linked to Climate and Food supply, *Science*, **305**, pp 513-515.

RYAN B.F. and HEEZEN B.C., 1976. Smothering of deep-sea benthic communities from natural disasters. *Tech. report prepared from marine ecosystems analysis program office of the NOAA Lamont-Doherty geological observatory of Columbia university*: 131.

SAGUEZ G., 1985. Etude de la morphologie, de la structure interne and de la lithologie des nodules polymétalliques de la zone Clarion-Clipperton. Relations avec l'environnement. Thèse de Doctorat, Université de Bretagne Occidentale, Brest: 1-228.

SALDANHA L., 1962. Régime alimentaire de *Synaphobranchus* au large des côtes européennes. *Cybium*, 3e série, **8**: 91-98.

SALONEN K., J. SARVALA, I. HAKALA and M.L. VILJANEN, 1976. The relation of energy and organic carbon in aquatic invertebrates. *Limnology and Oceanography*, **21**: 724-730.

SANDERS H. L., 1968. Marine benthic diversity : a comparative study. *American Naturalist*, **102**: 243-282.

SANDERS H.L. and R.R. HESSLER, 1969. Ecology of the deep-sea benthos. *Science*, **163**: 1419-1424.

SANDERS H.L. and R.R. HESSLER and G.R. HAMPSON, 1965. An introduction to the study of deep-sea benthic faunal assemblages along the Gay Head-Bermuda transect. *Deep-Sea Research*, **12** : 845-867.

SCHAREK R., L. TUPAS, D. KARL, 1999. Diatom fluxes to the deep-sea in the oligotrophic North Pacific gyre at station ALOHA. *Mar. ecol. Prog.Ser.*, **182**, 55-67.

SCHNEIDER J., 1981. Manganese nodules in the deep-sea. Formation, ocurrence and ecological consequences of mining. *Natur und Museum*, **3**: 114-124.

SCHNEIDER J.et H.THIEL,1988. Environmental problems of deep-sea mining. In : *The manganese Nodule Belt of the Pacific Ocean ; Geological Environment, Nodule Formation and Mining Aspects*. P. Halbach, G. Friedrich, U. von Stackelberg (eds.), F. Enke Verlag. Stuttgart: 222-228.

SCHRIEVER G., 1995, DISCOL-disturbance and recolonization experiment of a manganese nodule area of the Southeatsern Pacific. In : *Proc. ISOPE Ocean Mining Symp.*, Yamazaki T., Aso K., Okano Y., Tsurusaki K. (eds.), Tsukuba: 163-166.

SCHRIEVER G., AHNERT A., BLUHM H., BOROWSKI C. and THIEL H., 1997, Results of the large scale deep-sea environmental impact study DISCOL during eight years of investigation In : *Proc. 7th ISOPE Conf.*, **Vol I**, Chung J.S., Das B.M., Matsui T., Thiel H.(eds.), Honolulu: 438-444.

SEBENS K.P., 1984. Water flow and coral colony size: interhabitat comparisons of the octocoral *Alcyonium siderium*. *Proceedings of the National Academy of Sciences of the USA*, **81**: 5473-5477.

SEBENS K.P. and M.A.KOEHL, 1984. Predation on zooplankton by the anthozoans *Alcyonium siderium* (Alcyonacea) and *Metridium senile* (Actinaria) in the New England subtidal. *Marine Biology*, **81**: 255-271.

SHARMA, R and A. RAO, 1991. Environmental considerations of nodule mining in central Indian basin. *OTC, 6554*: 481-490.

SHARMA, R and A. RAO, 1992. Geological factors associated with megabenthic activity in the Central Indian Basin. *Deep-Sea Research*, **39(3/4) :** 705-13.

SHARMA R., N. NATH, S.M. GUPTA and Z.A. ANSARI, 1997. Benthic environment baseline investigations in the manganese nodule area of the central Indian Basin. *Proceedings of the ISOPE-Offshore and Polar Engineering Conference, May 25-30,1997*: 488-495.

SHIRAYAMA, Y. and D. SWINBANKS, 1986. Oxygen profiles in deep-sea calcareous sediment calculated on the basis of measured respiration rates of deep-sea meiobenthos and its relevants to manganese diagenesis, *La mer*, **24**: 75-80.

SHIRAYAMA Y and T. FUKUSHIMA, 1997. Benthic organism distribution in the Japanese Deep Sea Mining Claim Area. *Proceedings of International Symposium on Environmental Studies for Deep-Sea Mining, Tokyo, Japan*, November 20-21: 311-323.

SHIRAYAMA Y, FUKUSHIMA T., MATSU T. and KUBOKI E., 2001. The responses of deep-sea benthic organisms to experimental removal of the surface sediment. *Proceedings of the fourth ISOPE Ocean Mining Symposium (Szczecin, Poland*): 77-81.

SHOR G., 1959. Reflexion studies in the eastern equatorial Pacific. *Deep-Sea Research*, **5**: 283-285.

SIBUET M., 1974. Echinodermes de la mer d'Alboran. *Bulletin du Museum National d'Histoire Naturelle*, 3ème Série, **231**: 789-798.

SIBUET M., 1976. Le genre *Hymenaster* (Astérides) dans l'Océan Atlantique. *Bull. Mus. Hist. Nat. Paris*, **256**: 304-324.

SIBUET M., 1977. Répartition and diversité des échinodermes (holothurides-astérides) en zone profonde dans le golfe de Gascogne. *Deep-Sea Research*, **24** : 549-563.

SIBUET M., 1980. Adaptation des Echinodermes à la vie abyssale. In: *Echinodermes : Present and Past*, M. Jangoux Ed., A.D. Balkema/Rotterdam: 233-240.

SIBUET M., 1984. Les invertébrés détritivores dans l'écosystème abyssal. Sélection de la nourriture and régime alimentaire chez les holothuries. *Oceanis*, **10** : 623-639.

SIBUET M., 1985. Quantitative distribution of echinoderms (Holothuroidea, Asteroidea, Ophiuroidea, Echinoidea) in relation to organic matter in the sediment, in deep-sea basins of the Atlantic Ocean. In: *Echinoderms*, *Proceedings of the fifth international echinoderms conference, Galway, 24-29 September 1984,* B.F. KEEGAN and B.D.S. O'CONNOR Eds: 99-108.

SIBUET M., 1987. Structure des peuplements benthiques en relation avec les conditions trophiques en milieu abyssal dans l'Océan Atlantique. *Thèse de Doctorat d'Etat ès Sciences Naturelles*, Université P. and M. Curie, Paris: 1-280.

SIBUET M. and J.M. LAWRENCE, 1981. Organic content and biomass of abyssal holoyhuries (Echinodermata) from the Bay of Biscay. *Mar. Biol.*, **65**: 143-147.

SIBUET M. and M. SEGONZAC, 1985. Abondance and répartition de l'épifaune mégabenthique. In: *Peuplements profonds du Golfe de Gascogne (Campagnes Biogas*), L. Laubier and C.Monniot, editors, Ifremer, Brest: 143-156.

SIBUET M., D. DESBRUYERES and A. MAUVIEL, 1980. Etude des photographies de fond réalisées sur les stations du programme "Biogas" dans le golfe de Gascogne. *Rapport du contrat CEA TMC II/14265*.

SIBUET M., A. KHRIPOUNOFF, J. DEMING, R. COLWELL and A. DINET, 1982. Modification of the gut contents in the digestive tract of abyssal holothurians. In : *Proceedings of International Echinoderms Conference*, Tampa Bay, J.M. Lawrence Ed., A.A. Balkema, Rotterdam: 421-428.

SIBUET M., C. MONNIOT, D. DESBRUYERES, A. DINET, A. KHRIPOUNOFF, G. ROWE and M. SEGONZAC, 1984. Peuplements benthiques and caractéristiques trophiques du milieu dans la plaine abyssale de Demerara. *Oceanologica Acta*, **7(3)**.

SIBUET M., C. LAMBERT, R. CHESSELET and L. LAUBIER, 1989. Density of major size groups of benthic fauna and trophic input in deep basins of the Atlantic ocean. *Journal of Marine Research*, **47**: 851-867.

SLADEN W.P., 1889. Asteroidea, *Report of the Scientific Results of the Voyage of H.M.S. "Challenger" 1873-76*, **30** : 1-893.

SLOAN N., 1980. Aspects of the feeding biology of Asteroids. *Oceanogr. Mar. Biology Ann. Rev.*, **18**: 57-124.

SLUITER C., 1901a. Die holothurien der Siboga Expedition. *Siboga Exped.*, **44**: 1-142.

SMITH C. R., 1985. Food for the deep sea : Utilization, dispersal and flux of nekton falls at the Santa Catalina Basin floor. *Deep-Sea Research* **43 (4)** : 417-42.

SMITH C.R., 1992. Factors controlling bioturbation in deep-sea sediments and their relation to models of carbon diagenesis, in press in "*Deep-Sea Food Chains: Relation to the Global Carbon Cycle*, edited by G.T. Rowe, Kluwer, Dordrecht, the Netherlands.

SMITH C.R., 1994. Tempo and mode in deep-sea benthic ecology : punctuated equilibrium revisited. *Palaios* **9** : 3-13.

SMITH C.R., 1999. The biological environment in the nodule provinces of the deep sea. In : *Deep-Seabed Polymetallic Nodule Exploration : Development of environmental Guidelines*, Ed. N. Oduntun, Kingston, Jamaica: International Seabed Authority: 41-68.

SMITH C.R. and S. C. HAMILTON, 1983. Epibenthic megafauna of a bathyal basin off southern California : patterns of abundance, biomass, and dispersion. *Deep-Sea Research*, **30**: 907-928.

SMITH C.R. and R.R. HESSLER, 1987. Colonization and succession in deep-sea ecosystems. *Trends Ecol. Evol.* **2** : 359-365.

SMITH C.R. and KAUFMANN R.S., 1999. Long-term discrepancy between food supply and demand in the deep eastern north Pacific. *Science,* **284**:1174-1177.

SMITH C.R. and DEMOPOULOS A., 2003. Ecology of the deep Pacific ocean floor. In: *Ecosystems of the World*, Ecosystems of the Deep Ocean, Ed. P.A. Tyler, Amsterdam, the Netherlands : Elsevier, 28.

SMITH C.R., P. A. JUMARS and D. J. DEMASTER, 1986. In situ studies of megafaunal mounds indicate rapid turnover and community response at the deep-sea floor, *Nature*, **323**: 251-253.

SMITH C.R., R.S.KAUFMANN, J.L. EDELMAN and R.J. BALDWIN, 1992. Abyssopelagic fauna in the central North Pacific : comparison of acoustic detection and trawl and baited collections to 5800 m. *Deep-Sea Research*, **39(3/4)**: 659-685.

SMITH C.R., R.S.KAUFMANN and R.J. BALDWIN, 1994. Coupling of near-bottom pelagic and benthic processes at abyssal depths in the eastern North Pacific Ocean. *Limnology and Oceanography*, **39(5)**: 1101-1118.

SMITH C.R., BERELSON W., DEMASTER D.J., DOBBS F.C., HAMMOND D., HOOVER D.J., POPE R.H. and STEPHENS M., 1997. Latitudinal variations in benthic processes in the abyssal equatorial Pacific : control by biogenic particle flux, *Deep-Sea Res.*, II, **44** : 2295-2317.

SMITH K.F. and J.H. BROWN, 2002. Patterns of diversity, depth range and body size among pelagic fishes along a gradient of depth. *Global Ecology and Biogeography*, **11(4)**: 313-322.

SMITH Jr. K., P. WILLIAMS and E. DRUFFEL, 1989. Upward fluxes of particulate organic matter in the deep North Pacific. *Nature*, **337**: 724-726.

SMITH Jr. K.L., R.J. BALDWIN and J.L. EDELMAN, 1989. Supply of and demand for organic matter by sediment communities on two central north Pacific seamounts. *Deep-Sea Research*, **36**: 1917-1932.

SMITH Jr. K.L., R.S. KAUFMAN and R.J.BALDWIN, 1992. Coupling of near-bottom pelagic and benthic processes at abyssal depths in the eastern North Pacific *Ocean. Limnol. Oceanogr.*, **39 (5**) : 1101-1118.

SMITH Jr. K.L., R.S. KAUFMAN, J.L. EDELMAN and R.J.BALDWIN, 1992. Abyssopelagic fauna in the central North Pacific : comparison of acoustic detection and trawl and baited trap collections to 5800 m. *Deep-Sea Research*, **39**: 659-685.

SMITH Jr. K.L., R.S. KAUFMAN and WAKEFIELD, 1993. Mobile megafaunal activity monitored with a time-lapse camera in the abyssal North Pacific. *Deep-Sea Research*, **40(1-12)**: 2307-2324.

SNELGROVE P.V.R. and SMITH C.R., 2002. A riot of species in an environmental calm : the paradox of the species-rich deep sea. *Oceanography and Marine Biology Annual Review,* **40** : 311-342.

SOKOLOVA M.N., 1957. The feeding of some carnivorous deep-sea benthic invertebrates of the far eastern seas and the northwest Pacific Ocean. *Trudy Inst. Okeanol.*, **20**: 279-301. (traduction publiée en 1959 dans *Marine Biology* par l'American Institute of Biological Sciences, Washington, B.Y. Nikitin Ed : 227-244).

SOKOLOVA M.N., 1968. Relationships between feeding groups of bathypelagic macrobenthos and the composition of bottom sediments. *Oceanology*, **8(2)**: 141-151.

SOKOLOVA M.N., 1972. Trophic structure of deep-sea macrobenthos. *Marine Biology*, **16**: 1-12.

SOKOLOVA M.N., 1986. Data on the feeding of deep-water bottom invertebrates, in *Feeding of Marine Invertebrates in Natural Habitat*, Ed. by Shirshov Institut of Oceanography, Academy of Sciences of the USSR : 99-101.

SPIESS F.N. and P.F. LONSDALE, 1982. Deep Tow rise crest exploration techniques, *Marine Technology Society Journal*, **16**: 67-75.

SPIESS F.N. and M. WEYDERT, 1987. Operational aspects, geology and physical effects of dredging. In : *Environmental Effetcs of Deep-sea Dredging. Final report to the National Oceanic and Atmospheric Administration on contract NA 83-SAC-00659*, Reference 87-5: 1-23.

SPIESS F.N., R. HESSLER, G. WILSON and M. WEYDERT, 1987. Environmental effects of deep sea dredging, *NOAA Report*, **87-5:** 1-85.

STEELE J.M., 1974. The structure of marine ecosystems. Blackwell Sc. Publ., Oxford: 1-128.

STOCK J.H., 1978a. Abyssal Pycnogonida from the North-eastern Atlantic Basin, Part I. *Cahiers de Biologie Marine*, **19**: 189-219.

STOCK J.H., 1978b. Abyssal Pycnogonida from the North-eastern Atlantic Basin, Part II. *Cahiers de Biologie Marine*, **19**: 397-413.

STOCK J.H., 1984. The deep-water Pycnogonida of the Safari cruises to the Indian Ocean. *Bulletin du Museum National d'Histoire naturelle de Paris*, **6**: 701-709.

STOCKTON W.L. and T.E. DECALA, 1982. Food falls in the deep-sea : Occurrence, quality and significance. *Deep-Sea Research*, **29A**: 157-169.

STOYANOVA V., 2001. IOM BIE revisited : Meiobenthos at the IOM BIE site 5 years after the experimental disturbance. *Proceedings of the Fourth (2001) Ocean Mining Symposium*: 63-68.

STULL J. K. and C. I. HAYDOCK, 1982. Effect of bioturbation by *Listriolobus pelodes* (Echiura) on coastal shelf sediment modified by a major California wastewater discharge, *EOS*, **63**: 105.

SUN Z., D. YAO and D. XU, 1995. Growth wavy rates of polymetallic nodules from eastern Pacific Basin and its paleoenvironmental implications. *Marine science bulletin*, **14 (4)**: 50-58.

TABACHNICK KR and H.M. REISWIG, 2000. Porifera Hexactinellida: on *Euryplegma auriculare* (Schulze, 1886) and formation of a new order. Résultats des campagnes MUSORSTOM. *Mémoires du Muséum National d'Histoire Naturelle*, **21 (184)**: 39-52.

TABACHNICK K.R. and C. LEVI, 2004. Lyssacinosida du Pacifique Sud-Ouest (Porifera: Hexactinellida). *Mémoires du Muséum National d'Histoire Naturelle*, **191** : 11-71.

TAGHON G.L., A.R.M. NOWELL and P. A. JUMARS, 1980. Induction of suspension feeding in spionid polychaetes by high particulate fluxes, *Science*, **210** : 562-564.

TAYLOR J.D., N.J. MORRIS and C.N. TAYLOR, 1980. Food specialization and the evolution of predatory prosobranch gasteropods. *Paleontology*, **23**: 375-409.

TENDAL O., 1972. A monograph of the Xenophyophoria (Rhizopoda, Protozoa). *Galathea Report*, **12**: 3-103.

THAYER C. W., 1979. Biological bulldozers and the evolution of marine benthic communities, *Science*, **203** : 458-460.

THÉEL H., 1882. Report on the Holothurioidea dredged by *H.M.S. "Challenger"* during the years 1873-1876, I. *Report of the Scientific Results of the Voyage of H.M.S. "Challenger" 1873-76*, **4(13)**: 1-176.

THÉEL H., 1886a. Report on the Holothurioidea dredged by *H.M.S. "Challenger"* during the years 1873-1876, II. *Report of the Scientific Results of the Voyage of H.M.S. "Challenger" 1873-76*, **14(39)**: 1-290.

THÉEL H., 1886b. Report on the results of dredging by the United States Coast Survey Steamer "Blake". III. Report on the Holothuroidea. *Bulletin of the Museum of Comparative Zoology at Harvard University*, **13(1)** : 1-21.

THIEL H., 1975. The size structure of the deep-sea benthos. Int. *Revue Ges. Hydrobiol. Hydrogr.*, **60(5)**: 575-606.

THIEL H., 1978. The faunal environment of manganese nodules and aspects of deep-sea time scale. In :*Methods, Metals and Assessment,* W. E. Krumbein Eds., Ann Arbor Science, Michigan: 887-896.

THIEL H., 1979. Structure aspects of the deep-sea benthos in the deep-sea ecology and exploitation. *Rev. Ges. Hydrobiol. Hydrog.*, **60**: 575-606.

THIEL H., 2001a. Evaluation of the environmental consequences of polymetallic nodule mining based on the results of the TUSCH Research Association. *Deep-Sea Research II*, **48**: 3433-3452.

THIEL H., 2001b. Use and protection of the deep sea-an introduction. *Deep-Sea Research II*, **48**: 3427-3431.

THIEL H. and G. SCHRIEVER, 1990. Deep-sea mining, environmental impact and the DISCOL project, *Ambio*, **19(5)**: 245-252.

THIEL H., O. PFANNKUCHE, G. SCHRIEVER, K. LOCHTE, A. GOODAY, C. HEMLEBEN, R. MANTOURA, C. TURLEY, J. PATCHING and F. RIEMANN, 1988/1989. Phytodetritus on the deep-sea floor in a central oceanic region of the Northeast Atlantic, *Biol. Oceanogr.*, **6** : 203-239.

THIEL H., G. SCHRIEVER, C. BUSSAU and C. BOROWSKI, 1990. Manganese nodule crevice fauna. *Deep-sea Research* **40A(2)**: 419-23.

THIEL H., FOELL E. and G. SCHRIEVER, 1991. Megafauna observations and experiments with a time lapse camera. 6th deep sea biology Symposium (Copenhagen), p 98, 30 juin-5 juilet 1991.

THIEL H., H. BLUHM, C. BOROWSKI, C. BUSSAU, a. GOODAY, C. MAYBURY and G. SCHRIEVER, 1992. The impact of mining on deep sea organisms. The DISCOL-Project. *Ocean Challenge*, **3(1)**: 40-46.

THIEL H., M.V. ANGEL, E.J. FOELL, A.L. RICE and G. SCHRIEVER, 1998. Marine Science and technology-environmental risks from large-scale ecological research in the deep sea. A desk study. Office for Official Publications of the European Communities, Luxembourg.

THIEL H., G. SCHRIEVER, A. AHNERT, H. BLUHM, C. BOROWSKI and K. VOPEL, 2001. The large-scale environmental impact experiment DISCOL – reflection and foresight. *Deep-Sea Research II* **48**: 3869-3882.

THISTLE D., 1981. Natural physical disturbance and communities of marine soft bottoms, *Marine Ecology Progress Series*, **6**: 223-228.

THISTLE D., 1983. The role of habitat heterogeneity in deep-sea diversity maintenance, *Deep-Sea Res.*, **30A** : 1235-1245.

THISTLE D. and G.D.F. WILSON, 1987. A hydrodynamically modified, abyssal isopod fauna. *Deep-sea Research*, **34** : 73-87.

THISTLE D. and L. LEVIN, 1998. The effect of experimentally increased near-bottom flow on metazoan meiofauna at a deep-sea site, with comparison data on macrofauna. *Deep-Sea Research I*, **45**: 625-638.

THISTLE D.J., Y. YINGEST and K. FAUCHALD, 1985. A deep sea benthic community exposed to strong near bottom currents on the Scotian Rise (Western Atlantic). *Mar. Geol.*, **66**: 91-112.

THORNDIKE E.M., R.D. GERARD, L.G. SULLIVAN and A. Z. PAUL, 1982. Long-term, time-lapse photography of the deep ocean floor. In : The Ocean Floor, R. A. S. a. M. Talwani Eds., John Wiley & Sons Ltd.: 255-275.

THORSON G., 1974. Bottom communities. *Geological Society of America Memoirs*, **67**: 461-534.

THURSTON M.H., B.J. BETT, A.L. RICE and P.A. JACKSON, 1994. Variations in the invertebrate abyssal megafauna in the Northeast Atlantic Ocean. *Deep-Sea Research I*, **41**: 1321-1348.

THURSTON M.H., A.L. RICE and B.J. BETT, 1998. Latitudinal variation in invertebrate megafaunal abundance and biomass in the North Atlantic Ocean abyss, *Deep-Sea Res. II*, **45**: 203-224.

TIFFON Y., 1987. Ordre des Cerianthaires. Traité de zoologie, Tome III, Fasc. 3. Publié sous la direction de D. Doumenc: 212-256.

TILOT V., 1988. Review of Environmental Impact studies on deep-sea polymetallic mining in the Eastern Central Pacific Ocean. Contrat CEE CDC/88/7730/IN/01: 1-59.

TILOT V., 1989. Report on the german expedition DISCOL II. Contrat CEE CDC/89/7730/IN/01: 23.

TILOT V., 1990. The review of megafauna in the NIXONAUT cruise. Film présenté à une réunion de "United Nations Law of the Sea Treaty", Août 1990.

TILOT V., 1991. Who builds the deep-sea pyramids? *6th Deep-Sea Biology Symposium*, Copenhagen, (30/06/91 - 05/07/91): 66.

TILOT V., 1992a. Deep-sea exploratory means for analyzing epibenthic megafaunal assemblages in a nodule area of the tropical Northeast Pacific Ocean. *Symposium on Ocean Technology 27-29 Août 1992. National Institute of Oceanography, Dona Paula, GOA, Inde:* 76.

TILOT V., 1992b. Preliminary report on the description of megafaunal assemblages and manganese nodule coverage along transects taken during the benthic impact experiment (BIE) cruise June 24-July 14, 1991. *NOAA contract through The Research Corporation of the University of Hawaii*: 26.

TILOT V., 1992c. La structure des assemblages mégabenthiques d'une province de nodules polymétalliques de l'océan Pacifique tropical Est, *Doctorat (nouveau régime) en Sciences and Techniques*, Université de Bretagne occidentale, Brest, France: 1-380.

TILOT V., 2002. Megabenthic assemblages of polymetallic nodule ecosystems in the Clarion-Clipperton fracture zones within the abyssal tropical East Pacific Ocean. *Proceedings of the International Seabed Authority Preparatory meeting of scientists held in Kingston, Jamaica (29/7-3/8/2002).*

TILOT V., 2003. Les méthodes de suivi des fonds marins. *Cahiers des Explorateurs 28. Troisième millénaire. Soc de Géographie*. Avril 2003: 37-41.

TILOT V., R. LE SUAVE and M. SIBUET, 1988. Biological and environmental relationship in a manganese nodule province between Clarion and Clipperton fracture zones : Preliminary study to any benthic assessment in deep seabed mining. *5th Deep Sea Biology Symposium*, Brest: 86

TIXIER-DURIVAULT A., 1964. Stolonifera and Alcyonacea. *Galathea Report*, **7**: 43-58.

TKATCHENKO G. and T. RADZIEJEWSKA, 1998. Recovery and recolonisation processes in the area disturbed by a polymetallic nodule collector simulator, *8th. Int. Offshore and Polar Engineering Conference*, Montréal, Quebec, USA (24-29 May 1998): 282-286.

TKATCHENKO G, T. RADZIEJEWSKA, V. STOYANOVA, I. MODLITBA and A. PARIZEK, 1996. Benthic Impact Experiment in the IOM pioneer area: testing for effects of deep seabed disturbance. *Proceedings of the International seminar on deep sea-bed mining technology, Oct. 18-20, 1996*, COMRA, Pekin, PP China: C55-C68.

TRACEY J.I., G.H. SUTTON, W.D. NESTEROFF, J. GALEHOUSE, C.C. VONDERBORCH, T. MOORE, J. LIPPS, U. Z. BILAL UL HAQ and J.P. BECKMANN, 1971. Leg 8 summary. In : *Initial Reports of the Deep Sea Drilling Project*, Eds. U.S. Government Printing Office, Washington D.C.: 17-42.

TRUEBLOOD D.D. and OZTURGUT E., 1997. The Benthic Impact Experiment : a study of the ecological impacts of deep seabed mining on abyssal bentic communities. *Proc. 7th ISOPE Conf., Honolulu*: 481-487.

TURPAEVA E.P., 1971. Pycnogonida d'eaux profondes (Pantopoda) récoltés dans la fosse des Kouriles-Kamtchatka. *Tr. IN-TA Océanologie AN URSS*. **92** : 274-291.

TURPAEVA E.P., 1974. Pycnogonida de la mer d'Ecosse and des eaux environnantes. *IN-TA Océanologie AN URSS*. **98**: 277-305.

TYLER P.A., 1980. Deep-sea Ophiuroids. *Oceanog. Mar. Biology Ann. Rev.*, **18**: 125-153.

TYLER P. A., 1988. Seasonality in the deep sea, *Oceanogr. Mar. Biol. Ann. Rev.*, **26**: 227-258.

TYLER P.A., 1995, Conditions for the existence of life at the deep-sea floor: an update. *Oceanogr. Mar. Biol. Ann. Rev.*, **33**: 221-244.

UNDERWOOD J.R. and W. LAMBERT, 1974. Centroclinal cross strata, a distinctive sedimentary structure, *J. Sedim. Petrol.*, **44**: 1111-1113.

USUI A., 1979. Minerals, metal contents and mechanism of formation of manganese nodules from the central Pacific basin (GH76-1 and GH77-1 areas). In : *Marine Geology and Oceanography of the Pacific Manganese Nodule Province*, J.L. Bishoff and D.Z. Piper Eds., Plenum Press, New York: 651-689.

UZMANN J.R., R.A. COOPER, R.B. THEROUX and R.L. WIGLEY, 1977. Synoptic comparison of three sampling techniques for estimating abundance and distribution of selected megafauna: submersible vs camera sled vs otter trawl. *Marine Fisheries Review*, **39**: 11-19.

VADAN C. and A. GUILLE, 1984. Les Ophiuridae (Ophiuroidea, Echinodermata) de la campagne MD 32 du Marion Dufresne autour de l'île de la Réunion, *Bulletin du Museum d'Histoire Naturelle de Paris*, 4ème Série, **6(3)**: 583-615.

VALENTINE J.W., 1973. Evolutionary Paleoecology of the Marine Biosphere, Prentice-Hall, New Jersey.

VAN ANDEL T.J. and G.R. HEATH, 1973. Geological results of Leg 16. In: The central equatorial Pacific west of the East Pacific Rise. In : *Initial Reports of the Deep Sea Drilling Project*, Eds., U.S. Government Printing Office, Washington D.C.: 937-949.

VAN PRAET M., 1990. Food Intake and Digestion in Sea Anemones. Mellinger J. (ed.). Animal Nutrition and Transport Processes. 1. Nutrition in wild and Darostic. *Annals comp. Physiol. Bosel Kargers*, **5** : 24-35.

VERVOORT W., 1966. Bathyal and abyssal hydroids. *Galathea Report*, **8**: 98-174.

VINOGRADOV A.P., 1953. The elementary chemical comosition of marine organisms. *Memoir Sears Foundation for Marine Research*, **2**: 1-647.

VINOGRADOVA N.G., 1962. Vertical zonation in the distribution of the deep-sea benthic fauna in the ocean. *Deep-Sea Research*, **8**: 245-250.

VINOGRADOVA M.E. and V.B. TSEITLIN, 1983. Deep-Sea pelagic domain (aspects of bioenergetics). In : *Deep-Sea Biology, The Sea*, G.T. Rowe Ed, **8**, 123-165.

VON STACKELBERG U., 1979. Sedimentation, hiatuses and development of manganese nodules: Valdivia site Va 13/2, northern central Pacific. In : *Marine Geology and Oceanography of the Pacific Manganese Nodule Province*, J.L. Bishoff and D.Z. Piper Eds., Plenum Press, New York: 559-586.

VON STACKELBERG U., 1982. Influence of hiatuses and volcanic ash rains on the origin of manganese nodules of the equatorial north Pacific. In : *Marine Mining*, **3** : 3-4.

VON STACKELBERG U., 1984. Significance of benthic organisms for the growth and movement of manganese nodules, equatorial north Pacific. *Geo-Marine Letters*, **4**: 37-42.

VON STACKELBERG U. and V. MARCHIG, 1987. Manganese nodules from the equatorial north Pacific ocean. *Geologishes Jahrbuch*, **D87**: 123-227.

VON STACKELBERG U. and H. BEIERSDORF, 1991. The formation of manganese nodules between the Clarion and Clipperton fracture zones southeast of Hawaii. In : *Marine Geology*, **98**: 411-423.

VOSS G.L., 1967. The biology and bathymetric distribution of deep-sea. Cephalopods. *Stud. trop. Oceanogra. Inst. mar. Sci. Miami*, **5**: 511-535.

VOSS G., 1988. The biogeography of the deep-sea octopoda. *Malacologia*, **29 (1)**: 295-307.

VOSS G. and W. PEARCY, 1990. Deep-water octopods (Mollusca: Cephadopoda) of the Northeastern Pacific. *Proceedings of the Californian Academy of Sciences*, **47 (3)**: 47-94.

WAKEFIELD W. and GENIN A., 1987. The use of a Canadian (perspective) grid in deep-sea photography, *Deep-Sea Research*, **34**: 469-478.

WAKEFIELD W. and W. SMITHEY, 1989. Two camera sleds for quantitative study of deep-sea megafauna. *Vol 89-14, Scripps Institution of Oceanography Reference Series*, 1-25.

WANG Y., J. LI, X. HAN and Z. WU, 2001. The influence of terrain slope on the distribution of polymetallic nodules. *Acta Oceanologica Sinica*, **23(1)**: 65-23.

WANGERSKY P.J. and C.P. WANGERSKY, 1981. The manna effect : The structure of benthic populations. *Int. Rev. Ges. Hydrobiol.* **66**: 777-786.

WARNER G., 1982. Food and feeding mechanisms: Ophiuroidea. In: *Echinoderm nutrition*. M. Jangoux and J.M. Lawrence Eds, A.A. Balkema Publishers, Rotterdam: 161-181.

WENDT J., 1974. Encrusting organisms in deep-sea manganese nodules. *Spec. Publ. Inst. Ass. Sed*., **1**: 437-447.

WHEATCROFT R.A., SMITH C.R. and JUMARS P.A., 1989. Dynamics of surficial trace assemblages in the deep sea. *Deep-Sea Research*, **36 (1A)**: 71-91.

WICKINS J.F., 1983. Catches of large lysianassid amphipods in baited traps at the nuclear energy authority dump site during June 1979. *Deep-Sea Research*, **30** : 83-86.

WIGLEY R.L. and R.B. THEROUX, 1981. Macrobenthic invertebrate fauna of the middle Atlantic bight region : Part II. Faunal composition and quantitative distribution. U.*S. Geological Survey Professionnal Paper*, **529-N**: 1-198.

WILSON G.D.F., 1983. Systematics of a specimen complex in the deep-sea genus *Eurycope* with a revision of six previously described species (Crustacea, Isopoda, Eurycopidae). *Bulletin of the Scripps Institution of Oceanography of the University of California, San Diego*, **25** : 1-64.

WILSON G.D.F., 1990. Biological evaluation of a preservational reference area: BEPRA I cruise report. Scripps Inst. of Oceanography. *NOAA. RUM 3. R/V New Horizon cruise Quagmire II: 23 April - 17 May 1990. Post cruise report*: 1-34.

WILSON G.D.F. and R.R. HESSLER, 1987. The effects of manganese nodule test mining on the benthic fauna in the North équatorial Pacific. In : *Environmental Effetcs of Deep-sea Dredging. Final report to the National Oceanic and Atmospheric Administration on contract NA 83-SAC-00659, Reference 87-5*: 24-86.

WILSON Jr R.R., K.L. SMITH Jr and R.H. ROSENBLATT, 1985. Megafauna associated with bathyal seamounts in the central north Pacific basin. *Deep-Sea Research*, **32**: 1243-1254.

WOLFF T., 1960. The hadal community : An introduction. *Deep-Sea Research*, **32**: 1243-1254.

WOLFF T., 1962. The systematics and biology of bathyal and abyssal Isopoda Asellota, *Galathea Report*, **6**: 7-70.

WOLFF T., 1970. The concept of the hadal or ultra-abyssal fauna, *Deep-Sea Res.,* **17**: 983-1003.

WOLFF T., 1977. Diversity and faunal composition of the deep-sea benthos. *Nature*, **267**: 780-785.

WOLFF T., 1979. Macrofaunal utilization of plant remains in the deep-sea. *Sarsia*, **64 (1/2)**: 117-136.

WU S., M. YIN, C. SHI, W. ZENG, H. ZOU and X. ZENG, 1999. Determination of growth rates of deep-sea polymetallic nodules with super (10)Be accelerator mass spectrometry. Tropic oceanology/Redal Haiyang. Guangzhou, **18(1)**: 73-78.

YOUNG D.K., W.H. JOHN, M.D. RICHARDSON and A.W. LOHANICK, 1985. Photographs of deep-sea Lebenspuren : A comparison of sedimentary provinces in the Venezuela Basin, *Caribbean Sea. Mar. Geol*., **68** : 269-301.

ZENKEVITCH H., 1964. Nouveaux représentants Echiuroidea d'eaux profondes de l'Océan Indien. 1 : 178-182.

ZENKEVITCH H., 1966. The systematics and distribution of abyssal and hadal (ultra-abyssal) Echiuroidea. *Galathea report*, **8**: 175-184.

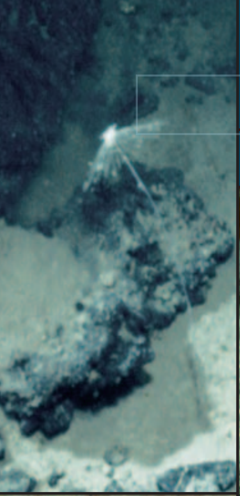
ZENKEVITCH H., 1970. Photographic atlas of the Pacific ocean seabed. *Trudy Instituta Okeanologii*, P.P. Shirshova: 265-266.

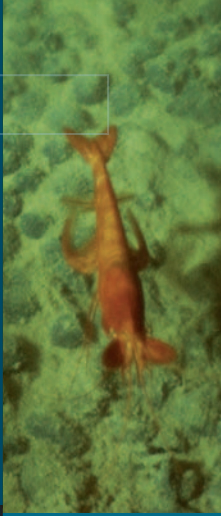
ZENKEVITCH H. and J.A. BIRSTEIN, 1956. Studies of the deep-water and related problems. *Deep-Sea Research*, **4**: 54-64.

ZENKEVITCH L.A., 1957. New genus and two new species of deep-sea Echiuroidea from the far eastern seas and northwestern part of the Pacific Ocean, *Trudy Instituta Okeanologii, Moskva*, **23**: 291-295.

ZEZINA O., 1975. On some deep-sea brachiopods from the Gay Head-Bermuda transect. *Deep-Sea Research*, **22**: 903-912.

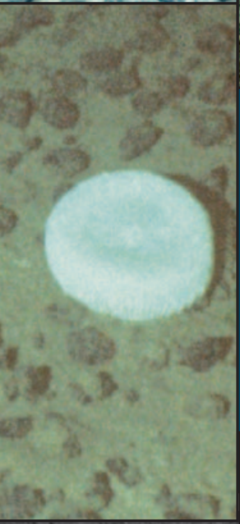
ZHOU H-Y., 1997. Chinese environmental investigations related to potential impact of deep-sea mining. *Proceedings of the ISOPE-Offshore and Polar Engineering Conference, May 25-30. 1997*: 496-498.





Appendix I

PANORAMA OF THE MEGAFAUNA WITHIN A POLYMETALLIC NODULE ECOSYSTEM IN THE EASTERN EQUATORIAL PACIFIC OCEAN AND COLOUR FIGURES ON THE THEME OF POLYMETALLIC NODULES



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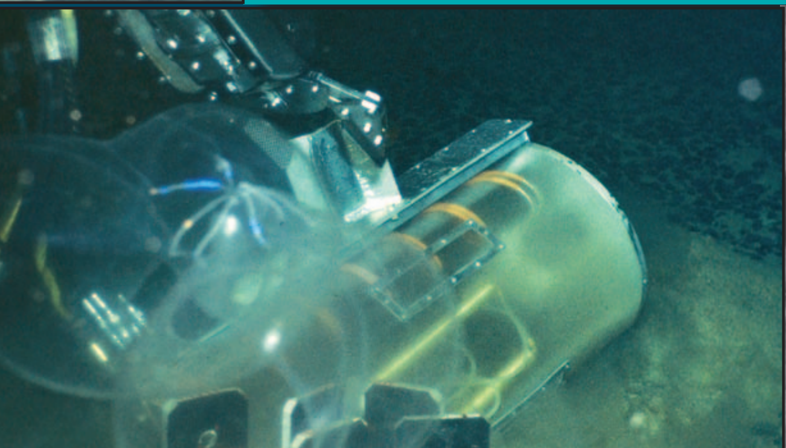
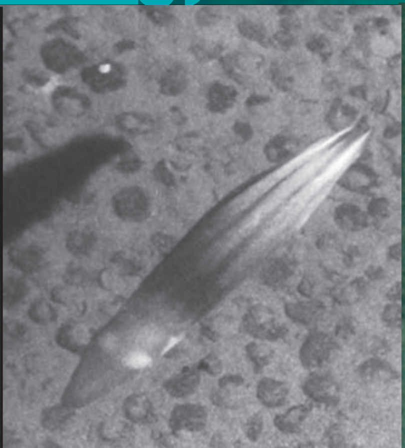




INTRODUCTION

This appendix shows a brief panorama of the suprabenthic megafauna in an abyssal ecosystem of polymetallic nodules. The echinoderm phylum is presented separately in greater detail in an annotated photographic atlas (IOC Tech Series N° 69, Vol. 2). As explained in the qualitative analysis, this atlas results from the compilation of a reference base of megabenthic assemblages and their various environmental parameters, based on about 200 000 photographs of the ocean floor and 55 hours of films collected by various towed devices (a troika, "Deep Tow", "R.A.I.E.") and remote vehicles ("ED1", the "Épaulard" and the manned submarine "the Nautile").

All our hypotheses of identification for the taxa present on the photographs and films from the Clarion-Clipperton fracture zone were complied on the advice of international specialists who are listed in Appendix 3. The accepted hypotheses are presented and commented in the annotated photographic atlas. The list of codes used for the taxa identified is presented in Appendix 2, and follows the classification of Parker (1982).

Most of the species in this zone have not yet been collected and are new to science. The images capture other valuable information, such as the appearance of the taxa in situ and their behaviour within faunal assemblages and on different substrata. The observation and spatio-temporal monitoring of the megafauna on a grand scale, by means of photography and video, proves to be a useful, low cost tool to evaluate the impact of exploiting nodule deposits. The megafauna, and especially certain faunal groups, are known to be good indicators in impact studies. Based on the hypotheses of identification proposed for each of the taxa observed in our study, a series of tables are presented in Appendix 4 synthesizing information provided by international specialists and by the literature.

The present data from research in the abyssal environment and especially in the Clarion-Clipperton fracture zone underlines the variation in biotic and abiotic conditions in space and time which have revolutionized previous notions of great stability based on unchanging environmental conditions.

Based on our results, the polymetallic nodule ecosystem appears to be a unique habitat for the suprabenthic megafauna. This megafauna is characterized by relatively great taxonomic richness, especially for suspension feeders, which are well represented in this panorama, and in particular for Cnidaria, which are the most diverse and abundant phylum. These images also illustrate the preferential habitats that we have demonstrated for the different faunal categories. As can be seen, faunal abundance is linked to edaphic heterogeneity and is especially marked for suspension feeders on facies O (without nodules) and with ancient sediments (Oligocene to Miocene) and on nodule-facies C+ (hummocky nodules of mean diameter 7.5 cm) on slopes and with nodule coverage C+20-40%. The edaphic preference for detritus feeders is nodule-facies C+10%.

These factors must be borne in mind in the proposition of recommendations for the conservation of the biodiversity and for building a strategy of monitoring in order to minimize the impact of the exploitation of polymetallic nodules.

Fig.1. Photograph taken by "the Nautile" during the NIXONAUT cruise: rocky facies, sponge Hexactinellida *Euplectella sp.* (SPO 13) © Ifremer

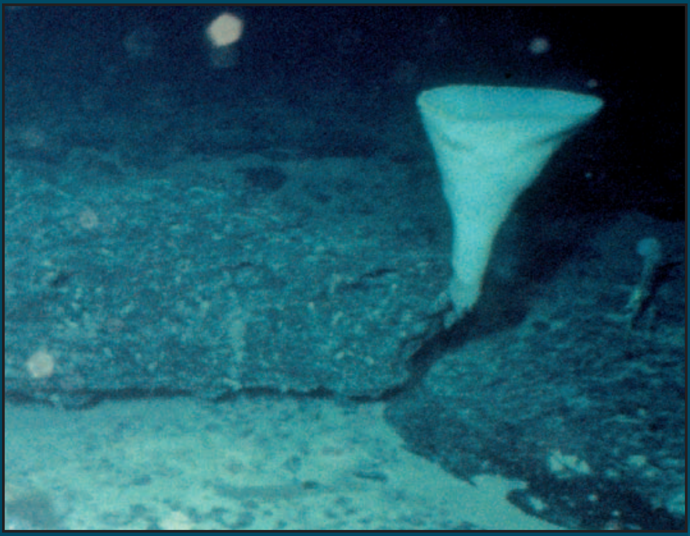


Fig.2. Photograph taken by the "the Nautile" during the NIXONAUT cruise: rocky facies, sponge Hexactinellida *Bathydorus sp.* (SPO 5) © Ifremer

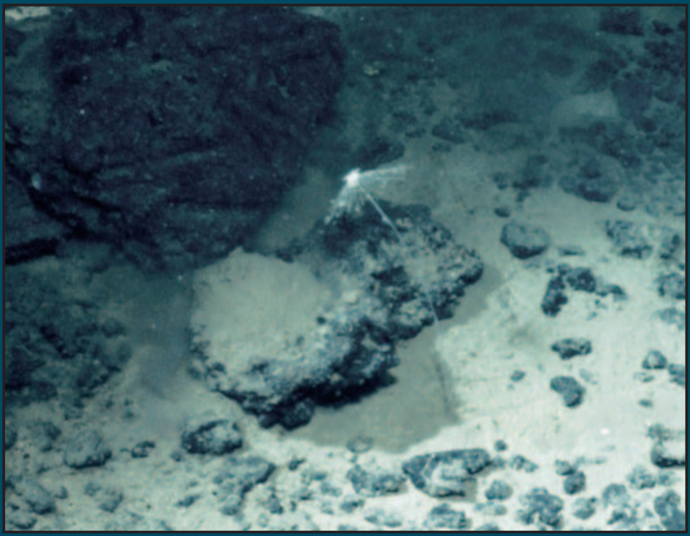


Fig.3. Photograph taken by the "the Nautile" during the NIXONAUT cruise: rocky facies, sponge Demospongiae *Cladorhizida sp.* (SPO 19) © Ifremer

Fig.4. Photograph taken by the "the Nautile" during the NIXONAUT cruise: nodule-facies C, sponge Hexactinellida "Two-pronged" Rossellidae (SPO 2) © Ifremer

Fig.5. Photograph taken by the 'Épaulard' at the NIXO 45 site: nodule-facies C, sponge Hexactinellida *Pheronema sp.* (SPO 14) with an actinid attached to the peduncle © Ifremer

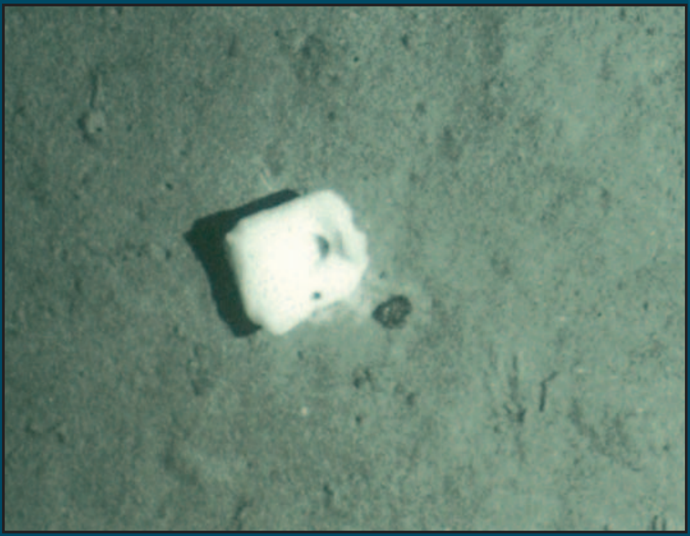


Fig.6. Photograph taken by the 'Épaulard' at the NIXO 45 site: nodule-facies C, sponge type "vase-shaped alveolate" Tetractinellida *Poecillastra sp.* (SPO 6) © Ifremer

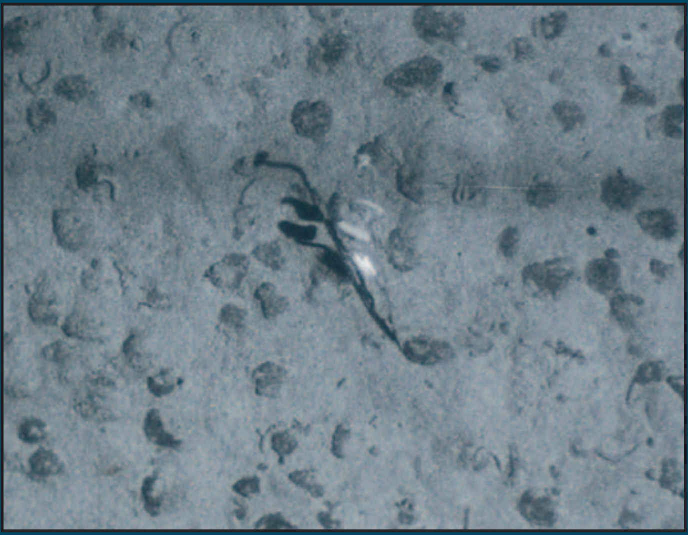


Fig.7. Photograph taken by the ‘Épaulard’ at the NIXO 45 site: nodule-facies C, colony of sponges Demospongiae *Caulophacus sp.* or *Esperiopsis sp.* (SPO 16) © Ifremer

Fig.8. Photograph taken by the ‘Épaulard’ at the NIXO 45 site: facies O, sponge Hexactinellida *Euplectella sp.* (SPO 12) © Ifremer

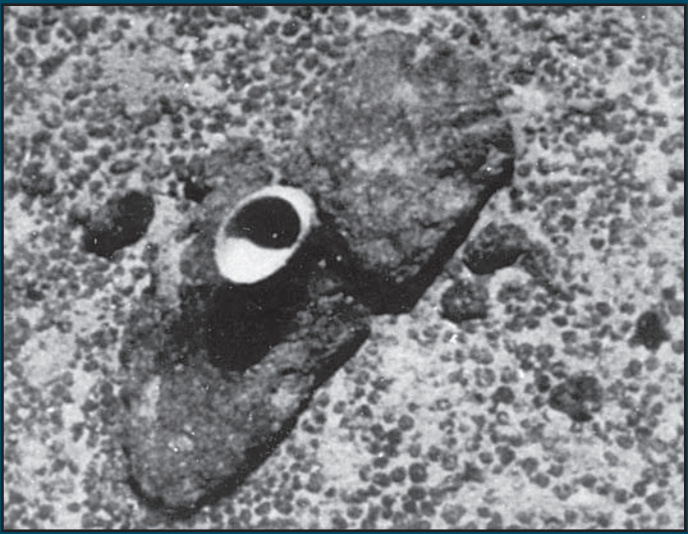


Fig.9. Photograph taken by the ‘Épaulard’ at the NIXO 45 site: mixed nodule-facies B with plates, sponge Demospongiae *Phakellia sp.* (SPO 4) © Ifremer

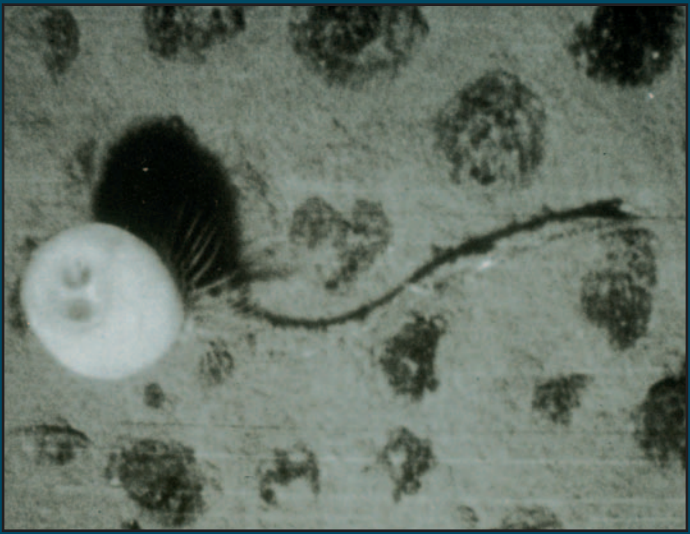


Fig.10. Photograph taken by ‘Deep Tow’ at the Echo I site (near DOMES C/CCFZ): nodule-facies C, sponge Hexactinellida *Hyalonema sp.* (SPO 15) © Ifremer

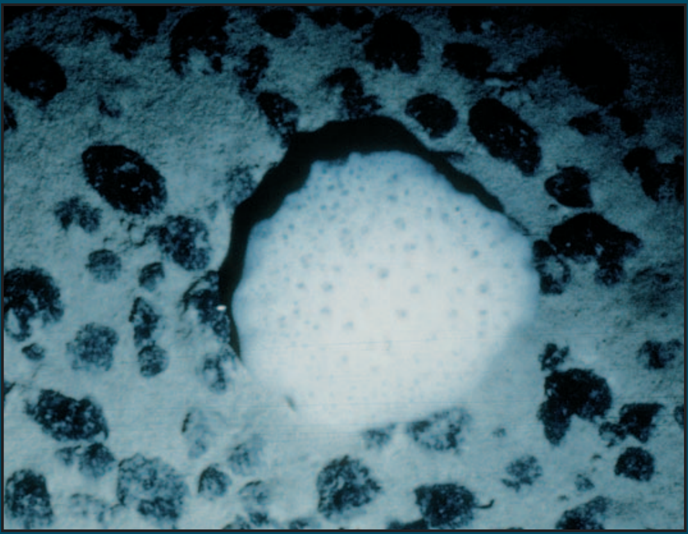


Fig.11. Photograph taken by ‘Deep Tow’ at the Echo I site: nodule-facies C, sponge type “alveolate cushion” Tetractinellida, *Poecillastra sp.* (SPO 8)

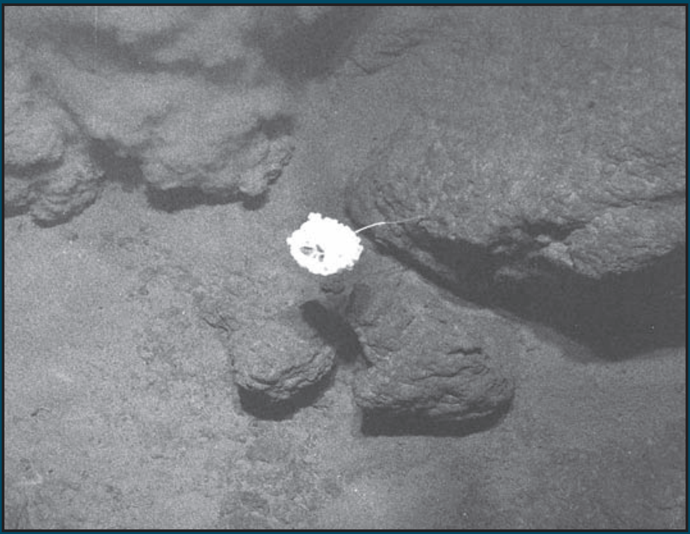


Fig.12. Photograph taken by the ‘R.A.I.E.’ at the NIXO 42 site: rocky facies, sponge Hexactinellida *Aulochone sp.* (A. cylindrica) (SPO 11) © Ifremer

Fig.13. Photograph taken by the 'Épaulard' at the NIXO 45 site: mixed nodule-facies with plates and B, hydrozoan *Branchiocerianthus imperator* (HYD 1) bending in the direction of the current © Ifremer

Fig.14. Photograph taken by the 'Épaulard' at the NIXO 45 site: facies O and some nodules of facies C, hydrozoan *Branchiocerianthus imperator* (HYD 1) © Ifremer

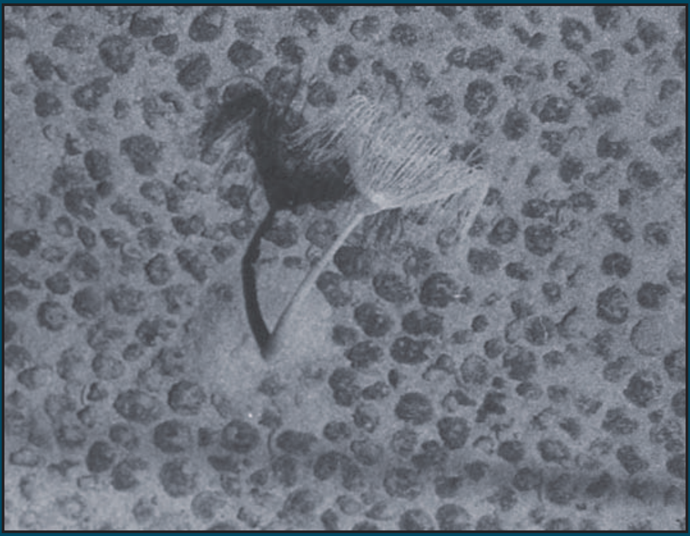


Fig.15. Photograph taken by the 'Épaulard' at the NIXO 45 site: nodule-facies C, hydrozoan *Branchiocerianthus imperator* (HYD 1) © Ifremer

Fig.16. Photograph taken by the 'Épaulard' at the NIXO 45 site: facies O, hydrozoan *Branchiocerianthus imperator* (HYD 1) © Ifremer

Fig.17. Photograph taken by the "the Nautile" during the NIXONAUT cruise: nodule-facies mixed with plates, scyphomedusa or hydromedusa *Chrysaora lysoscella* (MED 10) © Ifremer

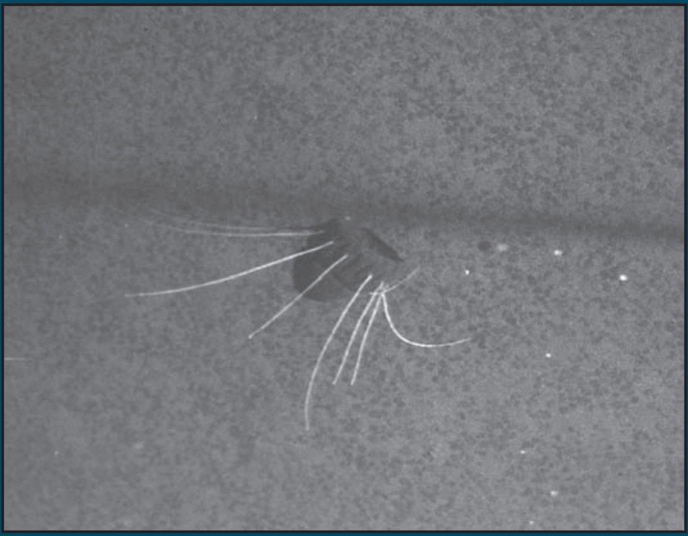


Fig.18. Photograph taken by the 'Épaulard' at the NIXO 45 site: Nodule-facies C, scyphomedusa, *Periphylla periphylla* (MED 9) © Ifremer

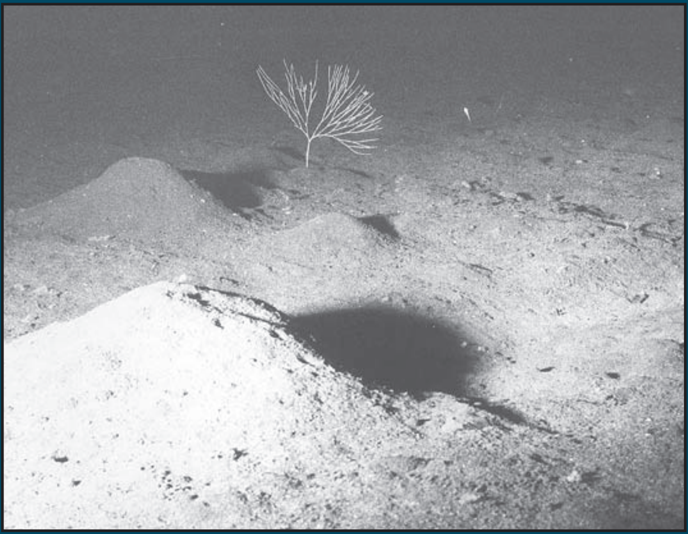


Fig.19. Photograph taken by a troika during the Copano 2 cruise: facies O, octocoralliarian Gorgonacea, Primnoidae (OCT 6) near mounds formed by echiurians © Ifremer

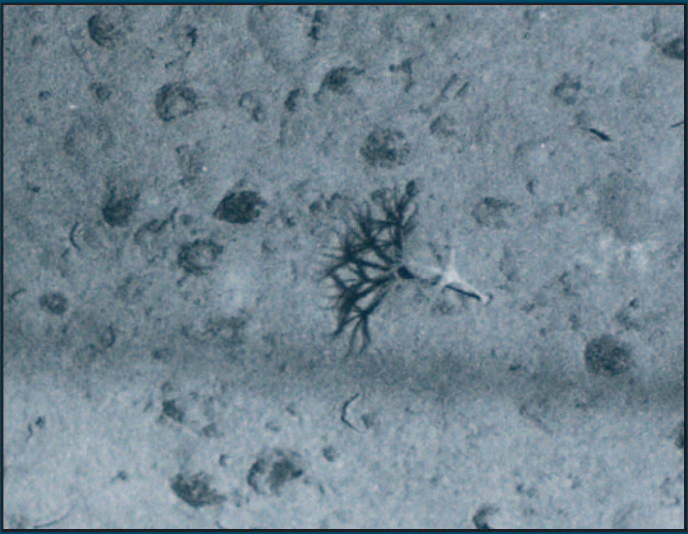


Fig.20. Photograph taken by the 'Épaulard' at the NIXO 45 site: nodule-facies C, octocoralliarian, complex form of *Umbellula sp.* (OCT 5) © Ifremer

Fig.21. Photograph taken by the 'Épaulard' at the NIXO 45 site: facies O and some nodules of facies C, octocoralliarid Pennatulacea (OCT 1) with actinian *Amphianthus sp.* (ACT 8) © Ifremer

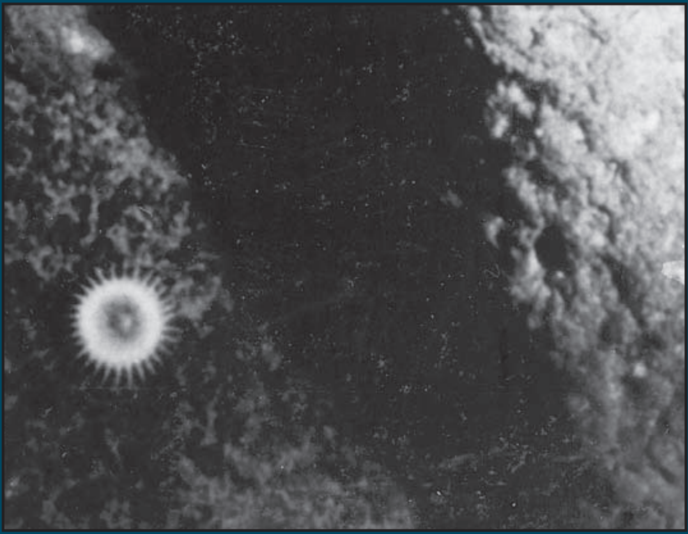


Fig.22. Photograph taken by the 'Épaulard' at the NIXO 45 site: cliffs and mixed nodule-facies B and plates, actinian Actinostolidae form with dark convex centre *Sicyonis biotrans* (ACT 6') © Ifremer

Fig.23. Photograph taken by a troika during the Copano 2 cruise: facies O, actinian *Ophiodiscus sulcatus* or *Bolocera sp.* (ACT 5) © Ifremer

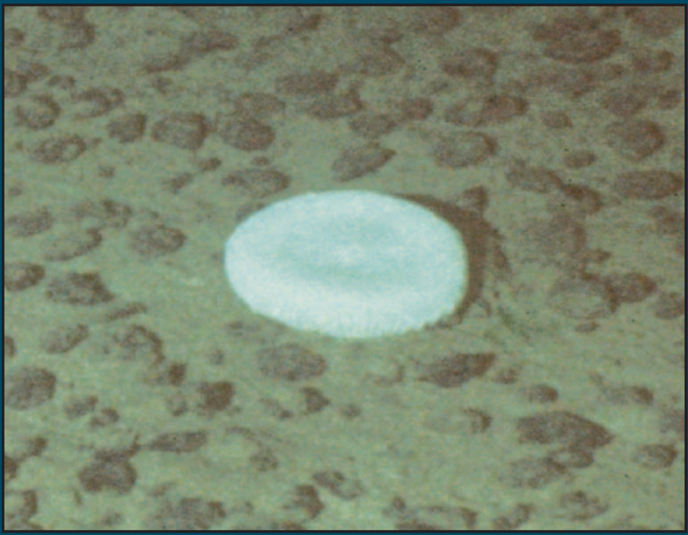


Fig.24. Photograph taken by the "the Nautile" during the NIXONAUT cruise: nodule-facies C, actinian type "white disc" *Liponema sp.* (ACT 1) © Ifremer

Fig.25. Photograph taken by the 'Épaulard' at the NIXO 45 site: nodule-facies C, actinian Actinostolidae not attached *Sicyonis biotrans* (ACT 4) © Ifremer

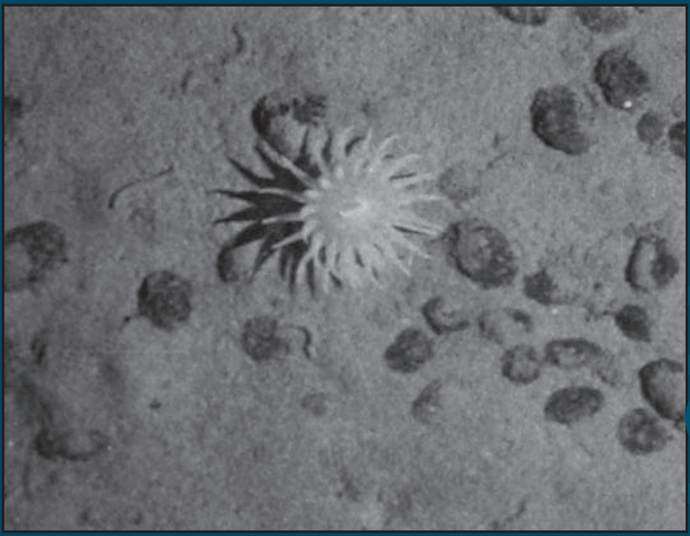


Fig.26. Photograph taken by the 'Épaulard' at the NIXO 45 site: nodule-facies C, actinian Actinostolidae *Actinernus sp.* (ACT 7) © Ifremer

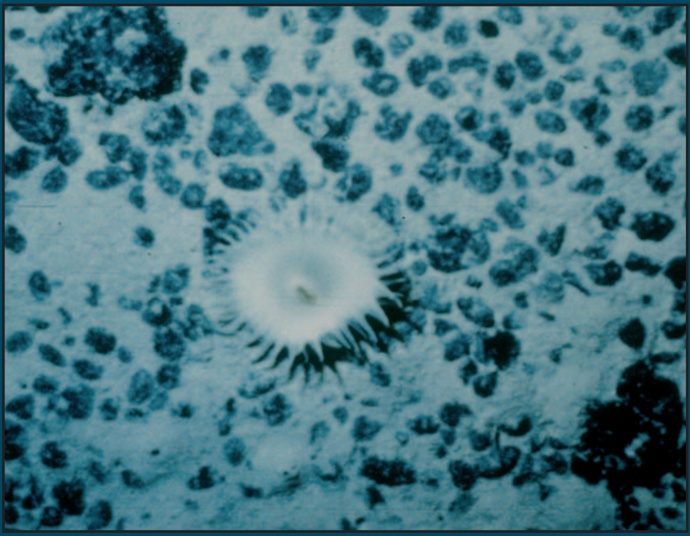


Fig.27. Photograph taken by 'Deep Tow' at the Echo I site: nodule-facies mixed B and plates, *actinian Hormathiidae* (ACT 6) © Ifremer

Fig.28. Photograph taken by a troika during the Copano 1 cruise: facies O, actinian Sagartiidae, *Thenaria sp.* (ACT 7) © Ifremer

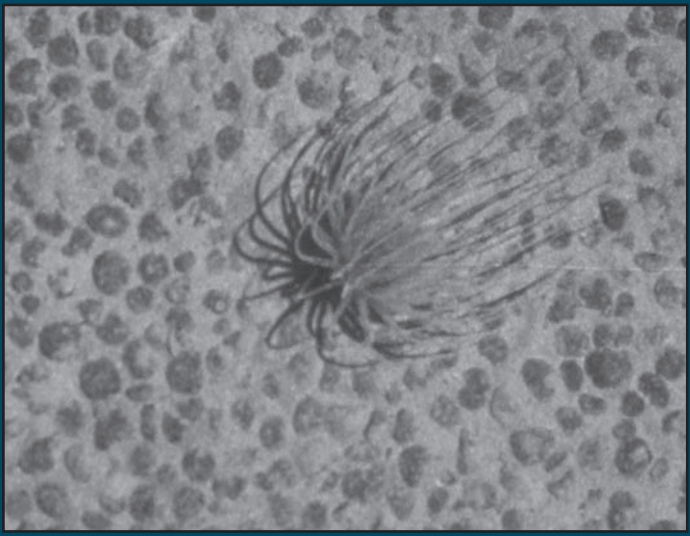


Fig.29. Photograph taken by the 'Épaulard' at the NIXO 45 site: nodule-facies B, ceriantharian Aliciidae, *Cerianthus sp.* (CER 1) © Ifremer

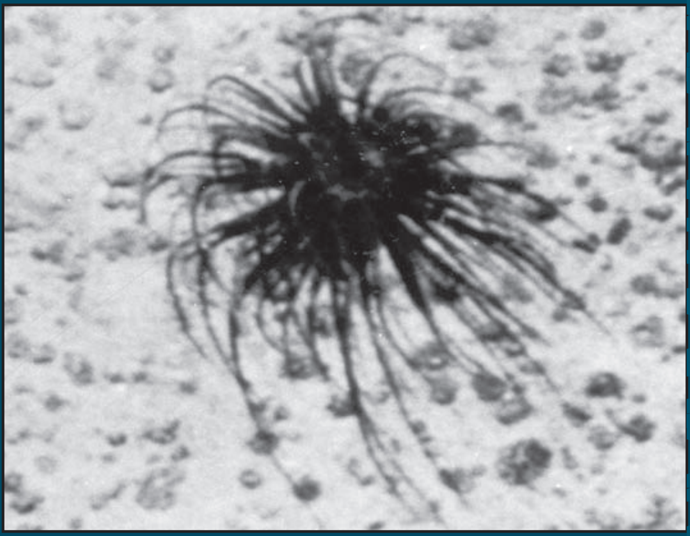


Fig.30. Photograph taken by the 'Épaulard' at the NIXO 45 site: nodule-facies B, dark ceriantharian, Aliciidae, *Cerianthus sp.* (CER 1') © Ifremer

Fig.31. Photograph taken by the "the Nautile" during the NIXONAUT cruise: rocky facies, antipatharian *Parantipathes larix* (ANT 7) © Ifremer

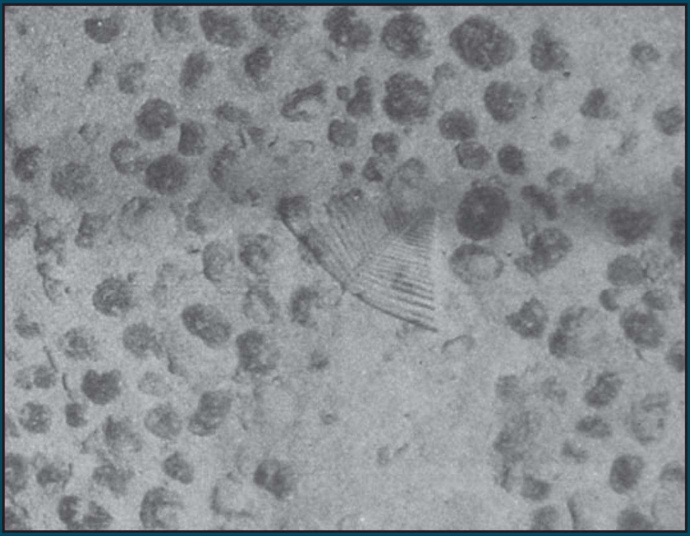


Fig.32. Photograph taken by the 'Épaulard' at the NIXO 45 site: nodule-facies C, antipatharian *Schizopathes crassa* (ANT 2) © Ifremer

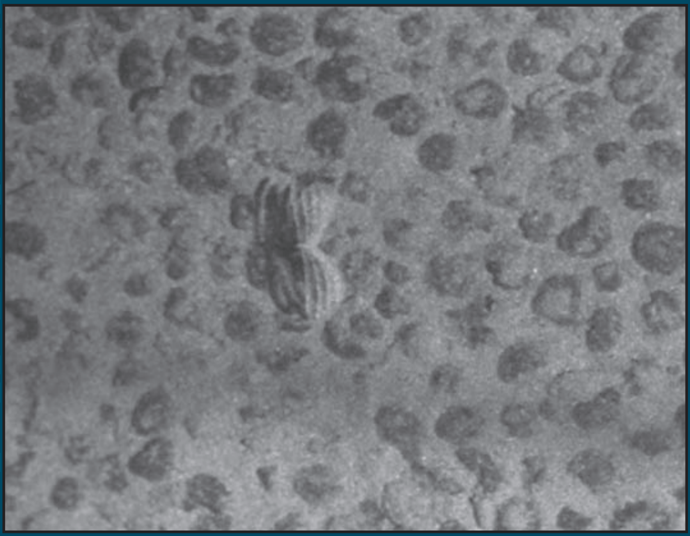


Fig.33. Photograph taken by the 'Épaulard' at the NIXO 45 site: nodule-facies C, antipatharian *Bathypathes lyra* (ANT 1) © Ifremer

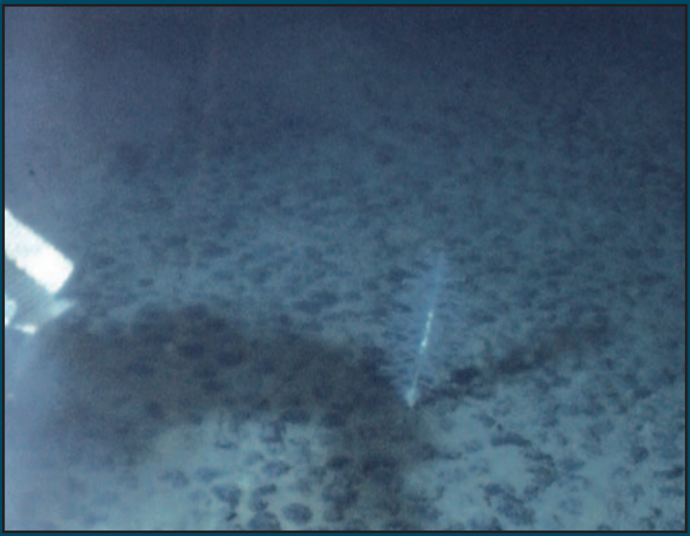


Fig.34. Photograph taken by the "the Nautile" during the NIXONAUT cruise: nodule-facies C, antipatharian *Bathypathes sp.* (ANT 10) © Ifremer

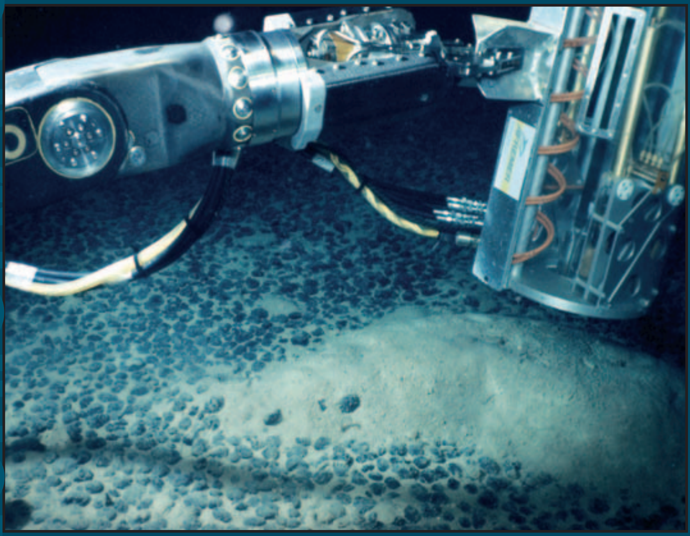


Fig.35. Photograph taken by the "the Nautile" during the NIXONAUT cruise: nodule-facies C, Field vane tester investigating the soil mechanics on a mound formed by the echiurian worm Bonneliidae *Jacobia birsteini* (ECH 2) © Ifremer

Fig.36. Photograph taken by the 'Épaulard' at the NIXO 45 site: nodule-facies C, round burrow and mound of the echiurian worm Bonneliidae *Jacobia birsteini* (ECH 2) © Ifremer

Fig.37. Photograph taken by the "the Nautile" during the NIXONAUT cruise: nodule-facies B, mound about 2.5 m formed by the echiurian worm Bonneliidae *Jacobia birsteini* (ECH 2) © Ifremer

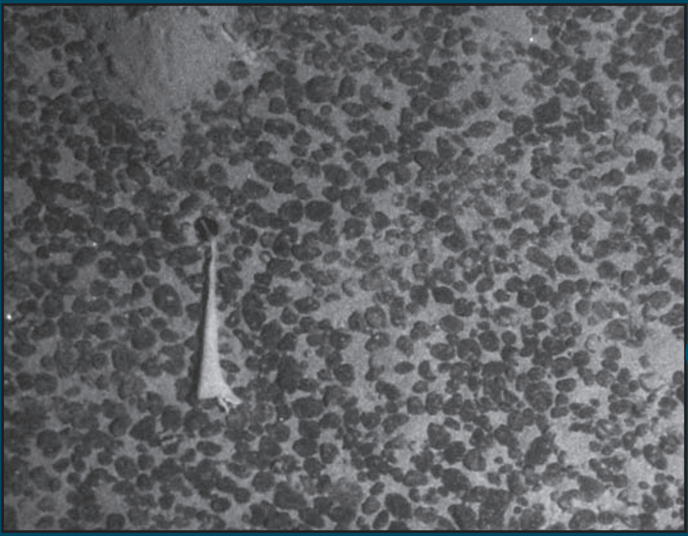


Fig.38. Photograph taken by the 'Épaulard' at the NIXO 45 site: nodule-facies B, proboscis of an echiurian worm Bonneliidae (ECH 3) extending from the hole close to its mound © Ifremer

Fig.39.Photograph taken by the 'Épaulard' at the NIXO 45 site: nodule-facies C, round mound constructed by an echiurian worm *Balanoglossus sp.* (ENT 4) © Ifremer

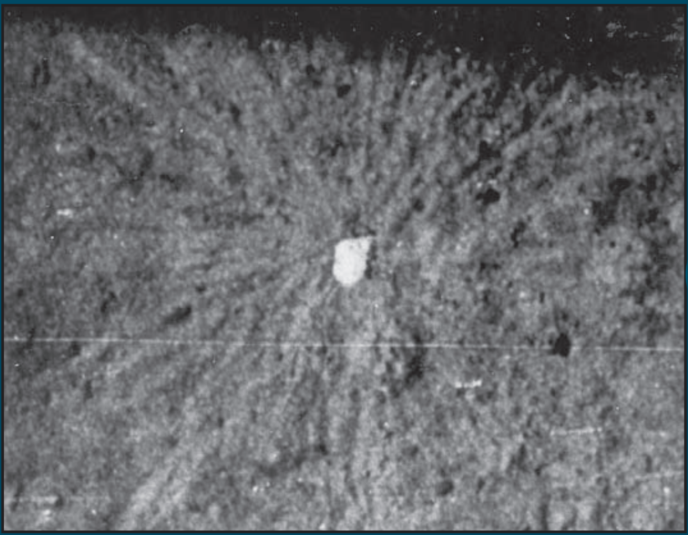


Fig.40. Photograph taken by the 'Épaulard' at the NIXO 45 site: facies O, proboscis of an echiurian worm retracted at the entrance of its burrow and radiating tracks Bonneliidae *Bruunellia bandae* (ECH 6) © Ifremer

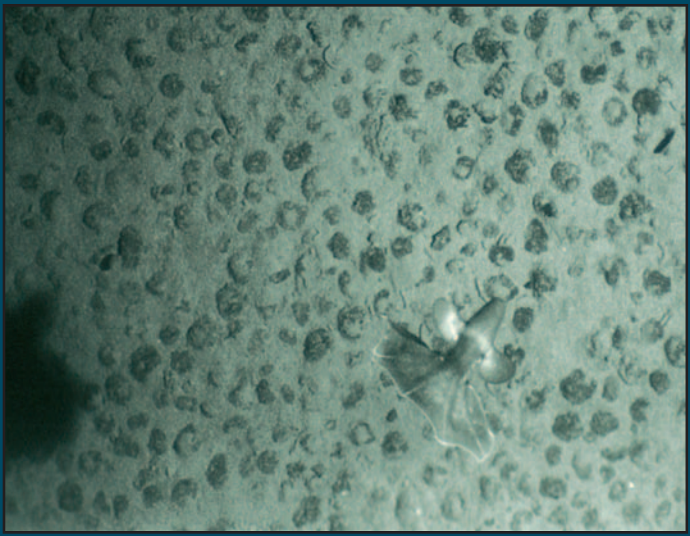


Fig.41. Photograph taken by the 'Épaulard' at the NIXO 45 site: nodule-facies C, cephalopod Cirrata *Cirroteuthis sp.* or *Cirrothauma sp.* (CEP 2) © Ifremer

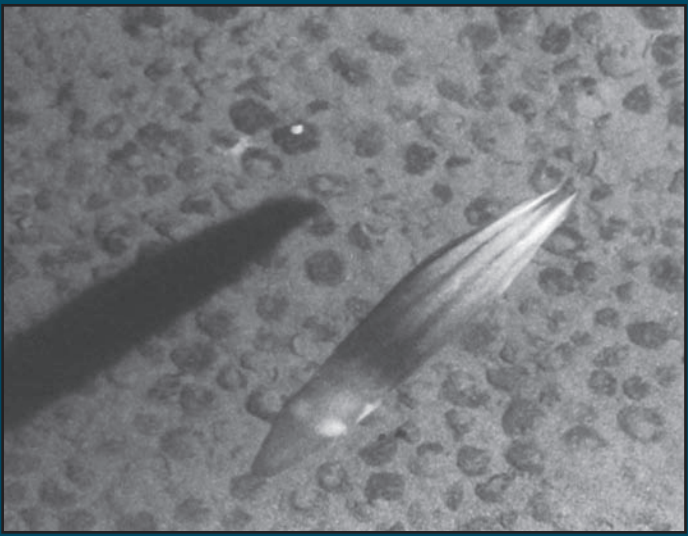


Fig.42. Photograph taken by the 'Épaulard' at the NIXO 45 site: nodule-facies C, cephalopod Cirrata during propulsion *Cirroteuthis sp.* (CEP 2) © Ifremer

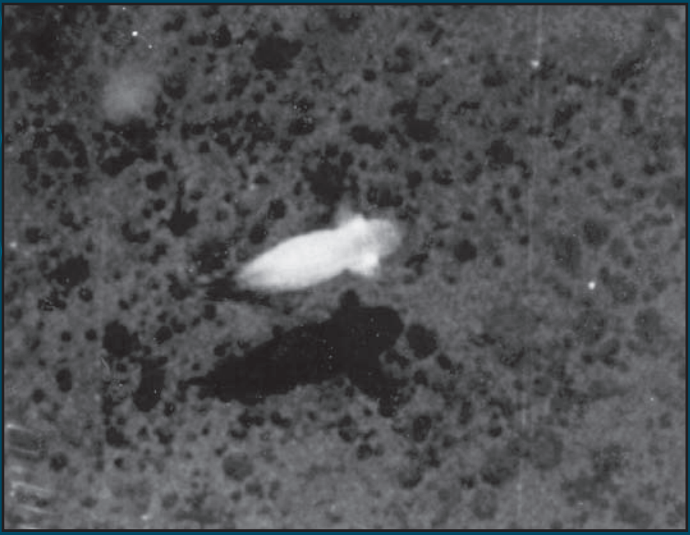


Fig.43. Photograph taken by the 'Épaulard' at the NIXO 45 site: nodule-facies mixed including B , cephalopod Cirrata during propulsion *Cirrotheuthis sp.* or *Stauroteuthis sp.* (CEP 1) © Ifremer

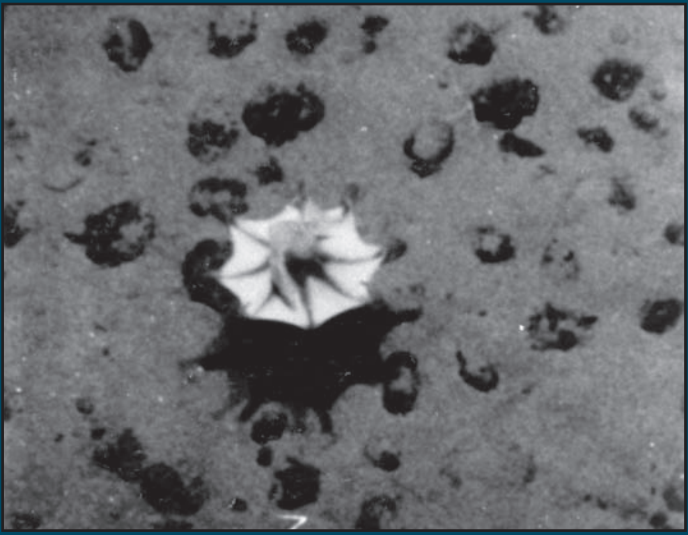


Fig.44. Photograph taken by the 'Épaulard' at the NIXO 45 site: nodule-facies C, Stationary cephalopod Cirrata *Grimpoteuthis sp.* or *Cirrothauma murrayi* (CEP 1) © Ifremer

Fig.45. Photograph taken by the "the Nautile" during the NIXONAUT cruise: mixed nodule-facies , crustacea Decapoda *Nematocarcinus sp.* (DEC 1) © Ifremer

Fig.46. Photograph taken by the "the Nautile" during the NIXONAUT cruise: nodule-facies C, crustacea Decapoda *Plesiopenaeus sp.* or *Aristaeomorpha sp.* (DEC 5) © Ifremer

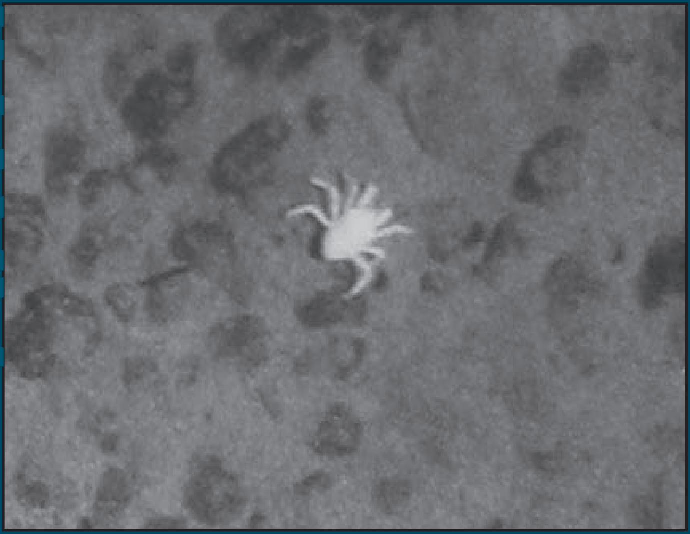


Fig.47. Photograph taken by the 'Épaulard' at the NIXO 45 site: nodule-facies C, crustacea Decapoda *Galathea sp.* (GAL 1) © Ifremer

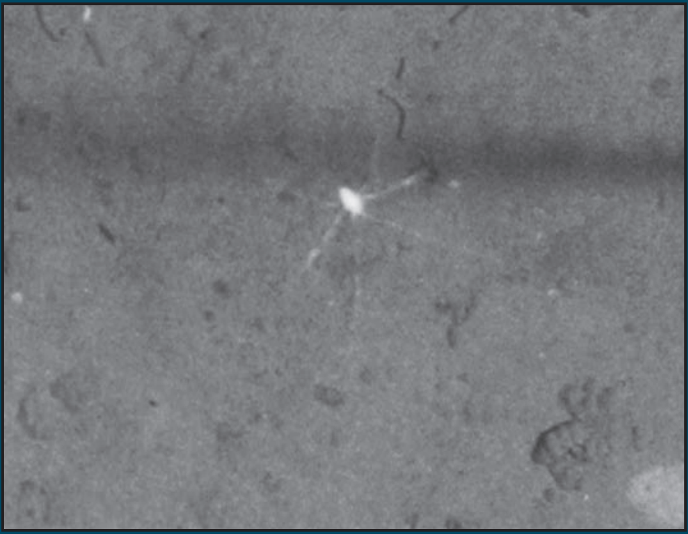


Fig.48. Photograph taken by the 'Épaulard' at the NIXO 45 site: facies O, crustacea Isopoda *Munnopsidae sp.* (ISO 1) © Ifremer

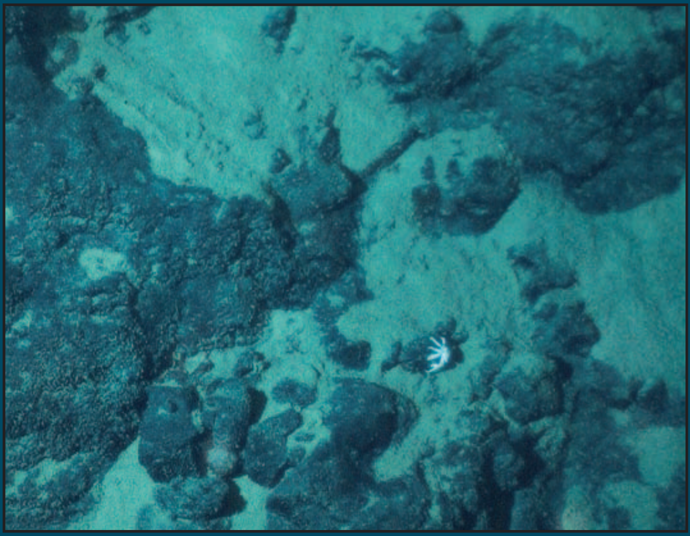


Fig.49. Photograph taken by the "the Nautile" during the NIXONAUT cruise: rocky facies, crustacea Decapoda *Munidopsis sp.* (GAL 3) © Ifremer

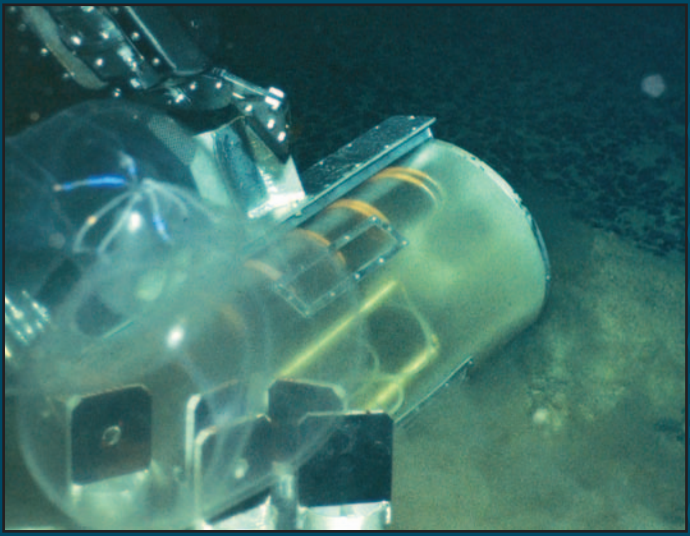


Fig.50. Exceptional photograph taken by the "the Nautile" during the NIXONAUT cruise, in front of a field vane tester: pycnogonid *Colossendeis colossea* (PYC) parasitising a lobed ctenophore © Ifremer

Fig.51. Photograph taken by the 'Épaulard' at the NIXO 45 site: facies O, enteropneusta Spengelitae *Glandiceps abyssicola* (ENT 3) © Ifremer

Fig.52. Photograph taken by the 'Épaulard' at the NIXO 45 site: facies O, spiral track of lophenteropneusta Ptychoderidae (ENT 1) and other traces of bioturbation © Ifremer

Fig.53. Photograph taken by the 'Épaulard' at the NIXO 45 site: nodule-facies C, ascidian Sorberacea *Phlebobranchiata sp.* (ASC 1) © Ifremer

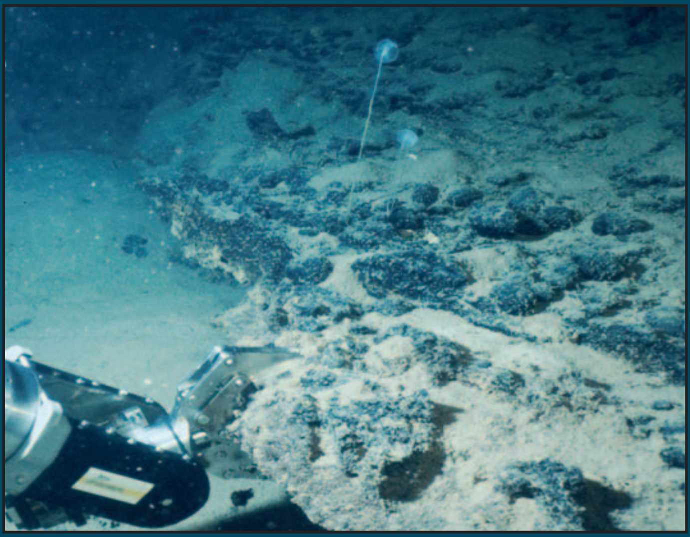


Fig.54. Photograph taken by the "the Nautile" during the NIXONAUT cruise: rocky outcrop, ascidian *Culeolus sp.* (ASC 4) © Ifremer

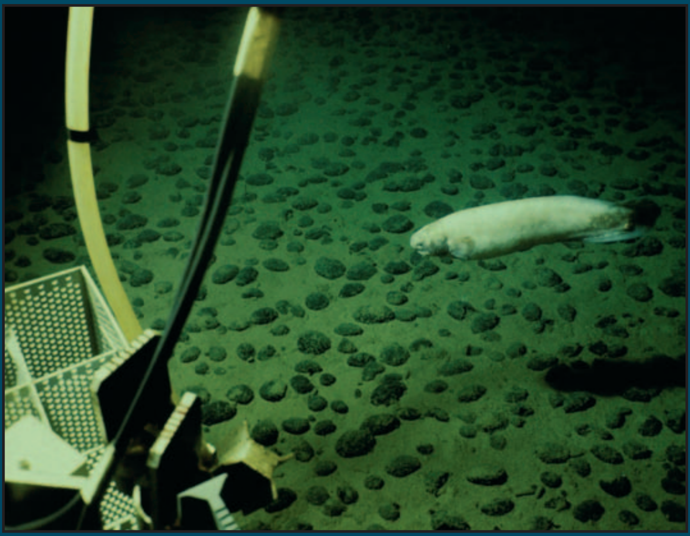


Fig.55. Photograph taken by the "the Nautile" during the NIXONAUT cruise: nodule-facies C, fish Ophidiidae *Barathrites sp.* (POI 14) © Ifremer

Fig. 56. Photograph taken by the "the Nautile" during the NIXONAUT cruise: nodule-facies C, fish *Bathysaurus mollis* (POI 7) © Ifremer

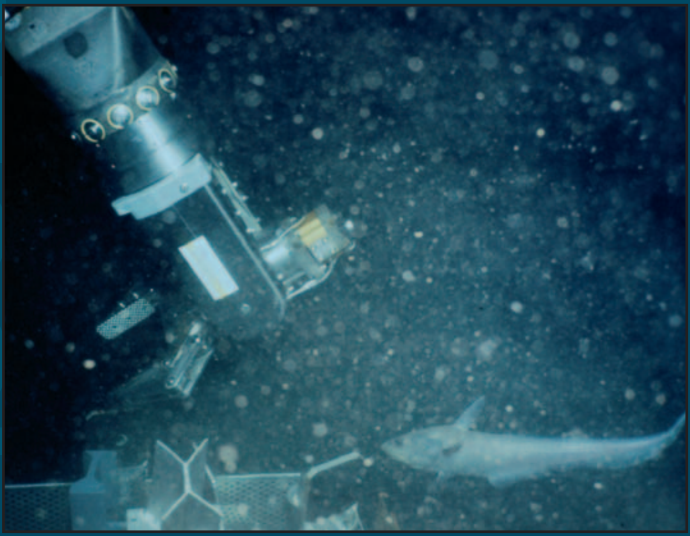


Fig.57. Photograph taken by the "the Nautile" during the NIXONAUT cruise: fish Macrouridae *Nematonurus sp.* (POI 1) attracted by activity © Ifremer

Fig.58. Photograph taken by the 'Épaulard' at the NIXO 45 site: nodule-facies C, fish Brotulidae *Typhlonus nasus* (POI 13) © Ifremer

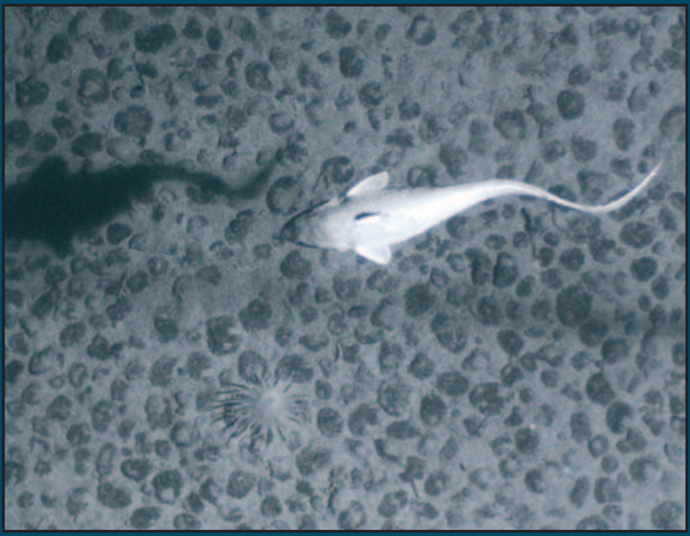


Fig.59. Photograph taken by the 'Épaulard' at the NIXO 45 site: nodule-facies C, fish Macrouridae *Coryphaenoides armatus* or *C. yaquinae* (POI 2) © Ifremer

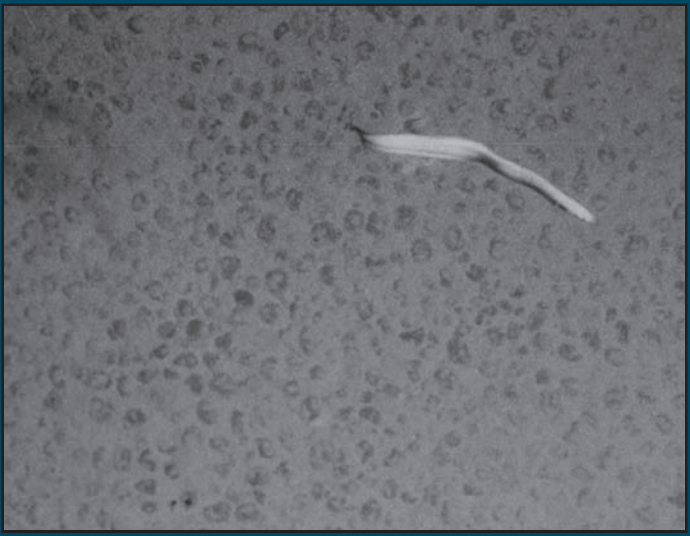


Fig.60. Photograph taken by the 'R.A.I.E.' at the NIXO 45 site: nodule-facies C, fish Synaphobranchidae (POI 8)

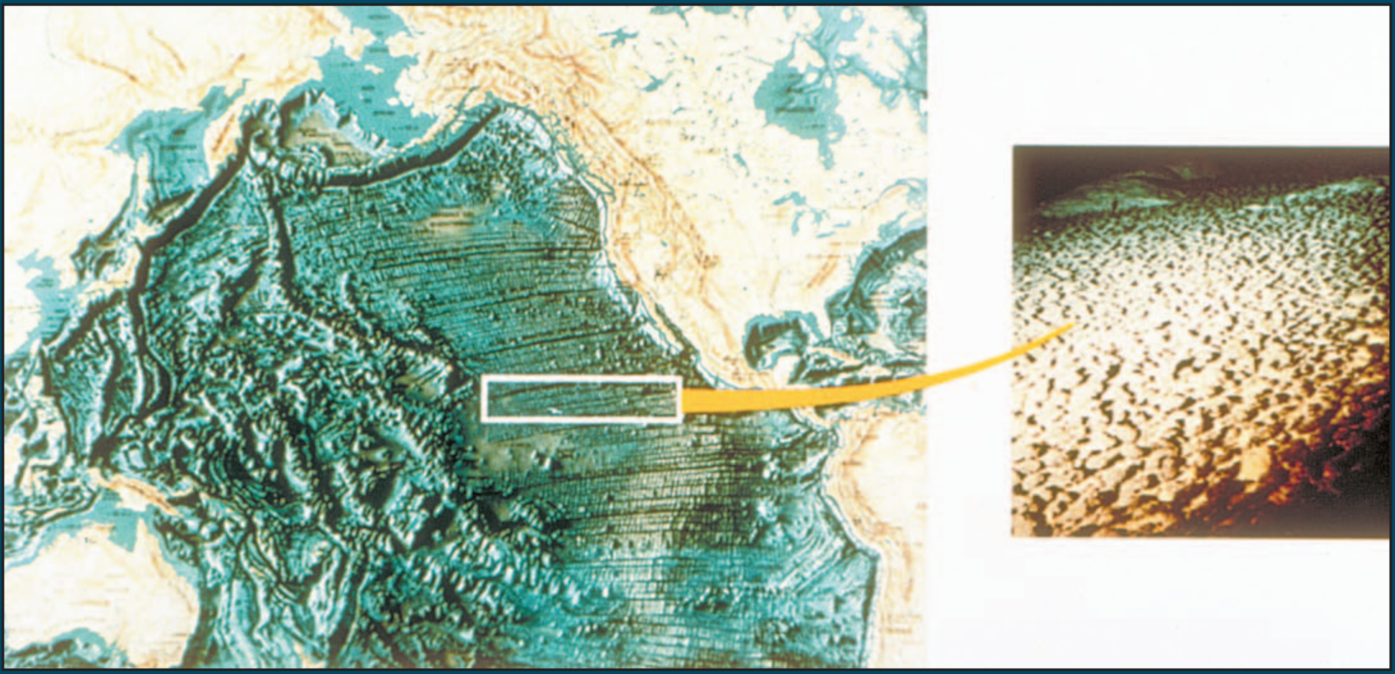


Fig.61. Location of deposits of polymetallic nodules in the Clarion-Clipperton fracture zone on a topographic map of the seabed of the Central North Pacific Ocean © Ifremer/GEMONOD

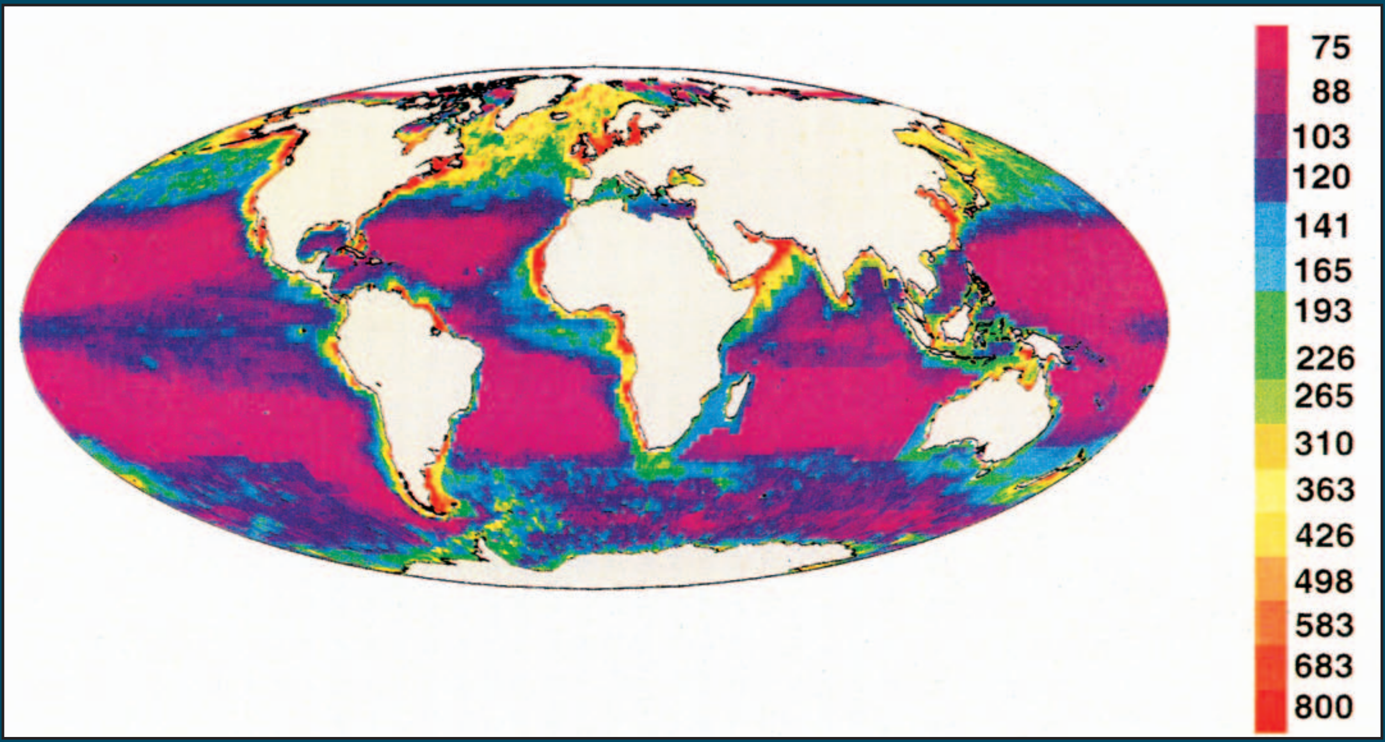
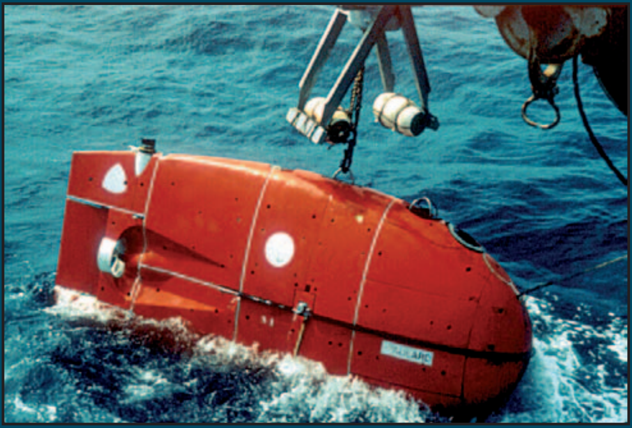


Fig.62. Geographical distribution on a world scale of the mean annual primary productivity (mg de C/m^2/y) calculated from C_{14} data (Longhurst *et al.* 1995) © Ifremer

Fig.63. Photograph of the remote submersible the ‘Épaulard’. © Ifremer



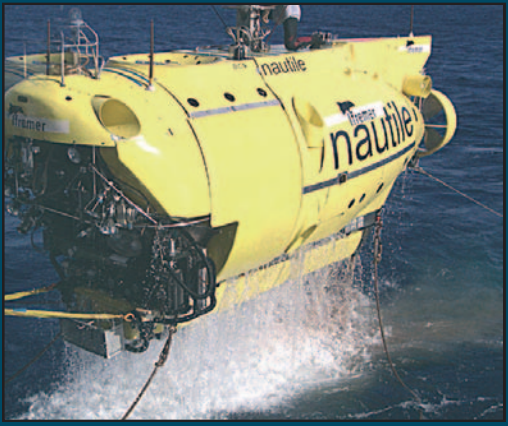


Fig.64. Photograph of the manned submersible “the Nautile”. © Ifremer

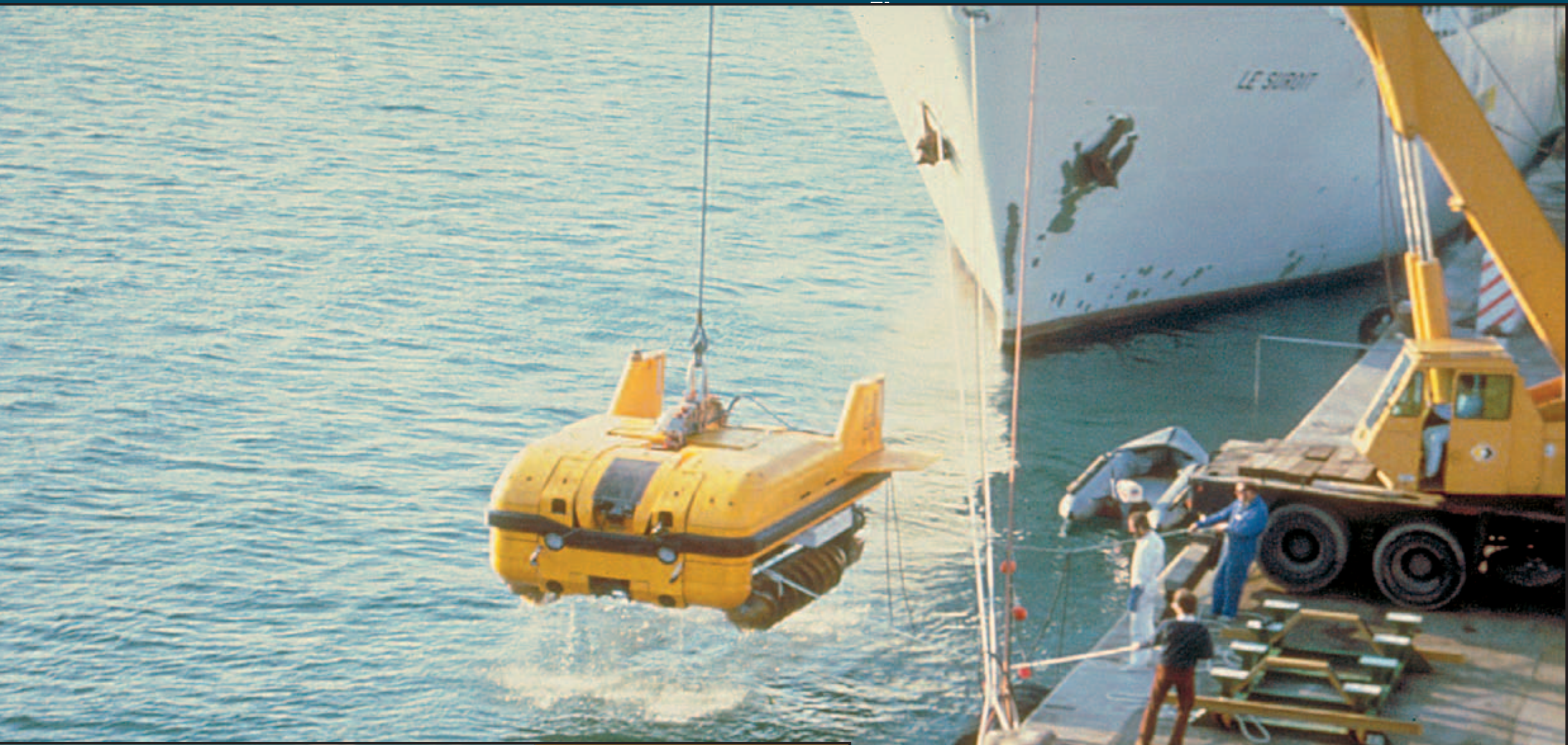


Fig.65. Photograph of the remote free-sampling device developed by Ifremer to collect polymetallic nodules © Ifremer

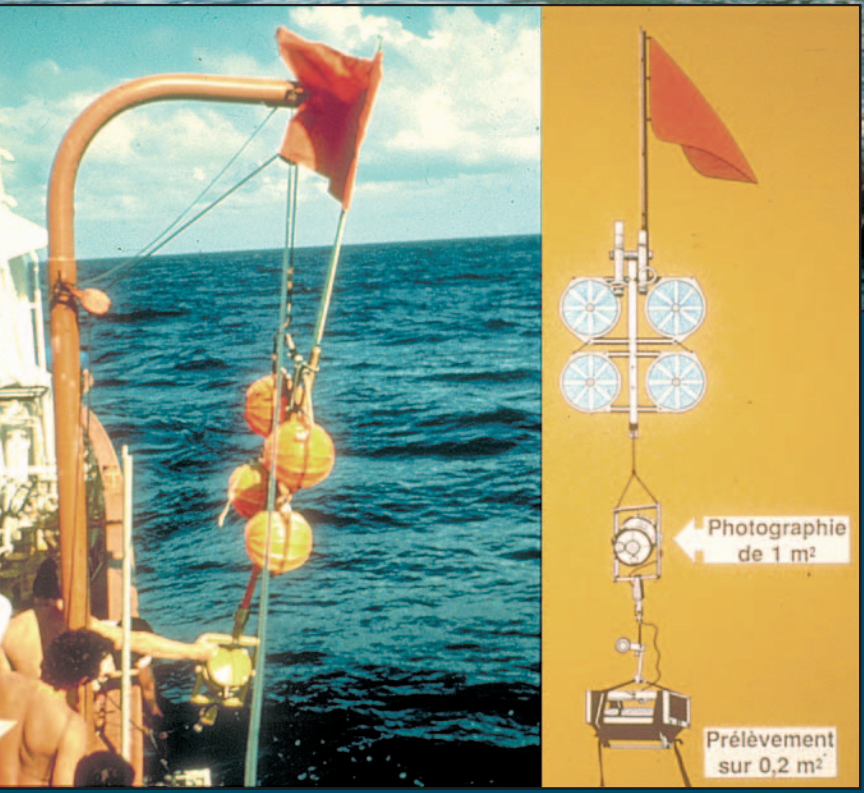


Fig.66. Diagram and photograph of the ‘ED1’ (camera coupled to a sampling device) © Ifremer

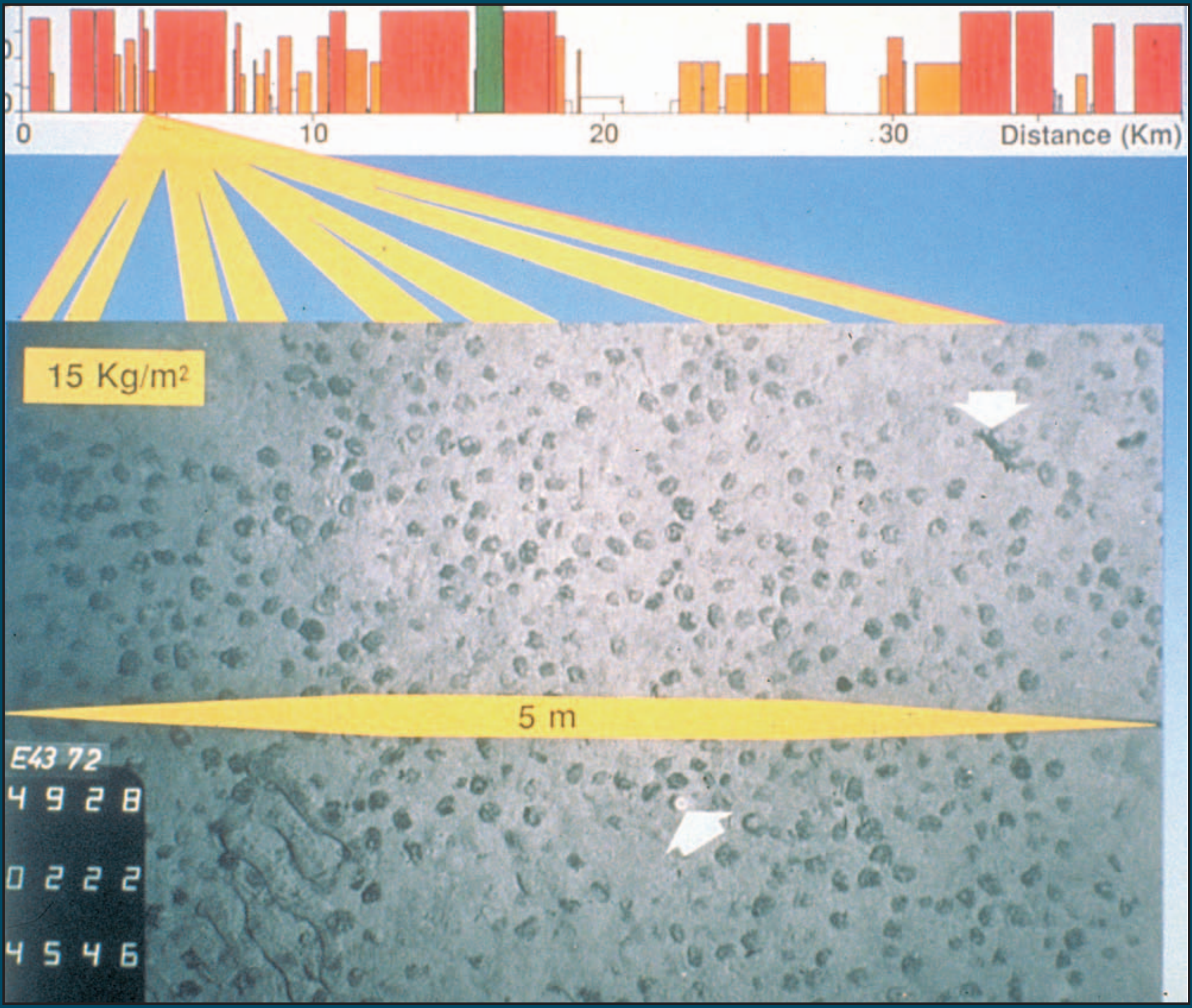


Fig.67. Example of a mineral bed with 15 kg of nodules per m^2. Megafauna indicated by white arrows © Ifremer

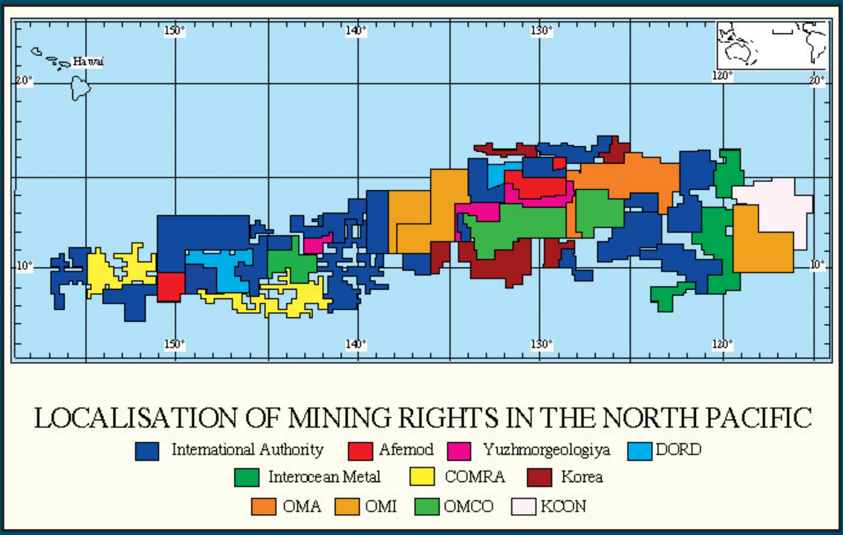
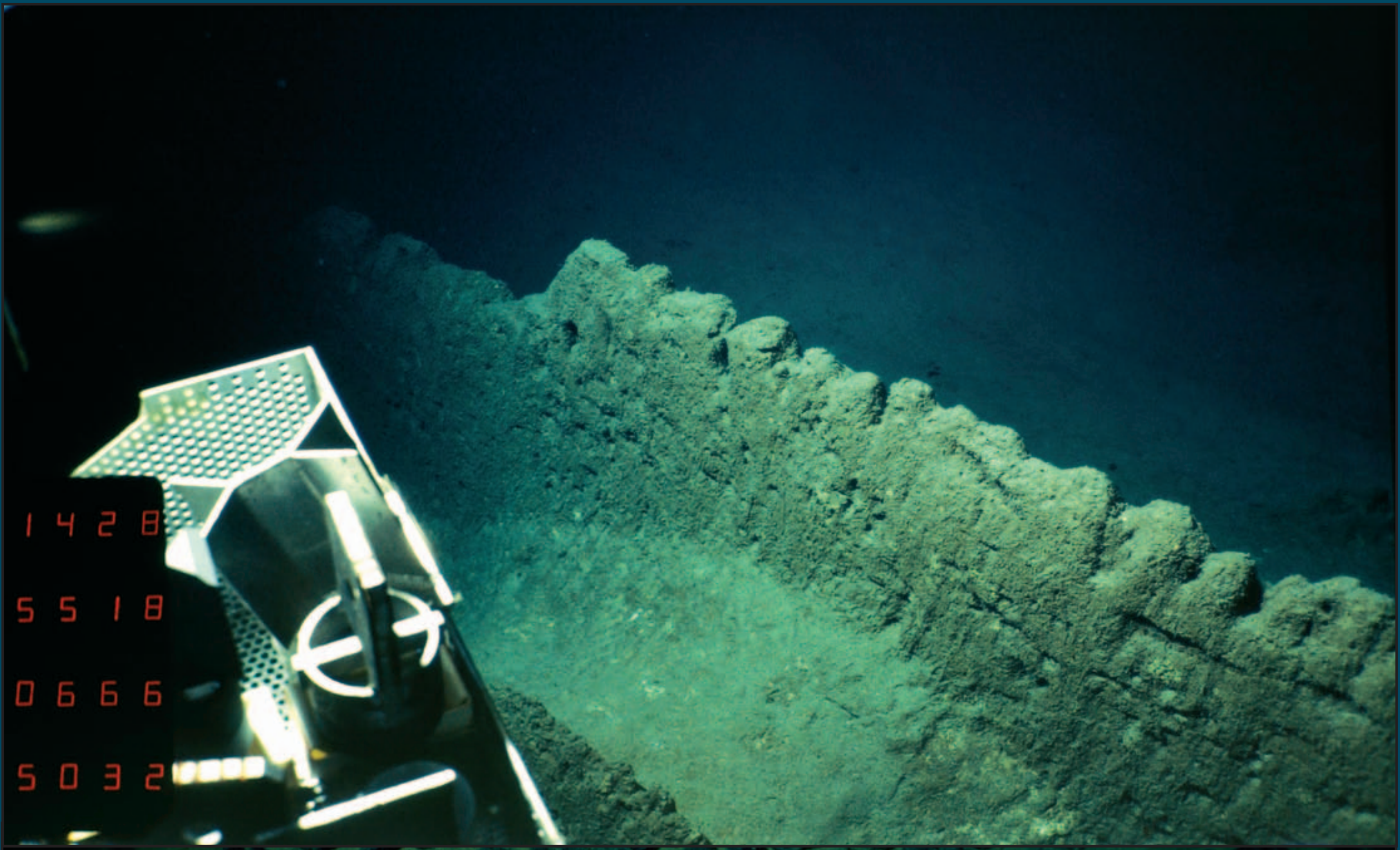


Fig.68. Areas covered by mining permits for the exploitation of polymetallic nodules in the equatorial eastern Pacific Ocean © Ifremer

Fig.69. Steps formed by the outcropping of hardened carbonated muds seen from "the Nautile" during the NIXONAUT cruise (PL 15) © Ifremer



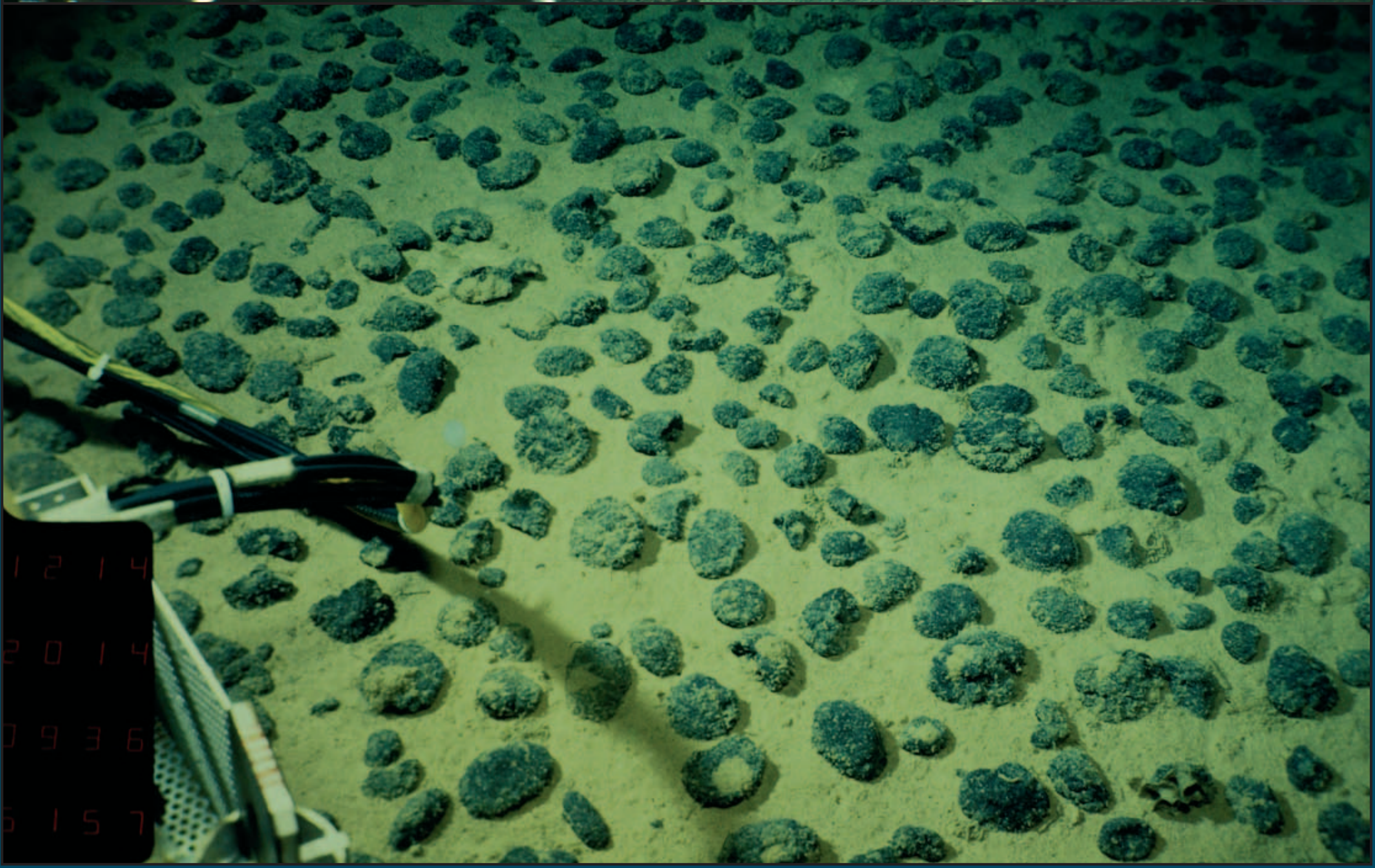


Fig.70. Nodule-facies C seen from "the Nautile" during the NIXONAUT cruise © Ifremer

Appendix II

List of codes based on the classification of Parker (1982)

XEN	Xenophyophora, Cl. Xenophyophorea, Supercl. Rhizopoda, Phyl. Protozoa
SPO	Sponges, Phyl. Porifera
HYD	Hydroids, O. Hydroidea, Cl. Hydrozoa, Phyl. Cnidaria
MED	Jellyfish, O. Coronatae and O. Semaeostoniae, Cl. Scyphozoa, Phyl. Cnidaria
SIF	Siphonophores, O. Siphonophora, Cl. Hydrozoa, Phyl. Cnidaria
OCT	Octocoralliarians, O. Gorgonacea and O. Pennatulacea, Cl. Anthozoa, Phyl. Cnidaria
CER	Ceriantharians, O. Ceriantharia, Cl. Anthozoa, Phyl. Cnidaria
CTEN	Ctenophorans, Phyl. Ctenophora
ANT	Antipatharians, O. Antipatharia, Cl. Anthozoa, Phyl. Cnidaria
ACT	Sea-anemones, O. Actinaria, Cl. Anthozoa, Phyl. Cnidaria
CEP	Cephalopods, Cl. Cephalopoda, Phyl. Mollusca
NUD	Nudibranchs, O. Nudibranchia, Cl. Gastropoda, Phyl. Mollusca
MOL	Molluscs, Phyl. Mollusca
POL	Polychaete worms, Cl. Polychaeta, Phyl. Annelida
SIP	Sipunculians, Phyl. Sipuncula
ECH	Echiurians, Phyl. Echiuria
PYC	Pycnogonids, Cl. Pycnogonida, Phyl. Arthropoda
PER	Peracarids, Super-O. Peracaridea, Cl. Crustacea, Phyl. Arthropoda
ISO	Isopods, O. Isopoda, Super-O. Peracaridea, Cl. Crustacea, Phyl. Arthropoda
DEC	Decapods, O. Decapoda, Super-O. Peracaridea, Cl. Crustacea, Phyl. Arthropoda
GAL	Galatheas, Fam. Galatheidea, Infra-O. Anomourea, O. Decapoda, Super-O. Peracaridea, Cl. Crustacea, Phyl. Arthropoda
CRI	Crinoids, Cl. Crinoïdea, Phyl. Echinodermata
AST	Seastars, Subcl. Somasteroïdea, Cl. Asteridae, Phyl. Echinodermata
OPH	Brittle stars, Subcl. Ophiuroidea, Cl. Asteridae, Phyl. Echinodermata
OUR	Sea urchins, Cl. Echinoidea, Phyl. Echinodermata
HOL	Sea cucumbers, Cl. Holothuridea, Phyl. Echinodermata
ENT	Epibenthic hemichordates, Cl. Enteropneusta, Phyl. Hemichordata
ASC	Ascidians, Cl. Ascidiacea, Subphyl. Tunicata, Phyl. Chordata
SAL	Salps, O. Salpidae, Cl. Thaliacea, Subphyl. Tuniciata, Phyl. Chordata
POI	Fish, Cl. Osteichthya, Subphyl. Vertebrata, Phyl. Chordata

Annexe III

LIST OF INTERNATIONAL SPECIALISTS CONSULTED

Phylum PROTOZOA	Cl. Xenophyophorea	A. Gooday	U.K.
		O. Kamenskaya	Federation of Russia
		L. Levin	U.K.
		C. Maybury	U.K.
		O. Tendal	Denmark
Phylum PORIFERA	Cl. Demospongiae	N. Boury-Esnault	Fr., Endume
	Cl. Hexactinellida	W. Hartman	E.U.
		V. Koltun	Federation of Russia
		C. Levi	Fr., Muséum
		D. Pawson	E.U.
		O. Tendal	Denmark
		J. Vacelet	Fr., Endume
Phylum CNIDARIA	Cl. Hydrozoa	J. Bouillon	Belgium
		J. Goy	Fr., Muséum
		M. Van Praët	Fr., Muséum
		W. Vervoort	Netherlands
	O. Siphonophora	C. Carré	Fr., Villefranche s/mer
		F. Pagès	Spain
		P. Pugh	U.K.
	Cl. Scyphozoa	J. Bouillon	Belgium
	Cl. Anthozoa	F.M. Bayer	E.U.
	subcl. Alcyonaria	M. Grasshoff	Fed. Rep. of Germany
	O. Gorgonacea	M.J. d'Hondt	Fr., Muséum
	O. Pennatulacea	M. Opresko	E.U.
		H. Zibrowius	(Fr., Endume)
	subcl. Zoantharia	D. Doumenc	(Fr., Muséum)
	O. Actinaria	D. Fautin	E.U.
		K. Riemann-Zürneck	Fed. Rep. of Germany
		M. Sokolova	Federation of Russia
		O. Zezina	Federation of Russia
		H. Zibrowius	Fr., Endume
	O. Scleractinia	H. Zibrowius	Fr., Endume
	O. Antipatharia	M. Grasshoff	Fed. Rep. of Germany
		M.J. d'Hondt	Fr., Muséum
		M. Opresko	E.U.
		H. Zibrowius	Fr., Endume
	O. Ceriantharia	D. Doumenc	Fr., Muséum
		D. Fautin	E.U.
		K. Riemann-Zürneck	Fed. Rep. of Germany
		H. Zibrowius	Fr., Endume
Phylum CTENOPHORA		C. Carré	Fr., Villefranche s/mer

Phylum ANNELIDA	Cl. Polychaeta	C. Bussau	Fed. Rep. of Germany
		D. Desbruyères	Fr., Ifremer
		L. Laubier	Fr., Ifremer
		T. Miura	Japan
		F. Pleijel	Sweden
		E. Southward	U.K.
Phylum ECHIURA		S. Edmonds	Australia
		S. Ohta	Japan
		C. Smith	E.U.
Phylum SIPUNCULA		C. Bussau	Fed. Rep. of Germany
		E. Cutler and N. Cutler	E.U.
		P. Gibbs	U.K.
		M. Rice	E.U.
Phylum MOLLUSCA	Cl. Bivalvia	P. Bouchet	Fr., Muséum
		M. Rex	E.U.
		A. Waren	Sweden
	Cl. Gastropoda	P. Bouchet	Fr., Muséum
		M. Rex	E.U.
		A. Waren	Sweden
	O. Nudibranchia	C. Poizat	Fr., Marseille
		R. Turner	E.U.
	Cl. Cephalopoda	G. Aldred	U.K.
		S. von Boletzky	Fr., Banyuls
		M. Clarke	U.K.
		T. Kubodera	Japan
		M. NIXOn	U.K.
		T. Okutani	Japan
		C. Roper	E.U.
		N. Voss	E.U.
		R. Young	E.U.
Phylum ARTHROPODA			
Subph. CHELICERATA	Cl. Pycnogonida	C. Allan Child	E.U.
		M. de Saint Laurent	Fr., Muséum
		J. Stock	Netherlands
		M. Türkay	Fed. Rep. of Germany
Subph. CRUSTACEA	Super O. Peracarida	J. Svavarsson	Iceland
		M. Türkay	Fed. Rep. of Germany
	O. Mysidacea	J.P. Lagardère	Fr., Endume
	O. Cumacea	M. Ledoyer	Fr., Endume
	O. Tanaidacea	C. Allan Child	E.U.
		A.B. Williams	E.U.
	O. Isopoda	C. Allan Child	E.U.
		R. Hessler	E.U.
		J. Stromberg	Sweden
		J. Svavarsson	Iceland
		D. Thistle	E.U.

		A.B. Williams	E.U.
		G. Wilson	Australia
	O. Amphipoda	Ph. Laval	Fr., Villefranche s/mer
	subo. Hyperiidea		
	O. Decapoda	C. Allan Child	E.U.
	Natantia	A. Crosnier	Fr., Muséum
		J.P. Lagardère	Fr., Endume
		M. Türkay	Fed. Rep. of Germany
		A.B. Williams	E.U.
	Reptantia	C. Allan Child	E.U.
		A. Crosnier	Fr., Muséum
		I. Gordon	U.K.
		J.P. Lagardère	Fr., Endume
	Reptantia (suite)	M. de Saint Laurent	Fr., Muséum
		J. Stock	Netherlands
		M. Türkay	Fed. Rep. of Germany
		A.B. Williams	E.U.
Phylum ECHINODERMATA			
Subph. CRINOZOA	Cl. Crinoidea	A. Clark	U.K.
		J. Durham	E.U.
		D. Pawson	E.U.
		M. Roux	Fr., Reims
Subph. ASTEROZOA	Cl. Stelleroidea	D. Blake	E.U.
	subcl. Asteroidea	A. Clark	U.K.
		L. Maluf	E.U.
		D. Pawson	E.U.
		M. Sibuet	Fr., Ifremer
	subcl. Ophiuroidea	A. Clark	U.K.
	O. Ophiurida	G. Hendler	E.U.
		L. Maluf	E.U.
		D. Pawson	E.U.
		M. Sibuet	Fr., Ifremer
Subph. ECHINOZOA	Cl. Echinoidea	A. Gebruk	Federation of Russia
		G. Hendler	E.U.
		D. Pawson	E.U.
		M. Roux	Fr., Reims
		M. Sibuet	Fr., Ifremer
	Cl. Holothuroidea	D. Billett	U.K.
		R.S. Carney	E.U.
		A. Gebruk	Federation of Russia
		M. Jangoux	Belgium
		L. Maluf	E.U.
		C. Massin	Belgium
		D. Pawson	E.U.
		M. Sibuet	Fr., Ifremer
Phylum HEMICHORDATA	Cl. Enteropneusta	M. Romero-Wetzel	Federation of Russia
		E. Southward	U.K.

Phylum CHORDATA			
Subph. TUNICATA	Cl. Ascidiacea	L. Cole	E.U.
		C. Monniot	Fr., Muséum
		F. Monniot	Fr., Muséum
	Cl. Thaliacea	J.C. Braconnot	Fr., Villefranche s/mer
Subph. VERTEBRATA	Cl. Osteichthyes	E. Anderson	South Africa
		P. Castle	New Zealand
		D. Cohen	E.U.
		P. Geistdoerfer	Fr., Muséum
		T. Iwamoto	E.U.
		N. Merrett	U.K.
		J. Nielsen	Denmark
		B. Seret	Fr., Muséum
	Cl. Mammalia	G. Demuizan	Peru
		E. Hussenot	Fr., Brest
		D. Robineau	Fr., Muséum

COMPARISON OF THE TAXONOMIC RICHNESS OF THE STUDY AREA WITH THE ABYSSAL ZONE OF THE WORLD'S OCEANS

TAXONOMIC RICHNESS PER PHYLUM IN THE CCFZ		NUMBER OF FAMILIES IN THE CCFZ	TOTAL NUMBER OF FAMILIES RECORDED IN THE ABYSSAL REALM	NUMBER AND DESIGNATION OF THE FAMILIES OTHER THAN THOSE REPORTED IN THE CCFZ WHICH COULD BE FOUND IN THE INFERIOR ABYSSAL REALM (3000m-6000m)			BIBLIOGRAPHIC REFERENCES
PROTOZOA (Xenophyophorea)	12	5	5				Tendal, 1972
PORIFERA	38	10	14	4	Cl. Desmospongiae	F. Mycalidae F. Chondrocladiidae F. Polymastiidae F. Theneidae	Birstein and Belyaev, 1955; Koltun, 1969; Lévi, 1964, 1972-1973; Zenkevitch, 1964
CNIDARIA	59	32	43(minimum)	11			
Scyphozoa	9	7	7 (minimum)				
Hydrozoa	12	8	12	4	O. Hydroida	F. Cytaeidae F. Campanulinidae F. Lafoeidae F. Sertulariidae	
Anthozoa	38	17	24	7	O. Stolonifera	F. Clavulariidae	Belyaev et Sokolova, 1960a; Carlgren, 1956; Kramp, 1956, 1959; Lemche et al., 1976; Madsen, 1956a; Menzies et al., 1973; Pasternak, 1958, 1960a, 1964, 1970, 1975; Tixier-Durivault, 1964; Vervoort, 1966
					O. Pennatulacea	F. Kophobelemnidae F. Pennatulidae F. Chunellidae F. Protoptilidae	
					O. Actinaria	F. Galantheanthemidae	
					O. Scleractinia	F. Fungiidae	
CTENOPHORA	2	1 (minimun)	1(minimum)	?			

COMPARISON OF THE TAXONOMIC RICHNESS OF THE STUDY AREA with the abyssal ZONE OF THE WORLD'S OCEANS

TAXONOMIC RICHNESS PER PHYLUM IN THE CCFZ		NUMBER OF FAMILIES IN THE CCFZ	TOTAL NUMBER OF FAMILIES RECORDED IN THE ABYSSAL REALM	NUMBER AND DESIGNATION OF THE FAMILIES OTHER THAN THOSE REPORTED IN THE CCFZ WHICH COULD BE FOUND IN THE INFERIOR ABYSSAL REALM (3000m-6000m)			BIBLIOGRAPHIC REFERENCES
MOLLUSCA	13	10	41(sans Ceph.)	31			
Gasteropoda	8	4 (minimun)	9	5	O. Planilabiata	F. Bathyphytophilidae	
					O. Archaeogasteropoda	F. Cocculinidae	
					O. Cephalaspidea	F. Philinidae F. Scaphandridae F. Trochidae	
Bivalvia	2	1	21	20	O. Nuculoida	F. Malletiidae F. Ledellidae F. Nuculidae F. Nuculanidae	
					O. Solemyoida	F. Solemyidae	
					O. Arcoida	F. Arcidae F. Limopsidae	
					O. Ostreoida	F. Ostreidae F. Pectinidae	
					O. Veneroida	F. Montacutidae F. Scrobiculariidae F. Kelliellidae F. Galatheavalvidae	Clarke, 1960, 1961, 1962a, 1962b; Bouchet et Waren, 1979, 1985;Filatova, 1960; Knudsen, 1964, 1970; Okutani, 1974; Minidier, 1969; Voss, 1967, 1969; 1988; Voss et Pearcy, 1990; Wolff, 1958, 1960, 1961
					O. Myoida	F.Mytilidae F. Poladomyidae F. Poromyidae F. Cuspidariidae F. Teredinidae F. Pholadidae F. Verticordiidae	

COMPARISON OF THE TAXONOMIC RICHNESS OF THE STUDY AREA with the abyssal ZONE OF THE WORLD'S OCEANS							
TAXONOMIC RICHNESS PER PHYLUM IN THE CCFZ	Z	NUMBER OF FAMILIES IN THE CCFZ	TOTAL NUMBER OF FAMILIES RECORDED IN THE ABYSSAL REALM e	NUMBER AND DESIGNATION OF THE FAMILIES OTHER THAN THOSE REPORTED IN THE CCFZ WHICH COULD BE FOUND IN THE INFERIOR ABYSSAL REALM (3000m-6000m)			BIBLIOGRAPHIC REFERENCES
Cephalopoda	2	4	7	3	O. Teuthoidea	F. Histioteuthidae	
					O. Vampyromorpha	F. Vampyroteuthidae	
					O. Octopoda	F. Bolitaenidae subF. Bathypolypodinae subF. Graneledoninae	
Scaphopoda	1	1 (minimun)	4	3	O. Dentaliida	F. Dentaliidae	
					O. Gadilida	F. Pulsellidae F. Siphonodentaliidae	
ANNELIDA (Polychaeta)	11	9	38	29	O. Phyllodocida	F. Sigalionidae F. Phyllodocidae F. Nereidae F. Nephtydidae F. Alciopidae F. Sphaerodoridae F. Glyceridae	Ushako, 1953, 1955; Kirkegaard, 1956; Levenstein, 1971, 1972; Jumars, 1974; Pasternak, 1975; Bailey-Brock et Knight-Jones, 1976; Fauchald, 1977; Desbruyères, 1980; Levenstein, 1984; Kolmer, 1985; Desbruyères et al., 1985; Borowski, 1995
					O. Amphinomida	F. Euphrosinidae	
					O. Eunicida	F. Dorvilleidae F. Onuphiidae F. Lumbrineridae F. Dorvilleidae F. Eunicidae	
					O. Orbiniida	F. Orbiniidae	
					O. Spionida	F. Spionidae	
					O. Chaetopterida	F. Chaetopteridae	

COMPARISON OF THE TAXONOMIC RICHNESS OF THE STUDY AREA with the abyssal ZONE OF THE WORLD'S OCEANS

TAXONOMIC RICHNESS PER PHYLUM IN THE CCFZ		NUMBER OF FAMILIES IN THE CCFZ	TOTAL NUMBER OF FAMILIES RECORDED IN THE ABYSSAL REALM	NUMBER AND DESIGNATION OF THE FAMILIES OTHER THAN THOSE REPORTED IN THE CCFZ WHICH COULD BE FOUND IN THE INFERIOR ABYSSAL REALM (3000m-6000m)			BIBLIOGRAPHIC REFERENCES
ANNELIDA (Polychaeta) *(suite)*					O. Flabelligerida	F. Chloraemidae F. Flabelligeridae F. Fauveliopsidae F. Acrocirridae	
					O. Ophelida	F. Scalibregmidae F. Ophelidae	
					O. Captellida	F. Capitellidae	
					O. Oweniida	F. Oweniidae	
					O. Terebellida	F. Ampharetidae F. Trichobranchidae	
					O. Sabellida	F. Sabellidae F. Serpulidae F. Spirorbidae	
ECHIURA	6	1	1	-			Bruun, 1953, 1956b; Zenkevitch, 1964, 1966; Wolff, 1976b; Datta Gupta, 1977, 1981; Wolff, 1979.
SIPUNCULA	1	2	4	2		F. Phascolosmatidae F. Aspidosiphonidae	Murina, 1957, 1961, 1964; Cutler et Cutler, 1980.
ARTHROPODA	20	12	58	46			
Pycnogonida	2	2	6	4		F. Nymphonidae F. Austrodecidae F. Endeidae F. Ammotheidae	

COMPARISON OF THE TAXONOMIC RICHNESS OF THE STUDY AREA with the abyssal ZONE OF THE WORLD'S OCEANS

TAXONOMIC RICHNESS PER PHYLUM IN THE CCFZ		NUMBER OF FAMILIES IN THE CCFZ	TOTAL NUMBER OF FAMILIES RECORDED IN THE ABYSSAL REALM	NUMBER AND DESIGNATION OF THE FAMILIES OTHER THAN THOSE REPORTED IN THE CCFZ WHICH COULD BE FOUND IN THE INFERIOR ABYSSAL REALM (3000m-6000m)			BIBLIOGRAPHIC REFERENCES
Crustacea	18	10	52	42	O. Cumacea	F. Lampropidae	Nordenstamm, 1955; Schellenberg, 1955; Turpaeva, 1956; Wolff, 1956b; Dahl, 1959; Wolff, 1962; Suyehiro et al., 1962; Birstein, 1963a; Barnard, 1964; Kudinova-Pasternak, 1965; Pasternak, 1966; Margulis, 1967; Franckenberg, 1968; Jones, 1969; Kudinova-Pasternak, 1970; Turpaeva, 1971; Menzies, 1972; Turpaeva, 1974; Wolff, 1976b; Lemche et al. 1976; Kudinova-Pasternak, 1977, 1978; Hessler et al., 1978; Hessler et al., 1979; Kensley, 1982; Gamo, 1983; Shin, 1984; Lincoln, 1985; Child, 1992; Child et Segonzac, 1996; Bamber, 2000; 2004.
						F. Bodotriinae	
						F. Vaunthompsoniinae	
						F. Diastylidae	
					O. Tanaidacea	F. Apseudidae	
						F. Neotanaidae	
						F. Paratanaidae	
						F. Pseudotanaidae	
						F. Agathotanaidae	
						F. Leptognathiidae	
						F. Paratanaidae	
						F. Anarthruridae	
					O. Isopoda		
					subO. Anthuridea	F. Anthuridae	
						F. Paranthuridae	
					subO. Valvifera	F. Arcturidae	
					subO. Asellota	F. Desmosomatidae	
						F. Echinothambematidae	
						F. Eurycopidae	
						F. Haploniscidae	
						F. Janirellidae	
						F. Ilyarachnidae	
						F. Ischnomesidae	
						F. Macrostylidae	
						F. Jaeropsidae	
						F. Munnidae	
						F. Janiridae	
						F. Mesosignidae	
						F. Nannoniscidae	
						F. Thambematidae	
						F. Abyssianiridae	
						F. Acanthaspidae	
						F. Dendrotionidae	
						F. Haplomunnidae	

COMPARISON OF THE TAXONOMIC RICHNESS OF THE STUDY AREA with the abyssal ZONE OF THE WORLD'S OCEANS

TAXONOMIC RICHNESS PER PHYLUM IN THE CCFZ		NUMBER OF FAMILIES IN THE CCFZ	TOTAL NUMBER OF FAMILIES RECORDED IN THE ABYSSAL REALM	NUMBER AND DESIGNATION OF THE FAMILIES OTHER THAN THOSE REPORTED IN THE CCFZ WHICH COULD BE FOUND IN THE INFERIOR ABYSSAL REALM (3000m-6000m)			BIBLIOGRAPHIC REFERENCES
Crustacea *(suite)*					O. Amphipoda	F. Phoxocephalidae	
					subO. Gammaridea	F. Ampeliscidae	
						F. Dexaminidae	
						F. Hyperiopsidae	
						F. Pardaliscidae	
						F. Stegocephalidae	
						F. Vitjazianidae	
						F. Hyperiidae	
					subO. Hyperiidea	F. Scinidae	
BRACHIOPODA	1	2 (minimun)	2(minimum)	?			
ECHINODERMATA	46	18	45	27			Koehler, 1909; Clark, 1920; Madsen, 1947-1948 ; Mortensen, 1951; Madsen, 1951, 1956 ; Gilsen, 1956; Hansen, 1956; Madsen, 1961; Belyaev et Vinogradova, 1961a; Menzies, 1963; Cherbonnier, 1964; Cherbonnier et Sibuet, 1972; Hansen, 1975; Ushakov, 1975; Macurda et Meyer, 1976; Lemche et al., 1976; Roux, 1980; Luke, 1982; Paterson, 1985; Bluhm et Gebruk, 1999.
Crinoidea	3	3	6	3	O. Bouergueticrinida	F. Phrynocrinidae	
						F. Porphyrocrinidae	
						F. Bourgueticrinidae	
Stelleroidea	8	5	8	3	O. Paxillosida	F. Astropectinidae	
					O. Valvatida	F. Goniasteridae	
					O. Spinulosida	F. Myxasteridae	
Ophiuroidea	2	2	10	8	O. Phrynophiurida	F. Euryalidae	
						F. Ophiomyxidae	
						F. Trichasteridae	
					O. Ophiurida	F. Ophiacanthidae	
						F. Ophioleucidae	
						F. Ophiactidae	
						F. Ophiodermatidae	
						F. Ophiolepididae	

COMPARISON OF THE TAXONOMIC RICHNESS OF THE STUDY AREA with the abyssal ZONE OF THE WORLD'S OCEANS							
TAXONOMIC RICHNESS PER PHYLUM IN THE CCFZ		NUMBER OF FAMILIES IN THE CCFZ	TOTAL NUMBER OF FAMILIES RECORDED IN THE ABYSSAL REALM	NUMBER AND DESIGNATION OF THE FAMILIES OTHER THAN THOSE REPORTED IN THE CCFZ WHICH COULD BE FOUND IN THE INFERIOR ABYSSAL REALM (3000m-6000m)			BIBLIOGRAPHIC REFERENCES
Echinoidea	2	2	9	7	O. Cidaroida	F. Cidaridae	
					O. Echinothurioida	F. Echinothuridae	
					O. Spatangoida	F. Holasteridae F. Pourtalesiidae F. Hemiasteridae F. Loveniidae F. Urechninidae	
Holothuriodea	31	6	12	6	O. Dendrochirotida	F. Cucumariidae	
					O.Dactylochirotida	F. Ypsilothuriidae	
					O. Apoda	F. Myriotrochidae F. Synaptidae	
					O. Molpadida	F. Molpadiidae F. Gephyrothuriidae	
HEMICHORDATA	4	3	3	?			Bourne et Heezen, 1965 ; Mauviel et al., 1987.
CHORDATA	27	18	26				
Tunicata	10	8	11	3	O. Phlebobranchiata	F. Octacnemidae	
					O. Stolidobranchia	F. Hexacrobylidae F. Styelidae	Grey, 1954; Nybelin, 1957; Millar, 1959; Nielsen, 1964; Rass et al., 1975; Lemche et al., 1976; Monniot et Monniot, 1978; Merret et Marshall, 1981; Okutami, 1982; Pearcy et al., 1982 ; Geistdoerfer, 1986, 1991 ; Smith et Brown, 2002.

COMPARISON OF THE TAXONOMIC RICHNESS OF THE STUDY AREA with the abyssal ZONE OF THE WORLD'S OCEANS

TAXONOMIC RICHNESS PER PHYLUM IN THE CCFZ		NUMBER OF FAMILIES IN THE CCFZ	TOTAL NUMBER OF FAMILIES RECORDED IN THE ABYSSAL REALM	NUMBER AND DESIGNATION OF THE FAMILIES OTHER THAN THOSE REPORTED IN THE CCFZ WHICH COULD BE FOUND IN THE INFERIOR ABYSSAL REALM (3000m-6000m)			BIBLIOGRAPHIC REFERENCES
Vertebrata	17	10	18	8	O. Anguilliformes	F. Nettastomatidae	
					O. Salmoniformes	F. Alepocephalidae F. Bathylagidae	
					O. Myctophiformes	F. Chlorophtalmidae	
					O. Gadiformes	F. Zoarcidae F. Aphyonidae	
					O. Beryciformes	F. Stephanoberycidae	
					O. Scorpaeniformes	F. Liparididae	

Appendix V

CLASSIFICATION OF THE ABYSSAL SUPRABENTHIC MEGAFAUNA ACCORDING TO TROPHIC AND FUNCTIONAL GROUPS

CLASSIFICATION OF THE ABYSSAL SUPRABENTHIC MEGAFAUNA BY TROPHIC AND FUNCTIONAL GROUPS			
Suspension feeders group			
Sessiles		Mobiles	
Taxonomic identification and bibliographic references	Number of taxons	Taxonomic identification and bibliographic references	Number of taxons
PORIFERA Bames, 1968; Bergquist, 1978; Brien et al., 1973; Hartman, 1982; Jørgensen, 1966	38 Taxons		
CNIDARIA Cl. Anthozoa, O. Gorgonacea, O. Pennatulacea Bames, 1968; Lewis, 1982; Tixier-Durivault, 1987 O. Ceriantharia Tiffon, 1987. O. Antipatharia Grasshof, 1981; Pax et al., 1987 O. Actinaria, principalement suspensivore sauf F. Actinoscyphiidae: *Actinoscyphia sp*, *Phelliactes sp* et F. Actinostolidae : *Sicyonis tuberculata* (ambivalents détritivores/suspensivores) Aldred et al., 1979; Lampitt et Paterson, 1987; Riemann-Zümeck, 1978;	9 taxons 1 taxon 10 taxons 15 taxons (dont 3 taxons ambivalents suspens./détrit./carnivore)	CNIDARIA - O. Corallimorpharia, F. Nectactis singularis Riemann-Zümeck, 1979. - O. Actinaria, F. Actinostolidae *Actinostola sp.* F. Actiniidae Riemann-Zümeck (com. pers.)	2 taxons 2 taxons 1 taxon (dont 3 taxons ambivalents suspens./détrit.)
ANNELIDA Cl. Polychaeta, O. Sabellida, F. Sabellidae, O. Terebillida, F. Sabellariidae O. Capitellida, F. Maldanidae Hessler et Jumars, 1974; Fauchald et Jumars, 1979; Jumars et Fauchald, 1977	1 taxon 1 taxon 1 taxon (ambivalent suspens./détrit.)		
		MOLLUSCA - Cl. Bivalvia, O.Veneroida, F. Vesicomyidae Allen et Morgan, 1981; Allen et Sanders, 1982; Boss, 1982; Knudsen, 1970; Morton, 1981,1983, 1987; Olivier, 1979; Poutiers, 1984; Reid et Reid, 1974; Sanders et Allen, 1973, 1985	2 taxons

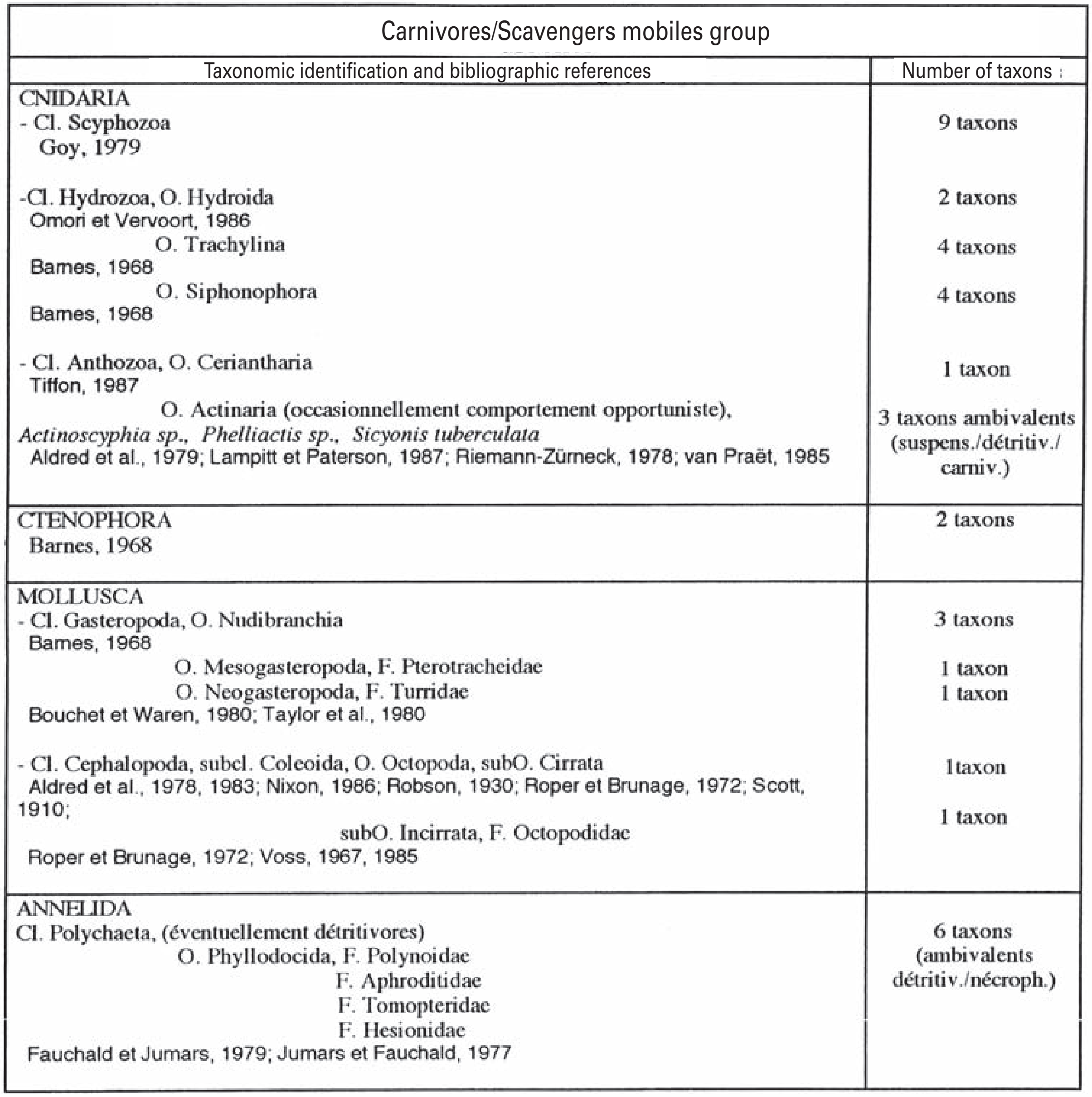
CLASSIFICATION OF THE ABYSSAL SUPRABENTHIC MEGAFAUNA BY TROPHIC AND FUNCTIONAL GROUPS			
Suspension feeders group			
Sessiles		Mobiles	
Taxonomic identification and bibliographic references	Number of taxons	Taxonomic identification and bibliographic references	Number of taxons
ARTHROPODA Cl. Crustacea, subcl. Cirripedia, O. Thoracica, F. Scalpellida Newman, 1967, 1974	1 taxon		
BRACHIOPODA O. Rhynchonellida O. Terebratulida Zezina, 1975.	1 taxon		
ECHINODERMATA Cl. Crinoidea (rheophiles), O. Millericrinida, F. Hyocrinidae O. Bouergueticrinida, F. Bathycrinidae, F. Phrynocrinidae, F. Porphyrocrinidae Fujita et al., 1987; Macurda and Meyer, 1976; Meyer, 1982; Roux, 1985	2 taxons	ECHINODERMATA - Cl. Crinoidea, O. Comatulida, superF. Antedonacea, F. Antedonidae Meyer, 1982. - Cl. Stelleroidea, subcl. Asteroidea, O. Forcipulata, F. Brisingidae principalement suspensivore Carey, 1972 - Cl. Stelleroidea, subcl. Ophiuroidea, O. Ophiuridea, subO. Chilophiurina, F. Ophiuridae (principalement suspensivore) subO. Gnathophiurina, F. Amphiuridae Fujita, 1988; Hendler, 1982; Litvinova et Sokolova, 1971; Ohta, 1988; Paterson et al., 1985; Pearson et Gage, 1984; Tyler, 1980; Warner, 1982; Woodley, 1975	1 taxon 3 taxons 2 taxons
CHORDATA subph Tunicata Cl. Ascidiacea, O. Stolidobranchia, F. Pyuridae, F. Molgulidae Incertae sedis Jørgensen, 1966; Monniot et Monniot, 1975	4 taxons		

Detritus feeders group			
Sessiles		Mobiles	
Taxonomic identification and bibliographic references	Number of taxons	Taxonomic identification and bibliographic references	Number of taxons
CNIDARIA O. Actinaria, F. Actinoscyphiidae, *Actinoscyphia sp.* occasionnellement détritivore (comportement opportuniste) F. Hormathiidae, *Phelliactis sp.* F. Actinostolidae, *Sicyonis tuberculata* Aldred et al., 1979; Lampitt et Paterson, 1987; Riemann-Zurnëck, 1978; van Praët, 1982, 1985, 1990	3 taxons ambivalents (suspens./détrit./carnivore)	CNIDARIA O. Actinaria, F. Boloceroididae *Bolocera sp.* van Praët, 1985. F. Actinostolidae *Actinostola sp.* van Praët, 1985. F. Actiniidae Riemann-Zurnëck (com. pers.): ces actinies peuvent glisser sur les sédiments	1 taxon 2 taxons 1 taxon
ANNELIDA Cl. Polychaeta, O. Capitellida, F. Maldanidae O. Cirratulida, F. Cirratulidae Fauchald et Jumars, 1979	1 taxon (ambivalent détrit./suspens.) 1 taxon	ANNELIDA Cl. Polychaeta, O. Terebellida, F. Terebellidae (peuvent quitter leurs tubes) Fauchald et Jumars, 1979. (ambivalents détrit./nécroph.), O. Phyllodocida, F. Polynoidae F. Aphroditidae F. Tomopteridae F. Hesionidae Fauchald et Jumars, 1979; Jumars et Fauchald, 1977;	1 taxon ambivalent (sédentaire/mobile) 6 taxons (ambivalents détrit./nécroph.)
ECHIURA O. Echiuroinea, F. Bonelliidae Datta Gupta, 1981; Dawydoff, 1959; Jaccarini et Schembri, 1977; Ohta, 1984; Zenkevitch, 1966	6 taxons		
SIPUNCULA F. Golfingiida, F. Sipunculidae Cutler et Cutler, 1980; Romero-Wetzel, 1987; Thomson, 1980; Vinogradov, 1953.	1 taxon		

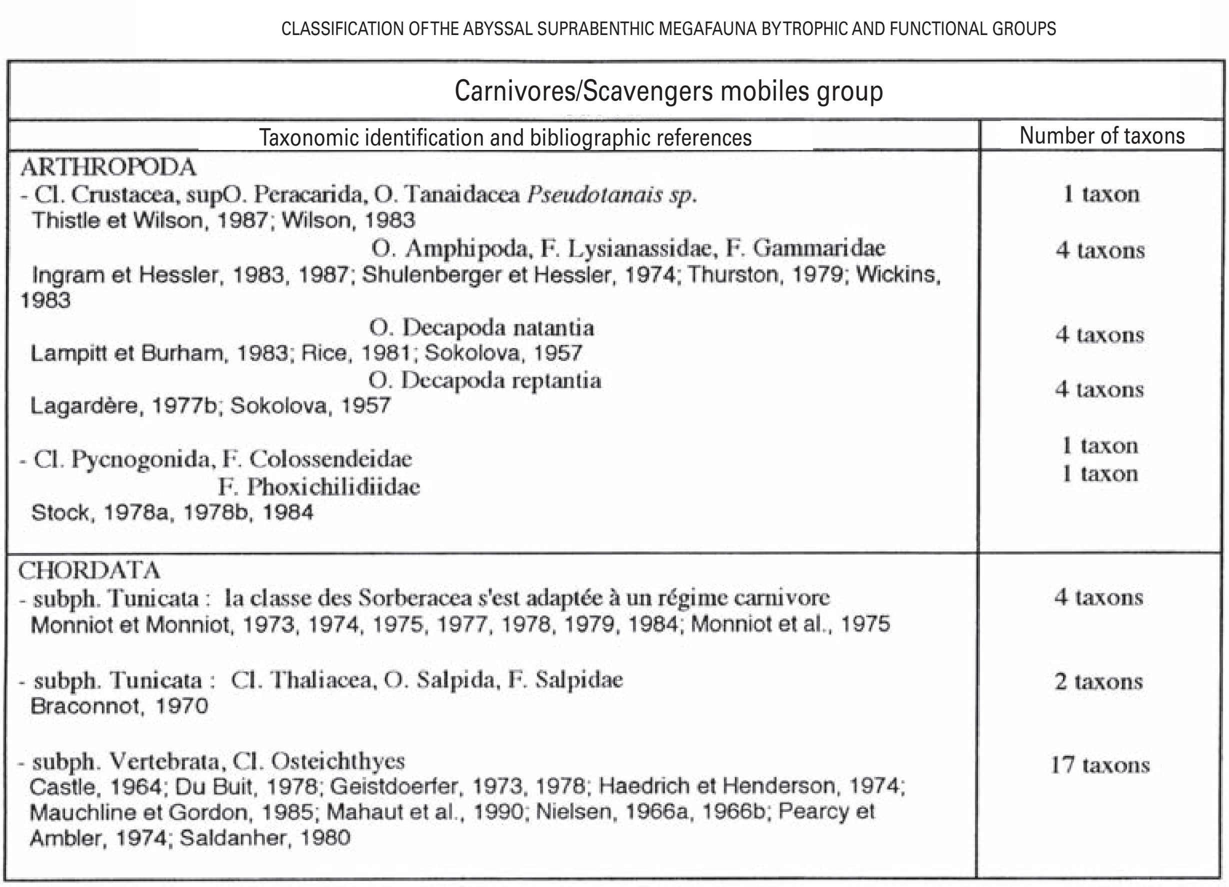
Detritus feeders group			
Sessiles		Mobiles	
Taxonomic identification and bibliographic references	Number of taxons	Taxonomic identification and bibliographic references	Number of taxons
		MOLLUSCA - Cl. Gasteropoda, O. Archaegastropoda Bouchet et Waren, 1979; Knudsen, 1979; Scheltema, 1981, 1985; Waren et Carney, 1981; Waren et Sibuet, 1981	3 taxons
		- Cl. Scaphopoda, F. Entallinidae Allen, 1983; Knudsen, 1964	1 taxon
		ARTHROPODA Cl. Crustacea, superO. Peracarida, O. Mysidacea, F. Mysidae O. Cumacea, F. Nannastacidae O. Tanaidacea (sauf Pseudotanais) O. Isopoda, F. Munnopsidae Hessler et Strömberg, 1989; Menzies, 1962; Wilson et Thistle, 1985; Wolf, 1962	5 taxons

Detritus feeders group			
Sessiles group		Mobiles	
Taxonomic identification and bibliographic references	Number of taxons	Taxonomic identification and bibliographic references	Number of taxons
		ECHINODERMATA - (occasionnellement) Cl. Stelleroidea, subcl. Ophiuroidea, subO. Gnathophiurina, F. Amphiuridae subO. Chilophiurina, F. Ophiuridae Paterson et al., 1985.	2 taxons
		- Cl. Echinoidea, O. Diadematoida, F. Aspidodiadematidae O. Spatangoida, F. Aeropsidae David et Sibuet, 1985; De Ridder et Lawrence, 1982	2 taxons
		- Cl. Stelleroidea, O. Paxillosida, F. Porcellenasteridae, F. Benthopectinidae O. Spinulosida, F. Pterasteridae O. Forcipulata, F. Zoroasteridae Carey, 1972; Jangoux, 1982; Madsen, 1961; Sloan, 1980;	5 taxons
		- Cl. Holothuroidea, O. Aspidochirotida, F. Synallactidae O. Elasipodida, F. Deimatidae, F. Laetmogonidae, F. Psychropotidae, F. Elpidiidae, F. Pelagothuriidae Khripounoff, 1979; Khripounoff et Sibuet, 1980; Massin, 1982; Miller et Pawson, 1985, 1989, 1990; Ohta, 1985; Pawson, 1976; Pawson et Foell, 1986; Sibuet, 1984, 1985, 1987; Sibuet et al., 1982	31 taxons
HEMICHORDATA Cl. Enteropneusta, F. Ptychoderidae Mauviel et al., 1986; Romero-Wetzel, 1989.	1 taxon	HEMICHORDATA Cl. Enteropneusta, F. Spengelidae, F. Ptychoderidae, F. Harrimanidae Bourne et Heezen, 1965.	3 taxons

CLASSIFICATION OF THE ABYSSAL SUPRABENTHIC MEGAFAUNA BY TROPHIC AND FUNCTIONAL GROUPS



Carnivores/Scavengers mobiles group	
Taxonomic identification and bibliographic references	Number of taxons
CNIDARIA - Cl. Scyphozoa Goy, 1979	9 taxons
-Cl. Hydrozoa, O. Hydroida Omori et Vervoort, 1986	2 taxons
O. Trachylina Bames, 1968	4 taxons
O. Siphonophora Bames, 1968	4 taxons
- Cl. Anthozoa, O. Ceriantharia Tiffon, 1987	1 taxon
O. Actinaria (occasionnellement comportement opportuniste), *Actinoscyphia sp., Phelliactis sp., Sicyonis tuberculata* Aldred et al., 1979; Lampitt et Paterson, 1987; Riemann-Zürneck, 1978; van Praët, 1985	3 taxons ambivalents (suspens./détritiv./carniv.)
CTENOPHORA Barnes, 1968	2 taxons
MOLLUSCA - Cl. Gasteropoda, O. Nudibranchia Bames, 1968	3 taxons
O. Mesogasteropoda, F. Pterotracheidae	1 taxon
O. Neogasteropoda, F. Turridae Bouchet et Waren, 1980; Taylor et al., 1980	1 taxon
- Cl. Cephalopoda, subcl. Coleoida, O. Octopoda, subO. Cirrata Aldred et al., 1978, 1983; Nixon, 1986; Robson, 1930; Roper et Brunage, 1972; Scott, 1910;	1taxon
subO. Incirrata, F. Octopodidae Roper et Brunage, 1972; Voss, 1967, 1985	1 taxon
ANNELIDA Cl. Polychaeta, (éventuellement détritivores) O. Phyllodocida, F. Polynoidae F. Aphroditidae F. Tomopteridae F. Hesionidae Fauchald et Jumars, 1979; Jumars et Fauchald, 1977	6 taxons (ambivalents détritiv./nécroph.)



CLASSIFICATION OF THE ABYSSAL SUPRABENTHIC MEGAFAUNA BY TROPHIC AND FUNCTIONAL GROUPS

Carnivores/Scavengers mobiles group Taxonomic identification and bibliographic references	Number of taxons
ARTHROPODA	
- Cl. Crustacea, supO. Peracarida, O. Tanaidacea *Pseudotanais sp.* Thistle et Wilson, 1987; Wilson, 1983	1 taxon
O. Amphipoda, F. Lysianassidae, F. Gammaridae Ingram et Hessler, 1983, 1987; Shulenberger et Hessler, 1974; Thurston, 1979; Wickins, 1983	4 taxons
O. Decapoda natantia Lampitt et Burham, 1983; Rice, 1981; Sokolova, 1957	4 taxons
O. Decapoda reptantia Lagardère, 1977b; Sokolova, 1957	4 taxons
- Cl. Pycnogonida, F. Colossendeidae F. Phoxichilidiidae Stock, 1978a, 1978b, 1984	1 taxon 1 taxon
CHORDATA	
- subph. Tunicata : la classe des Sorberacea s'est adaptée à un régime carnivore Monniot et Monniot, 1973, 1974, 1975, 1977, 1978, 1979, 1984; Monniot et al., 1975	4 taxons
- subph. Tunicata : Cl. Thaliacea, O. Salpida, F. Salpidae Braconnot, 1970	2 taxons
- subph. Vertebrata, Cl. Osteichthyes Castle, 1964; Du Buit, 1978; Geistdoerfer, 1973, 1978; Haedrich et Henderson, 1974; Mauchline et Gordon, 1985; Mahaut et al., 1990; Nielsen, 1966a, 1966b; Pearcy et Ambler, 1974; Saldanher, 1980	17 taxons

IOC TECHNICAL SERIES

No.	Title	Languages
1	Manual on International Oceanographic Data Exchange. 1965	(out of stock)
2	Intergovernmental Oceanographic Commission (Five years of work). 1966	(out of stock)
3	Radio Communication Requirements of Oceanography. 1967	(out of stock)
4	Manual on International Oceanographic Data Exchange - Second revised edition. 1967	(out of stock)
5	Legal Problems Associated with Ocean Data Acquisition Systems (ODAS). 1969	(out of stock)
6	Perspectives in Oceanography, 1968	(out of stock)
7	Comprehensive Outline of the Scope of the Long-term and Expanded Programme of Oceanic Exploration and Research. 1970	(out of stock)
8	IGOSS (Integrated Global Ocean Station System) - General Plan Implementation Programme for Phase I. 1971	(out of stock)
9	Manual on International Oceanographic Data Exchange - Third Revised Edition. 1973	(out of stock)
10	Bruun Memorial Lectures, 1971	E, F, S, R
11	Bruun Memorial Lectures, 1973	(out of stock)
12	Oceanographic Products and Methods of Analysis and Prediction. 1977	E only
13	International Decade of Ocean Exploration (IDOE), 1971-1980. 1974	(out of stock)
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15	Bruun Memorial Lectures, 1975 - Co-operative Study of the Kuroshio and Adjacent Regions. 1976	(out of stock)
16	Integrated Ocean Global Station System (IGOSS) General Plan and Implementation Programme 1977-1982. 1977	E, F, S, R
17	Oceanographic Components of the Global Atmospheric Research Programme (GARP) . 1977	(out of stock)
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20	A Focus for Ocean Research: The Intergovernmental Oceanographic Commission - History, Functions, Achievements. 1979	(out of stock)
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24	Time-Series of Ocean Measurements. Vol.1. 1983	e, f, s, r
25	A Framework for the Implementation of the Comprehensive Plan for the Global Investigation of Pollution in the Marine Environment. 1984	(out of stock)
26	The Determination of Polychlorinated Biphenyls in Open-ocean Waters. 1984	E only
27	Ocean Observing System Development Programme. 1984	E, F, S, R
28	Bruun Memorial Lectures, 1982: Ocean Science for the Year 2000. 1984	E, F, S, R
29	Catalogue of Tide Gauges in the Pacific. 1985	E only
30	Time-Series of Ocean Measurements. Vol. 2. 1984	E only
31	Time-Series of Ocean Measurements. Vol. 3. 1986	E only
32	Summary of Radiometric Ages from the Pacific. 1987	E only
33	Time-Series of Ocean Measurements. Vol. 4. 1988	E only
34	Bruun Memorial Lectures, 1987: Recent Advances in Selected Areas of Ocean Sciences in the Regions of the Caribbean, Indian Ocean and the Western Pacific. 1988	Composite E, F, S
35	Global Sea-Level Observing System (GLOSS) Implementation Plan. 1990	E only
36	Bruun Memorial Lectures 1989: Impact of New Technology on Marine Scientific Research. 1991	Composite E, F, S

No.	Title	Languages
37	Tsunami Glossary - A Glossary of Terms and Acronyms Used in the Tsunami Literature. 1991	E only
38	The Oceans and Climate: A Guide to Present Needs. 1991	E only
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54	Geological Processes on the Northeast Atlantic Margin (8th training-through-research cruise, June-August 1998). 1999	E only
55	Bruun Memorial Lectures, 1999: Ocean Predictability. 2000	E only
56	Multidisciplinary Study of Geological Processes on the North East Atlantic and Western Mediterranean Margins (9th training-through-research cruise, June-July 1999). 2000	E only
57	Ad hoc Benthic Indicator Group - Results of Initial Planning Meeting, Paris, France, 6-9 December 1999. 2000	E only
58	Bruun Memorial Lectures, 2001: Operational Oceanography – a perspective from the private sector. 2001	E only
59	Monitoring and Management Strategies for Harmful Algal Blooms in Coastal Waters. 2001	E only
60	Interdisciplinary Approaches to Geoscience on the North East Atlantic Margin and Mid-Atlantic Ridge (10th training-through-research cruise, July-August 2000). 2001	E only
61	Forecasting Ocean Science? Pros and Cons, Potsdam Lecture, 1999. 2002	E only
62	Geological Processes in the Mediterranean and Black Seas and North East Atlantic (11th training-through-research cruise, July- September 2001). 2002	E only
63	Improved Global Bathymetry – Final Report of SCOR Working Group 107. 2002	E only
64	In preparation	
65	Bruun Memorial Lectures, 2003: Gas Hydrates – a potential source of energy from the oceans. 2003	E only
66	Bruun Memorial Lectures, 2003: Energy from the Sea: the potential and realities of Ocean Thermal Energy Conversion (OTEC). 2003	E only
67	Interdisciplinary Geoscience Research on the North East Atlantic Margin, Mediterranean Sea and Mid-Atlantic Ridge (12th training-through-research cruise, June-August 2002). 2003	E only
68	Interdisciplinary Studies of North Atlantic and Labrador Sea Margin Architecture and Sedimentary Processes (13th training-through-research cruise, July-September 2003). 2004	E only
69	Biodiversity and Distribution of the Megafauna / Biodiversité et distribution de la mégafaune. 2006 Vol.1 The polymetallic nodule ecosystem of the Eastern Equatorial Pacific Ocean / Ecosystème de nodules polymétalliques de l'océan Pacifique Est équatorial Vol.2 Annotated photographic Atlas of the echinoderms of the Clarion-Clipperton fracture zone / Atlas photographique annoté des échinodermes de la zone de fractures de Clarion et de Clipperton	E F
70	Interdisciplinary geoscience studies of the Gulf of Cadiz and Western Mediterranean Basin (14th training-through-research cruise, July-September 2004). 2006	E only

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