Biodiversity and distribution of the megafauna

Vol. 1 The polymetallic nodule ecosystem of the Eastern Equatorial Pacific Ocean
Established in 1960, the Intergovernmental Oceanographic Commission (IOC) of UNESCO promotes international cooperation and coordinates programmes in research, services and capacity building, in order to learn more about the nature and resources of the ocean and coastal areas and to apply that knowledge for the improvement of management, sustainable development, the protection of the marine environment, and the decision-making processes of its 135 Member States.
Biodiversity and distribution of the megafauna:

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

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# Table of contents

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>PREFACE</td>
<td>V</td>
</tr>
<tr>
<td>ACKNOWLEDGEMENTS</td>
<td>VI</td>
</tr>
<tr>
<td>SUMMARY</td>
<td>VIII</td>
</tr>
<tr>
<td>1 – INTRODUCTION</td>
<td>1</td>
</tr>
<tr>
<td>2 – GENERAL CONTEXT</td>
<td>3</td>
</tr>
<tr>
<td>2.1 THE CLARION-CLIPPERTON FRACTURE ZONE</td>
<td>3</td>
</tr>
<tr>
<td>The oceanic meteorological environment</td>
<td>3</td>
</tr>
<tr>
<td>Physico-chemical characteristics of the water column and biological productivity</td>
<td>4</td>
</tr>
<tr>
<td>The abyssal suprabenthic fauna</td>
<td>5</td>
</tr>
<tr>
<td>Geological environment</td>
<td>6</td>
</tr>
<tr>
<td>2.2 POLYMETALLIC NODULES</td>
<td>8</td>
</tr>
<tr>
<td>Nodule composition</td>
<td>8</td>
</tr>
<tr>
<td>Formation and growth of nodules</td>
<td>9</td>
</tr>
<tr>
<td>Sustention of nodule deposits on the seafloor</td>
<td>10</td>
</tr>
<tr>
<td>2.3 THE COMMON HERITAGE OF MANKIND AND PIONEER INVESTORS</td>
<td>11</td>
</tr>
<tr>
<td>Actions taken by France concerning deposits of polymetallic nodules in the eastern equatorial Pacific ocean</td>
<td>13</td>
</tr>
<tr>
<td>2.4 ECONOMIC PERSPECTIVES OF MINERAL EXPLOITATION</td>
<td>14</td>
</tr>
<tr>
<td>2.5 DEFINITION OF THE “NODULE-FACIES”</td>
<td>15</td>
</tr>
<tr>
<td>2.6 THE NIXO 45 SITE</td>
<td>20</td>
</tr>
<tr>
<td>Structural and morphological features</td>
<td>20</td>
</tr>
<tr>
<td>The superficial layer of sediments</td>
<td>20</td>
</tr>
<tr>
<td>Distribution of the different nodule-facies</td>
<td>22</td>
</tr>
<tr>
<td>3 – MATERIALS AND METHODS</td>
<td>25</td>
</tr>
<tr>
<td>3.1 METHODS OF OBSERVATION</td>
<td>25</td>
</tr>
<tr>
<td>Towed devices</td>
<td>25</td>
</tr>
<tr>
<td>Remote-controlled devices</td>
<td>28</td>
</tr>
<tr>
<td>3.2 STRATEGIES OF DATA ANALYSIS</td>
<td>31</td>
</tr>
<tr>
<td>Strategy applied to the qualitative analysis</td>
<td>31</td>
</tr>
<tr>
<td>Strategy applied to the quantitative analysis</td>
<td>31</td>
</tr>
<tr>
<td>THE NIXO 45 SITE</td>
<td>32</td>
</tr>
<tr>
<td>Analysis of photographic data from the “Épaulard”</td>
<td>32</td>
</tr>
<tr>
<td>Analysis of photographic data from the “Nautile”</td>
<td>32</td>
</tr>
</tbody>
</table>
# Table of Contents

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>THE NIXO 41 SITE</td>
<td>32</td>
</tr>
<tr>
<td>THE ECHO 1 SITE</td>
<td>32</td>
</tr>
<tr>
<td>3.3 QUANTITATIVE ANALYSIS OF PHOTOGRAPHS FROM THE ‘ÉPAULARD’, ‘RAIE’ AND ‘DEEPTOW’</td>
<td>33</td>
</tr>
<tr>
<td>4 – QUALITATIVE ANALYSIS</td>
<td>35</td>
</tr>
<tr>
<td>4.1 COMPILATION OF AN ANNOTATED TAXONOMIC REFERENCE BASE</td>
<td>35</td>
</tr>
<tr>
<td>4.2 TAXONOMIC RICHNESS OF THE DEEP-SEA FAUNA OF THE CLARION-CLIPPERTON FRACTURE ZONE</td>
<td>36</td>
</tr>
<tr>
<td>4.3 TAXONOMIC RICHNESS BY TROPHIC AND FUNCTIONAL GROUPS</td>
<td>38</td>
</tr>
<tr>
<td>5 – QUANTITATIVE ANALYSIS</td>
<td>41</td>
</tr>
<tr>
<td>5.1 THE NIXO 45 SITE</td>
<td>43</td>
</tr>
<tr>
<td>Abundance and faunal composition by phylum</td>
<td>44</td>
</tr>
<tr>
<td>Abundance and faunal composition for the two dominant phyla</td>
<td>44</td>
</tr>
<tr>
<td>Abundance and faunal composition by nodule-facies</td>
<td>48</td>
</tr>
<tr>
<td>Faunal composition by trophic and functional groups</td>
<td>49</td>
</tr>
<tr>
<td>Faunal composition in relation to edaphic gradient</td>
<td>50</td>
</tr>
<tr>
<td>Faunal composition within each nodule-facies</td>
<td>51</td>
</tr>
<tr>
<td>Quantitative analysis at the level of taxa</td>
<td>54</td>
</tr>
<tr>
<td>Distribution of taxa in the three dominant faunal groups</td>
<td>55</td>
</tr>
<tr>
<td>Distribution of actinids and corallimorpharids on different facies</td>
<td>xx</td>
</tr>
<tr>
<td>Distribution of holothurians on different nodule-facies</td>
<td>xx</td>
</tr>
<tr>
<td>Distribution of sponges on different nodule-facies</td>
<td>xx</td>
</tr>
<tr>
<td>Multivariate analysis of benthic assemblages</td>
<td>55</td>
</tr>
<tr>
<td>Faunal affinities in relation to edaphic gradient</td>
<td>58</td>
</tr>
<tr>
<td>Spatial heterogeneity at nodule-facies level</td>
<td>60</td>
</tr>
<tr>
<td>Comparison of faunal data from the ‘Nautile’ and the ‘Épaulard’</td>
<td>61</td>
</tr>
<tr>
<td>5.2 THE NIXO 41 SITE</td>
<td>61</td>
</tr>
<tr>
<td>Faunal abundance and composition by phylum</td>
<td>61</td>
</tr>
<tr>
<td>Faunal composition by trophic and functional groups</td>
<td>63</td>
</tr>
<tr>
<td>Quantitative analysis at the level of taxa</td>
<td>64</td>
</tr>
<tr>
<td>Distribution of different holothurians on different facies</td>
<td>64</td>
</tr>
<tr>
<td>5.3 THE ECHO 1 SITE</td>
<td>65</td>
</tr>
<tr>
<td>Abundance and faunal composition by phylum</td>
<td>65</td>
</tr>
<tr>
<td>Faunal composition by trophic and functional groups</td>
<td>68</td>
</tr>
<tr>
<td>Quantitative analysis at the level of taxa</td>
<td>68</td>
</tr>
<tr>
<td>Distribution of holothurians on different facies</td>
<td>73</td>
</tr>
</tbody>
</table>
5.4 ESTIMATES OF BIOMASS AT THE STUDY SITES

Estimates of megafaunal biomass at the NIXO 45 and NIXO 41 Sites ......................................................... 73
Estimates of megafaunal biomass at the ECHO 1 Site .............................................................................. 75
Estimates of macrofaunal and meiofaunal biomass ............................................................................. 76
Estimates of flux in particulate organic carbon ...................................................................................... 77

6 – DISCUSSION .............................................................................................................................................. 79

6.1 COMPARISON OF DIFFERENT IN SITU OBSERVATION DEVICES ........................................................... 79
The ‘Nautile’ ..................................................................................................................................................... 79
The ‘R.A.I.E.’ ................................................................................................................................................ 79
The ‘Deep Tow’ ..................................................................................................................................... 80

6.2 COMPARISON OF SUPRABENTHIC ASSEMBLAGES AT THE STUDY SITES .................................................... 80
Taxonomic richness ........................................................................................................................................ 80
Faunal abundance ....................................................................................................................................... 81
Faunal composition .................................................................................................................................... 82
Trophic structure of suprabenthic assemblages ....................................................................................... 82
Preferential habitats and their faunal assemblages ................................................................................... 83

6.3 LIMITING FACTORS: CURRENTS, GEOMORPHOLOGY, EDAPHIC HETEROGENEITY AND ADAPTATIONS OF THE FAUNAL ASSEMBLAGES .................................................................................. 84

6.4 BIOTIC AND ABIOTIC STRUCTURING FACTORS .................................................................................... 86

BIBLIOGRAPHIC REFERENCES .................................................................................................................... 89

APPENDIX I ...................................................................................................................................................... 111
PANORAMA OF THE MEGAFAUNA WITHIN A POLYMETALLIC NODULE ECOSYSTEM OF THE EASTERN EQUATORIAL PACIFIC OCEAN

APPENDIX II .................................................................................................................................................. 127
LIST OF CODES BASED ON THE CLASSIFICATION OF PARKER (1982))

APPENDIX III .................................................................................................................................................. 128
LIST OF INTERNATIONAL SPECIALISTS CONSULTED

APPENDIX IV .................................................................................................................................................. 132
COMPARISON OF THE TAXONOMIC RICHNESS OF THE STUDY AREA IN THE ABYSSAL ZONE OF THE WORLD’S OCEANS

APPENDIX V .................................................................................................................................................. 140
CLASSIFICATION OF THE ABYSSAL SUPRABENTHIC MEGAFAUNA BY TROPHIC AND FUNCTIONAL GROUPS
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
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 “AssociationFrançaise 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 Mari-anne Cassaigne for digitizing the photographs and figures.
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 Q (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 ‘Nautilus’ 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
INTRODUCTION

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; Thiels et al., 1991; Sharma & Rao, 1991; Christiansen & Thiels, 1992; Smith et al., 1992; Christiansen, 1993; Bluhm, 1994; Bluhm & Thiels, 1996; Lauerman et al., 1996; Radziejewska, 1997; Pipenburg & Schmid, 1997; Hughes & Atkinson, 1997; Fukushima & Imajima, 1997; Kaufmann & Smith, 1997; Kottlowski & 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 (Aldred et al., 1979; Rice et al., 1979; Dyer et al., 1982; Wakefield & Smith, 1989; Nybakken et al., 1997), 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 accurate 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 & Thiels, 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; Pipenburg 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 northeast 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 Albatross 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, physicochemical 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.


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 megafauna, 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 Remorqueur Abyssal d’Instruments par l’Exploration or R.A.I.E., DeepTow 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’.

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

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/m²/an) to mesotrophic (150 gC/m²/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/m³ in summer and 0.12 mg/m³ in winter. That represents a low mean value for daily primary productivity of 1.5 mgC/m²/j in summer and 2.7 mgC/m²/j in winter when compared with a level of primary production in the euphotic zone of 43.8 gC/m²/an in summer and 52.5 gC/m²/an in winter (El-Sayed & Taguchi, 1979). The micronekton, zooplankton and neuston vary between 3 and 8 g/m³, with a maximum in winter due to greater insolation (16 % more than in summer according to Franceschini, 1979). The greatest

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**Fig. 2.** Map on the present-day pattern of deep ocean circulation in the Pacific Ocean (Demidova, 1999).
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 m²). 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; Lauerma 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 Niño/la Niña 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...
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 embayment 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 nanofossils, 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 nanno-fossils 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
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 characteris-
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 (sils, 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; Greenislate 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 (Mn²⁺, Fe³⁺, Mn⁴⁺) 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 & Özkar, 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; Krihhaswami 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 (10Be). 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 & Ebersdorff (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 Oligocene (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 & Özkar, 1979b). The nodular debris that served as kernels is evidence of a more ancient generation of nodules (19 to 20 Ma according to Ebersdorff, 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’Exploitation et la Recherche des NOdules’ (AFERNOD), a request for a permit of exploration covering a sector of 455 000 km². This permit request was modified on the 12th July 1982 by reducing the area to 300 000 km², 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 km² of which 94 500 km² 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.

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,

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 km² was based on sampling every 93 km. The Noria (Nodule Riches et Abondants) zone of about 450 000 km² 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:
2 GENERAL CONTEXT

• 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 km² 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 ‘Nautilus’, 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 ‘Nautilus’ 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 ‘Nautilus’ 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 ‘Nautilus’ 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 reference 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 reference 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. Economists 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
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 par-
GENERAL CONTEXT

Nodule-facies B is composed of isolated nodules. The nodules are never coherent. The concentration diminishes (2 to 10 kg/m²) with increasing nodule size. They cover only 15 to 20 % of the ocean floor and their abundance is limited to 8 kg/m². 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/m². 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/m². 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 (10Å²-manganate, buserite, todor- okite). These nodules form vast beds lying on the sediment, with a coverage of 30 to 50 % and concentration greater than 10 kg/m². 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/m². 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/m²) 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 in-
crease 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 AFRERNOD 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.
### Tableau. 1. Summary of the 5 types of nodule-facies based on visual observations and photographs of the seabed (Hoffert & Saget, 2004). © Ifremer

<table>
<thead>
<tr>
<th>Caractéristiques</th>
<th>Faciès O</th>
<th>Faciès Encroûtement et plaques (EP)</th>
<th>Faciès A</th>
<th>Faciès B</th>
<th>Faciès C</th>
</tr>
</thead>
<tbody>
<tr>
<td>Morphologie</td>
<td>Sphère</td>
<td>++</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Morphologie</td>
<td>Ellipse</td>
<td>++</td>
<td>++</td>
<td>+++</td>
<td></td>
</tr>
<tr>
<td>Morphiologie</td>
<td>Disque</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Polylébé</td>
<td>caractéristique</td>
<td>+</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Plaques</td>
<td>caractéristique</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td></td>
<td>Fragment de Nodules</td>
<td>fréquent</td>
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<td></td>
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<tr>
<td></td>
<td>Quelconque</td>
<td>possible</td>
<td></td>
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<td></td>
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<tr>
<td>Taille</td>
<td>&gt; 15cm</td>
<td>+++</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Très gros nodules</td>
<td>+</td>
<td>++</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>10 à 15 cm Grob nodules</td>
<td>+++</td>
<td>+</td>
<td>+++</td>
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<td></td>
<td>5 à 10 cm Taille moyenne</td>
<td>+</td>
<td>++</td>
<td>+++</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>2,5 à 6 cm Petits nodules</td>
<td>+++</td>
<td>+</td>
<td>++</td>
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</tr>
<tr>
<td></td>
<td>&lt; 2,5 cm Très petits nodules</td>
<td>++</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Aspect de la face supérieure</td>
<td>Base</td>
<td>+++</td>
<td>++</td>
<td>++</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Granulaire</td>
<td>+</td>
<td>++</td>
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<td></td>
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<tr>
<td></td>
<td>Boitroidal (mamelonné)</td>
<td></td>
<td></td>
<td>+++</td>
<td></td>
</tr>
<tr>
<td>Aspect de la surface extérieure</td>
<td>Cairenté équatorial</td>
<td>Non</td>
<td>rare</td>
<td>+++</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Indications de tendance à la fracturation</td>
<td>Non</td>
<td>+++</td>
<td>+++</td>
<td></td>
</tr>
<tr>
<td>Degré d’enroulement</td>
<td>Nul ou faible</td>
<td>faible</td>
<td>faible</td>
<td>+++</td>
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</tr>
<tr>
<td>Sédiment posé sur une partie de la face supérieure</td>
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<td>Non</td>
<td>+</td>
<td>+++</td>
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</tr>
<tr>
<td>Organismes fixés</td>
<td>Parfois sédiment induré</td>
<td>Possibilité de traces de volcanisme</td>
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<td></td>
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<tr>
<td>Remarques</td>
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</tbody>
</table>

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 km² 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.

Escarps 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 conical structures in steep slope. 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 reffering more precisely to the NIXO 45 area (Ricou, 1990) defines the “Bedded Series” as the formation of 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 contemporaneous 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.
- 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 m². 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 m² 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 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 Tows’ 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 3213 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 6000 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 5000 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 m² 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 6000 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 (3000 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 2090 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. 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. Seabead bathymetric map, showing the transects of the “Épaulard” and “R.A.I.E.”, indicating the various nodule-facies and density of nodules. © Ifremer
MATERIALS AND METHODS

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, Cyantor, 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 48,000 photographs along 75 km of transects performed by the ‘Épaulard’ 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 analyzed 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 (Pliocene-Quaternary).

A random selection of 48,000 photographs, covering an area of about 76,000 m², collected by the ‘Épaulard’ and the R.A.I.E. have been analyzed by units of 200 photographs of about 3,800 m² in the following way:

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

Analysis of photographic data from the ‘Nautili’

In order to compare the different means of photographic exploration from the ‘Nautili’ and the ‘Épaulard’, a 1250 m route, covered by the ‘Nautili’ 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 m².

**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 m². 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 SPADN 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; Matsu 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 fracture 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 (Vinogradova, 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, taxonomic 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.

![Histogram of taxonomic richness](image)
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.

Fig. 36. Histogram of the number of families in each phylum for the megafauna of the Clarion-Clipperton fracture zone.
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 echinurians 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 function, 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 opportunistic 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 octocorallariads (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.
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 fa-
cies 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% (88 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](image-url)  
**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.](image)
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 sipunculids 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.
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: *Pseudotichopis 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.

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 Amphiactis bathymbium 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 verrillii, 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 profundus 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, Cladophaga sp. are most abundant on facies O with ancient sediments and Poecillasta 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 Porcellenasteidae, 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

![Figure 46](image_url)

*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 m² 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 m²), 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.

- Octocorallians (OCT 7) of family Primnoidae are clearly most dense (221 ind/ha) on facies O with ancient sediments while other octocorallians (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 Ophiidioid 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 corallimorphs of the family Sideractidae. The most abundant detritus feeders are Munnopsid isopods and the holothurians Peniagone gracilis. Ophioid fish are the most abundant carnivores. Taxa exclusive to this facies are bivalves belonging to the Vesicomymidae.

Nodule-facies C+ 10% accommodates in great abundance a fauna that is largely mobile and detritus feeding such as the sipunculids Nephasoma elisa, the echinoids Plesiodiadema globulosum and the holothurians Mesothuria murrayi, Paenopatides sp. and Pannychia moselyi. The most abundant suspension feeders of this facies are Hexactinellid sponges of the Hyalonematidae and the octocoraliarids Primnoidae. Carnivores are medusas of the family Cladorhizidae and decapods of the genus Plesiopaneus, which are exclusive to this facies, as are demospangian 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 Actinocyphia sp. and polychaetes members of the Sabellidae. The most abundant detritus feeders are echinoids of the family Aeropsidea, 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 Focellastra and free crinoids belonging to the family Antedonidae. Detritus feeders are peracarids of the order Cumacea and the holothurians Meseres macdonalidi. 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 Benthescymus (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 Orphnurus 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 octocoralarid of the family Umbellulidae.
• Nodule-facies B 50% has only one abundant suspension feeder, the actinid Synyconis 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 Poeciliastrea, 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 profundus and Peniagone leander as 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 substrate. 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, Synyconis 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 m² and 15 400 m² respectively, 28 700 m² for nodule-facies C+ and nodule-facies BP with a surface area of 7 900 m².

The spatial distribution of taxa was estimated by means of relationships which combined the mean X and the variance $\sigma^2$ for the following different unit areas (or quadrats): 50 m², 100 m², 200 m², 400 m², 800 m², 1 600 m², 3 200 m², 6 400 m² (12 800 m² and 25 600 m² for nodule-facies C+). Following the recommendations of Elliot (1971), the following distribution indexes were calculated:

Fisher coefficient: $d = \frac{s^2}{X}$

Lexis index = $\frac{s^2}{\sqrt{X}}$

David & Moore index = $\frac{s^2}{X} - 1$

and Morisita index: $i_0 = \frac{n(S(x2) - Sx)}{(Sx)2 - Sx}$

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 Synyconis tuberculata is aggregated above 1600 m² according to the Lexis, David & Moore indexes and Fisher's coefficient, and random at 400 m² and 800 m².

• on nodule-facies O the distribution is random at 1 600 m² while at 800 m², it is aggregated. However, it may be that in an area of 1600 m² the population of Synyconis 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 quadrant areas within the four facies studied. A distinct peak occurs at 32 q suggesting that the size of aggregations of Synyconis tuberculata on facies O is 1600 m². Distributions on the three other facies follow similar trends, i.e. slightly aggregated at quadrat sizes of 100 m² up to 400 m² on nodule-facies C+ then random. Above 6 400 m² 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 m² and 800 m²;

• on nodule-facies C+, the distribution is aggregated at 100 m² and 400 m², and random between 800 m² and 1 600 m²,

• on nodule-facies BP, the distribution is aggregated with a peak at 800 m² and another lesser peak at 200 m²,

• on nodule-facies O, no holothurians belonging to Mesothuria murrayi are observed.

The peak of aggregation at 400 m² 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 m².

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.

<table>
<thead>
<tr>
<th>l/δ</th>
<th>50</th>
<th>100</th>
<th>200</th>
<th>400</th>
<th>800</th>
<th>1600</th>
<th>3200</th>
<th>6400</th>
<th>12800</th>
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<td>100</td>
<td>200</td>
<td>400</td>
<td>800</td>
<td>1600</td>
<td>3200</td>
<td>6400</td>
<td>12800</td>
<td>25600</td>
</tr>
<tr>
<td>Faciès C+</td>
<td>1,1</td>
<td>1,1</td>
<td>1,1</td>
<td>1</td>
<td>0,9</td>
<td>0,9</td>
<td>0,9</td>
<td>0,86</td>
<td>0,75</td>
</tr>
<tr>
<td>Faciès O</td>
<td>1,2</td>
<td>1</td>
<td>1,2</td>
<td>0,9</td>
<td>1,7</td>
<td>1,2</td>
<td>0,9</td>
<td>0,75</td>
<td></td>
</tr>
<tr>
<td>Faciès B</td>
<td>1,1</td>
<td>0,9</td>
<td>1</td>
<td>1</td>
<td>0,9</td>
<td>0,9</td>
<td>0,8</td>
<td>0,75</td>
<td></td>
</tr>
</tbody>
</table>

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

<table>
<thead>
<tr>
<th>l/δ</th>
<th>50</th>
<th>100</th>
<th>200</th>
<th>400</th>
<th>800</th>
<th>1600</th>
<th>3200</th>
<th>6400</th>
<th>12800</th>
</tr>
</thead>
<tbody>
<tr>
<td>l/δ</td>
<td>100</td>
<td>200</td>
<td>400</td>
<td>800</td>
<td>1600</td>
<td>3200</td>
<td>6400</td>
<td>12800</td>
<td>25600</td>
</tr>
<tr>
<td>Faciès C+</td>
<td>2,3</td>
<td>1,7</td>
<td>1,9</td>
<td>1,4</td>
<td>1,2</td>
<td>0,8</td>
<td>1,2</td>
<td>0,8</td>
<td>0,7</td>
</tr>
<tr>
<td>Faciès B</td>
<td>1</td>
<td>1,5</td>
<td>1,1</td>
<td>1,3</td>
<td>0,8</td>
<td>0,8</td>
<td>0,9</td>
<td>0,7</td>
<td></td>
</tr>
<tr>
<td>Faciès BP</td>
<td>0,6</td>
<td>1,4</td>
<td>1,1</td>
<td>2,2</td>
<td>0,5</td>
<td>0,9</td>
<td>0,9</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Comparison of faunal data from the ‘Nautil’ and the ‘Épaulard’**

To compare two different methods of photographic exploration, the ‘Épaulard’, equipped with a photographic camera, and the manned submersible ‘Nautil’, with its video camera, data were analysed from a transect 1 250 m long filmed by the ‘Nautil’. 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 ‘Nautil’ than in the data from the ‘Épaulard’. The total density of the megafauna was estimated from the ‘Nautil’ 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 ‘Nautil’ was less (2 500 m²) than that for the ‘Épaulard’ (3 850 m²).

These results contradict the suggestion that one would find a smaller number of taxa in the transects viewed by the ‘Nautil’ 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.
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 m², but usable data was more limited at NIXO 41 and the areas analysed were smaller, with nodule-facies A 30 % covering only 2 950 m², nodule-facies C+ 30 % 3 100 m² and nodule-facies B 35 %, 2 300 m².

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.

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.
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 greater.
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 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), 83 ind/ha for sea urchins Priesolodactyla globosum (OUR 1), 25 ind/ha for holothurians Psychronaetes hanseni (HOL 21), 23 ind/ha for polychaete worms Incertae sedis living in contorted tubes 40 cm long (POL 9), and 23 ind/ha for the actinids Actinernus verrill (ACT 7). Abundances distinctive to this zone are those of free crinoids Fariometra parvula (CRP 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 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 at the NIXO 45 site (18 ind/ha). 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 on the NIXO 45, the density is 5 ind/ha. In contrast, this taxon is present at a comparable density (25 ind/ha) on nodule-facies B 40% until ind/ha is reached at the density of 23 ind/ha.
• 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 (HOL 13) 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. This 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+ 40 % 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 echinoderms.

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 Enyuniastes 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 NIXO 45 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 m² with the 50 mm objective and 8 300 m² 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 octocorallariids 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), octocorallariids (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 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

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**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.

![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.](image-url)
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. Octocoral lariads 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 octocoral lariads (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 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 50 mm 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 echitarians 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 *Incertainae 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), octocoralliards of the family Plumularidae (OCT 1) and the polychaete worms *Incertainae sedis* with long contorted tubes (POL 9).

Detritus feeding echinoderms are the echinoids *Pleodiadema 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), octocoralliards of the family Plumularidae (OCT 1), sponges of the genus *Hyalonema* (SPO 15), sea urchins *Pleodiadema globulosum* (OUR 1), holothurians *Mesothuria murrayi* (HOL 9) and polychaete worms *Incertainae 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), echinarians *Jacobia birsteini* (ECH 1), sponges *Pheronema* sp. (SPO 14) and *Hyalonema* sp. (SPO 15), echinoids *Pleodiadema globulosum* (OUR 1), polychaete worms *Incertainae 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), octocoralliards 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 Pitlocrinus (CRI 3), which also belong to the 20 most abundant taxa at the NIXO 45 site, fish of the genus Ipnotus (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 Psychrosaetesi 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 Paelopatoides 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 Psychrosaetesi hanseni and Paelopatoides 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 profundus (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/m²) 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/m²) is about 11 times that for detritus feeders (32 mgC/m²) which is 16 times greater than that for carnivores and scavengers (2 mgC/m²). Fish have an estimated biomass of 119 mgC/m².
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/m² 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/m²) is 13 times greater than that of detritus feeders (48 mgC/m²), which is 7 times greater than that for carnivores and scavengers (7 mgC/m²). 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/m²) being about seven times greater than for detritus feeders (173 mgC/m²), whose biomass is four times greater than that of carnivores (43 mgC/m²).

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 echinurians and echiurids 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 echinurians is only 1 % of that for detritus feeders at the NIXO 45 site, contrasting with 12.5 % at NIXO 41. This is because echinurians preferentially inhabit facies with high nodule coverage, such as those selected at the NIXO 41 site, while echiurids 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/m² divided into 963.3 mgC/m² for suspension feeders (9 times greater than at ECHO 1), 97.42 mgC/m² for detritus feeders (3 times greater than at ECHO 1) and 40.28 mgC/m² 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 that 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 41 site. 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 (meta-
aceans, 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 30.8 % 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 meiofaunistic study sites of Reinaud-Mornant et al. (1997) at the BIE site in the Indian 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):

\[
J = \left(\frac{9 \times PP}{Z} + \frac{0.7 \times PP}{Z^{0.5}}\right)
\]

- \(J\) is the flux in particulate organic carbon expressed as \(\text{gC/m}^2/\text{y}\)
- \(PP\) is the primary production estimated at the surface of the study zone in \(\text{gC/m}^2/\text{y}\)
- \(Z\) 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 \(\text{gC/m}^2/\text{y}\) (compared with 90 \(\text{gC/m}^2/\text{y}\) 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 \(C_o\) 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/m²/day or 54.23 ± 20.8 gC/m³/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/m³/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/m³/y. Similarly, based on Berger et al. (1987), the meiofaunal study sites of Reinaud-Mornant & Gourbault (1990) fall within a zone of primary productivity of 125 gC/m³/y.
Consequently, for the more southerly study sites of NIXO 45 and 41, an estimated mean value for primary production of 150 gC/m²/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):

\[ J = \frac{(9 \times 150)}{5 \, 000} + \frac{(0.7 \times 150)}{5 \, 000}^{0.5} \]

The particulate flux \( J \) was thus calculated as 1.75 gC/m²/y or 4.79 mgC/m²/day. This value of particulate flux is greater than 0.2 mgC/m²/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/m²/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; Lauerma et al., 1997; Drazen et al., 1998; Thurston et al., 1998) related to variation in particulate organic carbon (Smith et 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/m²/y, while at the ECHO 1 site, the ratio is 35, taking into account its lower primary production of 125 gC/m²/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 Nautil” 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 ‘Épaulard’. The impression in colour and the scrolling of images in photographs and films of the ‘Nautil’ 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 ‘Nautil’ 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 ‘Nautil’ 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 ‘Nautil’. 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 ‘Nautil’ might cause animals to flee. As suggested by the quantitative analysis, this “overestimation” of densities could be because the surface area explored by the ‘Nautil’ was 2 500 m², and consequently less than the 3 850 m² sampled by the ‘Épaulard’, and because fish seem attracted by the presence of the ‘Nautil’ 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 echinarian burrows in images from the ‘Nautil’. These particular forms of bioturbation created by echinarians 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 ‘Nautil’.

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 echichurians.

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/m²/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 echichurians.

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 m² while the present study is based on an area of 71 070 m². 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 Peru 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 microfacades 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 Ozturkut 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 m² near DOMES C. Foell (1988) estimated a total density of 363 ind/ha based on a surface area of 9 260 km² situated 15°N-126°W near DOMES C and 361 ind/ha for an area of 1 087 542 m² 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 m² 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 m².

In contrast, the estimates of Morgan (1991) at a site neighbouring NIXO 45 and covering 11 068 m² 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 m²) 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 m². This value is nevertheless greater than the 123 ind/ha measured by trawling an area of 28 750 m² 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 (34-36 %) 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). Grasse 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, Özurtug 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/m²/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 trophic 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
DISCUSSION

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 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 pre-
vent 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, ceriantharids, actiniarids, corallimorpharids, antipatharids, archaeogastropods, sedentary polychaetes, cirripedes, brachiopods, crinoids, ophiuroids, brisingids and ascidians. Octocoralliarids and crinoïds predominate on sloping facies that favour the acceleration of currents (Du Castel, 1982). Evidence of currents commonly seen at the study sites are the crinoïds 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 & Pashon (1990), spending most of their time in the wa-
ter column. However, according to these authors, examination of their gastric contents indicates that they are not suspension feeders but they live in a mesopelagic 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 mesopelagic life style, similar to that lead by Psychropotes longicauda (Miller & Pawson, 1990), found in the study zone are: “facultative swimmers” according to the definition of body (Miller & Pawson, 1990). Holothurians that are movements by increasing the surface area of the for the lack of specialised respiratory organs, or to by beating it sails and podia, and so compensating of the Ekman layer adjacent to the ocean floor or sim-

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 theEkman 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 et 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).
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Appendix I

PANORAMA OF THE MEGAFANA WITHIN A POLYMETALLIC NODULE ECOSYSTEM IN THE EASTERN EQUATORIAL PACIFIC OCEAN AND COLOUR FIGURES ON THE THEME OF POLYMETALLIC NODULES

INTRODUCTION .............................................................. 112
SPONGES ................................................................. 113
HYDROZOANS ............................................................ 115
SCYPHOZOANS .......................................................... 115
OCTOCORALLIANS ......................................................... 116
ACTINIANS ................................................................. 116
CERIANTHARIANS ....................................................... 117
ANTIPATHARIANS ....................................................... 118
ECHIURIANS .............................................................. 118
CEPHALOPODS ........................................................... 119
ARTHROPODS .............................................................. 120
PYCNOGONIDS ............................................................ 121
ENTEROPNEUSTS .......................................................... 121
TUNICATES ................................................................. 121
PISCES ................................................................. 122
COLOUR FIGURES ON THE THEME OF POLYMETALLIC NODULES ................................................................. 123
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 compiled 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 *Poeciliaster* 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 Esperopsis 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 with plates, sponge Demospongiae Phakellia sp. (SPO 4) © Ifremer

**Fig. 10** Photograph taken by ‘Deep Tow’ at the Echo I site (near DO-MES 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 Auloche 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: nodule-facies C, hydrozoan Branchiocerianthus imperator (HYD 1) © Ifremer

**Fig. 15** Photograph taken by the “the Nautile” during the NIXONAUT cruise: nodule-facies mixed with plates, scyphomedusa or hydromedusa Chrysaora lysoscella (MED 10) © 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 Nautil” during the NIXONAUT cruise: nodule-facies mixed with plates, scyphomedusa or hydromedusa Chrysaora lyosenella (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 $O$, octocorallarian 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, octocorallarian, 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, octocorallarian 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 Nautilus” 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 ‘Deep Tow’ at the Echo I site: nodule-facies mixed B and plates, actinian Hormathiidae (ACT 6) © 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 the ‘Épaulard’ at the NIXO 45 site: nodule-facies B, ceriantharian Aliciidae, Cerianthus sp. (CER 1) © Ifremer

Fig. 29. Photograph taken by the ‘Épaulard’ at the NIXO 45 site: nodule-facies B, ceriantharian Aliciidae, Cerianthus sp. (CER 1) © 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. 24. Photograph taken by 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 Alicidae, Cerianthus sp. (CER 1) © Ifremer.

Fig. 30. Photograph taken by the "Épaulard" at the NIXO 45 site: nodule-facies B, dark ceriantharian, Alicidae, Cerianthus sp. (CER 1') © Ifremer.
Fig. 31. Photograph taken by the “Nautil” 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 “Nautil” during the NIXONAUT cruise: nodule-facies C, antipatharian *Bathypathes sp.* (ANT 10) © Ifremer

Fig. 35. Photograph taken by the “Nautil” during the NIXONAUT cruise: nodule-facies C, Field vane tester investigating the soil mechanics on a mound formed by the echiurian worm *BonnelliaJacobia birstei* (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 *Balanoglossus sp.* (ENT 4) © Ifremer

Fig. 37. Photograph taken by the “Nautil” during the NIXONAUT cruise: nodule-facies B, mound about 2.5 m formed by the echiurian worm *BonnelliaJacobia birstei* (ECH 2) © Ifremer

Fig. 38. 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. 39. Photograph taken by the Épaulard at the NIXO 45 site: nodule-facies C, cephalopod *Cirrothauma sp.* or *Cirroteuthis sp.* (CEP 2) © Ifremer
Fig. 37. Photograph taken by the "the Nautilus" 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 "Epaulard" 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 "Epaulard" 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 "Epaulard" at the NIXO 45 site: facies C, proboscis of an echiurian worm retracted at the entrance of its burrow and radiating tracks Bonneliidae Bruunellia bando (ECH 6) © Ifremer

Fig. 41. Photograph taken by the "Epaulard" at the NIXO 45 site: nodule-facies C, cephalopod Cirrata Cirrothethis sp. or Cirrothauma sp. (CEP 2) © Ifremer

Fig. 42. Photograph taken by the "Epaulard" at the NIXO 45 site: nodule-facies C, cephalopod Cirrata during propulsion Cirrothethis 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 Astaeomorpha 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 Nautilie” during the NIXONAUT cruise: rocky facies, crustacea Decapoda Munidopsis sp. (GAL 3) © Ifremer

Fig. 50. Exceptional photograph taken by the “the Nautilie” 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 Nautilie” during the NIXONAUT cruise: rocky outcrop, ascidian Culeolus sp. (ASC 4) © Ifremer
**Fig. 55.** Photograph taken by the “Nautile” during the NIXONAUT cruise: nodule-facies C, fish Ophidiidae *Barathrites* sp. (POI 14) © Ifremer

**Fig. 56.** Photograph taken by the “Nautile” during the NIXONAUT cruise: nodule-facies C, fish *Bathysaurus mollis* (POI 7) © Ifremer

**Fig. 57.** Photograph taken by the “Nautile” during the NIXONAUT cruise: fish Ophidiidae *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 *Typhonius 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/m²/y) calculated from C₁₄ 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 m². 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

LOCALISATION OF MINING RIGHTS IN THE NORTH PACIFIC

- International Authority
- Australia
- Yaqui Pangaeology
- COED
- Interocne Metal
- OMSA
- Korea
- OMA
- OME
- OMCO
- ROON
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)

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<thead>
<tr>
<th>Code</th>
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## List of International Specialists Consulted

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### Phylum CTENOPHORA

| C. Carré           | Fr., Villefranche s/mer |

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### Phylum ECHIURA

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<td>S. Edmonds Australia</td>
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### Phylum SIPUNCULA

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<td>E. Cutler and N. Cutler E.U.</td>
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### Phylum MOLLUSCA

#### Class Bivalvia

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<td>P. Bouchet Fr., Muséum</td>
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#### Class Gastropoda

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#### Order Nudibranchia

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#### Class Cephalopoda

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### Phylum ARTHROPODA

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#### Subphylum CRUSTACEA

##### Superorder Peracarida

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**Phylum ECHINODERMATA**

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  - 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**
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  - 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.
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## COMPARISON OF THE TAXONOMIC RICHNESS OF THE STUDY AREA WITH THE ABYSSAL ZONE OF THE WORLD'S OCEANS

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### Appendix V

#### Classification of the Abyssal Suprabenthic Megafauna According to Trophic and Functional Groups

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### Classification of the Abyssal Suprabenthic Megafauna by Trophic and Functional Groups

#### Suspension feeders group

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### Detritus feeders group

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# Detritus feeders group

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## Classification of the Abyssal Suprabenthic Megafauna by Trophic and Functional Groups

### Detritus feeders group

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<td>David et Sibuet, 1985; De Ridder et Lawrence, 1982</td>
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### Carnivores/Scavengers mobiles group

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### Classification of the Abyssal Suprabenthic Megafauna: By Trophic and Functional Groups

#### Carnivores/Scavengers Mobiles Group

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## IOC Technical Series

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<td>Catalogue of Tide Gauges in the Pacific. 1985</td>
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<td>Time-Series of Ocean Measurements. Vol. 3. 1986</td>
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<td>32</td>
<td>Summary of Radiometric Ages from the Pacific. 1987</td>
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<td>Time-Series of Ocean Measurements. Vol. 4. 1988</td>
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<td>Global Sea-Level Observing System (GLOSS) Implementation Plan. 1990</td>
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<td>Tsunami Glossary - A Glossary of Terms and Acronyms Used in the Tsunami Literature. 1991</td>
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<td>38</td>
<td>The Oceans and Climate: A Guide to Present Needs. 1991</td>
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<td>42</td>
<td>Calculation of New Depth Equations for Expendable Bathythermographs Using a Temperature-Error-Free Method (Application to Sippican/TSK T-7, T-6 and T-4 XBTs. 1994</td>
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<td>Design and Implementation of some Harmful Algal Monitoring Systems. 1996</td>
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<td>Equatorial Segment of the Mid-Atlantic Ridge. 1996</td>
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<td>Neotectonics and fluid flow through seafloor sediments in the Eastern Mediterranean and Black Seas - Parts I and II. 1997</td>
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<td>Global Temperature Salinity Profile Programme: Overview and Future. 1998</td>
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<td>51</td>
<td>L'état actuel de l'exploitation des pêcheries maritimes au Cameroun et leur gestion intégrée dans la sous-région du Golfe de Guinée (under preparation)</td>
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<td>Cold water carbonate mounds and sediment transport on the Northeast Atlantic Margin. 1998</td>
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<td>56</td>
<td>Multidisciplinary Study of Geological Processes on the North East Atlantic and Western Mediterranean Margins (9th training-through-research cruise, June-July 1999). 2000</td>
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<td>Bruun Memorial Lectures, 2001: Operational Oceanography – a perspective from the private sector. 2001</td>
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<td>Monitoring and Management Strategies for Harmful Algal Blooms in Coastal Waters. 2001</td>
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<td>Interdisciplinary Approaches to Geoscience on the North East Atlantic Margin and Mid-Atlantic Ridge (10th training-through-research cruise, July-August 2000). 2001</td>
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<td>64</td>
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<td>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</td>
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<td>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</td>
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<td>Interdisciplinary geoscience studies of the Gulf of Cadiz and Western Mediterranean Basin (14th training-through-research cruise, July-September 2004). 2006</td>
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Biodiversity and distribution of the megafauna

Vol.2 ANNOTATED PHOTOGRAPHIC ATLAS OF THE ECHINODERMS
OF THE CLARION-CLIPPERTON FRACTURE ZONE

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Table of Contents

Echinoderms of the Clarion-Clipperton fracture zone .......................2
  Crinoids ...........................................................................................................3
  Echinoids ..........................................................................................................6
  Ophiuroids .......................................................................................................8
  Asteroids ..........................................................................................................10
  Holothurians ..................................................................................................16

Appendix 1 .................................................................................47
  List of codes based on the classification of Parker (1982)

Appendix 2 ................................................................................48
  List of international specialists consulted

Appendix 3 ................................................................................52
  Identification, geographic and bathymetric distribution of echinoderms collected in the Pacific Ocean
The method of identification used in this photographic atlas, based on descriptions of organisms observed in situ, has already been used in several publications, notably those by Macurda & Meyer (1976), Roux (1980), Pawson (1983), Ohta (1985), Pawson & Foell (1986), Fujita et al. (1987), Pawson (1988), Miller & Pawson (1990) and Bluhm & Gebruk (1999). Most of the species of this zone are probably new to science since this part of the Pacific Ocean has scarcely been sampled. Also the in situ appearance of the megafauna differs considerably from that of preserved specimens, and especially so for the echinoderms, which often loose their superficial external gelatinous layer and delicate appendages at the time of collection (Bluhm & Gebruk, 1999). Photographic and video material are also the only means that allow the collection of valuable data on the behaviour and environment of each taxon identified in the midst of the faunal assemblages which compose the benthic and suprabenthic megafauna (Owen et al., 1967; Rowe, 1971; Grasse 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; Tilott 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; Lauer 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; Nybakken et al., 1999; Radziejewska & Kotlinski, 2002).

Often the study of the megafauna is 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) and sometimes limited to holothurians (Matsui et al., 1997). Echinoderms and especially holothurians are also known to be good indicator species in impact studies on the exploitation of polymetallic nodule deposits (Thiel et al., 1992; Bluhm et al., 1995; Bluhm & Gebruk, 1999) or in studies of the variation in particle flux of organic carbon (Smith et al., 1997).

The echinoderms of the Clarion-Clipperton fracture zone are presented here in the form of a photographic atlas accompanied by a commentary for each taxon. The gear that provided the photography and video of the seabed involved towed and free-moving vehicles:

The towed vehicles, generally multi-instrumented, are:

- the “Remorquage Abyssal d’Instrumentation pour l’Exploration” or “R.A.I.E.” developed for Ifremer
- an epibenthic camera sled or “troika” perfected by Commander Cousteau
- The “Deep Tow Instrumentation System” or “Deep-Tow” developed for the Scripps Institute of oceanography (USA)

The remote devices, all developed by Ifremer, are:

- the automatic sampler coupled to a camera or “E.D.1”
- the unmanned free-moving submersible “Epaulard”
- the manned deep-diving submersible “the Nautile”

In the photographic atlas, each commentary is presented in the following order:

- a morphological description,
- a description of certain aspects of behaviour (such as methods of locomotion, visible tracks, swimming movements, trophic behaviour ...),
• edaphic preferences (the occurrence of a taxon on a particular substratum or nodule-facies),
• hydrological preferences (such as orientation with respect to currents)
• hypotheses of identification made in agreement with international specialists for each group,
• information on morphology extracted from the literature,
• bathymetric and geographic distributions for each taxon in relation to the proposed identification(s),
• comparative observations in relation to taxa identified from other sites in the Clarion-Clipperton fracture zone, such as the DOMES sites, and more precisely the Echo 1 site located near DOMES C (14°40'N-125°25'W). These sites were investigated by the National Oceanic and Atmospheric Administration (NOAA) and the Scripps Institution of Oceanography. Similarities are also noted with the taxa identified from a station further north-east (34°50'N, 123°00'W) near the central part of the Californian coast at 4 100 m depth (Lauerman et al., 1996; Kaufmann & Smith, 1997). Other sites of comparison outside the Clarion-Clipperton fracture zone are in a polymetallic nodule area in the abyssal Peruvian Basin in the south-east Pacific Ocean (Bluhm, 1994; Bluhm & Gebruk, 1999)

Some remarks on the preceding ideas may conclude each commentary.

The list of codes used in the identifications, following the classification of Parker (1982), is presented as Appendix 1. The international specialists on whose advice the hypotheses of identification in this study were compiled are listed in Appendix 2. The accepted hypotheses of identification are presented and commented upon in the photographic atlas. Based on these, Appendix 3 presents, in the form of a table, a synthesis of information from both specialists and the literature on the echinoderms sampled in the Clarion-Clipperton fracture zone or in the eastern Pacific Ocean region. Also for each species identified are presented the author and date of identification, the bathymetric and geographic distributions and the substrata conditions in which it was collected. The last column displays the codes for the taxa and the name of the international specialists who participated in their identification.

**Crinoids**

**CRI 1**

This species often has five arms (figure 1) or a multiple of five arms, on which pinnules can sometimes be distinguished. The arms measure between 10 and 20 cm. The longest arm in Figure 1 is 20 cm and the crown of arms is spreading, as a “feeding net” to trap food particles efficiently. This species has also been observed moving around by the alternating motion of its arms. In this figure, its star-shaped tracks can be seen situated somewhat below the animal, as though produced during its displacement.

This species was observed on the facies of polymetallic nodules as well as on purely sedimentary substratum, facies O, as in Figure 1.

In reference to the literature (Carpenter, 1888; Hartlaub, 1895; Clark, 1923, 1967) and in the opinion of specialists, this free-living crinoid belongs to the family Antedonidae, Order Comatulida, subclass Articulata, class Crinoidea. The hypothesis of taxonomic identification for this comatulid is *Fariometra parvula* (Hartlaub, 1895), according to the specimens identified by Hartlaub (1895) and Clark (1923, 1967) between latitudes 32°N and 2°N in the Eastern Pacific Ocean, at depths between 589 m and 1 969 m and on substrata of green mud and globigerina ooze.

The family Antedonidae is represented in the Atlantic Ocean (Sibuet et al., 1980) and the Pacific Oceans between 1 200 m and 5 000 m (Carpenter, 1888). This species was listed by Lauerman et al. (1996) from a site in the north-eastern Pacific Ocean close to the central part of the Californian coast at 4 100 m depth and it has also been observed in the Peruvian Basin (Bluhm, 1994).
CRI 2

These crinoids are yellow-orange in situ as in photographs taken by the “Nautile”. Their open crown, formed of 10 pinnate arms, is 20 cm diameter and may be parallel to the substratum or flattened by the current. As rheophiles, they feed by the passive filtering of suspended particles (Roux, 1980). Their long peduncle, to which small actiniae or cirripeds are often attached, is anchored either in sediment or more often on a hard substratum such as rock outcrops or nodules (figure 2).

According to the literature (Carpenter, 1884; Clark, 1908; Roux, 1980; Luke, 1982), these fixed crinoids could be Bathycrinus equatorialis (Clark, 1908), a representative of the family Bathycrinidae, Order Bougueticrinida. Pawson & Foell (1983) suggested Rhizocrinus sp. or Bathycrinus sp. for the taxa they photographed at the DOMES C site in the Clarion-Clipperton fracture zone. This taxon was also listed by Lauerman et al. (1996) at a site in the north-east Pacific close to the central part of the Californian coast at 4 100 m depth.

In view of the difficulties of distinguishing differences in photographs, specialists have also suggested that this crinoid could perhaps be Bathycrinus affinis (Roux, 1980), Bathycrinus aff. australis (Roux, 1980), Rhizocrinus sp. (Carpenter, 1884) or Monachocrinus sp. (Clark, 1917). The latter has been reported at 32°N, on the Patton Escarpment, between 3 600 m and 3 676 m (Luke, 1982). These crinoids occur in the Atlantic, Indian and Pacific Oceans at a great variety of depths (Carpenter, 1884).

Similar sedentary crinoids, but very dark in colour and larger, were identified as Bathycrinus sp. in photographs from the Peruvian Basin (Bluhm, 1994). The Bathycrinids (Bathycrinus gracilis, Monachocrinus recuperratus, Zeuctocrinus gisleni) identified by Roux (1985) in the north-east Atlantic Ocean between 2 000 m and 5 000 m are represented in photographs from the Biogas cruise (Sibuet et al., 1980) and the Cymor cruise between 49°N and 30°N on the continental margin of the Bay of Biscay.

CRI 3

This small sedimentary crinoid has a peduncle 10 cm high and a crown of five arms fringed with long pinnules (figures 3, 4). Each arm measures a maximum of 5 or 6 cm.

According to specialists and information from the literature (Carpenter, 1884; Clark, 1907; Roux, 1980), the proposed identification is Ptilocrinus sp. (Clark, 1907), family Hyocrinidae, Order Millericrinida. Macurda & Meyer (1976) described a dense pinnulation specific to Ptilocrinus sp. Some specialists are undecided between Hyocrinus sp. and Ptilocrinus sp. (Roux, 1980).

Based on photographs from the DOMES C site, Pawson & Foell (1983) proposed the identification Hyocrinus bethelius (Wyville Thomson, 1876), which has a wide distribution from the equatorial Atlantic Ocean to the Crozet Islands in the Mid-Indian Ocean between 2 800 m and 3 300 m (Carpenter, 1884). This yellow hyocrinid has a smooth peduncle composed of ossicles of calcium carbonate which are shaped like dumbbells. The pinnules decrease in size distally along the arms. This hyocrinid was not found in the photographic analyses of Bluhm (1994) for the Peruvian Basin.

The crinoids identified by Roux (1980) as being Hyocrinus sp. were collected from a rocky substratum on the East Pacific ridge to the west of the Tres Marias Islands between 2 646 m and 2 665 m depth. A new species belonging to the family Hyocrinidae, Laubiericrinus pentagonalis, was described by Roux (2004) from specimens collected by submersible at 2 765 m depth in the south-west Pacific Ocean.

The Hyocrinidae Anachalypsicrinus nefertiti and Hyocrinus grimaldii were identified in photographs from the Cymor cruise exploring the Armorican margin at about 2 500 m depth and the Biogas cruise in the Bay of Biscay at about 3 000 m depth (Sibuet et al., 1980; Roux, 1985).

The collected crinoids, which on the advice of the specialists appear similar to the taxa identified in the Clarion-Clipperton fracture zone, are presented in appendix 3 with their geographic and bathymetric distribution.
Fig. 1. Photograph taken by the ‘Epaulard’ at the NIXO 45 site: nodule-facies O, crinoid *Achometra parvula* (CRI 1) © Ifremer

Fig. 2. Photograph taken by the “E.D.1” device during the Copano cruise: nodule-facies C+, crinoid *Bathyocrinus sp.* (CRI 2) and echinoid *Pleisiodiadema globulosum* (OUR 1) © Ifremer

Fig. 3. Photograph taken by the ‘Epaulard’ at the NIXO 45 site: crinoid *Hyocrinus bethellianus* on a cliff (CRI 3) © Ifremer

Fig. 4. Photograph taken by ‘Deep Tow’ at the DOMES C site: mixed nodule-facies, crinoid *Hyocrinus bethellianus* (CRI 3) © Ifremer
Echinoids

OUR 1

This echinid with long slightly recurved radioles about 10 to 15 cm long has a body 2 to 5 cm diameter (figure 5). In the images taken by the ‘Nautilite’ it appears violet, often with a paler region on the aboral face (lightly covered with sediment, reminiscent of the camouflage commonly found in littoral species). OUR 1 was observed on substrata with sediments and nodules as well as on the ocean floor in the Peruvian Basin.

Based on the literature (Agassiz, 1898, 1904, 1908; Mortensen, 1903, 1940, 1951; Downey, 1968) and the advice of specialists, the hypothesis of identification for this taxon is Pleisiodiadema globulosum (Agassiz, 1898), family Aspidodiadematidae, Order Diadematoida. It is a regular sea urchin which shares the abyssal environment of the Pacific and Atlantic Oceans with another genus, Aspidodiadema (Agassiz, 1898).

In the eastern Pacific Ocean, Pleisiodiadema globulosum has been collected between 8°N and 10°S, between Melpelo Island and Valparaiso from depths between 2830 m and 3900 m. This echinid was identified by Pawson & Foell (1983) from the DOMES C site in the Clarion-Clipperton fracture zone, and in the inventory of the megafauna of the Peruvian Basin, it was also present, along with Plesiodiana sp. and at least three other undetermined echinids (Bluhm, 1994).

Pawson & Foell (1983) identified this echinid in images and from specimens collected at the DOMES C site in the Clarion-Clipperton region. It has also been observed near Hawaii, off Japan and in the Indian Ocean at depths between 450 m and 4 800 m (Koehler, 1914), as well as amongst the megafauna of the Peruvian Basin (Bluhm, 1994).

Lauerman et al. (1996) and Kaufman & Smith (1997) identified an echinoid Echinocrepis sp. at 4 100 m at a station further north and close to the central part of the Californian coast.

The other regular and irregular echinids that can be observed and identified in the Clarion-Clipperton region are listed in appendix 3 with their geographic and bathymetric distribution.

OUR 2

One sees here a very sinuous track which could have been created by an animal living in the sediment. Similar tracks from the Peruvian Basin have been identified as having been made by irregular echinids (figure 6).

This irregular echinid has a fragile oral skeleton with a depressed region on the aboral surface encircled by a well-defined narrow brown band. The podia with terminal discs are localised in this depressed region and their function is similar to that of the sweeping podia of numerous burrowing spatangoids, which construct a chimney that communicates between the open water and the burrow (Smith, 1980). This irregular echinid has been identified as Aceste ovata (Agassiz & Clark, 1907), family Aeropsidae, suborder Aphisternata, Order Spatangoida. Since this sea urchin has an endobenthic way of life, its white skeleton can only be partially seen, lying on the sediment when it is dead, and it then resembles an ovoid sponge.

Pawson & Foell (1983) identified this echinid in images and from specimens collected at the DOMES C site in the Clarion-Clipperton region. It has also been observed near Hawaii, off Japan and in the Indian Ocean at depths between 450 m and 4 800 m (Koehler, 1914), as well as amongst the megafauna of the Peruvian Basin (Bluhm, 1994).

The spatangoids are heart-shaped sea urchins that feed on mud or are microphages. Their spines are very small and numerous. The cosmopolitan family Aeropsidae is exclusively abyssal and bathyal. It contains only two genera, Aeropsis and Aceste, collected in particular in the Bay of Biscay (Cuénot, 1948; David & Sibuet, 1985).

The other regular and irregular echinids that can be observed and identified in the Clarion-Clipperton region are listed in appendix 3 with their geographic and bathymetric distribution.
Fig. 5. Photograph taken by the "E.D.1" device during the Copano cruise: nodule-facies C+ sparse, echinoid Pleisiodiadema globulosum (OUR 1) © Ifremer

Fig. 6. Photograph taken by the "Epaulard" at the NIXO 45 site: nodule-facies C, tacks of irregular echinoid Aceste ovata (OUR 2) © Ifremer
Ophiuroids

**OPH 1**

This species is 6-14 cm diameter with a very white, flat central disc and five spindly arms, which are 4-5 times as long as the diameter of the central disc (figures 7 and 9). These taxa are found on all forms of substratum from rock outcrops to sediments with or without nodules.

In agreement with specialists and after referring to the literature (Lyman, 1882; Lütken & Mortensen, 1899; Clark, 1915; Koehler, 1922; Downey, 1969), the proposed identification is *Ophiomusium armatum* (Koehler, 1922), family Ophiuridae, suborder Chilophiurina, Order Ophiurida, subclass Ophiuroidea, class Stelleroidea. Members of the family Ophiuridae are relatively large with long, slender arms, and this family presents the characteristics of the true ophiuroids, in which the arms are never branched and not readily moved except in a horizontal plane. The discriminant characters for this family are only visible by microscope. The ophiuroids are one of the most ancient forms, dating from the Ordovician. They are cosmopolitan in abyssal environments with more than 30 species in the genus *Ophiomusium*. According to the specialists, OPH 1 could equally belong to the genus *Amphiophiura*, family Ophiuridae, or to the genus *Ophiura* or *Stegophiura*, although *Ophiomusium* has the longest legs. Superficially, all these ophiuroids closely resemble one another.

Several undetermined forms of ophiuroids have been reported from the Clarion-Clipperton fracture zone by Pawson & Foell (1983) and from the Peruvian Basin by Bluhm (1994), Lauerman et al. (1996) and Kaufman & Smith (1997) identified ophiuroids at a site in the northeast Pacific Ocean close to the central part of the Californian coast at 4100 m depth as *Ophiura bathybia, Amphilepsis patens* and *Amphiura carchara* on sediments, and *Ophiacantha* spp. on rocky substrata.

Various ideas on the feeding behaviour of these abyssal brittle stars have been proposed in the literature. According to David & Sibuet (1985), they selectively ingest detritus and sediment particles, whereas Litvinova & Sokolova (1971) and Pearson & Gage (1984) consider them to be non-selective euryphagous (omnivores), which are motile and opportunist, feeding on all prey or detritus found in their path. On the other hand, Sokolova (1972) says that abyssal cosmopolitan brittle stars are essentially carnivores, and in particular the semi-microphagous species. However, Fell (1961) suggests that some ophiuroids could be suspension feeders, based on observations of Antarctic specimens that produce a thread of mucus which is held between the spines of the arms in order to trap the small nekton, transported towards the mouth by movements of the flagella. Another way of being a suspension feeder, as in the case described by Fujita & Ohta (1988) for ophiuroids associated with gorgonians, involves capturing particles in suspension, transported by currents. In the Clarion-Clipperton study zone an association was frequently seen between ophiuroids and sponges of the genus *Hyalonema*, which are attached by long peduncles. This would confirm the hypothesis of Fujita & Ohta (1988) of suspension feeding by the ophiuroids of the Clarion-Clipperton fracture zone.

**OPH 1’**

According to the specialists, this ophiuroid is a dark version of the same genus as the preceding taxon, *Ophiomusium armatum* (Koehler, 1922). It appears smaller and more slender, and is difficult to identify from photographs (figure 8).

Another ophiuere, *Amphiophiura convexa* (Lyman, 1878), family Ophiuridae, suborder Chilophiurina, Order Ophiurida, has been identified from the Clarion-Clipperton Zone (Pawson & Foell, 1983). It is characterised by short arms that taper rapidly and bear three small spines on each side of the joints. The aboral surface of the central disc comprises large plates surrounding a single broad central plate. This generally small brittle star is difficult to detect in photographs and in addition, it generally lives buried close to the water-sediment interface. This taxon has been collected in many locations in the northern Atlantic Ocean, in the western part of the Indian Ocean and in the Arabian Sea at depths between 1 997 m and 6 810 m (Lyman, 1882; Bortsch, 1983; Vadan & Guille, 1984).

The collected ophiuroids, which according to specialists appear similar to the taxa identified in the Clarion-Clipperton fracture zone, are given in Appendix 3 with their geographic and bathymetric distribution.
Fig. 7. Photograph taken by ‘Deep Tow’ at the Echo I site: nodule-facies C, ophiuroid Ophiomusium armatum (OPH 1) © Ifremer

Fig. 8. Photograph of a sample from the Copano cruise, dark ophiuroid Amphiophiura convexa (OPH 1') © Ifremer

Fig. 9. Photograph taken by the ‘Nautilus’ during the NIXONAUT cruise: nodule-facies C sparse, ophiuroid Ophiomusium armatum (OPH 1)
Asteroids

**AST 1**

This asteroid is about 12 cm diameter, with thick, almost cylindrical arms that lack marginal spines, a slightly prominent disc and a somewhat rough appearance (figure 10). In some photographs, the central disc can sometimes be very swollen due to ingested sediment, indicating a detritivorous feeding habit. These asteroids are most often observed on substratum with a dense covering of nodules.

In agreement with specialists and after referring to the literature (Fisher, 1905, 1911, 1928, 1930; Ludwig, 1905; Clark, 1911, 1923; Madsen, 1951; Downey, 1970; Luke, 1982), the proposed identification is a representative of the family Zoroasteridae, in the Order Forcipulatida, either *Zoroaster hirsutus* (Ludwig, 1905) or *Zoroaster ophiurus* (Fisher, 1905). The latter has been collected in the south-eastern Pacific Ocean (Fisher, 1905) but has not been recorded in the photographs from the Peruvian Basin (Bluhm, 1994).

**AST 2**

This asteroid is about 15 cm diameter and is generally buried, leaving only its central disc of about 5 cm diameter prominent (figures 11 and 12). Pentahedral tracks on the circular mounds in which they are buried can probably be attributed to them. Similar asteroids have been observed in the Bay of Biscay (Sibuet et al., 1980).

Based on the literature (Sladen, 1883; Ludwig, 1905, 1907; Fisher, 1955; Madsen, 1961; Luke, 1982; Belyaev, 1985) and in agreement with specialists, the proposed identification for this taxon is a member of the family Porcellanasteridae, Order Paxillosida. Some specialists have suggested *Hyphalaster inermis* (Sladen, 1883), which has been reported in the Clarion-Clipperton region (Pawson & Foell, 1983), as have the following Porcellanasterids: *Eremicaster pacificus* (Ludwig, 1905), *Eremicaster crassus gracilis* (Sladen, 1883) and *Thoracaster cylindratus* (Sladen, 1883) (cf. Appendix 3). This asteroid has not been recorded in photographs from the Peruvian Basin (Bluhm, 1994).

Although they do not appear in the photographs, the distinctive characteristics of *Hyphalaster inermis* are the spines at the rounded extremity of the arms and the aboral marginal plates which join the arms midway (Madsen, 1961).

Because of the burrowing nature of this animal, which is rarely visible at the sediment surface, the distinctive characters of *Thoracaster cylindratus* (Sladen, 1883), i.e. the two single marginal plates on the dorsal and ventral sides at the centre of each inter-radius, cannot be seen either. In fact one part of the aboral surface is kept out of the sediment due to the presence of paxillae (small erect columns on the plates of the test that bear spreading spines at their free end), which on contact draw together to form an impenetrable roof (Fell, 1982).

**AST 3**

This asteroid has a fairly well developed disc and rigid, tapering arms with pointed ends. Its diameter is about 15 cm and it is seen especially on sedimentary substrata.

In accordance with the specialists and by reference to the literature (Ludwig, 1905; Fisher, 1910, 1911; Clark, 1913, 1920, 1923; Clark, 1981; Luke, 1982), the proposed identification of this asteroid is *Pectinaster sp.*, a representative of the family Benthopectinidae, Order Paxillosida. Sometimes aggregates can be distinguished along its arms, which could be attached to the well-developed spines found on the aboral marginals (Fell, 1982).

This taxon resembles *Pectinaster agassizii* (Ludwig, 1905), sampled notably in the north-east Pacific Ocean at medium depths (Clark, 1981), as well as another Benthopectinid, *Benthopecten acanthonotus* (Fisher, 1905), which has been collected in the tropical east Pacific Ocean between 1 157 m and 2 761 m (cf. appendix 3).
Fig. 10. Photograph taken by the 'Epaulard' at the NIXO 45 site: nodule-facies C, asteroid Zoroaster hirsutus (AST 1) © Ifremer

Fig. 11. Photograph taken by the 'Epaulard' at the NIXO 45 site: rock outcrop and nodule-facies O, asteroid Hyphalaster inermis (AST 2) © Ifremer

Fig. 12. Photograph taken by the 'Epaulard' at the NIXO 45 site: nodule-facies O, asteroids Hyphalaster inermis (AST 2) and Hymenaster violaceus (AST 5) © Ifremer
This species is about 5 cm in diameter with a pentagonal body. It was mostly observed on ocean floor with a dense covering of polymetallic nodules. It is present in some photographs from the Peruvian Basin (Bluhm, 1994). According to the literature (Ludwig, 1905; Clark, 1920; Madsen, 1951) and in agreement with the specialists, the pentahedral shape of this asteroid and the translucent membrane on the aboral surface are typical of representatives of the family Pterasteridae, in the Order Spinulosida. This level of identification must suffice as the elements for greater precision are lacking. In some photographs, long, fine, prickly adambulacra can be seen, perpendicular to the arms and enclosed in the membrane. In typical members of this family, with the exception of Hymenaster, the prickles on the adambulacra subtend two lateral palmar membranes (Fell, 1982).

In figures 12, 13 and 14, an asteroid 5 to 10 cm in diameter with a fleshy membrane can be distinguished. This species is sometimes violet in photographs taken by the “Nautil”.

According to the literature (Ludwig, 1905; Clark, 1920; Madsen, 1956) and in agreement with the specialists, the proposed identification for this taxon is Hymenaster violaceus (Ludwig, 1905). The distinctive features of the genus Hymenaster given by Sladen (1889) and Mortensen (1927) are a supradorsal membrane composed of numerous muscular fibres, well developed actinal prickles covered by a membrane, and adambulacral prickles that are free and not palmate.

This species has been reported from the DOMES C site (Pawson & Foell, 1983) and in the Peruvian Basin (Bluhm, 1994), as well as on rocky facies explored during the Cymor cruise (North Atlantic).

This asteroid might be expected to have omnivorous feeding habits, both detrivorous and carnivorous, based on the examination of the gastric contents of Hymenaster sp. and Hymenaster quadrispinosus (Fisher, 1905) collected at 1 600 m and 2 926 m (Carey, 1972). However, it may instead be a predominantly detrivorous opportunist, as many abyssal organisms are (Sokolova, 1959). This asteroid colonizes sediments as well as rocky substrata (Fisher, 1911; Clark, 1920; Madsen, 1951) and in photographs of the study zone, it was only found on substrata with polymetallic nodules.

Hymenaster quadrispinosus (Fisher, 1905), Hymenaster gracilis (Ludwig, 1905) and Hymenaster violaceus (Ludwig, 1905) have been collected at depths between 1 935 m and 3 436 m in the north, central and south-eastern Pacific Ocean (Appendix 3).
Fig. 13. Photographie prise par le «Deep Tow» sur le site d’Echo I : Faciès-nodules B, astéréide *Hymenaster violaceus* (AST 5)

Fig. 14. Photograph taken by the ‘Nautile’ during the NIXONAUT cruise: nodule-facies C, asteroid *Hymenaster violaceus* (AST 5)

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Fig. 15. Photograph taken by the ‘Nautile’ during the NIXONAUT cruise: nodule-facies C, brisingid asteroid with 6 arms captured by the ‘Nautile’, *Freyella benthophila* (AST 6)

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These asteroids have six arms, each measuring 5 to 20 cm in length (figures 15, 16, 17). The arms are very thin and clearly distinct from a small central disc, which gives this taxon the appearance of a brittle star. White or yellow-orange in colour, Freyella spp. are generally quite abundant and attached to nodules.

Similar Brisingidae have been reported in the Clarion-Clipperton fracture zone (Pawson & Foell, 1983) and in the Peruvian Basin (Bluhm, 1994).

Based on information from the literature (Sladen, 1889; Clark, 1920; Fisher 1928, 1930; Madsen, 1951, 1956) and the advice of specialists, the proposed identification for this asteroid is a member of the genus Freyella, family Brisingidae, Order Euclasterida (Downey, 1986). Freyella is cosmopolitan in abyssal environments and can have six or more arms. Some specialists have suggested this taxon might be Freyella benthophila (Sladen, 1889; Clark, 1920a) whose distribution extends across the eastern Pacific Ocean to the Indian Ocean in abyssal environments (Madsen, 1951, 1956; Fisher, 1928, 1930). Cherbonnier & Sibuet (1972) have also collected and identified Freyella benthophila in the Atlantic (45°13’N-5°30’W) at 4 700 m depth.

The majority of Freyella observed in the study zone had six arms but other Brisingidae had five, seven or eight arms (Freyella octoradiata, Clark, 1920), nine arms (Freyella heroina, Sladen, 1889) or 10 arms. The problem of number of arms as a means of determination in Freyella is tricky when one considers the frequency of autotomies and the regenerative power of a variable number of brachial buds, as in all the non-pentagonal asteroids which do not have arms largely united to the disc (Cuénot, 1948). Some specialists suggested that AST 6 could be a Freyastera (Downey, 1986). A Freyella with five arms has been observed in a single photograph from the Clarion-Clipperton fracture zone and could be an accidental case.

Some behavioural observations could be made on the feeding posture of this brisingid asteroid. Freyella generally has its arms slightly upturned in order to present the natural filter of their adherent podia to the current, thus trapping particles in suspension. This posture is similar to that of the comatulids. The position of the arms also indicates the direction of the current.

Figure 18 represents a Brisingidae with seven arms, each measuring about 20 cm. Freyella species with seven arms have also observed in the Peruvian Basin (Bluhm, 1994).

The Freyella sp. in figure 18 has a less typical posture, with its arms stretched out and their extremities sometimes raised. The arms are fringed with long thin podia that comb the water-sediment interface. This difference in posture could indicate a new species of Freyella (Pawson, 1982) or another, more detrititus feeding behaviour. Note also that this posture demonstrates maximum efficiency in the pursuit of food by dividing up equally the area to be searched.

According to Downey (1986), the Brisingidae can be separated from the Freyellidae by their feeding behaviour, the Brisingidae having their arms upturned in the current while the Freyellidae have theirs extended over the substratum. However, this statement does not seem justified as photographs from the Clarion-Clipperton fracture zone show that both taxa can have their arms in either position.

Figure 19 shows a Brisingidae of the same diameter as AST 7 with 10 arms. As in all the other Freyella species observed in the Clarion-Clipperton fracture zone, they are found preferentially on nodules. Freyella with 11 arms were seen in photographs from the Bay of Biscay (Sibuet et al., 1980).

By common agreement of the specialists and with reference to the literature (Sladen, 1889; Clark, 1920; Fisher 1928, 1930; Madsen, 1951, 1956), the proposed identification is Freyella sp. because neither Freyella brevispina (Clark, 1920) nor Freyella insignis (Ludwig, 1910), collected in the eastern Pacific Ocean, ever have 10 arms, but 11 and 13 respectively (A. Clark, pers. comm.).

The collected asteroids, which in the opinion of the specialists appear similar to the taxa identified in the Clarion-Clipperton fracture zone, are listed in Appendix 3 with their geographic and bathymetric distribution.
Fig. 16. Photograph taken by the ‘Epaulard’ at the NIXO 45 site: mixed nodule-facies B and rock outcrop, brisingid asteroid with 6 arms, *Freyella benthophila* (AST 6) © Ifremer

Fig. 17. Photograph taken by the ‘Epaulard’ at the NIXO 45 site: nodule-facies O, brisingid asteroid with 6 arms, *Freyella benthophila* (AST 6) © Ifremer

Fig. 18. Photograph taken by ‘Deep Tow’ at the Echo I site: nodule-facies C, asteroid with 7 arms *Freyella* sp. (AST 7) © Ifremer

Fig. 19. Photograph taken by the ‘Epaulard’ at the NIXO 43 site: mixed nodule-facies (A and C), asteroid with 10 arms *Freyella* sp. (AST 8) © Ifremer
Holothurians

HOL 1

This whitish holothurian measures 10 to 20 cm in length by 2 to 3 cm wide (figures 20, 21, 22). Its narrow body with attenuated extremities appears cylindrical with one ventral, plantar surface. Its rigid appearance suggests a thick cuticle, which is scarcely bristly with at least two rows of short, rudimentary dorsal papillae, sometimes irregularly arranged. In the study zone, this taxon was always relatively abundant, never seen in the water column and apparently indifferent to the type of substratum and sediments on which it feeds, and whether or not they are covered with nodules.

Similar Synallactes species were recorded by Pawson & Foell (1983) and Lauerman et al. (1996), as well as by Kaufman & Smith (1997) at a site in the north-eastern Pacific Ocean near the central section of the Californian coast at 4 100 m depth. This orange to brown taxon has also been found at great depths in the Peruvian Basin where they were identified as Synallactes sp. type 2 (Bluhm, 1994; Bluhm & Gebruk, 1999).

On the advice of specialists (Pawson, Sibuet, pers. comm.) and after referring to the literature (Ludwig, 1894; Clark, 1920; Madsen, 1953; Hansen, 1975), the identification proposed is a taxon belonging to the family Synallactidae, Order Aspidochirotida. The quality of the photographs did not allow further analysis and the recognition of Synallactes aenigma (Ludwig, 1894), which has been collected in the north-central Pacific Ocean (appendix 3). Bluhm & Gebruk (1999) suggested Synallactes reticulatus (Sluiter, 1901) as a second possible name for this taxon observed in the Peruvian Basin.

HOL 2

This whitish holothurian has a narrow, cylindrical body (figures 23, 24). Its dorsal surface is covered by at least two rows of numerous slender papillae of variable size but not however exceeding the width of the body. This species measures 12 to 20 cm long and 2 to 4 cm wide. Just as with the preceding taxon, this holothurian is found on all types of substratum, whether covered or not by nodules. It is not known to be mesopelagic (cf. appendix 3).

This holothurian is fairly cosmopolitan having been reported at depths between 2 700 m and 4 300 m in the Indian, Pacific and Atlantic Oceans on a great variety of substrata. Pawson & Foell (1983) identified it at the DOME C site, and Kaufman & Smith (1997) also identified it. It has also been found with a pink tinge in the abyssal depths of the Peruvian Basin (Bluhm & Gebruk, 1999), who referred to it as Synallactes sp. type 1. This taxon has also been reported in the Atlantic Ocean, notably in the Bay of Biscay (Sibuet et al., 1980).

The identification proposed in accordance with the literature (Koehler & Vaney, 1905; Clark, 1920; Madsen, 1953; Hansen, 1975) and specialists (Pawson, Massin, pers. comm.) is Synallactes profundi (Koehler & Vaney, 1905) in the family Synallactidae and Order Aspidochirotida. This taxon has been collected in the Indian, central and south Pacific and north Atlantic Oceans (appendix 3).
Fig. 20. Photograph taken by the ‘Epaulard’ at the NIXO 45 site: nodule-facies C, holothurian *Synallactes aenigma* (HOL 1) © Ifremer

Fig. 21. Photograph taken by a “Troika” during the Copano 1 cruise: nodule-facies C, holothurian *Synallactes aenigma* (HOL 1) © Ifremer

Fig. 22. Photograph taken by the ‘R.A.I.E.’ at the NIXO 45 site: nodule-facies C, holothurian *Synallactes aenigma* (HOL 1) © Ifremer

Fig. 23. Photograph taken by the ‘Epaulard’ at the NIXO 45 site: nodule-facies C, holothurian *Synallactes profundi* (HOL 2) © Ifremer

Fig. 24. Photograph taken by the ‘Epaulard’ at the NIXO 45 site: mixed nodule-facies (C and B), holothurian *Synallactes profundi* (HOL 2) © Ifremer
**HOL 3**

This white-coloured taxon can reach 25 cm long and 6 cm wide (figures 25, 26). It is remarkable in its elongated semi-cylindrical form with rounded extremities. The dorsal papillae are relatively long, thin and aligned in one row per radius, at the interior of which they are uniformly distributed. These papillae are rigid at the base and more flexible at the ends. This holothurian is not mesopelagic, it is generally found on substrata with a dense covering of nodules and it leaves characteristic tracks on the sediment which consist of a double row of small depressions that infer the existence of a double row of ventral podia and the absence of medio-ventral podia.

Pawson & Foell (1983) identified this holothurian from the DOMES C site, however, it does not appear in the identifications of Lauerman et al. (1996) nor of Kaufmann & Smith (1997). It was not reported from photographs of the depths of the Peruvian Basin (Bluhm, 1994). It is poorly represented in the Bay of Biscay (Sibuet et al., 1980).

By reference to the literature (Théel, 1879; Ludwig, 1893, 1894; Clark, 1901, 1913, 1920; Perrier, 1902; Grieg, 1921; Hansen, 1967, 1975) and in agreement with the specialists, we suggest that this taxon belongs to the genus *Orphnurgus* (Théel, 1879) in the family Deimatidae and Order Elasipodida. This holothurian demonstrates the visible characters of a member of the family Deimatidae by the presence of numerous long papillae, the mouth situated in the anterior part of the ventral sole and podia only on the external radius of the trivium. The genus *Orphnurgus*, previously known as *Scotodeima* (Ludwig, 1894), is characterised by the presence of 15 to 20 non-retractable tentacles and by the absence of peribuccal papillae.

**HOL 4**

This holothurian measures a maximum of 20 cm long and 4 cm wide, and is white with a rigid, cylindrical body (figures 27, 28). It closely resembles HOL 3 but is more thickset. Its dorsal surface has more numerous, long, delicate, rigid papillae distributed in several rows, with 4 to 35 pairs per dorsal row and 4 to 17 pairs per lateral row. The trail it creates makes a double row of small holes, indicating the absence of medio-ventral podia. This taxon has been observed on all types of substrata. It appears to ingest detritus and sediments in a non-selective manner, and is not known to be able to move in the water column.

Pawson & Foell (1983) identified this holothurian from the DOMES C site, and Lauerman et al. (1996) and Kaufman & Smith (1997) have also identified it from 4100 m at a site further north. It has been recorded from the Peruvian Basin (Bluhm, 1994; Bluhm & Gebruk, 1999) but appears somewhat different in their photographs, being narrower with two longer papillae on the anterior part of the body and two other perpendicular papillae on the dorsal posterior part. This taxon has been found also in the Bay of Biscay (Sibuet et al., 1980).

The proposed identification, after consulting the literature (Théel, 1879; Ludwig, 1894; Clark, 1901, 1913, 1920; Perrier, 1902; Grieg, 1921; Hansen, 1967, 1975) and specialists (Pawson, Sibuet, Gebruk, Massin, pers. comm.) is *Oneirophanta mutabilis* (Théel, 1879), family Deimatidae and Order Elasipodida. This cosmopolitan holothurian is characteristic of the abyssal region, having been recorded at depths between 1 800 m and 6 000 m in all explored parts of ocean depths. This taxon could be *Oneirophanta mutabilis affinis* (Ludwig, 1894), since that is peculiar to the region studied, in the tropical eastern Pacific Ocean, where it replaces the cosmopolitan *Oneirophanta mutabilis mutabilis* (Théel, 1879). However, HOL 4 is larger than *O. mutabilis affinis*, and from the description, it appears closer to *O. mutabilis mutabilis*. Less similar, *Oneirophanta setigera* (Ludwig, 1893) has been collected in the south-western Pacific Ocean (appendix 3).
Fig. 25. Photograph taken by the ‘Epaulard’ at the NIXO 45 site: mixed nodule-facies (C and B), holothurian Orphnurgus sp. (HOL 3) © Ifremer

Fig. 26. Photograph taken by the ‘Epaulard’ at the NIXO 45 site: nodule-facies C, holothurian Orphnurgus sp. (HOL 3) © Ifremer

Fig. 27. Photograph taken by the ‘Epaulard’ at the NIXO 45 site: nodule-facies C, holothurian Oneirophanta mutabilis (HOL 4) © Ifremer

Fig. 28. Photograph taken by the ‘Nautile’ at the NIXO 45 site: rock outcrop, holothurian Oneirophanta mutabilis (HOL 4) © Ifremer
HOL 5

This white holothurian is smaller, thickset and ovoid (figure 29), measuring a maximum of 15 cm long by 5 cm wide. Its papillae are less numerous, thicker and rigid. There are 5 to 16 pairs of dorsal papillae arranged in a double row and 3 to 7 pairs of lateral papillae. From observations in the study area, they are always found on the ocean bed, in areas with or without nodules, and consequently they may adopt a non-selective detritivorous feeding behaviour. The trail left by their passage does not indicate that medio-ventral podia are absent.

Pawson & Foell (1983) identified this holothurian from the DOMES C site, and it also appears in photographs from the Peruvian Basin (Bluhm, 1994; Bluhm & Gebruk, 1999) and the Bay of Biscay (Sibuet et al., 1980).

The identification proposed in accordance with the literature (Théel, 1879, 1882; Ludwig, 1894; Sluiter, 1901; Koehler et Vaney, 1905; Hérouard, 1923; Deichmann 1930; Hansen, 1967, 1975) and in agreement with specialists is *Deima validum* (Théel, 1879), family Deimatidae, Order Elasipodida. However, one would infer from the tracks created by HOL 5 that *Deima validum* is not characterised by an absence of medio-ventral podia, which contradicts the description of the podial sole made by Hansen (1975). According to him, *Deima validum* does not have medio-ventral podia, or at the very most, has one pair reduced to pre-anal podia. More precisely, HOL 5 may be the cosmopolitan *D. validum pacificum* (Ludwig, 1894) collected in the tropical north-eastern Pacific Ocean between 1 618 m and 2 487 m on various substrata (appendix 3). According to Sibuet et al. (1984), *Deima validum* is not a selective detritus feeder.

HOL 6

This holothurian measures 12 to 25 cm in length and 3 to 5 cm in width (figures 30 & 31). It appears semicircular and flattened, with the two extremities rounded. One can see on the dorsal surface a median groove and two rows of regularly distributed dorso-lateral papillae. The tegument appears soft and thick, and bluish or pale mauve in colour in photographs taken by the “Nautile” (figure 27). This taxon is found on all types of substratum, with or without nodules, as well as on rocky surfaces, but never in the water column.

The proposed identification, with reference to the literature (Théel, 1882, 1886; Ludwig, 1894; Perrier, 1896; Clark, 1920; Hansen, 1956, 1975) and to specialists, is a holothurian of the genus *Benthodytes*, family Psychropotidae and Order Elasipodida, referred to here as *Benthodytes sp.* type 1. Visible characteristics of the family are the medio-ventral podia and a body laterally fringed by anastomosing podia. Some members of the genus *Benthodytes* have been observed swimming (Pérès, 1965; Heezen & Hollister, 1971). Pawson & Foell (1983) identified several types of *Benthodytes* at the DOMES C site. In photographs from the Peruvian Basin, Bluhm & Gebruk (1999) identified a holothurian that was similar but very dark in colour and with some perpendicular dorsal papillae as *Benthodytes sp.* type 2.

Data on *Benthodytes* species collected near to or in the Clarion-Clipperton fracture zone are shown in appendix 3.
Fig. 29. Photograph taken by the ‘Epaulard’ at the NIXO 45 site: nodule-facies C, holothurian Deima validum (HOL 5) © Ifremer

Fig. 30. Photograph taken by the ‘Nautile’ during the NIXONAUT cruise: holothurian (collected) Benthodytes sp. type 1 (HOL 6) © Ifremer

Fig. 31. Photograph taken by the ‘Nautile’ during the NIXONAUT cruise: rocky facies, holothurian Benthodytes sp. type 1 (HOL 6) © Ifremer
HOL 7

This taxon has a cylindrical body with rounded extremities (figures 32, 33). It measures about 20 cm long and 6 cm wide. The whitish tegument is often covered by sediment or detritus, giving the appearance of a smooth surface. The mouth is ventral but the podia are not visible in the photographs. The distinctive feature of this taxon is the vertical notch situated at the posterior end of the body. This holothurian is invariably found on all facies with nodules and sediments but never in the water column.

The proposed identification, in agreement with specialists and the literature (Ludwig, 1894; Madsen, 1953) is Pseudostichopus mollis (Théel, 1886), family Synallactidae, Order Aspidochirotida.

This cosmopolitan holothurian has already been recorded from the Clarion-Clipperton fracture zone (Pawson & Foell, 1983), as well as elsewhere in the north-eastern and south-eastern Pacific, the south-eastern Atlantic and the Indian Oceans, at depths varying between 100 m and 5 203 m on a great diversity of substrata (appendix 3). This taxon does not appear in photographs from the Peruvian Basin (Bluhm, 1994; Bluhm & Gebruk, 1999).

As indicated by its spade-like tentacles, Pseudostichopus mollis adopts a distinctive feeding behaviour, raking up a thin film of superficial sediments (Massin, 1982).

HOL 8

This holothurian is 10 to 20 cm long and up to 5 cm wide (figure 24). It has a sub cylindrical or flattened and elongated form, wider than high, and with a marginal fringe. The dorsal surface of the tegument bears numerous small irregular papillae that trap epibenthic detritus (e.g. debris from nodules, Foraminifera, shells of pteropods etc.), and in consequence, its colour is similar to that of this soft substratum. Its trail is more accentuated on purely sedimentary facies where it appears half buried. It does not appear to be mesopelagic, always being found at the surface of sediments.

This holothurian has also been reported from the DOMES C site (Pawson & Foell, 1983), in the Peruvian Basin (Bluhm, 1994; Bluhm & Gebruk, 1999) and in the Atlantic, in the Bay of Biscay (Sibuet et al., 1980).

Literature references (Fisher, 1907) and the advice of specialists put this holothurian in the cosmopolitan species Mesothuria murrayi (Théel, 1886), family Synallactidae, Order Aspidochirotida. This taxon has been recorded from the western and eastern Pacific Ocean, as well as in the Indian Ocean at depths varying between 725 m and 4 064 m. It was not cited in the inventories of Kaufmann & Smith (1997) and Lauerman et al. (1996).

According to Heezen & Hollister (1971), Lemche et al. (1976) and Billet (1991) some Mesothuria and Pseudostichopus hollow out tracks about 1 cm deep by alternately extending and contracting the whole body, since the ventral podia are scarcely developed. These tracks are the most abundant form of bioturbation that disturbs the sedimentary surface to a significant degree in the depths of the Venezuelan Basin (Young et al., 1985), the Bay of Biscay (Mauviel & Sibuet, 1985) and the abyssal plain of Madeira (Hugget, 1987).

HOL 9

This holothurian measures up to 25 cm long and 5-6 cm wide and has a pointed structure at one end of the body (figure 25). Its body is bulging and cylindrical and has podia scattered all over. Those situated on the ventro-lateral surfaces are larger and could be seen in some photographs. This holothurian has a whitish tinge, and is brown to mauve in photographs in the rare instances when not covered by sediment. It is only seen on nodular substrata where it leaves a track that is clearly less deep than that of HOL 8. It is known to be a non-selective detritus feeder, and does not appear to be mesopelagic, never having been seen in the water column.

This holothurian has also been reported from the DOMES C site (Pawson & Foell, 1983), in the Peruvian Basin (Bluhm, 1994; Bluhm & Gebruk, 1999) and in the Atlantic, in the Bay of Biscay (Sibuet et al., 1980).

The proposed identification, after reference to the literature (Lemche et al., 1976) and in the opinion of the specialists, is a species of Meseres (Ludwig, 1894), family Synallactidae and Order Aspidochirotida. It could be Meseres macdonaldi (Ludwig, 1894; Sluiter, 1901), as were those reported from the central eastern Pacific Ocean between 1 644 m and 2 149 m (appendix 3).
Fig. 32. Photograph taken by the ‘Epaulard’ at the NIXO 45 site: mixed nodule-facies (C and B), holothurian *Pseudostichopus mollis* (HOL 7) © Ifremer

Fig. 33. Photograph taken by the ‘Epaulard’ at the NIXO 45 site: nodule-facies C, holothurian *Pseudostichopus mollis* (HOL 7) © Ifremer

Fig. 34. Photograph taken by the ‘Epaulard’ at the NIXO 45 site: nodule-facies O, holothurian *Meseres macdonaldi* (HOL 8) © Ifremer

Fig. 35. Photograph taken by the ‘Nautile’ during the NIXONAUT cruise: mixed nodule-facies (C and B), tumulus with holothurian *Mesothuria murrayi* (HOL 9) © Ifremer
HOL 10

This taxon measures 20 to 25 cm long and 5 to 7 cm wide (figures 36, 37). It appears translucid and bears a long tapering projection on top of its anterior end. Its ventro-lateral podia are easily distinguished, few in number, relatively well spaced and independent, giving the impression of raising the body. The loop formed by the intestinal tract can be distinguished through the dorsal translucid septum, and at the anterior end of the animal is a region that reflects light. This is situated exactly at the level of the peripharyngeal cavity where the radiating conjuncto-muscular flanges are encrusted with calcareous bodies capable of reflecting light.

The holothurian HOL 10 has been found on all types of substratum, including sedimentary rocky, and with poly-metallic nodules. It does not appear to be mesopelagic, never having been seen in the water column. It has not been observed in the Peruvian Basin nor the Bay of Biscay though forms morphologically similar to *Peniagone* sp. have been identified (Sibuet et al., 1980; Bluhm, 1994; Kaufman & Smith, 1997; Bluhm & Gebruk, 1999).

The proposed identification after referring to the literature (Hansen, 1975) and based on the opinion of specialists is *Peniagone papillata* (Hansen, 1975), family Elpidiidae, Order Elasipodida. This taxon has been collected particularly in the Clarion-Clipperton fracture zone at 3570 m. Its external characteristics are an elongated body, a soft, whitish tegument, eight to nine pairs of podia decreasing in size towards the posterior and situated in the posterior 2/3 of the ventral sole. It possesses four or five pairs of dorsal papillae of which the first and sometimes the second pair are independent, long and slender.

This taxon resembles a pink-tinted translucent species from the abyssal depths of the Peruvian Basin, identified as *Peniagone gracilis* (Bluhm & Gebruk, 1999). However, it was characterised by having podia only in the posterior half or 2/3rds of the body.

The independent movement of the ventro-lateral podia of HOL 10 is remarkable and recalls the model of locomotion proposed by Hansen (1972) for *Scotoplanes globosa* (Théel, 1879), another member of the Elpidiidae. Its podia communicate with wide water-filled cavities in the tegument, and local constriction of the latter, by peristaltic movements of the epidermal muscles, allows the independent movement of the podia. This suggests an adaptation to locomotion on soft substrata in abyssal environments (Hansen, 1975).

HOL 11

This holothurian, 17 to 20 cm long and 5 to 8 cm wide, resembles the previous taxon in its translucent texture through which one can see the loop of the intestinal tract, and a white mark, which reflects the light, situated at the peripharyngeal level (figure 38). Nevertheless, it appears flatter and bears marginal fringes that hide the ventro-lateral podia. A short velum in the nuchal part is formed by the fusion of the dorsal anterior papillae, and seems to unite four or five short projections. HOL 11 has been observed on all types of substrata but never in the water column.

Lauerman et al. (1996) and Kaufman & Smith (1997) recorded this taxon at their station further north at 4100 m, but it has not been found in the Peruvian Basin (Bluhm & Gebruk, 1999), nor does it appear to be present in the Bay of Biscay (Sibuet et al., 1980).

We propose as a hypothesis of identification a member of either the genus *Amperima* (Pawson, 1965) or *Peniagone* (Théel, 1882), family Elpidiidae and Order Elasipodida. HOL 11 and the following taxa (HOL 12 to HOL 15) share the characteristics of the groups *Peniagone* and *Amperima* (and part of the group *Ellipinion*), that is, an ovoid body, a wide velum consisting of two pairs of papillae, of which the median ones are generally longer than the laterals, podia bordering the posterior half or third of the body or distributed uniformly along the two lateral parts of the body.

Identification can not be taken further without a detailed study of the spicules. However, based on the literature (Théel, 1882; Ludwig, 1894; Clark, 1920; Hansen, 1975), one could compare this taxon with *Peniagone vitrea* (Théel, 1882) which has been collected in the region (between 10°N-10°S, cf. appendix 3). The external characteristics of this holothurian are an elongated body, a wide velum that can be folded either towards the anterior or the posterior, and 6 to 9 pairs of podia that decrease in size towards the posterior and border the posterior third of the ventral sole. As in most of the Elasipods, members of the genera *Amperima* and *Peniagone* comb a superficial film of sediments leaving few traces of their passage (Massin, 1982).
Fig. 36. Photograph taken by the 'Nautile' at the NIXO 45 site: cliff, holothurian Peniagone papillata (HOL 10)
© Ifremer

Fig. 37. Photograph taken by the 'Epaulard' at the NIXO 45 site: mixed nodule-facies B and plates: holothurian Peniagone papillata (HOL 10)
© Ifremer

Fig. 38. Photograph taken by 'E.D.1' during the Copano cruise: nodule-facies B, holothurian Peniagone vitrea (HOL 11)
© Ifremer
HOL 12

This taxon only differs from the preceding one by its velum, which is formed by two small anterio-dorsal projections (figure 39). It can reach 20 cm in length and 8 cm width, and is found on all substrata but never in the water column.

Pawson & Foell (1983) found this holothurian at the DOMES C site in the Clarion-Clipperton fracture zone. Lauerman et al. (1996) and Kaufman & Smith (1997) have also identified it at 4100 m at a station further north and close to the central part of the Californian coast. This taxon has also been found in the abyssal depths of the Peruvian Basin (Bluhm & Gebruk, 1999) where it appears translucid brown. In contrast, no similar holothurian has been found in the Bay of Biscay (Sibuet et al., 1980).

Based on the literature (Ludwig, 1894; Hansen, 1975), the proposed identification is a member of the genus *Amperima* (Pawson, 1965) or *Peniagone* (Théel, 1882), family Elpidiidae and Order Elasipodida, or *Achlyonice sp*. (Théel, 1879). *Achlyonice ecalcarea* has been collected between 2 780 m and 4 924 m in the Pacific Ocean (appendix 3), and therefore we suggest this latter identification.

HOL 13

This holothurian is distinguished from the preceding ones by the velum, which is formed of two pairs of dorso-papillae divided into two long projections, two other shorter ones arranged laterally, and a buccal orifice situated on a retractable tube (figures 40, 41). Its body is broader, ovoid and measures up to 30 cm long and 10 cm wide. Its ventral face is bordered by nine or ten pairs of podia decreasing in size towards the posterior.

This taxon has been observed on all types of substrata but never in the water column. This taxon has perhaps been found in photographs from the region of the DOMES sites, recorded as a *Peniagone sp.*, either type 1 or type 2 (Pawson & Foell, 1983). Lauerman et al. (1996) and Kaufman & Smith (1997) did not cite it in their faunistic inventories, nor has it been reported from the Bay of Biscay (Sibuet et al., 1980).

The proposed identification, based on the literature (Ludwig, 1894; Clark, 1920b; Hansen, 1975; Madsen, 1953) and in agreement with the specialists, is *Peniagone purpurea* (Théel, 1882), as in the case of specimens collected in the Indo-Pacific region (cf. appendix 3). *Peniagone purpurea* has the following external characteristics: a thickest body with seven to nine pairs of podia, the first two being independent and ventral while the other five to seven pairs are close together and partly fused. The velum consists of two pairs of very long, thin papillae joined together at the base. The edge of the velum is prolonged in a lateral fringe covering the podia.

In the figures, the velum sometimes appears folded towards the anterior with the extremities emerging on the substratum, or sometimes it is held high, almost perpendicularly. This could have various functions, sensory and perhaps even respiratory, by increasing the surface area of the body and facilitating the exchange of fluids in the water-vascular system by its movements (Hansen, 1975).
Fig. 39. Photograph taken by the ‘Epaulard’ at the NIXO 45 site: mixed nodule-facies C, holothurian Achlyonice ecalcarea (HOL 12) © Ifremer

Fig. 40. Photograph taken by the ‘E.D.1’ device during the Copano cruise: nodule-facies C, holothurian Amperima rosea (HOL 13) © Ifremer

Fig. 41. Photograph taken by a ‘Troika’ during the Copano 1 cruise: nodule-facies C, holothurian Amperima rosea (HOL 13) © Ifremer

Fig. 42. Photograph taken by the ‘Nautile’ during the NIXONAUT cruise: nodule-facies O, holothurian Peniagone purpurea (HOL 14) © Ifremer
HOL 15

This whitish taxon, maximum dimensions 20 cm long and 5 cm wide, seems to be quite rare in the study zone (figures 43, 44). It does not appear to have a preference in relation to substratum, occurring on nodules or sediments, and it does not appear to be mesopelagic.

This taxon has also been found in the Peruvian Basin (Bluhm & Gebruk, 1999) but was not recorded among the echinoderms in the Bay of Biscay (Sibuet et al., 1980).

Exception for its two large characteristic anterio-dorsal projections, it differs little from the other holothurians of the genera Amperima (Pawson, 1965) or Peniagone (Théel, 1882), family Elpidiidae and Order Elasipodida. As a more precise hypothesis of identification, based on the literature (Théel, 1882; Clark, 1920b; Madsen, 1953; Hansen, 1956, 1975) and the specialists, one could propose Amperima naresi (Théel, 1882), which has been collected in the study zone and is very similar. Its external characters are a body more ovoid than in the other members of the group, and eight to ten pairs of broad ventro-lateral podia, which border the whole sole, decrease in size towards the posterior, and are distributed more or less uniformly along the sides of the body. These podia are slightly fused in the posterior part. The velum, composed of two pairs of papillae, is well developed and can take different forms (Hansen, 1956).

Appendix 3 presents possible identifications for taxa HOL 10 to HOL 15 by describing the holothurians recorded belonging to the genera Amperima (Pawson, 1965) or Peniagone (Théel, 1882). Specimens of Amperima naresi would have come from between 10°S and the central eastern Pacific Ocean, between 2 010 m and 7 130 m depth.

HOL 16

This quite remarkable holothurian measures at the very most 40 cm long and 12 cm wide, with a very large caudal extension held perpendicular to the substratum, and which is about the same length as the body and as wide as the latter in its most expanded part (figures 45, 46). The body is very flattened on the ventral surface and arched dorsally. The extremities are strongly rounded and the whole body is bordered by a wide dark podial fringe on the trivium. The caudal appendage is fleshy and more indented along a median groove. This appendage originates in an upper dorsal region, about 1/4 to 1/3 of the way from the posterior end. This holothurian can be very dark or almost translucent, and the colour photographs taken by the “Nautil” show a bluish tinge for the translucent specimens.

This taxon has been observed on all types of substratum and occasionally in the water column. Pawson & Foell (1983) identified it from the DOMES C site though Kaufman & Smith (1997) did not see it at their station further north-east, and neither did Bluhm (1994; Bluhm & Gebruk, 1999) in the Peruvian Basin. On the other hand, it is present in the Bay of Biscay (Sibuet et al., 1980).

The proposed identification, based on the literature (Théel, 1882; Hérouard, 1902, 1923; Deichmann, 1940; Madsen, 1953) and on the advice of specialists, is Psychropotes semperiana (Théel, 1882), family Psychropotidae, Order Elasipodida. This holothurian has not yet been collected in the study zone nor elsewhere in the Pacific, but only in the Indian and Atlantic Oceans at depths of 3 460 m to 5 600 m.

The translucent versions of this taxon could be either juveniles that become darker in the adult stage (Miller & Pawson, 1990), or they could belong to another species, Psychropotes hyalinus, collected in the Pacific north-east at 5 891 m (Pawson, 1985). This latter species is very close to Psychropotes semperiana but differs in its transparency and the characteristics of its spicules. In addition, it is known to be a facultative swimmer, using its large marginal fringe as fins. Elsewhere it has been collected at 5 m above the substratum at a depth of 5890 m in the tropical north-eastern Pacific Ocean (Pawson, 1985). In films taken by the “Nautil”, one can see it making swimming movements when it contacts the manipulator arm, by twisting then gliding. This could be an avoidance behaviour in case of predation.

The tracks left by this taxon are difficult to see in the numerous photographs from the study zone. That might suggest Psychropotes semperiana, which has relatively small podia on the medio-ventral part of the plantar sole, distributed in two rows of 7 to 25. The nodules appear darker, as if cleaned by the animal’s passage.
Fig. 43. Photograph taken by the ‘Epaulard’ at the NIXO 45 site: nodule-facies C, holothurian, Amperima naresi (HOL 15) © Ifremer

Fig. 44. Photograph taken by the ‘Epaulard’ at the NIXO 45 site: nodule-facies O, holothurian, Amperima naresi (HOL 15) © Ifremer

Fig. 45. Photograph taken by the ‘Epaulard’ at the NIXO 45 site: mixed nodule-facies (C and B), holothurian Psychropotes semperiana (HOL) © Ifremer

Fig. 46. Photograph taken by the ‘Epaulard’ at the NIXO 45 site: nodule-facies C, holothurian Psychropotes semperiana (HOL 16) © Ifremer
**HOL 17**

This holothurian differs from the preceding one particularly in the location of the caudal appendage, which is in the extension of the posterior part of the body, behind the bivium (figures 47, 48, 49, 50). This taxon reaches a maximum of 50 cm in length and 15 cm width with a caudal appendage up to 30 cm long. The latter appears more fleshy and rigid in its first third, and more supple at its extremity, which can be flexed during swimming. The marginal fringe is much less developed than in the preceding species and demarcated from a well-developed peristomal membrane. In some photographs, the tail appears shorter, the peristomal membrane less spreading and the ventro-lateral podia more free and prominent.

This taxon appears very dark in black and white photographs but pale yellow to orange in the colour ones taken by the “Nautile”. In film from the NIXONAUT cruise, it performs a swimming motion, rhythmically arching the axis of its body after inducing a pulsation in its peristomal membrane, in opposition to movement in its caudal appendage. This taxon was only observed on ocean floor with a dense covering of nodules.

Pawson & Foell (1983) have identified this holothurian at the DOMES C site, while Kaufman & Smith (1997) did not see it at 4 100 m. Bluhm (1994) and Bluhm & Gebruk (1999) recorded it in the Peruvian Basin and it is also present in the Bay of Biscay (Sibuet et al., 1980).

Based on the literature (Théel, 1882; Ludwig, 1894; Clark, 1920; Madsen, 1953; Parker, 1963; Bayer, 1970; Hansen, 1975; Luke, 1982) and the advice of specialists, we propose as a hypothesis of identification, *Psychropotes longicauda* (Théel, 1882), family Psychropotidae, Order Elasipodida. This cosmopolitan holothurian has been reported between 2 210 m and 5 203 m (appendix 3). It bears between 7 and 25 pairs of independent podia, 18 peribuccal tentacles, a marginal fringe composed of two to nine pairs of podia and two to eight pairs of very small dorsal papillae. It can take on yellow to deep violet tones, always with the plantar sole darker.

According to Khripounoff & Sibuet (1980), *Psychropotes longicauda* is a detritus feeder, which selects the particles richest in assimilable compounds, and occasionally a scavenger. It has been recorded in all the oceans at depths between 2 210 m and 5 203 m on a great variety of substrata. According to Mortensen (1927), the caudal appendage is used in swimming, though Miller & Pawson (1990) stated that only the juveniles are mesopelagic and some of these have been collected 500 m above the benthos (Billet et al., 1985).
Fig. 47. Photograph taken by the ‘Nautile’ during the NIXONAUT cruise: nodule-facies C, holothurian (collected) Psychropotes longicauda (HOL 17) © Ifremer

Fig. 48. Photograph taken by the ‘Nautile’ during the NIXONAUT cruise: nodule-facies C, holothurian Psychropotes longicauda (HOL 17) © Ifremer

Fig. 49. Photograph taken by the ‘Nautile’ during the NIXONAUT cruise: nodule-facies O, holothurian Psychropotes longicauda (HOL 17) © Ifremer

Fig. 50. Photograph taken by the ‘Epaulard’ at the NIXO 45 site: nodule-facies C, holothurian Psychropotes longicauda (HOL 17) © Ifremer
HOL 18

This swimming holothurian is dark in colour and brown-violet in films taken by the “Nautile” (figures 51, 52, 53, 54). Its fleshy body (maximum dimensions 25 cm long and 10 cm wide), is slightly dorso-ventrally flattened. The anterior part bears a velum combining 12 to 14 broad dorso-ventral papillae into a membrane encircling 3/4 of the body. The anterio-ventral branch is encircled by 20 small tentacles whose extremities are divided in dendritic ramifications. The ventro-lateral podia are divided into two groups, one forming two fans each with six to nine pairs of long podia joined together posteriorily, and the other with three to six pairs of anterior, more rudimentary, podia.

Most of the time this holothurian is seen swimming over a great variety of facies of nodules and sediments. The tracks it leaves on the substratum are formed by the weight of the body resting on the ends of the three or four pairs membranous posterior podia and by the terminal parts of the folded tentacles. When following the swimming movements in film taken by the “Nautile”, the interval for each propulsion was estimated at 5 seconds. Miller & Pawson (1990) recorded a cycle of 7.5 seconds, during which the animal stayed vertical and beat the water by negative rheotropism with an undulating movement of its velum.

Pawson & Foell (1983) identified this holothurian at the DOMES C site although Kaufman & Smith (1997) did not find it at 4100 m at their station further northeast in the Pacific Ocean, perhaps because it has a more mesopelagic lifestyle. Bluhm (1994) and Bluhm & Gebruk (1999) definitely identified it in the Peruvian Basin, and it is also present in the Bay of Biscay (Sibuet et al., 1980).

The hypothesis of identification, based on the literature (Pawson, 1976, 1982; Ohta, 1985; Miller & Pawson, 1990) and the advice of specialists, is Enypniastes eximia (Théel, 1882), family Pelagothuriidae and Order Elasipodida. This holothurian has been observed swimming between 2.5 m and 5 m above the substrate, except for young specimens, which have been collected more than 3000 m above the bottom by Billett et al. (1985), or even at the ocean surface (Hérouard, 1923). Details of its swimming were described by Ohta (1985) and Miller & Pawson (1990). However, in photographs and films from the Clarion-Clipperton fracture zone, Enypniastes eximia adopts a swimming posture typical of currents, and uses its velum as a sail, opposed to the direction of the current, and its ventro-lateral podia as brakes. According to in situ observations, young E. eximia are smaller and translucent pink in colour (Billett et al., 1985; Miller & Pawson, 1990).

Enypniastes eximia is known to be cosmopolitan and has been recorded at depths between 516 m and 5689 m (appendix 3). This holothurian spends 10% of its time on the substratum in order to ingest sediment in a non-selective manner (Miller & Pawson, 1990). Thus it is not a suspension feeder and does not feed in the water column (Ohta, 1985). However, it could be at an intermediate stage of evolutionary adaptation to an essentially mesopelagic life, as seen in Pelagothuria natatrix (Ludwig, 1894; Chun, 1900; Etman, 1926). The latter is presumed to be a suspension feeder since it has only been collected in the water column (Ohta, 1985).
Fig. 51. Photograph taken by the ‘Epaulard’ at the NIXO 45 site: nodule-facies C, holothurian (swimming) Enypniastes eximia (HOL 18) © Ifremer

Fig. 52. Photograph taken by the ‘Nautile’ during the NIXONAUT cruise: nodule-facies C, holothurian (swimming) Enypniastes eximia (HOL 18) © Ifremer

Fig. 53. Photograph taken by the ‘Epaulard’ at the NIXO 45 site: nodule-facies C, holothurian Enypniastes eximia (HOL 18) © Ifremer

Fig. 54. Photograph taken by the ‘Epaulard’ at the NIXO 45 site: nodule-facies C, holothurian Enypniastes eximia (HOL 18) © Ifremer
HOL 19

This taxon with an ovoid body can measure up to 32 cm long by 10 cm wide (figures 55, 56, 57, 58, 59, 60), and in situ, it is bright pink. The velum is formed by four dorsal papillae of which the central pair is longer than the laterals. At the posterior of the body are four pairs of ventral, membranous podia, laterally arranged. The mouth is in a retractable tube oriented towards the posterior. About ten tentacles, branched at their ends, surround the mouth and folds mark the dorsal surface of the body. A membranous fringe joins the velum to the ventro-posterior podia laterally.

In photographs and film from the “Nautili,” this holothurian is mostly seen swimming. Whether suspended vertically and maintaining its flotation by beating its buccal tentacles, or with its body-axis parallel to the substratum, it propels itself by flexing its body, which is bent at the level of the velum, in rhythmic opposition to the pulsation of its ventro-posterior podia. When on the substratum, it feeds from the superficial film covering the nodules and sediments with the aid of its tentacles, which are forked at their ends (figure 60). The axis of the mouth and tentacles form a right angle in relation to the axis of the squat body, held up by the two series of ventro-posterior podia.

Pawson & Foell (1983) identified this holothurian at the DOMES C site although Kaufman & Smith (1997) did not find it, perhaps because it lives mostly in the water column. Bluhm (1994) and Bluhm & Gebruk (1999) did not record it in the Peruvian Basin, though it is present in the Bay of Biscay at a depth of 3000 m (Sibuet et al., 1980).

The hypothesis of identification proposed on the basis of literature (Théel, 1882; Herouard, 1899, 1902, 1923; Madsen, 1953; Barnes et al., 1976) and the advice of specialists is Peniagone diaphana (Théel, 1882), family Elpidiidae, Order Elasipodida. This species has been collected in the Pacific, Atlantic and Indian Oceans at depths between 1 520 m and 5 600 m (appendix 3). Peniagone diaphana has been observed from a submersible (Barnes et al., 1976) in such a way that its rhythmic swimming pulsations could be determined as 10 to 20 cycles per minute. It is known that it can maintain itself vertically in the water column for more than 12 hours and it was once found at more than 70 m above the bottom surface. According to Hansen (1975), the specific weight of this pelagic species is close to that of water, and it utilises currents as a means of displacement.

An interesting hypothesis for the function of its swimming movements has been proposed by Barnes et al. (1976). They suggest that they facilitate respiration and cause a current that puts particles of detritus from the water-sediment boundary into suspension, and which thus feed the animal. The hypothesis was proposed because Peniagone diaphana seems to be essentially mesopelagic, having been observed from a submersible to spend more than 12 hours continuously in the water column. It seems to be a suprabenthic detritus feeder on the basis of the contents of its digestive tract, which include the tests of Foraminifera, spicules of sponges and holothurians, as well as other detritus of benthic origin. Barnes et al. (1976) attributed a special feeding behaviour to it, that of a detritus feeder with the lifestyle almost of an agile suspension feeder. However, just as in Peniagone leander, this taxon may perhaps sometimes settle on the substratum in order to feed itself, like all detritus feeders, and the long time spent in the water column could perhaps be an artefact caused by the presence of the submersible disturbing its usual way of life.
Fig. 55. Photograph taken by the 'Nautile' during the NIXONAUT cruise: nodule-facies C, holothurian (swimming) Peniagone leander (HOL 19) © Ifremer

Fig. 56. Photograph taken by the ‘Epaullard’ at the NIXO 45 site: nodule-facies C, holothurian (swimming) Peniagone leander (HOL 19) © Ifremer

Fig. 58. Photograph taken by a ‘Troïka’ during the Copano 1 cruise: nodule-facies C, holothurian (swimming) Peniagone leander (HOL 19) © Ifremer

Fig. 57. Photograph taken by the ‘Epaullard’ at the NIXO 45 site: nodule-facies C, holothurian (swimming) Peniagone leander (HOL 19) © Ifremer

Fig. 59. Photograph taken by the ‘Nautile’ during the NIXONAUT cruise: nodule-facies C, holothurian on the ocean floor Peniagone leander (HOL 19) © Ifremer

Fig. 60. Photograph taken by the ‘Nautile’ during the NIXONAUT cruise: nodule-facies C, holothurian (swimming) Peniagone diaphana (HOL 20) © Ifremer
HOL 21

This holothurian measures up to 55 cm long and 5 cm wide and its body is cylindrical to fusiform (figures 61, 62, 63, 64, 65, 66). In colour it is dark purple or violet with paler patches. The dorsal papillae form an irregular fringe around the anterior dorsal extremity. The oral region bears tentacles and is directed ventrally. Two rows of small more or less protruding papillae are aligned on the dorsal surface. The posterior ends in a blunt point, sometimes with some short tapering projections. The non-gelatinous tegument resembles leather. This holothurian appears entirely benthic since it has never been reported from the water column. It has been found on different types of nodule substrata and purely sedimentary ones. Its tracks on sediments are characterised by a double row of relatively large and well-spaced ventro-lateral podia, and by an absence of medio-ventral podia.

Pawson & Foell (1983) identified this holothurian from the DOMES C site although it was not recorded in the inventories of Kaufman & Smith (1997) or Lauerman et al. (1996). Bluhm (1994) and Bluhm & Gebruk (1999) found it in the Peruvian Basin and it has been recognised in photographs from the Bay of Biscay in the north Atlantic Ocean (Sibuet et al., 1980).

The hypothesis of identification in agreement with Pawson (pers. comm.) is *Psychronaetes hanseni* (Pawson, 1983), family Laetmogonidae, Order Elasipodida, which has been collected in the central Pacific Ocean and especially in the study zone, between 4 800 m and 5 200 m (appendix 3). Externally, the holotype does not have peribuccal papillae but has 15 tentacles with broad oral discs and small short stalks. The 15 ventro-lateral podia per row are approximately 10 mm long and 8 mm wide, triangular in shape and evenly distributed. The dorsal papillae are arranged in two rows with 30 in each row. At the anterior end, about 15 papillae, measuring 15 mm long by 9 mm wide for the largest, form an irregular fringe.
Fig. 61. Photograph taken by the 'Nautile' during the NIXONAUT cruise: capture of a holothurian *Psychronaetes hanseni* (HOL 21) © Ifremer

Fig. 62. Photograph taken by 'Deep Tow' at the Echo I site: nodule-facies C, holothurian *Psychronaetes hanseni* (HOL 21) © Ifremer

Fig. 63. Photograph taken by the 'Epaulard' at the NIXO 45 site: nodule-facies C, holothurians *Psychronaetes hanseni* (HOL 21) and *Oniropranta mutabilis* (HOL 4) © Ifremer

Fig. 64. Photograph taken by the 'Nautile' during the NIXONAUT cruise: nodule-facies O, holothurian *Psychronaetes hanseni* (HOL 21) © Ifremer

Fig. 65. Photograph taken by the 'Nautile' during the NIXONAUT cruise: nodule-facies C, holothurian *Psychronaetes hanseni* (HOL 21) © Ifremer

Fig. 66. Photograph taken by the 'Nautile' during the NIXONAUT cruise: on ancient dredge tracks, two holothurians *Psychronaetes hanseni* (HOL 21) and *Mesothuria murrayi* (HOL 9) © Ifremer
HOL 22

This holothurian can reach up to 35 cm in length and 12 cm width (figure 67). It has a very dark tegument and in consequence, the detail of the dorsal surface is very difficult to discern. In some photographs, however, a double row or bands of dorsal papillae can be seen, as well as a marginal fringe bordering the sides of the body. In addition, it is characterised by the absence of a distinct anterior region, as was the case for the preceding taxon. HOL 22 is the only holothurian observed in the study zone that leaves a trail free of nodules on substrata with a dense covering of nodules. This gives an idea of its mass and power and the perturbation caused in the edaphic environment by its passage. It has never been seen in the water column.

Pawson & Foell (1983) identified similar holothurians from the DOMES C site, though Kaufman & Smith (1997) and Lauerman et al. (1996) did not record it. Bluhm (1994) and Bluhm & Gebruk (1999) reported comparable taxa in the Peruvian Basin, and it is also present in photographs from the Bay of Biscay in the northern Atlantic Ocean (Sibuet et al., 1980).

The hypothesis of identification proposed by reference to the literature (Théel, 1879, 1882, 1886a, 1886b; Ludwig, 1894; Madsen, 1953; Hansen, 1975; Luke, 1982) and specialists is a member of the Order Elasipodida and family Laetmogonidae, Laetmogone sp. Holothurians identified as Laetmogone wyville thomsoni (Theel, 1879; Madsen, 1953) have been collected in the north-east and south-east Pacific Ocean (cf. appendix 3).

HOL 23

This holothurian measures up to 30 cm long and 6 cm wide (figures 68, 69, 70, 71). Its dark body is semi-cylindrical, flattened on the ventral surface and supported by a broad podial fringe. In black and white photographs it appears dark, and in colour photographs, pale violet-brown on the dorsal surface with much darker shades on the ventral planter surface. In figure 69, one can distinguish two dorsal tapering papillae perpendicular to the axis of the body. One small dorsal apophysis is situated approximately 1/4 of the way from the posterior end. The broad podial fringe is used in swimming, putting the holothurian in a medio-transverse plane while keeping the dorsal apophysis upright (figure 71). This holothurian has been observed on all types of ocean floor and its tracks are easily discernible (figure 70).

Pawson & Foell (1983) identified it from the DOMES C site though it has not been recorded by Kaufman & Smith (1997) or Lauerman et al. (1996) at the station further north-east at 4100 m. Bluhm (1994) and Bluhm & Gebruk (1999) also found it in the Peruvian Basin, but it has not been seen in the Bay of Biscay in the north Atlantic Ocean (Sibuet et al., 1980).

The proposed identification, based on the literature (Ludwig, 1894; Koehler et Vaney, 1905; Clark, 1920; Madsen, 1953; Hansen, 1956, 1975) and the opinion of specialists, is Psychropotes verrucosa (Ludwig, 1894), family Psychropotidae and Order Elasipodida. This holothurian exhibits the external characters that can be seen in some photographs, such as 15 or 16 peribuccal tentacles, one to four pairs of small dorsal papillae, a conical and retractable dorsal appendage, a marginal fringe composed of ventro-lateral podia and their water-vascular system, and a tegument covered with excrescences that each contain a giant spicule in the form of a cross; in older individuals, the tegument has longitudinal bands of transverse ridges. One can explain the absence of definite tracks on the substratum by the fact that this taxon only has medio-ventral podia (56 pairs).

This species has been reported from many localities from the Indian to the eastern Pacific Ocean at depths varying between 2417 m and 7250 m (appendix 3), but never in the water column.
Fig. 67. Photograph taken by the 'Epaulard' at the NIXO 45 site: nodule-facies C, holothurian Laetmogone sp. (HOL 22) © Ifremer

Fig. 68. Photograph taken by the 'Epaulard' at the NIXO 45 site: nodule-facies O, holothurian Psychropotes verrucosa (HOL 23) © Ifremer

Fig. 69. Photograph taken by the 'Epaulard' at the NIXO 45 site: mixed nodule-facies (C and B), holothurian Psychropotes verrucosa (HOL 23) © Ifremer

Fig. 70. Photograph taken by the 'Epaulard' at the NIXO 45 site: nodule-facies C sparse, holothurian Psychropotes verrucosa (HOL 23) © Ifremer

Fig. 71. Photograph taken by the 'Nautili' at the NIXO 45 site: nodule-facies O, holothurian (swimming) Psychropotes verrucosa (HOL 23) © Ifremer
HOL 24

This holothurian measures 20 to 30 cm long and 5 to 7 cm wide (figure 72). Its very dark, smooth tegument reflects light, as though armoured and marked by transverse folds. A relatively thin podial fringe encircles the body. The anterior region is very distinct and almost hexahedral in shape. It occurs on sedimentary facies and rock outcrops but has never been observed in the water column, and its tracks can not be discerned. Outside the study zone, it has not been seen in photographs from the Peruvian Basin nor those from the Bay of Biscay.

The proposed identification is a member of the family Psychropotidae, Order Elasipodida. The identification can not be taken further, either by reference to the literature (Sluiter, 1901; Heding, 1940; Hansen, 1975) or to specialists, because this species was previously unknown to science. It has certain characteristics in common with Benthodytes sibogae (Sluiter, 1901; Hansen, 1975) that has been collected around Indonesia between 694 m and 2 798 m.

HOL 25

This taxon is about 30 cm long and 10 cm wide, very flattened and dark, and is found on all types of sedimentary facies and with nodules (figures 73, 74). The podial margin is developed and continuous with the widely spreading peribuccal tentacles. Unfortunately the dark dull colour of the tegument prevents any morphological detail from being distinguished, and the tracks left by its passage could not be seen either. One individual of HOL 25 was filmed on a voyage during the NIXONAUT cruise, raising itself half way up the side of a cliff and then diving, flattened, with the aid of its broadly spread fringe in order to alight several metres lower. This was perhaps a reaction to the approach of the “Nautilus” or done under the influence of its hydrodynamic turbulence.

The hypothesis of identification based on the literature (Théel, 1879, 1882, 1886a, 1886b; Ludwig, 1894; Madsen, 1953; Hansen, 1975; Luke, 1982) and specialists is a member of the Order Aspidochirotida, family Synallactidae, Paelopatides sp. (Théel, 1886). Paelopatides confundens (Théel, 1886) has been recorded in the north and south-east Pacific Ocean, especially in the study zone between 450 m and 4 070 m and P. suspecta at 2 323 m at 8°N in the Pacific (appendix 3).

Pawson & Foell (1983) identified Paelopatides species of similar appearance at the DOMES C site. Kaufman & Smith (1997) and Lauerman et al. (1996) did not find this genus at their station. Bluhm (1994) and Bluhm & Gebruk (1999) have also recorded Paelopatides in the Peruvian Basin that were brown-orange in colour and had a somewhat convex dorsal surface and two rows of short papillae. Similar taxa have been reported from the Bay of Biscay in the northern Atlantic Ocean (Sibuet et al., 1980).

According to Gage et al. (1985), holothurians identified as Paelopatides sp. have been photographed in the north-east Atlantic Ocean at 1942-1949 m and at 1100 m in the north-east Pacific Ocean. They appeared to flee with a sinusoidal motion at the approach of the trawl.
Fig. 72. Photograph taken by the 'R.A.I.E.' at the NIXO 42 site: mixed nodule-facies O and rock, holothurian Benthodytes sibogae (HOL 24) © Ifremer

Fig. 73. Photograph taken by the 'Epaulard' at the NIXO 45 site: nodule-facies O, holothurian Paelopatides confundens (HOL 25) © Ifremer

Fig. 74. Photograph taken by the 'Epaulard' at the NIXO 45 site: nodule-facies O, holothurian Paelopatides sp. (HOL 25) © Ifremer
HOL 26

This holothurian measures 16 to 20 cm in length and 7 cm width (figure 75). It is very flattened, paler in colour than HOL 25 and with the edges and the dorsal median groove darker. The extremities of the body are rounded. One distinctive external character is the presence of some long tapering dorsal papillae. This holothurian has only been observed on surfaces with nodules, where its tracks are indistinct, and never in the water column, although it has a morphology suitable for vertical movement due to the presence of a broad podial fringe (Hansen, 1975).

Pawson & Foell (1983) identified similar taxa from the DOMES C site. Kaufman & Smith (1997) and Lauerman et al. (1996) did not find this genus at their station, and neither did Bluhm (1994; Bluhm & Gebruk, 1999) in inventories from the Peruvian Basin. This taxon also seems to be absent from the Bay of Biscay in the north Atlantic Ocean (Sibuet et al., 1980).

The identification proposed, based on the literature (Théel, 1882; Ludwig, 1894; Perrier, 1896, 1902; Koehler et Vaney, 1905; Clark, 1913, 1920, 1923a, 1923b; Oshima, 1915, 1916, 1919; Grieg, 1921; Herouard, 1923; Deichmann, 1930, 1940, 1954; Heding, 1940; Madsen, 1953; Hansen, 1975) and on the advice of specialists is Pannychia moseleyi (Théel, 1882), family Laetmogonidae. It has been recorded in the north, south-east and south-west Pacific Ocean at depths varying between 212 m and 2 599 m (appendix 3). External characters of this taxon are 20 tentacles, ventro-lateral podia in a double row to the extremities (34 to 45 podia per row), which terminate in discs in the form of suckers, 40 smaller medio-ventral podia, numerous small papillae distributed over all the body, and 10-20 longer papillae arranged bilaterally on the dorsal radii.

HOL 27

This taxon is characterised by a flattened, elongated body with a well developed lateral fringe (figure 76). It measures a maximum of 20 cm long and 7 cm wide. The lateral fringe has a dark tinge contrasting with the pale or sometimes off-white dorsal surface that has a speckled appearance. It has never been seen swimming although its morphology would be suitable. Östergren (1938) suggested that this bicoloured pattern could be an aid to escaping predation by swimming, as in numerous Elasipods. This taxon has only been observed on facies with nodules and it does not leave any visible trail in photographs. A similar taxon appears in the photographs from the Bay of Biscay but it does not show the bicoloured pattern seen in the holotype HOL 27.

The identification proposed by reference to the literature (Théel, 1882, 1886; von Marenzeller, 1893; Ludwig, 1894; Perrier, 1896, 1902; Koehler et Vaney, 1905; Clark, 1913, 1920, 1923a, 1923b; Oshima, 1915, 1916, 1919; Grieg, 1921; Hérouard, 1923; Deichmann, 1930, 1940, 1954; Heding, 1940; Madsen, 1953; Hansen, 1975) and on the advice of specialists is a holothurian of the genus Benthodytes, family Psychropotidae, Order Elasipodida. It most closely resembles Benthodytes typica (Théel, 1882) which has been reported between 315 m and 4 700 m between 8°N and 6°S in the Pacific Ocean (appendix 3). The external characters of Benthodytes typica are, among others, 15 to 20 peribuccal tentacles, circum-oral papillae and well pigmented water-vascular system on the ventro-lateral podia that is equally visible from the dorsal and ventral surfaces. The dorsal papillae are few (three or four pairs), small and aligned in two rows along the anterior part of the dorsal radii. The tegument is soft and mucosal for most of the time. The speckled appearance of the dorsal tegument comes from the fact that it is covered with small mauve swellings on a dark back ground. The ventral surface is uniformly dark violet.

This taxon is fairly cosmopolitan having been reported at depths varying between 315 m and 4 700 m. According to Miller & Pawson (1990), specimens have been collected in the Atlantic Ocean up to an altitude of 3 400 m above the bottom, indicating that only the juvenile forms are bentho-pelagic (Grieg, 1921; Billett et al., 1985).

A similar form, Benthodytes sanguinolenta (Théel, 1882), from in the north-east Pacific Ocean, has also been found in the Peruvian Basin, where it is relatively abundant. It is an active swimmer and moves by rhythmic flexing.
Fig. 75. Photograph taken by ‘Deep Tow’ at the Echo 1 site: nodule-facies C, holothurian Pannychia moseleyi (HOL 26) © Ifremer

Fig. 76. Photograph taken by the ‘Epaulard’ at the NiXO 45 site: nodule-facies B, holothurian Benthodytes typica (HOL 27) © Ifremer
HOL 28

This holothurian measures 17 to 25 cm long by 2 to 4 cm wide (figures 77, 78). It appears flattened with the extremities rounded. In photographs taken by the “Nautile”, it is pale violet with clearly darker shades along the podial fringe and at the anterior extremity, which is slightly more developed. On the dorsal surface, two rows of long dispersed papillae can be distinguished, turned down towards the substratum. Just as in the preceding taxa, no trail could be detected after its passage over ocean floor covered in nodules. This taxon appears to prefer a habitat with a relatively dense covering of nodules and does not appear to be mesopelagic, never having been seen in the water column.

Pawson & Foell (1983) identified Benthodytes incerta at the DOMES C site. Kaufman & Smith (1997) and Lauerman et al. (1996) did not find it at their station further to the north-east, and neither did Bluhm (1994; Bluhm & Gebruk, 1999) in inventories of the Peruvian Basin. It also appears to be absent from the Bay of Biscay in the northern Atlantic Ocean (Sibuet et al., 1980).

The proposed identification, based on the literature (Ludwig, 1894; Oshima, 1915, 1915-1919; Clark, 1920; Madsen, 1953; Hansen, 1975) and on the advice of specialists, is Benthodytes incerta (Ludwig, 1894), family Psychropotidae, Order Elasipodida. Benthodytes incerta has been collected in the tropical east Pacific Ocean and around Japan at depths varying from 2 417 m to 4 087 m (appendix 3). It has as external characters a semi-cylindrical body, a firm tegument finely covered with swellings, 9 to 15 tentacles, a narrow podial fringe delimiting the well defined ventral sole, six to nine filiform or conical dorsal papillae in two rows, 9-15 tentacles, circum-oral papillae, a contractile peribuccal membrane, often turned down over the tentacles, and medio-ventral podia arranged irregularly in a double row.

HOL 29

This dark taxon measures between 15 and 20 cm long and 2-3 cm wide (figure 79). It has some long scattered dorsal papillae extending over the dorsal radii. The peribuccal region is clearly distinct from the rest of the body. It is never found in the water column but is present on all types of facies with nodules and it leaves no visible trail.

Pawson & Foell (1983) have identified three sorts of Benthodytes from the DOMES C site, Benthodytes sp., B. incerta and B. typica, one of which is similar to HOL 29. Kaufman & Smith (1997) and Lauerman et al. (1996) did not record Benthodytes sp. at their station. Bluhm (1994) and Bluhm & Gebruk (1999) reported two types of Benthodytes in their inventories from the Peruvian Basin, as well as Benthodytes sanguinolenta, which is very characteristic of this zone. This taxon was not recognised in photographs from the Bay of Biscay (Sibuet et al., 1980).

We propose as a hypothesis of identification, based on the literature (von Marenzeller, 1893; Ludwig, 1894; Perrier, 1896; Clark, 1920; Deichmann, 1930, 1940, 1954; Heding, 1940, 1942; Hansen, 1956, 1975) and the advice of specialists, a holothurian that is probably new to science and related to the genus Benthodytes, B. sp. type 2 (Théel, 1882), family Psychropotidae and Order Elasipodida. One possibility would be Benthodytes lingua (Perrier, 1896), which is characterised by a pedal sole scarcely differentiated from the rest of the body, filiform and conical dorsal papillae in up to 12 pairs, and rounded ends to the body. Benthodytes lingua has been collected in the Atlantic Ocean (04°05’N, 02°13’O) at 2 100 m depth.

HOL 30

This holothurian measures about 30 cm long by 5 cm wide (figures 77, 78). The tegument is off-white seems randomly speckled by numerous small papillae. The body appears cylindrical and rounded at the extremities. This taxon only appears on nodular ocean floor and does not seem to be mesopelagic.

In referring to the literatures (Ludwig, 1893, 1894; Clark, 1920; Hansen, 1966) and on the advice of specialists, we propose as a hypothesis of identification a species of the genus Mesothuria (Théel, 1886), family Synallactidae, Order Aspidochirotida. Three members of this genus have been collected not far from the study zone: Mesothuria megapoda (Clark, 1920) at 4 245 m in the central east Pacific Ocean, Mesothuria murrayi (Théel, 1886) corresponds to HOL 9 described previously, and Mesothuria multipes (Ludwig, 1893) from the Indian Ocean and the central east Pacific Ocean between 725 m and 4 064 m depth (appendix 3).

Pawson & Foell (1983) did not identify any Mesothuria species from the DOMES C area except for M. murrayi, and the same is true for Bluhm & Gebruk (1999) in the Peruvian Basin.
Fig. 77. Photograph taken by the ‘Epaulard’ at the NIXO 45 site: nodule-facies C, holothurian Benthodytes incerta (HOL 28) © Ifremer

Fig. 78. Photograph taken by the ‘Nautilie’ during the NIXONAUT cruise: facies of plates, holothurian Benthodytes sp. type 1 (HOL 6) © Ifremer

Fig. 79. Photograph taken by ‘Deep Tow’ at the Echo I site: mixed nodule-facies with plates (B and C), holothurian Benthodytes sp. type 2 (HOL 29) © Ifremer

Fig. 80. Photograph taken by the ‘Epaulard’ at the NIXO 45 site: nodule-facies C, holothurian Mesothuria sp. (HOL 30) © Ifremer

Fig. 81. Photograph taken by the ‘Epaulard’ at the NIXO 45 site: nodule-facies C, holothurian Mesothuria sp. (HOL 30) © Ifremer
HOL 31

These small holothurians 3-5 cm long and 1-2 cm wide are difficult to see and can be found on all types of ocean floor. They can sometimes be confused with other organisms such as sponges, molluscs or crustaceans. The body is almost globular and bears some long dorsal papillae and long, widely spaced, latero-ventral podia. This taxon is only seen on sedimentary surfaces. The small size of these holothurians is perhaps the reason why they were not distinguished in photographs from the Peruvian Basin.

Based on the literature (Clark, 1920; Hansen, 1956, 1967, 1975; Belyaev 1971; Lemche et al., 1976) and specialist advice, identification proposed is a member of the family Elpidiidae, Order Elasipodida. Scotoplanes globosa (Théel, 1879), a cosmopolitan holothurian which has been recorded in the study zone, is a possibility, or Scotoplanes clarki (Hansen, 1975), which has only been collected in the central eastern Pacific Ocean (10°N, 10°S) at depths between 3 570 m and 5 107 m (appendix 3). These holothurians both have two or three pairs of long dorsal papillae, five to seven pairs of ventral podia and 10 peribuccal tentacles. A smooth tegument and rigid dorsal papillae would correspond to the external characters of Scotoplanes globosa, while a tegument covered with swellings and long, thin dorsal papillae are characteristic of Scotoplanes clarki. These holothurians can measure up to 9 cm. They have a very special mode of locomotion, as mentioned previously for HOL 10, using their long latero-ventral podia activated independently by the constriction of cavities of the water-vascular system contained in the dermis (Hansen, 1972). Some Scotoplanes species are known to be occasional scavengers, feeding in fish carcasses (Pawson, 1976).

The collected holothurians, which on the advice of specialists appear similar to the taxa identified in the Clarion-Clipperton fracture zone, are presented in appendix 3 with their geographic and bathymetric distribution.
Appendix 1

List of codes

XEN  Xenophyora, Cl. Xenophyophorea, Supercl. Rhizopoda, Phyl. Protozoa
SPO  Sponges, Phyl. Porifera
HYD  Hydroids, O. Hydroidea, Cl. Hydrozoa, Phyl. Cnidaria
MED  Siphonophores, O. Siphonophora, Cl. Hydrozoa, Phyl. Cnidaria
SIF  Octocorallarians, O. Gorgonacea and O. Pennatulacea, Cl. Anthozoa, Phyl. Cnidaria
CER  Ceriantharians, O. Ceriantharia, Cl. Anthozoa, Phyl. Cnidaria
CTEN  Ceriantharians, O. Ceriantharia, Cl. Anthozoa, Phyl. Cnidaria
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. Echiurida
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
CRI  Crinoids, Cl. Crinoidea, Phyl. Echinodermata
AST  Seastars, Subcl. Somasteroidea, Cl. Asteridae, Phyl. Echinodermata
OPH  Brittle stars, Subcl. Ophiuroidea, Cl. Asteridae, Phyl. Echinodermata
OUR  Sea urchins, Cl. Echinoidea, Phyl. Echinodermata
HOL  Sea cucumbers, Cl. Holothuroidea, Phyl. Echinodermata
ENT  Epibenthic hemichordates, Cl. Enteropneusta, Phyl. Hemichordata
ASC  Ascidians, Cl. Ascidiacea, Subphyl. Tunicata, Phyl. Chordata
SAL  Salps, O. Salpidae, Cl. Thaliacea, Subphyl. Tunicata, Phyl. Chordata
POI  Fish, Cl. Osteichthya, Subphyl. Vertebrata, Phyl. Chordata
### List of international specialists consulted

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<td>R. Turner</td>
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#### Class Cephalopoda

<table>
<thead>
<tr>
<th>Authors</th>
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<tbody>
<tr>
<td>G. Aldred</td>
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<tr>
<td>S. von Boletzky</td>
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<tr>
<td>M. Clarke</td>
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</tr>
<tr>
<td>T. Kubodera</td>
<td>Japan</td>
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<tr>
<td>M. Nixon</td>
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<td>T. Okutani</td>
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<tr>
<td>C. Roper</td>
<td>E.U.</td>
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<tr>
<td>N. Voss</td>
<td>E.U.</td>
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<tr>
<td>R. Young</td>
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### Phylum ARTHROPODA

#### Subph. CHELICERATA

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<tr>
<th>Order</th>
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<td>Pycnogonida</td>
<td>C. Allan Child</td>
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<td>M. de Saint Laurent</td>
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<td>J. Stock</td>
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<tr>
<td>M. Türkay</td>
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#### Subph. CRUSTACEA

##### Superorder Peracarida

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##### Order Mysidacea

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<tr>
<td>J.P. Lagardère</td>
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##### Order Cumacea

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<td>M. Ledoyer</td>
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##### Order Tanaidacea

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<td>A.B. Williams</td>
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##### Order Isopoda

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<td>Phylum ECHINODERMATA</td>
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<td>Phylum HEMICHORDATA</td>
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### Phylum CHORDATA

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<th>Subph. TUNICATA</th>
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<td>Cl. Thaliacea</td>
<td>J.C. Braconnon</td>
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<th>Subph. VERTEBRATA</th>
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<th>E. Anderson</th>
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<td>P. Geistdoerfer</td>
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<tr>
<th>Cl. Mammalia</th>
<th>G. Demuizan</th>
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<td>D. Robinet</td>
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Identification, geographic and bathymetric distribution of echinoderms collected in the Pacific Ocean

### Identification, Geographic and Bathymetric Distribution of Crinoids Collected in the Pacific Ocean

<table>
<thead>
<tr>
<th>Taxonomic identification</th>
<th>Taxon</th>
<th>Authors + date of identification</th>
<th>Geographic distribution</th>
<th>Bathymetric distribution</th>
<th>Substratum</th>
<th>Codes of taxons on photographs and specialists consulted</th>
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</thead>
<tbody>
<tr>
<td>O. Comatulida Fam. Antedonidae</td>
<td>Feniometra parvula</td>
<td>Hartlaub, 1865 Clark, 1923 ; 1967</td>
<td>Escarpement Fatton à la Ride Cocos</td>
<td>589-1969 m</td>
<td>Boues vertes, Vases à globigerines</td>
<td>CRI 1 (M. Roux, A. Clark)</td>
</tr>
<tr>
<td>O. Bourguetichnida Fam. Bathycrinidae</td>
<td>Bathycrinus equatorialis</td>
<td>Roux, 1980</td>
<td>Ride Est Pacifique</td>
<td>4246 m</td>
<td>-</td>
<td>CRI 2 (A. Clark, M. Roux)</td>
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## IDENTIFICATION, GEOGRAPHIC AND BATHYMETRIC DISTRIBUTION OF CRINOIDS COLLECTED IN THE PACIFIC OCEAN

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<th>Taxon</th>
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<th>Bathymetric distribution</th>
<th>Substratum</th>
<th>Codes of taxons on photographs and specialists consulted</th>
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<tbody>
<tr>
<td>O. Cidaroida Fam. Cidaridae</td>
<td>Aporocidaris milleri</td>
<td>Agassiz, 1898</td>
<td>Alaska, Galapagos, O. Antartique</td>
<td>300 - 3937 m</td>
<td>Boues vertes, Sables fins, Vases vertes à diatomées et globigières</td>
<td>possible CCFZ*</td>
</tr>
<tr>
<td>O. Echinoturrida Fam. Echinoturridae</td>
<td>Tromikosoma hispidum</td>
<td>Agassiz, 1898</td>
<td>Guadeloupe, ride Galapagos (30°N-4°S)</td>
<td>1820 - 2763 m</td>
<td>Boues vertes, Sables, Roche, Vases grises à globigières</td>
<td>possible CCFZ</td>
</tr>
<tr>
<td>O. Echinoturrida Fam. Echinoturridae</td>
<td>Tromikosoma panamense</td>
<td>Agassiz, 1898</td>
<td>fosse Cedros, ride Malpelo</td>
<td>2054 - 3334 m</td>
<td>Vases vertes</td>
<td>possible CCFZ</td>
</tr>
<tr>
<td>O. Diadematoidea Fam. Diadematidae</td>
<td>Kamptosoma aestivis</td>
<td>Agassiz, 1881</td>
<td>Bassin Mazatlan, fosse du Perou</td>
<td>2988 - 4950 m</td>
<td>Boues grises</td>
<td>possible CCFZ</td>
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<tr>
<td>O. Diadematoidea Fam. Aspidodiadematidae</td>
<td>Pleiodioderme globulosum</td>
<td>Agassiz, 1898</td>
<td>Ride Malpelo, Valparaiso</td>
<td>2830 - 3900 m</td>
<td>Boues vertes, Vases vertes</td>
<td>OUR 1 (D. Pawson)</td>
</tr>
<tr>
<td>O. Diadematoidea Fam. Aspidodiadematidae</td>
<td>Pleiodioderme horni</td>
<td>Agassiz, 1898</td>
<td>Ride Cocos/Malpelo/ Galapagos</td>
<td>1625 - 3241 m</td>
<td>Boues vertes à globigières, Boues vertes, sables, roche</td>
<td>possible CCFZ</td>
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<tr>
<td>O. Spatangoida sub. O. Aphesterina Fam. Aeropidae</td>
<td>Acesta ovata</td>
<td>Agassiz et Clark, 1907</td>
<td>Bassin du Pérou, Hawaii, Japon, O. Indien</td>
<td>450 - 4800 m</td>
<td>Echinides enfouis dans les sédiments</td>
<td>OUR2 (D. Pawson)</td>
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<tr>
<td>O. Spatangoida sub. O. Aphesterina Fam. Hemimasteridae</td>
<td>Hemister tenuis</td>
<td>Agassiz, 1898</td>
<td>Golfe de Panama</td>
<td>980 - 4027 m</td>
<td>Boues volcaniques fines, Boues vertes, Vases vertes</td>
<td>possible CCFZ</td>
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<tr>
<td>O. Spatangoida sub. O. Aphesterina Fam. Schizasteridae</td>
<td>Brisaster latifrons</td>
<td>Agassiz, 1881,1898, 1901</td>
<td>Mer de Baring, Galapagos</td>
<td>1900 - 2817 m</td>
<td>Boues vertes, Sable, Vases à globigières, Silites</td>
<td>possible CCFZ</td>
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<td>O. Spatangoida sub. O. Aphesterina Fam. Aeropidae</td>
<td>Aeropals furva</td>
<td>Agassiz, 1898</td>
<td>Mer de Baring, O. Pacifique O</td>
<td>1455 - 5200 m</td>
<td>Boues vertes fines, Vases vertes</td>
<td>possible CCFZ</td>
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<td>Taxonomic identification</td>
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<td>Authors + date of identification</td>
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<td>O. spatangoida sub O. Aphiasterina Fam. Brissidiae</td>
<td>Brissopsis pacifica</td>
<td>Agassiz, 1896</td>
<td>Île Manta, Hawaii, Indo-Pacific</td>
<td>3279 m</td>
<td>Boues bleues et vertes, Siltes, Sables, Argiles</td>
<td>possible CCFZ</td>
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<td>O. spatangoida sub O. Aphiasterina Fam. Loneliidae</td>
<td>Echinocardium cordata</td>
<td>Pennant, 1777 Gray, 1851, 1855</td>
<td>Bassin Conception, O. Atlantique, O. Pacifique, O. Meditrranée</td>
<td>0-4900 m</td>
<td>Boues, Sables, Vases grises, Schiste argileux</td>
<td>possible CCFZ</td>
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<tr>
<td>O. spatangoida sub O. Aphiasterina Fam. Loneliidae</td>
<td>Heterolampas fulva</td>
<td>Agassiz, 1879</td>
<td>Bassin d’Amérique Centrale, O. Pacifique</td>
<td>3665-4500 m</td>
<td>Vases grises à globigerines</td>
<td>possible CCFZ</td>
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<td>O. spatangoida sub O. Holasterina Fam. Urechinidae</td>
<td>Urechisus tovern</td>
<td>Agassiz, 1898 Agassiz et Clark, 1907</td>
<td>Mer de Bering, O. Pacifique N, Guatemala</td>
<td>1571-3710 m</td>
<td>Boues, Vases à globigerines, Argiles bleues</td>
<td>possible CCFZ</td>
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<td>O. spatangoida sub O. Holasterina Fam. Urechinidae</td>
<td>Urechisus narinanus</td>
<td>Agassiz, 1879</td>
<td>Bassin de Californie, Chili, O. Antarctique, O. Atlantique, O. Pacifique</td>
<td>755-4400 m</td>
<td>Boues, Vases à globigerines, Boues</td>
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<td>O. spatangoida sub O. Holasterina Fam. Poupartialesidae</td>
<td>Cystochirinus setigerus</td>
<td>Agassiz, 1898</td>
<td>Bassin d’Amérique Centrale</td>
<td>2875-3438 m</td>
<td>Vases vertes à globigerines, Boues</td>
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<td>O. spatangoida sub O. Holasterina Fam. Poupartialesidae</td>
<td>Pouteriasia tanneri</td>
<td>Agassiz, 1898</td>
<td>Bassin de Guayamas, O. Atlantique N</td>
<td>1450-2454 m</td>
<td>Boues bleues, Vases à globigerines</td>
<td>possible CCFZ</td>
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### Identification, Geographic and Bathymetric Distribution of Ophiuroids Collected in the Pacific Ocean

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<tbody>
<tr>
<td>O. Ophiuroidea Fam. Ophiacanthidae</td>
<td>Ophiacantha cosmica</td>
<td>Lyman, 1876; Djakonov, 1954; Zenkevitch, 1969</td>
<td>O. Pacific (32°N-10°S), O. Indien, O. Atlantique N, O. Antarctique</td>
<td>415-4840 m</td>
<td>Sables fins et gris, Boues vertes</td>
<td>possible CCFZ</td>
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<td>O. Ophiuroidea Fam. Ophiacanthidae</td>
<td>Ophiacantha pacifica</td>
<td>Djakonov, 1954; Zenkevitch, 1969; Lütken et Mortensen, 1899</td>
<td>O. Pacific (32°N-0°)</td>
<td>362-2877 m</td>
<td>Vases vertes, Boues, Sables</td>
<td>possible CCFZ</td>
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<td>O. Ophiuroidea Fam. Ophiacanthidae</td>
<td>Ophiolima baeri</td>
<td>Djakonov, 1954; Zenkevitch, 1969; Lyman, 1883</td>
<td>O. Pacific (80°N-14°N)</td>
<td>578-2549 m</td>
<td>Boues vertes, Sables fins et gris, Vases à globigerines, Roches</td>
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<td>Ophiolita paucispina</td>
<td>Djakonov, 1954; Zenkevitch, 1969; Lütken et Mortensen, 1899</td>
<td>O. Pacific (14°N-0°)</td>
<td>2149-4082 m</td>
<td>Vases vertes à globigerines, Boues vertes, Sables, Roches</td>
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<td>O. Ophiuroidea Fam. Amphiuridae</td>
<td>Amphilepis patens</td>
<td>Djakonov, 1954; Zenkevitch, 1969; Lyman, 1879; Clark, 1911</td>
<td>Alaska, O. Pacific (60°N-60°S)</td>
<td>385-4087 m</td>
<td>Boues grises, Boues vertes</td>
<td>possible CCFZ</td>
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<td>O. Ophiuroidea Fam. Amphiuridae</td>
<td>Amphiopus clavata</td>
<td>Djakonov, 1954; Zenkevitch, 1969; Lyman, 1879</td>
<td>O. Pacific (32°N-10°S), O. Atlantique O</td>
<td>1170-5889 m</td>
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<td>Amphiura assimilis</td>
<td>Djakonov, 1954; Zenkevitch, 1969; Lütken et Mortensen, 1899</td>
<td>O. Pacific (28°N-2°N)</td>
<td>2996-5482 m</td>
<td>Vases vertes</td>
<td>possible CCFZ</td>
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<td>O. Ophiuroidea Fam. Amphiuridae</td>
<td>Amphiura dromedae</td>
<td>Djakonov, 1954; Zenkevitch, 1969; Lütken et Mortensen, 1899; McClendon, 1909</td>
<td>O. Pacific (60°N-4°S), Japon</td>
<td>44-3017 m</td>
<td>Boues vertes, Sable, Boues vertes à globigerines, Rhabdamminia</td>
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<td>O. Ophiuroidea Fam. Amphiuridae</td>
<td>Amphiura seminuda</td>
<td>Djakonov, 1954; Zenkevitch, 1969; Lütken et Mortensen, 1899</td>
<td>O. Pacific (60°N-10°N)</td>
<td>9-4096 m</td>
<td>Sables noirs, Boues vertes, Manganèse, Calcaires</td>
<td>possible CCFZ</td>
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### Identification, Geographic and Bathymetric Distribution of Ophiuroids Collected in the Pacific Ocean

<table>
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<th>Codes of taxons on photographs and specialists consulted</th>
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<tr>
<td>O. Ophiuraea</td>
<td>Ophiocenthe hastatum</td>
<td>Djakonov, 1964; Zenkevitch, 1969; Lyman, 1978; Lütken et Mortensen, 1899</td>
<td>O. Pacific (60°N-3°S), Japon, O. Atlantique E, Ooalans sud</td>
<td>824-4700 m</td>
<td>Vases à globigerines, Boues vertes, Rhabdammina</td>
<td>possible CCFZ</td>
</tr>
<tr>
<td>O. Ophiuraea</td>
<td>Ophioumuseum lymani</td>
<td>Djakonov, 1964; Zenkevitch, 1969; Thomson, 1873</td>
<td>O. Pacific (60°N-60°S), Indo-Ouest Pacifique, O. Atlantique N</td>
<td>51-2906 m</td>
<td>Vases jaunes à globigerines, Boues vertes, Sable, Rhabdammina</td>
<td>possible CCFZ</td>
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<tr>
<td>O. Ophiuraea</td>
<td>Ophiopetrum gibbum</td>
<td>Djakonov, 1964; Zenkevitch, 1969; Lütken et Mortensen, 1899</td>
<td>O. Pacific (32°N-60°S)</td>
<td>878-5203 m</td>
<td>Manganese, Vases à globigerines et radiales, Boues vertes, Sable, Rhabdammina</td>
<td>possible CCFZ</td>
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<tr>
<td>O. Ophiuraea</td>
<td>Ophioclype simplex</td>
<td>Djakonov, 1954; Zenkevitch, 1969; Koehler, 1887</td>
<td>O. Pacific E, O. Atlantique E, O. Indien</td>
<td>3652-3811 m</td>
<td>Vases à globigerines</td>
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<tr>
<td>O. Ophiuraea</td>
<td>Ophiura irrorata</td>
<td>Djakonov, 1954; Zenkevitch, 1969; Clark, 1911</td>
<td>O. Pacific (32°N-60°S), Indo-Pacifique, O. Atlantique</td>
<td>405-5869 m</td>
<td>Vases vertes à globigerines, Boues vertes, Sable, Manganese, Rhabdammina</td>
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<tr>
<td>O. Ophiuraea</td>
<td>Ophioplatheus seminudus</td>
<td>Djakonov, 1954; Zenkevitch, 1969; Lütken et Mortensen, 1899</td>
<td>O. Pacific (14°N-60°S)</td>
<td>840-4082 m</td>
<td>Sables fins, Vases à globigerines, Argiles, Boues vertes</td>
<td>possible CCFZ</td>
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## Identification, Geographic and Bathymetric Distribution of Asteroids Collected in the Pacific Ocean

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<th>Taxonomic identification</th>
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<th>Bathymetric distribution</th>
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<tr>
<td>O. Paxillosida Fam. Astropelcidae</td>
<td>Diphasaster anoplus</td>
<td>Fisher, 1910</td>
<td>Mer de Bering, O. Pacifique N</td>
<td>220-2200 m</td>
<td>Sables fins, Boues</td>
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<tr>
<td>O. Paxillosida Fam. Astropelcidae</td>
<td>Dysaster gilberti</td>
<td>Fisher, 1905; Ludwig, 1905</td>
<td>Escarpement Patton, Trujillo</td>
<td>1573-4335 m</td>
<td>Boues grises et vertes, Vases à globigènes, Sables</td>
<td>possible CCFZ</td>
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<td>O. Paxillosida Fam. Astropelcidae</td>
<td>Peilaster pectinatus</td>
<td>Fisher, 1905; Ludwig, 1905</td>
<td>De la Mer de Bering au Bassin de Panama</td>
<td>1600-3060 m</td>
<td>Boues et vases vertes, Sables</td>
<td>possible CCFZ</td>
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<tr>
<td>O. Paxillosida Fam. Porcellanasteridae</td>
<td>Erencaster crassus gracilis</td>
<td>Fisher, 1905; Sladen, 1883; Ludwig, 1905</td>
<td>Alaska à Valparaïso, O. Atlantique E</td>
<td>2420-5204 m</td>
<td>Vases à globigènes et diatomées, Boues bleues et grises, Sables verts, Argiles</td>
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<tr>
<td>O. Paxillosida Fam. Porcellanasteridae</td>
<td>Erencaster pacificus</td>
<td>Ludwig, 1905</td>
<td>Mer de Bering à Valparaïso, O. Atlantique E O. Pacifique N O</td>
<td>1463-5780 m</td>
<td>Vases à globigènes, Boues grises, Sables, Rhabdammina</td>
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<td>O. Paxillosida Fam. Porcellanasteridae</td>
<td>Thoracaster cylindrus</td>
<td>Sladen, 1883; Ludwig, 1907</td>
<td>Indo-Pacifique, O. Atlantique W</td>
<td>2600-5303 m</td>
<td>Boues grises et vertes, Argiles, Vases, Manganèse</td>
<td>possible CCFZ (O. Pawson)</td>
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<tr>
<td>O. Paxillosida Fam. Benthopelcidae</td>
<td>Berthopelcet aconethonotus</td>
<td>Fisher, 1905</td>
<td>Bassin de Californie, Galapagos, Bassin Guernes</td>
<td>1157-2726 m</td>
<td>Boues</td>
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<td>O. Paxillosida Fam. Benthopelcidae</td>
<td>Pacinaster aposizili</td>
<td>Ludwig, 1905; Fisher, 1910</td>
<td>Bassin de Californie, Galapagos, O. Indien O</td>
<td>790-2323 m</td>
<td>Vases à globigènes, Boues vertes et grises, Rhabdammina</td>
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<tr>
<td>O. Spinulosida Fam. Pterasteridae</td>
<td>Hymenaster gracilis</td>
<td>Ludwig, 1905</td>
<td>Galapagos</td>
<td>2416-3241 m</td>
<td>Vases à globigènes, Boues vertes</td>
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<td>O. Spinulosida Fam. Pterasteridae</td>
<td>Hymenaster quadrispinus</td>
<td>Fisher, 1905</td>
<td>Mer de Bering, golfe de Panama</td>
<td>1935-3240 m</td>
<td>Vases grises à globigènes, Boues vertes</td>
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<td>O. Spinulosida Fam. Pterasteridae</td>
<td>Hymenaster violaceus</td>
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<td>O. Pacifique Central</td>
<td>3193-3436 m</td>
<td>Vases à globigènes, Boues</td>
<td>AST 5 (O. Pawson)</td>
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<td>O. Forcipulatidae Fam. Zoroasteridae</td>
<td>Zoroaster hirsutus</td>
<td>Ludwig, 1905</td>
<td>O. Pacifique Central</td>
<td>3436 m</td>
<td>Boues, Vases à globigènes</td>
<td>AST 1 (A. Clarke, M. Sibuet)</td>
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<td>O. Forcipulatida</td>
<td>Zoroaster ophuoros</td>
<td>Fisher, 1905</td>
<td>Mer du Bering, O. Pacifique SE</td>
<td>695-2226 m</td>
<td>Sables fins, Boues</td>
<td>AST 1 (A. Clarke, M. Sibuet)</td>
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<td>O. Brislingida</td>
<td>Astrolitus panamensis</td>
<td>Ludwig, 1905</td>
<td>Galapagos</td>
<td>48-2418 m</td>
<td>Vases vertes à globigénes, Boues, Sables, Rhabdammina</td>
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<tr>
<td>O. Euclasterida</td>
<td>Freyella benthophila</td>
<td>Sladen, 1889, Clark, 1920a</td>
<td>Ride Est Pacifique Pointe Aguja</td>
<td>4064-4667 m</td>
<td>Vases à globigénes, Argiles, Boues fines, Manganese</td>
<td>(A. Clarke, M. Sibuet)</td>
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<td>O. Euclasterida</td>
<td>Freyella insignis</td>
<td>Ludwig, 1905</td>
<td>Bassin de Calilomie, Bassin de Panama</td>
<td>3180-4075 m</td>
<td>Boues, Vases vertes à globigénes</td>
<td>AST 8 (A. Clarke, M. Sibuet)</td>
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<td>O. Euclasterida</td>
<td>Freyella octorediata</td>
<td>Clark, 1920a</td>
<td>Ride Est Pacifique Pointe Aguja</td>
<td>4085-4430 m</td>
<td>Boues grises, Vases à radiolaires et à globigénes</td>
<td>possible CCFZ (A. Clarke, M. Sibuet)</td>
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<td>O. Euclasterida</td>
<td>Freyella pacifica</td>
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<td>Golf du Panama</td>
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<td>O. Euclasterida</td>
<td>Freyella tuberculata</td>
<td>Sladen, 1889</td>
<td>Galapagos, O. Indien, O. Atlantique E</td>
<td>3365-5300 m</td>
<td>Vases à globigénes</td>
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## Identification, Geographic and Bathymetric Distribution of Holothuroids collected in the Pacific Ocean

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<tbody>
<tr>
<td>O. Dendrochirotida Fam. Cucumariidae</td>
<td>Abyssocucumis abyssorum</td>
<td>Théel, 1886</td>
<td>O. Pacific N et SE, O. Atlantique</td>
<td>385-4087 m</td>
<td>Boues vertes, sable, Boues à globigériennes et Diatomées, Manganèse</td>
<td>possible dans CCFZ*</td>
</tr>
<tr>
<td>O. Dendrochirotida Fam. Cucumariidae</td>
<td>Abyssocucumis albatrossi</td>
<td>Cherbonnier, 1941</td>
<td>O. Pacific N et SE</td>
<td>1585-569 m</td>
<td>Boues vertes, Sable, Boues à globigériennes et diatomées, Manganèse</td>
<td>possible dans CCFZ</td>
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<tr>
<td>O. Dactylochirotida Fam. Ypsilothuriidae</td>
<td>Ypsilothuria batantacutata</td>
<td>Ludwig 1893</td>
<td>O. Pacific N, O et SE, O. Indien</td>
<td>225-4082 m</td>
<td>Boues à globigériennes, Sable, Boues vertes</td>
<td>possible dans CCFZ</td>
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<td>O. Aspidochiroidea Fam. Syniallactidae (Madsen, 1953; Hansen, 1975)</td>
<td>Capheira sulcata</td>
<td>Madsen, 1953; Hansen, 1975</td>
<td>8°N-10°S O. Pacific Central Est</td>
<td>2877-4334 m</td>
<td>Boues à globigériennes, Boues vertes, Manganèse</td>
<td>possible dans CCFZ</td>
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<td>O. Aspidochiroidea Fam. Syniallactidae</td>
<td>Meseeres macdonaldi</td>
<td>Ludwig, 1894; Sluter, 1901</td>
<td>2°N-8°N O. Pacific Central Est</td>
<td>1644-2149 m</td>
<td>Roche, Boues vertes, Sable</td>
<td>HOL 8 (D. Lawson)</td>
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<td>O. Aspidochiroidea Fam. Syniallactidae</td>
<td>Galeathethuria aequa</td>
<td>Théel, 1886</td>
<td>O. Atlantique</td>
<td>2500 m</td>
<td>-</td>
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<td>O. Aspidochiroidea Fam. Syniallactidae</td>
<td>Mesothuria megalapoda</td>
<td>Clark, 1920</td>
<td>2°N O. Pacific Central Est</td>
<td>4245 m</td>
<td>?</td>
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<td>O. Aspidochiroidea Fam. Syniallactidae</td>
<td>Mesothuria murrayi</td>
<td>Théel, 1886; Pfitzer, 1907</td>
<td>O. Pacific E et O, O. Atlantique N</td>
<td>300-3000 m</td>
<td>Sediments</td>
<td>HOL 9 (D. Lawson)</td>
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<td>O. Aspidochiroidea Fam. Syniallactidae</td>
<td>Mesothuria multipes</td>
<td>Ludwig, 1893</td>
<td>8°N-9°S O. Pacific Central Est, O. Indien O</td>
<td>725-4064 m</td>
<td>Boues, Manganèse, Nodules, Rhabdammina</td>
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<td>O. Aspidochiroidea Fam. Syniallactidae</td>
<td>Pseudopatricetes confundens</td>
<td>Théel, 1886</td>
<td>O. Pacific N et SE</td>
<td>450-4070 m</td>
<td>Boues vertes et noires, Vases à globigériennes</td>
<td>possible dans CCFZ Pseudopatricetes sp. (D. Lawson)</td>
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<td>O. Aspidochiroidea Fam. Syniallactidae</td>
<td>Pseudopatricetes suspecta</td>
<td>Ludwig, 1894</td>
<td>8°N O. Pacific</td>
<td>2323 m</td>
<td>Rhabdammina</td>
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<td>Pseudochiridotea molisi</td>
<td>Théel, 1886; Ludwig, 1894; Madsen, 1953</td>
<td>O. Pacific NE et SE, O. Atlantique SE, O. Antarctique, O. Indien</td>
<td>100-5203 m</td>
<td>Boues vertes, Vases à globigériennes, Manganèse, Sable</td>
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<td>O. Aspidochiroidea Fam. Syniallactidae</td>
<td>Pseudostichopus viticulosus</td>
<td>Théel, 1886</td>
<td>O. Pacific SO</td>
<td>8000 m</td>
<td>-</td>
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<td>Syniallactes euripus</td>
<td>Ludwig, 1894</td>
<td>8°N-10°S O. Pacific Central Est</td>
<td>2404-4334 m</td>
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<td>Syniallactes profundus</td>
<td>Koehler et Vaney, 1905</td>
<td>O. Indien, O. Pacific Central Est et S. O. Atlantique N</td>
<td>2700-4300 m</td>
<td>Sable, Vases à globigériennes, Manganèse, Boues vertes</td>
<td>HOL 2 (D. Lawson, C. Massain)</td>
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<td>O. Elasipodida Fam. Doliolidae</td>
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<td>1°N-2°N</td>
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<td>Bouses vertes, Sable, Manganèse, Vases à globigènes, Roche</td>
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<td>O. Elasipodida Fam. Doliolidae</td>
<td>Ophiothrix spinyicaudata</td>
<td>Clark, 1901</td>
<td>8°S-8°S</td>
<td>4335 m</td>
<td>Bouses vertes, Vases vertes</td>
<td>HOL 4</td>
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<td>O. Elasipodida Fam. Doliolidae</td>
<td>Ophiothrix mutabilis</td>
<td>Clark, 1901</td>
<td>14°N-10°S</td>
<td>3241-3670 m</td>
<td>Bouses vertes, Vases vertes</td>
<td>HOL 4</td>
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<tr>
<td>O. Elasipodida Fam. Doliolidae</td>
<td>Ophiothrix satigera</td>
<td>Théél, 1879</td>
<td>O. Pacific NE</td>
<td>1805-5000 m</td>
<td>Vases à globigènes et à diatomées, Bouses vertes, Sable</td>
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<td>O. Elasipodida Fam. Laemognoida</td>
<td>Laemognone wyville-thomseni</td>
<td>Théél, 1879</td>
<td>O. Pacific NE et SE</td>
<td>631-4410 m</td>
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<td>O. Elasipodida Fam. Laemognoida</td>
<td>Pennychia moseleyi</td>
<td>Théél, 1882</td>
<td>O. Pacific NE, SE et SO</td>
<td>212-2599 m</td>
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<td>Psychrophila hamreri</td>
<td>Théél, 1893</td>
<td>20°N-14°N</td>
<td>4800-5200 m</td>
<td>Vases à diatomées, Manganèse, Argile</td>
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<td>O. Elasipodida Fam. Psychropodidae</td>
<td>Benthodytes ascalonensis</td>
<td>Théél, 1882</td>
<td>8°N-8°S</td>
<td>315-4700 m</td>
<td>Vases gris à globigènes</td>
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<td>O. Elasipodida Fam. Psychropodidae</td>
<td>Benthodytes angulatus</td>
<td>Théél, 1882</td>
<td>2°N, O. Pacific NE, SE, O. Pacific SE et O. Atlantic</td>
<td>957-4060 m</td>
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<td>Psychrophila depressa</td>
<td>Théél, 1882</td>
<td>Cosmopolite</td>
<td>2210-5203 m</td>
<td>Vases gris à globigènes, Manganèse</td>
<td>HOL 17</td>
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### Identification, Geographic and Bathymetric Distribution of Holothuroids Collected in the Pacific Ocean

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<td>O. Elasipodida Fam. Psychropodidae</td>
<td>Psychropotes hyalinus</td>
<td>Pawson, 1985</td>
<td>O. Pacifique NE</td>
<td>5691 m</td>
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<td>O. Elasipodida Fam. Psychropodidae</td>
<td>Psychropotes semperiana</td>
<td>Théel, 1882</td>
<td>O. Atlantique N et S, O. Indien</td>
<td>3465-5600 m</td>
<td>Vases à diatomées, Boues grasses fines, Manganèse</td>
<td>Dans CCFZ, HOL 16 (D. Pawson)</td>
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<td>O. Elasipodida Fam. Psychropodidae</td>
<td>Psychropotes verrucosus</td>
<td>Ludwig, 1894</td>
<td>O. Indien, O. Pacifique SE</td>
<td>2417-7250 m</td>
<td>Vases grasses et jaunes à globigerines</td>
<td>HOL 23 (D. Pawson)</td>
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<td>O. Elasipodida Fam. Epbididae</td>
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<td>Cosmopolite, O. Atlantique, O. Indien, O. Pacifique NO</td>
<td>2780-4924 m</td>
<td>Vases, Roche</td>
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<td>O. Elasipodida Fam. Epbididae</td>
<td>Amperima narosi</td>
<td>Théel, 1882</td>
<td>Indo-Pacifique, 10°S, O. Pacifique Central Est</td>
<td>2010-7130 m</td>
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<td>O. Elasipodida Fam. Epbididae</td>
<td>Peniagone gracilis</td>
<td>Ludwig, 1894</td>
<td>2°N, O. Pacifique Central Est</td>
<td>2475 m</td>
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<tr>
<td>O. Elasipodida Fam. Epbididae</td>
<td>Peniagone purpurea</td>
<td>Théel, 1882</td>
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<td>3560-8000 m</td>
<td>Vases à globigerines</td>
<td>HOL 13</td>
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<tr>
<td>O. Elasipodida Fam. Epbididae</td>
<td>Peniagone intermedia</td>
<td>Ludwig, 1894</td>
<td>20°N-10°S, O. Pacifique Central Est</td>
<td>2418-5203 m</td>
<td>Vases à globigerines, Manganèse, Boues vertes et grasses</td>
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<tr>
<td>O. Elasipodida Fam. Epbididae</td>
<td>Peniagone papillata</td>
<td>Hansen, 1975</td>
<td>20°N-8°N, O. Pacifique Central Est</td>
<td>3570 m</td>
<td>Argiles sombres</td>
<td>HOL 10</td>
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<tr>
<td>O. Elasipodida Fam. Epbididae</td>
<td>Peniagone vitrea</td>
<td>Théel, 1882</td>
<td>10°N-10°S</td>
<td>1160-4507 m</td>
<td>Vases à globigerine, Boues grasses, Sable, Roche</td>
<td>HOL 11 (Hansen, 1975)</td>
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<tr>
<td>O. Elasipodida Fam. Epbididae</td>
<td>Peniagone elongata</td>
<td>Théel, 1879</td>
<td>O. Pacifique SO</td>
<td>3947-4065 m</td>
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<td>possible dans CCFZ</td>
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<tr>
<td>O. Elasipodida Fam. Epbididae</td>
<td>Peniagone diaphana</td>
<td>Théel, 1882</td>
<td>O. Pacifique, O. Atlantique, O. Indien</td>
<td>1520-5600 m</td>
<td>Manganèse, Vases, Sable</td>
<td>HOL 20 (D. Pawson)</td>
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<td>O. Elasipodida Fam. Epbididae</td>
<td>Scotoplanas starki</td>
<td>Hansen, 1975</td>
<td>10°N-10°S</td>
<td>3570-5107 m</td>
<td>Argiles sombres</td>
<td>possible dans CCFZ</td>
</tr>
<tr>
<td>O. Elasipodida Fam. Epbididae</td>
<td>Scotoplanes globosa</td>
<td>Théel, 1879</td>
<td>32°N, O. Pacifique SE, Cosmopolite</td>
<td>545-6770 m</td>
<td>Vases meubles</td>
<td>possible dans CCFZ</td>
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<tr>
<td>O. Elasipodida Fam. Pelagophurtidae</td>
<td>Pelagophurtia natantia</td>
<td>Ludwig, 1994</td>
<td>8°N-10°S, O. Pacifique Central Est</td>
<td>4504 m</td>
<td>Vases, Boues, Sable</td>
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<tr>
<td>O. Elasipodida Fam. Pelagophurtidae</td>
<td>Enypniesis eximia</td>
<td>Théel, 1882</td>
<td>Cosmopolite</td>
<td>516-5689 m</td>
<td>Suble fin, Boues grasses, Vases grasses</td>
<td>HOL 18 (S. Ohta ; D. Pawson)</td>
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</table>
### Identification, Geographic and Bathymetric Distribution of Holothuroids Collected in the Pacific Ocean

<table>
<thead>
<tr>
<th>Taxonomic identification</th>
<th>Taxon</th>
<th>Authors + date of identification</th>
<th>Geographical distribution</th>
<th>Bathymetric distribution</th>
<th>Substratum</th>
<th>Codes of taxa on photographs and specialists consulted</th>
</tr>
</thead>
<tbody>
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<td>O. Elasipodida Fam. Elpidiidae</td>
<td>Scotoplanes clarki</td>
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<td>10°N-10°S O. Pacific Central East</td>
<td>3570-5107 m</td>
<td>Argiles sombres</td>
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<tr>
<td>O. Elasipodida Fam. Elpidiidae</td>
<td>Scotoplanes globosa</td>
<td>Théel, 1879</td>
<td>31°N, O. Pacific SE, Cosmopolite</td>
<td>545-6770 m</td>
<td>Vases meubles</td>
<td>possible dans CCFZ</td>
</tr>
<tr>
<td>O. Elasipodida Fam. Pelagothuridae</td>
<td>Pelagothuria natatric</td>
<td>Ludwig, 1894</td>
<td>8°N-3°S, O. Pacific Central East</td>
<td>4504 m</td>
<td>Vases, Boues, Sable</td>
<td>possible dans CCFZ</td>
</tr>
<tr>
<td>O. Elasipodida Fam. Pelagothuridae</td>
<td>Enypniastes eximia</td>
<td>Théel, 1882</td>
<td>Cosmopolite</td>
<td>516-5689 m</td>
<td>Sable fin, Boues grises, Vases grises</td>
<td>HOL 18 (S. Otta, D. Pawson)</td>
</tr>
<tr>
<td>O. Apodida Fam. Synaptidae</td>
<td>Protodyphya pacifica</td>
<td>Ludwig, 1894</td>
<td>O. Pacific N et SE</td>
<td>870-4990 m</td>
<td>Sable fin, Boues grises, Vases grises</td>
<td>Enfouis, non visibles sur photographies du benthos</td>
</tr>
<tr>
<td>O. Molpadidae Fam. Molpadidae</td>
<td>Cerapiellina trachyderma</td>
<td>Clark, 1907</td>
<td>O. Pacific N et O</td>
<td>3188-6580 m</td>
<td>Boues fines et sombres, Argiles vertes</td>
<td>Enfouis, non visibles sur photographies du benthos</td>
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<tr>
<td>O. Molpadidae Fam. Molpadidae</td>
<td>Molpadia granulata</td>
<td>Ludwig, 1894</td>
<td>24°N-15°S</td>
<td>2690-5869 m</td>
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<td>Enfouis, non visibles sur photographies du benthos</td>
</tr>
<tr>
<td>O. Molpadidae Fam. Molpadidae</td>
<td>Molpadia intermedia</td>
<td>Ludwig, 1894</td>
<td>O. Pacific NE et S</td>
<td>55-2014 m</td>
<td>Boues à globigerines, Boues, Roche</td>
<td>Enfouis, non visibles sur photographies du benthos</td>
</tr>
<tr>
<td>O. Molpadidae Fam. Molpadidae</td>
<td>Molpadia musculus</td>
<td>Risco, 1826</td>
<td>O. Pacific NE et S, M. Mediterranee, O. Indien, O. Atlantique</td>
<td>4-5203 m</td>
<td>Boues grises, vertes et noires, Sable gris, Vases, Rhadaminna</td>
<td>possible dans CCFZ</td>
</tr>
<tr>
<td>Fam. Gephyrothauridae</td>
<td>Hadalothuria</td>
<td>Hansen, 1975</td>
<td>O. Pacific O et S</td>
<td>7000-8000 m</td>
<td>-</td>
<td>HOL 9 (Lenschke et al., 1976)</td>
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<tr>
<td>Fam. Gephyrothauridae</td>
<td>Parolecta sp.</td>
<td>Hansen, 1975</td>
<td>Cosmopolite, O. Pacific S</td>
<td>6650-7280 m</td>
<td>-</td>
<td>possible dans CCFZ</td>
</tr>
</tbody>
</table>
Biodiversity and distribution of the megafauna

Vol.2 Annotated photographic Atlas of the echinoderms of the Clarion-Clipperton fracture zone

Intergovernmental Oceanographic Commission (IOC)

United Nations Educational, Scientific and Cultural Organization (UNESCO)

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UNESCO
Biodiversity and distribution of faunal assemblages

Vol. 3 Options for the management and conservation of the nodule ecosystem in Clarion Clipperton Fracture Zone
Biodiversity and distribution of faunal assemblages

Vol.3 Options for the management and conservation of the nodule ecosystem in Clarion-Clipperton Fracture Zone: scientific, legal and institutional aspects

Dr Virginie Tilot
Membre correspondant de l’Académie des Sciences d’Outre-Mer

With the support of the Government of Flanders (Belgium)

UNESCO 2010
# Table of contents

FOREWORD \(\ldots\) V
PREAMBLE \(\ldots\) VI
ACKNOWLEDGEMENTS \(\ldots\) VII
ABSTRACT \(\ldots\) VIII
PREFACE \(\ldots\) IX

## 1 – INTRODUCTION

## 2 – SYNTHESIS OF A REFERENTIAL STATE OF THE ABYSSAL NODULE ECOSYSTEM IN THE CLARION-CLIPPERTON FRACTURE ZONE (CCFZ)

### 2.1 GENERAL CONTEXT

- Oceanographic and physical features \(\ldots\) 3
- Nodule deposits \(\ldots\) 4
- Study sites \(\ldots\) 5
- Megafaunal assemblages \(\ldots\) 6

### 2.2 MAIN RESULTS OF THE UNESCO/IOC BASELINE STUDY

- NORIA (AFERNOD) area \(\ldots\) 7
- NIXO 45 site \(\ldots\) 7
- NIXO 41 site \(\ldots\) 9
- ECHO I site \(\ldots\) 10
- IOM BIE site \(\ldots\) 12

### 2.3 MAIN RESULTS OF KAPLAN/ISBA/NODINAUT PROJECT

- Meiofaunal and Macrofaunal assemblages \(\ldots\) 14
- Kaplan/ISBA/Nodinaut project \(\ldots\) 14
- Main results of Kaplan/ISBA project \(\ldots\) 14
<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Main results of Nodinaut project</td>
<td>15</td>
</tr>
<tr>
<td>2.4 COMPARISON WITH ESTIMATES FROM DOMES STUDY</td>
<td>16</td>
</tr>
<tr>
<td>2.5 DISCUSSIONS</td>
<td>17</td>
</tr>
<tr>
<td>Intra-regional and within-site variability of the structure of benthic</td>
<td>17</td>
</tr>
<tr>
<td>faunal assemblages in the CCFZ</td>
<td></td>
</tr>
<tr>
<td>Comparison of data collected by different devices</td>
<td>20</td>
</tr>
<tr>
<td>2.6 RECOMMENDATIONS FOR FUTURE STUDIES</td>
<td>20</td>
</tr>
<tr>
<td>3 – RATIONALE FOR THE CONSERVATION OF THE BIODIVERSITY IN THE CCFZ ......</td>
<td>23</td>
</tr>
<tr>
<td>4 – PRINCIPLES, TOOLS AND CRITERIA FOR THE MANAGEMENT AND CONSERVATION</td>
<td>31</td>
</tr>
<tr>
<td>OF THE HIGH SEAS BIODIVERSITY</td>
<td></td>
</tr>
<tr>
<td>4.1 PRINCIPLES FOR SUSTAINABLE DEVELOPMENT AND CONSERVATION OF THE</td>
<td>31</td>
</tr>
<tr>
<td>MARINE ENVIRONMENT</td>
<td></td>
</tr>
<tr>
<td>4.2 TOOLS FOR BIODIVERSITY ASSESSMENT, MANAGEMENT AND MONITORING</td>
<td>32</td>
</tr>
<tr>
<td>Biodiversity assessment</td>
<td>32</td>
</tr>
<tr>
<td>Resilience</td>
<td>34</td>
</tr>
<tr>
<td>Multiple Systems management</td>
<td>34</td>
</tr>
<tr>
<td>Metapopulation approach in conservation</td>
<td>35</td>
</tr>
<tr>
<td>Environmental monitoring</td>
<td>36</td>
</tr>
<tr>
<td>4.3 CRITERIA FOR SITE SELECTION AND NETWORKING</td>
<td>38</td>
</tr>
<tr>
<td>Site selection</td>
<td>38</td>
</tr>
<tr>
<td>Networking sites</td>
<td>40</td>
</tr>
<tr>
<td>5 – CONSERVATION AND MANAGEMENT OF THE CCFZ</td>
<td>43</td>
</tr>
<tr>
<td>5.1 PREDICTED IMPACTS AND MANAGEMENT OPTIONS FOR POLYMETALLIC NODULE</td>
<td>43</td>
</tr>
<tr>
<td>MINING</td>
<td></td>
</tr>
<tr>
<td>Predicted impacts of nodule mining</td>
<td>43</td>
</tr>
<tr>
<td>Mining management options</td>
<td>44</td>
</tr>
<tr>
<td>5.2 INTERNATIONAL SEABED AUTHORITY’S MANDATE AND ACTIVITIES</td>
<td>45</td>
</tr>
<tr>
<td>5.3 PRESERVATION REFERENCE AREAS PROPOSED BY KAPLAN PROJECT</td>
<td>46</td>
</tr>
</tbody>
</table>
5.4 THE NETWORK OF SEABED PRESERVATION REFERENCE AREAS (SPRA) PROPOSED BY THE PRESENT UNESCO/IOC BASELINE STUDY ........................................................................................................48

6. FINAL CONCLUSIONS ..............................................................................................................................53

Biodiversity and driving factors of the nodule ecosystem in the CCFZ ................................................. 53
Principles, tools and criteria for the management conservation of High Seas biodiversity ..................... 54
Conservation and management of the CCFZ ............................................................................................... 54

ANNEXES

LIST OF ACRONYMS .................................................................................................................................55
BIBLIOGRAPHIC REFERENCES .......................................................................................................... 56

APPENDIX 1
Illustrations, Maps and Photographs of the deep sea bottom and of devices of exploration .............. 71

APPENDIX 2
List of codes based on the classification of Parker (1982) .................................................................. 95

APPENDIX 3
List of international specialists consulted ............................................................................................... 96

APPENDIX 4
Comparison of the taxonomic richness of the study area with the abyssal zone of the world’s oceans .......................................................... 100

APPENDIX 5
Classification of the abyssal suprabenthic megafauna by trophic and functional groups ............... 108

APPENDIX 6
List of IOC Technical Series ............................................................................................................... 115
My capacity as former Secretary-general of the United Nations could easily explain why I attached a great interest to the global issues as well as to the economic and social development of humanity. From my experience, I gained the conviction that the national or domestic dimension to deal with such issues is the expression of a world which has disappeared. The time of globalisation brought the consciousness of the urgency that the problems must be solved at the international level, at the United Nations level.

Today such a level implies a great number of stakeholders far beyond the participation of States only. The States should admit that they still could be key players if, and only if, they have the capacity to think and act beyond their national boundaries; if they are able to consider that the humanity problems are not lying within their own domestic limits.

Those views were verified on earth. They are much more relevant for the problems raised by the oceans and seas including the seabed issues. I am convinced that we should not repeat in the oceanic world the failures and the mistakes we, collectively, made in the exploitation of natural resources on Earth. Increasing our confidence in the United Nations institutions and spirit, we should be able to find the legal and political formula which could limit the selfishness of States in order to find out the appropriate measures to sustain the development of the marine resources for the benefit of mankind. The implementation of this idea is still to be undertaken and it is our responsibility towards the coming generations to protect and save the marine biodiversity.

The year 2010 is declared by the United Nations the Year of Biodiversity. This is an outstanding opportunity for the States and their leaders to express their political will to act within this framework of the United Nations by protecting the marine resources and allowing an equitable sharing of the benefices provided by the exploitation of such resources.

The work of Dr. Virginie Tilot is one major step on this road. The added value of her research lies in the ecosystemic approach she developed and her proactive view in strategic management of the resource. She and her colleagues in different parts of the world are at the forefront of the new paradigms needed for the sustainable use and management of our global resources.

Dr. Virginie Tilot must be congratulated for offering her work to the scientific community but also beyond, to all policy makers interested by increasing their knowledge in this particular field. Her vision is the fruit of an unusual experience that she acquired during twenty-five years in a large array of topics of research and teaching in marine environment and applied sciences mainly with developing countries. Her field of experience covers biological oceanography, marine ecology, fisheries, biodiversity and global change assessment, national and regional policy. She designed remarkable marine and coastal strategic management for different ecosystems from coastal to deep sea, tropical to temperate within the Atlantic, Pacific, Indian Ocean, Red Sea and the Mediterranean Sea including areas of more than fifty countries mostly appointed by different agencies of the United Nations, the European Commission, non governmental organizations, governmental organisms, private companies and universities.

Boutros Boutros-Ghali
Former Secretary-General of the United Nations
Preamble

Population growth and development have resulted in resource depletion of most known mineral deposits in all the planet’s continents. Demand is not decreasing but increasing, and as a result there is growing interest and financing available for deep sea exploration and mining.

Recognizing the inherent risks associated with mining in poorly known ecosystems, the global community established the International Seabed Authority to ensure that regulations were consistent and would be effective to guarantee that access to the resource and damage due to its extraction would be controlled.

Lessons learned from licensing and resource extraction in terrestrial areas have shown that regulation is sometimes difficult, and often the regulatory process fails as a result of conflicts of interests, transboundary management issues, and the ever-increasing demand of the manufacturing industries.

Global resource managers have learned from the failures and weaknesses associated with resource mining in terrestrial areas regardless of country. They are increasingly aware that, if mining is to take place on the seabed in international waters or on the seabed within national exclusive economic zones, a new and forward thinking paradigm has to be elaborated and agreed by all States. The linkages between the seabed and overlying waters of biological communities and ecological functions in three dimensions are much stronger than on land. Thus, environmental impacts are more difficult to limit and manage. The paradigm must acknowledge that activities in the sea are less visible and management enforcement therefore more difficult.

This new paradigm must also consider that the public globally remains poorly informed regarding the importance of the ocean and its physical, biological and chemical processes and, as such, is ill-equipped to consider, comment on, or take positions against damaging practices. Therefore an integrated and indissociable element of the paradigm must be an awareness campaign similar to those designed to inform the public of risks related to climate change, to ensure that the public is empowered to provide oversight of governance regarding this critical issue.

The issue that is addressed here is a global issue that could have planetary repercussions in terms of protecting and preserving the well-being and health of the oceans. Links between the health of the upper layers of the ocean and climate change are now known. As the significance of these connections is studied, it is becoming increasingly apparent that global changes and environmental impacts are affecting all marine organisms from phytoplankton, zooplankton to higher marine vertebrates and all oceanic processes. These changes also have a direct impact on the global human population, global warming, food security, the livelihoods of coastal populations and of course global economies. We have learned that we cannot disassociate activities on the seabed from the state of the ocean above up to the surface. Thus it would be irresponsible to ignore these connections in order to expedite resource extraction.

As there is presently a limited mandate of the International Seabed Authority with respect to overlying waters, there is thus no adequate legal regime for the creation and enforcement of the marine protected areas as recommended here. This highlights the urgent need to create a global legal framework for marine protected areas from the surface to the seabed beyond national jurisdiction, not only for seabed mining, but for fisheries management, waste disposal, carbon sequestration and other human activities.

Michael P. Pearson
Alain Jeudy de Grissac
Strategic Marine Resources Planners
Acknowledgements

We are very grateful to the Intergovernmental Oceanographic Commission of UNESCO and its former Executive Secretary, Dr Patricio Bernal, for agreeing to co-ordinate this project on the polymetallic nodule ecosystem in anticipation of future nodule mining in the abyssal Equatorial East Pacific ocean. Also to his team, among whom we acknowledge the late Dr Ümit Ünlüata for initiating this project and Dr Ehrlich Desa, Mr Julian Barbiere and Dr Salvatore Arico for their excellent advices during the production of this document. Our gratitude is also due to the Government of Flanders and especially to Dr Rudy Herman of the Science and Innovation Administration of the Ministry of Flanders for his enthusiasm in bringing to fruition this project.

I also thank for their precious input and comments Mr Jean Pierre Lenoble, marine geologist, former president of the “Association Française pour la Recherche et l’Exploitation des NODules polymétalliques” (AFER-NOD) and former member of the Legal and Technical Commission of the International Seabed Authority. All my reconnaissance and respect to Dr Jean Marie Auzende, marine geologist, formerly chief scientist at the “Institut Français pour la Recherche et l’Exploitation de la Mer” (IFREMER) and present member of the Legal and Technical Commission of the International Seabed Authority, and the professor Michel Hoffert, sedimentologist, vice-president of the Louis Pasteur University of Strasbourg, who designed the first geological model of the polymetallic nodules in the Clarion-Clipperton Zone from his numerous works in the equatorial Pacific ocean.

All my gratitude to the late Professor Lucien Laubier, former Director of the Oceanographic Institute in Paris for reviewing the first manuscript. This work would not have been possible without the collaboration of Dr Kotlinski, Director general of the Interoceanmetal Joint Organization (IOM), Poland and other deep sea specialists, Dr Teresa Radziejewska from the department of Palaeoceanology of the University of Szczecin, Poland, Dr Vulcana Stoyanova (IOM), Dr Stace Beaulieu from the Biology Department of the Woods Hole Oceanographic Institution, USA and the world known marine conservation specialists, Dr Alain Jeudy de Grissac, Dr Michael Pearson, Dr Andrew Price and Professor Callum Roberts.

I acknowledge also the valuable help of Mrs Anne-Marie Damiano and her team at the library of the oceanographic Museum of Monaco for bibliographic research.
Abstract

The principal ecological and biological characteristics of the nodule ecosystem in the CCFZ and their sensitivity to natural and anthropogenic impacts outlined in the UNESCO/IOC baseline study (IOC Technical Series 69, UNESCO/IOC, volumes 1 and 2) and the present interpretation of a referential state updated with recent literature and collaborative work on independent data sets from IOM BIE including the comparative analysis of DOMES and ISBA/Kaplan/Nodinaut studies, enable to draw a rationale for a conservation strategy of biodiversity in the CCFZ.

The diversity of the seabed fauna is characterized by true abyssal species adapted to the conditions of the abyssal environment with many species new to science which need to be protected from extinction. The management of natural resources and conservation of the biodiversity has to take into account the existence of intra-regional and within-site variability in biotic and abiotic conditions in space and time, the underlying driving factors and the existing patterns of faunal communities. Results evidence that habitat heterogeneity (“nodule facies”, microheterogeneity at nodule level, patches of detritus, biogenic structures and bioturbation) in correlation with other factors and conditions, i.e. bottom currents and sediment chemistry, is a significant factor defining the distribution pattern of nodule deposits in association with the structure of epibenthic megafaunal assemblages at different spatial and temporal scales.

The abundance and composition of faunal assemblages differ in each area. However within-area patterns are evidenced with a clearly marked faunal abundance and taxonomic richness for megafauna and macrofauna on nodule bearing areas, where prevail sessile fauna and infauna, while meiofauna prefer nodule-free areas. Results display the prevalence of sessile fauna and infauna on nodule deposits. Concerning sedimented areas, there is a faunal preference for nodule-free areas with old sediments (Oligocene to Miocene) versus more recent sediments (Plio-Quaternary). Overall, there is a higher taxonomic richness in the West due in part to a higher heterogeneity of substrates and conversely a higher abundance in the East because of an increased trophic input. There are also more suspension feeders in the western oligotrophic sites and more deposit feeders in the eastern sites. Preferential habitats, ranked according to nodule coverage and slope, are evidenced for specific megafaunal assemblages. Within sites, aggregative patterns of distribution are displayed for common species. There are key faunal groups in the CCFZ, such as cnidarians, echinoderms and sponges, for megafauna, and polychaete worms, nematode worms and protozoan foraminifera for macrofauna and meiofauna, which represent >50% of faunal abundance and species richness in abyssal sediments and display a broad range of ecological and life history types. Biological activity created on the sea floor affects the structure and chemistry of the sediment and would have an important role in maintaining nodules at the surface of the sediments. Megafauna, with its wide distribution and preferential habitats, would serve as good indicator of environmental change and mining impact, in particular the echiurian worms Bonellidae Jacobia birsteini producing conspicuous large mounds which could easily be monitored.

The need for a broader strategy of conservation and management of the biodiversity requires to define criteria and tools in ecologically meaningful ways that are practical to measure so that the effects of environmental degradation, remediation or conservation can be monitored.

A network of Seabed Preservation Reference Areas is proposed on basis of the rationale for conservation of the biodiversity which combines UNESCO/IOC and ISBA/Kaplan/Nodinaut studies. These proposed areas are representative of the main nodule and nodule-free facies and associated types of fauna described in the referential studies. A conservation strategy is based on the precautionary principle and is adaptive with the growing database on the region. A tridimensional concept could be replicated for the integrated conservation and management of the High Seas where multiple open seas activities occur.
Preface

The first phase of this UNESCO/IOC project has been completed in 2006 with the production of two documents which propose a comprehensive baseline reference on the description of the environment and the structure of megafaunal assemblages in the abyssal nodule province in the Clarion and Clipperton Fracture Zone (CCFZ). These documents are published in IOC Technical Series 69 and entitled "Biodiversity and distribution of the megafauna; Vol. 1: The polymetallic nodule ecosystem of the eastern Equatorial Pacific Ocean," 134 pp. + 4 annexes; Vol. 2 Annotated photographic atlas of the echinoderms of the Clarion-Clipperton Fracture Zones, 86 pp. +3 annexes, in English and in French versions,


and have been subject to communications at scientific symposiums (Tilot, 2006 d, e).

The second phase of the project produced in 2008-2010:

- (i) an updated synthesis of the referential state of the megafaunal assemblages in an abyssal nodule province in the eastern equatorial Pacific (Tilot, 2008a),

- (ii) a proposition of a conservation strategy of the ecosystem of polymetallic nodules in the Clarion-Clipperton Fracture Zone, NE Pacific Ocean. This document presents a description of the status of present and needed knowledge for the conservation of the marine environment, options for a conservation strategy of the biodiversity and tools for the management of the natural resources of the CCFZ (Tilot, 2008b).

- (iii) an electronic mail and a panel discussion organized at UNESCO/IOC (12 December 2008) with a large international pool of experts in deep sea affairs, science, industry, policy, management and conservation intergovernmental agencies (UN agencies, Law of the Sea, International Seabed Authority...) over the documents (i), (ii) (Tilot, 2008c). This pool of experts represents a link with the network of pioneer investors, international non governmental agencies (IUCN) and an international network concerned by High Seas issues.

- (iv) a final document produced after the panel discussion of international experts (iii) and entitled “Biodiversity and distribution of faunal assemblages”; Vol. 3: “Options for the management and conservation of the nodule ecosystem in the Clarion-Clipperton Fracture Zone (NE Pacific Ocean): scientific, legal and institutional aspects” which is presented here.
1. Introduction

Marine ecosystems have become degraded with the speed of change accelerating at an alarming rate in the past decades (Hughes et al., 2005). There has been a shift in the basic condition of the oceans from one of apparent abundance and accommodation to demands to one of growing scarcity and conflict among competing uses (Loreau et al., 2001). The growth in the intensity of these uses and in the number and magnitude of activities threatens to severely impinge on the carrying capacity of the oceans and on the levels of sustainable use. Formerly very productive grounds are now severely depleted and some habitats have been irreversibly destroyed (UNEP, 2006). In addition to global warming, increased carbon dioxide emissions are rapidly acidifying the world’s oceans and thus threatening calcifying organisms (Orr et al., 2005; Veron, 2008).

Pressures now extend to the High Seas and deep oceans (Ardron et al., 2008; Gianni, 2004; UNEP, 2005; Tilott, 2008c) hosting the least explored areas on the planet assumed to be the largest reservoirs of non-renewable resources, habitats and biomass which still harbour undiscovered ecosystems and species, serve as cradles of new species and contribute significantly to planetary biodiversity (Costanza et al., 1997; Gage and Tyler, 1991; Glover and Earle, 2004; Gray, 1997; Koslow, 2007; Laubier, 2008; Tyler, 2003). Also oceans, as self-contained entities are the main driving force for global climate and are of critical importance to the future well-being of humanity (Hoegh-Guldberg, 2005; Orr et al., 2005). These impacts are impairing the structure, productivity and resilience of marine ecosystems and placing an increasing number of species and habitats at risk of extinction (Folke et al., 2004; Myers and Worm, 2003; Scheffer and Carpenter, 2003; Scheffer et al., 2001; Worm et al., 2006). Thus the conservation of deep sea biodiversity is a priority for a sustainable functioning of the planet’s oceans (Dano-varo et al., 2007).

The resources of deep oceans are no longer safe from over-harvesting, pollution, dumping of extremely hazardous wastes and the direct and indirect impacts of climate change (Gardener et al., 2003; Harvell et al., 2004; Jackson et al., 2001, Jones et al., 2004; Palmer et al., 2004; Pandolfi et al., 2003; Pauly et al., 2002; Pitcher, 2001; Pyke, 2004; Roberts, 2002; UNEP WCMC, 2007). In the deep sea, there is an important lack of knowledge on species, biodiversity and the relationships with the functioning of deep sea ecosystems (Hooper et al., 2005).

Recent global conservation and biodiversity issues, particularly the concern for potential and real threats to the deep sea diversity, have provided an incentive to efforts aiming at exploring the structure and function of benthic communities in the abyss (e.g. Gage, 2001; Tilott, 2006a, b; Tilott et al, 2010) and at proposing different conservation strategies (e.g. Ardron et al., 2008; ISBA, 2008a; IUCN, 2005; Tilott, 2008c, 2010a). The benthic fauna is now increasingly targeted by studies testing human impact and global changes (e.g. Bluhm, 2001; Butler et al., 2001; IUCN, 2003; Jones et al., 2007; Radziejewska and Stoyanova, 2000; Rodrigues et al., 2001; Thiel et al., 2001).

Deep sea mining, which would be expected to occur in the near future because of increasing commercial and strategic interest, is envisioned to be the largest-scale human activity to directly impact the deep sea floor (Cressey, 2008; Lenoble, 2008; Glover and...
Smith, 2003). In addition there is limited knowledge on the mining technology that would then be used. Thus “the protection and sustainable development of the marine environment and its resources would require new approaches for management and development at global levels”; these should be “integrated in content and precautionary and anticipatory in ambit” (UN, 1992, RIO Conference on Environment and Development, Agenda 21, §17.1).

The richness and the dynamics of epibenthic faunal communities in an abyssal polymetallic nodule province in the Clarion-Clipperton Fracture Zone NE Pacific Ocean and the threats of major impacts due to future deep sea mining on a large scale have caught the interest of the scientific network of specialists (Foell and Pawson, 1986; Foell et al., 1989; Galeron et al., 2006a, b; Oebius et al., 2001; Ozurger et al., 1978; Radziejewska, 1997; 2002; Radziejewska and Modlitba, 1999; Radziejewska and Stoyanova, 2000; Tilot, 1988, 1990b, 1991b, 1992a, b, 1993, 1995, 2006a, Tilott et al., 2010; Tkatchenko and Radziejewska, 1998; Veillette et al., 2007a, b), the intergovernmental agencies and the international non governmental agencies (ISBA, 2002). These have expressed the need to draw a referential state on a regional scale which would serve as a benchmark against which epibenthic fauna subject to natural and anthropogenic impacts may be assessed at different scales (Tilot, 2006b, 2008a, 2010b, Tilot et al., 1988; 2010) in order to minimize the impacts of future nodule mining and provide elements to conserve the biodiversity in the region (ISBA, 2008a; Smith, 1999; Tilot, 2006d, e, 2008b, c, 2010a).

This document is organized in two main sections: the first section recapitulates the main features of the referential state of the abyssal nodule ecosystem in the Clarion-Clipperton fracture zone based upon an update of the UNESCO/IOC region-wide baseline assessment (Tilot, 1993, 2006b, c) published in IOC Technical Series 69, UNESCO/IOC, volumes 1 and 2. This represents the first additional information from recent literature and collaborative work on (IOM BIE) (Radziejewska and Stoyanova, 2000; Stoyanova, 2008; Tilot et al., 2010). It constitutes the first comparison, on a regional scale, of independent data sets collected by international research efforts in four different areas of the CCFZ (Sub chapters 1.1, 1.2). A comparative analysis of the results of Kaplan/ISBA/Nodinaut project and of the DOMES study (Sub chapters 1.3, 1.4) enables to discuss on a regional basis of all assessments for the three faunal categories (Sub chapter 1.5) in order to draw recommendations for future studies (Sub chapter 1.6) and propose a detailed rationale for the conservation of the biodiversity in the CCFZ (Chapter 2.).

The second section of the document relates to the conservation strategy proposed for the CCFZ and broadens to the High Seas, it encompasses a theoretical debate on the principles, tools and criteria that would be the best adapted to the management and the conservation of the biodiversity in the High Seas, in particular in the context of a nodule ecosystem (Chapter 3). The management of the polymetallic nodule ecosystem is defined in ecologically meaningful ways that are practical to measure so that the effects of environmental degradation, remediation or conservation can be monitored. The options of conservation and management of the CCFZ are examined in Chapter 4 with the proposal of a network of seabed preservation reference areas in line with the rationale for conservation. A strategy based on the precautionary principle and adapted to the growing database on the region is proposed. A tridimensional concept could be replicated for the integrated conservation and management of the High Seas where multiple open seas activities occur. The document concludes with a brief outline of each section in Chapter 6.
2. Synthesis of a referential state of the abyssal nodule ecosystem in the Clarion-Clipperton Fracture Zone (CCFZ)

2.1. General context

The comprehensive region-wide baseline assessment of the megafaunal assemblages in a polymetallic nodule ecosystem in the CCFZ (Tilot, 1993, 2006b, c) is published in IOC Technical Series 69, UNESCO/IAC, volumes 1 and 2. Additional information from updated literature and recent collaborative work on (IOM BIE) (Radziejewska and Stoyanova, 2000; Stoyanova, 2008; Tilot et al., 2010) forms the first comparison, on a regional scale, of independent data sets collected by international research efforts in four different areas of the CCFZ (Figure 1 in Appendix 1).

It constitutes an interpretation of the polymetallic nodule ecosystem to which changes, observed after anthropogenic activities will have begun in areas earmarked for future resource development (ISBA, 2008a), can be referred and against which they can be compared to assess the extent of impact on deep sea megafauna. A recent region-wide baseline study on mainly smaller faunal categories (macrofauna and meiofauna) has been achieved by ISBA/Kaplan and Nodinaut project (Galeron et al., 2006b; ISBA, 2008a) which completes this interpretation of a referential state.

The Clarion-Clipperton Fracture Zone (CCFZ), located in international waters of the NE Pacific between 118°W–157°W and 9°–16°N, is an abyssal area of more than 3 million km² in the sub-equatorial Pacific (Figure 1 in Appendix 1) that is targeted for mining activities on account of abundant polymetallic nodule deposits of most economical importance (Morel and Le Suavé, 1986; Ozturgut et al., 1978; Lenoble, 2004).

Mining claim holders, “The contractors”, which are presently eight (The Government of India, IFREMER/AFER-NOD, Deep. Ocean Resources Development Company (DORD) of Japan, State Enterprise Yuzmorgeologiya of the Russian Federation, China Ocean Mineral Resources Research and Development Association (COMRA) of the People's Republic of China, Interoceanmetal Joint Organization (IOM), a consortium formed by Bulgaria, Cuba, Czech Republic, Poland, Russian Federation and Slovakia, The Government of the Republic of Korea and The Federal Institute for Geosciences and Natural Resources of the Germany), are licensed by the International SeaBed Authority (ISBA) to explore nodule resources and to test mining techniques in their claim areas in anticipation of future commercial development which could reduce, if not remove, the dependence of some industrialized countries on other countries.

Oceanographic, physical and biotic features

The large equatorial polymetallic nodule belt of the CCFZ is located in international waters of the sub-equatorial NE Pacific between 118°–157°W and 9°–16°N. It covers about 2 million km² of abyssal hills often accompanied by escarpments and elongated in a north-south direction with irregular, elliptically domed summits and steep sides (Menard, 1964; Kotlinski, 1998).

The sedimentary cover is mainly biogenic in origin and has been subjected to diagenetic processes of various intensity, depending on temperature and pressure; the
surface layer is highly hydrated and can be several hundred metres thick depending on the crust age and sedimentation rate (Ilijn et al., 1997; Kotlinski, 1999; Menzies et al., 1975; Seibold and Berger, 1993; Tyler, 1995; Whitmarsh et al., 1996).

The hydrography in this area is shaped primarily by the westward-flowing Northern Equatorial Current and by the eastern-flowing Northern Equatorial Countercurrent which form a complex divergence system, due to seasonal variability (Fiedler and Talley, 2006; Sokov and Demidova, 1999). This flux is observed to be particularly intensive in spring (Yamazaki and Kajitani, 1996; Thiel et al., 1999; Seibold and Berger, 1993; Tyler et al., 1997; Kotlinski, 1998; Saguez, 1985). Vast stretches of nodule deposits on the seafloor are interspersed by larger or smaller nodule-free areas which differ in sediment properties (mean grain size, water content, shear stress, plasticity) as evidenced by geotechnical assays (Hoffert, 2008; Morel and Le Suavé, 1986; Radziejewska and Modlitba, 1999; Saguez, 1985).

The great variability of conditions in the geological environment at a regional scale (topography, erosion by deep ocean currents and regional deposition of sediments) has led to a classification of nodule deposits and the recognition of "nodule-facies" (Hoffert, 2008; Hoffert and Saget, 2004). This differentiation is based on a photographic study associated with samples and morphological and geochemical measurements of the types of nodule-facies (UNESCO/IOC, volume 1, Table 1 and in this document, Appendix 1, Figures 2-9).

The study of environmental and edaphic conditions supports a better understanding of the biodiversity and heterogeneity of epibenthic populations. The associations that may exist between some functional assemblages and particular biotopes, such as the different 'nodule-facies', are factors operating in these population dynamics. These nodule-facies are the following:

- **Nodule-facies C** is composed of large nodules (6-15 cm diameter or more), sunk well into the surface sediments if not completely, hillocky on the surface, heterogeneous and elliptical in outline. Attached organisms are frequent. They cover 5 to 40 % of the ocean floor (C 5 % to C 40 %) limited to 8 kg/m². Nodule-facies C 30 % is often associated to slopes > 15 %. The underlying silts have less clay and are richer in radiolarians than in the other nodule-facies. 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 %).

- **Nodule-facies B** is composed of smaller nodules that are ovoid and flattened with a poorly developed equatorial thickening. Their diameter varies from 4 to 7 cm and their abundance from 5 to 20 kg/m². Their surface is hummooky and rough except at the summit where it is smooth or sometimes granular. Some of these nodules are apparently fragments of older nodules, with some showing lines of fragment-
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 five), nickel (1-4%) and copper (1-4%), and low levels of iron and cobalt. These nodules differentiate from Facies C and are associated with claysey radiolarian silts forming vast deposits with a coverage of 30 to 50% (B 40%, B 50%).

- **Nodule-facies BP** consists of small flattened ovoid nodules, very frequently cohering and 2.5 to 4 cm in diameter. Their concentration varies from 4 to 10 kg/m². Polynodules and ancient fragments are very frequent. The surface appears smooth, their degree of burial varies from 0 to 30%, and their structure is porous, microgranular on the upper and lower surfaces. The kernel is sometimes a fragment of an older nodule. These nodules are generally close to rock outcrops and form beds with a coverage of 30% to 50% (BP 35%, BP 50%).

- **Nodule-facies A** groups together very numerous small nodules (3 to 6 kg/m²) with smooth surfaces that are 20 to 30 mm in diameter and irregular, often multilobed, in shape. Polynodules and older fragments are frequent, and they rest on the sediment, scarcely buried. They border crusts, plate formations and rock outcrops, covering about 50% of the substratum in large homogeneous deposits, sometimes in facies mixed with larger nodules or plates. 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. These are the nodules principally associated with red clay formations in the northern part of the Clarion-Clipperton fracture zone. They form beds with a coverage of 30% (A 30%) in average.

- **Nodule-facies O** has no nodules on the sediment surface nor any plates or crusts. It is possible that this facies is an ultimate form of a totally buried nodule-facies C except when located at the foot of cliffs, steps and escarpments. The substratum is composed either of ancient sediments (Oligocene to Miocene) or more recent sediments (Plio-Quaternary).

**Study sites**

The study sites (Figure 1) on which is based the interpretation of the referential state (Tilot, 1993, 2006b, c, 2008a, Tilot et al., 2010) in the CCFZ are French (NORIA, NIXO 45 and NIXO 41), American (ECHO I) and from the governments of Bulgaria, Cuba, Czech Republic, Poland, Russia Federation and Slovakia represented in the “Interoceanmetal Joint Organization” (IOM BIE). These sites have been sampled during surveys (1970s-2004) by means of towed devices (“R.A.I.E” “Troika”, “Deep. Tow Instrumentation System”, towed cameras from MIR-1 and NEPTUN, remote devices (spade box corers equipped with a photo camera in IOM BIE and the French “ED1” and “Epaullard”) and the submersible “Nautilus”. The description of the methodologies and strategies used during the different surveys is presented in UNESCO/IOC, volume 1, chapter 3 and here in Appendix 1, Figures 10-13.

**NIXO 45 site** represents the largest thoroughly sampled and analyzed site (du Castel, 1982, 1985; Morel and Le Suavé, 1986, Tilot, 1992b), thus has the highest resolution in terms of habitat identification (Tilot, 1993, 1996b, c). The site supports all the nodule-facies listed above (Hoffert and Saget, 2004; Tilot, 2006b), including nodule-free areas (nodule-facies O).

**NIXO 41 site** (Morel and Le Suavé, 1986; Tilot, 1992b, 1996b, c), located south and eastwards of NIXO 45 has been selected to explore nodule-facies A 30% (nodule cover of 30% of small smooth nodules, 20 to 30 mm diameter) and to compare faunistics data on nodule-facies B 35% and C 30%, also present at NIXO 45 site.

**ECHO I site** (Spiess and Lonsdale, 1982; Spiess et al., 1987) located in the vicinity of the American study area DOMES C site, between 13°30′N to 15°00′N and 124°00′W to 130°00′W, (Ozturgut et al., 1978), eastward to NIXO 45, was chosen in order to study three nodule-facies O, B 45% and C 40% which have homologues on NIXO 45 with the exception of the sedimentary context for nodule-facies B 45% and C 40%, dating from the Oligocene for the older layers instead of the Plio-Quaternary in NIXO 45. The megafauna has been previously described qualitatively by Foell and Pawson (1986) and quantitatively by Ozturgut et al. (1978), Foell et al. (1989), Tilot (1990b, 1991b) before the comparative study of Tilot (1992b, 1996b, c). This site has been chosen to assess the impact on faunal communities of pilot-scale mining tests conducted by Ocean Mining Inc. and Ocean Mining Associates (OMA) in 1978. The tracks (1.5 m large, 10 cm deep) of a prototype cross the different nodule-facies.

**IOM Benthic Impact Experiment (BIE) site** (Kotliński, 1998; Radziejewska, 1997; 2002; Radziejewska and Modlińska, 1999; Radziejewska and Stoyanova, 2000; Stoyanova, 2008; Tkatchenko and Radziejewska, 1998) serves as complementary source of information to complete the interpretation of the referential state of the CCFZ on a regional and latitudinal scale (Tilot et al., 2010). IOM BIE study site has for mid-point coordinates: 11°04′N; 119°40′W and can be described as undulating plains at an average depth of 4,300 m incised by longitudinal horsts and troughs. The sedimentary cover of siliceous radiolarian oozes supports dense deposits of polymetallic nodules, partially embedded in a semiliquid surficial sediment (Kotliński, 1998). The site has been surveyed by towed cameras MIR-1 and NEPTUN cameras (Tkatchenko and Radziejewska, 1998; Radziejewska, 2002). Also during 2004, a total of 158 stations has
been sampled with a 0.25m² spade box corer equipped with a photo camera (Stoyanova, 2008).

Video and photographic data were analysed over the following nodule facies: A 30%, C 5%, C 10%, C 15%, C 20%, C 30%, C 40%, B 40%, B 50%, BP 35%, BP 50%, O old sediments, O recent sediments (Radziejewska, 2007, 2008; Veillette et al., 2008). Megafauna still remains unexplored in vast areas of the deep sea floor and many aspects of the structure of their communities are still inadequately known (Gage and Tyler, 1991; Glover and Earle, 2004; Laubier, 2008; Tyler, 2003). However this faunal category plays an important role in deep sea epibenthic ecosystems and the conservation of the biodiversity. It is often neglected in biological assessments because of the difficulty to sample and identify taxa in their corresponding habitat among communities dispersed heterogeneously over large areas with some buried in the sediment (IUCN, 2003; Tilot, 2006b, 2010a). The study and assessment of megabenthic communities from bottom photographs represents one mobile and cost-effective possibility to obtain substantial data on environmental baseline surveys and it is also well adapted and cost effective for large scale impact assessments and monitoring (Tilot et al., 2001; 2008).

Most of the exploratory surveys in the CCFZ supplied important imagery and some sampling from which megafaunal assemblages are analyzed in their respective habitats, at different levels (seafloor level and nodule level), in particular, abundance, composition, distribution and diversity (e.g., Foell and Pawson, 1986; Foell et al., 1989; Galeron et al., 2006a; ISBA, 2008a; Mullineaux 1987, Ozturgut et al., 1978; Radziejewska, 1997; Radziejewska and Stoyanova, 2000; Tilot, 1989, 1990a, b, 1991b, 1992a, b, 1993, 1995, 2006 a,b,c, 2008 a,b ; 2010b; Tilot et al., 1988; 2010; Tkatchenko and Radziejewska, 1998; Veillette et al., 2007a, b).

Megafauna and smaller organisms are thought to be an important link in carbon cycling and mineralisation near and at the seafloor (Smith, 1992; Smith et al., 1996; Lauerman et al., 1997). Moreover, by their activity on the seafloor often leaving remarkable traces (e.g., Gaillard, 1991; Heezen and Hollister, 1971; Mauviel, 1982; Tilot, 1990b, 1992b, 1995, 2006b, c, 2010b), megafaunal assemblages affect the structure and chemistry of the sediment (Hoffert, 2008; Hughes et al., 2005; Wheatcroft et al., 1989) and would have an important role in maintaining nodules at the surface of the sediments, especially when considering the slow growth rate of nodules (1-10mm/million years). This action would be in addition to the action of erosion at certain geological periods (Hoffert, 2008; von Stackelberg, 1979, 1984, 1987; von Stackelberg and Beiersdorf, 1987; von Stackelberg and Marchig, 1987).

Piper and Fowler (1980) advance a theory that bioturbation would happen at two levels, firstly, organisms would feed on the deposited organic matter concentrated on the nodules, thus preserving nodules from sinking into the sediments, secondly, the digging and mound building fauna would move the small nodules and thus maintain them at the sediment-water interface. These diggers would also move the sediments which are subjacent to the nodules thus leaving the place to younger less compacted sediments. Sanderson (1985) found evidence that there is a differential sedimentation in a nodule field, with less organic matter in sediments under nodules than on the sediments around nodules at the sediment-water interface. This differential sedimentation would cause horizontal transport of material in the most bioturbated areas towards less bioturbated areas (under nodules) and thus would help to maintain nodules at the surface.

In addition, the potential of megafauna, with its wide distribution, would serve as good indicator of environmental change and anthropogenic impact such as for mining; in particular echinuran worms Bonellidae Jacobia birsteini (Figures 50-55 in Appendix 1) would be key indicators for monitoring (Tilot, 1995, 2010b) as developed further.

The terms “taxon and taxonomic richness” are used here rather than “species and species richness” because, only a few specimens were collected during the study surveys and, consequently, no definitive faunal identifications could be made (Belyaev, 1989; Gage and Tyler, 1991; Stoyanova, 2008). The taxonomic resolution of the photographic data being fairly high, some organisms are identified to the family, genus and species level in agreement with the literature and with consultation of world taxonomists experts (Tilot, 1990b, 1992b, 1993, 2006 b, c; Tilot et al., 2010) with the purpose to serve as an identification reference for megafaunal taxa which have been barely sampled (see Panorama in Appendix 1). These data have been integrated in several databases, e.g. http://www.whoi.edu/science/B/people/sbeaulieu/H2O_new/ (Beaulieu, 2006). Recently some identifications have been confirmed with the results of analysis of the megafauna specimens collected during the Kaplan/ISBA/Nodinaut surveys (Galeron et al, 2006a, b; ISBA, 2008a; Veillette et al., 2007).

The megafauna of the Clarion-Clipperton fracture zone has been classified into five trophic and functional groups that are corroborated by an exhaustive review
of the literature: sessile suspension feeders (Porifera, Pennatulacea, Ceriantharia, Antipatharia, Actinaria, Cnidaria, Asciidiacea...), motile suspension feeders (Antedonidae, Asteroidea, Brisingidae, Ophiuroidea...), sessile deposit feeders (some Actinaria, echinarian worms Bonellidae...), mobile deposit feeders (Stelleroidea, Echinoidea, Holothuroida, Enteropneusta...) and mobile carnivores/scavengers (Schyphozoa, Cephalopoda, Gasteropoda, Decapoda, Tunicata, Osteichthyes...)(Tilot, 1992b, 2006b).

2.2. MAIN RESULTS OF THE UNESCO/IOC BASELINE STUDY

The main results of the interpretation of the structural and functional characteristics of megafaunal assemblages in relation to ecological parameters within the CCFZ (Stoyanova, 2008, Radziejewska and Stoyanova, 2000; Tilot, 2006b; Tilot et al., 2010) for the overall study of the CCFZ and the four study sites are the following:

**NORIA (AFERNOD) area**
On the behalf of the “Association Française pour la Recherche et l’Exploitation des Nodules Polyvalent tres” (AFERNOD), the first French exploratory cruises carried by the Centre National pour l’Exploitation des Océans (CNEXO), which became IFREMER in 1984, had for objective to identify areas of nodule deposits and evaluate their economic potential. A systematic survey over about 2,500,000 km² was based on sampling every 93 km. The Noria (Nodule Riches et Abondants) zone of about 450,000 km² was then delimited between 125°W/135°W and 11°N/16°N and surveyed from 1974 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 (UNESCO/IOC, volume 1, p. 13).

Overall all CNEXO-IFREMER survey sites in the NORIA area, the analysis of the faunal communities recorded on imagery (Tilot, 1992b, 1993, 2006b, 2008a, Tilot et al., 2010) displays the following results:

- a total of 175 taxa (genera and species) covering 13 phyla over 5,500,000 m² (total benthos surface analysed from more than 200,000 photographs and 55 h video transects).
- some phyla have quite significant taxonomic richness (by decreasing order of importance): echinoderms (50 taxa including 32 holothurians), cnidarians (41 taxa), chordates (23 taxa including 17 fishes) and sponges (21 taxa) (UNESCO/IOC, volume 1, Figure 35, p. 36).
- the existence of more suspension feeders in the western oligotrophic sites and more deposit feeders in the eastern sites in relation to a gradient in productivity from West to East. However particular substrate, hydrological conditions above the bottom layer and the topography of the ocean floor also influence the structure of faunal assemblages.
- suspension feeders (68 taxa, among which 58 sessile taxa and 10 mobile taxa) display a higher taxonomic richness than deposit feeders (60 taxa, among which 50 taxa are mobile) and carnivores/scavengers (45 taxa).
- the taxonomic richness of suspension feeders is principally represented by cnidarians (41 taxa) and sponges (21 taxa) (UNESCO/IOC, volume 1, Figure 37, p. 39).
- the taxonomic richness for deposit feeders is principally expressed by holothurians (32 taxa).

**NIXO 45 site**
The analysis of the faunal communities of NIXO 45 site recorded on imagery (Tilot, 1992b, 1993, 2006b, 2008a, Tilot et al., 2010) displays the following results:

- an overall taxonomic richness of 134 taxa in 13 phyla over about 70,000 m² (total benthos surface analysed on photographs for 2600 replicates) of 13 different facies. Higher taxonomic richness is recorded in nodule areas, in particular on nodule-facies C (large hillocky nodules) covering 2-15 % of the seabed (48 taxa in average), than on facies O, nodule free areas (36 in average). However densely covering nodule-facies B (smaller ovoid and flattened nodules) and BP (small flattened and frequently cohering nodules) display a slightly lower taxa richness (34) than on facies O.
- an overall abundance of megafaunal taxa of 553 ± 333.73 ind/ha (UNESCO/IOC, volume 1, Figures 38-40, p. 42) including the following main phyla:
  - 258 ind/ha cnidarians, 46.7 % of total abundance (composed mainly of 135 ind/ha actinians and 105 ind/ha octocorallians, respectively 52 % and 41 % of the total cnidarian abundance),
  - 180 ind/ha echinoderms, 32.5 % of total abundance (composed mainly of 64 ind/ha holothurians and 61 ind/ha crinoids, respectively 36 % and 34 % of the total echinoderm abundance),
  - 56 ind/ha sponges, 10 % of total abundance.
- within the phyla, some taxa are more present e.g. among holothurians, by decreasing order of importance, Aspidochirotidae: Pseudostichopus mollis, Synallactes aenigma, Synallactes profundi and Elasipodidae: Benthodytes incerta and Peniagone leander.
• concerning trophic guilds, there is in overall more suspension feeders (389 ind/ha) than deposit feeders (113 ind/ha) and carnivores/scavengers (51 ind/ha) (UNESCO/IOC, volume 1, Figure 42, p. 47), this order in abundance is irrespective of either nodule-facies. In particular,
  - by decreasing order, there are more sessile suspension feeders (360 ind/ha) than mobile deposit feeders (108 ind/ha), mobile carnivores/scavengers (51 ind/ha), motile suspension feeders (29 ind/ha) and sessile deposit feeders (5 ind/ha).
  - Sessile suspension feeders are dominated by Actinaria (135 ind/ha), Octocorallia (105 ind/ha), fixed Crinoidea (57 ind/ha), Porifera (56 ind/ha) while Antipatharia, Ceriantharia and Ascidiae are scarce.
  - Among mobile deposit feeders, there are mainly holothurians (64 ind/ha) and echinoids (36 ind/ha) while asteroids are rarer (6 ind/ha).
  - Motile carnivores and scavengers abound with swimming polychaetes (21 ind/ha), hydromedusas and scyphomedusas (12 ind/ha), fish (9 ind/ha) while decapods, molluscs, siphonophoran and ceriantharids are scarce.
  - Among motile suspension feeders, ophiuroids (16 ind/ha) and brisingids (13 ind/ha) are more abundant than asteroids and Antedonidae.
  - Sessile deposit feeders, among which sedentary polychaetes, sipunculids and echuriarins, are scarce.
• at nodule-facies level, the results show that:
  - in decreasing order, overall faunal taxa are more abundant in the following nodule-facies: facies C 10 % 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 % (UNESCO/IOC, volume 1, Figure 41, p. 46).
  - some phyla are more abundant on specific nodule-facies, such as prevailing phyla, cnidarians (478 ind/ha), echinoderms (467 ind/ha) and sponges (126 ind/ha), on nodule-facies C 10 % (big nodules relatively scattered) and on nodule-facies C 30 % (more densely covered) on slopes (>15°), both on sediments dated from Plio-Quaternary (UNESCO/IOC, volume 1, Figure 42, p. 47).
  - other phyla prevail on other nodule-facies: annelids and chordates (58 ind/ha and 29 ind/ha respectively) on facies O with recent sediments, arthropods (21 ind/ha), brisingids (10 ind/ha) on facies C 20 to 40 %, with slope (>15°), mollusks (14 ind/ha) on facies C 15 % and echuriarins (10 ind/ha) on facies BP 35 %.
  - within the phyla, some taxa display affinities for specific habitats by marked relative abundance or exclusive presence on specific nodule-facies. e.g. among holothurians, Mesothuria murrayi are more present (40 ind/ha) on nodule-facies C 10 %, Benthodytes incerta and Synallactes profundi (25 ind/ha) on nodule-facies BP 35-50 %, Enypniastes eximia (25 ind/ha) on nodule-facies C 10 %, Synallactes enigma (21 ind/ha) on facies O with ancient sediments and Benthodytes sp. (13 ind/ha) on nodule-facies C 20-40 % with slope > 15°.
  - facies O with ancient sediments and nodule-facies C 15 % accommodate most exclusive taxa.
• these affinities are confirmed by the multidimensional positioning of taxa and facies given by the indexes of similarity extrapolated from the multivariate analysis of data which ordinate taxa and facies along 13 preferential habitats from the indices of effective overlap. (UNESCO/IOC, volume 1, Figures 46-47, pp. 54-55).
  As an example of preferential habitat, nodule-facies C 20 to 40 % on slopes > 15° is characterized by a relative abundance of fixed fauna mostly of suspension feeders such as ring-shaped Hexactinellida Rosseliidae sponges, Tetractinellida Poecillastra sp. type 1, Euretidae sponges, Cladorhizidae Demospongia sponges and polychaeta sedentaria, Protula sp. originating a calcareous tube. The most abundant deposit feeders on this sloping facies are echinoderms such as Brisingidae with 10 arms and holothurians Benthodytes sp. Carnivores are decapods, Nematomorcrinus sp. and Bythitidae fish, Typhlonus sp. Tanaidacea peracarids have only been seen on this nodule-facies (Tilot, 2006b).
• habitat heterogeneity is structuring the distribution of megafaunal assemblages at different scales. At tax level, an aggregative pattern within a nodule-facies is expressed as follows:
  - e.g. actinids Sincyonis tuberculata aggregating above 1600 m² on nodule-facies C and random at 400 m² and 800 m² on facies O according to the Levis, David and Moore indexes and Fisher's coefficient (UNESCO/IOC, volume 1, Table 2, p59),
  - e.g. holothurians Mesothuria murrayi aggregating at 100 m² and 400 m² on nodule-facies C and at 800 m² on nodule-facies BP (UNESCO/IOC, volume 1, Table 3, p59).
Concerning trophic guilds within nodule-facies,

- suspension feeders are more abundant on facies O with recent sediments and on nodule-facies C 10 % (big nodules, relatively scattered) on slopes. Among motile suspension feeders, a predominance of actinians is observed on nodule-facies C 30 %, B 50 %, C 15 %, O on recent sediments with a maximum density of 79 ind/ha on BP 35 %. Ophiuroids are the only mobile suspension feeders on rock outcrops, they are also observed on all nodule-facies and especially on nodule-facies BP 35 % at a density of 26 ind/ha.

- deposit feeders are more abundant on nodule-facies C 10 % (big nodules, relatively scattered). Echinoids and holothurians, the most recorded detritus feeders appear to be present in equal proportions on all nodule-facies. Echiurians (16 ind/ha) are more present on nodule-facies B 40 %, B 50 %, BP 35 % and BP 50 %.

In conclusion,

- the overall taxonomic richness on a photographed surface of 70,000 m² in NIXO 45, among which 2600 replicates covering 13 different facies, totals 134 taxa; Higher taxonomic richness is recorded on specific nodule areas, in particular on nodule-facies C covering 2-15 % of the seabed (48 taxa in average), while densely covered nodule-facies B 35 % and BP 50 % host a lower taxa richness (34) than facies O (36).

- the overall abundance of megafaunal taxa of 726 ± 438.14 ind/ha (UNESCO/IOC, volume 1, Figure 51, p. 62) including the following main phyla:
  - 364 ind/ha echinoderms, 50.1 % of total abundance (composed mainly of 178 ind/ha ophiuroids, 94 ind/ha holothurians and 83 ind/ha echinoids, respectively 48.9 %, 25.8 % and 22.8 % of the total echinoderm abundance),
  - 270 ind/ha cnidarians, 37.2 % of total abundance (composed mainly of 266 ind/ha actinians, 98.5 % of the total cnidarian abundance),
  - 43 ind/ha sponges, 5.9 % of total abundance.

- in overall, megafaunal taxa are more abundant in the following nodule-facies: 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 %.

- some phyla prevail on specific nodule-facies, e.g. cnidarians, echinoderms and sponges on nodule-facies C 10 % (big nodules relatively scattered) and on nodule-facies C 30 % (more densely covered) on slopes (>15°), both on sediments dated from Plio-Quaternary.

- facies O with ancient sediments and nodule-facies C 15 % accommodate most exclusive taxa.

- there are at least 13 preferential habitats ranked according to nodule coverage and slope as emphasized by a factor analysis of Reciprocal Averaging.

- habitat heterogeneity is important in structuring the distribution of megafaunal assemblages at different scales.

- there is a patchiness in the distribution of megafaunal populations analyzed at a taxa level e.g. actinids *Sincyonis tuberculata* aggregating above 1600 m² on nodule-facies C and at 800 m² on nodule-facies O.

**NIXO 41 site**

The analysis of the faunal communities recorded on imagery (Tilot, 1992b, 1993, 2006b, 2008a, Tilot et al., 2010) displays the following results:

- an overall taxonomic richness of 55 taxa (genera and species) on a photographed surface of 10 500 m² (over replicates of 3 different nodule-facies); As in NIXO 45, sampling on NIXO 41 shows a lower richness (31) for nodule-facies A 30 %, (30) for nodule-facies C 30 % and (26) for nodule-facies B 35 %.

- there are in overall more suspension feeders than deposit feeders and carnivores/scavengers irrespective of either nodule-facies.

- In particular, there are more sessile suspension feeders than mobile deposit feeders, mobile carnivores/scavengers, motile suspension feeders and sessile deposit feeders.

- suspension feeders are more abundant on facies O with recent sediments and on nodule-facies C 10 % (big nodules, relatively scattered) on slopes. Among motile suspension feeders, a predominance of actinians is observed on nodule-facies C 30 %, B 50 %, C 15 %, O with recent sediments with a maximum density on BP 35 %.

- deposit feeders are more abundant on nodule-facies C 10 % (big nodules, relatively scattered). Echinoids and holothurians, the main components, appear to be present in equal proportions on all nodule-facies.

- In conclusion, the overall abundance of epibenthic megafauna in NIXO 45 encompasses, in decreasing order, cnidarians (mainly actinians and octocorallians), echinoderms (mainly holothurians and crinoids) and sponges.

- there are in overall more suspension feeders than deposit feeders and carnivores/scavengers irrespective of either nodule-facies.
*berculata*, 174 ind/ha for the brittle stars *Ophiomu-


sium armatum* (their density at this site is unique),


83 ind/ha for sea urchins *Plesiodiadema globulo-


sum*, 25 ind/ha for holothurians *Psychronaetes han-


seni* and 23 ind/ha for actinids *Actinernus verrill*.


\[ \text{In conclusion,} \]


- the data from similar depths in two sites of the CCFZ


(NIXO 45 and NIXO 41) are comparable despite dif-


ferent methods of exploration and sampling strate-


gies (towed camera and camera from the subma


raine *Nautilus*): the same order of dominance and


proportionality of suspension feeders over deposit


feeders and carnivores is observed whatever node-


ule-facies with only the faunal components of the


tropic groups differing.


- no taxon is found to be exclusive to NIXO 41 since


all taxa recorded have already been identified on


NIXO 45.


- taxonomic richness, faunal composition and levels


of abundance on node-facies B 35 % are similar to


those of the same facies at NIXO 45 site.


- in contrast, node-facies C 30 % is different from


that facies in NIXO 45 by its greater faunal abun-


dance and by a reversal in the usual order of domi-


nance: echinoderms are the most abundant group,


with a high density of ophiuroids whose suspen-


sion-feeding behaviour maintains the predomi-


nance of suspension feeders over deposit feeders.


- node-facies A 30 % resembles node-facies B 40 % in its population of cnidarians, and resem-


bles sloping node-facies C+ 20 to 40 % in hav-


ing a majority of echinoderms. This facies is also


characterised by a relatively high density of sessile


deposit feeders with echinarian worms *Bonneliidae*.


**ECHO I site**


The analysis of the faunal communities recorded on


imagery through 50mm lens (Tilot, 1990b, 1991b,


1992, 1993, 2006b, c; 2008a, Tilot et al., 2010) displays


the following results:


- an overall taxonomic richness of 61 taxa over


around 25 200 m 2 (over replicates of 3 different


node-facies); and more richness (36) on node-


facies C 40 % than (23) for B 45 % and a minimum


(8) on facies O.


- an overall abundance of megafaunal taxa of 502 +


146.97 ind/ha including the following main phyla


(UNESCO/IOC, volume 1, Figure 54, p. 66):


- 179 ind/ha sipunculids,


- 123 ind/ha echinoderms, 24.5 % of total abun-


dance (composed mainly of 65 ind/ha echinoids


and 52 ind/ha holothurians, respectively 52.8 %


and 42.3 % of the total echinoderm abundance),


- 79 ind/ha echinarians,
- 48 ind/ha sponges, 9.6 % of total abundance,
- 42 ind/ha cnidarians, 8.4 % of total abundance (composed mainly of 38 ind/ha actinians, 90.5 % of the total cnidarian abundance),
- 19 ind/ha annelids,
- 11 ind/ha fish.

• the following taxa are among the 20 most abundant taxa at the NIXO 45 site: actinids Sincyonis tuberculata, echiurians Jacobia birsteini, sponges Phoronema sp. and Hyalonema sp., echinoids Pleiodiadema globulosum, holothurians Mesothuria murrayi and polychaete worms Incertae sedis with long contorted tubes.

• some other taxa are also among the most abundant at NIXO 41 such as: actinids Sincyonis tuberculata, echinoids Jacobia birsteini, sponges Phoronema sp. and Hyalonema sp., echinoids Pleiodiadema globulosum, polychaete worms Incertae sedis with long contorted tubes and holothurians Synallactes enigma, Synallactes profundi and Mesothuria murrayi.

• concerning trophic guilds, there is in overall more deposit feeders (389 ind/ha) than suspension feeders (103 ind/ha) and carnivores/scavengers (10 ind/ha), this order in abundance is irrespective of either nodule-facies. In particular,

- by decreasing order, there are more sessile deposit feeders (216 ind/ha) than mobile deposit feeders (173 ind/ha), sessile suspension feeders (99 ind/ha), mobile carnivores/scavengers (10 ind/ha) and motile suspension feeders (4 ind/ha),
- sessile deposit feeders are mainly represented by sipunculids (179 ind/ha), echinarians (37 ind/ha) and sedentary polychaetes,
- among mobile deposit feeders, there are mainly echinoids (65 ind/ha), holothurians (52 ind/ha), annelids (19 ind/ha) as asteroids and enteropneusta are rare,
- sessile suspension feeders are dominated by Porifera (48 ind/ha), Actinaria (38 ind/ha) and as fixed Crinoidea, Antipatharia, Octocorallia, Ceriantharia and Asciidiacea are rarer,
- mobile carnivores and scavengers are mainly fish (11 ind/ha) as medusas, decapods, molluscs, siphonophoran, swimming polychaetes and ceriantharids are scarce,
- among motile suspension feeders, ophiuroids, brisingids, molluscs and free crinoids are rare.

• at nodule-facies level, the results (UNESCO/IOC, volume 1, Figure 55, p. 67) show that:
- overall faunal taxa are more abundant on facies C 40 % (densely covered with big nodules) on recent sediments dated from Plio-Quaternary. 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), actinians (64 ind/ha), ascidians (8 ind/ha) and polychaetes (11 ind/ha). On this facies, the population densities of crinoids and asteroids are rare (5 ind/ha) and even more for sipunculids and molluscs.
- nodule-facies B 45 % on ancient sediments, where the pilot-scale mining tests were conducted by Ocean Mining Inc. and Ocean Mining Associates (OMA) in 1978. The tracks of a prototype would cross the photographs of this nodule-facies. The megafauna 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, sipunculids, ascidians, cephalopods to the same nodule-facies with recent sediments at 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 NIXO 41 site.
- nodule-facies O with ancient sediments is characterized by a high density of echinoderms (204 ind/ha), mostly echinoids, (151 ind/ha), as well as a relatively large population of sipunculids (122 ind/ha) and fish (16 ind/ha). The same facies O on 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 other sites is close to absent, as are those for holothurians, molluscs and fish (about 2 ind/ha).
- nodule-facies C 40 % on ancient sediments, preferentially supports holothurians Peniagone gracilis, which are exclusive to this nodule-facies. Other holothurians, mostly members of the family Elpidiidae, are unique to this nodule-facies, such as Amperima rosea, Peniagone gracilis and Benthodytes sp.. The highest abundances are seen with Synallactes enigma, showing a density of 11 ind/ha. These observations are confirmed at NIXO 45 site for the exclusive taxon Orphnurges sp. and for holothurians of the genus Benthodytes. In contrast, none of these results were observed at the NIXO 41 site.
• at taxa level, e.g. holothurians, 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.

In conclusion,

• ECHO 1 displays an overall taxonomic richness of 61 taxa over around 25 200 m² (replicates over 3 nodule-facies); and more richness (36) on nodule-facies C 40 % than (23) for B 45 % (where the tracks were seen) and a minimum (8) on facies O.

• there is a greater number of taxa on nodule-facies C 40 % (densely covered with big nodules).

• there is an overall dominance of deposit feeders over suspension feeders:
  - suspension feeders prevailing on facies-nodule B 45 % and C 40 %, with a majority of actinians among cnidarians,
  - deposit feeders prevailing on facies O with echinoderms, mainly echinoids and holothurians prevail.

• the overall predominance of echinoderms in photographs of ECHO I taken with a 50 mm lens differs from the results of NIXO 45 site but recalls those from NIXO 41, on nodule-facies A 30 % and C+ 30 %. This preponderance of echinoderms is not due to an overabundance of ophiuroids as in NIXO 41 but due to large numbers of holothurians and echinoids, whose respective densities vary according to nodule-facies. Considerable populations of sipunculids (50 ind/ha) and echiurians were also detected due the conspicuous bioturbation they create.

• deposit feeders, as indicated by the abundance of sipunculids, echinoids and holothurians, is particularly abundant on facies O with ancient sediments (332 ind/ha). Suspension feeders, dominated by actinians, are most numerous on nodule-facies C 40 % (167 ind/ha). These results differ from those observed on similar nodule-facies at NIXO 45 and 41.

IOM BIE site

The analysis of the faunal communities recorded on imagery (Stoyanova, 2008; Radziejewska and Stoyanova, 2000; Tilot et al., 2010) displays the following results:

• representatives of six high-level taxa are present however there are no record of molluscs, sipunculids, brachiopods, and hemichordates, as observed on study sites in NIXO 45 and ECHO 1 sites.

• the mean area-wide total abundance of the mega-fauna is assessed to vary 243.82 + 146.97 ind/ha., which is lower than the other three sites. This could also be due to the lower resolution of the imagery.

• there is a significant difference in abundance and taxa richness of mega fauna on the two main substrates that have been analyzed: nodule bearing (average nodule abundance 8.4 kg/m² which would correspond to facies B 45 % and C 40 % on the other sites) and nodule-free (facies O). The results show that taxa richness and abundance are more important on nodule bearing substrates.

• the most striking within-area difference compared to the other sites is a much higher relative abundance of holothurians, fish, and particularly ophiuroids on nodule-bearing facies than on facies O.

• in nodule-facies O, the highest taxonomic richness belongs to the echinoderms and more particularly to holothurians; the next taxonomically richest phylum are the sponges.

• concerning trophic groups, suspension feeders are taxonomically more diverse and more numerous than detritus feeders notwithstanding nodule coverages.

• there is evidence of high within-area variability in abundances.

• numerous ichnofacies are present especially on nodule-free areas.

From the 2004 surveys by the Interoceanmetal Joint Organization, the analyses reveal:

• the presence of 13 phyla as on the other sites of the CCFZ.

• an overall abundance of megafaunal taxa of 225 + 130.28 ind/ha, with more (148 ind/ha) on nodule bearing areas than on facies O (136 ind/ha).

• the presence of the following main phyla:
  - 84 ind/ha echinoderms (composed mainly of 63 ind/ha holothurians and 18 ind/ha ophiuroids respectively 28 % and 15.5 % of total abundance),
  - 34 ind/ha sponges, 26 % of total abundance,
  - 15 cnidarians (composed mainly of 8 ind/ha hydrozoans, 8.4 % of total abundance).

• concerning trophic guilds, there is in overall about the same amount of suspension feeders 68 ind/ha than deposit feeders 69 ind/ha however these proportions differ with the substrates:
more suspension feeders (76 ind/ha) on nodule bearing substrates than on facies O (32 ind/ha).

deposit feeders are slightly more numerous (39 ind/ha) on nodule free areas than on nodule bearing seafloor (30 ind/ha).

- at the substrate level, the composition of faunal assemblages differs:

- on nodule free areas, there is a predominance of holothurians (30.5 %), sponges (15.25 %), ophiuroids (10.17 %), echinarians (5.08 %), hydrozoans (3.4 %). This confirms the results of NIXO 45 where echinoderms predominate on facies O mainly because of echinoids and holothurians in almost equal parts and in lesser numbers crinoids. These results also corroborate with those of ECHO I where echinoderms prevail on facies O but principally because of echinoids.

- on nodule bearing areas, there is in overall a higher diversity with a predominance of sponges (32.29 %), holothurians (26.04 %), ophiuroids (18.75 %), hydrozoan (11.46 %), polychaetes (8.33 %), antipatharians (7.29 %), zoanthids (5.21 %) and hydrozoans (3.39 %). The predominance of sponges has not been reported on the other nodule-bearing sites of the CCFZ, however sponges as well as Echiura are particularly abundant on Facies C 40 % on ECHO I. Also holothurians are more present in ECHO I on facies C 40 % based on the analysis of imagery viewed through a 70 mm lens. The rank in abundance of ophiuroids on IOM BIE site would be replaced by echinoids on ECHO I. Antipatharians, zoanthids and polychaetes appear to be exclusive to nodule-bearing seafloor.

There is evidence of preferential habitats for megafaunal assemblages on specific seafloor types. These have been classified as: undulating plain, horst top, horst slope, trough axle, trough slope, volcanic slope. The results show that:

- the highest diversity is recorded on:

  - gently undulating plains, composed of ophiuroids (19 %), antipatharians (17 %), polychaetes (14 %), holothurians (14 %), xenophyophores (13 %), hydrozoans (13 %) and sponges (10 %),

  - horst slopes, composed of xenophyophores (11 %), sponges (22 %), antipatharians (11 %), hydrozoans (19 %), polychaetes (23 %), ophiuroids (8 %) and holothurians (6 %).

- intermediate diversities on:

  - horst tops, composed of xenophyophores (12 %), sponges (28 %), hydrozoans (12 %), polychaetes (17 %), ophiuroids (9 %), holothurians (22 %),

  - trough axles, composed of xenophyophores (19 %), sponges (11 %), antipatharians (23 %), ophiuroids (23 %) and holothurians (24 %).

- low diversity on trough slopes, composed of xenophyophores (22 %), sponges (9 %), hydrozoans (50 %) and holothurians (19 %).

- the lowest diversity on volcanic slopes, mainly composed of xenophyophores (23 %) and sponges (77 %).

An association of genetic nodule types and megafaunal assemblages has been outlined. The different genetic nodule types encompass: hydrogenically grown (H), hydrogenic-diagenically grown (HD), diagenically grown (D) and nodule free stations. The main results within these nodule types are:

- an abundance of taxa (68-92 %) is associated with nodules diagenically grown D-Type and D1 subtype (Cu>Ni>1.2 %),

- holothurians are not associated to nodules hydrogenic-diagenically grown HD types, only to diagenically D type and hydrogenically H types,

- polychaetes and hydrozoans are associated to nodules diagenically grown D type and intermediate nodules hydrogenic-diagenically grown HD types.

In conclusion,

- there is a greater abundance and richness of taxa on nodule bearing seafloor (corresponding to nodules facies B 45 % and C 40 % on the other sites).

- there is in overall about the same amount of deposit feeders than suspension feeders, however when considering substrates, suspension feeders prevail significantly on nodule bearing substrates while deposit feeders are slightly more abundant on facies O such as in ECHO I.

- the predominance of echinoderms is composed mainly of holothurians and ophiuroids in lesser proportions on all substrates while on other sites of CCFZ, echinoids replace ophiuroids in the rank of abundance.

- sponges have a marked preference for nodule-bearing substrates such as in ECHO I on nodule-facies C 40 % where Echiura are also particularly abundant.

- there is evidence of preferential habitats on specific seafloor types from the highest diversity recorded
on gently undulating plains and horst slopes, inter-
mediate diversities on horst tops and trough axles,
low diversity on trough slopes and the lowest diver-
sity on volcanic slopes.

• an association with genetic nodule types has also
been outlined such as the fact that megafaunal as-
semblages are more abundant on nodules diageni-
cally grown D-Type and D1 subtype (Cu>Ni>1.2 %).

2.3. MAIN RESULTS OF KAPLAN/ISBA/
NODINAUT PROJECT

Meiofaunal and macrofaunal assemblages

Meiofauna is defined as biota retained by the finest
screens down to a mesh opening of 40-62 microns or
smaller and the macrofauna as the part retained by
sieves with meshes of 250 microns-1 mm (Gage and
Tyler 1991; Grassle et al., 1975; Haedrich et al., 1975,
1980; Hecker and Paul, 1979; Hessler and Jumars, 1974;
McIntyre, 1969; Smith et al., 1997; Thiél, 1975). Together
with meiofauna, macrofauna makes up. by far the most
numerous and diverse component of the deep sea ben-
thos. Meiofauna, which is much less known than mac-
rofauna, consists of both multicelled (metazoan) ani-
mals traditionally regarded as meiofaunal and larger
single-celled protozoans as Foraminifera.

Kaplan/ISBA/Nodinaut project

The surveys achieved by the International Seabed
Authority for Kaplan project (ISBA, 2008a) and IFREMER /
Nodinaut project (Galeron et al., 2006a, b) were complet-
ed in May June 2004 with RV l’Atalante (Nodinaut cruise)
as part of the activities agreed upon in the contract for
nodule exploration in the CCFZ drawn up. between the
French authorities and the International Seabed Author-
ity (ISBA, 2008a). Previously two other surveys were
performed in February-March 2003 with RV New Horizon
and in February 2004 by RV Umiaka-Maru.

These surveys took place at three sites spaced at
1,500 km intervals across the CCFZ (W, C, E of the CCFZ).
Among these, two sites (C=NIXO 45 and E= IOM BIE)
are at the same locations as in the previously described
region-wide UNESCO/OIC baseline study of megafaunal
assemblages of the CCFZ (Stoyanova, 2008, Radziejews-
ka and Stoyanova, 2000; Tilot, 1993, 2006 b; 2008c; Tilot
et al., 2010). NIXO 41 is located in the area of Kaplan
site C, more south-east while Kaplan Site W is located
West of UNESCO/OIC baseline study sites. ECHO I is also
close to Kaplan site C and has been surveyed to assess
the recolonization rate on disturbed areas (Tilot, 1990b)
as it was a pilot-scale mining site where tests were con-
ducted by Ocean Mining Inc. and Ocean Mining Associ-
aties (OMA) in 1978 (Appendix 1, Figure 14).

The objectives of the Kaplan project were to gather en-
vironmental reference data on 3 study sites and to elu-
cidate regional-scale patterns of the structure and distri-
bution of macrobenthic and meiofaunal communities
(protozoan foraminifera, nematode worms and poly-
chaeta worms) in order to assess the impact of mining
activities on benthic populations and to propose recom-
endations to ISBA on minimizing the impact of mining
activities on deep sea biodiversity.

The spatial scale of the distribution and the gene flow of
these communities are important elements to the suc-
cessful recolonisation of disturbed areas. Polychaeta and
nematods dominating these faunal categories by abun-
dance and species richness are frequently used to evalu-
ate anthropogenic disturbance in shallow-water habi-
tats (Boucher and Lambshead, 1995; Brown et al., 2001;
Glover et al., 2001; Hannides and Smith, 2003; Lambs-
head and Boucher, 2003; Paterson et al., 1998; Smith and
Demopoulos, 2003). Foraminifera (~0.03 mm to 10's of
centimeters in size) are very broad ranged and the most
abundant protozoans in deep sea sediments (Gooday et
al., 1998). They substantially influence seafloor habitat
structure and energy flow in the Pacific nodule province
(Gooday, 1994). Foraminiferan community structure is
frequently used to infer disturbance and climate-change
impacts in fossil marine habitats.

The Nodinaut project (Galeron et al., 2006a, b) studied
these aspects on meio-, macro and in smaller propor-
tions, megabenthic communities, taking in account pre-
vious knowledge on one of the eastern French claim ar-
reas, NIXO 45 (Du Castel, 1985, Tilot, 1992b, 1993, 2006b),
recording and sampling in situ, with the submersible
Nautilis and specific devices, environmental parameters
and biological data of benthic communities. In addition
three autonomous colonisation modules have been
launched for a year on the seabed.

State-of-the-art molecular “DNA-friendly techniques”
and morphological methods were used essentially on
key components of foraminifera, nematode and poly-
chaeta to evaluate levels of species overlap. and rates of
gene flow over scales of 1,000-3,000 km.

Main results of Kaplan/ISBA project

The sampling programme involved three research cruises
which collected a total of 40 box core and 32 multiple
cores samples. Each “box core” sample is essentially a
50x50x50-cm cube of sediment recovered intact from the
seafloor; a “multiple core” consists of eight core tubes
of intact bottom sediment ~10 cm in diameter,

The main results are the following:

• the diversity of the seabed fauna is unique, by the
fact that it encompasses true abyssal species, many
new to science, adapted to abyssal environment
with reproductive viability and sustained species radiations, i.e., among Echinodermata (Billet, 1991), Isopoda (Hessler, 1970), Nematoda (Tietjen, 1989) and Foraminifera (Gooday, 1993). There would then be a characteristic fauna of the abyss, i.e., that abyssal habitats are not merely sinks of non-reproducing individuals transported from ocean margins as previously hypothesized (Rex et al., 2005).

- high, unanticipated, levels of species diversity for all three sediment-dwelling faunal components (foraminifera, nematodes and polychaetes) at the three study sites. Barcoding revealed novel lineages in small invertebrates that are hidden by cryptic morphology and the presence of numerous unique abyssal taxa. A total species richness of these faunal communities at a single site in the CCFZ could easily exceed 1,000 species. However there is still a large number of undescribed species.

- the abundance, species richness and community structure of foraminifera and polychaetes is heterogeneous on scales 1,000-3,000 km across the CCFZ. While morphotypes may be broadly shared at this scale, there is no evidence yet for high levels of gene flow.

- the abundance of the megafauna, macrofauna and meiofauna is lower in the western than in the eastern site because of an overall westward trend of reduced primary productivity in the central Pacific (Smith and Demopoulos, 2003).

- the assessment of the diversity of benthic communities is incomplete as the study sites appear to be undersampled and the molecular analyses present technical difficulties.

- for foraminifera, among the 252 morphospecies recognized at site E and C, most are rare. There is a large number of undescribed species.

- the within-site diversity of nematodes is very high with 73 hypothesized species from the 97 specimens collected on sites E and W.

- polychaetes, also exhibit very high within-site diversity and a high abundance of cryptic species. The estimates are at least the double of those based on morphological studies (Glover et al., 2002). Their abundances decrease from East to West (from 84.8 ind/m² to 18.4 ind/m²). Analysis of the polychaete composition at the family level strongly suggests reduced diversity at Sites C and W, compared to Site E where some families seem restricted revealing high endemcity.

- in nodule covered areas, megafaunal and macrofaunal densities are more abundant whereas meiofaunal densities are reduced.

- habitat heterogeneity also appears to be higher than previously appreciated.

**Main results of Nodinaut project**

The Nodinaut project contributed to Kaplan project with the comparison of all benthic community patterns between the eastern (Kaplan C=Nixo 45) and the western French claim (Kaplan W) sites (Galeron et al., 2006a, b). The main results are the following:

- the geological and chemical characteristics of the substratum (sediments and minerals) as well as the physico-chemical characteristics of the water-sediment interface at Kaplan C and W are investigated.

- for megafauna, although the sampling effort by video and photo was too low to appreciate correctly the results, the following trends have been recorded: the abundance is lower in the western area, with 147 ind/ha (sampled area of about 4 ha) while in the east, the figures are higher with 157 ind/ha on facies O and 330 ind/ha on facies B (smaller sampled areas). However, a total of 51 species have been collected among which 20 holothurians.

- macrofauna follows the same pattern with 160 ind/m² on nodule bearing areas of Kaplan W and higher estimates in the east, 263 ind/m² on facies O and 338 ind/m² on nodule bearing areas. More than 80 % of the macrofauna is composed of polychaetes (56-67 %), tanaids (12-15 %) and isopods (4-11 %). Species richness is of more than 200 species/ 4 m² with a great amount of unknown species, in particular Spionids. Only the composition of the communities differs in nodule free and nodule bearing substrates. Taxonomic identification is still in progress for the next years.

- meiofauna, conversely to macrofauna and megafauna, is more abundant and diverse in the eastern area than the western because partly of the nodule coverage factor. It is thus more abundant on facies O with 13 ind/cm² over a sampled area of 0.5 m². Nematodes totaled 250 species, belonging to 110 genera and 33 families; there is still a high percentage of unknown species.

- from the five samples of protozoans, the abundance is 18 ind/cm² with a richness of 180 species mostly of unknown species.

- the small encrusting protozoans, mainly foraminifers, living on nodules are more diverse in the eastern than in the western area (Veillette et al., 2007a, b). A total of 90 different morphospecies, among which 73 morphospecies of foraminifera, have been found on 235 nodules sampled by the Nautile.
2.4. COMPARISON WITH ESTIMATES FROM DOMES STUDY

Assessments for the macrofauna and the meiofauna of the CCFZ have been drawn previously (Burns et al., 1980; Hecker and Paul, 1979; Mullineaux, 1983; Paul and Hecker, 1977; Radziejewska, 1997; Radziejewska, 2002; Radziejewska and Kotlinski, 2002; Radziejewska and Modlitba, 1999; Radziejewska et al., 2003; Stoyanova, 2001; Trueblood and Ozturgut, 1997). Concerning the results from the DOMES study (Hecker and Paul, 1979), in particular DOMES C = ECHO I = Kaplan C, comparative analysis are presented (Tilot, 1992b, 2006b; Tilot et al., 2010; ISBA, 2008a).

Hecker and Paul (1979) and Paul and Hecker (1977) sampled the macrofauna and the meiofauna at three study sites, DOMES A, B and C. DOMES C is in the area of Kaplan site and ECHO 1 (UNESCO/IoC study).

Results on the macrofaunal assemblages at DOMES C analysed by Hecker and Paul (1979) are as follows:

- in overall, the faunal density (268 ind/m²) is higher at DOMES C than at DOMES A and B which supports UNESCO/IoC baseline study and ISBA/Kaplan/Nodinaut results and could be explained by the westward trend of reduced primary productivity in the central Pacific.
- a prevalence of deposit feeders (3.5 times greater) than suspension feeders. This corroborates with the results for megafauna in the UNESCO/IoC study at ECHO I site displaying the existence of more suspension feeders in the western oligotrophic sites and more deposit feeders in the eastern sites in relation to a gradient in productivity from west to east, habitat heterogeneity and local environmental conditions.

The importance of polychaetes as dominant components of the macrofaunal deposit feeders at DOMES C is also displayed in the results of Paul and Jumars (1976) who found 30.6 % polychaetes at the DOMES C site, while Hessler and Jumars (1974) found 55.1 % at a site in the central Pacific Ocean.

The estimates of Paul and Jumars (1976) at DOMES S C are slightly different concerning the contribution of suspension feeders, mainly cnidarians (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 and Jumars, 1974). Conversely, for megafauna on ECHO 1, cnidarians do not prevail, only sipunculids and by decreasing order: echinoderms, echiurians, sponges, cnidarians, annelids and fish.

The meiobenthos at DOMES C is characterized by a high biodiversity of two large groups, ostracods and nematodes. Estimates display more ostracods (87.61 %) than nematodes (12.38 %). However, these proportions were not confirmed by Renaud-Mornant and 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/m³, 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 recorded by Paul and Jumars (1976) at comparable depths at the DOMES C site, and similar proportions were confirmed.

There was a difference in sampling intensity between Domes and Kaplan. In Kaplan’s results, endemism in all families is found much higher than in Domes data as a proportion of the total number of species in each family. Kaplan plans to unify its datasets with those of Domes as it is an important step. to assessing morphological patterns.

2.5. Discussions

Intra-regional and within-site variability of the structure of benthic faunal assemblages in CCFZ

In overall, UNESCO/IOC baseline study (Tilot, 1992b, 2006b, 2008c, Tilot et al., 2010) and ISBA/ Kaplan/Nodinaut (ISBA, 2008a) show an intra-regional variability in faunal assemblages, biotic and abiotic conditions at different scales in space and time.

At a regional scale, within the CCFZ, the large contribution of particulate flow over the substratum may be a major factor contributing to faunal abundance (Drazen et al., 1998; Smith et al., 1997; Thurston et al., 1998). The CCFZ being included in the broadly defined mesotrophic abyss of Hannides and Smith (2003) characterized by a primary productivity (NECC) ranging from 210 to 327 mg C m⁻² d⁻¹ (Pennington et al., 2006) and by particulate organic carbon (POC) fluxes varying from ~0.5 to 1.6 g C m⁻² y⁻¹, the estimates of abundances of megafaunal assemblages of the UNESCO/IOC baseline study remain in the range reported for the deep. Pacific seafloor in different studies (summarised by Bluhm, 1994, Bussau et al., 1995).

Due to this overall westward trend of reduced primary productivity in the central Pacific (Smith and Demopoulos, 2003), the abundance of megafauna, macrofauna and meiofauna is lower in the western area than in the eastern (ISBA, 2008a, Tilot, 1992b, 2006b, Tilot et al., 2010), confirming the literature.

The community structure of faunal assemblages differs substantially for macrofaunal and meiofaunal populations, often displaying a major turnover in species, over a latitudinal range; the abundance, species richness and community structure of foraminifera and polychaetes is heterogeneous on scales 1,000-3,000 km across the CCFZ (ISBA, 2008a). For example, the fact that there are at least 10 species of foraminifera that are abundant at one of the Kaplan Sites C or E, but rare or absent at the other site suggests significant turnover of major components of the foraminiferal faunal over scales of roughly 1,000 km across the CCFZ (ISBA, 2008a). For megafauna, it is presumably at wider scales. Therefore diversity of the seabed fauna is unique, by the fact that it encompasses true abyssal species adapted to abyssal environment with reproductive viability and sustained species radiations, i.e., among Echinodermata, Isopoda, Nematoda and Foraminifera and are not merely sinks of non-reproducing individuals transported from ocean margins as hypothesized previously (Rex et al., 2005). Many species are new to science and therefore need to be protected from extinction.

ISBA/Kaplan/Nodinaut project concludes on basis of their results that the assessment of the diversity and abundance of benthic communities is incomplete as study sites are undersampled, technical difficulties with the molecular analyses are to be solved and as a great percentage of taxa are still to be identified taxonomically.

The influence of this overall westward trend of reduced primary productivity is partly verified in UNESCO/IOC baseline study (Tilot et al., 2010) by the relatively high abundances assessed at NIXO 45 (553 ind/ha), NIXO 41 (726 ind/ha) and ECHO I (502 ind/ha) sites which are in Kaplan site C area. But the more eastern site IOM/BIE (Kaplan E), with its relatively lower abundance (225 ind/ha), does not follow the pattern, this may be due to different factors among which the location of UNESCO/IOC sites which are more eastern and less distant from each other than the three DOMES sites; they correspond to Kaplan C (=DOMES C) and E and may be then in a richer area concerning primary productivity. In addition the sampling devices, efforts and methodology differ at each site. However since the other regional trends are observed at UNESCO/IOC sites, several other factors may intervene such as bottom topography, edaphic (substratum) characteristics, hydrological conditions and other regional and local characteristics.

Nodinaut project’s (Galeron et al., 2006a, b) assessments for megafauna over much smaller sampled areas are relatively lower but follow the same latitudinal trend with 147 ind/ha on a nodule bearing area at Kaplan W and 330 ind/ha on a nodule area at Kaplan C. Macrofauna displays 160 ind/m² on nodule bearing areas of Kaplan W and 338 ind/m² at Kaplan C. Thus higher densities have been reported at DOMES C (=Kaplan C) than at more western sites, DOMES A and B (Hecker and Paul, 1979; Morgan, 1991; Morgan et al., 1993; Paul and Jumars, 1976). However these estimates would be lower than those given by Wilson and Hessler (in Mullineaux, 1989).
Moreover meiofauna does not observe this latitudinal trend as abundances and species richness are greater in the east (13 ind/cm² at Kaplan C) than at Kaplan W because partly of the nodule coverage factor (Galeron et al., 2006a, b).

Concerning trophic guilds, one might expect to see more suspension feeders in the more western sites where primary productivity is the lowest at the surface and following an eastward gradient (Smith and Demopoulos, 2003). This trend is evidenced by the results in the UNESCO/IOC baseline study displaying more suspension feeders at NIXO 45 and NIXO 41, the more western sites, while at ECHO I there are more deposit feeders, in particular echinoderms (Morgan, 1991; Morgan et al., 1993; Paul and Jumars, 1976; Tilot, 2006b, Tilot et al., 2010). However IOM/BIE displays about the same amount of suspension feeders and deposit feeders. UNESCO/IOC baseline study demonstrates a gradient of dominance of actinoids to the West (NIXO 45 in the UNESCO/IOC baseline study displaying more abundance and following an eastward gradient (Smith and Demopoulos, 2003). This trend is evidenced by the results in the UNESCO/IOC baseline study displaying more suspension feeders at NIXO 45 and NIXO 41, the more western sites, while at ECHO I there are more deposit feeders, in particular echinoderms (Morgan, 1991; Morgan et al., 1993; Paul and Jumars, 1976; Tilot, 2006b, Tilot et al., 2010). However IOM/BIE displays about the same amount of suspension feeders and deposit feeders. UNESCO/IOC baseline study demonstrates a gradient of dominance of actinoids to the West (NIXO 45 and NIXO 41) and echinoderms to the East, echinoids in ECHO 1 and holothurians in IOM BIE). The relative abundance of actinians (52 %) and echinoderms (32.5 %) in NIXO 45 corroborates with the estimates of Morgan et al. (1993), which are 54 % and 32 % respectively for a study site further West (Domes A).

The most persistent within-area pattern is a higher faunal abundance and richness for megafaunal and macrofaunal assemblages in nodule bearing areas (Galeron et al., 2006a; ISBA, 2008a; Morgan, 1991; Mullineaux, 1987; Radziejewska, 1997; Radziejewska and Stoyanova, 2000; Stoyanova, 2008; Tilot, 1990b, 1991b; Tilot, 1992b, Tilot, 2006b, Tilot et al., 2010). The evidence of a trend of higher megafaunal and macrofaunal densities on nodule areas shows that these assemblages are not space limited. The inverse trend of lower meiofaunal densities in nodule areas may suggest competition between meio- and macro-infauna, e.g. both assemblages of spongiaids for the macrofauna and nematodes for the meiofauna shows a high species richness but dissimilar species compositions in areas with and without nodules. This general pattern is observed elsewhere in the deep sea such as in the Peru basin where nodule crevice fauna is distinctly different from the fauna living in the sediment at proximity of nodule fields (Tilot, 1989; Thiel et al., 1993).

There is also a high within-site heterogeneity in infaunal community structure which appears to covary with the abundance and size of manganese nodules, on scales of 0.1-10 kilometers at Kaplan sites C and W (ISBA, 2008a).

In UNESCO/IOC baseline study, the high values of standard deviations of the overall abundances indicate a high within-site variability resulting from non-random dispersion of faunal populations (225 - 130.28 ind/ha at IOM BIE site, 502 - 146.97 ind/ha at ECHO I site, 553 - 333.73 ind/ha at NIXO 45 site, 726 - 438.14 ind/ha at NIXO 41. These facts have serious consequences for the conservation of the biodiversity of the benthic fauna in areas earmarked for nodule mining.

Nodule coverage and abiotic factors such as the effect of slope are factors that partly determine the abundance and composition of faunal assemblages. This has been analyzed in detail in UNESCO/IOC baseline study for megafaunal assemblages where 13 preferential habitats have been identified. Some nodule-facies have exclusive taxa such as on facies O with ancient sediments (Oligocene to Miocene) and nodule-facies C 15 % in NIXO 45.

Thus megafaunal assemblages are more abundant on nodule-facies C 10 % on slopes (> 15°) and facies O on recent sediments (Plio-Quaternary) for NIXO 45, C 30 % and A 30 % for NIXO 41, C 40 % for ECHO I, nodule-facies B 45 % and C 40 % for IOM BIE. The taxonomic richness is higher on nodule-facies C 2-15 % for NIXO 45, on nodule-facies A 30 % for NIXO 41, on nodule-facies C 40 % for ECHO I and on nodule-facies B 45 % and C 40 % on IOM BIE.

On the other hand, meiofauna prefers nodule-free areas, where often sediments are softer. Nodinat project reports a greater abundance on facies O with 13 ind/cm² sampled on 0.5 m². There may be some competition between meiofauna and macro-infauna, e.g. nematodes and spongiaids show similar high species richness and dissimilar species composition in areas with and without nodules (Galeron et al., 2006a; ISBA, 2008a).

In general for sessile epibenthic and infaunal communities, nodule bearing areas represent a special habitat of higher heterogeneity in substratum which harbors more suspension feeders (mainly actinians, octocorallians and sponges), feeding on suspended organic particles, while nodule-free areas attract more deposit feeders.

Although the same order of dominance and proportionality of suspension feeders over deposit feeders and carnivores is recorded on some sites such as NIXO 45 and NIXO 41 what ever the nodule-facies, ECHO I differs with deposit feeders outnumbering suspension feeders and carnivores and IOM/BIE displays both trophic groups in equal amounts.

Among nodule bearing areas, sponges prevail among suspension feeders at IOM/BIE the most eastern site while actinians prevail at ECHO I, NIXO 41 and NIXO 45. Among deposit feeders, holothurians prevail on IOM BIE, holothurians and echinoids on NIXO 41 and NIXO 45 while echinoids and holothurians prevail on ECHO 1.

Conversely to the regional trend for abundance, taxonomic richness of megafaunal and macrofaunal as-
Foraminiferans, living on nodules are more diverse in evidence that the small encrusting protozoans, mainly with respect to ECHO 1 versus NIXO 45 and NIXO 41. The differences were most striking compared at the major taxonomic category level, NIXO 45, NIXO 41, ECHO 1, IOM BIE differ in their composition and structure. The differences were most striking with respect to ECHO 1 versus NIXO 45 and NIXO 41. This trend is not verified at the nodule level, for there is evidence that the small encrusting protozoans, mainly foraminiferans, living on nodules are more diverse in the eastern than in the western area (Veillette et al., 2007a, b). At a nodule-facies level, UNESCO/IOC baseline study detects more taxa richness for megafaunal assemblages on its western study site (NIXO 45) especially for facies C 2-15 % and nodule-facies C 30 % but not as much for nodule-facies O, B 35 % and B 35 %. When compared at the major taxonomic category level, NIXO 45, NIXO 41, ECHO 1, IOM BIE differ in their composition and structure. The differences were most striking with respect to ECHO 1 versus NIXO 45 and NIXO 41. This trend is not verified at the nodule level, for there is evidence that the small encrusting protozoans, mainly foraminiferans, living on nodules are more diverse in the eastern than in the western area (Veillette et al., 2007a, b).

The results (Galeron et al., 2006a; Tilot, 1990b, 1991b, 1992; Tilot et al., 2010) on the analysis of faunal communities on the dredge tracks, produced by pilot-scale mining tests conducted by Ocean Mining Inc. and Ocean Mining Associates (OMA) in 1978, are interesting as these tracks lay still undisturbed and recolonisation is evidenced. Megafaunal and macrofaunal assemblages display similar densities than in proximate nodule bearing areas but differ in faunal composition. The high rate of biological activity and oxygen flux at the sediment water interface, comparable to the neighbouring nodule bearing substrates, could be explained by the fact that the dense cover of nodules would limit the intensity of respiratory exchanges per surface unit. However these exchange rates are much higher in nodule free areas (which may be due to the fact that a layer of nodules may exist under the dredge tracks, pers. obs. Tilot, 1989).

The variability in biotic and abiotic conditions (Angel, 1998; Tyler et al., 1998) revolutionizes the preconceived notion of a very stable faunal environment moulded by an unchanging environmental context in “equilibrium” (Sanders, 1968) in which the high stable nature of the deep sea, over evolutionary time, allows species to diversify and evolve into highly specialized niches. For Grassle and Sanders (1973), the deep sea would in fact be a non-equilibrium community with a patch mosaic model set against a backdrop of environmental stability thus creating a mosaic of microhabitats on which species might specialize. The patch mosaic model would favour larvae and juveniles specializing on patches of different sorts in order to grow until they can effectively compete with other species and successfully coexist and reproduce (Jumars et al., 1990). Another disequilibrium model consistent with Rex’s (1981) pattern of highest diversity is Huston’s (1979) intermediate disturbance hypothesis where communities in highly stable environments experience competitive exclusion as the dominant take over and eliminate weaker competitors. Natural disturbances could also maintain epibenthic communities in “disequilibrium” as local perturbation produces heterogeneous habitats supporting populations at an early phase below carrying capacity where species coexist without competition (Gray, 1977). Data from research in the abyssal environment demonstrate a variability in biotic and abiotic conditions in space and time such as currents at depth, benthic storms and seasonal cycles in the vertical flow of detritus particles (Ailler, 1997; Angel, 1996; Drazen et al., 1998; Kontar and Sokov, 1994; Laueraman et al., 1997; Smith et al., 1997; Thurston et al., 1998; Tyler, 1995) related to variation in planktonic debris that originates in the eutrophic zone (Gehlen et al., 1997; Khrisponoff et al., 1998; Scharek et al., 1999; Smith et al., 1997; Thiel et al., 1988/1999). This flux is observed to be particularly intensive in spring (Yamazaki and Kajitani, 1999) and may result in the deposition of detritus on the sediment surface (Radziejewska, 2002; Smith et al., 1996; Thiel et al., 1988/1989) causing a significant change in the structure of dominant epibenthic megafaunal assemblages in shallower sites of the abyssal north-eastern Pacific (Ruhl and Smith, 2004). Radziejewska and Stoyanova (2000), Stoyanova (2008) report greatly elevated aphid abundances on the seafloor showing evidence of sedimentation. Knowledge of events that may underlie variation in organic carbon supply to the abyssal benthic communities in CCFZ is necessary if temporal changes are to be correctly interpreted.

There is evidence that other factors influence the structure of epibenthic assemblages:

- the horizontal contribution of nutritive sediment particles in suspension when currents originate in the west in specific zones of high primary production and decrease progressively eastwards.

- particular edaphic and hydrological conditions above the bottom layer and the topography of the ocean floor. For example, the morphology of the NIXO 45 site comprises horsts and grabens, which favour the acceleration of currents and the creation of slopes. Nodule-facies B and C+ appear to be where currents...
circulate according to the abundance of sessile suspension feeders and their orientation.

Epibenthic megafauna from various depths has been reported to display non-random distribution patterns (Sale et al., 2006). Analyses of the seafloor in the CCFZ have shown that spatial heterogeneity induces patchiness in megafaunal colonisation (Schneider et al., 1987; Tilot, 1993, 1995, 2006b, Tilot et al., 2010). Results in the UNESCO/IOC baseline study display an aggregative pattern within specific nodule-facies for some of the most frequently observed taxa on the study sites, e.g. aggregations of holothurians, sponges and actinians according to particular nodule-facies (Tilot, 2006b; Tilot et al., 2010). For example, on nodule-facies C+ of NIXO 45, the distribution of actinids Sincyonis tuberculata is aggregated above 1600 m$^2$ according to the Levis, David and Moore indexes and Fisher’s coefficient and random at 400 m$^2$ and 800 m$^2$ on facies O. 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. Also holothurians Mesothuria murrayi aggregate at 100 m$^2$ and 400 m$^2$ on nodule-facies C and at 800 m$^2$ on nodule-facies BP. Thus by identifying the spatial scales of the distribution of key benthic populations, impacts of mining activities can be assessed.

The heterogeneity in space and time of distributions of some populations can be caused also by biological interactions which are hardly known in the deep sea such as reproductive and social patterns, interspecific competitive or predatory interactions (Herring, 2002), bioturbation and biogenic structures and the micro-heterogeneity of habitats (Angel, 1998).

Using the pattern of hydrodynamic flow over the nodules to predict a priori the distribution of epibenthic organisms is a means of determining the relative importance of physical action on biological processes in the structure of abyssal communities. Two factors which give structure to epibenthic 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 deposit feeders colonise the base of nodules with rougher surfaces, weak cohesion, weak particle contact and a higher rate of deposition. Also individual nodules serve as permanent or semi-permanent attachment sites for numerous sessile and hemi-sessile organisms, members of both the megabenthos and smaller benthic compartments (Mullineaux, 1987; Tilot, 1992b, 2006b; Tilot et al., 2010; Veillette et al., 2007).

Potential indicators of environmental change and mining impact would be some taxa among the megafauna, characterized by their wide distribution and preferential habitats, in particular echiurian worms Bonelliaea Jacobia birsteini would be key indicators for monitoring (Tilot, 1991a, 2006b, 2010b).

Comparison of data collected by different devices

The variety of equipment used in the surveys, the different methodologies, sampling efforts and the frame examination procedures necessitate caution in the interpretation of results (Rice et al., 1982). While seafloor imaging (photographic transects, video surveys) is a preferred and cost-effective group of methods (Parry et al., 2002; Tilot et al., 2010), techniques and equipment applied have been evolving and remain different (e.g., single deployment camera of Piepenburg and Schmid, 1997; stationary time-lapse cameras used by Smith et al., 1993; towed gear used in this study, Tilot, 1992a, 2006b).

Results show that regional trends reported in the literature and by other surveys in the CCFZ are observed in the UNESCO/IOC baseline study despite different sampling devices, efforts and methodologies. The variations may also be due to several other factors such as the bottom topography, edaphic (substratum) characteristics, hydrological conditions and other regional and local characteristics.

The study and assessment of megabenthic communities from bottom photographs represent one mobile and cost-effective possibility to obtain substantial data on environmental baseline surveys and it is also well adapted and cost effective for large scale impact assessments and monitoring (Tilot et al., 2001, 2008).

2.6. Recommendations for future studies

ISBA/Kaplan/Nodinault and UNESCO/IOC baseline studies conclude that concerning the polymetallic nodule ecosystem, more information is required on the functioning of the natural processes on the seabed and in overlying watercolumn, on varying spatial and temporal scales. There is a lack of knowledge in truly understanding the dynamics of the ecological factors driving these community changes, on the physical features of the environment and the relationships with biodiversity, on species ranges, sensitivity to sediment burial and the spatial-scale dependence of recolonization on abyssal benthic communities (Bussau et al., 1995, Jumars 1981, Mullineaux 1987, Oebius et al., 2001; Sharma et al., 2001; Smith et al., 2008 in Polunin, 2008; Thiel et al., 2001; Tilot, 1988, 1992b, 2006b, 2008b; Tilot et al., 2010). Also some trends (e.g., greater abundance and high levels of biodiversity of infaunal macrobenthos and megafauna in areas of higher nodule abundance,
high habitat heterogeneity...) makes it “very difficult to predict the upper limit to biodiversity within and across sites in the CCFZ, and how precisely nodule mining activities might influence habitat variability” (ISBA, 2008a).

Recommendations are the following:

- As the biodiversity across the CCFZ is still undersampled, there should be unification of existing datasets in the CCFZ (an important step for assessing morphological patterns), “intercalibration of working-species collections, e.g. CeDAMar, from disparate sampling efforts in the CCFZ” (ISBA, 2008a) and additional photographic/video and in situ sampling on a regional basis, to ensure identification of all faunal categories in relation to their varying habitats and environmental conditions (Tilot et al., 2010). The identification should be pursued preferably corroborating state-of-the-art molecular “DNA-friendly techniques” and morphological identification to ensure proper identification (ISBA, 2008a, Brandt et al., 2007; Tilot et al., 2010), levels of species richness, endemism and gene flow.

- For the collect of larger benthic organisms, intensive sampling would be recommended by means of photography and video, epibenthic sled or in situ, by submersible, ROV’s (Gage and Tyler, 1991; Tilot et al., 2010). The epibenthic sled would have to be adapted to the special nodule environment, as nodules are often collected with macro and megafaunal samples and thus often grind them into morphologically unidentifiable specimens (Tilot, 1989) however these could still be identified by DNA techniques.

- As there is a lack of knowledge on reproductive capabilities of all faunal categories in the CCFZ, the evaluation of the reproductive status of sampled fauna (Gage and Tyler, 1991) should be encouraged to test if the CCFZ is a sink of non-reproductive communities from more productive areas of the ocean.

- (ISBA, 2008a) suggests to study the biota of hard substrates (rock outcrops associated with fracture zones and seamounts) in order to test if the manganese nodule biota is unique or more widely distributed in the rocky substrates of the region. Although one facies of NIXO 45 analyzed in the UNESCO/IOC baseline study (Tilot, 2006b; Tilot et al., 2010) was composed of rock outcrops (AR) and displayed a characteristic fauna with a prevailing amount of suspension feeders (sponges, octocorallians, actinins, crinoids), the sampling effort was too low to appreciate correctly the results.

- The collect of more statistically representative materials would help to fine-tune the perception of habitat preferences and colonisation patterns of the nodule field benthos. A robust sampling strategy would adjust to low densities and relatively high sample diversity in the CCFZ (ISBA, 2008a).

- Modelling efforts are needed in order to assess the errors (confidence limits) in estimating abyssal endemism from various levels of sampling effort and for predicting sampling effort to sufficiently characterize regional species pools (Glover et al., 2002).
3. Rationale for the conservation of the biodiversity in the CCFZ

The ecological characteristics of the deep sea floor habitats of an abyssal polymetallic nodule ecosystem are prone to a higher sensitivity to environmental change and human impacts than shallower habitats as there lies a cumulative effect of diverse natural and anthropogenic stressors and toxic agents dispersed over the vastness and continuum of the soft-sedimented plains and amplified in deep sea food webs (Smith et al., 2008). Direct human activities at the surface and upper water column, such as overfishing (Myers and Worm, 2003), would affect the structure and functioning of benthic ecosystems. Climate change would be another cumulating factor which would influence regional patterns of circulation, primary production and thus would affect the deep sea floor through changes in epipelagic ecosystems. The overall consequences are hard to predict, most probably there would be an impact at a regional scale on the deep sea floor, water column and surface of the ocean (and layer of air over the ocean). The recovery rate to anthropogenic impact, if ever possible, would be very long, decades for the benthos to a million of years for nodules. The following basic elements, displayed in Table 1, have to be considered for preservation purposes (Tilot, 2010a):

Table 1. Description of the ecological characteristics of the nodule ecosystem in the CCFZ and their sensitivity to natural and anthropogenic impacts

<table>
<thead>
<tr>
<th>General ecological characteristics</th>
<th>Description of ecological characteristics within the CCFZ</th>
<th>Sensitivity to natural and anthropogenic impacts</th>
</tr>
</thead>
<tbody>
<tr>
<td>Productivity</td>
<td>Generally located beneath the oligotrophic ocean with a very low organic-energy flux (typically 1-10 g Corg per m² per year), mainly based on remaining organic matter coming from the surface or the water column. There is an eastward increase in surface productivity and thus more oligothrophic sites are located in the west of the CCFZ. In addition, close to the seafloor, there is a horizontal contribution of nutritive sediment particles in suspension when currents originate in the west in specific zones of high primary production. The general pattern of stability in productivity can be marked by temporal and spatial variability of particulate organic flux coming from the surface (Gage and Tyler, 1991; Smith and Kaufmann, 1999). Productivity can also be enhanced by topography, bottom currents, carcasses. A seasonal cycle exists with a variation in the vertical flow of detritus particles (Smith et al., 1997; Lauerman et al., 1997; Drazen et al., 1998; Thurston et al., 1998) causing an alteration in the flux of particulate organic carbon (Smith et al., 1997; Scharek et al., 1999).</td>
<td>More sensitive</td>
</tr>
<tr>
<td>Topic</td>
<td>Description</td>
<td>Sensitivity</td>
</tr>
<tr>
<td>-------------------------------------------</td>
<td>-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------</td>
<td>-----------------------------------------------------------------------------</td>
</tr>
<tr>
<td>Biological rates (respiration, reproduction, growth, recolonization)</td>
<td>Low biological rates (Gage and Tyler, 1991; Smith and Demopoulos, 2003), slow metabolic growth, compensated by an extension of the longevity of faunal organisms (Roberts, 2006); slower recovery (re-sedimentation, reorganisation of food chains) after disturbance. High stability, however there can be marked temporal and spatial variability inducing a fluctuation in biological patterns (Gage and Tyler, 1991; Smith and Kaufmann, 1999)</td>
<td>More sensitive, Slower recovery rate</td>
</tr>
<tr>
<td>Biomass</td>
<td>Many animals are small in body size and biomass and are extremely delicate, feeding on a thin layer of organic matter at the water-sediment interface (Gage and Tyler, 1991; Smith and Demopoulos, 2003)</td>
<td>More sensitive</td>
</tr>
<tr>
<td>Temperature</td>
<td>1-4 °C, one of the characteristics of an extreme environment</td>
<td></td>
</tr>
<tr>
<td>Sedimentation rates and mixing</td>
<td>0.1-10 cm per thousand years (Gage and Tyler, 1991; Smith and Demopoulos, 2003); Information lacking on sensitivity to sediment burial</td>
<td>Rolinskia et al., (2001) predict a resettlement of sediment particles up. to 95 % of the total released within a period of 3 to 14 years depending on the depth of release. When released near the surface, the same sediment could drift over thousands of km</td>
</tr>
<tr>
<td>The deep sea floor and global geochemical cycles</td>
<td>The deep sea floor is essential to global geochemical cycles. The sediments are major sites of nutrient recycling and are responsible for much of the organic-carbon burial on the planet. In the Eastern Equatorial Pacific Ocean, the sediment coverage is about 20 % thicker in morphological depressions than on the ridges; this is probably due to the lateral transport of particles in suspension by weak currents (Shor, 1959), between 2 and 25 cm/sec (Amos et al., 1977). Sediment chemistry is important in the genesis of nodules (Hoffert, 2008).</td>
<td>More sensitive</td>
</tr>
<tr>
<td>Topography</td>
<td>The general appearance of the CCFZ is one of abyssal hills, covered by nodule fields with some nodule-free sedimented areas at an average depth of 5500m. These hills are elongated in a north-south direction, parallel to each other and accompanied by escarpments (cliffs). Rocky substrates and seamounts are rarer. At a local scale, habitat heterogeneity plays an important role in structuring megafaunal assemblages. In addition, patchiness in the distribution at taxa level has been evidenced. Also the morphology of some sites of the CCFZ, as NIXO 45, comprises horsts and grabens, which favour the acceleration of currents and the creation of slopes.</td>
<td>More sensitive as heterogeneity of the substrate plays an important role in the structure of faunal assemblages</td>
</tr>
</tbody>
</table>
### Growth of polymetallic nodules and processes to maintain nodules at the surface of the sediments

<table>
<thead>
<tr>
<th>Description</th>
<th>Details</th>
<th>Recovery Time</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nodules grow about 1mm in 10,000 years (UNEP, 2006). The time for reconstitution of nodules is estimated to 1 million year for 1 to 2 mm size nodule (Ghosh and Mukhopadhyay 2000; McMurtry 2001). The role of biological activity, in particular deposit feeders, and of currents, which are sufficient to transport fine particles and reduce the real rate of sedimentation, could maintain nodules at the sediment surface (Hartmann, 1979; Hoffert, 2008; Schneider, 1981; Tilot, 1992b).</td>
<td>Very slow recovery</td>
<td></td>
</tr>
</tbody>
</table>

### Physical energy

**Bottom currents**

<table>
<thead>
<tr>
<th>Bottom currents</th>
<th>Details</th>
<th>Recovery Time</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bottom currents are often considered very weak (Shor, 1959), between 2 and 25 cm/sec (Amos et al., 1977). If a current is 1cm per second, it would travel for about 315 km per year; For a similar speed, sediments released at the surface could then move for more than 3,000 km over a period of 10 years. Also variability in the current pattern at depth and benthic storms are evidenced (Kontar and Sokov, 1994; Aller, 1997).</td>
<td>More sensitive to disturbance</td>
<td></td>
</tr>
</tbody>
</table>

### Deep ocean circulation

<table>
<thead>
<tr>
<th>Deep ocean circulation</th>
<th>Details</th>
<th>Recovery Time</th>
</tr>
</thead>
<tbody>
<tr>
<td>Over the past 15 years, in situ research revealed an unexpected complexity of the deep ocean circulation with localized deep circulation patterns on smaller spatial scales that are governed by regional processes. As timescales are longer than expected on the regional scale, conservation of large scale potential vorticity is still believed to be a strong constraint on flow, resulting in a tendency for zonally-elongated circulation systems, particularly at low latitude and mid-depth. Boundary currents, topography, mixing “hotspots”, transient flow, and influences of the wind-driven circulation provide mechanisms for meridional transport (Hautala and Riser, 1993).</td>
<td>Unknown but most probably long lasting with multiple effects due to complexity</td>
<td></td>
</tr>
</tbody>
</table>

### Absence of light

<table>
<thead>
<tr>
<th>Absence of light</th>
<th>Details</th>
<th>Recovery Time</th>
</tr>
</thead>
<tbody>
<tr>
<td>Part of the characteristics of an extreme environment</td>
<td>Presumably the fauna is more robust but the biogeographical range is poorly known</td>
<td></td>
</tr>
</tbody>
</table>

### An ecosystem over an often large and continuous megahabitat of soft sediments

| Vastness of the abyssal plains composed of soft sediments over 100-1,000 km. | Presumably, the fauna would be more resistant to local perturbations; there would be a greater potential for recolonization however the size of source populations depends on the biogeographical ranges of deep sea species which are poorly known (Glover et al., 2002). |

### Abyssal epibenthic fauna in a nodule ecosystem

| The diversity of the seabed fauna is unique, characterized by true abyssal species, (Isopoda, Nematoda and Foraminifera, in particular Echinodermata for megafauna) adapted to abyssal environment with reproductive viability and sustained species radiations. Benthic fauna is thought to be an important link in carbon cycling and mineralisation near and at the seafloor and contributes to the genesis of polymetallic nodules. | More sensitive, many species are new to science and therefore need to be protected from extinction |

### Faunal distribution

| The community structure of faunal assemblages differs substantially, often displaying a major turnover in species, over a latitudinal range. For foraminifera and polychaetes, the turnover is at scales of 1,000-3,000 across the CCFZ. For megafauna, it is presumably at wider scales. There are more suspension feeders in the western oligotrophic sites and more deposit feeders in the eastern sites in relation to the gradient in productivity from West to East. | Sensitive                                                                 |

### Deep ocean circulation

| Over the past 15 years, in situ research revealed an unexpected complexity of the deep ocean circulation with localized deep circulation patterns on smaller spatial scales that are governed by regional processes. As timescales are longer than expected on the regional scale, conservation of large scale potential vorticity is still believed to be a strong constraint on flow, resulting in a tendency for zonally-elongated circulation systems, particularly at low latitude and mid-depth. Boundary currents, topography, mixing “hotspots”, transient flow, and influences of the wind-driven circulation provide mechanisms for meridional transport (Hautala and Riser, 1993). | Unknown but most probably long lasting with multiple effects due to complexity |
Species diversity (on local scales) | Substantial reservoir of biodiversity for megafauna, macrofauna and meiofauna, e.g. polychaetes, crustacean, mollusks... (Snelgrove and Smith, 2002); The levels of species diversity are still poorly known since populations are undersampled.

There are very high levels of within-site diversity for macrofauna and meiofauna which appear to co-vary with the abundance and size of manganese nodules, e.g., on scales of 0.1-10 kilometers at Kaplan sites C and W. For megafauna, the high within-site diversity results from the non-random dispersion of faunal populations.

More sensitive

The high within-site diversity has serious consequences for the conservation of the biodiversity of the epibenthic fauna

Species distribution | Broad, however poorly known

Information lacking on sensitivity to spatial-scale dependence of recolonization of benthic communities.

Presumably less sensitive

Species abundance | In overall, there is a clearly marked faunal abundance for megafauna and macrofauna on nodule bearing areas while meiofauna prefers nodule free areas (Galeron et al., 2006a; ISBA, 2008a; Morgan, 1991; Mullineaux, 1987; Radziejewska, 1997; Radziejewska and Stoyanova, 2000; Stoyanova, 2008; Tilot, 1992b, 2006b).

Nodule influences on sessile epifauna and infauna contributes to enhance the biodiversity of the abyssal benthos at regional scales.

More sensitive

By combining the results of UNESCO/IOC baseline study (Tilot, 2006b, 2008c, 2010a; Tilot et al., 2010) and ISBA/Kaplan/Nodinaut (ISBA, 2008a), the following evidenced elements are to be taken in account for conservation purposes:

- There is an intra-regional and within-site variability in biotic and abiotic conditions in space and time. The abundance and composition of megafaunal assemblages differ in each area and within.

- Area patterns are present.

- The diversity of the seabed fauna is unique, characterized by true abyssal species, (Isopoda, Nematoda and Foraminifera, in particular Echinodermata for megafauna) adapted to the abyssal environment with reproductive viability and sustained species radiations.

- Many species are new to science and therefore need to be protected from extinction.

- The levels of species diversity are still poorly known since populations are undersampled; There are very high levels of within-site diversity, e.g. many foraminifera are new to science and characterised by extreme, small-scale heterogeneity in community structure.

- There are key faunal groups in CCFZ, such as cnidarians, echinodermns and sponges, for megafauna, and polychaete worms, nematode worms and protozoan foraminifera for macrofauna and meiofauna, which represent >50% of faunal abundance and species richness in abyssal sediments and display a broad range of ecological and life history types.

- There is an importance of other faunal groups which constitute the ecosystem, not only the fauna in, on the surface of the sediments and above the surface but also of fauna influencing the ecosystem, dwelling in the water column up to the surface of the ocean as the main food resources originate from above.

- UNESCO/IOC baseline study shows an overall taxonomic richness of 175 megafaunal taxa (genera and species) covering 13 phyla over about 5,500,000 m² (total benthos surface analysed from more than 200 000 photographs and 55 h video transects). The overall taxonomic richness is relatively high and composed of echinoderms (50 taxa including 32 holothurians), cnidarians (41 taxa), chordates (23 taxa including 17 fishes) and sponges (21 taxa). Over a much smaller surface, Nodinaut identifies 51 species among which 20 holothurians.

- ISBA/Kaplan/Nodinaut assess that more than 80% of the macrofauna, is composed of polychaetes (56-67%), tanaids (12-15%) and isopods (4-11%). Species richness is of more than 200 species/4 m² with a great amount of unknown species, in particular Spionids; concerning meiofauna, nematodes
totalize 250 species, belonging to 110 genera and 33 families; there is still a high percentage of unknown species while taxonomic identification is still in progress for the next years.

- Over all five study sites of UNESCO/IUCN baseline study, there is a higher taxonomic richness for suspension feeders (68 taxa, among which 58 sessile taxa and 10 mobile taxa), than for deposit feeders (60 taxa, among which 50 taxa are mobile) and carnivores/scavengers (45 taxa). In particular, suspension feeders are principally represented by cnidarians (41 taxa) and sponges (21 taxa), and deposit feeders, by holothurians (32 taxa).

- The western area is characterised by a higher heterogeneity of the substrates at a local level (nodule vs facies level), which may contribute to the observed increase in richness of megafaunal and macrofaunal assemblages from East to West, confirming previous studies in CCFZ for macrofauna (Hecker and Paul, 1979) and the present UNESCO/IUCN baseline study. The latter shows a higher taxonomic richness on the western area (NIXO 45) especially for facies C 2-15 % and nodule-facies C 30 % but not as much for nodule-facies O, BP 35 % and B 35 %.

- The community structure of faunal assemblages differs substantially, often displaying a major turnover in species, over a latitudinal range. For foraminifera and polychaetes, the turnover is at scales of 1,000–3,000 across the CCFZ. For megafauna, it is presumably at wider scales.

- Variability in the structure of benthic communities and faunal turnovers may be driven by different trophic inputs because of:
  - an overall westward trend of reduced primary productivity in the central Pacific,
  - hydrological conditions above the bottom layer,
  - the varying habitat heterogeneity or topography of the seafloor (higher in the west).

- UNESCO/IUCN baseline study, ISBA/Kaplan/Nodinaut and IOM/BIE surveys have evidenced that habitat heterogeneity (“nodule facies”; microheterogeneity at nodule level, patches of detritus, biogenic structures and bioturbation) in correlation with other factors and conditions, i.e. bottom currents and sediment chemistry, is a significant factor defining the distribution pattern of nodule deposits in association with the abundance, composition and structure of epibenthic megafaunal assemblages at different scales.

- Polymetallic nodules clearly provide a habitat for infaunal communities and fixed (sessile) faunal assemblages which feed on suspended organic particles, like sponges and actinids, fixed crinoids, octocorallians, sedentary polychaetes, antipatharids and tunicates. Thus polymetallic nodules influence on sessile epifauna and infauna contribute to enhance biodiversity of the abyssal benthos at regional scales. This fact has important ramifications for biodiversity conservation in area earmarked for nodule mining.

- Habitat heterogeneity, e.g. nodule covered areas, is highly appreciated by faunal assemblages in particular megafauna and macrofauna. These faunal categories display higher densities on nodule covered areas than on nodule free areas while meiofauna displays higher densities on nodule free areas. The nature of sediments may also be the cause of this difference (softer sediments located out of nodule fields). This evidences that megafaunal and macrofaunal assemblages are not space limited.

- The influence of the type of sediments (old or recent) on megafaunal communities has been studied in UNESCO/IUCN baseline study revealing different preferential megafaunal assemblages for each nodule-facies. Results display a faunal preference for nodule-free areas with old sediments (Oligocene to Miocene) over more recent sediments (Pliocene). The presence of still perfectly visible dredge tracks produced by pilot-scale mining tests in 1978 (ISBA 2008a; Titot, 1990b, 1990c, 1991b) evidences a low sedimentation rate and only low speed bottom currents. Within the tracks, in the nodule free areas, there is a relatively high rate of biological activity and oxygen flux at the sediment water interface, comparable to the neighbouring nodule bearing substrates. Macrofaunal assemblages in the tracks display similar densities than in proximate nodule bearing areas but differ in faunal composition. However these exchange rates are much higher in nodule free areas because sediments are generally unconsolidated with a high porosity.

- On the study sites of the UNESCO/IUCN baseline study, the taxonomic richness of megafauna varies at the nodule-facies level as follows:
  - NIXO 45 (Kaplan C) displays a richness of 134 taxa on a photographed surface of 70 000 m² (replicates of 13 different nodule-facies) with a higher taxonomic richness (48 in average) on nodule-facies C 2-15 % (sparse large hillocky nodules) while B 35 % (numerous smaller ovoid and flattened nodules) and BP 50 % (small flattened and frequently cohering nodules) display a lower taxonomic richness (34) than facies O (36).
- NIXO 41 (South of Kaplan C) displays a richness of 55 taxa on a photographed surface of 10,500 m² (replicates of three different nodule facies) and as NIXO 45, shows a lower richness (31) than NIXO 45 for nodule-facies A 30 % (small nodules with smooth surfaces), (30) for nodule-facies C 30 % and (26) for nodule-facies B 35 %.

- ECHO I (East of Kaplan C) displays a greater richness of 61 taxa on a photographed surface of 25,200 m² (replicates of 3 different nodule-facies); and more richness (36) on nodule-facies C 40 % than (23) for B 45 % while a minimum (8) on facies O.

- IOM BIE (Kaplan E) shows a higher taxa richness of megafauna on nodule-bearing facies (nodule-facies B 45 % and C 40 %) than on facies O.

• UNESCO/IOC baseline study displays the existence of at least 13 preferential habitats for specific megafaunal assemblages ranked according to nodule coverage and slope as emphasized by a factor analysis of Reciprocal Averaging. Some nodule-facies have exclusive taxa such as on facies O with ancient sediments (Oligocene to Miocene) and nodule-facies C 15 % in NIXO 45.

• The abundance of the megafauna and macrofauna is lower in the western site than in the eastern (ISBA, 2006a; Tiliot, 1992b, 2006b) due to the overall trend of reduced primary productivity confirming the literature. Nodinaut’s project estimates the abundance of megafauna as lower in the western site, with 147 ind/ha on a nodule bearing area at Kaplan W and 330 ind/ha on a similar area at Kaplan C. Macrofauna displays 160 ind/m² on nodule bearing areas of Kaplan W and 338 ind/m² at Kaplan C. However meiofauna does not observe this latitudinal trend as abundances and species richness are greater in the East (13 ind/cm² at Kaplan C) than at Kaplan W because of, to a certain degree, the nodule coverage.

• This latitudinal trend is partly verified for megafauna in UNESCO/IOC baseline study concerning the relatively high abundances assessed at NIXO 45 (553 ind/ha), NIXO 41 (726 ind/ha) and ECHO I (502 ind/ha) sites which are in Kaplan site C area. But for the most eastern IOM/BIE (Kaplan E), megafauna is less abundant (225 ind/ha).

• UNESCO/IOC baseline study displays the overall existence of more suspension feeders in the western oligotrophic sites and more deposit feeders in the eastern sites in relation to a gradient in productivity from West to East. This trend is evidenced in the results by more suspension feeders at NIXO 45 and NIXO 41, the more western sites, while at ECHO I there are more deposit feeders, in particular echinoderms. However IOM/BIE has about the same amount of suspension feeders and deposit feeders. Also confirming the literature, there is a gradient of dominance of actinids to the West (NIXO 45 and NIXO 41) and echinoderms to the East, echinoids in ECHO 1 and holothurians in IOM BIE. The particular characteristics of the substratum, the hydrological conditions above the bottom layer and the topography of the ocean floor also influence this pattern.

• More specifically, UNESCO/IOC baseline study evidences a varying prevalence of the different trophic and functional guilds on each site:

- NIXO 45: suspension feeders>deposit feeders>carnivores/scavengers. More specifically:

  > overall dominance of sessile suspension feeders>mobile deposit feeders> mobile carnivores/scavengers> motile suspension feeders>sessile deposit feeders;

  > Coverall abundance order: cnidarians (mainly actinians and octocorallians), echinoderms (mainly holothurians and crinoids) and sponges,

  > preferential habitat of suspension feeders: facies O and facies C+ 10 % on slopes with recent sediments,

  > preferential habitat of deposit feeders: facies C+10 %; with recent sediments,
- **NIXO 41**: suspension feeders > deposit feeders > carnivores/scavengers. More specifically:
  
  > overall dominance of sessile suspension feeders > mobile deposit feeders > motile suspension feeders, sessile deposit feeders > mobile carnivores/scavengers;
  
  > overall abundance order: echinoderms (mainly ophiuroids and echinoids), cnidarians (mainly actinians) and sponges,
  
  > preferential habitat of suspension and deposit feeders: facies C + 30 % with recent sediments.

- **ECHO I**: deposit feeders > suspension feeders > carnivores/scavengers. More specifically:
  
  > overall dominance of sessile deposit feeders > mobile deposit feeders > sessile suspension feeders > mobile carnivores/scavengers > motile suspension feeders;
  
  > overall abundance order: sipunculids, echinoderms (mainly echinoids and holothurians), echiurians, sponges and cnidarians (mainly actinians),
  
  > preferential habitat of suspension feeders: facies B 45 % and C + 40 % on ancient sediments,
  
  > preferential habitat of deposit feeders: facies O on ancient sediments,

- **IOM/BIE**: deposit feeders = suspension feeders > carnivores/scavengers. More specifically:
  
  > in overall there is about the same amount of suspension feeders than deposit feeders,
  
  > overall abundance order: echinoderms (mainly holothurians and ophiuroids), sponges and cnidarians (hydrozoans),
  
  > preferential habitat of suspension feeders: nodule bearing facies,
  
  > preferential habitat for deposit feeders: slightly more on facies O than on nodule bearing areas.

- Another important factor important for assessing impacts of mining activities is the evidenced within-site heterogeneity in the community structure and the distribution of megafaunal populations at different spatial scales. In UNESCO/IOC baseline study, an aggregative pattern at the nodule-facies level appears with most common taxa, actinids *Synphonyis tuberculata* above 1600 m² on nodule-facies C (large nodules covering 5 to 40 % of the ocean floor) and random at 400 m² and 800 m² on facies O (no nodules).

- There is also a high within-site heterogeneity in infaunal community structure which appears to covary with the abundance and size of manganese nodules, on scales of 0.1-10 kilometers at Kaplan sites C and W. This has serious consequences for the conservation of the biodiversity of benthic fauna in areas earmarked for nodule mining.

- In UNESCO/IOC baseline study, the high values of standard deviations of the overall abundances indicate a high within-site variability resulting from non-random dispersion of faunal populations (225 + 130.28 ind/ha at IOM BIE site, 502 + 146.97 ind/ha at ECHO I site, 553 + 333.73 ind/ha at NIXO 45 site, 726 + 438.14 ind/ha at NIXO 41).

- Benthic fauna is thought to be an important link in carbon cycling and mineralisation near and at the seafloor and contributes to the genesis of polymetallic nodules.

- The biological activity (bioturbation) created on the sea floor affects the structure and chemistry of the sediment and would have an important role on maintaining nodules at the surface of the sediments.

- With its wide distribution and preferential habitats, mega fauna has a great potential as indicator for monitoring environmental change and mining impact. In particular, echiurian worms *Bonellidae Jacobia birsteini* would be key indicators (Tilbot, 2006b, 2010b).
4. Principles, tools and criteria for the management and conservation of the High Seas biodiversity

4.1. Principles for sustainable development and conservation of the marine environment

In the context of nodule mining, one should adopt the Brundtland Commission’s (1986) vision of sustainable development that meets the needs of the present generation without undermining the capacity of future generations. This approach has been refined at the 1992 Rio Earth Summit by commitment to ecological integrity (to protect biological diversity and maintain essential ecological processes and life support systems) and by incorporating social and economic dimensions of sustainability (UN, 2005).

The precautionary principle, calls for States and decision-makers to be more cautious when information is uncertain, unreliable or inadequate, i.e “the fact that lack of full scientific certainty should not be used as a reason for postponing a measure to prevent degradation of the environment where there are threats of serious irreversible environmental damage” (Environment Protection and Biodiversity Act 1999). It is a major component of the ecologically sustainable development underlying the environmental protection approach to efficient management of the renewable and non-renewable resources on which mining operations depend. Parties to the CBD agreed that a precautionary approach should be applied to the full range of human activities affecting marine biodiversity.

Ecosystem-based management, as defined by Parties to the CBD (Rio Declaration on Environment and Development, 1992), is “a strategy for the integrated management of land, water and living resources that promotes conservation and sustainable use in an equitable way. As such, the ecosystem approach provides for the comprehensive integrated management of human activities, based on best available scientific knowledge about the ecosystem and its dynamics, in order to identify and take action on influences which are critical to the health of the marine ecosystems, thereby achieving sustainable use of ecosystem goods and services and maintenance of ecosystem integrity.

Adopting this approach should:

- avoid degradation of ecosystems, as measured by indicators of environmental quality and system status,
- minimize the risk of irreversible damage to natural assemblages of species and ecosystem processes,
- obtain and maintain long-term socio-economic benefits without compromising the ecosystem,
- generate knowledge of ecosystem processes sufficient to understand the likely consequences of human actions.

Thus:

- Ecosystem managers should consider the effects (actual or potential) of their activities on adjacent and other ecosystems,
• Conservation of ecosystem structure and functioning, to maintain ecosystem services, should be a priority target of the ecosystem approach,

• Ecosystems must be managed within the limits of their functioning,

• The ecosystem approach should be undertaken at the appropriate spatial and temporal scales,

• Recognizing the varying temporal scales and lag-effects that characterize ecosystem processes, objectives for ecosystem management should be set for the long term,

• Management must recognize that change is inevitable,

• The ecosystem approach should seek the appropriate balance between, and integration of, conservation and use of biological diversity (part of the 12 principles of the Ecosystem Approach, in Sheppard, 2004.)

Ecosystem management has been adopted in varying degrees by natural resources and water and land-use management communities to support their respective missions to protect the quality of the environment. A favorable science policy on ecosystem management is adaptive to individual situations and yet should be built upon scientific grounds and standards of measurement (Morrissey, 1996). An ecosystem approach is appropriate for the global assessment and management of coastal and open marine waters (Sherman and Duda, 1999). High seas water column and deep sea bottoms and underground layers have to be considered separately and jointly. Keeping in mind the complexity of the system and the little knowledge available, it is important to consider as essential an adaptive management as soon as new information is made available.

Protection of ecosystem integrity encompasses three components: ecosystem health, capacity and resilience. Ecosystem health refers to its current state or condition at a point in time. The ecosystem’s capacity makes reference to its potential for continued self-development, regeneration and evolution under normal circumstances (Kay and Regier, 1999). Resilience refers to the ecosystem’s ability to absorb recurrent natural and human perturbations and continue to regenerate without slowly degrading or exhibiting varying degrees of hysteresis, i.e., shifting into alternate states (Berkes et al., 2003; Collie et al., 2004; Gundersen and Pritchard, 2002; Folke et al., 2004; Hughes et al., 2003; Nyström et al., 2000; Scheffer et al., 2001). Marine reserves contribute to the protection of ecosystem integrity by greatly strengthening and supporting each of the component parts of that wholeness (Tilot, 2004).

The temporal and spatial scales of disturbances will determine the faculty of ecosystems to regenerate or change to an extent that the original pristine state will never be recovered (Berkes et al., 2003; Gundersen and Pritchard, 2002). The consequences for management are crucial as it is easier to sustain a resilient ecosystem than repair it once shifted. During the post impact phase, changes in species composition occur often favouring short-lived species that can quickly colonize after disturbances (Hughes et al., 2003). These alternate states can be maintained by density-dependent mortality (e.g. owing to altered predator-prey ratios) or by density thresholds required for reproductive success (Cury and Shannon, 2004). As emerging multidisciplinary approaches stress the importance of assessing and actively managing resilience (Folke et al., 2004), it is likely to be important for deep sea protected or conservation areas to have extensive buffer zones, for added robustness and ‘insurance’, particularly given that these environments are one of the world’s few that remain relatively pristine (Tilot, 2010a).

4.2. TOOLS FOR BIODIVERSITY ASSESSMENT, MANAGEMENT AND MONITORING

It is necessary to define biodiversity assessment, conservation and management measures to put in place as well as the means to measure their effectiveness (Tilot, 2010a). Issues and questions for the deep sea are likely to take some time to resolve, but they may be more important than commonly supposed. As science is unable to deliver a proper answer to all phenomena, one should rely on a scientific theoretical approach based on all natural parameters (biodiversity and others). Biodiversity assessment is a major factor to identify priority areas, thus the selection of appropriate measures has serious implications for conservation.

Biodiversity assessment

Evaluations of the deep sea biodiversity have invariably focused on species richness (or Whittaker’s (1970) diversity, i.e. a count of the total number of species in a sampled area) and evenness (or equitability, i.e. the proportional abundance of each species). The biodiversity assessments drawn from these traditional measures have often the disadvantage to change on wide spatial and long time scales and often stay undetected until a very advanced stage of environmental degradation. In addition, spatial and temporal scales tend to be interrelated. Species diversity can also be very dependent on differences in natural environmental variables such as the composition of sediments for meiofauna or different nodule-facies for megafauna as described previously. Since biodiversity is a multi-dimensional concept, species richness (and metrics derived from it) can only be a partial estimation. It has been defined as the sum of taxonomic or numerical diversity and the ecological, genetic, historical and phylogenetic diversity (Van der Spoel, 1994). All these elements are impossible to unite
in order to provide a single biodiversity index and are therefore difficult to apprehend both in ecology and in conservation (Gray 2000, Margules and Pressey, 2000, Warwick and Clarke, 2001).

Inclusion of different measures would help. ensure more comprehensive characterization of biodiversity in the deep sea and broad scale conservation. Abyssal megafauna commonly encompasses many different phyla with a large number of species often distantly related. Also since organisms are not geographically or ecologically randomly distributed, as discussed previously for the CCFZ (Tilot et al., 2010), the geographical, temporal and taxonomic scales chosen for data collection will have a strong impact on the results of any analysis. Geographical distance provides one useful measure for change in species composition. Overall, spatial and temporal scales tend to be inter-related as ecological processes tend to dominate over short time-scales and local distances while over large time-scales and regional global distances, evolutionary processes are more important.

Over the past decade, a suite of more intuitive/comprehensive average measures reflecting complementarity, relatedness (beta-diversity), similarity (taxonomic distinctness) and other ‘average’ measures, have been developed (Izsak and Price, 2005; Price et al., 1999; Warwick and Clarke, 2001) to measure biodiversity over both small and large spatial scales.

Complementarity is essential for prioritizing areas in systematic conservation planning and should be expanded from a regional perspective as it weights the extent of unrepresented features (evolutionary characters, species richness and/or restricted range, habitats) from an area to other areas (Margules and Pressey, 2000; Price, 2002; Warwick and Clarke, 2001; Williams et al., 1996).

Taxonomic distinctiveness, an extension of Taxonomic Diversity measuring the relatedness for maximising biodiversity representation within a limited area, provides a means of weighting species in respect of priorities for conservation. It is less sensitive to the degree of sampling effort and preferred for selecting species from an inventory for conservation purposes as it would preserve more evolutionary history. Complementary subsets of species can also be selected to provide representativeness of the widest range of evolutionary characters. Taxonomic distinctness gives the ability to monitor changes in patterns of relatedness over space and time in community samples.

Taxonomic diversity/distinctness measures biodiversity at (within-habitat) and (within-region) scales in particular for large ocean provinces (Price et al., 1999) and is useful in environmental monitoring and assessment, in particular for conservation purposes (Gray, 1997; Izsak and Price, 2001; Warwick and Clarke, 1995, 2001).

While β-diversity, much neglected in the marine environment (Gray, 2000), is an estimate of spatial turnover of species along a gradient, e.g. changes of species composition from site to site (Whittaker 1975, Gray, 2000). As an example, populations of asteroids have been compared in coastal and deep sea waters for the entire Atlantic and results show that absolute species numbers are the same in deep. and shallow waters while β-diversity is greater in shallow waters (Price et al., 1998). In the deep sea, as Rex and Etter (2010) outline, β-diversity is closely related to α-diversity (sample richness) and standing stock (rate of change in species composition). “It mirrors the selective gradients that drive the evolutionary processes that ultimately generate deep sea biodiversity”. These processes are depth related environmental parameters and adaptive properties of species.

As taxonomic distinctness is higher in environmental stability (Warwick and Clarke, 1995), genetic diversity is higher in unstable stressed environments (Nevo et al., 1984) and the total genetic complement in any biome would be partitioned differently among the hierarchy of taxonomic units according to the age or successional stage of the assemblage.

Taxonomic similarity, analogous to taxonomic distinctness, is used to measure diversity using presence/absence species data and including evenness and taxon richness.

To summarize, these indices may have valuable applications in deep sea, biodiversity assessment and in the selection of protected area sites, for several reasons:

- all indices can be computed using presence/absence data, i.e. quantitative abundance information is not essential;

- they are robust to the effects of sampling area/thoroughness to a far greater extent than ‘species’ or absolute measures, with the exception of Simpson’s index;

- there is some evidence that ‘taxonomic’ i.e. relatedness measures, based on average properties, are more sensitive to disturbance effects than ‘species’ and other ‘absolute’ measures (e.g. Izsak et al., 2002; Warwick and Clarke, 1995).

Paradoxically, a particular area can be both a ‘hotspot’ and ‘coldspot’ of biodiversity depending on the diversity measure(s) selected (Price, 2002; Price and Izsak, 2005). For example, the biodiversity of deep sea vents is unimpressive when characterised merely as species richness. Yet this ecosystem emerges as a hotspot if the choice of metrics is expanded to include endemism, taxonomic distinctness and β-diversity.

The deep sea globally is not hyperdiverse at a regional scale as first assessed from extrapolation of species ac-
cumulation per distance curves (Boucher and Lambshead, 1995; Grassle and Maceiolek, 1992; Groombridge, 1992; Lambshead, 1993) but displays high local diversity through patch dynamics such as for rain forests (Grassle, 1988). This point has been confirmed for macrofauna (Gray, 1994) and nematodes (Lambshead and Boucher, 2003) as discussed previously for the CCFZ (Tilot et al., 2010).

Species diversity can influence the stability and productivity of ecosystems in a variety of ways. A diversity-stability hypothesis about the functional role of species diversity for ecological communities has first been proposed by MacArthur (1955) under the premise that energy flow in complex foodwebs will be least disrupted by disturbance because alternative pathways for energy flow will be used.

Alternatives to the diversity-stability hypothesis have been advanced by Ehrlich and Ehrlich (1981) with the Rivet hypothesis (some species may be redundant generating a nonlinear relationship between species richness and ecosystem function while “Rivets” are key species without which the ecosystem collapses beyond some threshold), the redundancy hypothesis (species within the same functional group. are to expand more in terms of ecosystem function thus compensating for species going extinct according to Walker (1992) and the idiosyncratic hypothesis (Lawton, 1994) for communities featuring higher-order interactions with very little relationship between species composition and ecosystem function. The progress in understanding the mechanisms of the critical functions of taxa emphasizes the functional importance of diversity within the context of a specific ecosystem (Johnson et al., 1996).

The logistical constraints on operating in the deep sea should not be underestimated. Whatever the choice of biodiversity metric is, species identification (or at least determination of recognisable taxonomic units) is generally still required, i.e., even for presence-absence data. For all but small areas of the deep sea, biological material and data are unavailable; hence the reliance on inferential data based upon physical features to characterize deep sea sites in different parts of the ocean (Tilot, 2010a; Tilot et al., 2010).

Resilience

The concept of resilience is an important factor to consider for an ecosystem and the sustainable management of its resources. Resilience is the capacity of the ecosystem to absorb recurrent natural and human perturbations and continue to regenerate without slowly degrading or exhibiting varying degrees of hysteresis, i.e., shifting into alternate states (Berkes et al., 2003; Collie et al., 2004; Gundersen and Pritchard, 2002; Folke et al., 2004; Hughes et al., 2003; Nyström et al., 2000; Scheffer et al., 2001). The temporal and spatial scales of disturbances will determine the faculty of ecosystems to regenerate or change to an extent that the original pristine state will never be recovered (Berkes et al., 2003; Gundersen and Pritchard, 2002) and the consequences for management are crucial as it is easier to sustain a resilient ecosystem than repair it once shifted.

During the post impact phase, changes in species composition often favouring short-lived species that can quickly colonize after disturbances (Hughes et al., 2003). These alternate states can be maintained by density-dependent mortality (e.g. owing to altered predator-prey ratios) or by density thresholds required for reproductive success (Cury and Shannon, 2004). Some small-scale experimental studies of biodiversity suggest that high species richness confers greater resilience to marine ecosystems (Loreau et al., 2004). Recent studies show that higher biodiversity can afford a degree of ecological insurance against ecological uncertainty when comparing species-rich and naturally depauperate marine systems (Steneck et al., 2004). But other studies indicate that biodiversity does not afford additional protection if all species in a functional group. respond similarly to global pressures (Elmqvist et al., 2003).

In order to improve assessment and management of marine resilience, it is a priority to develop new metrics that are process oriented and that account for ecosystem dynamics across temporal and spatial scales (Steneck, 2001), in particular by highlighting the importance of key functional groups, ecological roles and species interactions (Hughes et al., 2005), as has been described in the CCFZ (Tilot et al., 2010); thus it is likely to be important for deep sea protected or conservation areas to have extensive buffer zones, for added robustness and ‘insurance’, particularly in the case of the deep sea environment which still remains relatively pristine (Folke et al., 2004).

Multiple Systems management

An emerging approach to the management of marine resources prioritizes practices that recognize coupled social-ecological systems (SESs) that are characterized by complex dynamics and thresholds with multiple possible outcomes and inherent uncertainties (Folke et al., 2004; Hughes et al., 2005; Scheffer et al., 2001). Ecosystem-based management reverses earlier single-species approaches by supporting ecological processes and recognizing the diverse ecological role of the different functional guilds in the dynamics of complex ecosystems at temporal and spatial scales (Graham et al., 2003; Hughes et al., 2005; Steneck, 2001).

Also new conceptual models encompassing the role of history and nonequilibrium dynamics in ecosystem change in larger spatial and temporal scales are being developed (Hughes et al., 2002; Steneck and Carl...
The importance of biodiversity in the functioning and resilience of marine systems and in key processes undertaken by crucial functional groups is targeted. Thus conservation is shifting to active management of functional groups (Hughes et al., 2005; Steneck and Carlton, 2001).

In order to succeed, SES management should develop resilience for dealing with external change, understand ecosystem processes and functions, design management practices that measure, interpret and respond to ecological feedback and support flexible institutions and social networks in multi-level governance systems (Hughes et al., 2003).

The developing concept of adaptive governance of linked social-ecological systems, i.e. governance with a clearer understanding of resource and ecosystem dynamics, provides a new paradigm for responding to multi-scale environmental feedbacks and for managing resilience to ensure sustainable resources; This concept is a more mature ecosystem-based approach to management of the world’s oceans (Ardon et al., 2006; Hughes et al., 2005), such as for the Great Barrier Reef system in Australia or the high-seas marine mammal sanctuary in the Mediterranean sea, “Pelagos” (Tilot, 2004; 2007a, b).

In summary, a successful SES management must develop resilience to face external change such as climate change, build knowledge on resource and ecosystem dynamics, develop management practices that interpret and respond to ecological feedback and rely on multiple institutional linkages among user communities (Hughes et al., 2005).

Metapopulation approach in conservation

The metapopulation concept, first formalized by Levins (1969, 1970), has been described as an important component of modern ecology theory by Hanski (1999) and Hanski and Sumberloff (1997). Sale et al. (2006) have adopted the paradigm with the rediscovery of the powerful effects on populations of larval dispersal and subsequent settlement to juvenile and adult demersal and sessile populations; They outlined the uses of metapopulation theory in marine systems as primarily for cases when the spatial structure of populations is imposed by habitat patchiness, which is often interconnected, and by the perspective of a dynamic that maintains community structure in the patch network. This dynamic would be measured by the degree of replacement connectivity in the age structure of a population. Kritzer and Sale (2004, 2006) emphasize the need to develop techniques for measuring connectivity among marine populations.

Although patchy loss of habitats may result from natural disturbances, it can result in widespread degradation if extreme (Connell et al., 2004). The spatial scale of dispersal of larvae, pollutants, climate change, large scale mining, as for the CCFZ, is crucial to understand the dynamics of marine systems and their resilience; production and supply of larvae is not inexhaustible as previously assumed, but limited for many species and consequently, the local loss of reproductive adults can disrupt stock-recruitment relationships. Conversely, species with long-distance dispersal should be more resistant to habitat fragmentation (Hughes et al., 2000; Strathmann et al., 2002). If too many patches of habitat degrade, once a critical threshold is passed, the remaining healthy habitats can collapse and the dynamics of individual patches can propagate through larval dispersal to much larger scales, potentially leading to a phase shift of the entire system (Bascompte et al., 2002; Klaussmeier, 2001). Consequently, multi-scale dynamics requires multi-scale resilience-based management, (Folke et al., 2004; Gundersen and Pritchard, 2002; Hughes et al., 2005; Kinzig et al., 2003; Walker et al., 2004).

Natural impacts (climate change...) and anthropogenic disturbances (pollution, deep sea fishing, seabed mining...) will generally result in degradation and homogenization of habitats across broad areas. Regarding conservation management within a metapopulation approach, the knowledge of dispersal pattern would be needed to estimate the terms describing the transfer between habitat types, an emerging aspect on metapopulation persistence, which will provide valuable information for managers of marine conservation (Botford and Hastings, 2006). Also marine reserve concepts are evolving towards a dynamic metacommunity approach emphasizing managing biodiversity, trophic structure and function, and ecosystem resilience (Guichard et al., 2004; Lubchenco et al. 2003; Sobel and Dahlgren, 2004).

As an example, taxonomic similarity and species similarity between sites were assessed for echinoderms over three spatial scales, at a local scale (less than 10km), medium scale (10 to 100s km) and at a province scale (100s to 1,000s km) (Izsak and Price, 2001). Results show that both increase with spatial scale. One of the interpretations is that the large scale area represents a metapopulation of echinoderms including the smaller areas and that there is a greater biophysical instability and unpredictability at small scales. Thus on small spatial scales, a site's total species composition can be more likely influenced by effects of species migrations and extinctions or other effects of patch dynamics such as predation and competition (Izsak and Price, 2001).

As marine systems are more open than terrestrial or freshwater systems, barriers to dispersal are weak, thus local extinctions are easily resplenished by new recruits, which are often produced in large quantities by highly fecund adults. Primary producers are often very small, mobile with a rapid turnover. Thus environmental change in the sea has a much lower amplitude and longer frequency than on land on spatial and temporal scales (Grassle et al, 1991). Natural variability impacts...
and anthropogenic stresses, are more diffuse and widely dispersed physically and in the food chain (Heip et al., 1998). The diversity of higher taxonomic levels is much higher in the sea than on land, so that the total of genetic resources is very high. Furthermore the maintenance of marine biodiversity is essential to sustain a wide range of ecosystem functions, essential to humankind (Costanza et al., 1997).

These facts lead to a broader strategy for conservation of marine biodiversity with a need to define the management of the biodiversity in ecologically meaningful ways that are practical to measure so that the effects of environmental degradation, remediation or conservation can be monitored (Tilot, 2010a). Organismal diversity and Ecological diversity, in the terminology of Harper and Hawksworth (1994), should be prioritized in deep sea broad scale conservation.

Environmental monitoring

Deep-sea biology, due to the inaccessibility and the costs of deep sea research, observation and sampling, is still considered as a young science relying on many basic observational studies. Thus long-term time-series, which would provide information on the dynamics and functioning of deep sea ecosystems, are lacking for most of the deep sea. Data on taxonomy, species diversity and structure, biogeography, larval dispersion, habitat distribution are insufficient in relation to the size of the area concerned as about 60 % or the solid surface of the earth is considered as deep sea.

No biogeographical syntheses over basin scales and globally can yet be done, many species collected are new to science and have not yet been formally classified, most have been identified by using morphological methods. Thus comparisons from one area to another are quite difficult.

Long-term time-series are developed routinely in coastal ecosystems for research and management purposes, in temperate and tropical waters, such as for coral reefs and associated ecosystems (http://www.gcrmn.org/, Tilot, 2003a, b; 2007b). When designing a long-term monitoring strategy, critical issues arise, such as defining baselines, thresholds, key health indicators and the level of acceptability of decline of biodiversity when confronted to anthropogenic impacts. Long-term monitoring must be directly related to the baseline environmental survey using the same survey sites, sampling techniques and analysis methods to ensure data comparability. Sampling frequency should be random to prevent synchronising with natural biological cycles which are poorly known in the deep sea (Tilot, 2010a). Research shows that endogenous disturbances may be relatively frequent and variable and that the biological processes driven by these events can exhibit disequi-
<table>
<thead>
<tr>
<th>Ecology</th>
<th>habitat (pelagic, benthic)</th>
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<td>structural complexity and critical habitat which have been</td>
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<td>evidenced as key parameters for maintaining abundance,</td>
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<td>biodiversity and biomass in balance over space and time scales</td>
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<td>connectivity</td>
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<td>meta-communities</td>
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<td>species interactions</td>
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<td>importance of ecological roles</td>
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<td>Physic</td>
<td>bathymetry</td>
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<td>temperature (and thermocline)</td>
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<td>pressure</td>
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<td>current (direction and force at different levels in the water</td>
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<td>column), internal swell (current), tide (barotropic, baroclinic,</td>
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<tr>
<td></td>
<td>current)</td>
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<td></td>
<td>geological structures (plains, seamounts, guyots, fractures...)</td>
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<td></td>
<td>vertical zonation of the bottom (bathyal 800-3500 m, abyssal</td>
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<td>3-6,000 m, hadal &gt; 6500 m)</td>
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<td></td>
<td>vertical zonation of water column (Carbonate Compensation Depth</td>
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<td>(CCD) including Aragonite Compensation Depth (ACD) and</td>
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<td></td>
<td>Carbonate Compensation Depth (CCD))</td>
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<tr>
<td>Chemistry</td>
<td>O² Particulate Organic Carbon (POC) flux</td>
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<td></td>
<td>export of carbon to the benthos (and geochemistry)</td>
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<td></td>
<td>CO₂ sequestration and Fe Fertilization</td>
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<td>Biology</td>
<td>species richness</td>
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<td>endemism</td>
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<td>meio, macro, megafaunal abundance</td>
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<td>productivity and export</td>
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<td>larval dispersion</td>
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<td>resilience</td>
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<td>beta diversity (relatedness)</td>
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<td>meta population</td>
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<td>taxonomic diversity</td>
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<td>ecological, genetic, historical and phylogenetic diversity,</td>
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<td>complementarity, similarity (taxonomic distinctness)</td>
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<tr>
<td>Sea bottom types</td>
<td>basalt</td>
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<td></td>
<td>volcanism (and sedimentology)</td>
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<tr>
<td></td>
<td>sandy muddy substrate or hard (rocky) substrate, sulphids, other</td>
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<tr>
<td></td>
<td>metalliferous deposits from hydrothermalism</td>
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<td></td>
<td>polymetallic nodules</td>
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<td></td>
<td>manganese crusts</td>
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<tr>
<td>Economy</td>
<td>minerals, sulphids, metalliferous deposits from hydrothermalism</td>
</tr>
<tr>
<td></td>
<td>thermal energy, polymetallic nodule, flat area ( % slope)</td>
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<td></td>
<td>deep sea fisheries (if any)</td>
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<td>others</td>
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<tr>
<td>Others</td>
<td>pollution</td>
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<td>climate change</td>
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</table>

Table 2. Parameters to take in account for conservation measures including impact assessment, surveys and monitoring.
These elements are important for the definition of conservation measures, allowing to assess more precisely the impacts of seabed mining on the sea bottom, the water-column to the surface. They are necessary to define surveys and monitoring strategies in the CCFZ. The recovery time of benthic communities and their dynamics, if the impact is not too severe, will depend on all these parameters, their importance and their duration.

The monitoring programme in the CCFZ should cover most of the natural parameters, including the deep seabed and the water column (see Table 1 in “Rationale for the conservation of the biodiversity in the CCFZ”; Tilot, 2010a). As strict guidelines and indicators are necessary for management decisions (Boyle et al., 2001), a permanent tridimensional monitoring system with identified indicators related to natural parameters and the different activities on the deep seabed and the water column could be installed in a grid of multiple stations in the CCFZ area in order to detect the variability in space and time of natural processes and mining impacts and thus enable the management body to set up guidelines that could be adaptive due to time and space span of expected impacts (Tilot, 2010a). On the deep seabed, a strategy of epibenthic monitoring could be adapted.

There is a potential for megafauna, with its wide distribution and often conspicuous features and bioturbation on photographs and videos, to be a good indicator of environmental change and mining impact at a regional scale; in particular echinuran worms Bonellidiae Jacobia birsteini would be key indicators for monitoring, as discussed previously (Tilot, 1992b, 1995, 2010b, see Appendix 1, Figures 50-55). On the photographs and videos of the surveys (Tilot, 1990b, 1991b, 1993, 2006b, 2008b), these Bonellidiae are conspicuous, of good size (several meters long) and linked to specific environmental conditions. They are often seen when out of their circular burrows and along an elongated, crescent or V-shaped mound (in average 2m long, 60 cm wide, 40 cm high) that they build by the licking action of their proboscis. They are observed on specific habitats: recent (Plio-Quaternary) sediments densely covered (50 %) by small nodules (2-3cm) and linked to a relative higher abundance of deposit feeders. These Bonellidiae appear as important components of the nodule ecosystem and therefore would serve several purposes as indicators: specific conditions of currents, nodule coverage, nodule size, lithographic sediment features, trophic conditions favouring the presence of deposit feeders. By the mounds they build, they generate habitat heterogeneity and stimulate dynamics in epifaunal assemblages, they also have a salient role in sediment irrigation and mixing, thus have an action on nodule formation (diagenesis).

As some of these parameters indicate the commercial value of the nodule deposits, these key indicators would thus also interest the mining companies. In addition, when considering the exploitation phase of the nodules, if not to close to the impact, these animals would be active components for reworking the sediments and creating the best conditions for the recolonization of the fauna (Tilot, 2008b).

During nodule mining, each prospecting or mining operation could support these monitoring programmes for a better understanding of biodiversity and impacts by means of different technics such as videomonitoring. A cost-effective method would be to set video-monitors on the collectors or on ROVs with the possibility of fauna sampling for research and biotechnology purposes, which would be an added value to the marine resource (Tilot, 2010a).

When monitoring the mining operations, threshold impacts should be identified and tested during the mining activities by Feedback loop monitoring (i.e. the continuous testing of the effect of an ongoing project near and far from the development site, in reference to Gray and Jensen, 1993). Feedback monitoring is a cost-effective approach to the proactive or reactive management of activities, because the effort can be focused on monitoring only specific variables. It detects impacts as they occur, and provides a mechanism to stop the harmful action until conditions improve, or a mechanism to modify the action to prevent further damage. Feedback monitoring will be based on new threshold criteria for environmental parameters relevant to operation. These concepts are also variable in time and space, for example thresholds could be shifted by the extension and degree of seabed mining.

The strategy of monitoring programmes should follow the Before–After/Control–Impact (BACI) approach developed into ‘Repeated Measures’ designs by Green (1993) and Underwood (1993, 1994, 1996). In the original designs, rigorous monitoring of areas likely to be disturbed by a development is compared to control areas before and after the development project, and the data are subjected to analysis of variance to detect significant impacts.

4.3. CRITERIA FOR SITE SELECTION
AND NETWORKING

Site selection

The criteria are critical for the selection of preservation sites in the High Seas and the development of a management plan. A proper selection of preservation sites will have to consider all the criteria related to the seabed, water column, sea surface and air above. The criteria are thus biogeographical, biological, physical, oceanographic and relating to water column quality, ocean surface importance for species, the presence/absence of species on the benthos, in the pelagic domain or even in the air above (Roberts, 2006). These should be analyzed at different time and spatial scales.
### Biogeographic criteria (World Oceans Biogeographic zones from Roberts, 2006)

<table>
<thead>
<tr>
<th>Pacific westerly winds</th>
<th>Atlantic westerly winds</th>
<th>Indian Ocean trade winds</th>
<th>Antarctic westerly winds</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pacific trade winds</td>
<td>Atlantic trade winds</td>
<td>Indian Ocean coastal</td>
<td></td>
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<tr>
<td>Pacific polar</td>
<td>Atlantic polar</td>
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<tr>
<td>Pacific coastal</td>
<td>Atlantic coastal</td>
<td></td>
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</tbody>
</table>

### Ecological criteria (preliminary list)

<table>
<thead>
<tr>
<th>Habitats (pelagic, benthic)</th>
<th>Connectivity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Critical habitats (biodiversity and biomass)</td>
<td>Meta communities</td>
</tr>
<tr>
<td>Structural complexity</td>
<td>...</td>
</tr>
</tbody>
</table>

### Biological (preliminary list)

| Species diversity, distribution and abundance | Resilience |
| Endemism | Beta diversity |
| Micro, macro, mega-faunal abundance | Meta population |
| Productivity and export | ... |
| Biological rates (respiration, reproduction, growth) | |
| Biomass | |
| Faunal distribution | |
| Larval dispersion | |

### Physical, chemical and oceanographic criteria (preliminary list)

| Bathymetry | Temperature |
| Topography | Geology (hard bottom and soft bottom) |
| Habitats | Sedimentation rates and mixing |
| Pressure | Water quality (Oxygen, acidification...) |
| Tide | Geochemical cycles |
| Currents | Mineral resources on the seabed |
| Deep. ocean circulation | |
| Upwelling and downwelling | |

### Geological criteria (World Oceans bottom types and feature from Roberts, 2006)

<table>
<thead>
<tr>
<th>Sediment</th>
<th>Depth zonation</th>
<th>Features</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sediment Clays</td>
<td>Depth 1-200m (continental shelves/epipelagic)</td>
<td>Bathymetric complexity</td>
</tr>
<tr>
<td>Sediment Glacial deposits</td>
<td>Depth 201-1,000m (mesopelagic)</td>
<td>Ocean ridges</td>
</tr>
<tr>
<td>Sediment Continental margins</td>
<td>Depth 1001-4,000m (bathypelagic)</td>
<td>Hydrothermal vents</td>
</tr>
<tr>
<td>Sediment Siliceous diatom ooze</td>
<td>Depth 4,001-6,000m (abyssopelagic)</td>
<td>Cold seeps</td>
</tr>
<tr>
<td>Sediment Siliceous radiolarian ooze</td>
<td>Depth &gt; 6,000m (hadalpelagic)</td>
<td>Deep. coral reefs</td>
</tr>
<tr>
<td>Sediment Calcareous ooze</td>
<td></td>
<td>Ocean trench area</td>
</tr>
</tbody>
</table>

*Table 3. Description of the criteria for site selection for preservation in the High Seas (Roberts, 2006).*
The internationally agreed scientific criteria adopted in May 2008 by the Conference of the Parties to the Convention on Biological Diversity (COP to CBD Decision IX/20 paragraph 14) for identifying ecologically or biologically significant marine areas in need of protection in open-ocean waters and deep sea habitats are:

- uniqueness or rarity
- special importance for lifehistory stages of species
- importance for threatened, endangered or declining species and/or habitats
- vulnerability, fragility, sensitivity or slow recovery
- biological productivity
- biological diversity
- naturalness

And the five required properties and components for selecting MPA networks are:

- ecologically and biologically significant areas
- representativity
- connectivity
- replicated ecological features
- adequate and viable sites

On basis of these criteria and properties, areas beyond national jurisdiction are being identified as illustrated by the recent expert workshop in Ottawa in 2009 (Ardron et al., 2009).

Concerning the deep seabed, criteria used to identify candidate protected area sites have included biological assemblages derived mainly from macro-faunal species abundance (or presence-absence). However, recent research shows that knowledge of megafauna of the deep sea also contributes greatly to its biodiversity, but this has been neglected in most biological assessments (Tilot, 2006b). Irrespective of the type of fauna examined, only a very small percentage of the deep sea has been biologically characterized at all.

Physical features, including polymetallic nodule abundance, coverage, sediment/facies type, water movements and slope, are also an important means of characterizing and classifying different areas of the deep sea. Collection of physical data is generally more straightforward than the acquisition and analysis of biological material. From physical environmental data, inferences are possible about the likely biological composition and assemblages in different areas of the deep sea (Tilot, 2006b; Tilot et al., 2010). In the CCFZ preferential habitats composed of specific faunal and functional assemblages are evidenced for the nodule ecosystem (Tilot, 2006b), and would be better adapted as criteria for a deep sea conservation strategy (Tilot, 2010a).

Only if widely separated areas of the seabed have been assessed, directly or indirectly, is it possible to develop a representative listing of candidate sites for inclusion in a protected area system.

Candidate sites are selected on the basis of the smallest areas containing the highest levels of biodiversity – based not just on species richness but upon a range of measures. The rationale for this is that, at least in coastal and terrestrial environments, space is a commodity for which there is strong competition for different resources. However, in the deep sea, space may be an issue of lesser concern than in coastal environments, at least over the short-term, given the vast extent of the abyssal and other deep sea zones. Clearly it will be important for deep sea protected areas to have extensive buffer zones, for 'added robustness and insurance', particularly given that these environments are one of the world's few that remain relatively pristine.

Networking sites

Presently a global system of High Seas marine protected areas networks is fostered as the ultimate solution to protect the biodiversity in the High Seas (IDDRI, 2009; Laffoley, 2005; UNEP WCMC, 2008). A preliminary definition of a network of marine protected areas in the High Seas has been proposed (Roberts, 2006), using a grid of squares of 5 degrees latitude by 5 degrees longitude. One grid cell corresponds to an area of approximately 560 x 560 km at the equator, or 314,000 km², with the longitudinal dimension diminishing towards the poles. Between 70°N and 75°N, for example, each cell covers 93,600 km². The 5 degrees resolution is relatively robust to data errors and temporal variation.

The parameters of selection for each square of the grid are the following:

- The network should be representative of the full range of biodiversity,
- The network should be based on the coverage of all the physical factors such as bathymetry, sea bottom complexity (Ardron et al., 2002), sediments or geology and oceanographic features such as upwelling, currents or temperature,
- The network should replicate habitats in different protected areas in order to buffer human or natural impacts or catastrophes. Some authors suggest that all habitats should be replicated three times (Roberts and Hawkins, 2000),
- The network should be designed so that populations in different protected areas can interact and be mutually supporting. According to movements of adults, juveniles or larvae, the ecological connectivity could be ensured by protected areas separated by few kilometers to thousands of kilometers,
• The network coverage should be large enough to allow for long term persistence of species, habitats, ecological processes and services. The IUCN World Park Congress (2003) recommended a coverage of 20 to 30% for all habitats. Other authors go further with a recommendation of 20 to 50%. Roberts (2006) has chosen for the High Seas a coverage of 40% in relation to the large scales of oceanographic processes and species movements.

• The network should rely on the best available scientific information.

Based on the results of the compilation study, Roberts (2006) proposes as a conservation area the whole Clarion-Clipperton Zone as part of the Northeastern Pacific area, a large equatorial/sub equatorial area. As such, this global conservation area is not relevant as mining concessions are already established, but it shows the importance of the area in terms of biodiversity.
### 5. Conservation and management of the CCFZ

#### 5.1. Predicted impacts and management options for polymetallic nodule mining

**Predicted impacts of nodule mining**

Responses of deep sea ecosystems to human impacts are poorly known, especially at a regional scale, in the case of combined impacts.

From the elements stressed in UNESCO/IOC baseline study (Tilot, 2006b; Tilot et al., 2010) and ISBA/Kaplan/Nodinaut studies (Galeron et al., 2006a; ISBA, 2008), the synthesis of the ecological characteristics of the nodule ecosystem in the CCFZ and their sensitivity to natural and anthropogenic impacts is outlined previously in the rationale for conservation of the biodiversity of the CCFZ (Table 1). Deep sea ecosystems are more sensitive to natural stressors and anthropogenic activities than in shallow waters as there is a cumulative effect of the different impacts in the water column up to the deep sea floor which is amplified in deep sea food webs.

Although of much lower scale in intensity and space than would be commercial mining, the results of in situ experiments using different types of equipments have shown that on the sea floor, the collect of nodules would have a catastrophic impact on the benthos at different stages (Glover and Smith, 2003; Thiel, 2003; Thiel et al., 2001; Tilot, 1988, 89, 91b) such as:

- removal of the top 5 to 10 cm of sediment containing the nodules, the preferential habitat of the fauna (Bussau et al., 1995; Mullineaux, 1987; Tilot, 1989, 1993, 2002, 2006a, b; Tilot et al., 2010),
- suspension of an important part of the sediment into the water column (Oeibus et al., 2001; Thiel et al., 2001),
- sediment-dwelling fauna killed or displaced,
- faunal communities in mining vicinity buried under varying depths of sediment (Jumars, 1981; Oeibus et al., 2001; Sharma et al., 2001; Smith, 1999; Thiel et al., 2001),
- exposed underlayer of sediment, compacted and poor in organic matter,
- suspended sediment redeposited partly on the site or in the vicinity, burying epibenthic faunal communities,
- surviving animals most probably unable to adapt to the altered seabed habitat,
- food supply in the area reduced drastically,
- full sediment dwelling-communities would recover eventually in centuries if not more.

Glover and Smith (2003) have done a complete review of the potential impacts on the deep sea floor ecosystem:

- with the disposal of wastes (structures, radioactive wastes, munitions and carbon dioxide), surviving animals would reach the seabed but would most probably not be able to survive,
- concerning deep sea fishing, as shallow water fish-
ing is moving deeper with the depletion of stocks, the consequences are devastating for deep sea communities and their associated ecosystems,

- with oil and gas extraction, there is a potential pollution on the sea bottom, in the water column and at the surface, in addition to potential impacts of the platform and transport by ships or pipelines,

- concerning marine mineral extraction, the disturbance of the sea bottom would have long term effects at the site as well as in the surrounding areas sometimes to a distance of hundred of kilometres (re-sedimentation),

- with climate change, the effects in the deep sea are poorly known in particular concerning the water quality (temperature, acidification...).

The overall consequences of deep sea mining in the CCFZ are hard to predict, most probably there would be an impact at a regional scale, over an area of more than 3 million km² of the deep sea floor, water column and surface of the ocean (and layer of air over the ocean). The recovery rate to anthropogenic impact, if ever possible, would be very long, decades for the benthos to a million of years for nodules. More precisely, each mining operation (contractor) would disrupt 300-800 km² of the sea floor per year from the 150,000 km² of its claimed area (Oebius et al., 2001). At present there are eight claimed areas, thus the impact would be much greater than 1,200,000 km² due to combined effects.

Rolinska et al., (2001) predict a resettlement of sediment particles up to 95 % of the total released within a period of 3 to 14 years depending on the depth of release. The cloud of sediment from the mining plume or from the tailings when separating nodules and sediment will have an impact on hundreds to thousands of kilometers downstream or following currents, over large temporal and spatial scales. The redeposition process from the surface could take from five months to seven years according to the particle size and local conditions (Oebius et al., 2001; Thiel et al., 1991; 2001) and interfere with the feeding activities of particle grazers and suspension feeders over areas 2 to 100 km² of the mined areas (Hannides and Smith (2003); Smith, 1999; Thiel et al., 2001). From data from ISBA, Hannides and Smith (2003) predict that mining would affect severely benthic communities over 20,000 to 45,000 km².

If it is not possible to evaluate the time for reconstitution of the deep sea ecosystem in a mined area, the time for reconstitution of fields of polymetallic nodules is estimated to 1 million years for 1 to 2 cm size nodules (Ghosh and Mukhopadhyay 2000; McMurtry 2001), knowing that nodule’s growth has been assessed to be in average 1mm in 10,000 years in natural unimpacted conditions (UNEP, 2006).

In conclusion, deep seabed mining will constitute an important threat in terms of physical and biological damage in the area of operation and surrounding habitats, with inevitable severe disturbance to the associated ecosystems.

Among the information needed to enable to fully predict and manage commercial mining, would be detailed information on species ranges, sensitivity to sediment burial and spatial scale dependence of recolonization in abyssal benthic communities (Smith et al., 2008 in Polunin, 2008).

Mining management options

Best practice environmental management in mining demands a continuing, integrated process through all phases of mining operations. The Fundamental Principles for the Mining Sector (Berlin Guidelines 1991, revised UNDESA and UNEP, 2000) should be adapted to emerging activities in the deep oceans and High Seas such as those elaborated through the UN Fish Stocks Agreement (Kimball, 2005).

Detailed information on the natural resources and the human activities (mining, energy exploitation, waste disposal, and commercial fishing) associated to the abyssal seafloor, the water column, the surface of the ocean and the atmosphere above the surface should be incorporated to the management of the proposed MPAs as these data influence the processes and the structure of benthic communities in the CCFZ.

In the CCFZ, protection of the environment requires careful planning and commitment from all levels among and within mining consortia. The Mining Code issued by ISBA has for purpose to regulate prospecting, exploration and exploitation of marine minerals in the international seabed Area (defined as the seabed and subsoil beyond the limits of national jurisdiction). All rules, regulations and procedures are issued within a general legal framework established by the 1982 United Nations Convention on the Law of the Sea and its 1994 Implementing Agreement relating to deep seabed mining.

The Mining Code for the polymetallic nodules is not yet complete (www.isa.org.jm/en/documents/mcode, last consulted 9.12.2009). ISBA issued on 13 July 2000 regulations for prospecting and exploring polymetallic nodules in the Area. In addition, the Authority’s Legal and Technical Commission has issued recommenda-
tions for the guidance of contractors on the assessment of the environmental impacts of exploration for polymetallic nodules.

Under the pressure of a number of countries affirming their belief in implementing Agenda 21 as the programme for environmental management for the 21st century, the Natural Resources and Environment Management Branch and the United Nations Environment Programme (UNEP) have been requested to draw *environmental guidelines for the mineral sector* (UNDESA and UNEP, 1994) after the 1991 Berlin Round Table on Mining and the Environment organized by the United Nations and the German Foundation for International Development. These guidelines have been updated (UN, 2002) according to changes in the mining sector, in particular by defining and promoting a standardized best environmental practice in the management of mining operations to minimize environmental impacts. The principles of Best Practice (The Commonwealth Government of Australia and UNEP, 2002) include:

- Ecologically sustainable development
- Intra and inter-generational equity
- Accountability and compliance with international standards and principles
- The Precautionary Principle
- Well informed and trained staff
- Effective communication and openness
- Flexibility
- Continual improvement.

The general approach of these environmental guidelines is to address in an integrated approach: mining and sustainable development, regulatory frameworks, environmental impact assessments (EIAs), environmental management systems and programmes, environmental monitoring, environmental auditing and enforcement in particular during exploration and mining activities.

Environmental Management encompasses all the activities necessary to ensure that a mining project is designed, operated and closed in an environmentally sound and socially acceptable manner. The principles of good environmental management are:

- identifying all potentially significant adverse environmental impacts and social effects that would result without mitigation or control;
- defining control strategies to mitigate all potentially significant adverse impacts;
- implementing procedures to instigate control strategies in response to the unacceptable risk of adverse environmental impact;
- implementing procedures to review control strategies in response to performance evaluation;
- implementing procedures to promote the benefits of any positive environmental or social impacts.

To conclude, polymetallic nodule mining cannot be considered as a sustainable activity as the reconstitution of the initial status, if ever possible, would take at least 1 million years according to nodule growth. Restoration of the mining site (in terms of fauna and habitats, not of landscape) could also take centuries in relation to the slow processes occurring in the deep sea. Finally as technologies for extraction and recovery of polymetallic nodules are not yet totally defined, impacts cannot be correctly quantified over spatial and temporal scales and would also depend on combined effects of water movement and the scale of mining.

### 5.2. International Seabed Authority’s Mandate and Activities

On 13 July 2000, the International Seabed Authority (ISBA) adopted the Regulations on Prospecting and Exploration of Polymetallic Nodules in the Area (“the Regulations” - ISBA/6/A/18). The Regulations require the Authority to establish and keep under periodic review environmental rules, regulations and procedures to ensure effective protection for the marine environment from harmful effects which may arise from activities in the Area. Under each contract, the Contractor is required to gather environmental baseline data and to establish an environmental referential state against which to assess the likely effects of its programme of activities and a programme to monitor and report on such effects.

In 2001, recommendations by ISBA for the guidance of the contractors for the assessment of the possible environmental impacts arising from the exploration for polymetallic nodules in the Area have been issued. These include the delineation by contractors, sponsoring States and other interested States of *impact reference zones* and *preservation reference zones* as part of the establishment and implementation of programmes for monitoring and evaluation of the impacts of deep seabed mining on the marine environment.

According to ISBA, an *impact reference zone* should be selected based on the area being representative of the environmental characteristics, including the biota, of the site where testing would take place.
ISBA recommends that a **preservation reference zone** should be carefully located and be large enough so as not to be affected by the natural variations of local environmental conditions. The zone should be a non mining area and have species composition comparable (fauna and flora) to that of the **test area**, an area for testing nodule collecting systems and processing operations in the impact reference zone.

In 2007, ISBA has prepared draft regulations on prospecting and exploration for polymetallic sulphides in the Area. Within this document the same recommendations appear for impact reference and preservation reference zones (regulation 33). In 2008, the Legal and Technical Commissions of ISBA has issued recommendations on the design and implementation of **preservation reference zones** before test mining and during mining. The main elements are:

- to be large enough so as not to be affected by the natural variations of local environmental conditions,
- to have species composition comparable to that of the test mining area,
- to be located upstream of the test mining area (not influenced by the plume when processing the nodules in the water column).

The term “**Marine Protected Area (MPA)**” appears for the first time in the official documents of the Law of the Sea, of the Agreement and ISBA in the 2008 report of the Council (ISBA 14/C/2 of 14 February 2008): “Biodiversity, species range and gene flow in the abyssal Pacific nodule province: predicting and managing the impacts of deep seabed mining (paragraph 11):" In this document the MPA denomination is referred to “preservation reference zones” as specified in the Authority’s regulations and the MPA network is quoted as a “network of representative preservation zones" (paragraph 13).

ISBA is an organisation with a specific (sectoral) mandate, considering one activity, mineral exploration and exploitation. Thus it promotes research and knowledge on a part of the environment (the seabed and its subsoil and not on the water column), looks at the impacts of the activity on this restricted part of the environment and recommends to contractors and/or States to minimise if possible the impacts on the specific site of mining and on the surrounding areas (outside the mining site, in the water column and at the surface of the sea).

### 5.3. **Preservation Reference Areas proposed by Kaplan Project**

From the results of its surveys (ISBA, 2008a), Kaplan project produces a rationale and recommendations for the establishment of a network of preservation reference (representative) areas (ISBA, 2008b). Overall, Kaplan project concludes that the precautionary principle should be used as knowledge on biodiversity levels, species ranges and gene flow in the CCFZ is still limited. Thus the environment should be protected by Marine Protected Areas (MPAs) with the following recommendations:

- MPAs should be erected to safeguard biodiversity in the CCFZ.
- MPAs should be set up, at multiple locations across the CCFZ, at the very least in the eastern, central and western portions of the region of mining claims.
- MPAs should be designed to protect biodiversity across the entire width of the CCFZ, i.e., from 7°–17° N latitude, because of the steep latitudinal gradients in productivity and community structure within the equatorial Pacific.
- MPAs should be large enough to encompass major areas of the known benthic habitat types in the CCFZ, including abyssal hills with and without nodules, rocky ridges, and multiple seamounts of various elevations above the seafloor.
- MPAs should be large enough for most of its area to be buffered from the direct and indirect impacts of nodule mining activities, including influences from sediment plumes in the water column and at the seafloor.
- MPAs should be consistent with the concept of ecosystem-based management, and include the control of substantial human activities (mining, energy exploitation, waste disposal, and commercial fishing) from the abyssal seafloor to the ocean surface as benthic processes and community structure in the CCFZ are strongly influenced by processes in the water column above.
- that the “precautionary principle” should be applied while a database on biodiversity and species range should be developed.

The analysis of the nine preservation reference areas proposed by Kaplan project, displayed in Table 4a and 4b, has been achieved on basis of available data in the literature and discussion with experts in the field (Auzende, pers. comm.; Hoffert, pers. comm.; Volat et al., 1980; Wirmann, 1980). The description of the different nodule-facies and sediments at each preservation unit follows the classification (Hoffert, 2008; Hoffert and Saget, 2004) proposed previously in the UNESCO/IOC baseline study (Tilot et al., 2010). The localization in the CCFZ of the preservation reference areas proposed by Kaplan project is represented on Figure 15, Appendix 1.
### Table 4: Description of Marine Protected Areas proposed by ISBA/Kaplan project ISBA/14C/2 (2008).

<table>
<thead>
<tr>
<th>Coordinates (Centre of area)</th>
<th>Location in CCFZ</th>
<th>Average depth</th>
<th>Sediment Water content (250-300 %) in CCFZ</th>
<th>Sediment size</th>
<th>Sediment contents period</th>
<th>Nodule facies (prevailing)</th>
<th>Comments</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>MPA1</strong> 153W-13N</td>
<td>No</td>
<td>6,000m</td>
<td>&lt;150 % relatively low</td>
<td>large fraction &gt;63μ relatively coarse sed.</td>
<td>siliceous/ argileous</td>
<td>Eocene</td>
<td><strong>Facies A</strong></td>
</tr>
<tr>
<td><strong>MPA2</strong> 136W-16N</td>
<td>Partly</td>
<td>4,800m</td>
<td>&lt;170 % relatively low</td>
<td>large fraction &gt;63μ relatively coarse sed</td>
<td>siliceous/ argileous</td>
<td>Eocene/Quaternary</td>
<td><strong>Facies A</strong></td>
</tr>
<tr>
<td><strong>MPA3</strong> 129W-20N</td>
<td>No</td>
<td>4,000m</td>
<td>&lt;150 % relatively low</td>
<td>small fraction &gt;63μ relatively fine sed</td>
<td>Argileous</td>
<td>Quaternary</td>
<td><strong>Facies A</strong></td>
</tr>
<tr>
<td><strong>MPA4</strong> 149W-7N</td>
<td>Yes</td>
<td>variable</td>
<td>&lt;150 % relatively low</td>
<td>large fraction &gt;63μ relatively coarse sed</td>
<td>calcareous ooze</td>
<td>Eocene</td>
<td><strong>Facies A</strong></td>
</tr>
<tr>
<td><strong>MPA5</strong> 138W-10N</td>
<td>Yes</td>
<td>5,000m</td>
<td>300 % relatively high</td>
<td>Large fraction &gt;63μ relatively coarse sed</td>
<td>siliceous/argileous</td>
<td>Eocene/Quaternary/Miocene</td>
<td><strong>Facies B</strong></td>
</tr>
<tr>
<td><strong>MPA6</strong> 122W-16N</td>
<td>Yes</td>
<td>4,200m</td>
<td>= or&lt;200 % relatively low</td>
<td>small fraction &gt;63μ relatively fine sed</td>
<td>argileous ooze</td>
<td>quaternary period</td>
<td><strong>Facies B</strong></td>
</tr>
</tbody>
</table>

**Comments**: Seamounts are present in this area which is relatively deeper than the rest of the CCFZ.

**Comments**: This area is characterized by relief, cliffs, volcanoes, seamounts in the NE. The sediments are relatively coarse, related to relief.

**Comments**: This area is on the NE border of the CCFZ. Seamounts are located in its south-eastern part.

**Comments**: This site is located in an area of large relief with seamounts, 1,000 m of elevation over 400 km wide.

**Comments**: None.

**Comments**: None.
5.4. THE NETWORK OF SEABED PRESERVATION REFERENCE AREAS (SPRA) PROPOSED BY THE PRESENT UNESCO/IOC BASELINE STUDY

The rationale for conservation of the biodiversity in the CCFZ is based on the analysis of the results of UNESCO/IOC baseline study (Tilot, 2006b; Tilot et al., 2010) and ISBA/Kaplan/Nodinaut studies (Galeron et al., 2006a; ISBA, 2008). It outlines the principal ecological and biological characteristics of the nodule ecosystem in the CCFZ and their sensitivity to natural and anthropogenic impacts (detailed in chapter 2 of this document).

On basis of this rationale, a conservation strategy with the establishment of a network of seabed preservation reference areas is recommended to protect the biodiversity in the CCFZ in the face of future nodule mining. It is necessary to consider an important seabed area or a network of areas covering all the different facies and associated types of fauna. This recommendation would be made by precautionary principle, as there is a limited knowledge on environmental parameters, habitats, structure and dynamics of benthic communities due to heterogeneous sampling over vast regions, variable taxonomic expertise and the fact that modern molecular techniques have not been applied to most deep sea faunal groups. However, with the past baseline studies in particular with CNEXO-IFREMER surveys from the first explorations to presently (Tilot, 2006 a, b), there are sufficient data to identify representative areas of the CCFZ. Meanwhile with further in situ surveys, and consequently a growing database on fauna, habitats and environmental parameters, the conservation strategy would be adaptive.

The size of a unit within a network of Preservation Reference Areas being (400km/400km) on the seabed as proposed by Kaplan project (ISBA, 2008b), is indeed large enough for all faunal categories to contain areas of representative habitats and faunal communities in the general context of the CCFZ. Although ideally, MPAs within a network should have corridors to interconnect for recolonization purposes.

Nodule deposits do not cover uniformly large areas as observed during the surveys. Often several nodule-facies coexist and only prevailing facies would be observed at a certain scale. This size unit would be large enough to detect prevailing nodule-facies habitats and their associated faunal communities, all categories included. At this scale, one can observe, for example, that nodule-facies A often prevails while coexisting with nodule-facies B and C (Tilot et al., 2010).

Table 4. Description of Marine Protected Areas proposed by ISBA/Kaplan project ISBA/14C/2 (2008).

<table>
<thead>
<tr>
<th>Coordinates (Centre of area)</th>
<th>Location in CCFZ</th>
<th>Average depth</th>
<th>Sediment Water content (250-300 %) in CCFZ</th>
<th>Sediment size</th>
<th>Sediment contents Period dating</th>
<th>Nodule facies (prevailing)</th>
</tr>
</thead>
<tbody>
<tr>
<td>MPA7 142W-6N</td>
<td>No</td>
<td>5,000m</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Comments: This site is located out of the CCFZ, on the Clipperton Fracture and is characterized by relief with seamounts, volcanoes, rock outcrops. There are no nodule deposits nor sediments in general</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>MPA8 131W-7N</td>
<td>No</td>
<td>4,600m</td>
<td>&lt;150 % relatively low small fraction &gt;63μ relatively fine sed</td>
<td>siliceous ooze eocene period</td>
<td>Facies B and O in N</td>
<td></td>
</tr>
<tr>
<td>Comments: This site is located out of the CCFZ, on the Clipperton Fracture at 4600m. It is characterized by relief, cliffs, seamounts.</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>MPA9 125W-9N</td>
<td>Yes</td>
<td>4,300m</td>
<td>200-300 % Average of CCFZ small fraction &gt;63μ relatively fine sed</td>
<td>siliceous ooze quaternary period</td>
<td>Facies B</td>
<td></td>
</tr>
<tr>
<td>Comments: None</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

(Continued)
As discussed previously, there is significant evidence that the community structure of faunal assemblages differs substantially over a latitudinal range in the CCFZ due to topography, varying habitat heterogeneity and different trophic inputs partly originating in an overall westward trend of reduced primary productivity in the central Pacific (Smith and Demopoulos, 2003).

Therefore, for designing representative reference areas, it would indeed be relevant to select three major zones from West to East divided into two subzones North and South in the CCFZ instead of three as proposed by Kaplan project. Indeed several factors lead to this conclusion such as the topography of the CCFZ, the fact that the commercially interesting nodule deposits are included between the Clarion-Clipperton fracture zones and not on and beyond the fractures (as Kaplan’s PRA 3, 8, 7 and partly PRA 1 and 2 located in a higher variability of relief including seamounts with no nodule deposits).

Within the CCFZ, there are major characteristics of faunal communities related to specific nodule-facies and sediments types in nodule free areas, which are well represented in these subzones as described in the UNESCO/IOC baseline study. In addition, there is a major elevation (in average 1,000 km long, 400 km large, 1,000 m high) crossing the CCFZ in a NS direction which separates the most western zone from the rest of the CCFZ. Consequently environmental parameters such as currents, habitats and faunal communities differ substantially at either side of this elevation, thus the western part is not representative of the rest of the CCFZ.

Also in the few Kaplan’s PRAs located in the CCFZ, none include deposit beds where nodule-facies C prevail (large nodules more scattered on the seabottom). Now this nodule-facies is one of the most commercially important where megafaunal and macrofaunal communities are also the most abundant and diverse. The exploitation of this nodule-facies would have a greater impact on the general biodiversity of faunal assemblages. Additionally MPA 4 differs from the other areas in the CCFZ as it is located mostly on the large elevation described previously, crossing the CCFZ in a NS direction.

Based on existing knowledge in the literature and discussions with different experts in the field (Auzende, pers. comm.; Hoffert, pers. comm.; Volat et al., 1980; Wirmann, 1980), UNESCO/IOC thus proposes a network of seabed PRAs which are all included in the nodule deposits of the CCFZ (Figure 15). Although several parameters such as the nature of sediments, the type of nodule-facies and coverage are missing for some areas as displayed in Tables 5a and 5b, (but may be available in the ISBA and/or Russian databases), these Seabed Preservation Reference Areas (SPRAs) are well representative of the habitats outlined in the UNESCO/IOC study (Tilot, 2006b, Tilot et al., 2010).

According to the features of the environment and the faunal communities as well as the location of mining claims in the CCFZ, a set of seven SPRAs areas is proposed for the CCFZ (Figure 15 in Appendix 1; red squares delineate UNESCO/IOC Seabed Preservation Reference Zones 1 to 7). The seventh SPRA has been chosen because of its location at the most eastern and southern part of the CCFZ and because it includes the area of the Authority. It is also close to the German mining area and to the Clipperton Fracture Zone where seamounts and volcanoes are present.
<table>
<thead>
<tr>
<th>Coordinates (Center of area)</th>
<th>Location in CCFZ</th>
<th>Average depth</th>
<th>Sediment Water content (250-300 %) in CCFZ</th>
<th>Sediment size</th>
<th>Sediment contents period dating</th>
<th>Nodule facies (prevailing)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>SPRA 1</strong> 155W-8N</td>
<td>Yes</td>
<td>5,100m</td>
<td>&gt;250 % relatively high</td>
<td>Small fraction &gt;63μ relatively fine sed</td>
<td>siliceous Quaternary</td>
<td>Facies B on rock outcrops</td>
</tr>
<tr>
<td><strong>Comments</strong>: This area is lying West of a large N-S relief, 1,000 m high, 100 km long and 400 km large; this elevated area includes seamounts. There would be relatively more current than elsewhere in the CCFZ area.</td>
<td></td>
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</tbody>
</table>

| **SPRA 2** 150W-14N         | Yes             | 6,000m        | <200 % relatively low                   | small fraction >63μ relatively fine sed | siliceous/argileous Eocene/Quaternary | Facies B                    |
| **Comments**: This area is characterized by relief, cliffs, volcanoes, seamounts in the northeastern part. The sediments are relatively coarse, related to relief. |

| **SPRA 3** 140W-9N          | Yes             | 4,900m        | >200 % relatively high                  | large fraction >63μ relatively coarse sed | siliceous/argileous Eocene/Quaternary /Miocene | Facies B                    |
| **Comments**: Seamounts are present and the Clarion fracture is located in the most southern part of the MPA area. The sediments are relatively coarse, in relation to the relief expressed by rock outcropping on old sediments. There are relatively more currents than elsewhere in the CCFZ area. |

| **SPRA 4** 136W-15N         | Yes             | 4,800m        | <170 % relatively low                   | large fraction >63μ relatively coarse sed | siliceous/argileous Eocene/Quaternary | Facies A                    |
| **Comments**: This area is located in the CCFZ, a bit south of the formerly MPA 2 proposed by Kaplan/ISBA (2008). According to the bathymetric map, there is more relief (seamounts especially in the NE) than in formerly proposed MPA AREA 2. There is a majority of nodule-facies A in relation to the relief and relatively more currents than elsewhere in the CCFZ area. |

| **SPRA 5** 127W-12N         | Yes             | 4,600m        | >150 %<300 % relatively high            | small fraction >63μ relatively fine sed | siliceous/argileous Quaternary | Facies C                    |
| **Comments**: None          |

| **SPRA 6** 121W-16N         | Yes             | 4,200m        | <200 % relatively low                   | small fraction >63μ relatively fine sed | siliceous/argileous Quaternary | Facies A                    |
| **Comments**: This area is located in a setting of abyssal hills and plains including some fractures and seamounts in the NE. |

| **SPRA 7** 118W-9N          | Yes             | see ISBA database | see ISBA database | see ISBA database | see ISBA database | see ISBA database |
| **Comments**: This area has been chosen because of its location at the most eastern and southern part of the CCFZ, including an area of the Authority. It is close to the German mining area and to the Clipperton Fracture Zone where seamounts and volcanoes are present. The data are available in ISBA database. |

Table 5b Description of the Seabed Preservation Reference Areas (SPRAs) proposed in the UNESCO/IoC study.
In conclusion there is a need of additional information on:

- current patterns close to the seabed in the CCFZ. In the literature, the general pattern is described for the region as an east-western flow (Volat et al., 1980; Ryan et Heezen, 1976),
- variability of cover percentage of nodule deposits,
- topography, such as for cliffs (in average 200m large and 100m high), plateaus...,
- bathymetry and microtopography of the seabed to identify the seabed in particular fractures,
- percentage cover of nodules in the newly proposed MPA areas,
- percentage of water content in sediments and microfauna (as sampled in cores of the seabed),
- Photographs and samples of the benthos to analyse faunal communities, nodule percentage cover and possible preferential habitats and other ecological and biological relations.

This information may be partly found in the growing database of ISBA.

Presently, the ISBA mandate concerning mining is limited to soil and subsoil and impacts will occur also in the water column and at the surface. It is important that marine conservation in the High Seas takes into account an integrated approach for ocean management and conservation covering all the sectors of activities (such as mining and cables at the sea bottom, fisheries in the water column and maritime traffic at the surface), most of these being covered by existing instruments or institutions. Coordination between all the international instruments and institutions concerning the High Seas should be reinforced as emphasized in recent literature (IDDRI, 2009; Corrigan and Kershaw, 2008; Tilot, 2010a). On this matter and based on the results of discussions with different experts, a tridimensional management concept could be proposed for the High Seas in order to support an integrated approach.

Thus, the only options for the High Seas would appear to move towards an integrated Ocean/High Seas management, an integrated approach of natural processes and impacts of human activities. As fostered in the document ISBA 14C-2 08, it would be “Because benthic processes and community structure in the Clarion-Clipperton Zone are strongly influenced by processes in the water column above that it would be highly desirable for management of the Marine Protected Areas to include the control of substantial human activities (mining, energy exploitation, waste disposal and commercial fishing) from the abyssal seafloor to the ocean surface”. This recommendation is consistent with the concept of Ecosystem-based management and in line with the Convention on Biological Diversity.

For the potential mining areas, the hope is in the voluntary decision of individual or consortium of contractors, supported by States for increasing research activities.

As strict guidelines and indicators are necessary for management decisions (Boyle et al., 2001), a permanent tridimensional monitoring system with identified indicators related to natural parameters and the different activities on the deep seabed and the water column could be installed in a grid of multiple stations in the CCFZ area in order to detect the variability in space and time of natural processes and mining impacts. Thus it would enable the management body to set up, guidelines that could be adaptive due to a time and space span of expected impacts (Tilot, 2010a). On the deep seabed, a strategy of epibenthic monitoring could be adapted from rapid assessment technics and strategies as developed previously in this document.

This monitoring system would allow at the same time to increase the knowledge on the referential state and to better evaluate the potential impacts of the mining activities, thus enable to take proper decisions and improve regulations for future mining operations.
6. Final conclusions

Biodiversity and driving factors of the nodule ecosystem in the CCFZ

The present updated interpretation of a referential state in the nodule ecosystem of the CCFZ shows that the epibenthic faunal communities are highly diverse and composed of true abyssal species, with many species new to science, adapted to a regional and within-site variability in biotic and abiotic conditions, the underlying driving factors of this abyssal environment.

Habitat heterogeneity at different spatial and temporal scales (i.e. areas in the CCFZ, nodule-facies, microheterogeneity at nodule level, patches of detritus, biogenic structures and bioturbation) in correlation with other factors and conditions (i.e. bottom currents and sediment chemistry) is a significant factor defining the distribution pattern of nodule deposits in association with the abundance, composition and structure of epibenthic megafaunal assemblages at different scales.

The abundance and composition of megafaunal assemblages differ in each area. However within-area patterns are evidenced with a clearly marked faunal abundance and taxonomic richness for megafauna and macrofauna on nodule bearing areas where prevail sessile fauna and infauna, while meiofauna is more abundant and diverse on nodule-free areas. There are key faunal groups in the CCFZ, such as cnidarians, echinoderms and sponges, for megafauna, and polychaete worms, nematode worms and protozoan foraminifera for macrofauna and meiofauna. Preferential habitats, ranked according to nodule coverage and slope, are evidenced for specific megafaunal assemblages. Within sites, aggregative patterns of distribution are displayed for common species.

There is a higher taxonomic richness in the West due in part to a higher heterogeneity of substrates. More suspension feeders are found in the western oligotrophic sites. On the other hand, faunal abundance is higher in the East with a larger number of detritus feeders in correlation with a higher trophic input.

Megafauna, with its wide distribution and preferential habitats, would serve as good indicator of environmental change and mining impact. In particular the echiurian worms 

As biological activity on the sea floor affects also the structure and chemistry of the sediment, it has an important role on maintaining nodules at the surface of the sediments.

There is however a lack of knowledge on physical, faunal components of the nodule ecosystem in the CCFZ, e.g. the levels of species diversity are still poorly known due to undersampling. Also there is a lack of information on the other faunal groups which influence the ecosystem, the fauna dwelling in the water column up. to the surface of the ocean as the main food resources originates from the water column and
above. Therefore data collection, research and conservation should be encouraged in these directions.

Principles, tools and criteria for the management and the conservation of High Seas biodiversity

Discussions over the principles, tools and criteria for biodiversity assessment and monitoring show the need for a careful approach for the management and conservation of the deep sea. All the elements presented lead to a broader strategy for conservation of marine biodiversity which requires to define the management of the biodiversity in ecologically meaningful ways that are practical to measure so that the effects of environmental degradation, remediation or conservation can be monitored.

Conservation and management of the CCFZ

Polymetallic nodule mining cannot be considered as a sustainable activity as the reconstitution of the initial status, if ever possible, or an alternate state, would take at least one million years according to nodule growth. Most probably there would be an impact at a regional scale, over an area of more than 3 million km² of the deep sea floor, overall the water column and surface of the ocean (and layer of air over the ocean). As nodule mining is envisioned to be the largest-scale human activity to directly impact the deep sea floor, faunal communities particular to the nodule ecosystem need to be protected from extinction. Among the information needed to enable to fully predict and manage commercial mining would be knowledge on species ranges, sensitivity to sediment burial and spatial scale dependence of recolonization in abyssal benthic communities. Finally as technologies for extraction and recovery of polymetallic nodules are not yet totally defined, impacts cannot be correctly quantified over spatial and temporal scales. They would also depend on combined effects of water movement and of the scale of mining.

The preservation reference areas proposed by Kaplan project are discussed and a network of Seabed Preservation Reference Areas is proposed on basis of the rationale for conservation of the biodiversity which combines UNESCO/IOC and ISBA/Kaplan/Nodinaut studies. These areas are representative of the main nodule and nodule-free facies and associated types of fauna described in the referential studies. A conservation strategy is advanced on the precautionary principle; it is to be adaptive with the growing database on the region.

It is also outlined that marine conservation in the High Seas should take into account an integrated approach for ocean management and conservation covering all the sectors of activities and the tridimensional status of the oceans. Coordination between all the international instruments and institutions concerning the High Seas should be reinforced in this matter.
LIST OF ACRONYMS

ACD  Aragonite Compensation Depth
AFERNOD  Association Francaise pour la Recherche et l’Exploitation des NODules polymetalliques
BACI  Before–After/Control–Impact
CBD  Convention on Biological Diversity
CCD  Carbonate Compensation Depth
CCFZ  Clarion-Clipperton Fracture Zone
CeDAMar  Census of the Diversity of Abyssal Marine Life
CNEXO  Centre National pour l’Exploitation des Océans
CO₂  Carbon Dioxide
COMRA  China Ocean Mineral Resources Research and Development Association
COP  Conference of the Parties (governing body of CBD)
CBD  Convention on Biological Diversity
DORD  Deep Ocean Resources Development Company
EEZ  Exclusive Economic Zone
EIA  Environmental Impact Assessment
FAO  United Nations Food and Agriculture Organisation
HSTF  High Seas Task Force
IFREMER  Institut Francais pour la Recherche et l’ Exploitation de la Mer
IMO  International Maritime Organisation
IOC  Intergovernmental Oceanographic Commission of UNESCO
IOM  Interoceamenetal Joint Organization
IOM BIE  Interocceanmetal Joint Organization Benthic Impact Experiment
IPCC  Intergovernmental Panel on Climate Change
ISBA  International SeaBed Authority
IUCN  World Conservation Union
LTC/ISBA  Legal and Technical Commission of the International SeaBed Authority
MDG  Millennium Development Goals
MPA  Marine Protected Area
NGO  Non-Governmental Organisation
NORIA  NOduleRîches et Abondants
OMA  Ocean Mining Associates
POC  Particulate Organic Carbon
PRA  Preservation Reference Area
RFMO  Regional Fisheries Management Organisation
SES  Social-Ecological Systems (of management)
SPRA  Seabed Preservation Reference Areas
UN  United Nations
UNDESA  United Nations Department of Economic and Social Affairs
UNEP  United Nations Environment Programme
UNESCO  United Nations Economic, Social and Cultural Organisation
UNFSA  United Nations Fish Stock Agreement
UNGA  United Nations General Assembly
UNICPOLOS  United Nations Informal Consultative Process on Oceans and the Law of the Sea
WCMC  World Conservation Monitoring Centre
WCPA  World Commission on Protected Areas
WSSD  World Summit on Sustainable Development


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Appendix I

ILLUSTRATIONS, MAPS AND PHOTOGRAPHS OF THE DEEP SEA BOTTOM AND OF DEVICES OF EXPLORATION

Fig. 1. Localisation of “the Area” and the “Contractor Areas” within the Clarion-Clipperton Fracture Zone (CCFZ) in the NE equatorial Pacific Ocean (adapted from http://www.ISBA.org.jm) and the four study areas on which is based the interpretation of the referential state (Radziejewska and Stoyanova, 2000; Tilot, 1991b, 1992b, 1993, 2006b, c; Tilot et al., 2010): NIXO 45, NIXO 41, Echo I, BIE (IOM). Three of the study areas have been investigated by other projects: DOMES and ISBA/Kaplan/Nodinaut project (NIXO 45 =Kaplan C; BIE= Kaplan E; ECHO I=Kaplan C=DOMES C), a comparative analysis of the results is developed in this document.

Fig. 2. Photograph of nodule-facies A, with small irregular nodules (Hoffert and Saget, 2004). © Ifremer

Fig. 3. Photograph of nodule-facies B, regularly shaped nodules with numerous pieces of debris from old nodules (Hoffert and Saget, 2004). © Ifremer
Fig. 4. Photograph of nodule-facies C, hummocky nodules with an equatorial thickening (Hoffert and Saget, 2004). © Ifremer

Fig. 5. Photograph of nodule-facies O seen from the ‘Nautile’ during the NIXONAUT cruise. © Ifremer

Fig. 6. Photograph of nodule-facies C seen from the ‘Nautile’ during the NIXONAUT cruise. © Ifremer

Fig. 7. Photograph of nodule-facies B and C mixed, seen from the ‘Nautile’ during the NIXONAUT cruise. © Ifremer

Fig. 8. Photograph of steps in an outcrop of hardened carbonaceous silt, seen from the ‘Nautile’ during the NIXONAUT cruise. © Ifremer

Fig. 9. Photograph of nodule-facies A, associated with small plates (facies-EP), NIXONAUT cruise. © Ifremer
Fig. 10. Photograph of the remote-controlled submersible the ‘Épaulard’. © Ifremer

Fig. 11. Photograph of the manned submersible the ‘Nautilis.’ © Ifremer

Fig. 12. Photograph of the remote free-sampling device developed by Ifremer to collect polymetallic nodules. © Ifremer

Fig. 13. Diagram and photograph of the ‘ED1’ (camera coupled to a sampling device). © Ifremer
Fig. 14. Map of claimed areas in the CCFZ licensed to exploration contractors. Kaplan sites are indicated by E, C, W (the Kaplan East, Central and Western Sites). Site E is located in the IOM claim area at ~15° N, 119° W (3,990–4,096 m depth), Site C is located in the eastern IFREMER/AFRENOD claim area at ~14°5' N, 130° 5'W (4,997–5,054 m depth) and Site W is located in the western IFREMER/AFRENOD claim area at 9° 33' N, 150° 0.5' W (5,043–5,059 m depth). Reference: Biodiversity, species ranges and gene flow in the abyssal Pacific nodule province: predicting and managing the impacts of deep Seabed mining, ISBA Technical study, N°3.
Fig. 15. Proposal of a network of seven Seabed Preservation Reference Areas (red squares), each 400 x 400 km, representative of six subregions of the CCFZ with an additional site in option (UNESCO/IOC 2009) and the ISBA/Kaplan proposal of nine preservation reference areas (black squares). The CCFZ is divided into the nine management subregions, with one 400 x 400 km preservation reference area centered in each of the subregion (adapted from the Figure of the International Seabed Authority/14/LTC/2, Fourteenth session Kingston, 2008).
PANORAMA OF EPIBENTHIC MEGAFANAUL COMMUNITIES IN A DEEP SEA NODULE ECOSYSTEM OF THE CCFZ, NE PACIFIC OCEAN

INTRODUCTION ................... 77
PORIFERA ......................... 78-79
HYDROZOA ....................... 80
SCYPHOZOA ...................... 80
OCTOCORALLIA ................. 81
ACTINARIA ....................... 81-82
CERIANTHARIA .................. 82
ANTIPATHARIA ................. 83
ECHIURIA ......................... 83-84
CEPHALOPODA ................. 84-85
ARTHROPODA .................... 85
CRINOIDA ........................ 86
ECHINOIDA ....................... 86
ASTEROIDA ...................... 87
HOLOTHUROIDA ............... 88-92
ARTHROPODA PYCNOGONIDA 93
ENTEROPNEUSTA .............. 93
TUNICATA ....................... 93
PISCES .......................... 94
This panorama is drawn from the reference database compiling over 200,000 photographs, 55 hours of films and various environmental database of the seabed (and its vicinity) in the CCFZ on which is based the description of the referential state of the epibenthic megafaunal assemblages in an abyssal nodule ecosystem (Tilot, 2006d, e). These data were collected mainly by various towed devices (troika, 'Deep Tow', 'R.A.I.E.'), remote vehicles ('ED1', the "Épaulard") and the manned submarine 'the Nautile'. A total of 175 taxa (genera and species) covering 13 phyla has been identified over an area of 5,500,000 m² CCFZ. A pool of international specialists (listed in Appendix 3) concur with the hypotheses of taxa identification describing these photographs. 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. There are key megafaunal groups in the CCFZ, such as cnidarians, echinoderms and sponges. The present interpretation of a referential state of the polymetallic nodule ecosystem shows a relatively significant taxonomic richness (by decreasing order of importance): echinoderms (50 taxa including 32 holothurians), cnidarians (41 taxa), chordates (23 taxa including 17 fishes) and sponges (21 taxa). Suspension feeders (68 taxa, among which 58 sessile taxa and 10 mobile taxa) display a higher taxonomic richness than deposit feeders (60 taxa, among which 50 taxa are mobile) and carnivores/scavengers (45 taxa). The taxonomic richness of suspension feeders is principally represented by cnidarians (41 taxa) and sponges (21 taxa). For deposit feeders, it is principally expressed by holothurians (32 taxa).

Habitat heterogeneity is a significant factor defining the distribution pattern, abundance and characteristics of nodule deposits (nodule-facies) as well as faunal communities at different scales. Results of the UNESCO/IOC baseline study show that suspension feeders are more abundant on facies O with recent sediments and on nodule-facies C 10% (big nodules, relatively scattered) on slopes while deposit feeders are more abundant on nodule-facies C 10% (big nodules, relatively scattered).

Biological activity created on the sea floor affects the structure and chemistry of the sediment and would have an important role on maintaining nodules at the surface of the sediments. The observation and spatio-temporal survey of the megafauna on a large scale, by means of photography and video is a useful, low cost tool to evaluate the impact of natural and human-induced processes. Epibenthic megafaunal communities, characterized by their wide distribution and preferential habitats, in particular echiurian worms Bonellidae Jacobia birsteini, would be good indicators for monitoring changes.

This present UNESCO/IOC baseline study of a referential state enables to draw a rationale for a conservation strategy of the CCFZ taking in account the principal ecological and biological characteristics of the nodule ecosystem in the CCFZ and their sensitivity to natural and anthropogenic impacts.
Fig. 16. Photograph taken by ‘the Nautile’ during the NIXONAUT cruise: rocky facies, sponge Hexactinellida *Eulectella* sp. (SPO 13). © Ifremer

Fig. 17. Photograph taken by ‘the Nautile’ during the NIXONAUT cruise: rocky facies, sponge Hexactinellida *Bathydorus* sp. (SPO 5). © Ifremer

Fig. 18. Photograph taken by ‘the Nautile’ during the NIXONAUT cruise: rocky facies, sponge Demospongiae *Cladorhizida* sp. (SPO 19). © Ifremer

Fig. 19. Photograph taken by ‘the Nautile’ during the NIXONAUT cruise: nodule-facies C, sponge Hexactinellida “Two-pronged” Rossellidae (SPO 2). © Ifremer

Fig. 20. Photograph taken by the “Épaulard” at NIXO 45 site: nodule-facies C, sponge Hexactinellida *Pheronema* sp. (SPO 14) with an actinid attached to the peduncle. © Ifremer

Fig. 21. Photograph taken by the “Épaulard” at NIXO 45 site: nodule-facies C, sponge type “vase-shaped alveolate” Tetractinellida *Poecillastra* sp. (SPO 6). © Ifremer

PORIFERA
Fig. 22. Photograph taken by the ‘Épaulard’ at NIXO 45 site: nodule-facies C, colony of sponges Demospongiae Caulophacus sp. or Esperiopsis sp. (SPO 18). © Ifremer

Fig. 23. Photograph taken by the ‘Épaulard’ at NIXO 45 site: facies O, sponge Hexactinellida Euplectella sp. (SPO 12). © Ifremer

Fig. 24. Photograph taken by the ‘Épaulard’ at NIXO 45 site: mixed nodule-facies B with plates, sponge Demospongiae Phakellia sp. (SPO 4). © Ifremer

Fig. 25. Photograph taken by ‘Deep Tow’ at Echo I site (near DOMES C/CCFZ): nodule-facies C, sponge Hexactinellida Hyalonema sp. (SPO 15). © Ifremer

Fig. 26. Photograph taken by ‘Deep Tow’ at Echo I site: nodule-facies C, sponge type “alveolate cushion” Tetractinellida, Poecillastra sp. (SPO 8).

Fig. 27. Photograph taken by the ‘R.A.I.E.’ at NIXO 42 site: rocky facies, sponge Hexactinellida Aulochone sp. (A. cylindrica) (SPO 11). © Ifremer
HYDROZOA

Fig. 28. Photograph taken by the ‘Épaulard’ at NIXO 45 site: mixed nodule-facies B with plates, hydrozoan Branchiocerianthus imperator (HYD 1) bending in the direction of the current. © Ifremer

Fig. 29. Photograph taken by the ‘Épaulard’ at NIXO 45 site: facies O and some nodules of nodule-facies C, hydrozoan Branchiocerianthus imperator (HYD 1). © Ifremer

Fig. 30. Photograph taken by the ‘Épaulard’ at NIXO 45 site: nodule-facies C, hydrozoan Branchiocerianthus imperator (HYD 1). © Ifremer

Fig. 31. Photograph taken by the ‘Épaulard’ at NIXO 45 site: facies O, hydrozoan Branchiocerianthus imperator (HYD 1). © Ifremer

Fig. 32. Photograph taken by the ‘the Nautile’ during the NIXONAUT cruise: nodule-facies C mixed with plates, scyphomedusa or hydromedusa Chrysaora lysocella (MED 10). © Ifremer

Fig. 33. Photograph taken by the ‘Épaulard’ at NIXO 45 site: Nodule-facies C, scyphomedusa, Periphylla periphylla (MED 9). © Ifremer
Fig. 34. Photograph taken by a troika during Copano 2 cruise: facies O, octocorallian Gorgonacea, Primnoidae (OCT 6) near mounds formed by echiurians. © Ifremer

Fig. 35. Photograph taken by the ‘Épaulard’ at NIXO 45 site: nodule-facies C, octocorallian, complex form of Umbellula sp. (OCT 5). © Ifremer

Fig. 36. Photograph taken by the ‘Épaulard’ at NIXO 45 site: facies O and some nodules of facies C, octocorallian Pennatulacea (OCT 1) with actinian Amphianthus sp. (ACT 8). © Ifremer

Fig. 37. Photograph taken by the ‘Épaulard’ at NIXO 45 site: cliffs and mixed nodule-facies B and plates, actinian Actinostolidae form with dark convex centre Sicyonis biotrans (ACT 6'). © Ifremer

Fig. 38. Photograph taken by a troika during Copano 2 cruise: facies O, actinian Ophiodiscus sulcatus or Bolocera sp. (ACT 5). © Ifremer

Fig. 39. Photograph taken by the ‘the Nautile’ during the NIXONAUT cruise: nodule-facies C, actinian type “white disc” Liponema sp. (ACT 1). © Ifremer
Fig. 40. Photograph taken by the ‘Épaulard’ at NIXO 45 site: nodule-facies C, actinian Actinostolidae not attached Sicyonis biotrans (ACT 4). © Ifremer

Fig. 41. Photograph taken by the ‘Épaulard’ at NIXO 45 site: nodule-facies C, actinian Actinostolidae Actinernus sp. (ACT 7). © Ifremer

Fig. 42. Photograph taken by ‘Deep Tow’ at Echo I site: nodule-facies mixed B and plates, actinian Hormathiidae (ACT 6) © Ifremer

Fig. 43. Photograph taken by a troika during Copano 1 cruise: facies O, actinian Sagartiidae, Thenaria sp. (ACT 7). © Ifremer

Fig. 44. Photograph taken by the ‘Épaulard’ at NIXO 45 site: nodule-facies B, ceriantharian Aliciidae, Cerianthus sp. (CER 1) © Ifremer

Fig. 45. Photograph taken by the ‘Épaulard’ at NIXO 45 site: nodule-facies B, dark ceriantharian, Aliciidae, Cerianthus sp. (CER 1’) © Ifremer
Fig. 46. Photograph taken by the ‘the Nautil’ during the NIXONAUT cruise: rocky facies, antipatharian Parantipathes larix (ANT 7). © Ifremer

Fig. 47. Photograph taken by the ‘Épaulard’ at NIXO 45 site: nodule-facies C, antipatharian Schizopathes crassa (ANT 2). © Ifremer

Fig. 48. Photograph taken by the ‘Épaulard’ at NIXO 45 site: nodule-facies C, antipatharian Bathypathes lyra (ANT 1). © Ifremer

Fig. 49. Photograph taken by the ‘the Nautil’ during the NIXONAUT cruise: nodule-facies C, antipatharian Bathypathes sp. (ANT 10) © Ifremer

Fig. 50. Photograph taken by the ‘the Nautil’ 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. 51. Photograph taken by the ‘Épaulard’ at NIXO 45 site: nodule-facies C, round burrow and mound of the echiurian worm Bonneliidae Jacobia birsteini (ECH 2). © Ifremer
Fig. 52. Photograph taken by the ‘the Nautilus’ during the NIXONAUT cruise: nodule-facies B, mound about 2.5 m formed by the echiuran worm Bonneliidae Jacobia birsteini (ECH 2). © Ifremer

Fig. 53. Photograph taken by the ‘Épaulard’ at NIXO 45 site: nodule-facies B, proboscis of an echiuran worm Bonneliidae (ECH 3) extending out of its burrow close to its mound. © Ifremer

Fig. 54. Photograph taken by the ‘Épaulard’ at NIXO 45 site: nodule-facies C, round mound constructed by an echiuran worm Balanoglossus sp. (ENT 4). © Ifremer

Fig. 55. Photograph taken by the ‘Épaulard’ at NIXO 45 site: facies O, proboscis of an echiuran worm retracted at the entrance of its burrow and radiating tracks Bonneliidae Bruunellia bandae (ECH 6). © Ifremer

Fig. 56. Photograph taken by the ‘Épaulard’ at NIXO 45 site: nodule-facies C, cephalopod Cirrata Cirroteuthis sp. or Cirothauma sp. (CEP 2). © Ifremer

Fig. 57. Photograph taken by the ‘Épaulard’ at NIXO 45 site: nodule-facies C, cephalopod Cirrata during propulsion Cirroteuthis sp. (CEP 2). © Ifremer
Fig. 58. Photograph taken by the “Épaulard” at NIXO 45 site: mixed nodule-facies including B, cephalopod Cirrata during propulsion Cirrotheuthis sp. or Stauroteuthis sp. (CEP 1). © Ifremer

Fig. 59. Photograph taken by the “Épaulard” at NIXO 45 site: nodule-facies C, Stationary cephalopod Cirrata Grimpoteuthis sp. or Cirothauma murrayi (CEP 1). © Ifremer

Fig. 60. Photograph taken by the ‘the Nautile’ during the NIXONAUT cruise: mixed nodule-facies including C, crustacea Decapoda Nemato-carcinus sp. (DEC 1). © Ifremer

Fig. 61. Photograph taken by the ‘the Nautile’ during the NIXONAUT cruise: nodule-facies C, crustacea Decapoda Plesiopenaeus sp. or Aristaeomorpha sp. (DEC 5). © Ifremer

Fig. 62. Photograph taken by the “Épaulard” at NIXO 45 site: nodule-facies C, crustacea Decapoda Galathea sp. (GAL 1). © Ifremer

Fig. 63. Photograph taken by the “Épaulard” at NIXO 45 site: facies O, crustacea Isopoda Munnopsidae sp. (ISO 1). © Ifremer
Fig. 64. Photograph taken by the ‘Epaulard’ at NIXO 45 site: nodule-facies O, crinoid *Farinometra parvula* (CRI 1). © Ifremer

Fig. 65. Photograph taken by ‘Deep Tow’ at DOMES C site: mixed nodule-facies, crinoid *Hyocrinus bethellianus* (CRI 3) © Ifremer

Fig. 66. Photograph taken by ‘E.D.1’ device during Co-pano cruise: nodule-facies C+, crinoid *Bathyocrinus* sp. (CRI 2) and echinoid *Pleiosodiadema globulosum* (OUR 1). © Ifremer

Fig. 67. Photograph taken by the ‘Epaulard’ at NIXO 45 site: crinoid *Hyocrinus bethellianus* on a cliff (CRI 3) © Ifremer
Fig. 68. Photograph taken by the 'Nautile' during the NIXONAUT cruise: nodule-facies C, asteroid Hymenaster violaceus (AST 5). © Ifremer

Fig. 69. Photograph taken by the 'Nautile' during the NIXONAUT cruise: nodule-facies C, brisingid asteroid with 6 arms captured by the 'Nautile', Freyella benthophila (AST 6). © Ifremer

Fig. 70. Photograph taken by the 'Deep Tow' on ECHO I site: Asteroid Hymenaster violaceus (AST 5) on nodule-facies B.
Fig. 71. Photograph taken by the ‘Epaulard’ at NIXO 45 site: mixed nodule-facies (C and B), holothurian Orphnurgus sp. (HOL 3). © Ifremer

Fig. 72. Photograph taken by the ‘Epaulard’ at NIXO 45 site: nodule-facies C, holothurian Oneirophanta mutabilis (HOL 4). © Ifremer

Fig. 73. Photograph taken by the ‘Epaulard’ at NIXO 45 site: nodule-facies C, holothurian Orphnurgus sp. (HOL 3). © Ifremer

Fig. 74. Photograph taken by the ‘Nautile’ during the NIXONAUT cruise: rock outcrop, holothurian Oneirophanta mutabilis (HOL 4). © Ifremer
Fig. 75. Photograph taken by the ‘Nautile’ during the NIXONAUT cruise: nodule-facies C, holothurian (collected) *Psychropotes longicauda* (HOL 17). © Ifremer

Fig. 76. Photograph taken by the ‘Nautile’ during the NIXONAUT cruise: nodule-facies C, holothurian *Psychropotes longicauda* (HOL 17). © Ifremer

Fig. 77. Photograph taken by the ‘Nautile’ during the NIXONAUT cruise: nodule-facies O, holothurian *Psychropotes longicauda* (HOL 17). © Ifremer

Fig. 78. Photograph taken by the ‘Epaulard’ at NIXO 45 site: nodule-facies C, holothurian *Psychropotes longicauda* (HOL 17). © Ifremer
Fig. 79. Photograph taken by the ‘Epaulard’ at NIXO 45 site: nodule-facies C, holothurian (swimming) Enypniastes eximia (HOL 18) © Ifremer

Fig. 80. Photograph taken by the ‘Nautil’ during the NIXONAUT cruise: nodule-facies C, holothurian (swimming) Enypniastes eximia (HOL 18) © Ifremer

Fig. 81. Photograph taken by the ‘Epaulard’ at NIXO 45 site: nodule-facies C, holothurian Enypniastes eximia (HOL 18) © Ifremer

Fig. 82. Photograph taken by the ‘Epaulard’ at NIXO 45 site: nodule-facies C, holothurian Enypniastes eximia (HOL 18) © Ifremer
Fig. 83. Photograph taken by the 'Nautile' during the NIXONAUT cruise: nodule-facies C, holothurian (swimming) Peniagone leander (HOL 19). © Ifremer

Fig. 84. Photograph taken by the 'Epaulard' at NIXO 45 site: nodule-facies C, holothurian (swimming) Peniagone leander (HOL 19). © Ifremer

Fig. 85. Photograph taken by a 'Troika' during the Copano 1 cruise: nodule-facies C, holothurian (swimming) Peniagone leander (HOL 19). © Ifremer

Fig. 86. Photograph taken by the 'Epaulard' at NIXO 45 site: nodule-facies C, holothurian (swimming) Peniagone leander (HOL 19). © Ifremer

Fig. 87. Photograph taken by 'Epaulard' at NIXO 45 site: nodule-facies C, holothurian Peniagone leander (HOL 19). © Ifremer

Fig. 88. Photograph taken by the 'Nautile' during the NIXONAUT cruise: nodule-facies C, holothurian (swimming) Peniagone diaphana (HOL 20). © Ifremer
Fig. 89. Photograph taken by the 'Nautile' during the NIXONAUT cruise: collected holothurian *Psychronaetes hanseni* (HOL 21) © Ifremer

Fig. 90. Photograph taken by 'Deep Tow' at Echo I site: nodule-facies C, holothurian *Psychronaetes hanseni* (HOL 21) © Ifremer

Fig. 91. Photograph taken by the 'Epaulard' at NIXO 45 site: nodule-facies C, holothurians *Psychronaetes hanseni* (HOL 21) and *Oneirophanta mutabilis* (HOL 4) © Ifremer

Fig. 92. Photograph taken by the 'Nautile' during the NIXONAUT cruise: nodule-facies O, holothurian *Psychronaetes hanseni* (HOL 21) © Ifremer

Fig. 93. Photograph taken by the 'Nautile' during the NIXONAUT cruise: on old dredge tracks, two holothurians *Psychronaetes hanseni* (HOL 21) and *Mesothuria murrayi* (HOL 9) © Ifremer

Fig. 94. Photograph taken by the 'Nautile' during the NIXONAUT cruise: nodule-facies C, holothurian *Psychronaetes hanseni* (HOL 21) © Ifremer
Fig. 95. Photograph taken by the ‘the Nautile’ during the NIXONAUT cruise: rocky facies, crustacea Decapoda Munidopsis sp. (GAL 3) © Ifremer

Fig. 96. Exceptional photograph taken by the ‘the Nautile’ during the NIXONAUT cruise, in front of a field vane tester: pycnogonid Collossedes colossea (PYC) parasitising a lobed ctenophore. © Ifremer

Fig. 97. Photograph taken by the ‘Épaulard’ at NIXO 45 site: facies O, enteropneusta Spengellitae Glandiceps abyssicola (ENT 3) © Ifremer

Fig. 98. Photograph taken by the ‘Épaulard’ at NIXO 45 site: facies O, spiral track of lophenteropneusta Ptychodidae (ENT 1) and other traces of bioturbation. © Ifremer

Fig. 99. Photograph taken by the ‘Épaulard’ at NIXO 45 site: nodule-facies C, ascidian Sorberacea Phlebobranchiata sp. (ASC 1) © Ifremer

Fig. 100. Photograph taken by the ‘the Nautile’ during the NIXONAUT cruise: rocky outcrop, ascidian Culeolus sp. (ASC 4). © Ifremer
Fig. 101. Photograph taken by the ‘the Nautile’ during the NIXONAUT cruise: nodule-facies C, fish Ophidiidae Barathrites sp. (POI 14). © Ifremer

Fig. 102. Photograph taken by the ‘the Nautile’ during the NIXONAUT cruise: nodule-facies C, fish Bathysaurus mollis (POI 17). © Ifremer

Fig. 103. Photograph taken by the ‘the Nautile’ during the NIXONAUT cruise: fish Macrouridae Nematonurus sp. (POI 1) attracted by activity. © Ifremer

Fig. 104. Photograph taken by the ‘Épaulard’ at NIXO 45 site: nodule-facies C, fish Brotulidae Typhlonus nasus (POI 13). © Ifremer

Fig. 105. Photograph taken by the ‘Épaulard’ at NIXO 45 site: nodule-facies C, fish Macrouridae Coryphaenoides armatus or C. yaquinae (POI 2). © Ifremer

Fig. 106. Photograph taken by the ‘R.A.I.E.’ at NIXO 45 site: nodule-facies C, fish Synaphobranchidae (POI 8).
## Appendix 2

**LIST OF CODES BASED ON THE CLASSIFICATION OF PARKER (1982)**

<table>
<thead>
<tr>
<th>Code</th>
<th>Taxon Name</th>
<th>Subphylum/Suborder/Order/Class/Subclass/Phylum</th>
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<td>Sponges, Phyl. Porifera</td>
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<td>Hydrooids, O. Hydroidea, Cl. Hydrozoa, Phyl. Cnidaria</td>
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<td>Siphonophores, O. Siphonophora, Cl. Hydrozoa, Phyl. Cnidaria</td>
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<td>Octocorallarians, O. Gorgonacea and O. Pennatulacea, Cl. Anthozoa, Phyl. Cnidaria</td>
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<td>Ctenophorans, Phyl. Ctenophora</td>
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<td>Fish, Cl. Osteichthya, Subphyl. Vertebrata, Phyl. Chordata</td>
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## Appendix 3

### LIST OF INTERNATIONAL SPECIALISTS CONSULTED

<table>
<thead>
<tr>
<th>Phylum PROTOZOA</th>
<th>Cl. Xenophyophorea</th>
<th>A. Gooday</th>
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<tr>
<td></td>
<td>O. Kamenskaya</td>
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<td>Phylum PORIFERA</td>
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<td>J. Vacelet</td>
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<td>Fr., Endume</td>
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| 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 | Germany |
|                | O. Gorgonacea  | M.J. d’Hondt | Fr., Muséum |
|                | O. Pennatulacea | M. Opresko | E.U. |
|                | subcl. Zoantharia | D. Doumenc | (Fr., Muséum) |
|                | O. Actinaria   | D. Fautin  | E.U. |
|                | K. Riemann-Zürneck |          | Germany|
|                | M. Sokolova    |          | Russian Federation|
|                | O. Zezina      |          | Russian Federation|
|                | H. Zibrowius   |          | (Fr., Endume) |
|                | O. Scleractinia | H. Zibrowius | Fr., Endume |
|                | O. Antipatharia | M. Grasshoff | 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 |          | Germany|
|                | H. Zibrowius   |           | Fr., Endume|

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<thead>
<tr>
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<th>C. Carré</th>
<th>Fr., Villefranche s/mer</th>
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### Phylum ANNELEIDA

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### Phylum ECHIURA

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### Phylum MOLLUSCA

#### Class Bivalvia

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<td>A. Waren</td>
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<tr>
<td>C. Poizat</td>
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<td>R. Turner</td>
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#### Class Cephalopoda

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<tr>
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<td>M. NIXOn</td>
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<td>T. Okutani</td>
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### Phylum ARTHROPODA

#### Subphylum CHELICERATA

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#### Subphylum CRUSTACEA

#### Order Peracarida

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<td>M. Türkay</td>
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#### Order Cumacea

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## COMPARISON OF THE TAXONOMIC RICHNESS OF THE STUDY AREA WITH THE ABYSSAL ZONE OF THE WORLD'S OCEANS

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**COMPARISON OF THE TAXONOMIC RICHNESS OF THE STUDY AREA WITH THE ABYSSAL ZONE OF THE WORLD'S OCEANS**
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<td>F. Chlorophthalmidae</td>
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<td>O. Gadiformes</td>
<td>F. Zoarcidae</td>
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<td>O. Beryciformes</td>
<td>F. Aphyonidae</td>
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<td>O. Scorpaeniformes</td>
<td>F. Stephanoberycidae</td>
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<td>F. Liparidae</td>
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## Appendix 5

### Classification of the Abyssal Suprabenthic Megafauna According to Trophic and Functional Groups

#### Suspension feeders group

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<td><strong>PORIFERA</strong></td>
<td>38 Taxons</td>
<td>Barnes, 1968; Bergquist, 1978; Brien et al., 1973; Hartman, 1982; Jørgensen, 1986</td>
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<tr>
<td><strong>CNIDARIA</strong></td>
<td>9 taxons</td>
<td>O. Corallimorpharia, F. Nectactis singularis</td>
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<tr>
<td></td>
<td>1 taxon</td>
<td>O. Actinaria, F. Actinostolidae Actinostola sp.</td>
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<td></td>
<td>10 taxons</td>
<td>F. Actinidae</td>
<td>1 taxon</td>
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<td></td>
<td>15 taxons (dont 3 taxons ambivalents suspens/détrit/carnivo re)</td>
<td>Riemann-Zürneck (com. pers.)</td>
<td>(dont 3 taxons ambivalents suspens/détrit.)</td>
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<tr>
<td><strong>ANnelida</strong></td>
<td>1 taxon</td>
<td>Cl. Polychaeta, O. Sabellida, F. Sabellariidae</td>
<td>2 taxons</td>
<td></td>
</tr>
<tr>
<td></td>
<td>1 taxon</td>
<td>O. Terebellida, F. Sabellariidae</td>
<td></td>
<td></td>
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<tr>
<td></td>
<td>1 taxon</td>
<td>O. Capitellida, F. Malacidae</td>
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<tr>
<td></td>
<td>(ambivalent suspens/détrit.)</td>
<td>Heezen et Jumars, 1974; Fauchald et Jumars, 1979; Jumars et Fauchald, 1977</td>
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<tr>
<td><strong>MOLLUSCA</strong></td>
<td>2 taxons</td>
<td>Cl. Bivalvia, O. Veneroida, F. Vesicomyidae</td>
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### Classification of the Abyssal Suprabenthic Megafauna by Trophic and Functional Groups

#### Suspension feeders group

<table>
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<tr>
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<tr>
<td>BRACHIOPODA</td>
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<td>O. Rhyynchonellida, O. Terebratulida Zavina, 1975.</td>
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<th>Mobiles</th>
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<tr>
<td>ECHINODERMATA</td>
<td>Cl. Crinoidea, O. Comatulida, superF. Antedonaceae, F. Antedonidae Meyer, 1982.</td>
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<td></td>
<td>Cl. Stelleroidea, subcl. Asteroidea, O. Forcipulata, F. Brisingidae principalement suspensivore Carey, 1972</td>
<td>3 taxa</td>
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<tr>
<td>CHORDATA</td>
<td>4 taxa</td>
<td>Cl. Asciacea, O. Stolidobranchia, F. Pyuridae, F. Molgulidae incertae sedis Jørgensen, 1966; Monnot et Monnot, 1975</td>
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## Classification of the Abyssal Suprabenthic Megafauna by Trophic and Functional Groups

### Detritus feeders group

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<th>Taxonomic identification and bibliographic references</th>
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<tr>
<td><strong>Annelida</strong>&lt;br&gt;Cl. Polychaeta, O. Capitellidae, F. Maldanidae&lt;br&gt;O. Cirratulida, F. Cirratulidae&lt;br&gt;Fauclaud et Jumars, 1979</td>
<td>1 taxon (ambivalent détrit./suspend.)&lt;br&gt;1 taxon</td>
<td><strong>Annelida</strong>&lt;br&gt;Cl. Polychaeta, O. Terebellidae, F. Terebellidae (peuvent quitter leurs tubes)&lt;br&gt;Fauclaud et Jumars, 1979.&lt;br&gt;(ambivalents détrit./nécroph.). O. Phyllophoridae, F. Polynoidae&lt;br&gt;F. Aphroditidae&lt;br&gt;F. Tomopteridae&lt;br&gt;F. Hesionidae&lt;br&gt;Fauclaud et Jumars, 1979; Jumars et Fauclaud, 1977;</td>
<td>1 taxon ambivalent (sédentaire/mobile) 6 taxons (ambivalents détrit./nécroph.)</td>
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<td><strong>Echiura</strong>&lt;br&gt;O. Echiuroidea, F. Bonelliidae&lt;br&gt;Datta Gupta, 1961; Dawydoff, 1959; Jaccarini et Schembri, 1977;&lt;br&gt;Ohta, 1984; Zenkevitch, 1966</td>
<td>6 taxons</td>
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<tr>
<td><strong>Sipuncula</strong>&lt;br&gt;F. Golfingiidae, F. Sipunculidae&lt;br&gt;Cutter et Cutler, 1980; Romero-Wetzel, 1987; Thomson, 1980;&lt;br&gt;Vinogradov, 1953.</td>
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## Classification of the Abyssal Suprabenthic Megafauna by Trophic and Functional Groups

### Detritus Feeders Group

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<td><strong>Mollusca</strong></td>
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<td>- Cl. Gasteropoda, O. Archaeogastropoda</td>
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<td>- Cl. Scaphopoda, F. Entalididae</td>
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<td><strong>Arthropoda</strong></td>
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### Detritus feeders group

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<th>Taxonomic identification and bibliographic references</th>
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<tr>
<td><strong>ECHINODERMATA</strong>&lt;br&gt;- (occasionnellement) Cl. Stelleroidea,&lt;br&gt;subcl. Ophiuroidea, subO. Gnathophiurina, F. Amphiuridae&lt;br&gt;subO. Chilophiurina, F. Ophiuridae&lt;br&gt;Paterson et al., 1985.</td>
<td>2 taxons</td>
<td><strong>HSEMICHORDATA</strong>&lt;br&gt;Cl. Enteropneusta, F. Ptychodermidae&lt;br&gt;Mauviel et al., 1986; Romero-Wetzel, 1989.</td>
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<td>- Cl. Echinoidea, O. Diadematidae, F. Aspidodiadematidae&lt;br&gt;O. Spatangoidea, F. Aeropsidae&lt;br&gt;David et Sibuet, 1985; De Ridder et Lawrence, 1982</td>
<td>2 taxons</td>
<td>- Cl. Enteropneusta, F. Spengelidae, F. Ptychodermidae&lt;br&gt;F. Harrimanidae&lt;br&gt;Bourne et Heezen, 1968.</td>
<td>3 taxons</td>
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<td>- Cl. Stelleroidea, O. Paxillosida, F. Porcellenasteridae,&lt;br&gt;F. Benthopsectinidae&lt;br&gt;O. Spioulosida, F. Pterasteridae&lt;br&gt;O. Forcipulata, F. Zoroasteridae&lt;br&gt;Carey, 1972; Jangoux, 1982; Madsen, 1961; Sloan, 1980;</td>
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# Classification of the Abyssal Suprabenthic Megafauna by Trophic and Functional Groups

## Carnivores/Scavengers mobiles group

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<td>Omori et Vervoort, 1986</td>
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<td>O. Trachylina</td>
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<td>Barnes, 1968</td>
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<td>O. Siphanophora</td>
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<td>Barnes, 1968</td>
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<td>- Cl. Anthozoa, O. Ceriantharia</td>
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<td>Tifon, 1987</td>
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<td>O. Actinaria (occasionnellement comportement opportuniste),</td>
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<td><em>Actinoscyphia sp.</em>, <em>Phellicactis sp.</em>, <em>Sicyonis tuberculata</em></td>
<td>(suspens./détritiv./carniv.)</td>
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<td>Aldred et al., 1979; Lampitt et Paterson, 1987; Riemann-Züneck, 1978; van Praet, 1985</td>
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<td>Barnes, 1968</td>
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<td>O. Mesogasteropoda, F. Pterotacheidae</td>
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<td>O. Neogasteropoda, F. Turridae</td>
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<td>Bouchet et Warren, 1980; Taylor et al., 1980</td>
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<td>- Cl. Cephalopoda, subcl. Coleoidea, O. Octopoda, subO. Cirrata</td>
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<td>Aldred et al., 1978, 1983; Nixon, 1986; Robson, 1930; Roper et Brunage, 1972; Scott, 1910;</td>
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<td>subO. Incirriata, F. Octopodidae</td>
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<td>Roper et Brunage, 1972; Voss, 1967, 1985</td>
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<td><strong>ANNELEIDA</strong></td>
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<td>F. Tomopteridae</td>
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<td>F. Hesionidae</td>
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<td>Fauchald et Jumars, 1979; Jumars et Fauchald, 1977</td>
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### Carnivores/Scavengers mobiles group

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<td><strong>ARTHROPODA</strong></td>
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<td>- Cl. Crustacea, sup O. Pericarida, O. Tanaidacea <em>Pseudotanais</em> sp.</td>
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<td> Thistle et Wilson, 1987; Wilson, 1983</td>
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<tr>
<td> O. Amphipoda, F. Lysianassidae, F. Gammaridae</td>
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<td> O. Decapoda natantia</td>
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<tr>
<td> Lampitt et Burham, 1983; Fiese, 1981; Sokolova, 1957</td>
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<tr>
<td> O. Decapoda reptantia</td>
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<tr>
<td><strong>- Cl. Pycnogonida, F. Colossendeidae</strong></td>
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<tr>
<td> F. Phoxichiliidiidae</td>
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<tr>
<td> Stock, 1978a, 1978b, 1984</td>
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<td><strong>CHORDATA</strong></td>
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<tr>
<td>- subph. Tunicata : la classe des Sorberacea s’est adaptée à un régime carnivore</td>
<td>4 taxons</td>
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<td> Braconnier, 1970</td>
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<td>- subph. Vertebrata, Cl. Osteichthyes</td>
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# Appendix 6

## LIST of IOC Technical Series

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<td>Time-Series of Ocean Measurements. Vol. 3. 1986</td>
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<td>Summary of Radiometric Ages from the Pacific. 1987</td>
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<td>Tsunami Glossary - A Glossary of Terms and Acronyms Used in the Tsunami Literature. 1991</td>
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<td>IG0SS Plan and Implementation Programme 1996-2003. 1996</td>
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<td>Peace in the Oceans: Ocean Governance and the Agenda for Peace, the Proceedings of Pacem in Maribus XXIII, Costa Rica, 1995. 1997</td>
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<td>Neotectonics and fluid flow through seafloor sediments in the Eastern Mediterranean and Black Seas - Parts I and II. 1997</td>
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<td>Cold water carbonate mounds and sediment transport on the Northeast Atlantic Margin. 1998</td>
<td>E only</td>
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<td>Geological Processes on the Northeast Atlantic Margin (8th training-through-research cruise, June-August 1998). 1999</td>
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<td>Ad hoc Benthic Indicator Group - Results of Initial Planning Meeting, Paris, France, 6-9 December 1999. 2000</td>
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<td>Bruun Memorial Lectures, 2001: Operational Oceanography – a perspective from the private sector. 2001</td>
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<td>59</td>
<td>Monitoring and Management Strategies for Harmful Algal Blooms in Coastal Waters. 2001</td>
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