UNIVERSITÉ DU QUÉBEC À MONTRÉAL

ANALYSE DE LA DISTRIBUTION SPATIALE DE LA FAUNE ASSOCIÉE AUX NODULES POLYMÉTALLIQUES EN FONCTION DES FACTEURS ENVIRONNEMENTAUX EN MILIEU OCÉANIQUE PROFOND

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AVANT-PROPOS

Ce mémoire de maîtrise a été rédigé sous forme de deux articles scientifiques (Chapitre II et Chapitre III) qui seront soumis à la revue *Deep-Sea Research I.* D'autres auteurs ont participé à la rédaction de ces articles (voir chacun des articles pour l'énumération de ceux-ci). La mise en forme de ces deux articles respecte les exigences de cette revue. Le catalogue de la faune associée aux nodules polymétalliques (Chapitre I) sera soumis comme matériel supplémentaire avec l'article présenté au Chapitre II. Les références citées dans la préface du catalogue sont placées à la fin de cette préface et une liste de références est incluse dans la description de chaque taxon lorsque des références y sont citées. Le catalogue est également disponible électroniquement à julie.veillette.2@ulaval.ca. Par conséquent, les chapitres I, II, III et les appendices C et D sont écrits dans la langue anglaise. Pour chacun des articles, les figures et tableaux cités ont été placés à la suite des références, comme le demande la revue *Deep-Sea Research I.* Les références pour l'introduction et la conclusion sont placées à la toute fin du mémoire.

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RÉSUMÉ

La faune associée aux nodules polymétalliques demeure toujours méconnue même si les communautés associées à ce substrat dur sont répandues dans les grands fonds marins. L'exploitation des nodules, pour être rentable économiquement, devra être réalisée à grande échelle et par conséquent, produira un impact considérable sur la faune qui y est associée. Ce projet de mémoire porte sur l'analyse de la distribution spatiale de la faune associée aux nodules polymétalliques en fonction des facteurs environnementaux (courants près du fond, chimie de l'eau, substrat «nodule» et production primaire de surface) en milieu marin profond dans la zone Clarion-Clipperton située entre 7°N et 18°N de latitude et entre 157°W et 118°W de longitude. Trois échelles spatiales sont considérées pour cette étude: l'échelle régionale (latitude) représentant les deux zones explorées, soit la zone est située à 14°N, 130°W et la zone ouest située à 9°N, 150°W, l'échelle locale représentée par quatre types de faciès géologiques différents et la micro-échelle (le nodule). Afin d'analyser la distribution spatiale de la faune à l'échelle régionale et locale, la faune associée à 235 nodules, échantillonnés à l'aide d'un carottier USNEL ou du submersible français *Nautile*, a été examinée. Les nodules des faciès B et C échantillonnés à l'aide du submersible étaient plus gros que ceux récoltés avec le carottier. Néanmoins, ces différences de taille attribuées à la méthode d'échantillonnage sont très petites et ne contribuent pas à expliquer les différences de faune observées. 90 taxons associés à la surface des nodules ont été décrits: 73 protozoaires et 17 métazoaires. La faune recouvrait en moyenne 3% de la surface du nodule et ce, jusqu'à un maximum de 18%. La richesse des espèces augmentait avec la surface du nodule et ce, à l'échelle régionale et locale. Il n'y avait pas de relation entre le pourcentage de couverture et la surface estimée du nodule. Quelques différences statistiques entre les faciès ont été observées dans la distribution des espèces mais les faciès ne semblent expliquer qu'une petite portion de la variance totale. Enfin, la production primaire de surface est l'unique facteur environnemental considéré variable à l'échelle régionale, la zone est recevant un flux plus élevé de matière organique particulaire. Ceci pourrait contribuer à expliquer la plus grande richesse des espèces ainsi que le plus grand pourcentage de couverture par la faune observés dans la zone est. L'étude à la micro-échelle a montré que l'hétérogénéité des habitats, créée par les mamelons, ainsi que la texture de la surface des nodules pourraient influencer la distribution spatiale de la faune associée aux nodules.

Mots clés: Nodules polymétalliques, faune associée aux nodules, foraminifères agglutinants, distribution spatiale, facteurs environnementaux, impacts environnementaux

INTRODUCTION

Sujet de recherche

Mon projet de recherche porte sur l'analyse de la distribution spatiale de la faune associée aux nodules polymétalliques en fonction des facteurs environnementaux (courants près du fond, chimie de l'eau, substrat «nodule»et production primaire de surface) en milieu marin profond dans la zone Clarion-Clipperton située entre 7°N et 18°N de latitude et entre 157°W et 118°W de longitude. Trois échelles spatiales ont été considérées pour cette étude: l'échelle régionale (latitude) représentant les deux zones explorées, soit la zone est située à 14°N, 130°W et la zone ouest située à 9°N, 150°W (Fig. i), l'échelle locale représentée par quatre types de faciès géologiques différents et la micro-échelle (le nodule).

Ce projet s'insère dans un projet d'étude global de l'état de référence des zones à nodules françaises. Celui-ci est exigé par l'Autorité internationale des fonds marins (ISA) de tous les pays qui possèdent une zone d'exploration de nodules, dont la France fait partie (Fig. i). La campagne NODINAUT (NOdules-Diversité-NAUTile), qui a eu lieu du 18 mai au 27 juin 2004, a permis la réalisation de ce projet. Étant donné une éventuelle possibilité d'exploitation des nodules et l'impact potentiel que pourrait avoir une telle activité sur les organismes benthiques, il est primordial d'acquérir des connaissances de base sur l'état naturel des communautés associées à ces substrats durs ainsi que sur les caractéristiques de leur habitat. Alors que la faune de substrat meuble de l'océan profond a reçu une attention considérable de la part des écologistes, peu d'études se sont intéressées aux communautés de substrats durs avant la découverte des sources hydrothermales en 1977. L'approche écologique développée au cours de ce projet sera applicable au suivi d'autres communautés benthiques profondes qui risquent d'être affectées par les activités anthropogéniques.

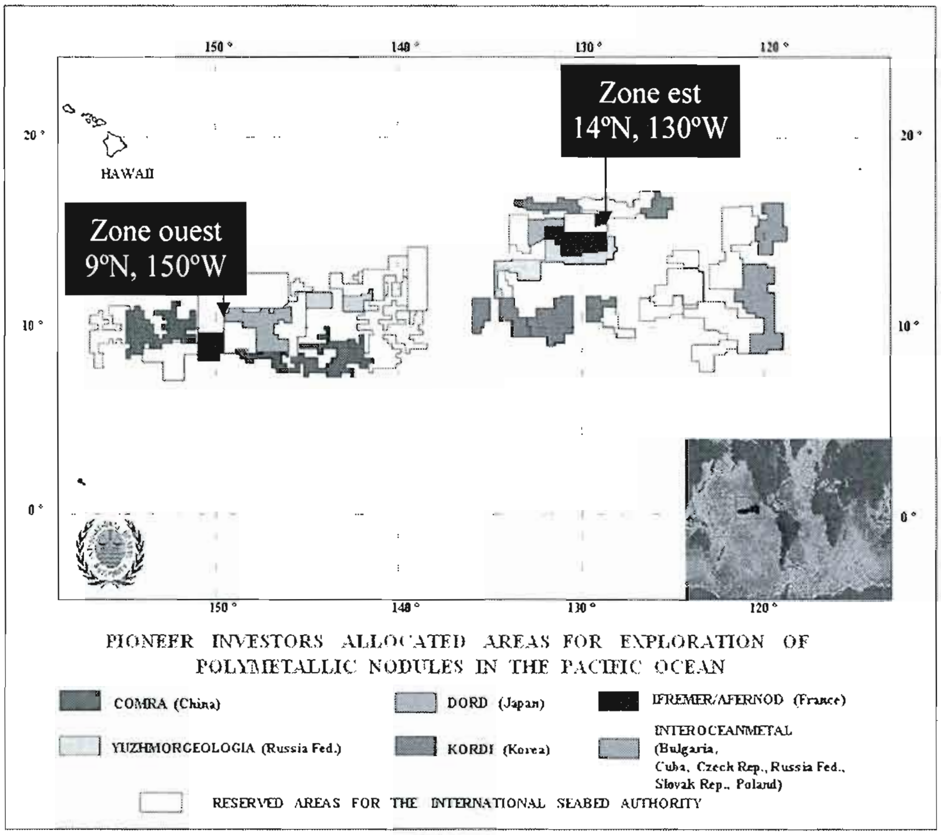

Figure i. Carte de l'océan Pacifique Nord Est indiquant les deux zones explorées lors de la campagne NODINAUT ainsi que les zones attribuées aux « investisseurs pionniers ».

Les nodules polymétalliques

Les nodules polymétalliques sont de petites boules de couleur brun-noir légèrement aplaties de 5 à 15cm de diamètre qui reposent sur le fond de la mer principalement entre 4000 et 6000m de profondeur. Ils sont composés de cuivre, de nickel, de cobalt, de fer et de manganèse en concentrations diverses. Les nodules ont été découverts en 1868 dans la mer de Kara et l'expédition britannique du H.M.S. *Challenger* autour du monde de 1873 à 1876 répertoriait des nodules dans tous les océans (Mero, 1972; Murray et Renard, 1891). La surface des fonds marins tapissée de nodules est estimée à 46 millions de km^2 (Glover et Smith, 2003), ce qui représente environ 15% des fonds marins (situés à plus de 1000m de profondeur) de tous les océans. Mero (1972) fut le premier à cartographier des fonds marins tapissés de nodules et ce, pour des fins économiques plutôt que scientifiques (Hoffert, pers.comm.).

Figure ii. Coupe transversale d'un nodule polymétallique.

Les nodules sont formés de la lente précipitation des éléments métalliques dissous dans l'eau de mer autour d'un noyau dur, tel une dent de requin ou un fragment lithique. Découpés en section, la plupart des nodules apparaissent formés de couches concentriques, comme un oignon (Fig. ii). Celles-ci correspondraient à des phases successives de croissance. Les deux principaux types de croissance des nodules sont: l'accrétion hydrogénée des éléments métalliques présents dans l'eau de mer et l'accrétion diagénétique d'éléments métalliques de l'eau interstitielle des sédiments (Halbach, *et al.*, 1988; Skornyakova et Murdmaa, 1992). Le concrétionnement serait favorisé par l'activité biologique de certains micro-organismes (Bignot et Lamboy, 1980; Dudley, 1978; Dudley et Margolis, 1974; Dugolinsky, 1976; Dugolinsky, *et al.*, 1977; Ehrlich, 1972; Graham et Cooper, 1959; Greenslate, *et al.*, 1974; Riemann, 1983; Riemann, 1985; Thiel, 1978; Thiel, *et al.*, 1993; von Stackelberg, 1984; Wendt, 1974). La vitesse de croissance des nodules est très lente (de l'ordre de quelques millimètres par million d'années) et suivrait un rythme irrégulier (Heye, 1978). De plus, des conditions de faible sédimentation, loin des apports terrigènes, semblent essentielles à leur formation (Horn, *et al.*, 1972a; Skornyakova et Murdmaa, 1992; von Stackelberg et Beiersdorf, 1991). L'accumulation des sédiments dans les zones à nodules (de l'ordre de 3mm par 1000 ans dans la zone de Clarion-Clipperton (Hoffert, pers.comm.)) est de trois ordres de grandeur plus rapide que leur croissance (Guichard, *et al.*, 1978). Or, les nodules demeurent à la surface des sédiments. La bioturbation créée par les mouvements de la mégafaune pour se déplacer ou s'alimenter dans ces zones présenterait l'explication la plus plausible de ce phénomène (von Stackelberg, 1984). Enfin, les nodules sont principalement présents sous la profondeur de compensation des carbonates (Skornyakova et Murdmaa, 1992). Cette dernière condition assure que les carbonates soient dissous avant qu'ils ne sédimentent. Ainsi, les nodules sont associés le plus souvent à des vases siliceuses (Skornyakova et Murdmaa, 1992). La région comprise entre les fractures de Clarion et de Clipperton dans le Pacifique Nord Est, entre 7°N et 18°N de latitude et 157°W et 118°W de longitude, présente la plus grande densité de nodules répertoriée connue. Par conséquent, cette région est la plus intéressante économiquement et elle est la plus explorée (Fig. i) (Horn, *et al.*, 1972b; Mero, 1972; Morgan, *et al.*, 1999).

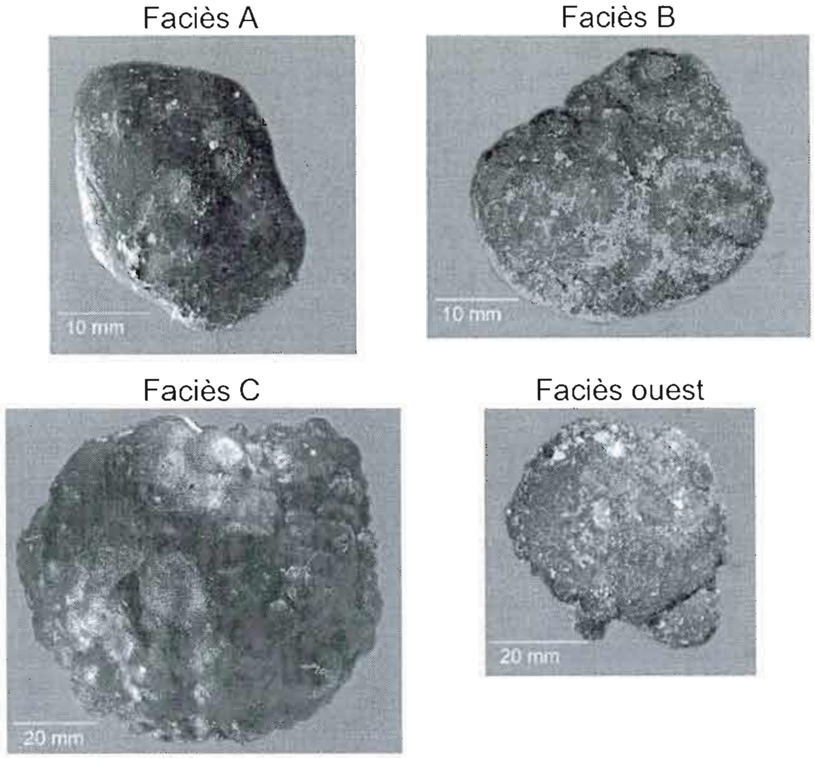

Figure iii. Vue de haut d'un nodule de chacun des faciès explorés.

La classification des faciès à nodules adoptée dans cette étude s'inspire de celle proposée par Hoffert et Saget (2004) et s'appuie principalement sur l'observation des nodules. Ces faciès sont identifiés selon quelques paramètres: la forme générale (régulière ou irrégulière), la taille (petit: moins de 5cm de longueur; moyen: entre 5 et 10cm de longueur; gros: plus de 10cm de longueur), l'aspect de la surface (lisse, rugueuse ou mamelonnée) et la relation avec leur environnement (s'ils sont enfouis ou non dans les sédiments et la topographie du fond). Trois faciès (A, B, et C) étaient distingués dans la zone est (Fig. iii). Brièvement, le faciès A se compose de petits nodules lisses accolés les uns aux autres de formes irrégulières, reposant sur le sédiment de pentes peu inclinées. Le faciès B présente des nodules ovoïdes de petites et moyennes tailles, de texture variant entre lisse et rugueuse, et enfouis légèrement dans le sédiment des plaines abyssales. Enfin, le faciès C est formé de moyens et de gros nodules, lisses et rugueux par endroits, mamelonnés avec un bord équatorial très net jusqu'où ils sont enfoncés dans les sédiments des plaines abyssales. La zone ouest, quant à elle, était tapissée de nodules ne correspondant à aucun des faciès décrits. Les nodules y sont de petites et moyennes tailles, de formes irrégulières, de textures très variées et sont enfouis dans le sédiment. Ce faciès est nommé « faciès ouest » dans cette étude (Fig. iii). Il est intéressant de constater qu'il existe des relations entre la morphologie et la composition chimique des nodules (Skornyakova et Murdmaa, 1992). En général, les nodules reposent sur des sédiments de boues non consolidées à très faible résistance mécanique et à forte teneur en eau (Paul, 1976; Piper et Fowler, 1980). Chaque faciès se distribue séparément sur le fond (Fig. iv) et recouvre des centaines de mètres carrés selon différentes densités, exprimées en pourcentage de couverture des fonds marins ou en kilogramme par mètre carré. Actuellement, parmi tous les endroits tapissés de nodules dans les océans, seulement les fonds marins de la zone est du permis minier français (Fig. i) sont cartographiés (Hoffert, pers.comm.).

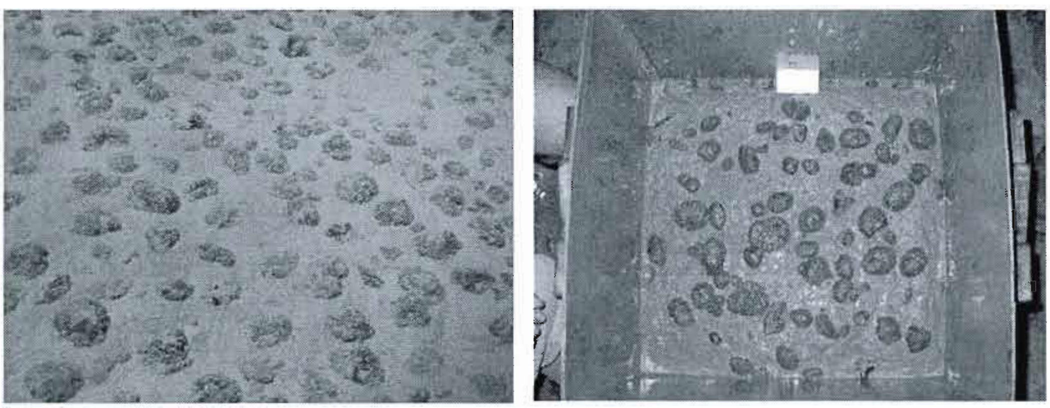

Figure iv. A) Des nodules du facies C tapissant les sédiments. B) Des nodules du faciès ouest à la surface d'un carottier USNEL.

La protection des ressources naturelles

Avec l'avènement de l'ère industrielle, les habitants des pays riches ont redéfini leur notion de besoin. Désormais, on exige de vivre dans le confort et l'abondance. De plus, les progrès technologiques ainsi que les moyens de communication permettent, pour l'instant, d'augmenter de façon régulière l'offre de biens et de services. Cette offre croissante augmente la demande des consommateurs, qui elle-même fait augmenter l'offre et ainsi de suite. Présentement, on peut affirmer indubitablement que la société occidentale en est une de consommation et même de surconsommation.

Or, cette consommation effrénée entraîne une exploitation des ressources naturelles terrestres et côtières comme jamais auparavant. Aussi, l'augmentation exponentielle de la population mondiale ainsi que les progrès technologiques accentuent les pressions exercées sur ces environnements.

L'exploitation des ressources des fonds marins

Les océans recouvrent 70 % de la surface de la Terre et les grands fonds marins, situés à plus de 1000m de profondeur en occupent 60% (Glover et Smith, 2003; Thiel, 2001). Ils représentent donc l'habitat le plus répandu sur la planète (Ahnert et Borowski, 2000; Brunn, 1956). De la base des continents jusqu'à plus de 11 000m de profondeur dans la fosse des Mariannes, les abysses abritent de nombreuses richesses, dont plusieurs restent inconnues. Depuis une cinquantaine d'années, l'industrie, aidée des avancements de la technologie, s'intéresse à l'exploration et à l'exploitation de cet environnement (Thiel, 2001). À l'heure actuelle, l'exploitation pétrolière offshore, la pêche et les développements biotechnologiques à partir d'organismes marins sont les principales ressources exploitées des fonds marins (Glover et Smith, 2003; Guilloux et Zakovska, 2004; Thiel, 2001). Les hydrates de gaz pourraient l'être également d'ici une dizaine d'années (Sarrazin, 2002). De plus, des nodules polymétalliques risquent d'être extraits des fonds marins dans un futur prochain (Glover et Smith, 2003). L'utilisation des fonds marins comme dépotoir permanent (munitions, rejets radioactifs, structures de toutes sortes et séquestration de carbone) et les changements climatiques (Danovaro, *et al.*, 2004) représentent aussi des menaces imminentes pour le milieu marin profond (Glover et Smith, 2003; Sarrazin, 2002; Thiel, 2001). Toutes ces activités doivent être réalisées à grande échelle afin d'être rentables, accentuant l'importance des impacts environnementaux potentiels (Thiel, 2001). Aussi, cet environnement est particulièrement vulnérable aux activités anthropogéniques. Cependant, son aspect lointain entrave la perception que les activités humaines peuvent l'influencer et engendrer des impacts à long terme. De plus, comme ces zones sont inhabitées, il est difficile d'avancer des arguments éthiques pour leur protection (Thiel, 2001). Malgré tout, l'immensité et l'accès limité des grands fonds marins y ont sans doute limité les impacts anthropogéniques. Comparativement à d'autres écosystèmes, les grands fonds marins demeurent encore peu influencés par les activités humaines (Glover et Smith, 2003).

Les nodules polymétalliques ont attiré l'intérêt des investisseurs dans les années 1960 pour leur important potentiel économique. Ils sont riches en métaux comme le cuivre, le nickel, le cobalt et le manganèse, ce dernier étant toutefois un métal moins précieux que les trois autres (Mero, 1972). À cette époque, la menace de l'épuisement des ressources terrestres en métaux a motivé la recherche de solutions alternatives (Glasby, 2002). Plusieurs pays industrialisés comme la France, l'Allemagne, les États-Unis, l'ancienne Union Soviétique et le Japon ont alors examiné les possibilités d'extraction des nodules des fonds marins (Glasby, 2002). Or, la baisse des prix des métaux, les demandes des pays en développement pour un accès équitable aux ressources, les défis technologiques pouvant permettre l'exploitation ainsi que des pressions importantes pour protéger l'océan profond ont agi comme des obstacles à la concrétisation de cette exploitation à brève échéance (Glasby, 2002; Sarrazin, 2002). Malgré cela, les recherches se poursuivent sur ces étonnantes boules ainsi que sur l'impact environnemental d'une éventuelle exploitation. L'intérêt économique de certains métaux contenus dans les nodules demeure d'actualité. Notamment, le cobalt est considéré comme un métal stratégique parce qu'il est essentiel à l'industrie de l'aéronautique et de la haute technologie (Glover et Smith, 2003). Aussi, le Japon, la Chine, la Corée et l'Inde s'intéressent désormais à l'exploitation des nodules afin de combler leurs besoins en métaux stratégiques puisqu'une pénurie déstabiliserait leur économie (Glasby, 2002).

Actuellement, plusieurs méthodes d'extraction de nodules des fonds marins sont proposées. L'une d'elles est celle d'un collecteur à nodules de la taille d'un wagon de train se baladant sur chenilles, à la manière d'un char d'assaut. Les nodules seraient concassés au fond afin de faciliter leur transport vers la surface jusqu'à un navire (Ifremer, 2003; Lenoble, 1996; Morgan, *et al.*, 1999). Les impacts environnementaux envisageables d'une telle exploitation sont, entre autres, des rejets de boues en profondeur et en surface, à partir du navire ou d'une plate-forme (Thiel et Tiefsee-Umweltschutz, 2001).En se redéposant sur le fond, ces rejets pourraient entraîner des perturbations plus ou moins graves dans les écosystèmes (Sharma, *et al.*, 2001). De plus, le transport des nodules jusqu'au port où sont situées les installations de traitement, ainsi que leur traitement métallurgique, pourraient engendrer des impacts environnementaux non négligeables (Morgan, *et al.*, 1999). Évidemment, comme la croissance des nodules est extrêmement lente, les fonds marins desquels seraient extraits ces nodules pourraient prendre des millions d'années à se régénérer. Ainsi, puisque les subtrats durs (autres que les nodules) sont extrêmement rares et dispersés dans les fonds marins et que la faune qui y est associée diffère de celle qui colonise les sédiments, on pourrait observer des extinctions locales de la faune associée aux nodules (Bussau, *et al.*, 1995; Mullineaux, 1987; Thiel et Tiefsee-Umweltschutz, 2001). Deux programmes de recherche ont étudié les impacts environnementaux potentiels de l'exploitation des nodules sur les communautés benthiques: le programme allemand DISCOL (« Disturbance and Recolonisation Experiment in a Manganese Nodule Area of the Deep South Pacific Ocean ») et BIEs (« Benthic Impact Experiments ») qui impliquaient les États-Unis, le Japon, l'« Interoceanmetal Joint Organization » et l'Inde (Ahnert et Borowski, 2000). Évidemment, les prédictions des impacts environnementaux de l'exploitation des nodules sur les communautés benthiques sont limitées par le manque d'information sur l'écologie des espèces (alimentation, dynamique des populations, dispersion des larves, relations trophiques, etc.) ainsi que par un effort d'échantillonnage insuffisant dans cet écosystème (Jumars, 1981). De plus, les moyens technologiques utilisés pour extraire les nodules des sédiments et les remonter à la surface influenceront ces impacts (Bardach, 1990). Néanmoins, Morgan et al. (1999) suggèrent que les impacts environnementaux de l'exploitation minière des grands fonds marins seraient moindres que ceux estimés pour une exploitation terrestre des mêmes métaux à ciel ouvert dans une région tropicale (l'endroit le plus probable pour l'ouverture de nouvelles mines). Il faudra toutefois s'assurer que l'exploitation des nodules est véritablement moins polluante que les mines terrestres et que ce n'est pas parce que ces zones sont plus « déconnectées » de notre réalité « terrestre » qu'elles sont prisées.

Contexte économique

L'exploitation de cette ressource minière devrait être économiquement rentable pour être réalisable. Parmi les facteurs qui influenceront la rentabilité de l'exploitation des nodules se trouvent: leur concentration sur les fonds marins, leur distribution de tailles, leur concentration en métaux précieux (manganèse, cuivre, nickel et cobalt), les caractéristiques physiques des sédiments avoisinants, la profondeur de l'eau, la topographie des fonds marins ainsi que la distance de la terre et des usines de traitement (Halbach, *et al.*, 1988; Mero, 1972). En effet, l'ensemble des moyens nécessaires à leur exploitation et à leur commercialisation est à considérer. L'extraction de cette ressource devra, pour être rentable, être organisée à grande échelle, impliquant de grandes quantités de nodules exploités et transportés, avec des moyens techniques importants créant ainsi des impacts à long terme sur l'écosystème (Thiel, 2003).

Entre 1984 et 1988, l'Ifremer (France) réalisa GEMONOD, une étude préliminaire de rentabilité. Cette dernière conclut que l'exploitation des nodules serait économiquement comparable à celle des minerais terrestres qui contiennent les mêmes métaux. Cependant, les contraintes d'extraction de la ressource sont importantes et demanderont l'élaboration de moyens technologiques novateurs. Pour l'instant, l'exploitation des nodules présente donc des risques et des coûts non négligeables qui doivent être minimisés. L'exploitation de cette ressource ne sera rentable que lorsque les prix des métaux retrouveront les cours des années 1970. Les perspectives économiques permettent d'envisager une rentabilité au moment où l'épuisement progressif des gisements de nickel entraînera une tension sur le marché et l'élévation durable du prix de ce métal. D'ici là, on peut aussi prévoir l'apparition de nouvelles techniques d'exploration et d'exploitation (Ifremer, 2003).

Les bénéfices de l'exploitation des nodules ne se limitent pas à la valeur des métaux. En fait, plusieurs autres bénéfices sont envisagés: revenus aux gouvernements sous forme de taxes, contributions des industries d'approvisionnement (études géophysiques, oléoducs), utilisation ultime des métaux (transport, électricité), application des nouvelles technologies développées à d'autres industries. Finalement, il ne faut pas négliger les bénéfices intangibles à la société comme l'avancement des connaissances (Cruickshank, 1972).

Contexte légal et politique

L'exploitation des ressources des grands fonds marins situées au milieu des océans dans des territoires de juridiction internationale, à l'extérieur des zones économiques exclusives de 200 milles nautiques, risque d'entraîner des problèmes uniques et sans précédent au niveau légal (Nordquist, 1972). En 1970, l'Assemblée générale des Nations Unies adopte une déclaration de principe constituant « patrimoine commun de l'humanité » le fond des mers et des océans ainsi que leur sous-sol au-delà des limites des juridictions nationales (International Seabed Authority, 2005a). Dès 1982, les lois internationales de la mer, codifiées par la Convention des Nations Unies sur le droit de la mer, sont adoptées et prennent en compte, entre autres, les questions environnementales ainsi que l'utilisation équitable des ressources provenant des océans. Or, ce n'est qu'en 1994 que cette Convention entre en vigueur (Lenoble, 1996; Thiel, 2003).

L'Autorité internationale des fonds marins (ISA), fondée en 1994, est l'institution des Nations Unies chargée de la gestion des fonds marins situés au-delà des limites de juridiction nationale; elle organise et contrôle les activités dans cette zone et assure également leur administration. Aussi, les objectifs de cette institution sont de protéger l'environnement marin des impacts de l'exploitation des ressources (en créant, entre autres, des zones de conservation) ainsi que d'assurer un partage équitable des bénéfices économiques de cette exploitation entre les pays exploitants et la communauté internationale (International Seabed Authority, 2005a). Aussi, en plus d'inciter la recherche scientifique dans les territoires de juridiction internationale, l'Autorité rassemble, analyse et rend disponible les données et résultats de cette recherche (International Seabed Authority, 2005b). L'exploration et l'exploitation minière dans les territoires de juridiction internationale, par une entreprise ou un État, nécessitent un contrat délivré par l'Autorité. Cette dernière, par l'intermédiaire de son Conseil, a des pouvoirs discrétionnaires étendus pour évaluer l'impact potentiel des activités minières menées dans l'environnement marin. Elle a pour mission de mettre en place un programme de surveillance, de recommander des changements, ou éventuellement d'émettre, via son Conseil, des directives visant à prévenir tout dommage grave pouvant être causé au milieu marin (International Seabed Authority, 2005a). Ainsi, les contractants sont responsables de tout dommage causé aux territoires relevant de leur juridiction. Dans le cas d'une éventuelle exploitation, les contractants devront payer des redevances à l'Autorité qui se chargera de les redistribuer équitablement en considérant les intérêts et les besoins des pays en voie de développement (International Seabed Authority, 2005a). En effet, comme les zones à nodules se trouvent dans un territoire de juridiction internationale, les bénéfices économiques de leur exploitation ne devraient pas revenir uniquement aux quelques pays qui possèdent la technologie ainsi que le capital nécessaire pour exploiter cette ressource (International Seabed Authority, 2005a). Enfin, en 2000, l'Autorité a adopté le code sur l'exploitation des nodules polymétalliques qui dicte, entre autres, que les contractants doivent évaluer les conséquences environnementales d'une exploitation éventuelle des nodules. Sept investisseurs pionniers, la France (Ifremer/AFERNOD), l'Inde, le Japon (DORD), la Russie (par une entreprise d'État), la Chine (COMRA), la Corée et un consortium (IOM) formé par la Bulgarie, Cuba, la République tchèque, la Pologne, la Fédération de Russie et la Slovaquie se partagent un territoire dédié à l'exploration des nodules dans la zone Clarion-Clipperton, qui représente plus de 6 millions km^2 de superficie (Fig. i). L'Inde possède un deuxième territoire d'exploration dans le sud de l'océan Indien central, entre 10°S et 17°S de latitude et entre 72°E et 82°E de longitude. Chacun de ces sept investisseurs pionniers détient un permis minier de 75 000 km^2 valide pour une durée de 15 ans (International Seabed Authority, 2005a).

L'éventuelle exploitation des nodules soulève également des questions touchant la politique internationale. Par exemple, du point de vue des États-Unis, le cobalt serait un métal stratégique puisque ce pays ne l'exploite pas. Ce métal se trouve principalement dans des mines en Afrique du Sud ainsi que dans les nodules. Étant donné la situation politique instable de l'Afrique du Sud, les États-Unis auraient intérêt à exploiter les nodules afin d'assurer leur approvisionnement en cobalt (Thurman, 2004).

L'écosystème abyssal et sa faune

Cinq caractéristiques générales décrivent bien la singularité de l'écosystème abyssal: une faible productivité, des conditions environnementales relativement stables mais extrêmes (températures froides, fortes pressions et absence de photosynthèse), une énergie physique très faible (courants), une biodiversité élevée malgré une faible biomasse (Dayton et Hessler, 1972; Hecker et Paul, 1979; Levin, *et al.*, 2001) et, sauf pour quelques habitats particuliers, un immense habitat d'apparence homogène (Dayton et Hessler, 1972; Smith, 1999). D'autre part, les récentes conclusions de Levin *et al.* (2001) énoncent que les sédiments abyssaux sont un environnement dynamique intimement lié à la biosphère globale. Plus récemment, les travaux de recherche tendent à montrer qu'il existerait une importante hétérogénéité spatiale dans cet habitat (Thistle et Eckman, 1990).

La faune abyssale est encore très méconnue de nos jours mais la science découvre peu à peu les secrets de son existence et de son écologie. Les ressources disponibles pour les organismes qui vivent sur les fonds océaniques sédimentent lentement de la surface. La quantité et la qualité de cette nourriture varient selon des gradients spatio-temporels qui sont liés à la production de surface des océans (Fabiano, *et al.*, 2001; Lampitt et Antia, 1997; Lampitt, *et al.*, 2001; Levin, *et al.*, 2001; Smith, *et al.*, 1997; Smith, *et al.*, 1996). Or, au cours de leur transport jusqu'au fond de l'océan, ces ressources diminuent progressivement (Fabiano, *et al.*, 2001; Rex, 1976; Sanders et Hessler, 1969; Tyler, 1988). Il est donc généralement admis que la quantité de nourriture (production primaire) est une ressource limitante pour les organismes des fonds marins (Dayton et Hessler, 1972). Selon certains auteurs, elle contrôlerait même la densité (Grassle, 1991; Rex, 1976) et la biomasse des organismes (Gage, *et al.*, 2000; Rex, 1976; Sanders et Hessler, 1969; Sokolova, 1972). Comme la biomasse du benthos diminue avec la profondeur plus rapidement que l'abondance, il est suggéré que les petites tailles des espèces abyssales constitueraient une adaptation aux faibles quantités de nourriture présentes (Rex, 1976).

La faune abyssale est caractérisée par une biodiversité très élevée (Dayton et Hessler, 1972; Hecker et Paul, 1979; Levin, *et al.*, 2001). Plusieurs hypothèses expliquant la présence d'une grande diversité sont proposées dans la documentation. Elles sont toutes basées sur la grande stabilité de l'environnement mais elles diffèrent selon l'importance relative attribuée aux interactions biologiques (Juniper et Sarrazin, comm. pers.). Selon Rex (1976), deux théories expliquent la grande biodiversité des fonds marins. Premièrement, elle serait attribuée aux interactions compétitives raffinées qui impliquent une division multidimensionnelle complexe des ressources disponibles. Deuxièmement, elle serait le résultat d'une prédation intensive qui aurait comme conséquence de réduire l'exclusion compétitive parmi les nombreux détritivores. De son côté, Grassle (1991) explique la grande diversité par les conditions relativement constantes des fonds marins. En fait, la « stability-time hypothesis » stipule que si des conditions physiques stables persistent sur une longue période, la spéciation et l'immigration vont faire augmenter la biodiversité graduellement. Chaque espèce devra alors occuper une niche écologique de plus en plus spécialisée. Thistle (1983) quant à lui, propose un modèle dans lequel l'hétérogénéité des habitats, créée par la présence de structures biologiques, joue un grand rôle.

Bien que Murray et Renard (1891) aient décrit la présence de plusieurs groupes d'organismes associés aux nodules, il a fallu attendre plusieurs années avant que les chercheurs des grands fonds s'intéressent aux communautés de substrats durs (sources hydrothermales, croûtes carbonatées des suintements froids et nodules polymétalliques; Mullineaux, 1987).

La faune associée aux nodules

Les études précédentes sur la faune associée aux nodules sont davantage axées sur son rôle sur la croissance des nodules (Bignot et Lamboy, 1980; Dudley, 1978; Dudley et Margolis, 1974; Dugolinsky, 1976; Dugolinsky, *et al.*, 1977; Ehrlich, 1972; Graham et Cooper, 1959; Greenslate, *et al.*, 1974; Riemann, 1983; Riemann, 1985; Thiel, 1978; Thiel, *et al.*, 1993; von Stackelberg, 1984; Wendt, 1974) que sur sa description et son écologie (Mullineaux, 1987; Mullineaux, 1988; Mullineaux, 1989). Les microorganismes colonisant la surface des nodules (Burnett et Nealson, 1981; Ehrlich, 1972) ainsi que la faune colonisant les anfractuosités des nodules (Maybury, 1996; Thiel, *et al.*, 1993) ont également été étudiés. La faune colonisant la surface exposée des nodule est dominée par des foraminifères agglutinants mais des métazoaires (éponges, hydrozoaires, scyphozoaires, mollusques, polychètes, crustacés, bryozoaires, brachiopodes et ascidies) sont également présents (Mullineaux, 1987). La faune associée aux nodules pourrait même être considérée comme une communauté écologique distincte de celle des sédiments (Mullineaux, 1987).

En plus d'une meilleure caractérisation de cette faune, l'identification des liens entre la distribution de la faune et les facteurs environnementaux du milieu à différentes échelles spatiales demeure cruciale pour notre compréhension de ces communautés distinctes. Comme plusieurs espèces animales habitant les fonds marins n'ont toujours pas été décrites et que plusieurs autres ne sont même pas connues, il est aujourd'hui impossible d'estimer la valeur que pourraient avoir ces organismes notamment pour l'industrie pharmaceutique ou médicale (Jumars, 1981).

Problématique spécifique

Avant tout, l'ambition de la présente étude est de contribuer à la recherche par l'acquisition de connaissances fondamentales nécessaires aux études d'impact destinées à conserver l'intégrité des océans et, plus précisément, celle des fonds marins. La recherche portant sur la faune associée aux nodules est primordiale et la connaissance des caractéristiques écologiques de base de cet habitat sont essentielles pour évaluer les impacts environnementaux de leur exploitation et de leur transformation (Bluhm, 2001; Jumars, 1981; Mero, 1972; Rex, 1981). Dans le cas d'une exploitation, la faune associée aux nodules extraits des fonds marins serait automatiquement détruite puisque les nodules seraient retirés des sédiments et remontés à la surface (Ahnert et Borowski, 2000; Thiel, *et al.*, 2001; Thiel, *et al.*, 1993; Thiel et Tiefsee-Umweltschutz, 2001). Les nodules constitueraient pour la faune benthique l'unique habitat de substrat dur dans plusieurs régions des océans et leur exploitation risquerait d'avoir des conséquences négatives sur la fragile communauté colonisatrice (Gooday, 1990). Évidemment, comme leur croissance est extrêmement lente, les nodules pourraient prendre des millions d'années à se régénérer.

La faune associée aux nodules nécessite des efforts supplémentaires de recherche. Une étude approfondie sur les caractéristiques de cet habitat et sur la faune qui y est associée est essentielle. En effet, il est pertinent de se questionner sur la distribution spatiale des organismes dans les deux zones explorées, dans les différents faciès et à l'échelle du nodule. L'hypothèse selon laquelle certains facteurs environnementaux (courants près du fond, chimie de l'eau, le substrat «nodule» et production primaire de surface à l'échelle des zones et des faciès, l'hétérogénéité des habitats et la texture de la surface des nodules à l'échelle du nodule) influencent la distribution spatiale des communautés associées aux nodules est posée.

L'objectif de cette recherche est d'analyser la distribution spatiale de la faune associée aux nodules polymétalliques en fonction des facteurs environnementaux mesurés *in situ* dans la zone Clarion-Clipperton (zone équatoriale du Pacifique Est) à différentes échelles spatiales.

La variable à expliquer (dépendante) est la distribution spatiale de la faune à l'échelle de la zone, du faciès et du nodule. À l'échelle de la zone et du faciès, les variables potentiellement explicatives (indépendantes) sont: les courants près du fond, le pH, la salinité, les concentrations en oxygène et en CO_2, les nitrates et phosphates, la température, la profondeur, la production primaire de surface, les interactions entre espèces ainsi que le substrat « nodule » (taille, composition géochimique, morphologie et texture). À l'échelle du nodule, les variables potentiellement explicatives sont l'hétérogénéité des habitats, créée par les mamelons, et la texture de la surface des nodules.

Mon hypothèse principale est que la quantité de nourriture disponible explique une partie de la variation de la distribution spatiale de la faune associée aux nodules à l'échelle de la zone, du faciès et du nodule.

Cette hypothèse est appuyée sur le fait que la quantité de nourriture disponible est limitante dans les fonds marins. Par conséquent, il est possible de penser que ce facteur aura une grande influence sur la faune associée aux nodules À l'échelle de la zone et du faciès, la quantité de nourriture disponible sera estimée à partir de la production primaire de surface. À l'échelle du nodule, l'hétérogénéité des habitats, créée par les mamelons, ainsi que la texture variable de la surface des nodules seront examinés comme facteurs pouvant influencer l'apport de nourriture disponible pour la faune associée aux nodules. L'importance relative d'autres facteurs sera également explorée.

CHAPITRE I

CATALOGUE OF NODULE FAUNA

PREFACE

Nodule fauna

This catalogue describes 90 organisms associated with nodule surfaces above the sediment line. For each form, description, size, remarks, geographical distribution, references and photographs are included when available. Following Dugolinsky (1976), abundant taxa were those present on more than 50% and common taxa were present on 10-50% of the nodules sampled. All the forms observed were considered to be permanently attached to the nodule substratum since each nodule had been rinsed off with sea water, removing any forms temporarily laying on nodule surfaces. "Free living" form associated with nodules has never been reported in other studies.

Seventy three protozoans, all foraminifers, comprised the large majority of nodule fauna. They were all attached directly to the nodule surface except for five taxa, found agglutinated in mats. More than three-quarters of protozoan taxa contained protoplasm suggesting that they were live when collected. Eleven forms were identified to species or genus and 21 were considered to correspond to taxa listed by Mullineaux (1987). Since foraminifers are commonly distinguished on the basis of chamber arrangement and test composition (Loeblich and Tappan, 1987), the description of the forms in this catalogue was made according to 1) test morphology, 2) test wall construction, 3) aperture location and 4) character of the protoplasm. Personal observations were enriched by a visit to Andrew J. Gooday at the National Oceanographic Centre Southampton in October 2004 and by regular internet interactions.

Seventeen metazoan taxa were also associated with nodules; they include sponges, scyphozoans, molluscs, polychaetes, bryozoans, brachiopods, ascidians and platyhelminths. The metazoan groups recorded on nodule surfaces by Mullineaux (1987) are similar to the ones reported in the present study. Only 29% of these metazoan taxa were considered to be live when collected. Eight taxa were identified to species or genus with the help of taxonomists.

Finally, some indeterminate forms encountered on nodules could not be assigned to protozoan or metazoan taxa since they lack any obvious structures. However, because they are recurrent, they are included in the catalogue.

Terminology

Foraminiferal tests can be either calcareous (composed of secreted $CaCO_3$), agglutinated (composed of foreign particles), or organic in composition (Loeblich and Tappan, 1987). Most of the foraminifers associated with nodules collected during this study had an agglutinated test wall. The majority of these were single-chambered monothalamous forms but some were multichambered (polythalamous). The monothalamous forms included domes, mats, tunnels, connected chambers, upright or recumbent tubes. Tubes with a small diameter in relation to their length are termed tubules. Thin, upright, very elongated, straight thin tubes are termed filaments. Another important feature used to classify foraminifers is the mode of test attachment to the substratum (Gooday and Haynes, 1983; Bertram and Cowen, 1994). In some forms, the test wall does not separate the cell body from the nodule substratum; these are referred as "adherent" (Bertram and Cowen, 1994) or "attached" (Gooday and Haynes, 1983). In other forms, the cell body is separated from the nodule substratum by the test wall; these are referred to as "pseudoattached" (Gooday and Haynes, 1983). The terms "attached" and "pseudoattached" are used herein.

The test morphology terminology used in this catalogue is derived from that of Mullineaux (1988) and Loeblich and Tappan (1964).

1) Mats: Uninterrupted crusts with irregular outlines or branching tubes radiating from a central location or anastomosing in an irregular pattern.
2) Hemispheres: Dome-shaped tests with a regular, circular and clearly defined outline.
3) Tunnels: Attached linear sections of the test.
4) Tubes: Pseudo-attached cylindrical tests.

Stercomata are intra- or extra-cellular pellets of waste material. They are generally dark spherical to oval bodies composed mainly of clay minerals; they sometimes contain manganese or iron oxides (Mullineaux, 1988).

Live or dead?

This is often difficult to determine. All organisms, whether live, dead or fragmented, are included in this catalogue. It is assumed that protozoans with unbroken tests and containing protoplasm were live when collected (Mullineaux, 1987). Robust coarsely agglutinated foraminiferal tests generally remain intact on the nodule surface long after death. Furthermore, in some taxa, the protoplasm is diffuse, small in volume compared to the test volume and therefore difficult to observe. Taxa that are clearly dead or present only as fragments are indicated.

Limits

This catalogue is not intended as an exhaustive inventory of nodule fauna, but it does include the main, commonly occurring forms found on the nodule surface. It is limited to organisms ≥100 µm which will include many of the foraminifera and most metazoans (Mullineaux, 1987). The observations were made using a binocular light microscope (83 X) supplemented where necessary by scanning electron microscopy (SEM). Since deep-sea foraminifers are not well known and that their observation is very time-consuming, the descriptions are not exhaustive. A particular problem is that the full range of morphological variability of the described forms is unknown. Metazoans were only briefly noted since few specimens of each group were observed.

Photography

The nodules samples were taken during the NODINAUT cruise (May 18th – June 27th 2004) to the Clarion-Clipperton fracture zone as part of a project funded by the Kaplan Foundation and the International Seabed Authority. Two geographical areas were investigated: the east zone (14°N, 130°W) and the west zone (9°N, 150°W). Three different nodule facies are found in the east zone (A, B and C) and an undescribed facies characterizes the west zone. Briefly, nodule facies are differentiated according to the general shape, size and the surface morphology of the nodules and the relation between the nodule and its environment (burying in the sediment and presence of volcanic material).

Photographs of nodule fauna were taken at IFREMER by Julie Veillette during part of her Master degree done in collaboration with Université du Québec à Montréal. All rights belong to IFREMER. Organisms were photographed in alcohol or water using a (Nikon E4300) digital camera mounted on a binocular microscope. Because the nodules and their attached fauna are very three-dimensional, a compromise between depth of field and exposure was necessary in order to obtain the clearest possible photographs. Two or more sources of light were used instead of the camera flash. Pale-coloured structures required the photographs to be under-exposed. Specimens were measured under a binocular microscope and scale derived from these measurements. SEM photos were taken using a microscope Philips model XL30LAB6.

Acknowledgements

I extent great thanks to Andrew J. Gooday without whom this catalogue would not have been the same. Thanks to the NODINAUT scientific party who gave me relevant advices concerning the art of the photography with a binocular microscope. The SEM photos could not have been realized without Philippe Crassous. Finally, great thanks to Ifremer for the NODINAUT cruise and for its financial support.

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CHAPTER I

PROTOZOAN TAXA

1.1 DOMES AND LUMPS

1) *Pseudowebbinella* sp.

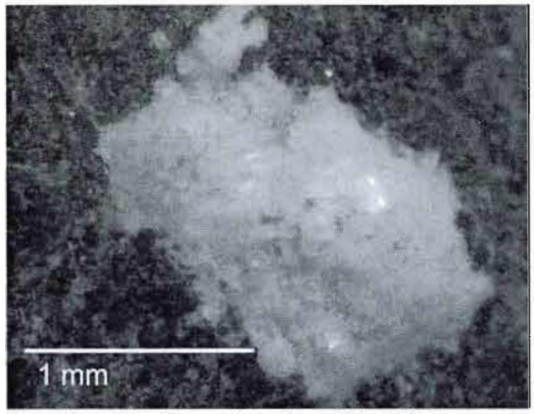
Foraminifera,Textulariina, Astrorhizacea, Hemisphaeramminidae

Description: Test hemispherical with a granular surface appearance reflecting the presence of internal chambers divided by septa. Test wall thick composed of sparse fine particles rigidly cemented in a whitish matrix. Aperture not observed. The inner structure, revealed when specimens are broken open, resembles a honeycomb. Stercome not observed.

Size: About 1mm in diameter.

Remarks: When you break a specimen, it looks like honeycomb because of the internal chambers.

Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific. Common in the west zone.



Pseudowebbinella sp. Location: 13°55.63 N, 130°12.20 W, depth: 4980m, nodule: PL1602-10-4.

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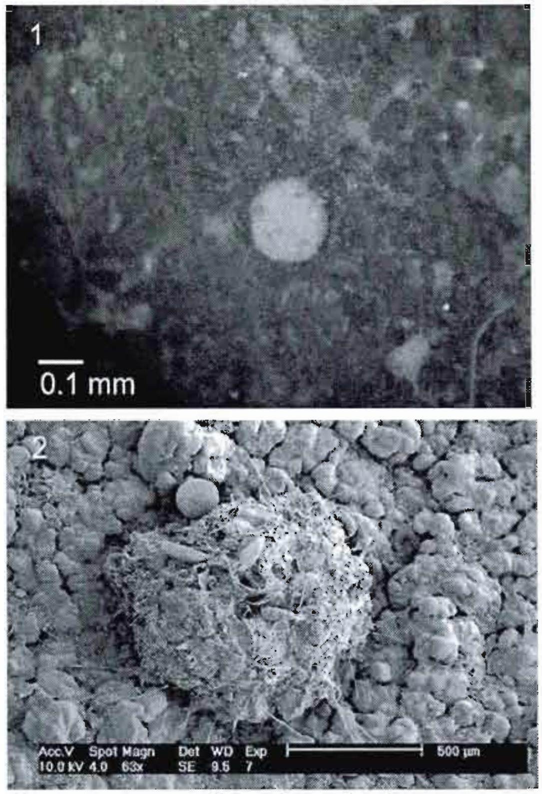
Mullineaux, L.S., 1988. Taxonomic notes on large agglutinated foraminifers encrusting manganese nodules, including the description of a new genus, Chondrodapis (Komokiacea). Journal of Foraminiferal Research 18, 46-53.

2) *Hemispherammina*-like, pale regular dome

Foraminifera, incertae sedis

Description: Test hemispherical, monothalamous, without obvious aperture. Test wall thick, composed of fine pale particles. No stercome.
Size: About 100 to 800µm in diameter.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific. Especially common on facies B and C.

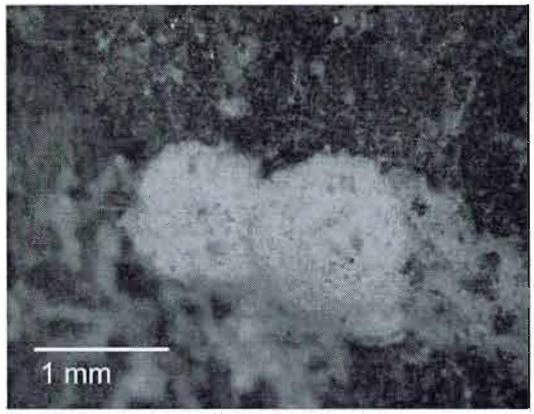


Hemispherammina-like, pale regular dome.
1) Location: 9°33.20 N, 150°0.41 W; depth: 5050m, nodule: KGS28-3. 2) Specimen on nodule surface.

3) *Hemispherammina*-like, pale granular dome

Foraminifera, incertae sedis

Description: Test hemispherical, monothalamous, with a granular surface without obvious aperture. Test wall thick, composed of fine, pale-coloured particles. No aperture observed. The interior of this form is full of stercomata.
Size: From 1 to 2mm in diameter.
Remarks: Larger than the "common" white patches found everywhere on the nodule. Similar to *Chondrodapis integra* but no tubule visible.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific. Especially common on facies B and C.

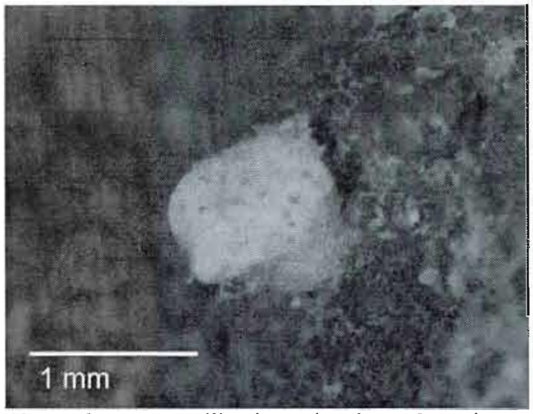


Hemispherammina-like, pale granular dome. Unknown nodule.

4) *Hemispherammina*-like, irregular shape

Foraminifera, incertae sedis

Description: Test hemispherical, monothalamous, without obvious aperture. Test wall thick and rigid, composed of fine pale particles cemented in a matrix. Stercomata are visible.
Size: Around 1.5mm in diameter.
Remarks: Different from "Komoki, mud-ball type" mainly because the test wall is rigid while the one of "Komoki, mud-ball type" is flexible.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific. Especially common on facies B and C.

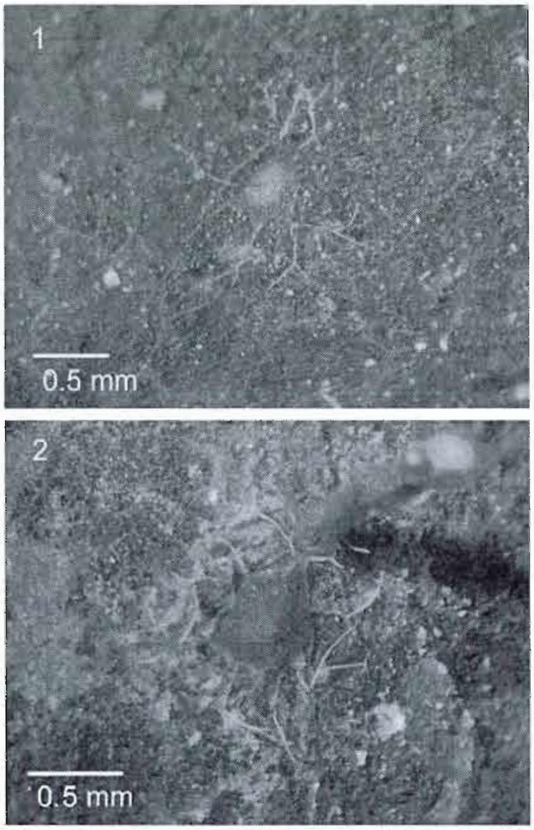


Hemispherammina-like, irregular shape. Location: 9°33.60 N, 150°0.84 W; depth: 5050m, nodule: KGS29-7.

5) Tholosina sp.

Foraminifera, Textulariina, Astrorhizacea, Saccaminidae

Description: Orange monothalamous, flexible test composed of fine agglutinated particles. Fine tubes extending out across the nodule surface from the margin of the test make this species look like a sun. No aperture visible.
Size: From 300 to 800µm in diameter.
Remarks: Most of the times, several specimens are observed on a nodule.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific. Commonly observed on facies C and located far from the sediment line. Indurated sediment in close proximity to vent sites are also colonized by *Tholosina* sp.



Tholosina sp. 1) Location: 14°3.0 N, 130°6.93 W, depth: 4974 m, nodule: KGS6-6. 2) Location: 13°55.63 N, 130°12.20 W, depth: 4971 m, nodule: PL1598-6_4-2.

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6) Tholosina-like

Foraminifera, incertae sedis

Description: Dark orange single-chambered hemisphere with a flexible wall composed of fine agglutinated particles and a white base. A few tubes spread out across the substratum from the margin of the test making this species looking like a sun. No aperture visible.
Size: Around 1mm in diameter.
Remarks: Very similar to *Tholosina* sp. but bigger and darker.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific. Mostly observed on facies C.

7) *Trochammina*-like

Foraminifera, incertae sedis

Description: Tiny orange multichambered test, shaped like a pointed cone and with trochospirally-arranged chambers. Test wall composed of fine to medium particles firmly cemented with a fine matrix. Occasionally, sediment is collected at the base of the dome. The aperture was not observed during this study but is described by Loeblich and Tappan (1964, p.C259) and Shröder (1986, p.52) as an aperture simple at the inner margin on the umbilical side of the last chamber opening into narrow umbilicus. Therefore, the form described in this study is assumed to be similar to *Trochammina* sp.
Size: Around 100µm in diameter.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific on every facies. Similar forms occur encrusting the interior of *Bathysiphon rusticus* tubes in the northeast Atlantic, on experimental substrates on Cross Seamount, on ice-rafted stones in northeast Atlantic and on indurated sediment in close proximity to vent sites. Also found in box-cores taken from the northwest Atlantic Ocean.

References

Bertram, M.A. and Cowen, J.P., 1994. Testate rhizopod growth and mineral deposition on experimental substrates from Cross Seamount. Deep-Sea Research I 41, 575-601.

Bignot, G. and Lamboy, M., 1980. Les foraminifères épibiontes à test calcaire hyalin des encroûtements polymétalliques de la marge continentale au nord-ouest de la péninsule ibérique. Revue de Micropaléontologie 23, 3-15.

Gooday, A.J. and Haynes, J.R., 1983. Abyssal foraminifers, including two new genera, encrusting the interior of *Bathysiphon rusticus* tubes. Deep-Sea Research 30, 591-614.

Jonasson, K.E., Schröder-Adams, C.J. and Patterson, R.T., 1995. Benthic foraminiferal distribution at Middle Valley, Juan de Fuca Ridge, a northeast Pacific hydrothermal venting site. Marine Micropaleontology 25, 151-167.

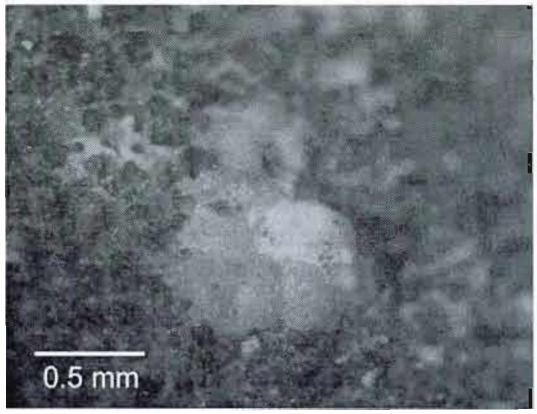
Loeblich, A.R.Jr and Tappan, H., 1964. Sarcodina, chiefly "Thecamoebians" and Foraminiferida. In: Moore, R.C. (Ed.), Treatise on Invertebrate Paleontology, Part C, Protista. The Geological Society of America and the University of Kansa Press, New York and Lawrence, KS, pp. 900 pages.

Schröder, C.J., 1986. Deep-water arenaceous foraminifera in the northwest Atlantic Ocean. Canadian Technical Report of Hydrography and Ocean Sciences 1-191.

8) *Placopsilina*-like

Foraminifera, incertae sedis

Description: Test orange in colour, multichambered, initial part planispirally coiled, becoming uniserial later. Wall composed of medium-sized agglutinated particles, rigidly cemented. Aperture terminal.
Size: Length around 750µm.
Remarks: According to Gooday and Haynes (1983), many tests of *Placopsilina* sp. had stained protoplasm which means that they were live when captured.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific. Mostly observed on facies B and C. A few similar specimens found encrusting the interior of *Bathysiphon rusticus* tubes in the northeast Atlantic and in box-cores taken from the northwest Atlantic Ocean.



Placopsilina-like. Location: 13°55.63 N, 130°12.20 W, depth: 4985m, nodule: PL1603-11_2-1.

References

Gooday, A.J. and Haynes, J.R., 1983. Abyssal foraminifers, including two new genera, encrusting the interior of *Bathysiphon rusticus* tubes. Deep-Sea Research 30, 591-614.

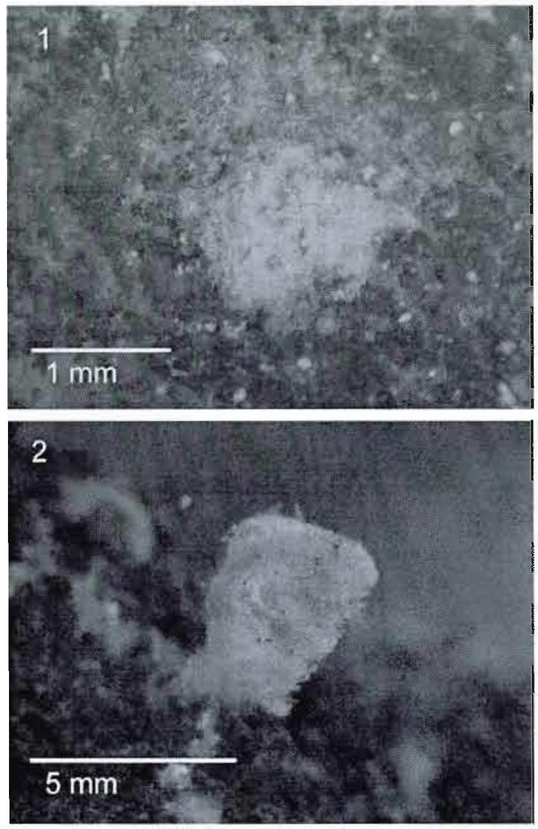
Loeblich, A.R.Jr and Tappan, H., 1964. Sarcodina, chiefly "Thecamoebians" and Foraminiferida. In: Moore, R.C. (Ed.), Treatise on Invertebrate Paleontology, Part C, Protista. The Geological Society of America and the University of Kansa Press, New York and Lawrence, KS, pp. 900 pages.

Schröder, C.J., 1986. Deep-water arenaceous foraminifera in the northwest Atlantic Ocean. Canadian Technical Report of Hydrography and Ocean Sciences 1-191.

9) Komoki, mud-ball type

Foraminifera, incertae sedis

Description: Beige dome, rounded and very cohesive. Tubules tightly packed. Test wall composed of agglutinated particles in a flexible organic matrix that contains stercomata. No cavity. No aperture. Rarely, the "ball" is held on the nodule surface by delicate filaments. This taxon includes a lot of different morphotypes; any spherical or hemispherical form of cohesive packed tubules with flexible test wall are assigned to this taxon.
Size: 1 to 5mm in diameter.
Remarks: Probably a new genus (Gooday, pers. comm.).
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific. Very common on every facies except A.

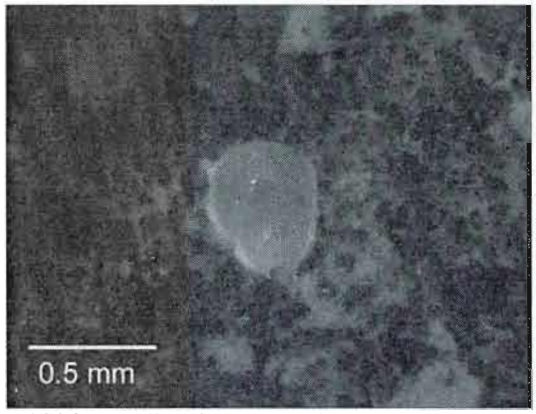


Komoki, mud-ball type. 1) Location: 13°55.63 N, 130°12.20 W, depth: 4970m, nodule: PL1598-06_4-1. 2) Location: 9°33.16 N, 150°0.89 W, depth: 5050m, nodule: KGS31-1.

10) Whitish sparkling dome

Foraminifera, incertae sedis

Description: Hemispherical test with whitish, translucent wall composed of tiny agglutinated particles.
Size: Around 400µm in diameter.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific.

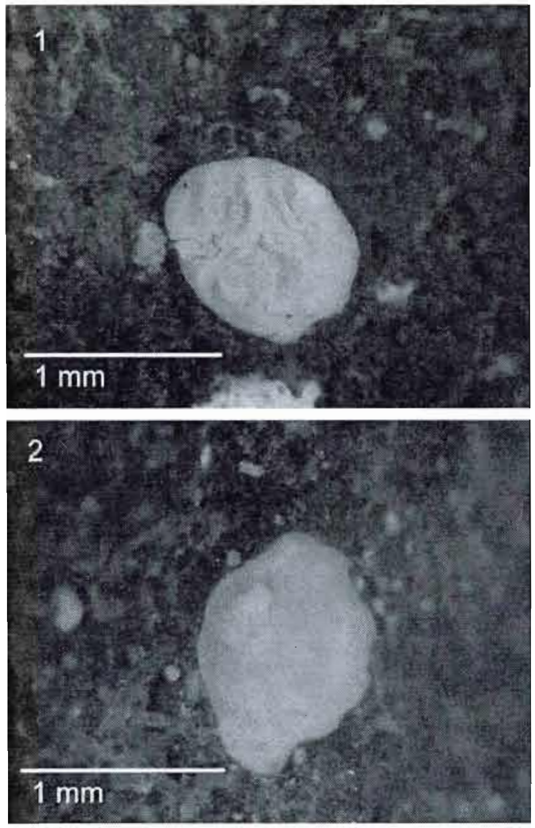


Whitish sparkling dome. Location: 13°55.63 N, 130°12.20 W, depth: 4985m, nodule: PL1593-1_3.

11) Whitish flattened dome

Foraminifera, incertae sedis

Description: Hemispherical test flattened and wrinkled. Test wall composed of fine agglutinated particles. No aperture observed. Looks as if surface has tubercle-like swellings.
Size: 1mm in diameter.
Remark: Similar to "Whitish, irregular flattened domes (WIFD)" described by Gooday and Haynes (1983).
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific. Only two specimens observed.



Whitish flattened dome. 1) Location: 9°33.16 N, 150°0.89 W, depth: 5050m, nodule: KGS31-6.
2) Location: 14°3.01 N, 130°6.93 W, depth: 4974m, nodule: KGS6-4.

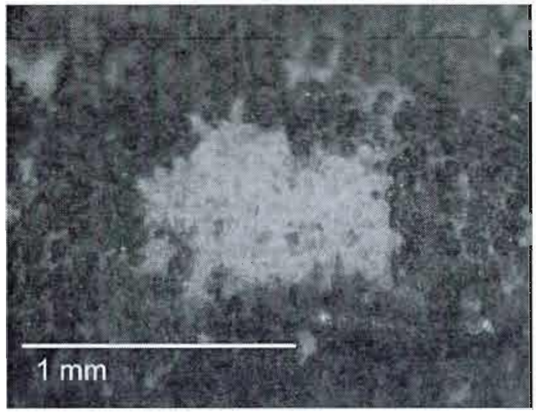
Reference

Gooday, A.J. and Haynes, J.R., 1983. Abyssal foraminifers, including two new genera, encrusting the interior of *Bathysiphon rusticus* tubes. Deep-Sea Research 30, 591-614.

12) White granular patches

Foraminifera, incertae sedis

Description: Tiny, irregularly-shaped, white or beige-coloured hemispheres. Test seems to be consisted of a mass of small chambers which give the surface a granular appearance. It is composed of fine agglutinated particles and organic material.
Size: Small, from 500μm to 1mm in diameter.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific. Ubiquitous taxon on every facies.

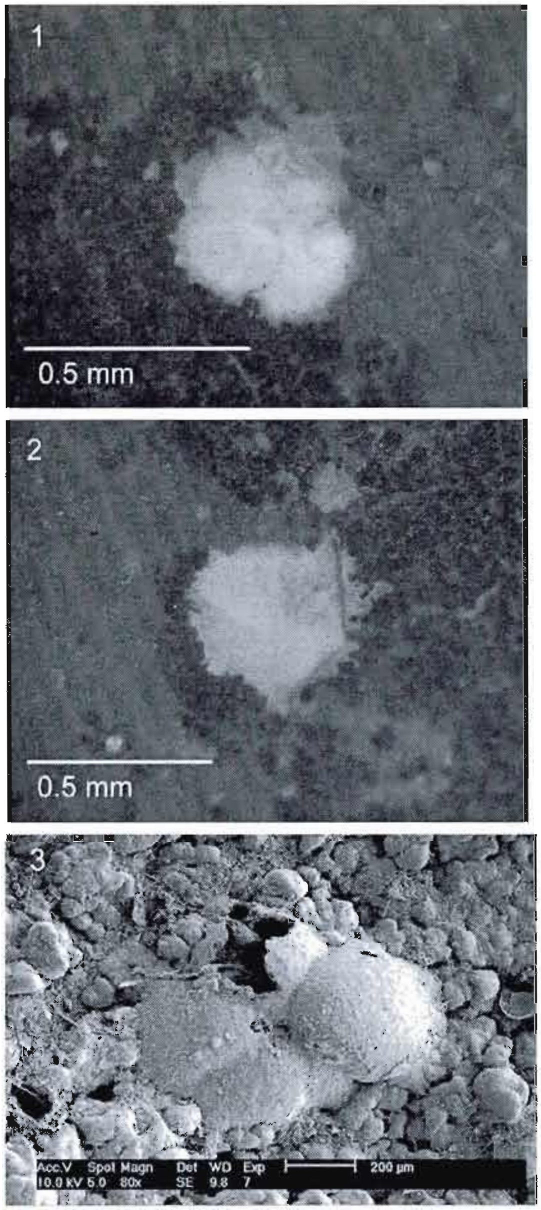


White granular patches. Location: 13°55.63 N, 130°12.20 W, depth: 5030m, nodule PL1593-01_4.

13) *Ammobicides*-like

Foraminifera, incertae sedis

Description: White, hemispherically-shaped, multi-chambered which chambers are twisted and formed by radial septa. Test wall calcareous with surface obscured by very fine agglutinated particles. Sometimes covered by fluffy beige sediment.
Size: 400µm to 1mm in diameter.
Remarks: Often, only dead, damaged tests of this taxon are observed.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific. Abundant on facies B and C. Bignot and Lamboy (1980) reported the presence of *Carpenteria Proteus*, a very similar form to *Ammocibicides*-like, on polymetallic crusts off Portuguese continental margin, between 2600 and 3100m.



Ammocibicides-like. 1) and 2) are two different specimens from the same nodule. Location: 13°55.63 N, 130°12.20 W, depth: 4970 m, nodule: PL1598-06_1-1. 3) Specimen on nodule surface.

References

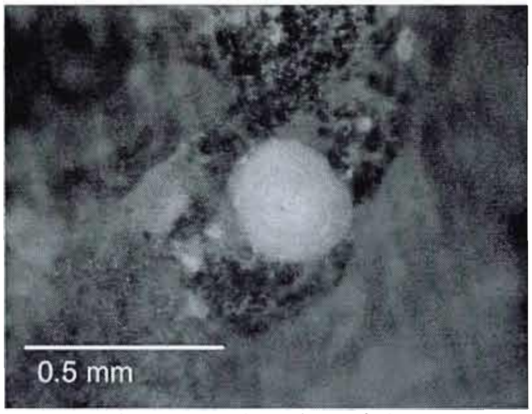
Bignot, G. and Lamboy, M., 1980. Les foraminifères épibiontes à test calcaire hyalin des encroûtements polymétalliques de la marge continentale au nord-ouest de la péninsule ibérique. Revue de Micropaléontologie 23, 3-15.

Janin, M.-C., 1983. *Ammotrochoides bignoti* n. gen. n. sp., foraminifère des croûtes ferromanganésifères des marges de l'océan Atlantique nord-est. Benthos 1983;2nd International Symposium of Benthic Foraminifera. Pau, pp. 327-337.

14) Fine agglutinated particles beige soft dome

Foraminifera, incertae sedis

Description: Flattened and wrinkled beige dome composed of fine agglutinated particles including plate-like particles (mica) that result in a reflective surface. Aperture located at central, highest point of dome, encircled by brown rings.
Size: Between 100 and 500μm in diameter.
Remarks: Similar to *Colonammina* (Loeblich and Tappan, 1964) but with finer agglutinated particles. The test shape and composition are close to the genus *Hippocrepina*.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific. Common on every facies.



Fine agglutinated particles beige soft dome.
Location: 9°23.69 N, 150°05.72 W, depth: 5040m, nodule: PL1605-13_1-13.

Reference

Loeblich, A.R.Jr and Tappan, H., 1964. Sarcodina, chiefly "Thecamoebians" and Foraminiferida. In: Moore, R.C. (Ed.), Treatise on Invertebrate Paleontology, Part C, Protista. The Geological Society of America and the University of Kansa Press, New York and Lawrence, KS, pp. 900 pages.

15) Brown granular shiny dome

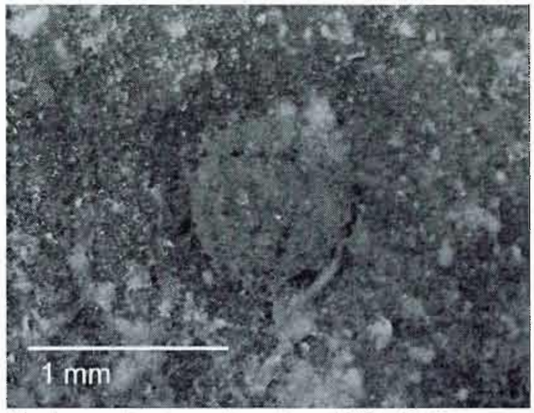
Foraminifera, incertae sedis

Description: Rounded brown dome composed of distinct chambers which give the surface a granular appearance. Test wall shiny, organic and flexible, without agglutinated particles. No aperture visible. Protoplasm contains numerous, tiny, very dark stercomata.
Remarks: Completely undescribed (Gooday, pers. comm.).
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific.

16) Black granular dome

Foraminifera, incertae sedis

Description: Rounded black dome of a granular appearance due to the presence of distinct chambers. Test wall organic, flexible and without agglutinated particles. No aperture visible. Chambers full of decayed stercomata.
Size: Up to 1.5mm in diameter.
Remarks: Judging from the presence of decayed, powdery stercomata, all specimens are dead.The test exhibits some similarities to xenophyophores. Some specimens are much bigger than the average size. Differs from "black soft dome" in the granular appearance of the test.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific.

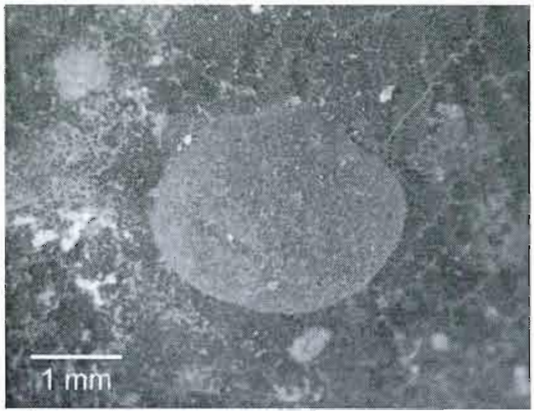


Black granular dome. Location: 13°55.63 N, 130°12.20 W, depth: 4980m, nodule: PL1602-10_20.

17) Black soft dome

Foraminifera, incertae sedis

Description: Rounded black dome. Test wall organic, flexible. Protoplasm contains stercomata.
Size: Around 2mm in diameter.
Remarks: Similar size as "black granular dome" but interior not subdivided into chambers.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific. Few specimens observed on every facies.

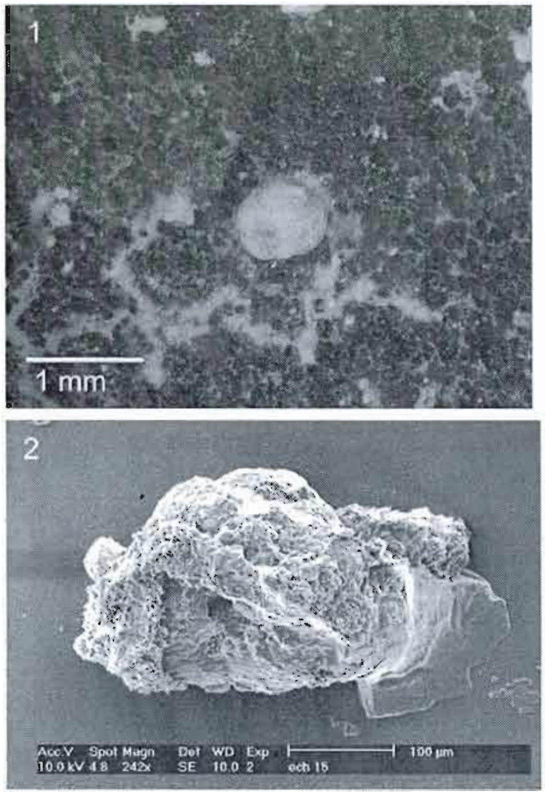


Black soft dome. Location: 14°3.01 N, 130°6.93 W, depth: 4974m, nodule: KGS6-5.

18) Orange dome

Foraminifera, incertae sedis

Description: Very rigid orange dome composed of agglutinated particles.
Size: Around 1mm in diameter.
Geographical distribution:
Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific.
Common in the east zone.



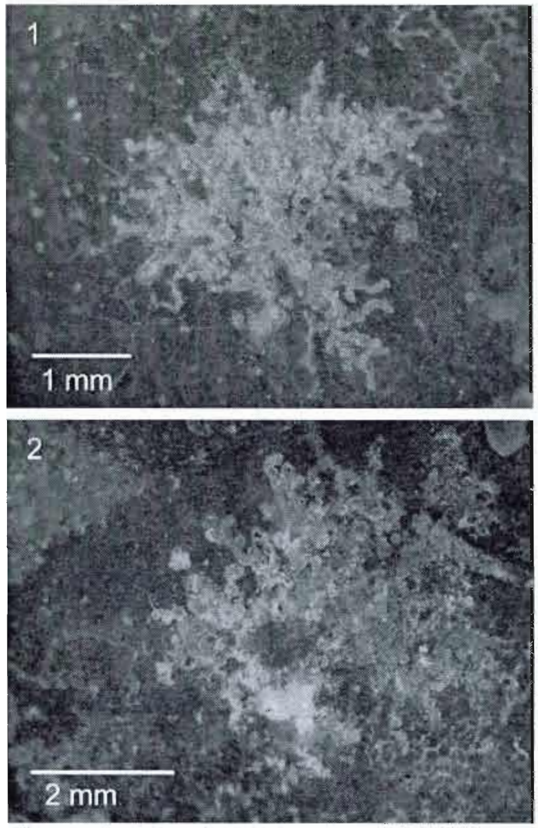
Orange dome. 1) Location: 14°3.01 N, 130°6.93 W, depth: 4974m, nodule: KGS6-5. 2) Specimen alone.

1.2 MATS

19) ***Chondrodapis hessleri*** Mullineaux, 1988

Foraminifera, Textulariina, Komokiacea, Baculellidae

Description: Radiating branching recumbent tubules arising from a central portion of the test where tubules are packed more densely (mat-like). Tubules are constricted at intervals, creating a granular appearance. Short beads with stercomata visible protude up of the recumbent tubules on the nodule surface. Test outline irregular. Wall of tubules composed of clay loosely bound in an organic matrix. Colour similar to the colour of the sediment surrounding the nodule. Interstices between tubules often filled with sediment making this taxon easy to mistake for a lump of agglutinated sediment. Stercomata present in the entire length of the tubule.
Size: Can cover up to 30mm^2 of nodule surface including pores.
Remarks: Occasionally, *Chondrodapis hessleri* develops an orange tinge probably due to iron oxide.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific. Abundant in the east zone, especially on the biggest facies C and B nodules. Very rare in the west zone.



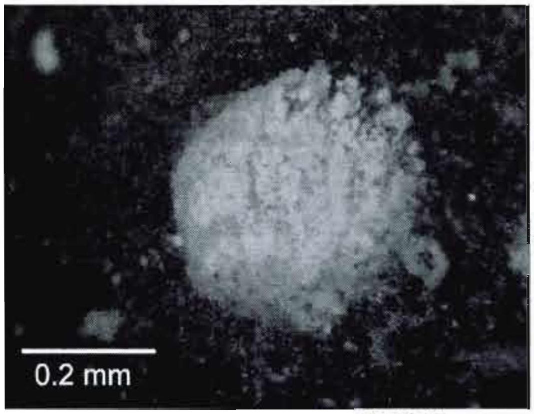
Chondrodapis hessleri. 1) Location: 14°3.10 N, 130°7.75 W, depth: 4954m, nodule: KGS22-5.
2) Location: 14°2.80 N, 130°8.18 W, depth: 4911m, nodule: KGS21-4.

Reference

Mullineaux, L.S., 1988. Taxonomic notes on large agglutinated foraminifers encrusting manganese nodules, including the description of a new genus, Chondrodapis (Komokiacea). Journal of Foraminiferal Research 18, 46-53.

20) ***Chondrodapis integra*** Mullineaux, 1988

Foraminifera, Textulariina, Komokiacea, Baculellidae



Chondrodapis integra. Location: 14°2.80 N, 130°8.18 W, depth: 4911m, nodule: KGS21-8.

Description: Test dome-shaped, consisting of tightly packed, short, upright, unbranched tubules. Test perimeter is well defined. Constrictions at the end of the tubules form beads in which stercomata are visible; this creates a granular appearance. Test wall made of clay loosely bound in an organic matrix. At the first glance, it looks like a granular dome with a very cohesive, flexible test. Colour similar to the colour of the sediment surrounding the nodule. Sediment often filling the interstices between tubules making the tubules hard to distinguish. Some specimens recovered by sediment have also been observed.

Size: Generally 1mm of diameter.

Remarks: The main difference between *Chondrodapis hessleri* and *Chondrodapis integra* is the morphology of the test; *Chondrodapis hessleri* having a network of horizontal radiating tubules that can cover up to 30mm^2 of nodule surface including pores while *Chondrodapis integra* is dome-shaped and smaller (1mm of diameter).

Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific. Abundant in the east zone, common in the west zone.

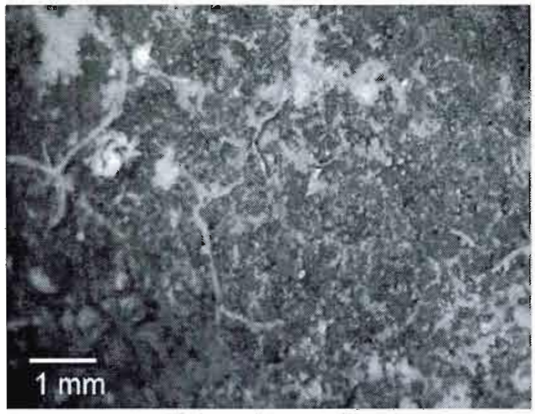
Reference

Mullineaux, L.S., 1988. Taxonomic notes on large agglutinated foraminifers encrusting manganese nodules, including the description of a new genus, Chondrodapis (Komokiacea). Journal of Foraminiferal Research 18, 46-53.

21) Area covered with komokiacean-like chambers linked with fine tubes

Foraminifera, incertae sedis

Description: Regular pattern of komokiacean-like chambers linked by fine tubes. Test made of clay loosely bound in an organic matrix. Colour similar to the colour of the sediment surrounding the nodule. Stercomata present in the chambers.
Size: Can cover up to $30mm^2$ including pores.
Remarks: The fine tubes are very similar to those of *Telammina* sp.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific. Common on every facies.

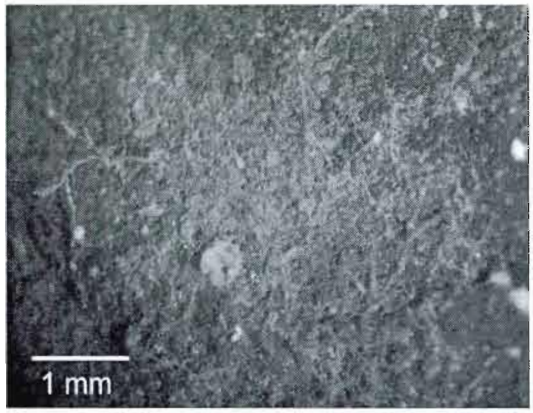


Area covered with komokiacean-like chambers linked with fine tubes. Location: 9°33.81 N, 150°0.98 W, depth: 5051m, nodule: KGS30-1.

22) Grey granular mat

Foraminifera, incertae sedis

Description: Spherical komokiacean-like chambers linked by fine tubules forming a mat of a granular appearance. Test made of clay loosely bound in an organic matrix. Stercomata visible.
Size: Can cover up to $40mm^2$.
Remarks: Similar to "area covered with komokiacean-like chambers linked with fine tubes" but the chambers are more tightly packed.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific. Common on every facies.

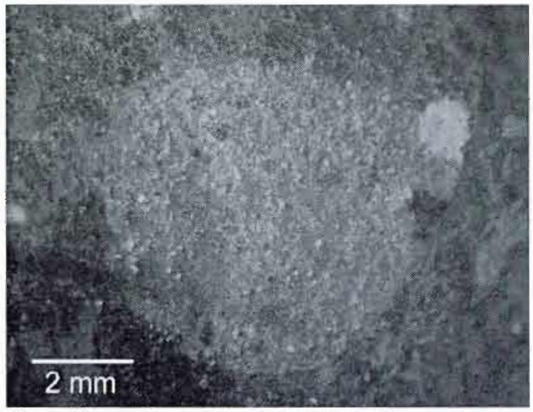


Grey granular mat. Location: 14°2.80 N, 130°8.18 W, depth: 4911m, nodule: KGS21-3.

23) Very thin muddy patches with komokiacean-like chambers

Foraminifera, incertae sedis

Description: Taxon very variable in shape. Komokiacean-like chambers gathered together more or less tightly to form a very thin mat. Test made of clay loosely bound in an organic matrix. Stercomata visible.
Size: Can cover up to 50mm^2 including pores.
Remarks: Appears sometimes like a beige filamentous mat.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific. Abundant in the east zone and especially ubiquitous on facies B.

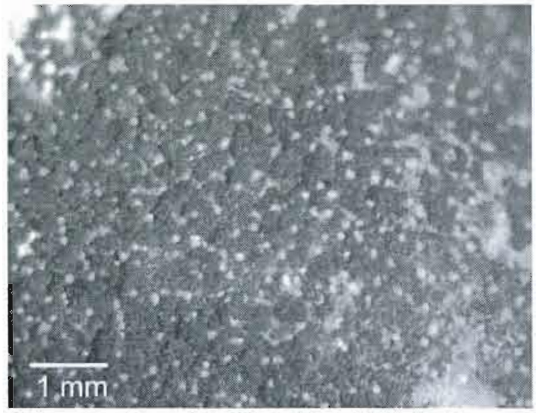


Very thin muddy patches with komokiacean-like chambers. Location: 13°55.63 N, 130°12.20 W, depth: 4970m, nodule PL1598-06_4-2.

24) *Telammina* Gooday and Haynes, 1983

Foraminifera, incertae sedis

Description: Network of tiny hemispherical chambers linked with very fine tubules spreading in anastomosing pattern across nodule surface; may form extensive meshworks. Test outline not well defined. Test wall thin with sparse, fine particles rigidly cemented in a whitish matrix. Aperture not observed. Stercome not apparent in protoplasm. This taxon is often observed over or under other rhizopod-like forms; seem to anastomose across nodule surface regardless of the community in place.



Telammina. Location: 9°33.89 N, 150°0.95 W, depth: 5054m, nodule KGS37-3. See also "upright filament".

Size: Networks can cover several cm^2 including pores. However, the actual surface covered by the taxon is about 5% of that area.

Remarks: *Telammina* sp. spreads as an anastomosing network on nodule surface, in a more regular pattern than "area covered with komokiacean-like chambers linked with fine tubes". It is impossible to estimate the number of individuals living in a meshwork.

Geographical distribution: Abyssal, found attached with manganese nodules below 4950m in the equatorial north Pacific, where it is common on every facies, and encrusting the interior of *Bathysiphon rusticus* tubes in the northeast Atlantic. Similar forms were observed on experimental substrates on Cross Seamount. Also reported on sponge stalks in the northeast Pacific and on ice-rafted stones in northeast Atlantic.

References

Beaulieu, S.E., 2001. Life on glass houses: sponge stalk communities in the deep sea. Marine Biology 138, 803-817.

Bertram, M.A. and Cowen, J.P., 1994. Testate rhizopod growth and mineral deposition on experimental substrates from Cross Seamount. Deep-Sea Research I 41, 575-601.

Gooday, A.J. and Haynes, J.R., 1983. Abyssal foraminifers, including two new genera, encrusting the interior of *Bathysiphon rusticus* tubes. Deep-Sea Research 30, 591-614.

Mullineaux, L.S., 1987. Organisms living on manganese nodules and crusts: distribution and abundance at three North Pacific sites. Deep-Sea Research 34, 165-184.

Mullineaux, L.S., 1988. Taxonomic notes on large agglutinated foraminifers encrusting manganese nodules, including the description of a new genus, Chondrodapis (Komokiacea). Journal of Foraminiferal Research 18, 46-53.

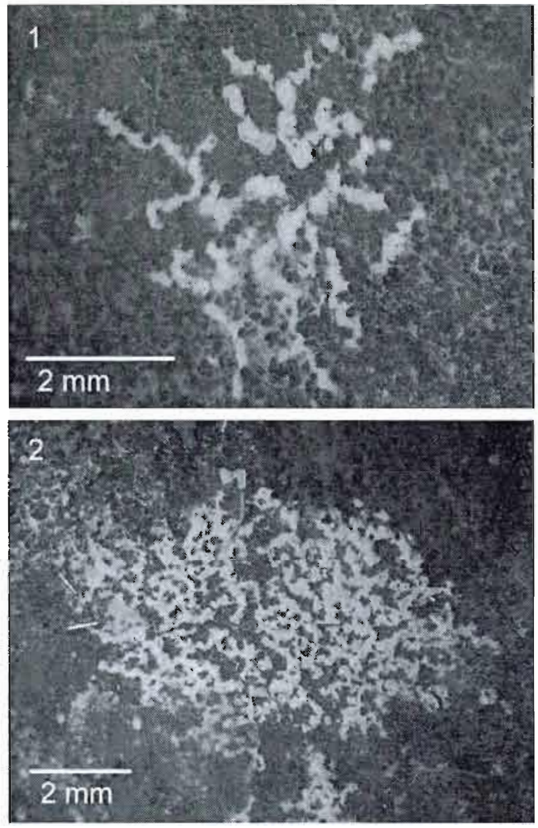
25) ***Tumidotubus*** Gooday and Haynes, 1983

Foraminifera, incertae sedis

Description: Test consists of anastomosing tubes with swellings at intervals, forming elongate chambers. The tubes radiate from a central point and sometimes branch. Test wall composed of occasional coarse particles rigidly cemented in a whitish matrix. No aperture observed. Protoplasm present in the chambers where stercomata are also observed.

Size: Can extend over an area of several cm^2, up to 60 cm^2. The actual surface covered by the test is generally 25% of that area but some specimens anastomose more tightly and the actual surface covered can be up to 60%.

Geographical distribution: Abyssal, found attached with manganese nodules below 4950m in the equatorial north Pacific. Abundant in the east zone, common in the west zone. Similar forms observed on experimental substrates on Cross Seamount and encrusting the interior of *Bathysiphon rusticus* tubes in the northeast Atlantic. Also reported on sponge stalks in the northeast Pacific at 4100m and on ice-rafted stones in northeast Atlantic at 4550m.



Tumidotubus. 1) Location: 14°3.41 N, 130°6.24 W, depth: 5005m, nodule KGS3-32. 2) Location: 13°55.63 N, 130°12.20 W, depth: 4985m, nodule PL1602-10_4.

References

Beaulieu, S.E., 2001. Life on glass houses: sponge stalk communities in the deep sea. Marine Biology 138, 803-817.

Bertram, M.A. and Cowen, J.P., 1994. Testate rhizopod growth and mineral deposition on experimental substrates from Cross Seamount. Deep-Sea Research I 41, 575-601.

Gooday, A.J. and Haynes, J.R., 1983. Abyssal foraminifers, including two new genera, encrusting the interior of *Bathysiphon rusticus* tubes. Deep-Sea Research 30, 591-614.

Mullineaux, L.S., 1987. Organisms living on manganese nodules and crusts: distribution and abundance at three North Pacific sites. Deep-Sea Research 34, 165-184.

Mullineaux, L.S., 1988. Taxonomic notes on large agglutinated foraminifers encrusting manganese nodules, including the description of a new genus, Chondrodapis (Komokiacea). Journal of Foraminiferal Research 18, 46-53.

26) *Xenophyophorea*-like, without agglutinated particles

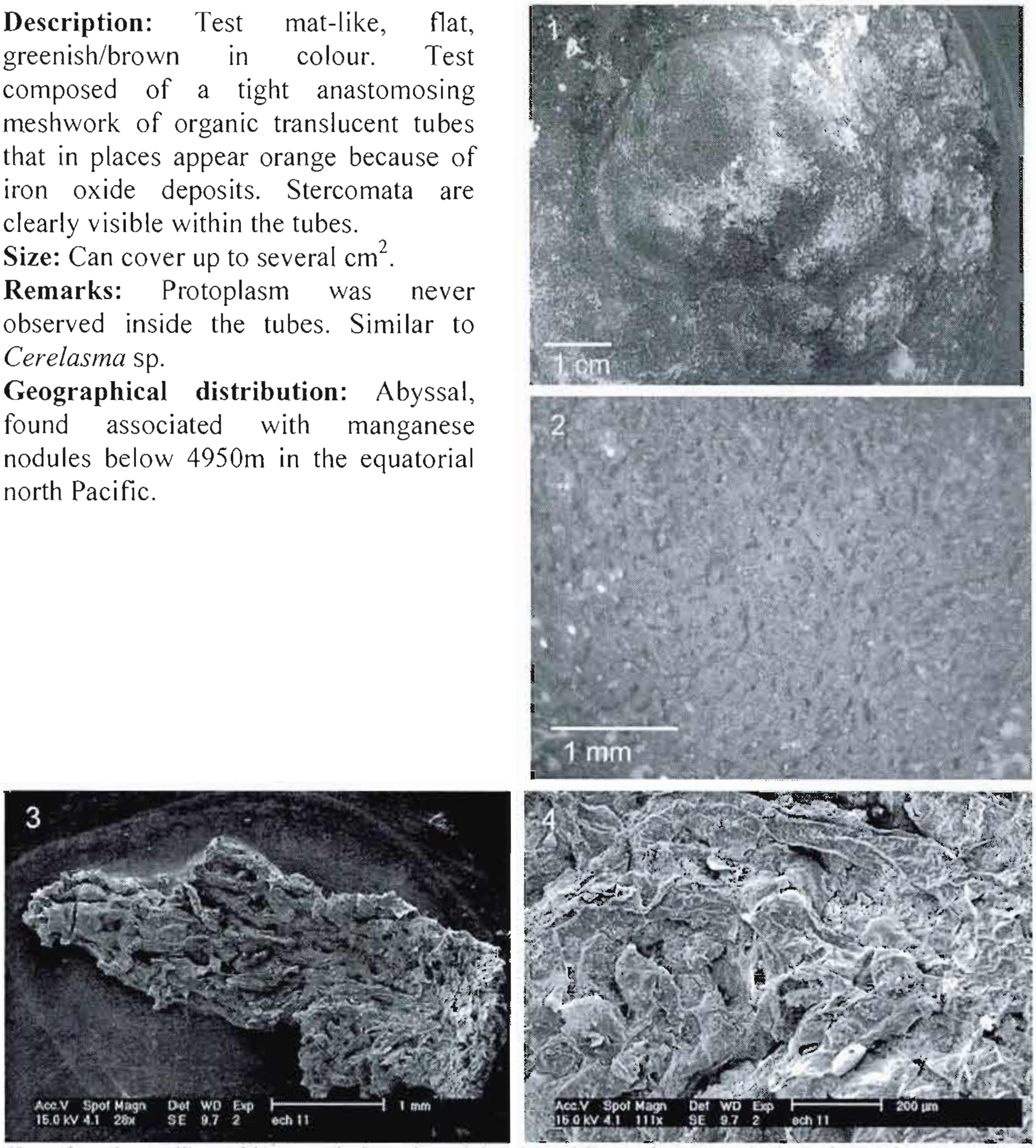
Foraminifera, incertae sedis

Description: Test mat-like, flat, greenish/brown in colour. Test composed of a tight anastomosing meshwork of organic translucent tubes that in places appear orange because of iron oxide deposits. Stercomata are clearly visible within the tubes.

Size: Can cover up to several cm^2.

Remarks: Protoplasm was never observed inside the tubes. Similar to *Cerelasma* sp.

Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific.

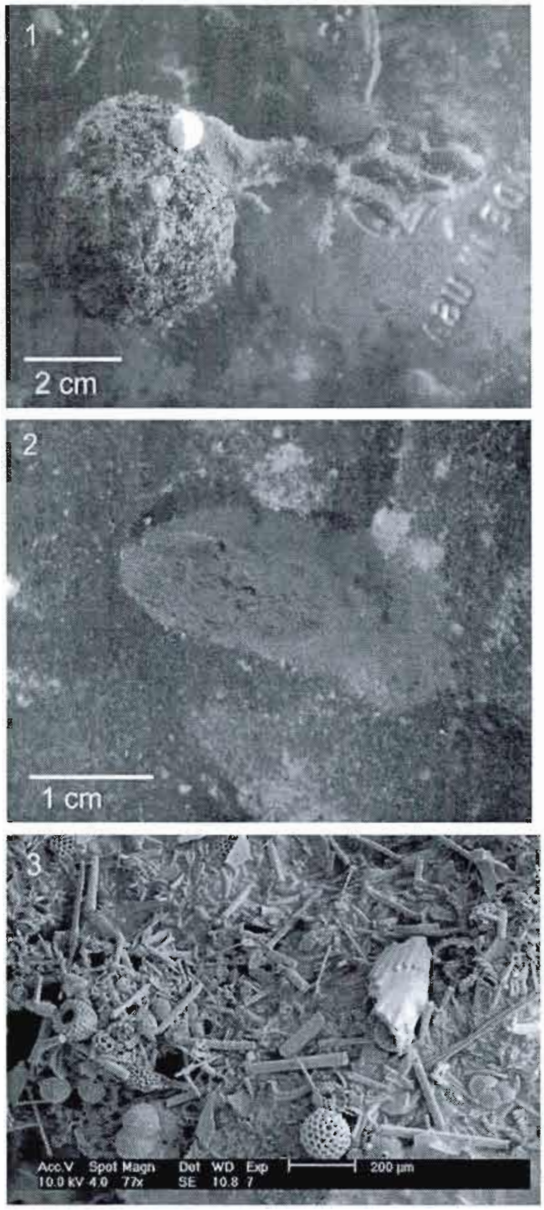


Xenophyophorea-like, without agglutinated particles. 1) and 2) are the same specimen but 2) is a closer view. Location: 13°55.63 N, 130°12.20 W, depth: 4980m, nodule PL1602-10-18. 3) and 4) Specimen alone.

27) *Xenophyophorea*-like, fan-shaped agglutinated

Foraminifera, incertae sedis

Description: Fan-shaped, fragile structure on upper surface of nodules. Test made of agglutinated particles of which sponge spicules are obvious. Stercomata visible but are in a decayed state.
Size: Could grow to several cm. Base cover several cm^2 of the nodule surface.
Remarks: All specimens were dead, judging from the decayed state of the stercomata.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific.

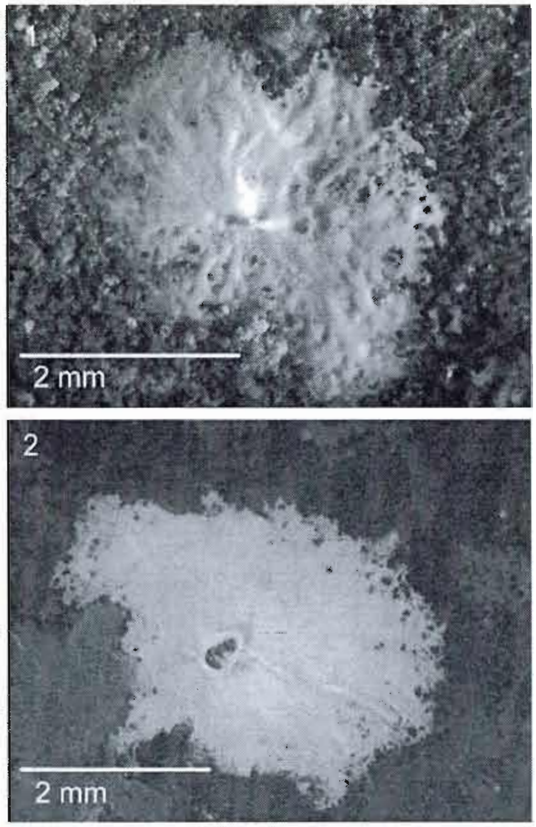


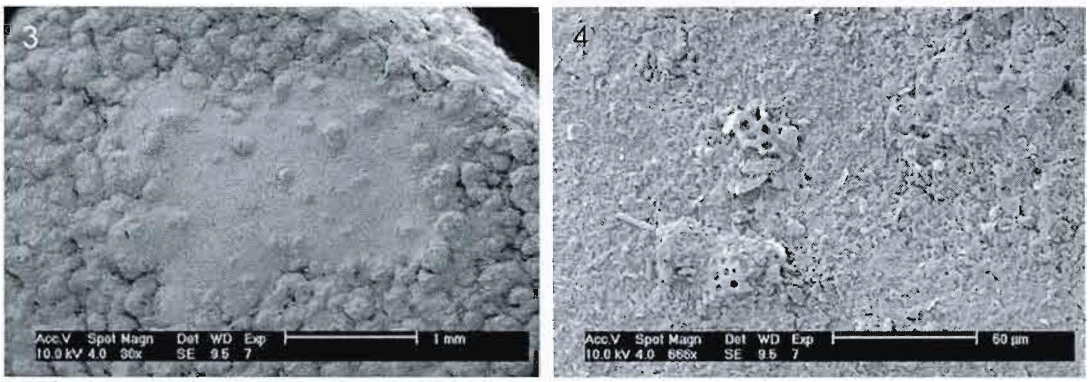
Xenophyophorea-like, fan-shaped agglutinated. 1) Unknown nodule. 2) Broken specimen, top view. Location: 13°55.63 N, 130°12.20 W, depth: 4980m, nodule PL1602-10-5. 3) Specimen test wall.

28) **"White crust"** Mullineaux, 1988

Foraminifera, Textulariina, Astrorhizacea

Description: Test colour varying from sparkling white to beige. Test outline irregular, not subdivided internally. Wall very thin, composed of fine agglutinated particles in a rigid matrix. Aperture can sometimes be observed. No stercome observed. However, Mullineaux (1988) mentioned that stercomata were abundant within protoplasm. Therefore, the taxon identified in the present study might be different from her.
Size: From 0.5 to 2mm in diameter.
Remarks: This taxon is one of the most distinctive of the nodule fauna. The protoplasm is not obvious thus it is hard to determine if this taxon was live when collected. The majority of the specimens observed were unbroken.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific.





"White crust". 1) Location: 14°2.63 N, 130°7.97 W, depth: 4930m, nodule KGS25-bizz2. 2) Location: 13°55.63 N, 130°12.20 W, depth: 4985m, nodule PL1598-6_1-1. 3) and 4) Specimen on nodule surface.

References

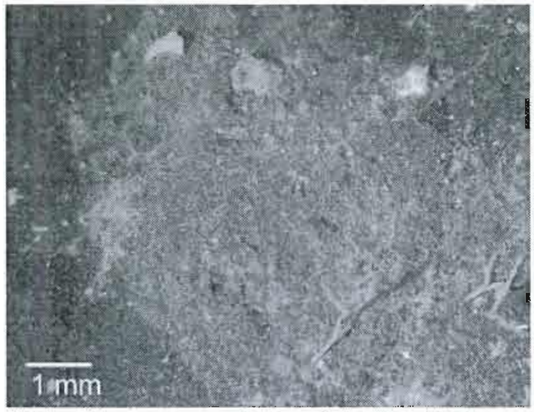
Mullineaux, L.S., 1987. Organisms living on manganese nodules and crusts: distribution and abundance at three North Pacific sites. Deep-Sea Research 34, 165-184.

Mullineaux, L.S., 1988. Taxonomic notes on large agglutinated foraminifers encrusting manganese nodules, including the description of a new genus, Chondrodapis (Komokiacea). Journal of Foraminiferal Research 18, 46-53.

29) **"Beige filamentous mat"** Mullineaux, 1988

Foraminifera, Textulariina, Astrorhizacea

Description: Mat-like test beige in colour, irregular in shape with a poorly-defined outline. Test wall thick composed of fine agglutinated particles loosely bound in an unconsolidated organic matrix. Underneath the test wall, there is visible an anastomosing network of organic tubes containing protoplasm. Sometimes, these tubes protrude out of the test wall and give a filamentous appearance to the mat. No stercome observed.
Size: Diameter up to 15mm.
Remarks: This taxon can easily be mistaken for sediment sticking to the nodule surface since particles on the outside of the mat are loosely bound and can easily be rinsed off during nodule sampling and preparation.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific. Common on facies C, rarely observed on facies A, B and in the west zone.



"Beige filamentous mat". Location: 14°3.10 N, 130°7.75 W, depth: 4954m, nodule KGS22-4.

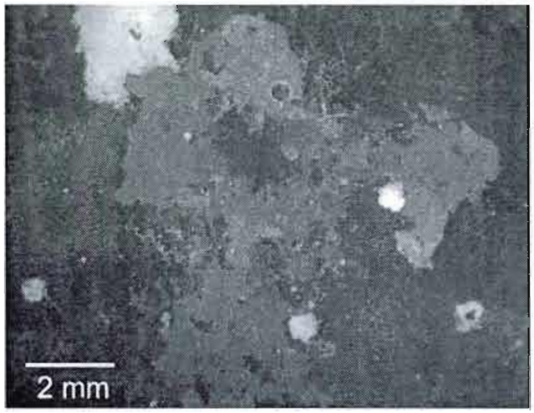
Reference

Mullineaux, L.S., 1988. Taxonomic notes on large agglutinated foraminifers encrusting manganese nodules, including the description of a new genus, Chondrodapis (Komokiacea). Journal of Foraminiferal Research 18, 46-53.

30) **"Dark chambered mat"** Mullineaux, 1988

Foraminifera, Textulariina, Astrorhizacea

Description: Thick mat divided into several large chambers by vertical septa. Test outline irregular. Test wall organic with fine clay particles agglutinated to the surface. Aperture not observed. Protoplasm dark (green to black) visible through the test. Stercomata very abundant in the protoplasm.
Size: Can cover up to 150mm^2 of nodule surface.
Remarks: Different from "flattened chambers" by the absence of small, discrete chambers.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific. Only observed on facies C.



"Dark chambered mat". Location: 13°55.63 N, 130°12.75 W, depth: 4970m, nodule PL1598-06_1-1.

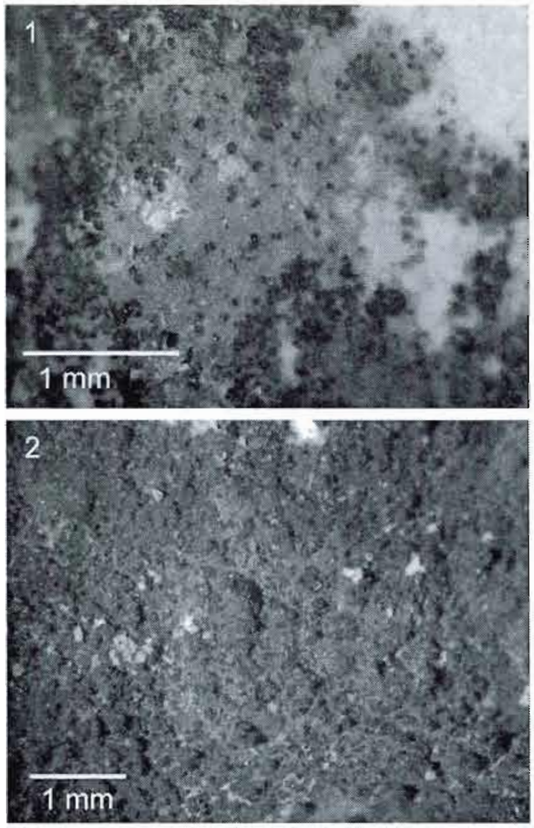
Reference

Mullineaux, L.S., 1988. Taxonomic notes on large agglutinated foraminifers encrusting manganese nodules, including the description of a new genus, Chondrodapis (Komokiacea). Journal of Foraminiferal Research 18, 46-53.

31) Thin grey mat

Foraminifera, incertae sedis

Description: Thin mat with a poorly-defined outline which conforms to the nodule surface and varies from clear grey to black in colour. There are no chambers or surface filaments. Test made of agglutinated particles loosely bounded in an organic matrix. Stercome not observed. This taxon has a very variable shape and probably include more than one distinct form. Sometimes, the mat-like test develops spaces and may break down into a series of tunnels.
Size: Can cover up to $50mm^2$ of nodule surface.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific. Abundant on facies B and C, common in the west zone.

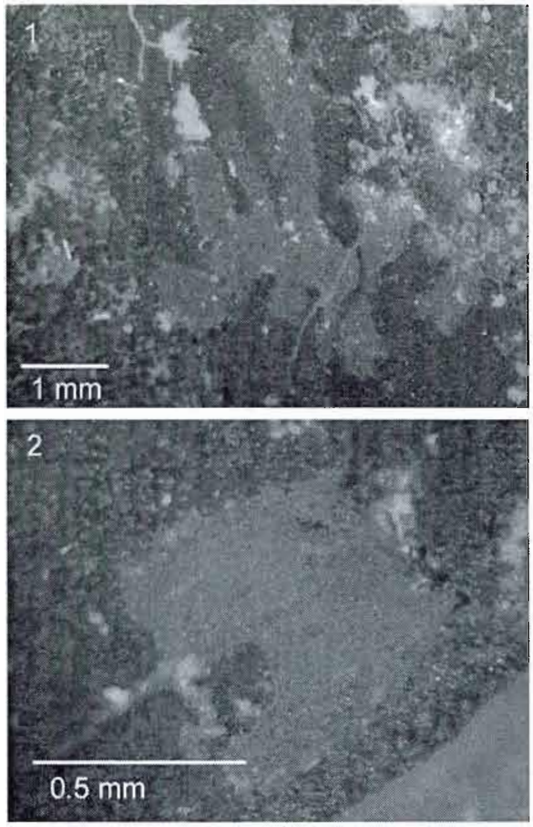


Thin grey mat. 1) Location: 13°55.63 N, 130°12.20 W, depth: 5030m, nodule PL1593-01_2.
2) Location: 9°33.20 N, 150°0.41 W, depth: 5050m, nodule KGS28-5.

32) Thin organic mat with dark grey stercomata

Foraminifera, incertae sedis

Description: Thin mat of variable shape conforming to the nodule surface. Test wall organic, without agglutinated particle. Stercomata clearly visible through the translucent test wall.
Size: Can cover several mm^2 of nodule surface.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific. Very common on every facies.



Thin organic mat with dark grey stercomata.
1) Location: 14°3.10 N, 130°7.75 W, depth: 4954m, nodule KGS22-4. 2) Location: 14°2.48 N, 130°8.44 W, depth: 4935m, nodule KGS23-4.

33) Beige thick mat with red interior

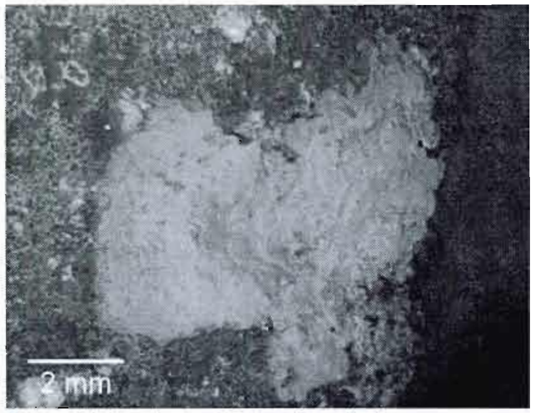
Foraminifera, incertae sedis

Description: Thick, beige-coloured mat composed of fine, weakly cemented particles. The interior is red and assumed to be the protoplasm.
Size: Can cover up to 50mm^2 of nodule surface.
Remarks: Very similar to "beige thick and smooth mat, interior brown" but the red-coloured interior is a distinguishing feature.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific.

34) Beige thick and smooth mat, interior brown

Foraminifera, incertae sedis

Description: Thick, beige-coloured mat with a smooth, rather lumpy surface. Wall composed of fine, agglutinated particles cemented loosely together. Test interior is brown. No obvious stercome.
Size: Can cover up to $75mm^2$ of nodule surface.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific. Common on facies B and C.

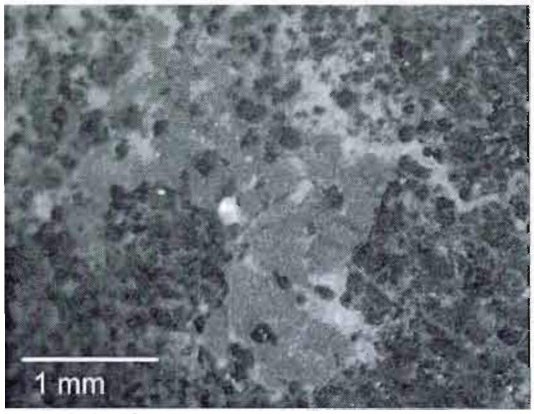


Beige thick and smooth mat, interior brown. Location: 14°2.80 N, 130°8.18 W, depth: 4911m, nodule KGS21-4.

35) Mat of blue flattened chambers

Foraminifera, incertae sedis

Description: Test form composed of flattened chambers connecting together. Wall blueish in colour with speckly refletive sheen; composed of agglutinated particles in an organic matrix.
Size: Diameter of 1 to 3mm.
Remarks: Very similar to "flattened chambers" but individual chambers are bigger and form a mat, not a chain.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific. Common in the east zone.

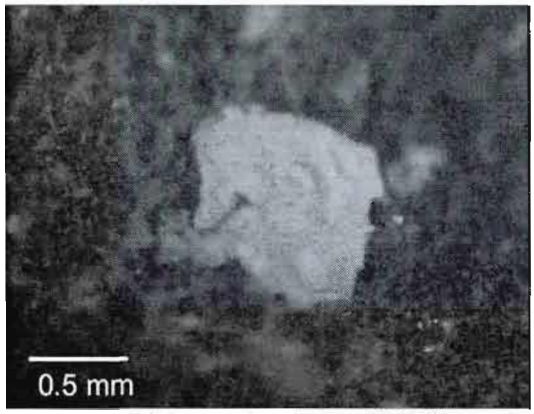


Mat of blue flattened chambers. Location: 14°3.41 N, 130°6.24 W, depth: 5005m, nodule KGS3-2.

36) White mat with lumps

Foraminifera, incertae sedis

Description: Delicate mat with clearly-defined, more or less circular outline. Wall thin like a sheet of paper, white, composed of fine particles. Underside of test is white and has the texture of wool. Stercomata are present in the interior.
Size: Around 1mm in diameter.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific. Common on facies B, C and in the west zone.

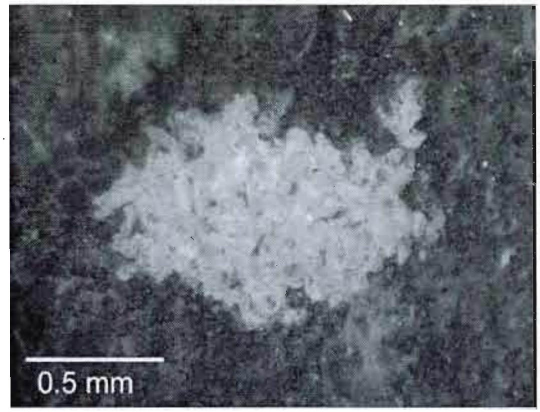


White mat with lumps. Location: 14°2.63 N, 130°7.97 W, depth: 4930m, nodule KGS25-bizz1.

37) White crusty mat with coarse particles

Foraminifera, incertae sedis

Description: White granular mat. Test wall composed of fine white agglutinated particles with scattered coarse particles.
Size: Around 1mm in diameter.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific.

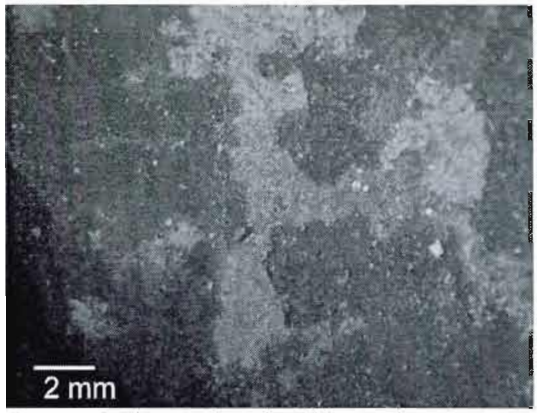


White crusty mat with coarse particles. Location: 9°33.12 N, 150°0.51 W, depth: 5043m, nodule KGS33-7.

38) Orange, rigid agglutinated wall in crevice

Foraminifera, incertae sedis

Description: Very coarsely agglutinated orange-coloured test wedged into crevices or attached to the lower areas of nodules.
Size: Can cover up to several cm^2 of nodule surface.
Remarks: All specimens of this taxon were dead.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific. Abundant on facies C, common on facies B and in the west zone. Seems to be present only on the biggest nodules and located in crevices close to the sediment line.

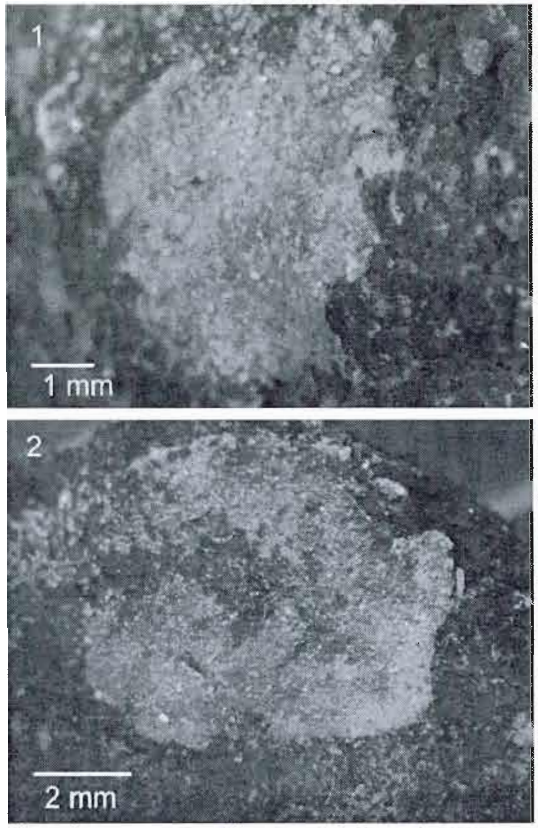


Orange, rigid agglutinated wall in crevice.
Location: 13°55.63 N, 130°12.75 W, depth: 4970m, nodule PL1598-06_4-2.

39) Mat of very coarse sediment agglutinated

Foraminifera, incertae sedis

Description: Very fragile mat composed of coarse, weakly-cemented sediment grains, including sponge spicules and radiolarians.
Size: Can cover up to several cm^2 of nodule surface.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific. Common on facies B, C and in the west zone.



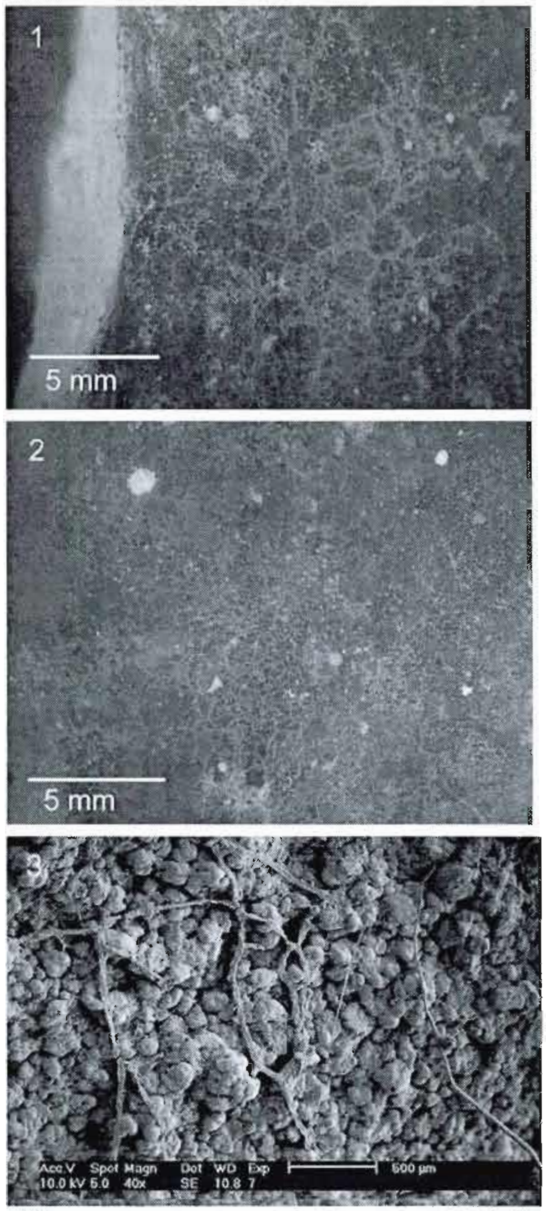
Mat of very coarse sediment agglutinated.
1) Location: 9°33.81 N, 150°0.98 W, depth: 5051m, nodule: KGS30-1. 2) Location: 9°33.81 N, 150°0.98 W, depth: 5051m, nodule: KGS30-8.

1.3 TUNNELS

40) **"Thin anastomosing tunnels"** Mullineaux, 1988

Foraminifera, Textulariina, Astrorhizacea

Description: Anastomosing tunnels spreading out across conforming to the nodule surface, mostly between botryoids. Test outline poorly-defined. Test wall thin composed of fine agglutinated particles. Aperture or stercome not observed.
Size: Can cover large areas, up to $3cm^2$ of nodule surface including pores. However, the actual surface covered by the taxon is about 20% of that area. Tunnels are narrow; less than 20µm in diameter.
Remarks: Taxon very similar to the anastomosing network of tubes underneath the test wall of "beige filamentous mat".
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific. Very abundant on every facies.



"Thin anastomosing tunnels". 1) Location: 13°55.63 N, 130°12.75 W, depth: 4970m, nodule PL1598-06_4-1. 2) Location: 13°55.63 N, 130°12.75 W, depth: 4970m, nodule PL1598-06_1-1. 3) Specimen on nodule surface.

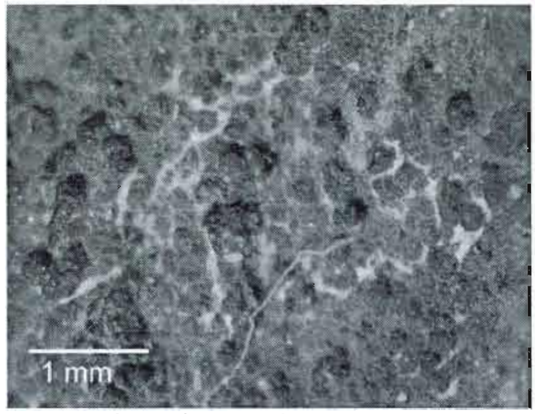
Reference

Mullineaux, L.S., 1988. Taxonomic notes on large agglutinated foraminifers encrusting manganese nodules, including the description of a new genus, Chondrodapis (Komokiacea). Journal of Foraminiferal Research 18, 46-53.

41) **"Cemented tunnels"** Mullineaux, 1988

Foraminifera, Textulariina, Astrorhizacea

Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific. Common on every facies.
Size: Cover areas less than 1mm^2 including pores.
Description: Anastamosing narrow tunnels between botryoids on nodule surface. Test wall rigidly cemented with white or orange matrix, sparse fine particles agglutinated to the surface. Aperture or stercome not observed.
Remarks: Test wall very similar to the one of "white crust" except for the colour varying from white to orange.



"Cemented tunnels". Location: 13°55.63 N, 130°12.20 W, depth: 4980m, nodule PL1602-10-18.

Reference

Mullineaux, L.S., 1988. Taxonomic notes on large agglutinated foraminifers encrusting manganese nodules, including the description of a new genus, Chondrodapis (Komokiacea). Journal of Foraminiferal Research 18, 46-53.

42) Reticulated dark tunnels

Foraminifera, incertae sedis

Description: Network of green-coloured flattened tunnels.
Remarks: Similar to the genus *Rhizammina* which has been reported on nodule surface by Dudley and Margolis (1974).
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific. Common on every facies.

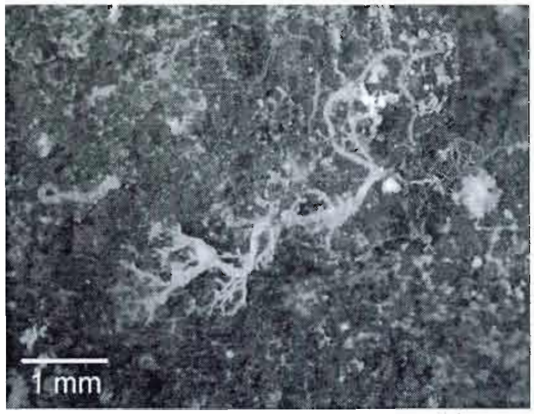
Reference

Dudley, W.C. and Margolis, S.V., 1974. Iron and trace element concentration in marine manganese nodules by benthic agglutinated foraminifera. Geological Society of America, Abstracts with Programs 6, 716.

43) Network of beige tunnels; horizontal tree with upright branches

Foraminifera, incertae sedis

Description: Recumbent beige-coloured tunnel from which upright fine branches with ramifications are protruding. Test wall organic and flexible with sparse particles agglutinated to the surface.
Size: Upright branches and the recumbent tunnel are several mm in length.
Remarks: Similar to *Rhizammina globigerinifera* (Hofker, 1930). In the west zone, where nodule surface is rough, this taxon is often deduced from the tips of the upright branches.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific. Common on every facies.



Network of beige tunnels; horizontal tree with upright branches. Location: 9°33.46 N, 150°0.03 W, depth: 5048m, nodule KGS36-1.

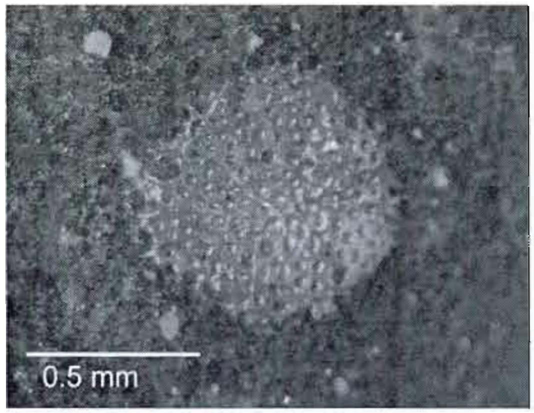
Reference

Dudley, W.C. and Margolis, S.V., 1974. Iron and trace element concentration in marine manganese nodules by benthic agglutinated foraminifera. Geological Society of America, Abstracts with Programs 6, 716.

44) Crystal star and tunnels

Foraminifera, incertae sedis

Description: Two morphotypes are observed: tunnels and a star. Monothalamous. Test wall are silvery in colour with reflective sheen.
Size: About 1mm in diameter for the star morphotype. The diameter of the tunnels morphotype is about 250µm.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific. Common on facies B and C.



Crystal star and tunnels. Location: 13°55.63 N, 130°12.20 W, depth: 4985m, nodule PL1603-11_2-1.

45) Spider network of grey tunnels

Foraminifera, incertae sedis

Description: Networks of anastomosing grey tunnels of variable shape with a well-defined outline, mostly located between botryoids. Aperture or stercome not observed.
Size: Networks can cover several cm^2. However, the actual surface covered by the taxon is about 25% of that area.
Remarks:. Similar to "thin anastomosing tunnels" but the tunnels of "spider network of grey tunnels" are much thicker. The well-defined outline of "spider network of grey tunnels" is also a distinguishing feature. This taxon includes all the different forms of anatomosing grey tunnels. Therefore, an unknown but probably large plasticity exists within this taxon.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific. Abundant on facies B and C, common on facies A and in the west zone.

46) White soft tunnels

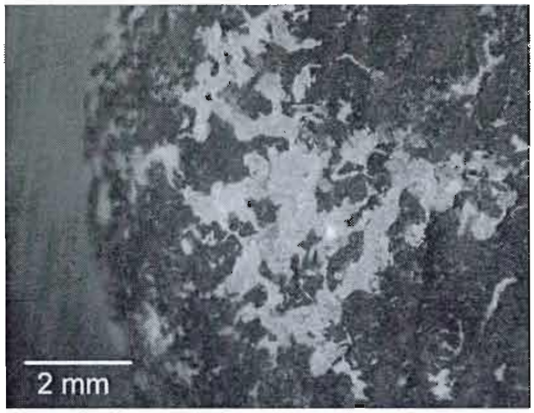
Foraminifera, incertae sedis

Description: White tunnels between bothryoids. Test wall organic and flexible with white fine particles agglutinated to the surface. Aperture or stercome not observed.
Size: Can cover 1 or 2cm^2. However, the actual surface covered by the taxon is about 25% of that area.
Remarks: Similar to *Tumidotubus* but the main difference is that the test wall of "white soft tunnels" are very flexible while the one of *Tumidotubus* is rigidly cemented. Also, the radiating pattern of the anastomosing tunnels of *Tumidotubus* is particular to this genus.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific. Abundant on facies C, common on facies A, B and in the west zone.

47) Network of empty beige tunnels

Foraminifera, incertae sedis

Description: Empty beige-coloured rounded tunnels of a large diameter. No stercome observed.
Size: Can cover up to 75mm^2.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific.



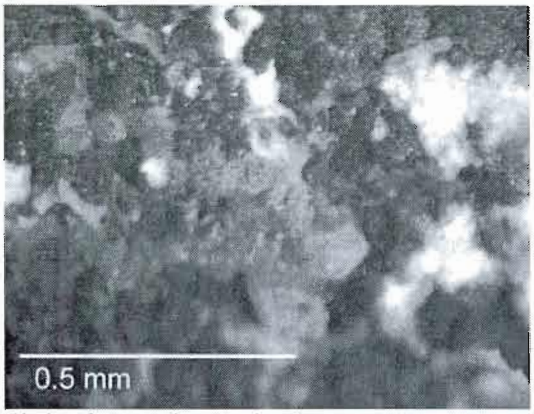
Network of empty beige tunnels. Location: 14°2.48 N, 130°8.44 W, depth: 4935m, nodule KGS23-5.

1.4 CONNECTED CHAMBERS

48) Chain of orange/brown chambers

Foraminifera, incertae sedis

Description: Single line of several rounded, empty chambers of similar size. Test wall made of agglutinated orange/brown sand grains, rigid surface. Aperture not observed.
Size: Chain of about 1mm in length.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific. Common in the east zone.

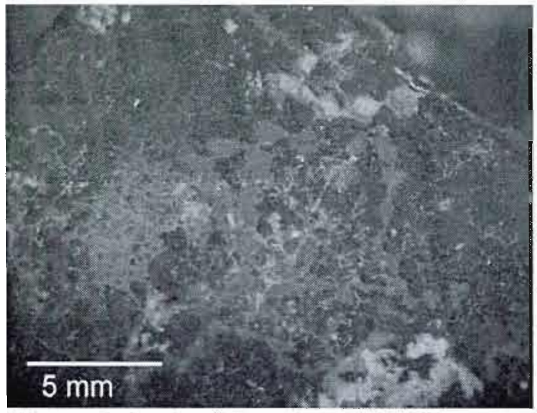


Chain of orange/brown chambers. Location: 14°2.80 N, 130°8.18 W, depth: 4911m, nodule KGS21-2.

49) **"Flattened chambers"** Mullineaux, 1988

Foraminifera, Textulariina, Astrorhizacea

Description: Several rounded and thin connected chambers of a similar size. Chambers outline regular and well defined. Test wall organic and thin with fine clay particles agglutinated on the surface. Aperture not observed. Protoplasm dark (green to black) visible through the test. Stercomata very abundant in the protoplasm and present in every chamber.



"Flattened chambers". Location: 14°2.80 N, 130°8.18 W, depth: 4911m, nodule KGS21-7.

Size: Can cover areas from 1 to 20 mm^2. However, the actual surface covered by the taxon is about half of that area. Chambers diameter is about 500 µm

Remarks: Test similar to "dark chambered mat".

Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific. Abundant on facies C and B, common on facies A and in the west zone.

References

Mullineaux, L.S., 1987. Organisms living on manganese nodules and crusts: distribution and abundance at three North Pacific sites. Deep-Sea Research 34, 165-184.

Mullineaux, L.S., 1988. Taxonomic notes on large agglutinated foraminifers encrusting manganese nodules, including the description of a new genus, Chondrodapis (Komokiacea). Journal of Foraminiferal Research 18, 46-53.

50) Chain of empty grey and rounded chambers

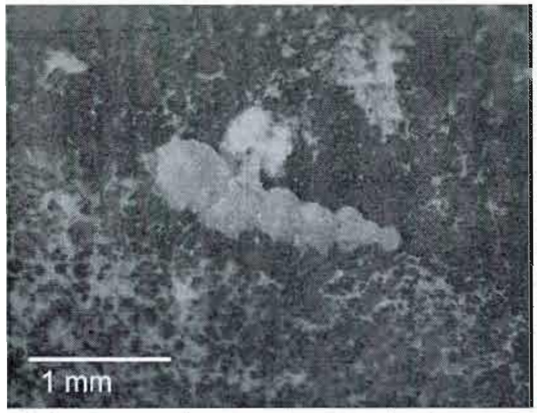
Foraminifera, incertae sedis

Description: Chain of several chambers. Test wall rigid, made of coarse agglutinated particles. Chambers are always empty.
Size: Several mm in length.
Remarks: Different from "flattened chambers" by the rounded appearance of the test.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific.

51) *Hormosina* sp.

Foraminifera, incertae sedis

Description: Chain of several rounded chambers decreasing regularly in size. Wall test made of orange grains cemented rigidly. Chambers always observed empty.
Size: About 2mm in length.
Remarks: An attached *Hormosina*. Similar to *H .globulifera* but chambers are less globular. Dudley and Margolis (1974) reported the presence of the genus *Hormosina* on nodule surface.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific. Several specimens present on every facies.



Chain of orange chambers decreasing in size. Location: 13°55.63 N, 130°12.20 W, depth: 5000m, nodule PL1593-01_4.

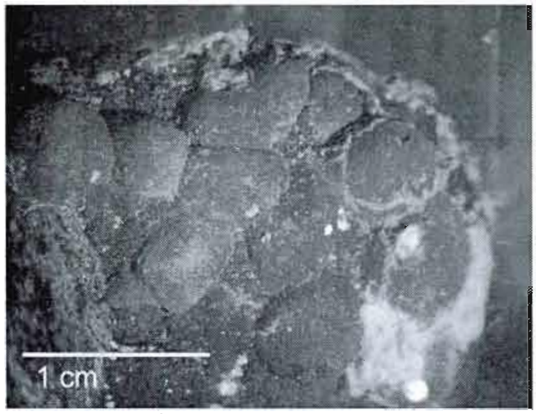
Reference

Dudley, W.C. and Margolis, S.V., 1974. Iron and trace element concentration in marine manganese nodules by benthic agglutinated foraminifera. Geological Society of America, Abstracts with Programs 6, 716.

52) Brown chain of spheres rigidly agglutinated

Foraminifera, incertae sedis

Description: Several very large hemispheres of varying size and shape linked together. Wall test made of brown sediment grains very rigidly agglutinated.
Size: Can cover large areas, up to 225 mm^2. However, the actual surface covered by the taxon is about 75% of that area.
Remarks: One of the largest form associated with nodule surface observed. Other foraminiferal forms seem to live on the taxon.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific.

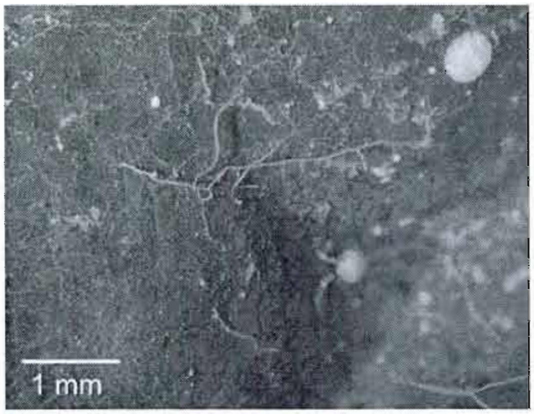


Brown chain of spheres rigidly agglutinated.
Location: 14°3.10 N, 130°7.75 W, depth: 4954m, nodule KGS22-bizz1.

1.5 UPRIGHT TUBES

53) Network of branched tubes either lying down on the nodule surface or standing

Foraminifera, incertae sedis



Network of branched tubes either lying down on the nodule surface or standing. Location: 9°33.60 N, 150°0.84 W, depth: 5050m, nodule KGS29-4.

Description: Tubes anastomosing on the nodule surface and vertically, creating a loose meshwork. Tube wall is organic and flexible. No stercome observed in the tubes.

Size: Often present on large areas, up to $3cm^2$.

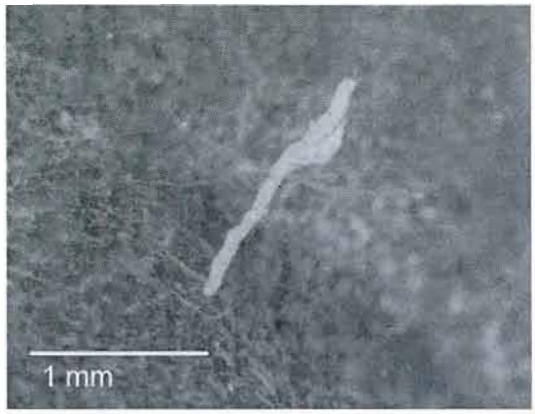
Remarks: Often mixed with other foraminiferal forms. In cases where only one or two upright tubes are observed, they can be identified as "branched upright tubules". In the west zone, this taxon is a little different, probably because of the difference in the nodule surface: tubes are shorter, more damaged and fluffy sediment covers the taxon.

Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific. Abundant on facies B and C, common on facies A and in the west zone.

54) *Psammotodendron indivisum*-like

Foraminifera, incertae sedis

Description: Upright beige tubule without chamber at the base.
Size: Few mm in length.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific.

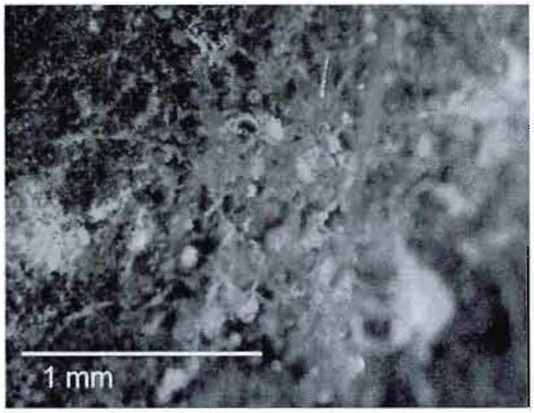


Psammotodendron indivisum- like. Location: 14°3.41 N, 130°6.24 W, depth: 5005m, nodule KGS3-3.

55) Komokiacean-like chambers on delicate filaments

Foraminifera, incertae sedis

Description: Network of upright tubules with swellings at their ends mixed with agglutinated sponge spicules and other sediment grains agglutinated. Test wall organic with sparse fine particles agglutinated on the surface. Stercomata obvious in the swellings at the end of the tubules.
Size: Few mm in diameter and in height.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific.

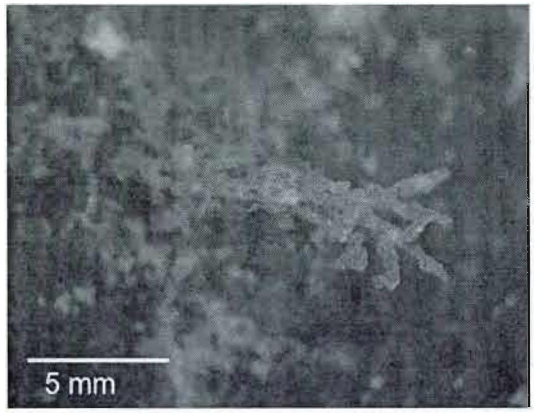


Komokiacean-like chambers on delicate filaments. Location: 14°2.80 N, 130°8.18 W, depth: 4911m, nodule KGS21-4.

56) Upright beige tubules with constrictions

Foraminifera, incertae sedis

Description: Upright beige tubules branching dichotomously and constricted almost every mm. Test wall is organic with fine particles agglutinated on the surface. Tubules are full of stercomata.
Size: Tubule length up to 15mm.
Remarks: Not a Komokiacea.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific.



Upright beige tubules with constrictions.
1) Location: 14°3.41 N, 130°6.24 W, depth: 5005m, nodule KGS3-3.

57) Upright beige structures

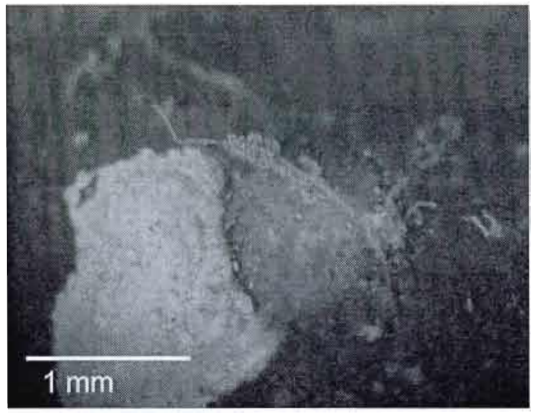
Foraminifera, incertae sedis

Description: 5 or 6 protruding upright beige structures, tubule-like, close together. Test wall organic with fine particles agglutinated on the surface.
Remarks: Similar to *Psammotodendron indivisum* (Rhabdammina) but no chamber at the base. Probably a new genus (Gooday, 2004, pers. comm.).
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific. Only one specimen observed.

58) Tube upright with komokiacean-like chambers

Foraminifera, incertae sedis

Description: Komokiacean-like chambers attached to a dead organic upright tube. Fine beige sediment particles agglutinated to the chambers. Chambers are full of stercomata.
Size: Several mm in length.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific.

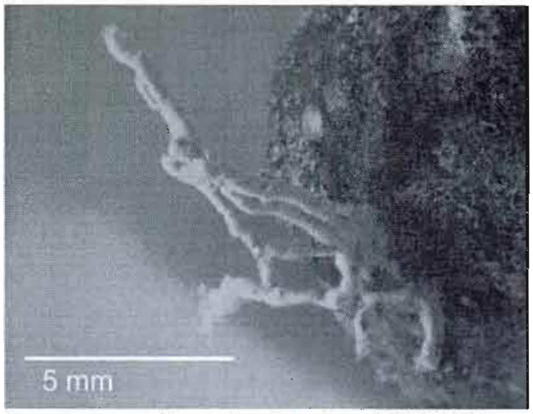


Tube upright with komokiacean-like chambers. (It is the structure in the foreground, in front of the sponge.) Location: 13°55.63 N, 130°12.20 W, depth: 4990m, nodule PL1593-01-4.

59) Branched upright tubules

Foraminifera, incertae sedis

Description: Beige-coloured tubules of a constant diameter branching in an irregular pattern. Test made of clay loosely bound in an organic matrix. Stercomata visibles.
Size: Length of the tubules up to 2cm.
Remarks: Similar to *Lana* sp. (Tendal and Hessler, 1977), but not forming a large mass of tubules. A distinguishing feature of the taxon is its branching.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific. Common on facies B and C.

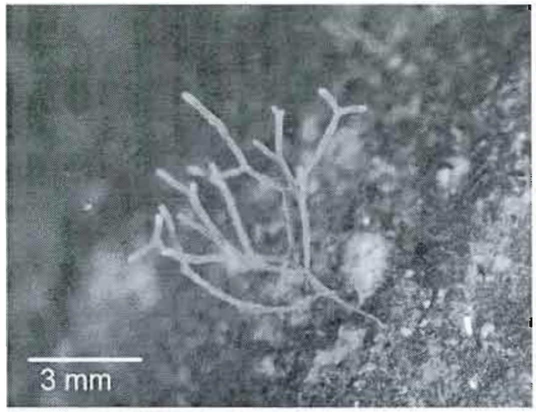


Branched upright tubules. Location: 13°55.63 N, 130°12.20 W, depth: 4980m, nodule: PL1593-02-1.

60) Upright tree

Foraminifera, incertae sedis

Description: Upright tubule branching a few times at a certain point. Test wall organic. Few stercomata observed.
Size: Up to a height of 15mm.
Remarks: Always only one tubule attaches to the nodule surface. It is certainly a new genus (Gooday, pers. comm.).
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific.

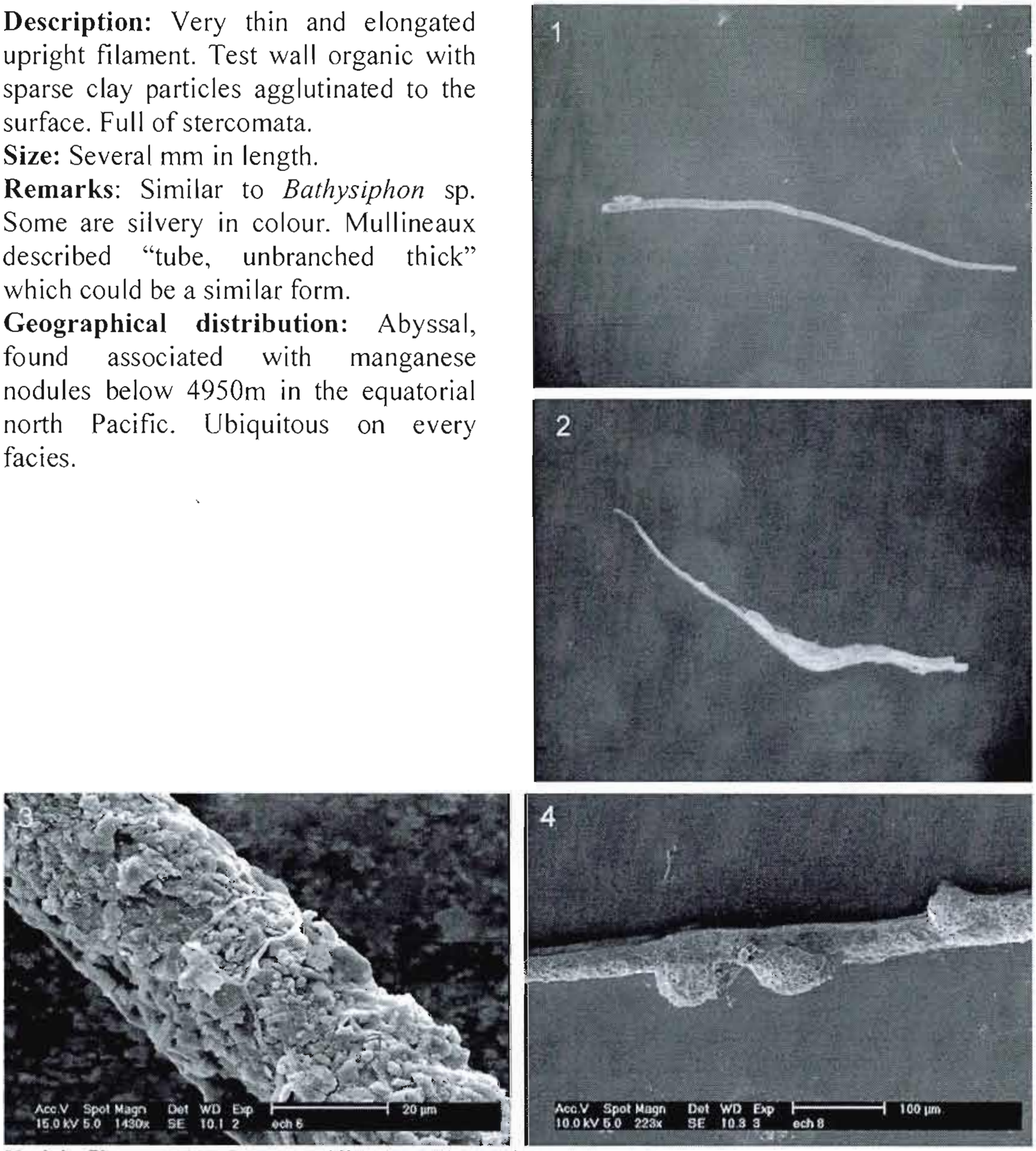


Upright tree. Location: 13°55.63 N, 130°12.20 W, depth: 4970m, nodule: PL1598-06_5-2.

61) Upright filament

Foraminifera, incertae sedis

Description: Very thin and elongated upright filament. Test wall organic with sparse clay particles agglutinated to the surface. Full of stercomata.
Size: Several mm in length.
Remarks: Similar to *Bathysiphon* sp. Some are silvery in colour. Mullineaux described "tube, unbranched thick" which could be a similar form.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific. Ubiquitous on every facies.



Upright filament. 1) and 2) Two different specimens from two unknown nodules. 3) Specimen alone. 4) Upright filament with three chambers of *Telammina* sp.

Reference

Mullineaux, L.S., 1987. Organisms living on manganese nodules and crusts: distribution and abundance at three North Pacific sites. Deep-Sea Research 34, 165-184.

62) Upright filament, branched dichotomously

Foraminifera, incertae sedis

Description: Exactly like "upright filament" but branched dichotomously.
Size: Several mm in length.
Remarks: One branching is the distinguishing feature of this taxon from "upright tree" or "network of branched tubes either lying down on the nodule surface or standing".
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific. Common in the east zone.

63) Upright beige tubule, two origins

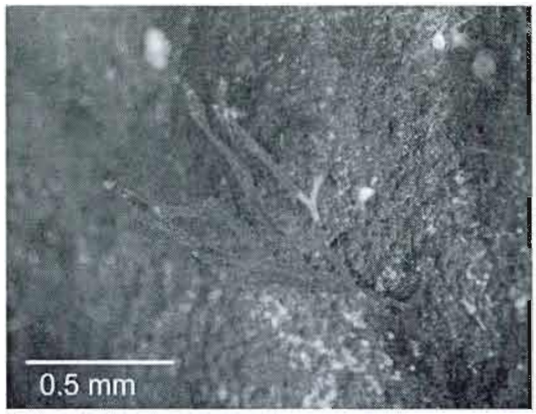
Foraminifera, incertae sedis

Description: Upright beige tubule with two origins; two tubules are attached together to the nodule surface and then, they merge to form a single tubule. Test wall made of clay loosely bound in an organic matrix. Stercomata visibles.
Size: Several mm in length.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific.

64) Branching stercomata-filled tube

Foraminifera, incertae sedis

Description: Thin translucent tube with one origin branching dichotomously. Test wall organic. Tubes are filled with stercomata.
Size: Several mm in length.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific. Common on facies C. A similar form "transparent, stercomata-filled tubes" found attached to the interior of *Bathysiphon rusticus* tubes. "Branched tubular foraminifer filled with brown and black stercomata" also observed on nodule surface by Riemann (1983).



"Branching stercomata-filled tube". Location: 13°55.63 N, 130°12.20 W, depth: 4980m, nodule: PL1602-10-1.

References

Gooday, A.J. and Haynes, J.R., 1983. Abyssal foraminifers, including two new genera, encrusting the interior of *Bathysiphon rusticus* tubes. Deep-Sea Research 30, 591-614.

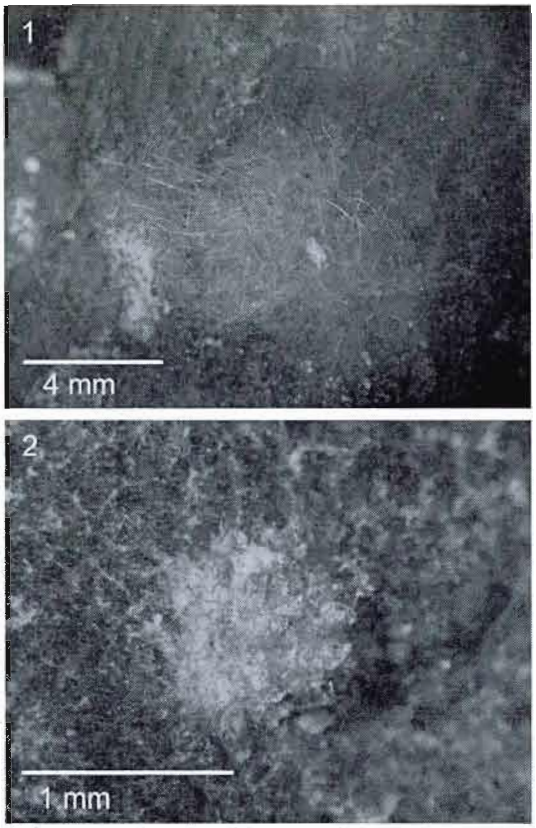
Mullineaux, L.S., 1987. Organisms living on manganese nodules and crusts: distribution and abundance at three North Pacific sites. Deep-Sea Research 34, 165-184.

Riemann, F., 1983. Biological aspects of deep-sea manganese nodule formation. Oceanologica Acta 6, 303-311.

65) Anastomosing *Rhizammina*-like tubes

Foraminifera, incertae sedis

Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific. Several specimens observed on every facies. Dudley and Margolis (1974) reported the presence of the genus *Rhizammina* on nodules.
Size: From 1 to 10mm in diameter.
Description: Anastomosing mesh-like network of tightly packed tubules. No upright filaments protruding out of the network. Test wall organic with fine particles agglutinated in the network. No stercome observed.
Remarks: Similar to *Lana neglecta* because of the anastomosing pattern and to *Rhizammina* because of the morphology of the tubes.



Tubes network; mix of *Lana neglecta* and *Rhizammina*. 1) Location: 13°55.63 N, 130°12.20 W, depth: 4980m, nodule: PL1602-10_15.
2) Location: 9°23.69 N, 150°05.72 W, depth: 5040m, nodule: PL1605-13_1-12.

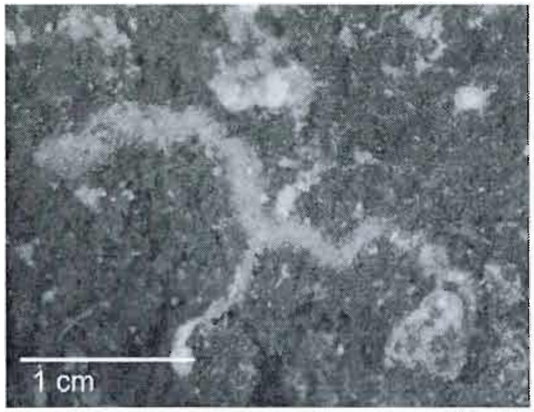
Reference

Dudley, W.C. and Margolis, S.V., 1974. Iron and trace element concentration in marine manganese nodules by benthic agglutinated foraminifera. Geological Society of America, Abstracts with Programs 6, 716.

1.6 RECUMBENT TUBES

66) *Saccorhiza ramosa*-like

Foraminifera, Textulariina, Hippocrepinacea, Astrorhizidae



Saccorhiza ramosa-like. Location: 9°33.92 N, 150°0.54 W, depth: 5051m, nodule: KGS38-6.

Description: Long recumbent tube, chaotically coiled and encrusted in the nodule surface. Test wall thick composed of agglutinated sponge spicules, protruding up almost at right angle of the test, and coarse sand grains. The general appearance of the test is spinose and sparkling. Most specimens are yellow. Apertures formed by open ends of tube (Loeblich and Tappan, 1964).
Size: Diameter of the tube is about 250μm and the length of the entire organism can be several cm.
Remarks: *Saccorhiza ramosa*-like leaves a remnant scar on the nodule surface. Normally, *Saccorhiza ramosa* sits erect in the sediment and is not attached. Also, since no intact specimen was observed, it was difficult to identify it as *Saccorhiza ramosa.*
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific, in the south Pacific and in the Southern Ocean. Also, found in box-cores taken from the northwest Atlantic Ocean.

References

Dudley, W.C., 1976. Cementation and iron concentration in foraminifera on manganese nodules. Journal of Foraminiferal Research 6, 202-207.

Dugolinsky, B.K., 1976. Chemistry and morphology of deep-sea manganese nodules and the significance of associated encrusting protozoans on nodule growth. PhD, unpublished.

Loeblich, A.R.Jr and Tappan, H., 1964. Sarcodina, chiefly "Thecamoebians" and Foraminiferida. In: Moore, R.C. (Ed.), Treatise on Invertebrate Paleontology, Part C, Protista. The Geological Society of America and the University of Kansa Press, New York and Lawrence, KS, pp. 900 pages.

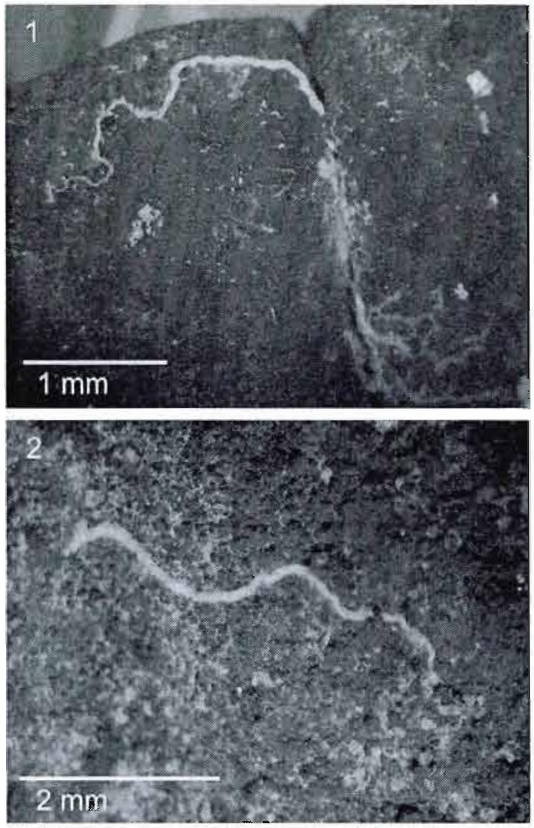
Mullineaux, L.S., 1987. Organisms living on manganese nodules and crusts: distribution and abundance at three North Pacific sites. Deep-Sea Research 34, 165-184.

Schröder, C.J., 1986. Deep-water arenaceous foraminifera in the northwest Atlantic Ocean. Canadian Technical Report of Hydrography and Ocean Sciences 1-191.

67) *Tolypammina* sp.

Foraminifera, Textulariina, Ammodiscidae

Description: Large globular proloculus followed by a long tubular second chamber of smaller diameter that winds irregularly on the nodule surface. Test wall composed of sparse agglutinated particles rigidly cemented in an orange or reddish matrix. Aperture observed at the open end of the second chamber.
Size: Diameter of the tube is about 50µm and the length of the organism can be several cm.
Remarks: *Tolypammina* sp. leaves a remnant scar on the nodule surface that can stay for a long period. The large majority of observed specimens were fragments or scars; only a few specimens were intacts.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific and in the Atlantic. Also reported in nodule crevices from abyssal southeast Pacific. It is the most abundant taxon on every facies. Dugolinsky (1976) also noted that *Tolypammina vagans* is one of the most widespread form found on nodules from the northeast Pacific. One specimen found encrusting the interior of *Bathysiphon rusticus* tubes and reported in box-cores taken from the northwest Atlantic Ocean. Indurated sediments in close proximity to vent sites are colonized by *Tolypammina* sp. as well.



Tolypammina sp. 1) Unknown nodule. 2) Location: 9°33.20 N, 150°0.41 W, depth: 5050m, nodule: KGS28-5.

References

Dugolinsky, B.K., 1976. Chemistry and morphology of deep-sea manganese nodules and the significance of associated encrusting protozoans on nodule growth. PhD, unpublished.

Gooday, A.J. and Haynes, J.R., 1983. Abyssal foraminifers, including two new genera, encrusting the interior of *Bathysiphon rusticus* tubes. Deep-Sea Research 30, 591-614.

Jonasson, K.E., Schröder-Adams, C.J. and Patterson, R.T., 1995. Benthic foraminiferal distribution at Middle Valley, Juan de Fuca Ridge, a northeast Pacific hydrothermal venting site. Marine Micropaleontology 25, 151-167.

Loeblich, A.R.Jr and Tappan, H., 1964. Sarcodina, chiefly "Thecamoebians" and Foraminiferida. In: Moore, R.C. (Ed.), Treatise on Invertebrate Paleontology, Part C, Protista. The Geological Society of America and the University of Kansa Press, New York and Lawrence, KS, pp. 900 pages.

Maybury, C., 1996. Crevice foraminifera from abyssal South East Pacific manganese nodules. In: Moguilevsky, A. and Whatley, R. (Eds.), Microfossils and Oceanic Environments. Aberystwyth-Press, University of Wales, pp. 281-295.

Schröder, C.J., 1986. Deep-water arenaceous foraminifera in the northwest Atlantic Ocean. Canadian Technical Report of Hydrography and Ocean Sciences 1-191.

Wendt, J., 1974. Encrusting organisms in deep-sea manganese nodules. International Association of Sedimentologists, Special Publications 1, 437-447.

68) Horizontal organic tube full of stercomata

Foraminifera, incertae sedis

Description: Black recumbent tube of a regular diameter. Test wall are organic and flexible. Tube full of stercomata visible through the translucent wall, giving a black colour to this taxon.

Size: Several mm in length.

Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific.

1.7 UNATTACHED FORMS

69) *Ammodiscus* sp.

Foraminifera, Textulariina, Ammodiscidae

Description: Test free. Thin planispiral. Proloculus followed by a long enrolled tubular chamber. Test wall made of fine agglutinated particles rigidly cemented. Aperture at the end of the tubular chamber. Protoplasm not observed.
Size: Around 100μm in diameter.
Remarks: Not attached directly with the nodule surface. Sometimes observed agglutinated in "mat of very coarse sediment agglutinated".
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific. Dugolinsky (1976) reported the rare presence of this taxon (found on less than 5% of nodules studied) from nodules in the northeast Pacific. Also found in nodule crevices from abyssal south east Pacific and in box-cores taken from the northwest Atlantic. Gooday and Haynes (1983) observed a single juvenile specimen present in *Bathysiphon rusticus* tubes in the northeast Atlantic. *Ammodiscus* sp. is present on ice-rafted stones in the northeast Atlantic at 4550m as well (Gooday, unpublished data).

References

Dugolinsky, B.K., 1976. Chemistry and morphology of deep-sea manganese nodules and the significance of associated encrusting protozoans on nodule growth. PhD, unpublished.

Gooday, A.J. and Haynes, J.R., 1983. Abyssal foraminifers, including two new genera, encrusting the interior of *Bathysiphon rusticus* tubes. Deep-Sea Research 30, 591-614.

Loeblich, A.R.Jr and Tappan, H., 1964. Sarcodina, chiefly "Thecamoebians" and Foraminiferida. In: Moore, R.C. (Ed.), Treatise on Invertebrate Paleontology, Part C, Protista. The Geological Society of America and the University of Kansa Press, New York and Lawrence, KS, pp. 900 pages.

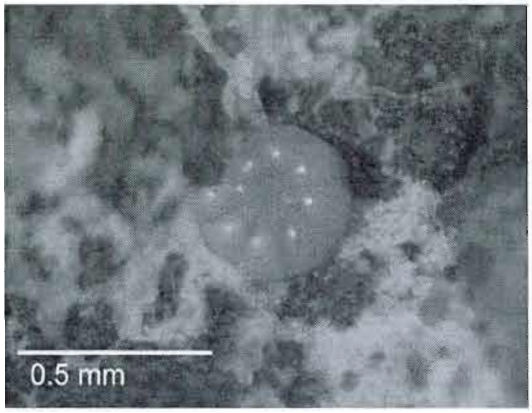
Maybury, C., 1996. Crevice foraminifera from abyssal South East Pacific manganese nodules. In: Moguilevsky, A. and Whatley, R. (Eds.), Microfossils and Oceanic Environments. Aberystwyth-Press, University of Wales, pp. 281-295.

Schröder, C.J., 1986. Deep-water arenaceous foraminifera in the northwest Atlantic Ocean. Canadian Technical Report of Hydrography and Ocean Sciences 1-191.

70) Orange snail

Foraminifera, incertae sedis

Description: Test free. Orange planispiral. Test wall calcareous. Aperture at the open end of the last chamber.
Size: Around 500μm in diameter.
Remarks: Not directly attached. Seems associated to the nodule surface by other networks of foraminifers.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific.

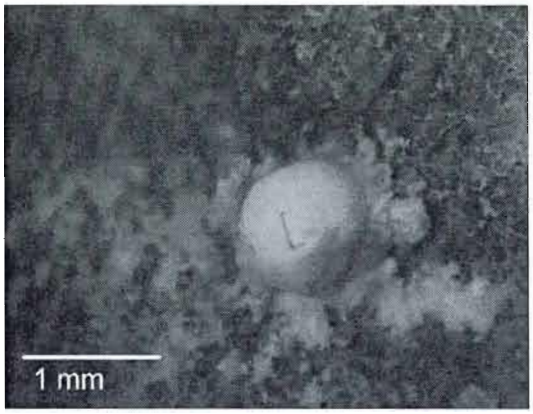


Orange snail. Location: 9°23.69 N, 150°05.72 W, depth: 5040m, nodule: PL1605-13_3-8.

71) *Biloculina* sp.

Foraminifera, incertae sedis

Description: Test free, spherical, composed of several chambers in a whorled shape. Similar to Miliolidae in morphology. White calcareous test. Aperture toward the top.
Size: Around 1.5mm in diameter.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific.

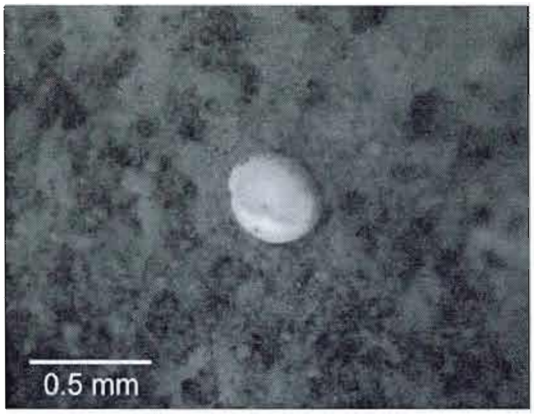


Biloculina sp. Location: 9°23.69 N, 150°05.72 W, depth: 5040m, nodule: PL1605-13_3-13.

72) *Quinqueloculina*-like

Foraminifera, incertae sedis

Description: Test free, coiled spherical form. Test wall white, calcareous. Aperture visible.
Size: Around 400µm in length.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific.

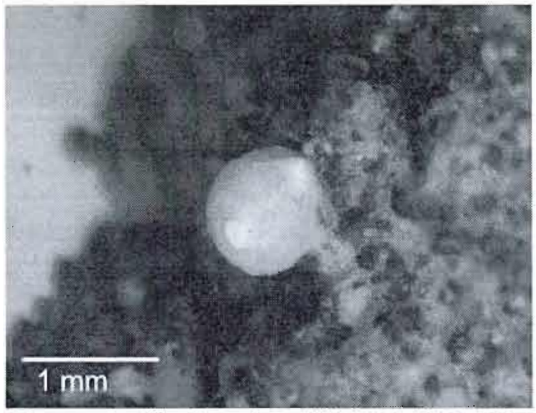


Quinqueloculina-like. Location: 14°3.10 N, 130°7.75 W, depth: 4954m, nodule: KGS22-4.

73) *Thurammina*-like

Foraminifera, incertae sedis

Description: Test free, one spherical chamber. Test wall fragile, very thin, build with fine whitish particles agglutinated. Several apertures located on small protuberances.
Size: Around 1 mm in diameter.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific. The presence of *Thurammina papillata* is reported on sponge stalks in the northeast Pacific at 4100meters. Indurated sediment in close proximity to vent sites is also colonized by *Thurammina*-like.



Thurammina-like. Location: 14°3.01 N, 130°06.93 W, depth: 4975m, nodule: KGS6-3.

References

Beaulieu, S.E., 2001. Life on glass houses: sponge stalk communities in the deep sea. Marine Biology 138, 803-817.

Jonasson, K.E., Schröder-Adams, C.J. and Patterson, R.T., 1995. Benthic foraminiferal distribution at Middle Valley, Juan de Fuca Ridge, a northeast Pacific hydrothermal venting site. Marine Micropaleontology 25, 151-167.

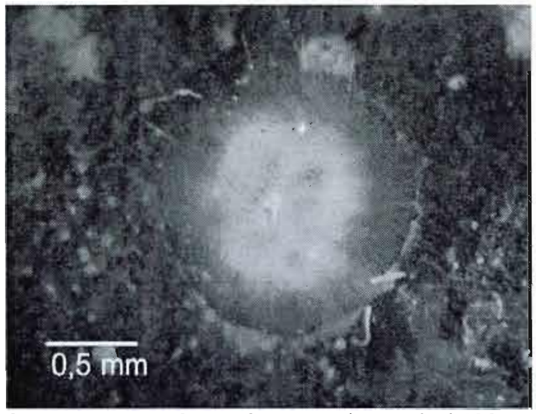
CHAPTER II

METAZOAN TAXA

2.1 SPONGES

M1) Taxon 1: Porcupine

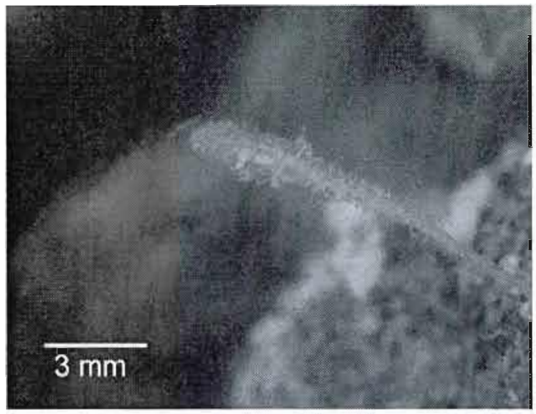
Description: Translucent hemisphere from which spicules radiate.
Size: Up to 5mm in diameter.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific.



Sponge taxon 1: Porcupine. Location: 14°2.97 N, 130°8.19 W, depth: 4904m, nodule: KGS24-7.

M2) Taxon 2: Sponge stalk with spikes

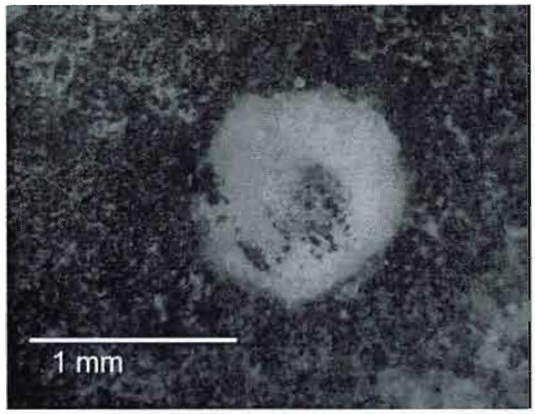
Description: Translucent sponge stalk with short spikes. Spikes start to appear at the middle height of the stalk.
Remarks: Always observed broken.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific.



Sponge taxon 2: Sponge stalk with spikes.
Location: 13°55.63 N, 130°12.20 W, depth: 4980m, nodule: PL1602-10-13.

M3) Taxon 3: White rigid stalk

Description: Very rigidly attached white sponge stalk to the nodule surface.
Size: The area covered by the sponge stalk on the nodule surface is around $1mm^2$.
Remarks: Always observed broken.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific.

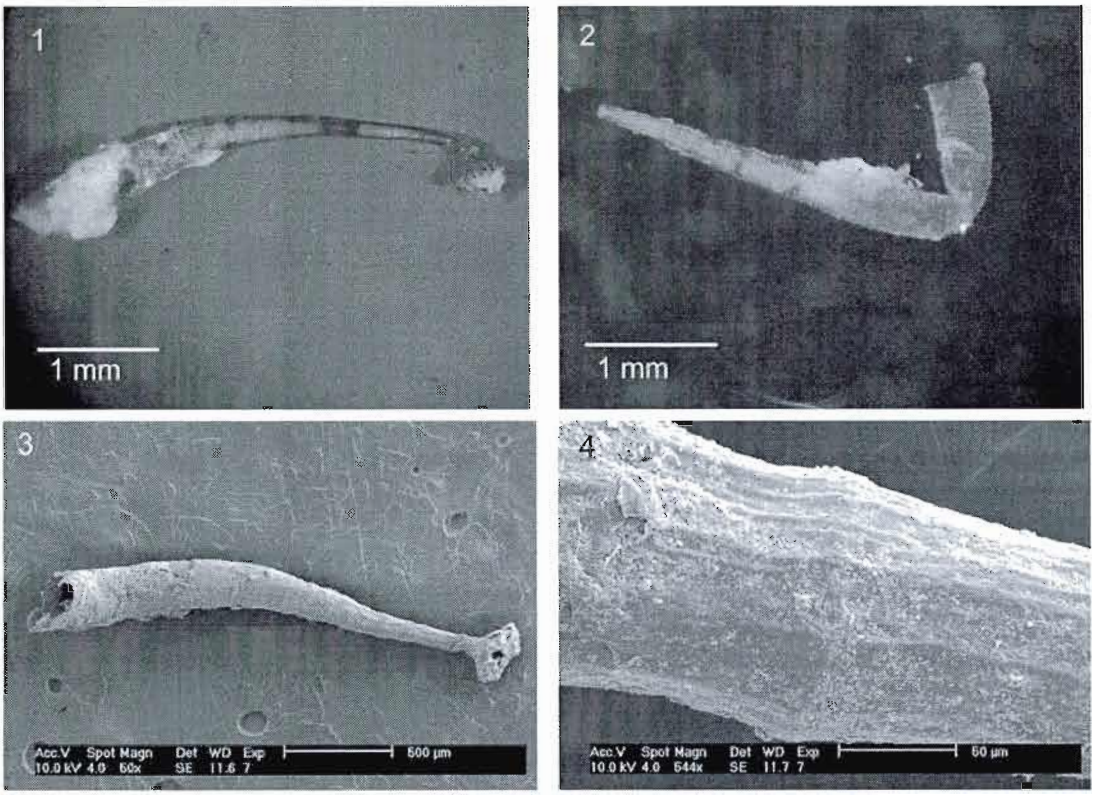


Sponge taxon 3: White rigid stalk. Location: 9°23.69 N, 150°5.72 W, depth: 5040m, nodule: PL1605-13_1-14.

2.2 SCYPHOZOANS

M4) *Stephanoscyphus* sp.

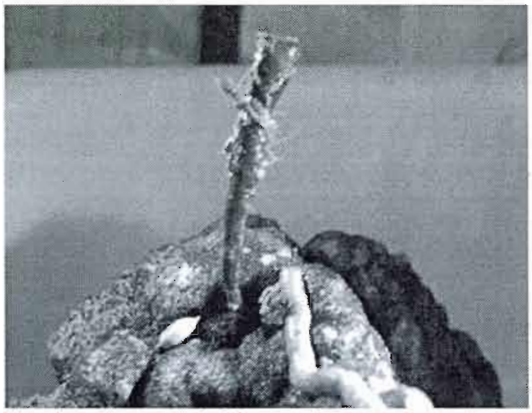
Size: Several mm in length.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific.



Stephanoscyphus sp. 1) Location: 14°2.80 N, 130°8.18 W, depth: 4911m, nodule: KGS21-3. 2) Location: 13°55.63 N, 130°12.20 W, depth: 4980m, nodule: PL1602-10-18. 3) and 4) Specimen alone.

M5) Taxon 1: Elongated scyphozoan

Description: Dark brown tube widens toward aperture.
Size: Several cm in length.
Remarks: Only one specimen observed. Tube covered with *Telammina* sp. and hydrozoans.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific.

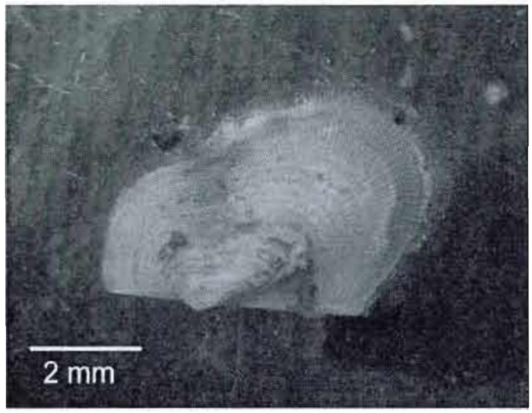


Scyphozoan taxon 1: Elongated scyphozoan.
Location: 13°55.63 N, 130°12.20 W, depth: 4980m, nodule: PL1602-10-2.

2.3 MOLLUSC

M6) *Bentharca asperula* Dall, 1881

Size: Around 4 to 6mm in length.
Remarks: Identified by Rudo von Cosel. Only one specimen observed. It needs a hard substratum.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific.



Bentharca asperula. Location: 14°3.01 N, 130°6.93 W, depth: 4974m, nodule: KGS6-1.

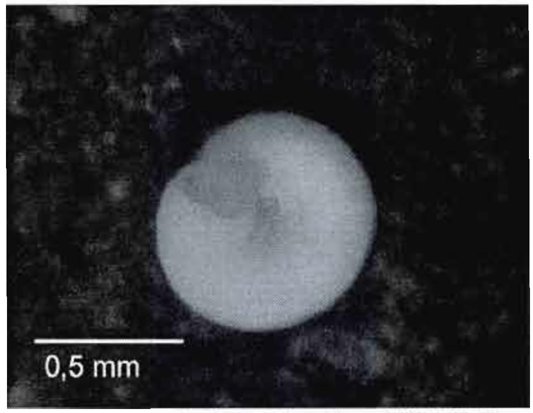
Reference

Dall, W.H., 1881. Preliminary report on the Mollusca. Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico (1877-78) and in the Caribbean Sea (1879-80), by the U.S. Coast Survey Steamer "Blake". Lieutenant-Commander J.R. Bartlett, U.S.N., commanding, 15. Bulletin of the Museum of Comparative Zoology at Harvard College 9 (2). Cambridge, Massachusetts.

2.4 POLYCHAETES

M7) Taxon 1: Spiral

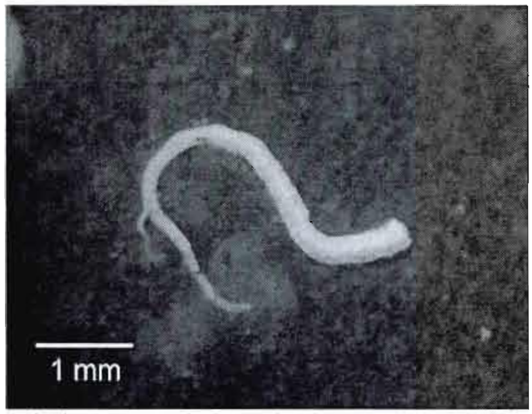
Description: White spiral very hard.
Size: The part attached to the nodule surface covered an area of around 500μm in diameter.
Remarks: Always observed empty.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific.



Polychaete taxon 1: Spiral. Location: 13°55.63 N, 130°12.20 W, depth: 4980m, nodule: PL1602-10-5.

M8) Taxon 2: Smooth tube

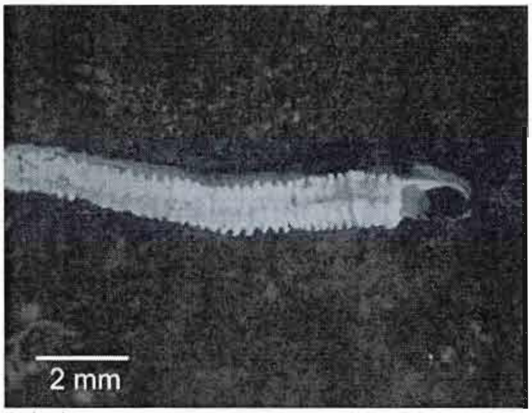
Description: White hard tube that winds on the nodule surface.
Size: The tube can be several mm in length. The tube diameter widens toward aperture.
Remarks: Always observed empty.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific.



Polychaete taxon 2: Smooth tube. Location: 13°55.63 N, 130°12.20 W, depth: 4980m, nodule: PL1602-10-5.

M9) Taxon 3: Tube with spikes

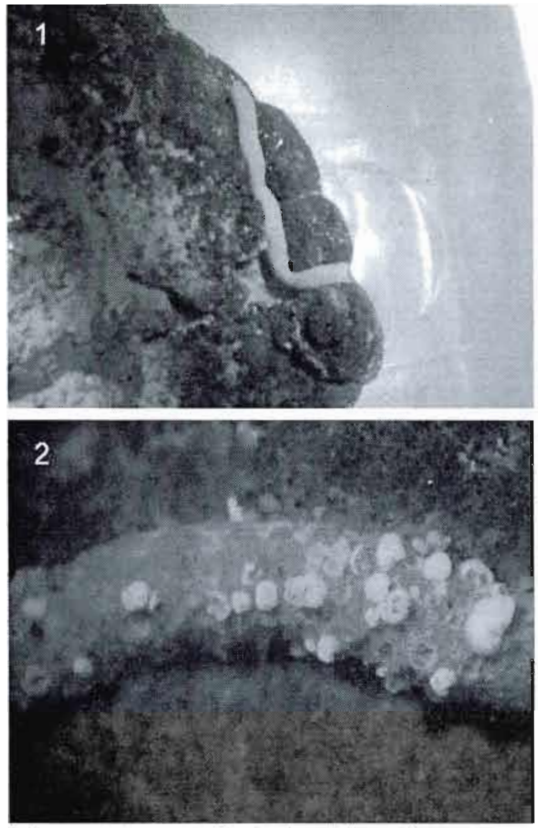
Description: Large white tube with rows of spikes. Interior filamentous.
Size: Tube around 20mm in length and 1.5mm in diameter.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific.



Polychaete taxon 3: Tube with spikes. Location: 13°55.63 N, 130°12.20 W, depth: 4980m, nodule: PL1602-10-5.

M10) Taxon 4: Mud tube

Description: Mud tube, sometimes with globigerinids.
Size: Several mm in length.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific.

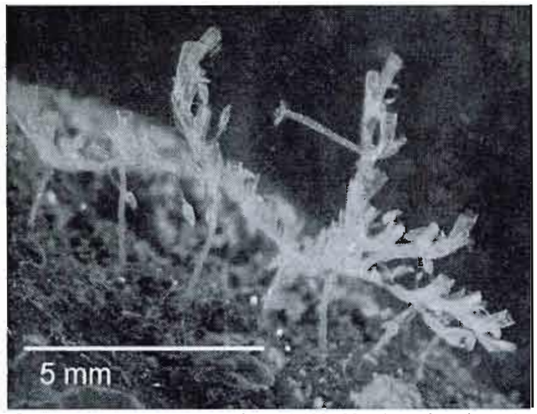


Polychaete taxon 4: Mud tube. 1) Location: 13°55.63 N, 130°12.20 W, depth: 4980m, nodule: PL1602-10-11. 2) Location: 13°55.63 N, 130°12.20 W, depth: 4980m, nodule: PL1602-10-5.

2.5 BRYOZOANS

M11) *Camptoplites* sp.

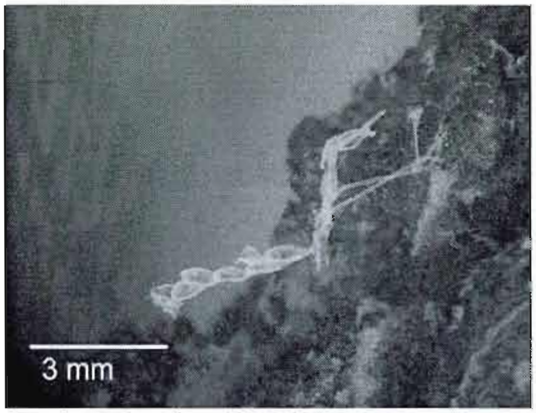
Description: White swellings on thin filaments.
Size: Several mm in height.
Remarks: Identified by Peter Hayward. Only fragments are found on nodules. According to Peter Hayward, this species is most similar to Antarctic/subantarctic *Camptoplites bicornis* (Busk, 1884) but it is too fragmentary for a confident identification.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific.



Camptoplites sp. Location: 14°2.63 N, 130°7.97 W, depth: 4930m, nodule: KGS25-bizz4.

M12) *Bugula* sp.

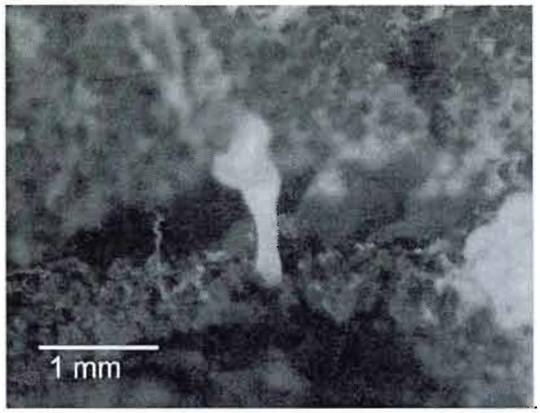
Size: Several mm in height.
Remarks: Only fragments of this genus are observed. Peter Hayward identified it judging from the outline of the proximal end of each zooid, which is "fishtailed" in basal view.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific.



Bugula sp. Location: 13°55.63 N, 130°12.20 W, depth: 4971m, nodule: PL1598-06_2-2.

M13) Cyclostomate

Size: Fragment of 1 to 2mm in height.
Remarks: Identified by Peter Hayward. This specimen is only a tiny piece and it is not possible to be sure which family it might belong to.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific.

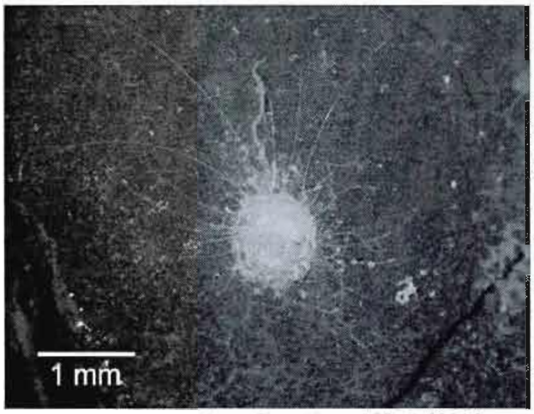


Cyclostomate. Location: 13°55.63 N, 130°12.20 W, depth: 4980m, nodule: PL1602-10-16.

2.6 BRACHIOPODS

M14) *Pelagodiscus atlanticus* King, 1868

Description: Inarticulated abyssal brachiopod anchored by tendril-like filaments to a hard surface. Limpet-like form.
Size: From 0.5 to 2mm in diameter.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific.



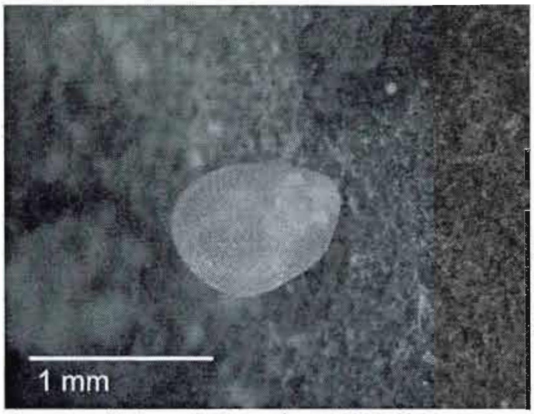
Pelagodiscus atlanticus. Location: 13°55.63′ N, 130°12.20′ W, depth: 4980m, nodule: PL1602-10-5.

Reference

King, W., 1868. On some Palliobranchiate shells from the Irish Atlantic. Proceedings of the Natural History Society of Dublin 5, 170-173.

M15) *Gwynia aff. Capsula* Jeffreys, 1859

Description: Two valves upright perforated and translucent. Attached to the nodule surface at the base.
Size: Several mm in length.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific.



Gwynia aff. Capsula. Location: 13°55.63 N, 130°12.20 W, depth: 4980m, nodule: PL1602-10-20.

Reference

Jeffreys, J.G., 1859. Further gleanings in Bristish Conchology. Annals and Magazine of Natural History 3(3), 30-43.

2.7 ASCIDIAN

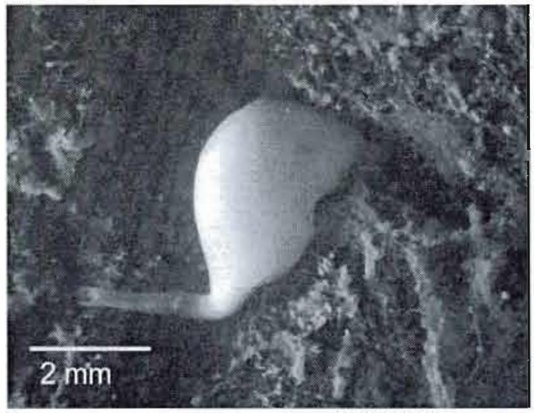
M16) *Cnemidocarpa sp.*

Size: Around 20 mm in length. Huge!
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific.

2.8 PLATYHELMINTHE, TURBELLARIA

M17) *Fecampia abyssicola* Christensen, 1981

Description: Pinkish cocoon sausage-shaped.
Size: Several mm in length.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific.



Fecampia abyssicola. Location: 14°3.02 N, 130°5.19 W, depth: 5036m, nodule: KGS1.

Reference

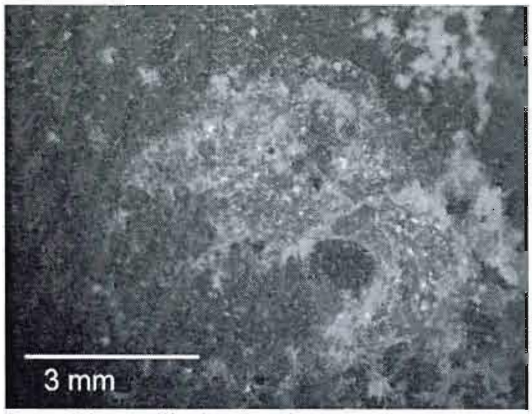
Christensen, A.M., 1981. *Fecampia abyssicola* n. sp. (Turbellaria: Rhandocoela) and five cocoon types of undescribed species of Fecampiidae from the deep sea. In: Wolff, T. (Ed.), Galathea Report. Scandinavian Science Press Ltd, Copenhagen, pp. 69-79.

CHAPTER III

INDETERMINATE FORMS

Saran-Wrap pellicule

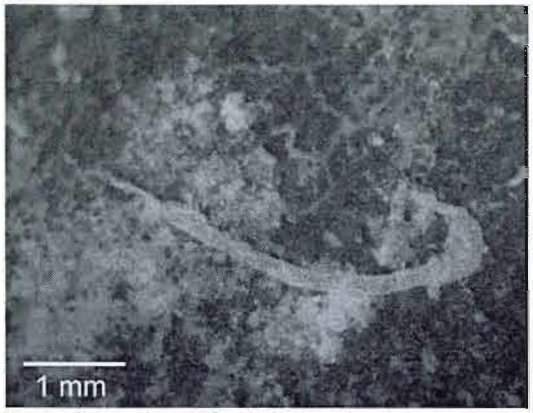
Description: Very thin film covering the nodule surface. No structure recognized. Sparkling appearance.
Size: Can cover up to $5cm^2$ of nodule surface.
Remarks: Probably not a foraminifer.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific.



Saran-Wrap pellicule. Location: 14°2.80 N, 130°8.18 W, depth: 4911m, nodule KGS21-2.

Recumbent tube perforated

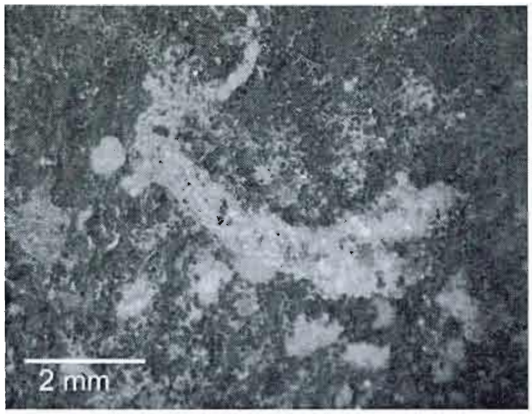
Description: Recumbent beige tube with lots of holes. Test wall flexible. No stercome observed.
Size: Several mm in length.
Remarks: Probably not a foraminifer.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific.



Recumbent tube perforated. Location: 14°3.10 N, 130°7.75 W, depth: 4954m, nodule KGS22-3.

Recumbent tube agglutinated

Description: Flattened tube made of agglutinated coarse and fine particles. Test wall are composed of a flexible matrix. Colour similar to the colour of the sediment surrounding the nodule. No stercome observed.
Size: Several mm in length.
Remarks: Probably not a foraminifer. It could be a worm tube.
Geographical distribution: Abyssal, found associated with manganese nodules below 4950m in the equatorial north Pacific.



Recumbent tube agglutinated. Location: 14°2.97 N, 130°8.19 W, depth: 4904m, nodule KGS24-8.

CHAPITRE II

FERROMANGANESE NODULE FAUNA IN THE EQUATORIAL NORTH PACIFIC OCEAN: SPECIES RICHNESS, FAUNAL COVER AND SPATIAL DISTRIBUTION

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Abstract

The poorly known ferromanganese nodule fauna is a widespread hard substratum community in the deep sea. Economically viable nodule mining will likely be large in scale and have a considerable impact on nodule ecosystems. The objective of this study was to analyze the spatial distribution of the fauna attached to nodules in the Clarion-Clipperton fracture zone, in relation to environmental factors (near-bottom currents, water chemistry and surface primary productivity) at two scales; a regional scale that includes the east (14°N, 130°W) and the west (9°N, 150°W) zones and a local scale in which different geological facies (A, B, C and west) are recognizable. The fauna associated with 235 nodules was quantitatively described: 104 nodules from the east zone (15 of facies A, 50 of facies B and 39 of facies C) and 131 nodules from the west zone. Percent cover was used to quantify the extent of colonization at the time of sampling and included 42 taxa out of the 62 live taxa observed. Faunal coverage reached up to 18% of exposed nodule surface with an average of about 3%. While species richness increased with exposed nodule surface, both at the regional and at the facies scales (except for facies A), total species density decreased (again except for facies A). There was no relation between faunal cover and exposed nodule surface when all nodules were included in the statistical analysis. Nevertheless, faunal cover decreased with exposed nodule surface for the east zone and for both facies B and C. Taxa distributions among facies were significantly different but explained only a very small portion of the variance (~5%). The analyses of species assemblage distribution resulted in the identification of two groups of associated taxa: a first

group of two taxa and a second group of six taxa. The other taxa (34) were independently distributed, suggesting that species interactions play only a minor role in the spatial distribution of nodule fauna. The flux of particulate organic carbon to the bottom is the only major environmental factor considered to vary between the two zones. We conclude that the higher species richness and higher percent faunal cover of the east zone can be partially attributed to greater food availability. Moreover, facies B and C nodule surfacc, located in the east zone, had a complex, knobby micro-relief, creating microhabitat heterogeneity for nodule fauna. This factor may have contributed to the greater species richness observed in the east zone.

Keywords: Ferromanganese nodules, fixed fauna, agglutinated foraminifera, geographical distribution, environmental factors, environmental impacts.

Regional terms: Pacific ocean, equatorial north Pacific ocean, Clarion-Clipperton fracture zone. 14°N, 130°W and 9°N, 150°W.

1. Introduction

Faunas that encrust ferromanganese nodules are poorly known, even though the hard substratum formed by the nodules is widespread in the deep sea (Gooday, 1990). While nodules are present in a few regions of the deep Atlantic ocean, they may cover more than 50% of the seafloor in the Pacific Ocean (Smith and Demopoulos, 2003; Thistle, 2003).

In order for nodule mining to be economically viable, exploitation will likely be at scales of tens to hundreds of thousands of square kilometres (Glover and Smith, 2003; Thiel, 2003). Among the potential impacts of nodule mining, it is clear that the fauna attached to the nodules will be destroyed (Thiel *et al.*, 1993) and that surrounding organisms will be affected by sediment blanketing (Morgan *et al.*, 1999; Sharma *et al.*, 2001; Thiel *et al.*, 2001). In order to manage and mitigate these impacts, it is critical that we better understand the composition and distribution of the nodule fauna and its relationship to the mineral substratum and other environmental factors.

The study of hard substratum communities in nodule fields has been neglected compared to sediment communities, probably because of the difficulties inherent in sampling remotely from the sea surface. Previous studies of nodule faunas focused on their role in nodule formation and growth (Graham and Cooper, 1959; Ehrlich, 1972;

Dudley and Margolis, 1974; Greenslate *et al.*, 1974; Wendt, 1974; Dudley, 1976; Dugolinsky, 1976; Dugolinsky *et al.*, 1977; Dudley, 1978; Thiel, 1978; Bignot and Lamboy, 1980; Riemann, 1983; von Stackelberg, 1984; Riemann, 1985; Thiel *et al.*, 1993). Mullineaux (1987; 1989) conducted the only detailed ecological study of organisms living on the surface of the nodules. The bacteria associated with nodules (Ehrlich, 1972; Burnett and Nealson, 1981) and the fauna found within nodule crevices have also been examined (Thiel *et al.*, 1993; Maybury, 1996). Other deep sea hard substratum communities have been studied systematically including sponge stalks (Beaulieu, 2001), whale skeletons (Thiel *et al.*, 1993; Baco and Smith, 2003), indurated sediment around hydrothermal vents (Jonasson *et al.*, 1995; Jonasson and Schröder-Adams, 1996), dropstones (Gooday, unpublished data), large foraminiferal tests (Gooday and Haynes, 1983; Waren and Bouchet; 2001), exposed seamount rocky bottom (Genin *et al.*, 1986), experimental substrates on seamounts (Bertram and Cowen, 1994) and sunken woods (Turner, 1973). Two major research programs investigated the impacts of nodule mining: DISCOL (Disturbance and Recolonization Experiment in a Manganese Nodule Area of the Deep South Pacific Ocean) (Borowski and Thiel, 1998; Ahnert and Schriever, 2001; Bluhm, 2001; Borowski, 2001; Thiel *et al.*, 2001; Vopel and Thiel, 2001) and BIEs (Benthic Impact Experiments) (Sharma *et al.*, 2000; Sharma *et al.*, 2001). However, these studies did not specifically consider the impact of nodule mining on the nodule-dwelling fauna.

The objective of this study was to improve knowledge of pristine nodule faunas in order to help the planning of valid conservation areas. The spatial distribution of nodule fauna in relation to environmental factors (near-bottom currents, water chemistry and surface primary productivity) has been analyzed at two scales: a regional scale that includes the east (14°N, 130°W) and the west (9°N, 150°W) zones and a local scale in which different nodule facies (A, B, C and west) were recognizable. Depth was similar between the different studied zones (varying from 4900m to 5050m). Four parameters of nodule substratum that could influence faunal distribution were also examined: nodule size, geochemical composition, morphology and surface texture. The distribution of taxa among the zones and the facies, and nodule grouping using faunal characteristics, were analyzed in order to determine the most influential factors on faunal spatial distribution. Then, species assemblages were investigated as a potential factor structuring faunal distribution on nodule. Finally, the conservation implications of nodule fauna distribution in the equatorial North Pacific ocean is discussed.

The present study extends previous work by Mullineaux (1987, 1989) in several key respects. First, we carried out sampling method comparison between nodules obtained with an USNEL box core and the scoop of the *Nautile* submersible. Secondly, the large number of nodules sampled in different locations permitted extensive characterization, quantification and distribution analysis of nodule fauna.

Finally, we examined the influence of a few environmental factors on the spatial distribution of this fauna.

2. Materials and methods

2.1. Sampling sites

The NODINAUT cruise (May 18th – June 27th 2004) explored and sampled two geographical zones located in the French mining claim in the equatorial Pacific: the east zone (14°N, 130°W) and the west zone (9°N, 150°W) (Fig. 1). The east zone had been visited before by the NIXONAUT cruise (November 18th – December 22nd 1988) (Cochonat *et al.*, 1992). The two locations sampled by the study of Mullineaux (1987) are the equatorial North Pacific (ENP) and the central North Pacific (CNP) (Fig. 1). Three different nodule facies were observed in the east zone (A, B and C) where they cover hundreds of square kilometers. Nodule facies were differentiated according to their general shape, size, surface morphology and the relation between the nodule and its environment (buried in the sediment, presence of volcanic material) (Saguez, 1985; Morel and Le Suavé, 1986). The facies A nodules were small spheres (less than 4cm in length) with smooth surfaces and lay at the surface of the sediments in slight slopes. Facies C nodules were the largest (average of 11cm in length) but their sizes varied considerably (from 2 to 15cm in length). They appeared as spheres half buried in the sediments. Knobs and protrusions characterized their smoothtextured summital region and their sides were rough. Facies B nodules were ovoid, medium in size (average of 5cm in length), most of their surface texture was rough and they were slightly buried in the sediments. An undescribed facies that characterizes the west zone is referred to as the "west facies". These nodules were generally ovoid but occurred in different shapes. They were small to medium in size (from 2 to 9cm in length), their texture surface was rough and they were slightly buried in the sediments. Even though our visual classification, commonly used by geologists, appears to be subjective, differences in the geochemical composition of the nodules from different facies provides support to this approach (Tilot, 1992; Hoffert and Saget, 2004). Both zones are located in the Clarion-Clipperton fracture zone at depths varying from 4950 to 5050m.

Primary productivity in the region is estimated to be moderate compared to the high equatorial productivity (DuCastel, 1985; Skornyakova and Murdmaa, 1992). Ambient bottom-water temperature is ~1°C in both zones. The east zone lies beneath the North Equatorial Current and the west zone beneath the North Equatorial Counter Current (DuCastel, 1985; Smith and Demopoulos, 2003). Near-bottom currents observed during the NODINAUT cruise (short term ADCP-WH300 measurements at ten meters above the bottom) are very weak and are of the same order in the two zones (3.5 – 4 cm s^{-1}). Their direction was toward east/south-east in the east zone and east/north-east in the west zone. There were some very slight speed and direction variations due to semi-diurnal tidal oscillations. Previous long-term data (Pujol, 1988;

Mauviel, 1990) indicated the existence of inertial oscillations (2 – 3 days) and longer term oscillations (around 2 – 3 months), the amplitude of which is the highest. According to these data, the current direction encountered during the NODINAUT cruise was always associated with higher current speeds. We assume therefore that the NODINAUT cruise took place during a period of high current speeds and that current speeds may be lower at other periods.

Bottom relief can influence current speed and direction (Morgan *et al.*, 1999). We attempted to estimate currents at the scale of the nodules at several cm above the bottom with a modified weathercock but results are too preliminary to be significant. Seawater chemical properties measured at the nodule scale (pH, water salinity, dissolved oxygen, alkalinity, dissolved organic carbon (DOC) and nutrients) were similar at the two zones. Moreover, the flux of particulate organic carbon to the bottom declines gradually from east to west along any line of latitude, and also declines steeply with distance from the equator (Smith and Demopoulos, 2003). Therefore, the east zone probably benefits from a greater flux of particulate organic carbon to the bottom since it is located to the east of the west zone and is closer to the equator (Skornyakova and Murdmaa, 1992; Smith and Demopoulos, 2003), although the sedimentation rate in the Clarion-Clipperton fracture zone is fairly low (Hoffert, pers. comm.).

2.2. *Sampling methods*

Nodules were sampled either using an USNEL box core or the manipulator of the *Nautile* submersible (Table 1 and 2). A top-view photo of each USNEL box core was taken before eight nodules randomly chosen were removed from the sediment and washed carefully with seawater. The sampled nodules were stored in 4% formaldehyde and transferred to 70% alcohol after several days. They were all carefully packed for transportation in jars of different sizes. Plastic packing was placed in the jars to immobilize the nodules. During all manipulations, nodules were never allowed to dry and were handled with the greatest care possible because of their high friability.

The two different sampling methods (USNEL box core versus *Nautile* submersible) were compared in order to test the effect of sampling method on our results, on nodule integrity and its fauna. We were particularly interested in two potential effects: 1) the influence of sampling method on the size of the nodules collected; 2) whether one sampling method could be more destructive than the other, damaging the most fragile living forms and decreasing species richness. The nodule surface above the sediment line was used as an indicator of nodule size.

2.3. Nodule substratum

Four characteristics of the nodule substratum were considered in relation to faunal distribution: nodule size, geochemical composition, morphology and texture. Nodule morphology and texture are considered in a separate study of the spatial distribution of the nodule fauna at the scale of the nodule itself (Veillette *et al.* submitted to Deep-Sea Research). The influence of nodule size on the nodule fauna was investigated by testing regressions of species richness, species density and percent faunal cover in relation to nodule surface above the sediment line. For the geochemical composition analysis, the metallic composition of a nodule cross section from each facies was determined. We were specifically interested in possible relationships between the fauna and the geochemical composition of the outer nodule layer.

2.4. Nodule surface area determination

Nodule surface area was calculated in order to compare zones and facies. Since nodule surfaces below the sediment line are rarely colonized, they were not taken into account in this study. Therefore, the nodule surface of interest lies above the sediment line. This surface area was determined differently for each facies since their nodules exhibit different morphologies. The fauna encrusting facies A nodules can colonize their entire surface since they lied at the surface of the sediments. For these nodules, surface area prone to faunal colonization was estimated with the sphere surface formula ($4\pi r^2$). Facies B and west nodules were mostly ovoid and buried in the sediment. Their surface area was determined using IP Lab Spectrum© image analysis software, assuming that top-view photos provided a good representation of nodule surface area above the sediment line. Facies C nodules appeared as spheres half buried in the sediment. When the vertical or near vertical sides of the nodules extended more than 30mm above the sediment, before flattening to form the summital region, the surface area was separated into top and side. In order to control for the irregular shape of most nodules, eight measures of the height of the sides were taken at every 45° around the nodule circumference. When the sides of facies C nodules were 30mm or less in height, nodule surface area was determined with the same methodology as for facies B and west. For nodules greater than 30mm in side heights, side surface area was calculated using the surface formula for an open cylinder (height x circumference). All measurements and surface determination with IP Lab Spectrum© were made in triplicate.

2.5. Faunal identification and quantification

The fauna associated with 235 nodules (greater than 18mm in length), collected either by a USNEL box core or by the *Nautile* from four different nodule facies, was described quantitatively (Table 3). The total nodule surface area examined was 0.715 m^2. Identification of living organisms on nodule surfaces was done using a binocular dissecting microscope. Light microscopy and scanning electron microscopy were also used to examine smaller forms or particular structures and to determine if the unusual forms observed were protozoan, metazoan or non-living. The tests of most foraminifera (protozoa) were partially broken in order to determine if protoplasm was present and therefore whether the organism was alive or dead.

Taxa that were considered to be alive at the time of collection (based on the presence of intact protoplasm) were quantified. However, some foraminiferal forms rarely contained visible protoplasm. In these cases, the presence of unbroken tests was used to classify the taxon as live when collected. Despite all precautions taken during handling of the nodules, some very fragile structures may have been destroyed or lost prior to identification. Thus, faunal identifications in this study could be biased towards more robust forms firmly attached to nodule surfaces.

While percent cover was the best way to quantify taxa that form mats or domes (Mullineaux, 1987), presence/absence was the more appropriate method to quantify upright structures. Presence/absence data were used to calculate species richness, defined as "the number of species present, without any regard for the exact area or number of individuals examined" (Hurlbert, 1971). The surface area covered by upright structures is negligible and thus, the percent cover includes all forms covering the nodule surface. In order to simplify the methodology of faunal cover analysis, every covering taxon was assumed to represent a circle or a rectangle. The dimensions of the form were then measured under a binocular microscope equipped with a scale. For taxa forming anastomosing networks, percent cover within the limits of the form was estimated. Density (number of individuals) was not used in this study since the vast majority of the living forms were foraminifera that are best quantified with percent cover (Mullineaux, 1987).

2.6. Statistical analyses

Between zones, quantitative comparison of faunal species richness, species density and percent cover included all nodules, since the sample sizes of both zones were relatively similar (n_{east}=104, n_{west} = 131). The non-parametric Mann-Whitney test was used to test for differences between the two zones because the two main assumptions for the *t*-test (homogeneity of variances and normal distributions) were never met. All nodules were also included in the inter-facies comparisons but unbalanced sample size was controlled for in the analysis since the sample sizes of the different facies were not equal (n_A= 15, n_B= 50, n_C= 39, n_{west}= 131). Spatial bias could not be controlled for because the number of sampling sites varied too much between facies (Table 3). The non-parametric Kruskal-Wallis test was used to test differences between the four facies since the two main assumptions for ANOVA (homogeneity of variances and normal distributions) were never met. When the result of the Kruskal-Wallis test was significant, the Tukey *a posteriori* test, was used to verify which distributions differed from the others. Nodules were classified in three size categories according to Hoffert and Saget (2004): small <5cm in length, medium between 5 and

10cm in length and, large >10cm in length. Nodules with overlapping size ranges (Table 4) were compared quantitatively in order to explore faunal differences caused by factors other than nodule surface area. The two zones could be compared but only three facies could be compared together since nodule sizes of facies A and C do not overlap (small: A, B and west, medium: B, C and west). The sample size used when comparing nodules of the same size, either small or medium, was the smaller one (of the groups being compared) in order to assure equal variances. Nodules of the two other groups were randomly chosen. When comparing nodules of the same size for the two zones, the *t*-test was used if the assumptions were met. Otherwise, the non-parametric Mann-Whitney test was used. When nodules of the same size for the three facies were compared, ANOVA was used if the assumptions were respected. The non-parametric Kruskal-Wallis test was used when they were not. When the ANOVA result was significant, the Tukey *a posteriori* test was used to verify which distributions differed from the others. All analyses were made at $\alpha = 0.05$.

The distribution of taxa among facies was analyzed to verify if the facies harboured specific taxa. Most of the taxa confined to one facies were found on facies C (Table 5), where the nodules are biggest. We tested the hypothesis that taxa were evenly distributed on every facies. Redundancy analyses (RDA) were performed on abundance as well as on presence/absence data. All data were Hellinger-transformed since this transformation is appropriate for the analysis of community composition data (Legendre and Gallagher, 2001).

Nodules were grouped using faunal characteristics and compared to grouping by facies type in order to test the influence of facies on the nodule fauna. Different grouping methods were explored using either abundance or presence/absence data: Jaccard index (presence/absence data), PCA, K-means Euclidean ordination (abundance data) and Ward agglomerative grouping (abundance data).

Kendall's coefficient of concordance (*W*) was used to identify species associations with Hellinger-transformed abundance data (Legendre, 2005). The objective of this analysis was to test if taxa were independent of one another, or if they formed significant faunal assemblages.

3. Results

3.1. Sampling methods

For facies B and C nodules, the two sampling methods yielded different size distributions (Table 4). The difference in nodule size was statistically significant; those sampled with the submersible *Nautile* were bigger for both facies (Fig. 2). The dominant taxa on the nodules sampled by the USNEL box core or the *Nautile* were slightly different, but in general all sampled nodules had similar numbers of delicate organisms (Table 6a and 6b). Sampling method did not seem to influence species richness for facies B and C since the species accumulation curves of the two sampling methods overlapped (Fig. 3). Facies west nodules collected with the *Nautile* had lower species richness than those collected with the USNEL box core. The number of nodules observed appeared to be sufficient since all accumulation curves tended towards an asymptote, where the number of new taxa observed no longer increased with increasing sample size (Fig. 3). However, some of these trends [Facies A, B (PL), C (KGS)] could also be artefacts due to the small number of observed nodules.

3.2. Nodule fauna composition

We identified a total of 73 protozoan and 17 metazoan forms associated with nodule surfaces (see "Catalogue of nodule fauna") (Fig. 4 and Table 5). Eleven protozoan and 8 metazoan forms were identified to species or genus level. The protozoan taxa were all foraminifera, with the exception of two probable xenophyophores. They were all attached directly to the nodule surface except for five taxa, found agglutinated in mats.

Around 70% (62 out of 90) of the taxa observed were considered to be living when collected. However, the proportion was substantially higher for protozoans (78%) than for metazoans (29%). Only these 62 live forms (57 protozoans and 5 metazoans) were included in the species richness analysis. Sixty percent of the protozoan taxa are believed to be suspension feeders based on the presence of stercomata-free protoplasm and, in some cases, an upright life position. The remainder (37%) are considered to be deposit feeders based on the accumulation of stercomata within the test (Gooday *et al.*, 1997). All metazoan taxa (except "mud tube") were classified as suspension feeders.

Percent cover was used to quantify the extent of colonization at the time of sampling. Out of the 62 live taxa, 41 protozoans (mostly mats, domes and tunnels) and one metazoan (the ascidian *Cnemidocarpa* sp.) were quantified by percent cover. Fauna covered up to 18% of the exposed nodule surface, with a mean of about 3%.

3.3. Species richness and density

Species richness per nodule was higher in the east zone than in the west zone (Fig. 5) even when nodules of the same size were compared. Moreover, at the facies scale, facies C followed by facies B were more species diversified than facies A or west as confirmed by the Tukey test (Fig. 6). Also, facies B nodules yielded more diversified assemblage than facies A or west nodules when only small nodules were considered. On the other hand, facies C nodules was more species rich than facies B or west nodules when only medium nodules were included in the analysis.

Species density (number of taxa per cm^2) was not significantly higher in the east zone than in the west zone (Fig. 5). However, when only small nodules were considered, species density was higher in the east than in the west zone. At the facies level, facies B had the highest species density, while facies A and west were not different, and facies C had the lowest species density according to the Tukey test (Fig. 6). These rankings still hold when only small nodules were compared but in this case, facies C was not included. For medium nodules, there was no significant difference in species density between facies B and C, or between facies C and facies west. However, facies B had a higher species density than facies west.

3.4. Percent cover

Percent faunal cover was significantly higher in the east zone than in the west zone even when the same nodule sizes were compared (Fig. 5). At the facies scale, facies B nodules were more heavily encrusted with fauna than facies C, followed by facies A and west according to the Tukey test (Fig. 6). These trends remained true for small nodules only but in this case, facies C was not included. However, there were no difference in percent cover between facies B, C and west for medium nodules.

3.5. Nodule substratum

Facies C nodules were larger than facies A, B or west nodules when nodules obtained using both sampling methods were pooled together (Fig. 2). There was no significant difference in nodule surface area between facies A, B and west. We examined the relationship between nodule size and species richness, species density and percent cover. It might be expected that the number of taxa would increase with nodule surface area. Figure 7 shows that the regression between the number of taxa and the exposed nodule surface is significant when all nodules are considered, at both the regional and the facies scales, except for facies A. These regressions exhibit positive slopes, as expected. The regressions between species density and exposed nodule surface are significant as well, again except for facies A (Fig. 7). Nevertheless, the slopes of these regressions are negative, meaning that the number of taxa per surface area decreases with nodule size. Furthermore, there is no relation between faunal cover and exposed nodule surface when all nodules are included (Fig. 7c). However, east zone as well as facies B and C nodules present significant regressions with negative slopes.

The geochemical analysis of the nodules showed some trends common to all facies: a patchy presence of highly concentrated iron, a uniform layer of highly concentrated cobalt and patches of highly concentrated calcium. There were also geochemical differences between facies. Facies A and C nodules showed silica correlated with calcium and manganese spots just beneath the surface. The outer metallic composition of facies west nodules was different from that of the other nodule facies, exhibiting high manganese and nickel concentrations and some sparse spots of copper.

3.6. Taxa distribution among facies

Tables 6a and 6b show the evenness of relative abundance among taxa in both zones (Table 6a) and among the four facies studied (Table 6b). 83% of taxa in the east zone and 75% of taxa in the west zone were abundant in both zones. 72%, 66%, 67% and 59% of taxa were abundant in facies A, B, C and west respectively. Two foraminiferal taxa were only observed on facies A nodules, one foraminiferal taxon was only found on facies B, one unattached foraminiferan and ten metazoan taxa were only noted on facies C nodules and two unattached forms of foraminifera only occurred on facies west (Table 5). Therefore, facies C nodules host 11 taxa that appear to be confined to this habitat. Ten of these are metazoans.

For all facies, the redundancy analyses show similar patterns with abundance and presence/absence data (Fig. 8). Taxa 1 and 36 seem to be strongly associated with facies west. Taxa 22, 23, 45, 19, 28 and 46 were found only in the east zone, while 28 and 46 were confined to facies C. However, these trends, although significant ($p= 0.0005$ and $p= 0.0001$), explain only a very small portion of the variance of the distribution of taxa among facies ($R^2= 0.054$ and $R^2= 0.063$).

3.7. Nodule grouping and species assemblages

Nodule grouping using the Jaccard index method yielded three groups of seven, two and 49 nodules. Nodules were at most 75% similar. The PCA, K-means Euclidean ordination and the Ward agglomerative grouping method used abundance data and yielded similar results. For the PCA, K-means Euclidean ordination, six groups of eight, five, four, two, ten and 26 nodules were formed. The Ward agglomerative grouping method also formed six groups, in this case of nine, two, 20 and three groups of eight nodules. The nodules composing these groups were similar irrespective of the method used.

Table 7 shows that two significant groups of associated taxa exist: one with two taxa and the other with six taxa. The remaining 34 taxa (out of 42) are independently distributed.

4. Discussion

4.1. Sampling methods

Although the *Nautile* pilot was instructed to collect nodules randomly, there still seems to have been a bias toward the sampling of larger nodules. However, nodule size differences were too slight to explain the observed faunal differences and nodules collected using both methods were therefore pooled.

A smaller surface area of the seafloor sampled could explain the observed lower species richness of the facies west nodules collected with *Nautile* submersible compared to those collected with the USNEL box core. Together, the ten USNEL box cores sampled a larger surface area of the west zone than the samples from the dive PL1605-13. To test this hypothesis, the fauna on six nodules from one USNEL box core were compared to six random nodules from PL1605-13. Species richness was not significantly different between the two sampling methods ($t_{0.05(2),10} = 2.228$, p=0.2545). Hence, the smaller surface area sampled on the seafloor rather than the sampling method can explain the different species accumulation curves obtained for this facies.

4.2. Comparisons with previous studies

Approximately 21 protozoans out of 73 recorded in this study may correspond to taxa listed by Mullineaux (1987) and the metazoan groups were similar to those observed by this author as well. The five species of agglutinated foraminifers described from the radial crevices of nodules by Maybury (1996) were close to forms observed in the present study. Almost all the protozoan and metazoan forms colonizing nodule surfaces have yet to be observed in the soft sediment (Dugolinsky, 1976; Mullineaux, 1987).

The nodule fauna analyzed in this study was dominated by foraminiferans in terms of species richness (92.4%), as also observed by Mullineaux (1987) and Dugolinsky (1976). This protozoan group may exert a more significant influence on deep-sea benthic community structure and dynamics than the metazoan macrofaunal taxa on which deep-sea ecological studies have traditionally focussed (Gooday and Haynes, 1983). It has been suggested that benthic foraminifera may reach their highest diversity on the abyssal plain (Buzas and Gibson, 1969). The number of taxa colonizing other hard substrata, such as the interior of *Bathysiphon rusticus* tubes (Gooday and Haynes, 1983) and experimental substrata on seamounts (Bertram and Cowen, 1994), was also dominated by foraminifers. On the other hand, sponge stalks were predominantly colonized by metazoans (Beaulieu, 2001) whereas corals (gorgonians and antipatharians) dominated exposed rocky substrata on seamounts (Genin *et al.*, 1986). Metazoans generally build more robust structures compared to protozoans and this could explain why more metazoan remnants are present on exposed nodule surfaces. Data on the abundance and diversity of foraminifera living in the sediment in nodule regions are difficult to compare with our observations since the assemblages were quantified in terms of numbers of individuals and fragments (Nozawa *et al.*, pers. comm.). These assemblages were dominated by monothalamous soft-shelled taxa and fragments of komokiaceans and tubular species.

The nodules examined in this study exhibited a species richness similar to that of nodules studied by Mullineaux (1987). However, the species richness values would be more convincing if species accumulation curves had clearly reached an asymptote (Fig. 3). Species richness depends upon the sampling effort and inter-site comparisons are relevant only if faunal characterization is sufficient (Etter and Mullineaux, 2001). Even if presence/absence data included more taxa than percent cover data, the latter provides a better indicator of the magnitude of faunal colonization. Species richness of sponge stalk communities (total number of taxa observed= 144; Beaulieu, 2001) is higher than nodule fauna but whale bone communities (total number of taxa observed= 36) are less specious than nodules (Bennett *et al.*, 1994; Baco and Smith, 2003). On the other hand, while nodule species density for the east (0.9 taxa cm^{-2}) and the west (0.7 taxa cm^{-2}) zones was slightly lower than for sponge stalks (1.1 taxa cm^{-2}; Beaulieu, 2001), species density on facies B nodules (1.4 taxa cm^{-2}) was higher. Percent faunal cover on nodules (average of 3%) was similar to that reported by Mullineaux (average of 10%) (1987). Sponge stalks were almost entirely covered by fauna (Beaulieu, 2001), and faunal coverage on experimental substrata from Cross Seamount (central North Pacific, 410m depth) reached 37% on basalt surfaces and 13% and 20% on ferromanganese-oxide and $CaCO_3$ substrata, respectively (Bertram and Cowen, 1994). The forms excluded from the faunal cover analysis were considered to occupy a negligible nodule surface area.

Only two functional groups (suspension and deposit feeders) have been identified in the nodule fauna while the sponge stalk fauna have many feeding types (detritivores, mobile predators, suspension and deposit feeders) (Beaulieu, 2001). Studies of deep-sea communities report that deposit feeders are dominant in sediments (Hessler and Jumars, 1974; Etter and Mullineaux, 2001) and that abyssal species are usually generalists (Dayton and Hessler, 1972). However, structures extending from the sediment into higher current flow above the benthic boundary layer, such as nodules, sponge stalks or rocks, can provide a hard substratum for suspension feeders (Beaulieu, 2001; Etter and Mullineaux, 2001). In the case of nodule mining, it is predicted that suspension and deposit feeders in adjacent parts to mined areas will be most heavily influenced by sediment resuspension and deposition (Jumars, 1981). Sponge stalk communities exhibit a structure different from that of nodule communities: a foraminiferan and a serpulid polychaete are dominant in percentage abundance in the former (Beaulieu, 2001), while several taxa dominate the latter, as observed in this study and by Mullineaux (1987). This is to be expected since abyssal assemblages generally exhibit evenness in their diversity (Gage and Tyler, 1991). Thus, no heterogeneity was detected at the regional or facies scales but it may exist at smaller scales (Jumars, 1976). The similarity of dominant taxa in both zones may also indicate that the slight differences in surface productivity and hence, food availability are not important enough to affect strongly the nodule community composition.

4.3. Environmental factors

Near-bottom currents can have a major influence on the fauna of hard substrata (Thistle, 2003). The current speeds measured during the NODINAUT cruise were very low and stable in both zones, as observed in other abyssal studies (Hayes, 1979; Thistle, 2003). Nevertheless, slow currents are sufficient to renew water surrounding nodules, replenishing particulate food and removing waste material (Thistle, 2003). There was no evidence for any significant small-scale temporal variability (4-5 days) in current velocity at our regional and local scales. Although we did not measure currents at the nodule scale, the observed temporal variability of currents (semi-diurnal oscillations) indicate that nodule faunas do not always experience unidirectional currents. From the NODINAUT data, it is clear that the current direction changed during the study; in the east zone (measured for five days) mean current was around 90-130° while it was 0-90° in the west zone (measured for four days). A previous study of suspension-feeder megafauna fixed to nodules in the Clarion-Clipperton fracture zone concluded that 60% of the specimens were oriented 40-50° north and that therefore, the current should be oriented in the same direction (DuCastel, 1985). At a smaller scale, turbulence could have an effect on faunal spatial distribution on nodule surfaces (Mullineaux, 1989).

The chemical properties of bottom-water masses in both study areas were similar and therefore unlikely to have influenced the nodule faunas.

Surface primary production is relatively higher in the equatorial North Pacific because of upwelling of nutrients (in particular nitrate and iron) along the equatorial divergence (Murray *et al.*, 1994). Moreover, in this food-limited region, flux of particulate organic carbon to deep-sea benthic ecosystems overrides the influence of all other environmental factors and is recognized to be the only important factor to vary (Smith and Demopoulos, 2003). Therefore, carbon flux to the seafloor could play a dominant role in controlling regional differences in the spatial distribution and diversity of nodule faunas composed of sessile, suspension- or deposit-feeding organisms. Thus, the higher species richness and percent faunal cover of the east zone compared to the west zone could be attributed to the greater food availability of the east zone. This conclusion is consistent with the results of Mullineaux (1987). She found that species richness and faunal percent cover at the ENP site (5°N, 125°W) were higher than at the CNP site (30°N, 157°W), even when rarefaction curves were used to avoid the bias that ENP nodules were larger and colonized by a greater number of individuals than CNP nodules. The ENP site presumably receives a more abundant food supply, which could favour a higher number of taxa and a greater extent of faunal colonization.

4.4. Nodule substratum

Nodule size can influence species richness, species density and percent faunal cover. In contrast to those of Mullineaux (1987), our data show that species richness increases with nodule size. The non-significance of the regressions between nodule size and these parameters in the case of facies A could be explained by the smaller sample size (n=15) and the fact that the nodules were small (Table 4). The negative slope of the regressions between species density and exposed nodule surface implies that the number of taxa observed on a nodule reaches a maximum value at a certain nodule surface area. This suggests that species richness is not limited by the space on the nodule surface available for colonization. The relationship of percent cover and nodule surface is negative for the east zone and facies B and C. However, the absence of a relation between faunal cover and nodule surface reported by Mullineaux (1987) implies that percent faunal cover is not limited by nodule surface either. Furthermore, there is no link between species richness and percent faunal cover.

In deep-sea sedimentary environments, small-scale heterogeneity has been invoked to explain high local species diversity in soft-bottom communities (Grassle and Maciolek, 1992; Snelgrove and Smith, 2002). The higher species richness on facies C and B nodules could be explained by the presence of morphological irregularities, such as knobs, protrusions and depressions, that create habitat heterogeneity and different ecological niches for the encrusting fauna. In contrast, the low species richness on spherical facies A nodules or on the regularly-shaped facies west nodules may reflect the relative lack of surface irregularities. Nodule surface texture, either rough or smooth, can also contribute to structuring faunal spatial distribution. Mullineaux (1989) showed that the distributions of common nodule taxa were correlated with surface roughness; 15 taxa occurred more abundantly on smooth surfaces and seven taxa on rough surfaces. This may be related to, among other factors, larval responses to surface texture. Moreover, Dugolinsky (1976) observed that nodules with a rough and gritty surface from the northeast equatorial Pacific supported a larger number of attached protozoans than nodules with a smooth surface from the southwest Pacific and the southern ocean, although regional environmental differences may also have contributed to these faunal differences. Nodule surface composition can also influence the distribution of organisms as demonstrated by Mullineaux (1988). In her colonization experiment, several taxa settled exclusively on natural nodules, avoiding ceramic nodules with surface textures similar to that of the nodules. See Veillette *et al.* (2006, submitted to Deep-Sea Research) for a more detailed discussion on the roles of nodule surface characteristics and microhabitats in structuring faunal communities.

The RDA analyses of taxa distribution among facies based on abundance and presence/absence yielded very similar results (Fig. 8). The analyses suggest that facies type significantly influences the composition of nodule fauna although it is probably not the main regulating factor.

4.5. Nodule grouping and species assemblages

Links to environmental factors were examined to ascertain why certain nodules grouped together. Nodules that did not join with the largest group obtained by the Jaccard index method were mostly facies A and west nodules. This suggests that the faunal composition of facies B and C nodules was more similar to one another than to facies A or west. Also, nodules coming from the same box core or dive tended to cluster more closely, indicating that their faunas were similar. Nodules grouping with the PCA, K-means Euclidean ordination and the Ward agglomerative grouping method did not correspond to any facies type, indicating again that facies type is not the main factor influencing the nodule fauna. Furthermore, no measured environmental factor was specific to any group, indicating that nodule faunas were mainly structured by random processes or by other factors not considered here at the facies scale. Cluster analyses of the fauna colonizing sponge stalks suggested that substratum complexity may have an influence on communities (Beaulieu, 2001). Moreover, sponge stalks act as isolated island habitats for encrusting organisms (Beaulieu, 2001) whereas nodules are often a dominant habitat, where space is not limiting, at both the regional and facies scales. Sponge stalk communities were at most 50% similar using the Jaccard index and the sponge species forming the substratum was the first criterion explaining the formation of a cluster rather than horizontal distance (on the scale of meters) or similarity in stalk height (Beaulieu, 2001).

Thirty-four taxa out of 42 are independently distributed, suggesting that species interactions play only a minor role in explaining the distribution of the fauna on the nodules. Species assemblage identification could not include metazoans since their abundance was not measured. Their occurrence was recorded only on the basis of presence or absence. The vast majority were dead when collected. Metazoans were mostly found on facies C nodules and this is probably related to the higher flow necessary for suspension feeding.

4.6. Vulnerability of nodule faunas to mining impacts

Not all nodule fields can be easily exploited (for example, steep escarpments are unsuitable for mining) and some are not economically viable because their chemical composition is unsuitable or the nodule density is too low (Thiel and Tiefsee-Umweltschutz, 2001). Hoffert (pers. comm.) suggests that less than 1% of the seafloor would be exploitable for nodule mining. Nevertheless, nodule mining will potentially affect tens to hundreds of thousands of square kilometres of deep sea (Glover and Smith, 2003). Nodule growth is extremely slow and ecosystem recovery to the pre-exploitation state would probably require millions of years (Glover and Smith, 2003). It is also important to note that no natural disturbance similar in magnitude (in terms of space and intensity) to large-scale nodule mining has ever been done in deep-sea regions where nodules are found (Jumars, 1981). The potential for mining to cause extinctions among nodule-dwelling species is a crucial issue. Our knowledge of the distribution and diversity of the fauna associated with nodules in the deep ocean is very limited. Further study of the geographic ranges of taxa living on nodule surfaces, and the comparison of these ranges with the extent of nodule regions potentially targeted for mining activities, will be essential in order to evaluate the possible impacts on nodule communities. At present, only speculation, based on the present study and that of Mullineaux (1987), is possible.

Twenty-one of the protozoans (out of 73), and all of the metazoan groups that we recognised appear to correspond to taxa observed by Mullineaux (1987) on nodules at central North Pacific (CNP) or equatorial North Pacific (ENP). Most of the protozoan taxa (83%) were observed in both zones (east and west). Even though species richness at the ENP site (78 taxa) was twice that at the CNP site (34 taxa), most taxa observed at the latter site were also found at the former (Mullineaux, 1987). Thus the geographic ranges of some taxa colonizing nodule surfaces extend at least over the entire Clarion-Clipperton fracture zone. Ten protozoan taxa identified in this study are similar to species associated with hard substrata other than nodules, suggesting that their geographic ranges are not confined to nodule fields. For example, some of the foraminifera in our samples (e.g. *Telammina*) resemble encrusting species reported from the Atlantic (Gooday and Haynes, 1983). Cosmopolitan distributions are well known among some free-living, abyssal foraminifera (Murray, 1991; Gooday *et al.*, 2004) and preliminary morphological analyses of polychaetes inhabiting nodule-field sediments suggest that other taxa may have similar distributions (Glover *et al.*, 2002). Thus the geographic ranges of the species may extend well beyond the spatial scales of areas impacted by individual mining operations, although these conclusions must be confirmed by molecular techniques (Glover *et al.*, 2002).

Nodule fields are widespread in the deep Pacific ocean and are characterized by homogeneous environmental parameters, leading to a high recruitment potential. Species associated with nodules are therefore likely to be less vulnerable to local disturbances and extinctions than those with more localized distributions (Glover and Smith, 2003). Nevertheless, the number of sites sampled is low (too low for identification of rare species) and we need to know much more about abyssal community structure, taxonomy and natural history of species in order to confirm this idea (Thiel and Tiefsee-Umweltschutz, 2001). For instance, we do not know whether source or "mother" populations of nodule-dwelling species exist and hence, the precautionary approach must be applied. In addition, we cannot assume that the nodule fauna of all sites has been identified to similar systematic levels or with a similar degree of accuracy (Thiel and Tiefsee-Umweltschutz, 2001). Present evidence suggests that facies C would be more vulnerable to exploitation. It is the most species rich facies, it includes most of the rare species, and has the greatest economical potential in terms of mining (Hoffert, pers. comm.). As a result, controlled nodule extraction would be essential to ensure the perennity of the nodule fauna in this area.

The DISCOL and BIEs programs established baseline data for the benthic ecosystem in nodule regions and evaluated the possible impacts of nodule mining by creating benthic disturbances mimicking the likely effects of mining (Borowski and Thiel, 1998; Sharma *et al.*, 2000; Ahnert and Schriever, 2001; Bluhm, 2001; Borowski, 2001; Sharma *et al.*, 2001; Thiel *et al.*, 2001; Vopel and Thiel, 2001). DISCOL compared pre- to post-disturbance assemblages of meiofauna (Nematoda and Harpacticoida at genus level), macrofauna (total and Polychaeta at species and higher taxa levels) and megafauna (higher taxa) in the disturbed areas of seafloor and adjacent parts affected by sediment blanketing, a major environmental consequence of nodule mining (Borowski and Thiel, 1998; Ahnert and Schriever, 2001; Bluhm, 2001; Borowski, 2001; Sharma *et al.*, 2001; Thiel and Tiefsee-Umweltschutz, 2001; Vopel and Thiel, 2001). Seven years after the artificial disturbance, the benthic community had still not recovered, as evidenced by the irregular distribution of species and different diversity patterns. The megafauna was not restored to its original densities after this time interval. In the long term, the re-establishment of a balanced community, with a different structure than the original one, would represent an acceptable outcome (Thiel and Tiefsee-Umweltschutz, 2001). Nevertheless, the nodule faunas cannot possibly recover if the substratum on which they live is removed from the mined zones.

In general, the results of the DISCOL and BIEs programs do not provide strong arguments against nodule mining (Thiel and Tiefsee-Umweltschutz, 2001). However, caution must be used in extrapolating from these limited results to the potential impact of large scale nodule exploitation since the disturbance created was much less extensive than what would occur during actual mining (Thiel and Tiefsee-Umweltschutz, 2001). Moreover, the impacts on the benthic ecosystem will also depend on local environmental conditions (Sharma *et al.*, 2001). If and when nodule mining does occur, conservation areas will be created by the International Seabed Authority (International Seabed Authority, 2005a). These will act as reference areas in order to assess the environmental impacts of nodule mining. Endemic species and species with limited recruitment potential will require particular attention. More research is needed to select and plan effective conservation areas and this must take into account the abundant and diverse communities of organisms living on the nodules themselves.

5. Conclusions

Flux of particulate organic carbon to the bottom is the only major environmental factor considered that seems to vary between the two zones studied. The higher species richness and percent faunal cover found on nodules of the east zone can be partially attributed to greater food availability. The complex, knobby micro-relief of facies B and C nodules probably creates microhabitat heterogeneity that could have contributed to the greater species richness of the east zone. Nodule size also exerted a significant influence on the nodule fauna; in most cases, species richness increased with the area of exposed nodule surface while species density decreased. The analysis of the distribution of taxa among facies explained only a very small portion of the variance and species assemblages only play a minor role in the spatial distribution of nodule fauna. Although the impact of nodule mining will not be negligible, it is unlikely that mining will pose a major threat to any identified member of the nodule fauna. Local extinctions are probable, but given the widespread distribution of the nodule fauna and the limited areas likely to be affected by mining operations, total extinctions are unlikely. Nevertheless, caution is necessary and this tentative conclusion needs to be supported by a much fuller understanding of the biodiversity and biogeography of nodule-dwelling species.

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Figures

Figure 1.

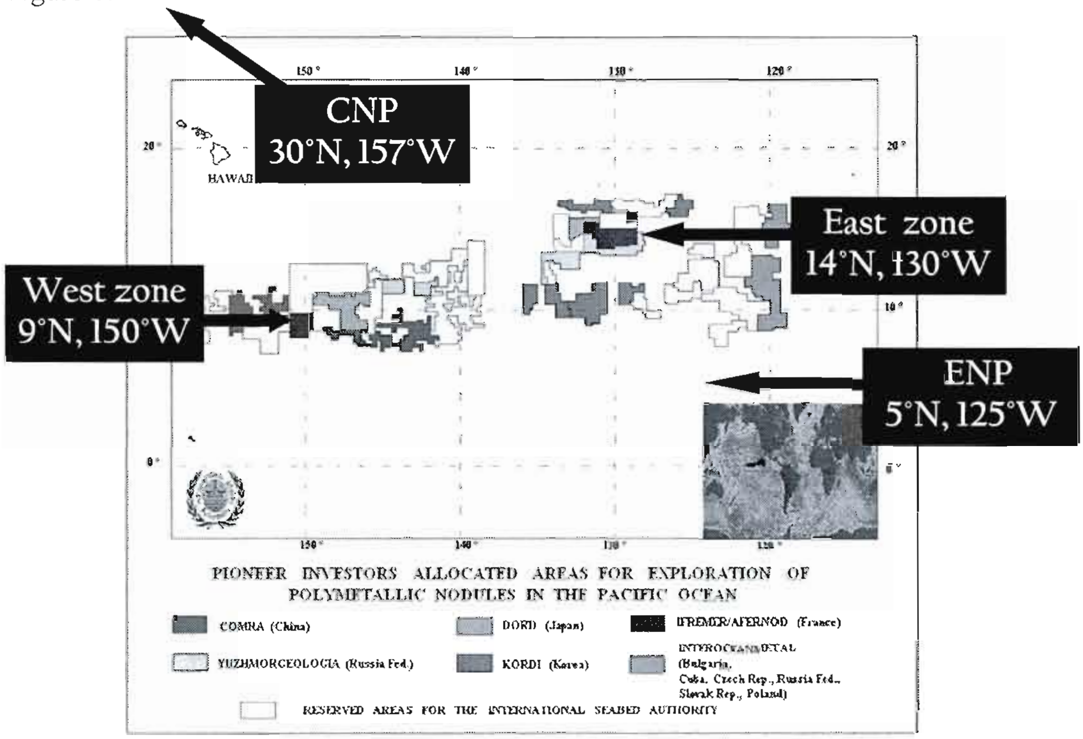
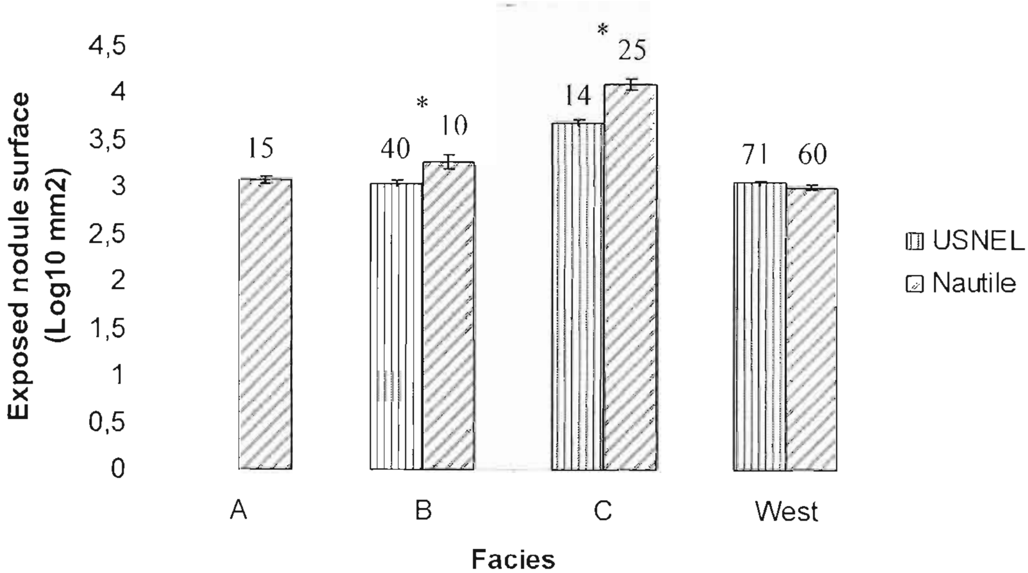
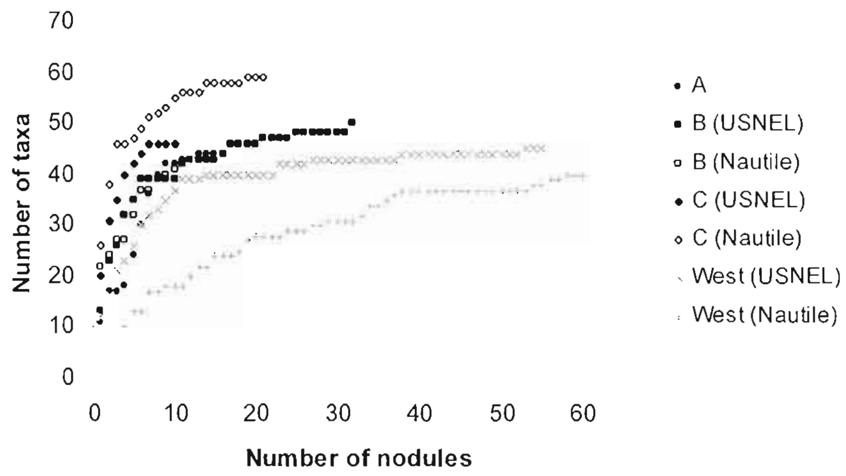


Figure 2.



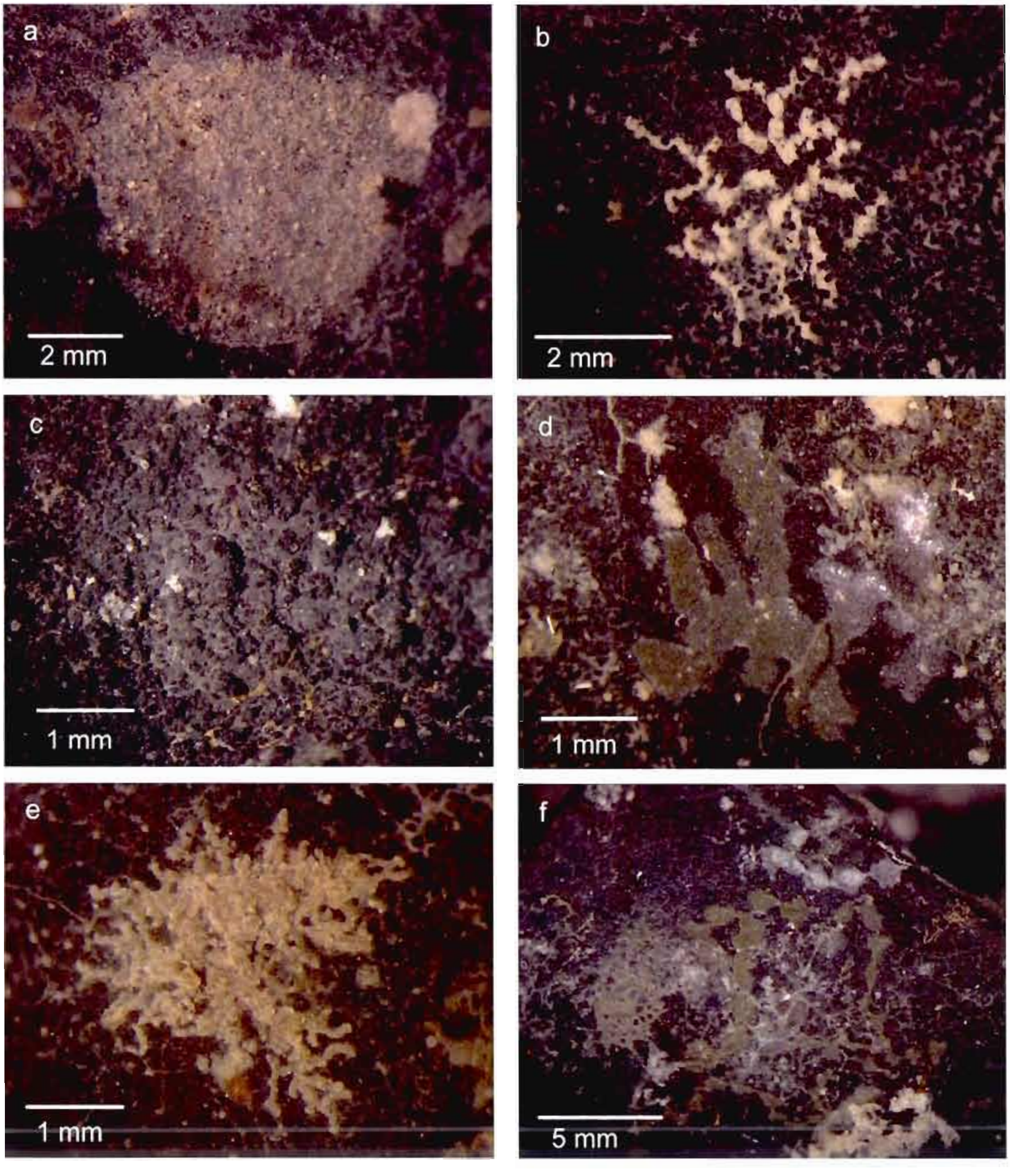
Exposed nodule surface (Log10 mm2)
4,5
4
3,5
3
2,5
2
1,5
1
0,5
0
15
40
*
10
14
*
25
71
60
USNEL
Nautile
A
B
C
West
Facies

Figure 3.



70
60
50
40
30
20
10
0
Number of taxa
0
10
20
30
40
50
60
Number of nodules
A
B (USNEL)
B (Nautile)
C (USNEL)
C (Nautile)
West (USNEL)
West (Nautile)

Figure 4.



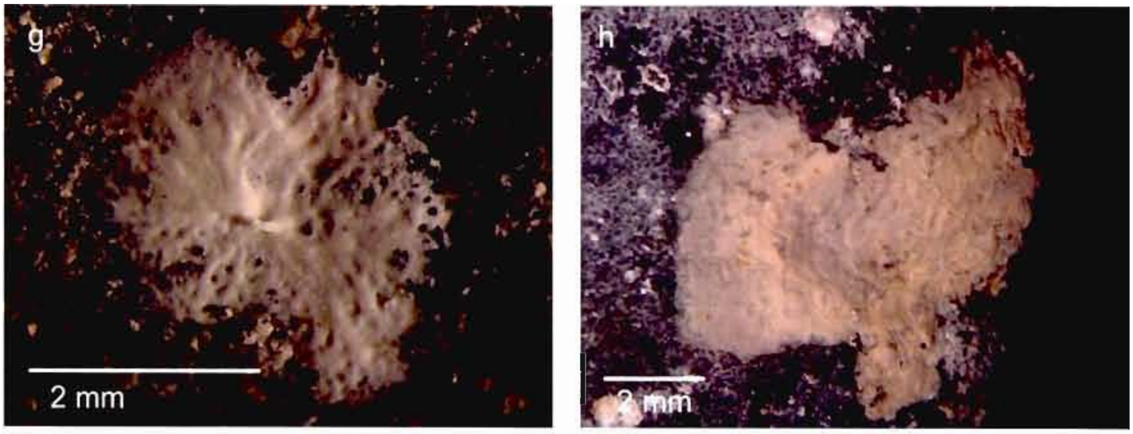

g
2 mm
h
2 mm

Figure 5.

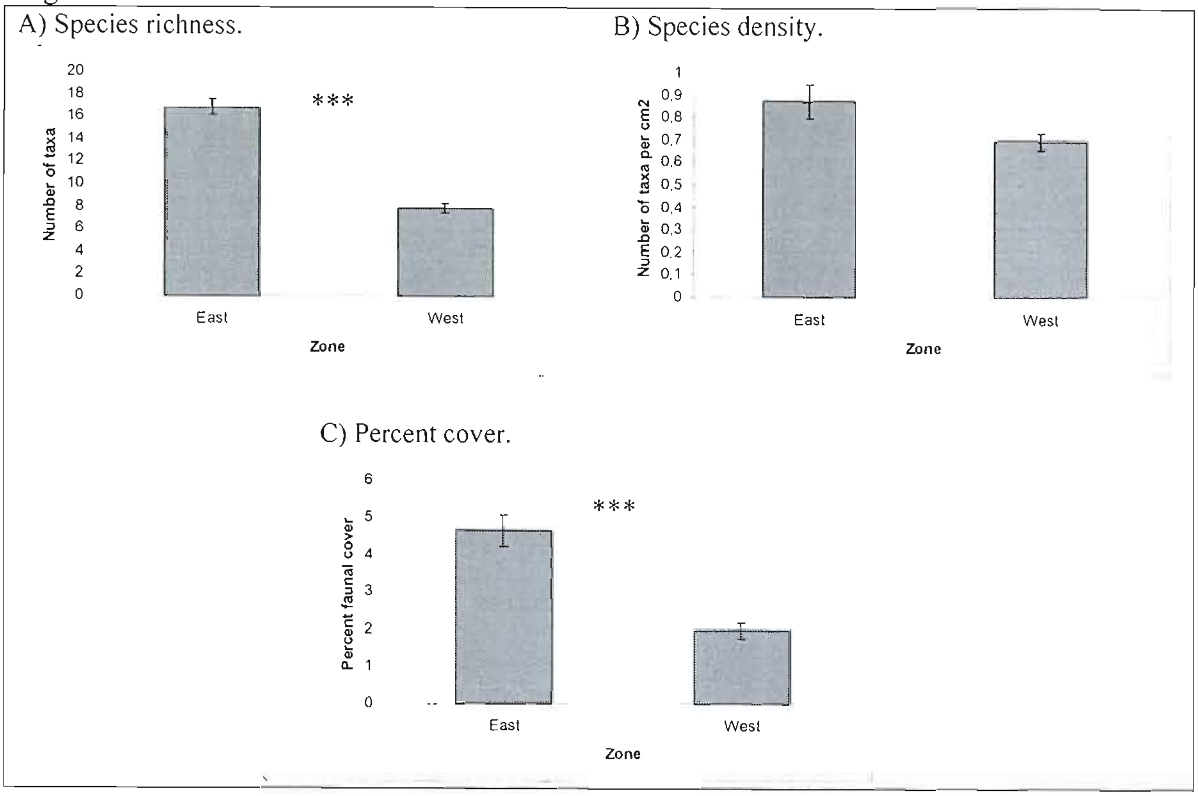

A) Species richness.
Number of taxa
20
18
16
14
12
10
8
6
4
2
0
***
East
West
Zone
B) Species density.
Number of taxa per cm2
1
0,9
0,8
0,7
0,6
0,5
0,4
0,3
0,2
0,1
0
East
West
Zone
C) Percent cover.
Percent faunal cover
6
5
4
3
2
1
0
***
East
West
Zone

Figure 6.

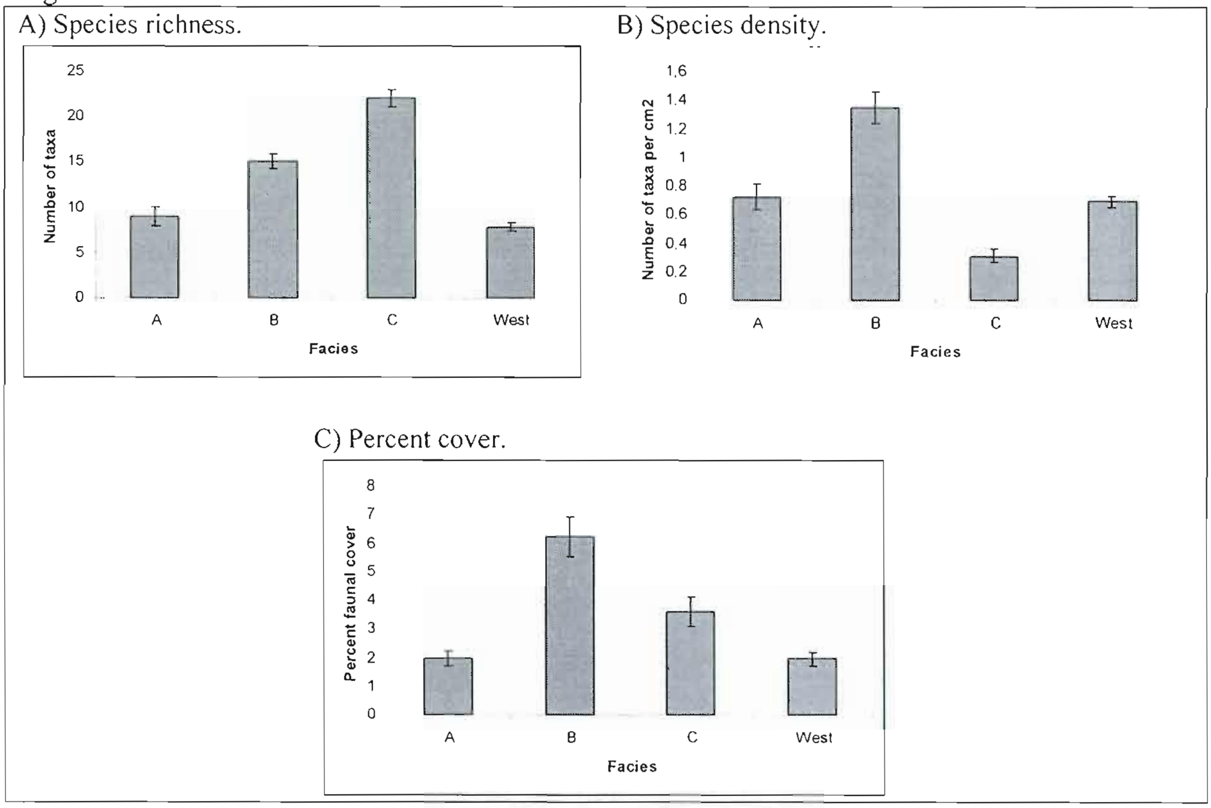
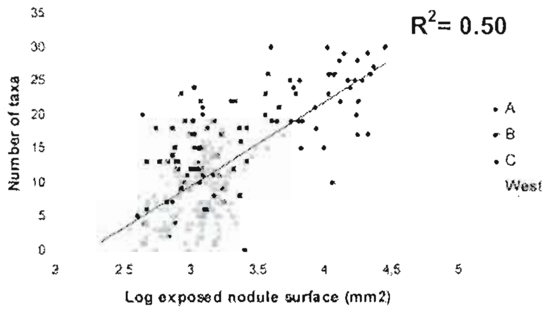
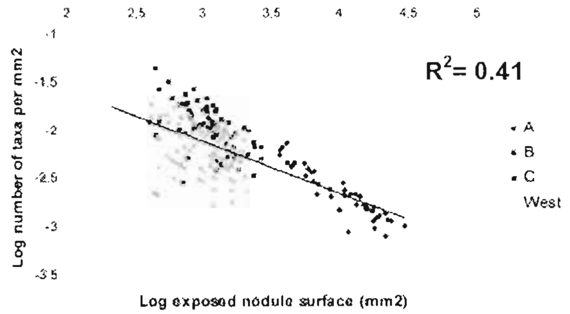

A) Species richness.
Number of taxa
25
20
15
10
5
0
A
B
C
West
Facies
B) Species density.
Number of taxa per cm2
1,6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
A
B
C
West
Facies
C) Percent cover.
Percent faunal cover
8
7
6
5
4
3
2
1
0
A
B
C
West
Facies

Figure 7.

A) Species richness in relation to exposed nodule surface.



B) Species density in relation to exposed nodule surface.



C) Percent cover in relation to exposed nodule surface.

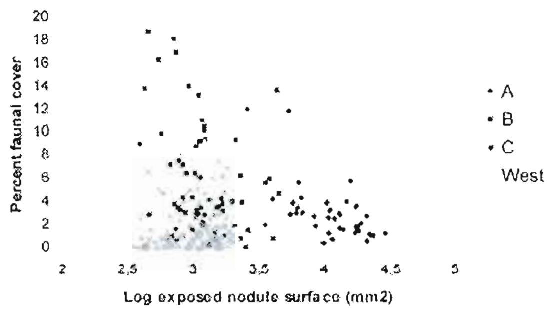
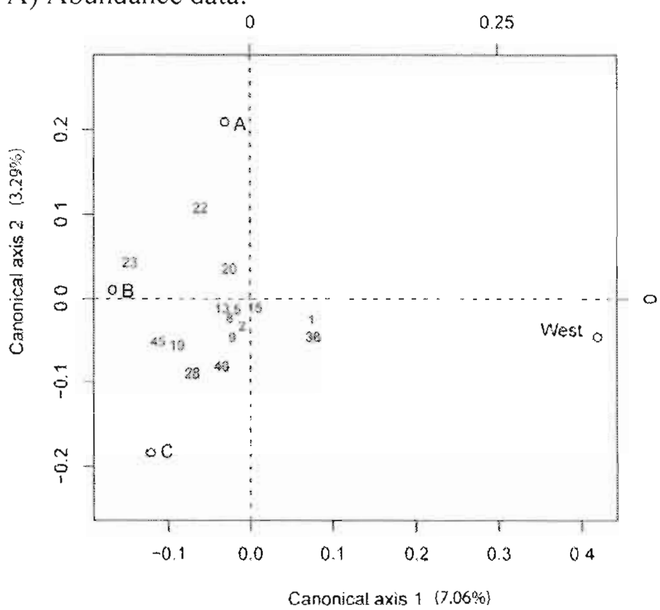


Figure 8.

A) Abundance data.



B)Presence/absence data.

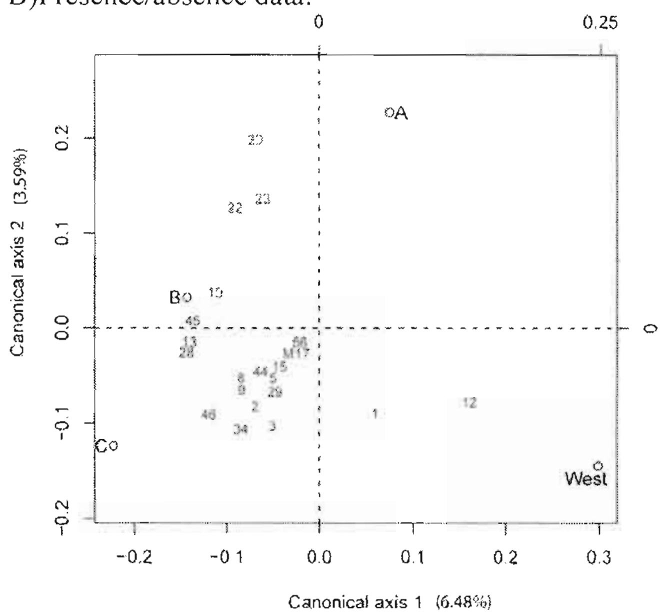


Figure captions

Figure 1. Map of the equatorial North Pacific ocean showing the east and west zones sampled during the present study and the two locations, equatorial North Pacific (ENP) and central North Pacific (CNP), sampled by Mullineaux (1987).

Figure 2. Nodule surface area (exposed above sediment line) for the two sampling methods, USNEL box core and the submersible *Nautile*, for nodules of facies B (50 nodules), C (39 nodules) and west (131 nodules). Numbers of nodules are indicated over bars. Error bars indicate SD. The non-parametric Wilcoxon/Kruskal-Wallis test was used to test differences between the two sampling methods. * α= 0.05. Facies B: Z= 1.96, p= 0,002. Facies C: Z= 1.96, p= 0,03. Facies west: Z= 1.96, p= 0,32. Facies C grouped alone and then, facies A, B and west grouped together according to the Tukey test when nodules of the same facies collected using both sampling methods were pooled together ($\chi^2_{0.05,3}$ = 7.815, p<0.0001).

Figure 3. Accumulation curves of taxa for the number of nodules in each facies. Nodules were collected using two sampling methods: USNEL box core and the submersible *Nautile*.

Figure 4. Some of the most common taxa living on nodule surfaces. a) Very thin muddy patches with komokiacean-like chambers; b) *Tumidotubus* sp.; c) Thin grey mat; d) Thin organic mat with dark grey stercomata; e) *Chondrodapis hessleri*; f) "Flattened chambers"; g) "White crust"; h) Beige thick and smooth mat, interior brown

Figure 5. Comparison at the regional scale of mean species richness (A), species density (B) and percent cover (C) using all 235 nodules analyzed. Error bars indicate standard error. * α= 0.05, ** α=0.01, ***<0.001. Species richness ($t_{0.05(2),\infty}$= Z= 1.96, p=0.0000) and percent faunal cover ($t_{0.05(2),\infty}$= Z= 1.96, p<0.0001) were significantly different between the two zones. Only species density ($t_{0.05(2),\infty}$= Z= 1.96, p= 0.5364) was similar between the two.

Figure 6. Comparison at the facies scale of mean species richness (A), species density (B) and percent cover (C) using all 235 nodules analyzed. Error bars indicate standard error of the mean. All tests show significant differences between facies ($\chi^2_{0.05,3}$ = 7.815, p<0.0001).

Figure 7. Regression of species richness (A), species density (B) and percent cover (C) as a function of exposed nodule surface for the 235 nodules analyzed.

Figure 8. Redundancy canonical analysis (RDA) of Hellinger-transformed abundance data (A) (42 taxa, R^2 = 0.054, p= 0.0005) and presence/absence data (B) (62 taxa, R^2

= 0.063, p= 0.0001) from 60 randomly-chosen nodules (15 nodules/facies). Nodules without fauna were excluded from the analysis. % of variance explained by each axis indicates between parentheses. Numbers refer to taxa numbers as detailed in Table 5. Only taxa for which >10% of variance is explained by facies type are shown. 9999 permutations were realized for every test.

Tables

Table 1. Nodule abundance and percent cover from USNEL box cores.

USNEL box cores	Depth (m)	Facies[1]	Total number of nodules[2]	Total nodule percent cover[3]	Number of nodules used for analyses[4]
East zone					
KGS-1	5036	C	Disturbed[5]	Disturbed	0
KGS-3	5005	C	Disturbed	Disturbed	2
KGS-6	4974	C	Disturbed	Disturbed	3
KGS-7	4996	C	Disturbed	Disturbed	2
KGS-21	4911	B	91	35.3	1
KGS-22	4954	B	92	48.7	3
KGS-23	4935	B	169	55.6	2
KGS-24	4904	B	114	52.8	0
KGS-25	4930	B	97	52.7	3
West zone					
KGS-28	5050	West	53	26.1	0
KGS-29	5050	West	22	22.6	2
KGS-30	5051	West	97	45	1
KGS-31	5055	West	78	8.2	1
KGS-32	5048	West	116	18.2	0
KGS-33	5043	West	19	8.9	0
KGS-36	5048	West	64	24.3	0
KGS-37	5054	West	16	4.5	0
KGS-38	5051	West	63	24.7	0
KGS-39	5051	West	88	37.9	0
KGS-40	5059	West	Disturbed	Disturbed	0
KGS-41	5050	West	Disturbed	Disturbed	0

[1] Facies A were not sampled with USNEL box core.
[2] Determined by direct counting in top-view pictures (average of triplicates).
[3] Determined with Image analysis software IP Lab Spectrum© (average of triplicates).
[4] Number of nodules used in inter-facies faunal comparisons (15 nodules of every facies collected by either sampling method).
[5] "Disturbed" means that the content of the box core was well mixed and that the number of nodules and the nodule percent cover were impossible to estimate.

Table 2. Sampling strategy used for nodules collected with the manipulator of the submersible *Nautile*.

Dive	Depth (m)	Facies	Sampling strategy	Number of nodules used for analyses [1]
PL1593-01	4955	A	All nodules were placed in a small box. 15 nodules were present.	15
PL1598-06	4971	C	Nodules were placed with difficulty in small boxes.	2
PL1602-10	4983	C	Nodules were placed directly in the basket.	6
PL1603-11	4987	B	Nodules were placed in small boxes in groups of 4.	5
PL1605-13	5040	West	Nodules were placed in small boxes full of sediments. The first 15 nodules encountered were taken (length >18mm).	11

[1] Number of nodules used in inter-facies faunal comparisons (15 nodules of every facies collected by either sampling method).

Table 3. Numbers and types of nodules analyzed and included in this study. Numbers of sampling sites are indicated between parentheses.

Facies	Number of nodules sampled with USNEL box core	Number of nodules sampled with *Nautile* submersible	Total number of nodules analyzed	Total surface area (m^2)
East zone				
A	0	15 (1)	15	0.019
B	40 (5)	10 (1)	50	0.074
C	14 (4)	25 (2)	39	0.457
West zone				
West	71 (12)	60 (1)	131	0.164
Total			235	0.715

Table 4. Numbers of nodules observed in three size categories as described by Hoffert and Saget (2004).

Sampling method	Facies	Number of nodules			Total number of nodules
		Small (<5cm in length)	Medium (5-10cm in length)	Large (>10 cm in length)	
Nautile	A	15	0	0	15
Box core	B	30	10	0	40
Nautile	B	3	7	0	10
Box core	C	3	9	2	14
Nautile	C	0	5	20	25
Box core	West	48	23	0	71
Nautile	West	42	18	0	60
Total					235

Table 5. List of taxa colonizing the four facies of the 235 nodules analyzed in this study.

	Protozoan taxa[1]	A[2]	B[2]	C[2]	West[2]	Live/ Dead[3]	Percent cover[4]	Feeding type[5]
	Domes and lumps							
1	*Pseudowebbinella* sp.	0	x	x	x	Live	x	S
2	*Hemispherammina*-like, pale regular dome	x	x	x	x	Live	x	S
3	*Hemispherammina*-like, pale granular dome	x	x	x	x	Live	x	S
4	*Hemisperammina*-like, irregular shape	x	x	x	x	Live	x	S
5	*Tholosina* sp.	0	x	x	0	Live	x	S
6	*Tholosina*-like	x	x	x	0	Live	x	S
7	*Trochammina*-like	x	x	x	x	Live		S
8	*Placopsilina*-like	x	x	x	x	Live	x	S
9	Komoki, mud-ball type	x	x	x	x	Live	x	D
10	Whitish sparkling dome	x	0	0	x	Live	x	S
11	Whitish flattened dome	x	0	0	x	Live	x	S
12	White granular patches	x	x	x	x	Live		S
13	*Ammocibicides*-like	x	x	x	x	Live	x	S
14	Fine agglutinated particles beige soft dome	x	x	x	x	Live	x	S
15	Brown granular shiny dome	0	x	x	x	Live	x	D
16	Black granular dome	0	x	x	x	Dead		D
17	Black soft dome	x	x	x	x	Live	x	D
18	Orange dome	x	x	x	x	Live	x	S
	Mats							
19	*Chondrodapis hessleri*	x	x	x	x	Live	x	D
20	*Chondrodapis integra*	x	x	x	x	Live	x	D
21	Area covered with komokiacean-like chambers linked with fine tubes	x	x	x	x	Live	x	D
22	Grey granular mat	x	x	x	x	Live	x	D
23	Very thin muddy patches with komokiacean-like chambers	x	x	x	x	Live	x	D
24	*Telammina*	x	x	x	x	Live		S
25	*Tumidotubus*	x	x	x	x	Live	x	S
26	*Xenophyophorea*-like, without agglutinated particles	x	x	x	x	Dead		D
27	*Xenophyophorea*-like, fan-shaped agglutinated	0	x	x	x	Dead		D
28	"White crust"	x	x	x	x	Live	x	S
29	"Beige filamentous mat"	0	x	x	x	Live	x	?

30	"Dark chambered mat"	0	x	x	0	Live	x	D
31	Thin grey mat	x	x	x	x	Live	x	S
32	Thin organic mat with dark grey stercomata	x	x	x	x	Live	x	D
33	Beige thick mat with red interior	x	0	0	0	Live	x	S
34	Beige thick and smooth mat, interior brown	x	x	x	x	Live	x	S
35	Mat of blue flattened chambers	x	x	x	x	Live	x	?
36	White mat with lumps	x	x	x	x	Live	x	S
37	White crusty mat with coarse particles	0	0	x	x	Live	x	S
38	Orange, rigid agglutinated wall in crevice	0	x	x	x	Dead		S
39	Mat of very coarse sediment agglutinated	0	x	x	x	Dead		S
	Tunnels							
40	"Thin anastomosing tunnels"	x	x	x	x	Live		S
41	"Cemented tunnels"	x	x	x	x	Live	x	S
42	Reticulated dark tunnels	x	x	x	x	Live	x	S
43	Network of beige tunnels; horizontal tree with upright branches	0	x	x	x	Live	x	D
44	Crystal star and tunnels	0	x	x	x	Live	x	S
45	Spider network of grey tunnels	x	x	x	x	Live	x	S
46	White soft tunnels	x	x	x	x	Live	x	S
47	Network of empty beige tunnels	0	x	x	x	Dead		S
	Connected chambers							
48	Chain of orange/brown chambers	x	x	x	x	Dead		S
49	"Flattened chambers"	x	x	x	x	Live	x	D
50	Chain of empty grey and rounded chambers	0	x	x	x	Dead		S
51	*Hormosina* sp.	x	x	x	x	Live	x	S
52	Brown chain of spheres rigidly agglutinated	0	0	x	0	Dead		S
	Upright tubes							
53	Network of branched tubes either lying down on the nodule surface or standing	x	x	x	x	Live		D
54	*Psammotodendron indivisum*- like	0	x	x	x	Live		S
55	Komokiacean-like chambers on delicate filaments	x	x	x	x	Live		D
56	Upright beige tubules with constrictions	0	x	x	x	Live		D
57	Upright beige structures	0	x	0	0	Live		S
58	Tube upright with komokiacean-like chambers	x	x	x	0	Live		D
59	Branched upright tubules	x	x	x	x	Live		D
60	Upright tree	0	x	x	x	Live		D

61	Upright filament	x	x	x	x	Live		D
62	Upright filament, branched dichotomously	x	x	x	x	Live		D
63	Upright beige tubule, two origins	x	0	0	0	Live		D
64	Branching stercomata-filled tube	x	x	x	x	Live		D
65	Anastomosing *Rhizammina*-like	x	x	x	x	Live	x	D
	Recumbent tubes							
66	*Saccorhiza ramosa*-like	0	x	x	x	Dead		S
67	*Tolypammina* sp.	x	x	x	x	Dead		S
68	Horizontal organic tube full of stercomata	0	0	x	x	Live	x	D
	Unattached forms							
69	*Ammodiscus* sp.	0	0	0	x	Dead		S
70	Orange snail	0	0	0	x	Dead		S
71	*Biloculina* sp.	0	x	x	x	Dead		S
72	*Quinqueloculina*-like	0	x	x	0	Dead		S
73	*Thurammina*-like	0	0	x	0	Dead		S
	Metazoan taxa							
	Sponges							
M1	Taxon 1: Porcupine	x	x	x	x	Dead		S
M2	Taxon 2: Sponge stalk with spikes	0	0	x	0	Dead		S
M3	Taxon 3: White rigid stalk	0	0	x	0	Dead		S
	Scyphozoans							
M4	*Stephanoscyphus* sp.	0	x	x	x	Dead		S
M5	Taxon 1: Elongated scyphozoan	0	0	x	0	Dead		S
	Mollusc							
M6	*Bentharca asperula*	0	x	x	0	Live		S
	Polychaetes							
M7	Taxon 1: Spiral	0	x	x	0	Dead		S
M8	Taxon 2: Smooth tube	0	x	x	x	Dead		S
M9	Taxon 3: Tube with spikes	0	0	x	0	Dead		S
M10	Taxon 4: Mud tube	0	0	x	0	Dead		?
	Bryozoans							
M11	*Camptoplites* sp.	0	x	x	0	Dead		S
M12	*Bugula* sp.	0	0	x	0	Dead		S
M13	Cyclostomate	0	0	x	0	Dead		S
	Brachiopods							
M14	*Pelagodiscus atlanticus*	0	0	x	0	Live		S

M15	*Gwynia aff. capsula*	0	x	x	0	Live		S
	Ascidian							
M16	*Cnemidocarpa sp.*	0	0	x	0	Live	x	S
	Platyhelminthe, Turbellaria							
M17	*Fecampia abyssicola*	0	0	x	0	Live		S

[1] Taxa in quotes have the same name as those described in Mullineaux (1987).
[2.] Presence (x) or absence (0) of the taxa on nodules.
[3.] Intact protoplasm was used to identify live specimens, and the "dead" designation was used when only remnant specimens were present on nodule surface.
[4.] Percent cover identifies taxa included in the percent cover study.
[5.] Feeding type (suspension feeder (S) or deposit feeder (D)) was deduced by the presence or absence of stercomata for Foraminifera (Gooday *et al.*, 1997), and from morphology and literature descriptions for metazoans (Mullineaux, 1987).

Table 6a. Ten most abundant taxa (out of 42) ranked in terms of percent cover of total fauna for all nodules analyzed in both zones (n= 104 for the east zone; n= 131 for the west zone). Grey shading indicates taxa abundant in both zones.

East zone		**West zone**	
Taxa	**%**	**Taxa**	**%**
Very thin muddy patches with komokiacean-like chambers	26.59	*Tumidotubus*	16.10
Spider network of grey tunnels	13.25	Very thin muddy patches with komokiacean-like chambers	14.10
Thin grey mat	9.45	Thin organic mat with dark grey stercomata	10.41
Thin organic mat with dark grey stercomata	6.72	Spider network of grey tunnels	9.79
Tumidotubus	6.40	Area covered with komokiacean-like chambers linked with fine tubes	4.99
Chondrodapis hessleri	5.76	"Flattened chambers"	4.85
"Flattened chambers"	4.59	Grey granular mat	3.97
"White crust"	4.11	"Beige filamentous mat"	3.84
Beige thick and smooth mat, interior brown	3.19	Komoki, mud-ball type	3.46
Grey granular mat	2.64	Thin grey mat	3.34

Table 6b. Ten most abundant taxa (out of 42) ranked in terms of percent cover of total fauna for all nodules analyzed in every facies (A, n= 15; B, n= 50; C, n= 39; west, n= 131). Grey shading indicates taxa abundant in the four facies.

Facies A		**Facies B**		**Facies C**		**Facies west**	
Taxa	**%**	**Taxa**	**%**	**Taxa**	**%**	**Taxa**	**%**
Very thin muddy patches with komokiacean-like chambers	36.62	Very thin muddy patches with komokiacean-like chambers	28.80	Very thin muddy patches with komokiacean-like chambers	25.47	*Tumidotubus*	16.10
Grey granular mat	7.74	Spider network of grey tunnels	17.07	Spider network of grey tunnels	12.08	Very thin muddy patches with komokiacean-like chambers	14.10
Spider network of grey tunnels	7.55	*Chondrodapis hessleri*	7.17	Thin grey mat	10.41	Thin organic mat with dark grey stercomata	10.41
Thin organic mat with dark grey stercomata	7.54	Thin grey mat	6.99	*Tumidotubus*	7.39	Spider network of grey tunnels	9.79
"Flattened chambers"	7.18	Thin organic mat with dark grey stercomata	6.44	Thin organic mat with dark grey stercomata	6.79	Area covered with komokiacean-like chambers linked with fine tubes	4.99
Thin grey mat	6.89	Grey granular mat	5.86	*Chondrodapis hessleri*	5.36	"Flattened chambers"	4.85
Tumidotubus	5.74	*Tumidotubus*	3.69	"Flattened chambers"	4.91	Grey granular mat	3.97
"Reticulated dark tunnels"	4.39	"Flattened chambers"	3.42	"White crust"	4.82	"Beige filamentous mat"	3.84
Beige thick and smooth mat, interior brown	3.62	Beige thick and smooth mat, interior brown	3.25	Beige thick and smooth mat, interior brown	3.15	Komoki, mud-ball type	3.46
Chondrodapis hessleri	2.71	"White crust"	2.30	White soft tunnels	2.90	Thin grey mat	3.34

Table 7. Results of the concordance tests among 42 nodule faunal taxa: A) overall test and B) *a posteriori* tests. To avoid spatial bias, 15 nodules were randomly selected from the four facies; five uncolonized nodules (one on facies B and four on facies west) were excluded from the analysis. Hellinger-transformed abundance data for the remaining 55 nodules were used. P= permutational probability based upon 9999 random permutations. P_H= Holm adjusted probability for multiple testing. C) Results based on the identification of associated taxa by K-means partitioning and Pearson correlation matrix. Only taxa significantly associated within each group by both methods are presented. (* α= 0.05.)

A) Overall test of the *W* statistic. H_0: The 42 taxa are not concordant with one another.		
Kendall's *W* =	0.09164	
Friedman's chi-square =	207.84010	P= 0.0001 *
H_0 is rejected. Taxa are not all independent of one another.		
B) *A posteriori* tests. H_0: This taxon is not concordant with the other 41.		
Pseudowebbinella sp.	P= 0.8427	P_H= 3.6864
Hemispherammina-like, pale regular dome	P= 0.0003 *	P_H= 0.0117 *
Hemispherammina-like, pale granular dome	P= 0.0472 *	P_H= 1.1064
Hemisperammina-like, irregular shape	P= 0.0471 *	P_H= 1.1064
Tholosina sp.	P= 0.0004 *	P_H= 0.0152 *
Tholosina-like	P= 0.0354 *	P_H= 0.9204
Placopsilina sp.	P= 0.0004 *	P_H= 0.0152 *
Komoki, mud-ball type	P= 0.0049 *	P_H= 0.1568
Whitish sparkling dome	P= 0.4252	P_H= 3.6864
Whitish flattened dome	P= 0.6639	P_H= 3.6864
Ammocibicides-like	P= 0.0001 *	P_H= 0.0042 *
Fine particles agglutinated beige soft dome	P= 0.0400 *	P_H= 1.0000
Brown granular shiny dome	P= 0.1287	P_H= 2.3166
Black soft dome	P= 0.1911	P_H= 2.8688
Orange dome	P= 0.1169	P_H= 2.2211
Chondrodapis hessleri	P= 0.0001 *	P_H= 0.0042 *
Chondrodapis integra	P= 0.1793	P_H= 2.8688
Area covered with komokiacean-like chambers linked with fine tubes	P= 0.0160 *	P_H= 0.4480
Grey granular mat	P= 0.2136	P_H= 2.9904
Very thin muddy patches with komokiacean-like chambers	P= 0.2562	P_H= 3.0744
Tumidotubus	P= 0.0006 *	P_H= 0.0216 *
"White crust"	P= 0.0002 *	P_H= 0.0080 *
"Beige filamentous mat"	P= 0.0103 *	P_H= 0.2987
"Dark chambered mat"	P= 0.2736	P_H= 3.0744
Thin grey mat	P= 0.0533	P_H= 1.1193
Thin organic mat with dark grey stercomata	P= 0.0247 *	P_H= 0.6669
Beige thick mat with red interior	P= 0.4096	P_H= 3.6864
Beige thick and smooth mat, interior brown	P= 0.0044 *	P_H= 0.1452
Mat of blue flattened chambers	P= 0.2191	P_H= 2.9904
White mat with lumps	P= 0.1554	P_H= 2.6418
White crusty mat with coarse sediments	P= 0.0096 *	P_H= 0.2880
"Cemented tunnels"	P= 0.0967	P_H= 1.9340

"Reticulated dark tunnels"	P= 0.6147	P_H= 3.6864
Network of beige tunnels; horizontal tree with upright branches	P= 0.4681	P_H= 3.6864
Crystal star and tunnels	P= 0.0029 *	P_H= 0.0986
Spider network of grey tunnels	P= 0.0461 *	P_H= 1.1064
White soft tunnels	P= 0.0006 *	P_H= 0.0216 *
"Flattened chambers"	P= 0.0065 *	P_H= 0.2015
Hormosina sp.	P= 0.6139	P_H= 3.6864
Anastomosing *Rhizammina*-like tubes	P= 0.4104	P_H= 3.6864
Horizontal organic tube full of stercomata	P= 0.9004	P_H= 3.6864
Cnemidocarpa sp.	P= 0.3645	P_H= 3.6450

C) Identification of associated taxa.

Group 1	- *Tholosina*-like
	- *Chondrodapis hessleri*
Group2	- *Hemispherammina*-like, pale regular dome
	- *Tholosina* sp.
	- *Placopsilina* sp.
	- Area covered with komokiacean-like chambers linked with fine tubes
	- White mat with lumps
	- Anastomosing *Rhizammina*-like tubes

CHAPITRE III

INFLUENCE OF SURFACE TEXTURE AND MICROHABITAT HETEROGENEITY IN STRUCTURING NODULE FAUNAL COMMUNITIES

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Abstract

The role of nodule surface texture and microhabitat heterogeneity in structuring nodule faunal communities was investigated. Facies C nodules were sampled either by an USNEL box core or the manipulator of the *Nautile* submersible during the NODINAUT cruise in the equatorial North Pacific in 2004. These nodules were characterized by a knobby summital region predominantly smooth, and by rough sides. Kruskal-Wallis tested if the percent cover of each of the 34 taxa examined was distributed evenly between the two surface textures and the three microhabitats. More than half taxa examined (20 out of 34) had a greater percent cover on smooth surfaces and the third of taxa (12 out of 34) preferred raised surfaces over hollows and nodule sides. These two results are closely interrelated since 78% of the raised surfaces are characterized by a smooth texture. Most of these taxa were suspension feeders. Flow velocity, involved in propagule transport and particulate food supply, may represent an important environmental factor explaining these faunal distributions as it is in other hard substrata communities.

Keywords: Ferromanganese nodules, fixed fauna, agglutinated foraminifera, surface texture, microhabitats, flow velocity.

Regional terms: Pacific ocean, equatorial north Pacific ocean, Clarion-Clipperton fracture zone. 14°N, 130°W.

1. Introduction

Foraminiferan taxa compose the vast majority of nodule fauna (Mullineaux, 1987; Veillette *et al.*, submitted). They are known to colonize different microhabitats that can be created, for example, by biological structures such as dead *Syringammina fragilissima* (Xenophyophorea) tests (Hughes and Gooday, 2004) and large agglutinated foraminifera (Gooday and Haynes, 1983; Gooday, 1984). Veillette *et al.* (submitted) suggested that microhabitat heterogeneity created by complex, knobby nodule micro-relief or remnant foraminiferan and metazoan tubes or tunnels can contribute to enhance species richness (Rex, 1981) and faunal cover. This source of habitat heterogeneity is of a smaller scale than those investigated at regional and local scales (Veillette *et al.*, submitted).

Substratum irregularities can affect boundary layer characteristics and so influence current velocities experienced by benthic organisms, many of which are filter- or suspension-feeders. Because of the dependence of hard substratum organisms on water currents, flow velocity is often considered as the most important environmental parameter structuring hard substrata communities (Jumars and Nowell, 1984; Mullineaux, 1988; Lutze and Thiel, 1989; Flach *et al.*, 1998; Pernet *et al.*, 2003; Thistle, 2003). It has been suggested that flow velocities vary between the different nodule microhabitats. Substrata characteristics, such as surface texture, can also influence the distribution of foraminifera (Mullineaux, 1988; Gooday, 1990; Bertram and Cowen, 1994, 1999) and were also observed to vary between different areas of the nodule surface in the analyzed nodules (Veillette *et al.*, submitted).

The objectives of this study are (1) to test if taxa are distributed evenly between the two surface textures and the three microhabitats and (2) to identify potential environmental factors that can explain these distributions.

2. Materials and methods

2.1. Sampling sites and methods

The NODINAUT cruise (May 18th – June 27th 2004) explored and sampled two geographical zones located in the French mining claim in the equatorial Pacific: the east zone (14°N, 130°W) and the west zone (9°N, 150°W). Both zones are located in the Clarion-Clipperton fracture zone at depths varying from 4950 to 5050m. Three different nodule facies were observed in the east zone (A, B and C) and an undescribed facies referred to as the "west facies" was found in the west zone. Nodule facies were differentiated according to their general shape, size, surface morphology and the relation between the nodule and its environment (buried in the sediment, presence of volcanic material) (Saguez, 1985; Morel and Le Suavé, 1986). Even though our visual classification, commonly used by geologists, appears to be subjective, differences in the geochemical composition of the nodules from different facies provides support for this approach (Tilot, 1992; Hoffert and Saget, 2004). Facies C nodules were chosen for this study because of their greater microhabitat heterogeneity and texture surface variations compared to facies A, B or west, although facies B nodules also had some knobs and texture variations as well. Only nodules whose vertical or near vertical sides extended more than 30mm above the sediment were included in this study.

Primary productivity in the region is estimated to be moderate compared to the high equatorial productivity (Du Castel, 1985; Skornyakova and Murdmaa, 1992). Ambient bottom-water temperature is ~1°C and near-bottom currents observed during the NODINAUT cruise (short term ADCP-WH300 measurements at ten meters above the bottom) are very weak (3.5 – 4 cm s^{-1}). Bottom relief can influence current speed and direction (Morgan *et al.*, 1999). We attempted to estimate currents at the scale of the nodules at several cm above the bottom with a modified weathercock but results are too preliminary to be significant.

Nodules were sampled using either an USNEL box core or the manipulator of the *Nautile* submersible. The sampled nodules were stored in 4% formaldehyde and transferred to 70% alcohol after several days. They were all carefully packed for transportation in jars of different sizes. Plastic packing was placed in the jars to immobilize the nodules. During all manipulations, nodules were never allowed to dry and were handled with the greatest care possible because of their high friability.

2.2. Nodule surface area determination

Nodule surface area was estimated in order to calculate percent cover on every texture and microhabitat. Since nodule surfaces below the sediment line were rarely colonized, they were not taken into account in this study. Therefore, the nodule surface of interest lies above the sediment line. The facies C nodules analyzed in this study (20 nodules) have their vertical or near vertical sides extended for more than 30mm above the sediment, before flattening to form the summital region. Their surface area was therefore separated into top and side. Top surface area was determined using IP Lab Spectrum© image analysis software, assuming that top-view photos provided a good representation of nodule surface area of the summital region. Side surface area was calculated using the surface formula for an open cylinder (height x circumference). In order to control for the irregular shape of most nodules, eight measures of the height of the sides were taken at every 45° around the nodule circumference. All measurements and surface determinations with IP Lab Spectrum© were made in triplicates.

2.3. Faunal identification and quantification

Identification of living organisms on nodule surfaces was done using a binocular dissecting microscope. Light microscopy and scanning electron microscopy were also used to examine smaller forms or particular structures and to determine if the unusual forms observed were protozoan, metazoan or non-living. The tests of most foraminifera (protozoa) were partially broken in order to determine if protoplasm was present and therefore whether the organism was alive or dead.

Taxa that were considered to be alive at the time of collection (based on the presence of intact protoplasm) were quantified. However, some foraminiferal forms rarely contained visible protoplasm. In these cases, the presence of unbroken tests was used to classify the taxa as live when collected. Despite all precautions taken during handling of the nodules, some very fragile structures may have been destroyed or lost prior to identification. Thus, faunal recognitions and descriptions in this study could be biased towards more robust forms firmly attached to nodule surfaces.

Percent cover was the best way to quantify taxa that form mats or domes (Mullineaux, 1987) and only these taxa were included in this study. Upright structures were excluded since their covered surface area was negligible. In order to simplify the methodology of faunal cover analysis, every covering taxa was assumed to represent a circle or a rectangle. The dimensions of the form were then measured under a binocular microscope equipped with a scale. For taxa forming anastomosing networks, percent cover within the limits of the form was estimated. Density (number of individuals cm^{-2}) was not used in this study since the vast majority of the living forms were foraminifera that are best quantified in terms of percent cover

(Mullineaux, 1987). The taxa included in this study were those found on at least two nodules.

2.4. Microhabitats and surface texture definitions

Data from twenty nodules were pooled to investigate the influence of microhabitats and surface texture on the distribution of nodule fauna. Three different types of microhabitats could be recognized on all nodules: the summital region was divided into raised and hollow surfaces, while the sides formed the third microhabitat. The hollows constituted the space between two knobs on the nodule surface (Fig. 1). Surface texture perception by organisms depends of their size scale: if the organism has about the same size as the protrusions creating the roughness of the surface, it might be influenced differently than a larger organism. Nonetheless, it has been suggested that differences between smooth and rough nodule surfaces are possibly large enough for tactile detection by foraminiferan larvae (Mullineaux, 1989). Surface texture was defined as either smooth or rough, although it was sometimes difficult to classify areas of moderate roughness. Surface area of each texture was estimated for the summital region of each of the 20 nodules analyzed by recording the texture under 20 random points of a grid placed over the nodule summit. Sides were assumed to present mostly rough surfaces.

2.5. *Statistical analyses*

A Kruskal-Wallis test was performed for the 34 live taxa included in this study in order to test if there were significant differences in cover between surface textures and microhabitats. Cover of every taxa on each surface texture was divided by the fraction of the nodule of that texture in order to calculate percent cover on every texture. The same was done for the comparisons between the three different microhabitats.

3. Results

When the 20 nodules were pooled together, 72% of the summital region had a smooth surface texture. When only raised surfaces were considered, 78% of the surface texture was smooth. However, only 30% of the area of hollows had a smooth surface texture. When the nodule surfaces of the three microhabitats were pooled together, smooth and rough surfaces were almost equally represented (48% versus 52%). Raised surfaces were dominant with more than 57% of the nodule surface while sides represented 33% and hollows areas, 10%. Eighty-six percent of the summital region was composed of raised surfaces, the remaining being hollows.

Out of the 34 taxa examined, percent cover for 20 taxa was significantly different between the two textures (Table 1). These taxa all had a greater percent cover on smooth surfaces. Of these, 13 were suspension feeders, six were deposit feeders and one had an unknown feeding type. Moreover, 12 of the 34 taxa preferred raised surfaces over hollows and nodule sides. Fourteen taxa preferred smooth and raised surfaces over hollows and nodule sides. Eight of the latter were suspension feeders and five deposit feeders. Overall, twelve taxa had no significant relationships with surface texture and microhabitat types.

4. Discussion

4.1. Influence of surface texture and microhabitat

The facies C nodules analyzed in this study were characterized by a summital region predominantly smooth, and by rough sides, as observed by Dugolinsky (1976) and Mullineaux (1988, 1989).

As in this study, Mullineaux (1989) observed more taxa present in higher abundance on smooth surfaces. In her study, 16 taxa were predominant on smooth surfaces and nine on rough surfaces. Nonetheless, she concluded that these texture-related faunal distributions resulted from interactions between texture, flow, and particulate food availability, rather than texture alone (Mullineaux, 1989). The same author suggested that the composition of the substratum may also influence the faunal distribution of nodule fauna (Mullineaux, 1988). In this study only one substratum type (facies C nodules) was examined. Moreover, smooth surfaces were only present in the summital region of the nodules where flow rates are almost certainly higher. This possibly explains why suspension feeders were more abundant on smooth surfaces. A rough surface texture, on the other hand, could contribute to the accumulation of fine particles and enhance food availability for deposit feeders, but here none of the taxa presented a significant relationship with rough surfaces.

Different authors have reported that most forms of foraminifera appear to colonize nodule surfaces located at or just above the sediment-water interface (Greenslate, 1974; Dugolinsky, 1976; Dugolinsky *et al.*, 1977; von Stackelberg, 1984) whereas the results of the present study showed that raised surfaces, located in the summital region, were most covered by the fauna. Mullineaux (1988) reported that 65% of the sessile organisms living on nodules belong to taxa whose abundance was related to vertical position on the nodule. This agrees with our results since almost half of the taxa analyzed covered more substratum surface in raised areas on the nodule summit than elsewhere. Conversely, other authors observed that sessile organisms prefer to settle in hollows or crevices of the nodule surface (von Stackelberg, 1984; Maybury, 1996). The search for shelter from predators and the greater concentration in nutrients for deposit feeders in these regions would explain this settlement preference (von Stackelberg, 1984; Maybury, 1996). This pattern was not observed for any of the taxa present.

4.2. Environmental factors

Flow velocity may play an important in structuring benthic communities (Mullineaux, 1988; Flach *et al.*, 1998; Pernet *et al.*, 2003). Near-bottom flow is crucial to fauna living on hard substrata since they depend on it for feeding (at least for suspension feeders) and to transport their propagules (Thistle, 2003). Suspension-feeding foraminifera are advantaged in areas with considerable flow in order to extend their pseudopodial network within the velocity profile of the near-bottom shear flow enhancing capture of food particles (Lutze and Thiel, 1989). According to Veillette *et al.* (submitted), 60% of the protozoan taxa observed on nodule surfaces are known to be suspension feeders. The feeding type and the spatial distribution of the main taxa colonizing other marine hard substrata demonstrate that they take advantage of being in an enhanced particle flux (Genin *et al.*, 1986; Mullineaux, 1988; Etter and Mullineaux, 2001). For instance, corals (suspension feeders) on seamounts appeared to benefit from flow acceleration and, current conditions can explain their distribution patterns (Genin *et al.*, 1986). Also, suspension-feeding organisms such as one zoanthid and one tunicate as well as ophiuroids and anemones preferentially colonized the top of sponge stalks (Beaulieu, 2001). A higher flow velocity is expected on the raised surface of nodules since these are the most removed from the sediment and most exposed to the flow. Therefore, raised surfaces were expected to be colonized mostly by suspension-feeding organisms. Surprisingly, almost half of the deposit feeder taxa identified (5 out of 13) were preferentially associated to smooth texture and to raised surfaces, the others being linked to either smooth texture (1) or to raised surfaces (1). The remaining six were not significantly linked to any particular texture or microhabitat.

Flow would have an influence on recruitment of encrusting benthic invertebrates in the deep-sea (Mullineaux and Butman, 1990). This study concluded that recruitment would be a function of propagule transport, which is highly influenced by hydrodynamic factors. This does not exclude the possibility that larvae could actively respond to flow conditions. Moreover, the results of a study on vertical distribution of the nodule fauna suggested that benthic organisms exhibit both settlement and post-settlement responses to flow (Mullineaux, 1989). One very interesting result of this study is that, after two years of colonization experiments, suspension feeders dominated nodules raised above the seafloor and deposit feeders dominated nodules resting on the sediment. Hence, the supply of particulate food was suggested to determine the composition of the nodule community (Mullineaux, 1989).

Biotic factors can also have a strong influence in structuring faunal communities. Vertical zonation on sponge stalks was suggested to be determined mostly by interactions among species (Beaulieu, 2001) which would not be the case for nodule surfaces, since species associations have been shown to have little influence on nodule fauna (Veillette *et al.*, submitted). Biotic disturbance including physical disruption, mortality due to predation and behavioural irritation of marine invertebrate larvae by predators may decrease larval settlement (Osman and Whitlatch, 1995; Dahms *et al.*, 2004).

5. Conclusion

This study aimed to determine the influence of surface texture and microhabitat heterogeneity on the structure of nodule faunal communities. Raised and smooth surfaces appeared to be preferred by fauna. Nonetheless, surface texture and microhabitat heterogeneity interacted together since most of the raised surfaces are also smooth. It is suggested that flow velocity, being higher on raised surfaces, would be an important environmental factor in structuring nodule faunal communities since most taxa were linked to these nodule characteristics. Therefore, vertical distance from the sediment would be a good predictor of faunal cover on nodule surfaces.

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Figure 1.

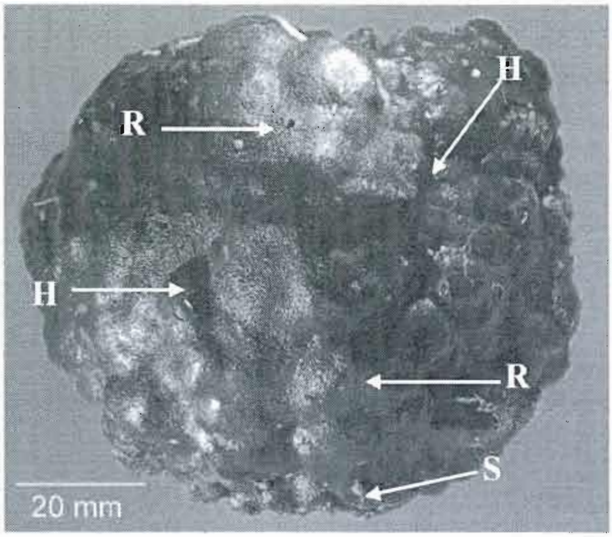


Figure caption

Figure 1. Top-view picture of a facies C nodule showing three microhabitats: raised surfaces (R), hollows (H) and sides (S).

Table 1. Distribution of the 34 taxa (percent cover) according to nodule surface texture (smooth and rough) and microhabitat (raised surfaces (R), hollows (H) and sides (S)). * α= 0.05, ** α=0.01, *** α=0.001. Known suspension (S) or deposit (D) feeding types are indicated after the name of the taxon. NS: non-significant.

	Taxa	Surface texture most covered	Microhabitat most covered
2	*Hemispherammina*-like, pale regular dome (S)	Smooth ***	R >H and S ***
3	*Hemispherammina*-like, pale granular dome (S)	Smooth **	NS
4	*Hemisperammina*-like, irregular shape (S)	Smooth **	NS
5	*Tholosina* sp. (S)	Smooth ***	R >H and S ***
6	*Tholosina*-like (S)	Smooth *	NS
8	*Placopsilina*-like (S)	NS	NS
9	Komoki, mud-ball type (D)	NS	NS
13	*Ammocibicides*-like (S)	Smooth *	R >H and S **
14	Fine agglutinated particles beige soft dome (S)	NS	NS
15	Brown granular shiny dome (D)	NS	NS
17	Black soft dome (D)	NS	R >H and S **
18	Orange dome (S)	NS	NS
19	*Chondrodapis hessleri* (D)	Smooth **	R >H and S *
20	*Chondrodapis integra* (D)	Smooth ***	R >H and S ***
21	Area covered with komokiacean-like chambers linked with fine tubes (D)	NS	NS
22	Grey granular mat (D)	Smooth **	R >H and S **
23	Very thin muddy patches with komokiacean-like chambers (D)	Smooth ***	NS
25	*Tumidotubus* (S)	NS	R and S >H **
28	"White crust" (S)	Smooth ***	R >H and S ***
29	"Beige filamentous mat"	NS	NS
30	"Dark chambered mat" (D)	NS	NS
31	Thin grey mat (S)	Smooth **	R >H; S=R; S=H ***
32	Thin organic mat with dark grey stercomata (D)	Smooth ***	R >H and S ***
34	Beige thick and smooth mat, interior brown (S)	Smooth *	R >H; S=R; S=H *
35	Mat of blue flattened chambers	Smooth ***	R >H and S ***
36	White mat with lumps (S)	Smooth *	NS
42	Reticulated dark tunnels (S)	Smooth *	NS
43	Network of beige tunnels; horizontal tree with upright branches (D)	NS	NS
44	Crystal star and tunnels (S)	Smooth **	R >S; H=R; H=S **
45	Spider network of grey tunnels (S)	Smooth **	R >H and S **
46	White soft tunnels (S)	NS	NS
49	"Flattened chambers" (D)	Smooth ***	R >H and S ***
51	*Hormosina* sp. (S)	NS	NS
65	Anastomosing *Rhizammina*-like (D)	NS	NS

CONCLUSIONS

Ce mémoire a apporté une meilleure caractérisation de la faune associée aux nodules, à l'échelle des zones, des faciès et du nodule, en explorant différents facteurs environnementaux pouvant influencer sa distribution spatiale. Comme très peu de travaux sont publiés sur le sujet, il constitue une contribution colossale à la recherche sur la faune associée aux nodules. Également, la comparaison des deux méthodes d'échantillonnage (carottier USNEL et la pince à godet du submersible *Nautile*) a mis en évidence que ces deux outils sont valables à la cueillette des nodules pour l'observation de la faune associée.

La documentation descriptive et photographique des 90 taxons observés sur les nodules analysés, dans le «Catalogue de la faune associée aux nodules», forme une contribution originale et présente un avancement considérable des connaissances sur cette faune abyssale singulière. Elle permettra de réaliser d'autres études sur cette faune ou encore, des études d'impact dans le cas d'une éventuelle exploitation. Aussi, l'analyse de l'influençe des facteurs environnementaux sur la distribution spatiale de la faune a permis d'en connaître davantage sur l'écologie de ces protistes. Néanmoins, une limite considérable à ce mémoire est l'incertitude découlant de la taxonomie des foraminifères qui est fondée sur les caractères morphologiques des taxons. L'identification précise des espèces avec leur nom binomial était, pour la grande majorité des structures organiques observées, impossible malgré l'expertise d'un spécialiste mondial des foraminifères Dr. Andrew Gooday. Par conséquent, cette étude ne possède pas l'assurance de pouvoir être répétée par un autre chercheur. La possibilité de répéter les observations d'une étude afin de les valider est un des principes de base de la méthode scientifique. Sans cette assurance, ce travail scientifique se doit de présenter ses conclusions avec beaucoup d'humilité. Toutefois, il est important de noter que l'auteure a fournit un effort respectable pour réduire ces incertitudes par l'élaboration du «Catalogue de la faune associée aux nodules». L'utilisation des méthodes modernes de génétique moléculaire permetttra, dans des études futures, de réduire les incertitudes taxonomiques. Ces technologies sont aujourd'hui utilisées couramment pour étudier la diversité des foraminifères (Gooday, pers. comm.). Par ailleurs, Masashi Tsuchiya, scientifique à JAMSTEN au Japon et participant au projet NODINAUT, est responsable de l'étude de la diversité génétique des espèces des foraminifères colonisant les sédiments et les nodules des zones à nodules françaises. Des techniques de génétique moléculaire seront employées pour la réalisation de son projet de recherche.

La faune associée aux nodules est dominée majoritairement par les foraminifères agglutinants en nombre de taxons. Le nombre de taxons observés dans cette étude est semblable à celui d'une étude précédente portant sur les nodules (Mullineaux, 1987) et dans le même ordre de grandeur que ceux obtenus pour d'autres substrats durs présents dans les grands fonds marins comme des tiges d'éponges (Beaulieu, 2001) et des os de baleines (Baco and Smith, 2003; Bennett, *et al.*, 1994). Il a été montré que la richesse des espèces augmentait avec la surface du nodule et ce, à l'échelle régionale et locale. Aucune relation entre le pourcentage de couverture et la surface estimée du nodule n'a été observée ce qui suggère que la surface du nodule n'était pas un facteur limitant la colonisation de la faune. Les résultats des tests de concordance ont suggéré que les interactions entre espèces n'exercent qu'une très faible influence sur la distribution spatiale de la faune sur les nodules. Quelques différences statistiques dans la distribution des espèces entre les faciès ont été observées mais le type de faciès ne semble expliquer qu'une petite portion de la variance totale de la faune. Les différentes méthodes de groupement utilisées n'ont pas permis l'identification de groupes de nodules spécifiques, correspondant, par exemple, à des conditions environnementales similaires.

L'analyse de l'influence des facteurs environnementaux sur la distribution spatiale de la faune a démontré qu'à l'échelle régionale, la production primaire de surface pourrait être, parmi les facteurs étudiés, le facteur le plus déterminant pour expliquer la plus grande richesse spécifique ainsi que le plus grand pourcentage de couverture par la faune de la zone est. L'hétérogénéité de l'habitat, créée par les mamelons et les différentes textures de la surface des nodules des faciès B et C, pourrait également contribuer à expliquer la plus grande richesse des espèces ainsi que le plus grand pourcentage de couverture de la faune observés dans la zone est. L'étude à l'échelle du nodule a confirmé l'influence de la texture de la surface des nodules et de l'hétérogénéité de l'habitat pour la faune associée. En effet, la moitié des taxons avaient un plus grand pourcentage de couverture sur les surfaces lisses et sur les régions élevées du nodule; les surfaces rugueuses, les creux ou les côtés étant moins recouverts par la faune.

Plusieurs facteurs environnementaux ont été mesurés *in situ* en collaboration avec d'autres chercheurs participant à NODINAUT: les courants près du fond par Annick Vangriesheim (DEEP/Ifremer), la chimie de l'eau par Jean-Claude Caprais (DEEP/Ifremer) et la composition géochimique des nodules par Joël Étoubleau (DROGM/Ifremer). Les grandes tendances de ces données environnementales sont incluses dans ce mémoire mais il est possible de contacter directement les chercheurs afin d'obtenir leurs données détaillées. La productivité primaire de surface ainsi que le flux de matière organique au fond de l'océan sont traités qualitativement à partir de la littérature de cette région de l'océan Pacifique. Ces facteurs n'ont pas été mesurés lors de NODINAUT et ils semblent être les seuls à varier significativement à l'échelle régionale étudiée. Il est certain que l'obtention des données quantitatives de ces facteurs renforcerait la crédibilité de cette étude.

Dans le futur, il serait intéressant d'étudier quel est le rôle de la faune associée aux nodules sur l'écosystème abyssal environnant et ce, afin de déterminer quelles modifications l'écosystème subirait-il sans cette faune. Est-ce que l'équilibre de l'écosystème serait perturbé et ce, pour une certaine période de temps ou irréversiblement? Des expérimentations de recolonisation de substrats durs ont déjà été réalisées en milieu profond avec des substrats artificiels (Bertram and Cowen, 1994). De plus, lors de NODINAUT, des nodules nettoyés de toute forme de vie ont été posés sur les sédiments afin d'étudier leur recolonisation et de répondre aux questions suivantes: à quel rythme s'effectue la recolonisation?, quels organismes colonisent les premiers?, quelle est la succession des espèces?

L'analyse des données de cette étude aurait été beaucoup plus simple si les mêmes faciès avaient été présents dans les deux zones étudiées. Il pourrait être intéressant de placer des nodules « nettoyés » de toute forme de vie de chacun des faciès dans les deux zones. De cette façon, les conclusions de la présente étude gagneraient en crédibilité. Par ailleurs, l'étude de la distribution des espèces colonisant les nodules à l'échelle des océans présente une perspective de recherche très pertinente, surtout s'il y a exploitation. En connaissant la distribution des espèces, il serait possible de veiller à leur conservation. Évidemment, des méthodes génétiques devront être employées afin d'identifier les organismes au niveau de l'espèce avec assurance.

En ce moment, la communauté scientifique reconnaît que les connaissances et la compréhension actuelles de l'écologie des grands fonds marins demeurent insuffisantes pour évaluer de façon probante les impacts d'une exploitation minière à grande échelle (International Seabed Authority, 2005a). Or, au cours du siècle prochain, avec la surexploitation des ressources minières terrestres et les progrès technologiques, les efforts pour développer et exploiter les ressources minières des grands fonds marins risquent de s'accentuer. Les incertitudes concernant les impacts environnementaux d'une éventuelle exploitation devraient être minimisées (Gage, 2001), d'autant plus que la conservation des grands fonds marins présente des défis uniques de par ses caractéristiques particulières.

Enfin, dans une perspective environnementale, l'histoire de l'exploitation des nodules pourrait être résumée comme étant, jusqu'à présent, une histoire chanceuse. En effet, comme leur exploitation n'est toujours pas favorable économiquement, les moyens technologiques s'affinent et les connaissances des impacts environnementaux s'approfondissent de telle sorte qu'il pourrait être possible de limiter les impacts négatifs d'une éventuelle exploitation. Évidemment, des événements politiques ou des changements dans l'usage des métaux pourraient modifier rapidement les marchés et retarder ou, au contraire, accélérer le développement de l'exploitation des nodules.

APPENDICE A

PROTOCOLE DE PRISE DE PHOTOS AVEC UNE CAMÉRA NUMÉRIQUE

Introduction

Les nodules polymétalliques ainsi que leur faune associée sont un réel défi à photographier pour les raisons suivantes: les nodules sont de forme plutôt sphérique ou ovoïde, leur surface est grenue et mamelonnée et ils sont très foncés.

Prise de photos avec Nikon E4300

But 1: Prendre une photo d'un nodule de haut avec une bonne résolution

Stratégie: En général, la forme d'un nodule se rapproche d'une sphère aplatie. Comme il est important que la résolution des bords ainsi que des creux entre les mamelons soit satisfaisante, il est important d'avoir une petite ouverture du diaphragme (F= 9 ou plus élevée). Cette petite ouverture implique un temps d'exposition assez long ce qui requiert l'utilisation d'un trépied. Personnellement, je trouve que le mode manuel (M) semble beaucoup plus adapté pour ces photos.

Luminosité: Selon mon expérience, il vaut mieux prendre les photos du nodule sous l'eau (ou alcool) pour éviter les réflexions de la lumière causées par la surface irrégulière du nodule. Aussi, il est préférable d'utiliser un fond blanc afin d'obtenir une définition plus claire du périmètre du nodule; je place une feuille blanche directement sur le fond du contenant. Si possible, le contenant doit être transparent pour laisser passer le maximum de lumière. Le flash ne doit pas être utilisé. Deux sources de lumière ou davantage doivent être utilisées. Elles ne doivent jamais éclairer le nodule directement; je les positionne à environ 45° par rapport à l'horizontale. Pour réussir de meilleures photos, il est important d'ajuster l'appareil photo en fonction de la source de lumière utilisée. Aussi, avec le mode manuel, le temps d'exposition peut être réglé. Lorsque c'est possible, il est bien de sous-exposer de un cran ou deux pour accentuer les contrastes.

Format: Toujours faire la meilleure qualité de photo possible (plus grande densité de pixels). Aussi, il est très important de toujours conserver le numéro de chaque photo.

Échelle: On doit s'assurer de toujours connaître l'échelle des photos, soit en mesurant deux points, soit en incluant une règle dans la photo.

But 2: Prendre une photo d'un taxon colonisant le nodule à l'aide du tube à photo monté sur la binoculaire

Stratégie: Pour la plupart des spécimens observés sur la surface du nodule, qui sont de très petite taille, il est nécessaire de les photographier à l'aide du tube à photo monté sur la binoculaire. Comme une petite ouverture du diaphragme (F= 4 ou plus élevée) ainsi qu'un court temps d'exposition sont désirés, ces photos sont une histoire de compromis. Une manière satisfaisante de les réaliser est d'utiliser le mode scène avec la scène « paysage » qui assure une ouverture de diaphragme correcte (F= 3 ou 4). Le temps est réglé automatiquement. Lorsque le spécimen est pâle, il est préférable de sous-exposer de un ou deux crans afin de mieux voir les reliefs. Aussi, choisir le déclenchement à retardement évite que l'appareil bouge lorsque le bouton de déclenchement est appuyé.

Luminosité: Il est préférable de laisser le nodule sous l'eau ou l'alcool afin que le spécimen soit bien déployé. Le flash ne doit pas être utilisé. Deux sources de lumière ou davantage doivent être utilisées. Elles ne doivent jamais éclairer le nodule directement, ni être d'une forte intensité. Je les positionne à environ 45° par rapport à l'horizontale. Pour réussir de meilleures photos, il est important d'ajuster l'appareil photo en fonction de la source de lumière utilisée.

Format: Toujours faire la meilleure qualité de photos possible (plus grande densité de pixels). Aussi, il est très important de toujours conserver le numéro de chaque photo.

Échelle: S'assurer de toujours connaître l'échelle sur les photos en mesurant le spécimen.

APPENDICE B

TABLE B1. TEN DOMINANT LIVE TAXA OF 42 DESCRIBED AS PERCENT COVER FOR EACH SAMPLING GROUP

Table B1. Ten dominant live taxa of 42 described as percent cover for each sampling group with % faunal cover summed over 10 nodules chosen at random from each group and rank cover relative to all taxa found in that sampling group. (-) indicates taxa that were absent from a sampling group.

Taxa	A	A rank	B KGS	B KGS rank	B PL	B PL rank	C KGS	C KGS rank	C PL	C PL rank	West KGS	West KGS rank	West PL	West PL rank
Very thin muddy patches with komokiacean-like chambers	0.845	1	0.407	1	0.052	1	0.009	2	0.012	1	0.037	3	0.009	1
Thin organic mat with dark grey stercomata	0.188	2	0.012	12	0.016	3	0.003	5	0.001	5	0.069	1	0.006	2
Thin grey mat	0.163	3	0.087	4	0.011	6	0.011	1	0.003	2	0.014	5	0.001	9
Grey granular mat	0.150	4	0.100	3	0.011	5	0.001	14	<0.001	13	0.007	9	-	-
Beige thick and smooth mat, interior brown	0.116	5	0.038	6	0.001	14	0.001	10	-	-	0.006	12	0.002	6
"White crust"	0.061	6	0.012	11	0.008	7	0.002	9	0.001	6	0.006	11	-	-
"Flattened chambers"	0.058	7	0.018	9	0.006	9	0.006	4	<0.001	10	0.008	8	0.003	5
Reticulated dark tunnels	0.053	8	0.002	20	0.002	11	<0.001	15	-	-	0.005	13	0.001	10
Spider network of grey tunnels	0.052	9	0.187	2	0.038	2	0.007	3	0.003	3	0.016	4	-	-
Chondrodapis hessleri	0.038	10	0.049	5	0.003	10	0.003	6	0.001	9	0.006	10	-	-
Tumidotubus sp.	-	-	0.008	16	0.015	4	0.001	12	0.003	4	0.040	2	-	-
"Beige filamentous mat"	-	-	-	-	0.007	8	0.001	13	-	-	0.012	6	-	-
"Cemented tunnels"	0.004	21	0.024	7	<0.001	23	<0.001	22	<0.001	17	0.004	15	-	-
Chondrodapis integra	-	-	0.022	8	-	-	-	-	-	-	-	-	-	-
Komoki, mud-ball type	-	-	0.014	10	<0.001	18	<0.001	19	<0.001	12	0.009	7	-	-
White mat with lumps	0.009	16	0.012	13	-	-	<0.001	26	0.001	7	0.007	8	-	-
Area covered with komokiacean-like chambers linked with fine tubes	0.027	12	-	-	<0.001	17	0.002	8	0.001	8	0.005	14	<0.001	11
White soft tunnels	0.005	20	0.011	14	0.002	12	0.003	7	<0.001	16	0.002	17	-	-
Tubes network; mix of *Lana neglecta* and Rhizammina	-	-	0.001	26	-	-	<0.001	28	<0.001	24	<0.001	26	0.005	3
Pseudowebbinella sp.	-	-	0.001	21	-	-	<0.001	34	<0.001	30	-	-	0.004	4
Mat of blue flattened chambers	0.023	13	-	-	-	-	<0.001	25	<0.001	11	-	-	0.002	7
Network of beige tunnels; horizontal tree with upright branches	-	-	-	-	<0.001	26	-	-	-	-	-	-	0.001	8

APPENDICE C

ANALYSES STATISTIQUES DU CHAPITRE II

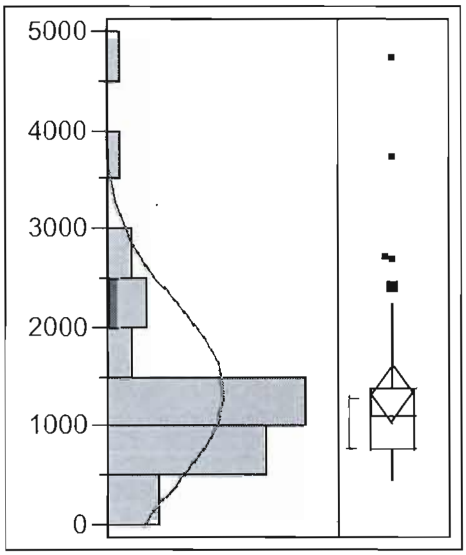
C.1 TESTING IF THE SAMPLING METHOD INFLUENCED THE SIZE OF NODULES (FIG 2).

Testing for difference between two means.
Assumptions of two-samples *t* test: 1) Normal distribution; 2) Equal variances. Better if samples sizes are equal or nearly equal.

H_0 : Nodule surface of nodules collected by the USNEL box core (KGS) and by the submersible Nautile (PL) are the same.
H_A : Nodule surface of nodules collected by the USNEL box core (KGS) and by the submersible Nautile (PL) are not the same.

Example of calculations for facies B nodules

KGS (mm^2)



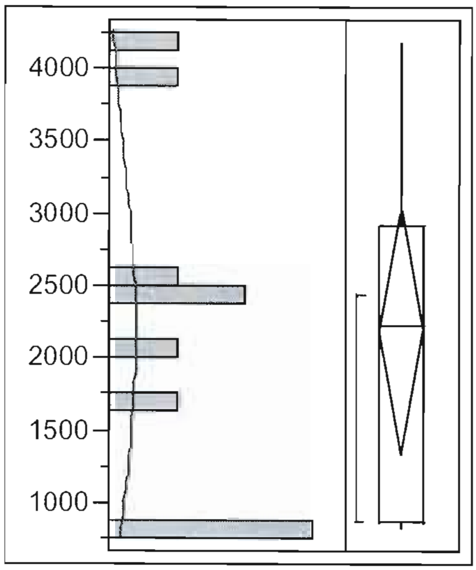
Mean	1314,3505
Std Dev	888,67217
Std Err Mean	140,51141
upper 95% Mean	1598,5616
lower 95% Mean	1030,1394
N	40

Shapiro-Wilk W Test

W	Prob<W		
		0,775075	<,0001

- Non-normal distribution
- Log10 transformation necessary

PL (mm^2)



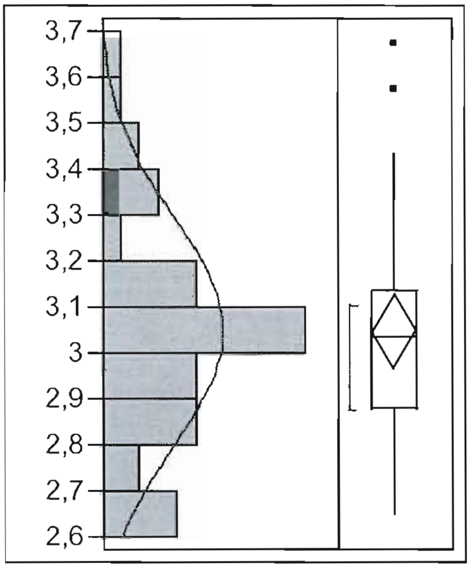
Mean	2181,0023
Std Dev	1190,0162
Std Err Mean	376,31618
upper 95% Mean	3032,2887
lower 95% Mean	1329,716
N	10

Shapiro-Wilk W Test

W	Prob<W
0,902171	0,2314

- Normal distribution

KGS (Log10 mm^2)



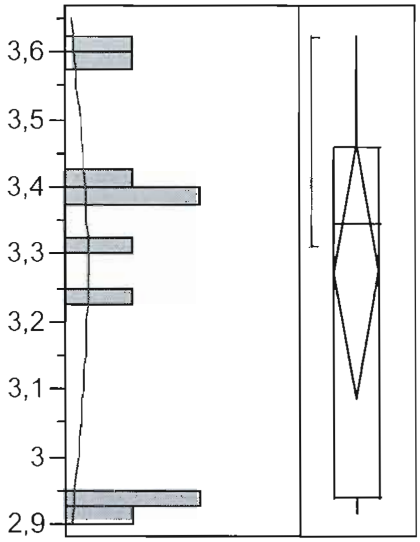
Mean	3,0466734
Std Dev	0,2423069
Std Err Mean	0,0383121
upper 95% Mean	3,1241669
lower 95% Mean	2,9691799
N	40

Shapiro-Wilk W Test

W	Prob<W
0,962532	0,2043

- Normal distribution
- Log10 transformed data will be used for the *t* test.

PL (Log10 mm^2)

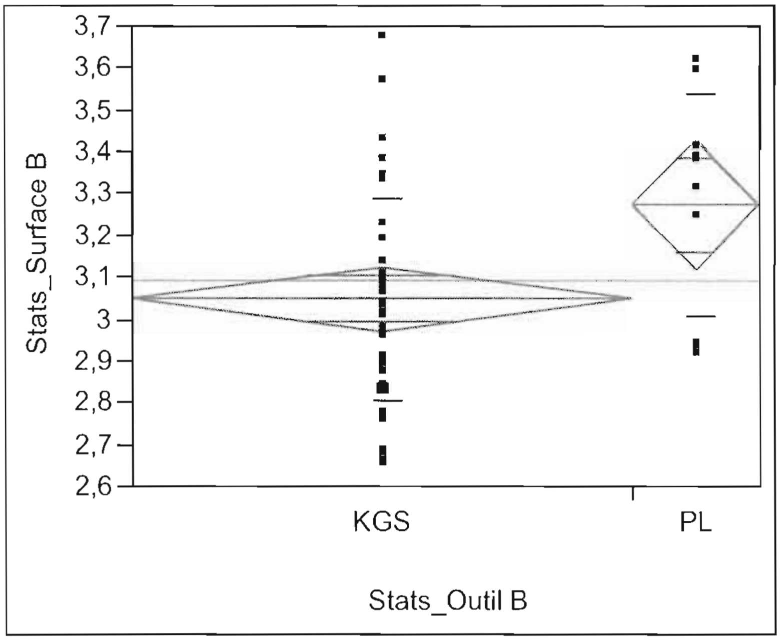


Mean	3,2724565
Std Dev	0,2634133
Std Err Mean	0,0832986
upper 95% Mean	3,460891
lower 95% Mean	3,084022
N	10

Shapiro-Wilk W Test

W	Prob<W
0,886234	0,1537

- Normal distribution
- Log10 transformed data will be used for the *t* test.



Rsquare	0,122761
Adj Rsquare	0,104485
Root Mean Square Error	0,246402
Mean of Response	3,09183
Observations (or Sum Wgts)	50

t Test
KGS-PL
Assuming equal variances

Difference	-0,22578	t Ratio	-2,59174
Std Err Dif	0,08712	DF	48
Upper CL Dif	-0,05062	**Prob > |t|**	**0,0126**
Lower CL Dif	-0,40094	Prob > t	0,9937
Confidence	0,95	Prob < t	0,0063

t Test
KGS-PL
Assuming unequal variances

Difference	-0,22578	t Ratio	-2,46255
Std Err Dif	0,09169	DF	13,07547
Upper CL Dif	-0,02782	Prob > |t|	0,0284
Lower CL Dif	-0,42374	Prob > t	0,9858
Confidence	0,95	Prob < t	0,0142

Tests that the Variances are Equal

Level	Count	Std Dev	MeanAbsDif to Mean	MeanAbsDif to Median
KGS	40	0,2423069	0,1824921	0,1819076
PL	10	0,2634133	0,2125357	0,2051041

Test	F Ratio	DFNum	DFDen	Prob > F
O'Brien[.5]	0,1315	1	48	0,7185
Brown-Forsythe	0,1683	1	48	0,6835
Levene	0,3066	1	48	0,5823
Bartlett	0,1017	1	.	0,7499
F Test 2-sided	1,1818	9	39	0,6669

Welch Anova testing Means Equal, allowing Std Devs Not Equal

F Ratio	DFNum	DFDen	Prob > F
6,0641	1	13,075	0,0284

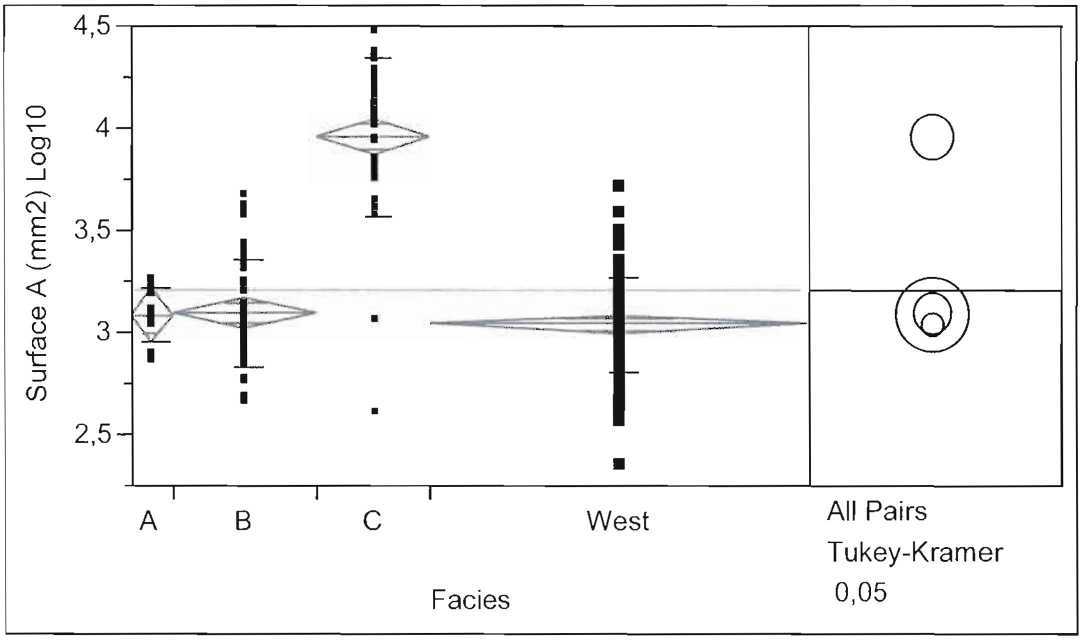
t Test
2,4625

2-Sample Test, Normal Approximation

S	Z	Prob>|Z|
346	2,19495	0,0282

- Variances are equal.
- ***T* test with equal variances is appropriate and significant.**

C.2 TESTING IF THERE ARE SIZE DIFFERENCES WHEN NODULES OF THE SAME FACIES COLLECTED USING BOTH SAMPLING METHODS WERE POOLED TOGETHER (FIG. 2).



Summary of Fit

Rsquare	0,620097
Adj Rsquare	0,615163
Root Mean Square Error	0,264478
Mean of Response	3,205413
Observations (or Sum Wgts)	235

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Ratio	Prob > F
Facies	3	26,374178	8,79139	125,6831	<,0001
Error	231	16,158186	0,06995		
C. Total	234	42,532365			

Means for Oneway Anova

Level	Number	Mean	Std Error	Lower 95%	Upper 95%
A	15	3,08682	0,06829	2,9523	3,2214
B	50	3,09183	0,03740	3,0181	3,1655
C	39	3,95479	0,04235	3,8713	4,0382
West	131	3,03925	0,02311	2,9937	3,0848

Std Error uses a pooled estimate of error variance

Comparisons for all pairs using Tukey-Kramer HSD

q*	Alpha
2,58785	0,05

Abs(Dif)-LSD	C	B	A	West
C	-0,15499	0,71674	0,66003	0,79069
B	0,71674	-0,13689	-0,19648	-0,06119
A	0,66003	-0,19648	-0,24992	-0,13899
West	0,79069	-0,06119	-0,13899	-0,08457

Level			Mean
C	A		3,9547908
B		B	3,0918300
A		B	3,0868165
West		B	3,0392476

Levels not connected by same letter are significantly different

Level	- Level	Difference	Lower CL	Upper CL
C	West	0,9155431	0,790694	1,040392
C	A	0,8679742	0,660029	1,075919
C	B	0,8629607	0,716741	1,009181
B	West	0,0525824	-0,061193	0,166358
A	West	0,0475689	-0,138994	0,234131
B	A	0,0050135	-0,196477	0,206504

Difference

1-way Test, ChiSquare Approximation

ChiSquare	DF	Prob>ChiSq
77,6406	3	<,0001

Tests that the Variances are Equal

Level	Count	Std Dev	MeanAbsDif to Mean	MeanAbsDif to Median
A	15	0,1302697	0,1021526	0,1010519
B	50	0,2603802	0,2060598	0,2047248
C	39	0,3865580	0,2808241	0,2681422
West	131	0,2307226	0,1852712	0,1815556

Test	F Ratio	DFNum	DFDen	Prob > F
O'Brien[.5]	4,5211	3	231	0,0042
Brown-Forsythe	3,8427	3	231	0,0103
Levene	5,2334	3	231	0,0016
Bartlett	9,2144	3	.	<,0001

Welch Anova testing Means Equal, allowing Std Devs Not Equal

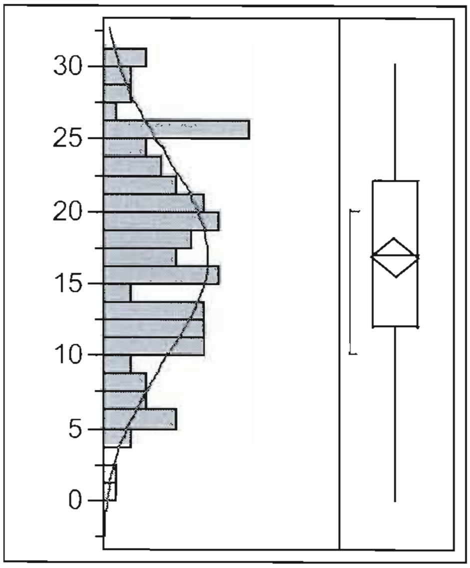
F Ratio	DFNum	DFDen	Prob > F
64,9660	3	59,472	<,0001

- The variances are not all equal.
- **Kruskal-Wallis non-parametric test is appropriate and significant. Facies C grouped alone and then, facies A, B and west grouped together according to the *a posteriori* Tukey test when nodules of the same facies collected using both sampling methods were pooled together.**

C.3 TESTING FOR FAUNAL DIFFERENCES BETWEEN ZONES AND FACIES (FIG. 5-6).

Example of calculations for species richness between zones

East

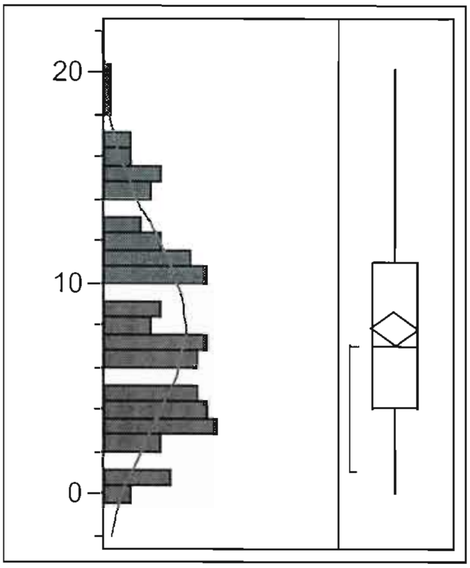


Goodness-of-Fit Test

Shapiro-Wilk W Test

W	Prob<W
0,982677	0,1926

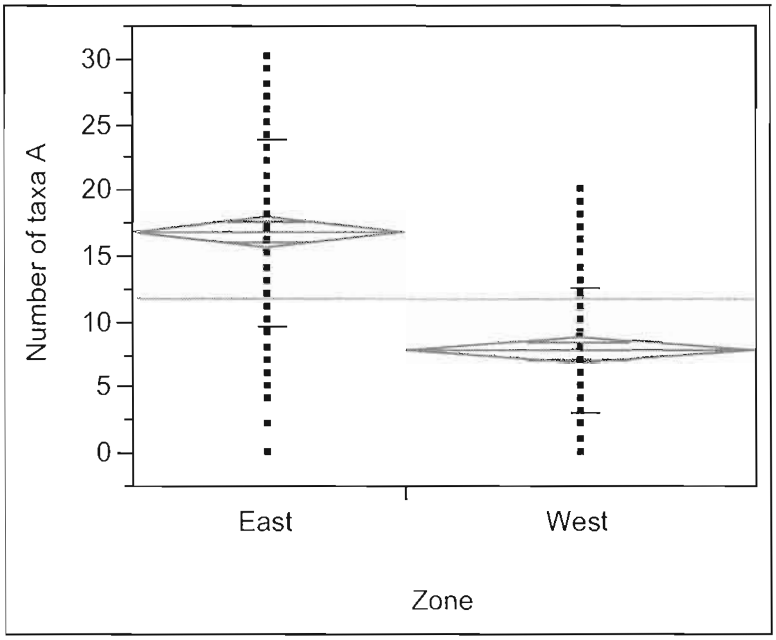
West



Goodness-of-Fit Test

Shapiro-Wilk W Test

W	Prob<W
0,963703	0,0014



Summary of Fit

Rsquare	0,36231
Adj Rsquare	0,359573
Root Mean Square Error	5,918257
Mean of Response	11,81277
Observations (or Sum Wgts)	235

t Test

East-West

Assuming equal variances

Difference	8,9431	t Ratio	11,50571
Std Err Dif	0,7773	DF	233
Upper CL Dif	10,4745	Prob > |t|	0,0000
Lower CL Dif	7,4117	Prob > t	0,0000
Confidence	0,95	Prob < t	1,0000

Tests that the Variances are Equal

Level	Count	Std Dev	MeanAbsDif to Mean	MeanAbsDif to Median

Level	Count	Std Dev	MeanAbsDif to Mean	MeanAbsDif to Median
East	104	7,101729	5,909763	5,894231
West	131	4,776742	4,028203	3,969466

Test	F Ratio	DFNum	DFDen	Prob > F
O'Brien[.5]	24,2524	1	233	<,0001
Brown-Forsythe	19,3688	1	233	<,0001
Levene	19,9001	1	233	<,0001
Bartlett	18,0816	1	.	<,0001
F Test 2-sided	2,2104	103	130	<,0001

Welch Anova testing Means Equal, allowing Std Devs Not Equal

F Ratio	DFNum	DFDen	Prob > F
121,3416	1	172,63	<,0001

t Test
11,0155

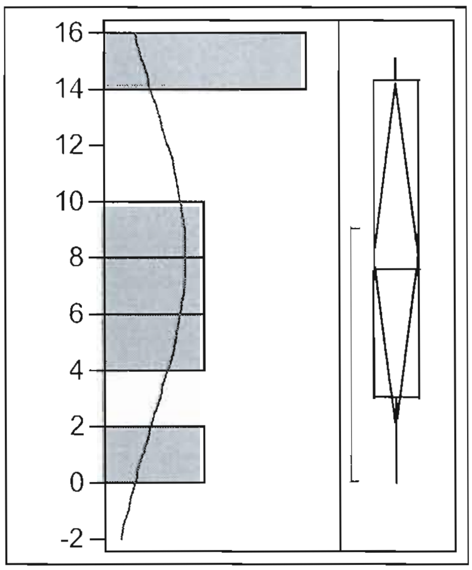
2-Sample Test, Normal Approximation

S	Z	Prob>|Z|
16963	9,07043	0,0000

- One distribution is not normal.
- **The non-parametric test of Kruskal-Wallis is therefore appropriate and significant.**

C.4 SPECIES ACCUMULATION CURVES: TESTING FOR SPATIAL BIAS OF FACIES WEST SAMPLING (SECTION 3.1.).

KGS



Moments

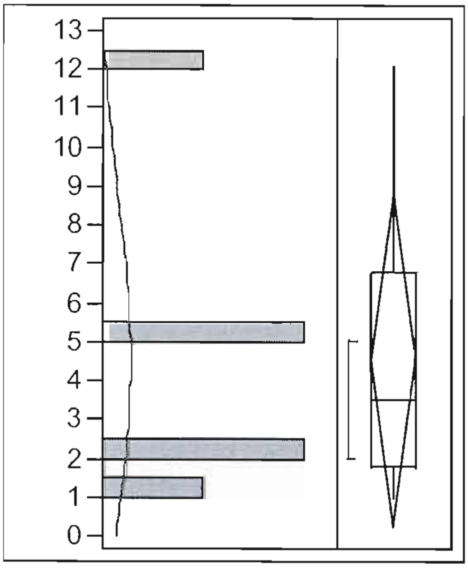
Mean	8
Std Dev	5,8309519
Std Err Mean	2,3804761
upper 95% Mean	14,119209
lower 95% Mean	1,8807913
N	6

Goodness-of-Fit Test

Shapiro-Wilk W Test

W	Prob<W
0,951224	0,7502

PL: randomly chosen: 1-11, 4-4, 2-3, 2-9, 4-9, 4-7



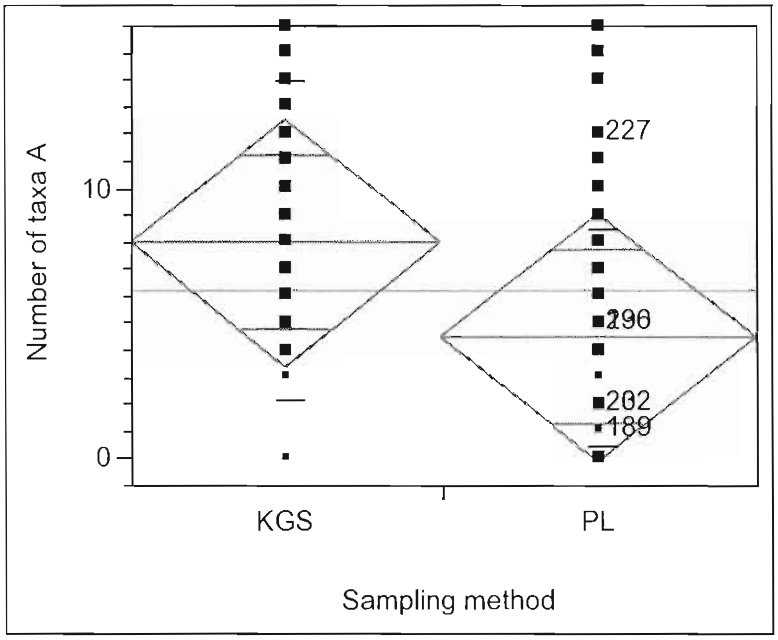
Moments

Mean	4,5
Std Dev	4,0373258
Std Err Mean	1,6482314
upper 95% Mean	8,7369136
lower 95% Mean	0,2630864
N	6

Goodness-of-Fit Test

Shapiro-Wilk W Test

W	Prob<W
0,820927	0,0899



Summary of Fit

Rsquare	0,127493
Adj Rsquare	0,040243
Root Mean Square Error	5,014978
Mean of Response	6,25
Observations (or Sum Wgts)	12

t Test

KGS-PL

Assuming equal variances

Difference	3,5000	t Ratio	1,208815
Std Err Dif	2,8954	DF	10
Upper CL Dif	9,9514	Prob > |t|	0,2545
Lower CL Dif	-2,9514	Prob > t	0,1273
Confidence	0,95	Prob < t	0,8727

Tests that the Variances are Equal

Level	Count	Std Dev	MeanAbsDif to Mean	MeanAbsDif to Median

Level	Count	Std Dev	MeanAbsDif to Mean	MeanAbsDif to Median
KGS	6	5,830952	4,666667	4,666667
PL	6	4,037326	2,833333	2,833333

Test	F Ratio	DFNum	DFDen	Prob > F
O'Brien[.5]	0,9318	1	10	0,3572
Brown-Forsythe	1,2578	1	10	0,2883
Levene	1,3876	1	10	0,2661
Bartlett	0,6009	1	.	0,4382
F Test 2-sided	2,0859	5	5	0,4389

Welch Anova testing Means Equal, allowing Std Devs Not Equal

F Ratio	DFNum	DFDen	Prob > F
1,4612	1	8,8982	0,2579

t Test
1,2088

2-Sample Test, Normal Approximation

S	Z	Prob>|Z|
32	-1,04449	0,2963

- **The *t* test is appropriate and significant.**

C.5 TESTING FOR FAUNAL DIFFERENCES BETWEEN NODULES OF DIFFERENT ZONES AND FACIES OF THE SAME SIZE (SECTIONS 3.3.-3.4.).

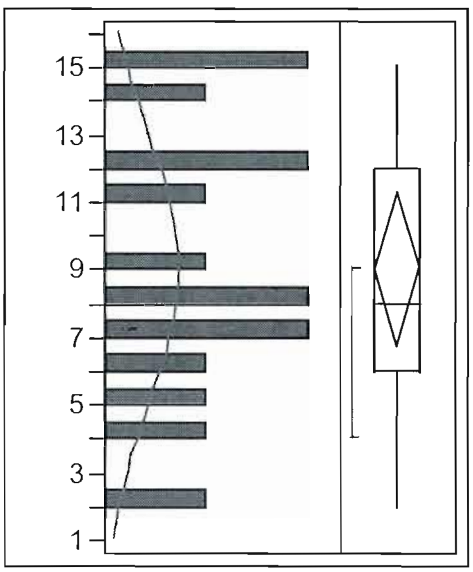
Testing for difference between three means.
Assumptions of ANOVA test: 1) Normal distribution; 2) Equal variances.

H_0: No difference between the three means.
H_A: The means are not all equal.

Example of calculations for species richness of small nodules:Facies A, B and west

Since ANOVA requires n equals or nearly equals, 15 small nodules of facies B and west were selected randomly.

Species richness
A

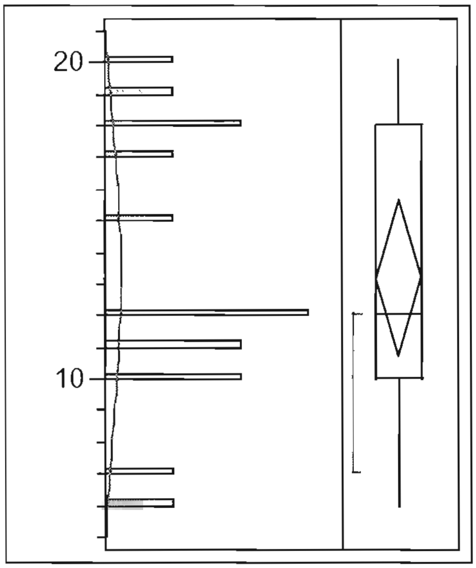


Goodness-of-Fit Test

Shapiro-Wilk W Test

W	Prob<W
0,957616	0,6511

B

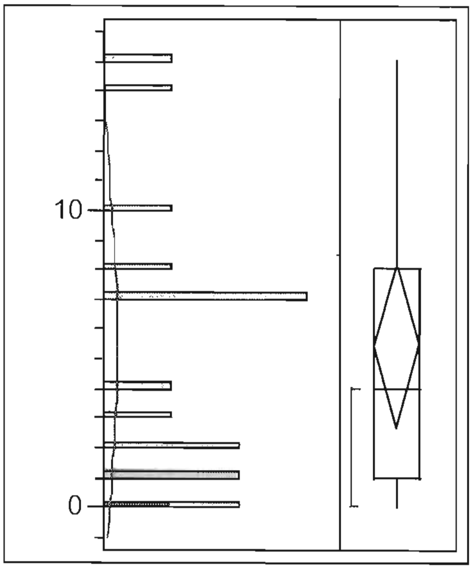


Goodness-of-Fit Test

Shapiro-Wilk W Test

W	Prob<W
0,934934	0,3229

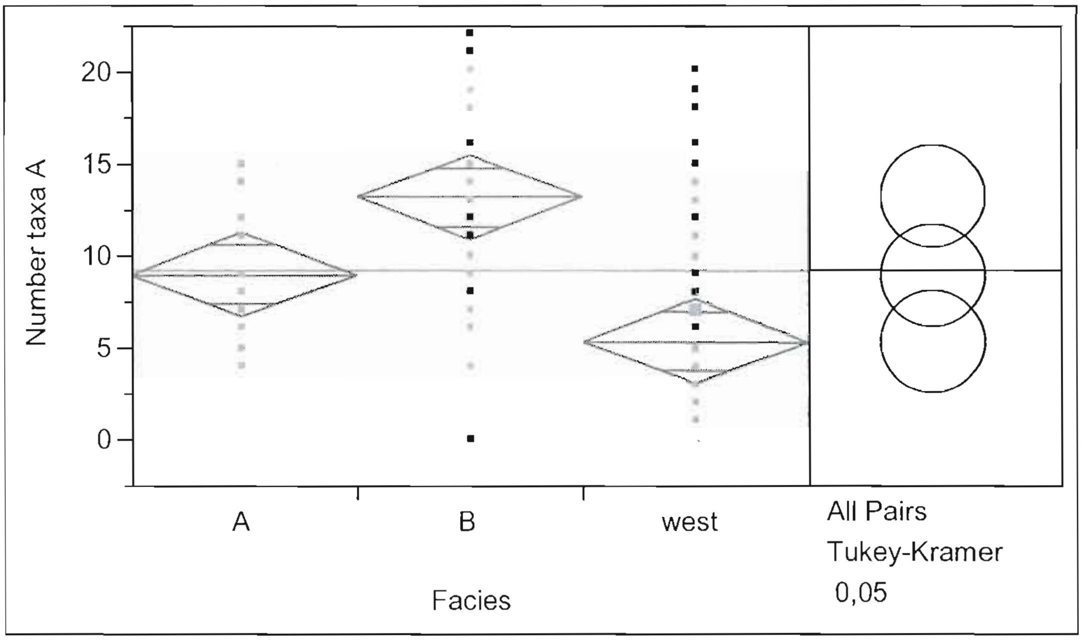
West



Goodness-of-Fit Test

Shapiro-Wilk W Test

W	Prob<W
0,898128	0,0891



Summary of Fit

Rsquare	0,356297
Adj Rsquare	0,325644
Root Mean Square Error	4,434712
Mean of Response	9,2
Observations (or Sum Wgts)	45

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Ratio	Prob > F
Facies	2	457,2000	228,600	11,6237	<,0001
Error	42	826,0000	19,667		
C. Total	44	1283,2000			

Means for Oneway Anova

Level	Number	Mean	Std Error	Lower 95%	Upper 95%
A	15	9,0000	1,1450	6,689	11,311
B	15	13,2000	1,1450	10,889	15,511
west	15	5,4000	1,1450	3,089	7,711

Std Error uses a pooled estimate of error variance

Comparisons for all pairs using Tukey-Kramer HSD

q*	Alpha
2,42949	0,05

q*	Alpha		
Abs(Dif)-LSD	B	A	west
B	-3,9341	0,2659	3,8659
A	0,2659	-3,9341	-0,3341
west	3,8659	-0,3341	-3,9341

Level			Mean
B	A		13,200000
A		B	9,000000
west		B	5,400000

Levels not connected by same letter are significantly different

Level	- Level	Difference	Lower CL	Upper CL	Difference
B	west	7,800000	3,86585	11,73415	
B	A	4,200000	0,26585	8,13415	
A	west	3,600000	-0,33415	7,53415	

Wilcoxon / Kruskal-Wallis Tests (Rank Sums)

Level	Count	Score Sum	Score Mean	(Mean-Mean0)/Std0
A	15	341,5	22,7667	-0,072
B	15	484,5	32,3000	3,356
west	15	209	13,9333	-3,272

1-way Test, ChiSquare Approximation

ChiSquare	DF	Prob>ChiSq
14,7584	2	0,0006

Tests that the Variances are Equal

Level	Count	Std Dev	MeanAbsDif to Mean	MeanAbsDif to Median
A	15	4,035556	3,333333	3,266667
B	15	4,378519	3,706667	3,466667
west	15	4,852098	4,026667	4,000000

Test	F Ratio	DFNum	DFDen	Prob > F
O'Brien[.5]	0,3884	2	42	0,6805
Brown-Forsythe	0,2896	2	42	0,7501
Levene	0,3612	2	42	0,6990
Bartlett	0,2323	2	.	0,7927

Welch Anova testing Means Equal, allowing Std Devs Not Equal

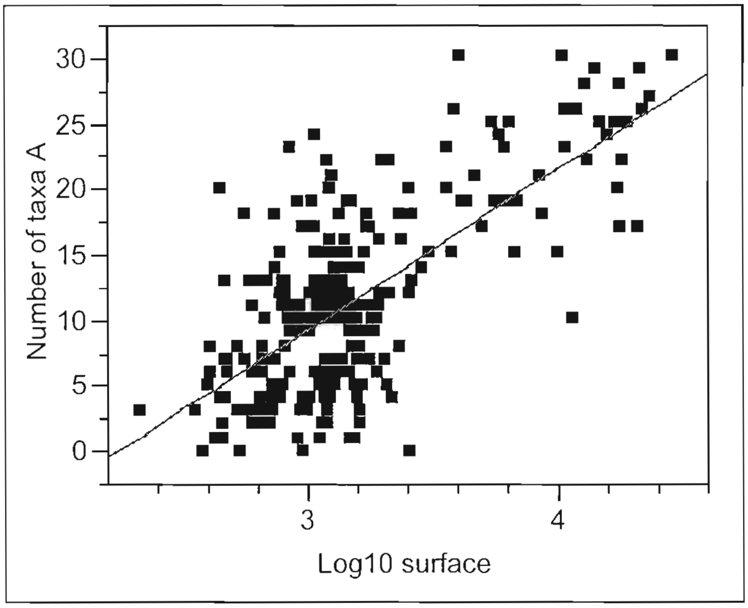
F Ratio	DFNum	DFDen	Prob > F
10,5662	2	27,846	0,0004

- Variances are equal
- The three distributions are normal
- **ANOVA is appropriate and significant.**

C.6 TESTING REGRESSIONS OF ECOLOGICAL FACTORS FOR THE 235 NODULES ANALYZED AS A FUNCTION OF EXPOSED NODULE SURFACE (FIG. 7).

Example of calculations for species richness

235 nodules



Linear Fit

Number of taxa A = -27,37312 + 12,22491 Log10 surface

Summary of Fit

RSquare	0,49668
RSquare Adj	0,49452
Root Mean Square Error	5,257885
Mean of Response	11,81277
Observations (or Sum Wgts)	235

Analysis of Variance

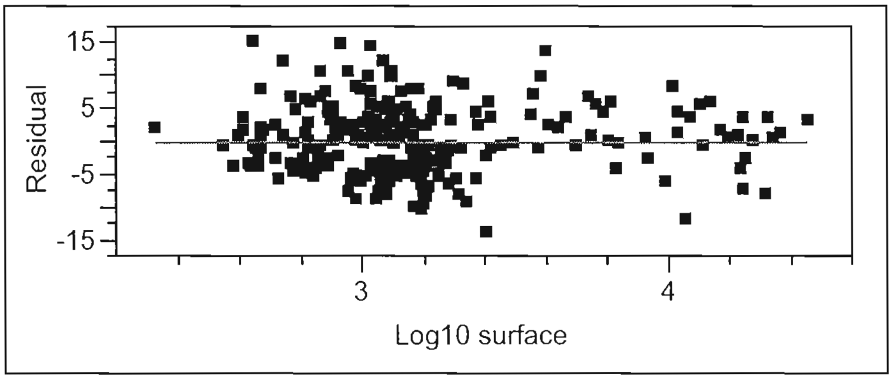
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	1	6356,395	6356,39	229,9264
Error	233	6441,367	27,65	Prob > F
C. Total	234	12797,762		<,0001

Parameter Estimates

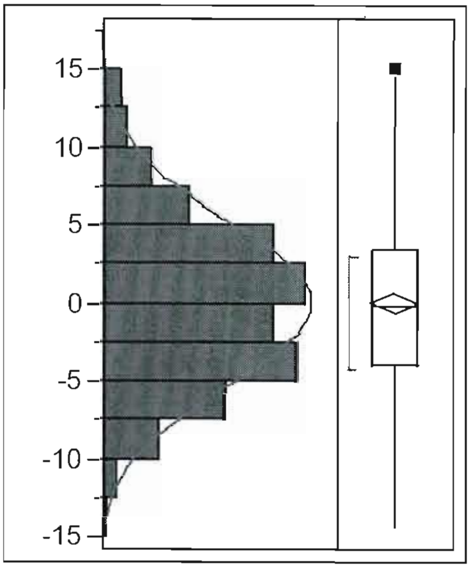
Term	Estimate	Std Error	t Ratio	Prob>|t|
Intercept	-27,37312	2,606916	-10,50	<,0001
Log10 surface	12,22491	0,806216	15,16	<,0001

Assumptions of regression analysis:

1) Linear relationship
2) Values of Y are independent of one another
3) Homogeneity of variances



4) Residuals are normally distributed



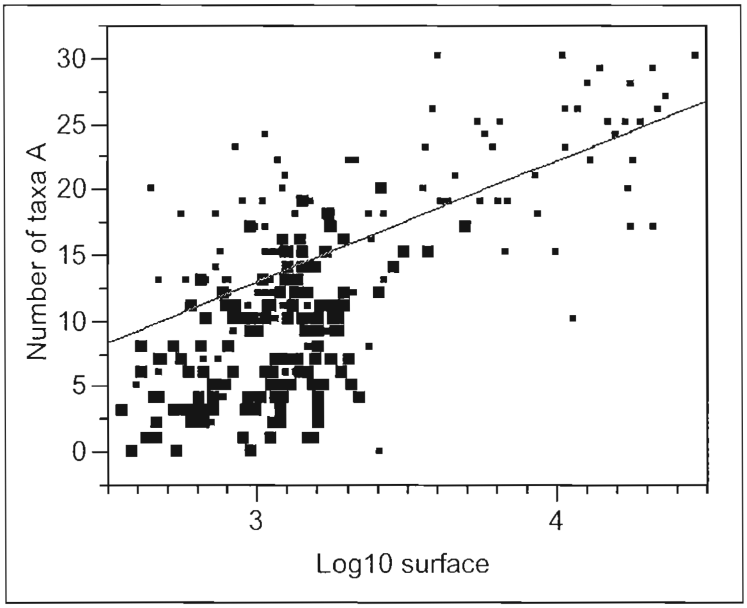
Goodness-of-Fit Test

Shapiro-Wilk W Test

W	Prob<W
0,993765	0,4369

- **The assumptions of the regression analysis are respected and the regression is significant.**

East zone



Linear Fit

Number of taxa A = -14,6513 + 9,2099504 Log10 surface

Summary of Fit

RSquare	0,448041
RSquare Adj	0,442629
Root Mean Square Error	5,301957
Mean of Response	16,79808
Observations (or Sum Wgts)	104

Analysis of Variance

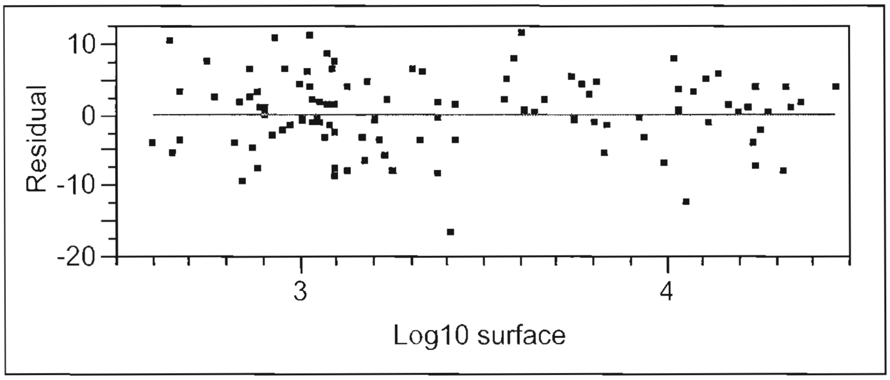
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	1	2327,4631	2327,46	82,7962
Error	102	2867,2966	28,11	Prob > F
C. Total	103	5194,7596		<,0001

Parameter Estimates

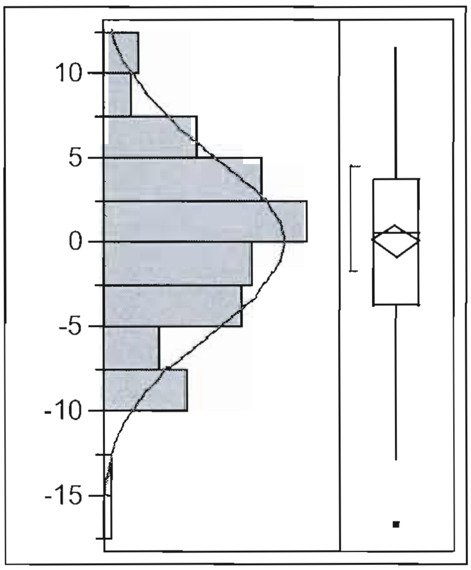
Term	Estimate	Std Error	t Ratio	Prob>|t|
Intercept	-14,6513	3,495147	-4,19	<,0001
Log10 surface	9,2099504	1,012167	9,10	<,0001

Assumptions of regression analysis:

1) Linear relationship
2) Values of Y are independent of one another
3) Homogeneity of variances



4) Residuals are normally distributed



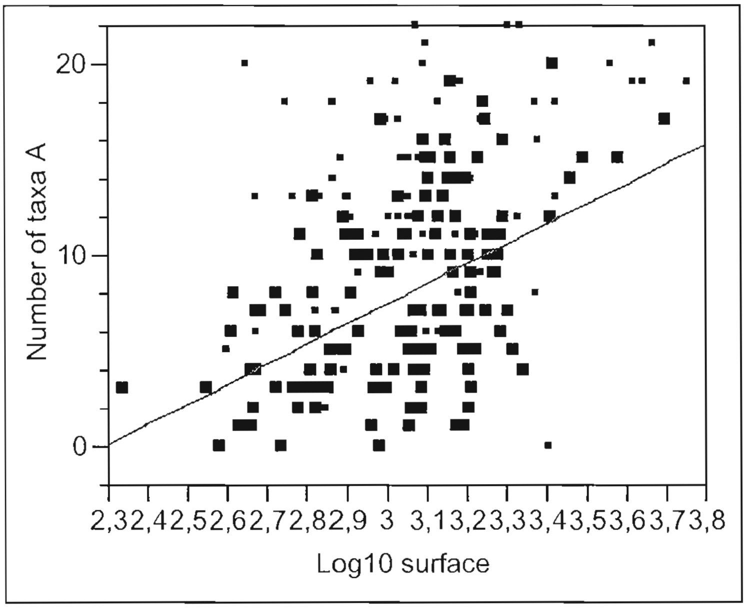
Goodness-of-Fit Test

Shapiro-Wilk W Test

W	Prob<W
0,988291	0,5009

- **The assumptions of the regression analysis are respected and the regression is significant.**

West zone



Linear Fit

Number of taxa A = -24,01718 + 10,486854 Log10 surface

Summary of Fit

RSquare	0,256571
RSquare Adj	0,250808
Root Mean Square Error	4,134552
Mean of Response	7,854962
Observations (or Sum Wgts)	131

Analysis of Variance

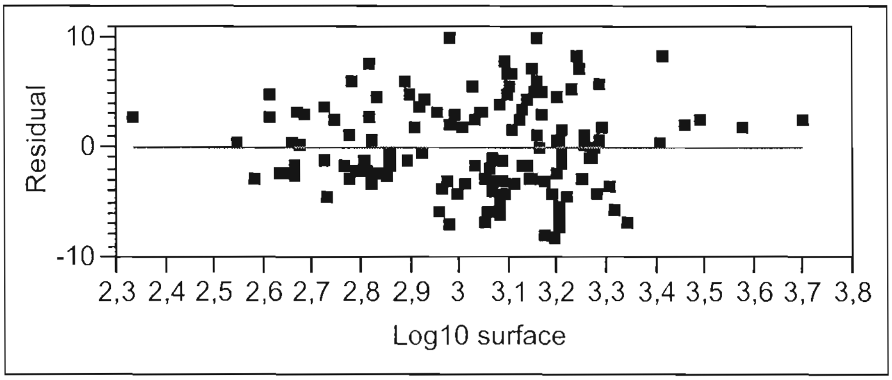
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	1	761,0514	761,051	44,5202
Error	129	2205,1929	17,095	Prob > F
C. Total	130	2966,2443		<,0001

Parameter Estimates

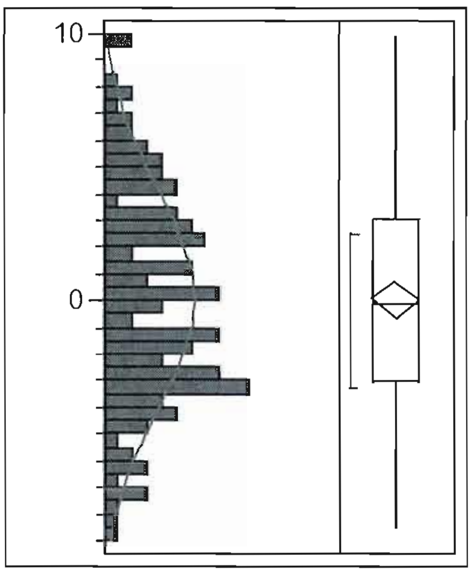
Term	Estimate	Std Error	t Ratio	Prob>|t|
Intercept	-24,01718	4,790392	-5,01	<,0001
Log10 surface	10,486854	1,571689	6,67	<,0001

Assumptions of regression analysis:

1) Linear relationship
2) Values of Y are independent of one another
3) Homogeneity of variances



4) Residuals are normally distributed

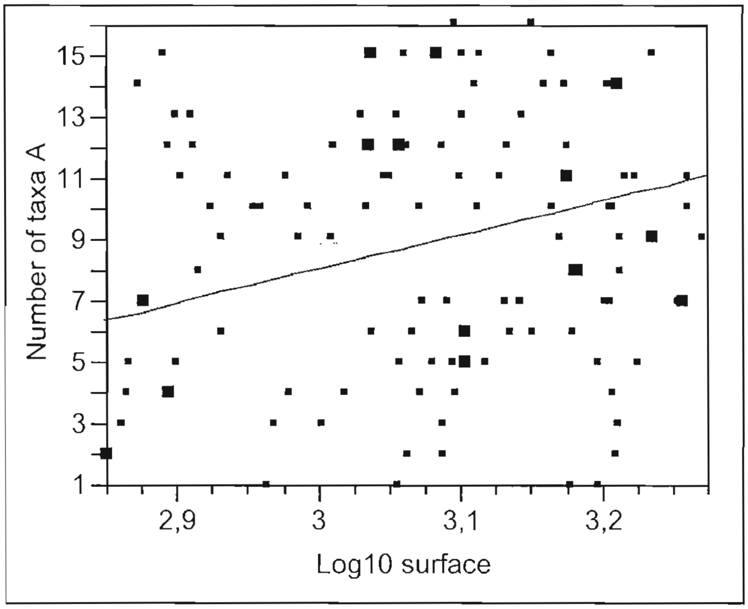


Goodness-of-Fit Test
Shapiro-Wilk W Test

W	Prob<W
0,986527	0,2261

- **The assumptions of the regression analysis are respected and the regression is significant.**

Facies A



Linear Fit
Number of taxa A = -25,37066 + 11,134661 Log10 surface

Summary of Fit

RSquare	0,129192
RSquare Adj	0,062206
Root Mean Square Error	3,908022
Mean of Response	9
Observations (or Sum Wgts)	15

Analysis of Variance

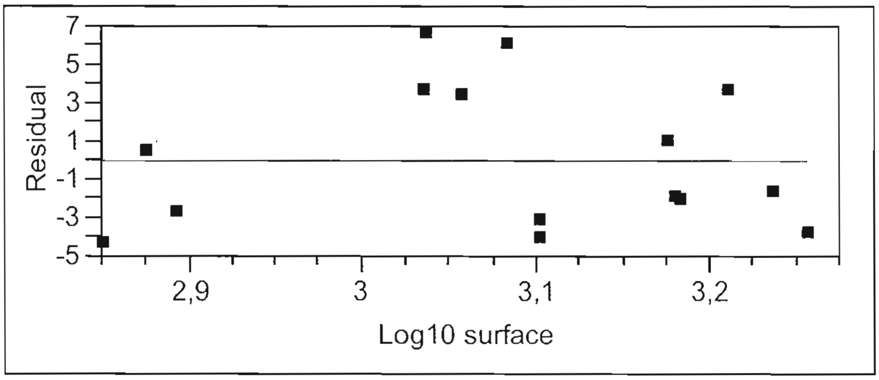
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	1	29,45568	29,4557	1,9287
Error	13	198,54432	15,2726	Prob > F
C. Total	14	228,00000		0,1882

Parameter Estimates

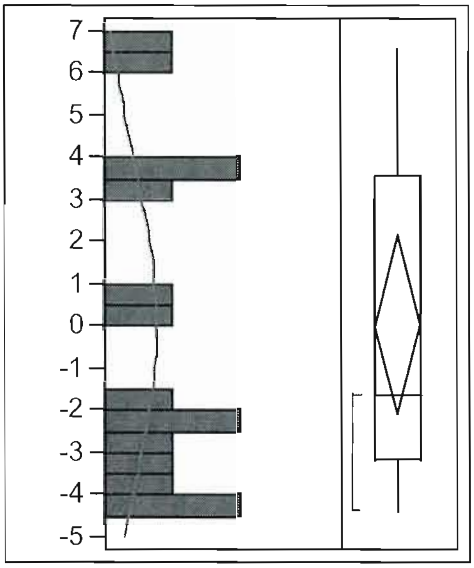
Term	Estimate	Std Error	t Ratio	Prob>|t|
Intercept	-25,37066	24,76971	-1,02	0,3244
Log10 surface	11,134661	8,017695	1,39	0,1882

Assumptions of regression analysis:

1) Linear relationship
2) Values of Y are independent of one another
3) Homogeneity of variances



4) Residuals are normally distributed



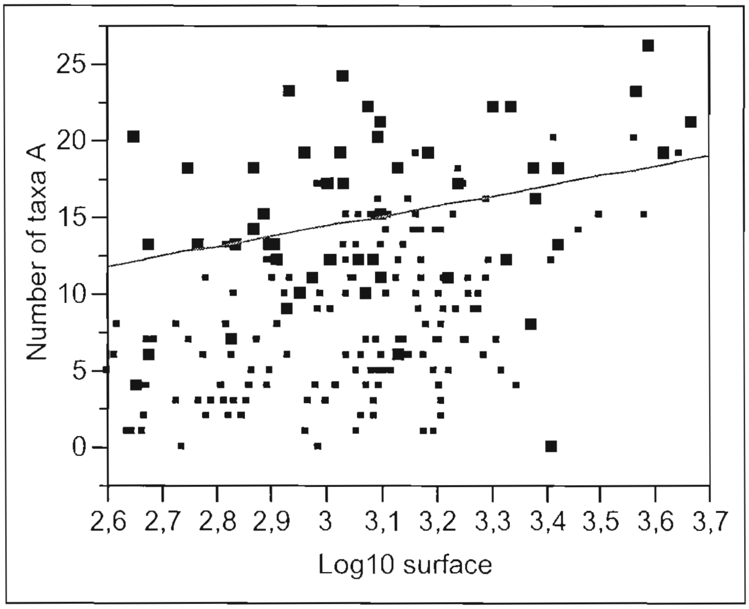
Goodness-of-Fit Test

Shapiro-Wilk W Test

W	Prob<W
0,898164	0,0892

- **The assumptions of the regression analysis are respected but the regression is non-significant.**

Facies B



Linear Fit

Number of taxa A = -5,337576 + 6,5907816 Log10 surface

Summary of Fit

RSquare	0,093347
RSquare Adj	0,074458
Root Mean Square Error	5,403728
Mean of Response	15,04
Observations (or Sum Wgts)	50

Analysis of Variance

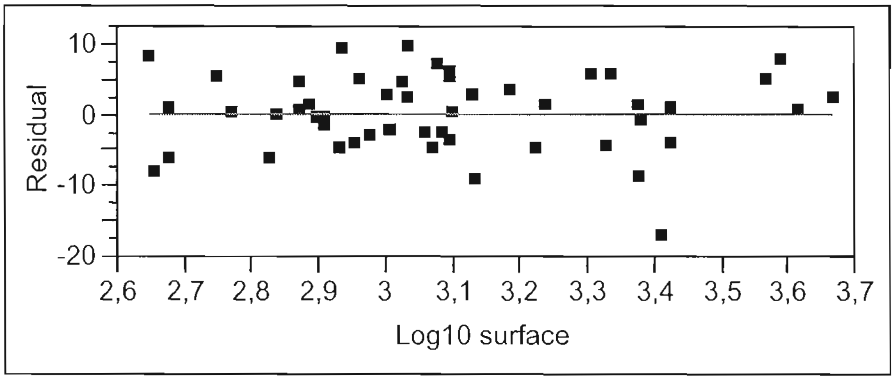
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	1	144,3065	144,307	4,9420
Error	48	1401,6135	29,200	Prob > F
C. Total	49	1545,9200		0,0310

Parameter Estimates

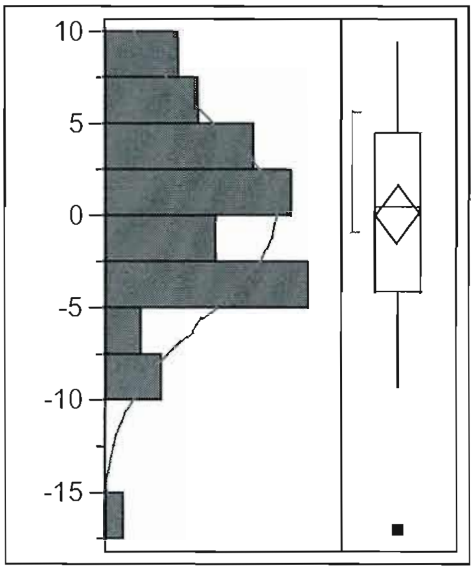
Term	Estimate	Std Error	t Ratio	Prob>|t|
Intercept	-5,337576	9,19829	-0,58	0,5644
Log10 surface	6,5907816	2,964746	2,22	0,0310

Assumptions of regression analysis:

1) Linear relationship
2) Values of Y are independent of one another
3) Homogeneity of variances



4) Residuals are normally distributed



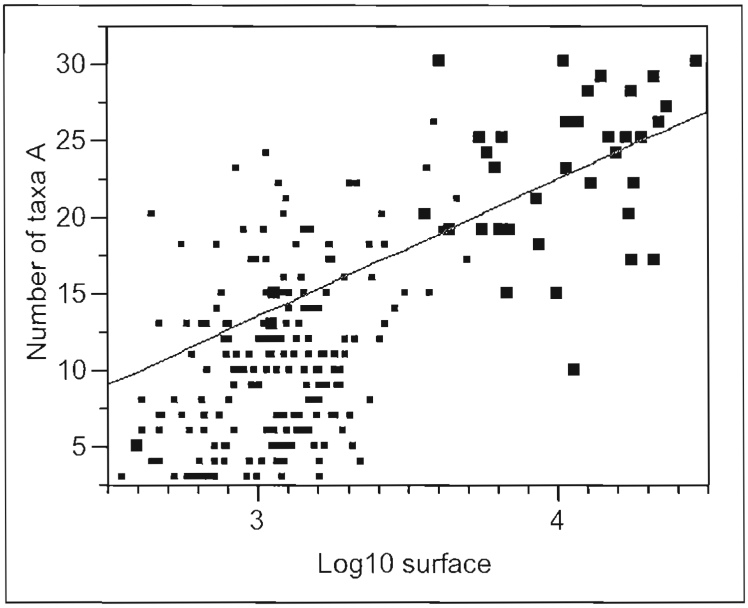
Goodness-of-Fit Test

Shapiro-Wilk W Test

W	Prob<W
0,970444	0,2412

❖ **The assumptions of the regression analysis are respected and the regression is significant.**

Facies C



Linear Fit

Number of taxa A = -13,32007 + 8,9439258 Log10 surface

Summary of Fit

RSquare	0,355446
RSquare Adj	0,338025
Root Mean Square Error	4,718206
Mean of Response	22,05128
Observations (or Sum Wgts)	39

Analysis of Variance

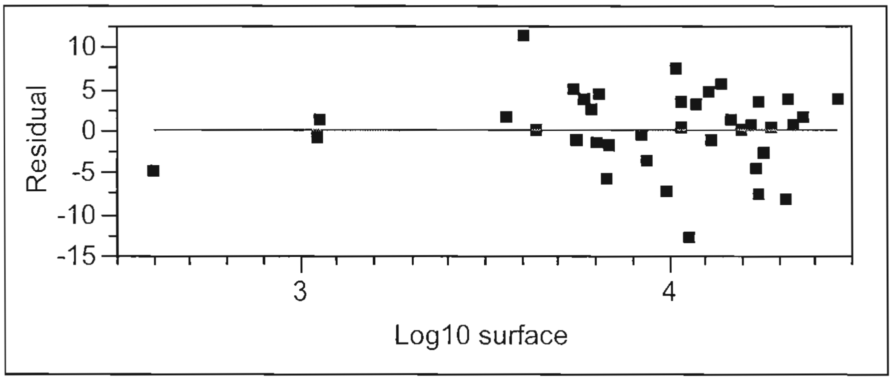
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	1	454,2232	454,223	20,4040
Error	37	823,6742	22,261	Prob > F
C. Total	38	1277,8974		<,0001

Parameter Estimates

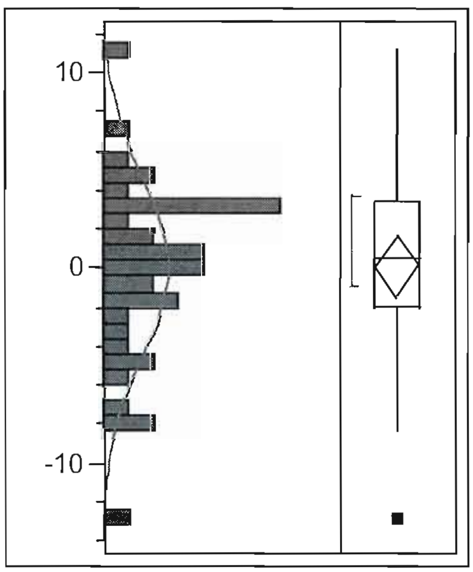
Term	Estimate	Std Error	t Ratio	Prob>|t|
Intercept	-13,32007	7,866943	-1,69	0,0988
Log10 surface	8,9439258	1,980024	4,52	<,0001

Assumptions of regression analysis:

1) Linear relationship
2) Values of Y are independent of one another
3) Homogeneity of variances



4) Residuals are normally distributed



Goodness-of-Fit Test

Shapiro-Wilk W Test

W	Prob<W
0,971023	0,4035

- **The assumptions of the regression analysis are respected and the regression is significant.**

Facies west (same as west zone)

C.7 RESULTS FROM REGRESSION AND CORRELATION ANALYSES OF THE RELATIONSHIPS BETWEEN DIFFERENT ECOLOGICAL FACTORS AND EXPOSED NODULE SURFACE (FIG. 7).

Results from regression and correlation analyses of the relationships between different ecological factors (species richness, density and percent cover) and exposed nodule surface. When residuals were not normally distributed according to Shapiro-Wilk test, the non-parametric Spearman's rank correlation was performed. * α= 0.05, ** α=0.01, ***<0.001.

	All	**Zone**		**Facies**		
		East	**West**	**A**	**B**	**C**
A) Species richness for the 235 nodules analyzed.						
n	235	104	131	15	50	39
R^2	0.50*	0.45*	0.26	0.13	0.09	0.36
p (F)	<0.0001*	<0.0001*	<0.0001*	0.1882	0.0310*	<0.0001*
Equation	y = 12.23x – 27.37	y = 9.21x – 14.65	y = 10.49x – 24.02	y = 11.13x – 25.37	y = 6.59x – 5.34	y = 8.94x – 13.32
B) Species density for the 231 nodules analyzed with fauna[1].						
n	231[1]	103[1]	128[1]	15	49[1]	39
R^2	0.41	0.82	0.07	-0.07	0.58	0.86
p (F)	<0.0001*	<0.0001*	0.001*	0.87	<0.0001*	<0.0001*
p(Rho)	<0.0001*	<0.0001*	0.0005*		<0.0001*	<0.0001*
Equation	y = -0.54x – 0.50	y = -0.73x + 0.27	y = -0.37x – 1.1	y = -0.08x - 1.95	y = -0.73x + 0.32	y = -0.75x + 0.32
C) Percent cover for the 235 nodules analyzed.						
n	235	104	131	15	50	39
R^2	0	0.14	0.02	0	0.10	0.42
p (F)	0.52	<0.0001*	0.07	0.35	0.02*	<0.0001*
p (Rho)	0.02*	0.0003*	0.002*			<0.0001*
Equation	y = -0.36x + 4.30	y = -3.14x + 15.36	y = 1.79x – 3.50	y = 2.12x – 4.55	y = -6.36x + 25.91	y = -5.51x + 25.40

[1]. 4 nodules without fauna are excluded from this analysis (1 of facies Band 3 of facies west).

APPENDICE D

ANALYSES STATISTIQUES DU CHAPITRE III

D.1 TESTING IF THE COVER OF EVERY OF THE 34 TAXA BETWEEN ROUGH AND SMOOTH SURFACES ARE DIFFERENT (TABLE 1).

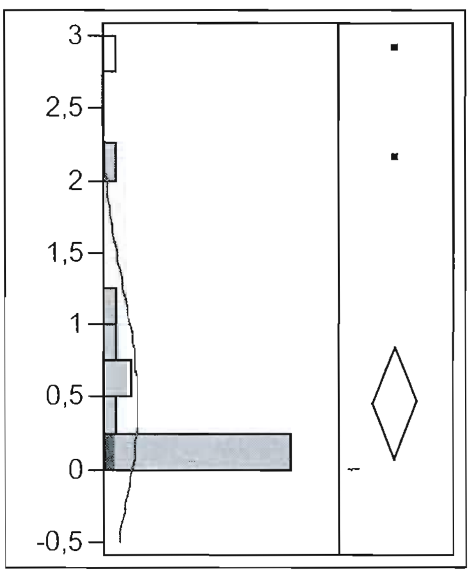
Testing for difference between two means.
Assumptions of two-samples *t* test: 1) Normal distribution; 2) Equal variances. Better if samples sizes are equal or nearly equal.

H_0 : Cover of every taxon on rough and smooth surfaces are the same.
H_A : Cover of every taxon on rough and smooth surfaces are different.

If these assumptions are violated, the non-parametric Wilcoxon/Kruskal-Wallis test is appropriate.

Example of calculations for *Hemispherammina*-like, pale regular dome

Cover on rough surfaces



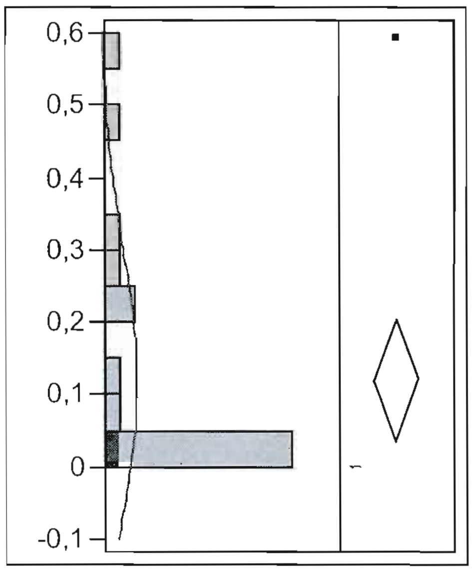
Moments

Mean	0,4466548
Std Dev	0,7954017
Std Err Mean	0,1778572
upper 95% Mean	0,8189143
lower 95% Mean	0,0743954

N 20
Goodness-of-Fit Test
Shapiro-Wilk W Test

W	Prob<W
0,641198	<,0001

- Data are log transformed according to Zar (1999): X'= log (X + 1)



Moments

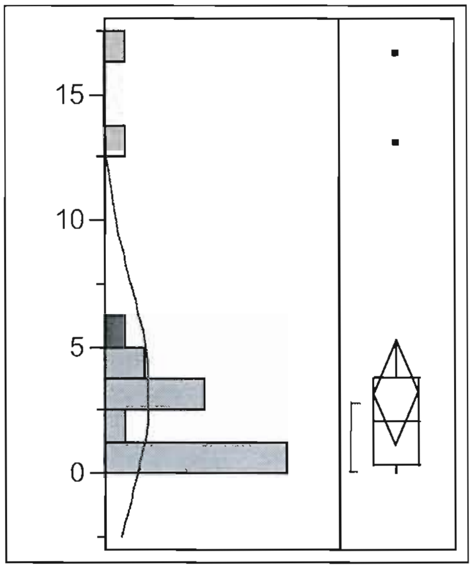
Mean	0,1178554
Std Dev	0,1797081
Std Err Mean	0,0401839
upper 95% Mean	0,2019614
lower 95% Mean	0,0337495
N	20

Goodness-of-Fit Test
Shapiro-Wilk W Test

W	Prob<W
0,719464	<,0001

- Data are not normally distributed when they are log transformed. Therefore, the non-parametric test will be preferred.

Cover on smooth surfaces



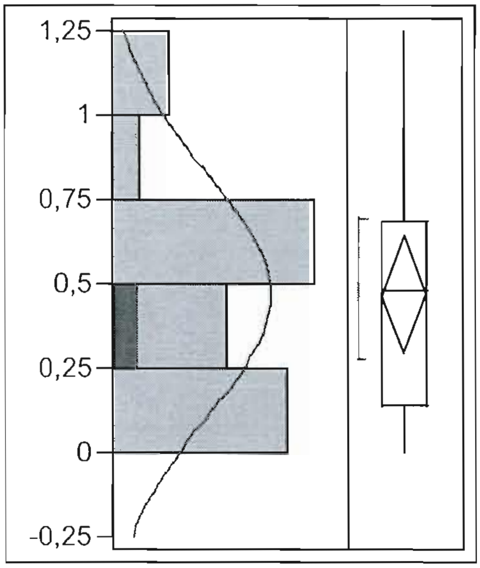
Moments

Mean	3,1696643
Std Dev	4,3084056
Std Err Mean	0,9633888
upper 95% Mean	5,1860602
lower 95% Mean	1,1532684
N	20

Goodness-of-Fit Test
Shapiro-Wilk W Test

W	Prob<W
0,689634	<,0001

- Data are log transformed according to Zar (1999): X'= log (X + 1)



Moments

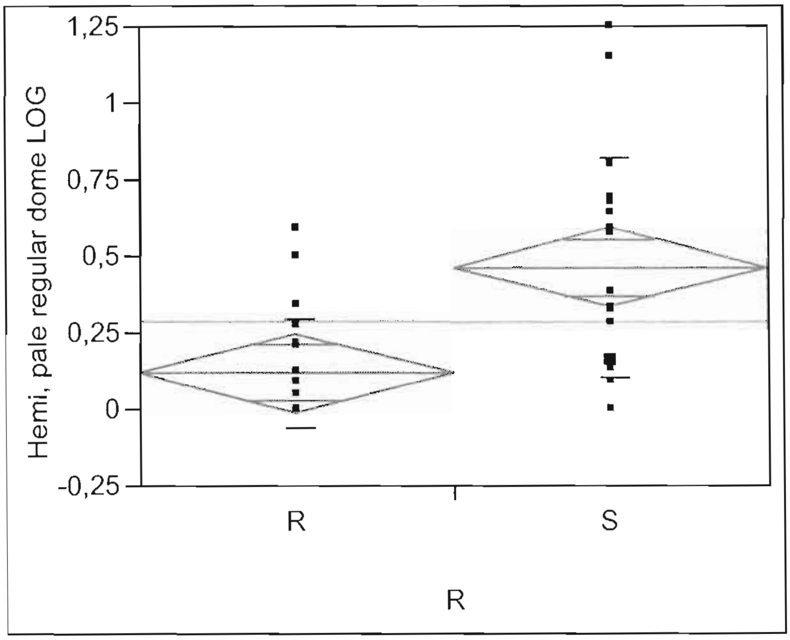
Mean	0,4640879
Std Dev	0,3603618
Std Err Mean	0,0805793
upper 95% Mean	0,6327424
lower 95% Mean	0,2954334
N	20

Goodness-of-Fit Test
Shapiro-Wilk W Test

W	Prob<W
0,931618	0,1659

- Data are normally distributed when they are log transformed.

Tests

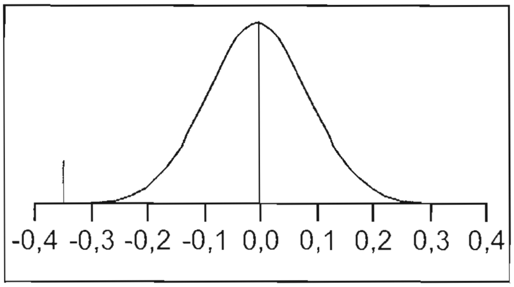


Summary of Fit

Rsquare	0,280104
Adj Rsquare	0,26116
Root Mean Square Error	0,284742
Mean of Response	0,290972
Observations (or Sum Wgts)	40

t Test
R-S
Assuming equal variances

Difference	-0,34623	t Ratio	-3,84518
Std Err Dif	0,09004	DF	38
Upper CL Dif	-0,16395	Prob > |t|	0,0004
Lower CL Dif	-0,52852	Prob > t	0,9998
Confidence	0,95	Prob < t	0,0002

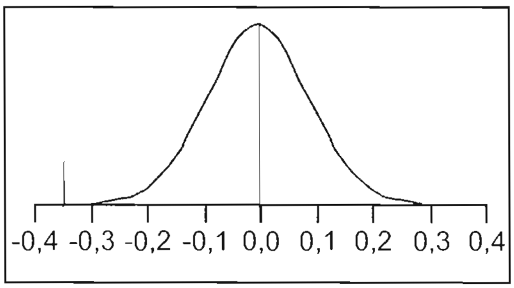


t Test

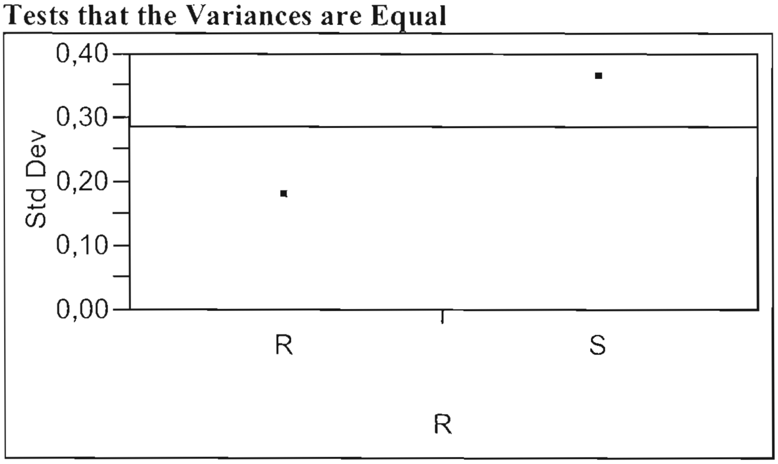
R-S

Assuming unequal variances

Difference	-0,34623	t Ratio	-3,84518
Std Err Dif	0,09004	DF	27,89979
Upper CL Dif	-0,16176	Prob > |t|	0,0006
Lower CL Dif	-0,53071	Prob > t	0,9997
Confidence	0,95	Prob < t	0,0003



Tests that the Variances are Equal



Level	Count	Std Dev	MeanAbsDif to Mean	MeanAbsDif to Median
R	20	0,1797081	0,1402609	0,1178554

Level	Count	Std Dev	MeanAbsDif to Mean	MeanAbsDif to Median
S	20	0,3603618	0,2961956	0,2961956

Test	F Ratio	DFNum	DFDen	Prob > F
O'Brien[.5]	5,7041	1	38	0,0220
Brown-Forsythe	9,0929	1	38	0,0046
Levene	9,9050	1	38	0,0032
Bartlett	8,3205	1	.	0,0039
F Test 2-sided	4,0211	19	19	0,0039

Welch Anova testing Means Equal, allowing Std Devs Not Equal

F Ratio	DFNum	DFDen	Prob > F
14,7854	1	27,9	0,0006

t Test
3,8452

Wilcoxon / Kruskal-Wallis Tests (Rank Sums)

Level	Count	Score Sum	Score Mean	(Mean-Mean0)/Std0
R	20	286,5	14,3250	-3,401
S	20	533,5	26,6750	3,401

2-Sample Test, Normal Approximation

S	Z	Prob>|Z|
533,5	3,40052	0,0007

1-way Test, ChiSquare Approximation

ChiSquare	DF	Prob>ChiSq
11,6578	1	0,0006

- **Kruskal-Wallis: $p < 0.05$ therefore, the cover of *Hemispherammina*-like, pale regular dome on the two texture surfaces are significantly different. The taxon is more present on smooth surfaces.**

Results of the analyses of differences in cover between rough and smooth nodule surfaces for the 34 taxa included. * α= 0.05, ** α=0.01, *** α=0.001. Feeding type, when known, is indicated after the name of the taxon (suspension-feeder (S) or deposit-feeder (D)). NS: non-significant.

Taxa	Kruskal-Wallis statistics	p	Texture most covered
Hemispherammina-like, pale regular dome (S)	Z= -3.401	0.0007 ***	Smooth
Hemispherammina-like, pale granular dome (S)	Z= 2.988	0.0028**	Smooth
Hemisperammina-like, irregular shape (S)	Z= 2.703	0.0069**	Smooth
Tholosina sp. (S)	Z= 3.450	0.0005***	Smooth
Tholosina-like (S)	Z= 2.052	0.0402*	Smooth
Placopsilina-like (S)	Z= 1.245	0.2132	NS
Komoki, mud-ball type (D)	Z= 1.531	0.1257	NS
Ammocibicides-like (S)	Z= 2.369	0.0170*	Smooth
Fine agglutinated particles beige soft dome (S)	Z= 1.396	0.1626	NS
Brown granular shiny dome (D)	Z= 0.633	0.5267	NS
Black soft dome (D)	Z= 1.723	0.0849	NS
Orange dome (S)	Z= 0.05	0.6147	NS
Chondrodapis hessleri (D)	Z= 2.755	0.0059**	Smooth
Chondrodapis integra (D)	Z= 4.276	<0.0001***	Smooth
Area covered with komokiacean-like chambers linked with fine tubes (D)	Z= 1.042	0.2977	NS
Grey granular mat (D)	Z= 3.158	0.0016**	Smooth
Very thin muddy patches with komokiacean-like chambers (D)	Z= 3.476	0.0005***	Smooth
Tumidotubus (S)	Z= 1.772	0.0764	NS
"White crust" (S)	Z= 3.788	0.0002***	Smooth
"Beige filamentous mat"	Z= -0.563	0.5737	NS
"Dark chambered mat" (D)	Z= 1.396	0.1626	NS
Thin grey mat (S)	Z= 2.546	0.01**	Smooth
Thin organic mat with dark grey stercomata (D)	Z= 3.875	0.0001***	Smooth
Beige thick and smooth mat, interior brown (S)	Z= 2.102	0.0355*	Smooth
Mat of blue flattened chambers	Z= 3.371	0.0008***	Smooth
White mat with lumps (S)	Z= 2.129	0.0333*	Smooth
Reticulated dark tunnels (S)	Z= 2.022	0.0432*	Smooth
Network of beige tunnels; horizontal tree with upright branches (D)	Z= 0	1	NS
Crystal star and tunnels (S)	Z= 3.078	0.0021**	Smooth
Spider network of grey tunnels (S)	Z= 3.027	0.0025**	Smooth
White soft tunnels (S)	Z= 1.869	0.0617	NS
"Flattened chambers" (D)	Z= 5.315	<0.0001***	Smooth
Hormosina sp. (S)	Z= -1.389	0.1649	NS
Anastomosing *Rhizammina*-like (D)	Z= -0.955	0.3497	NS

D.2 TESTING IF THE COVER OF EVERY OF THE 34 TAXA BETWEEN RAISED SURFACES, HOLLOWS AND SIDES MICROHABITATS ARE DIFFERENT (TABLE 1).

Testing for difference between three means.
Assumptions of ANOVAt: 1) Normal distribution; 2) Equal variances. Better if samples sizes are equal or nearly equal.

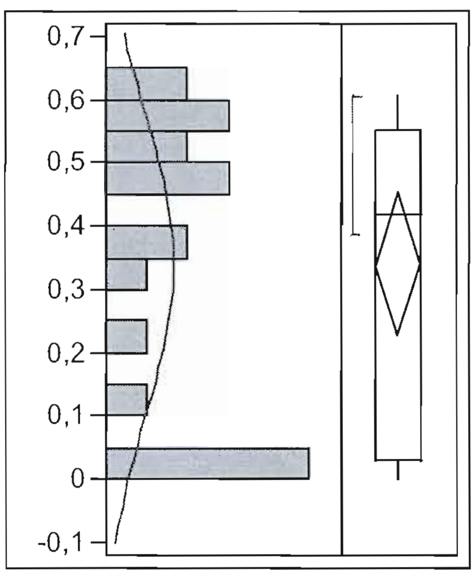
H_0 : Cover of every taxon on the three microhabitats are the same.
H_A : Cover of every taxon is different on at least one microhabitat.

If these assumptions are violated, the non-parametric Wilcoxon/Kruskal-Wallis test is appropriate.

Example of calculations for *Hemispherammina*-like, pale regular dome

- Data are all log transformed according to Zar (1999): X'= log (X + 1)

Cover on raised surfaces



Moments

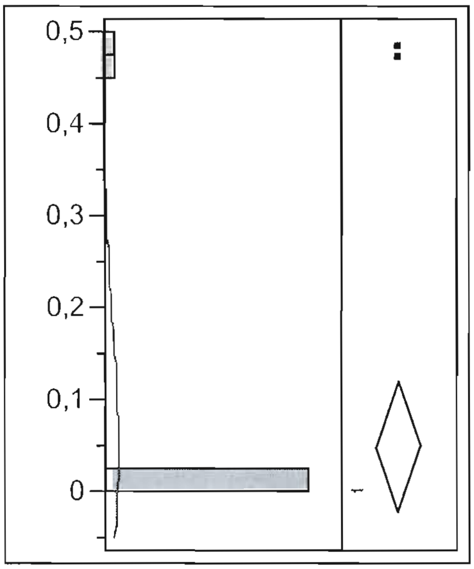
Mean	0,3383606
Std Dev	0,2354753

Std Err Mean	0,0526539
upper 95% Mean	0,4485664
lower 95% Mean	0,2281547
N	20

Goodness-of-Fit Test
Shapiro-Wilk W Test

W	Prob<W
0,845949	0,0046

Cover on hollows areas



Moments

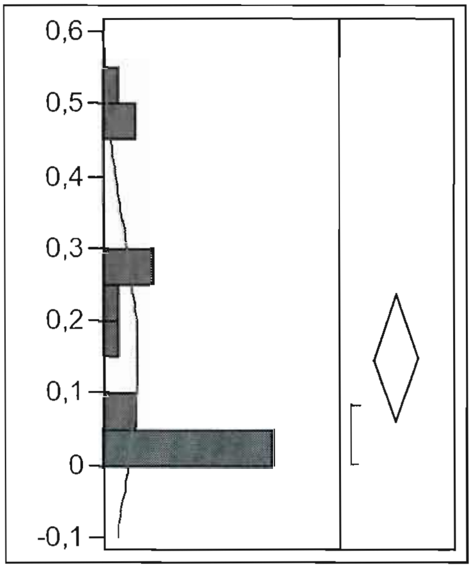
Mean	0,0476215
Std Dev	0,1465844
Std Err Mean	0,0327773
upper 95% Mean	0,1162251
lower 95% Mean	-0,020982
N	20

Goodness-of-Fit Test
Shapiro-Wilk W Test

W	Prob<W
0,352553	<,0001

W	Prob<W

Cover on sides



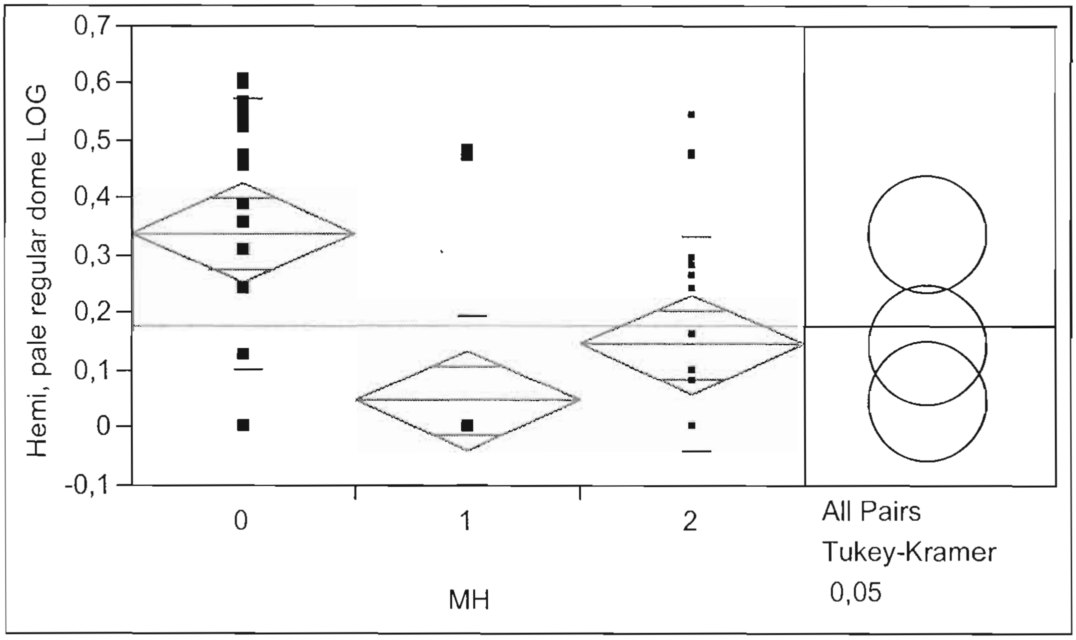
Moments

Mean	0,1455519
Std Dev	0,1857295
Std Err Mean	0,0415304
upper 95% Mean	0,232476
lower 95% Mean	0,0586278
N	20

Goodness-of-Fit Test
Shapiro-Wilk W Test

W	Prob<W
0,781238	0,0005

Tests



Summary of Fit

Rsquare	0,292498
Adj Rsquare	0,267674
Root Mean Square Error	0,192727
Mean of Response	0,177178
Observations (or Sum Wgts)	60

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Ratio	Prob > F
MH	2	0,8752983	0,437649	11,7826	<,0001
Error	57	2,1171908	0,037144		
C. Total	59	2,9924890			

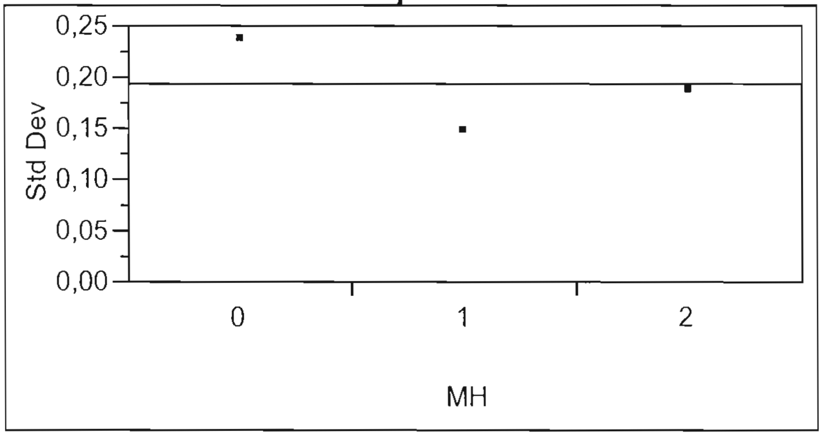
Wilcoxon / Kruskal-Wallis Tests (Rank Sums)

Level	Count	Score Sum	Score Mean	(Mean-Mean0)/Std0
0	20	830	41,5000	3,770
1	20	407	20,3500	-3,478
2	20	593	29,6500	-0,283

1-way Test, ChiSquare Approximation

ChiSquare	DF	Prob>ChiSq
17,6764	2	0,0001

Tests that the Variances are Equal



Level	Count	Std Dev	MeanAbsDif to Mean	MeanAbsDif to Median
0	20	0,2354753	0,2035974	0,1974636
1	20	0,1465844	0,0857187	0,0476215
2	20	0,1857295	0,1566631	0,1455519

Test	F Ratio	DFNum	DFDen	Prob > F
O'Brien[.5]	2,2654	2	57	0,1131
Brown-Forsythe	5,2392	2	57	0,0082
Levene	6,1737	2	57	0,0037
Bartlett	2,0483	2	.	0,1290

Welch Anova testing Means Equal, allowing Std Devs Not Equal

F Ratio	DFNum	DFDen	Prob > F
10,8460	2	36,7	0,0002

Comparisons for all pairs using Tukey-Kramer HSD

q*	Alpha
2,40642	0,05

Abs(Dif)-LSD	0	2	1
0	-0,14666	0,04615	0,14408
2	0,04615	-0,14666	-0,04873
1	0,14408	-0,04873	-0,14666

Level			Mean
0	A		0,33836057
2		B	0,14555189
1		B	0,04762152

Levels not connected by same letter are significantly different

Level	- Level	Difference	Lower CL	Upper CL

Level	- Level	Difference	Lower CL	Upper CL
0	1	0,2907391	0,144078	0,4374000
0	2	0,1928087	0,046148	0,3394697
2	1	0,0979304	-0,048731	0,2445914

- **Kruskal-Wallis: $p < 0.05$ therefore, the cover of *Hemispherammina*-like, pale regular dome on the three microhabitats is not the same. The Tukey-Kramer post test concludes that the cover of this taxon is significantly greater on raised surfaces than on hollows or sides.**

Results of the analyses of differences in cover between raised surfaces (R), hollows (H) and sides (S) for the 34 taxa included. * α= 0.05, ** α=0.01, *** α=0.001. Feeding type, when known, is indicated after the name of the taxon (suspension-feeder (S) or deposit-feeder (D)). NS: non-significant. Microhabitat most covered result is according to the Tukey test.

Taxa	Chi-Square statistics	p	Microhabitat most covered
Hemispherammina-like, pale regular dome (S)	17.676	0.0001***	R > H and S
Hemispherammina-like, pale granular dome (S)	7.671	0.0216*	NS
Hemisperammina-like, irregular shape (S)	7.938	0.0189*	NS
Tholosina sp. (S)	21.666	<0.0001***	R > H and S
Tholosina-like (S)	2.069	0.3555	NS
Placopsilina-like (S)	6.322	0.0424*	NS
Komoki, mud-ball type (D)	4.464	0.1073	NS
Ammocibicides-like (S)	11.658	0.0029**	R > H and S
Fine agglutinated particles beige soft dome (S)	4.068	0.1308	NS
Brown granular shiny dome (D)	4.219	0.1213	NS
Black soft dome (D)	9.97	0.0068**	R > H and S
Orange dome (S)	2.002	0.3675	NS
Chondrodapis hessleri (D)	8.834	0.0121*	R > H and S
Chondrodapis integra (D)	20.843	<0.0001***	R > H and S
Area covered with komokiacean-like chambers linked with fine tubes (D)	3.962	0.1379	NS
Grey granular mat (D)	13.319	0.0013**	R > H and S
Very thin muddy patches with komokiacean-like chambers (D)	3.828	0.1475	NS
Tumidotubus (S)	12.029	0.0024**	R and S > H
"White crust" (S)	19.127	<0.0001***	R > H and S
"Beige filamentous mat"	2.069	0.3555	NS
"Dark chambered mat" (D)	4.068	0.1308	NS
Thin grey mat (S)	15.823	0.0004***	R > H; S=R; S=H
Thin organic mat with dark grey stercomata (D)	20.024	<0.0001***	R > H and S
Beige thick and smooth mat, interior brown (S)	8.637	0.0133*	R > H; S=R; S=H
Mat of blue flattened chambers	17.92	0.0001***	R > H and S
White mat with lumps (S)	8.3	0.0158*	NS
Reticulated dark tunnels (S)	6.492	0.0389*	NS
Network of beige tunnels; horizontal tree with upright branches (D)	1.0178	0.6012	NS
Crystal star and tunnels (S)	11.699	0.0029**	R > S; H=R; H=S
Spider network of grey tunnels (S)	11.431	0.0033**	R > H and S
White soft tunnels (S)	7.4528	0.0241*	NS
"Flattened chambers" (D)	43.125	<0.0001***	R > H and S
Hormosina sp. (S)	5.694	0.058	NS
Anastomosing *Rhizammina*-like (D)	6.2057	0.045*	NS

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