
Influence of surface texture and microhabitat heterogeneity in structuring nodule faunal communities

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Abstract:

Manganese nodules provide an important habitat for sessile benthic organisms, many of them novel foraminifera, in the abyssal Pacific. The surface texture and microhabitat heterogeneity of nodules may play a significant role in structuring these communities. We analyzed the distribution of foraminiferal species on 20 nodules collected using either a USNEL box corer or the Nautilie submersible sampling tool at a 5000-m-deep site in the Tropical North Pacific. The nodules had an upper region characterized by two microhabitats, namely raised surfaces and intervening depressed surfaces. The more or less vertical sides of the nodules were regarded as a third microhabitat. The upper region had a predominantly smooth texture while the sides had a rough texture. We tested whether the percent cover of each of the 34 species examined was distributed evenly over the three microhabitats and the two surface textures (smooth vs rough). More than half (20 out of 34) of species covered a greater area on smooth surfaces than on rough surfaces, while one-third of the species (12 out of 34) occurred more on raised microhabitats than on depressed surfaces and nodule sides. These two results are closely interrelated, since 78% of the raised surfaces were characterized by a smooth texture. The nodule-encrusting species were feeding either on suspended particles or on particles deposited on the nodule surfaces. Because most species had a mat-like or domed morphology, we suspect that nodule surface feeding was more prevalent. Current flow, which transports propagules and particulate food, may be the main environmental factor explaining the observed faunal distributions, as it is in the case of other hard-substrate assemblages.

Keywords: Ferromanganese nodules; Epifauna; Agglutinated foraminifera; Surface texture; Microhabitats; Current flow

Pacific Ocean; Equatorial North Pacific Ocean; Clarion–Clipperton Fracture Zone (14°N; 130°W)

1. Introduction

Benthic foraminifera are often a dominant component of deep-sea, soft-bottom communities, particularly at abyssal depths (Snider *et al.*, 1984; Gooday, 2003). These testate protists are also abundant on hard structures in the deep ocean, mainly manganese nodules, glacial drop stones and biogenic structures including the tests of other, larger foraminifera, as well as experimental settlement plates (Lipps, 1983; Gooday 1990; Bertram and Cowen, 1999; Hughes and Gooday, 2004). In tropical latitudes, the most prevalent hard substratum in the deep ocean is provided by extensive tracts of manganese nodules, which are densely encrusted with organisms, most of them foraminifera (Dugolinsky *et al.*, 1977; Mullineaux, 1987). As in the case of sediment-dwelling communities, these sessile foraminifera are undoubtedly important in terms of their contribution to benthic biomass and diversity and, their ecological role, although both these aspects of their biology remain poorly understood.

In a companion paper to the present study, Veillette *et al.* (in press) described faunal assemblages from manganese nodules at two sites (east and west zones) in the Clarion-Clipperton Fracture Zone, eastern Equatorial Pacific. They recognized four facies defined by nodule characteristics: three (facies A, B and C) were found in the east zone and a single facies was identified in the west zone. They described the foraminiferan and metazoan assemblages associated with the nodules and related

faunal coverage, species richness and species density to nodule characteristics at the facies and regional (east vs west zones) scale. Veillette *et al.* (in press) suggested that microhabitat heterogeneity created by complex, knobby nodule micro-relief and the remnants of biogenic structures might enhance the species richness of sessile organisms and increase faunal cover. However, they did not investigate the spatial relationship between species and small-scale surface features (microhabitats) of the nodules.

Because of the dependence of sessile, hard-substrate organisms on currents, flow velocity is often considered to be the most important environmental parameter structuring sessile hard-substrate communities (Jumars and Nowell, 1984; Mullineaux, 1988; Lutze and Thiel, 1989; Flach *et al.*, 1998; Pernet *et al.*, 2003; Thistle, 2003). Currents can affect the way in which organisms colonize hard substrata. For example, interactions between boundary-layer flow and surface characteristics, including composition and microtopography, may influence where larvae and other propagules settle and hence the ways in which organisms colonize hard substrata (Mullineaux, 1989; Mullineaux and Butman, 1990). Similarly, small substratum irregularities may affect the current velocities experienced by sessile benthic organisms (Mullineaux 1989), many of which depend on the water flow for their food. Substratum characteristics, such as surface texture, can influence the distribution of foraminifera (Mullineaux, 1988; Goody, 1990; Bertram and Cowen,

1994, 1999) and were also observed to vary between different areas of the surfaces of nodules analyzed by Veillette *et al.* (in press).

In this paper, we explore the relation between different regions ('microhabitats') and surface textures (rough vs smooth) of individual nodules from our equatorial Pacific study area and the distribution of 34 species of encrusting foraminifera. Specifically, we ask: 1) Is there an association between particular species and specific microhabitats on the nodule surface? and 2) Are different species associated with areas of rough and smooth surface texture?

2. Materials and methods

2.1. Sampling sites and methods

Samples were collected during the NODINAUT cruise (RV *l'Atalante*; May 18th – June 27th 2004) in two areas, the east zone (14°N, 130°W) and the west zone (9°N, 150°W), of the French mining claim in the equatorial Pacific. Both are located in the Clarion-Clipperton Fracture Zone between 4950 and 5050 m water depth, below the carbonate compensation depth, where sediments are fine-grained clays (Skornyakova and Murdmaa, 1992). Primary productivity in this region is estimated to be moderate compared to the high equatorial productivity (Du Castel, 1985; Skornyakova and Murdmaa, 1992). Bottom-water temperature was ~1°C and near-bottom currents

observed during the NODINAUT cruise (short term ADCP-WH300 measurements at ten meters above the bottom, Vangriesheim, unpublished data) were very weak (3.5 – 4 cm s⁻¹).

The four nodule facies recognized by Veillette *et al.* (in press) differed in nodule shape, size, surface morphology and the degree to which nodules were exposed above the sediment-water interface. Twenty nodules from facies C in the east zone were chosen for this study, because they exhibited greater microhabitat heterogeneity and surface texture variations than other nodules. Facies C nodules formed spheres that were half buried in the sediment and covered an estimated 40% of the seafloor. They were generally larger (average diameter 11 cm) than nodules from other facies, but their sizes varied considerably, ranging from 2 to 15 cm diameter. The upper, summit region of the nodules was characterized by knobs and protrusions but otherwise had a generally smooth texture, whereas the sides were rough. Only nodules whose vertical or near-vertical sides extended more than 30 mm above the sediment were included in the present study.

Nodules were sampled using either a USNEL box corer or the manipulator of the *Nautilie* submersible (Veillette *et al.*, in press). The sampled nodules were preserved 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 above the sediment-water interface was estimated in order to calculate percent cover on the different textures and microhabitats. Since nodule surfaces below the sediment line were rarely colonized, they were not examined further. The 20 nodules analyzed in this study had vertical or near-vertical sides that extended for more than 30 mm above the sediment surface before flattening to form the upper region. We therefore differentiated between the upper and side regions of each nodule. Upper surface area was determined using IP Lab Spectrum© image analysis software, assuming that top-view photographs provided a good representation of the upper surface. Side surface area was calculated using the surface formula for an open cylinder (height x circumference). Because most nodules were irregular in shape, the height of the sides was measured at every 45° point around the nodule circumference. All measurements and surface area determinations with IP Lab Spectrum© were made in triplicate.

2.3. Faunal identification and quantification

Living organisms on nodule surfaces were identified using a binocular dissecting microscope. High power light microscopy and scanning electron microscopy were also used to examine smaller forms or to decide if particular forms were protozoans, metazoans or non-biogenic structures. 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. However, some foraminifera, for example, komokiacean-like forms in which the test interior is dominated by stercomata, rarely contained visible protoplasm. In these cases, unbroken tests were regarded as being 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, the recognition of species may have been biased towards more robust forms firmly attached to nodule surfaces. Two foraminiferal feeding types were distinguished based on test contents: species containing cytoplasm without obvious accumulations of stercomata and species that accumulate stercomata and have sparse cytoplasm (Gooday *et al.*, 1997, in press). We refer to these as 'feeding type I' and 'feeding type II', respectively.

The vast majority of the living organisms on the nodules were mat-like or dome-shaped foraminifera. Only these encrusting species were included in this study. Following Mullineaux (1987), they were quantified in terms of percent cover. For many species, the numbers of specimens, and hence faunal densities, could not be calculated easily because it was difficult to define the limits of an individual. Upright

structures were excluded, since the surface area that they covered was negligible. In order to simplify the estimation of surface area covered, each specimen was approximated to a circle or a rectangle. The dimensions of the test were then measured under a binocular microscope equipped with an eyepiece scale. For species forming anastomosing networks, the percentage of nodule surface covered within the boundaries of the test was estimated by eye. The species included in this study were those found on at least two nodules.

2.4. Microhabitats and definition of surface textures

Data from twenty nodules were pooled to investigate the influence of microhabitats and surface texture on the distribution of nodule fauna. Three different microhabitats were recognized on all nodules. Raised surfaces and depressed surfaces on the upper region constituted two distinct microhabitats, the depressions being the spaces between two or more raised areas of the nodule surface (Fig. 1). The sides of the nodule formed the third microhabitat.

We defined surface texture as either smooth or rough, although it was sometimes difficult to classify areas of moderate roughness. Smooth surfaces lacked protrusions visible to the naked eye, whereas rough surfaces had a gritty appearance similar to that of sandpaper. The surface area characterised by each texture was estimated for the upper 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 dominated by rough surfaces.

2.5. Statistical analyses

A Kruskal-Wallis test was performed for the 34 live species included in this study in order to test for significant differences in cover between (1) microhabitats and (2) surface textures. The area covered by each species on each microhabitat was divided by the fraction of the nodule represented by that microhabitat in order to calculate percent cover per microhabitat. The same was done for the comparisons between the two surface textures.

3. Results

When the 20 nodules were pooled, 86% of the combined upper area was occupied by raised microhabitats, the remaining areas being depressions (Fig. 1). Seventy-two percent of the combined upper area had a smooth surface texture. When only the raised microhabitat was considered, 78% of the surface texture was smooth, whereas only 30% of the depressed microhabitat had a smooth surface texture. When the areas occupied by the three microhabitats from the 20 nodules were combined, smooth and rough surfaces were almost equally represented (48% versus 52%, respectively).

Raised microhabitats represented 57%, sides 33% and depressed microhabitats 10% of the total exposed area of the nodule surface.

Twelve of the 34 species examined occurred more on raised surfaces than on depressed surfaces and nodule sides. The percent cover of 20 species (out of 34) was significantly different between the two surface textures (Table 1). In all cases, the percent cover was greater on smooth surfaces. Of these 20 species, 13 contain protoplasm (feeding type I), six accumulated stercomata (feeding type II) and one could not be assigned to either category. Fourteen species occurred more on smooth and raised surfaces than on depressed surfaces and nodule sides; 8 of them belonged to feeding type I and 5 to feeding type II. Overall, 12 species had no significant relationships with either microhabitat types or surface texture.

4. Discussion

4.1. Feeding types

Foraminifera that contain cytoplasm but are devoid of obvious stercomata and those that have sparse cytoplasm and large accumulations of stercomata (our feeding types I and II respectively) appear to represent different trophic strategies (Gooday *et al.*, 1997; in press). Type II species, which include the komokiaceans, are particularly abundant in abyssal, oligotrophic settings (Nozawa *et al.*, 2006) and it is not

surprising to find that they are common on nodule surfaces. Stercomata are waste pellets that consist largely of tiny, flake-like mineral grains (Riemann, 1983). Sediment-dwelling species that accumulate stercomata probably obtain grains from the surrounding sediment and therefore can be considered deposit feeders. However, foraminifera living on nodules, particularly those found on the upper region, do not have direct access to the sediment. Instead, the tiny clay-sized grains that form the stercomata of type II species must be taken directly either from the water column or from material deposited on the nodule surface (Burnett and Neelson, 1983). Type I species presumably feed on bacteria and other small particles and expel any sediment grains that they ingest. Food particles could be obtained either from suspension or from organic films and associated microorganisms present on the nodule surface (Burnett and Nelson, 1981; Bernhard and Bowser, 1992). Thus, foraminifera of both types may be feeding on material in suspension or material present on the nodule surface, or they may combine suspension and surface feeding. Xenophyophores, giant protozoans that accumulate large quantities of stercomata, seem to be capable of both suspension (Levin and Thomas, 1988) and deposit feeding (Goody *et al.*, 1993). Since all the species we analysed were encrusting forms with more or less flat, mat-like or domed morphologies, we speculate that nodule surface feeding was more prevalent. Occasional foraminifera with erect morphologies typical of suspension feeders (Lipps, 1983) were present on the nodule surfaces (see supplementary material of Veillette *et al.*, in press) but were not included in our analyses and represented a minor component of the assemblage.

4.2. Controls on distributions

Some authors have found that foraminifera usually colonize nodule surfaces at, or just above, the sediment-water interface (Greenslate, 1974; Dugolinsky, 1976; Dugolinsky *et al.*, 1977; von Stackelberg, 1984). Mullineaux (1988), however, reported that 65% of the sessile organisms living on nodules belonged to species whose abundance was related to vertical position on the nodule. This agrees with our observation that almost half of the species we analyzed covered more substratum area near the summit than on the sides of the nodules. In addition to nodule surface microhabitats, foraminifera can live in crevices and cavernous spaces within nodules, where they presumably gain shelter from predators and possibly access to bacterial food (von Stackelberg, 1984; Maybury, 1996). However, neither the crevice microhabitat nor the predominantly spherical foraminiferal morphotypes that inhabit it were represented in our material.

Surface texture perception by organisms depends partly on their size. An organism similar in size to the protrusions creating the surface roughness will probably be influenced differently compared to a larger organism. Nevertheless, differences between smooth and rough nodule surfaces may be large enough to be detected by invertebrate larvae (Mullineaux, 1989) and possibly also by foraminiferal propagules. The nodules that we examined had a predominantly smooth upper region and rough

sides, as also observed by Dugolinsky (1976) and Mullineaux (1988, 1989) in other parts of the Pacific Ocean. As in our study, Mullineaux (1989) found that more species (16) were concentrated on smooth surfaces than on rough surfaces (9 species). She concluded that these faunal distributions probably resulted from interactions between texture, flow, and particulate food availability, rather than on texture alone (Mullineaux, 1989).

Flow is a crucial parameter for sessile organisms living on hard substrata since it transports larvae and other propagules, influences their settlement, and delivers food to suspension feeders (Mullineaux, 1988; Mullineaux and Butman, 1990; Pernet *et al.*, 2003; Thistle, 2003). In areas characterized by strong currents, foraminifera often colonize stones and elevated biogenic structures (Schönfeld 1997, 2002; Lutze and Altenbach, 1988; Lutze and Thiel, 1989; Linke and Lutze, 1993). From these vantage points, they are able to extend their pseudopodial network into the velocity profile of the near-bottom shear flow and take advantage of the enhanced food supply (Lipps, 1983). Large, suspension-feeding animals colonizing other marine hard substrata also often occupy positions that allow them to take advantage of enhanced particle fluxes (Mullineaux, 1988; Etter and Mullineaux, 2001). For instance, suspension-feeding corals on seamounts appear to benefit from flow acceleration, and current conditions influence their distribution patterns (Genin *et al.*, 1986). According to Beaulieu (2001), suspension-feeding organisms, including a zoanthid, a tunicate, ophiuroids and anemones, preferentially colonized the tops of sponge stalks.

In our study, 12 out of 34 foraminiferal species, representing both feeding types, occurred mostly on raised nodule surfaces, i.e. elevated microhabitats (Table 1). The predominantly smooth upper surfaces of the nodules probably experience a higher flow velocity, because they project further into the benthic boundary layer (Thistle, 2003). As a result, and irrespective of whether the foraminifera were consuming suspended particles or organic material deposited on the nodule surface, the food supply is likely to have been enhanced in the summit region of the nodule. Thus location on the nodule, rather than texture, probably explains why many species were more abundant on smooth surfaces. A rough surface texture could also enhance the accumulation of fine particles and hence food availability for nodule surface feeders (Burnett and Neilson, 1983), although none of the species that we recognised exhibited a significant relationship with rough surfaces.

4.3. Other possible factors

Foraminifera may also mainly colonize raised nodule surfaces because these areas may favour propagule deposition. These may be areas where foraminiferal propagules are preferentially deposited from the water column. Biotic factors can structure attached faunal communities. For example, Beaulieu (2001) suggested that vertical zonation on sponge stalks was determined mostly by interactions among species. In the present case, however, such interactions seem to have little influence on nodule

fauna (Veillette *et al.*, in press). Biotic disturbance, including physical disruption and mortality due to predation, may also decrease larval settlement (Osman and Whitlatch, 1995). In hypoxic and sulphidic environments, foraminifera often climb up raised microhabitats in order to avoid oxygen depletion and hydrogen sulfide toxicity at the sediment-water interface (Linke and Lutze, 1993; Alve and Bernhard, 1996; Sen Gupta *et al.*, 2007). However, this is unlikely to be a factor in the well-oxygenated environment of the abyssal Pacific.

5. Conclusion

This study explored the influence of microhabitat heterogeneity and surface texture on the structure of foraminiferal assemblages attached to the surfaces of manganese nodules in the Clipperton-Clarion Fracture Zone. These assemblages may contribute substantially to overall levels of benthic diversity in this and other parts of the abyssal Pacific. Three microhabitats (raised surfaces, depressed surfaces, and nodule sides) and two surface textures (smooth and rough) were recognised. Most of the summit region of the nodules was occupied by raised microhabitats and had a smooth texture. These smooth, raised surfaces were the most colonized by many of the 34 species analysed. We suggest that current flow, which will be higher on raised surfaces, is the main environmental factor controlling the observed distribution pattern. Therefore, vertical distance from the sediment should be a good predictor of faunal cover on nodule surfaces. Given the possibility of future nodule mining, this type of

information is essential in order to establish an ecological baseline for attached nodule faunas.

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Table 1. Distribution of the 34 foraminiferal species (percent cover) according to microhabitat (raised surfaces (R), depressed surfaces (D) and sides (S)) and nodule surface texture (smooth and rough). * $\alpha=0.05$, ** $\alpha=0.01$, *** $\alpha=0.001$. Feeding types I (containing cytoplasm) and II (accumulations of stercomata, sparse cytoplasm) are indicated after the name of the species. NS: non-significant. See supplementary material of Veillette *et al.* (in press) for photograph and description of every taxon.

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

51	<i>Hormosira</i> sp. (I)	NS	NS
65	Anastomosing <i>Rhizammina</i> -like (II)	NS	NS

Figure 1.

