



Small-scale distribution of deep-sea demersal nekton and other megafauna in the Charlie-Gibbs Fracture Zone of the Mid-Atlantic Ridge

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Abstract

Videotapes from manned submersibles diving in the area of the Charlie-Gibbs Fracture Zone of the Mid-Atlantic Ridge were used to investigate the distribution of fishes, large crustaceans, epifaunal and sessile organisms, and environmental features along a series of transects. Submersibles MIR 1 and MIR 2 conducted paired dives in an area of mixed sediment and rock (beginning depth ca. 3000 m) and on a large pocket of abyssal-like sediments (depth ca. 4000 m). In the shallower area, the submersibles passed over extremely heterogeneous terrain with a diversity of nekton, epifaunal forms and sessile forms. In the first pair of dives, MIR 1 rose along the Mid-Atlantic Ridge from 3000 to 1700 m, while MIR 2 remained near the 3000 m isobath. Nekton seen in these relatively shallow dives included large and small macrourids (genus *Coryphaenoides*), shrimp (infraorder Penaeidea), *Halosaurus macrochir*, *Aldrovandia* sp., *Antimora rostrata*, and alepocephalids. The last two were more characteristic of the upper areas of the slope reached by MIR 1, as it rose along the Mid-Atlantic Ridge to depths less than 3000 m. Distributions of some forms seemed associated with depth and/or the presence of hard substrate. Sessile organisms such as sponges and large cnidaria were more likely to be found in rocky areas. The second pair of dives occurred in an abyssal area and the submersibles passed over sediment-covered plains, with little relief and many fewer countable organisms and features. The most evident of these were holes, mounds, small cerianthid anemones, small macrourids and the holothurian *Benthoctes* sp. A few large macrourids and shrimp also were seen in these deeper dives, as well as squat lobsters (*Munidopsis* sp.). Sponges and larger cnidaria were mostly associated with a few small areas of rocky substrate. Holes and mounds showed distributions suggesting large-scale patterning. Over all dives, most sessile and epifaunal forms showed clumped distributions. However, large holothurians and large nekton often had distributions not significantly different from random.

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1. Introduction

Submersibles have extended the range at which we can directly observe the natural history of deep-sea organisms, in particular their behavior (e.g., Cohen, 1977; Drazen et al., 2003; Uiblein et al., 2003) and small-scale distribution (e.g., Grassle et al., 1975; Smith and Hamilton, 1983; Kaufmann et al., 1989). Submersibles are especially useful

when investigating deep-sea regions of rough topography such as ridges and volcanic island slopes (e.g., Chave and Malahoff, 1998), hydrothermal vents (Gebruk et al., 2000) and in the open ocean (Vinogradov, 2005). Interactions of deep-sea organisms with their environment can be documented from videotapes taken from submersibles as well as by direct observations (Felley and Vecchione, 1994; Levin et al., 1994), providing insight into the environmental variables that affect the distribution of these forms.

The MAR-ECO pilot project of the Census of Marine Life provided an opportunity for a short series of submersible dives in the Charlie-Gibbs Fracture Zone to

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explore and photo-document the demersal nekton and benthic macrofauna in this very deep area of the Mid-Atlantic Ridge. The Charlie-Gibbs Fracture Zone is 'a major left lateral offset in the Mid-Atlantic Ridge at about 52°30'N' (Fleming et al., 1970). Our submersible dives were the first in that area and produced the videotapes and observations that we discuss here. We analyzed patterns of distributions of organisms, comparing the different dives and comparing habitats seen within each dive. Our primary goal was to examine the small-scale distribution of nekton, but for comparison we also conducted similar analyses of epibenthic megafauna and signs of infauna.

2. Materials and methods

2.1. Dives

Dives using the manned submersibles MIR 1 and MIR 2 of the Russian Academy of Sciences were conducted in the northwestern region of the Charlie-Gibbs Fracture Zone in June 2003 during a trans-Atlantic crossing of the R.V. *Akademik Mstislav Keldysh*. The dives were conducted in tandem (using both submersibles).

The first tandem set was on 11 June 2003 at 52°58'N; 35°01'W in an area where the bottom rose from a depth of about 3000–1000 m. Both MIR 1 and MIR 2 reached the bottom at ca. 3100–3000 m and spent about 8 h each on the bottom. Both submersibles passed over extremely variable topography, including areas of flat bottom covered with sediments, slopes with both rock and areas of sediment, rocky slopes and walls. MIR 1 followed the slope up to a depth of ca. 1700 m. The transect followed by MIR 2 proceeded along an isobath near 3000 m at the base of the slope.

The second set of dives occurred on 13 June 2003 at 52°47'N; 34°46'W in a large pocket of sediment similar to an abyssal plain at 4200–4500 m. The bottom was mostly flat sediment, with a few rocks and/or clumps of mud. The submersibles each spent ca. 7 h on the bottom. Videotapes were recorded during the period when each submersible was near the bottom.

2.2. Measurements and analyses

We measured environmental variables and counted megafaunal forms including nekton, epifauna, and infaunal signs (those benthic features that have been referred to as lebensspuren, e.g., Kaufmann et al., 1989). Counts were made from 1-min segments of the tapes, whenever the submersible was near the bottom and traveling slowly (ca. 1 m/s). This is similar to the visual fast count method shown by Strong et al. (2006) to be an effective way to quantify epibenthic organisms. The environmental variables recorded are listed in Table 1. Depth (m) was recorded whenever the value was noted by the observers either during or prior to the 1-min segment (the frequency that depth was stated varied by observer, and also by dive,

since some of the dives were over extremely fiat topography). The percentage of sediment was an estimate of the proportion of the bottom traversed during the 1-min segment that was covered with sediment. Other variables were counts of particular features. Holes were large and were distinguished from 'fairy rings' (Gage and Tyler, 1991), which consisted of sets of smaller holes forming a ring. Mounds were large, and were distinguished from large holothurian casts. One type of cast that we could identify specifically was a spiral cast formed by enteropneusts (Holland et al., 2005). Several morphotypes of sponges were counted separately. Tube sponges were single tubes rising from a base, while finger sponges had several to many tubes arising from a common base. Round sponges were essentially a short, fat tube, and round sponges that were bright yellow were counted separately. We also counted the remains of dead sponges. We counted morphotypes of sessile colonial cnidarians. Single stalks were called 'sea whips', those with a few branches were called 'branched gorgonians', while those with densely packed branches were called 'sea fans'. Several different types of echinoderms were counted, including stalked crinoids, feather stars (unstaked crinoids), brisingid stars, asteroids and various identifiable forms of holothurians. In MIR 1's deep dive, many small holothurians of the genus *Peniagone* were seen covering the bottom. These were too dense to count, so the occurrence of these was coded 1 (present) or 0 (absent) for segments in this dive. Finally, we counted gastropods.

Nektonic organisms were classified into morphological types, some of which could consistently be identified to genus or species. For example, some large macrourids could confidently be identified as *Coryphaenoides (Nematonurus) armatus*. Not all macrourids could be identified consistently to species; they have therefore been lumped into the morphotype 'large macrourids'. A similar 'taxon' included all small macrourids. In the analyses that follow, such morphotypes, or 'taxa' shall be the units of analysis and interest. Supplementary information provides images of nekton and environmental features for each dive.

Data from transects covered by the submersibles were described and analyzed separately. Statistical analyses were carried out with SYSTAT 11 (2006).

3. Results

3.1. Nekton forms seen

Table 2 lists the numbers and frequencies of different nekton forms seen in the dives. Small macrourids were the most abundant, and may represent more than a single species. They were most abundant and more frequent in the shallower dives, occurring in almost 50% of the 1-min segments. They were much rarer in the deep dives, occurring in one-quarter to one-third of the 1-min segments. Large macrourids were the next most common forms, and represented more than a single species. Those

Table 1

Means and standard deviations (in parentheses) of environmental variables recorded and features and organisms counted from 1-min segments of videotape taken by the MIR 1 and MIR 2 submersibles in dives in two different areas of the Charlie-Gibbs Fracture Zone of the Mid-Atlantic Ridge

Variable	Shallow		Deep	
	MIR 1 (n = 183)	MIR 2 (n = 87)	MIR 1 (n = 105)	MIR 2 (n = 90)
Depth (m)	3150–1740	3015–3000	4493–4361	4500–4200
% Sediment (95% CI)	70.4 (61.7–90.3)	77.8 (69.4–84.9)	100 –	100 (99.9–100)
Holes	0.62 (1.282)	0.98 (1.294)	1.36 (1.257)	3.59 (2.652)
Fairy rings	0.27 (0.784)	0.47 (1.274)	0.26 (0.621)	0.53 (0.939)
Mounds	0.22 (0.617)	0.68 (1.418)	28.5 (13.678)	18.7 (20.52)
Spirals	0.66 (1.300)	0.18 (0.518)	0.02 (0.137)	0.03 (0.235)
Sponges				
Dead	0.21 (0.995)	0.07 (0.397)		0.02 (0.211)
Tube	2.80 (5.920)	0.12 (0.387)	0.05 (0.322)	0.16 (0.652)
Encrusting	1.21 (2.443)	0.16 (0.525)		
Finger	0.44 (1.141)	0.12 (0.387)		0.08 (0.430)
Vase	1.14 (2.886)	0.12 (0.355)		0.06 (0.275)
Round	0.57 (2.361)	0.07 (0.367)		
Yellow	0.30 (1.237)	0.02 (0.151)		
Cnidaria				
Sea fans	0.10 (0.616)	0.10 (0.571)		
Gorgonians	0.16 (0.720)	0.44 (1.148)		
Sea whips	0.45 (1.147)	1.67 (2.769)		
Small anemones		0.05 (0.211)	0.83 (1.105)	1.66 (2.224)
Large anemones	0.01 (0.104)	0.02 (0.151)	0.01 (0.098)	0.07 (0.328)
Echinoderms				
Stalked crinoids	0.27 (0.681)	0.37 (0.764)		
Feather stars		0.44 (1.318)		
Brisingid stars	0.04 (0.192)	0.36 (1.034)		
<i>Benthothuria</i> sp.	0.07 (0.248)	0.84 (1.493)		
<i>Bentbodytes</i> sp.	0.02 (0.147)	0.07 (0.297)	0.08 (0.267)	0.08 (0.269)
<i>Peniagone</i> sp.	1.20 (3.509)	0.20 (0.662)		0.10 (0.475)
Green holothurian	0.03 (0.163)			
<i>Peniagone</i> sp. (presence)				0.61 (0.490)
Gastropod	0.08 (0.376)	0.03 (0.184)		
Nekton				
Small macrourids	0.80 (1.517)	1.25 (2.354)	0.22 (0.460)	0.63 (0.999)
Large macrourids	0.17 (0.443)	0.23 (0.564)	0.05 (0.255)	0.14 (0.412)
<i>Halosauropsis macrochir</i>	0.08 (0.339)	0.10 (0.342)		
<i>Aldrovandia</i> sp.		0.05 (0.260)		
<i>Antimora rostrata</i>	0.04 (0.230)			
<i>Bathysaurus</i> sp.	0.01 (1.04)	0.03 (0.184)		
Alepocephalids	0.04 (0.219)			
Shrimp	0.11 (0.405)	0.14 (0.347)	0.11 (0.320)	0.03 (0.181)
<i>Munidopsis</i> sp.		0.01 (0.107)	0.04 (0.192)	0.03 (0.181)

The depth range is provided for depth, 'n' is the number of usable 1-min transect segments on each dive. Means and 95% confidence intervals of percentage of sediment were calculated from arcsine transformed values of percentages.

seen clearly enough to identify included the abyssal grenadier *Coryphaenoides (Nematonurus) armatus* and probably the ghostly grenadier *Coryphaenoides (Chalinura) leptolepis* (the most abundantly caught macrourid of the subgenus *Chalinura* in the eastern Atlantic, Merrett et al., 1991). Both small and large macrourids were usually seen hovering over the bottom, and sometimes in contact with the bottom. Large macrourids (especially *C. armatus*) often approached the submersibles closely, investigating them. Macrourids large and small were the only fishes seen in the

deeper dives in the 1-min segments analyzed. A bathysaurid species (suspected to be *Bathysaurus mollis* because the sighting was deeper than 3000 m; e.g., Sulak et al., 1985; Haedrich and Merrett, 1988) was seen by MIR 2 in its deep dive but was not included in the analysis (for images of this individual see Supplementary Information).

Other fishes were seen during the two shallower dives, most commonly the halosaur *Halosauropsis macrochir*. This form was usually seen on the bottom with its belly on the substrate and its tail extended perpendicular to the

Table 2
Nekton counted from 1-min segments of videotape taken by the submersibles MIR 1 and MIR 2 during dives in two different areas of the Charlie-Gibbs Fracture Zone of the Mid-Atlantic Ridge

Taxon	Shallow		Deep	
	MIR 1 (n = 183)	MIR 2 (n = 87)	MIR 1 (n = 105)	MIR 2 (n = 90)
Small macrourids	147 (70)	109 (40)	23 (21)	57 (34)
Large macrourids	31 (26)	20 (15)	5 (4)	13 (11)
<i>Halosauropsis macrochir</i>	14 (11)	9 (8)		
<i>Aldrovandia</i> sp.	1 (1)	4 (3)		
Synphobranchid eel	1 (1)	1 (1)		
<i>Antimora rostrata</i>	8 (7)			
<i>Bathysaurus</i> sp.	2 (2)	3 (3)		
Ophidioid	2 (2)	1 (1)		
Alepocephalids	7 (6)			
Shrimp	20 (15)	12 (12)	12 (12)	3 (3)
Spider crab	1 (1)			
<i>Munidopsis</i> sp.		1 (1)	4 (4)	3 (3)
Pycnogonid	1 (1)			
Cirrate octopod	1 (1)	1 (1)		

Given are total numbers of individuals of a taxon seen in each dive and (in parentheses) number of 1-min segments in which a taxon was seen.

bottom. Another halosaur was a very skinny, pale form, identified as *Aldrovandia* sp. This form was usually seen with its lower jaw touching or close to the bottom, its body rigidly straight and extended up at an angle to the bottom. Bathysaurs, again suspected to be *B. mollis* (depths being deeper than 3000 m) were also seen by both MIR 1 and MIR 2, always motionless on the bottom. Several alepocephalids, blue hake *Antimora rostrata* and *Coryphaenoides rupestris* (classified as a large macrourid) were seen by MIR 1 during the shallower dive, as the submersible rose with the bottom. Alepocephalids typically were seen swimming several meters above the substrate, while individuals of *A. rostrata* were seen actively swimming close to the bottom. MIR 1 found two ophidioid individuals and a single synphobranchid eel, all swimming a meter or two over the substrate. MIR 2 encountered one individual each of these forms.

Invertebrate nekton were seen in all dives. Shrimp (infraorder Penaeidea) were the most common. The squat lobster *Munidopsis* sp. was seen in the deeper dives, and a single individual was seen by MIR 2 at the 3000 m depth. During the shallower dives, a spider crab and a pycnogonid were seen by MIR 1, both walking on the bottom, and in their shallow dives, MIR 1 and MIR 2 each saw a cirrate octopod hovering in the water column.

3.2. Description of dives

On its shallow dive, MIR 1 rose more than 1500 m, from below 3000 m to almost 1700 m (Table 1). The submersible traversed a variety of topographic features including flat sediment areas, areas of sediment with rocky outcroppings, rocky slopes, and steep rocky cliffs. The means for environmental variables recorded in the 1-min segments are presented in Table 1, and show the variability of the environment. In areas with sediment were found such

features as holes, mounds and casts such as the spiral casts of enteropneusts, as well as the holothurians *Benthothuria* sp., *Benthodytes* sp., and *Peniagone* sp. Areas with rock were characterized by attached sessile invertebrates such as sponges and cnidaria. MIR 1 traversed an area with numerous sea whips, branched gorgonians and sea fans (a cnidarian garden, where up to 16 were seen in a 1-min segment) and also an area with many sponges (a sponge garden, with up to 80 sponges seen in a 1-min segment).

3.3. Analyses of distributions

Means and standard deviations of numbers (Table 1) and the coefficients of dispersion that can be calculated from them (Sokal and Rohlf, 1981; Ludwig and Reynolds, 1988) suggested that most forms showed clumped (contagious) distributions, with more 1-min segments with high counts and more with very low (0) counts than expected for a random distribution. The coefficient of dispersion can be tested against a null hypothesis of random (Poisson) distribution of numbers using a χ^2 test. For 1-min segments from the MIR 1 shallow dive, we calculated χ^2 statistics for counts of 25 of the benthic features, sessile invertebrates, and nekton, using a Bonferroni correction for tables of tests (Rice, 1989). We excluded forms or features with low numbers (counts < 6), which in this dive excluded counts of large anemones, *Benthodytes* sp., the green holothurian and bathysaurs. The only forms that did not show a clumped distribution were large macrourids and the holothurian *Benthothuria* sp.

It was apparent that for some forms, clumped distributions were due to their occurrence in particular depth ranges, and also due to the different habitats traversed in each depth range. For the MIR 1 shallow dive (the only one that traversed a wide range of depths) we therefore divided up the 1-min segments by depth into four groups

Table 3

Means and standard deviations (in parentheses) of environmental variables recorded and features and organisms counted from 1-min segments of videotape from MIR 1's shallow dive

Variable	Depth			
	> 3000 m (n = 36)	3000–2500 m (n = 68)	2501–2000 m (n = 63)	< 2000 m (n = 21)
% Sediment (mean) (95% CI)	72.9 (53.4–100)	95.7 (92.0–100)	31.4 (39.0–48.0)	48.4 (30.5–64.4)
Holes	0.68 (1.077)	1.25 (1.740)	0.08 (0.326)	0.10 (0.436)
Fairy rings	0.24 (0.682)	0.60 (1.122)		
Mounds	0.64 (1.018)	0.24 (0.601)	0.06 (0.304)	
Spirals	0.64 (0.985)	1.46 (1.723)	0.02 (0.126)	
Sponges				
Dead	0.13 (0.341)		0.49 (1.625)	0.14 (0.478)
Tube	0.29 (0.588)		6.11 (8.619)	5.62 (2.958)
Encrusting	0.26 (0.445)		2.56 (3.222)	2.48 (2.839)
Finger	0.71 (1.039)		0.87 (1.661)	0.14 (0.478)
Vase			2.73 (4.289)	1.76 (1.998)
Round			0.93 (3.583)	2.14 (2.516)
Yellow			0.64 (1.937)	0.71 (1.140)
Cnidaria				
Sea fans	0.52 (1.387)		0.05 (0.280)	
Gorgonians	0.94 (1.548)			
Sea whips	1.61 (2.155)	0.06 (0.382)	0.30 (0.586)	0.48 (0.873)
Large anemones	0.03 (0.180)		0.02 (0.126)	
Echinoderms				
Stalked crinoids	0.74 (1.182)	0.03 (0.170)	0.40 (0.661)	
Brisingid stars		0.03 (0.170)	0.08 (0.272)	
<i>Benthothuria</i> sp.	0.10 (0.301)	0.13 (0.341)		
<i>Benthydotes</i> sp.	0.03 (0.180)	0.04 (0.207)		
<i>Peniagone</i> sp.	0.03 (0.180)	3.29 (5.152)		
Green holothurian		0.07 (0.263)		
Gastropod		0.15 (0.466)		
Nekton				
Small macrourids	0.52 (0.926)	1.16 (1.767)	0.79 (1.598)	0.10 (0.436)
Large macrourids	0.13 (0.341)	0.18 (0.487)	0.22 (0.490)	0.05 (0.218)
<i>Halosauropsis macrochir</i>	0.06 (0.250)	0.13 (0.486)	0.05 (0.215)	
<i>Antimora rostrata</i>		0.04 (0.207)	0.05 (0.280)	0.10 (0.402)
Alepocephalids			0.05 (0.280)	0.19 (0.402)
Shrimp	0.19 (0.477)	0.16 (0.536)	0.05 (0.215)	

This dive rose along a ridge from 3150 to 1750 m. 'n' is the number of 1-min segments in a depth range. Means and standard deviations for these forms are given for different depth ranges. Means and 95% confidence intervals of percentage of sediment were calculated from arcsine transformed values of percentages.

(Table 3). When MIR 1 was below 3000 m, it traversed a heterogeneous bottom with expanses of sediment and also large areas of rocky outcrops. Coefficients of dispersion were assessed for counts in 1-min segments below 3000 m, Bonferroni corrections were again applied, and the forms excluded because of low counts were dead sponges, large anemones, the three holothurians seen at that depth, large macrourids, and *H. macrochir*. Below 3000 m, clumped distributions were seen for the cnidaria and stalked crinoids (which were abundant, Table 3), forms strongly associated with the rocky bottom areas. Of the soft-bottom features, only the fairy rings showed a clumped distribution. None of the other counts or features showed significant deviations from random distributions.

MIR 1 traversed soft bottom environments from 3000 to 2500 m, with very few rocks. No sponges, branched gorgonians or sea fans were seen, and stalked crinoids, brisingid stars and sea whips were too few to analyze. Also excluded from further analysis were *Benthydotes* sp. and *A. rostrata*. In this depth range, large numbers of *Peniagone* sp. were seen, up to 23 in a 1-min segment. Counts of holes, fairy rings, spirals, *Peniagone* sp., small macrourids, *H. macrochir* and shrimp indicated clumped distributions. Other forms did not show significant deviations from random distributions.

From 2500 to 2000 m, the substrate was rocky with patches of sediment. Soft-bottom features such as holes and mounds were few and were excluded from analysis. No fairy rings were seen. Sponges were quite abundant

(Table 3) and all forms had significantly clumped distributions. Stalked crinoids showed a significantly over-dispersed distribution, the only such distribution seen in these dives. Other than sea whips (which were apparently randomly distributed), cnidarian forms were few and were not analyzed, and none of the holothurian forms were seen. The only nekton seen in enough numbers for analysis were small macrourids and large macrourids. Small macrourids had a clumped distribution, while large macrourids showed no significant deviation from random distribution.

Above 2000 m, the substrate was very rocky and rugged. Sponges were abundant. While there were areas of sediment, the only soft-bottom features counted were two holes that appeared in a single 1-min segment. Finger sponges and the remains of dead sponges were also rare in this depth range. No stalked crinoids were seen, and none of the large holothurians we counted were found in this range. Sea whips were the only type of sessile cnidarian seen and were distributed apparently at random. None of the nekton forms appeared in numbers large enough to allow analyses of distribution. Encrusting, vase, and round sponges showed significantly clumped distributions, while tube sponges and yellow sponges had distributions that were not significantly different from random.

MIR 2, traveling along the 3000 m isobath, also found the bottom to be mixed sediment and rock and the topography to be extremely variable. Like MIR 1, MIR 2 encountered a range of topographic features including flat sediment areas, areas of sediment with rocky outcroppings, rocky slopes, and steep rocky cliffs. The means for environmental variables recorded in the 1-min segments are presented in Table 2, and illustrate the variability of the environment. In areas with sediment were found such features as holes, mounds and casts such as the spiral casts of enteropneusts, as well as the holothurians *Benthothuria* sp., *Benthodytes* sp., and *Peniagone* sp. Areas with rock were characterized by attached sessile invertebrates such as sponges and cnidaria. This dive encountered an area of densely distributed cnidaria (up to 19 sea whips, gorgonians and sea fans in a 1-min segment), but did not encounter the type of dense sponge garden that was seen by MIR 1. Though individuals of *Peniagone* sp. were seen, no dense aggregations were seen by MIR 2.

Most of the forms commonly encountered by MIR 2 along the 3000 m isobath had clumped distributions. Dead sponges, round sponges and yellow sponges were not often seen, and were not included in these analyses. Anemones (both large and small), gastropods and the holothurian *Benthodytes* sp. were also excluded from analysis. Of the soft-bottom features, holes, mounds, fairy rings and spirals all had clumped distributions, reflecting their occurrence in the 1-min segments with much sediment. Also characteristics of these areas were the holothurians *Benthothuria* sp. and *Peniagone* sp. and both forms had clumped distributions. Sea fans, branched gorgonians, sea whips, brisingid seastars and stalked crinoids were more likely to be found in rocky areas, and they all demonstrated clumped

distributions. Feather stars co-occurred with cnidaria, and showed a clumped distribution. Results were not as clear-cut for sponges. Encrusting sponges were strongly associated with the rocks they encrusted, and had a clumped distribution. The distributions of tube sponges, vase sponges and finger sponges did not differ significantly from random. Of the nekton forms, small macrourids, large macrourids, *H. macrochir* and shrimp were common enough to examine distributions. Only small macrourids showed a distribution that was significantly different from random, and they showed a clumped distribution.

The second set of dives occurred in a much deeper area with habitats more characteristic of the abyssal plain. The environment was almost entirely soft bottom with many mounds and holes. There were very few hard-substrate areas. Both submersibles traversed generally similar areas, though MIR 2 did encounter an area with rocks and accompanying sessile organisms. In the areas traversed by both submersibles, fairy rings, mounds, and small cerianthid anemones had significantly clumped distributions. *Benthodytes* sp. had a distribution that did not differ significantly from random. In the MIR 1 deep dive, holes were distributed apparently at random, while in the area traversed by MIR 2, they were significantly clumped. Conversely, small macrourids were distributed in clumped fashion as seen by MIR 2, and were distributed apparently at random in the area covered by MIR 1. Shrimp (distribution apparently random) were seen by MIR 1, but not by MIR 2. For most of its dive, MIR 2 passed over a carpet of very small holothurians (*Peniagone* sp.) too numerous to count. These were seen in 61% of the 1-min segments. Large *Peniagone* sp. individuals were seen by MIR 2, and had a clumped distribution. MIR 2 passed a rocky area with tube and finger sponges. These two forms showed clumped distributions, as would be expected. Finally, MIR 2 saw several large macrourids, distributed apparently at random.

During all dives, data collection from videotape was interrupted at various times when the submersible stopped to collect samples or moved too high above the bottom to allow successful counts. Thus, contiguous 1-min segments were usually limited to single minutes to up to 7 min at a time, with interruptions of 1 to several minutes. In the MIR 1 deep dive, we were able to obtain 37 min of uninterrupted videotape. We used these data to calculate serial correlations between adjacent 1-min segments, to see if counts from one segment could be used to predict counts in the next segment. For this data subset, counts of holes, fairy rings, mounds, small anemones, *Benthodytes* sp., and large and small anemones were subjected to autoregressive integrated moving average analysis (ARIMA, Systat 11) (Ripley, 1981). Only holes and mounds showed significant serial correlations (0.72 and 0.97, respectively) of counts transformed as logarithm (count+1). Inspection of the data showed that during the 37-min period, the submersible moved from an area with relatively more holes and mounds to an area with fewer (averages of 1.6 holes and

41.7 mounds per 1-min segment in the first 10 min, 0.2 holes and 26.5 mounds per 1-min segment in the last 10 min).

4. Discussion

The area of the Charlie-Gibbs Fracture Zone shows similarities to other surveyed deep-ocean habitats, but differences as well. The cnidaria and sponge morphotypes seen were those characteristics of deep-ocean habitats. However, the densities of sessile cnidaria in the shallower dives were much less than have been documented in much shallower areas of Atlantic continental slopes (Gass and Willison, 2005; Reed et al., 2006; Roberts et al., 2006). The fishes found in the shallower of the two sets of dives were characteristic of Haedrich and Merrett's (1988) 'rise' fauna, found along continental slopes at depths <4500 m, while the few forms seen in the second set of dives were those they associated with the abyssal plain (depths >4500 m). The organisms counted were sparse in both sets of dives. In the shallower dives, there was an average of 9 countable organisms (sponges, cnidaria, epifauna, and nekton) per 1-min segment, ranging from 0 to 81 organisms per segment. The deeper set of dives covered areas much poorer in biota: an average of 2 countable organisms per segment, ranging from 0 to 13. Note that this count does not include the carpet of tiny *Peniagone* sp. seen in 55 of the 90 1-min segments from MIR 2, dive 2. The shallower set of dives found a more diverse fauna than the deeper set: 14 nektonic forms vs. 4, 6 morphotypes of sponges vs. 3, 4 types of sessile cnidaria vs. 2. No cnidarian gardens were found in the deeper dives, although a sponge garden was found on a patch of hard substrate. Interestingly, during the second (deeper) pair of dives, the submersibles both traversed similar habitats and depths, but the faunal observations differed substantially between the submersibles.

The lack of hard substrate in the deeper areas probably accounts for the fewer numbers of sessile forms such as sponges and sessile cnidaria. In the deeper dives, the few areas of rocky substrate were colonized by sponges and other sessile forms. However, even in shallower dives, presence of hard substrate was not a guarantor of finding sessile forms. In the shallow dives, there were 51 1-min segments with little sediment (<15% coverage), of which 21 had 5 or fewer sessile organisms counted in the segment. None of these low-sediment samples had any of the soft-bottom features such as holes, mounds, spirals or fairy rings. Apparently, fairly large patches of sediment are necessary for the animals making these lebensspuren. Conversely, large expanses of soft substrate did not guarantee high counts of soft-bottom features. In the shallow set of dives, 107 1-min segments had 85% coverage of sediment or more. In 10 segments, there were no soft-bottom features counted, and 77 had 5 or fewer soft-bottom features. Much like the deeper dives, hard substrate within these segments was colonized: in the 107 high-

sediment areas, 1 or more sessile organisms were found in 17 1-min segments.

We tested hypotheses concerning patterns of distribution of the various features and organisms. Clumped or random patterns of distribution characterized the counts of both features and forms, with only a single example of an over-dispersed distribution (stalked crinoids in the MIR 2 shallow transect). Some patterns were easily explained. The clumped distributions of sponges and cnidaria could be accounted for by their requirements for hard substrate. However, as mentioned above, this could not be the entire answer, as these forms did not heavily colonize many areas rich in hard substrate. Of the soft-bottom features, fairy rings and the fecal spirals formed by enteropneusts had consistently clumped distributions, perhaps reflecting variability in substrate quality. Holes and mounds were often distributed in clumped fashion, but an investigation of contiguous 1-min segments during the MIR 1 deep dive suggested that there were larger-scale processes influencing distribution of holes and mounds, as there was significant autocorrelation in these segments: numbers of holes and mounds in one segment were predictable from counts in adjacent segments. For the other counted features and taxa, 1-min segments seemed to represent independent samples.

Clumped patterns of distribution were the rule for soft-bottomed features in sediment-filled areas and for sessile organisms in rocky areas. Distributions of nekton and also of large holothurians were less easy to characterize. The blue hake *A. rostrata* and alepocephalids were seen only in the shallower parts of the ridge covered by MIR 1, coinciding with their known depth ranges (Merrett et al., 1991). Shrimp and the squat lobster *Munidopsis* sp. were more often seen below 3000 m. Large macrourids as a group tended to have distributions not significantly different from random. The halosaur *H. macrochir* had a clumped distribution in the area between 3000 and 2500 m covered by MIR 1, but was apparently distributed at random in the area covered by MIR 2. Small macrourids usually had clumped distributions. Some large holothurians tended to distribute apparently at random (*Benthodytes* sp. in the deep dives, *Benthothuria* sp. in the shallower dive between 3000 and 2500 m), while others showed clumped distributions (i.e., large *Peniagone* sp.).

The four MIR dives into the Charlie-Gibbs Fracture Zone are the first for that area and include the dive in MIR 1 reported by Vinogradov (2005). We were surprised by the prevalence of soft substrate on this mid-ocean ridge, as well as by the patchy high abundance of some fauna, such as the 'gardens' of sponges. We found evidence of spatial patterns ranging from depth-related structure to relatively small-scale patterns likely associated with habitat requirements and habitat quality. We also found some evidence of patterns on intermediate scales, as in the distribution of holes and mounds across large expanses of substrate. Some of the larger and more mobile forms seemed to be distributed in random fashion. These investigations of

distributional patterns suggest that there are interesting associations between deep-sea organisms and their environment, and also among the organisms themselves. Such observations as these can only begin to unravel the complexity that may exist in these deep-sea areas.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.dsr2.2007.09.021.

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