THE BENTHIC MACROINFAUNA OF A MUDDY DEPOSITIONAL BASIN IN THE NORTHWESTERN GULF OF MAINE

By

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Abstract

This communication begins to fill an identified gap in our knowledge of the Gulf of Maine marine benthic ecosystem. The benthic macroinvertebrate fauna of a muddy depositional basin in the northwestern Gulf of Maine was sampled with a 0.04 m^2 van Veen grab at nine stations in November 2010. The 100 m deep area was found to be physically homogeneous and inhabited by a limited benthic invertebrate community. Forty taxa from four phyla were identified and density averaged 1,055 individuals/m^2. Species accumulation curves suggest that additional sampling would result in a total of 75 species. Deposit-feeding polychaetes dominated the fauna qualitatively and quantitatively and accounted for over 90% of the community with the overall dominant being *Paraonis gracilis*. The community can be considered Boreal in its zoogeographic affinity. Multivariate analyses indicated that there was no significant difference between any of the stations. Comparisons with two previous mid-depth to deep-water studies indicate that soft bottom communities in the Gulf of Maine are similar in terms of quantitative parameters but differ qualitatively.

Introduction

The Gulf of Maine is one of the world's most productive fishing grounds and best-studied continental seas. Since the last glaciation, the Gulf has undergone a rapid and dynamic geological and oceanographic evolution that has produced the rich and intricate ecological system that we witness today (Bousfield and Thomas 1975, Shaw *et al.*, 2002). Interest in the benthic macrofauna of the Gulf began early and several classic investigations qualitatively documented the high invertebrate species richness of the region (Kingsley 1901; Mighels 1843; Stimpson 1853; Verrill 1872, 1874; and Webster and Benedict 1887; others). In more recent times, quantitative studies on the Gulf's macroinfauna have concentrated on the region's coastal embayments and estuaries (Hale 2010; Larsen 1979; Larsen and Gilfillan 2004; many others). Quantitative studies on the infauna of the offshore waters have been more limited and data on mid-depth depositional patches are especially lacking (Lewis Incze, Gulf of Maine Area Program, Census of Marine Life, personal communication, 2009). Two previous studies are relevant. Theroux and Wigley (1998) summarize the results of a series of cruises undertaken between 1956 and 1965. They report on 303 samples from the Gulf of Maine. Only nine of these, however, are from fine-grained sediments in less than 120 m depth in the northwest quadrant of the Gulf of Maine (Theroux *et al.* 1982). In the early 1970's, Rowe *et al.* (1975a) investigated the benthos of the deepwater Wilkinson and Murray Basins (280 m) in the west central Gulf.

In 2010 we had the opportunity to survey the benthic macroinfauna of a mud filled depression in search of an area suitable for the disposal of estuarine dredged material. Such information is of increasing interest to environmental managers not only because data are needed to evaluate the impacts of dredged material disposal but also the effects of the developing offshore wind power projects and the advent of large-scale offshore aquaculture. In this communication we describe the benthic infaunal community inhabiting a muddy depositional basin in 100 m of water between Jeffreys Ledge and the coast of southern Maine.

Methods and Materials

Sampling occurred at nine stations on November 1, 2010 within a 780m radius circle approximately 14 km east northeast of the Isles of Shoals in the northwestern Gulf of Maine (Fig. 1). At each station, samples for fauna and sediment analyses were retrieved using a 0.04 m^2 modified van Veen grab. The faunal samples were sieved on a 0.5 mm screen and fixed in 10% formalin solution with the vital stain Rose Bengal. In the laboratory, the formalin was removed from the samples by gentle washing on a 0.5 mm sieve and the samples were preserved in 70% ethanol. The benthic macrofauna in each sample was separated from the limited inorganic debris and identified to the lowest practical taxonomic level, usually the species level, and enumerated. Synonymies were made current using the World Register of Marine Species (www.marinespecies.org/). Sediment grain size was analyzed using sieve and hydrometer techniques following ASTM D 422-63 protocols.

Zoogeographic affinities and feeding types were determined using standard references such as Pettibone (1963), Gosner (1971), Bousfield (1973), Fauchald and Jumars (1979) and Watling (1979) as well as several websites including the World Register of Marine Species (www.marinespecies.org/).

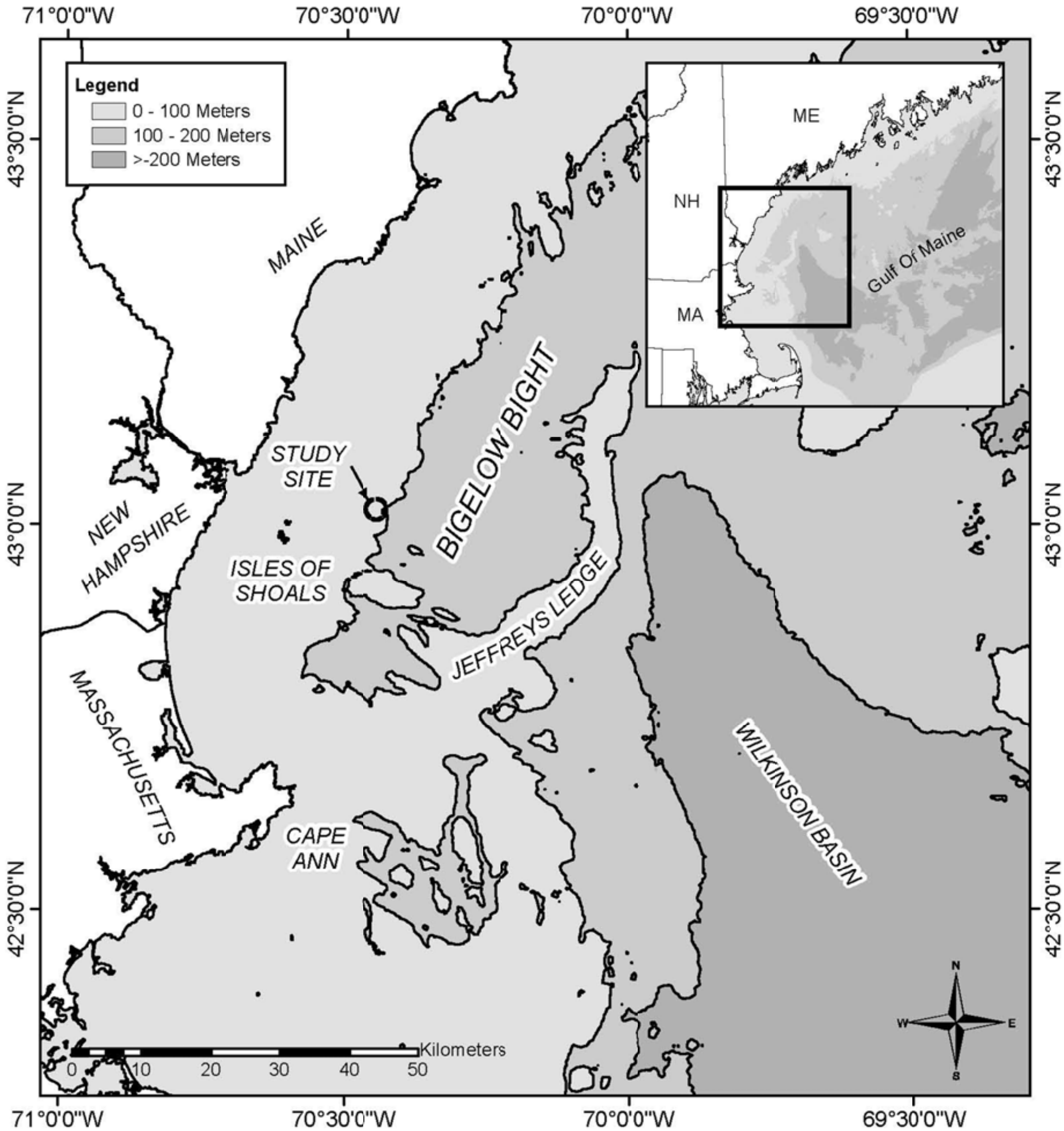

Fig. 1. Chart of the northwestern Gulf of Maine illustrating the sampling site and its relationship to major geographical features.

The numerical data were analyzed using the statistical package PRIMER v6 (Clarke and Gorley 2006). Univariate community structure analyses performed include density (N), species richness (S), Shannon diversity (H′, base *e*) and Pielou's Evenness (J′). The faunal relationships were also investigated using numerical classification and ordination. Species data were square root transformed to moderate the influence of abundant species. A hierarchical agglomerative classification scheme was employed using the Bray-Curtis similarity index. The group-average linking method was used to produce a dendrogram of sample relatedness and a 2-dimensional ordination of stations was accomplished using the non-metric multidimensional scaling (MDS) technique found in PRIMER. Multivariate analyses were limited to species that occurred at two or more stations.

Species accumulation curves were utilized to assess the adequacy of the sampling and to estimate the unknown biodiversity of the northwestern Gulf of Maine community. The Chao 2 formula was chosen. This is a presence-absence measure that relies on the number of species that occur in one sample and the number that occur in two samples to calculate an estimate of the maximum number of species expected (Colwell and Coddington 1994).

Results

Abiotic factors

Descriptive details of station location, depth and sediment type are presented in Table 1. The stations were in close proximity to one another; the maximum distance between any two stations being about 1.5 km. Depth was rather uniform as all stations occurred at depths between 95 and 100 m. The sediments can be characterized as fine grained. Seven of the nine stations exhibited silt/clay content in excess of 96%. Two stations, B and H, were somewhat coarser with silt/clay contents of 79.8 and 92.7%, respectively. The non-silt/clay fractions of all the samples consisted of sand. Moist, brown silty clay is the visual description of all of the samples. The Folk classification of these sediments is silt (Folk 1968).

Faunal composition, abundance and dominance

A total of 40 taxa from four phyla were identified from the nine stations (Table 2). Thirty-two taxa were identified to the species level. The number of taxa at the stations ranged from 7 to 19 with a mean of 10.7 (Table 3). The fauna was dominated by polychaetes that accounted for 25 of the 40 taxa or 62.5% of the fauna. Percentage representation of other taxa was 17.5% Arthropoda, 15% Mollusca and 5% Rhynchocoela. No echinoderms or colonial species were encountered.

Table 1. Location and environmental characteristics of the nine benthic stations from the northwestern Gulf of Maine.

Station	Latitude	Longitude	Depth (m)	% Sand	% Silt & Clay
A	43.028412	-70.45389	97.2	2.1	97.9
B	43.028527	-70.43678	95.7	20.2	79.8
C	43.023773	-70.45215	96.0	2.4	97.6
D	43.024674	-70.44097	96.9	3.4	96.6
E	43.021569	-70.44474	96.3	3.7	96.3
F	43.017613	-70.43885	97.8	2.4	97.6
G	43.018689	-70.45004	96.6	3.9	96.1
H	43.014840	-70.43541	100	7.3	92.7
I	43.015181	-70.45402	95.4	2.1	97.9

Density at the stations ranged from 400 to 1,950 individuals/m^2 with a mean density of 1,055/m^2 (Table 3). The numerical dominance of polychaetes was very pronounced. Polychaetes represented 93.2% of all individuals. Percentage of total individuals of Mollusca, Arthropoda and Rhynchocoela were 2.6, 2.1 and 2.1 percent, respectively. Numerical dominance of the most abundant species ranged from moderate to high (Table 3). The percentage of the fauna represented by the dominant species ranged from 14 to 61%. At eight of the nine stations the dominant species was the deposit feeding polychaete *Paraonis gracilis* that accounted for over 40% of the individuals at four of the nine stations. The only other species obtaining dominant status was another deposit feeder, the polychaete *Cossura longocirrata*.

Most of the Shannon informational diversity values (base log *e*) were constrained within a rather narrow range with low species richness (Table 3). Station C was something of an outlier because of low species richness and high dominance of *Paraonis gracilis*. The mean diversity for all stations was 1.811 with a diversity range of 1.184 to 2.367. Evenness also did not vary widely. Evenness values for all stations ranged from 0.6362 to 0.9182 with a mean of 0.7813.

Zoogeographic affinities and feeding guilds

It was possible to assign zoogeographic affinities to 32 of the 40 identified taxa (Table 2). Fifteen of the taxa, 47%, could be classified as Boreal in their distribution. Another 34% of the taxa were considered to have a Boreal-Virginian geographic range. Taxa characterized as being Arctic or Virginian in their zoogeographic affinities each represented nine per cent of the identified species.

On the basis of abundance, the distribution among the zoogeographic provinces was much more skewed. A full 71% of the individuals encountered could be defined as Boreal in character. The remaining individuals were divided rather evenly between Arctic, Boreal-Virginian and Virginian affinities.

Table 2. List of taxa collected from the Gulf of Maine depositional basin together with their zoogeographic affinities (A-Arctic, B-Boreal, V-Virginian) and feeding guilds.

	Zoogeographic Affinity	Feeding Guild
Phylum Rhynchocoela		
Micrura sp. Ehrenberg, 1971	BV	Carnivorous
Nemertean		Carnivorous
Phylum Mollusca		
Astarte undata Gould, 1841	B	Suspension
Bivavle juv.		Suspension
Parvicardium pinnulatum (Conrad, 1831)	BV	Suspension
Chaetoderma nitidulum (Loven, 1844)	B	Omnivorous
Thyasira gouldi (Philippi, 1845)	B+	Suspension
Thyasira sp. Lamarck, 1818		Suspension

Phylum Annelida		
Aglaophamus neotenus Noyes, 1980	B	Deposit
Ampharete arctica Malmgrem, 1866	A+	Deposit
Aricidea suecica (Eliason, 1920)	A+	Deposit
Ceratocephale loveni Malmgren, 1867	B	Deposit
Chaetozone setosa Malmgren, 1867	B	Surface deposit
Cossura longocirrata Webster & Benedict, 1887	B	Surface deposit
Harmothoe extenuata (Grube, 1840	B	Carnivorous
Lepidonotus squamatus (Linnaeus, 1758)	B	Carnivorous
Lumbrineris latreilli Audouin & Milne Edwards, 1834	BV	Carnivorous
Scoletoma tenuis Verrill, 1873	BV	Carnivorous
Maldane sarsi Malmgren, 1865	B	Subsurface deposit
Mediomastus ambiseta (Hartman, 1947)		Deposit
Nephtys incisa Malmgren, 1865	B	Deposit
Ninoe nigripes Verrill, 1973	BV	Carnivorous
Owenia fusiformis Delle Chiaje, 1844	BV	Surface deposit
Paramphinome pulchella Sars, 1869	BV	Carnivorous
Paraonis gracilis (Tauber, 1879)	B	Deposit
Praxillella gracilis (M. Sars, 1861)		Subsurface deposit
Praxillella praetermissa (Malmgren, 1865)	B	Subsurface deposit
Prionospio sp Malmgren, 1867.		Surface deposit
Sabaco elongatus (Verrill, 1873)	V	Subsurface deposit
Scalibregma inflatum Rathke, 1843	BV	Subsurface deposit
Syllid juvenile		Carnivorous
Tharyx acutus Webster & Benedict, 1887	B+	Surface deposit
Unknown		
Phylum Arthropoda		
Cyclaspis varians Calman, 1912	V	Deposit
Eudorella pusilla Sars, 1871	BV	Deposit
Harpinia propinqua Sars, 1891	B	Surface deposit
Leptocheirus plumulosus Shoemaker, 1932	V	Suspension
Leptostylis longimana (Sars, 1865)	A+	Deposit
Paracaprella tenuis Mayer, 1903	BV	Suspension/carnivorous
Photis sp. Kroyer, 1842	BV	Deposit

The taxa encountered were assigned to one of four feeding guilds for the purpose of analysis. Surface deposit feeders, subsurface deposit feeders and omnivores were grouped together as deposit feeders in this analysis. Deposit feeders were the most prevalent of the feeding guilds. Twenty-three of the 40 species, 59%, were classified as deposit feeders. Carnivores accounted for 23% of the taxa while only 18% were considered suspension feeders. A different pattern emerged when the analysis was done on the basis of individuals.

Here 88% of the community consisted of deposit feeders, nine per cent were carnivores, and suspension feeders represented only three per cent of the fauna.

Table 3. Community parameters and numerical dominance.

Station	Species richness	Density (m^2)	Evenness (J^1)	Diversity (H^1)	Numerical dominance
A	11	775	0.8561	2.053	*Paraonis gracilis* 26%
B	7	400	0.9182	1.787	*Paraonis gracilis* 14%
C	6	825	0.6609	1.184	*Paraonis gracilis* 61%
D	14	825	0.875	2.309	*Cossura longocirrata* 31%
E	10	1,425	0.7059	1.625	*Paraonis gracilis* 37%
F	10	950	0.7556	1.740	*Paraonis gracilis* 42%
G	8	475	0.8195	1.704	*Paraonis gracilis* 42%
H	19	1,875	0.8039	2.367	*Paraonis gracilis* 26%
I	11	1,950	0.6362	1.526	*Paraonis gracilis* 60%

Multivariate analyses

The dendrogram based on group-average sorting classification using the Bray-Curtis similarity measure on square-root transformed data did not present a clear-cut spatial pattern (Fig. 2). Only four stations were linked in pair-groupings. Stations C and F and stations H and I formed the two pair-groupings at a very high level of similarity. Station E was then linked to the C/F grouping and the five stations were joined at nearly 60% similarity. The remaining stations then were chain-linked to the five-station cluster, i.e. individual stations

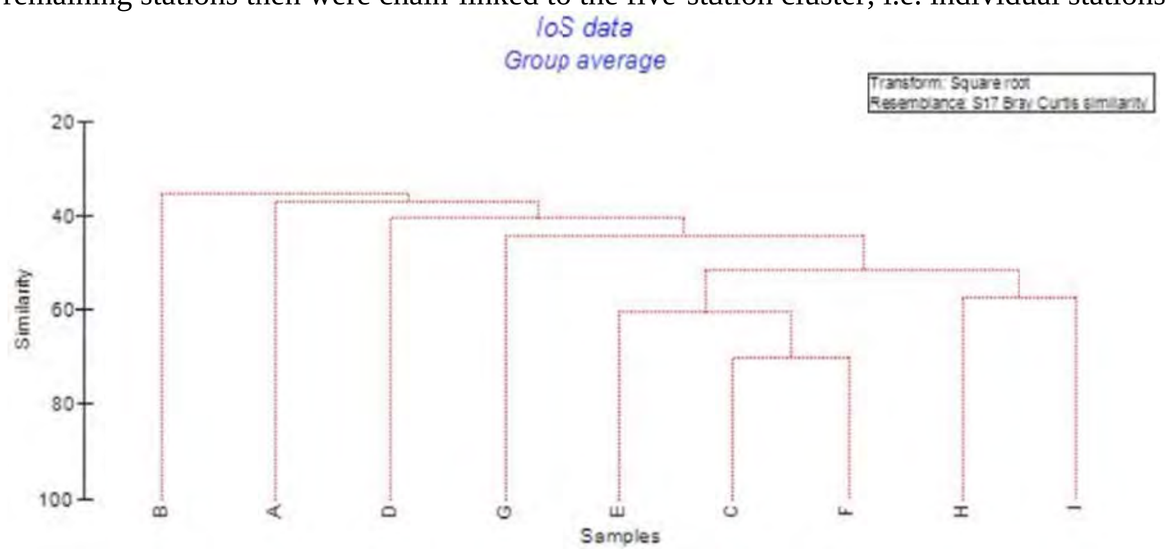

Fig. 2. Dendrogram based on a group-average sorting classification using the Bray-Curtis similarity measure on square root transformed data.

were sequentially and singly added to the dendrogram. There were no higher level dichotomies indicating basic dissimilarities in the station array. The SIMPROF routine of

PRIMER was run to test the null hypothesis that the set of samples do not differ from each other in the dendrogram structure. No two station pairs reject the null hypothesis and, hence, it can be concluded that all of the samples came from the same community.

The biological relationships among the nine samples were further investigated using a two dimensional non-metric multi-dimensional scaling (MDS) ordination also with the Bray-Curtis similarity measure calculated on square root transformed abundance data. Similar to the cluster analysis, the MDS did not reveal any segregation of groups of stations (Fig. 3). Stations C, E, F, H and I were grouped towards the center while Stations A, B, D and G were spaced around the periphery. The stress level of 0.07 indicates that the MDS is "a good ordination with no real prospect of misleading interpretation; 3- or higher dimensional solutions will not add any additional information" (Clarke and Warwick 2001).

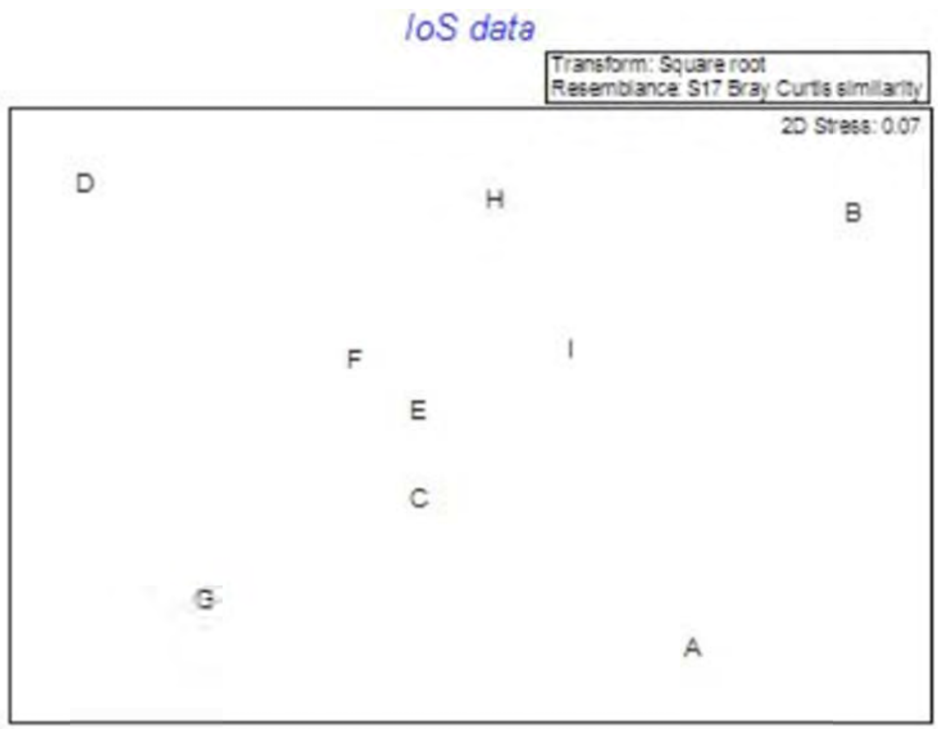

Fig. 3. MDS ordination of the nine samples based on square root transformed species abundances and Bray-Curtis similarities (stress = 0.07).

Species Accumulation Analysis

The observed species accumulation curve (Sobs) and the calculated Chao 2 values are plotted in Fig. 4. Tabulated values are presented in Table 4. The values are the product of 999 permutations at each step as the sample size is increased by adding samples randomly. The figure and table indicate that, while the Sobs curve continued to incline smoothly, the Chao 2 curve reached an asymptote when approximately six samples were accumulated. The Chao 2 estimator predicted that the number of macrofaunal species >0.5mm in this community is expected to be about 75 with a standard deviation of 20 under conditions of infinite sampling. The survey recovered slightly more than 50% of the theoretical total species number.

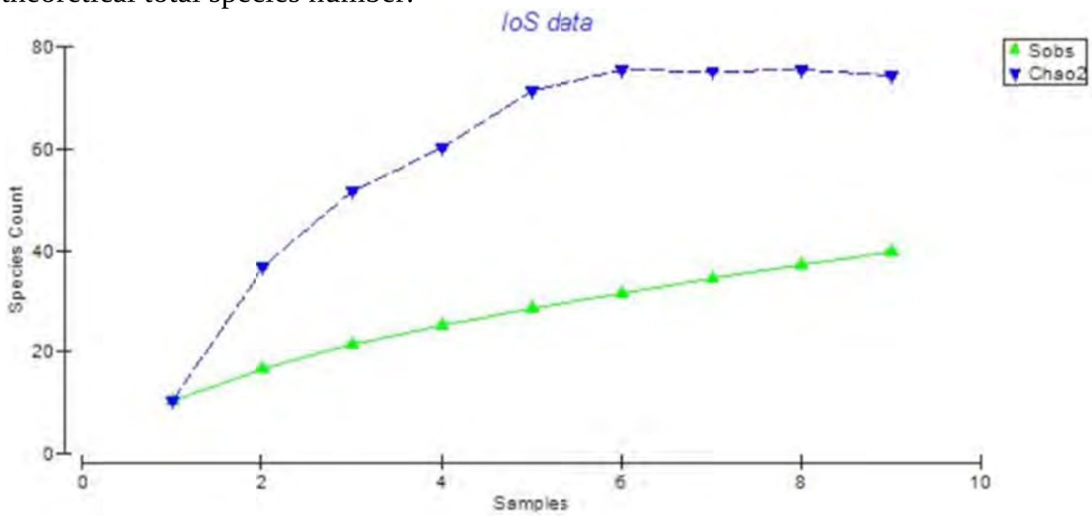

Fig. 4. Plot of observed species accumulation curve (Sobs) and the curve predicted by the Chao 2 extrapolator.

Table 4. Number of observed species (Sobs) and true total number of species predicted to be found (Chao 2) with infinite sampling following the same sampling protocol.

Station	Sobs	Sobs(SD)	Chao2	Chao2(SD)
1	10.62	3.66	10.62	12.69
2	16.65	3.91	36.05	15.56
3	21.42	3.91	50.39	24.20
4	25.43	3.54	60.79	28.43
5	28.89	3.28	70.93	33.98
6	32.07	2.85	76.53	33.15
7	34.85	2.31	75.54	27.57
8	37.54	1.56	76.50	24.95
9	40.00	0.00	74.57	20.56

Discussion

The salient result of this benthic survey in the northwest Gulf of Maine is the uniformity of the environment both physically and biologically. The stations occur over a very narrow depth range and the sediments have a very high silt/clay content that can be generally described as silt-clay (Table 1). In the limited area covered by the survey, there is no reason to suspect that temperatures and currents are not equally uniform.

The macroinvertebrate fauna at the site is limited. The benthic community consists of only 40 species representing just four phyla (Table 2). The assemblage is noteworthy for its lack of oligochaetes, nearly ubiquitous elsewhere, and the absence of echinoderms and colonial species. Polychaetes are the characteristic taxa overwhelmingly dominating the community in terms of numbers of species and individuals. Density is relatively low while the univariate statistics, species richness, diversity and evenness, are also at low to modest levels. One species, the polychaete *Paraonis gracilis*, is the numerical dominant at eight of the nine stations.

The zoogeographic affinities of the species that could be characterized range from Arctic to Virginian (Table 2). The largest group has a Boreal affinity followed by the Boreal-Virginian group accounting for about a third of the taxa. Fewer than one in ten of the taxa are considered to be either Arctic or Virginian. Numerically, however, individuals of the Boreal species make up nearly three-quarters of the community.

The functional group in this fine-grained habitat is overwhelmingly deposit feeders as would be expected in such fine sediments. Species in this generalized feeding guild partition the environment by practicing several variations of obtaining nutrition from the sediments. Some, such as the four maldanid polychaete species, feed relatively deeply within the subsurface sediments (Fauchald and Jumars 1979). Other subsurface feeders, *Scalibregma inflatum*, feed higher in the sediment column while several other species, *Cossura longocirrata* and *Tharyx acutus*, feed on the very sediment surface. Hence, a large number of deposit-feeders can be supported.

The biological homogeneity is confirmed by multivariate analyses of the community data. Cluster analysis does not dissect the stations into any discernible pattern. SIMPROF indicates that there are no statistically significant differences among the branches of the dendrogram (Fig. 2). MDS analysis, likewise, shows no separation of samples that would indicate any coherent underlying biological divisions (Fig. 3). It can be concluded that the samples were drawn from the same faunal community.

The species accumulation analyses are revealing. While the observed species curve climbs smoothly, the Chao 2 curve reaches an asymptote rather quickly (Fig. 4, Table 4). This suggests that the true species complement would be reached with a finite amount of additional sampling. The Chao 2 estimate of the true species number is less than twice the number of species actually observed (Table 4) indicating that further sampling would add rare species to the species list while not affecting the numerical dominance observed.

Comparisons of these results with the limited previous macroinfaunal studies of fine sediment bottoms of the Gulf of Maine brings to light noteworthy similarities and one significant difference. The summary statistics provided by Theroux and Wigley (1998), who principally used a 0.1 m^2 Smith-McIntyre grab and a 1.0 mm mesh sieve, found 86 taxa with a density of 718 individuals/m^2 in their silt-clay samples. This is close to the 75 taxa predicted by Chao 2 and the 1,055 individuals/m^2 reported in our results. It would be expected that Theroux and Wigley would find a few more species and a slightly lower density as they took over 300 samples over an extended depth range (18 to well over 200m). Density declines with increasing depth in the Gulf of Maine (Theroux and Wigley 1998) and the larger mesh sieve would not retain smaller individuals. Likewise, and similar to our results, Theroux and Wigley (1998) found that species with Boreal zoogeographic affinities predominated in the Gulf of Maine followed by Virginian species and small components of Arctic and Subarctic species.

Rowe *et al.* (1975a) surveyed Wilkinson and Murray Basins, two of the deep basins that are among the unique characteristics of the Gulf of Maine, using a variety of gear. We will limit the comparisons and contrasts to the results from their 0.15 m^2 van Veen grab and 0.42 mm sieve size. Their stations were from a predominantly clay bottom at a depth of 280 m and located about 70 km ESE of our stations. A total of 86 species were recovered from the basins, 68 from Wilkinson Basin and 58 from Murray Basin. Densities reported were

1,306 and 627 individuals/m^2 from Wilkinson and Murray Basins, respectively. Mean species diversity (H') were 2.25 from Wilkinson Basin and 2.56 from Murray Basin. These values are higher than our mean of 1.81 from the shallower silt-floored depression. This result might be expected considering Rowe *et al.* (1975a) took a larger number of samples and used a larger, deeper digging grab. Previous studies (Reish 1959, Gage *et al.* 2002) have demonstrated little or no difference in species retention between 0.5 (present study) and 0.42 mm (Rowe *et al.* 1975a) sieves. Consistent with our results, Rowe, *et al.* (1975b) found a high dominance of polychaetes. Four species accounted for over 50% of the individuals in the van Veen grabs. Indeed, 16 species accounted for over 90% of the individuals and 14 of these were polychaetes.

Whereas the quantitative results from Theroux and Wigley (1998), Rowe, *et al.* (1975a) and our 2010 survey are rather consistent, the similarities break down when qualitative community comparisons are made. The species list from the Rowe *et al.* (1975b) van Veen grabs and our own shows that they share just 11 species even though the sites are separated by only 70 km. Depth and small differences in sediment characteristics may be factors. We do not ascribe to this, however, as the species list of Rowe *et al.* (1975b) contains species such as the deposit feeding polychaete *Heteromastus filiformis*, the amphipods *Casco bigelowi* and *Leptocheirus pinguis*, and the molluscs *Nucula delphinodonta* and *Alvania carinata* that occur in a variety of Gulf of Maine habitats. This suggests a spatial heterogeneity in the mud bottom fauna of the Gulf of Maine and highlights the need for additional sampling over a larger geographic range.

In summary, the study area is physically homogeneous and inhabited by a limited benthic invertebrate community. Richness, at the species and higher taxonomic levels, and density are relatively low. Deposit-feeding polychaetes dominate the fauna qualitatively and quantitatively. The community can be considered Boreal in its zoogeographic affinity. Further sampling would undoubtedly add to the species total but would probably not modify the characterization of the community significantly. Comparisons with the limited previous available data indicate that soft bottom communities in the Gulf of Maine are similar in terms of quantitative parameters but differ qualitatively. This communication helps to fill an identified gap in our knowledge of the Gulf of Maine ecosystem while showing the need for expanded surveys to address the question of determinants of community composition over a geographic range.

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Appendix

Species data for individual stations

Isles of Shoals A

Number of Species:	11
Density (m^{-2}):	775
Diversity (H'):	2.053

Species	Total	Cum. Tot.	%	Cum. %	Higher Taxon
Paraonis gracilis	8	8	25.8	25.8	Annelida
Lepidonotus squamatus	6	14	19.4	45.2	Annelida
Ampharete arctica	6	20	19.4	64.5	Annelida
Nemertean	3	23	9.7	74.2	Rhynchocoela
Cossura longocirrata	2	25	6.5	80.6	Annelida
Scoletoma tenuis	1	26	3.2	83.9	Annelida
Ceratocephale loveni	1	27	3.2	87.1	Annelida
Tharyx acutus	1	28	3.2	90.3	Annelida
Unknown	1	29	3.2	93.5	Annelida
Harpinia propinqua	1	30	3.2	96.8	Arthropoda
Eudorella pusilla	1	31	3.2	100.0	Arthropoda

Isles of Shoals B

Number of Species: 11
Density (m^{-2}): 725
Diversity (H'): 1.787

Species	Total	Cum. Tot.	%	Cum. %	Higher Taxon
Paraonis gracilis	4	4	13.8	13.8	Annelida
Ampharete arctica	4	8	13.8	27.6	Annelida
Ninoe nigripes	3	11	10.3	37.9	Annelida
Cossura longocirrata	2	13	6.9	44.8	Annelida
Sabaco elongatus	2	15	6.9	51.7	Annelida
Mediomastus ambiseta	1	16	3.4	55.2	Annelida
Maldane sarsi	1	17	3.4	58.6	Annelida
Aglaophamus neotenus	1	18	3.4	62.1	Annelida
Paraonis gracilis	4	22	13.8	75.9	Annelida
Ampharete arctica	4	26	13.8	89.7	Annelida
Ninoe nigripes	3	29	10.3	100.0	Annelida

Isles of Shoals C

Number of Species: 6
Density (m^{-2}): 825
Diversity (H'): 1.184

Species	Total	Cum. Tot.	%	Cum. %	Higher Taxon
Paraonis gracilis	20	20	60.6	60.6	Annelida
Cossura longocirrata	7	27	21.2	81.8	Annelida
Ampharete arctica	2	29	6.1	87.9	Annelida
Owenia fusiformis	2	31	6.1	93.9	Annelida
Ceratocephale loveni	1	32	3.0	97.0	Annelida
Paracaprella tenuis	1	33	3.0	100.0	Annelida

Isles of Shoals D

Number of Species:	13
Density (m^{-2}):	725
Diversity (H'):	2.309

Species	Total	Cum. Tot.	%	Cum. %	Higher Taxon
Cossura longocirrata	9	9	31.0	31.0	Annelida
Sabaco elongatus	4	13	44.8	44.8	Annelida
Mediomastus ambiseta	4	17	58.6	58.6	Annelida
Prionospio sp.	2	19	65.5	65.5	Annelida
Ceratocephale loveni	2	21	72.4	72.4	Annelida
Paramphinome pulchella	1	22	75.9	75.9	Annelida
Syllid juvenile	1	23	79.3	79.3	Annelida
Paraonis gracilis	1	24	82.8	82.8	Annelida
Owenia fusiformis	1	25	86.2	86.2	Annelida
Nephtys incisa	1	26	89.7	89.7	Annelida
Chaetozone setosa	1	27	93.1	93.1	Annelida
Leptocheirus plumulosus	1	28	96.6	96.6	Arthropoda
Astarte undata	1	29	100.0	100.0	Mollusca

Isles of Shoals E

Number of Species: 10
Density (m^{-2}): 1425
Diversity (H'): 1.625

Species	Total	Cum. Tot.	%	Cum. %	Higher Taxon
Paraonis gracilis	22	22	38.6	38.6	Annelida
Cossura longocirrata	19	41	33.3	71.9	Annelida
Ampharete arctica	4	45	7.0	78.9	Annelida
Prionospio sp.	4	49	7.0	86.0	Annelida
Ceratocephale loveni	2	51	3.5	89.5	Annelida
Sabaco elongatus	2	53	3.5	93.0	Annelida
Ninoe nigripes	1	54	1.8	94.7	Annelida
Praxillella gracilis	1	55	1.8	96.5	Annelida
Thyasira sp.	1	56	1.8	98.2	Mollusca
Bivavle juv.	1	57	1.8	100.0	Mollusca

Isles of Shoals F

Number of Species: 10
Density (m^{-2}): 950
Diversity (H'): 1.740

Species	Total	Cum. Tot.	%	Cum. %	Higher Taxon
Paraonis gracilis	16	16	42.1	42.1	Annelida
Cossura longocirrata	9	25	23.7	65.8	Annelida
Ampharete arctica	3	28	7.9	73.7	Annelida
Mediomastus ambiseta	3	31	7.9	81.6	Annelida
Ceratocephale loveni	2	33	5.3	86.8	Annelida
Praxillella gracilis	1	34	2.6	89.5	Annelida
Owenia fusiformis	1	35	2.6	92.1	Annelida
Micrura sp.	1	36	2.6	94.7	Rhynchocoela
Paracaprella tenuis	1	37	2.6	97.4	Arthropoda
Astarte undata	1	38	2.6	100.0	Mollusca

Isles of Shoals G

Number of Species:	8
Density (m^{-2}):	475
Diversity (H'):	1.704

Species	Total	Cum. Tot.	%	Cum. %	Higher Taxon
Paraonis gracilis	8	8	42.1	42.1	Annelida
Cossura longocirrata	4	12	21.1	63.2	Annelida
Owenia fusiformis	2	14	10.5	73.7	Annelida
Sabaco elongatus	1	15	5.3	78.9	Annelida
Aricidea suecica	1	16	5.3	84.2	Annelida
Prionospio sp.	1	17	5.3	89.5	Annelida
Chaetoderma nitidulum	1	18	5.3	94.7	Mollusca
Micrura sp.	1	19	5.3	100.0	Rhynchocoela

Isles of Shoals H

Number of Species: 20
Density (m^{-2}): 1900
Diversity (H'): 2.367

Species	Total	Cum. Tot.	%	Cum. %	Higher Taxon
Paraonis gracilis	20	20	26.3	26.3	Annelida
Sabaco elongatus	15	35	19.7	46.1	Annelida
Ampharete arctica	7	42	9.2	55.3	Annelida
Praxillella gracilis	5	47	6.6	61.8	Annelida
Cossura longocirrata	4	51	5.3	67.1	Annelida
Prionospio sp.	4	55	5.3	72.4	Annelida
Scoletoma tenuis	3	58	3.9	76.3	Annelida
Mediomastus ambiseta	3	61	3.9	80.3	Annelida
Owenia fusiformis	2	63	2.6	82.9	Annelida
Ninoe nigripes	2	65	2.6	85.5	Annelida
Scalibregma inflatum	1	66	1.3	86.8	Annelida
Paramphinome pulchella	2	68	2.6	89.5	Annelida
Ceratocephale loveni	1	69	1.3	90.8	Annelida
Tharyx acutus	1	70	1.3	92.1	Annelida
Harmothoe extenuata	1	71	1.3	93.4	Annelida
Astarte undata	1	72	1.3	94.7	Mollusca
Thyasira gouldi	1	73	1.3	96.1	Mollusca
Parvicardium pinnulatum	1	74	1.3	97.4	Mollusca
Cyclaspis varians	1	75	1.3	98.7	Arthropoda
Leptostylis longimana	1	76	1.3	100.0	Arthropoda

Isles of Shoals I

Number of Species: 12
Density (m^{-2}): 1975
Diversity (H'): 1.526

Species	Total	Cum. Tot.	%	Cum. %	Higher Taxon
Paraonis gracilis	47	47	59.5	59.5	Annelida
Sabaco elongatus	7	54	8.9	68.4	Annelida
Cossura longocirrata	5	59	6.3	74.7	Annelida
Ampharete arctica	4	63	5.1	79.7	Annelida
Ninoe nigripes	3	66	3.8	83.5	Annelida
Mediomastus ambiseta	3	69	3.8	87.3	Annelida
Nemertean	3	72	3.8	91.1	Rhynchocoela
Praxillella praetermissa	2	74	2.5	93.7	Annelida
Owenia fusiformis	2	76	2.5	96.2	Annelida
Lumbrineris latreilli	1	77	1.3	97.5	Annelida
Lepidonotus squamatus	1	78	1.3	98.7	Annelida
Photis sp.	1	79	1.3	100.0	Arthropoda