THE MACROINVERTEBRATE FAUNA ASSOCIATED WITH FIVE SAND FLATS IN THE NORTHERN GULF OF MAINE¹

PETER F. LARSEN, LEE F. DOGGETT and ANNE C. JOHNSON
Bigelow Laboratory for Ocean Sciences
West Boothbay Harbor
Maine 04575

The macroinvertebrate fauna of five sand flats in the northern Gulf of Maine was sampled during the summers of 1975 and 1976. Seventy-one putative species were identified. Annelids were the dominant taxon in terms of both numbers of species and numbers of individuals. Diversity, species per station and density varied greatly both within and between sites. The fauna was also markedly heterogeneous and it is not possible to define a characteristic sand flat fauna in this geographic region.

La faune des macroinvertébrés de cinq plaines sablonneuses situeés dans la partie nord du golfe du Maine fut échantillonnée pendant les étés 1975 et 1976. Soixante et onze espèces putatives furent identifiées. Les annélides constituent le taxon dominant aussi bien du point de vue du nombre d'espèces que du nombre d'individus. La diversité, le nombre d'espèces par station et la densité varient beaucoup, aussi bien pour chacun des sites qu'entre les différents sites. La faune est remarquablement hétérogène et il n'est pas possible de définir une faune caractéristique des plaines sablonneuses de cette région.

Introduction

Quantitative data on the invertebrate communities of intertidal habitats in the northern Gulf of Maine are generally lacking. In an attempt to correct this situation and provide needed information for planners and managers, the Maine State Planning Office instituted an invertebrate resource inventory in 1975. This inventory defined nine discrete intertidal habitats—sand beaches, gravel beaches, cobble beaches, boulder beaches, sand flats, mud flats, low energy rocky shores, high energy rocky shores and salt marshes. Each type of habitat was sampled at several representative sites along the northern Gulf of Maine coast from the Isle of Shoals to the Quoddy region with the goal of defining the invertebrate fauna of each habitat. This communication presents the results of the sand flat sampling program.

A sand flat is a protected environment predominantly made up of sand, but containing varying percentages of silt, clay and organic detritus. Flats have a slight grade and usually exhibit sand waves (Larsen & Doggett 1981). Sand flats represent less than 6% of the intertidal habitat area in the region (Larsen & Doggett, in press) but, in addition to being prime shellfish harvesting areas, they are important feeding areas for shorebirds, gulls, wading birds and water fowl. The flats in eastern Maine and southwestern New Brunswick are especially important for migrating semi-palmated plovers, semi-palmated sandpipers, short billed dowitchers and black-bellied plovers (U.S. Fish and Wildlife Service, 1980).

Data on this important habitat are particularly needed at this time because of the potential development of tidal power resources in the upper Bay of Fundy. These developments could modify the tidal regime throughout the Gulf of Maine and hence alter dynamic sedimentary environments such as sand flats (Greenberg 1979; Larsen 1981).

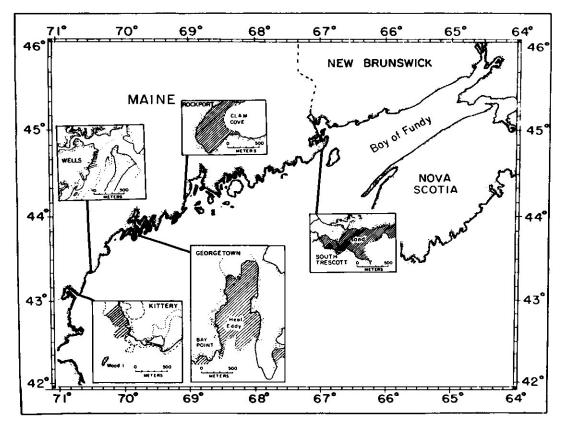


Fig 1. The locations of the sand flats studied in the northern Gulf of Maine.

Methods

Five sand flats representative of northern Gulf of Maine sand flats in terms of size, shape, slope and energy input were chosen for study (Fig 1) and sampled as close to spring tides as was practical. The sites selected and the dates of sampling were: Gerrish Island, Kittery (July 17, 1976); Wells Harbor, Wells (July 16, 1976); Heal Eddy, Georgetown (May 25, 1975); Clam Cove, Rockport (July 12, 1975); and Bailey's Mistake, Trescott (June 26, 1976).

Two transects were placed at each site. Four stations were occupied along each transect with the lowest station located at the low tide line and the highest station at the level of the last high tide. Intermediate stations were placed so as to dissect the intertidal zone into equal vertical segments. At each station a one-quarter meter squared quadrat with metal sides was forced into the sediment (Holme and McIntyre, 1971), and the enclosed area dug out to a depth of 15 to 20 cm. The sediment samples were transported in buckets to the laboratory or a field station and sieved on a 1.0 mm screen the day of sampling. The material remaining on the screen was fixed in 10% formalin containing the vital stain Rose Bengal. In the laboratory the samples were preserved in 70% ethanol and all organisms were removed, identified to the lowest taxonomic level practical (usually the species level), and counted. No attempt was made to identify nemerteans, nematodes, oligochaetes and insects to the species level.

Table I. Taxa found on northern Gulf of Maine sand flats.

Phylum Cnidaria sp.		Kittery	Wells	Georgetown	Rockport	Trescott
Phylum Rhynchocoela						
Unidentified Nemertea Phylum Aschelminthes Unidentified Nematoda Phylum Mollusca Hydrobia sp. Lacuna vincta Littorina littorea Nassarius trivittatus Odostomia bisuturalis Polinices heros Gemma gemma Macoma balthica Mya arenaria Mya arenaria Mytilus edulis Spisula solidissima Tellina agilis Fhylum Annelida Eteone longa Phyllodoce sp. Pholoe minuta Glycera dibranchiata Aglaophamus verrilli Nephtys bucera Nephtys locera Nepht						+
Phylum Aschelminthes	Phylum Rhynchocoela					
Unidentified Nematoda		+		+	+	+
Phylum Mollusca +						
Hydrobia sp. Lacuna vincta Littorina littorea Nassarius trivittatus Odostomia bisuturalis Polinices heros Gemma gemma Macoma balthica Mya arenaria Mya arenaria Hydrius edulis Spisula solidissima Tellina agilis Phylum Annelida Eteone longa Phyllodoce sp. Pholoe minuta Glycera dibranchiata Aglaophamus verrilli Nephtys bucera Nephtys caeca Nephtys longosetosa Exogene hebes Nereis diversicolor Nereis virens Capitella capitata Heteromastus filiformis Clymenella torquata Maldanid Polydora sp. Polydora ligni Pygospio elegans Scolecolepides viridis Spio setosa Spio setosa Spio setosa Spio setosa Spio setoso Spio penedicti H H H H H H H H H H H H H		+	+	+	+	+
Lacuna vincta Littorina littorea Nassarius trivittatus Odostomia bisuturalis Polinices heros Gemma gemma Macoma balthica Mya arenaria Mytilus edulis Spisula solidissima Tellina agilis Phyllum Annelida Eteone longa Phyllodoce sp. Pholoe minuta Glycera dibranchiata Aglaophamus verrilli Nephtys bucera Nephtys caeca Nephtys caeca Nephtys caeca Nereis virens Exogene hebes Nereis diversicolor Nereis virens Clymenella torquata Heteromastus filiformis Clymenella torquata Maldanid Polydora sp. Polydora ligni Pygospio elegans Spio setosa						
Littorina littorea Nassarius trivittatus Odostomia bisuturalis Polinices heros Gemma gemma Macoma balthica Mya arenaria Mytilus edulis Spisula solidissima Tellina agilis Phylum Annelida Eteone longa Phyllodoce sp. Pholoe minuta Glycera dibranchiata Aglaophamus verrilli Nephtys bucera Nephtys caeca Nephtys longosetosa Exogene hebes Nereis diversicolor Nereis virens Clymenella torquata Heteromastus filiformis Clymenella torquata Heteromastus filiformis Clymenella torquata Polydora sp. Polydora ligni Pygospio elegans Scolecolepides viridis Spio setosa Spi				+		
Nassarius trivittatus Odostomia bisuturalis Polinices heros Gemma gemma Macoma balthica Mya arenaria Mytilus edulis Spisula solidissima Tellina agilis Phyllum Annelida Eteone longa Phyllodoce sp. Pholoe minuta Glycera dibranchiata Aglaophamus verrilli Nephtys bucera Nephtys caeca Nephtys caeca Nephtys longosetosa Exogene hebes Nereis diversicolor Nereis virens Capitella capitata Heteromastus filiformis Clymenella torquata Haldanid Polydora sp. Polydora ligni Pygospio elegans Spio spl. Spio filicornis Spio setosa Spiophanes bombyx Strebiospio benedicti + + + + + + + + + + + + + + + + + + +				+		
Odostomia bisuturalis Polinices heros Gemma gemma Macoma balthica H + H + H Mya arenaria Mytilus edulis Spisula solidissima Tellina agilis Hhylum Annelida Eteone longa Phyllodoce sp. Pholoe minuta Glycera dibranchiata Aglaophamus verrilli Nephtys bucera Nephtys caeca Nephtys caeca Nephtys longosetosa Exogene hebes Nereis diversicolor Nereis virens Capitella capitata Heteromastus filiformis Clymenella torquata Maldanid Polydora sp. Polydora ligni Pygospio elegans Spio setosa Spio setosoi benedicti + + + + + + + + + + + + + + + + + + +			+	+	+	
Polinices heros Gemma gemma Macoma balthica Hya arenaria Hytilus edulis Spisula solidissima Tellina agilis Hyllum Annelida Eteone longa Hyhllodoce sp. Pholoe minuta Glycera dibranchiata Aglaophamus verrilli Nephtys bucera Nephtys longosetosa Exogene hebes Hexogene hebes Horeis diversicolor Nereis virens Capitella capitata Heteromastus filiformis Clymenella torquata Maldanid Polydora sp. Polydora ligni Pygospio elegans Spio splicornis Spio setosa Spiophanes bombyx Strebiospio benedicti + + + + + + + + + + + + + + + + + + +					+	
Gemma gemma Macoma balthica Mya arenaria Myta ilus edulis Spisula solidissima Tellina agilis Phyllum Annelida Eteone longa Phyllodoce sp. Pholoe minuta Glycera dibranchiata Aglaophamus verrilli Nephtys bucera Nephtys caeca Nephtys longosetosa Exogene hebes Nereis diversicolor Nereis virens Capitella capitata Heteromastus filiformis Clymenella torquata Maldanid Polydora sp. Polydora ligni Pygospio elegans Spio pelasos	Odostomia bisuturalis				+	
Macoma balthica	Polinices heros	+		+		
Macoma balthica	Gemma gemma			+		
Mytilus edulis Spisula solidissima Tellina agilis Phylum Annelida Eteone longa Fteone longa Fteone dibranchiata Aglaophamus verrilli Nephtys bucera Nephtys bucera Nephtys caeca Nephtys longosetosa Ftxogene hebes Nereis diversicolor Nereis virens Clymenella torquata Heteromastus filiformis Clymenella torquata Maldanid Polydora sp. Polydora sp. Polydora ligni Pygospio elegans Spio filicornis Spio setosa Spio setosa Spio setosa Spio setosa Spio benedicti H + + + + + + + + + + + + + + + + + +	Macoma balthica	+	+	+	+	
Mytilus edulis Spisula solidissima Tellina agilis Phylum Annelida Eteone longa Fteone longa Fteone dibranchiata Aglaophamus verrilli Nephtys bucera Nephtys bucera Nephtys caeca Nephtys longosetosa Ftxogene hebes Nereis diversicolor Nereis virens Clymenella torquata Heteromastus filiformis Clymenella torquata Maldanid Polydora sp. Polydora sp. Polydora ligni Pygospio elegans Spio filicornis Spio setosa Spio setosa Spio setosa Spio setosa Spio benedicti H + + + + + + + + + + + + + + + + + +	Mya arenaria	+	+	+	+	+
Spisula solidissima Tellina agilis Phylum Annelida Eteone longa Phyllodoce sp. Pholoe minuta Glycera dibranchiata Aglaophamus verrilli Nephtys bucera Nephtys caeca Nephtys caeca Nephtys longosetosa Exogene hebes Nereis diversicolor Nereis virens Capitella capitata Heteromastus filiformis Clymenella torquata Haldanid Polydora sp. Polydora ligni Pygospio elegans Spio spl. Spio spl. Spio setosa Spio planes bombyx Strebiospio benedicti + + + + + + + + + + + + + + + + + + +			+	+	+	+
Tellina agilis Phylum Annelida Eteone longa Phyllodoce sp. Pholoe minuta Glycera dibranchiata Aglaophamus verrilli Nephtys bucera Nephtys caeca Nephtys caeca Nephtys longosetosa Exogene hebes Nereis diversicolor Nereis virens Capitella capitata Heteromastus filiformis Clymenella torquata Maldanid Polydora sp. Polydora ligni Pygospio elegans Spio setosa Spio setosa Spio setosa Spio setosa Spio planes bombyx Strebiospio benedicti + + + + + + + + + + + + + + + + + + +					+	
Phylum Annelida Eteone longa		+			<u>.</u>	
Eteone longa + + + + + + + + Phyllodoce sp. + + + + + + + + + + + Phyllodoce sp. + + + + + + + + Pholoe minuta + + + + + + + Phylographical + + + + + + Phylographical + + + + + + + Phylographical + + + + + + + Phylographical + + + + + + Phylographical + + + + Phylographical + + Phylographical + + Phylographical	Phylum Annelida	•			•	
Phyllodoce sp. + Pholoe minuta + Clycera dibranchiata + + + Aglaophamus verrilli + Nephtys bucera + Nephtys caeca + + + + + + + + + Nephtys longosetosa + + + + + + + + + + + + + + + + + + +		+	+	+	+	+
Pholoe minuta Glycera dibranchiata Aglaophamus verrilli Nephtys bucera Nephtys caeca Nephtys longosetosa Exogene hebes HARE Spio setosa HEXOGENE HE		*.*	*.	•		*
Glycera dibranchiata + + + Aglaophamus verrilli + Nephtys bucera + + + + + + + + + + + + + + + + + + +				+		
Aglaophamus verrilli + Nephtys bucera + Nephtys caeca + + + + Nephtys longosetosa + Exogene hebes + + + + + Nereis diversicolor + + Nereis virens + + + Capitella capitata + + + Heteromastus filiformis + + Clymenella torquata + + Maldanid + Polydora sp. + + Polydora ligni + + Pygospio elegans + + + + + Scolecolepides viridis + + + + Spio sp. + Spio filicornis + Spio setosa + Spiophanes bombyx + + + Strebiospio benedicti + + +				i.	_	
Nephtys bucera		_			21 1 88	
Nephtys caeca + + + + + + + + + + + + + + + + + + +						
Nephtys longosetosa + Exogene hebes + + + + + + + + + + + + + + + + + + +			_	_	_	
Exogene hebes + + + + + + + + + + + + + + + + + + +				•	T	_
Nereis diversicolor Nereis virens H Capitella capitata Heteromastus filiformis H Clymenella torquata H Maldanid Polydora sp. Polydora ligni Pygospio elegans H Scolecolepides viridis Spio sp. Spio filicornis Spio setosa Spiophanes bombyx Strebiospio benedicti + + + + + + + + + + + + + + + + + + +		1		_L		_
Nereis virens + + + + + + + + + + + + + + + + + + +				-	T	T.
Capitella capitata + + + + Heteromastus filiformis + + + Clymenella torquata + + + Maldanid + Polydora sp. + + + Polydora ligni + + + Pygospio elegans + + + + + Scolecolepides viridis + + + Spio sp. + Spio filicornis + Spio setosa + Spiophanes bombyx + + + + Strebiospio benedicti + + +			4	_	-	120
Heteromastus filiformis + + + Clymenella torquata + + + Maldanid + Polydora sp. + + + Polydora ligni + + + Pygospio elegans + + + + + Scolecolepides viridis + + + + Spio sp. + Spio filicornis + Spio setosa + Spiophanes bombyx + + + + Strebiospio benedicti + + +		242	T	T		
Clymenella torquata + + + + H H H H H H H H H H H H H H H		□ ₩□		1		200
Maldanid + Polydora sp. + + Polydora ligni + + Pygospio elegans + + + + Scolecolepides viridis + + + Spio sp. + Spio filicornis + Spio setosa + Spiophanes bombyx + + + Strebiospio benedicti +				-	T	
Polydora sp. Polydora ligni + + + Pygospio elegans + + + + + Scolecolepides viridis + + + + Spio sp. + Spio filicornis + Spio setosa + Spiophanes bombyx + + + + Strebiospio benedicti + + +		T.			*	
Polydora ligni + + + Pygospio elegans + + + + + Scolecolepides viridis + + + Spio sp. + Spio filicornis + Spio setosa + Spiophanes bombyx + + + Strebiospio benedicti + +		T				
Pygospio elegans + + + + + + + + Scolecolepides viridis + + + + + + + + + + + + + + + + + + +	Polydora ligni			+	+	
Scolecolepides viridis + + + + Spio sp. + Spio filicornis + Spio setosa + Spiophanes bombyx + + + Strebiospio benedicti + +			400 a 20	*		+
Spio sp. + Spio filicornis + Spio setosa + Spiophanes bombyx + + + Strebiospio benedicti + +		1.	+	+	a t a	+
Spio filicornis + Spio setosa + Spiophanes bombyx + + + Strebiospio benedicti + +			+	+	+	
Spio setosa + Spiophanes bombyx + + + Strebiospio benedicti + +		120	+			
Spiophanes bombyx + + + + Strebiospio benedicti + +		+				
Strebiospio benedicti + +						+
		+		+	+	
Aricidea jeffreysii +					+	
	Aricidea jettreysii			+		

	Kittery	Wells	Georgetown	Rockport	Trescott
Paraonis fulgens		olevak ar	+	+	+
Lumbrineris fragilis				+	0.57
Orbinia sp.	+				+
Scoloplos sp.	+		+	+	
Tharyx acutus	•		+		
Fabricia sabella			+		
Unidentified Polychaeta	+				
Oligochaeta		+	+	+	+
Phylum Arthropoda					
Balanus balanoides				+	
Leptocuma minor			+		
Chiridotea coeca			+	+	+
Chiridotea tuftsi			+		+
Edotea triloba			+	+	
Idotea phosphorea	+				
Corophium insidiosum		+	+		
Corophium volutator			+	+	
Uniola irrorata	+				
Gammarus sp.			+		
Gammarus lawrencianus			+		+
Gammarus oceanicus			+		
Acanthohaustorius millsi	+		+		
Haustorius canadensis	+				
Protohaustorius deichmannae	+				
Jassa falcata			+		
Psammonyx nobilis	+		+	+	+
Carcinus maenas			+	+	
Crangon septemspinosa	+		+	+	
Insecta Larva					+
Ant	+				
Phylum Hemichordata					
Saccoglossus kowalevskii	+				
Unidentified					+

Results and Discussion

A total of 71 putative species was encountered at the five sand flats (Table I). Annelids accounted for 46% of the species encountered, followed by the arthropods, molluscs and miscellaneous phyla which represented 30, 17 and 7% of the species respectively. Likewise, annelids were the numerically dominant taxon accounting for 71% of the individuals while the arthropods, molluscs and miscellaneous phyla comprised 15, 6 and 7% of the total individuals respectively. These figures stand in contrast to the results of sand beach studies in the region which show an overwhelming dominance of crustaceans (Croker et al. 1975).

A great deal of variability in the biological parameters of diversity (H¹ log₂), species per station and density was manifested both within and between sites

Site	Diversity (H ¹)	Total Species	Species Per Station	Density/m ²
Kittery	1.47(0.85-1.95)	30	9.4(4-16)	1,218,(316-3316)
Wells	1.19(0.0-2.16)	13	4.3(0-9)	314(0-832)
Georgetown	2.67(1.83-3.25)	43	15.3(9-21)	994(440-2080)
Rockport	1.77(0.88-2.78)	34	14.3(8-20)	2,044(464-4216)
Trescott	2.07(0.24-2.86)	22	12.3(11-17)	3,471(696-16,832)

Table II. The mean and ranges of diversity, number of species and density at each of the sites sampled.

(Table II). Mean values and ranges over all stations for these parameters were: diversity 1.82 (0.0-3.25); species per station 12 (0-21); and density 1510/m² (0-16,832). Averaging the values from all the stations at each sandflat produces a range in diversity of 1.19-2.67, in species per station of 4.3-15.3 and in density of 314-3,741/m².

The sandflats at Kittery and Wells exhibited the lowest values for diversity and species per station, and below average densities. The morphology of these flats differed from the others in that they were adjacent to tidal channels and presumably experienced higher levels of current and wave energy. This undoubtedly increases sediment instability limiting the number of species that can maintain populations. The flat at Georgetown had the highest diversity and species richness (Table II) but a rather low density. We have no explanation for this phenomenon. Moderate levels of diversity and relatively high densities were encountered at the two most eastern sites.

The sandflats also differed significantly in taxonomic composition. The Kittery sandflat was the only one numerically dominated by arthropods (Fig 2). Crustacean

Table III. The five most abundant species and their mean density/m² at each of five sand flats.

Kittery		Wells		Georgetown			
Protohaustorius deichmannae Acanthohaustorius	406/m²	Mytilus edulis	78/m²	Gemma gemma	128/m²		
millsi	393	Nematoda	75	Scolecolepides viri	idis 121		
Pygospio elegans	186	Mya arenaria	68	Oligochaeta	116		
Nereis diversicolor	115	Oligochaeta	32	Nereis virens	102		
Tellina agilis	29	Pygospio elegans	22	Acanthohaustoriu:	s millsi 70		
Rockport		Trescot	it				
Oligochaeta	770/m²	Exogone hebes	2,763/m ²				
Spiophanes bombyx	417	Spio setosa	245				
Nematoda	306	Chiridotea coeca	89				

67

66

Capitella capitata

Unidentified

Scolecolepides viridis

Clymenella torquota

100

77

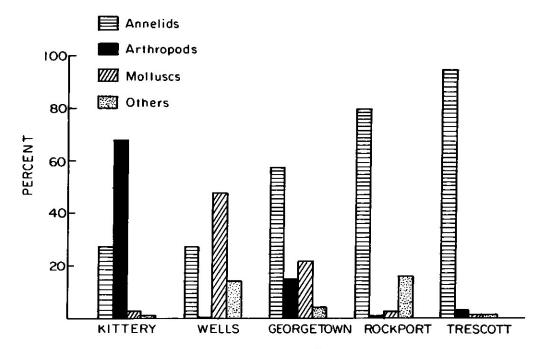


Fig 2. The percentage of individuals among four categories at each of five sand flats.

dominance was due to concentrations of the haustoriid amphipods, *Protohaustorius deichmannae* and *Acanthohaustorius millsi*, described (Croker et al. 1975) as being characteristic of sheltered and partly sheltered sand environments, respectively (Table III). The Wells sandflat was numerically dominated by molluscs, almost exclusively juvenile *Mytilus edulis* and *Mya arenaria*. This flat was characterized by large sand waves and it seems likely that the individuals encountered, especially of *M. edulis*, were washed in from adjacent environments and would not complete their life cycles on this flat. Only 13 species were found at this site (Table II).

The flats at Georgetown, Rockport and Trescott were dominated by annelids (Fig 2). With the exception of Gemma gemma and Acanthohaustorius millsi at Rockport, molluscs and amphipods were not numerically important at any of these sites. Consistent with the observation of Bousfield (1973) that the northern limit of haustoriid amphipods in the United States is central Maine, no haustoriids were found north of Rockport.

The invertebrate macrofauna of the five sand flats was markedly heterogeneous and it is not possible to define a characteristic sand flat fauna based on these results. The five most abundant species at each sampling site are listed in Table III. Nineteen taxa are represented, only five taxa being numerically dominant at more than one sand flat. These taxa are oligochaetes at Wells, Georgetown and Rockport, the haustoriid amphipod, Acanthohaustorius millsi, at Kittery and Georgetown, the polychaets, Pygospio elegans, at Kittery and Wells, and Scolecolepides viridis at Georgetown and Rockport.

The marked differences in community structure between individual sand flats, noted above in terms of number of species, diversity, density, and species domi-

nance, strongly suggest that ecological factors other than, or in addition to, gross sediment characteristics may be operative. Whether these factors are physical or biological in nature cannot be determined from the present results. Based on results from other intertidal habitats studied in the region, however, we do not believe that seasonal or interannual variation contributes significantly to the differences (Larsen & Doggett, unpublished).

Whereas most intertidal habitats are regarded to be physically controlled (sensu, Sanders, 1968), it is usually possible within a given geographic range to predict dominant species and/or characteristic fauna. This is true of sand beaches in the eastern United States (Croker et al. 1975) and mud flats in the northern Gulf of Maine (Larsen & Doggett, unpublished), but not of the sand flats studied. These flats, while superficially similar in appearance, are undoubtedly variously influenced by a wide range of physical factors that are not easily quantified. In addition, sand flats in this region are spatially isolated from one another unlike sand beaches south of, and mud flats north of, Cape Elizabeth, Maine. The nearly contiguous distribution of these latter habitats facilitates the development of a homogeneous fauna within a given geographic area. The disjunct distribution of sand flats in the northern Gulf of Maine may reduce recruitment between sand flats to the extent that community homogeneity does not develop. Further work on this important habitat with an emphasis on mechanisms influencing community development is definitely needed.

Acknowledgements

Initiation and major funding for this project were supplied by the Coastal Program of the Maine State Planning Office with monies from the Office of Coastal Zone Management, National Oceanic and Atmospheric Administration. Individuals and organizations too numerous to list contributed to several aspects of the program. We are grateful to all of them. We thank Robert A. Croker and Leon M. Cammen for reviewing the manuscript.

REFERENCES

- **Bousfield, E.L.** 1973. Shallow-water gammaridean Amphipoda of New England. Comstock Publishing Associates, Cornell University Press, Ithaca, NY.
- Croker, R.A., Hager, R.P. and Scott, K.J. 1975. Macroinfauna of northern New England marine sand. II. Amphipod-dominated intertidal communities. Can J. Zool. 53: 42-51.
- **Greenberg, D.A.** 1979. A numerical model investigation of tidal phenomena in the Bay of Fundy and Gulf of Maine. *Mar. Geodesy* 2: 161-187.
- Holme, N.A. and McIntyre, A.D. 1971. Methods for the study of marine benthos. ABP Handbook No. 16. Blackwell Scientific Publications, Oxford and Edinburgh.
- Larsen, P.F. 1981. Potential environmental consequences of tidal power development seaward of tidal barrages. Oceans 2: 908-912.
- **Larsen, P.F.** and **Doggett, L.F.** 1981. The Ecology of Maine's Intertidal Habitats. Maine State Planning Office. Augusta, Maine. 183 pp.
- Larsen, P.F. and Doggett, L.F. 1983. In Press. A Planner's Handbook on the Ecology of Maine's Intertidal Habitats. Maine State Planning Office. Augusta, Maine.
- Sanders, H.L. 1968. Marine benthic diversity: a comparative study. Am. Nat. 102: 243-282.
- U.S. Fish and Wildlife Service. 1980. An Ecological Characterization of Coastal Maine. FWS/OBS-80/29. U.S. Department of Interior, Washington, D.C.