

Pockmarks influence benthic communities in Passamaquoddy Bay, Bay of Fundy, Canada

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ABSTRACT: Physical characteristics of pockmarks in Passamaquoddy Bay, Bay of Fundy, Canada were measured, including depth, benthic area, sidewall slope, orientation at longest diameter and an out-of-roundness estimate. Sedimentary holes of uncertain origin, ranging from 2.69 to 36.02 cm² in area, were discovered. Mean densities of 4.78 holes m⁻² inside and 3.88 holes m⁻² outside pockmarks were found. Geochemical measurements of cores of ~100 cm depth suggested that sedimentary microbial metabolism was different inside than outside pockmarks. The megabiota consisted of the sea star *Asterias rubens*, commonest outside pockmarks; the sea cucumber *Cucumaria frondosa*, commonest on pockmark bottoms; an unidentified bryozoan/hydrozoan and the filamentous bacterium *Beggiatoa* sp., commonest on pockmark sidewalls. During this study, 2 habitat types (A and B) were characterized by differences in (1) multibeam acoustic data, and (2) community structure. Two different patterns of benthic macro-infaunal community structure were related to upper and lower areas within Habitat A. Compared to reference sites, upper Habitat A pockmarks had significantly fewer species and lower densities. Consequently, pockmark community structure was also different, notably with absence or lower densities of taxa appearing late in the succession. Lower Habitat A pockmarks had smaller and more subtle differences in macro-infaunal community structure than reference locations outside pockmarks and the equilibrium species number varied with benthic area of each pockmark. Circumstantial evidence, including nMDS and species–area plots, dominance patterns, accumulated species number and density of benthic macrofaunal communities, supports the hypothesis that upper Habitat A pockmarks are at various stages in a pre-equilibrium succession. By contrast, all lower Habitat A pockmarks had already reached equilibrium levels.

KEY WORDS: Pockmarks · Macro-infaunal communities · Megabiota · Sedimentary holes

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INTRODUCTION

The term 'pockmark' was first used by Canadian marine geologists to describe shallow, cone-shaped depressions in muddy, silt/clay sediments of the Scotian Shelf, off Canada's Atlantic coast (King & MacLean 1970). Subsequently, pockmarks have been found world-wide wherever suitable reducing sediments occur (Hovland & Judd 1988, Fader 1991, Judd & Carzi 2002), at water depths from 6 to 4800 m (Fader 1991). The formation of pockmarks has previously been hypothesized to involve various mechanisms, including (1) gas ebullition which entrains sediment followed

by its dispersion in local currents (Josenhans et al. 1978), (2) seismic activity which re-suspends large amounts of sediment, following the production and discharge of subterranean liquids (Fannin 1980), (3) meteorite impact (Solheim & Elverhoi 1993), (4) glacial erosion and tectonic activity leading to the formation of hill–hole pairs (Solheim & Elverhoi 1993), and (5) thermogenic gas which accumulates behind a gas hydrate seal where, following warming as the glacial seal disintegrates, an explosive release of gas occurs (Solheim & Elverhoi 1993). The force is sufficient to remove large quantities of surficial sediments which become re-distributed by currents. Released liquids include

brine, fresh water and gases such as methane. Sources of sedimentary methane are biogenic, produced by anaerobic bacteria able to reduce carbon dioxide to methane in surficial sediments, and thermogenic, produced deep in the bedrock where the high temperatures and pressure cause cracking of kerogens to methane (Fader 1991). It is not yet clear if less active pockmarks, such as those in the Bay of Fundy and North Sea, originally had a more active stage and evolved to their present condition by decreasing liquid emissions from sediments; or whether pockmarks can be formed without a continuous efflux of brines, sulphides or methane gas. In the latter case colonization of the freshly formed pockmark is from macrofauna found in the surrounding sediments.

In the only previous quantitative macro-infaunal study of a pockmark, of which we are aware, Dando et al. (1991) investigated a single pockmark in the North Sea. That study used the ship's navigation system and echo sounder to judge, by water depths on the sounder, where grab and core samples were collected. It included 11 grab samples of 0.1 m² from a single pockmark. A total of 67 taxa with combined densities ranging from 708 to 1550 ind. m⁻² were found.

Pockmarks were discovered in Passamaquoddy Bay on Canada's Atlantic coast by Fader (1988) and further described by Pecore & Fader (1990). Passamaquoddy Bay is a small (575 km²) semi-enclosed body of seawater (Fig. 1), situated at ~45°N, at the mouth of the St Croix river that opens into the Bay of Fundy and Gulf of Maine. Spring tides in the region are of the order of 8 m and salinities (25 to 32 PSU) and temperatures (-1.8 to 15°C) vary seasonally, with spring freshets from the St. Croix and 2 smaller rivers, the Digdeguash and Maguadavic (Trites & Garrett 1983). Sampling depths encountered during the present study were from 35 to 81 m. Sidescan sonar and high-resolution seismic reflection acoustic imaging studies in Passamaquoddy Bay by Fader (1988) suggested that there were over 11 000 pockmarks, in 2 areas totaling 87 km². This number was extrapolated from partial coverage (13 km² and 1320 pockmarks found) by acoustic mapping undertaken by Fader (1988). The latter found that the pockmarks varied in diameter from 1 to 300 m and were up to 29 m deep. More recent acoustic imaging using multibeam mapping has been undertaken by the University of New Brunswick (www.omg.unb.ca/Projects/SWNB/). The geological mechanism of formation and temporal history of any Passamaquoddy Bay pockmark is not known.

In this study, we present a descriptive and comparative investigation of the benthic macro-infauna in 17 pockmarks (Fig. 2) and 9 reference locations outside pockmarks in Passamaquoddy Bay for a total of 101 grab samples using precise positioning methods.

We address the following ecological question: Are the communities of benthic macrofauna and megafauna different inside versus outside pockmarks, and if so, how? The null hypothesis tested was that there was no difference in community structure of benthos within pockmarks versus outside (= reference locations). We also identify possible ecological mechanisms involved in the macrofaunal community differences that we found. We use available knowledge regarding the trophic capabilities of each species to infer the trophic functioning of the pockmark benthic community ecosystem.

MATERIALS AND METHODS

Physical characterization of pockmarks. Pockmarks in Passamaquoddy Bay were not bubbling during our survey and were free of sulphide or brine in benthic boundary layer seawater. Intermittent gas ebullition may occur as it does in nearby locations in Belfast Bay

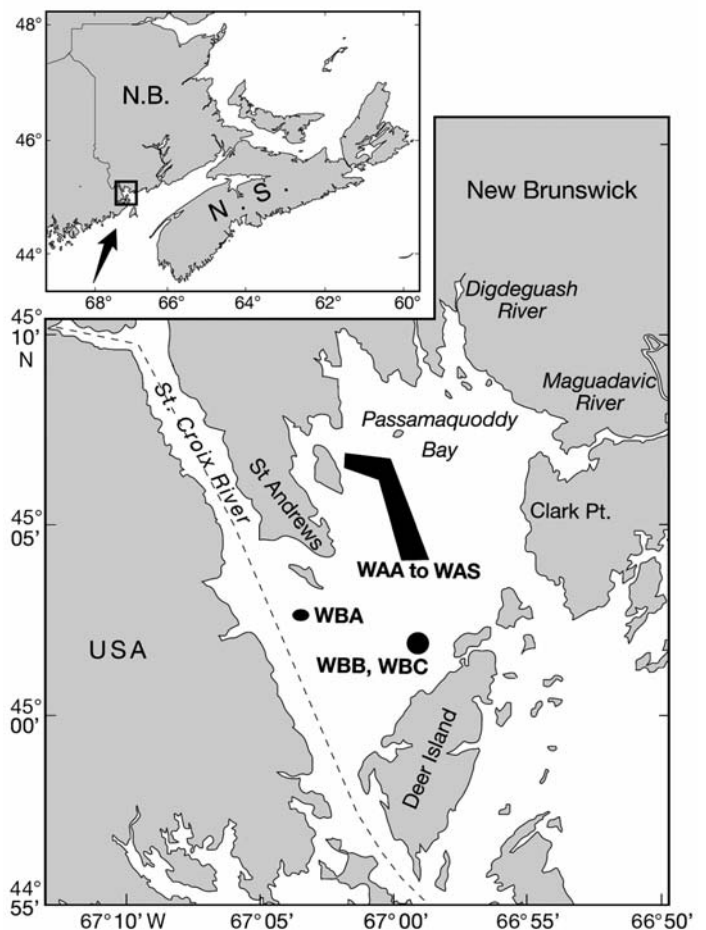


Fig. 1. Pockmark sampling sites in Passamaquoddy Bay, with dotted line indicating international boundary between Canada and USA. Codes identify pockmark sampling areas

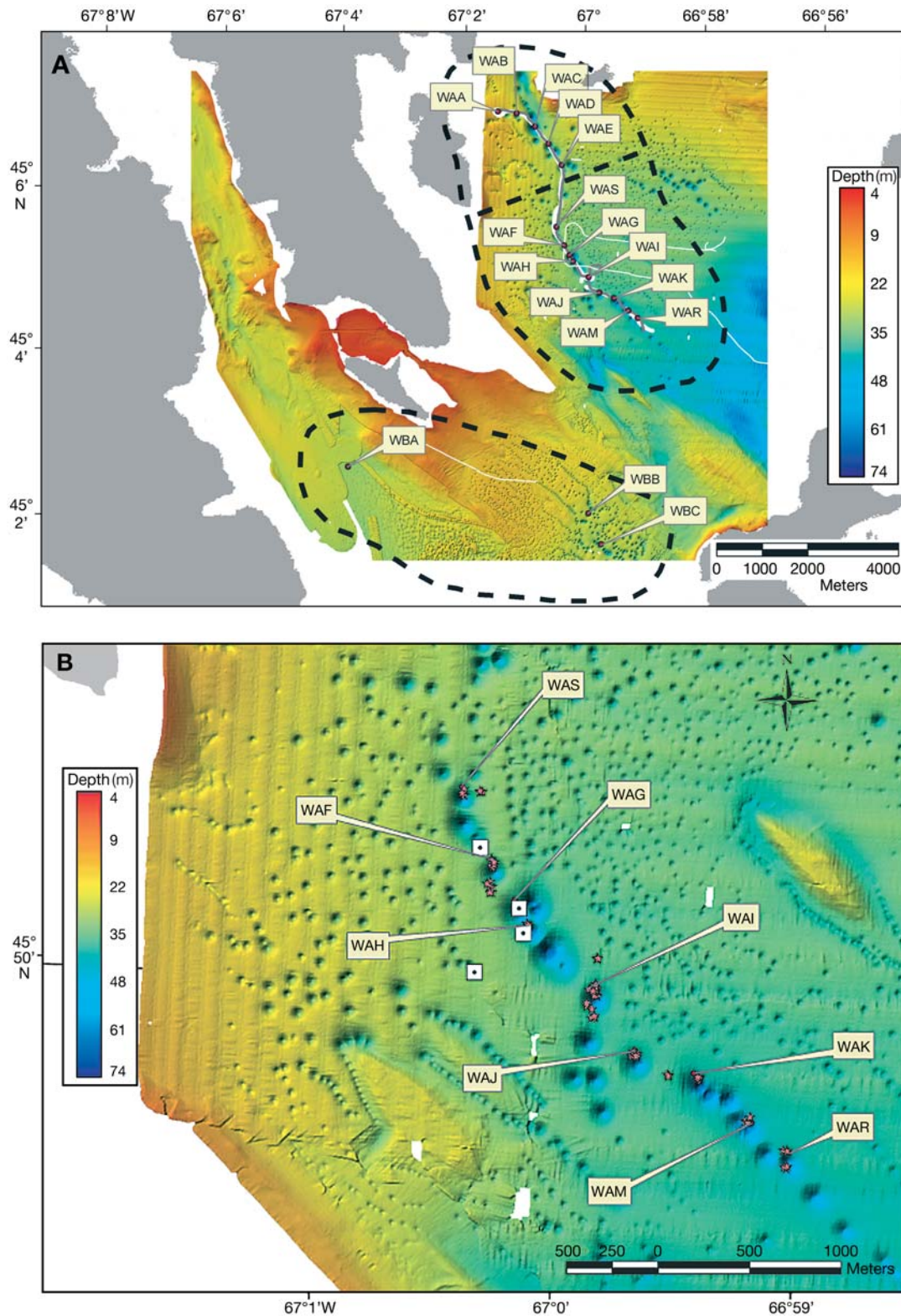


Fig. 2. (A) Multibeam, bathymetric, shaded relief image of Passamaquoddy Bay. Northern ellipse is Habitat A, divided into upper and lower sections; southern ellipse is Habitat B (second letter of pockmark designator indicates habitat). Grab-sampled pockmarks are labeled; grey and white lines represent TOWCAM cruise tracks. Pockmarks sampled only by TOWCAM (designated WT, see Table 1) are omitted for clarity. (B) Enlarged multibeam bathymetry of lower part of Habitat A, showing grab sample (orange star) and coring (white square) locations

(Rogers et al. 2006). Each pockmark was examined using multibeam acoustic data collected by Fisheries & Oceans Canada and the University of New Brunswick, 1988–2002 (www.omg.unb.ca/Projects/SWNB/). The central position of each pockmark was located and its coordinates recorded as decimal degrees. Pockmark depth from the lip to the deepest point on the bottom, and the average slope of the sidewall was determined. Simple planar areas at the top and bottom of the pockmark were estimated, with the sidewall area determined as a cone. Most pockmarks had an elliptical orientation and we determined the position of the major and minor axes of the ellipse to the nearest 45° quadrant. The degree to which pockmarks were elliptical, as opposed to circular, in outline is given as an out-of-roundness estimate, defined as (major axis length – minor axis length)/(major axis length). Thus, a value of 0.000 would be a circle; values greater than this indicate the degree to which the pockmark outline was elliptical, with a value of 1 being a straight line.

Other physical data included a backscatter map (available from www.omg.unb.ca/Projects/South_West_NB). Data on seismic events in Passamaquoddy Bay which might indicate dates of origin of individual pockmarks were obtained from www.earthquakes-canada.nrcan.gc.ca.

Sediment geochemistry. Four core samples were obtained for sediment profiling (Fig. 2B): 2 in pockmarks and 2 at nearby reference locations. We used a LeHigh corer weighted to 300 kg, with a 150 cm long core liner drilled at 5 cm intervals to take a plastic cut-off syringe. Sub-samples of sediment for determination of sulphide were taken with labeled, individual 5 cm³ syringes and sealed with a plastic cap, to prevent air entering the syringe. Samples were stored at 5°C until analysis 24 to 80 h later. Total sulphide was determined in pore water from the syringe samples, after stabilization in sulphide antioxidant buffer solution by Berner's (1963) ion analytical method. An Orion 9616 combination silver/sulphide electrode calibrated with sodium sulphide was used and the results expressed as micromoles l⁻¹ (μM).

Megafaunal sampling. TOWCAM is a towed, underwater, bottom referencing vehicle on which floodlights, analogue video- and digital still-camera were mounted. A pair of laser sources projected thin beams of light onto the seafloor to provide a reference scale for area calculation of both photographic and video images. TOWCAM towing speed was approximately 2 knots at ~1.5 m above the seabed. The continuously recorded video was viewed in real time on a monitor for still camera activation. Further operational and deployment details are described in Gordon et al. (2006). Photographic images (n = 107) suitable for

analysis were judged by the presence of clear laser point measuring origins. Large sedimentary holes were present and photographs (JPEGs) were used to calculate the opening area, by assuming that each hole was circular (although some had an irregular outline), and measuring the radius in pixels on each JPEG. From the calibrated relationship between pixels and cm² the area was calculated from πr^2 .

Approximately 4 h of video images for a distance of 14.451 km was analyzed on a DVD player/writer frame by frame for hole and megabiota density. Selected frames were saved as bitmaps identifiable by number and their GMT timestamp with Win DVD software. Megafauna and patches of filamentous bacteria, defined as visible characteristic shapes, were counted. Also counted were the largest sedimentary holes >2.5 cm². Frames selected as bitmaps (n = 1304) were those where laser points were clearly visible and with a time delay of 4 s, to ensure no frame overlap in counting epibiota and sedimentary holes. The area properly illuminated by TOWCAM lights was determined for each bitmap or JPEG by measuring the number of pixels not illuminated (by Image Pro Plus software) and subtracting from the total number of pixels for the whole frame area.

The density of sediment holes or megafauna, as number m⁻² was calculated by estimating the image area sampled by each JPEG or video bitmap. Images were rectangular in shape and project a quadrilateral area of the seafloor because TOWCAM tilts on both the roll and pitch axes. Thus, whilst the pixels are of constant size on the image, their corresponding dimensions varied when projected on the seafloor. We computed the dimensions of an average pixel at the midpoint of the image and multiplied by the total number of pixels to establish image area. (see Appendix 1, available in MEPS Supplementary Material at www.int-res.com/articles/suppl/m357p051_app.pdf). Based on in-water calibrations, an empirical correction for barrel distortion (Bradford 2005) was derived and applied to obtain the final area. The correction was of the order of 15% for most of the images analyzed.

Megafaunal abundance was estimated by counting the number of individuals per bitmap and adjusting the area sampled in each bitmap to 1 m². Our estimates include bitmaps with zero counts for that taxon. In the same manner the largest holes (>2.5 cm², equivalent diameter = 1.78 cm) were counted and the density (number per m²) estimated. Densities were compared using non-parametric statistics.

Macro-infaunal sampling. In Habitat A, 14 pockmarks (Fig. 2) and 9 reference locations (designated as REF1 to REF9) outside pockmarks were sampled. Only 3 pockmarks and no reference locations were sampled in Habitat B. Triplicate grab samples were taken at

each location with one exception. A Hunter-Simpson grab (Hunter & Simpson 1976) fitted with a multibeacon transponder (see below) was deployed from a 16 m research vessel. The maximum depth of penetration of the grab was 16 cm, sampling an area of 0.1 m². A full grab sample contained 12.5 to 16 l of sediment slurry. Macrofauna was separated from the sediment by sieving through 5 and 1 mm meshes with running seawater, with individual grab sample sievings placed in labeled plastic pails containing 5 to 10% formalin in seawater and sealed for storage. Pail contents were transferred to 70% isopropanol in the laboratory and stained with eosin for identification to the lowest possible taxon. The total isopropanol-wet biomass of each sample was determined to 0.01 g.

The Grab Acoustic Positioning System (GAPS) employed allows grab samples to be precisely related to acoustic backscatter or bathymetry maps. GAPS consists of (1) a GPS sub-system on the sampling vessel able to locate the vessel relative to the seafloor, (2) a transportable acoustic sub-system consisting of a Trackpoint multibeacon transponder and hydrophone (Accusonic Technologies), (3) an electronic sub-system to display and log the incoming position and time data, and (4) custom-designed software to process the logged data. McKeown et al. (2007) give a technical description of GAPS-assisted sampling. The transponder was attached to the wire just above the corer and grab. TOWCAM also carried a multibeacon transponder and thus underwater photographs and videographs could be positioned accurately, after coordination of spatial and temporal records.

Grab samples, denoted by lower case n, were taxonomically analyzed individually. Triplicate grab samples were available for each pockmark location, except for WAJ and WAK (n = 6), WAF (n = 9) and WAI (n = 15). Sampling was in the fall of 2001, 2002 and 2004, with the number of pockmarks sampled denoted by N. The macro-infaunal species × abundance data matrix of the study is available at www.marinebiodiversity.ca/cmb/research/passamaquoddy-bay-pockmarks.

Species × abundance data for all pockmark and reference locations (n = 3 to 15) were analyzed for community structure by non-metric multidimensional scaling (nMDS) with Primer 6.0 (Clarke & Warwick 2001). An nMDS and analysis of similarities (SIMPER) between upper (n = 15) and lower (n = 50) Habitat A pockmarks and appropriate reference samples (n = 6 and 18 respectively) allowed us to investigate the top 10 discriminating taxa between these habitats.

Macro-infaunal taxa were analyzed further by groups of locations, classified geographically as follows: Habitat B pockmarks: (WBA + WBB + WBC); upper Habitat A source population: (REF1 + REF2); lower Habitat A source population: (REF4 + REF5 +

REF6), (REF7 + REF8 + REF9); lower Habitat A pockmarks: (WAF + WAG + WAH), (WAI + WAJ + WAK), (WAM + WAR + WAS); upper Habitat A pockmarks: (WAA + WAB + WAE), (WAE + WAD + WAC).

Reference locations (REF) are referred to as source populations since they may provide colonizing propagules to newly formed pockmarks. Groups were chosen to represent geographic locations within Passamaquoddy Bay and to consist of the same number of grab samples (n = 9). Two exceptions were the groups containing WAF, where n = 8 due to the loss of one replicate sample, and the upper Habitat A source population (only 2 REF locations available). The abundance of each taxon was summed for all grab samples and the species ordered from highest to lowest abundance. Within each of the 9 groups of samples the density as number per m², the mean species number, \bar{S} (where n = 3 to 15) and the accumulated species number, S (where n = 9), was calculated. For the same 9 groups a presence/absence and density record for all taxa belonging to the Amphipoda and Cumacea was created.

\bar{S} and the sum of the conical and bottom of the pockmark area, A, expressed as hm² (100 × 100 m), were log normally transformed before regressing with log₁₀ \bar{S} on the ordinate and log₁₀ A on the abscissa, so that linear regression equations were obtained.

Trophic group characterization. Trophic group designations were based on taxon-specific data available in Pollock (1998) and Wildish & Peer (1983). The trophic groups employed were deposit feeders (Dep), suspension feeders (Sus), carnivore (Car), omnivore (Omn), and algal scrapers (Alg). *Thyasira flexuosa* and *Solemya* sp., 2 species of clam that occurred in our species list, contain chemosynthetic bacteria in their tissues (Southward 1986, Dando et al. 2004) and thus are able to metabolize chemosynthetically.

RESULTS

Sampling locations and physical pockmark characteristics

Details of the central position and the physical characterization of pockmarks sampled by grab and TOWCAM are shown in Table 1. Mean depth of pockmarks (N = 35) was 21.7 m (range 5.1 to 50.8 m), mean slope = 0.244 (range 0.185 to 0.336) and mean out-of-roundness = 0.096 (range 0.033 to 0.244). The planar surface area of a pockmark to the edges of the lip averaged 1.84 hm², compared to the total pockmark surface area (bottom plus sidewalls) of 3.59 hm² available for benthic colonization following pockmark formation. Pockmark formation can thus approximately double the

sediment–water interface. The total surface area among pockmarks ranged from 0.31 to 17.25 hm².

A profile view of one representative pockmark, WAI, derived from multibeam data (Fig. 3), shows 3 zones into which all samples could be assigned: the generally flat, or reference, area outside a pockmark; an inner zone within the pockmark where the walls slope, forming a narrowing cone, with the conical nature of the sidewall contributing most to total pockmark area; the pockmark central area where the bottom was often flat.

Sediment profiles

Cores showed a rapid increase in total sulphide from the sediment–water interface to a peak at ~15 cm depth, and by 20 cm depth sulphide was declining

(Fig. 4). For reference cores the decline continued exponentially reaching minimal sulphide levels at 90 cm depth. In contrast, total sulphide levels beneath 20 cm in pockmark cores WAG and WAH remained stable between 600 µM to 1200 µM to the maximum depth sampled at 96 cm.

Sedimentary holes

Many holes of different sizes were noticed in photographs and video bitmaps. Smaller holes of <2.5 cm² (diameter equivalent <1.78 cm), consistent with the openings of small polychaete worm burrows were present in photographs and excluded from the analysis. From a random selection of 25 photographs, 78 holes >2.5 cm² were measured, with a median value of 11.62 cm² (equivalent hole diameter = 3.85 cm). Hole

Table 1. Sampling coordinates at the centre and physical characterization of pockmarks examined in this study. Grab reference locations outside pockmarks are available at: www.marinebiodiversity.ca/cmb/research/passamaquoddy-bay-pockmarks. Physical characteristics for WBA and WBC are absent because of lack of multibeam data in this area. Depth: vertical distance from upper planar surface to bottom of pockmark. OOR: Out-of-roundness estimate

Pockmark	Latitude (°N)	Longitude (°W)	Depth (m)	Mean slope	Area (m ²)			Orientation	OOR
					Top	Bottom	Sidewall		
WAA	45.11466	67.02553	15.9	0.214	16033	1576	29239	NE–SW	0.064
WAB	45.11454	67.02029	19.0	0.256	15775	1830	28341	N–S	0.057
WAC	45.11249	67.01555	50.8	0.253	86570	3300	169159	SE–NW	0.033
WAD	45.10882	67.01089	34.0	0.259	40972	1755	79723	NE–SW	0.060
WAE	45.10464	67.00703	24.2	0.247	22405	1847	41733	E–W	0.079
WAF	45.08894	67.00525	20.2	0.270	16445	1299	30833	N–S	0.100
WAG	45.08703	67.00343	28.1	0.292	15904	1054	30322	E–W	0.040
WAH	45.08616	67.00254	31.1	0.310	13956	940	26641	E–W	0.132
WAI	45.08294	66.99781	25.5	0.263	21636	1656	40636	NE–SW	0.050
WAJ	45.07989	66.99478	20.0	0.235	21376	1857	39571	E–W	0.074
WAK	45.07894	66.99035	25.7	0.247	19187	1254	36407	N–S	0.204
WAM	45.07703	66.98689	25.8	0.205	22253	1557	41822	E–W	0.244
WAR	45.07545	66.98399	18.6	0.204	14941	1172	27822	N–S	0.078
WAS	45.09243	67.00773	23.2	0.300	13447	2005	23388	E–W	0.115
WBB	45.03651	66.99510	14.1	0.336	3821	430	6968	N–S	0.145
WTC01	45.11460	67.02305	18.7	0.213	23350	3555	40034	E–W	0.075
WTC02	45.11439	67.01605	36.3	0.254	36822	2152	70437	E–W	0.081
WTC03	45.10784	67.00907	30.1	0.244	36415	2329	69170	N–S	0.031
WTC04	45.10230	67.00618	17.2	0.252	11178	538	21613	E–W	0.043
WTC05	45.09913	67.00689	18.7	0.301	7051	877	12620	E–W	0.105
WTC06	45.10021	67.00694	19.0	0.262	11343	783	21475	E–W	0.038
WTC07	45.09944	67.00571	18.9	0.270	10396	859	19414	NE–SW	0.092
WTC08	45.09843	67.00721	9.5	0.185	3341	380	5972	SE–NW	0.172
WTC09	45.09646	67.00729	8.7	0.226	3568	830	5546	N–S	0.060
WTC10	45.09550	67.00690	5.1	0.198	1737	330	2841	SE–NW	0.036
WTC11	45.093737	67.006976	11.7	0.239	4657	540	8349	SE–NW	0.097
WTC12	45.091255	67.007537	25.2	0.275	16479	1103	31321	E–W	0.134
WTC13	45.090648	67.006682	18.3	0.198	12375	915	23144	N–S	0.191
WTC14	45.085213	67.001269	31.8	0.265	28330	2518	52513	N–S	0.178
WTC15	45.080828	66.998201	21.7	0.271	19532	1488	36740	E–W	0.052
WTC16	45.078587	66.989788	27.2	0.227	18452	1099	35147	N–S	0.151
WTC18	45.078359	66.988425	23.9	0.216	18212	1865	33071	NE–SW	0.113
WTC19	45.075772	66.985514	17.7	0.204	13815	1776	24325	NE–SW	0.155
WTC20	45.073809	66.982022	17.0	0.191	13664	1216	25121	N–S	0.034
WTC21	45.097115	67.006927	5.2	0.204	1649	191	2946	E–W	0.050

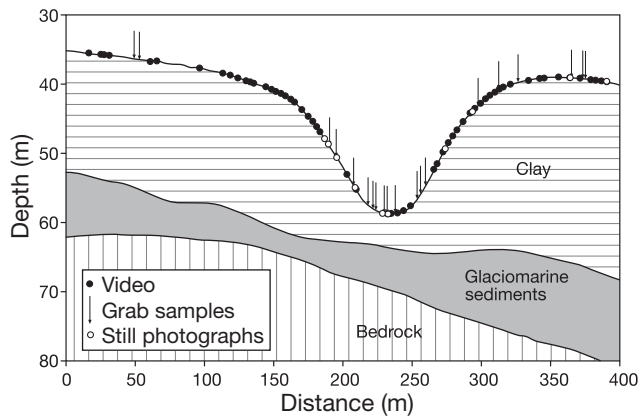


Fig. 3. Passamaquoddy Bay pockmark WAI depth profile with sampling locations (○ = video bitmaps, ● = still photographs, arrows = grab samples). Geological strata from Pecore & Fader (1990)

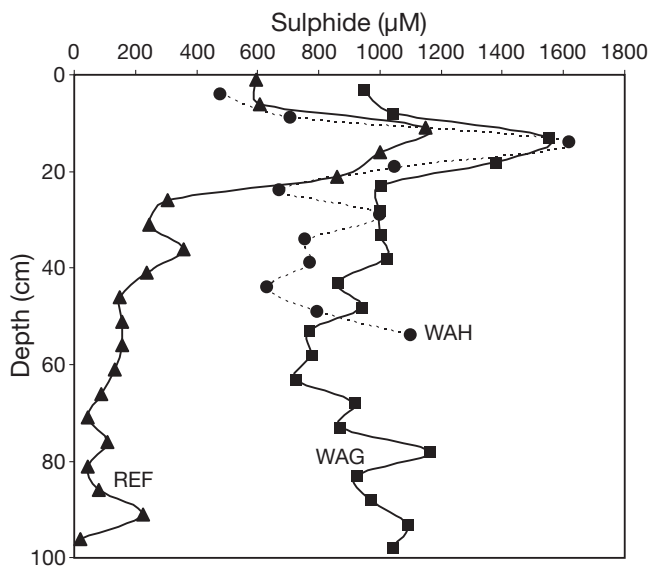


Fig. 4. Sediment profiles of total sulphide for WAG (sidewall), WAH (bottom) and a single reference (REF) location (the other omitted for clarity)

area ranged from 2.69 to 36.02 cm² (equivalent diameters = 1.85 to 6.77 cm) with the data negatively binomially distributed.

Hole density was determined for each of the bitmap images ($N = 1304$), but only the larger holes (>2.5 cm²) were counted. Among these, there were significantly more holes within any given pockmark than outside it (Table 2). The highest density of holes was found on the pockmark sidewalls and the lowest on the pockmark bottom. We also compared individual hole density within a pockmark and at nearby reference locations, which were outside pockmarks, as is shown in Table 3. For about half of the data, standard kurtosis and skewness values suggested a contagious distribution, and so a Mann-Whitney W -test was used to com-

pare pairs of medians. We excluded any pockmark where hole density was <15 due to insufficient numbers for statistical analysis. Significantly higher hole densities were found on pockmark sidewalls than outside pockmarks (Table 3), except in 3 pockmarks where the hole density medians were not significantly different (WAI, WTC01 and WTC16). Hole density appeared to be variable by location, particularly for locations outside pockmarks, with a low median of 1.98 (near WTC01) and high median of 7.37 (near WTC16) holes m⁻².

Megabenthos

Four species of sufficiently large megabenthos were identified from all bitmap images: the 5-armed sea star, *Asterias rubens* ($n = 174$), a scavenger/carnivore; the sea cucumber *Cucumaria frondosa* ($n = 29$), a

Table 2. Comparison of combined hole density, as number per m², between pairs of locations. Out = outside pockmarks, In = all within pockmarks, Side = sidewall of pockmarks, Bottom = flat bottom of pockmark. N = number of video-frames examined. W = Mann-Whitney W test statistic

Location	N	Median	W	p
In	719	4.78	166743	0.00000
Out	586	3.88		
Out	586	3.88	232614	0.00000
Side	620	5.03		
Out	586	3.88	22514	0.00036
Bottom	99	2.94		

Table 3. Comparison of hole density as the median (number per m²) of the sidewall (Side) and outside (Out) the pockmark. N = number of video-frames examined. W = Mann-Whitney W -test statistic. Where $N < 15$, pockmarks were excluded from this analysis

Pockmark	N		Median		W	p
	Out	Side	Out	Side		
WAB	58	45	2.36	3.45	1765	0.00225
WAC	73	58	2.96	5.21	3509	0.00000
WAD	32	27	3.54	5.88	690	0.00009
WAE	67	34	3.64	4.80	1517	0.00414
WAF	30	16	4.05	5.39	356	0.00772
WAI	141	43	4.55	5.63	4088	0.00055
WAI	59	37	5.91	5.45	945	0.46755
WTC01	25	27	1.98	2.21	414	0.16388
WTC03	41	36	3.60	5.97	1283	0.00000
WTC04	46	25	3.87	4.57	796	0.00808
WTC05	22	21	2.78	4.35	361	0.00165
WTC06	22	22	3.17	4.34	341	0.02142
WTC14	111	17	4.55	5.53	1314	0.00938
WTC15	24	16	5.05	6.47	319	0.00048
WTC16	38	16	7.37	5.56	227	0.14463

passive suspension feeder; an unidentified bryozoan/hydrozoan ($n = 14$); and white patches of a filamentous bacterium, probably *Beggiatoa* sp. ($n = 113$). The latter formed patches at the sediment–water interface and are indicative of anaerobic sediments overlain by well oxygenated benthic boundary-layer sea water (Jorgensen 1977).

We compared the densities of megafauna and *Beggiatoa* sp., within and outside pockmarks (Table 4). Standard deviation values in Table 4 are greater than the means in all cases and this, taken together with standardized kurtosis and skewness values >2 , is indicative of a contagious distribution. *Asterias rubens* reached a significantly higher density outside pockmarks than in them, while inside the pockmark, bottom and sidewall densities were similar. *Cucumaria frondosa* had similar low densities on the pockmark sidewall and outside the pockmark. However, within pockmarks sea cucumber density on the sidewall was significantly lower than on the bottom. In fact, aggregated clumps of this species only occurred on lower Habitat A pockmark bottoms and only single, occasionally 2, sea cucumbers were found outside and on pockmark sidewalls. The filamentous bacterium, *Beggiatoa* sp., occurred at highest densities on pockmark sidewalls. The cross section of pockmark WAI (Fig. 3) indicates the sampling intensity available for each pockmark. The pattern found for megafaunal density in an individual pockmark (not shown) is similar to that for the combined data in Table 4.

Macro-infauna

Surficial geological limits of Habitats A and B. The backscatter map of Passamaquoddy Bay (not shown) suggested that the Habitat A upper and lower pock-

mark sample areas were similar, with no evidence of a discontinuity in backscatter between the 2 areas. The low backscatter was indicated by uniform dark colour throughout, suggesting low sediment density and/or roughness, which is consistent with the silt/clay of the Holocene clay described by Pecore & Fader (1990) in Passamaquoddy Bay. In contrast, lighter areas of higher backscatter, e.g. a large oval area to the NE of our pockmark samples, represent hard bedrock protruding above the flat expanse of silt/clay (Fig. 2B). Other smaller areas of protruding rock can also be seen closer to some of the pockmarks that were sampled, although we only sampled soft sediments. Habitat B is separated from Habitat A by a gradation to lighter areas of higher backscatter, with a more grainy appearance to the backscatter signal, indicating harder sediment.

Multivariate statistics. The nMDS plot for macro-infaunal data of all 3 years (Fig. 5) suggests that there were 4 significantly different (ANOSIM test, $p = 0.1\%$) groupings (Fig. 5A). They are: Habitat B pockmark, Habitat A reference, lower Habitat A pockmark and upper Habitat A pockmark samples. Fig. 5A shows that upper Habitat A pockmark and Habitat B samples are distinct from the more closely related reference and lower Habitat A samples.

For pockmark WAI we found that there was inter-annual difference with nearby reference locations (Fig. 5B) and the difference between pockmark and reference samples persisted from 2001 to 2002.

Species–area curve for all samples. A scatter plot of \bar{S} for pockmark macro-infaunal samples, for which estimates of area were available, included 14 Habitat A pockmarks, but only one from Habitat B (WBB). The other Habitat B pockmarks (WBA and WBC) were not included in multibeam coverage and thus do not have estimates of area (Table 1). Although insufficient samples were available to construct a species–area (\bar{S} –A) curve for Habitat B, it is clear from the higher position of WBA that such a regression, assuming the same slope value, would predict higher values of \bar{S} per unit area than for Habitat A. This emphasizes the importance of including inputs to \bar{S} –A plots which are from the same habitat. The linear regression of \bar{S} –A was based on a subset of the Habitat A data, from 9 pockmarks of the lower Habitat A area (WAF, WAG, WAH, WAI, WAJ, WAK, WAM, WAR, WAS), for a total of 50 grab samples, and had the regression equation $\log_{10} \bar{S} = 0.3873 \log_{10} A + 1.3555$, $R^2 = 0.74$

All 9 pockmark faunal communities were assumed to have reached the succes-

Table 4. Comparison of megafaunal and *Beggiatoa* sp. densities as number per m^2 , between all locations. Out, Side, and Bottom locations as in Table 3. Although mean and standard deviations (SD) are shown, the significance test is based on non-parametric statistics. N = number of video-frames examined. W = Mann-Whitney W-test statistic

Species	Location	N	Mean \pm SD	W	p
<i>Asterias rubens</i>	Side	620	0.03 \pm 0.12	146859	0.00000
	Out	585	0.15 \pm 0.30		
<i>Cucumaria frondosa</i>	Side	620	0.02 \pm 0.18	183347	0.13278
	Out	586	0.01 \pm 0.07		
<i>Cucumaria frondosa</i>	Out	586	0.01 \pm 0.07	33216	0.00000
	Bottom	99	0.44 \pm 1.64		
<i>Cucumaria frondosa</i>	Side	620	0.02 \pm 0.18	34872	0.00000
	Bottom	99	0.44 \pm 1.64		
<i>Beggiatoa</i> sp.	Side	620	0.05 \pm 0.15	188356	0.02474
	Out	586	0.03 \pm 0.12		

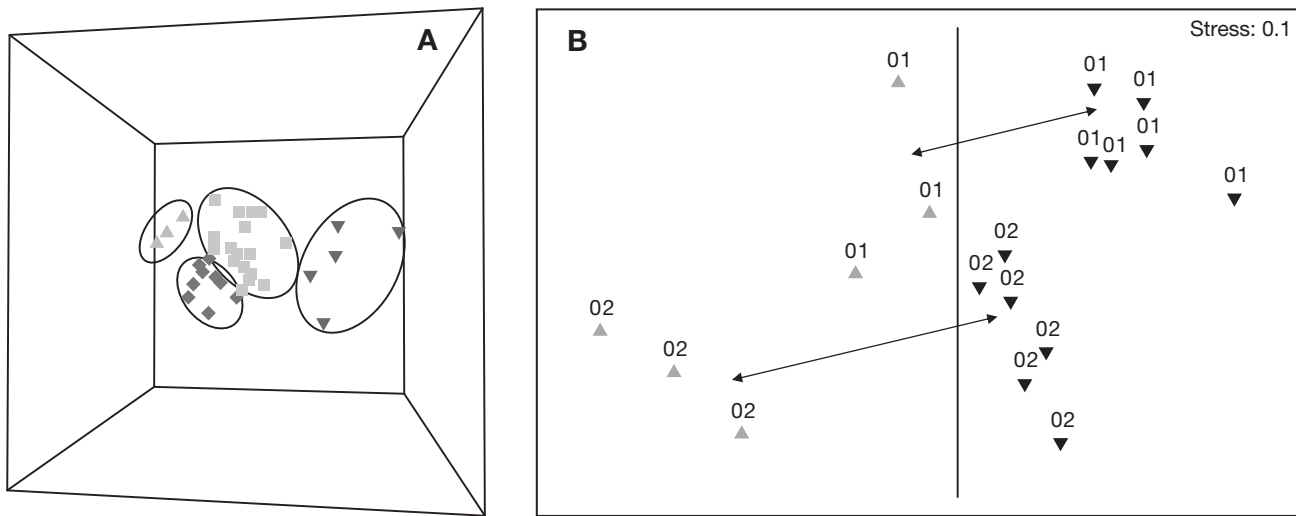


Fig. 5. (A) Mean 3D nMDS ordination plot for all Habitat A and B data in 2001, 2002 and 2004 (\blacktriangle = Habitat B, \blacktriangledown = upper Habitat A, \blacksquare = lower Habitat A, \blacklozenge = reference sites; 3D stress: 0.09). (B) 2D nMDS ordination of pockmark WAJ in 2001 and 2002, showing a difference in community structure ($R = 0.6$, $p = 0.1\%$) between macrofauna inside pockmarks with that of reference samples (arrows) maintained over time (vertical bar). \blacktriangle = samples from inside pockmark, \blacktriangledown = samples from reference locations outside pockmark; 01 = 2001, 02 = 2002

sional equilibrium number of taxa, \hat{S} . Grab samples from upper Habitat A, including WAA, WAB, WAC, WAD, WAE, appeared below the fitted regression line. This is consistent with these samples being at a pre-equilibrium stage in their succession and consequently originating later than samples at \hat{S} . We have calculated \hat{S} for each of the non-conforming samples with the equation above using the known area of each pockmark from which the sample originated (Table 5).

Species dominance for grouped samples. Dominance analysis of grouped data suggested differences in community structure between Habitats A and B (Table 6), notably the presence of the deposit feeding polychaete, *Diplocirrus hirsutus*, dominant in Habitat B (#4 in the hierarchy) but absent or rare (1 to 3 individuals) in all Habitat A locations.

Accumulated species number (S), density (D) and biomass (B). Comparisons between upper Habitat A source populations (REF1, REF2) and combined upper Habitat A pockmark samples showed mean values (\pm SD) for S (as number per 0.1 m^2) as follows: $S_{\text{source}} = 41.17 (\pm 3.19)$ versus $S_{\text{pocks}} = 23.4 (\pm 4.12)$, $t = 9.44$, $p = 0.000$. The mean values for D (as number per 0.1 m^2) were $D_{\text{source}} = 395 (\pm 70.47)$ versus $D_{\text{pocks}} = 137.07 (\pm 51.02)$, $t = 9.40$, $p = 0.000$. The mean values for B (as g wet weight per 0.1 m^2) were $B_{\text{source}} = 24.18 (\pm 13.75)$ versus $B_{\text{pocks}} = 18.51 (\pm 19.01)$ with $t = 0.66$, $p = 0.517$. We conclude that although accumulated species number and density were significantly less in upper Habitat A pockmark samples, this was not the case for biomass.

Similar comparisons between lower Habitat A source populations (REF4–9) and lower Habitat A pockmark

samples showed that $S_{\text{source}} = 41.0 (\pm 5.87)$ versus $S_{\text{pocks}} = 37.06 (\pm 5.44)$, $t = -2.58$, $p = 0.012$. The mean species number was significantly less in pockmark samples. Although S was normally distributed, this was not the case with D and B, which were skewed. The density and biomass were compared by non parametric statistics at the same confidence interval (not shown) and no significant difference between lower Habitat A source and pockmark samples was found.

Amphipoda and Cumacea. Gammaridean Amphipoda, and to a lesser extent Cumacea, were depauperate or absent altogether from upper Habitat A pock-

Table 5. Predicted equilibrium species number, \hat{S} , from $\log_{10} \bar{S} = 0.3873 \log_{10} A + 1.3555$, where \bar{S} = mean no. of species, and A = total pockmark benthic area

Pockmark	A (hm ²)	Observed \bar{S}	\hat{S}	\bar{S} as % \hat{S}
WAS	2.5	33	32	103
WAH	2.8	34	34	100
WAR	2.9	36	34	106
WAB ^a	3.0	27	35	77
WAA ^a	3.1	24	35	69
WAG	3.1	32	35	91
WAF	3.2	35	36	97
WAK	3.8	39	38	103
WAJ	4.1	39	39	100
WAI	4.2	38	40	95
WAM	4.3	42	40	105
WAE ^a	4.4	23	40	58
WAD ^a	8.1	24	51	47
WAC ^a	17.2	18	68	26

^aPockmark data not used in the equation

Table 6. Hierarchical order of dominant taxa in grouped samples from Habitats A and B. Each pockmark or REF location consists of 3 sample replicates, so n = 9 per group (except WAF where n = 2). Density is number per m²; na = absent. S = mean species number; S̄ = accumulated species number. Trophic types: Dep = deposit feeder, Sus = suspension feeder, Car = carnivore, Omn = omnivore, Alg = algal scraper

Taxon	WBA	WAF	WAI	WAM	REF1	REF4	REF7	WAA	WAE	Trophic type
	WBB	WAG	WAJ	WAR	REF2	REF5	REF8	WAB	WAD	
	WBC	WAH	WAK	WAS		REF6	REF9	WAE	WAC	
<i>Nucula proxima</i>	2	1	3	2	6	2	2	1	1	Sus/Dep
<i>Yoldia sapotilla</i>	3	2	5	5	4	6	9	4	2	Sus/Dep
Nemata	6	5	2	1	7	1	1	3	5	Dep/Car
<i>Mediomastus (ambiseta)</i>	9	3	1	3	2	3	6	2	3	Dep
<i>Ninoe nigripes</i>	7	4	4	6	5	4	4	5	6	Dep
<i>Terebellides stroemii</i>	1	9	6	10	1	7	3	26	42	Dep
<i>Nucula delphinodonta</i>	11	6	9	8	3	5	5	6	4	Sus
<i>Levinsenia gracilis</i>	16	7	8	4	23	8	17	16	8	Dep
<i>Frigidoalvania pelagica</i>	5	12	13	11	9	14	11	10	13	Omn/Alg
<i>Diplocirrus hirsutus</i>	4	na	71	na	na	na	na	34	27	Dep
Density (no. m ⁻²)	4917	2639	3966	5230	3948	4894	4033	1494	1361	
S̄	44	38	41	37	41	42	41	25	22	
Accumulated S	79	(70)	78	80	(?)	75	74	54	54	

marks (Table 7), i.e. from the successional younger samples. Only a single individual of *Deflexilodes (= Monoculodes) tessellatus* was present at WAD among upper Habitat A samples, whereas in all other groups from Habitat A 6 additional taxa occurred. For Cumacea in lower Habitat A, 9 taxa were present, but only 4 in upper Habitat A.

Discriminating taxa between upper Habitat A pockmark and reference samples. From a total of 138 taxa, the top 10 discriminating taxa contributed 38.7% of the difference between pockmark and reference samples

(Table 8). All of the taxa in Table 8 had significantly lower densities in pockmark samples. The SIMPER analysis (not shown) indicated that there were 6 taxa absent in pockmarks, but present in reference samples. The absent taxa in pockmarks were *Ampharete lindstroemi*, *Musculus niger*, *Rhodine gracilior*, *Phascolion strombus*, *Mayerella limicola* and *Lyonsia hyalina*.

Discriminating taxa between lower Habitat A pockmark and reference samples. In a similar analysis for lower Habitat A samples, the top 10 taxa were found to contribute 34.2% of the difference between pockmark

Table 7. Abundance of amphipod and cumacean taxa for the same grouped samples as in Table 6. Numbers indicate the total individuals per 0.9 m². Absence of a taxon is indicated by absence of an entry

Taxon	WBA	WAF	WAI	WAM	REF1	REF4	REF7	WAA	WAE	
	WBB	WAG	WAJ	WAR	REF2	REF5	REF8	WAB	WAD	
	WBC	WAH	WAK	WAS		REF6	REF9	WAE	WAC	
Amphipoda										
<i>Byblis serrata</i>	1									
<i>Leptocheirus pinguis</i>							1			
<i>Jassa marmorata</i>			1							
<i>Anonyx</i> sp.							2			
<i>Deflexilodes tessellatus</i>	1		8	2	2	31				
<i>Dyopodos monacanthus</i>	1									
<i>Mayerella limicola</i>		6	8	14	6	6	22			
<i>Casco bigelowi</i>	3	2	5	1	2	2	29			
<i>Megamoera dentata</i>					1					
Cumacea										
<i>Eudorella</i> sp.				3		6	8			
<i>Eudorella hispidata</i>	6	1	6	4		4		2		
<i>Diastylis</i> sp.							1			
<i>Diastylis quadrispinosa</i>	2	3	11	1	18	2	1	3	1	
<i>Diastylis sculpta</i>	2		2	2	1	2		2	1	
<i>Diastylis cornuifer</i>						1				
<i>Diastylis goodsiri</i>				1						
<i>Leptostylis longimana</i>						2				
<i>Campylaspis rubicunda</i>	7	3	10	3	1	2	4	1	1	

and reference samples (Table 9). Two species, *Yoldia sapotilla* and *Euchone incolor*, had significantly higher densities within pockmarks than at reference locations. Four taxa (*Nemata*, *Terebellides stroemii*, *Nucula delphinodonta* and *Anobothrus gracilis*) had significantly higher densities at reference than pockmark locations. The remaining 4 taxa had similar densities, non-significantly different between pockmark and reference samples. We found no taxa in the upper and lower Habitat A species list (not shown) that were unique to pockmarks when compared to reference locations. All 6 of the taxa absent in upper Habitat A pockmarks (see above) were present in lower Habitat A pockmarks.

Trophic group characteristics

Of the 138 invertebrates present in our list of taxa we were able to assign 89 taxa to a single trophic group as follows: 47 Dep, 22 Sus, 19 Car and 1 Omn. In addition, there were 20 taxa able to feed by more than one trophic mechanism, i.e. 6 Dep/Car, 5 Dep/Sus, 3

Sus/Alg, 3 Omn/Alg, 2 Dep/Omn and 1 Dep/Alg. All of these taxa were heterotrophic. We also found 2 taxa (*Thyasira flexuosa* and *Solemya* sp.) that are reported to metabolize chemosynthetically as is further discussed below.

Dominant taxa in both pockmark and reference samples was mixed, including both deposit and suspension feeders, but with a predominance of deposit feeders (Tables 6, 8 & 9).

DISCUSSION

Differences between macrofaunal communities inside and outside pockmarks

We have shown in this study of the benthic ecology of 14 pockmarks in Habitat A of Passamaquoddy Bay that pockmark benthic megafauna differs from nearby reference locations which are outside pockmarks, in that fewer *Asterias rubens* are present within pockmarks; aggregations of *Cucumaria frondosa* are only found on pockmark bottoms and *Beggiatoa* sp. is more

Table 8. Summary statistics of top 10 discriminating taxa between pockmark and reference locations within upper Habitat A. Densities rounded to nearest whole number. Pockmark densities for all listed species are significantly lower (95% confidence interval, by Mann-Whitney *W*-test) than for reference locations. Dep = deposit feeder, Sus = suspension feeder, Car = carnivore, Omn/Alg = omnivore/algal scraper

Taxon	Higher taxon	Rank	Mean contribution (%)	Mean density (no. m ⁻²)		Trophic type
				Pockmark	Reference	
<i>Terebellides stroemii</i>	Polychaeta	1	8.8	3	75	Dep
<i>Euchone incolor</i>	Polychaeta	2	4.0	8	41	Sus
<i>Nucula delphinodonta</i>	Bivalvia	3	3.9	24	54	Sus
<i>Anobothrus gracilis</i>	Polychaeta	4	3.7	3	34	Dep
<i>Periploma fragile</i>	Bivalvia	5	3.5	4	33	Sus
<i>Arctica islandica</i>	Bivalvia	6	3.5	1	30	Sus
<i>Aricidea</i> sp.	Polychaeta	7	3.3	9	35	Dep
<i>Crenella glandula</i>	Bivalvia	8	2.8	1	23	Sus
<i>Frigidoalvania pelagica</i>	Polychaeta	9	2.8	15	37	Omn/Alg
<i>Mediomastus (ambiseta)</i>	Polychaeta	10	2.5	38	54	Dep

Table 9. Summary statistics of top 10 discriminating taxa between pockmark and reference sites within lower Habitat A. Densities rounded to nearest whole number. *Significant difference in density (by Mann-Whitney *W*-test, confidence interval = 95%) between pockmark and reference samples. Dep = deposit feeder, Sus = suspension feeder, Car = carnivore

Taxon	Higher taxon	Rank	Mean contribution (%)	Mean density (no. m ⁻²)		Trophic type
				Pockmark	Reference	
<i>Nemata</i>		1	6.2	60	97*	Dep/Car
<i>Nucula proxima</i>	Bivalvia	2	5.0	71	85	Sus/Dep
<i>Levinsenia gracilis</i>	Polychaeta	3	3.8	40	28	Dep
<i>Yoldia sapotilla</i>	Bivalvia	4	3.5	59*	36	Sus/Dep
<i>Terebellides stroemii</i>	Polychaeta	5	3.3	33	47*	Dep
<i>Euchone incolor</i>	Polychaeta	6	2.8	26*	9	Sus
<i>Nucula delphinodonta</i>	Bivalvia	7	2.7	38	52*	Sus
<i>Mediomastus (ambiseta)</i>	Polychaeta	8	2.3	60	53	Dep
Oligochaeta		9	2.3	21	18	Dep
<i>Anobothrus gracilis</i>	Polychaeta	10	2.3	24	38*	Dep

abundant on pockmark sidewalls than at the bottom and outside pockmarks. Benthic macro-infauna within pockmarks showed 2 differences in comparison with reference locations outside, dependant on their position (upper or lower) in Habitat A: (1) upper Habitat A pockmarks (WAA, WAB, WAC, WAD, WAE) were depauperate in \bar{S} and density, and consequently showed major community structural differences; (2) lower Habitat A pockmarks (WAF, WAG, WAH, WAI, WAJ, WAK, WAM, WAR, WAS) showed minor differences in community structure, with similar taxa, but some at significantly higher and some at lower density when compared with reference locations. It was also established that larger pockmarks of lower Habitat A contained more equilibrium taxa.

Consequently, we are justified in rejecting the null hypothesis of no difference in community structure of benthos between the inside and outside of pockmarks, in favour of its alternative. Although Dando et al. (1991) did not include reference locations outside the single pockmark they studied in the North Sea, they compared their pockmark macrofauna results with previously published reference grab samples. As we also found for upper Habitat A pockmarks, the species per grab and density were all less in the pockmark studied by Dando et al. (1991) than at reference locations studied by others nearby.

Possible causes of macro-infaunal community differences

We propose 3 possible explanations for the community differences noted above:

- Disturbance theory. Physical conditions within pockmarks result in singular and/or intermittent disturbances which cause macrofaunal impoverishment. Following recolonization the macrofaunal community develops in a series of successional stages. The dispersal ability of each taxon can determine the rate at which it colonizes a recently formed pockmark
- Ecological niche theory. The pockmark niche has different environmental conditions than nearby reference locations. The differential suitability of colonizing propagules determines those taxa present in each niche at each stage of the succession
- Island biogeographic theory. Pockmark area itself, or factors related to it, influences equilibrium community structure as it does in some 'islands'.

These theories are all consistent with geological mechanisms 1, 2 and 5 proposed to form pockmarks, as briefly reviewed in the Introduction. The disturbance mechanism could involve seismic activity, which is known to occur in Passamaquoddy Bay (Burke & Stringer 1993, Burke 2004). The largest historical

earthquake in the area was a 5.9 event in 1904 (Leblanc & Burke 1985), with numerous smaller seismic events occurring up to the present time. A sudden displacement of a large volume of sediment and/or intermittent release of sediments or toxic liquids could result in the loss of the resident benthic macrofauna. We could also reasonably expect that the pockmarks so formed would have benthic communities at different successional stages.

Pockmark formation is likely to remove benthos on a scale comparable to ice scour. Conlan & Kvitek (2005) monitored the re-establishment of benthic macro-infaunal communities in the Canadian Arctic following disturbance by ice scour, which completely removed the benthic fauna from large areas of soft sediment. Estimates of the time required to achieve benthic recolonization and a near-equilibrium community (~80% of the mean species number at equilibrium, or \bar{S}) following ice disturbance was of the order of ~10 yr. Consequently, we would expect a similar time scale of ca. 5 to 15 yr for our upper Habitat A samples to reach near-equilibrium levels. The ages of origin, or time of last disturbance event, for these pockmark communities can be given as relative age for upper Habitat A pockmarks based on closeness to \bar{S} for each pockmark size (Table 5). Thus WAA > WAB > WAE > WAD > WAC, with WAC being the 'youngest' in this series.

Disturbance theory was applicable to upper Habitat A pockmark macro-infaunal communities, and perhaps to the North Sea pockmark community studied by Dando et al. (1991). Disturbance events may occur at the time of formation, or subsequent to formation, during the history of upper Habitat A pockmarks. Disturbance events may include dispersal of sediments and/or the presence of toxic liquids at the sediment-water interface resulting in extirpation of the macrofauna. This is followed by recolonization by larvae, or other propagules, which are carried in currents. Circumstantial evidence supporting the view that upper Habitat A pockmarks were at a pre-equilibrium stage of successional development when sampled is that in \bar{S} -A plots the pockmark data appear below the regression line for lower Habitat A pockmarks. A possible alternative hypothesis (that upper Habitat A pockmark colonists are from a different source habitat) can be discounted on the basis of backscatter similarities between upper and lower regions. During early development of benthic successional communities the competitive/supportive interactions which are so characteristic of mature equilibrium communities have not yet fully developed. The dissimilarity analysis for upper Habitat A identifies 7 early successional taxa (Table 8) which are not among the top 10 of the lower Habitat A equilibrium community (compare Tables 8 & 9). Evidence that amphipods and cumaceans are

under-represented in upper Habitat A pockmarks (Table 7) could be due either to niche differences between upper and lower regions, or to poor colonizing ability. We propose that it is poor colonizing ability, exemplified by these 2 groups, which results in the differences in distribution. It results because amphipods and cumaceans have direct development with eggs laid in a marsupium or brood pouch, where they spend the early part of their juvenile lives. In amphipods there is evidence of parental care within the marsupium (Thiel 1999). Egg sizes are relatively large and consequently numbers low, generally in the 10 to 100 range, in contrast to the thousands of small eggs and long pelagic larval life of many polychaetes, bivalves and echinoderms. The latter make up the bulk of our species list and dispersal of their pelagic larvae is passive and efficient in the dynamic tidal and wind currents of Passamaquoddy Bay. In contrast, dispersal in gammaridean amphipods is less efficient, either by passive rafting or by active swimming (Myers 1993, Kumagai 2006).

Our present data favor explanations based on disturbance rather than ecological niche theory, because no macrofaunal taxa were found which were unique to pockmarks (as would be required by the latter theory). Also, the 6 taxa absent in upper Habitat A pockmarks all occurred in lower Habitat A pockmarks, consistent with them appearing only in the mature equilibrium community. The megafaunal suspension feeder *Cucumaria frondosa* was the only example of a taxon especially suitable for the pockmark niche, as required by ecological niche theory. This holothurian occurred both inside and outside pockmarks, but reached high densities in small clumps only at the bottom of some lower Habitat A pockmarks. In all upper Habitat A pockmarks *C. frondosa* was absent.

Island biogeographic theory is applicable to lower Habitat A pockmarks as 'islands' because they fit the species–(pockmark) area curve. Modern interpretation of the log linear species–area curve is that it may be explained by several mechanisms (McGuinness 1984). These include random placement of taxa and individuals within 'islands', patch diversity increasing with area; the equilibrium theory of MacArthur & Wilson (1963), proposing larger 'islands' which have higher values of \hat{S} and density because of higher immigration and lower extinction rates; and modifications of disturbance theory, whereby disturbance event frequency increases with area. We were unable to examine these hypotheses further with present data. Future examination will require a more focused study, including field experimentation, before the macro-infaunal community differences between source population and lower Habitat A pockmarks can be explained.

These results imply that a pockmark geological disturbance event sufficient to extirpate benthic macrofauna occurred in the upper Habitat A area <15 yr prior to sampling. In contrast, the last pockmark geological disturbance event in lower Habitat A occurred >15 yr prior to sampling. Since all lower Habitat A pockmarks had reached macro-infaunal community equilibrium, we were unable to age them as we did for upper Habitat A samples.

Passamaquoddy Bay ecosystem

Our coring observations are consistent with a moderate carbon burial rate, with benthic fauna unable to process all of it, so that microfloral, anaerobic processes predominate at depths below a few millimetres in the sediment profile. Although based on very limited data, we propose the following hypothesis to explain the difference we observed between pockmark and reference cores: near the sediment–water interface, sulphate-reducing bacteria undertake anaerobic oxidation, $\text{SO}_4^{2-} + 2\text{CH}_2\text{O} > \text{H}_2\text{S} + 2\text{HCO}_3^-$. Anaerobic bacterial activity is limited by oxygen diffusing into the sediment. As sediments become more anoxic with increasing depth, sulphate-reducing anaerobic bacteria increase, producing a peak of sulphide at ~15 cm depth. Below this depth, available carbon (e.g. lactate and pyruvate) becomes limiting for sulphate reducers. The result is an exponential decline in sulphide with depth seen only in reference cores. We hypothesize that an increased supply of methane gas directly beneath pockmark sediments allows a second oxidation pathway there: $\text{SO}_4^{2-} + \text{CH}_4 > \text{HS}^- + \text{HCO}_3^- + \text{H}_2\text{O}$. Methane oxidation accounts for the continued microbial production of high sulphide levels (600 to 1200 μM) at increasing depths in the pockmark profile. If this interpretation is correct, then our limited sampling, to maximum depths of 96 cm, has not located the DNS (depth of no sulphate interface of Borowski et al. 1996), which is where sulphate itself becomes limiting for both anaerobic bacterial pathways shown above.

The discovery of small, well-spaced holes inside and outside pockmarks could be due to biogenic methane escaping from the sediment, or to burrowing by the mobile fauna. Similar holes of different sizes have previously been reported from the Gulf of Mexico by MacDonald et al. (1994), the Haakon Mosby mud volcano off Norway (Vogt et al. 1997, Milkov et al. 1999) and in the North Sea (Judd et al. 1997). As with these previous authors, we found little direct evidence of gas bubbling: one gas bubble in ~4 h of observation (from the sidewall of WAG at 105330 GMT) from the holes in our videographs. This is in contrast to active seep areas in the

Gulf of Mexico (MacDonald et al. 1989). One possible reason for the absence of bubbling may be that methane gas ebullition is episodic in nature, as has been shown in freshwater lakes by Mattson & Likens (1990) to occur only when air pressure is low, and in the sea due to tidal changes of pressure (Scranton et al. 1993, Leifer & Patro 2002). Whether air pressure or the hydrostatic pressure variations associated with tides changed the patterns of gas ebullition in Passamaquoddy Bay remains to be determined, e.g. by *in situ* time lapse photography. Alternatively, the holes are the result of burrowing (or at least secondarily used) by decapod crustaceans such as *Homarus americanus*, *Cran- gon* spp., and *Pandalus* spp., or the hagfish *Myxine* sp. All are well known from Passamaquoddy Bay by other sampling methods. Physical or biogenic causation of the holes cannot be confirmed with presently available data, but a physical cause is consistent with the absence of digging wastes around the holes, as might be expected if they were of biogenic origin. As the maximum grab digging depth was 16 cm, it is likely that strong burrowing forms such as lobsters and shrimp would be missed, and hence absence in grab samples is not conclusive evidence of their absence in sediments.

The dominant taxa by abundance are similar to the fine-sediment taxa in the Gulf of Maine described by Rowe et al. (1975) and Watling et al. (1988). Consideration of the trophic types of the macro-infauna of Passamaquoddy Bay show that most species are dependant on transported carbon, rather than on chemosynthesis of reduced sulphur or carbon sources. We found no evidence of authigenic carbonate-cement bioherms as reported by Hovland (2002) in the North Sea, although the occasional presence of patches of *Beggiatoa* suggests that the redox potential discontinuity is at the sediment–water interface here. Most of the macro-infauna within Passamaquoddy Bay consists of small deposit feeders with some being small suspension feeders and some carnivores/omnivores. Two species, *Thyasira flexuosa* and *Solemya* sp., are reported to carry chemosynthetic bacteria. These bivalves have chemoautotrophic, reduced sulphur-oxidising, symbiotic bacteria in the gill tissues (Southward 1986). Species of *Thyasira* lack a siphon and use the foot to construct a burrow to obtain both oxygen and dissolved sulphides, the latter for use by its endosymbiotic bacteria (Dando et al. 2004). *Thyasira flexuosa* has recently been shown by Dufour & Felbeck (2006) to utilize both a particulate carbon diet by suspension feeding, as well as utilizing chemosynthetic bacteria, probably in a facultative manner. The rarity of *Solemya* sp., only occurring in one pockmark, and relatively low mean densities of *Thyasira flexuosa* (12 ind. per m²), suggest that chemoautotrophy among macro-infauna is of relatively minor importance to the energy budget of the Bay.

The megafauna (Table 4) of the present study is typical of the Gulf of Maine silt/clay sediments (Langton & Uzzmann 1989, Langton et al. 1990) and occur at low densities. The large-bodied sea cucumber, *Cucumaria frondosa*, was found both in- and outside pockmarks, although aggregated populations only occur on some pockmark bottoms in Passamaquoddy Bay. Recent observations in Arctic waters made by remotely operated vehicle on the Chukchi Plateau (I. MacDonald, Texas A&M, pers. comm.) showed aggregations of a different species of sea cucumber (*Kolga hyalina*), smaller than *C. frondosa*, also within the center of depressions that are assumed to be pockmarks at depths exceeding 900 m. Dense aggregations of holothurians have previously been reported off southern California (Smith & Hamilton 1983) and in Antarctic seas (Gutt & Piepenburg 1991), which have not been associated with pockmarks. This suggests that the phenomenon may be geographically widespread, is not limited to shallow water, nor to a single species of holothurian. We propose that aggregations of sea cucumbers on the bottom of pockmarks are linked to the special hydrodynamic conditions found there, which cause turbulent re-suspension of material, as described by Josenhans et al. (1978). These conditions may present more favourable feeding opportunities for these megafaunal suspension feeders

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