Microbial Activity and Ultrastructure of Mineral-Based Marine Snow from Howe Sound, British Columbia[1]

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Electron microscopy and biochemical measurements of heterotrophic and enzymatic activities were made on marine snow and underlying sediments collected from Howe Sound, British Columbia. SEM showed the marine snow to be accretions of comminuted phytoplankton, fecal pellets, cellular material, and mineral particles bonded by films and coatings of an amorphous material. The amount of amorphous substance decreased as Howe Sound became increasingly marine. Rod, cocoidal, and filamentous bacteria were cultured from the marine snow. Heterotrophic microbial activity increased seaward and was found to be higher in marine snow than in underlying sediments. Phosphatase, protease, laminarinase, and xylanase were also more active in marine snow whereas sulfatase activity was found to be higher in the sediments. β-Glucosidase activity was demonstrated in marine snow only at sampling stations isolated from outer Howe Sound and the Strait of Georgia by a submarine sill.

Des débris marins en suspension et des sédiments sous-jacents prélevés dans le détroit Howe, en Colombie-Britannique, ont été examinés par microscopie électronique et ont fait l'objet d'une mesure biochimique de leurs activités hétérotrophes et enzymatiques. La microscopie a montré que les débris étaient constitués d'accrétions de fins débris de phytoplancton, de pastilles fécales, de matériaux cellulaires et de particules minérales liés par des films et des revêtements de matière amorphe. La quantité de substance amorphe diminuait à mesure que l'on se dirigeait vers la mer. Des bactéries en forme de bâtonnets, de coques ou de filaments provenant des débris en suspension ont été cultivées. L'activité microbienne hétérotrophe augmentait en direction de la mer et était plus importante dans les débris marins que dans les sédiments sous-jacents. La phosphatase, la protéase, la laminarinase et la xylanase des débris marins étaient aussi plus actives tandis que l'inverse était vrai pour la sulfatase. L'activité de la β-glucosidase n'a pu être démontrée que dans les débris marins provenant des stations de prélèvement isolées de la partie externe du détroit Howe et du détroit de Géorgie par un seuil sous-marin.

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Particulate matter in seawater is derived from a number of sources (Riley 1970; Cauwet 1978; Syvitski et al. 1985). The components comprising these particulates include minerals, fragments of phyto-zooplankton, fecal pellets, and particulate organic material formed from previously dissolved organic matter. Collectively, this material has traditionally been called marine snow (due to its appearance in deep green water), "floc", particulate matter, and several other terms. Syvitski and Murray (1981) used the term "agglomerate" to describe organic and inorganic matter weakly held together by ionic charge, surface tension, and organic cohesion. Bacteria can perform an important role in the formation and growth of marine particulates by both the recovery and conversion of dissolved organic matter into particulate form (Paerl 1978) and aggregating other particles together with secretion (Paerl 1973; Syvitski et al. 1985).

Research in the warm waters off the California coast (Alldredge 1976, 1979; Silver et al. 1978; Trent et al. 1978; Shanks and Trent 1979; Alldredge and Cox 1982; Knauer et al.

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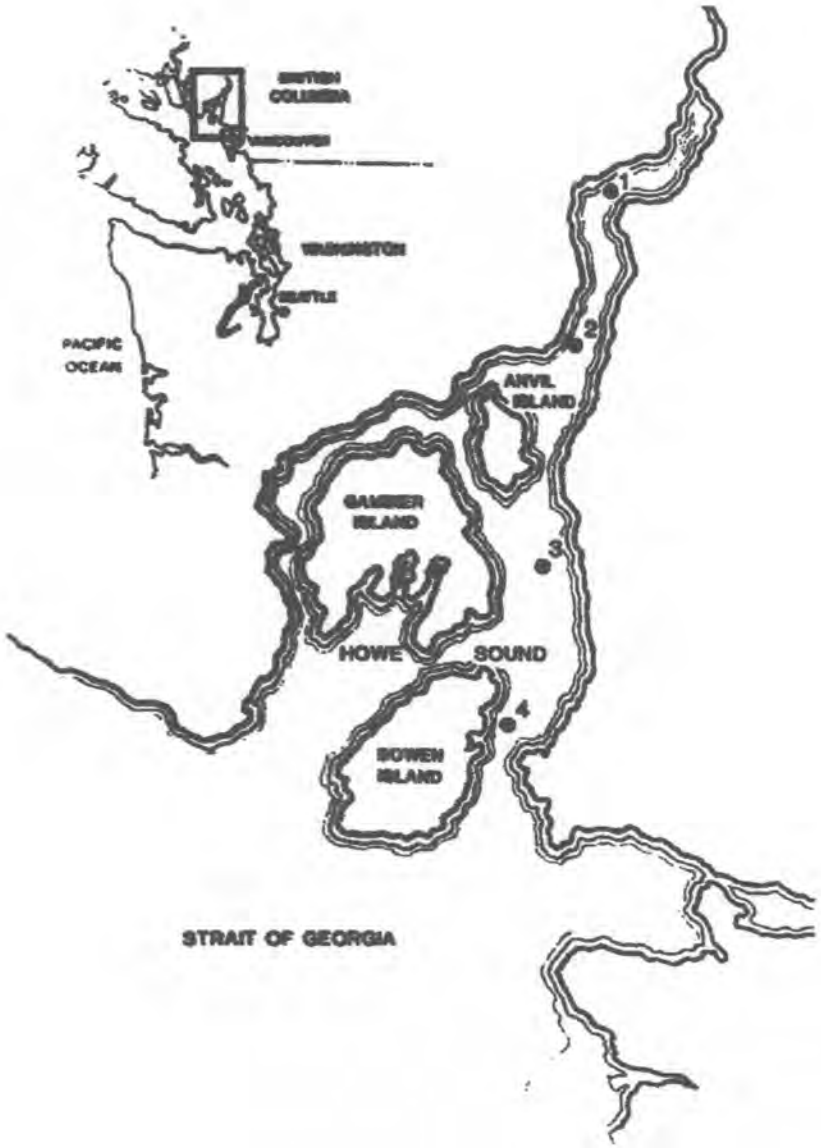

FIG. 1. Study area and sampling stations in Howe Sound, B.C.

1982; Prezelin and Alldredge 1983) and the Sargasso Sea (Riley et al. 1965; Caron et al. 1982) demonstrated the presence of a biologically based marine snow. Syvitski and Murray (1981), working in the cold waters of British Columbia, observed the presence of a second type of agglomerate which is mineral based and contains little biological material. This second type of marine agglomerate is the subject of this research. It is heavily laden with silt and clay from glacial runoff of rivers that discharge into fjords on the northwestern coast of Canada. Both types of agglomerate material may act as sites of nutrient enrichment and regeneration, contain high concentrations of bacteria/phytoplankton available for grazing by zooplankton, generate microscale habitat heterogeneity, and transport organic matter to the sediment at velocities different from individual planktonic organisms.

Little information has been available on the microbial productivity, heterotrophic activity, or enzymatic activities which are probably responsible for significant alterations in the structure and nutritive value of marine agglomerates. Because of the usual loss of nutrient-rich material from the photic zone toward depth in a water column, mechanisms to produce agglomerates which become increasingly richer in microbial cell mass are of interest to the total nutrient budget of benthic and water column organisms.

In this study, we have concentrated on the microbial activity, both by whole organisms in communities and by the enzymes that those organisms produce, of macroagglomerates in the water column and uppermost sediment layer of a Canadian fjord. In addition, we have evaluated the microstructure of the habitat available within marine snow macroagglomerates by scanning electron microscopy (SEM).

Materials and Methods

Sampling Site

Samples for this study were collected in April 1984 from Howe Sound, British Columbia, using the research submers-

ible *PISCES IV*. Howe Sound, located 20 km north–northwest from Victoria, B.C., is the fjord of the Squamish River drainage (~3636 km^2) from the Pacific Ranges of the Coast Mountains (Fig. 1). The 42-km-long fjord broadens from approximately 2 km at the Squamish River delta to 18 km at its terminus in the Strait of Georgia and has a mean water maximum depth of 325 m. The Squamish River is the source of most freshwater and terrestrially derived suspended materials discharged into Howe Sound.

The water masses of Howe Sound and the Strait of Georgia are partially separated by a submarine sill located across much of the mouth of the fjord (outer sill). A second sill (inner sill) crosses the fjord 25 km into the Sound, about 1.5 km north of Anvil Island, at a mean water depth between 35 and 70 m.

Samples were taken at the vicinity of 49°35′N, 123°14′W (station 1), 49°35′N, 123°15′W (station 2), 49°28.5′N, 123°16′W (station 3), and 49°23.5′N, 123°14′W (station 4), with dive sites fixed by bathymetry and by radar and visual triangulation. The four stations comprised a north–south transect along the middle of the main fjord channel. Two stations (1 and 2) were located north of the inner sill and two stations (3 and 4) were located between the outer and inner sills.

Comparison sampling was also done during dives made in Howe Sound and Bute Inlet (October 1983), in Saanich Inlet (March and April 1984), and in Howe Sound (October 1984).

Sampling Methods

Observations were made and samples collected using the manned research submersible *PISCES IV* operated from its support vessle, M.V. *PANDORA II*. Three sampling methods were used with *PISCES IV*.

One method used three butterfly samplers (Niskin) fixed to the submersible's crash bar and triggered by the hydraulic arm. These were used to obtain water samples from desired depths and locations.

Method 2 used an electrically operated water pump to draw samples through a flexible 8.0-cm-diameter plastic tube. The tube inlet, fastened to *PISCES IV*'s hydraulic arm, allowed specific agglomerates or locations (e.g. nephloid layer, layer of dense snow, single large agglomerates) to be sampled. Collections were pumped into numbered acrylic jars mounted by a rotating plate to sequentially position each jar at the pump's discharge port. A brushed nylon cloth filter supported by screening placed over the pressure relief outlet for each jar served to retain the collected material. By maintaining a desired depth, and pumping for several minutes, large quantities of marine snow could be accumulated by this mechanism. Samples were kept in the original water taken at depth after return to the surface. Material from cloth filters was resuspended in small volumes of seawater taken from the acrylic jars. The original structure of the flocculant material was disrupted but maximally recovered by this process. Flocculated material reaggregated with settling, but was resuspended to maintain even distribution for measurements of bacterial counting, heterotrophic glucose utilization, and enzymatic activity. Sediments were diluted 1:10 or 1:100 with filter-sterilized seawater to produce an even slurry for biochemical determinations. Agglomerate and sediment suspensions were then vacuum filtered onto 0.22-μm Millipore filters and air dried to obtain dry weight measurements.

A large rectangular box trap, with top and bottom ends retracted prior to launch, was mounted to the submersible's crash bar and used to recover undisturbed specimens of agglomerates for electron microscopy (EM) and microbial culture. *PISCES IV* could be maneuvered to position the open box to enclose an agglomerate. When the box ends were closed, a water-tight seal was formed which trapped the agglomerates with several litres of seawater.

Following retrieval of *PISCES IV* aboard *PANDORA II*, individual agglomerates captured with the box trap sampler were transferred to Petri dishes containing SLX agar (Amy and Morita 1983) and incubated 10 d at 10°C or prepared for EM.

Electron Microscopy

From the box trap sampler, intact agglomerate samples for EM were floated into glass vials. Seawater was replaced by 3% glutaraldehyde in filter-sterilized buffered seawater and the specimens were fixed for 2–4 h. Samples were transferred to the laboratory in 0.25% glutaraldehyde in filter-sterilized seawater.

For microscopy, samples were placed in dialysis tubing and placed in fresh tap water to remove sea salts and then floated onto 15-mm-diameter cover glasses and freeze dried 24 h at 1×10^{-3} torr. After drying, cover glasses were fastened to aluminum planchets using DUCO adhesive, coated for conductivity with 60:40 Au/Pd alloy by vacuum evaporation, and examined in an AMRAY 1000A scanning electron microscope. Several dozen agglomerates were examined and several hundred SEM images recorded.

Bacterial Counts

Bacterial counts were determined by the acridine orange direct count method (Hobbie et al. 1977; Daley and Hobbie 1975). Bacterial carbon values were determined as described by Albright (1983a, 1983b). Bacteria were released from particles by the pyrophosphate-sonication method of Velji and Albright (1986).

Heterotrophic Activity

Relative heterotrophic uptake of dissolved organic matter was assayed with a modification of the one concentration method of Griffiths et al. (1978). Five millilitres of agglomerate suspension or either a 1:10 or 1:100 sediment dilution (with filter-sterilized seawater) was incubated with 0.39 mCi [^{3}H] glucose (12.6 mCi·mmol^{-1}) for 1 h at in situ temperature. Microbial uptake was terminated by addition of 100 μL of 8% EM-grade glutaraldehyde. The samples were filtered onto 0.45-μm Millipore filters, air dried, and stored in 20-mL scintillation vials for return to Oregon State University. Glucose uptake was quantified using a Beckman LS-8000 liquid scintillation counter with quench correction by the channels ratio method. Uptake was calculated as picomoles of glucose per gram per hour.

Hydrolytic Enzymes

To provide a sufficient concentration of material for analysis, 1–50 cm^3 of agglomerate suspension was concentrated by gentle filtration onto 0.45-μm Millipore filters.

Phosphatase activity was measured using a modification of the spectrophotometric assay of Morita and Howe (1957) and Tabatabai and Bremner (1969). One cubic centimetre of sediment or a filter of concentrated particulate material was

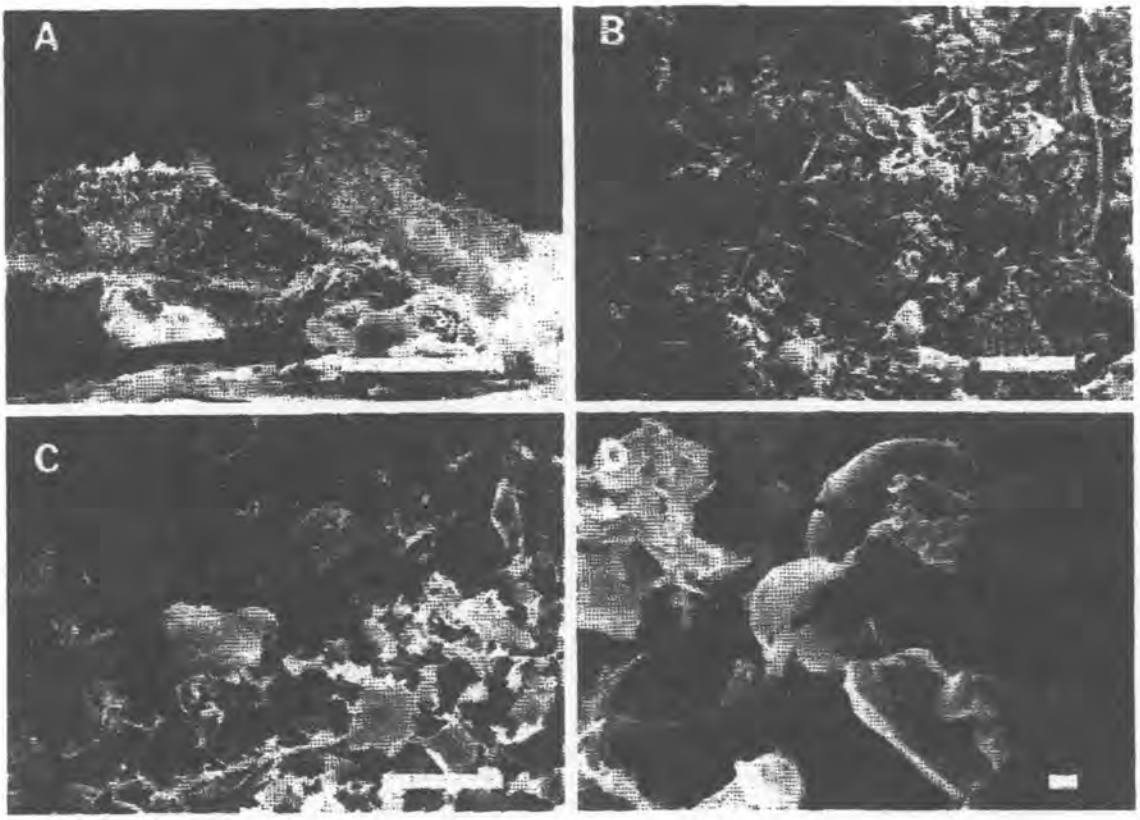

FIG. 2. Marine snow, Howe Sound, station 2, 250 m, October 1983. (A) Typical agglomerate flake structure; bar = 500 μm. (B and C) Agglomerate microstructure characterized by rough texture, great porosity, and much comminution of included particles; bars = 10 μm. (D) Agglomerate components including phytoplankton and planktonic debris (P), triptonic clay and silt particles (S), and amorphous thin films of organic material (OM); bar = 1.0 μm.

brought to a total volume of 2 mL with 0.1 *M* tris(hydroxymethyl)aminomethane (THAM) buffer (pH 7.5), and 1.0 mL of buffer containing 5 *mM* *p*-nitrophenylphosphate was added. After incubation for 1–6 h at 25°C, the reaction was terminated with 2 mL of 0.5 *N* NaOH and 0.5 mL of $CaCl_2$. Following centrifugation for 10 min at 2000 × *g*, the $OD_{410\,nm}$ of the supernatant was measured and enzyme levels were calculated as micromoles of *p*-nitrophenol released per gram per hour.

Sulfatase and β-glucosidase levels were measured using *p*-nitrophenylsulfate and *p*-nitrophenyl-β-D-glucoside as respective substrates and incubated for 2–24 h until color formation.

Protease levels in 1 cm^3 of sediment or from a filter of concentrated particulate material were measured using the method described in Griffiths et al. (1983), adapted from Ladd and Butler (1972). Results were expressed as micromoles of tyrosine equivalents released per gram per hour. The levels of three enzymes responsible for the hydrolysis of major plant (cellulose and xylan) and algal (laminarin) polysaccharides were measured in each sediment sample and one agglomerate sample. One cubic centimetre of sediment or a filter with the residue of 50 mL of agglomerate suspension (station 4) was mixed with 1 mL of 0.1 *M* acetate buffer (pH 5.5) and incubated with 1 mL of a 1% solution of either carboxymethylcellulose, laminarin, or xylan (Sigma Chemical Co.) and 0.2 mL of toluene at 25°C. After 17–24 h, the reaction mixture was centrifuged for 10 min and the reducing sugar content of the supernatant was determined with the dinitrosalicylic acid reagent of Bernfeld (1955). Enzyme levels were calculated as nanomoles of glucose equivalents released per gram per hour.

Results and Discussion

Over the duration of the study, marine snow agglomerates ranging in size from about 0.25 to 2500 mm^3 were seen. Agglomerates were observed to be in three forms: (1) flat, roughly circular flakes and sheets, (2) slender threadlike filaments, and (3) globular masses. Most flakes were 0.5–5.0 mm across (0.25–25.0 mm^2) by 50–100 μm thick (0.01–2.5 mm^3). Filamentous forms generally had diameters of 0.5–10.0 mm and lengths between 2 and 400 mm. Globular agglomerates were spheroidal (5.0–50.0 mm in diameter) to elliptoidal (5.0–10.0 mm in diameter by 10–30 mm long). All forms were very fragile and with only slight water turbulence were disrupted and disintegrated into many smaller fragments.

Figure 2A illustrates a typical agglomerate of Howe Sound marine snow. Figures 2B and 2C reveal that a great amount of material is accreated to form even small agglomerates. This results in a tremendously porous microstructure and a surface texture which is very roughened at the microscopic level. Hence, the actual surface area and the volume of agglomerates are very much different from what might be calculated from estimates based only on their macroscopic dimensions.

All agglomerates recovered from sample sites during the study were accretions of phytoplanktonic and zooplanktonic

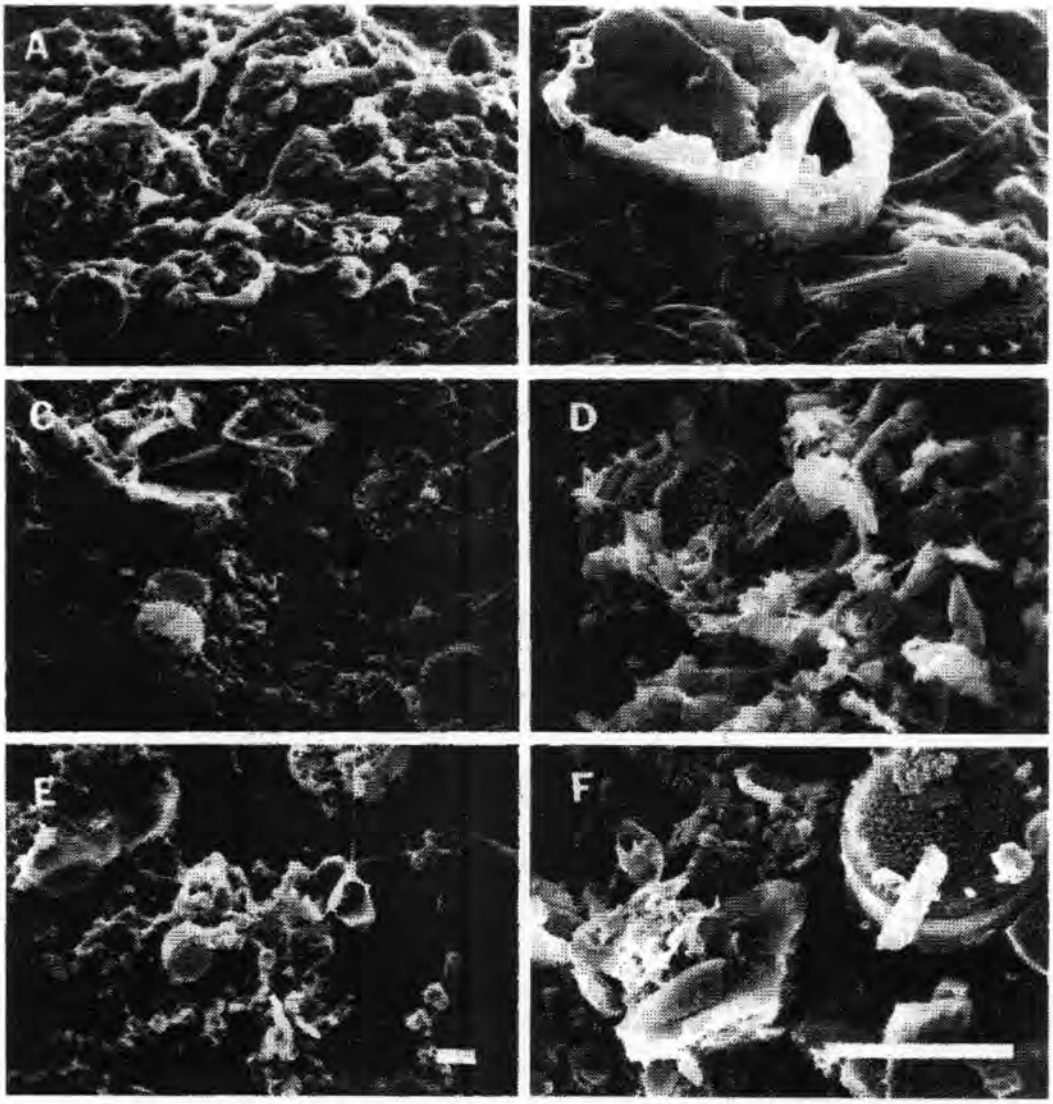

FIG. 3. Trend toward reduction in the amount of amorphous coating found adhering to agglomerates of marine snow from (A and B) station 1, 200 m, (C and D) station 2, 280 m, and (E and F) station 3, 100 m, collected in April 1984; bars = 10 μm.

cells and debris and particles of silts and clays. Many components had undergone partial dissolution and extensive physical breakage. The material adhered together by thin, amorphous interconnecting films and coatings (Fig. 2D). Ionic and electronic charge, chemical polarity and bonding, pH-related precipitation, and surface tension effects undoubtedly also affect structural cohesion (Scholkovitz 1976; Syvitski and Murray 1981; Avnimelech et al. 1982; Edzwald et al. 1974; Rashid et al. 1972), but these forces cannot be measured by microscopy.

Comparison of Fig. 2 with Fig. 3 shows that the fundamental composition of agglomerates appeared similar throughout the year and at all depths. All our samples of marine snow from various depths and times from Howe Sound, Bute Inlet, and Saanich Inlet were found to be compositionally similar when examined with SEM (data not shown). This suggests widespread general consistency in the biological and detrital components of marine snow found in water masses contiguous with the southern end of the Strait of Georgia and supports the findings of Syvitski and Murray (1981). However, other researchers have shown changes in the chemical composition of mineral components both in Howe Sound (Syvitski and MacDonald 1982) and adjacent Bute Inlet (Farrow et al. 1983; Syvitski et al. 1985).

Figure 3 demonstrates a progressive reduction in the amount of amorphous material and an increase in distinct components in marine agglomerates at three stations along a transect from station 1 to station 3. The agglomerates from station 1 (Fig. 3A and 3B) show a strikingly different structure from those from either station 2 (Fig. 3C and 3D) or station 3 (Fig. 3E and 3F). In the former the amorphous coating is more apparent and results in surface textural patterns which are larger and more rounded, giving the structure a noticeably more cohesive character. Similar observations have been reported for Howe Sound by Syvitski and Murray (1981), but the trend is not confined to the waters of southern British Columbia. Studies by Emery and Honjo (1979) and Honjo (1978), for example, reported finding more amorphous films associated with coastal

water agglomerates than with offshore agglomerates in samples taken off eastern Asia and between western Africa and the mid-Atlantic ridge.

Comparison of Fig. 2 and 3 shows that the relative amount of amorphous substance associated with agglomerates at station 2 in October 1983 (Fig. 2) appeared lower than the amount of amorphous component detected at the same station in April 1984 (Fig. 3C and 3D). In October, freshwater runoff is low, and in response to lower temperatures and shorter daylengths, the planktonic standing crop declines. In spring, freshwater runoff is higher and temperature and photoperiod increase, which results in an expanding plankton crop. We postulate that the organic matter available to precipitate with marine snow agglomerates probably shifts up or down the fjord on a seasonally cyclic basis corresponding with cycles in freshwater and terrestrially derived input, salinity, temperature, and photoperiod. The amorphous-dominated material in the upper fjord provides surfaces attractive for bacterial colonization whereas the more complex lower fjord agglomerates include numerous planktonic cells and debris. The potential significance of this has been suggested in Knight Inlet, B.C., where the distribution of benthic fauna may reflect feeding strategies related to composition of detritus (Syvitski et al. 1985).

Structural differences in the composition of marine snow cause variation in porosity, permeability, agglomerate density, surface area, and surface texture. Such variations can have significant consequences for the organism grazing on these agglomerates. While certain microbiological activities occur in marine snow in general, other specific activities may be limited to certain structural configurations within the total mass of the particulates present in the water mass.

Although SEM of agglomerates showed the absence of extensive microbial colonization, many colonies were readily cultured from the agglomerates placed on SLX agar. Rod, coccoidal, and filamentous bacteria were recovered in culture and documented by EM. These observations suggest that there is a great diversity of microorganisms associated with marine snow and that those microbes able to exploit the nutrients and microhabitats of marine snow may do so primarily as individual cells, microcolonies, or organisms intermittently associated with the agglomerates.

Results for heterotropic activity as [^{3}H]glucose uptake, bacterial counts, and carbon-based biomass and the levels of seven major hydrolytic enzymes involved in the degradation of organic matter and nutrient regeneration from agglomerate and sediment samples are listed in Table 1. The overall ranges of sediment enzymes detected in this study overlapped those reported in similar assays, except β-glucosidase, for sediments from a coastal embayment on the Aleutian Peninsula, Alaska (Griffiths et al. 1983), and the Yaquina River estuary on the Oregon coast (B. A. Caldwell, unpubl. data). In addition to differences between agglomerate and sediment samples at a given station, substantial differences were seen in many variables between stations.

Glucose uptake levels, by weight, were 2–60 times greater (station means) in the agglomerates than in the underlying sediments. The highest agglomerate to sediment ratio was found at station 2 and the lowest at station 3. Glucose uptake in the agglomerates increased seaward whereas a more complex pattern was found in the sediment. Here, uptake declined from station 1 to 2, station 3 had the highest, and the amount declined again at the most seaward station 4.

Comparison of bacterial counts and biomass, as bacterial carbon, was less clear. Greater bacterial counts were found in sediment at station 1, while numbers overlapped at stations 2 and 3. Sediment bacterial counts were not made at station 4. When expressed as bacterial carbon, the sediment biomass was higher than agglomerate biomass at station 1, much less than agglomerate biomass at station 2, and overlapped at station 3. Bacterial counts for water samples not containing agglomerates were between 2.3 and 6.8 $\times$ $10^5 \cdot mL^{-1}$, which is similar to previous reports for these waters (Albright 1983a, 1983b).

To evaluate the relative microbial activities of agglomerate and sediment samples and of the same material at different locations, glucose uptake was standardized on a per unit bacterial carbon basis (as picomoles of glucose per gram of bacterial carbon per hour). These values are listed in Table 1. Using this analysis, the range of values for the agglomerates from stations 1 and 2 (0.279–0.495 and 0.345–0.624) was much greater than the corresponding sediment ranges (0.016–0.018 and 0.050–0.083). This indicates that the microbial populations at these stations were more active in the agglomerates than those in the sediments. Station 3 produced overlapping ranges for agglomerate (0.217–0.747) and sediment (0.140–0.311) samples. One possible explanation for this is that more of the organic material at these seaward stations comes from readily usable planktonic sources, while recalcitrant terrestrial materials from river input influence the two more landward stations.

Phosphatase, which is involved in the mineralization of inorganic phosphate from organic matter, had higher levels in the agglomerate samples than in the sediments, and the highest levels were in stations 1 and 2 north of the inner sill. This may be because the enzyme is absorbed to riverine clay particles and humic materials in the agglomerates — a phenomenon known to occur in soils (Burns 1980). This is further supported by the previously mentioned decrease in amorphous material with which these enzymes may be associated, in the seaward transect from station 1 to 3.

Detectable levels of sulfatase, an enzyme responsible for the remineralization of sulfate from organic sulfate esters (Fitzgerald 1976), were found only in the sediment samples. Since this enzyme is typically inducible, its apparent absence in the agglomerate could be due to the abundance of sulfate in the surrounding seawater. In contrast, activities in the sediments could be indicative of sulfate regeneration to support anaerobic metabolism at some depth within the sediment (King and Klug 1980). Sediment sulfatase levels increased seaward to station 3, but to a greater extent than phosphatase, and then declined slightly.

Levels of β-glucosidase in agglomerate samples were detected only at stations 1 and 2 where they were 6 orders of magnitude greater than in the corresponding sediment levels. The absence of detectable enzyme levels at the two lower stations may be due to the same phenomenon that caused the rapid decline in agglomerate phosphatase activity, i.e. rapid sedimention with extensive coatings of amorphous material, including adsorbed enzymes. This is partially supported by the fact that the highest level of sediment β-glucosidase was at station 1 and the levels progressively dropped seaward.

In a limited sampling of protease and cellulase (stations 3 and 4) and laminarinase and xylanase (one concentrated sample from station 4), the levels in the agglomerates were also much greater than in the sediments, except for cellulase which was not detected in the sediment at station 4. The sediment levels of these enzymes were highest at stations seaward. This

TABLE 1. Bacterial biomass, heterotrophic activity, and hydrolytic enzyme levels, Howe Sound, October 1984. ND = not determined; 0 = below level of detection.

	Station 1		Station 2		Station 3		Station 4	
	Agglomerates	Sediments	Agglomerates	Sediments	Agglomerates	Sediments	Agglomerates	Sediments
Bacterial counts·g^{-1}	(6.54–10.80) × 10^9	(1.68–4.26) × 10^{10}	(1.29–1.47) × 10^9	(1.66–3.89) × 10^9	(1.35–3.52) × 10^{10}	(1.30–1.78) × 10^9	(6.86–12.70) × 10^9	ND
Bacterial biomass (μg C·g^{-1})	61.9–102	160–291	124–255	15.8–24.2	118–333	124–147	65.7–110	ND
Glucose uptake (pmol·g^{-1}·h^{-1})	30.9–50.8	2.82–5.35	77.4–87.7	1.26–1.31	48.7–95.9	20.6–43.5	104–168	9.60–15.9
Glucose uptake (pmol·g bacterial biomass^{-1}·h^{-1})	0.279–0.495	0.016–0.018	0.345–0.624	0.050–0.083	0.217–0.747	0.140–0.311	ND	ND
Phosphatase (μmol·g^{-1}·h^{-1})	41.2–100.0	0.750–0.825	61.0–76.2	1.00–1.22	6.8–10.4	2.91–3.99	3.55–4.36	1.48–1.97
Sulfatase (μmol·g^{-1}·h^{-1})	0	0.062–0.071	0	0.146–0.151	0	1.85–2.38	0	1.43–1.82
β-Glucosidase (μmol·g^{-1}·h^{-1})	228–300	0.406–0.466	223–476	0.068–0.076	0	0.114–0.208	0	0.007–0.016
Protease (μmol·g^{-1}·h^{-1})	ND	0.031–0.035	ND	0.041–0.045	11.06–15.69	0.191–0.219	1.57–2.18	0.089–0.194
Cellulase (nmol·g^{-1}·h^{-1})	ND	25.14–67.63	ND	40.78–48.20	ND	87.20–114.90	6069	0
Laminarinase (nmol·g^{-1}·h^{-1})	ND	72.55–101.50	ND	77.0–101.00	ND	325–400	12640	211–470
Xylanase (nmol·g^{-1}·h^{-1})	ND	116–176	ND	141–193	ND	177–200	16900	208–265

may indicate a drop in the terrestrially derived material (high in cellulose) and a rise in phytoplanktonic material (high in laminarin). However, the increasing xylanase levels seaward contradict this because xylans are generally found in higher terrestrial plants.

The high glucose uptake and enzyme levels of most sediments of station 3, and to a lesser extent station 4, indicate that this is a region of major organic matter deposition supporting the benthic community. The abundant populations of echinoderms, tube works, shrimp, and fish at these two stations supported this whereas virtually no macroorganisms were seen on the sediment surface at stations 1 and 2.

The regionally widespread agglomerate character of marine snow is well documented for the Strait of Georgia and its contiguous waters. Our study finds that there is a spatial and functional diversity of microscale habitats affecting the microbiota and the metabolic processes associated with them. The significance of this variability and diversity may be easily overlooked by studies that emphasize the macroscopic features of the fjord ecosystem.

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