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MARINE SNOW IN ANTARCTIC COASTAL WATERS

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Abstract: Fragile macroscopic aggregates consisting of a matrix of non-living organic material and inhabited by prokaryotic and eukaryotic microorganisms have been reported from many areas of the world's oceans. These aggregates, referred to as marine snow, are sites of enhanced biological activity. The abundance of marine snow in Antarctic coastal waters was investigated by using a video camera on a remotely operated vehicle in the 1991/92 summer. In the 1993/94 summer, marine snow was collected by divers in Kita-no-seto Strait near Syowa Station to investigate the species composition of the constituent organisms and their Enrichment Factor (defined as the concentration of organisms in marine snow divided by their concentration in the adjacent water devoid of marine snow). The abundance of marine snow aggregates >1 mm differed widely from $<0.1\ l^{-1}$ to $>10\ l^{-1}$. Marine snow collected in mid January 1994 consisted principally of diatoms and mucilage derived from the sea-ice community while the collections made at the end of that month contained much colonial *Phaeocystis*. The Enrichment Factor was around 10 for bacteria and varied from around 200 to over 600 for eukaryotic protists. The abundance of polysaccharide-containing particles remained approximately constant during January and early February but the size of these particles increased during this time reflecting an increase in the abundance of large colonies of *Phaeocystis*.

1. Introduction

Marine snow is the term given to macroscopic amorphous aggregates composed of organic and inorganic detritus and containing living organisms. The formation and fate of these aggregates, as well as the biological processes associated with them are of major importance in energy flow through marine ecosystems (ALLDREDGE and SILVER, 1988). Settling of these particles accounts for much of the vertical transport of surface material to the deep ocean and the sea floor (HONJO *et al.*, 1984; ASPER *et al.*, 1992). Marine snow particles are sites of high concentrations of microorganisms and elevated levels of biological activity (ALLDREDGE and SILVER, 1988; CARON, 1991; SMITH *et al.*, 1992). The abundance of bacteria and eucaryotic protists associated with marine snow particles is highly variable but can be up to 3 or 4 orders of magnitude higher than the concentration in the surrounding water. Only few investigations have reported the species composition of the these organisms (*e.g.* CARON, 1991; LAMPITT *et al.*, 1993; PATTERSON *et al.*, 1993). Zooplankton contribute to marine snow by the production of faecal material and mucus as well as feeding on it (ALLDREDGE and SILVER, 1988 and references therein, BOCHDANSKI and HERNDL, 1992; LAMPITT *et al.*, 1993). As pointed out by these

authors, particles and organisms too small to be individually retained by filter feeding and raptorial invertebrates could be ingested when associated with marine snow aggregates. That abundant nanoplanktonic organisms have been reported from the gut contents and faecal material of krill (MARCHANT and NASH, 1986) prompts the question of the extent to which krill and other grazers utilize marine snow in Antarctic waters.

Marine snow particles are usually extremely fragile and cannot be sampled using nets or water bottles. Most useful data on their distribution and abundance comes from *in situ* observations using photographic methods (HONJO *et al.*, 1984) and analysis of their composition following collection by divers (ALLDREDGE and SILVER, 1988). The characteristics of marine snow from tropical and temperate oceanic waters have been comprehensively reviewed by ALLDREDGE and SILVER (1988) but marine snow from polar waters has received only scant attention.

Recently, ALLDREDGE *et al.* (1993) and PASSOW and ALLDREDGE (1994) reported abundant polysaccharide-rich transparent exopolymer particles (TEP), apparently produced by phytoplankton and bacteria, as the major constituent of marine snow. TEP are apparently colonized by bacteria with 2 to 25% of the total number of bacteria attached to TEP. Further, TEP have been implicated in the flocculation of diatoms leading to enhanced settling rates (PASSOW *et al.*, 1994).

Considerable use has been made of sediment traps to investigate vertical flux of organic material in the Southern Ocean (KARL *et al.*, 1991 and references therein). Numerous studies have been undertaken by Japanese scientists to better understand the processes associated with vertical flux of particulate material in the fast ice area. These investigations have clearly demonstrated the close coupling of phytoplanktonic and ice algal production with vertical flux (FUKUCHI and SASAKI, 1981; MATSUDA *et al.*, 1987; HANDA *et al.*, 1992) and the role of this flux as the food source for benthopelagic and benthic consumers (MATSUDA *et al.*, 1990). However other than the recent report of ASPER *et al.* (1993) on the vertical profiles of the abundance of marine snow aggregates we are not aware of any study on the abundance and size of marine snow particles and the concentration of microorganisms associated with these particles compared with that in the surrounding water in the Southern Ocean. Here we present preliminary data on the abundance, size and concentration of microorganisms of marine snow in Antarctic coastal waters and discuss its potential role in vertical flux and trophodynamics, especially as a food source for krill and other grazers.

2. Materials and Methods

Video images were recorded at three sites in the 1991/92 austral summer; near Mawson Station on 17 January, in Prydz Bay near Davis station on 2 February and on Fram Bank on 6 February. The images were obtained with a video camera on a remotely operated vehicle (ROV). The abundance of marine snow particles were estimated from the video images by counting the number of particles going out of focus in successive frames as they got close to the camera. The size of these particles was estimated by comparison with a scale on the frame of the ROV. At least 100 particles were counted and measured at each site.

Samples were collected in mid-January 1994 in Kita-no-seto Strait, approximately

1 km north of the Japanese Antarctic Station of Syowa (69°S, 39°30′E). At the time of collection the sea was ice covered and most of the under-ice algal mat had detached. The water depth at the collection site was 18 m and the collection of marine snow was made at 15 m depth. The abundance of marine snow >2 mm was measured visually by a SCUBA diver counting the number of aggregates passing through a quadrat frame on four horizontal transects. Divers collected marine snow samples and seawater samples without aggregates using 50 m*l* catheter syringes.

On return to the laboratory the size of the marine snow particles was measured and each aggregate individually placed in 2 m*l* of 0.2 μm filtered seawater in wells of tissue culture plates and fixed with filtered glutaraldehyde, final concentration 1%. Before counting the abundance of organisms, the aggregates were dispersed by repeated pipetting with a fine bore pipette or by sonication. Microplankton were counted in settling chambers and nanoplanktonic autotrophs and heterotrophs and bacteria were counted in individual aggregates using epifluorescence microscopy of organisms collected on 0.2 μm pore size polycarbonate filters and DAPI stained (PORTER and FEIG 1980). Filters were examined using UV excitation to determine bacterial concentration and blue excitation to distinguish red autofluorescent autotrophs from heterotrophs. Aggregate-free samples were counted similarly to determine the enrichment factor (EF), defined as the concentration of organisms in aggregates divided by concentration of the same organisms in surrounding water.

Samples of 1% glutaraldehyde-fixed marine snow aggregates and water collections without marine snow were filtered using 0.8 μm Poretics polycarbonate filters and stained while moist for <5 s with 0.02% alcian blue in an aqueous 0.06% acetic acid solution (ALLDREDGE *et al.*, 1993) which had been filtered through a 0.2 μm Millipore filter. Alcian blue stains negatively charged polysaccharides. Stained 0.8 μm filters were placed on Poretics Cyto-Clear slides for microscopical examination. The concentration and size of the particles were determined from observations at 200× magnification.

3. Results

The abundance of marine snow particles in Antarctic waters became apparent on viewing the video images taken from a ROV used in an investigation of krill biology. The estimates of the concentration and size of marine snow aggregates obtained at three sites in Antarctic waters from video images are given in Table 1. There was an obvious difference in the abundance, size and shape of the aggregates. Those from both Prydz Bay and the Fram Bank were generally highly asymmetric "strings", possibly derived from tube diatoms detached from adjacent sea-ice. Abundant krill were seen associated

Table 1. Abundance and size of marine snow aggregates.

Date	Location	Abundance (particles l^{-1})	Size (mm)
17 January 1992	Mawson Harbour	0.1–2	<10–20
2 February 1992	Prydz Bay	0.1–0.5	<10–100
6 February 1992	Fram Bank	0.1–1	<10–50
12–14 January 1994	Kita-no-seto Strait	0.03–0.07	2–5

with the marine snow at the Fram Bank site. Some krill were seen associated with the aggregates at the Prydz Bay site but none in Mawson Harbour. The abundance of aggregates >2 mm was measured by divers to be $0.05 \pm 0.02\ l^{-1}$ on 12–14 January 1994. Turbidity made it impossible to measure marine snow abundance on 29 January but divers estimated it was substantially less.

On three separate occasions in January 1994 the concentrations of bacteria associated with marine snow particles and in collections of water which was devoid of aggregates were ascertained. The bacterial concentrations ranged from 3.6 to 8.4×10^5 per aggregate, which, when compared to the concentration in the water without aggregates indicated an EF of 5 to 13 (Table 2). On two of the sampling occasions the concentration and EF of autotrophs and heterotrophs were measured on the same samples as used for the bacteria. The autotroph concentrations were 6 and 3.9×10^3 per aggregate with EFs of 650 and 280 while the heterotroph concentrations were 4.4 and 3.5×10^3 and EFs of 460 and 210 (Table 2). Pennate diatoms, thick walled cysts likely to be dinoflagellates, Parmales, high numbers of heterotrophic nanoflagellates and choanoflagellates including *Acanthocorbis unguiculata, Diaphanoeca grandis* and *Bicosta spinifera* were the principal eucaryotes associated with marine snow aggregates collected on 14 January. Many of the diatoms and cysts lacked cytoplasmic contents. Such dead cells were not included in estimates of abundance or EF. On 20 January the eucaryotic composition of the aggregates had changed so that the autotrophs were mostly colonial *Phaeocystis* cells with fewer diatoms and cysts and Parmales. There was no readily apparent difference in the composition of the heterotrophs.

*Table 2. Concentration of bacteria, autotrophs and heterotrophs on marine snow aggregates collected from 15 m depth and the Enrichment Factor of each of these groups organisms. * no data.*

Date	Cells per aggregate	Enrichment Factor
	Bacteria	
14 January	$3.9–6.3 \times 10^5$	5–13
20 January	$3.9–8.4 \times 10^5$	5–12
29 January	$3.6–4.2 \times 10^5$	7–8
	Autotrophs	
14 January	6×10^3	650
20 January	3.9×10^3	280
29 January	nd*	
	Heterotrophs	
14 January	4.4×10^3	460
20 January	3.5×10^3	210
29 January	nd	

Table 3. Abundance and size of alcian-blue staining particles sampled at 15 m depth.

Date	Abundance (particles ml^{-1})	Mean size (range) (μm)	Number of particles
14 January	26±6	22 (5–150)	70
29 January	36±7	33 (10–250)	50
29 January	41±4	61 (15–350)	50
6 February	31±7	110 (5–500)	70

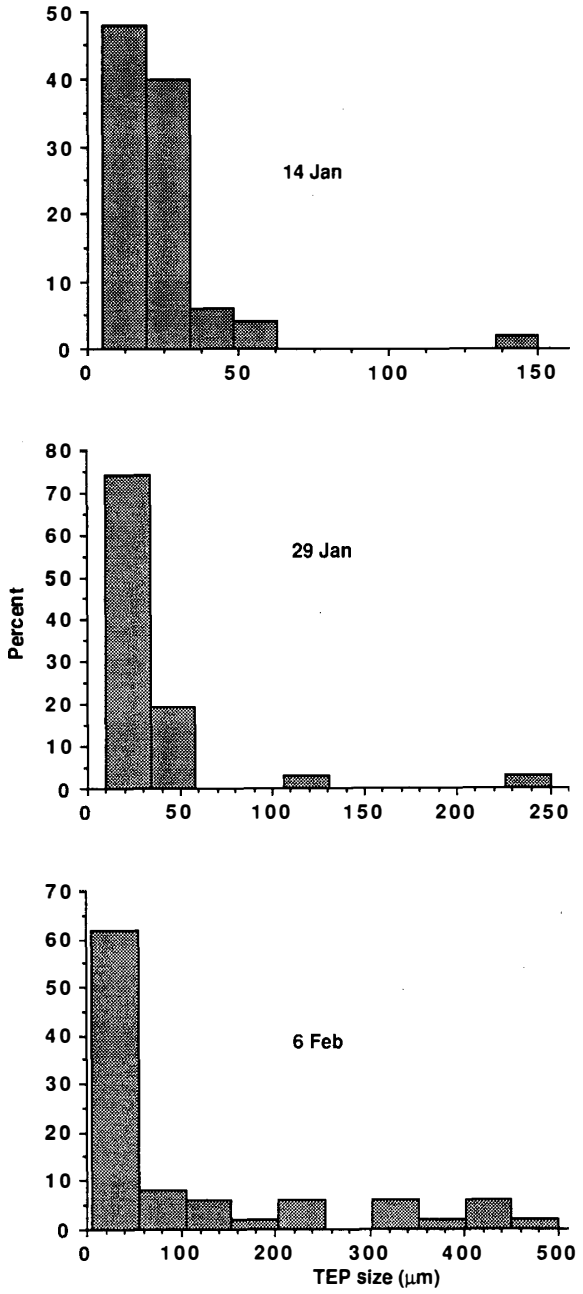

Fig. 1. Size frequency histograms of alcian-blue staining TEP collected at 15 m depth on three different dates in early 1994.

Table 3 indicates that although the abundance of alcian blue staining particles changed little during the period of observation, the size structure of the population of these particles did. As the size frequency histograms (Fig. 1) show, in all collections the smallest size classes of TEP dominated but with time there was an increased contribution by a few large particles. These were most often individual colonies of *Phaeocystis*. Smaller colonies of this alga stained much less intensely with alcian blue than the larger ones.

4. Discussion

Using a single video camera to measure the distribution and size of marine snow particles is obviously greatly inferior to direct observations, photographic or stereographic methods. Small particles escape detection and the estimation of abundance is inherently imprecise. The estimates of marine snow particle abundance here are generally much lower than those found by ASPER *et al.* (1993) at stations near the Antarctic Peninsula. In one profile they found aggregate concentration increased abruptly from less than 1 l^{-1} at around 100 m depth to 15 to 25 aggregates l^{-1} between 150 and 200 m. Another profile revealed >15 aggregates l^{-1} close to the surface, 5 to 10 aggregates l^{-1} from 10 to 150 m depth and around 25 aggregates l^{-1} near the seafloor at around 180 m. Thus the few investigations that have been conducted on the concentration of marine snow in Antarctic waters show marked differences. This is consistent with investigations from temperate and tropical waters (ALLDREDGE and SILVER, 1988) and also reflects the substantial variation in spatial and temporal variation in production and sedimentation in the Antarctic marine environment (KARL *et al.*, 1991).

Both diatoms and *Phaeocystis* have been reported to be involved in the formation of aggregates in cold waters (PASSOW and WASSMANN, 1994). Aggregates derived from the Antarctic sea-ice community have been observed to detach and sink (SASAKI and WATANABE, 1984; SASAKI and HOSHIAI, 1986) and ice algae formed fast-sinking aggregates in experiments simulating conditions during the melting of sea-ice (RIEBESELL *et al.*, 1991). The variety of organisms associated with Antarctic coastal marine snow, not surprisingly, reflected the organisms reported from the sea-ice community and found in the water column when sampled with water bottles. Most of these organisms were nanoplanktonic. Their Enrichment Factors found here fell well within the range reported for other parts of the world's ocean. There was apparently no concentration of cyanobacteria in the marine snow aggregates which have been reported to be in very low concentration in Antarctic waters (MARCHANT *et al.*, 1987) but present in the infiltration assemblage (MATHOT *et al.*, 1991) and seasonally associated with the bottom assemblage of Antarctic sea-ice (WALKER and MARCHANT, 1989). The essential absence of cyanobacteria in Antarctic waters is likely to represent a major qualitative difference between Antarctic and temperate and tropical marine microbial food webs (AZAM *et al.*, 1991). The species composition of the heterotrophic nanoflagellates, which consisted of a surprising diversity of different forms, was not investigated in detail. Such diverse assemblages have been previously reported (*e.g.* CARON, 1991; PATTERSON *et al.*, 1993) and it is likely that in these other cases the nanoflagellates play a major role in consuming the bacteria and detritus associated with the marine snow aggregates.

Transparent exopolymer particles (TEP) have recently been shown to be widespread in the world's oceans and to play a major role in trophodynamics and particulate flux (ALLDREDGE *et al.*, 1993). TEP contain polysaccharides and are thought to be derived by exudation from phytoplankton and bacteria. Experimental investigations have demonstrated their role in the aggregation of diatoms and in the formation of marine snow (PASSOW *et al.*, 1994). Alcian blue staining for polysaccharides reported here shows the presence of TEP in Antarctic waters and that *Phaeocystis* as well as

diatoms are associated with stained material. The role of TEP in Antarctic waters awaits further investigation.

There has been considerable interest in krill energetics, especially filtration rates and filtering efficiency (QUETIN *et al.*, 1994; CLARKE *et al.*, 1988; CLARKE and MORRIS, 1983; NICOL *et al.*, 1995). CLARKE *et al.* (1988) estimated that adult krill require around 20% of their body carbon per day, similar to the value found for other euphausiids. Thus a krill containing 75 mg C would require around 15 mg C day^{-1}. The concentration of chlorophyll *a* in Antarctic waters has been reported to be 0.1 to 1 $\mu g\ l^{-1}$ (EL-SAYED, 1988). Assuming a C: chlorophyll *a* is 50: 1, the carbon concentration is 5 to 50 $\mu g\ l^{-1}$. This value is ignoring any contribution by heterotrophs to the diet of krill. Thus to obtain 15 mg C day^{-1} a krill would have to have a filtration rate of 12.5 to 125 $l\ hr^{-1}$ at this chlorophyll *a* concentration. This is higher by around one or two orders of magnitude than the measured filtration rate of 1 to 4 $l\ hr^{-1}$ (QUETIN *et al.*, 1994). If krill are filtering at this rate the concentration of chlorophyll *a* must be 3 to 12.5 $\mu g\ l^{-1}$ to satisfy their nutritional requirements. Such a concentration is dramatically higher than the observed concentration of chlorophyll *a* and still much higher than the concentration of C even when heterotrophs are also included. The carbon concentration of marine snow is reportedly 1 to 2800 μg per particle for particles over the range 2.4 to 75 mm (ALLDREDGE and SILVER, 1988). Thus if krill are grazing marine snow, they need only consume some 30 particles per day that contain 500 μg C. However, at present there is only circumstantial evidence that krill consume marine snow.

Zooplankton and micronekton including copepods, euphausiid larvae, salps, doliolids and fish consume marine snow particles (ALLDREDGE and SILVER, 1988). LAMPITT *et al.* (1993) reported that ostracods, copepods and amphipods graze marine snow rich in cyanobacteria and eukaryotic picoplankton. These grazers are therefore taking organisms that would be too small for them to ingest by filter feeding or raptorially. In the microbial loop, picoplanktonic organisms are usually consumed by nanoplankton which are in turn consumed by microplankton on which metazoa graze (POMEROY, 1974; AZAM *et al.*, 1983). Thus taking up of picoplanktonic organisms aggregated in marine snow effectively short-cuts the food chain (ALLDREDGE, 1972). In contrast, BOCHDANSKY and HERNDL (1992) report that although the abundance of polychaete larvae and juvenile turbellarians was enriched in marine snow, the dominant copepod did not feed significantly on the phytoplankton associated with marine snow in the Northern Adriatic Sea. Similar to LAMPITT *et al.* (1993) we have previously presented evidence that krill have abundant, very small organisms in their gut contents and faecal pellets. MARCHANT and NASH (1986) report the presence of organisms $< 5\ \mu m$ in diameter in krill faeces and gut contents including diatoms, Parmales and flagellates. Such organisms were abundant components of marine snow aggregates investigated here. MCCLATCHIE and BOYD (1983) show that krill feed on particles smaller than 5 μm at around 25% of the efficiency than they do with particles 10 μm in size or larger. It is consistent with the observations of others therefore to suggest that krill ingest such small organisms by feeding on aggregates containing these organisms rather than by filtering these organisms individually from seawater. In addition, costal strips of choanoflagellates also have been reported to be abundant in krill faeces (MARCHANT and NASH, 1986; TANOUE and HARA, 1986). As choanoflagellates are commonly found in marine snow aggregates

(PATTERSON *et al.*, 1993), as we also found here, it is likely that marine snow is grazed by krill. In addition our underwater video has recorded krill associated with marine snow in Antarctic coastal waters. Clearly further investigations are needed to ascertain to what extent marine snow is a constituent of the diet of krill.

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