Primary productivity and chemical composition of marine snow in surface waters of the Southern California Bight

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ABSTRACT

The primary productivity of flocculent marine snow (fragile and amorphous macroscopic particulates) was measured for the first time using samples collected quantitatively in surface waters of the Southern California Bight. C^{14} production rates averaged 53 ± 12 times higher on macroscopic aggregates than in equal volumes of surrounding, aggregate-free seawater. Densities of marine snow were low, ranging from 0.1 to 1.1 aggregates • l^{-1}. Although only 0.1 to 9.1% of total primary production at 10 m occurred on flocculent marine snow at the time of sampling, the majority of photosynthetic activity in the water column may be associated with these particles during periods of high snow density. Chlorophyll *a* concentrations were 252 ± 61 times greater but carbon fixed per unit chl *a* was 4 times lower on marine snow than in the surrounding seawater. High chlorophyll content relative to carbon fixation may result from pigment enhancement due either to self-shading or nutrient loading of phytoplankton cells inhabiting marine snow. Overall chemical composition of aggregates also differed from that of surrounding seawater with aggregates showing significantly higher carbohydrate:protein ratios. Carbohydrates of aggregates were generally higher in the base and acid insoluble fractions (cellulose and long-chain β 1-3 linked glucans) probably because the matrices of some aggregates were derived from mucopolysaccharide remains of appendicularian houses. Laminarinase activity, an index of grazing, was significantly higher on marine snow than in the surrounding seawater, implying the existence of actively grazing microzooplankton and the potential for active nutrient recycling within the detrital community inhabiting marine snow.

1. Introduction

Marine snow, a collective term for a variety of fragile, amorphous particulates ranging in size from 0.5 mm to many cms in diameter, is now known to be a ubiquitous and abundant component of both epipelagic and bathypelagic waters (Suzuki and Kato, 1953; Johannes, 1967; Hamner *et al.*, 1975; Alldredge, 1976, 1979; Trent *et al.*, 1978; Silver and Alldredge, 1981). These macroscopic aggregates harbor many organisms, particularly healthy phytoplankton and cyanobacteria,

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at concentrations greatly exceeding those in surrounding water and communities on marine snow differ in composition from those freely dispersed in the water (Silver *et al.*, 1978; Silver and Alldredge, 1981). In addition, marine snow particles are enrichment sites for nutrients, particularly ammonia, which may reach concentrations 800 times higher than those in the surrounding seawater (Shanks and Trent, 1979). Snow particles are also sites of enhanced heterotrophic activity within pelagic communities (Silver and Alldredge, 1981; Pomeroy and Deibel, 1980). Moreover, they represent a source of spatial heterogeneity and microscale patchiness, an important pelagic food source and a mechanism for transporting surface-derived materials to depth at intermediate sinking rates (50-100 $m \cdot d^{-1}$) (Silver and Alldredge, 1981).

The high concentration of living, healthy phytoplankton on marine snow, coupled with the high nutrient concentrations found within these particles suggested to us that marine snow might be a significant site of primary productivity, particularly in surface waters of the neritic zone where macroscopic aggregates are particularly abundant. Previous reports of abundant protozoan grazers on these rich detrital communities (Silver and Alldredge, 1981) also suggested that grazing activity might be high on these particles. If so, the potential for rapid nutrient recycling within the aggregate detrital community is improved significantly.

Herein we document for the first time the primary production rates of marine snow and present evidence that significant primary production occurs on macroscopic particulates in nearshore waters of the eastern Pacific. Additionally, we examine marine snow as enrichment sites for protein, carbohydrate and chlorophyll and estimate potential grazing activity as measured by the activity of the digestive enzyme, laminarinase.

2. Materials and methods

a. Field collections. We collected 100 to 200 individual macroscopic aggregates by hand using SCUBA at depths of 10 m, 1 to 2 km due east of Isthmus Cove, Catalina Island, California on each of 7 days in the spring of 1981. Because of the fragile nature of marine snow, hand collection was necessary to obtain intact specimens. Aggregates were drawn individually into clean, open-ended, plastic syringes of 6 or 20 ml capacity. Because the time needed to collect large quantities of individual, small aggregates was prohibitive, we restricted collection and density counts to flocculent aggregates, most of which were at least 3 mm in longest dimension. These were randomly sampled by collecting the first flocculent aggregate encountered. Flakelike aggregates were not collected because of their small size; thus our estimates of the enrichment of both production rates and materials on snow represent minima.

We determined the density of flocculent marine snow visually with a General Oceanics digital flow meter, model #2030, containing a slow-speed rotor and at-

tached sidearm supporting a 4.2 cm diameter loop as described by Trent *et al.* (1978). At the same time, seawater lacking flocculent aggregates was aspirated from the same depth into collapsible polypropylene containers. Light levels were measured at 10 m with a Licor Corporation Model 155, quantum sensing light meter.

b. Production measurements. We measured primary production of flocculent marine snow and surrounding seawater using standard C^{14} tracer techniques (Vollenweider, 1974). Within 30 minutes of collection, 10 to 20 aggregates were pipetted with a 1 ml graduated pipette into each of 4 light and 2 dark BOD bottles (125 ml capacity) containing unfiltered seawater collected at the same time and depth. Four light and 2 dark BOD bottles containing unfiltered surrounding seawater served as controls. The volume of each aggregate was measured while within the pipette. We inoculated each bottle with 5 μCi of C^{14} (as Na $HC^{14}O_3$) and placed them in a running seawater bath (17°C) in natural light under neutral density filters giving light intensities equivalent to those at 10 m depths (about 10% of surface illumination). Incubations of 1.5 to 2.0 h were all carried out between 1030 and 1300 hours.

Following incubation, we filtered the entire contents of each bottle onto a Gelman metrical filter (0.45 μm pore size), rinsed the filter with distilled water, fumed it for 2 to 3 minutes over HCL, and placed it wet into a scintillation vial containing 16 ml of PCS scintillation cocktail (Amersham Co.). Activity was measured with a Beckman LS-100C Scintillation Counter. We subtracted the productivity of the surrounding seawater (determined from controls) from the total productivity of the bottles containing snow to obtain the productivity of the snow alone. The percentage contribution of flocculent marine snow to total productivity was calculated by multiplying the mean carbon fixed per aggregate by the number of aggregates per liter at each station. This value was then divided by the mean total carbon fixed (C fixed in seawater + C fixed on aggregates) per liter.

c. Chemical analysis. We determined chlorophyll *a* content of aggregates at each station by pipetting 3 aggregates onto each of 6 Whatman GF/F glass fiber filters, extracting the pigments in acetone and measuring the fluorescence of chlorophyll *a* by standard methods (Strickland and Parsons, 1972). Five to 10 large aggregates or 10 to 30 small aggregates were also pipetted, with minimal surrounding water, onto pre-ashed glass fiber filters and stored in a dessicator for later analysis for protein, carbohydrate and laminarinase activity. Replicate surrounding water samples of 1100 and 2100 ml volumes were also filtered onto glass fiber filters for these analyses.

Protein content of filters was determined by the Lowry method. Carbohydrate determinations were made by the method of Hitchcock (1971). Laminarinase activity was determined by grinding of the filter and subsequent treatment as a homogenate (corrected for volume displaced by the glass fibers of the filter) as previously described by Cox (1981). Differences between means were tested statis-

tically with a Student's t-test except for laminarinase values. High variances made a parametric test inappropriate, thus the difference between laminarinase means was tested with a Mann-Whitney U-test.

3. Results

Large, amorphous, flocculent particles of marine snow, ranging from 0.1 to greater than 1 ml in volume were abundant east of Catalina Island during March and April, 1981. Most were irregularly or spherically shaped particles a few mm to several cm in diameter and some contained the remains of internal filters, suggesting that they were the decaying, discarded houses of appendicularians (Alldredge, 1976). Large, comet-shaped particles several cm in length and of unknown origin also occurred occasionally on all sampling days and dominated on April 1. The density of marine snow ranged from 0.25 to 1.10 aggregates $\cdot\, l^{-1}$ (Table 1). Flocculent marine snow occupied 0.01 to 0.15% of surface waters by volume. Flakelike particles of marine snow, although also abundant, were not sampled in this study.

Estimates of *in situ* C^{14} uptake rates of macroscopic aggregates were high, averaging 0.24 ± 0.15 μg C fixed $\cdot$ aggregate^{-1} $\cdot$ h^{-1} (Table 1). This was equivalent to 270 ± 60 μg C $\cdot\, l$ of aggregate^{-1} $\cdot$ h^{-1} with a range of 100 to 500 μg C $\cdot\, l$ of aggregate^{-1} $\cdot$ h^{-1}. Although these high production rates averaged 53 ± 12 times higher than the production rates of an equal volume of surrounding seawater, densities of flocculent snow were low at the time of sampling. Thus the actual contribution of marine snow to total primary production in surface waters of the study area averaged 2.3%. As much as 9.1% of primary production occurred on marine snow particles on April 1, when snow particles were particularly large and abundant (Table 1).

Dark fixation averaged 28 ± 5% of light fixation in control bottles and 22 ± 6% of light fixation in bottles containing aggregates. Dark fixation in control bottles did not differ significantly from dark fixation in bottles containing aggregates. High dark fixation relative to light fixation may result, in part, from the low light levels at which samples were incubated, to bacterial activity and to adsorption of C^{14} onto microscopic particulates.

Chlorophyll *a* was also highly concentrated on marine snow. Chl *a* concentrations averaged 0.76 μg $\cdot$ aggregate^{-1} (Table 2). This was equivalent to 1010 ± 260 μg chl *a* $\cdot\, l$ of aggregate^{-1} with a range of 560-2,000 μg chl *a* $\cdot\, l$ of aggregate^{-1}. The concentration of chl *a* on flocculent snow was 252 ± 61 times higher than the chlorophyll content of an equal volume of surrounding water. Marine snow contained 7.2 ± 3.6% of the total chlorophyll *a* at the study site, although maximum contributions reached 27.2% on April 1. The ratio of chl *a* to phaeopigments did

Table 1. Mean(± S.D.) density, primary productivity and percent contribution of marine snow (aggs.) to total productivity in surface waters east of Catalina Island during spring, 1981. S.E. = standard error. *Not included in calculation of mean.

Date	No. agg. l^{-1}	Agg. vol. (ml)	Primary production			% Contribution of aggs. to total primary productivity
			$\mu g\ C \cdot agg.^{-1} h^{-1}$	$\mu g\ C \cdot l^{-1} \cdot h^{-1}$	$\mu g\ C \cdot l^{-1} \cdot h^{-1}$ in agg.	
Mar. 28	1.03	0.2 ± 0.1	0.10 ± 0.01	5.7 ± 0.4	0.10 ± 0.02	1.7
Mar. 30	0.25	0.1 ± 0.05	0.04 ± 0.01	7.4 ± 0.6	0.01 ± 0.004	0.1
Apr. 1	1.10	>1.0*	1.14 ± 0.23	12.5 ± 0.9	1.25 ± 0.25	9.1
Apr. 6	0.55	0.1 ± 0.05	0.01 ± 0.003	5.8 ± 2.7	0.006 ± 0.002	0.1
Apr. 8	0.26	0.1 ± 0.03	0.02 ± 0.003	6.7 ± 1.4	0.005 ± 0.001	0.1
Apr. 10	0.50	0.5 ± 0.1	0.11 ± 0.02	2.5 ± 0.9	0.06 ± 0.01	2.0
Apr. 14	0.52	1.5 ± 1.0	0.29 ± 0.03	5.1 ± 0.7	0.15 ± 0.02	2.9
Mean S.E.	0.60 ± 0.13	0.4 ± 0.2	0.24 ± 0.15	6.5 ± 1.2	0.23 ± 0.17	2.3 ± 1.2

Table 2. Mean(± S.D.) Chlorophyll *a* concentration, Chl. *a*: Phaeopigment ratios and carbon fixed per unit chlorophyll of marine snow (aggs.) and surrounding seawater from 10 m depths. *—Mean calculated deleting anomalously high value.

Date	μg Chl $a \cdot l^{-1}$	μg Chl $a \cdot agg.^{-1}$	Chl *a*: Phaeopigments		$\mu g\ C \cdot \mu g$ Chl $a^{-1} \cdot h^{-1}$	
			seawater	aggregates	seawater	aggregates
Mar. 28	7.68	0.26 ± 0.01	219.4	2.2	0.74	0.37
Mar. 30	4.80 ± 2.35	0.20 ± 0.05	2.4	1.9	1.52	0.19
Apr. 1	10.04 ± 1.48	3.41 ± 2.69	2.5	4.0	1.25	0.33
Apr. 6	5.99 ± 0.16	0.04 ± 0.02	6.3	2.9	0.96	0.28
Apr. 8	4.07 ± 1.60	0.18 ± 0.06	2.0	0.7	1.65	0.10
Apr. 10	2.49 ± 0.32	0.34 ± 0.13	0.7	0.7	1.01	0.32
Apr. 14	3.62 ± 2.55	0.84 ± 0.22	2.0	3.7	1.42	0.34
Mean ± S.E.	5.54 ± 0.98	0.76 ± 0.45	*2.7 ± 0.4	2.3 ± 0.5	1.22 ± 0.13	0.28 ± 0.04

not differ significantly between marine snow and the surrounding seawater ($P > 0.2$; Table 2).

The carbon fixed per unit chlorophyll *a* on marine snow was consistently and significantly ($P < 0.001$) lower than that of particles in the surrounding seawater.

The mean μg C fixed • μg chl a^{-1} • h^{-1} of seawater was 1.22 ± 0.13 while that of marine snow averaged 0.28 ± 0.04 (Table 2).

Marine snow particles were also enrichment sites for carbohydrates. Aggregates averaged 59 μg total particulate carbohydrates • aggregate^{-1} (Table 3), 352 ± 201 times more concentrated than particulate carbohydrates in an equal volume of surrounding seawater. Particulate carbohydrates on aggregates contributed a mean of 5.7 ± 1.7% to total carbohydrates in surface waters, ranging from 2.4 to 12%. Table 3 describes the carbohydrate composition of both marine snow and the surrounding seawater. Although marine snow did not differ significantly from the surrounding seawater in the proportion of the acid soluble fraction of total carbohydrates, snow did contain a significantly smaller proportion of base soluble carbohydrates ($P < 0.001$; Table 3). The proportion of residue fractions was generally higher on aggregates, although the differences were not statistically significant (Table 3).

Flocculent marine snow contributed a mean of 2.8 ± 1.0% to total particulate protein, with a mean of 8.1 μg protein • aggregate^{-1} (Table 4). Protein on marine snow was 87 ± 12 times more concentrated than protein in an equal volume of surrounding seawater. The particulate carbohydrate:protein ratio of marine snow was significantly higher than that of the surrounding seawater ($P < 0.01$; Table 4). Marine snow particles are thus carbohydrate rich and protein poor in comparison with particles in the surrounding water.

Table 4 describes the laminarinase activity of marine snow particles and particles from the surrounding seawater. Laminarinase is a digestive enzyme of marine zooplankton specific for laminarin found in marine phytoplankton. Thus it can be used as a measure of grazing activity (Cox, 1981). The laminarinase activity of marine snow was significantly higher ($P < 0.05$) than that of particles in the surrounding water, indicating that marine snow particles represent sites of increased grazing activity.

4. Discussion

Marine snow particles are highly enriched habitats with concentrations of phytoplankton, microorganisms and detritus two to four orders of magnitude higher than in surrounding seawater. Plant pigments, dinoflagellates, protozoans, and fecal matter are particularly concentrated on snow in California coastal waters (Silver *et al.*, 1978; Trent *et al.*, 1978; Silver and Alldredge, 1981). Additionally, marine snow may contain quantities of ammonia 3 to 860 times more concentrated than those in surrounding seawater. Concentrations of NO_2, NO_3 and PO_4 are not consistently higher on snow particles (Shanks and Trent, 1979). The high concentrations of ammonia, the preferred form of nitrogen for most phytoplankton (Dugdale and MacIsaac, 1971), and the high population densities of primary producers on snow suggest that production rates of marine snow would also be high relative to the

Table 3. Mean(± S.D.) carbohydrate composition of marine snow (aggregates) and surrounding seawater. Numbers in ( ) indicate the number of filters analyzed.

	Total carbohydrates		Carbohydrates fractions—%					
	seawater	aggregates		seawater			aggregates	
Date	($\mu g\ l^{-1}$)	($\mu g\ agg.^{-1}$)	acid sol.	base sol.	residue	acid sol.	base sol.	residue
Mar. 28	2340 ± 250(3)	104(1)	14 ± 4	5 ± 4	80 ± 6	13	7	80
Apr. 1	570 ± 40(2)	71(1)	41 ± 5	4 ± 2	55 ± 3	64	6	30
Apr. 8	410 ± 100(2)	39(1)	18 ± 5	18 ± 17	65 ± 23	0	0	100
Apr. 10	400 ± 70(2)	32(1)	21 ± 1	11 ± 1	68 ± 2	0	0	100
Apr. 14	420 (1)	49(1)	19	16	65	7	1	92
Mean ± S.E.	828 ± 380	59 ± 13	22 ± 5	11 ± 3	67 ± 4	17 ± 12	3 ± 2	80 ± 13

Table 4. Mean(± S.D.) protein and laminarinase composition of marine snow (aggregates) and surrounding seawater. *Very large aggregates which were not included in calculation of means. Numbers in ( ) indicate number of filters analyzed.

	Protein		Laminarinase activity ($X10^4\ \mu g$ glucose • μg prot.$^{-1}$ • min^{-1})		Carbohydrate:protein	
	seawater	aggregates				
Date	($\mu g\ l^{-1}$)	($\mu g\ agg.^{-1}$)	seawater	aggregates	seawater	aggregates
Mar. 28	470 ± 200(2)	8.5 ± 2.5(3)	13.4 ± 4.0(2)	18.2 ± 4.7(3)	5.0	12.2
Apr. 1	250 ± 10(3)	12.8 ± 0.3(2)	13.7 ± 2.3(3)	15.3 ± 7.8(2)	2.3	5.5
		*39 (1)		*14.4		
Apr. 8	100 (1)	1.2 ± 0.2(2)	12.9 (1)	25.0 ± 13.0(2)	4.1	32.5
Apr. 10	150 ± 10(2)	5.2 ± 2.9(3)	12.6 ± 2.7(2)	24.5 ± 9.6(3)	2.7	6.2
Apr. 14	130 ± 1(3)	13.0 ± 0.8(4)	22.5 ± 12.0(3)	16.9 ± 5.7(4)	3.2	3.8
Mean ± S.E.	220 ± 68	8.1 ± 2.3	15.0 ± 1.9	20.0 ± 2.0	3.5 ± 0.5	12.0 ± 5.3

surrounding seawater. We found production rates of marine snow two orders of magnitude higher than equal volumes of surrounding seawater. Our results confirm that marine snow communities do indeed support high production rates and represent sites of high photosynthetic activity which are spatially patchy on the scale of cm's.

The low contribution of marine snow to total productivity in the Southern California Bight results primarily from low densities of marine snow. Previously reported densities of marine snow in California coastal waters have generally been considerably higher. Densities of 2 to 28 aggregates $\cdot\, l^{-1}$ have been reported in Monterey Bay (Trent *et al.*, 1978; Silver *et al.*, 1978) and densities up to $8.0 \cdot l^{-1}$ are common in the Santa Barbara Basin (Alldredge, 1979). The snow particles described in these previous papers are quite similar in size, chlorophyll content and general characteristics to those described here, and thus, may have had very similar production rates. At concentrations of only 5 aggregates $\cdot\, l^{-1}$ marine snow would contribute over 20% to the total primary production in surface waters and at high snow densities the major photosynthetic activity in the water column could occur in association with these particles.

Our values represent minimum contributions of marine snow to primary production. Numerous flakelike particles of marine snow were not included in this study. Flakes have similar concentrations of algae per unit volume relative to larger flocculent aggregates (Silver and Alldredge, 1981). Thus, their small size suggests that their addition to production measurements would probably not have increased the total contribution of marine snow by a significant proportion. However, if production occurs primarily on the unshaded surfaces of snow particles, then the high surface-to-volume ratios of flakes suggest that they might be important centers of photosynthetic activity.

Carbon fixed per unit chlorophyll at *in situ* light intensities was significantly lower on snow than for particles in the surrounding seawater. These low numbers result in part from extremely high chlorophyll concentrations within phytoplankton cells inhabiting marine snow. Enhancement of pigment concentrations within organisms living on snow could result from self-shading. Phytoplankton cells living within the interior of the snow particles may receive considerably less light than do cells on the periphery. Phytoplankton inhabiting marine snow may also exhibit nutrient loading. Marine snow is a habitat rich in nutrients, much of which may be stored as plant pigments. Dinoflagellates, the most abundant phytoplankters on marine snow off California (Silver *et al.*, 1978) exhibit pigment enhancement under both low light and high nutrient conditions (B. Prézelin, pers. comm.).

Alternatively, photosynthetic rates on marine snow, although high, may be lower than might have been predicted from their nutrient and phytoplankton concentrations. Competitive or allelopathic interactions between the diverse inhabitants of

these semienclosed environments may reduce photosynthesis in some species. Marine snow particles are undoubtedly complex detrital communities experiencing a variety of intricate interspecific interactions which may affect both photosynthesis and chlorophyll content of the photoautotrophs inhabiting them.

Unlike Trent *et al.* (1978) who found much higher concentrations of phaeopigments on marine snow, reflecting their high detrital content, we found no difference between the ratio of chlorophyll *a* to phaeopigments on aggregates and that in the surrounding seawater. Many of the aggregates sampled during this study consisted of appendicularian houses either alone or aggregated together to form larger particulates. Since appendicularians collect large quantities of living, healthy phytoplankton on their houses during the process of feeding, it is likely that many of the marine snow particles in this study did contain less detrital and fecal material and more living algae than those sampled by Trent *et al.* (1978).

Production rates of seawater found in this study are similar to those of 50 to 75 mg $C \cdot m^{-3} \cdot day^{-1}$ reported by Eppley *et al.* (1972) during spring in the Southern California Bight. If we convert our production data to a daily rate by assuming a 12-hour day length, we obtain a range of about 30 to 150 mg $C \cdot m^{-3} \cdot d^{-1}$. The volumes and chlorophyll content of marine snow particles described here are also similar to those of aggregates from other coastal areas off California. Trent *et al.* (1978) report volumes of 0.004 to 2.1 ml and chlorophyll concentrations of 72.8 to 1,444.6 $\mu g \cdot l^{-1}$ of aggregate^{-1} for aggregates in Monterey Bay. Our chlorophyll values were only slightly higher, ranging from 560 to 2000 $\mu g \cdot l$ of aggregate^{-1}.

The high concentration of carbohydrates on aggregates relative to protein bears out previous reports of high Carbon:Nitrogen ratios on snow (Alldredge, 1976, 1979). Snow particles are sites of high enrichment of carbohydrates and some proteins, thus providing a potentially rich food source. Samples of aggregates were overwhelmingly dominated by high fractional percentages of the "residue" fraction of polysaccharides. The residue fraction typically consists of cellulose, chitin, and possibly other refractory polysaccharides in addition to high chain length β 1-3 linked polysaccharides. These results are consistent with a carbohydrate composition which is comprised largely of refractory mucopolysaccharide remains of larvacean houses and dinoflagellate constituents where the principal polysaccharide components would be expected to be cellulosic and long chain length β 1-3 linked glucans (Nevo and Sharon, 1969). The high acid-soluble percentage observed on April 1 indicates that, at times, labile and easily digestible carbohydrates can occur in association with aggregates, although the persistence of such biologically labile fractions may depend upon other factors.

Laminarinase is found only in negligible amounts in fecal material (Cox, 1981), a major component of marine snow (Silver *et al.*, 1978). Thus, the significantly higher concentration of laminarinase on marine snow suggests that a population of

grazers, predominantly ciliates (Silver *et al.*, 1978; Silver and Alldredge, 1981), are active on these particles. Laminarinase activity in surrounding water samples probably results from the inclusion of small numbers of planktonic grazers, particularly copepods and ciliates in these samples. An abundance of actively grazing protozoans on marine snow has several important implications. Such grazing activity may result in extensive excretion and nutrient recycling within the snow microcosm. Such nutrient recycling would contribute to the high production rates observed on these particles. Additionally, the consumption of a significant proportion of actively photosynthesizing phytoplankton by protozoan grazers, both associated with marine snow particles, suggests that a significant proportion of the primary production in the nearshore, pelagic zone may pass through a cilliate-detrital food chain rather than through the more traditional free-floating, phytoplankton-filter feeder type food chain generally believed to predominate in this system. Considerably more study of the complex communities inhabiting marine snow is needed to confirm these suggestions.

5. Conclusions

1) The first reported C^{14} uptake rates of marine snow indicate that primary production on marine snow is up to two orders of magnitude higher than in equal volumes of surrounding seawater. At low aggregate densities (up to 1.1 aggregates $\cdot\ l^{-1}$) between 0.1 and 9.1% of primary production at 10 m occurs on marine snow. At high densities of marine snow the majority of photosynthetic activity in the water column could occur in association with these particles.

2) Marine snow are enrichment sites for chlorophyll *a*, carbohydrate, protein and laminarinase. Chlorophyll *a* content of snow is high and the carbon fixed per unit chl *a* is low, suggesting pigment enhancement due to self shading or nutrient loading.

3) Chemical composition of marine snow differs from that of surrounding seawater: carbohydrate:protein ratios are higher as is the acid and base insoluble fraction of carbohydrates.

4) Laminarinase activity is higher on marine snow, suggesting active grazing by microzooplankton inhabiting these particles. Marine snow may represent sites of active nutrient regeneration. A significant proportion of primary production in the water column may pass through the detrital food chain on these particles.

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