Marine Snow: Microplankton Habitat and Source of Small-Scale Patchiness in Pelagic Populations

Abstract. *In near-surface waters of the neritic zone, the fragile aggregate material called "marine snow" is enriched by a variety of planktonic organisms and detrital products of plankton. Here marine snow is a source of patchiness and taxonomic diversity for microplankton populations and is a likely food resource and recycling agent for fecal particles.*

Oceanic biologists have recently begun to study a variety of pelagic phenomena that are studied effectively only by direct observation underwater. Using scuba, observers have characterized mucus structures of some planktonic organisms and suggested that the mucus provides a physical substrate in the open water environment (*1, 2*). Observations from submersibles and by scuba divers have revealed the existence of large quantities of amorphous, fragile particulates, referred to as "marine snow" (*3*) or "organic aggregates" (*1, 2, 4*) (Fig. 1). From an analysis of hand-collected samples, we present what is, to our knowledge, the first quantitative description of the flora and fauna of marine snow (aggregates > 0.5 mm) and report the contribution of these microplankton assemblages to the total community in the same water column. Occasionally all the individuals in selected phytoplankton and zooplankton taxa were found associated with aggregates and were not freely suspended in the water column. The particular taxonomic composition and relative enrichment of populations on marine snow demonstrates that these aggregates were sources of patchiness and taxonomic diversity for microplankton populations. The size of marine snow and the abundance of the associated organisms and waste products show that these aggregations could be food sources and, if consumed, would be agents for recycling of fecal-bound materials in near-surface waters of the sea.

Using scuba, we hand-collected water samples and individual specimens of marine snow from Monterey Bay, California (total water depth, 25 m; 36°57′N, 122°00′W), on dates and from depths shown in Table 1. While collecting samples, we also obtained data on the sizes and concentrations of aggregates from in situ photographic records and direct counts underwater (*4*). Although the aggregates were abundant (numbering about 2 to 28 per liter) and were conspicuous to the diver, we were unable to obtain intact aggregates with standard water bottles (*4*). We preserved separate samples of water and aggregates with formalin, and in the laboratory we identified and counted 500 to 2000 organisms from vigorously stirred samples of both water and marine snow. From the counts of aggregates and of water samples, and from data on sizes and concentrations of aggregates (*4*), we calculated the numbers and concentration of various organisms associated with the aggregates (*5*) (Table 1) and the contribution of the aggregates to the biomass in the study area.

The macroscopic aggregates are almost always enrichment sites for the microplankton groups studied. At times the aggregates contain all the individuals in the water column in the enumerated groups, except for the diatoms (Table 2). Variations in the concentration of organisms on aggregates may be related to the age of the aggregates. For statistical tests, we ranked the aggregates from the various depths and dates by age using the accumulations of fecal pellets on them, but we also made tentative calculations of their absolute ages. The absolute age was estimated from our separate measurements of the concentrations of pellets on aggregates and in the surrounding water (*5*), data on the projected surface areas of aggregates for these samples (*4*), and published values for pellet sinking rates (*6*). Such estimates suggest that aggregates average a few hours to several days or a week in age for our samples (*7*). If aggregates are ranked by increasing fecal pellet enrichment (Table 1), and thus by increasing age, we find correlative increases in dinoflagellate concentration [Kendall's τ for correlation, $\tau(12) = +0.56$, $P < .02$] and in protozoan concentration [$\tau(12) = +0.64$, $P < .01$]. As fecal pellet concentration increases in aggregates, so does concentration of empty diatom frustules [$\tau(12) = +0.56$, $P < .02$] but not overall diatom concentration [$\tau(12) = +0.44$, $P < .05$].

We recorded the general categories of large particles (particles > 0.5 μm) and, when possible, the genus and occasionally the species of the various phytoplankters. We compared diatom floral composition in aggregates to that in the

Table 1. Marine snow composition and enrichment factors (EF); EF = (number per aggregate)′× (number in equal volume of surrounding water)$^{-1}$. Tabled values are based on one to four ($\bar{X} = 2.8$) counts of aggregates and one to four ($\bar{X} = 2.7$) counts of water samples at each depth. Protozoa are mostly loricate ciliates (tintinnids) and naked ciliates, but smaller numbers of radiolaria and foraminifera are included also. Values for aggregate volumes are from photographs (*4*); A indicates all individuals are in aggregates (that is, none free in water).

Sample depth (m)	Aggregate volume (cm^3)	Diatoms (in hundreds)		Dinoflagellates		Protozoa		Fecal pellets	
		$\bar{X}$ ± S.E.	EF	$\bar{X}$ ± SE	EF	$\bar{X}$ ± SE	EF	± S.E.	EF
					23 July 1976				
3	0.03	51.9 ± 27.7	1.0	17 ± 3	53	0.8 ± 0.8	16	13 ± 3	431
8	0.26	41.8 ± 22.3	0.1	45 ± 15	33	1.8 ± 0.9	5	38 ± 15	350
12	0.01	15.4 ± 9.2	0.6	35 ± 4	1.3 ± 10^3	8.0 ± 4.3	4.7 × 10^2	36 ± 3	1.7 × 10^3
15	0.01	1.7	0.1	56	2.1 × 10^3	27.0	26.0 × 10^2	34	1.4 × 10^3
3	0.01	6.1 ± 3.6	0.0	34 ± 6	1.6 × 10^3	9.6 ± 4.3	23.7 × 10^2	32 ± 20	4.4 × 10^3
6	0.01	0.0 ± 0.0	0.0	11 ± 9	48	18.0 ± 3.9	1.0 × 10^2	21 ± 17	1.5 × 10^3
17	0.01	2.5 ± 1.6	0.2	13 ± 15	110	1.0 ± 1.1	10	24 ± 9	2.1 × 10^3
					25 August 1976				
3	0.03	9.7 ± 3.7	8.2	177 ± 70	A	8.4 ± 4.8	12.1 × 10^2	423 ± 220	A
11	0.03	20.3 ± 1.7	26.5	330 ± 37	A	52.0 ± 12.5	A	1509 ± 219	A
14	0.09	19.3 ± 1.2	3.7	1207 ± 255	A	132.7 ± 10.5	86.3 × 10^2	1929 ± 121	A
17	0.29	11.5 ± 2.3	2.4	306 ± 130	422	49.7 ± 14.5	A	1283 ± 303	A
					10 June 1977				
3	0.01	0.0 ± 0.0	0.0	1 ± 1	26	6.6 ± 5.2	48	12 ± 6	859
10	0.01	5.7 ± 2.3	1.4	0 ± 0	0	0.0 ± 0.0	0	24 ± 7	511

water surrounding aggregates with Whittaker's similarity index (*8*). Numerical values of this index indicate that the flora on aggregates resembles that on other aggregates more closely than in the surrounding water [t (9) = 4.08, $P < .01$]. The similarity of diatom populations in aggregates and in the surrounding water varies greatly for the dates and depths sampled (range of index, from 30 percent to 89 percent), with the flora of aggregates and surrounding water diverging increasingly in older aggregates (τ (11) = -0.53, $P < .05$). Only one group of diatoms—small, solitary pennate forms—was more common on aggregates than in surrounding water [t (10) = 4.25, $P < .01$], and this group became proportionately more abundant on the aggregates as the similarity indices declined between water and aggregates [r (10) = .76, $P < .01$].

Material associated with aggregates may accumulate by passive collection of sinking particles, by attraction of mobile organisms, or by enhanced growth of organisms associated with the aggregates. Particles such as fecal pellets, heavy-walled resting spores of diatoms, and empty diatom frustules must accumulate passively. Motile organisms such as dinoflagellates and ciliates may be attracted to aggregates or might remain nearby after encountering them through random swimming movements. [Even the more slowly swimming dinoflagellates should be able to swim the 0.2- to 1.0-m distances between aggregates (*4*) in a few hours (*9*).] Since the aggregates are also a locus for bacterial and microflagellate enrichment (our own observations) and possibly sites for the leaching or the bacterial regeneration of nutrients from fecal material, marine snow is a favorable site for dinoflagellates with their complex nutritional requirements and for the heterotrophic ciliates. The increasing enrichment of planktonic organisms on aggregates as the aggregates become older, as indicated above, is consistent with these interpretations. The diatom association with aggregates is more complex. Diatoms are not as concentrated on aggregates as are the mobile microplankton, and only one subpopulation, the small pennate group, is consistently enriched here. Similar pennates often grow rapidly to become the first dominants in seawater-enrichment cultures in our laboratory and may be basically substrate-dependent forms. Some of these pennates were found abundantly on valves and spines of other diatoms in this study and may have been inoculated onto aggregates from initially epiphytic populations. These pennates may be accumulating on aggregates as a result of rapid growth there; the maximum deviation in the proportion of pennates between aggregate and water samples is equivalent to five additional divisions on the aggregates.

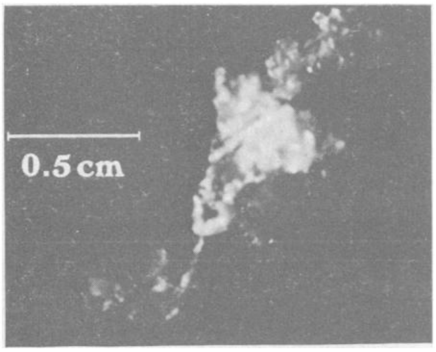

Fig. 1. Individual marine snow particle.

Table 2. Marine snow contribution as a percentage of total particle biomass in the water column; N indicates that no individuals were present in the water column, whereas 0.0 indicates that individuals were present but not in the aggregates. The volume occupied by aggregates was obtained from photographs (*4*).

		Percentage in aggregates of					
		Diatoms					
Water depth (m)	Volume occupied by aggregates (%)	Total (> 5 μm)	Empty frustules (> 5 μm)	Resting spores	Dino-flagel-lates	Proto-zoa	Fecal pellets
			23 July 1976				
3	0.036	3.6	9.0	N	1.9	0.6	13.4
8	0.330	2.2	9.1	N	9.8	1.7	53.7
12	0.011	0.7	2.2	N	12.2	4.9	15.9
15	0.011	0.1	0.9	N	18.8	22.2	13.6
			2 August 1976				
3	0.007	0.3	0.8	N	10.3	1.6	23.6
6	0.008	0.0	0.0	100.0	0.4	3.8	10.7
17	0.002	0.1	0.1	0.1	0.2	0.0	4.1
			25 August 1976				
3	0.011	8.3	100.0	100.0	100.0	11.8	100.0
11	0.006	13.7	100.0	100.0	100.0	100.0	100.0
14	0.029	9.8	100.0	100.0	49.9	71.5	100.0
17	0.078	15.7	100.0	100.0	24.8	100.0	100.0
			10 January 1977				
3	0.005	0.0	0.0	100.0	0.1	0.2	4.1
10	0.001	0.2	3.1	24.4	0.0	0.0	0.6

Marine snow contains abundant populations of microorganisms and small detrital particles, and the species and taxa there are present in different ratios from those from surrounding waters. The existence of pelagic microhabitats that simultaneously support different populations has been suggested as a mechanism for maintaining phytoplankton species diversity (*10*). However, the physical definition of such microhabitats has been poorly understood. Marine snow offers a physically distinct, benthic-like microenvironment with extensive surfaces, concentrations of organic waste products, and a microflora (*11*). Aggregates increase species diversity when they occur in water samples, since the different populations on disrupted aggregates will be mixed with those from surrounding water. Moreover, aggregates will also contribute to the small-scale patchiness of biomass for organisms concentrated here. Patchiness from aggregates will become more pronounced with smaller sample sizes, since the chance inclusion of an aggregate (volume < 1 in our studies) (*4*) in a subsample increasingly alters the apparent number of organisms per unit volume as sample volume decreases. Our results indicate that researchers could reduce the high variance of replicates of microplankton biomass associated with small sample volumes if they obtain larger (more than a liter) initial sample volumes, mix these well, and then withdraw the smaller portions. However, much of the information on true structure of communities will be lost after disruption of the aggregates, and such structural features may be of considerable ecological importance for the organisms themselves.

Because marine snow is enriched with fecal material, diatom frustules, and miscellaneous exoskeletons (such as crustacean molts), the fate of materials associated with such organic detritus will be affected if marine snow is consumed. The vertical transport of a number of chemical substances is thought to be governed by incorporation into sinking fecal pellets (*12*); if pellets are trapped and consumed on aggregates, the residence time of some fecally bound materials may be longer than suggested by sinking rates of individual pellets. Moreover, fecal material, which is a large and useful energy source for some grazers (*13*), may become more available after incorporation into larger-sized aggregates and with increased retention time in near-surface waters.

The apparent youth of marine snow and its abundance (*4*) suggests active turnover. Possible fates could be disruption in turbulent surface waters (not observed by us), sinking into deeper waters, or consumption by grazers. Although grazers of larger particulates are known (*1, 2*), we did not observe consistently any potential consumers near the aggregates. The enrichment of aggregates in phytoplankton, microzooplankton, and fecal pellets, however, indicates these are rich, localized food resources. Moreover, the aggregates provide a mechanism for converting small (on the order of micrometers) items into larger (millimeter- to centimeter-sized) particles for grazers that use the larger-size classes [see also (*2*)]. For example, the anchovy-like fish of the neritic and upwelling areas, which are major contributors to world fisheries, consume particles in the aggregate-size class (*14*). The importance of prey size to consumers is well known, and enlargement of plants through colony formation is assumed to be the basis for the shortening of food chains in upwelling areas (*15*). The large size and abundance of marine snow (*4*) and its concentrated communities of microplankton suggest a potentially rich food resource for organisms capable of using these particle sizes in neritic waters of the pelagic zone.

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5. The number of particles per aggregate (x) and the number per milliliter in surrounding (nonaggregate) water (y) are calculated from counts of aggregates in 1 ml of water and from portions of 1- to 4-liter water samples: number of particles in a 1-ml "aggregate" sample = $x + y(1 - V)$; number of particles in a 1-ml water sample = $(10^{-3})(Nx) + y[1 - (NV \times 10^{-3})]$, where N is the average number of aggregates per liter and V is the volume in 1 ml of an aggregate at that depth and date (*4*).
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7. Aggregate age = (number of fecal pellets per projected surface area of the aggregate)/(number of fecal pellets per surrounding water volume)/(fecal pellet sinking rate). Aggregate dimensions are known from (*4*) and fecal pellet sinking rates are calculated from a fecal pellet size–sinking rate relationship (*6*), with fecal pellet sizes from aggregates studied here (median size 70 μm and length-width ratio approximately 2). Fecal pellets from aggregate and water samples were of similar sizes. We assumed a constant number of fecal pellets in the surrounding water and a constant size for the aggregates during the time the aggregates are trapping pellets. We calculated ages from several estimates of trapping efficiency for the aggregates: if fecal pellets are deflected around the aggregates or fall through open areas in them, we have underestimated ages by the inverse of the trapping efficiency. We calculated ages on the basis of assumptions of no vertical motion of the aggregates (that is, pellet sinking rates 70 m/day relative to aggregates). Although the snow appears essentially motionless to the diver, we also calculate ages for slowly sinking aggregates (sinking at half the fecal pellet rate). The latter calculation simply provides an arbitrary measure of the effect of relative motion by the aggregate. For stationary aggregates, the average age is 1.5 hour [standard error (S.E.) =0.2, N = 9] for 100 percent trapping efficiency; if aggregates are only 10 percent or 1 percent efficient at trapping fecal pellets, the ages are 10 or 100 times greater than this. If the aggregates are sinking at half the fecal pellet rate, they are 2.9 hours old (S.E. = 0.1, N = 9), and they must be efficient at trapping fecal pellets (or their increased ages would be incompatible with the shallow depths at which they were captured).
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Early Maternal Separation Increases Gastric Ulcer Risk in Rats by Producing a Latent Thermoregulatory Disturbance

Abstract. *Rat pups that are separated early from their mothers, at postnatal day 15, become hypothermic when subjected to physical restraint on postnatal day 30. Restraint of separated pups also elicits an unusually high incidence of gastric erosions, as well as insomnia and an increase in quiet wakefulness. If hypothermia during restraint is prevented, neither the erosions nor the behavioral responses occur. Rat pups separated at the customary age (postnatal day 22) do not become hypothermic during restraint, and the restraint of such pups is not associated with either gastric erosion or insomnia.*

We reported previously (*1*) that the age at which the young rat is separated from its mother markedly influences its later susceptibility to gastric erosions when subjected to food deprivation and physical restraint. For example, when tested at postnatal day 30, rats that were separated from their mothers on day 15 develop gastric erosions with a probability of 95 percent. At the same test age, rats that were separated from their mothers on day 21 or later develop gastric erosions with a probability of only 10 percent.

Early maternal separation in rats evidently amplifies pathogenetic factors in comparison to normally reared rats. A comparison of the effects of restraint on rats separated early and rats reared normally should reveal pathogenetic variables in greater relief than the more customary strategy of comparing subjects within one relatively homogeneous group. Such a study should also indicate how early maternal separation exerts such profound effects on vulnerability to gastric erosions.

Body temperature regulation is one factor that may be related to the gastric erosions elicited during restraint. The probability of erosion formation is inversely related to ambient temperature during restraint (*2*). Some investigators have shown specifically that the probability of erosion formation is inversely related to body temperature during restraint, even when the ambient temperature is 22°C (*3*). Other investigators have not confirmed these observations on body temperature (*4*). Since physical restraint is well known to impair thermoregulation in the rat (*5*), the hypothesis that this impairment contributes to the development of gastric erosions in restrained rats remains an attractive one.

Alternatively, it has been proposed that the rat's behavioral response to restraint may be related to the production

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