
The characteristics and transparent exopolymer particle (TEP) content of marine snow formed from thecate dinoflagellates

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Abstract. Abundant marine snow containing diatoms and detritus, but dominated by large, bioluminescent thecate dinoflagellates and their temporary vegetative cysts, especially several species of the genus *Gonyaulax*, was observed at six stations in the Santa Barbara Channel, California, in 1989 and 1994. These aggregates were unusually cohesive and mucus rich, and contained 2–4 times more mass, particulate organic carbon (POC), particulate organic nitrogen (PON) and chlorophyll *a* per unit aggregate volume than more common types of marine snow formed from diatoms, fecal matter, larvacean houses or miscellaneous detritus. However, the relationship between aggregate size and the concentration of TEP (transparent exopolymer particles which form the mucus matrix of most marine snow) was similar to that of other types of aggregates, suggesting that much of the copious gel-like material within dinoflagellate aggregates was not TEP. While this is the first report of abundant thecate dinoflagellates occurring within large, rapidly sinking marine aggregates, the data do not support the conclusion that mass aggregation and subsequent sedimentation of blooms is part of the life history adaptations of thecate dinoflagellates, as it is for some diatoms. The high abundance of free-living dinoflagellate cells and temporary cysts, and the similar proportion of dinoflagellates relative to other algal and chemical components in both aggregates and the surrounding seawater, indicate that the dinoflagellates were not differentially aggregating. Even so, passive accumulation of dinoflagellates in marine snow through aggregation processes may result in more rapid transport of dinoflagellate-generated material to the deep ocean, alter the nature of sinking particulate matter following dinoflagellate blooms, and increase the nutritional value of marine snow as a food source for zooplankton and fish.

Introduction

Much of the suspended matter in the ocean exists as aggregates 0.5 mm or larger in diameter, known as marine snow, formed from phytoplankton, fecal pellets, inorganic particles, zooplankton feeding structures and detritus. These aggregates are enriched in carbon, nitrogen and nutrients, and harbor concentrated communities of microorganisms at abundances several orders of magnitude greater than found free living in the surrounding seawater (Alldredge and Silver, 1988). Moreover, they sustain unique chemical microenvironments (Alldredge and Cohen, 1987) and are the major form in which particulate organic matter sinks to the ocean floor (Fowler and Knauer, 1986).

Four types of marine snow have been reported previously based on the identity of their major components (Alldredge and Gotschalk, 1990). These include larvacean houses, formed from the discarded feeding structures of larvaceans, fecal aggregates composed primarily of zooplankton fecal matter, diatom flocs formed from the aggregation of diatoms at bloom termination (Smetacek, 1985; Alldredge and Gotschalk, 1989), and miscellaneous aggregates formed in ageing systems from unidentifiable debris. All but those formed as zooplankton feeding structures are generated by aggregation, the process whereby particles present in the water column are collided together by turbulent shear, differential settlement

and other physical processes, and subsequently stick together to form aggregates. These aggregates are held together by a matrix of sticky, gel-like particles known as TEP (transparent exopolymer particles) produced from the polysaccharides exuded by phytoplankton and bacteria (Allredge *et al.*, 1993).

Recently, we encountered a previously undescribed type of marine snow dominated by the cells and cysts of thecate dinoflagellates. These aggregates differed both biologically and chemically from other types of marine snow, and the abundance of dinoflagellates in rapidly sinking aggregates suggested a mechanism for the vertical transport of dinoflagellate resting stages to the deep sea that has not been previously considered for this taxon. In the present paper, we characterize dinoflagellate marine snow and discuss its significance for the life histories of thecate dinoflagellates. We also present the first data on the concentration of TEP within a wide variety of aggregate types.

Method

Sizing and collection of aggregates in situ

Marine snow containing abundant thecate dinoflagellates was observed, photographed and hand collected by divers at depths of 10–20 m at one station in November 1989, and five stations in December 1994, in the Santa Barbara Channel, California (all stations were located at 34°10'–34°20'N and 119°40'–120°30'W). The TEP content of other types of marine snow was also investigated for comparison: at two stations in September 1994 and three in June 1995 in the Santa Barbara Channel, five stations in Monterey Bay, California, (36°54.9'N, 121°56'W and 36°50'N, 121°56'W) in July 1993, and one station in East Sound, Washington (48°12'N, 122°54'W), in April 1994. Marine snow from each station was classified into general categories based on the identity of the dominant particles composing the aggregates, as revealed by microscopy. Two of these stations were dominated by larvacean houses, four by diatom flocs and five by miscellaneous aggregates. Larvacean houses consisted of the discarded houses of *Oikopleura dioica* and *O.longicauda*. Diatom aggregates were composed primarily of living, chain-forming diatoms of the genera *Chaetoceros*, *Nitzschia* and *Thalassiosira*, empty frustules, setae and other phytoplankton detritus. Miscellaneous aggregates were composed of detritus, naked flagellates and occasional fecal pellets [see Allredge and Gotschalk (1990) for additional descriptions of these aggregate classes]. Over 90% of the aggregates at any one station were of the same type, consistent with the findings of Allredge and Gotschalk (1990).

Ninety to 450 aggregates at each station were collected by scuba divers in 20 ml syringes in three size classes as described in detail in Allredge (1998) for measurements of particulate organic carbon (POC), particulate organic nitrogen (PON), dry mass, chlorophyll (Chl) *a* and TEP content. Surrounding seawater (seawater free of aggregates) was also collected by divers in syringes for microscopic counts. Bulk seawater was collected by divers in 2-l polyethylene bottles for the determination of the chemical and biological content of the background seawater. Ten to 11 aggregates, chosen because they were as close as possible in size to the prototype aggregate in each size class, were also photographed under

water with a Nikonos IV camera fitted with a strobe and 1:2 close-up attachment using Tri-X 400 black and white film. Aggregates were photographed in the plane parallel to their direction of sinking.

Divers determined the abundances of dinoflagellate aggregates visually by counting aggregates >3 mm in diameter passing through a 100 cm² rectangular frame as the diver swam transects. Horizontal distances were determined either with a hand-held General Oceanic flowmeter, Model 2030, or with a tether line of known length. Transects consisted of 25–250 l each.

Laboratory analysis for chemical content and size

On board ship the aggregates in each size class were pooled in a beaker and the total sample volume and number of aggregates collected were recorded. Aggregate concentrations ranged from 0.7 to 5 aggregates ml⁻¹ in these pooled samples. Three replicate subsamples of each size class were then filtered and later analyzed using standard methods for Chl *a* [2–5 ml samples; fluorometrically according to Parsons *et al.* (1984)], POC and PON [10–30 ml samples; using a Leeman Labs Model CE 440 CHN analyzer according to Sharp (1991)], dry mass [5–10 ml samples; using 0.4 µm Nuclepore filters and a Cahn Electrobalance Model 4600 according to Sharp (1991)] and TEP [four, 3–8 ml replicates; analyzed spectrophotometrically after staining with alcian blue according to Passow and Alldredge (1995)]. Three replicates of background seawater were also filtered and similarly analyzed for Chl *a* (25 ml samples), POC and PON (500 ml samples), dry mass (50 ml samples) and TEP (100 ml). Seawater blanks were subtracted from the aggregate slurries, assuming that the aggregates occupied 10% of the slurry by volume (estimated by wet settling), yielding the chemical content of the aggregates alone.

The equivalent spherical volume of each photographed aggregate was calculated from particle area determined by computerized image analysis of the film with a Megavision 1024 XM Image Analysis System containing a 1000-line video camera as described in Alldredge (1998). Regression lines of aggregate size versus mass, POC, PON and Chl *a* content were generated for dinoflagellate marine snow, and differences in slope and elevation between dinoflagellate aggregates and regressions for other types of marine snow reported in Alldredge (1998) were statistically compared using analysis of covariance, performed according to Snedecor and Cochran (1980).

Microscopy

The abundance of phytoplankton, protozooplankton and empty cysts within aggregates from the medium size class and in the surrounding seawater (collected by divers with a syringe so as to be aggregate free) was determined with an inverted microscope according to Utermöhl (1958). Cell numbers in the surrounding seawater were enumerated by settling and counting 50 ml of each sample. Aggregates were diluted with a known volume of artificial seawater and mixed vigorously. In some cases they were sonicated lightly, as they were held

together by material which was extremely sticky, cohesive and difficult to disperse. We determined that gentle sonication (1 min at 30%) did not destroy dinoflagellate or diatom cells. In some cases, we were not able to disperse the whole aggregate completely even by sonication and a detrital floc remained. These remaining flocs could not be dispersed even by the addition of EDTA. Closer investigations of these remaining flocs convinced us that negligible amounts of diatom or dinoflagellate cells remained in these flocs, although empty frustules were entangled in the very sticky detrital matter. The dispersed solution of the aggregate (minus the detrital floc) was filled directly into a counting chamber (1.94 ml) and >200 dinoflagellate and diatom cells each were counted per subsample. Two replicate subsamples were counted for each aggregate.

Phytoplankton cell numbers were converted to phytoplankton carbon according to Edler (1979) by multiplying the plasma volume of each cell by $0.13 \text{ pg } \mu\text{m}^{-3}$ for armored dinoflagellates and $0.11 \text{ pg } \mu\text{m}^{-3}$ for all other cells. The plasma volume of a thecate dinoflagellate is identical to its total volume, whereas for diatoms a correction for the large vacuole is needed (plasma volume = total volume - 0.9 vacuole volume). We also used Calcofluor stain to further investigate theca plates of dinoflagellates under a fluorescence microscope. This stain revealed the presence of many small fragments of theca which had not been observed under bright field. We used the fluorescence microscope to confirm that >98% of all dinoflagellates had been actively autotrophic.

Results

Aggregate characteristics

The aggregates of dinoflagellate marine snow observed in this study were very large (centimeters long), brown, sticky, and unusually strong and cohesive. They were held together with thick, viscous, mucus-like material. Unlike the more fragile, flocculent aggregates formed primarily by diatoms, these aggregates did not readily break apart when disturbed by a diver under water. Aggregates larger than 3 mm in diameter varied in abundance from 0.1 to 2 aggregates l^{-1} at the six sampling stations (Table I).

Microscopic examination revealed that these aggregates contained primarily diatoms, empty frustules, mucus-like material, and some zooplankton fecal matter and detritus. However, they also contained high abundances of very large, thecate dinoflagellates. *Gonyaulax polyedra*, *G.polygramma*, *G.grindleyi* and *G.koeffoidi* made up >90% of the dinoflagellates by number, but species of *Ceratium*, *Dinophysis*, *Prorocentrum* and *Protoberidinium* also occurred. Silicoflagellates and ciliates were observed regularly. The ciliates were often observed to contain *Gonyaulax* and had clearly been grazing on these organisms. While diatoms, predominantly small *Nitzschia* spp., were the most abundant algal component by number, making up 53–98% of the cells present (Table I), dinoflagellates contributed far more to the total carbon in the aggregates (because of their large size). Thirty-two to 95% of the algal carbon in aggregates consisted of dinoflagellate cells (Table II).

Table 1. The mean occurrence of dinoflagellates and diatoms in marine snow aggregates at six stations in the Santa Barbara Channel, California. The enrichment factor is the volume of surrounding seawater which would contain the same number of cells as a unit volume of aggregate

Date	Aggregate abundance (no. l ⁻¹)	Diatom abundance (cells agg ⁻¹)	Dino abundance (cells agg ⁻¹)	% occurring in aggregates		% of cells that are dinos		% of dinos that are cysts		Enrichment factor of aggregates			
				Diatoms	Dinos	Aggs	SW	Aggs	SW	Aggs	SW	Cysts	Dino cells
1989													
14 Nov.	0.1	1880	406	5.9	3.9	17	20	80	50	nd	nd	nd	nd
1994													
1 Dec.	2.0	719	53	2.1	4.3	2	nd	71	36	111	116	168	168
2 Dec.	0.1	2210	337	0.5	2.2	8	3	75	70	1413	12 076	546	546
3 Dec.	0.1	5978	1236	3.0	2.4	18	21	66	56	3803	2521	3882	3882
4 Dec.	0.5	411	251	0.5	8.7	47	3	69	35	8573	2015	167	167
5 Dec.	0.1	1428	347	1.7	1.4	20	23	56	43	2190	1292	2018	2018
Mean	0.5	2104	438	2.3	3.8	19	12	70	48	3218	3604	1356	1356
SD	0.8	2015	410	2.0	2.6	15	10	8	13	3278	4821	1605	1605

Agg. aggregate; SW, surrounding seawater; dinos, thecate dinoflagellates.

Table II. The average total particulate organic carbon (POC) and phytoplankton particulate carbon (PPC) in aggregates (Agg) and in seawater at five stations in the Santa Barbara Channel

Date in 1994	Aggregates ($\mu\text{g C agg}^{-1}$)				Seawater ($\mu\text{g C l}^{-1}$)				% of PPC in dinos	
	PPC in dinos	PPC in diatoms	POC in agg	% of POC in dinos	PPC in dinos	PPC in diatoms	Total POC	% of POC in dinos	Aggregates	Seawater
1 Dec.	0.43	0.91	19.2	2.3	nd	nd	nd	nd	32	nd
2 Dec.	0.69	0.23	15.6	4.4	18	9	156	12	75	69
3 Dec.	2.23	0.17	96.8	2.3	57	6	178	32	93	90
4 Dec.	7.31	0.37	31.8	23.0	15	12	129	12	95	58
5 Dec.	2.67	0.38	31	8.6	30	3	132	23	88	92
Mean	2.67	0.41	38.8	8.1	30	8	148	20	77	77
SD	2.77	0.29	33.2	8.7	19	3	20	10	26	17

Dinos, thecate dinoflagellates.

The majority (56–80%) of the thecate dinoflagellates in aggregates existed as cysts (Table I). These cysts had relatively thin cell walls and lacked internal pigmented bodies or exterior spines. From their appearance, we conclude that they were temporary, vegetative dinoflagellate cysts, presumably cysts of *Gonyaulax* spp. The presence of abundant empty thecae in the samples also suggested that these were temporary cysts. Neither thick-walled, spined hypnozygotes (the long-lived cysts produced through sexual reproduction commonly found in marine sediments) nor flagellated planozygotes (a stage lasting a minimum of 3–5 days preceding the formation of hypnozygotes; Walker, 1984; Anderson *et al.*, 1985) were observed.

The quantity of POC, PON, Chl *a* and dry mass of individual aggregates was a significant exponential function of aggregate volume (Figure 1). However, dinoflagellate aggregates contained from two to four times more of each of these components than other types of marine snow aggregates of identical size. Alldredge (1998) reported size to mass, POC, PON and Chl *a* relationships for common types of marine snow aggregates (shown as open circles in Figure 1). These relationships were similar in slope, but significantly lower in elevation (and intercept) than the relationships found for dinoflagellate snow ($P < 0.01$ for all four chemical

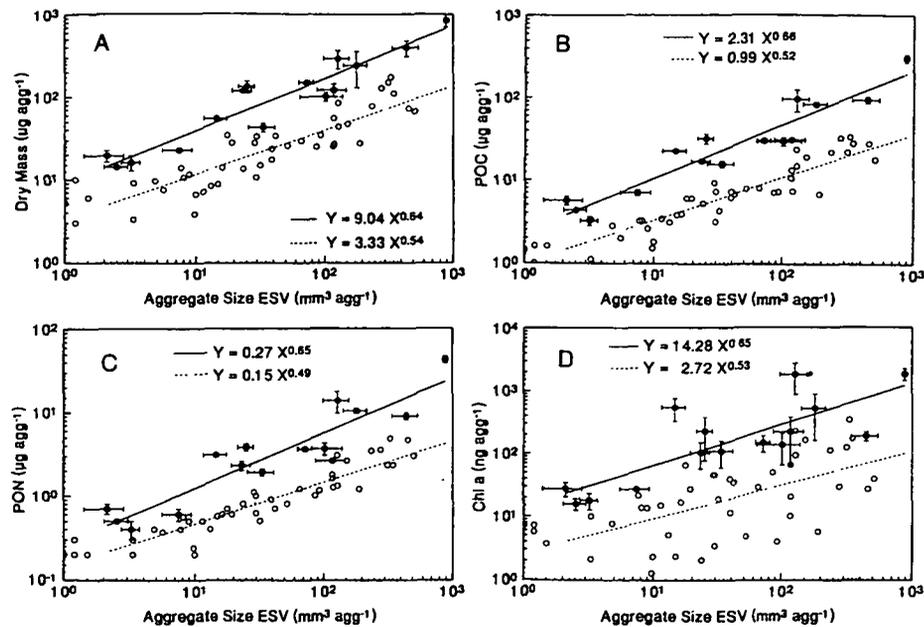


Fig. 1. The content of marine snow as a function of aggregate size for dinoflagellate aggregates (closed circles, solid line) and other types of aggregates combined including aggregates dominated by diatoms, fecal matter, miscellaneous debris, and larvacean houses (open circles, dashed line). Data for 'other types of aggregates' are from Alldredge (1998). Each data point represents an average of three replicates of 10–30 aggregates each for chemical analysis and 10–12 aggregates for size. Error bars (1 SE) are shown only for dinoflagellate aggregates in order to simplify the graphical presentation. The correlation coefficients below refer to the relationship for dinoflagellate aggregates. (A) Dry mass, $r^2 = 0.93$, $P < 0.001$; (B) POC, $r^2 = 0.88$, $P < 0.001$; (C) PON, $r^2 = 0.81$, $P < 0.001$; (D) Chl *a*, $r^2 = 0.43$, $P < 0.01$.

constituents). From estimates of dinoflagellate abundance and cell carbon content, we estimate that dinoflagellate carbon contributed up to 23% to total POC in the aggregates (mean 8%; Table II). Empty thecae composed primarily of cellulose, whose carbon content could not be estimated, were very abundant and likely to contribute substantially to the higher carbon and mass content as well.

The TEP content of marine snow was also found to be a significant exponential function of aggregate volume. However, the TEP content of dinoflagellate snow was not significantly different from that of other types of aggregates when normalized for aggregate size (Figure 2), suggesting that the higher mass content of dinoflagellate aggregates did not result from unusually high concentrations of TEP. Table III summarizes the abundance of TEP normalized to other aggregate components within a variety of types of marine snow. Aggregates containing few diatoms, such as larvacean houses, and aggregates composed of miscellaneous debris contain very little TEP relative to other components. However, diatom flocs and dinoflagellate aggregates (which contained abundant diatoms) had nearly identical concentrations of TEP per unit Chl *a*, POC, or mass, suggesting that these two aggregate types were very similar in TEP concentration.

Comparisons between snow and seawater

Dinoflagellates and diatoms were also the dominant phytoplankton taxa found suspended in the seawater surrounding the aggregates. In fact, a relatively small percentage of these major taxa occurred within marine snow. A mean of only 3.8% of all the dinoflagellates, 5.1% of dinoflagellate cysts and 2.3% of all the diatoms present at 10–20 m occurred in association with aggregates (Table I). However, because aggregates are concentrated assemblages of particles, dinoflagellates and diatoms were highly enriched within them, occurring at concentrations 100–1000 times higher within aggregates than in an equal volume of surrounding seawater (Table I).

A paired *t*-test for equivalence of means indicated that the percentage of total dinoflagellate cells relative to total phytoplankton within aggregates was not

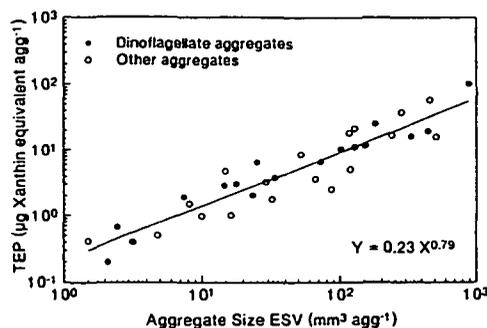


Fig. 2. The TEP content of marine snow as a function of aggregate size. The relationship is significant at $P < 0.001$ ($r^2 = 0.69$). TEP is expressed as µg equivalent of gum xanthan, a polysaccharide used as a standard in measuring TEP concentrations semiquantitatively (Passow and Aldredge, 1995).

significantly different from their percentage in the surrounding seawater (19% versus 12%, respectively, $P > 0.2$). However, a significantly higher proportion of the total dinoflagellates on marine snow existed as cysts than in the surrounding seawater (70% versus 48%, $P < 0.001$), indicating that cysts were significantly concentrated on marine snow (Table I). Owing to the high detrital content of marine snow, a significantly lower fraction of the total POC in dinoflagellate aggregates existed as dinoflagellate cells than in the surrounding seawater (mean of 8 and 20%, respectively, $P < 0.001$; Table II).

Discussion

Uniqueness of dinoflagellate marine snow

Dinoflagellate marine snow differed from other types of marine snow in three major ways. First, of course, it contained conspicuous abundances of large thecate dinoflagellates. Second, it contained several times more POC, PON, mass and Chl *a* per unit volume than reported for other types of marine snow (Alldredge, 1997). Third, it was held together by unusually copious and viscous mucus. The high concentrations of dinoflagellates were not adequate to explain the increased matter content observed. Moreover, while the abundant empty cellulosic theca present may have made a substantial contribution to the POC and mass of aggregates, they were unlikely to have contributed as much to PON and Chl *a*. Yet these components were also higher than in other types of marine snow.

Several hypotheses can be evaluated to explain the elevated matter content per unit volume of dinoflagellate aggregates. First, although the types of other component particles composing these aggregates, including fecal pellets, diatoms and detritus, did not appear to differ substantially from those found in other types of marine snow, these components may have been more densely packed together. Dense packing of component particles might be expected for aggregates formed under conditions of high shear and turbulence. Such conditions result in higher impact velocities during aggregation, thus generating more compact aggregates with higher fractal dimensions (Logan and Kilps, 1995). However, dinoflagellates flourish best under conditions of low turbulence (Taylor, 1987) and do not readily

Table III. TEP content of various types and sizes of marine snow. TEP is expressed semiquantitatively as μg xanthan equivalent, a TEP-like polysaccharide used as a standard

Type of snow	Date and location	<i>N</i>	TEP/agg ($\mu\text{g agg}^{-1}$)	TEP/Chl <i>a</i> ($\mu\text{g ng}^{-1}$)	TEP/POC ($\mu\text{g } \mu\text{g}^{-1}$)	TEP/mass ($\mu\text{g } \mu\text{g}^{-1}$)
Dinoflagellate	SB, 1–6 Dec., 1994	5	15.4 ± 15.0	0.04 ± 0.02	0.36 ± 0.02	0.12 ± 0.02
Larvacean	WA, 20 April, 1994	1	0.01	nd	0.01	nd
	SB, 21 June, 1995	1	0.4	0.02	nd	0.03
Miscellaneous	MB, July, 1993	4		0.01 ± 0.003	0.24 ± 0.02	0.07 ± 0.02
	SB, 22 June, 1995	1	5.1	0.03	nd	0.29
Diatom	SB, Sept., 1994	2	2.9 ± 0.6	0.06 ± 0.01	0.36 ± 0.01	0.11 ± 0.01
	MB, 29 July, 1993	1	nd	0.01	0.71	0.12
	SB, 19 June, 1995	1	18.0	0.27	nd	0.72

SB, Santa Barbara Channel; MB, Monterey Bay; WA, East Sound, Washington; *N*, number of stations.

replace diatoms in succession in nature when high shear or turbulence is present (Eppley *et al.*, 1978). Thus, the very presence of high abundances of dinoflagellates suggests that our stations had experienced conditions of low turbulence in the recent past. Wind speeds were low, generally $<5 \text{ m s}^{-1}$, throughout our study, further reducing turbulence. Thus, high collision impact does not adequately explain our results.

A high mucus content might increase aggregate mass content, but the size-specific TEP composition of dinoflagellate aggregates did not differ from other types of aggregates. Moreover, the TEP content normalized to POC, mass or Chl *a* content of dinoflagellate aggregates was very similar to that of diatom aggregates, suggesting that most of the TEP in the dinoflagellate aggregates probably originated from diatoms which were also abundant in the bloom. Staining of a dense laboratory culture of *G.polyedra* for TEP yielded almost no measurable TEP (A.L.Aldredge, unpublished data). Thus, the mucus-like material in dinoflagellate aggregates is probably not TEP (acidic polysaccharides containing sulfated half-ester groups) but some other type of mucus. Copious mucus is generated during the formation of temporary dinoflagellate cysts (Walker, 1984) and, from our observations, this mucus appears to be of considerably higher cohesiveness, density and stickiness than TEP. This viscous mucus might attach component particles together more tightly and generate more compact particles with higher mass content per unit size. This, combined with contributions from cysts and empty theca, may have generated the high matter content observed in dinoflagellate aggregates.

The matter content of dinoflagellate aggregates makes them particularly rich food sources for zooplankton. Dilling (1997) found that the euphausiid, *Euphausia pacifica*, and the copepod, *Calanus pacificus*, voraciously consumed dinoflagellate aggregates collected at our stations at rates higher than those at which they consumed other types of marine snow. The ability of bioluminescent *G.polyedra* and *G.polygramma* within aggregates either to attract or deter migrating aggregate consumers at night is not known, but is probably significant.

Implications for dinoflagellate biology

This is the first report of high abundances of armored dinoflagellates within large, rapidly sinking aggregates of marine snow. About 80% of total POC in healthy, growing dinoflagellate blooms is usually contained in living cells (Noji *et al.*, 1986). The low percentage of phytoplankton carbon relative to total POC at our stations suggests that we were investigating a declining bloom rich in detritus. Mass aggregation and sedimentation of declining blooms is adaptive for certain taxa, especially diatoms. Sedimentation of resting stages to the sea floor in rapidly sinking aggregates is a common adaptation among coastal diatom species and appears to be an integral part of their life histories (Smetacek, 1985). Diatoms excrete abundant polysaccharides, leading to the formation of TEP which facilitates this mass aggregation and sedimentation (Passow *et al.*, 1994). Does the occurrence of armored dinoflagellates in large, rapidly sinking aggregates indicate that these taxa are also adapted for mass aggregation and subsequent rapid

sedimentation to deep water? Our data do not support this conclusion for several reasons.

First, the dinoflagellate cysts we observed were short-lived temporary cysts, rather than the over-wintering, long-lived, resistant dinoflagellate and diatom cysts found in modern and fossil marine sediments. The lack of exterior spines, the thin cyst walls, the lack of pigmented intracellular bodies within the cysts themselves (Anderson and Wall, 1978; Dale, 1983) and the absence of planozygotes, long-lived flagellated stages which precede the formation of sexually generated hypnozygotes (Pfiester and Anderson, 1987), all support our identification of the dinoflagellate cysts within marine snow as temporary cysts. Temporary cysts, sometimes called pellicle cysts (Dale, 1983), are non-motile vegetative cysts known to form in cultures when conditions, such as temperature, salinity or nutrients, change rapidly or deteriorate (Dale, 1977; Walker, 1984). Their formation can be accompanied by extensive mucus formation (Walker, 1984). These cysts persist only a short time and have only rarely been observed in sediments (Nehring *et al.*, 1995). They appear to be a mechanism by which dinoflagellates survive brief, unfavorable periods in the water column rather than a stage which facilitates survival through sedimentation and later transport to the surface.

Second, the proportion of total dinoflagellates within marine snow, expressed both as the proportion of total algal carbon and the percentage of total algal cell number, was not significantly different from that in the surrounding seawater. If dinoflagellates were differentially aggregating, we would expect them to occur at higher proportions within aggregates than in the surrounding seawater relative to other types of algal cells. Diatom resting spores occur only within aggregates in the field, suggesting that they actually form within aggregates (Silver *et al.*, 1978; Alldredge *et al.*, 1995; Brzezinski *et al.*, 1998). Although a significantly higher percentage of dinoflagellates existed as temporary cysts within aggregates than in the surrounding seawater, the abundance of free-living cysts observed in our study clearly indicates that dinoflagellates need not be in aggregates to form temporary cysts. Moreover, an alternate mechanism may explain the differential concentration of dinoflagellate cysts within aggregates. Dinoflagellates are highly motile and are able to regulate their position in the water column (Taylor, 1987). These large, motile cells may avoid becoming stuck to the sticky surfaces of marine aggregates. The higher percentage of cysts in aggregates may reflect differential avoidance of aggregates by motile stages rather than differential aggregation of non-motile cysts or their formation within aggregates.

Our data indicate that mass aggregation at the end of blooms is unlikely to be an adaptation of the armored dinoflagellate species encountered here. Dinoflagellate cells appear to become aggregated in diatom marine snow through normal processes of coagulation, just as do non-living fecal and detrital particles. The common co-occurrence of dinoflagellates with diatoms in coastal blooms (Taylor, 1987) would facilitate the accumulation of dinoflagellates within diatom aggregates and would lead to more rapid sinking of some proportion of the dinoflagellate population into deeper waters. Dinoflagellates sink relatively slowly as single cells (6–11 m day⁻¹; Anderson *et al.*, 1985), but once incorporated in marine snow they may sink at rates of ~50–100 m day⁻¹ (Alldredge and Gotschalk, 1988).

Although temporary dinoflagellate cysts are rarely found in marine sediments (Dale, 1983), they have recently been described in the sediments of German coastal waters where they serve as food for benthic copepods and worms (Nehring *et al.*, 1995). This suggests that rapid transport to the sea floor can occur in some systems. The nutrient-replete microenvironment of the marine snow (Shanks and Trent, 1979; Allredge and Gotschalk, 1990; Brzezinski *et al.*, 1998), or the sinking of aggregates into more nutrient-replete water, may also facilitate transformation of temporary cysts back into motile cells which then escape the confines of the aggregate through active swimming before reaching the sea floor. These cells return to the water column and may eventually reach surface waters through passive transport and active swimming. This is a considerably different fate than that of diatom and dinoflagellate resting cysts which are commonly observed in marine sediments. Whether dinoflagellate resting cysts might become aggregated in marine snow is not known. Sedimentation of hypnozygotes from a bloom of *Peridinium hangoei* at rates higher than might be expected for single cells has been reported previously in the Baltic Sea (Heiskanen, 1993) suggesting that association of resting cysts with marine snow is also possible, although as yet undocumented.

TEP content of marine snow

Although the TEP content of all types of marine snow, including dinoflagellate snow, was a significant function of aggregate size, considerable variation existed among individual aggregates. TEP content varied by a factor of 2–20 times for any given size of aggregate. This variability reflects the age and sources of marine snow. Aggregates containing abundant diatoms, common sources of TEP, have higher TEP concentrations than aggregates formed from bacteria, larvacean houses, fecal matter and unidentifiable debris. However, the predictable quantities of TEP occurring in aggregates of all types provide further support for the hypothesis that TEP is essential for the formation of marine snow by processes of aggregation (Allredge *et al.*, 1993). TEP serves as the glue binding together the relatively unsticky detrital and algal particles in the water column, and occurred in all types and sizes of marine snow. Moreover, the persistence of TEP in ageing aggregates dominated by complex microbial communities and decomposing organic matter suggests that TEP is resistant to microbial decay or, alternatively, that the bacteria decomposing it produce similar mucus as capsular material (Heissenberger *et al.*, 1996). These processes may help explain how aggregates persist as they sink into the ocean interior.

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