

## Colonization of marine snow aggregates by invertebrate zooplankton: Abundance, scaling, and possible role

**Abstract**—I compiled literature observations of abundances of invertebrate zooplankters associated with marine snow aggregates in the euphotic zone. Abundances, normalized with ambient concentrations of colonizers, scale with equivalent aggregate radius raised to power 2.27. Different taxonomic groups showed different affinities for aggregates and copepods and crustacean nauplii were the dominant groups on aggregates. The encounter volumes (volume searched to find one aggregate) are substantial, e.g., >1 liter for a 1-cm aggregate, suggesting that some zooplankters actively search for aggregates. The scaling of the enrichment of invertebrates in aggregates over ambient water with aggregate radius ( $r$ ) was significantly different from that of bacteria,  $\propto r^{-0.73}$  and  $\propto r^{-2.25}$ , respectively, and for aggregates larger than 0.1 cm radius, invertebrates were one to several orders of magnitude more enriched than bacteria. Tentative estimates of the remineralization and degradation rates of aggregates due to the activity of invertebrate colonizers suggest that aggregate carbon is turned over within one to a few days. This is similar to or faster than turnover rates due to microorganisms. It is also estimated that between 20 and 70% of aggregate carbon is degraded by invertebrate colonizers before a sinking aggregate leaves a 50-m-deep euphotic zone. Thus, the majority of aggregated material may be degraded within the euphotic zone due to the combined activity of colonizing invertebrates, other grazers, and microorganisms.

Vertical material transport in the ocean happens mainly through the sinking of large aggregates and fecal pellets (Fowler and Knauer 1986). Aggregates may be formed from smaller primary particles by several processes, and physical coagulation has been implicated as one of the main mechanisms (e.g., Jackson 1990). Coagulation theory implies that flux increases as a power function of the concentration of suspended particles, with a power >1 (e.g., Kiørboe et al. 1996). However, summaries of ocean observations suggest that flux out of the euphotic zone increases less with particle concentration (e.g., Baines et al. 1994). Also, little material may leave the euphotic zone, even when formation rate and concentration of aggregates are very high (e.g., Kiørboe et al. 1998). Below the euphotic zone, the vertical flux declines with depth (e.g., Banse 1990). Together, these observations suggest that aggregates to a large extent are remineralized in the water column, both within and below the euphotic zone.

Microbes occur on aggregates at concentrations exceeding ambient concentrations by one to several orders of magnitude and aggregates are sites of elevated microbial activity (Allredge and Silver 1988). Bacteria may dissolve (Smith et al. 1992) and remineralize (Ploug et al. 1999) particulate material in aggregates at substantial rates, leading to expected turnover times of a few days to a week. Aggregates also provide a food source for zooplankton and fish (Lampitt

1992; Larson and Shanks 1996) that further contribute to aggregate remineralization. Banse (1990) suggested that below the euphotic zone, zooplankton in particular may be responsible for reducing the vertical flux. Some zooplankton groups appear particularly adapted to colonize sinking aggregates, inhabit them for shorter or longer periods, and feed on their constituents. While the colonization phenomenon has been known for quite some while (Allredge 1972), only recently have quantitative investigations of the abundance of mesozooplankters inhabiting marine snow aggregates been undertaken (Shanks and Edmonson 1990; Steinberg et al. 1994; Green and Dagg 1997; Shanks and Carmen 1997; Shanks and Walters 1997).

In this study I examine the potential role of colonizing invertebrates in degrading and remineralizing sinking aggregates within the euphotic zone. I compile available information from the literature on the abundance of zooplankton inhabiting aggregates and examine how abundance scales with aggregate size. I then combine these observations with information on the carbon content of marine snow particles and metabolic rates of zooplankters to evaluate the possible role of colonizing invertebrates in degrading sinking aggregates.

**Abundance of zooplankters on aggregates**—I identified only four studies with simultaneous quantitative information on abundances of invertebrate zooplankters inhabiting aggregates of known (average) sizes and concentrations of the same organisms in the ambient water (Shanks and Edmonson 1990; Green and Dagg 1997; Shanks and Carmen 1997; Shanks and Walters 1997). In these studies aggregates were collected in the photic zone at 3–15 m depth. One additional study had information on the abundance of zooplankters inhabiting aggregates of known size (Steinberg et al. 1994); this study was at a deep site and the aggregates were giant larvacean houses collected at 100–500 m depth.

Figure 1 summarizes this information. Abundances of invertebrate zooplankters per aggregate vary by almost four orders of magnitude and can be substantial (up to several 100 individuals per aggregate). There is a significant trend of increasing mesozooplankton abundance with increasing aggregate size ( $P < 0.001$ ), although there is a considerable scatter in this relation (Fig. 1).

Some of this scatter may be caused by the inclusion of somewhat different taxonomic groups in the different studies and by variable ambient abundances of colonizing organisms. I therefore normalized abundances of organisms on aggregates with their concentration in the water column (Fig. 2a) and also broke the relations down into taxonomic units to the extent possible (Fig. 2b–g). The normalization significantly reduces the scatter and suggests that abundances of invertebrates inhabiting aggregates scale approximately with

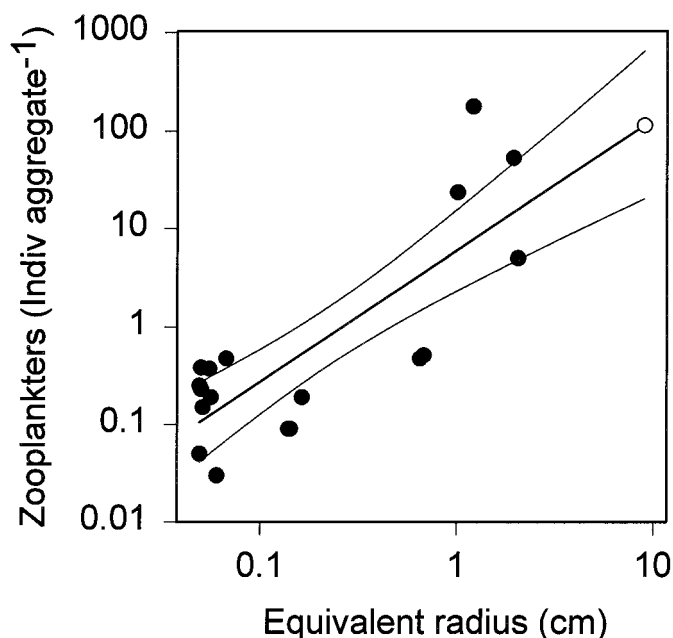


Fig. 1. Abundance of invertebrate zooplankters attached to marine snow aggregates as a function of aggregate size. Aggregates were in all cases collected individually by divers or submersible. Sizes of aggregates are here converted to equivalent radius from information on (average) volume, transsectional area, or diameter as reported in the original references. Data from the euphotic zone (closed symbols) are from Shanks and Edmonson (1990), Green and Dagg (1997), Shanks and Carmen (1997), and Shanks and Walters (1997) and are presented as averages for individual sampling sites and dates. Shanks and Carmen (1997) and Shanks and Walters (1997) report polychaetes and other invertebrates, respectively, from the same study; these data were combined here. One observation from below the euphotic zone (open symbol) is from Steinberg et al. (1994) and is the average over several sampling dates. The fitted regression is  $\log Y = 0.78 + 1.34\log X$ ,  $R^2 = 0.71$ .

aggregate radius squared. Deviations from this pattern (nauplii, nematodes) may be real or may be due to the scarcity of data or the nonspherical form of particles. The observations also suggest that some invertebrates are closer associates of aggregates than others. Harpacticoid copepods, for example, are more than one order of magnitude relatively more abundant than the mixed group of cyclopid, poecilostomatoid, and calanoid copepods (other copepods). Within the latter group, poecilostomatoid copepods, particularly of the genus *Oncaea*, are by far the relatively most abundant. Nematodes and polychaete larvae are likewise much more relatively abundant than nauplii. Other relatively abundant groups, for which a scaling analysis is not possible due to scarcity of data, include certain amphipods.

Due to the very different abundances in the pelagic environment of the various invertebrate groups considered in Fig. 2, the normalized abundances yield a biased impression of the actual occurrences of the different groups in aggregate metazoan communities. Therefore, average actual abundances from a number of field studies of the quantitatively most abundant groups have been shown in Table 1 for small ( $\sim 0.1$  cm radius) and large (1 cm radius) aggregates. Evidently, for

both small and large aggregates, crustacean nauplii are the most abundant group, followed by copepods. Particularly in small aggregates, invertebrate larvae are also relatively abundant. Despite their high affinity for aggregates, nematodes contribute relatively little. Typical carbon contents of the various groups are also shown. Weighted average carbon contents suggest that the typical size of an invertebrate attached to a small aggregate is less than that attached to a larger one.

*Encounter rates and mechanisms*—The normalized abundance of zooplankters on aggregates has units of  $\text{ml particle}^{-1}$ . It is equivalent to the volumes of ambient water that contains the same amount of organisms that is now sitting on the aggregate. Depending on the mechanism by which zooplankters and aggregates encounter each other, it can be interpreted as the volume of water scavenged for zooplankters by a sinking aggregate or as the volume of water that an individual zooplankter searches for aggregates. For the larger aggregates, this volume is substantial (up to 10 or more liters). The observed scaling of abundance of colonizers with aggregate size might suggest simple scavenging as the main encounter mechanism, because the scavenged volume (ignoring hydrodynamic effects) scales with radius squared (scavenged volume =  $\pi r^2 d$ , where  $r$  = aggregate radius and  $d$  = sinking distance). Sinking distances required to account for the observed abundances of colonizers are on the order of 1–10 m, consistent with these aggregates being collected at 3–15 m depth. However, Alldredge (1972), Shanks and Carmen (1997), and Shanks and Walters (1997) did behavioral observations of mesozooplankters associated aggregates. They all noted that most invertebrates only visit aggregates for short periods of time, a few minutes. If we assume a typical residence time of 3 min (Shanks and Walters 1997), the volumes in Fig. 2 can be turned into clearance rates by division with 3 min. With reference to the regression for all invertebrates, this implies that individual zooplankters clear 0.1-cm-radius aggregates at a rate of ca. 0.25  $\text{L h}^{-1}$  and 1-cm-radius aggregates at a rate of ca. 45  $\text{L h}^{-1}$  (or that the aggregates scavenge volumes at these rates). Simple scavenging and reported aggregate sinking velocities cannot account for such high encounter volumes. Aggregates sink at size-dependent velocities,  $v = \alpha r^b$ . Different values of  $b$ , ranging from 0.26 (Alldredge and Gotschalk 1988) to  $\sim 1.0$  (Alldredge and Gotschalk 1989) have been reported in the literature. If we assume the empirical relation found by Alldredge and Gotschalk (1989), then  $b \sim 1$  and  $v \cong 0.2r \text{ s}^{-1}$ . The volume scavenged by a sinking aggregate per unit time (disregarding hydrodynamical effects, thus a maximum estimate),  $\pi r^2 v \cong 0.2\pi r^3 \text{ s}^{-1}$ , is thus about 2.3  $\text{ml h}^{-1}$  for a 0.1-cm aggregate and about 2.3  $\text{L h}^{-1}$  for a 1-cm aggregate. Employing instead the empirical sinking velocity–size relation of Alldredge and Gotschalk (1988),  $v (\text{cm s}^{-1}) = 0.126r (\text{cm})^{0.26}$ , yields estimates of similar magnitudes (7.8  $\text{ml h}^{-1}$  and 1.4  $\text{L h}^{-1}$ ). These rates are one to two orders of magnitude less than those estimated above. These considerations suggest that (some) zooplankters actively search for aggregates, and that remote detection is required.

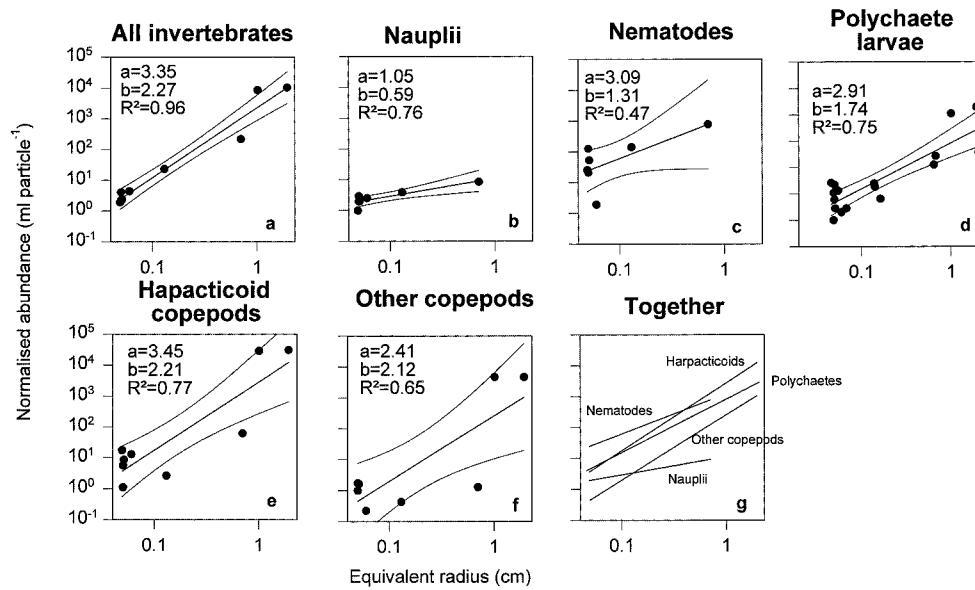


Fig. 2. Normalized abundances of invertebrate zooplankters associated marine snow aggregates as a function of aggregate size. Data from Shanks and Edmonson (1990), Green and Dagg (1997), Shanks and Carmen (1997), and Shanks and Walters (1997). Normalization is only possible for a subset of the data in Fig. 1. All aggregates were collected in the euphotic zone at 3–15 m depth. Other copepods refer to the mixed group of calanoid, cyclopoid, and poecilostomatoid copepods. Original observations were reported as numbers of zooplankters per aggregate or as a fraction of the zooplankton population attached to aggregates; these were normalized by division with ambient concentrations of zooplankters or aggregates, respectively. These two normalization procedures are identical. In several instances the original data required averaging over several sampling dates at each site depending on the degree of detail in the reports; this explains the different numbers of data points for each category. Regression parameters ( $\log Y = a + b \log X$ ) and  $R^2$  are given for each regression.

Table 1. Mean abundances of most abundant invertebrate groups attached to small ( $\sim 0.1$  cm radius) and large ( $\sim 1$  cm radius) aggregates in the euphotic zone. Abundances were normalized to aggregate sizes of 0.1 and 1.0 cm, respectively, by assuming the scaling of Fig. 2a for all invertebrates ( $\propto r^{2.27}$ ) and averaged over study sites and sampling stations. Data for large aggregates are from Green and Dagg (1997) (shallow sampling in the northern Gulf of Mexico) and data for small aggregates are from Shanks and Carmen (1997) and Shanks and Walters (1997) (shallow sampling in various coastal areas).

Invertebrate group	Small aggregates		Typical body carbon ( $\mu\text{g C}$ )
	Large aggregates (no. aggregate <sup>-1</sup> ), mean (SD)	(no. [100 aggregates] <sup>-1</sup> ), mean (SD)	
Calanoid copepods	8.8 (13.4)	—	
Cyclopoida	4.2 (6.6)	—	
Poecilostomatoida	4.8 (3.4)	—	
Calanoid + cyclopoid + poecilostomatoid copepods	17.7 (23.2)	0.6 (1.1)	5
Harpacticoid copepods	0.7 (0.5)	2.1 (3.6)	3
Crustacean nauplii	22.2 (22.6)	25 (41)	0.5
Polychaetes (larvae)	0.8 (1.1)	2.5 (3.4)	2
Nematodes	—	0.6 (0.8)	0.5
Gastropod veligers	—	0.3 (0.5)	1
Bivalve veligers	—	3.5 (3.5)	1
Weighted average body carbon ( $\mu\text{g C}$ )	2.5	0.9	

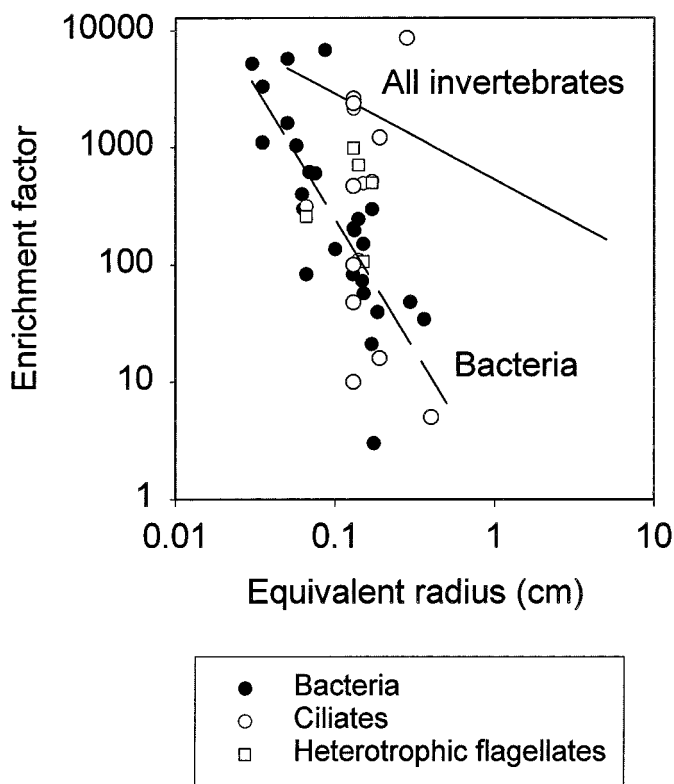


Fig. 3. Enrichment factors for bacteria, other heterotrophic microorganisms, and invertebrate zooplankters on marine snow aggregates as a function of aggregate size. Enrichment factor is computed as concentration in aggregate/concentration in ambient water. The full line for all invertebrates is derived from the regression in Fig. 2a (enrichment factor = normalized abundance/aggregate volume =  $534r \text{ (cm)}^{-0.73}$ ); the data points are not shown. Closed symbols represent bacteria and the dashed line is the regression for bacteria only (enrichment factor =  $1.39r \text{ (cm)}^{-2.25}$ ,  $R^2 = 0.60$ ). Open symbols are for ciliates (circles) and heterotrophic flagellates (squares). Data for microorganisms are from Silver et al. (1978), Alldredge et al. (1986), Davoll and Silver (1986), Turley and Mackie (1994), and Ploug et al. (1999).

*Remineralization and degradation rates of aggregates in the euphotic zone*—Invertebrates are normally considered to be inferior to microorganisms in accounting for pelagic remineralization rates (e.g., Fenchel 1987). This situation may be different on aggregates, because invertebrates appear to be more enriched in aggregates relative to ambient water than microorganisms. Reported enrichment factors (i.e., concentration in aggregate divided by concentration in ambient water) for pelagic bacteria and other microorganisms have been compiled in Fig. 3. Enrichment factors for invertebrates have also been shown (derived from the regression for all invertebrates in Fig. 2a). For both bacteria and invertebrates the degree of enrichment depends on aggregate size, but the scaling is significantly different (suggesting distinctly different accumulation dynamics). For aggregates exceeding 0.1 cm radius in size, invertebrates are one to several orders of magnitude more enriched than bacteria. Enrichment factors for very large (~10 cm radius) larvacean house aggregates are consistent with those for the smaller aggregates in

Fig. 3, i.e., 264 for invertebrates (Steinberg et al. 1994) and 0.5–15 for bacteria (Silver et al. 1998). Other heterotrophic microorganisms appear to be intermediate but without any clear relation to size. This would suggest that invertebrates are relatively much more important for remineralization rates on aggregates than in the pelagic realm. Figure 3 may somewhat overemphasize this difference, however, because attached bacteria typically are larger than free bacteria (e.g., Alldredge et al. 1986).

Alldredge (1998) examined the carbon content of various types of field-collected marine aggregates (diatom aggregates, detritus aggregates, aggregates formed from mucus feeding webs). Independent of the type of aggregate, she found that carbon content scales approximately with radius<sup>1.5</sup>. Given the above scaling of normalized abundance of colonizers to aggregate size ( $r^2$ ), this implies that numbers of zooplankters per unit carbon scale with  $r^2/r^{1.5} = r^{0.5}$ . Thus, fractional remineralization rate due to zooplankton activity increases with particle size. However, bigger particles have shorter residence times in the euphotic zone than smaller ones (residence time  $\propto v^{-1}$ ). Depending on the relationship between sinking velocity and aggregate size, the fraction of an aggregate's carbon content that has been grazed by colonizing invertebrates scales with  $r^{-0.5} - r^{0.24}$ . This (weak) scaling implicitly assumes that remineralization rate is proportional to the number of colonizers present. However, larger aggregates house on average larger grazers (Table 1). Thus, presumably, larger aggregates become more degraded per unit distance descended than smaller aggregates.

Absolute aggregate mineralization and degradation rates due to the activity of invertebrate colonizers depend on the grazing (degradation) and metabolic (mineralization) rates of the colonizers and on the abundance of colonizers on the aggregate that, in turn, depends on the ambient concentration of colonizers. A first estimate of the order of magnitude of the degradation can be obtained from estimates of typical concentrations and respiration rates. In the four studies conducted in the euphotic zone, ambient concentrations of the considered organisms varied between 2 and 200 liter<sup>-1</sup>; we will take the geometric mean of the reported concentrations, 37 liter<sup>-1</sup>, as a typical value. This yields estimated abundances of colonizers per aggregate (Table 2) that are consistent with those observed (Table 1). Banse (1982) reviewed metabolic rates of small aquatic metazoans. Mass specific rates depend on size and vary somewhat between groups, with nematodes at the lower end of the range and copepods at the higher end. For organisms in the relevant size range, 0.1–10  $\mu\text{g}$  dry mass, mass specific oxygen uptake (20°C) is on the order of 10 nl O<sub>2</sub> h<sup>-1</sup> ( $\mu\text{g}$  dry mass)<sup>-1</sup> ~ 10 ng C h<sup>-1</sup> ( $\mu\text{g}$  body C)<sup>-1</sup> (Banse's fig. 3). This is a conservative estimate for the dominant crustacean group of colonizers. If we further take 1.5  $\mu\text{g}$  body C as a representative size for an invertebrate colonizer (cf. Table 1), then a typical metabolic rate is ~15 ng C ind<sup>-1</sup> h<sup>-1</sup>. Grazing rate is about three times the metabolic rate (e.g., Kiørboe 1989); thus, about 45 ng C ind<sup>-1</sup> h<sup>-1</sup>. By combining the normalized abundance of colonizers for all invertebrates from Fig. 2 with the allometric equation describing the carbon content of aggregates (Alldredge 1998) and the above grazing and metabolic rate estimates, we can now estimate degradation and remineraliza-

tion rates for aggregates in the euphotic zone (Table 2). Fractional mineralization and degradation rates are substantial, 0.08–0.38 and 0.23–1.15  $d^{-1}$ , respectively, for aggregates in the size range 0.1–1.0 cm, leading to turnover times for aggregates of this size on the order of a day to a week or less. This is similar to or faster than recently estimated carbon turnover times due to microbial mineralization (Ploug et al. 1999). Due to the activity of colonizing mesozooplankton alone, between 20 and 70% of the aggregate carbon is degraded before the aggregate leaves a 50-m-deep upper mixed layer.

Of course the present estimates are bound only within very broad limits. Concentrations and activity of colonizers vary widely and depend on a variety of environmental factors. For example, the remineralization and degradation rates estimated here assume that the colonizers feed solely on aggregate material. Some nematodes and invertebrate larvae may use aggregates mainly as transport vehicles (Shanks and Edmonson 1990), and nematodes residing on aggregates may even add material that they capture from the ambient water (Shanks and Walters 1997). This would lead to overestimates of degradation rates, although these groups contribute relatively little to the present estimates (cf. Table 1). Conversely, most crustacean colonizers appear to reside on aggregates for only a small fraction of their time, spending more time cruising between aggregates. Assessing their role in aggregate degradation only from their numerical presence at any point in time may lead to gross underestimates. More accurate estimates of the role of metazoan zooplankton in aggregate degradation would require a much more detailed resolution of the biology of the numerically important organisms. In spite of these limitations, the present exercise does suggest that invertebrate zooplankters colonizing sinking aggregates may play a significant role in remineralizing and degrading aggregates and, thus, in retaining material within the euphotic zone.

The present estimates of aggregate remineralization and degradation rates due to invertebrate colonizers in the euphotic zone may be compared with observations and estimates from the mesopelagic and deeper environments. Steinberg et al. (1997) found, consistent with the present study, that metazoans were more important than microorganisms in accounting for community respiration in mesopelagic (2–500 m depth) giant (~10 cm radius) larvacean house marine snow particles. Fractional remineralization and degradation rates due to copepods averaged 2 and 6%  $d^{-1}$  and were up to 13 and 43%  $d^{-1}$ , respectively, when copepods were abundant. Considering the colder environment and the low ambient abundance of colonizers at depth, these estimates are not inconsistent with the much higher rates estimated here for the euphotic zone. Banse (1990) calculated that mesozooplankton respiration rates in the depth interval 70–200 m at two Pacific deep-water stations could account for between 50 and 100% of the observed decline in vertical particle flux with depth. Similarly, Lampitt (1992) estimated that net zooplankton respiration rates in the depth interval 4–5,000 m could account for 9% of the decline in vertical flux at a subtropical Atlantic station. These latter estimates include all mesozooplankton, not only those colonizing particles. Together, these observations suggest that the signifi-

Table 2. Typical abundances, grazing, and metabolic rates of invertebrate zooplankton associated marine snow particles and estimates of degradation turnover time of aggregates in the euphotic zone, computed for two sizes of aggregates.

Aggregate radius (cm)	Aggregate C-content* (μg)	Normalized abundance† (ml aggregate <sup>-1</sup> )	Abundance of zooplankters per aggregate‡	Zooplankton		Turnover time¶ (d)	Residence time in 50 m mixed layer# (d)	Fractional degradation in mixed layer#
				metabolic rates§ (μg C d <sup>-1</sup> ) (remineralization)	grazing rate   (μg C d <sup>-1</sup> ) (degradation)			
0.1	2	12	0.44	0.16	0.48	4.2	2.9/0.81	0.67/0.19
1.0	76	2,200	81	29	88	0.87	0.30/0.44	0.35/0.50

\* From Alldredge 1998.

† From Fig. 2a.

‡ Assuming 37 colonizers liter<sup>-1</sup>.

§ Assuming metabolic rate of 15 ng C ind<sup>-1</sup> h<sup>-1</sup> (see text).

|| Assuming grazing rate ~3 × metabolic rate.

¶ Aggregate carbon content/degradation rate.

# Assuming either of the two sinking velocity–size relations given in text (i.e.,  $v = 0.2r s^{-1}$  or  $v (cm s^{-1}) = 0.13r (cm)^{0.26}$ , from Alldredge and Gotschalk 1989 and 1988, respectively).

cance of zooplankton relative to microorganisms declines with depth, although the scarcity of data prevents definite conclusions.

If one considers the combined effect of colonizing invertebrates, flux feeders, other aggregate grazers, and attached microorganisms, it appears that aggregates are likely to often be largely decomposed within the euphotic zone. Thus, aggregation of smaller particles into rapidly sinking aggregates does not necessarily imply that this material is lost from the euphotic zone. On the contrary, aggregation may encourage remineralization rates and reduce sinking losses from the euphotic zone due to the localized enhanced abundance of heterotrophs and thus allow sustained high plankton biomass in the euphotic zone. Clearly, this potentially important but understudied phenomenon requires further attention in the future.

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