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Fragmentation of marine snow by swimming macrozooplankton: A new process impacting carbon cycling in the sea

Lisa Dilling¹, Alice L. Alldredge*

Department of Ecology, Evolution and Marine Biology, University of California, Santa Barbara, CA 93106, USA

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Abstract

Comparisons of the abundances and size distributions of marine snow (aggregated particles > 0.5 mm in diameter) in the upper 100 m of the water column at ten stations off Southern California in the late afternoon with those in the same parcel of water the following morning, after nocturnal vertical migration by zooplankton had occurred, revealed the existence of a previously undescribed process affecting marine particle dynamics. Aggregate abundances increased overnight and changes were positively and significantly correlated only with the abundance of the common euphausiid, *Euphausia pacifica*, and with no other biological or physical factor. Moreover, mean aggregate size decreased and aggregate size distributions shifted toward smaller size classes when euphausiids were abundant. The only conclusion consistent with these findings was that euphausiids were physically disaggregating marine snow into smaller, more numerous aggregates through shear stresses generated while swimming. Video-recording of both tethered and free-swimming *E. pacifica* in the laboratory dramatically confirmed that aggregates passing within 8–10 mm of the animal's abdomen were fragmented either by entrainment and direct impact with the beating pleopods or by eddies generated during swimming. At the abundances observed in this study, swimming *E. pacifica* would have sufficiently disturbed 3–33% of the water column each night to disrupt the aggregates contained therein. This is the first evidence for the fragmentation of large particles by the swimming activities of zooplankton and suggests that macrozooplankton and micronekton play a significant role in the particle dynamics of the water column regardless of whether they consume particles or not. Disaggregation of marine snow by swimming and migrating animals may alter the sizes of particles available to grazers and microbial colonizers and reduce the flux of

* Corresponding author. Fax: + 1-805-893-4724.

E-mail address: alldredge@lifesci.ucsb.edu (A.L. Alldredge).

¹ Current address: NOAA Office of Global Programs, 1100 Wayne Ave., Suite 1225, Silver Springs, MD, 20910, USA.

particulate carbon by generating smaller particles, which potentially sink more slowly and reside longer in the water column. This newly discovered process reduces carbon flux while simultaneously conserving carbon and provides a previously unconsidered link between animal behavior and the biogeochemistry of the sea. It may help explain the exponential reduction in particle flux with depth observed in parts of the ocean and help balance oceanic carbon models. © 2000 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Most of the particulate organic carbon sedimenting to the deep ocean settles as large, rapidly sinking, organic aggregates > 0.5 mm in diameter, known as marine snow (Fowler and Knauer, 1986; Alldredge and Silver, 1988; Silver and Gowing, 1991). The flux of particulate carbon in these and other large particles decreases exponentially below the mixed layer (Martin et al., 1987; Silver and Gowing, 1991) because of processes that either directly consume aggregates or that transform them into non-sinking or more slowly sinking forms. Smaller, more slowly sinking particles remain longer in the water column, making them more susceptible to processes that retain carbon in the upper ocean. Processes that reduce the quantity of particles sedimenting from the upper ocean alter the strength of the biological pump and decrease the ocean's ability to sequester carbon in the deep sea, thus impacting the global carbon cycle.

Several hypotheses have been formulated to explain the decrease in particle flux with depth, including microbial decomposition and solubilization, abiotic fragmentation to form smaller, more slowly sinking particles, and consumption by animals (Karl et al., 1988). However, microbial decomposition is not rapid enough to account for most of the decrease (Karl et al., 1988), and abiotic fragmentation by wind or current-generated fluid shear has been discounted because shear rates in most of the ocean do not appear sufficient to disrupt most types of marine snow (Alldredge et al., 1990). While still under intensive investigation (Karner and Herndl, 1992; Smith et al., 1992), solubilization, like decomposition, may not occur rapidly enough to explain observed decreases. Finally, although marine snow is consumed by many types of zooplankton (Alldredge, 1972; Dagg, 1993; Lampitt et al., 1993; Dilling et al., 1998) and intercepted by "flux feeders" (Jackson, 1993), the potential impact of zooplankton grazers on the abundance and size distribution of large aggregates and, by inference, on particle flux has not been investigated in the field.

We originally conceived the following study to test the hypothesis that abundant macrocrustaceans migrating into surface waters at night to feed could reduce the abundance and size distribution of marine snow in the upper water column over a single night sufficiently to potentially impact particle flux. We correlated the change in aggregate size and abundance in the upper 100 m overnight with the abundance of

vertically migrating *Euphausia pacifica*, a euphausiid species known to readily consume marine snow (Dilling et al., 1998). Nighttime reductions in aggregate concentrations correlated with euphausiid abundance would indicate that animal consumption was a significant process affecting particle abundance and sedimentation in nature.

Unexpectedly, the field study yielded convincing data indicating that a fifth, previously unconsidered process, physical fragmentation by the swimming activities of migrating macrozooplankton, may reduce the sizes and sedimentation rates of large, sinking particles in the ocean. Herein we present the first preliminary laboratory evidence of the existence of this newly discovered process and field evidence supporting its potential to significantly impact sedimentation rates, carbon cycling, and particle dynamics in the sea. This study provides an additional explanation for the reduction in particle flux with depth and reveals a previously unknown link between animal behavior and biogeochemical cycling in the sea.

2. Methods

2.1. General approach

The hypothesis that migrating euphausiids could alter the abundance and size distribution of marine snow particles in surface waters overnight was tested off the coast of southern California by comparing the size distribution and abundance of particles > 0.5 mm in diameter in the upper 100 m in the late afternoon, prior to vertical migration, with the size distribution and abundance of particles in the same parcel of water the following morning, after migrators had departed. *Euphausia pacifica* abundance in the upper 100 m at night and ancillary hydrographic and biological data were also collected. Thus, each station consisted of a pair of vertical profiles of aggregate size and abundance as well as supporting data on nocturnal zooplankton abundance and ancillary factors potentially impacting particle dynamics. *E. pacifica* was chosen for this study not only because it consumes marine snow (Dilling et al., 1998), but also because it is a large, omnivorous species very abundant in coastal waters off California that migrates from daytime depths of around 400 m into the upper 100 m during the night to feed (Brinton, 1967). *E. pacifica* often constitutes more than 50% of the night time, near-surface zooplankton biomass in coastal California waters (Brooks and Mullin, 1983). A depth range of 0–100 m was chosen so as to include all migrating *E. pacifica*. Although the highest density of adult *E. pacifica* are from 0–40 m at night, some members of the population can be distributed deeper (Brinton, 1962).

A 1 m by 1.5 m canvas drogue drifting at a depth of 10 m and attached to a small surface spar buoy was deployed in the late afternoon at the start of each station to mark the water parcel. All sampling occurred as close to this drogue as possible, generally within 50–400 m. Temperature/salinity diagrams for each pair of late afternoon and morning CTD casts at these stations matched very closely, indicating that the drogue accurately tracked water movement and that sampling occurred in the same parcel over the 12-h period investigated. Complete data sets for 9 stations in the Santa

Table 1

Contributions of various processes to the change in aggregate concentration and size observed overnight at 10 stations off Southern California. The gross change in aggregate concentration (Agg) (column 2) was the change observed in nature due to all production and loss processes. Net change in aggregate concentration (column 3) was the estimated change due to all processes except particle sinking. Net aggregate concentrations increased at all but one station, indicating that significant aggregate-generating processes counterbalanced sinking. The percent of available aggregates by number consumed by euphausiids was calculated as described in the text. The percent increase attributable to each production process was most accurately determined by dividing the calculated change for that process by the estimated total net change. ESD — Equivalent spherical diameter. Agg. = aggregate

| Date | Change in (Agg) | | Change in ESD mm | <i>E. pacifica</i> abundance No. m ⁻³ | % of aggs consumed per liter | % of net increase due to: | |
|-----------|---------------------------|-------------------------|------------------|--|------------------------------|---------------------------|------------------|
| | Gross No. 1 ⁻¹ | Net No. 1 ⁻¹ | | | | Euphausiid fecal pellets | Larvacean houses |
| 26-Jun-93 | -0.5 | 2.7 | 0.00 | 7.6 | 30 | 3 | 0.4 |
| 28-Jun-93 | 1.0 | 6.5 | -0.58 | 5.4 | 1 | 1 | 0.3 |
| 29-Jun-93 | -2.0 | 1.1 | -0.56 | 5.2 | 2 | 6 | 0.3 |
| 30-Jun-93 | 6.6 | 9.8 | -0.64 | 13.4 | 14 | 2 | 0.2 |
| 21-Sep-93 | 1.9 | 7.9 | -0.75 | 3.0 | < 1 | 1 | 0.3 |
| 22-Sep-93 | -2.4 | 7.7 | -0.63 | 3.6 | < 1 | 1 | 1 |
| 23-Sep-93 | -15. | 2.6 | 0.51 | 2.3 | < 1 | 1 | 4 |
| 24-Sep-93 | 0.5 | 6.0 | -0.63 | 4.5 | 1 | 1 | 1 |
| 25-Sep-98 | -27.2 | -6.4 | 0.34 | 1.3 | < 1 | 0 | 0 |
| 8-Sep-94 | -2.0 | 8.2 | -0.75 | 5.5 | 1 | 1 | 3 |
| Mean | -3.3 | 4.6 | -0.40 | 5.2 | 5 | 2 | 1.1 |

Barbara Channel (all stations located at 34°10' to 34°20'N and 119°40' to 120°30'W) and 1 station in the Santa Cruz Basin (33°51.1'N and 119°38.5'W) off southern California were acquired on 3 cruises in June and September, 1993 and September, 1994 (Table 1).

2.2. Measurement of particle abundance and size

Profiles of particle abundance and size from 0–100 m were obtained between 1700 and 1800 h Pacific Standard time, approximately 2 h prior to sunset and 0545–0630 h the following morning, about 1-h after sunrise. Particles were illuminated by a collimated beam of light 10.5 by 14.7 by 5 cm in size (0.78 l) and photographed on *T*-max 400 black and white film using a vertical-profiling in situ still camera and instrument package as described in MacIntyre et al. (1995). Photographs were taken at 10-s intervals, resulting in a sampling frequency of 2 to 3 frames per meter of vertical depth. Aggregate abundance and the equivalent spherical volume (ESV) of each particle were quantified from the still films using a Megavision 1024 *XM image* analysis system as described in MacIntyre et al. (1995). The resolution of the in situ camera (approximately 250 µm) was considerably finer than the size of marine snow, and particles smaller than 0.5 mm in equivalent spherical diameter were excluded from all analyses.

Oblique net tows from 100 m to the surface during the day at each station indicated that zooplankton in the marine snow size range constituted considerably less than 1% of the particles in each frame.

Frames were grouped into 2-m depth increments, and the average number, mean size, and total cumulative volume contained in aggregates in each depth bin was determined. The data were then integrated over the top 100 m to obtain average aggregate number and volume concentrations per liter in the top 100 m of the water column in each late afternoon and morning camera cast. Mean aggregate volume was determined by dividing total volume concentrations by number concentrations.

We estimated changes in the total carbon occurring in aggregates overnight, because this parameter was necessary to estimate the impact of euphausiid consumption on aggregates. Individual aggregate volume was converted to particulate organic carbon (POC) using a carbon to aggregate size relationship determined for natural hand-collected aggregates from the Santa Barbara Channel (Alldredge, 1998):

$$\text{POC} = 0.99 * V^{0.52}, \quad (1)$$

where POC is the particulate organic carbon content of an individual aggregate in μg and V is the aggregate volume in mm^3 .

2.3. Zooplankton sampling and enumeration

Zooplankton were collected with a 333mm-mesh meter net with a mouth opening of 0.79 m^2 in which was attached a General Oceanics Model 2030 flow meter. Net tows were performed at 2030 to 2200 h Pacific Daylight time, approximately 1–2 h after sunset. Nets were towed obliquely and sampled the upper 100 m at a forward velocity of 2 knots and an ascending and descending velocity of 10 m min^{-1} . Zooplankton were preserved in 70% ethanol and enumerated using a dissecting microscope and a Folsom plankton splitter.

2.4. Supporting hydrographic and biological data

Ancillary hydrographic and biological data including temperature, conductivity, and in vivo fluorescence were collected from 0–100m with a SeaBird SBE 19 CTD and a Seatech fluorometer attached to the camera package. Salinity and density were computed from these data with the equation of state of seawater (Fofonoff and Millard, 1983). Temperature/salinity diagrams were plotted and used to test whether the drogue had remained in the same parcel of water. Fluorescence, calibrated against readings on a Turner Fluorometer by standard fluorometric techniques (Strickland and Parsons, 1972), was integrated from 0 to 100 m to estimate total phytoplankton biomass and the availability of small particles for aggregation.

Wind velocity (m s^{-1}) was measured at each station with shipboard anemometers to estimate the intensity of the physical processes, especially shear, enhancing aggregation of small particles and disaggregation of large ones. Mean wind speed was used to estimate mean energy dissipation rate (ϵ) at 5 m depths at each station from Eq. (1) of MacKenzie and Leggett (1991). Shear, G , a major parameter in estimating particle

aggregation rates, was calculated from energy dissipation by the equation $G = (\epsilon/\nu)^{1/2}$, where ν is kinematic viscosity.

2.5. Laboratory studies

The interaction of *E. pacifica* with marine snow in the laboratory was video-recorded in order to elucidate the mechanisms by which these animals fragmented particles and to provide preliminary quantitative data with which to estimate their impact on marine snow in nature. Two approaches were used. First, aggregates produced on a rolling table (Shanks and Edmondson, 1989) from cultures of the chain-forming diatom *Chaetoceros affinis* were released and allowed to sink past adult *E. pacifica* (14–16 mm in length) tethered by monofilament line (as described in Paffenhofer et al., 1982) in both vertical and horizontal positions in a small seawater tank. Interactions were video-recorded simultaneously on a split screen by two video cameras set at 90° to each other. Interactive distances and particle velocities and trajectories were quantified from the videotapes with a Megavision 1024 XM image analysis system and frame grabber.

Second, free *E. pacifica* swimming in a field of the bioluminescent alga *Lingulodinium polyedrum* (previously *Gonyaulax polyedra*) were filmed in the dark with an image intensifying Dage-MTI VE-1000 Sit camera in order to verify that free-swimming animals produced a radius of influence around their bodies similar to that of tethered animals (e.g. this was a test of tethering artifacts). *L. polyedrum* luminesces at a threshold shear stress of 1 dyne cm⁻² (Latz et al., 1994). The shear stresses required to break natural marine snow reported in Alldredge et al. (1990) were converted to units comparable to those reported for *L. polyedrum* with equations in Latz et al. (1994).

2.6. Theoretical considerations

While this study focused primarily on the potential for one dominant migrating grazer, *E. pacifica*, to alter the abundance and size distributions of large particles, the impacts of other common, vertically migrating zooplankton were also considered. Moreover, other processes that act to increase or decrease aggregate abundance in the water column also required evaluation. The change in the volume or number concentration of aggregates > 0.5 mm in diameter over a specified time due to all such processes can be modeled as

$$\begin{aligned} \text{Change in aggregate concentration} &= \text{concentration gained} \\ &\quad - \text{concentration lost.} \end{aligned} \quad (2)$$

Several processes act to produce large particles. Aggregation is primarily a physical process dependent on the concentration of small, slowly sinking particles and their collision rate and stickiness (McCave, 1984; Jackson, 1995). Other processes generating marine snow depend primarily upon zooplankton. Animals create large fecal pellets, exuviae, and feeding structures such as larvacean houses and pteropod webs. Zooplankton may also fragment large aggregates into smaller, more numerous

particles still within the marine snow size range through their swimming or feeding activities (Alldredge and Silver, 1988). Thus,

$$\begin{aligned} \text{Concentration gained} = & \text{aggregation of } < 0.5 \text{ mm particles} \\ & + \text{new fecal pellets} + \text{new zooplankton feeding} \\ & \text{structures} + \text{disaggregation of larger particles.} \end{aligned} \quad (3)$$

Several physical and biological processes, in addition to animal consumption, also act to reduce marine snow concentrations. Aggregates have relatively rapid sinking rates, on the order of tens of meters per day, and may quickly sink out of surface waters (Alldredge and Gotschalk, 1988). Turbulence may cause some aggregates to disassociate into < 0.5 mm particles, and finally, bacteria can reduce aggregate concentrations through decomposition and solubilization (Karl et al., 1988). Thus,

$$\begin{aligned} \text{Concentration lost} = & \text{sinking} + \text{decomposition} \\ & + \text{solubilization} + \text{animal consumption} \\ & + \text{disaggregation to } < 0.5 \text{ mm particles.} \end{aligned} \quad (4)$$

Although detailed measurement of the effects of each of these processes on aggregate concentrations was far beyond the scope of this study, data relevant to these competing processes was collected and considered in evaluating the effects of macrozooplankton on aggregate abundance in nature.

3. Results

3.1. Field results

The nocturnal abundance of adult *Euphausia pacifica* ranged from 1.3 to 13.4 animals m^{-3} at the 10 stations investigated. Fig. 1 illustrates the type of data obtained for each pair of aggregate profiles. (The upper 2–5 m were not analyzed because interference from sunlight obscured some particles on the film.) The mean total volume and mean aggregate number concentration of particles > 0.5 mm in diameter at each depth were averaged for the upper 100 m of the water column for each profile in order to allow comparisons among profiles.

We expected aggregate abundance to decrease overnight as euphausiid abundance increased, because *E. pacifica* consumes marine snow, but exactly the opposite was observed. Instead, aggregate concentration increased significantly with increasing euphausiid abundance ($r^2 = 0.73$; $P < 0.001$), and gross increases, rather than the expected decreases, in aggregate abundance overnight were observed at 50% of the stations (Fig. 2A). This indicated that a significant, marine snow-generating process proportional to euphausiid abundance was occurring. Moreover, this production process was clearly discernible even against a backdrop of counterbalancing loss processes dominated by consumption and particle sinking. In order to estimate the

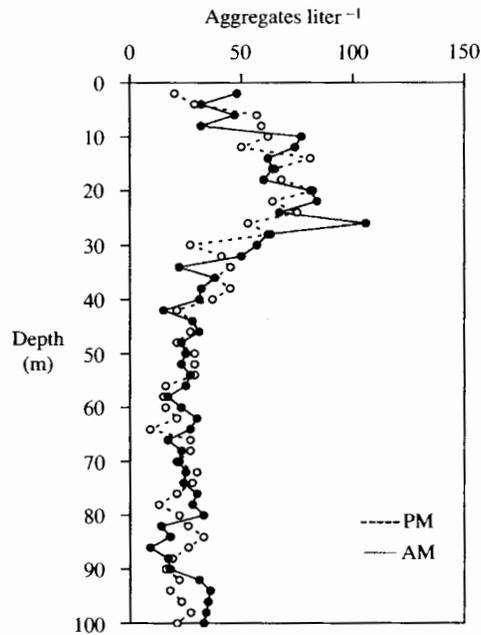


Fig. 1. An example of the pair of profiles generated for each station. Abundance of marine snow (aggregates > 0.5 mm in diameter) from the late afternoon on 28 June 1993 (open circles) and the early morning of 29 June (closed circles) are shown.

actual magnitude of this aggregate-generating process, we estimated the magnitude of the two major loss processes to attempt to correct for them.

3.1.1. Processes decreasing aggregate concentrations

Aggregate consumption: The greatest possible grazing impact of adult *E. pacifica* on aggregates was estimated from the maximum laboratory ingestion rate of $14 \mu\text{g C animal}^{-1}\text{h}^{-1}$ found for *E. pacifica* feeding on a variety of types of marine snow (Dilling et al., 1998). This ingestion rate was multiplied by the number of adult euphausiids per m^3 and an estimated feeding time of 6 h yielding the total carbon consumed by euphausiids as snow per night. The estimated potential maximum decrease in aggregate carbon overnight due to grazing by adult *E. pacifica* ranged from $0.1 \mu\text{g C l}^{-1}$ to $1.1 \mu\text{g C l}^{-1}$. Using Eq. (1) and the average volume of aggregates in the nighttime distributions, the maximum number of aggregates consumed per liter by *E. pacifica* alone was estimated. Because of the range of average aggregate volume ($0.2\text{--}0.85 \text{ mm}^3$) and the range of euphausiid abundance, estimates of the number of aggregates consumed per liter ranged from 0.03 to 2.4 aggregates l^{-1} . Only at two stations were these estimates more than 1 or 2% of the available aggregates (26 June, 30% and 30 June, 14%; Table 1). In addition, at those two stations we observed gross and net increases in aggregate abundance overnight, rather than decreases, further

suggesting that other processes counterbalanced aggregate consumption by *E. pacifica*. Euphausiid abundance was completely unrelated to integrated fluorescence at each station (data not shown), and none of the other dominant herbivorous zooplankton taxa, including copepods, euphausiid juvenile and larval stages, larvaceans, and total zooplankton, showed a trend with either initial aggregate concentration or change in aggregate concentration overnight (data not shown). Thus we discounted aggregate consumption as a major loss process at our stations.

Aggregate sinking: The major process likely to remove aggregates from the water column on times scales of hours is sinking. An equation describing empirically determined size-specific sinking relationships of marine snow from California surface waters (Alldredge and Gotschalk, 1988) was used to estimate the sinking rate of aggregates:

$$U = 51.085(V)^{0.0962} \quad (5)$$

where U is the aggregate sinking velocity in m day^{-1} and V is the equivalent spherical volume of an aggregate in mm^3 . Sinking speed is not highly sensitive to particle size; within a change of over 4 magnitudes of volume, sinking speed only doubles. We applied Eq. (5) to each individual aggregate in each late afternoon profile to determine which aggregates would sink out of the upper 100 m before morning. These particles were then removed from the late afternoon profile of each station and the sinking-corrected profiles compared to their morning counterparts to determine changes in aggregate abundance from processes other than sinking. Losses due to sinking do not account for any turbulence or mixing that may have been acting to retain particles above 100 m (although we estimate mixing to be low, see below), and, therefore, losses due to sinking can be considered maximum estimates.

When aggregates calculated to have been lost from the control volume overnight by sinking were removed from the analysis, a net gain in the abundance of marine snow overnight was estimated for 9 of the 10 stations, which was also significantly correlated with euphausiid abundance ($r^2 = 0.43$; $P < 0.05$; Fig. 2B). This suggested that the aggregate-generating process was of considerable magnitude. Changes in aggregate concentration overnight were not significantly correlated with any other factor examined, including abundance of other zooplankton taxa, initial phytoplankton biomass, wind speed, or stratification (data not shown).

3.1.2. Processes increasing aggregate concentration

Aggregate-generating processes correlated with euphausiid abundance could have arisen under two circumstances. First, *E. pacifica* might not have caused the aggregate increases but instead, co-varied with factors controlling processes that did, including particle aggregation or production of zooplankton feeding webs. Second, *E. pacifica* could have directly generated aggregates as fecal pellets or through fragmentation. We evaluated each of these four major processes generating marine snow-sized particles at our stations.

Aggregation: Aggregation, the process by which small particles collide and stick together, is primarily a physical process in the ocean. Particle aggregation rates are a function of the abundance and size distributions of particles available for

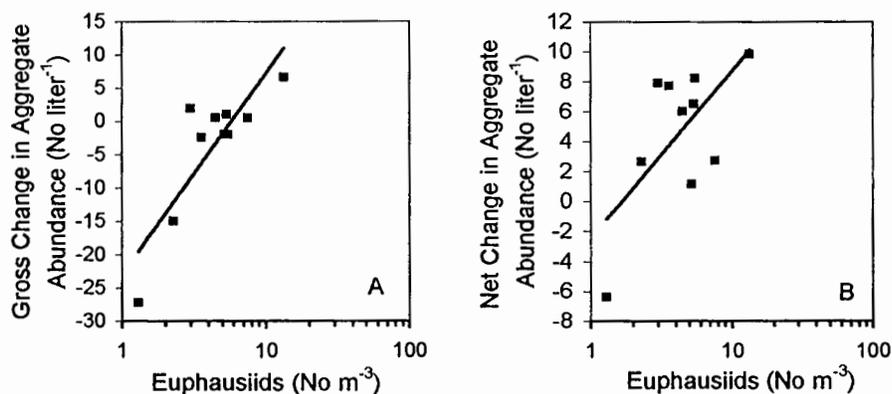


Fig. 2. Observed changes in the abundance of aggregates > 0.5 mm in diameter overnight versus the abundance of *Euphausia pacifica* at 10 stations off Southern California. (A) Actual gross changes observed from all production and loss processes. $r^2 = 0.73$, $P < 0.001$. (B) Changes in aggregate abundance after correction for losses overnight due to sinking. Losses due to sinking tend to mask the magnitude of aggregate-generating processes such as fragmentation. Thus net change more accurately reflects impacts of *E. pacifica*. $r^2 = 0.43$, $P < 0.05$.

aggregation (e.g. phytoplankton, fecal pellets, etc.), the intensity of the physical processes, especially shear, producing particle collisions, and the stickiness of the colliding particles (McCave, 1984).

Aggregation rates were potentially very low in this study for three reasons. First, fluid shear due to wind mixing was very low and was unrelated to changes in aggregate abundance overnight. Since, according to aggregation theory, aggregation rates in surface waters are linearly related to fluid shear generated largely by wind mixing (McCave, 1984), we might expect the production of new aggregates to be proportional to increasing wind speed. Average wind speeds overnight during this study were quite low, ranging from 1 to 6 m s⁻¹. Shear stress at 5 m estimated from wind speed was also very low and relatively constant, ranging from 0.011 to 0.021 s⁻¹ over the 10 stations. Moreover, shear rates dropped off exponentially below the water surface, reaching considerably lower values below 5 m. Neither wind speed nor shear stress at 5 m showed any relationships to observed changes in aggregate concentration (data not shown).

Second, phytoplankton abundance, estimated from in situ fluorescence, was unrelated to changes in aggregate abundance overnight. Phytoplankton were used as a proxy for the availability of small particles for aggregation, since phytoplankton are often the most abundant particles involved in marine snow formation (Jackson, 1990; Hill, 1992). Average phytoplankton abundance as estimated by in situ fluorescence was low (150–225 mg chlorophyll m² integrated over the upper 100 m). Moreover, changes in aggregate concentration overnight, corrected for sinking, showed no relationship with either initial integrated fluorescence or with changes in fluorescence overnight (data not shown). Were aggregation of these particles significant overnight, we would have expected some relationship with aggregate abundance.

While phytoplankton biomass is not a perfect proxy for estimating small particles available for aggregation, it is an estimate of the dominant type of particle active in aggregation processes in coastal waters. Thus, because shear was low and small particle abundances, as estimated by phytoplankton biomass, were not related to changes in aggregate concentration overnight, physical aggregation processes appear unlikely to explain the increases in aggregate concentration we observed. Finally, *E. pacifica* abundances did not co-vary with either phytoplankton biomass or wind speed, indicating that aggregation was unlikely to have generated the relationship between euphausiid and aggregate abundance shown in Fig. 2.

Larvacean house production: Larvaceans (primarily *Oikopleura dioica*), which produce marine snow-sized houses, were common at most stations. But, the abundances of larvaceans and *E. pacifica* did not co-vary. Moreover, at the abundances observed in this study, and assuming a maximum rate of house production for *O. dioica* at in situ temperatures of approximately 0.3 houses h^{-1} (Fenaux, 1985), larvaceans could have accounted for, at most, 4% of the increase in particle number (Table 1). Larvacean house production was an insignificant source of the net aggregate increases observed.

Fecal pellet production: Euphausiids produce fecal pellets that are large enough to be categorized as marine snow. Fecal pellet production might explain both the net increases in aggregate concentrations and their correlation with *E. pacifica* abundance. However, euphausiid fecal pellet production estimated from euphausiid abundance and maximum pellet production of 2 pellets animal h^{-1} under ideal feeding conditions for 6 h each night (Dilling et al., 1998) contributed a mean of only 2% to the estimated net increases in aggregate abundance. Even at the station with the highest euphausiid density, fecal pellet production would have resulted in a particle increase of only 0.16 particles l^{-1} . The observed increase in particle numbers after correction for sinking at that station was 9.8 particles l^{-1} , over 60 times higher. Moreover, fecal pellets were rare in the camera profiles. We conclude that fecal pellet production by *E. pacifica* was not a major process generating particles in this study.

Particle fragmentation: The final hypothesis we considered was that euphausiid swimming behavior fragmented large aggregates into smaller daughter particles, many still within the marine snow size range. Three pieces of field evidence support disruption of marine snow into multiple fragments by the swimming activities of *E. pacifica* as the only process consistent with our results. First, changes in both gross and net aggregate concentration were significantly positively correlated only with euphausiid abundance and no other factor (Fig. 2). Second, the mean size of marine snow that did not sink out of the control volume overnight decreased at 8 of the 10 stations by an average of 25% (Table 1). Thus, those stations with moderate to high euphausiid abundances experienced not only increases in aggregate abundance overnight, but the aggregates became smaller in average size as would be expected with fragmentation. (Only aggregates remaining in the control volume overnight were considered for size comparisons, because sinking favors the loss of larger particles and would automatically have skewed the results toward smaller aggregates.) Finally, changes in the size distribution of aggregates overnight supports fragmentation by *E. pacifica*. All stations with relatively fewer *E. pacifica* (< 3 animals m^{-3}) experienced

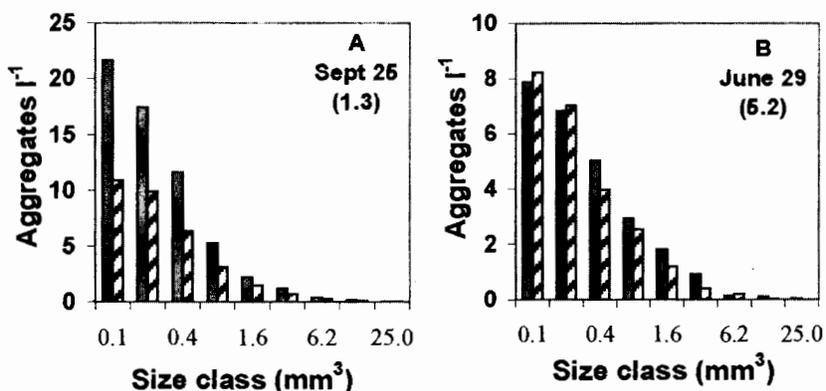


Fig. 3. Examples of typical changes in size class distributions of marine snow overnight. (A) When *Euphausia pacifica* was scarce all size classes experienced losses overnight. (B) When *E. pacifica* was abundant large size classes declined and small size classes increased. (Solid bars) late afternoon, (striped bars) the next morning. Euphausiid abundance per liter in parentheses.

a loss in aggregate abundance across all aggregate size classes (Fig. 3A). However, at 75% of the stations where euphausiids were relatively abundant (> 3 animals m^{-3}) the abundance of particles in the larger size classes decreased and that of the smaller size classes increased overnight (Fig. 3B), a result also consistent with fragmentation.

These three types of evidence strongly support the conclusion that *E. pacifica* was fragmenting marine snow in nature. Other zooplankton taxa, including copepods, euphausiid larval stages, and total zooplankton, were also examined to determine if these groups might also potentially contribute to fragmentation. However, changes in aggregate mean size and number concentration were not significantly correlated with the abundance of any other zooplankton taxon except *E. pacifica*.

3.2. Laboratory observations

Video-recordings of 10 tethered *E. pacifica* (14–16 mm in length) interacting with marine snow in the laboratory verified the effectiveness of these animals as aggregate fragmentors and demonstrated the major mechanism by which fragmentation occurs. The beating pleopods generated a substantial flow field underneath and parallel to the animal's abdomen and tail. Any aggregate passing within 4.0 to 4.2 body widths of the animal's abdomen (approximately 7.6–8.1 mm away from the 2 mm diameter animals investigated) was entrained by the flow and drawn rapidly toward the animal's ventral surface. There the aggregates were struck by the pleopods, shredded into multiple pieces, many still within the marine snow size range (> 0.5 mm), and ejected in a stream under the animal's tail at velocities of 2.7 – 7.4 $cm\ s^{-1}$ for distances up to 3 cm (Fig. 4). Aggregates passing near the edge of this flow field (8–10 mm from the abdomen) were sheared and disrupted by the flow without striking the pleopods.

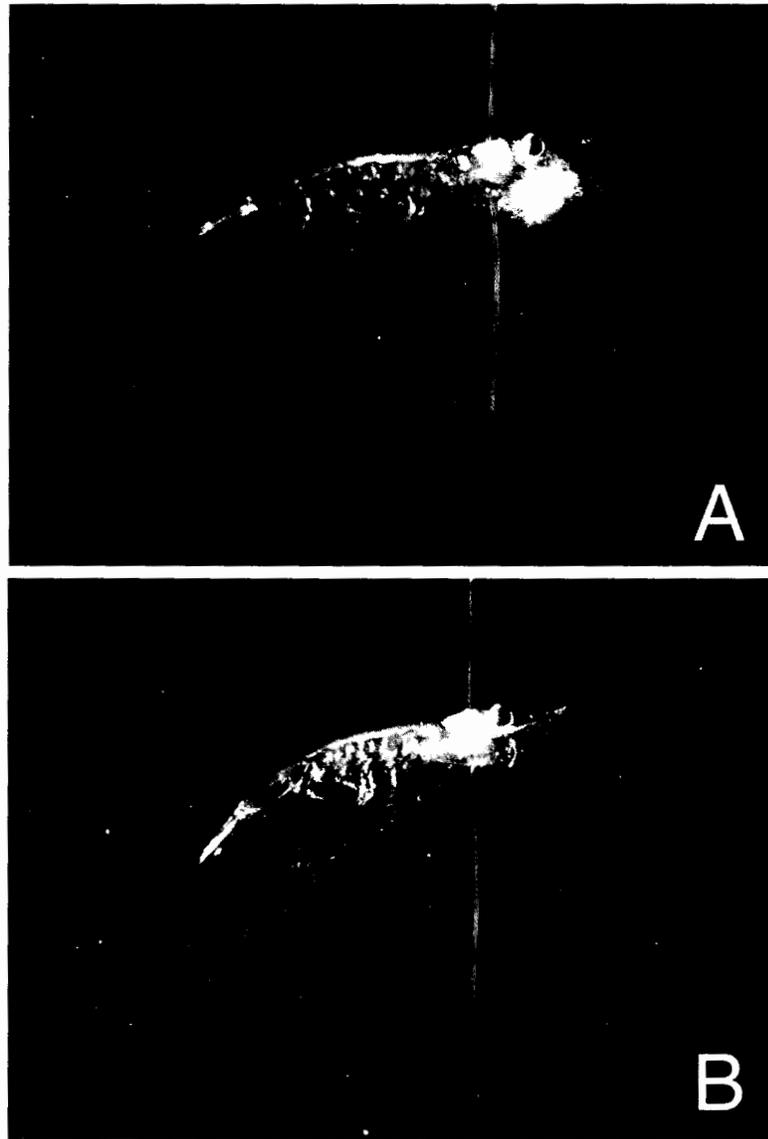


Fig. 4. Disruption of a fragile diatom aggregate by a tethered *Euphausia pacifica* adult (16 mm in length). (A) A 4-mm aggregate sinking past the side of the animal's head. (B) The aggregate has been entrained, struck by the beating pleopods, and ejected as a stream of fragments. Most marine snow is stronger than diatom snow and would break into a few, larger pieces. Aggregate strength is a function of aggregate size (Alldredge et al., 1990; Hill, 1998), and very small aggregates (1–2 mm diameter) required direct contact with a pleopod to fragment while larger aggregates were also fragmented by fluid shear in eddies generated by swimming.

Free-swimming *E. pacifica* were also video-recorded with an image-intensifying camera in the dark in seawater containing bioluminescent dinoflagellates, in order to reveal any artifacts due to tethering. Free-swimming euphausiids produced luminescent trails 7.0 ± 0.4 mm in diameter, similar in size to those observed for tethered animals. *L. polyedrum* luminesces at a threshold shear stress of 1 dyne cm^{-2} (Latz et al., 1994), 5 times higher than that required to disrupt many types of marine snow (Alldredge et al., 1990). Thus the slightly larger impact diameters obtained from tethered animals probably more accurately reflect fragmentation distances in nature.

4. Discussion

Our field study indicates that euphausiids can significantly alter aggregate size distributions and abundances in nature over a single night through their swimming activities alone. Three pieces of evidence support the conclusion that zooplankton were fragmenting marine snow in nature. First, increases in aggregate abundance overnight were significantly positively correlated only with euphausiid abundance, and with no other biological or physical factor; second, mean aggregate size decreased overnight; and third, aggregate size distributions shifted toward smaller aggregate size classes when euphausiids were abundant. Other abundant zooplankton present were apparently not significantly involved in this process since their abundances did not correlate with changes in aggregate concentration. This suggests that only macrozooplankton were large enough or fast enough to physically disrupt marine snow.

The laboratory observations indicate that *Euphausia pacifica* can disrupt marine snow aggregates through small-scale fluid shear generated by their swimming activities alone. The action of the pleopods and the flow field produced by them appears to be the main source of shear around the animals. However, during feeding by compression filtration euphausiids rapidly expand their thoracic limbs, arranging them in a formation known as the feeding basket, which induces particle flow toward the maxillae. The thoracic limbs are then rapidly compressed and water is expelled through the setae, while food particles are retained (Hamner, 1988). Compression filtration may generate turbulence around the entire perimeter of the feeding basket, resulting in the disruption of nearby aggregates through the process of feeding as well as by swimming. *E. pacifica* readily consumes marine snow and disrupts aggregates while feeding on them in laboratory vessels (Dilling et al., 1998). However, they ingest most of the fragments generated, suggesting that superfluous feeding may be a relatively minor source of aggregate fragmentation in nature.

4.1. Consistency of field and laboratory results

The laboratory results provide preliminary quantitative estimates of the radius of impact surrounding swimming euphausiids within which marine snow would encounter sufficient shear to be fragmented. Are the field results consistent with these laboratory observations? Did the euphausiids encounter an adequate number of aggregates

Table 2

Comparison between the percentage of the water column disturbed by euphausiid swimming (column 7) and the percentage required to be disturbed in order to generate the changes in net aggregate abundance actually observed overnight (column 6) at 10 stations off Southern California. Net changes (column 3) were estimated changes due to all processes except particle sinking. The number of fragmented aggregates required to generate the net increases in aggregate abundance estimated at each station (column 5) was calculated assuming aggregates fragmented into 3 pieces. (Agg.) — aggregate number concentration, euph. — euphausiids, na — not applicable due to net loss of aggregates

| Date | Mean initial [Agg.] No. l ⁻¹ | Net change in [Agg.] No. l ⁻¹ | <i>E. pacifica</i> abundance No. m ⁻³ | Number of aggs. disrupted No. l ⁻¹ | % of water column disturbed by euph | |
|-----------|---|--|--|---|--|-----------|
| | | | | | Required | Estimated |
| 26-Jun-93 | 7.3 | 2.7 | 7.6 | 0.9 | 23 | 19 |
| 28-Jun-93 | 33.0 | 6.5 | 5.4 | 2.2 | 9 | 13 |
| 29-Jun-93 | 25.6 | 1.1 | 5.2 | 0.4 | 2 | 13 |
| 30-Jun-93 | 16.6 | 9.8 | 13.4 | 3.3 | 29 | 33 |
| 21-Sep-93 | 25.4 | 7.9 | 3.0 | 2.6 | 16 | 8 |
| 22-Sep-93 | 32.8 | 7.7 | 3.6 | 2.6 | 12 | 9 |
| 23-Sep-93 | 50.6 | 2.6 | 2.3 | 0.9 | 3 | 6 |
| 24-Sep-93 | 25.5 | 6.0 | 4.5 | 2.0 | 13 | 11 |
| 25-Sep-98 | 60.0 | -6.4 | 1.3 | na | na | 3 |
| 8-Sep-94 | 28.5 | 8.2 | 5.5 | 2.7 | 13 | 14 |
| Mean | 30.8 | 4.6 | 5.2 | 1.9 | 13 | 13 |

within their impact radius while swimming in the field to account for the increases in aggregate abundances actually observed overnight at our field stations?

In order to evaluate this, we estimated contact rates between euphausiids and aggregates at our stations by assuming that an average adult *E. pacifica* swam at a conservative average cruising speed of 1.1 cm s⁻¹ (Torres and Childress, 1983) for 8 h each night. The effective impact diameter for each animal, estimated from the tethering study, was 10 mm (8mm impact distance + 2 mm abdomen diameter). Thus, each animal generated a long tunnel of disturbed water as it swam throughout the night. We also assumed that aggregates were evenly dispersed throughout the water column. Under these assumptions the percentage of the water column sufficiently disturbed by the euphausiids to disrupt aggregates contained within it ranged from a low of 3% at the lowest euphausiid abundance observed in this study to almost 33% at the highest abundance (Table 2), averaging 13%.

Clearly, when *E. pacifica* is abundant, a high degree of random contact with suspended marine snow can occur. Is this rate of contact adequate to explain the particle increases we observed in the field? Alldredge et al. (1990) found that disaggregation of natural marine snow by shear in the laboratory produced 2 fragments in 70% of cases, 3 fragments in 14% of cases, and greater than 10 fragments in 11.5% of the cases, thus averaging about 3 fragments per aggregate. If we assume each aggregate encountered broke into 3 fragments and that only encounters with aggregates larger than 0.13 mm³ are relevant (the smallest marine snow size class, 0.65–0.13 mm³,

breaks into daughter particles smaller than the minimum cut-off size of marine snow, and thus, the results of fragmentation would not be seen), then we can calculate the numbers of aggregates per liter that would be required to be disrupted to generate the observed net particle increase at each of our stations on the basis of disaggregation alone. This calculation is reported in Table 2 and ranged from 0.9 to 3.3 aggregates per liter.

The percentage of the water column required to be disturbed in order to produce 0.9–3.3 aggregates per liter ranged from 2 to 29% and averaged 13%. This was nearly identical to the 3 to 33% of the water column estimated to be actually disturbed by the euphausiids (Table 2). The estimated percent contact by euphausiids was lower than that required to produce the observed increases in aggregate abundance at only 3 of the stations, and then only slightly so. Aggregate-generating processes such as fecal pellet and larvacean house production might also augment particle abundances slightly, thus reducing the required contact rates somewhat. Clearly, euphausiid contact rates with aggregates were sufficient to explain the observed changes in aggregate abundances at our stations. The laboratory and field results were surprisingly consistent.

4.2. Implications of fragmentation

While models of oceanic particle dynamics have predicted that disaggregation is an important process affecting particle abundances, size distributions, and diel patterns (Jackson, 1995; Ruiz, 1997), none have considered the role of swimming animals in particle disaggregation. The field evidence indicates that particle disaggregation by swimming macrozooplankton is significant and detectable even over a single night. Cumulative effects over successive nights would be even greater, suggesting that fragmentation may be a dominant process in oceanic particle dynamics. Moreover, *E. pacifica* is only one zooplankton species, although clearly an important one in the eastern Pacific. All large, rapidly swimming zooplankton, including other macrocrustacean species, fish larvae, salps, pteropods, medusae, and ctenophores probably fragment marine snow and impact particle size distributions in the ocean. These larger zooplankton, as well as micronekton taxa, can attain the swimming speeds and generate the shear stresses necessary to fragment marine snow.

The fragmentation of marine snow by rapidly swimming macrozooplankton and micronekton has several major implications for ocean biogeochemistry and ecology. First, fragmentation will reduce the overall flux of particulate carbon to the deep sea, assuming, as predicted by Stokes Law, that fragments sink more slowly than their parent particles and would remain longer in the water column. Since fragmentation via swimming does not involve consumption or transformation of carbon, it may be a particularly unique process in balancing ocean carbon budgets. Particle flux would be reduced while simultaneously conserving carbon. Fragmentation is likely to have the biggest impact in shelf, slope, and polar seas, where macrozooplankton, especially macrocrustaceans, are most abundant.

Second, zooplankton disaggregation represents a new mechanism to help explain the exponential decrease in particle flux with depth. The abundance of zooplankton and micronekton decreases exponentially with depth throughout the ocean (Angel,

1984) and reductions in mass flux, attributed to zooplankton consumption, have been correlated with declines in zooplankton abundance below the surface layer (Bishop et al., 1986). Fragmentation is an additional process that could reduce flux in proportion to animal abundance.

Third, fragmentation by macrozooplankton is likely to generate diel patterns in aggregate abundance, size, and particle flux, such as those reported in midwater by Lampitt et al. (1993) and in California surface waters by Graham et al. (2000). Marine snow is most abundant in the surface ocean (Alldredge and Silver, 1988; MacIntyre et al., 1995), and fragmentation will be greatest at night when zooplankton migrate vertically into the surface layer, generating pulses of smaller, more slowly sinking particles on a diel cycle. Diel pulses of sinking particles may have important implications for the feeding behavior and ecology of oceanic animals dependent on these particles and may generate pulsed arrivals of sinking particulate food to the benthos.

Fourth, while fragmentation conserves carbon, it may indirectly increase the rate of particulate carbon utilization and overall microbial activity in the water column by increasing the surface area of particles available for microbial colonization, decomposition, and solubilization. Finally, the fragmentation of marine snow changes its suitability for various types of particle grazers. Large aggregates are fed upon primarily by grazers capable of consuming whole particles or by small grazers, such as the copepod *Oncaea* spp., which sit on particles and scrape material from them (Alldredge, 1972). Snow fragments, on the other hand, may be more available to medium-sized suspension feeding herbivores including copepods. The longer residence time of fragments in the water column will also increase their availability for consumption.

Fragmentation of large sinking particles by macrozooplankton swimming behavior clearly has the potential to impact food web structure, carbon cycling, and particle dynamics in the ocean. This newly discovered process provides a previously unconsidered link between animal behavior and biogeochemical cycling in the sea. Since all large macrozooplankton and micronekton potentially fragment marine snow, this process may be of considerable magnitude throughout the ocean. Additional research will be needed to clearly evaluate its significance relative to other processes affecting particle dynamics and sedimentation in the sea.

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