Can chaetognath fecal pellets contribute significantly to carbon flux?

Lisa Dilling, Alice L. Aldredge

Department of Biological Sciences and Marine Science Institute, University of California, Santa Barbara, California 93106, USA

ABSTRACT: The high abundance of chaetognaths and the relatively large size of their fecal pellets suggest that these planktonic predators might make a substantial contribution to the vertical carbon flux in some regions. Although fecal pellets of the epipelagic species Parachaetogaster euxenitica and the mesopelagic species Solidogaster reticulata and Peniodesmita maximus had high sinking speeds, 27 to 113 m d⁻¹, they sank 5 to 10 times more slowly than comparably sized herbivore fecal pellets. Chaetognath fecal pellets had densities around 1.015 g cm⁻³. Estimates using published pellet production rates and animal abundances, and measured pellet carbon content show that chaetognaths fecal pellets could contribute modestly (4 to 6 %) to carbon flux in the euphotic zone and substantially (8 to 60 %) at depth.

INTRODUCTION

The abundance and sinking velocities of large particles, such as fecal pellets and marine snow (detrital aggregates larger than 500 μm in diameter), determine the magnitude of carbon flux which reaches the bottom (Powler & Knauer 1986). Due to their high sinking speeds, large particles are not consumed or remineralized in the water column as readily as small, suspended particles. Fecal pellets in particular have been hypothesized to play an important role in carbon flux to the bottom, since they are one of the few types of particles with sufficient mass and sinking speeds to be removed rapidly from surface waters.

Several predominantly herbivorous zooplankton, including salps, euphausiids, large copepods, and pteropods, produce large, rapidly sinking fecal pellets (Wilbe et al. 1979, Bruisland & Silver 1981, Anderson & Nival 1988). Predatory zooplankton also produce relatively large fecal pellets. The most abundant planktonic predators in many areas of the ocean are chaetognaths, which produce large compact fecal pellets enclosed in a membrane (Reeve et al. 1975). Densities of 500 ind. m⁻³ have been reported in the California (USA) coast (Mullin 1979), while more typical oceanic densities range from 20 to 50 ind. m⁻³ (Stur & Mullin 1981). While therole of fecal pellets produced by predatory zooplankton in carbon cycling in the ocean has been largely unexplored, the abundant and ubiquitous distribution of chaetognaths and the characteristics of their fecal matter suggest that they may, in particular, be important sources of sinking particles.

In this study we investigated the hypothesis that chaetognath fecal pellets could contribute significantly to carbon flux. We determined fecal pellet carbon content and sinking speeds, and combined this information with published values on feeding rates and abundance to estimate pellet fluxes to different zones in the water column.

METHODS

Epipelagic chaetognaths of the common species Parachaetogaster euxenitica Alvarado were obtained throughout 1991 and 1992 using a 0.75 m diameter plankton net with 500 μm mesh. Specimens were collected in April of both years off Point Conception, California and in August, October, November, December 1991 and February 1992 in the Santa Barbara Channel, California. While the larger mesh size probably did not retain some smaller chaetognaths, it also...
did not retain most prey items so that within-net feeding was minimized. Specimens with prey items in their guts were removed from the transparent cod ends using a large-bore pipette, placed into beakers containing 5 μm filtered seawater, and allowed to defecate at 5 °C overnight. Supplementary data on chaetognath abundances were gathered in the Santa Barbara Channel using a 1 m diameter net with 333 μm mesh equipped with a Censel Oceanics Inc. Flowmeter (model 2030) suspended in the mouth opening.

Mesopelagic chaetognaths of the species Pseudosagitta maxima Conant and Solidsagitta zetesios Fowler were collected in deep water off the central coast of California in July 1991 and June 1992. A 10 m² Tucker trawl with 30 μm thermally protective cod end (Childress et al. 1978) was towed at a speed of less than 1 knot to minimize damage to the specimens. Chaetognaths were selected by hand, placed into beakers of filter-sterilized seawater and allowed to defecate at 5 °C for at least 30 h.

Fecal pellets were collected at the end of the incubation from the beakers by pipette. The amount of degradation which might have taken place after the relatively short period at that temperature was assumed to be negligible (Honjo & Roman 1978). Pellet sinking rates were determined in a 2 l graduated cylinder filled with filtered seawater at room temperature (20 °C) to minimize convection currents. As each pellet sank, 4 or 5 consecutive measurements of the time required for the pellet to sink a distance of 1.6 cm through the cylinder were determined with a stopwatch. Sinking speed was measured on a total of 11 pellets from Parasagitta eueneatica and 20 pellets from the 2 midwater species.

Additional pellets were rinsed in distilled water, placed onto pre-weighted nucleopore filters, dried at 75 °C for 24 h and reweighed on a Cahn Electrobalance (Model 4600) to obtain dry weights. Pellets were also rinsed and collected onto pre-weighted, ashed foil boats or C/F filters, dried in a drying oven, and stored in a desiccator for CHN content determination with a Lesman Labs Inc. CE CHN Analyzer (Model 440). (See Table 1 for numbers of pellets analyzed.) Chaetognaths and fecal pellets were sized using calipers and a dissecting microscope with a micrometer.

To corroborate measured sinking rates, densities of individual pellets were measured independently at a controlled temperature of 15 °C by suspending them in seawater layers in a series of Percoll solutions of different density (Pennington & Strathmann 1990). Crystalline NaCl was added to pure Percoll, to match the osmolality of seawater at 33 psu and then diluted with filtered seawater to produce solutions of 5 densities. A total of 28 pellets were gently dropped into the top seawater layer in 28 individual test tubes. These test tubes contained seawater layered over 8 solutions at 1.025 g cm⁻³, 1.03 g cm⁻³, 1.035 g cm⁻³, 1.04 g cm⁻³, and 1.1 g cm⁻³. If they sank through both layers, their density was recorded as greater than the solution in the test tube, and if they were suspended at the interface of the Percoll and seawater, it was recorded as less than that of the solution. In this way, a density range for fecal pellets from eupelagic chaetognaths was determined. While this method does not give precise density information, it does allow comparison with estimates based on sinking rates, and gives an adequate range to distinguish gross density differences between chaetognath pellets and herbivorous zooplankton pellicels. The density of mesopelagic chaetognath pellets was not measured.

Pellet production rate was estimated using published daily prey rations. Daily prey rations can be estimated from gut transit time and percent of specimens containing prey at a given time. Since gut transit time was not measured in this study, daily prey ration could not be directly derived. Instead, the percent of individuals containing prey in this study was compared with results of published studies to derive if literature values for daily prey ration could be used, assuming digestion time was similar. In this study, the percent of all species containing food in their guts was determined by examining live chaetognaths by eye captured during a 24 h period.

RESULTS

Pellets of Parasagitta eueneatica, the common neritic species off the central coast of California, were characterized by a long and slender shape, tapering at one end to a thin, tail-like structure (Fig. 1a). Much of the pellet was highly translucent with regions of opaque or pigmented material. Cepodopod body parts, when present, were visible through the membrane. In addition, all pellets were extremely sticky and had to be handled in water.

Pellets from the midwater species, Pseudosagitta maxima and Solidsagitta zetesios, varied in appearance, with some resembling those of Parasagitta eueneatica, and others more square in shape (Fig. 1b). Many of the pellets had an orange coloration, presumably a reflection of their midwater prey, which often have orange pigments. S. zetesios feeds mainly on cepods and other chaetognaths, with euphausiids and ostracods being minor components of the diet (Terao & Marumo 1982). Sizes, dry weights, carbon contents, and C:N ratios of chaetognath pellets are detailed in Table 1. Pellets from the 2 midwater species were much larger than
Fig. 1. Chaetognath (fecal) pellets. (a) Pellet of Parasagitta wenceslea. Scale bar = 1 mm. (b) Pellet of mudwater species, Solenocrypta zetesana. Scale bar = 1 mm. Note that the tapered, tail-like structure on this pellet has been folded and is stuck to the main body of the pellet.
those of *Parasaggita* eunectes, reflecting the larger body size of the midwater species. Midwater pellets had 50 times more carbon and a higher C:N ratio than *P. eunectes* pellets.

The sinking rates of fecal pellets from epipelagic chaetognaths ranged from 27 to 196 m d⁻¹, with a mean of 58 ± 49 (SD) (Fig. 2). The sinking rates of fecal pellets from midwater species ranged from 83 to 1313 m d⁻¹ with a mean of 382 ± 306. Both groups had sinking rates which varied by an order of magnitude. Sinking rates increased significantly with pellet size, ($r^2 = 0.62, p < 0.01$) (Fig. 2). Approximately 15% of the fecal pellets of midwater species and 5% of the pellets of epipelagic species did not sink at all, remaining neutrally buoyant or floating to the surface of the container. These pellets were not included in the sinking rate or density measurements.

The measured density of *Parasaggita eunectes* fecal pellets was 1.033 g cm⁻³ (Table 2). This is close to the mean density of 1.04 ± 0.02 g cm⁻³ (SD) calculated with the formula of Komar et al. (1981) using sinking rates and volumes of 11 epipelagic pellets.

The proportion of animals that contained prey, i.e., the food-containing ratio (FCR), was consistent with values reported for other epipelagic species (Fig. 3). Epipelagic chaetognaths do not generally contain more than one prey item at a time and gut transit time ranges from 1 to 3 h (Spyker 1978, Feigenbaum 1979, Nagasewa 1985). Chaetognaths also tend to process their prey discontinuously rather than on a constant basis (Reeve et al. 1975). It was assumed, therefore, that the number of pellets produced per day is equal to the number of pellets tested per day in each solution.

### Table 1. Pellet characteristics of epipelagic (*Parasaggita eunectes*) and midwater (*Pseudosaggita maxima* and *Solidosaggita zoeana*) chaetognaths

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Mean (± SD)</th>
<th>No. of samples</th>
<th>No. of pellets sample⁻¹</th>
<th>Total no. of pellets sampled</th>
</tr>
</thead>
<tbody>
<tr>
<td>Epipelagic species</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Length of pellet (mm)</td>
<td>1.3 ± 0.3</td>
<td>62</td>
<td>1</td>
<td>62</td>
</tr>
<tr>
<td>Width of pellet (mm)</td>
<td>0.3 ± 0.1</td>
<td>62</td>
<td>1</td>
<td>62</td>
</tr>
<tr>
<td>Dry wet pellet⁻¹ (µg)</td>
<td>7.9 ± 1.5</td>
<td>5</td>
<td>5–8</td>
<td>35</td>
</tr>
<tr>
<td>C content (µg pellet⁻¹)</td>
<td>0.9 ± 0.3</td>
<td>6</td>
<td>8–20</td>
<td>82</td>
</tr>
<tr>
<td>N content (µg pellet⁻¹)</td>
<td>0.2 ± 0.1</td>
<td>5</td>
<td>8–20</td>
<td>66</td>
</tr>
<tr>
<td>C:N ratio (by weight)</td>
<td>7.2 ± 1.1*</td>
<td>5</td>
<td>8–20</td>
<td>66</td>
</tr>
</tbody>
</table>

**Midwater species**

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Mean (± SD)</th>
<th>No. of samples</th>
<th>No. of pellets sample⁻¹</th>
<th>Total no. of pellets sampled</th>
</tr>
</thead>
<tbody>
<tr>
<td>Length of pellet (mm)</td>
<td>3.9 ± 0.4</td>
<td>20</td>
<td>1</td>
<td>20</td>
</tr>
<tr>
<td>Width of pellet (mm)</td>
<td>1.5 ± 0.6</td>
<td>20</td>
<td>1</td>
<td>20</td>
</tr>
<tr>
<td>Dry wet pellet⁻¹ (µg)</td>
<td>102.7 ± 66</td>
<td>2</td>
<td>11–13</td>
<td>24</td>
</tr>
<tr>
<td>C content (µg pellet⁻¹)</td>
<td>45.8 ± 16.8</td>
<td>6</td>
<td>4–13</td>
<td>53</td>
</tr>
<tr>
<td>N content (µg pellet⁻¹)</td>
<td>5.8 ± 3.4</td>
<td>6</td>
<td>4–13</td>
<td>53</td>
</tr>
<tr>
<td>C:N ratio (by weight)</td>
<td>9.1 ± 3.8*</td>
<td>6</td>
<td>4–13</td>
<td>53</td>
</tr>
</tbody>
</table>

* C:N of individual samples was averaged to obtain mean C:N, therefore mean C and N contents of pellets will not average to the same ratio.

### Table 2. Primary density of *Parasaggita eunectes* fecal pellets as measured by a series of Percoll solutions of different density

<table>
<thead>
<tr>
<th>Density of solution (g cm⁻³)</th>
<th>No. of pellets with density:</th>
<th>Total no. of pellets tested in each solution</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Less than solution</td>
<td>More than solution</td>
</tr>
<tr>
<td>1.025</td>
<td>0</td>
<td>8(100 %)</td>
</tr>
<tr>
<td>1.03</td>
<td>0</td>
<td>4(100 %)</td>
</tr>
<tr>
<td>1.035</td>
<td>3 (60 %)</td>
<td>2 (40 %)</td>
</tr>
<tr>
<td>1.04</td>
<td>7 (8 %)</td>
<td>1 (12 %)</td>
</tr>
<tr>
<td>1.1</td>
<td>3 (100 %)</td>
<td>0</td>
</tr>
</tbody>
</table>

Fig. 2. Sinking rates of epipelagic species *Parasaggita eunectes* and midwater species *Pseudosaggita maxima* and *Solidosaggita zoeana* increase as a function of pellet size ($r^2 = 0.62, p < 0.01$).
lower temperatures under lower food concentrations, they may have a slower digestion time. In order to estimate the contribution of midwater chaetognath fecal pellets to flux from the mesopelagic zone, a conservative daily ration of 1.2 × 10^{-4} (and thus 1 pellet d^{-1}) was used.

**DISCUSSION**

Chaetognath fecal pellets sink rapidly enough (27 to 13.1 m d^{-1}) to be important components of carbon flux. These pellets sink more slowly than similarly-sized herbivore pellets, however. Using the data compiled by Bruland & Silver (1981) we calculate that comparably-sized herbivore pellets sink roughly 10 times faster than epipelagic chaetognath pellets and 5 times faster than midwater chaetognath pellets (Fig. 5). Volume was calculated as an ellipsoid, which is the closest geometric shape to approximate chaetognath pellets.

One reason chaetognath pellets might sink more slowly for a given size is that their density or specific gravity is lower. Particle density is a major variable determining a particle's sinking rate (Komar et al. 1981). For comparison, euphausiid falcal pellet densities are around 1.5 g cm^{-3} (Komar et al. 1981), considerably higher than chaetognath pellet densities reported here (1.035 g cm^{-3}).

Density difference may result from differences in content and packaging; pellets containing exoskeletal copepod remains may be packed less tightly than pellets containing the remains of phytoplankton cells. The shape of the pellet may be constrained by the undi-
Table 3. Potential percent contribution of chaetognath fecal pellets to carbon flux out of the euphotic zone in 2 production regimes

<table>
<thead>
<tr>
<th>Upwelling region (Coastal California)</th>
<th>Oligotrophic region (North Pacific Central Gyre)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Carbon (µg pellet^-1)</td>
<td>0.9</td>
</tr>
<tr>
<td>No. of pellets m^-2 h^-1</td>
<td>2^2</td>
</tr>
<tr>
<td>Total pellet C (µg ind.^-1)</td>
<td>1.8</td>
</tr>
<tr>
<td>No. of ind. m^-2 h^-1</td>
<td>32^2-116^2</td>
</tr>
<tr>
<td>upper euphotic zone 0-35 or 50 m</td>
<td>3.8-3.5</td>
</tr>
<tr>
<td>lower euphotic zone 50-100 m</td>
<td>2.8-10.8</td>
</tr>
<tr>
<td>Fecal carbon production rate (mg C m^-2 d^-1)</td>
<td>5.9</td>
</tr>
<tr>
<td>Total daily particulate flux at 100 m mg C m^-2 d^-1</td>
<td>1.1-4.2</td>
</tr>
<tr>
<td>% pellet of total flux</td>
<td>5.9</td>
</tr>
</tbody>
</table>

* Fecal pellets were assumed to be identical in this region for purposes of this estimate. See text for further assumptions.
As described in "Results"

Fecal carbon production rate (mg C m^-2 d^-1) =

\[ \text{mg C pellet}^{-1} \times \text{no. of pellets ind}^{-1} \times \text{d}^{-1} \times \text{no. of ind. m}^{-2} \times \text{height of zone (m)}^{(1)} \]

A carbon content of 0.9 µg C pellet^-1 and 2 pellets produced d^-1 were used in Eq. 1 (above) for the euphotic zone. The euphotic zone depth was assumed to be 100 m. For the midwater calculations, 45.8 µg C pellet^-1 and 1 pellet d^-1 were used. The midwater zone was assumed to start at 500 m and be 400 m deep. This zone depth was arbitrarily chosen to approximate the depth that the pellets might sink in 1 d. Chaetognath abundances ranged greatly depending on season, geographic location, and production regime. A range of published values was used in Eq. 1 to determine maximum and minimum contributions to flux. A range of published values was used in Eq. 1 to determine maximum and minimum contributions to flux. A range of published values was used in Eq. 1 to determine maximum and minimum contributions to flux. A range of published values was used in Eq. 1 to determine maximum and minimum contributions to flux. A range of published values was used in Eq. 1 to determine maximum and minimum contributions to flux.

*1 A carbon content of 0.9 µg C pellet^-1 and 2 pellets produced d^-1 were used in Eq. 1 (above) for the euphotic zone. The euphotic zone depth was assumed to be 100 m. For the midwater calculations, 45.8 µg C pellet^-1 and 1 pellet d^-1 were used. The midwater zone was assumed to start at 500 m and be 400 m deep. This zone depth was arbitrarily chosen to approximate the depth that the pellets might sink in 1 d. Chaetognath abundances ranged greatly depending on season, geographic location, and production regime. A range of published values was used in Eq. 1 to determine maximum and minimum contributions to flux. A range of published values was used in Eq. 1 to determine maximum and minimum contributions to flux. A range of published values was used in Eq. 1 to determine maximum and minimum contributions to flux. A range of published values was used in Eq. 1 to determine maximum and minimum contributions to flux. A range of published values was used in Eq. 1 to determine maximum and minimum contributions to flux.
The potential contribution of chaetognath fecal pellets to flux from the midwater zone, although more variable, can be relatively large when compared with the contribution of pellets produced in the euphotic zone (Table 4). In an upwelling region, the chaetognath fecal carbon production rate could be 0.2 to 2.2 mg C m\(^{-2}\) d\(^{-1}\), or 0.5 to 5.9 % of the total flux at 900 m, and 0.2 to 2.6 mg C m\(^{-2}\) d\(^{-1}\), or 4 to 37.7 % of the total flux at 900 m in an oligotrophic region. The wide range in these calculations results from high variations in chaetognath abundance in the mesopelagic zone. The calculations would benefit from a more refined measurement of chaetognath abundance in the mesopelagic zone as well as from a study of diet in these larger organisms to better determine a daily prey ration and hence pellet production rate.

Using the particulate organic carbon (POC) pigment ratio in total suspended particles versus phytoplankton alone, Small (1969) inferred that omnivorous and carnivorous zooplankton in the Southern California upwelling must contribute to fecal pellet production. While the calculations of the present study are merely estimates, they indicate that predator pellets may indeed play a significant role in the carbon budget. Sediment trap studies have not identified chaetognath fecal pellets as a flux component, but since they resemble copepod coprophages or other zooplankton remains, they may be missed when the trap sample is counted. Moreover, even though pellets have high sinking speeds in the lab, they may be kept from sinking in the field by mixing (Aldredge et al. 1987). While this may be likely for pellets in the euphotic zone, it is less likely for pellets in the midwater zone, where little turbulence occurs. If chaetognath pellets are not in fact sedimenting out, then they must be eaten, decomposed, or otherwise recycled within the water column.


Manuscript first received: June 20, 1992

This article was presented by K. Banse, Seattle, Washington, USA.