



ELSEVIER

Available online at www.sciencedirect.com

SCIENCE @ DIRECT®

Deep-Sea Research I 51 (2004) 865–884

DEEP-SEA RESEARCH
PART I

www.elsevier.com/locate/dsr

A vertical model of particle size distributions and fluxes in the midwater column that includes biological and physical processes—Part I: model formulation

Lars Stemann^{*1}, George A. Jackson, Debby Ianson²

Department of Oceanography, Texas A&M University, College Station, TX 77843-3146, USA

Received 22 November 2002; received in revised form 12 August 2003; accepted 2 March 2004

Abstract

The downward transport of surface particle production constitutes an important mechanism for carbon sequestration by the ocean. Only a small fraction ($\approx 10\%$) of the flux that leaves the euphotic zone reaches 1000 m depth because the particulate organic matter is consumed and transformed in the oceanic midwater column. The depth at which this transformation occurs is crucial to estimate carbon sequestration. Description of the particle flux and remineralization with depth below the euphotic zone has previously been limited to empirical relationships that neglect physical and biological mechanisms. Because several particle properties and functions (settling speed, rates of coagulation and consumption) are related to particle size, measurements of particle size spectra provide an important tool to understand particle dynamics. Most of the mechanisms affecting particle dynamics known for the surface layer should continue in the mesopelagic region. We review the different mechanisms and formulate equations describing changes in particle size distributions throughout the water column as a result of particle sinking, coagulation, disaggregation, and bacterial and zooplankton consumption. The resulting model describes the midwater particle population by its mass distribution for the size range 1 μm to 1 cm. Most of the particle data sets have a narrower size range but we suggest that model results are not greatly affected by the lack of data on particles smaller than 200 μm because most of the particle mass is in particles larger than 100 μm , as seen in a full size-range particle spectrum. The combination of this model with a unique particle size spectra data set, obtained during an inter-annual survey at the French JGOFS site in the NW Mediterranean Sea, give an insight into the key processes for particle dynamics in the unknown midwater layers.

© 2004 Elsevier Ltd. All rights reserved.

1. Introduction

Particle sedimentation to the deep-sea is a major mechanism for the redistribution of carbon, other nutrients (P, N, Si) and trace elements (e.g., Th, Pb, Ag, Se) in the water column (Broecker and Peng, 1982; Fowler and Knauer, 1986; Hebel et al.,

^{*}Corresponding author. Tel.: +33-(0)4-93-76-38-18; fax: +33-(0)4-93-76-38-34.

E-mail address: stemmann@obs-vlfr.fr (L. Stemann).

¹Present address: Laboratoire d'Océanographie de Villefranche, BP 28, 06234 Villefranche sur Mer, France.

²Present address: Institute of Ocean Sciences, P.O. Box 6000, Sidney, BC, Canada V8L 4B2.

1986; Lee and Fisher, 1993). Because particle settling speed generally increases with particle length (Shanks and Trent, 1980; Alldredge and Gotschalk, 1988, 1989; Syvitsky et al., 1995), the particle size distribution can be used to predict the potential vertical flux of a marine ecosystem. For this reason, macroscopic aggregates in the euphotic zone have been studied during the last two decades to determine their properties, including geometry, chemical content, and size distributions. The results allow investigation of the linkage between particle size spectra and bio-physical processes (settling, aggregation, solubilization and remineralization).

Particles range from individual organisms to assemblages of highly degraded detritus; they can be formed directly by such biological processes as cell division and fecal pellet production or indirectly by coagulation of other particles. Once formed, particle size can be reduced by remineralization, solubilization and physical fragmentation caused by microbial and zooplankton communities living and feeding on aggregates (Alldredge, 1972; Silver et al., 1978; Davol and Silver, 1986; Steinberg et al., 1994; Turley and Mackie, 1994; Green and Dagg, 1997; Kiørboe, 2000, 2001). Particle size can also increase by coagulation (Jackson, 1990) and fecal production. These changes in particle sizes can dramatically affect the vertical flux by changing particle sinking speeds as well as particle concentrations. As a result, the vertical distributions of all the elements carried by particles are changed and the knowledge of the processes affecting particle size is important for understanding the distribution of these elements in the water column.

Descriptions of carbon flux as a function of depth are based on empirical relationships which fit discrete sediment trap data to either power law or exponential functions (e.g., Martin et al., 1987; Bishop, 1989; Armstrong et al., 2002). The observed spatio-temporal variations of the two resulting parameters do not involve any mechanisms. Dadou et al. (2001) developed a model that predicts the vertical flux of elements in midwater and deepwater as a function of surface inputs. They did apportion the particles into two size classes and used ad hoc functions to move particles

between the two. Their simple particle dynamics models yielded a better estimation of the POC flux than did a simple depth–flux relationship. However, their model was unable to reproduce the observed temporal variations in particle flux to the benthos. Dadou et al. suggested that adding zooplankton behavior or marine snow dynamics could improve their results. Jackson and Burd (2002) have developed a series of models to describe interactions between particle flux and zooplankton population dynamics in the subsurface region. They indicated that the animal prey–predator interactions can affect the particle vertical flux. Their models results are sensitive to zooplankton behavior (e.g., feeding and death formulations) for which we have little information. The implication of Dadou et al. (2001) and Jackson and Burd (2002) is that understanding of processes affecting particles transformation is crucial in any attempt to estimate what controls the vertical flux of material.

Many of the processes affecting particle size in the surface layer (settling, coagulation, bacterial and zooplankton activity) should continue in the midwater region, although at different rates. Therefore, models of particle dynamics developed for the surface layer can also be used deeper. By comparing observed particle size spectra and model results, we can estimate the relevant process rates and direct future studies. The aim of this paper is to describe the processes affecting particle dynamics and to assemble them into a mathematical framework that can be used to model the midwater particle processes. Our region of interest is the sub-euphotic midwater zone with a nominal depth range of 100–1000 m. We first review particle properties and dynamics as inferred mostly from surface studies and we discuss their relevance to midwater conditions. We then develop mathematical formulations describing the different processes and assemble them into an integrated model. In the companion paper, we test the model against a unique 3 years data set of midwater particle distributions in the NW Mediterranean (Stemmann et al., 2004) in order to estimate the relative effect of the different mechanisms on particle distribution.

2. Particle properties

2.1. Particle length and mass

Particles in the ocean range from the “almost dissolved” colloids about 1 nm long to aggregates longer than 1 cm. We will use the generic term “particle” to describe non-motile particles and aggregates without distinction.

Visual observation of particles in the surface ocean reveals considerable variation in characteristics ranging from individual phytoplanktonic cells and fecal pellets to aggregates composed of multiple particle types embedded in a mucilaginous matrix (Allredge and Silver, 1988). It is useful to describe the particle abundance as a function of an important particle property, such as diameter, mass, surface area or carbon content. These properties are generally correlated but the relationships are not simple both because aggregates are porous objects whose porosity increases with their size and because they are formed from different constituents having different densities. Typical densities of aggregate constituents are 1.03–1.1 g cm⁻³ for cytoplasm, 1.23 g cm⁻³ for a fecal pellet and 2.6 g cm⁻³ for the silicon wall of a diatom (Komar et al., 1981; Mann and Lazier, 1991). To determine the mass of each aggregate accurately, we need to know the exact composition and size of each constituent. Reliable data at this level of detail are not currently available for any of the complex natural particles described as marine snow. Fractal scaling has been used as a tool to describe the relationship between particle mass and length. This approach usually assumes that an aggregate is formed from one source particle type, although more comprehensive descriptions exist (e.g., Jackson, 1998). The fractal dimension characterizes the relationship between particle mass and diameter (see below). Calculated fractal dimensions for natural surface water and laboratory aggregates range from 1.59 to 2.67 (Logan and Wilkinson, 1990; Li and Logan, 1995; Jackson, 1995a; Jackson et al., 1997).

Much less is known about aggregates in the midwater layers, but aggregates of phytoplanktonic origin tend to dominate the mass and abundance of particles in both coastal (Peinert

and Miquel, 1994; Passow and Wassman, 1994) and oceanic regions (Billet et al., 1983; Lampitt, 1985; Takahashi, 1986; Sancetta et al., 1992).

2.2. Particle size spectrum

2.2.1. Concepts

The particle size spectrum provides a useful way to characterize the relationship between particle abundance and size. If \hat{N} is the cumulative particle concentration, the total number concentration of particles larger than a given mass m , then $n(m) = -d\hat{N}/dm$ is the number spectrum. Here n and \hat{N} are both functions of particle mass but they can be expressed as functions of particle diameter d or any other particle properties and converted between each other.

The number spectra is usually estimated by counting the number of particles within a given length and dividing that number by the extent of the range and the volume sampled. Length is a useful particle descriptor because several particle properties such as mass and settling speed (Allredge and Gotschalk, 1988), colonization by microbes and zooplankton (Kjørboe, 2000, 2001) and coagulation rate (Jackson and Lochmann, 1993) depend on it. Biogeochemical activity such as aggregates remineralization by bacterial activity or zooplankton consumption can also be a function of length (Jackson, 1993; Ploug and Grossart, 2000; Kjørboe and Thygesen, 2001). Because it is easily measured with optical techniques, many marine particle studies measure particle distribution as a function of length (Table 1).

2.2.2. In situ observations

Most in situ instruments observe only a narrow range of particle sizes present in nature because the lower size limit is set by instrumental sensitivity and the upper size limit is set by the rarity of large particles in the limited water volumes observed. Moreover, different instruments use different ways of measuring physical properties that are affected differently by the fractal nature of aggregates (Jackson et al., 1995). Particle size has been commonly measured either with impedance instruments (which measure a property that

Table 1

Different instruments used to measure particle size spectra in midwater. The instrument characteristic are as reported by the respective authors

Instrument	Size range	Depth range	Reference
Underwater Video Profiler II	> 100 μm –1.5 mm	0–1000 m	Gorsky et al. (1992)
UVP III	> 400 μm –~5 mm	0–1000 m	Gorsky et al. (2000)
UVP IV	> 90 μm	0–1000 m	Gorsky et al. (2000)
Marine Snow Profiler (MSP)	> 600 μm	0–4300 m	Lampitt et al. (1993)
Large Aggregate Profiling System (LAPS)	0.5 mm–~5 mm	0–1000 m	Walsh et al. (1997)
SNOWCAM	> 35 μm	0–100 m	MacIntyre et al. (1995)
MAPPER LFC	> 50 μm		Costello et al. (1992)
High Resolution Camera System (Parca)	> 50 μm	0–1000 m	Ratmeyer and Wefer (1996)
Floc Camera Assembly	> 50 μm		Syvitski et al. (1995)
Aggregate Settling Collector and Observation Tower	> 500 μm	0–700 m	Diercks and Asper (1997)

approximately corresponds to the volume of the solid particles composing an aggregate) or optical instruments that measure light transmission and scattering by a particle or the size of its image. Impedance instruments (such as the Coulter Counter) are used for particles with $0.5\ \mu\text{m} < d < 200\ \mu\text{m}$ in water samples returned to the laboratory. Imaging systems have been used to measure in situ particles with $d > 50\ \mu\text{m}$ (Table 1). In situ observations of particles using non-intrusive methods are preferred to water collection because aggregate fragility can cause their disruption during sampling.

A means to cover a wide particle size range is to combine results from different instruments. In a unique set of studies, Jackson et al. (1995, 1997) combined results from multiple instruments to describe the length spectra for $1\ \mu\text{m} < d < 1\ \text{cm}$, first in a mesocosm and then in the surface layer in Monterey Bay, California. They observed that the number of particles was greatest in small ($< 50\ \mu\text{m}$) particles, but that the mass was predominantly in larger particles ($d > 100\ \mu\text{m}$, Fig. 1).

3. Processes affecting particle size and spatial distributions

3.1. Settling

Particle settling occurs at a speed that is a function of particle mass and diameter. Typical settling speeds in the surface layer increase with

particle length and range from $< 1\ \text{m d}^{-1}$ for small algae to $> 100\ \text{m d}^{-1}$ for fecal pellets and large marine snow particles (Fig. 2).

The considerable variability in the relationship between aggregate diameter and settling speed is not surprising given the heterogeneity of particles, particularly the aggregates. In midwater, Diercks and Asper (1997) measured particle settling speeds of subsurface particles, finding no statistical relationship between settling speed and diameter for $0.5\ \text{cm} < d < 5.5\ \text{cm}$ and concluded that the variation in the density of particle constituents controlled the aggregate settling speed. Their observation of regional differences in average settling speed suggests that different marine systems produce different types of particles. Berelson (2002) has argued that there are vertical differences in settling speed, with an average increased by a factor of 2–10 between the depth of 100 and 2000 m as a result of differential mineralization.

These results indicate that a universal relationship between settling speed and particle diameter likely does not exist but that local relationships may be applicable. Such a conclusion agrees with the analysis of Kriest (2002). No studies have been carried out to measure simultaneously settling speed and diameter over the full $1\ \mu\text{m}$ –1 cm size range.

3.2. Coagulation

Coagulation is the process by which two particles are brought into contact by physical

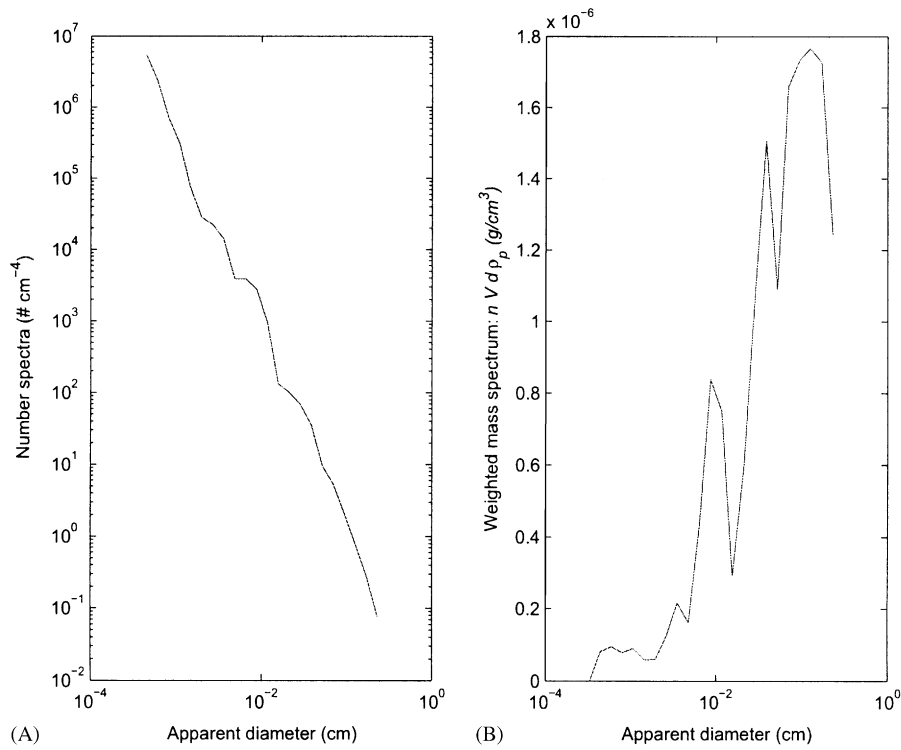


Fig. 1. (A) Sectional number and (B) mass spectra obtained in the mixed layer by Jackson et al. (1997). The mass spectrum is calculated assuming that $\rho_p = 1.068 \text{ g cm}^{-3}$, that aggregates are composed of a unique particle source ($d_1 = 5 \mu\text{m}$) and that the porosity can be described using fractal theory ($D_3 = 2.3$).

mechanisms and join together to form a single, larger particle. The physical mechanisms include Brownian motion, shear and differential settling (e.g., O'Melia, 1978). Coagulation models have been used by different authors to model the phytoplankton dynamic in the surface layer and in a mesocosm (Jackson, 1990; Hill, 1992; Riebesell and Wolf-Gladrow, 1992; Jackson, 1995a; Ruiz, 1997). Coagulation can have a major impact in determining particle size distribution in the mixed layer and may explain the rapid export of surface phytoplanktonic production, even in the absence of zooplankton grazing (Jackson, 1990).

In the midwater region much less is known about the rates, although the decreasing particle concentrations and shear rates should decrease particle encounter rates. Sediment trap observations in the Black Sea (Honjo et al., 1987; Izdar et al., 1987) and in the Gulf of Lyon (Monaco

et al., 1990) have discovered specific situations in continental margin nepheloid layers where fine-grained particles were intercepted in midwater by settling organic matter produced during a surface phytoplankton bloom.

While the encounter rates leading to aggregation depend on particle concentrations, sizes and masses, the probability that colliding particles join depends on their stickiness. The stickiness is nominally described as the probability α that two colliding particles stick together. Studies have shown that α varies from less than 0.1 to 1 in algal cultures (Kiørboe et al., 1990; Kiørboe and Hansen, 1993; Hansen et al., 1995) and 0.6–0.8 for aggregates of different natures (Alldredge and McGillivray, 1991). Stickiness can be affected by the concentration of mucus, such as “transparent exopolymeric particles” (TEP), around the particle and particle shape (Alldredge et al., 1993, 1995;

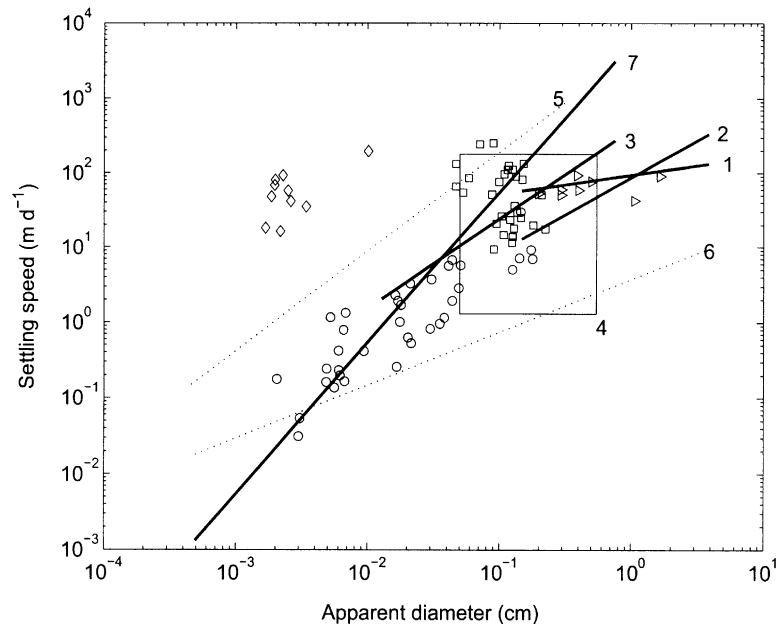


Fig. 2. Particle settling speed function of particle diameter measured by different authors. We report either the data points for (○) Smayda (1970), (▷) Shanks and Trent (1980), (◇) Carder et al. (1982), (□) Azetsu Scott and Johnson (1992) or the empirical relationships reported by different authors, 1—Allredge and Gotschalk (1988), 2—Allredge and Gotschalk (1989), 3—Syvitski et al. (1995), 4—Diercks and Asper (1997). Settling speeds calculated using our model with different parameter values (5— $\Delta\rho=0.08$, $D_3 = 2.33$, $d_1 = 5$, 6— $\Delta\rho=0.01$, $D_3 = 1.79$, $d_1 = 5$) are also reported. The regression line 7 is the settling speed predicted by Stokes Law. See Table 2 for parameter descriptions.

Dam and Drapeau, 1995; Jackson, 1995b; Passow, 2002). There is no evidence that α varies with particle size, although this may reflect a lack of systematic investigation.

3.3. Fragmentation

3.3.1. Physical fragmentation

Physical disaggregation breaks an aggregate into smaller pieces without consuming particle mass. Larger aggregates tend to have higher disaggregation rates because shear caused by turbulence exerts stronger forces on them and because their greater porosity weakens them. Given the size dependence, disaggregation has been invoked to explain the observation that there is a maximum size for aggregates in a coagulating system (e.g., Parker et al., 1972).

Allredge et al. (1990) measured the break up of diatom aggregates in a laboratory experiment as a

function of shear intensity. They concluded that physical disaggregation is important only in the upper layer during a storm event when high turbulence is generated ($\epsilon > 10^{-3} \text{ cm}^2 \text{ s}^{-3}$). This conclusion explained Riebesell's (1992) observation that the disappearance of large marine flocs from the surface layer (presumably via disaggregation) coincided with drastic increases in wind speed. In a model study of a mesocosm diatom bloom experiment, Jackson (1995a) showed that including both coagulation and disaggregation was required for the best description of the particle dynamics. An additional model describing diel variations in surface layer particle dynamics showed that a diel cycle in turbulence could lead to diel cycle in particle size due to diel fragmentation (Ruiz, 1997).

Thus, physical disaggregation is likely to be most important in the mixed layer where turbulence is common and variable. In the quiescent

midwater region, values of the energy dissipation rate are typically 2–3 orders of magnitude smaller than the values observed to be important for breakup for aggregates of the same strength (10^{-6} – 10^{-5} cm²s⁻³, Polzin, pers. comm.). Hill (1998) argued that breakup could occur from settling stresses on large and fragile marine flocs. We expect disaggregation by natural shear to be less important in midwater. Disaggregation is more likely controlled by biological mechanisms: bacterially mediated dissolution, zooplankton mining or zooplankton-caused shear. These mechanisms are discussed below.

3.3.2. Biological fragmentation

The flow field associated with swimming or feeding zooplankton has been observed to fragment aggregates several millimeters long by Dilling and Alldredge (2000). They suggested that aggregate breakup by vertically migrating euphausiids was responsible for their observed day–night variation in marine snow size distribution in the upper 100 m depth. Steinberg et al. (1997) observed a different mechanism for ctenophores and gelatinous zooplankton, in which these organisms became entangled in appendicularian houses and disrupted them with the movement of their cilia or the pulsing of their swimming bells. There are undoubtedly more ways in which organism can affect particle size distributions than these sparse observations have shown.

3.4. Zooplankton feeding

Particles form the base of any midwater food web and there are numerous indications that zooplankton consume aggregates. Gut contents of midwater copepods such as *Scopalatum vorax* (Steinberg, 1995) or *Lucicutia* aff. *L. grandis* (Gowing and Wishner, 1998) include amorphous detritus and other materials associated with aggregates. Many species colonize aggregates in the euphotic zone (Alldredge, 1972; Green and Dagg, 1997; Shanks and Walters, 1997) and in the midwater (Steinberg et al., 1994, 1997). Kiørboe (2000) calculated that the zooplankton feeding on aggregate in the mixed layer were responsible for a specific loss of aggregate POC on the order of 0.1–

0.2 d⁻¹. There are no such rates published deeper, but estimates that zooplankton metabolic demand accounts for 9–64% of the decrease in POC flux suggest that this rate could be also high (Sasaki et al., 1988; Banse, 1990; Koopelmann and Weikert, 1992; Lampitt, 1992; Steinberg et al., 1997; Yamaguchi et al., 2002).

3.4.1. Encounter rate

Three mechanisms for zooplankton–particle encounter have been proposed: volume filtering, flux feeding and plume searching. Filter feeders process a volume of water, interacting with particles at rates proportional to particle concentrations; flux feeders interact with falling particles at rates proportional to particle settling velocities (essentially catching particle as they fall); plume searchers seek out falling particle by sensing the hydrodynamic or chemical disturbance caused by them.

Filter feeding is a well-described mechanism for many organisms including larvaceans, salps and numerous species of crustaceans (e.g., Huntley and Boyd, 1984). The rate of particle removal for filter feeding is generally proportional to particle concentration, although feeding can saturate at high concentrations.

Flux feeding has been more recently described as a potentially effective mechanism to reduce vertical flux (Jackson, 1993). Pteropods behave like miniature sediment traps, collecting particles on their large mucus webs (Gilmer and Harbison, 1986). The midwater copepod, *Calanus cristatus*, can also flux-feed, remaining sedentary and using its disproportionate antennae to sense settling particles (Dagg, 1993). More rapidly settling particles are preferentially removed by a flux feeder because the probability of a particle falling onto a zooplankton's collecting apparatus depends on the particle flux, equal to the settling speed times the concentration (Jackson, 1993).

Kiørboe and Thygesen (2001) proposed a variant to the flux feeding where animals remotely search for aggregates looking for hydro-mechanical disturbances or chemical signatures from the falling particles. The solute distribution behind the sinking particles is long and slender and may be detected by swimming copepods. They suggest that small poecilostomatoid copepods of genus

Oncaea, found to feed on and colonize aggregates, could be effective plume finders. Theoretical calculations suggest that the ability of animals to find particles this way is proportional to the particle fall velocity. Because the dependence on particle size appears to be similar, we are combining this mode of plume searching, with flux feeding. We term this behavior “active flux feeding” to distinguish with the more traditional “passive flux feeding” discussed above.

3.4.2. Zooplankton behavior on aggregates

The standard way to describe zooplankton feeding is that an animal ingests all food particles it encounters and assimilates only a fraction of them. However, feeding behavior depends on the size of the animal relative to the size of the particle. A zooplankton larger than the particle can either engulf the entire particle (Larson and Shanks, 1996; Dilling et al., 1998) or feed on a fraction of it (Alldredge, 1972; Shanks and Walters, 1997; Steinberg et al., 1997). A fundamental difference from a particle dynamics perspective between the two feeding modes is that the first decreases the number of particles while the other makes them smaller. Total ingestion causes the removal of 100% of the encounter particles while mining causes the removal of a fixed amount of mass invariant with particle size. Therefore, the fraction of mass uptake will depend on the size of the particle and may range from few percent to 100% for, respectively, a very large particle and a very small particle compared to the size of the animal.

A small zooplankton can only consume a small amount of a large aggregate during short contacts with the particle. This mining can represent a large total consumption of aggregate material because of the large number of such individuals found on aggregates. Among the different groups, the poecilostomatoid copepods of genus *Oncaea* spp. have been found to feed on and colonize aggregates (Lampitt et al., 1993; Green and Dagg, 1997; Steinberg et al., 1997; Kiørboe, 2000). *Oncaea* is widespread and abundant; it can be the numerically dominant species in midwater (Scotto Di Carlo et al., 1984; Böttger-Schnack, 1994). Therefore, mining may be an important process altering particle size spectra in midwater.

3.4.3. Production of detritus

Zooplankton not only consume particles but they also produce fecal material (e.g., Pomeroy and Deibel, 1980; Urrere and Knauer, 1981) and mucus-feeding structures (Alldredge and Silver, 1988). Both types of particles have mass–length relations different than those of typical aggregates (Komar et al., 1981; Alldredge and Gotschalk, 1988; Jackson, 2001). However, we argue that grouping the particles produced by zooplankton with the typical aggregates is a reasonable approximation. First, discarded feeding structures such as pteropod web and appendicularian houses are rapidly incorporated into aggregates. Second, fecal pellets are much less abundant than aggregates (e.g., Turner, 2002; Stemann, unpublished data). Lastly, fecal pellets are consumed or broken up rapidly by zooplankton (Lampitt et al., 1990; Gonzalez and Smetacek, 1994; Bathmann et al., 1987; Peinert et al., 1987; Riser et al., 2001), developing a fluffy consistency similar to that of aggregates (Lampitt et al., 1990). For these reasons, the description of particle size spectra based on a unique relation between mass and length may be a reasonable first approximation.

3.5. Microbial activity

Several studies have found that bacterial concentrations in aggregates are greater by a factor of up to 10^3 relative to the surrounding waters (Silver et al., 1978; Davol and Silver, 1986; Alldredge and Silver, 1988; Turley and Mackie, 1994). Protozoa are also commonly important members of detrital communities (Caron et al., 1982; Silver et al., 1984; Silver and Gowing, 1991).

Attached bacteria metabolize and solubilize the particulate organic matter (POM) composing aggregates. The rate of POC solubilization has been estimated to range from 0.075 to 0.2 d^{-1} (Smith et al., 1992; Grossart and Simon, 1998). Ploug and Grossart (1999, 2000) found that the loss of POC by solubilization was smaller (0.023 d^{-1}) than by respiration (0.10 d^{-1}) and suggested that the particle-specific mass loss may be constant with particle size ranging from 1 to 6 mm. Direct metabolism and solubilization both represent losses to particle mass, but solubilization provides

food for the free living bacteria and creates a chemical plume that allows a particle to be detected.

Microbial consumption of particle mass can also affect particle geometry by hollowing out the particle or by shrinking it. In either case, it can change the mass–length relationship. Biddanda and Pomeroy (1988) described a characteristic pattern of decomposition: growth of attached bacteria, aggregation of detritus, growth of protozoa feeding upon bacteria and, after 8 d, disaggregation. A similar pattern of microbial succession and particle alteration has been described for discarded larvacean houses (Davol and Silver, 1986) and tunicate feces (Pomeroy and Deibel, 1980). Ploug and Grossart (2000) measured the POC release rate and the shrinking of decomposing diatom aggregates, finding that after 4 days both POC mass and apparent volume decreased by about 37–40%. The latter result suggests that the porosity was constant during decomposition.

Thus, the process of particle decomposition appears to consist of a mass loss caused by bacteria and a size reduction caused by protozoa.

4. Mathematical description

4.1. Particle size spectrum

The use of particle size spectra provides a powerful approach to describe a particle population and its dynamics because several particle properties are related to particle size. The total number of particles per unit volume dN in a size range between m and $m + dm$, where dm is a small mass increment, is $dN = n dm$. The total number of particles per unit volume between one mass (m_1) and another (m_2) is the sum (integral) of the particles in all the size intervals between m_1 and m_2 . We can also integrate to find the total mass of particles per unit volume ΔM :

$$\Delta M = \int_{m_1}^{m_2} mn(m, z, t) dm. \quad (1)$$

Note that n is a function of position (x, y, z), time t , and mass m . For simplification, we will focus on

vertical processes and ignore horizontal transport, although its inclusion is a straightforward extension of what we present. As a result, $n = n(m) \equiv n(m, z, t)$, where z is the depth.

Particle mass does not uniquely determine other important properties, such as particle diameter or settling speed. It is clear from the weak relationship between particle diameter and settling speed (Fig. 2) that there can be a range of particle densities. This problem can be addressed with a two-dimensional size spectrum $n_2(m, d, z, t)$ where d is the particle diameter (Jackson, 1998). In this case, the total number of particles in the size region bounded by m , $m + dm$, d and $d + dd$ is $dN = n_2(m, d) dm dd$. While this approach has been used to describe marine food chains with diverse particle sources, ranging from colloids to phytoplankton and fecal pellets, it is more difficult to implement and requires more information to set up (Jackson, 2001). Therefore, we will describe the particle population with a one-dimensional mass spectrum $n(m, z, t)$.

The variability of the particle size spectrum provides clues for studying by means of models the processes that affect particle distributions in a continuous manner. Unfortunately, the resulting equations are not easily solved. For example, the equations that describe coagulation result from a complex set of integro-differential equations with no general analytical solution. Numerical solutions of these equations can be found by the *sectional approach*, in which size spectrum is approximated in pieces (“sections”) similar to a histogram approximating a smooth curve (Gelbard et al., 1980). We will denote the i th section as S_i . The lower bound (m_i) of S_i has a particle mass half that of its upper bound ($2m_i = m_{i+1}$).

In the sectional approach, the particle number spectrum is assumed to be the product of two parts, one varying with time, the other with particle mass (Jackson, 1990). Within S_i , n is approximated as

$$n = \frac{Q_i(z, t)}{mm_i} \quad \text{for } m_i \leq m < 2m_i, \quad (2)$$

where $Q_i(t)$ is the total particulate mass concentration in S_i . Mass concentration can be mol C l^{-1} , g C cm^{-3} , or conserved volume of C ($= m/\rho_p$, where

ρ_p is the density of the unit particle) per unit volume.

4.2. Mass–length relation

Fractal scaling provides the means of relating particle mass m to its diameter d . According to fractal theory, if an aggregate of mass m is composed of sub-particles, each of the same mass m_1 and diameter d_1 , the relationship between the aggregate diameter and the mass can be described as a fractal by

$$\frac{m}{m_1} = \left(\frac{d_v}{d_1}\right)^3 = A_f \left(\frac{d_g}{d_1}\right)^{D_3}, \quad (3)$$

where d_v is the conserved diameter (the diameter the aggregate would have if no water was trapped between particles composing the aggregate), d_g is the gyration diameter (the root-mean-square diameter, a size close to the visual diameter), A_f is a fitting constant and D_3 is the fractal dimension (Jackson, 1995a). A_f is calculated from Eq. (3) for the case of the initial cell. For a solid sphere, $d_g = \sqrt{0.6}d_v$ and $A_f = 0.6^{-D_3/2}$.

4.3. Model

We have developed a model that describes the change in midwater particle concentration by all the processes reviewed above: settling, coagulation, fragmentation, microbial activity and zooplankton consumption. At any depth and time, the rates from the processes sum to yield the total rate of change of particle concentration. Thus, the rate of change of the number size spectrum is

$$\frac{\partial n}{\partial t} = \sum_{o=1}^f \left(\frac{\partial n}{\partial t}\right)_o, \quad (4)$$

where $(\partial n/\partial t)_o$ are the rate of change of n from the o th mechanism and f is the number of mechanisms considered (see Table 2 for a list of symbols).

The sectional approximation to Eq. (4) is

$$\frac{\partial Q_i}{\partial t} = \sum_{o=1}^f \left(\frac{\partial Q_i}{\partial t}\right)_o. \quad (5)$$

In the following paragraphs, we will describe mathematically processes ($o=1-8$) that affect particles in the mesopelagic region.

4.4. Vertical flux of particles

The settling speed of an aggregate can be calculated from a modified Stokes fall velocity that uses fractal scaling (Jackson, 1995b):

$$w = am^b \quad (6)$$

with $a = g(\rho_p - \rho_f)(18\rho_f\nu)^{-1}(\rho_p\pi/6)^{1/D_3-1}A_f^{1/D_3}d_1^{3/D_3-1}$, $b = 1 - (1/D_3)$, g is the gravitational acceleration, ρ_f the fluid density and ν is the kinematic viscosity.

The net loss or gain at a given depth due to settling ($o=1$) is a function of the vertical gradient in particle concentration:

$$\left(\frac{\partial n}{\partial t}\right)_1 = -w \frac{\partial n}{\partial z}, \quad (7)$$

where $w = w(m)$. The equivalent equation for the sectional approach results from integrating Eq. (7) over S_i

$$\begin{aligned} \left(\frac{\partial Q_i}{\partial t}\right)_1 &= - \int_{m_i}^{2m_i} mw \frac{\partial n}{\partial z} dm \\ &= - w_i \frac{\partial Q_i}{\partial z}, \end{aligned} \quad (8)$$

where $w_i = \int_{m_i}^{2m_i} wm_i^{-1} dm$ is the average settling speed over S_i .

While n is a function of space, particle mass, and time, the spatial dependence is explicit only for the transport terms. This would include any advection or mixing processes as well as particle settling. The various biological and coagulation processes that affect the particle distribution depend only on the local concentrations and rates.

4.5. Coagulation

Coagulation models simulate the particle size distribution resulting from the collision and subsequent sticking together of particles over a

Table 2

List of model parameters and their values. M, L, and T represents mass, length and time

Symbol	Description	Dimension
a	Constant for $w(m)$	$L T^{-1} M^{-b}$
A_f	Constant in fractal relationship	—
b	Constant for $w(m)$	—
c	Clearance rate for filter feeder	$L^3 T^{-1}$
d	Particle diameter	L
d_1	Diameter of primary particle	L
d_g	$2 \times$ radius of gyration	L
d_v	Diameter of conserved volume	L
D	Detritus production function	$L^{-4} T^{-1}$
D_i	Detrital production rate in S_i	$M L^{-3} T^{-1}$
D_3	Fractal dimension	—
e	Total zooplankton encounter rate	T^{-1}
e_c	Encounter rate for filter feeders	T^{-1}
e_f	Encounter rate for flux feeders	T^{-1}
e_m	Encounter rate for miners	T^{-1}
f	Total number of rate terms	—
g	Gravitational acceleration	$L T^{-2}$
l	Total number of particle sections	—
m	Particle mass	M
m_1	Mass of primary particle	M
n	Particle number spectrum	L^{-4}
\hat{N}	Cumulative particle concentration larger than a given mass or length range	L^{-3}
N	Particle concentration in a given mass or length range	L^{-3}
o	Indice of the mechanism	—
p	Fraction of food to detritus	—
Q_i, Q_q	Mass concentration in S_i, S_q	$M L^{-3}$
r	Specific loss rate from bacteria	T^{-1}
S_i	i th section	—
T	Mass transfer function for feces	M^{-1}
w	Particle settling speed	$L T^{-1}$
Z_c	Concentration of filter feeders	ind L^{-3}
Z_f	Concentration of flux-feeders	ind L^{-3}
Z_m	Concentration of particle miners	ind L^{-3}
α	Stickiness	—
β	Coagulation kernel	T^{-1}
${}^1\bar{\beta}_{q,i}, {}^2\bar{\beta}_{q,i}, {}^3\bar{\beta}_{q,i}, {}^4\bar{\beta}_{i,i}, {}^5\bar{\beta}_{q,i}$	Sectional coefficients for change in S_i	$M^{-1} L^3 T^{-1}$
$\Delta\rho$	Particle excess density	$M L^{-3}$
δ_m	Mass uptake per mining	M
ε	Energy dissipation rate	$L^2 T^{-3}$
ν	Seawater viscosity	$L^2 T^{-1}$
ξ_b	Breakup rate for binary fission	T^{-1}
ξ_c	Breakup rate to cloud	T^{-1}
ρ_p	Density of primary particle	$M L^{-3}$
ρ_f	Fluid density	$M L^{-3}$
σ	Flux-feeding cross-sectional area	L^2

wide range of sizes. The change in concentration of particles of any mass with time from coagulation ($o=2$) results from a cascade of mass up the particle size spectrum: gain from the collision of smaller particles and loss from the collision with other particles. These changes can be

described as

$$\left(\frac{\partial n}{\partial t}\right)_2 = 0.5\alpha \int_0^m \beta(m', m - m')n(m')n(m - m') dm' - n(m)\alpha \int_0^\infty \beta(m, m')n(m, m') dm', \quad (9)$$

where α is the particle stickiness and $\beta(m, m')$ is the coagulation coefficient describing the interaction rates between particles of masses m and m' .

The transformation of Eq. (9) to the sectional form after integration is

$$\begin{aligned} \frac{dQ_i}{dt} = & \alpha Q_{i-1} \sum_{q=1}^{i-1} {}^1\bar{\beta}_{q,i} Q_q \quad \text{gain from collision } q, i-1 \\ & + \alpha Q_i \sum_{q=1}^{i-1} {}^2\bar{\beta}_{q,i} Q_q \quad \text{gain from collision } q, i \\ & - \alpha Q_i \sum_{q=1}^{i-1} {}^3\bar{\beta}_{q,i} Q_q \quad \text{loss from collision } q < i, i \\ & - \alpha^4 \bar{\beta}_{i,i} Q_i^2 \quad \text{loss from collision } q = i, i \\ & - \alpha Q_i \sum_{q=i+1}^l {}^5\bar{\beta}_{q,i} Q_q \quad \text{loss from} \\ & \quad \text{collision } q > i, i, \end{aligned} \quad (10)$$

where l is the total number of sections, (${}^1\bar{\beta}_{q,i}$, ${}^2\bar{\beta}_{q,i}$, ${}^3\bar{\beta}_{q,i}$, ${}^4\bar{\beta}_{i,i}$, ${}^5\bar{\beta}_{q,i}$) are the sectional coefficients used by Jackson and Lochmann (1993) and α is assumed to be independent of size in the absence of more detailed information.

4.6. Fragmentation

Several models have been proposed for particle fragmentation by velocity shear and the resultant particle distribution (Hill, 1992, 1996; Jackson, 1995a; Ruiz, 1996). These models are complex and we have a poor understanding of shear and particle breakup rates below the surface due to the lack of observation. Does fragmentation occur through the erosion of the surface aggregate, or does the aggregate split into several daughter particles and what is the resulting size distribution? How fast does this happen and what is the size dependence of the processes? A complete description would use a transfer function that depends on the masses of both parent and daughter particles times the spectral density of the parent particle. In the absence of in situ data and to reduce the model complexity, we model physical disaggregation in a very simple manner by considering two extreme cases: a binary splitting into two equal mass

particles and splitting into clouds of elemental or source particles.

The change in the concentration of particle with mass m by splitting of a parent particle into two equal daughters ($o=3$) can lose particles by breakup to smaller particles and add them by breakup of larger particles

$$\left(\frac{\partial n(m)}{\partial t} \right)_3 = -\xi_b(m)n(m) + 2\xi_b(2m)n(2m), \quad (11)$$

where $\xi_b(m)$ is the breakup rate, a function of shear, including that induced by zooplankton.

The sectional equivalent for binary splitting is

$$\left(\frac{\partial Q_i}{\partial t} \right)_3 = -\xi_{b,i} Q_i + \xi_{b,i+1} Q_{i+1}. \quad (12)$$

The change in the concentration of particle with mass m by fragmentation into a cloud of source particles of mass m_1 ($o=4$) results in an increase of elemental particles and a loss of parent particles such as

$$\begin{aligned} \left(\frac{\partial n(m_1)}{\partial t} \right)_4 &= \int_{m_1}^{\infty} \xi_c(m)n(m) \frac{m}{m_1} dm, \\ \left(\frac{\partial n(m)}{\partial t} \right)_4 &= -\xi_c(m)n(m) \quad \text{for } m > m_1. \end{aligned} \quad (13)$$

The sectional equation for fragmentation in a cloud of elemental particles is

$$\begin{aligned} \left(\frac{\partial Q_1}{\partial t} \right)_4 &= \sum_{i=2}^l \xi_{c,i} Q_i, \\ \left(\frac{\partial Q_i}{\partial t} \right)_4 &= -\xi_{c,i} Q_i, \quad i \neq 1. \end{aligned} \quad (14)$$

As discussed above (Section 3.3) midwater turbulence is considered to be too low to break up particles, but sufficient shear may be created locally by the action of swimming zooplankton. Therefore, ξ_b and ξ_c should be a function of the volume of water affected by zooplankton while swimming. This volume can be approximated from swimming speed, cross-sectional surface area of the zooplankton and the number concentration of the organisms. We estimate the length-scale of the flow field to be larger than the length of the organism itself.

4.7. Zooplankton

As a first approximation, we consider that large zooplankton consume entire aggregates when they encounter them and that they are filter and flux feeders. In contrast, small zooplankton can consume only a portion of each aggregate and they are active flux feeders.

4.7.1. Encounter rate

The rate at which any particle encounters zooplankton equals an encounter kernel times the zooplankton concentration. For the rate of encounter by filter feeders,

$$e_c = cZ_c, \quad (15)$$

where Z_c is the number concentration of filter-feeding zooplankton and c is the average volume clearance rate.

For flux feeders, the encounter kernel is the product of w and a cross-sectional area σ , such as $e_f = w\sigma Z_f$,

$$(16)$$

where Z_f is the number concentration of flux-feeding zooplankton. Note that values of Z_f , Z_c , c and σ can vary in space and time, depending on the zooplankton community present, while c and σ can vary with food concentration and particle size.

4.7.2. Total particle consumption

The net effect of animal particle consumption when the total particle is consumed must account for the formation of fecal pellets, whose rate is indicated by D and which is developed further below. The net effect of filter feeding ($o = 5$) and flux feeding ($o = 6$) on the particle size spectrum is then

$$\left(\frac{\partial n}{\partial t}\right)_{5+6} = -(e_c + e_f)n + D. \quad (17)$$

In the sectional representation of filter feeding, the change of mass in section i due to full consumption is

$$\begin{aligned} \left(\frac{\partial Q_i}{\partial t}\right)_5 &= - \int_{m_i}^{2m_i} (e_c mn) dm + D_i \\ &= - e_c Q_i + D_i \end{aligned} \quad (18)$$

if e_c is independent of m and $D_i = \int_{m_i}^{2m_i} Dm dm$.

For flux feeding, the sectional equation is

$$\begin{aligned} \left(\frac{\partial Q_i}{\partial t}\right)_6 &= - \int_{m_i}^{2m_i} w\sigma Z_f mn dm + D_i \\ &= - a\sigma Z Q_i m_i^b (b+1)^{-1} \\ &\quad \times (2^{b+1} - 1) + D_i \quad \text{if } w = am^b. \end{aligned} \quad (19)$$

4.7.3. Partial particle consumption—mining

By consuming only a small amount (δ_m) from an aggregate at each contact, a small animal can cause the particle to shrink rather than disappear. This mining makes particles smaller but does not change the total number of particles. The rate at which miners find particles having mass m is $e_m(m)n(m, t)$, where $e_m(m)$ is the specific encounter rate for the miners. Since each encounter with particle m decreases the mass of the particle to $m - \delta m$ and each encounter with a particle of mass $m + \delta m$ increases the number of m particles, the change in $n(m, z, t)$ after a small time dt by mining ($o = 7$) can be described by

$$\begin{aligned} (n(m, t + dt) - n(m, t)) &= e_m(m + \delta_m)n(m + \delta_m, t) dt \\ &\quad - e_m(m)n(m, t) dt. \end{aligned} \quad (20)$$

The shrinkage causes loss of particles of a given size but also their gain from shrinkage of larger particles.

The lowest order terms for a Taylor expansion in δ_m and dt yield $e(m + \delta_m) \approx e(m) + (\partial e(m)/\partial m)\delta_m$, $n(m + \delta_m, t) \approx n(m, t) + (\partial n(m, t)/\partial m)\delta_m$ and $n(m, t + dt) \approx n(m, t) + (\partial n(m, t)/\partial t)dt$. Substituting these terms into Eq. (20), collecting terms and adding detrital production yields

$$\left(\frac{\partial n}{\partial t}\right)_7 = e_m \delta_m \frac{\partial n}{\partial m} + n \delta_m \frac{\partial e_m}{\partial m} + D. \quad (21)$$

The sectional representation of Eq. (21) must take into account that we have assumed that the shape of n is fixed within each S_i (see Eq. (2)) and that the mass is lost by shrinkage out of the section as well by consumption of S_i while mass gain in S_i by shrinkage from S_{i+1} . The mass loss from feeding is

$$\begin{aligned} - \int_{m_i}^{2m_i} e_m \delta_m \frac{Q_i}{mm_i} dm &= - ab^{-1} \delta_m \sigma Z_f m_i^{b-1} \\ &\quad \times Q_i (2^b - 1), \end{aligned} \quad (22)$$

where the right-hand side of Eq. (22) assumes that $w = am^b$ and that the search strategy for miners is the same as for plume finders ($e_m = w\sigma Z_m$, Z_m is the concentration of mining zooplankton).

The mass loss due to shrinking from S_i to S_{i-1} is the rate at which particles between m_i and $m_i + \delta_m$ are found:

$$\begin{aligned} & - \int_{m_i}^{m_i + \delta_m} e_m n \delta_m dm \\ & \approx - e_m(m_i) \frac{Q_i \delta_m}{m_i} \\ & = - am_i^{b-1} \sigma Z_m \delta_m Q_i \quad \text{for } w = am^b, \end{aligned} \quad (23)$$

assuming that $e_m(m_{i+1}) \approx e_m(m_{i+1} + \delta_m)$. Finally, the mass gain from S_{i+1} is

$$am_{i+1}^{b-1} \sigma Z_m \delta_m Q_{i+1} \quad \text{for } w = am^b \quad (24)$$

again assuming that $e(m_{i+1}) \approx e(m_{i+1} + \delta_m)$.

The total change due to mining is the sum of these three terms and the detrital production:

$$\begin{aligned} \left(\frac{\partial Q_i}{\partial t} \right)_7 & = ab^{-1} \sigma \delta_m Z_m \\ & \times (m_{i+1}^{b-1} Q_{i+1} - 2^b m_i^{b-1} Q_i) + D_i. \end{aligned} \quad (25)$$

4.7.4. Detrital production

Zooplankton feeding involves the consumption of one set of particles and the production of a second set as feces. It, $T(m', m)$, represents the rate that particles of mass m' are converted to fecal particles of mass m , then the total fecal particle production D can be described by

$$D(m) = \int_0^\infty T(m', m) e(m') n(m') dm'. \quad (26)$$

T incorporates the effects of all zooplankton feeding and fecal release. Feces, as particles, participate in the same coagulation processes as other particles. Describing these interactions involves the use of mass–length relationships. While it is possible to use separate relationships for fecal pellets (Jackson, 1998, 2001), it is simpler to assume that fecal pellets have the same mass–length relationship as aggregates (discussed above) and are indistinguishable from other particles of the same mass.

To simplify the incorporation of feces into the sectional equations, we further assume that a fraction p of all the material zooplankton consume is released as feces and that this material is released equally to all sections ranging from a minimum size characteristic of section S_{i_c} to the maximum S_l . Thus,

$$\begin{aligned} D_i & = p(l - i_c)^{-1} \sum_{q=1}^l e_q Q_q \quad \text{for } i > i_c, \\ & = 0 \quad \text{for } i \leq i_c. \end{aligned} \quad (27)$$

Note that i_c represents the minimum size of a fecal pellet released by zooplankton. Such an equal redistribution of mass among sections implies that the number spectra of the fecal pellets decreases with pellets size. Eq. (27) is required in each of the sectional equations for filter feeding (18), passive flux feeding (19) and active flux feeding (25) for all sections larger than i_c .

4.8. Microbial activity

Microbial activity ($o = 8$) consumes particulate mass and causes particles to shrink. If the specific rate of mass loss r is constant with particle size, a particle of mass m at t becomes a particle of mass $m - rm dt$ at $t + dt$ for small dt . For the spectra, that means that $n(m, t) = n(m - rm dt, t + dt)$. Making the Taylor expansion of this and keeping lowest order terms yields

$$\left(\frac{\partial n}{\partial t} \right)_8 = rm \frac{\partial n}{\partial m}. \quad (28)$$

The conversion of Eq. (28) to the sectional equivalent must account for the fact that the shape of n within a section cannot change. Changes in Q_i include losses from respiration and shrinking as well as a gain from shrinkage of S_{i+1} :

$$\begin{aligned} \left(\frac{\partial Q_i}{\partial t} \right)_8 & = -rQ_i - rQ_i + rQ_{i+1} \\ & = -2rQ_i + rQ_{i+1}. \end{aligned} \quad (29)$$

5. Discussion

5.1. Ecological interest of the model

In the surface region of the ocean, several studies (Alldredge and Gotschalk, 1988, 1989; Syvitsky et al., 1995; Kjørboe, 2000) have shown that particle properties and function can be related to their size spectra. Most of the surface processes should continue in the midwater zone and in the absence of more direct measurement of the processes and their rates, observed particle size distribution can be used as clues to find the relevant processes. Therefore, the knowledge of particles size and their variation in time can be used with models to understand the mechanisms of particle transformation. This is of special interest in the mesopelagic depths where sampling is difficult but where recent imaging techniques can be used to obtain particle size spectra.

Not unexpectedly, much of what we conclude is that more information is needed. Because settling speed is so important to estimate the flux, in situ accurate measurement at various depths and locations should be a priority for future research. Because both the colonizing zooplankton and the attached microbes modify the particle size distribution and hence the settling speed, the understanding of their respective physical effect on the micro scale is needed. In addition, the biochemical nature of midwater marine particles is not well known and needs further investigations.

We have catalogued different mechanisms known to affect particle concentrations and, therefore, fluxes. Our goal has been to show how other parts of the oceanic ecosystem affect particles in ways that have characteristic signatures. In Stemmann et al. (2004), we combine the equations describing settling (Eq. (8)), coagulation (Eq. (10)), disaggregation (Eqs. (12), (14)), zooplankton consumption (Eqs. (18), (19) and (25)) and microbial activity (Eq. (29)) in a series of models which are tested against a 3 year survey of particle size spectra. The results allow us to gain an understanding of the important processes and their rates in the oceanic midwater column and they suggest specific field work or experiment that

can be done to test the importance of the difference processes.

5.2. Model properties

The model developed in this paper can be used to predict vertical and temporal changes in particle size spectra in a one-dimensional system, given surface forcing and a prescribed zooplankton community and microbial activity. Physically, the model is suitable for regions where horizontal gradients of particles are small or where the 3D circulation is minimal. The model can be easily extended to three dimensions by adding the standard terms to describe the effects of advection and eddy mixing. However, this expansion requires more parameters and would introduce additional sources of uncertainty in a system where considerable information is lacking.

This analysis emphasizes particle interactions over a large size range (nominally 1 μm to 1 cm). However, most data sets of subsurface particle distribution cover only a narrow size range (Table 1) often skewed toward the larger size of the spectra. We hypothesize that small particles in much of the ocean have a small impact on the mass spectra as a whole. This hypothesis can be tested with the model by calculating those concentrations of small particles necessary to significantly alter the rates of change calculated using only the larger particles. We do this by separating the terms in our equations into two parts separated by a critical mass, m_c . The small particles have unknown concentrations. For example,

$$\frac{\partial n(m)}{\partial t} = \int_0^{m_c} J(m, m') dm' + \int_{m_c}^{\infty} J(m, m') dm', \quad (30)$$

where $J(m, m')$ is one function of the model mechanism. We considered mechanisms that transfer mass from the lower end to the larger end (i.e., zooplankton feeding and coagulation). We can calculate the mass of particles smaller than m_c needed to equal the change in the known part occurring in isolation from other processes such that $\int_0^{m_c} J(m, m') dm' = \int_{m_c}^{\infty} J(m, m') dm'$. This critical concentration of particles can be compared to

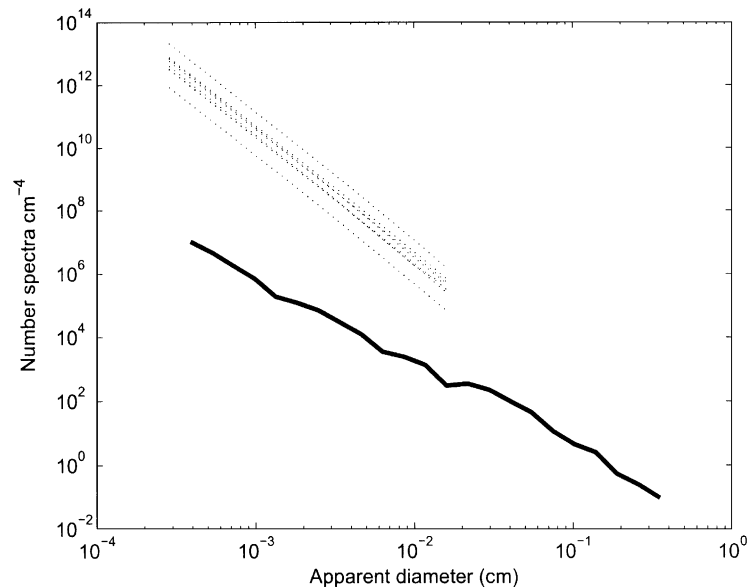


Fig. 3. Critical particle ($<200\ \mu\text{m}$) mass concentration needed to modify the model output for coagulation (dotted line) and (solid line) observed number spectra by Jackson et al. (1997). Each dotted line corresponds to a critical spectrum for one known section in the observed spectrum.

other field observation such as total POC or can be compared to complete size spectra in order to evaluate the validity of the hypothesis.

As an example, we have applied (Eq. (30)) with the process of coagulation to the size spectrum obtained in Monterey Bay by Jackson et al. (1997) (Fig. 1). Particle mass was estimated from particle length using the values for D_3 , d_1 given in Jackson et al. (1997) and we have assumed typical values of surface water for $\alpha = 0.4$ and $\varepsilon = 1.7 \times 10^{-2} \text{ cm}^2 \text{ s}^{-3}$. The sectional size spectrum was calculated as in Jackson (1995a). We assume that unknown sections contain particles of apparent diameter less than $200\ \mu\text{m}$. We choose this length as a limit because it corresponds to the minimal diameter of particles observed by the UVP in the sole inter-annual study of marine size spectra over the 100–1000 m depth range available (Stemmann et al., 2002).

Results indicate that the number concentrations of particles smaller than $200\ \mu\text{m}$ required to impact the model output are many orders of magnitude higher than those observed, confirming our

hypothesis (Fig. 3). Only the particles having a length close to $200\ \mu\text{m}$ may affect the model output. This result is not surprising given the sharp transition in particle mass spectra occurring at 100–800 μm (Fig. 1b). We speculate that in the midwater layers away from a source of small particles, such as phytoplankton growth, the particle dynamics inferred from the model should not be affected by the lack of data on small particles. This should be tested with more complete data sets.

Acknowledgements

We thank Richard Lampitt for helpful information. We also thank the three anonymous reviewers for their extensive, thoughtful, and helpful comments. They have done a heroic job. This work was supported by Grants OCE9986765 and OCE9981424 from the Ocean Sciences Division of NSF.

References

- Allredge, A.L., 1972. Abandoned larvacean houses: a unique food source in pelagic environment. *Science* 177, 885.
- Allredge, A.L., Gotschalk, C., 1988. In situ settling behavior of marine snow. *Limnology and Oceanography* 33, 339–351.
- Allredge, A.L., Gotschalk, C.C., 1989. Direct observations of the flocculation of diatoms blooms: characteristics, settling velocity and formation of diatoms aggregates. *Deep-Sea Research I* 36, 159–171.
- Allredge, A.L., McGillivray, P., 1991. The attachment probabilities of marine snow and their implications for particle coagulation in the ocean. *Deep-Sea Research I* 38, 431–443.
- Allredge, A.L., Silver, M.W., 1988. Characteristics, dynamics and significance of marine snow. *Progress in Oceanography* 20, 41–82.
- Allredge, A.L., Granata, T.C., Gotschalk, C.C., Dickey, T.D., 1990. The physical strength of marine snow and its implications for particle disaggregation in the ocean. *Limnology and Oceanography* 35, 1415–1428.
- Allredge, A.L., Passow, U., Logan, B.E., 1993. The abundance and significance of a class of large, transparent organic particles in the ocean. *Deep-Sea Research I* 40, 1131–1140.
- Allredge, A.L., Gotschalk, C., Passow, U., Riebesell, U., 1995. Mass aggregation of diatom blooms: insights from a mesocosm study. *Deep-Sea Research II* 42 (1), 9–27.
- Armstrong, R.A., Lee, C., Hedges, J.I., Honjo, S., Wakeham, S.G., 2002. A new, mechanistic model for organic carbon fluxes in the ocean based on the quantitative association of POC with ballast minerals. *Deep-Sea Research Part II* 49, 219–236.
- Azetsu-Scott, K., Johnson, B.D., 1992. Measuring physical characteristics of particles: a new method of simultaneous measurements for size, settling velocity and density of constituent matter. *Deep-Sea Research* 39, 1057–1066.
- Banse, K., 1990. New views on the degradation and disposition of organic particles as collected by sediment traps in the open ocean sea. *Deep-Sea Research* 37, 1177–1195.
- Bathmann, U.V., Noji, T.T., Peinert, R., 1987. Copepod fecal pellets: abundance, sedimentation and content at a permanent station in the Norwegian Sea in May/June 1986. *Marine Ecology—Progress Series* 38, 45–51.
- Berelson, W.M., 2002. Particle settling rates increase with depth in the ocean. *Deep-Sea Research Part II* 49 (1–3), 237–251.
- Biddanda, B.A., Pomeroy, L.R., 1988. Microbial aggregation and degradation of phytoplankton-derived detritus in seawater. 1. Microbial succession. *Marine Ecology—Progress Series* 42 (1), 79–88.
- Billet, D.M.S., Lampitt, R.S., Rice, A.L., Mantoura, R.F.C., 1983. Seasonal sedimentation of phytoplankton to the deep-sea benthos. *Nature* 302, 520–522.
- Bishop, J.K.B., 1989. Regional extremes in particulate matter composition and flux: effects on the chemistry of the ocean interior. In: Berger, W.H., Smetacek, V.S., Wefer, G. (Eds.), *Productivity of the Ocean: Present and Past*. Wiley, Chichester, pp. 117–137.
- Böttger-Schnack, R., 1994. The microcopepod fauna in the Eastern Mediterranean and Arabian Seas: a comparison with the Red Sea fauna. *Hydrobiologia* 292/293, 271–282.
- Broecker, W.S., Peng, T.H., 1982. *Tracers in the Sea*. Lamont–Doherty Geological Observatory, Palisades, New York, 690pp.
- Carder, K.I., Steward, R.G., Betzer, P.R., 1982. In situ holographic measurements of the size and settling rates of oceanic particles. *Journal of Geophysical Research* 87, 5681–5685.
- Caron, D.A., Davis, P.G., Madin, L.P., Sieburth, J.M.N., 1982. Heterotrophic bacteria and bacterivorous protozoa in oceanic macroaggregates. *Science* 218, 795–797.
- Costello, D.K., Carder, K.L., Hou, W., 1992. Structure visible diode laser illumination for quantitative underwater imaging. In: Gilbert, G.D. (Ed.), *Ocean Optics*, Vol. XI, Proceedings of the SPIE, Vol. 1750. Society of Photo-optical Instrumentation Engineers, Bellingham, WA, pp. 95–103.
- Dadou, I., Lamy, F., Rabouille, C., Ruiz-Pino, D., Andersen, V., Bianchi, M., Garçon, V., 2001. An integrated biological pump model from the euphotic zone to the sediment: a 1-D application in the Northeast tropical Atlantic. *Deep-Sea Research Part II* 48, 2345–2381.
- Dagg, M., 1993. Sinking particles as a possible source of nutrition for the large calanoid copepod *Neocalanus cristatus* in the subarctic Pacific Ocean. *Deep-Sea Research Part I* 40, 1431–1445.
- Dam, H.G., Drapeau, D.T., 1995. Coagulation efficiency, organic-matter glues and the dynamics of particles during a phytoplankton bloom in a mesocosm study. *Deep-Sea Research Part II* 42, 111–123.
- Davol, P.J., Silver, M.W., 1986. Marine snow aggregates: life history sequence and microbial community of abandoned larvacean houses from Monterey Bay, California. *Marine Ecology Progress Series* 33, 111–120.
- Diercks, A.-R., Asper, V.L., 1997. In situ settling speeds of marine snow aggregates below the mixed layer: Black Sea and Gulf of Mexico. *Deep-Sea Research Part I* 44, 385–398.
- Dilling, L., Allredge, A.L., 2000. Fragmentation of marine snow by swimming macrozooplankton: a new process impacting carbon cycling in the sea. *Deep-Sea Research Part I* 47 (7), 1227–1245.
- Dilling, L., Wilson, J., Steinberg, D., Allredge, A., 1998. Feeding by the euphausiid *Euphausia pacifica* and the copepod *Calanus pacificus* on marine snow. *Marine Ecology—Progress Series* 170, 189–201.
- Fowler, S.W., Knauer, G.A., 1986. Role of large particles in the transport of elements and organic compounds through the entire water column. *Progress in Oceanography* 16, 147–194.
- Gelbard, F., Tambour, Y., Seinfeld, J.H., 1980. Sectional representation for simulating aerosol dynamics. *Journal of Colloid and Interface Science* 76, 541–556.

- Gilmer, R.W., Harbison, G.R., 1986. Morphology and field behavior of pteropod mollusks—feeding methods in the families Cavolinidae, Limacinidae, peracrididae (*Gastropoda thecosomata*). *Marine Biology* 91 (1), 47–57.
- Gonzalez, H.E., Smetacek, V., 1994. The possible role of the cyclopoid copepod *Oithona* in retarding vertical flux of zooplankton faecal material. *Marine Ecology Progress Series* 113, 233–246.
- Gorsky, G., Aldorf, C., Kage, M., Picheral, M., Garcia, Y., Favole, J., 1992. Vertical distribution of suspended aggregates determined by a new underwater video profiler. Inst. Oceanographique, Paris, France.
- Gorsky, G., Picheral, M., Stemann, L., 2000. Use of the underwater video profiler for the study of aggregate dynamics in the North Mediterranean. *Estuarine Coastal and Shelf Science* 50, 121–128.
- Gowing, M.M., Wishner, K.F., 1998. Feeding ecology of the copepod *Lucicutia* aff. *L.-grandis* near the lower interface of the Arabian Sea oxygen minimum zone. *Deep-Sea Research Part II* 45, 2433–2459.
- Green, E.P., Dagg, M.J., 1997. Mesozooplankton associations with medium to large marine snow aggregates in the northern Gulf of Mexico. *Journal of Plankton Research* 19 (4), 435–447.
- Grossart, H.P., Simon, M., 1998. Bacterial colonization and microbial decomposition of limnetic organic aggregates (lake snow). *Aquatic Microbial Ecology* 15 (2), 127–140.
- Hansen, J.L.S., Timm, U., Kjørboe, T., 1995. Adaptive significance of phytoplankton stickiness with emphasis on the diatom *Skeletonema costatum*. *Marine Biology* 123 (4), 667–676.
- Hebel, D., Knauer, G.A., Martin, J.H., 1986. Trace metals in large agglomerates (marine snow). *Journal of Plankton Research* 8, 819–824.
- Hill, P.S., 1992. Reconciling aggregation theory with observed vertical fluxes following phytoplankton blooms. *Journal of Geophysical Research* 97 (C2), 2295–2308.
- Hill, P.S., 1996. Sectional and discrete representations of floc breakage in agitated suspensions. *Deep-Sea Research Part I* 43 (5), 679–702.
- Hill, P.S., 1998. Controls on floc size in the coastal ocean. *Oceanography* 11 (2), 13–18.
- Honjo, S., Hay, B.J., Manganini, S.J., Asper, V.I., et al., 1987. Seasonal cyclicity of lithogenic particle fluxes at a southern Black sea sediment trap station. *Mitt Geol-Palaontologie Institution, University of Hamburg*, 62, 19–39.
- Huntley, M., Boyd, C., 1984. Food-limited growth of marine zooplankton. *American Naturalist* 124 (4), 455–478.
- Izdar, H., Konuk, T., Ittekkot, V., Kempe, S., Degens, E.T., 1987. Particle flux in the Black sea; nature of organic matter. *Mitt Geol-Palaontologie Institution, University of Hamburg*, 62, 1–18.
- Jackson, G.A., 1990. A model for the formation of marine algal flocs by physical coagulation processes. *Deep-Sea Research* 37, 1197–1211.
- Jackson, G.A., 1993. Flux feeding as a mechanism for zooplankton grazing and its implications for vertical particulate flux. *Limnology and Oceanography* 38, 1328–1331.
- Jackson, G.A., 1995a. Comparing observed changes in particle size spectra with those predicted using coagulation theory. *Deep-Sea Research Part II* 42, 159–184.
- Jackson, G.A., 1995b. TEP and coagulation during a mesocosm experiment. *Deep-Sea Research Part II* 42, 215–222.
- Jackson, G.A., 1998. Using fractal scaling and two-dimensional particle size spectra to calculate coagulation rates for heterogeneous systems. *Journal of Colloid and Interface Science* 202, 20–29.
- Jackson, G.A., 2001. Effect of coagulation on a model planktonic food web. *Deep-Sea Research Part I* 48, 95–123.
- Jackson, G.A., Burd, A.B., 2002. A model for the distribution of particle flux in the mid-water column controlled by subsurface biotic interactions. *Deep-Sea Research Part II* 49, 193–217.
- Jackson, G.A., Lochmann, S.E., 1993. Modeling coagulation of algae in marine ecosystems. In: Buffle, J., Leuwen, H.P.V. (Eds.), *Environmental Particles*. Lewis, Boca Raton, FL, USA, pp. 387–414.
- Jackson, G.A., Logan, B.E., Alldredge, A.L., Dam, H.G., 1995. Combining particle size spectra from a mesocosm experiment measured using photographic and aperture impedance (Coulter and Elzone) techniques. *Deep-Sea Research Part II* 42, 139–157.
- Jackson, G.A., Maffione, R., Costello, D.K., Alldredge, A., Logan, B.E., Dam, H.G., 1997. Particle size spectra between 1 μ m and 1 cm at Monterey Bay determined using multiple instruments. *Deep-Sea Research Part I* 44 (11), 1739–1767.
- Kjørboe, T., 2000. Colonization of marine snow aggregates by invertebrate zooplankton: abundance, scaling, and possible role. *Limnology and Oceanography* 45 (2), 479–484.
- Kjørboe, T., 2001. Formation and fate of marine snow: small-scale processes with large-scale implications. *Scientia Marina* 65 (2), 57–71.
- Kjørboe, T., Hansen, J.L.S., 1993. Phytoplankton aggregate formation: observations of patterns and mechanisms of cell sticking and the significance of exopolymeric material. *Journal of Plankton Research* 15, 993–1018.
- Kjørboe, T., Thygesen, U.H., 2001. Fluid motion and solute distribution around sinking aggregates. II. Implications for remote detection by colonizing zooplankters. *Marine Ecology—Progress Series* 211, 15–25.
- Kjørboe, T., Andersen, K.P., Dam, H.G., 1990. Coagulation efficiency and aggregate formation in marine phytoplankton. *Marine Biology* 107 (2), 235–245.
- Komar, P.D., Morse, A.P., Small, L.F., Fowler, S.W., 1981. An analysis of sinking rates of natural copepod and euphausiid fecal pellets. *Limnology and Oceanography* 26, 172–180.
- Koopelmann, R., Weikert, H., 1992. Full-depth zooplankton profiles over the deep bathyal of the NE Atlantic. *Marine Ecology—Progress Series* 86 (3), 263–272.
- Kriest, I., 2002. Different parameterizations of marine snow in a 1D-model and their influence on representation of marine snow, nitrogen budget and sedimentation. *Deep-Sea Research I* 49, 2133–2162.

- Lampitt, R.S., 1985. Evidence for seasonal deposition of detritus to the deep-sea floor and its subsequent resuspension. *Deep-Sea Research* 32, 885–897.
- Lampitt, R.S., 1992. The contribution of deep-sea macroplankton to organic remineralization: results from sediment trap and zooplankton studies over the Madeira Abyssal Plain. *Deep-Sea Research* 39 (2A), 221–233.
- Lampitt, R.S., Noji, T., Von Bodungen, B., 1990. What happens to zooplankton fecal pellets? Implication for material flux. *Marine Biology* 104, 15–23.
- Lampitt, R.S., Wishner, K.F., Turley, C.M., Angel, M.V., 1993. Marine snow studies in the Northeast Atlantic Ocean: distribution, composition and role as a food source for migrating plankton. *Marine Biology* 116 (4), 689–702.
- Larson, E.T., Shanks, A.L., 1996. Consumption of marine snow by two species of juvenile mullet and its contribution to their growth. *Marine Ecology Progress Series* 130 (1–3), 19–28.
- Lee, B.-G., Fisher, N., 1993. Release rate of trace elements and protein from decomposing debris I. Phytoplankton debris. *Journal of Marine Research* 51, 391–421.
- Li, X., Logan, B.E., 1995. Size distributions and fractal properties of particles during a simulated phytoplankton bloom in a mesocosm. *Deep-Sea Research Part II* 42, 125–138.
- Logan, B.E., Wilkinson, D.B., 1990. Fractal geometry of marine snow and other biological aggregates. *Limnology and Oceanography* 35, 130–136.
- MacIntyre, S., Alldredge, A.L., Gotschalk, C.C., 1995. Accumulation of marine snow at density discontinuities in the water column. *Limnology and Oceanography* 40, 449–468.
- Mann, K.H., Lazier, J.R.N., 1991. *Dynamics of Marine Ecosystems: Biological-Physical Interactions in the Oceans*, Blackwell, Cambridge, 466pp.
- Martin, J.H., Knauer, G.A., Karl, D.M., Broenkow, W.W., 1987. VERTEX: carbon cycling in the Northeast Pacific. *Deep-Sea Research* 34, 267–285.
- Monaco, A., Courp, T., Heussner, S., Carbonne, J., Fowler, S.W., Deniaux, B., 1990. Seasonally and composition of particulate fluxes during ECOMARGE-1, western Gulf of Lions. *Continental Shelf Research* 10 (9–11), 959–987.
- O'Melia, C.R., 1978. Coagulation in wastewater treatment. In: Ives, K.J. (Ed.), *The Scientific Basis of Flocculation*. Sijthoff and Noordhoff, Alphen ad, Rijn, pp. 219–268.
- Parker, D.S., Kaufman, W.S., Jenkins, D., 1972. Floe breakup in turbulent flocculation processes. *Journal of the Sanitary Engineering Division, Proceedings of the American Society of Civil Engineers* 98 (SA1), 79–99.
- Passow, U., 2002. Transparent exopolymer particles (TEP) in aquatic environments. *Progress in Oceanography* 55, 287–333.
- Passow, U., Wassmann, P., 1994. On the trophic fate of *Phaeocystis Pouchetii* (Hariot). 4. The formation of marine snow by *P-Pouchetii*. *Marine Ecology—Progress Series* 104 (1–2), 153–161.
- Peinert, R., Miquel, J.-C., 1994. The significance of frontal processes for vertical particle fluxes: a case study in the Alboran Sea (SW Mediterranean Sea). *Journal of Marine Systems* 5 (3–5), 377–389.
- Peinert, R., Bathmann, U., Bodungen, B.V., Noji, T., 1987. The impact of grazing on spring phytoplankton growth and sedimentation in the Norwegian Current. *Mitt Geol-Palaontologie Institution, University of Hamburg* 62, 149–164.
- Ploug, H., Grossart, H.P., 1999. Bacterial production and respiration in suspended aggregates—a matter of the incubation method. *Aquatic Microbial Ecology* 20 (1), 21–29.
- Ploug, H., Grossart, H.P., 2000. Bacterial growth and grazing on diatom aggregates: Respiratory carbon turnover as a function of aggregate size and sinking velocity. *Limnology and Oceanography* 45 (7), 1467–1475.
- Pomeroy, L.R., Deibel, D., 1980. Aggregation of organic matter by pelagic tunicates. *Limnology and Oceanography* 25, 643–652.
- Ratmeyer, V., Wefer, G., 1996. A high resolution camera system (parca) for imaging particles in the ocean—system design and results from profiles and a three-month deployment. *Journal of Marine Research* 54 (3), 589–603.
- Riebesell, U., 1992. The formation of large marine snow and its sustained residence in surface waters. *Limnology and Oceanography* 37 (1), 63–76.
- Riebesell, U., Wolf-Gladrow, D.A., 1992. The relationship between physical aggregation of phytoplankton and particle flux: a numerical model. *Deep-Sea Research* 39 (7–8A), 1085–1102.
- Riser, C.W., Wassmann, P., Olli, K., Arashkevich, E., 2001. Production, retention and export of zooplankton faecal pellets on and off the Iberian shelf, north-west Spain. *Progress in Oceanography* 51 (2–4), 423–441.
- Ruiz, J., 1996. The role of turbulence in the sedimentation loss of pelagic aggregates from the mixed layer. *Journal of Marine Research* 54, 385–406.
- Ruiz, J., 1997. What generates daily cycles of marine snow? *Deep-Sea Research I* 44 (7), 1105–1126.
- Sancetta, C., Villareal, T., Falkowski, P., 1992. Massive fluxes of rhizosolenoid diatoms: a common occurrence? *Limnology and Oceanography* 36, 1452–1457.
- Sasaki, H., Hattori, H., Nishizawa, S., 1988. Downward flux of particulate organic matter and vertical distribution of calanoid copepods in the Oyashio Water in summer. *Deep-Sea Research* 35, 505–515.
- Scotto di Carlo, B., Ianora, A., Fresi, E., Hure, J., 1984. Vertical zonation patterns for Mediterranean copepods from the surface to 3000m at a fixed station in the Tyrrhenean Sea. *Journal of Plankton Research* 6 (6), 1031–1056.
- Shanks, A.L., Trent, J.D., 1980. Marine snow: sinking and potential role in vertical flux. *Deep-Sea Research* 27A, 137–143.
- Shanks, A.L., Walters, K., 1997. Holoplankton, meroplankton, and meiofauna associated with marine snow. *Marine Ecology Progress Series* 156, 75–86.

- Silver, M.W., Gowing, M.M., 1991. The 'particle' flux: origins and biological components. *Progress in Oceanography* 26, 75–113.
- Silver, M.W., Shanks, A.L., Trend, J.D., 1978. Marine snow: microplankton habitat and source of small-scale patchiness in pelagic populations. *Science* 201, 371–373.
- Silver, M.W., Gowing, M.M., Brownlee, D.C., Corliss, J.O., 1984. Ciliated protozoa associated with oceanic sinking detritus. *Nature* 309, 246–248.
- Smayda, T.R., 1970. The suspension and sinking of phytoplankton in the sea. *Oceanography and Marine Biology Annual Review* 8, 353–414.
- Smith, D.C., Simon, M., Alldredge, A.L., Azam, F., 1992. Intense hydrolytic enzyme activity on marine aggregates and implications for rapid particle dissolution. *Nature* 359, 139–142.
- Steinberg, D.K., 1995. Diet of copepods (*Scopelatum vorax*) associated with mesopelagic detritus (giant larvacean houses) in Monterey Bay, California. *Marine Biology* 122 (4), 571–584.
- Steinberg, D.K., Silver, M.W., Pilskaln, C.H., Coale, S.L., Paduan, J.B., 1994. Midwater zooplankton communities on pelagic detritus (giant larvacean houses) in Monterey Bay, California. *Limnology and Oceanography* 39 (7), 1606–1620.
- Steinberg, D.K., Silver, M.W., Pilskaln, C.H., 1997. Role of mesopelagic zooplankton in the community metabolism of giant larvacean house detritus in Monterey Bay, California, USA. *Marine Ecology—Progress Series* 147, 167–179.
- Stemmann, L., Gorsky, G., Marty, J.-C., Picheral, M., Miquel, J.-C., 2002. Four-year study of large-particle vertical distribution (0–1000m) in the NW Mediterranean in relation to hydrology, phytoplankton, and vertical flux. *Deep-Sea Research Part II* 49 (11), 2143–2162.
- Stemmann, L., Jackson, G.A., Gorsky, G., 2004. A vertical model of particle size distributions and fluxes in the midwater column that includes biological and physical processes—Part II: application to a three year survey in the NW Mediterranean Sea. *Deep-Sea Research Part I*, this issue (doi:10.1016/j.dsr.2004.03.002).
- Syvitski, J.P.M., Asprey, K.W., Leblanc, K.W.G., 1995. In situ characteristics of particles settling within a deep-water estuary. *Deep-Sea Research Part II* 42, 223–256.
- Takahashi, K., 1986. Seasonal fluxes of pelagic diatoms in the subarctic Pacific, 1982–1983. *Deep-Sea Research* 33, 1225–1251.
- Turley, C.M., Mackie, P.J., 1994. Biogeochemical significance of attached and free-living bacteria and the flux of particles in the NE Atlantic Ocean. *Marine Ecology—Progress Series* 115, 191–203.
- Turner, J.T., 2002. Zooplankton fecal pellets, marine snow and sinking phytoplankton blooms. *Aquatic Microbial Ecology* 27 (1), 57–102.
- Urrere, M.A., Knauer, G.A., 1981. Zooplankton fecal pellets fluxes and vertical transport of particulate organic matter in the pelagic environment. *Journal of Plankton Research* 3, 369–387.
- Walsh, I.D., Gardner, W.D., Richardson, M.J., Chung, S.P., Plattner, C.A., Asper, V.L., 1997. Particle dynamics as controlled by the flow field of the eastern equatorial Pacific. *Deep-Sea Research Part II* 44 (9–10), 2025–2047.
- Yamaguchi, A., Watanabe, Y., Ishida, H., Harimoto, T., Furusawa, K., Suzuki, S., Ishizaka, J., Ikeda, T., Takahashi, M., 2002. Community and trophic structures of pelagic copepods down to greater depths in the western subarctic Pacific (WEST-COSMIC). *Deep-Sea Research Part I* 49, 1007–1025.