REVIEW

Zooplankton fecal pellets, marine snow and sinking phytoplankton blooms

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ABSTRACT: Zooplankton fecal pellets have long been thought to be a dominant component of the sedimentary flux in marine and freshwater ecosystems, but that view is changing. The last 2 decades have seen publication of >500 studies using sediment traps, which reveal that zooplankton fecal pellets often constitute only a minor or variable proportion of the sedimentary flux. Substantial proportions of this flux are from organic aggregates ('marine snow') of various origins, including phytoplankton blooms, which sediment directly to the benthos. It now appears that mainly large fecal pellets of macrozooplankton and fish are involved in the sedimentary flux. Smaller fecal pellets of microzooplankton and small mesozooplankton are mostly recycled or repackaged in the water column by microbial decomposition and coprophagy, contributing more to processes in the water column than flux to the benthos. The relative contributions of fecal pellets, marine snow and sinking phytoplankton to the vertical flux and recycling of materials in the water column are highly variable, dependent upon multiple interacting factors. These include variations in productivity, biomass, size spectra and composition of communities in the overlying water columns, and trophic interactions between various components of the plankton and nekton communities at various times, locations and depths. Other factors include differences in sinking rates, sizes, composition and pollutant contents of fecal pellets produced by various sizes of zooplankters, and zooplankton feeding-fecal pellet production interactions in relation to upwelling and El Niño periods, seasonal life-history-related zooplankton vertical migrations and long-term oceanographic regime shifts. There are also suggestions from the geological record that zooplankton fecal pellets may have been important in ancient oceans. The ecological roles of marine snow and phytoplankton aggregates in sedimentary flux also depend on a variety of interacting factors, including sources of origin, degrees of microbial colonization, depth distributions, sinking rates and ingestibility by consumers. Perhaps the major reversal of the previous paradigm on the role of fecal pellets in the sedimentary flux over the last 2 decades has been the realization that much, if not most, of the organic rain from the epipelagic to the abyss is due to direct sedimentation of aggregated phytoplankton, which does not appear to undergo consumption in the water column, and which may be related to seasonality of surface production cycles. Further, there is emerging evidence for benthic responses to sedimented phytodetritus, including apparent synchrony of reproductive cycles of some deep-sea benthic animals with seasonality of sinking of surface blooms. Such episodic input of surface phytodetritus may help resolve apparent discrepancies between average supply and demand of organic matter required to maintain benthic community metabolism. The sedimentary flux of fecal pellets, marine snow and sinking phytoplankton is an important component of the biological pump that not only transports and recycles materials in the sea but also may help scrub greenhouse gases from the atmosphere.

KEY WORDS: Zooplankton fecal pellets · Marine snow · Sinking phytoplankton blooms · Sedimentary flux

INTRODUCTION

The ocean is aphotic and therefore aphotosynthetic below the upper few tens to hundreds of meters, yet there is animal and microbial life throughout, including down to the greatest depths. Except for communities around hydrothermal vents, which produce organic matter by bacterial chemosynthesis, the

organic matter required to maintain deep-water pelagic and benthic ecosystems must ultimately derive from the photosynthetic system in the epipelagic. This has been recognized at least since Agassiz (1888) proposed that '…deep-sea organisms are nourished by a "rain" of organic detritus from overlying surface waters.' Since sedimenting organic particles are subject to a gauntlet of microbial degradation, it has long been thought that fast-sinking materials such as zooplankton fecal pellets are primary agents of the downward flux in the sea.

Turner & Ferrante (1979) reviewed literature on transport potential, nutritional content, recycling by decomposition and coprophagy, and pollutant content of zooplankton fecal pellets in marine and freshwater ecosystems. During the intervening 2 decades, it has become apparent that zooplankton fecal pellets remain important agents of vertical flux under some circumstances, but that in other cases, most fecal pellets are reprocessed in the water column by microbial decomposition or coprophagy. Further, in many instances, most of the vertical flux is due not to fecal pellets, but to marine snow or sedimenting phytoplankton blooms that descend to the benthos without entering water-column consumer food webs. It is also apparent that the dynamics of fecal pellets, marine snow and sinking phytoplankton blooms are important not only in the flux to the benthos but also to pelagic communities throughout the water column.

Removal of carbon dioxide from the atmosphere, and its processing by the photosynthetic system in the upper ocean, with subsequent descent and sequestering in the deep sea may be important aspects of the 'biological pump' (Longhurst & Harrison 1988) mitigating anthropogenic increases in greenhouse gases (Longhurst 1991, Sarmiento 1991). The sedimentary particulate flux from varying combinations of sinking fecal pellets, marine snow and phytoplankton is generally considered much more important than the active downward flux due to vertical migrations of zooplankton and nekton (Longhurst & Harrison 1988, Longhurst et al. 1989, 1990, Longhurst & Williams 1992), although there may be exceptions to this (Bradford-Grieve et al. 2001, Hays et al. 2001), and vertically migrating zooplankton may contribute substantially to the flux of dissolved organics and inorganics (Dam et al. 1995, Hays et al. 1997, Zhang & Dam 1997, Steinberg et al. 2000, Al-Mutairi & Landry 2001). Important reviews and analyses of vertical flux processes have appeared over the last 2 decades (Angel 1984, Smetacek 1984, Hargrave 1985, Fowler & Knauer 1986, Alldredge & Silver 1988, Michaels & Silver 1988, Angel 1989, Bishop 1989, Bruland et al. 1989, Legendre & Gosselin 1989, Longhurst & Harrison 1989, Peinert et al. 1989, Toggweiler 1989, Wefer 1989, Banse 1990, Fowler

1991, Longhurst 1991, 2000, Noji 1991, Silver & Gowing 1991, Wassmann 1991a, 1998, Fortier et al. 1994, Wassmann 1994, Legendre & Le Fèvre 1995, Thingstad & Rassoulzadegan 1995, Bathmann 1996, Kiørboe 1996, Legendre & Rassoulzadegan 1996, Wassmann et al. 1996a,b, Butterfield 1997, Lampitt & Antia 1997, Azam 1998, Legendre & Michaud 1998, Falkowski et al. 2000). The present review will update and extend that of Turner & Ferrante (1979) to present the emerging view that zooplankton fecal pellets are often less important in the sedimentary flux than marine snow and sinking phytoplankton blooms.

IMPORTANCE OF ZOOPLANKTON FECAL PELLETS

'Indeed, this concern for bioenergetics, energy flow, and processes has been so pervasive that biological oceanography now suffers from an agricultural mentality that would have us believe that bioenergetics is the only valid subject of investigation. At times this narrow outlook has even degenerated into the peculiar belief that the waste products of an animal are somehow more important than the animal itself.'

Hamner (1985) p. 417

Much of the early evidence for the importance of fecal pellets in the sedimentary flux came from studies employing sediment traps. Turner & Ferrante (1979) cited only the first few of the flurry of studies, beginning mainly in the mid-1970s, using sediment traps (Moore 1931, Schrader 1971, Steele & Baird 1972, Ansell 1974, Wiebe et al. 1976, Soutar et al. 1977, Honjo 1978, Spencer et al. 1978a,b, Knauer et al. 1979) or large-volume filtration systems (Bishop et al. 1977, 1978) to quantify vertical flux in the open sea, as well as in coastal waters (Hargrave & Taguchi 1978, Smetacek et al. 1978, Taguchi & Hargrave 1978). Publications (>500) from most sediment-trap studies appeared after the Turner & Ferrante (1979) review (Table 1).

Many sediment-trap studies have revealed that zooplankton fecal pellets or fecal matter are important components of rapid particulate flux in the sea. Perhaps the most dramatic evidence for this was the discovery that radionuclides from the Chernobyl disaster were present in zooplankton fecal pellets in sediment traps at 200 m depth in the Mediterranean an average of 7 d after peak radioactivity was delivered to the surface and <2 wk after the explosion (Fowler et al. 1987). On the basis of theoretical considerations, Jumars et al. (1989) have also concluded that the principal pathway of dissolved organic carbon from phytoplankton back to bacterioplankton (i.e., 'closing the microbial loop') is through rapid release from zooplankton fecal pellets.

Table 1. Publications from marine studies with sediment traps, particle interceptor traps and large-volume filtration systems appearing since the review of Turner & Ferrante (1979)

1979: Crisp et al., Hargrave & Burns, Hinga et al., Larrance et al., Rowe & Gardner

1980: Bishop et al., Brewer et al., Gardner a,b, Honjo, Honjo et al., Iseki et al., Tanoue & Handa, Volkman et al., Wakeham et al.

1981: Blomqvist & Kofoed, Chester & Larrance, Deuser et al. a,b, Dunbar & Berger, Dymond et al., Fellows et al., Iseki, Knauer & Martin, Landing & Feely, Lorenzen et al., Sasaki & Nishizawa, Syvitski & Murray, Takahashi & Honjo, Thunell & Honjo, Urrère & Knauer

1982: Ducklow et al., Feely et al., Gagosian et al., Honjo, Honjo et al. a,b, Lee & Cronin, Repeta & Gagosian, Staresinic et al., Taguchi a,b, Wefer et al.

1983: Burns & Villeneuve, De Baar et al., Deuser et al. a,b, Falkowski et al., Fowler & Fisher, Fowler et al., Gagosian et al. a,b, Gardner et al., Gowing & Silver, Gulliksen, Lee et al., Livingston & Anderson, Lorenzen & Welschmeyer, Lorenzen et al. a,b, Small et al., Staresinic et al., Wassmann

1984: Andrews et al., Betzer et al. a,b, Bishop & Marra, Cowen & Silver, Davies & Payne, Dunbar, Gardner et al., Ittekkot et al., Izdar et al., Jickells et al., Karl & Knauer a,b, Karl et al., Knauer et al., Lee & Cronin, Murphy & Dymond, Repeta & Gagosian, Silver et al., Tett, Wakeham et al., Wassmann, Welschmeyer et al.

1985: Altabet & Deuser, Bacon et al., Baker et al., Bé et al., Burns et al., Cadée, Cowen & Bruland, Deming, Deming & Colwell, Downs & Lorenzen, Ducklow et al., Dymond & Lyle, Gowing & Silver, Noriki et al. a,b, Schnack, Wassmann, Welschmeyer & Lorenzen

1986: Bishop & Joyce, Bishop et al. a,b, Bodungen, Bodungen et al., Cadée, Deuser, Emerson et al., Feeley et al., Fowler et al., Harada & Tsunogai, Kajihara et al., Knap et al., Larsson et al., Matsueda & Handa, Müller et al., Noji et al., Noriki & Tsunogai, Peinert, Pisias et al., Simoneit et al., Skjoldal & Wassmann, Takahashi, Taylor et al., Tsunogai et al. a,b, Wassmann, Wassmann et al.

1987: Asper, Atkinson & Wacasey, Bathmann et al., Benli, Bernstein et al., Bodungen et al., Broman et al., Buesseler et al., Carey, Coale & Bruland, Deuser, Emerson & Roff, Fowler et al., Harding et al., Heussner et al., Honjo et al., Hsiao, Izdar et al., Kempe & Nies, Kempe et al., Liebezeit, Martin et al., Michaelis et al., Nelson et al., Peinert et al., Pilskaln & Honjo, Richardson & Hollister, Small et al., Smith, Smith et al., Takahashi a,b,c, Tambiev, Tanoue & Handa, Tsunogai & Noriki

1988: Altabet, Baker et al., Bathmann, Biscaye et al., Bodungen et al., Deuser et al., Dymond & Collier, Emerson & Hedges, Fischer et al., Fisher et al., Hedges et al. a,b, Heussner et al., Honjo & Doherty, Honjo et al., Karl et al., Kempe & Jennerjahn, Kusakabe et al., Laws et al., Lee et al., Maita et al., Moore & Dymond, Morris et al., Naes et al., Sancetta & Calvert, Sasaki et al., Walsh et al. a,b, Wefer et al.

1989: Altabet a,b, Bhosle et al., Costello et al., Deuser & Ross, Faganeli, Fleeger et al., Graf, Hargrave et al., Laws et al., Longhurst et al., Lutter et al., Nair et al., Nöthig & Bodungen, Pedros-Alio et al., Riebesell, Sancetta a,b, Small et al., Smith, Smith et al. a,b, Takahashi, Taylor, Tremblay et al., Wakeham & Lee, Wassmann

1990: Banse, Bathmann et al., Berger & Wefer, Bernstein et al., Buesseler et al., Coale, Deuser et al., Gadel et al., Grimalt et al., Gundersen & Wassmann, Hay et al., Huh et al., Jahnke et al., Knauer et al., Longhurst et al., Meinecke & Wefer, Michaels et al., Monaco et al. a,b, Montgomery et al., Novitsky, Peterson & Dam, Reemtsma et al., Rowe et al., Sakugawa et al., Takahashi et al., Vangriesheim & Khripounoff, Wakefield & Smith, Wassmann a,b, Wassmann et al., Wefer et al.

1991: Abelmann & Gersonde, Altabet et al., Bathmann et al.,

Bodungen et al., Buesseler, Fabry & Deuser, Fowler et al., Hebbeln & Wefer, Ittekkot et al., Karl & Knauer, Karl et al., Knauer, Leventer, Posedel & Faganeli, Proctor & Fuhrman, Rutgers van der Loeff & Berger, Sancetta et al., Sautter & Thunell, Taylor & Karl, Tsunogai & Noriki, Voss, Wassmann a,b, Wassmann et al., Wefer & Fischer

1992: Abelmann a,b, Asper et al., Ayukai & Hattori, Bianchi et al., Bishop et al., Cadée et al., Cowen, González, Honjo et al., Lampitt, Landry et al., Lee et al., Lohrenz et al., Puàkarić et al., Rau et al., Reimers et al., Simon et al., Small & Ellis, Smith et al., Waite et al.

1993: Bauerfeind et al., Boltovskoy et al., Gardner et al., Gowing, Haake et al., Head & Horne, Honjo & Manganini, Lampitt et al. a,b, Lenz et al., Lochte et al., Martin et al., Miquel et al., Noji et al., Passow & Peinert, Passow et al., Pfannkuche & Lochte, Reinfelder et al., Wakeham et al., Weeks et al.

1994: Anderson et al., Biscaye & Anderson, Carlson et al., Falkowski et al., González & Smetacek, González et al. a,b, Hargrave et al., Head et al., Karl & Tilbrook, Kiørboe et al., Landry et al. a,b, Lane et al., Marty et al., Michaels et al. a,b, Miquel et al., Peinert & Miquel, Rowe et al., Sayles et al., Smith et al., Thunell et al. a,b, Turley & Mackie, Walsh, Wassmann et al.

1995: Bodungen et al., Buck & Newton, Buesseler et al., Deuser et al., Heiskanen, Heiskanen & Leppänen, Honjo et al., Lampitt et al., Landry et al., Luo et al., Riebesell et al., Turley & Mackie, van der Wal et al.

1996: Andreassen et al., Bacon et al., Dymond & Collier, Etcheber et al., Fischer et al., Jickells et al., Karl & Lukas, Karl et al., Keck & Wassmann, Kiørboe et al., Michaels & Knap, Murray et al., Osinga et al., Pilskaln et al., Reigstad & Wassmann, Rivkin et al., Smith et al., Witte

1997: Berelson et al., Christian et al., Conte, Curry & Ostermann, Diercks & Asper, Dortch et al., Duineveld et al., Emerson et al., François & Bacon, Hansell et al. a,b, Honjo, Honjo & Weller, Karl et al., Koning et al., Lampitt & Antia, Lundsgaard & Olesen, Rodier & Le Borgne, Roman & Gauzens, Thunell, Valdes et al., Wakeham et al.

1998: Andreassen & Wassmann, Baldwin et al., Beaulieu & Smith, Bode et al., Carroll et al., Conte et al., Druffel et al., Dunbar et al., Heiskanen et al., Lazzari et al., Lee et al., Shaw et al., Sherrell et al., Silver et al. a,b, Smith & Druffel, Smith et al., Steinberg et al., Thunell a,b

1999: Altabet et al., Antia et al., Asper & Smith, Beaufort & Heussner, Bishop et al., Boyd et al., Cailliau et al., Charette et al., Danovaro et al., Druffel & Robison, Heussner et al., Honjo et al., Noji et al. a,b, Peña et al., Pfannkuche et al., Radakovitch & Heussner, Scharek et al., Smith & Kaufmann, Thibault et al., Urban-Rich et al., Viitasalo et al., Wassmann et al., Wong et al., Wu et al.

2000: Alleman et al., Andruleit, Broerse et al. a,b, Collier et al., Conan & Brummer, Danovaro et al. a,b,c, Duineveld et al., Fischer et al., Gardner et al., Giraudeau et al., Goericke et al., González et al. a,b, Gust & Kozerski, Gyldenfeldt et al., Haidar et al., Hebbeln, Hebbeln et al., Honjo et al., Kemp et al., Kincaid et al., Lampitt et al., Loh & Bauer, Prahl et al., Reigstad et al., Rixen et al., N. Romero et al., O. E. Romero et al., Roy et al., Sempéré et al., Stavrakakis et al., Sumida et al., Thunell et al., Waite et al., Waniek et al., Wassmann et al., Young & Ziveri, Ziveri & Thunell, Ziveri et al., Zonneveld & Brummer

2001: Antia et al., Bauerfeind et al., Benitez-Nelson et al., Christiansen et al., Conte et al., Dadou et al., Gowing et al., Hamm et al., Harada et al., Harris et al., Hedges et al., Herman et al., Hernes et al., Hidaka et al., King & Howard, McCave et al., Müller & Fischer, Nodder & Northcote, Nodder & Waite, Olesen, Passow et al., Prahl et al., Romero et al., Scholten et al., Smith et al., Steinberg et al., Wollast & Chou, Zeldis

The relative importance of zooplankton fecal pellets in sedimentary flux and water-column recycling depends on various factors. These include fecal pellet sinking rates, chemical and particulate contents (including pollutants), fate of fecal pellets in terms of microbial decomposition or coprophagy and organisms producing (and therefore sizes of) fecal pellets, and the possible importance of zooplankton fecal pellets in oceans of the geological past. These will be reviewed before addressing the variable contribution of zooplankton fecal pellets to the sedimentary flux in the present-day ocean and the emerging view that much of the sedimentary flux in the ocean is due to marine snow and direct sedimentation of phytoplankton blooms.

Fecal pellet sinking rates

Fecal pellets sink rapidly. All published sinking rates for fecal pellets reviewed by Turner & Ferrante (1979) were for fecal pellets of unknown origin or those produced by copepods or euphausiids. These rates ranged from <10 to typically hundreds of meters per day. Subsequent sinking rate data for fecal pellets of various other animals (Table 2) considerably broaden the range of sinking rates.

Fecal pellets of salps and pteropods generally sink from hundreds to thousands of meters per day, whereas less dense, more flaky pellets of doliolids (Bruland & Silver 1981, Madin 1982, Deibel 1990) or

discarded houses and fecal pellets of the appendicularian *Oikopleura dioica* (Gorsky et al. 1984) sink only tens to hundreds of meters per day.

The high rates of sinking of fecal pellets from salps and pteropods appear related to the larger volumes of these pellets. Due to the widespread abundance of salps and pteropods in oceanic waters, the high organic content of their fecal pellets (Bruland & Silver 1981, Madin 1982) and the rapid defecation rates of salps (Madin 1982), fecal pellets of these gelatinous zooplankters may contribute disproportionately to the vertical flux to the benthos.

A mass occurrence of salps was recorded by Wiebe et al. (1979) in the northwest Atlantic. *Salpa aspera* performed diel vertical migrations over distances of 800 m, resulting in evacuation of 85 to 90% of the zooplankton biomass from the upper 500 m during daylight. Since salps feed upon small particles in the epipelagic, such a migration would have removed massive amounts of primary production to depth. Salp fecal pellet production and mortality during this event were estimated to contribute over 100% of the daily energy requirements of the deep-sea benthos. Other mass occurrences of salps that produced episodic fecal pellet fluxes in the benthos were recorded by Bathmann (1988), Morris et al. (1988), Pfannkuche & Lochte (1993), and Perissinotto & Pakhomov (1998).

Variations in consumer diets can affect sinking rates of resulting fecal pellets. Small et al. (1979) reported that natural copepod fecal pellets sank at higher and more variable rates than those produced on laboratory phytoplankton diets. This was presumably due to variations in fecal pellet contents and densities, since pellets produced from diets of cultured phytoplankton mixed with sediment sank faster than those produced on phytoplankton diets alone. Small et al. (1979) recommended against extrapolating measurements of sinking rates made on pellets produced on laboratory diets to those of fecal pellets produced on natural diets. For natural fecal pellets of both small copepods and the large copepod *Anomalocera patersoni*, collected under calm sea conditions, there was an increase in sinking rates with increases in fecal pellet volumes, but there was no such relation for fecal pellets collected in rough seas. Bienfang (1980) found no relationship between fecal pellet sinking rates and volumes for pellets of the copepod *Calanus finmarchicus* produced on

Table 2. Sinking rates of zooplankton fecal pellets, marine snow and phytodetritus

Particles	Sinking rate (m d^{-1})	Source
Fecal pellets of:		
Copepods	5–220	Smayda (1971), Turner (1977), Honjo & Roman (1978), Paffenhöfer & Knowles (1979), Small et al. (1979), Bienfang (1980), Yoon et al. (2001)
Euphausiids	16–862	Fowler & Small (1972), Youngbluth et al. (1989), Yoon et al. (2001)
Doliolids	41–504	Bruland & Silver (1981), Deibel (1990)
Appendicularians	25–166	Gorsky et al. (1984)
Chaetognaths	27–1313	Dilling & Alldredge (1983)
Pteropods	120–1800	Bruland & Silver (1981), Yoon et al. (2001)
Heteropods	120–646	Yoon et al. (2001)
Salps	43–2700	Madin (1982), Yoon et al. (2001)
Marine snow	16–368	Alldredge (1979), Shanks & Trent (1980), Silver & Alldredge (1981), Taguchi (1982b), Gorsky et al. (1984), Asper (1987), Alldredge & Gotschalk (1988)
Phytodetritus	100–150	Billett et al. (1983), Lampitt (1985)

diets of diatoms versus flagellates but found that the fecal pellets produced on the diatom diets sank significantly faster. Bienfang (1980) suggested that this difference was due to higher densities of pellets containing remains of diatom frustules. Komar et al. (1981) concluded that a modified version of the Stokes equation gave a reasonable approximation of measured rates of Small et al. (1979) for sinking rates of cylindrical fecal pellets of copepods and euphausiids, and that most variations in sinking rates of such fecal pellets were due to diet-related pellet densities. Indeed, euphausiid fecal pellets in the Antarctic were larger and sank faster when produced on diets dominated by diatoms than on non-diatom phytoplankton (Cadée et al. 1992, González 1992a). Deibel (1990) discovered that doliolid fecal pellets produced on diets of natural particulates did not sink but that pellets produced on diets of microflagellate, dinoflagellate and diatom cultures sank at rates of 59 to 405 m d^{-1}. Dilling & Alldredge (1993) concluded that while chaetognath fecal pellets were large (approximately 1 to 4 mm long), due to their contents (copepod parts) pellet density was low, and with sinking rates 5 to 10 times slower than those of comparably sized herbivores such as salps and doliolids. Urban et al. (1993a) reported that densities of fecal pellets of a larvacean and a copepod varied with season, depending on types of phytoplankton ingested and the extent to which remains were compacted in pellets. Frangoulis et al. (2001) found that sinking rates of copepod fecal pellets decreased from 100 to 70 m d^{-1} during the transition from diatom- to *Phaeocystis*-dominated spring blooms, and suggested that the lower sinking rates were due to decreases in pellet density and volume when feeding on *Phaeocystis* sp.

Sinking rates of copepod fecal pellets vary with pellet size, and pellet size varies with food concentration, food composition and ingestion rate. Dagg & Walser (1986) found that pellet size increased with increasing food concentration up to chlorophyll levels of 3 µg l^{-1}, above which size remained constant. Below this level, ingestion and defecation were balanced so that copepod guts did not fill and fecal pellet size was smaller, but above this level, copepod guts did fill, producing fecal pellets of maximum size. Dagg & Walser (1986) concluded that fecal pellets produced by copepods under low food conditions would likely sink at lower rates than pellets produced by the same copepods at higher food levels. Ayukai & Nishizawa (1986) also reported that pellet sizes were smaller at lower food concentrations and that the ratio of defecated volume to ingested volume was higher with a dinoflagellate than a diatom diet. Tsuda & Nemoto (1990) found that ingestion rates, fecal pellet production rates and fecal pellet size increased with increasing food

concentrations. Feinberg & Dam (1998) reported that various characteristics (length, width, density, calculated sinking rate) of fecal pellets of the copepod *Acartia tonsa* were significantly different with different laboratory diets of diatoms, photosynthetic and heterotrophic flagellates, dinoflagellates and ciliates. Sinking rates of fecal pellets from other copepods vary with food conditions (Butler & Dam 1994) and size of the fecal pellet producer (Harris 1994). Rates of sinking of salp fecal pellets can vary with the decomposition state of the pellets (Yoon et al. 1996). Dam & Feinberg (2001) found significant relationships between fecal pellet sinking rate and weight of fecal pellet producers, and between fecal pellet sinking rate and volume.

Silver & Bruland (1981) and Bruland & Silver (1981) concluded that diets of salps and pteropods in the California Current differed considerably, and that this would affect the vertical chemical fluxes resulting from their fecal pellets. Salps fed mainly upon small phytoplankton, so when coccolithophorids were abundant, their fecal pellets presumably contributed to enhanced calcite flux. Pteropods in the same area fed primarily upon larger phytoplankton, especially diatoms, so their fecal pellets would be expected to facilitate enhanced silicate flux.

In an exaggerated example of the effects of ingested mineral particles on fecal pellet sinking rates, Taghon et al. (1984) and Komar & Taghon (1985) found that fecal pellets of a deposit-feeding polychaete were large (up to 9.7 mm long), had high density due to ingested sediment (1.086 to 1.282 g cm^{-3}) and high sinking rates (2618 to 5132 m d^{-1}). Similar processes might also apply to planktonic organisms, since abundant fine-grained lithogenic particles were filtered by *Oikopleura dioica* (Dagg et al. 1996) and by copepods (Turner 1984a,b, 1987) in the plume of the Mississippi River.

Fecal pellet contents

Contents of fecal pellets have long been used to examine the diets of the zooplankters that produce them (Fig. 1). These analyses include studies of copepods (Turner 1977, 1978, 1984a,b,c, 1985, 1986a,b, 1987, 1991, Turner & Anderson 1983, Bathmann et al. 1990a,b, Voss 1991, Urban et al. 1992, 1993b, González et al. 1994a,b), euphausiids grazing on epontic (under-ice) algae (O'Brien 1987, González et al. 1994a) and protists (Buck & Newton 1995).

Levels of photosynthetic pigments and phaeopigments, and other chemicals such as carbon, nitrogen, phosphorus and radiolabeled compounds in fecal pellets have also been used to examine patterns of zooplankton feeding and fecal pellet decomposition
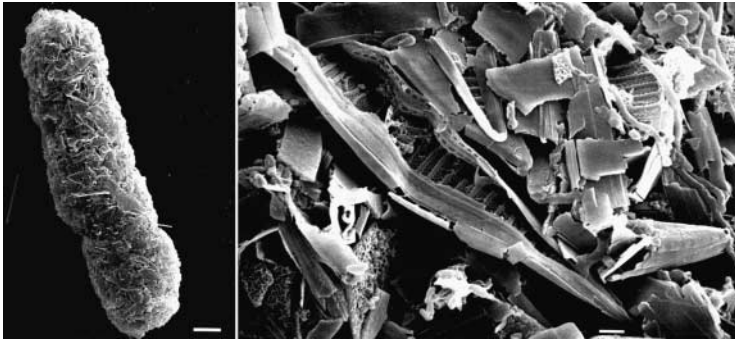
Fig. 1. Fecal pellet of the copepod *Acartia tonsa* produced while feeding on the toxic diatom *Pseudo-nitzschia multiseries*. Photograph at left shows entire fecal pellet; line scale = 10 µm. Photograph at right is high magnification, showing fragments of broken diatoms; scale bar = 1 µm

(Honjo & Roman 1978, Turner 1979, Welschmeyer et al. 1984, Downs & Lorenzen 1985, Welschmeyer & Lorenzen 1985, Vernet & Lorenzen 1986, Bathmann & Liebezeit 1987, Dagg & Walser 1987, Morales 1987, Head 1988, Head et al. 1988, Sapozhnikov & Pasternak 1988, Dagg et al. 1989, Nelson 1989, Ayukai 1990, González & Biddanda 1990, Roy & Poulet 1990, Head 1992a,b, Head & Harris 1992, 1996, Lee & Fisher 1992, Head & Horne 1993, Otsuki et al. 1993, Pfannkuche & Lochte 1993, Anderson 1994, Butler & Dam 1994, Harris 1994, Landry et al. 1994a,b, Madin et al. 1997, Urban-Rich et al. 1998, McLeroy-Etheridge & McManus 1999, Thibault et al. 1999, Goericke et al. 2000, Hayashi et al. 2001). Altabet & Small (1990) found that nitrogen isotope ratios in zooplankton fecal pellets indicated that grazers were important modifiers of nitrogen contents of particles sinking in the sea. Copepod fecal pellets can also be highly concentrated sources of dimethylsulfoniopropionate (DMSP) (Kwint et al. 1996, Tang 2001) and may be important in the vertical flux of this compound (Daly & DiTullio 1996).

The feeding ecology of various zooplankters has been related to rates of production, size, volume and enzymatic activity of fecal pellets (Clarke et al. 1988, Butler & Dam 1994, Harris 1994, Paffenhöfer 1994, Bochdansky et al. 1995, Dagg 1995, Carlotti et al. 1997, Nejstgaard et al. 1997, Rey et al. 1999, Thibault et al. 1999, Huskin et al. 2000), and sizes of fecal pellets have been examined in relation to sizes of fecal pellet producers (Uye & Kaname 1994).

There have been several reports of intact or even live phytoplankton cells in fecal pellets. Johnson et al. (1982) found intact *Synechococcus* cells in *Calanus* sp. fecal pellets, and ultrastructural studies revealed that the cells were apparently undigested. Pfannkuche & Lochte (1993) found apparently undigested chlorophyll-bearing cyanobacteria cells in salp feces. Conversely, Silver & Bruland (1981) observed many cocco-

lithophorid and diatom cells in fecal pellets of salps and pteropods that appeared intact based upon scanning electron microscopy of external morphology, but transmission electron microscopy revealed that internal protoplasm had been digested. Cells that appear to be identical to the aphotic zone 'olive-green cells' described by Fournier (1970, 1971) have been found in fecal pellets of salps and pteropods by Silver & Bruland (1981) and bathypelagic marine snow (Silver & Alldredge 1981). These were suggested to be waste products from either partial degradation of algae ingested by herbivores, cells that had undergone autolysis, egested vacuolar residues of protozoans or fecal pellets of microzooplankton, which had been eaten by consumers, evacuated in fecal pellets and then after subsequent fecal pellet sinking and degradation were released back into the water column at depth. The finding of photosynthetically competent phytoplankton cells from 1000 m prompted Platt et al. (1983) to suggest that the cells had reached depth after surviving grazer gut passage and fecal pellet sinking and decomposition.

The existence of viable phytoplankton cells in euphausiid fecal pellets was confirmed by Fowler & Fisher (1983). Fecal pellets from sediment traps as well as those produced by euphausiids grazing on laboratory diets contained live cells, mostly diatoms. Viability was confirmed by growth of cells both in fecal pellets and subsequently in unenriched seawater. In some cases, cells had survived in natural fecal pellets for up to 10 d.

Bathmann & Liebezeit (1986) found that many fecal pellets produced by copepods during a declining spring phytoplankton bloom in the Baltic contained high levels of chlorophyll *a* (chl *a*) but low levels of phaeopigments, indicating that pellets contained undigested cells. Scanning electron microscopy of these fecal pellets confirmed that they contained abundant intact diatom cells. As the bloom became terminated, chl *a* and intact diatoms in copepod fecal pellets progressively declined.

The lipid, amino acid and fatty acid contents of fecal pellets of copepods, euphausiids and other consumers can differ with changes in the levels of these compounds in ingested food or with fecal pellet age (Tanoue et al. 1982, Prahl et al. 1984a,b, 1985, Tanoue 1985a,b, Corner et al. 1986, Matsueda et al. 1986, Neale et al. 1986, Poulet et al. 1986, Tanoue & Hara 1986, Bradshaw et al. 1989, Wakeham & Lee 1989, Roy & Poulet 1990, Claustre et al. 1992, Marty et al. 1994, Yoon et al. 1996, Hamm et al. 2001). Fecal pellets of the pelagic crab *Pleuroncodes planipes* accounted for a

significant portion of the lipids collected in sediment traps deployed over the upper 1500 m in the equatorial North Pacific (Wakeham & Canuel 1986).

Fecal pellets and pollutants

Anthropogenic compounds showing elevated concentrations in fecal pellets or other sedimented materials (in addition to references in Turner & Ferrante [1979] for trace metals, radionuclides, chlorinated hydrocarbons and petroleum hydrocarbons) include polycyclic aromatic hydrocarbons (Prahl & Carpenter 1979), chlorinated hydrocarbons (Osterroht & Smetacek 1980, Sleeter & Butler 1982, Burns et al. 1985, Fowler et al. 1986, Harding 1986, Knap et al. 1986), petroleum hydrocarbons (Burns et al. 1985, Broman et al. 1987), fly-ash particles from coal-burning power plants (Deuser et al. 1983b), metals (Cowen & Bruland 1985, Krishnaswami et al. 1985, Noriki et al. 1985a,b, Fisher et al. 1991, Reinfelder & Fisher 1991, Nott & Nicolaidou 1996), transuranics (Fowler et al. 1983, Gorsky et al. 1984, Reinfelder & Fisher 1991, Reinfelder et al. 1993, Lee & Fisher 1994) and radionuclides (Fowler et al. 1983, 1987, Livingston & Anderson 1983, Bacon et al. 1985, Krishnaswami et al. 1985, Harada & Tsunogai 1986, Buessler et al. 1987, Kempe & Nies 1987, Kempe et al. 1987, Fisher et al. 1988, Kusakabe et al. 1988, Moore & Dymond 1988, Reinfelder et al. 1993).

The Chernobyl nuclear power plant accident on 26 April 1986 provided a serendipitous 'tracer experiment' for measuring vertical flux of radionuclides into the deep sea at 3 distant European locations (Bacon 1987). Fowler et al. (1987) recorded peaks of the signature radionuclides [141]Ce and [144]Ce from Chernobyl in zooplankton fecal pellets in time-series sediment traps at 200 m in the Mediterranean off Corsica from 8 to 15 May, within a few days of delivery of these radionuclides to the surface by a pulse of rainfall on 4 to 5 May. The sediment traps had been deployed prior to the Chernobyl event, and their particulates were primarily (>70%) composed of zooplankton fecal pellets in the size range of those produced by copepods. Kempe & Nies (1987) and Kempe et al. (1987) also recorded Chernobyl radionuclides within 10 d in sediment traps already in place at 222 m depth in the North Sea off Norway. This was during the time of the spring diatom bloom. Chernobyl radionuclides were also recorded in sediment traps deployed in the Black Sea prior to the accident (Buessler et al. 1987, Kempe et al. 1987). Radionuclides arrived at a depth of 1071 m over the course of the 2 months following the accident, during the time of the normal summer bloom of the coccolithophorid

Emiliania huxleyi. Kusakabe et al. (1988) also recorded Chernobyl radionuclides at depths of 110 to 780 m in June and July of 1986 in the North Pacific and Bering Sea, indicating long-distance transport over several months. Levels of Chernobyl radionuclides in sediment traps in the Black Sea continued to decline throughout the fall and winter of 1986, and by a year after the explosion were undetectable (Buesseler et al. 1990). The Chernobyl episode clearly showed that biologically mediated vertical flux mechanisms in the sea can deliver pollutants to depth with previously unappreciated rapidity.

Fate of fecal pellets

'Utilization of fecal particles would appear to be a race between microorganisms and coprophages, both working against the effects of gravity on the falling particles.'

Pomeroy et al. (1984) p. 434

There is increasing evidence that many zooplankton fecal pellets are recycled in the water column through microbial decomposition and coprophagy. Urban-Rich et al. (1999) compared potential fecal pellet carbon flux, determined from fecal pellet production rates, fecal pellet carbon and zooplankton abundance, with actual levels of carbon flux due to zooplankton fecal pellets recovered from sediment traps off Norway (see Wassmann et al. 1999). Potential fecal pellet carbon flux was estimated to be 2 to as much as >100% of the measured fecal pellet carbon flux in the upper 200 m, but recovery of fecal pellets in sediment traps, which amounted to only 5 to 35% of total carbon flux, suggested that substantial recycling of fecal pellets was occurring in surface waters. Using a similar approach, Viitasalo et al. (1999) calculated that >99% of potential copepod fecal pellet production in the Baltic was recycled in the upper water column, although this varied somewhat with season, location, composition of the zooplankton community and turbulence. Much of the loss of fecal pellet carbon in the water column appears to be through release of dissolved organic carbon from fecal pellets during their descent (Noji et al. 1999a, Urban-Rich 1999, 2001). Also, despite extensive biodegradation (>98%), the bulk organic composition of sinking particulate matter appears to undergo minimal changes (Hedges et al. 2001), suggesting that organic matter in sinking particles such as fecal pellets might be protected from degradation by inorganic components.

Some zooplankton fecal pellets become repackaged through coprophagy by other zooplankters. Gowing & Silver (1986) have found recognizable zooplankton fecal pellets in the guts of deep-sea copepods. Paffenhöfer & Knowles (1979) and Ayukai (1986) have shown

that adult copepods feed upon fecal pellets of conspecific juveniles, often at higher filtering rates than on co-occurring diatoms. Neal et al. (1986) fed fecal pellets of barnacle nauplii to copepods. Green et al. (1992) found that nauplii of the large copepod *Calanus helgolandicus* ingested fecal pellets of nauplii of the smaller copepod *Pseudocalanus elongatus*.

Lampitt et al. (1991) reported that copepods break up their own fecal pellets while ingesting only a small portion of the pellets, and named this behavior 'coprorhexy.' These authors speculated that copepods strip the peritrophic membrane off fecal pellets and consume the membrane in order to ingest attached microbiota. Indeed, Youngbluth (1982) observed mysis larvae of pelagic shrimps feeding on microbes, phytoplankton, protozoans and metazoans attached to the peritrophic membrane of their own fecal material, as well as fecal pellets of other zooplankters.

Noji et al. (1991) distinguished 3 types of behavior by copepods when feeding on fecal pellets, all of which can potentially modify particle-size spectra of particle assemblages. Coprorhexy, or the fragmentation of fecal pellets, resulted in decreasing the number of large particles and increasing the abundance of smaller particles. At the same time, the smallest size fractions of particles had an increase in particle sizes, due to addition of larger particles from broken fecal pellets, which were larger than the small natural particles most abundant in the water. Coprophagy, or ingestion of fecal pellets, removes large particles. 'Coprochaly' was defined as disruption of peritrophic membranes of fecal pellets by copepods, resulting in partial dispersal of fecal pellet contents into the water, thereby increasing the relative abundance of small particles. Noji et al. (1991) suggested that disruption of fecal pellets by these processes would increase residence times of fecal materials by converting large particles to smaller ones with lower sinking rates. This could also enhance microbial degradation of feces by increasing microbial substrate by converting larger particles to smaller ones. Additional effects might include enhancement of diffusion processes oxygenating the interior of fecal particles (Alldredge & Cohen 1987), as well as leaching of dissolved organics and inorganics from such particles to the surrounding water (Jumars et al. 1989). All of these processes would be expected to convert large fast-sinking particles to smaller suspended ones, thereby increasing the recycling of fecal pellets in the upper layers of the sea, while retarding their transport to depth.

The copepod *Oithona similis* has been shown to ingest fecal pellets of several calanoid copepods, whereas the calanoids did not appreciably ingest their own fecal pellets (González & Smetacek 1994, González et al. 1994b). This led González & Smetacek (1994) to speculate that specialization for coprophagy by *O. similis* may contribute to the ubiquitous abundance of this species in the ocean. Coprophagy of fecal pellets produced by calanoid copepods by cyclopoids (mainly *Oithona* spp.) was also indicated by results from mesocosm studies of Svensen & Nejstgaard (2001).

There is also indirect evidence for zooplankton reprocessing of fecal pellets by coprophagy at depth. Honjo (1978) collected 'green' and 'red' fecal pellets in sediment traps in the Sargasso Sea, which had different composition. The green pellets contained abundant phytoplankton pigments, coccoliths and diatom fragments, and appeared to have resulted from zooplankton grazing in the surface layer, with rapid sedimentation to depth. The red pellets, however, contained clay particles and few phytoplankton remains, and were collected only in the deepest sediment traps. Honjo (1978) concluded that red pellets had been produced at depth by deep-water zooplankters reprocessing fecal pellets and other particulates sinking from above. Similarly, Urrère & Knauer (1981) found an increased fecal pellet flux in sediment traps at 1500 m, relative to traps at 500 m, and Conte et al. (2001) found increased lithogenic fluxes between 500 and 3200 m compared to depths closer to the surface. Both of these increases in fluxes at depth suggested repackaging of fecal pellets through coprophagy by mesopelagic and bathypelagic zooplankton.

Fecal pellets are subject to microbial decomposition, and questions have been raised as to whether fecal pellets contain bacteria primarily on surfaces or internally, and whether pellet decomposition is primarily from the 'inside out' or from the 'outside in'.

There is increasing evidence for decomposition of fecal pellets by internal bacteria. Gowing & Silver (1983) confirmed that natural fecal pellets collected from either sediment traps or freshly produced by pelagic crabs contained bacteria primarily inside the pellets, and that pellet surfaces had few attached bacteria. This was in contrast to observations of laboratory-produced fecal pellets, which were reported to have few internal bacteria (Honjo & Roman 1978). Further, Gowing & Silver (1983) discovered that with aging in the laboratory, fecal pellets that initially had few surface bacteria developed a 'surface microbial lawn' over time during laboratory incubations, similar to observations of Turner (1979). Gowing & Silver (1983) concluded that extensive rapid bacterial colonization of fecal pellet surfaces was likely an artifact of laboratory conditions, and that decomposition of most fecal pellets in the sea initiates with internal bacteria that are either enteric or ingested, or both. Since guts of copepods have been reported to contain an extensive microbial flora (Ogawa 1977, Sochard et al. 1979),

Gowing & Silver (1983) concluded that fecal pellet decomposition in the sea is primarily from the inside out. However, Nott et al. (1985) reported that bacteria were present in copepod fecal pellets only during periods of feeding, and no bacteria were found in empty guts of non-feeding copepods, suggesting that bacteria in fecal pellets were ingested along with food and not derived from resident populations in the gut. Lawrence et al. (1993) concluded that bacteria were abundant in copepod fecal pellets produced from feeding on food that contained bacteria, but bacteria were absent from fecal pellets produced from feeding on axenic food. Bacteria within copepod fecal pellets grew during incubation, suggesting that some had survived gut passage, and high aminopeptidase activity in fecal pellets suggested that internal bacteria participated in pellet degradation. Nagasawa & Nemoto (1988) found bacteria in the guts, within the interior of fecal pellets and colonizing the outside of fecal pellets of marine amphipods and copepods. In some cases, bacteria within copepod fecal pellets were more abundant than, and taxonomically different from, bacterial assemblages in surrounding waters (Delille & Razouls 1994). Hansen & Bech (1996) observed that copepod fecal pellets became colonized by bacteria from the surrounding water but could not dismiss the possibility that some bacteria were from inside fecal pellets or copepod guts.

Bianchi et al. (1992) identified both methanogenic (obligate anaerobes) and nitrifying (areobic) bacteria in natural fecal pellets from sediment traps and copepods, and suggested that the bacteria originated from copepod guts, most likely as ingested species for nitrifiers and enteric for methanogens. Karl & Tilbrook (1994) concluded that most methane in the upper layers of the Pacific is associated with sinking particles, and suggested that methane leaking from settling fecal pellets into the water column may explain the typical supersaturation of highly oxygenated surface waters with methane that forms only under anaerobic conditions.

Raghukumar & Raghukumar (1999) discovered that salp fecal pellets in the Arabian Sea contained abundant bacteria and unicellular, heterotrophic fungoid protists known as thraustochytrids. In addition to internal thraustochytrids, during experimental incubations, fecal pellets became colonized by thraustochytrids that were in the water column. Isolates of these protists from fecal pellets grew during incubations designed to simulate temperature and pressure conditions of the deep sea. This suggests that thraustochytrids survive gut passage through salps and continue to decompose salp fecal pellets during their rapid descent to the abyss.

Some fecal pellets have been shown to become rapidly colonized by bacteria and other microorganisms from seawater. Jacobsen & Azam (1984) found that within 24 h of egestion copepod fecal pellets had bacteria from the surrounding seawater covering nearly a third of the fecal pellet surface area. Sinking of pellets through a column of natural seawater increased the rate of initial colonization compared to fecal pellets lying on the bottoms of laboratory containers. Growth rates of bacteria associated with fecal pellets and those of bacteria free in the water were not significantly different, and mineralization of fecal pellet carbon amounted to no more than 1% d^{-1}. Jacobsen & Azam (1984) concluded that bacteria colonizing fecal pellets may not be a major remineralization pathway in the epipelagic.

Guidi & Tito de Morais (1983) observed that both fresh and aged fecal pellets of an ascidian were ingested by an epibenthic amphipod and that aged fecal pellets became progressively colonized by bacteria, which increased pellet organic carbon content. Peduzzi & Herndl (1986) also confirmed that fecal pellets of a gastropod became quickly colonized by bacteria within 12 h, after which bacterial abundance on pellets declined.

There is a microbial succession of colonizers of fecal pellets. Pomeroy et al. (1984) observed that bacteria originating in feces of salps and doliolids developed rapidly within the first 24 h, causing increases in respiration, net uptake of phosphate, loss of total primary amines and little change in ammonium. After 24 h protozoans invaded the feces and rapidly consumed most bacteria. After about 2 d fecal pellet microbial activity had largely ceased. Pomeroy et al. (1984) concluded that the efficiency of conversion of tunicate feces to microbial biomass was 10 to 20% and that fecal pellets were rapidly biodegraded by their own internal microbial community. In contrast, Caron et al. (1989) found that fecal pellets of oceanic salps remained intact over 10 d periods of experimental decomposition, despite becoming colonized by abundant bacteria and protozoans. Silver et al. (1984) also found that detrital particles collected in sediment traps had abundant ciliates, which were suggested to be endemics within consumer guts, rather than colonists from the surrounding water.

Fecal pellet degradation rates may depend on the diets producing the fecal pellets. Hansen et al. (1996) fed the copepod *Acartia tonsa* unialgal diets designed to simulate the boreal seasonal succession of phytoplankton dominated by diatoms in spring, nanoflagellates in summer and dinoflagellates in fall. Fecal pellets produced on diatom diets degraded significantly more slowly than those produced on nanoflagellate or dinoflagellate diets. Bacteria decreased over time on diatom-based pellets but increased on nanoflagellate- and dinoflagellate-based diets. Hansen et al. (1996)

concluded that flagellate-based fecal pellets produced during summer and fall periods are most likely degraded in the epipelagic, whereas diatom-based fecal pellets are more likely to sediment to the benthos in spring.

Smetacek (1980a) also found evidence for considerable reprocessing of copepod fecal pellets in Kiel Bight. The contribution of calanoid copepod fecal pellets to particulate carbon in detritus averaged <10% from April through September and <5% for the rest of the year. Periods of lowest fecal pellet contribution were those of highest zooplankton abundance and vice versa. Calculated residence times for fecal pellets in the 20 m deep water column were only a few hours in summer. Smetacek concluded that reprocessing of fecal pellets by zooplankton coprophagy and microbial degradation was high in summer and that this conserved essential nutrients in the water column.

Hofmann et al. (1981) simulated the contribution of fecal pellets by the various stages of dominant small copepods of the genus *Paracalanus* to the benthos of the southeastern USA continental shelf. The model indicated that nauplii produced daily averages of 50% of total fecal pellet mass, but only 4% of pellet flux. Adults produced daily averages of 13% of total fecal pellet mass but only 63% of pellet flux. Because most copepod fecal pellets were small, would sink slowly and were presumably consumed by coprophagy or microbially degraded in the epipelagic, the model indicated that only 0.2% of the average daily primary production reached the sea floor (35 m depth) as fecal pellets.

Krause (1981) suggested that most fecal pellets are biodegraded in near-surface waters and questioned the notion that fecal pellets sink at all. During a study of vertical distributions of fecal pellets in the North Sea, fecal pellets were generally found above the main thermocline, within 30 m of the surface. Most fecal pellets appeared to be those of the copepod *Calanus finmarchicus*. Even when this copepod migrated below the thermocline, the fecal pellet maximum remained in the uppermost layers of the water column. Krause (p. 325) conjectured that 'faecal pellets, probably enriched with bacteria in the gut of the copepod, inevitably have an anaerobic metabolism. The gas bubbles which develop during the bacterial activity in the faeces, at first cause a floating or even a buoyancy of the faecal pellets. This causes them to remain in the euphotic zone, where they can be re-cycled.' Krause then speculated that the high sinking rates for various types of fecal pellets recorded from laboratory investigations (references in Turner & Ferrante 1979) were artifacts caused by such things as storage of fecal pellets in cold water or 'counting and measuring under a warm light microscope, where the material is heated.'

He concluded that fecal pellets remain in the upper mixed layer because they are, in fact, buoyant and do not naturally sink. This conclusion is at odds with the numerous studies conducted prior to his showing that fecal pellets are collected in deep-sea sediment traps. An alternative explanation might be that fecal pellets sometimes remain in the upper mixed layer because it is mixed. Indeed, Alldredge et al. (1987) observed that large fecal pellets, probably produced by euphausiids, had sustained residence times in the upper 20 m off California, even though these pellets had measured sinking rates of 18 to 170 m d^{-1}. Alldredge et al. (1987) attributed this accumulation of large fecal pellets in surface waters to turbulent mixing, which retained the pellets in the upper mixed layer. Martens & Krause (1990) also found that most fecal pellets were at depths above 100 m in the North Sea in summer.

Microzooplankton fecal pellets

Most studies of zooplankton fecal pellets have focused on pellets produced by larger mesozooplankters such as copepods, euphausiids and tunicates, which have high sinking rates. However, some microzooplankters such as protozoans and small metazoans are now known to produce tiny fecal pellets, which presumably do not sink and are likely remineralized in the epipelagic.

Gowing & Silver (1985) discovered that small fecal pellets from 3 to 50 μm in diameter were ubiquitous and abundant in sediment traps and water samples throughout the upper 2 km of the eastern tropical Pacific. These 'minipellets' were thought to be wastes of radiolarians, other protozoans and small metazoans. Fluxes of minipellets exceeded those of larger fecal pellets (>50 μm) by 3 orders of magnitude, and carbon flux of minipellets was 11 to 49% that of larger pellets. Minipellets contained intact bacteria and picoplankton cells, some of which appeared identical to previously described olive-green cells. Gowing & Silver (1985) concluded that minipellet producers are major reprocessors of detritus originating in the euphotic zone and that these organisms are important in biological transformation of organic matter in the sea.

Nöthig & Bodungen (1989) observed that small fecal pellets (30 to 150 μm) were abundant in the water column and in sediment traps in the Weddell Sea. These pellets were suggested to originate from protozoan grazers such as ciliates, heterotrophic dinoflagellates, radiolarians and foraminiferans. They constituted 36% of the total sedimented feces volume in sediment traps. The majority of fecal pellets remaining in sediment traps were larger (150 to 300 μm) spherical fecal pellets, suggested to be those of small metazoans.

Other studies have confirmed that protozoans produce minipellets. Stoecker (1984) found that tintinnids and aloricate ciliates produce small fecal aggregates (18 × 32 µm), which overlap in size with cells of their dinoflagellate prey (16 × 22 µm). Buck et al. (1990) confirmed that a phagotrophic athecate dinoflagellate found in Antarctic sea ice produced small fecal pellets that averaged 30 µm in diameter and were filled with frustules of the pennate diatom *Nitzschia cylindrus*. Buck et al. (1990) suggested that the release of such fecal pellets from melting ice into the underlying water column may constitute a substantial portion of the flux of organics from the euphotic zone to depth. González (1992b) also found that minipellets (5 to 100 µm) were abundant in the Antarctic. These minipellets contained numerous unbroken diatom frustules and originated from heterotrophic unarmored dinoflagellates and phaeodarian radiolarians. Gowing et al. (2001) reported that minipellets from athecate heterotrophic dinoflagellates and ciliates were the dominant types of fecal pellets in sediment traps at several stations in the Ross Sea.

Dinoflagellate minipellets have also been reported from temperate localities. Buck & Newton (1995) found that during a spring bloom in Dabob Bay (Puget Sound, Washington, USA) the dominant diatom *Thalassiosira pacifica* was extensively eaten by an unarmored dinoflagellate of the genus *Gymnodinium*, which produced abundant fecal pellets. These pellets averaged 69 × 83 µm, were covered with a peritrophic membrane and were packed with *Thalassiosira* frustules, which were devoid of cytoplasm. Dinoflagellate minipellets accounted for an average of 29 % of the total fecal pellet flux to 50 m depth. Elbrächter (1991) showed that a variety of photosynthetic and heterotrophic dinoflagellates and other protists produce minipellets.

Other studies have revealed abundance of fecal pellets from metazoan microzooplankton. Minipellets from copepod nauplii also contained frustules of the diatom *Nitzschia sicula* during a bloom of this species in the Adriatic (Vilicic et al. 1994), and pellets <80 µm in the longest dimension, likely from copepod nauplii, were important components of the fecal pellet assemblage in a Norwegian fjord (Pasternak et al. 2000).

Fish fecal pellets

The fecal pellets of fish also appear to be important in some marine ecosystems. Fecal matter of 7 species of mid-water fish sank at rates of hundreds to thousands of meters per day (Robison & Bailey 1981), and pellets of larger volumes sank faster. Due to the high abundance of mid-water fish in many oceanic environments and the high nutrient content of their fecal pellets, mid-water fish fecal matter may be a major source of organic export from the pelagic community to the benthos. Bray et al. (1981) have shown that fish that forage during the day on pelagic zooplankton and then return to shelters in a rocky reef at night import substantial amounts of carbon to the reef through defecation in nocturnal shelters. Fecal pellets of reef fishes also appear important in the import of minerals to reef communities (Geesey et al. 1984). Similarly, Robertson (1982) showed that many coral reef fishes are coprophagous on feces of other fish, which can have high nutritional content (Bailey & Robertson 1982). Fecal pellets of reef fishes that prey on cnidarians that contain zooxanthellae, themselves contain live zooxanthellae, which are photosynthetically active and capable of re-establishing symbioses with cnidarians (Parker 1984).

Fecal matter of anchovies in the Peru upwelling system was a major component of the downward flux into sediment traps (Staresinic et al. 1983). Fecal fragments sank at rates averaging >1 km d^{-1}, and had high organic carbon and nitrogen contents as well as abundant diatom fragments. Due to fast sinking rates, anchovy feces have a relatively short residence time in the water column, and since they fall into sediments that are primarily anoxic below the superficial layers, fecal organic matter should remain intact before burial in deeper sediments. Staresinic et al. (1983) speculated that the decline in anchovy stocks off Peru in the early 1970s might have led to reduced fluxes of particulate organic matter and that a relative increase in the contribution of smaller slower-sinking particles such as phytoplankton cells and zooplankton fecal pellets might have contributed to the increased denitrification recorded off coastal Peru since the decline of fish stocks (Codispoti & Packard 1980). An alternative hypothesis by Walsh (1981) suggested that the decline in anchovy stocks off Peru would decrease utilization of organic matter in the water column by anchovies, making more organic matter available for deposition. Either way, feeding and fecal production by anchovies off Peru, and presumably in other coastal upwelling systems, are potentially important processes. In fact, Scheidegger & Krissek (1983) have suggested that unusually fine-grained terrigenous sediments confined to the inner continental margin off Peru are due to fecal pelletization of these particles by zooplankton and anchovies while feeding upon phytoplankton. Since zooplankton and fish populations increase together with phytoplankton during enhanced upwelling intensity in December through April, also a period of peak river discharge, the coincidence of maximum biological removal of terrigenous sediments at

the time of their maximum input may explain why so few terrigenous sediments are found beyond the continental margin. Scheidegger & Krissek (1983) concluded that such a biological 'filter' or barrier to seaward transport of terrigenous sediments in the wind-driven surface layer enhanced deposition of terrigenous and pelagic particulates into anoxic sediments off Peru, thereby helping to preserve the sedimentary record of upwelling characterized by various chemical and biological indicators (references in Scheidegger & Krissek 1983).

Zooplankton fecal pellets in ancient oceans

There is paleontological evidence for zooplankton fecal pellets. Porter & Robbins (1981) discovered what appear to be fossil zooplankton fecal pellets in black shales 11 to 300 million yr old that represent coastal, epicontinental sea and lake environments. These black shales are associated with phosphate, oil and coal deposits. Porter & Robbins (1981) suggested that zooplankton fecal pellets contributed to the deposition of organic matter in anoxic basins, contributing to formation of the black shale deposits. Robbins et al. (1985) described microfossils resembling fecal pellets of modern zooplankters in Middle Cambrian and Early Proterozoic shale. These microfossils were in rocks that also preserved sulfides analogous to modern anoxic environments that preserve fecal pellets. Rocks containing putative pellets were 0.53×10^9 to 1.9×10^9 yr old. Similar rocks of Archaean age (2.68×10^9 to 3.8×10^9 yr old) did not contain pellet-like microfossils. Robbins et al. (1985) argued that if the Proterozoic microfossils were fossilized fecal pellets, then they provided evidence of metazoan life and a complex food web 1.9×10^9 yr ago, which predates macroscopic metazoan body fossils 0.67×10^9 yr ago, animal trace fossils 0.9×10^9 to 1.3×10^9 yr ago and fossils of unicellular eukaryotic algae 1.4×10^9 yr ago.

Fecal pellets may have facilitated oxygenation of the ocean, leading to the Cambrian 'explosion' of multicellular life (Walter 1995, Oliwenstein 1996). G. A. Logan et al. (1995) found that hydrocarbons extracted from Terminal Proterozoic to Early Cambrian marine sediments (570 to 590 million yr old) were derived mainly from bacteria and other heterotrophs rather than from autotrophs. They proposed that prior to the Cambrian, slowly sinking organic matter in the sea was repeatedly reworked by bacterial degradation, leading to sulfate reduction and oxygen depletion in the surface layer of the sea. High ^{13}C:^{12}C ratios in sediments suggested long heterotrophic microbial food webs. An abrupt decline in ^{13}C:^{12}C ratios at the beginning of the Cambrian, coincident with evolution of the

metazoan gut, suggests that organic matter in the sea became increasingly packaged in rapidly sinking fecal pellets, which plummeted to depth before they could be extensively decomposed, resulting in increases in ocean oxygenation and allowing the Cambrian radiation of multicellular animal life.

Butterfield (1997) has proposed that the advent of metazoan guts and increased zooplankton grazing in the sea at the Proterozoic-Cambrian interface would have had the opposite effect from that described above, namely a decrease in export to depth via zooplankton fecal pellets. By removing phytoplankton and packaging it as animal biomass, which stayed in the upper water column, Butterfield suggested that zooplankton grazing might have reduced carbon burial, causing the observed drop in ^{13}C:^{12}C ratios at the beginning of the Cambrian. If this were the case, then the drop in carbon ratios would be a consequence, rather than a cause, of the Cambrian explosion.

Kitchell (1983) and Haberyan (1985) have suggested that if zooplankton fecal pellet sedimentation is a dominant means by which phytoplankton remains reach the seafloor and become part of the micropaleontological fossil record, then selective feeding by the zooplankton producing the fecal pellets might heavily bias the fossil record toward phytoplankton species preferred by grazers.

The variable importance of fecal pellets in sedimentary flux

Numerous studies have shown that the contribution of zooplankton feces to sedimentary flux can be substantial (Table 3). Bishop et al. (1977) estimated that in the upper 400 m of the equatorial Atlantic, zooplankton fecal pellets and fecal matter constituted only 4% of the total suspended mass concentration but accounted for 99% of the vertical mass flux through the upper 388 m. Urrère & Knauer (1981) reported that fluxes of recognizable zooplankton fecal pellets varied with depth, accounting for 10 to 19% of total carbon fluxes for near-surface waters (35 to 150 m), declining to 9.7% at 500 m and 3.4% at 1500 m. Fowler et al. (1991) found that fecal pellet carbon fluxes increased with depth, accounting for 25, 29 and 33% of total particulate carbon fluxes at 50, 150 and 250 m, respectively. Graf (1989) concluded that a pulse of fecal pellets from the copepod *Calanus finmarchicus* accounted for 92% of the total carbon settling to the deep North Atlantic at the end of a spring bloom in May. Fecal pellets constituted averages of 11 to 37% but up to 66% of the vertical flux of particulate organic carbon (POC) over the upper 200 m off Norway (Wassmann et al. 1999). Roy et al. (2000) found that zooplankton fecal

Table 3. Zooplankton fecal pellet contribution to total particulate organic carbon flux

Depth (m)	Fecal pellets (%)	Source
High		
1430	92	Graf (1989)
200	Up to 66	Wassmann et al. (1999)
150	3 to >100	Roy et al. (2000)
120	'Almost all'	Small et al. (1983)
400	99 % of total mass	Bishop et al. (1977)
200	92.8 (sum of all sizes)	Wassmann et al. (2000)
1500	84.0 (sum of all sizes)	Wassmann et al. (2000)
Low		
389 to 5068	5 to 10	Pilskaln & Honjo (1987)
74	2 to 25	Maita et al. (1988)
390	'Insignificant'	Asper (1987)
200	6	Taylor (1989)
100	0.4 to 1.7	Ayukai & Hattori (1992)
42	<1	Lane et al. (1994)
500	Mean 20, range 10 to 30	Passow et al. (2001)
Moderate to variable		
100	10 to 19	Urrère & Knauer (1981)
500	10	Urrère & Knauer (1981)
1500	3	Urrère & Knauer (1981)
50	25	Fowler et al. (1991)
150	29	Fowler et al. (1991)
250	33	Fowler et al. (1991)
2300	3 to 35	Carroll et al. (1998)
1000	1.6 to 62.0	Miquel et al. (1994)
860	18 to 199	Small & Ellis (1992)
500	10 to 30 %	Bauerfeind et al. (2001)
300 Pre-El Niño	5 to 10	González et al. (2000a)
El Niño	24 to 38	González et al. (2000a)
Post-El Niño	3 to 11	González et al. (2000a)
200	5 to 48	Gowing et al. (2001), Asper & Smith (1999)

pellets accounted for 3 to >100 % of total POC flux over the upper 150 m in the Gulf of St. Lawrence but that during June, the period of maximum fecal pellet carbon flux, all values were >66 %. The average contribution of zooplankton fecal pellets to POC flux at 50 m in this study was 50 % over the annual cycle. Other studies show that euphausiid and copepod fecal pellets can be the dominant components of flux during major blooms of the prymnesiophyte *Phaeocystis pouchetii* (Lutter et al. 1989, Riebesell et al. 1995, Hamm et al. 2001) and coccolithophorids such as *Emiliania huxleyi* (van der Wal et al. 1995, Fischer et al. 1996).

Small et al. (1983) investigated the proportions of vertical particulate flux made up of fecal pellets and amounts of primary production converted by zooplankton to fecal pellets and dissolved excretions in the tropical Pacific. Both small (<300 µm) and large (300 to 500 µm) zooplankton (not counting euphausiids, salps and red crabs) constituted <2 % of daily primary carbon and nitrogen production into fecal pellets. If all such fe-

cal pellets sank below 100 m and into the oxygen minimum zone without being eaten or decomposed, then upward nutrient flux from below 100 m would only have to be equivalent to a loss of 2 % or less to maintain daily production. That would mean that 'new production' (Dugdale & Goering 1967, Eppley & Peterson 1979) would have to be only 2 % of total production, and 98 % could be recycled production, if the only losses were due to sedimentation of fecal pellets from small and large zooplankton (mostly copepods). Considering that there are other fecal pellet producers and that some small fecal pellets are recycled in the epipelagic and do not sink below 100 m, whereas other small pellets are exported to depth via attachment to marine snow, Small et al. (1983) estimated that total fecal pellet removal of carbon and nitrogen from surface waters would not exceed 10 % of daily primary production and would more closely approximate 5 %. The percentages of vertical flux measured at 120 m composed of various types of fecal pellets were much greater. Small et al. (1983) estimated that 41 % of the carbon flux to this depth came from fecal pellets of small and large zooplankton, and that 21 % came from the red crab *Pleuroncodes planipes*. Small et al. (1983) concluded that after adding contributions from all other organisms that were not accounted for in these categories, 'almost all' of the carbon flux to 120 m could result from fecal pellet flux.

Other studies have shown the proportion of vertical fluxes attributable to fecal pellets is comparatively low. Despite collection of large numbers of zooplankton fecal pellets in sediment traps at various depths, fecal pellets contributed averages of only <5 to 10 % of the vertical fluxes of organic, carbonate, silicate and lithogenic materials at several oceanic deep-water sites (Pilskaln & Honjo 1987). However, since fecal pellets had elevated C:N ratios and high organic content, they may have been an important source of organic carbon for deep-sea benthos. Fecal pellet fluxes accounted for only 2 to 4 % and 5 to 25 % of the total organic carbon fluxes in summer and winter, respectively, to a depth of 74 m in Funka Bay, Hokkaido (Maita et al. 1988). Particulate flux to 390 m in the Panama Basin was dominated by marine snow, and fecal pellet flux was insignificant (Asper 1987). Taylor (1989) found that fecal pellet flux was only 6 % of total particulate carbon flux in the upper 200 m in the North Pacific central gyre, and Ayukai & Hattori (1992) reported that fecal pellet carbon flux was only 0.4 to 1.7 % of total POC flux to 100 m off Japan. Lane et al. (1994) estimated that copepod fecal pellet flux in the upper 42 m over the Virginia continental shelf

constituted <1% of total particulate carbon collected in sediment traps and 0.3% of particulate carbon in the water column. The contribution of zooplankton feces to particulate carbon flux at 80, 200 and 1000 m depths in the Mediterranean was variable over the annual cycle (1.6 to 62%) (Miquel et al. 1994). Similarly, Carroll et al. (1998) found that fecal pellet flux over 2300 m in the Mediterranean varied with depth and season, and in terms of types of fecal pellets collected, and that the proportion of total carbon flux attributable to fecal pellets averaged 18%, ranging from 3 to 35%. Lundsgaard & Olesen (1997) concluded that most copepod fecal pellets produced in the Kattegat sank out of the surface layer but that, due to the large component of vertical flux from sources other than copepod fecal pellets, copepod fecal pellet contribution to flux was insignificant. Roman & Gauzens (1997) calculated that the proportion of export flux due to copepod fecal pellets in the equatorial Pacific was small, suggesting that most copepod fecal pellets produced in the euphotic zone decomposed or were ingested by other zooplankton. Landry et al. (1995) calculated that mesozooplankton (>200 µm) grazing in the Southern California Bight seasonally accounted for 16 to 44% of phytoplankton growth but that only 23 to 32% of this grazing was lost rapidly enough from the euphotic zone to be recovered as fecal pellets in sediment traps down to 100 m. Zeldis (2001) concluded that <4% of the POC in sediment traps was due to copepod fecal pellets during an iron enrichment experiment in the Southern Ocean.

The relative contribution of zooplankton fecal pellets to vertical carbon flux can depend on the depth interval being considered. In the euphotic zone of an oligotrophic oceanic station in the sub-tropical North Pacific, there was a 2-layered system (Small et al. 1987) where, in the upper 40 m, there was higher primary production, low chlorophyll concentration and low zooplankton biomass, and the zooplankton produced mainly small fecal pellets that were recycled. In the lower layer from 40 to 100 m depth, there was low primary productivity but high chlorophyll and zooplankton, and many larger zooplankton fecal pellets. There was no fecal pellet flux into sediment traps at 30 m but at 120 m, fecal pellet flux was 30% of total carbon flux. Small et al. (1987) concluded that zooplankton fecal pellets are coupled more to carbon flux out of the bottom layers of oligotrophic euphotic zones than to the carbon flux of unlayered eutrophic euphotic zones. In contrast, Altabet (1989a) concluded that in the Sargasso Sea, the recycling of nutrients in the upper half of the euphotic zone was less efficient than that in the euphotic zone as a whole.

The relative contribution of fecal pellets to vertical flux also depends on epipelagic community structure. Michaels & Silver (1988) simulated the size distribu-

tions of pelagic producers and trophic positions of consumers, and their effects on the composition and amounts of sinking fluxes. Picoplankton were the dominant producers in the model, but they contributed little to downward fluxes due to the large number of trophic steps between picoplankton and producers of fecal pellets. Net phytoplankton, though less abundant than smaller phytoplankton, were important contributors to the vertical flux because of the comparatively few trophic steps between them and their consumers, which produce large sinking fecal pellets, and because blooms of netplankton can sink to the benthos directly. The vertical flux varied strongly with community composition of consumers producing fecal pellets. Generalist grazers, which ingest a broad size spectrum of prey from pico- and nanoplankton, were major exporters of fecal pellets to depth. Such generalists that form swarms, including salps and doliolids, may have important episodic impacts on the overall average export from the epipelagic.

The contribution of fecal pellet carbon to total particulate carbon flux out of the euphotic zone can also vary with size and relative carnivorous versus herbivorous feeding patterns of the zooplankton community. Small & Ellis (1992) found that the percentage of total carbon flux attributable to fecal pellet flux from larger zooplankton (>500 µm) in the Santa Monica Basin off California also varied with season, from 10% in October to 172% in May. Assuming no carnivory and adding in fecal pellet flux from smaller (200 to 500 µm) zooplankton, much of which may have been recycled in the epipelagic, percentages of total carbon flux represented by fecal pellet flux ranged from 18% in January and February to 199% in May.

The relative contribution of fecal pellets to total particulate flux can vary in relation to El Niño conditions (González et al. 2000a,b). In January 1997, prior to the 1997-1998 El Niño in the northern Humboldt Current off Chile, zooplankton fecal pellets accounted for means of 5 to 10% of the total POC in sediment traps over the upper 300 m depth. This was during a period when the zooplankton assemblage was dominated by copepods. In July 1997, during the onset of El Niño, the deepening of the thermocline led to a reduction of nutrient input by upwelling, and chlorophyll levels were low. The zooplankton during this period included abundant salps and euphausiids, and zooplankton feces, primarily fecal strings of euphausiids, accounted for means of 24 to 38% of total sediment-trap POC. In post-El Niño conditions in January 1998, when copepods were again dominant, zooplankton fecal pellet carbon had declined to 2.7 to 11.3% of total sediment-trap carbon.

The relative contributions of zooplankton fecal pellets compared to ungrazed phytoplankton can also

vary in relation to upwelling seasons and copepod life cycles. Smith (2001) concluded that zooplankton grazing in the Arabian Sea could control vertical flux variations. During June at the onset of upwelling, large copepods in the epipelagic grazed extensively on diatoms, preventing diatom blooms. The largest vertical flux events were recorded near the end of the upwelling season in August and September, after the dominant copepods had migrated to depth to begin diapause, when ungrazed diatoms constituted the dominant component of sediment-trap contents (Passow et al. 1993).

The apparent importance of fecal pellet flux to depth may also depend on benthic conditions. Pilskaln (1991) found that zooplankton fecal pellets were extremely abundant in anoxic surface sediments of the Black Sea. These fecal pellets were packed with coccolithophorid remains and contributed substantially to the white coccolith-rich sediments. Pilskaln concluded that abundant fecal pellets in these anoxic sediments substantiated the claim that the widespread lack of fecal pellets in sediments deposited under aerobic conditions was due to remineralization by benthic microbes and consumers.

Part of the variability in estimates of the importance of fecal pellets in sedimentary flux may be due to patchiness of fecal pellets and the animals producing them. Using a submersible, Youngbluth et al. (1989) observed abundant fecal pellets (50 to 325 m^{-3}) *in situ* in the Gulf of Maine and canyons south of Georges Bank, where pellets were accumulated at night in 5 to 24 m thick layers in the pycnocline. Positions of these layers in the water column varied with time of day. The pellets were produced by the vertically migrating euphausiids *Meganyctiphanes norvegica*, which were present in enormous aggregations (up to 10^4 m^{-3}), usually near the seabed. These pellets sank rapidly (means of 200 to 211 ± 32 m d^{-1}) and were estimated to transport large amounts of organic matter (means of 7 to 12 mg C m^{-2} d^{-1}) to the bottom. Youngbluth et al. (1989) concluded that amounts of vertical flux due to zooplankton fecal pellets can vary considerably with hydrography and zooplankton behavior.

MARINE SNOW

'When I think of the floor of the deep sea…I see always the steady, unremitting, downward drift of materials from above, flake upon flake, layer upon layer…the most stupendous "snowfall" the earth has ever seen.'

Rachael Carson (1951) p. 74

'Marine snow' refers to organic aggregates >500 µm in size (Alldredge & Silver 1988). Such aggregates are abundant and ubiquitous in the ocean, and comprise many types of particles, originating from a variety of sources. As reviewed by Alldredge & Silver (1988), the study of marine snow began with *in situ* observations and collections from submersibles, primarily by Japanese researchers beginning in the 1950s (Tsujita 1952, Suzuki & Kato 1953, Nishizawa et al. 1954, Inoue et al. 1955, Nishizawa 1966, 1969, Kajihara 1971). Field studies by primarily North American scientists in the 1960s and 1970s focused on samples named 'organic aggregates' collected from water bottles (Riley 1963, 1970, Johannes 1967, Gordon 1970, Wiebe & Pomeroy 1972, Wangersky 1974). Other studies, primarily in the laboratory, addressed the role of bubbles, turbulence and bacteria in the conversion of dissolved organic material to particulate organics (Baylor et al. 1962, Sutcliffe et al. 1963, Menzel 1966, Sheldon et al. 1967, Batoosingh et al. 1969, Johnson 1976, Johnson & Cooke 1980, Kranck & Milligan 1980, Biddanda 1985), and whether such particles supported nutrition of filter-feeding animals (Baylor & Sutcliffe 1963). Since the late 1970s and 1980s, there has been a coalescence of *in situ* study using SCUBA and submersibles (Silver et al. 1978, Trent et al. 1978) with laboratory and shipboard field studies (reviewed below).

Marine snow and other macroscopic organic aggregates may originate from a variety of sources. These include abandoned larvacean houses, diatom and dinoflagellate flocs, fecal aggregates and aggregates of miscellaneous detritus (Alldredge & Gotschalk 1990, Alldredge et al. 1998). Marine snow particles contain sticky microbially produced exopolymers that have high efficiencies of aggregation (Alldredge & McGillivary 1991, Stolzenbach 1993, Stolzenbach & Elimelech 1994). Large marine snow macroflocs form under conditions of high phytoplankton biomass and low wind speeds, and dissipate with wind-induced turbulence (Riebesell 1992). Marine snow also accumulates at water-column density discontinuities (MacIntyre et al. 1995).

Marine snow becomes enriched by a variety of attached planktonic organisms and other particles. These include bacteria, photosynthetic picoplankton, diatoms, diatom resting spores, dinoflagellates, other primary producers, protozoans, small detrital particles, minerals and fecal pellets (Silver et al. 1978, 1998a, Trent et al. 1978, Silver & Alldredge 1981, Knauer et al. 1982, Prézelin & Alldredge 1983, Biddanda 1985, 1986, 1988, Alldredge et al. 1986, 1998, Beers et al. 1986, Caron et al. 1986, Davoll & Silver 1986, Silver et al. 1986, Taylor et al. 1986, Amy et al. 1987, Eisma 1987, Biddanda & Pomeroy 1988, Herndl 1988, Herndl & Peduzzi 1988, Davoll & Youngbluth 1990, Simon et al. 1990, Turley 1991, Bochdansky & Herndl 1992a,b, Kaltenböck & Herndl 1992, Müller-Niklas & Herndl 1992, Smith et al. 1992, Buck & Chavez 1994, Kilps et

al. 1994, Steinberg et al. 1994, Turley & Mackie 1994, Artolozaga et al. 1997, Holloway & Cowen 1997, Leppard et al. 1997, Noji et al. 1997, Rath et al. 1998, Ploug & Grossart 2000). Various zooplankters also appear to be associated with marine snow (Alldredge 1972, 1976, Shanks & Edmonson 1990, Steinberg et al. 1994, 1997, Walters & Shanks 1996, Green & Dagg 1997, Shanks & del Carmen 1997, Shanks & Walters 1997, Kiørboe 2000).

Marine snow aggregates provide small-scale patchiness of larger particles that may be nutritionally enhanced parcels when consumed by larger pelagic organisms. Microscale chemical patches of oxygen and pH around marine snow particles and fecal pellets were confirmed by Alldredge & Cohen (1987). Ploug et al. (1999) found that marine snow aggregates were net heterotrophic communities that were hotspots of microbial respiration in the water column. Alldredge (2000) found that dissolved organic carbon associated with marine snow can be up to 31% of the total organic carbon in aggregates and suggested that previous measurements of sedimenting carbon that only included particulate carbon may have underestimated the total vertical flux of organic carbon.

Macroscopic aggregates (>1 mm) are abundant in epipelagic as well as mesopelagic and bathypelagic waters (Silver & Alldredge 1981, Honjo et al. 1984, Davoll & Youngbluth 1990, Gardner & Walsh 1990, Pilskaln et al. 1998, Silver et al. 1998b). In Monterey Bay, California, phytoplankton-containing aggregates constituted about half the aggregates in the upper 40 to 250 m layers but declined to only 5% of aggregates at 400 m, prompting Silver et al. (1998b) to suggest that many sub-euphotic zone aggregates were derived from sources not tied to phytoplankton production cycles.

Aggregates are resistant to disaggregation (Alldredge et al. 1990) and are typically chemically enriched with higher concentrations of organic carbon, nitrogen, protein, carbohydrate, lipid, phaeopigments, chlorophyll and particulate weight than of those in the surrounding water column (Alldredge 1979, 1998), as well as with high levels of trace metals (Hebel et al. 1986).

Concentrations of attached bacteria, phytoplankton and heterotrophic protozoan cells (many of which appear alive), zooplankton, fecal pellets, other biogenic debris, and organic carbon on marine snow and other large particles can exceed those suspended in the surrounding water by as much as 2 to 4 orders of magnitude (Fellows et al. 1981, Silver & Alldredge 1981, Caron et al. 1982, Bochdansky & Herndl 1992a,b, Lampitt et al. 1993b, Steinberg et al. 1994, Turley & Mackie 1994, Ploug et al. 1999, Waite et al. 2000). Levels of primary productivity and chlorophyll of algae attached to marine snow can exceed those of the surrounding water column by up to 2 orders of magnitude (Alldredge & Cox 1982), but only marine snow of phytoplankton origin contributes significantly to primary production in surface waters (Alldredge & Gotschalk 1990). For marine snow in the mesopelagic zone, however, even though bacteria attached to marine snow were >100 times more abundant than in surrounding seawater, since marine snow was rare (0.4 to 5.0 aggregates m^{-3}), the contribution made by bacteria attached to marine snow to total mesopelagic zone bacterial production was insignificant, ranging from 0.01 to 0.39% (Alldredge & Youngbluth 1985). Plumes of dissolved organics leaking from sinking aggregates may attract bacteria from the water column to attach to marine snow (Kiørboe & Jackson 2001). There are also suggestions that bacteria attached to marine snow and other organic aggregates appear to be taxonomically different from those dominating water-column assemblages (DeLong et al. 1993).

Marine snow and other sinking particles may contain enhanced levels of viruses (Proctor & Fuhrman 1991). Large virus-like particles have been found in bulk sediment-trap material, in zooplankton guts and fecal pellets, and in phaeodarian radiolarians, which may have acquired viruses while feeding on sinking or suspended particulates (Gowing 1993).

Depending on their sizes, shapes and densities, marine snow particles may sink tens to hundreds of meters per day, which is either faster or slower than many types of zooplankton fecal pellets (Shanks & Trent 1980, Silver & Alldredge 1981, Taguchi 1982b, Gorsky et al. 1984, Asper 1987, Alldredge & Gotschalk 1988, Diercks & Asper 1997). Since marine snow particles 'scavenge' smaller particles including fecal pellets from the surrounding water as they sink (Hill & Nowell 1990), adherence to marine snow particles may either enhance or retard sinking rates of fecal pellets (Alldredge 1979). A model by Jackson (2001) suggests that sinking rates of marine snow particles may be enhanced if high-density fecal pellets become embedded in the marine snow. Rapidly sinking mucous aggregates from web-feeding euthecosomatous pteropods scavenge picoplankton-sized particles, thereby greatly accelerating their sinking rates (Noji et al. 1997), and Waite et al. (2000) observed massive sedimentation of picoplankton embedded in organic aggregates in the South Pacific.

Some forms of marine snow are fecal pellets. Pomeroy & Deibel (1980) found that up to 4 d old fecal ribbons from pelagic tunicates (salps and doliolids) resembled the flocculent organic aggregates colonized with microorganisms that are typically described as 'marine snow' in productive parts of the ocean. Older particles of feces resembled the uncolonized aggregates that appear to be ubiquitous throughout the

ocean. There was a microbial succession on fresh aggregates that initially contained phytoplankton remains but that subsequently developed populations of larger bacteria cells and later protozoans such as flagellates and ciliates. The microbial populations appeared to originate both from cells contained in the feces and from others colonizing from the surrounding water column. However, most bacteria cells in the feces were larger 1 to 3 µm rods and cocci, which were different from the <1 µm minibacteria in the seawater.

Marine snow is a food source for pelagic organisms. Lampitt et al. (1993a) found that marine snow particles in the northeast Atlantic exhibited diel variability in abundance and depth, and suggested that this was due to ingestion by vertically migrating mesopelagic fauna. Lampitt et al. (1993b) confirmed from both gut contents produced on natural diets and feeding experiments conducted at sea that several species of ostracods, copepods and the micronektonic amphipod *Themisto compressa* consumed marine snow. This implied that a food-web shortcut by which picoplankters attached to marine snow, which are too small to be efficiently consumed by mesozooplankton and micronekton, can become part of the diets of these upper-trophic-level consumers when they eat marine snow. Amphipod fecal pellets contained such picoplankters, and gut passage times for vertically migratory amphipods were long enough to allow marine snow consumed at night in the epipelagic to be eliminated at mesopelagic daytime depths. Lampitt et al. (1993b) calculated that such 'gut flux' for the amphipod population might constitute as much as 2% of the vertical flux measured simultaneously in sediment traps. Dagg (1993) suggested from both energy-budget imbalances and gut contents that the large (7 to 9 mm long) copepod *Neocalanus cristatus* in the sub-Arctic Pacific must be ingesting large detrital particles such as marine snow. There are other reports or suggestions that zooplankton ingest various types of marine snow, mainly originating from planktonic tunicates (Alldredge 1972, 1976, Hamner et al. 1975, Alldredge & Madin 1982, Ohtsuka & Kubo 1991). Also, Lawrence et al. (1993) found that copepods ingested and assimilated bacteria attached to detrital particles such as marine snow, again suggesting a shortcut between the microbial loop and the grazing food chain. Laboratory investigations have confirmed that marine snow is consumed by copepods and euphausiids (Bochdansky & Herndl 1992a, Dilling et al. 1998), and fish (Larson & Shanks 1996). Graham et al. (2000) attributed a nighttime reduction in amounts of marine snow in near-surface waters off California to consumption or disruption by euphausiids and large copepods that had migrated upward into the epipelagic. Indeed, Dilling & Alldredge (2000) and Goldthwait et al. (2001) found that euphausiids caused fragmentation of marine snow particles by the activity of swimming.

A particular type of macroscopic aggregate is the mucilage phenomenon in the Adriatic Sea (reviewed by Stachowitsch et al. 1990, Herndl 1992). These events have been known for centuries and can cause beach fouling on a massive scale (*mare sporco* or 'dirty sea' in Italian), and benthic anoxia. The mucilagenous accumulations are thought to be initially produced by diatoms (Heissenberger et al. 1996, Leppard et al. 1996, Najdek 1996). The intermittent timing and interannual variability of mucilage outbreaks makes pinpointing a cause difficult.

Alldredge et al. (1993) and Kiørboe & Hansen (1993) described previously unknown forms of organic aggregates in the sea known as transparent exopolymer particles (TEP). TEP are small, transparent and extremely abundant, and are formed from dissolved exopolymers exuded by phytoplankton and bacteria. TEP range in the longest dimension from 3 to hundreds of micrometers, and in abundance from 28 to 500 ml^{-1} in coastal California waters. TEP are sticky (B. E. Logan et al. 1995), have high levels of attached bacteria, and are major agents in the aggregation of diatoms and in the formation of marine snow. Alldredge et al. (1993) suggested that TEP might transform dissolved organic matter into particulates by a rapid abiotic pathway, in addition to remineralization by microbes. The abundance, size and extent of bacterial colonization of TEP are quite variable (Passow & Alldredge 1994, Mari & Kiørboe 1996), and TEP can be important in the flocculation and mass sinking of diatom blooms (Passow et al. 1994, Alldredge et al. 1995, Passow & Alldredge 1995, Waite et al. 1997, Ploug & Jørgensen 1999, Ramaiah et al. 2001) and blooms of *Phaeocystis* spp. (Hong et al. 1997). However, Engel & Schartau (1999) found that diatom aggregates without TEP sank faster than those with TEP, because TEP reduced the density of aggregates. TEP appear to form from dissolved precursor material (Passow 2000), and phytoplankton appear to be the most important source of TEP, although bacteria may possibly enhance phytoplankton production of TEP (Passow et al. 2001). Schuster & Herndl (1995) concluded that turbulence was more important than bacteria in the water column in the formation of TEP particles in the Adriatic. Krembs & Engel (2001) found that TEP were abundant in Arctic sea ice. Colloidal TEP can be eaten by protozoans (Shimeta 1993, Tranvik et al. 1993) and larvaceans (Flood et al. 1992). Passow & Alldredge (1999) showed that TEP-nanoplankton clusters were readily grazed by euphausiids, and that this process shortcircuited the microbial loop by making cells normally too small to be efficiently grazed available to euphausiids after incorporation into TEP clusters.

Long & Azam (1996) found abundant proteinaceous fibrous particles in the sea that were 3 to 13 times more abundant than TEP, with up to 2 orders of magnitude greater area. Bacteria had colonized 20 to 40 % of these particles. Long & Azam (1996) suggested that these proteinaceous particles may serve as nitrogen sources for bacteria and other organisms.

An important summary of both theoretical and empirical studies in the emerging fields of TEP, and the roles of aggregation and stickiness of phytoplankton and other particles in vertical flux was presented in a special issue of 'Deep-Sea Research' (Part II, Vol. 42, No. 1) entitled 'Aggregation in marine systems' (Alldredge & Jackson 1995, and papers referenced therein).

PHYTOPLANKTON SEDIMENTATION

'…Huxley was certainly wrong in his interpretation of [*Bathybius haeckeli*] as a new and primitive life form, but his error was not quite so foolish as many of his contemporaries and subsequent commentators have suggested. Perhaps later generations of oceanographers are much more open to criticism for not recognizing a phenomenon of such potential significance [i.e., sedimented phytoplankton blooms] for so long!'

Rice (1983) p. 179

Phytoplankton were not considered to be a major component of the sedimentary flux until recently. This was because laboratory studies of sinking rates of phytoplankton cells gave sinking rates typically <1 to tens of m d^{-1} (Smayda 1970, 1971, Smayda & Bienfang 1983, and references therein). However, field studies over the last 2 decades revealed that some ungrazed phytoplankton blooms can sink directly to the benthos at unexpectedly rapid rates.

Bloom sedimentation was first shown for shallow coastal waters (20 m depth) of Kiel Bight (Smetacek et al. 1978, 1984, Smetacek & Hendrikson 1979, Smetacek 1980a,b, 1984). Peaks in phytoplankton sedimentation occurred during the spring diatom bloom in March and April. The low C:chl *a* ratios of sedimented materials indicated that it was primarily fresh phytoplankton. Phytoplankton sedimentation declined from May through August during a period when the phytoplankton was dominated by dinoflagellates and microflagellates, and zooplankton were abundant. The high C:chl *a* and C:N ratios of sedimented materials during summer indicated that it was highly degraded, due to decomposition under warmer temperatures or zooplankton grazing, or both. Sedimentation increased again during fall diatom and dinoflagellate blooms, when low C:chl *a* ratios again indicated that sedimented material was primarily phytoplankton instead of detritus. The highest rates of sedimentation were

during winter, when most material collected in sediment traps was resuspended bottom sediments, with high C:chl *a* ratios, that had been mixed into the water column by turbulence from frequent storms.

There are other recent reports of episodic mass sedimentation of phytoplankton blooms in coastal waters. Bodungen et al. (1981) similarly reported that a spring bloom in the Baltic, comprising mainly the diatom *Skeletonema costatum*, sank to the benthos. This occurred under calm sea conditions, prior to seasonal thermal stratification. Calculated sinking rates for the *S. costatum* bloom were 30 to 50 m d^{-1}. Cadée (1985) found that macroaggregates with intact cells of the coccolithophorid *Emiliana huxleyi* embedded in mucoid materials were collected in floating sediment traps in the epipelagic, but below the euphotic zone (40 to 70 m depth), during a spring bloom in the North Sea, just after the maximum abundance of this coccolithophorid in the surface layer. Sedimentation of seasonal blooms has also been observed in other nearshore waters off northern Europe (Peinert et al. 1982, Davies & Payne 1984, Cadée 1986, Nicolaisen & Christensen 1986, Noji et al. 1986, Peinert 1986, Skjoldal & Wassmann 1986, Rey & Skjoldal 1987, Kempe & Jennerjahn 1988, Lutter et al. 1989, Wassmann et al. 1991, Passow & Wassmann 1994, Trimmer et al. 1999, Reigstad et al. 2000, Olesen 2001), the Canadian Arctic (Atkinson & Wacasey 1987, Hsiao 1987, Tremblay et al. 1989, Riebesell 1993), British Columbia (Sancetta & Calvert 1988, Sancetta 1989a), California (Alldredge & Gotschalk 1989, Gotschalk & Alldredge 1989, Logan & Alldredge 1989), Washington (Kiørboe et al. 1996), Alaska (Laws et al. 1988, Hansell et al. 1989, Waite et al. 1992), Narragansett Bay (Riebesell 1989) and Antarctica (Bathmann et al. 1991, Karl et al. 1991, Leventer 1991, Rutgers van der Loeff & Berger 1991, Gowing et al. 2001). Walsh (1983) has speculated that mass sedimentation of phytoplankton blooms to continental shelf sediments may represent substantial global sinks of carbon and nitrogen, and a simulation by Boyd & Newton (1999) suggests that sinking of large ungrazed phytoplankton cells, probably diatoms, may be a major determinant of the flux of particulate organics in several ocean habitats.

Smetacek (1985) has argued that rapid mass sinking of diatom blooms may be a transition from growing to resting stages in the life histories of these algae. Smetacek suggested that sinking is of survival value in diatom species that survive long periods in cold and dark, but not warm nutrient-depleted surface waters. Formation of mucous diatom flocs would accelerate sinking rates of diatoms to depth, away from surface strata with high population levels of zooplankton, during or immediately prior to seasons of maximum grazing pressure. Smetacek (1985) also suggested that

diatom sinking may 'seed' coastal sediments with diatom resting spores, contributing to persistence of diatom species in an area by providing seed populations for the next growing season. Bodungen et al. (1986) found evidence for such a scenario in the Antarctic Peninsula region. Formation of diatom aggregates has also been shown to enhance sedimentation in the North Sea (Riebesell 1991a,b) and in the Antarctic (Riebesell et al. 1991).

Mass sedimentation of diatoms appears to have been occurring for tens of thousands to millions of years. Jordan et al. (1991) invoked flocculation as a mechanism explaining a 3 cm thick layer of well-preserved diatom sediments from the upper Pleistocene in the Antarctic. Sancetta et al. (1992) summarized data on sinking of rhizosolenid diatoms and concluded that this is a common occurrence now, as well as in the past (Sancetta 1993). Schubert et al. (1998) used organic chemical biomarkers in sediments to reveal that the relative proportions of diatoms and dinoflagellates remained similar but that combined phytoplankton abundances tracked changes in ocean productivity in the Arabian Sea over the last 200 000 yr.

Sapropels (sediment layers with high concentrations of organic carbon) from the Pliocene to the Pleistocene age (5 million to 10 000 yr old) from the eastern Mediterranean are composed primarily of rhizosolenid diatoms (Kemp et al. 1999, Sancetta 1999). These appear to have formed dense mats during summer, which would be expected to be an oligotrophic period. However, such diatoms have endosymbiotic nitrogen-fixing cyanobacteria, which might have enabled them to survive during stratified nitrogen-depleted conditions. Mass sedimentation of these diatoms appears to have contributed to the widespread coincident hypoxia or anoxia recorded in these sediments.

Seasonal mass sedimentation of large diatoms is still a major feature in modern seas (Kemp et al. 2000, Smetacek 2000, Trull & Armand 2001). Examination of laminated sediments and diatom fluxes from sediment traps from the Gulf of California and the Mediterranean led Kemp et al. (2000) to propose that where there is a strong seasonal thermocline and nutricline, several taxa of 'giant' (>50 µm in longest dimension) diatoms may be able to generate substantial production at depth during the summer. Included would be several species of the genera *Rhizosolenia*, other rhizosolenids such as *Proboscia* and *Pseudosolenia*, and species of *Stephanopyxis*, *Thalassiothrix* and *Coscinodiscus.* Some large diatoms such as these appear to be adapted to low light (Goldman 1993) and able to vertically migrate between the euphotic zone and nutrient-rich deeper layers by controlling buoyancy (Villareal et al. 1993, 1996, 1999). Their large size and robust thecae may also make them harder for grazers to eat; thus,

they may live longer, allowing a biomass buildup (Smetacek 2000). If these giant diatoms persist at depth throughout the stratified summer period, autumn mixing may cause a 'fall dump' of these diatoms, which can produce as much, if not more, export production of diatoms as the typical spring bloom. This might prompt re-evaluation of the common assumption that diatomaceous sediments are paleontological evidence of upwelling because they might have been deposited under oligotrophic conditions instead.

Kiørboe et al. (1998) found that diatom aggregates in the Benguela Current upwelling were extremely sticky and contributed little to vertical flux. This was because aggregates became colonized by the heterotrophic dinoflagellate *Noctiluca scintillans* (Tiselius & Kiørboe 1998), which not only grazed on the diatom aggregates but also imparted buoyancy to them so that they did not sink.

Svensen et al. (2001) tested the hypotheses that increased levels of silicate would favor diatom growth, with consequent increases in sedimentation, and that increased turbulence would increase diatom sedimentation through increased aggregation. Neither hypothesis was upheld. While increased silicate did enhance diatom growth, this did not increase phytoplankton sedimentation, relative to communities dominated by flagellates, and increased turbulence had no effects on sedimentation of diatom- versus flagellate-dominated assemblages.

There can be a rapid benthic response to organic input from sinking phytoplankton blooms in shallow water. Graf et al. (1982, 1984) found that there was immediate stimulation of benthic microbial activity following sedimentation of a spring phytoplankton bloom in Kiel Bight. The bivalve *Macoma baltica*, a macrobenthic sediment surface feeder, commenced accumulation of lipid and glycogen reserves immediately following bloom sedimentation. Responses of other macrobenthic animals were less clear. It appeared that the organic material contributed by this bloom was remineralized within 2 to 3 wk, so its overall contribution to the annual benthic energy budget was only 15 to 25%. During sedimentation of subsequent phytoplankton blooms in Kiel Bight, Graf et al. (1983) found that an autumn phytoplankton bloom was not consumed rapidly by microbial processes, but a spring bloom was consumed within 5 to 6 wk. A simulation of the responses to the fall bloom agreed with field observations (Graf 1987). Supply of food from the surface layer to the benthos, as deduced from sediment samples, appears to be an important factor affecting macrobenthic community structure, biomass and metabolism on the continental shelf in the Bering and Chukchi Seas (Graebmeier et al. 1988, 1989, Graebmeier & McRoy 1989). Meiofauna gave varied re-

sponses to sedimenting phytodetritus, in that it was extensively ingested by harpacticoid copepods but not by other meiofauna (Rudnick 1989) or that there were no apparent relationships between interannual variations in meiofaunal abundance and supply of sedimenting phytodetritus in Auke Bay, Alaska (Fleeger et al. 1989). In the Cretan Sea (northeast Mediterranean), seasonal deposition of phytodetritus stimulated benthic responses by bacteria (Danovaro et al. 2000c) and meiofauna (Danovaro et al. 2000a). Deposition from phytoplankton blooms can also alter sediment nutrient regimes (Conley & Johnstone 1995) and production of dimethylsulfide (DMS) (Osinga et al. 1996).

Phytoplankton blooms can also sink directly into deep water (reviewed by Rice et al. 1986). Deuser & Ross (1980) and Deuser et al. (1981a) found that the flux of organic carbon and particles to the deep (3200 m) Sargasso Sea near Bermuda appeared closely tied to the annual cycle of phytoplankton primary production in surface waters. This signal persisted despite interannual variations (Deuser 1986, 1987, Deuser et al. 1990, 1995). This suggested that there was an efficient mechanism for rapid export (<60 d) of even fine particles from the surface to abyssal depths.

Billett et al. (1983) confirmed the rapid seasonal sedimentation of intact phytoplankton cells to depths of 1 to 4 km in the deep sea off Scotland. Phytoplankton was part of an amorphous organic matrix of fluffy detritus, which time-lapse photography revealed arrived on the sea floor within time intervals of a few hours during the spring-summer bloom period of April to July. Surface sediment samples revealed that the detrital matrix contained intact phytoplankton assemblages resembling those of spring and summer blooms in the overlying near-surface waters during periods immediately prior to sedimentation events. Spring blooms were dominated by diatoms, whereas summer blooms contained proportionately more coccolithophorids. Such rapid sedimentation implied sinking to depths of 2000 m over periods of as little as 2 to 3 wk, or sinking rates of 100 to 150 m d^{-1}. Incorporation of phytoplankton cells into fecal pellets may help explain the rapid descent in summer but not in the early spring, when zooplankton abundance was low, and fecal pellets were scarce in the settled detritus. It was suggested that incorporation of phytoplankton cells into gelatinous matrices enhanced sedimentation rates. Lampitt (1985) showed in subsequent years that the phytoplankton sedimentation recorded by Billett et al. (1983) was not an isolated incident but rather a regular summer occurrence, and extended the recorded depth of this phenomenon from 2000 m to 4000 m. Phytodetrital aggregates sinking from surface layers to 4500 m in the North Atlantic contained a rich community of active bacteria and cyanobacteria

(Turley & Mackie 1995), which rapidly degraded and transformed the sedimented material in the deep sea (Lochte & Turley 1988, Pfannkuche 1993), as well as phaeodarian radiolarians and their fecal pellets (Riemann 1989). The formation of phytoplankton aggregates relates partly to coagulation efficiency ('stickiness'), which increases when cell growth decreases and nutrient limitation increases (Kiørboe et al. 1990). Such phytodetrital material is also utilized as food by a wide variety of benthic animals (Thiel et al. 1988) and benthic foraminifera (Gooday 1988). Widespread and abundant phytodetrital aggregates have also been photographed on the sea floor between 450 and 2400 m after the spring bloom on the continental slope of the northwestern Atlantic (Hecker 1990).

Similar linkages between seasonality of surface productivity patterns and vertical flux to the deep sea have been recorded for many areas. These include the Panama Basin (Honjo 1982), the Black Sea (Hay et al. 1990), the Arabian Sea (Haake et al. 1993), the Antarctic (Wefer et al. 1990, DiTullio et al. 2000), the North Pacific (Scharek et al. 1999), the North Atlantic (Honjo & Manganini 1993, Passow & Peinert 1993, Pfannkuche 1993), the Cretan Sea (Danovaro et al. 2000a) and the Barents Sea (Wassmann 1989, Wassmann et al. 1990, 1994, Andreassen et al. 1996, Andreassen & Wassmann 1998). Seasonally atypical transient-episodic vertical fluxes in the Sargasso Sea can also deliver labile phytoplankton-derived detritus not associated with the spring bloom to the deep Sargasso Sea to depths of 3400 m (Conte et al. 1998).

It has been suggested that mucoid agglomerations collected from the deep North Atlantic in 1857, which were described in 1868 by Thomas Henry Huxley as *Bathybius haeckelli*, may have actually been collections of settled detrital 'fluff' containing phytoplankton (Rehbock 1975, Rice 1983). The story is frequently repeated in introductory oceanography textbooks of how Huxley thought that *B. haeckelli* was a primordial life form, but his explanation was subsequently discredited during the circumglobal expedition of the HMS 'Challenger' (1872 to 1876), when it was concluded that *B. haeckelli* was nothing more than a precipitate caused when seawater samples were preserved in alcohol. Rice (1983) has shown, however, that in Huxley's descriptions of *B. haeckelli*, he noted inclusions that he called 'coccoliths', which had likely originated from coccolithophorids, although Huxley was unaware of this at the time. Subsequent drawings of *B. haeckelli* by Haeckel (reproduced by C. Wyville Thomson [1873], Fig. 63, presented in Rice 1983) show what are clearly coccoliths and coccolithophorids in the *B. haeckelli* matrix. Rice (1983) concluded that there is strong circumstantial evidence that the original samples of *B. huxleyi* collected in June and July of

1857 in the northeast Atlantic may have been sedimented blooms of coccolithophorids in a gelatinous matrix, such as those described for the same area and season by Billett et al. (1983). There is increasing evidence of seasonal sedimentation of particulates to various locations in the deep sea (Deuser & Ross 1980), including coccolithophorid blooms (Honjo 1982) and pine pollen (Hinga et al. 1979), which becomes incorporated into copepod fecal pellets (Turner 1991).

There are apparent deep-sea benthic responses to seasonality of phytoplankton and other particulate sedimentation (reviewed by Tyler 1988, Gooday & Turley 1990). Tyler et al. (1982, 1990) found that annual reproductive periodicities and between-species synchrony in the reproductive cycles of several species of deep-sea echinoderms in the northeast Atlantic matched the productive cycle in the overlying surface waters. Echinoderm spawning occurred in late winter and early spring, coincident with the spring bloom. Witte (1996) found similar seasonal reproduction in deep-sea sponges coincident with episodic vertical flux. Lampitt (1990) presented photographic evidence for a single barnacle on the deep-sea floor that its growth rate over a period of 7 mo was high and enhanced by the annual deposition of phytodetritus from the surface layer. Smith & Baldwin (1984) found that sediment community oxygen consumption (SCOC) off California and Hawaii at depths of 3800 to 5900 m was seasonal, with the highest values in early summer, suggesting a benthic response to seasonality of surface productivity. Cole et al. (1987) found that of the organic carbon that sedimented to 3856 m, comprising largely coccolithophorids and associated macroaggregates, 50 to 85 % was remineralized within 1 yr, and the decomposition of these surface-derived particulates accounted for virtually all of the benthic decomposition at this site. Turley & Lochte (1990) confirmed the potential for microbial processing of phytodetritus in laboratory experiments in which sterile detritus was incubated with deep-sea microbial communities under simulated abyssal conditions of high pressure and low temperature. Williams et al. (1987) used carbon isotopes to estimate that maximum estimates for turnover of organic carbon was 4 to 18 yr in chronologically old bathy- and abyssopelagic fish and crustaceans from the North Pacific, and that rapid sinking of organic detritus from the surface was the primary source of organic carbon in the diets of these animals. Gooday & Lambshead (1989) found that phytodetritus seasonally settled to the deep sea in the northeast Atlantic was a microhabitat for benthic foraminiferans, and that patchiness of phytodetritus caused patchiness and species distributions of foraminiferans. Graf (1989) found that a pulse of copepod fecal pellets to the deep-sea benthos in the Norwegian Sea was utilized in < 8 d by burrowing infauna. A detrital layer on the bottom of the northeast Pacific was seasonally composed of diatoms in summer or radiolarians in fall (Beaulieu & Smith 1998), but there was no significant correlation between distribution and abundance of deep-sea echinoderms and seafloor phytodetritus (Lauerman & Kaufmann 1998). Pfannkuche et al. (1999) found that the benthic community response to sedimentation of a spring bloom in the North Atlantic included transient increases in metabolic activity but not in benthic biomass.

Supply and demand of organic matter for the deep-sea benthos

There have been several studies indicating that episodic input of organic matter to the deep-sea benthos appears to be an important aspect of supply and demand relationships. Comparisons of the supply of POC sedimenting to the floor of the North Pacific and SCOC, normalized to mineralization to CO_2, indicated shortfalls of carbon supply in meeting sediment consumption demands of as much as 97 % of mean values (Smith 1987, 1989). These results were based on short-term measurements (14 d) of sediment-trap accumulations of POC and measurements of SCOC with *in situ* benthic respirometers. However, in a long time series (> 2 yr) of these measurements in the same area (Smith et al. 1992), when episodic input of POC was included in supply, there was agreement within 15 % between organic carbon supply and demand. Smith et al. (1992) concluded that episodic inputs of organic matter can be critical for sustaining abyssal benthic communities below surface layers where seasonal inputs of primary production sediment to depth. In fact, Riebesell & Wolf-Gladrow (1992) simulated particle flux due to phytoplankton bloom aggregation and found that particle flux to the deep ocean could be solely explained by this process. Smith et al. (1994) confirmed concurrence of increased SCOC with episodic seasonal input of POC, and time-lapse photography revealed that mobile epibenthic megafauna such as holothuroids and echinoids were twice as active when detrital aggregates reached the sea floor at 4100 m in spring as during other periods of the year.

Long-term time-series studies reveal that sedimentation patterns in the oligotrophic oceanic waters have seasonal, interannual and decadal components, as well as responses to major environmental perturbations such as upwelling or El Niño-Southern Oscillation events (Karl et al. 1996, Michaels & Knap 1996, Pilskaln et al. 1996, Baldwin et al. 1998, Drazen et al. 1998, Lee et al. 1998, Smith & Druffel 1998, Thunell 1998a, Hanson et al. 2000). The range of vertical

flux, excluding highly variable polar regions, varies about 11-fold world-wide, and there is a general linear relationship between surface primary productivity and organic carbon flux to 2000 m (Lampitt & Antia 1997). However, there are still major uncertainties regarding amounts of primary productivity exported by vertical flux and how these vary between locations, over time and with water-column food-web structure (Michaels et al. 1994a, Rivkin et al. 1996, Boyd & Newton 1997, Doney 1997, Emerson et al. 1997, Hansell et al. 1997a, Karl et al. 1997, McGillicuddy & Robinson 1997). Climate-induced domain shifts toward an ecosystem dominated by prokaryotes over the last 3 decades may be occurring in the North Pacific (Karl et al. 2001a), and this may have altered nutrient stoichiometry and flux pathways (Karl et al. 2001b) as well as export processes (Christian et al. 1997).

There is evidence, however, that at least some portions of the deep sea may be undergoing sustained reductions in the supply of organic matter supplied by vertical flux, and that these reductions may be related to processes in the overlying water column and atmosphere. A 7 yr time series of supply of POC sedimenting to the sea floor at 4100 m in the northeastern Pacific and SCOC revealed a pronounced decline in POC (52 to 59%) without any significant reduction in SCOC from 1989 to 1996 (Smith & Kaufmann 1999). This coincided with a period of increasing sea surface temperatures and declines in primary production, zooplankton biomass, kelp production and seabird abundance in the North Pacific (Druffel & Robison 1999). Smith & Kaufmann (1999) suggested that if these temperature increases are related to anthropogenic increases in greenhouse gases in the atmosphere, and if the decline in food supply to the deep sea is not reversed, concomitant shifts in the characteristics and composition of deep-sea benthic communities and the role of the ocean in the global carbon cycle could result. This apparent 7 yr deficit was reversed in the eighth year, by an increase in sedimentary flux (Smith et al. 2001). What remains to be seen is whether much of the ocean bottom periodically experiences deficits of sedimented POC relative to SCOC. In the only other long-term study of these parameters, in the Sargasso Sea off Bermuda, SCOC appears relatively constant over time, and sedimented POC appears sufficient to balance it (Sayles et al. 1994). Smith et al. (2001) suggested that additional sources of organic matter undersampled by sediment traps, such as episodic lateral advection, terrestrial discharges or long-term climate variations in the oceanic production system, may be important in resolving discrepancies between organic matter supply and demand in the deep sea.

SUMMARY

The vertical flux in the sea is due to intertwined combinations of zooplankton and nekton fecal pellets, marine snow and phytoplankton detritus. Some fecal pellets attach to marine snow, some forms of marine snow are fecal pellets, and some phytoplankton detritus forms marine snow. Portions of this flux reach the benthos, but much, if not most, is repackaged or recycled in the water column. Synthesis of the relative contributions of fecal pellets, marine snow and sinking phytoplankton to vertical flux and water-column recycling is elusive, since these processes are highly variable, situation specific and dependent on multiple interacting factors. Within the last 2 decades a major discovery is that the deep sea is not as unvarying as earlier thought, but rather is subject to seasonal and episodic inputs of sedimenting organic matter, which may provoke benthic biological responses. Further, the sedimentary flux of fecal pellets, marine snow and phytodetritus is important not only to communities on the sea bottom but also to those in the water column. Together, fecal pellets, marine snow and sinking phytoplankton are major components of the 'biological pump' that not only transports and recycles materials in the sea but also may scrub greenhouse gases from the atmosphere.

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