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Detritus in the pelagic ocean

Michael R. Stukel[1], K. A. S. Mislan[2], Moira Décima[3], and Laura Hmelo[4]*
[1]University of Maryland Center for Environmental Science, Horn Point Laboratory
[2]Princeton University, Atmospheric and Ocean Sciences Program
[3]University of California – San Diego, Scripps Institution of Oceanography
[4]University of Washington, Department of Microbiology

Abstract

Detritus is a ubiquitous and diverse component of the pelagic ecosystem. It comprises a wide class of particles created by such diverse processes as cell death, egestion, and aggregation. Detrital particles span several orders of magnitude in size and have distinctly different chemical and physical properties. As a consequence, the propensity of detrital particles to serve as substrates for bacteria or grazers, passive particles drifting through the ocean, or conduits for rapid flux into the deep ocean is highly variable. In this chapter, we review the diverse nature of detrital particles and corresponding production and loss terms in the pelagic ocean, as well as current attempts to include detritus in ecological and biogeochemical models. Our goal is to bridge the gap between field experiments and modeling studies by highlighting properties of detritus that vary predictably between classes and can be both measured in the field and incorporated into the next generation of pelagic ecosystem models.

Section 1. Introduction

Detritus (nonliving particulate material) is an important, but under-studied, component of marine food webs. It is produced by a variety of distinct biotic and abiotic processes including (but not limited to) grazing, organismal death, and aggregation. As a consequence of a wide range of production mechanisms, detrital particles and aggregates can vary widely in their chemical and physical properties. In particular, size, porosity, and lability (the chemical composition of a particle that determines nutritional availability to bacteria and grazers) strongly affect the role and fate of different components of the detritus. Detritus can be used by both particle-associated bacteria and grazers and plays a distinct role in marine biogeochemical cycles as it sinks out of the euphotic zone or is redistributed by advective transport.

Detritus dominates the standing stock of particulate matter in the oceans, comprising over 50% of particulate organic matter (POM) in most surface ocean regions and an even higher fraction at depth (Riley 1970; Yanada and Maita 1995). Yet, compared with living organic matter, the detrital pool remains understudied (for a review of total POM in the ocean, see Volkman and Tanoue 2002). Early studies of nonliving material in aquatic ecosystems focused primarily on dissolved material (Wood 1968) or detritus in lacustrine, fluvial, and coastal environments (Melchiorri-Santolini and Hopton 1972) and were conducted prior to the discovery of abundant marine bacterial populations. A decade later, another symposium (Roman and Tenore 1984) began to highlight a modern view of marine detritus as a micro-habitat for bacteria (Jacobsen and Azam 1984; Pomeroy et al. 1984) and protozoans (Goldman 1984), food source for mesozooplankton (Roman 1984a), and transporter of carbon to depth (Karl and Knauer 1984). In the three decades since, a wealth of new instruments and techniques (including the proliferation of three-dimensional biogeochemical models) has added greatly to the body of detritus literature. Yet conversely, this proliferation of new techniques has led to specialization and disconnect between different sub-disciplines. Few studies consider multiple components of the broader detrital pool, and ecosystem models typically conflate this diverse class of particles into one or a few model compartments. This coarse representation of a class of particles with important biogeochemical roles is likely hindering our understanding of heterotrophy in the surface ocean and supply of organic matter to the mesopelagic.

The importance of detritus in marine ecological models is

*Corresponding author: E-mail: mstukel@umces.edu

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highlighted by the fact that detritus is one of only four state variables included in simple nutrient, phytoplankton, zooplankton, detritus (NPZD) models (Olson and Hood 1994; Anderson 2005). Nevertheless, detritus has typically been treated as little more than a pragmatic tool to introduce a time-lag in remineralization or mediate vertical flux, whereas many of the ecological roles of detritus have been neglected. In fact, with few exceptions, the only way in which model treatment of detritus is validated (if at all) is by comparison of vertical detritus flux to total particulate organic carbon (POC) export. Yet even this simple model validation is highly misleading, as models typically assign detritus a slow sinking rate (e.g., Fasham et al. 1990) that may be an order of magnitude lower than in situ measured rates (McDonnell and Buesseler 2010). This imbalance implies that many models may drastically overestimate the standing stock of sinking detritus, with concomitant effects on its availability to grazers and bacteria. Depiction of accurate detritus dynamics will require both an attempt by field investigators to frame their results in a manner that is accessible to modelers and a willingness by modelers to rethink model construction.

In this chapter, we synthesize field and laboratory studies detailing the nature, production, and loss terms of detritus in the pelagic ocean, while also highlighting how detritus has been treated in biogeochemical and ecosystem models. Our goal is to simultaneously reveal gaps in our knowledge of detritus and suggest opportunities for incorporating a more sophisticated view of detritus into models. Whereas conceding that the diversity of goals of biogeochemical models makes it foolish to suggest a single approach for incorporating detritus into models, we hope to facilitate the development of a common language for exchange between modelers and experimentalists.

This review is broken into four parts. In the first section, we highlight the diversity of marine detrital particles (including organic material and minerals) and formation processes. In the second, we discuss biotic and abiotic loss terms for detritus. Together, these production and use processes determine the detrital makeup, and hence, role of detritus within a given ecosystem. We then review current model treatment of detritus, before finally addressing potential avenues of future research.

Section 2. Components of detritus

Detritus, broadly defined as nonliving particulate matter, constitutes a heterogeneous class of marine particles that is often treated simplistically in representations of the pelagic ecosystem. Marine detritus includes, but is not limited to, 'dead' phytoplankton, fecal pellets, molts and dead organisms, aggregates, and terrigenous material (Fig. 1). These types of detritus vary widely in size, porosity, and chemical composition, with different classes playing distinct biogeochemical roles, including export of matter to depth, support of epipelagic and benthic particle feeders, and host for particle-attached bacteria and hence sites of intense remineralization and nutrient regeneration. The balance of sinking, advection, and remineralization of detritus determines not only bulk export rates, but also the depth of penetration of sinking particles into the ocean interior, and hence the duration that carbon will be sequestered from the atmosphere. For instance, when salp fecal pellets are a dominant form of surface ocean detritus, we can expect efficient carbon flux to the local benthos (Pfannkuche and Lochte 1993; Phillips et al. 2009). However, a detrital pool comprised largely of porous aggregates will likely be remineralized near the base of the euphotic zone (Jackson and Checkley 2011) and/or transported long horizontal distances as it sinks, resulting in a decoupling of production and export (Plattner et al. 2005). Thus two ecosystems with equal new production rates can have vastly different carbon export and sequestration potentials depending on their detrital composition. Elucidation of the diversity of detrital particles, as well as characterization of the similarities and differences within, is thus critical for accurate coupling of pelagic food web processes to global biogeochemical cycles. In this section, we will address the myriad forms of detritus found in the ocean, while paying particular attention to the distinct ecological roles of each. We will also address some of the methods used to sample these particles.

Dead phytoplankton

As the base of the pelagic food web, phytoplankton dominate production processes, and hence dead phytoplankton potentially form a dominant class of detrital particles. Nevertheless the term 'dead phytoplankton' needs some explanation as it can be used to refer to a range of particles from non-photosynthesizing phytoplankton (Berden-Zrimec et al. 2009) to the phytoplankton membranes and organelles remaining after sloppy feeding by mesozooplankton (Roy et al. 1989) or viral lysis (Fuhrman 1999; Balch et al. 2007). Sandwiched between those extremes are biochemically inert phytoplankton, including resting spores (McQuoid and Hobson 1996), and non-vital cells that may have permeable membranes or lack nuclei (Alonso-Laita and Agusti 2006; Bidle and Bender 2008; Hayakawa et al. 2008). Some phytoplankton transported beneath the euphotic zone on aggregates or through subduction may be treated effectively as detrital particles, yet still be able to regain full metabolic health if returned to the surface. Even cells contained within fecal pellets have been shown to remain vital at times (Jansen and Bathmann 2007). Fluorescent stains (Timmermans et al. 2007), transmission electron microscopy (Bidle and Bender 2008), membrane permeability tests (Agusti and Sanchez 2002; Hayakawa et al. 2008), and fluorescence methods (Berden-Zrimec et al. 2009) have all been used to assess the vitality of phytoplankton cells. Few studies have, however, applied these techniques in marine ecosystems and generally phytoplankton cells in the surface ocean are considered vital, whereas phytoplankton below the euphotic zone are considered a part of detritus. For the remainder of this section we will use the term 'dead phytoplankton' to refer to all phytoplankton that are unlikely to

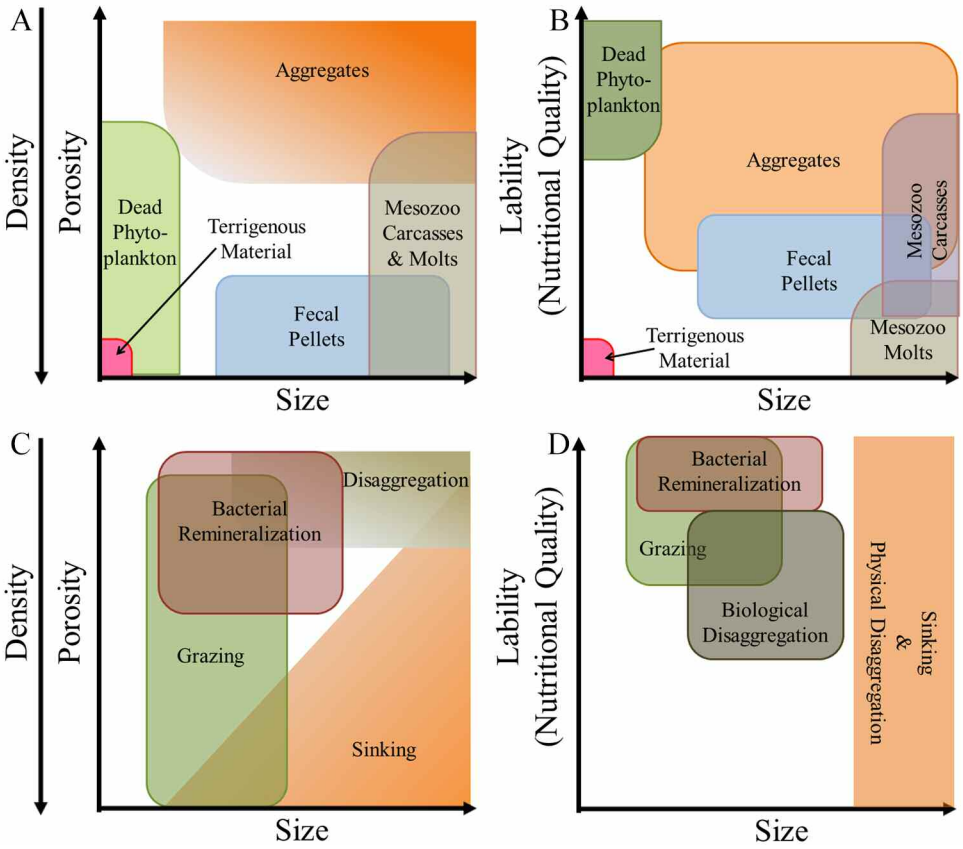

Fig. 1. Conceptual diagram of detritus properties. Panels A and B show properties of different components of the detrital communities, whereas panels C and D show the likelihood of different detrital loss mechanisms acting on particles with different properties. Panels A and C show size versus porosity (or density), and panels B and D show size versus lability. All graphs should be considered simple conceptual diagrams, as consistent and comparable data for accurately classifying detritus is scarce.

photosynthesize in the future (including resting stages and viable cells in the deep ocean). Although we focus on phytoplankton in this section as a result of their high biomass and production, we note that many of the same discussions apply to other nonvital protists and bacteria.

Dead phytoplankton exist in all regions of the ocean, including the euphotic (Agusti and Sanchez 2002; Alonso-Laita and Agusti 2006; Hayakawa et al. 2008), mesopelagic (Knappertsbusch and Brummer 1995; Martin et al. 2011), bathypelagic (Silver and Alldredge 1981), and benthic zones (Garrison 1981; Pfannkuche and Lochte 1993; Smith et al. 1996). Within the euphotic zone, dead phytoplankton comprise a highly variable proportion of the total phytoplankton cells (Alonso-Laita and Agusti 2006; Baudoux et al. 2008; Hayakawa et al. 2008), and at times, may exceed 88% of total phytoplankton (Alonso-Laita and Agusti 2006) and 80% to 90% of total biogenic silica (Krause et al. 2010). Whether or not dead phytoplankton are counted amongst the living phytoplankton depends on the physiological state of the cells (e.g., presence or absence of chlorophyll) and the method of enumeration used. Euphotic zone cell viability has been shown to be related to nutrient and irradiance levels (Timmermans et al. 2007) and season (Hayakawa et al. 2008). Nevertheless, the differences in biogeochemical fate of living and dead phytoplankton remains to be seen. Viable and nonviable cells likely behave similarly with respect to grazing, aggregation, and export except in taxa where active buoyancy control or grazer-deterrence are common.

Phytoplankton are often a dominant component of sinking particles. Laboratory experiments have typically found very low sinking rates for individual phytoplankton (Smayda 1970; Smayda and Bienfang 1983). However, the large export flux following the termination of diatom (Honjo and Manganini 1993; Martin et al. 2011) and coccolithophorid (Foster and Shimmield 2002; Fischer and Karakas 2009) blooms suggests that at times phytoplankton may sink much more efficiently. Large phytoplankton flux events may be triggered by aggregation events (Alldredge et al. 1995) or packaging into fecal pellets (Pfannkuche and Lochte 1993). Phytoplankton with mineral shells (siliceous and calcium carbonate) also play a distinct role in vertical flux through a mineral ballasting effect (Armstrong et al. 2002) that increases the sinking rate of not only cells, but of other particles that contain the phytoplankton remains.

Fecal pellets

Globally, mesozooplankton directly graze roughly 12% of total phytoplankton primary production (Calbet 2001). Total mesozooplanton ingestion rates are likely significantly higher due to grazing on protozoans and detrital particles (Zeldis et al. 2002; Diodato and Hoffmeyer 2008) as well as carnivory by higher trophic level mesozooplankton (Le Borgne et al. 2003). Since mesozooplankton typically egest 30% of ingested carbon (Conover 1966; Pagano and Saintjean 1994; Cowie and Hedges 1996; Liu et al. 2006), fecal pellet production is a significant fraction of primary production and hence total detritus production.

Fecal pellets vary widely in their physical and chemical properties, which are dependent not only on the taxonomic origin of the fecal pellets, but also the diet and metabolic state of the zooplankton. Zooplankton fecal pellets vary in size from 3 μm "mini-pellets" (Gowing and Silver 1985) to centimeter-sized salp fecal pellets (Matsueda et al. 1986). (We will not consider the much less abundant fecal pellets of fish and marine tetrapods in this review). While some fecal pellets are amorphous, many mesozooplankton taxa produce recognizable fecal pellets that vary from tiny nondescript spheres to the long cylindrical pellets of euphausiids or the tabular pellets of salps (Turner 2002; Wilson et al. 2008). Most crustacean fecal pellets are encased within a chitinous peritrophic membrane (Fowler and Knauer 1986) that slows remineralization and mechanical disruption, but may serve as an active site of bacterial colonization (Jacobsen and Azam 1984).

As fecal pellets contain ingested but unassimilated material, they presumably have reduced nutritional quality compared with the prey of mesozooplankton. In particular, they often have increased mineral contents (Knappertsbusch and Brummer 1995; Dagg et al. 2003; Ploug et al. 2008b) and high C:N ratios (Checkley and Entzeroth 1985). Labile organic matter, including polysaccharides, amino acids, and fatty acids, are preferentially used by zooplankton and hence depleted in fecal pellets (Cowie and Hedges 1996; Mayzaud et al. 2007). However, some prey species resist digestion (Cowie and Hedges 1996; Gorsky et al. 1999; Paffenhöfer and Koster 2005), suggesting that their presence in the water column may increase the content of labile organic matter contained in fecal pellets. Additionally, gut passage time is inversely related to ingestion rates so at high feeding rates in prey-rich regions fecal pellets likely have lower C:N ratios and higher amounts of amino acids than fecal pellets produced by mesozooplankton existing in near starvation conditions.

Fecal pellet sinking speed is generally considered to be a function of size and density (Komar et al. 1981; Yoon et al. 2001; Turner 2002), although at times in situ sinking velocities of small particles may exceed those of larger particles (McDonnell and Buesseler 2010). Nevertheless, the general trend of faster sinking speed for large pellets suggests that the size spectra of fecal pellets directly impact their biogeochemical role. Few studies have sampled the distributions of fecal pellets suspended in the water column, hence size spectra of euphotic zone fecal pellets can only be estimated from production and removal rates. The taxonomic composition of both the zooplankton and prey communities determine the size spectra of produced fecal pellets. However, the size distribution of the standing stock of fecal pellets in the surface ocean is likely dominated by small pellets at all times. In fact, a simple calculation suggests that if grazing was partitioned between salps capable of producing large fecal pellets sinking at 1 km d^{-1} (Caron et al. 1989) and copepods producing small fecal pellets that sink at only 20 m d^{-1} (Small et al. 1979), then even if salps dominated grazing rates by a ratio of 10:1, their large fecal pellets would only represent 17% of the carbon in the euphotic zone. Such calculations are complicated, however, by the fact that pellet disruption can lead to significantly decreased sinking rates and retention in the surface (Alldredge et al. 1987). Compared with their contribution to surface ocean standing stocks, large fecal pellets typically dominate the rate of carbon export, particularly in richer ecosystems (Wilson et al. 2008). They have been suggested to potentially control the rate of carbon export during spring conditions in an eastern boundary current ecosystem (Stukel et al. 2011) and are often found to be the dominant form of POC in sediment trap contents (Turner 2002; Ebersbach and Trull 2008; Gleiber et al. 2012).

Crustacean molts

Crustacean molts are chitinous structures that are shed routinely as organisms mature from one stage to the next. Given the prevalence of crustaceans among the pelagic mesozooplankton, crustacean molts are most likely an important component of the detrital pool. Jerde and Lasker (1966) found that krill in the California Current region produced molts equal to approximately 10% of their dry weight, with a frequency of 1 molt every 5-6 d, and suggested that *Euphausia pacifica* alone could produce almost 1.5 g m^{-2} of molt material every year. Escribano and McLaren (1992) showed that copepod intermolt duration was inversely related to temperature and averaged 2 days at 10.2°C compared with 5-6 days at 3.0°C for *Eurytemora herdmani*. Molts are likely of low nutritional quality, due to the difficulty of breaking down chitin, which can persist in the marine environment for over a month (Kirchner 1995). However, molts and mesozooplankton carcasses do serve as an important substrate for particle-attached bacteria (Kirchner 1995; Tang et al. 2010).

Dead mesozooplankton

Relatively little work has been done on the role of mesozooplankton carcasses in the marine environment, but they may play a significant role in vertical flux of detritus. Mesozooplankton carcasses are large, dense particles that likely sink rapidly. For example, small copepod carcasses sink at speeds > 800 m d^{-1} (Elliott et al. 2010). Krill molts and remains have been shown to be a significant portion of the diet of particle

feeders in an Antarctic midwater ecosystem (Hopkins 1985) and their vertical flux exceeded that of fecal pellets in an oligotrophic area of the Western Mediterranean (Frangoulis et al. 2011). In shallow water regions where resuspension prevents the rapid removal of carcasses by sinking, carcasses may be a significant fraction of the apparent mesozooplankton biomass (Genin et al. 1995; Elliott and Tang 2009) and even in deeper regions carcasses may have a significant standing stock (Haury et al. 1995; Tang et al. 2009).

Aggregates and marine snow

Aggregates, also known as "marine snow" when > 500 μm, can vary in size from tiny aggregates of picoplankton (Albertano et al. 1997) to web-like aggregates that are several meters in size (Precali et al. 2005). As a result of both the difficulty of sampling aggregates without disruption and the range of sizes involved, few studies have systematically sampled the full size-spectrum of marine aggregates. Jackson et al. (1998) used a combination of instruments to assess the size-spectra of particles in Monterey Bay, and found that particle mass was concentrated in 100 μm–1 mm particles. Aggregates can be composed of all the marine detritus types mentioned above, and also contain still living material including bacteria and protists that have actively colonized the aggregates (Caron et al. 1986; Azam 1998; Kiorboe et al. 2002) and living phytoplankton that sink out of the euphotic zone on marine snow particles (Passow et al. 1994). By transforming the size-spectrum of particles in the ocean, aggregation provides additional food sources for large zooplankton (Dilling and Brzezinski 2004; Wilson and Steinberg 2010), increases vertical flux rates out of the ocean (Alldredge and Gotschalk 1988; Ebersbach and Trull 2008; Guidi et al. 2008), and creates refugia for particle-associated bacteria and microzooplankton (Ploug et al. 1999; Simon et al. 2002).

The formation of aggregates is primarily by coagulation processes that are controlled by both collision rates of smaller particles and the probability that colliding particles will stick together. At present, there is a vast gap between aggregation theory (Burd and Jackson 2009) and in situ ecosystem and biogeochemical measurements, due to the inability to measure or constrain many of the parameters used in coagulation models. In particular the 'stickiness' parameter, which defines the probability that two colliding particles will stick together, is critical to coagulation models, but poorly understood and likely to be highly variable. However, clever combinations of new field instruments with model concepts are beginning to allow for more direct assessment of the role of aggregates in the pelagic realm (e.g., Jackson and Checkley 2011).

While aggregates can form by the collision of any two marine particles, there are distinct classes of aggregates that are common in the marine pelagic (Alldredge and Silver 1988). On the small end of the size spectrum are micro-aggregates formed abiotically by coagulation of colloids and nanogels (Wells and Goldberg 1993). Formation rates of such aggregates can be enhanced in surface waters by bubble adsorption (Kepkay and Johnson 1988; Zhou et al. 1998) and laminar shear (Passow 2000). Some precursors of such particles are fibrils small enough to pass through 8 kDa dialysis bags (Passow 2000), though other studies have found that > 2 μm colloids are necessary for coagulation (Johnson et al. 1986). The aggregation of colloidal material into particulate form likely increases their bioavailability, stimulating bacterial respiration and remineralization (Kepkay 1994). The adhesion of colloids and DOM is the only form of aggregation that can truly be considered to create detritus (other forms of aggregation simply alter the detritus size-spectrum). These micro-aggregates are often transparent exopolymer particles (TEP), which are a particularly abundant form of acid polysaccharide and are visualizable with use of alcian blue stain (Passow 2002). Since TEP can exist as discrete particles and are often associated with aggregates, they are thought to play an important role in coagulation (Passow et al. 1994; Passow 2002), though many other exopolymers may also play a role (e.g., Samo et al. 2008). These exopolymers are primarily produced abiotically from coagulation of exudates (Mopper et al. 1995; Passow 2000) produced by phytoplankton when high bacterial concentrations are present or during periods of nutrient-stress that exist during the decline phase of blooms (Staats et al. 2000; Passow et al. 2001),

Many aggregates are formed by coagulation of phytoplankton. All types of phytoplankton, from micron-sized cyanobacteria (Albertano et al. 1997) to large diatoms (Alldredge and Gotschalk 1989), are capable of forming aggregates, although most studies of phytoplankton aggregates have focused on coagulation processes in diatom blooms (Thornton 2002). Phytoplankton aggregation is believed to be controlled by the production of exopolymers (high molecular weight, carbon-rich polysaccharides) that increase the 'stickiness' of individual cells and chains. Exopolymers, including TEP, combined with the high particle concentrations at the end of blooms, may lead to mass flocculation events (Alldredge et al. 1995), which have been observed in several regions (Alldredge and Gotschalk 1989; Boyd et al. 2005; Martin et al. 2011) and even been hypothesized to control maximum phytoplankton concentrations in the ocean (Jackson and Kiorboe 2008).

Another prevalent class of detritus is formed around the discarded mucilaginous food webs of appendicularians and pteropods. While appendicularians strain their prey out of the water, their food webs (houses) eventually get clogged with living and dead organic matter and are discarded. Appendicularians are common throughout the oceans, and can produce between 2 and 40 houses d^{-1} (Sato et al. 2003). Houses vary greatly in size and deflate after being discarded. Deflation leads to a loss of particles that were collected on the active house, and leads to an increased density and sinking speed of detritus formed from houses (Lombard and Kiorboe 2010). Discarded houses accumulate additional particles of various types as they sink through the water column, and may form a

large fraction of the 300-500 μm particles in some ocean regions (Lombard and Kiorboe 2010; Berline et al. 2011). Houses created by large, less abundant appendicularian species can be > 30 cm and have been shown to constitute a significant and undersampled portion of carbon export in Monterey Bay (Robison et al. 2005). Houses serve as food for mesozooplankton (Alldredge 1976) and also as sites of elevated bacterial and zooplanktonic respiration (Davoll and Youngbluth 1990; Steinberg et al. 1997). Typical houses sink at rates of 10-70 m d^{-1} (Lombard and Kiorboe 2010), though sinking rate is likely higher for large houses or for houses with high mineral content.

It is also important to consider the true heterogeneity in aggregate composition and ecological and biogeochemical roles (Alldredge and Gotschalk 1990). Aggregates can be formed by the disruption and subsequent coagulation of fecal material and may contain detrital particles ranging from colloidal picoplankton to rapidly sinking fecal pellets. Their highly fractal nature, porosity, and variable density can lead to widely varying sinking rates. Thus while aggregation is typically considered to increase sinking rates, it can also retard the sinking velocities of the fastest sinking particles. Aggregates can unquestionably serve as sites of increased microbial activity; though it is less certain that the aggregates support greater microbial production than their constituent parts would have prior to aggregation. While aggregation serves to make micron-sized particles available for sinking and ingestion by mesozooplankton (Waite et al. 2000; Wilson and Steinberg 2010), mesozooplankton may not actually derive nutrition from ingested picoplankton as cyanobacteria are often found intact in fecal pellets (Gorsky et al. 1999).

Terrigenous material

Lithogenic and terrigenous material dominates marine sediments near the coast (Mayer et al. 2007; Goni et al. 2008). Near river mouths, entire communities can be controlled by terrigenous input (Ayers and Scharler 2011). Even far from land its role should not be ignored. Colored dissolved organic matter originating from the Amazon River has been observed as part of a plume > 1000 km from the river mouth (Del Vecchio and Subramaniam 2004; Hu et al. 2004). Atmospheric deposition also transports large quantities of nutrients, particularly Fe, from land to open ocean areas downwind of major deserts (Jickells 1999; Krishnamurthy et al. 2010). The variable speciation and solubility of these Fe inputs greatly affects the fraction of Fe available to phytoplankton as opposed to that adsorbed to detritus (Johnson et al. 1997; Barbeau 2006). Trace elements believed to be of lithogenic origin have also been found to be part of sinking flux in the open ocean and attributed to atmospheric deposition at station ALOHA in the North Pacific subtropical gyre or lateral shelf inputs at station K2 in the northwest Pacific subarctic gyre (Lamborg et al. 2008a). Nepheloid layers have also been shown to transport terrigenous material from the continental shelf to pelagic regions (McCave et al. 2001; Karakas et al. 2006; Hwang et al. 2009), and may play a role in restructuring marine snow before it reaches the seafloor (Ransom et al. 1998).

Sampling detritus

The study of marine detritus is difficult for many reasons including: the dilute nature of particulate matter in the pelagic ocean, the fragile nature of aggregates which get destroyed during traditional sampling, and the difficulty in distinguishing between organisms that were dead in the ocean and organisms that died during collection or sample processing. The study of detritus has typically proceeded by use of one of four broad types of approaches. 1) Measurement of production or sinking rates from which detrital importance is inferred. 2) In situ measurement of particle size spectra (including living particles). 3) Detrital stains that can discriminate living from detrital plankton. 4) Collection of sinking material, particularly by sediment traps.

The estimation of detrital production rates is relatively straightforward for the production of detritus by mesozooplankton. Both fecal pellet (Small and Ellis 1992; Poulsen and Kiorboe 2006) and mucous feeding web (Sato et al. 2003) production rates can be measured on plankton collected in situ, and while the results of such studies can be highly variable, the methods are robust and when combined with in situ abundance data allow for the estimation of in situ production rates. For detrital phytoplankton and aggregates, however, estimating production rates is much more difficult. Non-grazer related plankton death rates are difficult to assess (Brum et al. 2013), while aggregate production rates are obfuscated by our inability to directly measure particle stickiness (Burd and Jackson 2009).

In situ measurement of particle size-spectra has been a field of rapid, instrument-driven growth in recent years and is of particular importance to the study of aggregates. Laser optical plankton counters, and particularly those mounted on autonomous gliders and profilers allow rapid measurement of in situ particle sizes (Checkley et al. 2008), though it can be difficult to differentiate zooplankton from aggregates, and have been used to estimate aggregate formation and loss rates (e.g., Jackson and Checkley 2011). Video plankton recorders (Davis et al. 1992; Ashjian et al. 2005) and underwater vision profilers (Stemmann et al. 2008; Picheral et al. 2010) generate particle size-spectra while also photographing particles and hence can be used to differentiate between aggregates and organisms. In situ holography provides information about the distribution of particles in the ocean, and can potentially provide incredibly useful information about the porosity and fractal structure of aggregates (Katz et al. 1999; Malkiel et al. 2006; Graham and Smith 2010). Carbon Explorers (autonomous free-drifting floats designed for carbon measurements) have been developed with the ability to autonomously produce profiles of particulate organic and

inorganic carbon, or measure the sedimentation of particles onto a glass plate at depth (Bishop 2009). Taken together, these methods are just beginning to provide us with a wealth of particle data that could previously only be found by intensive in situ observation.

Detrital stains for protists (Williams et al. 1995; Verity et al. 1996) and mesozooplankton (Elliott and Tang 2009) allow differentiation of living and detrital plankton collected in situ. Further advances in confocal, epifluorescence, and scanning electron microscopy enable researchers to probe the microstructure of aggregates, the relationship between viruses, bacteria, and aggregates, and the molecular composition of aggregates (Holloway and Cowen 1997; Schumann and Rentsch 1998; Luef et al. 2009; Cattaneo et al. 2010).

Vertical particle flux rates, as well as the composition of sinking material, has traditionally been studied with the use of sediment traps, which are prone to both hydrodynamic (Baker et al. 1988) and 'swimmer' (Knauer et al. 1979) biases. Recently introduced neutrally buoyant sediment traps have minimized hydrodynamic biases by traveling with water parcels along an isopycnal layer, thus effectively eliminating shear above the trap mouths (Buesseler et al. 2000; Lampitt et al. 2008). Simultaneously, advancements in the study of material collected within the traps has generated new information on the nature of sinking particles. Acrylamide gels have been deployed in the base of traps to prevent disruption of sinking aggregates, and hence allow new information about the size and porosity of sinking particles (Lundsgaard 1995; Waite et al. 2000). Molecular and genetic techniques, in addition to the microscopic techniques mentioned above, are now used to infer the origin of organic matter found in traps from classification of pigments (e.g., McCave et al. 2001; Lamborg et al. 2008b), lipids (e.g., Yamamoto et al. 2007; Christodoulou et al. 2009; Fischer and Karakas 2009), amino acids (e.g., Salter et al. 2010), and nucleic acids (e.g., Dell'anno et al. 1999; Suzuki et al. 2003).

Section 3. Fate of detritus and mechanisms of loss

The downward flux of POM in the upper ocean exhibits a non-linear decrease with increasing depth (Martin et al. 1987). This pattern of exponential decrease in flux is consistently found in all types of ocean regimes (Berger et al. 1988). Because most of the sinking is done by particles in the larger size categories (see Fowler and Knauer 1986), significant processes leading to the fragmentation and loss of these particles must be occurring in the upper water column. Current flux models, which rely heavily on empirical observations of sinking material collected in traps, provide little insight into the specific mechanisms responsible for flux attenuation (Martin et al. 1987; Armstrong et al. 2001). POM flux is reduced by a continuum of mechanisms ranging from purely physical, abiotic mechanisms to biologically mediated mechanisms. These processes include grazing, disaggregation, remineralization, and solubilization.

Mechanical disruption

Disruption of large particles into small particles will result in an increase in residence time in the upper water column, effectively decreasing the downward flux of POM. Multiple mechanisms of mechanical disruption exist, including both biotic and abiotic processes. In understanding the potential effect of mechanical disruption on the particle spectrum of the ocean, we must remember that the minimal fluid shear required to fragment aggregates increases exponentially with decreasing size (Smith and Kitchener 1978), implying that the larger aggregates are in fact more susceptible to this process. Abiotic fragmentation of aggregates can be caused by fluid shear, while biotic fragmentation can be induced by processes associated with swimming and ingestion.

Physical fragmentation

The hydrodynamic regime in the ocean is generally turbulent. Although large-scale motions contain most of the energy in the ocean, they do not dissipate aggregates. The range of scales of turbulence that can impact aggregates is on the scale of microns to centimeters. For turbulence to affect aggregates, it is necessary to have variations in fluid shear across the length of the aggregate (Parker et al. 1972; Tomi and Bagster 1978). Several theoretical mechanisms have been proposed, including erosion (where small subunits detach), instantaneous pressure fluctuations across the aggregate (resulting in fragmentation), and filament fracture (where organic filaments of the particle break) (Alldredge et al. 1990). The strength of four types of large marine aggregates (>0.5 mm, marine snow) were empirically investigated by Alldredge et al (1990), by measuring the dissipation energy required for their fragmentation in the laboratory. The only types of marine snow found to fragment at dissipation rates < 1cm^2 s^{-3} were the diatom flocs, whereas aggregates of miscellaneous nature and appendicularian houses did not fragment at rates > 1 cm^2 s^{-3}. Because the normal dissipation rates in the ocean range between10^{-2} and 10^{-4} cm^2 s^{-3} (Dillon and Caldwell 1980), physical turbulence is not likely to be one of the major processes leading to fragmentation of marine snow.

Biological fragmentation

There are a few processes induced by marine organisms that can lead to fragmentation of detritus. Fragmentation can occur due to turbulence created by swimming or direct fragmentation during swimming (Dilling and Alldredge 2000), or by handling of aggregates without ingestion (e.g., Banse 1990; Iversen and Poulsen 2007).

Due to their size and numerical abundance, mesozooplankton are major contributors to biological fragmentation. Disruption of marine snow by swimming euphausiids was suggested as an important mechanism of particle fragmentation in a field study in the California Current (Dilling and Alldredge 2000). The direct action of beating pleopods on aggre-

gates was shown to disrupt large particles into a variable number of daughter particles in the laboratory (Dilling and Alldredge 2000; Goldthwait et al. 2004). The radius of effect, i.e., the distance from which particles could be pulled in and fragmented, as by Goldthwait et al (2004), is 6.7 mm for a euphausiid of 1-2 cm in length. This means that in areas with high concentrations of euphausiids and marine aggregates, abundances of 1-10 animals m^{-3} would result in an interaction with 5% to 50% of aggregates, and densities > 20 animals m^{-3} would lead to 100% of particles being affected (Goldthwait et al. 2004). Dilling and Alldredge (2000), found the diel cycle of increase in particle abundance and decrease in average particle size to correlate only with the abundance of the regionally dominant euphausiid species, implying that this process might also be important in the field.

Other mesozooplankton can also potentially affect the particle field via fragmentation during swimming. Ctenophores have been observed to fragment appendicularian houses (Steinberg et al. 1997), and larger animals with greater swimming speeds such as salps and shrimps may also fragment aggregates significantly (Goldthwait et al. 2004).

Handling of aggregates can significantly alter particle size and composition, without the requirement of ingestion. Copepods have been observed to fragment appendicularian houses (Steinberg et al. 1997) and sloppy feeding may break up marine snow (Banse 1990), but most studies have focused on the effect of zooplankton on fecal pellets, which are an important component of the aggregate particle assemblage. There are three processes through which copepods can affect fecal pellets in the field. The first involves grazing on the fecal particle itself, called coprophagy, and has been shown for a number of marine invertebrates (Frankenberg and Smith 1967). The other two important processes involve the handling of fecal pellets. Handling of fecal pellets with consumption of only the peritrophic membrane, which leads to a conservation of most of the POC but significant fragmentation of the particle, is called coprorhexy (Lampitt et al. 1990). Finally, coprochaly involves handling of fecal pellets with no ingestion, which can lead to subsequent fragmentation (Noji et al. 1991). Because these processes, and the relative importance of each, are usually investigated together in laboratory experiments, we will discuss them in a separate section. It is important to remember that of the three, coprochaly would be the only biologically disruptive process involving no ingestion, and therefore technically should be listed with the processes discussed above.

Grazing—Fecal pellet degradation

Mesozooplankton can alter fecal pellets by three processes already mentioned: coprophagy (consumption of fecal pellets), coprorhexy (fragmentation of fecal pellets, usually due to consumption of parts of the peritrophic membrane), and coprochaly (loosening of fecal pellets with no ingestion) (Paffenhöfer and Strickland 1970; Lampitt et al. 1990; Noji et al. 1991).

Coprophagy was determined to be an important feeding strategy in a number of invertebrate species (Frankenberg and Smith 1967), and significant rates of consumption were determined for copepods in the laboratory (Paffenhöfer and Strickland 1970). Coprophagy was also found in a laboratory study using three species of copepods, but only for one small copepod species; the other two fragmented pellets via coprochaly and coprorhexy (Noji et al. 1991). Laboratory experiments showed that the main effect of copepods on fecal pellets were of coprorhexy and not coprophagy (Lampitt et al. 1990). Electron micrograph images show clear damage to the peritrophic membrane after interaction with copepods, a behavior hypothesized to take advantage of the higher nutritional status of the membrane (Lampitt et al. 1990), due to active bacterial colonization in the few hours after egestion (Jacobsen and Azam 1984; Lampitt et al. 1990). These same experiments showed that microbial degradation is low before fragmentation, suggesting this process is essential for the initiation of significant microbial decomposition. Field studies have speculated on the importance of coprophagy by the cyclopoid *Oithona* spp., based on negative correlations between abundance and fecal material in the water column, suggesting it as a key foraging strategy in oligotrophic environments (Gonzalez and Smetacek 1994). Other studies, however, challenge this notion based on combined field and laboratory experiments and suggest that, instead, *Oithona* spp. is an indicator taxa of environments characterized by high degradation rates (Poulsen and Kiorboe 2006), or mediates fragmentation without actual consumption (Kobari et al. 2010). Two different laboratory studies, together investigating the behavior of four different calanoid copepods and the cyclopoid *Oithona* spp. concluded that coprorhexy is the main effect of copepods on fecal pellets (Poulsen and Kiorboe 2005; Iversen and Poulsen 2007). Fecal pellets were generally encountered during foraging and rejected as food items, fragmenting in the process. Consumption of fecal pellets was observed to vary inversely proportional to size, supposedly consumed unintentionally with other food items (Iversen and Poulsen 2007).

The picture that emerges from both laboratory and field studies is that while coprophagy might be an important strategy to procure enough carbon for metabolic demands, the main effect of the zooplankton community on fecal pellets' standing stock and size spectrum is that of fragmentation, usually without significant consumption. A recent study found that the protozooplankton were also significant degraders of zooplankton fecal material, contributing 15% to 53% of the total degradation rate (Poulsen and Iversen 2008). The combined effect of fragmentation by mesozooplankton, degradation by protozooplankton and remineralization by bacteria are intricately related in reducing particle size and therefore POC flux and detritus standing stock in the upper ocean.

Feeding on detritus

Mesozooplankton are generally thought to consume detritus, including fecal pellets, marine snow, copepod carcasses, etc., but direct evidence is generally limited. The first study to document copepods feeding on detritus was by Paffenhöfer and Strickland (1970), where copepods were found to feed at highest rates on diatom flocs, followed by fecal pellets, and negligible rates on naturally occurring aggregates. Roman (1984b) showed that copepods can supplement their diets by consuming and assimilating detritus, but may require other nutritional sources to grow. Two vertically migrating species of California Current zooplankton were shown to feed on marine snow in the laboratory, irrespective of the composition of these aggregates, in the absence of other food choices (Dilling et al. 1998). Consumption rates were on the low end of the range reported for these two species, but assimilation efficiencies were high, ranging from 64% to 83%, depending on the nature of the aggregate (Dilling et al. 1998). As discussed above, the importance of fecal pellets as dietary resources has been actively debated, and most recent evidence suggests that coprophagy is of minor importance, especially in the presence of other diet choices. A study comparing the consumption of euphausiids on diatoms and aggregates made by the same diatom species found higher rates for the aggregates, even while in the presence of individual diatoms (Dilling and Brzezinski 2004). This result is not surprising given the general preference of zooplankters for larger particles (Frost 1972), and the lack of nutritional difference between these two choices, which is uncharacteristic of aggregates in the water column. Evidence from stable isotopes suggests that detritus can be an important dietary component for euphausiids in the field, at least for some life history stages of *E. Pacifica* (Park et al. 2011). The importance of consumption of detritus depends on the availability of other food items, primarily phytoplankton, and therefore will probably vary depending on season, depth, and ecosystems studied (discussed further below). Roman (1984a) used 3H-thymidine to assess mesozooplankton feeding on particle-attached bacteria and found that grazing was higher in productive regions (warm core rings) than oligotrophic regions (the Sargasso Sea). Studies of mesozooplankton inhabiting depths below the euphotic zone, unlike the species mentioned above which inhabit rich upwelling systems and migrate to shallow depths for nighttime feeding, show significant consumption of aggregates and marine snow. Schnetzer and Steinberg (2002) found that marine snow and detritus were important diet items in three vertically migrating zooplankters in the Sargasso Sea, but seasonally variable. Steinberg et al (1997) found significant zooplankton communities and higher metabolisms associated with large appendicularian houses in the bathypelagic depths of Monterey Bay, and marine snow and houses were also important components in the guts of a mesopelagic copepod (Steinberg 1995). Zooplankton in the Southern Ocean were found to rely heavily on detritus during the fall season, when phytoplankton is in short supply (Hopkins 1985). Jackson (1993) pointed to the importance of 'flux feeding' by web-making zooplankton, e.g., pteropods, capturing particles falling out of the euphotic zone. Mesopelagic zooplankton have been found to contain autotrophic picoplankton in their guts (Wilson and Steinberg 2010), cells that when alive are too small for direct consumption, again indicating the importance of aggregate feeding for deep dwelling organisms.

Despite this strong evidence for mesozooplankton ingestion of aggregates and fecal pellets, it remains unclear to what extent they assimilate detrital carbon in situ. It is possible that energy and nutrients derived from particle ingestion are ultimately gleaned primarily from the diverse microbial communities associated with detritus, rather than from potentially refractory detrital particles.

Variability in the effects of zooplankton on detritus

The first conclusive evidence for variability at both the seasonal and diel scale was presented by Lampitt et al. (1993), where marine snow at 270 m sampled with a camera system was found to show a strong signal at both these scales. The diel variability was investigated in a particle dynamics model by Ruiz (1997), who concluded that turbulence was sufficient to account for this daily pattern. However, laboratory results have shown that turbulent energy dissipation rates in the ocean are usually insufficient to break even the most fragile of particle aggregates (Alldredge et al. 1990). A theoretical study by Kiorboe (2000) suggested that 20% to 70% of aggregate carbon was degraded before it left a 50 m euphotic zone, and suggested a major role for biology in this degradation of particulate matter. Diel variations in particulate flux were also detected by Graham et al. (2000) in the Santa Barbara Channel (California). Particle concentrations increased, and average particle size decreased, simultaneously correlating with the abundance of large zooplankters (euphausiids), and further implying a significant role in particulate fragmentation due to biological processes (Dilling and Alldredge 2000). There is debate on the ability of zooplankton to mix the ocean, but some evidences does suggest that significant mixing in the upper ocean is due to biology (see Huntley and Zhou 2004; Kunze et al. 2007; Visser 2007). Given the strong correlations found for the productive California Current region (Dilling and Alldredge 2000), and the possibility that swimming of zooplankton mixes the euphotic zone (Huntley and Zhou 2004), we can speculate that this process and this diel pattern might be present wherever the standing stock and size of zooplankters is significant.

For organisms that inhabit the bathypelagic zones, and rely mainly on detritus as food items, there should be no significant change in the relative proportion of detritus to their diet with season, although the absolute contribution probably increases when productivity is highest. However, studies on the seasonal variability of organisms exclusively inhabiting this part of the ocean are lacking. For organisms that switch

their diets relative to prey availability, such as many vertically migrating crustaceans, detritivory should increase in relative proportion during low phytoplankton conditions. In fact, seasonal variability in consumption of marine snow, where dietary shifts were correlated with the phytoplankton community and detrital material increased in importance during times of low phytoplankton standing stock was documented by Schnetzer and Steinberg (2002). The reliance of the Antarctic mesozooplankton community on detritus during austral fall also points to the importance of this feeding strategy during low productivity seasons (Hopkins 1985). Prevalence of a detrital food web under ice during the Arctic winter (Sampei et al. 2009) further indicates a stronger reliance on detritus as a food source when phytoplankton are in short supply.

Photolysis and abiotic oxidative processes

Exposure of POC to high-intensity light in the euphotic zone can induce a number of photodegradative mechanisms including photolysis and oxidative degradation that increase the lability of detritus. Photolysis and abiotic degradation by oxidative processes, while not as widely recognized as disaggregation, contribute to the remineralization and solubilization of POC in the upper ocean. Photolysis leads to the conversion of high molecular weight organic compounds to low molecular weight organic compounds. Since lower molecular weight compounds tend to be more soluble than high molecular weight compounds, this results in the partitioning of this carbon from the particulate into the dissolved phase (Mayer et al. 2006; Mayer et al. 2009).

Oxidative degradative processes fall into two categories: photooxidation and autooxidation; both processes can lead to complete remineralization of organic carbon to dissolved inorganic carbon. Alternatively, by modifying the size and/or oxidation state of POC (and thereby its solubility), these processes can convert POC to dissolved organic carbon.

Photooxidative processes in phytoplankton (or phytodetritus) result from the activity of singlet oxygen, an excited free-radical form of oxygen. Singlet oxygen is generated as a result of the photosensitization of chlorophyll and effectively degrades the lipid components of cells (Girotti 2001; Rontani et al. 2011). If enough singlet oxygen is produced, such that it overwhelms the photoprotective capacity of the algal cell, it can migrate outside the chloroplast and cause damage to nearby heterotrophic cells. Thus, photooxidative damage to phytodetritus-containing organic aggregates may impact subsequent biodegradation of the material by limiting heterotrophic degradative processes in the euphotic zone (Rontani et al. 2011 and refs therein). On the other hand, dissolved organic carbon (DOC) produced by photooxidation is often more labile and accessible to bacterial degradation (Mayer et al. 2009).

In contrast to photooxidation, autooxidation involves the activity of free radicals derived from fragments of organic molecules. These radicals can be produced during the course of viral infection, autocatalytic cell death, or the hemolytic cleavage of photosensitized organic molecules.

As is the case for the other degradative mechanisms we have discussed, oxidative processes can affect different types of particles in different ways. Aged particles may be more susceptible to remineralization to dissolved organic carbon by photodegradation than fresh algal biomass, but algal biomass is more likely to be oxidized to smaller organic molecules (Estapa and Mayar 2010). Oxidized, dissolved organic carbon released from detrital phytoplankton is available for microbial remineralization and thus photooxidation is an important step in the process of biological degradation (Estapa and Mayar 2010).

Bacterial solubilization and remineralization

It is well known that bacteria are important solubilizers and remineralizers of POC, yet the relative contribution of bacteria and zooplankton to remineralization at a given site can be challenging to assess and is geographically variable (Steinberg et al. 2008). Bacteria colonize POC at densities up to three orders of magnitude greater than their free-living counterparts (Simon et al. 2002). In addition, particle-attached (PA) bacteria display significantly higher (potential) extracellular hydrolytic enzyme activity (e.g., aminopeptidase, phosphatase, lipase and glucosidase activity) than their free-living (FL) counterparts (Smith et al. 1992). Although it is known that bacteria significantly contribute to POC flux attenuation, the regulation of bacterial organic matter degradation largely remains a black box.

Several recent reviews of microbial oceanography have been written (Simon et al. 2002; Azam and Malfatti 2007; Aristegui et al. 2009; Grossart 2010; Yokokawa and Nagata 2010; Arnosti 2011; Stocker 2012), and it is not our goal to exhaustively summarize their findings. Instead we plan to highlight recent work of particular importance to bacteria-detritus interactions, with a focus on methodologies and approaches that can supply unique new information on the controls of bacterial remineralization of detritus.

Incubation of aggregates with associated microbial communities allows investigation of the joint detritus-microbe system. Incubations have shown that internal cell state appears to influence bacterial colonization rates with both iron depletion (Tang and Grossart 2007) and starvation (Yam and Tang 2007) leading to decreased swimming speeds and particle encounter rates. The interaction of PA bacteria with iron is complicated by the fact that bacteria also mediate the release of iron from aggregates (Balzano et al. 2009). Mesocosm experiments have also suggested that growth rates are lower and bacterivory higher for PA bacteria with only a 21-min mean residence time for bacteria on aggregates (Tang et al. 2006). Kiorboe et al. (2004) found that motile flagellates could colonize particles and exert grazing control on PA bacterial concentrations.

PA bacteria incubated with natural aggregates exhibited higher uptake rates for glucose and leucine than their FL coun-

terparts, though uptake rates for the PA bacteria decreased as the aggregate aged, highlighting the variable lability within discrete classes of detritus (Azua et al. 2007). Microbial degradation has also been linked to a decrease in short-chain and monounsaturated fatty acids as aggregates age (Balzano et al. 2011). PA bacterial activity, including production of sugar and protein-degrading enzymes was increased when aggregates were incubated at higher temperatures, though the associated increased degradation of aggregates was offset by increased aggregate formation rates (Piontek et al. 2009). Carbon-specific degradation of copepod fecal pellets was unrelated to copepod diet (and hence composition of fecal pellets), though sinking rates were controlled by mineral ballasting with profound effects on the remineralization length scale (Iversen and Ploug 2010).

The use of fluorescently labeled substrates (Arnosti 2003) provides additional valuable information on the lability of different fractions of the detrital pool. Since bacteria can only transport small molecules across their cell membranes, to use the complexed organic nutrients contained within POM they must first cleave the material into digestible units with extracellular hydrolytic enzymes (EHE). EHE from PA bacteria cleave many distinct polysaccharides (Ziervogel and Arnosti 2008), though PA bacteria may more rapidly break down proteins than carbohydrates and chitins (Kellogg et al. 2011). Compared with FL bacteria, PA bacteria may exhibit higher cell-specific cleavage rates (Kellogg et al. 2011), though perhaps not on all substrates (Ziervogel et al. 2010), and also used a wider diversity of substrates (Lyons and Dobbs 2012). EHE produced by PA bacteria may also remain active in the water column, with potential roles in degradation of DOM (Ziervogel et al. 2010).

The activity of extracellular hydrolytic enzymes within organic aggregates is likely regulated by numerous mechanisms including substrate induction and microbial interactions. Whereas it has yet to be demonstrated in POC, bacteria from deep-sea sediments (ultimately derived from sinking POC) have been shown to produce more enzyme activity in response to amendments of plankton-derived POC (as compared with DOC) (Boetius and Lochte 1994). Although the specific component of POC-inducing enzyme activity was not identified, Boetius and Lochte (1994) were able to demonstrate that the enzyme activity of deep-sea sediment microbial communities is dependent on the amount of POC added to the incubation rather than the bacterial biomass present in the sediments. Knowledge of specific inducers of degradative enzymes might help to explain seasonal or geographic variability in the bacterial contribution to total POC flux attenuation.

Genetic methods have been used to assess the taxonomic similarity of FL and PA communities, but with mixed results. At times the communities are quite similar (Ghiglione et al. 2009), suggesting rapid exchange between the communities, which is in agreement with the incubation study of Tang et al. (2006). However, other studies have found distinct differences between FL and PA groups (Kellogg and Deming 2009; Fuchsman et al. 2011). Hodges et al. (2005) found that this variability may be related to the formation of algal blooms, which can lead to growth of a PA specialist microbial community. Alternately, genetic studies can be used to assess the biogeochemical role of PA bacteria and have shown that particle interiors may be sites of manganese and sulfate reduction and sulfur oxidation (Fuchsman et al. 2011). A novel single-cell sorting and genome sequencing approach suggested chemolithoautotrophy by PA bacteria (Swan et al. 2011), whereas more traditional methods have found that aerobic anoxygenic phototrophic bacteria are sometimes present in aggregates (Lami et al. 2009).

Taken together, these studies suggest a multiplicity of approaches for connecting metabolic pathways, bacterial taxonomy, and detritus substrate composition with biogeochemical function. Nevertheless, it is clear from the paucity of data, and at times, conflicting results that this field is still in its infancy, and much work is needed before we reach predictive ability with detritus-bacteria interactions.

Sinking

Gravitational carbon export from the surface to the deep ocean, both in models and field studies, is generally considered to be mediated solely by detritus. This assumption stems from the contents of sediment traps, which are often dominated by dead phytoplankton, fecal pellets, and aggregates (Turner 2002), and the supposition that net flux can only occur through particles that sink down to depth and do not return to the surface (e.g., not diel-migrating zooplankton). Whereas there are a few classes of living particles that may contribute to net gravitational flux, such as resting stages of phytoplankton (Smayda 1970; McQuoid and Hobson 1996) and benthic meroplankton, there is little doubt that detritus dominates gravitational carbon export.

However, the heterogeneity of detrital particles suggests that it is foolish to consider all components of the detritus equally likely to sink out of the euphotic zone. Just as grazing and bacterial colonization rates are dependent on the character and nature of detrital particles, sinking rates are determined by properties of detritus, particularly density (or porosity) and size (De La Rocha and Passow 2007; Trull et al. 2008). Detritus sinking rates can vary by more than four orders of magnitude (see Fig. 2 and references therein). Mineral ballasting, whether by $CaCO_3$, biogenic Si, or terrigenous particles, has been shown to significantly increase detritus sinking rates and hence penetration into the ocean interior (Armstrong et al. 2009; Biermann and Engel 2010). Repackaging of organic matter into fecal pellets can significantly increase sinking rates (Bruland and Silver 1981; Turner 2002), whereas incorporation of the smallest size-classes of detritus into aggregates can promote sinking of otherwise neutrally buoyant material.

Particle settling velocities are generally considered to behave according to Stokes' Law, which states that settling

velocity is proportional to the density differential between the particle and water and the square of the particle radius, although it is important to note that Stokes' Law is only actually valid for a sphere of uniform density. Settling rates have been determined in several different ways including direct observation of rapidly sinking larger particles (e.g., fecal pellets and aggregates), relative concentration changes between the top and bottom sections of settling chambers (Bienfang 1981), specially designed sediment traps with rotating cups (Peterson et al. 2005), time-series analysis of multi-depth sediment trap arrays recording temporal lags between flux events, and inferences made from paired in situ flux and standing stock measurements. Direct observations of sinking rates, both laboratory measurements and in situ imaging techniques, tend to find a strong relationship between size and settling rate in rough agreement with Stokes' Law (see Smayda 1970; Turner 2002; Stemmann et al. 2004b). However, there is a distinct difference between the sinking rates of fecal pellets and marine snow, with both typically showing positive relationships with size, but fecal pellets generally having faster sinking rates than aggregates (Fig. 2).

Despite the strong positive correlation between size and sinking rate found amongst distinct types of particles, the heterogeneity of in situ detrital particles and aggregates obfus-

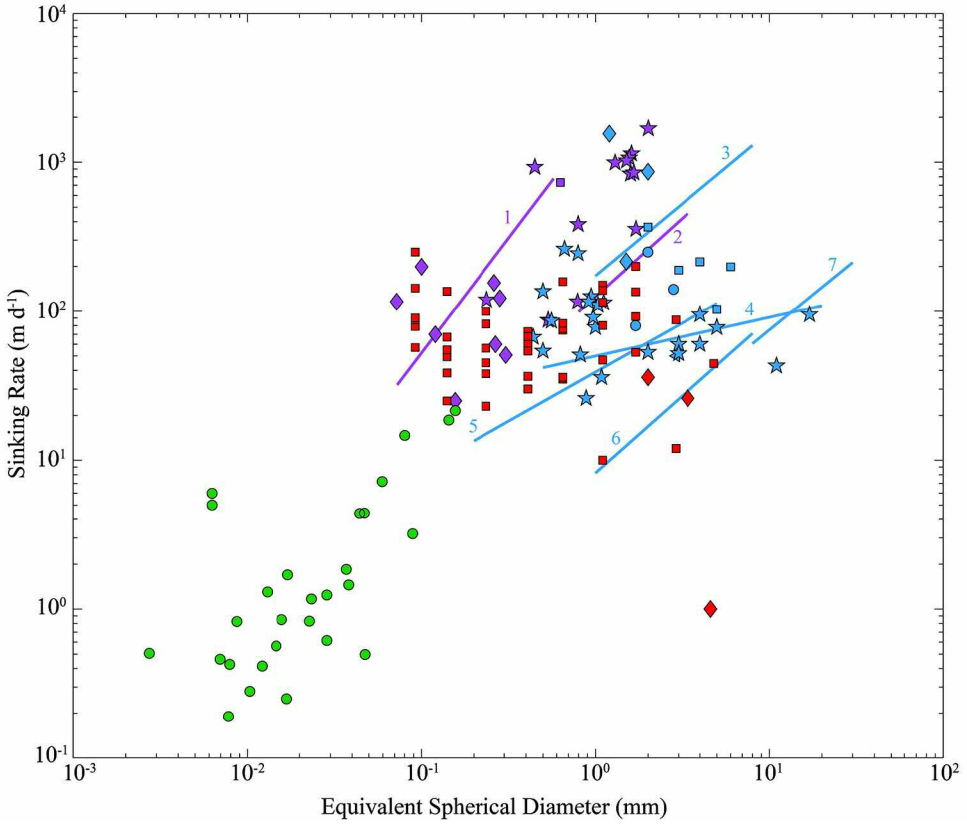

Fig. 2. Sinking rate as a function of equivalent spherical diameter. Green circles are intact individual phytoplankton (Smayda 1970). Purple symbols are mesozooplankton fecal pellets. Blue symbols are marine snow particles. Red symbols are in situ settling rates of mixed particle assemblages assessed by dividing fluxes by stocks. Note that strong correlations exist between size and sinking rate for phytoplankton and mesozooplankton feces, with these two types of particles falling on a similar line. Whereas individual experiments typically show correlations between size and sinking rate for marine snow aggregates, there is not a strong trend across studies (likely reflecting the highly variable density of aggregates) and in general marine snow has a lower sinking rate than fecal pellets of a similar size. By contrast, bulk in situ particles do not show a strong trend, and in fact, may decrease slightly in sinking rate with increasing size. Blue diamonds represent aggregates made from calcifying *Emiliania huxleyi* cells (Ploug et al. 2008a; Engel et al. 2009; Biermann and Engel 2010). Blue circles are aggregates formed from the diatom *Skeletonema costatum* (Ploug et al. 2008a). Blue triangles are natural marine snow particles from the Southern California Bight (Ploug et al. 2008a). Blue stars are natural marine snow particles from Monterey Bay, CA and Bedford Basin (Shanks and Trent 1980; Azetsu-Scott and Johnson 1992). Blue squares are appendicularian houses (Taguchi 1982). Purple squares are appendicularian fecal pellets (Ploug et al. 2008a). Purple diamonds are copepod and euphausiid fecal pellets (Smayda 1971; Turner 1977; Yoon et al. 2001; Ploug et al. 2008a). Purple stars are salp, doliolid, and pteropod fecal pellets (Bruland and Silver 1981; Madin 1982; Yoon et al. 2001). Red diamonds are measurements of bulk in situ sinking rates made by comparing size-distributions of particles collected in a sediment trap by optical determinations of water column size-spectra made by Asper (1987), whereas red squares are similar measurements made by McDonnell and Buesseller (2010). Lines represent relationships found by different authors for (1) crustacean fecal pellets (Small et al. 1979); (2) Chaetognath fecal pellets (Giesecke et al. 2010); (3) noncalcifying *E. huxleyi* aggregates (Engel et al. 2009); (4) Marine snow (Alldredge and Gotschalk 1988); (5) Marine snow (Syvitski et al. 1995); (6) appendicularian houses (Lombard and Kiorboe 2010); and (7) marine snow (Alldredge and Gotschalk 1989).

cates this simple relationship. McDonnell and Buesseler (2010) used a combination of underwater visual imaging of water column particles with acrylamide gels affixed to sediment traps beneath them to assess sinking rate as a function of size for particles sinking off of the Western Antarctic Peninsula. They found a bi-modal distribution of sinking rates during a January cruise with high sinking rates for large particles (equivalent spherical diameter [ESD] of > 1 mm) and small particles (ESD < 100 mm), but in February they found a strong inverse correlation between ESD and sinking rate. They attributed this difference to the presence of large, rapidly sinking fecal pellets in January, while most other large and medium-sized particles were aggregates that sank slower than individual siliceous cells of diatoms and radiolarians. Considered from a broader perspective, the different size-dependencies of sinking for discrete detritus types and in situ particles and aggregates, suggest the possibility that the importance of different types of detritus to POC flux is a function of size, with fecal pellets comprising a large portion of the 100-200 μm size fraction and aggregates dominant in the larger size fraction (Fig. 2). Attempts to estimate fluxes from particle size spectra (e.g., Jackson and Checkley 2011) may therefore hinge on the ability to differentiate rapidly sinking particles from slowly sinking particles of the same size.

Section 4. Modeling detritus

Detritus in typical biogeochemical models

Many types of models have been developed to address different aspects of ocean biology (see Fennel and Osborn 2005 for an overview). State variable models that cycle biomass (e.g., NPZD type models that track a fixed number of ecosystem compartments) tend to be the type of model that incorporates detritus as a dynamic of interest within a larger ecosystem context (see Fig. 1 in Travers et al. 2007). Because detritus is often considered as a closure term tuned to improve phytoplankton results, reviews of ecosystem models that thoroughly analyze phytoplankton and zooplankton components (Arhonditsis and Brett 2004; Tian 2006) do not extend their scope to detritus. History provides some explanation. Ecosystem models have been used as a tool since the middle of the twentieth century and were first developed to explore and understand the growth of phytoplankton (Riley 1946). A transformative development in the field of ecosystem modeling occurred when, in a seminal paper, Fasham et al. (1990) connected an ecosystem model to ocean circulation. The focus of the study was to reproduce and understand the observed patterns of phytoplankton production at an ocean site near Bermuda. The Fasham et al. (1990) model was a seven-compartment model that included nitrate, ammonium, dissolved organic nitrogen, phytoplankton, zooplankton, bacteria, and detritus. Sources of detritus in the Fasham et al. (1990) model were mortality of phytoplankton and egestion from zooplankton. The sinks of detritus were grazing by zooplankton, decay, and sinking. After publication of the Fasham et al. (1990) model, the number of ecosystem models proliferated, and there was also a rapid evolution in the number of applications of ecosystem models.

To explore how detritus is generally characterized in models, we used Web of Knowledge℠ database to find papers published between 1990 and 2010 that cite Fasham et al. (1990). A total of 561 studies were found: 313 included ecosystem modeling and 182 included an original model or a substantial change to an existing model. We analyzed the pelagic ecosystem component of the 182 models with the assumption that some characteristics of each model were unique. In particular, we were looking for the following in the ecosystem models: the total number of state variables, the number of detritus state variables, the sources of detritus, the sinks of detritus, and physiological constraints on detritus production and/or loss. We also tracked the coupling with physical models and the geographic location of the model implementation. Overall, this analysis of the processes controlling detritus in models will help identify potential improvements, including recent experimental and observational results that can be made to models.

Detrital compartments comprised an average of 14.6 ± 12% of the total compartments in the models and ranged from 0% to 60% depending on the focus of the study. Many of the models without detritus variables also had fewer total variables. The goal of the simpler models was to model a particular process, frequently primary productivity, but still allow the modeler to understand the underlying dynamics. In primary productivity models that did not explicitly consider detritus, the essence of detritus was incorporated when phytoplankton and/or zooplankton were recycled back to nutrients or disappeared from the system. An additional benefit to simpler models was the low computational cost, and there was a clear increase in the total number of state variables in more recent models as computing resources increased. The majority, 70 models, had a single detritus variable (Fig. 3). Fasham et al. (1990) included a single detritus variable so this finding may be related to the original search criteria. Furthermore, the four compartment NPZD model was a popular starting point for more complicated models because it includes what many consider to be the essential ecosystem components. In Fig. 3, Lee et al. (2002) had the model that included 6 detritus variables. The detritus variables were partitioned by nutrients (carbon, nitrogen, and silica) and the origin (detritus, phytodetritus). The Lee et al. (2002) included a high number, 19, of total state variables and was one of the most complicated models analyzed. Dunne et al. (2005) had the model with the highest percentage, 60%, of detritus variables. This model had only 5 total state variables, and was focused on mechanistically modeling detritus to better quantify the particle export ratio. Thus, there are a range of detritus parameterizations in ecosystem models that may have unanticipated effects on the model simulations, depending on how each detrital process is incorporated in the model.

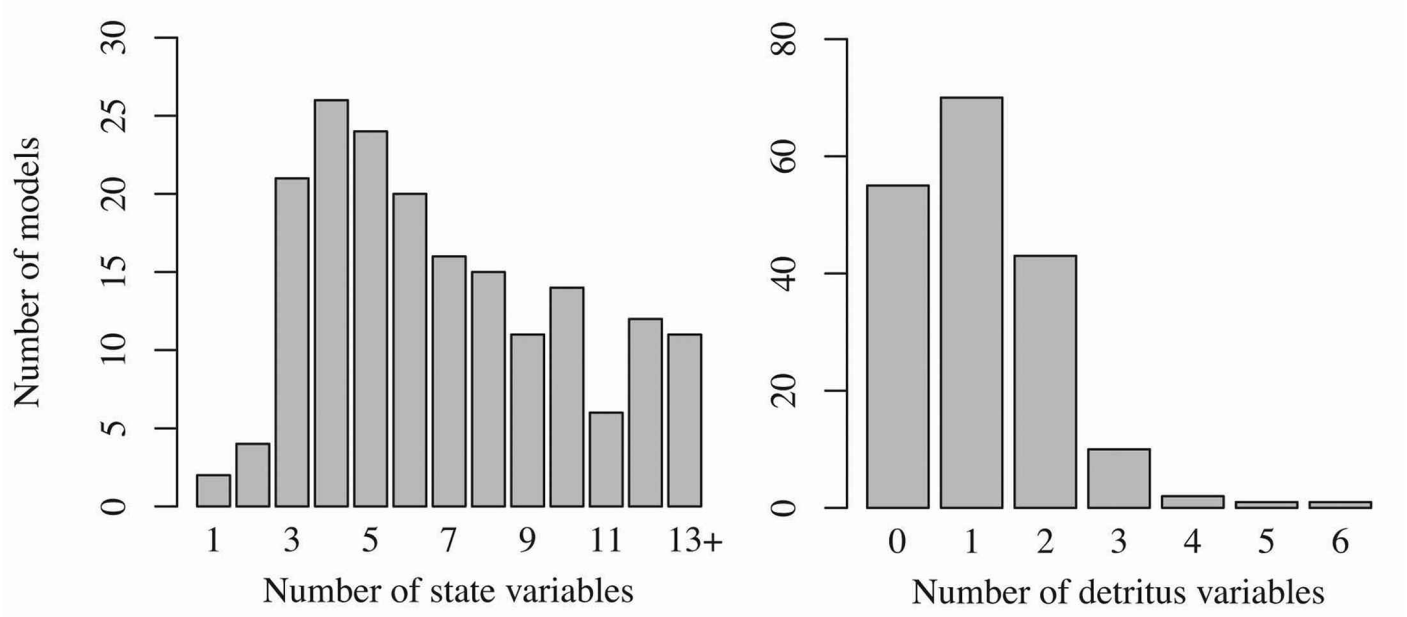

Fig. 3. A comparison of the distributions of the total number of state variables to the number of detritus state variables in the 182 original models found to cite Fasham et al. (1990) in the Web of Knowledge database. Panel A is a histogram of the number of models of a given number of total state variables, whereas Panel B is a histogram of the number of models with a given number of detritus variables.

Table 1. The frequency of occurrence of detritus components and rates among the 182 original models found by searching the Web of Knowledge for papers that cited Fasham et al. (1990).

	Number of models
Detritus partitions	
Nutrients	32
Size	13
Origin	10
Sinking speed	8
Lability	1
Sources of detritus	
Egestion	101
Mortality phytoplankton and zooplankton	94
Mortality phytoplankton	19
Sloppy feeding	9
Sinks of detritus	
Remineralization	122
Sinking	111
Zooplankton grazing	50
Bacterial grazing	3

Fifty-seven models had two or more detritus variables (Fig. 3). The detritus variables were typically distinguished by one of the following characteristics: nutrient type (carbon, nitrogen, phosphorus, and silica), size, lability, sinking speed, or origin (Table 1). Nutrient type was the most frequently used partition because many of the models included multiple elemental cycles, although it is important to note that nutrient partitioning of the detritus simply implies variable stoichiometry for the detritus, but does not suggest the inclusion of detrital pools that behave differently or have different origins. Size was used to distinguish detritus with different sinking and remineralization rates (e.g., large detritus typically had faster sinking speeds than small detritus). The remineralization rates of large versus small detritus varied greatly between studies. Fennel et al. (2006) had a faster remineralization rate, 0.03 d^{-1}, for small detritus compared with large detritus, 0.01 d^{-1}. Touratier et al. (2003) had equivalent remineralization rates for both small and large detritus, 0.1 d^{-1}. Slagstad et al. (1999) had a faster remineralization rate, 0.33 d^{-1}, for large detritus compared to small detritus, 0.05 d^{-1}. On the other hand, many of the models had sinking speed as a specific partition rather than size, although in many cases, these partitions were equivalent. Origin of detritus was also used to distinguish between, for example, phytoplankton aggregations and zooplankton fecal pellets (Druon and Le Fèvre 1999; Jackson 2001; Skliris et al. 2001). This type of partitioning had a more fluid connection between detritus creation and loss because the detritus variables were not grouped then redivided to calculate the transfer of organic matter within the system. Lability was a specific characteristic considered in Stock and Dunne (2010), which divided detritus into semilabile small detritus, labile small detritus, and large detritus. The semilabile and labile small detritus were nonsinking, and the large detritus was rapidly sinking. The lability differentiated between detritus that decays at different rates: labile decayed immediately and the semilabile decayed to labile on monthly to seasonal time scales. Overall, models are inconsistent in how they incorpo-

rate detrital types, which may prove important, especially when the sources and sinks of detritus within models are considered.

Sources of detritus in the ecosystem models were typically from phytoplankton and zooplankton mortality and zooplankton egestion. Similar to Fasham et al. (1990), 21 models included phytoplankton mortality but not zooplankton mortality as a source of detritus. Fasham et al. (1990) considered zooplankton mortality to be a closure term that included both natural mortality and predation by higher predators. Rather than including zooplankton mortality as detritus, a portion was instantly exported from the mixed layer and another portion was instantly converted to ammonium to simulate the effect of higher predators on zooplankton without explicitly including them in the model. The Fasham et al. (1990) model was able to make this set of assumptions because it was a 0D model in the mixed layer. However, most models, 94 in Table 1, considered both phytoplankton and zooplankton mortality as sources of detritus because they did not use the Fasham et al. (1990b) set of assumptions. The inclusion of both phytoplankton and zooplankton mortality fits with the observational evidence described previously. Sloppy feeding was included in some of the models (Table 1). In some cases, the term "sloppy feeding" was used to refer to the unassimilated material that was ingested, and in other cases, it referred to uningested products of grazing. Using the former definition, sloppy feeding and egestion (fecal pellet production) were equivalent, but in the latter definition, sloppy feeding was separate from egestion. Three of the models included both egestion and sloppy feeding (Haupt et al. 1999; Tian et al. 2000; Besiktepe et al. 2003). In Haupt et al. (1999), the rates of detritus production due to egestion and sloppy feeding were different, and both were parameterized as part of the slow-sinking detritus state variable. Besiktepe et al. (2003) had only a single detritus variable, and like Haupt et al. (1999) detritus from egestion and sloppy feeding were produced at different rates. Tian et al. (2000) had two detritus variables with sloppy feeding producing small detritus and egestion producing large sinking detritus. Last, in models that included small and large sizes of detritus, there was frequently an aggregation rate that represented the transformation of small detritus into large detritus. Despite the differences among models in the division of detritus into types, there was a consistency in having both phytoplankton and zooplankton mortality and zooplankton egestion as the main sources of detritus.

The main sinks of detritus in the ecosystems models were remineralization and sinking (Table 1). Grazing of detritus by zooplankton was also frequently included in the models and was a feature of the original Fasham et al. (1990) model. Edwards (2001) used existing NPZD models to theoretically analyze the effect of zooplankton grazing on detritus (Steele and Henderson 1981). He found that the addition of a detrital compartment to a nutrient-phytoplankton-zooplankton model made little difference to the qualitative behavior of the model if zooplankton were not allowed to graze on the detritus. However, the addition of grazing on detritus significantly altered the dynamics by decreasing the range of model parameters over which the model showed unforced oscillations and slowing these oscillations. Forty percent of the models included grazing on detritus so, based on the analysis of Edwards (2001), there would likely be differences in results across ecosystems based on this parameter alone. A small number of models included bacteria as a sink of detritus. Bacteria are a major consumer of detritus, and, in the models, the influence of bacteria on the decomposition of detritus was typically included in the remineralization rate. If bacteria were included as a state variable, their interaction was restricted to the dissolved organic matter. However, detritus and bacteria were explicitly linked in three of the models (Tian et al. 2000; Kantha 2004; Nogueira et al. 2006). Nogueira et al. (2006) acknowledge the "bacterial action on detritus," but the parameterization was still mainly a remineralization closure term. In contrast, Kantha (2004) and Tian et al. (2000) had a fraction of the bacteria actively consume the particulate organic matter. By incorporating a detailed microbial loop, ecosystem dynamics extended below the euphotic zone. In contrast to the sources of detritus, there were major discrepancies in the sinks of detritus in the models analyzed. Most of the models did not include grazing of detritus by zooplankton or remineralization by explicit bacteria as sinks of detritus which, based on the model analysis by Edwards (2001) and the observational evidence, have been found to be important.

Modeling detritus

This treatment of detritus in ecosystem models contrasts with the output from detritus models, which indicate that the complex processes controlling detritus are important. One of the major questions that still needs to be addressed is: How many detrital compartments, at a minimum, should be included in an ecosystem model? Ruiz et al. (2002) experimentally determined that there need to be multiple size classes of detritus with explicit representation of aggregates in biogeochemical models to accurately represent detritus flux to deeper depths. Kriest and Oschlies (2008) used 198 size classes to explore the increase in detritus sinking speed with depth and particle size distributions in a one-dimensional model; however, this many classes cannot be reasonably incorporated into physically coupled 3D models. An alternate approach, which explicitly models the size-spectra of POC (Burd and Jackson 2009), has benefits in its ability to directly reflect in situ size spectra measurements that are becoming increasingly common. Such models, particularly when used in conjunction with size-structured plankton models (Poulin and Franks 2010), are powerful tools because of the intrinsic inter-relationships between size, aggregation, disaggregation, and sinking rate. However, classification of all detritus based solely on size neglects the important role of lability in determining the fate of detritus, which may be particularly important when

attempting to answer questions related to bacteria or zooplankton usage of detritus. Furthermore, the computational cost of carrying a full discretized size-spectrum of detritus makes such a model infeasible for inclusion in large-scale three-dimensional models. Alternate size-spectra schemes, particularly the use of moments to describe the particle size-spectrum with only a few parameters (Kriest and Evans 1999; Gehlen et al. 2006), are computationally more efficient, but less accurate and more difficult to assimilate with the variable nature of in situ particle production by plankton.

A small subset of these size-structured models focuses on the biological and physical processes altering detritus explicitly. Jackson and Burd (2002) incorporated zooplankton with different modes of feeding as well as bacteria and predators in a theoretical model to explore the impact on sinking detritus. Stemmann et al. (2004b) developed the most comprehensive detritus model, which included the processes of settling, coagulation, fragmentation, microbial activity, and zooplankton consumption. These theoretical one-dimensional models determined that a diversity of processes influence variation in sinking and degradation of detritus.

Compared with the active research being done on aggregation in marine systems, few modeling studies have specifically targeted the interaction between grazers or bacteria and multiple detrital classes. Blackburn et al. (1997) showed that micro-scale nutrient patches around particles were available to chemotactic bacteria, whereas Kiorboe and Jackson (2001) showed that motile bacteria can use the solute enriched plume behind a sinking particle to locate nutrient-rich particles. Similarly, measurements of bacterial motility have been used to model bacterial encounter and colonization of aggregates (Kiorboe et al. 2002). Micro-scale and optimal foraging models such as these have great potential for generating and testing specific hypotheses about microbial-detritus interactions, but are not generally applicable to large-scale simulations. An alternate approach was taken by Miki and Yamamura (2005) who addressed competition between DOC-specialist, POC-specialist, and generalist bacteria in a homogeneous water parcel, and hence constructed a model that would be more amenable to inclusion in general circulation models. Anderson and Tang (2010) used a flow analysis model to compare the loss of sinking detritus in the mesopelagic to three pathways (remineralization by particle-attached bacteria, solubilization and subsequent remineralization by free-living bacteria, and consumption by detritivorous zooplankton) and found a dominant role for attached bacteria.

In a novel pair of papers, Stemmann et al. developed (2004a) and tested (2004b) a one-dimensional ecosystem model that explicitly dealt with particle aggregation and detritus feeding on zooplankton at the DYFAMED site in the Mediterranean Sea. The comparison provided some critical insights into the processes determining the loss of detritus. Particle size was determined to be important because the consumption of large detritus in the shallower depths by mesozooplankton in models was necessary to explain the patterns in the observational data. Microbial degradation rates were more important than zooplankton degradation rates at depths greater than 200 m. Three years of data from 1993-1995 were used in the analysis. The fit between the model and data were much higher in 1995 compared with 1993 or 1994. The authors suggested a potential reason to be the increased sampling interval which was every ~ 5 days in 1995 compared to ~ 40 days in 1993 and 1994. There were also differences in the dominant phytoplankton groups which caused differences in particle size and lability between years that also may have contributed to differences in fit. The processes governing particle degradation are proving to be complex, and further model development and comparisons with data may provide additional insights.

Perhaps even more important than models that focus on detrital interactions is a systematic approach for validating detritus behavior in general plankton models. Unfortunately the paucity of in situ detritus measurements makes model validation more complicated for detritus than for other state variables. Model phytoplankton distributions, for instance, are routinely validated with some combination of microscopy, pigment, and sea surface chlorophyll measurements. Nevertheless, there are paths forward. The increased use of automated tools for generating particle size-spectra in the epi- and mesopelagic (Checkley et al. 2008; Graham and Smith 2010) provides valuable data for testing size-structured detrital models (Stemmann et al. 2004a; Jackson and Checkley 2011), but could also be used as validation for mesopelagic detrital standing stocks predicted by three-dimensional ecosystem models. In situ imaging devices offer potential to further divide particles into explicit classes (e.g., aggregates, fecal pellets, organisms) that more fluidly parse into the detrital compartments used in most models. Comparison of model rates of detritus formation and destruction to in situ rates is another powerful avenue for model validation. Biogeochemical models already routinely compare detritus flux rates to estimates of carbon export, but such methods can be expanded upon greatly. Fecal pellet (Conover 1966) and appendicularian (Sato et al. 2003) house production are reasonably well known functions of zooplankton abundance and grazing. Likewise, estimates of aggregate formation rates can be made from phytoplankton concentrations (Jackson and Kiorboe 2008; Burd and Jackson 2009). Meanwhile, estimates of sinking rates (McDonnell and Buesseler 2010), export flux (Buesseler et al. 2008), bacterial remineralization and solubilization (Mevel et al. 2008; Ploug et al. 2008a; Kellogg et al. 2011), and grazing (Wilson et al. 2010; Park et al. 2011), made on discrete detrital classes can be used to constrain detritus loss terms.

Our analysis has also identified some key parameterizations of detritus that could be improved. We suggest that "sloppy feeding" needs to be used more frequently and carefully in models. In addition, since phytoplankton fragments are distinct in shape and size from intact phytoplankton cells or fecal

pellets and likely are more labile and have slower sinking speeds, we recommend separate consideration of these compartments. With respect to sinks of detritus, zooplankton grazing has been identified as an important loss term and warrants more consistent use (Edwards 2001; Stemmann et al. 2004b). In general, within the models we analyzed, physiology was rarely considered and detritus loss rates were rarely temperature-dependent. Respiratory physiology in particular will become increasingly important if hypoxic regions continue to expand.

Section 5. Recommendations

It is clear that there is a large disconnect between the heterogeneous nonliving POC pool in the ocean, and the parameterization of simple detrital compartments in ecosystem models. Bridging this gap will require a concerted effort by both experimentalists and modelers. Of immediate importance is the need for systematic characterization of the properties of different detrital classes (e.g., Ploug et al. 2008a). Most projects to date focus on either a single detrital class (e.g., appendicularian houses) or use automated methods that typically discriminate particles only on size (not origin). Whereas such studies have elucidated potential roles of different types of detritus, such a reductionist approach is difficult to incorporate into ecosystem models, which cannot reasonably be expected to carry multiple detrital compartments for each class of detritus. Instead, there is a need for integrative studies that compare and contrast different detrital classes, and hence allow for an informed approach to amalgamating heterogeneous classes of particles into representative detrital pools that may vary based on (for instance) size and lability. In much the same way that sinking rate has been systematically studied as a function of size for different detrital classes and unified with Stokes' Law (with the caveat that a priori prediction of excess density remains difficult) and coagulation theory has formed a basis for study of aggregation (with a similar caveat about a priori prediction of the 'stickiness' parameter), we need to address other relationships of detritus properties and loss terms. While some questions (e.g., the relationship of bacterial remineralization to particle size) may be amenable to our current methodological practices, others may require a fundamental reassessment of how detritus is studied. For instance, lability is an important determiner of the final fate of detritus, and is hence important to include in models. However, it is difficult to assess because it is a function of many different physico-chemical parameters. One approach may be to measure relative lability by simultaneously collecting multiple forms of detritus and incubating them with natural assemblages of marine bacteria. However, a more fruitful approach may stem from current research into bacterial use of the chemical constituents (e.g., simple carbohydrates, hydrocarbons, fatty acids, etc.) of detritus (Ziervogel et al. 2010; Lyons and Dobbs 2012). If such methods can be extended to include zooplankton use of detritus (e.g., Koski et al. 2010) and combined with chemical fingerprinting of different types of detritus to assess their relative chemical compositions (Tsukasaki and Tanoue 2010), lability could begin to serve as a concrete structuring principle for model detrital compartments.

These focused experimental approaches must be paired with a more fluid treatment of model detritus. It is of crucial importance that detrital compartments be explicitly linked to particular detritus production mechanisms so that losses may correspond to a relevant suite of remineralization rates, sinking rates, and grazing rates. The actual definition (and number) of different compartments will depend on the results of experimental studies. For instance, if appendicularian houses and phytodetrital aggregates are found to both have much higher lability than mesozooplankton fecal pellets and molts, and microzooplankton egesta are shown to behave similarly to individual detrital phytoplankters, it may be possible to conflate these different categories into small detritus, large porous labile detritus, and large dense refractory detritus. Regardless, each class of detritus should have distinct properties— including sinking, remineralization, and grazing rates— that are directly constrained by in situ measurements. Alternately, it may be possible to model detritus using size and lability spectra, with each source, loss, and transformation process explicitly acting on the moments and cross-products of size and lability (see Burd and Jackson 2009). Such a method may allow for a more accurate depiction of the full heterogeneity of the detrital pool (for instance allowing lability to vary continuously with bacterial remineralization or incorporating full aggregation/disaggregation dynamics), but with significantly increased model complexity. Whichever approach is undertaken, it is of paramount importance that the heterogeneity of processes producing and consuming detritus is considered and that model results are validated with in situ measurements of detritus standing stocks and related rates. Only a concerted joint effort between experimentalists and modelers will allow this often dominant form of particulate matter in the ocean to be mechanistically incorporated into ecosystem models.

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