Journal of Oceanography, Vol. 58, pp. 265 to 279, 2002

Review

Chemical and Biological Studies of Particulate Organic Matter in the Ocean

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(Received 10 September 2001; in revised form 1 October 2001; accepted 2 October 2001)

This paper presents a review of the past decade's highlights of research on the isolation and characterisation of particulate organic matter (POM) in the world's oceans. The emphasis is on chemical studies but, in keeping with the growing interdisciplinary nature of marine science, advances in other disciplines are also discussed, particularly those in biological sciences. Increasing evidence for the importance of picoplankton, bacteria and viruses as POM constituents is highlighted, including the recent recognition of large populations of autotrophic bacteria able to harvest light for energy. The transport of POM to bottom waters was thought to be largely confined to large, rapidly sinking faecal pellets. However, recent studies have highlighted the importance of organic aggregates and flocs formed by diatoms such as *Rhizosolenia* and other microalgae. Ascending particles have also been discovered, many of which are lipid-rich. Several studies have shown that resuspension of bottom sediments and lateral advection of material from continental shelves can lead to anomalously high particle fluxes measured in sediment traps moored in deep water. Many new approaches for characterizing POM have emerged, such as pyrolysis gas chromatography-mass spectrometry and direct temperature-resolved mass spectrometry for analysis of higher molecular weight materials and biopolymers. Lipid biomarker techniques have also advanced, exciting new possibilities being raised by the ability to measure stable and radioactive carbon isotopes for individual compounds. The techniques of molecular biology, such as the polymerase chain reaction (PCR), are being increasingly applied to provide complementary information to more conventional microscopy and flow cytometry on the identity of organisms in the sea. The combination of these techniques with advanced chemical analysis methods promises to greatly increase our knowledge of the origins, transport and fate of organic matter in the oceans.

Keywords:
· Bacteria,
· faecal pellets,
· flocs,
· flow cytometry,
· flux,
· lipids,
· mass spectrometry,
· particulate organic matter,
· proteins,
· phytoplankton,
· picoplankton,
· polymerase chain reaction,
· pyrolysis,
· sediment traps,
· viruses.

1. Introduction

Organic matter in the ocean occurs as particulate organic matter (POM, sometimes termed seston) and dissolved organic matter (DOM). Earlier research on the origins, composition and cycling of POM in the sea has been well covered in the valuable reviews by Lee and Wakeham (1988, 1992), Wakeham and Lee (1989) and Wakeham and Volkman (1991). Over the past decade this topic has continued to attract a considerable amount of new research, reflecting the importance of particulate matter in biogeochemical cycles in the ocean. This interest has been maintained despite logistic difficulties and the high cost of oceanographic cruises required to obtain field data.

Over the past decade some fundamental new insights and observations have been made which we attempt to summarize in this review. We have focused on papers published since 1993, although references to earlier fundamental work are also included. Although many recent papers have discussed the origins and fate of organic matter in estuarine and near-shore environments (e.g., Mannino and Harvey, 2000 and references therein), we

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have chosen to restrict our attention here largely to studies of POM in the open ocean. Although dissolved organic carbon (DOC) is the largest actively exchanging pool of organic carbon in the ocean (Druffel and Bauer, 2000), we have not attempted a comprehensive review, but rather we discuss it in connection with POM cycling.

2. What is POM?

The first difficulty that one must confront in any definition of POM is to define the term "particulate". Usually it has an operational definition as any material that does not pass through a given filter—usually a 0.5 μm filter. Glass fiber filters are widely used for the collection and analysis of organic substances, but quite different filter types have been used in different studies. Thus, one needs to be aware that a "particle" collected by a given filter may not be the same as a "particle" collected by another. Material that passes through the filter is termed "dissolved" (DOM), although in reality a broad spectrum of particle sizes exists. Some material, such as colloidal matter, does not fit neatly into either category.

The smallest particles (0.5–10 μm) comprise microalgal cells, bacteria, fine organic detritus and inorganic particles such as coccoliths, diatom skeletons and clay particles which often have an organic coating. The size range of tens to hundreds of μm includes the larger microalgae (especially diatoms), detritus and faecal pellets; these particles often result from biological repackaging of organic matter through feeding and excretion. Larger particles are known as marine snow (or fluff) which consist of detritus, phytoplankton and bacterial cells, and some clays and other inorganic matter. Thus the term "POM" can comprise a complex mixture of living and nonliving organic matter having a broad size range, form and reactivity.

3. Types of POM

3.1 Suspended POM and marine snow

Suspended POM is a mixture of living organisms and that, quite small, fraction of detritus that escapes from short time-scale remineralization. To distinguish between living and detrital carbon, labile chemical markers (biomarkers) such as chlorophyll and carotenoids, ATP and DNA are measured as indicators of phytoplankton or living biomass. Although this estimation has some inherent bias due to variability in carbon/marker ratios caused by biological responses to environmental differences, it is generally thought that non-living POM, or detritus, exceeds that of plankton (detritus:plankton = 10:1), although their relative abundances vary both temporally and spatially (e.g., Kirchman *et al.*, 1993; Yanada and Maita, 1995). The plankton is thus the initial source of detrital POM (e.g., Boyd and Newton, 1995, 1999; Smith and Asper, 2001; Bury *et al.*, 2001) and its community structure plays a key role in controlling the recycling and export of organic materials into and out of the euphotic zone.

It is now widely recognized that small organisms can be major components of the plankton in many oceanic regimes (e.g., Bidigare and Ondrusek, 1996; Binder *et al.*, 1996; Blanchot and Rodier, 1996; Landry *et al.*, 1997; Blanchot *et al.*, 2001). For example, Ishizaka *et al.* (1994, 1997) reported that autotrophic picoplankton (<3 μm in size) contributed more that 60% of depth-integrated chlorophyll *a* along 175°E from 45°N to 8°S in the Pacific, except the area north of the subarctic boundary (between 42° and 43°N). Even in the northern North Pacific (the area north of the subarctic boundary), large phytoplankton (>100 μm) including large diatoms and dinoflagellates were always minor components (Takahashi *et al.*, 2000). In simple terms, the phytoplankton community structure can be thought of as composed of two main groups: an ubiquitous basic structure made up of diverse algal groups including green algae, diatoms and haptophytes, and a flourishing diatom population limited by area and season, superimposed on the basic structure (Obayashi *et al.*, 2001).

The biomass of heterotrophic bacteria comprises a significant fraction of the living biomass of POM in oceanic surface waters. Bacteria are particularly dominant in oligotrophic areas (e.g., Caron *et al.*, 1995; Kirchman, 1997; Bradford-Grieve *et al.*, 1999). The interplay between their abundance and bacterial secondary production significantly contributes to the carbon dynamics in the oceanic euphotic zone (Ducklow, 1999, and references therein). Wilhelm and Suttle (1999) estimated that prokaryote biomass including photosynthetic prokaryotes contributed over 90% of the total biological carbon in the entire ocean.

Recently, exciting work by two groups of researchers has demonstrated that the oceans contain large numbers of aerobic bacteria that are able to utilise sunlight for energy and thus contribute energy to marine food webs (Béjà *et al.*, 2000; Kolber *et al.*, 2000). These widespread bacteria may account for as much as 20% of bacteria in some oceanic regions and their abundance relative to oxygenic phototrophs is higher in oligotrophic waters. Béjà *et al.* (2000) showed that these bacteria contain the light-harvesting protein rhodopsin which functions as a proton pump. Although these rhodopsins are commonly associated with archaea, this study showed that they are distributed across a range of taxa, including true bacteria. It is not clear whether these bacteria fix inorganic carbon, but clearly they might play a major role in global carbon cycling.

This increased recognition of the importance of bacteria has stimulated investigations of bacterivory, i.e., viruses and heterotrophic protists including nanoflagellates and ciliates (e.g., Mathias *et al*., 1995; Hennes and Simon, 1995; Fuhrman, 1999; Sherr and Sherr, 2000). Although viruses are often numerically dominant (see review by Wommack and Colwell, 2000), it is unlikely that viruses and protists are significant fractions of surface POM in terms of their organic matter contribution. However, they are important members of the microbial loop wherein DOM produced by phytoplankton is transferred to bacterial POM which is in turn grazed by protists and/or infected by viruses so that bacterial POM is reintroduced to DOM. It appears that an average of 10–20% of heterotrophic bacteria and 5–10% of cyanobacterial cells in the sea is destroyed daily by viral infections (Fuhrman and Suttle, 1993; Suttle, 1994), and cell lysis represents a significant source of organic carbon, nutrients and trace elements in the microbial loop (e.g., Thingstad *et al*., 1993; Gobler *et al*., 1997). Protist grazing has been suggested to cause a significant loss of bacteria (e.g., Davidson, 1996; Sherr *et al*., 1997), and has a major influence on bacterial community structure (e.g., Weinbauer and Höfle, 1998; Hahn and Höfle, 1999; Suzuki, 1999). Using mesocosm experiments, Fuhrman and Noble (1995) reported that bacterial mortality due to grazing by protists was about equal to that attributed to viruses.

Models suggest that 3–26% of photosynthetically produced organic carbon is recycled back to DOC by viral lysis (Wilhelm and Suttle, 1999). Cell lysis due to viral infection is the major cause of decline in some phytoplankton blooms (e.g., Bratbak *et al*., 1993; Brussaard *et al*., 1995, 1996; Yager *et al*., 2001). Ingestion of picoplankton as well as detrital POM by protists is also a potential source of bioavailable DOC (e.g., González, 1996; Posch and Arndt, 1996; Strom *et al*., 1997; Christaki *et al*., 1998). Barbeau *et al*. (1996) pointed out that protist grazing was a possible mechanism for relieving the iron limitation of phytoplankton because bioavailable iron is generated from refractory colloidal iron in the acidic food vacuoles of protist grazers.

Viral lysis and protist grazing may have different effects on carbon dynamics. Protist grazing may give rise to the transfer of more carbon to higher trophic levels, because POC grazed by protists produces less DOC, but is incorporated, respired and egested as POC (Pelegri *et al*., 1999; Nagata, 2000). Protists themselves are a significant food source for zooplankton (Brussaard *et al*., 1995; Sherr *et al*., 1997). In contrast, viral lysis transfers more carbon to DOC as soluble cytoplasmic materials and membrane materials (e.g., Middelboe *et al*., 1996; Wilhelm and Suttle, 1999).

Marine snow is the term generally used to describe large aggregates of organic matter. Marine snow is most abundant in surface waters, but it is almost completely recycled in the top 1000 m (e.g., Kiorboe *et al*., 1998). Sampling marine snow can be difficult because of its large size and fragility and thus divers are often used to collect it. Natural aggregates photographed and collected *in situ* by SCUBA divers from stations off coastal California were studied by Alldredge (1998). The POC (17–39% of the aggregate by weight), PON (1.7–6.0%) and dry mass content were highly significant exponential functions of aggregate volume. C:N ratios increased with increasing aggregate size, suggesting that larger aggregates were older and more refractory than smaller ones.

Aggregates can be broken up by physical disturbance into smaller particles. Dilling and Alldredge (2000) have shown that the shear forces from the swimming motions of zooplankton such as euphausiids are sufficient to disaggregate marine snow. This work showed that the activities of macrozooplankton and micronekton can play a significant role in the particle dynamics of the water column, regardless of whether they consume particles or not, and accounts for diel variations found in particle abundances in surface waters (e.g., Graham *et al*., 2000). This activity reduces the sizes of particles available to grazers and microbial colonizers and reduces the downward flux of particulate carbon since the smaller particles sink more slowly and reside longer in the water column.

Large amounts of mucilage are produced by some species of phytoplankton which can entrain a great variety of particles. A massive event occurred in the northern Adriatic Sea in July 1991. Analysis by light and epifluorescence microscopy (Baldi *et al*., 1997) revealed a variety of autotrophic species, cyanobacteria and heterotrophic bacteria embedded in a gelatinous matrix. Cytoplasm and particulate polysaccharides leaking from the envelopes of broken cells in the matrix were identified by scanning confocal laser microscopy (SCLM) and fluorescent molecular probes indicating extensive cell lysis. High concentrations of triacylglycerols (30% of total lipids) and free fatty acids (22%) along with very low concentrations of phospholipids (2%) also indicated massive cell degradation. Such aggregates can be hotspots of microbial respiration which cause a rapid and efficient respiratory turnover of particulate organic carbon in the sea (Ploug *et al*., 1999; Ploug and Grossart, 2000). Rates of photosynthesis, nutrient regeneration and decomposition are often much higher than in the surrounding waters.

3.2 Sinking POM

Dead or metabolically stressed microalgal cells settle slowly in seawater according to Stoke's law. However, this need not be the case for metabolically active cells. Waite *et al*. (1997) showed that there are at least two different controls on sinking rate: the ballasting component, which is driven by changes in cell composition and volume which, when dominant, causes sinking rates to be proportional to cell volume; and the energy-requiring, protoplast and vacuolar component which, when active, allows sinking rates to become independent of cell volume.

Given the slow sinking speeds of algal cells, faecal pellets have generally been considered as the important means by which surface POC is transported to bottom sediments, but this is now debated. Certainly, zooplankton faecal pellets are a significant fraction of sinking POM in some areas (e.g., Andreassen *et al.*, 1996), but many reports have now demonstrated that faecal pellets can be a minor component in the sinking POM (e.g., <0.05% of POC sedimentation; Viitasalo *et al.*, 1999).

Temporal and spatial variations in hydrography, together with differences in phyto- and zooplankton community structures, can significantly affect faecal pellet sedimentation fluxes (Viitasalo *et al*., 1999; Sarnelle, 1999; González *et al*., 2000). Much early work focused on the larger animals in faecal pellet transport, such as copepods and amphipods (e.g., Honjo and Roman, 1978). Recently, attention has turned to abandoned larvacean shells (Hansen *et al*., 1996) as a significant source of marine snow. Aggregates composed of the abandoned house of the larvacean *Oikopleura dioica* were found to contain numerous diatoms, fecal pellets, ciliates, and amorphous detritus. The concentrations of diatoms and fecal pellets in the aggregates exceeded ambient concentrations by 3 to 5 orders of magnitude. The suspended larvacean shells are rapidly turned over and can be important in driving the vertical flux of particles with high vertical flux rates ($20–120 \times 10^3$ houses $m^{-2} \cdot d^{-1}$) and settling velocities (an average of 120 $m \cdot d^{-1}$).

Gorsky *et al*. (1999) showed that appendicularians such as *Megalocercus huxleyi* efficiently collect small particles such as cyanobacteria and other prokaryotic picoplankton and excrete them in faecal pellets. However, larger picoeukarotes and the prochlorophyte *Prochlorococcus* were only found in very low quantities in the larvacean fecal pellets. Calculations showed that at an average concentration of five cells of *M. huxleyi* per m^3, about 7% of the small particulate matter will be daily removed from the water. Appendicularians are important in the cycle of both organic and inorganic carbon and their grazing activity can represent a major pathway of carbon transformation in the tropical ecosystem.

Another form of sinking POM consists of large phytoplankton mats (flocs) such as those formed by large diatoms of the genus *Rhizosolenia* (Villareal *et al*., 1993, 1996, 1999). Picoplankton can also be sedimented in this way, through being imbedded in large (>0.5 mm diam.) organic aggregates. For the high nutrient low chlorophyll (HNLC) waters over the Chatham Rise east of New Zealand (Waite *et al*., 2000), it was estimated that 9.3 mg C $m^{-2}yr^{-1}$ of prokaryotic picoplankton biomass could be transported below the euphotic zone by this mechanism. Picoplankton were found within heterotrophic flagellates, within copepod fecal pellets, and within organic matrices of the aggregates. A key factor mediating picoplankton carbon fluxes in moderately productive ecosystems, and in determining the overall particle structure of sedimenting aggregates is likely to be their changing porosity and reduction in picoplankton cell numbers by heterotrophy (Waite *et al*., 2000).

3.3 Ascending POM

One of the more interesting observations in recent years is that the vertical ascending flux of particulate matter in the ocean can be surprisingly high. Mats formed by the diatom *Rhizosolenia* (Villareal *et al*., 1999) not only sink through the water column, but migrate upwards as well (Hayward, 1993). Phytoplankton production in the surface waters of stratified oceans is fed mainly by nitrogen which has been recycled within the euphotic zone. The nitrogen that is lost from surface waters as organic matter exported to the deep ocean must be balanced by inputs of new nitrogen to the upper ocean. Sediment trap studies have shown that the rich nitrate pool below the euphotic zone is the source of “new” nitrogen for the upper ocean, yet steep vertical concentration gradients suggest that diffusive upward transport of nitrate is extremely limited. This conundrum was solved when Villareal *et al*. (1993) showed that abundant *Rhizosolenia* mats migrate vertically between surface waters and deep nitrate pools in the central North Pacific Ocean. This could transport the equivalent of 50% of the new nitrogen requirements into the surface waters of the North Pacific gyre.

In the central North Pacific gyre, chemical composition data indicated that negatively buoyant mats were physiologically stressed compared to positively buoyant mats; negatively buoyant mats had significantly higher C:N ratios and carbohydrate per mat, and lower protein:carbohydrate ratios and internal NO_3^- pools than positively buoyant mats. The maximum ascent rate of mats was 6.4 $m \cdot h^{-1}$ with no relationship to mat size or biovolume. Waite *et al*. (1997) showed that there is no obligate correlation between cell volume and sinking rate for metabolically active cells. They suggest that the minimum cell volume necessary for active sinking rate control is *ca*. 200 μm^3, and that this represents a lower limit for the theoretical minimum volume necessary for positive buoyancy.

Villareal *et al*. (1996) estimated that mats could transport 3.9–40 μmol N $m^{-2}day^{-1}$ into the euphotic zone which is the average equivalent of 3–35% of the new NO_3^- consumed in the surface mixed layer. *Rhizosolenia* mats are also an overlooked source of silica production in the open sea (Shipe *et al*., 1999). Such mats account for about 3% of the standing stock of biogenic silica and 26% of silica production in the upper 150 m of the Sargasso Sea and the daily silica production is 50–76% of the total silica production.

In many cases, these ascending particles have a high content of positively buoyant lipids. For example, Wakeham *et al*. (2001) analysed lipid-rich ascending particles from the hydrothermal plume at Endeavour Segment at the Juan de Fuca Ridge and found that the ascending flux of lipid was up to six-fold greater than the descending flux. Ascending particles contained up to 200 times more lipid than descending particles. Comparison with zooplankton collected above the plume suggested that a large fraction of this lipid was derived from zooplankton that were opportunistically feeding on organic matter from the plume.

3.4 *Lateral transport and resuspension of benthic particles*

In bottom waters much of the POM can be derived from lateral transport of material from continental shelves or from resuspension in the benthic boundary layer (BBL), rather than directly from the overlying surface waters. It is now clear that ocean margins are a significant source of organic matter to the deep open ocean (Bauer and Druffel, 1998). Bianchi *et al*. (1998) used pyrophaeophorbide-*a* (a breakdown product from chlorophyll thought to be predominantly formed by grazing processes in sediments as well as in the water column) to examine this process in waters of the north-east Pacific margin. In this case, an observed deep maximum in the pyrophaeophorbide-*a*/POC ratio was attributed to lateral transport of “older” resuspended sediments from the continental slope rather than to local vertical resuspension in the BBL. In support of this, pyrophaeophorbide-*a* concentrations were negatively correlated with $\Delta^{14}C$ values of the suspended POC.

Thomsen *et al*. (2001) collected particulate matter with sediment traps moored at 610, 1840 and 1950 m water depth in the Barents Sea continental margin. The compositions of the organic material in the two near-bottom traps differed significantly. A combination of quantitative microscopy and bulk parameter determinations together with measurements of alkenone distributions demonstrated that a turbidity plume event at the shelf edge transported organic and lithogenic particles at high velocities to the benthos of the lower continental margin. It was suggested that fine particles were advected into the trap at 1850 m, whereas the coarser fraction with higher settling velocities passed through several resuspension loops before entered the lower trap. Ratios of chlorophyll to phaeopigments (degraded chlorophylls) were used to estimate the contribution from fresh microalgal material.

Studies of POM in the benthic nepheloid layer (BNL) of the deep Arabian Sea by Boetius *et al*. (2000) revealed a high chlorophyll *a* to POC ratio and that the organic carbon concentrations were higher than the sinking particles or the particulate matter at the sediment surface. The carbon demand of the bacterial community in the BNL (20 mg C $m^{-2}d^{-1}$), which was estimated by leucine incorporation experiments, exceeded the vertical POC flux leading the authors to conclude that the enhanced microbial activity and biomass close to the seafloor was mainly supported by the resuspension of small phytodetrital particles and by the DOC flux.

3.5 *Terrestrial inputs*

A major source of particles in coastal areas is transport from the land. The fate and transport of terrestrial organic matter across the continental margin in the Gulf of Mexico was reported by Bianchi *et al*. (1997). Lignin phenols were utilized as biomarkers for terrestrial inputs and their distributions indicated that much of the terrestrial organic matter inputs were deposited on the shelf break and slope. The lignin-phenol concentrations (normalized to carbon) in POC, high molecular weight (HMW) DOC, and sediments in slope waters were considerably higher than at other open ocean sites studied previously. It was suggested that the dominant mechanism for the transport of terrestrially-derived POC and HMW DOC across the shelf and slope is advection of riverine and estuarine discharges through benthic nepheloid layers. Based on loliolide concentrations in the water column, the authors proposed that lateral transport of these materials at the shelf break (through extensions of benthic nepheloid layers) may have been an important mechanism for the injection of terrestrially-derived organic matter into deep slope waters.

Saliot *et al*. (2001) used lipid markers (sterols, fatty acids and pigments) in the POM isolated from Amazon River waters during a high flood period in June 1989 to estimate the relative portion of the terrigenous and autochthonous fractions. Particles showed a highly variable organic carbon content (1.8–29.0%) and corresponding organic carbon concentrations in the water varied from 0.36 to 1.13 $mg \cdot L^{-1}$. Sterol distribution patterns were similar to other equatorial rivers, but distinct patterns were found in the Trombetas and Tapajos rivers, reflecting the different vegetation types of drainage basins and distinct planktonic populations. Pigment concentrations showed that in the main river and most tributaries plant-derived carbon represented no more than 2% of the total.

4. New Approaches to Characterizing POM

A continuing goal of marine chemists is to identify at a structural level the constituents of POM isolated from oceanic waters. Data for a variety of compound types including hydrocarbons, fatty acids, sterols, alkenones, amino acids, pigments, sugars and the like are now available, but these collectively represent a small fraction of the total organic matter. Wakeham *et al.* (2000) systematically examined an inventory of the major particulate biochemicals (amino acids, carbohydrates and lipids) in plankton, sinking POM and sediment. They demonstrated that amino acids comprised about 67% of organic carbon, carbohydrates about 4%, and lipids about 15% in plankton. The quantities of these biochemicals decreased dramatically with depth. Amino acids and lipids accounted for most of the loss and their proportion to organic carbon decreased from 82% in plankton to 20% in sediments. Selective degradation of amino acids in POM has been frequently reported (e.g., Lee *et al.*, 2000; Wakeham *et al.*, 2000 and references therein). As much as 80% of organic carbon in sediment remains unidentified and is not amenable to conventional molecular level analyses. Nevertheless, solid-state ^{13}C NMR indicated that minimal changes occur between the bulk chemical compositions of surface phytoplankton and sinking POC, and amino acid-like material predominates throughout the water column (Hedges *et al.*, 2001).

Unidentified molecules in DOM and sediment have been assumed to be "humic material", which is formed by heteropolycondensation by Maillard-type reactions in which simple biochemicals condense abiotically to form a biologically refractory and extremely complex assemblage of molecules. A more recent view is that organic matter degradation processes are more important than the formation of humic materials in controlling and maintaining the reactive pool of organic matter on the earth's surface. There is growing evidence that many of the major component of the nonliving organic pool could be remnants of biomacromolecules (e.g., see review by Hedges *et al.*, 2000). A better understanding of organic matter degradation and selective preservation is needed. Detrital POM has been thought of as biomacromolecules that escape from short time-scale remineralization. Detrital macromolecules in POM are thought to be a first step in the sequential flow of organic matter from organisms to DOM and eventually to sediment. According to this point of view, chemical characterization of detrital POM is necessary not only for understanding the source and dynamics of POM but also for clarifying the mechanistic processes by which macromolecules survive in the environments. This suggests that new approaches to characterizing POM at the molecular level are still required.

Pyrolysis-gas chromatography/mass spectrometry (Py-GC/MS) analyses have recently been used to extend the more traditional description of the abundance and chemical composition of suspended particulate organic matter (POM) in open and coastal waters of the southern Black Sea (Coban-Yildiz *et al.*, 2000). Thermal degradation of the POM retained on the filters was used to generate depth profiles of the relative concentrations of 23 marker compounds characteristic of chlorophylls, lipids, carbohydrates and proteins. Strangely, no terrestrial markers characteristic of lignin or of plant waxes were observed. The advantage of this technique is that it can provide a rapid screening and ready identification of compositional changes with depth. In surface waters the suspended POM consisted mainly of detritus. Beneath the 0.1% light depth the absence of intact phytoplankton cells and the presence of bacteria and faecal pellets was accompanied by a change in the protein composition as shown by the changes in the ratio of pyrrole:indole markers. Lipid markers increased markedly from the euphotic zone into the oxycline and remained almost constant in the suboxic waters; decreased concentrations in the sulphidic interface were attributed to consumption of lipids by anaerobic bacteria.

An alternative technique to characterize bulk POM is direct temperature-resolved mass spectrometry (DT-MS; Minor *et al.*, 1998, 1999, 2000; Minor and Eglinton, 1999). DT-MS is a form of temperature-resolved, in-source pyrolysis mass spectrometry. Previously, it has been used to provide qualitative information about complex organic samples, but Minor *et al.* (2000) have shown that low voltage electron impact DT-MS can provide rapid (two minute analysis) semi-quantitative information on molecular-level characteristics of desorbable and pyrolyzable components in POM samples. These authors determined relative response factors of some of the common compound classes identified in marine organic matter which were then used to quantify the relative contribution of the compound classes in two natural POM samples. POC:chlorophyll ratios in natural POM samples were also compared with the same ratios determined by the more commonly used techniques of elemental analysis and liquid chromatography (HPLC).

There is growing evidence that different biomacromolecules survive in marine systems for varying time scales (e.g., Hedges *et al.*, 2000). Although the idea has mainly come from studies on dissolved organic matter (DOM) and sedimentary organic matter (e.g., Tanoue *et al.*, 1995; Aluwihare *et al.*, 1997; McCarthy *et al.*, 1997, 1998; Knicker and Hatcher, 1997; Pantoja and Lee, 1999; Mongenot *et al.*, 2001; Nguyen and Harvey, 2001; Knicker *et al.*, 2001), POM is no different in this respect. Particulate combined amino acids that are liberated after acid hydrolysis of POM have been termed "proteinaceous materials", but their chemical nature has not been well documented (e.g., Tanoue, 2000 and references therein). Gel electrophoresis has provided direct evidence that specific protein molecules universally survive in POM samples examined from surface to deep waters at stations in the subarctic, subtropical and equatorial Pacific Ocean, and in the surface waters of the Indian and the Southern Oceans (Tanoue, 1996, 2000; Tanoue *et al.*, 1996 and references therein). Proteolytic digestion indicated that peptides, particularly phytoplankton membrane components, are preferentially enriched in estuarine POM (Laursen *et al.*, 1996). Nguyen and Harvey (2001) showed in laboratory experiments using size-exclusion chromatography coupled to an evaporative light-scattering detector that proteolytic digestible peptides were preserved in the diatom detritus by the formation of large aggregates.

5. New Approaches to Isolating POM

The wider availability of flow cytometry has considerably broadened our knowledge of the smallest particles in the sea: the so-called picoplankton (cells smaller than 2–3 μm). These cells dominate in most open oceanic regions, such as the Pacific Ocean. Flow cytometric sorting allows the physical separation of particle subclasses on the basis of morphological and chemical criteria including size, shape, and autofluorescence characteristics. A protocol for the characterization of oceanic particles using flow cytometric sorting in combination with direct temperature-resolved mass spectrometry has recently been published by Minor *et al.* (2000).

The power of flow cytometry has been increased with the introduction of two new stains (fluorochromes; Veldhuis *et al.*, 1997). These can be used for the quantitative detection of cellular DNA in a wide variety of marine phytoplankton and they are suitable for direct use in seawater using most modern low-power flow cytometers (e.g., 15 mW, 488 nm excitation). The high sensitivity allowed the DNA of the smallest known phytoplankter (*Prochlorococcus*) to be quantified as well as bacteria found in some of the algal cultures. The combination of the dyes also allows live and dead cells to be discriminated in some algal groups (*Prochlorococcus*, diatoms, prasinophytes, and pelagophytes).

A combination of tangential-flow filtration and split flow thin-cell fractionation techniques can now be used to achieve a functional separation of suspended and settling POC. Gustafsson *et al.* (2000) have developed accurate settling velocity cut-offs in the range >0.1 – >10 $m \cdot d^{-1}$. Organic carbon and phosphorus were mainly associated with slowly settling particles (≤1–2 m/d), decoupled from more rapidly settling Si-containing and Fe-containing particles (>4 m/d).

6. Identifying Sources of POM

6.1 Biomarkers

Lipid biomarkers have been widely used to ascertain the sources of POM in marine environments. Much of this has been a qualitative assessment, but a more quantitative approach has been adopted recently. For example, Bodineau *et al.* (1998) used fatty acids and sterols to show that POM within the estuarine turbidity maximum zone in the macrotidal Seine estuary in France was derived from phytoplankton, bacteria, sewage and terrestrial sources. The concentrations of source-specific biomarkers were used to trace temporal changes. Terrestrial matter was a major contributor of POM at low ebb tide (35–58% of the POC) and at high slack tide (10–20% of the POC), whereas sewage organic matter was a relatively minor component (<4% of POC). Phytoplankton was a predominant component of POM during the slack period of the flood tide (12–31% of POC). This prominence was associated with a diatom bloom in the estuary.

Later work by Bodineau *et al.* (1999) extended this approach to the English Channel. Fresh phytoplankton was relatively important in September in coastal waters with a predominance of diatom species, whereas during winter there was a low to undetectable contribution. The bacterial contribution tended to vary in concert with the algal component, becoming important in bloom or post-bloom conditions. Terrestrial organic matter was restricted to coastal areas in September, but in November and February terrigenous organic matter was clearly identified over the whole transect.

Note that such calculations assume that a particular ratio of biomarker to POC is characteristic of the various sources. Clearly, such ratios can vary greatly between species and due to changing environmental conditions. Literature data are rather sparse since few algal studies report lipid data normalised to carbon content, so that field data from the environment being studied often need to be obtained. Despite these limitations, the technique has promise since a great variety of biomarkers are available (both lipids and pigments) and so the calculations allow for cross-checking. A systematic approach to the characterization of phytoplankton populations based on their pigment distributions is increasingly being used (Mackey *et al.*, 1998).

Sterols and fatty acids, in conjunction with several bulk parameters (total suspended solids, chlorophyll *a*, and particulate carbon and nitrogen concentrations), were also used by Canuel and Zimmerman (1999) to determine sources of particulate organic matter in the southern Chesapeake Bay. Suspended and sedimentary organic matter was mainly derived from autochthonous sources including a mixture of fresh and detrital phytoplankton, zooplankton, and bacteria. The dominant factor contributing to the observed temporal variability was phytoplankton productivity.

Much recent work has focussed on an unusual class of compounds called alkenones which are synthesized by certain haptophyte microalgae such as *Emiliania* and *Gephyrocapsa* (e.g., see Conte *et al.*, 1994). The distribution of these compounds is strongly affected by the temperature of the water in which the microalgae are found (Brassell *et al.*, 1986; reviewed by Volkman, 2000), and thus they have proved to be very useful as paleotemperature proxies in the sediment record. This subject was the focus of an NSF-funded workshop held at Woods Hole, Massachusetts in October, 1999 (Eglinton *et al.*, 2001). A good review of recent developments discussed at the meeting can be found in papers published in the electronic journal *Geochemistry Geophysics Geosystems* (e.g., Bijma *et al.*, 2001; Schneider, 2001). Several more recent papers have discussed the temporal (e.g., seasonality) variations of alkenone fluxes to the sea floor (Müller and Fischer, 2001; Prahl *et al.*, 2001).

6.2 Stable and radioactive carbon isotopes

Stable and radioactive carbon isotopes have given invaluable information on the source and the dynamics of POM in the sea. Stable carbon isotope (δ^{13}C) values of bulk POC have been used to identify the source of organic matter based on isotopic differences between C_3 and C_4 terrestrial plants and C_3 marine phytoplankton (e.g., see review by Fogel and Cifuentes, 1993). The δ^{13}C signature of oceanic POM (and DOM as well) provides the key evidence that it is substantially of marine origin (e.g., Trumbore and Druffel, 1995).

Radioactive carbon isotopes (Δ^{14}C) have given information on the dynamics (^{14}C-ages and turnover time) of POC in the sea. Druffel *et al.* (1996) found a large gradient (124–160‰) with depth and seasonal variability (by 20–30‰) in the suspended POC Δ^{14}C values throughout the water column in the northeast Pacific Ocean, even though it had been assumed that the turnover of suspended POC was relatively quick (≤10 years) and that sinking particles originating from surface water were the source of the suspended POC in the middle and deep waters. The Δ^{14}C value of sinking POC collected by deep-moored sediment traps also showed a semiannual trend and lower Δ^{14}C values were recorded during the period of high flux. From these observations they postulated that lower Δ^{14}C values of deep suspended and sinking POC were caused by the sorption (or biological incorporation) of "old" DOC onto particulate matter (Druffel *et al.*, 1998a, b). They further hypothesized that DOC was transported from surface to deep waters through this mechanism.

The ^{14}C content in individual compounds can now be measured through the combination of automated preparative capillary gas chromatography and accelerator mass spectrometry (Eglinton *et al.*, 1996). This technique has been successfully applied to the *n*-alkanes in sediments (Eglinton *et al.*, 1997). Application of such "state of the art" techniques promises to provide clues to explain the variability of Δ^{14}C values in suspended and sinking POC in the entire water column.

In marine environments, coastal areas receive large inputs of various organic compounds from different sources, and the dynamics of organic matter production, decomposition, transport and burial, display considerable spatial and temporal variability. A knowledge of the sources and reactivity of organic matter, as well as factors controlling its distribution, is therefore important in understanding the role of these areas in regional and global biogeochemical cycles (Bianchi and Canuel, 2001). Measurements of carbon isotopes and biomarkers have been applied to POM in coastal systems (Canuel *et al.*, 1995; Qian *et al.*, 1996; Raymond and Bauer, 2001). Canuel *et al.* (1995) found that the δ^{13}C ratios of tissues of suspension-feeding bivalves in San Francisco Bay were affected by freshwater algae, even though the bulk $\delta^{13}C_{POC}$ indicated that phytoplankton was the major source of POM in the entire bay system.

POM in coastal estuaries has multiple sources and the measurement of $\delta^{13}C_{POC}$ is often insufficient for determining the sources of organic carbon (e.g., Qian *et al.*, 1996). Raymond and Bauer (2001) emphasized the utility of the paired ^{14}C and ^{13}C measurements for better understanding carbon budgets of complex sites such as estuarine and near-shore environments. They applied a two-isotope, three-source mass balance mixing model (Kwak and Zedler, 1997) to evaluate the relative contributions of the different potential sources of DOC and POC to the observed Δ^{14}C and δ^{13}C distribution. Sources of DOC and POC were quite different in waters of the Mid-Atlantic Bight continental margin. The majority of DOC (as much as 97%) originated from offshore DOC, but DOC derived from estuarine and contemporary production was also evident. For POC, between half and all of the POC came from *in situ* primary production, up to half was from riverine/terrestrial material, and a smaller fraction (up to 25%) might have originated from older, resuspended shelf sediments.

In the past decade, compound specific isotope analysis (CSIA) using gas chromatography/combustion/isotope ratio mass spectrometry (GC/C/IRMS) has been applied to various geochemical samples. CSIA has been increasingly used to identify the sources of sedimentary organic compounds (e.g., Goñi *et al.*, 1997; Boschker *et al.*, 1999; Cifuentes and Salata, 2001; Shi *et al.*, 2001), and has provided a more robust interpretation of the fate and dynamics of terrestrial material that is transported to the sea. For example, the oxidation products of lignin, an indicator of terrestrial input, from surface sediments of the Gulf of Mexico showed that the offshore lignins derived from erosion of the grassland (C_4 plants) soils of the Mississippi River drainage basins, and nearshore lignins originated from C_3 plant detritus from coastal forests and swamps (Goñi *et al.*, 1997). Shi *et al.* (2001) suggested that the deposition pattern of POM depended on its source based on results of CSIA of sedimentary fatty acids in the Altamaha River estuarine in Georgia. They reported that POM from terrestrial plant material was dominant during the initial, upper estuary mixing, while marine POM was mainly deposited at a more intensive mixing zone, indicating that terrestrial plant-derived POM might not be significantly transported across the mixing zone.

6.3 *PCR-based molecular biology*

The techniques of molecular biology are increasingly being applied to identify the living components of POC in seawater. These powerful techniques promise to provide a level of detail virtually unobtainable by more traditional techniques such as microscopy and more recently flow cytometry, but we hasten to add that the techniques are complementary. An early example is the work of Palenik (1994) who used the polymerase chain reaction (PCR) to amplify DNA-dependent RNA polymerase gene sequences from the cyanobacterial populations in Sargasso Sea seawater. Sequencing and analysis of the cloned fragments showed that the population consisted of two distinct clusters of *Prochlorococcus*-like prokaryotes and four clusters of *Synechococcus*-like cyanobacteria.

A more recent example is the work of Moon-van der Staay *et al.* (2000). Total genomic DNA was isolated from 3 μm filtered samples collected in the Pacific Ocean from which small subunit (18S) ribosomal RNA genes (rDNA) were amplified by PCR using universal eukaryotic primers. 18S rDNA libraries from five samples were screened using a prymnesiophyte-specific oligonucleotide probe, and 14 nearly complete 18S rDNA sequences were retrieved. Phylogenetic analysis of these sequences established the presence of several prymnesiophyte lineages which had no equivalent among cultivated species. The interpretation of such data is presently constrained by the limited availability of sequence data for marine species, but this is rapidly changing as PCR techniques become widely adopted.

7. POM Reactivity

One of the more important components of POM in ocean waters is the fraction of photosynthetically produced POM that is transported from surface euphotic waters to the deep by sinking particles. This so-called “biological pump” plays a key role in biogeochemical cycles in the sea, such as the uptake of atmospheric CO_2 and the fuelling of marine food webs in the ocean interior and in the benthos (e.g., Druffel and Robison, 1999 and references therein). The export flux (flux at the base of the euphotic zone) must depend on primary production in the surface water, but a defined relationship between the two parameters has been unclear. Time-series field observations have demonstrated that the export flux of POC and depth-integrated primary production are poorly correlated at the Atlantic BATS station (Michaels and Knap, 1996) and at the Pacific HOT station (Karl *et al.*, 1996). Indeed, during the ENSO period an inverse correlation was observed at the HOT station (Karl *et al.*, 1996).

One of the difficulties for determining fluxes with confidence is overcoming methodological problems during sample collection. Although sediment traps are a valuable tool for collecting sinking POM, particularly settling particles in the marine snow size range ($d > 0.5$ mm), the accuracy of the fluxes measured in surface water has been questioned (Gardner, 1997). Sediment trap fluxes often do not correlate well with the total particulate mass concentration determined using transmissometers (Walsh and Gardner, 1992). Furthermore, the contribution from living zooplankton “swimmers” to the collected material has generated much attention (e.g., Lee *et al.*, 1988; Karl and Knauer, 1989). More recently, substantial biases have been reported due to the solubilization of collected particles (Noji *et al.*, 1999). Kähler and Bauerfeind (2001) showed that much of the solubilized organic matter in a shallow time-series trap originated from swimmers, as well as from passively trapped material. When this was considered, the calculated vertical organic carbon flux was 2.7 times larger than the estimate based on recovered particles alone. For organic nitrogen this correction was up to 6 times greater. Other problems in trapping efficiency have also been reported related to the geometries and deployment characteristics of traps (Nodder and Alexander, 1998; Gust and Kozerski, 2000; Buesseler *et al.*, 2000), and to the effect on lateral transport of materials (Yu *et al.*, 2001).

The ^{234}Th deficit method is another approach for determining particle fluxes from the euphotic zone. In the Equatorial Pacific the export flux determined from traps is 4–21% of primary production, whereas the values are between 3 and 5% based on the ^{234}Th method (Murray *et al.*, 1996). The correction of the trap flux using ^{234}Th data is problematic, however, because the ^{234}Th method also has some uncertainties (Gardner, 1997). These include variability of the C/^{234}Th ratio (e.g., Buesseler, 1998) and differences in the affinity of Th for different particle types (e.g., Hirose and Tanoue, 1999, 2001). Buesseler (1998) compared ^{234}Th-based export flux and primary production in a wide range of open ocean setting and seasons, and found that the export flux of POC is less than 5–10% of total primary production in much of the ocean, irrespective of the level of the primary production. Exceptions are found during blooms at high latitudes, accompanying spring blooms at mid-latitudes and at the sites of high export characterized by food webs dominated by large phytoplankton such as diatoms.

The concept that the export flux of bio-elements (C, N, P) balances new production in the surface water is attractive, but the idea is oversimplified because organic matter produced in the euphotic zone is removed not only by the particulate phase but also in the dissolved phase and through the vertical migration of zooplankton (Carlson *et al*., 1994; Emerson *et al*., 1997; Hernández-León *et al*., 2001; Hidaka *et al*., 2001). Kähler and Koeve (2001) examined nutrient consumption in relation to the dynamics of DOM in surface water and concluded that the export flux of DOM is of minor importance because DOM is moved mainly by convection, its capacity for export is limited, and because the C:N:P ratio of DOM is different from the Redfield ratio (e.g., Karl *et al*., 1993; Kähler and Koeve, 2001). In contrast, the C:N:P ratio in POM generally conforms to Redfield stoichiometry as does deep-ocean chemistry.

Lampitt and Antia (1997) examined the relationship between primary production and fluxes calculated from deep sediment traps. Rigorous criteria were applied so the results are comparatively unbiased. They found that there is a positive correlation between primary production and POC flux at the depth of 2000 m for primary production levels below 200 gC/m^2/year, but above this level, the flux remained constant at about 3.5 gC/m^2/year. They also commented that the eight planktonic climatological categories proposed by Longhurst (1995) provided a most useful means for examining the variability of flux data. Globally, the open ocean flux of organic carbon at 2000 m is 1% of the total net primary production with the highest flux recorded in monsoonal environments (1.7%) and the lowest in Antarctica (0.1%).

8. Concluding Remarks

Much has been learned about the chemical composition, production, transport and fate of particulate organic matter in the oceans over recent decades, but research continues to produce new insights into carbon cycling in the oceans. In part this is due to the introduction of new technologies for identifying living and detrital particles (e.g., flow cytometry, laser microscopy, techniques of molecular biology) and of chemical techniques for its characterization (e.g., lipid and pigment biomarkers, stable and radioactive carbon isotopes, pyrolysis techniques in conjunction with mass spectrometry, compound specific GC-MS). Our increased knowledge is also the result of the implementation of far-sighted large-scale multidisciplinary research programs such as JGOFS and the commitment of several nations to expensive, but vital, large-scale oceanographic expeditions. The true benefits of this chemical research can only be realised when it is carried out in combination with studies of marine physics and biology. Recent advances in the latter particularly in the field of molecular biology promise to provide much more information about the organisms involved in production and recycling of carbon in marine waters. We can confidently assert that sufficient significant research gaps still remain to entice a new generation of researchers into the field.

Abbreviations

ATP	adenosine triphosphate
BBL	benthic boundary layer
BNL	benthic nepheloid layer
C:N	carbon to nitrogen ratio
CSIA	compound specific mass spectrometry
DNA	deoxyribonucleic acid
DOC	dissolved organic carbon
DOM	dissolved organic matter
DT-MS	direct temperature resolved mass spectrometry
ENSO	El Niño-Southern Oscillation
GC-C-IRMS	gas chromatography-combustion-isotope ratio mass spectrometry
HMW	high molecular weight
HNLC	high nutrient-low chlorophyll
HPLC	high performance liquid chromatography
NMR	nuclear magnetic resonance
PCR	polymerase chain reaction
POC	particulate organic carbon
POM	particulate organic matter
PON	particulate organic nitrogen
Py-GC-MS	pyrolysis gas chromatography-mass spectrometry
RNA	ribonucleic acid
SCLM	scanning confocal laser microscopy
SCUBA	self-contained underwater breathing apparatus

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