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# Role of Large Particles in the Transport of Elements and Organic Compounds Through the Oceanic Water Column

SCOTT W. FOWLER* and GEORGE A. KNAUER†

**International Laboratory of Marine Radioactivity, Musée Océanographique, MC 98000, Monaco*

†*Center for Marine Science, University of Southern Mississippi, National Space Technology Laboratories, NSTL, Mississippi 39529, U.S.A.*

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**Abstract**—During the past decade data from a variety of sources have been obtained which show conclusively that the relatively rare, large particles sinking through the water column are responsible for the majority of the downard vertical mass flux in the sea. This finding has important implications for understanding the transfer, distribution and fate of elements and organic compounds in marine waters. The "large" ($> 100\,\mu m$) detrital particles responsible for vertical flux are primarily biogenic and range in size and composition from small, discrete fecal pellets and plankton hard parts to large, amorphous aggregates or "snow" which contain both organic and inorganic constitutents. Depending on size, shape and density, these particles sink at rates ranging from $< 1$ to $> 1000\,m\,day^{-1}$. Several methods have been developed for sampling these particles of which *in situ* sediment trapping has probably furnished the most comprehensive qualitative and quantitative information on the role large particles play in material transport. Flux studies have highlighted the importance of marine heterotrophs in packaging fine, suspended particulate matter into large rapidly sinking particles which accelerate the movement of incorporated materials to depth. Large particle production via biological packaging is not restricted to the euphotic zone but can occur at all depths and information is now accruing on rates of production of large particles in the water column. Chemical analyses of sedimenting particles collected in sediment traps and those sampled by other means have allowed quantifying vertical fluxes and residence times of elements, radionuclides and organic compounds (natural and anthropogenic) in various oceanic regimes. Pertinent studies dealing with the above aspects are reviewed and several areas for future research are suggested.

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## 1. INTRODUCTION

OCEANIC particulate matter, consisting of both biotic and abiotic materials, is derived from a variety of sources. These include authigenic production by biota, precipitation of inorganic minerals, resuspension of sedimentary material, fluvial and aeolian inputs, submarine vulcanism, and a number of inputs associated with lateral transport processes. The size of "large" marine particles is difficult to define precisely but is usually considered to encompass particles in the range of roughly $10^2$–$10^4$ $\mu$m in diameter or length. These are particles which are generally biogenic (planktonic remains, fecal pellets, molts, eggs, etc.) but can also contain a large inorganic component, as in the case of fecal pellets (DUNBAR and BERGER, 1981; DEUSER, ROSS and ANDERSON, 1981; DEUSER, BREWER, JICKELLS and COMMEAU, 1983). For the purposes of our discussion, we are not considering biogenic particles greater than $10^4$ $\mu$m in diameter which include the larger marine organisms.

Although large, rapidly sinking particles are far less numerous than the fine, suspended particulates, the former are primarily responsible for the vertical transport of material (mass flux) and elements in the sea (see MCCAVE, 1975, 1984; BISHOP, EDMOND, KETTEN, BACON and SILKER, 1977; HONJO, 1978, 1980). Various aspects of particle concentration, size distribution and particle dynamics have recently been reviewed by SIMPSON (1982). In this review we primarily discuss recent advances in knowledge concerning the composition, production, collection methods and transport dynamics of these so-called "large" marine particulates.

## 2. COMPOSITION

### 2.1. *Biogenic particles*

2.1.1. *Fecal pellets.* All consumer species produce fecal material of some sort. Fecal material can occur as relatively loose, amorphous aggregates which readily disintegrate, such as those produced by ciliates (STOECKER, 1984), or as dense, tightly packed pellets which maintain their integrity like those of many micro-crustaceans (see TURNER and FERRANTE, 1979). They range in size from a few $\mu$m for the recently identified "minipellets"

from protozoans (3–50 $\mu$m) (GOWING and SILVER, 1985) to several mm for pellets from larger crustaceans (FOWLER and SMALL, 1972), gelatinous zooplankton (BRULAND and SILVER, 1981; ISEKI, 1981) and fish (ROBISON and BAILEY, 1981). The size of the fecal pellet is a function of organism size; the smallest are produced by protozoans and larval stages of plankton, intermediate sizes by copepods, appendicularians and other microplankton, and the largest by euphausiids, salps, pelagic shrimp and fish. Fecal aggregates (13–25 $\mu$m) produced by planktonic ciliates and tintinnids lack a distinct membrane and quickly break up into smaller particles (STOECKER, 1984). Fecal material from other protozoans (foraminifera, radiolarians, etc.) is likely to be of a similar nature although it has not yet been examined. Micro- and macro-crustaceans normally produce ovoid, ellipsoid, cylindrical and spherical pellets which are usually encapsulated by a peritrophic membrane (FORSTER, 1953; GAULD, 1957); however, in the case of some larval forms the membrane does not separate from the organism's abdomen and thus provides a substratum termed "fecal mass" on which microbes, organic debris and planktonic organisms accumulate (YOUNGBLUTH, 1982). The peritrophic membrane is composed of chitin and is a key factor in determining the half-life of a degrading pellet. It is not clear how long these membranes can resist degradation. Some laboratory studies have shown that pellets produced by animals on laboratory diets are degraded in periods of several hours to several days at high temperatures between 20–25°C; at lower temperatures (5°C) membranes can remain intact for 20–35 days (HONJO and ROMAN, 1978; TURNER, 1979). In contrast pellets produced by marine zooplankton feeding on a natural diet have been shown to remain intact for several weeks at temperatures as high as 18°C (SMALL and FOWLER, 1973). Likewise natural pellets from freshwater copepods showed no membrane breakdown after six days (BATHELT and SCHELSKE, 1983). Evidence from geological studies clearly shows that zooplankton fecal pellets reach the deep sediments intact in many areas, particularly those which are exposed to anoxic conditions (PORTER, 1984). Considering these observations, pellets produced from natural diets (i.e. field produced pellets) may be more resistant to microbial attack than would be inferred from studies with animals feeding on specific algal cultures in the laboratory. This contention is supported by recent evidence from both bacterial colonization experiments (JACOBSEN and AZAM, 1984) and sediment trap studies which suggests that bacterial decomposition of large particles in the upper and lower water column is slow (DUCKLOW, HILL and GARDNER, 1985).

Pellets from macroplanktonic euphausiids and micronektonic shrimp are thin cylinders enclosed in a peritrophic membrane sometimes reaching several mm in length (MOORE, 1931; FOWLER and SMALL, 1972; FOWLER, personal observation). Pellets from other large macroplankton and micronekton, particularly the gelatinous forms, differ considerably. Salps (*Salpa*) produce large rectangular flakes (2–3 mm on a side) which are not membrane-bound (BRULAND and SILVER, 1981; ISEKI, 1981; MADIN, 1982; POMEROY, HANSON, MCGILLIVARY, SHERR, KIRCHMAN and DEIBEL, 1984). Often these flakes are connected end to end in long ribbons and the contents appear to be loosely held together by mucoidal substances. Other species such as the doliolids (*Dolioletta*) produce less compact, more irregularly shaped flakes (BRULAND and SILVER, 1981). Pellets from the pelagic pteropods (e.g. *Corolla* and *Euclio*) are typically coils of high density and cylindrical shape (BRULAND and SILVER, 1981; FOWLER, personal observation). Little is known about degradation rates of these types of pellets but they probably break down more rapidly than crustacean pellets because they lack discrete membranes. Midwater fish produce large cylindrical pellets which are not bound by a peritrophic membrane except in the case of some species of *Melanostigma*

(ROBISON and BAILEY, 1981). The material is somewhat adhesive which increases its probability to agglutinate with other smaller particles. During long-term aging experiments with fish feces, primary amines are released indicating that protein degradation does occur albeit slowly. Owing to the rapid sinking rates and slow decomposition of fish fecal pellets, it is suggested that this material will reach deep water or the bottom with nutrients and other elements virtually intact.

Although not numerous, several attempts have been made to characterize and categorize marine fecal pellets by size, shape, color, contents and sinking rates (see for example MOORE, 1931; MARTENS, 1978; URRERE and KNAUER, 1981). Despite these scattered works there still remains a need for a comprehensive key which could be used to help identify pellets sampled *in situ* by sediment traps.

The composition of fecal pellets is highly diverse and generally reflects the feeding habits of the producer organisms. Pellets from herbivore grazers contain a myriad of unialgal, protozoan and bacterial forms. Some copepod fecal pellets are luminescent due to enteric marine luminous bacteria egested with the pellet (ANDREWS, KARL, SMALL and FOWLER, 1984). Detailed description of pellet contents including excellent electron micrographs can be found in the works of TURNER (1977); BISHOP, EDMOND, KETTEN, BACON and SILKER (1977); BISHOP, KETTEN and EDMOND (1978); HONJO (1978, 1980); SILVER and BRULAND (1981); BRULAND and SILVER (1981); SILVER and ALLDREDGE (1981) and GOWING and SILVER (1985) to mention a few. Interestingly, it has been observed that many of the phytoplankton cells contained in pellets appear to be intact (SILVER and BRULAND, 1981). It has been further demonstrated using culture techniques that many of these algal cells in field-collected pellets are indeed viable after passing through the gut of grazers (FOWLER and FISHER, 1983). Recent evidence indicates that freshly-voided pellets contain gut-derived microflora, the activity of which decreases rapidly with time after voidance (ANDREWS, KARL, SMALL and FOWLER, 1984). This observation is in accordance with electron microscopic studies which suggest that bacteria inside pellets are the major cause of pellet decomposition rather than by external micro-flora colonization (GOWING and SILVER, 1983). Microscopic examination of pellets collected *in situ* and preserved showed little evidence of bacterial colonization of the peritrophic membrane (GOWING and SILVER, 1983), a finding which contrasts with studies that have used pellets produced in the laboratory on artificial diets (HONJO and ROMAN, 1978; TURNER, 1979). This discrepancy should be examined in more detail with various types of pellets since the location of the degrading bacteria could have profound effects on the cycling of elements and compounds contained in fecal pellets. Nevertheless, the process of bacterial decomposition of these particles in the sea may be slower than previous believed (JACOBSEN and AZAM, 1984; DUCKLOW, HILL and GARDNER, 1985).

In addition to their biogenic content, zooplankton fecal pellets often contain considerable amounts of fine alumino-silicate particles (DUNBAR and BERGER, 1981; DEUSER, ROSS and ANDERSON, 1981; SCHEIDEGGER and KRISSEK, 1983; KRISHNASWAMI, BASKARAN, FOWLER and HEYRAUD, 1985). This occurs when normally herbivorous forms like copepods indiscriminately filter suspended clays when feeding. It has been shown that packaging of these relatively heavy particles results in ballasting of the pellets and subsequent enhanced sinking velocities (SMALL, FOWLER and UNLU, 1979). These trapped inorganic particles are eventually released to the water column or sediments when the organic portion of the pellet is finally degraded. In fact the ingested minerals actually undergo chemical and mineralogical

transformations that depend on the initial mineralogy and particle residence times in the gut (SYVITSKI and LEWIS, 1980; LEWIS and SYVITSKI, 1983).

The composition of pellets from larger omnivorous and carnivorus zooplankton and nekton differs considerably. These pellets generally show a high protein content because of the packaged animal remains (ROBISON and BAILEY, 1981). These types of pellets, many of which are not enclosed by a peritrophic membrane (e.g. fish), contain more friable organic matter and less siliceous material and, as a result, will degrade more readily than those containing "hard parts" (diatom frustules, coccoliths, etc.) of microplanktonic species.

2.1.2. *Intact organisms and plankton hard parts.* Evidence from sediment trap and large volume filtration studies indicates that a substantial portion of the large particle flux is comprised of intact organisms and the hard parts of plankton. Intact radiolarians (BISHOP, EDMOND, KETTEN, BACON and SILKER, 1977; TAKAHASHI and HONJO, 1983), coccoliths (HONJO, 1978), foraminifera (HONJO, 1980; HONJO, MANGANINI and POPPE, 1982), diatoms (SCHRADER, 1971; HONJO, 1978; WASSMANN, 1983; SMETACEK, 1985), microcrustacean molts (BISHOP, EDMOND, KETTEN, BACON and SILKER, 1977; FOWLER, SMALL, ELDER, UNLU and LAROSA, 1979; HONJO, 1980; HONJO, MANGANINI and COLE, 1982; WEFER, SUESS, BALZER, LIEBEZEIT, MULLER, UNGERER and ZENK, 1982), pteropod shells, fish scales and bits of epiphytic plants (e.g., *Sargassum*) (HONJO, 1980) have all been found in particulate material at depth. In some cases where pronounced seasonal blooms take place, diatoms and other phytoplankton species appear to reach the deep-sea floor relatively intact (BILLET, LAMPITT, RICE and MANTOURA, 1983; LAMPITT, 1985). SMETACEK (1985) hypothesizes that mass diatom sinking is accelerated by aggregate formation of mucus-secreting cells. Furthermore, he contends that during descent these large sticky diatom aggregates may scavenge other particles which, if heavier, could increase the sinking rate. Nevertheless, despite rapid sinking, the organic fraction of these diatom aggregates undergoes some reworking and degradation as evidenced by the high phaeophorbide and C/N ratios characteristic of these particles (BILLET, LAMPITT, RICE and MANTOURA, 1983).

Other types of detrital material will eventually undergo dissolution although at differing rates. For example, the fact that molts are only rarely found in sediment traps, particularly deep ones, is attributable to their rapid degradation within a few days (SMALL and FOWLER, 1973). Those that are collected have either been in fairly shallow water (e.g. in traps $< 100$ m, FOWLER, SMALL, ELDER, UNLU and LA ROSA, 1979; CHESTER and LARRANCE, 1981; on filters $< 400$ m, BISHOP, EDMOND, KETTEN, BACON and SILKER, 1977) or were perhaps produced by deep water populations (WISHNER, 1980) dwelling just over the traps (HONJO, MANGANINI and POPPE, 1982). For example, recent samples collected within 10 m of the sea bed at depths of 5440 m in the region of Madiera Abyssal Plain by the RRS *Discovery* contained copepod material 60–70% of which consisted of carapaces and corpses (BOXSHALL, personal communication). Owing to their friable nature, molts produced in the surface layers probably have little chance of reaching great depth despite rapid sinking speeds. The rate of dissolution of calcium carbonate tests of foraminifera, coccoliths and aragonite shells of pteropods is a function of the degree of carbonate undersaturation in the surrounding waters (CORLISS and HONJO, 1981; THUNELL and HONJO, 1981; BETZER, BYRNE, ACKER, LEWIS, JOLLY and FEELY, 1984). Individually sinking diatom frustules would also undergo some dissolution especially in deep water columns (KAMATANI, 1982). In some instances hard part remineralization is rapid as shown by rates for aragonite shell dissolution of 4–14% per day (BETZER, BYRNE, ACKER, LEWIS, JOLLY and FEELY, 1984).

Nevertheless, interpretation of dissolution rates from sediment trap studies is confounded by a lack of knowledge about the effects of trap conditions (e.g. deployment times, preservatives, pH, etc.) on carbonate and opal dissolution.

Carcasses of organisms are another source of large particles, however, most originating in the upper layers of the water column are probably eaten before reaching great depth. In this respect, large animal remains have rarely been observed on the deep-sea floor. Recently, SMITH (1985) has reported that visual surveys from submersibles off southern California yielded one large carcass (mean wet weight $\sim 2$ kg) and four small carcasses (mean weight $\sim 50$ g) of potentially pelagic origin per 8100 $m^2$. This translates to roughly 270 mg imported material $m^{-2}$. The experimental results of SMITH (1985) indicate that these falls would be rapidly consumed (within hours to days) and are energetically important in that perhaps 11% of benthic community respiratory requirements are met from this food source. Large amounts of macrophytic detritus (e.g. *Thalassia* grass and *Sargassum* blades) are occasionally found at great depth and apparently also serve as food for many benthic organisms (ROWE and STARESINIC, 1979).

2.1.3. *Marine snow and amorphous aggregates.* The amorphous, flocculent detrital material loosely termed "marine snow" is ubiquitous in the world's oceans. Although derived from many sources, it probably represents the major component of the material caught in sediment traps and is thought to serve as an important site for most of the water-column related production/decomposition processes. It is difficult to consider marine snow as a specific type of particle such as fecal pellets, molts, etc., because of the varied processes, both organic and inorganic, which produce this material. These macroscopic aggregates are better thought of as both active and passive scavengers as well as sites for housing a variety of phyla and concomitant metabolic processes. A general discussion of their origins and roles can be found in TRENT, SHANKS and SILVER (1978). Examples of the roles played by this material include its contribution to vertical flux (SHANKS and TRENT, 1980; WASSMANN, 1983) and as a microhabitat for numerous bacteria, microzooplankton and their detrital products (SILVER, SHANKS and TRENT, 1978; CARON, DAVIS, MADIN and SIEBURTH, 1982; SILVER, GOWING, BROWNLEE and CORLISS, 1984). Marine snow has also been shown to represent a significant reservoir for numerous elements and compounds, such as trace metals (HEBEL, KNAUER and MARTIN, in press), $NH_4$, $NO_2$, $NO_3$ and $PO_4$ (SHANKS and TRENT, 1979), and C, N, protein, carbohydrate and lipid (ALLDREDGE, 1979). These aggregates often display bioluminescence (ORZECH and NEALSON, 1984; ANDREWS, KARL, SMALL and FOWLER, 1984) and are also the site for considerable primary production (KNAUER, HEBEL and CIPRIANO, 1982; ALLDREDGE and COX, 1982) and heterotrophic metabolic activity (ALLDREDGE and YOUNGBLUTH, 1985). While the above list is not exhaustive, it underscores the diversity of processes associated with these "particles" as well as their potential importance to the water column large particle pool, and by inference, element flux by large particles.

## 2.2. *Inorganic particles*

2.2.1. *Clay aggregates.* Fine inorganic particles such as clays enter the sea from land and sink very slowly through the water column (0.5 m $day^{-1}$, see LAL, 1980). Concentrations of these particles will vary both temporally and spatially but have been estimated to be

approximately $10\,\mu g\,l^{-1}$ in the deep ocean (LAL, 1980). If they are impacted with larger, more rapidly sinking particulates, the fine suspended particles can be entrained and carried downward by a "piggy-back" mechanism (LAL, 1980). This could take place by direct accretion of colliding fine particles on the sticky organic material that coats them (LAL, 1977; BALISTRIERI, BREWER and MURRAY, 1981) or by incorporation into the mucoid-type matrix of "marine-snow" (BISHOP, EDMOND, KETTEN, BACON and SILKER, 1977; SILVER, SHANKS and TRENT, 1978; SILVER and ALLDREDGE, 1981). These sorts of small aggregates could be further packaged by the grazing/filtering action of pelagic organisms, each time resulting in aggregates containing larger quantities of clay with greater sinking speed. Accretion, aggregation and packaging is probably the ultimate fate of most fine, suspended inorganic particles (see HONJO, SPENCER and FARRINGTON, 1982; HONJO, MANGANINI and POPPE, 1982; DEUSER, BREWER, JICKELLS and COMMEAU, 1983; MCCAVE, 1984).

2.2.2. *Sediment particles.* Large grain-size, suspended sedimentary particles (coarse sediment, sand, pebbles, etc.) are extremely rare in the ocean, particularly in open waters. Because of their high density, those put into suspension rapidly sediment near their point of origin. Sources could be lateral transport from the continental margins (HONJO, SPENCER and FARRINGTON, 1982), riverine input suspensions and resuspension via turbidity currents. Because much energy is needed to keep particles such as these in suspension, they would occur more commonly near shore, in high velocity currents and along bottom boundary interfaces (see HOLLISTER and MCCAVE, 1984; WEATHERLY, 1984).

2.2.3. *Benthic fluffs or flocs.* The presence of unconsolidated marine fluff or floc layers has been reported in the "benthic transition layer" (HONJO, MANGANINI and COLE, 1982), the zone covering the first few meters above the sediments (HONJO, personal communication; LAMPITT, 1985). The fluff layer, 2–5 cm thick, is very fluid, apparently structureless and reddish-brown in color. Comparison of this material with sediment trap samples collected 200 m above the bottom indicates that the fluff material is of different composition (HONJO, MANGANINI and COLE, 1982). COLE, HONJO, GRASSLE and HOBBIE (1982) hypothesize that the fluff zone is an area where decomposition and dissolution transform the particulate flux (highly biogenic) into surface sediment (mainly inorganic). Little is known about the composition of the particles comprising the fluff but it likely has a significant inorganic component. It is also probable that deep-sea benthopelagic plankton (WISHNER, 1980) process this material into fecal pellets. This material appears to be distinctly different from the pulses of phytodetritus that periodically arrive at the sea floor at depths as great as 4000 m (LAMPITT, 1985).

## 3. SAMPLING METHODS

### 3.1. *Sediment traps*

Since it is now recognized that standard water bottles fail to sample the ocean particle field adequately, moored or floating sediment traps are being used to intercept sinking particles (SIMPSON, 1982). This tool seems to be the most versatile means of sampling and experimenting with large particles in a variety of marine environments (see HONJO, 1978, 1980; KNAUER, MARTIN and BRULAND, 1979; PRAHL and CARPENTER, 1979; SASAKI and NISHIZAWA, 1981; ISEKI, 1981; DYMOND, FISCHER, CLAUSON, COBLER, GARDNER,

RICHARDSON, BERGER, SOUTAR and DUNBAR, 1981; DUNBAR and BERGER, 1981; FOWLER, BALLESTRA, LA ROSA and FUKAI, 1983; KARL and KNAUER, 1984; WASSMANN, 1983, 1984; and many others). Generally speaking, there has been little effort expended in addressing inherent problems involved with sediment trapping (BLOMQVIST and HAKANSON, 1981) other than the question of trapping efficiency (KNAUER, MARTIN and BRULAND, 1979; GARDNER, 1980a, b). Limited information is available on the trapping of extraneous materials (e.g. "swimmers", KNAUER, MARTIN and BRULAND, 1979; KNAUER, KARL, MARTIN and HUNTER, 1984) and the advantages and disadvantages of various preservatives (KNAUER, KARL, MARTIN and HUNTER, 1984). In water columns with large concentrations of zooplankton (e.g., copepods, pteropods, etc.), considerable contamination of trap materials can occur by animals actively swimming into the traps regardless of preservative. For example, KNAUER, KARL, MARTIN and HUNTER (1984) report that at shallow depths "swimmer" associated carbon can be as high as 400% of that due to passive particulate flux. In the absence of preservatives or poisons in sediment traps, carbon and nitrogen will be lost from the organic particles through biodegradation (LORENZEN, WELSCHMEYER and COPPING, 1983; LORENZEN, WELSCHMEYER, COPPING and VERNET, 1983; MANGANINI and HONJO, 1985). KNAUER, KARL, MARTIN and HUNTER (1984) discuss the effects and potential problems that can occur with various preservatives and poisons (i.e., compounds such as formaldehyde and gluteraldehyde are preservatives; mercury chloride and sodium azide are poisons). Depending on the questions being asked, employment of a proper preservative may be paramount if quantitative results are to be obtained. GARDNER, HINGA and MARRA (1983) who observed the degradation of biogenic material in the deep ocean have also discussed several aspects of this problem with respect to the accuracy of sediment trap fluxes. They found that even when poisons were used there was a measurable loss of organic matter from biogenic materials, on the order of 0.1–0.5% $day^{-1}$. Rates were higher for unpoisoned material (0.5–1.0% $day^{-1}$) but, in any case, loss was assumed to be exponential resulting in rapid decay of the labile carbon and a slower decay of the refractory component. Both GARDNER, HINGA and MARRA (1983) and KNAUER, KARL, MARTIN and HUNTER (1984) conclude that preservatives like formaldehyde might be the best agent for retarding decay of the organic matter.

There have been a number of studies indicating that a considerable amount of the analyte of interest is lost from the particulate phases of trap-collected material. These problems have been discussed for some organic compounds (MANGANINI and HONJO, 1985) and certain metals such as Mn, Fe, Zn and Cd. MARTIN and KNAUER (1980, 1982) specifically address this problem for Mn. They have overcome the problem by using a high density NaCl solution in the bottom of the traps that retards flushing and whose chemical properties can be controlled. Thus, it is possible to analyse this solution for solutes in order to calculate a total flux for the parameter of interest. Another important reason for using such density solutions in trap cod-ends is that various kinetic and metabolic processes involving sedimenting particles can be studied *in situ*. For example, KARL, KNAUER, MARTIN and WARD (1984), using $^{3}$H-adenine, discovered a zone of chemolithotrophic activity well below the euphotic zone which may be a ubiquitous feature of the world's oceans.

One problem often overlooked in sediment trap studies is the effect on biogenic particle flux of variations in temporal and spatial distribution of the organisms in the water column. This is particularly important if vertical flux rates are fast. Although through long-term deployments the variability may be smoothed out in terms of its influence on observed profiles of elements in the water column, it may introduce major difficulties into the

interpretation of sediment trap collections, particularly with short-term deployments and subsequent extrapolations. As an example, "patchiness" in time and space of many marine species is well-documented. Similarly, mesoscale features and oceanic fronts also produce substantial changes in the structure of pelagic communities (see e.g. FAIRBANKS, WIEBE and BE, 1980) which may greatly modify particle flux. To date this aspect of organism heterogeneity as it relates to particle source terms and particle flux has been little studied.

### 3.2. *Hand collections*

Several *in situ* studies have attempted to characterize directly large aggregates (i.e. 1 mm to several meters) in the upper 100 m of the water column. Such collections have typically involved SCUBA and have provided a considerable amount of data ranging from size distributions of marine snow (TRENT, SHANKS and SILVER, 1978; SILVER, SHANKS and TRENT, 1978) to associated bacteria and protozoa (CARON, DAVIS, MADIN and SIEBURTH, 1982). Mixed-gas saturation diving has extended hand collection of marine snow aggregates down to 260 m (ORZECH, 1983). In addition to the use of SCUBA and saturation diving to collect particles in the upper layers, a new tool, the one-person submersible "WASP", is now available which allows various particles to be collected by hand down to depths of 700 m (ALLREDGE, ROBISON, FLEMINGER, TORRES, KING and HAMNER, 1984).

### 3.3. *Freshly-produced biogenic material*

The simplest method for sampling particles released from zooplankton and nekton (fecal pellets, molts, eggs, etc.) is to place recently collected individuals into small aquaria and allow them to defecate or molt. These materials can then be removed with forceps or small-bore pipets. However, the proximity of the organism to the fragile particulates often results in the rapid disintegration of the particulates through mechanical action of the swimming animal and/or reingestion attempts. Also this method is inefficient if relatively large amounts of biodetritus are needed for chemical analyses. Far more effective are the large volume collection systems which were first described by LA ROSA (1976) and later modified (SMALL, FOWLER and UNLU, 1979; SMALL, FOWLER, MOORE and LA ROSA, 1983). These have the advantage of allowing collection of several hundred mg of material (e.g. fecal pellets) over short time intervals ($< 12$ hr) and allow for isolation of the biogenic material from the organisms producing it. Basically the collection system consists of a two-piece plastic funnel (Buchner type) which sits in a large outer container filled with filtered sea water (64 $\mu$m nylon mesh). The top part of the funnel fits snugly into the top of a lower tapered section between which monofilament netting is stretched taut to create an upper and lower chamber. A large number of freshly-collected zooplankton or nekton are sorted of debris and immediately placed in the upper chamber. The aperture size of the netting is chosen to retain live animals in the upper chamber, but allow passage of their fecal pellets into the lower chamber. Sizes between 140–180 $\mu$m have proven ideal for most species of copepods. A much larger aperture (1000–2000 $\mu$m) is used for larger micronekton like euphausiids, salps, shrimp and fish. The opening at the bottom of the lower chamber (the funnel tip) is screened with a finer-mesh netting (68 $\mu$m) to retain fecal pellets but allow passage of the finer material. This method has proved successful for organisms collected in the upper water layers but should serve as well for deeper species provided they survive transit to the surface.

Using large aperture size netting, the same systems can be used for collecting crustacean molts, however, holding organisms (e.g., euphausiids) individually in small glass jars is a more effective method since the animals can be maintained live more easily during the several days needed to produce molts (SMALL and FOWLER, 1973). In the same way pure samples of euphausiid and copepod eggs have been collected but difficulties often arise in separating the fecal pellets and eggs, both of which pass through the separation net and are trapped together in the bottom of the funnel. Other difficulties that could occur deal with plankton eggs which are neutrally boyant or sticky such as those of certain pelagic ostracods (ANGEL, 1972).

Samples collected by these systems are unique in that they represent relatively pure biogenic particles of known age from known sources living in the natural environment, are relatively undegraded (i.e. minutes to hours old), and are in sufficient quantity (10–100 mg amounts) to allow performing a variety of chemical and biological analyses (e.g. FOWLER, 1977; ELDER and FOWLER, 1977; HIGGO, CHERRY, HEYRAUD and FOWLER, 1977; SLEETER and BUTLER, 1982; CUTTER, 1982; ANDREWS, KARL, SMALL and FOWLER, 1984; REPETA and GAGOSIAN, 1984; BURNS, VILLENEUVE and FOWLER, 1985; KRISHNASWAMI, BASKARAN, FOWLER and HEYRAUD, 1985).

### 3.4. *Large volume* in situ *filtration*

Several attempts have been made to assess large particle distribution, size classes, chemistry and vertical transport through the use of large volume filtration techniques. A Large Volume *in situ* Filtration System (LVFS) filtering from 5–30 $m^3$ of water has been employed successfully in the equatorial Atlantic (BISHOP, EDMOND, KETTEN, BACON and SILKER, 1977), South Atlantic (BISHOP, KETTEN and EDMOND, 1978), Panama Basin (BISHOP, COLLIER, KETTEN and EDMOND, 1980), and warm-core Gulf Stream rings (BISHOP, CONTE, WIEBE and ROMAN, in press). These studies have provided fundamental information on particle size distribution, particulate dry weight, C, N, P, Ca, Si, K, Mg, Sr, Fe, various natural-series radionuclides, isotopic ratios (e.g. $\delta$ $^{13}C$) and characterization of biogenic particles including fecal pellets and so-called "fecal matter". Because of the large volume of water filtered, LVFS samples include particles in the size range of 1 $\mu$m to 1 cm. Furthermore, the morphology of the collected particles is not significantly altered since the speed of filtration ($< 2\,cm\,sec^{-1}$) is of the same magnitude as the sinking speeds of these particulates (BISHOP, 1982). Another advantage with LVFS samples is that filtered particles do not undergo post-collection aging and degradation prior to analysis as is often the case with particulates collected in sediment traps. Recent technical developments of this pumping system have resulted in an improved version (Multiple-unit LVFS) which is small, light weight and takes only 6–8 hr to complete one 12-sample profile to 1000 m (BISHOP, SCHUPACK, SHERRELL and CONTE, 1985). It was designed specifically for rapid spatial sampling of dynamic ocean environments such as warm-core Gulf Stream rings and has been optimized for deployment in rough seas and under harsh weather conditions. Since this device employs an electromechanical cable for power, its operation at present is limited to the upper 1000 m of the ocean.

Another large volume *in situ* pump is the IOS deep water particle sampler (DWPS) developed by SIMPSON, GWILLIAM, LAWFORD, LEWIS and FASHAM (submitted). This battery-powered instrument is not depth-limited and is capable of filtering $10^3\,l\,hr^{-1}$. The sampler also houses an *in situ* particle counter which provides data that can be used to estimate

particle mass concentration and flux profiles. The DWPS has been used successfully to elucidate particulate rare earth profiles to 5470 m in the NE Atlantic (W. R. SIMPSON, personal communication).

A third type of pump that has proved useful in sampling marine particulates is the Woods Hole *In Situ* Pump (WHISP). The basic system is an impeller pump connected to a 300 mm filter sandwich driven by a large fiberglass prop. The entire package can be placed on the hydrowire and towed at any depth at speeds of about 1.5 knots. If towed correctly, filtration rates of as much as 150 $l\,hr^{-1}$ can be obtained. WHISPs have been used successfully to filter sufficient suspended particulates to measure various organic compounds (WAKEHAM, FARRINGTON and GAGOSIAN, 1984; WAKEHAM, GAGOSIAN, FARRINGTON and CANUEL, 1984) and transuranium elements (FOWLER, BALLESTRA, LA ROSA and FUKAI, 1983). While these filtration systems appear to be efficient in sampling the finer suspended particles, because of the slow towing speed and limited diameter of the pump intake, it is doubtful that it samples the larger, rapidly sinking particulates discussed above.

Large volume *in situ* filtration is a versatile and extremely useful tool for assessing many aspects of particle fields in the ocean water column. Data on particle number and size distribution coupled with assumptions about particle density have allowed calculating vertical flux estimates with some success (see papers by BISHOP and co-workers). Nevertheless, it is still unclear whether or not this filtration technique samples "suspended" particles, "large fast-sinking" particles, or some combination of both. In this respect the combined use of LVFS and particle traps would appear to offer the best approach to defining particle fields and fluxes (BISHOP, COLLIER, KETTEN and EDMOND, 1980; BÉ, BISHOP, SVERDLOVE and GARDNER, 1985).

### 3.5. *Submersible collections*

Although samples of various kinds have been collected throughout the water column by submersible (*viz.* ALVIN and JOHNSON-SEA-LINK), only few studies have employed the use of this tool to explicitly look at large aggregates. In one such study, SILVER and ALLDREDGE (1981) collected marine snow from ALVIN using a horizontally mounted, transparent Van Dorn bottle (50 cm long, 10 cm diameter) which was triggered after enclosing the aggregates. Similar collections of undisturbed marine aggregates have been made by the JOHNSON-SEA-LINK utilizing a rack of eight, specially designed 6.5 l acrylic tubes (35.4 cm long, 17.6 cm diameter) which are sealed automatically by sliding lids across the openings once the particles enter the tube (YOUNGBLUTH, 1984a).

### 3.6. *Optical assessment*

Very large aggregates (tens of mm) can be determined by standard deep sea photography (LAMPITT, 1985). Recent advances in marine optical techniques have allowed assessing size, spatial distribution and flux of macroscopic aggregates ($> 0.2$ mm) by *in situ* photography (HONJO, DOHERTY, AGRAWAL and ASPER, 1984; ASPER, 1985) and video techniques (ORZECH and NEALSON, 1984). Likewise, *in situ* holographic techniques also have been used to measure the sizes and settling rates of these types of oceanic particulates (CARDER, STEWARD and BETZER, 1982).

### 3.7. *Plankton nets*

Plankton nets of various aperture sizes are commonly used to sample particles in the microplankton range ($\sim 20$–$200\ \mu m$). Because of limitations in mesh size that can be used, nanoplankton ($\sim 2$–$20\ \mu m$) and picoplankton ($\leqslant 2\ \mu m$) which together may comprise most of the phytoplankton biomass (TAKAHASHI and BIENFANG, 1983) are not normally sampled in this way. Living particles should, in principal, be caught in a net if the diameter of the mesh is smaller than that of the particle, however, in practice this does not always occur. First, many motile forms of plankton can avoid an oncoming net by swimming away. The degree of avoidance is a function of size of net opening, net towing speed, net filtration efficiency and plankton swimming speed (BOUGIS, 1976). Second, most plankton forms are not perfectly spherical and while their diameter may be greater than that of the mesh, they can readily slip through the mesh according to the way they are oriented. This is particularly critical for pennate diatoms, "soft" phytoplankton cells and non-living particles like molts and fecal pellets which are generally elongate or cylindrical. Even in the case of spherical plankton eggs, it has been shown that owing to their plasticity, only a fraction are trapped by mesh of marginally smaller diameter (see BOUGIS, 1976). While small biogenic particles like fecal pellets, marine snow and molts are routinely caught in towed plankton nets, it is almost certain that this trapping is neither qualitative nor quantitative. Nevertheless, in a relative sense they are useful in particle collections for discerning the spatial and temporal distribution of particles throughout the water column. Fine mesh nets have classically been used in this way in the euphotic zone to help assess primary and secondary production. More recently they have been successfully employed in deeper waters (1000–2000 m) and have demonstrated the presence of large populations of small copepodites and their fecal pellets hitherto unknown at those depths (TUEL and KNAUER, unpublished results).

## 4. SINKING SPEED

### 4.1. *Laboratory evidence*

Several laboratory studies have addressed the sinking rate of small compact biogenic particles such as fecal pellets (see KOMAR, MORSE, SMALL and FOWLER, 1981, for review). FOWLER and SMALL (1972) and SMALL, FOWLER and UNLU (1979) determined the sinking rate of natural zooplankton fecal pellets as a function of pellet volume. They found that rates varied between approximately 20 and 900 m $day^{-1}$ over 3 orders of magnitude in pellet volume. These rates appear to be highly dependent upon density (hence compaction) of the pellet (SMALL, FOWLER and UNLU, 1979) as well as diet of the organism producing them (SMALL, FOWLER and UNLU, 1979; BIENFANG, 1980a). Furthermore, pellets from microzooplankton ingesting sediments are ballasted and sink more rapidly than those produced from a diet of pure organic matter (SMALL, FOWLER and UNLU, 1979). Fecal pellets from large gelatinous zooplankton sink at higher rates (approximately 400–2700 m $day^{-1}$) (BRULAND and SILVER, 1981; MADIN, 1982) than those of the smaller zooplankton. Possibly the highest velocities have been found for fish feces; sinking rates average 1028 m $day^{-1}$ for fecal matter (2–6 mm) from a variety of midwater species (ROBISON and BAILEY, 1981) and 1100 m $day^{-1}$ for feces from anchoveta inhabiting the Peru coastal zone (STARESINIC, FARRINGTON, GAGOSIAN, CLIFFORD and HULBURT, 1983). Because sinking rate is a function of the density difference between the pellet and surrounding water, the rate of descent generally decreases

with decreasing water tempreature (ROBISON and BAILEY, 1981; GORSKY, FISHER and FOWLER, 1984). However, this effect could be partially offset, particularly in deeper waters, where increased pressure may result in interstitial water exchange through compression of loosely aggregated materials. KOMAR, MORSE, SMALL and FOWLER (1981), modelling the sinking rate of zooplankton pellets, found Reynolds numbers $\geqslant 0.5$ for pellets from some of larger zooplankton and concluded that Stokes Law sinking was inapplicable in these cases. They derived semi-empirical equations for the sinking rate of cylindrical and ellipsoid pellets which fit the observed data reasonably well. Using these formulae they were able to calculate the density of zooplankton fecal pellets ($1.22\,g\,cm^{-3}$) which agreed closely with a direct measurement ($1.23\,g\,cm^{-3}$) made on the same fecal material. Shape, size and density will also affect the sinking rate; this may be one reason why the large, flat fecal flakes of certain salps do not fit the regression relationship derived by SMALL, FOWLER and UNLU (1979) (BRULAND and SILVER, 1981; MADIN, 1982). A recent compilation of fecal pellet sinking rates has been made by ANGEL (1984).

Other classes of biogenic partiles sink at varying rates. For example, measurements with marine snow and appendicularian houses indicate that these more flocculent materials sink at rates ($\sim 50$–$150\,m\,day^{-1}$) somewhat slower than fecal pellets (SHANKS and TRENT, 1980; SILVER and ALLDREDGE, 1981; TAGUCHI, 1982; GORSKY, FISHER and FOWLER, 1984). However, somewhat higher speeds ($300$–$1020\,m\,day^{-1}$) have been reported for aggregates of phytodetritus (1–6 mm diameter) collected from the sea floor at 2695 m (LAMPITT, 1985). Sinking rates of fresh crustacean molts and macrozooplankton carcasses are much greater ($1500$–$4000\,m\,day^{-1}$) but decrease with time as the material degrades (SMALL and FOWLER, 1973). The relatively heavy skeletal remains of radiolarians sink at speeds ranging between $13$–$416\,m\,day^{-1}$ (TAKAHASHI and HONJO, 1983). Likewise sinking rates of Foraminifera vary greatly ($\bar{x}$ sinking speeds $= 198$–$2475\,m\,day^{-1}$) and are governed primarily by shell weight and presence/absence of spines (TAKAHASHI and BÉ, 1984). For example some spinose species sink at rates 3 times slower than non-spinose forms because of increased drag caused by the spines (TAKAHASHI and BÉ, 1984). Live or senescent phytoplankton cells sink very slowly at rates ranging between $0.1$–$10\,m\,day^{-1}$ in still water (SMAYDA, 1971) but normally less than $2\,m\,day^{-1}$ in the natural environment (BIENFANG, 1980b). Plankton and nekton eggs, being nearly neutrally buoyant, sink little, if at all.

### 4.2. *Field evidence*

Only recently have rates of large particle sinking been confirmed by *in situ* methods. From surface phytoplankton production data and observations of the appearance of detritus of phytoplankton origin at 2000 m (BILLET, LAMPITT, RICE and MANTOURA, 1983) and 4000 m (LAMPITT, 1985), it was calculated that the diatoms were sinking through the water column at rates of at least $100$–$150\,m\,day^{-1}$. SMETACEK (1985) discusses several sediment trap studies that also have documented the rapid, mass sinking of diatom cells following blooms. LORENZEN and WELSCHMEYER (1983), using a novel approach of following maxima of phaeopigment flux as directly measured in sediment traps, estimated that zooplankton fecal pellets sink between $31$–$122\,m\,day^{-1}$, rates not unlike those derived from the laboratory studies using similar pellet types. Likewise SCUBA divers have observed that marine snow aggregates sink about $70\,m\,day^{-1}$ in surface waters (SHANKS and TRENT, 1980), whereas photographic evidence from 3800 m suggests somewhat slower sinking speeds ($1$–$36\,m\,day^{-1}$) for large aggregates in the deep sea (ASPER, 1985). It would thus

appear that rates derived in the laboratory under static conditions give fairly reliable estimates of the sinking process occurring *in situ*.

## 5. PRODUCTION IN WATER COLUMN

The currently accepted model concerning POM production in the water column is that most of the organic material is derived from free-living primary producers (i.e. autotrophic activity not associated with particulates or aggregates) in the euphotic zones of the world's oceans. These small particles interacting with surface food webs are then "packaged" through biological processes (e.g. grazing–fecal pellets; biologically derived marine snow, e.g. diatom mats, cast-off larvacean houses, etc.) or abiotic processes, (e.g. flocculations, agglomeration). These large particles then begin their descent to meso- and bathypelagic regions via passive sinking or active transport through overlapping food chains VINOGRADOV (1962).

However, current sediment trap research being conducted by the VERTEX group indicates that the postive relationship between large particles and surface production as suggested by some researchers (SUESS, 1980; BETZER, SHOWERS, LAWS, WINN, DI TULLIO and KROOPNICK, 1984) is an oversimplification, and that large particle production can occur throughout the water column as a result of *in situ* or advective horizontal processes (FELLOWS, KARL and KNAUER, 1981; URRERE and KNAUER, 1981; KARL and KNAUER, 1984; KARL, KNAUER, MARTIN and WARD, 1984). In addition, when considering large particle production in the water column, it is difficult to assign these particles to a purely biotic or abiotic category, since both organic and inorganic phases are closely associated. Thus, one can speak of fecal pellet production as a biotic process, but it must be kept in mind that pellet production can also interact with inorganic materials through incorporation (see Section 2.2 above).

Additionally, flocculation of purely inorganic particles will in time incorporate organic detritus to form an agglomerate. Agglomerations are organic and inorganic matter weakly bound by surface tension and organic cohesion due to biological activity, while floccules are inorganic particles that are held together by electrostatic force (SYVITSKI and MURRAY, 1981) which can later be colonized by bacteria and protozoans. Thus, in the following discussion of water column particle production, it must be noted that these particles are extremely complex and variable in origin and composition.

### 5.1. *Surface production and concentrations*

Aside from small particles resulting from microbial and phytoplankton primary production, one readily "identifiable" group of large particles is "marine snow" which includes a multitude of specific particles such as diatom mats, cast-off larvacean houses, mucus, fecal pellets, molts, etc.

5.1.1. *Aggregates.* Production of snow-like particles appears to be a variable process, although production is normally higher in coastal waters. There are examples of reported densities for zooplankton-produced aggregates (0.4–0.87 agg. $l^{-1}$) and those of unknown origin (1–3 agg. $l^{-1}$) from the Gulf of California (ALLDREDGE, 1979). SHANKS and TRENT (1980), studying aggregates in Monterey Bay (size range from 1–17 mm in longest dimension) found concentrations ranging from 0.7–14 agg. $l^{-1}$. They calculated an average flux

for the aggregates of $31 \times 10^4$ m$^{-2}$ day$^{-1}$, which if in steady state represents a considerable production. Concentrations such as these are in agreement with optical measurements made in the same area which show approximately 7 agg. l$^{-1}$ at 45 m (HONJO, DOHERTY, AGRAWAL and ASPER, 1984). HEBEL, KNAUER and MARTIN (in press) studying marine snow–metal relationships off central California also found aggregate concentrations of approximately 10 l$^{-1}$, whereas somewhat lower concentrations (0.2–0.6 agg. l$^{-1}$) have been measured at 60 m in southern California coastal waters (ORZECH and NEALSON, 1984). In contrast, a very low aggregate (> 3 mm in longest dimension) density of approximately 1 agg. m$^{-3}$ was reported in the upper 30 m off the Bahama Islands (ALLDREDGE and YOUNGBLUTH, 1985). The large range in reported aggregate concentrations underscores their variable production rates in different oceanic areas. As mentioned earlier, these types of particles represent important sites for nutrient regeneration, scavenging, transport and primary productivity in surface waters. Indeed, KNAUER, HEBEL and CIPRIANO (1982) found that up to 58% of the primary production in Monterey Bay, California, could be associated with these particles.

5.1.2. *Fecal pellets.* As discussed above, fecal pellets can be extremely important as transporters of energy (food) as well as numerous kinds of compounds. The production of fecal pellets in coastal surface waters is generally high as indicated by fluxes greater than $3 \times 10^5$ total pellets m$^{-2}$ day$^{-1}$ (KNAUER, MARTIN and BRULAND, 1979; CHESTER and LARRANCE, 1981). URRERE and KNAUER (1981) calculated that 10–20% of the C flux in the upper 150 m of a coastal California water column was derived from fecal pellets. At an oligtrophic station off Mexico (VERTEX II) KNAUER and MARTIN (unpub. data) found that up to 40% of the C flux could be accounted for by very large pellets produced by the pelagic crab *Pleuroncodes planipes*. Offshore, surface production of large pellets is considerably lower, e.g. fluxes less than 1500 pellets m$^{-2}$ day$^{-1}$ have been measured (KNAUER, MARTIN and BRULAND, 1979). In contrast, fluxes of minipellets in offshore waters are as high as $5 \times 10^6$ m$^{-2}$ day$^{-1}$, however, because of their small size the volume flux of corresponding large fecal pellets can be nearly a factor of 10 greater (GOWING and SILVER, 1985). Within the euphotic zone of a given water column, fecal pellet production and corresponding fluxes may be higher at night due to the diel maximum in zooplankton grazing activity which occurs during the hours of darkness (WELSCHMEYER, COPPING, VERNET and LORENZEN, 1984). Furthermore, fecal pellet concentrations vary greatly throughout the euphotic zone; for example strong concentration gradients for cylindrical fecal pellets (> 1 mm) decreasing from approximately 400 m$^{-3}$ at 40 m to 2 m$^{-3}$ at 110 m have been observed in warm-core rings of the Gulf Stream (BISHOP, CONTE, WIEBE and ROMAN, in press). Such gradients which vary seasonally in strength are a result of changes in zooplankton grazing pressure and particle repackaging in the euphotic zone.

### 5.2. *Subsurface production and concentrations*

With the exception of regions in the immediate vicinity of hydrothermal vents, living particle production in the mesopelagic and bathypelagic zone is primarily a result of deep water plankton (e.g. copepods) and nekton feeding directly on surface-derived organic matter. As one example, large communities of deep sea benthopelagic plankton, including copepods, ostracods, isopods, and chaetognaths, have been found in the 10–100 m layer above the bottom at 1100–3200 m (WISHNER, 1980). The benthopelagic copepods are

predators and generalized particle feeders and feed in the benthic boundary layers where suspended particles are most abundant. These organisms also serve as food for deep sea predators such as benthopelagic fish which will produce larger particles through egestion. Unfortunately little is known about the production rates of either the small or large deep sea benthopelagic organisms or their biogenic particulate products.

5.2.1. *Marine snow.* Numerous workers have observed the presence of snow-like particles throughout the water column (e.g. see HAMNER, MADIN, ALLDREDGE, GILMER and HAMNER, 1975; BISHOP, EDMOND, KETTEN, BACON and SILKER, 1977; TRENT, SHANKS and SILVER, 1978; SILVER, SHANKS and TRENT, 1978; SHANKS and TRENT, 1979, 1980; HONJO, DOHERTY, AGRAWAL and ASPER, 1984; YOUNGBLUTH, 1984b). SILVER and ALLDREDGE (1981) have tried to estimate their concentration and importance in the deep sea, nevertheless data which would be useful for interpreting the role these particles play in the deep sea, or on their origins and specific composition, are sparse. The only published data indicate that macroscopic aggregate densities in subsurface waters vary greatly in both time and space. For example concentration of aggregates ($>0.5$ mm) off central California were observed to range from 1 $l^{-1}$ at layers deeper than 210 m to 0.7 $l^{-1}$ at 2650 m (HONJO, DOHERTY, AGRAWAL and ASPER, 1984). In oligotrophic subtropical Atlantic waters ALLDREDGE and YOUNGBLUTH (1985) report low densities of aggregates ($>3$ mm) between 130 and 650 m ranging from 0.5 to 4 $m^{-3}$; however, they also note that concentrations 2 orders of magnitude greater have been observed at the same site during other seasons. Recent photographic evidence indicates that in some areas of the deep sea (e.g. Panama Basin) fluxes of aggregates larger than 0.5 mm can reach $10^5$ $m^{-2}$ $day^{-1}$ (ASPER, 1985). These sorts of data for the deep sea are important since lack of high-frequency vertical migrations by organisms at depths $>1500$ m means that bathypelagic and abyssopelagic communities depend almost totally on sedimenting particles and aggregates for their food supply.

5.2.2. *Fecal pellets.* The presence of fecal pellets as measured by sediment traps and large volume filtration techniques has been noted throughout the water column (WIEBE, BOYD and WINGET, 1976; BISHOP, EDMOND, KETTEN, BACON and SILKER, 1977; HONJO and ROMAN, 1978; KNAUER, MARTIN and BRULAND, 1979; ROWE and GARDNER, 1979; FOWLER, SMALL, ELDER, UNLU and LA ROSA, 1979; GOWING and SILVER, 1985; and others). Few of these studies have dealt with points of origin and in general have assumed that these large particles are derived primarily from surface injections; however, one study by URRERE and KNAUER (1981) presents convincing evidence indicating multiple points of new pellet production at different depths in the water column. Such sub-euphotic zone production has consistently been observed by the VERTEX group and it is now thought that there are discontinuity zones throughout the water column where new large particle production can occur (KARL and KNAUER, 1984). ANGEL (1984) further stresses the potential importance of fecal pellet production by nekton in the deep mesopelagic and shallow bathypelagic zones and presents evidence to suggest that, despite low standing crops of organisms, these relatively large forms will have a significant influence on fluxes of carbon and other elements because of their production of large, fast sinking feces.

5.2.3. *New particle production at depth.* KNAUER and MARTIN (1981) observed a significant increase in C flux at 1500 m relative to the C flux at 500 and 750 m. The increased C flux was correlated with the increase in fecal pellet flux mentioned above and reported in

URRERE and KNAUER (1981). These latter authors concluded that increases of these two parameters at depth were the result of *in situ* repackaging processes. It was surmised that the primary energy source for these *in situ* processes was most probably due to some interaction between microbial populations and the various DOC-POC pools along the lines suggested by POMEROY (1974). That such aphotic zone processes could be involved was also suggested by FELLOWS, KARL and KNAUER (1981) who found considerable amounts of ATP in association with trap-collected particles indicating the presence of a viable assembly of microorganisms with large subsurface particles. Indeed, they found that the amount of ATP per sediment trap actually increased from low concentrations at 210 m to high concentrations at 1100 m. Their results also indicated that within the surface waters (0–385 m) of the area investigated, the ATP concentrations associated with the rapidly sinking particles exceeded those in the slow sinking suspended materials (on a daily basis) by factors ranging between 1.4–15.4. In deeper waters the quantitative role of the ATP-large particle association was even greater relative to the suspended pool with ratios ranging up to 106 at 1550 m. Thus, it appears that large particles have the potential to support greater bacterial populations than the smaller, suspended matter.

In a further study of these processes, KARL and KNAUER (1984) using $^{3}$H-adenine to measure the potential for C production in sediment trap materials, observed that a considerable amount of new carbon was produced by microorganisms between 700–900 m at the VERTEX I site, 160 km off Point Sur, California. Such areas of activity have now been found in association with large particle collections at a number of depths below the euphotic zone in the northeast Pacific (KNAUER, MARTIN and KARL, 1984) and it may in fact be a ubiquitous ocean feature.

One hypothesis put forward to account for these zones of large particle-associated new carbon production is that chemolithotrophic bacteria are responsible with the most likely energy sources being $NH_4^+$ or $HS^-$ brought in vertically or horizontally. This hypothesis was initially tested during one of the sediment trap experiments and indeed, it was found that chemolithotrophy in association with large particles accounted for 90% of the total production at 550 m (KARL, KNAUER, MARTIN and WARD, 1984).

Thus, although only a few studies have been conducted to date concerning the role of large particle production in the pelagic zone, it is obvious that such particles play a significant if not major role in water column biology and particle transport. Some information can be gleaned from particle flux measurements (see Sections 5.1 and 5.2.3 above) but fluxes are generally the net result of production and consumption occurring above the sediment traps.

### 5.3. *Biodetritus production rates*

At present there are no adequate techniques for directly measuring the *in situ* production rate of biodetritus. Most production estimates therefore have to be derived from laboratory experiments aimed at measuring rates of egestion, molting, egg deposition, etc., and these are then coupled to population estimates. In this respect microcrustacean molts have been suggested as an important component of detritus as well as instrumental in recycling elements (JERDE and LASKER, 1966; FOWLER and SMALL, 1967; MARTIN, 1970). For example, copepods molt 12 times until reaching adulthood whereas euphausiids, depending upon the temperature, regularly molt on average once per week throughout their entire lifespan. Based on knowledge of fractional weight loss during molting, molting rates and euphausiid

distribution, JERDE and LASKER (1966) estimated that the species *Euphausia pacifica* could contribute roughly 1.5 g dry detritus $m^{-2}$ $yr^{-1}$ in the form of molts. Copepods, which molt less frequently during their life but are far more abundant and may lose a greater percentage of their body weight at molt, probably account for the majority of the molt-derived detritus produced in the sea. In fact, measured fluxes of unidentified zooplankton molts have been reported to be as high as $4.6 \times 10^4$ $m^2$ $day^{-1}$ in shallow bays of Cook Inlet, Alaska (CHESTER and LARRANCE, 1981), a finding which indicates relatively high biodetrital production rates in the form of molts. Molting rates generally decrease with decreasing temperature (FOWLER, SMALL and KECKES, 1971); however, judging by the large number of benthopelagic copepod molts found *in situ* (up to 1800/1000 $m^3$, WISHNER, 1980) and the fact that they are roughly 2–7 times more abundant than living copepods, it would seem that this mechanism of detrital production is also important in the cold, deep sea.

Whereas calculations have shown that euphausiids may lose about 1% of their dry body weight per day as molts, depending upon feeding conditions these organisms can produce 2–5% of their weight per day as fecal pellets (SMALL and FOWLER, 1973; HEYRAUD, 1979). The production rate of feces clearly depends upon the feeding rate, but in most cases appears to be a more important contributor to detrital production than molts. Furthermore, smaller individuals of a given species produce a greater fraction of body weight as feces (HEYRAUD, 1979; ANGEL, 1984). For the euphausiid *Meganyctiphanes norvegica*, HEYRAUD (1979) derived an expression for determing fecal production ($E$) as $E = 0.35\ W^{0.42}$ where $W$ is the animal's body weight. Some gelatinous zooplankton may far surpass these microcrustacean rates given adequate food supply. MADIN (1982) reported fecal pellet productioan rates for 7 species of salps that ranged from 3.7–27.7 μg fecal C mg body $C^{-1}$ $hr^{-1}$. Using data on salp density and typical values for their defecation rate, WIEBE, MADIN, HAURY, HARBISON and PHILBIN (1979) estimated a fecal production rate for an average salp population of 8.5–139 mg C $m^{-2}$ $day^{-1}$. Combining this with an estimate of salp carcass production (3.6 mg C $m^{-2}$ $day^{-1}$), the authors concluded that salp fecal pellet flux alone could provide about 180% of the metabolic needs of the local benthic infauna.

Other gelatinous zooplankton like the appendicularian *Oikopleura longicauda* produce copious amounts of fecal pellets. The daily production rate for this species living in a subtropical bay has been measured at 243 ± 105 pellets, many of which are retained in the cast larvacean houses. House production estimates range from 5–10 houses per day (TAGUCHI, 1982; GORSKY, FISHER and FOWLER, 1984), and concentrations of detrital houses often become extremely dense (YOUNGBLUTH, 1984b).

The net fecal pellet flux through any given depth is a function of the fecal pellet production and consumption rate in the overlying waters. It is now well established that zooplankton fecal pellets, especially the smaller ones, are grazed in the water column (TURNER and FERRANTE, 1979; PAFFENHOFFER and KNOWLES, 1979; BISHOP, COLLIER, KETTEN and EDMOND, 1980; HOFMANN, KLINCK and PAFFENHOFER, 1981; BISHOP, CONTE, WIEBE and ROMAN, in press). As ANGEL (1984) points out, the general lack of direct observations of coprophagy probably reflects the technical difficulties involved in demonstrating its occurrence rather than its infrequency. Fecal pellets most likely serve as an important food source in regions where primary producers are not present, i.e. below the photic zone. For example, as mentioned above recent evidence indicates an increase in biological activity and fecal pellet production in the mesopelagic zone between 700–900 m (KARL and KNAUER, 1984) which is believed to result from a chemolithotrophic-based carbon production system supported by reduced inorganic compounds in association with

sinking particles (KARL, KNAUER, MARTIN and WARD, 1984). It is possible that a large portion of the increase in particulate flux comes by way of "repackaging" fecal pellets descending from overlying waters into new fecal pellets (URRERE and KNAUER, 1981).

Production rates of other materials such as released eggs and dead zooplankton (carcasses) are yet more difficult to assess. Using fecundity data for the euphausiid *M. norvegica*, SMALL and FOWLER (1973) calculated that female euphausiids could lose about 0.37% of their body weight per day in terms of egg production. This is far less than that lost for production of fecal pellets and molts and, given the fact that most of the eggs would hatch, egg laying would be of lesser importance in the production of detrital particles by this species. SMALL and FOWLER (1973) also estimated the production of euphausiid carcasses based on available mortality data for the same species and several assumptions. The estimate of about 0.2% of euphausiid weight per day over an entire year was also very low suggesting that this mechanism of particle production is also of limited importance compared to fecal pellet production.

### 5.4. *Effect of vertical migration*

Input sources of large biogenic particles from heterotrophs depend on the position of the producer-organisms in the water column. The effect of epipelagic community "patchiness" on large particle assessment by sediment traps has been mentioned above in Section 3.3. Equally important may be the diel vertical migration patterns of many plankton and micronekton species (VINOGRADOV, 1962). As the model studies of ANGEL (1984, 1986) point out, diel vertical migration (often several hundred meters in range) is primarily restricted to approximately the top 700 m for plankton and top 1000–1500 m for micronekton. Particle collectors moored in deep water beneath these depth limits should collect an integrated particle flux consisting of all biogenic particles, new or residual, which are generated in the overlying waters. On the other hand, sediment traps or large volume pumps located in epipelagic or mesopelagic waters would miss all material carried down in the stomachs of vertical migrants which fed in the overlying waters and defecated at depth beneath the collectors. This short-circuit mechanism, which leads to an underestimate of particle flux to the deep sea, will be particularly important for larger species whose migration rates are commensurate with or faster than the settling rates of larger fecal pellets, and for those species whose gut retention times are long enough for the animal to reach maximum depth before defecation, but short enough to assure that the organism will not transport ingested material back up in the water column during its next ascent. ANGEL (1984) cites evidence in support of the required food retention times (a few hours) at typical temperatures encountered in the water column and, based on theoretical biological transport models, suggests that migrants make a substantial contribution to the actual flow of particulate material and associated elements into deep water which may not be readily assessed by sediment traps in the upper layers. Furthermore, ANGEL (1984) points out that downward seasonal migrations performed by many organisms prior to overwintering could result in the same effect, i.e. gross changes in the depth of input of biodetrital particles and of the resultant pattern of vertical particulate flux. Unfortunately, hard data with which to test these hypotheses are lacking, and only carefully-designed sediment trap experiments coupled with quantitative plankton and nekton sampling will enlighten our understanding of how this potential mechanism alters large particle transport.

## 6. ELEMENT AND ORGANIC COMPOUND TRANSPORT

As the principal mode of vertical transport of material (mass flux) to the bottom is through the relatively rare, large, fast-sinking biogenic particles (e.g. fecal pellets, molts, other biogenic debris), it follows that these particles will be instrumental in determining the distribution of elements associated with them. Because of their high sinking speeds, large particles will inject elements into the deep sea, whereas elements associated with the biodegradable fraction of slowly sinking, fine suspended particulates will be remineralized and recycled in the upper water layers and hence involved in controlling near-surface elemental distribution.

### 6.1. *Nitrogen, phosphorus and organic carbon*

Evidence for large particle element transport comes from a wide variety of oceanographic studies. Sediment-trap measurements of particulates in the North Atlantic mesopelagic and bathypelagic zones indicate that biogenic carbonate particles and organic matter contribute 10 to 55% and 10 to 20% of the flux, respectively (HONJO, 1980). Organic carbon and nitrogen concentrations in large particles characteristically decrease with depth (ROWE and GARDNER, 1979; KNAUER, MARTIN and BRULAND, 1979; KNAUER and MARTIN, 1981; WASSMANN, 1985; GARDNER, SOUTHARD and HOLLISTER, 1985). For example, KNAUER and MARTIN (1981) found that of the total carbon fixed by primary producers in the northeast Pacific, approximately 22% reached 65 m in the form of large particles and only 3–4% remained at the depth of the oxygen minimum (500–750 m). In another study in the same area under coastal upwelling conditions, fluxes as high as 36, 4.1 and 0.2 m moles of C, N and P $m^{-2}$ $day^{-1}$ were observed at 50 m (KNAUER, MARTIN and BRULAND, 1979). These fluxes represented 53, 39 and 32% of the computed surface primary productivity of these elements, respectively. The calculated C : N : P ratios suggested that the materials falling into the traps were similar to living phytoplankton. In the oligotrophic Pacific ocean, C in large particles increased relative to N and P in a manner that indicated marked losses of both P and N even at the shallowest depth. It would appear that during their descent large particles lose P and N relative to C via natural decomposition and/or reingestion by detritivorous organisms. In fact, labile organic P is probably the most rapidly remineralized; for example, WEFER, SUESS, BALZER, LIEBEZEIT, MULLER, UNGERER and ZENK (1982) found in circumpolar waters of the Drake Passage that only $< 5\%$ of the labile organic P escaped recycling within near surface waters and reached depths of 1000 m. Likewise DYMOND and LYLE (1985), comparing fluxes between sediments and sediment traps at a MANOP site in the eastern tropical Pacific, found that $> 97\%$ of the total particulate phosphate and 95% of total particulate organic carbon are regenerated at depths less than 1500 m.

KNAUER, MARTIN and BRULAND (1979) also showed that rates of change for C, N and P and inferred rates of oxygen change varied widely in relation to surface productivity. In a similar study using more closely-spaced sampling intervals, increases in carbon and nitrogen flux via large particles actually were detected between 700–900 m suggesting the *in situ* production of organic matter in the aphotic zone based on chemolithotrophy (KARL and KNAUER, 1984; KARL, KNAUER, MARTIN and WARD, 1984).

Numerous other studies have confirmed that most of the surface-produced carbon is consumed before reaching the sea floor. For example, during a 10 day period in the north

Pacific off Washington carbon flux decreased non-linearly with depth from 34 mg C $m^{-2}$ $day^{-1}$ at 250 m to 18.5 mg C $m^{-2}$ $day^{-1}$ at 3000 m (LORENZEN, WELSCHMEYER and COPPING, 1983). The carbon sinking to the sea floor at 4200 m was equivalent to 3.7% of the daily primary production, and of that only 0.14% was incorporated into the sediments (LORENZEN, WELSCHMEYER and COPPING, 1983). In the equatorial Pacific beneath an area of high primary productivity, organic C flux into traps 20 m above the bottom (2670 m) was 1.5% of the primary production in the euphotic zone (COBLER and DYMOND, 1980). Most of all the carbon data published through 1980 was examined by SUESS (1980) who determined an empirical relationship that predicts organic carbon flux at any depth of the ocean below the base of the euphotic zone as a function of the mean net primary production rate at the surface and depth dependent consumption. Nevertheless, as pointed out by KNAUER, MARTIN and KARL (1984), Suess's model fails to differentiate between new and regenerated primary production, the ratio of which is known to vary between different marine waters. Furthermore, the model does not take into account depth dependent variations in the rate of new particle production observed by several authors (see above discussion). While a relationship between primary production and subeuphotic zone particle flux most certainly exists (see e.g. ALTABET and DEUSER, 1985), the exact nature of the relationship is unclear as exemplified by the primary production and new production data for the north Pacific shown in Table 1. In oligotrophic waters KNAUER, MARTIN and KARL (1984) argue for the presence of a two layered system in the euphotic zone with an upper layer displaying tight coupling between organic production and consumption, and a lower layer with new production values on the order of 40%. They buttress their argument with sediment trap data indicating negligible particulate C flux at 50 m in contrast to considerable flux out of the 50–160 m depth (see N flux in Table 1). Based on their two-layered euphotic zone model, these authors calculated that from 18–41% of the total integrated primary production in the euphotic zone occurs in the lower layer (50 m to base of euphotic zone), and concluded that mean new production estimates in this layer may be higher

TABLE 1. ESTIMATES OF NEW PRODUCTION ASSUMING A TWO-LAYERED EUPHOTIC ZONE IN OLIGOTROPHIC OCEAN WATERS IN THE NORTH PACIFIC (From KNAUER, MARTIN and KARL, 1984)

| Location | Integrated primary production in the 0–50 m upper layer (mg C $m^{-2}$ $day^{-1}$) | Integrated primary production in the 50 m base of euphotic zone (lower layer) (mg C $m^{-2}$ $day^{-1}$) | Nitrogen flux at reference trap depth† (mg N $m^{-2}$ $day^{-1}$) | New production N‡ fixed in the lower layer/N‡ flux (100) |
|---|---|---|---|---|
| VERTEX 2 | | | | |
| Mexico | 595 | 165 (22%)* | 7 | 24 |
| VERTEX 3 | | | | |
| Mexico | 390 | 85 (18%)* | 8.5 | 57 |
| VERTEX 4 | | | | |
| N.E. Pacific | 235 | 165 (41%)* | 5 | 17 |
| VERTEX 5a | | | | |
| N.E. Pacific | 155 | 90 (37%)* | 6.2 | 39 |
| VERTEX 5b | | | | |
| N.E. Pacific | 205 | 120 (37%)* | 9 | 42 |

*Numbers in parentheses: percentage of total integrated production in the euphotic zone.
†100 m for Vertex 2 and 3, 150 m for Vertex 4, 125 m for Vertex 5a and 5b.
‡Nitrogen estimated from C : N ratio = 6.6 : 1 (REDFIELD, KETCHUM and RICHARDS, 1963).

(~35%) than the average value of about 10% (EPPLEY and PETERSON, 1979). Recent work has also shown that much of the carbon associated with sedimenting particles is in fact derived from living organisms (e.g. bacteria, microheterotrophs, etc.) which play a major role in particle decomposition processes (FELLOWS, KARL and KNAUER, 1981).

Although, if not consumed, carbon can be rapidly transported to the benthos via fecal pellets, etc., in reality much of it is continually recycled in the upper layers (BISHOP, KETTEN and EDMOND, 1978; DUCKLOW, 1983; GARDNER, SOUTHARD and HOLLISTER, 1985). The idea that production, consumption and remineralization of nutrients are primarily recycled in the upper water column is further supported by the recent finding of the relatively low bomb $^{14}C$ content of many bathypelagic and abyssobenthic fish and invertebrates (PEARCY and STUIVER, 1983). However, it is perhaps noteworthy that the deep water organisms which were anlayzed for $^{14}C$ inhabited an oceanic area of the North Pacific in which there is no strong seasonal cycle of phytoplankton abundance (see MILLER, FROST, BATCHELDER, CLEMONS and CONWAY, 1984). In areas where pronounced phytoplankton blooms are common (e.g. North Atlantic) pulses of phytoplankton and attendant detritus rapidly reach great depth (LAMPITT, 1985) presumably carrying surface derived bomb $^{14}C$. It would thus be of interest to compare $^{14}C$ concentration in deep North Atlantic fauna with those reported for similar species from the North Pacific.

Besides "trapped" particulates, other large aggregates (i.e. marine snow) have been analyzed for nutrient content. SHANKS and TRENT (1979) found that hand-collected marine snow aggregates at times served as nutrient-rich patches, 1.1 to 860 times more concentrated in $NH_3$, $NO_2$, $NO_3$ and $PO_4$ than the surrounding water. Their data also indicated that dissolved phosphate was adsorbed onto the aggregates. In a similar study it was shown that macroscopic aggregates of recognizable zooplankton origin represented 26–34% of the total particulate carbon, nitrogen, protein, carbohydrate, lipid and dry weight of surface waters off California (ALLDREDGE, 1979).

### 6.2. *Organic compounds*

Because of their predominantly biogenic nature, large rapidly sinking particles contain a variety of organic compounds. Sedimenting fecal pellets resulting from intense zooplankton grazing activities in the euphotic zone typically contain chlorophyll a and phaeopigments (HARGRAVE and TAGUCHI, 1978; LORENZEN and WELSCHMEYER, 1983; LORENZEN, WELSCHMEYER and COPPING, 1983; LORENZEN, WELSCHMEYER, COPPING and VERNET, 1983). For example in the Bedford Basin (max. depth, 70 m) during the summer, chlorphyll a concentrations in large particles (i.e. fecal pellets) correlate closely with the biomass of herbivorous zooplankton (HARGRAVE and TAGUCHI, 1978). In contrast to nutrient elements like C and N, the vertical phaeopigment flux behaves conservatively indicating that there is no significant loss of these pigments from sinking herbivorous fecal pellets over a depth range from 20–100 m (LORENZEN and WELSCHMEYER, 1983). Significant concentrations of carotenoid dehydration products have been measured in zooplankton fecal pellets by REPETA and GAGOSIAN (1984). These authors proposed that phytoplankton derived carotenoids are rapidly metabolized by heterotrophs (e.g. zooplankton and anchovy) within the water column, and the resulting metabolites transported to the surface sediments. Dihydrophytol, a metabolite of dietary phytol, has also been found in the fecal pellets of certain calanoid copepods, and fecal pellet transport has been proposed to explain the presence of this compound in many marine sediments (PRAHL, EGLINTON, CORNER and O'HARA, 1984).

Lipids, amino acids, natural hydrocarbons, sugars, sterols and wax esters have also been measured in large particles (WAKEHAM, FARRINGTON, GAGOSIAN, LEE, DE BAAR, NIGRELLI, TRIPP, SMITH and FREW, 1980; WAKEHAM, FARRINGTON and GAGOSIAN, 1984; WAKEHAM, LEE, FARRINGTON and GAGOSIAN, 1984; WAKEHAM, 1982, 1985; WEFER, SUESS, BALZER, LIEBEZEIT, MULLER, UNGERER and ZENK, 1982; SALIOT, GOUTZ, FEVRIER, TUSSEAU and ANDRIE, 1982; LEE and CRONIN, 1982, 1984; GAGOSIAN, NIGRELLI and VOLKMAN, 1983; LEE, WAKEHAM and FARRINGTON, 1983). Working at a 5288 m sediment trap station in the north Atlantic, WAKEHAM, FARRINGTON, GAGOSIAN, LEE, DE BAAR, NIGRELLI, TRIPP, SMITH and FREW (1980) showed that while total organic carbon fluxes in the deep ocean decrease only slightly throughout the water column, the composition of portions of the organic fraction changes dramatically. Furthermore, many of the organic compounds in large particles are recycled and/or remineralized in the mesopelagic layer in this part of the ocean. For instance, lipids were rapidly depleted in the upper 1000 m of the water column resulting in decreasing lipid fluxes with depth. Lipids became a proportionally smaller fraction of the organic flux indicating that they were consumed preferentially with respect to some other components of the organic pool. Dominant hydrocarbons in particles from all depths were those of planktonic origin ($n$-$C_{17}$, $C_{19}$ and pristane). Sterenes were detected primarily at mid-depths suggesting active microbial transformations of organic matter in particles and rapid biogeochemical formation of sterenes. From detailed analyses of the particulates WAKEHAM (1982) concluded that zooplankton fecal matter and intact zooplankton probably represented the most important input of these compounds to traps at 389 to 988 m while particulates at 3755 and 5068 appear to have been biogeochemically altered. The finding of biogeochemically important compounds, often unsaturated, confirmed the rapidity with which the particles transited through the water column. A similar conclusion was reached by SALIOT, GOUTZ, FEVRIER, TUSSEAU and ANDRIE (1982) who found polyunsaturated $C_{20}$ and $C_{22}$ fatty acids, and $n$-$C_{17}$ hydrocarbons plus pristane in large particles ($> 50\,\mu m$) netted at 1000 m in the Arabian Sea. Finally, the intermittent appearances of large amounts of wax esters along with the changing fatty acid composition of the large particles found in deeper waters has led WAKEHAM, LEE, FARRINGTON and GAGOSIAN (1984) to conclude that there are deep water sources for these compounds, most likely a result of production of fecal pellets by mesopelagic carnivores. Amounts and fluxes of the various organic components of large particles from the equatorial North Atlantic are given in Table 2.

In the Peru upwelling region approximately 2–6% of the sterols of phytoplankton origin that are found in large particles survive water column and sediment degradative processes (GAGOSIAN, NIGRELLI and VOLKMAN, 1983). Much of the sterol flux was found to be mediated by zooplankton feeding activity since sterol fluxes were 10 times greater at night than in the daytime. Furthermore, these diatom derived sterols appear to be rapidly delivered to the sediment via sinking anchovy fecal pellets (GAGOSIAN, VOLKMAN and NIGRELLI, 1983). In the same region, the highest wax ester fluxes were measured in shallow sediment traps (10–14 m) at night and are attributed to increased inputs from surface-feeding zooplankton (WAKEHAM, 1985). Higher tricylglycerol fluxes were measured during the night than in the day in both deep (50 m) and shallow traps, an observation consistent with inputs of both zooplankton and phytoplankton lipids (WAKEHAM, 1985).

In the Panama Basin, amino acids in large particles collected at 1267 m made up 15–35% of the total organic carbon flux and 35–75% of the total organic nitrogen flux (LEE, WAKEHAM and FARRINGTON, 1983). Corresponding percentages (20–30% and 40–65%) in

TABLE 2. AMOUNTS AND FLUXES OF ORGANIC CONSTITUENTS IN SAMPLES FROM THE PARFLUX E SEDIMENT TRAP STATION IN THE NORTH ATLANTIC. FROM WAKEHAM, FARRINGTON, GAGOSIAN, LEE, DE BAAR, NIGRELLI, TRIPP, SMITH AND FREW (1980)

| Depth | Particulate matter | Organic matter | Organic carbon | Hexane-soluble lipids | Hydrocarbons | Total fatty acids | Free fatty acids | Wax esters | Steroid ketones | Amino acids (lipid fraction) | Free fatty alcohols | Free sterols | Steryl esters | Triacylglycerols |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | (g) | | | (mg) | Amount of material per trap ($\mu$g) | | | | | | | | | |
| 389* | 6.6 | 1.4 | 0.7 | 225 | 1,200 | 39,100 | 4,100 | 770 | 4,720 | 300 | 20,500 | 19,100 | 170 | 390 |
| 389† | 3.6 | 0.6 | 0.3 | 70 | 250 | 16,500 | 2,600 | 530 | 130 | 90 | 4,100 | 7,400 | 60 | 90 |
| 988* | 6.7 | 1.2 | 0.5 | 170 | 1,120 | 17,400 | 470 | 180 | 3,300 | 43 | 1,800 | 31,400 | 2,300 | 2,100 |
| 988† | 0.5 | 0.1 | 0.04 | 20 | 170 | 5,100 | ND | 20 | 20 | 3.2 | 980 | 3,360 | 200 | 110 |
| 3,755* | 6.8 | 0.7 | 0.2 | 25 | 140 | 1,280 | ND | 16 | 530 | 13 | 6,300 | 900 | 8 | 17 |
| 5,068* | 6.9 | 0.7 | 0.2 | 13 | 97 | 910 | 200 | 49 | 590 | 14 | 760 | 550 | 9 | 12 |
| | | | | | Fluxes | | | | | | | | | |
| | | | ($mg\,m^{-2}\,day^{-1}$) | | | | | | | | ($\mu g\,m^{-2}\,day^{-1}$) | | | |
| 389* | 45.1 | 9.7 | 4.7 | 1,530 | 8.2 | 270 | 27.9 | 5.3 | 32.1 | 2.0 | 140 | 130 | 1.2 | 2.6 |
| 389† | 24.2 | 3.9 | 2.0 | 470 | 1.7 | 110 | 17.8 | 3.6 | 0.9 | 0.6 | 30 | 50 | 0.4 | 0.6 |
| 988* | 45.9 | 7.9 | 3.7 | 1,160 | 7.6 | 120 | 3.2 | 1.2 | 22.4 | 0.3 | 12 | 214 | 15.9 | 14.3 |
| 988† | 3.3 | 0.7 | 0.3 | 130 | 1.2 | 35 | ND | 0.1 | 0.1 | 0.02 | 7 | 23 | 1.3 | 0.7 |
| 3,755* | 46.4 | 4.8 | 1.7 | 170 | 1.0 | 8.7 | ND | 0.1 | 3.6 | 0.1 | 43 | 6 | 0.06 | 0.12 |
| 5,068* | 47.0 | 4.9 | 1.7 | 85 | 0.7 | 6.2 | 1.4 | 0.3 | 4.0 | 0.1 | 5 | 4 | 0.06 | 0.08 |

ND Not detectable relative to blank.
* Particle size > 1 mm
† Particle size < 1 mm

particles from the productive Peru upwelling area are similar (LEE and CRONIN, 1982). The Peru data also suggest that 10% of the primary production is decomposed as particulate amino acids between 14 and 50 m, and up to 12% may reach the sea floor. When amino acid and productivity data are compared from several different oceanic regions, a close relationship is found between amino-acid flux on sinking particles and primary productivity (LEE and CRONIN, 1984). However, the extent of amino acid decomposition varied in areas of different productivity. LEE and CRONIN (1984) found that faster decomposition took place below surface waters in areas of high productivity and suggested that this was due either to more efficient zooplankton feeding in more productive regions, or to production of amino acids in more resistant organic matrices in less productive areas.

From sediment trap studies in the southern ocean WEFER, SUESS, BALZER, LIEBEZEIT, MULLER, UNGERER and ZENK (1982) found decreasing protein (amino acids) and increasing carbohydrates in particles with depth reflecting preferential degradation of proteinaceous material. Amino sugars comprised a relatively stable fraction of both organic C and N at all depths indicating the presence of poorly degradable chitinaceous matter probably originating from crustacean molts. Work by LIEBEZEIT (1985) carried out in the same general area indicates that in high productivity zones where grazing pressure is evident, particulate amino acids are rapidly degraded; e.g. amino acid flux at 100 m in the Bransfield Strait was about 11% of their production in the euphotic zone. In contrast, for areas where grazing pressure is considerably less, this degree of degradation may not be reached until approximately 1000 m.

ATP and RNA are other compounds which have commonly been found in large particles collected in traps from depths above 2000 m (FELLOWS, KARL and KNAUER, 1981; KARL and KNAUER, 1984). Their presence is attributed to the metabolic activities of living microorganisms associated with sedimenting particles (see Section 5.2.3). Subsurface flux maxima have been interpreted as zones of enhanced metabolic activity and C production based on chemolithotrophy (KARL and KNAUER, 1984; KARL, KNAUER, MARTIN and WARD, 1984).

Anthropogenic hydrocarbons are also common components of large biogenic particles. ELDER and FOWLER (1977) measured relatively high PCB concentrations (4.8–38 $\mu g\, g^{-1}$ dry) in zooplankton fecal pellets and suggested that sinking pellets would be instrumental in transporting these compounds in the deep sea. Recent sediment trap studies in the coastal Mediterranean have confirmed the presence of PCBs in large particles (including fecal pellets) collected at depth, and the changes in concentration with depth indicate that PCBs are relatively stable in the sinking particles (FOWLER, SMALL, ELDER, UNLU and LA ROSA, 1979; BURNS, VILLENEUVE and FOWLER, 1985). Measured PCB fluxes through 100 m depth averaged approximately $4\, ng\, cm^{-2}\, yr^{-1}$ and agreed well with sediment deposition data (BURNS, VILLENEUVE and FOWLER, 1985). These fluxes of particulate PCBs are lower than those measured in the Kiel Bight ($\sim 15\, ng\, cm^{-2}\, yr^{-1}$) where primary production is higher and the water column much shallower ($\sim 20$ m) (OSTERROHT and SMETACEK, 1980).

DDT residues, lindane and hexachlorobenzene (HCB) have also been measured in fecal pellets and sediment trap material (BURNS, VILLENEUVE and FOWLER, 1985); non-soluble DDE behaves like PCB and is rapidly deposited in the sediment whereas the more soluble lindane ($\gamma$-hexachlorocyclohexane) and HCB may be partially leached from the particles before they reach the sea floor. In the coastal waters of the northwestern Mediterranean, based on these measurements residence times in the top 100 m were computed to be 2.6 and 55 yr for PCB and lindane, respectively. Fecal pellet analyses clearly indicate that much of the transport is occurring via these biogenic particles. In the case of PCBs, it appears that

this cleansing mechanism is at least partially responsible for the decrease in PCB concentrations over time noted in Mediterranean coastal waters (BURNS, VILLENEUVE and FOWLER, 1985).

The same mechanism is involved in the removal of petroleum hydrocarbons (PH) which enter surface waters (PRAHL and CARPENTER, 1979; SLEETER and BUTLER, 1982; BURNS, VILLENEUVE and FOWLER, 1985). Zooplankton fecal pellets collected at 60 m in Dabob Bay, Washington accounted for essentially 100% of the polycyclic aromatic hydrocarbon (PAH) fluxes measured in $^{210}$Pb dated sediments, implying the pellets were controlling PAH removal to the sediments. In the central basin of Puget sound, Washington, the flux of PAH through the 50 and 100 m depths accounted for 84% of the PAH accumulating in the underlying surface sediments (BATES, HAMILTON and CLINE, 1984). Based on fecal pellet analyses for petroleum hydrocarbons (PH), SLEETER and BUTLER (1982) estimated PH removal from surface waters of the Sargasso Sea by defecation to be 8–23 mg m$^{-2}$ yr$^{-1}$, a rate not much lower than the input (18–70 mg m$^{-2}$ yr$^{-1}$) to the region. In the coastal Mediterranean, petroleum fluxes via sedimenting particles averaged 80 mg m$^{-2}$ yr$^{-1}$, with fecal pellets acting as prime carriers (BURNS, VILLENEUVE and FOWLER, 1985). The resultant residence time in the upper 100 m was thus about one year. However, these compounds in the particles were rapidly degraded and comparison with bottom sediment data indicated that 90% of the PHs transported to depth (100 m) were degraded before incorporation into compacted sediments. These findings are similar to those of PRAHL, BENNETT and CARPENTER (1980) who showed that aliphatic hydrocarbons (e.g., pristane and unsaturated compounds) are rapidly remineralized at or near the sediment–water interface.

### 6.3. *Biogenic and lithogenic constituents*

Large particles are also carriers of various inorganic components and mineralogical phases which arise primarily from the biological origin of materials comprising these particles. These include such materials as carbonate tests, opaline shells, barite and aluminosilicates (non-biogenic). Sediment trap experiments in the Atlantic and Pacific have shown that 60–90% of the total particle flux is biogenic, with the contribution of biogenic material decreasing with increasing depth (HONJO, MANGANINI and COLE, 1982). HONJO, MANGANINI and COLE (1982) found that carbonate hard parts accounted for 30–60% of the flux. Their data and those of THUNELL and HONJO (1981) indicate that except for small foraminifera ($< 150\ \mu$m), major dissolution and remineralization of the carbonate does not take place even upon reaching the undersaturated bathypelagic layer due to the very fast transit time in fecal pellets and aggregates. In the southern circumpolar waters of the Drake Passage it was found that the calcium carbonate and aluminosilicate fractions increased in relative importance with depth due to the more rapid disappearance of opal and organic matter (WEFER, SUESS, BALZER, LIEBEZEIT, MULLER, UNGERER and ZENK, 1982). It was also demonstrated that the entire calcium carbonate flux in that particular region was attributable to the single species of foraminifera present in their trap samples. From recent measurements in the eastern tropical Pacific, it appears that in contrast to the more labile components of large particle flux (C, N and P), much of the $CaCO_3$ is in fact regenerated at the sea floor (DYMOND and LYLE, 1985).

Quantitative X-ray diffraction analyses of large particles from the Atlantic ocean (BERNER and HONJO, 1981) indicate that a minimum of 12% of the total flux of calcium carbonate is made up of aragonite; however, the degree of dissolution which may have

occured in the traps is not known. Some of the aragonite is derived from sinking planktonic remains (e.g. pteropods) while the remainder appears to be laterally transported from shallow water regions. More recently, short-term (1–1.5 day) sediment trap experiments in the North Pacific have demonstrated the importance of aragonitic pteropods in large particle flux (BETZER, BYRNE, ACKER, LEWIS, JOLLEY and FEELY, 1984), hitherto possibly underestimated because of dissolution during long-term studies. Contributions of these pteropods to total mass flux ranged from 24% at 100 m to 6% at 220 m, an observation which indicates that approximately 90% of the aragonite flux is rapidly remineralized from biogenic hard parts in the upper 2.2 km of the water column. Nevertheless, pteropods are very patchy in time and space and the absence of detectable aragonite flux over longer time scales may also reflect a true event.

Diatomaceous debris ($SiO_2$) is often the dominant constituent of large particle flux especially in high latitude waters (WEFER, SUESS, BALZER, LIEBEZEIT, MULLER, UNGERER and ZENK, 1982). The recycling of opal from diatom frustules can be especially rapid. From the work of HONJO, MANGANINI and COLE (1982) it is evident that the major region of opal dissolution is in the upper few hundred meters; this results at least partially from the higher temperatures found in the surface layers (KAMATANI, 1982). Some dissolution also occurs with radiolarians; for example partial dissolution of opal was evident in about 10% of the shallow trap samples and 36% in the deep trap at 5582 m (TAKAHASHI and HONJO, 1981). In one long-term study at 2670 m in the north equatorial Pacific, COBLER and DYMOND (1980) found that at least 80% of the opal in sinking particles was consumed at the sediment–water interface. The rates of loss of $SiO_2$ into the bottom water was calculated to be 14.2 $\mu$mole $cm^{-2}$ $yr^{-1}$.

Investigations of lithogenic particles collected in sediment traps indicate an increase in lithogenic flux with depth in many regions of the open sea (HONJO, 1982; HONJO, SPENCER and FARRINGTON, 1982; HONJO, MANGANINI and POPPE, 1982). Where increased lithogenic fluxes with depth have been noted (e.g. Panama Basin) it has been suggested that smectite and other clay minerals are laterally transported from the bottom sediments on the continental slope, and the fine suspended particles are then entrapped by large, settling particulates. On the other hand, the fluxes of hemipelagic clays, i.e. kaolinite and chlorite, have been found to be constant at all depths in the Panama Basin; this was thought to occur by incorporation of these particles in fecal pellets which rapidly settled to depth (HONJO, MANGANINI and POPPE, 1982). However, these trends are not always the same; at the Demerara Abyssal Basin station, fluxes of illite and chlorite particles increased with depth and the smectite flux was constant (HONJO, MANGANINI and POPPE, 1982).

In other studies SEM and electron microprobe analyses of suspended particulates have revealed the presence of barite crystals (DEHAIRS, CHESSELET and JEDWAB, 1980). These crystals were found in fecal material which was observed throughout the water column. It is thought that the abundant organic material in this debris may provide the micro-environment necessary for the precipitation of $BaSO_4$. Furthermore strong correlation between barite crystals and nutrient content suggests a control of barite formation by biological activity (DEHAIRS, CHESSELET and JEDWAB, 1980). As mentioned in Section 2.1.1 above, there is substantial evidence that many of the fine inorganic particles like clay are passively filtered by zooplankton with subsequent encapsulation in fecal pellets and removal to depth (see also BRONGERSMA-SANDERS, 1983). It seems clear that fecal deposition is the main mechanism by which lithogenic particles reach the sediments.

### 6.4. *Trace elements*

The production, sinking and decomposition of large biogenic particles are important factors controlling the distribution of trace elements within the oceans (BRULAND, 1983; COLLIER and EDMOND, 1984; MURPHY and DYMOND, 1984; NORIKI, ISHIMORI and TSUNOGAI, 1985; NORIKI, ISHIMORI, HARADA and TSUNOGAI, 1985). Upon sinking these particles can adsorb and "scavenge" many trace elements from the dissolved phase and thereby remove them to depth and/or release adsorbed and incorporated elements as the debris is oxidized and resolubilized.

An examination of the adsorption properties of sinking particulate matter in the deep sea (BALISTRIERI, BREWER and MURRAY, 1981) suggests that the adsorptive properties of the particles are controlled primarily by organic coatings. Recent work by HUNTER (1983) has shown that the residence times of at least 8 elements are quantitatively consistent with the surface chemical model of BALISTRIERI, BREWER and MURRAY (1981) using likely model ligands. The probable functional groups involved are carboxylic acid and phenols. A good correlation between experimentally-derived, trace metal concentration factors in phytoplankton and the solubility products of the metal hydroxides suggests that metal uptake by these living particles is determined similar to that for inert particulates (FISHER, in press). Besides sorptive and ion exchange processes, many elements can become associated with large particles following direct uptake across cell membranes into phytoplankton and zooplankton by active metabolism. Such elements are those which play important roles in metal-requiring enzyme systems like V, Cr, Mn, Fe, Co, Ni, Cu, Zn and Mo.

Recently, COWEN and SILVER (1984) reported an association of metal depositing bacteria with rapidly sinking particulates in the open ocean. This association represents another mechanism by which metals such as Fe and Mn are accumulated on large particles. These authors suggest that the capsule polymer-metal complex may contribute a major portion of the weakly bound fraction of the particulate iron flux.

The release of particulate-bound elements back to the sea water ("J-flux", LAL, 1977) may occur by desorption or ion exchange processes with surface-bound trace elements, or dissolution of elements that were bound to labile (e.g. organic) constitutents within the particles (COLLIER and EDMOND, 1984). The exchange kinetics between particle and water and resultant oceanic trace element distributions are highly dependent upon the element, the large particle constituents and the particular oceanographic regime. BRULAND (1983) has extensively examined the relationships between particulate and dissolved trace element profiles, and an exhaustive review of these concepts will not be attempted here. Rather certain examples will be discussed which illustrate specifically the role played by large particles in these processes. As BRULAND (1983) points out, in many cases the nature of the vertical profiles has allowed elucidating the major processes controlling the trace element's distribution. In this respect he has described seven distinct basic types of profile involving various degrees of element depletion or enrichment with depth. With the use of sediment traps it has become possible to describe rates of change in large particle trace metal concentrations and how vertical transport of particles leads to either element enrichment or depletion in the water column.

Large biogenic particles are often extremely rich in trace elements. For example, trace element concentrations in freshly-collected zooplankton fecal pellets and those collected by deep sediment traps, molts and Atlantic surface particulates are shown in Table 3. Concentrations of many trace elements are often higher in these types of biogenic debris

TABLE 3. TRACE ELEMENTS# ($\mu g\,g^{-1}$ DRY WEIGHT) IN ATLANTIC SURFACE PARTICULATES AND IN ZOOPLANKTON FECAL PELLETS AND MOLTS

| Element | Atlantic surface particulates | Fecal pellets | | | Molts |
|---|---|---|---|---|---|
| | | Fresh* | Sediment trap* | Sediment trap† | Fresh |
| Al | 3000 | 28,490 | 20,800 | 74,900 | – |
| Sc | 0.5 | 2.8 | 4 | 15 | 0.03 |
| V | 22 | – | 76 | 114 | – |
| Cr | 125 | 38 | – | – | 5.3 |
| Mn | 140 | 243 | 2110 | 768 | 12 |
| Fe | 8800 | 24,000 | 21,600 | 43,600 | 232 |
| Co | 5 | 3.5 | 15 | 10 | 0.8 |
| Ni | 70 | 20 | – | – | 6.7 |
| Cu | 145 | 226 | 650 | 308 | 35 |
| Zn | 640 | 950 | < 20 | < 20 | 146 |
| Se | 8 | 6.6 | – | – | 1.9 |
| Ag | 4 | 2.1 | – | – | 2.9 |
| Sb | 7 | 71 | < 5 | < 5 | 0.8 |
| Au | 0.4 | – | < 0.1 | 0.16 | – |
| Hg | 16 | 0.34 | – | – | 0.17 |
| Pb | 180 | 34 | – | – | 22 |
| Th | 0.4 | 4 | – | – | – |
| La | – | – | 24 | 49 | – |
| I | – | – | 496 | 83 | – |
| Ba | – | – | 192 | 526 | – |
| Ti | – | – | 0.13 | 0.31 | – |
| Cd | – | 9.6 | – | – | 2.1 |
| Ce | – | 200 | – | – | 1.2 |
| Cs | – | 6.0 | – | – | 0.02 |
| Eu | – | 0.66 | – | – | 0.0077 |
| Sr | – | 78 | 1430 | 50 | 350 |

*"Green" fecal pellets.
†"Red" fecal pellets.
# Data from FOWLER (1977); SPENCER, BREWER, FLEER, HONJO, KRISHNASWAMI and NOZAKI (1978); BUAT-MENARD and CHESSELET (1979); KRISHNASWAMI, BASKARAN, FOWLER and HEYRAUD (1985).

than in the organisms producing them (FOWLER, 1977; KRISHNASWAMI, BASKARAN, FOWLER and HEYRAUD, 1985). Since much of the biogenic debris is produced in the surface layers, it is not surprising that these particles are instrumental in removing many trace elements from the upper water column and transporting them to depth (e.g. FEELY, CHESTER, PAULSON and LARRANCE, 1982; IZDAR, KONUK, HONJO, ASPER, MANGANINI, DEGENS, ITTEKKOT and KEMPE, 1984). In fact, based on these sorts of data and mass balance considerations of river input and sediment output, some studies have concluded that the settling of fecal pellets and fecal aggregates is the most important mechanism effecting the vertical transport, and thus residence time, of many trace elements (CHERRY, HIGGO and FOWLER, 1978; LI, 1981).

Cadmium and zinc are two trace elements whose profiles show a marked surface depletion and enrichment at depth. As such these elements are closely correlated with phosphate, nitrate and silica concentrations at all depths, suggesting a nutrient-type regeneration pattern (BOYLE, SCLATER and EDMOND, 1976; BRULAND, KNAUER and MARTIN, 1978a, b). Based on sediment trap data cadmium residence times in the upper

65 and 750 m of the northeast Pacific were computed to be approximately 1 and 250 yr, respectively (KNAUER and MARTIN, 1980). In contrast, Cu profiles in the open Pacific are characterized by a near-linear increase with depth (BRULAND, 1980). This pattern is typical when *in situ* scavenging onto sinking particles is taking place. The mean residence time for Cu due to scavenging in the deep sea was computed to be on the order of $10^3$ yr. The observed enrichment of Cu in bottom waters is due to particle regeneration processes and injection from sediments. Copper may behave somewhat differently in nearshore waters; for example at a 100 m station in the Gulf of Alaska, LANDING and FEELY (1981) found that organically-associated Cu in large particles was remineralized at a rate of approximately 79 pg cm$^{-2}$ day$^{-1}$ which represents about 3.6% of the total Cu flux to the underlying sediments. Likewise TSUNOGAI, UEMATSU, NORIKI, TANAKA and YAMADA (1982) found decreasing metal/Al concentration ratios with depth for Cu as well as Ni and Cd in sinking particles and concluded that these elements were being remineralized in deeper water as a result of decomposition.

Particulate manganese cycling is far more complex because of its various inputs and redox chemistry. In the northeast Pacific equatorial water, labile Mn fluxes via large particles slowly increased from 270 at 125 m to 450 ng Mn cm$^{-2}$ yr$^{-1}$ at 900 m (MARTIN and KNAUER, 1982). These rates, although only determined over a 28 day period, were consistent with those estimated for "excess Mn"* accumulation in open ocean sediments which implies that biogenic transport is a major factor in oceanic Mn cycling. Much of the Mn transported biogenically is adsorbed to the surfaces of the $CaCO_3$ phases and can be removed from particles by weak acid leaches (MARTIN and KNAUER, 1983).

MARTIN and KNAUER (1984) examined Mn transport off central Mexico and found that Mn is released from particles as they sink through the oxygen minimum. Manganese fluxes decreased from 381 ng cm$^{-2}$ yr$^{-1}$ at 120 m to 72 ng cm$^{-2}$ yr$^{-1}$ at 400 m. Regeneration rates of Mn up to 0.24 ng kg$^{-1}$ yr$^{-1}$ occurred in the upper oxygen minimum (120–200 m); this accounts for only 30% of the dissolved Mn in this zone. The remainder was thought to be transported horizontally from the continental slope. Below the $O_2$ minimum, dissolved Mn was scavenged back onto particles as the $O_2$ level increased. Scavenging rates ranged from $-1.65$ to $-4.94$ ng kg$^{-1}$ yr$^{-1}$ at depths from 700–1950 m, and resulted in Mn residence times via sinking particles of 16–19 yr. Mn removal by particles below these depths is balanced by Mn released along continental boundaries and transported horizontally by advection–diffusion. Later work by MARTIN and KNAUER (1985) in the open ocean demonstrated conclusively that the processes responsible for the excess Mn accumulating on the sea floor are a combination of continental weathering input, dissolved Mn lateral transport, and sinking biogenic particle scavenging output.

Mn fluxes via large particles can also vary seasonally in certain areas. In Funka Bay, Japan (100 m deep) UEMATSU and TSUNOGAI (1983) observed that the downward flux of total Mn during the winter (0.47–1.0 mg cm$^{-2}$ yr$^{-1}$) was generally an order of magnitude greater than that in summer (0.05–0.16 mg cm$^{-2}$ yr$^{-1}$). Furthermore, the Mn fluxes during both seasons were higher than the net accumulation rate of Mn in the sediments (0.04 $\mu$g cm$^{-2}$ day$^{-1}$). Based on their data a compound Mn residence time in bottom water was about 1 to several months, values which suggest active recycling of Mn between the water column and sediments in the coastal zone.

*i.e. sedimentary Mn supplied neither by dissolved Mn in sea water nor by hydrothermal inputs – see BENDER, KLINKHAMMER and SPENCER, 1977.

COBLER and DYMOND (1980) set two closely spaced traps for 234 days in the equatorial Pacific near the bottom (20 and 100 m above) at 2670 m and compared trap fluxes for several elements with those accumulating in the sediments. Based on these relatively long-term deployments they found that fluxes of Mn and Ni to the sediment were two to three times greater than those in the benthic interface zone, an indication that these elements were mobilized in surface sediments. In contrast Si, Ca, Cu and Zn had larger fluxes into the traps than into the sediment. This observation implied that the elements are being released from particles into the bottom water. Al, Fe and Ba fluxes into traps and sediments were nearly similar; this is probably due to their association with relatively stable phases in particles (e.g. alumino-silicates and barite). With evidence from sediment trap studies DEUSER, BREWER, JICKELLS and COMMEAU (1983) have shown that Al is swept from the upper 100 m of the Sargasso Sea with residence times ranging from 14 to 80 days and rapidly transported to depth as particulate Al associated with organic matter. Likewise WALLACE, MAHONEY, DULMAGE, STORTI and DUDEK (1981) computed a 30-day residence time for particulate Al in the top 30 m of the Gulf Stream. From 30 to 100 m they measured an exponential decrease in particulate aluminium and attributed this first order removal ($K_{const} = 3.8 \times 10^{-2}\,m^{-1}$) to sinking fecal pellets, particularly those of salps. The recent finding of high Al concentrations (2.84%) in freshly excreted salp fecal pellets (KRISHNASWAMI, BASKARAN, FOWLER and HEYRAUD, 1985) supports their hypothesis. Below 100 m the Al flux increased with depth as has been noted in other studies from the Atlantic (BREWER, NOZAKI, SPENCER and FLEER, 1980) and the Pacific (TSUNOGAI, UEMATSU, NORIKI, TANAKA and YAMADA, 1982).

Major ions such as Ca, Sr, Na, K and Mg are also rapidly removed from the surface layer by their association with large particles (BISHOP, EDMOND, KETTEN, BACON and SILKER, 1977; BISHOP, KETTEN and EDMOND, 1978; DEUSER, BREWER, JICKELLS and COMMEAU, 1983). In addition BISHOP, KETTEN and EDMOND (1978) found that at least excess Ca and K were involved in shallow regenerative cycles and were present in deep samples only in areas of high primary productivity.

Vertical transport of a variety of other elements is intimately linked to large particle flux. Studying chemical fluxes in the deep Sargasso Sea, SPENCER, BREWER, FLEER, HONJO, KRISHNASWAMI and NOZAKI (1978) normalized trace element concentrations in trapped particles to Al and concluded that Fe, Mg, Ti, Mn, Ba, V, La, Sc and Co were carried downward by large particles (i.e. fecal pellets) consisting principally of surface-derived clays and also via flux from the biological aggregation of fine particles resuspended from the bottom. Furthermore, they found that fluxes of Ca and Sr in carbonates (from foraminifera and pteropods), C and I in organic phases, and an Fe–Mn hydroxide component with atmospherically-derived alumino-silicates were responsible for the principal primary fluxes from the upper water column. Similar sediment trap experiments in the equatorial Pacific have also demonstrated that biogenic particles are the major carrier of the rare earth elements, particularly in shallow depths, and that the fraction of these elements regenerated from particles at the sea floor is small (MURPHY and DYMOND, 1984).

BREWER, NOZAKI, SPENCER and FLEER (1980) studying elemental fluxes throughout the water column in the North Atlantic found constant metal/Al ratios in particles with depth for K, Ti, La, V and Co. This observation suggested that these elements were carried in terrigenous materials. For Ca, Sr, Mg, Si, Ba, U and I, metal/Al ratios decreased with depth indicating their initial association with biogenic particles. In contrast metal/Al ratios for Mn, Cu, Fe and Sc increased with depth which was interpreted to result from the scavenging

of the surface active elements by sinking particulates. These direct measurements allowed calculating residence times for the scavenging elements; values were 20, 77, 230 and 500 yr for Mn, Fe, Sc and Cu, respectively.

Closely related studies in the Sargasso Sea (JICKELLS, DEUSER and KNAP, 1984) have revealed that fluxes of Al, Cd, Cu, Fe, Mn, Ni, P, Pb, V and Zn in the deep ocean (3200 m) are temporally variable and are controlled by the seasonal cycle of primary production in the overlying surface waters. From total trace element inventories in the water column and measured particulate element fluxes, total residence time for these elements (particulate plus dissolved) in the top 100 m were estimated to range from 0.1 to 30 yr (except for V, 250 yr). Residence times for particulate trace elements in surface waters were shorter ($< 150$ yr) and JICKELLS, DEUSER and KNAP (1984) concluded that those elements rapidly converted to particulate forms by biogenic or abiotic processes, and not easily recycled, display the shortest residence times due to their rapid removal from the euphotic zone. In a similar study enrichment factors relative to aluminium were computed for several trace metals in sinking biogenic debris during bloom conditions in Funka Bay, Japan (NORIKI, ISHIMORI, HARADA and TSUNOGAI, 1985). The resultant order of affinity for biogenic particles was Cd > Pb, Ni, Cu > Co > Mn, Fe, Al.

Comprehensive data on trace element flux through a 2000 m water column have been reported by MARTIN and KNAUER (in press) for large particles sinking through the sub-oxic zone in waters off Mexico. They found similar flux patterns for Cd, Ag, Mo, Zn, Ni, Pb, Co, Mn, Cu and Ba, i.e. fluxes were highest in the 120 m trap and then decreased until flux minima were reached at mid-depths. The similarity between this pattern and that noted for organic carbon suggested that these 10 elements were taken up in the biogenic phases (Si, $CaCO_3$, organic C) in near surface waters and then upon sinking were regenerated fairly rapidly between 200–700 m (sub-oxic zone) in the water column. Below 700 m some fluxes remained roughly constant with depth (Cd, Ag, Mo, Ni and Zn) while other fluxes (Co, Pb, Mn, Cu and Ba) increased due to scavenging between 1400 to 1950 m. At the same station Al and Fe fluxes were relatively constant at all depths, indicating a close association with alumino-silicates and no interaction with the biota. Marked *in situ* scavenging onto particles was noted for Cr and V in that their fluxes were low in the upper layers and then increased steadily with depth up to a point (200 m for V, 800 m for Cr) after which the fluxes began to decrease. These patterns indicated greater particle reactivity for these elements, including Mn, in the reducing conditions of the oxygen minimum layer. Residence times of particulate metal phases, a measure of particle reactivity, were calculated for the upper 120 m in these waters; they were 0.82 (Ag), 1.1 (Cd), 2.4 (Co), 3.7 (Cr), 5.0 (Mn), 7.8 (Cu), 10.8 (Pb), 12.5 (Ni), 570 (V) and 21,000 yr (Mo).

Trace metal regeneration from settling biogenic particles has been specifically examined with sediment trap experiments in the shallow waters ($\sim 100$ m) of Funka Bay (NORIKI, ISHIMORI and TSUNOGAI, 1985). Net fluxes normalized to Al were calculated at 1, 40 and 80 m. Decreasing fluxes with depth indicated that Cd was actively regenerated (70% of that in surface flux) in the layers above 80 m, primarily in the top 40 m, while Mn ($\sim 50\%$) was released from the particles mainly in the lower layer between 80 m and the sediments. In contrast, constant net fluxes of Fe with depth showed no apparent Fe regeneration in either the water column or at the sea floor under these conditions.

All the above-mentioned evidence for scavenging and/or regeneration of trace elements in large particles is derived from field studies. Because of the technicalities involved, direct measurements of rates of element scavenging or release by large particles would be difficult,

TABLE 4. *REMINERALIZATION HALF-TIMES (DAYS) FOR ELEMENTS AND RADIONUCLIDES IN TYPICAL BIOGENIC PARTICLES†#

| Element/RN | Fecal pellets | Molts | Euphausiid carcasses |
|---|---|---|---|
| Zn | 2.0 | 1.7 | 7.8 |
| Hg (Inorg.) | 14.1 | 2.3 | 3.1 |
| Hg (Org.) | 6.0 | 4.1 | 2.6 |
| Se | 3.9 | – | – |
| $^{239+240}$Pu (+VI) | 9.7 | 4.7 | 5.3 |
| $^{239+240}$Pu (+IV) | 23.0 | – | – |
| $^{241}$Am | 41.0 | 2.9 | – |
| $^{144}$Ce | 7.5 | 10.6 | 17.3 |
| $^{210}$Po | 3.5 | – | – |

*Temperature = 13°C.
†Particles were produced by the zooplanktonic euphausiid *Meganyctiphanes norvegica*.
# Data taken from FOWLER (1982); FISHER, BJERREGAARD and FOWLER (1983b).

if not impossible, to do *in situ*. However, some insight into the time scales involved can be obtained from radiotracer studies carried out under laboratory conditions. For example, laboratory radiotracer studies have shown that elements such as Cs, Zn, Pa, Sn and Th adsorb rapidly (hours to days) to sediment trap material and fecal pellets, reaching distribution coefficients ($K$d) ranging from $10^2$ to $10^6$ after several days (NYFFELER, LI and SANTSCHI, 1984). During decomposition, zooplankton fecal pellets, molts and carcasses labelled with radio-isotopes characteristically release or desorb these elements to the surrounding water at rates which follow a single exponential (FOWLER, 1982). Table 4 gives the half-times for release of Zn, Hg, Se, Cu, Pu and Po from typical debris; these elements differ greatly in their reactivities for particles, however, release rates for complexed or adsorbed forms of these elements in decomposing biodetritus only vary within approximately an order of magnitude. It is also evident that fecal pellets retain the elements to a greater degree than either microcrustacean molts or carcasses principally because the latter detrital forms decompose more rapidly than fecal pellets. This indicates that fecal pellets would have a greater potential to transport trace elements downward than other biogenic particles like molts and dead zooplankton. In fact, several studies modelling vertical transport of trace metals and radionuclides have come to this conclusion (see FOWLER, 1982, for review). For example, in one such study BURNETT and PATTERSON (1980), modelling Pb transport in the NE Pacific, calculated that sinking zooplankton fecal pellets containing Pb-rich phytoplankton residues could account for 95% of the estimated 1200 ng Pb $m^{-2}$ $day^{-1}$ removed from the mixed layer (upper 100 m) by biological mechanisms.

### 6.5. *Radionuclides*

Like their stable isotopes, the water column distributions of many radioactive elements are also controlled to a large extent by large particle transport processes. Radionuclides, particularly those in the natural series ($^{234}$Th, $^{230}$Th, $^{228}$Th, $^{210}$Po, $^{210}$Pb), often serve as unique tracers for studying particle dynamics because of their differences in parent–daughter chemistries and their known radioactive decay constants which are useful for assessing the time dimension of these processes. Various artificial radionuclides originating from

atmospheric nuclear testing are of equal interest owing to their differing reactivities and their single point of entry (i.e. ocean surface). Several works (N.A.S., 1971; SACKETT, 1978; SIMPSON, 1982; BROECKER and PENG, 1982) have comprehensively reviewed the overall oceanic distribution and geochemistry of dissolved and particulate radionuclides; therefore, in the following treatment emphasis has been placed on recent literature that pertains specifically to transport by large particles.

Some of the first evidence (indirect but convincing) that radionuclides move rapidly downward in association with large biogenic particles came from the observation of the short-lived fission products $^{95}Zr$–$^{95}Nb$ and $^{141,144}Ce$ in sea cucumbers living at 2800 m (OSTERBERG, CAREY and CURL, 1963). Sinking rates of fallout particles based on Stokesian settling were far too low to account for the activity levels of these short-lived radionuclides at that depth. Differences in radionuclide levels in sea cucumbers from shallow waters and from depth indicated that the nuclides must have transited the 2800 m distance in 7 to 12 days. This implied a sinking rate of roughly 230–400 m day$^{-1}$ and OSTERBERG, CAREY and CURL (1963) suggested sinking zooplankton fecal pellets as a possible mechanism. Later works showed conclusively that sinking rates of this order were indeed typical of natural fecal pellets (see Sections 4.1 and 4.2). Based on these findings, several studies went on to model the role of biodetritus in the vertical transport of radionuclides and trace elements (LOWMAN, RICE and RICHARDS, 1971; SMALL and FOWLER, 1973; FOWLER, HEYRAUD, SMALL and BENAYOUN, 1973; CHERRY, FOWLER, BEASLEY and HEYRAUD, 1975; HIGGO, CHERRY, HEYRAUD and FOWLER, 1977; HIGGO, CHERRY, HEYRAUD, FOWLER and BEASLEY, 1980, BEASLEY, HEYRAUD, HIGGO, CHERRY and FOWLER, 1978; FISHER, BJERREGAARD and FOWLER, 1983b; GORSKY, FISHER and FOWLER, 1984; KRISHNASWAMI, BASKARAN, FOWLER and HEYRAUD, 1985; FISHER and FOWLER, in press). Most of these studies were based on either known concentrations of radionuclides in natural biogenic debris in conjunction with various assumptions about the production and sinking of particles, or laboratory experimentation using radiotracers. The general conclusion from all these model studies was that biogenic particles are of prime importance in affecting radionuclide distribution; direct supportive evidence from the field was forthcoming.

With the advent of sediment traps and large volume filtration systems (LVFS), it has been possible to collect and directly measure radionuclide concentrations in the large, rapidly sinking particles (KRISHNASWANI, LAL, SOMAYAJULU, WEISS and CRAIG, 1976; BISHOP, EDMOND, KETTEN, BACON and SILKER, 1977; SPENCER, BREWER, FLEER, HONJO, KRISHNASWAMI and NOZAKI, 1978; BREWER, NOZAKI, SPENCER and FLEER, 1980; BRULAND, FRANKS, LANDING and SOUTAR, 1981; BACON and ANDERSON, 1982; TANAKA, TAKEDA and TSUNOGAI, 1983; FOWLER, BALLESTRA, LA ROSA and FUKAI, 1983; ANDERSON, BACON and BREWER, 1983; LIVINGSTON and ANDERSON, 1983; COALE and BRULAND, 1985; BACON, HUH, FLEER and DEUSER, 1985). These sorts of data coupled with knowledge of the radionuclide field in the dissolved and suspended particulate phase have given new insight into the processes controlling the vertical transport and distribution of elements in the sea.

Thorium isotopes have a high reactivity with suspended particles and are readily scavenged from the water column (KRISHNASWAMI, LAL, SOMAYAJULU, WEISS and CRAIG, 1976). SPENCER, BREWER, FLEER, HONJO, KRISHNASWAMI and NOZAKI (1978) trapped sinking particulates from 5367 and 5581 m in the Atlantic and found that the particulate $^{228}Th$ and $^{234}Th$ flux was derived principally from the overlying waters whereas much of the particulate $^{230}Th$ came from resuspended sediments in the nephaloid layer. From analyses of thorium parent–daughter ratio data, they concluded that most of the material trapped

TABLE 5. RESIDENCE TIMES* OF THORIUM, LEAD AND POLONIUM IN SEAWATER AT A STATION IN FUNKA BAY (FROM TANAKA, TAKEDA AND TSUNOGAI, 1983)

| Date | Sampling interval (day) | Th (day) | Pb (day) | Po (day |
|---|---|---|---|---|
| 1979 25 April | 37 | 49 (36) | – (–) | – (–) |
| 1 June | 45 | 56 (48) | – (–) | – (–) |
| 16 July | 35 | 210 (55) | – (–) | – (–) |
| 20 Aug. | 28 | 109 (125) | 64 (161) | 137 (184) |
| 17 Sept. | 65 | † (110) | † (110) | † (324) |
| 21 Nov. | 21 | 73 (91) | 130 (145) | 157 (303) |
| 12 Dec. | 76 | 27 (80) | 65 (143) | 117 (267) |
| 1980 26 Feb. | | (27) | (71) | (345) |

*Those in parentheses are the residence times calculated from a steady state model.
†Not calculated when there was exchange with the outside bay.

at that depth consisted of a primary flux derived from rapidly settling particles from the surface. Unlike the short-lived Th isotopes, $^{232}$Th is derived from terrigenous sources and is therefore associated with the clay phases in large particles (BREWER, NOZAKI, SPENCER and FLEER, 1980). They also elaborated a two-box scavenging model which accounted for the different Th scavenging rates in the euphotic zone and deep waters.

There is much recent evidence to show that in the productive surface layers, Th and other radioisotopes are rapidly removed by biological processes (BHAT, KRISHNASWAMI, LAL, RAMA and MOORE, 1969; MATSUMOTO, 1975; TANAKA, TAKEDA and TSUNOGAI, 1983; COALE and BRULAND, 1985; BACON, HUH, FLEER and DEUSER, 1985); for example in Funka Bay, Japan, the $^{234}$Th, $^{210}$Po and $^{210}$Pb inventories were at a minimum during the spring phytoplankton bloom (TANAKA, TAKEDA and TSUNOGAI, 1983). TANAKA, TAKEDA and TSUNOGAI (1983) also showed that residence times for these radionuclides varied considerably with season and concluded that steady state models were not applicable for computing residence times of these reactive nuclides in surface waters (Table 5). These authors reported residence times on the order of 60 days (median value) for $^{234}$Th. Lead-210 estimates ranged between 60–130 days and were roughly half that of $^{210}$Po. Interestingly, from known $^{210}$Po concentrations in zooplankton biodetritus, CHERRY, FOWLER, BEASLEY and HEYRAUD (1975) estimated a mixed-layer $^{210}$Po removal time by large biogenic particles alone of roughly 330 days.

Based on observed dissolved and particulate disequilibria for $^{234}$Th and parent $^{238}$U, COALE and BRULAND (1985) calculated the rate of removal from dissolved to particulate form (scavenging rate), and the removal rate of particulate $^{234}$Th in highly productive waters of the California Current. They found that the residence time of dissolved thorium ($\tau_d$) with respect to the first order scavenging rate constant varied from 6–50 days and was a function of primary productivity or particle abundance, while the very short particle residence times for $^{234}$Th (2–20 days) in the upper 50 m were a function of zooplankton grazing and fecal pellet production. Salps, which were in high concentration during one of the study periods, were believed to be responsible for the rapid production of large particles. For the surface waters they argued that irreversible scavenging onto particles and rapid removal of the particles were good assumptions, especially for highly productive waters. Direct measurements with sediment traps indicated that large particles were removing $^{234}$Th

from the overlying waters at rates ranging between 0.8–2.2 dpm $m^{-2}$ $day^{-1}$. COALE and BRULAND (1985) also found that the scavenging rate constant for $^{234}Th$ varied between 0.005 $day^{-1}$ in oligotrophic gyres to 0.02 $day^{-1}$ in areas like the California Current. That salps are effective agents in removing Th isotopes from the upper water column has recently been corroborated by KRISHNASWAMI, BASKARAN, FOWLER and HEYRAUD (1985) who found that salp fecal pellets are indeed highly enriched in thorium (e.g. 750 dpm $^{234}Th$ $g^{-1}$ dry wt).

In contrast, NOZAKI, HORIBE and TSUBOTA (1981) and BACON and ANDERSON (1982) have concluded that irreversible thorium scavenging is not taking place in the deep ocean where fine particles have residence times of 5–10 yr. In this case a reversible exchange model best describes the distributions of particulate and dissolved $^{234}Th$, $^{228}Th$ and $^{230}Th$. The rate of reversible exchange is rapid (adsorption rate constant $\sim 1\ yr^{-1}$, desorption rate constant $\sim 3\ yr^{-1}$) compared with the removal time of the particulate matter, i.e. $\sim$ 5–10 yr (BACON and ANDERSON, 1982). Interestingly, similar adsorption rate constants for Th on sediment trap material have been measured in laboratory radiotracer studies (NYFFELER, LI and SANTSCHI, 1984).

Added information on thorium behaviour was obtained from the sediment trap studies of ANDERSON, BACON and BREWER (1983) in the Atlantic and Pacific. Examination of radioisotope ratios suggested that in the open ocean rapidly sinking particles are delivering most of the unsupported $^{230}Th$ and $^{231}Pa$ to the sediments. Their data also indicated that Th is preferentially adsorbed relative to Pa; the difference in distribution coefficient on particles was about a factor of 10. Most of the $^{230}Th$ is thus scavenged and removed by sinking particles whereas less than half of the $^{231}Pa$ produced by uranium decay in the deep sea is removed by adsorption to settling particles; the remaining Pa is transported to other sinks by horizontal mixing. Seasonal studies at a deep water (3200 m) station in the Sargasso Sea indicated that chemical scavenging of $^{230}Th$ and $^{231}Pa$ responded quickly to seasonal fluctuations in the supply of particles sinking from above (BACON, HUH, FLEER and DEUSER, 1985). It was proposed that particle aggregation by physical and/or biological mechanisms, occurring at all depths in the water column, was the process responsible for the removal of these natural radionuclides to sediments. In fact, from a recent assessment of much of the published data on the disequilibrium of U/Th nuclides in the ocean, SANTSCHI (1984) concluded that particle flux was the prime variable controlling Th (IV) concentrations and residence times in the marine environment.

Large particles are effective carriers for several other reactive radionuclides. At the same sediment trap stations in the Pacific and Atlantic discussed above, it was found that dissolved uranium is fixed to biogenic particles in the surface layers and transported to the bathypelagic zone where it is remineralized (ANDERSON, 1982). ANDERSON (1982) demonstrated that the carrier phase for U was not $CaCO_3$ as expected but rather the organic content of the particles trapped at depth. Although not examined in this study, some of the U in the water column scavenged by these large particulates may be in the form of particles greater than 1 $\mu$m (see e.g. HODGE, KOIDE and GOLDBERG, 1979). Surface-introduced $^{7}Be$ is also transported to depth via sinking particulates; nothing is known about its loci in the carrier phase although it is thought to be associated with snow-like organic aggregates (TANAKA and TSUNOGAI, 1983). Lead-210 is another nuclide which is believed to be readily adsorbed onto particles and removed by sinking, even though SPENCER, BACON and BREWER (1981) suggest that boundary scavenging with diffusive and advective $^{210}Pb$ fluxes from the interior ocean may be an equally effective removal mechanism. $^{210}Pb$

concentrations in fresh, natural fecal pellets of zooplankton living in surface waters are typically about 23 dpm $g^{-1}$ dry (BEASLEY, HEYRAUD, HIGGO, CHERRY and FOWLER, 1978), and particularly noteworthy is the fact that the $^{210}Po:^{210}Pb$ activity ratio in these fecal pellets ($\sim 2.2$) is very similar to that found for suspended particulates in surface waters ($\sim 2.0$) (BACON, SPENCER and BREWER, 1976) and sediment trap material from deep water (1.5–1.7) (SPENCER, BREWER, FLEER, HONJO, KRISHNASWAMI and NOZAKI, 1978). Lead-210 concentrations in trapped particulates have been found to range from 51 to 250 dpm $g^{-1}$ dry in various basins off southern California (BRULAND, FRANKS, LANDING and SOUTAR, 1981); the higher values found in large particles from deep water are thought to result from active scavenging of dissolved $^{210}Pb$.

Transuranic radionuclides and their activity ratios have also been examined in fecal pellets and trapped particulates (HIGGO, CHERRY, HEYRAUD and FOWLER, 1977; HIGGO, CHERRY, HEYRAUD, FOWLER and BEASLEY, 1980; FOWLER, BALLESTRA, LA ROSA and FUKAI, 1983; LIVINGSTON and ANDERSON, 1983; BACON, HUH, FLEER and DEUSER, 1985). Zooplankton fecal pellets often contain relatively high concentrations at about 200 dpm $^{239,240}Pu$ and 160 dpm $^{241}Am$ $kg^{-1}$ dry (HIGGO, CHERRY, HEYRAUD and FOWLER, 1977; HIGGO, CHERRY, HEYRAUD, FOWLER and BEASLEY, 1980; FOWLER, BALLESTRA, LA ROSA and FUKAI, 1983). Examining particles in the upper few hundred meters in the northeast Pacific, FOWLER, BALLESTRA, LA ROSA and FUKAI (1983) found that both transuranic (Pu and Am) concentrations in large particles and transuranic flux tended to increase with depth to 750 m, suggesting active scavenging of the radionuclides through these strata. Americium was scavenged by these particles (principally fecal pellets) to a greater degree than $^{239,240}Pu$ as shown by increasing Am : Pu ratios with depth. Clearly, transuranics accumulated by a phytoplankton bloom observed in the surface waters were being repackaged by zooplankton grazing and rapidly removed to depth by sinking fecal pellets. Flux-derived particulate residence times for two depth intervals in the upper mixed layers (0–80 m and 0–250 m layers) were computed to be 2 and 13 yr for $^{239,240}Pu$ and 4.5 yr for $^{241}Am$.

LIVINGSTON and ANDERSON (1983) measured transuranics and other radionuclides in trapped particles from deeper waters in the equatorial Pacific and also found increasing transuranic concentration and flux to a certain depth. While transuranic concentrations in the sinking particles were roughly similar to those measured off California (FOWLER, BALLESTRA, LA ROSA and FUKAI, 1983), the fluxes were lower due to the much lower particle fluxes in the equatorial Pacific between 378 and 5582 m depth. Their deep water studies also showed a decreasing $^{239,240}Pu:^{137}Cs$ ratio with depth. LIVINGSTON and ANDERSON (1983) hypothesized a possible mechanism to explain their observation by which more $^{137}Cs$ (in an insoluble form) than $^{239,240}Pu$ was scavenged from the deep water by these particles, or that Pu was remineralized more rapidly from sinking particles than some refractory form of $^{137}Cs$, or that the two processes were working simultaneously. The $^{239,240}Pu:^{55}Fe$ ratios in particulates also decreased with depth and the authors invoked similar mechanisms to explain the decrease. They concluded that much of the dissolved Pu and Am in the deep ocean was supplied by surface-derived large particles with subsequent near-bottom dissolution. In the deep-sea, Pu flux varies seasonally in the same manner as described for Th and Pa above; during the period 1978–1980 Pu fluxes ranging between approximaely 0.008–0.025 dpm $m^{-2}$ $yr^{-1}$ were measured at 3200 m in the Sargasso Sea (BACON, HUH, FLEER and DEUSER, 1985).

Based on much of the above data and known sinking rates for planktonic debris, FISHER and FOWLER (in press) derived model calculations which suggest that the large, faster

TABLE 6. RADIONUCLIDE CONCENTRATIONS# IN ZOOPLANKTON AND THEIR PARTICULATE PRODUCTS

| Radionuclide | Macroplankton | Fecal Pellets | pCi $kg^{-1}$ dry molts ( )* | Microplankton+ |
|---|---|---|---|---|
| $^{239+240}Pu$ | 0.4 | 98 | 4.8 (90) | 4.0 |
| $^{241}Am$ | 0.09 | 72 | – | 3.2 |
| $^{210}Po$ | 1100 | 24,500 | 306 (2.5) | 3400 |
| $^{210}Pb$ | 60 | 10,400 | – | 30–1000 |
| $^{228}Th$ | 107 | 973 | – | 39 |
| $^{232}Th$ | 0.35 | 250 | 2.6 (57) | 17 |
| $^{234}Th$ | 21,170 | 338,000 | – | 6200 |
| $^{238}U$ | 21 | 520 | 245 (90) | 340 |

*Represents fraction of whole body concentration contained in molt.

+ Organisms that serve as food for macroplankton.

# Data from HEYRAUD, FOWLER, BEASLEY and CHERRY (1976); HIGGO, CHERRY, HEYRAUD and FOWLER (1977); BEASLEY, HEYRAUD, HIGGO, CHERRY and FOWLER (1978); HIGGO, CHERRY, HEYRAUD, FOWLER and BEASLEY (1980); FOWLER, BALLESTRA, LA ROSA and FUKAI (1983); FISHER, BJERREGAARD and FOWLER (1983b); KRISHNASWAMI, BASKARAN, FOWLER and HEYRAUD (1985).

sinking fecal pellets and crustacean molts have the potential to transport transuranic radionuclides to deep water and sediment, whereas slower sinking phytoplankton cells, gelatinous houses and small fecal pellets are probably involved in remineralization and recycling of these nuclides at intermediate depths. Their model underscores the potential impact of sinking zooplankton fecal material in removing transuranic elements from surface waters and indicates that residence times of these elements in surface waters are largely a function of the zooplankton biomass.

Besides direct adsorption (scavenging) of radionuclides from the water column, large biogenic particles like fecal pellets can become enriched with these radionuclides by organisms ingesting matter which has already accumulated the elements. For example, phytoplankton take up transuranics principally by surface adsorption and exhibit relatively high concentration factors ranging from $10^5$–$10^6$ (FISHER, BJERREGAARD and FOWLER, 1983a). Zooplankton feeding on phytoplankton strip the essential nutrients and organic constituents from the cells and leave the more refractory, hard parts laden with transuranics as a residue in the fecal pellets. Thus freshly-excreted fecal pellets can contain higher transuranic levels on a unit weight basis than the food which formed them (HIGGO, CHERRY, HEYRAUD and FOWLER, 1977; FOWLER, BALLESTRA, LA ROSA and FUKAI, 1983). Examples of radionuclides concentrations in zooplankton, their food, fecal pellets and molts are given in Table 6.

There is also evidence that in the absence of further radionuclide scavenging, slowly decomposing fecal pellets can release radionuclides back to the water column (Table 4). Polonium is leached at a relatively rapid rate as reflected by a half-time for loss of only 3.5 days (HEYRAUD, FOWLER, BEASLEY and CHERRY, 1976). On the other hand, results from radiotracer studies suggest that Am and reduced Pu (+4) may be retained for much longer periods of time, e.g. half-times for loss of several weeks (FOWLER, HEYRAUD and CHERRY, 1976; FISHER, BJERREGAARD and FOWLER, 1983b). Decomposition of pellets and other biogenic debris with concomitant transuranic resolubilization could account in part for the presence of the subsurface maxima of Pu and Am that have been observed throughout the Pacific, however, more study is needed on transuranic concentrations in both the fine

suspended particles and large particulates in order to elucidate the exact mechanism responsible for this feature (FOWLER, BALLESTRA, LA ROSA and FUKAI, 1983; FISHER and FOWLER, in press).

## 7. RECOMMENDATIONS FOR FUTURE STUDY

(1) The inherent problems with sediment trapping notwithstanding, measurements of element concentrations in sediment trap samples in conjunction with similar measurements in the dissolved and suspended particulate phases offer much promise for elucidating the mechanisms responsible for maintaining observed element distributions throughout the water column.
(2) In addition to routine stable element measurements in these materials, more emphasis should be placed on natural series and artificial radionuclides, in particular activity ratios of selected radioisotopes, since their differing physical half-lives and chemical behaviour can be excellent tracers for discerning temporal and spatial scales of a given process.
(3) Detailed characterization of the material caught in sediment traps with simultaneous characterization of biogenic particles produced over the traps will allow further assessment of the role of large biogenic particles in effecting the vertical transport of elements. As fecal pellets are often the most important biogenic aggregate involved in these processes, characterizations of this nature could be helpful in identifying the principal organisms responsible for their production in a given area.
(4) Efforts should be made in the field and in the laboratory to study element adsorption (scavenging) and desorption processes during decomposition of sinking biogenic particles. An initial understanding of the rates involved can be gained from carefully designed, laboratory radiotracer studies.
(5) Although difficult to characterize in terms of its origin, the ubiquitous "marine snow" has been shown to be a prime mediator of vertical transport of many elements and compounds. The production, behaviour and fate of this material should be examined in more detail.
(6) Because of the predominantly organic nature of large biogenic particles, detailed analyses of their organic constituents will be a key tool for studying the origin of these particles as well as their role in the remineralization and cycling of materials. In addition knowledge of the rates of degradation effected by bacterial and microheterotrophic activities is essential for assessing the lifetime and ultimate fate of these particles.
(7) More effort should be made to quantify the influence that the vertical movements of active, grazing organisms have on the spatial and temporal distribution of large particules and, hence, organic and inorganic materials in the water column.

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