Radiolaria: Major exporters of organic carbon to the deep ocean

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[1]   Very large pulses of particulate organic matter intermittently sink to the deep waters of the open ocean in the Northeast Atlantic. These pulses, measured by moored sediment traps since 1989, can contribute up to 60% of the organic flux to 3000 m in a particular year and are thus a major cause of the variability in carbon sequestration from the atmosphere in the region. Pulses occur in the late summer and are characterized by material that is very rich in organic carbon but with low concentrations of the biominerals opal and calcite. A number of independent lines of evidence have been examined to determine the causes of these pulses: (1) Data from the Continuous Plankton Recorder (CPR) survey show that in this region, radiolarian protozoans intermittently reach high abundances in the late summer just preceding organic pulses to depth. (2) CPR data also show that the interannual variability in radiolarian abundance since 1997 mirrors very closely the variability of deep ocean organic deposition. (3) The settling material collected in the traps displays a strong correlation between fecal pellets produced by radiolaria and the measured organic carbon flux. These all suggest that the pulses are mediated by radiolarians, a group of protozoans found throughout the world's oceans and which are widely used by paleontologists to determine past climate conditions. Changes in the upper ocean community structure (between years and on longer timescales) may have profound effects on the ability of the oceans to sequester carbon dioxide from the atmosphere.

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1.   Introduction

[2]   The past few decades have seen a massive increase in interest in the sequestration of carbon from the atmosphere by the oceans. A key factor in CO_2 drawdown is the gravitational settling of particulate organic carbon (POC) from the upper ocean and the relationship of this flux with that of particulate inorganic carbon (PIC), mainly as calcite, both of which are of biological origin [*Holligan and Robertson*, 1996; *Antia et al.*, 2001; *Ridgwell*, 2003]. The key to enhanced sequestration is not only elevation of the downward flux of carbon but also increase of the POC: PIC ratio of the material produced in the upper ocean. The reason for this is that production of organic matter removes CO_2 from solution, while the process of calcification decreases surface ocean alkalinity, and in addition releases CO_2 to solution thereby partly counteracting this biological pump [*Iglesias-Rodriguez et al.*, 2002]. The relative partial pressures of CO_2 in the atmosphere and seawater determines the direction of the CO_2 flux and the potential for carbon sequestration is therefore influenced by the balance between calcifying and noncalcifying organisms. Sequestration is therefore enhanced if POC is synthesized in preference to PIC (i.e., if noncalcifying organisms dominate net production). The majority of synthesized POC is remineralized to dissolved inorganic carbon (DIC) in the upper few hundred meters of the ocean as a result of biological activity. However, some of it escapes and any material that is transported below the maximum depth of winter mixing (100–800 m) is isolated from atmospheric exchange for climatically relevant timescales of the order several centuries [*Antia et al.*, 2001].

[3]   Material collected by time series sediment traps provides not only a direct measure of the downward particle flux but also crucial information on the chemical and microscopic characteristics of the sedimenting material. In general the POC:PIC ratio of this sinking material decreases with depth to values of about 1.0 at 3000 m because of the fact that POC is remineralized at a faster rate than PIC dissolves [*Lampitt and Antia*, 1997]. In many tropical and subtropical environments this ratio changes little seasonally or between years, with POC contributing about 6% to the dry weight flux (DW) [*Lampitt and Antia*, 1997; *Neuer et al.*, 1997; *Wong et al.*, 1999; *Conte et al.*, 2001; *Waniek et al.*, 2005]. However, this is not always the case and in the Northeast Atlantic, at the site of the JGOFS North Atlantic Bloom Experiment (1989–1991) (Joint Global Ocean Flux Study) there was an example of a mass sedimentation event characterized by very high POC content, up to 25% of DW and a POC:PIC ratio of 9.0

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[*Newton et al.*, 1994]. The factors responsible for this mass flux of organic carbon could not be determined at the time and microscopic analyses of the material collected shed no significant light on the vehicles responsible for this flux. The amorphous gelatinous matrix collected in the traps gave no clues as to its origin. Nevertheless the event was of major significance with about 60% of the annual POC flux occurring in this one event lasting only a few weeks. At the same location, a few years earlier, Franz Riemann collected some phytodetrital aggregates from the surface of seabed cores and came to the highly significant conclusion that phaeodarian radiolarians were important in the formation of fast-sinking gelatinous aggregates. This, he speculated, could be relevant to the rapid sedimentation of material previously reported [*Lampitt*, 1985]. He stated that the most prominent components of the material in terms of numbers and volumes were small fecal pellets [*Gowing and Silver*, 1985] having a diameter of 5 to 80 μm, and consisting of unidentifiable detrital material, folded membranes, and masses of green chlorophyte cells. "The fecal pellets were identical to those found inside phaeodaria (radiolaria), which were collected at the same time in the water column." [*Riemann*, 1989, p. 533].

[4] Radiolarians are exclusively marine planktonic single-celled organisms (protists). They usually dwell in open-ocean waters, and are rare near the coast. Individual radiolarians are normally in the size range of 10–1000 μm, but some form colonies many centimeters in length. As with most other related planktonic protists, radiolarians are omnivorous particle feeders which catch their prey (small algal cells, other protists, small crustaceans, etc.) with the aid of sticky cytoplasmic strands protruding from the cell body, the pseudopodia [*Swanberg*, 1983; *Anderson*, 1993; *Michaels et al.*, 1995; *Dennett et al.*, 2002].

[5] Some species of radiolarians secrete siliceous skeletons while others are characterized by "enormous gelatinous and frothy peripheral structures (1.5–15 mm diameter)" [*Anderson*, 1993, p. 34]. They are closely related to foraminifera with calcite tests and to acantharia with tests of strontium sulphate. Two major groups, or superorders, are recognized within the radiolaria: the polycystina and the phaeodaria. Among other traits, the two differ in the composition of their skeletons: while in the polycystina these are made up of amorphous silica, in the phaeodaria the silica is supported by an organic matrix. Representatives of both groups sink to the ocean floor upon death, but because of differences in their composition, polycystine skeletons can withstand dissolution during and after descent while phaeodarian skeletons usually dissolve before reaching the bottom [*Takahashi et al.*, 1983]. Thus, large areas of the ocean floor are covered with a thick layer of polycystine shells known as radiolarian ooze.

[6] Polycystine radiolarians provide one of the few tools available for investigating past climate changes in the oceanic realm. The techniques are based on comparisons of the radiolarian assemblages in the water column and/or in the topmost sedimentary layer (assumed to reflect the living populations), with those retrieved from sediments buried deeper under the seafloor (and therefore older in age). Each
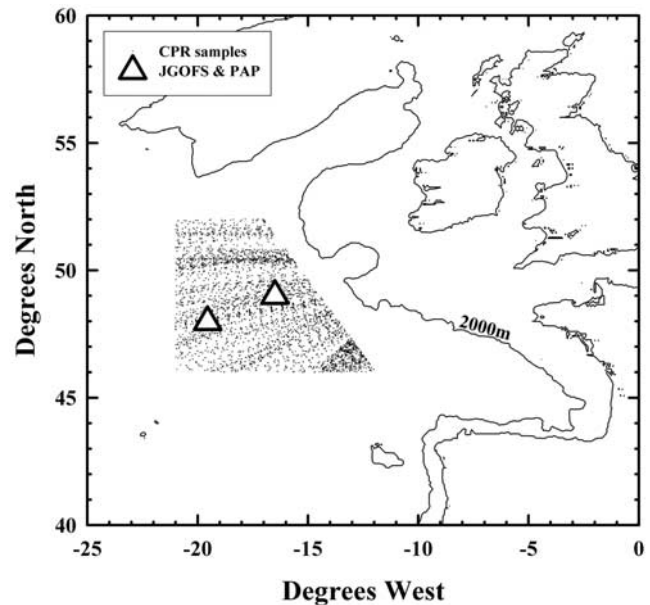

Figure 1. The two sediment trap mooring locations (PAP being to the east) and points where samples were taken by the Continuous Plankton Recorder (CPR) for assessment of the abundance of radiolaria and foraminifera. These points represent the middle of 15 km long sections of the CPR transects. The continental slope is indicated by the 2000 m contour.

assemblage is characterized by a particular combination of species in more or less defined proportions. Because radiolarians are sensitive to environmental conditions, different species and species proportions in the assemblages are indicative of different living conditions, in particular water temperature and productivity and from this, historical trends can be inferred reaching as far back as the start of the Cambrian period (570 M years BP). A crucial assumption in such palaeoreconstruction is that the relationship between polysystine radiolarian flux to the seafloor (and preservation) and the upper water column environmental conditions has not changed with time [e.g., *Lazarus et al.*, 2006].

[7] The deep seafloor of the Northeast Atlantic has experienced significant regime shifts over the past 2 decades [*Billett et al.*, 2001; *Wigham et al.*, 2003] and the hypothesis advanced is that this is related to quantitative and qualitative changes in the downward flux of organic material, although the exact mechanism has not been determined. Changes in the species composition of the upper ocean are likely to have a significant effect on the deep ocean downward flux [e.g., *Boyd and Newton*, 1999] but the ways in which this is manifest and the affects of such changes have usually been impossible to determine with any confidence.

[8] In this paper we examine the temporal trends in deep ocean downward flux of POC in the context of observations on the variability of upper ocean populations of radiolaria. This is to determine if these organisms could be responsible
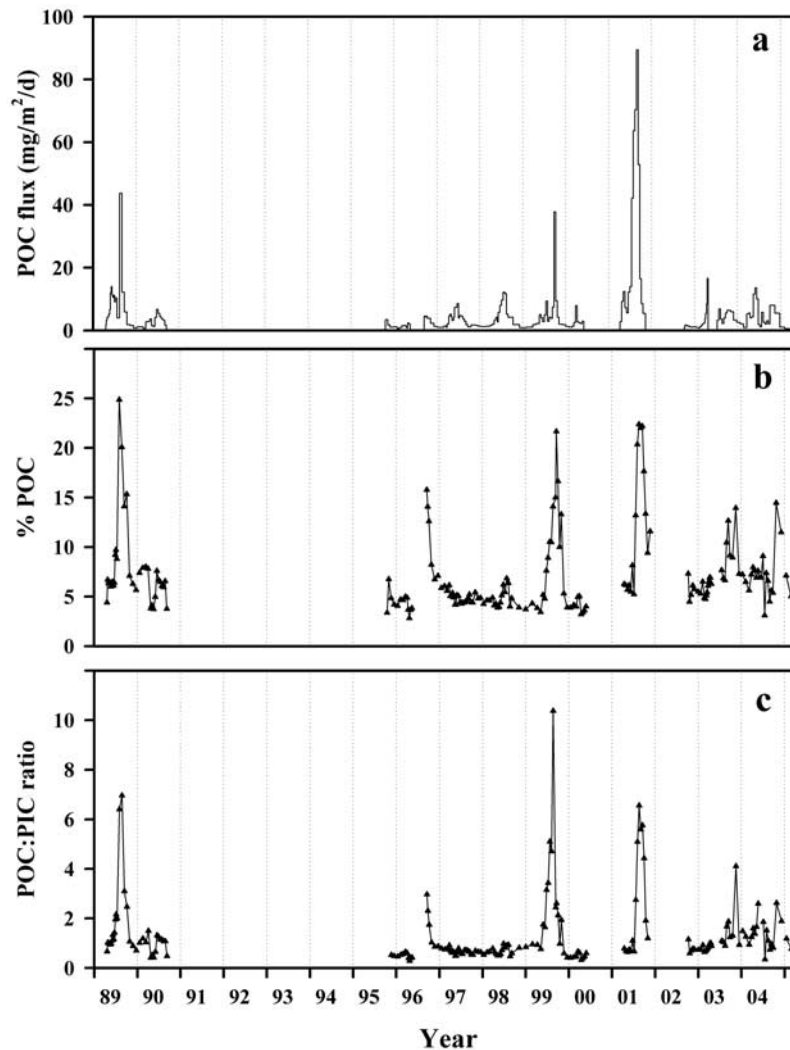
Figure 2. Temporal trend at 3000 m depth in (a) POC flux, (b) POC as a percent of the dry weight of material, and (c) POC: PIC ratio. Data in Figures 2b and 2c are expressed at the midpoint of the sampling period of the trap cups.

for the massive depositions of highly enriched material that are an intermittent feature of the Northeast Atlantic.

2. Material and Methods

2.1. Particle Flux

[9] The downward flux of particulate material has been measured at a depth of about 3000 m over the Porcupine Abyssal Plain (PAP) in a water depth of 4800 m for much of the period since 1989. This has been achieved using time series sediment traps attached to a bottom-tethered mooring. These devices collect sinking particles in a funnel of surface area 0.5 m^2 below which is a carrousel carrying a number of sampling cups filled with formalin preservative in a slightly hypersaline solution. The carrousel rotates at predetermined time intervals (typically 2 or 4 weeks) to give a time series of downward flux. The material collected in the sample cups has been processed in a consistent manner over the years to provide flux in terms of dry weight, organic and inorganic

carbon, opaline silica and opportunistically, various other components of the material. [*Newton et al.*, 1994; *Lampitt et al.*, 2001]. In 1989 and 1990 the traps were deployed at about 48°N 20°W (JGOFS NABE) but subsequently (1996–2005) were at 49°N 16.5°W (PAP) (Figure 1). In 1990 microscopic analysis of the material was carried out to determine the abundance of minipellets defined as fecal pellets of size 5–50 μm.

2.2. Upper Ocean Plankton Community

[10] Since 1949 zooplankton have been collected in the Northeast Atlantic using a net towed at a depth of 10 m behind merchant ships. This has constituted the Continuous Plankton Recorder (CPR) survey, the longest-running survey of its kind in the world. The net comprises a long strip of silk with an effective mesh size of 270μm which is mechanically driven between two spools with only a small portion exposed to the collecting funnel at any one time. This then provides numerous samples along each transect
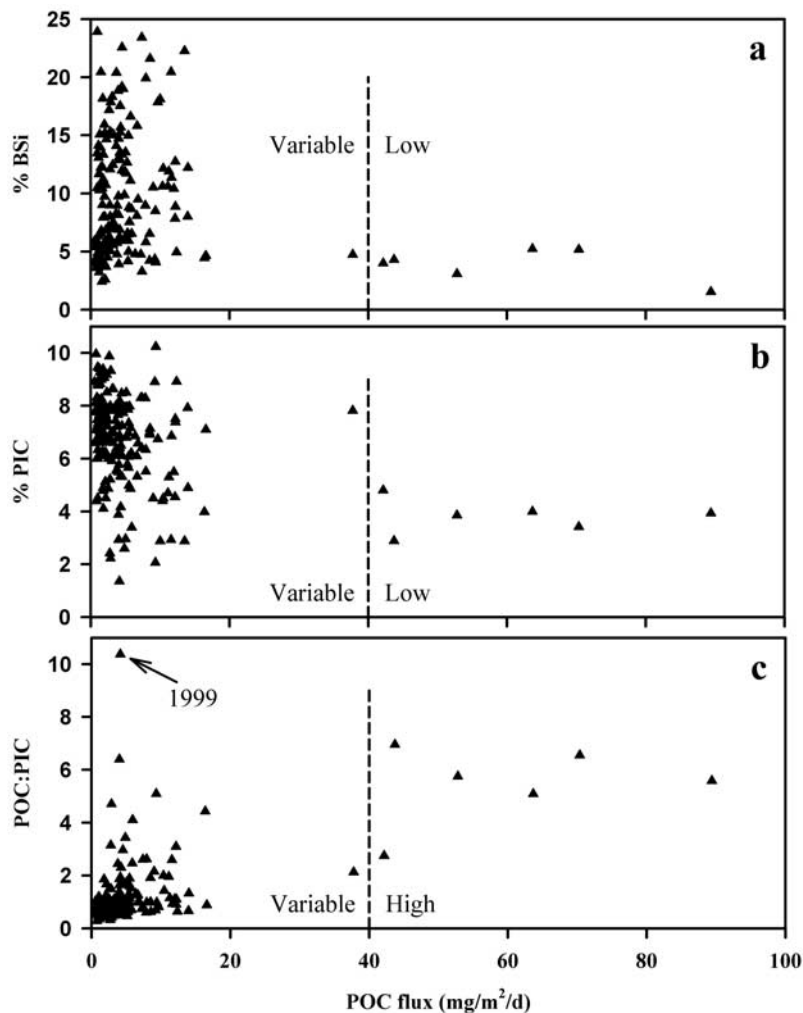
Figure 3. Relationship between POC flux and (a) the concentration of BSi and (b) the concentration of PIC (both are expressed as a percentage of the dry weight of these elements). (c) POC: PIC ratio.

and hence information on the spatial distribution of the plankton community [*Batten et al.*, 2003]. On return to shore the silk is cut into sections, representing 15 km of distance traveled, and the collected specimens enumerated.

[11] The spatial variability of the planktonic community along these shipping lanes is large but in order to examine temporal variability in the region of study, an area was selected that is unlikely to be influenced by the continental slope or major frontal regions but is still large enough to obtain sufficient sample numbers (Figure 1). Since 1997 the sampling intensity in the PAP region has been increased substantially and furthermore the analysis of the material collected has, since that time, been expanded to include the radiolaria, the larger specimens of which will be retained by the silk. The larger specimens of foraminifera are also collected and these have been enumerated since 1993. The data are archived and freely available at http://www.sahfos.ac.uk/.

[12] Chlorophyll concentration was calculated using the satellite based SeaWiFS (Sea-viewing Wide Field-of-view Sensor) merged into 8-day composites at a resolution of

18 km, taking into account dissolved organic material. Data were extracted from a circle around the sediment trap mooring of radius 200 km which is considered to be the source location for most of the material entering the trap at 3000 m.

3. Results and Discussion

[13] The downward flux of POC at 3000 m was sometimes enhanced as a result of an increase in dry weight flux but more particularly by a massive increase in the richness of the material deposited, from a normal POC concentration of about 6% of DW up to 25% (Figure 2). Such levels are almost unheard of in other regions of the world where similar sediment trap studies have been carried out and where values in the range 4 to 10% are the norm [*Lampitt and Antia*, 1997]. These peaks occur exclusively in the late summer and autumn and are not only characterized by high POC content but by low concentrations of opal expressed as biogenic silica (BSi) and PIC (Figure 3). Above a POC flux of 40 mg/m^2/d the contribution of BSi and PIC
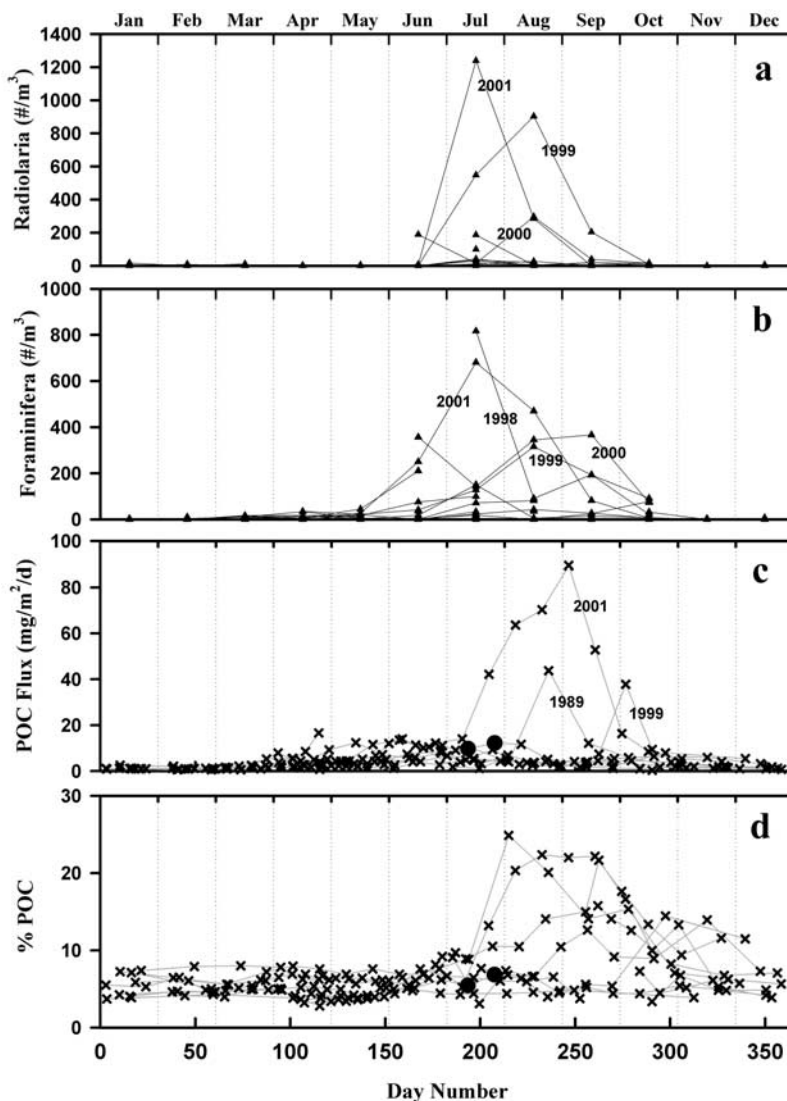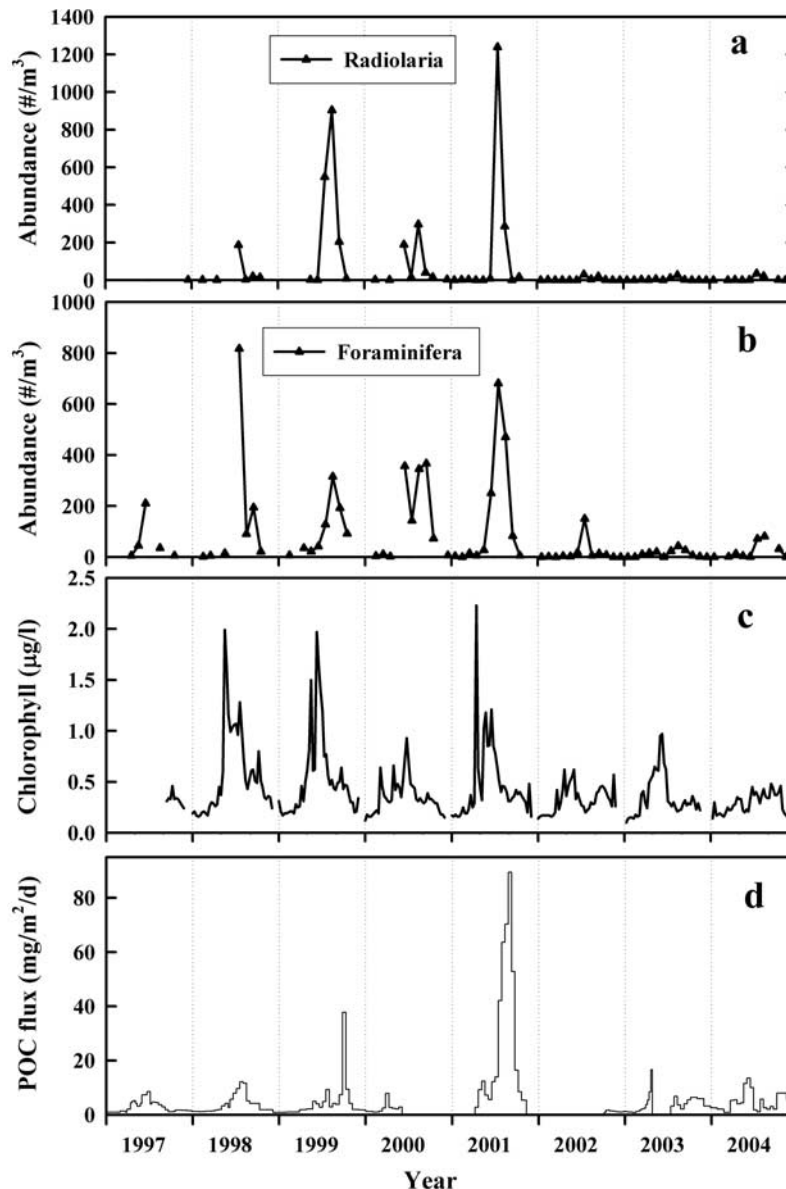
Figure 4. Seasonal variation in (a) abundance of radiolarian, (b) abundance of foraminifera, (c) POC flux at 3000 m depth, and (d) POC as percent of dry weight of material in the traps. The solid circles in Figures 4c and 4d represent the data from July 1998 when foraminifera were particularly abundant in the upper ocean as discussed in section 3.

were very constant at about 4% of dry weight for both elements and which are near to the lowest recorded in the sediment trap record at the PAP site. During the 9 years for which good data are available in the late summer, this organic-rich deposition has occurred three times; 1989, 1999 and 2001 associated with large POC flux and several other times; 1996, 2003 and 2004 when there was high POC concentration but no enhanced flux (Figure 2).

[14] These data pose several questions about the origin of the material and the implications for our understanding of the factors that affect downward particle flux. They may also affect our interpretation of sediment down core variations of palaeoproxies if subtle changes in the upper ocean plankton community should cause a large change to the depositional flux and hence the sedimentary record.

[15] The CPR provides a unique insight into seasonal and long-term trends in planktonic abundance and in this case, after reviewing the abundance data of 25 biotic categories it was immediately clear that the foraminifera and radiolaria at 10 m depth have seasonal maxima in the late summer just prior to the massive organic depositions at 3000 m (Figure 4). The time lag is about 6 weeks but as the CPR are monthly averages and the particle flux data usually have a resolution of 2 weeks, the precision in such estimates is low.

[16] Population growth of foraminifera and radiolaria was noted at the JGOFS NABE site during September 1996 and in the case of the foraminifera this was thought to be due to entrainment of deeper nutrient-rich water which stimulated phytoplankton growth while the phytoplankton biomass was kept in check by grazing [Schiebel et al., 2001]. In

Figure 5. Temporal variation in (a) abundance of radiolarian and (b) abundance of foraminifera, (c) mean chlorophyll concentration around the PAP site, and (d) POC flux at 3000 m.

addition to the seasonal trends, the longer-term record since 1997 for POC flux and protistan abundance show extraordinary interannual similarity (Figure 5) with the high abundances and flux in 1999 and 2001and low abundances and flux in 1998, 2003 and 2004.

[17] The obvious explanation for this association between deep ocean flux and the protistan community is that some ecological factor such as enhanced productivity caused an increase in abundance of radiolaria and foraminifera as well as in deep ocean flux. We have examined the temporal variability of over 20 biotic categories including diatoms, dinoflagellates, chaetognaths and all the common species of copepod and no similar seasonal or interannual patterns were found. Satellite-derived chlorophyll variations demonstrate some similarities in interannual pattern with high

levels in 1998, 1999 and 2001 and low concentrations in the last 3 years (Figure 5c) [*Hartman et al.*, 2009] also characterized by very low abundances of foraminifera and radiolaria (Figures 5a and 5b). Chlorophyll maxima occur in the spring and one might come to the conclusion that this indicates that such springtime events have a prolonged effect on the upper ocean leading for instance to growth in the late summer of populations of protists. This may indeed be the case but it should be borne in mind that the satellite only provides data on the near surface layer whereas the phytoplankton below this layer (eg at 40 m) exert a substantial effect on upper ocean biogeochemistry and tend to have maxima later in the year [*Hartman et al.*, 2009].

[18] Our evidence, albeit circumstantial, strongly indicates that the protists are key factors in the enhanced autumnal
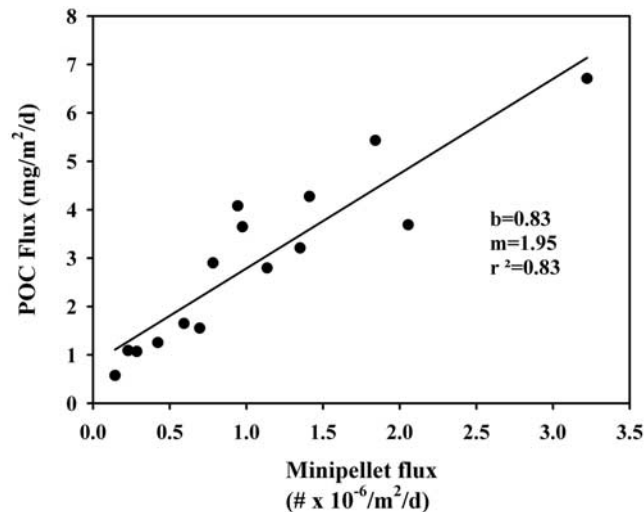
Figure 6. Relationship between downward flux of mini-pellets and POC during 1990 at 3000 m depth.

POC flux in the region. The final evidence to support this hypothesis comes from the microscopic analysis. In years with high flux, the material is extremely difficult to analyze microscopically because of its agglutinated nature and such analysis has only been possible for the material collected in 1990 which was not a year characterized by high POC flux. Nevertheless during 1990 the relationship between POC flux and the flux of minipellets, thought to be produced by protists is extremely close, with a R^2 value of 0.83 (Figure 6).

[19] In spite of the fact that sediment traps have been widely used for the past 2 decades with large data sets on chemical fluxes, insights into the species of organism that contribute to the flux of organic carbon has been very limited. The reason for this is that usually it is impossible to identify most of the material collected to species origin (whether body parts or fecal). PIC is more easily categorized as it is in the form of coccolithophores, their liths, foraminifera or pteropod shells. There are several examples where particular faunal groups have made a major contribution to POC flux, in particular gelatinous organisms [*Perissinotto and Pakhomov*, 1998; *Billett et al.*, 2006] but in the majority of cases the species contributing most to flux are unknown.

[20] The evidence we present is highly compelling that there is an intimate association between autumnal pulses in the flux of organic rich material to the deep water mass and the abundance of protists in the overlying planktonic community. The issue now is to determine which protists are most likely to be responsible. The two likely candidates for involvement are the foraminifera and the radiolaria both of which follow similar seasonal and interannual patterns. Even though the two groups have radically different mineral compositions they occupy similar trophic positions [*Anderson*, 1993] feeding as they do in similar ways.

[21] Although foraminifera capture food using rhizopods which will have a high organic content, the POC: PIC ratio of living specimens is low because of their heavy calcite

tests. Furthermore these tests are unlikely to dissolve before reaching the sediment traps, whereas the PIC concentration in the collected material at these times of very high POC flux was at its lowest level (Figure 3b). An additional point is that in 1998 the abundance of foraminifera was at its highest in July while POC flux at 3000 m was not particularly high at about 10 mg m^{-2} d^{-1} and POC concentration about 6% DW (solid circles in Figures 4c and 4d). It therefore seems unlikely that foraminifera were intimately involved in the autumnal POC flux events observed.

[22] The same might be said for the radiolaria as the BSi concentration was similarly at a minimum during these POC flux peaks (Figure 3a). Unfortunately, information is not available on the species of radiolarian present in the CPR samples but a viable hypothesis is that they were either species that do not secrete a siliceous test or were phaeodarians, the tests of which dissolve rapidly as mentioned above. It is possible that the environmental conditions that are responsible for the seasonal and interannual variations in the radiolarian populations also promote downward flux of a gelatinous and unidentifiable material in the deep sediment traps. Indeed the enhanced chlorophyll concentration suggests that productivity is high in years which are characterized by enhanced POC flux. However, this would not, on its own, have produced the gelatinous material in the sediment traps. As mentioned above the enhanced chlorphyll tends to be in the spring and furthermore is only enhanced by a factor of about two while the flux was enhanced by much more. Clearly another link in the chain is required and we believe the role of phaeodarian radiolaria to be highly significant.

[23] *Armstrong et al.* [2002] proposed that the correlation between the flux of POC and that of biominerals (calcite and silicate) indicated a causal relationship and that the enhanced specific gravity of the biominerals over organic carbon increased the sinking rate of particles and led to greater POC export. More recently it has been suggested that the biominerals are in fact simply caught up in the sticky matrix of organic matter as it settles and that they do not necessarily enhance flux [*Passow and De La Rocha*, 2006]. The results we have presented demonstrate conclusively that massive POC flux can and does occur in the Northeast Atlantic during times when biomineral flux is very low; our results are thus consistent with the hypothesis of *Passow and De La Rocha* [2006]. As the material is of such high POC concentration, it is likely that it has undergone little degradation during settlement and therefore had a very high sinking rate. Because of postcollection changes, it is not possible to state with certainty the size or sinking rate of the particles that originally settled into the sediment traps. However, on occasions when the massive organic flux pulses occurred, the material in the cups had a granular appearance with the mucous particles appearing to be several millimeters in diameter. If this is the form in which they settled through the water column, one would expect the sinking rate to be high and hence subject to limited processing during descent.

[24] The implications from the hypothesis we present are profound in that it first enhances our belief that the structure of the upper ocean planktonic community can have a major

influence on the sequestration of carbon from the atmosphere. As described above, sequestration will be enhanced if either carbon flux increases (with constant POC: PIC ratio) or if the POC: PIC ratio increases (with constant carbon flux). As can be seen from Figure 2c, the autumnal POC peaks are characterized by increases in POC: PIC ratio from about 1 to 8–11. Again during times of high POC flux, POC: PIC ratios are consistently high (Figure 3c) although interestingly in 1999, flux with the highest POC: PIC ratio occurs before the major peak in POC flux. If the radiolaria are responsible for such a major shift in the POC:PIC ratio of the sedimenting material and for deposition of massive quantities of POC, small changes in the upper ocean community could have major changes in carbon sequestration. Knowledge of the population dynamics of radiolaria is at present poor and the reasons for the very large interannual variations we report cannot be surmised although there is clearly a link to the chlorophyll concentration and hence probably to primary production. Furthermore the CPR samples are from the single depth of 10 m so we do not have information about their population size over their entire depth range.

[25] In addition to the significance of our observations on the effect of upper ocean communities, it casts some doubt on palaeoreconstructions based on the abundance of polycystine radiolaria in the sedimentary record. Even a comparatively small change from one group of radiolaria to another may have a major influence on the sedimentary record and until the causes of the large interannual variability can be determined and the reasons why one class of radiolaria is more successful than another, some caution should be applied to reconstructions based on such palaeoproxies.

4. Conclusions

[26] The significance of the observations we present here on large autumnal depositions of organic carbon and the conclusions about the fauna responsible for this are far-reaching.

[27] 1. The massive organic carbon deposition and high POC concentration recorded in 1989 during the JGOFS North Atlantic Bloom Experiment was not an extraordinary event but has been repeated several times since then and may in fact be a common but intermittent feature of the temperate North Atlantic.

[28] 2. The very high POC:PIC ratio of this material implies substantial sequestration of atmospheric CO_2 during the late summer period but with significant interannual variability.

[29] 3. A high proportion (<60%) of the annual POC flux can occur at times when the mineral flux is at its lowest, a feature that is in contradiction to implication from the "ballast hypothesis" which is that biominerals are required for high flux of POC.

[30] 4. Changes to the planktonic community structure such as may occur in response to global environmental perturbations may have a very great effect on the ocean's ability to sequester CO_2 from the atmosphere. At present it is not possible to determine if the anticipated changes to mixed layer depth, water temperature and productivity are likely to enhance or depress populations of radiolaria and hence sequestration flux but the very great interannual

variation in POC flux highlights the magnitude of this potential change.

[31] 5. If the implications from these observations can be corroborated by further analyses, additional care may be required when using radiolarian abundance and diversity in sediment cores as palaeoproxies.

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