Transformations of biogenic particulates from the pelagic to the deep ocean realm


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Abstract

This overview compares and contrasts trends in the magnitude of the downward Particulate Organic Carbon (POC) flux with observations on the vertical profiles of biogeochemical parameters in the NE subarctic Pacific. Samples were collected at Ocean Station Papa (OSP, 50°N, 145°W), between 18–22 May 1996, on pelagic stocks/rate processes, biogenic particle fluxes (drifting sediment traps, 100–1000 m), and vertical profiles of biogeochemical parameters from MULVFS (Multiple Unit Large Volume Filtration System) pumps (0–1000 m). Evidence from thorium disequilibria, along with observations on the relative partitioning of particles between the 1–53 µm and > 53 µm classes in the 50 m mixed layer, indicate that there was little particle aggregation within the mixed layer, in contrast to the 50–100 m depth stratum where particle aggregation predominated. Vertical profiles of thorium/uranium also provided...
evidence of particle decomposition occurring at depths ca. 150 m; heterotrophic bacteria and mesozooplankton were likely responsible for most of this POC utilisation. A water column carbon balance indicated that the POC lost from sinking particles was the predominant source of carbon for bacteria, but was insufficient to meet their demands over the upper 1000 m. While, the vertical gradients of most parameters were greatest just below the mixed layer, there was evidence of sub-surface increases in microbial viability/growth rates at depths of 200–600 m. The C:N ratios of particles intercepted by free-drifting and deep-moored traps increased only slightly with depth, suggesting rapid sedimentation even though this region is dominated by small cells/grazers, and the upper water column is characterised by long particle residence times ( > 15 d), a fast turnover of POC (2 d) and a low but constant downward POC flux.

1. Introduction

The fate of particulate organic matter originating in the upper ocean is controlled by the relationship between pelagic particle production and the resulting transformations of such particles in transit to the deep ocean (Peinart et al., 1989; Silver and Gowing, 1991). The magnitude of change in biogenic particle flux with depth has been estimated primarily using sediment traps deployed at a range of depths (e.g. Martin et al., 1987). In several cases the timing and the magnitude of pelagic events such as the spring bloom, as recorded by primary production measurements, have been compared and contrasted with the corresponding signal at depth in free-drifting and/or deep-moored sediment traps (Asper et al., 1992; Karl et al., 1996). However, while POC fluxes from traps provide a record of the attenuation of the bulk particulate signal, they offer few insights into the processes that may influence the transformation of biogenic particles as they sink to depth (Boyd and Stevens, submitted).

In the last decade, studies have elucidated processes that will influence strongly both the magnitude of the downward particle flux and the depth strata at which process-specific particle transformations occur in the water column. In the mixed layer region, Boyd and Newton (1995,1999) reported that planktonic community structure may strongly influence the magnitude of the downward particulate flux. Indeed, based on marine snow vertical profiles from mounted underwater camera systems, the upper ocean is the primary site for aggregate formation in the NE Atlantic (Lampitt et al., 1993a). Using microscopy, such aggregates have been shown to be heterogeneous in nature (Lochte and Turley, 1989; Lampitt et al., 1993b). Others have revealed the importance of phytoplankton abundance/coagulation (Jackson, 1990), biological glues (Dam and Drapeau, 1995), and other modes of particle interactions (see reviews by Turley, 1992; Kepkay, 1994) in the initiation of aggregation ‘events’ between particles in the upper ocean. In this zone, radionuclide studies have provided estimates of particle residence times (Coale and Bruland, 1985), and disaggregation rate constants (Murnane et al., 1996).
In addition to studies of particle formation, other research has focussed on the factors controlling the breakdown of particles, such as heterotrophic bacterial activity, or the activity of interzonal migrating mesozooplankton (Longhurst et al., 1990). There are marked vertical gradients in bacterial activity (Hoppe et al., 1993) and the degree of particle solubilisation over the upper 500 m depth stratum (Karl et al., 1988; Smith et al., 1992). Azam et al. (1995) and Christian and Karl (1995) have identified and characterised bacterial enzyme systems responsible for solubilisation processes. Giovannoni et al. (1990,1995) and Fuhrman and Davis (1997) have reported the existence of distinct bacterial groups occupying discrete depth strata. Such processes of particle aggregation and breakdown may be reflected by the observed vertical gradients of biological, biochemical and/or geochemical parameters. Thus, changes with depth in the signatures associated with microbial activity (Karl and Knauer, 1984), organic constituents (Wakeham and Canuel, 1988), stable isotopes (Altabet et al., 1991), and particle populations (Bishop et al., 1999) may be indicative of changes in the dominant particle transformation processes throughout the water column.

Although the 30 year Ocean Station Papa (OSP) time series is relatively comprehensive for the open ocean (Banse, 1991), virtually all of these data were obtained from the upper 200 m. Similarly, the SUbarctic Pacific Ecosystem Research (SUPER) programme focused primarily on pelagic foodweb processes (Miller, 1993). Prior to the present study, the main biogeochemical water column research conducted at depth in this region was by the VERTical EXchange (VERTEX) programme (Martin et al., 1987). In addition, Takahashi (1986) analysed data obtained from a deep-moored sediment trap deployed at OSP in the 1980s. Thus, relatively few studies in this region have examined biogeochemical processes at depth. Joint consideration of the vertical gradients of biogenic particulate fluxes and of the processes transforming particles within depth strata may lead to a better mechanistic understanding of the factors controlling downward POC flux in this region.

The data presented here represent a synthesis of the majority of the vertical process studies from surface waters to ca. 4 km depth carried out during a 5-d occupation of OSP as part of the Joint Global Ocean Flux Study-Canada (JGOFS-Canada).

2. Methods/datasets

Data were available on vertical processes at five stations from the coastal (station P04, 48 39°N, 126 40°W) to the open ocean (OSP, 50°N, 145°W); see map in Whitney and Freeland (1999) from six cruises between September 1995 and June 1997. Consideration of all data was beyond the scope of this overview, which instead attempts to synthesise data obtained at OSP between 18–22 May 1996. Although the synthesis is based on a 5-d period at one location, it is more than likely representative of a larger region of ocean, over a wider time period. The OSP region is characterised by weak upper ocean current flows (which decrease with depth) from west to east (Tabata, 1975; Bograd et al., 1999), and pelagic biological observations to the west and the east of OSP indicate that the waters are High Nitrate Low Chlorophyll (HNLC) in character (see discussion in Boyd et al., 1998). Bishop et al. (1999) report that based on
surveys of POC levels, using optical characterisation, the POC field was relatively uniform in the vicinity of OSP (scale of kms) in May 1996. Furthermore, OSP is characterised by relatively low seasonality with respect to phytoplankton processes compared to other regions such as the NE Atlantic (Parsons and Lalli, 1988). The low seasonality at OSP likely impacts that observed for foodweb and vertical processes (see Table 1).

The majority of the data presented are subsets of other studies in this volume, and the complete dataset from stations P04-OSP in all seasons, and the methodologies employed, are presented in the respective papers (Table 2). The data presented may be divided into three groups: firstly the potential source material for particulate aggregates, as represented by particles that are components of (such as ciliates) or are derived from (such as faecal pellets) the pelagic foodweb and associated trophic interactions. Such particles will henceforth in this study be referred to as the ‘living’ particle population. Secondly, data relating to particle aggregation in the upper ocean (0–100 m depth) such as \( ^{234}\)Th activity distributions, or size distributions for Particulate Organic Carbon (POC); both obtained (as were the majority of the data

Table 1

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Seasonal variation</th>
<th>Data source</th>
</tr>
</thead>
<tbody>
<tr>
<td>(A)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chlorophyll (a)</td>
<td>2 fold</td>
<td>Parslow (1981); Boyd and Harrison (1999)</td>
</tr>
<tr>
<td>Primary production</td>
<td>3–4 fold</td>
<td>Wong et al. (1995); Boyd and Harrison (1999)</td>
</tr>
<tr>
<td>Algal size structure(^b)</td>
<td>&lt; 2 fold</td>
<td>Welschmeyer et al. (1993); Boyd and Harrison (1999)</td>
</tr>
<tr>
<td>Heterotrophic bacterial biomass</td>
<td>2 fold</td>
<td>Boyd et al. (1995a); Sherry et al. (1999)</td>
</tr>
<tr>
<td>Heterotrophic bacterial production</td>
<td>3-fold</td>
<td>Boyd et al. (1995b); Sherry et al. (1999)</td>
</tr>
<tr>
<td>Microzooplankton biomass</td>
<td>2-fold</td>
<td>Boyd et al. (1995a)</td>
</tr>
<tr>
<td>Microzooplankton grazing</td>
<td>3-fold</td>
<td>Boyd et al. (1995b)</td>
</tr>
<tr>
<td>Mesozooplankton biomass</td>
<td>35-fold(^c)</td>
<td>Fulton (1978)</td>
</tr>
<tr>
<td>(B)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Downward POC flux</td>
<td>3-fold</td>
<td>Charette et al. (1999)</td>
</tr>
<tr>
<td>Export ratio</td>
<td>&lt; 2 fold</td>
<td>Charette et al. (1999)</td>
</tr>
<tr>
<td>Upper ocean POC levels</td>
<td>2-fold</td>
<td>Bishop et al. (1999)</td>
</tr>
<tr>
<td>(f) ratio</td>
<td>&lt; 2-fold</td>
<td>Varela and Harrison (1999)</td>
</tr>
<tr>
<td>Heterotrophic bacterial respiration</td>
<td>&lt; 3 fold</td>
<td>Sherry et al. (1999)</td>
</tr>
<tr>
<td>Faecal pellet production</td>
<td>2 fold</td>
<td>Thibault et al. (1999)</td>
</tr>
<tr>
<td>DOC levels</td>
<td>(+ 10 \mu\text{mol Kg}^{-1}) (^d)</td>
<td>Wong et al. (1999a)</td>
</tr>
<tr>
<td>DIC levels</td>
<td>(+ 10 \mu\text{mol Kg}^{-1}) (^d)</td>
<td>Wong et al. (1999a)</td>
</tr>
</tbody>
</table>

\(^a\) Denotes occasional evidence of ten-fold increases in chlorophyll \(a\) levels, interpreted by Boyd et al. (1998) to represent episodic Fe-mediated diatom blooms.

\(^b\) Based on size-fractionated production and biomass data.

\(^c\) Denotes variations due to seasonal ontogenetic migration of copepods.

\(^d\) Denotes seasonal change over ‘growth season’.
Table 2
Summary of the suite of measurements carried out in May 1996 at OSP. Details of the depth range of sampling over the water column, and the source of the methodologies employed are included.

<table>
<thead>
<tr>
<th>Measurement</th>
<th>Depth range</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Phytoplankton processes</td>
<td>0–50 m</td>
<td>Boyd and Harrison (1999)</td>
</tr>
<tr>
<td>Heterotrophic bacterial processes</td>
<td>0–1000 m</td>
<td>Sherry et al. (1999)</td>
</tr>
<tr>
<td>Mesozooplankton faecal pellet production</td>
<td>0–100 m</td>
<td>Thibault et al. (1999)</td>
</tr>
<tr>
<td>POC/PON levels</td>
<td>0–1000 m</td>
<td>Bishop et al. (1999)</td>
</tr>
<tr>
<td>POC and PON downward flux</td>
<td>0–1000 m drifting traps</td>
<td>Wong et al. (1999)</td>
</tr>
<tr>
<td>Algal protease activity</td>
<td>0–1000 m</td>
<td>Berges and Falkowski (1996)</td>
</tr>
<tr>
<td>$^{234}\text{Th}/^{238}\text{U}$</td>
<td>0–1000 m</td>
<td>Charette et al. (1999)</td>
</tr>
<tr>
<td>Algal pigments</td>
<td>0–1000 m</td>
<td>Thibault et al. (1999)</td>
</tr>
<tr>
<td>Community Respiration</td>
<td>0–1000 m</td>
<td>Sherry et al. (1999)</td>
</tr>
<tr>
<td>$\delta^{13}\text{C}-\text{POC}$</td>
<td>0–1000 m</td>
<td>Wu et al. (1999)</td>
</tr>
<tr>
<td>POC/PON downward flux</td>
<td>1000 and 3800 m traps</td>
<td>Wong et al. (1999)</td>
</tr>
<tr>
<td>RNA/DNA ratio</td>
<td>0–1000 m</td>
<td>Kemp (1995)</td>
</tr>
</tbody>
</table>

presented here) from the MULVFS pumps (Multiple Unit Large Volume Filtration System, see Bishop et al., 1985). Thirdly, data indicative of particle-removal/transformations – such as solubilisation/respiration or mesozooplankton grazing in the upper ocean and in midwater.

Ancillary data, on chlorophyll $a$ fluorescence from a bio-optical mooring in the vicinity of OSP, were obtained every 10 min (mean of 60 readings) from a calibrated Biospherical Instruments INF-300 fluorometer deployed at ca. 30 m (depth range ± 1.5 m over 14 d) below the ocean surface. These data provided estimates of temporal variability in chlorophyll $a$ levels over this period, and thus of whether the algal biomass levels observed during the May 18–22 occupation of OSP were representative of events before or after this period (Fig. 1); particles intercepted by free-drifting sediment traps at depth between May 18–22 probably originated in the mixed layer prior to when the May pelagic measurements were made.

Data on the size/abundance of pelagic particles were used to construct a ‘living’ particle size-distribution (after Sheldon et al., 1972), and these data were transformed using published bioparticle volume conversions (see Table 3) into estimates of POC for each component of the food web (Table 4). This enabled a comparison of the partitioning, into size-classes, of the calculated ‘living’ POC with that of POC collected by the MULVFS pumps in the upper ocean (Bishop et al., 1999).

The magnitude of observed downward POC fluxes during late May 1996 was compared with those predicted from an existing vertical flux modelling approach (Boyd and Newton, 1995,1999; Fig. 2 in present study). The model (Michaels and Silver, 1988) was used in conjunction with data on size-fractionated primary and bacterial production (see Fig. 2 Legend) to predict the downward POC flux from the mixed layer, and as employed by Boyd and Newton, the flux from the mixed layer was extrapolated to 100 m using a published algorithm (Bender et al., 1993).
Fig. 1. Time-series of chlorophyll $a$ levels obtained from a moored fluorometer (solar-stimulated fluorescence, no data during darkness) at 30 m depth in the vicinity of OSP during May 1996 – prior to and after the occupation of OSP – (mixed layer depth was ca. 50 m). The instrument was calibrated (using discrete samples) both at the start and end of a 100 d deployment.

Table 3
Summary of the data sources for the abundance of each foodweb component, and of the carbon/biovolume conversion (including carbon : chlorophyll $a$ ratio) factors used to convert the abundances of the components of the mixed layer at OSP in May 1996 to units of carbon

<table>
<thead>
<tr>
<th>Foodweb component</th>
<th>Data source</th>
<th>Biovolume reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Phytoplankton$^*$</td>
<td>Boyd (unpublished)</td>
<td>Strathmann (1967); Montagnes et al. (1994)</td>
</tr>
<tr>
<td>Size-fractionated chlorophyll $a$</td>
<td>Boyd and Harrison (1999)</td>
<td></td>
</tr>
<tr>
<td>Heterotrophic flagellates$^*$</td>
<td>Boyd (unpublished)</td>
<td>Kirchman et al. (1993)</td>
</tr>
<tr>
<td>Heterotrophic bacteria$^*$</td>
<td>Sherry et al. (1999)</td>
<td>Borshiem and Bratbak (1987)</td>
</tr>
<tr>
<td>Cyanobacteria$^*$</td>
<td>Sherry (unpublished)</td>
<td>Booth et al. (1993)</td>
</tr>
<tr>
<td>Autotrophic flagellates/dinoflagellates$^*$</td>
<td>Boyd (unpublished)</td>
<td>Montagnes et al. (1994)</td>
</tr>
<tr>
<td>Heterotrophic ciliates$^*$</td>
<td>this study</td>
<td>Putt and Stoecker (1989)</td>
</tr>
<tr>
<td>Heterotrophic dinoflagellates$^*$</td>
<td>this study</td>
<td>see Boyd et al. (1995a)</td>
</tr>
<tr>
<td>Mesozooplankton$^*$</td>
<td>Goldblatt et al. (1999)</td>
<td>see Boyd et al. (1995a)</td>
</tr>
</tbody>
</table>

$^*$Denotes abundance data.
Table 4
(A) Calculated particle and POC distribution based on the living foodweb components within the mixed layer at OSP in May 1996. Cells < 1 μm made up > 95% of abundance and ca. 40% of POC.
(B) Estimated faecal pellet production in the upper ocean at OSP in May 1996 from pellet production experiments (see Thibault et al., 1999) and mesozooplankton abundance data (Goldblatt et al., 1999)

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Abundance (l⁻¹)</th>
<th>Proportion of community abundance</th>
<th>Mean length (μm)</th>
<th>Calculated POC (μg l⁻¹)</th>
<th>Proportion of community biomass</th>
</tr>
</thead>
<tbody>
<tr>
<td>(A)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Het. bacteria</td>
<td>1.3 × 10⁹</td>
<td>0.94</td>
<td>submicron</td>
<td>26.0</td>
<td>0.24</td>
</tr>
<tr>
<td>Cyano-bacteria</td>
<td>7.0 × 10⁷</td>
<td>0.05</td>
<td>1.0</td>
<td>14.7</td>
<td>0.14</td>
</tr>
<tr>
<td>Het/Auto nanoflagellates</td>
<td>4.7 × 10⁶</td>
<td>&lt; 0.01</td>
<td>3</td>
<td>34.0</td>
<td>0.33</td>
</tr>
<tr>
<td>Het. ciliates</td>
<td>5.7 × 10³</td>
<td>&lt; 0.01</td>
<td>21</td>
<td>5.4</td>
<td>0.05</td>
</tr>
<tr>
<td>Autotrophic dinos</td>
<td>5.8 × 10⁴</td>
<td>&lt; 0.01</td>
<td>15</td>
<td>1.3</td>
<td>0.01</td>
</tr>
<tr>
<td>Het. dinos</td>
<td>3.0 × 10³</td>
<td>&lt; 0.01</td>
<td>19</td>
<td>0.8</td>
<td>0.01</td>
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<tr>
<td>Diatoms</td>
<td>2.0 × 10⁵</td>
<td>&lt; 0.01</td>
<td>32</td>
<td>9.3b</td>
<td>0.09b</td>
</tr>
<tr>
<td>Copepods</td>
<td>0.6</td>
<td>&lt; 0.01</td>
<td>3000</td>
<td>15.0</td>
<td>0.14</td>
</tr>
<tr>
<td>Total</td>
<td>1.38 × 10⁹</td>
<td>1.0</td>
<td></td>
<td>106.5</td>
<td>1.00</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Species</th>
<th>Abundance m⁻³ (0–100 m)</th>
<th>Pellet production (indiv⁻¹ d⁻¹)</th>
<th>Pellets produced (l⁻¹ d⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>(B)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Neocalanus plumchrus</td>
<td>59</td>
<td>21.6</td>
<td>1.2</td>
</tr>
<tr>
<td>N. flemingeri</td>
<td>35</td>
<td>12.5–21.1</td>
<td>0.4–0.7</td>
</tr>
<tr>
<td>N. cristatus</td>
<td>8.3</td>
<td>24.0–32.4</td>
<td>0.2–0.3</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td></td>
<td>1.4–2.3</td>
</tr>
</tbody>
</table>

Denotes counted by light microscopy and therefore could not discriminate between auto- and heterotrophs. The proportion of POC in living particles > 53 μm was 0.14 (copepods), 0.03 (diatoms) and faecal pellets (0.015, from Thibault et al., 1999) = 0.19.

Denotes mixed population of diatoms 85% of which are ca. 5 μm in length, 30% of diatom carbon was in cells > 50 μm.

3. Results

3.1. Pelagic particles

Heterotrophic bacteria (1.3 × 10⁹ L⁻¹), followed by cyanobacteria (Table 4A), were the most abundant ‘living’ particles in the mixed layer; this trend also has been reported for the Sargasso Sea (Roman et al., 1995). The size range (length scale) of the ‘living’ particles was < 1.0 μm → 1 mm. Faecal-pellet production by the main mesozooplankton species present in the upper ocean was ca. 2 pellets l⁻¹ d⁻¹ (Table 4B). The algal assemblage was dominated by small nanoflagellates, while autotrophic
cells $>53 \mu m$ made up 3% of ‘living’ biomass and were mainly diatoms (Table 4A, see the appendix). No data were available on transparent exopolymers (TEPS; Alldredge et al., 1993) nor on the abundance of detritus-like particles in the mixed layer. The ‘living’ particle size distribution indicated that $>99\%$ of particles were submicron, and that 70% of the POC associated with ‘living’ particles was $<5 \mu m$. The $>53 \mu m$ particles contributed ca. 19% to the total ‘living’ POC (Table 4A legend). POC levels calculated for the ‘living’ particles in the mixed layer (ca. 105 $\mu g \text{C} \cdot l^{-1}$) were ca. three-fold greater than POC estimates derived from pumps (Fig. 3A, 30 $\mu g \text{C} \cdot l^{-1}$). The greatest disparity between the calculated and measured POC levels was for the submicron fraction. Reasons for these disparities are discussed later.

3.2. Particle aggregation/residence times

POC and PON levels were highest in the mixed layer and decreased rapidly with depth (Figs. 3A and B). The POC size distributions derived from the foodweb (Table 4A) were compared with the partitioning of POC into size classes, as sampled by the MULVFS pumps (Fig. 3C). Despite differences between the calculated and
measured POC levels, the 1–53 μm fraction dominated both the partitioning of POC (Fig. 3C) and the population of ‘living’ POC in the upper ocean (Table 4A). Submicron particles made up > 20% of POC (ca. 6 mg C m$^{-3}$) sampled by the pumps, whereas heterotrophic and cyano-bacteria comprised 35% of the ‘living’ carbon (41 mg C m$^{-3}$). The partitioning of POC into particles > 53 μm was less (Fig. 3C) than that observed for the ‘living’ carbon (19% of POC > 53 μm). Although it is likely that some of the large but rare ‘living’ particles (such as sarcodines; Michaels et al., 1990) were not sampled by bottles, and there are discrepancies between the magnitude of ‘living’ and pump POC levels, these observations suggest that the majority of the POC in the > 53 μm fraction can be attributed to ‘living’ particles in the mixed layer. As such there was likely little particle aggregation within this zone; an observation
supported by the thorium vertical profile that indicates a small deficit of $^{234}$Th relative to the parent $^{238}$U in the mixed layer relative to that at the base of and below the mixed layer (Fig. 4).

A comparison of calculated pelagic particle abundance with that of critical particle concentrations required to initiate coagulation (Jackson, 1990) indicates that there are insufficient particle abundances, in any of the size classes considered, to initiate coagulation of particles (Table 5). While data were not available on the abundance of TEPS, addition of observed abundances of TEPS (10–1000 ml$^{-1}$ for large and small TEPS, respectively, Passow and Alldredge, 1994) to particle abundances at OSP would not exceed the particle threshold required to initiate coagulation (sensu Hill, 1992). Under these circumstances it is probable that processes such as differential sinking (Kepkay, 1994) will be particularly important in particle aggregation, which based on the $^{234}$Th/$^{238}$U profiles, probably occurred between 50 and 100 m depth.

Fig. 4. Vertical profiles of (A) $^{234}$Th disequilibria in relation to the parent $^{238}$U, (B) total, particulate and dissolved $^{234}$Th distributions. Samples were obtained from MULVFS pumps (night cast) in May 1996 at OSP. $^{234}$Th activities less than those of $^{238}$U signify particle removal, whereas higher activities than $^{238}$U are indicative of rapid particle remineralisation. In most cases the error bars were smaller than the symbols for dissolved, particulate and total $^{234}$Th (i.e. < 10% at all depths).
Table 5
A comparison of observed abundances of ‘living particles’ in the upper mixed layer at OSP in May 1996 with predictions of critical particle concentrations (CPC) for aggregation (based on coagulation thresholds – from Fig. 7 in Jackson (1990)). Cell dimensions were obtained from Table 4.

<table>
<thead>
<tr>
<th>Cell mean length (μm)</th>
<th>Cells (l⁻¹)</th>
<th>CPC (l⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>&lt; 1</td>
<td>1.3 × 10⁹</td>
<td>&gt; 10¹⁰</td>
</tr>
<tr>
<td>1–3</td>
<td>4.0 × 10⁶</td>
<td>&gt; 10⁸</td>
</tr>
<tr>
<td>3–5</td>
<td>5.0 × 10⁵</td>
<td>&gt; 10⁷</td>
</tr>
<tr>
<td>5–10</td>
<td>2.0 × 10⁵</td>
<td>5 × 10⁸</td>
</tr>
</tbody>
</table>

Estimation of the turnover and residence times of POC (from pumps) in the mixed layer in May 1996 (after Coale and Bruland, 1985) suggested that POC turnover (POC levels/regenerated production; regenerated production was assumed to be primary production – export production) was ca. 2.5 d, whereas residence time (POC levels/export production; export production was assumed to be downward POC flux) was 17 d. Bishop et al. (1999) reported POC residence times (calculated from the diurnal variation of POC levels/POC levels from the MULVFS pumps) of < 5 d. The particulate (> 1 μm) thorium residence times in the upper ocean ranged from 31 to 59 d (Charette et al., 1999); Murray et al. (1989) reported that the upper ocean residence time of thorium in the Equatorial Pacific was twice that for POC.

3.3. Downward biogenic fluxes

Observed POC fluxes, from surface-tethered free-drifting sediment traps, were ca. 65 mg C m⁻² d⁻¹ at 100 m depth and decreased rapidly with depth (Fig. 5A). This trend also was observed for downward PON fluxes (Fig. 5B). The estimated downward POC fluxes at 100 m from thorium activity distributions and POC/thorium ratios (see Charette et al., 1999) were two-fold lower than observed for the drifting traps, suggesting ‘over-trapping’ or the non-removal of cryptic swimmers from trap cups (Michaels et al., 1990) at this depth. Thibault et al. (1999) estimate that mesozooplankton faecal pellets contributed > 30% to this downward POC flux. The downward POC flux in the deep-moored traps at 1000 and 3800 m in early July 1996 was 1.7 and 1.6 mg C m⁻² d⁻¹, respectively (Wong et al., 1999b). These data represent the flux at depth that probably originated in the upper ocean in late May 1996 (i.e. ca. 40 d after the pelagic sampling took place, based on a 100 m d⁻¹ sinking rate). The observed POC flux in the 1000 m deep-tethered trap was five-fold lower than that recorded in the surface-tethered drifting trap at 1000 m; due to the different time-scales of sampling (2.5 d versus 17 d in the deep traps) and the different trap designs employed, a comparison is problematic.

As chlorophyll a levels changed little either 7 d prior to, or after the occupation of OSP (Fig. 1), it is likely that the pelagic ‘snapshot’ obtained between 18–22 May was representative of events before and after. Thus a comparison of the predicted and
observed POC fluxes at 100 m and at depth was valid. The predicted downward POC fluxes, using the foodweb modelling approach, were 71 and 33.3 mg C m$^{-2}$ d$^{-1}$ at 50 m (base of the mixed layer) and 100 m depth, respectively. The downward POC flux at 3800 m (1.7 mg C m$^{-2}$ d$^{-1}$) predicted using the Boyd and Newton (1995) modelling approach was comparable to that observed in the deep-moored trap (3800 m) in early July 1996.

3.4. Particle removal

In the zone from the base of the mixed layer to 100 m depth, there were ca. two-fold increases in the proportion of particles > 53 μm, a decrease in the proportion of 1–53 μm particles, and little change in the proportion of submicron particles (Fig. 3C). Such increases in the proportion of large particles occurred in a zone where POC levels decreased significantly with depth (Fig. 3A), which may therefore represent repackaging of POC, such as by grazing activity or particle aggregation. The shallowest surface-tethered free-drifting trap was located at 100 m. The magnitude of the

![Graph showing downward POC and PON fluxes](image-url)
downward POC fluxes, from drifting traps, decreased with depth; the flux at 100 m was three-fold higher than at 400 m and ten-fold higher than that at 1000 m (Fig. 5A). A similar decrease in POC levels (comprising both sinking and suspended particles, see Wakeham and Canuel, 1988) also was observed over the water column (Fig. 3A). In addition, an excess of $^{234}$Th (relative to $^{238}$U) around 150 m depth indicates particle breakdown (Fig. 4).

Between 100 and 200 m, where particle breakdown was occurring, the partitioning of POC within size classes indicates little change in the proportion of particles > 53 μm (Fig. 3C). In contrast, the proportion of submicron particles progressively decreased, while the proportion of 1–53 μm particles increased. At ca. 200 m depth, the proportion of particles > 53 μm increased by two-fold, possibly representing repackaging of material by interzonal migrants (see later). At depths greater than 200 m, the proportion of large particles progressively decreased until 500 m depth, whereas the proportion of those in the 1–53 μm class progressively increased over this part of the water column (Fig. 3C). POC associated with submicron particles made up a low and constant fraction of total POC from 200 to 1000 m depth.

The C : N ratio of biogenic particles has been used as an index of solubilisation/remineralisation (Newton et al., 1994). The ratios (atomic) derived from particles intercepted by the surface-tethered drifting traps approximated the Redfield ratio (Redfield et al., 1963) in the upper ocean, and although the ratios increased with depth, the changes were small, attaining 8.7 in midwater, and ca. 8.3 at 1000 m (Fig. 6). The C : N ratios of particles (atomic), intercepted by bottom-tethered traps at 1000 and 3800 m in early July were around 7.5 (data not shown, see Wong et al., 1999b), with little difference between the ratios derived from particles intercepted by the 1000 and

![C:N ratio](image)

Fig. 6. Vertical profiles of C : N ratios derived from POC and PON downward fluxes from surface-tethered drifting traps (open squares), and POC and PON levels from MULVFS pumps (ratios based on 1–53 μm data only, solid circles) at OSP in May 1996.
3800 m traps for concurrent time periods (data not shown). In contrast, the C : N ratio of POC and PON levels (for the 1–53 µm fraction only) collected by pumps (including both suspended and sinking particles) ranged from 5.5 to 6.5 in the upper ocean, with a subsurface peak at ca. 200 m, and with values of between 4.5 to 7.6 in deeper water (Fig. 6).

3.5. Removal mechanisms

The main agents for the removal and transformation of particles include heterotrophic bacteria/protozoa and interzonal migrants (Azam et al., 1995). The vertical profile of heterotrophic bacterial abundance displays a pattern similar to that of downward POC flux, i.e. a six-fold decrease in abundance below 50 m (Fig. 7A). However, while 7% of the bacterial assemblage in the mixed layer was viable (i.e. metabolically active and with intact membranes as inferred by exclusion of the fluorescent stain propidium iodide; Lloyd and Hayes, 1995), the viability of the population increased three-fold below 100 m (Fig. 7B), attaining 25% at 200 m, and then declining between 400 and 800 m depth. This results in a vertical profile of (viable) bacterial abundance that does not exhibit such a pronounced decrease with depth (see Fig. 7A). Bacterial activity, measured using Thymidine and Leucine incorporation (but not incubated at ambient pressure for deep water samples), displayed a marked decrease with depth, particularly between 50 and 300 m, but exhibited increases at 400 m depth (data not shown, but see Fig. 7D). The thymidine/leucine ratio (ratio of nucleic acid:protein synthesis) also showed marked decreases with depth, except at 400 m (not shown).

Conversion of thymidine incorporation into net bacterial carbon uptake after Kirchman et al. (1993) yielded a mixed layer uptake rate of ca. 0.7 µg C l⁻¹ d⁻¹ (Fig. 7D). This compares with a community respiration rate of ca. 30 µg C l⁻¹ d⁻¹ at OSP (Fig. 7C). Del Giorgio et al. (1997) and Cherrier et al. (1996) recently reported that the assimilation efficiency (AE) of heterotrophic bacteria was ca. 0.1–0.2. In addition, Tortell et al. (1996) report that the AE of bacteria under Fe-stressed conditions ranges from 0.1 to 0.3. As bacteria at OSP are likely Fe-stressed in the upper ocean (Tortell et al., 1996), the gross bacterial C uptake will likely be in the range 2.3–7.0 µg C l⁻¹ d⁻¹. From size-fractionated respiration measurements, heterotrophic bacteria are reported to contribute between 25 and 80% to community respiration at OSP (Sherry et al., 1999). On this basis, a bacterial AE at OSP of 0.1 (and hence a ca. 25% contribution to community respiration) is more likely than one of 0.3 (8% contribution to community respiration). Although community respiration data were only available for the upper 60 m (Fig. 7C), bacterial respiration at depths > 60 m were estimated by scaling them to the relative magnitude of thymidine incorporation over the 0–1000 m. If it is assumed that bacterial AE did not alter with depth (see later), then respiration rates should decrease by seven-fold from 0 to 1000 m.

Bacterial growth rates (bacterial biomass divided by production) were < 0.05 d⁻¹ over the water column (Fig. 7E); such a turnover time appears low relative to phytoplankton (ca. 1 division d⁻¹, Booth et al., 1993), which provide substrates
Fig. 7. Vertical profiles of heterotrophic bacterial (A) abundance (closed symbols denote all cells, open symbols denote live cells (total abundance x cell viability); (B) viability; (C) community respiration (expressed as µg C L⁻¹ d⁻¹, converted to carbon uptake using an RQ of 0.85); (D) production expressed in units of carbon; (E) growth rate, estimated for production/biomass of all cells, (F) growth rate, estimated for production/biomass of active cells only. Note as incubations were conducted on deck at simulated in situ temperatures, pressure effects which may markedly reduce the magnitude of rate processes (Turley, 1993; Turley and Mackie, 1995) were not considered.

(via exudation) used by bacteria, or to bacterivores ( > 1 division d⁻¹, Fenchel, 1982). However, the estimation of bacterial growth rates, based on viability, resulted in rates of 0.4 d⁻¹ in the upper ocean (Fig. 7F). Indeed, bacterial growth rates of 0.3 d⁻¹ were calculated for midwater populations at 400 m depth – this zone is thought to be
characterised by ‘carbon-poor’ substrates (see Fig. 5 in Cherrier et al., 1996). Such high growth rates suggest that substrates are being utilised efficiently at depth.

RNA/DNA ratios represent another approach to estimating heterotrophic bacterial growth rates (Kemp, 1995). These ratios for particles 1–53 μm likely represent both free-living and attached bacteria, and indicate a decrease in growth rate with depth at OSP. In both the day and night profiles, there is evidence of subsurface increases in growth rate (Fig. 8A) at shallower (night cast) and similar depth stratum (day cast), respectively, than observed from other growth rate estimates (Fig. 7F). The ratios from the submicron particles are likely indicative of free-living bacterial growth rates, and while the dataset is limited there is again a subsurface increase in growth rate at around 200 m (Fig. 8B). There is some evidence that ratios from the 1–53 μm and > 53 μm particles are several fold higher than those for the submicron fraction (Fig. 8C); this may either reflect higher numbers of eukaryotes in these fractions (larger

![RNA/DNA ratio graph](image)

Fig. 8. Vertical profiles of the RNA/DNA ratio of particles (A) 1–53 μm, night (closed circles), day (open squares); (B) < 1 μm, day; (C) > 53 μm, day, collected using MULVFS pumps from casts at OSP in May 1996.
3.6. Other biogeochemical gradients

The vertical profiles of biochemical parameters, such as algal protease activity, which may play a role in accelerating the solubilisation of sinking aggregates (Berges and Falkowski, 1996), showed 6–10 fold decreases in levels/activity at depths below 100 m (Fig. 9A–C). However, when normalised to soluble protein levels, there was little difference in caseinolytic activity over the upper 1000 m, whereas leucine aminopeptidase activity (LAP) declined at depths > 150 m (Fig. 9D). Mesozooplankton data from a Tucker trawl (150–250 m depth) indicate that while abundances were low (Table 6) the assemblage contained several important and efficient suspension feeders such as *Neocalanus cristatus* CV. Particle-ingestion rates by animals at
Table 6
Estimates of mesozooplankton ingestion rates of particles in the midwater column derived for the main species sampled by a Tucker trawl between 150–250 m in May 1996 at OSP (see Goldblatt et al. (1999) for methodological details). Ingestion rates were obtained for Neocalanus cristatus CV from the mean of the day/night abundance in conjunction with grazing data presented by Dagg (1993), and were assumed for the other species (scaled to 10% of body weight of each species per day).

<table>
<thead>
<tr>
<th>Species</th>
<th>Abundance (m^{-3})</th>
<th>Ingestion rate (µg C cop^{-1} d^{-1})</th>
<th>POC removed (mg C m^{-2} d^{-1})</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eucalanus bungii</td>
<td>6.7</td>
<td>15</td>
<td>10</td>
</tr>
<tr>
<td>Neocalanus cristatus CV</td>
<td>7.0–23.0</td>
<td>24.8–47.0</td>
<td>61.8</td>
</tr>
<tr>
<td>Oithona spp.</td>
<td>3.7</td>
<td>0.04</td>
<td>0.01</td>
</tr>
<tr>
<td>Conchoecia spp.</td>
<td>15.6</td>
<td>2</td>
<td>3.1</td>
</tr>
<tr>
<td>Eukrohnia hamata</td>
<td>4.4</td>
<td>10</td>
<td>4.3</td>
</tr>
<tr>
<td>Microcalanus pygmaeus</td>
<td>19.3</td>
<td>0.1</td>
<td>0.2</td>
</tr>
<tr>
<td>Total</td>
<td>56.7–72.7</td>
<td>79.4</td>
<td></td>
</tr>
</tbody>
</table>

depth, estimated using published rates (Dagg, 1993) in conjunction with observed abundances in May 1996 at OSP, indicate that ca. 79 mg C m^{-2} d^{-1} are ingested by mesozooplankton over this depth stratum (Table 6). However, ca. 30% of this carbon likely will be returned to the water column, as faecal pellets (Dagg, 1993), and hence contribute to the downward POC flux at depth.

Vertical gradients of algal pigment levels (data not shown, see Thibault et al., 1999) revealed marked decreases in pigment levels beneath the mixed layer and a ca. ten-fold decrease over the upper 1000 m, with little variation in either day or night, or between pigment groups, such as fucoxanthin (diatoms) or hexanoyloxy-fucoxanthin (prymnesiophytes) in this trend. Pyropheophorbide a levels (a marker for copepod faecal material) derived from the MULVFS pumped samples, exhibited a sub-surface maximum at 80–100 m depth (data not shown). The isotope signature of δ^{13}C in particles, collected by MULVFS pumps, displayed strong vertical gradients over the upper 1000 m (Fig. 10) with a value of −27.5_{oo} in the mixed layer, declining by 2.5_{oo} at 100 m, and thereafter remained in the range −25 to −23.45_{oo} at depth.

4. Discussion

4.1. Sources of particles in the mixed layer

The magnitude of phytoplankton stocks in May 1996 at OSP was similar to that observed in May 1993, May 1994 (Boyd et al., 1996), May 1995 and June 1997 (Boyd and Harrison, 1999). In addition, the reported biomass of microbial components of the food web in May 1996 were similar to those previously observed in late spring at OSP for bacterial (Kirchman et al., 1993; Sherry et al., 1999) and microzooplankton
Fig. 10. Vertical profile of stable isotopes ratio ($\delta^{13}$C, \%) for POC obtained from MULVFS pumps (night cast) in May 1996 at OSP.

biomass (Booth et al., 1993; Rivkin et al., 1999), respectively. Thus, in addition to the observed low seasonality at OSP, there is also evidence of low interannual variability in the magnitude of ‘living’ particles during late spring for this region. Mesozooplankton abundance, which displayed the largest seasonal variation of the all pelagic foodweb components, was relatively high in May 1996 at OSP; late spring is characterised by the highest levels of grazers over the annual cycle (Fulton, 1978). These foodweb components will be the building blocks for particle aggregates (Silver and Gowing, 1991; Lampitt et al., 1993b).

Calculated POC levels for ‘living carbon’ ($105 \mu g C l^{-1}$) in May 1996 were comparable to those reported previously at OSP for late spring (see Booth et al., 1993 (autotrophs/heterotrophs $60 \mu g C l^{-1}$); Kirchman et al., 1993 (bacteria $30 \mu g C l^{-1}$), but were ca. three-fold greater than those collected by the pumps. Reasons for this disparity probably include the cumulative error associated with using 5–6 specific biovolume conversion factors (up to three-fold, see discussion in Caron et al., 1995), the inability to size each individual cell for the foodweb components, and the likelihood that the pumps may not have captured particles with the same efficiency as water bottles; submicron POC calculated from biovolume factors was ca. $40 \mu g C l^{-1}$ compared with $6 \mu g C l^{-1}$ sampled by the pumps. Although pumps have been reported as collecting lower PN levels than bottle samplers in the Sargasso Sea (Altabet et al., 1992) and fewer microbial particles in the NW Mediterranean (Turley and Stutt, 1999), Caron et al. (1995) report that in a Sargasso Sea study $< 10\%$ of total heterotrophic bacterial abundance was observed in GF/F filtrates. Thus, as reported by Caron et al., the bacterial carbon content ($20 fg C cell^{-1}$) used in many studies may be an overestimate for open ocean bacteria. Despite such disparities between POC levels from these two approaches, changes in the partitioning of POC between size fractions over the water column may provide indirect evidence of particle transformations.
The calculated fast turnover times and long residence times for particles in the mixed layer at OSP are consistent with insufficient particle abundances to initiate aggregation via coagulation, a ‘living’ particle population dominated by cells too small to exit the water column directly, and high levels of pigment markers for grazing activity. Such observations suggest that the water column at OSP is characterised by a low and constant downward flux of material where decomposition of particles is dominant, and this conclusion supports the theoretical description of the region by Legendre and Le Fevre (1991). The modelling study of Michaels and Silver (1988) suggests that the main particles contributing directly to downward POC flux will be large algae such as diatoms, and faecal pellets from meso-grazers (copepods and salps). Such particles are present at relatively low levels at OSP (see Table 4A; salps (< 0.1 L$^{-1}$, Purcell and Madin, 1991; Goldblatt et al., 1999)). Cells < 5 µm may contribute indirectly to this flux via particle pumping (Gardner et al., 1993).

4.2. Particle transformations in the upper ocean

The low seasonal variability at OSP in autotrophic and heterotrophic biomass (Boyd et al., 1995a) is due, in part, to high grazer activity (Landry et al., 1993; Gifford, 1993). Initial particle transformations are therefore mainly associated with grazing activity, in conjunction with particle aggregation by differential sinking. Data from thorium disequilibria, the presence of a sub-surface pyropheophorbide $a$ maxima, and changes in the partitioning of POC within size classes all indicate that the main region of particle formation is between 50 and 100 m depth. This also has been observed in the NE Atlantic by Lampitt et al. (1993b).

4.3. The attenuation of downward POC fluxes – a mass balance approach

The availability of concurrent POC data from drifting traps and pumps with estimates of heterotrophic bacterial respiration (BR)/mesozooplankton grazing (MZ) permits an assessment of whether the rates of attenuation of POC (both suspended and sinking) balance biogenic carbon demands over the upper 1000 m. In this carbon balance calculation, three zones of the water column were considered, 100–150 m (BR data only), 150–250 m (BR and MZ data), and 100–1000 m (BR data only) (Fig. 11). The number of terms to be considered in this calculation were reduced since horizontal advection in this region is low (Tabata, 1975; Bograd et al., 1999), and although no data were available for May 1996, DOC and DIC levels changed little (10 µmol kg$^{-1}$ or less) over the 100–1000 m water column during the period May 1995 to September 1995 (Wong et al., 1999a). Furthermore, Bishop et al. (1999) report that water column POC levels increased slightly over the period of May to September 1996; suspended particles are thought to have long residence times in the deep ocean (Druffel et al., 1992). Therefore DIC, DOC and POC can be assumed to be in quasi-steady-state and thus not considered in the mass balance; the main POC source is probably the proportion of sinking particles ‘lost’ to the water column (58.3 mg C m$^{-2}$ d$^{-1}$ (66.5–8.2)) between 100 and 1000 m.
Column-integrated BCD for the water column between 100 and 1000 m depth was 609 mg C m$^{-2}$ d$^{-1}$ (a BCD (152.6 mg C m$^{-2}$ d$^{-1}$) based on an AE of 0.4 is included for comparison). In the present study, data on particle ingestion by large copepods at depth were only available from the 150–250 m depth stratum where they ‘removed’ ca. 79.4 mg C m$^{-2}$ d$^{-1}$; 30% of this carbon was likely returned to the water column as egested pellets. The total carbon required daily over the 100–1000 m water column ranged from 232 to 688 mg C m$^{-2}$ d$^{-1}$. The total carbon demand, based either on a bacterial AE of 0.1 or 0.4 is ca. four-fold to > ten-fold higher, respectively, than the available carbon. The total carbon demand (using bacterial AEs of 0.1 or 0.4) was also in excess of the available carbon for the 150–250 m, but not for 100–150 m (AE of 0.4) horizon (see Fig. 11).
4.4. Comparison with the NE Atlantic

In contrast to the present study, Turley and Mackie (1994) report that the fraction of sinking POC lost between 150 and 3100 m in the NE Atlantic was capable of supplying ca. 90% of the BCD (455 mg C m\(^{-2}\) d\(^{-1}\)). However, there appear to be several important differences between these two locales: firstly, Turley and Mackie (1994) used an AE of 0.4 (see their Table 9; NE Atlantic waters are not characterised by subnanomolar iron levels (Martin et al., 1993)) whereas an AE of 0.1 was used at OSP. This will result in a higher BCD at OSP. Secondly, the downward POC flux in the NE Atlantic was three-fold higher in the late spring period than that observed at OSP. Turley and Mackie (1994) invoked the possibility of the vertical supply of DOC contributing to the BCD in the NE Atlantic. While care must be taken when comparing processes occurring on different timescales (Taylor and Karl, 1991), it is probable that both the solubilisation of POC from suspended particles and the bacterial utilisation of DOC are the only other sources to supply the BCD. However, since DOC Wong et al. (1999a) and POC Bishop et al. (1999) levels increase from spring to summer, they cannot supply the missing carbon; the supply of > 95% of the highest BCD (0.1 AE) would remove > 10% of suspended POC (100–1000 m column integrated POC 6.2 g C m\(^{-2}\)) or < 1% of the DOC pool (100–1000 m column integrated ca. 750 g C m\(^{-2}\) DOC) at OSP.

4.5. Does Fe supply determine bacterial carbon demand?

The elevated BCD at OSP depends critically on the assumption that the low bacterial AE estimated for the upper ocean is applicable throughout the water column. Dissolved Fe levels increase from 0.02 to 0.6 nmol kg\(^{-1}\) from surface waters to 1000 m (Martin and Gordon, 1988). Furthermore, the nitracline (150 m) appears to be shallower than that for Fe (300 m, Martin and Gordon, 1988), suggesting that there is a stronger sink for iron than for nitrate in this region (assuming that the diffusion coefficient is the same for both nitrate and Fe). These factors will likely alter the BCD with depth. While more information is needed on how bacterial AE changes with depth, the lack of closure of the water column carbon balance suggests that bacterial cells may have a higher AE/lower BCD (consistent with higher Fe supply) at depth at OSP. Alternatively, the inability to consider the effects of pressure on altering bacterial production (see Fig. 7 legend) resulted in artificially elevated BCD for the water column.

4.6. Solubilisation of particles – C : N ratios

Smith et al. (1992) reported that the nitrogen associated with particles was preferentially solubilised resulting in an elevated C : N ratio of particles with depth. Indeed, an inverse relationship has been observed between the magnitude of downward POC flux and the C : N ratio of the associated particles, i.e. faster deposition of particles results in less solubilisation (Newton et al., 1994; Turley and Mackie, 1995). The C : N ratio of particles intercepted by free-drifting traps at OSP increased only slightly with
depth (ratios of 8.2 (150 m) and 8.1 (600 m)), suggesting that particles sank relatively quickly. At the HOT site in the N Central Pacific Gyre, Karl et al. (1996) observed C : N ratios of ca. 8 and > 10 for particles intercepted by drifting traps at 150 and > 600 m depth, respectively. At OSP, the C : N ratios of particles intercepted by deep-moored traps at 1000 and 3800 m in early July are at the lower end of the range of C : N ratios (6.6—> 10 over the annual cycle) of particles intercepted by deep traps (3200 m) in the NE Atlantic (Newton et al., 1994), again suggesting a rapid settling of material to depth at OSP. Indeed, Takahashi (1986) and Wong et al. (1999b) have estimated particle sinking rates at OSP of up to 175 m d\(^{-1}\) and ca. 130 m d\(^{-1}\), respectively. These are similar to rates associated with the NE Atlantic spring bloom (Newton et al., 1994).

In contrast, the C : N ratios of the suspended (plus sinking) material at OSP were 5.5–6.5 and relatively uniform in the upper ocean, with a slight decrease with depth. Given the high residence times/low sinking rates of suspended POC at OSP, it will likely be subject to heterotrophic bacterial solubilisation (see Fig. 2 in Christian et al., 1997) in the upper ocean and at depth. Thus, it is likely that these suspended particles are heavily colonised by bacteria, which have a C : N ratio of ca. 4–5 (estimated from ratio of submicron POC/PON in Fig. 3A/B), which would potentially offset the influence of differential solubilisation on the C : N ratios. Despite the region being dominated by small cells and being characterised by a relatively low and constant downward particle flux, it appears that this flux is dominated by a small proportion of fast-settling particles.

4.7. The role of mesozooplankton in particle transformations — evidence of seasonality?

Longhurst et al. (1990) have demonstrated in the NW Atlantic that interzonal migrants may transport considerable amounts of C and N to depth via respired carbon and dissolved inorganic nitrogen excretion, respectively. In spring at OSP, the upper ocean is characterised by little diel zooplankton vertical migration (Mackas et al., 1993; Goldblatt et al., 1999), and thus the magnitude of biogenic fluxes associated with interzonal migrants is unlikely to be a pronounced mechanism for the downward transport of carbon in this region. Nevertheless, mesozooplankton appear to be a key determinant of the particle transformations which alter the magnitude of the downward POC flux; Thibault et al. (1999) report that the flux of faecal pellets/pheopigments contributed ca. 30% to the downward POC flux in May 1996.

There is evidence that particles exiting the mixed layer at OSP are an important source of nutrition for mesozooplankton, in particular *Neocalanus cristatus*, within discrete depth strata below the mixed layer (Dagg, 1993). In the present study, large copepods at depth, such as *N. cristatus*, ingested ca. 79 mg C m\(^{-2}\) d\(^{-1}\) POC from the 150–250 m depth stratum. These findings do not concur with Lampitt et al. (1993b) who observed relatively low rates of particle ingestion by grazers in the NE Atlantic. Since Thibault et al. (1999) observed a considerably lower contribution of faecal pellets to the downward flux of POC in summer, the seasonal ontogenetic migration of mesozooplankton may be one of the main sources of seasonal variability in downward POC flux over the annual cycle.
4.8. Discrete depth strata for distinct particle transformations?

The availability of vertical profiles of biogeochemical parameters enables the investigation of the possibility of vertical zonation in particle transformation processes. The permanent pycnocline at OSP is at ca. 150 m depth (Tabata, 1975), above which multiple thermoclines exist (Denman and Gargett, 1988). These zones of rapid density change may influence particle distributions either by forming a temporary barrier to some forms of sinking particles (Alldredge and Crocker, 1995), or by isolating different groups of organisms. In addition, the relatively shallow depth of the permanent pycnocline, cf. NE Atlantic depth of 500 m (see Turley and Mackie, 1994), may have implications for the ratio of ‘sequestered’ to ‘recycled’ export production (sensu Riebesell and Wolf-Gladrow, 1992; see below).

Medders et al. (1997) reported the presence of a novel δ protobacterial lineage within a distinct depth stratum in the midwater region (160–500 m) of the OSP water column. Such a vertical distribution also has been described by Giovannoni et al. (1990) in the Sargasso Sea. Medders et al. (1997) suggested that such a stratified distribution, i.e. higher abundances of these protobacteria at depth, may reflect a functional adaptation to the utilisation of substrates. Most of the vertical profiles of parameters in the present study point to marked ten-fold gradients. However, the maxima observed by Medders et al. (1997) are coincident with the elevated proportion of large particles relative to surface waters (Fig. 3C). In addition, such reports of functionally adapted bacterial communities may explain the presence of increases in both bacterial viability (200–350 m depth) and growth rate (200 m depth – from RNA/DNA ratios; 400 m depth – from thymidine) in the midwater column at OSP; such trends are consistent with the efficient utilisation of substrates, thought to be of ‘poor’ quality, at depth. While the observed increases in bacterial growth rate at depth, from these different approaches, do not match with respect to depth range in midwater, nevertheless, the few available data suggest that this area of research requires further investigation.

4.9. Other biogeochemical gradients

Although proteases from microalgae have been measured and characterised to some extent (Berges and Falkowski, 1996), their precise functions remain unknown. Given their very high extracellular stability, it is likely that they could play a role in accelerating the solubilisation of sinking aggregates. Thus, it is of interest to note that when normalised to soluble protein, the depth distribution of the two proteolytic activities examined – LAP and caseinolysis – were markedly different. In the case of LAP, there were marked decreases at depths > 150 m, whereas with caseinolysis there was little change. The lack of significant variability of caseinolysis activity with depth probably reflects the very broad optimal conditions for this activity and its high stability (Berges and Falkowski, 1996). While it is difficult to assign unambiguously these proteolytic activities to specific organisms (e.g. phytoplankton versus bacteria), it is prudent to assume that phytoplankton as well as bacteria may contribute to the pool of extracellular activity (Berges and Falkowski, 1996). Furthermore, high LAP
and caseinolytic activity have been associated with dark-mediated cell-death events in some species (Berges and Falkowski, 1998).

The range of LAP activity observed at OSP at first appeared to be several orders of magnitude lower than reported for the oceanic waters off California by Smith et al. (1992) using an identical technique. However, it has since been established that the hydrolysis rates reported in Smith et al.’s Table 2 are nmol ml$^{-1}$ h$^{-1}$, not µmol ml$^{-1}$ h$^{-1}$, and that the volume considered in Smith et al.’s measurements was that of the aggregate, not the volume of seawater in which the measurement was made (D. Smith, personal communication). Taking these factors into account, the results from OSP become much closer; for example, the first value quoted in Smith et al.’s Table 2 corresponds (in seawater) to $5.2 \times 10^{-8}$ µmol min$^{-1}$ l$^{-1}$, which is very comparable to the mean upper water column values at OSP of ca. $6 \times 10^{-8}$ µmol min$^{-1}$ l$^{-1}$.

Vertical profiles of $\delta^{13}$C-POC from MULVFS pumps show extremely light values in the upper ocean, a marked trend towards heavier values (by 4$\%_{oo}$) between 100 and 250 m depth, and fairly constant values in deeper waters. Bishop et al. (1977) suggested that the lightening of surface values in pump samples from the equatorial Atlantic was due to the inclusion of heterotrophic bacteria (which are isotopically light ($< -30\%_{oo}$); they compute that based on observed POC values of $-28\%_{oo}$, 20% of the pelagic POC must be heterotrophic bacteria in this depth range. However, this explanation does not seem to be appropriate in the present study, where the pumps appeared to under-sample the submicron fraction relative to samples obtained from water bottles. Thus, the reason for the lightening of the surface values in the pump samples in the present study is not known. The marked shift with depth towards isotopically heavier POC at OSP may be due to the loss of isotopically lighter labile material by bacterial solubilisation; photomicrographs of pelagic marine aggregates (see Lampitt et al., 1993b) indicate that they are composed of considerable amounts of what appears to be labile material, since such material is not observed in mid-water aggregates.

4.10. Observed POC downward fluxes vs predicted

The predicted downward POC flux at 100 m, from the modelling approach, was two-fold lower than the observed flux in the drifting traps at 100 m. In addition, estimates of downward POC flux from thorium disequilibria/Th : C ratios also point to an over-estimation of POC flux in the drifting traps. Such an over-estimation may be due to the non-removal of cryptic swimmers (Michaels et al., 1990), hydrodynamic effects (Gust et al., 1994), and/or the presence of mesozooplankton in the vicinity of the shallow traps resulting in ‘swimmer’ effects elevating trap fluxes (see Discussion in Boyd and Newton, 1997; Rivkin et al., 1997).

Although the OSP region is characterised by low and constant downward biogenic fluxes, it is possible that the presence of a relatively shallow permanent pycnocline (150 m) may elevate the proportion of export production sinking to the deep ocean. For example, in the NE Atlantic only POC that sinks deeper than ca. 500 m, the depth of the permanent pycnocline, may be termed ‘sequestered export production’ (term defined by Riebesell and Wolf-Gladrow, 1992), whereas in the case of OSP material
settling deeper than 150 m depth will be ‘sequestered’. Thus, slow sinking particles or material that is solubilised between 150 and 500 m depth will be part of the ‘sequestered’ production in the NE subarctic Pacific but not the NE Atlantic. This may represent the additional removal of ca. 30 mg C m$^{-2}$ d$^{-1}$ (POC flux at 200 m minus that at 500 m, 49.5–19.3 mg C m$^{-2}$ d$^{-1}$).

4.11. Conclusions

(i) The open NE subarctic Pacific appears to be characterised by relatively low seasonality for the majority of pelagic and downward biogenic flux processes, and hence the magnitude of vertical processes recorded during May 1996 period are likely to be representative of a larger spatial area and wider time period. However, the seasonal ontogenetic vertical migration of mesozooplankton into the upper ocean may be one of the main sources of seasonal variability in downward POC flux over the annual cycle.

(ii) The upper ocean at OSP in May 1996, below the mixed layer and above 100 m, is a region of particle aggregation, whereas at depths > 100 m decomposition dominates particle transformations. Mixed layer residence times for POC are > 15 d and POC turnover within the mixed layer is ca. 2 d.

(iii) Despite estimated long residence times in the upper ocean, particles that sink to depth display relatively little change in C : N ratios, suggesting a rapid transit to depth. In contrast, suspended particles have relatively low C : N ratios when they might be expected, on the basis of differential solubilisation, to have elevated ratios.

(iv) The bacterial gross carbon demand (BCD) in the water column (100–1000 m depth) was, depending on assumptions, up to ten-fold greater than could be supplied by available POC. The inability to close the water column carbon budget suggests that the BCD may have been over-estimated. High Fe levels at depth at OSP may result in a greater bacterial assimilation efficiency and hence a reduced BCD. More information is needed on how BCD changes with depth.

(v) Both bacterial and interzonal migrant activity dominate midwater particle transformations. There is evidence of elevated midwater microbial activity (viability, growth rates) despite the availability of ‘poor’ quality substrates. This points to functionally adapted microbial populations, such as δ protobacterial groups at various depth strata below the mixed layer.

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Table 7

<table>
<thead>
<tr>
<th>Group</th>
<th>Spp or size (length scale)</th>
<th>Cell (l⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cyanobacteria</td>
<td><em>Synechococcus</em></td>
<td>7 × 10⁷</td>
</tr>
<tr>
<td>Diatoms</td>
<td>pennates &lt; 10 μm</td>
<td>2.0 × 10⁵</td>
</tr>
<tr>
<td></td>
<td>pennates 10–25 μm</td>
<td>2 × 10⁴</td>
</tr>
<tr>
<td></td>
<td>centrics &gt; 25 μm</td>
<td>3 × 10³</td>
</tr>
<tr>
<td>Dinoflagellates</td>
<td>&lt; 25 μm</td>
<td>5.5 × 10⁴</td>
</tr>
<tr>
<td></td>
<td>&gt; 25 μm</td>
<td>3 × 10³</td>
</tr>
<tr>
<td>Nanoflagellates</td>
<td>&lt; 5 μm</td>
<td>4.3 × 10⁶</td>
</tr>
<tr>
<td></td>
<td>5–20 μm</td>
<td>4 × 10⁵</td>
</tr>
</tbody>
</table>

*Denotes mainly *Thalassiosira* species.

*Denotes mainly *Gymnodinium*.

*Denotes mainly *Micromonas pusilla*.

*Denotes counted by light microscopy and therefore could not discriminate between auto- and heterotrophs.

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**Appendix A**

A list of the abundances of the main phytoplankton functional groups from May 1996 at OSP are given in Table 7.

**References**


