PERGAMON

Deep-Sea Research II 46 (1999) 2761–2792

DEEP-SEA RESEARCH
PART II

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

P.W. Boyd[a,*], N.D. Sherry[a], J.A. Berges[b], J.K.B. Bishop[c,1], S.E. Calvert[a], M.A. Charette[d], S.J. Giovannoni[e], R. Goldblatt[a], P.J. Harrison[a], S.B. Moran[d], S. Roy[f], M. Soon[a], S. Strom[g], D. Thibault[f], K.L. Vergin[e], F.A. Whitney[h], C.S. Wong[h]

[a]*School of Earth and Ocean Sciences, University of British Columbia, Vancouver, BC, Canada V6T 1Z4*
[b]*School of Biology and Biochemistry, Queen's University, Belfast Northern Ireland, BT9 7BL, UK*
[c]*School of Earth and Ocean Sciences, University of Victoria, Victoria, BC, Canada*
[d]*Graduate School of Oceanography, University of Rhode Island, Narragansett, RI 02882, USA*
[e]*Department of Microbiology, Oregon State University, Corvallis, OR 97331, USA*
[f]*INRS-Oceanologie, 310 Allee des Ursulines, Rimouski, Quebec, Canada G5L 3A1.*
[g]*University of Western Washington, Bellingham, WA, USA*
[h]*Institute of Ocean Sciences, DFO, P.O. Box 6000, Sidney, BC, Canada V8L 4B2*

Received 18 February 1998; received in revised form 4 September 1998; accepted 4 September 1998

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

* Corresponding author. National Institute of Water and Atmospheric Research, Centre for Chemical and Physical Oceanography, Department of Chemistry, University of Otago, Dunedin, New Zealand. Fax: 0064-3-479-5248.

E-mail address: pboyd@alkali.otago.ac.nz (P.W. Boyd)

[1] Present Address: UC Berkeley National Laboratory, One Cyclotron Road, M/S 90-1116, Berkeley, CA 94720, USA.

PII: S0967-0645(99)00083-1

evidence of particle decomposition occuring 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
Observed seasonal variations (winter versus summer) in (A) ecosystem components, (B) downward biogenic flux processes at OSP

Parameter	Seasonal variation	Data source
(A)		
Chlorophyll *a*	2 fold	Parslow (1981)[a]; Boyd and Harrison (1999)
Primary production	3–4 fold	Wong et al. (1995); Boyd and Harrison (1999)
Algal size structure[b]	< 2 fold	Welschmeyer et al. (1993); Boyd and Harrison (1999)
Heterotrophic bacterial biomass	2 fold	Boyd et al. (1995a); Sherry et al. (1999)
Heterotrophic bacterial production	3-fold	Boyd et al. (1995b); Sherry et al. (1999)
Microzooplankton biomass	2-fold	Boyd et al. (1995a)
Microzooplankton grazing	3-fold	Boyd et al. (1995b)
Mesozooplankton biomass	35-fold[c]	Fulton (1978)
(B)		
Downward POC flux	3-fold	Charette et al. (1999)
Export ratio	< 2 fold	Charette et al. (1999)
Upper ocean POC levels	2-fold	Bishop et al. (1999)
f ratio	< 2-fold	Varela and Harrison (1999)
Heterotrophic bacterial respiration	< 3 fold	Sherry et al. (1999)
Faecal pellet production	2 fold	Thibault et al. (1999)
DOC levels	$+ 10$ μmol Kg^{-1} [d]	Wong et al. (1999a)
DIC levels	$+ 10$ μmol Kg^{-1} [d]	Wong et al. (1999a)

[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

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

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 $\pm$ 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 bi^{p}ovolume conversions (see Table 3) into estimates of POC for each component of the foodweb (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).

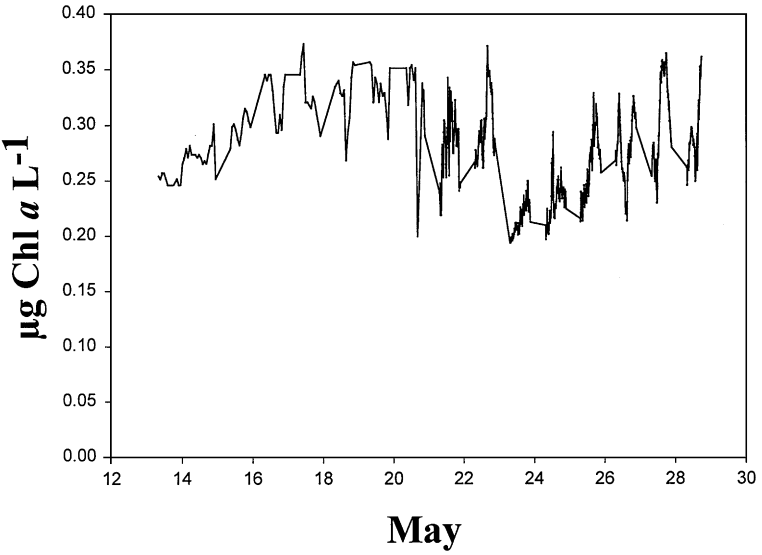

Fig. 1. Time-series of chlorophyll *a* levels obtained from a moored fluorometer (solar-stimulated fluorescence, no data during darkness) at 30 m depth in the vicinity of OSP during May 1996 – prior to and after the occupation of OSP – (mixed layer depth was ca. 50 m). The instrument was calibrated (using 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

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

[a]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 $< 1\,\mu m$ 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)

Parameter	Abundance (l^{-1})	Proportion of community abundance	Mean length (μm)	Calculated POC ($\mu g\ l^{-1}$)	Proportion of community biomass
(A)					
Het. bacteria	1.3×10^9	0.94	submicron	26.0	0.24
Cyano-bacteria	7.0×10^7	0.05	1.0	14.7	0.14
Het/Auto nano-flagellates[a]	4.7×10^6	< 0.01	3	34.0	0.33
Het. ciliates	5.7×10^3	< 0.01	21	5.4	0.05
Autotrophic dinos	5.8×10^4	$\ll 0.01$	15	1.3	0.01
Het. dinos	3.0×10^3	$\ll 0.01$	19	0.8	0.01
Diatoms	2.0×10^5	$\ll 0.01$	32	9.3[b]	0.09[b]
Copepods	0.6	$\ll 0.01$	3000	15.0	0.14
Total	1.38×10^9	1.0		106.5	1.00

Species	Abundance m^{-3} (0–100 m)	Pellet production ($indiv^{-1}\ d^{-1}$)	Pellets produced ($l^{-1}\ d^{-1}$)
(B)			
Neocalanus plumchrus	59	21.6	1.2
N. flemingeri	35	12.5–21.1	0.4-0.7
N. cristatus	8.3	24.0–32.4	0.2-0.3
Total	102.3		1.4-2.3

[a]Denotes counted by light microscopy and therefore could not descriminate between auto- and heterotrophs. The proportion of POC in living particles $> 53\,\mu m$ was 0.14 (copepods), 0.03 (diatoms) and faecal pellets (0.015, from Thibault et al., 1999) = 0.19.
[b]Denotes mixed population of diatoms 85% of which are ca. 5 μm in length, 30% of diatom carbon was in cells $> 50\,\mu m$.

3. Results

3.1. Pelagic particles

Heterotrophic bacteria ($1.3 \times 10^9\ L^{-1}$), 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 $< 1.0\,\mu m$ – $> 1\,mm$. 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

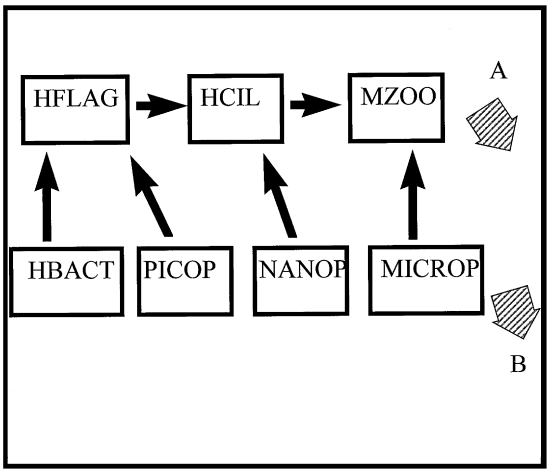

Fig. 2. Diagram of the pelagic foodweb structure used to predict the downward POC flux from the mixed layer at OSP. The algal flux version of the Michaels and Silver (1988) model, which permits 50% of large algal cells to sink ungrazed out of the upper ocean was used. As algal biomass at OSP is observed to vary little in magnitude over the annual cycle (Frost, 1993; Wong et al., 1995) the model was run in steady-state i.e. all inputted daily primary (from Boyd and Harrison, 1999) and bacterial production (from Sherry et al., 1999) is either grazed and/or sinks to depth. The fate of bacterial and primary production in the model is represented by foodweb flows between compartments (solid arrows). The trophic transfer efficiency of carbon at each foodweb flow is as described in Michaels and Silver (1988). The resulting downward POC fluxes in the model are represented by shaded arrows A and B which denote the fluxes resulting from foobweb interactions, and direct algal sinking, respectively. HBACT, PICOP, NANOP, MICRO, HFLAG, HCIL and MZOO denote, heterotrophic bacteria, picophytoplankton, nanophytoplankton, microphytoplankton, heterotrophic flagellates, heterotrophic ciliates and mesozooplankton, respectively.

cells > 53 μm made up 3% of 'living' biomass and were mainly diatoms (Table 4A, see the appendix). No data were available on transparent exoploymers (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 μm. The > 53 μm 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 μg $C\,l^{-1}$) were ca. three-fold greater than POC estimates derived from pumps (Fig. 3A, 30 μg $C\,l^{-1}$). 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

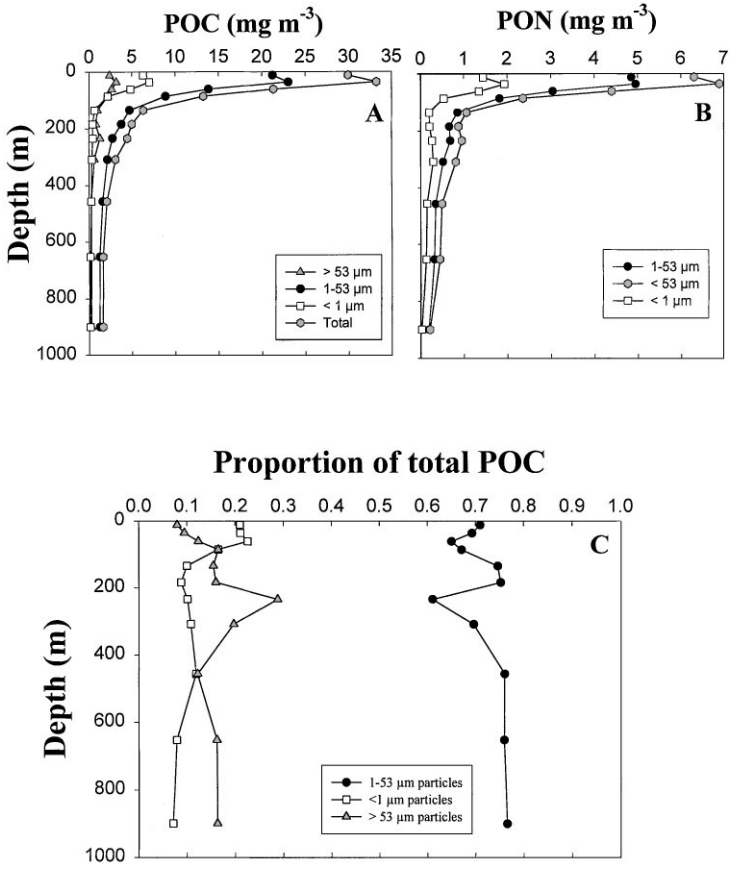

Fig. 3. Vertical profiles from MULVFS pumps (night-cast) of (A) POC concentrations for the < 1, 1–53 and > 53 µm fractions, total material collected is the sum of these fractions (B) PON concentrations – as for (A) but no data are available for material collected on 53 µm filters, (C) the partitioning of POC between the size-fractions, expressed as a proportion of total POC concentration from OSP in May 1996.

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.

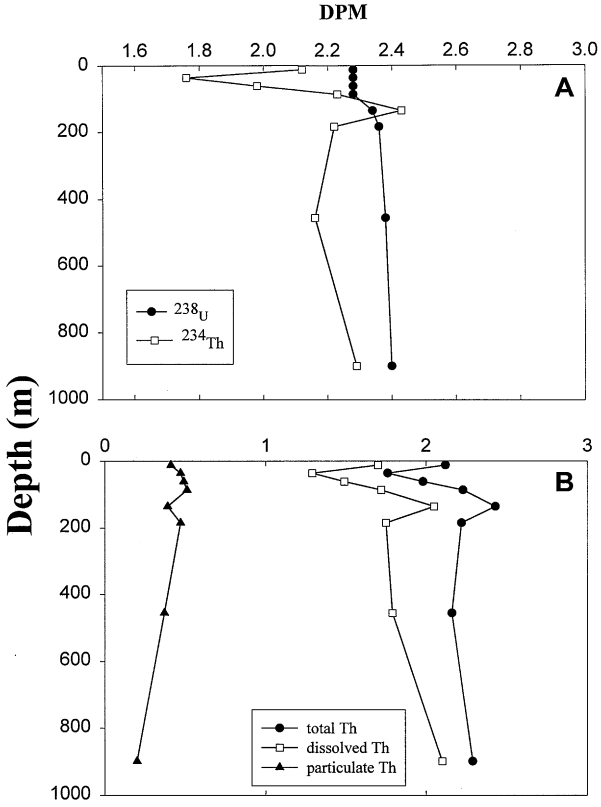

Fig. 4. Vertical profiles of (A) ^{234}Th disequilibria in relation to the parent ^{238}U, (B) total, particulate and dissolved ^{234}Th distributions. Samples were obtained from MULVFS pumps (night cast) in May 1996 at OSP. ^{234}Th activities less than those of ^{238}U signify particle removal, whereas 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

Cell mean length (μm)	Cells (l^{-1})	CPC (l^{-1})
<1	1.3×10^{9}	$\gg10^{10}$
1–3	4.0×10^{6}	$\gg10^{8}$
3–5	5.0×10^{5}	$>10^{7}$
5–10	2.0×10^{5}	5×10^{8}

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 timescales 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

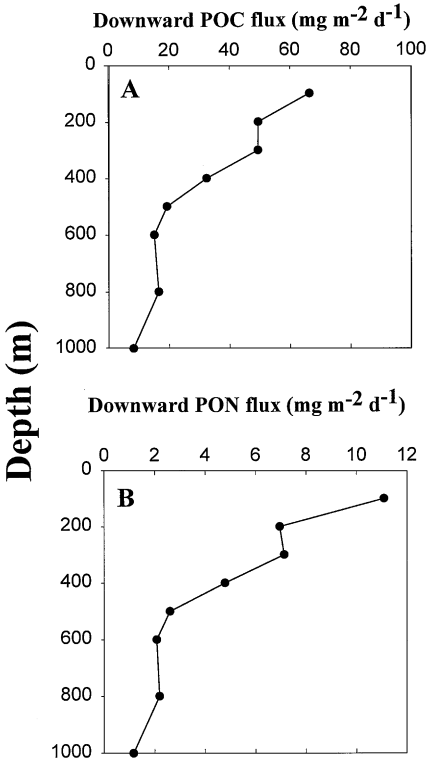

Fig. 5. Vertical profiles of downward flux of (A) POC (B) PON, estimated from a 72 h deployment of surface-tethered free-drifting sediment traps at OSP in May 1996.

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

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

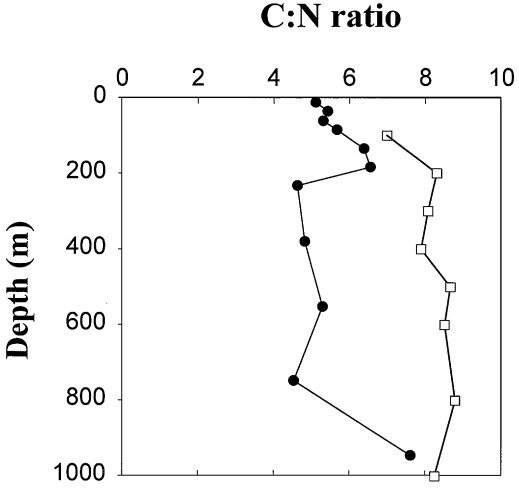

Fig. 6. Vertical profiles of C : N ratios derived from POC and PON downward fluxes from surface-tethered drifting traps (open squares), and POC and PON levels from MULVFS pumps (ratios based on 1–53 μm data only, solid circles) at OSP in May 1996.

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 $\mu g\ C\ l^{-1}\ d^{-1}$ (Fig. 7D). This compares with a community respiration rate of ca. 30 $\mu g\ C\ l^{-1}\ d^{-1}$ 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 $\mu g\ C\ l^{-1}\ d^{-1}$. 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 that 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

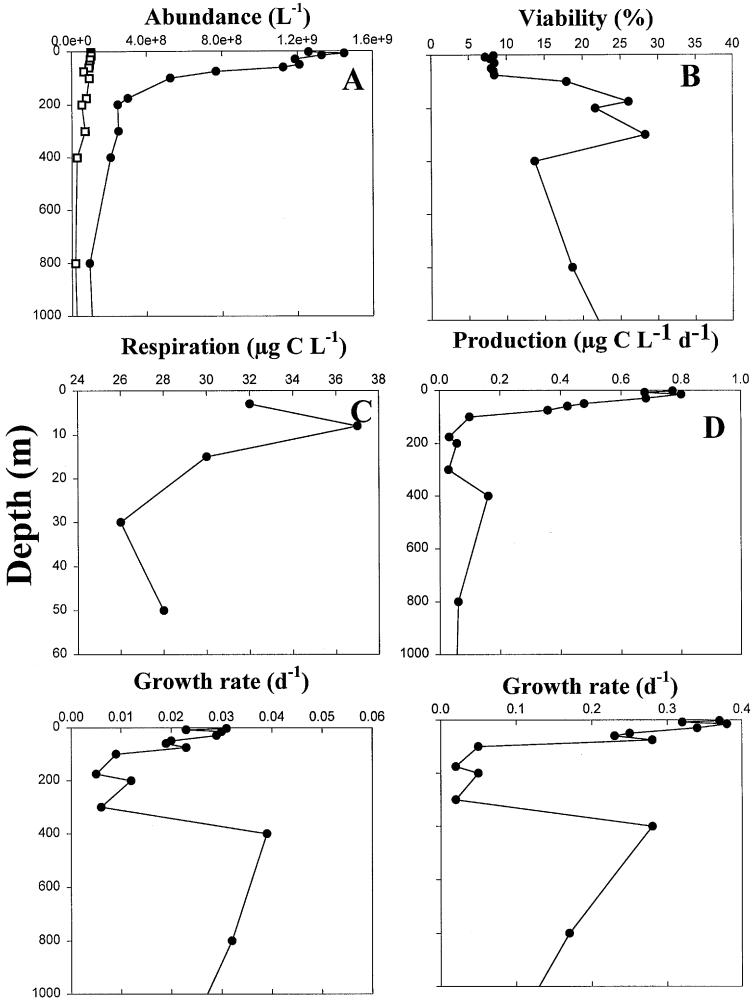

Fig. 7. Vertical profiles of heterotrophic bacterial (A) abundance (closed symbols denote all cells, open symbols denote live cells (total abundance * cell viability); (B) viability; (C) community respiration (expressed as µg C l^{-1} d^{-1}, converted to carbon uptake using an RQ of 0.85); (D) production 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

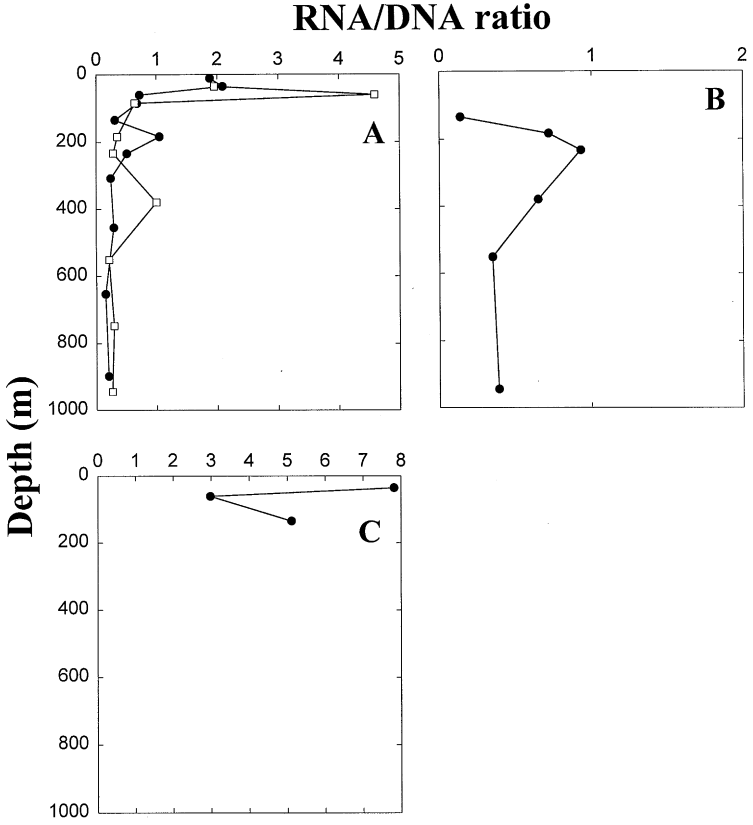

Fig. 8. Vertical profiles of the RNA/DNA ratio of particles (A) 1–53 μm, night (closed circles), day (open squares); (B) <1 μm, day; (C) >53 μm, day, collected using MULVFS pumps from casts at OSP in May 1996.

cells tend to have higher RNA/DNA ratios) or faster growth rates by attached bacteria, although the latter seems less likely (see DeLong et al., 1993).

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

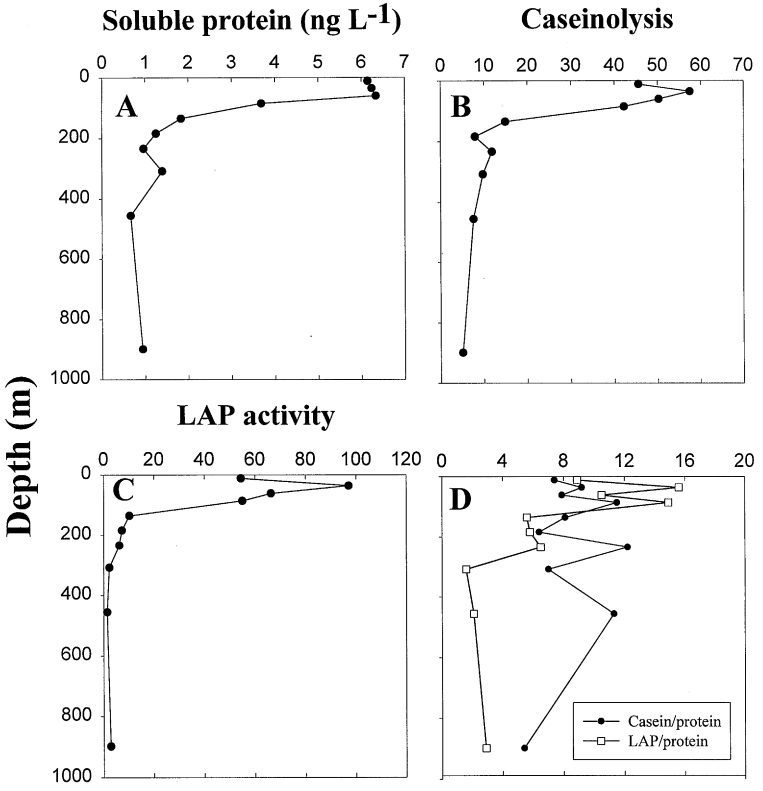

Fig. 9. Vertical profiles of (A) Soluble protein; (B) Caseinolysis (10^{-9} μmol FTC min^{-1} l^{-1}); (C) Leucine aminopeptidase activity (LAP) activity (10^{-9} μmol min^{-1} l^{-1}); (D) Caseinolysis (10^{-9} μmol FTC min^{-1} $prot^{-1}$) and LAP (10^{-9} μmol min^{-1} $prot^{-1}$) activity normalised to soluble protein. Samples were obtained from MULVFS pumps (night cast) in May 1996 at OSP.

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)

Species	Abundance (m^{-3})	Ingestion rate ($\mu g\ C\ cop^{-1}\ d^{-1}$)	POC removed ($mg\ C\ m^{-2}\ d^{-1}$) (150–250 m)
Eucalanus bungii	6.7	15	10
Neocalanus cristatus CV	7.0–23.0	24.8–47.0	61.8
Oithona spp.	3.7	0.04	0.01
Conchoecia spp.	15.6	2	3.1
Eukrohnia hamata	4.4	10	4.3
Microcalanus pygmaeus	19.3	0.1	0.2
Total	56.7–72. 7		79.4

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 $\delta^{13}C$ in particles, collected by MULVFS pumps, displayed strong vertical gradients over the upper 1000 m (Fig. 10) with a value of $-27.5‰$ in the mixed layer, declining by $2.5‰$ at 100 m, and thereafter remained in the range -25 to $-23.45‰$ 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

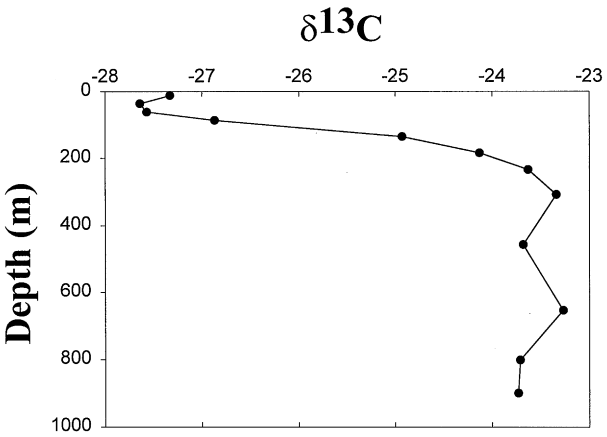

Fig. 10. Vertical profile of stable isotopes ratio ($\delta^{13}C$, ‰) for POC obtained from MULVFS pumps (night cast) in May 1996 at OSP.

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 μg 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 μg C l^{-1}); Kirchman et al., 1993 (bacteria 30 μg 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 μg C l^{-1} compared with 6 μg 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 $< 5\ \mu m$ 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 ($10\ \mu mol\ kg^{-1}$ 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.

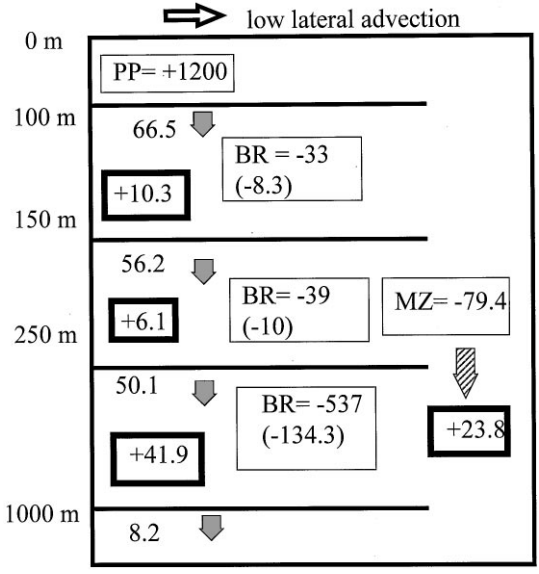

Fig. 11. A carbon budget comparing the POC (as the fraction of sinking particles lost between each depth horizon over the water column) available to bacteria/mesozooplankton (positive values in bold boxes), and the carbon demand by biota (negative values in boxes). The solid arrows denote the downward POC flux at each depth horizon. Bacterial carbon demand based is on an assimilation efficiency (AE) of 0.1 (BCD based on an AE of 0.4 is in parentheses) for three depth horizons (100–150 m, 150–250 m and 250–1000 m) at OSP in May 1996. All fluxes are in mg C m^{-2} d^{-1}. BR denotes bacterial respiration and represents the sum of the utilisation of Dissolved Organic Carbon (DOC) and the solubilisation of Particulate Organic Carbon (POC) to DOC (Smith et al., 1992). Note DIC and DOC fluxes were not considered as they change little in magnitude over the growth season. MZ represents the ingestion of particles by mesozooplankton, PP denotes primary production. The shaded arrow denotes the flux of faecal pellets from interzonal migrants. Calculations of BCD at OSP are under-estimates since that do not take into account the requirements of attached bacteria; Turley and Mackie (1994) report that they may comprise 25–34% of the biomass of free-living cells.

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 artifically 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 5.2×10^{-8} μmol min^{-1} l^{-1}, which is very comparable to the mean upper water column values at OSP of ca. 6×10^{-8} μmol min^{-1} l^{-1}.

Vertical profiles of δ^{13}C-POC from MULVFS pumps show extremely light values in the upper ocean, a marked trend towards heavier values (by 4‰) 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‰); they compute that based on observed POC values of -28‰, 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.

Acknowledgements

We thank the Captain and officers of the vessel *John P. Tully* for their skills and co-operation. We wish to acknowledge the skilled assistance provided by Hugh Maclean (UBC), Tim Soutar, Ron Bellegay, Reg Bingham, John Love (IOS, Canada). We thank Bruce Johnson for his unstinting support and selfless guidance of the JGOFS-Canada programme. We are grateful to three anonymous reviewers for their helpful comments and advice which improved substantially this manuscript, to David Smith (University of California) for a personal communication and to Ken Denman

Table 7

Group	Spp or size (length scale)	Cell (l^{-1})
Cyanobacteria	*Synechococcus*	7×10^7
Diatoms	pennates < 10 μm	2.0×10^5
	pennates 10–25 μm	2×10^4
	centrics > 25 μm[a]	3×10^3
Dinoflagellates	< 25 μm[b]	5.5×10^4
	> 25 μm	3×10^3
Nanoflagellates[c]	< 5 μm[d]	4.3×10^6
	5–20 μm	4×10^5

[a]Denotes mainly *Thalassiosira* species.
[b]Denotes mainly *Gymnodinium*.
[c]Denotes mainly *Micromonas pusilla*.
[d]Denotes counted by light microscopy and therefore could not discriminate between auto- and heterotrophs.

for useful comments on the manuscript. This research was performed as part of the Canadian JGOFS Program. Principal support for Canadian JGOFS comes from the Natural Sciences and Engineering Research Council and from the Department of Fisheries and Oceans, Canada.

Appendix A

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

References

Alldredge, A.L., Passow, U., Logan, B.E., 1993. The abundance and significance of a class of large transparent organic particles in the ocean. Deep-Sea Research 40, 1131–1140.

Alldredge, A.L., Crocker, K.M., 1995. Why do sinking mucilage aggregates accumulate in the water column?. The Science of the Total Environment 165, 15–22.

Altabet, M.A., Deuser, W.G., Honjo, S., Stienen, C., 1991. Seasonal and depth-related changes in the source of sinking particles in the North Atlantic. Nature 354, 136–139.

Altabet, M.A., Bishop, J.K.B., McCarthy, J.J., 1992. Differences in particulate nitrogen concentration and isotopic composition for samples collected by bottles and large volume pumps in Gulf Stream warm-core rings and the Sargasso Sea. Deep-Sea Research 39, S405–417.

Asper, V.L., Deuser, W.G., Knauer, G.A., Lohrenz, S.E., 1992. Rapid coupling of sinking particle fluxes between surface and deep ocean waters. Nature 357, 670–673.

Azam, F., Smith, D.C., Long, R.A., Steward, G., 1995. Bacteria in ocean carbon cycling as a molecular problem. In: Joint, I. (Ed.) Molecular ecology of aquatic microbes, NATO ASI Series, vol. G38. Springer, Berlin, pp. 39–54.

Banse, K., 1991. Iron availability, nitrate uptake and exportable new production in the subarctic Pacific. Journal of Geophysical Research 96, 741–748.

Bender, M., Ducklow, H., Kiddon, J., Marra, J., Martin, J., 1993. The carbon balance during the 1989 spring bloom in the North Atlantic Ocean, 47°N, 20°W. Deep-Sea Research I 39, 1707–1725.

Berges, J.A., Falkowski, P.G., 1996. Cell-associated proteolytic enzymes from marine phytoplankton. Journal of Phycology 32, 556–574.

Berges, J., Falkowski, P.G., 1998. Physiological stress and cell death in marine phytoplankton: Induction of proteases in response to nitrogen or light limitation. Limnology and Oceanography 43, 129–135.

Bishop, J.K.B., Edmond, J.M., Ketten, D.R., Bacon, M.P., Silker, W.G., 1977. The chemistry, geology and vertical flux of particulate matter from the upper 400 m of the equatorial Atlantic Ocean. Deep-Sea Research 24, 511–548.

Bishop, J.K.B., Schupack, D., Sherrell, R.M., Conte, M., 1985. A Multiple Unit Large Volume in-situ Filtration System (MULVFS) for sampling oceanic particulate matter in mesoscale environments. In: Zirino, A. (Ed.) Mapping Strategies in Chemical Oceanography, Advances in Chemistry Series, 209. American Chemical Society, Washington, DC, pp. 155–175.

Bishop, J.K.B., Calvert, S.E., Soon, M., 1999. Spatial and temporal variability of POC in the northeast subarctic Pacific. Deep-Sea Research II 46, 2699–2733.

Bograd, S.J., Thomson, R.E., Rabinovich, A.B., Paul, H.L. (1999). Near-surface circulation of the northeast Pacific Ocean derived from WOCE–SVP satellite-tracked drifters. Deep-Sea Research II, this volume.

Booth, B.C., Lewin, J., Postel, J.R., 1993. Temporal variation in the structure of autotrophic and heterotrophic communities in the subarctic Pacific. Progress in Oceanography 32, 57–99.

Borshiem, K.Y., Bratbak, G., 1987. Cell volume to cell carbon conversion factors for a bacterivorous Monas sp. Enriched from seawater. Marine Ecology Progress Series 36, 171–175.

Boyd, P., Newton, P., 1995. Evidence of the potential influence of planktonic community structure on the interannual variability of particulate carbon flux. Deep-Sea Research I 42, 619–639.

Boyd, P.W., Strom, S., Whitney, F.A., Doherty, S., Wen, M.E., Harrison, P.J., Wong, C.S., Varela, D.E., 1995a. The NE subarctic Pacific in winter. Biological standing stocks. Marine Ecology Progress Series 128, 11–24.

Boyd, P.W., Whitney, F.A., Harrison, P.J., Wong, C.S., 1995b. The NE subarctic Pacific in winter. Biological rate processes. Marine Ecology Progress Series 128, 25–34.

Boyd, P.W., Muggli, D., Varela, D., Goldblatt, R.H., Chretien, R., Orians, K.J., Harrison, P.J., 1996. In vitro iron enrichment experiments in the NE subarctic Pacific. Marine Ecology Progress Series 136, 179–193.

Boyd, P.W., Newton, P., 1997. Measuring biogenic carbon flux in the ocean. Science 275, 554.

Boyd, P.W., Harrison, P.J., 1999. Phytoplankton dynamics in the NE subarctic Pacific. Deep-Sea Research II 46, 2405–2432.

Boyd, P.W., Wong, C.S., Merrill, J., Whitney, F., Snow, J., Harrison, P.J., Gower, J., 1998. Atmospheric iron supply and enhanced vertical carbon flux in the NE subarctic Pacific – is there a connection? Global Biogeochemical Cycles 12, 429–441.

Boyd, P.W., Newton, P.P., 1999. Does planktonic community structure determine downward particulate organic carbon flux in different oceanic provinces. Deep-Sea Research I 46, 63–91.

Boyd, P.W., Stevens, C.L., 1999. A coupled C flux/particle dynamics model to assess factors controlling the transfer of material to the deep ocean. Deep Sea Research I, submitted for publication.

Caron, D.A., Dam, H.G., Kremer, P., Lessard, E.J., Madin, L.P., Malone, T.C., Napp, J.M., Peele, E.R., Roman, M.R., Youngbluth, M.J., 1995. The contribution of micro-organisms to particulate carbon and nitrogen in surface waters of the Sargasso Sea near Bermuda. Deep-Sea Research I 42, 943–972.

Charette, M.A., Moran, S.B., Bishop, J.K.B., 1999. ^{234}Th as a tracer of particulate organic carbon export in the northeast Pacific Ocean. Deep-Sea Research II 46, 2833–2861.

Cherrier, J., Bauer, J.E., Druffel, E.R.M., 1996. Utilization and turnover of labile dissolved organic matter by bacterial heterotrophs in eastern North Pacific surface waters. Marine Ecology Progress Series 139, 267–279.

Christian, J.R., Karl, D.M., 1995. Bacterial ectoenzymes in marine waters: activity ratios and temperature responses in three oceanographic provinces. Limnology and Oceanography 40, 1042–1049.

Christian, J.R., Lewis, M.R., Karl, D.M., 1997. Vertical fluxes of carbon, nitrogen and phosphorus in the North Pacific Subtropical Gyre near Hawaii. Journal of Geophysical Research 102, 15667–15677.

Coale, K.H., Bruland, K.W., 1985. $^{234}Th : ^{238}U$ disequilibria within the California current. Limnology and Oceanography 30, 22–32.

Dagg, M., 1993. Sinking particles as a possible source of nutrition for the large calanoid copepod Neocalanus cristatus in the subarctic Pacific Ocean. Deep-Sea Research I 40, 1431–1445.

Dam, H.G., Drapeau, D.T., 1995. Coagulation efficiency, organic matter glues and the dynamics of particles during a phytoplankton bloom in a mesocosm study. Deep-Sea Research II 42, 111–123.

DeLong, E.F., Franks, D.G., Alldredge, A.L., 1993. Phylogenetic diversity of aggregate-attached vs. free-living marine bacterial assemblages. Limnology and Oceanography 38, 924–934.

del Giorgio, P.A., Cole, J.J., Cimbleris, A., 1997. Respiration rates in bacteria exceed phytoplankton production in unproductive aquatic systems. Nature 385, 148–151.

Denman, K.L., Gargett, A.E., 1988. Multiple thermoclines are barriers to vertical exchange in the subarctic Pacific during SUPER, May 1984. Journal of Marine Research 46, 77–103.

Druffel, E.R., Williams, P.M., Bauer, J.E., Ertel, J.R., 1992. Cycling of dissolved and particulate organic matter in the open ocean. Journal of Geophysical Research 97, 15639–15659.

Fenchel, T., 1982. Ecology of hetrotrophic microflagellates: II Bioenergetics and growth. Marine Ecology Progress Series 8, 225–231.

Frost, B.W., 1993. A modelling study of processes regulating plankton standing stock and production in the open subarctic Pacific Ocean. Progress in Oceanography 32, 17–56.

Fuhrman, J.A., Davis, A.A., 1997. Widespread Archea and novel bacteria from the deep sea as shown by 16S rRNA gene sequences. Marine Ecology Progress Series 150, 275–285.

Fulton, J.D., 1978. Seasonal and annual variations of net zooplankton at Ocean Station P, 1965–1976. Canadian Fisheries Marine Services Data Report, 49.

Gardner, W.D., Walsh, I.D., Richardson, M.J., 1993. Biophysical forcing of particle production and distribution during a spring bloom in the North Atlantic. Deep-Sea Research II 40, 171–198.

Gifford, D.J., 1993. Protozoa in the diets of Neocalanus spp. In the oceanic subarctic Pacific Ocean. Progress in Oceanography 32, 223–238.

Giovanonni, S.J., Britschgi, T.B., Moyer, C.L., Field, K.G., 1990. Genetic diversity in Sargasso Sea bacterioplankton. Nature 345, 60–63.

Giovannoni, S.J., Mullins, T.D., Field, K.G., 1995. Microbial diversity in oceanic systems: rRNA approaches to the study of unculturable microbes. In: Joint, I. (Ed.) Molecular ecology of aquatic microbes, NATO ASI Series, G38. Springer, Berlin, pp. 217–248.

Goldblatt, R.H., Mackas, D.L., Lewis, A.G., Wen, M.E., 1999. Mesozooplankton community characteristics in the NE subarctic Pacific. Deep-Sea Research II 46, 2619–2644.

Gust, G., Michaels, A.F., Johnson, R., Deuser, W.G., Bowles, W., 1994. Mooring line motions and sediment trap hydromechanics: in situ intercomparison of three common deployment designs. Deep-Sea Research I 41, 831–857.

Hill, P.S., 1992. Reconciling aggregation theory with observed vertical fluxes following phytoplankton blooms. Journal of Geophysical Research 97, 2295–2308.

Hoppe, H.G., Ducklow, H., Karrasch, B., 1993. Evidence for the dependency of bacterial growth on enzymatic hydrolysis of particulate organic matter in the mesopelagic Ocean. Marine Ecology Progress Series 93, 277–283.

Jackson, G.A., 1990. A model of the formation of marine algal flocs by physical coagulation processes. Deep-Sea Research 37, 1197–1211.

Karl, D.M., Knauer, G.A., 1984. Vertical distribution, transport and exchange of carbon in the northeast Pacific Ocean: evidence for multiple zones of biological activity. Deep-Sea Research 31, 221–243.

Karl, D.M., Knauer, G.A., Martin, J.H., 1988. Downward flux of particulate organic matter in the ocean: a particle decomposition paradox. Nature 332, 438–441.

Karl, D.M., Christian, J.R., Dore, J.E., Hebel, D.V., Letelier, R.M., Tupas, L.M., Winn, C.D., 1996. Seasonal and interannual variability in primary production and particle flux at Station ALOHA. Deep-Sea Research II 43, 539–568.

Kemp, P.F., 1995. Can we estimate bacterial growth rates from ribosomal RNA content. In: Joint, I. (Ed.) Molecular ecology of aquatic microbes, NATO ASI Series, G38. Springer, Berlin, pp. 279–302.

Kepkay, P.E., 1994. Particle aggregation and the biological reactivity of colloids. Marine Ecology Progress Series 109, 293–304.

Kirchman, D.L., Keil, R.G., Simon, M., Welschmeyer, N.A., 1993. Biomass and production of heterotrophic bacterioplankton in the oceanic subarctic Pacific. Deep-Sea Research 42, 967–988.

Lampitt, R.S., Hillier, W.R., Challenor, P.G., 1993a. Seasonal and diel variation in the open ocean concentration of marine snow aggregates. Nature 362, 737–739.

Lampitt, R.S., Wishner, K.F., Turley, C.M., Angel, M.V., 1993b. Marine snow studies in the Northeast Atlantic Ocean: distribution, composition and role as a food source for migrating plankton. Marine Biology 116, 689–702.

Landry, M.R., Monger, B.C., Selph, K.E., 1993. Time-dependency of microzooplankton grazing and phytoplankton growth in the subarctic Pacific. Progress in Oceanography 32, 205–222.

Legendre, L., Le Fevre, J., 1991. From individual plankton cells to Pelagic marine ecosystems and to global biogeochemical cycles. In: Demers, S. (Ed.) Particle Analysis in Oceanography. Springer, Berlin, pp. 261–300.

Lloyd, D., Hayes, A.J., 1995. Vigour, vitality, and viability of microorganisms. FEMS Microbiological Letters 133, 1.

Lochte, K., Turley, C.M., 1989. Bacteria and cyanobacteria associated with phytodetritus in the deep sea. Nature 333, 67–68.

Longhurst, A.R., Bedo, A.W., Harrison, W.G., Head, E.J.H., Sameoto, D.D., 1990. Vertical flux of respiratory carbon by oceanic diel migrant biota. Deep-Sea Research 37, 685–694.

Mackas, D.L., Sefton, H., Miller, C.B., Raich, A., 1993. Vertical habitat partitioning by large calanoid copepods in the oceanic subarctic Pacific during spring. Progress in Oceanography 32, 259–294.

Martin, J.H., Gordon, R.M., 1988. Northeast Pacific iron distributions in relation to phytoplankton productivity. Deep-Sea Research, Part A 35, 177–196.

Martin, J.H., Knauer, G.A., Karl, D.M., Broenkow, W.W., 1987. Vertex: Carbon cycling in the northeast Pacific. Deep-Sea Research 34, 267–285.

Martin, J.H., Fitzwater, S.E., Gordon, R.M., Hunter, C.N., Tanner, S.J., 1993. Iron, primary production and carbon–nitrogen flux studies during the JGOFS North Atlantic Bloom Experiment. Deep-Sea Research II 40, 115–134.

Medders, T.D., Vergin, K.L., Boyd, P.W., Giovannoni, S.J., 1997. A novel δ-subdivision Proteobacterial lineage from the Lower ocean surface layer. Applied Environmental Microbiology 63, 1441–1448.

Michaels, A.F., Silver, M.W., 1988. Primary production, sinking fluxes and the microbial food web. Deep-Sea Research 35, 473–490.

Michaels, A.F., Silver, M.W., Gowing, M.M., Knauer, G.A., 1990. Cryptic zooplankton 'swimmers' in upper ocean sediment traps. Deep-Sea Research 37, 1285–1296.

Miller, C.B., 1993. Pelagic production processes in the Subarctic Pacific. Progress in Oceanography 32, 1–17.

Montagnes, D.J.S., Berges, J.A., Harrison, P.J., Taylor, F.J.R., 1994. Estimating carbon, nitrogen, protein and chlorophyll *a* from volume in marine phytoplankton. Limnology and Oceanography 39, 1044–1060.

Murnane, R.J., Cochran, J.K., Buessler, K.O., Bacon, M.P., 1996. Least-squares estimates of thorium, particle and nutrient cycling rate constants from the JGOFS North Atlantic Bloom Experiment. Deep-Sea Research I 43, 239–258.

Murray, J.W., Downs, J.N., Strom, S., Wei, C.L., Jannasch, H.W., 1989. Nutrient assimilation, export production and ^{234}Th scavenging in the eastern equatorial Pacific. Deep-Sea Research 36, 1471–1489.

Newton, P.P., Lampitt, R.S., Jickells, T.D., King, P., Boutle, C., 1994. Temporal and mesoscale variability of biogenic particle fluxes in the context of the JGOFS north-east Atlantic process studies at 47N 20W (1989–1990). Deep-Sea Research I 41, 1617–1642.

Parslow, J.S., 1981. Phytoplankton–zooplankton interactions: data analysis and modelling (with particular reference to Ocean Station Papa [50°N 145°W] and controlled ecosystem experiments), PhD Thesis, University of British Columbia, Canada.

Parsons, T.R., Lalli, C.M., 1988. Comparative oceanic ecology of the plankton communities of the subarctic Atlantic and pacific Oceans. Oceanography and Marine Biology Annual Review 26, 317–359.

Passow, U., Alldredge, A.L., 1994. Distribution, size and bacterial colonization of transparent exoploymers in the ocean. Marine Ecology Progress Series 133, 185–198.

Peinart, R., von Bodungen, B., Smetacek, V.S., 1989. Foodweb structure and loss rate. In: Berger, W.H., Smetacek, V.S., Wefer, G. (Eds.) Productivity of the Ocean: Present and Past. Wiley, New York, pp. 35–48.

Purcell, J.E., Madin, L.P., 1991. Diel patterns of migration, feeding, and spawning by salps in the subarctic Pacific. Marine Ecology Progress Series 73, 211–217.

Putt, M., Stoecker, D.K., 1989. An experimentallly determined carbon : volume ratio for marine 'oligotrichous' ciliates from estuarine and coastal waters. Limnology and Oceanography 34, 1097–1103.

Redfield, A.C., Ketchum, B.H., Richards, F.A., 1963. The influence of organisms on the composition of seawater. In: Hill, M.N. (Ed.) The Sea. Wiley, New York, pp. 26–77.

Riebesell, U., Wolf-Gladrow, D.A., 1992. The relationship between physical aggregation of phytoplankton and particle flux: a numerical model. Deep-Sea Research 39, 1085–1102.

Rivkin, R.B., 1997. Measuring biogenic carbon flux in the oceans. Science 275, 554–555.

Rivkin, R.B., Putland, J.N., Deibel, D., Anderson, M.R., 1999. Microzooplankton bacterivory and herbivory in the NE subarctic Pacific. Deep-Sea Research II 46, 2579–2618.

Roman, M.R., Caron, D.A., Kremer, P., Lessard, E.J., Madin, L.P., Malone, T.C., Napp, J.M., Peele, E.R., Youngbluth, M.J., 1995. Spatial and temporal changes in the partitioning of organic carbon in the plankton community of the Sargasso Sea off Bermuda. Deep-Sea Research I 42, 973–992.

Sheldon, R.W., Prakash, A., Sutcliffe, W.H., 1972. The size distribution of particles in the ocean. Limnology and Oceanography 17, 327–340.

Sherry, N.D., Boyd, P.W., Sigimoto, K., Harrison, P.J., 1999. Seasonal and spatial patterns of heterotrophic bacterial production, respiration, and biomass in the NE subarctic Pacific. Deep-Sea Research II 46, 2557–2578.

Silver, M.W., Gowing, M.M., 1991. The 'particle' flux: Origins and biological components. Progress in Oceanography 26, 75–113.

Smith, D.C., Simon, M., Alldredge, A.L., Azam, F., 1992. Intense hydrolytic enzyme activity on marine aggregates and implications for rapid particle dissolution. Nature 359, 139–142.

Strathmann, R.R., 1967. Estimating the organic carbon content of phytoplankton from cell volume or plasma volume. Limnology and Oceanography 12, 411–418.

Tabata, S., 1975. The general circulation of the Pacific Ocean and a brief account of the oceanographic structure of the North Pacific Ocean. Part I – Circulation and volume transports. Atmosphere 13, 133–168.

Takahashi, K., 1986. Seasonal fluxes of pelagic diatoms in the subarctic Pacific, 1982–1983. Deep-Sea Research 33, 1225–1252.

Taylor, G.T., Karl, D.M., 1991. Vertical fluxes of biogenic particles and associated biota in the eastern north Pacific: implications for biogeochemical cycling and productivity. Global Biogeochemical Cycles 5, 289–303.

Thibault, D., Roy, S., Wong, C.S., Bishop, J.K., 1999. The downward flux of biogenic Material in the NE subarctic Pacific: importance of algal sinking and mesozooplankton herbivory. Deep-Sea Research II 46, 2669–2697.

Tortell, P.D., Madonado, M.T., Price, N.M., 1996. The role of heterotrophic bacteria in iron-limited ocean ecosystems. Nature 383, 330–332.

Turley, C.M., 1992. Formation, vertical flux and remineralisation of aggregates in the ocean: a short review. Archiv. Fur Hydrobiologie Beiheft Ergebnisse der Limnologie 37, 155–163.

Turley, C.M., 1993. The effect of pressure on leucine and thymidine incorporation by free-living bacteria and by bacteria attached to sinking particles. Deep-Sea Research I 40, 2193–2206.

Turley, C.M., Mackie, P., 1994. Biogeochemical significance of attached and free-living bacteria and the flux of particles in the NE Atlantic Ocean. Marine Ecology Progress Series 115, 191–203.

Turley, C.M., Mackie, P., 1995. Bacterial and cyanobacterial flux to the deep NE Atlantic on sedimenting particles. Deep-Sea Research I 42, 1453–1474.

Turley, C.M., Stutt, E.D., 1999. Depth related cell specific leucine incorporation rates on particles and its biogeochemical significance in the NW Mediterranean. Limnology and Oceanography, submitted for publication.

Varela, D.E., Harrison, P.J., 1999. Seasonal variability in the nitrogenous nutrition of natural phytoplankton assemblages in the northeastern subarctic Pacific. Deep-Sea Research II 46, 2505–2538.

Wakeham, S.G., Canuel, E.A., 1988. Organic geochemistry of particulate matter in the eastern tropical North Pacifc Ocean: Implications for particle dynamics. Journal of Marine Research 46, 183–213.

Welschmeyer, N.A., Strom, S., Goericke, R., DiTuillio, G., Belvin, B., Petersen, W., 1993. Primary production in the subarctic Pacific Ocean: Project SUPER. Progress in Oceanography 32, 101–135.

Whitney, F.A., Freeland, H., 1999. Variability in upper ocean water properties along Line P in the NE Pacific Ocean. Deep-Sea Research II, this volume.

Wong, C.S., Whitney, F.A., Iseki, K., Page, J.S., Zeng, J., 1995. Analysis of trends in primary productivity and chlorophyll-a over two decades at Ocean Station P (50°N 145°W) in the Subarctic Northeast Pacific Ocean. Canadian Journal of Fisheries and Aquatic Science 121, 107–117.

Wong, C.S., Yu, Z., Johnson, W.K., Matear, R.J., Whitney, F.A., 1999a. Dissolved organic carbon in Sub-Arctic Northeast Pacific Ocean. In: Handa, N., Tanoue, E., Hama, T. (Eds.), Dynamics and Characterization of Marine Organic Matter, Terra Scientific Publishing Co., Tokyo, pp. 107–116.

Wong, C.S., Whitney, F.A., Crawford, D.W., Johnson, W.K., Iseki, K., Matear, R.J., Page, J.S., Timothy, D., 1999b. Seasonal and interannual variability in particle fluxes of carbon, nitrogen and silicon from time series of sediment traps at Ocean Station P, 1982–1993: relationship to changes in subarctic primary productivity. Deep-Sea Research II 46, 2735–2760.

Wu, J., Calvert, S.E., Wong, C.S., Whitney, F.A., 1999. Carbon and nitrogen isotopic composition of sedimenting particulate material at Station Papa in the subarctic northeast Pacific. Deep-Sea Research II 46, 2793–2832.