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Benthic community responses to pulses in pelagic food supply: North Pacific Subtropical Gyre

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Abstract

Time-series measurements of particulate organic carbon (POC) and particulate nitrogen (PN) fluxes, sediment community composition, and sediment community oxygen consumption (SCOC) were made at the Hawaii Ocean Time-series station (Sta. ALOHA, 4730 m depth) between December 1997 and January 1999. POC and PN fluxes, estimated from sediment trap collections made at 4000 m depth (730 m above bottom), peaked in late August and early September 1998. SCOC was measured in situ using a free vehicle grab respirometer that also recovered sediments for chemical and biological analyses on six cruises during the 1-year study. Surface sediment organic carbon, total nitrogen and phaeopigments significantly increased in September, corresponding to the pulses in particulate matter fluxes. Bacterial abundance in the surface sediment was highest in September with a subsurface high in November. Sediment macrofauna were numerically dominated by agglutinating Foraminifera fragments with highest density in September. Metazoan abundance, dominated by nematodes was also highest in September. SCOC significantly increased from a low in February to a high in September. POC and PN fluxes at 730 m above bottom were significantly correlated with SCOC with a lag time of $\leqslant 14$ days, linking pelagic food supply with benthic processes in the oligotrophic North Pacific gyre. The annual supply of POC into the abyss compared to the estimated annual demand by the sediment community (POC:SCOC) indicates that only 65% of the food demand is met by the supply of organic carbon. © 2002 Elsevier Science Ltd. All rights reserved.

Keywords: Benthic community; Abyssal zone; North Pacific Ocean; Carbon cycling

1. Introduction

Extensive efforts have been made in the last two decades to understand the cycling of carbon in the ocean. Long time-series studies were initiated at one station (Sta. ALOHA) in the Pacific as part of the Joint Global Ocean flux study (JGOFS) to study the temporal variations in the exchange rates of carbon between the atmosphere, ocean, seafloor and continental margins. This station was chosen as representative of the expansive North Pacific Subtropical Gyre (NPSG), one of the largest ecosystems in the world.

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Recent evidence at Sta. ALOHA revealed a dramatic shift in the photoautotrophic production of organic matter in the euphotic zone of the NPSG over the past decade from one dominated by eukaryotic algae to one based largely on cyanobacteria (Karl, 1999). The microbial domination of the production of organic matter in the surface waters creates a more intense remineralization of nutrients within the upper water column, reducing the amount of particulate matter exported to the deep sea. Sediment communities at abyssal depths in the ocean rely on the supply of reduced organic carbon that settles to the sea floor. The question is then raised as to the impact of a reduction of food export on deep-sea communities.

Major shifts in the planktonic communities resulting in rapid recycling of nutrients through the microbial loop and reduced export of particulate matter to the deep ocean with the possible consequence of an "abyssal famine" (Karl, 1999) is of major ecological concern. The export of newly produced organic carbon from the euphotic zone to the deep sea and the regeneration at depth, the "biological pump", is a key control of carbon dioxide in the atmosphere (Sarmiento and Siegenthaler, 1992). Measurements of the organic carbon export flux at Sta. ALOHA have indicated that the vast region represented by this station may be responsible for up to half of the global-ocean biological carbon pump (Emerson et al., 1997). However, in what Karl (1999) refers to as "oligotrophic ocean ecology and evolution *par excellence*", the phytoplankton–bacterial interactions have now been replaced with bacterial–bacterial interactions, resulting in a decrease in the export of carbon out of the euphotic zone within the past decade (Karl et al., 1997). It is critical that we examine the long-term changes in abyssal regions of the ocean and evaluate the influence of such climatic shifts on these remote communities since they cover such vast areas of the earth and represent an integral part of the oceanic ecosystem. The objective of our study was to address the question: Is there a temporal relationship between the utilization of organic carbon by the sediment community and the production and downward flux of particulate matter through the water column?

2. Area of investigation

The study site is located at Sta. ALOHA (22°45′N, 158°00′W; water depth of 4730 m), approximately 100 km north of Oahu (Karl and Lukas, 1996). This station is situated upwind of the Hawaiian Island chain over an abyssal area with little topographic relief and located more than one Rossby radius (50 km) from any steep topography (Fig. 1). The sediments are fine-grained pelagic clay with no manganese nodules encountered during our sampling program.

Mean annual net primary production at Sta. ALOHA measured on 74 cruises over a 9-year period (1989–1997) was 14.5 mol C m^{-2} yr^{-1} (Karl, 1999). A recurring seasonal trend in primary production exhibits winter minima and late spring maxima. Particulate matter fluxes from the euphotic zone show two major export periods per year, one in late winter and the other in late summer (Karl et al., 1996). The winter pulse is believed to be related to nitrate supplied through stochastic upwelling; the summer pulse is supported by nitrogen from N_2 fixation (Karl et al., 1997).

Results of previous work at this study site show particulate matter fluxes through the deep water column exhibit temporal coherence with particulate matter export from the euphotic zone, reflecting an estimated sinking rate of >200–300 m day^{-1} following a major export event (Karl et al., 1996). These measurements, based on the sediment trap collections at 800 and 4000 m depth, would result in a sinking time of 11–19 days. Moored sediment traps collected sinking particulate matter at 4000 m depth (730 m above bottom) with a sampling frequency of 14–17 days. From April 1997 through January 1999 (time period selected for comparison with our benthic studies), there were pronounced peaks in both particulate organic carbon (POC) and particulate nitrogen (PN) fluxes in July 1997 and then again in late August to early September of 1998 (Fig. 2). The lowest particulate fluxes of organic carbon and nitrogen were in fall and winter, with the exception of a minor peak in December 1998. The molar C:N of this particulate matter was highest in August and September of 1997 and February of 1998,

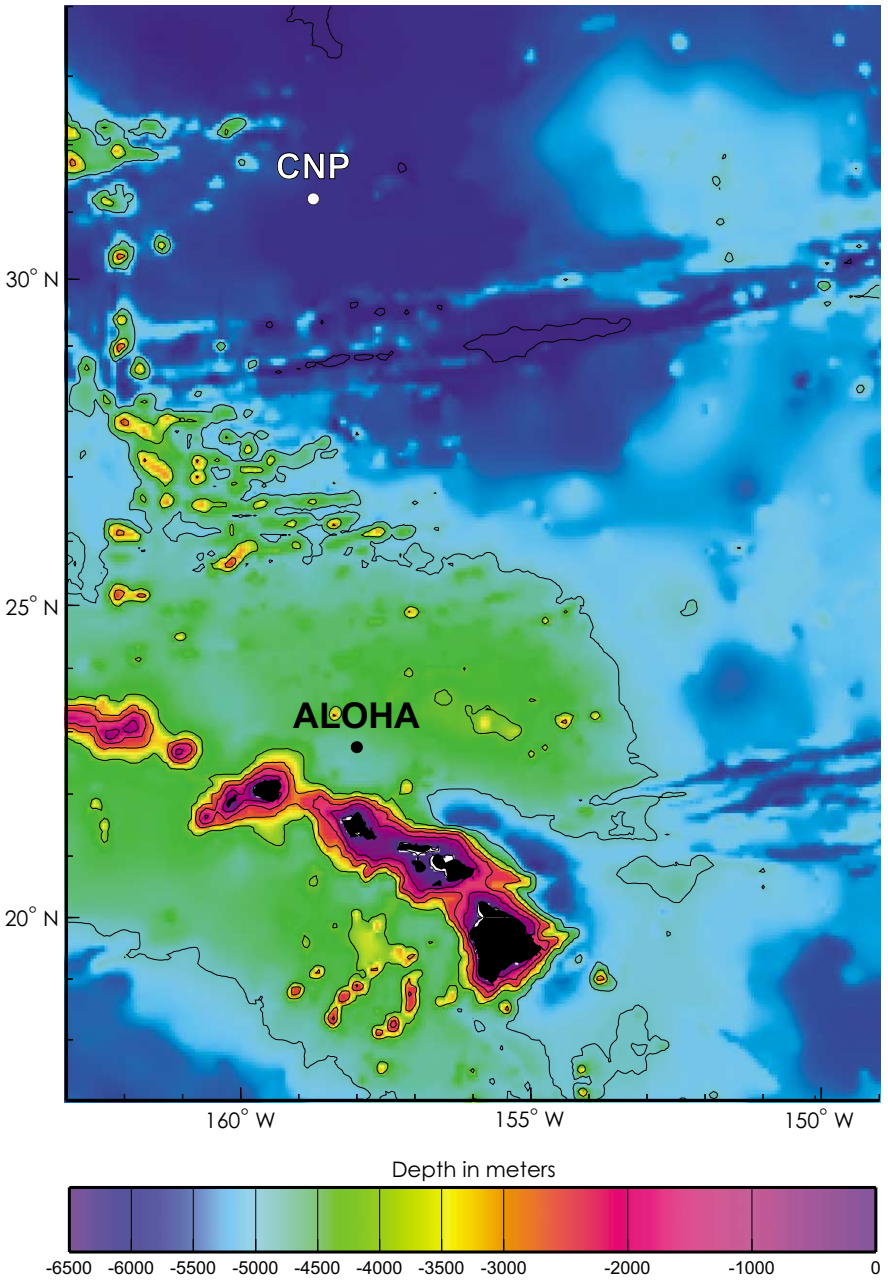


Fig. 1. Topographic chart of the central North Pacific and Hawaiian Island Chain showing the location of Stas. ALOHA and CNP.

when the fluxes were low, but then fell to a relatively consistent ratio between 10 and 15 for the rest of the monitoring period. No sediment trap samples were collected between 1 October 1997 and 6 January 1998.

3. Methods

In situ measurements of sediment community oxygen consumption (SCOC) and sampling of the overlying water and sediments were made with the

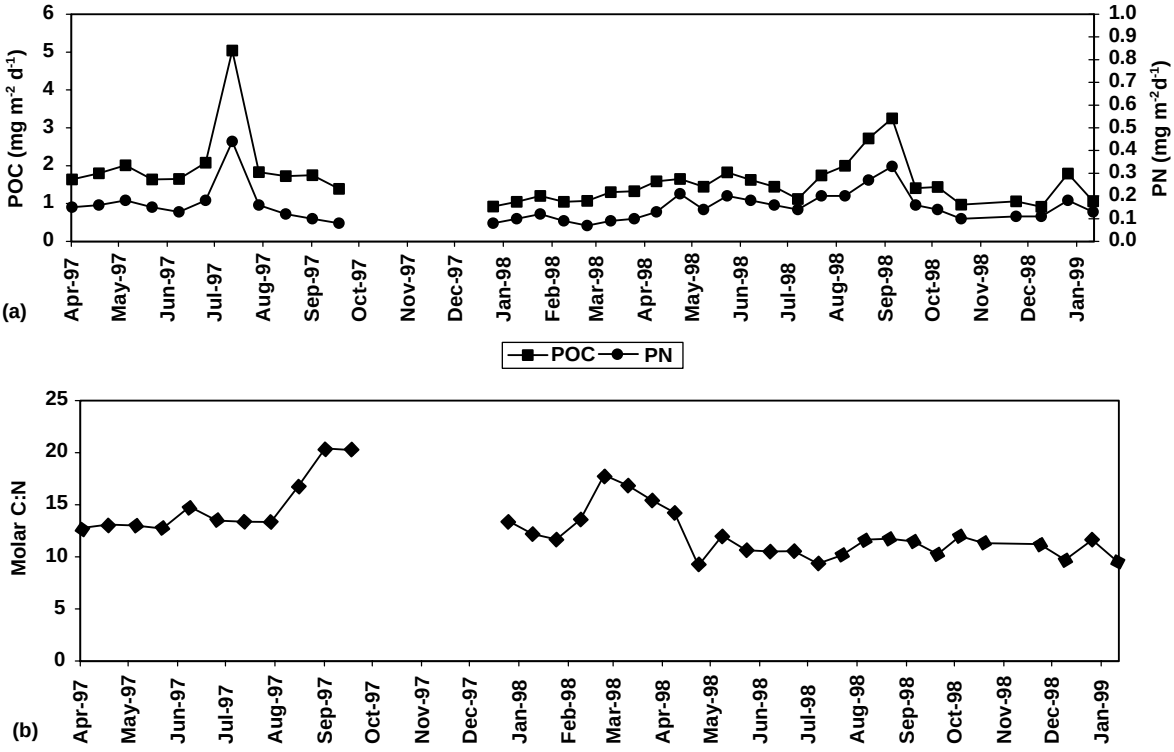


Fig. 2. The flux of POC and PN at 4000 m depth at Sta. ALOHA. (a) POC and PN flux from April 1997 to January 1999. (b) The molar C:N of the particulate matter flux for the same sampling period. A hiatus in sampling occurred between September and December 1997.

free vehicle grab respirometer (FVGR) (see Smith (1987), for a full description of this instrument). The FVGR is an autonomous instrument, ~2 m on a side and 4 m high and consisting of flotation, a centrally located instrument package and a ballast release mechanism. This instrument was deployed for periods of 40–44 h on each of six cruises to Sta. ALOHA between December 1997 and January 1999.

One hour after landing on the sea floor, the central instrument package, consisting of four stainless steel grabs, was slowly pushed into the sediment by a hydrostatic piston actuated with an electronic timer. Each grab enclosed 413 cm^2 of sediment surface to a depth of ~15 cm, leaving an overlying water column of ~15 cm. A polarographic oxygen sensor in each grab monitored the dissolved oxygen concentration during the entire incubation, with the enclosed water constantly stirred to simulate natural current flow and prevent stratification. At the end of the incubation, the grab jaws on each chamber were closed, the ballast weights were released, and the instrument rose to the surface for recovery.

Two 5-l Niskin bottles, attached to the lower portion of the FVGR frame, were triggered by burnwire releases (one to close at the initiation of the incubation and the other to close at the end of the incubation). On recovery, the enclosed bottom water was immediately analyzed for dissolved oxygen by a Winkler titration method. The difference between the oxygen concentrations in the initial and final water samplers, an estimate of the oxygen consumption associated with organisms in the overlying water in each grab, was consistently negligible.

The depth of the overlying water in each grab was measured and the water removed. One grab

was subcored (8.2 cm inside diameter core) for chemical analyses; the three remaining grabs were sieved through a 300-μm mesh screen and preserved in 10% formalin for macrofaunal analyses. The subcore for chemical analysis was held at ambient bottom temperature (1.5°C) and sectioned at 2.5 mm intervals to a depth of 40 mm. Nine sediment subsamples (0.5 cm^3) were taken from each section, six frozen at −70°C for chemical analyses and 3 placed in 5% formalin for sediment bacteria counts.

In the laboratory, the frozen sediment samples were thawed, lyophilized, ground and weighed. Subsamples were analyzed in duplicate for total carbon and nitrogen with a Perkin-Elmer CHN analyzer, and for inorganic carbon with a coulometer (Smith et al., 1994). The organic carbon fraction was calculated as the difference between the total and inorganic carbon. Additional sediment subsamples from each depth were analyzed in triplicate for chlorophyll *a* and phaeopigments (Parsons et al., 1984) with a Turner Designs fluorometer. All mass determinations were corrected for salt content.

Samples of bacterial numbers were prepared according to the method of Velji and Albright (1986) with 1 min of sonification on ice (output: 50 W, LABSONIC U, BRAWN). Each sample was diluted 1:2400 before concentration of a known volume on a filter. The high-dilution factor was necessary to avoid coverage of the filter with clay particles, limiting the counts per grid to a maximum of 10 cells. Bacterial numbers were determined by epifluorescence microscopy (ZEISS AXIOSKOP) after staining with acridine orange (Meyer-Reil, 1983). Each value represents the mean of 50 grid counts from one filter.

The macrofauna samples were stained with a protein stain, Rose Bengal, sorted to major taxa, and counted. The agglutinated Foraminifera generally broke into fragments during the sieving and sorting procedure so we have presented only the number of fragments for each sampling period as an estimate of their relative abundance between sampling periods, including only those stained pink and assumed to be living when sampled.

Statistical comparisons of each measured parameter with sampling period were first examined with the Kruskall–Wallis H test and then the Mann–Whitney U paired test to differentiate significance between each sampling period. The Spearman rank test was used to examine correlations between measured parameters (Zar, 1998). The primary production, flux of POC and nitrogen at 4000 m depth, and SCOC were compared by a parametric cross-correlation analysis followed by a Spearman rank test for those periods of maximum positive correlation. Each data set was treated as a stationary time series, and paired correlations in 14-day increments were computed from 0 to 140 days (second data set lagged relative to first data set; cf. Wei, 1990).

4. Results

4.1. Sediment chemistry

Sediment organic carbon was generally highest at the surface and declined with increasing depth (Fig. 3a). The highest concentration of organic carbon was measured in September 1998, coinciding with increased POC fluxes (Fig. 2a). The lowest concentration of organic carbon in the surface sediment was measured in February 1998 when the profile was almost vertical in the upper 4 cm of the sediment and the sinking particulate fluxes were low. The subsurface sediment organic carbon was consistently between 2.5 and 3 mg C $gdwt^{-1}$ ($gdwt^{-1}$ = per gram dry weight) below 2 cm depth except in December 1997, when the concentrations dropped below 2 mg C $gdwt^{-1}$. The mean organic carbon content for the upper 10 mm of the sediment for each sampling period was low in February 1998, significantly increasing to a high in September 1998 (Mann–Whitney test, $p = 0.01$; $U_{(2),8,8}$) and then declining again in November 1998 (Fig. 4a).

Profiles of sediment total nitrogen declined with increasing depth, being most pronounced in December 1997 and September 1998, when the surface concentrations were the highest (Fig. 3b). The lowest nitrogen concentrations were measured in June 1998 and January 1999. Total nitrogen in the upper 10 mm of the sediment was highest in December 1997, declining to a low in June 1998

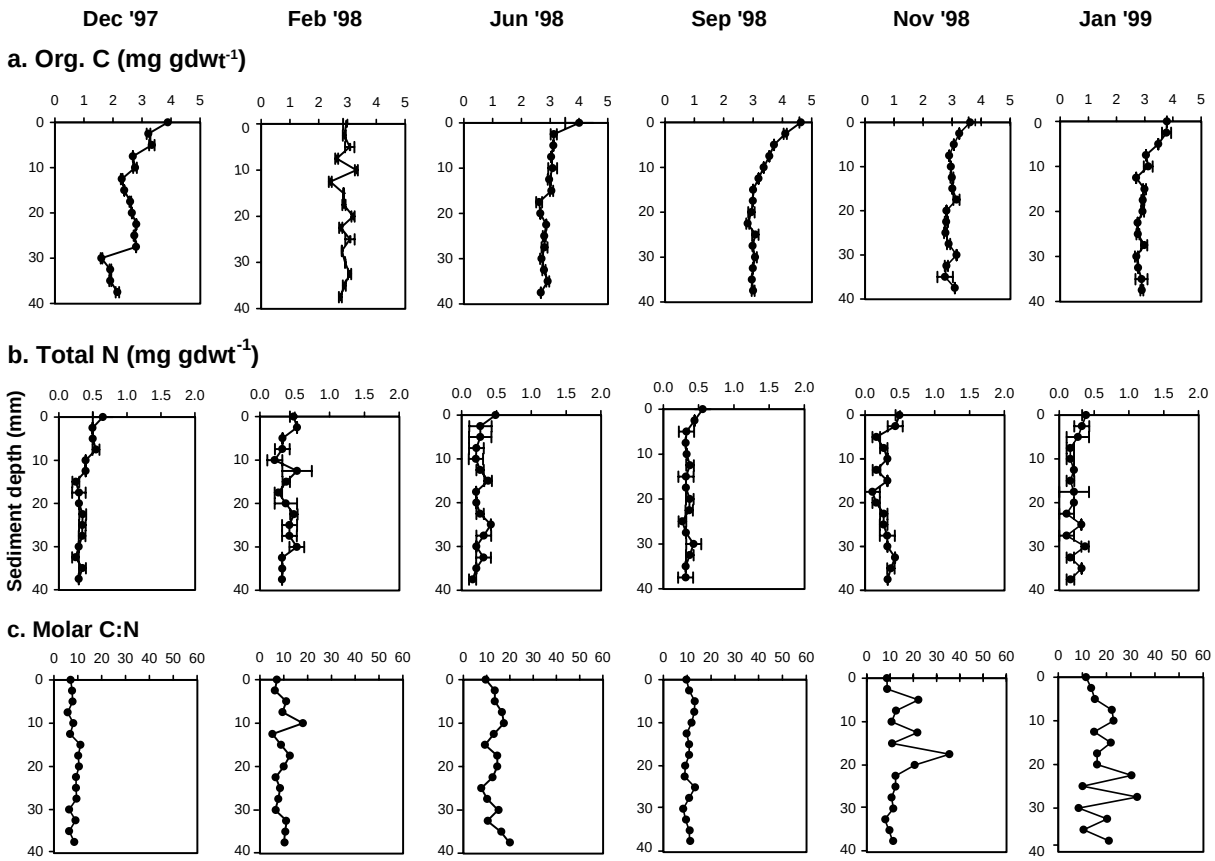


Fig. 3. Vertical profiles of sediment chemical parameters measured in triplicate (mean ± SD) at 2.5 mm depth intervals to a depth of 40 mm from December 1997 to January 1999 at Sta. ALOHA: (a) organic carbon, (b) total nitrogen, and (c) molar C:N.

and then increasing significantly to a second high in September 1998 ($p = 0.009$; $U_{(2),7,8)}$) before declining again until January 1999 (Fig. 4a).

The molar ratio of organic carbon:total nitrogen consistently ranged from 7 to 11 with subsurface depth ratios of 40 in November 1998 and January 1999 (Fig. 3c). The ratio in the surface sediment was highest in June 1998, significantly declining in sampling periods before ($p = 0.028$; $U_{(2)4,4}$) and afterwards ($p = 0.028$; $U_{(2)4,4}$) (Fig. 4b). There was no obvious relationship between the C:N of the sediments and the C:N of the particulate matter fluxes (Fig. 2b).

Chlorophyll *a* concentrations in the sediment declined with depth from the surface. Highest concentrations of chlorophyll *a* occurred in September 1998 ranging from a mean of $13.2\,\mu g\,gdwt^{-1}$ at the surface (September 1998) to levels of $\leqslant 5\,\mu g\,gdwt^{-1}$ (Fig. 5a). During February 1998 and June 1998 there was little variability between replicate sampling, in contrast to September 1998, which exhibited the greatest variability from the surface to the maximum depth of collections at 40 mm. There was no significant difference (Kruskall Wallis, $H_{5,47}$; $p > 0.05$) between the four sampling periods in the upper 10 mm of the sediment, possibly because of the high variability in chlorophyll *a* concentrations within sampling periods indicating the patchy distribution of phytoplankton particles (Fig. 4c).

Phaeopigments, degradation products of chlorophyll, had higher concentrations in the surface

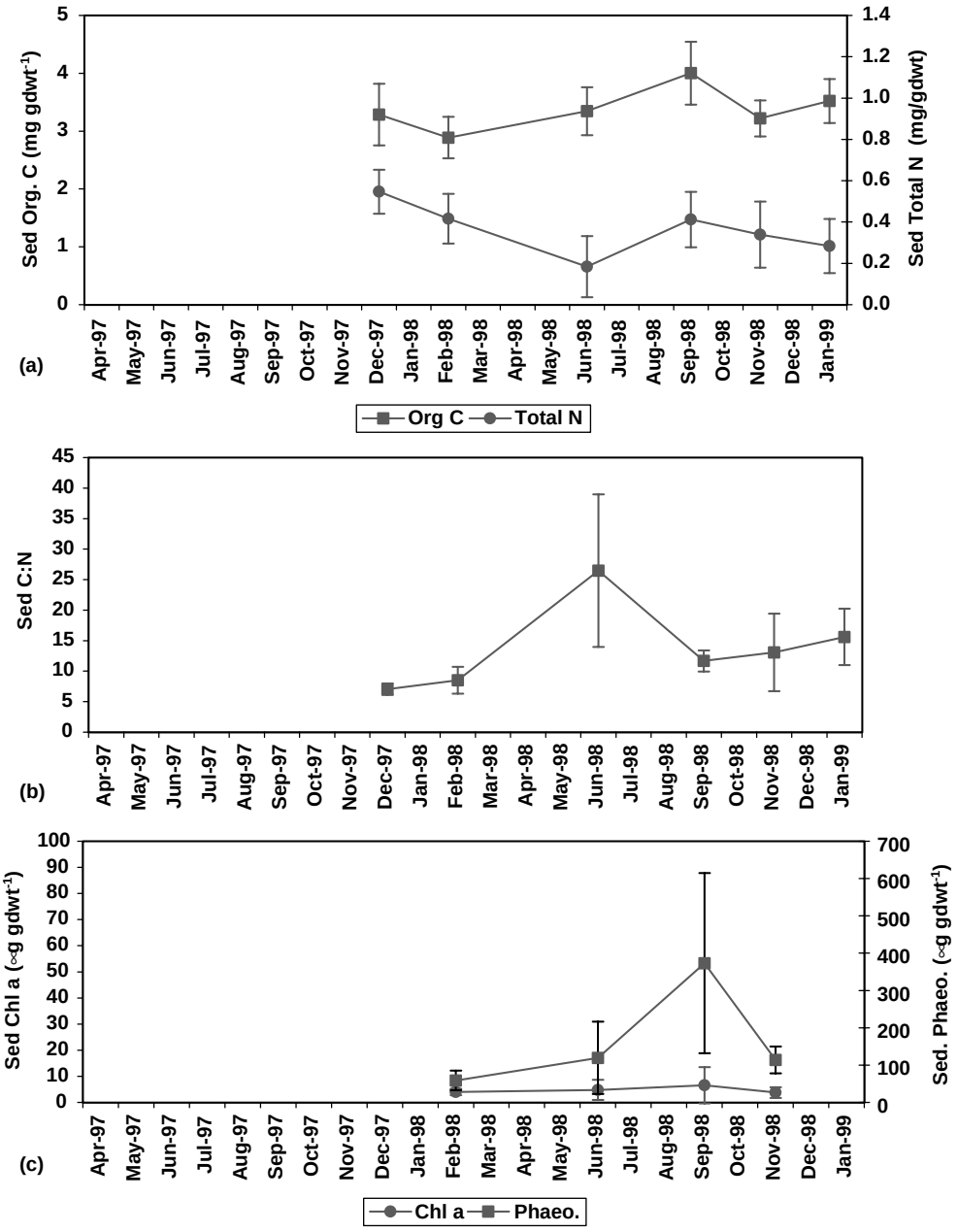


Fig. 4. Surface sediment chemical parameters taken at 2.5 mm depth intervals to a depth of 10 mm (mean ± SD) from December 1997 to January 1999 at Sta. ALOHA: (a) organic carbon and total nitrogen, (b) molar C:N and (c) chlorophyll *a* and phaeopigments. Pigment concentrations were not available for December 1997 and January 1999.

layer of sediments, reaching stable concentrations below 5 mm (Fig. 5b). The exception was September 1998, when the surface phaeopigment concentration was highest, 734 μg gdwt^{-1}, precipitously declining to 148 μg gdwt^{-1} at 10 mm depth. Below 10 mm there was a distinct increase to 15 mm,

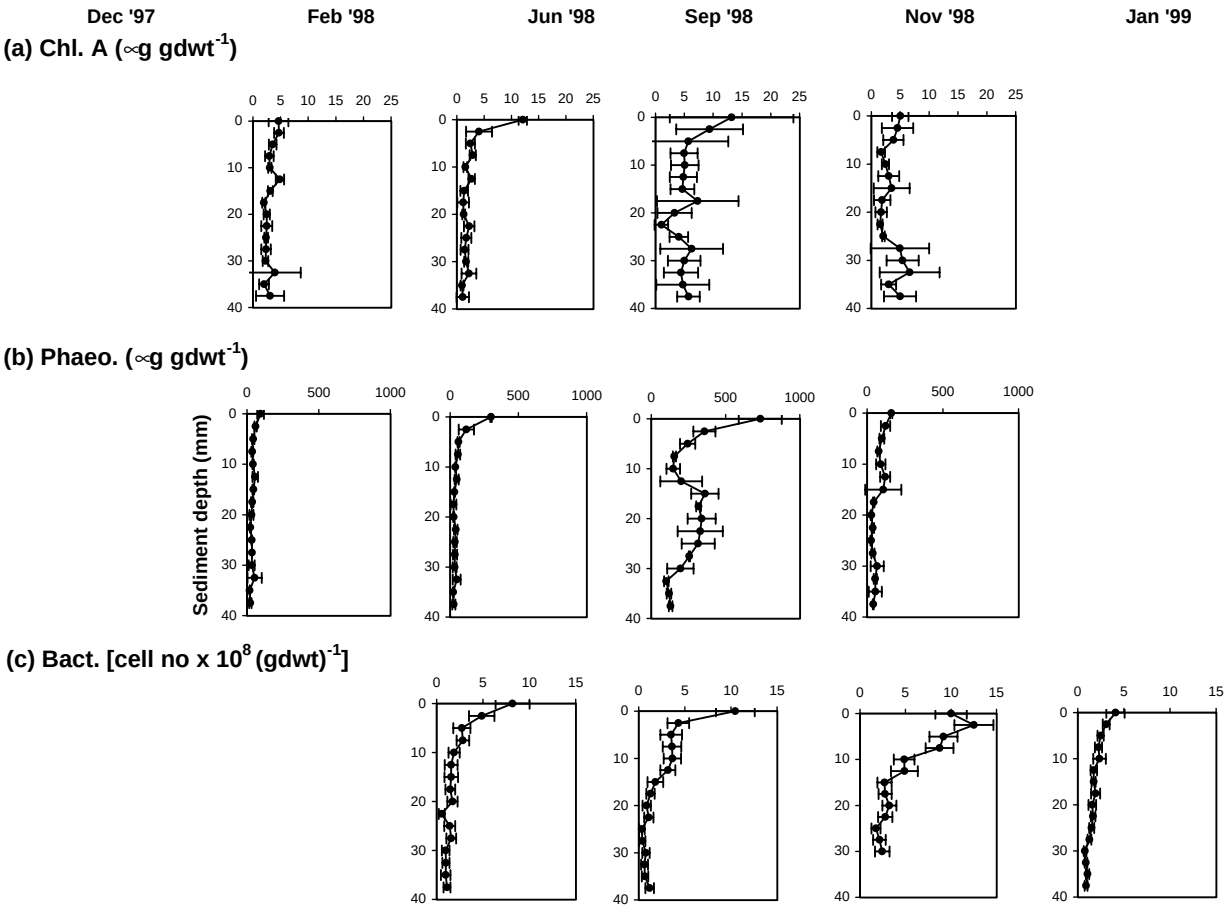


Fig. 5. Vertical profiles of sediment chemical parameters (mean ± SD) and bacterial count (mean ± C.I.) taken at 2.5 mm depth intervals to a depth of 40 mm from December 1997 to January 1999 at Sta. ALOHA: (a) chlorophyll *a*, (b) phaeopigments and (c) bacterial count. Bacterial counts were not available for December 1997 and February 1998; pigment concentrations were not available for December 1997 and January 1999.

suggesting that a mixing event may have occurred during this period of maximum particulate fluxes to the sea floor. Such a mixing event was not evident in any of the other sediment parameters measured in this study.

Surface phaeopigment concentrations follow a pattern similar to that of surface chlorophyll *a*, but the increase from June 1998 to a peak in September 1998 was significant ($p = 0.0007$; $U_{(2),11,12}$) (Fig. 4c). The high phaeopigment values in September 1998 corresponded to peaks in particulate carbon and nitrogen fluxes recorded in August and September 1998 at 4000 m (Fig. 2a). After the September 1998 peak, phaeopigments significantly declined in the next sampling period, November 1998 ($p = 0.0001$; $U_{(2),12,12}$).

4.2. Sediment community composition

Sediment bacteria were most abundant at the sediment-water interface and generally decreased in number with increasing depth (Fig. 5c). The highest bacterial abundance occurred in September 1998 with a bacterial cell count of 10.47×10^8 (gdwt sediment)$^{-1}$ in the surface sediment, declining to a low of 0.34×10^8 cells (gdwt sediment)$^{-1}$ at 27.5 mm depth. In November 1998, there was a subsurface maximum at 2.5 mm depth, 12.51×10^8

cells (gdwt sediment)$^{-1}$, which remained high through 10 mm depth before declining with increasing depth.

In the uppermost 2.5 mm of the sediment, bacterial abundance was highest in September 1998 (Fig. 6a), coinciding with the periods of highest fluxes of particulate organic matter and highest concentrations of sediment carbon, nitrogen and chlorophyll *a*. Considering the combined bacterial counts in the upper 10 mm of the sediment, abundance was highest in November, following the high particulate matter fluxes in September. The lowest bacterial abundance occurred in January 1999, when there was little subsample variability and the numbers declined gradually with depth (Fig. 6a). The high bacterial counts in November 1998 were significantly higher than those in June 1998 ($p = 0.03$; $U_{(2)4,4}$) and January1999 ($p = 0.02$; $U_{(2)4,4}$) but not significantly different from those in September 1998.

Sediment macrofauna were numerically dominated by agglutinating Foraminifera fragments, accounting for $\geqslant 90\%$ of the abundance, with highest density in September 1998 and lowest density in February 1998. Other dominant protozoans, calcareous Foraminifera and Komokiacea, were of minor numerical importance compared to the agglutinating Foraminifera, indicating no obvious seasonal variability. The combined protozoan abundance integrated over 15 cm, the average depth of grab penetration, ranged from a low of $10{,}863 \pm 5789$ units m^{-2} in February 1998 to $18{,}491 \pm 3929$ units m^{-2} in September 1998 (Fig. 6b), with no significant variation between sampling periods ($H = 2.6$; $p = 0.76$). Protozoan biomass is difficult to assess because of our inability to separate the disproportionate weight of the test from the small quantity of protoplasm, especially in the agglutinating species. Being cognizant of this problem, we found the protozoan biomass ranged from 1.2 ± 0.6 g m^{-2} in June 1998 to a high of 3.8 ± 2.9 g m^{-2} in December 1997 (Fig. 6b) with no significant variation between sampling periods ($H_{5,15} = 1.86$; $p = 0.86$).

Metazoan numerical abundance was considerably less than that of the protozoans, ranging from 517 ± 196 m^{-2} in February 1998 to 839 ± 331 m^{-2} in September 1998 (Fig. 6c) with no significant variation between sampling periods ($H = 4.29$; $p = 0.51$). The trend in the two lines representing the abundance of protozoans and metazoans is quite similar with peaks in September 1998. The metazoan component of the infauna was generally dominated by nematodes that reached a significant peak abundance in September 1998 ($p = 0.04$; $U_{(2)3,3}$) and were least prevalent in November 1998 and December 1997 (Fig. 7a). Other prominent metazoan taxa were the crustaceans, consisting largely of calanoid and harpacticoid copepods, which were most abundant in November 1998 and constituted over 50% of the metazoan animals. Polychaetes and bivalve mollusks were minor contributors to the overall metazoan abundance. A benthic sampling program at Sta. ALOHA in July 1992 also found the metazoan component to be dominated by nematodes (Brown et al., 2001) and the total macrofaunal abundance to be 290 ± 33 m^{-2} (from Fig. 9b in Smith et al., 1997).

Metazoan biomass revealed no significant seasonal variation ($H = 5.4$; $p = 0.36$), being lowest in September 1998, 0.01 ± 0.01 g m^{-2}. The metazoan biomass was an order of magnitude higher in January 1999 (0.13 g m^{-2}), but it was based on a single grab sample (Fig. 6c). Polychaetes and crustaceans were the gravimetrically dominant metazoans with nematodes contributing negligibly (Fig. 7b). Crustacean biomass was highest in September 1998 during the peaks in particulate carbon flux; the polychaete biomass was highest during four other sampling periods in February 1998, June 1998, November 1998 and January 1999. The dominance of the "other" category, especially in December 1997 and February 1998, was attributable to small ophiuroids, sponges and tunicates not present in samples from the other periods.

4.3. Sediment community oxygen consumption

SCOC significantly increased ($H = 17.0$; $p = 0.004$) after a low in February 1998 of 1.64 ± 0.12 mg C m^{-2} day^{-1} (0.16 mmol O_2 m^{-2} day^{-1}) and continued to increase through June to a peak of 3.55 ± 0.26 mg C m^{-2} day^{-1} (0.34 mmol O_2 m^{-2} day^{-1}) in September 1998, coinciding with the peak in POC and PN fluxes

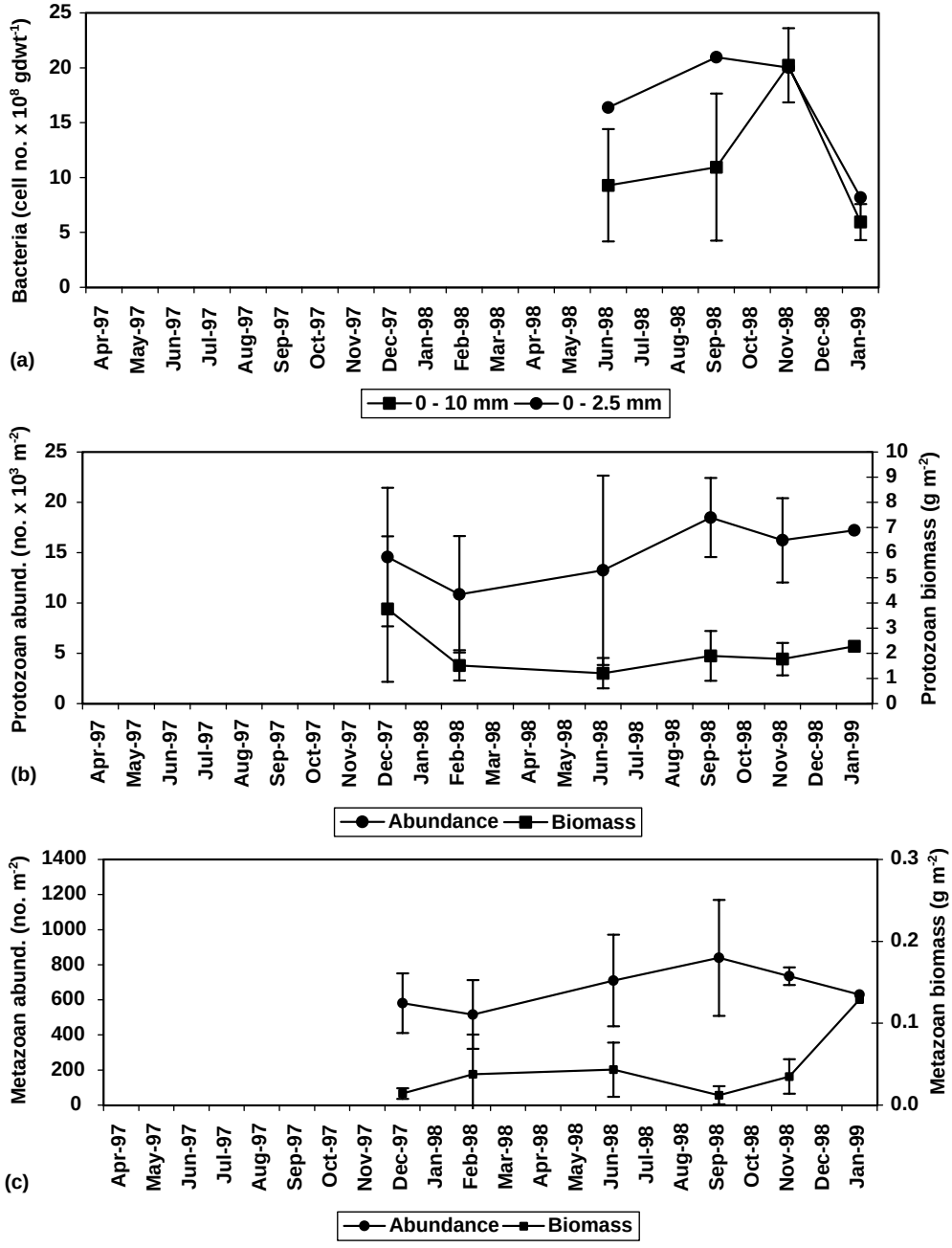


Fig. 6. Sediment biota in the surface sediments at Sta. ALOHA: (a) sediment bacterial count (mean ± C.I.) taken at 2.5 mm depth intervals to a depth of 2.5 and 10 mm from June 1998 to January 1999, (b) protozoan and (c) metazoan abundance and biomass from December 1997 to January 1999 at Sta. ALOHA.

(Fig. 8a and b). After the September peak in SCOC, the rates decreased in November 1998 and January 1999 to levels similar to those measured the previous winter. The September 1998 peak in SCOC corresponded to highs in surface sediment organic carbon, total nitrogen, chlorophyll *a*,

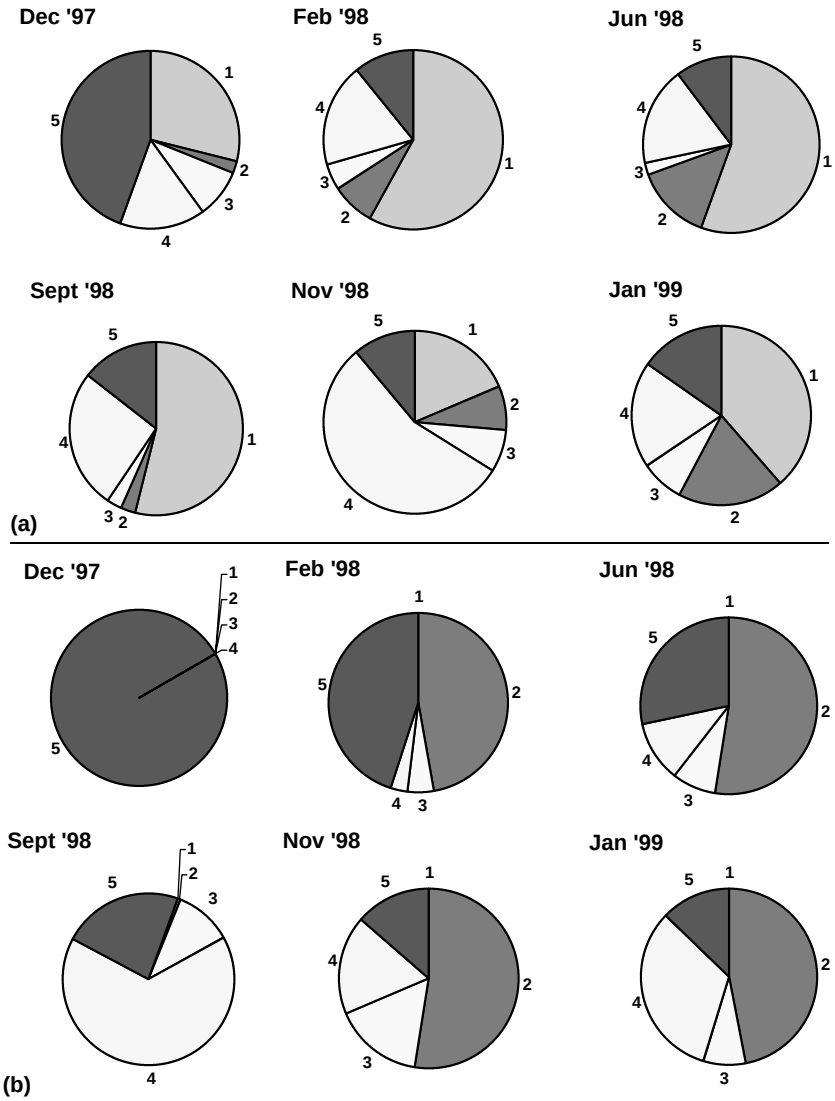
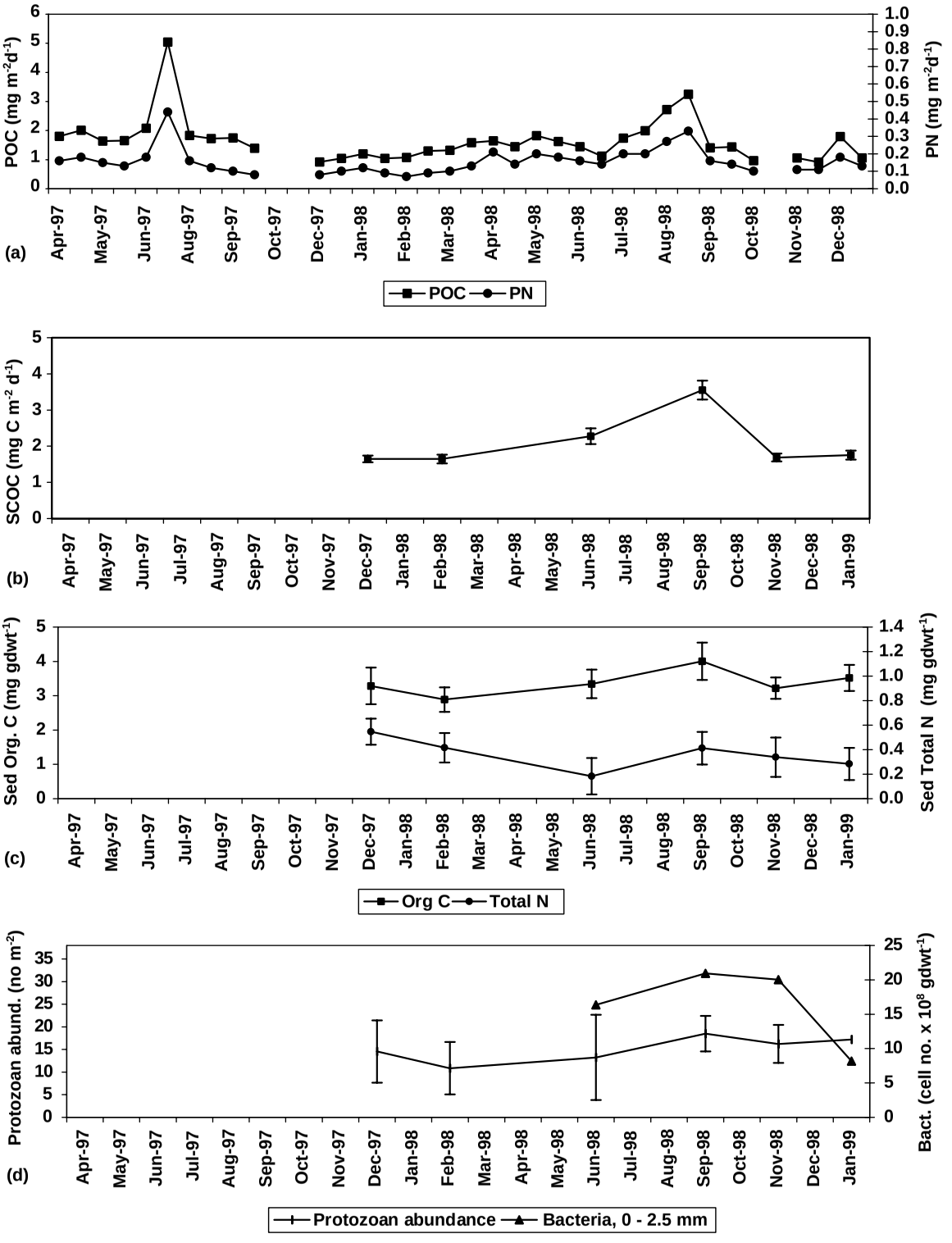


Fig. 7. Sediment metazoan abundance and biomass frequencies sampled on six cruises December 1997 to January 1999 at Sta. ALOHA: (1) nematodes, (2) polychaetes, (3) molluscans, (4) crustaceans, and (5) other. (a) abundance (no. m^{-2}) and (b) biomass ($g\,m^{-2}$).

phaeopigments and bacterial abundance (Fig. 8c and d). Sediment infaunal abundance, dominated by Foraminifera, also reached a peak in September 1998. SCOC was significantly correlated with sediment organic carbon ($r = 0.44$; $p = 0.03$) and phaeopigments ($r = 0.53$; $p = 0.04$).

The pulse of sinking particulate organic matter to the sea floor in September obviously stimulates the sediment community activity, supporting a coupling between the supply of organic matter and its utilization by the sediment community. A cross-correlation analysis of particulate matter fluxes


POC (mg m-2d-1)
PN (mg m-2d-1)
(a)
POC
PN
SCOC (mg C m-2 d-1)
(b)
Sed Org. C (mg gdwt-1)
Sed Total N (mg gdwt-1)
(c)
Org C
Total N
Protozoan abund. (no m-2)
Bact. (cell no. x 10^8 gdwt-1)
(d)
Protozoan abundance
Bacteria, 0 - 2.5 mm
Apr-97
May-97
Jun-97
Jul-97
Aug-97
Sep-97
Oct-97
Nov-97
Dec-97
Jan-98
Feb-98
Mar-98
Apr-98
May-98
Jun-98
Jul-98
Aug-98
Sep-98
Oct-98
Nov-98
Dec-98
Jan-99

(4000 m depth) and SCOC revealed the most significant correlation at $\leqslant$14 days for POC_{4000} flux ($r = 0.90$, $n = 5$; $p = 0.037$) and PN_{4000} flux ($r = 0.97$, $n = 5$; $p = 0.0048$). Hence, the sinking particulate matter settles from 4000 m to the sea floor at 4730 m depth and elicits a significant response in the sediment community within 14 days.

The annual flux of POC at 4000 m depth, estimated by integrating the area under the POC flux curve in Fig. 8a from 1 January 1998 until 1 January 1999, yielded an organic carbon input of 470 mg C m^{-2} yr^{-1}. This supply of organic carbon into the abyssal zone at 730 mab can be compared with the demand for organic carbon, as estimated by integrating the curve representing SCOC over the same time period (Fig. 8b). The demand for organic carbon by the sediment community is 727 mg C m^{-2} yr^{-1}, exceeding the annual supply by 257 mg C m^{-2} yr^{-1}. The POC:SCOC is 0.65, indicating that only 65% of the demand is met by the supply of organic carbon collected with sediment traps at 730 mab.

5. Discussion

5.1. Comparisons with CNP and equatorial Pacific stations

One of the most studied abyssal regions of the ocean is located approximately 1100 km north of Sta. ALOHA (Fig. 1). Although this station (Sta. CNP; Smith, 1992) was not studied with a long time-series in mind, it warrants some comparison with Sta. ALOHA. Sta. CNP is located in the abyssal hill region north of the Murray Fracture Zone with water depths of 5700–5900 m (Smith et al., 1983). The oxygenated clay sediments had a surface organic carbon content of 3.4–5.7 mg C gdwt^{-1}(Smith, 1987), which is very similar to the range measured at Sta. ALOHA (Fig. 4a). Macrofauna abundance of 201–841 individuals m^{-2} at Sta. CNP, collected and analyzed in the same manner as in this study (Smith, 1987), fell within the range of metazoan abundance at Sta. ALOHA (Fig. 6c).

In situ measurements of SCOC (total $n = 63$) were made intermittently with the FVGR at Sta. CNP from August 1978 through June 1987 (Fig. 9a). SCOC reached a high of 3.86 mg C m^{-2} day^{-1} (0.37 mmol O_2 $m^{-2}$$day^{-1}$) in June 1982 and a low of 0.44 mg C m^{-2} day^{-1} (0.04 mmol O_2 m^{-2} day^{-1}) in November 1982. We compared the SCOC measured during the same months but different years at Sta. CNP and found no significant difference between years, with the exception of June 1982 and June 1987 ($p = 0.007$). At Sta. ALOHA more than a decade later, the SCOC reached a high comparable to those at Sta. CNP of 3.87 mg C m^{-2} day^{-1} (0.38 mmol O_2 m^{-2} day^{-1}) in September 1998 (Fig. 9b). However, the SCOC at Sta. ALOHA never fell below 1.5 mg C m^{-2} day^{-1} (0.15 mmol O_2 m^{-2} day^{-1}), three times greater than that of the lowest SCOC measured at Sta. CNP (Fig. 9a and b).

When the SCOC measurements for both stations are plotted by month regardless of year, it is evident that the rates at Sta. ALOHA are generally higher with the exception of June, when they are similar (Fig. 9c). For the two months when SCOC was measured at both stations, June and November, in only November were the rates significantly higher at Sta. ALOHA ($r = 0.75$; $p = 0.03$). As there are obvious interannual variations in SCOC at Sta. CNP (Fig. 9a), longer time scale variability also must be considered.

In the central Equatorial Pacific to the south of Sta. ALOHA, SCOC was measured along two transects, one east–west along the equator in January 1992 and one north–south across the equator in December 1992 (Hammond et al., 1996). SCOC was considerably higher along the equator (0.42–0.80 mmol O_2 m^{-2} day^{-1}) between 2°S and 5°N latitude and 140°W longitude than SCOC measured at either Sta. ALOHA or Sta.

Fig. 8. A comparison of POC and PN flux measured at 4000 m depth, with sediment chemical and biological parameters and SCOC measured at 4730 m at Sta. ALOHA: (a) POC and PN flux, (b) SCOC, (c) surface sediment organic carbon and total nitrogen, (d) protozoan abundance and bacterial count.

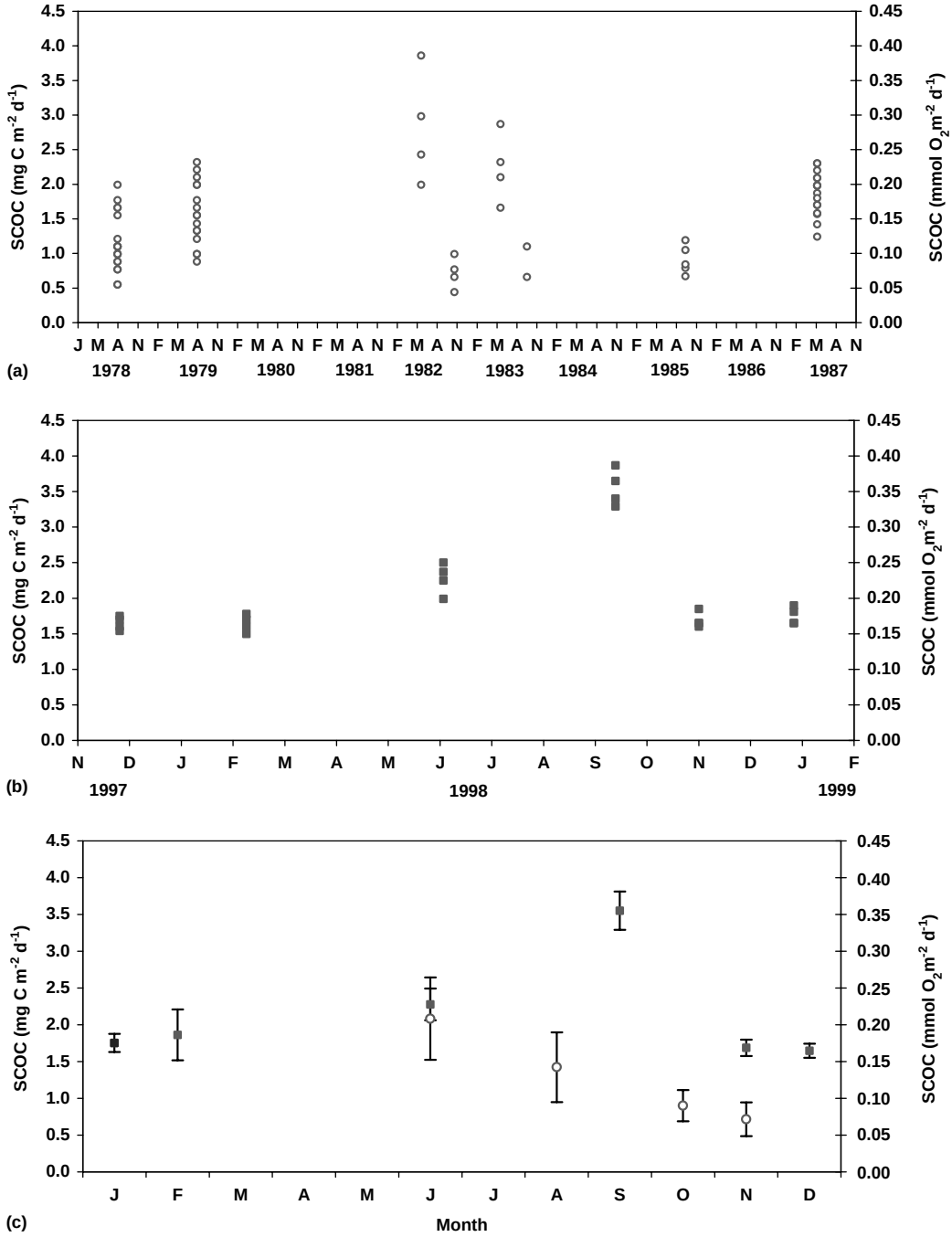


Fig. 9. Comparison of SCOC measured over a 21-year period at Sta. CNP and Sta. ALOHA: (a) individual SCOC measurements at Sta. CNP from 1978 to 1987, (b) individual SCOC measurements at Sta. ALOHA from Dec 1997 to January 1999, (c) comparison of SCOC by month (mean + SD) for Stas. CNP (○) and ALOHA (■).

CNP (Fig. 9). However, SCOC rates at Stas. ALOHA and CNP were comparable to those measured for the same season at a single station at 12°S (0.14 mmol $O_2\,m^{-2}\,day^{-1}$; Hammond et al., 1996), which was located beyond the influence of the enriched equatorial upwelling region.

These intermittent point measurements in the Equatorial Pacific and at Sta. CNP are difficult to compare to long time-series measurements given the known variability in such measurements on seasonal, interannual and decadal time scales (Smith and Kaufmann, 1999; Smith et al., 2001). There is accumulating evidence that decadal scale climatic shifts influence coastal and upper ocean communities (Mantua et al., 1997; McGowan et al., 1998; Hare and Mantua, 2000). Major climatic regime shifts in the North Pacific occurred in 1977 with minor shifts recorded in 1989 (Overland et al., 2000). Preliminary evidence now suggests that another major regime shift occurred in 1998–1999 (Bogard et al., 2000). In the major regime shift of 1976–1977, atmospheric forcing drove the Aleutian low-pressure system southward, which led to intensified westerly winds. As a result, sea surface temperature increased in the eastern North Pacific and decreased in the central North Pacific. Mixed layer depth shoaled in the subarctic Pacific and deepened in the central Pacific (Hayward, 1997). During this period, the central Pacific experienced increased chlorophyll *a* and primary production in the euphotic zone (Hayward, 1987; Venrick et al., 1987; Karl, 1999), impacting the export of organic matter to the abyss.

5.2. Pelagic–benthic coupling

The coupling between the pelagic supply of food originating in surface waters and its ultimate arrival and utilization by the sediment community has been shown in several studies of abyssal regions in the North Atlantic (Pfannkuche and Lochte, 1993; Pfannkuche et al., 1999) and the North Pacific (Smith et al., 1992, 1994; Lauerman et al., 1997). At Sta. ALOHA, we have identified coupling between the flux of particulate organic matter entering the benthic boundary layer and its arrival on the sea floor that appears to be correlated with the increase in bacterial and Foraminifera abundance. These positive responses of the sediment community standing stocks to peaks in particulate organic matter fluxes also are associated with increased SCOC. Similarly, seasonal pulses of POC fluxes to the abyssal sea floor in the eastern North Pacific (Sta. M) were temporally correlated with increased SCOC in summer and fall (Drazen et al., 1998). However, at the eastern North Pacific site the sediment Foraminifera and metazoans increased in abundance in winter months, after pulses of POC flux had subsided.

Time-series studies of abyssal activity in the eastern North Atlantic have shown similar responses to those in the North Pacific. Seasonal deposition of phytodetritus on the sea floor resulted in increased abundance of benthic organisms including bacteria, foraminiferans, and nematodes (Gooday and Turley, 1990; Pfannkuche, 1993). For example, at >4500 m (BIOTRANS site) the sediment bacterial biomass doubled immediately after a sedimentation event of phytodetritus reached the seafloor in July. Similarly, the SCOC doubled between April and July at the same site (Pfannkuche, 1993). However, these benthic responses vary from year to year depending on the quantity and quality of the sedimenting particulate organic matter (Pfannkuche et al., 1999). During sedimentation events, the microbial community response in the sediments can vary from almost immediate to delayed or undetectable (Turley and Lochte, 1990; Boetius and Lochte, 1994, 1996).

The documented changes in photoautotrophic production in the surface waters at Sta. ALOHA from a eukaryotic to a cyanobacteria based system between 1991 and 1999 (Karl et al., 2001) suggests that the export of particulate organic matter to the deep sea will be reduced (Karl, 1999). How important are such shifts in photoautotrophic production on the export of particulate organic matter from the euphotic zone and its ultimate arrival at abyssal depths? Large eukaryotic photoautotrophs such as diatoms contribute significantly to the sinking flux of particulate organic matter from the euphotic zone; bacterial photoautotrophs on the other hand are largely recycled through the microbial food loop (Legendre and Le Fevre, 1989).

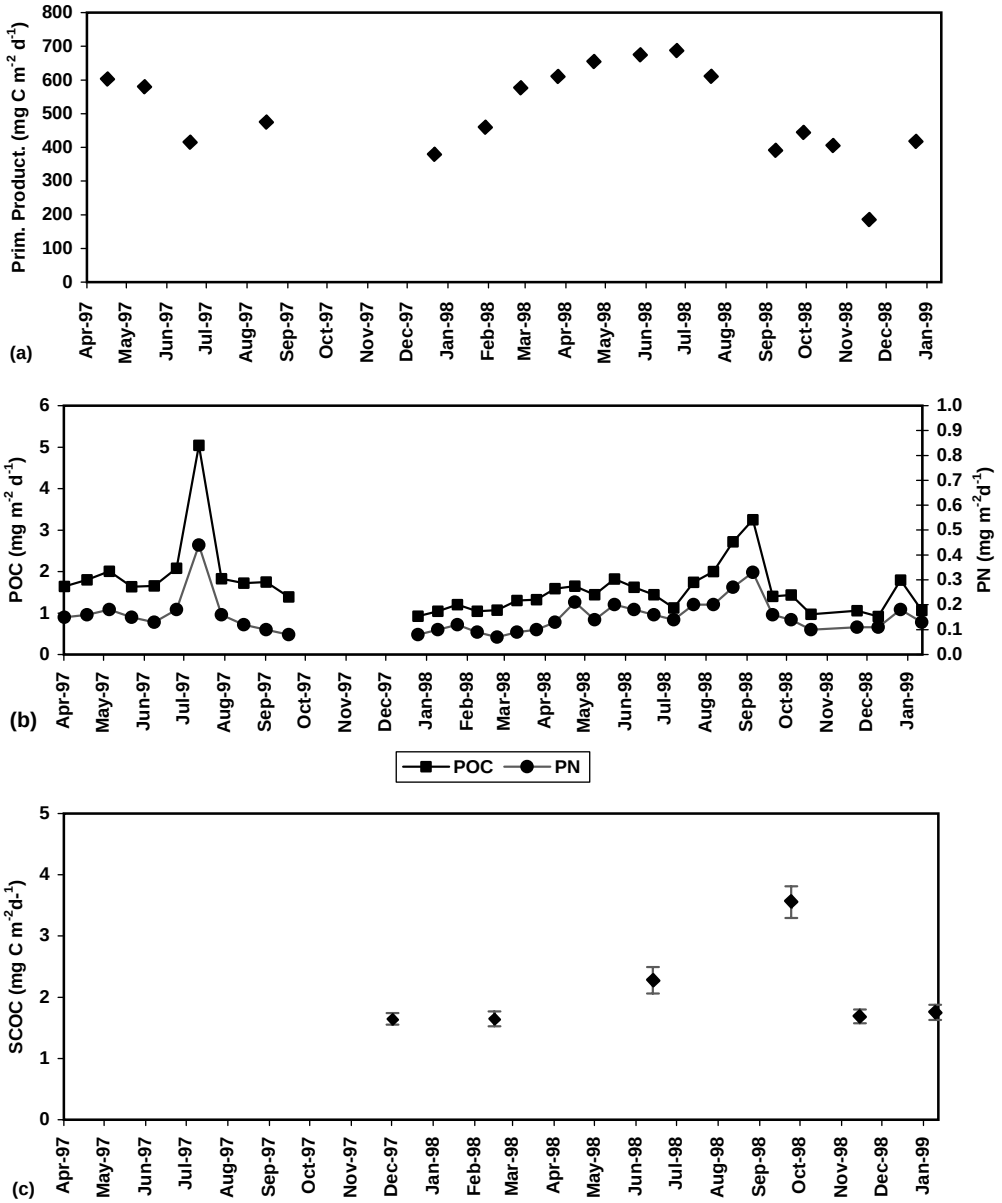


Fig. 10. Comparison of surface primary production, POC and PN flux at 4000 m with sediment community response (SCOC) at Sta. ALOHA: (a) primary production, (b) POC and PN flux, and (c) SCOC.

We examined the temporal correlation between integrated primary production (measured at monthly intervals) with the POC and PN fluxes (estimated from sediment trap collections at 4000 m depth at Sta. ALOHA) over a period from April 1997 through January 1999 (Fig. 10a and b). Cross-correlation analysis was used by holding the primary production data set fixed, lagging the POC and PN fluxes in 14-day steps, and calculating correlation coefficients at each lag step. A

significant correlation existed between primary production and POC flux$_{4000\,m}$ with a time lag of 42 days ($r = 0.61$, $n = 15$; $p = 0.015$) and similarly with PN flux$_{4000\,m}$ after 42 days ($r = 0.70$, $n = 15$; $p = 0.039$). This suggests that the major spring peaks in primary production are being exported from the euphotic zone (0–200 m depth) and reaching abyssal depths (4000 m) with a sinking rate of $\sim 90\,m\,day^{-1}$, or 42–44 days from primary production peak to collection at depth. Similar sinking rates of particulate organic matter were estimated from spring blooms at the surface to abyssal depths in the eastern North Atlantic (Pfannkuche, 1993). The major peaks in primary production at Sta. ALOHA are then largely the result of eukaryote production and are exported either directly from the euphotic zone or after passing through the "classic" food web of zooplankton and fish (Karl, 1999). In late July 1992 and August 1994 during times of high-particle flux at Sta. ALOHA, sediment trap collections at 4000 m depth contained 500–1250 fold increases over the average flux of cytoplasm-containing diatom cells (Scharek et al., 1999). Scharek and associates (1999) estimated sinking rates for these diatoms at 100–200 $m\,day^{-1}$, which is higher than our flux estimate of 90 $m\,day^{-1}$, but their fluxes were based on discrete events that lasted 5 weeks at most. Such sinking rates can be achieved only if the diatoms are aggregated (Diercks and Asper, 1997).

Further transfer of organic matter between 4000 m and its estimated utilization by the sediment community at 4730 m also exhibit a strong temporal correlation (Fig. 10c). The correlation between POC flux and SCOC was highest with a lag of $\leqslant 14$ days ($r = 0.90$, $n = 5$; $p = 0.037$). A similar correlation exists between PN flux and SCOC with a lag of $\leqslant 14$ days ($r = 0.97$, $n = 5$; $p = 0.0048$).

5.3. Annual carbon and nitrogen budgets

We compared the ratio of the POC and nitrogen flux to that of the consumption of organic carbon and nitrogen as estimated from SCOC at Sta. ALOHA over a 1-year period from November 1997 through November 1998. The POC:SCOC was 0.65, revealing a food deficit of 35% (Table 1). The burial rate of organic carbon at Sta. ALOHA was estimated from that of Sta. CNP, a station further to the north but still within the NPSG. The slow burial rate in this oligotrophic region has a negligible impact on the overall discrepancy between food supply and demand. To make similar comparisons for nitrogen, we estimated that for every 10 mmol carbon consumed in SCOC, 1 mmol of reduced nitrogen was oxidized in aerobic respiration (Williams and Carlucci,

Table 1
Annual organic carbon and nitrogen budgets, including particulate fluxes and sediment processes, at Sta. ALOHA and Sta. M

	Sta. ALOHA, 1998	Sta. M, 1998
Carbon budget		
POC flux ($g\,C\,m^{-2}\,yr^{-1}$)	0.53	1.45
SCOC ($g\,C\,m^{-2}\,yr^{-1}$)	0.81	3.37
POC flux:SCOC	0.65	0.43
Burial rate[a] ($g\,C\,m^{-2}\,yr^{-1}$)	0.0015[a]	0.13
POC flux—burial rate	0.53	1.32
(POC flux—burial rate):SCOC	0.65	0.39
Nitrogen budget		
PN flux ($g\,N\,m^{-2}\,yr^{-1}$)	0.051	
PTN flux ($g\,N\,m^{-2}\,yr^{-1}$)		0.14
SCNO ($g\,N\,m^{-2}\,yr^{-1}$)	0.078	0.32
PN flux:SCNO	0.65	
PTN flux:SCNO		0.44
Burial rate[a] ($g\,N\,m^{-2}\,yr^{-1}$)	0.0001[b]	0.013
PN flux—burial rate	0.051	
PTN flux—burial rate		0.13
(PN flux—burial rate):SCNO	0.65	
(PTN flux—burial rate):SCNO		0.40

[a] POC burial rate (Smith, 1992).
[b] PTN burial rate calculated from the POC burial rate and a C:N ratio of 12.5 at 4 cm depth.
POC and PN fluxes estimated from sediment trap collections at 730 mab at Sta. ALOHA. POC and PTN fluxes estimated from sediment trap collections at 50 mab at Sta. M. POC = particulate organic carbon, PTN = particulate total nitrogen which is comparable to that reported as PN for Sta. ALOHA, SCOC = sediment community oxygen consumption, SCNO = sediment community nitrogen oxidation. Annual averages were calculated from November to November for 1997–1998.

1976; Smith et al., 2001). Therefore, 8.15 mmol O_2 was used to oxidize organic carbon and 1.85 mmol was used to oxidize other reduced ions such as NH_4^+, Fe^{2+} and Mn^{2+}. However, since the principal aerobic process is nitrification in deep-sea sediments, we assumed the entire 1.85 mmol was consumed in this process. Hence, 22% of the SCOC can be estimated to be a result of nitrification. We calculated sediment community nitrogen oxidation (SCNO) by assuming 22% of the SCOC was used in nitrification and then converting this value to $g\,N\,m^{-2}\,yr^{-1}$ (Table 1). The annual PN:SCNO was 0.65 with the estimated burial rate for Sta. ALOHA being negligible on an annual basis.

Concurrent annual measurements in 1998 of fluxes at an abyssal station in the eastern North Pacific (Sta. M) revealed POC and PTN (comparable to PN fluxes at Sta. ALOHA) fluxes almost 3 times higher than at the more oligotrophic Sta. ALOHA (Table 1). SCOC was four times higher at the more eutrophic Sta. M. However, both stations exhibited an insufficient food supply to meet the demands of the sediment community. This discrepancy was more pronounced at the eutrophic Sta. M, where the burial rate was two orders of magnitude higher yielding a (POC flux—burial rate): SCOC of 0.39 compared to 0.65 at Sta. ALOHA (Table 1). Similar magnitude changes were evident in the nitrogen fluxes and SCNO for Sta. M.

Although a 1-year time-series study of benthic processes in the abyssal ocean is rare, this study at Sta. ALOHA still leaves many questions regarding year to year variability and ultimately changes which occur on longer time scales of decades to interdecades. It is also very apparent that in order to interpret long time-scale changes at abyssal depths, critical data concerning climate change and upper ocean processes are required. Ideally, an entire oceanic ecosystem from the sea surface to the sea floor should be studied with adequate temporal and spatial resolution over decadal time scales. The difficulty in funding such an undertaking is daunting even considering remote sensing systems that now make sampling of some of the parameters a reality. Measurements of surface and seafloor processes over the course of a year at Sta. ALOHA do provide insights into the interrelationships between these processes and stress the importance of studying biogeochemical cycling throughout the water column and sediments.

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