Pelagic-Benthic Coupling in the Abyssal Eastern North Pacific: An 8-Year Time-Series Study of Food Supply and Demand
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Reviewed work(s):
Source: *Limnology and Oceanography*, Vol. 46, No. 3 (May, 2001), pp. 543-556
Published by: American Society of Limnology and Oceanography
Stable URL: http://www.jstor.org/stable/2670946
Accessed: 01/02/2013 19:16

Limnol. Oceanogr., 46(3), 2001, 543–556

Pelagic–benthic coupling in the abyssal eastern North Pacific: An 8-year time-series study of food supply and demand

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Abstract

An 8-yr time-series study of the trophic coupling between a pelagic food supply and its utilization by the sediment community was conducted at 4,100-m depth in the eastern North Pacific between 1989 and 1998. Supply of sinking particulate organic carbon (POC) and particulate total nitrogen (PTN) was estimated from collections made with sediment traps moored at 3,500- and 4,050-m depth (600 and 50 m above bottom). Sediment community oxygen consumption (SCOC), an estimate of aerobic utilization of organic matter, was measured in situ. POC and PTN fluxes at both depths declined significantly from October 1989 through 1996 then increased in 1998. Organic carbon : total nitrogen (C : N) of the sinking particulate matter fluctuated ~10 throughout the study, except for a major peak (84.8) at 50 m above bottom in summer 1995, indicating lateral advection of organic material of terrestrial origin. POC : SCOC declined progressively over the first 7 yr, from a high of 0.99 in 1989–1990 to 0.22 in 1995–1996. In 1998, there was an increase in POC : SCOC to 0.43, suggesting that the food deficit was reduced by an increase in sinking flux. A continuing deficit in food supply cannot be sustained without ultimately affecting the structural and functional characteristics of the sediment community. The importance of undersampling by sediment traps, lateral advection of marine and terrestrial organic matter from the continental slope and shelf, and dissolved organic matter is evaluated. These other sources of nutrients for benthic organisms may be important in explaining some of the observed discrepancy between supply and demand in the abyssal Pacific. Decadal-scale climate variations that influence marine primary production and terrestrial discharges into the ocean may be extremely important in understanding biogeochemical processes in the deep sea.

The food supply for deep-sea benthic communities originates almost entirely from primary producers in surface waters and is transferred to the sea floor either directly, in the case of phytoplankton blooms, or indirectly, through the pelagic food web. Sediment traps have been employed routinely to measure the passive flux of sinking particulate organic matter (POM) in the water column as an estimate of food supply. Long time-series measurements of POM fluxes have indicated considerable temporal variability in food supply to the deep sea on both seasonal and interannual timescales (Deuser 1986; Smith et al. 1994; Baldwin et al. 1998). Photographic monitoring of the sea floor has shown episodic sedimentation events of phytodetrital material on the abyssal sea floor in the Atlantic and Pacific Oceans (Lampitt 1985; Rice et al. 1986; Smith et al. 1994, 1998).

The impact of a varying food supply on benthic communities has been examined directly by measuring the combined community activity, reflected in rates of oxygen consumption, and indirectly by estimating the organic carbon utilized by the sediment biota (Smith and Baldwin 1984; Smith et al. 1992; Pfannkuche 1993; Lampitt et al. 1995; Witbaard et al. 2000). Indicators of biological activity, such as concentrations of metabolic enzymes and adenosine triphosphate (ATP), have been used to evaluate relative changes before and after deposition of POM (Graf 1989; Pfannkuche 1993). One major problem with such comparisons has been the lack of concurrent, long time-series measurements of particulate matter fluxes and benthic community activities at a single location.

The need for long time-series measurements to examine

Acknowledgments

This long time-series research would not have been possible without the help of countless participants on our 36 cruises to Sta. M and the expertise of the ships' crews on RV *New Horizon,* RV *Wecoma,* RV *Atlantis II*/DSRV *Alvin,* and RV *Sproul.* We specifically thank our colleagues, Rob Glatts, Fred Uhlman, and Bob Wilson, for their support throughout this study. Critical comments by Ellen Druffel, Jeff Drazen, Henry Ruhl, and Anders Tengberg improved the manuscript. We especially thank Fred Sayles and Tim Shaw for providing valuable insights into the evaluation of our data and making the presentation significantly clearer; their constructive and in-depth comments were very thought-provoking. This research was supported by NSF grants OCE89-22620, OCE92-17334, and OCE98-07103.

concurrently (1) the input of a pelagically derived food supply, and (2) its impact on benthic community processes prompted us to establish a long-term study site (Sta. M) in the eastern North Pacific in June 1989. Work at this location continued until December 1998, with one hiatus in sampling (October 1996–November 1997). A primary goal of this study was to determine if there was a temporal relationship (coupling) between the flux of POM entering the benthic boundary layer (BBL) and benthic community utilization of organic matter, estimated from sediment community oxygen consumption (SCOC). Over the first 1.5 yr of this study, there was a definite seasonal fluctuation in POM fluxes, with peaks in late spring and fall that were reflected directly in elevated SCOC (Smith et al. 1994). Periods of high POM fluxes were coincident with the appearance on the sea floor of detrital aggregates that were similar in species and chemical composition to the POM entering the BBL (Beaulieu and Smith 1998). However, the annual contribution to SCOC of these aggregates, while visible on the sediment surface, was minimal (Smith et al. 1998). As this time-series study continued, we discovered a surprising long-term deficit in food supply (POM flux) compared to estimated food demand (SCOC) over a 7-yr period (Smith and Kaufmann 1999). This finding raised questions concerning the continuation of such a downward trend in food supply and its impact on the sediment community. We report the results of the final year of this study (November 1997–December 1998) and evaluate the entire 8-yr time series of POM fluxes into the BBL, organic matter in the surface sediments, and the response of the sediment community.

Area of investigation—This long time-series study was conducted at Sta. M (centered at 34°50′N, 123°00′W; 4,100-m depth) in an abyssal area 220 km west of the California coastline on the Monterey Deep Sea Fan (Smith and Druffel 1998). The sea floor in this area has little topographic relief (<100 m over 1,600 km²) and is covered with silty-clay sediments. The California Current supports a meandering along-shore jet that spawns cyclonic and anticyclonic eddies westward from spring to fall (Strub and James 2000). These eddies transport nutrient-rich water offshore, leading to high chlorophyll and zooplankton concentrations along the central California coast (Haury et al. 1986; Pelaez and McGowan 1986).

Coastal upwelling along the central California coast typically is highest in the spring but displays considerable interannual variability. Sea surface temperature, measured daily off the Farallon Islands, 290 km north of Sta. M, generally increased from 1989 through 1998 (Fig. 1). An upwelling index (Bakun Index; Bakun 1973) was compiled by the National Oceanic and Atmospheric Administration for a 3° by 3° area north of Sta. M from January 1989 to December 1998, based on surface pressure fields provided by the Fleet Numerical Oceanographic Center (http://www.pfeg.noaa.gov/products/products.html). The highest indices were related to intense upwelling periods (1989, 1991, 1994, 1996, and 1998) and were associated with lower sea surface temperatures (Fig. 1). The periods of least upwelling, as indicated by the index, were associated with El Niño events in 1991–1993, 1994–1995, and late 1997–early 1998 when sea surface temperatures were high. The Bakun Upwelling Index for the area centered at 36°N, 122°W was correlated positively with particulate mass fluxes measured at 3,500-m depth, 600 m above bottom (mab), from October 1990 to October 1996, with a significant ($P < 0.05$) temporal lag of 50 d (upwelling occurred 50 d before the arrival of particulate matter at 600 mab; Baldwin et al. 1998).

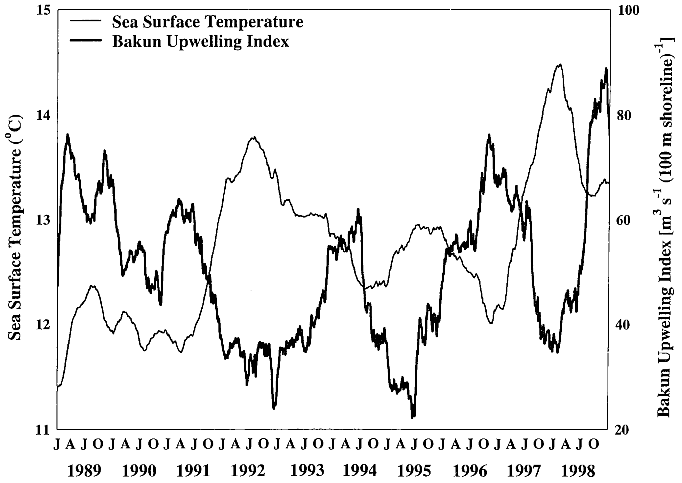

Fig. 1. SST at the Farallon Islands and the Bakun Upwelling Index over the 10-yr period from January 1989 to December 1998. Traces are 365-d centered running means based on daily measurements (SST) or estimates (Bakun Index; *see* text). JAJO = January, April, July, and October in this figure and all others.

We have studied Sta. M for the past 10 yr and have made the following observations. Detrital aggregates consisting of diatoms and radiolarians occurred seasonally on the sediment surface at Sta. M (Smith et al. 1994; Beaulieu and Smith 1998; Lauerman and Kaufmann 1998), covering up to 4.9% of the sea floor (Smith et al. 1998). Concentrations of total and organic carbon, total nitrogen, chlorophyll *a* (Chl *a*), and phaeopigments in the aggregates were similar to those of the sinking particulate matter collected at 50 mab, but aggregates contained higher concentrations of these components than the underlying surface sediments (Smith et al. 1998). However, the estimated annual oxygen consumption associated with these detrital aggregates was of minor importance compared to the total annual SCOC (Smith et al. 1998). Protozoan and some metazoan taxa of macrofauna in the sediments increased in density during winter months, after detrital aggregates disappeared from the sediment surface (Drazen et al. 1998). However, these elevated densities of macrofauna occurred during the winter when SCOC was lowest (Smith and Kaufmann 1999), suggesting that these infauna had little influence on SCOC unless their predation on the smaller, more abundant biota resulted in lower rates of community respiration.

Materials and methods

Particulate matter settling through the water column was collected continuously with single conical sediment traps having a mouth opening of 0.25 m² and suspended at 600 and 50 mab on a single mooring. The 600-m altitude was chosen to collect sinking material not influenced by resuspension from the bottom; the 50-m altitude was selected to represent the BBL as identified by higher turbidity extending up to 80 m above the sea floor (Beaulieu and Baldwin 1998). Each Teflon™-coated fiberglass sediment trap had a baffle across the mouth and was equipped at the base with a sequencer (Honjo and Doherty 1988) programmed to collect sinking particulate matter over 10-d intervals (sampling intervals were 30 d from October 1989 to June 1990 at 600 mab and from October 1989 to October 1990 at 50 mab). These sediment traps were serviced every 4 months. The collection cups of each sequencer were filled before each deployment with water collected from the deployment depth, then filtered and poisoned with $HgCl_2$ (3.0 mM). Processing of the samples followed the procedures described by Baldwin et al. (1998). In the laboratory, particulate matter was analyzed in duplicate for total carbon and nitrogen using a Perkin-Elmer 2400C elemental analyzer, and inorganic carbon was measured using a Coulometrics carbon analyzer (Smith et al. 1994) with corrections for salt content estimated from total chloride (determined by $AgNO_3$ titration; Strickland and Parsons 1972). Organic carbon was determined as the difference between total and inorganic carbon concentrations. Duplicate measurements of percentage total and inorganic carbon generally were within 0.1%. Because organic carbon was calculated as the difference between total and inorganic carbon, the reproducibility of the organic carbon was ±0.2%. Failure of the sequencing mechanism prevented sampling at 50 mab from November 1989–February 1990 and October 1992–July 1993. Sequencer problems prevented sampling at 600 mab from July 1989–October 1989 and November 1997–August 1998. The sediment trap at 600 mab also failed to collect samples from July 1994–October 1994 due to a presumed clogging event resulting from very high fluxes of sinking POM (*see* Baldwin et al. 1998).

SCOC, an indicator of the aerobic oxidation of organic matter in the sediments, was measured in situ during 2-d incubations on seasonal cruises using a free-vehicle grab respirometer (FVGR; Smith 1987). This respirometer was deployed from a ship and sank autonomously to the sea floor. After landing, four stainless steel grab chambers were pushed slowly into the sediment; each chamber enclosed up to 15 cm of overlying water and up to 15 cm of sediment with a surface area of 413 cm^2. Polarographic oxygen sensors in each chamber continuously recorded the depletion of oxygen in the overlying water due to the respiring sediment community. Each sensor was calibrated with chilled, oxygen-saturated, and nitrogen-purged seawater as limits, and SCOC was calculated in mmoles O_2 per square meter per day for each grab chamber following the methods described by Smith (1987). SCOC then was converted to organic carbon utilization (mg C m^{-2} d^{-1}), assuming a respiratory quotient of 0.85 for mixed carbohydrate and lipid (Smith 1989). Additional measurements of SCOC were made in situ using tube core respirometers operated by the submersible RV *Alvin* (*see* Smith et al. 1998 for a full description of methods and measurements) and a remotely operated bottom-transecting vehicle, ROVER (*see* Smith et al. 1997 for a full description of methods and measurements).

After each FVGR deployment, a 10-cm-diameter core of sediment was taken from one chamber, held in a cold room at 2°C, and sectioned at 2.5-mm intervals to 4 cm and then at 1-cm intervals to 8-cm depth. Triplicate subsamples from each section were frozen in liquid nitrogen and stored at −70°C for later analysis of carbon and nitrogen content. Subsamples also were frozen at −20°C for ATP analysis. In the laboratory, the carbon/nitrogen samples were thawed, dried at 60°C, weighed, and ground to a fine powder. Each sample was analyzed in duplicate for total carbon and nitrogen and for inorganic carbon (as described above). Organic carbon was calculated as the difference between total and inorganic carbon. Other subsamples were analyzed in triplicate for ATP (Craven et al. 1986) following methods described by Smith et al. (1994).

To compare data sets, 10-d means were calculated for sea surface temperature (SST) and the Bakun Upwelling Index to cover the same time periods with the same temporal resolution (10 d) as the sediment trap collections. Mean SST and Bakun Index values were generated by averaging daily values over contiguous, nonoverlapping 10-d intervals. Particulate organic carbon (POC) and particulate total nitrogen (PTN) flux measurements represent the means of two replicate measurements for each 10-d sampling period. Relationships between data sets were examined over eight complete annual cycles (October 1989–October 1996, November 1997–November 1998) using the Spearman rank correlation procedure (Zar 1998) and omitting periods during which sediment trap data were unavailable (*see* above). Cross-correlations were obtained by holding one data set fixed and lagging the second data set in 10-d steps, calculating correlation coefficients at each lag step. This procedure was used for the period from October 1990 to October 1996, during which samples were collected with 10-d resolution. To calculate POC : SCOC ratios for the entire time series, 10-d mean POC flux measurements (mg C m^{-2} d^{-1}) from 600 and 50 mab were divided by 10-d estimates of SCOC (mg C m^{-2} d^{-1}) interpolated between empirical SCOC measurements. The complete data set for the 8-yr time series is presented as Web Appendix 1 (http://www.aslo.org/lo/pdf/vol_46/issue_3/0543a1.pdf).

Results

Supply—Water column: Ten-day averaged fluxes of POC at 50 and 600 mab varied from a high of 27.9 mg C m^{-2} d^{-1} (600 mab) in June 1991 to a low of 0.16 mg C m^{-2} d^{-1} (50 mab) in May 1996 (Fig. 2A,B). PTN fluxes ranged from 3.69 mg N m^{-2} d^{-1} (600 mab) in July 1993 to below analytical levels of detection (<0.004 mg m^{-2} d^{-1}) in July 1995 (600 mab) and May 1996 (50 mab) (Fig. 3A,B). POC and PTN fluxes generally were high in late spring/early summer, often with a secondary peak in fall. The lowest annual fluxes were in 1992 and 1995–1996, corresponding to periods of documented reduction in upwelling off the coast of central California (*see* Baldwin et al. 1998 for a discussion). A large El Niño event between summer 1997 and summer 1998, reflected in a decline in the Bakun Index (Fig. 1), coincided with decreased POC and PTN fluxes that only began to rise in fall 1998 before termination of our sampling (Figs. 2, 3).

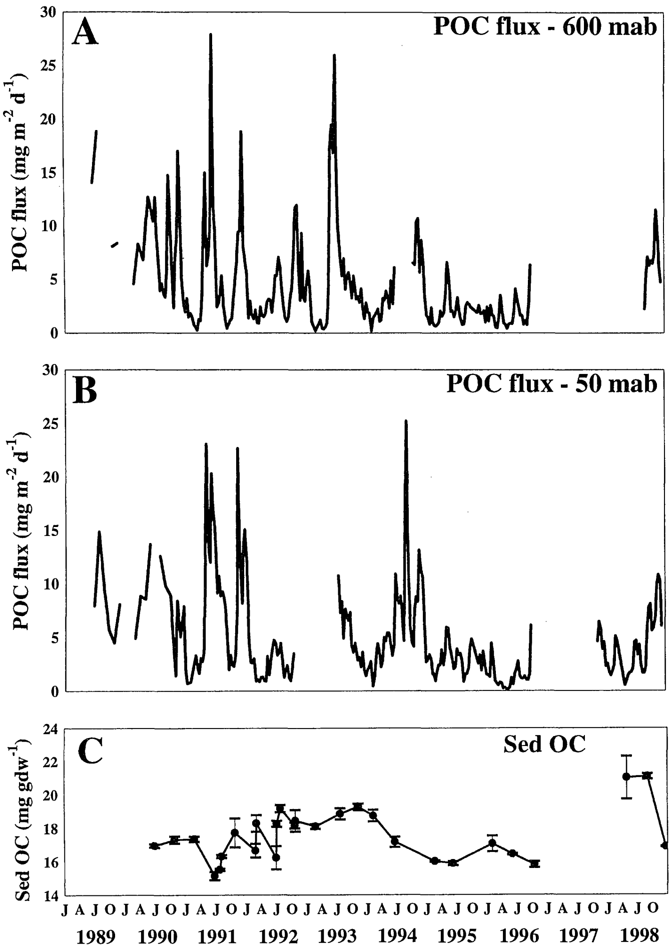

Fig. 2. (A) POC flux measured with sediment traps moored at Sta. M at 600 mab. Gaps in the data set of <30 d are connected by linear interpolation; gaps of >30 d are depicted as breaks in the record with no interpolation between data points. (B) POC flux measured with sediment traps moored at Sta. M at 50 mab. Gaps are represented as in panel A. (C) Mean, maximum, and minimum concentration of organic carbon (SedOC) in the uppermost 10 mm of the sediments. Each value calculated as the mean of concentrations from sediment sections taken at 2.5-mm intervals below the sediment surface (four sections). Symbols represent empirical measurements of sediment organic carbon concentrations. Lines connecting means are the result of linear interpolation between data points.

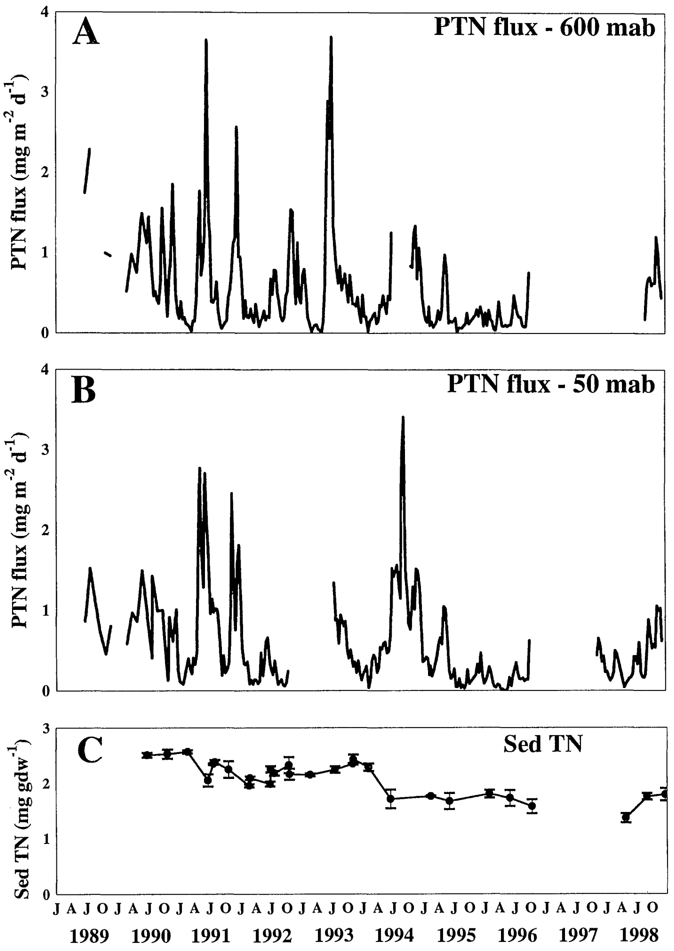

Fig. 3. (A) PTN flux measured with sediment traps moored at Sta. M at 600 mab. Gaps in the data set of <30 d are connected by linear interpolation; gaps of >30 d are depicted as breaks in the record with no interpolation between data points. (B) PTN flux measured with sediment traps moored at Sta. M at 50 mab. Gaps are represented as in panel A. (C) Mean, maximum, and minimum concentration of total nitrogen (SedTN) in the uppermost 10 mm of the sediments. Each value calculated as the mean of concentrations from sediment sections taken at 2.5-mm intervals below the sediment surface (four sections). Symbols represent empirical measurements of sediment total nitrogen concentrations. Lines connecting means are the result of linear interpolation between data points.

The Bakun Index was correlated positively and significantly with POC flux at 600 mab ($P = 0.011$) and 50 mab ($P = 0.009$) and with PTN fluxes at 50 mab ($P = 0.017$) but not at 600 mab ($P = 0.070$). A cross-correlation of the Bakun Index with POC and PTN fluxes at 50 mab between October 1990 and October 1996 revealed maximum correlations with time lags of 20–60 d ($r = 0.29$–0.31, $P < 0.001$). These time lags are comparable to that found between the Bakun Index and POC fluxes at 600 mab at this same station by Baldwin et al. (1998). The time lag seems reasonable, considering (1) the time necessary for an upwelling event to occur, (2) the subsequent uptake of nutrients, (3) increased primary productivity (Hayward et al. 1994), and (4) time for the newly generated organic matter to transit 4,100 m through the water column. This time lag is consistent with sinking speeds of 100–200 m d^{-1}, as reported by Alldredge and Silver (1988).

POC fluxes over eight complete annual cycles between October 1989 and November 1998 were correlated significantly between 600 and 50 mab ($r = 0.80$, $P < 0.001$), as were PTN fluxes ($r = 0.75$, $P < 0.001$), but both generally were higher at 50 mab. This difference may be the result of material advected laterally from distant sources on the slope and shelf (*see* below). The disparity between fluxes at the two sampling depths was highest during 1990–1991 and 1994–1995, with the annual difference being as much as 21.4% (POC) and 24.5% (PTN). A cross-correlation analysis revealed a positive correlation with no significant time lag from October 1990 to October 1996 between 600 and 50 mab fluxes of both POC and PTN ($P < 0.001$). A 365-d

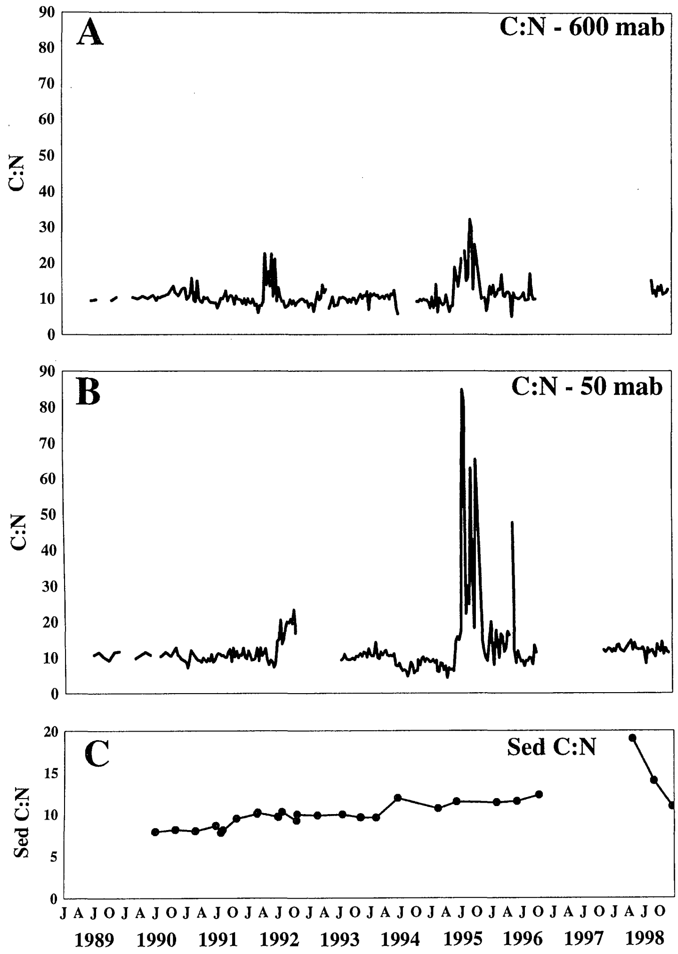

Fig. 4. (A) Molar C : N for sinking material collected in sediment traps moored at Sta. M at 600 mab. Gaps in the data set of <30 d are connected by linear interpolation; gaps of >30 d are depicted as breaks in the record with no interpolation between data points. (B) Molar C : N for sinking material collected in sediment traps moored at Sta. M at 50 mab. Gaps are represented as in panel A. (C) Molar C : N in the uppermost 10 mm of the sediments. Each value calculated as the mean of concentrations from sediment sections taken at 2.5-mm intervals below the sediment surface (four sections). Symbols represent molar C : N based on empirical measurements of sediment organic carbon and total nitrogen concentrations. Lines connecting symbols are the result of linear interpolation between data points.

centered moving average of the POC and PTN fluxes at both sampling altitudes declined significantly (negative slope, $P < 0.001$) from October 1989 through October 1996. The 1998 data were not included in this statistical analysis because of the 1-yr hiatus in sampling during 1997 (Figs. 2, 3). There was an increase in POC and PTN fluxes in 1998 compared to the low levels measured in 1995–1996 but not to the magnitude measured in the early 1990s.

The molar ratio of organic carbon to total nitrogen (C : N) in the sinking POM over the time series was generally $\sim$10, but several peaks and lows created a wide range of values from 4.96 to 32.2 at 600 mab and from 4.31 to 84.8 at 50 mab (Fig. 4A,B; excluding times when PTN levels were below detection limits). There was no significant correlation ($P > 0.05$) between the C : N of the sinking POM fluxes and the Bakun Index at either altitude. The highest C : N occurred in 1992 and 1995–1996 (Fig. 4A,B) when the Bakun Index was relatively low (Fig. 1) and POC and PTN fluxes were lowest (Figs. 2, 3). These two periods also were characterized by warmer surface waters and lower primary production (Baldwin et al. 1998). In 1992, the peak in C : N began at 600 mab in April and continued through June, followed by a peak in C : N at 50 mab from late June into October. The temporal shift in C : N peaks from 600 mab in spring to 50 mab in summer suggests vertically linked events in particulate flux during 1992. In contrast, the peaks in C : N during 1995 were concurrent at 50 and 600 mab but were substantially higher at 50 mab, reaching 84.8 at 50 mab in July 1995. During these 1995 peaks in C : N, POC fluxes generally were higher but PTN fluxes lower at 50 mab.

The principal current flow vector at 50 mab during the 1995 peaks in C : N was southwest (Beaulieu and Baldwin 1998), suggesting possible transport from the shelf and slope to the northeast of Sta. M. Local resuspension of bottom sediments was possible during a brief period in July 1995 when current speeds measured at 2.5 mab exceeded 14 cm s^{-1} (Beaulieu and Baldwin 1998), but the low C : N of the surface sediments at the time (<12) argues against this contribution to the high C : N peaks at 50 mab. The higher C : N in the samples collected at 50 mab, particularly apparent in the peaks of 1995, likely reflected the presence of more refractory organic material transported laterally from distant sources on the shelf and slope to the east (Bianchi et al. 1998; Druffel et al. 1998; Sherrell et al. 1998).

Supply—Sediments: Organic carbon content of the surface sediment (integrated over the upper 1 cm) ranged from a low of 15.1 mg gdw^{-1} in July 1991 to a high of 21.8 mg gdw^{-1} in April 1998 (Fig. 2C). The low sediment carbon followed a period of low POC flux 4 months earlier, while the second largest high, in October 1993, followed a peak in POC flux the previous summer. The highest peak in sediment carbon in April 1998 did not correspond to any flux we measured but might have resulted from an event that occurred the previous year when we did not sample. There was no significant trend in sediment organic carbon content over the 8-yr sampling period, and there was no significant correlation between sediment organic carbon and POC flux at either 600 or 50 mab ($P > 0.05$). This lack of correlation is not surprising since the annual POC flux is a very small fraction of the standing stock of organic carbon in the surface sediments (*see* below).

Sediment total nitrogen (also integrated over 1-cm depth) showed a declining trend from the first measurements in 1990 and 1991–1996 and then increased over the last two sampling periods in August and December 1998 (Fig. 3C). Sediment total nitrogen declined significantly ($P < 0.001$) from October 1989 through October 1996 in conjunction with the decline in PTN fluxes at 50 and 600 mab. However, there was no significant correlation ($P > 0.05$) between PTN fluxes and sediment total nitrogen, which is plausible given the small annual input of PTN compared to the large standing stock of nitrogen in the surface sediment.

In contrast to the POM flux, molar C : N in the surface

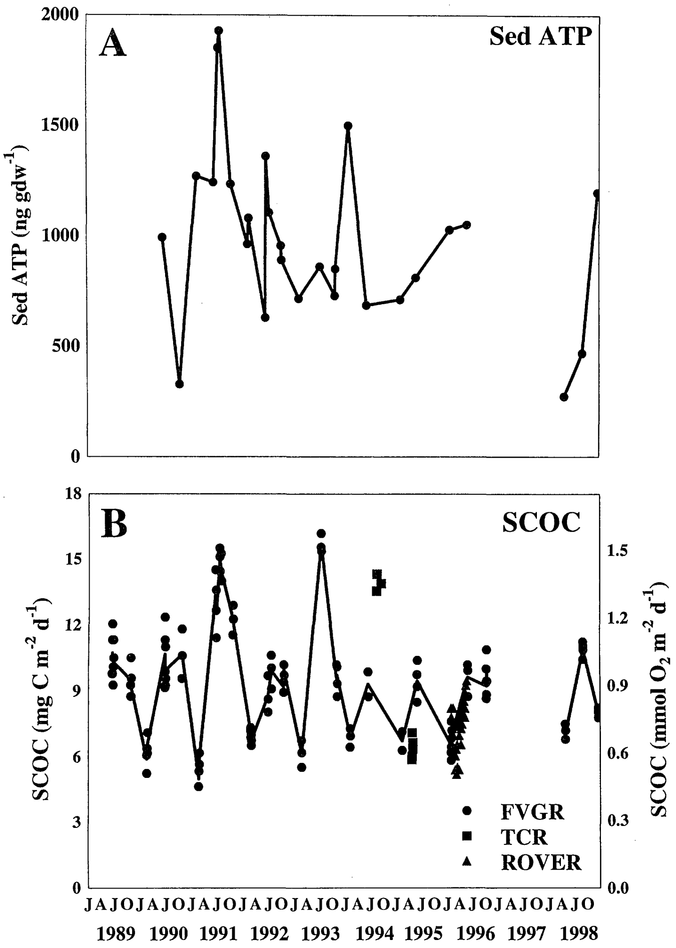

Fig. 5. (A) Concentrations of ATP for the uppermost 10 mm of the sediments. Each value calculated as the mean of concentrations from sediment sections taken at 2.5-mm intervals below the sediment surface (four sections). Lines connecting symbols are the result of linear interpolation between empirical data points. (B) Measured rates of SCOC at Sta. M. Symbols represent individual measurements of SCOC made with an FVGR, Alvin-placed tube core respirometers, and ROVER, a bottom-transecting vehicle. Trace is linear interpolation between means of synoptic replicate FVGR measurements.

sediment increased noticeably from 7.7 in June 1990 to a high of 12.3 in October 1996 (Fig. 4C). Resumed sampling in 1998 revealed the highest ratio measured in the sediments (19.0) in April, followed by a precipitous decline to 10.9 at the end of sampling in December. The trend of increasing C:N in the surface sediments did not coincide with the C:N of the sinking POM at either 600 or 50 mab.

Demand—Sediments: ATP content of the surface sediment can be used as an indicator of microbial biomass (Craven et al. 1986; Smith et al. 1987). Sediment ATP content (also integrated over 1-cm depth) was highly variable but displayed summer peaks in concentration in 1991, 1992, and 1996 with a winter peak in 1994 (Fig. 5A). High ATP concentrations during the summer of 1991 coincided with peaks in POM fluxes (Figs. 2, 3) but with a low in sediment organic carbon (Fig. 2C). The high ATP in 1992 corresponded temporally to highs in POM fluxes and sediment organic carbon. However, during 1994, the peak in ATP was coincident with a low in POM fluxes but highs in both sediment organic carbon and nitrogen. During 1998, the ATP concentration climbed to levels comparable to those measured before fall 1994. Of all the parameters measured, ATP was correlated positively only with sediment total nitrogen ($P = 0.017$).

SCOC, an estimate of organic carbon utilization by the sediment community, fluctuated seasonally in relative synchrony with the POC flux, showing peaks in summer and fall and lows in the winter (Fig. 5B). The highest peaks in SCOC during July 1991 and July 1993 corresponded to highs in POM fluxes during the same time periods (Figs. 2, 3). There was no obvious correlation between SCOC and sediment organic carbon, nitrogen, or ATP. Over the entire time series, SCOC remained remarkably consistent from year to year, fluctuating seasonally around a mean (±SD) of 9.11 ± 0.86 mg C m^{-2} d^{-1}. Regularity from year to year also was evident in the C:N of the sinking POM, with the exception of obvious spikes in 1992 and 1995.

Supply versus demand—The relationship between POC flux and SCOC (in mg C m^{-2} d^{-1}) can be represented as a ratio, POC:SCOC, with values greater than unity indicating a surplus and values less than unity reflecting a deficit of POC. During the first 7 yr of the time-series study, POC:SCOC declined progressively and reached the lowest values in mid-1996 (Fig. 6). However, there was a prominent peak in POC:SCOC during fall 1994 at 50 mab (Fig. 6B) that coincided with a period of very low C:N (4.76–10.11) in the sinking particulate matter, indicating a large pulse of "nitrogen-rich" food, which brought the POC:SCOC above three. Concurrently, the 600-mab sediment trap was clogged (Baldwin et al. 1998), and large phytodetrital aggregates were abundant on the sea floor (Smith et al. 1998). The total POC flux from October 1989 to October 1996 contributed only 52.1 and 59.2%, estimated from 600 and 50 mab, respectively, of the estimated sediment community demand based on SCOC (Smith and Kaufmann 1999). After the hiatus in sampling during 1997, POC:SCOC remained <0.5 until fall 1998, when values rose to a peak of 1.25 before declining below unity by December. The significant decline in POC:SCOC through 1996 appears upheld in 1998, but the peak in fall 1998 indicates possible signs of recovery (toward unity) not seen since 1994.

Discussion

A continuing deficit in food supply relative to the estimated demands of the sediment community cannot be sustained without ultimately affecting the structural and functional characteristics of the community. One possible explanation for the observed deficit entails the existence of food sources that are not quantified by sediment traps. These sources include large particles not collected effectively by sediment traps, laterally advected material from the continental margin to the east, and dissolved organic matter in the water column.

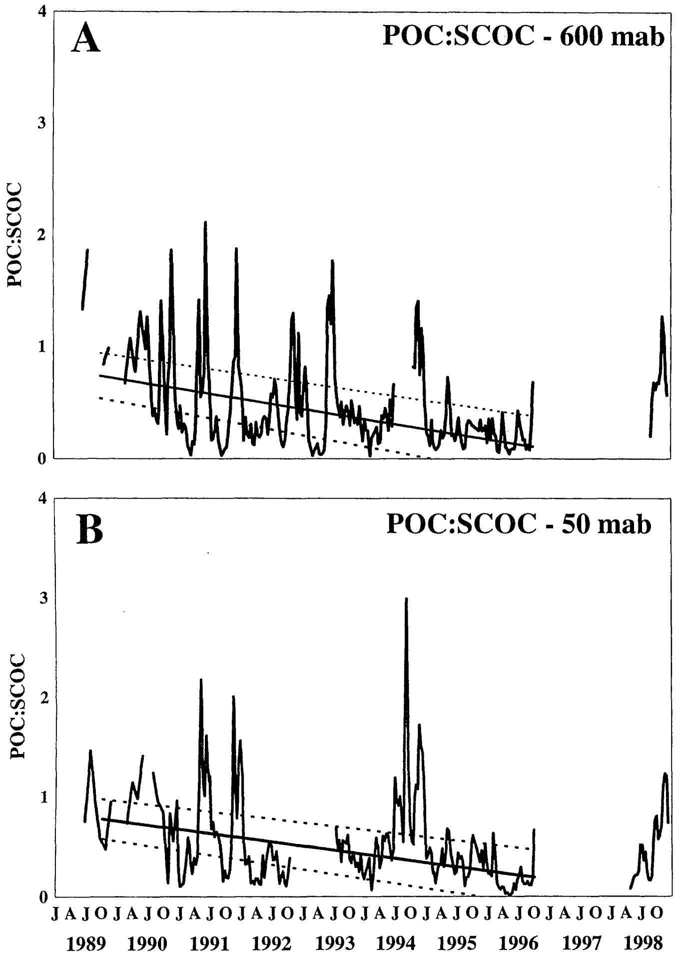

Fig. 6. (A) Ratio of sinking POC flux (food supply) to SCOC (food demand) based on sinking flux rates at 600 mab. Sampling resolution was not identical for POC flux and SCOC, and ratios were calculated for 10-d intervals using empirical measurements (POC flux) and interpolated measurements (SCOC). Solid line is based on a linear regression using only empirical data during the period between October 1989 and October 1996. Dashed lines indicate 95% confidence interval for the regression. (B) Ratio of sinking POC flux (food supply) to SCOC (food demand) based on sinking flux rates at 50 mab. Data and regression results are represented as in panel A.

Undersampling—Sediment traps may have undersampled the particulate matter settling to the sea floor at Sta. M. Sinking particulate matter collected in the sediment trap moored at 50 mab was different in composition from phytodetritus collected concurrently on the sea floor, suggesting undersampling in the water column (Beaulieu and Smith 1998). Clogging of the baffle on one sediment trap by large detrital aggregates was suggested at 600 mab during a period of high particulate matter flux, preventing collections for 3 months from July to October 1994 (Baldwin et al. 1998). In the summer and fall of 1994, large detrital aggregates observed and collected on the sea floor contributed up to 20 times more organic carbon to the sediment community than was measured concurrently with sediment traps (Smith et al. 1998). This heavy carpet of detrital material was not noted in hourly photographs of the sea floor during previous years (Smith et al. 1994; Lauerman and Kaufmann 1998); however, events of this magnitude may be uncommon.

One method of measuring the efficiency of sediment traps is through the accumulation of radionuclides produced in the water column. In a related study, Shaw et al. (1998) found that the sediment trap-determined flux of ex^{210}Pb at Sta. M significantly underestimated water-column production over the period from August 1994 through July 1995. Further, the sediment trap-determined flux of ex^{230}Th underestimated the sediment accumulation at Sta. M by nearly an order of magnitude (Shaw et al. 1998). Shaw et al. were able to reconcile these differences based on the additional delivery of ex^{230}Th via large aggregate deposition events (missed by sediment traps). Using mass flux estimates for aggregate deposition events and an average organic carbon concentration in collected phytodetritus of 5.5% (Beaulieu and Smith 1998), Shaw et al. (1998) estimated that a single aggregate deposition event delivered ~0.07 g m^{-2} d^{-1}. Four such deposition events annually would reconcile the ex^{230}Th accumulation and provide an estimated average flux of 15 mg C m^{-2} d^{-1} associated with large aggregate deposition at Sta. M. The estimated annual POC flux measured in sediment traps is ≤5 mg C m^{-2} d^{-1}, approximately one-third of the estimated large aggregate deposition.

Large aggregates of phytoplankton (Alldredge and Gotschalk 1989) and large mucous aggregates of zooplankton origin, such as pteropod-feeding webs (Gilmer and Harbison 1986) and larvacean "houses" (Hamner and Robison 1992), have been observed throughout the water column in the North Pacific. These large aggregates may be rare enough to escape sediment trap collection or, if encountered, clog the baffles across the opening of the trap (Silver et al. 1998). At mesopelagic depths in Monterey Bay, the estimated monthly POC flux from aggregates was up to two times greater than POC fluxes calculated from sediment trap collections (Pilskaln et al. 1998). Thus, a substantial portion of the discrepancy we observed between supply and demand could have resulted from sinking aggregates that were not sampled adequately by sediment traps or that reduced the traps' sampling efficiency.

Lateral advection: Lateral advection of particulate matter from the continental shelf and slope to the vicinity of Sta. M was suggested by the lower ("older") radiocarbon content of suspended particulate matter below 2,500-m depth (Druffel et al. 1998). Relatively high concentrations of pyrophaeophorbide *a,* a degradation product of Chl *a,* in proximity to the sea floor indicated lateral transport from the continental margin within the benthic mixed layer (Bianchi et al. 1998). We examined the difference between the POM fluxes at 600 and 50 mab as an indicator of lateral advection, since the lower sediment trap was in the BBL, as identified by higher turbidity in this altitude range (15–80 mab; Beaulieu and Baldwin 1998). We assumed that any advected material reaching the sea floor would have been captured in the 50-mab sediment trap, i.e., input to the 50-mab trap was representative of fluxes reaching the sea floor. It should be noted that our estimate of lateral advection is an underestimate, accounting only for that fraction of laterally advected sinking

Table 1. Annual POC and PTN flux at 50 mab compared with SCOC, SCNO, POC, and PTN burial at Sta. M. POC, particulate organic carbon; PTN, particulate total nitrogen; SCOC, sediment community oxygen consumption; SCNO, sediment community nitrogen oxidation. Flux for the 600-mab trap was not included but can be calculated by subtracting the lateral transport from the 50-mab flux. Annual averages were calculated from October to October for 1989–1990 through 1995–1996 and from November to November for 1997–1998.

	89–90	90–91	91–92	92–93	93–94	94–95	95–96	96–97	97–98	Mean±SD
POC flux (g C m^{-2} yr^{-1})	3.18	2.51	1.63	2.32	1.91	1.53	0.67		1.45	1.90±0.77
SCOC (g C m^{-2} yr^{-1})	3.21	3.75	3.34	3.81	3.12	2.94	3.06		3.37	3.33±0.31
POC flux : SCOC	0.99	0.67	0.49	0.61	0.61	0.52	0.22		0.43	0.57±0.22
POC burial rate* (g C m^{-2} yr^{-1})	0.29	0.23	0.15	0.21	0.17	0.14	0.06		0.13	0.17±0.07
POC flux − burial rate	2.89	2.28	1.48	2.11	1.74	1.39	0.61		1.32	1.73±0.70
(POC flux − burial rate): SCOC	0.90	0.61	0.44	0.55	0.56	0.47	0.20		0.39	0.52±0.20
Lateral transport§ (g C m^{-2} yr^{-1})	0.42	0.48	0.19	0.04	0.18	0.32	0.01		0.04	0.21±0.18
PTN flux (g N m^{-2} yr^{-1})	0.25	0.30	0.17	0.30	0.27	0.19	0.06		0.14	0.21±0.09
SCNO (g N m^{-2} yr^{-1})	0.30	0.36	0.32	0.36	0.30	0.28	0.29		0.32	0.32±0.03
PTN flux : SCNO	0.81	0.83	0.54	0.83	0.93	0.69	0.20		0.44	0.66±0.25
PTN burial rate* (g N m^{-2} yr^{-1})	0.030	0.024	0.015	0.022	0.017	0.014	0.006		0.013	0.017±0.007
PTN flux − burial rate	0.22	0.27	0.16	0.28	0.26	0.18	0.05		0.13	0.19±0.08
(PTN flux − burial rate): SCNO	0.71	0.76	0.49	0.77	0.87	0.64	0.18		0.40	0.60±0.23
Lateral transport† (g N m^{-2} yr^{-1})	−0.003‡	0.059	0.000	0.003	0.018	0.047	−0.011‡		0.003	0.016±0.024

* POC burial rate calculated using an organic carbon burial efficiency of 9% of the POC flux (Reimers et al. 1992; Reimers' Sta. N is the same as our Sta. M), PTN burial rate calculated from the POC burial rate and a C : N ratio of 10.28 at 8-cm depth.

† Lateral transport calculated as the flux at 50 mab minus the flux at 600 mab (*see* text for details).

‡ Means less than zero treated as no lateral transport for that year.

particulate material at ≥50 mab. Given the constraints on this assumption, the annual advective input ranged from a high of 0.48 g C m^{-2} yr^{-1} in 1990–1991 to a low of 0.01 g C m^{-2} yr^{-1} in 1995–1996 (Table 1), constituting 1.5–20.9% of the annual POC flux at 50 mab (Fig. 7A). A 365-d running mean of the percent lateral advection of organic carbon [(POC flux$_{50mab}$ − POC flux$_{600mab}$)/(POC flux$_{50mab}$)] exhibited a primary peak in 1991 and a secondary peak in July 1995 (Fig. 7B). The increased lateral advection in 1995 corresponded to increased current flow in the BBL measured at 600, 50, and 2.5 mab at Sta. M during the same period (Beaulieu and Baldwin 1998).

The total nitrogen difference between 600 and 50 mab (lateral flux of PTN) ranged from a positive 0.059 g N m^{-2} yr^{-1} in 1990–1991 to a negative 0.011 g N m^{-2} yr^{-1} in 1995–1996 (Table 1). PTN advection thus accounted for up to 24.5% of the PTN flux at 50 mab based on a net lateral advective flux of 0.27 g N m^{-2} yr^{-1} in 1990–1991 (Table 1). The calculated flux due to lateral advection here is probably an underestimate of the flux to the sea floor. At Sta. M, the upper limits of the BBL varied from 15 to 80 mab, with an average of 40 mab (Beaulieu and Baldwin 1998), and advection through this layer could have provided additional organic matter undetected by the sediment trap at 50 mab.

The high C : N in the sinking particulate matter at 50 mab in 1995 compared to that at 600 mab strongly suggests that a major event occurred in the BBL (Fig. 4). Local resuspension is possible, as discussed above, but the C : N of surface sediments was considerably less than that measured in the sinking particulate matter at 50 mab from July through October 1995 (Fig. 4). River discharge into the ocean of highly degraded, nitrogen-poor organic matter of terrestrial origin is significant on a global scale, sufficient in quantity each year to supply the entire organic carbon standing stock in marine sediments (Hedges et al. 1997). Intrusion of high C : N particulate matter of terrestrial origin could have occurred, triggered by coastal events such as high precipitation and river discharge. Significant contributions of terrestrial material to the sinking POC flux in the deep sea have been identified at an oceanic station in the subarctic Pacific Ocean, based on depleted $\delta^{13}C$ (Druffel et al. 1986). Riverine input of black carbon, highly refractory carbon produced during terrestrial burning and fossil fuel combustion, also could have contributed to a high C : N in the sinking particulate matter at Sta. M (Masiello and Druffel 1998). Other sources of highly refractory organic matter with high C : N in riverine discharges can be decomposing estuarine macrophytes (C : N of 13 to >70; Rice 1982; Kuehn et al. 2000) and degradation products from terrestrial vascular plants (C : N of 17 to >100; Meyers and Lallier-Verges 1999).

We examined flow rates of California rivers extending from the Klamath River near Crescent City in the north to the Santa Clara River near Ventura in the south. Daily flow rates were averaged over 10-d intervals and compared to the C : N of sinking POM fluxes measured at Sta. M. Cross-correlation analysis revealed a strong correlation ($r = 0.70$) between flow in the San Joaquin River (monitoring station near Newman, California; USGS Sta. 11274000) and the C : N of the sinking POM when lagged by 110 d. A very conspicuous peak in river flow was apparent in spring 1995, 110 d before the major peak in C : N of the particulate matter fluxes measured at 50 mab (Fig. 8). A similar but less pronounced pattern was seen the following year. The San Joaquin River is a major central California river that drains an extensive region from the Sierra mountain range to the rich agricultural region of the San Joaquin Valley before entering San Francisco Bay. River flows from the other seven rivers we examined did not show correlations with the particulate fluxes at Sta. M as strong as the San Joaquin River, suggesting that river flow originating from central California has the strongest influence at Sta. M, located to the southwest. A 110-d period between the river discharge into San Fran-

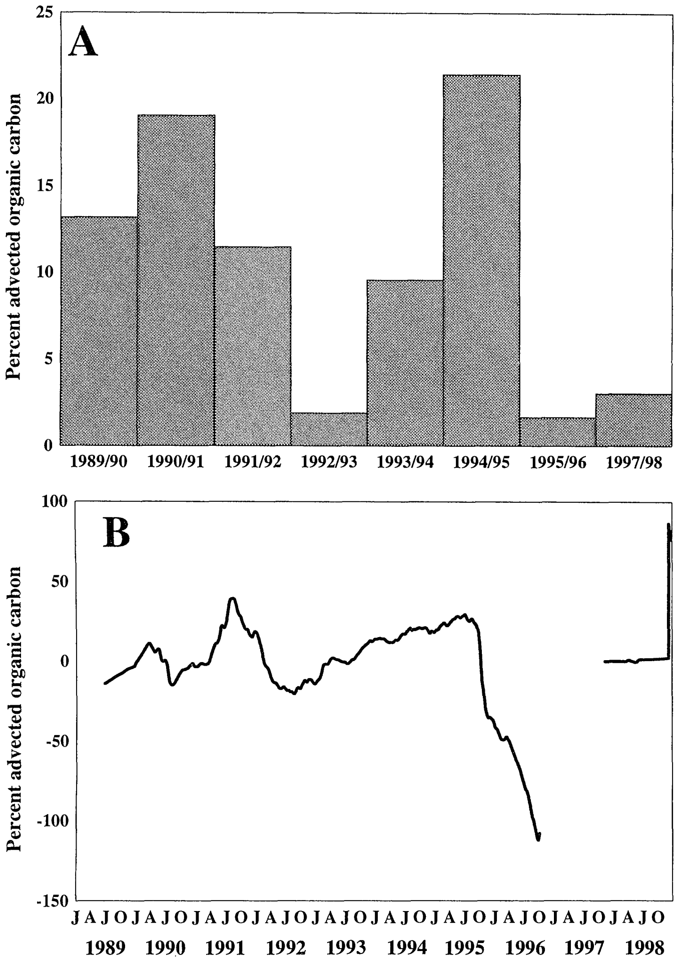

Fig. 7. Percentage of sinking POC flux supplied by lateral advection [(POC $\text{flux}_{50\text{ mab}}$ − POC $\text{flux}_{600\text{ mab}}$)/(POC $\text{flux}_{50\text{ mab}}$)]. Data based on composite data records in which flux measurements from the 600-mab trap were used to fill gaps in the 50-mab record and vice versa. *See* Materials and methods for time periods affected by this procedure. Lateral advection estimates were zero during filled gaps in either the 600-mab traps or 50-mab records; thus, lateral advections during time periods containing gaps were biased toward zero. (A) Annual means for complete annual cycles running from October to October (1989–1990 through 1995–1996) or November to November (1997–1998). *See Table 1 for annual flux totals.* (B) The 365-d centered running mean based on daily estimates of flux rates.

cisco Bay and the arrival of terrestrially derived POM with high C:N at 50 mab seems reasonable. The San Joaquin River flow might be a general indicator of river discharge in central California and may not be the specific source of material reaching Sta. M, the relationship being governed by the more extensive data set for this river compared to many of the other surrounding river systems. However, this strong correlation indicates a relationship between peaks in river flow and the supply of organic matter to the deep ocean.

Dissolved organic material: The largest pool of organic matter in the ocean is in the dissolved state. Dissolved organic carbon (DOC) concentrations are orders of magnitude higher than suspended and particulate fractions in the water column. DOC concentration in the BBL waters at Sta. M is ~40 μM (Bauer et al. 1998), increasing an order of magnitude in the surface sediments (279–753 μM in the top 10 cm; Bauer et al. 1995). Bauer et al. (1995) used a Fickian diffusion model to estimate an annual flux of 12.8 g C m^{-2} yr^{-1} from the sediment at Sta. M. The DOC fraction in the sediments has a higher ^{14}C content than the DOC in the overlying water, indicating that this carbon is more recent in age. This "young" DOC is likely derived from sinking POC that organisms in the sediment community have metabolized

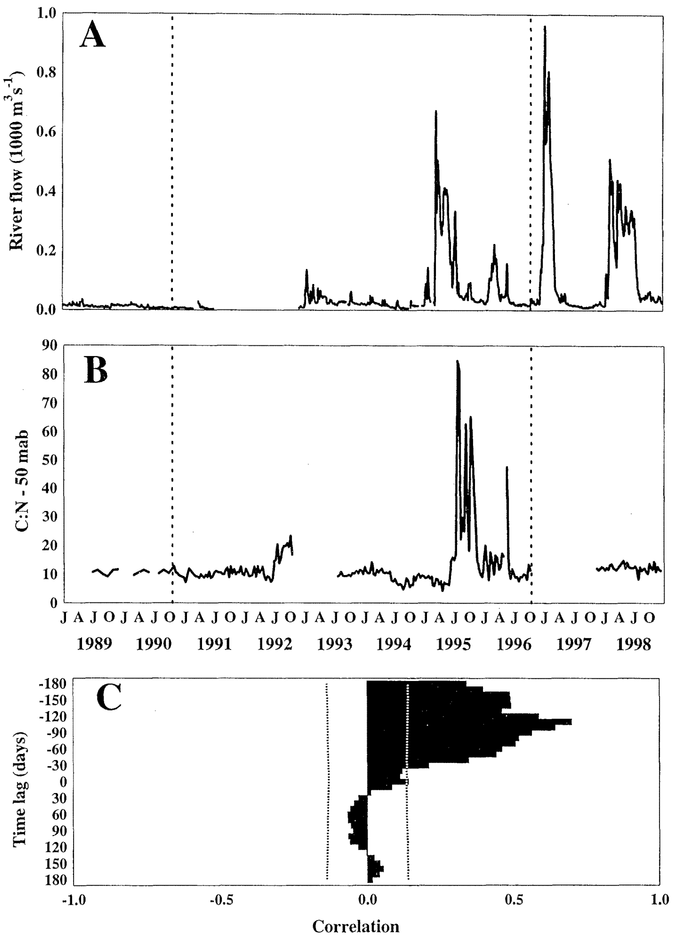

Fig. 8. (A) Daily flow rates for the San Joaquin River, measured near Newman, California (USGS 11274000). Gaps in the trace reflect gaps in the data record. Dashed vertical lines delimit period used for cross-correlation analysis between flow rate and molar C:N in 50-mab sediment trap at Sta. M (panel C). (B) Molar C:N for sinking material collected in sediment traps moored at Sta. M at 50 mab. Gaps in the data set of <30 d are connected by linear interpolation; gaps of >30 d are depicted as breaks in the record with no interpolation between data points. Dashed vertical lines delimit period described in panel A. (C) Cross-correlation between 10-d mean flow rate for the San Joaquin River, measured at Newman, California, and molar C:N in the 50-mab sediment trap at Sta. M between October 1990 and October 1996. Mean flow rates were calculated as the mean of daily flow rates measured over the previous 10 d, corresponding to molar C:N of organic material collected by the 50-mab sediment trap over the previous 10 d. Dotted lines indicate two-tailed 5% significance levels.

incompletely, leaving residual DOC in sufficient concentrations to create a diffusion gradient out of the sediments. However, this flux of DOC from the sediment exceeds the annual SCOC by a factor of 3.4–4.4 (Table 1). Such high DOC fluxes have been questioned because of the possible contamination from carbon in sediment-dwelling organisms and also from the transitional reduced phases in carbon mineralization (*see* Jahnke 1996; Alperin et al. 1999). Because DOC in the surface sediments appears to originate largely from sinking POC, this pool of organic carbon cannot reduce the POC : SCOC deficit. However, utilization of some fraction of the large pool of "older" water-column DOC by organisms in the sediment with either direct access or through burrow irrigation may reduce some of the apparent deficit in food supply.

Carbon and nitrogen budgets: The measured components of the carbon and nitrogen budget in the BBL at Sta. M are presented in Table 1. To simplify our budgets, we chose the POC and PTN fluxes at 50 mab to represent the food input to the sediment community, because these constitute our best estimates of the material reaching the sea floor, local resuspension not being a major factor in this environment (Beaulieu and Baldwin 1998). The annual flux of POC ranged from a high of 3.18 g C m^{-2} yr^{-1} in 1989–1990 to a low of 0.67 g C m^{-2} yr^{-1} in 1995–1996. The demand for this food input, as estimated from SCOC, was relatively consistent from year to year, with a range from 3.81 g C m^{-2} yr^{-1} in 1992–1993 to 2.94 g C m^{-2} yr^{-1} in 1994–1995 (Table 1). The ratio of POC flux, an estimate of carbon supply, to SCOC, an estimate of carbon utilization, varied from almost unity, 0.99, in 1989–1990, to a low of 0.22 in 1995–1996. This estimated discrepancy in food supply increases when the calculated amount of the organic carbon supply unavailable to the sediment community because of deep burial in the sediments is subtracted from the total POC measurements. Reimers et al. (1992) estimated that burial efficiency of organic carbon was 9% of the POC flux for Sta. M (their Sta. N). When this loss from the system is subtracted from the POC flux and the remainder is compared to the carbon demand, the ratio of available organic carbon to SCOC ranges from a high of 0.90 in 1989–1990 to a low of 0.20 in 1995–1996 (Table 1). The (POC flux minus burial rate): SCOC, based on the summation of fluxes over the 8-yr sampling period, is 0.52 (Table 1), indicating that almost 50% of the organic carbon to fuel the sediment community is derived from sources other than the measured sinking POC flux.

Examining the measured components of the nitrogen budget, the annual PTN flux was highest in 1990–1991 and 1992–1993 (0.30 g N m^{-2} yr^{-1}) and lowest in 1995–1996 (0.06 g N m^{-2} yr^{-1}) (Table 1). To estimate the amount of PTN utilized by the sediment community, we started with SCOC values and assumed that for every 10 mmol carbon consumed, 1 mmol of reduced nitrogen was oxidized in aerobic respiration (Williams and Carlucci 1976), the predominant metabolic process at Sta. M (Reimers et al. 1992). Therefore, for every 10 mmol of O_2 consumed by the sediment community, 8.15 mmol was used to oxidize organic carbon (Williams and Carlucci 1976), and 1.85 mmol was available to oxidize other reduced ions such as NH_4^+, Fe^{++}, and Mn^{++}. We further assumed that the entire 1.85 mmol O_2 was used in nitrification, because it is the major aerobic process in deep-sea sediments. Therefore, 22% (1.85/8.15) of the SCOC value gives us an estimate of O_2 used in nitrification. In nitrification, each millimole of reduced nitrogen requires 2 mmol of O_2 (Reimers et al. 1992), 1.5 mmol to oxidize ammonia and 0.5 mmol to form H_2O. Sediment community nitrogen oxidation (SCNO) in Table 1 was calculated assuming 22% of the O_2 consumption measured in SCOC was used in nitrification and then converting to grams N per square meter per year.

SCNO was quite consistent, as expected from the SCOC rates, with the highest rates in 1990–1991 and 1992–1993 (0.36 g N m^{-2} yr^{-1}) and the lowest rate in 1994–1995 (0.28 g N m^{-2} yr^{-1}) (Table 1). The PTN flux : SCNO indicated a deficit in the nitrogenous food supply, particularly evident in 1995–1996, corresponding to the period of lowest POC flux : SCOC. As with POC, we need to take into account the PTN burial rate to obtain the amount available for the sediment community. We determined PTN burial rate from the molar ratio of PTN to POC, assuming the same burial efficiency as POC (9%). Subtracting the PTN burial rate from the PTN flux and dividing by the SCNO yielded values ranging from 0.87 in 1993–1994 to 0.18 in 1995–1996. Over the 8-yr sampling period, this ratio indicated that sinking POM supplied 60% of the nitrogen required to meet the estimated aerobic respiration demand of the sediment community.

Supply versus demand—The deficit of ~50% in sinking POM to meet the demands of sediment community aerobic respiration requires other sources of food. To evaluate the standing stocks and fluxes more thoroughly, we examined the carbon and nitrogen budgets for the sediment community during two extreme periods when full data sets existed: a period of close agreement between supply and demand (1990–1991) and a period of great discrepancy (1995–1996). In generating our budgets, we assumed that the sediment community was limited primarily to the upper 3 cm of the sediment, the depth of penetration of oxygen and the assumed depth of bioturbation at Sta. M. (Reimers et al. 1992), and the bottom 10 cm of the water column (arbitrary vertical range for infauna that extend into the water column).

The standing stock of organic carbon in the water column included the large DOC pool and the much smaller suspended particulate organic carbon (SPOC) pool (Table 2). In the sediment, the organic carbon (SedOC), which consisted of both particulate and dissolved fractions, was the largest pool, three orders of magnitude larger than the DOC pool in the water column. We assumed that the quantity of DOC in the sediment did not change between 1991, when it was measured (Bauer et al. 1995), and 1995–1996. The organic carbon content of the benthic organisms in the sediments was a minor contribution to this standing stock (Smith et al. 1992). Sediment bacterial biomass, estimated from sediment ATP concentrations, represented the largest fraction of living carbon, while the foraminiferans and metazoans contributed orders of magnitude lower quantities to the overall standing stock (Table 2). Combined, the pools of living carbon were <0.2% of the SedOC both years (Table 2). It should be noted

Table 2. Annual carbon and nitrogen budgets for overlying water and sediment at Sta. M during 1990–1991 and 1995–1996. POC and PTN flux were measured in a trap 50 m above the bottom. Sediment bacterial carbon in the upper 3 cm was estimated by multiplying the ATP concentration by 250 (Smith et al. 1987). Metazoans that were retained on a 300-μm mesh sieve were preserved and weighed in 1-cm depth intervals (Drazen et al. 1998), and wet weights for each taxon were considered to be 10% organic carbon (*see* Smith 1992) and 0.6% nitrogen. Agglutinated foraminiferal weight, including the tests, was estimated to be 1% organic carbon; calcareous foraminiferal weight was estimated to be 10% organic carbon and 0.6% nitrogen. SedOC, sediment organic carbon; DON, dissolved organic nitrogen; SPON, suspended particulate organic nitrogen; PTN, particulate total nitrogen; SedTN, sediment total nitrogen.

	1990–1991	1995–1996
I. Carbon budget		
A. Overlying water		
1. Standing stocks		
a. DOC (g m^{-2} to 10 cm above sediment)	0.046*	0.044†
b. SPOC (g m^{-2} to 10 cm above sediment)	<0.001‡	<0.001§
2. Fluxes		
a. POC flux (g m^{-2} yr^{-1})	2.51	0.67
lateral advection portion of POC (g m^{-2} yr^{-1})	0.48	0.01
Flux to the sediment	**2.51**	**0.67**
B. Sediment		
1. Standing stocks		
a. DOC (g m^{-2} to 3 cm below sediment surface)	0.162‖	0.162‖
b. SedOC (g m^{-2} to 3 cm below sediment surface)	149	150
(1) bacteria (ATP) (g m^{-2} to 3 cm below sediment surface)	3.30	2.28
(2) metazoans (g m^{-2} to 3 cm below sediment surface)	0.03	0.03
(3) foraminiferans (g m^{-2} to 3 cm below sediment surface)	0.02	0.02
2. Fluxes		
a. SCOC (g m^{-2} yr^{-1})	3.75	3.06
b. Burial rate (g m^{-2} yr^{-1})	0.23	0.06
Fluxes: a + b (organic carbon utilization and loss in the sediments)	**3.98**	**3.12**
II. Nitrogen budget		
A. Overlying water		
1. Standing stocks		
a. DON	0.014¶	0.014¶
b. SPON	<0.001	<0.001
2. Fluxes		
a. PTN flux (g m^{-2} yr^{-1})	0.30	0.06
(1) lateral advection portion of PTN (g m^{-2} yr^{-1})	0.059	0#
Flux to the sediment	**0.30**	**0.06**
B. Sediment		
1. Standing stocks		
a. DON	0.02¶	0.02¶
b. SedTN (g m^{-2} to 3 cm below sediment surface)	24.8	12.1
(1) bacteria (ATP) (g m^{-2} to 3 cm below sediment surface)	0.66	0.49
(2) metazoans (g m^{-2} to 3 cm below sediment surface)	<0.002	<0.002
(3) foraminiferans (g m^{-2} to 3 cm below sediment surface)	<0.002	<0.002
2. Fluxes		
a. SCNO (g m^{-2} yr^{-1})	0.36	0.29
b. burial rate (g N m^{-2} yr^{-1})	0.029	0.007
Fluxes: a + b (PTN utilization and loss in the sediments)	**0.389**	**0.297**

* From Bauer et al. 1998 (JGR).
† From Bauer et al. 1998 (DSR II).
‡ From Druffel et al. 1996.
§ From Druffel et al. 1998.
‖ From Bauer et al. 1995.
¶ Calculated from unpubl. data of Bauer for 1991 (estimated for 1995–1996).
\# Lateral advection (flux at 50 mab minus flux at 600 mab) is a negative number (*see Table 1*) for this year; therefore, zero is used in calculation.

that the SedOC we measured included most of the living carbon with the exception of larger sediment biota selectively removed prior to analysis. We assumed that including these organisms would not significantly increase the percentage living carbon above 1% of the SedOC (Smith 1992).

Above, we compared the carbon fluxes from sinking POC and lateral advection to the demands of the sediment community combined with the loss due to burial. In 1990–1991, there was a discrepancy of 1.47 g C m^{-2} yr^{-1} (derived from Table 2) between the supply and demand. This deficit could have been met easily by the standing stocks of carbon in the sediment, which would sustain the SCOC beyond the seasonal inputs of POC. Since the organic carbon in the sediment includes benthic organisms, it is reasonable to assume that predation by mobile, epibenthic, or pelagic predators could account for some of the food deficit by consuming living carbon in the sediments. However, this living carbon source is ultimately derived from the sinking POC flux on temporal scales ranging from months to decades, depending on the age and growth of the predators and prey. A portion of the nanobiota, including bacteria and small eukaryotes such as flagellates, yeasts, and amoebae (Snider et al. 1984), consumes DOC from the sediment pool, which is more recent than the DOC supply in the water column (Bauer et al. 1995). These organisms make up a component of measured SCOC but do not consume sinking POC directly, contributing to the observed POC : SCOC discrepancy. Considering these biotic interactions within the sediment carbon pool, there appears to be sufficient organic carbon to meet the carbon deficit in 1990–1991.

In contrast, the discrepancy in the annual supply of and demand for organic carbon in 1995–1996 was much more apparent. The combined fluxes of organic carbon supplying the sediment community were 0.67 g C m^{-2} yr^{-1}, which only accounted for 20% of the demand by the sediment community and loss to burial (Table 2). The deficit of 2.45 g C m^{-2} yr^{-1} was more than twice that in 1990–1991. The carbon pools in the sediment still could have accounted for this larger deficit in organic carbon supply and sustained SCOC. However, the higher C : N (Fig. 4B) during this period indicated a change in the quality of this food source.

For the nitrogen budget in 1990–1991, there was a deficit of 0.09 g N m^{-2} yr^{-1} in the supply, such that the demand by sediment community nitrogen oxidation plus burial was almost met (Table 2). However, the reverse was true in 1995–1996, when the supply was sufficient to account for only 20% of the demand by the sediments. The deficit of 0.237 g N m^{-2} yr^{-1} could have been met adequately by the surface sediment pool of organic nitrogen, including both living and nonliving fractions. However, sediment total nitrogen showed a trend of decreasing concentrations during this period compared to previous years (Fig. 3B).

Conclusions

On initial inspection, it is disconcerting to find a discrepancy between the supply of food to and the demand for food by the deep-sea benthos, especially over a period of time (8 yr), during which episodic, seasonal, and interannual variability would be expected to average out. However, it is possible that the utilization of organic matter by the sediment community is fueled by sources (e.g., sediment DOC and POC, lateral transport, etc.) not adequately quantified by our measurement techniques and that major food supply events occur on decadal timescales. This possibility and the extensive temporal variability apparent in our data strongly emphasize the need for detailed studies over long timescales in order to evaluate the cycling of nutrients in the deep ocean. Based on our results, there appeared to be adequate supplies of food to sustain the sediment community during periods of low food supply, such as in 1995–1996 and 1997–1998. However, we would expect that a long-term decline in the flux of sinking POM reaching the deep-sea floor, e.g., as a result of the effects of climate change on the upper ocean ecosystem, would lead to substantial changes in the structure and function of benthic communities as well as the geochemistry of marine sediments. The correlation of climatic events such as El Niño and the concomitant increase in precipitation and river discharge along the western U.S. coast suggest that climate influences the quantity and quality of organic matter input to the deep ocean. Decadal-scale climate variations that affect marine primary production as well as terrestrial discharges into the ocean may be extremely important influences on biogeochemical processes in the deep sea.

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Received: 27 July 2000
Accepted: 4 January 2001
Amended: 11 January 2001