methionine [D. J. Leahy, W. A. Hendrickson, I. Aukhil, H. P. Erickson, *Science* **258**, 987 (1992)]. RNA and protein were mixed to equimolar concentration and crystals grown by sitting drop vapor diffusion from 50 mM sodium cacodylate (pH 6.5), 15% polyethylene glycol (PEG) 600, 80 mM $Mg(OAc)_2$, 100 mM KCl, and 0.2 mM $Co(NH_3)_6Cl_3$ at 37°C. The crystals typically had a size of 0.1 mm by 0.1 mm by 0.2 mm. The space group is $P4_32_12$ with unit cell dimensions $a = b = 150.68$ Å and $c = 63.84$ Å. The crystallographic asymmetric unit contains two complexes.

5. Diffraction data for selenomethionyl and native crystals were collected at beamline X4A, Brookhaven National Laboratories, Brookhaven, NY. Heavy-atom positions were determined with the program SOLVE [T. C. Terwilliger, *Methods Enzymol.* **276**, 530 (1997); www.solve.lanl.gov] and an experimental phase set generated with the program MLPHARE [Z. Otwinowsky, in *Isomorphous Replacement and Anomalous Scattering, Proceedings of the CCP4 Study Weekend*, W. Wolf, P. R. Evans, A. G. W. Leslie, Eds. (Science and Engineering Research Council Daresbury Laboratory, Warrington, UK, 1991), p. 80] in the resolution range 10.0 to 4.2 Å (Table 1). Experimental electron density maps were improved by solvent flattening with the SOLOMON procedure [J. P. Abrahams and A. G. W. Leslie, *Acta Crystallogr. D* **52**, 30 (1996)] and twofold noncrystallographic symmetry averaging. A model of L11-C76 (*13*) was fitted into the density with the Se-atom positions as a guide. A model of the RNA was built into the electron density map with the program O [T. A. Jones, J. Y. Zou, S. W. Cowan, M. Kjelgaard, *Acta Crystallogr. A* **47**, 110 (1991)]. During the initial stages of model building, the program SIGMAA [R. J. Read, *ibid.* **42**, 140 (1986)] was used to improve the electron density maps by phase recombination. Model refinement was performed with X-PLOR version 3.8 [A. T. Brünger, J. Kuriyan, M. Karplus, *Science* **235**, 458 (1987)]. A final round of model building and refinement (including grouped B factor refinement) against the native data set to 2.8 Å resolution was performed. The final crystallographic *R* factor is 24.0% against all reflections in the resolution range 8.0 to 2.8 Å (15,433 reflections) with an R_{free} [A. T. Brünger, *Nature* **355**, 472 (1992)] of 32.1% (1324 reflections) (Table 1). The model contains residues 6 to 72 of L11-C76 and all 58 nucleotides of the RNA. The two complexes in the asymmetric unit have a root-mean-square deviation (rmsd) of 0.60 Å on all protein and RNA backbone atoms (when aligned on Cα and phosphorus). The coordinates have been deposited in the RCSB Protein Databank (accession number 1QA6). Figures 1D, 2A, 2B, and 3B were generated with Setor [S. V. Evans, *J. Mol. Graphics* **11**, 134 (1993)] and Fig. 3C with Molscript [P. J. Kraulis, *J. Appl. Crystallogr.* **24**, 946 (1991)] and Raster3D [E. A. Merritt and D. J. Bacon, *Methods Enzymol.* **277**, 505 (1997)].
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Long-Term Discrepancy Between Food Supply and Demand in the Deep Eastern North Pacific

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A 7-year study of food supply [sinking particulate organic carbon (POC)] and food demand [sediment community oxygen consumption (SCOC)] in the abyssal eastern North Pacific revealed a long-term deficit in food supply. The POC:SCOC ratio decreased by 52 to 59 percent between 1989 and 1996. A possible explanation for this trend is the documented sea surface temperature increase and concomitant plankton biomass decrease in the eastern North Pacific, resulting in an apparent reduction in POC export from surface waters to the deep ocean. Continuation of this trend could profoundly impact geochemical cycling as well as the structure and dynamics of deep-sea communities.

Recent long-term increases in sea surface and upper water column temperatures in the eastern North Pacific have led to shoaling of the mixed layer, resulting in a reduced nutrient supply to the euphotic zone (*1*). Concomitantly, there has been a decline in primary productivity accompanied by decreases in zooplankton and seabird abundances as well as kelp production (*1–4*). Deep-sea communities rely on food produced in the euphotic zone, and a long-term reduction in surface productivity could severely impact the supply of food to the deep ocean.

Efforts to examine the coupling between pelagic food sources and the utilization of this food by deep-sea communities have been hampered by a number of problems. These include qualitative and quantitative diversity in food sources, the diffuse nature of the mechanisms by which this food is transported from its source to the abyssal ocean, and variability in metabolic demands by deep-sea communities on a variety of temporal and spatial scales. Short-term studies of trophic coupling between a pelagic (water column) food supply and benthic (surface sediment) communities in the deep ocean have been inconclusive. These studies have revealed both acceptable agreement and unexplained discrepancies, depending on geographic location and time of year (*5–7*). These inconsistencies have prompted long-term studies of temporal variation in the flux of sinking particulate organic carbon (POC), as a measure of food supply reaching the sea floor from the overlying water column, and sediment community oxygen consumption (SCOC), as an estimate of metabolic demand for organic carbon (*8*, *9*).

A 7-year study was conducted to examine

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the relation between food supply and demand in an area of the deep sea with strong seasonality in primary production in the overlying waters. We measured the flux of sinking POC at 600 and 50 m above bottom (mab) continuously from June 1989 until October 1996 at an abyssal station (Station M; 4100 m water depth), 220 km off the central California coast (*8*, *10*, *11*). This station is described in detail elsewhere (*8*, *9*). Here we report results from October 1989 through October 1996, representing seven complete annual cycles.

In situ measurements of SCOC were made with a free-vehicle grab respirometer (FVGR) (*5*) on seasonal cruises throughout the study (*6*, *8*, *12*, *13*). For comparison with the FVGR data, in situ measurements of SCOC were made with two other, independent instruments during this study. Thirty-nine measurements of SCOC were collected with tube core respirometers (TCRs) placed by the submersible Alvin, and high-temporal-resolution measurements of SCOC were made with an autonomous bottom-transecting vehicle (ROVER) (*14*) from January through May 1996 at 17 sites. Synchronous measurements of SCOC by the FVGR and TCRs (Fall 1994 and Spring 1995) and the FVGR and ROVER (Spring 1996) were not significantly different (*14*, *15*).

The flux of sinking POC at 600 and 50 mab varied considerably on both intra- and interannual scales, with 10-day–averaged fluxes ranging from 0.16 to 27.87 mg C m^{-2} day^{-1} between October 1989 and October 1996 (Fig. 1A). The highest peaks in POC flux occurred in summer and fall with the lowest fluxes in winter. On an annual basis, the highest POC fluxes were in 1991, 1993, and 1994 and the lowest fluxes in 1992, 1995, and 1996. POC fluxes were consistently higher at 50 mab than at 600 mab, suggesting local resuspension or lateral input from the continental margin to the east (*8*, *11*, *16*).

Seasonal measurements of SCOC showed fluctuations similar to those in POC flux, with highest rates in summer and fall and lowest rates during the winter months (Fig. 1). However, the magnitude of the fluctuations in SCOC varied by a factor of 3 (5.0 to 15.7 mg C m^{-2} day^{-1}), whereas POC fluxes varied by a factor of 174. The greater variation in POC flux compared with SCOC may be attributable to two factors. First, POC flux was sampled with higher temporal resolution than SCOC, and thus the POC flux record includes fine-scale variability that is absent from the coarser-resolution SCOC record. Second, the magnitude of the SCOC may be related to the quality of the incoming POC, not just the quantity (*17*), resulting in a decoupling of POC flux and SCOC. Interannual variations in SCOC measured with the FVGR were most pronounced in 1991 and 1993, corresponding to the highest peaks in POC flux. From January 1995 through the end of our study in October 1996, SCOC was consistently higher than POC flux.

SCOC measured with the TCRs was high during the fall peak in POC flux in 1994 and similar in magnitude to POC flux in April 1995, but lower than SCOC interpolated between FVGR measurements in February and June (Fig. 1B). Contiguous measurements of SCOC made with the ROVER between January and June 1996 closely paralleled interpolated measurements of SCOC made with the FVGR in February and June. During this time period both SCOC records were consistently higher than the POC fluxes.

The balance between POC flux and SCOC was expressed as a ratio, with values greater than unity indicating a surplus of POC and values less than unity indicating a deficit in sinking POC. POC:SCOC exhibited considerable variability between 1989 and 1995, then declined sharply in 1995 and 1996 (Fig. 2). POC:SCOC for both collection depths decreased progressively beginning in October 1989 and reached values approaching 0.1 in mid-1996. Between October 1989 and October 1996, this relation was significantly negative at both 600 ($P = 0.004$) and 50 mab ($P = 0.007$). Total POC fluxes from 4 October 1989 until 3 October 1996 were 12.11 g C m^{-2} at 600 mab and 13.75 g C m^{-2} at 50 mab. Compared with the total SCOC of 23.24 g C m^{-2}, the food supply estimated at 600 and 50 mab contributed only 52.1% and 59.2%, respectively, of the sediment community demand. A comparison between food supply and demand on an annual basis revealed the best agreement in 1989 to 1990 with 99.3% at 50 mab and the largest discrepancy in 1995 to 1996 of 21.4% at 600 mab.

A likely explanation for the progressive decline in POC:SCOC between 1989 and 1996 is the observation since the late 1970s of increasing sea surface and upper water column temperatures in the eastern North Pacific (*18*). Surface warming can lead to a

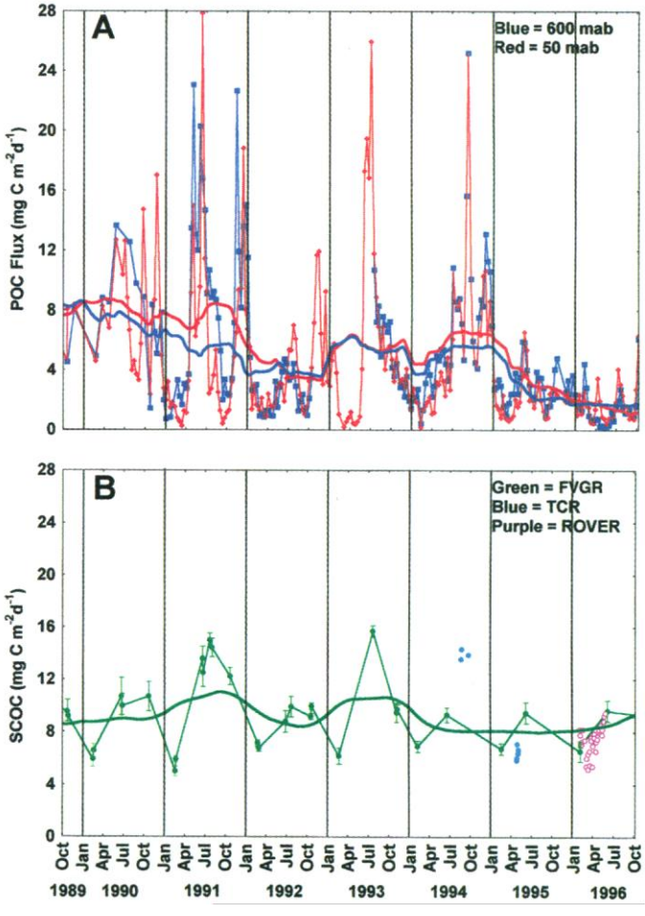

Fig. 1. POC flux and SCOC measured at Station M between October 1989 and October 1996. (**A**) POC measurements were averaged over a 30-day sampling period before June (600 mab) or October 1990 (50 mab) and a 10-day sampling period thereafter and are expressed as daily fluxes. Individual symbols represent the means of two replicate measurements for each sampling period. Replicate measurements typically differed by less than 10%. "Swimmers" (zooplankton capable of swimming into the sediment trap rather than sinking in as carcasses) were found in all traps, but the abundance of swimmers did not exhibit a significant trend over the time period reported here. POC fluxes at 600 mab (blue, filled squares) and 50 mab (red, filled diamonds) are plotted separately, but during periods when one trap failed to collect a sample, data from the other trap have been substituted (October 1992 to July 1993 at 50 mab; July 1994 to October 1994 at 600 mab). Thick traces represent 365-day centered moving averages for the two flux records. (**B**) SCOC measurements are based on incubations of 2 days (FVGR: green, filled circles), 1 to 6 days (TCR: blue, filled circles), and 6.3 days (ROVER: purple, open circles). TCR and ROVER symbols are individual measurements, whereas FVGR measurements are presented as means ± 1 SD. Lines connecting FVGR measurements represent linear interpolations between adjacent data points. Thick traces represent 365-day centered moving averages for the SCOC records.

reduction in the depth of the mixed layer and can decrease the supply of nutrients to the euphotic zone, resulting in lower rates of primary production and, consequently, less export production (*1*). Because the magnitude of export production directly affects the flux of sinking POC to the deep ocean (*19*), it is likely that the deficit in POC supply to the deep-sea floor is a result of sea surface warming and its associated effects.

Long-term increases in sea surface temperature in the eastern North Pacific have been related to a number of biological impacts. Near shore, the abundance and stipe number (an index of individual size) of southern California populations of the kelp *Macrocystis pyrifera* have undergone a substantial decline since 1990, following the trend of increasing sea surface temperature (*3*). In addition, long-term faunal changes have been reported in rocky intertidal communities on the central California coast. These changes include a shift in species composition toward warmer-living forms, apparently as a result of increases in sea surface temperature over the 60-year period ending in 1994 (*20*). Offshore, sea surface warming has been correlated with declining populations of zooplankton (*2*) and pelagic birds (*4*, *21*). Since the late 1970s, macrozooplankton volume in the California Current has declined over 70%, in concert with increasing sea surface temperatures (*1*, *2*). Reduced macrozooplankton abundance has had a major impact at higher trophic levels. Sea bird abundance declined 40% within the California Current between 1987 and 1994, largely as a result of a 90% decline in the population of the dominant pelagic species, the sooty shearwater *Puffinus griseus* (*4*). The decrease in macrozooplankton abundance, estimated from quarterly offshore sampling in surface waters of the California Current (*22*), is significant ($P = 0.015$) and similar in timing and magnitude to the decrease we observed in POC:SCOC between 1989 and 1996.

A long-term deficit in the supply of food necessary to meet the metabolic demands of the sediment community certainly is unsustainable. We therefore must consider the possibilities that either the POC fluxes estimated from our collections are erroneously low or that alternate sources of nutrition to the benthos exist, besides the sinking POC collected in our sediment traps. There is evidence at this station that sediment traps tend to "clog" and undersample sinking particles during periods of high particulate matter fluxes (*11*, *23*). Methodological problems like clogging could contribute to the discrepancy but are difficult to quantify. However, if this mechanism were solely responsible for the observed flux discrepancies, one would conclude that the frequency of sediment trap clogging was increasing between 1989 and 1996, presumably because of an increase in the flux of sinking particles. This explanation is strongly contrary to the observations of reduced surface production and the expectation of reduced export production over this time period and seems unlikely to account for the observed POC flux discrepancies.

A second possibility is that our sediment traps do not quantitatively sample certain types of food inputs—for example, very large parcels of organic material (*11*). Such parcels could substantially supplement the smaller POC collected by our sediment traps, providing an important source of nutrition for the benthic community. However, in seasonal tows of a camera sled across several kilometers of sea floor at Station M over the 7-year monitoring period, we found no evidence of large, discrete food falls (*24*). Further, although this mechanism could provide the benthic community with a source of food apart from the sinking POC collected in our sediment traps, the existence of episodic organic falls would not explain the observed decline in our measurements of POC:SCOC between 1989 and 1996.

Considerable evidence from trace metal and isotopic measurements of suspended particulate matter in the water column at Station M suggests the input of horizontally transported material from the continental shelf and slope to the east (*9*, *16*, *25*). The advective input of organic material was reflected in the sediment trap collections as consistently higher fluxes at 50 mab, compared with 600 mab (Fig. 1) (*11*). However, even the elevated fluxes at 50 mab account for only 59% of the estimated benthic metabolic demand between 1989 and 1996, far below the levels necessary to achieve a balance between food supply and demand.

It seems unlikely that the discrepancy we measured between POC flux and SCOC over a 7-year period could continue indefinitely without producing visible changes in benthic community structure and affecting rates of metabolism, growth, and reproduction among the benthic fauna. In the future, we would expect this unsustainable condition to be resolved either by periodic increases in POC flux sufficient in magnitude to compensate for the deficit we observed between 1989 and 1996 or by long-term shifts in the dynamics of deep-sea benthic communities and their faunal components. These shifts may affect not only biological processes but also geochemical cycling in the sediments and ultimately the sedimentary record.

Climatic changes appear to exert a strong influence on physical conditions within the upper ocean and thus impact the dynamics of shallow-water marine communities. These effects in turn are translated throughout the water column and into the deep sea. If long-term climatic changes cause a progressive warming of the waters in the eastern North Pacific, our data suggest that the result may be a reduction in the supply of food to the deep-sea benthos. This reduction could produce a concomitant shift in the characteristics and, perhaps, in the composition of the abyssal community.

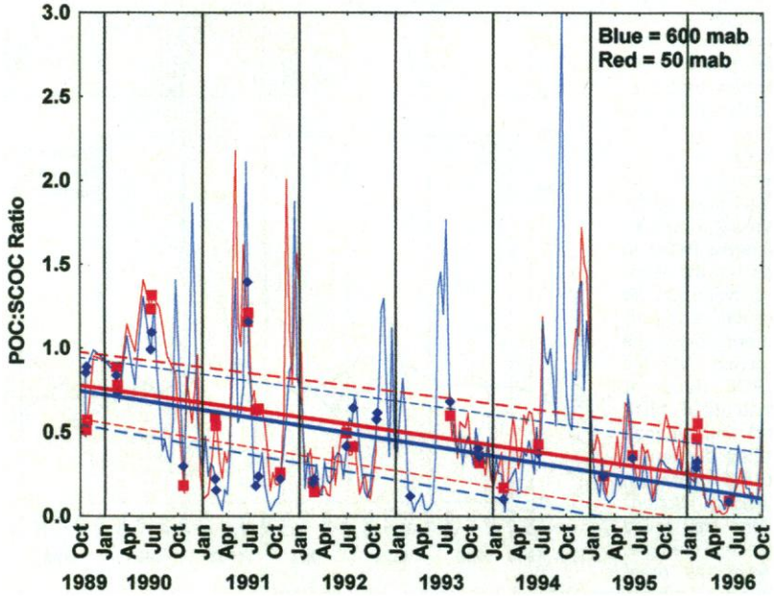

Fig. 2. The ratio of POC:SCOC on the basis of POC flux measurements at 50 and 600 mab and on SCOC measured with the FVGR. POC:SCOC was calculated at 10-day intervals with sinking POC flux data (Fig. 1A) and interpolated SCOC (Fig. 1B). Thin traces show "raw" POC:SCOC values. Symbols indicate POC:SCOC during 10-day time periods when measurements of both POC flux and SCOC were made. Thick solid lines are based on linear regressions with only data presented as symbols. Dashed lines indicate 95% confidence intervals for the regressions.

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Net Primary Production of a Forest Ecosystem with Experimental CO_2 Enrichment

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The concentration of atmospheric carbon dioxide was increased by 200 microliters per liter in a forest plantation, where competition between organisms, resource limitations, and environmental stresses may modulate biotic responses. After 2 years the growth rate of the dominant pine trees increased by about 26 percent relative to trees under ambient conditions. Carbon dioxide enrichment also increased litterfall and fine-root increment. These changes increased the total net primary production by 25 percent. Such an increase in forest net primary production globally would fix about 50 percent of the anthropogenic carbon dioxide projected to be released into the atmosphere in the year 2050. The response of this young, rapidly growing forest to carbon dioxide may represent the upper limit for forest carbon sequestration.

Combustion of fossil fuels and deforestation, particularly in tropical regions, are rapidly increasing the concentration of CO_2 in the atmosphere (*1*, *2*). Trees that use the C_3 mechanism of photosynthesis are carbon-limited at the current atmospheric CO_2 concentration (*3*); therefore, the stimulation of photosynthesis by elevated CO_2 may increase the capacity of forests to store carbon in wood and soil organic matter. Because of their imposing contribution to global productivity (*2*), forests have the potential to reduce the anthropogenic increase in atmospheric CO_2.

Seedlings or saplings exposed to two times the current atmospheric concentration of CO_2 in growth chambers, greenhouses, or open-top chambers have ~54% greater photosynthesis and ~31% greater biomass (*4*). These enhancements are considerably reduced when plants receive suboptimal amounts of other important resources such as nitrogen (*5*). Most studies of tree rings (*6*) show no increase in growth rate in response to the increase in atmospheric CO_2 that has occurred from the pre-industrial concentration of ~280 μl $liter^{-1}$ to the current 360 μl $liter^{-1}$. Resource limitations in natural ecosystems and other ecological interactions including competition (*7*) may constrain the potential for forests to respond to increasing concentrations of CO_2.

To examine the response of an intact forest ecosystem to projected elevated concentrations of CO_2, we installed a gas-delivery system in a 13-year-old loblolly pine (*Pinus taeda* L.) plantation in the Piedmont region of North Carolina (35°97′N 79°09′W) (*8*). The free-air CO_2 enrichment (FACE) system (*9*) increases the concentration of atmospheric CO_2 in 30-m-diameter experimental plots nested within this continuous pine forest (Fig. 1). Each FACE ring (plot) consists of a large circular plenum that delivers air to an array of 32 vertical pipes. The pipes extend from the forest floor through the 14-m-tall forest canopy and contain adjustable ports at 50-cm intervals. These ports are tuned to control the atmospheric concentration of CO_2 ($[CO_2]$) through the entire volume of forest. In the three elevated CO_2 plots, CO_2 was injected to maintain the atmosphere at ambient $[CO_2]$ plus 200 μl $liter^{-1}$ (~560 μl $liter^{-1}$); three ambient CO_2 plots were treated identically

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