Deep ocean communities impacted by changing climate over 24 y in the abyssal northeast Pacific Ocean

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The deep ocean, covering a vast expanse of the globe, relies almost exclusively on a food supply originating from primary production in surface waters. With well-documented warming of oceanic surface waters and conflicting reports of increasing and decreasing primary production trends, questions persist about how such changes impact deep ocean communities. A 24-y time-series study of sinking particulate organic carbon (food) supply and its utilization by the benthic community was conducted in the abyssal northeast Pacific (~4,000-m depth). Here we show that previous findings of food deficits are now punctuated by large episodic surpluses of particulate organic carbon reaching the sea floor, which meet utilization. Changing surface ocean conditions are translated to the deep ocean, where decadal peaks in supply, remineralization, and sequestration of organic carbon have broad implications for global carbon budget projections.

carbon cycle | deep-sea ecology | climate change

Contemporary climate change marked by increasing water temperature, density stratification, and acidification is impacting the world ocean. These changes are especially evident in oceanic surface waters and coastal areas (1), where surface water production of organic carbon and trophic exchanges are affected. However, little is known of how these changes influence the food supply to the deep ocean. Can we expect decreased production of organic carbon produced in the upper ocean, and thus less food delivered to the sea floor? Because the deep ocean occupies the vast majority of the world, such answers are critical to evaluating impacts of climate variation on the global carbon cycle, particularly regarding long-term carbon sequestration.

A major unknown component of the global carbon cycle is the amount of organic carbon that reaches the deep ocean and its ultimate utilization or long-term sequestration in the sediments. This supply starts with primary production by phytoplankton in surface waters. There is no consensus on whether phytoplankton biomass is decreasing as a result of a reduction in upwelled nutrients, caused by warming surface waters and increasing stratification (2). In open ocean areas, these conditions can lead to a decrease in primary production by phytoplankton (1, 3) and a geographic expansion of oligotrophic (low chlorophyll) waters (3). In contrast, along-shore winds and increased land–sea temperature disparities are leading to increased nutrient supply and primary production in coastal upwelling areas (1, 2, 4–6). A portion of the organic carbon produced in surface waters is exported to the deep ocean by a variety of mechanisms, including mineral ballasting, aggregation, fecal pellet production, and sinking or vertical migration of large zooplankton (7–12).

How do such conditions impact the food supply to the deep ocean, which relies on surface water primary production? Previous studies have shown an unexpected shortage of food reaching deep ocean depths to sustain benthic communities over an 18-y period, with carbon utilization consistently exceeding local supply over that time scale (13, 14). New technology added to long

time-series studies now allows us to compare high-resolution measurements of food supply and benthic community carbon consumption to trends over the past 24 y to resolve the question of food shortage, and to examine how it might be changing in the context of global warming. We set out to test the hypothesis that food produced in and settling from overlying surface waters cannot sustain benthic community utilization on multiyear to decadal scales at an abyssal station in the northeast Pacific. To test this hypothesis, we used a combination of autonomous instrumentation on the sea floor and water column, along with satellite-derived measurements, to estimate sinking particulate food as organic carbon reaching and being used by deep-sea communities. These studies were conducted as part of an ongoing 24-y time series at Station M, where measurements of deep-sea processes, combined with atmospheric and surface ocean conditions, have been monitored since 1989 (15). Overlying waters at this abyssal site (~4,000-m water depth) show strong seasonal primary production corresponding to upwelling events within the California Current.

Results

Surface ocean chlorophyll *a*, net primary production (NPP), and export flux (EF) estimated from satellite ocean color over a 100-km-radius circle around Station M (*SI Materials and Methods*), exhibited a distinct seasonal pattern that was highest in summer and fall (Fig. 1 *A–C*). Over the measured period from 1997 through 2012, average NPP was significantly higher from 2003 to 2012 than in years prior (Mann–Whitney *U* test, *P* < 0.001), with peaks more prevalent from 2006 onward. EF estimates were
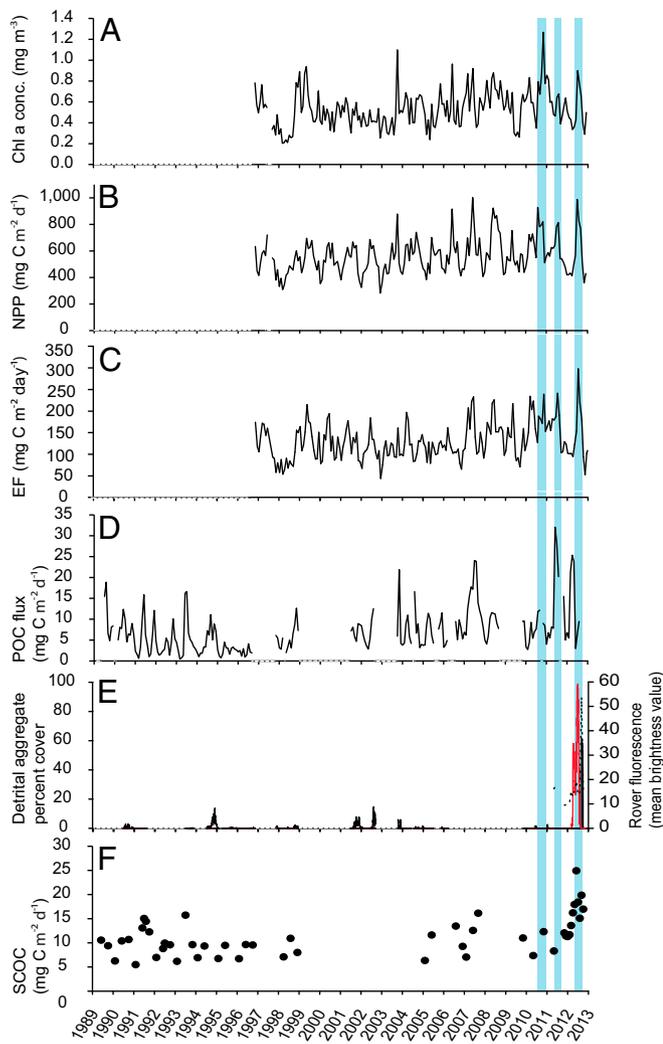
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Fig. 1. Long time-series measurements of surface-ocean and abyssal processes from July 1989 through November 2012 at Station M in the northeast Pacific Ocean on a monthly basis. Blue bars highlight the timing of peaks in NPP from 2010 to 2012. Dashed lines on *x* axes indicate data gaps longer than 1 mo. (*A*) Chlorophyll *a* concentration within 100-km-radius circle around Station M. (*B*) Net primary production within 100-km-radius circle around Station M. (*C*) Satellite estimated EF in a 100-km-radius circle around Station M, calculated for a nominal depth of 100 m. (Dataset S1). (*D*) POC flux. (*E*) Phytodetrital (black) and salp (red) aggregate percent cover on the sea floor (daily averages). Benthic Rover fluorescence images relative brightness value (dashed line). (*F*) Monthly averages of SCOC measured seasonally from 1989 until 2011 and daily from 2011 through 2012 (oxygen consumption has been converted to milligrams of carbon assuming a respiratory quotient of 0.85).

higher in 2012 than in any previous year (Fig. 1*C*). Sinking particulate organic carbon (POC) flux exhibited seasonal, interannual, and episodic rate variations over the entire time series from 1989 through autumn 2012 (Fig. 1*D*). Two major peaks in POC flux occurred over the last 18 mo of the time series, one from June to August 2011 and another between March and May 2012. The peak POC flux in spring/summer 2011 was the highest recorded over the 24-y time series (Fig. 1*D*), with the predominant constituent being the diatom *Rhizosolenia* (*Rhizosolenia setigera* and *Rhizosolenia styliformis*). The peak in POC flux in spring 2012 (Fig. 1*D*) included a relatively high abundance of tunics and fecal material from salps, *Salpa* spp., which were tentatively identified from high-definition video in the upper 600 m of the water column

with a remotely operated vehicle in June 2012 (*SI Materials and Methods*). This spring peak was soon followed by another major sedimentation event to the sea floor in September 2012, which consisted of a combination of salp fecal pellets and phytodetritus (Fig. 1*E*). This pulse corresponded with strong peaks in surface chlorophyll, NPP, and EF (Fig. 1 *A–C*).

The daily presence of detrital aggregates on the sea floor did not exceed 15% coverage over the period from 1990 to 2007. Detrital aggregates showed distinct seasonal variation, reaching the highest peaks in the summer of 2002 (< 15% cover), fall of 1994 (< 14% cover), and summer and fall of 2001 (<8% cover) (Fig. 1*E*). The highest sea-floor coverage by detrital aggregates measured throughout the 24-y time series occurred between March and August 2012, when salp detritus ranged from <1% cover in early March to a high of 98% cover on 1 July (Fig. 1*E*). This was the only measurable deposition event of salps observed during the entire time series. Following this salp pulse, phytodetrital aggregates combined with some salp detritus formed another major deposition event beginning in late August and peaking in mid-September. This pulse covered up to 61% of the sea floor (Fig. 1*E*), the largest primarily phytodetrital aggregate peak recorded during the time series. Highs in relative sea-floor fluorescence accompanied both of these depositional events (Fig. 1*E*). The pulse of *Rhizosolenia* detected by the sediment traps in 2011 was not apparent in the time-lapse photographs because there were no large aggregations with dissimilar coloration from the background sediment.

Once on the sea floor, the phytodetritus and salp detritus became a food source for the organisms living in and on the surface sediments and overlying water. The utilization of organic carbon on the sea floor, estimated from measurements of sediment community oxygen consumption (SCOC), exhibited a strong periodicity, highest in summer and fall and lowest in winter months (Fig. 1*F*). Over the entire time series, SCOC fluctuated substantially from year to year in synchrony with POC flux but with less variance. However, more recently there was a major increase in SCOC, reaching a high of 25 mg C m^{-2}·d^{-1} and coinciding with the peak in the deposition of salp detritus in spring 2012 (Fig. 1 *E* and *F*). This peak was 54% higher than any pre-2011 measure of SCOC. SCOC decreased after the salp aggregate peak, only to increase again corresponding to a secondary peak in September of a detrital aggregate deposition that clogged the sediment traps (Fig. 1 *E* and *F*), although not eliciting the same magnitude in response. There was no increase in SCOC during the major phytodetrital (*Rhizosolenia*) peak in POC flux the previous year (2011). However, with only seasonal SCOC measurements until November 2011, any increase might not have been detected. With SCOC measured daily starting in November 2011, it was possible to document the rapid response of SCOC to the pulses of salps or detrital aggregates on the sea floor in 2012 (Fig. 1 *E* and *F* and Fig. S1). SCOC spiked from 12 mg C m^{-2}·d^{-1} in February 2012 to its peak of 25 mg C m^{-2}·d^{-1} in June 2012, and then declined to 15 mg C m^{-2}·d^{-1} 2 mo later.

We compared the organic carbon supply as POC flux to the estimated utilization by the sediment community (SCOC). The highest POC fluxes and SCOC occurred in the last 2 y of the time series (Fig. 2*A*). The ratio of POC flux to SCOC increased above unity nine-times over the time series (*n* = 55 monthly estimates), four of which occurred in 2011 and 2012. POC flux:SCOC reached a high of 1.6 in spring 2012 (Fig. 2*B*). These results suggest that food utilization by the benthic community at Station M tracks POC flux (Spearman-rank correlation, r_s = 0.67, *P* < 0.001) (Fig. S2). However, the hypothesis that there is insufficient food to sustain the benthic community at Station M on multiyear to decadal time scales still cannot be rejected based on these most recent POC flux and SCOC measurements alone.

A more comprehensive view of carbon supply to and utilization on the sea floor considers input from detrital aggregates as
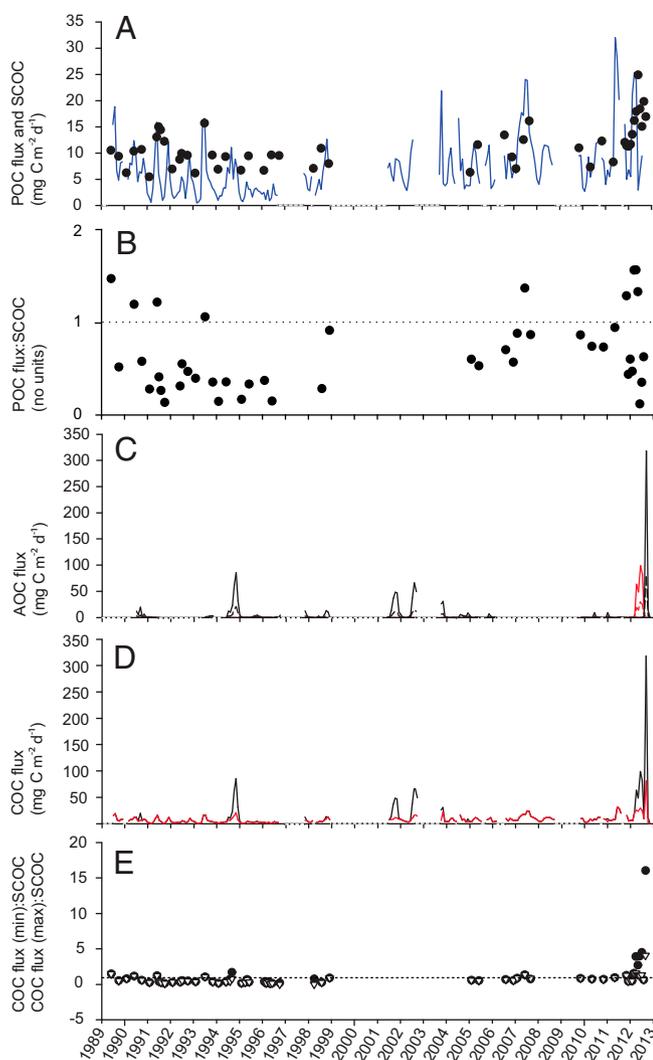
Fig. 2. Comparisons of food supply as POC and sea floor AOC with food utilization by the benthic community (SCOC) at Station M from July 1989 through November 2012. Dashed lines on *x* axes indicate data gaps exceeding 1 mo. (*A*) POC flux (line) and SCOC (dots). (*B*) Ratio of POC flux to SCOC. (*C*) Monthly estimated organic carbon flux of detrital aggregates (AOC) on the seafloor expressed in milligrams of C m^{-2}·d^{-1}. Phytodetrital AOC flux (black lines) minimum (dashed line) and maximum (solid line) based on the "August" model and the "September" model of Smith et al. using residence times of 45 h and 95 h. (16) (*SI Materials and Methods*). Salp AOC flux (red lines) maximum (solid line) using a residence time of 109 h, and minimum (dashed line) using a residence time of 365 h. (*D*) COC flux, the higher of POC flux or AOC flux for each time period, maximum (black line) and minimum (red line) estimates. (*E*) The ratio of COC flux minimum estimates [(salp + AOC fluxes) or POC] to SCOC (triangles), the ratio of COC flux maximum estimates [(salp + AOC fluxes) or POC] to SCOC (circles), dashed line indicates unity (COC flux:SCOC = 1).

well as POC flux, because POC flux might not include larger aggregates or salp tunics blocked by the small apertures in the sediment trap baffle (*SI Materials and Methods*). To calculate aggregate organic carbon (AOC) flux, the rate at which detrital aggregates supply organic carbon to sediments, we converted the measured coverage of detrital aggregates on the sea floor (Fig. 1*E*) to carbon content per area coverage, combined with a visible decay rate component. Separate observation-based conversions were generated for salp and phytodetrital aggregates, respectively (16, 17) (Fig. 2*C* and *SI Materials and Methods*). Combined phytodetrital and salp AOC fluxes ranged from ≤30 (minimum

estimate) to 99 (maximum estimate) mg C m^{-2}·d^{-1} in June 2012 during the salp deposition and up to 81 (minimum estimate) to 318 (maximum estimate) mg C m^{-2}·d^{-1} during the subsequent phytodetrital aggregate deposition in September 2012 (Fig. 2*C*). Because AOC flux measured from photographs and POC flux measured with sediment traps are simply alternative methods of measuring POC arriving on the sea floor, we chose the highest estimate from either method (*SI Materials and Methods*) and defined this value as the combined organic carbon (COC) flux (Fig. 2*D*).

Recent pulses of high COC flux at Station M exceeded utilization (SCOC) at the greatest ratios measured in 24 y (Fig. 2*E*). The monthly COC:SCOC peaked at 4.1 (minimum estimate) to 16.1 (maximum estimate) in September 2012, suggesting that a single monthly surplus alone could supply food to sediment communities for many months or even in excess of a year. The average COC:SCOC for the majority of the time series (1989–2007) was 0.57, whereas the 2008–2012 COC:SCOC averaged 2.5 using the maximum COC estimate and 1.1 using the minimum COC estimate. The combined magnitude of the COC flux suggests that the deficit seen in food supply during the earlier portion of the time series could be met by episodic pulses of particulate organic matter, such as those in 2011 and 2012. Based on these recent large food pulses to the seafloor, we would reject the original hypothesis that there is insufficient food supply to meet the benthic community utilization over the 24-y time series. However, this interpretation infers that there were previous pulses of high food supply before our study or possibly missed during periods of no data collection.

Discussion

Over long periods of time, the deep sea can be sustained on the episodic supply of food from surface waters, which may be increasing in frequency and magnitude over the last several years at Station M. The recent large pulses of food suggest that changing surface water conditions have contributed to increased delivery of POC to the abyssal sea floor. The two major pulses of POC, phytodetritus, and salp detritus that we observed in 2012 were the result of rapid vertical transport of planktonic organisms containing chlorophyll pigments to the sea floor (Fig. 1*E*), suggesting a high-quality food source (18, 19). This food then rapidly elicited a utilization response by the sediment community. Although the peaks of this consumption response were relatively short-lived, the oversupply of organic carbon is available for remineralization well into the future.

The abyssal area surrounding Station M is influenced by the California Current, which is experiencing increased wind stress, resulting in increased upwelling of nutrient-rich subsurface waters (4, 5), contributing to increased primary production (2, 20, 21). With increasing primary production there has been a corresponding increase in POC flux and detrital aggregate accumulation on the sea floor over the past several years. This increase has led to a food supply sufficient to offset deficiencies of the magnitude documented over the 24-y time series at Station M. This result suggests that global warming-related processes enhance food supply to the deep ocean.

Some studies based on satellite and in situ time-series measurements suggest that primary production in the ocean is increasing globally (2, 22). Other studies indicate a reduction in primary production in mid to low latitudes because of increasing vertical stratification (3, 23) and global reductions in primary production overall. It is not yet clear whether there might be an increasing trend in the food supply to other deep-ocean time-series stations. Climate-driven variability in primary production is expressed differently on a regional scale as a function of local ocean and air circulation, as well as changing climate conditions. An examination of satellite-estimated EF of organic carbon since 1997 from long time-series research stations, including PAP

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(Porcupine Abyssal Plain, northeast Atlantic), DELOS (Deep-Ocean Long-Term Envirnonmental Research Station, south Atlantic), Hausgarten (Arctic), and CARIACO (Cariaco Basin, Caribbean) also suggest that the highest monthly fluxes from the euphotic zone occurred in 2011–2012 (Fig. S3). Relatively oligotrophic stations, such as the Bermuda Atlantic Time-Series (BATS), Hawaii Ocean Time-series (HOT), North Atlantic Oligotrophic Gyre (NOG), and South Atlantic Oligotrophic Gyre (SOG), however, show no such recent increase (Fig. S3).

In the northeast Pacific (Station M), the abyssal community is sustained by episodic pulses of food originating in surface waters. These pulses have increased in magnitude over the past several years, together with increases in surface water primary production. Although environmental variation, such as air temperature and winds, affect the physical dynamics of this upwelling ecosystem, the specific mechanisms behind the changes in food-supply composition and food-web processes corresponding with the peaks in 2011 and 2012 remain unknown. Such increases in food supply appear to change the structure and functioning of deep-sea communities. We already are observing significant changes in populations of benthic fauna that can be correlated with food supply (24, 25) (*SI Materials and Methods*). With increased supply of POC to the deep sea, there is a concomitant increase in the utilization of this food through sediment community metabolism. Organic carbon not consumed readily by the benthic community becomes incorporated in the sediments and can be used in subsequent periods of low food supply. It is not known whether this increase in food supply will continue and, if so, on what geographic scales. Alternatively, these observed variations in the carbon cycle may be only part of interannual or multidecadal variations, unrelated to global climate change (26). We cannot predict whether this abyssal community at Station M is in long-term equilibrium, being sustained by previous pulses of food either before our study or missed during more recent periods of no data collection, or is in a state of change reflecting climatic variation.

Carbon remineralization and sequestration in the deep ocean are major unknown components in attempts to realistically model the global carbon cycle. Long time-series studies, such as the 24-y continuing study at Station M, remain the key mechanisms to resolving such carbon-cycle questions.

Methods

The continuous monitoring efforts at Station M were begun with sediment traps moored at 3,400- and 3,950-m depth, 600 and 50 m above the bottom, respectively, to sequentially collect sinking particulate matter as an estimate of food supply reaching the sea floor (27, 28). Concurrently, a time-lapse camera at the bottom of the mooring photo-documented hourly changes in sedimentation events and megafaunal movements over ~20 m^2 of the sea floor (29, 30). Seasonal measurements of SCOC, used to estimate organic carbon utilization, were made with a free vehicle-grab respirometer (31). Year-round measurements of SCOC began in 2011, using an autonomous bottom-transiting vehicle (29, 32) (Fig. S1) (Benthic Rover). The Benthic Rover also takes high-resolution images of the sediment surface, filtered to the approximate wavelength of chlorophyll *a* fluorescence (29, 32).

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