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California Current Ecosystem (Station M, 34° 50'N, 123° 00'W, 4,000-m depth; 1989 to 2017). Such Eastern Boundary Coastal Upwelling systems can account for over 10% of global new production (23). Station (Sta.) M was chosen in 1989 because of expected high seasonality in surface production manifested in deep-ocean processes (24, 25). Over time it has become evident that interannual and longer-term processes also provide important variation in the area. Ocean basin-scale climate forcing has cascading influences on local winds, ocean circulation including upwelling, fronts, filaments, and eddies, and related variations in hydrographic structure, sea surface temperature (SST), and sea surface height (e.g., refs. 26 and 27). El Niño Southern Oscillation forcing has been linked further to changes in nutrient availability, primary production, zooplankton dynamics, POC export flux, and ultimately abyssal sea-floor ecosystem function (e.g., refs. 8, 21, and 28). For example, SST exhibited seasonal and interannual variation from 1989 through 2017 in the region over Sta. M, with increasing peaks during El Niño periods in 1997 to 1998 and 2014 to 2016 significantly exceeding 18 °C (mean + 2 σ ; Fig. 1A). Surface Chla concentration, NPP, and EF derived from ocean-color imaging, within a 100-km-radius circle overlying Sta. M, showed significant decreases during these El Niño periods (Fig. 1B). We evaluated lagged relationships between high-magnitude “pulse” events (i.e., ≥ 1989 -to-2017 time-series mean + 2 σ) of surface EF, abyssal POC flux (3,400-m depth; 600 m above bottom), sea-floor detrital aggregate (DA) % cover (4,000-m depth), and SCOC (4,000-m depth). We analyzed

a subset of the time series, from 2011 through 2017, when high-resolution organic carbon supply and demand fluxes were available for both the water column (sediment traps) and at the sea floor (time-lapse camera and mobile sea-floor respirometer) on temporal scales comparable to satellite-derived surface-ocean production (export flux). Lastly, we discuss the implications of our findings in the context of interpreting both observations and model estimates of EF and abyssal carbon fluxes.

Results

Twenty-Nine-Year Time Series: 1989 Through 2017. The POC flux at 3,400-m (600 m above bottom) depth showed seasonality and interannual variability over the entire time series, with the highest peak reaching 57 mg C·m⁻²·d⁻¹ (Fig. 1C). POC flux peaked in spring and summer periods, with highest spikes in 2011, 2016, and 2017. Mean POC flux was 8.1 mg C·m⁻²·d⁻¹ through the entire time series. For years with $\geq 50\%$ sampling coverage, significant pulses (mean + 2 σ = 22.5 mg C·m⁻²·d⁻¹) occurred in 2007, 2011 to 2013, and 2016 to 2017, contributing from 25 to 63% of the annual POC flux (Fig. 2).

On the sea floor, detrital aggregate % cover had a time-series mean of 6.4, becoming sharply higher beginning in 2011 compared with the preceding 21-y period (Fig. 1D). Significant peaks (mean + 2 σ = 46.6%) in DA % cover were evident in 2012, 2016, and 2017 exceeding 90%. Short-term seasonal measurements of SCOC were made from 1989 until 2011, with rates generally below the mean of 12 mg C·m⁻²·d⁻¹ for the entire 29-y period (Fig. 1E). Beginning in 2011, the benthic transecting Rover came on-line. This autonomous underwater vehicle provides contiguous measurements of SCOC that revealed elevated rates in 2012 reaching 24 mg C·m⁻²·d⁻¹, significantly above 18.7 (mean + 2 σ), before declining to lower seasonal peaks in 2016 and 2017.

Seven-Year Time Series: 2011 Through 2017. Mean export flux over this 7-y period was 113.4 mg C·m⁻²·d⁻¹. Six significant EF peaks exceeded the 1989-to-2017 pulse threshold (139.6 mg C·m⁻²·d⁻¹), bracketing the low fluxes during the El Niño event in 2015 to 2016 (Fig. 3A). From 2011 to 2017, POC flux mean + 2 σ was 33.1 mg C·m⁻²·d⁻¹. Six significant POC flux peaks above the 1989-to-2017 mean + 2 σ pulse threshold (22.5 mg C·m⁻²·d⁻¹) occurred from 2011 to 2017 that could be analyzed from the surface to the sea floor—one each in 2011 and 2012 before decreasing during the El Niño event, and then four more in 2016 and 2017 (Fig. 3B). The mean POC flux over the 7-y period, 11.7 mg C·m⁻²·d⁻¹, exceeded the entire time-series POC flux mean of 8.1 mg C·m⁻²·d⁻¹.

Detrital aggregate % cover from 2011 to 2017, mean 14.9%, was more than twice that for the entire time series, mean 6.4% (Fig. 3C). There were five significant DA peaks above the 1989-to-2017 mean + 2 σ threshold (46.6%), two in 2012 following POC pulses in 2011 and three in 2016 and 2017 matching POC peaks over the same period. The longest sustained period of high DA % cover was in summer and fall 2017. Mean SCOC during the 2011-to-2017 period, 12.7 mg C·m⁻²·d⁻¹, was only slightly higher than for the entire time series (12.1 mg C·m⁻²·d⁻¹; Fig. 3D). SCOC was significantly higher than the 1989-to-2017 pulse threshold (18.7 mg C·m⁻²·d⁻¹) during two periods, a major rate increase in 2012 corresponding to a peak in DA % cover and in winter and spring 2015 (Fig. 3C). Lower spikes in SCOC corresponded to the POC flux and DA % cover events in 2016 and 2017.

Pulse Events. Temporal lags and correlations between POC flux pulses at abyssal depths and remineralization on the sea floor were highly variable between each event at Sta. M (Fig. 3). The duration and magnitude of these events, and the time between surface-ocean conditions related to carbon production, delivery

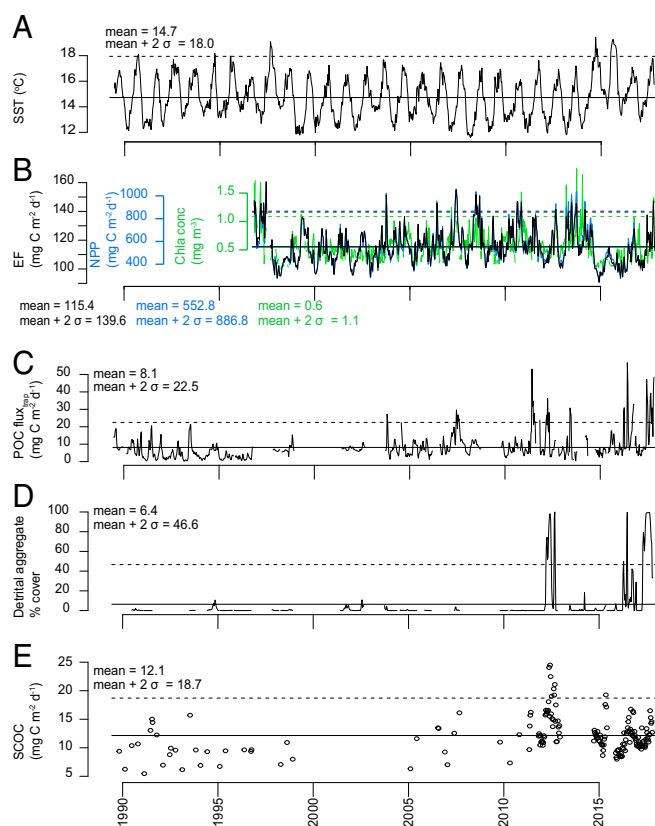


Fig. 1. (A and B) Full Station M time series of sea surface temperature (A) and surface chlorophyll a concentration (green lines), net primary production (blue lines), and export flux (black lines) (B) estimated from satellites with a 100-km radius around Station M. (C–E) Trap-measured particulate organic carbon flux (C), detrital aggregate % cover on the sea floor (D), and sediment community oxygen consumption (E). Time-series mean, and mean + 2 σ threshold, are shown as solid and dashed lines, respectively.

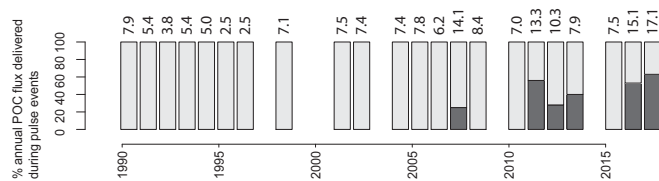


Fig. 2. Contribution of pulse events to annual carbon flux to 3,400-m depth, for years with >50% sampling coverage, based on sediment trap measures. Dark gray bars represent the proportion of annual POC flux that arrived during pulse periods, while light gray bars represent the proportion that arrived during nonpulse periods. Mean annual POC flux ($\text{mg C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) is given above each bar.

of organic carbon to abyssal depths, and remineralization on the sea floor, showed considerable variation. EF and POC flux pulse events were usually, but not always, followed by changes in the carbon flux at greater depths. Three principal components of the carbon cycle from surface production to sea-floor remineralization are EF, POC flux, and SCOC. Six POC flux pulse events exceeding the 1989-to-2017 mean + 2σ ($22.5\text{ mg C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) were identified and compared across all three of these components: spring 2012, spring, summer, and fall 2016, and summer and fall 2017 (Fig. 3).

The spring 2012 POC flux pulse event (no. 1; $1,480\text{ mg C}\cdot\text{m}^{-2}$) was 23% of the correlated EF ($6,340\text{ mg C}\cdot\text{m}^{-2}$) with a 40-d lag (Fig. 3A and B and Table 1). The corresponding SCOC ($1,220\text{ mg C}\cdot\text{m}^{-2}$) over a 60-d period was 82% of the POC pulse and significantly correlated ($P \leq 0.0005$) with a lag of 70 d. The SCOC event was 19% of the associated EF event. The organic carbon supply at 3,400 m was similar in magnitude to the estimated remineralization on the sea floor exceeding the demand (SCOC) by 18% during this event. It must be noted that our methods did not account for differences in the duration of responses following changes in EF and POC flux. If SCOC response to changes in POC flux is more prolonged than the duration of the POC flux pulse event itself, then we have underestimated the total carbon consumed by the sediment community in response to the POC flux pulse.

The spring 2016 POC flux pulse event (no. 2; $590\text{ mg C}\cdot\text{m}^{-2}$) was preceded by a suggestive increase ($P \leq 0.05$) in EF ($2,100\text{ mg C}\cdot\text{m}^{-2}$) 10 d earlier (Fig. 3A and B). Twenty days after this POC flux pulse event, there was a significant response ($P \leq 0.0005$) in SCOC ($220\text{ mg C}\cdot\text{m}^{-2}$) on the sea floor (Fig. 3D). Estimated POC flux during this 20-d event was 28% of the EF and exceeded the remineralization on the sea floor by 2.7 times. In summer of 2016, EF ($2,330\text{ mg C}\cdot\text{m}^{-2}$) coincided with the POC flux pulse (no. 3; $1,010\text{ mg C}\cdot\text{m}^{-2}$) with no lag (Fig. 3A and B). This 20-d POC flux pulse event was followed 30 d later by a period of increased SCOC ($280\text{ mg C}\cdot\text{m}^{-2}$). Supply of POC during this event was 43% of the EF and exceeded the estimated consumption of carbon (SCOC) by 3.6 times (Table 1). The final 2016 POC pulse event in the fall (no. 4; $1,210\text{ mg C}\cdot\text{m}^{-2}$) occurred over a 40-d period from September 26 to November 4. This POC flux event followed a peak in EF ($4,940\text{ mg C}\cdot\text{m}^{-2}$) by 10 d (Fig. 3A and B), with 25% being collected in the abyssal sediment traps (Table 1). There was a 0-d lag between POC flux and SCOC ($540\text{ mg C}\cdot\text{m}^{-2}$), which was not suggestive (Fig. 3B and D). The POC supply over this 40-d event was 2.2 times greater than the demand by the sediment community (Table 1).

In 2017, there were two POC flux pulse events, summer and fall. The 30-d summer POC flux (no. 5; $1,180\text{ mg C}\cdot\text{m}^{-2}$) event followed a local peak in EF ($3,810\text{ mg C}\cdot\text{m}^{-2}$) by 10 d ($P \leq 0.01$; Fig. 3A and B). EF exceeded the POC flux by a factor of three over this period (Table 1). In turn, this POC flux, with a significant lag of 10 d ($P \leq 0.005$), was three times higher than SCOC ($370\text{ mg C}\cdot\text{m}^{-2}$). Pulse event no. 6 ($2,600\text{ mg C}\cdot\text{m}^{-2}$) was recorded

over a prolonged 80-d period in the fall from September into mid November 2017 (Fig. 3). POC flux followed by 20 d a local peak in EF ($10,080\text{ mg C}\cdot\text{m}^{-2}$) and preceded a local peak in SCOC ($1,170\text{ mg C}\cdot\text{m}^{-2}$) by 20 d. Over this 80-d period, EF was 3.9 times greater than the POC flux, which in turn was 2.2 times greater than SCOC (Table 1).

A composite illustration showing average estimated fluxes of organic carbon and associated time lags related to the six POC flux pulse events from the surface (EF) through remineralization on the sea floor (SCOC) is shown in Fig. 4A. Average EF carbon preceding POC flux pulse events was $4,933\text{ mg C}\cdot\text{m}^{-2}$ with a time lag between 0 and 40 d to changes in POC flux (Fig. 4B and Table 1). Average POC flux pulse event carbon was $1,345\text{ mg C}\cdot\text{m}^{-2}$. SCOC averaged $633\text{ mg C}\cdot\text{m}^{-2}$ with a lag after POC flux of 0 to 70 d. Between January 6, 2011 and December 31, 2017, there were 130 10-d periods for which POC flux, EF, and SCOC data coincided. During this period, summed carbon content was as follows. EF: $117,700\text{ mg C}\cdot\text{m}^{-2}$ during nonpulse periods ($n = 1,100\text{ d}$) and $23,600\text{ mg C}\cdot\text{m}^{-2}$ during pulse periods ($n = 200\text{ d}$); POC flux: $8,580\text{ mg C}\cdot\text{m}^{-2}$ during nonpulse periods ($n = 1,100\text{ d}$) and $6,860\text{ mg C}\cdot\text{m}^{-2}$ during pulse periods ($n = 100\text{ d}$); and SCOC: $13,310\text{ mg C}\cdot\text{m}^{-2}$ during nonpulse periods ($n = 1,100\text{ d}$)

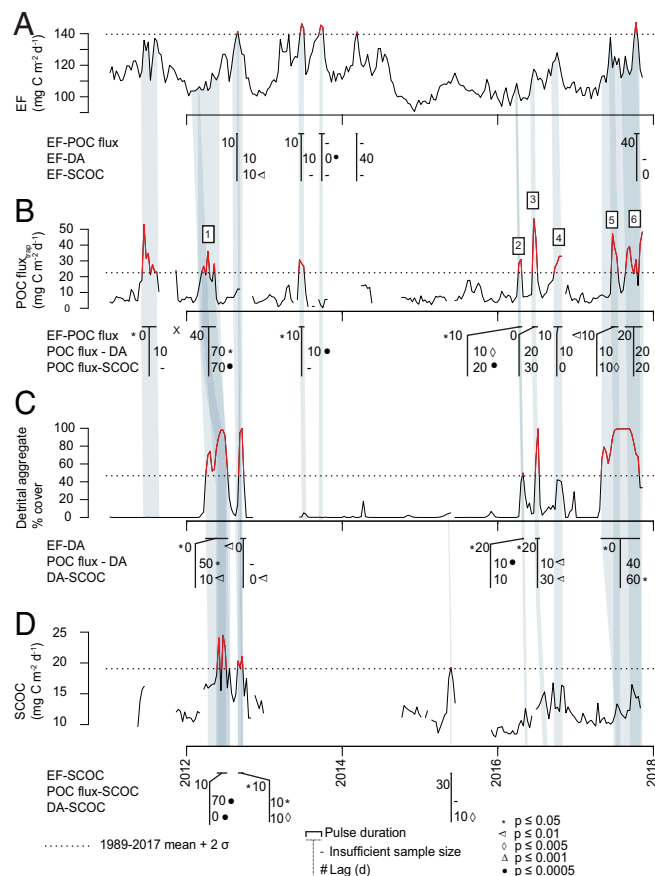


Fig. 3. Time lags in days associated with pulse periods of EF (A), POC flux to 3,400 m (B), DA % cover (at 4,000 m) (C), and SCOC (at 4,000 m) (D). Red lines identify periods when values exceeded the 1989-to-2017 time-series mean + 2σ (dotted lines), the threshold for pulse events used in the analysis. Graphics below the time-series plots show timing of peaks in cross-correlations and lags between the plotted pulse events and EF, POC flux, DA, and SCOC. P -value ranges for lagged correlations are noted. The duration of pulses is illustrated as a horizontal line above the associated lags and P -value symbols. Transparent gray shading has been added to illustrate the sequence of lags between variables. Numbered POC flux peaks (B) refer to events analyzed from surface to sea floor.

ID	Dates (no. of days)	EF_100 km, mg C·m ⁻²	POC flux, mg C·m ⁻²	SCOC, mg C·m ⁻²
1	3/21/2012 to 5/19/2012 (60)	6,340	1,480	1,220
2	4/9/2016 to 4/28/2016 (20)	2,100	590	220
3	6/18/2016 to 7/7/2016 (20)	2,330	1,010	280
4	9/26/2016 to 11/4/2016 (40)	4,940	1,210	540
5	6/23/2017 to 7/22/2017 (30)	3,810	1,180	370
6	9/1/2017 to 11/19/2017 (80)	10,080	2,600	1,170
Average	(42)	4,933	1,345	633
Minimum	(20)	2,100	590	220
Maximum	(80)	10,080	2,600	1,220

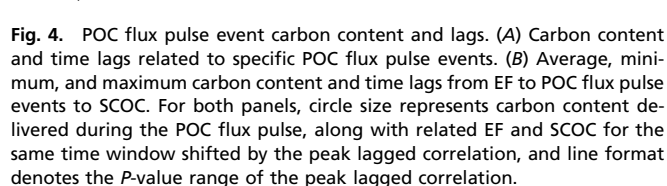
Discussion and Conclusions

The observed variation betw

Previous work has shown that ecosystem structure and dynamics might explain a significant portion of variation in the biological carbon pump (32, 33). Communities that produce fast-sinking particles (34) are especially important for determining POC flux export from surface waters and transfer to the deep sea. Faster-sinking particles are assumed to experience less exposure to consumption by heterotrophs, and therefore less carbon attenuation, than slower-sinking particles during vertical transport through the water column (35, 36). The high variability we observed in lags between surface and abyssal carbon dynamics related to POC flux pulse events suggests variability in food web dynamics and particle sinking rates. However, we also recognize that correlations with only a few time points describing individual events can contribute to variance in the results. Salp fecal pellets are very fast-sinking (37), carbon-rich particles which can be responsible for significant carbon delivery to the deep sea (36). They were evident during POC flux pulse no. 1 in 2012 (19), for which we estimated a lag of 40 d from EF to POC flux, which elicited a strong SCOC response 70 d after reaching 3,400 m. The fact that some, but not all, POC flux pulse events were followed by depositions of detrital aggregates visible in sea-floor images suggests variability in the biological carbon pump due to clumping of particles in marine snow and larger aggregates (e.g., ref. 38). Variable lags between POC flux pulse events and SCOC

High-resolution sampling has improved the capability to estimate surface-ocean organic carbon production to sea-floor consumption at Sta. M. Over the period from 2011 to 2017, the remineralization of organic carbon on the sea floor (SCOC) accounted for an estimated 11% of the EF, matching well the measured POC flux (*SI Appendix, Table S1*). Previous analysis using a ratio of monthly and yearly POC flux and SCOC averages from 1989 to 2015 estimated a 37% shortfall in POC flux to account for SCOC over the time series at Sta. M (23).

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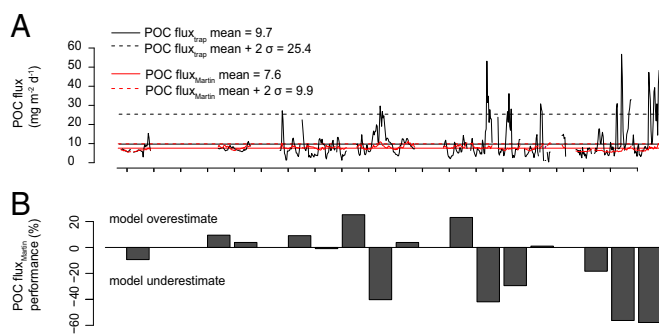


Fig. 5. Performance of Martin POC flux model estimates for Station M from 1989 to 2017 compared with sediment trap measures. (A) Full time series. (B) Model over/underestimate of POC flux on an annual scale for years with >50% sampling coverage: $(\text{POC flux}_{\text{Martin}} - \text{POC flux}_{\text{trap}}) / \text{POC flux}_{\text{trap}} \times 100$.

$[f_z = f_{z_0}(z/z_0)^{-b}]$, where z_0 is export depth (here 100-m depth), f_{z_0} is flux at export depth, and f_z is flux at depth z (here 3,400-m depth), and the coefficient of flux attenuation (b) parameter can be set to vary with midwater temperature parameterized with a spatially variable dataset (2). Using this variable b formulation of the Martin curve over time at Sta. M along with satellite-estimated EF, for 10-d periods when trap measurements and EF data were available ($n = 130$), the POC flux at 3,400-m depth (600 m above bottom) is estimated by the Martin curve to be $6.8 \pm 0.9 \text{ mg C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ when averaged over the period from 2011 to 2017 (SI Appendix, Table S1; T at 250-m depth at Sta. M ranged from 6.96 to 8.46 °C). Thus, Martin curve-estimated flux is ~57% of the measured POC flux (average $11.9 \pm 10.8 \text{ mg C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$). The measured POC flux reaching 3,400-m depth at Sta. M accounted for 11% of the EF during this period, while the Martin curve estimated only 6% of EF (SI Appendix, Table S1). This difference between trap measurements and model estimates is evident when examining the 1989-to-2017 POC flux time series as well (Fig. 5). Martin curve estimates of POC flux showed major divergences from trap measurements during high-flux periods, suggesting this model significantly overestimates attenuation during pulse events (Fig. 5A; pulse period POC flux trap measured vs. Martin curve model POC flux, two-tailed paired Wilcoxon signed-rank test P value < 0.0001 , $V = 666$, $n = 36$). However, the Martin curve model was remarkably close in estimating the background POC flux (nonpulse period POC flux trap measured vs. Martin curve model POC flux, two-tailed paired Wilcoxon signed-rank test P value = 0.757, $V = 51,678$, $n = 458$). These deviations in the overall POC flux estimates (all periods POC flux trap measured vs. Martin curve model POC flux, two-tailed paired Wilcoxon signed-rank test P value = 0.015, $V = 68,832$, $n = 494$) were more evident in recent years (Fig. 5B).

Reasons for the measured-versus-model discrepancies could include errors in EF, carbon attenuation rates, and/or model form and application. Biological carbon pump efficiency varies globally (32, 33, 41), and our results suggest temporal changes are also substantial. Export flux here is modeled from satellite

estimates of surface Chla, which does not fully reflect changes in available POC for vertical processing and transport (42). Our application of the Martin curve considered variation in attenuation due to temperature (2) but not to other parameters, which can lead to errors when modeling the biological carbon pump, especially in high-export-production situations (32). Our results corroborate the assertion of Marsay et al. (2) that the power-law equation appears to be an oversimplification for the whole water column.

The definition of pulse events influences their accounting. While using multiples of SD to evaluate extreme events is common in climatology research (e.g., refs. 43 and 44), others define extreme events as those exceeding the 95th percentile (e.g., ref. 45). Here the application of a mean + 2σ threshold equates to the 95th percentile in POC flux and is a reasonably simple and conservative pulse episode definition (SI Appendix).

High-magnitude pulse events of POC sinking through the water column can have a major impact on the oceanic carbon cycle and need consideration in future modeling efforts to balance carbon budgets. While models suggest on the order of $\leq 5\%$ surface production reaching abyssal depths at the global scale (3, 4), at Sta. M we found a much larger percentage reaching the sea floor at 4,000 m (11%) and equally remineralized between 2011 and 2017 (11%; SI Appendix, Table S1). These values are even greater during POC flux pulse periods, when an estimated average of 29% of surface production reached abyssal depths (SI Appendix, Table S1). These pulses likely play an important role in resolving the long-term carbon deficit reported for abyssal communities including Sta. M (21, 22).

Methods

We defined pulse events according to variation within a 29-y data record (≥ 1989 -to-2017 mean + 2σ) and then analyzed lagged cross-correlations between ranked EF, POC flux, and SCOC pulse events for a subset of the time series (2011 to 2017) when high-resolution organic carbon supply and demand fluxes were available for the water column (sediment traps) and at the sea floor (time-lapse camera and mobile sea-floor respirometer). Data were binned into commonly aligned 10-d averages. Export flux was generated for a 100-km radius around Sta. M using Kelly et al. (46). Carbon content of pulse events and associated leading/lagging variables were calculated for a window spanning the POC flux pulse, and shifted to correspond to the temporal lag with the peak correlation. POC flux to 3,400 m was modeled using the Martin power-law equation (3) with an attenuation coefficient (b) that varied according to temperature (2). Because debate exists as to whether P values should be interpreted more conservatively when assessing significance of new discoveries (47), we report multiple ranges of P values in the figures. Following the recommendation of Benjamin et al. (47), we used a threshold for statistical significance of $P \leq 0.005$. Correlations with P values $0.005 < P \leq 0.05$ were interpreted as suggestive. Further details about methods can be found in SI Appendix.

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