



Eighty years of food-web response to interannual variation in discharge recorded in river diatom frustules from an ocean sediment core

John B. Sculley^a, Rex L. Lowe^{b,1}, Charles A. Nittrouer^c, Tina M. Drexler^{c,2}, and Mary E. Power^{a,3}

^aDepartment of Integrative Biology, University of California, Berkeley, CA 94720; ^bDepartment of Biological Sciences, Bowling Green State University, Bowling Green, OH 43402; and ^cSchool of Oceanography, University of Washington, Seattle, WA 98195

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Little is known about the importance of food-web processes as controls of river primary production due to the paucity of both long-term studies and of depositional environments which would allow retrospective fossil analysis. To investigate how freshwater algal production in the Eel River, northern California, varied over eight decades, we quantified siliceous shells (frustules) of freshwater diatoms from a well-dated undisturbed sediment core in a nearshore marine environment. Abundances of freshwater diatom frustules exported to Eel Canyon sediment from 1988 to 2001 were positively correlated with annual biomass of *Cladophora* surveyed over these years in upper portions of the Eel basin. Over 28 years of contemporary field research, peak algal biomass was generally higher in summers following bankfull, bed-scouring winter floods. Field surveys and experiments suggested that bed-mobilizing floods scour away overwintering grazers, releasing algae from spring and early summer grazing. During wet years, growth conditions for algae could also be enhanced by increased nutrient loading from the watershed, or by sustained summer base flows. Total annual rainfall and frustule densities in laminae over a longer 83-year record were weakly and negatively correlated, however, suggesting that positive effects of floods on annual algal production were primarily mediated by “top-down” (consumer release) rather than “bottom-up” (growth promoting) controls.

paleoproxy | diatom frustule | food-web controls | river discharge variation | ecological upscaling

Tracking food-web responses to environmental changes over long timescales (1–3) can be difficult, as species interactions do not generally preserve well (4, 5). Where records can be recovered, as from varved sediments, proxy indicators can reveal changes in density or biomass, which suggest that food-web structures have changed over time. In the absence of experimental manipulations or prolonged, direct observations of processes, however, inferences of ecological causes for recorded change remain uncertain. For example, to what extent are changes in biomass through time a result of changes in environmental conditions or resource availability, versus altered impacts of consumers or other natural enemies? Species interactions, in particular top-down (trophic) interactions, are often difficult to observe even in contemporary time, and hence are commonly underestimated as drivers of ecological change (6).

In the Eel River of northern California, 28 y of ecological research has linked annual hydrologic regimes to alternative food-web structures with contrasting algal abundance (7–10). Under winter-rain, summer-drought Mediterranean seasonality, the Eel shows striking year-to-year variation in algal accrual during its biologically productive summer low flow period. Large proliferations of attached green macroalgae, with average filament lengths peaking in midsummer at >50 cm, often follow winters with at least one bed-scouring flood. In summers following winters without scouring floods, river substrates remain relatively barren over the summer, and attached algal filaments are generally <5- to 15-cm long. These green versus barren years could occur because of either

“bottom-up” or “top-down” effects of winter floods (9). Floods extirpate large overwintering grazers, releasing spring and early summer algal growth from consumer control. Wetter winters could also sustain higher nutrient fluxes or flows and temperatures that are more favorable for algal growth longer into the summer. Tentative support favoring the top-down hypothesis (that floods released algae from grazer control) came from the partial recovery of algal biomass following experimental removal of large grazing caddisflies from instream enclosures during one summer that followed a flood-free winter (11) (Fig. S1), but little evidence is available to evaluate the relative importance, over the scale of decades, of top-down versus bottom-up food web controls in regulating variation in annual algal production.

Here we take advantage of the offshore transport, deposition, and storage of freshwater riverine diatoms in coastal marine sediments to reconstruct changes in epiphyte abundance in relation to disturbance, food web, and climatic events. Freshwater diatoms have proven extremely useful as paleoenvironmental indicators in lake and marine depositional environments, because silica in their cell walls (frustules) preserves well in sediments and retains taxonomically diagnostic characters that distinguish taxa with different environmental tolerances (12, 13). Although sedimentary records are frequently absent from erosional riverine environments, many coastal rivers deposit markers of freshwater communities and processes in the near-shore

Significance

Are plants limited by resources or by consumers? Feeding interactions are difficult to observe in nature, so their impacts are commonly underestimated. A record of freshwater diatom frustules in a sediment core collected off the mouth of the Eel River in northern California correlated positively with algal biomass during years when upstream river reaches were surveyed. Our short-term experiments have suggested that year-to-year variation in river algal biomass during the summer growth season was driven by whether or not armored grazers had been scoured away by winter floods. The marine core record also suggests that over 83 years, controls of summer algal production were mediated more by hydrologic impacts on grazers than by their influence on growth conditions for algae.

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Data deposition: The data from this study are available at the Eel River Critical Zone Observatory Sensor Database, criticalzone.org/eel/data. The correlation raw data have been deposited at erczo.berkeley.edu/datasets.

¹Present address: Center for Limnology, University of Wisconsin–Madison, Madison, WI 53705.

²Present address: ExxonMobil Upstream Research Company, Spring, TX 77389.

³To whom correspondence should be addressed. Email: mepower@berkeley.edu.

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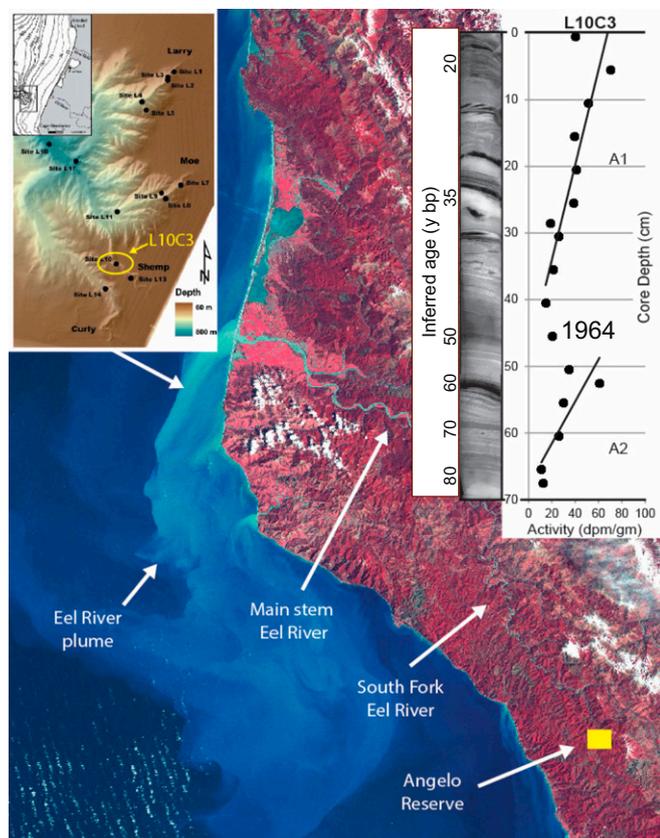


Fig. 1. The Eel River watershed and Eel submarine canyon. Draining 9,546 km², the Eel is the third largest river in California, and is representative of mid-sized mountain rivers that collectively account for ~45% of global sediment discharge to the ocean, 18% of global river-to-ocean discharge, and 10% of global drainage area (1). Rivers of this size class are understudied relative to smaller and larger rivers (2). (Left Inset) Shemp Channel of the canyon about 15-km offshore of the Eel River mouth where the core L10C3 used in this study was collected (yellow arrow and circle). (Right Inset) An X-radiograph of the layered sediment and a plot of depth vs. excess ²¹⁰Pb activity that shows two periods of steady accumulation rate that allowed annual temporal resolution. A change in the rate of sediment accumulation occurs in the mid-1960s, when a superflood destabilized the Eel River banks, and the channel became wider. Thereafter, annual rates of sediment deposition in the canyon increased from 4 (preflood) to 11 (postflood) mm/y. Relationship A1 is used correlating frustule density in cores with algae biomass surveyed along river transects from 1988 to 2001 (Fig. 3), but both lines are used to examine the relationship (or lack thereof) between rainfall at Eureka (near the Eel mouth) from 1918 to 2001 to frustule accumulation in corresponding laminae (Fig. 4). [Figure modified from Drexler et al., (20) © Society for Sedimentary Geology; background Landsat 1 image courtesy of USGS and NASA].

marine environment (14–17). For example, the Eel River, which cuts through steep topography along the tectonically active northern coast of California (18, 19), has few depositional areas in its watershed. Offshore, however, a submarine canyon carved at low sea stands (Fig. 1) provides nearly ideal conditions for river sediment deposition (20). Sediment budget studies using isotopic tracers and fixed ocean-floor monitors in the canyon entrances confirm that the submarine Eel canyon typically receives about half of the Eel River's annual sediment flux (21–23) at rates high enough to inhibit bioturbation (20). An extensive marine coring program (24) has yielded hundreds of cores of this sediment deposited onto the adjacent continental shelf and slope, including some cores from an adjacent submarine canyon in which ²¹⁰Pb-estimated sediment age is linearly correlated with burial depth at near annual resolution for nearly a century (20) (Fig. 1). We took advantage of this stable depositional environment and sampled

three cores (SI Methods) for identification of freshwater diatoms remains. A fourth core was selected for quantitative estimates of frustule density and to assess potential environmental and ecological changes in the river over the past century.

Summer algal proliferations in the Eel and many similar temperate rivers worldwide are dominated by the green macroalga *Cladophora glomerata* (L.) Kütz., which becomes heavily overgrown by epiphytic diatoms over time. Two exclusively freshwater diatoms (25) with distinctive, robust frustules in the family Rhopalodiaceae [*Epithemia sorex* Kütz., *Epithemia turgida* (Ehrenb.) Kütz.] (Fig. 2) dominate mid- to late-summer epiphyte assemblages on *C. glomerata* in the Eel River, while other diatoms (e.g., *Rhoicosphenia abbreviata* Agardh, *Cocconeis placentula* Ehr., and *Cocconeis pediculus* Kütz.) are dominant earlier in the low flow season. We developed an 83-y record of freshwater diatoms exported from the Eel River to Eel canyon sediments and evaluated their utility as a proxy for biomass accrual of *Cladophora* proliferations in the Eel River basin by examining the relationship between freshwater diatom frustule counts in annual laminae and the magnitudes of *Cladophora* proliferations surveyed in the upper basin from 1988 to 2001 (Tables S1–S3).

Methods

Based on the ²¹⁰Pb geochronology observed for core L10C3, sediment in the upper ~40 cm accumulated at a relatively steady rate of 11 mm/y. This is based on calculations from the ²¹⁰Pb profile shown in Fig. 1, and the corresponding regression coefficient ($r^2 = 0.73$) developed by Drexler et al. (20). Following Smol et al. (13) and Abrantes (15), we made slides from core sediments by withdrawing 1 g of sediment from the full depth of the lamina in the upper 40 cm of core L10C3, sampling at 11-mm increments, measured using a micrometer. Care was taken to ensure that the sediment was fully suspended and disaggregated. Because freshwater diatoms were much less abundant in cores than marine diatoms, we counted all freshwater diatoms on each slide and subsampled the common marine taxa (12) at 400–1,000×

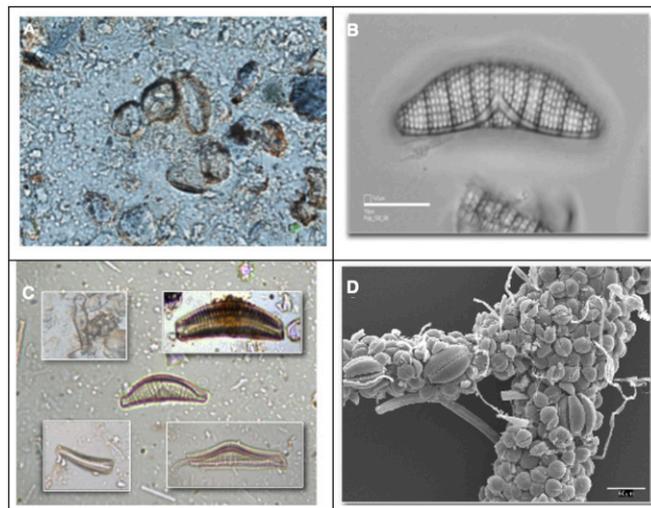


Fig. 2. (A) Frustules of *E. sorex* and *C. pediculus* from core L10C3. *Epithemia* spp. often co-occur with and subsequently replace *Cocconeis* late in the summer growing season. The robust frustule of *Epithemia* allows better preservation than thinner frustules of *Cocconeis* or *Rhoicosphenia*. (B) Scanning electron micrograph (SEM) of an *Epithemia* frustule showing the distinctive curved raphe and robust silica walls that aid in identification and preservation in sediments. Photo by R.L.L. (Scale bar, 10 μ .) (C) *R. abbreviata* (Bottom, Left) is a midsuccessional epiphytic diatom that often co-occurs with *Gomphonema acuminatum* (Upper Left) and is supplanted by *E. sorex* (Center), *E. turgida* (Upper Right), and *Rhopalodia gibba* (Lower Right) as the growing season progresses. Frustules are from core L10C3 and other Eel submarine canyon sedimentary cores. (D) SEM of a heavily epiphytized strand of *C. glomerata*. Almost all of the epiphytes are *E. turgida* and *E. sorex*. SEM courtesy of R.L.L. and the Society for Freshwater Biology ©2010. (Scale bar, 50 μ .)

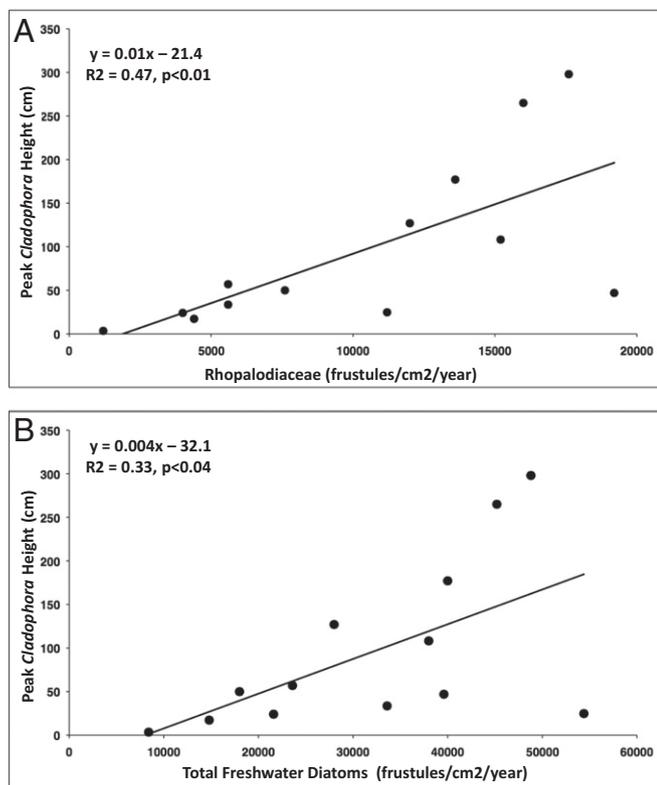


Fig. 3. Peak modal height of *C. glomerata* streamers plotted against (A) Rhopalodiaceae frustules and (B) total freshwater diatom frustules from core L10C3. Each point shows data for the algal survey and the corresponding sampled sediment layer from 1988 to 2001 (*SI Methods*).

We converted our diatom totals from each slide to estimates of frustule accumulation rates for the entire annual lamina following standard procedures (*SI Methods*) (15).

Diatom frustule densities in cores were compared with the magnitude of algal proliferations surveyed by one of us (M.E.P.) across four permanent cross-stream transects during summers from 1988 through 2001. These transects were established over a 5-km reach along the upper South Fork Eel River within the Angelo Coast Range Reserve, about 210-km upstream from the mouth of the Eel River. Modal height of attached filaments (hereafter “proliferation heights”), the percentage cover, and the condition of algae were all recorded within an estimated $\sim 100\text{-cm}^2$ area under each transect point (additional methodological details are in *SI Methods*).

Results and Discussion

Annual peaks of spatially averaged *Cladophora* proliferation heights surveyed along the South Fork of the Eel River near Branscomb, California, for a given year were positively related to the abundance of freshwater Rhopalodiaceae frustules recovered from the corresponding lamina in the marine core (Fig. 3A). Total counts of all epiphytic freshwater diatom taxa (including *C. placentula*, *C. pediculus*, *R. abbreviata*, and *Gomphonema* spp.) were also positively correlated with *Cladophora* proliferation height during a given year (Fig. 3B). The abundance of Rhopalodiaceae diatom frustules in a lamina for a given year explains 47% of the year-to-year variation in surveyed *Cladophora* peak modal height averaged over surveyed transects, and the total freshwater epiphytic diatom frustules in a lamina for a given year explains 33% of interannual variation in this index of peak *Cladophora* biomass. Paleolimnological studies of periphyton in the St. Lawrence River have also reconstructed *Cladophora* biomass from epiphytic diatoms (26), including the same or similar species found in the Eel flora.

Both Rhopalodiaceae and total freshwater diatom frustule counts were weakly negatively correlated with precipitation during

a given year (Fig. 4). This suggests that top-down controls as a result of release from grazers were more significant than were bottom-up effects linked to increased annual precipitation, such as increased nutrient fluxes, or more prolonged periods of favorable flow velocities or temperatures. In mixed-size gravel-bedded rivers, scour of the bed occurs as a threshold event, when flood discharges reach “bankfull,” estimated as that magnitude with a recurrence interval of ~ 1.5 y (27, 28). A flood of this magnitude appears necessary for extirpating predator-resistant overwintering grazers. After this flow threshold is crossed, however, summer algal proliferation magnitude is not correlated with flood magnitude or with the number of subsequent floods (9). In some years after scouring floods, early summer algal growth was exported by late June spates, with modest subsequent recovery, as waning, warming late-summer flows became less favorable for *Cladophora* proliferation. These complications and nonlinearities added noise to the relationship between flood peak magnitudes and summer algal biomass, which suggested that frustule abundance in an annual lamina was a true paleoproductivity record, rather than a result of river discharge.

It was surprising that frustule counts representing annual flux from the entire $9,546\text{-km}^2$ Eel basin were strongly related to proliferation heights surveyed over a relatively small (5 km) study reach draining $116\text{--}137\text{ km}^2$ of the upper South Fork of the Eel River. For successful upscaling, three assumptions would have to be met: (i) annual algal proliferation sizes were positively correlated among subbasins across the Eel River because of correlated or compensatory trends in the annual hydrologic, environmental, and food-web controls that limit accrual of *Cladophora*, and *Epi-themia*, and other epiphytic diatoms during a given year; (ii) frustules were not stored in depositional riverine environments (deep pools, off channel water bodies or wetlands) even during low flow years, so that most frustules are exported offshore during the year in which they were produced (*SI Methods*); and (iii) most exported frustules were deposited in their final canyon repository during the

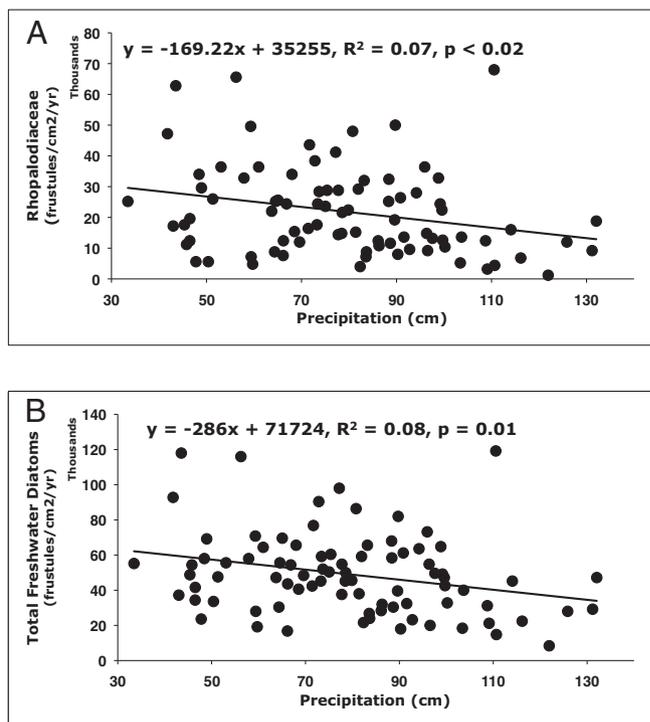


Fig. 4. (A) Rhopalodiaceae diatom frustules per year and (B) total freshwater diatom frustules per year from core L10C3 plotted against annual total precipitation measured at Eureka, California (NWS Station 42910) from 1918 to 2001.

same water year that they were produced. We examine each of these assumptions in turn below.

Hydrologic mediation via food-web interactions has been established as a major mechanism releasing *Cladophora* proliferations in the Upper South Fork Eel River basin (3), but has not been examined elsewhere in the basin. Counts of Rhopalodiaceae and total epiphytic diatom frustules recovered from the marine core suggest that large algal proliferations tended to follow bed-scouring winter floods across the entire Eel River basin during the interval recorded in the core. This congruence may suggest similar release of *Cladophora* following flood scour of predator-resistant grazers, but the pattern could also arise from flood-mediated effects that enhanced algal accrual by enhancing environmental conditions or nutrient fluxes. In the eastern portions of the basin, there is less forest cover and a potential for a different combination of hydrologically mediated top-down and bottom-up controls to influence algal accrual during a given year (*SI Methods*). The negative correlation of frustule densities in laminae with total annual rainfall, however, favors grazer release rather than bottom-up controls as a basin-wide explanation (Fig. 4). Overwinter storage of a summer's diatom production in the river channel or basin could produce time lags, complicating the relationship between annual algal production and frustule densities in laminae. If summer algal production were stored over low-flow winters until flushed during a subsequent high flow year, we would expect the abundance of frustules in a lamina to increase with the magnitude of the peak winter flood that follows a given summer growth period. However, the relationship of frustule counts to actual surveyed peak algal biomass surveyed in the upper South Fork Eel watershed in a given year was stronger than the relations of either Rhopalodiaceae frustules, or total freshwater diatom frustules to that water year's peak hourly maximum discharge during the subsequent winter (Fig. S2). The geomorphology of the Eel, a steep, canyon-bound river, and the apparent lack of frustule storage even over drought winters suggest that the Eel River has only one major repository: its submarine canyon (*SI Methods*) (29, 30). Storage of frustules in shelf deposits for one or more years before their transport to the canyon would, like river channel storage, complicate the relationship between riverine algal production and frustule density in the lamina assumed to record deposition from a given year. The sinking rates of diatoms in still columns of salt water have been estimated to range from 0.6 to 8 m d⁻¹ in marine diatoms similar in size (long axes 10–50 μ) to the two *Epithemia* species we studied (*SI Methods*) (31). If diatom cells or frustules in this size range traveled rapidly (within hours or days) offshore from the Eel mouth with the wash load (finest sediment visible in surface currents) during high river discharges (30), then sank (with no turbulent displacement) 130 m to the sea floor at site L10C3 in thalweg at the head of the Shemp canyon, frustules would arrive on the canyon floor (130 m deep) 16–217 d after their export from the river, permitting deposition within the year following summer production of these diatom cells or frustules. The confirmed presence of ⁷Be in Eel Canyon sediments supports a rapid (sub-annual) deposition of Eel River sediments (20–23, 29). If freshwater diatoms aggregated with marine phytoplankton or detritus, they would sink more rapidly (32, 33). We have little information, however, on the degree to which diatoms or frustules might be resuspended or displaced by currents, smaller scale turbulence, or even zooplankton feeding or other food-web interactions in the coastal ocean. All of these events would complicate the trajectories and fates of freshwater diatom cells or frustules on their journey from the river mouth to the canyon floor.

Despite these three potential sources of spatial and temporal noise, our results (Fig. 3) suggest that the signal of interannual variation in riverine algal production remains discernable in the offshore record, as indicated by the significant correlation of peak

biomass of riverine algae produced during a given year with the density of freshwater diatom frustules in lamina estimated, from ²¹⁰Pb dating (20), to correspond to that year.

Freshwater diatom frustules recovered from submarine canyon cores appear to be useful as a paleoproductivity (proliferation size) proxy of algae and algal-based food-web dynamics during the period of overlap between the core and survey record. Our results suggest that we can use *Epithemia* and other freshwater epiphytic diatoms to extend temporal inferences about hydrologically controlled food-web states (e.g., the alternative food-web structure with contrasting algal abundance as a response to sub- vs. super-bankfull discharge during the preceding winter) (Fig. S1) back nearly a century for the L10C3 core (34). The results are also encouraging for spatial upscaling. Similar research with a lower-resolution core from coastal Portugal established a correlation between freshwater diatom frustules and instrumental records of river flood stages (15, 16). Work in the Murray-Darling River basin of Australia, St. Lawrence River of Canada, and the Amazon River has also shown that diatom frustules recovered from freshwater off-channel deposits recorded basin-wide environmental changes (17, 26, 35).

Based on frustule recovery from marine cores, we are able to estimate the size attained by past riverine algal proliferations up until the 2001 core collection, primary production that can support consumers and predators. Paleoproxies that provide such a record of primary production may expand the time domain of food-web analyses beyond not only the period of contemporary research, but also beyond that of the instrumental record. The dynamics of food-web interactions that involve long-lived organisms or slow feedbacks often unfold over decades to centuries or millenia. In such ecosystems, paleoproduction proxies may allow hypotheses about trophic controls to be evaluated over more appropriate time scales. Ecosystem change will also be driven by external forcing processes with long time scales. With the increased understanding of the importance of long-period climate cycles, such as the Pacific Decadal Oscillation for marine and freshwater food webs, the need for long time-series data on responses has become more apparent. The widespread geographic dominance of *C. glomerata* in temperate freshwater rivers and lakes globally (25, 36, 37) suggests that its epiphytic diatoms could be used as proxies in other temperate fresh waters where highly resolved, integrative depositional records have accumulated: at river mouths, in reservoirs or off-channel lakes, or within depositional subbasins. These records would expand the spatial and temporal scales of inferences linking food webs to environmental change, enhancing our understanding of how freshwater webs may respond to future changes in climate, land cover, biota, and other factors affecting riverine runoff and conditions.

Finally, the development of a paleoproductivity proxy using freshwater diatoms recovered from marine sediments provides a quantitative tool for measuring the transfer of riverine biota, nutrients, and organic matter into marine ecosystems. In rivers that do not retain their sediments for longer than 1 y (e.g., small steep rivers in tectonic settings along colliding continental margins), marine records may contribute to our understanding of interannual variation in the interactions of climate with freshwater and marine productivity (13, 38–40).

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