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 scouried 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.*

Author contributions: J.B.S., R.L.L., and M.E.P. designed research; J.B.S., C.A.N., and T.M.D. performed research; J.B.S. analyzed data; and J.B.S. and M.E.P. wrote the paper.

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

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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., *Rhicosphenia abbreviata* Agardh, *Cocconeis placenta* 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. 1. The Eel River watershed and Eel submarine canyon. Draining 9,536 km$^2$, 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).](image)

![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 *Rhicosphenia*. (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 μm) (C) *R. abbreviata* (Bottom, Left) is a mid-successional epiphytic diatom that often co-occurs with *Gompsochroma 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 μm).](image)
area under each transect point (additional methodological
biomass from epiphytic diatoms (26), including the
Peak modal height of \( \sim \) Eel basin were strongly related to pro-
C. pediculus proliferation height during a given year
biomass. Paleolimnological studies
Height (cm)
Height (cm)
[Image 0x1 to 19x816]

counts were weakly negatively corre-
Cladophora lamina for a given year explains 33% of interannual variation in
transects, and the total freshwater epiphytic diatom frustules in a
in surveyed
Height (cm)
Height (cm)

Sculley et al.

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 corres-
ponding lamina in the marine core (Fig. 3A). Total counts of all
epiphytic freshwater diatom taxa (including C. placenta, C. peliculus, R. abbreviata, and Gomphonema spp.) were also positively corre-
lated 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 Rhopalodiaceaeen 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 \( \sim 1.5 \) 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 pro-
leration 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 warming, 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
apaleoproductivity record, rather than a result of river discharge.

It was surprising that frustule counts representing annual flux
from the entire 9,546-km² Eel basin were strongly related to pro-
leration heights surveyed over a relatively small (5 km) study
reach draining 116–137 km² 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 corre-
lated 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-
thermia, and other epiphytic diatoms during a given year; (ii) frus-
tules 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

We converted our diatom totals from each slide to estimates of frustule
accumulation rates for the entire annual lamina following standard pro-
dures (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 21
Reach draining 116–137 km² of the upper South Fork of the Eel
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Fig. 3. Peak modal height of C. giomerata 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).

y = 0.01x – 21.4
R² = 0.47, p < 0.01

y = 0.004x – 32.1
R² = 0.33, p < 0.04

Fig. 4. (A) Rhopalodiaceae diatom frustules per year and (B) total freshwater
diatom frustules per year from core L10C3 plotted against annual total pre-
cipitation measured at Eureka, California (NWS Station 429110) 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 Rhopalodiales 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 Rhopalodiales 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 assumed to record deposition from a given year. The dynamics of food-web interactions in the Upper South Fork Eel River basin (3), but has not been examined elsewhere in the basin. 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biomass of riverine algae produced during a given year with the density of freshwater diatom frustules in lamina estimated, from

a 20Pb 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 millennia. In such ecosystems, paleoproductivity 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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34. Sculley JB (2013) From Cobble to Canyon: Inferring the effects of discharge, climate and trophic interactions on primary productivity in a northern California river, over reach to watershed to coastal ocean and annual to multi-decadal scales. PhD dissertation (University of California, Berkeley, Berkeley, CA).