Paleocological and evolutionary implications of phytoplankton "suicide"

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Millimeter-scale laminae composed of *Chaetoceros* resting spores (CRS) are present in Quaternary diatomaceous marine sediments from the Santa Barbara Basin ODP Site 893) of California and the Japan Sea (ODP Site 798). In the modern ocean, each CRS sedimentation event occurs at the termination of an upwelling-induced, phytoplankton bloom event. SEM investigation of CRS laminae (CRSL) reveals that very delicate surface ornamentation and setae are unbroken, demonstrating that CRS did not experience the abrasion and fragmentation that characterizes heterotrophic grazing (Fig. 1). CRS are effectively self-sedimenting via spore formation, resulting in efficient (e.g. ungrazed) export of biosilica (and organic carbon) from the photic zone to the sediments. Modern CRS sedimentation events require several days to weeks to complete; hence, each discrete CRSL preserves the highest resolution snapshot of an ecological succession / sedimentation event that has been recognized in the sedimentary record (Fig. 2).

Natural selection operates at all levels of biological organization. For an individual cell, the Darwinian fitness of self-sedimentation seems very low or negative; accelerated settling contributes to high individual mortality. From the perspective of evolutionary ecology, each individual CRS in a series of CRSL was a failed participant in a reproductive gamble that has been successfully employed since at least the Early Cretaceous. These observations present a paradox for simple Darwinian interpretation.

The CRS/self-sedimentation strategy has adaptive value at the level of the population (opportunistic recruitment and utilization of a spatially and temporally discontinuous nutrient resource; successful competition with rival species) and the species (the resting spore strategy enhanced diatom survivorship of some episodes of short-duration, broad-scale ecological collapse that drove many other species to extinction; e.g. K/

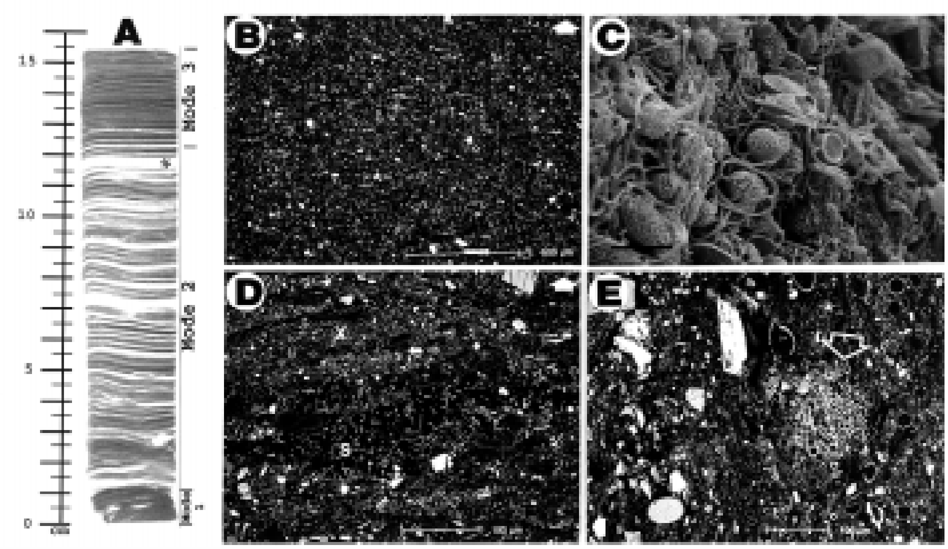

Figure 1. Laminated biosiliceous sediment from the Santa Barbara Basin, California.

- **a) Contact print of x-radiograph of slab sample (ODP 893B-8H-4; 92-107cm) showing distinctly-laminated fabric with light-colored laminae consisting of unfragmented *Chaetoceros* resting spores (Mode 2); asterisk marks thick monospecific lamination of *C. vanheurckiii*, that demarcates the abrupt termination of thick *Chaetoceros* laminae attributed to self-sedimentation. Mode 1 corresponds to very indistinctly-laminated sediment where diatom bloom laminae are absent; Mode 3 corresponds to very thinly-laminated sediment where thick diatom bloom laminae are absent [*Grimm et al.,* 1996].**
- **b) Backscattered electron photomicrograph (BSEP) of epoxy-impregnated sediment consisting of unfragmented *Chaetoceros cinctus* resting spores.**
- **c) Secondary electron photomicrograph of lamination consisting of unfragmented *Chaetoceros cinctus* resting spores. Scale bar = 20 μm.**
- **d) BSEP of laminated diatomaceous sediment; S marks a silicoflagellate (*Dictyocha speculum*) lamination. Adjacent sediments include thin *Chaetoceros* resting spore laminae, and laminae consisting of extensively-fragmented biosilica (X); we attribute the latter to maceration associated with heterotrophic grazing. Arrow at upper right points in stratigraphic up direction.**
- **e) Hollow arrow points to a typical aggregate of silicoflagellate skeletons (*Dictyocha speculum*), which we interpret as a preserved floc. Solid arrow at lower left points in stratigraphic up direction. Surrounding sediments contain various diatom taxa, including *Stephanopyxis* and *Chaetoceros* setae.**

T boundary Event). In addition, our observations suggest that organic carbon burial rates over ecological and short to intermediate geological time spans may be governed by intrinsic ecological changes in grazing efficiency and biologically-mediated sedimentary flux, in a manner which may supercede the roles of phytoplankton production and organic carbon preservation. Testing such a geophysiological hypothesis may provide more accurate understanding of how the Earth system regulates atmospheric CO_2 over centennial to millenial time scales.

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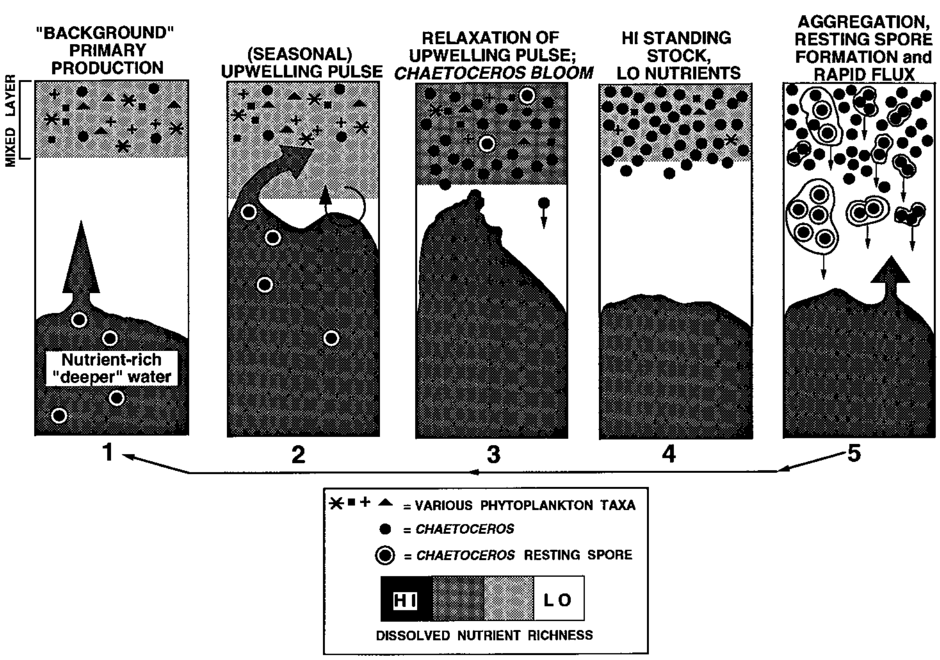

Figure 2. Interpretative environmental diagram, showing the dynamics of a *Chaetoceros* bloom and self-sedimentation event. In the modern, the ecological succession from background to bloom to self-sedimentation occurs over time spans periods of weeks [*Grimm,* 1992b]. Stage 5 illustrates TEP formation, resting spore formation, and the rapid vertical descent of *Chaetoceros*-bearing flocs; recent experimental results confirm earlier field data indicating that resting spores (circled black ovals) form only within settling flocs [*Alldredge et al.,* 1995].