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Continental-shelf sediment as a primary source of iron for coastal phytoplankton

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The availability of iron, an essential nutrient, controls rates of phytoplankton primary productivity in the open-ocean, upwelling ecosystems of the equatorial Pacific^{1,2}. Upwelling injects large amounts of macronutrients into the euphotic zone of eastern boundary currents, such as the California Current System (CCS), where iron can become the limiting factor on productivity^{3,4}. Iron addition to samples from some areas of the CCS has been shown to increase rates of biomass production^{5,6}, but the processes that control iron availability in these systems remain poorly understood. Here we report measurements of dissolvable iron (that is, dissolved plus leachable iron at pH 3) in transects across the CCS in March of 1997 and 1998. We found high concentrations of iron in 1997 during strong upwelling conditions. During the 1998 El Niño, the concentration of dissolvable iron in surface waters was low, even though that year was marked by high river flow and low offshore salinity. These results indicate that the primary source of iron in the CCS is resuspension of particles in the benthic boundary layer, followed by upwelling of this iron-rich water, rather than direct riverine input. This source of iron must be an essential but variable component of the high productivity found in upwelling ecosystems.

Upwelling along eastern boundary currents sustains some 11% of the global ocean primary production⁷ and 50% of the global fish production⁸. The waters that come to the surface in these systems are enriched in macronutrients. However, there is no corresponding subsurface enrichment of iron in the offshore areas that are the source of the upwelled waters³. Consequently, there must be additional sources of iron at the continental margin to sustain elevated rates of primary production. Large concentration gradients of dissolved and particulate iron across both eastern⁹ and western¹⁰ ocean boundaries demonstrate that ocean margins are important sources of iron. It has been hypothesized that elevated iron concentrations in coastal regions may arise from riverine input, resuspended sediment or atmospheric deposition⁹, but so far we do not know the relative importance of these mechanisms or how they vary over time.

We have made measurements of dissolvable iron, nitrate and chlorophyll in March 1997 (cruise S197) and March 1998 (cruise S298) at a depth of 2 m along transects from Monterey Bay in a southwesterly direction across the CCS (Fig. 1). Conditions in March of 1997 were representative of typical spring upwelling, with strong winds from the northwest (Fig. 2c). A sharp drop in surface temperature, driven by strong winds that favoured upwelling, was recorded just before the S197 cruise at the MBARI M1 mooring in Monterey Bay¹¹ (Fig. 2a). Temperatures remained low throughout the cruise and dissolved nitrate concentrations near the

surface were as high as 25 μM . Surface salinities measured along the transect were >32.8 , which is typical of the CCS in this region¹². The shipboard measurements of dissolvable iron at stations within 100 km of the coast averaged 6 nM, but values as high as 20 nM were observed near the core of the upwelling system at Año Nuevo, which feeds Monterey Bay¹³. In the open ocean waters more than 200 km offshore (west of 124.2° W), the dissolvable iron concentration was 0.2 ± 0.1 (mean \pm standard deviation) nM. High chlorophyll concentrations developed near the coast under these conditions (Fig. 1c).

Wind conditions that favoured upwelling were rare during the El Niño conditions of late winter and early spring of 1998. High-wind events were primarily from the south (Fig. 2c), which would have suppressed offshore transport, and the surface ocean was nearly 3 °C

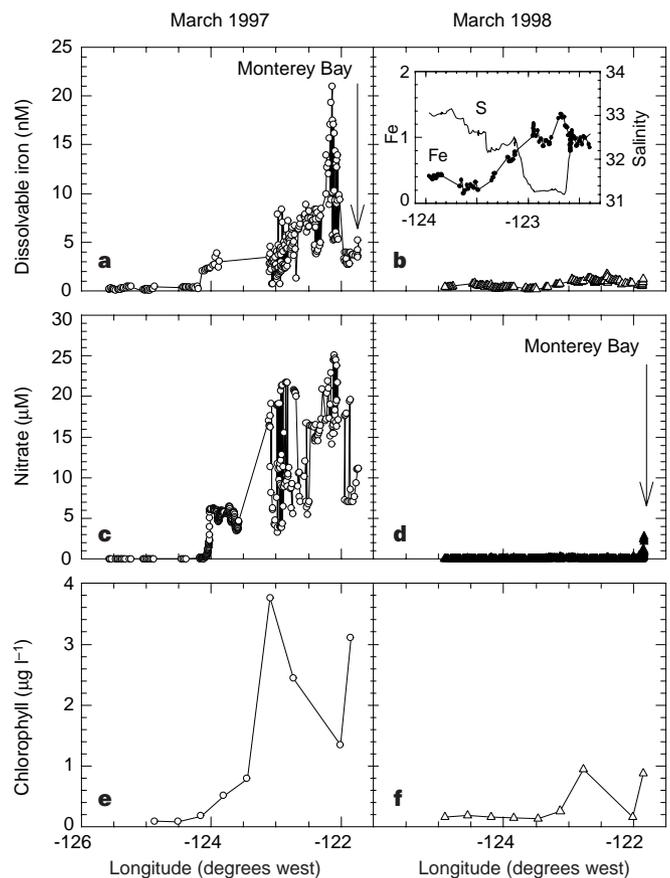


Figure 1 Dissolvable iron, nitrate and chlorophyll on transects across the CCS. Measurements were made from Moss Landing in Monterey Bay (36.80° N, 121.79° W) to a point 390 km offshore (35.07° N, 125.57° W) on cruise S197 (3–9 March 1997) and 317 km offshore (35.46° N, 124.90° W) on cruise S298 (March 18–23 1998). The inset to **b** shows iron concentration on an expanded scale and the salinity on S298, which is anomalously low over the inner 150 km. Dissolvable iron was measured by flow-injection analysis with chemiluminescence detection at 6-min intervals²⁴. Sea water was sampled with an all-teslon pump system towed at 1–2 m depth. Nitrate in this sample stream was determined colorimetrically aboard ship using an automated continuous-flow analysis system²⁵. Sea water from the pump was passed through a 10- μm polypropylene filter and acidified to pH 3 for ~0.5 min before iron analysis. Laboratory experiments demonstrate no difference between the amount of iron desorbed from particles at pH 3 in 1 min and in >6 h²⁶, indicating that we detected dissolved plus all adsorbed iron. The dissolvable iron/nitrate relationship in the data was similar to that reported previously for Monterey Bay³. Chlorophyll was determined by extracting the pigment and measuring fluorescence in a shore-based laboratory. The nitrate data near the upwelling front at 124° W on S197 were obtained on the inshore leg of the cruise to replace data missing on the offshore transect.

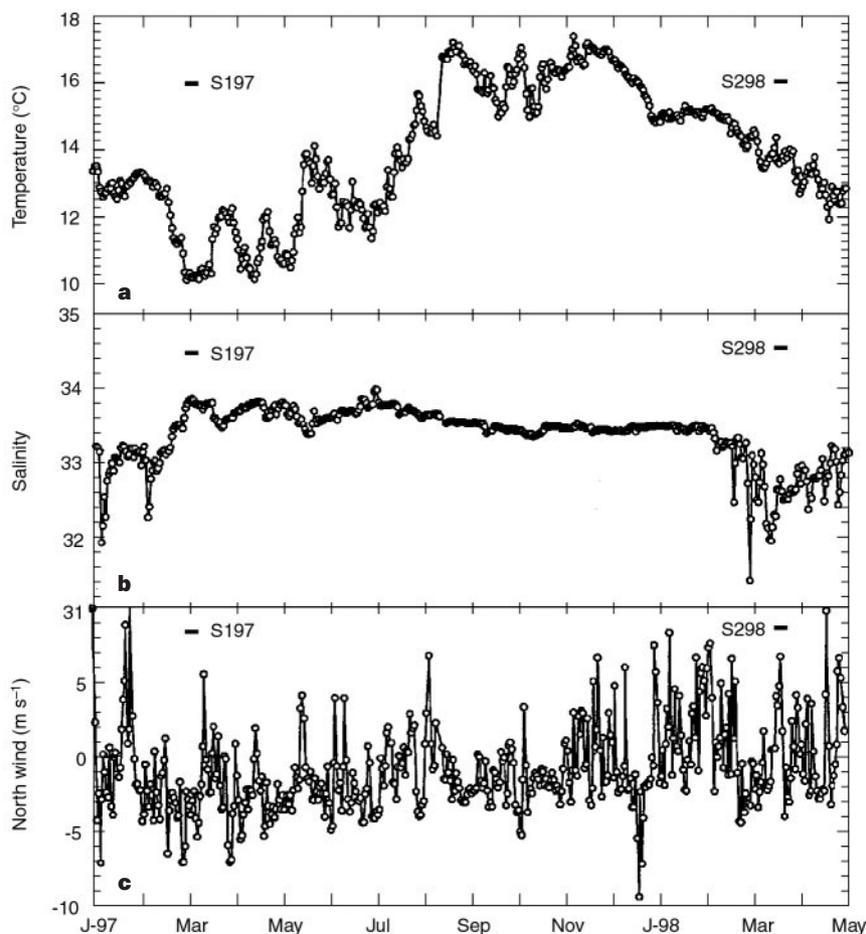


Figure 2 Daily average values of temperature, salinity and north windspeed. Parameters were measured from 1 January 1997 to 30 May 1998 on the M1 mooring in Monterey Bay (36.73° N, 122.01° W). The time spans of the S197 and

S298 cruises are shown. Data are available from the MBARI database located on the Internet at www.mbari.org.

warmer than in 1997 (Fig. 2a). Rainfall during the winter of 1997/98 was double the annual average at meteorological stations throughout the central California region. Salinity across the inner 150 km of this transect was less than 32.8 to depths of 10–15 m (Figs 1b, 2b), which is anomalously low¹². Drifting buoys drogued with 10-m holey socks of the WOCE design and equipped with ARGOS satellite transmitters were deployed at three stations along the cruise track. The inner two drifters deployed near 122.5° and 123.8° W moved continuously south for the next month at an average speed of 10 cm s⁻¹. The mean speed increased to 20 cm s⁻¹ when the wind was from the north. The drifter tracks show that the low salinities must have been produced by outflow from the Sacramento/San Joaquin River system that has been carried south in the CCS. These two rivers, which discharge 100 km to the north of the transect through San Francisco Bay, combine to form one of the 60 largest systems in the world. The dissolvable iron concentrations in the offshore waters were slightly higher (0.4 ± 0.1 nM) than the values recorded in 1997, whereas values in the river-influenced inner 100 km of the transect had an average value of 0.9 ± 0.2 nM (Fig. 1b). Little chlorophyll was found in this system except in plumes of low-salinity water at 122.8° W and 121.8° W (Fig. 1f).

Our measurements confirm previous observations that iron concentrations in coastal systems can be elevated, relative to open-ocean concentrations^{9,10}. However, the high-resolution ship-board measurements also provide significant new information on the mechanism by which iron is introduced in coastal systems; this information cannot be obtained by classical methods for iron analysis⁹. Periods of low salinity from freshwater runoff regularly occur each winter along the central California coast¹⁴ (Fig. 2b).

Although these low-salinity events clearly carry elevated iron (Fig. 1b, inset), the concentration increase of <1 nM is extremely modest when compared with upwelled water. Large amounts of the dissolved (<0.4 μm) iron in rivers are present mainly as colloids. These colloids aggregate as salinity increases and settle out in estuaries, which prevents most riverine iron from reaching offshore waters¹⁵. Atmospheric deposition also seems to be a relatively minor source as offshore winds were more frequent during 1998 when dissolvable iron concentrations were lowest.

The iron source in the upwelled water does not appear to originate from diffusion of dissolved Fe from shelf sediments. Measurements of the flux of dissolved iron across the sediment-water interface on the continental shelf in Monterey Bay, using benthic flux chambers^{16,17}, average 5 ± 3 μmol Fe m⁻² d⁻¹ (standard error, n = 11; K.S.J., unpublished results). If the shelf has a mean depth of 50 m, then the flux of dissolved iron can add only 0.1 nM Fe d⁻¹, which is an insignificant amount.

Vertical profiles of dissolvable iron were collected along the transect during the S298 cruise to assess the amount of dissolvable iron in the subsurface waters (Fig. 3a). The concentrations of dissolvable iron at a station 200 km offshore are no higher than 2.3 nM Fe in the upper 1,000 m of the water column. Concentrations below the mixed layer at the Monterey Bay station are as high as 110 nM, in contrast to the low values seen at the surface (Fig. 3a). There is little difference in the profiles of nitrate concentration at these two stations (Fig. 3c). The high dissolvable iron concentrations in subsurface waters of Monterey Bay must be derived from resuspended sediments⁹, as light transmission is markedly lower in waters with high iron (Fig. 3b).

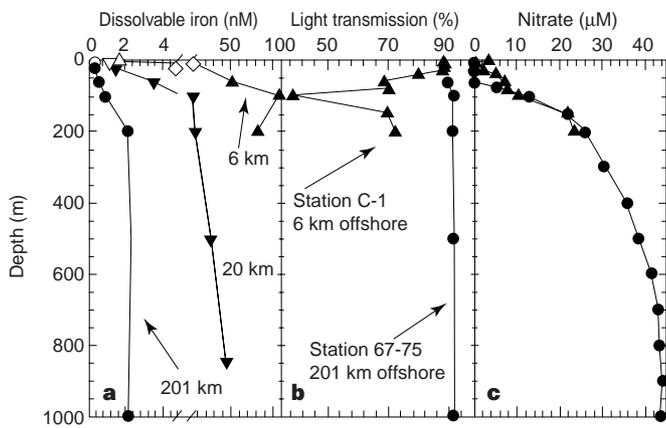


Figure 3 Vertical profiles of dissolvable iron, light transmission and nitrate. Measurements were made on cruise S298 at station 67–75 (35.95° N, 123.84° W), 201 km offshore near the offshore end of the transect shown in Fig. 1, and at station C-1 (36.80° N, 121.85° W), 6 km offshore. An iron profile is also shown from station M-1 (36.78° N, 122.01° W), 20 km offshore. Dissolvable iron was determined as described above, except that samples were acidified at pH 3 for as long as 8 h before analysis. Iron measurements made immediately using the pumping system are shown as open symbols, whereas filled symbols represent samples collected with a rosette. The iron concentrations determined on rosette samples in the mixed layer at C-1 (open diamonds) appear to be too high, perhaps owing to inadequate flushing of the rosette bottles as they were raised to the surface, rather than to the longer time at low pH, as evidenced by laboratory experiments²⁶ and the agreement of pump and surface-rosette samples at other stations. Light transmission was determined with a SeaTech 25 cm transmissometer. Nitrate was determined by colorimetry on frozen samples returned to a shore-based laboratory.

The large amounts of dissolvable iron found at the surface during upwelling conditions must be introduced by resuspension of particles into the benthic boundary layer as the upwelling source waters flow over the continental shelf. This iron-enriched water is then upwelled to the surface. These conclusions are supported by recent observations on the New Zealand shelf¹⁸. Resuspension of iron clearly occurred during the El Niño conditions of 1998, but either a lack of offshore transport trapped the iron in the inner-shelf region or weaker mixing trapped it below the surface, and surface concentrations remained low.

Upwelled water requires a large amount of iron to make use of all of the nitrate quickly. A C/Fe ratio of 27,000 was estimated from increases in particulate carbon and iron concentrations during the diatom bloom observed in the IronEx II equatorial iron fertilization experiment (K.S.J. *et al.*, manuscript in preparation). Similar C/Fe ratios are observed in cultures of coastal diatoms growing at their maximum rate¹⁹. Upwelled water with 20 µM nitrate would need at least 5 nM Fe (20 µM N × 106 µmol C/16 µmol N × 1 µmol Fe/27,000 µmol C) for diatoms to consume all of the nitrate. Dissolved (<0.4 µM) iron concentrations in the upwelled source waters are less than 1.5 nM (ref. 3), which is not sufficient to support use of the upwelled nitrate. The measurements of dissolvable iron reported here include both dissolved and labile particulate iron. A fraction of the iron in particles will be unavailable to plankton and some will be lost as particles sink from the system. These measurements must represent an upper limit on the amount of biologically available iron in the upwelled water. However, large decreases in the Fe/Al ratio in particles sampled within the CCS are strong evidence that some of this particulate iron is consumed³.

Concentrations of dissolvable iron that were sufficient for full utilization of the nitrate were observed on the S197 cruise to the coastal upwelling front. These high iron concentrations (>2 nM at the surface, up to 200 km offshore) (Fig. 1a) seem to have originated

close to shore (Fig. 3). This has important consequences as upwelling processes do not always originate in the inner-shelf region. Dynamic processes associated with the jets and eddies of the CCS⁴ or large-scale geostrophic adjustments of the thermocline²⁰ have been implicated as important for stimulating phytoplankton productivity in eastern boundaries. Coastal upwelling from the inner-shelf region, which can be important in the CCS²¹, must be the most efficient mechanism for injection of iron from the benthic boundary layer. The other processes bring macronutrients into the euphotic zone, but they may lack the continental iron source, which leads to development of high nitrate, low chlorophyll conditions. The region of the upwelling source can also migrate from the inner shelf to the shelf break as the wind strength increases in some eastern boundary current systems²², which would result in a time-varying iron source. Although high nitrate, low chlorophyll conditions have been observed in the CCS^{4,6}, their abundance and persistence have not been well resolved. When the coastal upwelling process dominates, such as during March 1997 and the spring and early summer of 1987 (ref. 4), high nitrate, low chlorophyll conditions are unlikely.

These differences in iron-source strength must contribute to the variability of the biological response to upwelling seen in coastal upwelling ecosystems throughout the world²³. The low iron concentrations observed during the S298 cruise also demonstrate that iron may be deficient at ocean margins where upwelling does not occur, even if there is a large riverine input. These conclusions indicate that iron limitation of coastal systems could have been universal phenomena during the low stands of sea level at glacial maxima, when narrow continental shelves are a global feature. □

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Archaeopteris is the earliest known modern tree

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Archaeopteris is an extinct plant which is of botanical interest for two reasons. It was the main component of the earliest forests until its extinction around the Devonian/Carboniferous boundary^{1–3}, and phylogenetically, it is the free-sporing taxon that shares the most characteristics with the seed plants^{4,5}. Here we describe the largest group of anatomically preserved *Archaeopteris* remains ever found, from the Famennian marine beds of south-eastern Morocco⁶, and provide the first evidence that, in terms of development and branching strategies, these 370-million-year-old plants were the earliest known modern trees. This modernization involved the evolution of four characteristics: a lateral branching syndrome similar to the axillary branching of early seed plants; adventitious latent primordia similar to those produced by living trees, which eventually develop into roots on stem cuttings; nodal

zones as important sites for the subsequent development of lateral organs; and wood anatomy strategies that minimize the mechanical stresses caused by perennial branch growth.

Archaeopteris is thought to have been an excurrent tree, with a single trunk producing helically arranged deciduous branches growing almost horizontally⁷. All studies relating to the development of *Archaeopteris* support the view that these ephemeral branches arise from the pseudomonopodial division of the trunk apex^{8–11}. Apical branching also characterizes all other contemporaneous non-seed-plant taxa including those that had also evolved an arborescent habit, such as lepidosigillarioid lycopsids and cladoxylean ferns. This pattern, which can disadvantage the tree if the trunk apex is damaged, contrasts with the axillary branching reported in early seed plants¹². Analysis of a 4 m-long trunk from the Famennian of Oklahoma has shown that *Archaeopteris* may produce adventitious organs¹³. These have been interpreted as being branches of limited lifespan that increase the survival potential of the plant.

About 150 specimens were collected in three localities of the Mader Basin and Tafilalt Platform in eastern Anti-Atlas⁶. They were found in dark-grey shales with calcareous concretions of the lowermost Famennian age (Kellwasser facies, *crepida* zone). They range from 2.5 mm-wide distal axes to portions of trunks nearly 40 cm in diameter. Developmental analyses were conducted on one 5 m-long decorticated portion of trunk, which was presumed to be that of a young individual given its proximal diameter of less than 10 cm (ref. 14). Three types of appendage were identified from the size, structure, length and spatial arrangement of vascular traces along a 40 cm-long portion of its distal part (Fig. 1a). Developmentally, type A organs correspond to the ephemeral, apically produced branches previously recognized in *Archaeopteris*. We interpret them as being physiologically homologous to seed-plant leaves and assume that they were not significant in the large-scale architectural structure of the tree.

Type H adventitious organs are also short-lived. Their traces, which occur singly or in serial groups, compare well in size, structure and horizontal course with traces to small adventitious appendages in Trivett's¹³ *Archaeopteris* trunk from Oklahoma. New

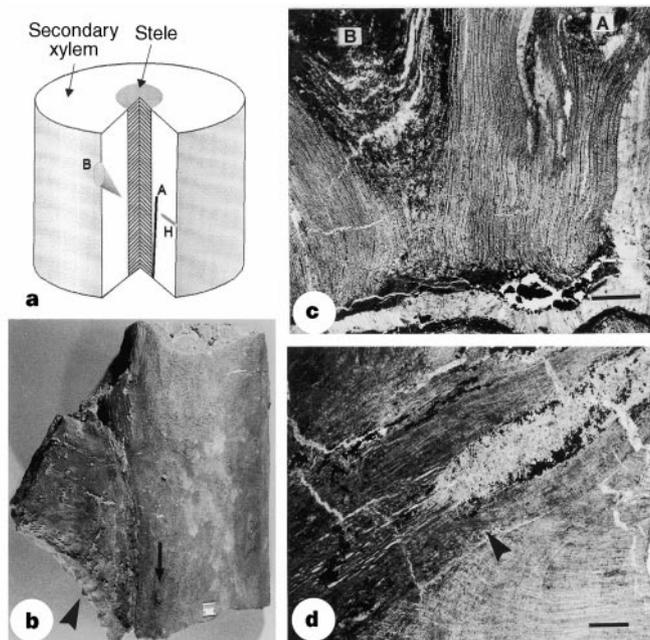


Figure 1 *Archaeopteris*, Early Famennian of Morocco. **a**, The relative arrangement of type A, B and H traces in the trunk. **b**, Trunk exterior with a large branch on the left that has a pronounced collar of trunk wood surrounding its base, showing transverse waves of wood on the branch bottom (arrowhead) and a cluster of

small buried traces on the branch flank (arrow). **c**, Cross-section of trunk showing a type B trace lateral to a type A one at the level of occlusion. **d**, Type B trace in radial section showing trace to lateral appendage (arrowhead). Scale bars: **b**, 1 cm; **c**, **d**, 1 mm.