conferring chloroquine resistance (Wellems *et al.* were unaware of this at the time). The sensitive parent had a single copy, and the resistant parent four copies. Despite these differences, the phenotypes of the chloroquine-resistant recombinants, whether they possessed a single copy from the sensitive parent or between two and four copies from the resistant parent, were identical with respect to the chloroquine concentration giving 50 per cent inhibition of parasite growth, and the chloroquine efflux rates. So the *mdr* genotype and copy number cannot alone determine these parameters. This suggests that other genes are more important in controlling them, and that the *mdr* mutations may simply facilitate the export of chloroquine, perhaps by altering the affinity of the MDR protein for the drug. Because the rates of accumulation of chloroquine were not measured in these or other related studies, it is quite feasible that other gene(s) affect chloroquine uptake, perhaps by being associated with intracellular chloroquine binding.

The argument for *mdr* being necessary but insufficient for chloroquine resistance is a circumstantial but strong one and relies on the high concordance of mutant alleles and gene amplification with the resistant phenotype. That Foote *et al.* identified two chloroquine-resistant parasites with apparently wild-type *mdr* genes would seem to contradict the basic hypothesis. Unfortunately, these isolates were not clones and it is not clear how many individual products of the polymerase chain reaction the authors sequenced. Also, because they examined only small areas of the genes, they may have missed novel mutations in other regions.

If a multigenic mechanism of resistance is a correct interpretation of the new data, then two further problems arise. First, the high degree of accuracy of phenotype prediction based on *mdr* genotype by Foote *et al.* would be surprising. The authors explain this by the excess of chloroquine-resistant parasites in their sample and the fact that the chloroquine-sensitive lines came from areas where there was no resistance at the time of isolation. Second, Wellems *et al.*'s interpretation of linkage data from a single cross where it was suspected that several genes may be involved is fraught with potential problems.

Both groups nevertheless agree that genes other than *mdr*1 are involved in chloroquine resistance. With the cloned recombinants available from the cross it should now be possible to start to search for these genes by linkage analysis. The biggest stumbling block in these types of studies is the difficulty of carrying out sufficient numbers of genetic crosses with *P. falciparum* to give reliable linkage data. The final answer to whether or not *mdr* in addition to other genes is involved will be arrived at only when a more detailed understanding of the mechanisms of chloroquine resistance is forthcoming or the other gene(s) are identified. In the meantime, individuals exposed to malaria and with limited access to drugs other than chloroquine will continue to be at risk. □

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OCEANOGRAPHY

Diving into the organic soup

J. R. Toggweiler

On land, the massive trunks and limbs of trees and woody shrubs make up one of the main repositories of organic matter. In contrast, in the ocean, most plants are microscopic and have no need to produce and maintain massive structures. And so the living biomass of the ocean is tiny when compared with the living biomass on land. Another large repository of terrestrial organic matter is the 'saprosphere'[1], the decaying organic matter in soils. The ocean too has a saprosphere which consists of dissolved organic matter (DOM) and particulate detritus. The marine saprosphere is hundreds of times larger than the pool of living organic material, and roughly the same size as the combined terrestrial organic repositories[1]. About two per cent of the marine saprosphere consists of large particles that can be examined visually with a microscope. The remaining 98 per cent is contained in dissolved, colloidal and submicrometre particle pools that largely defy characterization. Why there is so much of this material, how it forms and how this huge pool of material relates to the ecology of the ocean are some of the questions that, until now, we have not even begun to answer. On page 242 of this issue, Koike *et al.*[2], by means of a few simple experiments, have distilled some new facts from this unyielding organic soup.

Koike *et al.* examined oceanic particles with a spherical diameter between 0.38 and 1.0 μm. Most of these particles would be classified as 'dissolved' in routine oceanographic filtrations. The authors determined the number of particles in this size range using a non-destructive particle counter. They counted bacteria in this size range separately using epifluorescence microscopy and were able to show that more than 95 per cent of submicrometre particles are non-living. These particles are very fragile — exposure to high-frequency sound drastically reduces the number of particles that are not bacteria — and flexible enough to sneak through pore sizes nominally only one-quarter of their diameter. Ultra-centrifugation has no effect, indicating that the particles are rather loose aggregations enclosing a large quantity of water. The highest number of particles in this size range is at the surface; at a depth of 200 m the number of submicrometre particles falls to 1/30 of that found at the surface. Variations with depth show a close association between the number of submicrometre particles and bacterial biomass, chlorophyll and the larger-sized particulate organic carbon caught on glass fibre filters. The measurement techniques do not, however, provide an estimate of the carbon content or mass of material in the submicrometre pool.

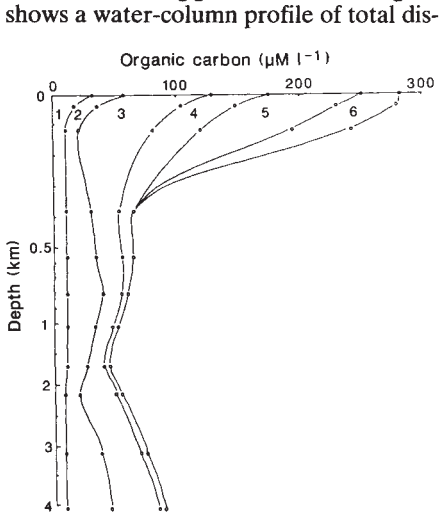
Using filters of ultra-fine pore size (about 0.02 μm) Koike *et al.* found that they could remove 99.5% of these tiny particles from the sea water. Incubations of this highly filtered water inoculated with a small amount of seawater filtered through a 0.6-μm glass-fibre filter produced more bacteria, but no more submicrometre particles. The inoculum in this case included only bacteria and the non-living particles described above; the bacteria in the inoculum multiplied by consuming the dissolved organic matter in the highly filtered solution. But when the inoculum was prepared by passing sea water through a 5-μm filter, 10–20 times more submicrometre particles were produced during the incubation than bacteria. Small animals in the 5-μm filtrate apparently began eating bacteria and presumably produced the submicrometre particles by egestion or in the process of lysing bacterial membranes.

This finding is consistent with the arguments of Jumars *et al.*[3] regarding the origin of the organic matter fuelling the heterotrophic microbial community in the sea. Between 20 and 40 per cent of the primary production of oceanic plants passes through the bacteria[4], and it is not clear how this happens. Many have argued that the organic substrates feeding the microbial community come directly from the phytoplankton as dissolved organic exudates[5]. According to this view, these relatively simple compounds, if not immediately utilized by bacteria, can react to form complex unreactive geopolymers, which build up in the ocean and account

for the huge size of the oceanic DOM pool. In contrast, Jumars *et al.* argue that marine zooplankton, in the process of eating phytoplankton cells, other animals or bacteria, egest or leak unassimilated materials in sufficient quantities to account for the level of microbial activity observed in the ocean. It is not clear, however, that dissolved organic material associated with animal egesta will persist long enough in the ocean to accumulate as high concentrations of DOM. Despite these shortcomings, the animal model is attractive because it easily accounts for the relatively low C/N ratio in the oceanic DOM, and does not require any hypothetical chemical reactions.

Not too many years ago the marine saprosphere was thought to consist mainly of very refractory organic compounds which circulated through the oceans for thousands of years before breaking down[7]. The dissolved organic pool in the ocean was thought to be equivalent in many ways to the pool of decaying organic matter in soils. Within the past few years, Suzuki *et al.*[7] and Sugimura and Suzuki[8] have perfected a technique for the catalytic oxidation of marine organic matter and as a result of this work, ocean chemists have come to recognize a new pool of organic material. The new pool rivals the old pool in its size (such that the total pool is now twice the size of the old pool), but not in its inactivity. Whereas the old pool of DOM was more or less evenly distributed throughout the ocean, the new pool is concentrated near the surface and appears to be actively involved in the biogeochemical cycling of carbon and nitrogen[9].

One largely unrecognized aspect of Suzuki and Sugimura's work is their attempt to break the DOM pool down by size fraction using gel filtration. The figure shows a water-column profile of total dissolved organic carbon (DOC) from the western Pacific broken down into six size fractions, where size fraction 6 is the largest. Most of the DOM extracted by older methods is composed of smaller molecules, corresponding roughly to size fractions 1 and 2. Most of the gradient in DOC between the upper ocean and the deep ocean is contained in the larger size fractions 3–6. To first order, the larger sizes represent the difference between the old and new material.



Concentration of total dissolved organic carbon with depth at 5° N 135° E in the western Pacific divided among six size classes: 1, <1,800; 2, 1.8–4 × 10^3; 3, 4–20 × 10^3; 4, 2–6 × 10^4; 5, 6–10 × 10^4; 6, >1 × 10^5 daltons (from ref. 8).

Fractions 5 and 6 largely disappear in the upper few hundred metres of the ocean, as do Koike *et al.*'s submicrometre particles. The largest molecular weight fraction (>100,000 daltons) probably overlaps the size range inhabited by the Koike *et al.* particles, such that size 6 and the submicrometre particles may indeed be the same material. Break-up of fragile submicrometre particles into smaller and more typically 'dissolved' entities could conceivably account for the larger pool of smaller compounds that comprise the bulk of Suzuki and Sugimura's DOM pool (size fractions 3, 4 and 5). To the extent that this might be true, the experiments of Koike *et al.* may herald the start of a new approach for the study of the marine saprosphere. □

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GEOCHEMISTRY

Granulites and the lead paradox

Robert Zartman

NEW isotopic and chemical data for rocks that are rarely seen at the surface of the Earth, but which may play an important role in understanding the evolution of the continental crust, are always exciting. And Rudnick and Goldstein[1] now report on the lead isotopic composition of three suites of mafic granulite xenoliths — essentially doubling our knowledge of lead isotopes in this largely neglected rock type originating in the lowermost crust.

Petrologically, most mafic granulites appear to be variants of metamorphosed basaltic rocks, that presumably have been injected into the crust from the underlying mantle. Geobarometry and geothermometry suggest that the granulites crystallized at depths of 35–50 km and temperatures substantially above the normal continental geothermal gradient. Together with Sr and Nd isotope ratios and other chemical data on the same xenoliths, these new analyses challenge previous ideas about the composition, age and mode of formation of the Earth's continental crust. Although the xenolith suites occur in areas with Proterozoic basement rocks (about 1,500 million years old), the isotopic evidence points to a much younger emplacement age for the precursors of the mafic granulites. If mafic granulites constitute a major lithostratigraphic unit in the lower crust, it may be necessary to contemplate a crust that is more mafic in composition and younger in age than usually assumed, and one that can be progressively thickened from below by the introduction of mantle-derived magmas.

Much of the earlier modelling of the lower crust, including my own[2], has been based on the premise that felsic granulites — often of great age and very low μ ($^{238}U/^{204}Pb$ ratio) — are the dominant rock type below mid-crustal levels. (The low value of μ will retard the further growth of radiogenic lead.) A perplexing problem of Pb isotope systematics was thus avoided. The difficulty comes from the so-called lead paradox[3], which arises when the apparent bulk-Earth Pb isotopic composition plots off the geochron (the line on a $^{207}Pb/^{204}Pb$ versus $^{206}Pb/^{204}Pb$ diagram representing the closed-system lead isotopic evolution of the Earth since its origin 4.57 thousand million years ago, see figure). Because the fields of the upper crustal and mantle reservoirs are fairly well-defined and lie to the right of the geochron, for balance, a complementary reservoir to the left of the geochron is needed. Old, low-μ lower crust composed mainly of felsic granulites held promise of offering a solution to this paradox[4]. By contrast, from Rudnick and Goldstein's results it seems that the lower crust has a younger 'tectonothermal' age and an isotopically less-retarded lead content than has usually been assumed. If their findings are generally applicable, we must almost certainly look elsewhere for the missing complementary reservoir (possible candidates are the subcontinental lithosphere, lower mantle or core) — or, alternatively, entertain the notion of a significantly younger age for