crepancy among these findings regarding the importance of isolation to biodiversity is puzzling because the various measures used to assess isolation are all related, as are the measures of diversity (*6*, *10*).

The empirical finding of a relationship between habitat area and reef biodiversity is not without precedent (*10*). It is consistent with theoretical models based on the notion of metapopulations (that is, groups of partially isolated and partially interconnected populations) (*11*, *12*). Recent studies of Pacific reef fishes and corals (*13*, *14*) suggest that, as required by metapopulation models, new recruits to the reefs are a mixture of offspring produced by local and more distant parents.

The dependence of diversity on habitat area is particularly troubling in light of the progressive destruction of reef habitats worldwide (*15*), and this finding clearly has important implications for conservation. First and foremost, coral reefs need to be protected now in order to prevent future species extinctions. The fact that such extinctions are not yet conspicuous is no cause for complacency, because models predict a substantial time lag between loss of habitat and species extinction (*12*). Moreover, these models also suggest that the coral species at greatest risk are the long-lived species that are rarely recruited to reefs but form the three-dimensional structure of reefs on which many other species depend. Finally, as noted by Bellwood and Hughes (*6*), low diversity regions may be especially vulnerable to damage and destruction because they lack entire families of species that might help the reef ecosystem to recover. The relationship between coral reef biodiversity and ecosystem productivity and resilience (*16*) is poorly understood (*17*). Thus, it is crucial that our conservation strategies err on the side of caution.

If reefs are the rainforests of the sea, then the corals and fishes counted by Bellwood and Hughes are equivalent to trees and birds. Even though most of the diversity in rainforests is contributed by insects, the insect equivalents that inhabit reefs have not been well characterized as yet. Indeed, the only estimates available for total reef biodiversity are based on an extrapolation from rainforests (*2*) and the counting of taxa found in a 5-cubic-meter reef microcosm in Baltimore harbor (USA) (*3*)! As we computerize and analyze existing taxonomic data and contemplate the contribution of reef loss to the global biodiversity crisis, we should remember that most of the organisms at risk on reefs are not only countless but also uncounted.

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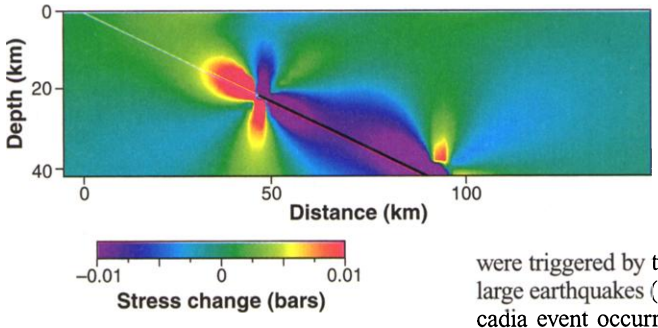
PERSPECTIVES: GEOPHYSICS

Silent Slip on the Cascadia Subduction Interface

Wayne Thatcher

Geodetic satellites of the Global Positioning System (GPS) now permit continuous recording of surface motions around earthquake faults and volcanoes with millimeter precision. Data from distinct points on Earth's surface can be combined to infer the locations of the sources of deformation at depth in the crust. These data are radically altering our understanding of earthquake processes, justifying ambitious new sensor arrays to image active deformation sources in Earth's crust. In recent years, large continuous GPS arrays have been deployed in Japan and southern California, and smaller networks have been installed in other seismically active regions. On page 1525 of this issue (*1*), Dragert *et al.* provide a glimpse of the kinds of insights we can expect from these arrays.

Dragert *et al.* use data from a 14-station continuous GPS net located in southwestern British Columbia and northern Washington to detect an episode of silent (aseismic) slip on a major fault that surfaces offshore and dives eastward beneath the continent. This fault defines the Cascadia subduction zone, which separates the large, ~100-km-thick blocks of the Juan de Fuca and North American plates (see the figure on the next page). Geological studies (*2*) have shown that large earthquakes occur along the Cascadia plate boundary roughly every 600 years. Modeling of geodetic data (*3*) indicates that the shallow, upper ~20 km of the plate boundary fault is currently "locked" (not slipping) because of frictional resistance on the fault interface. Continued relentless motion of the plates and aseismic slip increase stresses on the overlying earthquake fault. These stresses will eventually be relieved by abrupt shallow slip in a large earthquake.



A small step toward failure. Cross section showing elastic stress changes due to silent slip as inferred by Dragert *et al.* on fault segment shown in black. Positive stress changes (warm colors) bring earthquake faults like that shown by the white line closer to failure.

The Cascadia slip episode studied by Dragert *et al.* is unique and important because it occurred beneath an apparently completely locked plate boundary fault and was unrelated to any local earthquake activity. Aseismic events reported elsewhere occurred at the transition between locked and freely sliding fault segments (*4*), and many of them were triggered by transient adjustments after large earthquakes (*5*, *6*). In contrast, the Cascadia event occurred on the downward extension of the locked earthquake-generating fault, where aseismic slip or distributed ductile shearing (*7*) was expected to occur at a uniform speed. The physical processes responsible for all such deformation instabilities are not much studied or well understood. If similar episodes are identified elsewhere, they will doubtless stimulate new work directed toward understanding their mechanisms.

Aseismic events of the kind identified by Dragert *et al.* have potentially important implications for earthquake occurrence. Each aseismic slip episode perturbs the local stress field and may bring a fault closer to failure. No single deformation episode is necessarily an earthquake precursor, but if

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the locked fault is near the end of its stress buildup cycle, an episodic slip event may be sufficient to trigger a large earthquake (*8*).

The Cascadia slip episode, which took about 35 days, increased stresses across the shallower, earthquake-generating part of the plate boundary fault (white line segment in the figure on the previous page). This stress increase associated with the event is very small, equivalent to about half a year of steady stress buildup, bringing the fault very slightly closer to failure. The maximum change is about a factor of 10 smaller than the stress changes caused by earthquake slip that have triggered subsequent earthquake events (*9*).

The Cascadia subduction zone last experienced a great earthquake in 1700 (*10*) and so may be only about halfway through its ~600-year earthquake cycle. Therefore, even events substantially larger than the 1999 aseismic slip episode may not soon push this fault over the brink. However, other regional faults may be closer to failure and such episodic events could lead to large earthquakes. Continuous monitoring of these faults, in Cascadia and elsewhere, is thus of major importance.

Much remains to be learned about earthquake stress buildup. We do not yet know whether aseismic episodes are rare or common, large or small. For earthquakes, the numbers of events increases roughly tenfold for each unit decrease in earthquake magnitude. For aseismic events, we must determine the relation between frequency of occurrence, slip, and slipped area to understand what causes them and evaluate whether such episodes will trigger large earthquakes. For the Cascadia episode, the ratio of fault slip to fault area was quite small, about two orders of magnitude less than that typical for earthquake slip. This ratio is proportional to the stress change caused by the event, so the magnitude of the effects like those shown in the figure is less important when the ratio is small.

The Cascadia subduction zone. Subdiction of the Juan de Fuca plate beneath the North American plate results in the formation of the Cascade Range.

Recent work (*1*, *4*–*6*) has revealed a rich spectrum of aseismic behavior in seismically active regions but has also raised many new questions. Further progress in understanding these processes depends on the deployment of dense networks. Focused instrument clusters are needed to spatially resolve buried sources of deformation, many of which could be much smaller or more localized than that identified with the relatively sparse array used by Dragert *et al.* These arrays should also include ultrastable borehole strain meters, which are increasingly more sensitive than continuous GPS for time intervals of a month or less. Parallel developments are needed in refining analysis and modeling techniques aimed at extracting the maximum information from these large data sets (*11*).

Local prototype arrays of continuous GPS and borehole strain meters have recently been installed by the U.S. Geological Survey at Parkfield on the central San Andreas fault and at Long Valley caldera, a region of volcanic unrest in eastern California. Additional clusters in a range of geological environments will ensure timely acquisition of the kinds of data needed to capitalize on the capabilities of continuous GPS and borehole strain meter technology and rapidly expand our understanding of how earthquakes occur and why volcanoes erupt.

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PERSPECTIVES: PALEONTOLOGY

Digging Up Fresh Clues About the Origin of Mammals

André Wyss

The last two decades have been exhilarating for paleontologists and evolutionary biologists seeking to unravel phylogenetic relationships among living and extinct mammals. Stunning fossils have been unearthed from key locations worldwide and new methods have facilitated the comparison of these fossils with their living counterparts. The fossil reported by Luo *et al.* (*1*) on page 1535 of this issue is the latest gem in this string of paleontological pearls. They describe a beautifully preserved skull of a new synapsid taxon called *Hadrocodium* (synapsids are the group of legged vertebrates to which mammals belong), unearthed from the famous Early Jurassic (~195 million years old) Lufeng deposits of Yunnan Province in China.

Although the last 65 million years of Earth history (the Cenozoic Era) are often regarded as "the age of mammals," the major branches of the mammalian evolutionary tree diverged tens of millions of years earlier, during the Mesozoic Era (see the figure). We have known about fossils of Mesozoic mammals for about 200 years. But it is only recently that significant numbers of reasonably complete skulls and skeletons have become available. Prior to this, information was limited to what could be gleaned from skeletal bits and pieces, such as teeth and jaw fragments. Indeed, much of our knowledge about mammalian evolution stems from analyses of the highly specialized teeth for which mammals are noted. The availability of exquisitely preserved skulls and skeletons of many early mammalian lineages has diminished the influence of this tooth-centric perspective, leading to the emergence of a highly integrated understanding of mammalian phylogeny.

A consideration of the outwardly undemanding question "How old is the oldest mammal?" reveals one recent improvement in the naming of groups of organisms. Traditionally, formal taxonomic names, such as Mammalia, have been equated with "key" or "defining" morphological traits—for example, mammary glands, hair, or a dentary-squamosal jaw

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