PERSPECTIVES

GEOSCIENCE

Sea-Floor Depth and the Lake Wobegon Effect

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Geophysicists are directing renewed attention to the long-standing question of how to discriminate "normal" versus "anomalous" depths of portions of the oceans. The seemingly prosaic challenge of assessing whether depths deviating from an assumed norm are significant or simply artifacts of the reference model used (as in the mythical town of Lake Wobegon in the radio show Prairie Home Companion "where all children are above average") is surprisingly crucial to modern concepts of how the solid Earth functions. Put simply, sea-floor slopes and bumps provide much of our ideas about how Earth's heat engine operates and why it differs from those of neighboring planets.

Although sea-floor topography is complicated, three primary effects were identified after the recognition of plate tectonics in the late 1960s. Plates of oceanic lithosphere form at mid-ocean ridges, move away from those ridges, and eventually subduct into the deep Earth. It was recognized that seafloor depth increases approximately as the square root of lithospheric age and that the flow of heat through the sea floor decreases similarly. Because square-root-of-time behavior characterizes diffusion processes, depth and heat flow can be described by treating the lithosphere as the upper layer of a half space that cools, thickens, and contracts as it ages (1). The oceanic lithosphere thus forms the cold, strong outer boundary layer of the convection system removing heat from Earth's interior.

A great deal of old sea floor is, however, shallower than predicted by a simple model of half-space cooling. This shallowing is typically treated in terms of two processes thought to jointly describe heat addition to the lithosphere from below. In one, diffuse heating below most old lithosphere balances heat lost at the sea floor, causing old lithosphere to approach equilibrium thermal structure, depth, and heat flow (2). In addition to the general "flattening" due to diffuse heating, some localized shallowing appears to reflect concentrated plumes of upwelling mantle material. Plumes move slowly relative to plates moving over them, causing linear shallow hotspot swells often marked by volcanic islands such as Hawaii (3).

In this view, the terrestrial heat engine is characterized by the balance between three modes of heat transfer from Earth's interior: (i) the overall plate tectonic cycle (evidenced by half-space cooling and flattening), (ii) three planets is thus a "hot" (as it were) topic.

Considerable effort has thus been directed toward estimation of the relative thermal effects of plate tectonics, mantle plumes, and other local phenomena. The challenge is that the primary observables, depth and heat flow, reflect combinations of possible effects. The approach taken is to develop reference models predicting depth and heat flow for normal oceanic lithosphere as functions of age, and then identify anomalous areas where predictions misfit data, presumably because processes not depending on age (such as plumes) operate. The simplest model, a cooling half-space, is reasonably successful for lithosphere younger than 70 million years age but overpredicts depths and underpredicts heat flow for older areas. Alternatively, a model of a cooling plate with an isothermal lower boundary accounts for heat addition from below the lithosphere and thus better fits data. However, a commonly used plate



Geophysical Rorschach test. (**Upper left**) Sea-floor topography in the Darwin Rise (shown corrected for sediment loading) showing linear swells and broad regions between them. This topography can be viewed as three quite different depth anomaly maps, depending on the reference model used: (**upper right**) PSM model; (**lower left**) GDH1 model; and (**lower right**) half-space cooling model. Depth anomalies are divided into those within 500 m (~1 σ) of that predicted (green), those shallower (red), and those deeper (blue). [OJP, Ontong Java Plateau (not a swell); Midpacs, Mid-Pacific Mountains; and Wake Gyts, Wake Guyots]

mantle plumes (evidenced by swells), which are another feature of the convective system, and (iii) heat conduction through continents (which do not participate directly in the convective system owing to their low density relative to oceanic lithosphere). Hence, seafloor topography provides the primary evidence for present estimates that about 70% of terrestrial heat loss occurs by means of plate tectonics and 5% by means of plumes (4, 5). In contrast, although direct measurements are not available, Mars and Venus seem to function quite differently, because large-scale plate tectonics is presumed absent (6). The question of how and why mantle convection takes place differently on the model with parameters given by Parsons and Sclater (PSM) (7) still results in a systematic misfit of depths and heat flow for most old lithosphere, implying widespread depth and heat-flow anomalies. Hence, regions were considered anomalous despite not differing from others of similar age.

This situation prompted a recent joint inversion of depth and heat-flow data, which found that these anomalies can be reduced significantly by a reference model, termed GDH1, with a thinner thermal plate than previously assumed (8). Depth, heat flow, and satellite gravity data not inverted in deriving GDH1 are also better fit by the thinlithosphere model (9). As a result, possible

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depth and heat-flow anomalies have come under renewed scrutiny.

Of special interest have been possible anomalies over hotspot swells. The GDH1 model reduced inferred anomalies at swells like Hawaii, implying that reheating of the lithosphere was less than previously thought (10). This reduction leads naturally to the consideration of "superswells", such as the Darwin Rise region (see figure), where multiple hotspot tracks may indicate that in the Cretaceous (before 65 million years ago), an unusual outpouring of mantle heat produced a broad upwelling. Depth anomalies relative to different reference models yield quite different maps and hence tectonic inferences (see figure). The entire Darwin Rise is shallow relative to a half-space model (11). Relative to PSM, much of the area is also shallow, suggesting a remnant regional thermal signature of the volcanism that formed the swells (12). However, because almost all lithosphere of this age is shallower than these models predict, the anomalies need not indicate that the Rise currently differs from lithosphere of this age elsewhere. In contrast, relative to GDH1, swells associated with volcanic chains are shallow, whereas depths between them are within a standard deviation of that predicted. Because of the three models GDH1 best describes average old lithosphere, it indicates that much of the Darwin Rise is not significantly deeper than lithosphere of the same age elsewhere, implying that the region between the swells retains no significant large-scale thermal signature of the Cretaceous events (10).

The superswell region near Polynesia, considered a possible present analog to the Darwin Rise, is also receiving new scrutiny. Although the extent of the depth anomaly is under debate (13), the region is shallow relative to all three reference models, which make similar predictions because the lithosphere is relatively young. The suggestion that the depth anomaly and weakening of the lithosphere inferred from satellite gravity observations reflected regional thermal thinning of the lithosphere (14) now seems precluded by heat-flow data (10, 15). Hence, the weakening seems likely to be mechanical, with the plate acting as though it were broken (10). The extent and cause of the depth anomaly remains an active research area, because of the challenge of separating any regional shallowing due to large-scale mantle upwelling from the effects of localized volcanism.

The revived interest in depth and heat flow anomalies seems likely to continue. New thermal models are being proposed (16), and new analysis techniques are being developed. The growing availability of data on the World Wide Web—including depths from combined shipboard and satellite observations (17), sea-floor ages (18), sediment

thickness (19), and heat flow (5)—provides useful tools. Geophysicists will thus be inverting data, improving models, reducing misfits, pondering alternative depth anomaly maps, and debating their implications for years to come.

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TRANSCRIPTION

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Paths to Activation of Transcription

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The activities of genes are frequently regulated "up front", at the initiation step of transcription. The molecular picture of how this occurs is far from completion, but lots of progress is currently being made on many fronts, and work on the relatively simple bacteria continues to provide new insights. Two reports, on page 1658 and page 1655 of this issue (1, 2), describe incisive experiments on the mechanisms that regulate the initiation of transcription in bacteria, with implications for understanding common mechanisms of all transcription.

NtrC (nitrogen regulatory protein C) is a transcriptional regulator that activates transcription. In a process that requires energy in the form of adenosine 5'-triphosphate (ATP) hydrolysis, NtrC converts polymerase-promoter complexes of the σ^{54} -RNA holoenzyme $E\sigma^{54}$ (E designating the core enzyme and σ^{54} the promoter-recognizing and initiation-specific subunit) from a closed state to a transcription-ready open state. NtrC is brought to the region of its target transcription units by binding to enhancers, which characteristically have two binding sites for dimeric NtrC.

Wyman, Rombel, and co-workers have

now examined the binding of NtrC to an enhancer by scanning force microscopy (SFM) in coordination with an analysis of transcriptional activation in vitro (1). They show, in a visually striking way, that large oligomers, comprising more protein mass than the expected pair of phosphorylated NtrC dimers, accumulate on DNA when the transcriptionally active phosphorylated form of NtrC binds to its enhancer. With the use of SFM, these authors estimated the sizes of these large complexes, which appear as mounds piled up on ribbons of DNA. The mounds comprise protein-protein sandwiches, the functional significance of which has been demonstrated by a striking complementation: NtrC that can still bind DNA but that cannot activate RNA polymerase and NtrC that can activate RNA polymerase but not bind DNA can cooperate to activate transcription. Under these conditions, these molecules also form large protein oligomers on the enhancer.

Other experiments from the Kustu laboratory (3), and further work by others (4), indicate that the formation of these large phosphorylated NtrC oligomers is required for ATP hydrolysis, which is in turn directly coupled to the opening of the promoter. One might imagine that ATP hydrolysis would directly drive DNA strand separation at the transcriptional start site, but this is not the case (5): Until it is subjected to the

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