A Thermal Filter to Extinction

A paleontologist argues that periodic global refrigeration has been the main proximal agent of extinction throughout Earth history

Anyone who searches for a single, general cause of the series of mass extinctions that have punctuated the history of life may be doomed to failure. Simply, because the striking pattern of mass dyings through the past 600 million years might well be the product of a complex interaction of many different influences, both biotic and abiotic. Steven Stanley, a paleontologist at Johns Hopkins University, is prepared to argue, nonetheless, that temperature fluctuation, particularly refrigeration, is responsible for a very large part of the overall extinction pattern, in the marine realm at least.

Stanley's interest in the idea was piqued while he was studying fossil data on the longevity of mollusc species on the Atlantic and Pacific coasts of Central and North America during the past 3.5 million years, since the Panama Isthmus was formed. He began to notice a dramatic elimination of Atlantic species around 3 million years ago, which coincided with the onset of the most recent major series of glaciations. The Pacific molluscs of the time, by contrast, suffered hardly at all.

Not only did this observation dispel the notion that the Plio/Pleistocene glaciation had come and gone without any important marine extinction, but it also revealed a biogeographic pattern that appeared to emphasize both the impact and complexity of temperature change on species' survival. The molluscs of the Pacific Panama region were apparently able to migrate southwards to warmer climes during the glaciation, and therefore escape extinction, whereas their Atlantic cousins perished in a geographical and climatic trap formed by the Caribbean Basin.

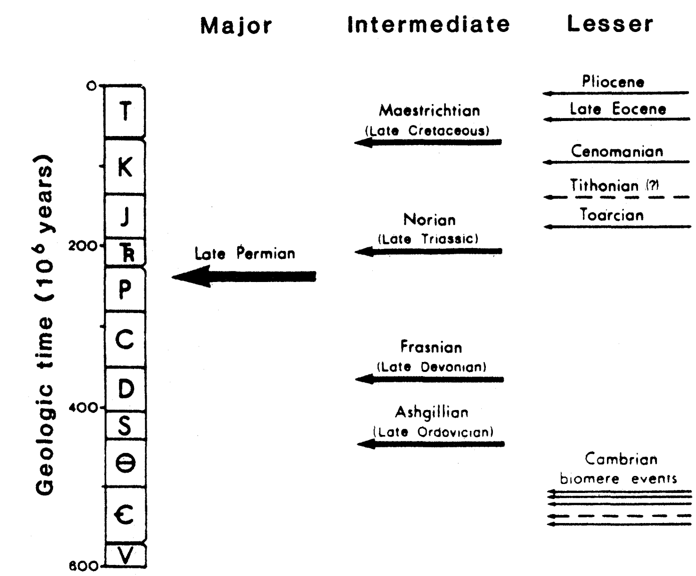
There is, of course, a suite of environmental factors that impose potential constraints on a marine species' distribution, such as salinity, dissolved oxygen, food resources, competitive interactions, predation, and temperature. Of these, Stanley reasons, temperature is surely the one most likely to have global impact. Thus began "a thin thread of logic that strengthened as I pursued it," says Stanley.

That thread runs counter to the currently most popular idea for a common denominator between all the major marine extinctions: to wit, the loss of habitable area on the continental shelves through a substantial drop in sea level or marine regression. Stanley also does not see persuasive evidence in temperature-related data for a general role of truly catastrophic and abrupt extinction that might result from periodic asteroid impact, which is currently gaining wide attention.

There is an important distinction to be made between proximal and ultimate causes, however, which Stanley is careful to do. Temperature change, as a proximal influence, might be the result of any one of many ultimate causes, which includes certain aspects of marine regression and asteroid collision. Changes in the solar constant is a more direct ultimate cause that has to be considered, as do the less direct effects of certain galactic cycles. It is, however, "temperature as a proximate agent of extinction" that Stanley is focusing on presently.

Paleontologists have been interested in mass extinctions for a very long time, not least because they represent the most dramatic signatures in the fossil record. Aside from one or two notable exceptions, however, the rigorous search for general mechanisms is a very recent phenomenon, spurred at least in part by the excitement provoked by the asteroid hypothesis. As climatic change, including refrigeration, is an obvious candidate for adverse impact on communities, it is not surprising that temperature has cropped up from time to time as a potential agent of extinction. Stanley's is among the most recent, most general, and most bold presentation of the idea.

Although no one would deny that refrigeration has left its mark in the extinction record, few would espouse its generality. "You can make a good case for temperature effects at certain extinction events," says Anthony Hallam of the University of Birmingham, England, "but you simply cannot argue for it as a general phenomenon. I see too many instances of extinctions without refrigeration and refrigeration without extinction for this to be correct." David Jablonski, of the University of Texas, Austin, essentially agrees with this assessment: "It's a little oversimplified," he says.



Extinction record

Data from the marine record (compiled mainly by J. J. Sepkoski) show periodic extinction through the Phanerozoic, that is the last 600 million years.

Strong support for the temperature hypothesis, however, comes from Erle Kauffman of the University of Colorado in Boulder. "Temperature effects must be an important part of the general extinction pattern," he says. "I have been recording a regular 26 million year climatic fluctuation, together with marine salinity and oxygenation, that correlates with the extinction pattern over the last 180 million years." The magnitude of the extinctions that result when these regular climatic instabilities hit depends, suggests Kauffman, on how robust biotic communities are in the face of other environmental factors, such as sea level.

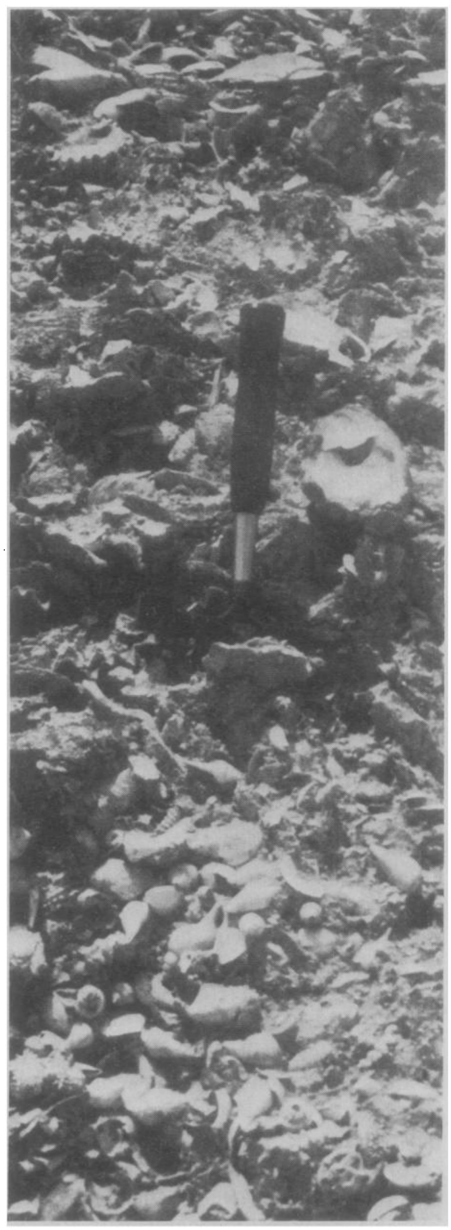
Many problems stalk the unwary investigator who seeks to correlate extinction events with environmental changes of one sort or another, not least of which are the difficulties involved in pinning down the timing of these events in the geological record. With paleotemperatures there is the additional frustration caused by the steady fading of the temperature signal—specifically, the ratio of certain oxygen isotopes—as one goes further and further back in the record. Beyond 160 million years or so researchers must rely on indirect inference, such as the shift from tropical to temperate faunas for instance.

The essence of Stanley's hypothesis is very simple. During global cooling events organisms in temperate regions will, if they are able, migrate towards the equator, and thus for the most part avoid extinction. Tropical biotas, however, have no place to which to escape, and so become extremely vulnerable. This neat model fits perfectly with what is surely the strongest signal common to all marine mass extinctions, namely, the strong differential loss of tropical as against temperate species. In addition to this main signal, however, certain geographic configurations will block the equatorward migration in some cases, and therefore produce a patchwork of more or less severe extinctions throughout temperate faunas. "This is precisely the geographic pattern that we observe for most ancient mass extinctions," says Stanley.

Stanley develops his thread of logic by comparing its associated evidence and predictions with those of its main competitor, marine regression. The periodic rise and fall of sea level, which is sometimes associated with plate tectonic movement, sometimes with major polar glaciation, will by turns increase and decrease available habitat for shallow-water organisms. Paleobiologists borrowed from ecologists an equation embodied in the species-area hypothesis that implies an inevitable loss of species numbers as habitat area dwindles. A major reduction in habitat area through major marine regression would, it was argued, cause a mass extinction.

The species-area argument does not impress Stanley, for several reasons. First, a fall in sea level, which reduces available continental shelf, will increase habitable shallow-water habitats around oceanic volcanic islands, because they are conical in shape. Moreover, these islands today "harbor enormous shallow-water marine faunas, which include a large majority of all species-rich families of benthos occupying warm, shallow seas."

Another argument centers on the rich diversity of mollusc species that live today in the Panamic-Pacific Province, which constitutes a very narrow shelf. Similarly, the Hawaiian archipelago supports a large shallow-water fauna in spite of its relatively small habitat area. "These observations oppose the idea that regressions should entirely eliminate some biogeographic provinces by way of species-area effect," contends Stanley. Jablonski agrees that the species-area effect is a poor candidate as an extinction mechanism, and, like Stanley, suggests that specific habitat destruction and a more continental climatic regime, both of which might be associated with marine regression, could cause significant loss of species in discrete localities.



Thermal filter in the Pinecrest beds

Organisms of both narrow (tropical) and broad temperature tolerance ranges lived off the coast of Florida 3.5 million years ago. Subsequent glaciations caused widespread extinctions in the fauna, the survivors of which were primarily species that could tolerate cool conditions.

In comparing marine regression as an agent of extinction with impacts of refrigeration, Stanley suggests that the former should be expected to have a uniform global effect whereas the pattern produced by the latter would be more complex. The simultaneous episodes of refrigeration and marine regression during the past 3 million years offers a simple test of this hypothesis. According to species-area calculations, the regression should have caused a worldwide 25 percent reduction of species numbers. "What we find is little or no excessive extinction in some areas but heavy mass extinction in others. The latter represented biogeographic traps where temperatures fell."

In the biogeographic trap represented by the Caribbean only 20 percent of mollusc species made it to the present through the periodic glaciation of the past 3 million years, compared with more than 70 percent on the California coast.

An impressive signal of extinction as a thermal filter comes from the nature of survivors in certain tropical fauna, such as the Pinecrest beds of central and southern Florida. "If refrigeration caused the mass extinction, the extant residue of this fauna should consist of species that can tolerate cool conditions," reasons Stanley. "This is precisely what we find." A similar thermal filter can be seen to have operated in an extinction event among earlier populations of the Mediterranean.

A second comparison of the regression and temperature models involves a natural experiment on a grand scale, during the Eocene and Oligocene epochs, 55 million to 25 million years ago. At the boundary of the two epochs, about 38 million years ago, global cooling was accompanied by only a minor drop in sea level. Later on during the Oligocene a major marine regression developed during which there was no excessive cooling. Here, it seems, is an opportunity to separate the effects of the two environmental phenomena.

According to Stanley, the outcome supports the temperature hypothesis, although Hallam for one would object to some of the time correlations used. During the late Eocene refrigeration there was a step-wise, global loss of planktonic foraminifers, the survivors of which were typical cold-water species. About 50 percent of all families of shallow marine species disappeared at this point, making it a major event. This was at a time of little marine regression.

By contrast, the large Oligocene regression was not accompanied by excessive extinctions among shallow-water organisms. "If the species-area effect were ever to have devastated species of shallow-water marine benthos globally, it should have done so at this time."

Looking to mass extinctions earlier in the geological record, Stanley believes he can make an argument for associated global refrigeration in most cases, and this includes that most notorious of mass extinctions, the Cretaceous/Tertiary boundary 65 million years ago, which, among other things, saw the demise of the dinosaurs.

The connection between extinction and refrigeration events is not always easy to make, however, partly because of the problems of inferring temperature regimes far back into the record, and partly because of a distinction that has to be made between polar and global refrigeration. Although polar glaciation might appear to be a potentially dramatic occurrence, it can in fact be rather localized, so that the tropics are little affected.

By contrast, general global cooling of an earth that has equilibrated to a balmy climate with gentle temperature gradients between the poles and equator could have a devastating effect, particularly in the tropics. Many organisms on such an earth would be adapted to a narrow range of temperatures, so even a slight cooling would initiate a squeeze to the tropics, with casualties lost in geographic traps. This pattern—of a balmy world being particularly vulnerable to even slight cooling—might seem somewhat counterintuitive.

Although some species are able to tolerate a wide range of environmental conditions and therefore potentially can be geographically widespread, many must remain within narrow limits, which is known as stenotopy. In Stanley's view—supported here by Kauffman—stenotopy is in large measure stenothermy, or narrow temperature tolerance. This, combined with the known climatic fluctuations that have tracked Earth history, must imply that episodes of cooling have a strong potential as a proximal agent of occasional mass extinction. Whether it is *the* agent in the markedly periodic history of life remains to be proved. As Hallam cautions—and Stanley would agree—"No one can afford to be dogmatic about anything yet."

—ROGER LEWIN

Additional Reading

Mass Extinctions, Matthew H. Nitecki, Ed. (University of Chicago Press, Chicago, to be published in May 1984).

Receptor Reconstituted

The purification of the β-adrenergic receptor protein is opening new ways of studying how this important receptor mediates the responses of cells to catecholamines, the physiological activators of the receptor. Robert Lefkowitz, Marc Caron, and their colleagues at Duke University Medical Center have reported that the purified protein can be inserted into the membranes of cells that ordinarily lack the receptor, conferring on them the ability to respond to a catecholamine.* "The molecule does all the things one thought a receptor should do," Lefkowitz says.

About a year ago, Lefkowitz and his colleagues purified the β-adrenergic receptor of frog erythrocytes; it turned out to be a single protein chain with a molecular weight of 58,000. More recently, they purified the receptors from hamster and guinea pig lungs. Each of these receptors also consists of a single protein chain, but the molecular weight is higher, 64,000.

Receptors must both bind to their ligands with appropriate specificity and also evoke a response in the cell. Although ligand binding can be studied with a purified receptor, the cellular consequences of the binding cannot. The β-adrenergic receptor must activate the enzyme adenylate cyclase to produce the "second messenger," cyclic AMP, to bring about its effects on the cell. "Our group had shown that we could purify a molecule with all the basic binding characteristics of a β-adrenergic receptor," Lefkowitz says. "But did it also contain the machinery for activating the adenylate cyclase?"

As the first step to answering this question the Lefkowitz group incorporated the purified protein into phospholipid vesicles. They then fused the vesicles with red blood cells of the African clawed toad, which have few or no β-adrenergic receptors of their own. However, they do have the other proteins needed for the cyclic AMP response. After fusion with vesicles containing a β-adrenergic receptor protein, the red blood cells gained the ability to respond to a catecholamine by producing cyclic AMP. Martin Schramm and his colleagues at Hebrew University in Jerusalem and Steen Pedersen and Elliott Ross of the University of Texas Health Science Center in Dallas had previously shown the feasibility of such reconstitution experiments but had used unpurified receptor preparations.

The experiments by the Lefkowitz group show that a single protein chain performs both the ligand-binding and cyclase-activating functions of the β-adrenergic receptor. This receptor appears simpler than the others that have been characterized so far. The receptors for insulin, acetylcholine, and immunoglobulin E are composed of multiple subunits.

The β-adrenergic receptor, an important regulator of the circulatory and respiratory systems, is a frequent target of therapeutic drugs. The ability to reconstitute the receptor response with purified protein opens the way to studying such problems as drug desensitization, Lefkowitz says. Cells frequently lose their responsiveness to a receptor activator, whether it be the endogenous one or a drug mimic, after varying periods of exposure. Densensitization can be a problem in the treatment of many conditions, including asthma.

Often the diminished responsiveness is caused by an actual decrease in the number of receptors in the membrane. But it can also be caused by a reduced effectiveness of the receptor in activating the cellular response. The Lefkowitz group found that the β-adrenergic receptor of turkey erythrocytes, when exposed to catecholamines, loses its ability to activate adenylate cyclase. This change appears to be caused by phosphorylation of the receptor, perhaps by the protein kinase that is activated by cyclic AMP.

In any event, it will now be possible to isolate the receptor from desensitized cells and see how effectively this protein works in the reconstitution assay. Or the protein can be modified in defined ways to study its interactions with the other components needed to activate the cells. "If we understand desensitization, it might be possible to develop ways to interdict it," Lefkowitz notes.—JEAN L. MARX

*R. A. Cerione, B. Strulovici, J. L. Benovic, R. J. Lefkowitz, M. G. Caron, *Nature (London)* **306**, 562 (1983).