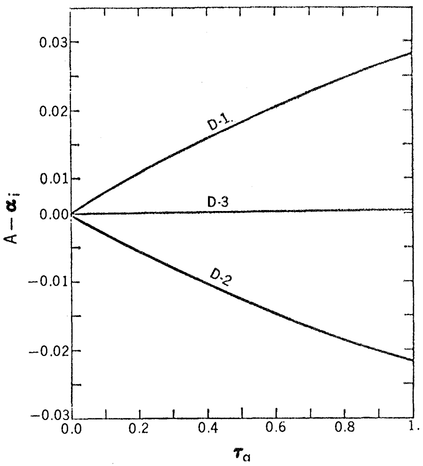
Fig. 3. Relative heating, $A - \alpha_i$, plotted as a function of aerosol optical depth with the same distributions of aerosol as in Fig. 1. The values $\omega_a = 0.9$, $\omega_a \beta_a = 0.1$, $\tau_c = 2.0$, and $r_s = 0.20$ were chosen so that $A - \alpha_{\overline{ac}} \simeq 0$.



bedo, in order for added aerosol to result in heating, the critical absorption-to-backscatter ratio for the aerosol is least when the aerosol is distributed above the cloud. Greater absorption relative to backscatter by the aerosol is necessary if the distribution is either mixed with or below preexisting atmospheric scatterers. In particular, at the annual global average albedo of 0.29, the critical ratio is 0.9 when the aerosol is distributed above the cloud, 1.3 when mixed with the cloud, and 3.2 when between the cloud and the surface.

In a second set of calculations, the results of which are plotted in Fig. 2, we set the atmospheric optical depth, τ_c, at 2.0 (a value which, together with $r_s = 0.12$, gives the global average albedo of 0.29) and vary the surface reflectivity. In this case also the distribution D-3 gives critical ratios that are intermediate between the D-1 and D-2 distributions, with the lowest values of absorption relative to backscatter required for heating to occur when the aerosol is distributed above the cloud. Convergence of the critical ratio occurs at high surface reflectivities.

Equation 1, applicable to the D-1 distribution, indicates that the critical point of transition from heating to cooling resulting from added aerosol is independent of its optical depth. Our calculations for the other distributions indicate that this is also true within the limits of error of the convergence criteria in the range of aerosol optical depth investigated, 0.1 to 2.0.

Finally, to further illustrate the effect of aerosol distribution on heating, we choose a set of values for ω_a, β_a, r_s, and τ_c such that $A - \alpha_{\overline{ac}} \simeq 0$. We then plot $A - \alpha_i$ as a function of the aerosol optical depth, τ_a, in Fig. 3 from which it is clear that the aerosol leads to net heating when distributed above the preexisting atmospheric scatterers but to net cooling when distributed below them.

As with the calculations of Chýlek and Coakley (*4*), the validity of the results reported here are limited by the approximations inherent in the radiative calculations. In particular, it is limited to the global average situation since solar zenith angle dependency has not been taken into account. Also in our calculations we have assumed a diffuse thin atmospheric cloud rather than a system composed partially of thick cloud and partially clear atmosphere. These limitations do not detract from the general conclusion that the effect of added aerosol on radiative balance is dependent not only on its intrinsic optical properties but also on its distribution within the atmospheric system and the preexisting atmospheric and surface reflectivities.

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28 May 1974; revised 19 July 1974

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Environmental and Evolutionary Stability in Bivalve Mollusks

Abstract. *There is no relationship between environmental stability* [*as indicated by infaunal (stable) versus epifaunal (unstable) habits*] *and the generic duration of extinct marine bivalve mollusks when the effects of cosmopolitanism (which is associated with long generic durations) and other paleontological "noise" are excluded. This is contrary to the "depauperate gene pool" hypothesis of extinctions.*

The nature is the relationship between environmental stability and evolutionary stability has been the object of much recent concern (*1–3*). Does an unstable environment produce frequent extinctions and rapid taxonomic change? Or does it provide continuous selection for genetic diversity so that taxa are better able to survive eventual major changes of the environment? The latter is predicted by the "depauperate gene pool" hypothesis of extinctions (*4*).

Neontologic evidence is contradictory (*1*) and cannot provide the necessary time perspective. Paleontology does, but the definition and recognition of unstable ancient environments is a fundamental problem. Bretsky (*5*) assumed that benthic environments became more stable as water depth (approximated by distance from the ancient shore) increased. From an inferred evolutionary sequence of communities, he concluded that environmental instability favored evolutionary and taxonomic stability, but this result has been questioned (*1*, *6*).

I consider here an alternative measure of environmental stability: infaunal versus epifaunal habit. Epifaunal organisms live on the surface of the substratum and are subject to the full range of environmental fluctuations. Infaunal animals live within the sediment and are insulated from short-term changes of the environment (*7*). Although genetic variability is not in general related to environmental stability (*1*), reduced genetic variability is indicated in the relatively uniform "underground" environments occupied by fossorial rodents and infaunal bivalve mollusks (*3*, *8*). If infauna are sufficiently insulated with respect to epifauna, the depauperate gene pool hypothesis predicts that infauna should be evolutionarily less stable than epifauna.

In terms of geologic time, the rodent "experiment" has just begun (*9*) and its record is poorly preserved. In contrast, the bivalve mollusks are an ancient group (*10*) with commonly fossilized infaunal and epifaunal representatives which can be reliably distinguished (*11*). In this report, six superfamilies of suspension feeders and one order of deposit feeders are analyzed (*12*). The mean generic durations of epifaunal and infaunal groups are tested for significant differences [90 percent confidence (*13–16*)].

Table 1. Durations of genera of bivalves (*13*): Ostreacea, Pteriacea, Pectinacea, Hippuritacea, Veneracea, Lucinacea, Nuculoida. Extant and cosmopolitan genera were not included in the number of genera used. Abbreviation: S.D., standard deviation.

Group	Number of genera				Mean duration ± S.D. (million years)
	Total	Extant	Cosmopolitan	Used	
			Epifaunal		
Suspension feeders					
Ostreacea	42	8	10	30	31.1 ± 27.6
Pteriacea	86	7	14	68	31.4 ± 30.0
Pectinacea	101	15	23	66	38.6 ± 44.0
Hippuritacea	105	0	0	105	15.8 ± 14.6
			Infaunal		
Suspension feeders					
Veneracea	98	57	2	41	31.2 ± 22.0
Lucinacea	89	45	0	44	32.6 ± 23.0
Deposit feeders					
Nuculoida	63	17	16	41	56.1 ± 39.4

Extant genera are excluded. They may reduce mean generic duration because they represent incomplete experiments (*17*), or they may have longer ranges than extinct taxa because the real "last occurrence" is known (*18*). Analysis of extinct genera confirms the dominance of the latter effect; all mean durations are less than with extant genera included. The maximum reduction (10 million years) occurs in the Ostreacea and Lucinacea.

Cosmopolitan genera are omitted because they have greater durations than noncosmopolitans. Bretsky (*19*) found this in Paleozoic bivalves, and my results agree; in each group, the mean generic duration is significantly (90 percent) greater in cosmopolitan genera (*20*). However, both studies are subject to reservations because their data came exclusively from the *Treatise* (*14*): (i) A genus inhabiting first one hemisphere and then the other could be called cosmopolitan. A long-lasting genus would have a greater chance of attaining such nonsynchronous cosmopolitanism. (ii) The complete duration is more likely to be known for cosmopolitans because they are more likely to be discovered than endemics. (iii) Broadly defined genera have greater geographic and chronostratigraphic ranges than finely divided genera (*21*).

The reality of the relationship between geographic distribution and duration of taxa is indicated by other studies (*22, 23*). The detailed work of Rohr and Boucot (*16*) and Boucot (*24*) on Silurian and Devonian brachiopods is particularly important because it eliminates objections (i) and (iii), while minimizing (ii). There is a substantial biological basis for the observed relationship: (i) large populations evolve more slowly than small ones (*16, 23–25*); (ii) cosmopolitans can survive local changes causing extinctions of endemics (*26*); and (iii) taxa may become cosmopolitan through eurytopy (*19, 26*), although this is not always the case (*27*). Such taxa would be well equipped to survive environmental changes.

Vermeij (*27*) found that the gastropods of stable environments are largely cosmopolitan, and inferred a causal relationship. If so, cosmopolitanism may be a route by which inhabitants of stable environments achieve greater generic longevity. However, in the bivalves considered here, cosmopolitans are common only among the epifauna and the infaunal Nuculoida (Table 1). Cosmopolitanism in nuculoids may be due largely to broadly defined genera. Their shells have a large proportion of biodegradable organic matrix and are usually preserved as molds, which fail to reveal taxonomically critical internal structures. In addition, the optimum habitat of the Nuculoida is in fine-grained clastic sediments, and the sparse, poorly preserved faunas of such sediments have been relatively neglected by paleontologists. In any case, the infaunal habit (environmental stability) is not linked with cosmopolitanism in fossil bivalves; the greater generic longevity of cosmopolitans is a separate effect. In accord with this conclusion, Jackson (*26*) reports that recent bivalves from unstable, nearshore environments have wider geographic distributions than those from stable, deeper-water environments.

Table 1 shows only two significant differences in mean generic durations. The infaunal Nuculoida exceeded all other groups, while the epifaunal Hippuritacea (rudists) were lower than all others. The rapid evolution of the rudists has been ascribed to intense competition for solid substrata in their reef habitat (*28*). The effect of finely divided genera may also be involved; because of their unique form and massive, well-preserved shells, the rudists have probably attracted more study than most bivalves (*29*).

Nuculoids may have greater generic durations than suspension feeders because they exploit a relatively stable food source (*30*). However, the substantial resistance to starvation of suspension feeders (*31*) and the apparent superabundance of their food (*28*) weaken this argument. The long durations of many nuculoids may be due to broadly defined genera.

If stability of the physical environment were an important determinant of evolutionary stability, its effects should be more apparent: the generic durations of the infaunal Veneracea and Lucinacea should differ significantly from those of the Ostreacea and Pteriacea, for all four are localized in "unstable" nearshore environments (*32*). In any case, the inverse relationship between environmental and evolutionary stability predicted by the depauperate gene pool hypothesis of extinctions is not found. A growing body of evidence indicates either that this hypothesis is invalid or that the catchall parameter of environmental stability is too generalized to be considered a practical control of evolutionary rates.

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12. To be included, a superfamily or order had to contain numerous genera, all of which could be assigned with reasonable confidence to a single habit (epifaunal or infaunal).
13. I used the two-tailed *t*-test, assuming no uncertainty in the chronostratigraphic ranges of genera, which were taken from the *Treatise* (*14*). If the reported time span included a given chronostratigraphic unit, I assumed that the genus lived for the entire duration of the unit. Absolute dates are linear interpolations from F. W. B. Van Eysinga, *Geological Time Table* (Elsevier, New York, 1972). Ranges and genera preceded by a question mark, "unrecognizable" genera, and all subgenera were omitted. *Labrostrea* and *Oretia* were included. In the Hippuritacea "subfamily uncertain" was included, "family uncertain" omitted.
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33. I thank P. W. Bretsky, J. B. C. Jackson, J. S. Levinton, A. L. McAlester, D. C. Rhoads, and S. M. Stanley for the comments on the manuscript.

18 June 1974

Blood Velocity Measurements in Human Retinal Vessels

Abstract. *Laser Doppler velocimetry was used to measure the velocity of blood in human retinal vessels. The mean flow velocities obtained were 1.9 centimeters per second in a retinal vein and 2.2 centimeters per second in a retinal artery. Scattered light from a weak helium-neon laser beam focused on the vessel was detected by a photomultiplier, and the temporal correlation of the intensity fluctuations was measured with a photon counting autocorrelator. Autocorrelation functions for blood flowing through glass capillaries were used for calibration.*

The feasibility of using laser Doppler velocimetry to measure blood flow velocity in retinal vessels of rabbits was previously demonstrated (*1*). It was speculated then that such measurements could be performed in humans if the recording time could be short enough to minimize the effects of slow eye drifts and if the retinal irradiance could be decreased to permissible levels. These requirements have now been satisfied, and we report here in vivo measurements of the flow velocity of blood in human retinal vessels.

Laser Doppler velocimetry is a conventional technique for measuring the velocity of particles suspended in a fluid (*2*). It is based on the Doppler effect. The laser light scattered from a moving particle is shifted in frequency by an amount f according to the Doppler relation

$$f = (1/2\pi)\ (\mathbf{K}_S - \mathbf{K}_i)\cdot\mathbf{V}$$

where $\mathbf{K}_i$ and $\mathbf{K}_s$ are the wave vectors of the incident laser beam and the scattered beam, respectively, and $\mathbf{V}$ is the velocity of the particle. The magnitude of the frequency shift can be measured by optical heterodyning. With this method, the light scattered from the moving particles is combined at the surface of a photodetector with a local oscillator or reference beam which is, in general, a portion of the laser beam initially incident on the scattering re-

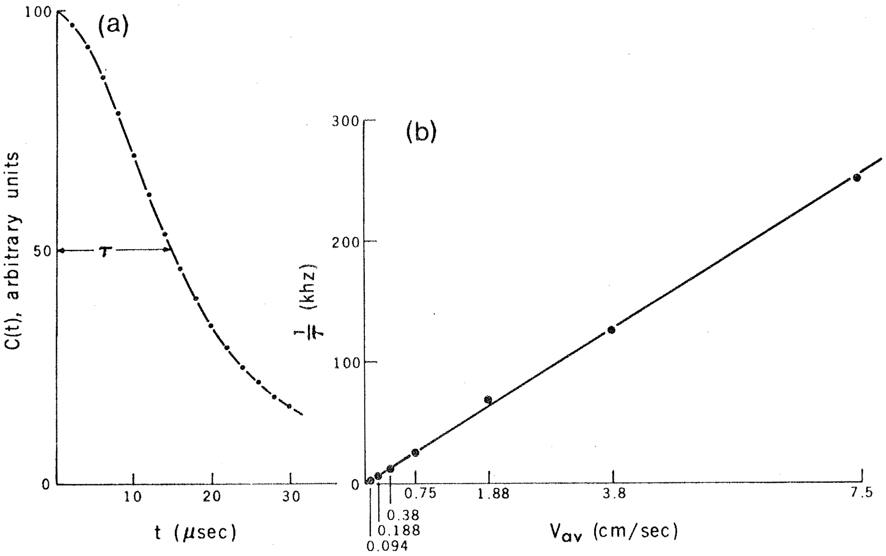

Fig. 1. (a) Correlation function for light scattered from the blood flowing in a glass capillary with an internal diameter of 160 μm; the flow velocity was 2.0 cm/sec. The half-width of the correlation function is denoted by τ. (b) Plot of 1/τ as a function of average velocity of blood flowing in a glass capillary with an internal diameter of 160 μm.