Environmental Trends in Extinction During the Paleozoic

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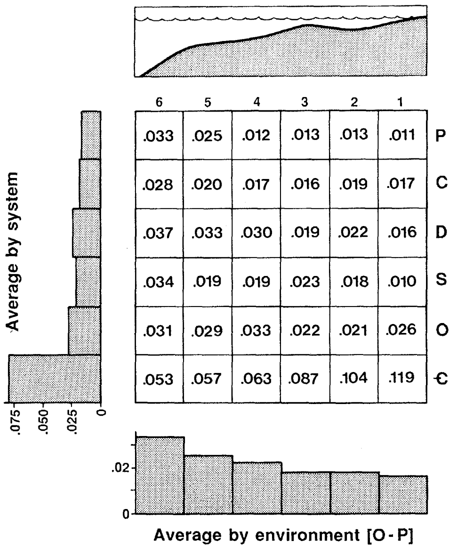
Extinction intensities calculated from 505 Paleozoic marine assemblages divided among six environmental zones and 40 stratigraphic intervals indicate that whole communities exhibit increasing extinction offshore but that genera within individual taxonomic classes tend to have their highest extinction onshore. The offshore trend at the community level results from a concentration of genera in classes with low characteristic extinction rates in nearshore environments. This finding is consistent with the ecologic expectation that organisms inhabiting unpredictably fluctuating environments should suffer more extinction than counterparts living under more predictably equitable conditions.

ONE OF THE MORE PERPLEXING PAleontologic generalizations concerning extinction in the oceans is that its intensity tends to increase offshore from shallow to deep marine environments. This generalization is surprising because it seems to contradict basic ecologic expectations: taxa in unpredictably fluctuating environments, such as found in nearshore regions, should suffer more extinction than those inhabiting more predictably equitable environments (*1*), as might occur offshore. An apparent offshore increase in extinction was first noted by Bretsky (*2*) in his synthesis of benthic community groups through the Paleozoic Era; he observed that brachiopod-dominated offshore communities tend to change more rapidly through time than do mollusk-dominated, nearshore communities. Subsequent workers (*3*) have documented environmental patterns of extinction or taxonomic longevity among various higher taxa and, in general, have found some tendency for extinction to increase, albeit irregularly, toward deeper water, although some exceptions (that is, onshore increase or lack of pattern) have been noted (*4, 5*). These exceptions may in fact be the rule. Analysis of extinction patterns for a variety of Paleozoic taxa indicates that extinction within taxonomic classes tends to increase toward shore and that it is only the domination of classes with low characteristic turnover rates in nearshore regions that causes whole communities to display higher apparent extinction offshore.

The analysis is based on a data set of 505 well-documented marine fossil assemblages of Cambrian through Permian age. These assemblages comprise published paleocommunities as well as biostratigraphic faunal lists covering all preserved macroinvertebrates and vertebrates collected from well-circumscribed lithofacies in both marginal shelf and cratonic settings (*6*). These data were compiled with as even an environmental and temporal distribution as possible while restricting sampling mostly to North America in order to avoid biogeographic complications.

The fossil assemblages are divisible into six broad environmental zones (Fig. 1, top): 1, nearshore zone, encompassing tidally influenced and estuarine environments; 2, nearshore subtidal "quiet" zone, including shelf lagoons and delta-top environments; 3, offshore "turbulent" zone, including some oolite shoals, bioherm-rich areas, and delta-front sands; 4, middle shelf zone, below normal wave base but influenced by storm activity; 5, outer shelf zone, near the shelf edge and influenced only weakly, if at all, by storms; 6, "deep" water zone, including slope, deep ramp, deep basinal, and offshore low-oxygen environments. These six zones are broadly analogous to Boucot's (*5*) benthic assemblages but are recognized by lithologic criteria rather than faunal content.



	6	5	4	3	2	1	
	.033	.025	.012	.013	.013	.011	P
	.028	.020	.017	.016	.019	.017	C
	.037	.033	.030	.019	.022	.016	D
	.034	.019	.019	.023	.018	.010	S
	.031	.029	.033	.022	.021	.026	O
	.053	.057	.063	.087	.104	.119	Є

Fig. 1. Average per-genus rates of extinction in six marine environmental zones within the systems of the Paleozoic (major mass extinctions excluded). Each cell of the matrix lists the mean (in units of genera per genus per million years) of three to eight extinction rates computed for subdivisions of the systems; standard errors of estimate average 30% of the listed mean values. Systems are denoted at the right of the matrix by standard symbols. The inset at the top of the figure shows a very generalized environmental model used to divide the data into the six zones. The histogram to the left of the matrix displays average values for each system and shows high extinction intensities in the Cambrian and lower intensities through the remainder of the Paleozoic. The histogram below the matrix displays average extinction intensities within the environmental zones for the Ordovician through Permian and shows increasing intensities from onshore to offshore at the community level. P, Permian; C, Carboniferous; D, Devonian; S, Silurian; O, Ordovician; and Є, Cambrian.

The total time represented by the assemblages was divided into 40 stratigraphic intervals, with the use of mostly North American units (*7*); these intervals average 7.5 million years in duration. Each contained an average of 12.6 assemblages (standard deviation, 4.8) and 120 genera (standard deviation, 48.5), many of which occurred in more than one environmental zone. The analytic design thus generated a 40 by 6 matrix with cells containing lists of genera known to occur in a given environmental zone during a given stratigraphic interval of the Paleozoic. Extinction intensities were calculated as the proportion of genera within a cell becoming globally extinct (*8*) during the stratigraphic interval (*9*), divided by the estimated duration of the interval. This produced a per-genus rate, or probability, of extinction.

The matrix in Fig. 1 lists the average per-genus extinction rates in each environmental zone in each system of the Paleozoic, with the stratigraphic intervals containing major mass extinctions [Richmondian, Frasnian, and Capitanian-Ochoan (*10*)] excluded. Averages across the row for each system are illustrated by the histogram at the left of the matrix. These averages show that extinction intensities were high during the Cambrian and considerably lower afterward, with a gentle, if irregular, decline to the end of the Paleozoic. This same pattern has been observed in global compilations of genera (*11*) and families (*10*), indicating that the local data analyzed here are not generating aberrant temporal trends.

The histogram at the bottom of Fig. 1 illustrates the average extinction intensities for the six environmental zones, with the high intensities of the Cambrian excluded. This display corroborates Bretsky's (*2*) observation that total turnover rates for entire communities increase toward deeper water. Average per-genus extinction rates over all Ordovician to Permian taxa increase by more than 50% from the shoreline to shelf edge and by more than 100% into deep water (*12*). Although there is variance within the individual systems, the overall trend appears statistically significant (*13*).

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Table 1. Per-genus rates of extinction, in units of genera per genus per million years, for entire communities in six environmental zones during intervals of major mass extinction in the Paleozoic Era. Data are insufficient to calculate a rate for zone 4 in the Late Permian.

Stratigraphic interval	Rates for environmental zones					
	6	5	4	3	2	1
Late Permian (Capitanian-Ochoan)	0.102	0.123		0.118	0.101	0.103
Frasnian	0.042	0.074	0.070	0.055	0.045	0.043
Ashgillian (Maysville-Richmond)	0.060	0.080	0.069	0.077	0.071	0.038

This whole-community trend is deceptive, however, as suggested by the average extinction rates for the Cambrian: these increase by 125% in the opposite direction, from offshore to onshore. The data for the Cambrian, in contrast to the other Paleozoic systems, are dominated by a single class, the trilobites, which are abundant in all environmental zones and increase their extinction intensity toward shore. However, this same pattern is seen in other major taxa when they are isolated from the data. Figure 2 illustrates average per-genus extinction rates for the five most common and widespread classes. Except for articulate brachiopods, each class exhibits some tendency for increasing extinction toward shore, attaining a maximum in environmental zone 1 or 2 (*14*). Weighted averages for the five classes, illustrated at the bottom of Fig. 2, display a 150% increase from deep to shallow water, although there appears to be little variation across the middle to outer shelf region (zones 3 to 5); a nearly identical trend results if Cambrian trilobites are eliminated and the analysis is restricted to the Ordovician through Permian. These patterns are consistent with the previously noted expectation that organisms in unpredictably fluctuating environments should experience higher frequencies of extinction than those inhabiting more predictably equitable environments (*15*).

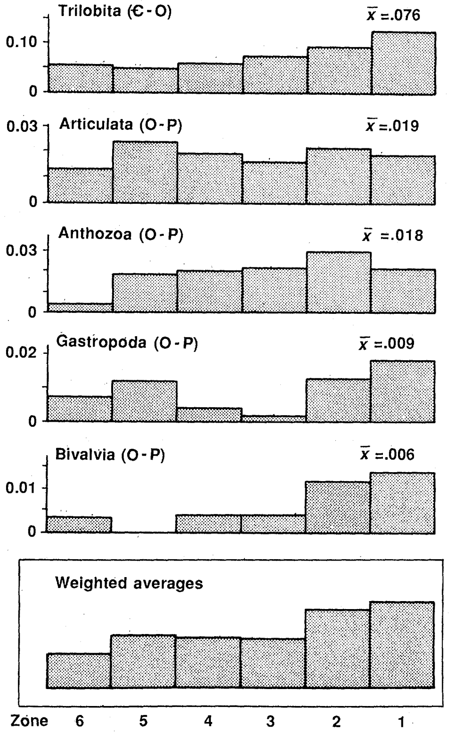

Fig. 2. Histograms displaying average per-genus extinction rates (major mass extinctions excluded) in six marine environmental zones for the five most common and widespread taxonomic classes in the Paleozoic data. The histograms are scaled such that the maximum value in each has the same height. The average rates, in units of genera per genus per million years, were calculated over those systems, indicated in parentheses for each class, in which members of the classes were common in the data. (The four classes other than trilobites are rare to absent in the data for the Cambrian, and trilobites are rare in most environmental zones after the Ordovician.) Mean values over all six environmental zones reflect the average, characteristic intensity for each class and indicate low turnover for bivalves and gastropods, moderate turnover for articulate brachiopods and anthozoans (rugosans and tabulates), and high turnover for trilobites. The unscaled histogram at the bottom of the figure displays weighted averages, calculated by converting the six values within each class to a percentage of the maximum for that class and then computing the mean within each environmental zone over the five classes. This histogram indicates a general increase in extinction intensity from offshore to onshore, opposite to the whole-community trend in Fig. 1.

The opposing trends of extinction in the whole-community versus individual-taxon analyses result from a simple source: classes differ considerably in their characteristic turnover rates and are heterogeneously distributed across the shelf in the Ordovician through Permian. Genera of articulate brachiopods, anthozoans, and several other classes with moderate characteristic turnover rates (Fig. 2) are concentrated in middle to outer shelf environments during the Paleozoic, whereas genera of bivalves and gastropods with low turnover rates are concentrated in the nearshore (*2, 16*). Because among-taxon differences in average extinction intensity are greater than among-environment differences, the variance resulting from the heterogeneous environmental distribution swamps the fundamental variance among environments, causing extinction rates to increase offshore in the whole-community analysis. Only the Cambrian trilobites, with their higher turnover rate, tend to be homogeneously distributed, resulting in whole-community extinction intensities that appear to increase toward shallow water.

Environmental patterns for major mass extinctions exhibit only some of the trends seen for extinction during "normal" times. Table 1 lists per-genus rates of extinction for the entire fauna in the six environmental zones for the Ashgillian, Frasnian, and Late Permian events. Calculated extinction intensities for all three events tend to exhibit some increase from shoreline to shelf edge but then decline into deeper water (*17*). This trend again reflects concentration of genera within the more extinction-resistant bivalves and gastropods in nearshore environments, although proportional differences in extinction rates between these molluscan classes and the articulate brachiopods and anthozoans are considerably smaller than during normal times. The reason for the decline in intensity off the shelf in zone 6 is not clear, although greater survivorship of off-shelf taxa has been observed for other extinction events (*18*). Within the major classes, there are no obvious trends in extinction across the shelf during the three events in Table 1, suggesting that mass extinction may be less discriminant with respect to environment than is normal extinction. Although the data are not really sufficient to test this suggestion rigorously, it is consistent with the recent inference (*19*) that different processes may be operating during times of mass extinction than those operating during normal extinction.

REFERENCES AND NOTES

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5. A. J. Boucot, *Evolution and Extinction Rate Controls* (Elsevier, Amsterdam, 1975).
6. Earlier versions of the data set are described in (*16*); the version analyzed here is considerably larger and more evenly distributed with respect to time and environment.
7. The stratigraphic intervals are *Fallotaspis* and *Nevadella* zones; *Bonnia-Olenellus* zone; *Plagiura-Poliella* and *Albertella* zones; *Glossopleura* and *Bathyuriscus-*

Elrathina zones; *Bolaspidella* zone; Dresbachian; Franconian; Trempealeauan; Gasconadan; Beekmantownian; Whiterockian; Chazyan; Blackriverian; Trentonian; Edenian; Maysvillian and Richmondian; lower and middle Llandoverian; upper Llandoverian; Wenlockian; Ludlovian and Pridolian; Lochkovian; Pragian; Emsian; Eifelian; Givetian; Frasnian; Famennian; Kinderhookian; Osagean; Meramecian; Chesterian; Morrowan and Atokan; Desmoinesian; Missourian; Virgilian; lower Wolfcampian; upper Wolfcampian; Leonardian; Wordian; and Capitanian and Ochoan.

8. No attempt was made to distinguish between true extinction (that is, lineage termination) and pseudoextinction (that is, phyletic transformation resulting in change of generic name).
9. Times of extinction were derived from a compilation of stratigraphic ranges of marine genera described in (*11*).
10. D. M. Raup and J. J. Sepkoski, Jr., *Science* **215**, 1501 (1982); L. Van Valen, *Nature (London)* **307**, 50 (1984); J. J. Sepkoski, Jr., in *Search for Extraterrestrial Life: Recent Developments*, M.D. Papagiannis, Ed. (Reidel, Dordrecht, 1985), p. 223.
11. J. J. Sepkoski, Jr., in *Patterns and Processes in the History of Life*, D. Jablonski and D. M. Raup, Eds. (Springer, Berlin, 1986), p. 277.
12. The large extinction intensities in environmental zone 6 reflect in part the inclusion of pelagic and nektonic taxa, including graptoloids and ammonoids, with very high characteristic turnover rates.
13. Friedman's test [S. Siegel, *Nonparametric Statistics* (McGraw-Hill, New York, 1956)] for five rows (Ordovician through Permian) and six columns yields $\chi_r^2 = 15.74$ ($P < 0.01$), indicating significant differences among the columns. Inclusion of the Cambrian, however, decreases χ_r^2 to 7.49, which is not significant ($0.10 < P < 0.20$). These and subsequent tests are only partially valid, however, since the rows and columns are not entirely independent (many genera occur in more than one environmental zone, more than one system, or both).
14. Friedman's test for the five rows (classes) and six columns (environmental zones) illustrated in Fig. 2 yields $\chi_r^2 = 11.40$ ($P < 0.05$).
15. These results suggest that possible adaptations to fluctuating environments, such as expanded niche breadth and greater larval dispersal, were not sufficient to counteract increased extinction intensities in the nearshore during the Paleozoic.
16. J. J. Sepkoski, Jr., and P. M. Sheehan, in *Biotic Interactions in Recent and Fossil Benthic Communities*, M. J. S. Tevesz and P. L. McCall, Eds. (Plenum, New York, 1983), p. 673; J. J. Sepkoski, Jr., and A. I. Miller, in *Phanerozoic Diversity Patterns: Profiles in Macroevolution*, J. W. Valentine, Ed. (Princeton Univ. Press, Princeton, NJ, 1985), p. 153.
17. Friedman's test for the three rows and six columns in Table 1 yields $\chi_r^2 = 11.95$ ($P < 0.05$).
18. A. R. Palmer, *J. Paleontol.* **39**, 149 (1965); J. G. Johnson, *Geology* **2**, 479 (1974); P. M. Sheehan, in *Proceedings of the Third North American Paleontological Convention*, (Business & Economic Service, Limited, Ontario, 1982), p. 477; R. Ludvigsen and S. R. Westrop, *Alcheringa* **7**, 301 (1983).
19. D. Jablonski, *Science* **231**, 129 (1986).

20. I thank A. I. Miller for his help with data compilation; P. W. Bretsky, D. J. Bottjer, A. J. Boucot, D. Jablonski, A. I. Miller, and P. M. Sheehan kindly provided comments on manuscript drafts. Supported in part by NSF grant DEB 81-08890 and NASA grant NAG 2-282.

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Delayed Transneuronal Death of Substantia Nigra Neurons Prevented by γ-Aminobutyric Acid Agonist

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In an investigation of the mechanism by which brain lesions result in delayed degeneration of neurons remote from the site of injury, neurons within the caudate nucleus of rats were destroyed by local injection of the excitotoxin ibotenic acid. Treatment resulted in the rapid degeneration of the striatonigral pathway including projections containing the inhibitory neurotransmitter γ-aminobutyric acid (GABA) and delayed transneuronal death of neurons in the substantia nigra pars reticulata. The distribution of nigral cell loss corresponded to the loss of GABAergic terminals. Neuronal death was prevented by long-term intraventricular infusion of the GABA agonist muscimol. Delayed transneuronal degeneration may be produced by neuronal disinhibition consequent to loss of inhibitory inputs. Replacement of inhibitory transmitters by suitable drugs may prevent some forms of delayed neuronal death.

WITHIN THE CENTRAL NERVOUS system (CNS), neurons may die when deprived of their afferent input (*1*). This form of neuronal degeneration, termed anterograde transsynaptic or transneuronal cell death (*1*), is believed to underlie some of the systemic degenerative diseases of the human nervous system (*2*). Its mechanism is unknown.

One example of anterograde transsynaptic degeneration is the death of neurons in the substantia nigra pars reticulata (SNr) after destruction by excitotoxins of neurons of the caudate nucleus (CN) (*3, 4*). Excitotoxin treatment results in death of the neurons in the CN (*5, 6*). Included are neurons projecting to the SN over the striatonigral tract, many of which contain the amino acid neurotransmitter γ-aminobutyric acid (GABA) (*7*). Because GABA is a potent and ubiquitous inhibitor of neuronal discharge (*8*) and because excessive excitation of neurons elicited, for example, by excitatory neurotoxins can lead to neuronal death (*9, 10*), the transneuronal death of SNr neurons produced by CN lesions may be due to loss of an inhibitory GABAergic input.

To test this hypothesis we have elicited transneuronal degeneration of neurons in the SNr by destroying CN neurons with the excitotoxin ibotenic acid (IBO) (*11*). We sought to establish (i) whether the neuronal loss is topographically related to the magnitude of the loss of GABAergic innervation and (ii) whether the death of neurons in SNr could be prevented by intraventricular administration of a highly specific agonist of GABA, muscimol (*12*).

Table 1. Effects of microinjection of ibotenic acid (IBO) into one caudate-putamen (CP) with or without intraventricular administration of muscimol on the neuronal and glial density in the CP.

Group (n)	Density (neurons per 10^6 μm^3)	
	Neuronal	Glial
Control (3)	78.0 ± 10.1	63.3 ± 7.9
Lesion (3)	2.3 ± 0.3*	292.3 ± 19.7*
Lesion + muscimol (3)	3.0 ± 0.2*	268.5 ± 14.7*

*Differs only from control ($P < 0.001$) (Newman-Keuls test of multiple comparisons). Cannulas were implanted into the lateral ventricle (*11*). Animals receiving muscimol were treated (10 ng/μl) for 15 days. On day 15 after IBO treatment, rats were killed by perfusion (*12*), and neuronal or glial density was assessed (*13*).

Male Sprague-Dawley rats were anesthetized with halothane. IBO was stereotaxically injected unilaterally into three sites (4 μg of IBO in 0.4 μl of saline at each site) in the CN. Control animals received an equal volume of saline. In some animals, in the same operation, a cannula was inserted into the lateral ventricle contralateral to the lesion, fixed to the skull, and sealed for subsequent intraventricular injections (*13*). Wounds were closed aseptically and the animals returned to their cages. The animals had no evidence of convulsive activity upon awakening.

At various times thereafter, the animals were reanesthetized and perfused transcardially with phosphate-buffered 4% paraformaldehyde. Brains were removed, sectioned, and stained with thionine or, in some instances, with antibodies to GABA to establish the distribution of the GABAergic innervation of SNr (*14*). We calculated the extent of the IBO lesion of the CN by measuring the area of neuronal loss on serial transverse sections of the striatum. To facilitate analysis, the SNr was divided into four regions at the level of the accessory optic nucleus (AON) (Fig. 1). These were designated as area 1, medial; area 2, dorsal central; area 3, ventral central; and area 4, lateral (Fig. 2). The dorsal and ventral central areas together were termed the central core. The extent of neuronal death in the SNr was assessed as a function of the reduced density of neurons (*15*).

In agreement with our earlier observation

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