

Decoupling of taxonomic and ecologic severity of Phanerozoic marine mass extinctions

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ABSTRACT

There have been five major mass extinctions among the marine biota during the ~0.6 b.y. history of metazoan life on Earth. These mass extinctions have been ranked from the largest to the smallest by the severity of taxonomic diversity losses, but they have not been ranked by the severity of the ecologic changes that they produced. Here we utilize a system of paleoecological levels that allows for the ranking of ecological degradation or shifts associated with significant taxonomic events, along with an analysis of large-scale paleoenvironmental patterns of two of the great evolutionary faunas, to compare the relative ecologic degradation caused by two major mass extinctions. The Late Ordovician and Late Devonian mass extinctions produced similar taxonomic losses (marine families declined ~22% and 21%, respectively). However, our analyses show that whereas the Late Ordovician extinction resulted in only minimal permanent ecological change, the Late Devonian extinction resulted in the complete restructuring of many components of the marine ecosystem. Thus, the large-scale taxonomic and ecological significance of these extinction events are decoupled, implying that some taxa are ecologically more critical than others.

Keywords: paleoecological levels, Devonian mass extinction, Ordovician mass extinction.

INTRODUCTION

Although various paleoecological approaches have been utilized to study the effects of mass extinctions, no systematic method comparable to the taxonomic approach of Raup and Sepkoski (1982) has previously been developed to compare ecologic changes between mass extinctions. However, changes in paleoecological systems can be expressed in terms of scales of change, and some changes are far more important than others. This structuring provides a means to rank paleoecological changes, which can be categorized into four types that are termed paleoecological levels (Droser et al., 1997) (Table 1). Changes at the first level are of the greatest magnitude and represent the advent of new ecosystems. Changes at the second level occur within an established ecosystem, and represent major structural changes at the largest ecological scale. Structural changes include the first appearance or replacement of ecologically dominant higher taxa within an ecosystem. Large-scale shifts in ecospace utilization are also included and can be recognized by large-

scale changes in adaptive strategies (Bambach, 1983) or Bambachian megaguilds (Droser et al., 1997). Changes at the third level include community-scale shifts within an established ecological structure, in particular the appearance or disappearance of community types (Bambach

and Bennington, 1995). Changes at the fourth level involve the appearance and disappearance of paleocommunities such as a succession of similar brachiopod-dominated communities; these changes are common through the Phanerozoic record and are similar in magnitude to most

TABLE 1. DEFINITION OF PALEOECOLOGICAL LEVELS AND CHARACTERISTIC SIGNALS FOR EACH LEVEL

LEVEL	DEFINITION	SIGNALS
First	Appearance/disappearance of an ecosystem	1. Initial colonization of environment
Second	Structural changes within an ecosystem	1. First appearance of, or changes in ecological dominants of higher taxa. 2. Loss/appearance of metazoan reefs. 3. Appearance/disappearance of Bambachian megaguilds.
Third	Community-type level changes within an established ecological structure	1. Appearance and/or disappearance of community types. 2. Increase and/or decrease in tiering complexity. 3. "Filling-in" or "thinning" within Bambachian megaguilds.
Fourth	Community-level changes	1. Appearance and/or disappearance of communities. 2. Taxonomic changes within a clade.

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minor ecological changes. While it is not possible to develop a hierarchical or quantitative measure of these types of ecological change, these levels are scaled and provide a method of ranking change (Droser et al., 1997).

We utilize this system of paleoecological levels to analyze the paleoecological effects of the Late Ordovician (ca. 440 Ma) and the Late Devonian (ca. 364 Ma) marine mass extinctions. These two mass extinctions are similar in that both occurred while marine assemblages were dominated primarily by the Paleozoic evolutionary fauna, one of the three Phanerozoic great evolutionary faunas of Sepkoski (1981), and both produced very similar taxonomic losses at the family level (Raup and Sepkoski, 1982).

LATE ORDOVICIAN EXTINCTION

The Late Ordovician extinction, one of the five largest mass extinctions in the history of marine life, had the second-largest family-level loss, exceeded only by the end-Permian extinction (Raup and Sepkoski, 1982). In spite of severe taxonomic losses, ecological changes were minor in reef, pelagic, and benthic settings. Metazoan reef communities were strongly affected by the cool temperatures during this mass-extinction interval, but the Silurian reefs that appeared soon after the extinction were composed mostly of the same families of rugose and tabulate corals and stromatoporoid sponges that were present in latest Ordovician reefs. Therefore, Silurian reef faunas can be regarded as Lazarus taxa (Copper, 1994), and thus the end-Ordovician extinction was not a major event for the reef system (Copper, 1994).

In the pelagic realm, graptolites were ecologically dominant early Paleozoic filter feeders. Although Late Ordovician graptolites had a huge taxonomic loss, being reduced to only a few species, they diversified quickly after the extinction and, ecologically, were as abundant in Silurian seas as they had been in the Ordovician (Berry, 1996). Pelagic conodonts also declined to fewer than 20 species, but returned to near pre-extinction diversity in the Early Silurian, so that conodonts reattained a dominant ecological position following the extinction event (Armstrong, 1996). Similarly, Ordovician nautiloid cephalopods were dominant in the pelagic carnivore megaguild, and during this extinction nautiloid diversity declined to levels not seen since their origination in the Early Ordovician. By the middle Silurian nautiloids had regained their ecologically prominent position in this megaguild (Crick, 1990), so that changes in this megaguild were only at the third and fourth level.

Brachiopods were a dominant component of Late Ordovician benthic communities. Diversity declined among all groups of brachiopods during the Ordovician extinction, but none of the megaguilds were vacated (Sepkoski, 1981; Boucot, 1975; Sheehan, 1996). Most changes

were at the fourth level. For example, among the biconvex brachiopods, which were the most common form, species diversity declined substantially, but Silurian recovery of community dominance was rapid (Watkins, 1994). An important new group of brachiopods, the wide-hinged spire-bearers, was added to the epifauna-attached suspension-feeding megaguild. The rise to prominence of spire-bearing brachiopods is an example of third-level filling of Bambachian megaguilds.

Other prominent members of benthic communities, such as rugose corals (Elias and Young, 1998), bryozoans (Tuckey and Anstey, 1992), and stalked echinoderms (Foote, 1999), also declined but then recovered to be important community components in the Silurian. It is interesting that crinoid disparity changed little across the event despite significant loss of taxonomic diversity (Foote, 1999). Ordovician trilobites, which had declined from their Cambrian dominance, were more permanently affected than most other groups (Sepkoski, 1981). Adrain et al. (1988) showed that trilobites from groups that originated in the Middle Ordovician were the primary survivors, while trilobites from groups present in the Early Ordovician (during the reign of the Cambrian evolutionary fauna) were nearly eliminated. Third- and fourth-level changes resulted from this extinction event. Thus, in reef, pelagic, and benthic settings, the severe taxonomic losses during this extinction resulted in only third- and fourth-level changes.

LATE DEVONIAN MASS EXTINCTION

In contrast to the Late Ordovician, the Late Devonian mass extinction triggered second-level changes. Devonian metazoan reef ecosystems have been described as the most extensive reef development in the planet's history (Copper, 1994), constituting almost 10 times the areal extent of reefal ecosystems present on Earth today. Metazoan reef ecosystems were virtually destroyed in the Late Devonian mass extinction, shrinking in geographic extent by a factor of 5000 from the Frasnian Stage to the Famennian (Copper, 1994; McGhee, 1996). Tabulate corals and stromatoporoid sponges, major elements of the Devonian reef biota, did not recover their diversity losses or ecological role for the remainder of the Paleozoic (Copper, 1994). The Late Devonian mass extinction thus precipitated a permanent change in the structure of global metazoan reef ecosystems in geologic time, a change at the second paleoecological level.

In the pelagic realm, the cricoconarids and conodonts were the two dominant elements of the Bambachian pelagic-suspension feeding megaguild during the Devonian. Only three species of the pelagic conodonts recovered their ecological position in the later Famennian (Sandberg et al., 1988). All of the cricoconarids

were driven to extinction in the Late Devonian, representing the permanent loss of a major element of the oceanic zooplankton (McGhee, 1996; Hallam and Wignall, 1997). The total loss of the cricoconarids and the major changeover in dominant conodont taxa were permanent second- and third-level changes in the structure of pelagic-suspension megaguilds.

Most elements of marine benthic ecosystems were adversely affected by the Late Devonian mass extinction (McGhee, 1996; Stanley, 1993). In particular, the Devonian was the golden age of brachiopods, which were the dominant element of benthic shellfish in Paleozoic seas, an ecological position occupied by the molluscs today. The dominant biconvex brachiopods of the Bambachian epifauna-attached-suspension megaguild lost more than 75% of their genera in the Late Devonian extinction (Boucot, 1975; McGhee, 1995), and were ecologically replaced by nonbiconvex brachiopods of the Bambachian epifauna-reclining-suspension megaguild in the post-Devonian Paleozoic (McGhee, 1996). This shift in ecological dominance between Bambachian megaguilds constitutes a second-level change in the structure of benthic marine ecosystems precipitated by the Late Devonian mass extinction. Similar dominance shifts in other major elements of the benthos (e.g., selective survival of unilaminar bryozoan species; McKinney, 1986) were also triggered by the event.

In the nekton, ammonoids and fish are the dominant elements of the Bambachian pelagic-carnivore megaguild during the Devonian. Only six genera of ammonoids survived the Frasnian Stage, although the ammonoids (like the conodonts) recovered their ecological position in the Famennian with the evolution of totally new families of goniatites (Becker and House, 1994). More than half of the species of placoderm fish did not survive, and one-third of the surviving placoderm families lost all of their marine members and became exclusively fresh water as a consequence of the ecological selectivity of the Late Devonian mass extinction (McGhee, 1996; Long, 1993). Major losses also occurred in chondrichthyan and osteichthyan dominants, but in the Carboniferous fishes recovered their ecological position with the evolution of entirely new fish faunas (Long, 1993; Benton, 1993). The Late Devonian evolution of new ammonoid familial dominants and changeover in fish faunas constituted a major change in the dominance structure of pelagic-carnivore megaguilds from the Devonian to the Carboniferous.

Therefore, while the Late Ordovician mass extinction had only third- and fourth-level paleoecological changes, the Late Devonian mass extinction had second-, third-, and fourth-level changes. Taxonomically, the Late Ordovician extinction was slightly larger than the Devonian. In contrast, the Late Devonian extinction had more lasting ecological impact and produced

greater changes in ecosystem structure. Thus, the ecological impact of a mass extinction can be decoupled from its overall taxonomic impact.

PALEOENVIRONMENTAL PATTERNS

The ecological impact of these extinctions can be viewed in another way. Sepkoski and Miller (1985) studied the ecological distribution of marine communities in the Paleozoic by compiling a data matrix consisting of the taxonomic composition, environmental position along an onshore-offshore environmental gradient, and temporal position of 540 communities. Factor analysis of this data matrix extracted the position of the Cambrian, Paleozoic, and modern evolutionary faunas in space and time (Fig. 1). The boundary between the Cambrian and Paleozoic evolutionary faunas (dashed line in Fig. 1) and the boundary between the Paleozoic and modern evolutionary faunas (solid line) give the contour of the 0.33 factor loadings of the communities. The pattern of interaction between the Paleozoic and modern evolutionary faunas is complex (Sepkoski and Miller, 1985; also see Cowen, 1995, p. 105). The offshore displacement of the Paleozoic evolutionary fauna by the modern evolutionary fauna was reversed twice; the Paleozoic evolutionary fauna briefly reinvaded shallow-water inner shelf regions. The more severe of these two reversals was in the middle of the Late Devonian, and a more moderate displacement of the modern evolutionary fauna occurred in the Late Carboniferous (Fig. 1).

Of importance here is the fact that the factor analytic study of Sepkoski and Miller (1985) can be used to quantitatively demonstrate the differential ecological severities of the Late Ordovician and Late Devonian mass extinctions. The position of the Late Ordovician mass extinction in the time-environment diagram is given by the arrowhead and the number 1 in the right margin of Figure 1, and the position of the Late Devonian mass extinction by the arrowhead and the number 2. Note that there is no displacement in either bathymetric direction of the boundary between the Paleozoic and modern evolutionary faunas during the Late Ordovician mass extinction. The Late Ordovician mass extinction thus is not registered in the paleoenvironmental distribution of marine communities; this extinction had no major ecological effect.

The Late Devonian mass extinction had a different pattern. In the middle of the Late Devonian (at the end of the Frasnian Stage; see McGhee, 1996) the modern evolutionary fauna is replaced in the inner shelf region by the Paleozoic evolutionary fauna (Fig. 1). The ecological severity of this major reversal for the modern evolutionary fauna can be further seen by the duration of the reversal. The Paleozoic evolutionary fauna remains dominant in inner shelf regions throughout the remainder of the Late Devonian (the Famennian Stage; see McGhee,

1996) and into the Early Carboniferous. Only in the late Early Carboniferous does the modern evolutionary fauna recover from the ecological effect of the Late Devonian mass extinction, and again begin to replace the Paleozoic evolutionary fauna in deeper water regions.

DISCUSSION

The different ecological signatures revealed through these analyses imply that although taxonomically the two mass extinctions were similar in size, some proportion of the organisms lost during each mass extinction had a different ecological importance. Hence, in terms of retaining ecological structure after a mass extinction, some taxa are much more important than others.

Metazoan reefs provide the most dramatic example. The Late Ordovician and Late Devonian extinctions eliminate 70% and 80% of the tabulate corals, respectively. Tabulate corals are a common and important component of Ordovician and Devonian buildups, but in both cases the dominant constructional metazoans of these buildups are stromatoporoids. Stromatoporoids were hit hard during the Late Ordovician extinction; however, they rebounded in the Silurian to form similar buildups along with tabulates. In contrast, after the Late Devonian extinction stromatoporoids lost nearly half of their genera and did not recover ecologically to build reefs. Scrutton (1988) linked the failure of the tabulates to recover after the Late Devonian extinction to the ecological structure provided by stromatoporoids, because the stromatoporoids created many of the reefal niches within which tabulates flourished. Thus, while the disappearance of buildups after the Devonian can in part be tied to the loss of stromatoporoids, the failure of the tabulates to recover to a position of some ecological importance was due to the loss of the three-dimensional physical structure created by the stromatoporoids. There were important changes during the Devonian, including shifts in predators (Bambach, 1999) as well as changes in terrestrial vegetation and concomitant change in nutrient supply to the oceans (Algeo and Scheckler, 1998). These events may have been influential in determining both the keystone and dominant taxa of the post-Devonian extinction as well as influencing biotic turnover during the Devonian, and these types of changes were not occurring during the Ordovician. However, much more work will be needed to determine the role of such factors in the ecosystem restructuring that occurred during the Late Devonian mass extinction.

Modern ecological studies recognize the importance of the relatively high ecological values of dominant taxa (e.g., Power et al., 1996). The key feature of dominant taxa in a community is that they have a very high biomass, which gives them their great ecological impact (Power et al., 1996). They play a major role in controlling the direc-

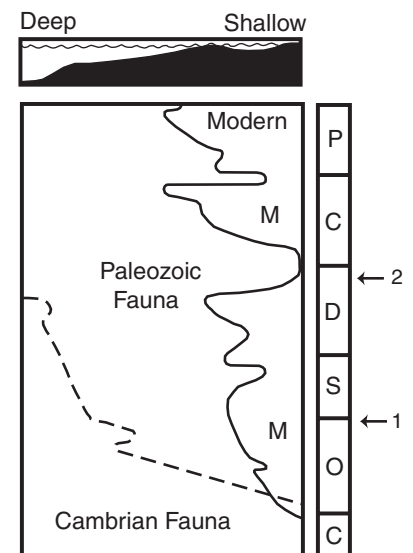


Figure 1. Paleozoic time-environment diagram of Sepkoski and Miller (1985), showing environmental and temporal distribution of Cambrian, Paleozoic, and modern (M) evolutionary faunas. Boundary between Cambrian and Paleozoic evolutionary faunas is indicated by dashed line in figure, and boundary between Paleozoic and modern faunas is indicated by solid line. Horizontal axis gives environmental position along bathymetric gradient (top margin of figure), and vertical axis is geologic time (right margin of figure) going from Cambrian to Permian. Figure is after Sepkoski and Miller (1985) and Cowen (1995). From bottom to top, C, Cambrian; O, Ordovician; S, Silurian; D, Devonian; C, Carboniferous; P, Permian.

tion and rates of community processes, and commonly provide the major energy flow or three-dimensional structure that supports a community (e.g., Scrutton, 1988). Modern examples of dominant taxa include forest trees, giant kelp, prairie grass, and reef-building corals (Power et al., 1996). Other types of taxa in a community also have relatively great ecological value, such as keystone species, which have relatively low biomass in a community, but a relatively large ecological impact, commonly as great as that of dominants (Power et al., 1996; Paine, 1969).

The general premise is that loss of taxa with high ecological value forces restructuring of an ecological system. Recognition of these taxa is based on criteria developed from modern habitats within an ecological (or generational) time scale. It is not clear whether this type of ecological phenomenon can be scaled up, in this case, both spatially and temporally. However, results from this study confirm that there are taxa that are ecologically more significant than others when operating within an evolutionary time scale and over large spatial dimensions. Furthermore, removal of these taxa during a mass extinction results in a significant and permanent restructuring of an ecosystem. Thus, modern dominants and keystones, which are significant in structuring local

ecosystems at a particular time, may be significant on a long-term basis.

Our results, along with others (McKinney et al., 1998), demonstrate that the taxonomic evaluation of a mass extinction represents only one aspect of the impact of a mass extinction. Thus, taxonomically, a mass extinction may be very large or relatively minor, but the ecological impact may be quite different. Early approaches to protecting modern ecosystems focused on preserving species diversity, while ignoring the ecological characteristics of species (Hooper and Vitousek, 1997). Recent studies of modern ecosystems, however, indicate that the ecological value of component species in an ecosystem is at least as important as species diversity in maintaining the integrity of the ecosystem (e.g., Hooper and Vitousek, 1997). In evaluating the differential ecological outcomes of the Late Ordovician and Late Devonian mass extinctions for mitigating the ecological effects of the current global biodiversity crisis, the value of a strategy emphasizing preservation of taxa with high ecological value is greatly reinforced.

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