

# Selective extinction among end-Triassic European bivalves

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## ABSTRACT

Ongoing controversies surrounding the end-Triassic extinction highlight the need for identifying a causal mechanism leading to extinction. Bivalve data from Lombardia (Italy), Northern Calcareous Alps (Austria and Germany), and northwest Europe (England and Wales) provide the biologic signal of selective extinction to compare two competing extinction hypotheses: (1) sea-level change and associated anoxia and (2) reduced primary productivity. The end-Triassic extinction eliminated 71% of Lombardian species, 85% of northern alpine species, and 90% of northwest European species. The extinction was independent of body size and geographic distribution. With respect to living habits, species from the three regions show a significantly greater proportion of infaunal bivalve extinction. The greater survival of epifaunal bivalves is correlated to their more efficient feeding and suggests that the infaunal bivalves may not have been able to meet their nutritional requirements. This pattern of selective extinction is inconsistent with anoxia and/or sea-level change as a causal factor in which higher survival of infaunal detritus and filter feeders would be predicted. Instead, the pattern is consistent with a reduction of primary productivity. Several regional and global mechanisms, including bolide impact, would have been capable of altering primary productivity levels to affect the food sources for Late Triassic bivalves, thus leading to extinction.

## INTRODUCTION

Recent analyses on the extinction at the end of the Triassic (Hallam, 1990a; Allasinaz, 1992) have highlighted the severity of the biotic crisis but have failed to identify clearly any causal mechanism. Of the many suggested causes for the end-Triassic extinction, only a regression-transgression coupled with anoxia (Hallam, 1981, 1990a) or an extraterrestrial impact (Badjukov et al., 1987, 1988; Bice et al., 1992) remain plausible hypotheses. Although both mechanisms rely on sedimentary, mineralogical, and geochemical evidence, neither has been tested against the biologic signal of selective extinction. The two extinction scenarios should provide distinctly different extinction patterns with regard to several ecologic, biologic, and physiologic attributes that can be inferred from fossil evidence. Because of their variety in life habits, bivalve mollusks are suited for this type of extinction analysis (Raup and Boyajian, 1988; Stanley, 1986a, 1986b). This paper examines the biologic signals provided by diversity and extinction data on European bivalves from the latest Triassic to earliest Jurassic. Furthermore, this report highlights the relation of bivalve life habits with respect to selective extinction and suggests a test for causal mechanisms that can be applied to other mass extinctions.

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## EUROPEAN EXTINCTIONS

### Bivalve Data

Species-level bivalve data were compiled from both the primary and summary literature sources and, where possible, supplemented with first-hand examination. The data used are derived from the Penarth Group of England and Wales (Hallam, 1981, 1990b; Hallam and El Shaarawy, 1982), the Kössen and Zlambach beds of the Northern Alps of Austria and Germany (Zapfe, 1967; Hallam, 1981, 1990b; Hallam

and El Shaarawy, 1982; Golebiowski, 1990; Golebiowski and Braunstein, 1988; Johnson and Simms, 1989), and the Zu and Sedrina Limestones of the Southern Alps of Italy (Allasinaz, 1992; McRoberts et al., 1995). Bivalves from the west Tethyan and northwest European seaways were chosen for this analysis because these bivalves have been well studied and the stratigraphic succession is relatively unambiguous. The data for diversity (measured as species richness) and extinctions are provided in Tables 1 and 2, respectively.

From the Lombardian Alps of Italy, 30 of the 42 species (71.4%) had become extinct by the end of deposition of the Rhaetian Zu Limestone. These 30 extinct species include all 18 (100%) infaunal elements and only 12 of the 24 (50%) epifaunal elements. The survivors in Lombardia are dominated by cemented and byssally attached pectinaceans, along with a few epibyssate pteriod, mytiloid, and arcoïd species. The bivalve species data from the Penarth Group of England and Wales show a loss of 23 species or 85.5% of the standing diversity. The 23 extinct species include 13 of the 14 (92.9%) infaunal elements and 10 of the 13 (76.9%) epifaunal bivalves. The four surviving species include two pectinaceans, one mytiloid, and one infaunal siphonate pho-

TABLE 1. RHAETIAN BIVALVE SPECIES RICHNESS

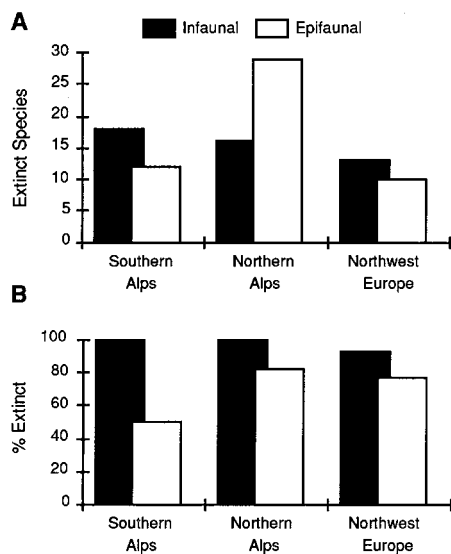
Life habit	Trophic level	Southern Alps	Northern Alps	Northwest Europe
Burrowing protobranch	Detritus feeder	1	2	2
Burrowing nonsiphonate*	Filter feeder	8	6	2
Burrowing siphonate	Filter feeder	10	8	9
Epifaunal byssate	Filter feeder	10	22	9
Epifaunal cemented	Filter feeder	5	4	3
Endobyssate	Filter feeder	4	4	1
Epibyssate zooxanthellate	Filter feeder	3	4	0

Note: Data (numbers of species) are derived from numerous sources given in text.  
\*Includes species with very small siphons.

TABLE 2. SPECIES EXTINCTIONS AND PERCENT EXTINCTIONS OF END-TRIASSIC EUROPEAN BIVALVES

	Southern Alps	Northern Alps	Northwest Europe
Infaunal species	18/18 = 100%	16/16 = 100%	12/13 = 92.3%
Epifaunal species	12/24 = 50%	29/34 = 82.3%	10/13 = 76.9%
Total species	30/42 = 71.4%	45/50 = 90%	23/27 = 85.3%
Pooled Binomial Prob.*	0.0064	0.1185	0.1114
Paired Binomial Prob.†	<0.001	<0.001	0.1203

\*Testing from mean extinction rate of pooled infaunal and epifaunal bivalves.  
†Testing difference between infaunal and epifaunal extinction.



**Figure 1. Comparisons of infaunal vs. epifaunal bivalve extinction from each of three European regions, measured as both (A) number of extinct species and (B) as percent extinction of standing diversity.**

ladomyoid. The data from the northern alpine regions of Austria and Bavaria show a cumulative loss of 90% of the Kössen and Zlambach bivalves. The 45 extinct species include all 16 (100%) infaunal species and 29 of the 34 (79%) epifaunal species. The northern alpine survivors include five cementing and byssate pectinaceans, an epibysate arcoid, and an endo- or epibysate mytilacean.

Although the numbers of extinct epifaunal and infaunal bivalve species (Table 2, Fig. 1) vary between regions (Fig. 1A), the percent of extinction is consistent across the sample areas. The percent of extinction better illustrates the pattern of selective survival for epifaunal bivalves at the expense of infaunal bivalves. As shown in Table 2, the selective extinction of infaunal bivalves in Lombardia is significantly greater than an expected pooled extinction rate of 71% (binomial probability  $p = 0.0064$ ). The small sample size from the other two regions makes it impossible to document a significant difference for these regions (pooled binomial probability 0.1114–0.1185). Clearly, the 92.5% to 100% infaunal extinction rate among European bivalves is ecologically significant and is counter to the benefits (protection from predators and environment) that may be afforded to infaunal bivalves.

Although all three regions underwent changes in sea level (regression followed by transgression) which may locally have affected the bivalve populations (e.g., Hallam, 1981; McRoberts, 1994), such changes do not account for either the magnitude or selective pattern of extinction. The Late Triassic paleogeography of the western Tethys,

with numerous islands and seamounts (Marcooux et al., 1993), would have provided insular refugia during times of regression, as has been argued by Jablonski (1985) for Permian-Triassic and Holocene invertebrate distributions. In addition, other regressive periods in geologic history were times of little or no marine extinction (Stanley, 1986a), which suggests that regression alone cannot account for the end-Triassic bivalve extinctions.

### Selective Extinction: Causes and Implications

The traditional explanations for selective extinction among bivalve mollusks—body size, larval dispersion, and geographic distribution—do not account for the selective extinction of infaunal elements, because these characters are similarly distributed between both infaunal and epifaunal life-habit groups. Two alternative hypotheses that may show selectivity along life-habit groups include (1) selection against bivalves ill adapted to oxygen-stressed environments or (2) selection against bivalves unable to compete for food resources during times of low primary productivity.

Anoxia as a causal factor is not consistent with the observed pattern of selective extinction. Most low-oxygen bivalve faunas are dominated by infaunal detritus and filter feeders; an exception is the exaerobic (or shelly laminate) biofacies (Savrda and Bottjer, 1987, 1991) which is characterized by “flat-clams” and other specialized epifauna. These infaunal life habits are typical of bivalves in modern dysaerobic environments (Rhoads and Morse, 1971; Theede, 1973; Thompson et al., 1985; see also Wignall, 1994) and are also known from oxygen-poor biofacies for several Jurassic examples (Morris, 1979, 1980; Oschmann, 1991; Wignall and Hallam, 1991). Given the empirical evidence, one would predict a relative dominance of infaunal filter feeders and burrowing deposit feeders over epifaunal filter feeders in oxygen-stressed bivalve faunas.

Physiological factors may have been important. Modern infaunal and epifaunal bivalves show pronounced physiological differences between feeding capacity, feeding requirements, and respiration. Available data on Holocene bivalves indicate that, as a group, epifaunal species can ventilate up to an order of magnitude more of suspension-laden water per gram of body weight than can infaunal species (Cranford and Grant, 1990; Jørgensen, 1975). Filtration rates are better determined by gill area, valve gape, and the diameter of the siphonal aperture rather than body mass (Bayne and Newell, 1983; Jørgensen, 1990). It is not clear, however, that the lower filtration rates of infaunal bivalves correspond to lower nutritional

requirements. Indirect measures of metabolic demands suggest that the two life-habit groups have roughly equivalent energy requirements per unit of body mass. There is no apparent difference between the two life-habit groups with respect to the amount of food necessary before excess food is rejected as pseudofeces (see data in Bayne and Newell, 1983; Griffiths and Griffiths, 1987). In addition, both life-habit groups have roughly equivalent metabolic demands measured as oxygen consumption rates (Griffiths and Griffiths, 1987). The pseudofeces threshold and respiratory rate data are counter to the idea that infaunal bivalves have greater food requirements necessitated by their supposed greater mobility (Rhodes and Thayer, 1991). Both infaunal and epifaunal groups have highly variable life habits and mobility levels (Stanley, 1970). It can thus be suggested that both infaunal and epifaunal life-habit groups would fare well in times of abundant food, yet during periods of low food availability, the epifaunal bivalves are better able to extract the required amount of food from sea water.

### DISCUSSION

The data presented here suggest a role for reduced primary productivity in the bivalve extinctions at the end of the Triassic. A comparable pattern of selective extinction of infaunal bivalves occurred during the end-Cretaceous mass extinction (Rhodes and Thayer, 1991; although see Raup and Jablonski, 1994), which has also been linked to a productivity crisis (Arthur et al., 1987; see also Hansen et al., 1993). Selection patterns of this sort suggesting productivity declines have not been documented for all first-order extinctions, including the end-Permian biotic crises (Rhodes and Thayer, 1991), but may be a common factor among second-order events (Paul and Mitchell, 1994).

Available geochemical evidence in support of reduced primary productivity is equivocal. The negative shift in  $\delta^{13}\text{C}$  values at the Triassic-Jurassic boundary from Kandelbach, Austria (Hallam and Goodfellow, 1990), might be construed as resulting from a productivity crisis, but it also corresponds to a lithologic change from the dominantly carbonate Kössen Formation to the overlying shales of the Grenzmergel. Further geochemical substantiation (or refutation) of the hypothesized productivity crisis must await additional analyses from lithologically homogeneous sections spanning the boundary.

Several regional and global mechanisms could have been capable of altering primary productivity levels to affect the food sources for Late Triassic bivalves. Although temperature fluctuations are known to alter the

levels of phytoplankton in modern oceans, geochemical evidence does not support temperature change for the end-Triassic crises (Hallam and Goodfellow, 1990). Productivity levels could also be altered by cessation of coastal upwelling, yet diminishing upwelling on the global scale necessary for the observed magnitude of marine extinctions would be difficult, and it could not account for the terrestrial crises. A reduction in primary productivity can be achieved through atmospheric darkening (Milne and McKay, 1982) as might be expected during prolonged periods of explosive volcanism or as a result of the impact of a large extraterrestrial bolide. There is currently no evidence of extended explosive volcanism at the Triassic-Jurassic boundary (Hallam, 1990a). The presence of shock-metamorphosed quartz grains in a Triassic-Jurassic interval in Tuscany (Bice et al., 1992) is evidence that is consistent with the hypothesis of bolide impact at the close of the Triassic Period and could explain the selective extinction among European bivalves.

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