THE EFFECT OF THE GREAT PERMIAN EXTINCTION ON SURVIVAL OF CHEMOSYMBIOTIC BIVALVES: HOW ALTERNATE DIETS AND METABOLIC PROCESSES ALLOW ORGANISMS TO SURVIVE MARINE HYPOXIA

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ABSTRACT: As fertilizer runoff and other nitrogen rich pollutants cause dead zones in the ocean, there are many implications of what types of organisms will survive modern marine hypoxia. The purpose of this project is to determine if the Permian-Triassic Extinction, also known as the P-T event, approximately 252 million years ago caused mass marine extinction via hypoxia. This is one of the most common theories regarding the Permian extinction. According to this theory, the meteor strike sent debris and smoke into the atmosphere, blocking out the sun. Marine plants and algae, which rely on sunlight for photosynthesis, produce less oxygen. Dissolved oxygen in the water is quickly consumed, and marine animals suffocate en masse. Chemosynthetic bacteria can live without light because they capture energy from chemical bonds instead. Multicellular organisms are incapable of chemosynthesis by themselves, but they can survive by hosting chemosynthetic bacteria within themselves. If this were the case, the Permian Extinction would not have affected the survival of bivalve species with a chemosymbiotic diet. The author of this paper determined the effect diet had on survivability by comparing the numbers of chemosymbiotic bivalves before and after the Permian Extinction using data from the Paleobiology Database, an online data archive of fossils including their contemporary location, species, surrounding rock matrix type, and other specific information. The numbers of bivalve species of various chemosymbiotic diets in two time ranges were compared: from 300 to 250 million years ago and from 250 to 200 million years ago. These time ranges cover the late Permian and early Triassic periods, respectively. The hypothesis was wrong in that the Permian extinction did significantly affect the number of chemosymbiotic species. The number and distribution of chemosymbiotic bivalves actually increased following the Permian extinction.

Keywords: Bivalve, Chemosynthesis, Chemosymbiosis, Hypoxia/Anoxia, Great Permian Extinction, Deposit feeding, Suspension feeding

Introduction

The effect of the P-T event on isolated ecosystems such as deep-sea vents and burrowing animals is a common topic in the scientific community, and more insight into and interpretations of data will better our overall understanding of what actually happened 250 million years ago. Oxygen deprivation inducing mass extinction during the Permian is one interpretation of events, justified by the dominance of anaerobic brachiopods in the rock layer formed during that time (Wignail and Hallam 1992). Chemosynthesis uses chemical bond forces to generate energy. The specific method here uses carbon dioxide and hydrogen sulfate. Unlike the most common methods of generating energy (photosynthesis from fixing atmospheric carbon dioxide with sunlight, aerobic respiration from converting oxygen and glucose into carbon dioxide and water) chemosynthesis does not require light or oxygen. Chemosymbiotic organisms generally cannot synthesize by themselves and instead host chemosymbiotic bacteria (Mae et al. 2007).

Bivalves are aquatic mollusks of the class Bivalvia enclosed in two hinged shells. They are an excellent model organism because their hard shells fossilize easily, are found in marine environments all over the world, and modern bivalves are very similar in form and living conditions to their ancestors. Because of this, the author believes the effect of hypoxia on ancient bivalves would relate closely to the effect of hypoxia on modern bivalves. Bivalves, such as the well-known oysters, scallops, and clams, are also important to modern human culture and economy, and any changes for them will likely affect us.

In this paper, the hypothesis, the number of chemosymbiotic bivalve species being unaffected by the Permian extinction because they did not rely on photosynthesis related food sources, is tested. The author predicts the number of chemosymbiotic bivalve species did not change before and after the Permian Extinction.

Methods

A X2 test to determine the validity of a hypothesis by calculating the likelihood of the null hypothesis being statistically significant was conducted. The bivalve data were separated into six categories: obligate chemosymbiotes, deposit feeding + chemosymbiosis, and suspension feeding + chemosymbiosis between the earlier 300 and 250 mya, and obligate chemosymbiotes, deposit feeding + chemosymbiosis, and suspension feeding + chemosymbiosis between the later 250 and 200 mya. Deposit feeders eat small pieces of organic material fallen to the sea floor. This is commonly known as bottom feeding. Suspension feeders eat even smaller pieces of organic material afloat in the water. Most bivalves are suspension feeders. All of these variables are categorical. The data were downloaded from the Palaeobiology Database on October 24th, 2018, using the genus “Bivalvia”, palaeoenvironment = marine, and a species-level specificity, with the time range from 300 to 200 million years ago. R Studio, a programming language for statistical computing, was used to create subsets containing only the relevant data and Microsoft Excel was used to conduct a six-category X2 test with an alpha of 0.025 and generate the figure below. The author chose an alpha value of 0.025 because the relatively small number of chemosymbiotic bivalve species in comparison to total bivalve species of all diets within these time periods requires more precision. The purpose of this test was to determine if the differences between these categories are significant.

Results

To test the author’s hypothesis that the Permian extinction had no effect on the number of chemosymbiotic bivalve species, the resulting p

	200-250 mya (million years ago), pre-extinction	250-300 mya, post-extinction
Obligate chemosymbiote species	21	188
Deposit feeding, Chemosymbiotic species	60	7
Suspension feeding, chemosymbiotic species	0	2

Fig. 1: Time Ranges and Diet Types of Bivalve Species

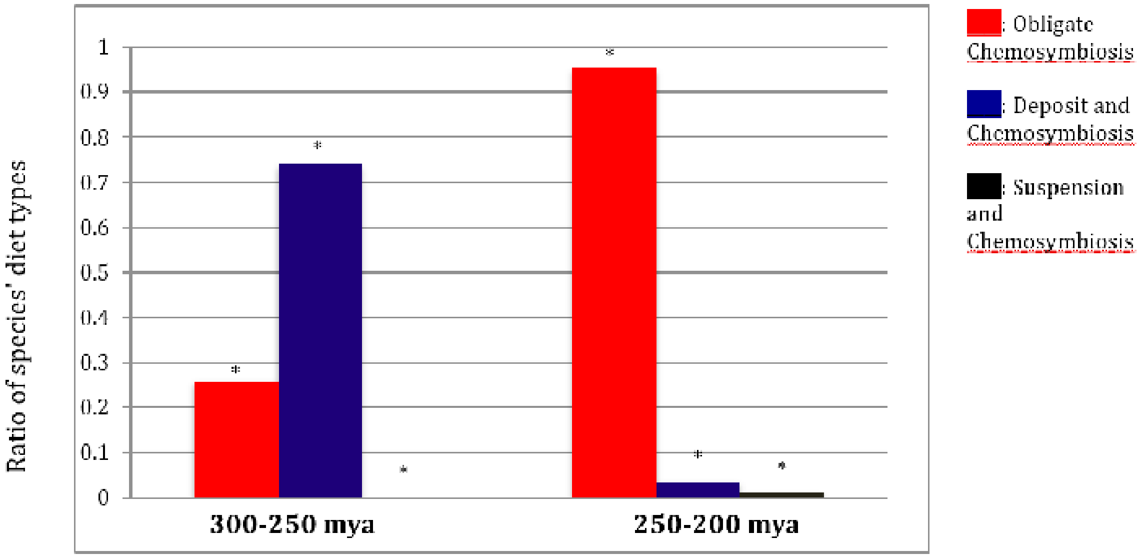

Fig. 2: Frequencies of various feeding patterns of chemosymbiotic bivalve species (obligate chemosymbiotes, chemosymbiosis and deposit feeders, and chemosymbiosis and suspension feeders) between 300-250 mya and 250-200 mya, p = 7.62E-18, α = 0.025

must be greater than 0.025 for it to be significant. The X2 test result for all chemosymbiotic bivalves is much less at 7.62E-18. The null hypothesis and research prediction are rejected. There is a significant difference in number of chemosymbiotic bivalve species before and after the extinction. As seen in the red leftmost bars in Figure 2, the proportion of obligate chemosymbiotic bivalve species increased, with very few post-extinction chemosymbiotic bivalves having alternate forms of diet. Additionally, the total number of chemosymbiotic species increased from 81 in pre-extinction to 197 in post-extinction.

Post-hoc (further and more specific statistical analysis done after the first test) X2 tests done in pairs between obligate and chemosymbiosis + deposit feeding bivalves had a resulting p of 1.05E-18, meaning there is a significant difference between the proportions of pure chemosymbiotes and bivalves capable of chemosymbiosis and deposit feeding. Between chemosymbiosis + deposit and chemosymbiosis + suspension, the p value is 9.56E-11, meaning this difference is also significant. Between obligate and chemosymbiosis + suspension, the p value is 8.22E-10. This difference is also significant. This means the diet of bivalves has a significant effect on their survivability.

Discussion

The number and diet diversity of chemosymbiotic bivalves did not remain unaffected by the Permian extinction as hypothesized, but they increased in number of species and reliance on chemosymbiosis. The hypothesis of the bivalve species being unaffected by the extinction was false. Initial reasoning of chemosymbiotic bivalves not relying on photosynthetic food sources can still be applied here. From the decreased number of deposit feeding bivalves, it can be inferred the extinction of other marine species led to less organic detritus from organisms that require oxygen to support their diet.

A very recent study of marine life during the P-T event provides an alternate explanation. Hypoxia may have been caused or exacerbated by the P-T event increasing the surface temperature of oceans, which also increases the metabolic rate of cold-blooded organisms in the water, causing them to consume oxygen at a much higher rate and then suffocate (Penn et al. 2018). Many chemosymbiotic bivalves are found in deep-sea vents and cold seeps, which are full of sulfur compounds required for chemosynthesis (Mae et al. 2007). These environments are far from the surface and likely change temperature less drastically. Even if the metabolisms of organisms in these environments increase, they do not require oxygen and are unlikely to suffocate. This theory would be supported if other deep-sea vent and cold seep organisms followed the same survival patterns as bivalves, but other chemosymbiotic organisms in these environments, such as tube worms and polychaete worms, have changed greatly following the P-T event despite their apparent isolation from climate change (Little and Vrijenhoek 2003).

It may be a far reach to assume distantly related organisms had the same reaction to the P-T event as bivalves. Brachiopods are similar to bivalves, with the most obvious differences being upper and lower shells, as opposed to the usually symmetric shells of bivalves, and a stalk anchoring the brachiopod to the ocean floor. Brachiopods are common throughout evolutionary history and chemosymbiotic brachiopods were found in the same environments as chemosymbiotic bivalves in many eras including the Permian (Campbell and Bottjer 1995). Similar to the increased survival of obligate chemosymbiotic bivalves, immediately following the Permian Extinction event, obligate chemosymbiotic brachiopods of the genus Lingula were the most common fossils found in the sedimentary layer, dated to immediately after the extinction event (Wignail and Hallam 1992). Anaerobic brachiopods in the Lingula genus today, although they continue to evolve genetically, have traits and living environments superficially identical to their ancient ancestors (Luo et al. 2015). It is a mark of great efficiency and adaptability for chemosymbiosis that it has allowed these organisms to survive the Permian extinction, remain relatively unchanged to today, and may potentially survive any future mass extinctions if current environmental trends continue.

Acknowledgements

Many thanks to Dr. Price for giving such a good clarification of proper X2 graph formatting that I was able to fix my original figure from a ten-minute office visit. I am immensely grateful towards fellow BES 301 student Alex Wachter for reviewing my paper even though it wasn't assigned. Also thanks to Linda Simonsen for assigning R programming homework that happened to be extremely useful for this project. I acknowledge my friend Arnold for trying and failing to fix my computer.

Supplemental Material

	Pre Extinct	Post Extinct	Type Totals
pure chemosymbiosis	21	188	209
chemo and deposit	60	7	67
chemo and suspension	0	2	2
Time range totals	81	197	278

Fig. 3: Excel Data Used to Conduct Tests

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