AMMONOIDEA: AN EXCEPTION TO THE TEMPERATURE SIZE RULE

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ABSTRACT: A phenomenon exists where the size of animals living in colder regions are larger than those living in warmer regions. Scientists call this phenomenon the temperature size rule. Although there is no conclusive explanation for why the temperature size rule occurs there is much research that has been done on it and some studies have found exceptions to the rule. This study looks at whether ammonoids, an extinct subclass of cephalopods, are an exception to the rule because they had unique growth patterns and evolved rapidly. A linear regression was run using width as the dependent variable and paleolatitude as the independent variable. The null hypothesis, which supports my prediction, was not rejected because of a large p-value and a small r^2 value. Because of the lack of relationship between the two variables, as well as other factors, I conclude that ammonoids are an exception to the temperature size rule. Future studies should look at specific ammonoid species and explore more variables such as depth.

Keywords: Temperature Size Rule, Latitude, Ammonoidea, Exception

Introduction

The temperature size rule (TSR) is a widespread phenomenon where the size of adult animals living in colder regions are larger than those living in warmer regions; average animal size increases as temperature decreases (Walters & Hassall, 2006). When it was first discovered in 1847, the rule was thought to apply to endotherms, warm blooded animals, because of a resistance to heat loss (Walters & Hassall 2006). However, about 80% of ectotherms, cold blooded animals, also followed this trend (Walters & Hassall, 2006). As widespread as it is there is no current explanation for why the TSR happens (Walters & Hassall, 2006). Among many possible explanations, one study found a tentative working hypothesis where temperature variation caused changes in diet which led to variations in size (Lee et al., 2015), and another found that size may be influenced by predation patterns at different temperatures (Manyak-Davis et al., 2013). Current databases allow for more extensive research, but many of these studies analyzing the TSR were conducted with regards to only one or two organisms. Consequently, there is still no conclusive explanation that applies to all species. In fact, some scientists believe there is no one reason for why it happens (Kingsolver et al., 2007).

Even though individual studies analyzed one or two organisms at a time, over the years a wide range of species have been studied with regard to the TSR. These organisms include grasshoppers (Walters & Hassall, 2006), pulmonate snails (Arendt, 2015), fish (Rijn et al., 2017), and other ectotherms. In these studies, some exceptions to the TSR have been found including aquatic ectotherms (Atkinson, 1995). By analyzing these exceptions to the TSR, and finding new exceptions to the rule, new information about its cause(s) may be found which is why it is important to search for new species that may be exceptions to the rule.

Cephalopods are a very diverse class of marine animals that includes squids, octopuses, and nautiloids, which look like octopuses with curved shells covering most of their body. Some species of common Cephalopods were studied in one project and seem to follow the TSR (Rosa et al., 2012). However, one extinct subspecies of Cephalopod has not been studied and may be an exception to TSR. Ammonoids were marine animals with soft bodies and external shells similar to current day nautiloids (Moriya, 2015). Studies concerning ammonoid ecology are ongoing, but there is evidence that they lived near the ocean floor and ate aquatic organisms such as plankton (Moriya, 2015). Their spiral shells, which grew throughout their entire life and contained chambers, are thought to have helped the animals regulate their buoyancy (Arai & Wani, 2012). Because their shells grew along with their bodies, ammonoid size is easily measured using their shells (Arai & Wani, 2012). Ammonoid growth was done in four steps, and the characteristics caused by this growth vary greatly between ammonoid species (Arai & Wani, 2012). This implies that their growth is independent of patterns such as the TSR. Also, ammonoids evolved rapidly (Moriya, 2015). If ammonoids were diverse and able to adapt quickly to their environment, then whatever factor, or group of factors, influence the TSR may not have applied to them. Thus, I suggest that ammonoids may not follow the TSR because of their unique growth methods and rapid evolution.

My hypothesis is that ammonoids, as a subclass, are an exception to the TSR. In this research project, I predict that ammonoids will not follow the common trendline of the TSR, showing that they are an exception to the rule. If ammonoids are an exception to the rule, then more research into their species may help provide other explanations for why the TSR occurs. According to the Paleobiology Database, the most occurrences for the subclass Ammonoidea are from the Cretaceous Period (PBDB, 2017), so this study will focus on the subclass Ammonoidea from the Cretaceous period.

Materials and Methods

Data on species, age, and location were downloaded from the Paleobiology Database on October 18th, 2017 using the parameters Ammonoidea and Cretaceous. Occurrences that slightly overlapped the Jurassic were included to ensure all Cretaceous occurrences were accounted for. Data on shell width were downloaded from fossilworks.org on October 25th, 2017 and added to the occurrence data. The absolute value of the midpoint of latitudinal range was used to represent temperature since it indicates distance from the equator.

The accompanying file shows the three columns which were used to run the statistical test. A linear regression was run in Excel using width as the dependent variable and latitudinal range as the independent variable. The significance level was chosen as $\alpha = 0.05$. For the linear regression, my research hypothesis was that the relationship between ammonoid size and latitude would be negative rather than the positive relationship shown by the TSR. My null hypothesis was that there would be no relationship at all between the two variables.

Results

The linear regression generated a p-value of 0.1 which means that my results had a 10% chance of being random, and an R^2 value of 0.003 which means that the difference in latitude is only responsible for 0.3% of the variation in size. Thus, I failed to reject my null hypothesis that there is no significant relationship between temperature and size and subsequently rejected my research hypothesis that the relationship would be a negative slope. This statistical test supported my prediction that ammonoids are an exception to the TSR; there is no significant relationship between ammonoid size and latitudinal range. Figure 1 shows my graph of the data for size and latitude along with a linear trend line. This almost horizontal trend line illustrates that there is no relationship between size and latitude.

Discussion

In my results, the p-value was very large and the R^2 value was very small, causing me to accept my null-hypothesis. Because I did not reject my null hypothesis, I concluded that ammonoids are an exception to the TSR. If ammonoids had followed the TSR, I would have seen a steeply positive slope, showing a relationship where size decreased the closer it got to the equator. As shown in Figure 1 and explained in the Results section, I did not get these results; the linear regression I ran showed a trend line with a slope of 0.0029, which is almost completely

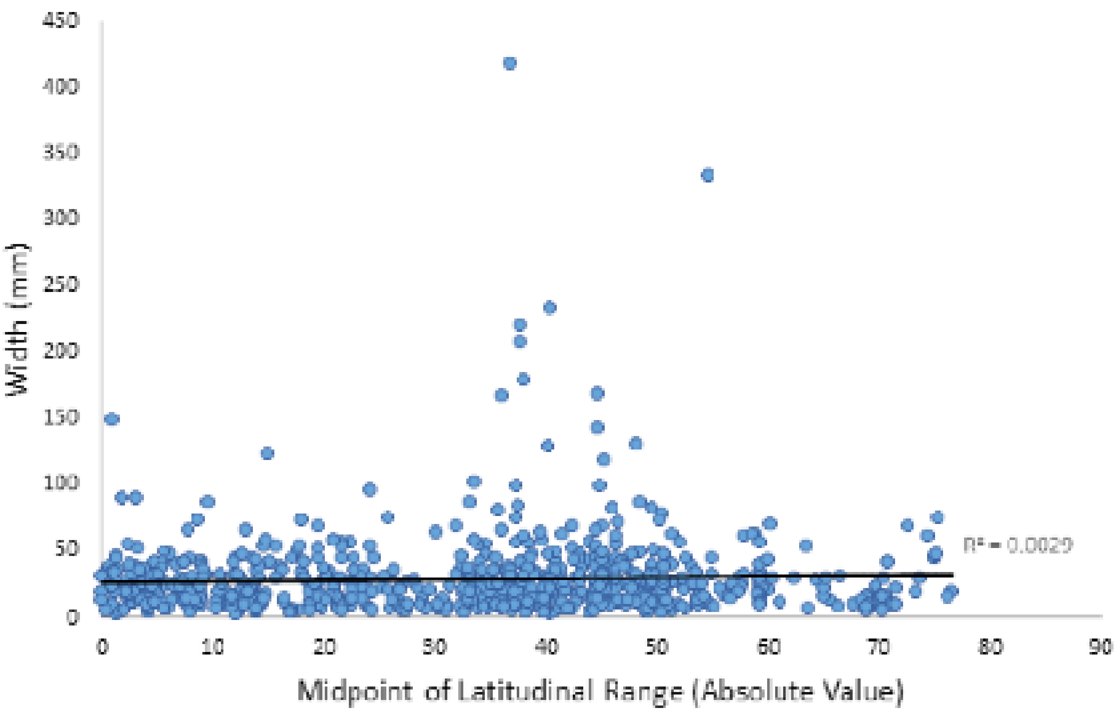

Figure 1. Lack of significant correlation between width (mm) of Ammonoidea shells and the midpoint of their latitudinal range (absolute value). (Linear regression, P = 0.1, and R^2 = 0.003).

flat. Because the results show no significant relationship, positive or negative, between latitudinal range and size, ammonoids must be totally independent of the TSR and exceptions to the rule.

If we take into account differences in ocean circulation during the Cretaceous Period, it is even more impressive that there is no relationship between latitude and size. According to one study, during the Cretaceous Period, strong ocean currents greatly influenced where species were located and wide circulation patterns caused a severe differentiation between temperate and arctic waters (Gordon, 1973). I would expect my results to have an even steeper positive trend line if ammonoids followed the TSR because the severe difference between warm and cold water should have caused a dramatic difference in shell size. As seen from the results, that is not the case, which all the more supports ammonoids being an exception to the TSR.

As I explained in the Materials and Methods section, I represented temperature using the paleolatitude of the occurrences. I used latitude to portray water temperature because it seemed like a straightforward way of representing it and had been used in other studies (Rosa et al., 2012). In fact, Bergmann's Rule, another version of the TSR, compares body size to latitude (Angilletta & Dunham, 2003). Nevertheless, latitude might not be the best representation of water temperature when analyzing aquatic organisms because aquatic environments are impacted by many factors such as the weather, sea level, atmospheric temperature (Yin, 1988), and depth. Depth has major implications for the size of the animals. In fact, Rosa et al. states that, in general, the deeper the animal, the larger its size (Rosa et al., 2012). When latitude has been used in other studies to represent water temperature the studies occurred in shallower environments (Rosa et al., 2012), but my study included fossils from every depth. Depth has even bigger implications for ammonoids because many species of Ammonoidea are bottom dwelling animals (Moriya, 2015). This possible misrepresentation of temperature may have impacted my results and should be considered when analyzing my data.

Another related matter I would like to bring up is the outlying occurrences shown in Figure 1. Between 30 and 60 degrees, especially around 40 degrees, there are a number of occurrences that are far above the average size. It would appear that a large number of ammonoid occurrences that are from temperate regions are larger than those in tropic and polar regions. If this is true, then ammonoids definitely do not follow the TSR.

Limitations and Future Work

Future studies should take into account more factors than just latitude in representing water temperature when considering ammonoids. Also, rather than generalizing the data and using each species once, future studies should analyze ammonoid species individually to see if there are trends in some species and not in others. I think that future studies should additionally include other measurements of size. I included width as a representation of shell size, but height and length could be added to provide a more accurate representation of size. Lastly, research should be done by dividing the latitude of ammonoid occurrences into different bins rather than using latitude as a continuous variable. They should look into whether ammonoids are actually larger in temperate regions, or whether there is a difference in size between the Northern and Southern hemispheres.

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