

**Can changes in the Larval Developmental Modes of *Olivella*
in the Caribbean Neogene be used as a reliable
productivity proxy?**

-

John H. Wilbur III
Washington and Lee University
Bachelor of Science in Geology
Senior Thesis

Introduction:

We do not understand if it is environmental or ecological change that drives evolution. (Vermeij 1986, Jablonski and Sepkoski 1996, Jablonski 2003, Jackson and Erwin 2006). For a long time paleontologists have been limited in their ability to make broad, ecological inferences about the fossil record because of the lack of ecological context; ecological context here meaning both the biotic and physical properties of the system.. By accurately reconstructing the past environment and examining the fossil record, we can attempt to determine quantitatively which has a greater effect on macroevolutionary trends.

The Closure of the Isthmus of Panama functions as an excellent natural experiment because of our knowledge of the geologic record and the changing environment that influence the temperature, salinity, nutrients, and productivity of each area. The modern day Caribbean resembled the Pacific before the Closure of the Isthmus of Panama. The present day Pacific can serve as an analogue for the ancient Caribbean (Erwin et. al 2011). Extending this thought, life modes that are common within the modern Pacific should be present in the ancient Caribbean (Fortunato 2004). This provides an opportunity to examine how evolution was influenced by the changing productivity within each environment. The Closure of the Isthmus of Panama provides a clear study area in which to test whether environmental or ecological change drives evolution. The two environments generated by the closure provide an excellent opportunity to see how organisms evolve in response to their environments. In this paper, I will be focusing primarily

on the physical changes in the environment, specifically planktonic productivity. The fossilized remains of gastropods, bivalves and bryozoans provide an opportunity to study and track these changes.

The closure of the Isthmus of Panama, and the effects of that closure, are recorded in the geologic record (Allmon 2001, Henderson et al. 2002, O'Dea et al. 2007). Deep-water circulation between the Caribbean and the Pacific halted no later than 3.6Ma and shallow water circulation no later than 3.0Ma (Allmon 2001). The blockage of water flow had a major impact on the Caribbean. The Caribbean lacks upwelling, is relatively nutrient poor, and has much smaller seasonal variability in sea surface temperature (Allmon 2001, Todd et al. 2002, O'Dea et. al 2007). The Pacific possesses inter-annual and seasonal variations along with changes in temperatures and upwelling that promotes planktonic feeders (Allmon 2001, Todd et al. 2002, O'Dea et. al 2007). The western direction of the trade winds enable the cooler nutrient-rich water to cycle to the surface and replace the warmer and nutrient-poor water in the Pacific. Environmental changes such as the lack of nutrients have been known to drive distinct evolutionary events (Fortunato 2004, Nutzal et al. 2006, O'dea and Jackson 2009, Leonard-Pingel et. al 2012,).

Fossils are used to better understand the past environment by comparing the fossils to their living analogues. This allows assumptions to be made about the past environment. The newly formed Caribbean changed benthic communities and promoted expansion of coral reefs (Todd et al. 2002, Travis 2007, Smith and Jackson

2009, Leonard-Pingel et al. 2012). The increase in reefs and sea grasses in the early Pleistocene due to the decline in productivity in the Caribbean was a major factor in the turnover of bivalve assemblages (Leonard-Pingel et al. 2012). In particular, gastropods, bivalves and bryozoans can help better construct past environments by comparing the past organisms to their modern analogues in the western Caribbean. Currently bryozoans (O'Dea and Jackson et. al 2009) and bivalves (Travis 2007) are the best understood within the Panama system. (Todd et al. 2002, Nutzel et al. 2006, Smith 2007, O'Dea and Jackson et. al 2009, Smith and Jackson 2009). In particular, the extreme turnover of the American scallop shows a dramatic change in scallop diversity in the southwest Caribbean over the past 12 Myr but not in the eastern Pacific (Travis 2007, Smith and Jackson 2009). The species that did survive in the Caribbean had larger eggs and shorter larval durations than those that went extinct (Smith et al. 2003, Travis 2007, Smith and Jackson 2009). These changes can be directly tied to a decrease in production and a lack of nutrients necessary for planktotrophic organisms to survive (Allmon 2001, Nutzel et al. 2006, Kirby and Jackson 2009, Leonard-Pingell et al. 2012). These traits in bivalves are extremely similar to those in gastropods. Thus we can infer how gastropods were developing at the same time. Due to their similarity in larval development, gastropods make an ideal candidate to further reinforce the changing environment during the closure of the Isthmus.

By examining the gastropods before, during, and after the closure of the Isthmus of Panama, I hope to provide support for using gastropods as another

reliable proxy for environment. Gastropods are numerous, present in many types of environments and a common fossil found in oceanic environments (Allmon 1988). Gastropods keep their larval stage (protoconchs) throughout their adult lives and therefore the larval modes are preserved in the fossil record.

Gastropods are divided into two distinct larval categories: 1) Planktonic or suspension feeders and 2) non-planktonic, which includes both lecithotrophic and direct developers (Allmon 1988, Fortunato 2004, Nutzel 2014). In gastropods, the type of development can be directly measured in the size of the protoconch, or larval shell. Adult gastropods retain this development in the size and shape of their protoconchs. The diameter of the embryotic protoconch and number of whorls depends on the egg yolk and egg size (Allmon 1988, Van Osselear 1999, Fortunato 2004, Nutzel et al. 2006, Nutzel 2014). The number of whorls within the protoconch denotes the amount of time spent within the water column: the longer the time, the more whorls the protoconch is likely to have. Planktonic gastropods survive by preying upon plankton and other primary developers in the photic zone. This allows them to possess a smaller egg size because they are able to feed within the water column. Lecithotrophic gastropods have larger egg size because they are only able to survive for a limited time through suspension feeding. They spend shorter amounts of time in the embryotic stage and quickly metamorphose into their juvenile forms. Direct developers cannot feed within the water column and require a larger egg yolk than lecithotrophic and planktotrophic developers. They must

metamorphose into their juvenile forms before they can begin feeding (Fortunato 2004, Nutzel et al. 2006).

This study seeks to look at fossil data of the gastropod *Olivella* in order to understand the macro-evolutionary trends since the closure of the Isthmus of Panama. The number of modern non-planktonic neogastropods in the Caribbean is significantly higher than in the Eastern Pacific (Fortunato 2004) due to the decrease in productivity in the Caribbean after the closure of the Isthmus of Panama, we predict that non-planktotrophic feeders will survive preferentially because of the changing environment. This change may appear after a 'lag time' of an estimated 1-2Ma. This lag time is predicted because the environment would not change suddenly when the Isthmus closed. Instead, the Caribbean would adjust and reach its new equilibrium slowly over several million years. During this lag time, planktotrophic and non-planktotrophic gastropods could coexist in the Caribbean (O'Dea et al 2007). It is after this time the effects of the closure were seen throughout the Caribbean. Thus there is an expected gap before planktonic gastropods are selected against in the Caribbean. I expect to see that if the size of the protoconchs increases with time in the Caribbean then evolution in response to the changing environment is responsible for this change.

Methods:

The gastropods used in the analysis were from 15 sites collected from eastern Panama. The sample sites were determined by possessing specimens with five or more viable protoconchs. Viable meaning that the protoconchs were intact and able to be examined under the Scanning Electron Microscope. The collections were made as part of the Panama Paleontology Project (PPP) and build on previous studies of stratigraphy, age dating, paleoenvironments, and faunal composition (Coates et al. 1992, 2003, 2004, 2005; Collins 1993, 1996; Collins et al. 1995, 1996 a,b; Coates 1999a; Jackson et al. 1999; Aubrey and Beggren 1999; McNeill et al. 2000; O'Dea et al. 2007; Johnson et al. 2007; O'Dea and Jackson 2009; Smith and Jackson 2009). Samples are naturally time-averaged, providing a more accurate picture of the community composition through time (Kidwell and Flessa 1995; Kowalewski et al. 1998; Kidwell 2001, 2002a). Samples were processed by repeated freezing and thawing in Glauber's salt solution, which breaks down the consolidated sediment matrix while reducing damage to fragile fossils (Surlyk, 1972). After the freezing and thawing, the samples were washed on a 2mm sieve and sorted to genus following the classification and nomenclature of Todd (2001a).

For the analysis of protoconch size changes, I choose the genera *Olivella*. I attempted to choose 10 specimens from each faunule selected. For faunules with more than 10 specimens, each sample was randomly selected by hand and examined underneath an optical microscope for the best protoconch. The samples

were selected based off the most intact and clean protoconchs from the specimens available. After selecting the specimens, each individual gastropod was placed in a separate container and labeled clearly. The *Olivella* were examined using a Scanning Electron Microscope (SEM) to provide a clear picture of the protoconchs (Figure 1). The SEM's internal software was used to provide an accurate measurement of the diameters of the first whorl of each protoconch.

The number of whorls of the embryotic protoconch was counted using Nutzel's method (Nutzal, 2014). *Olivella* lacks the common abrupt transition between the teloconch and protoconch that many other gastropods possess. After viewing all of the samples, the end of protoconch II was determined by searching for the end of the micro-pustular surface and the beginning of the filament channel. The true transition lies somewhere between the transition of the micro-pustular to smooth accretionary teloconch and the beginning of the filament channel. Due to the micro-pustular surface closely resembling weathering, the end of the protoconch was determined to be at the beginning of the filament channel (Figure 2).

The diameters and volutions were inputted into R to create bin plots comparing diameter size to age and volutions to age. Spearman's rank correlation and Kruskal-Wallis rank sum test determined if the change in times were significant. The relationship between the maximum diameter of the embryotic protoconch over the number of volutions of the protoconch II was recorded. Using the guidelines in

Jackson, direct developers were assumed to have <1.5 whorls, lecithotrophic /planktotrophic were between 1.5 and 3.0 whorls and planktotrophic possessed >3.0 whorls (Jackson et al. 1996).

Results:

Embryonic Shell Diameters

There were a total of 129 diameter measurements taken. A Kruskal-Wallis rank sum test shows a significant increase in the median size in the diameter of the embryonic protoconch through time, which increases from 225nm in bin 1 (age range) to 300nm in bin 3 (age range). Diameter of the embryonic protoconch is more variable in Bin 2 than bin 3. However, Bin 3 has a tighter set of constraints that are, on average, higher than bin 2.

Bin 2 contains the greatest total number of specimens (5-3Ma) while bin 1 (9.6-5) possessed the fewest number of samples. There is a distinct gap between 9.6 and 6.35 Ma, but the environment remained similar throughout this period. This should mean there are similar species throughout these times.

Protoconch Volution Data:

There were a total of 76 volution measurements taken. A Kruskal-Wallis rank sum test shows a significant decrease in the median volutions of the protoconchs through time. There is a significant degree of variability within the

modern samples with some samples only having 1 whorl and others possessing as many as 2.5.

Discussion:

We know today that the number of non-planktonic neogastropods in the Caribbean is significantly higher than in the Eastern Pacific (Fortunato 2004). The species that did survive in the Caribbean had larger eggs and shorter larval durations than those that went extinct (Smith et al. 2003, Travis 2007, Smith and Jackson 2009). Gastropods preserve the effects of the changing environment within their larval stage in both their shell diameters and the number of volutions.

The diameter data for the gastropods shows a trend of increasing median diameter through the Closure of the Isthmus. Based on Fortunato's modern analogues, direct developers possess larger protoconchs. (2004). This data suggests that there is an increase in direct developers through time, which was expected with a decrease in planktonic productivity in the Caribbean. There appears to be a gradual selection against planktotrophic to direct developers in Bin 2. There is thought to be a mixture of planktotrophic and lecithotrophic protoconchs that would have coexisted during the final closing of the Isthmus. Due to the general trend of increasing protoconch I diameters, this allows for the diameter of *Olivella* to be used as reliable productivity indicators for the environment

The whorl data is not as reliable due to the difficulties determining where the protoconch ended. The number of whorls within the protoconch denotes the amount of time spent within the water column: the longer the time, the more whorls the protoconch is likely to have (Fotunato 2004, Nutzal et al. 2006). On the samples collected, there appears to be a general trend of less volutions over time, which supports the decreasing productivity of the Caribbean. However, there is a very high range of variability in the most recent samples. This might represent that the number of volutions is indicative of the individual species rather than the genus.

Conclusion:

In future studies, I would like to examine a larger sample pool, especially in gastropods from before the Closure. Future studies need to compare the diameter data against other genera of gastropods in order to see if this trend is common across all gastropods. I suspect that the whorl data would be much easier to determine using a gastropod other than *Olivella*. In addition, the whorl data needs to be further worked on to determine what is the cause of the high degree of variability in bin 1.

Figures and Tables:

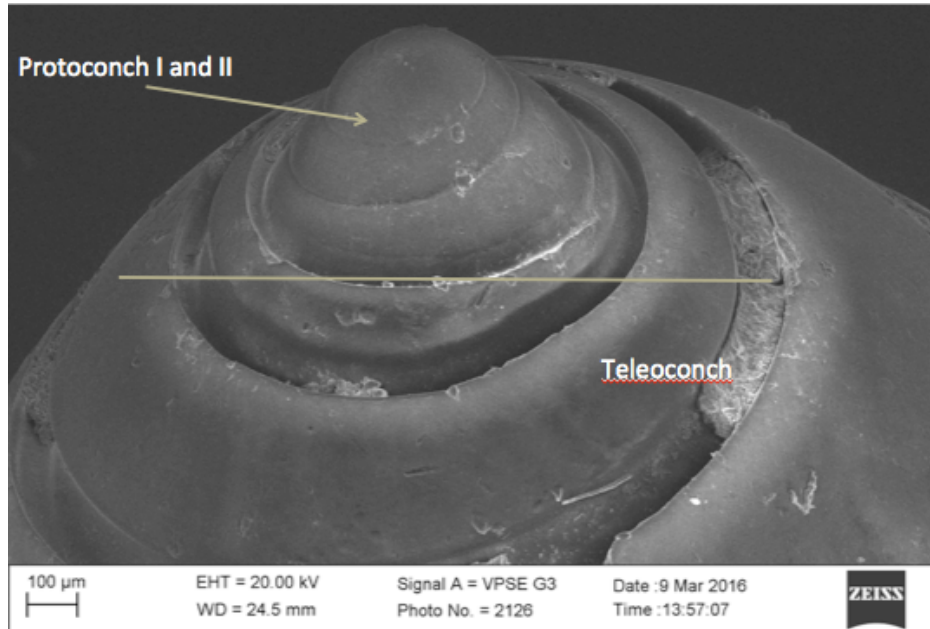


Figure 1: Picture of both the Protoconch I and II and the transition to the Teloconch in an *Olivella* sample.

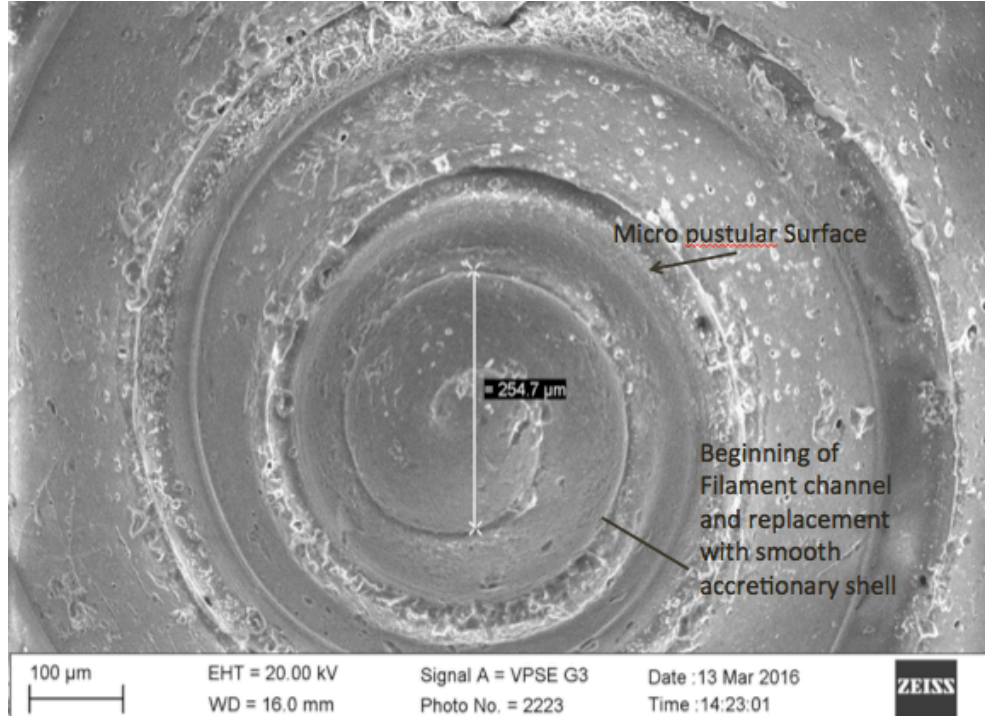


Figure 2: Picture of both the embryonic protoconch measure from the first whorl and the end of the juvenile protoconch. The true transition between the protoconch II and teloconch is somewhere in between the micro pustular surface and the beginning of the filament channel. However, during the data collection the end of the protoconch II was determined to be the beginning of the filament channel.

Age (Ma)	1.4	1.6	2.05	3.55	4.25	6.35	9.6
# of Samples	8	30	14	48	15	4	9
Mean Diameter (nm)	324.25	289.65	295.69	294.79	288.42	336.33	214.23

Table 1: The mean change in diameters throughout time. The large increase in size from 6.35Ma is thought to come from the low amount of samples present within that faunule. The degree of variability from 3.55 to 4.25 signals a high variability in environments during the Closure of the Isthmus.

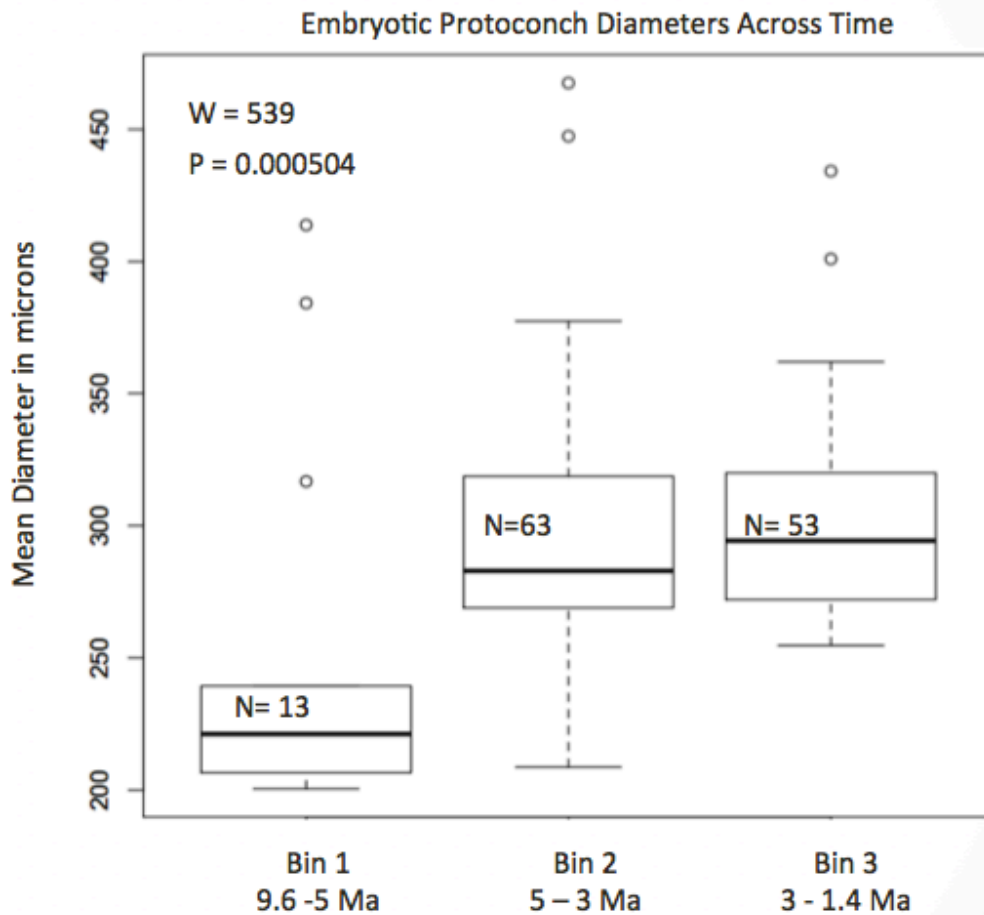


Figure 3: The analyzed faunules ranging in age from 9.6Ma to 1.4Ma. The most complete data set comes from the Upper Lomas with 20 samples. The results were compiled in to a bin plot with bin 1 representing all samples from 9.6-5Ma, bin 2 representing samples from 5-3Ma, and bin 3 representing 3-1.4Ma. The p value represented here shows a significance difference in the range of shell diameters. The P-value comes from a Kruskal-Wallis rank sum test ran in R.

Age (Ma)	1.40	1.60	2.05	3.55	4.25	6.35	9.60
# of Samples	8	16	14	43	11	1	8
Mean Volutions	1.69	2.19	2.35	1.92	2.18	2.25	2.47

Table 2: The mean change in volutions throughout time. The variations of size are thought to come from the small sample sizes within some of the faunules. There is a general trend of decreased whorl counts through time; however, the difference is not significant.

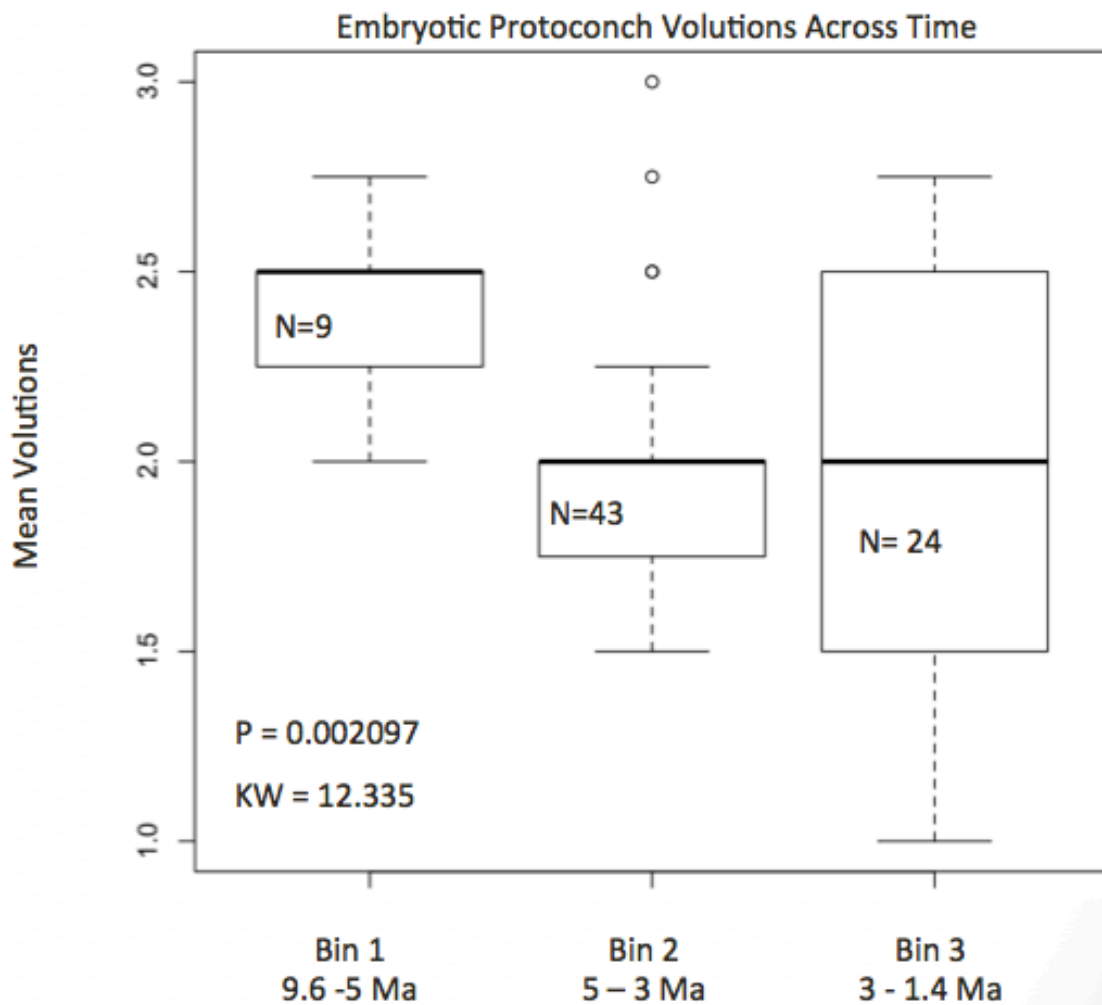


Figure 4: The analyzed faunules ranging in age from 9.6Ma to 1.4Ma. The results were compiled in to a bin plot with bin 1 representing all samples from 9.6-5Ma, bin 2 representing samples from 5-3Ma, and bin 3 representing 3-1.4Ma. The p value represented here shows a significance difference in the range of shell volutions. However, these results are skewed because of the much smaller sample sizes within each bin. The P-value comes from a Kruskal-Wallis rank sum test ran in R.

Literature Cited:

Allmon, W.D. 2001. Nutrients, temperature, disturbance, and evolution: a model for the late Cenozoic marine record of the western Atlantic. *Palaeogeography, Palaeoclimatology, Palaeoecology*. 166 (2001) 9-26

Allmon, W.D. 1988. Ecology of Recent Turritelline Gastropods (Prosobranchia, Turritellidae): Current Knowledge and Paleontological Implications. *Palaios*. V. 3: 259-284.

Erwin, Douglas H, Marc Laflamme, Sarah M. Tweedt, Erik A. Sperling, Davide Pisani, and Kevin J. Peterson. 2011. The Cambrian Conundrum: Early Divergence and Later Ecological Success in the Early History of Animals. *Science*. Vol 334, Issue 6059: 1091-1097.

Fortunato, Helena. 2004. Reproductive strategies in gastropods across the Panama seaway. *Invertebrate Reproduction and Development*. 46:2-3 (2004) 139-148.

Jablonski, D. 2003. The interplay of physical and biotic factors in macroevolution. Pp. 235–252 in L. Rothschild and A. Lister, eds. *Evolution on planet Earth*. Elsevier, Amsterdam.

Jablonski, D, and J. J. Sepkoski Jr. 1996. Paleobiology, community ecology, and scales of ecological pattern. *Ecology* 77: 1367-137.

Jackson, J. B. C., A. F. Budd, and A. G. Coates, eds. 1996. *Evolution and environment in tropical America*. University of Chicago Press, Chicago

Jackson, J.B.C and D.H. Erwin. 2006. What can we learn about ecology and evolution from the fossil record? *Trends in Ecology and Evolution*. 21: 322-328.

Kirby, M. X., and J. B. C. Jackson. 2004. Extinction of a fast growing oyster and changing ocean circulation in Pliocene tropical America. *Geology* 32:1025–1028.

Leonard-Pingel, Jill, J.B.C Jackson, and Aaron O’Dea. 2012. Changes in bivalve functional and assemblage ecology in response to environmental change in the Caribbean Neogene. *Paleobiology*, 38(4):509–524.

Nutzell, Alexander, Oliver Lehnert, Jiri Fryda. 2006. Origin of planktotrophy-evidence from early molluscs. *Evolution and Development*. Jul-Aug;8(4):325-30.

Nutzell, Alexander. 2014. Larval ecology and morphology in fossil Gastropods. *Paleontology*. Vol. 57, Part 3: 479–503.

O'Dea, A., J.B.C. Jackson, H. Fortunato, J.T. Smith, L. D'Croze, K.G. Johnson, and J.A. Todd. 2007. Environmental change preceded Caribbean extinction by 2 million years. *Proceedings of the National Academy of Sciences*. USA 104: 5501-5506.

O'Dea, A., and J. B. C. Jackson. 2009. Environmental change drove macroevolution in cupuladriid bryozoans. *Proceedings of the Royal Society of London B* 276:3629-3634.

Smith, J. T, N. Nakanishi, and J. B. C. Jackson. 2003. Late Neogene divergence in life span of scallop larvae across the Isthmus of Panama. *GSA Abstracts with Programs* 35(6):318.

Smith, J. Travis and Jeremy B.C. Jackson. 2009. Ecology of extreme faunal turnover of tropical American scallops. *Paleobiology*. 35(1): 77-93.

Todd, J.A. 2001a. Identification and taxonomic consistency in Neogene marine biota of tropical America. <http://nmita.geology.uiowa.edu/mollusc/molluscintro.htm>

Travis, James Smith. 2007. Ecology and environments of an extreme faunal turnover in tropical American Scallops. Unpublished. 1-94.

Todd, J.A., J.B.C. Jackson, K.G. Johnson, H. Fortunato, A. Heitz, M. Alvarez, and P. Jung. 2002. The ecology of extinction: molluscan feeding and faunal turnover in the Caribbean Neogene. *Proceedings of the Royal Society of London B*. 296:571-577.

Van Osselear, C. 1999. Counting shell whorls. Remarks. *Labortoire de Bio-Ecologie*. APEX 14(2):33-42.

Vermeij, G. J., and E. J. Petuch. 1986. Differential extinction in tropical American molluscs: endemism, architecture, and the Panama land bridge. *Malacologia* 27:29-41.