#### MSc Research Project Report, Biology, Leiden University

#### **Small mollusks and big cooling**

Molluskan response to the Eocene-Oligocene Transition

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#### **General Background**

The early Eocene was a relatively warm period during with large numbers of tropic and warm-water biotas. Global surface temperature decreased through the Middle Eocene and into the Late Eocene by 4 to 5 degrees (Prothero et al, 1994). At the end of the Late Eocene a much more rapid cooling took place, the Eocene Oligocene transition (EOT). During the EOT a stepwise increase in  $\delta^{18}$ O occurred (Lear et al, 2008). The buildup to the most positive oxygen isotope values took two steps, each of 40 kyr and with a 200 kyr interval. The first increase in  $\delta^{18}O$  was caused by cooling and the second by an increase in ice volume and a drop in sea level. After the EOT,  $\delta^{18}$ O had increased by 1‰ and the temperature had dropped by 4 degrees (Pearson & Coxall, 2007). The Eocene Oligocene boundary (EOB) itself is defined by the extinction of the foraminifer Hantkeninia, which went extinct during the 200 kyr interval (Berggen et al, 1995). Also, re-organization of continents coincide with changes in ocean circulation and the thermal isolation of Antarctica(Pearson & Coxall, 2007). These changes might have caused the increase in oceanic mixing and higher nutrient availability. During the Eocene several extinction events can be distinguished, one at the end of the Middle Eocene, one during the Late Eocene and one during the EOT (Hansen et al., 1987). This research focuses on the EOT extinction. Some of these EOT extinctions have already been described, for example the extinction of certain planktonic foraminifera (Cotton & Pearson, 2011) and certain nanofossils (Dunkley Jones et al, 2008). The response of mollusks to the EOT however has not been extensively studied.

### **Specific Background**

Mollusks provide a unique insight into environmental conditions due to their specific life habits, feeding and reproduction (Hansen et al., 2004). However, little detail is known about their exact response during the EOT. Few complete shallow water EOT sections exist due to the sea level fall, which is associated with an increased ice volume in Antarctica, which led to subsequent erosion. Deep-water sections are even more rare or have not been investigated for mollusks. Additionally, many of those that do exist do not contain a well preserved mollusk fauna. The mollusk record across the EOT therefore remains patchy with the majority of studies based on North American localities (Prothero et al, 2003). In 2009, three drill sites, part of the Tanzania Drilling Program (TDP), span the EOT and contain a diverse, well-preserved deep-water mollusk fauna. The Tanzania Drilling Project is an enterprise to recover and investigate Cretaceous-Paleogene sediments for climatic and paleontological research (Bown et al., 2008). The mollusk fossils from these three cores have been used in this project to reconstruct mollusk response to the EOT at high resolution (Bown et al., 2008).

### **Methods**

During the Tanzanian Drilling Project three sites (11, 12 and 17, figure 1) were drilled to recover EOT sediments (Pearson et al., 2008). They were within 3 kilometers from each other (TDP 11 — UTM 37L; 560250 8983211; TDP 12 — UTM 37L; 560222 8981309; TDP 17 — UTM 37L; 560539 8984483; Nicholas et al., 2006, For detailed information on the TDP cores; Nicholas et al, 2006.) The lithology of these sites consists of clay-rich, hemipelagic sediments which contain exceptionally well preserved calcareous fossils. The cores contain a wide variety of mollusk shells. Apart from the mollusks, the site has already been extensively studied. Pearson et al (2008) studied the same cores (11, 12 and 17) and they have generated an age model using biostratigraphic datums and geochemical tie-points. (5) This model can be used to look at the mollusk ranges and tie them to climatic events.



*Figure 1. The location and geological maps of the Tanzanian Drilling Project EOB sites 11, 12 and 17. Additional sites in the area are also shown (picture from: Cotton, 2011)*

The hemiplegic clays were washed down with a 63 micrometer sieve and the residues dried (Pearson et al, 2008). The samples from the TDP cores were packaged in plastic bags containing an identification code (TDP core section). These samples were filtered using a 500 micrometer sieve. Using a microscope, any present fossil mollusks were transferred to a plastic microscopic slide. The resulting 188 fossil depth assemblages were sorted into different morphotypes and, if possible, identified up to genus level. The

identifications were made under the guidance of F.P. Wesselingh (Naturalis). No literature exists on Paleogene deep-water mollusks to my knowledge and identifications were not able to carry out to species level. Counts of mollusks through the cores were carried out.

## *Data analysis*

A sample rarefaction (figure 10, addendum) was computed using PAST ver. 2.17c and this revealed that the sample sizes were too small; too small to get a comparison between depths, (data not shown). Using the rarefaction, minimal sample size should be at least 100. To reach this amount, data was binned for each 10 meter composite depth (mcd). This resulted in nine consecutive samples ranging from 40 to 120 mcd.

# *NMDS*

On the species x 10mcd sample database we first performed a non-metric multidimensional scaling (NMDS). The nine binned samples were analyzed using PAST, using the Bray-Curtis distance measure (df=8). Depth in the core and the Oxygen isotope as an indicator for temperature were used for the environmental variables.

## *Total mollusk abundance*

Total abundance of mollusks was plotted for each 10mcd bins

# *Biodiversity*

To account for the possible change in biodiversity two diversities were measured with the x10 mcd sample database; the standing diversity (amount of mollusk species found at each depth interval) and the range-through diversity (amount of mollusk species found at each depth interval + species that are present both before and after the interval). However, due to unequal sample size, no additional statistics were possible.

### *Functional groups, ANOVA*

To investigate functional group turnover, the mollusks were grouped together. This resulted in five functional groups (chemosymbiont, herbivore detrivore, parasite, carnivore and filter feeder) and one rest group (unknown). These groups were then compared to each other and their combined total was set at 100% for each of the nine binned samples. Afterwards, three groups would be compared to each other; the three Eocene samples (100-120), earliest Oligocene (70-90) and later Oligocene (40-60) and for each functional group. Comparing these two factors, depth and functional group, was done using an Analysis of Variance (ANOVA)(H0; no interaction between depth and functional group). To analyze the interaction, the interaction table was calculated. This was all done using IBM SPSS Statistics 21. *Functional groups, species details*

Seven highly abundant species were selected for a detailed analysis. These seven contain four herbivore detrivore species, two carnivore species and one filter feeder. They were adjusted for the amount of sediment sampled, so they now are all 'specimen found per centimeter composite depth'. They were combined with the  $\delta^{18}O$  isotope data from the same cores (Lear et al, 2008), which is the  $\delta^{18}O$  response over the EOT. Using this response, the isotope stepd (temperature drop and the sea level drop) could be shown.

### **Results**

### **1-species identified**

The three TDP cores conveyed a total of 188 depth samples with 89 mollusk morphotypes, 20 bivalves and 69 gastropods. A total of 58 gastropod and 19 bivalves species were identified.

#### **2-Mollusk reaction to the EOT**

The depth binned data with three Eocene data points (mcd 120-100) and six Oligocene, subdivided in three earliest Oligocene (mcd 70-90) and three later Oligocene data points (mcd 40-60), reveal a grouping of the three periods (figure 2). On the right, the three Eocene samples are grouped together. On the top left, the three earliest Oligocene are close together and on the bottom left the later Oligocene. This first data indicates that there is a response by the mollusks during the EOT. The stress value of 0,08088 indicates a good representation.



*Figure 2. Non-metric multidimensional scaling (NMDS) with three groups, Eocene, Early Oligocene and Late Oligocene. The two variables are DEPTH (40, 50, 60, ..., 120 mcd) and ISOTOPE (average* δ<sup>18</sup>O at *each depth; -2.35, -2.30, -2.17,… -2.98). The three groups can be sorted; Eocene in the right, Early-Oligocene in the top left and Late Oligocene in the bottom left. The stress value is 0,08088. (PAST output)*

## **3-Total number of specimens**

The total number of mollusks found is shown in figure 3. The amount of mollusks that were found differs over time, or mcd. From 130 to 200 mcd the amount of specimens found was extremely low, at around 10 specimens every ten meters or one specimen per meter. After 130 mcd the mollusks became more abundant, rising to around 300 per 10 meters. Around the EOB I found less specimens, just over one hundred. Immediately after the EOB they returned to more than 300 specimens. At 60 mcd the amount peaked at approximately 550 specimen. However, due to unequal sampling, no statistics were possible.



*Figure 3. Graph showing the total amount of Mollusks found in different depth intervals (10 mcd). The red line indicate the EOB, with the Oligocene on the left and the Eocene on the right. (Excel output)*

### **4-Diversity**

Figure 4 (left) depicts the Mollusk standing biodiversity during the EOT. A first glance reveals a slight peak at 60 mcd and a minor decline at 100 mcd, the EOB (102 mcd). The outer data points, at 120 mcd and 40 mcd are also lower. The highest biodiversity was found at 60 mcd, with just over fifty mollusk species. However, the biodiversity shows no discernable pattern over time and the number of species is consistently over 30 and averages around 45 different species. Figure 4(right) shows the range-through diversity. This data shows a peak at the center, at 80 mcd and a gradual decline towards the ends, 40 mcd and 120 mcd. The range-through diversity shows no discernable pattern either.



*Figure 4. Graphs showing the total number of species found in different depth intervals (10 mcd), left is standing diversity, right is range through diversity. The red line indicates the EOB and the lower part is the Eocene and the top part the Oligocene. (Excel output)*

# **5-Response of functional groups**

The identified mollusk species were grouped into five different functional groups, based on their feeding strategies. The five categories are chemosymbiont (CB), herbivore detrivore (HD), parasite (P), carnivore (C) and filter feeder (F). The unidentified species compose the sixth category unknown (U). The Herbivore Detrivore group increase from 30 to 40 percent when it crosses the EOB (figure 5). This result is almost significant (p=0,051, figure 6, A) and is significant when we compare the Eocene with the Late Oligocene (p=0,034, figure 6, B). In contrast, the Parasite group plunges when it crosses the EOB (p=0,016, figure 6, C), dropping from 25 percent to just over 10 % in the early Oligocene and just under 10% in the later Oligocene. The filter feeders show little response over the EOB, but during the Oligocene they rise. This increase is almost significant (p=0,074, figure 6, D).



*Figure 5. Graphs showing the response of five functional groups of Mollusks during the EOT. The five functional groups are carnivore (C, Blue), chemosymbiont (Cb, green), filter feeder (F, brown), herbivore detrivore (HD, Purple) and parasite (P, Yellow). The last group is unknown (U, Red). The vertical red line indicates the EOB, with on the left the Oligocene and on the right the Eocene. Stars indicate a significant response(p<0.05) and circles indicate an almost significant response (p<0,10). Data is in percentages and binned for each thirty meters. (SPSS output)*



Based on estimated marginal means

\*. The mean difference is significant at the ,05 level.

b. Adjustment for multiple comparisons: Least Significant Difference (equivalent to no adjustments).

*Figure 6. Analysis of Variance (ANOVA) showing the comparisons between the depth intervals for each Functional Group. Almost significant differences are indicated with A (Hd difference between 10-12 and 7-9) and C (F difference between 7-9 and 4-6). Significant differences (<0.05) are indicated with B (Hd difference between 10-12 and 4-6) and D (P difference between 10-12 and 4-6). Data is binned for each thirty meters. (SPSS output)*

#### **6-Functional group response**

Seven highly abundant (>100 specimen) species, four from the herbivore detrivore group, two from the carnivore group and one from the filter feeder group, were examined in detail. They are all plotted next to the high resolution *ΔO₂ isotope record* (Lear et al, 2008) *to compare them with the events of the EOT. These events include the cooling period and the sea level drop.* Three of the herbivore detrivore species, both *Rissoa* species (1 and 4) and *Teinostoma* have a very similar pattern (figure 7, ABC). They are all present in the Eocene in relatively low numbers and only *Rissoa* spec. 1 is consistently present though the temperature decrease. It is only after the EOB that they start to become more abundant. The fourth HD species, *Bittium* has a dissimilar pattern (figure 7, D). They are present at deeper stratigraphic depths and they are highly abundant right before the EOB, during the main temperature decrease . After the EOB, they are still present, but their numbers have decreased dramatically.





*Figure 7. Bar charts showing the herbivore detrivore response to the EOT. Four different species are shown;* Rissoa *spec. 1 (A),* Rissoa *spec. 4 (B),* Teinostoma *(C) and* Bittium *(D). Bars show the amount of specimen found at different depths (corrected for depth interval) .The red line indicates the* δ18Ο *change over the EOT. The blue line indicates the EOB. The right orange square indicates the first isotope drop, associated with temperature drop and the left orange square indicates the second, associated with a sea level drop. (Excel output)*

*Kelliella*, a filter feeder, shows a similar pattern to the three HD species. It is present before the EOB and is abundant after. This increase does not occur immediately after the EOB however, but after the sea level drop. This delay is similar to delay found in the overall filter feeder group (figure 8).



*Figure 8. Bar chart showing filter feeder (F) response to the EOT. The depicted species is* Kelliella*. Bars show the amount of specimen found at different depths (corrected for depth interval) .The red line indicates the*  $\delta^{18}$ O *change over the EOT. The blue line indicates the EOB. The right orange square indicates the first isotope drop, associated with temperature drop and the left orange square indicates the second, associated with a sea level drop. (Excel output)*

The two carnivore species, *Limacina* and *Turridae*, also have different patterns over the EOT (figure 9). *Limacina* is very abundant before the EOB, during the temperature drop. They show a slow decline during the EOT. The other carnivore species, *Turridae*, is almost absent before the EOB, but right after the boundary they increase in numbers.



*Figure 9. Bar charts showing carnivore response to the EOT. Two different species are shown;* Limacina

*(A) and* Turridae *(B). Bars show the amount of specimen found at different depths (corrected for depth interval) .The red line indicates the* δ18Ο *change over the EOT. The blue line indicates the EOB. The right orange square indicates the first isotope drop, associated with temperature drop and the left orange square indicates the second, associated with a sea level drop. (Excel output)*

## **Discussion**

## **1-Biodiversity**

The EOT is well known for its rapid decline in global temperature. However, bottom water temperatures measured from  $\delta^{18}O$  of benthic foraminifera do not show such a dramatic shift and remain fairly constant, between 18 and 20°C (Lear et al, 2008). As the molluscs are also living in the bottom water could this be a reason that no decline in mollusk biodiversity was detected in this study. In contrast, calcareous nanofossils from the same cores did respond with a decline in biodiversity (Dunkley Jones et al, 2008). This might be due to the different living habitats of mollusks and the nanofossils. While the majority of the mollusks identified/found lived in the deeper waters, the calcareous nanofossils lived in the surface waters. The surface-waters are more susceptible to changing temperatures, and during the EOT the surface water temperature decreased by at least two degrees. (Lear et al, 2008). Previous research on mollusk responses to the EOT do show a correlation with temperature changes, but they are also shallow-marine molluscan faunas (Prothero et al, 2003).

## **2-early Eocene depletion**

Mollusk densities in the 130-200 mcd interval were low (figure 3). Possibly, deep marine mollusks had a very low presence in the area during this time period. In Baja California, Mexico and West coast of the United States they found mostly shallow-water mollusks from Paleocene through middle Eocene (Prothero et al, 2003). Their increase after 130 mcd, which coincides with the temperature drop of the EOT (Lear et al , 2008), is noteworthy. However, stable deep water temperatures could rule out a temperature-dependent explanation of this sudden increase in mollusk population. A possible rationalization of this increase in specimens might be an increase in nutrient availability due to ocean mixing and circulation changes (Pearson & Coxall, 2007).

# **3-Functional Group Turnover**

The Mollusk population shows a clear and significant turnover in some of their functional groups. The most noteworthy is the increase in the herbivore detrivore group. This group is the largest of them all, increasing from thirty to over forty percent of the total population. The detailed examination of some of the herbivore detrivore species indicates a different reaction of some species within the group. For instance, *Bittium* shows a different trend to the overall group response over the EOB; This species is abundant before the EOB and decreases afterwards. Whilst the other herbivore detrivore species, both *Rissoa* specs and *Teinostoma*, show an increase right after the EOB and are not abundant before. A possible explanation is a difference in feeding strategies. While *Bittium* has a mostly detritus feeding strategy, *Rissoa* feeds on algae. This indicates more eutrophic feeding strategies in the Oligocene (Anderson et al, 2002) and oligotrophic in the late Eocene: "…differences in epiphyte biomass seem to

support the notion that eutrophic conditions would favor food webs based in algae, whereas oligotrophy would favor sea grass detritus…" (Gacia et al, 2009). This is further backed by findings of algal limestones above the EOB (Adams et al., 1986). In the same time period, a similar decline is found in oligotrophic foraminifera (Pearson, 2008) and a turnover from in calcareous nanofossils favoring oligotrophic conditions to those favoring more nutrient rich conditions.(Dunkley Jones et al, 2008).

The filter feeder species *Kelliella* seems to represent its group well, by increasing after the sea level drop. Even though it is not a significant increase group-wise, a delayed increase of this group, compared to the herbivore detrivore group, is interesting. It indicates a latent increase of planktonic species. Another explanation might be a possible impact of the sea level drop on the accessibility of planktonic species. However, it is debatable whether a drop of no more than 100 meters would have an impact on deep water fauna composition (Pearson & Coxall, 2007).

The statistical analysis indicates no increase or decrease in numbers of the carnivore group. However, detailed examination of two carnivore species, *Limacina* and *Turridae* do indicate a response by this group. This response can be explained by a possible turnover of their prey species, a further indication that deep water fauna is affected by the EOT. In contrast to the carnivore group, the parasite group did show a significant difference; a decline over the EOT. This might be explained as follows. The decline of the Parasite group is only in ratio to the other mollusk species. Their absolute response however is much less severe and their numbers actually remains rather constant during the EOT. This deep water Parasite group might not be affected by the EOT, and its species not correlated with cooling or eutrophication. However, low amounts of Parasite specimens mean the response and explanation remain uncertain

### **4-Response**

Deep marine Mollusk species respond to the EOT. The results found in this research do not indicate a swift, rapid turnover. Gastropod extinctions in the US Gulf were found to be up to 97% and bivalve species to 89% (Hansen et al, 1987; Prothero et al, 1994). It might have taken several million years for the Eocene species to reach this extinction level. This is in sheer contrast to the larger benthic foraminifera (LBF) that had a rapid extinction (Cotton & Pearson, 2011). Previous mollusk research also take a longer mollusk extinction period in consideration (Prothero et al, 2003). Exact comparisons are difficult, because all mollusk research on the EOT I could find was on shallow marine species and temperature changes and shelf area have more impact there than on deep marine fauna (Lear et al, 2008).

# **Conclusion**

The results from this paper align with the concept that there were gradual extinctions and speciations and that deep-water species increase over the EOT because of the changing currents and nutrient enrichment (Pearson & Coxall, 2007). Deep-water Mollusks seem to have very little response to the cooling of the EOT.

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### **Addendum**



*Figure 10. Rarefaction of mollusk species*

Table 1: list of mollusks found, their morphotypes, identification and corresponding group. Number correspond to plates.

























