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Prey-size selectivity in the bivalve *Chione* in the Florida Pliocene-Pleistocene: A re-evaluation

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Prey-size selectivity in the bivalve *Chione* in the
Florida Pliocene-Pleistocene: A reevaluation

by

Shubhabrata Paul

A thesis submitted in partial fulfillment
of the requirements for the degree of
Masters of Science
Department of Geology
College of Arts and Science
University of South Florida

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Dedication

This thesis is dedicated to my dear sister, Sampi. Although she is younger than me, she has taught me how to stand tall in difficult times. She has always been a great source of inspiration and motivation.

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I would like to express my deep and sincere gratitude to my supervisor, Dr. Gregory S. Herbert for his enthusiasm, his inspiration, his great efforts to explain things clearly and his patience to improve my writing skill. Throughout my thesis-writing period, he provided encouragement, sound advice, good teaching, lots of good ideas and some crazy songs.

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Prey-size selectivity in the bivalve *Chione* in the
Florida Pliocene-Pleistocene: A reevaluation

Shubhabrata Paul

ABSTRACT

Previous study of drilling predation on the bivalve *Chione* during the late Neogene of Florida suggested that prey-size selectivity of predators was disrupted by species turnover and morphological change within the prey genus. More recent experimental work, however, showed that at least some of these changes can be attributed to the confounding effects of facies shifts between naticid-dominated, muricid-dominated, and mixed predator assemblages. As muricids have the most abundant and continuous fossil record and are most responsible for predation on the *Chione* bivalve in modern benthic ecosystems of Florida, we use new criteria to isolate the muricid component of the *Chione* drillhole record and analyze the history of this type of predator independently. Our analysis, based on drilled *Chione* from four Plio-Pleistocene formations in Florida, does not support the previous scenario of disruption at the end of the Pliocene followed by predator recovery. Rather, selected prey size has steadily increased since the middle Pliocene, although the stereotypy of prey-size selection behaviors has decreased. In order to explain this trend, I performed a series of statistical analyses to explore factors most likely to have influenced muricid prey-size stereotypy. The timing of Species turnover within the prey lineage or change in prey phenotype does

not correlate with the timing of changes in prey-size stereotypy and, therefore, cannot explain the observed changes in muricid behavior. Presence of secondary predators may also influence predator-prey interactions, because predators forage sub-optimally to ensure greater safety in the presence of enemies. Results indicate that secondary predation pressure decreased at the Caloosahatchee-Bermont boundary without any evident change in muricid prey-size stereotypy and hence refute the hypothesis that secondary predation induced sub-optimal foraging. A third factor tested is prey density, which plays a major role in predator-prey interactions in other systems by thwarting a predator's ability to single out the preferred individual prey. Increased *Chione* prey density correlates with and provides support for increased confusion among the muricid predators and hence driving the increased sub-optimal behavior reflected by the increased variability in prey-size selection. This is the first time prey density effect has been considered and its importance here over all other factors suggests that it may be a critical factor in short- and long-term predator behavior trends in fossil record.

Chapter 1

Introduction

The Late Neogene molluscan community of Florida experienced a regional extinction at the end of Pliocene, but the magnitudes of biodiversity loss and ecological disruption as well as subsequent recovery remain controversial (Woodring, 1966; Stanley, 1986; Vermeij and Petuch, 1986; Jackson et al., 1993; Petuch, 1995; Allmon et al., 1993, 1996; Roopnarine, 1996, 1997; Allmon, 2001; Doming, 2001; Todd et al., 2002). Dietl et al. (2004) suggested that the late Neogene extinction altered predator-prey interactions in the post-extinction molluscan community and that there was no evident recovery in last 2 myr. On the other hand, Roopnarine & Beussink (1999) suggested a recovery in the foraging behavior of predatory gastropods from middle Pleistocene to recent. Here, I present a new dataset involving the prey bivalve *Chione* and borehole traces from muricid predators to determine the magnitude of disruption in this predator-prey interaction across the extinction boundary and into the Pleistocene recovery interval.

To assess the influence of the Late Neogene extinctions on this predator-prey interaction, Roopnarine and Beussink (1999) examined predatory drillholes records from *Chione* valves in Plio-Pleistocene sediments of Florida. Drillholes on the bivalve shells are the most reliable indicators of gastropod predation (Kelly and Hansen, 2003). Information regarding both prey size and predator size can be obtained from a single

drilled valve. Previous studies (Kitchell et al., 1981) suggest that predatory gastropods are selective in choosing the prey size in order to maximize the net energy gain from drilling. Variability within the selected prey size is defined as the prey-size stereotypy. Roopnarine and Beussink (1999) suggested that predatory gastropods were more selective in preferred prey size in the pre-extinction Pliocene community, and prey-size stereotypy declined significantly in the post-extinction Bermont community. They concluded that introduction of a new species due to a turnover within *Chione* occurred during an extinction event at the boundary between the Caloosahatchee and Bermont formations as the possible cause of the decline in prey stereotypy.

However, Roopnarine and Beussink (1999) assumed that all drillholes were produced by naticid gastropods and overlooked the fact that some drillholes may have been produced by muricids. Daley et al. (2007) has shown that separating naticid and muricid drillhole traces results in different relationships reconstructed for predator-prey size selectivity. Failure to properly identify different predators based on their traces risks confounding real trends in stereotypy with changes in the relative proportions of either predator type between time intervals. For example, Herbert and Dietl (2002, in prep.) suggest that drillholes on the umbonal region of *Chione* are produced by naticids exclusively. Muricid gastropods almost always drill at the central or ventral region of prey valves. Therefore, mixing predator identities may confound the prey-size stereotypy trend of predatory gastropods.

Because muricids have the most continuous and abundant record of predatory interactions with the venerid bivalve *Chione* in the Neogene of Florida (Dietl et al. 2004),

we isolate the muricid-predator component of the *Chione* drillhole record on the basis of drillhole position following the approach of Herbert and Dietl (2002, in prep.). Because of its abundance, this interaction is easier to quantify than the naticid-*Chione* and it is also presumably the more important from an evolutionary standpoint. Here, we present a new dataset involving *Chione* prey species and their muricid predator to determine the magnitude of disruption in this predator-prey interaction across the extinction boundary and following recovery of biotic interaction.

After reconstructing the muricid-*Chione* interaction, we ask the question what are the factors that could cause the disruption in this predator-prey relation. Other than turnover in prey or predator lineages, several ecological factors can govern predator-prey interactions in general. Firstly, we discuss our results in the light of change in prey *Chione* shell thickness (Roopnarine and Beussink, 1999). Prey shell thickness could be treated as a cost of drilling by predatory gastropods (Kitchell et al., 1981), where increasing thickness should drive selection of smaller, thinner prey or should interrupt stereotypy.

Secondly, the presence of secondary predators could be treated as a potential factor in influencing the predator-prey interactions for predators in general (Brown and Kotler, 2004; Lima and Dill, 1990) and predatory muricid gastropods in particular (Paul et al., in prep). Because predators generally prefer specific-sized prey to maximize energy gain (Kitchell et al., 1981; Kowalewski, 2004) and likelihood of success, introduction of a secondary predator should result in suboptimal foraging, which may be expressed as increased variability in prey-size selection. In the present study, we test the applicability

of this hypothesis of secondary predation pressure as a driving factor of changes in our muricid-*Chione* interaction. Although this hypothesis is valid in other predator-prey systems, it has not been tested in molluscan communities previously or considered in paleoecological studies of drilling predation.

Lastly, we test the hypothesis that increasing prey density can play a pivotal role in modification of predator-prey interactions in ecological communities. Prey density has manifold influences in predator-prey interactions, including the early warning of an approaching predator and increased potential for escape (Treisman 1975; Treherne and Foster 1981), reduced probability of detecting prey (Treisman 1975; Inman and Kerbs 1987), and increased confusion predators (Jeschke and Tollrian 2007). According to Krause and Ruxton (2002) this confusion effect hinders a predator's ability to single out individual optimal-size prey individuals. This hypothesis has also not been tested for molluscan communities; however, a number of other predator-prey systems support this argument (see Jeschke and Tollrian 2007). Increases in prey density are known to reduce prey selectivity in the case of predators that locate prey using tactile or chemical sensing organs. The muricid gastropods studied here are chemosensory predators (Kitchell 1981). If prey density affects change in muricid prey-size stereotypy, we should expect to see sub-optimal foraging behavior or a decline in muricid prey-size stereotypy in the case of higher *Chione* relative abundance and the opposite in times when *Chione* are less abundant.

To test these three hypotheses, prey thickness, presence of secondary predators and prey density, I carried out a series of comparisons between changes in muricid prey-

size stereotypy with simultaneous change in the possible governing factors. In an attempt to discern the processes underlying the changes in muricid prey-size stereotypy, we focus on the applicability and implications of these factors in the present study.

Chapter 2

Materials and Methods

The age and stratigraphic relationships among different Pliocene-Pleistocene in Florida is still poorly understood and in part controversial (Lyons 1991). Several researchers have proposed different relationships between Tamiami Formation and Pinecrest beds of Pliocene deposit (Mansfield, 1939; Olsson, 1964; Hunter, 1968; Brooks, 1974; DuBar, 1974; Petuch, 1982; Vokes, 1988). In the present study, I will follow Lyons's (1991) approach and use the name "Tamiami Formation" to refer to middle Pliocene deposits in Florida, and Pinecrest beds is the uppermost member of the Tamiami Formation. The late Pliocene Caloosahatchee Formation is distinguished from the Early Pleistocene Bermont Formation by the extinction of Caloosahatchee index taxa at the Pliocene-Pleistocene boundary (Lyons 1991). The age of the Caloosahatchee Formation is tentatively placed between 2.5-1.8 myr (Bender, 1972, 1973). The age of the Bermont Formation is also controversial. The Bermont Formation has been placed in the Early Pleistocene (Vokes, 1963; Taylor, 1966; Walker, 1969; Hoerle, 1970) and also in the Middle Pleistocene (DuBar, 1974; Blackwelder, 1981). The most recent evidence confirms the Early Pleistocene age (1.8-1.1 myr) of the Bermont Formation (Hulbert and Morgan, 1988; Webb et al., 1989). Ft. Thompson Formation is assigned as the middle Pleistocene (Lyons 1991). Webb et al. (1989) suggested the age of 0.95-0.55 myr for the

Ft. Thompson Formation based on the Sr⁸⁷/Sr⁸⁶ isotope data. However, at least one study (Tiling, 2004) has assigned the age of 0.125 myr which is also the age of the last interglacial episode for the Ft. Thompson formation from Caloosa Shell Pit.

This stratigraphic framework was also followed in other faunal studies of Florida fossils (Roopnarine and Beussink 1999; Vermeij, 2005) with some difference, specifically by subdividing the Pinecrest beds into Upper and Lower Pinecrest beds (Petuch 1986, 2004). In the present study, I used samples collected from Pinecrest member, Tamiami Fm., the Caloosahatchee Fm., the Bermont Fm. and the Ft. Thompson Fm. Three sites were analyzed from each formation. Table 1 presents a synthesis of stratigraphic ranges of the collection sites with number of samples collected from each location.

Table 1: Stratigraphic sequence of collection sites. ‘†’ indicates bulk samples.

Stratigraphic Formation	Stratigraphic range	Location	Sample no.
Pinecrest member, Tamiami Fm.	Middle Pliocene	APAC Pit [†]	32
Pinecrest member, Tamiami Fm.	Middle Pliocene	Mac Asphalt Pit	94
Pinecrest member, Tamiami Fm.	Middle Pliocene	Quality Aggregates Pit	118
Caloosahatchee Formation	Late Pliocene	Brantley Shell Pit	64
Caloosahatchee Formation	Late Pliocene	Bonita Grande Pit	199
Caloosahatchee Formation	Late Pliocene	Florida Shell & Dirt Pit [†]	34
Bermont Formation	Early Pleistocene	Longan Lake	100
Bermont Formation	Early Pleistocene	GKK Pit	70
Bermont Formation	Early Pleistocene	Florida Shell & Dirt Pit [†]	92
Ft. Thompson Formation	Middle Pleistocene	Leisey Pit	120
Ft. Thompson Formation	Middle Pleistocene	Caloosa Shell Pit	60
Ft. Thompson Formation	Middle Pleistocene	Bermont Pit [†]	57

Measurements:

Three drilling parameters are measured on each *Chione* valve (Fig. 2). Prey size is measured as valve height. Studies have shown that outer borehole diameter can be used as a proxy of predator size in case of naticids (Kitchell et al., 1981) and muricid (Kowalewski, 2004) predatory gastropods. In this study, predator size is assessed from the outer borehole diameter (OBD). Both prey valve height and outer drillhole diameter are measured with a slide calipers to the nearest 0.1 mm. Thickness of the prey *Chione* valve is measured with a screw gauge micrometer to nearest 0.1 mm. Data are transformed using natural log.

When shell height is regressed relative to the OBD, the change in the y-intercept indicates a change in preference for overall smaller or larger prey. A change in the slope indicates relative change in the range of selected prey sizes for juvenile and adult muricid predators. A low slope, for example, shows that juveniles and adult predators selected similarly-sized prey or lower prey-size selectivity. In other words, increasing selectivity (meaning increasingly selective foraging where juveniles and adults feed on very different size prey) is indicated by a steeper slope and lower y-intercept.

Prey-size stereotypy refers to variability in selection and is determined as the correlation (R^2) between predator and prey sizes for each formation. Ontogenetic change in thickness is measured by regressing shell thickness relative to shell height. When compared between formations, changes in the slope of the regression lines indicate relative change in thickness. Relationships between valve height, OBD and thickness

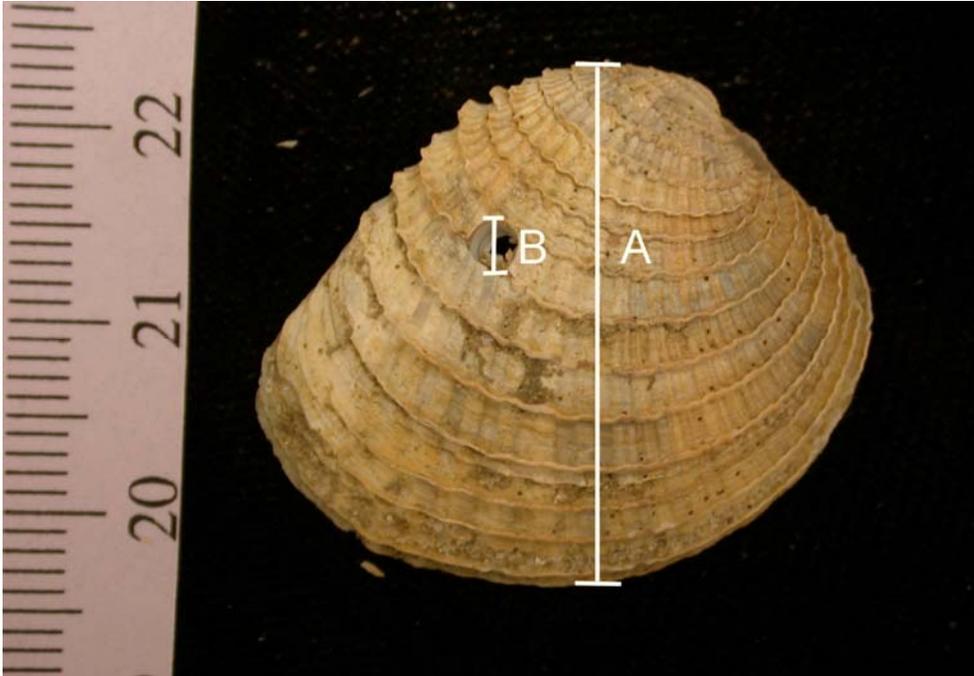


Figure 1: Measurements on the *Chione* valve. (A) – prey valve height indicative of the prey size, (B) outer borehole diameter, indicative of the predator size.

were determined using Model I regression. Muricid prey-size stereotypy was measured in two different ways- (1) different sites within a formation considered in unison (i.e. pooled), (2) considering different sites within a formation individually (i.e. non-pooled)

Predatory muricid gastropods use edge-drilling in the presence of secondary predators (Paul et al., in prep) and competitors (Dietl et al., 2004; Dietl and Herbert, 2005). We used the frequency of muricid edge-drilling on *Chione* as a proxy for secondary predation pressure. This dataset was taken from Dietl et al. (2004). Edge-drilling frequency is measured as: (number of edge drilled valve/number of total drilled valves)*100.

Chione relative density is determined from its abundance relative to all prey

bivalves in the various bulk samples studied. Bulk samples were collected by participants in the NSF-funded Research Experience for Undergraduates (REU) 2004-2007 programs run at USF and by the author in 2008.

Chapter 3

Results

Analysis of Prey-Size Stereotypy

When prey size (valve height) is regressed relative to predator size (as inferred by OBD) for each formation (Fig. 2), the slope of the least square regression line decreases significantly (t-value 10.56, $p < 0.001$) after the middle Pliocene Tamiami Formation indicating a decrease in prey-size selectivity (difference between selected prey size for juvenile and adult predator). The slope of the regression line increases minimally (t-value -3.92, $p < 0.001$) from across the Caloosahatchee-Bermont boundary. There is no evident change in the slope between the early Pleistocene Bermont and the middle Pleistocene Ft. Thompson formation (t-value 2.40, $p > 0.001$). Although the slope declines after the Tamiami formation, intercept of the regression line increase from the Tamiami to Caloosahatchee formation. Thus, different sizes of muricid predators preyed on similarly sized *Chione* following the middle Pliocene, with the bulk of this shift reflecting a general increase in the size of prey selected by smaller muricids so that both small and large predators fed on a similar size range of prey.

Model I regression analysis of prey size on drillhole size for pooled samples indicates that prey-size stereotypy was reduced (i.e., variability of selection also

increased) in two steps. The correlation between prey-size and predator size as measured by R^2 , decreased at the Tamiami-Caloosahatchee boundary from 0.63 to 0.45.

Interestingly, prey stereotypy did not change substantially across the main extinction boundary between the Latest Pliocene Caloosahatchee Fm. and the Bermont Fm. as R^2 values for these units are nearly identical (0.45 to 0.49). Another decrease in prey-size stereotypy from 0.49 to 0.32 took place between the Early Pleistocene Bermont Fm. and the middle Pleistocene Ft. Thompson Fm.

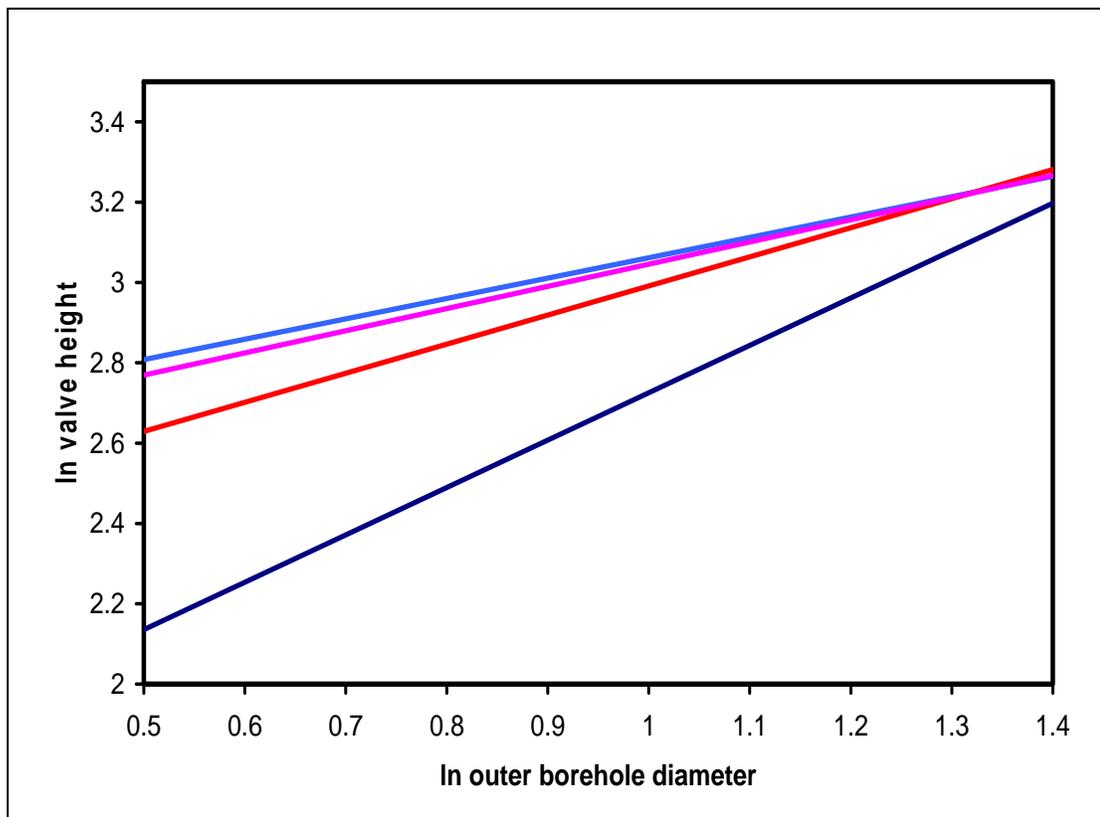


Fig. 2 Comparison of prey size selection between formations. Valve height is regressed on the outer borehole diameter. Color code follows: dark blue-Pinecrest member, Tamiami Fm. [$\ln H = 1.18 \ln OBD + 1.55$ ($R^2 = 0.63$, $p < 0.001$)] light blue-Caloosahatchee [$\ln H = 0.51 \ln OBD + 2.56$ ($R^2 = 0.45$, $p < 0.0001$)], red-Bermont [$\ln H = 0.73 \ln OBD + 2.27$ ($R^2 = 0.49$, $p < 0.0001$)], Pink- Ft. Thompson [$\ln H = 0.55 \ln OBD + 2.49$ ($R^2 = 0.32$, $p < 0.0001$)]. Note that the Tamiami Fm. is different than other formations in both slope and intercept. The slope and intercept did not vary from the Caloosahatchee Fm. to the Ft. Thompson Fm. R^2 values, however, decreased at the end of Tamiami Fm. and again at the end of the Ft. Thompson Fm.

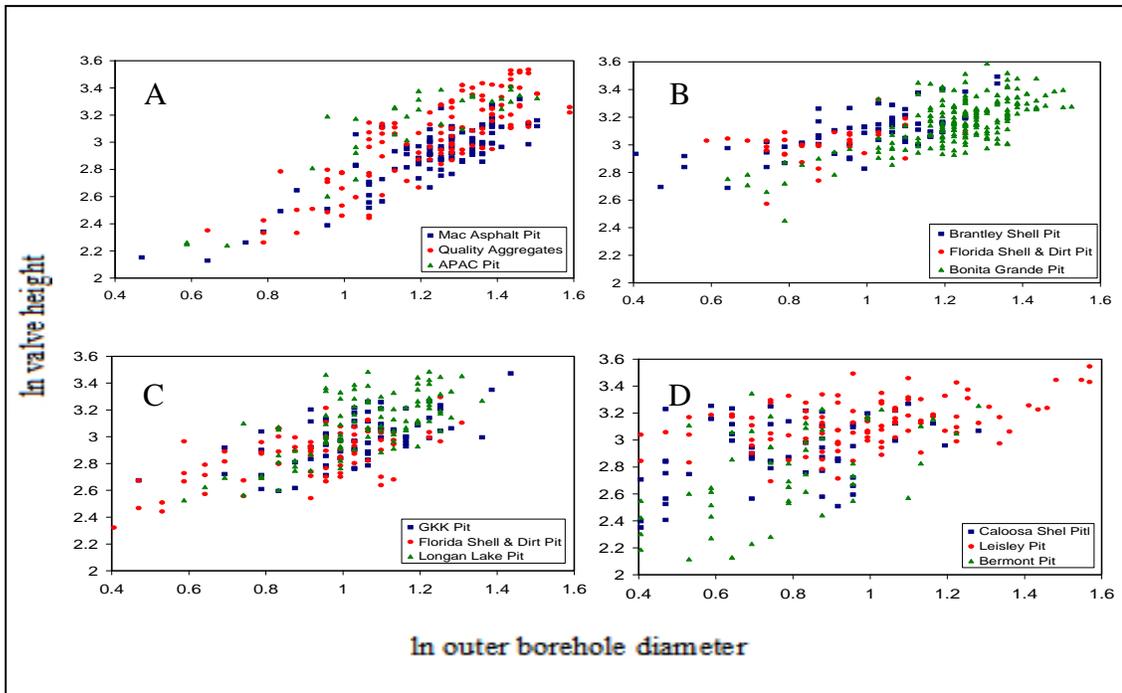


Fig. 3: Comparison of muricid prey-size stereotypy between localities of each formation. (A) Pinecrest member, Tamiami Fm., (B) Caloosahatche Fm., (C) Bermont Fm., (D) Ft. Thompson Fm. Note that outer borehole diameter- prey valve height relation is least correlated in Ft. Thompson Formation.

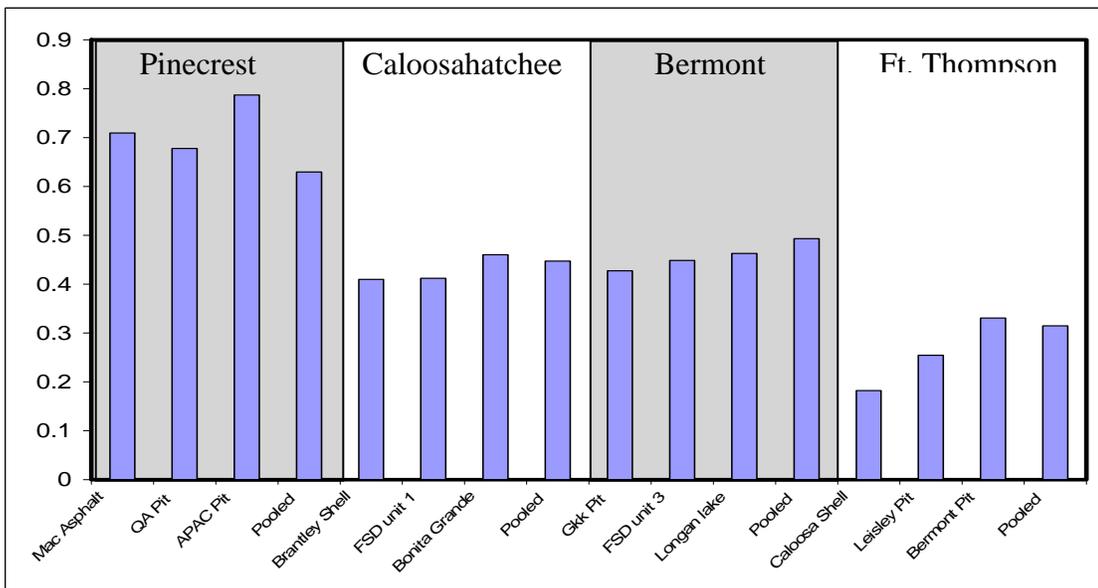


Fig. 4: Comparison of correlation-coefficient of prey-size selection between localities of each formation. R^2 values did not change significantly within samples of individual formations. However, there is a stepwise decrease in R^2 value between-formations.

When samples from different localities (within a formation) are pooled, a locality with a larger sample size may have more influence on the mean value for the formation than a locality with smaller sample size. To examine the extent of variability between different localities of the same formation, we performed prey-size selection analysis on different localities individually (Fig. 3). Our results show that within each individual formation, prey-size stereotypy (R^2) did not vary between different localities (Fig. 4). It indicates that our pooled results (Fig. 2) are not influenced by any single locality result.

Analysis of Prey Shell Thickness

When shell thickness is regressed against shell height (Fig. 5), the Tamiami Fm. and the Caloosahatchee Fm. do not differ in shell thickness. The slope and intercept remained nearly identical in these formations. Prey shell thickness increased in the Early Pleistocene Bermont Fm. Although intercept did not change significantly, the slope of the regression line increased from the preceding Pliocene formations. Major increase in the prey shell thickness occurred by the middle Pleistocene Ft. Thompson Fm. The slope and intercept of the regression line are different from those of preceding formations.

Analysis of Secondary Predation Pressure

Results (Table 2, Fig. 6) show that edge-drilling frequency declined significantly at the Pliocene-Pleistocene boundary from 4.37% to 0% (Chi-square test,

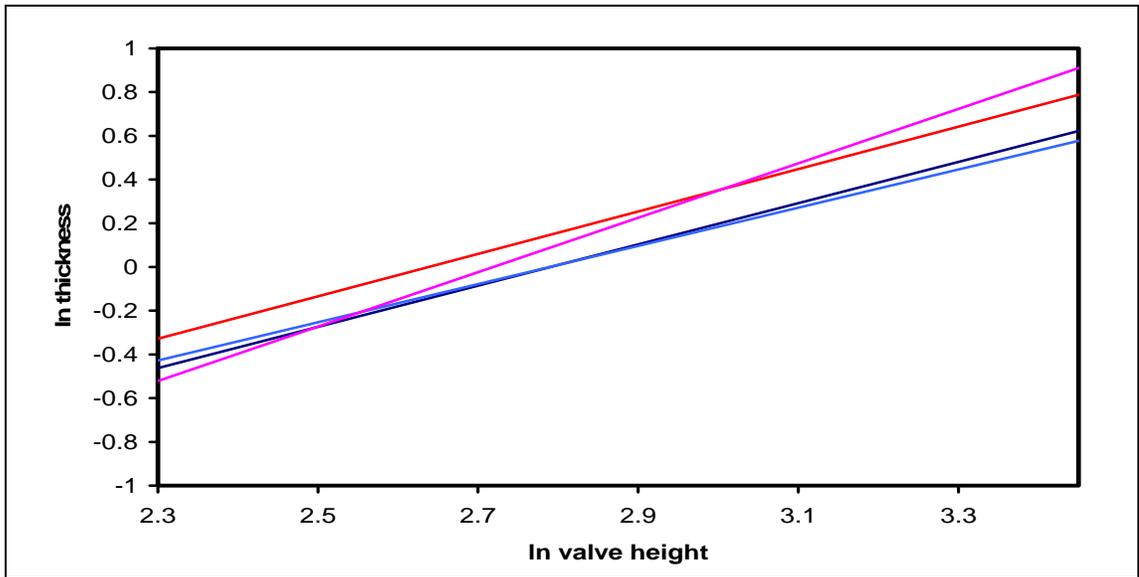


Fig. 5: Valve thickness (lnTh) regressed on valve height (lnH). Color code follows: dark blue-Pinecrest member, Tamiami Fm. [$\ln Th = 0.94 \ln H - 2.63$ ($p < .0001$)], light blue-Calooahatchee [$\ln Th = 0.87 \ln H - 2.44$ ($p < .0001$)], red- Bermont [$\ln Th = 0.97 \ln H - 2.55$ ($p < .0001$)], Pink- Ft. Thompson [$\ln Th = 1.24 \ln H - 3.38$ ($p < .0001$)]. Note that the specimens from the Bermont Fm. are thicker than the Pliocene formations. Ft. Thompson Fm. is different than others, indicating an increase in valve thickness from the middle Pleistocene.

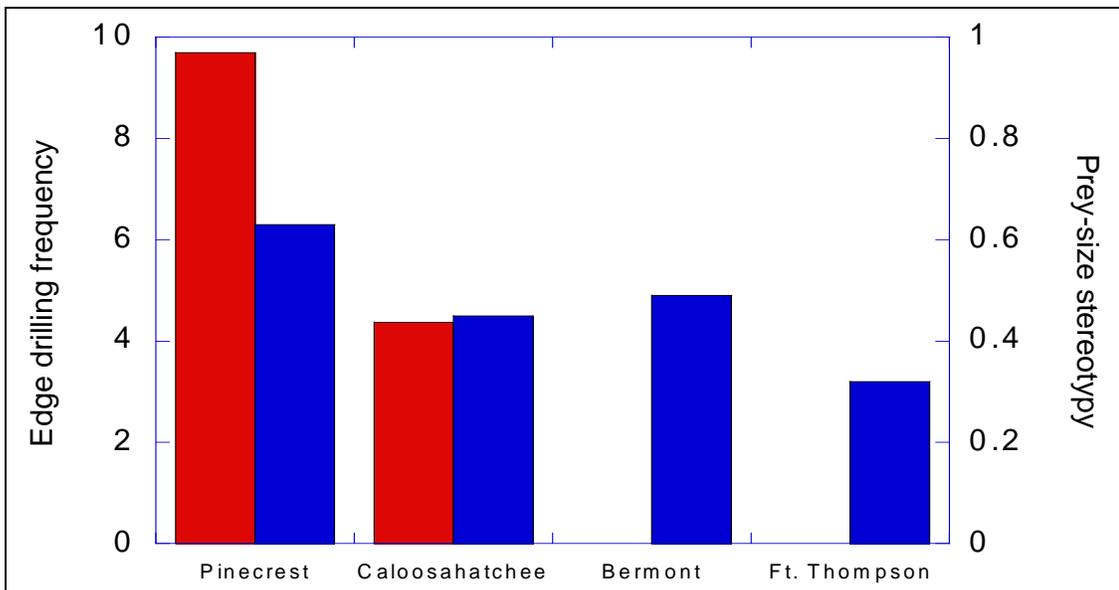


Fig. 6: Comparison of edge-drilling frequency and prey-size stereotypy. Color code follows: red- edge drilling frequency; blue-prey-size stereotypy. Note that edge-drilling decreased significantly across the Caloosahatchee-Bermont Fm. without any change in prey-size stereotypy.

$p < 0.05$). Edge-drilling frequency also declined from 9.69% in the middle Pliocene Tamiami to 4.37% in the Caloosahatchee, but this difference was not statistically significant (Chi-square test, $p > 0.05$). The absence of any edge-drilled *Chione* in the Pleistocene indicates a decline in secondary predation or competition pressure on predatory muricid gastropods. In comparison with the results of our prey-size stereotypy analysis, muricids were most stereotyped with respect to prey-size in the middle Pliocene Tamiami Fm., when secondary predation pressure was also highest. Muricid prey-size stereotypy also declined at the end of the Tamiami Fm. and also at the end of the Ft. Thompson Fm. but without any evident change in secondary predation pressure.

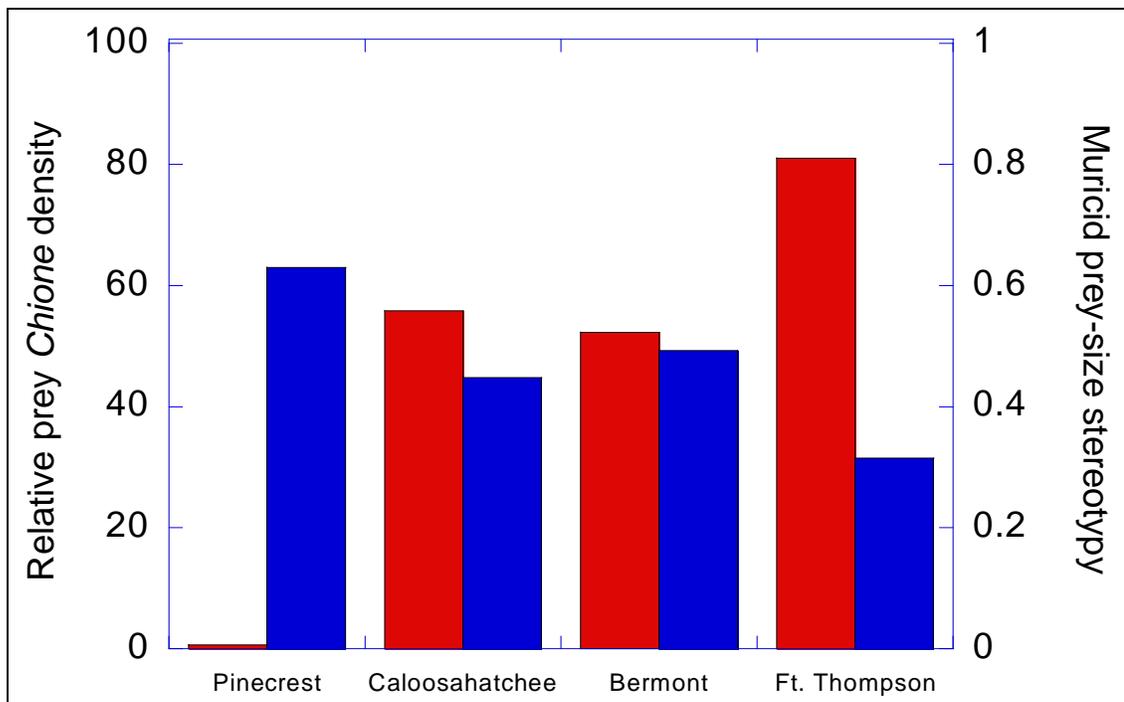


Fig. 7: Comparison of prey *Chione* relative density and prey-size stereotypy. Color code follows: red - *Chione* prey relative abundance; blue-prey-size stereotypy (R^2). Note that prey relative abundance increased from the Tamiami (0.7%) to the Caloosahatchee Fm. (55.84%) and at the Bermont Fm. (52.24%) - Ft. Thompson Fm. (81.01%).

Analysis of Prey *Chione* Density

Our results (Table 2, Fig. 7) show that the relative *Chione* abundance (total number of *Chione*/total number of prey bivalves) increased significantly (Chi-square test, $p < 0.05$) between the middle Pliocene Tamiami Formation (<1% of all bivalves) and the Late Pliocene Caloosahatchee Formation (55% of all bivalves). Although Pliocene *C. erosa* was replaced by Pleistocene *C. elevata* in the Bermont formation, there was no significant change in relative *Chione* density at this time (Chi-square test, $p < 0.05$) (52% of all bivalves in Bermont formation). Another significant increase in prey density took place between the Early Pleistocene Bermont Fm. and the middle Pleistocene Ft. Thompson Fm (Chi-square test, $p < 0.05$) (81% of all bivalves).

Chapter 4

Discussions

Regression analyses do not support the results of Roopnarine and Beussink (1999). They suggested that predator-prey interactions were disrupted by prey turnover at the Caloosahatchee-Bermont boundary and recovered by the middle Pleistocene. By contrast, we observe an earlier shift in muricid prey-size selectivity as well as an earlier and a later decline in prey-size stereotypy. These changes cannot be explained by the replacement of Pliocene *C. erosa* by the Pleistocene *C. elevata*, which occurred at the end of the Caloosahatchee Formation (Roopnarine, 1995, 2001; Vermeij and Roopnarine, 2000). Although *C. erosa* was replaced by the *C. elevata* in post-Pliocene Florida molluscan community, *C. elevata* was not more escalated than the pre-extinction *C. erosa* (Roopnarine and Beussink, 1999). Our results suggest that any morphological differences between *C. erosa* and its replacement *C. elevata* did not pose novel challenges for muricid predators and did not interrupt their prey-foraging or prey-handling behaviors. Other than species turnover within a prey or predator lineage, a number of factors can potentially influence interactions in a specific system. In order to evaluate the role of these factors, I performed independent analyses of these factors and then compared the results with change in muricid-prey stereotypy results. Results suggest that *Chione* shell thickness increased with simultaneous decline in muricid prey-size stereotypy at the

Table 2: Muricid prey-size stereotypy, edge drilling frequency (data taken from Dietl et al. 2004) and relative abundance of prey *Chione* across the studied stratigraphic formations. Note that muricid prey-size stereotypy decreased simultaneously with increasing relative *Chione* abundance. Decline in muricid edge drilling behavior is not concurrent with change in prey-size stereotypy.

Stratigraphic Formation	Muricid prey-size stereotypy	Edge drilling frequency	Relative <i>Chione</i> density
Pinecrest member, Tamiami Fm.	0.63	9.69	0.70
Caloosahatchee Formation	0.45	4.37	55.84
Bermont Formation	0.49	0	52.24
Ft. Thompson Formation	0.32	0	81.01

Bermont-Ft. Thompson boundary. Therefore, an increase in thickness cannot be ruled out as a potential factor driving the decline in prey-size stereotypy at the end of the Bermont Fm. However, a causal relationship between these two factors can be rejected by two lines of argument. First, a change in the prey size-thickness relation after the Caloosahatchee was accompanied by no changes in predator behavior. Secondly, changes in predator behavior after the Tamiami were not accompanied by changes in prey thickness. Therefore, the correlation between thickness and predator behavior after the Bermont appears to be coincidental only.

Increasing variability for prey-size selection can be viewed as increasing sub-optimal foraging for a specific predator. In the presence of enemies, foragers typically decrease risk through reduced activity, shifting to less productive but safer habitats, restricting foraging time to reduce exposure time, or foraging in similar habitats but with less selectivity (Houston et al., 1993; Walters and Juanes, 1993; Brown, 1999; Kotler et al., 2004; Heithaus et al., 2007). For example, foragers reduce their foraging activity in order to gain greater safety in presence of enemies. Mule deer (*Odocoileus hemionus*)

spent less time in foraging in high risk areas. This risk factor comes from the secondary predation pressure of mountain lions (*Puma Concolor*) (Altendorf et al., 2001). A shifting of habitat is found within green sea turtle (*Chelonia mydas*) community as a response of the predation pressure from tiger sharks (*Galeocerdo cuvier*). Green sea turtles forage in low quality seagrass when tiger shark is abundant. When number of tiger shark is reduced, i.e., in time of less predation pressure turtles are found to forage in high quality seagrass near to the river banks (Heithaus et al., 2007). A forager may also restrict foraging time to reduce exposure time to enemies. Experimental study (Paul et al., in prep) show that predatory snail *Chicoreus dilectus* attacks on the edge of their clam prey *Chione elevata* at least two-times higher in presence of secondary predators such as crabs. This edge-drilling technique shortens the foraging time and subsequently the exposure time to enemies.

I tested the possibility that increasing predation pressure on muricid gastropods is driving sub-optimal foraging, and hence decline in prey-size stereotypy. Higher edge-drilling frequency indicates higher secondary predation pressure in the Pliocene molluscan community. My preliminary prediction was that any decrease in secondary predation pressure should have been accompanied by an increase prey-size stereotypy. My results do not support this prediction. Muricids were most stereotyped (prey-size) in the middle Pliocene Tamiami Fm., when our edge-drilling proxy for secondary predation pressure was also highest. This is opposite of the prediction. Muricid prey-size stereotypy also declined at the Tamiami-Caloosahatchee as well as the Bermont-Ft. Thompson boundary without any evident change in secondary predation pressure. These results

refute the hypothesis that secondary predation induced sub-optimal foraging over last 3 Ma in this predator-prey system.

Predator-prey interactions can also be influenced by changing prey-density. A predator becomes confused when faced with higher number of prey. For example, Jeschke and Tollrian study (2007) suggest that, larvae of *Aeshna cyanea* becomes less efficient predator when *Daphnia magna* prey density gradually increases from 10 to 250. This negative correlation between attack efficiency and prey density indicates the increasing confusion factor among the *Aeshna cyanea* larvae. Confusion factor also increases with higher prey density in case of *Chaoborus obscuripes* predator and *Daphnia obtuse* prey (prey density changed gradually from 5 to 70). In both of these two cases negative correlation between attack efficiency and prey density indicates that predator forage less efficiently (i.e., sub-optimally) with increasing prey density.

Predator confusion is a widespread response when faced with higher prey density (Jeschke and Tollrian 2007). Failing to single out individual prey results in sub-optimal foraging behavior of different tactile, visual and chemosensory predators. If this true for our system, we expect to see that predatory muricids became more confused, as reflected in decreased prey-size stereotypy, when faced with higher number of *Chione*.

Comparison of prey *Chione* density with prey-size stereotypy shows a pattern that supports this hypothesis. Muricid prey-size stereotypy was highest in the Tamiami Fm. when relative *Chione* density was lowest. Muricids were least selective in choosing the prey size in the Ft. Thompson Fm. when *Chione* was most available. Moreover, stasis in prey-size stereotypy coincided with stasis in *Chione* prey abundance between the

Caloosahatchee and Bermont Fm. In addition to these, comparison of prey *Chione* density with prey stereotypy shows that neither parameter was influenced by the species turnover event at the Caloosahatchee-Bermont boundary. These results indicate that increase in prey density cannot be ruled out as a potential factor in driving the changes in muricid prey-size stereotypy.

This argument is supported by another line of evidence. Studies suggest that confusion factor decreases when the prey population contains a greater variety of ‘prey types’, including presence of odd individuals (Ohguchi, 1981; Landeau and Terborgh, 1986; Krakauer, 1995; Tosh et al., 2006). For example, hyenas spend a considerable time in choosing their prey during hunting. Usually hyenas hunt old or weak individuals. When Kruuk placed a marker on some of the individuals within the prey group, hyenas almost always targeted those odd, marked individuals (Kruuk, 1972). This ‘variety of prey types’ may also refer to the availability of prey of different genera (Jeschke and Tollrian, 2007). A predator faces more ‘prey types’ when species abundances within the prey community are more even (i.e. each prey genus is represented by nearly similar number of individuals) and hence confusion factor will be reduced. As *Chione* dominance relative to other bivalve prey increased after the Pinecrest, we would expect a decrease of prey community evenness and hence increasing confusion factor within predatory muricid gastropods. Further work is needed to test this hypothesis in detail.

Although this study is an important step in understanding the nature of predatory response in face of changing prey density in molluscan community, these results also raise the question about the magnitude of muricid predation intensity on *Chione*. Kelly

and Hansen (1996) argued that decline in predator behavioral stereotypy is associated with higher drilling frequency. This argument was based on the assumption of selective removal of highly escalated prey immediately after the mass the mass extinction. In Neogene Florida, the Pliocene *C. erosa* was not more escalated than the Pleistocene *C. elevata*. So, decline in predator behavioral stereotypy in the studied stratigraphic formations was not due to the change in magnitude of prey escalation. If we consider increased variability in prey-size stereotypy as the reflection of increased sub-optimal foraging behavior driven by increased confusion factor for muricid gastropods, we would expect to see a decline in predation intensity on *Chione* relative to other available prey types. With suboptimal foraging, foraging time should go up and prey consumed per unit time should go down only when muricids are foraging on *Chione*, not other bivalves. This factor may result in decline in predation intensity on *Chione* relative to other prey bivalves. However, present lineage-level dataset is insufficient to test this hypothesis. Assemblage-level dataset is required to conclusively answer this question.

Beyond predation intensity, sub-optimal foraging may be reflected through other parameters like frequency of unsuccessful attack. As this study suggests that sub-optimal foraging behavior of predatory muricid gastropods may be driven by increased confusion to identify the preferred prey size class, we expect to see an increase in frequency of the unsuccessful attacks. In a review of the incomplete or multiple drillholes on bivalves, indicating prey effectiveness, Kelly and Hansen (2003) found that frequency of failed attacks increased from the Cretaceous to the Oligocene indicating that predatory gastropods became less effective in handling prey in the Oligocene. Following Vermeij's

escalation hypothesis (1987) they suggested that the increase in failed attacks was a reflection of the increasing effectiveness of prey anti-predatory traits (e.g. shell thickness) relative to predator efficiency. However, none of these studies examined relative prey density in relation to the failed attack or prey effectiveness. The present study indicates that increasing prey density effect may play an important role in determining predator efficiency. Future work will be aimed to test the hypothesis.

Chapter 5

Conclusions

Previous study of predation on *Chione* prey was confounded by the mixed signature of naticid and muricid foraging behavior. As, muricids are the most common predators of the *Chione* bivalve in Neogene fossil record and modern ecosystem in Florida, present study deals with the independent muricid component of the fossil record. Present study suggests that in the muricid-*Chione* system, prey-size stereotypy declined at the Tamiami-Caloosahatchee boundary as well as at the Bermont-Ft. Thompson boundary. There was no evident change in muricid prey-size stereotypy at the Caloosahatchee-Bermont boundary. These results indicate that a late Neogene regional extinction did not alter muricid prey-size stereotypy.

This trend cannot be explained by the prey species turnover event at the Pliocene-Pleistocene boundary. Increased sub-optimal foraging behavior of muricids at the Tamiami-Caloosahatchee boundary cannot be explained by the change in prey phenotype (shell thickness). Muricid prey-size stereotypy declined at the end of the Tamiami Fm. without any evident change in prey thickness. At the Caloosahatchee-Bermont boundary, thickness increased without any increase in sub-optimal foraging behavior. Although, *Chione* shell thickness increased simultaneously with the decline in prey-size stereotypy at the Bermont- Ft. Thompson boundary, the correlation between thickness and predator

behavior after the Bermont appears to be coincidental only.

Increased variability of prey-size selection after the middle Pliocene was not a reflection of change in secondary predation pressure on the muricid gastropods. Muricids expressed optimal foraging behavior when secondary predation pressure was highest in the Tamiami formation. Secondary predation pressure decreased significantly at the end of Caloosahatchee formation without any evident change in muricid prey-size stereotypy.

Increased prey density may cause the increased confusion factor within the predators to select the preferred prey-size class and hence driving the decline of prey-size stereotypy. Relative abundance of *Chione* prey increased simultaneously with decrease in muricid prey-size stereotypy. My results suggest that temporal pattern of prey density plays a more important role than species-replacement within the prey lineage or change in prey phenotype or influence of secondary predation pressure in our specific muricid predator-*Chione* prey system.

Literatures 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*, v. 166, p. 9-26.
- Allmon, W. D., Rosenberg, G., Portell, R. W., and Schindler, K. S., 1993, Diversity of Atlantic Coastal Plain mollusks since the Pliocene. *Science*, v. 260, p. 1626-1629.
- Allmon, W. D., Emslie, S. D., Jones, D. S., and Morgan, G. S., 1996, Late Neogene oceanographic change along Florida's west coast: Evidence and mechanisms. *Journal of Geology*, v. 104, p. 143-162.
- Altendorf, K. B., Landré, J. W., González, C. A. L., Brown J. S., 2001, Assessing effects of predation risk on foraging behavior of mule deer. *Journal of Mammalogy*, v. 82, p. 430-439.
- Bender, M. L., 1972, Notes on the fauna of the Chipola Formation—XI. Helium-uranium dating studies of corals. *Tulane Stud. Geol. Paleont.*, v. 10, p. 51-52.
- Bender, M. L., 1973, Helium-uranium dating of corals. *Geochimica et Cosmochimica Acta*, v. 37, p. 1229-1247.
- Blackwelder, B. W., 1981, Late Cenozoic stages and molluscan zones of the U.S. middle Atlantic Coastal Plain. *Paleontology Society Memoirs*, v. 12, p. 1-34.
- Brooks, H. K., 1974, Lake Okeechobee. Pp. 256-286 in P. J. Gleason ed. *Environments*

- of south Florida: Present and past. Miami Geol. Soc., Mem. 2.
- Brown, J.S., 1999, Vigilance, patch use and habitat selection: Foraging under predation risk. *Evol. Ecol. Res.*, v. 1, p. 49–71.
- Brown, J.S. and Kotler, B.P., 2004 Hazardous duty pay and the foraging cost of predation. *Ecology Letters*, v. 7, p. 999–1014
- Daley, G. M., Ostrowski, S. and Geary, D.H., 2007, Paleoenvironmentally correlated differences in a classic predator-prey system: The bivalve *Chione elevata* and its gastropod predators. *Palaios*, v. 22, p. 166-173.
- Dietl, G.P., Herbert, G.S., and Vermeij, G.J., 2004, Reduced competition and altered feeding behavior among marine snails after a mass extinction: *Science*, v. 306, p. 2229–2231.
- Dietl, G.P. and Herbert, G.S., 2005, Influence of alternative shell-drilling behaviours on attack duration of the predatory snail, *Chicoreus dilectus*. *Journal of Zoology*, v. 265, p. 201–206
- Domning D. P., 2001, Sirenians, seagrasses, and Cenozoic ecological change in the Caribbean. *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 166, p. 27–50.
- DuBar, J. R., 1974, Summary of the Neogene stratigraphy of the southern Florida. Pp. 206-231 in R. Q. Oaks and J. R. DuBar, eds. *Post-Miocene stratigraphy central and southern Atlantic coastal plain*. Utah State Univ. Press, Logan.
- Herbert, G. S. and Dietl, G. P., 2002, Tests of the escalation hypothesis: The role of multiple predators. *Geological Society of America Annual Meeting*, Abstract 236-

14.

Herbert, G. S. and Dietl, G. P., (in prep) Tests of the escalation hypothesis: The role of multiple predators.

Houston, A.I., McNamara, J.M. and Hutchinson, J.M.C., 1993, General results concerning the trade-off between gaining energy and avoiding predation. *Phil. Transac. R. Soc. Lond. B*, v. 341, p. 375–397.

Heithaus, M. R., Frid, A., Wirsing, A. J., Dill, L. M., Fourqurean, J. W., Burkholder, D., Thomson, J., and Bejder, L., 2007, State-dependent risk-taking by green sea turtles mediates top-down effects of tiger shark intimidation in a marine ecosystem. *Journal of Animal Ecology*, v. 76, p. 837–844.

Hoerle, S. E., 1970 Mollusca of the “Glades” Unit of the southern Florida: Part II; list of molluscan species of the Belle Grade Rock Pit, Palm Beach County, Florida. *Tulane Stud. Geol. Paleont.*, v. 8, p. 56-68.

Hulbert R. C. Jr., and Morgan, G. S., 1989, Stratigraphy, paleoecology, and vertebrate fauna of the Leisey Shell Pit Local Fauna, early Pleistocene (Irvingtonian) of southwestern Florida. *Papers in Florida Paleontology*, v. 2, p. 1–19.

Hunter, M. E., 1968, Molluscan guide fossils in the late Miocene sediments of the Southern Florida. *Trans. Gulf Coast Assoc. Geol. Soc.*, v. 18, p. 439-450.

Inman, A. J. and Krebs, J., 1987, Predation and group living. *Trends in Ecology & Evolution*, v. 2, p. 31-32.

Jackson, J. B. C., Jung, P., Coates, A. G., and Collins, L. S., 1993, Diversity and extinction of tropical American mollusks and emergence of the Isthmus of

- Panama. *Science*, v. 260, p. 1624-1626.
- Jeschke, J. M. and Tollrian, R., 2007, Prey swarming: which predators become confused and why? *Animal Behaviour*, v. 74, p. 387-393.
- Kelley, P. H. and Hansen, T. A., 1996, Recovery of the naticid gastropod predator-prey system from the Cretaceous-Tertiary and Eocene-Oligocene extinctions. In Hart, M. B., ed., *Biotic Recovery from Mass Extinction Events*, p. 373-386. Geological Society Special Publication No. 102.
- Kelly, P. A. and Hansen, T. A., 2003, The fossil record of drilling predation on bivalves and gastropods. In Kelly, P. H., Kowalewski, M. and Hansen, T. A., eds., *Predator-prey interactions in the fossil record*, p. 113-140. Kluwer Academic/Plenum Publishers, New York.
- Kitchell, J. A., Boggs, C. H., Kitchell, J. F., and Rice, J. A., 1981, Prey selection by naticid gastropods: experimental tests and application to the fossil record. *Paleobiology*, v. 7, p. 533-552.
- Kotler, B.P., Brown, J.S. and Bouskila, A., 2004, Apprehension and time allocation in gerbils: The effects of predatory risk and energetic state. *Ecology*, v. 85, p. 917–922.
- Kowalewski, M., 2004, Drill holes produced by the predatory gastropod *Nucella lamellosa* (Muricidae): paleobiological and ecological implications. *J. Mollus. Stud.*, v. 70, p. 359–370.
- Krakauer, D. C., 1995, Groups confuse predators by exploiting perceptual bottlenecks: a connectionist model of the confusion effect. *Behavioral Ecology and*

- Sociobiology, v. 36, p. 421- 429.
- Krause, J. and Ruxton, G. D., 2002, Living in Groups. Oxford: Oxford University Press.
- Kruuk, H., 1972, The Spotted Hyena: a Study of Predation and Social Behavior.
University Chicago Press.
- Landeau, L. and Terborgh, J., 1986, Oddity and the 'confusion effect' in predation.
Animal Behaviour, v. 34, p. 1372-1380.
- Lima, S.L. and Dill, L.M., 1990, Behavioral decision making under the risk of predation:
a review and prospectus. Can. J. Zool., v. 68, p. 619-640.
- Lyons, W.G., 1991, Post-Miocene species of *Latirus* Montfort, 1810 (Mollusca:
Fascioliidae) of southern Florida, with a review of regional marine
biostratigraphy. Bulletin of the Florida Museum of Natural History (Biological
Sciences), v. 35, p. 131-208.
- Mansfield, W. C., 1939, Notes on the upper Tertiary and Pleistocene mollusks of
peninsular Florida. Florida Geol. Surv., Geol. Bull., v. 18, p. 1-75, pls. 1-4.
- Ohguchi, O., 1981, Prey density and selection against oddity by three-spined
sticklebacks. Advances in Ethology, v. 23, p. 1-79.
- Olsson, A. A., 1964, The geology and stratigraphy of south Florida. Pp. 511-526 in A. A.
Olsson and R. E. Petit. Some Neogene Mollusca from Florida and Carolinians. Bull.
Amer. Paleont., v. 47, p. 505-574.
- Petuch, E. J., 1982, Notes on the paleoecology of the Pinecrest beds at Sarasota, Florida
with the description of *Pyruella*, a stratigraphically important genus (Gastropoda:
Melongenidae). Proc. Acad. Nat. Sci. Philadelphia, v. 134, p. 12-30.

- Petuch, E. J., 1986, The Pliocene reefs of Miami: their geomorphological significance in the evolution of the Atlantic coastal ridge, southeastern Florida, U.S.A. *Journal of Coastal Research*, v. 2, p. 391–408.
- Petuch, E. J., 1995, Molluscan diversity in the late Neogene of Florida: evidence for a two-staged mass extinction. *Science*, v. 270, p. 275-277
- Petuch, E. J., 2004, *Cenozoic seas: the view from eastern North America*. CRC Press, Boca Raton, Fla.
- Paul S. and Herbert G.S., (in prep) Influence of secondary predation pressure on drilling habit of the predatory snail, *Chicoreus dilectus*.
- Roopnarine, P. D., 1995, A re-evaluation of evolutionary stasis between the bivalve species *Chione erosa* and *Chione cancellata* (Bivalvia: Veneridae). *Journal of Paleontology*, v. 69, p. 280-287.
- Roopnarine, P. D., 1996, Systematics, biogeography and extinction of chionine bivalves (Early Oligocene - Recent) in the Late Neogene of tropical America. *Malacologia*, v. 38, p. 103-142.
- Roopnarine, P. D., 1997, Endemism and extinction of a new genus of chionine (Bivalvia: Veneridae) bivalve from the late Neogene of Venezuela. *Journal of Paleontology*, v. 71, p. 1039-1046.
- Roopnarine, P. D., 2001, A history of diversification, extinction, and invasion in tropical America as derived from species-level phylogenies of chionine genera (Family Veneridae), *Journal of Paleontology*, v. 75, p. 644–657.
- Roopnarine, P.D., and Beussink, A., 1999, Extinction and naticid predation of the bivalve

- Chione* von Mühlfeld in the late Neogene of Florida: Palaeontographica Electronica, v. 2, no. 1, 718 KB. http://palaeo-electronica.org/1999_1/bivalve/issue1_99.htm. Checked November 2006.
- Stanley, S. M., 1986, Anatomy of a regional mass extinction: Plio-Pleistocene decimation of the Western Atlantic bivalve fauna. *Palaios*, v. 1, p. 17-36.
- Taylor, D. W., 1966, Summary of the North American Blancan non-marine mollusks. *Malacologia*, v. 4, p. 1-172.
- Tiling, G., 2004, Aminostratigraphy of the Plio-Pleistocene of Florida. MS thesis, University of South Florida.
- Todd, J. A., Jackson, J. B. C., Johnson, K. G., Fortunato, H. M., Heitz, A., Alvarez, M., and Jung, P., 2002, The ecology of extinction: molluscan feeding and faunal turnover in the Caribbean Neogene. *Proceedings of the Royal Society of London B* v. 269: p. 571-577.
- Treherne, J. E. and Foster, W. A., 1981, Group transmission of predator avoidance behaviour in a marine insect: the Trafalgar effect. *Animal Behaviour*, v. 29, p. 911-917.
- Treisman, M., 1975, Predation and the evolution of gregariousness. I. Models for concealment and evasion. *Animal Behaviour*, v. 23, p. 779-800.
- Tosh, C. R., Jackson, A. L. and Ruxton, G. D., 2006, The confusion effect in predatory neural networks. *American Naturalist*, v. 167, p. 52-65.
- Vermeij, G. J., 2005, One-way traffic in the western Atlantic: causes and consequences of Miocene to early Pleistocene molluscan invasions in Florida and the Caribbean.

- Paleobiology, v. 31, p. 624-642.
- Vermeij, G. J. and Petuch, E. J., 1986, Differential extinction in tropical American molluscs: Endemism, architecture, and the Panama land bridge. *Malacologia*, v. 17, p. 29-41.
- Vermeij, G. J., 1987, *Evolution and escalation: An ecological history of life*. Princeton University Press, Princeton, NJ.
- Vermeij, G. J. and Roopnarine, P. D., 2000, One species becomes two: the case of *Chione cancellata*, the resurrected *C. elevata*, and a phylogenetic analysis of *Chione*, *J. Moll. Stud.*, v. 66, p. 517–534.
- Vokes, E. H., 1963, Cenozoic Muricidae of the Western Atlantic Region. Part I- *Murex sensu stricto*. *Tulane Stud. Geol.*, v. 1, p. 93-123.
- Vokes, E. H., 1988, Muricidae (Mollusca: Gastropoda) of the Esmeraldas beds, northwestern Ecuador. *Tulane Stud. Geol. Paleont.*, v. 21, p. 1-50.
- Waller, T.R., 1969, The evolution of the *Argopecten gibbus* stock (Mollusca: Bivalvia) with emphasis on the Tertiary and Quaternary species of eastern North America. *Paleontology Society Memoirs*, v. 3, p. 1–125.
- Walters, C. and Juanes, F., 1993, Recruitment limitation as a consequence of natural selection for use of restricted feeding habitats and predation risk taking by juvenile fishes. *Canadian Journal of Fisheries and Aquatic Sciences*, v. 50, p. 2058–2070.
- Webb, S. D., Morgan, G. S., Hulbert Jr., R. C., Jones, D. S., Mac-Fadden, B. J. and Mueller, P. A., 1989, Geochronology of a rich early Pleistocene vertebrate fauna,

Leisey Shell Pit, Tampa Bay, Florida. *Quaternary Research*, v. 32, p. 96–110.

Woodring, W.P., 1966, The Panama land bridge as a sea barrier. *American Philosophical Society Transactions*, v. 110, p. 425-433.