

Faculty Scholarship Collection

The faculty at Allegheny College has made this scholarly article openly available through the Faculty Scholarship Collection (FSC).

Article Title	Did shell-crushing crabs trigger an escalatory arms race in the aftermath of a Late Neogene regional mass extinction event? An experimental test
Author(s)	Lisa Whitenack (Allegheny College) and Gregory Herbert
Journal Title	*Palaeogeography, Palaeoclimatology, Palaeoecology*
Citation	Whitenack, Lisa B. and Gregory S. Herbert. 2015. "Did shell-crushing crabs trigger an escalatory arms race in the aftermath of a Late Neogene regional mass extinction event? An experimental test." *Palaeogeography, Palaeoclimatology, Palaeoecology* 417: 57-65.
Link to article on publisher's website	http://dx.doi.org/10.1016/j.palaeo.2014.09.026
Version of article in FSC	Published version
Link to this article through FSC	https://dspace.allegheny.edu/handle/10456/37706
Date article added to FSC	March 16, 2015
Terms of Use	© 2014 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license http://creativecommons.org/licenses/by-nc-nd/3.0/

Information about Allegheny's Open Access Policy is available at http://sites.allegheny.edu/scholarlycommunication/
For additional articles from this collection, visit https://dspace.allegheny.edu/handle/10456/34250

Palaeogeography, Palaeoclimatology, Palaeoecology 417 (2015) 57–65

Contents lists available at ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

journal homepage: www.elsevier.com/locate/palaeo

Did shell-crushing crabs trigger an escalatory arms race in the aftermath of a Late Neogene regional mass extinction event? An experimental test

Lisa B. Whitenack [a,*], Gregory S. Herbert [b]

[a] Department of Biology, Allegheny College, 520 N. Main St., Meadville, PA 16335, USA
[b] School of Geosciences, University of South Florida, 4202 E. Fowler Ave., Tampa, FL 33620, USA

ARTICLE INFO

Article history:
Received 27 May 2014
Received in revised form 23 September 2014
Accepted 24 September 2014
Available online 5 October 2014

Keywords:
Menippe
Strombus
Extinction
Escalation
Florida

ABSTRACT

A regional mass extinction event in the late Neogene western Atlantic is widely thought to have generated evolutionary opportunities for survivors, including enemy-related adaptation (escalation). The *Strombus alatus* species complex is one potential example of this phenomenon. Strombid gastropods are abundant in the Plio-Pleistocene fossil record and Recent in subtropical Florida, and the percentage of these shells bearing a row of short spines on the last whorl increased from nearly zero to almost 100% over this time. As shell ornamentation is one of the most frequently cited defenses against both peeling and crushing predators, we exposed live spined and spineless *S. alatus* to the stone crab *Menippe*, one of its natural enemies and the predator responsible for shells scars commonly found on modern and fossil *S. alatus* shells, to test whether the increase in expression of shell spines in this species complex is consistent with an adaptive or induced response to intensifying predation pressure from durophagous crabs. We also utilize random variation in prey shell length, diameter, and lip thickness to quantify the relative importance of additional shell parameters thought to deter attacks from durophagous crabs. The central finding of this study is that neither thicker shell lips nor the modern configuration of spines determine whether *S. alatus* will be more likely to survive *Menippe* attacks or have less severe shell damage. In our experiments, the only shell trait associated with reduced damage and increased probability of survival was whorl diameter. We conclude that menippid crabs, at least those crabs within the range of large, adult sizes used in this experiment, probably did not play a primary role in the changing expression of *Strombus* spines on the last whorl in the post-Pliocene of Florida or elsewhere in tropical America. This conclusion is consistent with the position that faunal-scale increases in expression of defensive shell traits in the post-Pliocene of Florida were driven more by differential extinction of lightly armored species than escalatory responses to increasing crab predation pressure. However this conclusion is tentative and additional data are needed to explore this hypothesis fully.

© 2014 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (http://creativecommons.org/licenses/by-nc-nd/3.0/).

1. Introduction

A period of environmental upheaval that triggered a regional extinction event in the late Neogene western Atlantic is widely thought to have generated evolutionary opportunities for survivors in the form of speciation (Allmon et al., 1993; Jackson et al., 1993; Allmon, 2001; Johnson et al., 2007) and enemy-related adaptation (i.e., escalation) (Vermeij and Petuch, 1986). Escalation, the idea that biological hazards, such as competition and predation, and adaptations to those hazards have increased over time (Vermeij, 1987, 1994), was inferred by Vermeij and Petuch (1986) from a "moderate" post-Pliocene increase in the percentage of sand-dwelling gastropod genera that possess anti-predatory shell traits specific to lip-peeling crabs, such as an occluded or reinforced aperture. The notion that escalation could begin so rapidly (within 1 Ma) after loss of up to 70% of Pliocene taxa (Stanley and Campbell, 1981; Stanley, 1986; Allmon et al., 1993), however, is controversial. Disruptions or reversals of escalatory trends, even if temporary, are the normal outcome of extinction events (Vermeij, 2013) where dominant, high-powered predators or competitors are lost and not immediately replaced by invasion, and environmental stresses, such as a decline in primary productivity, impose selection pressures on survivors (e.g., reduced body size, earlier sexual maturation, etc.) that run counter to trends in adaptation to biotic factors (e.g., increased body size, investment in adult defenses, etc.) (Vermeij, 1987). If post-extinction escalation did occur, it would imply both the (1) rapid recovery of primary productivity, perhaps through the shift in ecological dominance from one type of primary producer to another, and (2) the rapid return of intense top-down pressure by competitors and consumers (Vermeij, 2004: 242). Although it can take substantial time for high-powered competitors and predators to re-evolve, invasion of high-powered species form adjacent areas less affected by extinction would speed up this phase of recovery.

* Corresponding author at: Department of Biology, Allegheny College, Meadville, PA 16335, USA. Tel.: +1 814 332 2888.
E-mail addresses: lwhitena@allegheny.edu (L.B. Whitenack), gherbert@usf.edu (G.S. Herbert).

http://dx.doi.org/10.1016/j.palaeo.2014.09.026
0031-0182/© 2014 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (http://creativecommons.org/licenses/by-nc-nd/3.0/).

At present, the increase in proportion of armored taxa in the aftermath of this extinction event is suggestive of intensified selection from enemies, but this, as noted by Vermeij and Petuch (1986), this conclusion is not yet supported by any specific ecological data. Additionally, no data were presented on changes in the relative abundance of narrow- versus broad-apertured gastropods, which may be a better indication of the average escalation state of the community as a whole before and after the Pliocene (e.g. Jemvall and Fortelius, 2002). Other plausible instances of escalation in the post-Pliocene of Florida, such as microevolutionary increases in shell thickness and size of some bivalves, have also been portrayed convincingly as isolated, co-evolutionary responses to highly specialized gastropod predators rather than as a broad, assemblage-level phenomenon involving generalist durophagous enemies (Rooperaine and Beussink, 1999; Dietl, 2003). An alternative hypothesis is, thus, that trends documented by Vermeij and Petuch (1986) reflect differential extinction of broad apertured taxa due to incidental factors unrelated to escalation, although it is unclear what incidental factors those might be.

If shell-crushing or peeling predators did trigger escalation in gastropods following the late Neogene extinction event, its most conspicuous manifestation would be the simultaneous, independent acquisition of shell spines and knobs – putative anti-predatory adaptations (Palmer, 1979) – across several genera of soft-sediment dwelling strombid gastropods (*Lobatus costatus* and *Lobatus raninus* species complexes, *Eustrombus gigas* species complex; *Strombus alatus* species complex) from the Pliocene to the Recent in subtropical Florida (Guest et al., 2008; Landau et al., 2008, 2011). Extant *Strombus* species are subjected to a wide array of predation pressures from durophagous enemies. Vertebrate predators, such as the cownose ray *Rhioptera bonasus*, the loggerhead sea turtle *Caretta caretta*, and various durophagous teleosts have been known to crush whole *Strombus* using oral or pharyngeal jaws (Yamaoka, 1978; Palmer, 1979; Taylor et al., 1980). The mantis shrimp *Gonodactylus* has been reported to peel the shell of young *S. alatus* and attempt to hammer a hole through the ultimate whorl via its smasher-type dactylus (Bertness, 1982; Balukm and Radwanski, 1996). Crabs such as *Menippe* and *Calappa* are capable of peeling and crushing adult *S. alatus*.

The *S. alatus* complex is of particular interest as it is represented in Florida as a single, morphologically changing lineage, and Pliocene to Recent trends in its morphology are well documented (Hargreave, 1995). *Strombus* is also one of the most abundant survivors of this extinction event in both Pleistocene fossil deposits (Geary and Allmon, 1990) and modern coastal habitats (Clench and Abbott, 1941). This population characteristic is important, because common taxa are more likely to exhibit general adaptive trends than rare taxa, whose specializations may not be representative of assemblage-level patterns (Jernvall and Fortelius, 2002).

Since the Pliocene, the percentage of *Strombus* spp. shells in Florida bearing a row of short, conical spines on the last whorl has increased from close to zero to nearly 100%, while the maximum number of spines on the last whorl has increased from less than three to around eleven (Goodrich, 1944; Petuch, 1994; Hargreave, 1995; Herbert et al., 2004) (Fig. 1). Similar trends are seen in other fossil *Strombus* species from the Caribbean (Landau et al., 2008, 2010, 2011; Freiheit and Geary, 2009). Following Vermeij and Petuch (1986), Herbert et al. (2004) speculated that morphological changes in the *S. alatus* complex were possibly an escalatory response triggered by intensifying attacks from durophagous crabs, which are abundant in modern habitats and Plio-Pleistocene shell beds where *S. alatus* and its fossil predecessors occur (Britton and Morton, 1989; Portell and Agnew, 2004). The distinctive scars left by crab chelae are the most common predation trace on fossil and modern *Strombus* shells (Herbert et al., 2004), which suggests that crab predators were potentially important selective agents of *Strombus* morphology (Ditel and Herbert, 2010).

Here, we employ an experimental approach to test the hypothesis that the shell spines acquired by *Strombus* spp. in the aftermath of the late Neogene extinction event deter predatory attacks by the most common decapod predator of gastropods in coastal habitats in the Gulf of Mexico, the stone crab *Menippe* (Bert, 1985; Brown and Haight, 1992; Beck, 1995, 1997). Random variation in prey shell length (columella height), diameter, and lip thickness between mature *S. alatus* used in this experiment allowed us to quantify the relative importance of additional shell parameters previously cited to deter attacks from durophagous crabs in other gastropod species (e.g., Hughes and Elner, 1979; Vermeij, 1982; West et al., 1991; Rochette et al., 2007). Testing whether shell spines do, in fact, increase survival in *Strombus* prey exposed to crabs is a critical test of the hypothesis that spine evolution in *Strombus* occurred, at least partly, in response to durophagous crabs. We conducted a predator–prey experiment with live *Menippe* fed extant *S. alatus*, where we compared the outcomes of *Menippe* attacks on *S. alatus* having the modern morphology of 11 spines with the outcomes of attacks on *S. alatus* that had been mechanically altered

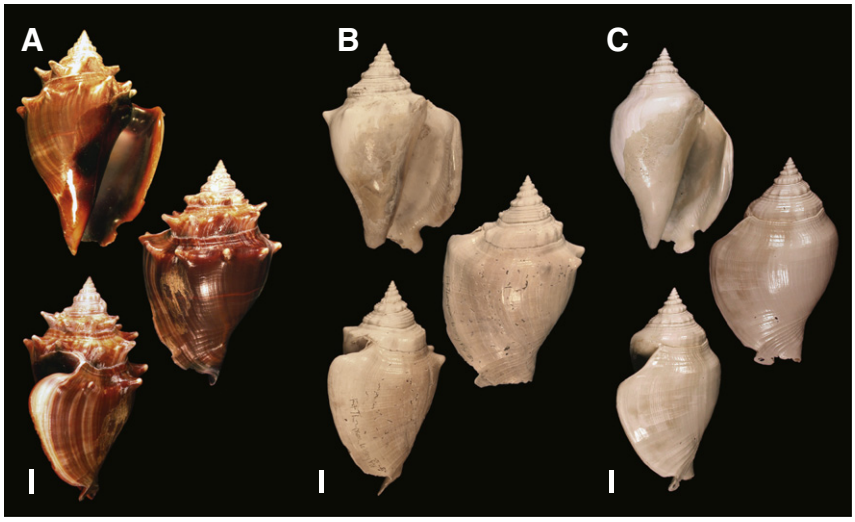


Fig. 1. *Strombus* sp. shells from Florida showing changes in the typical number and placement of shell spines through time. A. Recent *S. alatus* from Bonita Beach, Lee County, Florida. B. *S. alatus*, Ft. Thompson Formation (0.95–0.22 Ma), Leisey Shell Pit, Ruskin, Hillsborough County, Florida. C. *Strombus evergladesensis* Petuch, 1991, Bermont Formation (1.6–1.1 Ma), Longan Lakes Shell Pit, Naples, Collier County, Florida. Scale bar = 1 cm.

(i.e., shell spines removed) to mimic phenotypes that were common in the Pliocene and early Pleistocene but are exceedingly rare (<1%) today (Goodrich, 1944). These "ancient" phenotypes include shells having no spines on the ultimate whorl (here called the "no spine" condition) and shells having three spines roughly 180° from the aperture on the ultimate whorl ("three spine" condition) (Fig. 1).

2. Materials and methods

Seven adult *Menippe mercenaria–adina* hybrids (carapace width = 84.0–96.3 mm), hereafter simply referred to as *Menippe*, were obtained from Gulf Specimen Marine Laboratories (Panacea, Florida). Both male and female crabs were used in this study. All crabs used in this experiment were right-handed; that is, the right chela was always the larger crusher claw. Each crab was housed in its own 38 L tank with 0.5 cm of coarse sand and crushed shell substrate, and recirculating seawater. The sides and tops of aquaria were covered with black paper to prevent the crabs from seeing crabs in adjacent tanks and from being startled by lab personnel monitoring the experiment. This also served to simulate the dark burrow environment in which stone crabs typically feed. *Menippe* is typically nocturnal (Powell and Gunter, 1968); however they readily fed during the day in this study.

Adult male and female *S. alatus* were collected from Bonita Beach, Florida and west of Marco Island in the Gulf of Mexico (24° 29.87′ N, 81° 90.11′ W). None of the specimens chosen had any shell breakage or repair from previous predation attempts. Snails were housed in groups of 10 in 38 L tanks with approximately 2 cm of coarse sand substrate and recirculating seawater. All organisms were maintained at 23 °C and a salinity of 34–36 ppt.

S. alatus were divided into three groups based on lip thickness as measured by digital calipers at the lip margin, halfway between the posterior and anterior ends of the lip. The three groups were thin-lipped (0.4–1.5 mm, mean ± SD = 1.0 ± 0.34 mm), medium-lipped (1.6–2.5 mm, 2.02 ± 0.29 mm), and thick-lipped (2.6–4.8 mm, 3.15 ± 0.44 mm). In addition to measuring lip thickness (mm), columella length (mm) and diameter of the ultimate whorl between spines (mm) were also measured. Within each lip thickness grouping, snails were haphazardly assigned to one of three ornamentation treatments: maintaining all spines ("all spines"), removing all spines from the last, or ultimate, whorl ("no spines"), and removing spines from the first 180° of the ultimate whorl, with degrees measured beginning with the terminal lip ("three spines") (Fig. 2). Spines for the "no spine" and "three spine" condition were removed by mechanical abrasion with a polishing lap.

2.1. Effects of spine removal on shell strength

In order to determine whether the process of mechanically removing spines weakened *S. alatus* shells, a possible confounding factor in our study, we employed indentation testing. An aluminum cast of a *Menippe* "crusher" propodus (length = 55.46 mm) (Fig. 3A) was mounted to a MTS 858 MiniBionix II universal testing system (Eden Prairie, Missouri). Twenty live thick-lipped *S. alatus* were used: ten "all-spine" and ten "no spine" (mean ± SD for "all spine" and "no spine" respectively: lip thickness: 4.0 ± 0.5 mm, 3.9 ± 0.2 mm; columella length: 71.2 ± 4.0 mm, 71.6 ± 3.7 mm; shell diameter: 32.0 ± 2.3 mm, 31.8 ± 2.3 mm). Each *S. alatus* was individually placed aperture-down on a walled steel platform lined with a thin piece of leather, which allowed the shell to be held firmly in place and prevent slipping during tests (Fig. 3B). The platform rested upon a 5 kN load cell to obtain force magnitudes at the time of shell breakage. The molar tooth of the propodus was positioned to contact the shell just below the spine row (or abraded spine row) on the ultimate whorl. Trials were run at a displacement rate of 0.3 mm/s, based on loading rates in previous studies (Miller and LaBarabera, 1995; Stefaniak et al., 2005) and stopped once the shell failed. For each trial, we recorded force at shell failure ($F_{failure}$, N). However, the amount of applied force required to break a structure is related to the thickness of a structure; thicker materials require more force to fail compared to thinner materials, when all other material properties are held equal. As we could not control for natural variation in internal shell thickness in the *S. alatus* used in these mechanical tests, we also measured shell thickness (mm) at the site where the aluminum claw contacted the shell to use as a covariate in subsequent statistical analyses. If shell strength is not affected by the mechanical removal of spines, any differences among shell conditions in our predation experiments may be attributed to morphology.

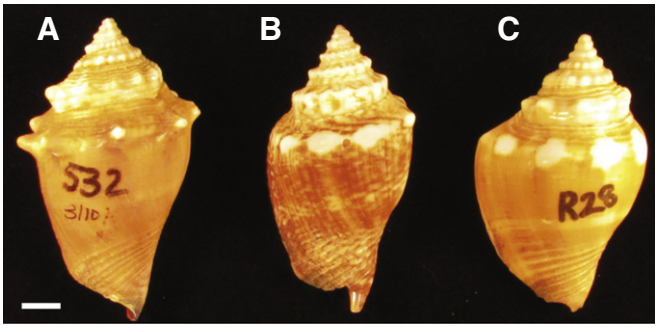


Fig. 2. *Strombus alatus* shells demonstrating spine condition. A. "All spine" condition. B. "Three spine" condition. C. "No spine" condition.

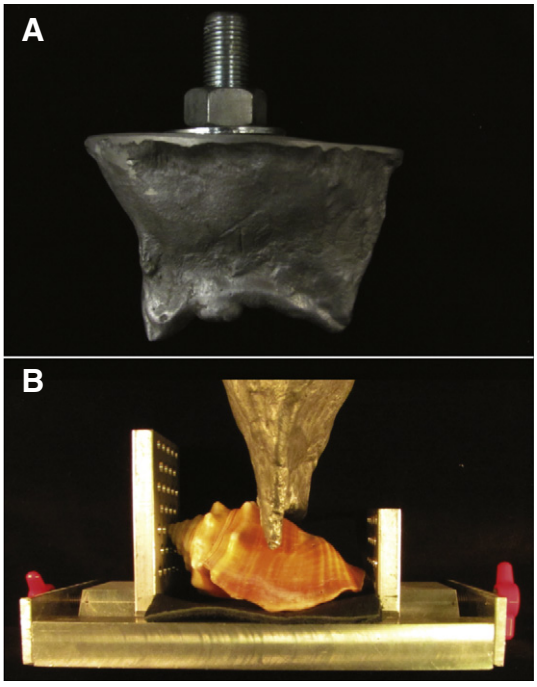


Fig. 3. Shell strength testing apparatus. A. Aluminum cast of *Menippe* propodus. B. Walled platform used to secure *S. alatus* shells during testing with aluminum propodus in place for testing.

2.2. Predation experiments

To test the effect of *S. alatus* shell morphology on survival of *Menippe* predation attacks, each crab was offered a single live *S. alatus* in each of the spine-lip thickness combinations by placing the *S. alatus* in the crab's aquarium. Snails were assigned to crabs haphazardly, which included three replicates of each of the nine lip-spine combinations presented to each crab. Due to occasional crab mortality, some crabs received fewer prey, resulting in 181 trials overall (all spine $N = 61$, three spine $N = 51$, zero spine $N = 69$). We also directly observed eleven total predation attempts by four crabs to survey prey handling behavior.

Each *S. alatus* was left in the crab tank for 72 hours and then removed whether it was eaten or not. If the snail was eaten, the crab was not fed again for 7 days to ensure that the crab would be hungry and motivated to attack the next prey item. If the snail was not eaten, it was immediately exchanged for a different *S. alatus*. If this snail was not eaten within 72 hours, the snail was removed and a *Mytilus* mussel was given to the crab to meet the crab's basic dietary needs; crabs were given 7 days before being fed again. All non-eaten *S. alatus* were euthanized immediately following the predation trial.

All *S. alatus* used in the predation experiments, whether eaten or not, were examined for shell damage following removal from the crab tanks. For damage to the spire, siphonal canal, and columella, a simple absence/presence was recorded. Damage to the spines was also recorded as absence/presence, as well as whether damaged spines were on the ultimate whorl, penultimate whorl, or both whorls. For shells in which the lip had been peeled back, the extent of damage was recorded as an angle from the terminal lip, where 360° = peeling of the entire ultimate whorl, 180° = peeling of half of the ultimate whorl, etc. To collect angle data, shells were oriented "upright," markers were placed on the ultimate whorl at the point of furthest damage from the lip and at the lip of the shell (or identifiable remnants of the lip near the suture), and the angle of damage was measured in SigmaScan (SPSS, New York) from the lip to the shell axis to the point of furthest damage (Fig. 4). In some cases, the damage to the lip was minor and did not extend past the shoulder. For these shells, we assigned a value of 1° to allow for statistical testing. Shells with not even minor lip damage were scored as 0°.

2.3. Statistical analysis

To confirm that shell thickness was correlated with $F_{failure}$, we used a Pearson's product moment correlation, followed by an ANCOVA with shell thickness as the covariate to determine whether mechanically removing spines decreased shell strength. The influence of shell morphology on the ability of *S. alatus* to survive predation attacks by *Menippe* was investigated by multiple logistic regression. The dependent variable was whether *S. alatus* was consumed or not (a consumed snail was considered a positive response), and the independent variables were lip thickness, shell diameter, columella length, and spine condition (all spines, no spines, three spines), with the latter coded as a set of two dummy variables (SC1, SC2) to satisfy the conditions of the multiple logistic regression. Lip thickness was not treated as a categorical variable, as it was used as a guide to ensure a somewhat even distribution of spine conditions across lip thickness values. Significance of the overall regression was determined by a likelihood ratio test statistic (D), while significance of the dependent variables was determined by Wald statistics. A similar series of multiple regressions was used to determine whether these same independent variables contributed to presence of damage in presence/absence damage categories (spihonal canal, spines, and columella). Damage to the spire could not be analyzed this way, as there were too few individuals with this type of damage to run a multiple logistic regression. Angle of damage was analyzed using a multiple linear regression with the same independent variables as the other damage regressions. Differences in damage between consumed and non-consumed *S. alatus* were assessed with a series of chi-square tests of independence, and this same test was used to further illustrate the influence of spine condition on damage metrics. For all tests, an α level of 0.05 was used to determine significance. All statistical analyses were performed in PAST (Hammer et al., 2001) or SigmaStat (SPSS, New York).

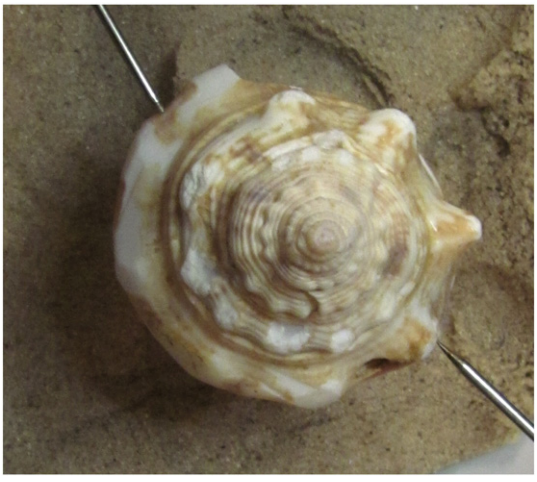


Fig. 4. *Strombus alatus* shell in position for measuring angle of damage. Markers are placed at the point of furthest damage from the lip and at the lip of the shell. Angle of damage is measured using these points and the shell apex as the vertex of the angle.

3. Results

3.1. Effects of spine removal on shell strength

As expected, $F_{failure}$ was correlated with shell thickness ($r = 0.472$, $p = 0.036$). When accounting for the effect of shell thickness (mean ± SD spineless = 0.7 ± 0.2 mm, intact = 0.7 ± 0.3 N), mechanically removing the spines did not have an effect on $F_{failure}$ (mean ± SD spineless = 1182.7 ± 440.2 N, intact = 1020.9 ± 383.6 N; $F_{1,17} = 0.854$, $p = 0.368$).

3.2. Predation experiments

3.2.1. Prey handling behaviors of Menippe

Prey handling was observed in 11 trials plus numerous feedings in the pre-experiment acclimation period, all on *S. alatus* with all spines intact (Fig. 5). Predation attempts lasted anywhere from 2 to 15 minutes and began with an initial phase in which the crab would orient and then re-orient the prey shell repeatedly with the legs and chelae to find an optimal handling orientation. This process was combined with frequent testing of the prey shell for weak points in which the crab used its right claw (the crusher) to crush or peel the shell. Shells that sustained little or no damage within this preliminary manipulation and testing phase were dropped, but dropped shells were often recaptured and subjected to further predation attempts.

The orientation of the prey shell to the crab varied between predation attempts, depending on the stage of the attack. In the earliest attack stage, the prey shell was typically oriented aperture up, with the spire facing the crab. In this phase, the left chela (the pincer or cutting claw) was used to hold the prey shell at the spire, lip, columella, or siphonal canal, while the right chela (crusher claw) closed on the spire or columella in an attempt to crush the shell outright. In some instances, *Menippe* used the left chela and arm to cradle the shell against its body without grasping it with the claw. If outright crushing failed, lip peeling attempts often followed. In peeling attempts, the prey shell was generally manipulated so that its axis was perpendicular to the anterior–posterior axis of the crab, aperture up (Fig. 5A) or down (Fig. 5C), and with the spire of the prey shell near the right chela and the siphonal canal closest to the left chela. To break the shell, the right chela would close over the posterior portion of the lip. If the aperture of the shell was pointed upward, the entire right appendage would then rotate either dorsally or ventrally, similar to a human using a bottle opener. In one trial, the crab made a small chip in the shell lip with its pincer claw instead of its crusher, while holding the columella with the crusher, such that the aperture faced up and spire toward the crab's body. If the aperture was pointed downward, the crusher claw would close over the shell with the molar tooth over posterior-most edge of the lip, near the suture, as well as part of the spire and the middle part

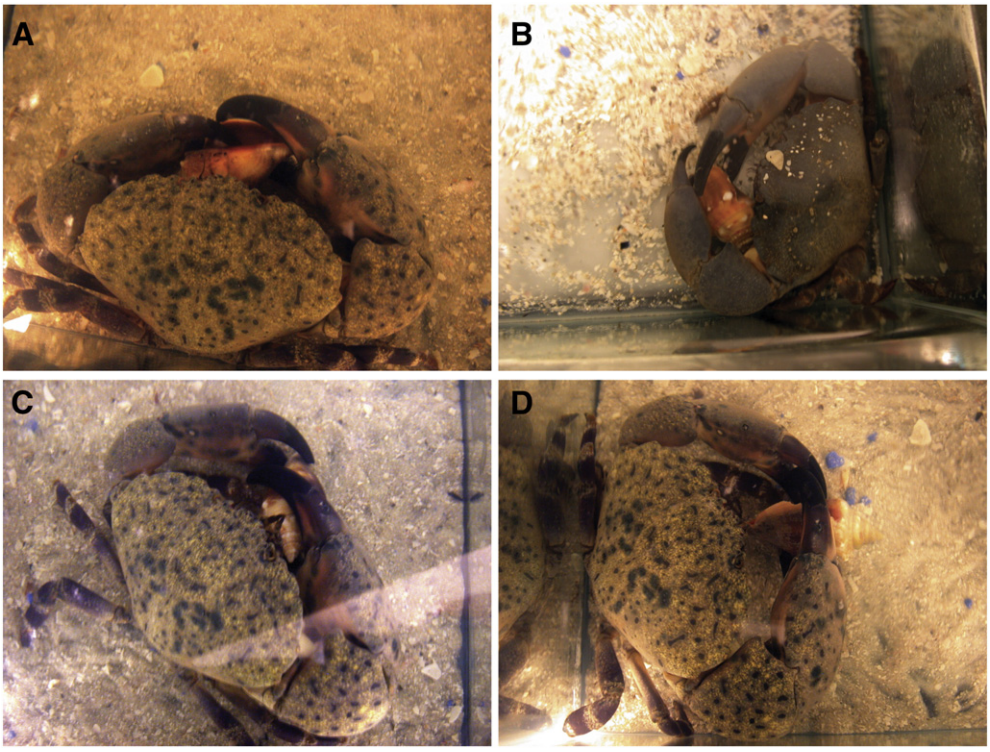


Fig. 5. Prey handling by *Menippe* showing interaction between *Menippe* claws and *Strombus* shell. A. *Strombus* held aperture up by the pincer (left) claw, with the crusher (right) claw breaking the columella and siphonal canal. B. *Menippe* cradling the shell with its pincer claw and peeling the shell lip with the crusher claw. C. *Strombus* held aperture down by the pincer claw over the siphonal canal, with the crusher claw crushing the shell spire. D. *Menippe* holding the shell with its crusher claw and inserting its pincer claw into the aperture to reach the snail.

of the claw over the body whorl (Fig. 5C). This orientation typically led to crushing damage rather than lip peeling.

Between, and occasionally before, breakage attempts, *Menippe* would attempt to extract the soft tissue from the shell with the pincer claw (Fig. 5D). In two trials, the same individual crab unsuccessfully attempted to pull the snail out of the shell with its crusher. If initial attempts at extraction were unsuccessful, crabs would return to damaging the shells. Successful predation attempts ended when *Menippe* was able to extract soft tissue out of the shell with the pincer claw. Unsuccessful predation attempts ended when the crab dropped the shell and did not attempt to recapture the snail.

Crabs had varying amounts of success removing the gastropod from its shell once it was able to grasp the snail's body. In one case, the gastropod's operculum was torn from the body, though the snail was not ultimately killed and consumed. In most cases, when shells of consumed snails were removed from the crabs' tanks and cleaned, snails were only partially consumed, with some parts of the visceral mass (e.g., gonads, digestive glands) left in the upper shell whorls.

3.2.2. Prey behavior of S. alatus

In the trials described above, we did not observe any attempts by the prey to escape *Menippe*. Snails were already withdrawn into their shells as they were placed in the tank and remained so throughout the predation attempt. During the overall experiment, we did observe snails in their non-withdrawn state, crawling along the tank floor, after failed predation attempts.

3.2.3. General types of shell damage

Out of 181 total trials, 175 (96.7%) of all prey shells offered exhibited some degree of damage. Five (3%) of the 175 damaged *S. alatus* shells were completely destroyed (i.e., reduced to fragments). In such cases, some damage metrics, such as the angle of damage, could not be measured. All completely destroyed shells belonged to the "no spine" (2 snails, 2.8%) and "three spine" (3 snails, 5.9%) treatments, but given the rarity of this type of damage, the relationship between complete shell destruction and spine condition could not be assessed statistically (Table 1).

Overall, lip peeling and chipping of the columella were the most common types of damage (79.9% and 79.0%, respectively), followed closely by damage to spines (75.7%) (Fig. 6, Table 1). When the three spine and all spine conditions are considered, ultimate whorl spine damage occurred in 57.7% of individuals. When all of the spine conditions for *S. alatus* are taken into account, penultimate whorl spine damage occurred in 64.8% of individuals, and damage to spines on whorls above the penultimate whorl was found on 35.8% of individuals. Approximately half of the prey had part of the siphonal canal removed (52.5%). The least common types of damage were clipping of the spire (10.5%) and punching through the ultimate whorl away from the aperture (2.2%). The angle of peeling for all attacks damage ranged from 0° (no damage to the lip) to 360° (entire ultimate whorl removed), with a mean ± SD of 112.6 ± 75.2° (Table 1).

3.2.4. Influence of shell traits on shell damage

In general, spine condition did not contribute to the likelihood of exhibiting any particular type of damage (Table 2), and damage types were not statistically different across the three spine conditions ($\chi^2_2 = 0.06$–4.91, $p > 0.05$ for all tests). This was primarily due to large standard deviations in measured effects, which is particularly evident in the extent of peeling damage on shells (mean + SD: no spine = 119.0 ± 70.6°, three spine = 117.5 ± 70.9°, all spine = 102.1 ± 82.9°) (Table 1). Likelihood of damage to the columella did not have a relationship with any measured shell characteristic (spine condition, columella length, shell diameter, and lip thickness), as indicated by a nonsignificant multiple logistic

Table 1
Percent and number (in parentheses) of *S. alatus* shells consumed, damaged, and displaying each type of damage measured in this study ($N = 181$). Shells are divided by spine treatment type. C = consumed, N = not consumed, N/A = not applicable, Total = overall for that spine condition, regardless of whether the snail was consumed or not. Total measurement across shells for spine damage to ultimate whorl is only for the three spine and all spine conditions ($N = 112$). Mean ± SD given for angle of damage (degrees).

	No spine			3 spine			All spines			Total across all shells ($N = 181$)
	C ($N = 39$)	N ($N = 30$)	Total ($N = 69$)	C ($N = 32$)	N ($N = 19$)	Total ($N = 51$)	C ($N = 28$)	N ($N = 33$)	Total ($N = 61$)	
Columella	94.9% (37)	63.3% (19)	81.2% (56)	100.0% (32)	52.6% (10)	82.4% (42)	96.4% (27)	54.6% (18)	73.8% (45)	*79.0% (143)*
Spines	81.1% (32)	63.3% (19)	71.0% (51)	93.8% (30)	36.8% (7)	72.5% (37)	96.4% (27)	72.7% (24)	83.6% (51)	*75.7% (137)*
Ultimate whorl	N/A	N/A	N/A	59.3% (19)	21.1% (4)	45.0% (23)	71.4% (20)	33.3% (11)	68.9% (31)	*48.2% (54)*
Penultimate whorl	64.1% (25)	56.7% (17)	60.8% (42)	84.3% (27)	31.5% (6)	64.7% (33)	78.6% (22)	57.6% (19)	67.2% (41)	*64.1% (116)*
Above penultimate whorl	33.3% (13)	13.3% (4)	24.6% (17)	40.6% (13)	10.5% (2)	29.4% (15)	50.0% (14)	9.0% (3)	27.9% (17)	*27.1% (49)*
Siphonal canal	56.4% (22)	40.0% (12)	49.3% (34)	65.6% (21)	31.6% (6)	52.9% (27)	82.1% (23)	33.3% (11)	55.7% (34)	*52.5% (95)*
Spire	18.0% (7)	3.3% (1)	11.6% (8)	18.8% (6)	10.5% (2)	15.7% (8)	7.1% (2)	3.0% (1)	4.9% (3)	*10.5% (19)*
Whorl punch	0.0% (0)	3.3% (1)	1.4% (1)	3.1% (1)	0.0% (0)	2.0% (1)	3.6% (1)	3.0% (1)	3.3% (2)	*2.2% (4)*
Peeling damage	97.1% (38)	70.0% (21)	85.5% (59)	96.6% (31)	57.9% (11)	83.3% (42)	96.4% (27)	51.5% (17)	72.1% (44)	*79.9% (145)*
Angle of damage	158.0 ± 51.6	73.43 ± 62.4	119.0 ± 70.6	157.6 ± 48.1	56.3 ± 54.4	117.5 ± 70.9	166.5 ± 60.5	47.39 ± 55.5	102.1 ± 82.9	*112.6 ± 75.2*
Completely destroyed	5.2% (2)	0.0% (0)	2.8% (2)	9.4% (3)	0.0% (0)	5.9% (3)	0.0% (0)	0.0% (0)	0.0% (0)	3.0% (5)
Consumed	56.5% (39)			62.7% (32)			45.9% (28)			54.7% (99)
Damaged	100.0% (69)			96.1% (49)			95.10% (58)			93.7% (175)

regression ($D = 4.02$, $p = 0.546$). The regression for spine damage to any whorl and shell characteristics was nonsignificant overall ($D = 9.60$, $p = 0.087$) (Table 2).

Other traits, however, did influence the likelihood and severity of certain types of shell damage. The multiple logistic regression for angle of peeling damage was significant ($F_{5,165} = 3.211$, $p = 0.009$); *S. alatus* with smaller diameters exhibited significantly larger angles of damage (Table 2). Lip thickness exhibited a significant relationship with the presence of spine damage, where thinner-lipped *S. alatus* were more likely to exhibit spine damage (Table 2). Lastly, the regression for siphonal canal damage was marginally nonsignificant ($D = 10.68$, $p = 0.058$). However, both columella length and shell diameter exhibited significant relationships with this damage type (Table 2). *S. alatus* exhibiting damage to the siphonal canal were more likely to have a longer columella and smaller shell diameter. Due to the small number of whorl punches, we did not run a regression on this metric.

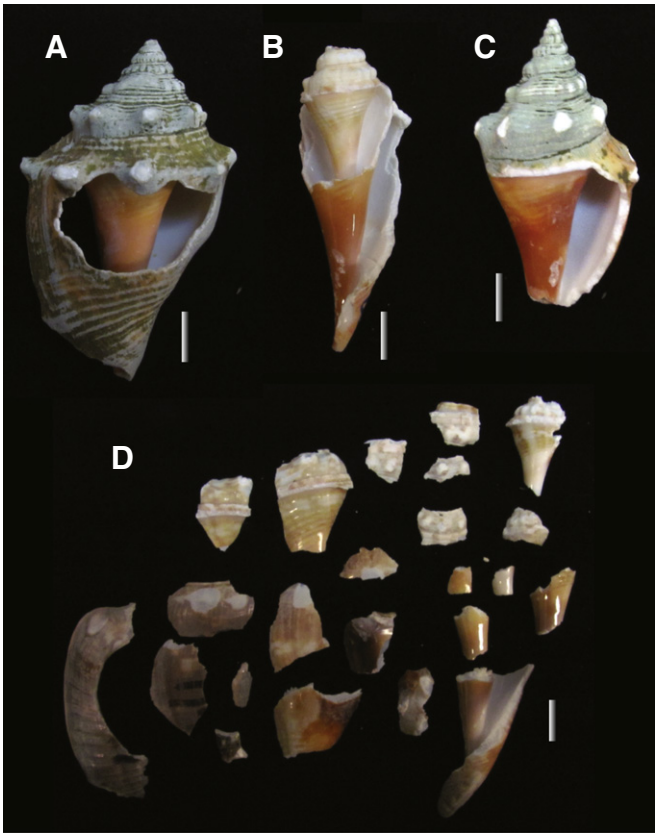


Fig. 6. Representative damage caused by *Menippe* during predation attempts. A. *S. alatus* ("all-spine" condition) showing damage to the spines and a whorl punch. Shell length: 67 mm. B. *S. alatus* ("three spine" condition) with damage to the spire, columella, and shell lip. Shell length as pictured: 63 mm. C. *S. alatus* ("three spine" condition) with damage to the columella, siphonal canal, spines, and shell lip. Damage to spine on ultimate whorl due to removal by experimenter. Shell length as pictured: 59 mm. D. *S. alatus* completely destroyed. Length of lip piece on left side of figure: 48 mm.

3.2.5. Influence of shell traits and damage types on prey survival

Out of 181 total trials, 99 (54.7%) prey were killed and partly or completely consumed. Based on the results of the significant multiple logistic regression ($D = 19.24$, $p = 0.002$), neither spine condition, columella length, nor lip thickness predicted whether *S. alatus* was more likely to survive predation attempts by *Menippe*. The only significant predictor of prey survival was large shell diameter (Table 3). All consumed *S. alatus* exhibited some sort of damage (Table 1), but consumed *S. alatus* exhibited more damage in all categories, compared to those that were not consumed, with the exception of ultimate whorl punch (2.0% for both) (Table 4). However, 45.9% of "all spine" shells

Table 2
Results of significant multiple regressions to determine which *S. alatus* shell characteristics contribute to the likelihood of damage by *Menippe* (nonsignificant regressions not shown). For all dependent variables, presence of the damage category is the positive response. SC1 and SC2 = dummy variables for spine condition, CL = columella length, DS = shell diameter, LT = lip thickness, * = significant *p*-value, $^{+}$ = *t*-test used for linear regression.

Dependent	Independent	Coefficient	Standard error	Wald statistic	*p*-Value
Spines	Constant	−1.30	2.32	0.32	0.574
	SC 1	0.30	0.43	0.49	0.482
	SC 2	0.69	0.44	2.46	0.117
	CL	0.05	0.05	1.37	0.241
	DS	−0.02	0.08	0.04	0.837
	LT	−0.49	0.20	5.71	0.017*
Siphonal canal	Constant	−2.07	1.95	1.13	0.288
	SC 1	0.24	0.37	0.40	0.527
	SC 2	0.21	0.36	0.36	0.551
	CL	0.11	0.04	7.34	0.007*
	DS	−0.17	0.07	6.88	0.009*
	LT	0.04	0.17	0.05	0.831
Angle of damage	Constant	258.80	68.29	3.79^{+}	<0.001*
	SC 1	5.25	13.47	0.39^{+}	0.697
	SC 2	−17.81	12.78	−1.39^{+}	0.165
	CL	0.95	1.36	0.70^{+}	0.488
	DS	−5.65	2.25	−2.51^{+}	0.013*
	LT	−10.71	6.13	−1.75^{+}	0.082

Table 3
Results of multiple logistic regression to determine which *S. alatus* shell characteristics contribute to the likelihood of being consumed by *Menippe*. The dependent variable is whether *S. alatus* was consumed by *Menippe*, with consumption being the positive response. SC1 and SC2 = dummy variables for spine condition, CL = columella length, DS = shell diameter, LT = lip thickness, * = significant *p*-value.

Variable	Coefficient	Standard error	Wald statistic	*p*-Value
Constant	4.51	2.05	4.82	0.028*
SC 1	0.44	0.39	1.30	0.255
SC 2	−0.53	0.37	2.04	0.153
CL	0.04	0.04	1.02	0.312
DS	−0.20	0.07	8.80	0.003*
LT	−0.23	0.17	1.75	0.186

were consumed compared to 56.5% of "no spine" shells and 62.7% of "three spine" shells (Table 1). The standard deviations for the mean angle of damage were high, and in one case (all spines, not consumed) larger than the mean angle of damage (47.39 ± 55.5°), indicating that the data tended to fall at the extremes of very little or very high amounts of peeling damage (Table 1).

4. Discussion

Modern shells of *S. alatus* typically have a row of 11 evenly-spaced spines on the last whorl (Goodrich, 1944), while spines on fossil *Strombus* from the Pliocene and Pleistocene are greatly reduced in number and have irregular spacing or are absent entirely (Goodrich, 1944; Petuch, 1994; Hargreave, 1995; Herbert et al., 2004). Shell ornamentation is one of the most frequently cited defenses against both peeling and crushing predators, and several predator–prey experiments have largely confirmed this (Hughes and Elner, 1979; Vermeij, 1982; West et al., 1991; Rochette et al., 2007). Therefore, to test whether the modern number and regular spacing of *Strombus* shell spines on the last shell whorl are consistent with an evolutionary or induced response to intensifying predation pressure from durophagous crabs, we exposed live spined and spineless *S. alatus* to the stone crab *Menippe*, one of its natural enemies and the predator responsible for shells scars commonly found on modern and fossil *S. alatus* shells (Herbert et al., 2004; Portell and Agnew, 2004). Given previous work on spine function in gastropods, we expected the presence of spines to deter successful attacks and reduce damage by making prey shells stronger or more difficult to manipulate (Vermeij, 1974; Palmer, 1979; Savazzi, 1991; Miller and LaBarabera, 1995). The central finding of this study is that neither the modern configuration of 11 spines nor even a thick shell lip determines whether *S. alatus* will be more likely to survive *Menippe* attacks or have less severe shell damage than *S. alatus* with fossil configurations of three or zero spines. In our experiments the only shell trait associated with reduced damage and increased probability of survival was a large whorl diameter.

4.1. The effect of shell morphology on deterring Menippe predation

While adding spines does locally increase the amount of material that must be broken and should increase the amount of force necessary to break through that region of the shell, it is only a local effect. Indeed, crabs such as *Carpilius* will break off knobs and spines on gastropods such as *Vasum* and *Drupa* without significant damage to other parts of the shell (Vermeij, 1978), and in mechanical tests similar to those in this study, removing ornamentation on *Chicoreus dilectus* did not affect the overall strength of the shell (Miller and LaBarabera, 1995). Spines occur at the level of the shoulder, and therefore would only serve to protect that area. The rest of the ultimate whorl is left at the baseline thickness and thus is weaker than the shoulder region.

Palmer (1979) argued that crabs manipulate their claws precisely to avoid spines of the type exhibited in *S. alatus* and should not be deterred by such ornamentation. We find that this statement is true, although not in the manner expected. Several attacks we observed were initiated along the lip away from (anterior to) the spine row (Fig. 5B) and were likely unaffected by the presence or absence of spines. However, most attacks by *Menippe* involved direct interaction between the crab's crusher claw and the strombid spines, as evidenced by the fact that 67% of attacks on individuals with a full spine row resulted in damage to those spines, including shearing of spines at their bases. In fact, spine damage was the most common type of shell damage we measured. Not only do crabs not avoid spines, but they seem to be drawn to the portion of the lip closest to the spine row when initiating an attack.

There are two primary reasons why crabs may be drawn to rather than avoid the general area near the spine row. First, the aperture at this point is widest and offers relatively deeper access (i.e., better leverage) for the large claws of *Menippe* (Savazzi, 1991). We also observed in our experiments that *Menippe* may use *Strombus* spines to stabilize its claw against lateral slippage during lip peeling. In several of the attacks we observed, *Menippe* rested its molar tooth in the saddle-like depression between adjacent spines. Damage to spines may be occurring due to (1) top-down compression as the crab tests claw positions and/or (2) lateral shearing by the molar tooth, which is most likely to occur as the crab rotates its appendage. We also occasionally observed *Menippe* losing control of the shell during breakage attempts. This could cause the spines to shear off as the snail slips from the crab's grasp.

Shell thickness of the dorsal shell whorl and lip was also not effective in deterring predation by *Menippe* because of the amount of force that *Menippe* is capable of generating. Our tests of *S. alatus* shell strength at the dorsal part of the ultimate whorl revealed mean failure forces of just 1021 ± 383 and 1183 ± 440 N for shells with spines removed and intact, respectively. By comparison, some *Menippe* can produce nearly 1500 N of force (Whitenack et al., unpublished data), well beyond the mechanical strength of fossil or modern *S. alatus* shell whorls. The lip is also subject to attacks where *Menippe* seizes the shell lip with the crusher claw and rotates the entire arm, in a similar style to a human using a bottle opener. Adding this rotation, or torque, turns the shell lip into a cantilever beam, where one end of the beam is free (in this case, the edge of the lip) and the other is fixed. When loaded in this manner, the shell lip experiences compression on one face and tension on the other. Molluscan shells, including those of strombids (Currey, 1980), are anisotropic; their material properties vary with the direction of loading and are stronger in some loading regimes (e.g., compression) compared to others (e.g., tension) (Currey and Kohn, 1976; Laraia and Heuer, 1989). Given the high forces these crabs are capable of producing, *Menippe* may simply be strong enough to overcome lip thickness defense by applying tension during peeling.

Shell diameter had a significant effect on *S. alatus* damage and survival metrics, which is in agreement with numerous studies on the importance of large size as a defense against durophagous predators (e.g., Hamilton, 1976; Hughes and Elner, 1979; West et al., 1991; Kitching et al., 1966; Rochette et al., 2007;). Given the manner in which *Menippe* preys upon *S. alatus*, we suggest that claw gape limitation is why shell diameter matters. *Menippe* grasps *S. alatus* in its cutting claw, usually around the penultimate whorl, to secure the shell for

Table 4
Percentage and number (in parentheses) of all consumed and non-consumed *S. alatus* ($n = 181$) exhibiting specific damage types and χ^2 results. No test was run on whorl punches, as the percentages are identical. * = significant *p*-value.

	Consumed ($N = 99$)	Not consumed ($N = 82$)	χ^2	*p*-Value
Columella	97.0% (96)	57.0% (47)	40.16	<0.001*
Spines	87.9% (87)	61.0% (50)	16.21	<0.001*
Siphonal canal	66.7% (66)	35.0% (29)	16.39	<0.001*
Spire	15.2% (15)	18.3% (4)	4.50	0.034*
Whorl punch	2.0% (2)	2.4% (2)	–	–

crushing or peeling by the larger claw. Given that the cutting claw is relatively small, *S. alatus* with wider whorls, in general, should be more difficult to handle and stabilize, as the crab may not be able to generate sufficient force to firmly hold the shell during the breaking attempt. Interestingly, the Recent *Strombus pugilis* from the tropical western Atlantic typically has very long spines on the penultimate whorl but reduced or no spines on the ultimate whorl. We propose that this peculiar distribution of spines on *S. pugilis* shells is consistent with an adaptive response to gape-limited, durophagous crabs (e.g., *Menippe*) that grasp the penultimate whorl with the smaller cutter claw but are not deterred by spines on the ultimate whorl. Furthermore, we predict that if similar crab predators had any influence on the evolution of *Strombus* spp. in the Plio-Pleistocene of Florida, then ongoing work on *Strombus* morphological evolution (e.g., Herbert et al., 2004; Kosloski et al., 2008; Ditel and Herbert, 2010) should find a trend of increasing effective diameter of the penultimate whorl due to: (1) actual increase in diameter of the penultimate whorl, (2) addition of spines to the penultimate whorl, and/or (3) increasing spine size or number on the penultimate whorl.

4.2. Possible causes of increased expression of shell spines in Strombus s.s. since the Pliocene

Although we have ruled out large menippid crabs as possible selective agents driving the increase in spine expression on the ultimate whorl of Neogene *Strombus*, we have not ruled out an escalatory origin in general. Our experimental design does not consider the role of smaller and weaker menippid crabs or large vertebrate predators, including the cownose ray *R. bonasus*, the loggerhead sea turtle *C. caretta*, and various durophagous teleosts, which attack small mollusks by crushing the entire shell between the oral or pharyngeal jaws (Yamaoka, 1978; Taylor et al., 1980). Small shell spines are already known to increase an individual snail's fitness in attacks by these gape-limited vertebrates by increasing the shell's effective diameter but also by redistributing crushing forces over the thickest parts of the shell (Palmer, 1979).

The possible influence of vertebrate predators in the evolution of shell spines in *Strombus* in the post-Pliocene of Florida is supported by patterns of morphological change in co-occuring strombid genera (Guest et al., 2008), which were possibly interacting with the same selective agents. In the *Lobatus* species complex, where shells often exceed 200 mm in length, Recent and Pleistocene shells from Florida typically possess a single, large, “knuckle”-shaped, dorsal knob and five or more smaller knobs, while Pliocene shells tend to have no knobs (Guest et al., 2008). The function of the dorsal knob in large strombids has been shown experimentally to reduce the risk of overturning, which exposes the aperture and soft parts of the animal to nipping by predators, especially fish (Berg, 1974, 1975). The dorsal knob also changes the orientation of an overturned shell so that the aperture is closer to the sediment surface, and less shell rotation and fewer attempts are required for righting (Berg, 1974, 1975; Savazzi, 1991). Dorsal knobs are probably not effective deterrents to attacks by lip peeling crabs such as *Menippe* since these knobs are never close to the terminal lip and prey shell overturning is not required for attacks by crabs. Given that the trend toward increased expression of a row of short spines in smaller *Strombus* spp. coincided with increased expression of shell knobs in larger *Eustrombus* spp. and *Lobatus* spp., and that both traits could potentially deter vertebrate predators, the most parsimonious explanation for morphological trends in both small and large strombids of Florida is increasing influence of one or more vertebrate predators.

The ultimate whorl spines in Pliocene and early Pleistocene *Strombus* were positioned roughly 90° to 180° from the terminal lip (Fig. 1B). In this position on a mature shell (i.e., one possessing a terminal lip), spines are absent from the dorsal portion of the ultimate whorl and could not interact with a vertebrate predator's jaws in way that would significantly increase the shell's effective diameter or ability to withstand dorsal–ventral crushing. However, these same spines would cover much of the dorsal part of the shell on a sub-adult *Strombus* and could have increased effective diameter and resistance to crushing. Thus, if vertebrates were influential selective agents in the evolution of *Strombus* spines, their influence was, at least initially, probably strongest on sub-adults rather than adults having a terminal lip.

An alternative, non-escalatory mechanism for the spread of anti-predatory shell armor in strombid gastropods in Florida is hybrid introgression between Caribbean species possessing defensive shell structures and Floridian species lacking them. Several fossil species of *Strombus* from the Caribbean (e.g., *Strombus bifrons* Sowerby, 1850, *Strombus proximus* Sowerby, 1850; *Strombus pugiloides* Guppy, 1873) possessed defensive shell structures (i.e., spine row or dorsal knob) no later than the Early Pliocene and as early as the early Middle Miocene (Landau et al., 2008, 2010, 2011; Freiheit and Geary, 2009), well before the introduction of similar traits in congeners in Florida. Unpublished molecular data suggest that hybridization between Florida and Caribbean *Strombus* spp. likely occurred in the Pleistocene (Dietl and Slaughter, 2005). Hybridization could also account for the spread of the dorsal shell knob in larger strombids, such as *Lobatus*, as this feature was also present much earlier in Caribbean fossil taxa (e.g., *Lobatus galliformis* Pilsbry and Johnson, 1917; *Lobatus vokesae* Landau et al., 2008; *Lobatus pascaleae* Landau et al., 2010) than in Florida fossil taxa.

5. Conclusions

Thickened shell lips and shell spines on the ultimate whorl of modern *S. alatus* are not effective deterrents against shell crushing or peeling attacks by large *Menippe*.

Increasing expression of spines on the ultimate whorl of *Strombus* shells through geologic time in Florida, therefore, cannot be interpreted as an escalatory response to large *Menippe*, although smaller crabs and vertebrate predators, such as fish and turtles cannot be ruled out. We can also not yet rule out non-escalatory mechanisms, such as the spread of shell spines through hybrid introgression.

The diameter of the outer whorl of *S. alatus*, however, did result in reduced damage and higher probability of survival in attacks by *Menippe*, regardless of spine condition. If crabs were influential in evolution of *Strombus* shell traits in the Plio-Pleistocene of Florida, the best test of this effect would be measured in the evolution of whorl diameter in the fossil record.

Acknowledgements

This research would not have been possible without the assistance of S. Platukyte, T. Bourn, and R.S. Kowalke. We are also grateful to S. Rice for allowing us to use the facilities at the University of Tampa for holding spare *Strombus*, and to D. Chattopadhyay and an anonymous reviewer for comments and critique which improved this article. Funding for this study came from a University of South Florida post-doctoral fellowship to L.B.W., a shiptime grant from the Florida Institute of Oceanography, and NSF EAR-0719029 to G.S.H. All specimens used in this study were collected under Special Activity License 08SR-901 issued to G.S.H. by the Florida Fish and Wildlife Conservation Commission.

References

Allmon, W.D., 2001. Nutrients, temperature, disturbance, and evolution: a model for the late Cenozoic marine record of the western Atlantic. Palaeogeogr. Palaeoclimatol. 166, 9–26.

Allmon, W.D., Rosenberg, G., Portell, R.W., Schindler, K.S., 1993. Diversity of Pliocene to Recent Atlantic coastal plain mollusks. Science 260, 1626–1628.

Balukm, W., Radwanski, A., 1996. Stomatopod predation upon gastropods from the Korytnica Basin and from other classical Miocene localities in Europe. Acta Geol. Pol. 46, 279–304.

Beck, M.W., 1995. Size-specific shelter limitation in stone crabs: a test of the demographic bottleneck hypothesis. Ecology 76, 2487–2503.

Beck, M.W., 1997. A test of the generality of the effects of shelter bottlenecks in four stone crab populations. Ecology 78, 2487–2503.

Berg Jr., C.J., 1974. A comparative ethological study of strombid gastropods. Behavior 51, 274–322.
Berg Jr., C.J., 1975. Behavior and ecology of conch (Superfamily: Strombacea) on a deep subtidal algal plain. Bull. Mar. Sci. 25, 307–317.
Bert, T.M., 1985. Geographic variation, population biology, and hybridization in *Menippee mercenaria* and evolution in the genus *Menippee* in the Southwestern North Atlantic Ocean(Ph.D. dissertation) Department of Biology, Yale University, (306 pp.).
Bertness, M.D., 1982. Shell utilization, predation pressure, and thermal stress in Panamanian hermit crabs: an interoceanic comparison. J. Exp. Mar. Biol. Ecol. 64, 159–187.
Britton, J.C., Morton, B., 1989. Shore Ecology of the Gulf of Mexico. University of Texas Press, Austin.
Brown, K.M., Haight, E.S., 1992. The foraging ecology of the Gulf of Mexico stone crab *Menippe adina* (Williams et Felder). J. Exp. Mar. Biol. Ecol. 160, 67–80.
Clench, W.J., Abbott, R.T., 1941. The genus *Strombus* in the western Atlantic. Johnsonia 1, 1–15.
Currey, J.D., 1980. Mechanical properties of mollusc shell. Symp. Soc. Exp. Biol. 34, 75–98.
Currey, J.D., Kohn, A.J., 1976. Fracture in the crossed-lamellar structure of *Conus* shells. J. Mater. Sci. 11, 1615–1623.
Dietl, G.P., 2003. Coevolution of a marine gastropod predator and its dangerous bivalve prey. Biol. J. Linn. Soc. 80, 409–436.
Dietl, G.P., Slaughter, C., 2005. Hybridization and adaptive evolution in Plio-Pleistocene strombid snails from Florida. Geol. Soc. Am. Abstr. Programs 37, 87.
Ditel, G.P., Herbert, G.S., 2010. Unexpected escalation of antipredatory shell defneses in strombid gastropods in the Pleistocene of Florida. Geol. Soc. Am. Abstr. Programs 42, 322.
Freiheit, J.R., Geary, D.H., 2009. Neogene paleontology of the northern Dominican Republic. Strombid gastropods (genera *Strombus* and *Lobatus*; Mollusca: Gastropoda: Strombidae) of the Cibao Valley. Bull. Am. Paleontol. 376, 1–54.
Geary, D.H., Allmon, W.D., 1990. Biological and physical contributions to the accumulation of strombid gastropods in a Pliocene shell bed. Palaios 5, 259–272.
Goodrich, C., 1944. Variations in *Strombus pugilis alatus*. Occasional Papers of the Museum of Zoology No. 490. University of Michigan, pp. 1–10.
Guest, R.L., Herbert, G.S., Gastaldo, R.A., Harries, P.J., Oches, E.A., Portell, R., Dietl, G., 2008. Can predator–prey arms races intensify during a mass extinction event: strombid gastropods from the Late Neogene of Florida. Geol. Soc. Am. Abstr. Programs 40, 142.
Hamilton, P.V., 1976. Predation of *Littorina irrorata* (Mollusca: Gastropoda) by *Callinectes sapidus* (Crustacea: Portunidae). Bull. Mar. Sci. 26, 403–409.
Hammer, Ø., Harper, D.A.T., Ryan, P.D., 2001. PAST: paleontological statistics software package for education and data analysis. Palaeontol. Electron. 4, 1–9.
Hargreave, D., 1995. An ontogenetic approach to understanding changes in shell morphology over time: the *Strombus alatus* complex in the Plio-Pleistocene of southern Florida. Tulane Stud. Geol. Paleontol. 27, 1–51.
Herbert, G.S., Dietl, G.P., Vermeij, G.J., 2004. Pleistocene escalation in strombid gastropods of Florida and a possible catalyst role for glacial 'super-El Niño' conditions. Geol. Soc. Am. Abstr. Programs 36, 480.
Hughes, R.N., Elner, R.W., 1979. Tactics of a predator, *Carcinus maenas*, and morphological responses of the prey, *Nucella lapillus*. J. Anim. Ecol. 48, 65–78.
Jackson, J.B.C., Jung, P., Coates, A.G., Collins, L.S., 1993. Diversity and extinction of tropical American molluscs and the emergence of the Isthmus of Panama. Science 260, 1624–1626.
Jernvall, J., Fortelius, M., 2002. Common mammals drive the evolutionary increase of hypsodonty in the Neogene. Nature 417, 538–540.
Johnson, K.G., Todd, J.A., Jackson, J.B.C., 2007. Coral reef development drives molluscan diversity increase at local and regional scales in the late Neogene and Quaternary of the southwestern Caribbean. Paleobiology 33, 24–52.
Kitching, J.A., Muntz, L., Ebling, F.J., 1966. The ecology of Lough Ine. XV. The ecological significance of shell and body forms in Nucella. J. Anim. Ecol. 35, 113–126.
Kosloski, M.E., Dietl, G.P., Herbert, G.S., 2008. Are museum collections adequate to test the escalation hypothesis? Geol. Soc. Am. Abstr. Programs 40, 371.
Landau, B., Kronenberg, G.C., Herbert, G.S., 2008. A large new species of *Lobatus* (Gastropoda: Strombidae) from the Neogene of the Dominican Republic, with notes on the genus. Veliger 50, 31–38.
Landau, B.M., Kronenberg, G.C., da Silva, C.M., 2010. A new species of *Lobatus* (Mollusca: Caenogastropoda: Strombidae) from the Neogene of the Dominican Republic, with notes on further species from the Dominican assemblages. Basteria 74, 95–109.
Landau, B., Kronenberg, G.C., Herbert, G.S., da Silva, C.M., 2011. The genus *Strombus* (Mollusca, Caenogastropoda, Stombidae) in the Neogene of the Bocas del Toro area, Panama, with the description of three new species. J. Paleontol. 85, 337–352.
Laraia, V.J., Heuer, A.H., 1989. Novel composite microstructure and mechanical behavior of mollusk shell. J. Am. Ceram. Soc. 72, 2177–2179.
Miller, D.J., LaBarabera, M., 1995. Effects of foliaceous varices on the mechanical properties of *Chicoreus dilectus* (Gastropoda: Muricidae). J. Zool. 236, 151–160.
Palmer, A.R., 1979. Fish predation and the evolution of gastropod shell sculpture: experimental and geographic evidence. Evolution 33, 697–713.
Petuch, E.J., 1994. Atlas of Florida fossil shells (Pliocene and Pleistocene marine Gastropods). Department of Geology, Florida Atlantic University and The Graves Museum of Archaeology and Natural History. Chicago Spectrum Press, (394 pp.).
Portell, R.W., Agnew, J.G., 2004. Pliocene and Pleistocene decapod crustaceans. Florida Fossil Invertebrates Part 4, pp. 1–29.
Powell jr., E.H., Gunter, G., 1968. Observations on the stone crab, *Menippe mercenaria* Say, in the vicinity of Port Arkansas, Texas. Gulf Res. Rep. 2, 285–299.
Rochette, R., Doyle, S.P., Edgell, T.C., 2007. Interaction between an invasive decapod and a native gastropod: predator foraging tactics and prey architectural defenses. Mar. Ecol. Prog. Ser. 330, 179–188.
Rooperaine, P.D., Beussink, A., 1999. Extinction and naticid predation of the bivalve *Chione* von Mühlfeld in the late Neogene of Florida. Palaeontol. Electron. 2 (24 pp.).
Savazzi, E., 1991. Constructional morphology of strombid gastropods. Lethaia 24, 311–331.
Stanley, S.M., 1986. Anatomy of a regional mass extinction: Plio-Pleistocene decimation of the western Atlantic bivalve fauna. Plaios 1, 17–36.
Stanley, S.M., Campbell, L.D., 1981. Neogene mass extinction of Western Atlantic molluscs. Nature 293, 457–459.
Stefaniak, L.M., McAtee, J., Shulman, M.J., 2005. The costs of being bored: effects of a clinoid sponge on the gastropod *Littorina littorea* (L). J. Exp. Mar. Biol. Ecol. 327, 103–114.
Taylor, J.D., Morris, N.J., Taylor, C.N., 1980. Food specialization and the evolution of predatory prosobranch gastropods. Palaeontology 23, 375–409.
Vermeij, G.J., 1974. Marine faunal dominance and molluscan shell form. Evolution 28, 656–664.
Vermeij, G.J., 1978. Biogeography and Adaptation: Patterns of Marine Life. Harvard University Press, Cambridge (352 pp.).
Vermeij, G.J., 1982. Gastropod shell form, breakage, and repair in relation to predation by the crab *Calappa*. Malacologia 23, 1–12.
Vermeij, G.J., 1987. Evolution and Escalation: an Ecological History of Life. Princeton University Press, Princeton (527 pp.).
Vermeij, G.J., 1994. The evolutionary interaction among species: selection, escalation, and coevolution. Annu. Rev. Ecol. Syst. 25, 219–236.
Vermeij, G.J., 2004. Nature: an Economic History. Princeton University Press, Princeton (445 pp.).
Vermeij, G.J., 2013. On escalation. Annu. Rev. Earth Planet. Sci. 41, 1–19.
Vermeij, G.J., Petuch, E.J., 1986. Differential extinction in tropical American molluscs: endemism, architecture, and the Panama land bridge. Malacologia 27, 29–41.
West, K., Cohen, A., Baron, M., 1991. Morphology and behavior of crabs and gastropods from Lake Tanganyika, Africa: implications for lacustrine predator–prey coevolution. Evolution 43, 589–607.
Yamaoka, K., 1978. Pharyngeal jaw structure in labrid fishes. Publ. Seto Mar. Biol. Lab. 24, 410–426.