Palaeogeography, Palaeoclimatology, Palaeoecology 363–364 (2012) 163–171

Contents lists available at SciVerse ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

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

Size refugia from predation through time: A case-study of two Middle Devonian brachiopod genera

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ARTICLE INFO

Article history:
Received 28 May 2012
Received in revised form 8 September 2012
Accepted 11 September 2012
Available online 19 September 2012

Keywords:
Repair-frequency
Crushing-predation
Atrypida
Strophomenida
Arms-race
Traverse Group

ABSTRACT

Predation scars offer insight into ancient predator–prey relationships and evolutionary processes. One approach to studying predation in fossils is through repair scars, which indicate a failed attempt at predation as the prey survives the attack and repairs its shell. A change in repair frequency is ambiguous as it may indicate either a change in the number of attacks on the prey or a change in the success of the predator. Size refugia, the size of the prey at which the predator will no longer take the prey, can potentially be used to differentiate between these two possibilities. The goal of this study is to examine predatory traces and size refugia in lineages of atrypide and strophomenide brachiopods to determine the relative performance of predators to prey through time in the Middle Devonian of Michigan.

We reviewed 1197 specimens of *Pseudoatrypa* and 896 specimens of *Strophodonta* for crushing predation through multiple shales in the Middle Devonian Traverse Group of Alpena and Presque Isle Counties of Michigan, USA. The sampled units, in stratigraphic order, are Bell Shale, Ferron Point Fm., Genshaw Fm., Dock Street Clay, Norway Point, and Potter Farm Fm.; these shales were deposited in broadly similar environments. Repair frequency (R%), the percent of shells with repairs, was determined for each unit. Body size was measured for all specimens and the body size at the time of attack was measured for the specimens that had repair scars. The maximum size-at-attack for each unit was used as a proxy for size refuge.

The results for the atrypides showed a U-shaped trend in R% through time, with the lowest R% in the Genshaw, and a size refuge that was roughly inverse to R%, showing an N-shaped trend, with the greatest size refuge in the Genshaw. Atrypides in the Genshaw likely never truly reach a size refuge (the predators could take any size of prey). There were no strongly significant results with respect to changes between R% and size refuge from unit-to-unit but this is likely due to the poor sample sizes for the Ferron Pt. and Dock St. Clay. The general trends, however, are statistically significant and suggest that the adaptive gap (the relative effectiveness) between predators and prey is fluctuating through time: during Genshaw time, the predators grew more effective relative to their prey, as indicated by the predator's ability to take larger prey, whereas pre- and post-Genshaw, the predators were less effective. This may imply that an evolutionary arms race occurred between predators and prey. No significant changes to the morphology of the prey through time were found but further research is needed to determine whether there was a change in morphology in the predators through time.

The results for the strophomenides indicated that R% and size refuge almost completely track each other through time, which is in contrast to the atrypides in which these variables change in opposition to each other in almost every unit. The general trend suggests that the change in repair frequency of strophomenides from unit to unit is due to a change in the predator attack frequency instead of a change in the success of the predator. Further research is needed to determine if the presence of one brachiopod genus had an effect on the other, as there is no hard evidence that they lived in any of the same localities at the same time.

1. Introduction

Predation in the fossil record can give insight into ancient predator–prey relationships and behaviors (Berg and Nishenko, 1975; Anderson et al., 1991; Kowalewski et al., 1997), ancient ecosystem dynamics and population biology (Thomas, 1976; Sheehan and Lesperance, 1978), and evolutionary processes and adaptive differences between predators and prey (Kitchell et al., 1981; Vermeij, 1977; Allmon et al., 1990; Leighton, 2003a). In particular, crushing predation has been a major source of mortality on shelled marine invertebrates through much of the Phanerozoic (Vermeij, 1987; Leighton, 2003b); possible Mid-Devonian crushing predators include ptychodontid placoderms and phyllocarids (Leighton, 2003b). Multiple methods and proxies

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http://dx.doi.org/10.1016/j.palaeo.2012.09.012

have been used to estimate predation intensity, the mortality frequency from predation, in the fossil record (Leighton, 2002; Huntley and Kowalewski, 2007). One of the most common proxies for estimating crushing predation is the repair frequency (Vermeij et al., 1980, 1981; Allmon et al., 1990; Kowalewski et al., 1997Dietl et al., 2000), calculated either as the number of repaired individuals out of the total population or as the total number of repairs out of the total population (Alexander and Dietl, 2003), because repairs have the advantage of being clear indicators of a predatory attack. However, because repair scars are examples of failed predatory attacks, the quantitative interpretation of the repair frequency may be ambiguous: it could be that an increase in repair frequency is due to an increase in attack frequency of the predator, but it also could be due to a decrease in the success frequency of the predator (Vermeij, 1987).

Leighton (2002) suggested that interpretation of changes in repair frequency could be more tractable by examining the relationship between repairs and prey size at the time of attack, as the adaptive gap (the relative effectiveness in abilities) between the predator and prey would influence the maximum size at which a predator would attack the prey. The present work is the first empirical study using this approach.

As mentioned above, there are two principal causes for an increase in repair frequency through time (Vermeij, 1987; Leighton, 2002): the first possibility is that the repair frequency increases simply because the attack frequency of the predator is increasing. Because the predator is attacking the prey more frequently, the repair frequency and the mortality frequency of the prey increases. In contrast, with the second case, the repair frequency increases because the success frequency of the predator is decreasing as the prey becomes stronger relative to the predator. The predator fails to kill the prey as often and therefore there are more repairs and less mortality in the prey. Note that the mortality of the prey increases in the first scenario and decreases in the second scenario. The reverse of these situations (due to a decrease in repair frequency) is true as well: either the attack frequency of the predator is decreasing or the success frequency of the predator in killing the prey is increasing.

Distinguishing between these two interpretations is crucial for avoiding incorrect conclusions. In the past, workers have used changes in repair frequency through time to corroborate hypotheses of adaptive gaps in predators and prey and that morphological changes in the prey are responses to predation pressures. However, only the second interpretation (the change in repair frequency in the prey is related to the success frequency of the predator) would unequivocally support this hypothesis. The first interpretation (the change in repair frequency in the prey is related to the attack frequency of the predator) does not necessarily support the hypothesis that a change in prey morphology is an anti-predatory response. An increase in attack frequency could be a function of any one of several factors such as an increase in the number of individual predators, increased metabolic rates due to temperature change, prey-switching etc., and not all of these situations would constitute an increase in selective pressure on the prey as mortality is not necessarily associated with natural selection (Vermeij, 1982). Note that to have selection implies differential mortality, wherein one segment of the population is preyed upon and, concurrently, another segment is not. In the case of increased attack frequency, there may be increased mortality, but not necessarily change in differential mortality and, therefore, no actual increase in selective pressure. In contrast, a change in the predator's success rate is most likely due to a change in the relative abilities – the adaptive gap – of the predator and the prey, and such a change would be a selective pressure. Thus, this latter scenario provides better corroborative support for a hypothesis that a concurrent change in prey morphology is an anti-predatory response. If a successful method to distinguish between these two interpretations was found, this would enhance tests of evolutionary arms-races or escalation.

To potentially differentiate between these two interpretations, we can use the size refugia technique, as proposed by Leighton (2002). The size refuge is the size of the prey at which the predator is unable or unwilling to take the prey (i.e., the prey is too large for the predator's gape, or there are other prey that would be significantly easier for the predator to capture and kill) (Vermeij, 1976; Leighton, 2002). There have been many documented cases of size refugia in both the ecological and paleoecological literature (Elner and Hughes, 1978; Sheehan and Lesperance, 1978; Boulding, 1984; Harper et al., 2009; among others).

In using the size refugia technique, we expect the position of the size refuge, the size at which the prey is safe, to change as the adaptive gap between predators and prey changes. For example, if the predator evolved through time to become stronger or faster, and thus became stronger relative to the prey, it would be able to take larger individuals within the prey species, leading to an increase in the position of the size refuge in the prey; larger individuals would become vulnerable to stronger predators (Fig. 1). In contrast, if the prey becomes more effective relative to the predator, the position of the size refuge would decrease as the predator would be forced to take smaller individuals. In this example, the predator's effectiveness changed through time, but it should be noted that this approach could also be used through space, such as along an environmental gradient, in which the abilities of the predators might vary.

To summarize, we would conclude that the first interpretation, that the change in repair frequency is dependent on the number of predator attacks, is true when there is no change in the position of the size refuge, that is, there is no change in the relative abilities of the predator and prey. The repair frequency will simply increase or decrease because of an increase or decrease in the number of attacks.

In contrast, with the second interpretation we would observe a change in the repair frequency as well as a change in the position of the size refuge through time, that is, the size at which the prey achieves a size refuge changes. This does not require a change in the overall body size of the prey population; instead, a change in size refuge indicates that the size threshold at which the prey will not be attacked by the predator has grown larger or smaller. Two opposing situations may result from this: a) if the predator gets more powerful relative to the prey, then the predator should succeed more often, resulting in fewer failed attacks (and therefore a decrease in repair frequency), and be able to take larger prey, resulting in an increase in the size refuge of the prey (that is, the size at which the prey is safe from the predator increases) through time, or b) if the prey improves its defenses relative to the predator then the predator would fail more often, resulting in more failed attacks (and therefore an increase in repair frequency), and be forced to take smaller, easier, prey, resulting in a decrease in the size refuge of the prey through time.

2. Methods

We borrowed 1197 specimens of the atrypide brachiopod *Pseudoatrypa* and 896 specimens of the strophomenide brachiopod *Strophodonta* from the University of Michigan Museum of Paleontology and examined them for signs of crushing predation. The specimens are from the Middle Devonian (Givetian) Traverse Group, a section consisting of alternating limestones and shales, and were originally collected by multiple collectors from six shale units and localities of Alpena and Presque Isle Counties of Michigan. These units, from base upwards, are the Bell Shale, Ferron Point Fm., Genshaw Fm., Dock Street Clay, Norway Point Fm., and Potter Farm Fm. (Fig. 2). Though we cannot be completely positive because the samples are museum specimens that were collected decades ago, we believe that the samples were all collected in place, without bias, because the collectors in question tended to indicate when they collected from float. The specimens used herein are only from the shales because it is virtually impossible to get whole, complete specimens

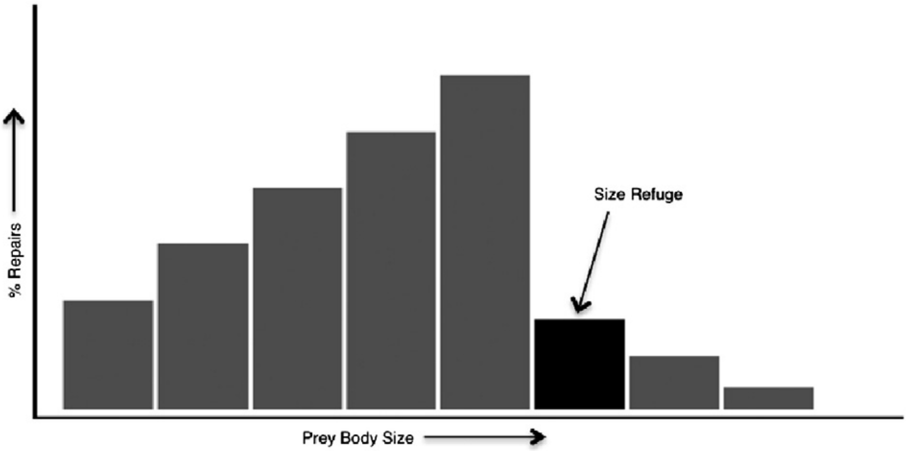


Fig. 1. Example of a hypothetical size refuge for a single prey population at a single time. Repair frequency increases with successively larger size-bins of the prey as the predator is increasingly likely to fail with larger members of the prey population. At some threshold in prey size, the larger prey are too large for the predator to take easily; at this size, the repair frequency drops abruptly as the predator is less likely to even attack such prey. Prey larger than the threshold are in a size refuge.

from the intervening limestones without damaging the fossils. All shales were deposited in roughly similar environments (Ehlers and Kesling, 1970). Ehlers and Kesling (1970) have divided the Traverse Group into environmental zones/facies. The Genshaw and Potter Farm Formations were from the Coral-Brachiopod Zone (Zone III of Ehlers and Kesling, 1970), a subtidal zone, below normal wavebase but above storm wavebase, with good circulation and the occasional stronger current, consisting mainly of corals and large brachiopods. Zone III typically consists largely of medium to fine-grained limestone, but in deeper parts of the zone, the beds change to a calcareous shale and the fauna becomes more diverse; the Genshaw and Potter Farm specimens are from such shales. The Bell Shale, Ferron Pt., and Norway Pt. units were located in the Diverse Fauna Zone (Zone IV), found at slightly greater depths than Zone III and characterized by deep mud flats, mainly claystones or shales with a low calcareous content, and high diversity. The Dock St. Clay was located in the interbioherm between Zone IV and Zone V (Biohermal Flank) and resembled Zone III in wave energy and diversity. Note that zone numbers do not necessarily reflect increasing depth. Thus, all units are subtidal, level-bottom habitats close to storm wavebase. The alternating cycles of limestones and shales seen in the Traverse Group are thought to be allocyclic, caused by eustatic sea-level changes, as opposed to autocyclic, which would involve only local depositional processes (Bartholomew and Brett, 2007; Brett et al., 2011). Note that although environmental differences definitely could have an effect on predation, the repair frequency and sizes-at-attack are the actual data; even if the environment influenced predation, the patterns of predation can still be observed and tested.

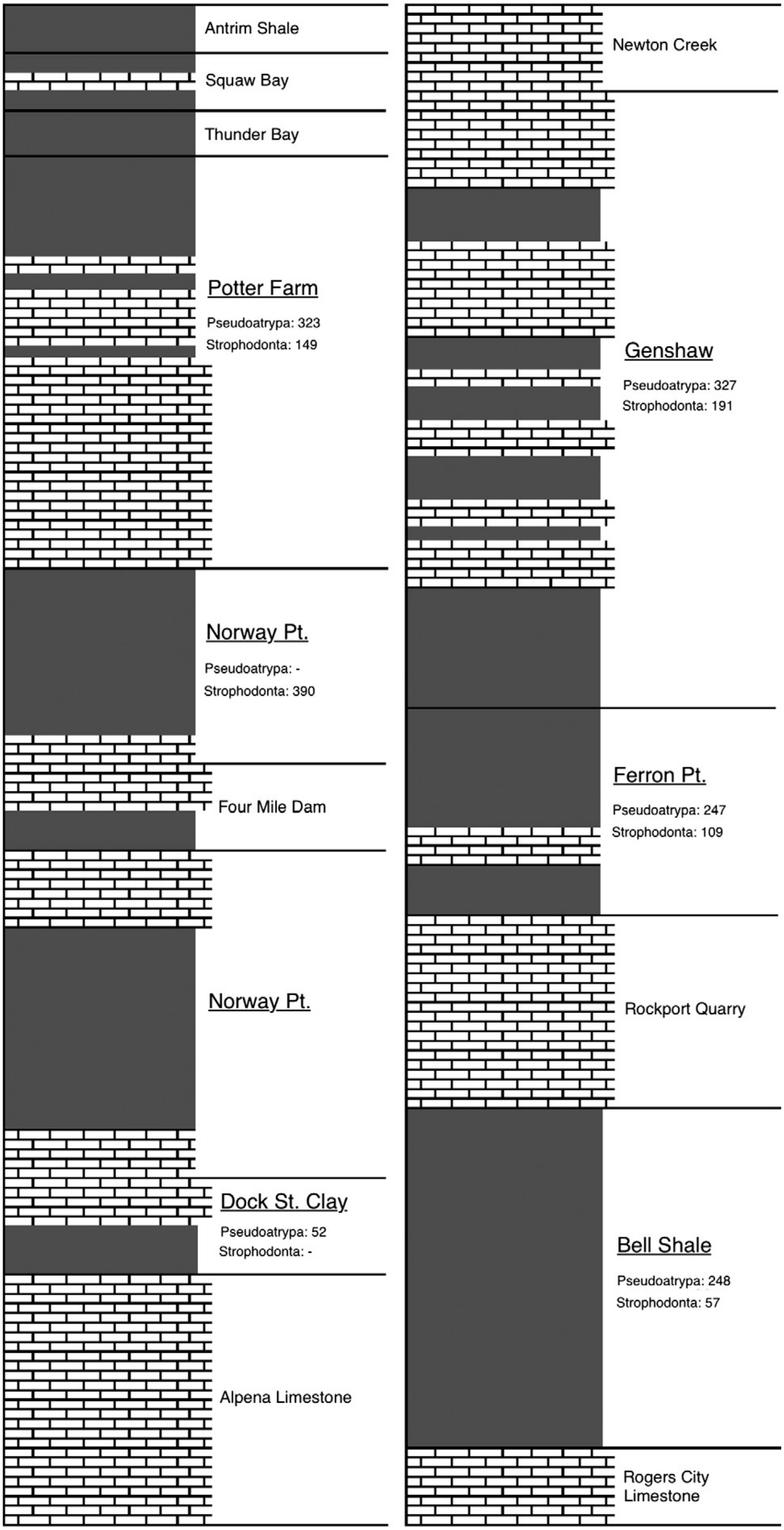
We examined two species of *Pseudoatrypa* (Phylum Brachiopoda, Order Atrypida), *Pseudoatrypa lineata* and *P.* sp. A (Bose et al., 2011), and two species of *Strophodonta* (Phylum Brachiopoda, Order Strophomenida), *Strophodonta extenuata* and *Strophodonta erratica* for crushing predation scars. *P. lineata* differs from *P.* sp. A in having a more rounded, rather than arched, brachial valve; a more circular outline in plain view; a shorter hingeline; and finer, more closely-packed ribbing (Bose et al., 2011). These two species of *Pseudoatrypa* may possibly be two plastic morphotypes of the same species as they are relatively similar in form and ornamentation.

The systematics of Michigan *Strophodonta* is in need of revision; Imbrie (1959) described more than 25 species and subspecies of Traverse Group *Strophodonta*, but many of these species are limited in distribution to a single outcrop, suggesting that the Michigan representatives of the genus are badly oversplit. Quantitative revision of the genus is currently in progress, but for the purposes of this paper, we identify two easily distinguishable morphotypes. *S. extenuata* is larger than *S. erratica* when fully grown and more prone to be wider along the hingeline than long, whereas *S. erratica* is more likely to be equidimensional in shape or longer than wide. The most reliable characteristic for distinguishing between these two species, however, is that *S. extenuata* has weaker ribbing than *S. erratica*, which has a very strong, sharp ribbing, almost to the point of being plicate. These two forms of *Strophodonta* are likely two different species rather than two plastic morphotypes because their form and ornamentation differ greatly and they were generally not found in the same units.

We took care to make sure that the scars on the shells were due to predation instead of taphonomy. The most convincing evidence that damage is predatory is when the damage is repaired on the shell (Leighton, 2011). If a brachiopod was able to repair its shell damage after an attack, then obviously it was still alive and the damage would thus not have been caused by compaction after death. Brachiopods grow by accretion along the commissure. After surviving an attack, the brachiopod will attempt to regrow its shell, often resulting in distortions in the growth lines or radial ornament (Fig. 3). The scar shape and position are important as well. The scar shape should be non-random as it mirrors the shape of the attack structure (Alexander, 1986; Leighton, 2011). The location of the scar will likely not be perfectly parallel to the growth lines (a conservative criterion) and, unlike with compaction in which the whole shell may be damaged, the scar usually involves only a small area (Alexander, 1986; Elliot and Bounds, 1987). Another good indication that a trace is predatory rather than taphonomic in origin is that the attack will be stereotypic (the predator attacks in a consistent pattern — in the same position or on the same valve on multiple specimens) and biologically meaningful (the predator attacks in the most efficient method to take the prey) whereas taphonomic damage is more often random (Leighton, 2011).

Repair frequency, in which the number of scarred specimens is divided by the total number of prey specimens, was determined for each species separately within each unit. This “individual repair frequency” is considered to be a conservative estimation of the repair frequency compared to an alternative approach in which the number of scars is divided by the total number of prey specimens (Leighton, 2011). Using calipers, we measured the length from hinge to commissure for all specimens and used it as a proxy for body size. Length is an appropriate proxy for body size because it is the primary growth direction in brachiopods.

We also measured the body size at the time of attack for all scarred specimens to be used in refuge analysis, as if the prey successfully repairs its shell, its size may be larger at death than it was when attacked


Antrim Shale
Squaw Bay
Thunder Bay
Potter Farm
Pseudoatrypa: 323
Strophodonta: 149
Norway Pt.
Pseudoatrypa: -
Strophodonta: 390
Four Mile Dam
Norway Pt.
Dock St. Clay
Pseudoatrypa: 52
Strophodonta: -
Alpena Limestone
Newton Creek
Genshaw
Pseudoatrypa: 327
Strophodonta: 191
Ferron Pt.
Pseudoatrypa: 247
Strophodonta: 109
Rockport Quarry
Bell Shale
Pseudoatrypa: 248
Strophodonta: 57
Rogers City
Limestone

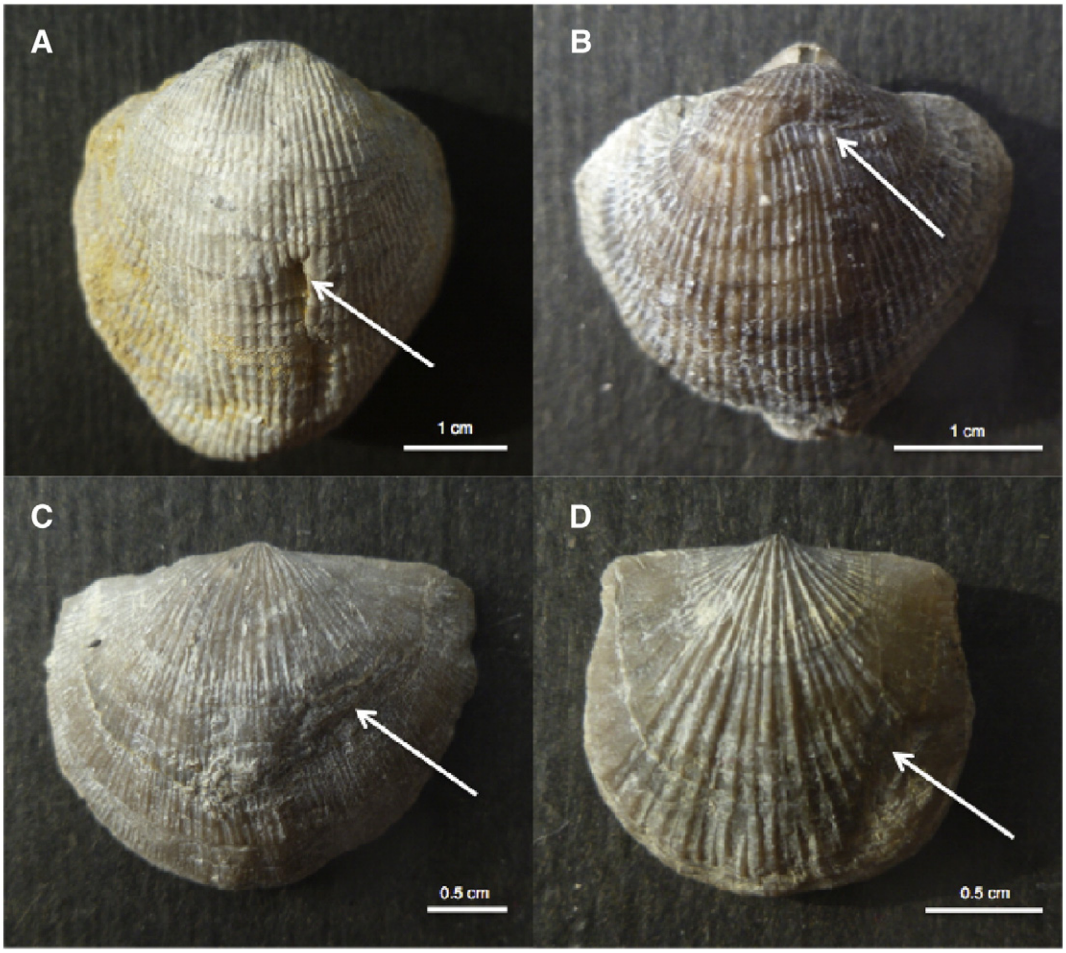


Fig. 3. Examples of the focal taxa and repair scars. A and B, brachial valve view of *Pseudoatrypa*; C and D, pedicle valve view of *Strophodonta*.

(Leighton, 2011). This was done by locating the distortion in the growth line caused by the attack and then following the growth line to the midline of the brachiopod. The length between that point and the midpoint of the hingeline is the minimum possible shell length at the time of attack (Fig. 4). The measurement is taken at a point along the midline because it is necessary to take the measurement in a consistent growth direction; otherwise, differently-shaped specimens could bias the results. The maximum size-at-attack length for each species of each unit was used as a proxy for the size refuge of that unit. This is a conservative estimate as we have only negative evidence that the predator could not take a larger brachiopod. When measuring the maximum size-at-attack lengths, we used the 95th percentile of the size-at-attack data, assuming the upper 5% is not representative of the prey size that a predator would take, to avoid any anomalous results or outliers. All these measurements were collected from both species of *Pseudoatrypa* and *Strophodonta*. The measurements were then compared between species, *P. lineata*/*P.* sp. A and *S. extenuata*/*S. erratica*, to determine whether they differed substantially.

To analyze changes in the size refuge for each unit, brachiopods were separated into size interval bins, represented on the x-axis, and the repair frequency within that size interval was found and plotted as bars in the y-axis, as seen in Fig. 1. Theoretically, repair frequency will generally increase as the size of the brachiopod gets larger because the predator will fail more often in its attack. Repair frequency will reach its maximum at the size interval at which the predator will gain the greatest amount of food while still being able to take the prey. The next greatest size interval should have a sudden drop-off in repair frequency as prey at this size are attacked less frequently — this is the size refuge, the size at which the predator is unable or unwilling to take the prey (assuming that one exists for the given prey).

To test whether there was a significant change in each species' repair frequency from unit to unit, we used a 2×2 Chi-square test ($\alpha = 0.05$) in which the unit of interest (observed) was compared with the preceding sampled unit (expected). Even though they are not stratigraphically adjacent shales, we also performed a 2×2 Chi-square test ($\alpha = 0.05$) between the Bell and Genshaw Formations, excluding the Ferron Pt. Formation, and between the Genshaw and Potter Farm Formations, excluding the Dock St. Clay Formation, to test the significance of the overall trend of repair frequency through time. Values were standardized so that the two columns each equaled the column that originally had the smaller sum. This transformation is conservative as Chi-square tests are increasingly conservative with less data.

If either *Pseudoatrypa* or *Strophodonta* demonstrated contrasting changes and trends through time in repair frequency and size refuge, indicative of a change in adaptive gap, then further measurements were taken to determine if there were any changes in morphology from unit to unit that may have been making the prey more or less effective relative to the predators: a) the sphericity of the sampled atrypide

Fig. 2. Stratigraphic column of the Middle Devonian (Givetian) Traverse Group. The base of the column is the lower right and the top of the column is the upper left of the figure. The units in which specimens were examined are underlined. The number of examined *Pseudoatrypa* and *Strophodonta* specimens for each unit is adjacent to the relevant units. Modified from Ehlers and Kesling (1970).

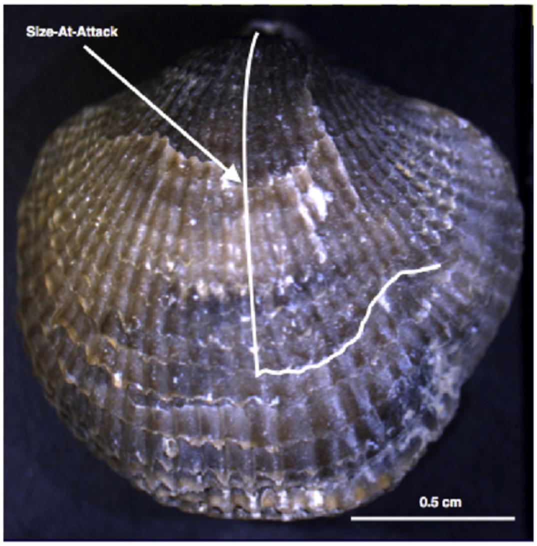


Fig. 4. A demonstration of how to measure the body size of a repaired brachiopod at the time of attack (the size-at-attack). See text for further discussion.

specimens, in which the height (distance from the most convex part of the pedicle valve to the most convex part of the brachial valve) to length ratio was used as a proxy for sphericity; all other things being equal, a more spherical shape resists point-loading, such as would be inflicted by a crushing predator, better than other shapes (Alexander, 1990); and b) the ontogenetic growth rates, measured as the averaged distances between each lamella of a sampled group of the largest specimens and plotted to compare the differences between each unit, to determine if the growth rates were faster for specimens in any of the units; brachiopods with faster growth rates would potentially have a better chance at surviving an attack if they can repair themselves more quickly (Leighton, 2003a). Measuring the thickness of the shell would have been desirable, but as the specimens were almost always articulated, it was impossible to get consistent thickness measurements from the same locations on each individual shell non-destructively and without large margins of error.

3. Results

The size ranges for the *Pseudoatrypa* for all five units in which they are present were similar, ranging from 5 mm to 40 mm. Repair frequency through time showed a U-shaped trend, with the lowest repair frequency in the Genshaw Fm. (Fig. 5). The size refuge, plotted using the maximum size-at-attack as a proxy, was roughly inverse to the repair frequency, showing an N-shaped trend, with the greatest size refuge in the Genshaw (Fig. 5). From the Bell Shale to Ferron Pt., there is a significant decline in the repair frequency ($X^2=3.94$, $P=0.047$), but we do not see an opposing increase in the size refuge. In contrast, from the Ferron Pt. to Genshaw, we see a significant decline in the repair frequency ($X^2=9.77$, $P=0.002$) as well as an opposing increase in the size refuge. For both Genshaw to Dock St. Clay and Dock St. Clay to Potter Farm, there is an increase in repair frequency and an associated decrease in size refuge. The unit-to-unit Chi-Square comparisons between the Genshaw and Dock St. Clay ($X^2=1.36$, $P=0.244$) and between the Dock St. Clay and Potter Farm ($X^2=1.61$, $P=0.688$) were not significant, however, likely because the Dock St. Clay, the unit that separates the Genshaw and Potter Farm units, has such a small number of specimens that the data may not be representative of the unit. Using Chi-square tests to examine the overall U-shaped trend in repair frequency found in the atrypides, the change in repair frequency is extremely significant from the Bell Shale to Genshaw when the Ferron Pt. is excluded ($X^2=23.1$, $P\ll 0.001$) and from the Genshaw to Potter Farm when the Dock St. Clay is excluded ($X^2=16.3$, $P\ll 0.001$).

The *Pseudoatrypa* size refugia for Bell Shale, Ferron Pt., Dock St. Clay, and Potter Farm was 35–40 mm, 30–35 mm, 30–35 mm, and 15–20 mm, respectively, as at these sizes there is a drop-off in the percentage of brachiopods that had repair scars (Fig. 5). The Genshaw Fm. was the only unit in which *Pseudoatrypa* never reached a size refuge: 50% of brachiopods between 35 and 40 mm in length were attacked and there were no brachiopods larger than 40 mm for predators to take.

The size ranges among the five units in which the *Strophodonta* are present are also similar to each other but tended to be smaller than the *Pseudoatrypa*, ranging from 5 mm to 30 mm. *Strophodonta* repair frequency was considerably higher than the *Pseudoatrypa* repair frequency, with the greatest repair frequency in the Ferron Pt. unit and

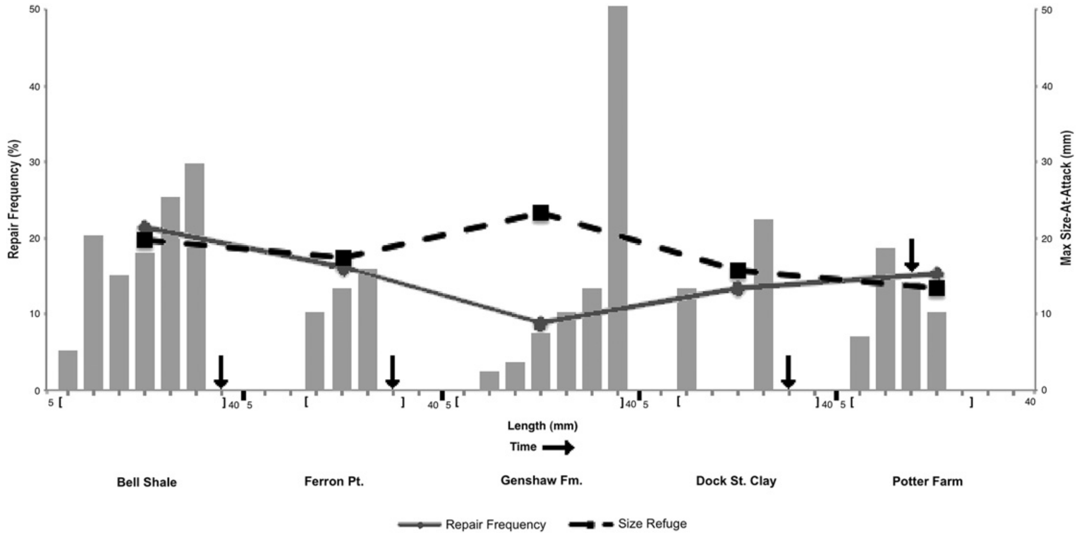


Fig. 5. Graph showing the relationship between repair frequency (%) and maximum size-at-attack (mm) through time for the *Pseudoatrypa* specimens. Columns indicate the repair frequency for different body sizes in each unit, ranging from 5 mm to 40 mm in increments of 5 mm. The size refuge for each unit is the sudden drop-off in column height, indicated by the arrows. In some units, there is a drop-off to zero indicating that no brachiopods in that size increment had a repair scar. Brackets below the x-axis indicate the actual size range that is occupied for each unit. The atrypide brachiopods of the Genshaw do not appear to ever reach a size refuge as there is no drop-off.

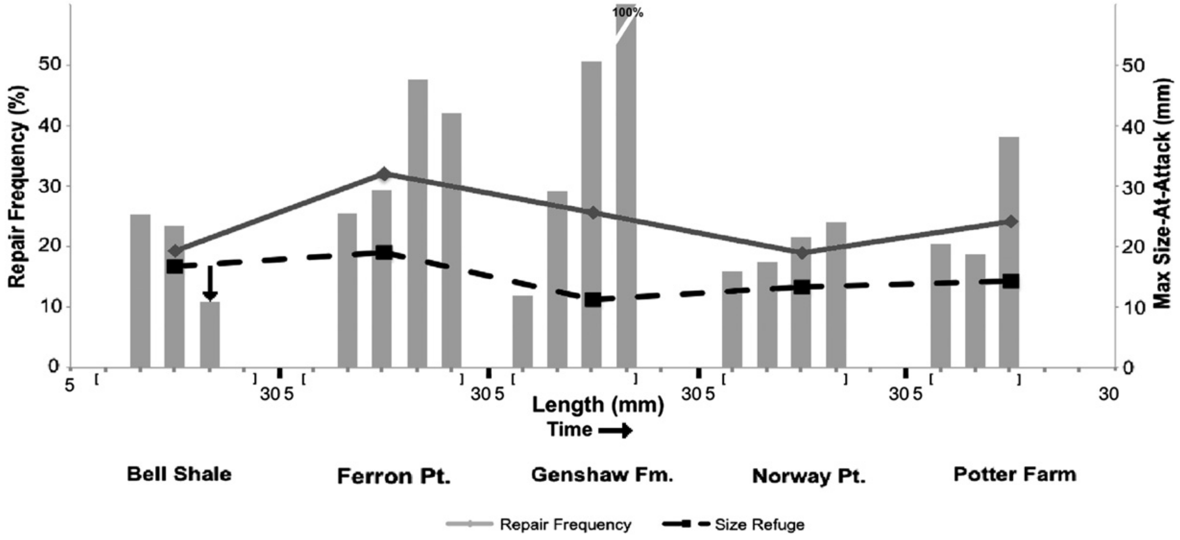


Fig. 6. Graph showing the relationship between repair frequency (%) and maximum size-at-attack (mm) through time for the *Strophodonta* specimens. Columns indicate the repair frequency for different body sizes in each unit, ranging from 5 mm to 30 mm in increments of 5 mm. The size refuge is the sudden drop-off in column height, indicated by the arrow. Brackets below the x-axis indicate the actual size range that is occupied for each unit.

the least in the Norway Pt. unit (Fig. 6). In contrast to the *Pseudoatrypa* size refuge, which was approximately opposite to the repair frequency, the *Strophodonta* size refuge roughly tracks the repair frequency, with the smallest size refuge in the Genshaw (Fig. 6). The repair frequency and the size refuge track each other in every unit-to-unit transition except from the Genshaw to Norway Pt., where the repair frequency decreases and the size refuge increases. For the sampled atrypides, the Genshaw Fm. was the only unit that did not have a size refuge, but for the sampled strophomenides, none of the units reached a size refuge except for the Bell Shale (20–25 mm) (Fig. 6). In the Ferron Pt., Genshaw, Norway Pt., and Potter Farm units, there were no size drop-offs in the percentage of brachiopods that had repair scars, indicative of a size refuge. The predators were capable of taking any *Strophodonta* found in these units, regardless of size. Therefore, there is no evidence for a change in the size refuge in the sampled strophomenides through time, and so any changes in repair frequency are probably not due to changes in the adaptive gap. Consequently, any further analysis, including any statistical calculations and additional measurements to determine whether there was a significant change in the adaptive gap between predators and prey through time, is unnecessary.

We acknowledge that there may be two different species of *Pseudoatrypa* present in our specimens from the Middle Devonian of Alpena and Presque Isle Counties of Michigan (Bose et al., 2011) or possibly two plastic morphotypes, but they are similar enough in form and ornamentation that, from a predator's standpoint, there was no preference as there was no major difference in repair frequencies between *P. lineata* and *P.* sp. A. These two potential *Pseudoatrypa* species were also likely coexistent as, to the best of our knowledge and the locality information provided, *P. lineata* and *P.* sp. A were found concurrently in similar environments. For these reasons, we chose to treat *P. lineata* and *P.* sp. A together as one prey item when plotting graphs and performing analyses.

There are two different species of *Strophodonta* that are very different in form and morphology, with *S. erratica* having much stronger ornamentation than *S. extenuata*. Whereas *S. extenuata* is present in all examined units, *S. erratica* was only present in the Genshaw Fm., in which it represents a large majority (82.72%) of the specimens that we studied in the unit. Also, within the Genshaw, the *S. erratica* specimens were not found in the same localities as the *S. extenuata* specimens (all *S. erratica* specimens that we examined are originally from the west side of Long Lake Road, Sec. 1, T.33N., R.8E., Alpena County, whereas the *S. extenuata* specimens from the Genshaw were found in a ditch along old Long Lake Road, Sec. 22, T.32N., R.8E., Alpena County), suggesting that these two species were not living together. It is probable that the presence of a second species, *S. erratica*, in the Genshaw had an effect on the repair frequency as there is a substantial difference in the repair frequencies when *S. extenuata* and *S. erratica* are analyzed on their own (57.58% and 18.99%, respectively, compared to 25.65% when the two species are combined), but the repair frequency and size refuge still track each other well when the Genshaw unit, or *S. erratica*, is removed.

Because the sampled atrypides demonstrated contrasting changes in repair frequency and size refuge, they were subjected to additional measurements (sphericity and ontogenetic growth rates) to determine whether the specimens of each unit had any variation in their morphology that would make them potentially more or less effective relative to predators. The results were inconclusive and not significant. There were no discernible patterns (i.e. more spherical brachiopods or brachiopods with faster growth rates in the units with the higher repair frequencies and vice versa) indicative of differences in the morphology of the brachiopods pre- and post-Genshaw that would suggest a response to increased predation pressure.

4. Discussion

We wanted to provide an empirical example of the size refugia technique, first proposed by Leighton (2002), in which the hypothesis of a change in the adaptive gap between predators and prey would be corroborated when the repair frequency and the size refuge change in opposite directions and not corroborated when these variables do not change in opposite directions. Fig. 5 displays the relationship between the repair frequency and the size refuge from unit to unit in *Pseudoatrypa*. From the Bell Shale to Ferron Pt., there is a decrease in the sampled atrypide repair frequency but we do not observe an inverse increase of the size refuge, suggesting that this decline in both repair frequency and size refuge is simply due to a decrease in the number of predator attacks and not due to a change in the relative abilities of predators and prey. From the Ferron Pt. to Genshaw Fm., there is a decline in the repair frequency as well as a corresponding increase in the size refuge, which corroborates the hypothesis of an increase in the adaptive gap between predators and prey (the predator becomes stronger relative to the prey). In contrast, from both Genshaw to Dock St. Clay and Dock St. Clay to Potter Farm, there is an increase in repair frequency and an associated decrease in size refuge, which corroborates the hypothesis of a decrease in the adaptive gap between predators and prey (the prey's defensive capabilities were improved relative to the predator's attack abilities).

Predators in the Genshaw could take larger sizes of *Pseudoatrypa* prey than in any other unit (Fig. 5). The Genshaw is the one unit that never appeared to reach a size refuge as there is no sudden drop-off at a certain size increment as there are in the other four units: 50% of the sampled atrypides between 35 and 40 mm in length were attacked in the Genshaw and there were no *Pseudoatrypa* larger than 40 mm for predators to take so, therefore, presumably the predators in the Genshaw could take any size of *Pseudoatrypa*. Although there is a possibility that Genshaw predators were capable of taking larger *Pseudoatrypa* prey than those observed, we are being conservative in using the maximum size data, rather than maximum size-at-attack, as the position of the size refuge. Despite this, the Genshaw data still support the hypothesis that Genshaw predators probably had a larger adaptive gap relative to atrypide prey than did predators in any other Traverse shale.

There were significant changes in repair frequency between the Bell Shale to Ferron Pt. and Ferron Pt. to the Genshaw. There were no significant changes to repair frequency between the Genshaw to Dock St. Clay and Dock St. Clay to Potter Farm, but this is likely because the Dock St. Clay, the unit that separates the Genshaw and Potter Farm units, has such a small number of specimens, only 52, that the data may not be representative of the unit. There is a significant increase in repair frequency from the Genshaw to Potter Farm (9 to 15%) but the low sample numbers of the unit in between mask this significance. When focusing on the overall U-shaped trend in repair frequency through time, there was an extremely significant change in repair frequency between the Bell Shale and Genshaw units, excluding the Ferron Pt., and between the Genshaw and Potter Farm units, excluding the Dock St. Clay.

Unlike for the *Pseudoatrypa*, in which the plots for the repair frequency and the maximum size-at-attack, used as a proxy for size refuge, trended approximately opposite to each other, the relationship between these variables in the *Strophodonta* roughly track each other through time (Fig. 6). The Bell Shale is the only unit that exhibited a size refuge, as there is a drop-off in the percentage of *Strophodonta* that had repair scars at the 20–25 mm size interval (Fig. 6). None of the other units exhibited a size refuge as there were no *Strophodonta* of size intervals larger than the highest repair scar percentage interval. Therefore, there is no evidence for a change in predator ability and thus, any apparent change in the size refuge for the sampled strophomenides probably has more to do with a change in absolute body size than with size-at-attack. Although a change in prey body-size could constitute a change in defense, there was no evidence in this case that the change in body-size was effective at resisting predation; the predators were still able to take the largest specimens. Because there is no relationship between repair frequency and size refuge, any changes in repair frequency are probably due to a change in predator attack frequency rather than changes in the relative abilities of predators and prey. At the very least, there is no evidence for a biologically significant change in the adaptive gap between predators and *Strophodonta*.

Though there was no evidence of a change in the adaptive gap between the predators and the sampled strophomenides, there was evidence of a changing adaptive gap with the atrypide specimens from the Ferron Pt. to Genshaw, in which the predator becomes more powerful relative to the prey, and between Genshaw to Potter Farm, in which the predator becomes less effective relative to the prey through this time interval. This could mean that there is a possibility of an evolutionary arms race occurring between the predators and atrypide prey. We cannot be completely sure that an evolutionary arms race is occurring, however, as the units sampled for this study are non-consecutive because we analyzed shales only. There is no way of knowing how the intervening limestones would affect the overall trends due to the logistic difficulties in removing specimens from the matrix without damaging them.

To test whether there is a possibility of an evolutionary arms race occurring within the atrypides through time between the predators and prey, atrypide brachiopods were inspected for any changes to their morphology pre- and post-Genshaw that would have made it more or less difficult for the predators to successfully prey upon them (i.e. sphericity and ontogenetic growth rates of the specimens). One explanation for why the atrypides of the Genshaw had the lowest repair frequency and the highest size refuge was that they may have had less spherical shells, and therefore were less resistant to point-loading by crushing predators. The sphericity would have increased through time from the Genshaw to Potter Farm unit because the adaptive gap between predators and prey decreases through this time interval, however, no discernible pattern was found that would support our expected result and, therefore, no further tests were performed. Another possible explanation to support the pattern that we observed in the atrypides is an increase in growth rates in the atrypides through time post-Genshaw; an increase in growth-rates would enable faster repair of damage, presumably a benefit to potential prey. However, there was no discernible pattern in the ontogenetic growth rates of the specimens from the Genshaw to Potter Farm either. Sclerochronology could potentially provide more information relevant to this problem, but as a first approximation, the growth-line data do not support the hypothesis.

Though examples of evidence of changes in the morphology of prey through time in response to predation pressures are common (Vermeij, 1977; Kitchell et al., 1981; Boulding, 1984; Leighton, 2003a; among others), we did not find evidence within the atrypides of differences from unit to unit. However, we cannot exclude the possibility of changes in other potential defenses, especially shell-thickness. As noted earlier, capturing shell-thickness data would have been impossible without using destructive techniques as the specimens were almost all fully articulated. We also did not have predators from the Traverse Group to determine if there were any changes to their morphology that may have made them more powerful in the Genshaw, and therefore, exploring morphological changes in predators through time is a possibility for future research. Because there is a decline in atrypide repair frequency in the Genshaw and an associated increase in the size refuge, it is plausible that the predators became stronger in this unit.

Possible Mid-Devonian crushing predators that could have preyed upon the studied specimens include ptychodontid placoderms and phyllocarids (Leighton, 2003b). Ptychodontid placoderms may have been durophages (shell-crushers) because they had molariform teeth which, due to their low and broad shape, would be ideal for crushing brachiopods. Like other durophages, ptychodontids also had a fixed jaw structure (Moy-Thomas and Miles, 1971). Certain arthropods, like phyllocarids, could have used their calcified, raptorial appendages (or gnathobases) to crush brachiopod prey (Leighton, 2003b).

This study could also benefit from examining more atrypide specimens, specifically from the Dock St. Clay, in which the sample numbers were relatively low compared to the other units, but which were included for the sake of completeness. If we had a more substantial sample size for the Dock St. Clay, there may have been a more significant change in repair frequency from the Genshaw to Dock St. Clay and from the Dock St. Clay to Potter Farm. Unfortunately, the Dock St. Clay locality is no longer accessible to obtain more specimens.

We allow for the possibility that the specimens of *Pseudoatrypa* and *Strophodonta* that we examined lived together in the same localities. In this regard, it should be noted that the maximum size of *Pseudoatrypa* in any given unit was roughly 10 mm larger than that of *Strophodonta*; moreover, the atrypides would have been considerably larger in height (strongly biconvex), and so large specimens of *Pseudoatrypa* would have been much more difficult for a gape-restricted predator (most shell-crushers are gape-restricted) to handle than would the concavo-convex *Strophodonta*. If the two prey taxa were living together, it would not be surprising then that the Traverse *Strophodonta* did not typically achieve a size refuge against predators capable of taking larger *Pseudoatrypa*. The greater repair frequencies on *Strophodonta* would most likely be a reflection of greater attack frequencies on the more vulnerable prey, rather than a function of lower success rates for the predator. However, in many cases there is not a clear record of the specifics of the localities (e.g. horizons) from where the brachiopods were collected. Because we have no hard evidence that our atrypide and strophomenide specimens lived together, we choose to treat them as independent groups, and as such, we cannot determine if the two prey taxa had an effect on each other's repair frequencies and size refugia. Other avenues for future research would be to determine the effect of the presence of one genus on the other and whether predators had a prey preference between *Pseudoatrypa* and *Strophodonta* through time. This would be especially pertinent in the Genshaw where the size refuge was at its highest for the atrypides and at its lowest for the strophomenides across all units.

This first empirical study of the size refugia technique, in which the interpretation of a change in repair frequency was determined by the presence of a change in the adaptive gap between predator and prey, evinced the utility of the method. By excluding the size refugia and examining the data using only the repair frequencies, one might have mistakenly argued that the sampled *Strophodonta*, or their predators, had evolved to either increase or decrease the adaptive gap. By adding the size refuge data, however, it becomes evident that, while a change in the adaptive gap through time is a plausible hypothesis for the change in repair frequency examined in the sampled *Pseudoatrypa*, such a hypothesis is probably incorrect for the sampled *Strophodonta*.

5. Conclusion

Our goal in this study was to provide the first empirical case of the size refugia technique, as proposed by Leighton (2002), to determine whether a change in the adaptive gap between predators and brachiopod prey has occurred through time. The data are consistent with the hypothesis that, within the sampled atrypide specimens, there was a change in the adaptive gap because the repair frequency and the size refuge changed in opposite directions. In contrast, there was no evidence for a change in the adaptive gap within the sampled strophomenide specimens because these variables tracked each other through time. The identification of prey morphological changes related to changes in the adaptive gap and any implications of a change in the adaptive gap between the predators and atrypide prey (i.e. the possibility of an evolutionary arms race) were beyond the reach of this study, but further research on these topics is warranted.

Acknowledgments

The first author gratefully acknowledges support from an NSERC Undergraduate Research Award. The research was also made possible by an NSERC Discovery Grant to the second author. Also thank you to Dan Miller and the University of Michigan Museum of Paleontology for loaning us the specimens and to Dr. Patricia Kelley and Dr. Gary Vermeij for their thoughtful reviews.

References

Alexander, R.R., 1986. Resistance to and repair of shell breakage induced by durophages in Late Ordovician brachiopods. Journal of Paleontology 60, 273–285.

Alexander, R.R., 1990. Mechanical strength of shells of selected extant articulate brachiopods: implications for Paleozoic morphologic trends. Historical Biology 3, 169–188.

Alexander, R.R., Dietl, G.P., 2003. The fossil record of shell-breaking predation on marine bivalves and gastropods. In: Kelley, P.H., Kowalewski, M., Hansen, T.A. (Eds.), Predator–prey Interactions in the Fossil Record. Kluwer Academic/Plenum Publishers, New York, pp. 141–176.

Allmon, W.D., Nieh, J.C., Norris, R.D., 1990. Drilling and peeling of turritelline gastropods since the Late Cretaceous. Paleontology 33, 595–611.

Anderson, L.C., Geary, D.H., Nehm, R.H., Allmon, W.D., 1991. A comparative study of naticid gastropod predation on *Varicorbula caloosa* and *Chione cancellata*, Plio-Pleistocene of Florida, USA. Palaeogeography, Palaeoclimatology, Palaeoecology 85, 29–46.

Bartholomew, A.J., Brett, C.E., 2007. Correlation of Middle Devonian Hamilton Group-equivalent strata in east-central North America: implications for eustasy, tectonics and faunal provinciality. Special Publication. Geological Society of London 278, 105–131.

Berg, J.C., Nishenko, S., 1975. Stereotypy of predatory boring behavior of Pleistocene naticid gastropods. Paleobiology 1, 258–260.

Bose, R., Schneider, C.L., Leighton, L.R., Polly, P.D., 2011. Influence of atrypid morphological shape on Devonian episkeletobiont assemblages from the lower Genshaw Formation of the Traverse Group of Michigan: a geometric morphometric approach. Palaeogeography, Palaeoclimatology, Palaeoecology 310, 427–441.

Boulding, E.G., 1984. Crab-resistant features of shells of burrowing bivalves: decreasing vulnerability by increasing handling time. Journal of Experimental Marine Biology and Ecology 76, 201–223.

Brett, C.E., Baird, G.C., Bartholomew, A.J., DeSantis, M.K., Ver Straeten, C.A., 2011. Sequence stratigraphy and a revised sea-level curve for the Middle Devonian of eastern North America. Palaeogeography, Palaeoclimatology, Palaeoecology 304, 21–53.

Dietl, G.P., Alexander, R.R., Bien, W.F., 2000. Escalation in Late Cretaceous–Early Paleocene oysters (Gryphaeidae) from the Atlantic Coastal Plain. Paleobiology 26, 215–237.

Ehlers, G.M., Kesling, R.V., 1970. Devonian Strata of Alpena and Presque Isle Counties, Michigan. Michigan Basin Geological Society, MI.

Elliot, D.K., Bounds, S.D., 1987. Causes of damage to brachiopods from the Middle Pennsylvanian Naco Formation, central Arizona. Lethaia 20, 327–335.

Elner, R.W., Hughes, R.N., 1978. Energy maximization in the diet of the shore crab, *Carcinus maenas*. Journal of Animal Ecology 47, 103–116.

Harper, E.M., Peck, L.S., Hendry, K.R., 2009. Patterns of shell repair in articulate brachiopods indicate size constitutes a refuge from predation. Marine Biology 156, 1993–2000.

Huntley, J.W., Kowalewski, M., 2007. Strong coupling of predation intensity and diversity in the Phanerozoic fossil record. Proceedings of the National Academy of Sciences of the United States of America 104, 15006–15010.

Imbrie, J., 1959. Brachiopods of the Traverse Group (Devonian) of Michigan: Bulletin of the AMNH, 116. article 4.

Kitchell, J.A., Boggs, C.H., Kitchell, J.F., Rice, J.A., 1981. Prey selection by naticid gastropods: experimental tests and application to the fossil record. Paleobiology 7, 533–552.

Kowalewski, M., Flessa, K.W., Marcot, J.D., 1997. Predatory scars in the shells of a recent lingulid brachiopod: paleontological and ecological implications. Acta Palaeontologica Polonica 42, 497–532.

Leighton, L.R., 2002. Inferring predation intensity in the marine fossil record. Paleobiology 28, 328–342.

Leighton, L.R., 2003a. Morphological response of prey to drilling predation in the Middle Devonian. Palaeogeography, Palaeoclimatology, Palaeoecology 201, 221–234.

Leighton, L.R., 2003b. Predation on brachiopods. In: Kelley, P.H., Kowakewski, M., Hansen, T.A. (Eds.), Predator–prey Interactions in the Fossil Record. Kluwer Academic/Plenum Publishers, New York, pp. 215–237.

Leighton, L.R., 2011. Analyzing predation from the dawn of the Phanerozoic. In: Laflamme, M., Schiffbauer, J.D., Dornbos, S.Q. (Eds.), Quantifying the Evolution of Early Life: Numerical Approaches to the Evaluation of Fossils and Ancient Ecosystems: Topics in Geobiology, 36, pp. 73–109 (Chapter 4).

Moy-Thomas, J.A., Miles, R.S., 1971. Palaeozoic Fishes, second ed. Saunders, Philadelphia.

Sheehan, P.M., Lesperance, P.J., 1978. Effect of predation on population dynamics of a Devonian brachiopod. Journal of Paleontology 52, 812–817.

Thomas, R.D.K., 1976. Gastropod predation on sympatric Neogene species of *Glycymeris* (Bivalvia) from the eastern United States. Journal of Paleontology 50, 488–499.

Vermeij, G.J., 1976. Interoceanic differences in vulnerability of shelled prey to crab predation. Nature 260, 135–136.

Vermeij, G.J., 1977. The Mesozoic marine revolution: evidence from snails, predators and grazers. Paleobiology 3, 245–258.

Vermeij, G.J., 1982. Unsuccessful predation and evolution. American Naturalist 120, 701–720.

Vermeij, G.J., 1987. Evolution and Escalation. Princeton University Press, Princeton, NJ.

Vermeij, G.J., Zipser, E., Dudley, E.C., 1980. Predation in time and space: peeling and drilling in terebrid gastropods. Paleobiology 6, 352–364.

Vermeij, G.J., Schindel, D.E., Zipser, E., 1981. Predation through geological time: evidence from gastropod shell repair. Science 214, 1024–1026.