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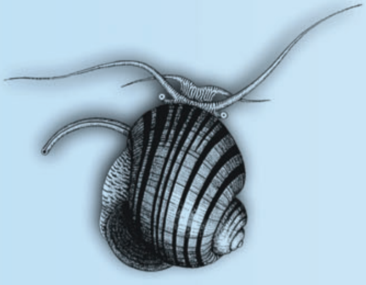

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Behavioural versatility of the giant murex *Muricanthus fulvescens* (Sowerby, 1834) (Gastropoda: Muricidae) in interactions with difficult prey

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ABSTRACT

Muricanthus fulvescens, one of the largest muricid gastropods in the world, was once thought to be a behavioural specialist, using its shell to grind feeding holes in bivalve prey. New experimental observations, however, reveal that this predator employs up to four modes of predation, including selective use of shell grinding and edge drilling in interactions with the large, thick-shelled venerid clam *Mercenaria campechiensis*. Shell-grinding attacks were found to be slightly faster than edge-drilling attacks, but had a lower success rate. Choice of predatory mode was more strongly correlated with the prey's anterior–posterior shell length than predator size. Smaller clams were attacked more frequently by shell grinding, while larger, thicker prey tended to be attacked by edge drilling. Several larger predators edge-drilled their prey successfully after first failing with the faster grinding behaviour; trial-and-error initiation of attacks with the more rapid grinding behaviour, however, was rare and expressed only by the largest predators. We also report an anecdotal observation of wall drilling and morphological evidence consistent with two modes of edge-drilling attacks, including drilling of larger holes for proboscis insertion and feeding and smaller, barely detectable (<1 mm) holes for toxin injection. Toxin use is further supported by a lack of correlation between predator size and inner drill-hole dimensions. The occurrence of previously undetected diversity in predatory modes of *M. fulvescens*, a common, easily accessible species, demonstrates how much we have to learn about ecological versatility in muricids and its role in muricid evolution.

INTRODUCTION

Most species of the neogastropod family Muricidae feed on shelled invertebrates, accessing the soft tissues by drilling a hole through the prey's shell wall using a combination of mechanical abrasion with the mineralized feeding teeth (radula) and acidic secretions of an accessory boring organ (ABO) (Taylor *et al.*, 1980). Drilling a prey bivalve through its central valve wall, however, can take up to a week or longer (Dietl & Herbert, 2005) and, during that time, drilling snails are vulnerable to competitors and other predators (Hutchings & Herbert, 2013). Some muricids have been found to switch to faster modes of attack more often when exposed to such enemies (Dietl, Herbert & Vermeij, 2004; Chattopadhyay, Zuschin & Tomašových, 2014; Paul, Herbert & Dietl, 2014). Examples of such behaviours include selective placement of drill holes over the thin commissure of bivalve prey (edge drilling) (Dietl *et al.*, 2004; Dietl & Herbert, 2005), use of anaesthetizing toxins secreted by the accessory salivary and hypobranchial glands that cause bivalve prey to gape (e.g. Andrews, Elphick & Thorndyke, 1991; Roller, Rickett & Stickle, 1995; Roseghini *et al.*, 1996) and use of several types of shell-lip spines to grind or wedge open feeding holes in bivalves (Paine, 1966; Perry, 1985; Vermeij, 2001; Peharda & Morton, 2006). When threats from competitors and other predators are reduced, however, selection of one predatory mode over another should be determined, in part, by other fitness considerations, such as which mode of attack maximizes the likelihood of success for a given prey type (e.g. Morton, Peharda & Harper, 2007) and, for snails that use their own shell to grind holes in prey armour, which mode of attack minimizes damage to the snail's own shell.

In this study, we investigated predatory mode selection by the giant eastern murex *Muricanthus fulvescens* (Sowerby, 1834), a muricid from the subtropical western North Atlantic. Initial observations by Wells (1958) suggest that *M. fulvescens* uses just one mode of attack—grasping a bivalve prey with its foot and pressing small spines on its own shell lip against the margin of one of the prey valves. Repeated contractions of *M. fulvescens*' columellar muscle draw the prey's shell across the predator's shell lip, grinding and breaking away slivers of prey shell, ultimately opening a hole at the commissure that is large enough for the predator to insert its proboscis to feed. Wells (1958) argued that *M. fulvescens* was, in fact, a shell-grinding specialist due to its large size (up to 17 cm in shell length), thick shell lip and powerful columellar muscle. However, Wells (1958) did not ask how smaller, thinner-shelled and less powerful subadults of *M. fulvescens* might feed, or how large adults feed when faced with difficult, thick-shelled prey.

Following Wells' (1958) initial work, Carriker & Yochelson (1968) and Radwin & Wells (1968) both reported anecdotal observations of *M. fulvescens* using a second predatory mode, edge drilling, in attacks on the venerid bivalve *Mercenaria*, one of the predator-prey interactions studied by Wells (1958); however, no comparative data on sizes of predators and prey were provided in those follow-up reports that could be used to determine whether drilling is used by *M. fulvescens* selectively. More recently, anatomical work by Kool (1993) described the ABO of *M. fulvescens* as well developed rather than vestigial; the ABOs of muricids that do not drill are reduced or lost (Kool, 1993). In combination, these observations suggest that *M. fulvescens* is a competent drilling predator and, more importantly, that it might optimize nutrient intake in each feeding event by weighing the relative costs and benefits associated with edge drilling and grinding modes of attack. Although grinding attacks by muricids may be up to three times faster than edge drilling (Peharda & Morton, 2006), grinding attacks on the largest bivalves should have a lower likelihood of success due to increased prey shell thickness and strength (Morton *et al.*, 2007) and should also bring increased risk of damage to the predator's own shell. Prey clams used by Wells (1958) were of small- to mid-range size for the genus *Mercenaria* (4.8 to 8.2 cm in antero-posterior length) and would therefore have had relatively thin valve edges. We hypothesized that in interactions involving larger, thick-lipped *Mercenaria* clam prey, the dominant shell grinding behaviour of *M. fulvescens* will predictably give way to the regular expression of slower modes of attack such as drilling, which increase success rates and minimize risk of injury to the predator.

MATERIAL AND METHODS

Laboratory experiments

Fifteen *Muricanthus fulvescens* ranging from 6.9 to 12.9 cm in shell length were collected in St Andrews Bay, Florida (30°07′25 N, 85°43′54 W) at depths between 2 and 5 m. Each animal was housed separately in a 38-l tank with 10 cm of coarse sand and recirculating seawater kept at 35 ppt and room temperature (22 °C) at the University of South Florida. Because experience can influence prey-handling behaviours and handling times of predators (Hughes & Dunkin, 1984; Rovero, Hughes & Chelazzi, 1999), predators were fed *Mercenaria campechiensis*, the prey item used in this study, *ad libitum* for 3 months to standardize predator experience levels with this prey species. The length of this standardization period was determined by previous findings that predators—whether fish, crabs or snails—generally require five to ten attacks for the handling efficiency of inexperienced predators to reach an asymptote (see review by Hughes *et al.*, 1992). Muricids typically take 1 to 7 d to initiate an attack and complete feeding, followed by several days of rest before foraging again (Dietl & Herbert, 2005).

Mercenaria campechiensis prey, ranging in size from 3.7 to 14.2 cm in antero-posterior shell length, were collected as needed from intertidal seagrass and sandflats in Miguel Bay near Tampa, Florida (27°34′39 N, 82°26′35 W) and maintained for up to a month on a phytoplankton diet in holding tanks isolated from predators until used for one of the experimental trials. Clams were haphazardly chosen for each trial and were used only if the animals showed signs of vigour (i.e. fast response times for valve closure) and if their shells bore no evidence of prior drilling or grinding attacks.

Following the habituation period, each predator was starved for a period of 24 h and then offered a single *M. campechiensis* prey. Within predator tanks, clams were manually positioned as collected in life, i.e. with only the postero-ventral region of the shell exposed above the sediment surface. Predator tanks were checked daily and new prey were offered to predators immediately following removal of valves of consumed prey. Predators showed no signs of stress during the experiment, which lasted over a year, although several of the smaller predators stopped feeding to grow new shell. When this happened, they were removed from the experiment because new shell is thinner and possibly a deterrent to use of the shell-grinding behaviour. For ten grinding and eleven drilling attacks, predation events were monitored continuously to record the duration of the interactions, which were measured beginning from the time the predator stabilized its position on its prey until feeding stopped and the predator crawled away.

Assessing predation evidence

Valves of consumed prey were examined macroscopically for evidence of predation. Attacks were scored as shell grinding or edge drilling. The antero-posterior prey length and the types and dimensions of predation traces on the valves were recorded for each predation event. The relationship between prey size (antero-posterior length) and prey handling method (both attempted and successful) was explored using binary logistic regressions, as this allowed us to ask whether certain prey sizes were more likely to be subjected to one prey handling method or the other. Drilling attacks were coded as the positive response (1) for all logistic regressions, while grinding was coded as 0. As we included only consumed prey as indicated above, it was unnecessary to include a category of 'not attacked.' We then assessed the relationship between predator size and the frequency with which an attack was initiated by grinding or edge drilling with an ordinary least squares (OLS) linear regression. For the subset of predation events with duration data, we used a series of OLS regressions to test for relationships between the duration of grinding or edge-drilling attacks and antero-posterior prey length and predator size. We also used an analysis of covariance (ANCOVA) to determine whether grinding and edge-drilling attacks differed in duration, with prey size as a covariate to remove the effect of size from this particular analysis. All regression analyses in this study were performed in SigmaStat v. 3.10 and the ANCOVA was performed in SYSTAT v. 10. All statistical tests in this study used a significance level of 0.05.

Drill-hole analysis

Drill-hole dimensions were measured to the nearest 0.1 mm using digital callipers. Inner drill-hole diameter (IDD) of edge-drilling traces was measured by pressing plasticine clay into the hole while the valves were in a closed position and measuring the drill-hole cast. While the outer drill-hole diameter (ODD) is a function of predator size (Palmer, 1988; Kabat, 1990; Mendez & Cancino, 1990; Kowalewski, 2004), the dimensions of the smaller, inner drill hole provide information about whether the hole was a larger opening used for proboscis feeding or a smaller opening used only for injecting toxins that cause the prey to gape. Functional feeding holes are expected to increase in both IDD and ODD with increasing predator size, to accommodate the proboscis, while drill holes used only for injecting toxins are expected to increase only in ODD, because the inner hole does not need to be enlarged for feeding. This prediction has been verified elsewhere for muricid gastropods (McGraw & Gunter, 1972; Gunter, 1979; Urrutia & Navarro, 2001).

Based on experimental observations of drilling by naticid gastropods, Kitchell *et al.* (1986) established a threshold for functional feeding holes as those having an IDD:ODD > 0.5. This threshold should be used with caution in application to other drilling predators, such as muricids, due to anatomical differences in relative sizes of the proboscis and ABO. Additionally, when dealing with drill holes of irregular or unusual shape, as is the case in the present study, use of IDD:ODD ratios is potentially misleading (Urrutia & Navarro, 2001). For slit-like edge drills produced by *M. fulvescens*, we consider inner drill hole height

(IDH), which is the smallest inner drill hole dimension, and inner drill hole area (IDA = [IDD/2][IDH/2][π]), the total area available for proboscis entry, as better measures of constraints on proboscis entry than width (IDD). Both IDH and IDA should be positively correlated with predator size for functional feeding holes but not for toxin-injection holes. To assess this relationship, we used a series of Pearson's correlations to deterimine if predation trace dimensions (ODD, IDH, IDA) were correlated with prey size. Pearson's correlations were performed with SigmaStat v. 3.10.

RESULTS

Prey handling

Muricanthus fulvescens initiated attacks on clams either by pulling the clam completely out of the sediment so that the shell could be oriented for grinding or drilling, or by attacking the exposed end of the clam near the siphon without pulling it free of the sediment. Fifty-nine attacks were initiated by grinding, which had a success rate of 85%. In the nine unsuccessful grinding attacks, predators switched to edge drilling and completed the attacks successfully. Fifty-one attacks were initiated by edge drilling, which was successful 100% of the time.

Grinding attacks began with a careful docking stage in which the predator held one valve of the clam with its foot and pressed its shell lip slowly and at an oblique angle against the valve margins of its prey (Fig. 1A). When the two shells were in contact, the predator contracted its foot muscle, driving the predator's shell lip into the clam's valve edges. These contractions lasted for roughly half a minute, followed by a brief rest. This cycle was repeated until small fractures developed along the valve margins of the prey shell to create a hole.

Predators used short, ventrally pointed crenulations of their shell lips to grind the prey shell. Crenulations develop as outgrowths of grooves between spiral cords along the apertural lip (Fig. 1B). Due to the oblique angle of the predator's shell lip relative to the commissure of its prey, only crenulations between the first (P1) and second (P2) varical spines contacted and damaged the lip of the prey shell (developmental cord/spine terminology after Merle, 2005). The oblique angle of the predator's shell lip to its prey tended to localize prey shell damage to a relatively small region of the commissure. The remaining crenulations between varical spines P2 and P5 (i.e. anterior to P2) did not dig into the prey shell's lip but were instead pressed flat over the prey valve's outer surface, stabilizing the prey shell during the grinding attack (Fig. 1A). The varical spines P1–P5 are not ventrally pointed (Fig. 1A, C) and, thus, did not contact the prey shell at any point during the attack. Damage to the predators' shell lips in grinding attacks included only superficial abrasion of lip crenulations.

Edge-drilling attacks began with a similar docking stage and relative orientation of both shells, but the predator did not move until the attack was completed.

Influence of prey and predator size on mode of attack

The probability of a snail initiating an attack with shell grinding rather than the edge-drilling behaviour decreased sharply with increasing prey size (logistic regression, $b = 0.06$, Wald statistic = 34.84, $P < 0.001$), as did the probability of a grinding attack being successful (logistic regression, $b = 0.08$, Wald statistic = 32.20, $P < 0.001$). None of the 55 clams between 8.3 and 14.2 cm in antero-posterior length was attacked successfully by shell grinding by a predator of any size. Grinding was only successful for prey between 3.7 and 8.3 cm.

Shell-grinding behaviour was expressed by both the smallest and largest predators used in our experiment, and the relationship between predator size and the frequency with which an attack was initiated by grinding, given the same range of prey sizes offered, was only marginally significant (linear regression, $r^2 = 0.33$, $F_{1,11} = 5.31$, $P = 0.04$). Larger snails, however, were more likely to test the physical limits of their shell-grinding behaviour in interactions with larger prey (Fig. 2). All nine unsuccessful grinding attempts observed in this study were recorded for predators in the larger half of the predator size range studied (9.6 cm in length or larger), attacking medium-sized to very large prey (6.8 to 14.2 cm valve length). Overall, predators within this larger half of the predator size range studied were successful in 83% (45/54) of attempted grinding attacks. In comparison, predators smaller than 9.6 cm employed grinding successfully 100% of the time in six attempts, although all six of these prey were small (less than 4.6 cm in length). Smaller predators were offered a total of 18 large clams in the 6.8 to 14.2 cm size range, but these were attacked exclusively by edge drilling.

Duration of attacks

For the subset of attacks that were timed ($n = 21$), grinding attacks ranged from 2 to 5 d in duration compared to 3 to 7 d for edge drilling and were of significantly shorter mean duration ($X \pm SD = 3.1 \pm 1.0$ d, $n = 11$) than edge-drilling

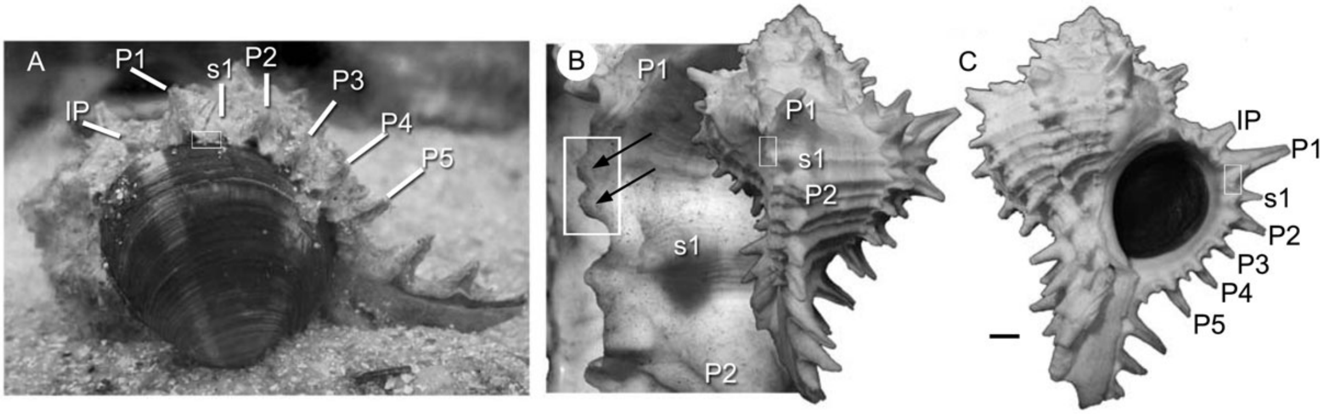

Figure 1. *Muricanthus fulvescens*. **A.** Shell-grinding attack on *Mercenaria* clam. Abbreviations: IP, infrasutural primary cord; P1–P5, primary cords; s1, secondary cord. **B.** Crenulations (arrows) of *M. fulvescens* apertural lip used to damage prey shell. **C.** Primary and secondary cords. Only lip crenulations (white boxes) between P1 and P2 cause damage to the prey shell. Scale bar **C** = 1 cm.

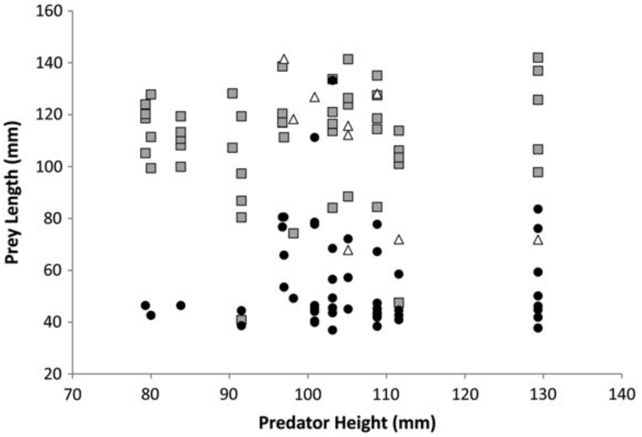

Figure 2. Bivariate scatter plot showing relationship between predator size (shell height), prey size (anterior-posterior shell length), mode of attack and attack success or failure, for *Muricanthus fulvescens* preying on *Mercenaria*. Symbols: black circles, successful shell grinding attacks; gray squares, successful edge drilling attacks; open triangles, unsuccessful shell grinding attacks.

attacks ($X \pm \mathrm{SD} = 4.5 \pm 1.1$ d, $n = 10$). However, prey attacked by grinding also tended to be smaller than those attacked by edge drilling. With the effect of prey size removed, grinding attacks by *M. fulvescens* are still of significantly shorter mean duration than edge-drilling attacks (ANCOVA, $F_{1,18} = 6.61$, $P = 0.019$). Within either the subset of smaller prey attacked by grinding and the subset of larger prey attacked by edge drilling, there was no relationship between the duration of an attack and either prey or predator size (linear regression, edge drilling: $r^2 = 0.47$, $F_{3,6} = 1.79$, $P = 0.25$; grinding: $r^2 = 0.32$, $F_{3,7} = 1.08$, $P = 0.42$).

Predation traces

Grinding attacks resulted in damage of 2 to 4 cm of the prey's ventral shell margin and ranged from shallow abrasion of the outermost shell layers (Fig. 3A, C) to deeper, scallop-shaped breakage over one or both valves (Fig 3B). In nine cases, shallow abrasion (i.e. abrasion not resulting in a hole between the valves) co-occurred with a complete edge drill. These were interpreted as unsuccessful grinding attacks followed by a switch to edge drilling. One grinding attack on a small clam resulted in complete failure of one prey valve (Fig. 3D). There was no apparent preference for

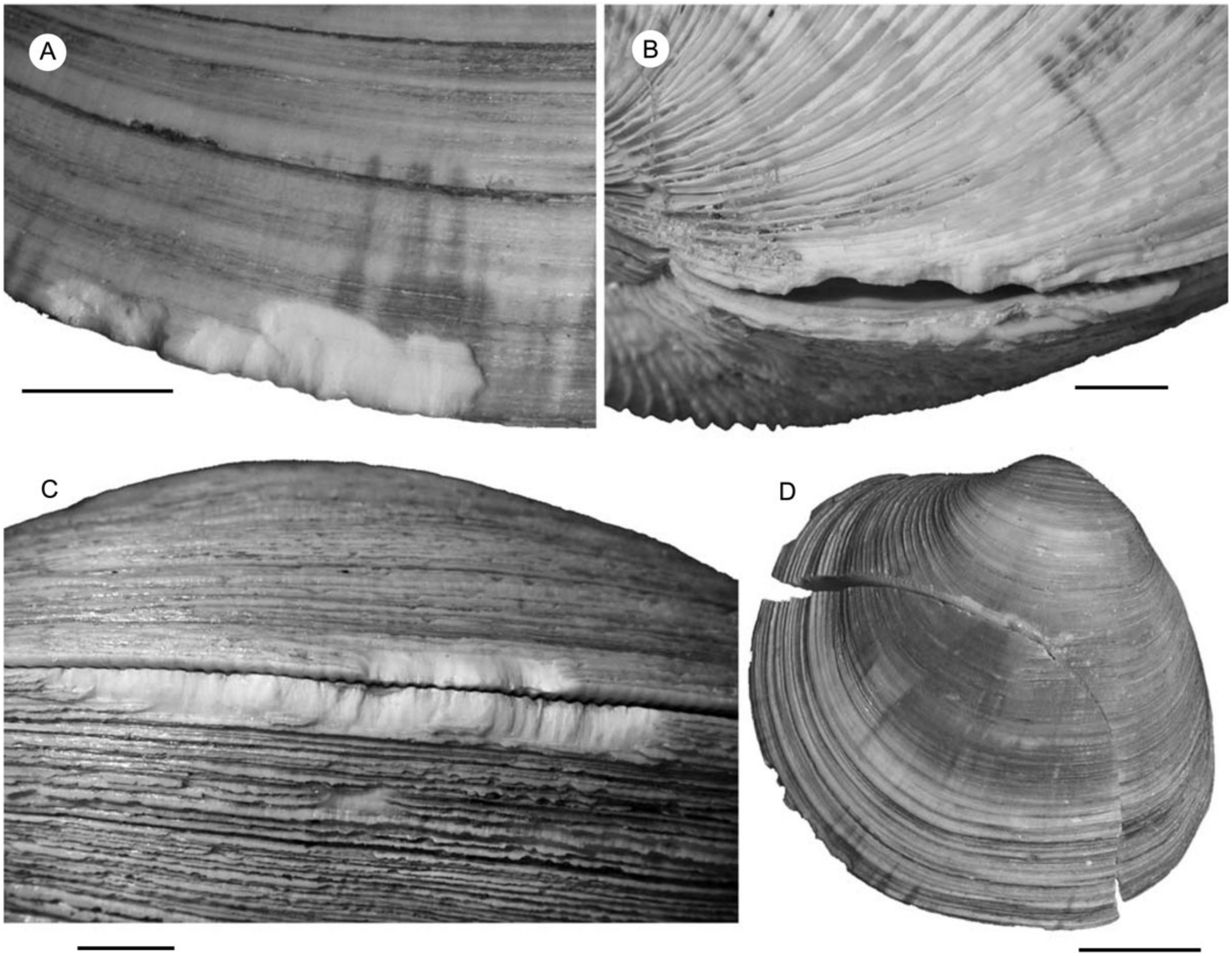

Figure 3. Examples of unsuccessful and successful shell grinding attacks by *Muricanthus fulvescens* on *Mercenaria*. **A.** Minor abrasion of outermost shell layers of one valve; unsuccessful attack. **B.** Deep, scallop-shaped breakage over both valves; successful attack. **C.** Minor abrasion to both valves; unsuccessful attack. **D.** Complete failure of prey valve; successful attack. Scale bars: **A**–**C** = 0.5 cm; **D** = 1 cm.

one valve over another during grinding attacks. Out of the 50 successful predation attempts that employed grinding, 39 prey (78%) had damage to both valves, four prey (8%) had damage to only the right valve and six (12%) had damage to only the left valve. For the 39 grinding attacks that damaged both valves, damage was more severe on one valve than the other for 19 prey.

Edge-drilling attacks left a trace characterized by two co-occurring features: (1) a countersunk (Fig. 4A–C) or straight-sided (Fig. 4D–F) drill hole orientated parallel to the plane of the commissure and penetrating through both valves; (2) a chemically-etched 'halo' on the interiors of both valves surrounding the drill hole and expanding away from it roughly 1 cm in all directions (Fig. 4B, C, F). Most edge-drilling attacks left slit-shaped holes that were indistinct on the surface (Fig. 4D, E). These were often detected only after examining the valve interior and locating the chemical etching trace that marks the site of drilling (Fig. 4F). Etching accompanied all edge drilling traces of *M. fulvescens*, including attacks on clams initiated by grinding followed by a switch to drilling. However, etching was absent from valves displaying grinding damage but no conspicuous drill hole.

ODD was positively correlated with predator size (Pearson correlation, $r_P = 0.362$, $n = 56$, $P = 0.006$). Despite being a significant correlation, a single predator could still produce a large range of hole sizes, as supported by low *r*-value (Fig. 5B). Further, mean ODD for one of the smallest predators (7.9 cm shell length) used in the experiment was 6.0 mm ($SD = 0.9$ mm, range = 5.0 to 7.0 mm, $n = 4$), while the mean ODD for the largest predator (12.9 cm shell length) was just 6.2 mm ($SD = 0.6$ mm, range = 5.4 to 7.0 mm, $n = 6$). The largest and smallest observed ODDs were made by predators in the middle of the size range used in this experiment; the largest observed ODD (8.6 mm) was produced by a predator having a shell length of 10.3 cm, while the smallest ODD (3.5 mm) was produced by a predator with a shell length of 9.2 cm.

Inner drill holes had broad diameters (IDD range = 3.2 to 7.9 mm, $X \pm SD = 5.3 \pm 1.1$, $n = 56$) but low height (IDH range = 0.5 to 1.5 mm, $X \pm SD = 0.9 \pm 0.3$, $n = 56$), resulting in a slit-like opening. IDD:ODD ratios ranged from 0.7 to 1.1, with a mean of 0.9, and all ratios exceeding the 0.50 threshold for functional feeding holes. However, IDH and IDA were not correlated with predator size (Pearson correlation for IDH, $r_P = -0.055$, $n = 56$, $P = 0.69$; Pearson correlation for IDA, $r_P = 0.188$, $n = 56$, $P = 0.17$). The largest predator (12.9 cm shell length) produced IDAs ranging from 2.4 to 7.8 mm^2, while the smallest predator used in this study (7.9 cm shell length) produced IDAs ranging from 3.4 to 7.0 mm^2 (Fig. 5A). The entire range of IDAs observed for all predators was 1.2 to 7.8 mm^2.

DISCUSSION

Muricanthus fulvescens is a versatile predator that selectively employs at least two predatory modes, shell grinding and edge drilling, in attacks on *Mercenaria* clam prey. Inner drill-hole dimensions, such as IDA, which did not correlate with predator size and were as small as 1.2 mm^2, suggest that this predator may also complete some edge-drilling attacks using a third mode, toxin injection. Wells' (1958) original observations of the

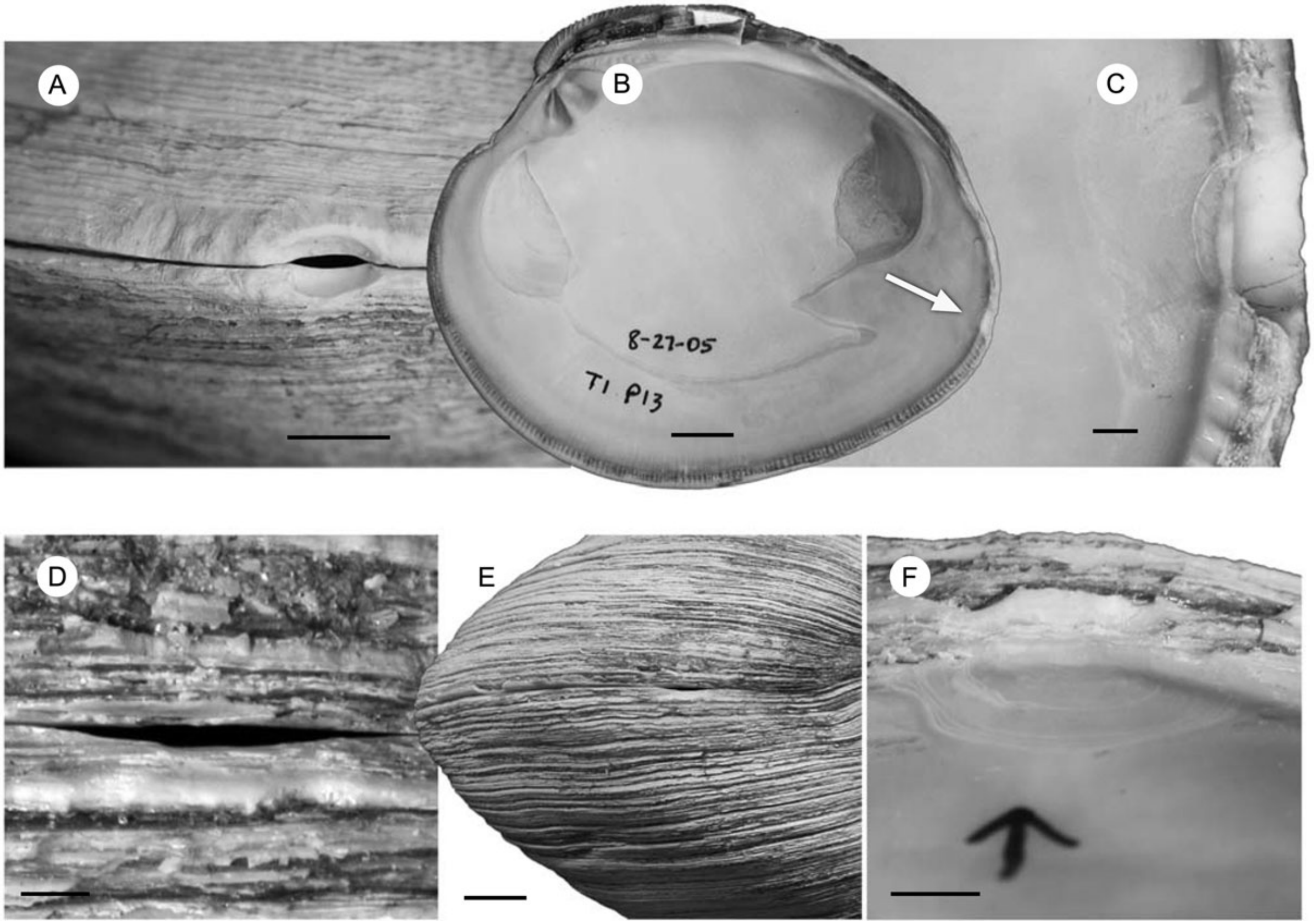

Figure 4. ***A–F.*** *Examples of successful edge-drilling attacks* by *Muricanthus fulvescens on* Mercenaria. **A.** Rounded, countersunk hole. **B.** Posterior placement of drill hole. **C.** Halo trace, inner surface of *Mercenaria*. **D.** Slit-shaped, straight-sided hole. **E.** Posterior placement of drill hole. **F.** Halo on inner surface of *Mercenaria*. Scale bars: **A** = 0.5 cm; **B, E** = 1 cm; **C, D** = 0.1 cm; F = 0.3 cm.

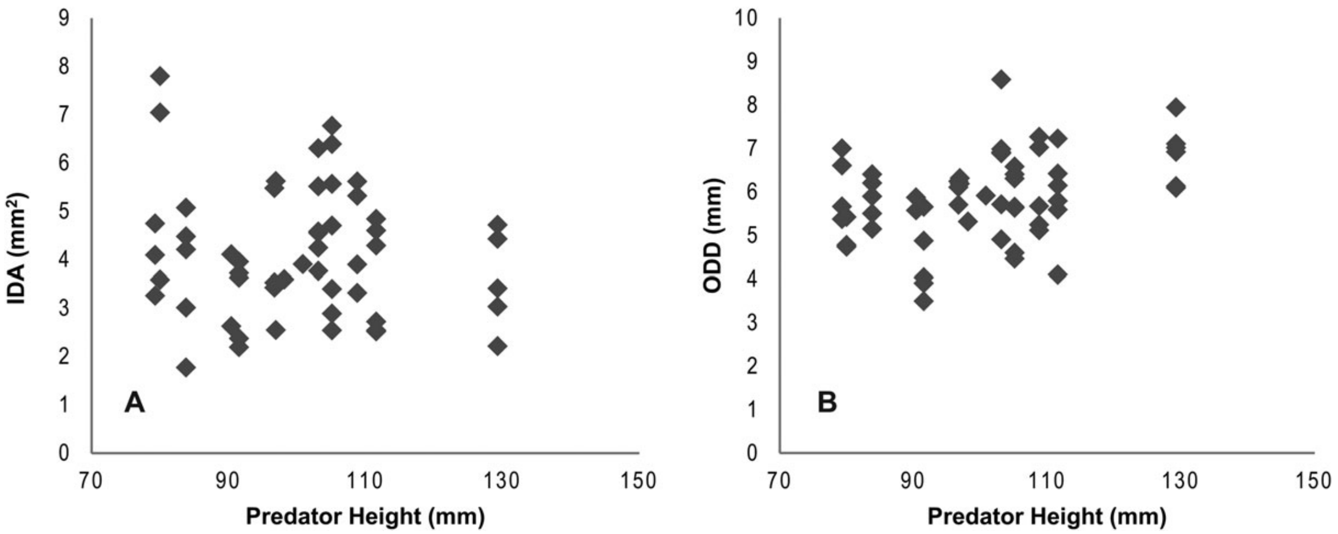

Figure 5. Bivariate scatter plots of size of *Muricanthus fulvescens* predator (shell height) *vs* inner drill hole area (IDA) (**A**) and outer drill hole diameter (ODD) (**B**).

predation behaviours of *M. fulvescens* included predation traces consistent with edge drilling, although he interpreted those differently. Wells (1958) listed 'halos', areas of shell etching around the entry point of the predator's proboscis, among the predation traces associated with grinding attacks. In our study, halos were associated exclusively with edge-drilled holes and we often used the halos to locate the smooth-sided drill-hole traces; the slit-like shape of edge drills produced by *M. fulvescens* rendered many of the holes nearly undetectable from the shell's outer surface. Wells (1958) attributed halo traces to acidic lubricants secreted by the proboscis to ease its entry through the narrow openings created by grinding; however, none of the shells attacked exclusively by grinding in our study had any signs of etching. While there are some examples of muricids secreting shell-dissolving agents from the proboscis (e.g. Herbert *et al.*, 2009; see also Carriker, 1981; Andrews *et al.*, 1991), species known to do this are exceedingly rare compared with the nearly ubiquitous distribution in the Muricidae of shell-dissolving secretions from the ABO in the foot, which is used in shell drilling attacks. We propose that halo traces in *M. fulvescens* attacks do not originate from the proboscis during feeding following grinding attacks, but from seepage from the ABO during drilling.

Factors in the selective expression of alternative predatory modes

Ontogeny plays an important role in the expression of predatory modes of some muricids (Hart & Palmer, 1987; Urrutia & Navarro, 2001; Herbert, Merle & Gallardo, 2007; Morton *et al.*, 2007). We found no evidence for differences between the range of behaviours used by small and large *M. fulvescens*. However, our study did not include predators smaller than 6 cm in shell as none were found at any of our field sites. Because small muricids are usually wall-drilling specialists (Herbert *et al.*, 2007; G.S. Herbert, unpublished), and because the smallest *M. fulvescens* shells are possibly too thin for their shell lip to be used in shell grinding, we predict that *M. fulvescens* smaller than the ones used in this study should have a more limited repertoire of predation behaviours, perhaps including only drilling. A single, unpublished observation of predation by a small *M. fulvescens* (shell length between 4 and 5 cm) on a venerid clam (*Chione elevata*) revealed the use of wall drilling (G. P. Dietl, personal communication), which is consistent with this prediction. If confirmed, the range of predatory modes expressed by *M. fulvescens*, which include four modes of attack involving three offensive 'weapons' (drilling, grinding and toxins), would be one of the most diverse described for any neogastropod.

Prey size was a dominant factor in the expression of predatory modes by *M. fulvescens* used in this study; larger, thicker prey were found to be difficult to damage by shell grinding and were attacked instead by edge drilling. Of particular interest is the fact that *M. fulvescens* tends to initiate attacks on *M. campechiensis* with the predatory mode most likely to be successful, even if that method is, on average, slower—rather than by a testing, trial-and-error approach beginning with the fastest mode of attack. Some other predators (e.g. *Octopus*) initiate attacks on bivalve prey with faster valve pulling by brute force and finish with the slower drilling mode only if brute force is unsuccessful (Steer & Semmens, 2003). In the case of *M. fulvescens*, the rapidly decreasing probability of attack success as prey size increases is likely the driving factor inhibiting expression of trial-and-error behaviour, but other factors could also contribute to this pattern. For example, there is potentially a greater risk of the predator injuring its own shell when attempting to grind feeding holes in clams with very thick shell margins. Shell grinding is also only slightly faster than edge drilling (3.1 *vs* 4.5 d; this study; see also Peharda & Morton, 2006). Thus, if a grinding attack on a large prey is unsuccessful, and the attack must be restarted and completed by edge drilling, then the total attack time could be nearly doubled compared with *M. fulvescens* individuals that choose the correct mode first by initiating the attack with edge drilling. In predators that always initiate attacks with faster, brute force methods, such as *Octopus*, the brute force mode is substantially faster than drilling (Steer & Semmens, 2003). For such predators, total attack time is not substantially increased if the brute force method fails. Time is a significant cost for animals like *M. fulvescens* that forage in the open exposed to enemies and whose prey-handing times are measured in days. Given how costly a trial-and-error approach would be for *M. fulvescens*, it is not surprising that this species initiates most attacks with the prey-handling method most likely to succeed at the first attempt.

In future studies, it would be worthwhile to test whether this predator increases the frequency of attacks initiated by shell grinding when exposed to additional risk factors, such as the presence of food-stealing competitors or other predators (e.g. other gastropods, durophagous crabs, turtles and rays). Such risk factors could, in theory, override the perceived risks and costs of shell grinding and lead to an increased percentage of attacks being initiated by faster grinding, as well as to a higher percentage of failed attacks. Increased risk taking in the presence of enemies has been confirmed for a wide range of animals (e.g. VanValkenburgh & Hertel, 1993; Dietl *et al.*, 2004). A key test of this hypothesis could be performed by examining fossil *Muricanthus* shells from the Pliocene of Florida, which was characterized by Dietl *et al.* (2004) as a time of intense competition among muricid gastropods and their enemies. Pliocene *Muricanthus* from Florida are predicted to possess a higher frequency of grinding-induced shell repair compared with *Muricanthus* shells from the Pleistocene and Recent of Florida, when predator abundances and competition intensity were reduced severely (Dietl *et al.*, 2004; Alvarez *et al.*, 2008; Paul & Herbert, 2014).

Evidence for toxin use

There is no direct, easy way to observe toxin use by muricids, because these animals cover the proboscis with their foot during the attack (Perry, 1985). Extracts of salivary and hypobranchial glands would have an anaesthetizing effect on prey (Andrews *et al.*, 1991; Roller *et al.*, 1995) and toxin use has been inferred from forced entry into bivalve prey without damaging the shell (Smith, 1983) or from a hole too small for proboscis entry and feeding (e.g. Luckens, 1970; McGraw & Gunter, 1972; Gunter, 1979; Palmer, 1982; West, 1986; Taylor & Glover, 1999; Urrutia & Navarro, 2001; Herbert, 2004). Toxin use is thought to be a plesiomorphic condition for the Neogastropoda rather than a derived trait in the Muricidae (Taylor, 1998), but the distribution of toxin use across the family is unknown. Although *M. fulvescens* produces drill holes approaching 9 mm in ODD, the slit-like shape of many of its edge drills suggests that some of these traces may not be functional feeding holes. Kitchell *et al.* (1986) considered an IDD:ODD ratio of 0.5 as the threshold for functional feeding holes for naticids. None of the edge drills recorded in our experiments fell below the 0.5 threshold, although some were close (e.g. IDD:ODD = 0.7). However, no such standard has been established for muricids or for drill holes of irregular or unusual shape, as is the case in the present study, where use of IDD:ODD ratios is potentially misleading (Urrutia & Navarro, 2001).

A preferable method for testing the functions of irregularly-shaped drill holes is to examine relationships between predator size and IDH or IDA, which represent the smallest inner drill hole dimension and total area available, respectively, for proboscis entry. Drill-hole size should increase predictably with increasing predator (and ABO) size in muricids that drill only functional feeding holes (Kowalewski, 2004); however, this should not be the case for muricids that produce both functional feeding holes and toxin-injection holes or only the latter (e.g. McGraw & Gunter, 1972; Gunter, 1979; Urrutia & Navarro, 2001). In this study, we find that neither IDH nor IDA are correlated with predator size, and the range of IDAs varied for one large *M. fulvescens* by more than 5 mm^2. Some drill holes produced by this large *M. fulvescens* had an IDA as low as 1.2 mm^2. These observations are consistent with at least some edge drills being used as sites of toxin injection rather than feeding, but are not conclusive. A more definitive approach, following that of Carriker, Schaadt & Peters (1974), might be to entice a large *M. fulvescens* predator to extend its proboscis into pre-drilled holes through valves attached to a glass plate. By pre-drilling holes of different sizes, particularly in the range of the smallest drill holes documented in this study, it could be determined conclusively whether a small IDH or IDA, interpreted here as an indicator of a toxin-injection function, actually precludes feeding.

Conclusions

The adaptive radiation of the Neogastropoda is commonly attributed to the evolution of feeding specializations that decreased niche breadth and allowed for species-packing in near-saturated ecosystems (e.g. Paine, 1962, 1963; Taylor, 1998; Vermeij & Carlson, 2000; Fedosov *et al.*, 2014). The role of ecological versatility of feeding adaptations in the neogastropod radiation, however, is relatively unexplored and the issue is contentious in evolutionary biology in general (reviewed by Ghalambor *et al.*, 2015). Ecological versatility refers to the degree of adaptive flexibility or plasticity organisms have in exploiting and converting local resources to fitness (MacNally, 1995; Feranec, 2007; Gavrilets & Losos, 2009); such versatility could potentially facilitate differential diversification among clades by (1) reducing the likelihood of competitive exclusion among species with overlapping niches (Mitter, Farrell & Weigmann, 1988; Thompson, 1988; Dial & Marzluff, 1989), (2) enhancing the persistence of founder populations in habitats with novel resources or conditions (Mayr, 1976; Moran, 1988; Dial & Marzluff, 1989; Ozinga *et al.*, 2012) and (3) reducing extinction rates of source populations (Hoenigsberg, 2003; Liow & Stenseth, 2007).

Ecological versatility is usually examined in the context of single traits, such as life-history characteristics that permit populations to track fluctuating resources and recolonize areas quickly following local extinction (Dial & Marzluff, 1989), or single innovations that have a diversity of trophic applications (e.g. gnawing in rodents; Simpson, 1961). However, versatility may also be enhanced when each individual of a species possesses its own ‘arsenal’ of foraging adaptations, either ancestral or derived, that can be employed selectively to allow flexible navigation through challenging environments (e.g. MacNally, 1994; Dietl & Herbert, 2005). Exemplary cases of this latter type of versatility within the Neogastropoda are already well documented, such as in the Conidae, where individual snails produce up to 200 venom peptides that target a diversity of prey, predators and competitors (Olivera, 2002). Taylor (1998: 196) acknowledged that the *combination* of predatory weapons rather than any single tool gives muricids “extraordinary flexibility in dealing with the wide variety of often heavily armoured food items.” It is the evolution of these combinations and their effects on ecology and diversification that deserve more attention. In the present study, we have shown that *M. fulvescens* has ecological versatility that extends far beyond what was known of this species previously. Despite the potential value of the versatility concept, recent discoveries of novel feeding adaptations (Simone, Herbert & Merle, 2007) and behaviours (Dietl *et al.*, 2004; Dietl & Herbert, 2005; Herbert *et al.*, 2007) of common, well-studied, intertidal muricids, such as *M. fulvescens*, highlight the need for continued experimental studies of the diversity and distribution of predatory modes within the Muricidae.

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