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Drilling and chipping patterns of bivalve prey shell penetration by *Hexaplex trunculus* (Mollusca: Gastropoda: Muricidae)

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The predatory caenogastropod *Hexaplex trunculus* employed different methods to access different species of bivalve prey characterized by different shell thicknesses. *Hexaplex trunculus* drilled *Callista chione* and *Venus verrucosa* at their shell margins but the latter species also laterally. It also attempted to drill two species of *Tapes* but successfully penetrated these only after chipping the shell margin. Chipping, whereby a labral spine is forcibly pushed between the prey's valves, especially posteriorly, to break them followed by proboscis insertion, was typically applied to access the thinner shelled prey *Cerastoderma glaucum* whereas *Modiolus barbatus* and *Mytilus galloprovincialis* were either chipped or drilled. The pattern of *M. galloprovincialis* shell penetration appears related to predator and prey size. Small (40 mm shell height) *H. trunculus* tended to drill rather than marginally chip *M. galloprovincialis*. Medium sized (55 mm shell height) *H. trunculus* either chipped or drilled *M. galloprovincialis* in approximately equal proportions but also at the valve margin. Larger (70 mm shell height) *H. trunculus* tended to laterally drill average sized (35 mm shell length) and the biggest (65 mm shell length) *M. galloprovincialis*. When larger *M. galloprovincialis* are attacked it thus becomes increasingly more difficult for *H. trunculus* to chip and drill the shell margin, possibly because the periostracum is thicker here in such individuals, and the predator resorts to lateral drilling. This is possible because as the mytilid ages its surface periostracum becomes progressively eroded and thus thinner and easier to access. Scanning electron microscopy (SEM) identified shell microstructure damage which shows that the chipping and drilling behaviours of *H. trunculus* result from labral spine damage and dissolutional etching, respectively, rather than mechanical radula rasping. These observations have implications for the use of such predation marks to identify the predator taxon implicated from holes in either empty Recent shells or fossil material.

INTRODUCTION

Muricid gastropods (Caenogastropoda) play an important role in regulating the population dynamics of their prey that includes mussels, barnacles, limpets and tubeworms (Menge, 1974; Morton, 2004) and in so doing regulate community structure. Hence, by feeding on barnacles, *Nucella lapillus* (Linnaeus, 1758) helps to create an important microhabitat (the empty tests) for numerous smaller organisms including the juveniles of dominant intertidal species such as littorines (Hughes, 1986). *Hexaplex trunculus* (Linnaeus, 1758) is one of the most widespread Mediterranean muricids and lives on rocky, sand and mud substrata. In the Adriatic Sea, *H. trunculus* is a widely distributed and commercially and ecologically important species (Benović, 1997). It is harvested for human consumption and used frequently as fish bait although the species probably has a greater significance with regard to its consumption of cultured bivalve species (Peharda & Morton, 2006). For example, although populations can be dense on the soft seabed, *H. trunculus* is most abundant (densities of up to 120 individuals m^{-2}) at aquaculture sites of the European flat oyster, *Ostrea edulis* Linnaeus, 1758 and black mussel, *Mytilus galloprovincialis* Lamarck, 1819 (Zavodnik & Šimunović, 1997).

Most studies that have examined *Hexaplex trunculus* are related to the occurrence of imposex in this species along Mediterranean shores (Axiak et al., 1995, 2000, 2003; Terlizzi et al., 1998, 1999, 2004; Chiavarini et al., 2003; Prime et al., 2006). Hence, despite its ubiquity, relatively little is known about the behaviour of *H. trunculus*. Research has generally shown it to be an opportunistic feeder, exhibiting both carnivory and scavenging but, throughout its wide range feeding on a variety of bivalve taxa including *Arca noae* Linnaeus, 1758, *Mytilus galloprovincialis*, *M. edulis* (Linnaeus, 1758), *Brachiodontes pharaonis* (P. Fischer, 1870), *Mytilaster minimus* (Poli, 1795), *Ostrea edulis*, *Crassostrea gigas* Thünberg, 1793, *Cerastoderma edule* (Linnaeus, 1758) and *Ruditapes decussatus* (Linnaeus, 1758) as well as other gastropods, barnacles, tunicates, bryozoans and even conspecifics and carrion from both rocky and sandy substrata (Lorenzini & Orlando, 1997; Zavodnik & Šimunović, 1997; Rilov et al., 2004; Marin & López Belluga, 2005; Peharda & Morton, 2006; Prime et al., 2006) (Table 1).

Hexaplex trunculus has similarly been little studied in Croatian waters although there is abundant anecdotal evidence that here too it is a generalist predator and scavenger which has thrived in locations where, as noted above, mussel and oyster culture takes place. It is a significant pest of cultured *Mytilus*

Table 1. *Bivalve species recorded as prey of* Hexaplex trunculus *with, where observed, the method of shell penetration adopted.*

Prey species	Type of attack	Reference
Arca noae	Not specified	Marin & López Belluga, 2004
	via byssal gape	Peharda & Morton, 2006
Mytilus galloprovincialis	Drilling, chipping	Lorenzini & Orlando, 1997; Peharda & Morton, 2006
Mytilus edulis	Not specified	Vasconcelos et al., 2004
Modiolus barbatus	Lateral drilling, chipping	This study
Brachiodontes pharaonis	Drilling	Rilov et al., 2004
Mytilaster minimus	Not specified	Rilov et al., 2004
Ostrea edulis	Not specified	Rilov et al., 2004
Crassostrea gigas	Not specified	Vasconcelos et al., 2004
Cerastoderma edule	Not specified	Vasconcelos et al., 2004
Cerastoderma glaucum	Chipping	This study
Ruditapes decussatus	Not specified	Vasconcelos et al., 2004
Ruditapes decussatus	Chipping	This study
Tapes rhomboides	Chipping	This study
Venus verrucosa	Drilling	This study
Callista chione	Drilling	This study

galloprovincialis in Croatian waters (Peharda & Morton, 2006).

The current study was undertaken to extend our understanding of the feeding behaviour of *Hexaplex trunculus* using experiments that involved: (i) an analysis of the attack patterns made upon a number of different species of burrowing bivalves in comparison with *Mytilus galloprovincialis*; (ii) a comparative analysis of lateral and edge drilling predation on *M. galloprovincialis* prey of different shell lengths; and (iii) an analysis of drill hole sizes in relation to predator size and the chosen prey identity and size. The study is complemented by an SEM examination of different prey shells, either chipped or edge- or side-drilled to determine, respectively: (i) the type of chips made; and (ii) the method(s) of shell penetration.

MATERIALS AND METHODS

Bivalve species were collected by SCUBA divers from coastal sites in the central Adriatic Sea during late 2004 and transported to the Institute of Oceanography and Fisheries laboratory in Split, Croatia. Species collected included *Mytilus galloprovincialis*, *Modiolus barbatus* (Linnaeus, 1758), *Cerastoderma glaucum* (Poiret, 1789), *Venus verrucosa* Linnaeus, 1758, *Callista chione* (Linnaeus, 1758), *Tapes aurea* (Gmelin, 1791) and *Ruditapes decussatus*. All these bivalves are commercially important species in Croatia and have a wide range of shell morphologies, thicknesses and microstructures.

Prior to experimentation, the bivalves (of standard shell lengths ranging between 30 and 40 mm—except for *Mytilus galloprovicialis* [see below])—were inspected for signs of previous predator attacks, grouped according to species and placed in separate aquaria with aerated seawater. *Hexaplex trunculus* individuals, ranging in shell height from 40 to 70 mm, that had been starved for 14 days prior to study, to standardize hunger levels, were added to these aquaria. Each day, over a period of the following four weeks, the empty shells of attacked bivalve prey items were removed, washed in distilled water and examined microscopically. The positions of drill holes, including predation attempts, and chip marks, were plotted on master drawings of the shell outlines of each species. Outer and inner drill hole diameters were measured to the nearest 0.01 mm and correlated with predator shell height. Because of their positions at the prey's valve margins, it was not possible to measure accurately the diameters of 22 of the drill holes studied. Similarly, when individual predators either drilled an extremely curved area of the prey's shell to produce an abnormally shaped hole or when they attacked *M. galloprovincialis* by inserting their proboscis between marginal apertures created by non-drilling methods, such information was, following Ishida (2004), removed from subsequent analyses.

In a second experiment, *Mytilus galloprovincialis* individuals with a range of sizes that encompassed the broad categories of large, medium and small, that is, with shell lengths of around 65, 35 and 20 mm were placed in aquaria with similarly large (70 mm shell height), medium (55 mm shell height) and small (40 mm shell height) individuals of *Hexaplex trunculus*. The procedures adopted in the first experiment were replicated in this one and a regression plotted against predator shell height and drill hole size. Methods of attack adopted by the former, that is, either marginal chipping or lateral or marginal drilling were noted. Differences in size between outer and inner drill hole diameters were analysed using a paired *t*-test.

Predator attack marks were examined using a scanning electron microscope (JEOL 820) at the University of Cambridge, following ultrasonic cleaning and gold sputter coating.

RESULTS

Attacks on different prey species and drill hole/chip characteristics

Our experiments showed that individuals of *Hexaplex trunculus* were capable of attacking and feeding successfully on all potential prey taxa offered. The method of attack varied between taxa, however, and sometimes between

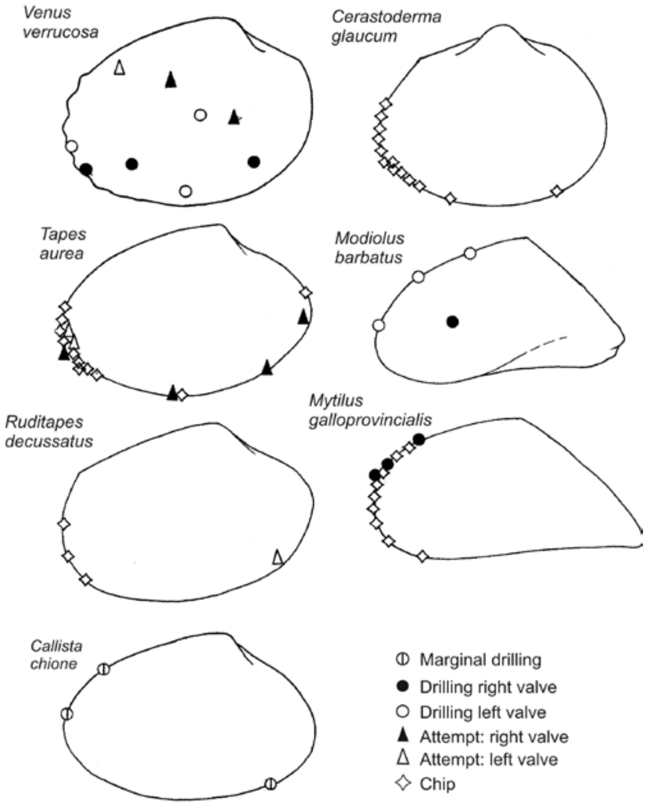

Figure 1. Shell outlines of different bivalve prey species attacked by *Hexaplex trunculus* showing the types of attacks and their positions.

different sizes of individuals of a given taxon. The process of 'chipping' whereby a labral spine is forcibly pushed between, usually the posterior margins of the prey's valves to break the shell has been illustrated by Peharda & Morton (2006, figure 1). The process of drilling is similar in that the prey is firmly held by the foot and the tip of the proboscis held against the area of shell chosen for attack (see Figure 5, to be discussed).

Venus verrucosa. *Hexaplex trunculus* penetrated *Venus verrucosa* individuals by drilling the valves laterally or at their margins. Of six successful attacks, two drill holes were located at the valve margins whereas four were located laterally (Figure 1A). Of these, three attacks were on the right valves and three on the left. In addition, one shell that had a complete hole in one valve had an additional attempt on the opposite one. Similarly, one *V. verrucosa* that was drilled successfully at the margin had evidence of two lateral drilling attempts. Chipping attempts were never identified.

Tapes aurea and *Ruditapes decussatus*. *Tapes aurea* and *Ruditapes decussatus* were attacked exclusively at the shell margin. In the case of *T. aurea*, 12 chipping attacks were identified but six of these also involved marginal drilling attempts (Figure 1B). All three attacks on *R. decussatus* involved chipping of the valve margins, while one of these included a drilling attempt (Figure 1C).

Callista chione. Two attacks of the *Callista chione* shells were recorded, both involving drilling at the posterior valve margins (Figure 1D).

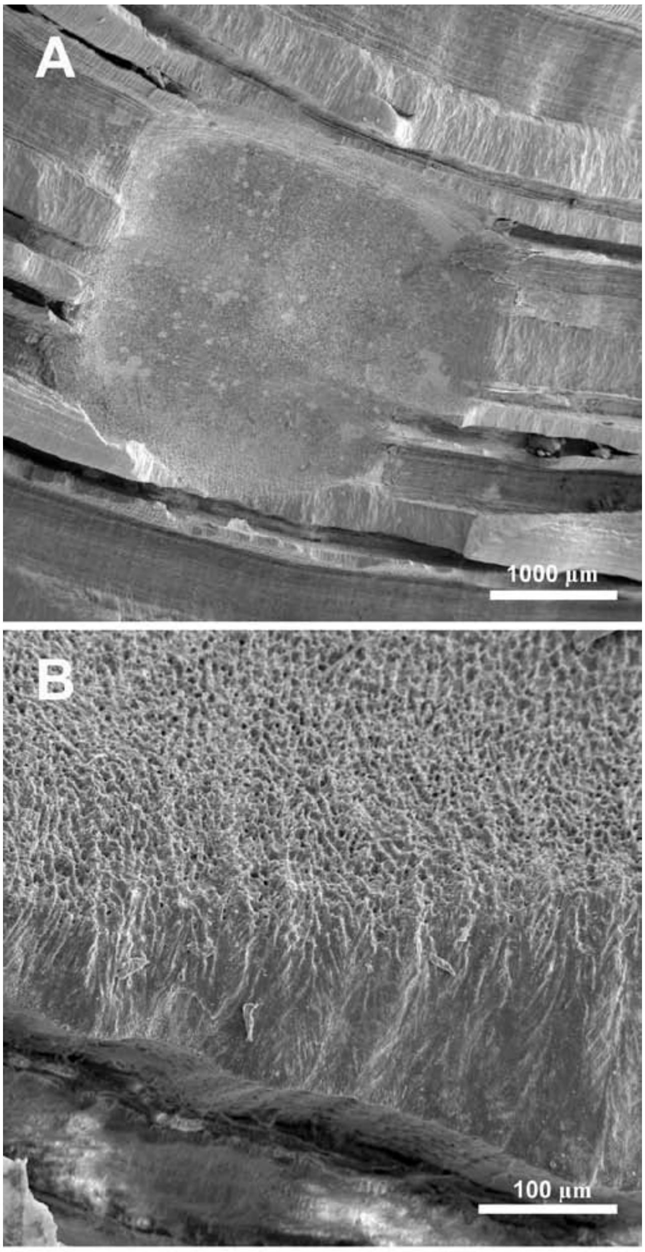

Figure 2. (A) Scanning electron micrograph of a drilling attempt made in the shell of *Venus verrucosa* by *Hexaplex trunculus*; (B) at greater magnification showing breakage of the prey shell lamellae around the drill hole.

Cerastoderma glaucum. All predation marks made by *Hexaplex trunculus* on *Cerastoderma glaucum* shells (Figure 1E) were located at the posterior shell valve margin. Of the 13 recorded attacks, four were on the right valve and nine on the left. In some cases, chip marks were barely discernible, being represented by small indentations at the valve edges.

Modiolus barbatus. Four individuals of *Modiolus barbatus* were attacked by *Hexaplex trunculus*. Three *M. barbatus* were marginally chipped while one individual was drilled through the centre of the right valve (Figure 1F).

Mytilus galloprovincialis. *Hexaplex trunculus* attacked *Mytilus galloprovincialis* by marginal chipping, edge drilling and side drilling. Of the total of 100 attacks identified, 55 (55%) were by marginal chipping, while 30 (30%) and 15 (15%: although

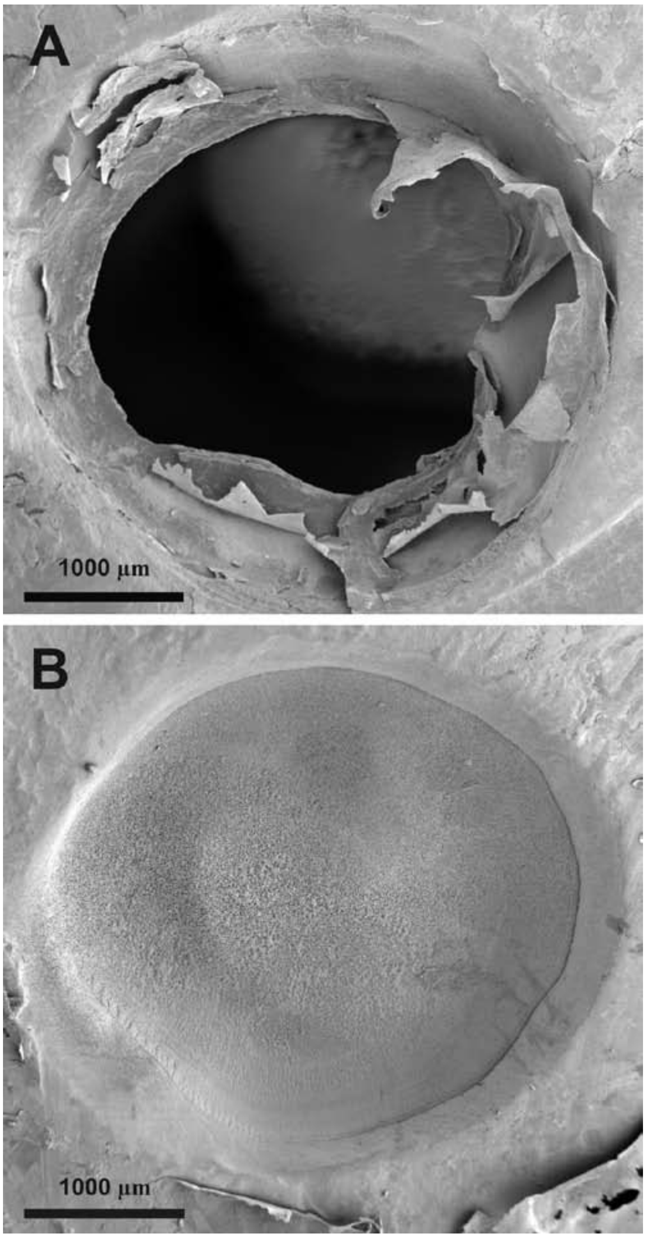

Figure 3. (A) Scanning electron micrograph of a drill hole made by *Hexaplex trunculus* in a shell of *Mytilus galloprovincialis*; (B) an attempted drill-hole made in the shell of *M. galloprovincialis*.

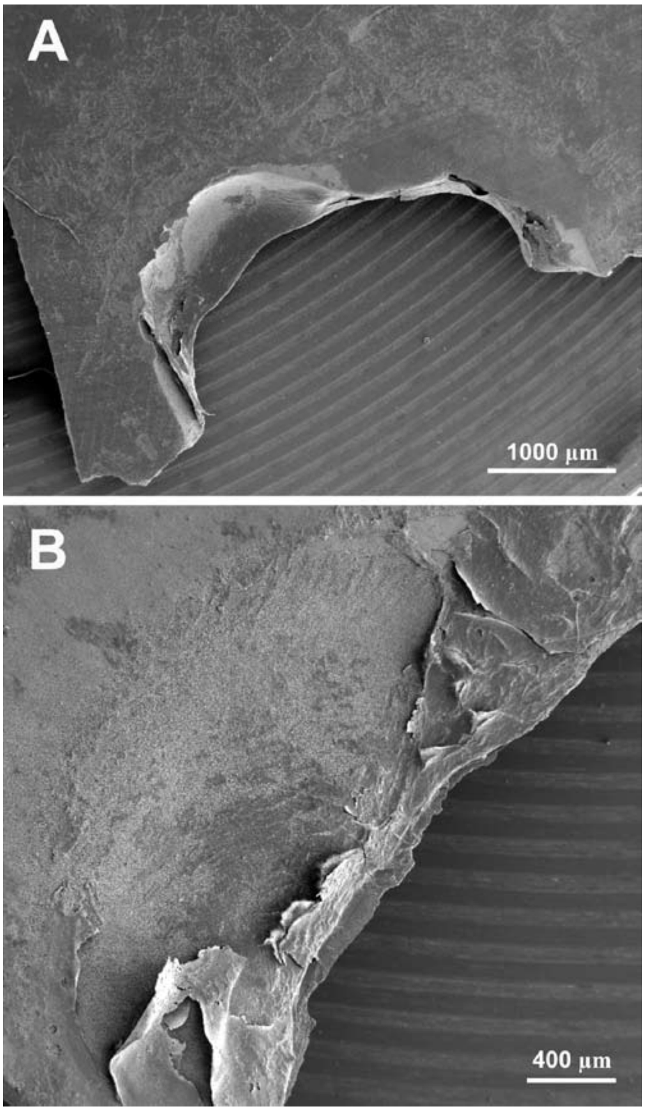

Figure 4. (A) A SEM micrograph of a shell of *Mytilus galloprovincialis* edge drilled by *Hexaplex trunculus*; (B) a SEM micrograph of the valve opposite to the drilled side showing the etched scar made by the accessory boring organ secretions.

four of these also showed signs of marginal chipping) were attacked by drilling at the shell margins and laterally, respectively. This dataset is analysed further below.

Drill hole characteristics

The drill holes made by *Hexaplex trunculus* in the sides of prey shell valves were circular in plan view and ranged from 2.8 to 4.0 mm in outer diameter, for example in *Venus verrucosa* (Figure 2A). The inner perforation was typically of a smaller diameter, and the outer perforation, again of *V. verrucosa*, more irregular in outline (Figure 2B). It was also noticed that the valve lamellae of *V. verrucosa* were broken in the areas around drill holes (Figure 2B).

The mean outer diameter of each drill hole made in the shell of *Mytilus galloprovincialis*, (x=2.48 mm) was significantly larger than the inner (x=1.88 mm) (paired t-test t=10.57, P<0.001, N=31) (Figure 3A). The floors of incomplete drill holes, again in *M. galloprovincialis* (Figure 3B), had central raised bosses. Detailed examination of all drill holes revealed that their edges were sharp and there were no obvious signs of radula scraping. The shell microstructure exposed on the walls of the drill holes similarly showed clear signs of chemical etching and no evidence of radula scrapings.

Drill holes made at the valve margin of *Mytilus galloprovincialis* were typically semi-circular in outline (Figure 4A). Similarly, in all such instances, the inner surfaces of the opposite valves showed dark etching marks as the drilled valves were accessed (Figure 4B). A *Hexaplex trunculus* individual is illustrated attacking *M. galloprovincialis* in Figure 5A. Illustrated in greater detail in Figure 5B, the successful drill hole, with adjacent attempts, shows a smooth margin with the inner surface of the opposite valve also scarred (grey area).

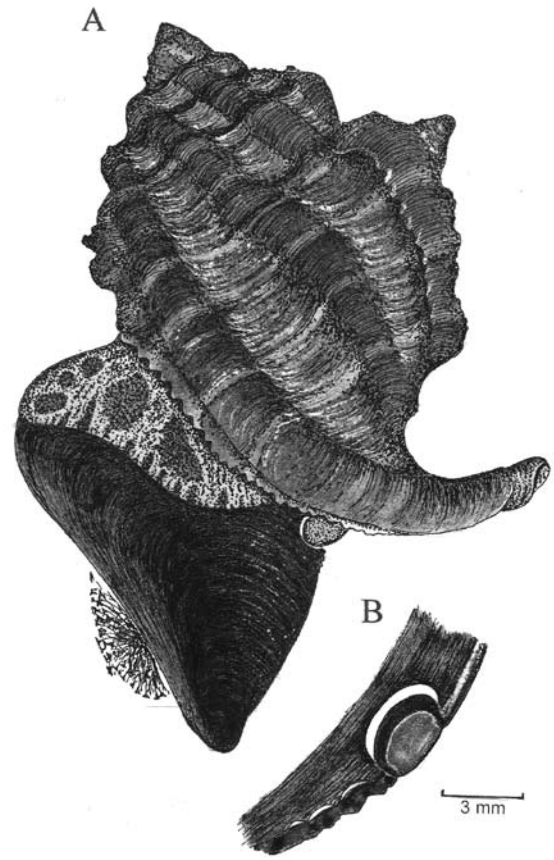

Figure 5. (A) A *Hexaplex trunculus* individual drilling *Mytilus galloprovincialis*. The drill hole is illustrated in greater detail in (B) and shows the smooth margin and how the opposite valve is also scarred in the etching process (grey area).

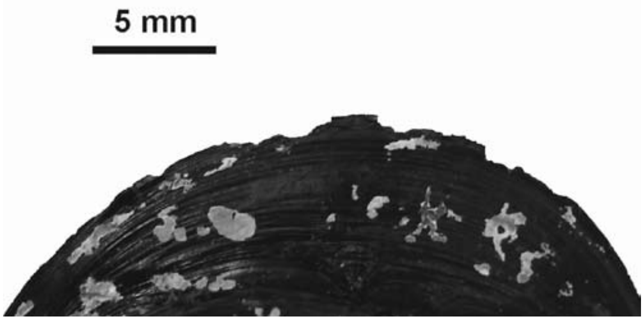

Figure 6. A photograph of the valve margin of a *Mytilus galloprovincialis* that has been chipped by *Hexaplex trunculus*.

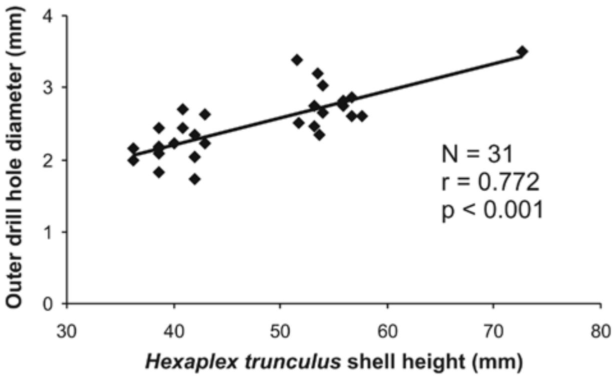

Figure 7. *Hexaplex trunculus*. The relationship between predator shell height and drill hole diameter in the valves of *Mytilus galloprovincialis*.

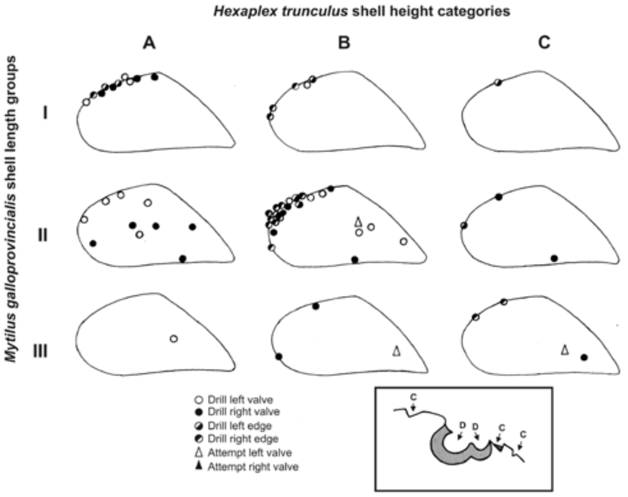

Figure 8. The numbers, positions and categories of drill holes (either edge or side drilled plus failed attempts) made in the shells of *Mytilus galloprovincialis* of different shell length groups (I, II & III) by *Hexaplex trunculus* individuals of different shell height categories (A, B & C). (Inset: a drawing of one *Mytilus galloprovincialis* valve margin that shows evidence of chipping [C] and drilling [D]).

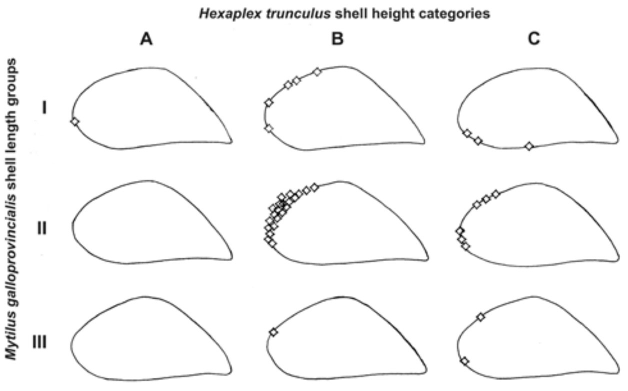

Figure 9. The numbers and positions of chip marks made in the valve margins of *Mytilus galloprovincialis* of different shell length groups (I, II & III) made by *Hexaplex trunculus* individuals of different shell height categories (A, B & C).

Chip characteristics

Many prey items, particularly of *Mytilus galloprovincialis*, were attacked by *Hexaplex trunculus* using the technique of 'chipping' with the labral spines (see Perharda & Morton, 2006, figure 1). These attacks generally resulted in small arcuate chips being removed from the margins of the shell (Figure 6). These would be classified as 'scalloped' attacks according to the scheme adopted by Alexander & Dietl (2001), although occasionally deeper and more angular pieces of shell regarded as 'clefts' were produced.

Predation on Mytilus galloprovincialis

Figure 7 plots the heights of individual *Hexaplex trunculus* against the size of drill holes they produced in *Mytilus galloprovincialis*. There is a positive correlation (r^2=0.772) between the two parameters that is also highly significant

(P=<0.001). The pattern of *M. galloprovincialis* shell penetration does, however, appear related to predator size (Figures 8 & 9). Small (40 mm shell height) *H. trunculus* tended to drill rather than chip *M. galloprovincialis* at the valve margin. Medium sized (55 mm shell height) *H. trunculus* either chipped or drilled *M. galloprovincialis* in approximately equal proportions, but also at the valve margin. Larger (70 mm shell height) *H. trunculus* tended to laterally drill average sized (35 mm shell length) and the biggest (65 mm shell length) *M. galloprovincialis*. Such results confirm the earlier observations made by Peharda & Morton (2006) on these two species but with the added information pertaining to the incidences and locations of chipping and drilling of different size-classes of *M. galloprovincialis*.

DISCUSSION

It is clear that *Hexaplex trunculus* can attack a wide variety of prey including several species of bivalves (Table 1). In some cases, both chipping and drilling behaviours are employed when attacking the same prey species. Our experiments show, however, that different attack strategies are employed, depending on prey characteristics. Thick-shelled prey, such as the venerids *Venus verrucosa* and *Callista chione*, were only drilled. Thinner shelled *Cerastoderma glaucum* (Cardiidae) was penetrated exclusively by marginal chipping while *Tapes aurea* and *Ruditapes decussatus* (Veneridae) were penetrated by marginal chipping albeit with evidence of unsuccessful drilling attempts also at the shell margin. *Cerastoderma glaucum* cannot shut its valves tightly and is therefore highly susceptible to predation attacks by *H. trunculus* with little expenditure spent accessing the shell and involving proboscis insertion only. The patterns observed in the mytilid prey, *Modiolus barbatus* and *Mytilus galloprovincialis*, were more complicated with both successful drilling and chipping attacks recorded.

Our analysis indicates that there is a progressive change in the attack method adopted according to the size of the predator, perhaps suggesting an ontogenetic shift in behaviour. Small (40 mm shell height) *H. trunculus* tended to drill rather than chip *M. galloprovincialis* but always at the valve margin rather than laterally. Medium sized (55 mm shell height) *H. trunculus* either chipped or drilled *M. galloprovincialis* in approximately equal proportions, also by drilling only at the valve margin. Larger (70 mm shell height) *H. trunculus* tended to drill average sized and larger (range=35–65 mm shell length) *M. galloprovincialis* laterally. Similar patterns of changing attack methods during ontogeny have been reported for other muricids (Hart & Palmer, 1987; Urrutia & Navarro, 2001). McQuaid (1994) showed that *Octopus vulgaris* changes its attack methods according to prey size.

Marginal drilling is an attack method in which a predatory gastropod excavates a hole at a point along the periphery of the closed valve margin of a bivalve prey item (Vermeij, 1980) and is most commonly associated with naticid gastropods (Ansell & Morton, 1987). It may represent a faster means of accessing the prey, particularly as the shell of most bivalves is thinner at the ventral margin. Dietl & Herbert (2005) estimate that the muricid *Chicoreus dilectus* (A. Adams, 1855) edge drills *Chione elevata* (Say, 1822) three times faster than by side drilling. It is then, however, difficult to understand why this strategy is not used on larger prey. It seems possible that when larger prey items are attacked, it becomes increasingly more difficult to chip and drill the valve margin, possibly because in such individuals the periostracum is thicker here and the predator hence resorts to lateral drilling. This is possible, according to Harper & Skelton (1993), because as the bivalve ages the earliest formed periostracum becomes eroded progressively and is thus thinned, even lost, thereby making the shell easier to access. The regular positioning of most attacks observed in this study of *H. trunculus* preying on *M. galloprovincialis* posterodorsally, suggests that the adductor muscle located in this quadrant of the body may be the principal object of each predation event.

The morphologies of the drill holes made by *Hexaplex trunculus* are of interest. This large predator produces large holes, with clear signs of them being the result of chemical etching. Although it has not been identified specifically in this taxon, all other muricids are known to possess an accessory boring organ (ABO) located in the foot (Taylor, 1998). The ABO secretes a mixture of acids, enzymes and chelators that attack the shell (Carriker, 1981). The lack of evidence for radula marks on our shells predated upon by *H. trunculus* suggests that this structure plays a subordinate role in the drilling process although it is likely, as suggested by Carriker et al. (1974), that it may be used to remove weakened material which is then eaten. In contrast, holes made by the muricid *Rapana bezoar* (Linnaeus, 1758) studied by Morton (1994) were less well defined and created by radula raspings. Radula rasping marks have also been identified in the drill holes made by the muricid *Lepsiella paivae* (Crosse, 1864) in the shells of the venerid *Katelysia scalarina* (Lamarck, 1818) (Morton, 2005, figure 4A)

Muricids are thought, typically, to drill cylindrical, straight sided, holes (Carriker, 1981). Incomplete holes usually have flat bases. The holes made by *Hexaplex trunculus* have conspicuously narrower jagged inner perforations and near-complete examples have bosses at their bases, a trait more typically associated with naticids (Carriker, 1981) but also marginellids (Ponder & Taylor, 1992). This departure from the typical muricid drill hole morphology has also been observed in trophonids (Gordillo, 1998; Harper & Peck, 2003) and has implications for the use of such a character to identify the predator taxon implicated from holes in either empty Recent shells or fossil material.

It is often suggested that outer drill hole diameter is a good proxy for ABO use and predator size (Carrriker & van Zandt, 1972; Palmer, 1990). This relationship is well demonstrated for naticids (Kitchell et al., 1981). Previous studies of the holes drilled by known muricids have shown, however, that an individual may create holes of different sizes (Harper & Morton, 1997; Harper & Peck, 2003; Kowalewski 2004). Similarly, Urrutia & Navarro (2001) have shown for the muricid *Chorus giganteus* (Lesson, 1829) that larger individuals often made relatively small perforations compared with smaller conspecifics.

In conclusion, therefore, *Hexaplex trunculus*, like *Dicathais orbita* (Gmelin, 1791) on rocky shores in Western Australia (Morton & Britton, 1993), has a catholic diet. Both species also attack the various components of their diet in different ways. This has herein been demonstrated for *H. trunculus* feeding on a range of naturally available prey of different sizes. The results of this study show that *H. trunculus* predates a variety of commercially important bivalve species and that this needs to be taken into account when setting up and managing bivalve aquaculture schemes in the sea. *Hexaplex trunculus* is a natural predator of commercially important, wild caught, molluscan fishery resources although details of its impacts remain unquantified. This study, however, demonstrates that the components of the very catholic diet of *H. trunculus* are attacked in different ways during the ontogenic histories of both prey and predator. *Hexaplex trunculus* is also an aquaculture candidate and the fact that it readily consumes carrion (Zavodnik & Šimunović, 1997) suggests that commercially important bivalves need not be sacrificed for its growth.

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