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ORIGINAL PAPER

Finding the sweet spot: drilling precision on shelled molluscs by *Octopus vulgaris* type III in False Bay, South Africa

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Abstract

Octopus vulgaris type III preys upon molluscs by drilling a hole in the shell, through which it injects venom, weakening the muscles and allowing the octopus to remove and eat the mollusc flesh. In False Bay, South Africa, the abalone *Haliotis midae,* the kelp limpet *Cymbula compressa* and the helmet snail *Semicassis zeylanica,* are all common octopus prey, but each has a very different shell morphology and underlying anatomy. It is hypothesized that *O. vulgaris* type III targets the muscle attachment site of all three species and that the precision of drilling should correlate with the relative size of these muscle attachment sites. Measurements of the locations of drill holes from collected shells of each species showed that drilling locations were significantly non-random. In the abalone and limpet, the muscle attachment site was targeted two and 4.5 times more frequently than expected, respectively. *Octopus vulgaris* type III drilled helmet snails with extreme precision, with over half the holes drilled on the spire at an angle of 45° and 90° from the lip. Kernel density heat maps demonstrated that octopus drilled abalone with low precision, limpets with medium precision and helmet snails with high precision. The reason for the high precision in the helmet snail remains speculative, as the main drilling location did not align with the columellar muscle attachment and no target could be defined. This study is the first to assess octopus drilling in temperate southern Africa and to compare drilling precision across different prey species.

Keywords *Octopus vulgaris* type III · Predation · Behaviour · Abalone · Limpet · Gastropod snail · Drilling precision

Introduction

The South African common octopus *Octopus vulgaris* type III, is an opportunistic, generalist predator, feeding on readily available and easily accessible prey, such as crustaceans, molluscs, teleosts and polychaetes (Smale and Buchan 1981; Smith 2003). In False Bay, South Africa, its diet consists largely of molluscs and crustaceans (Smith 2003). Both of these groups, particularly molluscs, pose the additional challenge of extracting the meat from within a hard exoskeleton or shell. This problem can be overcome using extreme pulling force (McQuaid 1994), by chipping away at the edges of the shell (Anderson and Mather 2007), or by drilling through the shell and injecting venom to weaken the muscle (Pilson and Taylor 1961; Arnold and Arnold 1969; Nixon 1980; Nixon and Maconnachie 1988.) The octopus drills through the shell using its salivary papillae, an accessory organ to the radula (Nixon 1980). Chemical dissolution of the shell by secretions from the posterior salivary gland assists with the drilling process (Arnold and Arnold 1969; Nixon 1980; Wodinsky 1973) but is not required to make an effective drill hole (Wodinsky 1973). The octopus injects venom through the drilled hole, which weakens the muscle of the prey, allowing the octopus to overpower it and access the meat (Arnold and Arnold 1969; Nixon and Maconnachie 1988).

The selection of the drilling location is of particular interest, as a certain degree of accuracy is required. Previous authors have shown that octopuses target specific regions of the shell which correspond to underlying anatomical structures and that there also appear to be interspecific differences between octopuses regarding the region targeted.

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Octopus vulgaris type III drills over the heart of the Brown mussel *Perna perna* (McQuaid 1994). *Octopus americanus* (Avendaño et al. 2020), previously identified as *Octopus vulgaris*, drills over the muscle attachment site in cowries (Blustein and Anderson 2016); into specific regions on the spire on the gastropod *Strombus rainus* (Arnold and Arnold 1969); and along the shell margins of the bivalves *Pitaria chione* and *Venus verrucosa* (Ambrose and Nelson 1983). *Octopus dierythraeus*, like *O. americanus*, drills along the margins of bivalves (Steer and Semmens 2003), while *O. mimus* and *O. rubescens* both drill over the adductor muscles (Anderson et al. 2008; Cortez et al. 1998) and *Enteroctopus dofleini* drills at the thinnest part of the shell over the heart (Anderson and Mather 2007). *Octopus djinda* (Amor and Hart 2021), previously identified as *Octopus aff tetricus,* targets the muscle attachment site of the abalone *Haliotis laevigata* (Greenwell et al. 2019). *Octopus dierythraeus*, *O. mimus*, *O. joubini* and *O. americanus* all target regions on the spire when drilling gastropods (Arnold and Arnold 1969; Cortez et al. 1998; Merlino 2013; Steer and Semmens 2003), although the reasons behind this are interpreted differently by these different authors. No work has focussed on investigating octopus drill holes on limpets, but in their study of muricid drill holes on limpets in Patagonia, Archuby and Gordillo (2018) acknowledge the presence of the oval drill holes associated with octopus predation.

To drill in a specific location on the shells of prey, octopus must hold these at an exact position and orientation. The mouth of the octopus is positioned under its web and out of sight to the animal, so it must rely on chemo-tactile or proprioceptive information to orientate the shell (Anderson and Mather 2007; Mather and Dickel 2017). Knowing how precisely octopuses are able to drill into the shells of different prey taxa not only advances ecological understanding of their feeding methods, but is important to better appreciate the cognitive abilities of these intelligent invertebrates. It has been suggested that octopuses learn the right drilling location through trial and error-based learning (Anderson and Mather 2007; Merlino 2013). When a drill location is unsuccessful in weakening the muscle after envenomation, additional holes may be drilled until the octopus is successful in removing the mollusc from its shell. Once the octopus finds a successful location, it may remember this for application on future shells (Arnold and Arnold 1969). Different groups of molluscs, such as abalone, snails and limpets, however, have very different shell morphologies and anatomies, and therefore require different drilling locations. The octopus thus needs to learn the most effective location to drill for each prey type independently. Such memory formation and problem solving is something which has historically only been attributed to mammals and some birds. While the intelligence of octopuses is widely recognized (Mather and Dickel 2017), the precision with which octopuses drill shells shows that they measure and analyse the shell before commencing the drilling process, thus providing another perspective on their high level of intelligence.

The hypothesis that octopuses target specific regions on the shells of molluscan prey to drill into has been well supported. However, apart from a brief mention by McQuaid (1994) on octopus drilling into mussel shells on the east coast of South Africa, no such work on octopus drilling has been conducted in Southern Africa. Although drilling on a range of prey species has been investigated, no comparisons have been made among different prey types. This study investigates the drilling location of *O. vulgaris* type III on three prey models: an abalone, a limpet and a snail, each displaying very different shell morphology and underlying anatomy. The aim is to determine whether the location of drill holes corresponds to the underlying anatomy and, if so, which anatomical structures are targeted and to investigate the precision of drilling within the target region. The regions targeted among the three prey models are compared to determine if there are any consistent patterns. It is hypothesized that *O. vulgaris* type III targets the muscle attachment site of all three species and that the precision of drilling should correlate with the relative size of the muscle scar.

Methods

Selection and collection of prey species

The abalone *Haliotis midae*, the kelp limpet *Cymbula compressa,* and the helmet snail *Semicassis zeylanica* are all common prey of *O. vulgaris* in False Bay (Smith 2003), but each of these species displays very different shell morphology and underlying anatomy. These species therefore provide three unique prey models that the octopus needs to independently learn how best to drill. To gain a clear anatomical understanding of the different prey models, specimens of each species were collected and dissected. Live specimens of helmet snails and limpets were collected from Miller's Point in False Bay (S 34° 13.8′, E 18° 28.6′), while cultivated abalone were obtained from an aquaculture facility. The specimens were removed from their shells and anatomical regions of interest were mapped relative to the location on the shell.

All sampling for drilled shells was undertaken along the eastern shores of the Cape Peninsula in False Bay, between Fish Hoek and Cape Point. Samples were taken from multiple sites to account for any patterns that may be present due to the particular drilling location preferences of individual octopus, or the possibility of learnt locations at a particular site. Empty shells of the three prey species were collected in the intertidal and subtidal zones (0–10 m depth) from the middens of octopus dens, or scattered around their habitat. The octopus drill holes have a distinctive oval to round shape, which tapers towards the inner orifice (Fig. 1) and range in diameter from less than 1 mm to a maximum of around 4 mm. Only those shells with clear octopus drill holes were collected. Subtidal collections were made using snorkelling gear.

Drilled shells previously collected in False Bay by Craig Foster (Sea Change Project) were also included to supplement the field collections. This collection has been built up over the past 10 years and thus further accounts for any individual, spatial or temporal preferences and patterns in drilling location by local octopus.

Data analysis and statistics

Collected shells were photographed and measurements obtained using Fiji biological-image analysis software (Schindelin et al. 2012). The locations of drill holes were visually determined and *X*–*Y* coordinates were obtained to plot the position of holes relative to their % distance along both the length and width of each shell. Only holes that were distinctly drilled by an octopus were recorded and incomplete drilling attempts were ignored. Where multiple holes were present on a shell, all were accounted for and treated as independent data points. This data set comprised 15 shells with two complete drill holes each, and no shells were recorded having three or more drill holes.

Landmark morphometric analysis using the tps software (Rohlf 2015) and the 'geomorph' package (Adams et al. 2021; Baken et al. 2021) in R (R Core Team 2021) was used to create a two-dimensional model specimen for the abalone and limpet, which accounted for natural variation, displaying the major anatomical regions (Fig. 2). The relative area for each region was obtained using Fiji (Schindelin et al. 2012).

In the helmet snail, the upper spire, where drill holes typically occurred, incorporated the digestive glands and other organs that could not be accurately defined for the target analysis. Because landmark morphometric analysis could not be done in the same way as for the other two species, a different approach was taken for this model and the spire was divided into eight 45° segments measured from the lip, which served as the regions for further analysis.

A chi-squared goodness of fit test was used to determine if the proportion of drill holes in each region differed significantly from the relative area of that region. A significant result would indicate non-random targeting of a particular region. If significant, for the abalone and the limpet, a second chi-squared goodness of fit test was used to determine if the adductor muscle was selectively targeted. All other anatomical regions were pooled and it was tested whether the proportion of drill holes within and outside the adductor muscle scar differed significantly from the expected frequency. This second test was not relevant for the helmet snail and so for that species only a single chi-squared test was conducted to determine whether drilling was non-random.

Heat maps were produced using a two-dimensional kernel density estimation in R using the 'MASS' package (Venables and Ripley 2002) as a visual representation of the relative density of drill holes on different regions of the shell (Fig. 3). Accuracy of measurements and plots using XY coordinates obtained from the proportions of length and width was verified by manual measurements and plotting.

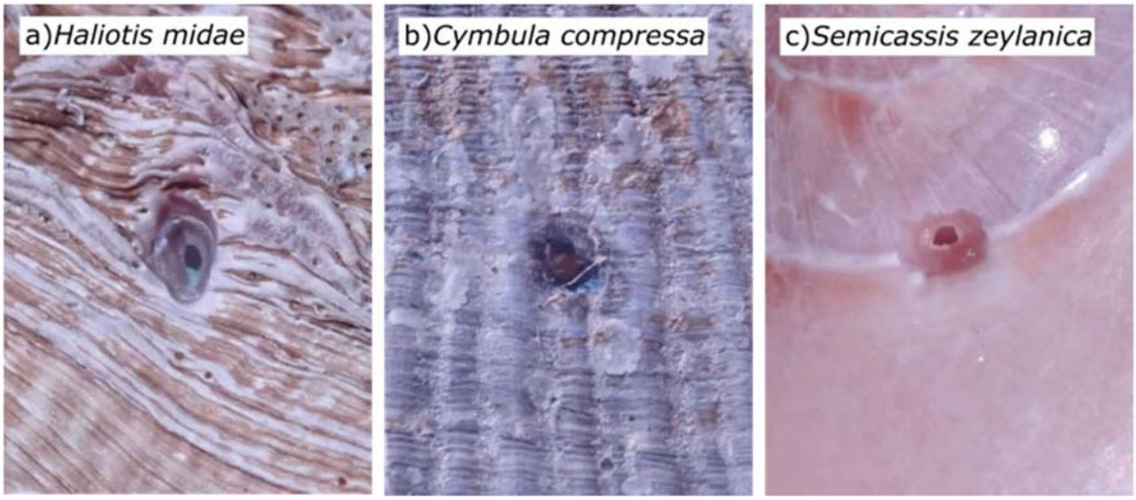

Fig. 1 Drill holes made by *Octopus vulgaris* type III on three different prey species studied herein

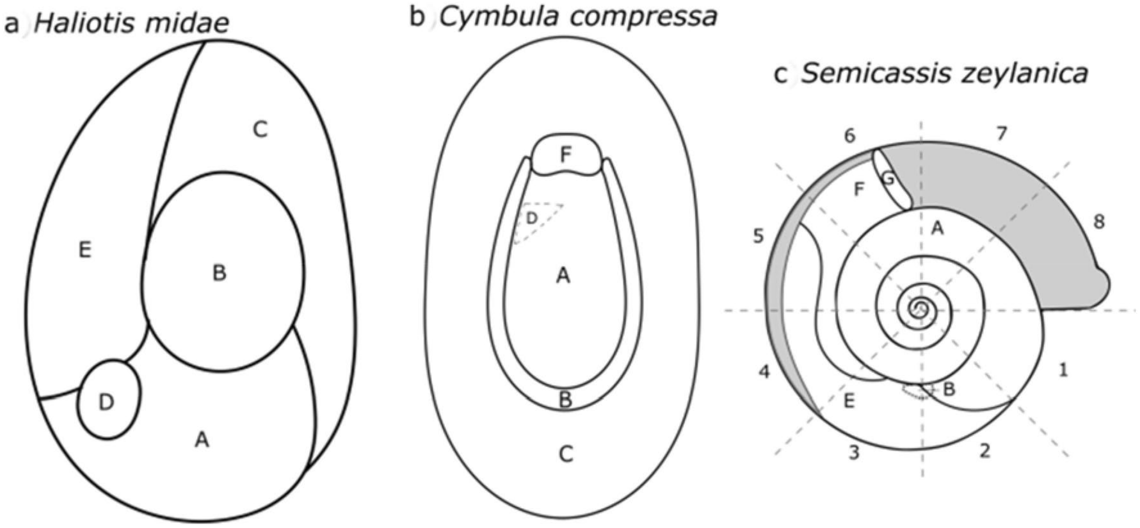

Fig. 2 Regions on the shell models of the three prey species studied herein, corresponding to different underlying anatomical structures: A—guts, B—muscle, C—mantle, D—heart, E—respiratory organs, F—head and G—operculum. Sections 1–8 in *Semicassis zeylanica* show the 45° segments analysed while the grey area shows empty regions

Results

Anatomy

The abalone has a circular muscle in the center of its ear-shaped shell. The digestive and reproductive organs lie at the posterior end, under the spire (labelled 'guts') with the heart positioned laterally on the left side within this region. Above the heart lie the respiratory organs, the position of which can be easily identified from external shell morphology, due to the respiration holes along the ridge of the shell. On the opposite side, under the lip of the shell, is the mantle (Fig. 2a).

The limpet's thin, U-shaped muscle scar extends approximately two-thirds of the way up the shell, posterior to the apex. At its base is the limpet's head, anterior to the apex. The muscle and head surround the guts. The heart lies on the left side of the guts, just behind the head, but cannot be easily distinguished from the other organs and therefore was not plotted as a separate region. The approximate region has been shown in Fig. 2b.

The snail has a cylindrical shell with a low spire and large body whorl. The apex of the shell contains the visceral mass (digestive organs and gonads). Leading on from this are the respiratory and other organs, which occupy the body whorl when the snail has retracted into its shell (Fig. 2c). The relative shell area of different anatomical structures could not be clearly quantified due to its three-dimensional shell morphology and because the upper area of the spire (where nearly all drill holes occurred) covers only the visceral mass. The retractor muscle attaches to the columella in the last body whorl and is therefore not directly accessible to the octopus by drilling through the external shell.

Drill hole location

179 shells containing 191 octopus drill holes were collected and analysed. These comprised 49 abalone (*Haliotis midae*) shells with 51 holes; 52 limpet (*Cymbula compressa*) shells with 56 holes and 78 helmet snail (*Semicassis zeylanica*) shells with 84 holes.

The density of holes drilled in the abalone shells was highest in the middle of the shell (Fig. 3a), the region over the adductor muscle scar. A chi-squared test of holes in all regions showed that drilling location differed significantly from the expected frequency ($X4 = 27.24$, $P < 0.001$). The adductor muscle was selectively targeted two times more often than expected (chi-squared test, $X1 = 22.03$, $P < 0.001$) (Table1).

No holes were drilled in the anterior or posterior extremes of the limpet. The majority of holes were located laterally within the middle band, with the highest density in the right half of the shell (Fig. 3b). A chi-squared test of holes in all regions showed that drilling was significantly non-random $X3 = 59.89$, $P < 0.001$. Selective targeting of the U-shaped muscle scar occurred nearly five times more often than expected (chi-squared test, $X1 = 57.51$, $P < 0.001$) (Table 1).

Drill holes on the helmet snail proved to be extremely precisely positioned, all being clustered within a small region on the lower right side of the spire (Fig. 3c). Drilling was significantly non-random with the majority of holes occurring at an angle between 45° and 89.9° from the lip, four times more often than expected (chi-squared

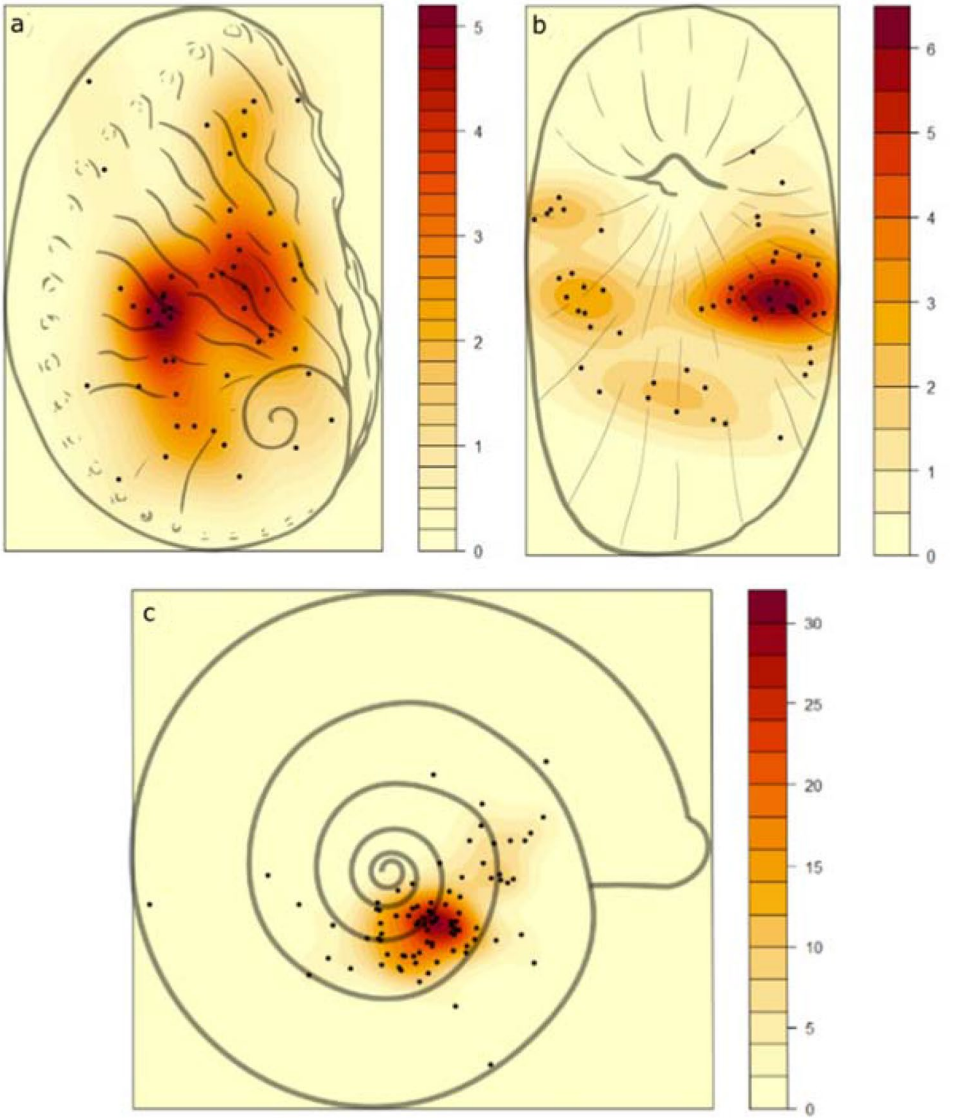

Fig. 3 Location of *Octopus vulgaris* type III drill holes on the shells of three prey species collected in False Bay: **a** *Haliotis midae* ($n = 51$), **b** *Cymbula compressa* ($n = 56$) and **c** *Semicassis zeylanica* ($n = 84$). Location was obtained as a proportion of both length and width of the shell. Density of drill holes is depicted by the colour gradient from low (yellow) to high (red)

test, $X7 = 152.76$, $P < 0.001$) (Table 1). Out of the 78 shells, only three were drilled on the body whorl, but all of these included a second hole on the spire in the commonly drilled location.

Discussion

The three prey species investigated have very different shell morphologies and underlying anatomies. For all three species, the location drilled by octopus was significantly non-random. This supports the findings of other studies which show that octopus selectively target specific regions of prey shells when drilling (Anderson et al. 2008; Anderson and Mather 2007; Cortez et al. 1998; Steer and Semmens 2003). For abalone and limpets, this selectivity was related to the position of the muscle attachment site. In the abalone, 59% of drill holes occurred in the region of the circular muscle attachment site, a region that makes up only 29% of the shell (double the predicted ratio). Similarly, 34% of drill holes in the shells of the limpet occurred within the U-shaped muscle scar, which makes up only 7.4% of the shell (more than 4.5 times the predicted ratio). On the helmet snail 52% of holes were drilled between 45° and 89.9° with another 38% drilled in the adjacent segments (Table 1).

The density of drill holes on each prey model (Fig. 3a–c) gives a clear visual indication of the precision of drilling. For both the abalone and limpet, the patterns of drill holes align with the shapes of the muscle scars. In the abalone, drill holes were more widely distributed across the shell, although the highest density occurred within the region of the central muscle scar. Holes on the limpet were clustered around the U-shaped muscle scar. Although many attempts missed their mark, penetrating the gut or mantle, the drill

Table 1 Frequencies at which *Octopus vulgaris* type III drilled shell regions (observed) and the expected frequency based on its relative area beneath the shell

Model species	Region	Proportion of shell area	Expected frequency	Observed frequency	Preference ratio (O/E)
Abalone (*N* = 51)					
	Guts	0.173	8.823	10	1.13
	Heart	0.039	1.989	2	1.01
	Mantle	0.259	13.209	7	0.53
	Muscle	0.29	14.79	30	2.03
	Respiratory	0.239	12.189	2	0.16
Limpet (*N* = 56)					
	Guts	0.198	11.088	12	1.08
	Muscle	0.074	4.144	19	4.58
	Head	0.021	1.176	0	0.00
	Mantle	0.707	39.592	25	0.63
Helmet snail (*N* = 84)					
	0–44.9°	0.125	10.5	18	1.71
	45–89.9°	0.125	10.5	44	4.19
	90–134.9°	0.125	10.5	14	1.33
	135–179.9°	0.125	10.5	2	0.19
	180–224.9°	0.125	10.5	0	0.00
	225–269.9°	0.125	10.5	0	0.00
	270–314.9°	0.125	10.5	1	0.10
	315–359.9°	0.125	10.5	5	0.48

holes were still within the vicinity of the muscle and therefore drilled with higher precision relative to the abalone. It is not clear why a larger proportion of holes were drilled on the right-hand side of the shell. The heart lies on the left hand side of the animal and thus was ruled out as a potential influencing factor. One speculation is that the limpets anus and kidney openings are on this side, and thus a chemical cue could be attracting the octopus.

The helmet snail presents an interesting case. Holes were tightly clustered in a region of the spire just below the apex—a region that does not seem to correlate with any specific anatomical feature. The visceral mass is located under this region extends into the entire upper spire of the shell. The high density of drill holes within the small area indicates extreme precision is shown by octopus when drilling this type of prey, but the reasons for this remain unclear.

The findings from both the abalone and limpet support the hypothesis that *O. vulgaris* type III is targeting the muscle. This is expected, as the purpose of the drill hole is to create access through which venom that weakens the muscle can be injected, allowing the octopus to overpower the mollusc and access the meat (Arnold and Arnold 1969; Nixon and Maconnachie 1988). The results from the helmet snail, however, are inconclusive. Although the muscle attaches to the central columella in the body whorl, within the vicinity of the targeted drill site, the octopus generally drills in the upper spire region. This means that a layer of internal shell would block the octopus from reaching the muscle attachment site, which does not seem to be the targeted organ, unless the injected venom spreads through the tissue to reach the columella. Arnold and Arnold (1969) showed that octopus use the lip of gastropods as a point of orientation, and when drilling individual octopuses showed a strong preference for a sector of the spire. When the lip was removed from the shells they were, however, drilled at random. This may explain how the octopuses manage to drill so precisely, but unfortunately does not answer the question of what the target is for the helmet snail in this study. The octopus studied by Arnold and Arnold (1969) did not all drill in the same location, but rather each had their own individual preferences. Their findings thus contrast the results of this study, where drilling location was consistent across the predator population. Merlino (2013) also suggested that the aperture was used as a reference point, based on the observation that drill holes were commonly found on the same side as the aperture, a finding similar to this study.

Another theory is that the octopus select drill sites according to shell thickness (Anderson and Mather 2007). The spire is known to be the thinnest part of the shell and after the gastropod has retracted, drilling higher up on the spire increases the chances of penetrating the flesh (Merlino 2013; Steer and Semmens 2003). A rather intriguing idea is that the high precision of drilling location observed on the helmet snail may be a result of combined learning from drilling the gastropod *S. zeylanica* and hermit crabs *Paguristes gamianus*, which are very common in this area and often use this shell type as shelter (Gareth Fee pers. observ.). Octopus are known to drill shells used by hermit crabs (Cortez et al. 1998; Merlino 2013), but when hermit crabs retreat into their shells, they are too large to retreat fully into the apex. The drilling location observed in this study may be the most successful location to drill for both potential prey species living in the helmet shell. However, this would need to be tested by conducting further and more detailed field or laboratory experiments.

Although the limpet appears to be drilled with higher precision than the abalone, the hypothesis that precision of drilling matches the relative size of the actively targeted region could not be tested, as the area targeted in the helmet snail could not be accurately identified or quantified. Not only is this study comparing different models of prey anatomy, but it is also the first to investigate octopus drilling on limpets. Although limpets are known to be preyed upon by octopuses (Ambrose 1986; Archuby and Gordillo 2018; Smith 2003), they have not previously been thought of as a preferred food choice. *Cymbulla compressa* is, however, a readily available prey item in the kelp forests of False Bay and hence it is not surprising that it forms a common prey species for this generalist predator (Smale and Buchan 1981; Smith 2003). The shell of *C. compressa* is relatively thin for a limpet and thus may not require a large amount of energy to drill and consume, making it an ideal food source. The anatomy of limpets is very different to that of other molluscan prey, particularly with regards to the U-shaped muscle scar. As this study has shown, octopus drill in this U-shaped pattern with medium to high precision.

As a generalist predator, the octopus needs to figure out how to find and process a wide variety of prey. Our results show that octopus recognize the need to drill in different locations on different prey models. They are also able to learn, possibly through trial and error (Anderson and Mather 2007; Merlino 2013), the most successful location for each prey model and apply this knowledge routinely. Mather et al. (2012) found that individual octopus within a population sometimes specialize on a particular prey item. This has also been observed in False Bay (Craig Foster, Sea Change Project, pers. comm.). For example, early in 2021, Foster monitored an individual octopus over a period of about six weeks and during that time it fed almost exclusively on the giant chiton *Dinoplax gigas,* a common species in the region but one not previously recorded as prey for *O. vulgaris* type III. Further investigations into the prey choice and drilling behaviour for individual octopuses in situ would be useful to determine whether individuals specialize not only in their preferred prey species, but also in terms of their drilling location, as suggested by Arnold and Arnold (1969).

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Author contributions All authors contributed to the study conception and design. Data collection and analysis were performed by GNF. The first draft of the manuscript was written by GNF and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data availability The datasets analysed in this study are available from the corresponding author on request.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

Ethics approval This research was authorised by scientific research permit number RES/2021/72 issued to the Department of Biological Sciences, University of Cape Town by the South African Department of Environment, Forestry and Fisheries (now Forestry, Fisheries and the Environment). No ethical clearance was required as only gastropod molluscs were collected from the field.

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