

Hole drilling in crab and gastropod shells by *Eledone cirrhosa* (Lamarck, 1798)*

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SUMMARY: *Eledone cirrhosa* readily feeds on crabs (e.g. *Carcinus maenas*) and gastropods (e.g. *Nucella lapillus* and *Littorina littorea*) in the laboratory. Penetration of the shells of these prey can be readily followed, with little or no disturbance, by suspending a microphone in the water and recording the sounds. The characteristic sound consists of a series of short bursts, resembling the noise of rasping, separated by quieter periods. A bore hole is formed through the shell of the prey with a morphology typical of the type of shell. In the gastropod this is located in a small area near the top of the shell, while in the crab nearly 60% were located in the carapace with 80% of these occurring in the lower left quadrant. Bore holes not in the carapace were located in the eyestalk or in the cuticle of the eye socket, in these cases the duration of the feeding sound was significantly shorter. The duration of the quiet periods are shortest at the initiation and at the completion of the bore hole. The central radula tooth can fit into the hole made in the shell of the crab and the characteristic pattern of wear indicates that it is subject to considerable abrasion when used. Chemical etching of the shell is involved in the formation of the bore hole. It is concluded that there is an alternation of periods of rasping by the radula and chemical etching during the making of the borehole.

Key words: *Eledone cirrhosa*, octopus, hole drilling, radula, saliva, chemical etching, boreholes.

RESUMEN: PERFORACIÓN DE AGUJEROS POR *Eledone cirrhosa* (LAMARCK, 1798) EN CONCHAS DE GASTERÓPODOS Y CAPARAZONES DE CANGREJOS. – En el laboratorio, *Eledone cirrhosa* come fácilmente cangrejos (p. e. *Carcinus maenas*) y gasterópodos (p. e. *Nucella lapillus* y *Littorina littorea*). Se puede seguir con facilidad la penetración de las conchas y caparazones de estas presas, sin apenas molestar al pulpo, registrando mediante un micrófono suspendido en el agua los sonidos que aquél hace. El sonido característico consiste en una serie de cortos ataques, que se parecen al ruido de raspar, separados por períodos más tranquilos. En la concha o caparazón se forma una perforación cuya morfología depende del tipo de concha. En el gasterópodo, la perforación se localiza en una pequeña región cerca del ápice de la concha, mientras que en el cangrejo cerca del 60% se situaban en el caparazón, y de ellos el 80% se hallaban en el cuadrante inferior izquierdo. Las perforaciones que no se encuentran en el caparazón se sitúan en el pedúnculo ocular o en la cutícula del cuenco ocular; en estos casos la duración del sonido de alimentación fue significativamente menor. La duración de los períodos de reposo es menor al inicio y al final de la perforación. El diente central de la rádula encaja en la perforación efectuada en el caparazón del cangrejo, y el modelo de desgaste característico indica que está sujeto a considerable abrasión cuando se ha gastado. En la formación de la perforación interviene la abrasión química. Se llega a la conclusión de que durante la perforación existe una alternancia de períodos de raspado por parte de la rádula y de abrasión química.

Palabras clave: *Eledone cirrhosa*, pulpo, perforaciones, rádula, saliva, abrasión química

*Received November 1995. Accepted September 1996.

INTRODUCTION

Many species of incirrate octopods spend most of their life in shallow seas living on the sea bottom and preying on a variety of invertebrates and small fish (Boyle, 1983; Boucaud-Camou and Boucher-Rodoni, 1983). *Eledone cirrhosa* is common offshore around the North Wales coast and common prey items are gastropods and crabs.

In a variety of octopods feeding frequently involves first boring a hole through the tough shells of their prey. The location of these holes is not random on the shell but appears to be in a position fairly characteristic of each prey species (Ambrose *et al.*, 1988; Arnold and Arnold, 1969; Boyle and Knobloch, 1981; Guerra and Nixon, 1987; Mather and Nixon, 1995; Nixon, 1979a; Nixon and Boyle, 1982; Wodinsky, 1969). Production of such boreholes has been investigated by a number of workers and two mechanisms have been identified, namely rasping by the radula (Wodinsky, 1969) and the action of as yet unidentified chemicals in the saliva aided by the actions of the salivary papilla (Nixon, 1979b, 1980; Nixon and Boyle, 1982). The relative importance of these two mechanisms remains uncertain. Once the hole has been completed saliva is injected and this appears to have two effects, paralysis of the prey (Ghiretti, 1959) and detachment of the muscles from the shell which considerably aids extraction of the flesh (Grisley, 1993).

Isgrove (1909) provides a clear description of the structures associated with hole boring and feeding in *E. cirrhosa* and this has been extended by more recent workers, e.g. Nixon and Boyle (1982). Through the mouth, situated at the centre of the ring of arms, the overlapping dark brown dorsal and ventral jaws are visible. These form the front wall of the buccal cavity from which arises dorsally the oesophagus, and protruding into it from the postero-ventral region, the odontophore, over which is extended the radula. The radula is supported by a pair of cartilaginous rods. Beneath the anterior region of the odontophore there is a small aperture through which can be protruded the salivary papilla. Ducts from the paired posterior salivary glands join to form a single duct which discharges via this papilla. Paired anterior and a single median salivary gland also discharge into the buccal cavity. A very complex mass of muscle surrounds the buccal cavity to form the characteristic buccal mass.

In the Mollusca, hole boring to obtain food has also been described in a number of gastropod species. Of these the oyster drills, e.g. *Urosalpinx cinerea*, are important pests on commercial oyster beds. From detailed studies of these Carriker (1969) concludes that the radula is used in combination with secretions from the accessory boring organ, to drill through the shells of oysters.

The aim of this study was to investigate the production of holes in the shell of their prey by our common local octopus *Eledone cirrhosa*.

MATERIALS AND METHODS

Eledone cirrhosa (Lamarck, 1798) were obtained from fishermen who collected them around the island of Anglesey and maintained in the laboratory in Bangor. Animals were maintained at 10-15°C in circulating seawater. The water, salinity 34-36‰, was passed through a large biological filter and refreshed weekly by the replacement of approximately 10% with fresh locally collected seawater. The 200-500 g octopods were fed on small crabs (*Carcinus maenas*) or the snails *Littorina littorea* and *Nucella lapillus*.

Animals were normally maintained in small groups (<10) in 500 l aquaria. For experimental study they were isolated in smaller 100 l tanks for the duration of that experiment.

For the shell boring study animals were isolated with their prey. When at least 10 well drilled shells had been obtained the animals were killed so that the relationship between the size of the radula teeth and the holes bored by that individual could be compared. For each prey item at least five *E. cirrhosa* were isolated and examined in this way. The teeth were studied by removing the buccal mass, opening the cavity dorsally and fixing the radula *in situ* over the odontophore cartilage. In order to retain the radula in a normal position it is important to cut as few muscles as possible when exposing it. Glutaraldehyde diluted with sea water was used for fixation. Following washing the odontophores were removed from the remainder of the buccal mass, dehydrated in an alcohol series, transferred to acetone and critical point dried using carbon dioxide. The odontophores were then attached to aluminium stubs using Araldite adhesive and coated with gold in a Polaron coating unit before examination in an Hitachi SE 520 scanning electron microscope (SEM).

The position of the drill holes in the arthropod and gastropod shell was determined using a micrometer and, for the gastropods, a circular protractor.

Recordings of the noises made by the radula during the drilling process were made with sensitive microphones manufactured by Mr. T. Davies or Mr. D. A. Davies. Microphones were suspended in the tanks and recordings made with an Ultra domestic cassette recorder. Recordings were analysed using EPIC software.

A method for collecting saliva from *Octopus* has been reported by Ballering *et al.* (1972) and we repeated this on *E. cirrhosa* to obtain saliva for experiments not reported here. An animal with its arms held back over its body to expose the mouth region, is placed inside a clear plastic bag and held with the mouth close to the plastic. Gentle stimulation of the mouth then produces a clear behaviour sequence involving the radula, salivary papilla and ejection of saliva. When the animal is returned to the aquarium there is no evidence that this procedure has caused it any stress.

RESULTS

Characteristics of the radula and radula wear

As illustrated by Isgrove (1909) each transverse row of teeth in the radula consists of a tall pointed central or rachidian tooth, flanked on each side with three lateral and a single small marginal tooth (Fig. 1). Where the teeth emerge from the radula gland they have sharp pointed cusps but anteriorly these become severely worn, so that at the extreme anterior edge the teeth are only represented by flat remnants of the teeth bases. The central teeth start to wear many rows before any affect on the other teeth can be observed. The tip of the central cusp becomes rounded and the cusp is reduced in height, as it is lowered so the lateral cusps on the tooth are worn and removed until eventually no cusps are visible. Occasionally larger parts of the tooth including most of the main cusp break off leaving a sharp edged remnant, which is in contrast to the rounding typical of normal wear. Thus during normal wear the central teeth are held clear of the lateral and marginal teeth, and they become progressively worn down from the tip.

The radula is tightly stretched over the anterior tips of the odontophore cartilages (Fig. 2). Extending laterally from the radular membrane the cuti-

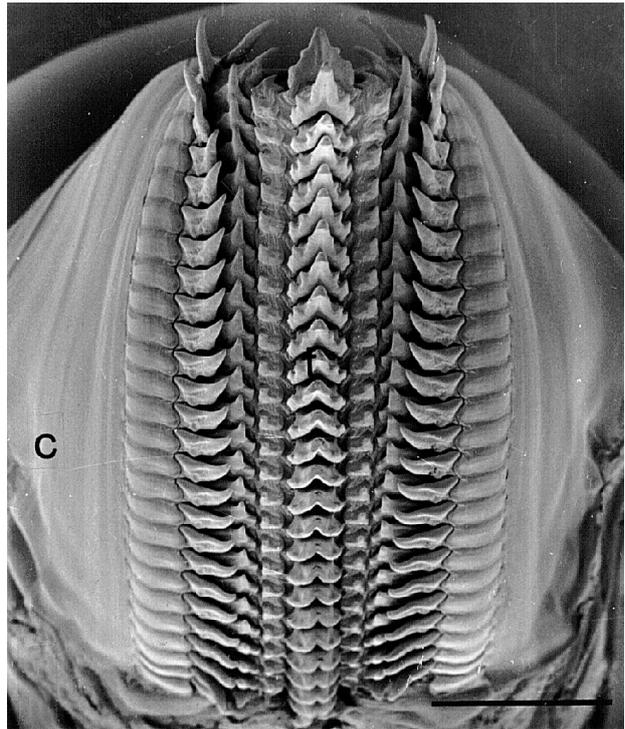


FIG. 1. – An SEM micrograph of an *Eledone cirrhosa* odontophore viewed from the antero-ventral surface. The most anterior region of the radula, continuous with the cuticle (c) over the lateral walls of the odontophore, is stretched over the underlying odontophore cartilages. The progressive wear of the central radula tooth (t) is clearly visible. The bar represents 1 mm.

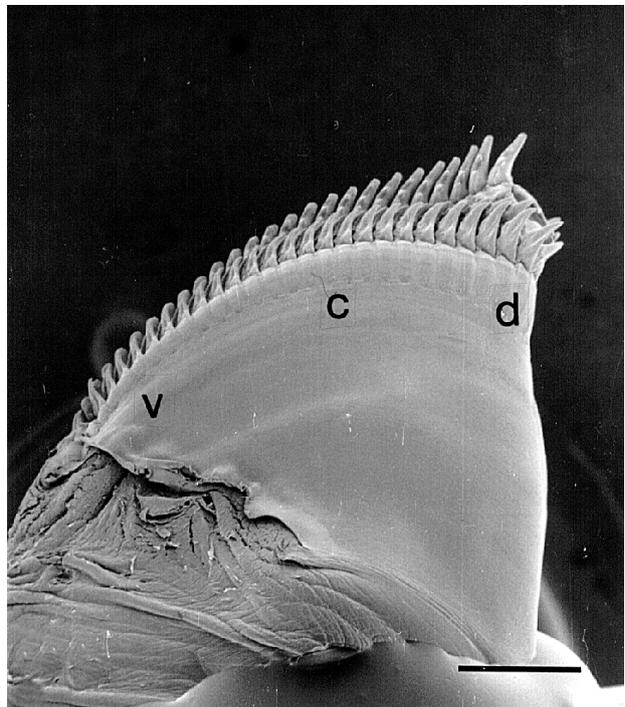


FIG. 2. – An SEM micrograph of an *Eledone cirrhosa* odontophore viewed from the lateral surface. There is a clear decrease in height of the central tooth from the dorsal (d) to the ventral surface (v). The lateral edges of the radula merge with the cuticle (c) covering the rest of the odontophore. The bar represents 1 mm.

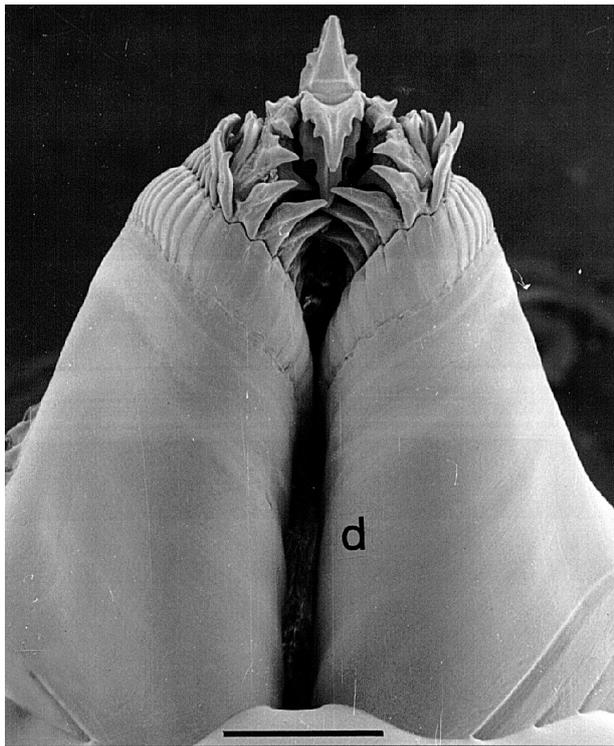


FIG. 3. — An SEM micrograph of an *Eledone cirrhosa* odontophore viewed from the dorsal surface. Teeth on the antero-ventral surface are drawn backwards into the dorsal groove (d) which leads into the radula gland. As the almost flat radula passes over the anterior edge the teeth rotate from an anteriorly projecting position to one directed posteriorly, and the radula becomes folded to form a tube with all teeth pointing inwards. The bar represents 1 mm.

cle covered epithelium covers the lateral surfaces of the odontophore and continues on to cover most of the inner surface of the buccal cavity. On the ventral surface of the odontophore the teeth are well exposed and the cusps of the teeth are directed forwards (Fig. 1). At the anterior tip of the odontophore the teeth move into a very narrow dorsal groove leading into the radula gland and come to point posteriorly (Fig. 3). The anterior tip of the odontophore is narrow and the central tooth is directed forwards clear of the other teeth which are located on the lateral walls. As in most molluscs the radula starts the feeding stroke maximally exposed on the surface of the odontophore, and during the rotation of the odontophore while feeding it is drawn back over the surface into the dorsal groove. As the teeth move over the edge of the odontophore they move rapidly from an anteriorly directed orientation to point posteriorly. When filmed from a lateral viewpoint the long series of central teeth are visible moving rapidly towards this anterior edge before disappearing into the groove.

How is the radula used?

It has proved impossible so far, to see the radula in use while the octopus is boring through the shell of its prey. The animal pounces and envelopes its prey in its arms so that very little is visible to view. However typical rasping noises are made as in other molluscs, and these can easily be recorded, a technique pioneered by Wodinsky (1969).

In all recordings made, whether the prey was a crab or a snail, analysis indicated that while it was actively boring there were short periods of noise separated by much longer quiet periods (Fig. 4). The total duration of this boring activity varied considerably between individual octopuses, between different prey and between different sizes of prey (Table 1). Over the main part of the recording there appeared to be a gradual increase in both the duration of the quiet periods and the length of the period

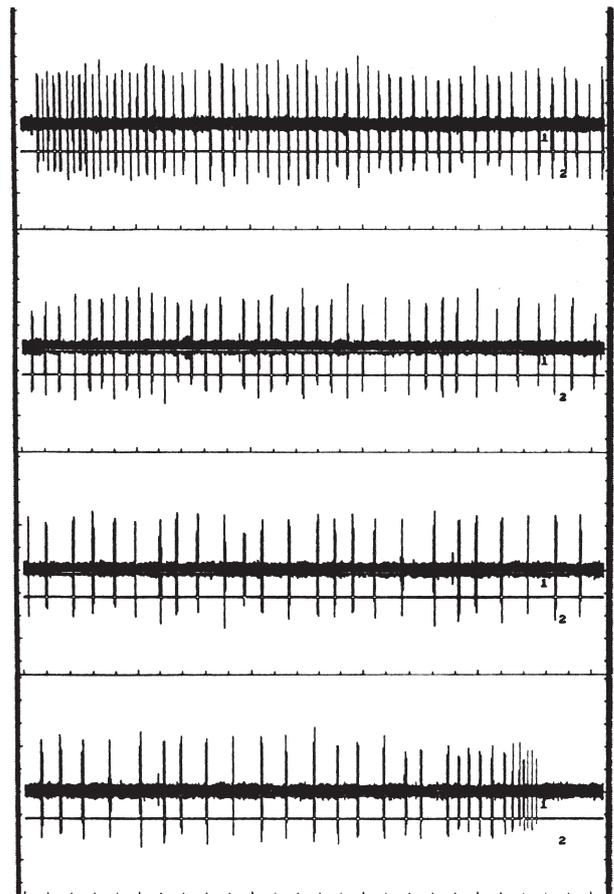


FIG. 4. — A sound recording of *Eledone cirrhosa* making a borehole in the carapace of a crab *Carcinus maenas*. 3 traces are shown, 1 is the sound record, 2 is an unused trace and the third is the timebase of 4 secs per division.

TABLE 1. – Analysis of sound recordings of two *Eledone cirrhosa* making boreholes in the crab *Carcinus maenas*.

<i>Eledone</i>	Parameter	Borehole in carapace	No. of observations	Mean±S.D.
402	No of rasps	Present	7	99.6±27.9
	No of rasps	Absent	1	20
	Secs to first rasp	Present	7	21.4±10.7
	Secs to first rasp	Absent	1	9
	Rasping duration	Present	7	542.1±190.9
	Rasping duration	Absent	1	51
209	No of rasps	Present	1	100
	No of rasps	Absent	9	26.8±13.9
	Secs to first rasp	Present	1	34
	Secs to first rasp	Absent	9	25.8±24.7
	Rasping duration	Present	1	515
	Rasping duration	Absent	9	81.8±68.6

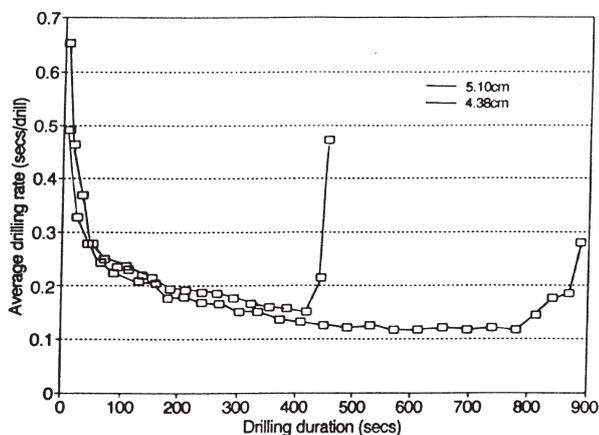


FIG. 5. – The change in drilling rate with time for a 405 g *Eledone cirrhosa* boring through two carapaces of the crab *Carcinus maenas*.

of noise (Fig 5). However in all cases the lengths of the quiet periods were much shorter at the start and at the end of the period of boring. All feeding on these prey organisms was associated with this characteristic pattern of noise which always resulted in the formation of a hole through the gastropod shell, while there appeared to be some variation with crabs. Boring activity on crabs usually resulted in the formation of a hole through the dorsal carapace (57% of animals recorded) but sometimes (43%) the hole appeared to be absent. Similar recordings of rasping activity were produced (Table 1) but these were much shorter in duration than normal (51 to 542±190.9 and 81.8±68.6 to 515 secs) and started later after envelopment by the predator (9 to 21.4±10.7 and 25.8±24.7 to 34 secs). In these cases holes were found through the basal segment of the antenna, or through the thin carapace around it,

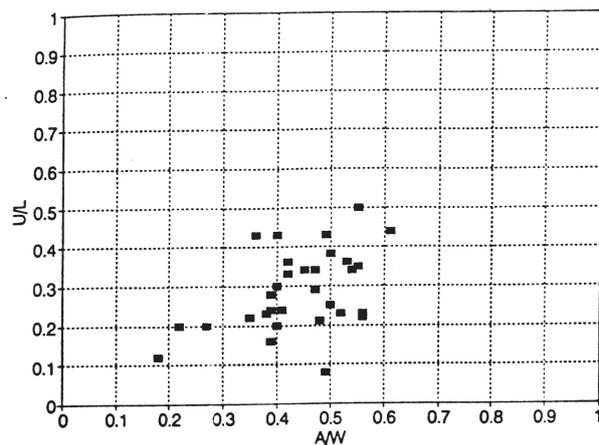


FIG. 6. – Position of boreholes observed on 31 carapaces of *Carcinus maenas* collected after boring by a 402 g *Eledone cirrhosa*. W, carapace width; L, carapace length; A, distance of borehole from left side of carapace; U, distance of borehole from lower edge of carapace.

when these regions were still present after dismemberment of the shell by the octopus.

Bore holes

Measurements of hole locations in the carapace clearly indicated that the highest concentration was located in the posterior left quadrant of the carapace (Fig. 6). Holes in the gastropod shells were equally small and their location varied with the species, thus in *Littorina* the greatest concentration of holes was

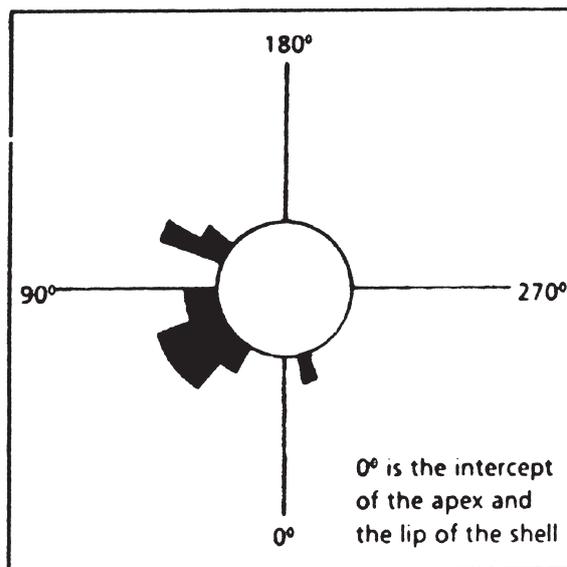


FIG. 7. – Frequency of position of boreholes made by a 292 g *Eledone cirrhosa* in shells of *Littorina littorea*. The position is measured in degrees from the position of the lip.

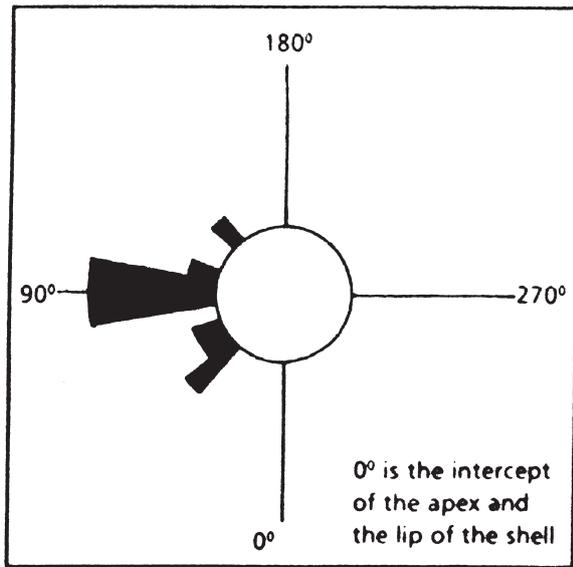


FIG. 8. – Frequency of position of boreholes made by a 292 g *Eledone cirrhosa* in shells of *Nucella lapillus*. The position is measured in degrees from the position of the lip.

close to the top of the spire (7% of the height) and 50° from the lip (Fig. 7) while in *Nucella* they were concentrated at 15° and 90° (Fig. 8) respectively.

Holes in the carapace of the crab were invariably oval in shape with smooth sloping walls to a small



FIG. 9. – An SEM micrograph of a borehole drilled by *Eledone cirrhosa* in the carapace of the crab *Carcinus maenas*. The bar represents 250 μm .

TABLE 2. – Characteristics of a borehole made by *Eledone cirrhosa* in the carapace of *Carcinus maenas*

Weight of <i>Eledone</i> (g)	415
Hole in <i>Carcinus</i> Length (μm)	918
Width (μm)	522
Thickness of carapace (μm)	400
Central tooth height (μm)	520
base width (μm)	400
angle at tip ($^{\circ}$)	22

round aperture at its base (Fig. 9). Great care was taken to compare the size with that of the central tooth of the predator that had made the hole as it could have contributed to the boring of the hole e.g. Table 2.

In contrast, most holes through the gastropod shells were highly irregular and larger (Fig. 10). Sometimes the outer part of the hole resembled the hole in the crab carapace but the inner part was invariably less regular. The shells studied were much thicker (1.1 ± 0.2 mm in *N. lapillus* and 0.85 ± 0.15 mm in *L. littorea*) than the crab carapaces (0.38 ± 0.12 mm) but there was no common shape to the hole. Holes most commonly looked as if they were produced by the merging of 2 or 3 separate bore holes.

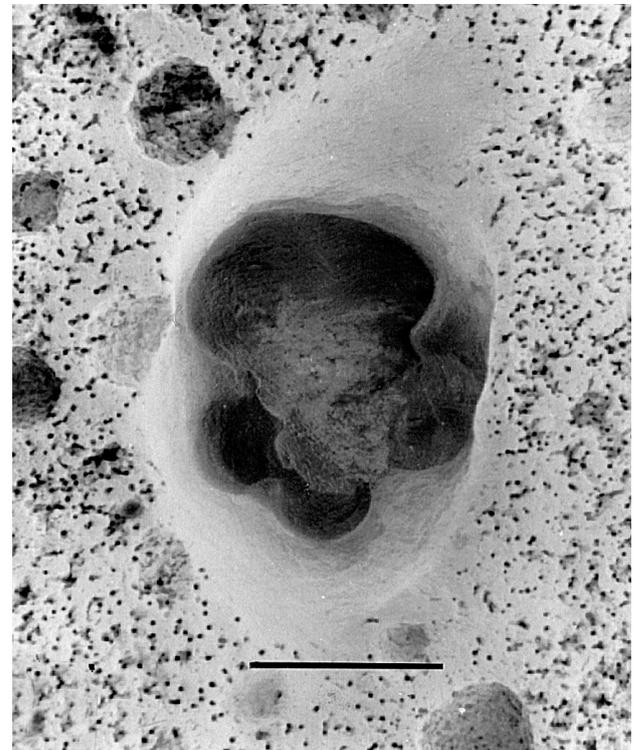


FIG. 10. – An SEM micrograph of a borehole drilled by *Eledone cirrhosa* in the shell of the winkle *Littorina littorea*. The bar represents 250 μm .

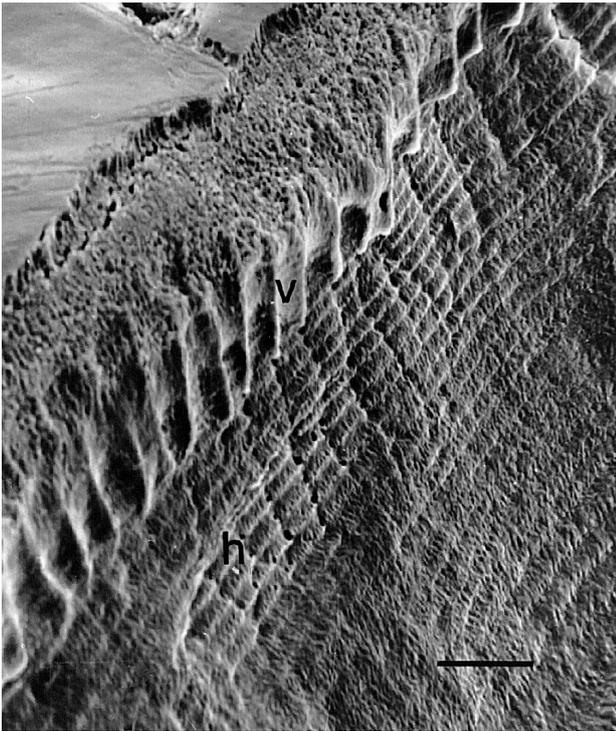


FIG. 11. – An SEM micrograph of the edge of a borehole drilled by *Eledone cirrhosa* in the carapace of the crab *Carcinus maenas*. The horizontal layers in the endocuticle (h), the vertically oriented crystallites (v) and the thin epicuticle are clearly visible. The bar represents 10 μ m.

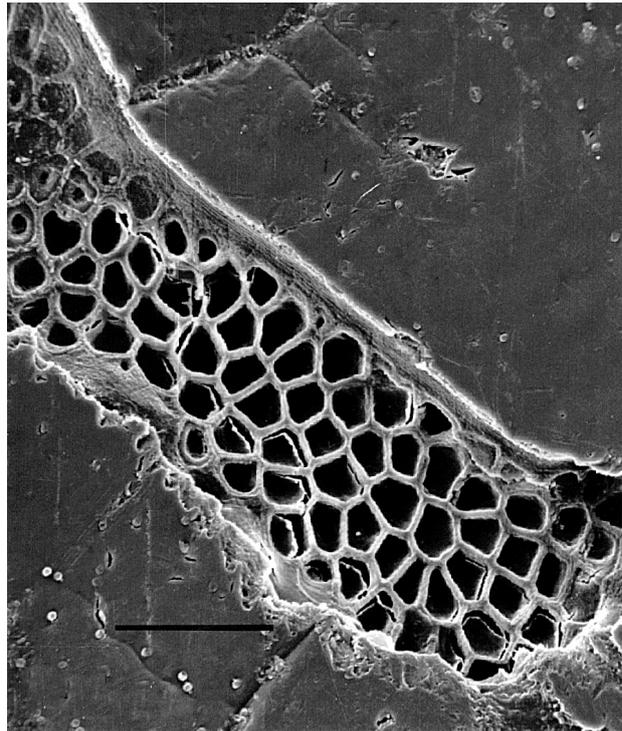


FIG. 12. – An SEM micrograph of the carapace surface of the crab *Carcinus maenas* close to the edge of a borehole drilled by *Eledone cirrhosa*. Etched outlines of the crystallites are clearly visible. The bar represents 30 μ m.

Examination of the bore holes in both types of prey clearly indicated that some chemical etching had taken place. No clear scratches were observed in the walls of completed holes and the outlines of crystallites in the shells were clearly visible in some small areas (Fig. 11) and occasionally on the surface of the shell around the hole (Fig. 12).

With both types of prey the final hole through the shell was smooth in outline with a very sharply defined edge (Fig. 13). Some possible signs of etching were occasionally visible on the inside surface of the shell immediately around the hole.

The salivary papilla and its use

Examination of the odontophore reveals a small aperture beneath its anterior tip close to the most anterior and most worn of the rows of radula teeth. In the fresh buccal mass, pressure applied to the posterior lateral walls can express the salivary papilla out through this aperture. When successful the salivary papilla is seen to consist of a conical basal region and a much narrower tubular apical region. SEM examination of the papilla reveals that the conical base is covered by narrow processes which vary

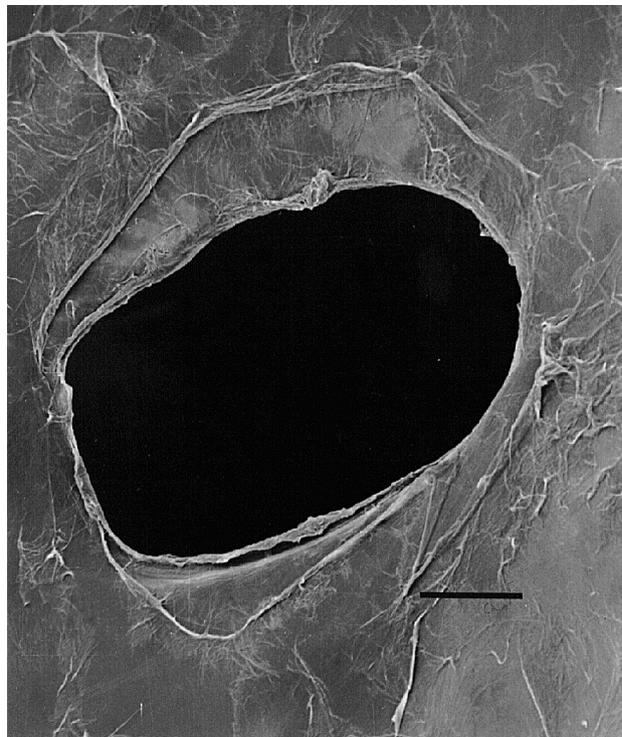


FIG. 13. – An SEM micrograph of the inner surface of borehole drilled by *Eledone cirrhosa* in the carapace of the crab *Carcinus maenas*. The edge of the borehole is well defined and there is little evidence here of any etching on this surface. The bar represents 50 μ m.



FIG. 14. – An SEM micrograph of the salivary papilla of *Eledone cirrhosa*. The conical base (b) of the papilla is covered by closely spaced pointed projections and the tubular tip (t) bears longitudinal rows of large irregularly shaped projections. The bar represents 200 μm .

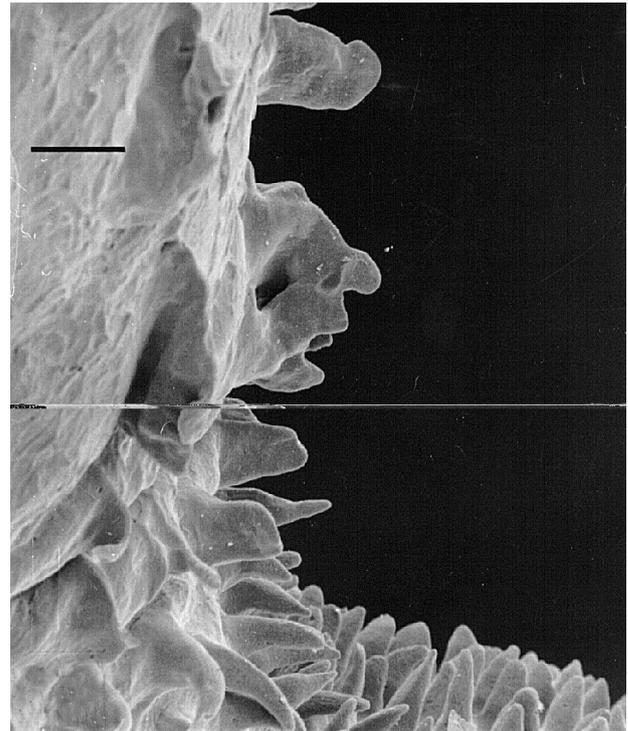


FIG. 15. – An SEM micrograph of the salivary papilla of *Eledone cirrhosa*. The narrow pointed projections on the base can be clearly distinguished from the larger irregular ones on the tip. No signs of wear are visible on these projections. The bar represents 20 μm .

in height from the densely packed elongated processes in its upper regions grading into the more sparsely arranged shorter and more irregular ones in the lower regions. The apical tube has on its surface 8 longitudinal rows of very irregular processes, approximately 10 occurring in each longitudinal row.

Light microscope sections revealed that the whole papilla is covered by a cuticle and that the various processes are projections from its surface (Fig. 14). The cuticle is thickest over the tubular region of the papilla. No signs of wear were ever observed on the surface processes (Fig. 15).

When saliva was collected a clear behavioural sequence involving the radula and salivary papilla was observed and on six occasions this was recorded on video. The mouth opens and the jaws are used to bite through the bag. The radula is then pushed out and executes a clear rasp with the central teeth visibly moving over the tip of the odontophore. This is then withdrawn and the salivary papilla everted with the narrow tubular region visible at its tip. Saliva is often then ejected forcibly through the papilla and may jet for a distance of up to 1 metre. This sequence of rasping followed by salivary papilla eversion was repeated up to three times under these conditions.

DISCUSSION

There is considerable discussion in the literature concerning the relative contributions made by the radula and the saliva to the boring of holes through the shells of their prey (Nixon, 1979b, 1980; Nixon and Boyle, 1982; Wodinsky, 1969). Some authors claim that the radula teeth are too large to produce the hole, others that the hole is produced solely by the action of the saliva or a mixture of the two factors. The work reported supports the view that both elements are important and that their use is highly integrated.

In all cases, boring is associated with short periods of rasping alternating with longer quiet periods. The videos of animals ejecting saliva reveal an alternation between periods of radula rasping and eversion of the salivary papilla with jetting of saliva. This behaviour was only observed for short periods but, with the clear evidence from the sound recordings, there appears to be support for the hypothesis that rasping by the radula alternates with periods of shell softening by the saliva. Further work is needed to extend these observations but it appears to be closely comparable to the well established mecha-

nism of boring established for the gastropod *Urosalpinx* (Carriker, 1969).

Wodinsky (1978) has reported that *Octopus vulgaris* will pull gastropods from their shells without first boring through the shell. This was not observed with *E. cirrhosa* feeding on *Littorina littorea* or *Nucella lapillus*. Some doubt has been expressed about hole boring being essential for *E. cirrhosa* feeding on crabs, as in some cases a hole is not found (Nixon and Boyle, 1982). When an octopus opens the shell of a crab the thinner arthrodiral membranes around the edge of the carapace can be hard to identify and may remain attached to the leg bearing portion rather than to the dorsal carapace. It has been concluded that where no hole was found, poison to paralyse the prey reached it via the membranes of the gills, via injection through the mouth or by some undiscovered route. Our observations clearly indicate that with all recordings of feeding on a crab the sequence of sounds associated with boring is present. The duration of the feeding sequence is shorter when holes through the carapace are absent, probably indicating that the hole is made through a thinner material and our observations indicate that the antennae and their surroundings are the probable location of this site.

The frequency of the rasping sequence is much higher at the start of boring. As the shells of both arthropods and gastropods have an outer layer, the epicuticle and periostracum respectively, with a much higher concentration of organic material than is found in the main thickness of the shell (Ruppert and Barnes, 1994), this could reflect the greater importance of the radula in penetrating these layers. Once access has been gained to the inner layers with their predominantly CaCO_3 content, decalcification could be more important and might account for the longer periods between rasps. How the octopus detects this situation and then controls the boring cycle is unknown but the recently postulated concentration of proprioceptors at the tip of the odontophore cartilages (J.Z. Young; personal communication) could be involved.

Where holes in the shell of the crab were compared to the height and width of the central radular teeth of the animals that created those holes, in all cases it was possible for those teeth to have generated them (e.g. Table 2). This relationship was noted by Nixon (1979), 'Only the mesocone of the central rachidian tooth could reach to the bottom of the cavity and penetrate the shell...'. Examination of the extracted radula on a flat surface (Isgrove, 1909), or

the odontophore when the radula is not fully stretched over its surface (Nixon and Boyle, 1982), give a misleading impression of the position of the teeth during rasping. When the radula is tightly stretched over the tips of the odontophore cartilages (Figs. 2, 3) the central teeth erect clear of the lateral teeth; this was also visible in video film of the radula during envenomation and agrees with the nature of the wear on the central compared to the lateral teeth. The pointed narrow shape of the hole closely matches the shape of the central teeth and it is difficult to understand how the tubular salivary duct could have produced this shape. Holes in gastropod shells are more difficult to interpret, however. While the teeth cusps can penetrate these holes to a considerable depth it is not entirely clear what their role is in making them. The appearance of several merged holes suggest that there were several attempts at making the hole and so the contribution of the teeth is obscured.

In all cases the walls of holes had a predominantly smooth surface indicating a major contribution from chemical etching rather than rasping alone. The areas of exposed crystallites at the edges appear to confirm this and there is often some etching around the outside of the hole, particularly on the surface of the *Nucella lapillus* shell where the periostracum can be largely absent. All such evidence indicates that there is a decalcifying effect of the saliva on the inner shell layers. While it is likely that this could be due to secreted acid this has not yet been established.

It can be concluded that the most likely method by which holes are produced through these calcified shells is that the radula is primarily used to remove the organic components of the shell while the saliva removes the calcium carbonate. As decalcification will leave behind the organic rich material surrounding the crystallites these would need to be removed by radula action to maximise the effect of the saliva.

What is the function of the teeth-like processes on the salivary papilla? Envenomation of *E. cirrhosa* indicates that saliva can be ejected at considerable pressure, although it is uncertain what pressure is involved when the papilla is within the hole. If it is ejected into the hole with a comparable pressure then it is necessary for there to be a mechanism for holding the papilla in place while this is happening. The salivary papilla can obviously be expanded by a combination of blood pressure and muscular action so that its wall will come to be

closely apposed to the walls of the surrounding hole. Teeth on the outside of the papilla will both aid its retaining a purchase on the walls and also permit the saliva to pass through the spaces between the teeth. If saliva does pass from the exit at the tip of the papilla and upwards between its outer surface and the wall of the hole between the teeth then there will be fast laminar flow of the fluid through this space, maximising the etching effect of the saliva. A role of this kind would explain the apparently completely unworn nature of the teeth on this salivary papilla and the apparent absence in the underlying epithelium of a mechanism to replace wear to these structures.

Much remains to be studied of this boring mechanism, it is very effective and it remains an interesting problem involving many areas of biological interest. While the radula and saliva are apparently both involved in boring, clearer details of their separate roles must be established. Holes appear to be located in specific regions of the shells of their prey and this must be determined by the handling behaviour of the octopus, but very little is known of this behaviour.

REFERENCES

- Ambrose, R.F., B.J. Leighton and E.B. Hartwick. – 1988. Characterisation of boreholes by *Octopus dofleini* in the bivalve *Saxidomus giganteus*. *J. Zool. Lond.*, 214: 491-503.
- Arnold, J.M. and K.O. Arnold. – 1969. Some aspects of hole-boring predation by *Octopus vulgaris*. *Am. Zool.*, 9: 991-996.
- Ballerig, R.B., M.A. Jalving, D.A. van Tresca, L.E. Hallercher, J.T. Tomlinson and D.R. Wobber. – 1972. *Octopus* envenomation through a plastic bag via the salivary proboscis. *Toxicon*, 10:245-248.
- Boucaud-Camou, E. and R. Boucher-Rodoni. – 1983. Feeding and digestion in cephalopods. In: K. Wilbur and S.M.S. Saleuddin (eds.), *The Mollusca* 5:149-187. Academic Press, New York.
- Boyle, P.R. – 1983. *Eledone cirrhosa*. In: P. R. Boyle (ed.): *Cephalopod Life Cycles* 1: 365-386. Academic Press. London, New York.
- Boyle, P.R. and D. Knobloch. – 1981. Hole boring of crustacean prey by the octopus *Eledone cirrhosa* (Mollusca, Cephalopoda). *J. Zool. Lond.*, 193: 1-10.
- Carriker, M.R. – 1969. Excavation of boreholes by the gastropod, *Urosalpinx*: An analysis by light and scanning electron microscopy. *Am. Zool.*, 9: 917-933.
- Ghiretti, F. – 1959. Cephalotoxin: the crab-paralysing agent of the posterior salivary glands of cephalopods. *Nature*, Lond., 183: 1192-1193.
- Grisley, M.S. – 1993. Separation and partial characterisation of salivary enzymes expressed during prey handling in the octopus *Eledone cirrhosa*. *Comp. Biochem. Physiol.*, 105: 183-192.
- Guerra, A. and M. Nixon. – 1987. Crab and mollusc shell drilling by *Octopus vulgaris* (Mollusca: Cephalopoda) in the Ria de Vigo (north-west Spain). *J. Zool. Lond.*, 211:513-523.
- Isgrove, A. – 1909. *Eledone*. In: W. A. Herdman (ed.), *Liverpool Marine Biology Committee, Memoirs* 18:1-105.
- Mather, J.A. and M. Nixon. – 1995. *Octopus vulgaris* (Cephalopoda) drills the chelae of crabs in Bermuda. *J. Moll. Stud.*, 61: 405-406.
- Nixon, M. – 1979a. Hole-boring in shells by *Octopus vulgaris* Cuvier in the Mediterranean. *Malacologia*, 18: 431-443.
- Nixon, M. – 1979b. Has *Octopus vulgaris* a second radula? *J. Zool. Lond.*, 187: 291-296.
- Nixon, M. – 1980. The salivary papillae of *Octopus* as an accessory radula for drilling shells. *J. Zool. Lond.*, 190: 53-57.
- Nixon, M. and P.R. Boyle. – 1982. Hole drilling in crustaceans by *Eledone cirrhosa* (Mollusca: Cephalopoda). *J. Zool. Lond.*, 196: 439-444.
- Ruppert, E.E. and R.D. Barnes. – 1994. *Invertebrate Zoology*. 6th ed. Saunders. Fort Worth.
- Wodinsky, J. – 1969. Penetration of the shell and feeding on gastropods by *Octopus*. *Am. Zool.*, 9: 997-1010.
- Wodinsky, J. – 1978. Feeding behaviour of broody female *Octopus vulgaris*. *Anim. Behav.*, 26: 803-813.