FEEDING BEHAVIOR OF *NUCELLA EMARGINATA* (GASTROPODA:THAIDIDAE) WHEN PREYING ON MUSSELS

by

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Drill-site and prey-size selection, and the ability to regenerate the proboscis were studied on Nucella emarginata when preying on mussels. These three parameters were investigated in relation to the use of toxic secretions by this neogastropod, as well as to the importance of the accessory boring organ (ABO) in its predatory process. Nucella emarginata consistently preys upon Mytilus edulis smaller than itself, and strongly prefers to attack the mussels along the edges rather than drilling a hole through the shell. Nucella uses a paralyzing agent on the mussel prey during the edge attacks. The toxin is probably derived from the hypobranchial gland. The ABO is of secondary importance in this snail's predatory behavior. The feeding behavior of N. emarginata is consistent with its overall ability to reduce time during its predatory activity and to minimize its exposure at low tide.

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TO THE MEMORY OF MY FATHER
EDUARDO GOMEZ-CORNEJO C.

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CHAPTER I

INTRODUCTION

Nucella emarginata (DESHAYES, 1839) is one of the most common carnivorous snails on the rocky shores of the Pacific coast of North America. It occurs over a wide variety of exposure conditions (from high energy shores to quiet bay waters) from Alaska to northern Baja California (MORRIS et al., 1980; RICKETTS et al., 1985). It is a member of the family Thaididae (KOOL, 1987, 1988; SMITH & CARLTON, 1975) or Nucellidae (e.g., KOZLOFF, 1987) in the superfamily Muricacea.

The diverse diet of *N. emarginata* includes largely sessile invertebrates: barnacles (*Balanus glandula*, *Semibalanus cariosus*, *Chthamalus dalli*, *C. fissus*, *Pollicipes polymerus* and *Tetraclita rubens*) and mussels (*Mytilus edulis* and *M. californianus*) (PALMER, 1984; PARIS, 1960; WEST, 1986). To a lesser extend *N. emarginata* may also attack snails such as *Littorina*, *Acmaea* and *Collisella* (SPIGHT, 1981; WEST, 1986). The two species that represent the largest percentage of its diet are *M. edulis* and *B. glandula*, which promote relatively higher body growth in *N. emarginata* (PALMER, 1983). When both barnacles and mussels are available, *N. emarginata* prefers musssels (SPIGHT, 1981).

Nucella is a non-visual predator, and relies solely on chemical and tactile cues to detect its prey (PALMER, 1984). This

chemoreceptive capability resides in the osphradium (KOHN, 1983). Prey items can be detected at a considerable distance (CARRIKER & VAN ZANDT, 1972a; MORGAN, 1972; PRATT, 1974; WOOD, 1968).

The process of penetration through the calcareous shell of the prey by the muricacean and naticacean snails, the two most important hole-boring gastropods, in order to gain access into the flesh of the prey, has been summarized by Carriker (1981). This process is a cyclic two step mechanism that alternately involves radula and the accessory boring organ (ABO). The mechanical portion is performed by the radula that moves over the cartilaginous odontophore in a back-and-forth motion, operating as a band-over-a-pulley (CARRIKER, 1943; GUNTER, 1952), in the buccal mass at the tip of the proboscis. The proximal bulb-shape end of the long radula sac, where the radular teeth are formed, projects freely towards the hemocoel of the snail (CARRIKER, 1943; HEMINGWAY, 1973a, b; HYMAN, 1967). In addition, the odontophore is able to rotate by muscular action at least 180 degrees to the right or to the left, in such a way that it covers the whole circumference of the drill-hole (CARRIKER, 1981).

The chemical portion involves the ABO. This gland is located in the mid-ventral sole of the foot in the muricaceans, and under the tip of the proboscis in the naticaceans (CARRIKER, 1981). The muricacean ABO is a small disc that projects and poses on the incomplete hole, deposits its secretions and is retracted back to its original position in the tubular vestibule. The shape and size of this gland determines the shape and size of the hole (CARRIKER & VAN ZANDT, 1972a). Carriker found the ABO in 33 species of boring gastropods (muricaceans and naticaceans) from around the world, including the thaidids N.

emarginata and N. lamellosa. The chemical step is longer than the mechanical step in every radular rasping cycle (CARRIKER, 1981; CARRIKER & VAN ZANDT, 1972a).

It has been hypothesized (CARRIKER & WILLIAMS, 1978) that these shell boring predators use a combination of enzymes, an inorganic acid and chelating agents in a hypertonic medium, to dissolve the calcareous structure of the shell. Smarsh et al. (1969) have already shown the presence of carbonic anhydrase (CA) (an enzyme that catalyzes CO2 + H2O = H2CO3) in the active and inactive ABO of Urosalpinx cinerea, as have Chetail and Fournie (1969) in the ABO of Nucella lapillus. Although CA is largely required in the shell dissolution process during boring by U. cinerea, it has not been confirmed as the direct demineralizing agent (CARRIKER & CHAUNCEY, 1973).

Both the whole organ complex of the buccal mass in the proboscis and the ABO were able to be completely regenerated after artificial amputation in the muricids Urosalpinx and Eupleura (CARRIKER at al., 1972; CARRIKER & VAN ZANDT, 1972a), and Thais haemastoma (DEMORAN & GUNTER, 1956; GUNTER, 1968, 1979). The very effective response of the molluscan immunological defenses in cases of wounds is well known (BAYNE, 1983). Radwin and Wells (1968) have found abnormally short radulae in some specimens of I. floridana and Carriker and Van Zandt (1972a) in individuals of U. cinerea, from the field, which suggests that they were able to regenerate the proboscis after its amputation by natural means.

Different aspects of the feeding behavior of predatory muricaceans when attacking bivalves have been described (CARRIKER &

VAN ZANDT, 1972a; CARRIKER et al., 1974; FRETTER & GRAHAM, 1962; HUGHES & DUNKIN, 1984, HUGHES & DREWETT, 1985; HEMINGWAY, 1973). After the snail has positioned itself in a suitable place on the shell of the prey, the proboscis is extended out of the mouth ready to drill, and the proboscis is enveloped by the lobes of the propodium (the front part of the foot). It is thus virtually impossible to observe the actual process of shell penetration unless artificial methods are used. Immediately after the drill-hole is completed the predator inserts the proboscis through the hole and starts tearing pieces of flesh by radular action, swallowing them through the proboscis and into the oesophagus. The proboscis in boring prosobranchs is as long as the shell height (CARRIKER, 1981), which allows them to reach the soft body of the prey in a wide radius. Hughes and Dunkin (1984), Hughes and Drewett (1985) and Menge (1974) have concentrated on the foraging aspects of the predatory behavior of neogastropods.

Carefoot (1977), Carriker (1981) and Kohn (1983) noted that the mechanism by which a boring gastropod selects a specific site to drill is unclear. Some attempts have been made, however, and possible explanations advanced (ANSELL & MORTON, 1987; BERG & NISHENKO, 1975; BLACK, 1978; EDWARDS & HUEBNER, 1977; HUGHES & DUNKIN, 1984; NEGUS, 1975; PALMER, 1980, 1982, 1988; VERMEIJ, 1980, 1987; WICKENS & GRIFFITHS, 1985).

The presence of choline esters in muricaceans has long been known. It is concentrated in the hypobranchial gland (HG) (Appendix A), which is located in the roof of the mantle cavity (HYMAN, 1967). Dubois (1909, cited in Hemingway, 1973a:3) suggested that a toxin from the HG could be used by the snail to aid in the predatory process.

Several authors have presented experimental or circumstantial evidence that a toxin secreted by the gastropod relaxes, paralyzes, anesthetizes or kills the prey. Examples include Acanthina algelica (MALUSA, 1985); A. spirata (HEMINGWAY, 1973a); A. punctulata (MENGE, 1974; SLENDER, 1981); N. canaliculata, N. emarginata, N. lamellosa and N. lima (PALMER, 1980, 1982, 1983); Ocenebra lurida (PALMER, 1988) and Thais haemastoma (GUNTER, 1968, 1979). The presence of toxins in the HG or salivary glands (SG) in non-drilling gastropods (Buccinidae, Conidae, Cymatiidae, Cassidae) has been reported (CORNMAN, 1963; DAY, 1969; ENDEAN, 1972; HOUBRICK & FRETTER, 1969; RUSSEL, 1984).

Other workers have concluded that the muricaceans Concholepas concholepas (CASTILLA, et al.,1979), Murex fulvescens (WELLS, 1958), N. lapillus (BARNETT, 1979; LARGEN 1975; MORGAN, 1972), and Nucella spp. (CAREFOOT, 1977), use the strength of the foot in order to access the flesh of prey items such as barnacles or mussels. Behavioral observations made by Carriker and Van Zandt (1972a) did not confirm the hypothesis of a venom or toxin in U. cinerea when preying on oysters. In addition, Palmer (1980, 1983) indicated that for Nucella the toxic saliva is only useful when preying on barnacles to reduce handling time, but not when consuming mussels.

The present research sheds light, particularly, on the last component of the feeding behavior of N. emarginata when preying on mussels; that is, attacking the prey (HUGHES & DUNKIN, 1984). I have studied the drill-site selection in the laboratory as well as in the field; the technique this thaidid uses to gain access into the mussel (mechanical or chemical), the effect of the HG extract on the behavior of the mussel, the regeneration rate of the proboscis after artificial

amputation, the possibility that the snail may lose part of the proboscis (with the buccal mass) in the field, and, finally, the importance of the ABO in its predatory behavior.

CHAPTER II

MATERIALS AND METHODS

Study Area

Field observations and sample collections were made on the concrete pilings under the semi-protected Oregon Institute of Marine Biology dock (OIMB dock). This area bears mixed populations of barnacles (Balanus glandula, B. cariosus and Pollicipes polymerus) and small to medium sized mussels (Mytilus edulis and M. californianus) together with a variety of other typical rocky intertidal invertebrates. The two most conspicuous invertebrate predators here were the neogastropod Nucella emarginata in the mid and upper intertidal level, and the asteroid Pisaster ochraceus in the lower zone. No other gastropod predator occurs at this site. The sea water temperature varies between 10 and 12.8 degrees centigrade (C) throughout the year (US Department of Commerce, 1986).

General Methods

Experiments were performed in flow-through sea water tables. The experimental animals (Mytilus edulis and Nucella emarginata) were maintained, unless otherwise indicated, in permanently submerged

plastic containers of different sizes whose walls had perforations for water circulating. The containers were covered with transparent plexiglass lids. The water temperature was 11 to 12 degrees centigrade.

Only healthy, fresh mussels were used in the experiments as prey for the snails. The criteria for healthy mussels were: 1) normal valve gaping, and 2) the ability to form byssal threads. Only mussels lacking previous radular marks on the shells were offered to the snails.

Snail shell height (or size) represents the distance from the apex to the tip of the siphonal canal. Mussel size is the length of the longitudinal axis of either shell.

As controls for the mussels' death rate in the experiments I used 5 to 25 mm mussels (the same size range as used in the treatment experiments) in groups of 50 to 100. These were placed in plastic containers in the same water table for two to four weeks. Considering that the death rate for the control mussels was less than 2%, that they were put in the containers directly from the field, and that the experimental mussels were checked for health condition, then the death rate for the experimental mussels will be assumed as zero.

For experiments where mussels were glued to a substratum, the controls consisted of six to eight small mussels glued by the center of one valve to the outside wall of 10 cm plastic petri dishes. "Krazy Glue" (instant glue, cyanoacrylate) provided excellent results when attaching the mussels to plastic or non-porous pieces of gravel. A portable electric drill with interchangeable drills (from 0.5 to 1.0 mm) was used to make the artificial holes on the mussel shells.

Drill-site and Prey-size Selection in the Field

For the purpose of studying the drill-site selection by N. emarginata in the field I collected empty mussels from different sites at the OIMB dock and nearby places during several low tides (March 11 and 18 (two samples), and April 02, 08 and 09). Broken or eroded shells, as well as single valves, were discarded and only the empty shells most recently preyed upon were considered.

In the laboratory the shells were checked for evidence of radular attacks. These were recorded on a "prototype" mussel figure and the approximate relative shell thickness at the attack site was noted, based upon the 1 to 10 scale of Carefoot (1977) for small to medium size M. edulis. In this scale the thickest site is the umbo (10), followed by the hinge (8), the posterior region of the hinge where the valves start merging (6), the region immediately posterior to the umbo (5), and the center (4), narrowing in thickness toward the posterior edge (1) following the direction of shell growth. The thickness at the ventral edge is equivalent to 2.

While small M. californianus may be thicker than M. edulis (HARGER, 1972), I used the same scale for both species, as this is a relative scale, and the thickness of the shells of these two species may not differ significantly for the same shell regions. In addition, due to the selective preference by N. emarginata on M. edulis over M. californianus (HARGER, 1972; SUCHANEK, 1978; personal observations) this problem was limited to a very low number of mussel shells (more than 95% were clearly M. edulis). That is, less than five percent of

the empty shells were M. californianus or were undeterminable due to the difficulty in telling apart one species from the other when the mussels are very small (SUCHANEK, 1978).

In order to study prey-size selection in the field I observed snails in actual predatory attitudes when attacking mussels. The sizes of snail and mussels were recorded.

Drilling-site Selection in Relation to Mussel Size

This experiment was design to test whether there was a similar pattern of selectivity considering the drilling-site on the preyed mussels among different age-classes of Nucella emarginata.

Three age-classes of N. emarginata were used: small (6-8 mm), medium (11-13 mm) and large (17-19 mm). The snails were placed individually in plastic containers immediately after being collected from the field.

Medium (M) and large (L) snails were placed in plastic compartments of about 0.8 l; small (S) snails were in containers of about 0.03 l. Ten snails were used for each of the two larger age-classes and 16 for the smaller class. I offered about 10 to 15 mussels per snail, in the range of 5 to 15 mm in size for the S, and 10 to 22 mm for the M and L snails.

Every 10 days the containers were checked and empty mussels retrieved, labeled individually and stored for analysis. Live mussels were then added to maintain the same quantitative availability for each snail. The experiment was run three weeks for the L, and six weeks for the M and S snails.

At the conclusion of the experiment, the size of the preyed mussels, type of radular attack and valve attacked (right or left) were recorded. The following categories were used for attack type: holes, small holes (which clearly could not have allowed the proboscis to penetrate because they were at the center of an incomplete drill-hole; these were very few and commonly found on the posterior margin), radular raspings or scratches (on the margin), and edge notches. Radular raspings far from the edges and incomplete drill-holes were not counted since they by themselves do not constitute a potentially mortal attack on the mussel.

Physical Strength or Chemical Means Used by the Snail to Gain Access into the Mussel

Notches, of a small fraction of a circumference, are commonly found along the posterior edge of the mussels preyed upon by N. emarginata. These notches leave a space too small to allow the snail's proboscis to penetrate when the valves are tightly closed.

The following experiment was then designed to test whether N. emarginata, when not drilling, uses the strength of its foot or a paralyzing secretion (applied or injected into the mantle tissue) to open a mussel's valves

In a 20 l aquarium connected to a running sea water system, a 1 l rectangular plastic container was placed on its side with the open top against a wall of the aquarium, so that it was easily observable from the outside (Figure 1). This "cage" was divided into two compartments with a piece of 1.6 mm thick plexiglass board, in such a way that the board was horizontal and perpendicular to the aquarium

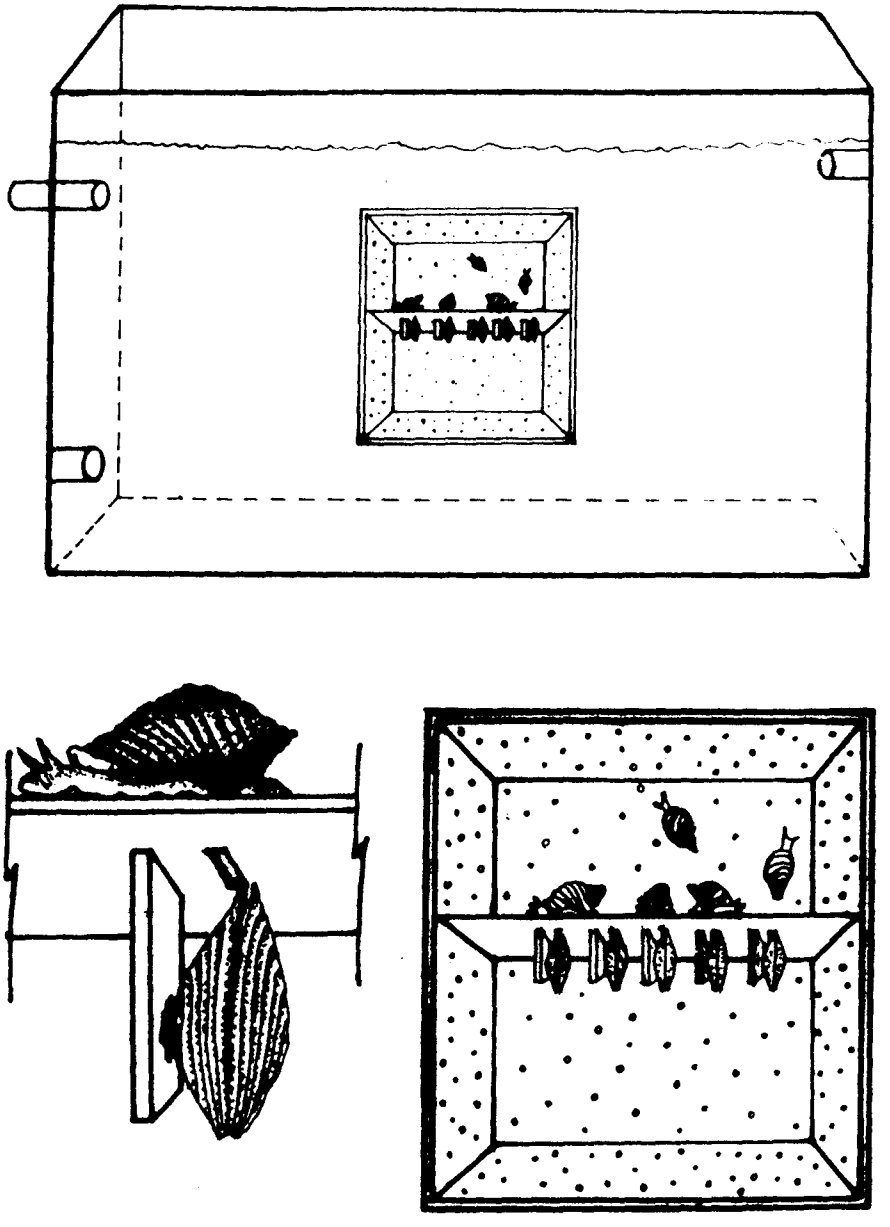

FIGURE 1. Experimental design to investigate whether N. emarginata uses physical strength or chemical means to gain access into the mussel.

wall. The dividing plastic had 5 parallel rectangular slits (perpendicular to the aquarium wall) of about 1.5 x 7.0 mm.

Five 20 mm M. edulis were glued by the left valve to individual small rectangular pieces of 1.6 mm thick plexiglass. Then, each of these were glued underneath the board in such a way that the posterior edge of the mussel was located underneath one of the slits of the board and about 2 mm from the board. The ventral edge of the mussel faced the aquarium wall. The mussels were placed slightly toward the right of the slit, such that if the snail could put its foot through the slit, it only had access to the left valve.

After checking the normal behavior of the mussels for several hours, I released 4 or 5 snails in the upper compartment allowing them to search and make contact with the mussels. This experiment was run twice, using a different set of snails each time. During an additional (third) trial I used a video camera to record predatory events. For this purpose a video camera (QUASAR VHS movie X8 auto focus) with close up lenses (PRINZ 49 mm #4) was placed in front of the aquarium.

Effect of Hypobranchial Gland Extract on Mussel Behavior

The effect of an extract of the hypobranchial gland of N. emarginata on the behavior of small M. edulis was examined. These extracts were injected in the pallial cavity. As controls I used extracts of foot tissue and filtered (through 30 um filter) sea water (in all treatments referred to as sea water).

Twenty large (18 to 22 mm) N. emarginata were sacrificed by carefully breaking their shells, and their hypobranchial gland (HG),

together with some surrounding tissue (in a volume ratio of about 1:1), were dissected, and pooled in a 10 ml beaker. Small pieces of foot were removed from the same snails and pooled in other 10 ml beaker. In each case the tissues were homogenized in 2 ml of sea water. The pooled tissues of the HG corresponded to 0.10 gr in weight and to 0.20 gr in the case of the foot. Four ml of sea water were added to the homogenates. These preparations were then centrifuged at 12000g for 10 minutes in a refrigerated centrifuge. The extracts were maintained on ice (2-3 C) until used.

To select 22 experimental mussels (8 for HG, 8 for foot and 6 for plain sea water treatments), I glued 50 small M. edulis, of 20±1 mm in length, with the posterior margin upwards on individually numbered pieces of gravel. These were then submerged in the sea water tables. The 22 mussels with the most uniform behavior (in terms of valve motion and intervalve distance), were selected for the experiment.

The mussels for each treatment were chosen at random, and placed at random in 4 rectangular uncovered plastic baskets, five or six mussels per container. The mussels were located about 12 cm apart. The baskets were about 15 cm apart (Figure 2).

Extracts or sea water injections (of 10 to 12 C) of 0.2 ml were delivered into the mussel's pallial cavity, without damaging the tissues, using a 1 ml syringe with a 23G needle. The pallial cavity of such small mussels is large relative to a 0.2 ml injections. At the same time the cavity is full of water and thus at the moment of the injection most of the solution may flow out of the pallial cavity. For these reasons injections were slowly (10 to 15 seconds) administered

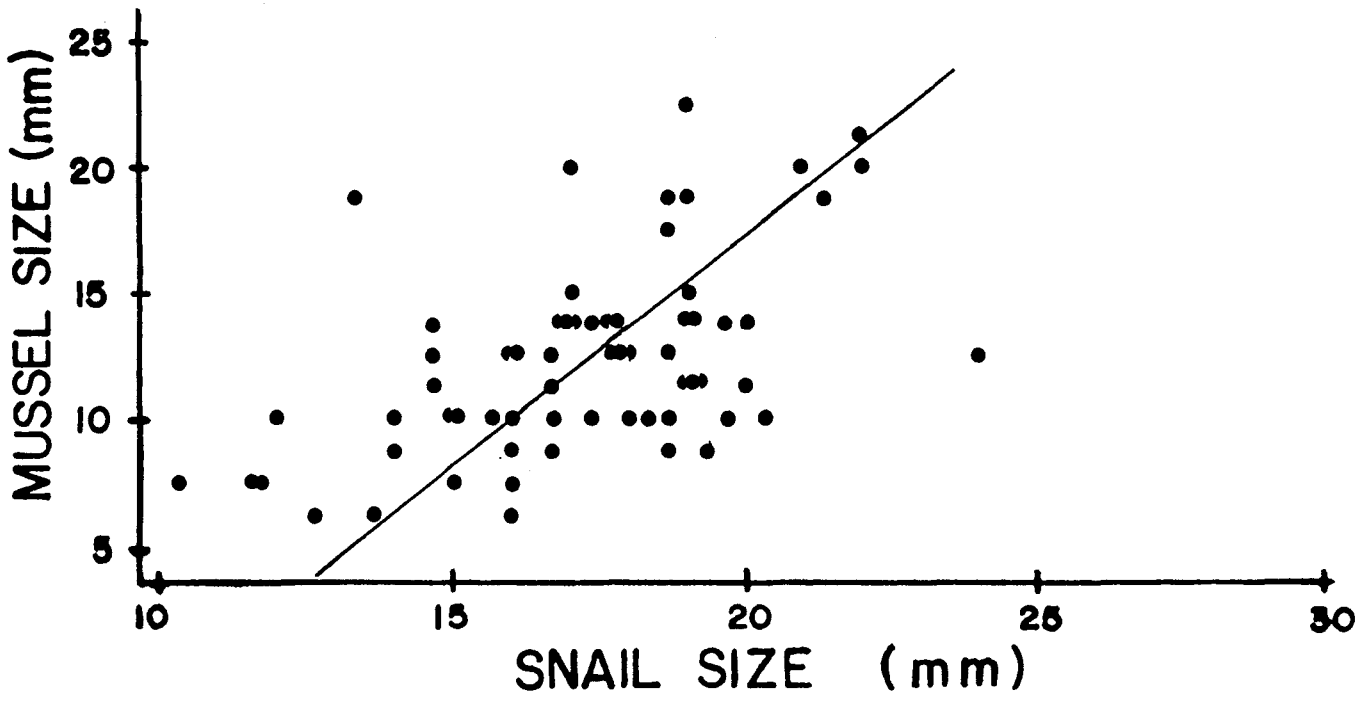

FIGURE 2. Experimental set up to test the effect of the hypobranchila gland extract of N. emarginata on the mussel's behavior. (Each circle represents a mussel glued to a piece of gravel; H=hypobranchial gland extract; F=foot; W=plain sea water; C=extra control out of the containers (no treatment))

in order to allow the active components of the solution to make contact with the mussel's tissues.

After the injection, the mussels were tested for their response. The mussel's mantle was gently stimulated with the tips of steel forceps. I then waited for 15 seconds to see how fast or slowly the valves shut and open, and also how widely the valves remained when gaping. The behavior of the experimental mussels was compared with that of six other mussels that did not receive any treatment (non-treated control mussels). The latter ones were in the same water table.

The resulting response by the treated mussels was recorded on a scale of "0" to "4": "4" corresponded to a response similar to non-treated control mussels; "0" was recorded when the valves remained tightly closed for the observation period before the application of the stimulus; "1" to "3" were thus increasing degrees of response between these extremes.

These observations began one hour after all injections were administered, and continued for every mussel for 2, 3, 4, 8, 12, 18, 24, 36, 48, 60, 72, 84, 96, 120 and 144 hours thereafter.

A preliminary experiment was performed in order to test the effect of the crude HG extract of N. emarginata when injected in the posterior adductor muscle (PAM) of small (20 to 25 mm) M. edulis. Five large N. emarginata were sacrified and their HG dissected and pooled in 3 ml of sea water, homogenated but not centrifuged. A 0.1 ml injection of the extract was administered with a 1 ml syringe (and 26G needle) into the PAM of seven mussels and in the pallial cavity of five mussels. As controls I used four mussels to which 0.1 ml of sea

water was injected into the PAM. The 16 experimental mussels (glued to individually numbered pieces of gravel) were scattered in an area of 15 by 60 cm, submerged in the sea water table. The observations on the responsiveness of the mussels (probing the mantle tissue with the tips of a small steel forceps), started 30 minutes after the injections were administered. These observations continued for 2, 10, 24, 72 and 96 hours thereafter. For this preliminary test, during each individual observation I recorded the responsiveness of the mussels, I paid particular attention to the difference between the prolonged valves closure and the gaping paralysis (unresponsive condition).

Proboscis Regeneration after Experimental Amputation

It has been reported that other muricacean species possess the ability to fully regenerate the proboscis (after artificial amputation), as an adaptation for the risk of losing the proboscis they face during the feeding process in the field. These experiments focus then on the ability of Nucella to recover (successfully feed) from the removal of the proboscis and associated buccal mass (and occasionally the radular sac itself). These "proboscisectomies" were performed as described below.

Eight live M. edulis (20 to 25 mm in size) were split by the hinge ligament, leaving each valve with its whole flesh. At the center of each valve a 1 mm hole was electrically drilled. Each of these valves, with the flesh side upward, were put on top of each of sixteen 3 mm holes made in a rectangular piece of 1.6 mm plexiglass of the size of a plastic ice cube tray. This plexiglass was then placed

tightly over a plastic ice cube tray. Each of the 3 mm holes corresponded to the center of each of the 16 divisions of the ice cube maker (Figure 3). Sixteen snails (six small and 10 medium to large) were then placed in individual divisions of the ice cube tray. The ice cube tray, plexiglass board and mussel valves were firmly kept in place with rubber bands.

Within 12 hours several Nucella had their probosces exposed through the holes and were eating the mussel flesh by "chunks". The buccal mass in feeding motion is clearly distinguishable, due to its reddish color and the transparent tissues of the proboscis sheath.

In these circumstances, with the use of a fine scalpel, I proceeded to excise the exposed probosces of the snails. For this experimental set up small (10 cm long) iris scissors did not work as well as the scalpel. Carriker (1972) used iris scissors to perform a proboscisectomy in the muricaceans Urosalpinx and Eupleura, and also observed that the retraction of the proboscis of those snails was significantly slower after they were eating (oyster flesh) for a long while, so the proboscis was easier to cut. This "slowing down" was not clearly noticeable in N. emarginata.

All the cut probosces tips were kept in labeled vials with 10% neutralized formalin for further examination. In all cases the buccal mass was found, and in some cases the whole radula sac was included. The snails with amputated proboscis were individually kept in submerged containers of 400 cm3. From the moment of amputation they were offered ad libitum mussels M. edulis of 5 to 25 mm in size.

The snails were checked every two days and, after the 20th day, every day to see if they were in a predatory position and to verify if

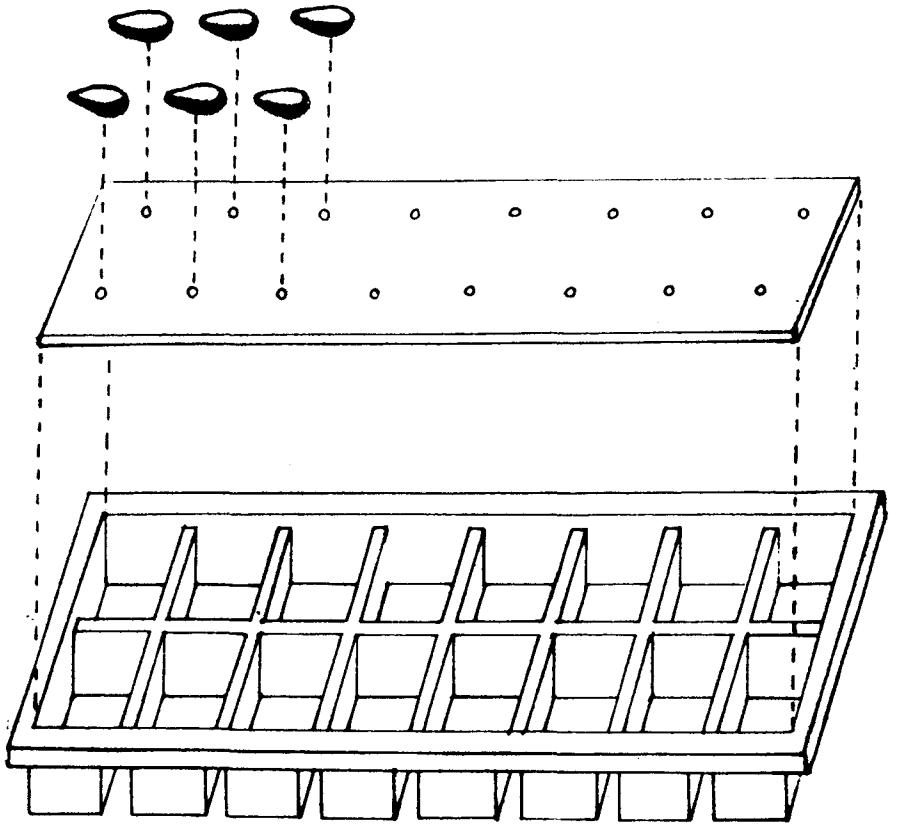

FIGURE 3. Method of proboscis amputation in N. emarginata

they were drilling, or, at least, starting to make radular scratchs on the surface of the mussel shell. Empty preyed mussels were individually labeled with a permanent marker and stored for further analysis.

Twenty N. emarginata in the same range of sizes of the operated snails were collected from OIMB dock. They were then sacrified in order to measure the length of the buccal mass and radula for comparison with those of the operated snails (in case regeneration occurred). The radula was measured from the tip (distal end) of the buccal mass to the proximal end of the radula sac. Measurements were made with an ocular micrometer.

Loss of the Proboscis in the Field

The purpose of this experiment was to determine the probability of N. emarginata's losing the proboscis by natural means.

In May 1989 I collected 175 snails and sorted them into three groups: 10.0 to 13.5 mm (N=47), 13.6 to 17.0 (N=57), and 17.1 to 20 mm (N=71). I split each group in two and put each subgroup in a separated plastic container of about 2 l with live mussels. These mussels (50 to 60 per container) were glued, uniformly spaced, to the walls and bottom of the containers. The size range of the mussels was about the same as the size of the snails from each group. I used this size relationship, and not smaller mussels, to avoid the possibility of finding a mussel totally eaten, and the snail already away from the preyed mussel. Had the latter occurred I would not have been able to detect the snail in a predatory what would have not let me detect it

in predatory attitude given the time interval between observations.

Every 6 hours thereafter I checked for the snails that were in a predatory posture and actually drilling or eating the prey. I checked for any of these three situations: 1) with the fore foot over the shell and an incomplete drill-hole underneath, 2) with the proboscis inserted through a hole, or 3) with the proboscis inserted between the valves. The mussel was then taken out from the container and the snail measured and segregated.

All remaining snails that were not clearly drilling or preying after three days of observations were dissected in order to examine the condition of the proboscis and/or absence of buccal mass as evidence that these structures were lost in their natural habitat.

Importance of the Accessory Boring Organ (ABO) in the Predatory Process of N. emarginata

The ABO has been found in all the shell boring neogastropods in which this gland has been sought. Considering the critical importance of this organ in shell boring neogastropods and the preference of N. emarginata for attacking mussels along the shell edges, occasionally without leaving any evidence of attack on the mussel's shell, the following experiment was performed to test the degree of importance of the ABO for this thaidid.

The ablation of the ABO was performed on several mid-size (11.5 to 15.5 mm) N. emarginata anesthetized in 7.5% MgCl2 for 2 to 4 hours. After the animals were totally relaxed the operculum was gently pulled out to expose the foot sole in an upward position. (The operculum is kept out and against the snail's shell with the help of the thumb nail

of the hand that is holding the snail). When the whole sole was exposed, creases in the anterior mid-ventral region of the foot sole, converging to a deep depression, indicated the location of the opening of the ABO vestibule. Another depression located immediately posterior to the one of the ABO is found in females. This is the ventral pedal gland or egg capsule gland (Carriker, 1981). In the depth of the vestibule (about 3 mm long in large snails) the pedunculate gland is located.

The sharp tips of curved fine forceps are introduced into the vestibule and the ABO, about 1 mm in diameter, is pulled out. The snails were then measured and numbered with a permanent marker after the shell was dried with paper towel. After the operation the snails were placed back in running sea water for recovery.

Eight ABOdissected snails were used as experimental animals. Five N. emarginata of the same size range, anesthetized but not operated on, were used as controls. These two groups were placed in two different compartments of a submerged 2 l container, together with mussels (8 to 18 mm) ad libitum. The snails were checked every day to see if they were preying and to determine the precise method of attack. The time from introduction (to containers) to the first incidence of predation, and the method of attack, were recorded.

CHAPTER III

RESULTS

Drill-site and Prey-size Selection in the Field

More than three-quarters of the mussels (78.4%, N=282) were attacked along the edges by means of a small semicircular (less than one fourth of a circumference) notch made by the radula. Holes were drilled in 21.6% of the mussels ($X^2=90.78$, $P<.001$). In very few cases only an incomplete drill-hole, with a small perforation at the center that would not allow the proboscis to penetrate, was observed (Table 1).

Locations of the snails' attacks are shown in Figure 4. The notches are concentrated at the opposite edge of the pedal gape, and the holes are far from the margins. The mean size of the mussels with holes (Table 2) was significantly greater than the mean size for the mussels with notches (Two-Way ANOVA, $P=.007$ for site vs way of attack interaction).

A varying percentage of empty mussel shells (16.9 to 43.2%) was found with no evidence of potentially mortal radular nor any other means of attack.

Eight (2.0%) of the 393 mussel shells from the field showed recent multiple attacks (more than one), in combinations of

TABLE 1. Mussels collected at the OIMB dock during low tides of March and April of 1989, preyed upon by *N. emarginata*. (H=hole through the shell; E=edge notches, marginal small holes and marginal radular raspings; N=number of empty mussels; X= mean size of mussels; S= standard deviation; all measurements are in mm).

	MUSSELS					
	MEANS OF ATTACK					
SAMPLES	H			E		
	N	X	S	N	X	S
Mar11	9	11.3	4.4	35	9.6	2.6
Mar18(1)	14	16.5	4.9	27	15.7	3.5
Mar18(2)	10	11.9	1.8	98	11.7	2.4
Apr02	2	19.8	1.1	23	11.3	5.4
Apr08	17	19.2	3.3	26	14.2	3.5
Apr09	9	20.9	5.9	12	20.5	3.8
TOTAL	61			221		

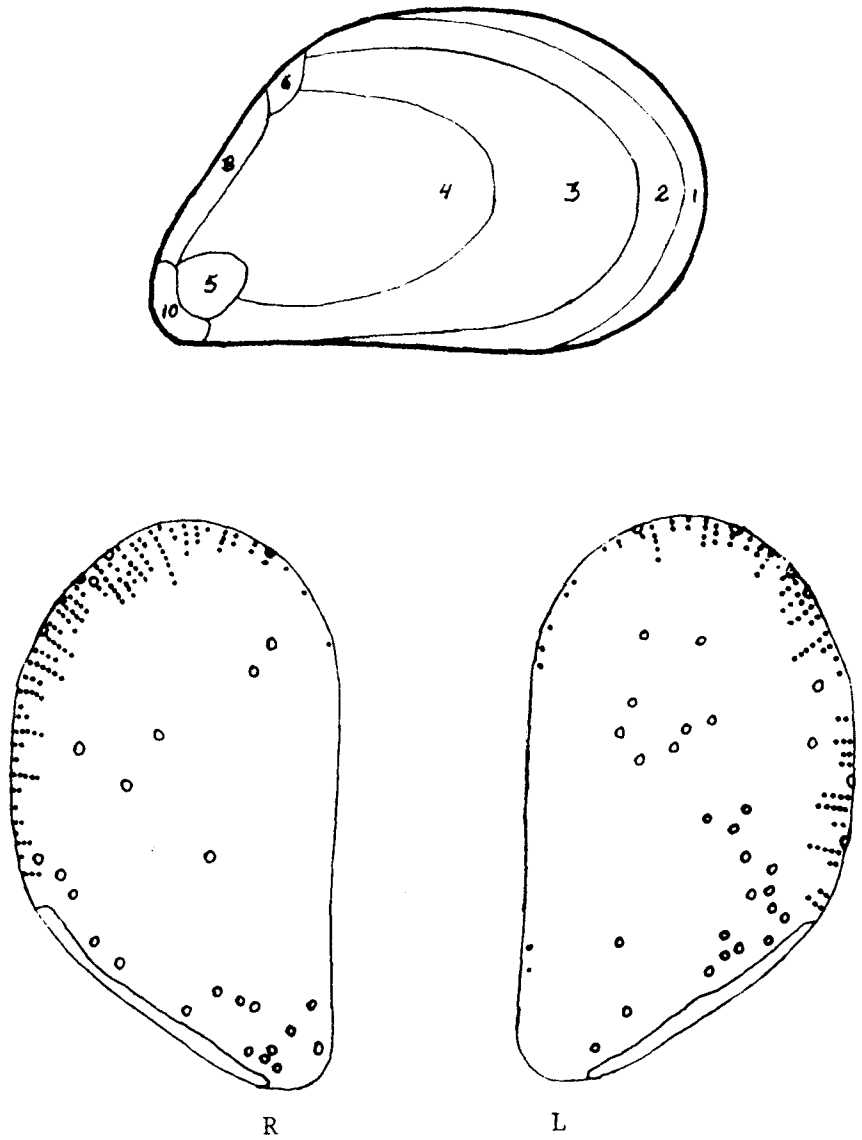

FIGURE 4. Drill-site selection in the field. (Upper shell=relative thickness in M. edulis shell; lower shells: circles=drill-holes, points= edge notches in a site perpendicular to the edge; R=right valve; L=left valve)

TABLE 2. Mussel size vs snail attack mode collected from OIMB dock. Two way ANOVA. (df=degrees of freedom; F=F distribution; P=Probability).

SOURCE	df	F	P
site	5	30.786	.000
attack	1	15.278	.000
site X attack	5	3.237	.007
error	270		

two holes, two notches, or one hole and one notch; two of these cases had three attacks. I have only seen on two occasions (of 163 observations) two N. emarginata feeding on the same M. edulis.

With respect to the preference of N. emarginata for size of prey (Figure 5), a simple linear regression showed that larger snails prey on larger mussels (ANOVA, F=23,13, P<.001). The mean size of snails was smaller than mean mussel size (t-value=9.12, df=62, P<.001).

Size-class Drilling-site Selection

Statistical analysis (pairwise contrast of One-Way ANOVA for the three attack modes: holes, edge and non-radular attack) showed (Table 3) that the mussels with complete holes were significantly larger than those with notches, as well as the mussels with no evidence of attack, for both the small and medium N. emarginata (Table 4).

Large snails drilled a complete hole in only one of the 97 mussels. Since the size range of mussels offered to the medium snails

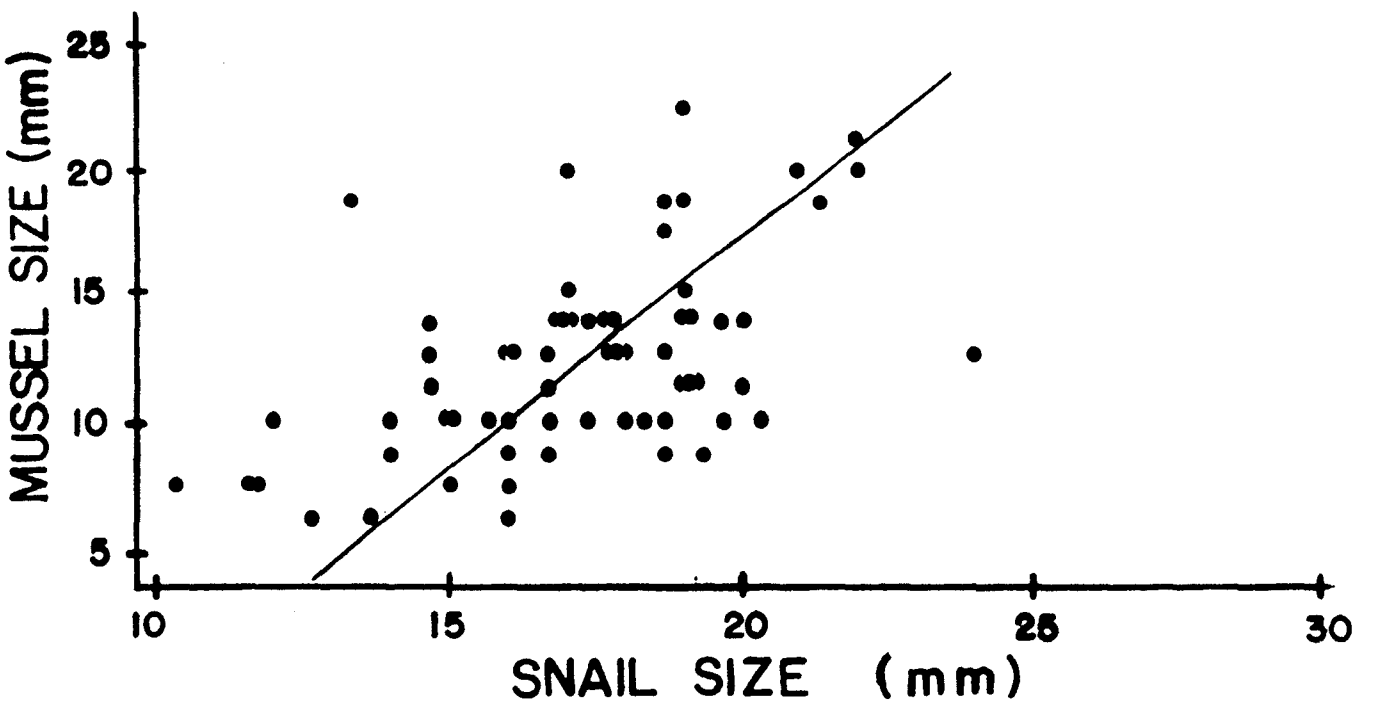

FIGURE 5. Simple linear regression for the relationship between the size of the N. emarginata and size of mussel prey in the field.

TABLE 3. Age-class drilling-site selection. (R=right valve; L=left valve; M-A=means of attack; n=no evidence of radular attack; X^2=chi-square value comparing shell attack frequency; the rest of the symbols as in pevious tables)

SNAILS	M-A	MUSSELS PREYED			VALVE ATTACKED		X^2	P
		N (%)	X	S	R	L		
	H	190 (60)	10.6	2.2				
SMALL	E	96 (30)	8.8	2.0				
	n	31 (10)	9.0	1.9				
	Total	317(100)	9.9	2.3	140	140	.000	1.0
	H	77 (28)	16.1	3.9				
MEDIUM	E	152 (55)	12.5	3.2				
	n	46 (17)	14.3	4.2				
	Total	275(100)	13.8	3.9	114	105	.369	>0.5
	H	1 (1)	15.8	0.0				
LARGE	E	78 (81)	14.0	3.6				
	n	18 (18)	15.4	4.8				
	Total	97(100)	14.2	3.8	45	33	1.846	>0.1

TABLE 4. Pairwise contrasts (one-way ANOVA) of mussel size with different attack modes for two size classes of *Nucella emarginata*. (Symbols as in previous tables)

	df	F	P
SMALL SNAILS			
H vs E		49.553	.000
H vs n	314	16.385	.000
E vs n		0.220	.638
MEDIUM SNAILS			
H vs E		54.571	.000
H vs n	272	8.532	.004
E vs n		8.443	.004

was the same as that for the large ones, then for the medium snails the mussels were relatively larger with respect to the size of the snail than for the large ones. Therefore, the preference for the snails to attack along the edges in smaller mussels is also reflected in this size class.

Neither size-class showed a significant predilection to bore one or the other valve (Goodness of Fit Test, Table 3).

For each of the three size groups there was a certain percentage of mussels (10, 17 and 18%, for small, medium and large snails, respectively) killed without leaving any evidence of radular attack.

Physical Strength or Chemical Means Used by the Snail to Gain Access into the Mussel

Nine of the ten mussels (two replicates pooled) were consumed. Six bore a small notch on the posterior edge of the left valve; three showed no signs of attack. I observed the mussels to remain with their valves gaping open while the snail consumed the tissues (by tearing off chunks with radular strokes). The snails had physical contact with only one valve (the left one) of the mussel during the whole predatory process. (In one case a snail was able to get access slightly to both valves with its propodial lobes).

About 80 to 100% of the soft parts of the mussels were consumed. The whole feeding process, from the time the snail accessed the left valve of the mussel with its propodium the until the snail finished eating, lasted 13 to 24 hours. The last portion of flesh eaten by the snails, or left partially consumed, was usually the posterior adductor muscle and remains of the mantle rim.

During an additional (third) replicate (not considered among the results above), I segregated one of the mussels after it had been under attack by a snail for two hours. The mussel did not show tissue damage, even though did not respond to mechanical probing with metal forceps tips on the mantle tissue. After about three days in running sea water (during which time it was gaping open), the mussel responded to the forceps' stimulus and returned to normal valvular movements. It took days for the mussel to recover its ability to form byssal threads. I have observed the same phenomenom a number of times in small mussels which did not suffer significant tissue damage after being preyed upon by N. emarginata.

Effect of Hypobranchial Gland on Mussels Behavior

There is a strong response in the mussels that received the hypobranchial gland (HG) extract injected in the pallial cavity, in contrast to the mussels that received either of the control (foot and sea water) solutions (Figure 6, wherein I average the degree of response of all the mussels for each time observation, with standard error bars). Although the response was strong in the former case, there was no apparent paralysis in the experimental mussels, whose valves remained closed much than the control mussels. There did not appear to be a correlation with circadian rhythms (AMEYAN-AKUNFI & NAYLOR, 1987).

The HG extract is light green. A perceivable amount of green mucus was produced by six of the eight mussels that received the HG treatment. It would appear that the mussels eliminated some amount of

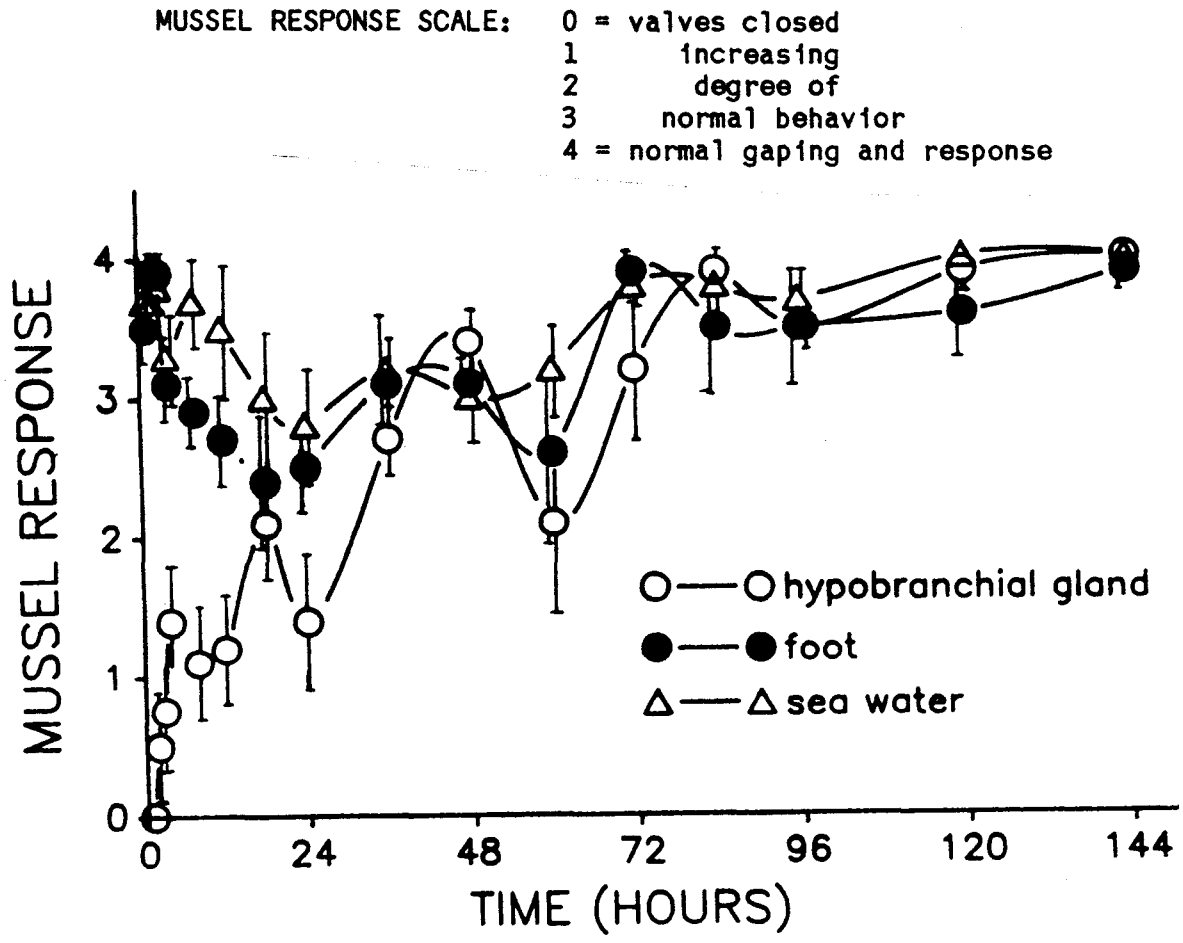

FIGURE 6. Experiment to test the effect of the hypobranchial gland extract of N. emarginata on the behavior of M. edulis. (The vertical bars represent the standard errors)

the HG extract in gill-produced mucus as pseudofecal material. No mucus was produced by control mussels. I have also observed a fairly large amount of mucus whenever Nucella attacked the mussels along the edges, although this mucus was not green.

After about 24 hours (Figure 6) the HG-treated mussels were reacting in a similar fashion as the other mussels, indicating the effect of the HG extract was wearing off. By the sixth day (144 hours) all the mussels from each treatment showed normal valvular motion and responsiveness.

Five of the mussels that received the HG extract in the posterior adductor muscle (PAM), in the preliminary experiment, showed paralysis after half an hour of the injection (no response to forceps tips probing on the mantle). The other two (of the seven) remained with valves tightly closed; all the control mussels (treated with sea water in the PAM and HG extract in the pallial cavity) remained closed. Twenty four hours after the injections three of the mussels that received the HG extract in the PAM were still unresponsive, but on the fourth day five mussels were dead, starting to decompose, and the other two were gaping normally. The control mussels after 24 hours still showed an irregular valvular movement, but not paralysis, and by the fourth day after the injections these mussels appeared to be gaping quite normally.

Proboscis Regeneration

All of the N. emarginata "proboscisectomized" survived the operation. In 36 to 43 days (Table 5) they fully recovered their

TABLE 5. Nucella emarginata individuals "proboscisectomized" and mussels preyed upon during the first month after drilling resumed. (SH=shell height; D=time (days) to resume drilling after amputation; the rest of symbols as in previous tables)

SNAILS		MUSSELS PREYED				
SH	D	N	X	S	R	L
11.1	37	9	14.7	4.2	3	6
11.5	36	8	11.7	4.0	2	6
12.1	36	8	13.8	4.1	4	4
15.8	37	10	14.3	3.8	5	5
16.6	37	9	12.7	2.8	5	2
17.2	37	9	12.8	3.7	6	2
17.2	41	6	13.1	5.5	3	3
17.5	43	5	14.7	4.7	2	3
18.5	37	5	13.5	2.7	5	0
19.0	43	7	14.6	5.1	5	2
19.4	38	9	14.8	4.3	6	3
21.1	39	10	12.7	4.8	4	4

ability to prey and drill.

During the whole recovery period they were unable to successfully prey in spite of having available live mussels of a wide range of sizes. Approximately two weeks after the operations, I offered fresh mussels with the PAM recently severed (cut) and the recovering snails were still not able to scavenge. Neither snail layed capsules during the recovery period. Two females started laying capsules seven and 10 days, respectively, after they resumed preying.

As soon as the snails resumed feeding they remain preying on the mussels regularly. The number of mussels eaten per snail during the first month after the amputation of the proboscis was computed (Table 5). The amount of mussels eaten by them in one month does not differ significantly from the number normally eaten in the same period of time by unoperated snails. They did not show a preference for either valve (right or left).

In a period of no more than 100 days after surgery (Table 6) the regenerated buccal mass reached a size similar to that of "normal" Nucella from the field, although the radulae were still only half full size. The shell sizes were not significantly different when the two groups of snails are compared (t-value=.55, P>.5).

TABLE 6. Comparison of sizes of buccal mass, radula and shell height of N. emarginata from the field with individuals "proboscisectomized 100 days after the operation. (t=t-test value; the rest of symbols as in previous tables; all measurements are in mm)

	SNAILS					
	NORMAL (N=20)		OPERATED (N=12)		t	P
	X	S	X	S		
BUCCAL MASS	2.3	0.4	2.3	0.2	0.00	> .9
RADULA	10.6	1.6	5.5	0.7	12.40	< .001
SHELL HEIGHT	16.9	2.6	17.4	2.4	0.55	> .5

Larger snails had larger radular (Figure 7) and buccal masses (Figure 8) in both operated and normal snails. The results are highly significant for both comparisons (Table 7).

Loss of the Proboscis in the Field

Of the 175 experimental N. emarginata, 90.3% showed an active predatory attitude during the first 24 hours of observations (Table 8), 6.3% the second and 1.7% the third 24 hours. The remaining 1.7% (N=3, belonging to the large class) on the fourth day did not show an apparent ability to prey. These three snails were immediately dissected. The size of their radulae and buccal mass were measured. Buccal masses were 2.4, 2.4 and 2.6 mm, and radulae were 6.0, 5.9 and

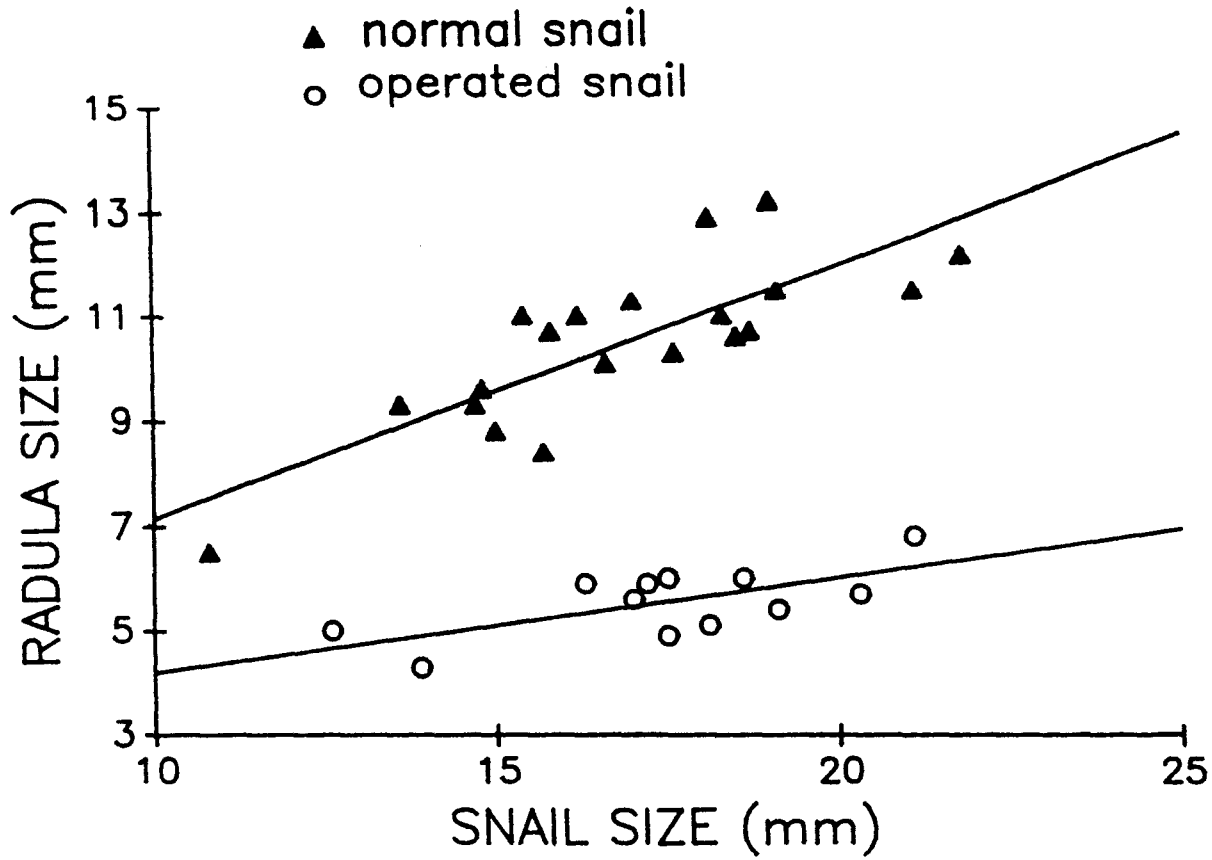

FIGURE 7. Proboscis amputation experiment: comparison of radula size between normal and operated N. emarginata

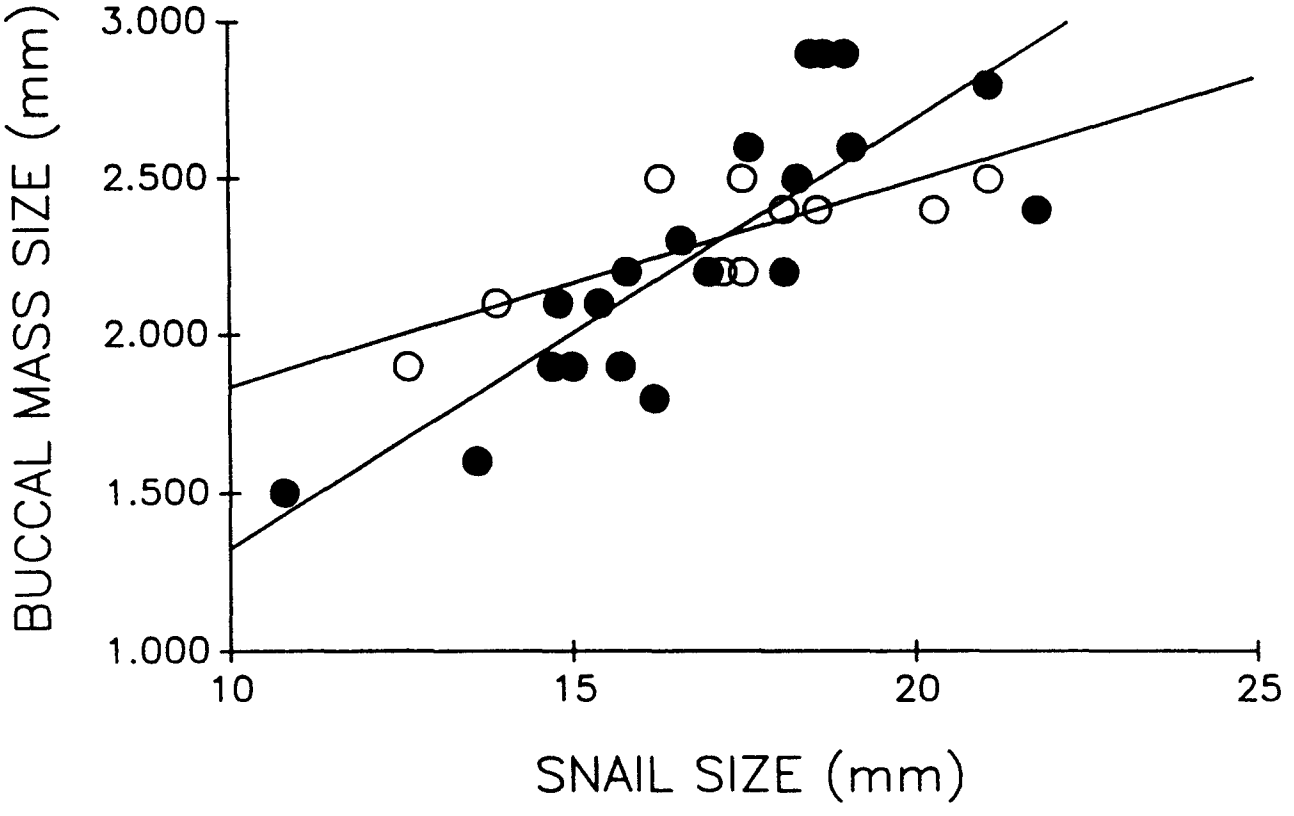

FIGURE 8. Proboscis amputation experiment: comparison of buccal mass sizes between normal (o) and operated (o) N. emarginata

TABLE 7. Simple linear regression analysis between shell height (SH) and buccal mass (BM) and radula (Ra) of *N. emarginata* (normal and operated)

	F	P	Multiple R^2
NORMAL			
SH vs BM	38.13	<.001	.679
SH vs Ra	32.94	<.001	.647
OPERATED			
SH vs BM	14.79	.003	.597
SH vs Ra	7.90	.018	.441

TABLE 8. Probability of losing the proboscis in the field. Percentage of snails of each size class that showed evidence of predatory ability by the end of the first, second and third 24-hour period of the experiment (see text for details)

	24-hour period of experiment:		
	1st	2nd	3rd
SNAILS			
SMALL (N=47)	89.4	8.5	2.1
MEDIUM (N=57)	98.2	1.8	0.0
LARGE (N=71)	87.5	8.5	2.8
TOTAL (N=175)	90.3	6.3	1.7

6.0 mm. These values fell in the corresponding range values of the normal snails. Thus, none of the 175 snails from the field either lacked the ability to prey on the mussels or had the proboscis damaged.

Predation after Ablation of Accesory Boring Organ

All ABO dissected N. emarginata recovered, as well as the controls. Both groups of snails started attacking the mussels four to six hours after the operation or after anesthetization (controls).

The experiment lasted six days. There was no significant difference in the mean size of the snails between the two groups (t-value=.40, df=11, P>.5), nor between the sizes of mussels preyed upon by the snails from the two treatments (t-value=.55, df=33, P>.5) (Table 9).

In the case of the mussels edge-attacked by the operated snails, there were only superficial radular scratches at the margins (somewhat circular or semicircular in shape). These scratches were only on the periostracum without reaching the calcareous layers of the valve. On the contrary, the radular marks along the posterior edge of the mussels eaten by the controls were true notches.

TABLE 9. ABO dissection experiment. Comparison between N. emarginata individuals, mussels preyed and number of mussels by means of attack. (Symbols as in previous tables)

	SNAILS			MUSSELS					
	SIZE			SIZE			MEANS OF ATTACK		
	N	X	S	N	X	S	H	E	n
CONTROL	5	14.2	1.3	18	13.5	2.0	12	5	1
ABO-DISSECT	8	13.9	1.3	17	13.1	2.2	0	8	9

CHAPTER IV

DISCUSSION

The neogastropod Nucella emarginata is a mid to high intertidal predator. It shows a consistent preference for attacking small mussels along the edges as opposed to boring a hole through the shell. The same edge-attack mode on bivalves has also been found in various degrees of preference in other species of gastropods: Polinices tumidus (ANSELL & MORTON, 1987), Acanthina spirata (HEMINGWAY, 1973,a, b), Thais floridana (RADWIN & WELLS, 1968), I. chocolata (personal observations), Nucella canaliculata and N. emarginata (PALMER, 1980), Murex fulvescens (WELLS, 1958), Muricanthus radix (VERMEIJ, 1978), and numerous naticid gastropods from Guam (VERMEIJ, 1980).

A difference in the degree of this preference for edge-drilling among populations from different localities of N. emarginata and N. canaliculata has been reported (PALMER, 1980). Edge-attack by the former species is much higher (PALMER, 1980), which agrees with my observations. The degree of preference may also depend on the mussel species (PALMER, 1980).

The preference in N. emarginata to make edge attacks along the posterior margin of the mussels may be because the ventral edge is thicker (CAREFOOT, 1977). The posterior edge is also more readily available in nature relative to the normal position (posterior edge

upward) of attached mussel in clumps. The snails may respond instinctively, attacking the most exposed part of the bivalve (PALMER, 1980). In the laboratory Thais chocolata (South American Pacific coast) attacks the thin-shelled mussels Semimytilus algosus preferentially either along the pedal gape (ventral anterior edge) or the posterior edge (personal observations), although these mussels clump in nature in just the same way as Mytilus edulis. Thus, the former explanation seems more plausible.

More interestingly, the data in this study strongly suggest a dependence of the attack mode on the size of the prey. Nucella emarginata drills holes more frequently on larger mussels than on smaller ones. In small mussels the alternative way of attack was "filing" a notch with the radula on the posterior edge of one of the valves. No significant difference was found on the frequency of attacks in either of the valves, right or left. Those patterns of preference were verified in experiments in the laboratory using three size-classes of snails.

These results would suggest that differences in age (size) structure in mussels and N. emarginata subpopulations or populations between localities may be an important cause for the observed percent differences among modes of attack on preyed mussels. That is, the larger the Nucella individuals are with respect to the mussels, the larger the probability of finding preyed mussels with notches rather than with holes.

Nucella emarginata most frequently selects mussels smaller in size than itself. In 19 of 20 individual predatory events observed at the OIMB dock, I noted that N. emarginata was preying on a

significantly smaller mussel compared to others close by (within a radius of 5 cm) around the attacked mussel. In addition, I have never seen N. emarginata preying on mussels larger than 25 mm at the OIMB dock, nor have I found here an empty mussel of more than 35 mm with potentially lethal radular attacks. The preference for attacking smaller prey than the gastropod predator itself has been found in other species: Ocenebra lurida (PALMER, 1988), Nucella canaliculata, N. emarginata, N. lamellosa and N. lima (when preying on barnacles, HART & PALMER, 1987), Natica maculosa (BROOM, 1982), Polinices duplicatus (EDWARDS & HUEBNER, 1977). Nucella lapillus showed a positive hyperbolic relationship with preyed M. edulis when shell sizes are compared, and the prey was smaller than the predator (BAYNE & SCULLARD, 1978). Paris (1960) also noticed that N. emarginata selected significantly smaller mussels (about 17 mm, N=5), when compared with mussels preyed by N. canaliculata and N. lamellosa, in Washington state. Gastropods do not prey at random, relative to either prey species or prey size (EMLEN, 1966; KITCHELL ET AL., 1981; PALMER, 1984).

It would appear to be a "useful" strategy for a gastropod predator that predominantly lives in the harsh environment of the upper intertidal zone, such as N. emarginata, to prey on mussels not too small (or the predatory process would not be worthwhile) yet small enough so that the snail can avoid either "interlopers" or "hangers-on". I have seen more than one N. emarginata preying on the same mussel in the field in only two of 163 observations. Moreover, on both occasions each snail had made its own entrance (notch or hole) into the prey.

This type of opportunism may significantly diminish the profitability of a prey item for the predatory snail that spends an important part of its handling time and energy in trying to gain access into the barnacle or mussel (DUNKIN & HUGHES, 1984; EMLEN, 1966; HUGHES & DUNKIN, 1984). For example, there is room for only one N. emarginata on top of the small Balanus glandula, but more than one snail can prey on an already-attacked Semibalanus cariosus (EMLEN, 1966). Emlen found "hangers-on" in eight of 46 feeding events of N. emarginata preying on S. cariosus of more that 5 mm in size.

Why does N. emarginata opt for drilling a hole (instead of attacking along the edge) when the mussel is larger? Larger mussels have stronger adductor muscles, which pose a risk to the snail. The snail's foot can be nipped by the closing valves of large mussels (M. edulis), and the snail is forced to move away or roll down (WAYNE, 1987). I have also frequently seen live and dead N. emarginata and N. canaliculata (rocky point of Pirate's Cove, Bastendorff Beach, 1 Km south of OIMB) attached to byssal threads inside M. californianus beds, but never in patches of small mussels where N. emarginata prefers to forage. Petraitis (1987) reported a similar phenomenon in for N. lapillus, which tries to avoid M. edulis beds.

It does not appear that N. emarginata selects a specific place to drill a hole. Nucella has a proboscis at least as long as its own shell length, and can thus access most of the inside of the mussel. It has been shown, however that N. lapillus can, through a learning process, drill a specific area where the snail has quicker access to the nutritious digestive gland (HUGHES & DUNKIN, 1984).

Results from the experiments of limiting the access of N.

emarginata to *M. edulis* valves strongly support the thesis of the use of some sort of toxin for the snail to gain access into the mussel. This toxin appears to cause flaccid paralysis (HEMINGWAY, 1973) particularly on the adductor mussels. Its effect is temporary. It seems that vital functions may continue: under the dissecting microscope ciliary currents are observed on the mussel when it is under the effect of the HG extract.

After the mussel is attacked, the valves gape and the snail feeds on it. The intervalve distance in these circumstances (limited access of the snail through the plexiglass hole to the mussel), is much wider than that during an actual predatory event in nature when the snail feeds between the valves. In the latter case, during most of the feeding process, the valves are only slightly separated (0.2-0.3 mm), compressing the proboscis sheath into the "slit" between the valves. These observations suggest that *N. emarginata* somewhat controls the intervalve distance with its propodium lobes, trying to keep the valves as close together as possible, to overcome the stretching strength of the hinge while the adductor muscles are relaxed. This behavior would let the snail limit the amout of metabolites being released by the mussel, in such a way as to avoid attracting competitors.

On several opportunities I have detached the foot of a snail from the mussel when the snail has been feeding for a long while between the valves, and the valves remained closed or slightly closed for several minutes while the snail had its proboscis "caught". At first it might appear that the mussel shut its valves. But, this phenomenon may be explained by the fact that the most voluminous and

the harder structure in the proboscis tip is the buccal mass. The latter is what basically defines the proboscis diameter (about 1 mm in a 15 mm snail). Therefore, what may not allow the proboscis to be freed when I pull the snail apart from the mussel is the buccal mass, until the paralyzed mussel slowly gapes again, opened by the hinge ligament strength.

Emlen (1966) and Palmer (1980, 1982) have observed that whenever Nucella emarginata, as well as other Nucella species, preys on barnacles it feeds through the opercular plates while the bore-hole is located elsewhere (such as lateral plates or sutures). Those holes were also too small to allow the proboscis to pass through (PALMER, 1980, 1982). Palmer assumed that these Nucella species are equipped with a powerful toxic saliva, which is injected through the hole to relax the opercular plates.

In contrast, when Nucella drills a hole, it always feeds through the hole until emptying the mussel. A plausible explanation is that there is a differential effect of the toxin on the physiology of these two phylogenetically different types of prey. There is a wide diversity in the effects produced by several choline esters when applied to the muscular tissue of different vertebrate groups (BULBRING et al., 1953). In addition, the condition of the musculature in molluscs is not comparable with that of the arthropods or vertebrates (HOYLE, 1964). There is also the presence of the peculiar adductor muscles (where the "catch mechanism" resides) in bivalves which is composed of both striated ("fast" portion) and smooth ("slow" portion) fibers (HOYLE, 1964).

Even more interestingly, during most of the feeding process of

N. emarginata when eating a mussel through a drill-hole, the mussel commonly keeps its valves closed. Only when there are some remains of the posterior adductor muscle left in the mussel does it start to gape. Carriker and Van Zandt (1972a) observed the same thing in Urosalpinx cinerea when preying on oysters. In contrast, as mentioned above, the feeding mode between the valves by Nucella, as a consequence of an edge-attack, suggests a relaxing paralysis in the mussel. This differential behavior of the mussel as a function of the snail's attack mode may depend upon the organ source of the toxin(s), and consequently the way in which the pharmacologically active compound(s) is (are) administered during each attack mode. The two most plausible sources of toxins in muricaceans seem to be the hypobranchial gland (HG) and the salivary glands (SG) (including the tubular salivary glands (TSG) which are unique features in muricacean gastropods, CARRIKER, 1981).

There is a surprising diversity of cases concerning the toxicity of these glands. In Acanthina spirata the active choline esters composition of both groups of glands seems to be identical (HEMINGWAY, 1978). In the case of Thais haemastoma the toxic fraction of the HG produced opposite physiological effects with respect to that of SG when tested on similar vertebrates (HUANG & MIR, 1971,1972). In other muricaceans the TSG did not show toxicity on Cardium heart (GRAHAM, 1941, cited by CARRIKER, 1981). It has been suggested that there may be as many choline esters (or combinations?) as muricacean gastropods exist (HEMINGWAY, 1978). Nucella emarginata bears choline esters different in character than acetylcholine which show dose-response relationships impossible to establish (BENDER et al., 1974). In this

study, I have shown that chemical compounds from the HG of N. emarginata significantly affect the behavior and the physiology of M. edulis. The preliminary test of the HG extract into the PAM of the mussel suggested that the flaccid paralysis, produced on the mussel when it is edge-attacked by N. emarginata, may be caused by toxins derived from this gland.

While the HG does not have a duct to deliver its products (HYMAN, 1967; HUANG & MIR, 1972) the mucus produced there is transported through ciliary currents (FRETTER & GRAHAM, 1962; HYMAN, 1967) in the mantle and on the propodium (foot), together with the toxins. On the other hand, the SG and the TSG have ducts that discharge into the buccal cavity; consequently, the method of administration of their products is only through the proboscis. Then, when Nucella attack the mussel between the valves, it can apply to the mussel's mantle both the HG secretions with the propodium and the proboscis (externally impregnated due to its constant contact with the propodium lobes) and/or the SG and/or TSG secretions injected via the proboscis. The preliminary test of the HG extract into the PAM of small Mytilus did not necessarily mimic the real administration method of the HG toxin(s). However, the results suggest that the flaccid paralysis could be produced if during the attack the snail damages the tissues of the mussel with the radula, exposing the mussel's circulatory system. Since paralysis occurs a considerable period of time after the snail started attacking the mussel (as observed here in the experiment of limiting the access of the snail to the mussel), it may suggest that paralysis could result after prolonged contact of the snail's secretions with the mussel's tissues. Hemingway (1978) found

similar results (flaccid paralysis) when the HG extract of A. spirata was injected directly into the PAM of M. edulis, compared to the lack of effects when delivered into the pallial cavity of the mussel.

On the other hand, when the snail feeds through a hole it is more likely that the salivary (SG and/or TSG) products are discharged into the mantle cavity of the mussel. Considering that the drill-hole seems to be narrower than the swelled proboscis (personal observations), and that the internal edges of the hole are commonly sharp, most of the HG secretion externally impregnated in the proboscis would be wiped clean upon insertion. All this would then result in the snail having two distinct ways to administer its toxin(s), with correspondingly different physiological effects on the prey.

These two attack modes (edge vs hole) have different advantages for the predator and the prey. When the snail is preying through a hole, the mussel typically remains tightly closed. This may be a natural protective behavior of the mussel or a physiological response to snail's toxin(s). For the predator, this means that the mussel does not release metabolites, and thus additional conspecifics, that may compete with the snail, may not be attracted. For the prey, this means that one snail is attacking it, and there is the possibility that the predatori would be interrupted by some external factors (after which the mussel might be able to recover). Several lines of evidence indicate that mussels can recover from a hole drilled through the shell (but from which the snail has been dislodged prior to commencing eating). I have seen complete bore holes filled from the inside with an irregular calcareous layer in about five percent of the empty

shells of M. edulis collected in the field. The formation of this extra layer may take a few weeks (personal observations in the laboratory on Mytilus which recovered completely from artificial holes (made by an alectrical drill) and from Nucella holes).

When the mussel is attacked on the edge the effect can (as mentioned above) last for several days as a flaccid paralysis. (Recovery from a drill hole is quicker, suggesting that the effect of the saliva "toxin" on the mussel, if any, is less toxic than the HG secretions). The mussel can recover from an edge attack in the laboratory, although it is uncertain or doubtful that the mussel will normally have an opportunity to recover in the field, due to the presence of other predators and scavengers that would easily feed on the gaping bivalve. For the predator, the adaptive preference for edge attacks (over holes) may result from three factors: (1) entrance (and therefore consumption) time is shortened, (2) the snail avoids (because of the mussel size) competitors, and (3) the snail can consume the whole prey because of its size, to avoid the risks of prolonged low-tide exposure (EMLEN, 1966; PALMER, 1980).

The results of the experiment of the snails' risk of losing the proboscis by natural means, I can speculate that the probability of that risk is less than 1/175=0.0057. This value is perhaps too liberal for two reasons: (1) I chose in the field the snails from hidden crevices, that is, neither crawling nor preying, nor females laying capsules (I assumed from the results of the proboscisectomy experiment, in which the snails with cut proboscis remained most of the time in a corner, that the snail in the field would behave basically the same way), and (2) the proboscis regeneration time (in

the same experiment) was about 40 days, and thus field collections would have detected snails whose proboscis was naturally amputated up to at least 30 days before the day of the collection.

The risk, then, for the snail to lose its proboscis when feeding in the field by either attacking mode is low. Four factors contribute to this: (1) this snail does not seem to risk its proboscis while preying between the valves of the prey; (2) Nucella has a very lubricated and fast retracting proboscis, such as to be quickly withdrawn from a hole or between the mussel valves when a threat is posed; (3) the strong foot allows the snail to firmly attach to the surface of the prey with a varying tenacity, depending on the wave exposure, (MILLER, 1974), in such a way that the snail would not likely be swept away before having time to withdraw the proboscis if it is inserted into the mussel; and (4) valve closure by the mussels normally selected by the snail does not pose a risk, because of the small size of the mussel and the presence of the paralyzing toxin(s) in the snail's secretions. These observations suggest that there is a very low probability for N. emarginata to have its proboscis amputated in the field by natural means when compared to other muricaceans (CARRIKER et al., 1972; GUNTER, 1979;RADWIN & WELLS, 1968).

The experimental results herein confirm the above conclusion. Nucella emarginata's close relatives, and common side-by-side neighbors, N. canaliculata and N. lamellosa, also have the ability to resume drilling and feeding after their probosces were amputated (personal observations), although they live in the low intertidal zone, conditions milder than in the habitat of N. emarginata (PALMER, 1980). Carriker believes (personal comunication) that all the

shell-boring neogastropods may have the ability to regenerate the proboscis as an adaptive response of their permanent risk to lose this structure in the field.

With respect to the amputation of the accessory boring organ (ABO) experiment, the two sets of data (operated and control snails) are not independent. While the snails of both treatments were in separated containers all of the snails of one treatment were together in the same compartment, in which case there may have been some behavioral interaction. Judging, however, from observations made on other occasions on healthy N. emarginata of the same size range of the snails and mussels used in the experiment, I conclude that the number of mussels attacked in each way by the two groups is clearly different. Therefore, the results of the present investigation strongly suggest that N. emarginata's preference for edge drilling is adaptive. The evidence for this is its ability to successfully attack and prey upon small mussels, producing only radular raspings at the mussels' margin or nothing at all, within a few hours after ablation of the ABO. In contrast, when I performed the same operation on N. canaliculata, these snails not only did not resort to edge attacking on the mussels, as N. emarginata did, but also remained posed in the same position on the center of the mussel valve for periods of one to three days. After that time they produced only superficial radular scratches clearing the shell of most of the periostracum within the rasping area.

I did not determine regeneration time of ABO in either Nucella species. In Urosalpinx and Eupleura resumption of shell boring parallel to feeding after ABOdissection happened between the 10th and

the 20th day, when the ABO is regenerated (CARRIKER & VAN ZANDT, 1972b). My results suggest that the ABO plays a critical chemical role during the penetration of the uncalcified structure of the periostracum of mussels (GREGOIRE, 1972) in addition to aiding in the dissolution of the calcareous part of the shell (CARRIKER, 1981). The periostracum in M. edulis is a protective structure even harder than the lower calcareous layers of the shell (CARRIKER, 1969).

It was noted throughout this study that N. emarginata in the laboratory can kill and access mussels between the valves without leaving any shell marks. (Most feeding by Nucella takes place at high tide (EMLEN, 1966), and thus this phenomenon, while not observed in the field, probably takes place there as well). The existence of preyed-upon shells without any trace of marks or holes means that we may underestimate mussel mortality due to carnivorous snails. A similar phenomenon has been reported in naticids, which kill many bivalves by enveloping (soffocating) before drilling is iniciated; this may have further importance for paleontological interpretations (VERMEIJ, 1980).

Natural death rate observations of M. edulis at the OIMB dock were hampered by a storm that apparently destroyed the mussel patches from several pilings on June of 1989. Thus I was not able to estimate the actual percentage of empty mussels that were preyed upon without drilling by N. emarginata. Such an ability has also been reported in Thais haemastoma when preying on oysters (GUNTER, 1968,1979). This preference is much stronger after the thaidid reached 50 mm (GUNTER, 1979). This behavioral shift might be related to the proportionately smaller size of the ABO in adult snails compared to young individuals

(CARRIKER, 1981). This ontogenetic shift was slightly suggested for N. emarginata during this study.

CHAPTER V

CONCLUSIONS AND RECOMMENDATIONS

The present investigation has shown in the neogastropod Nucella emarginata the existence in its feeding biology of behavioral, biochemical and anatomical adaptations for this mid and high intertidal inhabitant that can reduce natural risks posed to invertebrate predators in this harsh environment.

Nucella emarginata consistently looks for smaller Mytilus edulis (over M. californianus) than its own size. In addition, its preferred attack mode is by the edges, almost invariably along the posterior margin. In these cases, this thaidid drills a very small notch commonly unnoticeable by the naked eye.

During the edge-attack, the snail may apply toxic secretions, possibly from the hypobranchial gland, on the mussel mantle or in the pallial cavity. The toxin(s) promotes a flaccid relaxation on the mussel. Then, Nucella uses its propodium lobes to regulate the intervalvar distance while its proboscis, inserted between the valves, eats the prey flesh.

When the mussels chosen by N. emarginata are larger (relative to the snail's own size), the snail commonly opts for drilling a hole through the shell, preferentially away from the margins to avoid the threat of the mussel's valvular motion.

This study has demonstrated in N. emarginata a novel mode of attack among muricaceans when preying on mussels. Nucella can prey without the necessity of drilling a hole or filing a notch. A high percentage of recently preyed mussels from the field and from laboratory experiments, with no evidence of radular scratches, as well as by direct observations of predatory events in the laboratory, are evidence of this. Toxic secretions may be an important part in this mode of attack.

The accessory boring organ, when artificially removed, does not significantly diminish feeding rate. Nucella emarginata without the ABO resorts to edge attack while for other snails of similar size the length of the mussel would justify the attack mode of drilling a hole. The ABO appears to be of more critical importance for the predatory process in other shell boring muricaceans.

N. emarginata has the ability to regenerate the buccal mass and associated structures in about 40 days, during which time the snail was incapable of feeding. Although the radula by that time is functional, after 100 days following amputation the radula is only half the normal size. In spite of this ability, the present study has shown that probabilities are very scarce for the snail to lose its proboscis by natural means.

Further studies should be devoted to estimate the real impact on the natural death rate of mussels by each of the attack modes of N. emarginata. Particular attention must be paid with respect to what factor(s) determine(s) whether to drill a notch or not attack the shell at all. It would be worthwhile to study the precise method of administration of the toxic secretions (during each type of attack

mode) when Nucella preys both on mussels and on barnacles, and the differential handling time in each case. Finally, a multispecific comparative investigation in all these aspects would be useful, in order to have a better understanding of the ecological and phylogenetic implications of this versatility in attack modes.

APPENDIX A.

SOME PHARMACOLOGYCALLY ACTIVE CHOLINE ESTERS (OR TOXINS) STRUCTURES FOUND IN MURICACEAN GASTROPODS.

KEY
ST=structure; HG=hypobranchial gland; WO=whole organism extract;
SG=salivary gland; S-T=salivary gland-tubular salivary gland complex;
Toxin=chemical nature not mentioned;
Urocanylcholine=Murexine;
Several=several choline esters found.

FAMILY Species (ST)	CHOLINE ESTER	REFERENCE
Muricidae		
Murex trunculus (HG)	Urocanylcholine	EARSPAMER, 1948
M. brandaris (HG)	Urocanylcholine	EARSPAMER, 1948
M. fulvescens (HG)	Urocanylcholine	KEYL et al., 1957*
Ocenebra erinacea (HG)	Urocanylcholine	EARSPAMER, 1948
Urosalpinx cinerea (WO)	Urocanylcholine	kEYL et al., 1957*
Concholepas concholepas (HG)	Urocanylcholine	ROSEGHINI et al., 1970
Thaididae		
Thais chocolata (HG)	Senecioylcholine	ROSEGHINI at al., 1970
T. haemastoma (HG)	Dihydromurexine	ROSEGHINI et al., 1971
(HG)	Toxin(s)	HUANG & MIR, 1971
(SG)	Toxin(s)	HUANG & MIR, 1972
Nucella emarginata (HG)	Urocanylcholine + N-Methylmurexine	BENDER et al., 1974
N. lapillus (WO)	Toxin(s)	WHITTAKER & MICHELSON, 1954
(HG)	Toxin(s)	ROAF & MIERENSTEIN, 1907
Acanthina spirata (HG)	Urocanylcholine	BENDER et al., 1974
(HG)	Several	HEMINGWAY, 1978
(S-T)	Several	HEMINGWAY, 1978
A. punctulata (HG)	Toxin(s)	SLENDER, 1981

*Cited in BENDER et al., 1974.

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