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RESEARCH ARTICLE

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Feeding habits and phenotypic changes in proboscis length in the southern oyster drill, *Stramonita haemastoma* (Gastropoda: Muricidae), on Florida sabellariid worm reefs

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Abstract The southern oyster drill, *Stramonita* (= *Thais*, Kool 1987) *haemastoma*, is a common intertidal and subtidal predator in the southeastern United States. It uses specialized feeding structures and foraging strategies to bore holes through the shell of its bivalve prey. However, on the east coast of Florida, *S. haemastoma*, is common on sabellariid worm reefs constructed by the polychaete *Phragmatopoma lapidosa* (Walton Rocks Beach, Florida, 27°17′N, 80°12′W), a habitat where the snail's typical prey are scarce. From 1999 to 2001, we examined the feeding habits of *S. haemastoma* on sabellariid reefs and the behavioral and morphological responses of *S. haemastoma* that accompanied switching from a diet of bivalves to sabellariids. On worm reefs *S. haemastoma* feeds on *P. lapidosa* by inserting the proboscis deep into a worm's tube. Worm-feeding snails had longer proboscises (~3.7 times shell height) than bivalve-feeding conspecifics (~2.0 times shell height). Snails raised on different diets showed significant differences in proboscis length suggesting that the proboscis length is phenotypically plastic. Whereas typical oyster drills must bore holes for days before ingesting prey, *S. haemastoma* on worm reefs avoids boring and attacks and consumes worms in 15–50 min. In the laboratory, oyster drills consumed 1.7 worms per day, spending < 1 h each day feeding. On sabellariid reefs, differences in feeding, handling costs, and prey value, are likely to have a significant effect on the ecology and life history of *S. haemastoma* in this habitat.

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Introduction

Many predators exhibit specialized foraging strategies and morphological adaptations that have arisen in response to selective pressures imposed by specific types of prey (Schoener 1971). Shell-boring in gastropods is a feeding strategy that permits some snails to feed on bivalves and other shelled benthic invertebrates— prey whose defenses present significant challenges to attackers. To circumvent these defenses, shell-boring gastropods drill a hole through the calcareous shell of their prey using a combination of radular scraping and chemical dissolution. An accessory boring organ secretes enzymes intermittently, which helps soften and dissolve the area being drilled (Carriker 1978, 1981). After a hole is made in the shell, a long proboscis extends into the shell and the soft tissue is torn off and ingested. Thus, the ability to bore through shell and then feed on its contents required the evolution of several anatomical, physiological, and behavioral innovations.

Feeding on an individual shelled prey item may take several hours to several days, requiring a substantial commitment of both time and energy. The significant handling costs associated with shelled prey have led to the evolution of foraging strategies that reduce handling time and other costs, and maximize energy intake (Hughes 1980). When given a choice, shell-boring snails tend to select prey of optimal size and will choose more easily accessible or energetically rich species of prey over others (Garton 1986; Brown and Richardson 1987; Brown 1997). Feeding behaviors such as attacking the margin or lip of shells where defenses are weakest

(Gunter 1979), or foraging in groups (Brown and Alexander 1994) save time and energy. Some larger oyster drills may avoid boring altogether by secreting a toxin that causes bivalves to gape (McGraw and Gunter 1972).

Given the specialized nature of their feeding structures and foraging habits, shell-boring gastropods often occur where bivalves and other shelled prey are abundant. In the southeastern United States, the southern oyster drill, *Stramonita haemastoma*, feeds on the eastern oyster, *Crassostrea virginica* (reviewed by Butler 1985), mussels, *Ischadium recurvum*, and clams *Rangia cuneata* (Brown and Richardson 1987). In the Florida Keys, they feed on two species of tree oysters, *Isognomon bicolor* and *I. radiatus*, the mussel *Brachidontes exustus*, and the barnacle *Tetraclita squamosa* (Ingham and Zishke 1977). They also attack the bivalves *Donax variabilis*, *Perna perna, Anomia simplex, Mercenaria mercenaria*, and the gastropod *Crepidula plana* and cannibalize smaller conspecifics (Butler 1985).

However, on the Atlantic coast of Florida, populations of *S. haemastoma* occur on sabellariid worm reefs, a habitat where large populations of bivalve prey are unavailable to them. Sabellariid reefs are formed by large aggregations of the tube-building polychaete *Phragmatopoma lapidosa* (Sabellariidae). Huge intertidal and subtidal mounds consisting of thousands of sand tubes form reefs, and each mound may cover several square meters (Kirtley 1968). We witnessed *S. haemastoma* living directly on the worm mounds and sheltering in the cracks and crevices of the reef when not feeding. On sabellariid reefs, oyster drills feed primarily on *P. lapidosa*. For a predator that specializes on bivalves, switching to a diet of tubeworms is a major shift in foraging strategy. Differences in prey defense also present challenges that must be overcome for *S. haemastoma* to survive on sabellariid reefs.

Stramonita haemastoma is considered a pest of the commercial oyster industry and as a result, its feeding habits on oysters and on other bivalves have been extensively studied (review by Butler 1985). However, no information exists on the feeding habits of *S. haemastoma* on *P. lapidosa* worm reefs. We examined feeding behavior, feeding rate, and handling time of *S. haemastoma* feeding on *P. lapidosa* tubeworms. The long proboscis of *S. haemastoma* is its most functionally important feeding structure on worm reefs, so we compared the proboscises of worm predators with those of bivalve predators from another habitat to see if differences in habitat and prey were correlated with proboscis length. Finally, snails from different habitats were maintained on diets of worms or bivalves to determine if changes in proboscis length are inducible.

In the southeast United States, two subspecies, *S. haemastoma canaliculata* (Gray 1839) and *S. haemastoma floridana* (Conrad 1837) have been described based on differences in shell and radular morphology. A population genetics study of snails in this region identified two genetically differentiated groups of *S. haemastoma* (Liu et al. 1991). Snails characterized as *canaliculata*-like are more common along the Gulf coast of Louisiana, Mississippi, and Florida, while *floridana*-like snails are more prevalent in Texas and at two sites on the Atlantic coast of Florida. However, the same study found that genetic differences did not correlate with differences in shell or radular morphology, characteristics previously used to differentiate the subspecies. In this study, we collected bivalve-feeding *S. haemastoma* from a site on the Atlantic coast of Florida where Liu et al. (1991) found 114/128 *floridana*-like snails, 7/128 *canaliculata*-like, and 7/128 possible hybrids. Unfortunately, no genetic analyses have been conducted on sabellariid reef populations of *S. haemastoma* where our other snails were collected. In the absence of any information to the contrary, we assume that snails from both our study sites belong to the subspecies *floridana*. Other than allozyme differences revealed by Liu et al. (1991), no significant biological differences between the subspecies have been established.

Materials and methods

Study sites

Stramonita (= *Thais*, Kool 1987) *haemastoma* were collected from two sites on the east coast of Florida, USA, between 1999 and 2001. Walton Rocks Beach (27°17′N, 80°12′W) (WR) is located on the ocean side of a barrier island, approximately 65 km north of Palm Beach, Florida. A sandy beach slopes into the sea where scattered limestone coquina foundations support mounds of intertidal and subtidal *P. lapidosa* worm reef. Snails < 25 mm in shell height were collected at low tide primarily between the months of November and February. Clumps of worm tubes were collected regularly to feed the snails and for use in experiments. Both worms and snails were transported in buckets of seawater to our laboratory at Harbor Branch Oceanographic Institution (HBOI) where they were maintained in aquaria at room temperature (~23°C).

Stramonita haemastoma from WR were compared with snails at Marineland, Florida (29°40′N, 81°12′W) (ML), approximately 270 km further north. At this site, snails occur on intertidal limestone boulders that form groins perpendicular to the beach. Wave action and sand surrounding the boulders probably prevents emigration from the study site. *P. lapidosa* does not occur at this site and snails were found feeding on the small (~7 mm) bivalve *Lyonsia hyalina* and the barnacle *Balanus amphitrite* which occurs slightly higher in the intertidal. Snails of shell height 20–35 mm were collected at low tide and transported in buckets of seawater to the laboratory. We measured shells with vernier calipers to the nearest 0.1 mm from the siphon to the tip of the spire. Prior to the experiments, WR snails were maintained on a diet of *P. lapidosa*. Because the bivalve *Lyonsia hyalina*, was not readily available near the laboratory, ML snails were fed the oyster *C. virginica*, collected from a nearby seawall.

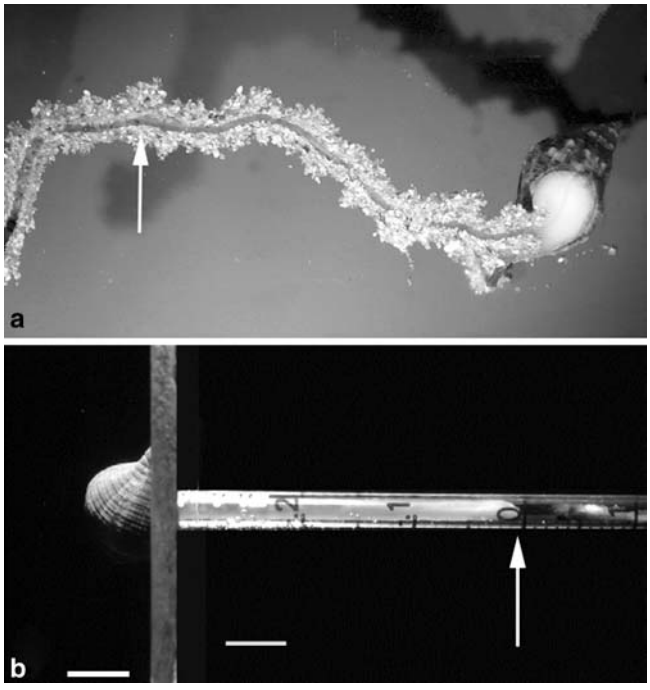

Fig. 1 *Stramonita haemastoma*. Attack on *Phragmatopoma lapidosa* in **a** A sand tube constructed *by P. lapidosa* on plexiglass. **b** A 1-ml plastic pipette (Photo W. Tyler). Time-lapse video and lines on pipette were used to measure length of snail proboscis. *Arrow* indicates tip of snail's proboscis. *Scale bar* 10 mm

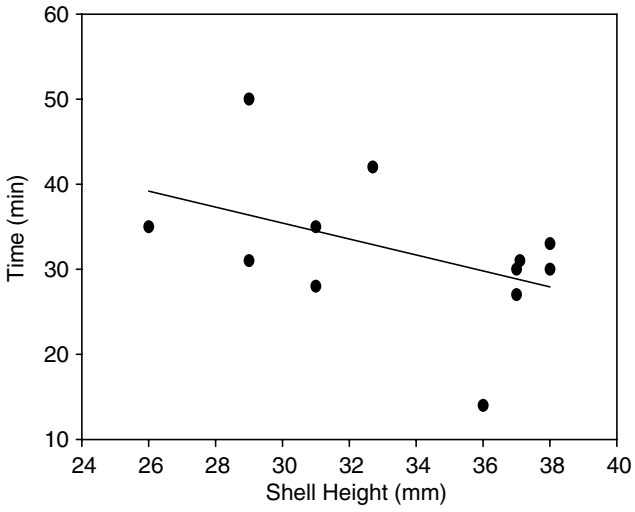

Fig. 2 *Stramonita haemastoma*. Relationship between shell height and time to consume a single *P. lapidosa* in a synthetic tube ($n = 12$, $y = 0.938x + 63.575$, $r^2 = 0.208$)

Feeding behavior, handling time, and proboscis length

Stramonita haemastoma attack and consume *P. lapidosa* within the worm tubes, making it difficult to observe feeding. We, therefore, developed two new methods to observe the feeding behavior of *S. haemastoma* on *P. lapidosa*. Individual tubeworms were cultured on transparent acrylic sheets and encouraged to build natural sand tubes on the transparent surface (Fig. 1a). A similar technique was previously used to observe the behavior of *P. lapidosa* within sand tubes (J. Pawlik, personal communication). We broke apart clumps of worm reef and isolated individual *P. lapidosa* within their sand tubes. Each tube was shortened to ~15 mm, making the tubes approximately the same size as the worms, and placed them on 10×10 cm^2 clear acrylic sheets in an aerated seawater aquarium. The remaining tube fragments were crushed into individual sand grains. A trail of sand was placed in front of each worm tube. When left undisturbed for 2–3 weeks, the worms reconstructed tubes on the acrylic sheet. This created an 'ant farm' effect that allowed a view of the worm within the tube. During tube building, worms were fed the diatom *Chaetoceros gracilis*. *Stramonita haemastoma* was then placed with the worm and the sheet was inverted under water. Under a dissecting microscope, feeding behavior was observed from above with the worm and snail on the opposite side of the clear sheet.

Snail feeding behavior was also observed in artificial tubes made from 1-ml clear graduated plastic pipettes (Fig. 1b). Six tubes (interior diameter 3 mm) were mounted and glued in a frame of two 15×20 cm^2 acrylic sheets. The sheets had holes to hold the tubes in place, which were spaced two per row, with openings mounted flush with one sheet. Six tubes were used to increase the likelihood that a snail would encounter a worm. Individual worms were removed from their sand tubes and placed inside the pipettes, posterior end first, with the head towards the opening of the pipette. Three or four snails at a time were labeled with nail polish and introduced to a 15-l seawater aquarium containing the pipettes and worms. Using a Panasonic time-lapse video recorder, we videotaped the aquarium for 72 h to observe feeding behavior over extended periods of time. As snails fed, they extended their proboscis down the tube, and the worms either retreated or were pushed by the proboscis. As the worms retreated, *S. haemastoma*, extended its proboscis further. Markings on the tube visible in the video replay enabled measurement of proboscis length. Whenever possible, handling time (the time from initial proboscis extension until the worm was consumed) was recorded from video footage or real-time observations. The aquarium was near a window and so natural light and dark cycles existed during the duration of the experiment.

We compared the proboscis lengths of snails from the WR and ML sites to determine if different types of available prey (and the different methods of handling these prey) were related to proboscis length. After each proboscis was measured, we removed the snail from the aquarium and measured shell height. Shell height to proboscis length regressions were compared between the two sites, using ANCOVA, with shell height as a covariate to eliminate the effects of snail size.

Phenotypic plasticity

Stramonita haemastoma feeding on worms had much longer proboscises than snails feeding on oysters. To determine if proboscis length changes phenotypically with a change in diet, we maintained separate groups of snails from WR and ML on diets of either *C. virginica* (~65 mm from hinge to posterior shell edge) or *P. lapidosa*. At the beginning of the experiment, snails from WR were slightly smaller (22.8 ± 2.4 mm) than those from ML (26.3 ± 3.2 mm). Snails of this size range have not yet attained reproductive maturity and were recruited within 6 months of collection (unpublished). *Stramonita haemastoma* may attain shell heights of >100 mm and live for several years and have been known to grow 25 mm in just 30 days in the laboratory (Butler 1987).

Snails were maintained in five, 47-l aquaria, each divided into 12, 12 × 6 × 14 cm^3 chambers. Snails were paired within chambers because the experiment also measured reproductive output (Watanabe 2002). Each tank had six snails from each habitat fed with each type of prey. Each chamber received either one clump of *Phragmatopoma lapidosa* (>200 individuals) every 4 weeks, or one cracked *C. virginica* oyster every 10–14 days. Oysters were cracked open with a hammer so that regular feeding intervals could be maintained and feeding would not be delayed by individual differences in the timing of shell-boring. This method should not affect the way the proboscis is extended when feeding on oysters. A preliminary study showed no significant difference in growth of snails that fed on opened or closed oysters (Watanabe 2002).

After 11 months, snails were removed from aquaria and proboscises were measured as described previously. Fifteen snails from each of the four site-prey combinations were measured. Proboscis lengths were compared using a two-way factorial ANCOVA with prey (fixed) and site (random) as the factors and shell height as the covariate.

Feeding rate

We estimated feeding rate of *S. haemastoma* on *P. lapidosa* in an experiment in April 2001. We put *S. haemastoma* (mean shell height 23.3 ± 0.8 mm) in 11 replicate, 2-l plastic containers of aerated seawater with clumps of worm reef (11–15 worms $clump^{-1}$) for 7 days. Three 2-l containers holding only worm clumps were used as controls. Prior to the experiment, all snails were kept in tanks with an ample supply of *P. lapidosa* clumps. After 7 days, the remaining worms were counted to determine the number of worms consumed. Half the water in each container was replaced twice during the experiment and all containers were kept at room temperature (~23 C). After 7 days, worm clumps were broken apart and the number of worms remaining in each replicate was subtracted from the initial number to determine the number consumed by the snail. Feeding rate (worms per day) was calculated as the number of worms consumed during the experiment, divided by days of the study.

Phragmatopoma lapidosa tissue dry-mass

To determine the amount of tissue consumed by the snails, we calculated the average dry tissue weight of individual *P. lapidosa* collected at WR in April 2001. One hundred worms were removed from their tubes and fixed in 10% formalin and sea water. Body length of each worm was measured to the nearest 0.01 mm from a digital photograph, using University of Texas Health Science Center San Antonio (UTHSCS1A) imaging program version 2.0. Undamaged worms ($n = 41$) were then oven-dried at 60°C for 24 h and weighed on a Mettler AE 163 analytical balance. After total body weight was measured, the operculum was removed from the worm and weighed to determine the percentage of worm mass attributable to the operculum, the only part of the worm that is not consumed by the snail.

The dry tissue consumed per day was calculated by multiplying the number of worms eaten per day from the feeding experiment by the average dry tissue weight without the operculum. *P. lapidosa* spawns when stressed, and dry mass did not account for missing mass due to release of eggs or sperm when worms were originally removed from their tubes. When *P. lapidosa* are being consumed by *S. haemastoma*, the worms may likely spawn before being eaten, and snails may not recover that biomass anyway. This was not, however, observed in our feeding experiments because worms released their gametes during the experimental setup prior to the introduction of the snails. *Phragmatopoma lapidosa* are capable of spawning the year round (McCarthy 2001), but at WR settlement was heaviest in September and October and abundance declined by August (Watanabe 2002).

Profitability of prey, (Brown and Richardson 1987), was calculated as the amount of dry tissue consumed per hour of feeding effort. The mean dry mass of *P. lapidosa* (without the operculum) was divided by the mean time it took snails to consume a single worm (as determined by the handling time studies). This yielded the amount of dry tissue consumed per hour of handling time.

Results

Feeding behavior and handling time

After *S. haemastoma* were placed in tanks containing *P. lapidosa*, the snails either searched for prey, or became inactive and did not move for some time. Videotaped observations over 72 h showed an apparently random activity pattern that did not correlate with any diurnal or tidal patterns.

Like other predatory gastropods, *S. haemastoma* made lateral movements of the siphon while searching for prey, presumably testing the water from different directions. Snails found the opening of the worm tubes with their siphons, often touching the tentacles of *P. lapidosa* in the process. The worms retracted upon contact but generally did not retreat down their tubes immediately. Snails initiated feeding by covering the external opening of the worm tube with the anterior portion of the foot. The snails then inserted their proboscises into the opening of the tube. When the proboscises touched the tentacles or chitinous operculum of *P. lapidosa*, the worms retreated into the tube. The snails followed the worms with their proboscises, rasping with their radula in an apparent attempt to slow down or capture the retreating worm. *P. lapidosa* was captured when it could not retreat any deeper, or when the radula of *S. haemastoma* caught the opercular plate of the worm. The operculum was slightly smaller than the diameter of the tube and allowed movement of the worm up or down the tube while keeping the head of the worm covered. *S. haemastoma* scraped at the operculum until it tilted to one side, rendering the soft head of *P. lapidosa* vulnerable to attack. Once the soft tissue was accessed, *S. haemastoma* tore bits of flesh from its prey. In the tube, some snails slowly retracted the proboscis as they fed, pulling the worm toward the opening of the tube. Near the tip of the proboscis, microscopic particles of detritus and sand moved rhythmically back and forth as the snail fed, suggesting a sucking or pumping force during feeding. When feeding on bivalves, the muscular proboscis pumps liquefied oyster tissue from the shell of prey. In addition to bringing particles to the mouth, the suction helped *S. haemastoma* slow down the retreat of *P. lapidosa* and pulled the worm toward the proboscis. *S. haemastoma* used two different methods of ingesting the remainder of the prey. In some cases, snails consumed the worms with the proboscis extended into the tubes; in other cases, they pulled the worms to the opening of the tube before ingestion. Tiny pieces of tissue moved in rhythmic pulses down the length of the semi-transparent proboscis. *S. haemastoma* ate all soft parts of the polychaete but never consumed the chitinous operculum.

Stramonita haemastoma rapidly attacked and consumed individual *P. lapidosa* when compared to other types of prey. Feeding times on *P. lapidosa* ranged from 14 to 50 min. In 13 timed attacks in artificial tubes, *S. haemastoma* consumed *P. lapidosa* in a mean time of 32.2 ± 8.3 (SD, range 14–50) min. In another study, similarly sized *S. haemastoma* took 20 h to feed on the mussel *I. recurvum*, and up to 70 h to consume clumped *C. virginica* (Brown and Richardson 1987). Snails fed continuously once they began ingesting the tissue and stopped only after all soft tissue was eaten. The size of snails did not show a strong relationship with feeding time (Fig. 2). Profitability for snails feeding on worms was 6.76 mg DW h^{-1} of handling time.

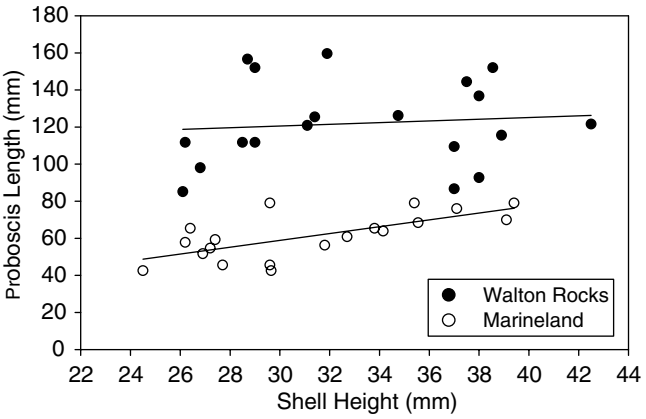

Fig. 3 *Stramonita haemastoma*. Relationship between shell height and proboscis length for snails from two populations with different prey ($n = 19$ for each). Shell height was not a good predictor of proboscis length for snails from WR ($y = 0.458x + 106.795$, $r^2 = 0.010$) nor snails from ML ($y = 1.839x + 3.695$, $r^2 = 0.477$). Proboscises of snails preying on *P. lapidosa* predators from WR were significantly longer than bivalve predators from ML (Table 1)

Proboscis length

Stramonita haemastoma from WR that fed on *P. lapidosa* had much longer proboscises than conspecifics from ML that fed on bivalves (Fig. 3, Table 1). Differences in proboscis length varied with habitat and were not explained by differences in shell height. Individuals from WR 26.1 to 42.5 mm shell height had proboscises 85.1–159.6 mm long. Proboscis length was not significantly correlated with shell size; proboscises ranged from 2.34 to 5.46 times the height of the

Table 1 *Stramonita haemastoma* ANCOVA table comparing the effect of habitat on proboscis lengths with shell height as the covariate

Source of variation	df	SS	MS	F	P
Shell	1	984.46	984.46	3.01	0.091
Site	1	31,443.95	31,443.95	96.27	< 0.001
Error	35	11,431.33	326.61		
Total	37	47,533.87			

Table 2 *Stramonita haemastoma* ANCOVA table comparing the effect of habitat and diet on proboscis lengths of snails with shell height as the covariate for groups of snails in the laboratory

Source of variation	df	SS	MS	F	P
Shell	1	648.51	648.51	2.20	0.144
Site	1	6.15	6.15	0.02	0.886
Prey	1	3,049.74	3,049.74	10.33	< 0.01
Site × Prey	1	913.35	913.35	3.09	0.085
Error	55	16,237.43	295.23		
Total	59	20,291.90			

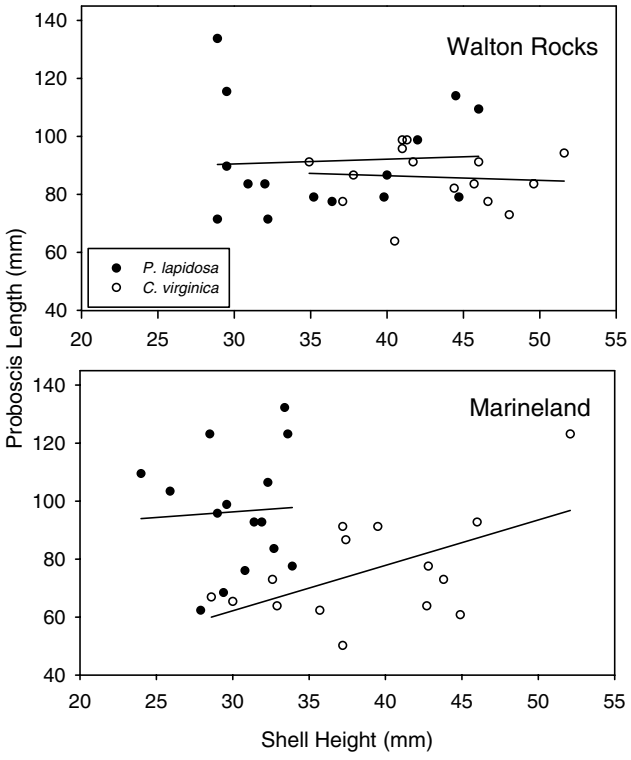

Fig. 4 *Stramonita haemastoma*. Relationship between shell height and proboscis length from two different sites (WR and ML) maintained for 9 months on diets of *P. lapidosa* or *Crassostrea virginica*. Proboscises of snails fed *P. lapidosa* were proportionally longer than those fed *C. virginica* (Table 2). Regressions indicate that shell height was not a good predictor of proboscis length for snails from WR maintained on *P. lapidosa* ($y = 0.171x + 85.884$, $r^2 = 0.003$) or on *C. virginica* ($y = 0.336x + 99.745$, $r^2 = 0.025$) nor for snails from ML maintained on *P. lapidosa* ($y = 0.387x + 84.660$, $r^2 = 0.01$) or on *C. virginica* ($y = 1.671x + 11.492$, $r^2 = 0.376$)

snail's shell (mean 3.74 ± 0.85 SD). One individual with a 28.7 mm shell had a proboscis 156.6 mm long.

Snails from ML 24.5 to 39.4 mm shell height had proboscises 42.6–79.0 mm long. Proboscises ranged from 1.44 to 2.67 times the height of their shells, with a mean of 1.96 ± 0.30 (SD) times shell height. Thus, snails from WR that normally feed on worms can extend their proboscises about 1.9 times further than snails from ML that normally feed on bivalves.

Stramonita haemastoma maintained in the laboratory for 11 months on a diet of *P. lapidosa* had significantly longer proboscises than snails fed oysters irrespective of size or original habitat (Fig. 4, Table 2). Regressions indicate that shell height was not a good predictor of proboscis length for snails from WR maintained on *P. lapidosa* ($y = 0.171x + 85.884$, $r^2 = 0.003$) or on *C. virginica* ($y = 0.336x + 99.745$, $r^2 = 0.025$), nor for snails from ML maintained on *P. lapidosa* ($y = 0.387x + 84.660$, $r^2 = 0.01$) or on *C. virginica* ($y = 1.671x + 11.492$, $r^2 = 0.376$).

Snails from WR fed tubeworms had proboscises 2.62 ± 0.73 times shell height, whereas snails from the same site fed *C. virginica* had shorter proboscises,

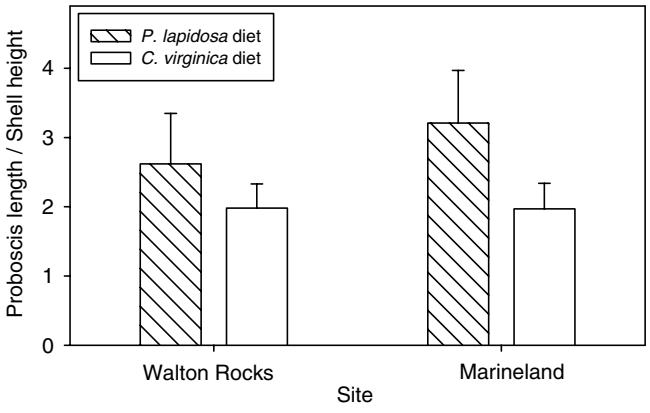

Fig. 5 *Stramonita haemastoma*. Ratio of proboscis length to shell height for snails from two different sites (WR and ML) maintained for 9 months on diets of *P. lapidosa* or *C. virginica*. *Error bars* = 1 SD ($n = 16$ for each site-prey combination)

2.02 ± 0.34 times shell height (Fig. 5). On a diet of *Phragmatopoma lapidosa*, snails from ML had proboscises 3.21 ± 0.76 times the height of the shell, whereas snails from the same site fed oysters, had proboscises only 1.97 ± 0.38 times the shell height. By the end of the experiment, nearly all snails raised on oysters had larger shells than snails fed *P. lapidosa*, irrespective of where the snails had originated.

Phragmatopoma lapidosa length and mass

Phragmatopoma lapidosa collected in April 2001 had a mean length of 14.55 ± 2.92 mm (range 8.34–20.94) and a dry mass of 4.233 ± 1.584 mg mm^{-1} worm^{-1} ($n = 41$) (range 1.2–8.8 mg mm^{-1} worm^{-1}). The average amount of consumable tissue (without the operculum) was 3.664 ± 1.419 mg. The operculum of *P. lapidosa* made up

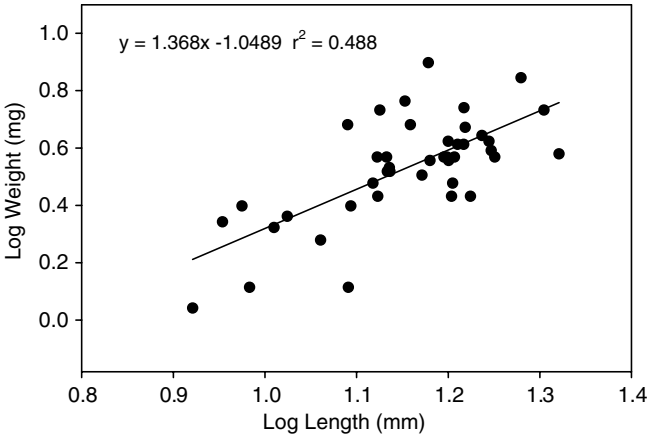

Fig. 6 *Phragmatopoma lapidosa*. Relationship between length and dry mass of worms from WR in April 2001 ($n = 41$) All values were log transformed and mass increased significantly with length. Worm length increased with mass ($y = 1.368x - 1.0489$, $r^2 = 0.488$)

approximately 13.6 ± 3.6% of the total dry mass of the worm. Dry mass of *P. lapidosa* was positively related to worm length (Fig. 6).

Feeding rate

Stramonita haemastoma consumed a total of 10.8 ± 2.7 (SD) *Phragmaopoma lapidosa* in 7 days. Snails ate about 5 to 14 worms during the feeding period. Their mean daily feeding rate was 1.57 ± 0.38 worms snail^{-1} day^{-1}, equivalent to 5.76 ± 1.40 mg DW snail^{-1} day^{-1}. All control worms remained alive during the duration of the experiment. One snail that escaped from its tank and died was not included in the measurements.

Discussion

The feeding habits of *S. haemastoma* living on sabellariid worm reefs differ from conspecifics in more typical habitats. Major differences in handling costs, prey defense, and mode of feeding affect foraging on the reefs. A diet of worms does not require snails to bore through shell, drastically reducing the amount of time and energy required to feed. Instead, the successful capture and consumption of *P. lapidosa* is dependent upon reaching the worms deep within their tubes. *Phragmatopoma lapidosa* can only escape if it retreats beyond the reach of the snail's extendable proboscis. Although *P. lapidosa* possesses a chitinous operculum that seals the opening of the tube and protects the worm from environmental stress (Kirtley 1968), it is not adequate protection against the probing proboscis and scraping radula of *S. haemastoma*.

On sabellariid reefs, a long proboscis is the most important feeding structure of *S. haemastoma*. The proboscis serves the same function on the worm reef as it does in oyster beds; by extending the reach of the mouth, the proboscis allows the snail to feed on items that it cannot approach because of its bulky shell. When feeding on bivalves, the proboscis reaches well-protected soft tissue inside the valves of prey (Carriker and Van Zandt 1972; Gunter 1979). We also observed that, when feeding in groups, a long proboscis allows several snails to feed simultaneously on a single gaping oyster. Without a long proboscis, *S. haemastoma* would be incapable of capturing *P. lapidosa* and thus unlikely to establish populations on sabellariid reefs.

Stramonita haemastoma collected from sabellariid reefs had proboscises nearly twice the relative length of snails from Marineland that feed on bivalves (3.74 compared to 1.96 times shell height). A longer proboscis greatly extends the reach of *S. haemastoma* and facilitates feeding on tubeworms. A short proboscis in this environment would make the capture of prey more difficult or impossible. Most proboscises of worm-fed snails were > 70 mm long (many were > 100 mm) suggesting that *P. lapidosa* must retreat at least 70 mm to escape an attack. Using grains of sand, *P. lapidosa* increases the length and diameter of its tube as it matures. The most recently constructed part of the tube is near the opening and is wider than older parts of the tube which are built when the worm is smaller. Even though sabellariid reefs may be > 1 m tall, the length of tube occupied by the worm is much shorter, leaving worms within reach of *S. haemastoma*. Worms could potentially respond to predation pressure by building longer tubes, but this would create larger worm mounds that are less stable and more likely to break under wave pressure. Also, longer tubes in the intertidal might reach above the water line and would increase exposure and stress during low tide.

At WR two non-shell-boring gastropods, *Pollia tincta* (Buccinidae) and *Leucozonia nassa* (Fasciolaridae), were observed feeding on *P. lapidosa* with long proboscises inserted in worm tubes, though these species were rare compared to *S. haemastoma*. Decapod crustaceans (Gore et al. 1978) and *S. haemastoma* probably account for the greatest predation pressure on *P. lapidosa* where they co-occur.

Differences in proboscis length between snails collected from WR and ML are attributable to phenotypic plasticity of the feeding structure and probably not to genetic differences. *Stramonita haemastoma* kept on a diet of *P. lapidosa* grew significantly longer proboscises than snails fed oysters, irrespective of where the snails had originated suggesting that differences in proboscis length are inducible. Phenotypic plasticity is common in a number of morphological traits among gastropods. Variations in shell morphology can be induced by the presence of predators (Hughes and Elner 1979) and climatic differences (Vermeij 1978; Trussell 2000). Shell shape and height, and size of the foot vary with wave energy (Trussell 1997), and radular teeth of some snails can vary in shape depending on prey (Padilla 1998; Reid and Mak 1999). Phenotypic plasticity is particularly advantageous for species with dispersive larvae that may settle in environments with a wide range of conditions. For *S. haemastoma*, flexibility in proboscis morphology permits the snail to broaden its diet and survive in a habitat where its typical food is absent.

Snails from WR are probably genetically similar to those found at ML because larval *S. haemastoma* spend several months in the plankton (Scheltema 1971; Dobberdeen and Pechenik 1987), a trait that promotes genetic exchange and reduces the likelihood of locally specialized, genetically distinct populations (Janson 1987). In fact, population dynamics observations at WR and at other sabellariid reef sites suggest that snails on sabellariid reefs disappear (probably perish) before reproducing (Watanabe 2002). Thus, a new population of *S. haemastoma* is established each year from larvae produced elsewhere, probably from shell-boring populations. Populations on sabellariid reefs appear to be genetic sinks for other populations, though genetic analysis is required to confirm this.

The energetic cost of foraging on sabellariid reefs is quite different than the cost of foraging on bivalves in other habitats. Time and energy, two related components of foraging models, are used to determine the value of prey (Hughes 1980). *Stramonita haemastoma* save a tremendous amount of time feeding on tubeworms, consuming worms in a fraction of the time (< 1 h) it takes to eat bivalves (1–3 days). Bivalve prey are larger than tubeworms and *S. haemastoma* feeding on bivalves may fast for several days between meals (Gunter 1979). In contrast, *S. haemastoma* on sabellariid reefs eat less tissue per meal while feeding more frequently. Laboratory feeding rates of *S. haemastoma* were between 1.5 and 1.7 worms snail^{-1} day^{-1} and snails thus spent < 2 h day^{-1} feeding. Boggs et al. (1994) found that when prey was artificially altered to reduce handling time, boring gastropods increased their feeding rates. Since feeding on worms is fast, snails could potentially increase their daily energy intake. It is important to note that feeding rates were calculated with snails of only one size class and that feeding rates of *S. haemastoma* vary with temperature, salinity (Garton and Stickle 1980), presence of predators (Richardson and Brown 1992), and wave action (Richardson and Brown 1990). In addition, *P. lapidosa* shows a seasonal growth cycle (McCarthy 2001), so differences in energy value per worm may also influence feeding rates and the amount of tissue ingested.

Shell-boring snails expend energy by scraping the surface of a shell with their radula for hours or days. In addition, the production of enzymes used for the chemical dissolution of shells and wear and tear on the radula (Carriker 1978, 1981) are also costs associated with boring. Because *S. haemastoma* on worm reefs do not drill when feeding on tubeworms, there may be striking differences in the amount of energy required to feed compared with conspecifics in other habitats. When handling costs are low, prey become more profitable. Most bivalves contain more tissue than *P. lapidosa*, but comparisons of the amount of tissue ingested for every hour of handling time allows meaningful comparisons of food values. Solitary *S. haemastoma* feeding on solitary mussels (wet mass < 2.0 g), clumped oysters (wet mass ~35.1 g), and solitary clams (wet mass ~63.6 g), ingested 0.61, 1.48, and 0.34 mg DW h^{-1}, respectively (Brown and Richardson 1987). Snails feeding on *P. lapidosa* are much more efficient, ingesting an average of 6.76 mg DW h^{-1} of handling time. Prey such as *P. lapidosa* that provide relatively more return in a given time period are, by definition, more optimal prey (Hughes 1980). Feeding more efficiently can affect the snail's energy budget, and possibly manifest itself as changes in growth or reproductive output (Bayne and Newell 1983). However, the energy contents of *P. lapidosa* and bivalve tissue need to be determined in order to make more meaningful comparisons. Despite saving time and energy, laboratory feeding experiments and field population studies have shown that shell-boring *S. haemastoma* grow much more rapidly and attain much larger sizes while feeding on *C. virginica* or other bivalves than non-boring *P. lapidosa* consumers (Watanabe 2002). Nutrition may play an even larger role than time and energy on the overall growth and fitness of *S. haemastoma*.

A diet of *P. lapidosa* may be advantageous for a number of other reasons. Because feeding on tubeworms takes less time, snails may quickly feed and then retreat to shelter. Boring requires snails to remain in place for long periods of time. In the intertidal zone, boring snails often must endure exposure over multiple tidal cycles and drastic changes in the environment over the course of a single meal (Menge 1974). Extended bouts of drilling render snails vulnerable to desiccation or thermal stress (Menge 1978a, b). In the intertidal and subtidal zones, disturbance by waves (Menge 1974; Burrows and Hughes 1989; Richardson and Brown 1990) and attack by predators (Richardson and Brown 1992) can result in death or the abandonment of a meal with a commensurate loss of many hours of shell drilling. Although tidal heights and emersion times along the east coast of Florida are not extreme, sabellariid reefs are exposed to high temperatures, intense solar radiation, and moderate wave action during tidal exchanges (Watanabe 2002). By feeding quickly, *S. haemastoma* avoids most of the hazards associated with extremely long handling times.

Stramonita haemastoma survives and feeds on sabellariid reefs despite the absence of its typical bivalve prey. Although *S. haemastoma* possesses feeding structures specialized for penetrating shells, a phenotypically plastic proboscis as well as adaptable foraging strategies allow this species to broaden its diet to include tube-dwelling polychaetes.

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