Comparative feeding biology of *Acteocina canaliculata* (Say, 1826) and *Haminoea solitaria* (Say, 1822) (Opisthobranchia: Cephalaspidea)

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Abstract. The southern New England cephalaspidean *Acteocina canaliculata* (Say, 1826) feeds on bivalves, including *Gemma gemma* (Totten, 1834), and Foraminifera belonging to three suborders: Textulariina, Miliolina, and Rotaliina. The proportion of miliolid foraminiferans in the diet of *A. canaliculata* decreased with increasing snail size. Snails > 5.0 mm in shell length fed increasingly on bivalves, probably reflecting an inability of small snails to ingest large prey. The snails appear to locate prey with the aid of Hancock's organ and sensory patches (here reported for the first time) situated along the anterior edge of the cephalic shield and foot. Individual prey are grasped with the radula and pulled whole into the buccal cavity. Sediment particles appear to be removed passively by the jaws. *Haminoea solitaria* (Say, 1822) indiscriminately ingests sediment containing diatoms, unidentified algae, and detritus. Hancock's organ and sensory palps in *H. solitaria* probably do not aid in selection of specific food particles, but could be involved in location of areas where diatoms and algae are abundant.

Cephalaspidean opisthobranchs are common members of the shallow water marine benthos. Previous studies revealed that cephalaspids feed on a variety of food items, including bivalve and gastropod mollusks (Hurst, 1965; Berry, 1988; Berry and Thompson, 1990; Morton and Chiu, 1990), foraminiferans (Burn and Bell, 1974a, b; Shonman and Nybakken, 1978; Berry, 1988; Berry and Thompson, 1990), polychaete worms (Hurst, 1965; Rudman, 1972a, b; Yonow, 1989), and algae (Fretter, 1939; Rudman, 1972a). Few studies have dealt with the feeding habits of cephalaspids in detail. Two species, *Acteocina canaliculata* (Say, 1826) and *Haminoea solitaria* (Say, 1822), occur commonly along the New England coast (Abbott, 1974) and offer an opportunity to investigate and contrast the feeding biology of two genera in detail.

Acteocina canaliculata is a small (4-6 mm) opistho-branch found commonly in both oceanic and estuarine environments in bare or vegetated, sandy to muddy subtidal habitats (Franz, 1971; Gosliner, 1979; Mikkelsen and Mikkelsen, 1984). The only species of *Acteocina* studied previously with regard to feeding, *A. culcitella* (Gould, 1852), is a selective predator on foraminiferans (Shonman and Nybakken, 1978).

Haminoea solitaria, another small (10-12 mm) opistho-branch, occurs in environments similar to those of *Acteocina canaliculata*. Except for *H. brevis* (Quoy and Gaimard, 1833), which is reported to feed on bivalve mollusks (MacPherson and Gabriel, 1962), members of the genus *Haminoea* are

reportedly herbivorous (Fretter, 1939; Rudman, 1971a,b; Gibson and Chia, 1989). Diet and feeding behavior have been described for *H. hydatis* (Linnaeus, 1758) and *H. zelandiae* (Gray, 1843) (Fretter, 1939; Rudman, 1971a, b). Both species feed on filamentous green algae using the jaws and radula to break pieces of algae and the gizzard plates to grind them. This paper presents information on the dietary composition, changes in diet, and behaviors associated with the location and consumption of food by *A. canaliculata* and *H. solitaria*.

MATERIALS AND METHODS

Acteocina canaliculata and *Haminoea solitaria* were collected in summer 1989 and spring 1990 from a sandy-mud flat in Bluff Hill Cove, Point Judith Salt Pond, Galilee, Rhode Island, USA (41° 23'N, 71° 30'W) (Fig. 1). Qualitative field observations on the relative abundance of both snails were made approximately every month from April 1989 to September 1990.

Individuals for diet analysis were collected by passing the flocculent top 1 cm of substratum through a 1.0 mm sieve. The animals were fixed in 5% buffered formalin immediately after collection and transferred to 75% ethanol after 24 to 48 hours. The digestive tract of *Acteocina canaliculata* was removed with the aid of a dissecting microscope, and the contents spread on a microscope slide. Food items were transferred with the aid of a small camel hair brush to double-stick tape mounted on a microscopic slide. Items were identified to the lowest possible taxonomic level utilizing Loosanoff *et al.* (1966), Abbott (1974), Cushman (1976), and
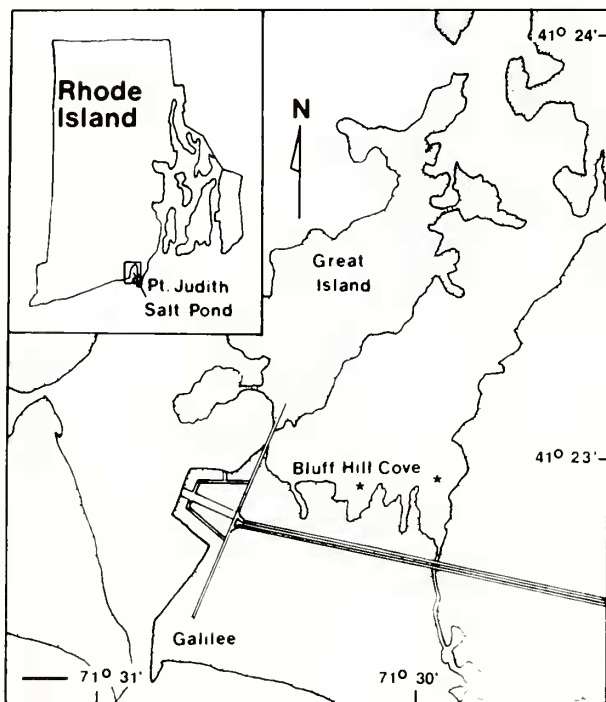
Fig. 1. Location of study site where *Acteocina canaliculata* and *Haminoea solitaria* were collected. Specific collecting sites are marked with an asterisk (scale bar = 200 m).

Todd and Low (1981).

Preliminary observations revealed that *Haminoea solitaria* feeds on diatoms and detritus. Therefore, the contents of the digestive tract were determined following the methods of Kesler *et al.* (1986). The digestive tract was removed, the contents mixed with a small amount of water, and evenly distributed on a glass slide. A grid containing 50 evenly spaced fields was viewed at 100x and scored for the presence of diatoms, filamentous algae, animal parts, sand, and detritus. The presence of each food type was quantified as the proportion of total fields containing that food item out of all fields that contained one or more food items. This procedure assumes that the proportion of fields containing an item reflects the amount of the food item in the diet. Items were identified utilizing Kennett and Hargraves (1988). Additionally, fecal remains from ten individuals were spread on a slide and viewed at 100x to determine which of the ingested material was being digested.

Multivariate analysis of variance (MANOVA) was performed on dietary proportions with respect to shell length and sample date (Sokal and Rohlf, 1981). Shell length of each animal was measured to the nearest 0.1 mm. Three size groups were chosen to give equal sample sizes between groups. Statistical analyses were performed using Statistical Analysis System (SAS Institute, Cary, NC). The results are presented as an F-ratio (F), with the appropriate degrees of freedom

(d.f.), and level of significance (P).

Snails used for feeding observations were collected as above and maintained in small aquaria. Algal and sediment samples were taken at the same time and location as the snails in order to present the same potential food sources to the snail as are found in their natural habitat. Feeding behavior was recorded with a video camera, mounted so as to view the ventral region of the snail, and a video cassette recorder that allowed frame-by-frame analysis of behavioral events.

Potential food items of *Acteocina canaliculata* (foraminiferans and bivalves) were selected carefully from substratum samples and placed in small petri dishes. These prey organisms were acclimated to laboratory conditions for at least 24 hr prior to observations. Attempts were made to remove sediment particles clinging to foraminiferans to improve the clarity of viewing feeding activity. A variety of potential food items, including a thin layer of sand containing micro-organisms and various algal species found in the sediments at the mudflat, was presented to *Haminoea solitaria* in a small glass chamber (10 x 10 x 12 cm).

Voucher specimens of *Acteocina canaliculata* (MCZ 302559) and *Haminoea solitaria* (MCZ 302560), collected from the study site, are located in the collections of the Museum of Comparative Zoology (MCZ), Harvard University.

RESULTS

ACTEOCINA CANALICULATA

Acteocina canaliculata was present on the Bluff Hill Cove mud flat throughout 1989 and 1990, with the highest abundances occurring during July and August 1989. Larger snails (shell length > 3.9 mm) were more abundant during these two months (Fig. 2). Juveniles (shell length > 1.0 mm) first appeared in March and April 1990.

1. DIET

Sixty-eight percent of the snails (n = 97, 2.0-6.8 mm shell length) contained food particles (Table 1). Food remains, consisting of foraminiferans and bivalves, were found in the esophagus, gizzard, stomach, and intestine. Ninety-eight percent of the food remains in the stomach and intestine were crushed yet remained as discrete particles. Food remains found posterior to the stomach consisted mainly of shell or test fragments and fecal material. Sediment grains were found in only nine individuals. The gizzard plates of all dissected individuals showed no obvious sign of physical damage.

Foraminiferans found in the digestive tract belonged to three suborders: Textulariina, Miliolina, and Rotaliina. The majority of miliolid foraminiferans recovered from the digestive tract was crushed. Some fragments did allow generic identification. The remaining fragments were classified as "miliolid spp." due to the porcelaneous appearance of the
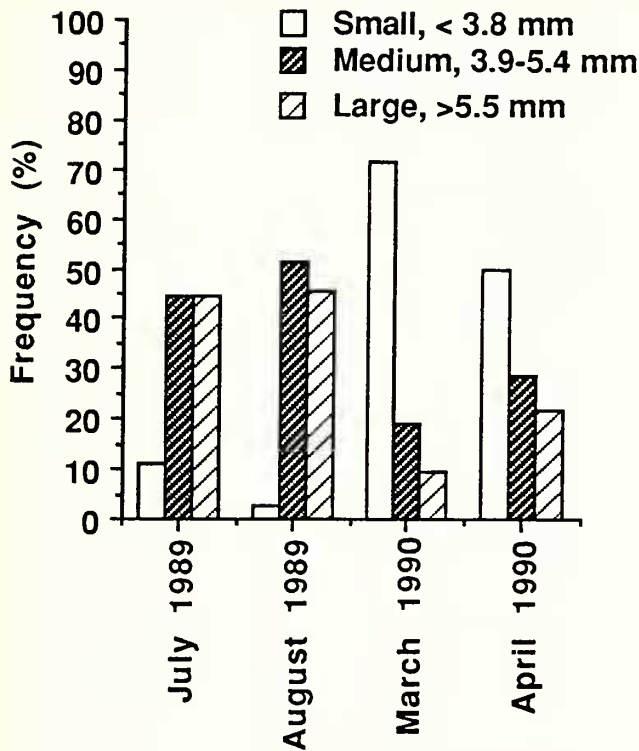
Fig. 2. Percentages of three sizes of *Acteocina canaliculata* collected over a four-month period from July 1989 to March 1990.

test (Todd and Low, 1981). Other foraminiferan fragments could not be identified and were classified as "unidentified forams." Eighty-three percent of Textulariina and Rotaliina found in the esophagus and gizzard were whole and showed no obvious signs of chemical or physical damage.

No bivalves were found in the esophagus, and all bivalves found in the gizzard, stomach, and intestine were crushed, making identification impossible in some cases. However, *Gemma gemma* (Totten, 1834) was usually identifiable based on the purplish coloration of its shell (Abbott, 1974).

Snail size was correlated with the type of food item in the gut (Fig. 3). The proportion of miliolid foraminiferans was significantly lower in medium and large snails (MANOVA: F = 4.07, d.f. = 1, 61, P = 0.0481). In addition, there were fewer unidentified foraminiferan fragments in larger snails, probably an artifact because "fragments" taken from larger cephalaspids were larger and therefore more readily identifiable. A significantly higher abundance of bivalves was found in the guts of medium and large animals (MANOVA: F = 10.61, d.f. = 1, 61, P = 0.0018). In fact, only one animal < 5.0 mm had a crushed bivalve in its intestine.

The proportion of bivalves in the diet was significantly higher in July and August than in March and April

(MANOVA: F = 12.44, d.f. = 1, 61, P = 0.0008) (Fig. 4). Unidentified foraminiferans were significantly higher in March than in other months (MANOVA: F = 4.33, d.f. = 1, 61, P = 0.0417). Again, this was probably due to the relative ease of identifying the larger foraminiferan fragments taken from larger animals.

2. BEHAVIORAL OBSERVATIONS: MOVEMENT

Movement was observed in 18 individuals (size = 3.6-5.2 mm). *Acteocina canaliculata* burrows into the top few millimeters of the substratum using the combined cephalic shield and tentacles as an efficient plow (Fig. 5). Sediment particles are carried by ciliary action along the dorsal surface of the cephalic shield and the posteriorly directed tentacles, and are sloughed off along either side of the shell. Typically, when moving, the head-foot extends forward, gliding across the substratum. With the foot extended anteriorly, the shell is retracted towards the head and the cycle repeated. Moving in this manner, the average speed for *A. canaliculata* was 17.6 mm per min on glass (n=3).

3. BEHAVIORAL OBSERVATIONS: FEEDING

A number of sense organs are located along the leading edge of the cephalic shield and foot. Two slightly darker sensory patches are located on either side of the mouth along the anterior edge of the cephalic shield (Fig. 6). Two other similar patches exist in corresponding positions on the foot. This area is highly active and was observed repeatedly touching the substratum and potential food items. Hancock's organs are located on either side of the head in antero-posterior grooves created by the cephalic shield and the foot. The animal characteristically swings the foremost part of the

Table 1. List of recovered food remains (including fragments) from 66 *Acteocina canaliculata* arranged by taxonomic group. % in Gut refers to the frequency of a food item in the gut. % Snails refers to the percent of snails in which a food item was present.

| Food Item	% in Gut	% Snails	# of Particles
Suborder Textulariina			
Trochammina	23.7	57.4	77
Suborder Miliolina			
Miliommina	9.2	23.5	30
Quinqueloculina	8.3	27.9	27
Miliolid spp.	26.2	50.0	85
Suborder Rotaliina			
Pseudononion	2.2	7.4	7
Astrononion	1.9	7.4	6
Haynesina	0.6	2.9	2
Nonionella	0.3	1.5	1
Elphidium	0.3	1.5	1
Suborder Unknown			
Unidentified Forams	6.8	22.1	22
Class Bivalvia			
Gemma gemma	14.2	26.5	46
Unidentified bivalves	6.5	17.7	21
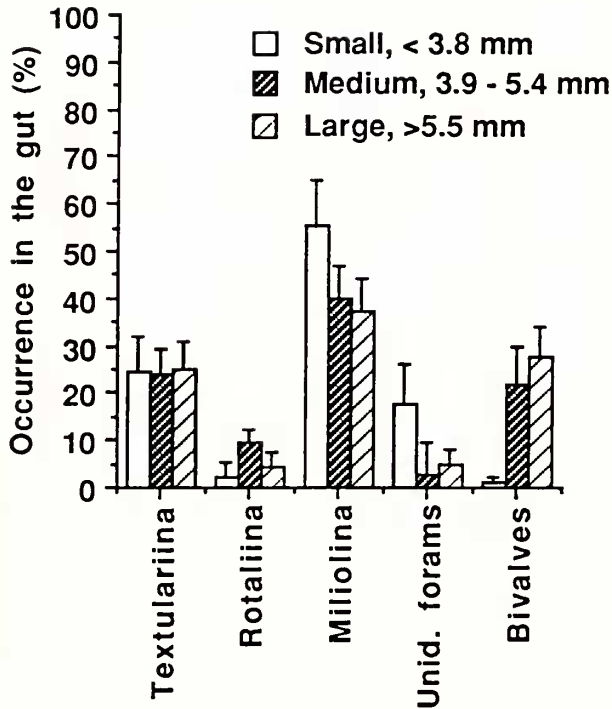
Fig. 3. Percentage of food items in the gut of three sizes of *Acteocina canaliculata* (bar = standard error of the mean).
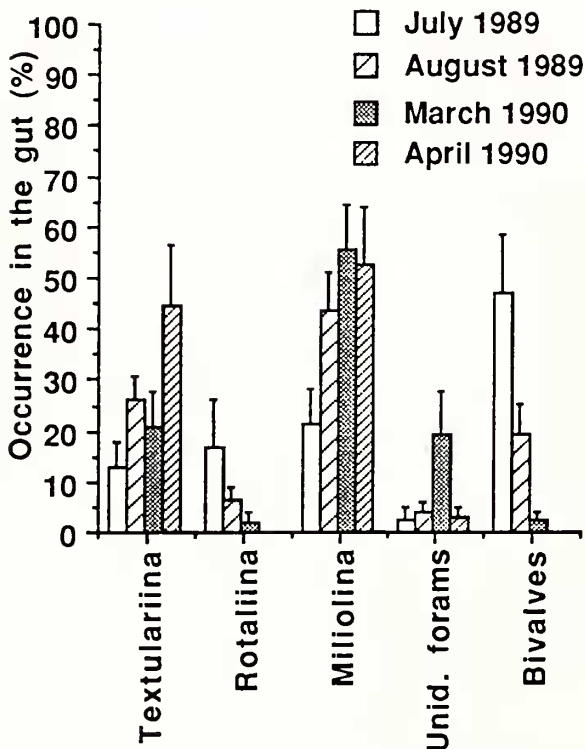

Fig. 4. Percentage of food items in the gut of *Acteocina canaliculata* collected in a four-month period from July 1989 to April 1990 (bar = standard error of the mean).

head back and forth, apparently searching for food. On six separate occasions, *Acteocina canaliculata* turned towards a prey items from a distance of 1 to 3 mm.

Feeding was observed in five individuals of *Acteocina canaliculata* (size = 4.5-5.2 mm). Upon contact, a potential food item is touched repeatedly by the sensory patches. The anterior edge of the cephalic shield and foot is compressed into a funnel-shaped cavity with the mouth in the center and sensory patches on either side. The mouth is then pressed against the food item, the buccal mass contracted, the odontophore protruded through the mouth, and the item gripped with the radula. The food item is then pulled into the buccal cavity. The jaws, located near the anterior end of the buccal cavity, appear to scrape off most of the sand grains clinging to the food item as it is drawn past the jaws into the mouth.

All foraminiferans ingested by *Acteocina canaliculata* were alive when eaten. Living foraminiferans are differentiated easily from empty tests because they are surrounded by detritus and sediment grains gathered by the reticulopodia (Cushman, 1976). Empty tests were ignored consistently by *A. canaliculata*, and they were passed up and over the cephalic shield along with sediment particles.

Capture and ingestion of a living bivalve *(Gemma gemma)* was observed only once. In this instance, a 5.2 mm snail turned towards the bivalve from a distance of 1.6 mm, and repeatedly touched it with its sensory patches. The bivalve was approximately 350 μm in height. It was gripped by the radula along the anterior edge, just anterior to the umbo, with the ventral opening facing down. Several attempts were made to draw the bivalve through the mouth and, after approximately two minutes, it was ingested.

HAMINOEA SOLITARIA

Haminoea solitaria was abundant seasonally, and it first appeared in mid-June 1989. The smallest individual collected during that summer was 3.0 mm in shell length. Field observations revealed that *H. solitaria* was extremely abundant during summer 1989, with large individuals more prevalent than small individuals in July and August. None were found after 17 November 1989. *H. solitaria* was first collected in 1990 on 13 July. The smallest individual collected during 1990 was 3.7 mm.

1. DIET

Sixty-seven percent of the snails (n = 106, 3.8-12.0 mm shell length) contained food items in their digestive system. Diatoms accounted for 36% and detritus accounted for 34% of the material ingested. Diatoms found included *Grammatophora, Thalassiosira, Coscinodiscus, Peridinium, Navicula, Gyrosigma, Skeletonema,* and *Chaetoceros*. Sand also constituted a large portion (26%) of the material found in the gut. Algae composed 3% of the diet. No attempt was
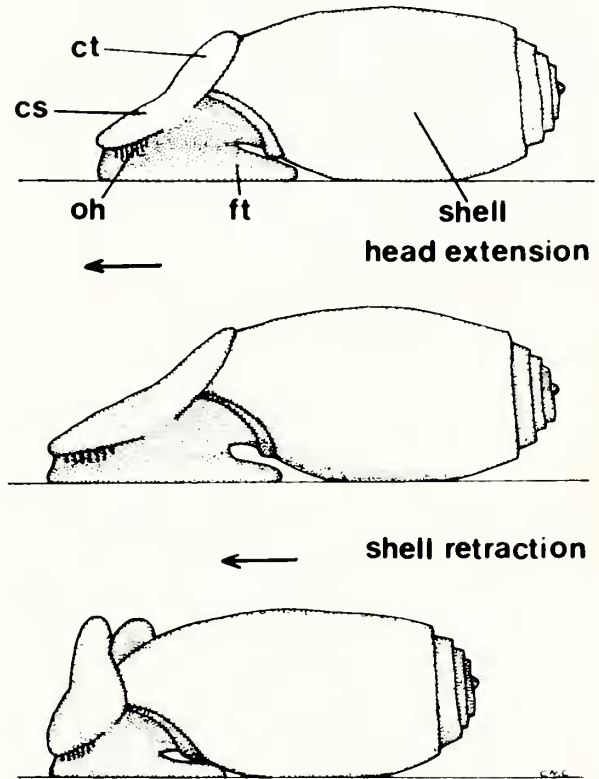
Dorsal View
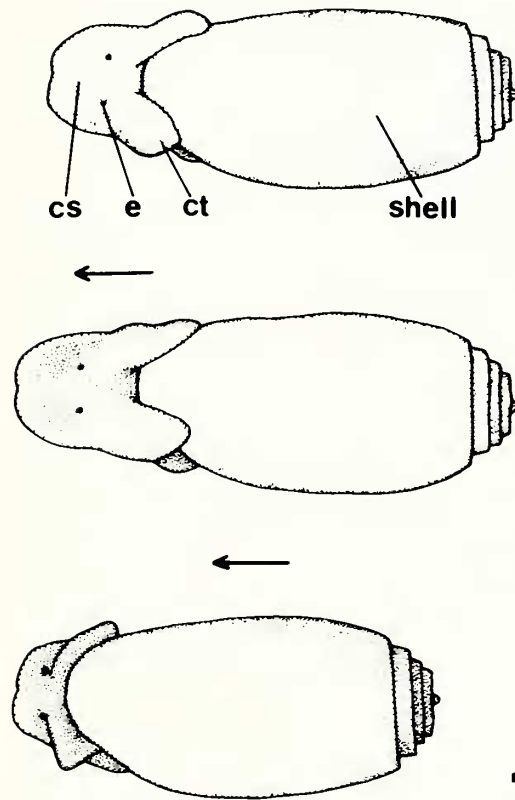
Lateral View

Fig. 5. Dorsal and lateral view of *Acteocina canaliculata* movement: cs, cephalic shield; ct, cephalic tentacle; e, eyespot; ft, foot; oh, Hancock's organ (scale bar = 1 mm).

made to identify algal species because of the small size of the fragments recovered. Additionally, a small fraction of the diet consisted of animals parts (1%). Animal parts included nematodes, copepods, nauplii larvae, ostracods, polychaete setae, oligochaetes, bivalves, and foraminiferans. The bivalves and foraminiferans showed no obvious signs of physical or chemical damage. Qualitative observations made of the fecal remains revealed that nearly all diatoms and animal parts consisted of empty tests suggesting that a large percentage of the diatoms and animals were digested.

The gizzard plates in 56 of the 106 *Haminoea solitaria* examined showed signs of damage. The outer, horny layer was usually torn away, creating pits in the plates. This was particularly apparent in larger individuals.

The proportion of sand and algae in the diet of *Haminoea solitaria* increased significantly with increasing snail size (MANOVA: sand, $F = 10.43$, d.f. $= 1$, 69, P $= 0.0002$; algae, $F = 6.02$, d.f. $= 1$, 69, P $= 0.0166$) (Fig. 7). Conversely, the amount of diatoms and detritus in the diet was significantly less in large animals (MANOVA: diatoms,

$F = 8.71$, d.f. $= 1$, 69, P $= 0.0043$; detritus, $F = 15.64$, d.f. $= 1$, 69, P $= 0.0002$). There was no significant change in the proportion of animal remains in the diet of small and large snails.

The diet was highly variable among sample dates, even when the dates were only a few days apart. Significant differences existed between sample dates in the summer of 1989 for detritus, sand, and algae (MANOVA: detritus, $F = 3.73$, d.f. $= 7$, 69, P $= 0.0019$; sand, $F = 4.53$, d.f. $= 7$, 69, P $= 0.0004$; algae, $F = 3.58$, d.f. $= 7$, 69, P $= 0.0026$) but not for diatoms or animals parts (Fig. 8). The proportions of diatoms in the diet decreased over time. There was no apparent trend in detritus and sand, but the percent of algae did exhibit an increase through August, a drop at the end of August and at the beginning of September, followed by a subsequent increase during September.

2. BEHAVIORAL OBSERVATIONS: MOVEMENT

Movement was observed in 18 individuals of *Haminoea solitaria* (size $= 3.3$-11.2 mm). The foot of *H. solitaria* is
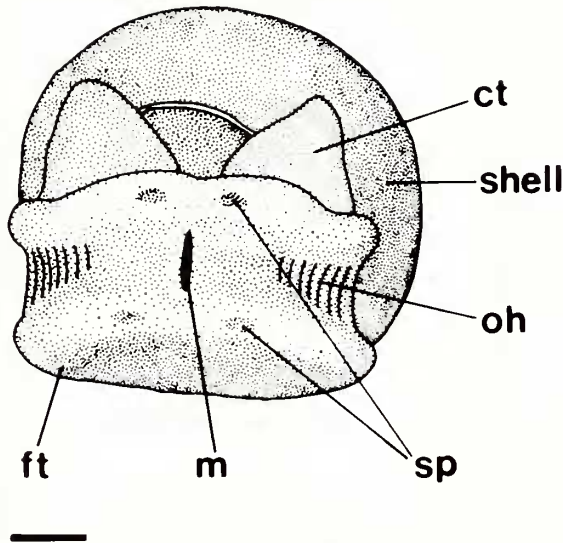
Fig. 6. Anterior view of *Acteocina canaliculata*: ct, cephalic tentacle; ft, foot; m, mouth; oh, Hancock's organ; sp, sensory patches (scale bar = 0.5 mm).

relatively larger than that of *Acteocina canaliculata* and has two parapodial lobes which curve up and around the anterior of the shell, often meeting mid-dorsally (Fig. 9a). Posterior to the foot, the floor of the mantle cavity extends postero-ventrally beyond the shell, forming the posterior mantle lobe. When moving, *H. solitaria* glides smoothly through the substratum. The foot secretes an almost complete tube of mucus which helps prevent sediment particles from clogging the mantle cavity. Sediment particles are moved along the ciliated cephalic shield where they are entrapped in the mucous secretions of the foot and sloughed off posteriorly. *H. solitaria* moves much faster than *A. canaliculata*, traveling an average of 97 mm per min on glass (n=3).

3. BEHAVIORAL OBSERVATIONS: FEEDING

Hancock's organs are located on either side of the head in antero-posterior grooves created by the cephalic shield and foot (Fig. 9b). They are smaller than in *Acteocina canaliculata*, and consist of slightly wavy ridges. In addition to Hancock's organ, two sensory palps are located on either side of the mouth, also in the antero-posterior groove. Sensory patches were observed in a few individuals, but could not be consistently found in all animals that were observed. *Haminoea solitaria* swings its head back and forth while moving forward. The leading edge of the cephalic shield and foot is highly active and repeatedly touches anything with which the animal comes in contact.

Feeding was observed in seven individuals (size = 4.6-10.9 mm). The feeding behavior of *Haminoea solitaria* is similar to that of *Acteocina canaliculata*. The buccal mass contracts, the odontophore protrudes through the mouth, and the radula grasps a mouthful of sediment. The odontophore

is then withdrawn and the buccal mass relaxes. All individuals observed appeared to ingest sediment at random with no selection of food particles. However, on several occasions *H. solitaria* rejected ingested particles by expectorating them.

DISCUSSION

Among opisthobranch gastropods, cephalaspids show the greatest diversity in feeding strategies, ranging from herbivores that graze algal mats or consume pieces of algae to carnivores that engulf whole prey animals (Kohn, 1983). The two species studied here have very different diets and exhibit two different feeding modes. *Acteocina canaliculata* seeks out and ingests whole foraminiferans and bivalves, while *Haminoea solitaria* consumes mouthfuls of sediment containing diatoms, detritus, and algae. Hard-shelled prey pass through *H. solitaria* apparently undigested.

In general, foraminiferans are ingested by two types of predators, unselective predators that ingest sediments containing foraminiferans, and selective predators that preferentially ingest foraminiferans (Lipps and Valentine, 1970; Murray, 1973). The diet and feeding behavior observed demonstrate that *Acteocina canaliculata* is a selective predator of foraminiferans in the sense that the snails are not selecting random sediment samples. Selective predation of forams
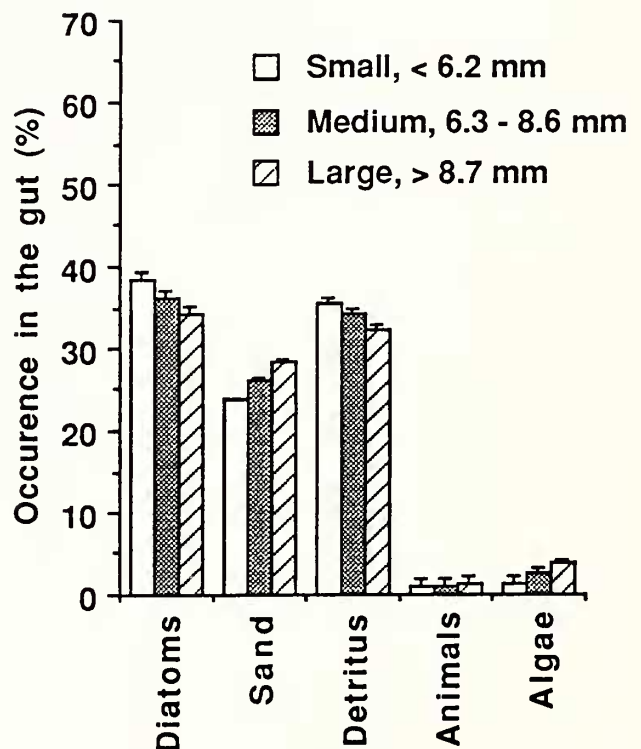

Fig. 7. Percentages of food items in the gut of three sizes of *Haminoea solitaria* (bar = standard error of the mean).
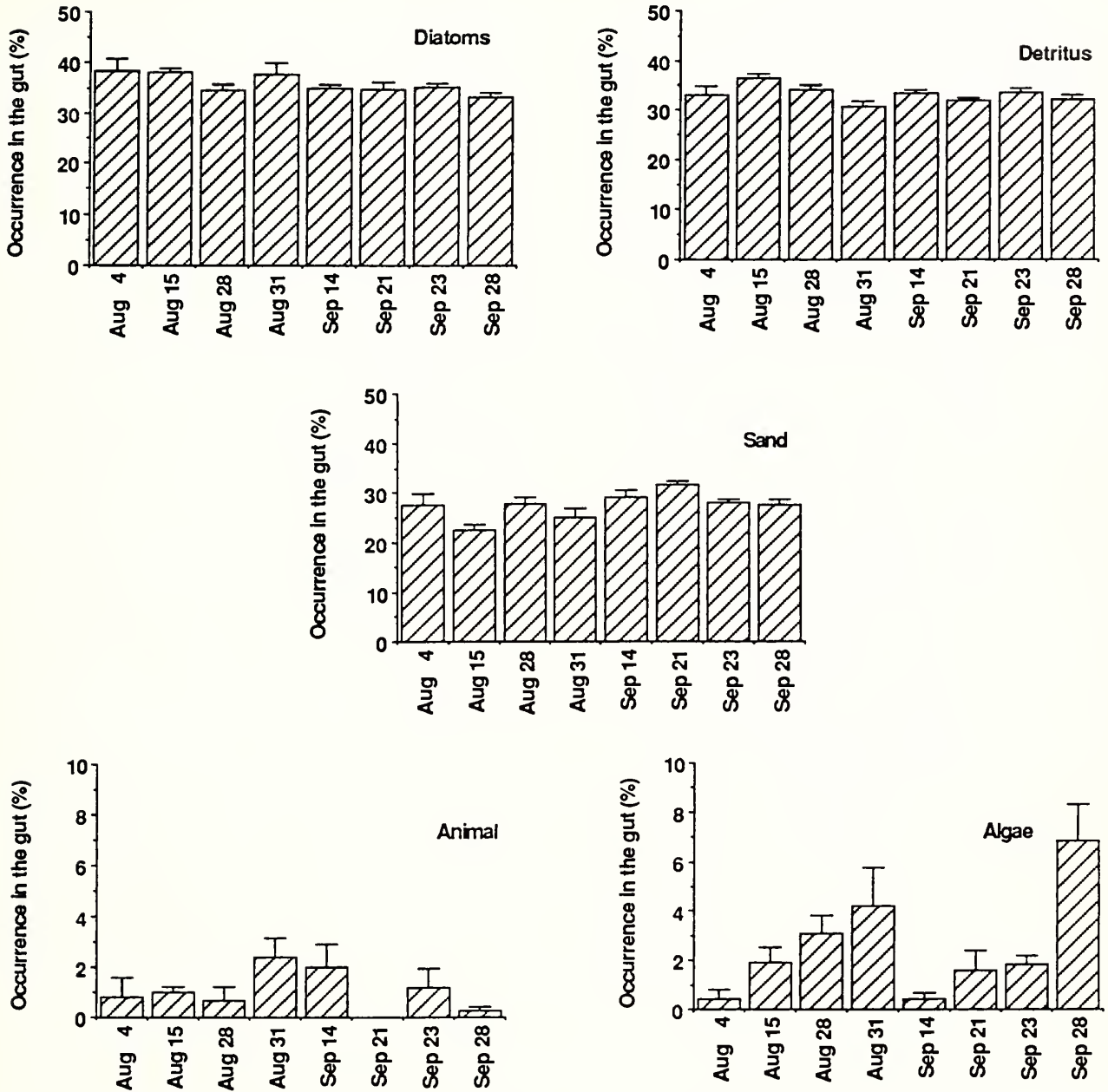
Fig. 8. Percentages of food items in the gut of *Haminoea solitaria* for eight sample dates in 1989 (bar = standard error of the mean).

has also been observed in *A. culcitella* (Shonman and Nybakken, 1978) and other cephalaspids (Hurst, 1965; Burn and Bell, 1974a,b; Berry, 1988; Berry and Thomson, 1990). These observations further suggest that *A. canaliculata* locates food items before they are physically contacted using Hancock's organ and sensory patches. Hancock's organ functions as a chemosensory organ in other cephalaspids (Lemche, 1956; Hurst, 1965; Edlinger, 1980; Kohn, 1983). Sensory patches have been observed in the genus *Philine* (Hurst, 1965; Rudman, 1972c). In *P. aperta* Linnaeus, 1766 they are believed

to aid in prey location and capture (Hurst, 1965). These organs, in *A. canaliculata*, appear to play a specific role in food acquisition, that of locating individual foraminiferans. In *A. canaliculata*, sensory patches appear to play a similar role.

Ontogenetic changes in diet have been observed in other gastropods, as well as in seastars, chitons, and fish (Hurst, 1965; Hughes, 1980; Taylor, 1980; Berry, 1988; Paine, 1988; Berry and Thomson, 1990). The diet of *Acteocina canaliculata* changed with shell size. As size increased, the
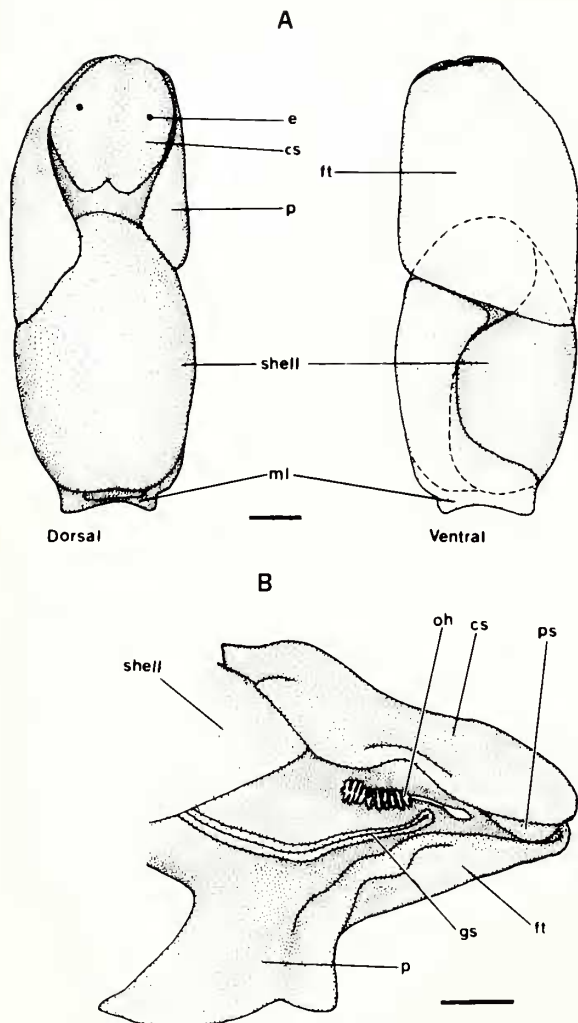
A

Dorsal   Ventral

B

Fig. 9. External anatomy of *Haminoea solitaria.* A. Dorsal and ventral views (scale bar = 2 mm). B. Lateral view of head-foot with lateral parapodia reflected ventro-laterally (scale bar = 1 mm): cs, cephalic shield; e, eyespot; ft, foot; gs, external seminal groove; ml, posterior mantle lobe; oh, Hancock's organ; p, parapodial lobes; ps, sensory palps.

abundance of miliolid foraminiferans in the gut decreased. Additionally, there was an increase in the proportion of bivalves in the guts of snails larger than 5.0 mm. This dietary pattern could represent an inability of small *A. canaliculata* to ingest large prey items. Foraminiferan size is generally between 50 μm and 300 μm (Cushman, 1976). Bivalves are typically larger than 200 μm when they settle. For example, *Mya arenaria* Linnaeus, 1758, has a minimum shell size at metamorphosis of 225 x 209 μm (Loosanoff *et al.*, 1966), thus representing the smallest bivalve species that is potentially available to *A. canaliculata* at Galilee. Snails smaller than 5.0 mm in length could be restricted to ingesting only foraminiferans due to the size of their digestive tract. From about 5.0 mm shell length the diameter of the digestive tract

or size of the radula would be large enough to allow *A. canaliculata* to incorporate bivalves, as well as larger foraminiferans, into its diet. Unfortunately, the number of measurable food remains was too small to adequately test this hypothesis.

A shell length of 5.0 mm could also represent a practical limit to the size at which the energy gained by eating foraminiferans is greater than the energy expended in searching for and ingesting them. Assuming that there is more energy to be gained by eating bivalves compared to foraminiferans, and that *Acteocina canaliculata* is maximizing its energy intake, then bivalves may be more profitable to snails larger than 5.0 mm (see Hughes, 1980).

A significantly higher proportion of bivalves was found in the diet of *Acteocina canaliculata* in July and August when larger snails were more common. This suggests that seasonality of prey species may be another factor in determining diet. This has been demonstrated in *Retusa obtusa* (Berry, 1988; Berry and Thomson, 1990) and other gastropod predators, such as *Conus, Thais,* and *Polinices* (Hughes, 1980, 1986). Unfortunately, no data concerning natural abundances and seasonality of the prey species at Galilee were made during this study.

In contrast with *Acteocina canaliculata*, the diet and feeding behavior of *Haminoea solitaria* revealed that it indiscriminately ingests sediments containing diatoms, algae, and detritus. No apparent selection of food items was observed, indicating that the sensory organs do not play as specific a role in food selection as they do in *A. canaliculata*. However, these organs could be more generally involved in locating patches of sand containing a high abundance of diatoms or other organic material, or not involved in feeding at all.

The diet of *Haminoea solitaria* changed with respect to both sample date and snail size. The indiscriminate feeding behavior observed in *H. solitaria* suggests that the abundances of specific food items in the diet should parallel their relative abundances in the habitat. As with planktonic diatoms, benthic diatoms show a definite seasonal cycle in abundance and species composition (Kennett and Hargraves, 1988). Typically, there is a spring bloom characterizing certain species, a low abundance during July, August or September, followed by a bloom in October characterizing other species. The trends observed in the diet of *H. solitaria* with respect to predator size and sample date might be the result of seasonal changes in abundance of prey species.

Future studies on these animals should concentrate on a number of areas. The diets of *Acteocina canaliculata* and *Haminoea solitaria* reveal the importance of food abundance and seasonal distribution in fulfilling dietary requirements. Additionally, the size of ingested food items appeared to be important in the diet of *A. canaliculata*. Future studies should examine not only the abundance of prey organisms in the en-

vironment, but the life cycle and size of ingested prey species to understand fully the relationships between predator and prey. Sensory organs appear to have a specific role in food acquisition in *A. canaliculata*, but the role of such organs in *H. solitaria* is unclear. Further research is necessary to determine more specifically the role sensory organs play in food detection and selection in these cephalaspids.

ACKNOWLEDGMENTS

LITERATURE CITED

Abbott, R. T. 1974. *American Seashells,* 2nd ed. Van Nostrand Reinhold, New York. 663 pp.

Berry, A. J. 1988. Annual cycle in *Retusa obtusa* (Montagu) (Gastropoda, Opisthobranchia) of reproduction, growth, and predation upon *Hydrobia ulvae* (Pennant). *Journal of Experimental Marine Biology and Ecology* 117:197-209.

Berry, A. J. and D. R. Thomson. 1990. Changing prey size preferences in the annual cycle of *Retusa obtusa* (Montagu) (Opisthobranchia) feeding on *Hydrobia ulvae* (Pennant) (Prosobranchia). *Journal of Experimental Marine Biology and Ecology* 121:145-158.

Burn, R. and K. N. Bell. 1974a. Description of *Retusa chrysoma* Burn sp. nov. (Opisthobranchia) and its food resources from Corner Inlet, Victoria. *Memoirs of the National Museum of Victoria* 35:115-119.

Burn, R. and K. N. Bell. 1974b. Description of *Retusa pelyx* Burn sp. nov. and its food resources from Swan Bay, Victoria. *Journal of the Malacological Society of Australia* 3:37-42.

Cushman, J. A. 1976. *Foraminifera, Their Classification and Economic Use,* 4th ed. Harvard University Press, Cambridge. 605 pp.

Edlinger, K. 1980. Beiträge zur Anatomie, Histologie, Ultrastructur und Physiologie der chemischen Sinnesorgane einiger Cephalaspidea (Mollusca, Opisthobranchia). *Zoologischer Anzeiger* 205:90-112.

Franz, D. R. 1971. Development and metamorphosis of the gastropod *Acteocina canaliculata* (Say). *Transactions of the American Microscopical Society* 90:174-182.

Fretter, V. 1939. The structure and functioning of the alimentary canal of some tectibranch molluscs, with a note on excretion. *Transactions of the Royal Society of Edinburgh* 59:599-646.

Gibson, G. D. and F.-S. Chia. 1989. Description of a new species of *Haminoea, Haminoea callidegenita* (Mollusca: Opisthobranchia), with a comparison with two other *Haminoea* species found in the northwest Pacific. *Canadian Journal of Zoology* 67:914-922.

Gosliner, T. M. 1979. A review of the systematics of *Cylichnella* Gabb (Opisthobranchia: Scaphandridae). *Nautilus* 93:85-92.

Hughes, R. N. 1980. Optimal foraging in the marine context. *Oceanography and Marine Biology Annual Review* 18:423-481.

Hughes, R. N. 1986. *A Functional Biology of Marine Gastropods.* Croom Helm Publishers, London. 245 pp.

Hurst, A. 1965. Studies on the structure and function of the feeding apparatus of *Philine aperta* with a comparative consideration of some other opisthobranchs. *Malacologia* 2:281-347.

Kennett, D. M. and P. E. Hargraves. 1988. Benthic marine diatoms. *In: Freshwater and Marine Plants of Rhode Island,* R. G. Sheath and M. M. Harlin, eds. pp. 127-135. Kendall/Hunt publishers, Dubuque.

Kesler, D. H., E. H. Jokinen, and W. R. Munns. 1986. Trophic preferences and feeding morphology of two pulmonate snail species from a small New England pond, U.S.A. *Canadian Journal of Zoology* 64:2570-2575.

Kohn, A. J. 1983. Feeding biology of gastropods. *In: The Mollusca,* Vol. 5. *Physiology,* Part 2, A. S. M. Saleuddin and K. M. Wilbur, eds. pp. 2-53. Academic Press, London.

Lemche, H. 1956. The anatomy and histology of *Cylichna* (Gastropoda: Tectibranchia). *Spolia Zoologica Musei Hauniensis* 16:1-278.

Lipps, J. H. and J. W. Valentine. 1970. The role of Foraminifera in the trophic structure of marine communities. *Lethaia* 3:279-286.

Loosanoff, V. L., H. C. Davis and P. E. Chanley. 1966. Dimensions and shapes of larvae of some marine bivalve mollusks. *Malacologia* 4:351-435.

MacPherson, J. H. and C. J. Gabriel. 1962. *Marine Molllusks of Victoria.* Melbourne University Press, Melbourne. 475 pp.

Mikkelsen, P. S. and P. M. Mikkelsen. 1984. Comparison of *Acteocina canaliculata* (Say, 1826), *A. candei* (d'Orbigny, 1841), and *A. atrata* spec. nov. (Gastropoda: Cephalaspidea). *Veliger* 27:164-192.

Morton, B. and S. T. Chiu. 1990. The diet, prey size and consumption of *Philine orientalis* (Opisthobranchia: Philinidae) in Hong Kong. *Journal of Molluscan Studies* 56:289-299.

Murray, J. W. 1973. *Distribution and Ecology of Living Benthic Foraminiferids.* Crane, Russak and Co., New York. 274 pp.

Paine, R. T. 1988. Food webs: road maps of interactions or grist for theoretical development? *Ecology* 69:1648-1654.

Rudman, W. B. 1971a. Structure and functioning of the gut in the Bullomorpha (Opisthobranchia), Part I, Herbivores. *Journal of Natural History* 5:647-675.

Rudman, W. B. 1971b. On the opisthobranch genus *Haminoea* Turton and Kingston. *Pacific Science* 25:545-559.

Rudman, W. B. 1972a. Structure and functioning of the gut in the Bullomorpha (Opisthobranchia), Part II. Acteonidae. *Journal of Natural History* 6:311-324.

Rudman, W. B. 1972b. Structure and functioning of the gut in the Bullomorpha (Opisthobranchia), Part IV. Aglajidae. *Journal of Natural History* 6:547-560.

Rudman, W. B. 1972c. Structure and functioning of the gut in the Bullomorpha (Opisthobranchia), Part III. Philinidae. *Journal of Natural History* 6:459-474.

Sokal, R. R. and F. J. Rohlf. 1981. *Biometry,* 2nd ed. W. H. Freeman and Co., New York. 859 pp.

Shonman, D. and J. W. Nybakken. 1978. Food preference, food availability, and food resource partitioning in two sympatric species of cephalaspidean opisthobranchs. *Veliger* 21:120-126.

Taylor, J. D. 1980. Diets of sublittoral predatory gastropods of Hong Kong. *In: The Marine Fauna and Flora of Hong Kong and Southern China.* B. C. Morton and C. K. Tseng, eds. pp. 907-920. Hong Kong University Press, Hong Kong.

Todd, R. and D. Low. 1981. Marine fauna and flora of the northeastern United States. Protozoa: Sarcodina: benthic Foraminifera. *National Oceanographic and Atmospheric Administration (NOAA) Technical Report (National Marine Fisheries Service) Circular* 439. 51 pp.

Yonow, N. 1989. Feeding observations on *Acteon tornatilis* (Linnaeus) (Opisthobranchia: Acteonidae). *Journal of Molluscan Studies* 55:97-102.