J. exp. Biol. 136, 89–102 (1988)
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RADULAR KINETICS DURING GRAZING IN *HELISOMA TRIVOLVIS* (GASTROPODA: PULMONATA)

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Accepted 12 November 1987

Summary

Three models for radular feeding in gastropod molluscs have been proposed: (1) odontophoral licking, where the radula is fixed to, and is directed by, a dynamic cartilage; (2) rope-and-pulley rasping, where the radula is dynamic and slides over a static cartilage; and (3) moving-conveyor-belt rasping, which involves independent though concurrent movements both of the radula and of the underlying cartilage. The implications of these alternative mechanical processes with regard to machine efficiency and to feeding optimality are considered. During radular feeding, individual *Helisoma trivolvis* (Say) employ the model which affords optimality both of food excavation and of food transport. Results showed that the radula of this species slides over the underlying cartilage while the cartilage independently accelerates across the substrate during each effective feeding stroke. Relative velocities (of the ribbon and of the odontophoral cartilage, VR: VO) ranged from 0·67: 1 to 0·92: 1 and these values were positively correlated with food availability.

Introduction

The radula, odontophoral cartilage, and muscles of the molluscan buccal mass work collectively to provide a steady stream of finely divided food material to the oesophagus (Russell-Hunter, 1979). This material may include plant tissue or a variety of animal prey including sessile erect or encrusting invertebrates. Although buccal architecture varies among cephalate molluscs and may be associated with specialized predatory habits (Carriker, 1943; Crampton, 1977; Shimek & Kohn, 1981), the fundamental elements of feeding are similar throughout members of this group. While grazing, the radula (a flexible, toothed membrane) and its supporting cartilage is protruded through the mouth, accelerated across the substrate (or into the prey) and withdrawn. During radular retraction, food particles carried on the surface of the radula are passed to the oesophagus and to the posterior alimentary canal.

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Key words: gastropod, radula, feeding-optimality, mechanics, kinetics.

Although malacologists generally agree on most aspects of radula function, until recently they had been divided on the precise mechanism of this small, structurally complex, organ system. Specifically, the functional relationships between the radula ribbon and the odontophoral cartilage have been debated. The first detailed report of radular activity appeared in the early nineteenth century. Cuvier (1817) [see also Geddes (1879) and Amaudrut (1898)] suggested that radular movements in *Buccinum* were akin to licking. In this view the radula is fixed to, and its movements are directed by, the underlying cartilage. In contrast, Huxley (1853) [see also Oswald (1893) and Pelseneer (1906)] used the analogy of a block-and-pulley to describe radular movements in *Buccinum* and other molluscs, including certain Heteropoda. In this view the radula is dynamic and slides over the cartilage, which is passive during feeding. Herrick's (1906) review of this debate concluded by settling the conflict in Huxley's favour. Little further work was done on the mechanism of radular feeding [with the exception of studies by Ankel (1936, 1938) and Eigenbrodt (1941)] until the middle 1950s when a new school of thought arose and controversy was rekindled. Hubendick (1957) advocated the idea of a fixed radula supported by a dynamic cartilage [*sensu* Cuvier (1817)], while Carriker (1943, 1946*a*) suggested that both the radula and the cartilage are dynamic during feeding. Recent reviews of gastropod feeding (Runham, 1975; Kohn, 1983) have recognized that the radular mechanism possesses mechanical characteristics of both a rasp (for excavation) and a conveyor belt (for transport) [mechanism *sensu* Carriker (1943, 1946*a*)]. Neurophysiological investigations of the gastropod buccal complex have been numerous (Rose, 1971; Kater & Rowell, 1973; Kater, 1974; Benjamin & Rose, 1979; Bulloch & Dorsett, 1979; Rose & Benjamin, 1979; Brace & Quicke, 1981; McClellan, 1982) but have contributed little to a more precise understanding of the mechanics of these movements.

The present investigation employed microcinematography as well as micro-videomicrography to evaluate the feeding mechanism of *Helisoma trivolvis* (Gastropoda: Pulmonata: Basommatophora). Specifically, the following points were addressed: (1) the precise mechanism of feeding; (2) the theoretical consequences of different modes of buccal function; and (3) the adaptive significance of variations in buccal activity, as observed in natural snail populations.

Materials and methods

Helisoma trivolvis is one of the more common gastropod molluscs of central New York State, USA. This euryoecic pulmonate snail is found in eutrophic environments including lakes, ponds and streams, and in man-made impoundments such as farm ponds and drainage ditches. Like the majority of freshwater gastropods *H. trivolvis* is a primary consumer of *Aufwuchs* [a scum flora consisting mostly of filamentous green algae, diatoms and blue-green algae (Russell-Hunter, 1978)].

Images of encapsulated snail embryos (performing effective feeding behaviours) were produced with an RCA CKCO21 colour video camera which had been mounted on a Wild compound microscope. Filming utilized an egg capsule (containing 10–20 embryos) attached to a glass plate which was inverted to permit viewing through its transparent underside. Consecutive video images were traced onto clear acetate for motion analysis.

A high-speed Fastax camera provided 16 mm images of adult snails. The camera was prefocused, tripod-mounted, and fixed on a specific area of a small, plate-glass aquarium within which feeding would take place. A small area on the front glass of the container had been designated as a stage and outlined. An individual snail was induced to crawl on a thin glass plate which was then fitted flat behind the stage. The mouth was kept within this area by adjustments of the plate on which the snail was crawling. Brewers' yeast was used to elicit feeding for both film recording and video imaging.

Although no EMG or similar recordings were made, preserved snails were dissected to detail the precise spatial and functional relationships among muscles constituting the buccal complex of *Helisoma trivolvis*. This also enabled the identification of antagonistic sets of muscles described below. Specimens were relaxed in a solution of Nembutal in pond water (250 mg l^{-1}) and then fixed in 7 % formalin. Sources for the identification of muscles included Carriker (1946*b*), Demian (1962) and Hembrow (1973). Specific nomenclature follows Demian (1962).

To record the rasp impressions of snails, thin three-dimensional feeding surfaces were prepared. Quantities of beef fat were rendered from suet, filtered, and then frozen. When needed, a quantity of solid fat was melted and poured liberally over a clean microscope slide. Once coated, the slide was shaken vigorously to remove the excess fat and to ensure that the remaining film was uniformly thin (approximately 250 μm). Individual snails were allowed to graze on these plates until they produced satisfactory radular impressions (usually within 2–24 h).

Aufwuchs standing crop biomass (dry mass) was quantified for five field sites in central New York State (Eaton Reservoir, 75°42·27′ W, 42°51·10′ N; Ithaca, 76°22·96′ W, 42°25·78′ N; Meadowbrook Pond, 76°07·08′ W, 43°01·59′ N; Otter Pond, 76°32·83′ W, 43°09·52′ N; Remsen, 75°08·19′ W, 43°20·97′ N). In August 1985, 10 microscope slides (75×25 mm) were set out in plastic slide boxes which had their side panels replaced with plastic-mesh screening. Samples were harvested after 2 weeks. *Aufwuchs* dry mass was determined by drying the slides to constant weight, weighing, acid cleaning, redrying and reweighing.

Results

The muscles which control the buccal mass of *Helisoma trivolvis* are arranged in three concentric and integrated envelopes (Smith, 1987). One muscle group includes fibres which pass from the body wall to the outer walls of the buccal mass. These assist in protraction and retraction of the mass. The second system includes muscles which pass from the walls of the buccal mass to the cartilage. These assist in rotation, protrusion and retraction of the entire odontophore (the radular ribbon, radular sac and odontophoral cartilage). The third muscle system consists of fibres which originate from the cartilage and insert on the radular ribbon. These affect the to-and-fro movement of radular feeding. There are other minor systems which open and close the mouth, stiffen the cartilage, and suspend the radula sac. For detailed accounts of buccal morphology in selected pulmonate snails see Carriker (1946*b*), Demian (1962), Goldschmeding & DeVlieger (1975) and Smith (1987, figs 21, 22, and appendix 6).

Radular feeding in *Helisoma trivolvis* may be divided into five dynamic processes as well as a rest stage (Fig. 2). [Radular feeding in gastropod molluscs has alternatively been divided into either four, five or six stages (Carriker, 1946*a*; Hubendick, 1957; Rose, 1971; Kater, 1974; Goldschmeding & DeVlieger, 1975).] These stages overlap in time (for example, radular protraction may proceed while the cartilage is at rest as well as while the cartilage is rotating during buccal protraction) and may be dissected into eight, non-overlapping, mechanical phases. Therefore, in addition to describing the six overlapping stages of feeding in *Helisoma*, the following also describes feeding in terms of the eight component phases of buccal activity (Fig. 1I–VIII).

Rest – phase I (Fig. 1I, Fig. 2)

At rest the buccal mass of *H. trivolvis* lies parallel to the floor of the cephalic haemocoel. Within the lumen of the mass, the spoon-shaped cartilage is inclined at an angle of approximately 45° to the floor of the buccal cavity with its convex surface facing anteroventrally. The radular sac lies within the concavity of the cartilage. T (time) = 225 ms. (Of more than 250 recorded sequences of radular feeding in *Helisoma*, five were selected for quantitative analysis. The times quoted for each stage are therefore average, rounded values based on these observations. The coefficient of variation for the duration of any single phase was less than 10 %.)

Radular protraction – phases II–IV (Fig. 1II–IV, Fig. 2)

A feeding stroke is initiated by contraction of the inframedian radular tensors which draw the radula over the tip and down the anterior (convex) face of the cartilage. Radular protraction results in collapse of the dorsal rim of the cartilage which stores energy in this vesiculomuscular cushion (Curtis & Cowden, 1977). Before the entrance to the radular sac reaches the leading edge of the cartilage, the buccal mass and cartilage initiate simultaneous rotations. Radular protraction lasts approximately 425 ms.

The structure of the radula is such that at rest the portion of the ribbon that lies within the concavity of the cartilage is folded into a U-shaped gutter. As the radula is drawn over the cartilage tip (during phases II–IV) consecutive tooth rows reflect over that edge and fold open (see Runham, 1969). As tooth rows pass the tip of the cartilage, individual teeth pivot about their bases and swing in wide arcs. This

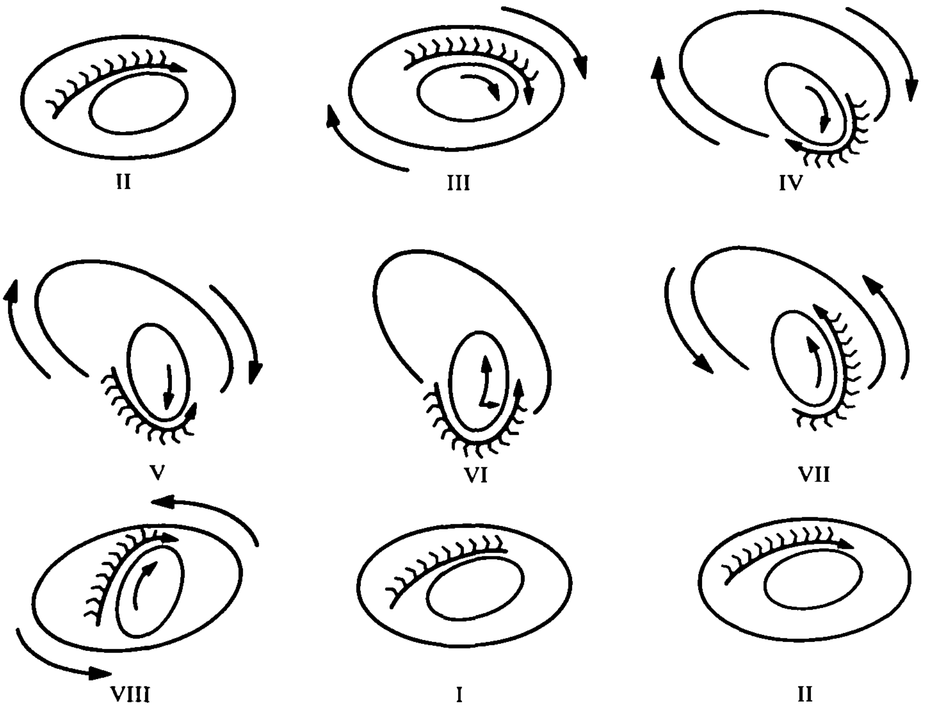

Fig. 1. Schematic representation of one cycle of feeding in *Helisoma* (constructed from observations of video recordings of encapsulated embryos). (In live preparations the radula ribbon lies within the median concavity of the cartilage. In this schematic representation, the radula has been drawn outside and above the cartilage for clarity.) The snail is moving to the right and the grazed substrate is below. Large ovals represent the buccal mass, small ovals represent the odontophoral cartilage. I = rest, T = 225 ms; II, III, IV = radular protraction, T = 425 ms; III, IV, V = buccal protraction, T = 325 ms; V, VI, VII = radular retraction, T = 400 ms; VI, VII = buccal retraction, T = 300 ms; VIII = buccal hyper-retraction, T = 325 ms. Elapsed time for a complete cycle is approximately 1·0 s. Arrowheads show movements of the cartilage and radular ribbon.

movement does not involve a cutting action (and could not, even if the teeth were brought into contact with the substrate). Although the cusps of the teeth point anteriorly when at the tip and when along the convex face of the cartilage (they point anteriorly after passing the bending-plane), they pass the leading edge of the cartilage in reverse (backside-of-cusp-first). In contrast, during phases V–VII (the rasp) the radula teeth (pointing anteriorly) pass the tip of the cartilage in a functional direction and this constitutes the cutting motion of feeding.

Buccal protraction (rotation) – phases III–V (Fig. 1III–V, Fig. 2)

During protraction, the buccal mass is rotated anteroventrally through an arc of approximately 65° in relation to the mouth (Fig. 1, note the change from phase III to phase V). The dorsolateral protractors, preventral protractors and anterior

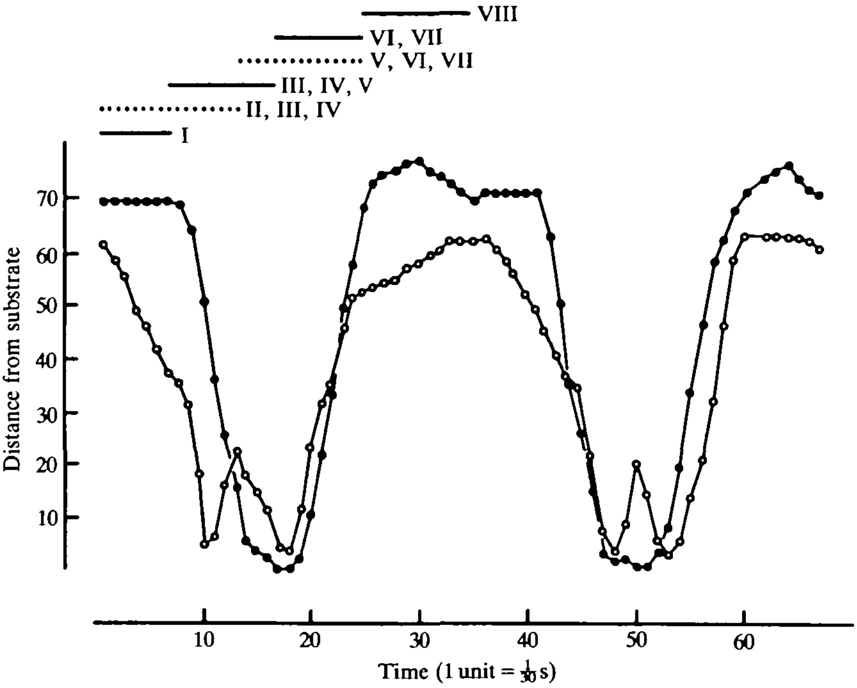

Fig. 2. Plot of radular and cartilage movements during two feeding cycles of *Helisoma trivolvis* (data taken from video recordings of encapsulated embryos). Closed circles represent the distance of the cartilage tip from the substrate, open circles represent the distance of the proximal tip of the radular ribbon from the substrate. Distances (in mm) are measured from a video display. I = rest; II, III, IV = radular protraction; III, IV, V = buccal protraction; V, VI, VII = radular retraction; VI, VII = buccal retraction; VIII = buccal hyper-retraction. Phases I–VIII as set out in Fig. 1. Dotted lines above represent radular activity, solid lines represent activity of the cartilage.

jugalis pull the buccal mass forward and down, while the postventral levators elevate the posterior. Odontophoral rotation is initiated almost simultaneously by activity of the dorsal odontophoral flexors, anterior jugalis and the posterior jugalis. Protraction of the cartilage occurs at an approximately constant velocity of 0·75 cm s^{-1} (Fig. 3, top). During phases III, IV and V, the odontophore rotates approximately 45° (Fig. 1, note the change from phase II to phase V). When rotation of both the buccal mass and cartilage are complete (passing the tip of the cartilage through a total arc of approximately 110°), the tip of the cartilage rests within the open mouth. Buccal protraction lasts approximately 325 ms.

With regard to the apparent reversal of direction during radular protraction (Fig. 1, phases II–IV). The radula begins protraction by sliding along the (posteriorly facing) concave surface of the cartilage. The ribbon then turns around the tip of the (stationary) cartilage and proceeds ventrally along the convex surface (Fig. 1, phase III). As the ribbon passes over the cartilage tip the cartilage rotates (during the latter portion of phase III). Therefore, during the first 300–350 ms of

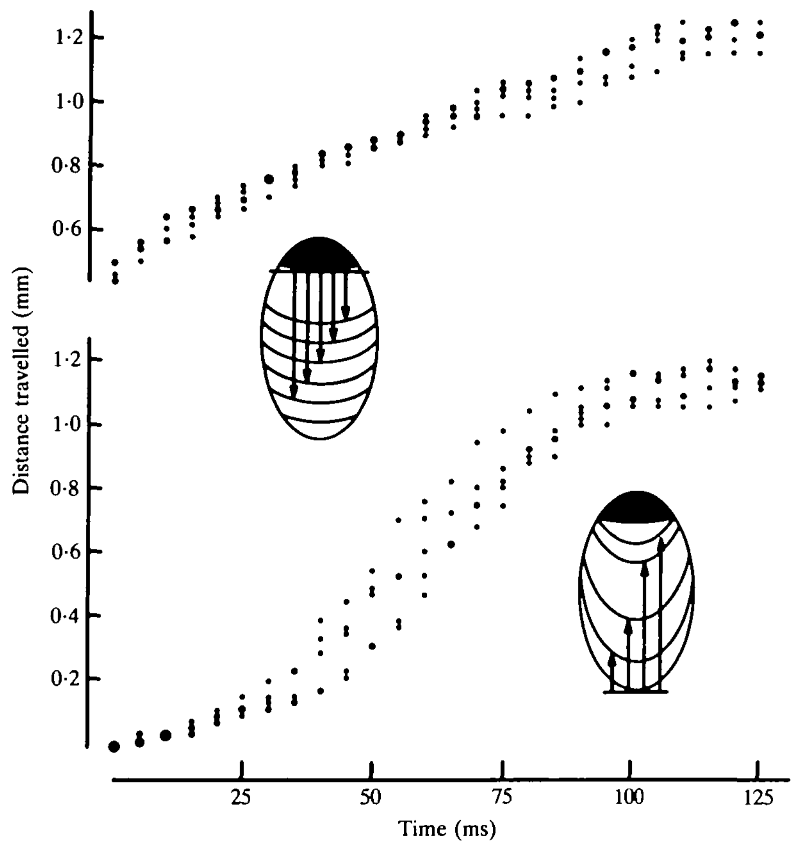

Fig. 3. Cumulative distance travelled by the cartilage during odontophoral protraction (top). Distances were measured from the edge of the mandible to the receding tip of the cartilage (top inset). Cumulative distance travelled by the cartilage tip during cartilage retraction (bottom). Distances were measured from the posterior limit of the mouth to the receding tip of the cartilage (bottom inset). Points represent, in order of size, 1, 2, 3, 4 and 5 observations. Data were taken from 16 mm images of freely crawling adults.

radular protraction the radular ribbon travels ventrally (mostly along the convex face of the cartilage). For the next 75–125 ms (after buccal rotation), the radula travels dorsally towards the ceiling of the lumen of the buccal mass (still along the convexity of the cartilage; Fig. 1, phase IV, see also Fig. 2).

Radular retraction – phases V–VII (Fig. 1 V–VII, Fig. 2)

Before the odontophore completes the protraction initiated in phase III, the radula begins to retract along the cartilage (Fig. 1, phase V). Radular retraction is rapid and is accomplished by contractions of the supramedian and supralateral radular tensors. When the ribbon passes the edges and tip of the cartilage, radula teeth swing about their bases approximately 270° from beneath the rim of the cartilage (the convex face, now positioned posteriorly) to above the rim (within the concavity, facing anteriorly). Movements of the lateral teeth occur in the tooth-column axis. Marginal teeth pass over the lateral edges of the cartilage and down towards the median concavity. Their movements take place across the tooth-row axis. Lateral tooth movement about the leading edge of the cartilage generates the cutting action of the ribbon, and this constitutes the effective 'rasping'. When in contact with the substrate, each lateral tooth gathers food along the tooth cusp, shaft and radular membrane. After radula retraction has been initiated, the cartilage initiates its rasp stroke. Phases V–VII last approximately 400 ms.

Rasp phase (buccal retraction) – phases VI, VII (Fig. 1 VI, VII, Fig. 2)

The rasp stroke is characterized by acceleration of the cartilage across the substrate. This is initiated by contractions of the infraventral and ventral odontophoral protractors. Once in contact with the ground the tip of the cartilage accelerates towards the mandible at a maximum velocity of approximately $1{\cdot}5\,\mathrm{cm\,s^{-1}}$ (Fig. 3, bottom). The additional snapping motion of the cartilage tip observed during phase VII is generated by the release of energy stored during earlier deformation of the cartilage (see phase II). During the rasp stroke, radula teeth move at a velocity which is the sum of the independent cartilage and ribbon velocities. Different relative velocities of the radula and of the cartilage are of considerable adaptive significance since these influence the radula's food-gathering capacity (see Discussion). After the cartilage has passed the mandible it travels dorsoposteriorly towards the oesophagus. Phases VI and VII last approximately 300 ms.

Buccal hyper-retraction – phase VIII (Fig. 1 VIII, Fig. 2)

At the end of phase VII, the long axis of the cartilage lies approximately perpendicular to the floor of the buccal cavity. As phase VIII proceeds, hyper-retraction brings the cartilage back towards the opening of the oesophagus. This is facilitated by pressures generated from collapse of the cephalic haemocoel and by contractions of the anterior jugalis muscle. Movements of the marginal teeth, as they converge from the lateral edges of the cartilage, assist in holding food onto the ribbon during radular collapse within the cartilage. When hyper-retraction is complete, the buccal mass is returned to its resting position by contractions of the buccal retractors, postventral levators and preventral levators ($T = 325\,\mathrm{ms}$). It should be noted that the durations set out above for each of the five dynamic processes involve overlap (see Fig. 2); the total elapsed time for a complete cycle (rest to rest) is approximately 1·0–1·5 s. Although this elapsed time agrees with that quantified by Carriker, Schaadt & Peters (1974) for *Lymnaea*, it is unclear why it differs so significantly from that of 2–5 s reported by Kater (1974) for *Helisoma*.

Although the vast majority of feeding seen in *Helisoma* followed the patterns described here (Fig. 1) several other (rare) alternative patterns of radular activity were also observed. The radula of this species sometimes acted as a true rasp [*sensu* Cuvier (1817)], and at other times it acted as a rope-and-pulley [*sensu* Huxley (1853); see also Kater (1974)]. In addition, feeding stroke reversals, which clear the radula of fouled material, were observed. Other studies have demonstrated that the serial elements of gastropod feeding (fixed-action patterns) are controlled by distinct neural arrays (Kater, 1974; Rose & Benjamin, 1979; Brace & Quicke, 1981). Observations from the present study indicate that there may be a neural hierarchy involving certain sensory inputs which can override such programmes. Therefore, feeding in this species may be somewhat flexible within a larger framework of behavioural canalization.

The relative rates of radula and cartilage motion were calculated from examinations of three-dimensional rasp impressions left in solidified beef fat. Distance travelled by the odontophore in unit time (VO) was equivalent to the total length of an individual rasp stroke. Distance travelled by the radula (VR) in the same unit time was equal to the number of tooth rows to hit the substrate over the distance for VO multiplied by the distance between tooth rows [determined from the dissected and slide-mounted radula, see Märkel (1965)]. Relative velocities (of ribbon and of cartilage, VR: VO) ranged from 0·67: 1 to 0·92: 1 among snails sampled from five sites, and mean values (VR: VO) were positively correlated with standing crop of *Aufwuchs* biomass [$y = 0{\cdot}834x^{0{\cdot}151}$, $N = 5$, $r^2 = 0{\cdot}955$, $P < 0{\cdot}01$, where y is VR: VO, x is *Aufwuchs* biomass ($\mathrm{g\,m^{-2}}$)] (Fig. 4). Snails from sites with low *Aufwuchs* biomass had low VR: VO values (0·67: 1) (low ribbon velocity) when feeding on beef-fat films, and snails from sites with high *Aufwuchs* biomass had relatively higher VR: VO values (0·92: 1). Although food

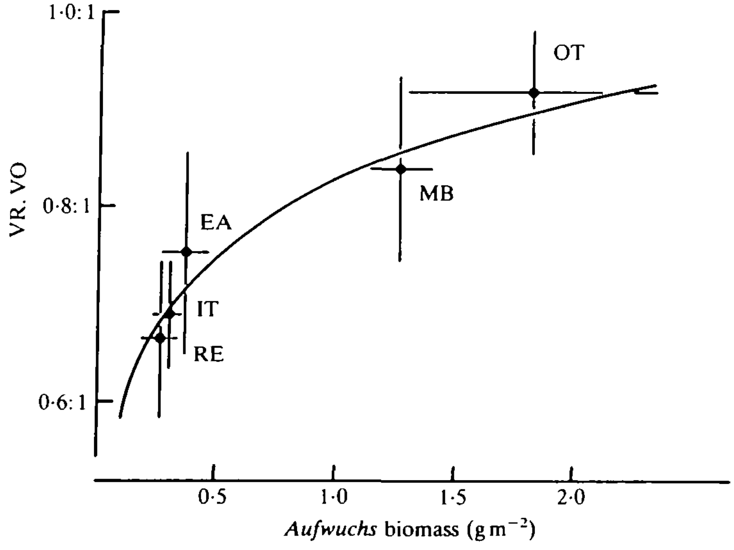

Fig. 4. The relationship of VR: VO (±S.D., $N = 10$) and *Aufwuchs* standing crop biomass (±S.D., $N = 10$) at five sites in central New York State. Regression equation for fitted line is $y = 0{\cdot}834x^{0{\cdot}151}$, $N = 5$, $r^2 = 0{\cdot}955$, $P < 0{\cdot}01$. EA, Eaton Reservoir; IT, Ithaca; MB, Meadowbrook Pond; OT, Otter Pond; RE, Remsen.

quality (as C:N) and diatom species diversity differed among sites these differences [among others, see Smith (1987)] could not explain the observed differences in VR:VO.

Discussion

Results from the present study agree with recent ideas about the mechanism of gastropod feeding and have shown that the radula of *Helisoma trivolvis* slides over the underlying cartilage (the 'rasp'), while the cartilage accelerates (the 'lick') independently across the substrate during each effective radular stroke. It is important to consider the implications of these alternative mechanical processes with regard both to machine efficiency and to feeding optimality.

Three dynamic models can be considered. (1) If the radular mechanism acts as a true rasp [*sensu* Cuvier (1817), fixed radula, moving cartilage] and if a hypothetical ribbon has five teeth per transverse row, then a single feeding stroke would result in the excavation of 5 long troughs, each 25 units in length (Fig. 5A). (2) In contrast, if the buccal mechanism is like that of a rope-and-pulley [*sensu* Huxley (1853), moving radula, fixed cartilage] a radula with five teeth per row would

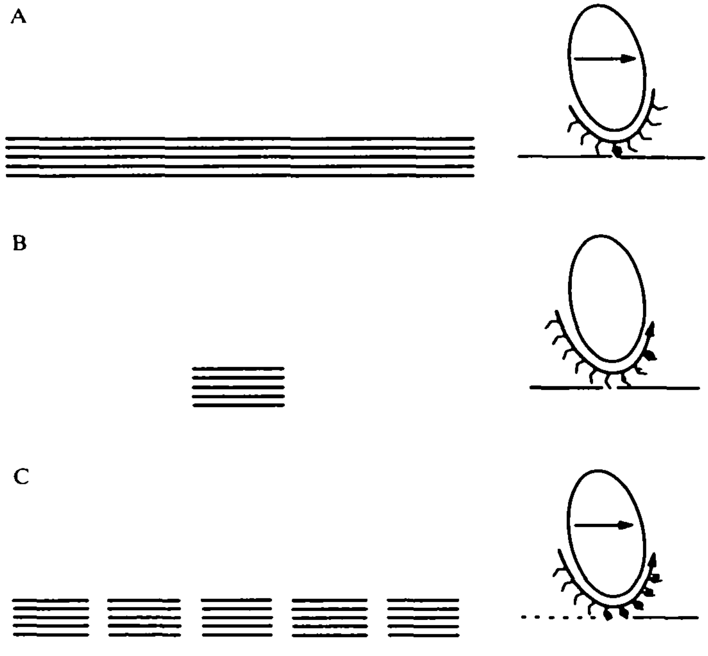

Fig. 5. Schematic representation of grazing traces and of relative buccal kinetics for three models of radular action. (A) Odontophoral licking; (B) rope-and-pulley rasping; (C) moving-conveyor-belt rasping (see Discussion for further details). The snail is moving to the right, the grazed substrate is below. Large ovals represent the odontophoral cartilage. Arrowheads show movements of the cartilage and radular ribbon.

excavate five shorter troughs, their size being proportional to the size of the proximal thickness of the cartilage, for example 5 units long (Fig. 5B). (3) If the radula functions like a moving conveyor-belt (moving radula, moving cartilage, as demonstrated here) each rasp stroke would produce five groups of tooth marks along 25 units of substrate (alternating troughs and gaps) (Fig. 5C).

In the first of these models a single row of the radula teeth remains at the proximal edge of the cartilage (corresponding to the bending-plane of the radula), while it (that single tooth row) is dragged along an area of substrate equivalent to the distance traversed by the moving cartilage. In the second model the radula slides over a static cartilage exposing many tooth rows to a single patch of substrate. In the third model consecutive rows of teeth are drawn over the proximal edge of the cartilage as the cartilage travels across the substrate. These tooth rows are therefore exposed to individual patches of previously uncleared substrate during a single feeding stroke.

In addition to differences in the efficiency of substrate excavation, these relative movements also affect food transport by the radula. In the first of these models, the space between tooth cusp, shaft and radular membrane rapidly becomes filled with food material. Although additional food particles may be available on the substrate, the radula does not expose more than a single tooth row in a single stroke. As that tooth row moves through uncleared substrate additional material cannot be gathered owing to a lack of space. Because the radula is fixed, marginal-tooth convergence (in the tooth-row axis) does not occur and therefore marginal teeth contribute little to food transport for ingestion. It had always been assumed (with little earlier observational evidence) that marginal teeth play a central role in the transport of food into the oesophagus. Observations from the present study have shown that while the marginal teeth of *H. trivolvis* do play an important role in the transport of food from substrate to oesophagus, they are not specifically involved in the transport of material from the surface of the ribbon. Numerous, incomplete annuli of strong cilia are located in the region immediately around the opening to the oesophagus. Direct observations of currents produced by these cilia-bands indicated that they are responsible both for food reception from the surface of the radula and for food delivery into the alimentary canal. Folding of the marginal teeth about the lateral edges of the cartilage (during radular retraction) serves to hold food onto the surface of the ribbon during the last part of each feeding cycle (hyper-retraction, Fig. 1, phase VIII).

In the second model, food material is gathered as the first tooth row contacts the substrate. As consecutive rows do the same, the substrate they contact may already have been cleared and therefore they do not collect significant amounts of additional material. In this rope-and-pulley model, marginal teeth do swing about the lateral edges of the cartilage (during radular retraction) and provide food-securing activity.

In the third model, consecutive rows of teeth, with empty spaces between cusp, shaft and membrane, are continually exposed to previously uncleared substrate. In this case the marginal teeth provide food-securing activity.

Simple odontophoral licking (first model) is relatively inefficient because food is lost owing to a lack of space in which to store material. Rope-and-pulley feeding, or radular rasping alone (second model), is also inefficient because uncleared substrate is not available to the ribbon. The third mechanism (concurrent but independent motions of radula and of cartilage, as detailed in this paper) is the most efficient because consecutive radular rows are drawn across uncleared substrate, resulting in more food rasped and in more food transported to the oesophagus per unit time.

Several workers have documented patterned feeding by snails (Woodward, 1906; Barnard, 1913; Longstaff, 1913; Ankel, 1936, 1938; Eigenbrodt, 1941; Märkel, 1955, 1957, 1965; Storey, 1971; Dawkins, 1974; Voigt, 1977; Zeldis & Boyden, 1979; Juch & Boekschoten, 1980; Zalucki & Kitching, 1982; Hickman & Morris, 1985). For generalized grazers (like *Helisoma*) no previous study has indicated any adaptive significance in relating specific patterns of feeding to relative mechanics of radular movements. Five intensively studied populations of *H. trivolvis* could be distinguished from one another on the basis of the relative speeds with which their radulae and cartilages moved while feeding on artificially prepared substrate. The relative rates of radula and cartilage motion (VR: VO) were positively correlated with *Aufwuchs* standing crop at each of the sites from which snails were sampled for analysis. Specifically, snails from sites with low *Aufwuchs* biomass had low VR: VO (low radula velocity), while snails from sites with high *Aufwuchs* standing crop biomass had higher VR: VO (relatively high radula velocity).

The present study has demonstrated that of three possible mechanical programmes, snails of the species *Helisoma trivolvis* normally employ the one which affords mechanical optimality of both food excavation and of food transport. Application of the methods used in this study to more specialized radular systems in other molluscs could prove fruitful.

I would like to thank Dr W. D. Russell-Hunter and two anonymous reviewers for their critical reading of this manuscript. Work was supported, in part, by Senate Research Committee Grants (Syracuse University) to Dr W. D. Russell-Hunter and to the author, and by a grant from the Theodore Roosevelt Memorial Fund to the author. This is contribution no. 84 of the Upstate Freshwater Institute.

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