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GRAZING OF THE SEAGRASS HALOPHILA HAWAIIANA (HYDROCHARITACEAE)

BY THE SNAIL SMARAGDIA BRYANAE (NERITIDAE)

A THESIS SUBMITTED TO THE GRADUATE DIVISION OF THE
UNIVERSITY OF HAWAII IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

IN BOTANICAL SCIENCES

AUGUST 1984

By

Catherine Craine Unabia

Thesis Committee:

Kent W. Bridges, Chairman
E. Alison Kay
Charles H. Lamoureux
Dieter Mueller-Dombois

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THESIS COMMITTEE

W. H. Bridges
Chairman

E. Alison Gray

Charles H. Ransome

Dieter Mueller-Dombois

Acknowledgements

Gratitude is expressed to E. Alison Kay for the use of unpublished data, to Regina Kawamoto of the Bishop Museum for extraction and preparation of snail radulae, and to Armand Unabia for field work and support. Laboratory facilities were provided by the Pacific Biomedical Research Center at Kewalo.

ABSTRACT

The snail Smaragdia bryanae grazes the blade tissue of the seagrass Halophila hawaiiana. In the laboratory snails grew and reproduced on this diet, and did not graze any macroalgae found in the seagrass meadows. Examination of the grazing damage with light and Scanning Electron Microscopy revealed that upper epidermal cell walls of the blade lamina are scraped off or punctured, presumably to gain access to the protoplast. The snail radula features large, double pointed first marginal teeth close in size to the holes cut in the cells.

Leaf area, width, length and density measured from field samples create a picture of the grazing theater. Blade width was identified as useful in differentiating populations. The size of the average snail is close to the overall blade width of leaves sampled.

Grazing damage occurred in all samples, with frequencies above 90% in some. Grazed area per blade was measured, and its location on the blade recorded. Snails usually graze both halves of the lamina between midrib and margin, avoiding vascular sections. This "preferred area" averages 40% of total leaf area. Frequencies of grazing patterns indicate that snails graze the blade surface selectively, and are likely to begin in the central section and follow a fairly predictable path as they graze.

From estimates of snail densities and grazing rates it is calculated that snails consume about 2% of the Halophila standing crop daily. It seems likely that under usual conditions daily production of new leaves compensates for this loss.

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PART I. LITERATURE REVIEW

This review provides background information for a study of an association between a species of the seagrass Halophila and a small neritic snail in the Hawaiian Islands.

Characteristics of the Seagrasses

Den Hartog (1970) introduced his monograph on the seagrasses of the world with the following observation:

When considering the marine flora what strikes one immediately is its complete domination by the algae, which occur in great diversity, followed by the fungi, which are widespread, although their optimum development is obviously terrestrial. Bryophytes, Pteridophytes and Gymnosperms are completely absent, and there is, as far as I know, not a single indication that they have ever inhabited the sea. The Angiosperms are only very sparsely represented. No marine dicotyledon exists and under the monocotyledons there is only one order which has produced some marine representatives, viz. the Helobiae.

In the Helobiae, Den Hartog recognizes 12 genera with 49 species which are restricted to the marine environment. Nine are assigned to the family Potamogetonaceae (Amphibolis, Gymnocoa, Halodule, Heterozostera, Phyllospadix, Posidonia, Syringodium, Thalassodendron, and Zostera), and three to the family Hydrocharitaceae (Enhalus, Halophila and Thalassia). Both are aquatic plant families which also contain fresh-water and brackish-water species.

The seagrasses are restricted to shallow waters such as coastal areas or shallow seas where enough light penetrates for their photosynthesis. Most species are found in sheltered areas away from strong wave action, but the genus Phyllospadix has roots that can attach to rock, and grows in the surf zone.

Though few in species, seagrasses are a conspicuous part of the marine vegetation in most coastal areas, where they are noted for binding sediments with extensive root and rhizome systems. Thalassia beds enhance sedimentation by protection from wave and current erosion and by acting as a baffle that slows currents as they pass over the bed, causing deposition of the water's suspended load of particles (Ginsburg and Lowenstam 1958). Lynets (1966) found a layer of semi-motionless water within Thalassia in Florida, with no resuspension of sediments from the root system. This quiet water, with its protective vegetation, forms an excellent habitat for small organisms, and the thick, stable sediments beneath are ideal for burrowing organisms.

Seagrasses also supply biogenic calcium carbonate to the sediment substrate in the form of epibionts, especially Foraminifera, and shells from invertebrates and calcareous algae (Brasier 1975). In some areas the net result may be the formation of carbonate banks.

Seagrasses are known for high productivity (Odum et al. 1960; Qasim and Bhattathiri 1971; McRoy and McMillan 1977). The fall and decay of leaves produces a large amount of organic detritus available for deposit feeders. The living leaves provide a substrate for many

small epiphytic algae and associated epifauna contributing further to the production and diversity of the ecosystem. Qasim and Bhattathiri note that coral reefs are frequently in close association with seagrass beds, and suggest that where corals occur in tropical waters of impoverished phytoplankton content, seagrasses may be the major source of food for the diverse fauna of the coral ecosystem.

Since seagrasses seem to exert a strong influence over the ecology of shallow water habitats, Brasier (1975) thought that their gradual entry into the sublittoral in late Cretaceous and Tertiary times would have been a significant event, marked by a change in community structure. She felt that seagrasses would have had important effects on faunal development such as an increase in habitat diversity, the eutrophication of sediment substrates, and the provision of an additional means of dispersal for sessile organisms (rafting). These factors were thought to have contributed to the development of deposit feeding organisms, especially prosobranch gastropods and miliolid foraminifera, two groups which have diversified greatly since the Miocene.

Seagrass communities are complex. Seagrasses, associated benthic and epiphytic algae, epifauna, infauna and swimming animals are the more obvious components of the community. Seagrasses seem to be uniquely stable "frame elements" (Den Hartog 1979) capable of supporting the diverse biota complete with symbioses, mimicry, and species-specific associations expected in an ecosystem. The intricate relationships that exist within the numerous structural elements are

just beginning to be described. Study of the relationship between Halophila hawaiiiana and its neritid grazer Smaragdia bryanae will add to this description.

Characteristics of the Neritacea

The Neritidae and the Helicinidae are two closely related families that together form the superfamily Neritacea (Mollusca: Archaeogastropoda). Fretter (1965) considers the Neritacea to be an isolated group within the prosobranchs whose evolution has paralleled that of other groups of gastropods, and is characterized by the acceleration of some adaptive trends and relatively slow change in others. They are sometimes separated from the Archaeogastropoda and considered a more advanced order. Fretter stated that Neritaceans are recorded from the mid-Devonian, and through a long period of independent evolution have developed characters enabling them to live under stringent intertidal conditions, to invade freshwater and the land. The Helicinidae are pulmonate land snails which have lost most primitive features.

The family Neritidae is a group of herbivorous snails represented by the amphibious intertidal snail Nerita (three species in Hawaii), the estuarine and brackish water Theodoxus (three endemic Hawaiian species), Neritilia (one Hawaiian species) found in low salinity tide pools, the freshwater stream dweller Neritina (one Hawaiian species)

and the semiterrestrial Neritodryas of Indonesia (Morton 1958; Kay 1979). Major changes from the basic archaeogastropod plan found in the Neritidae (Fretter 1965) include separate sexes with complex elaboration of the reproductive ducts, internal fertilization and production of resistant egg capsules, loss of the right kidney (probably incorporated in the genital tract), adaptations of the respiratory and circulatory systems in intertidal and semiterrestrial species, and specializations of the radula and the digestive system.

Molluscan Diet

According to Graham (1955), ancestral mollusks were microphagous, their diet consisting of diatoms, minute algae and detritus raked up by the radula. Most of the more primitive forms retain this habit, but through the molluscan line a steady drift toward macrophagy has occurred. The characteristic diet of higher snails is large plants or sedentary animals. This change has required adaptations in the radula and the digestive system. Larger, chemically complex particles cannot be handled by the simple intracellular digestion that occurs in the digestive gland or caeca of more primitive forms. With the change in diet came the much more efficient extracellular digestion found in higher snails. The stomach evolved as the place where this process occurs, and the digestive gland became the site for enzyme secretion rather than digestion. Such adaptations are found in Neritidae (Fretter 1965). The caecum is lost or poorly developed. The stomach

is a more voluminous sack in the neritid, capable of dealing with larger quantities of food, and the intestine is long and doubly looped.

Relationship of Animals to Aquatic Macrophytes

Invertebrates associated with the larger aquatic plants are usually found to eat minute algae, bacteria, protozoa and vother organisms growing on the surface of the leaves. Shelford (1918) described how animals such as snails may rasp the surface of aquatic plants for food without eating the plant tissues themselves. He wrote, "one could probably substitute glass structures of the same form and surface texture without greatly affecting food relations", but noted that the plants are important for habitat and shelter. Vahl (1971) contrasts this to the terrestrial situation where macrophytes directly provide the food for many species. She notes that surprisingly few animals feed on the large attached algae, although marine macrophytes have been shown to be highly productive.

The tendency to eat the **periphyton** rather than the leaf itself seems strong in the invertebrates associated with seagrasses. According to the Consumer Ecology Working Group of the International Seagrass Workshop (Kikuchi and Peres 1973), "few organisms depend directly upon green seagrass blades as an energy source". They recommended study of any direct grazing found.

A detailed study of the animals in a California estuary where Zostera was the dominant plant (MacGintie 1935) showed that very few animals fed directly on Zostera or other macrophytic plants (Enteromorpha and Polysiphonia). Those that did, of which he mentions the sea hare Tethys californicus which grazed quantities of Zostera, were not abundant enough to have any appreciable effect upon the food chain. He estimated that 95% of the animals fed upon microscopic materials, many being detritivores. The other 5% were carnivores. In the estuary food chain, Zostera forms the base, but its primary role is in its contribution of detritus, and its secondary role is as a substrate for epiflora and epifauna. Large numbers of bacteria colonize seagrass detritus, providing a rich food for detritivores (Phillips 1970). Seagrass may also contribute dissolved organic carbon that is taken up directly by the epibiota (Thayer 1978, Wetzel and Penhale 1979).

Marsh (1976) found 23 species of gastropods in the invertebrate epifauna of Zostera in a Virginia estuary, with not one eating Zostera directly. The most common gastropod was a detritivore, grazing on the surface of the Zostera blades. Others were mostly carnivores, with one filter feeder, and one herbivore grazing filamentous algae. Marsh described how the Zostera plants became heavily laden with large amounts of epiphytes and sessile organisms over the growing season. A similar situation was found in mollusks associated with Thalassia in Jamaica. Jackson (1972) recorded two species of epiphyton grazers as the only herbivorous gastropods present.

Macroherbivorous Prosobranch Mollusks

There are a few examples of more primitive gastropod mollusks that do graze macrophytes. Fralick et al. (1974) described heavy grazing of the kelp Laminaria and other algae in New Hampshire during a population explosion of the littorinid snail Lacuna vincta. The fronds and stipes of the kelp were riddled with holes produced by the grazing snails. Vahl (1971) composed a list of 29 species of macroherbivorous prosobranchs from published records of diet, more than half of which were limpets or abalone.

Limpets seem to graze macrophytes frequently, a capability attributed by Steneck and Watling (1982) to the excavating abilities unique to their feeding apparatus, the docoglossan radula. Vahl (1971) found the kelp Laminaria hyperborea to be the sole source of food for adults of the limpet Patina pellucida living on it in Western Norway. The kelp Egregia laevigata is host to the grazing limpet Acmaea insessa in the intertidal zone of Santa Barbara, California (Black 1976). Acmaea testudinalis preferentially grazes the coralline alga Clathromorphum circumscriptum in the Gulf of Maine (Steneck 1982).

Seagrass Herbivory

There are some marine herbivores that do include seagrass as a part of their diet, and a few even that specialize in it. In the

Caribbean the queen conch, Strombus gigas, feeds in seagrass beds (Randall 1964). In dense Thalassia beds the conch rasps epiphytes from the leaves, but in sparse beds of Cymodocea or Halophila the seagrass blades are consumed. Grazing of Thalassia by the emerald nerite, Smaragdia viridis, was reported by Zieman (1982), who noted that the small snail can be numerous although it is difficult to see because its color matches the lower portion of the turtle grass blades where it grazes.

The sea urchins (echinoderms) Lytechinus and Tripneustes were observed to graze Thalassia by Jackson (1972). Vadas et al. (1982) found that in addition to fresh Thalassia, urchins also ate much detrital and senescent Thalassia and sediments. Greenway (1976) found that Lytechinus variegatus was the major herbivore in Thalassia beds in Kingston, Jamaica. She found that at a mean density of 22 echinoids per square meter, the urchins consumed about 50% of Thalassia blade production. A small amount was eaten by fish. Greenway found that urchin grazing rates dropped with increasing population density, but concluded that occasional overgrazing might occur if herbivore populations explode. Camp et al. (1973) reported massive destruction of offshore Thalassia meadows in Dixie County, Florida as a moving aggregate of Lytechinus with densities reaching 636 echinoids per square meter cut large swathes through the meadows.

Grazing of Zostera capricorni by the gammarid amphipod Cymadusa was reported by Kirkman (1978) from Queensland, Australia. The grazing, which was discovered during laboratory culture of the plant

when the number of detached leaves floating on the surface increased concurrent with the number of amphipods present, was said to markedly affect production. The amphipods remained in position on a leaf, sometimes all day, until a relatively large piece of leaf was eaten away.

Many herbivorous fishes have been found to include seagrass in their diets. Randall (1965) showed that parrotfishes (Scarus and Sparisoma) and surgeonfishes (Acanthurus) graze heavily on seagrasses in the West Indies. These fish remain close to the shelter of coral reefs, and venture only about 30 feet into surrounding seagrass beds to graze, resulting in a conspicuous strip of bare sand separating the reef from the seagrass meadows. A small parrotfish, Sparisoma radians, lives in seagrass beds and feeds only on seagrass.

Sea turtles and the marine mammals, manatees and dugongs, feed predominantly on seagrass. Populations of these animals are now greatly reduced due to the activities of man, but in former times they may have harvested much of seagrass production. Johnstone (1978) described an unusual meadow at Rabouin Island, New Guinea which showed evidence of heavy grazing activity, attributed to the turtles which inhabit the island's waters because blades were cropped close to the sand with ends torn, different from fish grazing damage. He suggested that within historical times large populations of turtles could have kept seagrass standing crops at low levels, perhaps explaining in part why so few other herbivores have evolved a seagrass-based diet.

Lipkin (1975) analyzed the stomach contents of numerous dugongs obtained along the coast of the Sinai, and concluded that they eat only seagrasses and do not digest algae. He said that the dugong, or sea cow, returned to the sea during the Eocene, a time when the continents were covered to a great extent by shallow seas. Seagrasses probably had been around for some time by then and there were extensive meadows in many areas.

Study Proposal and Hypotheses

The snail genus Smaragdia seems to be specialized to feed on seagrasses. In Hawaii Smaragdia bryanae grazes the seagrass Halophila hawaiiiana. The occurrence of this association in Hawaii where there is only one seagrass species offers a unique opportunity for a study which would contribute to ecological knowledge in several ways. Most obvious would be the addition of an animal to the relatively short list of seagrass herbivores, perhaps helping to understand why there are so few. The study will consist of:

1. laboratory culture of snails to test nutritional dependence on the seagrass
2. microscopic examination of the grazing damage and the snail's radula
3. measurement of grazing damage from field samples to evaluate the

significance of the interaction in terms of the amount of damage sustained by the plant

Observation of the association has generated the following hypotheses:

1. Smaragdia bryanae obtains its primary nutrition from Halophila hawaiiiana
2. the amount grazed by the snail is significant in terms of frequency, total surface area and percent of surface area grazed

If these hypotheses are accepted, then the association would be classified as an example of specialized herbivory where Halophila hawaiiiana is the host of the monophagous herbivore Smaragdia bryanae.

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PART II. GRAZING OF THE SEAGRASS HALOPHILA HAWAIIANA

BY THE SNAIL SMARAGDIA BRYANAE

INTRODUCTION

Plant-animal interactions are interfaces of the plant and animal kingdoms which occur when aspects of the ecologies of a plant and an animal are bound together, usually involving food for the animal. Some interactions are general, while others are very specific, with one animal concentrating solely on one plant species. When an herbivore is monophagous its complete specialization to its host plant will be reflected in many aspects of its physiology, anatomy, sensory capabilities, reproduction and behavior. It is in cases like these that the coevolution of plant and herbivore may be most successfully worked out, especially the details of the pattern of herbivory. In the shallow coastal waters of some of the Hawaiian Islands the small snail Smaragdia bryanae Pilsbry 1917 appears to be involved in such an obligate grazing association with the seagrass Halophila hawaiiiana Doty and Stone 1966.

The Smaragdia-Halophila association in Hawaii seems to be part of a widespread phenomenon. Species of Smaragdia are associated with seagrasses in many areas, and the overall distribution of the snail genus coincides closely with that of the seagrasses (Unabia 1980). Like the dugong, Smaragdia may be a true "seagrass animal", ecologically dependent upon the marine angiosperms.

Since most invertebrate herbivores associated with seagrasses, or other large aquatic plants, feed on the epiphytes or other small organisms found on the surface of the leaves, it is unusual if Smaragdia is really eating the seagrass. It might just be scraping the seagrass tissues in the process of gathering algal epiphytes, much as limpets have been observed (Southward 1964) scraping up bits of rock with their sharp radulae as they graze.

Specialization to one host plant appears to be rare in marine herbivores, with few examples having been reported, but there has been little work done on the smaller herbivores (Lubchenco and Gaines 1981). Limpets of the genus Acmaea appear to have developed some degree of feeding specialization. Acmaea insessa was reported to graze only Egregia laevigata in Santa Barbara, California (Black 1976) causing conspicuous damage to the majority of the larger kelp plants. This isn't an obligate relationship since this limpet may graze different plant species in other parts of its range (Vahl 1971). Steneck (1982) studied an almost mutualistic interaction where regular grazing by Acmaea testudinalis, with consequent removal of epiphytes, seems essential to the health of the coralline alga Clathromorphum circumscriptum. Despite the plant's apparent dependency, the limpet's feeding is not completely host specific. Although Clathromorphum is preferred, other unbranched corallines will be grazed but not other types of algae.

The association between Smaragdia and Halophila in Hawaii appears to be an example of specialized, monophagous herbivory, one of the most

intimate cases of plant-animal interactions. If it can be shown that these animals are associated closely enough and with sufficient impact upon one another to expect coevolution, then we could begin to look for adaptations in the plant for tolerance of or escape from the herbivore, and in the animal for specialization to its food source. In addition, the animal might have beneficial effects upon the plant that might help to balance the negative.

MATERIALS

Halophila hawaiiiana Doty and Stone 1966

The genus Halophila du Petit Thouars belongs to the family Hydrocharitaceae, one of two aquatic plant families that contain seagrasses. Although completely marine, Halophila is similar in rhizome structure to Hydrocharis, the freshwater plant that is the type for the family. Halophila is a very geographically widespread genus, growing in coastal areas of all oceans from tropical through warm temperate zones in both hemispheres.

Den Hartog (1970) considered H. hawaiiiana to be a subspecies of H. ovalis. It is one of five subspecies placed in the H. ovalis complex, a "collective species" of closely allied taxa whose phenotypes overlap in some characters such as blade width. However, Doty and Stone (1966) felt that subspecies hawaiiiana was sufficiently distinct to merit

recognition as a separate species. Their separation, on the basis of blade width, the manner in which the blade joins the petiole, and the pattern of leaf venation, was supported by Sachet and Fosberg (1973), who pointed out that the Hawaiian plant also has fewer ovules.

Den Hartog (1970) preferred not to elevate any of the ovalis subspecies to full species rank until a complete revision was done of the entire complex. A study of isozymes from seven enzyme systems (McMillan and Williams 1980) of members of the Halophila complex has shown that Halophila hawaiiiana is sufficiently different from the others to be recognized a species.

Halophila hawaiiiana is the only seagrass in Hawaii. It grows in sheltered areas in sediments of sand or mud. Plants accumulate sediment and form elevated mounds or ridges. These Halophila patches may be small islands between algae covered coral or rock, scattered meadows surrounded by open sand and often tenuously connected by rhizomes, or rows of densely covered ridges like an underwater mountain range. Most patches change from time to time in shape, size and location, but some have persisted for years with only slight variation.

Like other species of Halophila, the Hawaiian species is a low, creeping plant. Profuse branching leads to a dense mat of foliage in which neighboring plants intertwine. Each node of the rhizome bears a pair of foliage and scale leaves and a root. The plants are said to be dioecious, but little is known of local reproductive biology. Male and

female flowers and ripe fruit with seeds have been seen.

The anatomy of the Halophila hawaiiiana plant and leaf blade are illustrated in Figures 1 and 2. Figure 2 is adapted from Balfour (1878) whose detailed description of Halophila ovalis collected at Rodrigues Island in the Indian Ocean was found to apply quite well with only slight modification to Halophila hawaiiiana, and is followed here.

The foliage leaf consists of an oblong-elliptical lamina, often spatulate, supported on a slender petiole. The petiole contains an axial fibrovascular bundle and two lateral bundles. The axial bundle continues in the lamina as the midrib, and the lateral bundles diverge and form the intramarginal vein, which joins the median bundle (midrib) at the leaf tip. The median bundle gives off lateral branches that pass outwards through the lamina and join the intramarginal vein. Extra development of parenchyma tissue around the bundles makes the lamina thicker at these points. Cells over the midrib and the intramarginal vein have thick cell walls.

The midrib is surrounded above and below by two layers of parenchyma and then a small-celled epidermis (Figure 2). On either side of the midrib there are intracellular canals amid parenchyma layers. In the lamina the intermediate parenchyma cells gradually disappear until there are just two epidermal layers loosely in contact, separated here and there by the lateral veins. According to Balfour, epidermal cells are the same on both surfaces of the leaf and contain

chlorophyll and starch grains. It is assumed that the epidermis is the sole photosynthetic tissue as it is in Thalassia (Tomlinson 1972). At the margin there is a layer of small cells between the intramarginal vein and the epidermal layers. The margin is made firm by several rows of cells with thickened walls.

Smaragdia bryanae Pilsbry 1917

Smaragdia bryanae (Figure 3) is a neritid snail described (as Neritina bryanae) by Pilsbry in 1917 from specimens collected by W.A. Bryan at Paumalu (Sunset Beach), Oahu. The description reads:

The snail is very small, semiglobose, polished pale gray with four principal bands of oblong, opaque white spots, two zones of fine, reddish longitudinal lines, and with length 2.1 mm and diameter 2.2 mm.

Shell markings and coloration are variable, but the dark green body gives the snail an overall green color that blends with the seagrass.

The genus Smaragdia was separated from Nerita and Neritina by Issel (1869) because the eyes are sessile, not stalked. The bright green Smaragdia viridis (Nerita) Linnaeus 1758, inspired the generic name: Smaragdus is Greek for emerald. Smaragdia has a pantropical distribution. According to Morton (1958) Smaragdia is a terrestrial neritid that has gone back to marine life.

In Hawaii, adult snails are found on seagrass blades. Aquarium behavior is described here, because field observations were

brief. Activities include feeding, general locomotion over the blade surfaces, mating and egg laying. A feeding snail may remain in a single scar for hours or may move on after a short time. Snails are observed to remain attached to the aquarium wall with operculum closed for periods of several hours. They also "swim" up or down to a leaf surface by floating upside down and moving their long tentacles like paddles. Contact is made with a leaf by extending the foot and then flipping over onto the leaf surface. Snails drift with the aquarium current by "swimming" to the surface and extending the foot upwards onto the water surface film. Eggs are laid on Halophila blades, and sometimes the aquarium wall. Egg masses are found on Halophila in the field. Eggs hatch in two weeks releasing numerous swimming veligers.

METHODS

Field work was done by skin diving (snorkeling) close to shore during periods of calm weather and low tides. Although plants occur from depths where leaves are exposed at low tide down to 15 meters or more, no diving was done in water over three meters deep or outside the reefs.

Photomicroscopy

Leaves collected from the field were prepared for microscopic examination and photography. For light microscopy leaves collected at Kaimana (10/8/79) were mounted fresh between glass slides and

photographed with a Zeiss Photomicroscope II. Sections were made to compare anatomical details to Balfour's (1878) descriptions and drawings. For scanning electron microscopy, pieces of leaves were air dried and glued onto plugs. This technique did not prevent collapsing of undamaged cells, but the general nature of the damage could be seen. Leaves for SEM were collected at Paiko (3/31/80) and at Kailua (4/16/80).

A radula from a large Smaragdia bryanae individual collected at Kihei, Maui was extracted and prepared for SEM by Regina Kawamoto.

Core Samples

To measure grazing damage, samples of leaves were obtained at six sites representing a variety of environmental conditions (Table 1, Figure 4). Samples were obtained near the center of homogeneous patches of Halophila with a coring device made from 3.81 cm diameter PVC pipe. Core samples were used so that measurements could be related to substrate area.

At most sites, core samples were obtained from several patches of seagrass, each called a sample (Table 2). If the patch was large, two cores were obtained and combined into one sample; if not, only one core was obtained to minimize disturbance. One set of samples was obtained at each site, since sample processing was time consuming. Because variation in grazing damage between samples was large at Kailua, sampling was repeated at that site (with the samples designated as Kailua-1 and Kailua-2).

Fresh leaves from core samples were wetted with seawater and sandwiched between two glass microscope slides, then wrapped in saran to minimize drying. In the darkroom, each slide was unwrapped and placed directly in a photographic enlarger to make prints for detailed examination and measurement. Slides were then rewrapped in saran for future reference.

On the leaves, grazed areas were outlined in ink on the photographic print and then total leaf area and grazed area on each leaf were measured with a Hewlett Packard coordinate digitizer and planimetry program. Blade area and length were measured from the blade apex to the junction with the petiole as distinguished by the transition from green pigmented cells to the colorless cells of the petiole (Doty and Stone 1966). Blade and midrib widths were measured at the broadest point. Margin width was measured in 25 leaves whose photographs clearly showed the inner boundaries of the margin. The number of leaves in each core gave leaf density. Mean leaf area from each sample multiplied by leaf density for that sample gave leaf area index (LAI).

The location on the blade of each grazed area was noted as basal, central or apical (or a combination of these), and as occurring on one or on both sides of the midrib in each section. Boundaries between sections were defined operationally as the points at which the blade narrows towards the apex and towards the base, but are not exact spots since narrowing is gradual and depends upon blade shape. The intent of

the division was to identify general regions of the blade and the classification proved adequate for the purpose of exploring the general pattern of feeding damage. The boundary between the central and apical sections generally is the point at which blade widths were measured, the broadest point. The relative areas of the sections were determined by weighing paper blades cut from photostated copies of the core sample photographs of enlarged leaves. Seven broad (width > 4.0 mm) and seven narrow (width < 2.2 mm) blades were cut into basal, central and apical sections. Sections were combined for broad and for narrow blades and weighed on a Mettler balance to the nearest 1/10,000 of a gram.

A total of 790 leaves were measured. Forty-six partial leaves were noted as damaged or undamaged but not measured. Leaf fragments and immature leaves were excluded. Data were processed using the SAS (Statistical Analysis System) program package on an IBM 360/158 computer.

Laboratory Experiments with Snails

Snail Maintenance experiment. Snails collected from Halophila growing in shallow water at Kuliouou, Oahu in September, 1980 were kept for four months with Halophila in a small tank with running seawater at the Pacific Biomedical Research Station (PBRC, Kewalo Laboratory). Seagrass plants were fed to the mollusks, floated freely in the water. Adult snails were measured at intervals to record growth, and a

rough count of eggs produced and leaves consumed (Appendix A) was kept.

Feeding rate experiment. A short feeding experiment was conducted with five snails kept in each of three petri dishes for eight days in January, 1976. Ten Halophila leaves were put into each dish. After three days the leaves were removed and area consumed estimated. Fresh leaves (10 to a dish) and water were then provided. Area consumed was again estimated three days later.

Algae/seagrass feeding experiment. A second feeding experiment in 7 petri dishes May, 1976 tested the question as to whether snails would graze macroalgae. Six dishes were started, each containing five snails. Three dishes were fed Halophila, three with species of algae collected in the seagrass patch where snails were found. Fresh algae and seawater were provided each day, but seagrass was only added the third day as it did not deteriorate as did the algae. Activity and feeding behavior were observed each day.

Field Counts of Snails

Several field counts were made to estimate population density per square meter. Except for one count (Kaimana 7/23/75) which was from a core sample that included sediment, only seagrass blades were searched for snails. (It is not known whether snails spend time in the sediments). Three careful counts of snails on leaves were made in 25 cm quadrats on 7/11/75, two at Kahala and one at Kaimana. It is difficult to count snails accurately in the field because they are so

small and well camouflaged, but water was very shallow and calm and visibility excellent.

A mark-recapture survey was conducted at the Paiko mudflat on March 6-7, 1976. Twenty-five snails were collected from leaf blades in a marked square meter of lush Halophila surrounded on all sides by more Halophila. Snails had to be found by touch because the water was turbid, but the required number of snails (25) was quickly found. Snails were dried and marked immediately with red nail polish then released. (In an aquarium test, nail polish marks did not seem to inhibit snail's movement, nor did they come off). Twenty-five snails were collected from the same location the following day. An additional 20 snails were collected from the adjacent seagrass blades.

Snails collected in the field were measured, yielding a total of 22 snails measured from five locations.

RESULTS

The Monophagous Herbivore

Aquarium culture and examination of the feeding damage and the snail radula provide evidence that Smaragdia bryanae is specialized to feed on Halophila hawaiiiana.

Nutritional dependence. Smaragdia bryanae individuals can be maintained indefinitely in an aquarium with Halophila as their

food. They consume seagrass steadily. Growth (Table 3) and reproduction were observed under aquarium conditions with this diet. Egg production was steady and plentiful. Egg masses were found especially on leaves with snail damage. Eggs were deposited on ungrazed portions of the blade, and consumption of egg masses by grazing snails seems unlikely. In a field sample from Malaekahana (2/13/81), 17 egg masses were found on 14 blades, with grazing damage on all but one blade. Three of the blades had two egg masses.

In the aquarium the snails did not eat any of the macroalgae found growing with Halophila in the field. Algae tested include Ulva reticulata, Halimeda sp., Padina sp., Dictyota sp., and unidentified red species. The snails were not tested to see if they consume any epiphytic micro-algae growing on the surface of the Halophila blade. The amount of Halophila eaten daily was estimated at half a leaf per snail in the seagrass feeding experiment. Leaves were more thoroughly grazed than is usual in the field, but that should not affect the estimate which is supported by the record of leaves added and consumed during the culture experiment (Appendix A).

Evidence of the snail's feeding activity. The characteristic damage pattern of grazing Smaragdia bryanae (Figure 5) typically occurs in the leaf lamina between the intramarginal vein and the midrib. Usually the clear grazed areas, which contrast obviously with the ungrazed tissue, form a connected but irregular strip on both sides of the midrib. Grazing scars often narrow or stop at lateral veins where the thin borders of intact tissue are usually wider, giving a scalloped

effect to the edge of the grazing scar. Small, isolated spots and patches of damage indicate that feeding is not always a continuous process.

Examination of grazing damage using a light microscope (Figure 6) suggests that during grazing the snail scrapes off one epidermal layer, leaving most of the opposite epidermis intact. Occasionally damage goes through both layers. When grazing occurs close to the midrib the lower layer of parenchyma cells can sometimes be seen. Extra tissue often remains around lateral veins if they are grazed over.

Scanning electron micrographs (Figures 7 and 8) reveal that actually it is only the upper cell wall, or a portion of it, that is removed during grazing, leaving the side walls intact. Apparently the snail punctures or peels away the upper wall and then perhaps sucks or rakes out the protoplast. Intact cells are interspersed among the damaged cells, and diatoms cling to the surface. Damaged areas photographed in leaf B were only lightly grazed. Diameter of the hole cut in these cells is 13 microns. Damage to leaves A and C was more obvious to the naked eye, and SEM shows that more tissue was removed from the cells. Cell diameter is 21 microns.

Smaragdia grazing equipment. The Smaragdia bryanae radula shown (Figures 10 and 11) was taken from a fairly large snail, about 3 mm in length. The big, double pointed first marginal teeth apparently accomplish most of the grazing damage. The slender, featherlike teeth on the outside may sweep the grazed material into the mouth. The

distance across the large tooth at its base is approximately 20 microns, and from point to point, 10 microns, about the size of grazing damage in leaf epidermal cells (13-21 microns).

The width of the radula in its preserved state is 150 microns. It would take about seven strokes of this radula to cover the width of a typical grazing scar. The portion bearing the large teeth measures 75 microns. The pair of teeth would cover the width of a grazing scar in 14 passes. Lengthwise, several pairs of teeth would be at work at the same time. The effective width of the active portion of the radula during a grazing stroke may be different in the living snail than it is in the flat ribbon configuration usually shown, which is an artifact of the relaxation process that allows extraction of the radula from a preserved snail. Morris and Hickman (1981) have found that in a live snail (Tegula funebris) during feeding the radula is actually tightly rolled with the teeth in a semicircular configuration. In a rolled configuration Smaragdia's first marginals would still be the main tools used in grazing the cells, but the distance between them might be different.

Grazing Theater

The average leaf. The Halophila hawaiiiana leaf blades are the theater where Smaragdia bryanae grazes. Dimensions of the leaf blade

delimit the space in which the food is gathered. Leaf areas, combined with leaf densities, define the amount of food available to local snail populations.

A Halophila patch presents a uniform appearance. The most noticeable difference between leaves is their width and, less obviously, their length. Some areas may be characterized by broad or narrow leaf blades, although both may be found at a single site. Since the snail occupies the blade surface, blade width may restrict snail size. An especially narrow blade might present problems such as dislodgement for a grazing snail of average size. Dimensions of the grazing theater are summarized in Table 4. Composite drawings were made of "the average leaf" based on the mean width and length with standard deviations (Figure 9).

Distributions of blade width and length. Relative within-site variation in leaf parameters indicated that samples could be lumped together. Leaf width and length are normally distributed at each site (Appendix B). When these distributions were compared using Duncan's Multiple Range Test (Tables 5 and 6), two sets of leaf-dimension categories could be recognized: broad or narrow, and long, moderate or short. The fact that leaf dimensions from the two Waikiki sites (Queen's Surf and Kaimana) are so obviously different indicates that geographical location is not the determining factor. Groupings based on width are different from those based on length, except that leaves from Queen's Surf and Kihei had the largest means in both parameters and leaves from Kailua-2 had the smallest mean width and length.

Mean width and length by site along with standard deviation, range and sample size are shown in Figures 10 and 11. Blade width seems the most discriminating and relevant parameter, so sites are arranged in order of increasing mean width in all subsequent figures and tables.

Snail size. The size of Smaragdia bryanae itself is well suited to the size of the Halophila hawaiiiana blade, particularly the width. In the original description Pilsbry (1917) gave the dimensions of the snail as 2.2 mm in length and 2.1 mm in diameter. Kay (1979) lists 2 mm for both dimensions. Snails were measured from several field collections (Table 7). Mean length is 2.9 plus or minus .5 mm and mean diameter 2.5 plus or minus .4 mm for $n = 22$. The average snail would be wider than most of the leaves at sites in the narrow category (Figure 10). In fact, many snails would be more than twice as wide as the narrower Halophila blades. Snails were collected at both narrow and broad sites, and snails from the narrow sites do not seem to be smaller. Overall blade width is close to average snail size.

The fact that Queen's Surf and Kihei are characterized by long and broad leaves and that at Kailua-2 most of the leaves are short and narrow suggests a positive correlation for length and width. The Pearson product-moment correlation coefficient (r) for this relation is 0.68, with $p = 0.0001$. Correlation is better for some samples than others (Table 8).

A plot of width to length (Figure 12) for all leaves shows that there is a fairly large group of long and narrow leaves and a few

short, broad leaves that detract from a linear correlation. Leaves are concentrated below the mean in the short and narrow category from 2 to 3 mm in width (just the size of the usual snail), but the range is greater above the mean in both dimensions.

Distributions of blade areas. The generally positive interaction between length and width creates a wider variation in mean area between the sites (Figure 13). Mean leaf area at Kihei is more than three times that at Kailua-2, a much larger meal per leaf for a grazing snail. Snail consumption was estimated at half of a leaf per day. Since the overall mean blade area is 48.5 mm^2 , the daily grazing ration is about 25 mm^2 per snail.

Measured leaf area is strongly correlated with both blade length and width (Table 8), especially width, but plots (Figures 14 and 15) show that a great deal of residual variation remains, especially in the larger leaves. Width to log area and width² to area transformations were tested but did not decrease the variation.

Leaf and snail density and leaf area index (LAI). Leaf density (Table 9) is another important aspect of food availability. Densities range from approximately 5,000 to 19,000 leaves per square meter, or in terms appropriate to the snail, one-half to nearly two leaves per square centimeter.

Several collections and counts of Smaragdia bryanae made in the field can be used as a rough estimate of the number of snails per unit area of Halophila hawaiiiana (Table 10). Two hundred to 400 snails per

square meter seems a reasonable estimated range for most areas.

LAI gives a measure of the total surface available to a population of grazing snails (Figure 16). LAI is fairly constant over the narrow sites, approximately $.5 \text{ cm}^2$ leaf per cm^2 substrate, but high leaf densities boost the index to 0.62 at Kailua-1. At Malaekahana the LAI is in the range of the narrower sites because leaves there were sparse. Queen's Surf and Kihei have leaf area indices twice that of the narrow sites, approximately 1 cm^2 leaf per cm^2 substrate.

Preferred grazing surface. Since snail damage is not usually seen on midrib or margin, the actual preferred area may be much smaller than the total area of the leaf blade. Dimensions of the "preferred area" were measured in 25 leaves from the dataset. Mean "preferred area" for these leaves is 40.16% of leaf total area, rounded to 40% for subsequent calculations.

The Grazed Leaves

Grazing frequency. Of the 836 leaves sampled, 556 were damaged giving an overall grazing frequency of 66.5% (Table 11). No sample escaped grazing entirely, at lowest grazing frequency, 30% of the leaves suffered damage. Damage occurred on more than 90% of the blades in several samples. The following analysis of the patterns of grazing

damage will include only the grazed subset, about two thirds of the whole.

Grazed surface area per leaf. Mean damage per leaf (by site, Figure 17; by sample, Table 12) is high at Kailua-1, Malaekahana, and Queen's Surf. Mean grazing damage increases with increasing blade width at the other sites.

Overall mean damage per leaf is 8.21 mm^2 . More than half of the damaged leaves were grazed less than the mean value (Figure 18). If the average snail really consumes 25 mm^2 of leaf surface daily, it must usually feed on several leaves to do so. Site maximum values of grazed surface per leaf are all at or above 25 mm^2 , possibly representing a day of grazing by a single snail. The highest damage measured on a blade was 49.12 mm^2 , equivalent to two day's grazing. This grazed area would be larger than whole leaves at most of the sites, but represents only 52.68% of this large leaf blade at Queen's Surf.

To explore the concept of maximum grazing further, a group of leaves that appeared very thoroughly damaged was chosen from the dataset (Table 13). Mean total damage per leaf for this group ($n = 36$) is 20.38 mm^2 and mean percent grazed per leaf is 39.66%. These figures may approach the maximum damageable surface under ordinary circumstances. They are very close to the measurements of the proposed preferred grazing surface.

Relation of damage to leaf dimensions. Total damage plotted against leaf area (Figure 19) seems to have a rather fixed upper limit

at approximately 40% of leaf area. This limit is assumed to correspond to the preferred grazing area discussed above.

Total grazing damage per leaf is positively correlated with width, length and area, except at Malaekahana (Table 14). Correlation is much stronger for sites characterized by narrow blade widths. Apparently, at sites where most of the leaves are smaller than a critical size, which may be related to the daily meal required by the individual snail (estimated at 25 mm^2 per day), more is grazed on larger leaves. Mean preferred area per leaf would be smaller than this amount at narrow sites (Table 15) where only the larger leaves would provide a full meal. At broad sites most leaves are larger than the critical size, and snails seem to graze the same amount on smaller as on larger leaves.

Percent of leaf surface grazed. If the preferred grazing surface is only about 40% of the leaf blade, then snails are actually utilizing the food source to a higher degree than might be thought. Snails graze an average of 10.9% of the total surface on each leaf (Table 16), but this corresponds to 27.3% of the preferred surface.

Looking at percent grazed per leaf rather than at total damage should allow us to focus on grazing patterns peculiar to leaf dimension. The relationships might otherwise be hidden by the more obvious correlation of amount grazed to leaf size because there is more to eat on a larger leaf. There is no overall correlation of percent grazed per leaf with leaf dimension (Table 17). However, the narrow

sites show a modest positive correlation, especially with blade width. Where blades are mostly narrow, the larger preferred area available on the broader blades might become significant. If snails had a grazing strategy that could take advantage of differences in blade widths encountered, then perhaps narrower leaves might escape some grazing pressure.

At Malaekahana the correlation is negative. Leaves there were sparse, and under these conditions the feeding strategy might be for snails to graze their fill on whatever leaf they encounter. A plot of percent grazed per blade to blade area (Figure 20) shows that most of the leaves with very high percent grazed are from Malaekahana. Only 22 leaves (4% of the grazed subset) showed damage greater than the theoretical limit of 40%. Leaves larger than 80 mm² are from the broad sites. Percent grazed tends to be lower on the largest leaves.

Damage in vascular sections. The combined areas of midrib and margin make up about 60% of the leaf surface. Despite apparent avoidance by grazing snails, small incursions into these vascular areas were seen in the leaf samples (Table 18). Out of all leaves grazed (511 leaves), 15.88% had damage in the midrib, 4.31% had damage in the margin, and 5.69% were damaged at the apex where midrib and margin join. These frequencies compare to 100% damage frequency for the lamina between midrib and margin. Since the vascular sections account for more than half the total blade area, the low frequency of damage there is significant.

When it grazes Thalassia, Smaragdia viridis is reported to make furrows about 1 mm wide and half the thickness of the blade (Zieman 1982). Judging from a photograph of the damage, it appears that grazing occurs between the numerous regular veins that run vertically through the Thalassia blade (Tomlinson 1972).

Patterns of feeding damage on leaf blades. The lamina between midrib and margin was subdivided to find out whether grazing occurs more frequently in some parts of the blade than others, and to analyze patterns of feeding damage on the leaf blade. The midrib divides the blade in half longitudinally, and for purposes of analysis the blade was further divided into three sections: base, center and apex (Figure 21) which make up approximately 29.3, 47.5 and 23.2 percent of the blade area respectively. These relative areas are the same in both broad and narrow blades.

Presence of damage in a section was recorded as double or single (on one or both sides of the midrib), but the halves were not differentiated. Blades grazed on both halves of a section were counted twice in frequency totals. Since damage to one or to both sides of a section are included as possible patterns for each section, there are 26 possible patterns as classified.

The most obvious pattern recognized by tabulation of frequencies of grazing damage in each section is that 78.7% of the blades were grazed on both sides of the midrib (Figure 21). This pattern is especially strong in the central section (78.6%), and fairly strong in

the apical section (60.4%), but damage to both halves of the basal section is relatively rare (24.9%).

Frequencies of grazing damage in each section indicate that the snail grazes the blade selectively (Table 19). Significant departure from random grazing is indicated by the high Chi-square value of 188. By the large positive deviation from the frequency expected from its relative area, the apical section seems to be preferred. The low frequency of grazing in the basal section might be related to the greater width of the midrib there.

Figure 22 shows the relative frequencies of the patterns of feeding damage. Diagrams are grouped by the number of sections grazed: one, two or three; and in subgroups by apical, central and basal sections. Damage in two sections is the most common situation, usually apical and central. The basal and apical sections are usually grazed in combination with one or both of the other sections, rarely alone. The basal section is generally grazed only when all three sections are grazed, that is, on a heavily damaged leaf.

The ten most frequent patterns (Figure 23) account for damage to 91% of the leaves. The prevalence of damage in the central section stands out. All ten patterns include damage in the central section. Because the patterns with damage only in the central section are so common (second and fourth), it is likely that the snail begins feeding in that section. By contrast, the frequencies for

patterns with damage only in the apical or basal sections are quite low.

Knowing the frequencies of the damage patterns, the probable path of the feeding snail may be diagrammed (Figure 24). The path shown is where a leaf is entirely consumed. After grazing most of the tissue on one side of the central section the snail crosses the midrib and feeds on the other half of that section. Next the snail usually moves on to the apical sections, and finally to the basal sections. Occasional alternative paths include the snail proceeding from the central to the basal sections without grazing (Figure 23 pattern 8) or only partly grazing the apical sections (Figure 23 patterns 6 and 10).

DISCUSSION

The evidence gathered in this study supports the hypothesis that Smaragdia bryanae is a monophagous herbivore. The snail apparently obtains nutrition directly from Halophila hawaiiiana blades, and does so in a systematic way that implies a greater degree of complexity in grazing behavior than might be imagined. Further observation of grazing behavior to confirm the "preferred pathway" should be interesting. Specializations of the animal which "fit" it to its host plant include size, coloration, and radula structure, and there are undoubtedly many more.

Specialization of the Radula

The unusual structure of the Smaragdia radula is probably important in its specialization to seagrass as food. Baker (1923) studied the radulae of the Neritidae and the Helicinidae. He felt that the radula of the subfamily Smaragdiinae is the most peculiar in the Neritacea, particularly because of the enormous first marginal tooth which bears the remaining marginals almost as vestiges. He claimed that functionally the radula of Smaragdia is 7-toothed, and thought that it illustrates how the taeniglossate type of radula may have developed.

The rhipidoglossate radulae of the Archaeogastropoda is characterized by very numerous marginal teeth. The more advanced Mesogastropoda have taeniglossate radulae with only seven teeth in a row, each with a particular function, reflecting specialization to more complex food. The tendency within the rhipidoglossa for the lateral teeth nearest the marginals to become enlarged and specialized is emphasized in the Neritidae (Fretter 1965); the last lateral is the most powerful tooth of the radula and works with a shovelling action. The marginals are few compared with other rhipidoglossate radulae.

Steneck and Watling (1982) analyzed feeding capabilities of herbivorous mollusks and assigned them to functional groups based on

radula structure. Snails with the rhipidoglossan type broom radulae are primarily limited to grazing microalgae and delicate filaments; snails with taeniglossan type rake radulae mostly graze microalgae but can graze macrophytes; and the true limpets, with their docoglossan type shovel radulae, specialize in grazing macrophytes. Ability to graze macrophytes, or "excavation ability", was said to increase with reduction in the number of functional points (teeth) per row contacting the substrate, which ranges from more than 500 in the Rhipidoglossa to only 4 in the Docoglossa.

Extent and Impact of Grazing Damage

Despite the problems of locating and maintaining contact with the host plant that larval and adult snails must face due to the patchy distribution of the seagrass around the islands, it seems that the grazing damage inflicted by the snails is a daily fact of life for the seagrass. Grazing occurs at high frequency. Significance of the total surface area and percent surface grazed will be demonstrated in the next few sections by calculation from measured values. Grazing damage per blade averaged over the entire dataset, with the undamaged leaves included, gives an overall mean of 5.32 mm^2 grazed per blade for a hypothetical population where every blade is grazed equally. The area of the average leaf is 48.5 mm^2 , so this damage amounts to 11% of the surface of the standing crop in an average Halophila meadow.

This percentage is close to grazing losses measured in other herbivory systems. Sea urchins Lytechinus variegatus were found by Greenway (1976) to graze 8.1% of Thalassia standing crop (20.2 g per week where Thalassia standing crop = 249 g/m^2). Anderson (1972) measured grassland losses due to grasshoppers at 6 - 12% of "available forage" annually.

Total surface grazed per square meter at a site (Figure 25) gives an index of grazing pressure. The index, which will be called Grazed Area Index (GAI), is estimated by combining leaf density at a site with the average grazing damage per Halophila blade at that site (Table 20). This index is analogous to the leaf area index in that it reflects the grazing impact relative to the productive area of the plants. The highest GAI estimate is nearly 0.1.

The GAI can be used to estimate the likely snail density responsible for the grazing damage measured. For example, a snail population with a density of 500 snails/m^2 , each consuming 25 mm^2 per day would graze $0.0125 \text{ m}^2/\text{m}^2/\text{day}$. This relatively dense snail population would remove 0.1 m^2 of blade area (equivalent to our highest GAI value) in approximately eight days. Eight days seems a reasonable interval for the damage measured in the samples to have occurred, assuming no leaf turnover, and this figure will be used to estimate a minimum snail density corresponding to overall grazing damage in each sample (Table 20). These snail population estimates are within the range of snail densities found in field samples.

An idea of the impact that snail grazing has on the seagrass is given by the percentage of total surface area that is damaged. The mean percent surface grazed (Figure 26) indicates the extent of damage to every blade in the average population represented by each site. If the level of damage were constant at all sites, we would expect high impact on the small leaves at Kailua-2, with progressively less impact as leaves get larger. Percent damage at Kihei and at Queen's Surf (where the leaves are largest) are lower as expected, but levels at Paiko through Malaekahana are nearly equal, and grazing impact at Kailua-2 is actually low due to the low levels of damage measured.

Grazing impact is influenced by the interaction of leaf area and grazing damage levels (Table 21). If leaves were larger at a spot where snail grazing was heavy, the impact of that grazing would not be as severe as a lower rate of grazing would be on smaller leaves. For example, the level of damage (GAI) is nearly the same at Kihei, sample 5 and Queen's Surf, sample 1, but the impact is less on the extremely large leaves in the Kihei sample. Impact level is very close at Kailua-2, sample 4 and Kihei, sample 3, but the damage or, by inference, the snail population supported would be nearly four times greater at the Kihei sample because the leaves are much larger.

Fraction of Standing Crop Occupied and Consumed by Snails

Aside from grazing damage, the basic spatial relationship of snails to seagrass can be quantified. Calculating from the mean LAI of 0.65 (0.65 m² Halophila surface per m² meadow area), there is on

average a leaf surface area (one-sided) of $650,000 \text{ mm}^2$ per m^2 . The average snail occupies a space approximately 6.5 mm^2 (mean snail diameter = 2.8 mm , $\pi r^2 = 6.2 \text{ mm}^2$). With a density of 500 snails, 0.5% of the leaf surface would be covered by snails. In a Halophila patch of average density ($13,000 \text{ leaves}/\text{m}^2$), there would be one snail to every 26 leaves.

Using the consumption estimate of 0.5 blade/snail/day, average daily consumption of seagrass for populations of snails at various densities per square meter was calculated and expressed as a fraction of the average seagrass standing crop (Table 22). A population of 500 snails would consume at least 250 leaves, or 2% of the standing crop daily. The degree of impact of consumption at this level would depend upon the rate of production of new leaves and the rate of leaf turnover.

Estimated Production of New Leaves

Since Halophila hawaiiiana maintains its abundance despite the regular grazing damage suffered, it is assumed that daily consumption by snails is offset by production of new leaves. Extrapolating from core sample data¹, a square meter of Halophila with density of 13,000 leaves would contain 2708 terminal buds. Since a pair of leaves is produced at each bud, there are 5,416 new leaves that will develop in the near future. Leaf turnover rate is not known, but from laboratory

1. Paiko, 15.6 cm diameter cores taken 6/18/75, 6/25/75

observation there is little change over a period of about a week. We assumed that leaf turnover was longer than the eight day grazing interval used earlier, so for calculation let us say that all the new leaves fully develop over the interval of 14 days. This would give 193 leaf pairs, or 386 leaves developing per day, representing 3% gross growth. Buesa (1974) measured 2.9% gross daily growth in Thalassia on the Cuban shelf. With losses due to herbivory, senescence, etc. included, net growth was 1.2% per day. Jacobs (1979) measured 1.5% net daily growth for Zostera in France.

Snail field density was thought to range from 200 to 500 snails per m^2 . At 350 snails per m^2 , 45% of the estimated Halophila new leaf production would be consumed by grazing snails. This is consistent with Greenway's (1976) findings that at mean field densities Lytechinus consumed about 50% of Thalassia blade production. If the figures for Smaragdia consumption and Halophila production are reasonable, new leaf production would ordinarily more than compensate for snail grazing losses. However, during a snail population boom or seagrass decline, tissue loss might equal or even exceed leaf production. Mature leaves seem to senesce slowly. It might be that leaf production is high because of snail grazing, but the effect of that grazing may be little more than to clear the way for new leaves. Gathering numbers for rates of leaf production and development, leaf longevity and turnover would be important objectives for further study. Firm numbers for snail population densities and grazing rates are also needed.

Plant Adaptation for Tolerance of Herbivory

In plant-animal interactions such as pollination and seed dispersal, the plant is aided in the perpetuation of the species by the interaction with the animal. These are mutually positive relationships with direct contributions to the survival of both partners. The attraction of animals has been a primary force in the evolution of flowers and fruit (Faegri and Van der Pijl 1966, Taktajan 1969).

Although some authors contend that herbivory is also beneficial to plants (Owen 1980, Owen and Wiegert 1976, 1981, 1982), herbivory and seed predation interactions have negative effects upon plants. Plant responses primarily consist of defense or escape activities. Since Smaragdia bryanae seems to graze only the specific host Halophila hawaiiiana, coevolutionary theories of herbivory would predict a continuing series of adaptations in the seagrass for defense or escape. With the information gathered so far, we can point out a few directions to look for possible escape, defense or, at least, tolerance strategies or mechanisms.

Snails most frequently graze the lamina between midrib and margin, especially in the central section, the widest portion of the blade. This may be the area of most active photosynthesis and thus a serious loss for the plant. However, it might be an advantage for the plant that the vascular systems in midrib and margin are not usually

attacked. Since most leaves are only partly damaged, the blade can continue to function.

Incursion into the vascular sections occurred more often at Malaekahana, Kailua-2 and Paiko than at the other sample sites. At Malaekahana total leaf surface area is low compared to the amount of damage sustained. Leaves at Kailua-2 and Paiko tend to be narrow and small. Under these conditions snails may be forced to graze on less desirable portions of the leaf blade. When leaf supply was scarce in the laboratory, snails grazed more of the leaf surface, especially the midrib. Damage in the apical margin seems especially high at Paiko, perhaps warranting investigation into possible causes.

The "preferred" grazing area seems to be largest in broad leaves, perhaps giving a selective advantage to production of narrow blades where grazing pressure is high. Data does not clearly support this hypothesis, but the situation is complex and deserves more investigation.

The selection pressure for plant adaptation may be related to the amount of damage involved, and to the extent of injury caused by that damage. However, there may also be benefits in some cases that might help to balance the negative effects of the animal. For example, herbivory can be combined with seed dispersal where sticky seeds or burrs become attached to grazing animals.

Black (1976) noted that Egrefia laevigata maintains its abundance despite regular grazing by Acmaea insessa, and described a possible

benefit provided by the limpet to host kelp plants. Grazed kelp branches break off at grazing scars, and this pruning effect may save the entire plant from detachment by heavy surf, a leading cause of mortality for large kelp plants.

Without grazing by Acmaea testudinalis, the coralline alga Clathromorphum circumscriptum becomes covered with epiphytes (Steneck 1982). The elaboration of up to ten layers of epithelial tissue protects the alga from grazing injury, but interferes with independent removal of epiphytes which other corallines accomplish by sloughing off their single layer epithelium. Halophila patches have been observed where each blade bore a thick furry covering of epiphytes which must interfere with photosynthesis. Grazing by Smaragdia may help to control epiphyte populations.

The patchy distribution of Halophila may provide some escape from grazing. It appears, however, that Smaragdia and seagrasses have been partners over long stretches of time and space. Therefore it would not be surprising if it is found that the grazing is well tolerated.

Table 1. Description of core sample locations with depth at low tide

Site name	Date	Description
Kaimana	5/31/77	Small bay near pier, subject to strong current; large patch surrounded by open sand. 1.5 m deep
Kailua-1	8/07/78	Near Flat Island, long band of grass-mounds parallel to shore. Depth 1 m
Queen's Surf	10/22/78	Small patches between algae covered rocks. Very close to shore and to breakwater. Depth 0.25 m
Kihei, Maui	12/27/78	Many patches in mud flat area mixed with coral rubble, algae. Close to shore near sandbar. 0.25 m
Paiko	2/26/79	Series of dense patches in mudflat and sand along Kuliouou coast inside reef. Exposed at low tide
Malaekahana	5/31/79	Small patches near beach exposed to some wave action. 0.5 m
Kailua-2	7/12/79	Same as Kailua-1 except more patches were sampled

Table 2. Summary of samples and cores at each site

Date	Site	Number of samples	Cores per sample
5/31/77	Kaimana	2	1
8/07/78	Kailua-1	3	2
10/22/78	Queen's Surf	2	2
10/27/78	Kihei	5	1
2/26/79	Paiko	1	2
5/31/79	Malaekahana	4	1
7/12/79	Kailua-2	5	1 - Samples 1 and 5 2 - Samples 2, 3, 4

Table 3. Growth (mm) of snails in PBRC laboratory during maintenance experiment 10/06/80 to 12/19/80

Initial snail length	Month 1		Month 2	
	Net growth	Percent growth	Net growth	Percent growth
3.52	0.25	7.1	0.08	2.1
3.20	0.49	15.3	0.09	2.4
3.04	0.24	7.9	0.20	6.1
3.04	0.08	2.6	0.28	9.0
2.72	0.06	2.2	0.13	4.6
1.89	*		0.23	12.2

* Snail introduced at end of Month 1

Table 4: Dimensions of the grazing theater: overall summary of measurements from leaves collected at all sites (n = 790)

Dimension	Mean	Standard deviation	Coefficient of variation %	Minimum	Maximum
Leaf area (mm ²)	48.67	28.45	58.46	9.61	167.70
Leaf length (mm)	21.42	5.98	27.91	8.90	43.18
Blade width (mm)	3.24	1.26	39.04	1.04	7.00
Midrib width (mm)	0.75	0.24	32.82	0.25	1.52
Margin width (mm)*	0.05	0.02	40.00	0.02	0.07
Leaf density (leaves/m ²)**	13,400	2,800	20.90	5,323	19,744
Leaf area index LAI (m ² /m ²)	0.65	0.40	61.54	0.24	1.86

*Measured where margin is midway between its broadest, at the apex and narrowest, towards base n = 25

** n = 26 samples

Table 5. Duncan's Multiple Range Test groupings for blade width (mm). Means with the same letter are not significantly different at alpha level = .05 with 783 degrees of freedom (n = 790)

Duncan grouping	Mean	n	Site	Category
A	4.78	103	Queen's Surf	broad
B	4.26	126	Kihei	"
C	3.90	79	Malaekahana	"
D	2.95	49	Kaimana	narrow
D	2.71	187	Kailua-1	"
E	2.39	39	Paiko	"
E	2.32	207	Kailua-2	"

Table 6. Duncan's Multiple Range Test groupings for blade length (mm). Means with the same letter are not significantly different at alpha level = .05 with 783 degrees of freedom (n = 790)

Duncan grouping	Mean	n	Site	Category
A	30.07	103	Queen's Surf	long
B	24.54	126	Kihei	"
C	21.04	79	Malaekahana	moderate
C	20.96	49	Kaimana	"
C	20.01	187	Kailua-1	"
D	17.51	39	Paiko	short
D	16.56	207	Kailua-2	"

Table 7. Measurements of *Smaragdia bryanae* collected in the field, length (mm) X diameter (mm). Overall mean length 2.9 ± 0.5 , mean diameter 2.5 ± 0.4 (n = 22)

Site Date	Queen's Surf 6/15/82	Kihei 7/18/79	Paiko 9/18/79	Malaekahana 10/7/80	Kailua 1/30/80
	3.8 X 2.9	3.3 X 2.5	3.5 X 2.6	1.9 X 1.0	3.4 X 2.2
	3.0 X 2.4	3.1 X 2.4	3.2 X 2.4		3.0 X 1.9
	2.9 X 2.3	2.9 X 2.1	3.0 X 1.9		2.7 X 2.2
	2.9 X 2.2	2.8 X 2.1	3.0 X 1.9		2.6 X 1.9
	2.1 X 1.7	2.7 X 2.0	2.7 X 1.8		2.1 X 1.4
		2.4 X 1.9			
Mean	2.9 X 2.3	2.9 X 2.2	3.1 X 2.1	-	2.8 X 1.9
Std*	0.6 0.4	0.3 0.2	0.3 0.4	-	0.5 0.3

* Standard deviation

Table 8. Values of Pearson product-moment correlation coefficients(r) for leaf dimensions and the probability (p) of a larger value of r

Site	n	Width-Length		Width-Area		Length-Area	
		r	p	r	p	r	p
Kailua-2	17	.46	.0629	.84	.0001	.79	.0001
	43	.41	.0065	.89	.0001	.68	.0001
	48	.54	.0001	.90	.0001	.82	.0001
	68	.71	.0001	.94	.0001	.83	.0001
	31	.45	.0001	.78	.0001	.86	.0001
Paiko	39	.59	.0001	.82	.0001	.89	.0001
Kailua-1	64	.46	.0001	.82	.0001	.81	.0001
	75	.61	.0001	.90	.0001	.82	.0001
	48	.38	.0083	.80	.0001	.80	.0001
Kaimana	21	.69	.0005	.81	.0001	.87	.0001
	28	.58	.0013	.90	.0001	.78	.0001
Malaekahana	39	.15	.6531	.81	.0023	.63	.0379
	11	.47	.0349	.83	.0001	.84	.0001
	20	.49	.0636	.92	.0001	.66	.0073
	15	.54	.0013	.92	.0001	.79	.0001
Kihei	21	.76	.0001	.89	.0001	.93	.0001
	19	.52	.0239	.90	.0001	.75	.0002
	37	.56	.0003	.90	.0001	.68	.0001
	21	.59	.0048	.88	.0001	.82	.0001
	28	.68	.0001	.90	.0001	.85	.0001
Queen's Surf	46	.69	.0001	.89	.0001	.76	.0001
	57	.72	.0001	.92	.0001	.84	.0001

Table 9. Density of leaves by site and sample from core samples described in Tables 1 and 2 except as noted

Site	Sample	Leaves ₂ per cm ²	Site mean leaves *** per m ²
Kailua-2	1	0.82	12,582
	2	1.09	
	3	1.19	
	4	1.69	
	5	1.50	
Paiko	1	1.50	15,001
	2*	1.48	
	3*	1.21	
Kailua-1	1	1.72	15,888
	2	1.86	
	3	1.19	
Kaimana	1	1.02	11,856
	2	1.35	
	3**	1.03	
Malaekahana	1	0.53	9,557
	2	0.97	
	3	0.73	
	4	1.60	
Kihei	1	1.02	12,775
	2	0.97	
	3	1.89	
	4	1.06	
	5	1.45	
Queen's Surf	1	1.14	12,582
	2	1.38	
Kahala	1**	1.97	19,744

* Data from 15.6 cm diameter core sample 6/25/75

** Data from 25 cm² quadrats sampled 7/8/75

*** Mean includes only grazing study core samples, except at Kahala, where no grazing study samples were obtained

Table 10. Field counts of snails and calculation of estimated snail density per square meter. Counts arranged in order of confidence in their accuracy

Date	Location	Number of snails	Area searched	Estimated snail density	Count description
7/23/75	Kaimana	8	0.019 m ²	421	Core (15.6 cm diameter) care taken not to lose snails
7/11/75	Kahala				Careful visual search of
	a. shore	8	25 cm ²	128	quadrat marked with string water shallow and clear
	b. reef	20	25 cm ²	240	(shore patch very small)
6/20/75	Paiko	20	30 cm ²	180	Casual visual search, area estimated tide low, sea-grass nearly exposed*
9/18/80	Kuliouou	11	25 cm ²	176	Area estimated, time short (collecting snails for experiment) much damage
3/6/76	Paiko	25	1 m ²		Zero visibility, snails found by touch, marked
3/7/76	Paiko	45	1 m ²	625	Recapture: 1 snail out of 25 collected in study area was marked**, 20 from surrounding <u>Halophila</u> also unmarked

* Snails may remain in the sediments when seagrass exposed at low tide
 ** Assumed nail polish marks may have come off some snails, or that procedure might have caused death of some marked snails. Alternatively, the population was indeed large or marked snails migrated

Table 11. Frequency of damage in sampled leaves

Site	Number of samples	n*	Percent leaves damaged	Lowest sample frequency	Highest sample frequency
Kailua-2	5	213	56.34	35.48	94.12
Paiko	1	62	90.32	-	-
Kailua-1	3	197	64.97	34.69	79.22
Kaimana	2	49	81.63	75.00	90.18
Malaekahana	4	79	74.68	36.36	93.33
Kihei	5	132	65.91	30.00	87.18
Queen's Surf	2	104	63.46	46.81	77.19
Overall	22	836	66.51		

* Partial leaves included

Table 12. Grazed surface per leaf (mm^2) in grazed subset by₂ sample. Overall mean ($n = 511$) = 8.21 plus or minus 7.05 mm^2

Site	n	Mean grazed area	Standard deviation	Minimum damage	Maximum damage
Kailua-2	16	13.60	8.12	3.61	29.80
	17	3.59	3.66	0.06	10.64
	35	4.64	3.95	0.13	13.54
	36	3.89	3.25	0.06	12.19
	11	2.86	3.32	0.19	11.03
Paiko	33	6.51	5.47	0.30	25.98
Kailua-1	43	10.20	7.88	0.38	32.82
	59	10.40	6.58	0.71	30.00
	16	7.41	4.77	1.05	17.06
Kaimana	19	7.61	7.20	0.35	26.57
	21	6.94	3.05	1.40	12.87
Malaekahana	4	8.27	8.07	1.20	19.80
	16	11.04	6.90	3.40	30.60
	14	13.34	6.36	1.40	20.00
	25	7.21	6.35	0.60	26.40
Kihei	12	2.48	1.70	0.50	5.31
	16	10.61	7.96	0.26	25.28
	32	8.13	5.71	0.64	22.45
	14	7.73	7.11	1.29	27.09
	7	12.75	11.33	1.10	30.60
Queen's Surf	21	8.86	5.39	0.99	18.09
	44	11.35	11.02	0.33	49.12

Table 13. Amount of damage on "very damaged" leaves (n = 36)
 Mean damage per leaf = 20.38 plus or minus 8.61 mm², mean
 percent damaged = 39.66 plus or minus 8.79% per leaf

Site	Leaf*	Damage mm ²	Percent damaged	Comment
Kailua-2	1-1-2	14.90	36.78	
	1-1-5	29.79	45.83	
	1-1-6	29.03	41.21	
	1-3-2	25.16	46.32	
	3-1-10	11.61	45.34	
	3-3-5	10.00	38.85	
	3-3-6	10.19	36.66	
	3-5-6	11.35	30.45	not all eaten
Paiko	1-3-1	15.10	43.02	
	1-5-2	25.98	41.50	
Kailua-1	1-6-5	9.20	31.83	small leaf
	1-1-1	22.86	31.96	
	1-3-6	32.82	42.53	
	1-4-1	15.76	43.07	
	1-7-1	21.33	44.81	
	1-7-4	24.54	39.05	
	2-1-9	13.63	26.50	
	2-2-2	15.34	37.87	
	2-2-4	14.31	45.43	
	2-2-5	19.66	44.86	
	2-2-6	17.75	31.06	
	2-7-2	10.84	28.70	narrow blade
	Kaimana	1-2-3	9.16	26.69
1-2-5		26.57	42.42	
1-3-6		21.87	37.00	
Malaekahana	3-1-2	20.0	54.4	
	3-1-3	18.8	37.4	
	3-2-3	19.8	68.0	
	3-2-5	19.2	52.3	
Kihei	2-1-2	25.28	29.25	very large leaf
	2-1-6	14.96	27.95	
	2-3-6	24.77	40.85	
Queen's Surf	2-1-3	32.25	35.69	
	2-3-4	34.19	32.24	huge leaf
	2-4-6	16.54	37.42	
	2-7-2	49.12	52.68	

* Numbers refer to sample-picture-leaf

Table 14. Values of Pearson product-moment correlation coefficients (r) for total grazed area per leaf with leaf dimensions, and probability (p) of a larger value of r. Undamaged leaves excluded

Site	n	Width		Length		Area	
		r	p	r	p	r	p
Kailua-2	115	.60	.0001	.65	.0001	.71	.0001
Paiko	23	.55	.0009	.27	.1273	.49	.0036
Kailua-1	118	.68	.0001	.53	.0001	.71	.0001
Kaimana	40	.55	.0003	.32	.0429	.49	.0012
Malaekahana*	59	.10	.4528	-.16	.2321	-.05	.7339
Kihei	81	.38	.0005	.13*	.2658	.35	.0013
Queen's Surf	65	.25	.0406	.27	.0287	.31	.0115
Overall	511	.41	.0001	.29	.0001	.39	.0001

* Value of p too high to accept relationship

Table 15. Average mm^2 "meal* per leaf" (preferred area = 40% mean area) available to grazing snails at each site compared to correlation of grazed area per leaf with leaf area

Site	Mean area	Mean preferred area "meal per leaf"	Correlation of damage to leaf area	Width category
Kailua-2	26.4	10.6	.71	narrow
Paiko	34.6	13.8	.49	"
Kailua-1	39.2	15.7	.71	"
Kaimana	38.9	15.6	.49	"
<hr/>				
Malaekahana	54.2	21.7	-.05	broad
Kihei	83.3	33.3	.35	"
Queen Surf	74.0	29.6	.31	"

* Daily requirement per snail estimated to be 25 mm^2 , is larger than mean preferred area at narrow sites

Table 16. Percent leaf surface grazed per leaf (grazed area/ leaf area X 100) in grazed subset, and expression as percentage of preferred grazing area (40% of total leaf area)

Site	n grazed leaves	Sample mean percent	Sample maximum percent	Site mean percent	Percent preferred area
Kailua-2	16	24.62	46.32	15.94	39.88
	17	13.47	34.79		
	35	17.10	45.34		
	36	13.88	39.55		
	11	10.16	23.67		
Paiko	33	17.70	43.02	17.70	44.25
Kailua-1	43	21.63	44.81	21.25	53.13
	59	21.97	46.69		
	16	17.59	35.52		
Kaimana	19	17.58	42.42	18.40	46.00
	21	19.15	31.82		
Malaekahana	4	19.02	45.10	19.83	49.58
	16	19.00	47.66		
	14	34.26	68.04		
	25	12.40	50.77		
Kihei	12	4.88	10.66	9.84	24.60
	16	14.84	40.85		
	32	8.21	22.45		
	14	11.44	34.08		
	7	11.11	26.24		
Queen's Surf	21	11.19	28.87	14.62	36.55
	44	16.26	52.68		

Table 17. Values of Pearson product-moment correlation coefficients (r) for percent damage per leaf with leaf dimensions, and probability (p) of a larger value of r. Undamaged leaves excluded

Site	n	Width		Length		Area	
		r	p	r	p	r	p
Kailua-2	115	.29	.0014	.34	.0002	.33	.0003
Paiko	23	.24	.1815	-.17	.3499	.02	.9175
Kailua-1	118	.37	.0001	.18	.0474	.29	.0014
Kaimana*	40	.16	.3220	-.09	.5792	.14	.8279
Malaekahana	59	-.19	.1436	-.45	.0003	-.39	.0020
Kihei	81	.06	.5723	-.10	.3562	-.01	.9140
Queen's Surf	65	-.06	.6261	-.03	.8422	-.01	.9244
Overall*	511	-.02	.5802	-.14	.0021	-.11	.0160

* Value of p too high to accept relationship

Table 18. Frequency of damage in vascular sections of leaf blade, midrib, margin and apex (n = 511)

Site	Midrib		Margin		Apex	
	frequency	%	frequency	%	frequency	%
Kailua-2	29	25.44	7	6.14	12	10.57
Paiko	6	18.18	2	6.06	7	21.21
Kailua-1	17	14.40	5	4.24	4	3.39
Kaimana	4	10.00	0	0.00	2	5.00
Malaekahana	14	23.73	1	1.69	2	3.39
Kihei	3	4.47	0	0.00	2	2.98
Queen's Surf	8	9.88	7	0.64	0	0.00
Overall	81	15.88	22	4.31	29	5.69
Margin + apex			51	9.19		

Table 19. Chi-square contingency table test for departure from random grazing on blade surface

	Base	Center	Apex
Expected	484	784	383
Observed	241	884	526
Deviation	-243	+100	+143

Chi-square = 188 highly significant

Table 20. Total surface area grazed per square meter: Grazed Area Index (GAI), an indication of the snail population

Site	Mean grazed area mm ² /leaf	Density leaves/m ²	GAI m ² /m ²	Estimated* minimum population snails/m ²
Kailua-2	2.94	12,582	0.037	185
Paiko	5.51	15,001	0.083	413
Kailua-1	6.19	15,888	0.098	492
Kaimana	5.92	11,856	0.070	350
Malaekahana	7.30	9,557	0.070	350
Kihei	5.23	12,775	0.067	334
Queen's Surf	6.65	12,582	0.084	418

* Calculated from GAI assuming 8 day grazing interval,
25 mm²/snail/day grazing consumption and no leaf turnover

Table 21. Impact of snail grazing (percent surface grazed) by sample shown in relation to the grazed area (GAI, estimated snail population) and the leaf area

Site	Sample	GAI	Estimated snails m ² *	Percent surface grazed	Mean leaf area mm ²
Kailua-2	1	0.105	526	23.18	53.9
	2	0.015	73	4.98	22.4
	3	0.040	200	12.47	24.9
	4	0.035	174	7.35	25.8
	5	0.015	77	3.61	20.4
Paiko	-	0.083	413	14.97	34.6
Kailua-1	1	0.018	581	14.81	39.1
	2	0.152	762	17.28	42.4
	3	0.029	146	5.86	34.3
Kaimana	1	0.070	350	15.91	41.8
	2	0.070	352	14.36	36.7
Malaekahana	1	0.016	80	6.92	44.4
	2	0.085	427	15.20	58.3
	3	0.090	452	31.98	40.1
	4	0.087	436	9.40	61.3
Kihei	1	0.014	72	2.79	46.8
	2	0.086	432	12.50	79.0
	3	0.133	663	7.10	96.8
	4	0.055	275	7.63	77.3
	5	0.046	232	2.78	98.0
Queen's Surf	1	0.045	230	5.11	83.1
	2	0.121	604	12.55	66.7

* Calculated from GAI assuming a snail grazes 25 mm² per day and that the samples represent an 8 day grazing interval

Table 22. Theoretical daily consumption of seagrass by snails at different densities per square meter compared to average standing crop (13,000 leaves or 650,000 mm²/m²)

Snails per m ²	Amount grazed / day		Fraction of standing crop consumed / day
	leaves	surface area (mm ²)	
25	12.5	625	.001
100	50.0	2,500	.004
350	175.0	8,750	.014
500	250.0	12,500	.019

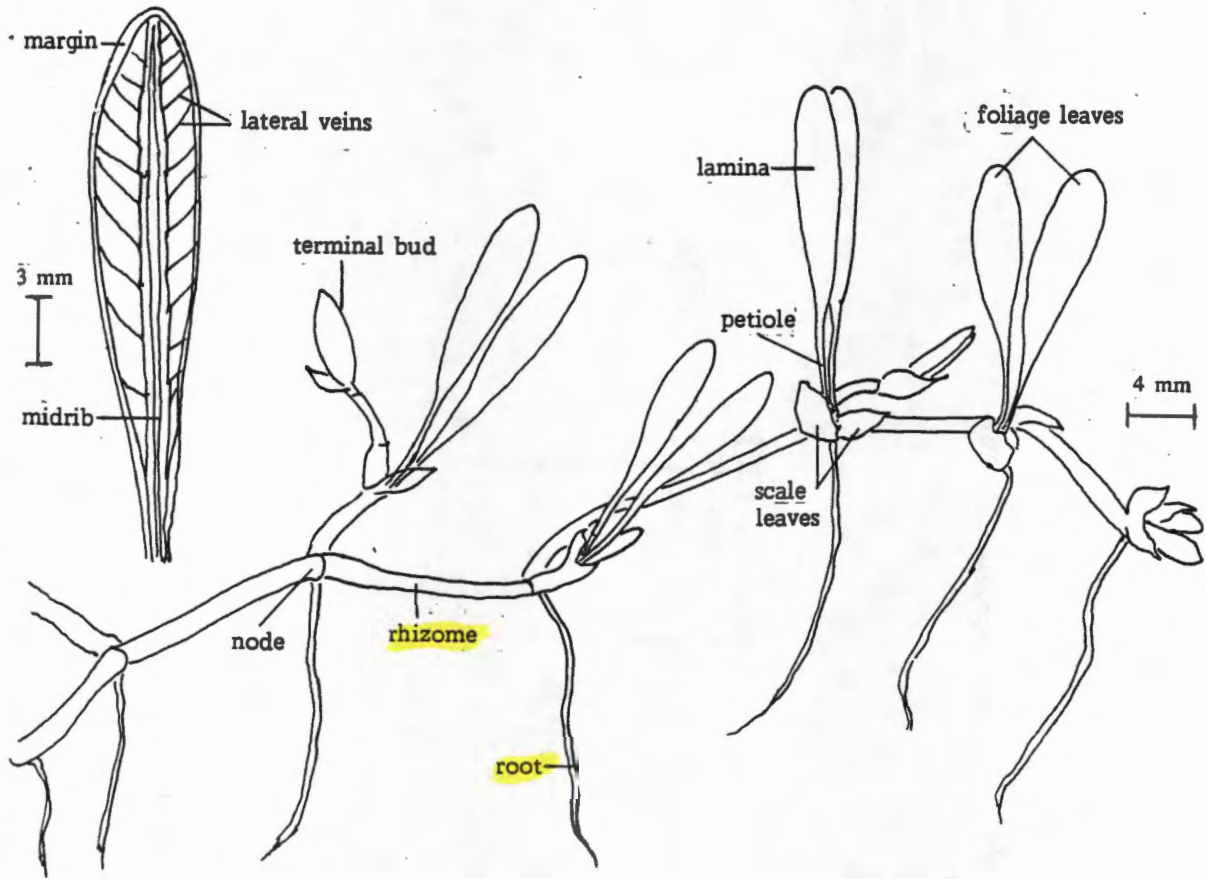


Figure 1. Habit of *Halophila hawaiiiana*

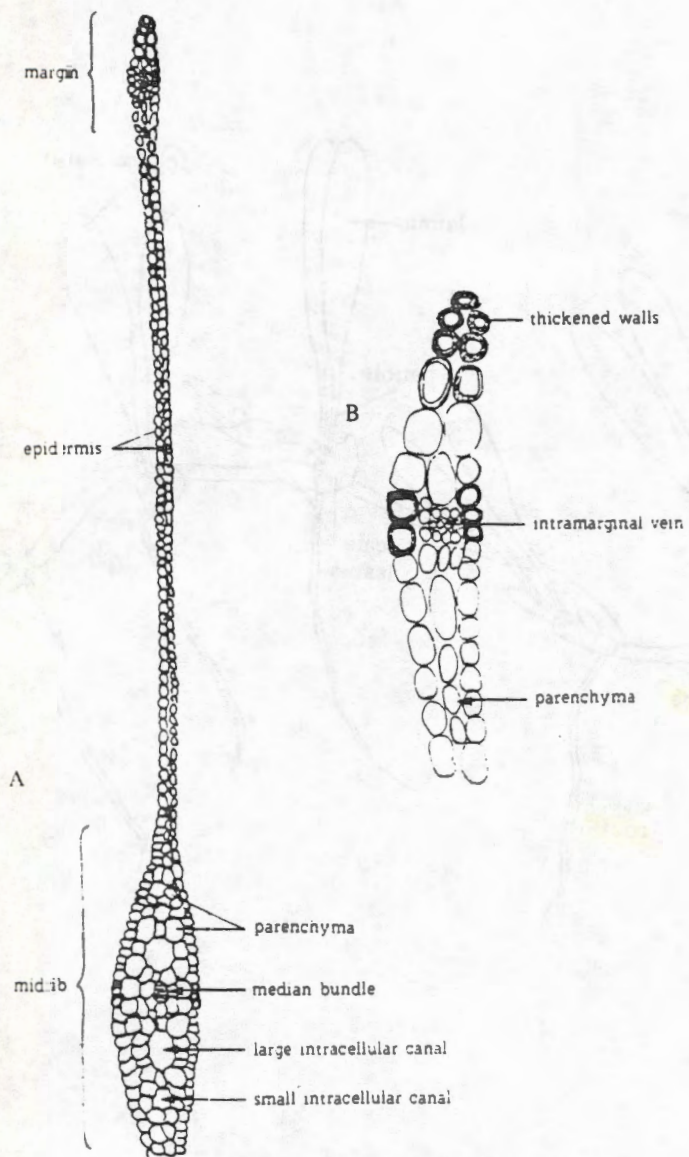


Figure 2. Section of *Halophila* blade adapted from Balfour (1878).
 A, midrib with one side of lamina. B, enlargement of margin)

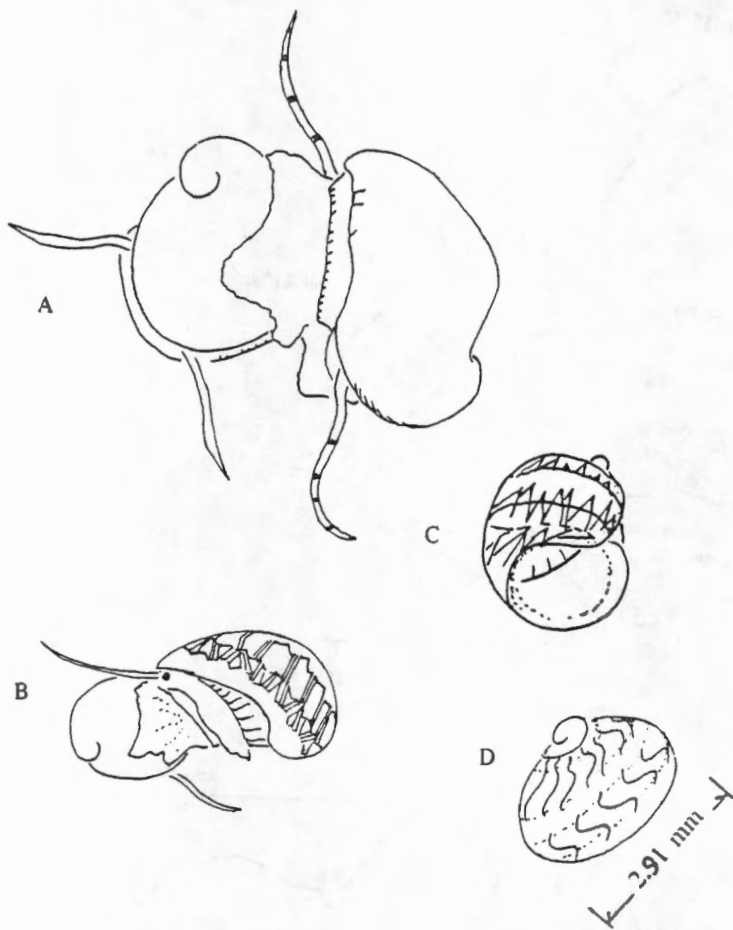


Figure 3. Adult Smaragdia bryanae. A, B, mating pairs.
 B, C, D, examples of marking patterns. B, dark lines on yellow
 background. C, dark lines and orange bands. D, reddish lines
 separated by opaque white bands

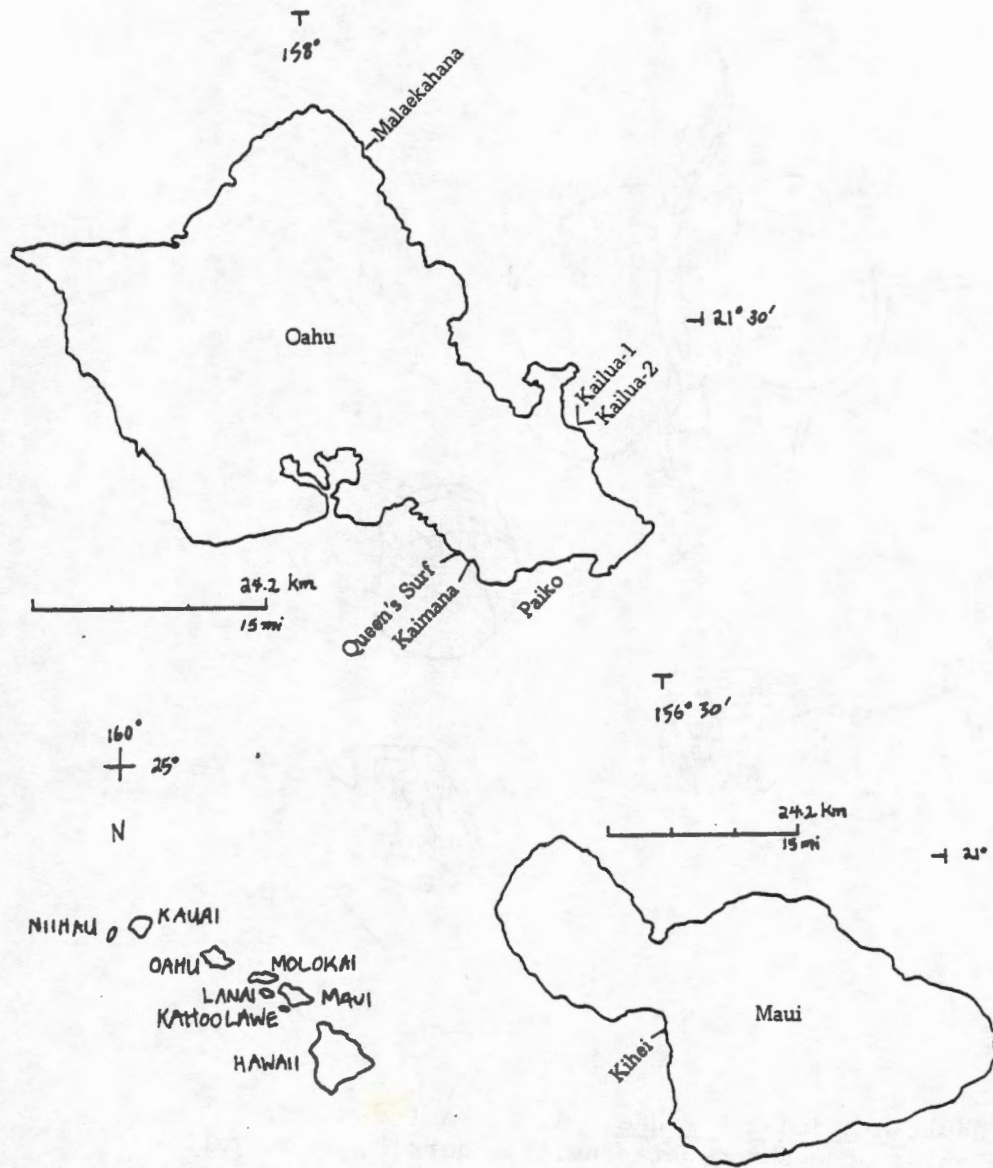


Figure 4. Map of the Hawaiian Islands showing locations of the sample sites on Oahu and Maui

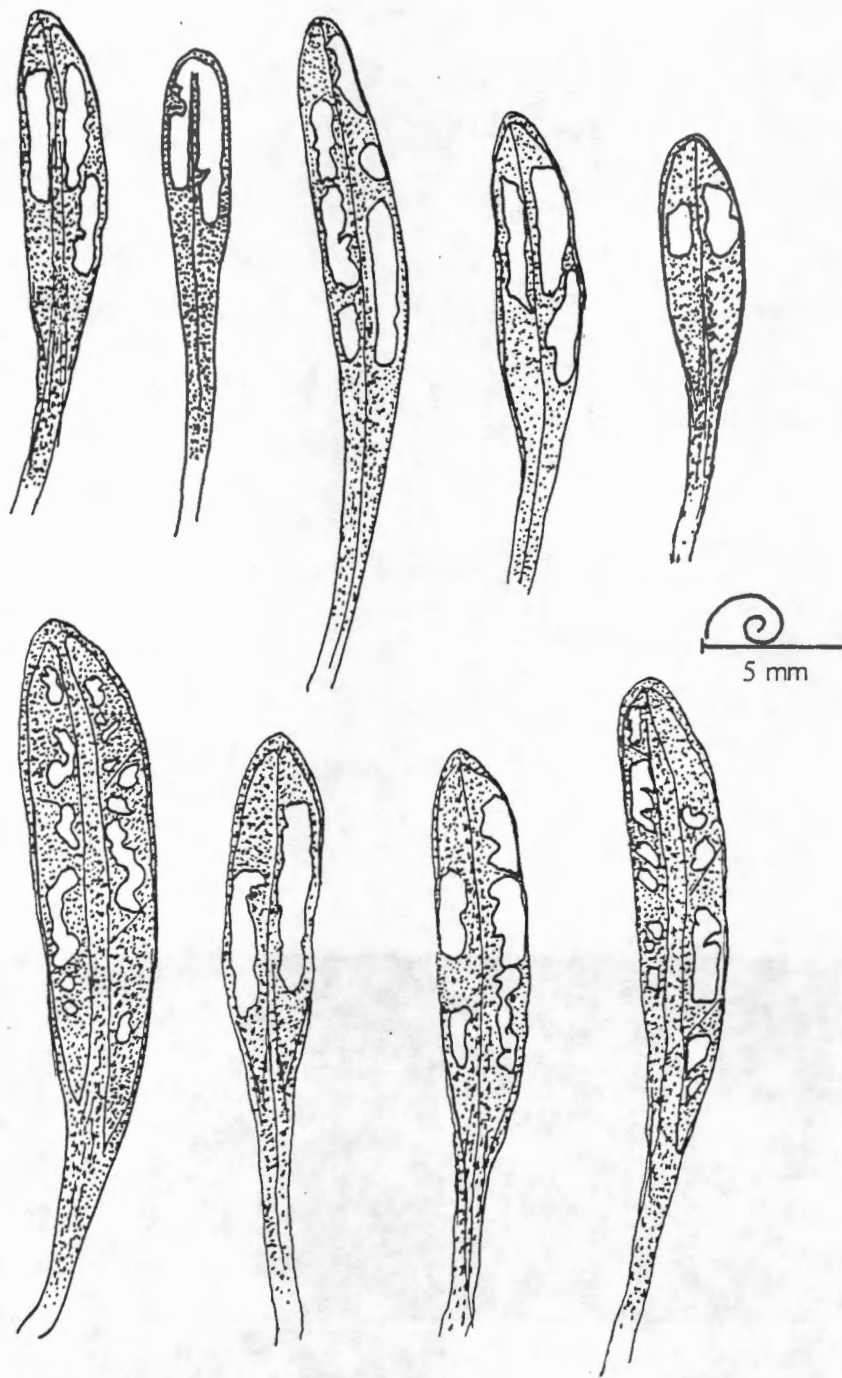
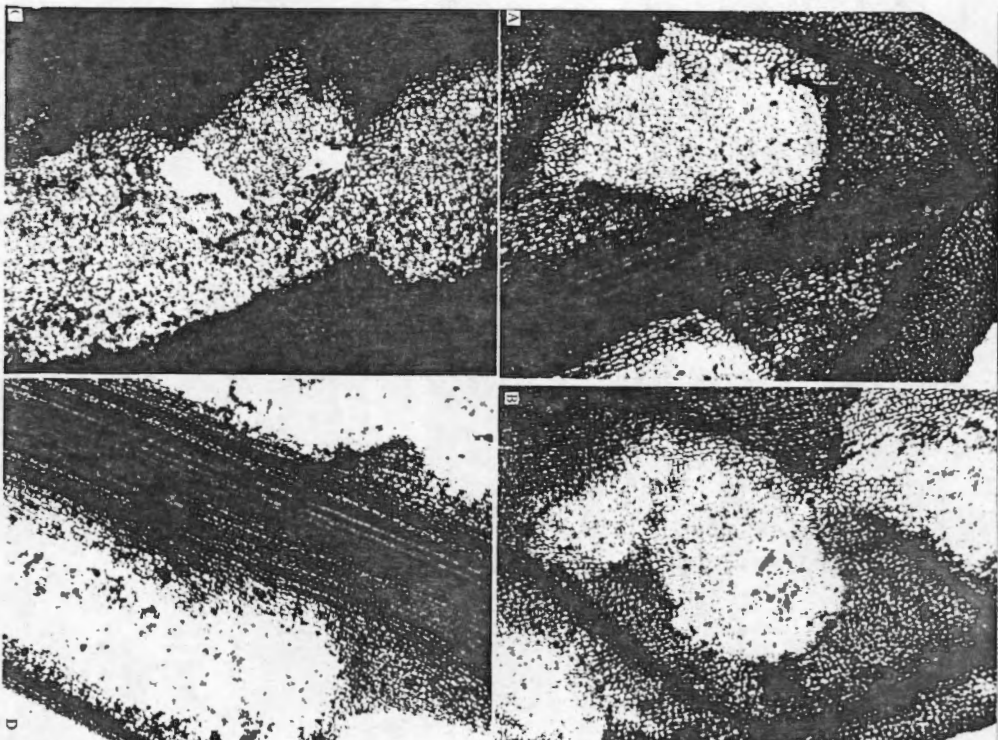


Figure 5. Examples of typical grazing damage traced from leaves in Kailua-2 samples. Scale indicates size of average snail

Figure 6. Light Micrographs of grazing damage. A, blade apex with damage bounded by midrib, intramarginal and lateral veins. B, damage frequently narrows at lateral veins, at times both cell layers are removed. C, typical strip of damage with scalloped edges. D, midrib with damage on both sides. (All X 100)



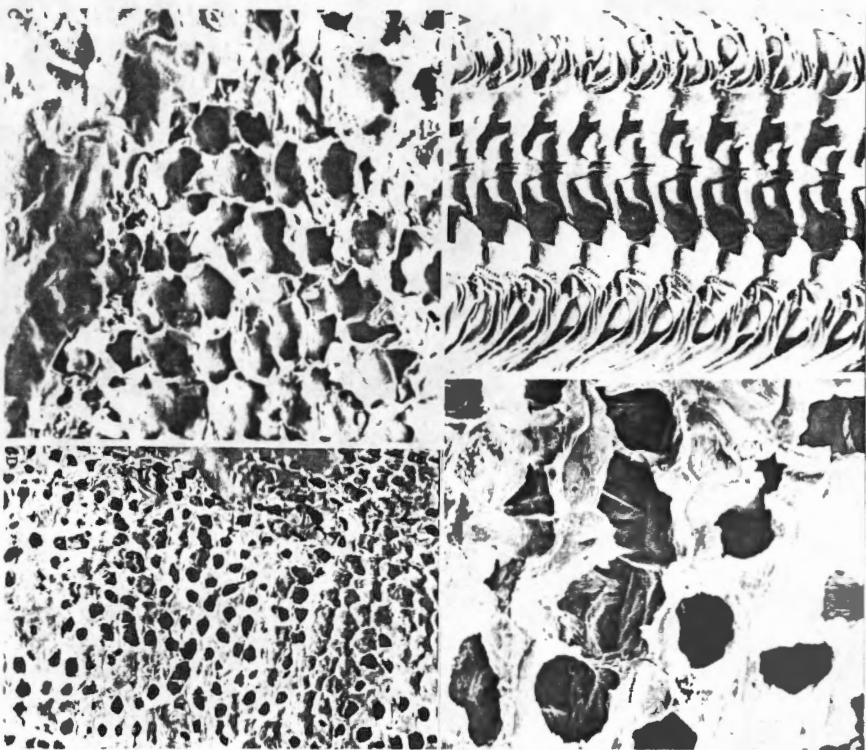


Figure 7. Scanning Electron Micrographs of *Halophila havaiiana* leaf surface damaged by grazing and of small radula. A, *Smaragdia bryanae radula* 525 X. B, leaf A 170 X. C, leaf B 525 X. D, leaf A 850 X. Leaves A and B were more heavily grazed than leaf C.

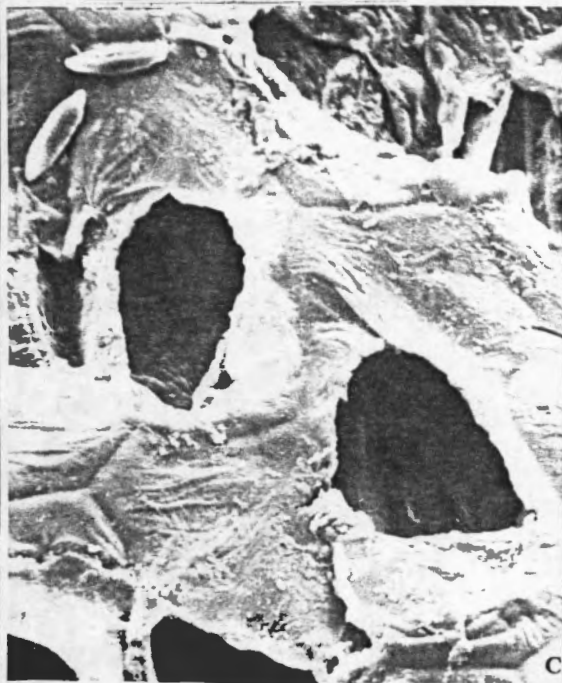
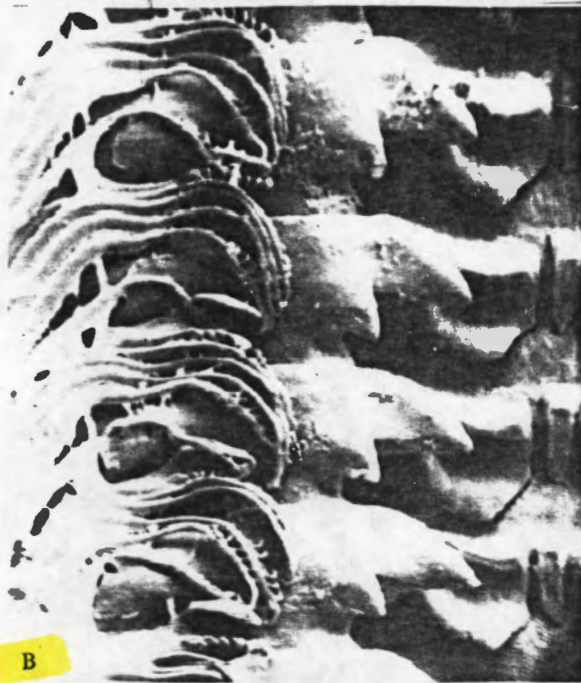
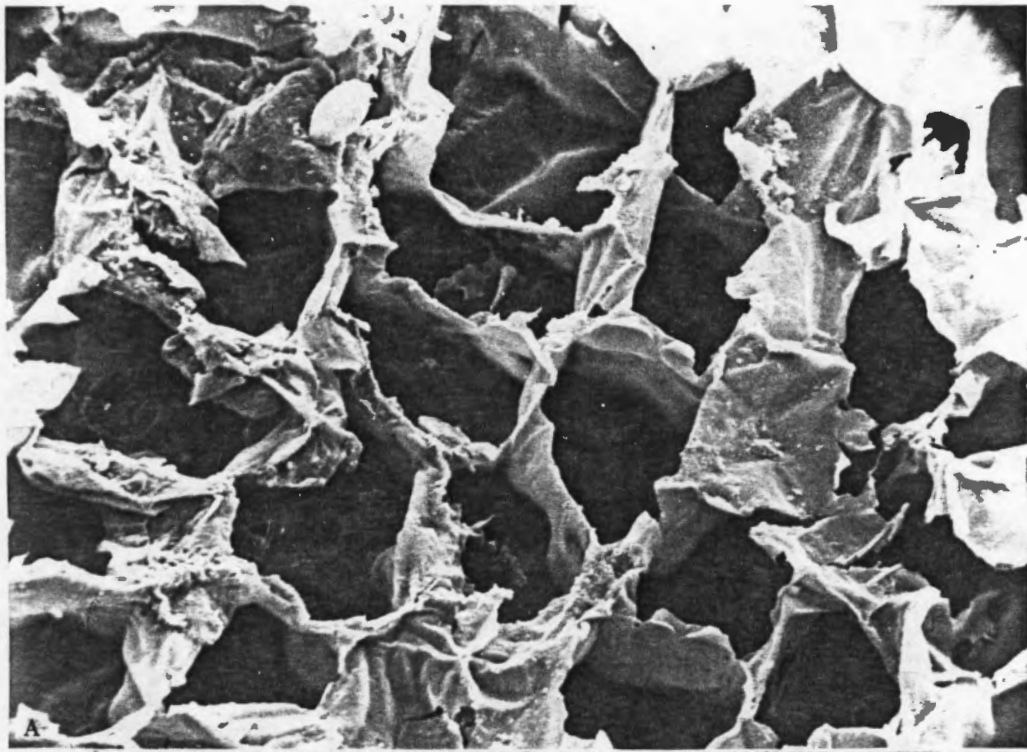


Figure 8. SEM of grazing damage and radula. A, leaf C 1050 X.
B, radula 1050 X. C, leaf A 1780 X. Leaf C was only lightly grazed

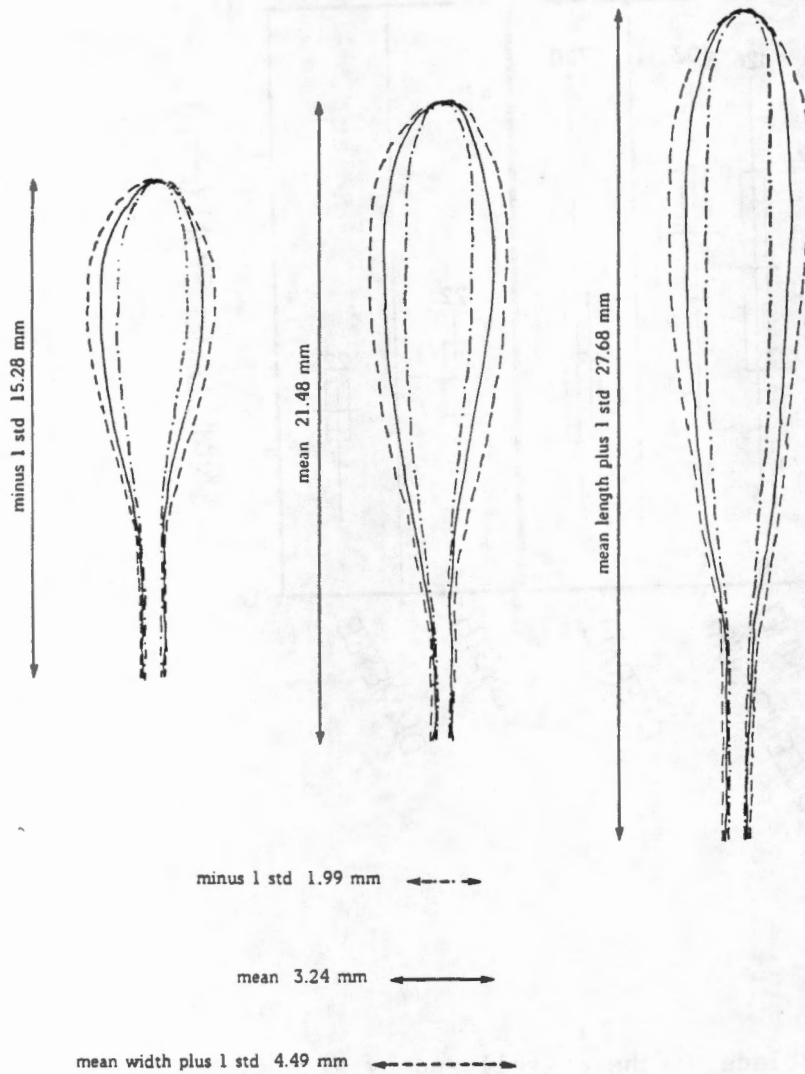


Figure 9. The average leaf: mean width and length (mm) plus and minus one standard deviation (std) X 4

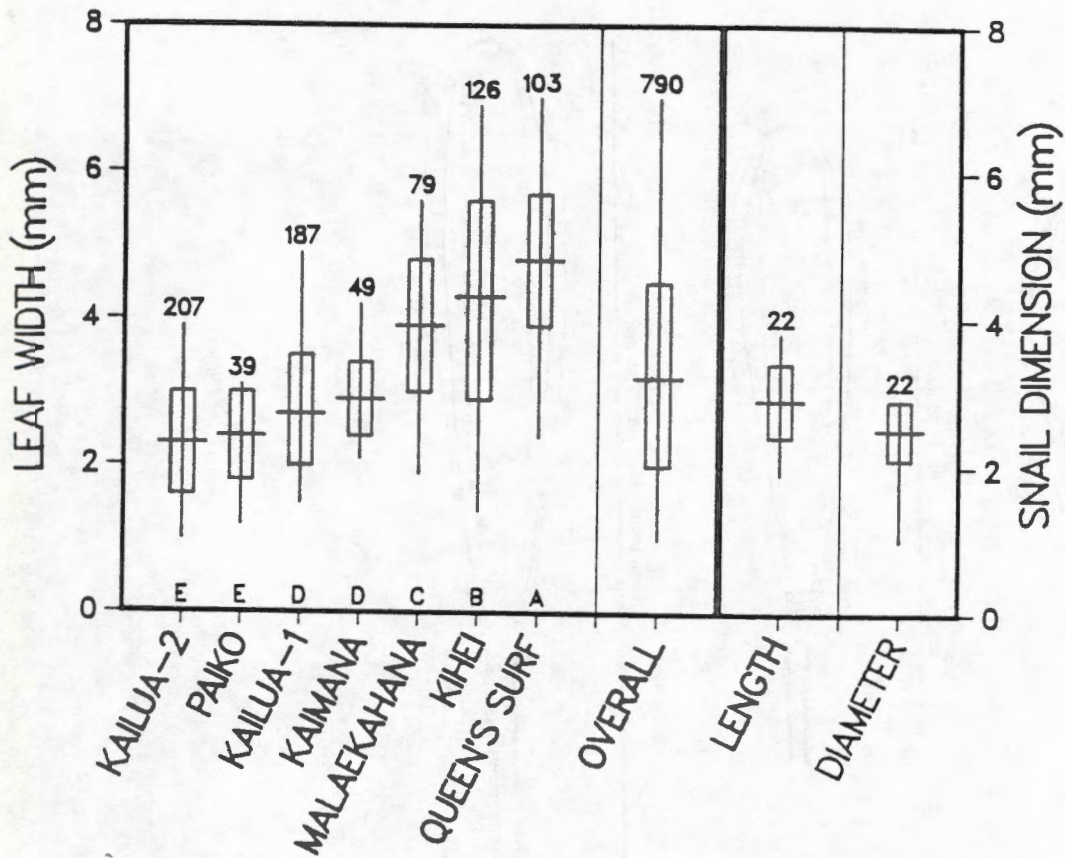


Figure 10. Distributions of blade widths overall and by site with means, standard deviations, ranges and sample sizes. Letters refer to Duncan grouping, sites with the same letter have mean widths that are not significantly different. Snail dimensions are summarized from Table 7

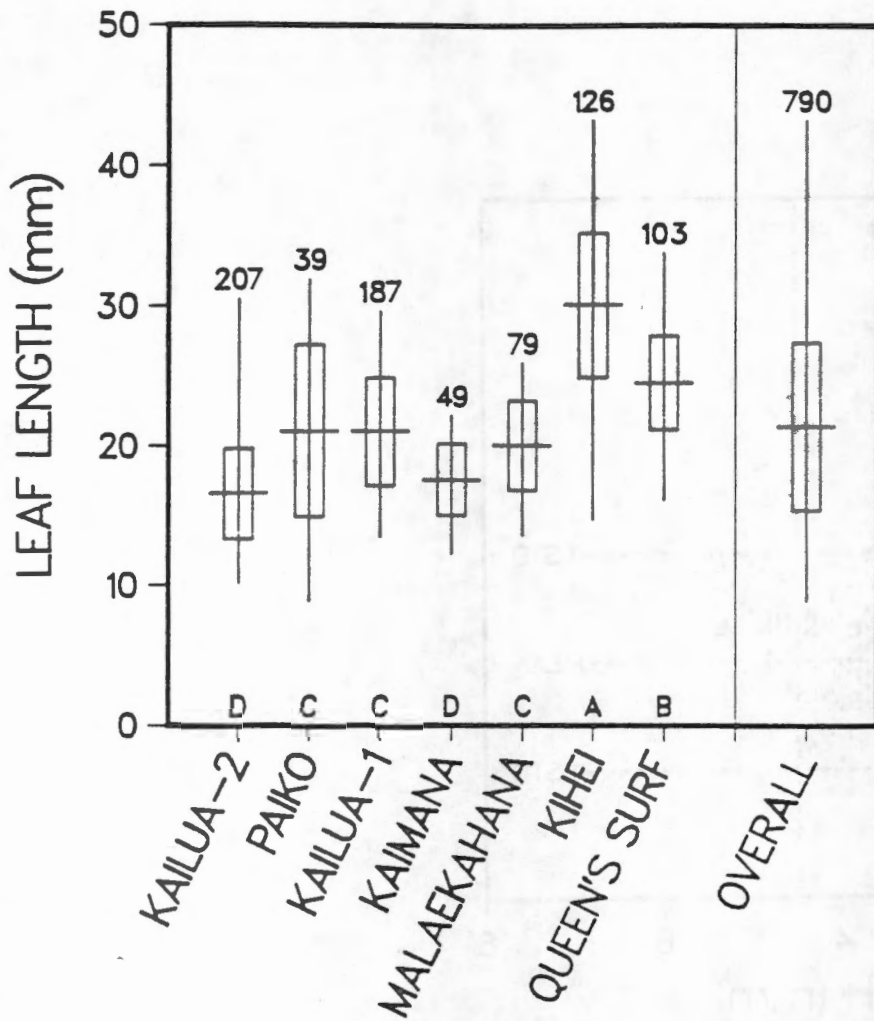


Figure 11. Distributions of blade lengths overall and by site with means, standard deviations, ranges and sample sizes. Letters refer to Duncan grouping, sites with the same letter have mean lengths that are not significantly different

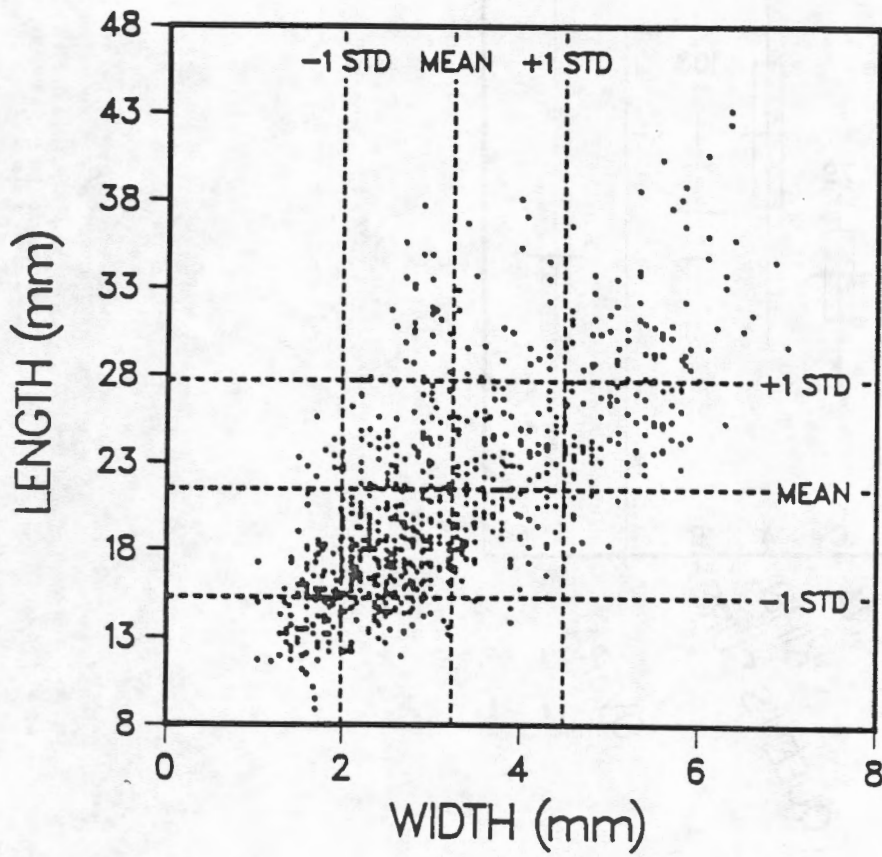


Figure 12. Plot of blade width to length with standard deviations from the mean indicated (n = 790)

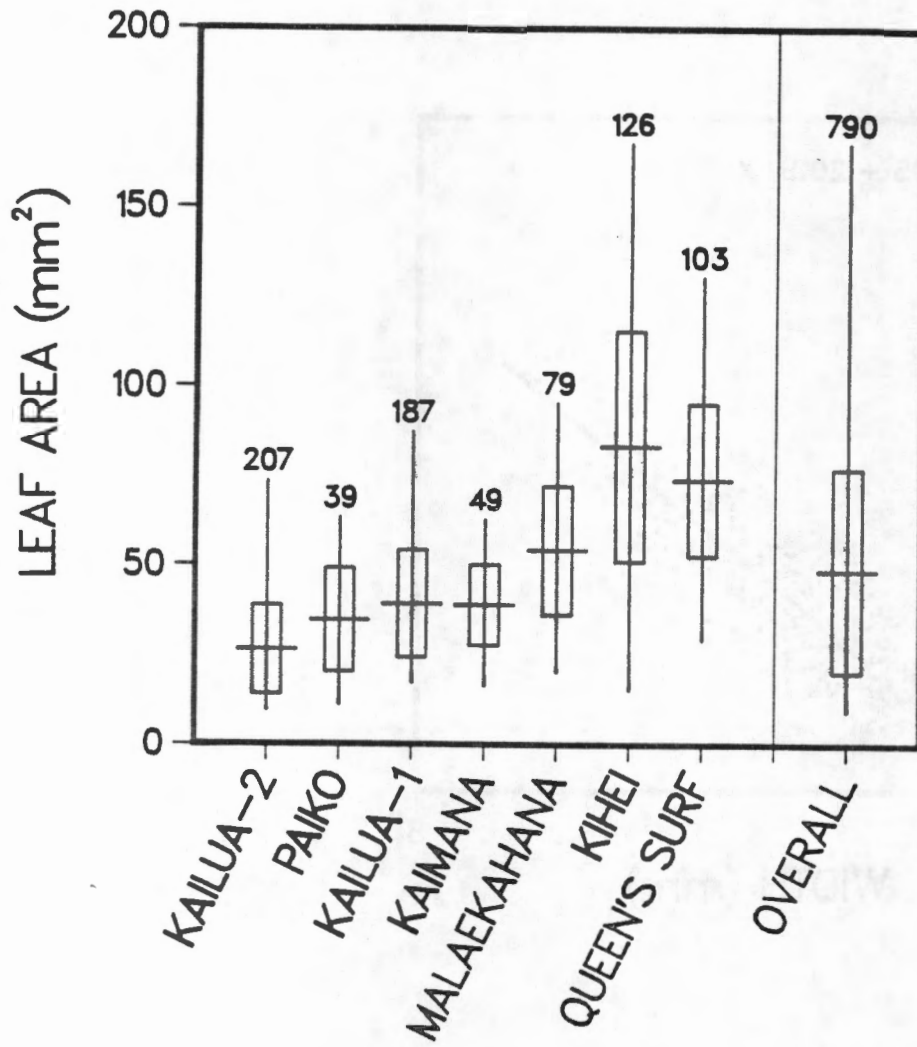


Figure 13. Distributions of leaf area values overall and by site, with mean, standard deviation, range and sample size. Arranged by ascending mean width

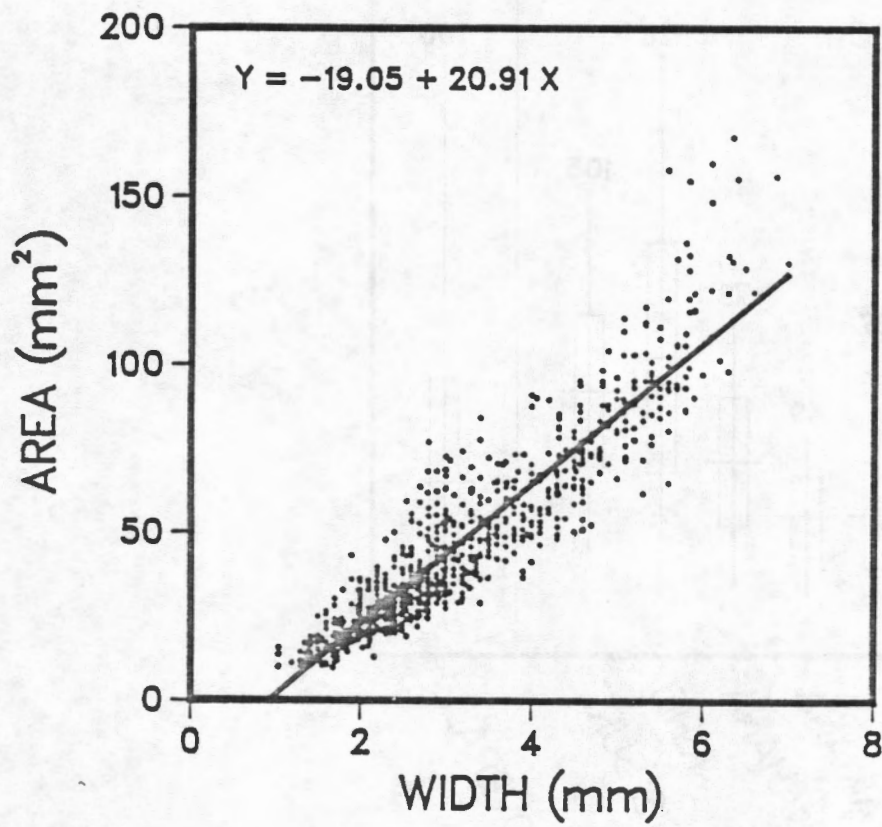


Figure 14. Plot of leaf area to blade width with regression line and equation (n = 790)

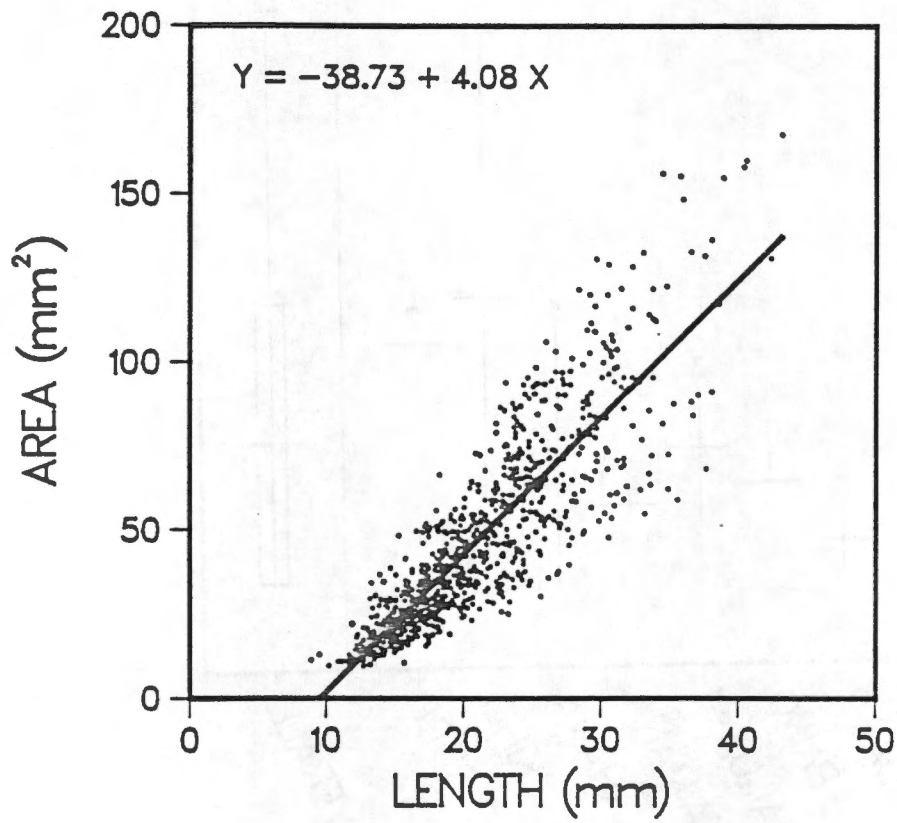


Figure 15. Plot of leaf area to blade length with regression line and equation (n = 790)

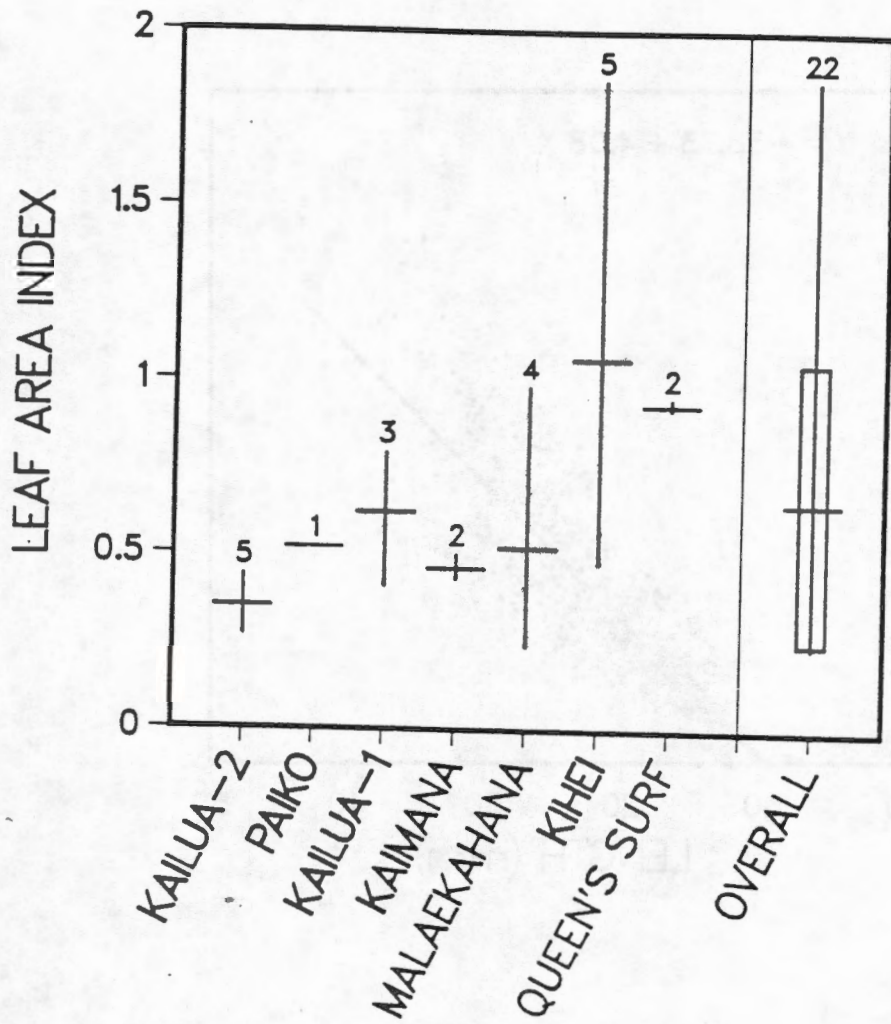


Figure 16. Distributions of Leaf Area Index values by site with mean, range and number of samples. Standard deviation is given only overall. Sites arranged by ascending mean width

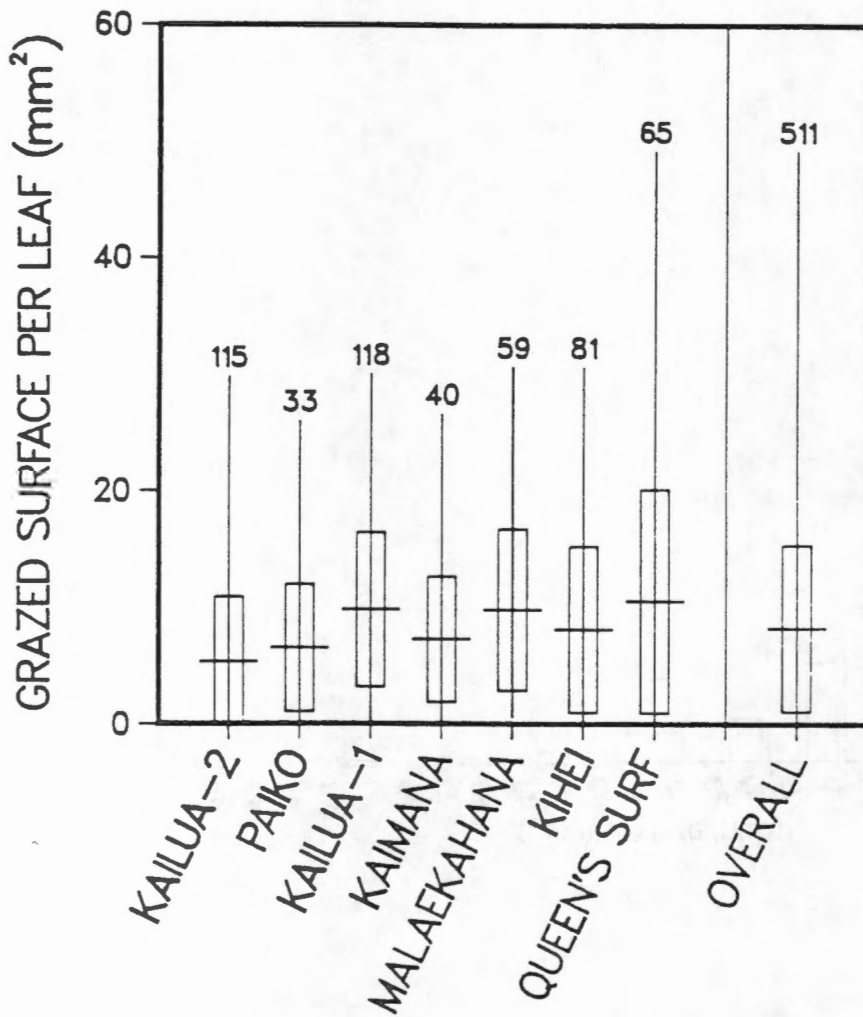


Figure 17. Distributions of amount of grazing damage per leaf by site in damaged subset with mean, standard deviation, range and sample size. Sites arranged by ascending mean width

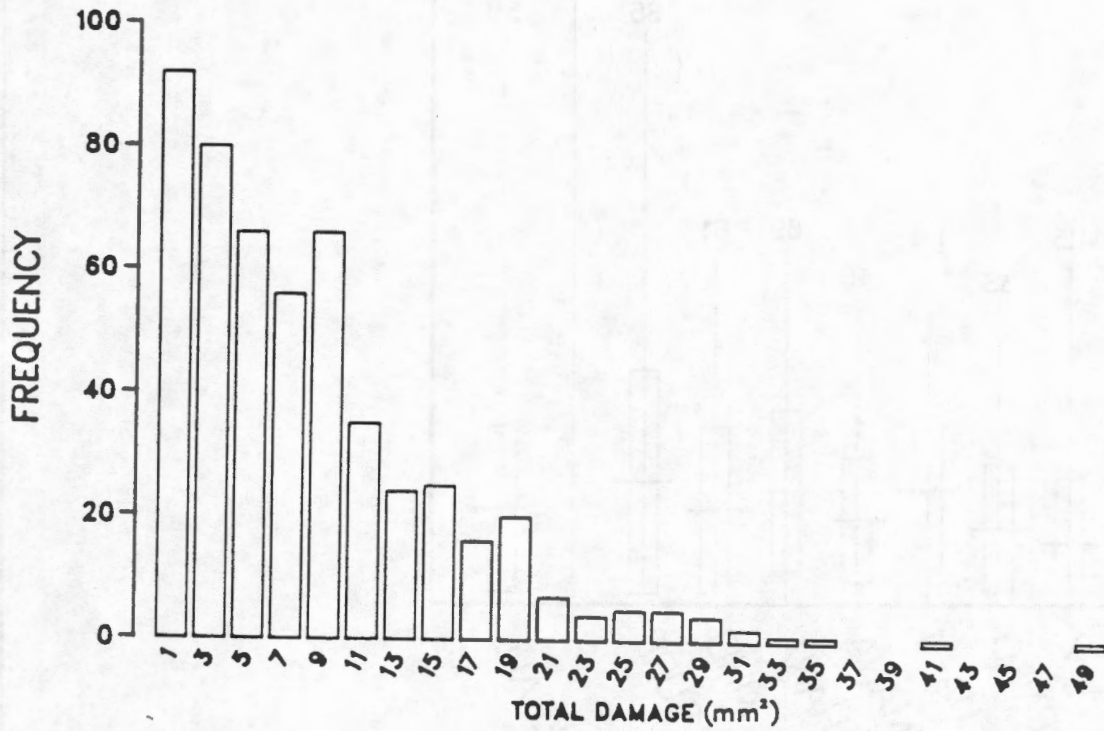


Figure 18. Histogram of the values of total damage per leaf in the grazed subset

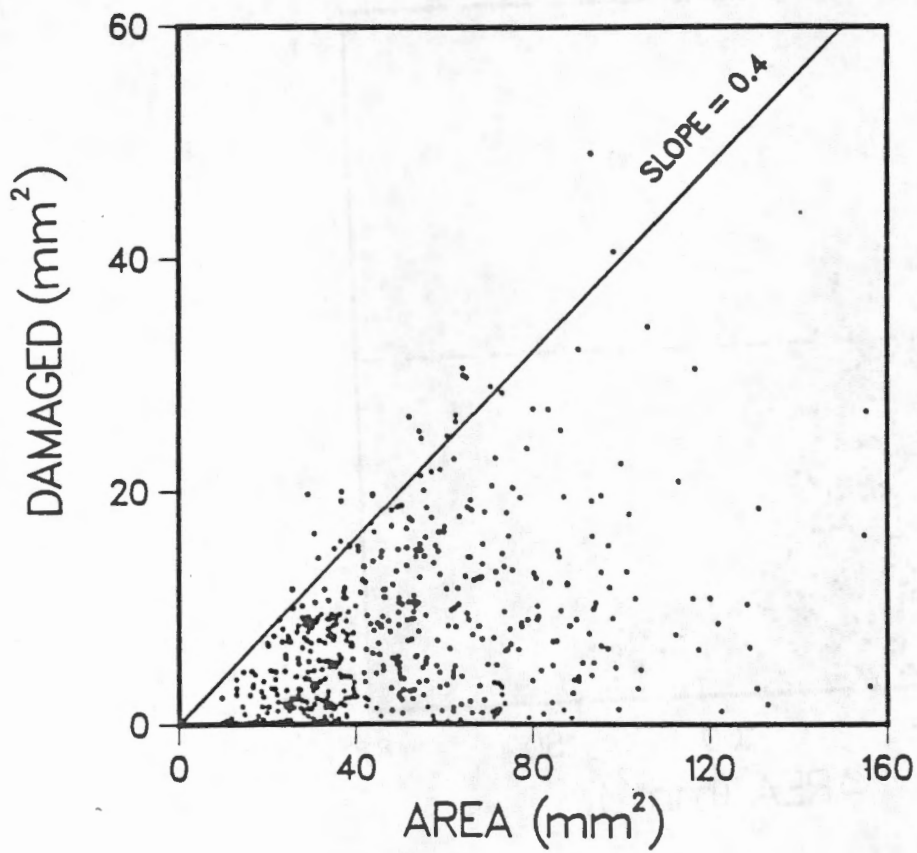


Figure 19. Plot of leaf area to total damage per leaf with reference line where damage = .4 leaf area (n = 511)

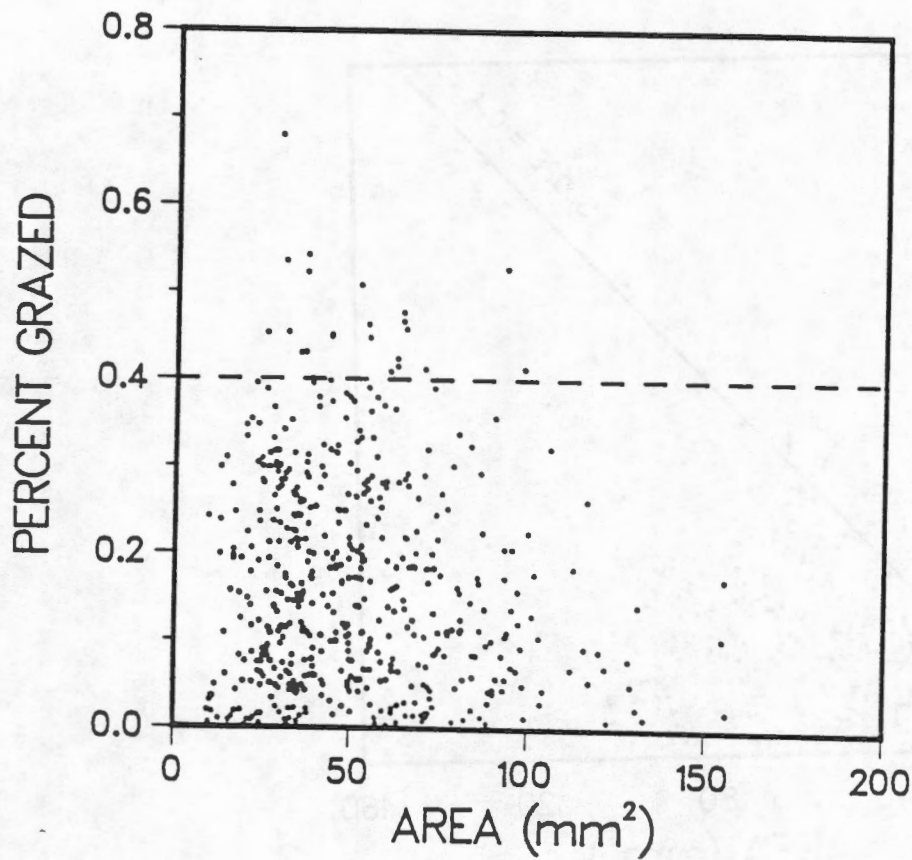


Figure 20. Plot of leaf area to percent damage per leaf with reference line at 40%, the assumed "preferred area" (n = 511)

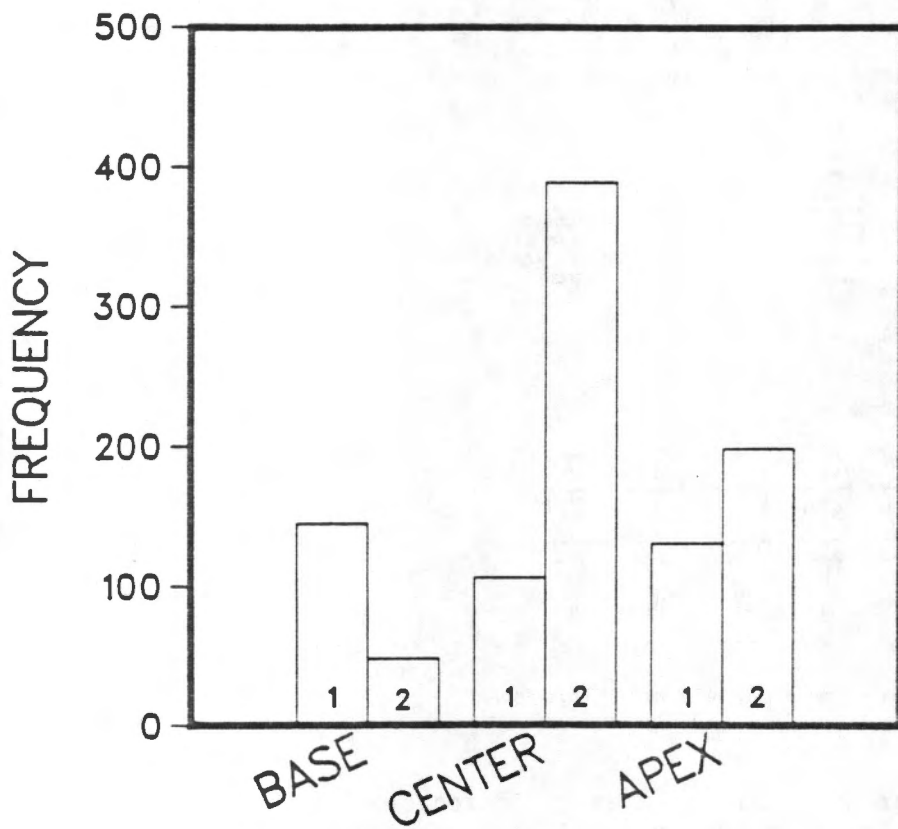
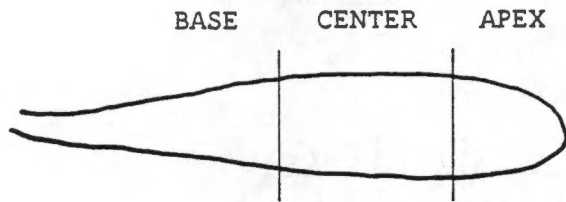


Figure 21. Division of the blade into sections and frequency of grazing damage on one or on both sides of the midrib in each section

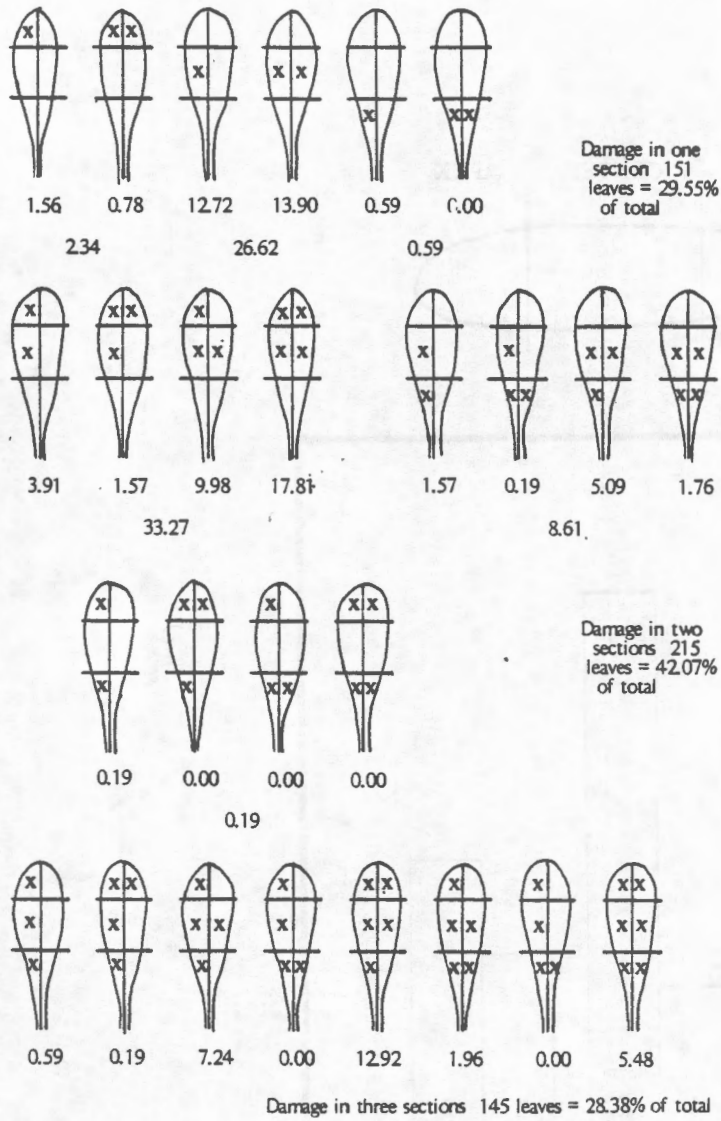


Figure 22. Frequencies of grazing damage in each section or sections. Frequency of each pattern is expressed as a percentage of the total (n = 511)

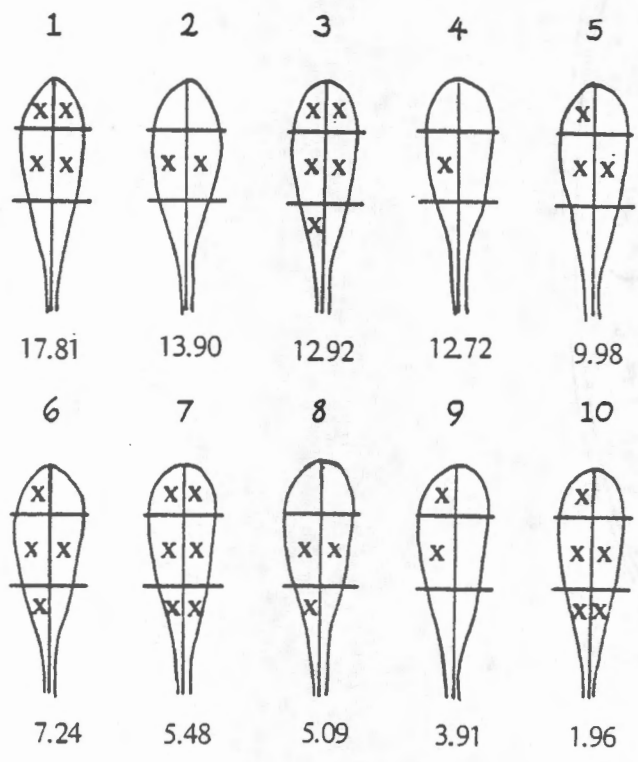


Figure 23. Ten most frequent damage patterns, accounting for 91.01% of damage seen on leaves in samples

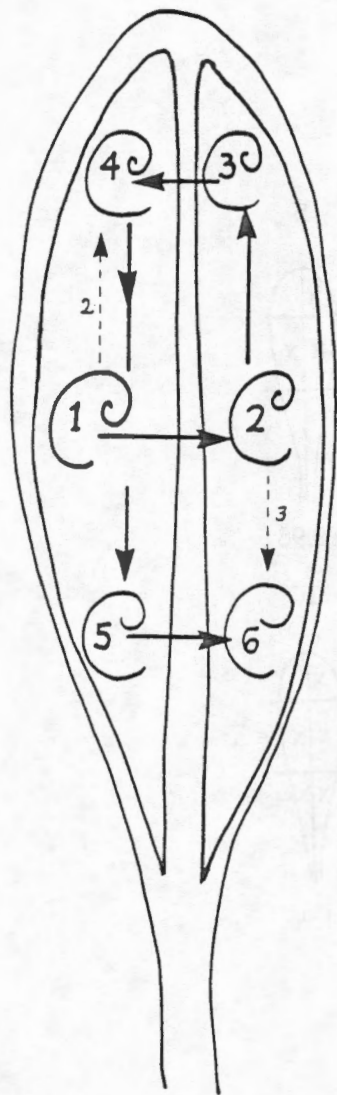


Figure 24. Probable path of the feeding snail. Values indicate the proposed sequence of feeding stations

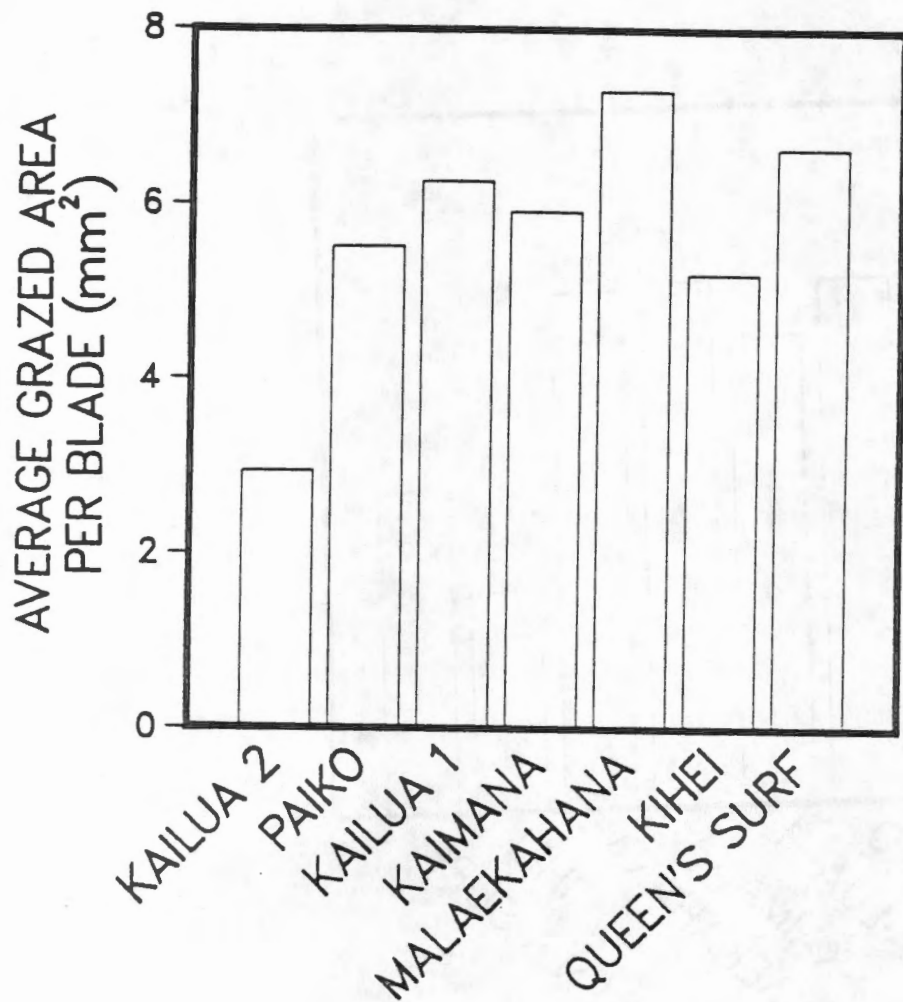


Figure 25. Average grazed area per leaf at each site, based on all leaves (the grazed subset values were given in Table 12). Sites arranged in order of increasing mean blade widths

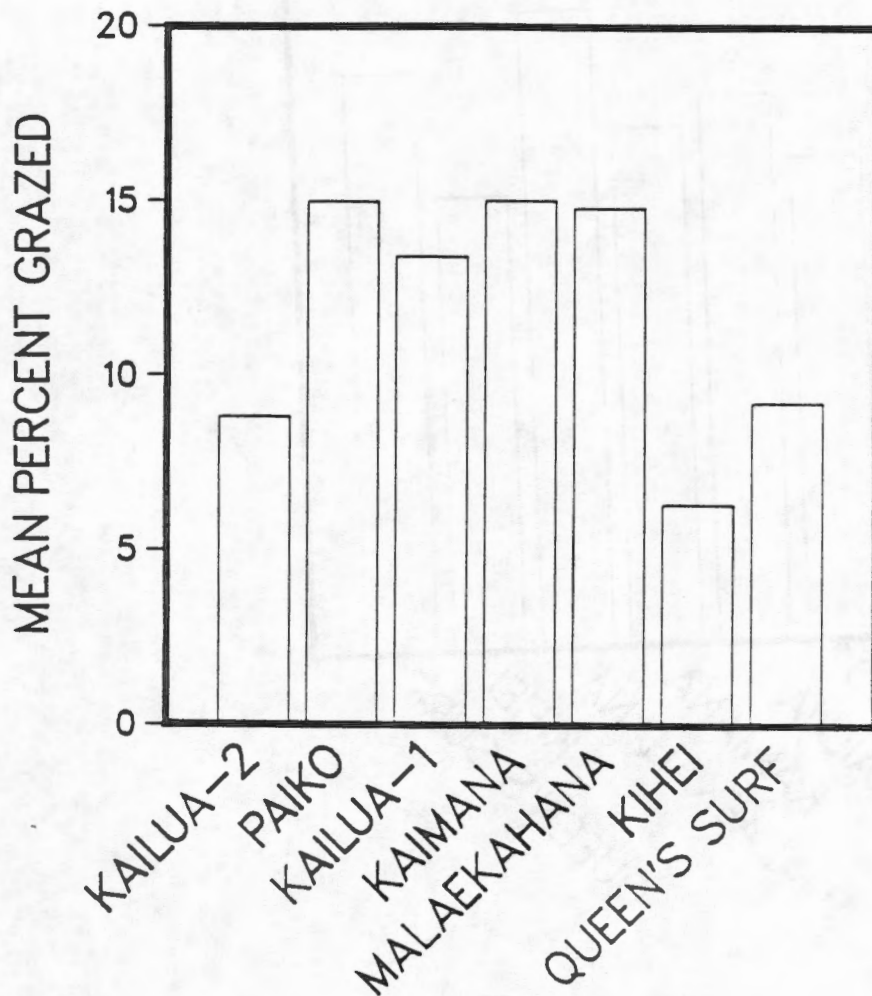


Figure 26. Mean percent leaf surface damaged at each site, based on all leaves (the grazed subset values were given in Table 16). Sites are arranged in order of increasing mean blade widths

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Appendix A.

An additional estimate of the amount eaten by the average snail can be obtained from the record of the number of leaves added and consumed in the PBRC tank during the maintenance experiment (Table 23). From this data it seems that each snail consumes about one leaf per day. This estimate is far from exact due to variation in the amount of leaves added each time, in the size of the leaves provided, and in the time interval between additions. The amount of seagrass that had to be provided for the snails turned out to be more than had initially been expected, and unplanned trips had to be made to supply the animals with food. Since the object was to keep the animals alive and well fed over an interval of several days, enough seagrass was usually provided so that some would be left. The time interval between additions is important to the accuracy of the estimate because older leaves senesce eventually if not eaten. Young leaves and leaf buds continued to develop and unfold in the tank, but they were smaller than in the field, and true growth did not occur.

Table 23. Record of leaves added and consumed during PBRC maintenance experiment. Leaves/day/snail = (previous addition - remainder)/(number of snails) (days in interval)

Date	Number of days	Leaves remaining	Leaves added	Total leaves	Number of snails	Leaves / day / snail
9/18	-	expt. start	10	10	5	-
9/19	1	5	10	15	5	1.0
9/23	4	0	20	20	5	0.8
9/26	3	0	20	20	5	1.3
9/30	4	0	23	23	5	1.0
10/03	3	0	20	20	5	1.5
10/06	3	0	34	34	5	1.3
10/09	3	few	20	35	5	2.0
10/14	5	0	26	26	5	1.0
10/17	3	0	200	200	6	1.7
10/25	8	75	0	75	6	2.6 long*
10/28	3	-	16	-	6	-
10/31	3	0	80	80	6	-
11/10	10	0	129	129	6	1.3
11/18	8	some	25	-	6	-
11/24	6	-	60	-	6	-
12/01	7	-	20	-	6	-
12/09	8	0	110	110	6	1.3
12/11	2	-	150	-	6	-
12/19	8	few	300	-	6	-
12/29	10	about 75	60	-	6	-

* Leaves may be lost due to senescence over longer intervals

Appendix B.

Table 24. Kurtosis and skewness in blade width and length at each site

Site	n	Kurtosis*		Skewness	
		width	length	width	length
Kailua-2	207	-0.21	+1.76	+0.50**	+1.06***
Paiko	39	-0.08	-0.90	+0.13	+0.21
Kailua-2	187	-0.16	-0.01	+0.77**	+0.52**
Kaimana	49	-0.22	-0.54	+0.18	-0.32
Malaekahana	79	-0.59	-0.97	-0.17	-0.05
Kihei	126	-1.00	+0.87	+0.28	-0.31
Queen's Surf	103	-0.31	-0.10	-0.17	+0.05

* No significant kurtosis

** Slightly skewed

*** Skewed

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