

Indirect Evidence of a Morphological Response in the Radula of *Placida dendritica* (Alder & Hancock, 1843) (Opisthobranchia: Ascoglossa/Sacoglossa) to Different Algal Prey

by

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Abstract. Examination of radulae from the ascoglossan mollusk *Placida dendritica* (Alder & Hancock, 1843) collected in New Zealand, Australia, Japan, and west coast North America revealed two morphological types. Each was correlated with the type of alga from which the slugs were collected. Those feeding on perennial *Codium* had smaller teeth, more teeth, and a tight radular coil in an enlarged ascus. Those feeding on seasonal *Bryopsis* and *Derbesia* had larger teeth, fewer teeth, and only a slightly curved radular ribbon (never a coil) in the ascus. This apparent morphometric response of radular structure to algal structure and defenses may explain similar sporadic size discrepancies observed in populations of three other ascoglossan genera, *Alderia*, *Elysia*, and *Limapontia*.

INTRODUCTION

For several species of ascoglossans, the radular teeth can, numerically and morphologically, (1) vary ontogenetically within an individual; (2) vary seasonally within one species; (3) have a reversal of the normal process of producing sequentially larger teeth; and (4) vary in the rate of tooth production as determined by comparing body lengths to the total number of teeth (RAYMOND & BLEAKNEY, 1987; BLEAKNEY, 1988). This paper reports a fifth category that had not previously been suspected, namely that the size of and production rate of teeth can vary in response to the type of algae eaten. Presumably this is a response to the degree of mechanical difficulty in penetrating algal filaments and to the effort required to suck out the cell sap.

BLEAKNEY (1989) recently demonstrated consistency over much of the Pacific Basin in the ultrastructure of the cutting edge of teeth of *Placida dendritica*. However, he noted in particular a perplexing lack of direct relationship between body size and total number of teeth. In most cases the largest animals, 14–20 mm in length, had fewer teeth than many animals only 3–4 mm in length. He concluded that this discrepancy was a reflection of either long geographic isolation and had a genetic basis, or was merely a temporal extreme such as he had observed in Nova Scotia populations of *Elysia chlorotica* Gould, 1870 (RAYMOND &

BLEAKNEY, 1987). However, after examining a series of *P. dendritica* from Oregon, a third and more plausible explanation is now available.

MATERIALS

Dr. Cynthia Trowbridge sent me three separate lots of *Placida dendritica* collected from three species of alga—*Codium fragile* (Suringar) Hariot, *Codium setchellii* Gardner, and *Bryopsis corticulans* Setchell—in the hopes that I might discover radular differences. She felt that differences in the general appearance and behavior of *Placida* on these algae indicated possible specialization and speciation. However, and without exception (based on examination of 10 slugs from each alga), the pronounced morphological variation observed fell into only two categories and these were directly correlated with the two genera of algae. These observations prompted a re-examination of my notes and collections of *P. dendritica* from British Columbia, Japan, Australia, and New Zealand, and some of those data are included in Figure 1.

RESULTS

In every case, the largest animals had been collected from *Bryopsis* or the related genus *Derbesia*. The radular ribbon

of *Bryopsis*-feeding *Placida dendritica* had fewer but much larger teeth and a slightly curved, descending radular limb (Figures 2, 3). In sharp contrast, slugs from *Codium* had many more teeth but much smaller ones (Figures 4, 5) and their strongly coiled descending radular limbs were already evident at body lengths of only 3 and 4 mm. Even with body lengths of 14 mm, slugs from *Bryopsis* had only a slightly curved ribbon in the ascus area.

Figures 2 to 5 are of two equally large buccal masses from two 8 mm *Placida dendritica*, photographed at the same magnification, yet the tooth bases in the ascending series of the *Bryopsis* feeder are at least twice as large as the *Codium* example. The differences in the size and number of teeth do not seem to effect the relative size of the buccal mass in the two categories, although a larger sample might emphasize an incipient divergence indicated by query arrows in Figure 6. The numerous additional teeth produced by the *Codium*-feeding slugs are accommodated outside the buccal mass within an enlarged ascus area.

DISCUSSION

Available morphological information indicates that *Placida dendritica* is a single species, at least within the Pacific Basin (BLEAKNEY, 1989). Among the three collections from Oregon, there were no differences in the ultrastructure of the serrated edge of the radular teeth. If *P. dendritica* actually consisted of a *Codium*-species and a *Bryopsis*-species, one would expect real differences in the teeth reflecting the considerable differences in structure of the two algae. The only radular differences detected were the relative size of teeth and the total number of teeth, two variables common to any population. That these two variables, as well as the category of maximum body size, were directly related to the different algal prey is significant. That the two algal genera were *Codium* and *Bryopsis* is equally significant for the former is perennial (pseudoperennial) and the latter highly seasonal. Perennial or pseudoperennial plants should (as predicted by evolutionary theory) partition more resources into anti-herbivore defenses. This becomes manifest as degrees of edibility and digestability, and ultimately affects the growth rates of predators. CLARK & DEFREESE (1987) emphasized the strong evolutionary interplay of algal life histories, physiology, and structure with that of alga-sap-sucking ascoglossans.

Because *Codium* is a perennial, it undoubtedly has developed defenses to reduce grazing efforts of ascoglossans, which are generally directed at the coenocytic filaments of siphonaceous algae because one puncture by a radular tooth gains access to the entire thallus system. Access to *Codium* must be frustrated in part by its peculiar surface which consists of a carpet of erect, compacted, clavate, utricles whose exposed apices are capped by a lamellate cuticle (WOMERSLEY, 1984). These utricle subunits almost amount to a septate condition, as the feeding slug must shift from one utricle to another to extract sap. Narrow radular teeth may be more effective than stout ones in penetrating this armor, but at the same time, under this

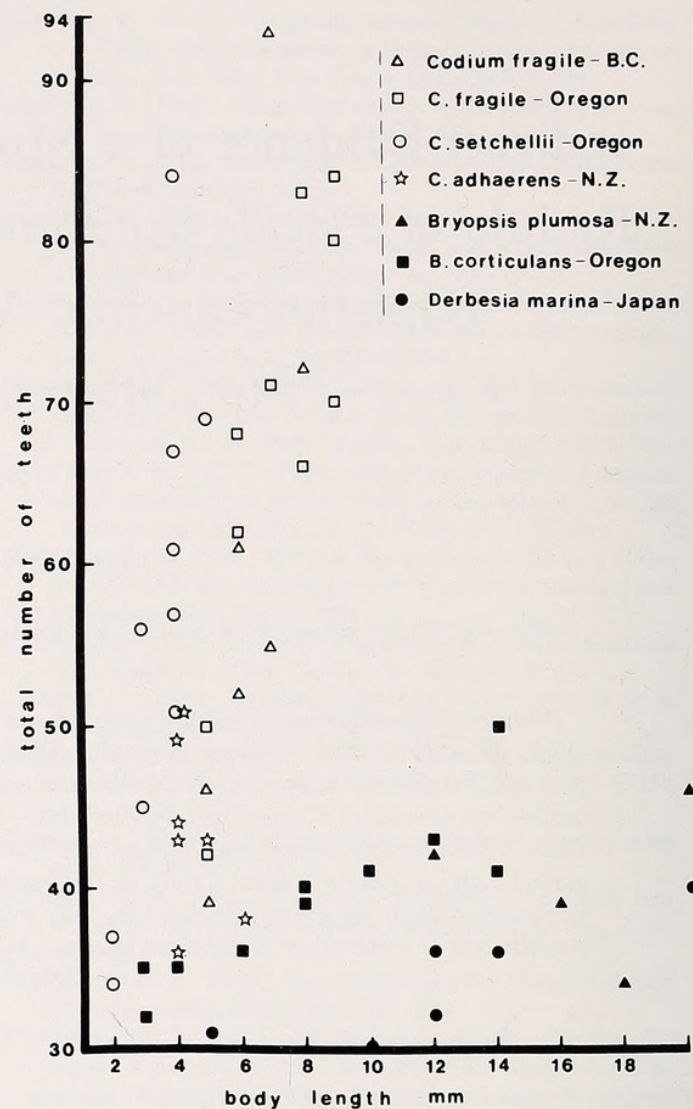
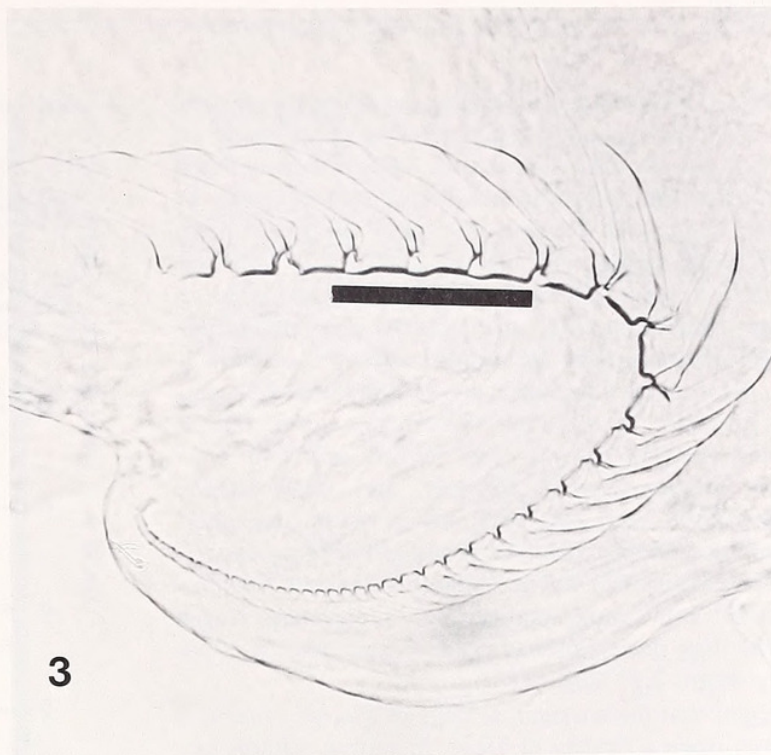
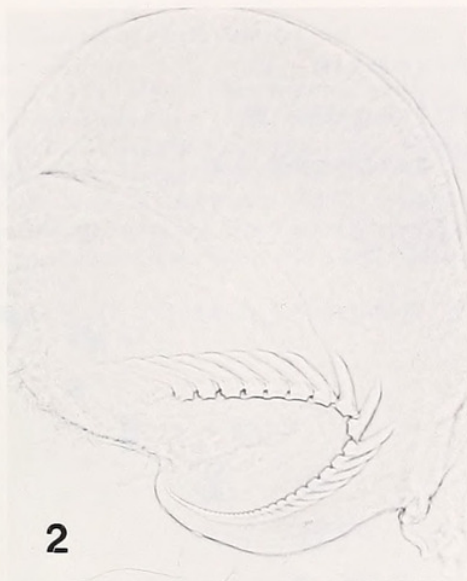


Figure 1

Relationship of body length and total number of teeth of *Placida dendritica* from various geographic regions to type of alga fed upon. *Codium* species are plotted as open symbols, and *Bryopsis*/*Derbesia* are solid symbols.

repetitious puncturing of numerous utricles, the serrations may wear down faster and tips break off and pieces chip out (see photographs in BLEAKNEY, 1989).

The life history of *Bryopsis*, in contrast, involves a seasonal appearance of irruptive, transient populations with little necessity to evolve major protective toxins or mechanical barriers. The thin-walled, plumose thallus of *Bryopsis* may be most effectively penetrated and split open by a large diameter tooth, and certainly the amount of cell sap extracted per puncture must be far greater from *Bryopsis* than from *Codium*. The nutrient value is probably far higher as well, for as CLARK & DEFREESE (1987) pointed out, perennial algae tend to produce a spectrum of secondary metabolites whose toxic effects are not necessarily direct, but which may serve the alga by inhibiting (or slowing) growth and reproductive processes in the attacking ascoglossans.



Explanation of Figures 2 to 5

Figures 2, 3. Entire buccal mass and enlargement of the radular area of an 8-mm-long *Placida dendritica* found on *Bryopsis corticulans* in Oregon, July 1988. Scale bar = 80 μ m.

Figures 4, 5. Entire buccal mass and enlargement of the radular area of 8-mm-long *Placida dendritica* found on *Codium fragile* in Oregon, July 1988. Scale bar = 80 μ m.

JENSEN (1989) conducted feeding experiments utilizing *Elysia viridis* (Montagu) by transferring slugs found on *Codium fragile* to the cellular alga *Chaetomorpha linum* (Miller) Kützing, and those found on *Chaetomorpha* to the coenocytic *Codium*. In general, the slugs experienced great difficulty in changing their feeding habits, with time lags of up to two weeks. These time delays were attributed to learning periods but may have reflected in part the time necessary to restructure the radular apparatus. Unfortunately, the respective radulae were not examined and compared. However, as there are three regional populations of *Elysia viridis* in Europe, each feeding primarily on a different genus—*Codium*, *Bryopsis*, and *Chaetomorpha* (JENSEN, 1989)—any real difference in radular morphology could be verified prior to prolonged feeding experiments. In passing, it is worth noting that Jensen's *Codium*-derived *E. viridis* were smaller ($n = 17$; average length 1.45 cm) than those collected off *Chaetomorpha* ($n = 30$; average length 2.13 cm).

I suggest that the survival strategy of *Placida dendritica* is to prey upon a variety of algae, including reliable perennials and desirable transients. If the veligers settle upon *Codium* they must contend with defensive chemicals and structures, and the result is a relatively small body size, rapid production of slender teeth, and fewer eggs laid. If the veligers find *Bryopsis* instead, they grow rapidly, produce fewer, more massive teeth, reach body lengths twice that of the *Codium*-limited individuals, and produce far more eggs.

Such a biochemical interplay between alga and ascoglossan, involving defenses, feeding effort, and nutrient value could explain the startling size discrepancies that one encounters sporadically when sampling populations over extended time periods. For example, the European ascoglossan *Limapontia depressa* Alder & Hancock, 1862, is usually only 2–3 mm in length, but in August 1969, in the Isefjord, Denmark, the late Henning Lemche (*in litt.*) found a swarm of hundreds of spawning animals most of which were an exceptional 8 mm in length, and their egg masses contained 800–1000 eggs. In contrast, collections of specimens of the usual 2 mm size, gathered on the same day but at a different locality, had egg masses containing only 155 eggs. Similarly, in the Minas Basin, Nova Scotia, the ascoglossan *Alderia modesta* (Loven, 1844) can grow to 15 mm, nearly twice its "normal" size, but this happens at irregular intervals, often years apart. *Elysia chlorotica* is usually considered "large" at 20–30 mm, but on occasion, in Minas Basin tidal marshes, entire populations can reach 35–45 mm. GIBSON *et al.* (1986) reported an exceptional phenomenon concerning this species. Much of the local population in the summer of 1983 and 1984 was without chloroplasts. Apparently, viable chloroplasts from *Vaucheria* were unavailable, yet the slugs appeared healthy and were actively spawning. Most of the non-green *Elysia* were 6–12 mm in length and only the few green individuals attained larger body sizes.

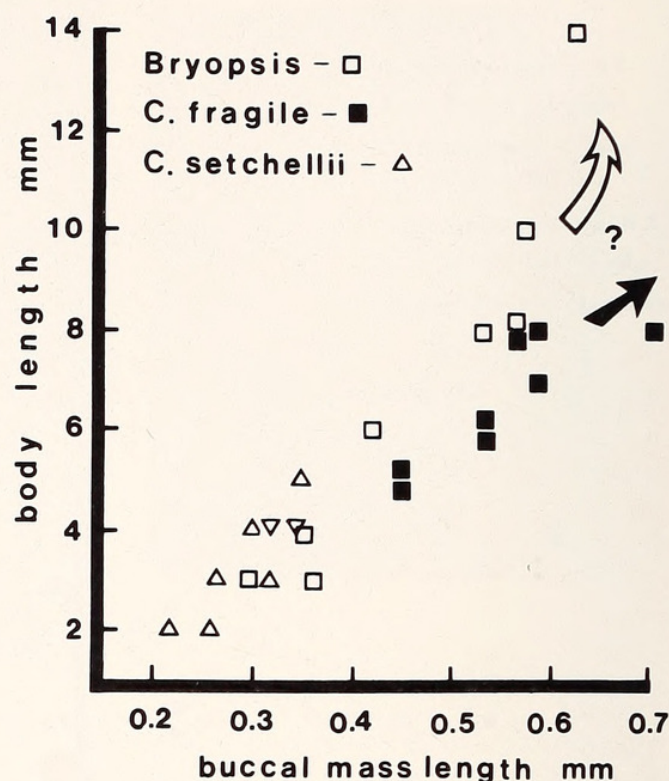


Figure 6

Relationship of body length and length of buccal mass to type of alga fed upon by *Placida dendritica* from Oregon.

CONCLUSIONS

The above observations, considered with the ecological studies of CLARK & DEFREESE (1987), emphasize how entrained and responsive are the life histories and anatomies of ascoglossans to their algal prey. It is also evident that these responses are open to experimental verification and manipulation at laboratories where controlled culturing techniques are available for both larvae and algae. The standard method of testing of adult ascoglossans using algal choice situations to establish a food preference spectrum for a particular slug species could be misleading. The "preferred" food of adults may simply depend upon the alga that veligers or larvae first encountered and to which they effectively adapt morphologically and physiologically during their brief life history period.

ACKNOWLEDGMENTS

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