# Predation by the Prosobranch Mollusk *Lamellaria diegoensis* on *Cystodytes lobatus*, a Colonial Ascidian

BY

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(1 Text figure)

## INTRODUCTION

THE LAMELLARIID GASTROPODS are highly specialized for predation on ascidians (HERDMAN, 1893; FRETTER & GRAHAM, 1962; GHISELIN, 1964). All the lamellariids are cryptically colored; some resemble their prey while others resemble the general substrate of their surroundings (THOMPSON, 1973). Their overall biology is poorly understood, however, because collections have been of only one or a few specimens at a time, and lengthy studies have not been carried out. The present paper describes the predator-prey relationship between *Lamellaria diegoensis* Dall, 1885, and the compound ascidian *Cystodytes lobatus* (Ritter, 1900). The results of several feeding experiments and calorimetric measurements of the ascidian colonies and mollusk feces are included, with a partial energy budget for *L. diegoensis* computed from these data. All observations and experiments were carried out on a single *L. diegoensis* because although *C. lobatus* is very common in the low intertidal and subtidal zones in central California, only one *L. diegoensis* was collected despite a concerted effort to find more over a six-month period. In spite of the drawbacks of the small sample size, this work was carried out because it may well be that the only way we shall ever gain a fairly comprehensive knowledge of the biology of the lamellariids is from the compilation of many separate studies.

## METHODS

One *Lamellaria diegoensis* was collected on March 7, 1978, on a piece of *Cystodytes lobatus* colony from the low intertidal zone during a −18 cm tide at Pt. Pinos, Pacific Grove, California. The piece of *C. lobatus* colony and additional colonies were maintained in an aquarium with running sea water at the Hopkins Marine Station; the mollusk was not actually observed on the colonies until March 23, even though the colonies had been examined daily in conjunction with another study (LAMBERT, 1979).

The mollusk was maintained solely on a diet of *C. lobatus* from March 7 until August 31, 1978. For most of this period it was kept cool on the water table in a Pyrex baking dish loosely covered with black plastic. This partial darkness was provided because like *Lamellaria stearnsii* Dall, 1871, studied by GHISELIN (1964), *L. diegoensis* reacted strongly and negatively to bright light. The water was changed once a day and a new piece of ascidian colony offered every two to three days.

During July and August, a total of 15 daily fecal pellet counts, wet weights and dry weights were made with the aim of ultimately using these values to determine the amount of prey consumed and therefore the calories ingested. To this end, pieces of fresh ascidian colonies and the *Lamellaria* fecal pellets were dried to constant weight at 55° C (Table 1), and the caloric content determined using a Parr model 1411 semimicro bomb calorimeter (Table 2). Ash determinations were made with a muffle furnace for the *C. lobatus* colonies; there were not enough mollusk feces for this procedure, so the percent ash given in Table 2 was calculated from the bomb residue. In both cases the ash content has been corrected for $CaCO_3$ endothermy according to PAINE (1966, 1971) because of the large quantity of ascidian spicules. No acid corrections were made because of the large amount of naturally occurring acid in these animals.

## Table 1

Wet and dry weights (mg) of *Cystodytes lobatus* colonies and *Lamellaria diegoensis* fecal pellets.

| *Cystodytes lobatus* | | | *Lamellaria diegoensis* fecal pellets/24 hrs | | | | |
|---|---|---|---|---|---|---|---|
| Wet | Dry | Ratio | Date | # Pellets | Wet | Dry | Ratio |
| 2877 | 294.5 | 0.102 | 7/13/78 | 207 | 88.0 | 22.8 | 0.259 |
| 3277 | 318.5 | 0.097 | 7/14 | 162 | 84.9 | 23.3 | 0.274 |
| 3393 | 327.0 | 0.096 | 7/17 | 147 | 80.6 | 18.3 | 0.227 |
| 2786 | 253.0 | 0.091 | 7/20 | 128 | 58.9 | 11.8 | 0.200 |
| 3573 | 331.5 | 0.093 | 7/26 | 186 | 88.7 | 26.1 | 0.294 |
| 3462 | 297.0 | 0.086 | 8/1 | 134 | 81.4 | 18.9 | 0.232 |
| 3210 | 284.5 | 0.089 | 8/6 | 172 | 95.1 | 22.6 | 0.238 |
| 3299 | 275.0 | 0.083 | 8/10 | 104 | 49.4 | 12.6 | 0.255 |
| 3261 | 290.4 | 0.089 | 8/11 | 150 | 81.3 | 19.5 | 0.240 |
| 3418 | 284.6 | 0.083 | 8/14 | 112 | 62.5 | 15.9 | 0.254 |
| | | | 8/15 | 177 | 87.1 | 21.5 | 0.247 |
| $\bar{x}$ 3256 | 295.6 | 0.091 | 8/16 | 165 | 84.0 | 17.6 | 0.210 |
| | | ±0.006 | 8/19 | 132 | 62.6 | 13.1 | 0.209 |
| | | | 8/20 | 136 | 64.8 | 13.1 | 0.202 |
| | | | 8/21 | 162 | 78.9 | 12.1 | 0.153 |
| | | | | 152 | 76.5 | 17.9 | 0.233 $\bar{x}$ |
| | | | | ± 28 | ±13.4 | ± 4.7 | ±0.035 |

## Table 2

Average energy values (calories/g ash-free dry wt) of *Cystodytes lobatus* colonies and *Lamellaria diegoensis* fecal pellets.

| | $\bar{x}$ cal $g^{-1}$ ash-free dry wt (±SD) | # det. | % ash (bomb det.) | % ash (muffle furnace det.) | # det. |
|---|---|---|---|---|---|
| *Cystodytes lobatus* whole colonies | 3679 ± 244 | 7 | 62.9 | 63.3 | 3 |
| *Lamellaria diegoensis* fecal pellets | 5578 ± 107 | 5 | 78.8 | – | |

## RESULTS AND DISCUSSION

### External Morphology of *Lamellaria diegoensis*

The following description of the living mollusk adds to Behrens' (1980) redescription (this issue) of this species. The shell was completely internal, with no opening on the mid-dorsal mantle surface to expose the shell. The pale pink mantle glistened with many shiny refractile spots. Flecks of black pigment were scattered everywhere, but they were especially numerous on the variable-sized contractile tubercles, which were largest mid-dorsally. Small tubercles extended right to the mantle edges and were also pale pink. Orange pigment could be seen inside some of the largest tubercles; its color closely matched the orange yolk of tadpole larvae developing in the ascidian colonies. White material was concentrated at the base of some of the tubercles; it resembled the white calcareous spicules that occur in large numbers in *Cystodytes lobatus* and form sacs that surround each zooid abdomen (Lambert, 1979). Many yellow pigment spots occurred on the inside of the mantle and on the top and bottom of the foot that were not visible in a dorsal view. The foot, visible posteriorly only when the animal was moving, also had a large number of red pigment spots. Like all the lamellariids (Fretter & Graham, 1962; Thompson, 1969), the mantle contained numerous acid glands that produced sulfuric acid, as indicated by barium sulfate precipitation when barium chloride was added to a drop of mantle fluid. In this respect it again resembled its prey, for the test of *C. lobatus* is packed with numerous sulfuric acid filled

bladder cells (Abbott & Newberry, in press) 35 to 50 μm in diameter (Lambert, 1979).

The anterior end of the mantle formed a siphon that was usually greatly extended when the mollusk was moving. When it was resting or feeding on *Cystodytes,* its siphon and dorsal tubercles were considerably shortened and its body much flattened. The lateral mantle edges became spread out, giving the animal an almost circular outline (Figure 1). The mantle edges became thin, translucent and nearly colorless, blending in with the bladder cell filled tunic of *C. lobatus* so well that the outline of the mollusk was difficult to distinguish.

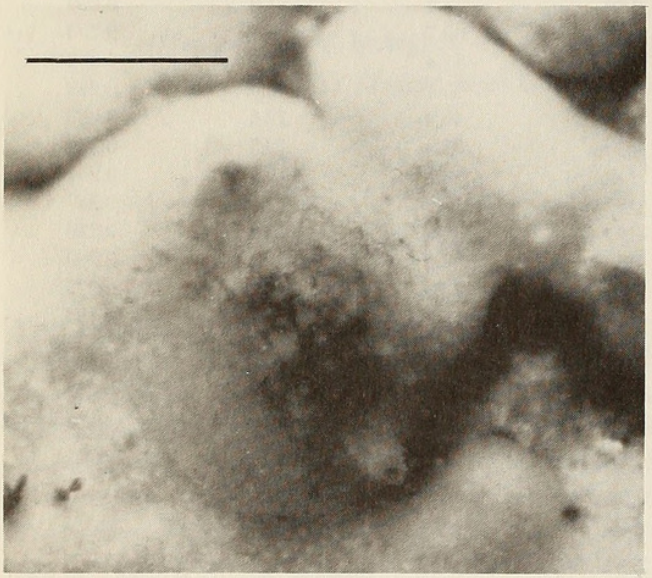

**Figure 1**

***Lamellaria diegoensis*** **at rest on a colony of** ***Cystodytes lobatus*** **scale bar 2 cm**

### Feeding on *Cystodytes lobatus*

*Cystodytes lobatus* occurs primarily in two color forms, translucent white and pale pink. The *Lamellaria diegoensis* blended somewhat better on the pink colonies and was originally collected on a pink colony but showed no feeding preferences between the two color types. The method of feeding has been described in detail by Fretter & Graham (1962): The animal rasps through the ascidian test and sucks up the zooids, leaving a hole with scalloped edges. In *Cystodytes* the zooid abdomens are surrounded by spicular sacs made up of closely overlapping disc-shaped calcium carbonate spicules. Inserting a fine probe into the tunic ruptures some of the acid-filled bladder cell membranes beyond the spicular sac, resulting in immediate dissolution of nearby spicules and release of $CO_2$ bubbles. The *L. diegoensis* ate right through the tunic, ingesting large numbers of spicules along with the zooids, and many of the spicules appeared in the feces almost undamaged in appearance, indicating that the mollusk was somehow able to neutralize the bladder cell contents quickly. The feces were either white or pink depending on the color of the tunicate colony being eaten. The feces had a striped appearance, with layers of spicules and tunic material alternating along the length of the pellet. This might reflect the alternating order in which these parts were in-

## Table 3

Results of *Lamellaria diegoensis (L.d.)* feeding on *Cystodytes lobatus (C.l.)*

| | Beginning wet wts. (g) | | | End wet wts. (g) | | | Difference (g) | | | Fecal Pellets Total | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Date | *L.d.* | *C.l.* | Control *C.l.* | *L.d.* | *C.l.* | Control *C.l.* | *L.d.* | *C.l.* | Control *C.l.* | # of pellets | wet wt. (g) |
| 8/4 beg<br>8/6 end<br>(2 days) | 6.528 | 10.286 | 8.999 | 5.154 | 9.219 | 9.079 | −1.374<br>*C.l.* Net loss = −0.987<br>= −0.4935 g/day | −1.067 | +0.08 | 266<br>= 133/day | 0.147<br>= 0.074/day |
| 8/8 beg<br>8/12 end<br>(4 days) | 5.17 | 13.65 | 16.044 | 5.145 | 11.696 | 15.532 | − .025<br>*C.l.* Net loss −1.442<br>= −0.3605 g/day | −1.954 | −0.512 | 366<br>= 92/day | 0.188<br>= 0.047/day |
| 8/18 beg<br>8/21 end<br>(3 days) | 5.672 | 20.864 | 34.696 | 5.986 | 18.08 | 33.01 | +0.314<br>*C.l.* Net loss = −1.098<br>= −0.366 g/day | −2.784 | −1.686 | 521<br>= 174/day<br>$\bar{x}$ = 128<br>± 38/day | 0.250<br>= 0.083/day<br>$\bar{x}$ = 0.065<br>± 0.017/day |

gested. In Table 1 are the wet and dry weights for 10 pieces of *C. lobatus* colonies and for 15 daily fecal pellet accumulations for *L. diegoensis*. The calorimetric analysis of these dried materials is given in Table 2.

Several feeding experiments were carried out (Table 3) to determine the average amount of food eaten per day and correlate this with the number and weight of fecal pellets produced per day. Unfortunately the handling, blotting dry and weighing of *Lamellaria* had a definite negative effect. The results indicate, however, that the animal was acclimating (compare beginning and end weights for each of the feeding runs), and better results would probably have been obtained if the experiments had been continued longer. The feeding experiments appear so variable as to be unusable, but internal checks show a surprisingly close correlation. For example, the ratio of the number of fecal pellets produced per day during the feeding experiments (128) to the average number from Table 1 (152) is nearly the same as the ratio of the weight of dry feces produced per day during the feeding trials (15 mg) to the average dry wt. from Table 1 (17.9 mg). These two sets of numbers were obtained independently by direct measurements and counts. Between May 3 and August 4, 1978, the 3 months prior to the feeding trials, the animal increased in weight from 2.2 to 6.5 g, indicating a steady gain. Assuming that *Lamellaria* had maintained a constant weight during the feeding experiments, the average net weight loss of *Cystodytes* was 0.392± .058 g wet wt/day (all losses added together and divided by 9 days total feeding time). This value is equivalent to 0.036 g dry wt/day, or 0.013 g ash free dry wt/day after subtracting for the 63.3% ash content (Table 3). The result is 48.6 calories ingested per day.

The lamellariid produced an average of 0.065 g wet weight of feces per day during the feeding experiments. Multiplying this by the dry/wet wt ratio from Table 1 results in a value of 0.015 g dry feces/day, or 0.003 g ash free dry wt/day after subtracting the 78.8% ash content. This is equivalent to 17.9 calories/day lost in the feces. Thus, the net caloric intake for *Lamellaria diegoensis* was 30.7 calories/day (=48.6 - 17.9 cals/day). Given that the *Lamellaria* weighed 6.53 g at the start of the feeding experiments, on a per gram basis its daily intake would be 4.7 calories/g body wt/day. This value is probably low when compared to the average number of fecal pellets produced per day when the animal is undisturbed (Table 1). Using this latter value, one can compute that the average net caloric intake would be 36 calories/day when the animal is undisturbed, or 5.5 calories/g body wt/day.

To determine feeding preferences, a few of the ascidian species growing next to *Cystodytes* colonies in nature were offered to *Lamellaria diegoensis*. The mollusk was starved for 3 days, then placed with *Aplidium* sp., *Polyclinum planum* (Ritter & Forsyth, 1917) or didemnids (unid.) for 24 hours. In no case were any of these ascidians eaten. When the *Lamellaria* was then offered *Cystodytes* it immediately began to feed, even in rather bright light before its dish was covered with black plastic.

## SUMMARY

*Lamellaria diegoensis*, a prosobranch gastropod, was collected intertidally on the compound ascidian *Cystodytes lobatus* at Pacific Grove, California. A description is given of the mollusk's external morphology and coloration in order to compare it with its prey. *Lamellaria diegoensis* closely resembles its prey in color and texture, and certain behavioral traits enhance its cryptic nature. It was maintained in the laboratory on a diet of only *C. lobatus* for 6 months; during this period its weight nearly tripled, from 2.2 to 6.5 grams. Several feeding experiments were performed, and these results together with bomb calorimeter values for the ascidian colonies and mollusk feces were used in computing a partial energy budget for *L. diegoensis*. During the feeding experiments, the animal ingested 48.6 calories/day, of which 17.9 calories/day were lost in the feces, resulting in a net caloric intake of 30.7 calories/day, or 4.7 calories/g body wt/day.

The caloric values given here are only preliminary; they are included in the hope that if this work is repeated they can be used on a comparative basis. All the lamellariids share a similar mode of existence; therefore their energy budgets should be comparable. Because their diet is so restricted, if a reliable conversion can be made between number of feces and calories ingested, a variety of feeding experiments are possible with little perturbation to the mollusk.

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