

The Impact of Plant Morphology of
Potamogeton richardsonii on the Feeding
Choices of *Lymnaea stagnalis* and *Physa sp.*

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Abstract

A previous feeding choice experiment found that the snails *Physa sp.* and *Lymnaea stagnalis* preferentially fed on periphyton rather than the macrophyte *Potamogeton richardsonii* (Chambers and Lodge, unpublished). Many reasons have been postulated to explain this, one of them being the structural toughness of the macrophyte as compared to nonvascular plants. In order to study the impact of this plant's structural components in the snails' feeding preferences, the macrophyte was reduced to a powder and then offered as an alginic gel to the snails, in addition to the natural macrophyte form. Experiments were run with both of the aforementioned species of snails, with snails placed in glass dishes with one-square inch of each food choice. The results show that both species consumed significantly more of the plant in alginic gel form and had a higher weight specific feeding rate on the gel.

Introduction

Until recently, the paradigm in the field of limnology had been that live macrophytes found in freshwater were rarely consumed by herbivores. This had been attributed primarily to their structural toughness or a relatively low nutritive value (Lodge et al. 1998). Since then, the impact of freshwater herbivores has been recognized, and the identification of specific grazers has been attempted. Thus far, we have little quantitative information about the particular feeding preferences of freshwater herbivores, and even less still is known about the plant traits that cause those preferences (Cronin 1998).

The impact of snails upon the distribution, abundance, and diversity of macrophytes in freshwater is a subject that has been under much debate (Bronmark 1989 and Sheldon 1987). A compilation of studies found that the foraging of snails has no impact on macrophytes, but that they do substantially reduce periphyton, especially microalgae (Lodge et al. 1998). Freshwater snails have been recognized as significant

grazers in the littoral food web and have been named a major factor in the regulation of periphyton species composition, standing crop, and productivity (Turner 2000).

Chambers and Lodge recently found that both snails *Lymnaea stagnalis* and *Physa sp.* preferentially fed on periphyton rather than the *P. richardsonii* macrophyte. The snails consumed the macrophyte only when otherwise starved (Chambers and Lodge, unpublished).

This experimental work has some correlation with observations in the field. In general, herbivores impact nonvascular plants in freshwater more than vascular plants (Lodge et al. 1998). Possible explanations for this pattern include the following. Algae generally lack structural materials (cellulose, lignin, cuticles) that may render vascular plants difficult to digest. Also, without the vascular tissues, algae are unable to efficiently transport compounds that may pose a deterrent for foraging organisms. Finally, the higher growth rate typical of algae may allow them to suffer and tolerate herbivory better than vascular plants (Lodge et al. 1998).

In the experiment reported here, I test the hypothesis that structural characteristics make macrophytes less desirable. Specifically, I evaluate the impact of the structural morphology of the plant *Potamogeton richardsonii* on the feeding preferences of *Lymnaea stagnalis* and *Physa sp.*

Materials and Methods

We collected *Lymnaea stagnalis* and *Physa sp.* snails at University of Notre Dame Environmental Research Center (UNDERC) in the Upper Peninsula of Michigan near the Wisconsin border. The *Lymnaea* were collected from Tenderfoot Lake, and the

Physa were collected from both Tenderfoot and Brown lakes. We kept the snails in aerated containers and starved them for at least 24 hours before the start of the experiment.

We harvested the freshwater macrophyte *Potamogeton richardsonii* from Tenderfoot Lake on June 14th (all shoots were collected within a 30 meter area along the shore, at about 0.5 to 1 meter in depth). Then we washed the plants, gently scrubbing with fingers to remove epiphyte, snails, and any other organisms residing on the leaves, and air-dried the plants. The dried macrophyte was frozen and shipped to the University of Notre Dame where it was freeze-dried, ground into a fine powder, and returned to UNDERC. We stored it at -20° C until used in the experiments.

We then reconstituted the *Potamogeton* powder into the form of an alginic gel in order to offer a feeding alternative to fresh macrophyte leaves. The gel was made by mixing a measured amount (see below) of the powder with a 2% solution of sodium alginate and then spreading the gel into a 2.5 centimeter wide by 30.5 centimeter long by 0.25 mm deep mold which was underlain by fiberglass window screening material. When making the gel, we added the same percentage of water to the plant powder that had been removed from the plant in the freeze-drying. After we spread and molded the gel onto the window screening, we poured a 0.25 M solution of calcium chloride over the gel mixture to harden the material; sodium alginate is soluble in water, but calcium alginate is insoluble in water. The gel was 0.25- 0.3 mm thick cut into 2.5 cm squares.

The experiment itself was conducted in the laboratory at the UNDERC property near a window that provided natural lighting throughout the experiment. We conducted the test with *Lymnaea* from June 27, 2000 to June 29, 2000 and from July 18, 2000 to

July 22, 2000 with *Physa*. The *Lymnaea* experiment was performed in glass dishes 18 cm in diameter and 7 cm deep, and the *Physa*, which were considerably smaller in size compared to the *Lymnaea*, were placed in glass dishes 11 cm in diameter and 5 cm in depth. Equal areas (2.5 cm squares) of alginic gel and fresh *P. richardsonii* leaf (which had been collected the morning of the experiment and washed free of any epiphyte) of known weights (weighed to nearest .0001 g) were placed in the dish and secured to the bottom of the dish using small rubber suction cups. We then filled all of the containers approximately halfway to the top with Tenderfoot Lake water, which ranged in temperature from 17°C to 19°C throughout the experiment. This was within one or two degrees of the actual lake temperature.

We placed two snails at the center of a glass dish, and the two food choices were placed at opposing sides of the dish to give equal probability or opportunity to reach and consume both food alternatives. In accordance with recommended analysis in feeding preference experiments (Peterson and Renaud 1989), we performed the same number of controls and replicates in the experiment, fifteen of each for *Lymnaea* and nine for *Physa*. This prevented the repression of variance in the control data or “correction factors.” The controls in this experiment consisted of placing both food choices in a glass dish of water without snails to measure any autogenic mass change in each of the alternative foods.

Due to the difference in the snail sizes and feeding rates, the experiment with *Lymnaea* was run for only 36 hours, while the *Physa* were kept in the feeding experiment for 4 full days in order to see noticeable consumption of the plant. After this time, the snails were removed and the plant gel and leaf were reweighed. Consumption of the plant tissue was calculated by subtracting the autogenic change in mass of the gel and

macrophyte in the randomly assigned control from the change in mass of the respective food in the treatment dishes (with snails). (Equation: (mass of treatment plant tissue at start of experiment – mass of treatment plant tissue at end of experiment) – (mass of randomly pre-assigned control plant tissue at start of experiment – mass of randomly pre-assigned control plant tissue at end of experiment) = consumption of plant tissue).

We also calculated the snails' weight specific feeding rate on the two different food choices. This was determined by selecting 16 *Lymnaea* and 12 *Physa* of various shell lengths within the range of variation used in the experiment. The range of length of snail shells used in the experiment was 5.1 mm to 19.5 mm for *Physa* and 18.2 mm to 51.1 mm for *Lymnaea*. These snails were frozen in order for the bodies to be easily removed. We dried the snail bodies in an oven at 105°C for eighteen hours. The dry, shell-free bodies were then weighed. We constructed a regression of the log (shell length in millimeters) versus log (snail mass in grams) for each species. The following are the regression equations for each species of snail:

$$\textit{Lymnaea stagnalis}: y = 3.4782x - 6.3494 \quad (R^2 = 0.9535, P < 0.001)$$

$$\textit{Physa sp.}: y = 2.3877x - 4.5698 \quad (R^2 = 0.9066, P < 0.001)$$

These linear equations allowed the interpolation of the total biomass of the two snails used in each replicate of the experiment. The mass estimates were then used to determine the weight specific feeding rate on the plant feeding alternatives. The feeding rate was expressed as grams of food/gram dry snail/day.

Results

When offered the feeding choice of either the *Potamogeton* macrophyte or the same plant reconstituted as a gel, both the *Lymnaea* and *Physa* snails seemed to prefer to eat the tissue in the form of a gel. From personal observation, we noticed that the snails spent the majority of their time on the plant tissue as a gel rather than the macrophyte leaf. Although the surface area of the two feeding choices was not used in this experiment to quantify plant consumption, it was also observed that a noticeable portion of the gel was missing at the end of the experiment in most dishes (especially with the *Lymnaea*), while few of the *Potamogeton* leaves showed any evidence of herbivory damage.

A t-test was performed to compare the mass consumed of the two different types of plant offered, (gel and leaf), for each of the two species of snails. Both the *Lymnaea* ($P = <0.001$) and the *Physa* ($P = 0.005$) snails consumed significantly more of the plant tissue offered in the alginic gel form as compared to the macrophyte leaf. The mean mass of macrophyte consumed was 0.00268g for *Lymnaea* (standard deviation of 0.00527) and -0.0144g for *Physa*, while the mean mass of the gel consumed was 0.51063g for *Lymnaea* (standard deviation of 0.173) and 0.18189g for *Physa*.

The data were further analyzed by the weight specific feeding rate of the snails, expressed in the units grams of food consumed per gram of snail dry weight per day, using the aforementioned regression curves. The feeding rates were compared using a Kruskal-Wallis one-way analysis of variance on ranks. The results of the test found that the feeding rates for both species of snails were significantly higher for the alginic gel as compared to the macrophyte leaf ($P < 0.001$) (Figure 1). The *Lymnaea* had mean weight specific feeding rates of 2.6871g gel/g snail/day and 0.01514g fresh leaf/g snail/day. The

Physa had mean weight specific feeding rates of 3.8426g gel/g snail/day and -0.7357g fresh leaf/g snail/day.

Discussion

The conceptual model that has been used to guide studies of plant selection by freshwater herbivores suggests that generalist herbivores may base their feeding decisions on a number of plant traits. Plant morphology and structure, the absence of any chemical deterrents, and the nutritive value of plants all seem to be factors playing some role in the foraging of herbivores (Lodge et al. 1998). The importance of each of these factors in a specific herbivore's food choices is still a topic that needs further study.

From the results of this experiment, it appears that the structure of *P. richardsonii* has a substantial impact on the grazing of the two species of snails used in the study. This finding seems reasonable, since the ability of the snail to handle, shred, and ingest different materials is a function of its mouthpart capabilities. From this experiment, however, it is difficult to suggest that the structural component of the plant was the only obstacle in the foraging of these snails, but rather the destruction of any structural impediment of the macrophyte led to the alginic gel being the more preferable food choice. Also, this experiment relies on the assumption that the process of freezing and freeze-drying the plants alters nothing but the structural component of the plant. The same amount of water is added back into the plant, and presumably the nutritive value and taste of the plant is little altered in this process. However, this method can affect some plant metabolites (Cronin 1998). In addition to this, there is one more criticism that could be voiced. The macrophytes for the gel were harvested much earlier (June 14th) than the macrophytes used as fresh tissue collected at the time of the experiment. Plant

characteristics could have changed between collections, however no obvious differences existed.

The role of plant morphology in determining the diet of some herbivores has already been found to be significant. One study noted the importance of plant structure on the susceptibility of seaweed for herbivore damage. Littler and Littler (1980) found that hard encrusting forms of seaweed are among the least susceptible to herbivores, whereas those plants that are highly branched and filamentous are more susceptible (Cronin 1998). Also, the fact that macrophytes are consumed more often as detritus than living tissue is more realistically explained by the reduction of structural integrity of the plant rather than any “microbial conditioning” or “chemical defense leaching,” explanations that receive less attention (Cronin 1998).

One particular study that used methods similar to this experiment, found that plant structure and chemistry are important determinants of crayfish feeding choices (Cronin 1998). Cronin found that often plants, when freeze-dried, ground, and reconstituted in an alginic gel, became more highly preferred by the crayfish. The feeding preferences of crayfish were apparently altered when the plant was offered in a form lacking its structural qualities.

In general, of the multiple plant traits affecting the foraging of herbivores, the structure and morphology of the plant seems to be one of the most substantial and more frequently studied attributes. The model of food selection put forth in Lodge et al. (1998) orders the three main factors in diet composition as plant structure, chemical deterrents, and finally nutritive value. However, chemical deterrents seem to have less affect on freshwater herbivores, since watercress (*Nasturtium officinale*) is the only example of an

aquatic plant having an identified chemical defense that deters herbivores from eating it (Lodge et al. 1998).

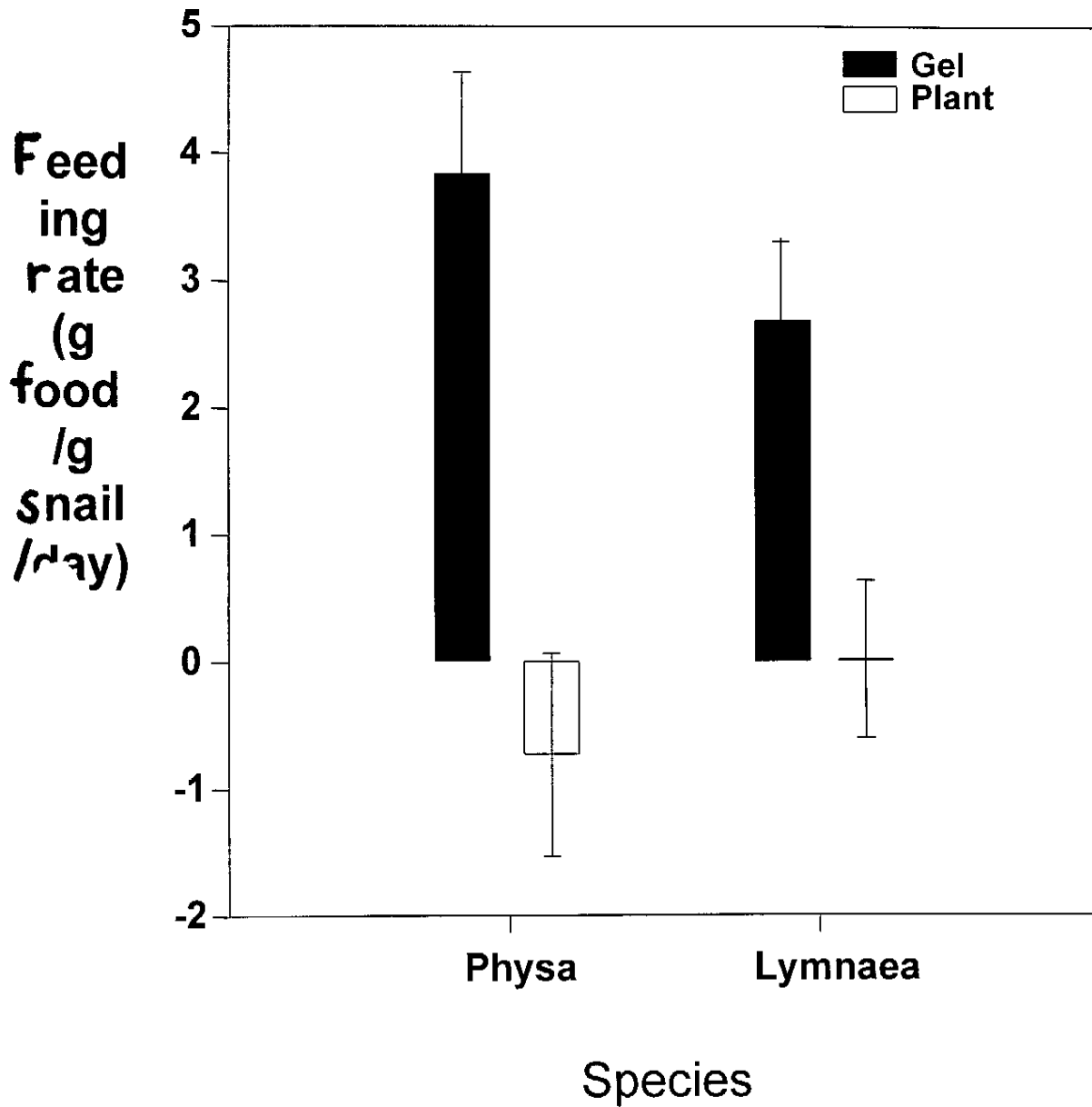
Finally, although it has been observed that snails tend not to directly consume macrophytes, the role of freshwater snails in macrophyte dominated lentic habitats must be acknowledged. Snail populations tend to be positively associated with aquatic macrophytes in nature. Competitive inhibition between macrophytes and periphyton or epiphyton has been named a factor in the loss of macrophytes. In turn, this is influenced by the presence of grazing snails because of high-density snail populations' ability to dramatically decrease periphyton (Daldorph 1995). This delicate balance is articulated in the naming of snails as the predominate keystone species in this type of habitat. Results lend credence to the mutualistic theory that snails act as cleaning symbionts by removing epiphyton and preventing it from harming the macrophyte. Since freshwater macrophytes are regarded as a major factor in the productivity, species diversity and stability, and aesthetic appeal of these littoral habitats (Daldorph 1995), snails' role in this food web must not be discounted, rather instead should be studied in more depth when concerned with the conservation and management of freshwaters.

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Figure 1. Feeding rate (expressed as grams of food/ gram dry snail/ day) for the two species of snails used in the laboratory experiment. Mean with 95% confidence intervals and significant differences detected by Kruskal-Wallis one-way analysis of variance ($P < 0.001$).



snail speci	type of pla	treatment	start weigh	end weight	weight cha	control	start weigh	end weight
Lymnaea	plant	T1	0.056	0.0504	0.0056	C1	0.06	0.0642
Lymnaea	plant	T2	0.0443	0.0427	0.0016	C2	0.0634	0.0709
Lymnaea	plant	T3	0.0589	0.0607	-0.0018	C3	0.0643	0.0612
Lymnaea	plant	T4	0.0562	0.0552	0.001	C4	0.0574	0.0562
Lymnaea	plant	T5	0.0526	0.0479	0.0047	C5	0.0511	0.0492
Lymnaea	plant	T6	0.0517	0.0473	0.0044	C6	0.0511	0.05
Lymnaea	plant	T7	0.07	0.0684	0.0016	C7	0.0668	0.0654
Lymnaea	plant	T8	0.0582	0.0517	0.0065	C8	0.0688	0.0685
Lymnaea	plant	T9	0.0609	0.0604	0.0005	C9	0.0646	0.0655
Lymnaea	plant	T10	0.0572	0.0531	0.0041	C10	0.044	0.0498
Lymnaea	plant	T11	0.0442	0.0465	-0.0023	C11	0.0639	0.0618
Lymnaea	plant	T12	0.0474	0.0458	0.0016	C12	0.0478	0.0522
Lymnaea	plant	T13	0.0547	0.0474	0.0073	C13	0.0473	0.0458
Lymnaea	plant	T14	0.0628	0.0682	-0.0054	C14	0.0647	0.0637
Lymnaea	plant	T15	0.0471	0.0488	-0.0017	C15	0.0571	0.0618
Lymnaea	gel	T1	1.2498	0.08796	0.3702	C1	0.9042	0.913
Lymnaea	gel	T2	1.2635	0.7517	0.5118	C2	1.1054	1.2154
Lymnaea	gel	T3	0.09769	0.4499	0.527	C3	1.1166	1.1368
Lymnaea	gel	T4	1.0978	0.7657	0.3321	C4	1.0224	1.0469
Lymnaea	gel	T5	1.1523	0.4289	0.7234	C5	1.1463	1.169
Lymnaea	gel	T6	1.2442	0.6687	0.5835	C6	1.1958	1.2702
Lymnaea	gel	T7	1.1337	0.3306	0.8031	C7	1.1157	1.1678
Lymnaea	gel	T8	1.2814	0.8253	0.4561	C8	1.0481	1.0521
Lymnaea	gel	T9	1.0492	0.6963	0.3529	C9	1.1599	1.2599
Lymnaea	gel	T10	1.2938	0.9042	0.3896	C10	1.1554	1.1682
Lymnaea	gel	T11	1.2649	0.9596	0.3053	C11	1.2825	1.2922
Lymnaea	gel	T12	1.0748	0.653	0.4218	C12	1.1064	1.1378
Lymnaea	gel	T13	1.3319	0.6683	0.6636	C13	1.2177	1.2812
Lymnaea	gel	T14	1.3085	1.0603	0.2482	C14	0.9899	1.0423
Lymnaea	gel	T15	1.2027	0.8765	0.3262	C15	1.137	1.1949
Physa	plant	T1	0.0539	0.0602	-0.063	C1	0.0552	0.0581
Physa	plant	T2	0.0554	0.0545	0.009	C2	0.0613	0.0649
Physa	plant	T3	0.0533	0.0569	-0.036	C3	0.0657	0.0681
Physa	plant	T4	0.0678	0.0679	-0.001	C4	0.0696	0.0757
Physa	plant	T5	0.0531	0.0587	-0.056	C5	0.0706	0.0727
Physa	plant	T6	0.0579	0.0613	-0.034	C6	0.0352	0.0356
Physa	plant	T7	0.0442	0.0377	0.0065	C7	0.0443	0.0507
Physa	plant	T8	0.0453	0.05	-0.0047	C8	0.0779	0.0661
Physa	plant	T9	0.0424	0.0442	-0.0018	C9	0.0424	0.0452
Physa	gel	T1	0.952	0.7511	0.2009	C1	0.8802	0.9522
Physa	gel	T2	1.0379	1.1004	-0.0625	C2	1.0097	1.0946
Physa	gel	T3	0.9643	1.0318	-0.0675	C3	1.0316	1.0765
Physa	gel	T4	0.8566	0.6268	0.2298	C4	0.9473	1.0088
Physa	gel	T5	0.8433	0.8479	-0.0046	C5	1.0354	1.085
Physa	gel	T6	1.0369	1.0421	-0.0052	C6	1.1586	1.249
Physa	gel	T7	0.9724	0.9691	0.0033	C7	0.9808	1.0413
Physa	gel	T8	0.9587	1.0062	-0.0475	C8	1.0453	1.0973
Physa	gel	T9	1.0687	1.1074	-0.0387	C9	1.0056	1.0662

weight change (g)

-0.0042

-0.0075

0.0031

0.0012

0.0019

0.0011

0.0014

0.0003

0.0009

-0.0058

0.0021

-0.0044

0.0015

0.001

-0.0047

-0.0088

-0.11

-0.0202

-0.0245

-0.0227

-0.0744

-0.0521

-0.004

-0.1

-0.0128

-0.0097

-0.0314

-0.0635

-0.0524

-0.0579

-0.029

-0.0036

-0.0024

-0.0061

-0.0021

-0.0004

-0.0064

0.0118

-0.0028

-0.072

-0.0849

-0.0449

-0.0615

-0.0496

-0.0904

-0.0605

-0.052

-0.0606

snail species	mass consumed (g)	type of plant	replicate
lymnaea	0.379	gel	1
lymnaea	0.6218	gel	2
lymnaea	0.5472	gel	3
lymnaea	0.3566	gel	4
lymnaea	0.7461	gel	5
lymnaea	0.6579	gel	6
lymnaea	0.8552	gel	7
lymnaea	0.4601	gel	8
lymnaea	0.4529	gel	9
lymnaea	0.4024	gel	10
lymnaea	0.315	gel	11
lymnaea	0.4532	gel	12
lymnaea	0.7271	gel	13
lymnaea	0.3006	gel	14
lymnaea	0.3841	gel	15
lymnaea	0.0098	plant	1
lymnaea	0.0091	plant	2
lymnaea	-0.0049	plant	3
lymnaea	0.0002	plant	4
lymnaea	0.0028	plant	5
lymnaea	0.0033	plant	6
lymnaea	0.0002	plant	7
lymnaea	0.0062	plant	8
lymnaea	-0.0004	plant	9
lymnaea	0.0099	plant	10
lymnaea	-0.0044	plant	11
lymnaea	0.006	plant	12
lymnaea	0.0058	plant	13
lymnaea	-0.0064	plant	14
lymnaea	0.003	plant	15
physa	0.2729	gel	1
physa	0.0224	gel	2
physa	-0.0226	gel	3
physa	1.14387	gel	4
physa	0.045	gel	5
physa	0.0852	gel	6
physa	0.0638	gel	7
physa	0.0045	gel	8
physa	0.0219	gel	9
physa	-0.034	plant	1
physa	0.0126	plant	2
physa	-0.0336	plant	3
physa	0.0051	plant	4
physa	-0.0539	plant	5
physa	-0.0336	plant	6
physa	0.0129	plant	7
physa	-0.0065	plant	8
physa	0.001	plant	9

snail speci	shell lengt	snail mass	snail speci	shell lengt	snail mass (g)
Lymnaea	35.3	0.0985	Physa	17.4	0.0243
Lymnaea	36.6	0.0729	Physa	19.5	0.0255
Lymnaea	25.8	0.0447	Physa	6.2	0.0021
Lymnaea	31.8	0.0619	Physa	5.1	0.0014
Lymnaea	47.4	0.2507	Physa	7.8	0.0043
Lymnaea	34.7	0.0995	Physa	7.1	0.0046
Lymnaea	51.1	0.4864	Physa	6.3	0.0022
Lymnaea	34.4	0.084	Physa	5.6	0.001
Lymnaea	32.8	0.0772	Physa	8.3	0.0035
Lymnaea	18.2	0.0103	Physa	10.1	0.0129
Lymnaea	44.5	0.2889	Physa	8.2	0.003
Lymnaea	42.4	0.2191	Physa	8.1	0.0036
Lymnaea	26.2	0.0431			
Lymnaea	39.4	0.219			
Lymnaea	47.4	0.3802			
Lymnaea	24.5	0.0371			

species of	mean mas	mass of pl	feeding rat	mass of g	feeding rate (ggel/gsnail/day)
Lymnaea	0.1029	0.0098	0.0635	0.379	2.455
Lymnaea	0.1271	0.0091	0.0477	0.6218	3.261
Lymnaea	0.1241	-0.0049	-0.0263	0.5472	2.94
Lymnaea	0.1115	0.0002	0.0012	0.3566	2.132
Lymnaea	0.2166	0.0028	0.0086	0.7461	2.296
Lymnaea	0.1177	0.0033	0.0187	0.6579	3.726
Lymnaea	0.2603	0.0002	0.0005	0.8552	2.19
Lymnaea	0.105	0.0062	0.0394	0.4601	2.921
Lymnaea	0.0942	-0.0004	-0.0028	0.4529	3.205
Lymnaea	0.1025	0.0099	0.0644	0.4024	2.617
Lymnaea	0.102	-0.0044	-0.0288	0.315	2.059
Lymnaea	0.0916	0.006	0.0437	0.4532	3.298
Lymnaea	0.1999	0.0058	0.0193	0.7271	2.425
Lymnaea	0.0984	-0.0064	-0.0434	0.3006	2.037
Lymnaea	0.0933	0.003	0.0214	0.3841	2.745
Physa	0.0129	-0.034	-0.6589	0.2729	5.289
Physa	0.0021	0.0126	1.5	0.0224	2.667
Physa	0.0029	-0.0336	-2.897	-0.0226	-1.948
Physa	0.0169	0.0051	0.0754	1.1438	16.921
Physa	0.0044	-0.0539	-3.063	0.045	2.557
Physa	0.005	-0.0336	-1.68	0.0852	4.26
Physa	0.0052	0.0129	0.6202	0.0638	3.067
Physa	0.0028	-0.0065	-0.5804	0.0045	0.4018
Physa	0.004	0.001	-0.0625	0.0219	1.369