

**Food choice among littoral macrophytes by  
*Parponyx* (Lepidoptera) and *Limnephilus* (Trichoptera) larvae**

Bios 569 - Practicum in Aquatic Biology

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## ABSTRACT

*Paraponyx* (Lepidoptera) larvae and *Limnephilus* (Trichoptera) larvae are generalist herbivores which feed on littoral macrophytes. Laboratory feeding assays were conducted in which *Paraponyx* and *Limnephilus* were offered several species of macrophyte fragments at one time. The change in plant biomass due to consumption and, in the case of *Paraponyx*, domicile construction was measured using wet weights. Also, the effect of *Limnephilus* herbivory on *Nuphar* seedlings was tested by comparing the mass of seedlings with and without insects. In the preference experiments, *Limnephilus* showed a significant preference for *Potamogeton richardsonii*. *Paraponyx* showed significant preference for consuming *P. richardsonii* in one assay, but no significant preferences in further assays. Preferential domicile building material varied among the assays between submerged *Nuphar variegatum* leaves, *Potamogeton richardsonii*, and *Potamogeton zosteriformis*. The *Limnephilus* larvae had no significant effect on the weight of the *Nuphar* seedlings.

## INTRODUCTION

Traditionally, live, freshwater, littoral macrophytes were considered too tough and too nutrient poor to contribute significantly to the diets of invertebrate aquatic herbivores (Gregory, 1983; Sheldon, 1918). However, recent reviews (Lodge, 1991; Newman, 1991) demonstrate that nitrogen contents of aquatic plants are comparable to those found in heavily grazed terrestrial plants. It seems unreasonable that macrophytes would remain unused as a food resource (Lodge, 1991). In fact, recent research has shown that significant aquatic invertebrate herbivory occurs (Wallace and O'Hop, 1985; Sheldon, 1987; Sand-Jensen and Madsen, 1989; Cyr and Pace, 1993).

Because of the historical bias against its importance, herbivory on macrophytes is poorly documented (Lodge et al., 1988; Lodge, 1991; Newman, 1991), but the topic is important to a general understanding of the dynamics of the littoral zone of lakes. For instance, Martin et al. (1992) have found evidence for a littoral cascade where the presence of fish actually inhibits macrophyte growth via an intermediate herbivore. This study strengthens the assertion of Lodge et al. (1988) that the littoral zone offers a more species rich environment to test traditionally pelagic theories such as that of trophic cascades. Also, Sand-Jensen and Madsen (1989) have shown that invertebrate herbivory is sometimes an important factor governing the plant composition of an area. This suggests that herbivory is critical for determining the composition of the littoral zone.

The extent of invertebrate effects on freshwater macrophyte populations, ranges from consumption of 2.5-20.3% of plant biomass (Kornijow, 1994) to 51% of annual primary production (Cyr and Pace, 1993). Such variability in the effect of herbivores on aquatic plants is partially explained by Jacobsen and Sand-Jensen's (1995) suggestion that the

presence and significance of herbivory depends on the presence of the herbivore (as determined by factors such as predation and habitat choice), the abundance of the herbivores relative to the plants, and the food choice of the herbivore. Season is also a factor in the amount of herbivore damage (Jeffries, 1990).

In studies dealing with underwater herbivory, the orders Trichoptera and Lepidoptera stand out as important insect herbivores. Specifically, *Limnephilus* (Trichoptera) and *Paraponyx* (Lepidoptera) are generalist herbivores which consume large amounts of macrophytes (Soszka, 1975; Jacobsen and Sand-Jensen, 1992). The food choice of these insects is not consistent through the literature, but *Potamogeton* species seem to be consistent favorites (Cronin, 1996; Jacobsen, 1992; Newman, 1991). These experiments focus on surveys of natural environments where environmental factors such as predation may affect macrophyte choice. Controlled laboratory choice experiments with insect herbivores have not been published.

The purpose of this study is to enhance the understanding of freshwater herbivory on macrophytes by two invertebrate herbivores, *Paraponyx* larvae and *Limnephilus* larvae, using controlled laboratory experiments. Both insects previously have been observed to be generalist herbivores feeding on the macrophytes found in lakes at the University of Notre Dame Environmental Research Center (UNDERC) in Gogebic county, Michigan and Vilas county, Wisconsin (Cronin, 1996; Froelich, unpublished data). The *Paraponyx* larvae use macrophytes as building material for "domiciles" (small tent-like structures), so this study considered the difference between consumptive and non-consumptive usage in the case of the *Paraponyx*. Other studies have shown that insects of these genera show preference for certain macrophytes (Jacobsen, 1992; Cronin, 1996; Soszka, 1975). This study seeks to discover which macrophytes are chosen over others.

I tested choice among macrophytes commonly found in lakes in this locality using laboratory preference assays. In these assays, the insects were offered a choice of plants, and the magnitude of damage to each plant type was measured. Also, since the stage of the plant may contribute to the significance of herbivory, the effect of *Limnephilus* larvae on *Nuphar* seedlings was tested by comparing the weights of seedlings exposed to larvae to the weights of those not exposed to herbivores.

## METHODS

### *Plants and Animals*

*Limnephilus* (Trichoptera) larvae were collected from Paul Lake at UNDERC in Gogebic county, Michigan. The larvae were collected from littoral surfaces covered with periphyton. *Paraponyx* larvae were collected in the north-east corner of Tenderfoot Lake at UNDERC in Gogebic county, Michigan. *Paraponyx* larvae were collected from

*Nuphar variegatum* and from *Potamogeton zosteriformis*. The Lepidoptera were all of the genus *Paraponyx*, however some of the individuals were thin and green, while others were fat and yellow. When necessary, the larvae were held in aerated lake water and were fed a selection of macrophytes.

*Nymphaea* leaves were collected from Tenderfoot Creek (at UNDERC) near its source, Tenderfoot Lake. Only leaves which had not yet reached the surface and those which had just reached the surface were used. *Myriophyllum* was collected from Kickapoo Lake at UNDERC. *Ranunculus*, *Potamogeton richardsonii*, *Potamogeton zosteriformis*, and *Scirpus* were collected from a shallow, productive bay in the north-east corner of Tenderfoot Lake. *Nuphar variegatum* has both submersed and floating leaves. Only new floating leaves which had not yet surfaced were used. When necessary, plants were held submerged in lake water at room temperature.

### *Preference Experiments*

The experimental containers for the preference experiments consisted of uncovered, 17x14.5x4.5 cm clear plastic deli trays filled with water from Tenderfoot Lake. Plants were rinsed, spun in a salad spinner, blotted with paper towels, cut into fragments, and weighed to the nearest milligram. Attempts were made to standardize the surface area of the plant fragments within each experiment in order to equalize the rate of encounter with each plant type. Since the leaves were different shapes, this standardization relied on human approximation. Fragments were secured to the bottom of the containers using the suction cups of rubber bath mats. The bath mats were soaked in deionized water for at least 24 hours prior to usage. With the exception of the third *Paraponyx* experiment and second *Limnephilus* experiment (in which the plants were placed in a circle and their orientation randomized), the plants were randomly placed in the container. Except for the third *Paraponyx* experiment and second *Limnephilus* experiment which was run in a dimly lit room, experimental lighting was variable. All experiments occurred at room temperature (approximately 19°C).

At the end of each experiment, the remains of the plant fragments were again weighed to the nearest milligram. In the experiments with *Paraponyx*, the plant material used in domiciles was weighed separately from the rest of the remaining fragments. Visual observations were made of the composition of the domiciles and of the amount of damage to each plant fragment.

Each replicate consisted of an experimental container with plants and animals and a control container with only plants. If two different experimental containers existed in each replicate, for example one with *Limnephilus* and one with *Paraponyx*, then only one control container was used for both experimental containers.

The first *Limnephilus* experiment was conducted for 72 hours on 16-19 June, 1996. Leaves were collected and stored overnight. Approximately 9 cm<sup>2</sup> leaf fragments of floating *N. variegatum* (0.287-0.469 g), *P. richardsonii* (0.083-0.378 g), and *P. zosteriformis* (0.068-0.120 g) were used. No attempt was made to assure that the leaves for each trial were from different plants. Each of 10 replicates consisted of one container with 5 *Limnephilus* larvae and a control container.

The first *Paraponyx* experiment was conducted for 85 hours on 20-25 June, 1996. Leaf fragments from floating *N. variegatum* (0.901-1.239 g), submerged *N. variegatum* (0.389-0.620 g), *Ranunculus* (0.260-0.596 g), *P. zosteriformis* (0.179-0.287 g), and *P. richardsonii* (0.120-0.316 g) were collected. The *N. variegatum* was cut into 25 cm<sup>2</sup> pieces, and approximately equal surface areas from the other plants were used. Because of the thin *Ranunculus* leaves, it was necessary to approximate the amount of leaves which would allow for an equal encounter rate between *Ranunculus* and the other plant types. No attempt was made to assure that each fragment was cut from a separate plant. Submerged fragments were stored overnight in the experimental containers, before the start of the experiment. Each of 20 replicates consisted of one container with a *Paraponyx* larva and one with no larva.

The second *Paraponyx* experiment was conducted for 97 hours on 24-28 June, 1996. Approximately 25 cm<sup>2</sup> fragments of *Nymphaea* (0.660-1.528 g), *P. zosteriformis* (0.165-0.308 g), and *P. richardsonii* (0.145-0.255 g) were used. No attempt was made to assure that each fragment was cut from a separate plant. Each of 20 replicates from this experiment consisted of a container with a *Paraponyx* and one with no animal.

The second *Limnephilus* experiment and third *Paraponyx* experiment were conducted for 36 hours on 2-4 July, 1996. Leaves were collected and stored overnight. Leaf fragments of *P. richardsonii* (0.054-0.064 g), *P. zosteriformis* (0.082-0.141 g), submerged *N. variegatum* (0.182-0.214 g), *Scirpus* (0.250-0.909 g), and *Myriophyllum* (0.304-0.382 g) were used. The surface area of the fragments was standardized by human approximation, and each fragment was from a separate plant. Each of 10 replicates consisted of a container with 2 *Paraponyx* of the thin green variety, one with 2 *Limnephilus* larvae, and one with no larvae.

In all the preference experiments, the proportion of damage done to each plant fragment was calculated using the formula:  $[E_i(C_f/C_i) - E_f]/[E_i(C_f/C_i)]$ , where E = weight of the experimental fragment, C = weight of the corresponding control fragment, i = initial weight, and f = final weight.

A Friedman's test ( $\alpha = 0.05$ ) was used to determine if proportions of insect damage differed between plants.

### *Limnephilus* Effects on Seedling Nuphar

An experiment to determine the effect of *Limnephilus* on *Nuphar* seedlings from South Bend, Indiana was conducted in a sunny outdoor area between 30 June and 20 July, 1996. Five dish pans were divided in half using nylon screen and aquarium safe silicon caulk. Sediment from Tenderfoot Lake was collected and approximately 4 cm was placed in each container. The pans were filled with lake water and placed in larger water filled containers as an insulation against extreme temperature changes. Four seedlings were planted in each side of each replicate. The next day (30 June) 4 *Limnephilus* larvae were added to one half of each replicate; the other half served as a control.

Periodic observations were made of the state of the seedlings. On 20 July, the seedlings and the larvae were removed. Seedling leaves were separated from the seedling roots, and all plant parts were dried at 40° C for 78 hours. After drying, leaves and roots were weighed separately to the nearest milligram. Experimental and control mean weights were compared using a t-test ( $\alpha = 0.05$ ).

## RESULTS

### *Limnephilus* preference experiments

In the first *Limnephilus* experiment using floating *N. variegatum* leaves, *P. richardsonii*, and *P. zosteriformis*, *P. richardsonii* was preferred and was the only species which was damaged significantly (fig. 1).

In the second *Limnephilus* experiment using *Myriophyllum*, *P. richardsonii*, *P. zosteriformis*, *Scirpus*, floating *N. variegatum* and submerged *N. variegatum*, *Myriophyllum*, *P. richardsonii*, and *P. zosteriformis* were preferred. Only *P. richardsonii* and *Myriophyllum* were damaged significantly, and *P. zosteriformis* was not significantly damaged (fig. 2).

### *Paraponyx* preference experiments

In the first *Paraponyx* experiment using *P. richardsonii*, *P. zosteriformis*, submerged *N. variegatum*, floating *N. variegatum* and *Ranunculus*, *P. richardsonii* was preferentially consumed over submerged *N. variegatum* and *Ranunculus*. *P. richardsonii* was also the only species which was significantly consumed (fig. 3a). Submerged *N. variegatum* leaves were preferred as domicile material and were the only leaves significantly damaged by this use (fig. 3b).

In the second *Paraponyx* experiment using *Nymphaea*, *P. richardsonii*, and *P.*

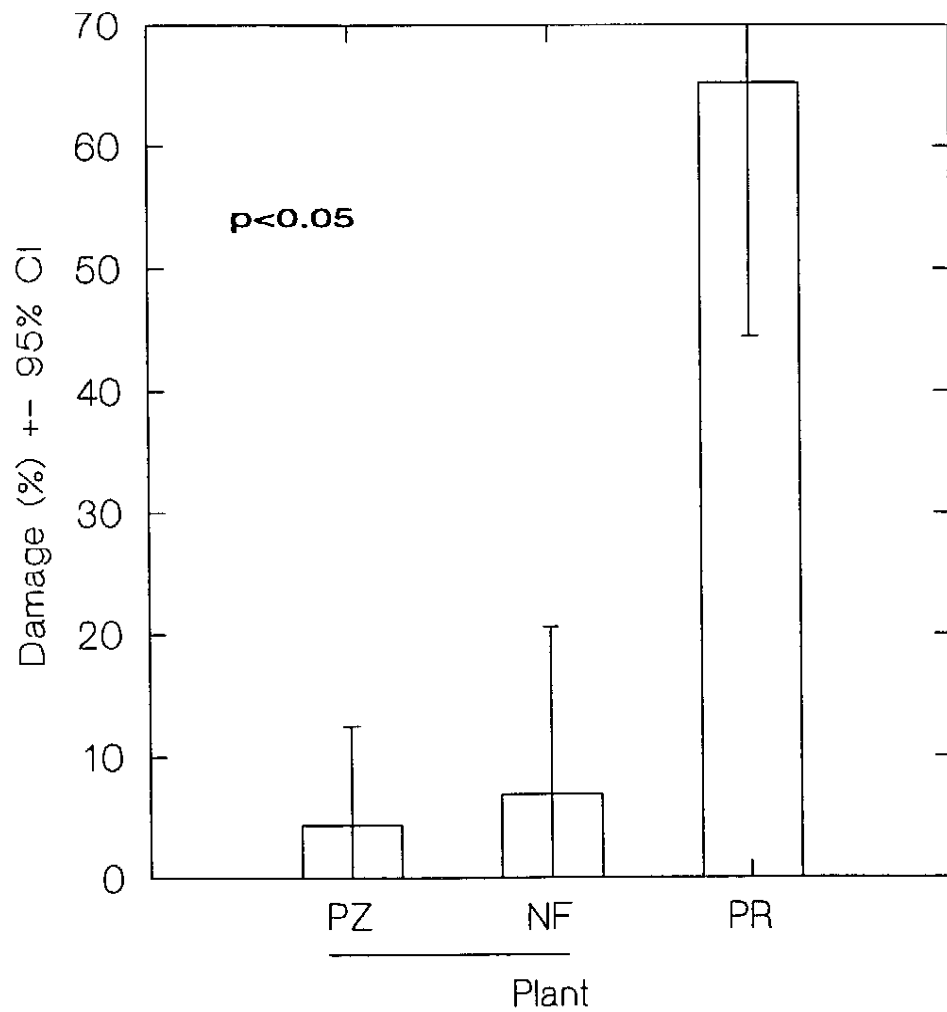


Figure 1: *Limnephilus* larvae damage to *P. Richardsonii* (PR), floating *Nuphar variegatum* (NF) and *P. Zosteriformis* (PZ) in laboratory preference experiments. Horizontal lines connect species for which damage did not differ (Friedman test).

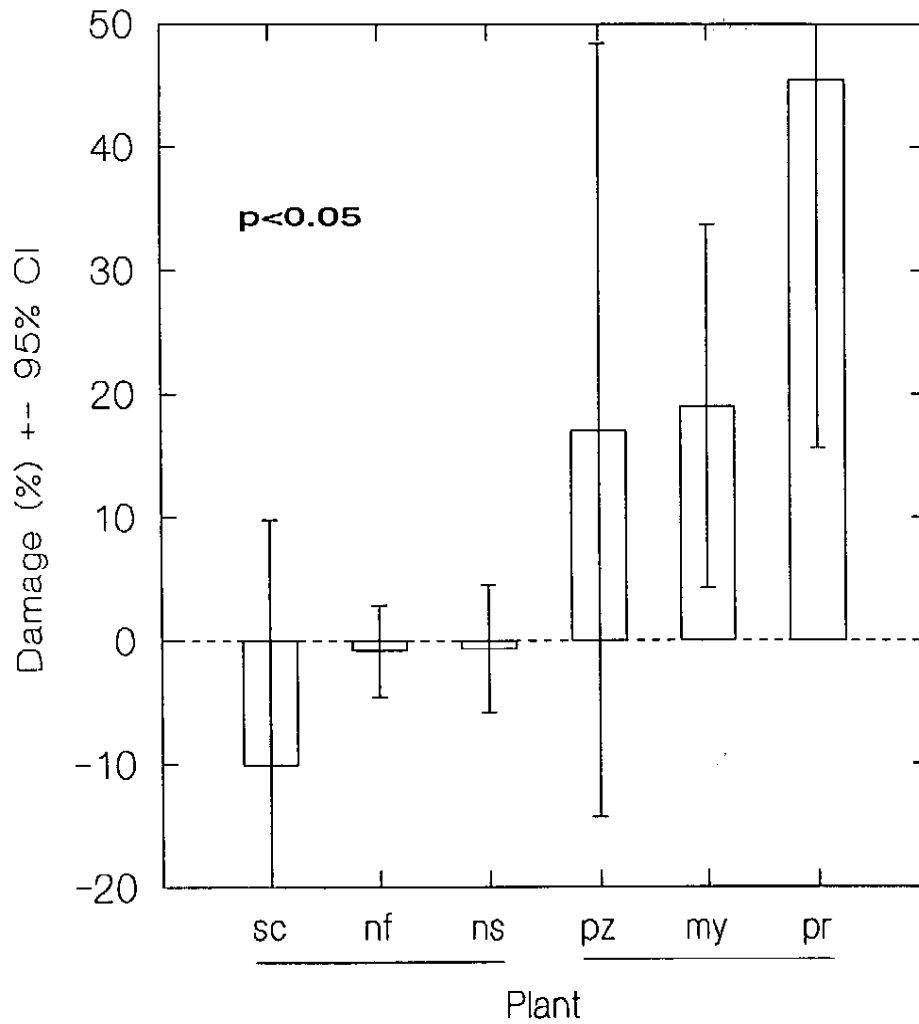


Figure 2: *Limnephilus* larvae damage to *P. Richardsonii* (PR), *N. variegatum* floating and submerged leaves (NF and NS) and *Scirpus* (SC) in laboratory preference experiments. Horizontal lines connect species for which damage did not differ (Friedman test).

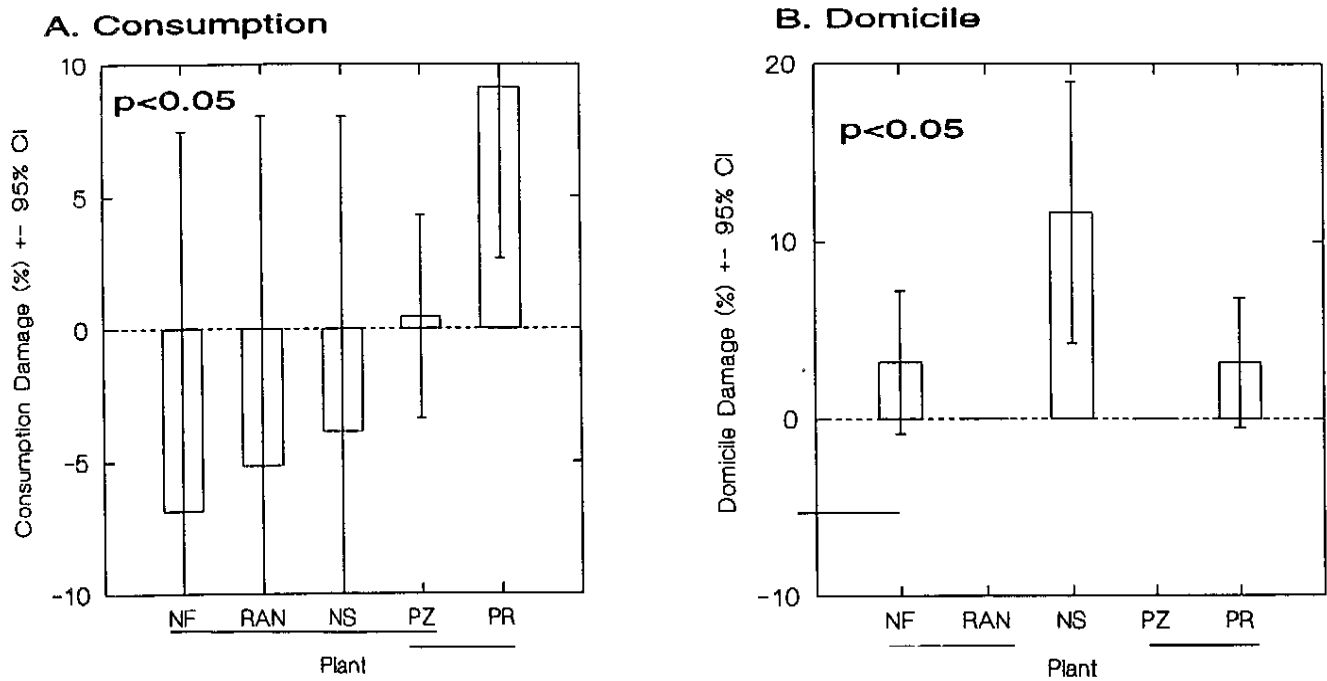


Figure 3: *Paraponyx* larvae damage to floating and submerged *N. variegatum* (NF and NS), *Ranunculus* (RAN), *P. zosteriformis* (PZ) and *P. richardsonii* (PR) in laboratory preference experiments. Horizontal lines connect species for which damage did not significantly differ (Friedman test).

*zosteriformis*, there was no preference between plants for consumption or domicile building. No significant damage was caused by consumption (fig. 4a), but significant damage due to domicile construction occurred for *Nymphaea* and *P. richardsonii* (fig. 4b).

In the third *Paraponyx* experiment using *Myriophyllum*, submerged *N. variegatum*, floating *N. variegatum*, *P. richardsonii*, *P. zosteriformis*, and *Scirpus* there was no difference in consumption of the plants. Only *P. zosteriformis* was significantly damaged due to consumption (fig. 5a). *P. richardsonii* and *P. zosteriformis* were preferred over the other choices as domicile building material, but only the damage of *P. zosteriformis* was significant (fig. 5b).

#### *Seedling Nuphar experiment*

The seedlings exposed to *Limnephilus* larvae showed a mean root weight of  $0.046 \pm 0.031$  g. This did not differ significantly from the mean root weight of the controls,  $0.054 \pm 0.150$  g ( $p=0.654$ ). The mean leaf weight of the experimental treatments,  $0.056 \pm 0.053$  g, also did not significantly differ from the experimental leaf weight,  $0.042 \pm 0.064$  g ( $p=0.643$ ). The mean total weight of the experimentals,  $0.096 \pm 0.077$  g did not significantly differ from the mean total weight of the controls,  $0.102 \pm 0.065$  g ( $p=0.888$ ).

Observations at the end of the experiment showed that the experimental treatments contained far less algae than the controls. Also, the plants in the experimental containers appeared healthier than those in the controls.

## DISCUSSION

The focus of this study were laboratory preference experiments ranking the macrophyte preference of the generalist aquatic insect larvae, *Limnephilus* (Trichoptera) and *Paraponyx* (Lepidoptera). Previous studies have suggested that macrophytes can constitute a large portion of the diet of these insects and that the insects preferentially damage particular macrophytes (Jacobsen, 1992; Cronin, 1996; Soszka, 1975). Also, to further understand how insect herbivory may affect the macrophyte composition of a habitat, *Limnephilus* effects on seedling *Nuphar* was observed.

Soszka (1975) noted heavy damage in the field to *Potamogeton lucens* and *perfoliatus*, with coincident lesser damage to *Elodea* and *Myriophyllum*. Similarly, the laboratory preference experiments in this study showed *Limnephilus* larvae preferring *P. richardsonii* over *Nuphar* and *Scirpus* a result which, in conjunction Soszka's work, could suggest a general preference for *Potamogeton*. However, the current study showed

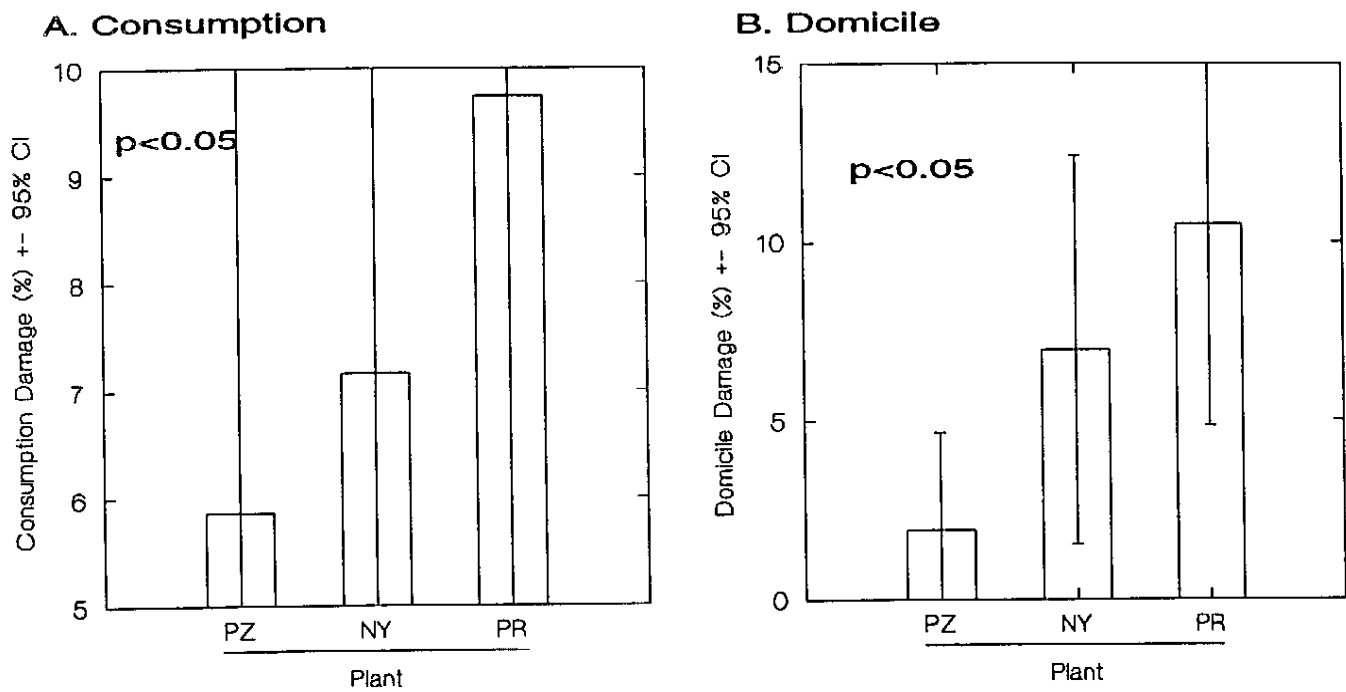


Figure 4: A. Consumption damage to *P. Richardsonii* (PR), *P. zosteriformis* (PZ), and *Nymphaea* (NY) by *Paraponyx* larvae in laboratory preference experiment. B. Damage of the plants due to domicile construction. Horizontal lines connect species for which damage did not significantly differ (Friedman test).

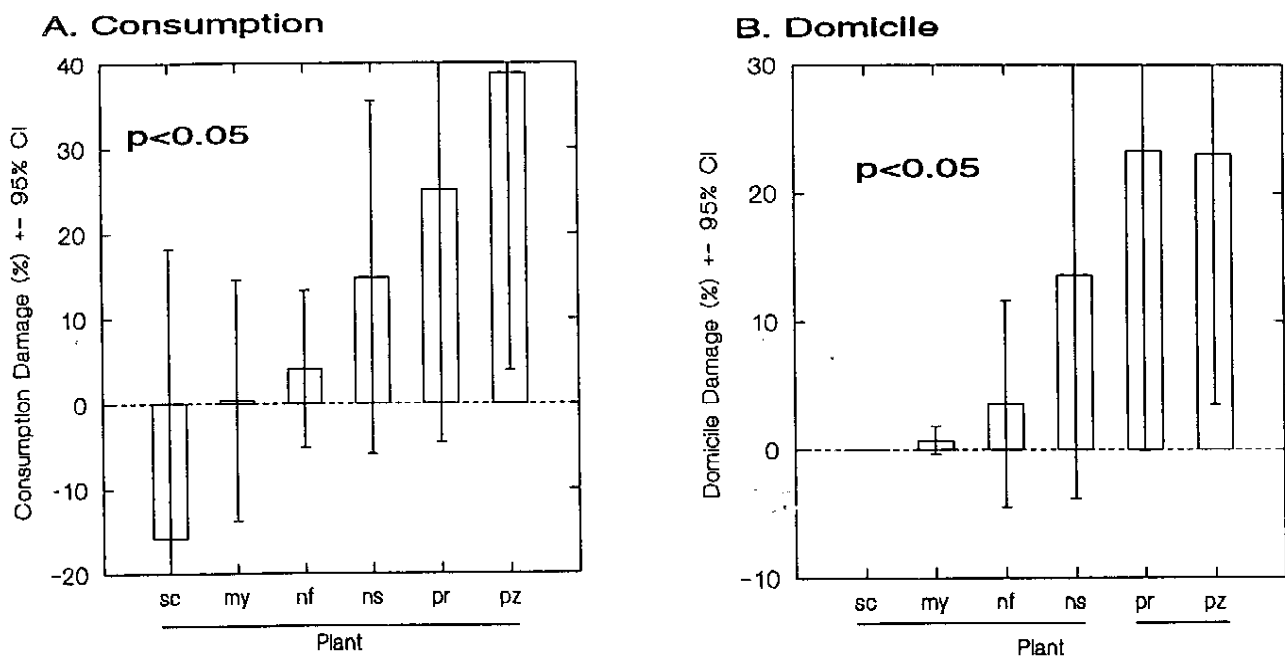


Figure 5: A. Consumption damage to *Myriophyllum* (MY), floating and submersed *N. variegatum* (NF and NS), *P. richardsonii* (PR), *P. zosteriformis* (PZ), and *Scirpus*(SC) by *Paraponyx* larvae a laboratory preference experiment. B. Damage due to domicile construction by *Paraponyx*. Horizontal lines connect species for which damage did not significantly differ (Friedman test).

no significant bias for or against *P. zosteriformis*, and *Limnephilus* showed a preference for *P. richardsonii* over *P. zosteriformis* in the second *Limnephilus* experiment. This points to the conclusion that the larvae can distinguish between *Potamogeton* species.

In my *Limnephilus* experiments, *Scirpus* and *Nuphar* were not favorites. Although no systematic testing of "toughness" was conducted, it is of note that *Nuphar* and *Scirpus* have leaves which are noticeably thicker and harder to tear than the other plants tested. Possibly, the accessibility of the leaves is a factor governing the preference of *Limnephilus* for macrophytes. This would be a particularly important factor in the damage done by herbivores such as *Limnephilus* which use the macrophytes primarily for food, as opposed to herbivores such as the *Paraponyx* larvae which also create structures out of the macrophytes. Of note is the fact that Newman (1991) discounts physical resistance as a reason for low herbivory on macrophytes in general. However, structural defenses may govern the herbivory which does exist in macrophytic systems.

Structure may be the key to explaining the negative mean damage done to *Scirpus* both by *Limnephilus* and *Paraponyx*. *Scirpus* has a tough outer layer which surrounds spongy inner tissue. It is easily conceivable that, when the *Scirpus* was cut, the inner tissue absorbed water. If insects were grazing on the outer layer of *Scirpus*, the plant fragment may absorb more water than if no insect were present. This would explain results opposite from those expected.

*Paraponyx* damage to macrophytes has also previously been documented (Soszka, 1975; Cronin, 1996; Jacobsen, 1992). *Paraponyx* damage differs from *Limnephilus* damage in that it is due to consumption and domicile building. Thus, in laboratory experiments where larvae are presented with several plants in close proximity to each other, it may be expected that the insects would consume one plant and build with another. In fact, in the first *Paraponyx* preference experiment, this occurred. *P. richardsonii* was the favored food, while submersed *Nuphar* leaves were the favored building material. It is not necessarily logical to transfer this laboratory result to the field, because it is easier for an animal to move between plants in the smaller scale of the laboratory containers than in the larger scaled littoral zone.

One explanation for the above results is that the *Paraponyx* larvae build their domiciles out of structurally sound material while eating less resistant leaves. However, a good deal of variation existed within these experiments. For instance, the third *Paraponyx* experiment showed the *Potamogeton* species as the favorite domicile material, while *P. zosteriformis* had the highest mean damage due to consumption (although this result was not statistically significant).

An explanation for these varying experimental results may be the timing of the experiments. The first experiment was conducted in very early spring, before most of the

macrophyte species had reached significant biomass. Furthermore, most of the *Paraponyx* larvae were collected from *Nuphar*. The later experiments were conducted after macrophyte species other than *Nuphar* had become abundant. The insects in these experiments were collected from plants other than *Nuphar*. It is reasonable to suggest that the preference of the larvae for particular macrophytes may be linked to the season or, even more probably, to their location as dictated by the season.

Collin (1989) suggests that the amount of exposure of benthic organisms to foraging fish ought to cause large amounts of time to be spent in "risk-reducing" postures. Such foraging would be an even greater risk to insects such as *Paraponyx* larvae before macrophytes grow enough to provide sufficient cover and shade. Thus, early in the season *Paraponyx* may create domiciles from tougher, more protective material, while later, when predation is not as great a factor, they may move to more pliable material. This hypothesis is, of course, based on several assumptions, such as the assumption that domiciles are essentially protective structures. It is, however, a testable explanation for the variation in preference shown by the *Paraponyx* larvae.

Besides the variation in preference between experiments, the variation within experiments in this study was extremely high. Most of the resulting percentages of damage were not significantly different from each other because the confidence intervals were as large or larger than the means themselves. Possibly, this points to a general variation in preference in natural population of these insects. More probably, the number of replicates in this study was too low.

In summary, both *Paraponyx* larvae and *Limnephilus* larvae showed some preference for *Potamogeton richardsonii* as food. However, variation in the study did not allow a ranking of other food choices. Furthermore, the *Paraponyx* larvae varied in their preference for the macrophyte of which they chose to build domiciles, a source of non-consumptive damage to plants. A general conclusion is that these organisms preferentially damage certain macrophytes, but the reason for their preference at any one time is still in need of investigation.

This study can best be viewed as the predecessor to future work. Later research ought to include more replicates and a more systematic choice of plants offered to the insects. Also, this study did not address the question of why insects would chose one plant over another. Future research could consider the effect that leaf toughness has on insect preference. Seasonal variation is another factor which ought to be considered.

Since insect herbivores can cause significant damage to common macrophytes in the laboratory, they may play an important role in determining the macrophytic species composition of the littoral zones of lakes. For example, a lake with a high population of *Limnephilus* may have a depressed population of *P. richardsonii*. Conversely, a lake

with a high population of *N. variegatum* may show a high population of *Paraponyx*, since these insects prefer to build domiciles from *Nuphar*. Future studies could consider if such correlations exist and test if natural populations of insect larvae are sufficient to have significant effects on natural populations of macrophytes.

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WORKS CITED

- Collins, N.C. 1989. Daytime exposure to fish predation for littoral benthic organisms in unproductive lakes. *Canadian Journal of Aquatic Sciences* 46:11-15.
- Cronin, G. 1996. Life at the water-air ecotone makes water-lilies (*Nymphaeaceae*) vulnerable to aquatic and terrestrial insects. Unpublished.
- Cyr, H. And M.L. Pace. 1993. Magnitude and patterns of herbivory in aquatic and terrestrial ecosystems. *Nature* 361:148-150.
- Daehler, C.C. and D.R. Strong. 1995. Impact of high herbivore densities on introduced smooth cordgrass, *Spartina alterniflora* invading San Francisco Bay, California. *Estuaries* 18:409-417.
- Froelich, A. 1996. Unpublished data.
- Gregory, S.V. 1983. Plant-herbivore interactions in stream systems. Pages 157-189 in J.R. Barnes and G.W. Minshall (editors). *Stream ecology: application and testing of general ecological theory*. Plenum Press, New York.
- Jacobsen, D. And K. Sand-Jensen. 1992. Herbivory of invertebrates on submerged macrophytes from Danish freshwaters. *Freshwater Biology* 28:301-308.
- Jacobsen, D. and K. Sand-Jensen. 1995. Variability of invertebrate herbivory on the submerged macrophyte. *Freshwater Biology* 34:357-365.
- Jeffries, M. 1990. Evidence of induced plant defenses in a pondweed. *Freshwater Biology* 23:265-269.
- Kornijow, R. 1994. The importance of invertebrates as consumers of freshwater macrophytes. *Wiadomosci Ekologiczne* 40:181-195.
- Lodge, D.M. 1991. Herbivory on freshwater macrophytes by invertebrates: a review. *Journal of the North American Benthological Society* 10:89-114.
- Lodge, D.M., J.W. Barko, D. Strayer, J.M. Melack, G.G. Mittelbach, R.W. Howarth, B. Menge, and J.E. Titus. 1988. Spatial heterogeneity and habitat interactions in lake communities. Pages 181-208 in S.R. Carpenter (editor). *Complex interactions in lake communities*. Springer-Verlag, New York.
- Martin, T.H., L.B. Crowder, C.F. Dumas, and J.M. Burkholder. 1992. Indirect effects of fish on macrophytes in Bays Mountain Lake: evidence for a littoral cascade. *Oecologia* 89:476-481.
- Newman, R.M. 1991. Herbivory and detritivory on freshwater macrophytes by invertebrates: a review. *Journal of the North American Benthological Society* 10:89-114.
- Sand-Jensen, K. And T.V. Madsen. 1987. Invertebrates graze submerged rooted macrophytes in lowland streams. *Oikos* 55:420-423.
- Sheldon, S.P. 1987. Effects of herbivorous snails on submerged macrophyte communities in Minnesota lakes. *Ecology* 68:1920-1931.
- Shelford, V.W. 1918. Conditions of Existence. Pages 21-60 in H.B. Ward and G.C. Whipple (editors). *Freshwater biology*. John Wiley and Sons, New York.
- Soszka, G.J. 1975. Ecological relations between invertebrates and submerged macrophytes in the lake littoral. *Ekologia Polska* 23:393-415.

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Wallace, J.B. and J. O'Hop. 1985. Life on a fast pad: water lily leaf beetle impact on water lilies. *Ecology* 66:1534-1544.