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**Experimental Studies of Population Growth and Predator-Prey  
Interactions of South Florida Fishes**

*Defining the roles of common small-bodied consumers in the  
Food web of the Everglades periphyton-mat complex*

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## SUMMARY

Floating periphyton mats and their resident macroinvertebrate communities function as self-contained systems in oligotrophic wetlands. Trophic relationships between this “periphyton-mat complex” and externally feeding macroinvertebrates and fishes have not been described. We conducted a mesocosm experiment to delineate this relationship with three common consumers: eastern mosquitofish (*Gambusia holbrooki*, “picking” omnivore), sailfin molly (*Poecilia latipinna*, “picking” herbivore), and grass shrimp (*Palaemonetes paludosus*, “milling” omnivore). We installed four cages in each of 36 mesocosm tanks and stocked them with 962 cm<sup>2</sup> of floating periphyton (≈ 36% cover). To further understand the relationship between the mat and the consumers, primary productivity was stimulated through a daily load of phosphorus (P) to the water column for two weeks prior to addition of consumers (control = 0, low = 0.6, high = 2.0 g P/m<sup>2</sup>/yr above ambient). We then added one of four consumer treatments to each cage: no consumers, species A only, species B only, and species A+B. All consumer communities were comprised of 13 individuals and all three pairwise consumer combinations were used. Analysis of water column and periphyton TP confirmed that P loads were readily assimilated by periphyton. There was no change in average periphyton biomass with enrichment. *P. latipinna* yielded the greatest per capita (change in periphyton biomass/g consumer) impact on periphyton biomass, and consumer impact on periphyton biomass generally increased with increased levels of P addition. Per capita impact on macroinvertebrate densities (change in density (no./g

AFDM) per g consumer) were also most apparent in *P. latipinna* monocultures and combinations. Multi-species consumer treatments were often associated with a significantly lower impact on both periphyton biomass and macroinvertebrate density suggesting some degree of interference competition. While macroinvertebrate density increased with increased levels of P, effects of consumers in low and high P treatments were also greater than effects observed in ambient P treatments. We did not observe any difference in the ability of *G. holbrooki* and *P. paludosus* to access macroinvertebrates within the mat. Gut content analyses will be performed to help us understand the negative impact on mat-dwelling macroinvertebrates by herbivorous *P. latipinna*. Our results indicate important indirect trophic effects on the periphyton-mat complex from externally feeding consumers.

## INTRODUCTION

The passage of energy between members of a community and the food web are fundamental concepts of ecosystem ecology (Slobodkin 1960). Food webs are traditionally based entirely on feeding relationships, and have developed from simple linear chains into complex food webs. Recent food-web studies have introduced many new concepts which should be considered in studies of trophic dynamics. Among these emerging ideas are (1) the relative strength of top-down and bottom-up forces (Hunter & Price 1992, Power 1992, Strong 1992, Polis 1994, Brett & Goldman 1997, Leibold *et al.* 1997, Chase 1999), (2) nutrient transport and recycling (Owen 1980, Sterner 1990, Ramcharan *et al.* 1996, Schindler & Eby 1997, Vanni & Layne 1997, McCollum *et al.* 1998), and (3) indirect effects and interaction webs (Abrams *et al.* 1996, Morin 1999).

Habitat complexity and the presence of refuges within an ecosystem create interesting indirect effects that are rarely discussed in the literature. Often the physical structure of the environment can have great implications for trophic interactions within a system. More complex habitats create new habitat types and resources, while indirectly altering the intensity of biotic processes within the system (Menge *et al.* 1983). Relatively few manipulative studies of the role of habitat complexity in structuring trophic interactions have been reported. Dudgeon (1993) found no difference in the abilities of predators consuming prey in microhabitats of different architectural complexities since the refuges were easily destroyed by the fish, allowing them access to the invertebrates. A study in a stream riffle system in Australia observed that a

complex boulder-cobble riffle system created a refuge from grazing for algae by restricting the movement abilities of grazers. Weakened trophic interactions between algae and their grazers were observed, while interactions between fish predators and the grazers may have been strengthened (Robson 1996). The complexity of trophic interactions increases significantly when the habitat structure is also food, as described in the La Jolla/Scripps Canyon system. In this study, as the density of prey populations increased and/or the thickness of the detritus mat was reduced, predation rate of fishes on detritus-associated crustaceans increased (Vetter 1998). It is clear that more research is needed to better describe the trophic interactions within these types of systems.

The open marsh of the Florida Everglades provides an excellent study system for investigations of complex trophic interactions. Expansive periphyton mats are a striking characteristic of the Florida Everglades ecosystem. Even though this system is highly oligotrophic, the lowest estimates of standing crops of periphyton in the Everglades exceed literature values for algal standing crops in most other aquatic systems (Goldsborough & Robinson 1996, Turner *et al.* 1999), and periphyton contributes to over 50% of the primary-producer standing stock in the system (E. Gaiser, *personal communication*; Turner *et al.* 1999). The periphyton-mat complex acts as a microcosm within the larger system with numerous species of small animals living in or on its surface (oligochaetes, rotifers, copepods, cladocerans, hemipterans, etc.) (Browder *et al.* 1994). Small fishes patrolling the mat's perimeter consume the

invertebrates it supports, while herbivorous fishes and freshwater prawns graze directly on it.

The periphyton-mat complex in the Florida Everglades serves a unique dual-role, by serving as a primary food source for invertebrate grazers, as well as, a refuge from externally feeding predators. Geddes and Trexler (2003) suggested that in the Everglades, mat structure actually deters herbivory and is a fundamental control in periphyton-consumer interactions, but very little attention has been paid to the specific dynamics of these interactions. Outlining the relationship between the periphyton mat (as both structure and nutrition), its resident invertebrates, and the externally patrolling fishes and large invertebrates is critical in understanding the response of this system to the ecosystem-level changes associated with eutrophication. An understanding of the specific relationships between members of the periphyton complex can then be extended to create models of the consumer community response to phosphorus (P) enrichment and will aid in the interpretation of existing data, such as those from the flume dosing project in northern Shark River Slough.

The complex role of the periphyton mat in the Everglades system leads to interesting indirect trophic interactions, although these indirect effects have not been well documented (Figure 1). Geddes and Trexler (2003) proposed that the combination of calcification, low nutritional value, and structure and arrangement of palatable algal taxa in a matrix of unpalatable ones serves to reduce herbivory. It is also proposed that the feeding capabilities of Everglades grazers and the structure and composition of the periphyton mat are not well matched, making grazing these taxa physically challenging

(Steinman 1996). The structure of the thick periphyton mat allows invertebrates to move freely, while predatory fish are only able to reach exterior portions (personal observation). This allows the invertebrates to use the mat as a refuge, producing a negative indirect effect on macroinvertebrate-eating consumers. Consumers whose feeding strategies give them access to internal portions of the periphyton mat (e.g. shrimp, who tend to use their front appendages to mill through periphyton) may have an advantage over those whose feeding strategies only allow them external access. Consumers who graze directly on the periphyton mat may also impact the mat-dwelling macroinvertebrates indirectly by way of reducing their available habitat.

The response of the algae comprising the periphyton mat to enrichment is well-documented and is often used as a water quality indicator, as eutrophication alters both species composition and productivity (McCormick & Scinto 1999). The response of the consumer community to these changes, however, is significantly less well defined. Addition of P causes a cascade of effects on Everglades periphyton mats. The effects nutrient enrichment include decrease in filamentous blue-green algae that are responsible for the precipitation of calcite within the mat, and a decrease in the amount of calcium carbonate in the remaining mats. Since calcium carbonate crystals make grazing of the mat difficult, it is suggested that this decrease in calcium carbonate increases its edibility (McCormick & Stevenson 1998). A handful of studies have documented both invertebrate and fish community densities along nutrient gradients, but these studies reach conflicting conclusions. Rader and Richardson (1992) found that

in the northern Everglades enrichment led to an increase in invertebrate density. Another study in the northern Everglades found that there was a higher density of fishes in enriched areas, while crustacean densities did not vary significantly from unenriched sites (Jordan 1996). Similar to those findings, Turner et al. (1999) sampled fish and invertebrate densities in WCA-2A, -3A, -3B, as well as Everglades National Park, and found that while fish density was higher in enriched than unenriched areas, invertebrate density did not change. They attributed this pattern to a trophic cascade, where increased primary productivity stimulates invertebrate population growth that is consumed by fish, keeping invertebrate density in check. While these studies are a good preliminary look at the dynamic interaction of the periphyton mat changes with the associated faunal community, they only point out correlations and fail to directly test mechanisms driving such changes.

This study sought to examine the organization and biotic interactions between the complex Everglades periphyton mat and the animals associated with it. This was accomplished by altering the rate of mat production through manipulation of both nutrients and consumers. We designed and conducted a multifactorial mesocosm study to address whether individual consumer species have different trophic relationships with the periphyton-mat complex. Specifically, we sought to determine if consumers' trophic position and/or feeding strategies influence their impact on the periphyton complex (both periphyton biomass and macroinvertebrate densities). Finally, we

determined if and how these consumer-periphyton-mat complex relationships change with increased levels of eutrophication.

## METHODS

### *Selection of Study Species*

To help us understand the relationship between externally feeding consumers and the periphyton-mat complex, we selected 3 consumer species with different trophic positions and feeding strategies. Study species were chosen based on the relative density of individuals and their contributions to total biomass, as well as their diet documented in the literature and observed feeding habits. Relative densities were based on quarterly throw-trap sampling in Shark and Taylor sloughs from October 1993 to December 2000 (J. Trexler, Florida International University, unpublished data).

*Palaemonetes paludosus* (grass shrimp) constitute 51% of the total number of invertebrates, while the next most common invertebrate (*Pelecopsis femoratus*) were only 10% of the total invertebrates. *P. paludosus* feed primarily on algae throughout the year (Hunt 1952), and have been observed to “mill” through the periphyton mat with their chelipeds and maxillipeds, able to access internal portions of the mat (personal observation). *Heterandria formosa* (least killifish) are the most commonly found fish in throw-traps (32% of total fish collected), while *Gambusia holbrooki* (eastern mosquitofish) are almost as common (24% of total fish collected). Since *G. holbrooki* are significantly larger than *H. formosa*, *G. holbrooki* were chosen for this study, because they represent a larger portion of the total fish biomass. *G. holbrooki* are omnivorous, eating mostly

invertebrates in the summer wet season, and changing their diet to mostly algae in the winter (Browder *et al.* 1994). Since *G. holbrooki* are fairly large-bodied with respect to the tightly-knit mat, they appear to have only external access to the mat, picking only at its peripheral edges (personal observation). *G. holbrooki* and *P. paludosus* collected in the southern Everglades have also been seen to have similar carbon and nitrogen stable isotope signatures (A.J. Williams, Florida International University, unpublished data). In contrast to these two species, sailfin mollies (*Poecilia latipinna*) are also quite common (9% of total fish collected), representing the most common herbivorous fish. *P. latipinna* are also assumed to have only peripheral mat access, similar to *G. holbrooki*.

#### *Mesocosm experiment*

A mesocosm tank experiment with a factorial design (3 P levels x 3 consumer combinations x 4 community compositions x 4 replicates = 144 experimental units) was carried out in 36- 213 x 106 cm concrete crypts located at the Daniel Beard Research Center, Everglades National Park in Fall 2002 (Table 1; Figure 2). Mesocosm tanks were filled with well water and four 29 cm diameter (3.18 mm) nylon-mesh cages were installed in each tank. Each cage was stocked with artificial vegetation (10- ¾ x 12" plastic strips tied to a base on the cage bottom), and floating periphyton. We collected the periphyton mat by carefully lifting 320 480-cm<sup>2</sup> pieces of floating mat from the Madeira Ditch area of Taylor Slough, Everglades National Park. Two of these floating periphyton samples were then randomly placed in each cage, providing cover to ≈36 % of the cage surface (960 cm<sup>2</sup>). Periphyton was placed in the mesocosms within 3 hours

of collection. All tanks were then covered with 1.59-mm vinyl-mesh screening and remained covered for the duration of the experiment. The 32 remaining periphyton samples were used for initial estimates of periphyton volume, wet weight, dry weight (DW), and ash-free dry weight (AFDW).

Periphyton was allowed to acclimate in the mesocosm cages for 5 days prior to 14 days of daily phosphorus loading. We established 3 P-loading levels: control (no added P), low (0.6 g P/m<sup>2</sup>/yr), and high (2.0 g P/m<sup>2</sup>/yr). Previous studies in the Everglades have added annual P loads within the same range, and noted enrichment effects in flora and fauna after 5 months (Newman *et al.* 2004). We loaded 41.7% (<sup>5</sup>/<sub>12</sub>) of the annual P load for each of our nutrient levels over the course of 14 days to mimic the total load that would be applied in 5 months. We prepared a 0.04 M solution of sodium phosphate (Na<sub>2</sub>HPO<sub>4</sub>) daily, of which 30mL was added to low P tanks and 100 mL was added to high P tanks. Loads were delivered to tanks daily by sprinkling the solution evenly across the surface of the water from 120 mL sample cups with holes in their lids. Cups containing P loads were rinsed 3x with well water, delivering the 'rinse' to the tanks in the same manner. Control (no added P) treatments received only the 3 "rinse" treatments.

Consumer communities within each mesocosm consisted of all 3 pairwise combinations of our focal species (*G. holbrooki*, *P. latipinna*, and *P. paludosus*). Each of the 4 cages within each mesocosm was randomly assigned one of the following consumer treatments: no consumers (control), species A only, species B only, species A + B. Consumer density was 13 consumers per cage in all consumer treatments, but their

relative density in the combination treatment (A+B) varied based on relative average densities in throwtrap samples collected in Shark and Taylor sloughs between 1993 to 2000 (Table 2). Consumers were placed in cages for 14 days, after which they were removed, anesthetized with MS-222 and euthanized with formalin (10% formaldehyde) for gut content analyses. All study organisms were collected from Shark River Slough and Taylor Slough, ENP, and Water Conservation Area 3A and housed in large outdoor tanks prior to stocking in the experiment.

#### *Sampling and Laboratory Analyses*

One 125-mL water sample was taken from each mesocosm and 1 20-mL periphyton sample was taken from each cage for TP analysis prior to initial P loading (T<sub>1</sub>), prior to adding consumers to cages (T<sub>2</sub>), and at the end of the experiment (T<sub>3</sub>). Periphyton samples collected from the field that were not stocked in cages (T<sub>0</sub>) were also sub-sampled for TP analysis. Measurements of pH and water temperature (Orion 150 A+ pH meter) were also taken for each tank at the end of the experiment (T<sub>3</sub>). An additional periphyton sample (avg. wet weight=22.31±0.31 g, avg. dry weight= 2.07±0.03 g) was collected from each cage prior to consumer addition (T<sub>2</sub>) and at the end of the experiment (T<sub>3</sub>) for analysis of macroinvertebrate densities. All remaining periphyton was removed from cages to determine total remaining biomass. Water samples were refrigerated and kept in the dark, and periphyton samples were frozen until laboratory processing and analyses.

Periphyton samples collected for nutrient analysis were processed by first thawing them and, when present, manually removing embedded *Eleocharis* spp. stems. Samples were dried at 70-80 °C for at least 48 hours and crushed to a fine powder, and analyzed for total phosphorus (TP), total nitrogen (TN), and total carbon (organic (OC) and inorganic (IC)) using standard procedures (Fourqurean *et al.* 1992). Water samples were analyzed for TP only. Dry weights (DW) and ash-free dry weights (AFDW) were obtained for periphyton removed from each cage at the end of the experiment.

Periphyton samples collected for macroinvertebrate analyses were thawed, stained with Rose Bengal solution and refrigerated for a minimum of 12 hours. Each sample was rinsed in a 250- $\mu$ m sieve and transferred to a petri dish for processing. Under a dissecting microscope, samples were carefully teased apart and all animals greater than approximately 1 mm in length were removed, identified to the lowest feasible taxonomic level and preserved in 70% EtOH. We froze our field samples rather than chemically preserve them in order to obtain measures of periphyton dry mass and AFDM, allowing a standardization of densities (no. animals per unit periphyton). The freezing and thawing process greatly reduced the integrity of oligochaetes rendering them impossible to quantify with any confidence, so we excluded this group from further analyses (no effect was observed with any other taxa). With all animals removed, remaining periphyton was dried at 70°C for at least 48 hours and incinerated at 500°C for 3 hours. Ash-free dry mass (AFDM) of substrate from each sample was then calculated.

Prior to being stocked into cages, lengths (standard lengths (SL) for fish, carapace lengths (CL) for shrimp) were obtained for 1 consumer of each species per cage (total measured: 11% of *G. holbrooki*, 12% of *P. latipinna*, 9% of *P. paludosus*). At the end of the experiment lengths were obtained for all consumers removed from cages and weights were obtained for any other large macroinvertebrates that may have been present (odonates, etc.).

### *Statistical analyses*

We conducted analyses of variance using Proc Mixed (SAS) to test for changes in water chemistry, periphyton chemistry and biomass, and macroinvertebrate densities across consumer and nutrient treatment levels through the course of the experiment. To fulfill assumptions of variance homogeneity and normality, water and periphyton TP, and water pH data were  $\ln(y+1)$  transformed. To correct for differences in the size of our consumer species in the analysis of consumer effects, we used established length-weight regressions to estimate biomass of consumers remaining in cages at the end of the experiment (Kushlan et al. 1986):

$$G. holbrooki: \text{ weight (g)} = (10^{(-4.786 + (3.032 * \log_{10}(\text{length}(\text{mm}))))}) * 0.2$$

$$P. latipinna: \text{ weight (g)} = (10^{(-4.750 + (3.142 * \log_{10}(\text{length}(\text{mm}))))}) * 0.2$$

$$P. paludosus: \text{ weight (g)} = (10^{(-3.8045 + (2.7878 * \log_{10}(\text{length}(\text{mm}))))})$$

Average biomass of periphyton stocked into cages was estimated from the extra periphyton samples collected from the marsh, and the assumption was made that this biomass did not change significantly between the time it was placed into the tanks ( $T_0$ )

and when consumers were introduced (T<sub>2</sub>). Periphyton biomass was analyzed in terms of the change in biomass with consumer addition per gram of consumer:

$$\text{per capita } \Delta \text{ periphyton DW} = \frac{\ln(\text{average } T_0 \text{ biomass(g)} + 1) - \ln(\text{biomass remaining at } T_3(\text{g}) + 1)}{\ln(\text{total consumer weight (g)} + 2)}$$

Macroinvertebrate densities were calculated as the number of macroinvertebrates per gram AFDM of periphyton. Changes in macroinvertebrate densities with consumer addition per gram of consumer were calculated as:

$$\text{per capita } \Delta \text{ density} = \frac{\ln(T_3 \text{ density (no./g AFDM)} + 1) - \ln(T_2 \text{ density (no./g AFDM)} + 1)}{\ln(\text{total consumer weight (g)} + 2)}$$

## RESULTS

### *Nutrient Effects*

TP analyses indicate that our P loads were rapidly assimilated from the water column by periphyton. Water and periphyton TP varied significantly across nutrient treatments and through the course of the experiment (Figure 3A&B). Tukey's pairwise comparisons indicated TP in the water column did not vary significantly through the course of the experiment in our control P tanks ( $P \geq 0.994$ ) or across nutrient levels prior to P addition ( $P > 0.999$ ). Immediately following P loading (T<sub>2</sub>), water TP was significantly higher in both low and high P treatments (low:  $P = 0.001$ ; high:  $P < 0.001$ ). At the end of the experiment (T<sub>3</sub>), TP in low P treatments was not significantly different

from that of T<sub>2</sub> (P=0.409), but TP in high P treatments was slightly lower (P=0.004). Periphyton TP did not vary significantly through the course of the experiment in control P tanks (P≥0.862) or across nutrient levels prior to P addition (P≥0.629). Furthermore, TP of periphyton stocked into tanks (T<sub>0</sub>) was not significantly different from TP of all tanks at T<sub>1</sub> (P≥0.148) or control tanks through the course of the experiment (P≥0.102). Immediately following P loading (T<sub>2</sub>), periphyton TP was significantly higher in both low and high P treatments (low: P<0.001; high: P<0.001). At the end of the experiment (T<sub>3</sub>), TP in low P treatments was not significantly different from that of T<sub>2</sub> (P=0.997), but TP in high P treatments was slightly higher (P=0.018). At the end of the experiment, pH in the low and high P treatments was slightly higher than control P treatments (F<sub>2,23</sub>=18.353, P<0.001;  $\bar{X}_C = 8.85 \pm 0.07$ ,  $\bar{X}_L = 9.39 \pm 0.07$ ,  $\bar{X}_H = 9.32 \pm 0.07$ ).

Periphyton AFDW adjusted for consumer mass increased significantly with P addition (F<sub>2,123</sub>=7.42, P=0.0009), but there was no significant difference between low and high P treatments (F<sub>1,123</sub>=0.59, P=0.442). We also observed an increase in consumer-mass adjusted density of several abundant macroinvertebrate taxa (*Hyalella azteca*, Heteroptera, and adult Coleoptera) and total macroinvertebrates. Tipulidae was the only macroinvertebrate group that decreased with P addition (Table 3).

### *Consumer Effects*

The proportions of consumers successfully recovered from cages at the end of the experiment were relatively high (Table 4). Small proportions of consumers were

found outside of cages (loose in tanks) or in other cages. Small to moderate proportions of consumers were not recovered, and mortality was assumed. One marsh killifish (*Fundulus confluentus*) was inadvertently stocked into a cage stocked with only *G. holbrooki* but was considered equivalent to *G. holbrooki* for analyses since they are also considered a “picking omnivore.” Sex determination of consumers removed from tanks at the end of the experiment, indicated a considerably higher proportion of females than males of each fish species (Table 4). While we did find a few relatively large macroinvertebrates in our cages (gastropods, *Pelocoris femoratus*, coenagrionids), we did not find any odonates.

We found not evidence that consumer lengths (SL and CL) changed through the course of the experiment. Paired t-tests indicated average lengths of *G. holbrooki* and *P. latipinna* were smaller at the beginning of the experiment than at the end ( $t_{42}=5.038$ ,  $P<0.001$ ;  $t_{42}=2.209$ ,  $P=0.033$ ), though the magnitude of the effects was small. This probably indicates that the small subset of consumers measured initially was not completely representative of the populations actually placed in the cages. Average length of *P. paludosus* did not change significantly throughout the experiment ( $t_{44}=-0.482$ ,  $P=0.632$ ).

While consumers had only a few statistically significant impacts on periphyton biomass, several trends are apparent from our data (Figure 4A). Consumer treatments consisting of *P. latipinna* (both alone and in combination with *G. holbrooki*) consistently had the greatest impacts on periphyton biomass. *G. holbrooki* and *P. paludosus* monocultures had very little impact on periphyton biomass. In most cases, these

consumer effects increased with increased levels of enrichment, although this increase was only significant in *G. holbrooki* + *P. latipinna* treatments.

We identified 26 macroinvertebrate taxa in our periphyton samples, but our statistical analyses focused only on those taxa present in at least 5% of samples. We saw significant consumer effects on each of our 14 numerically dominant taxa, although these effects varied greatly (Figure 4B-P). Monocultures of our consumer species consistently had one of the greatest top-down impacts on macroinvertebrate densities. This was especially evident in *Hyalella azteca*. Multi-species consumer combinations generally had higher means and variances than monocultures. Our data also indicate that these consumer effects are generally greatest at high levels of P enrichment. Contrary to our hypotheses (Figure 1), we did not observe significant differences in the ability of *P. paludosus* and *G. holbrooki* to access macroinvertebrates within periphyton mats.

## DISCUSSION

This study shows both direct and indirect effects of consumers on periphyton mats and their resident macroinvertebrate communities (Figure 5). Although all 3 of our consumers readily consumed periphyton in our cages, *P. latipinna* had the greatest impact on periphyton biomass even when their impact was scaled to their relatively larger body size. Everglades periphyton mats seem to be a very effective refuge for

macroinvertebrates, the magnitude of which varied across macroinvertebrate taxa. Many macroinvertebrate taxa were seemingly unaffected by the addition of predatory consumers to cages (i.e. adult Coleoptera, dipteran pupae, *Dasyhelea*, Stratiomyidae, non-tanypod Chironomidae, Tanypodinae), especially in ambient P conditions. We also found that consumer monocultures have a greater impact on macroinvertebrate communities than multi-species combinations. Interference competition seems to play an important role in these interactions as fewer resources are consumed by the combined communities than their individual components.

To assure that consumers could be adequately contained in 3.18 mm mesh cages, larger members of each consumer community were selected for this experiment. This was especially important for *G. holbrooki* whose slender bodies may have more easily moved through the mesh. As a result, we selected a disproportionately high number of *G. holbrooki* females, and a slightly higher proportion of female *P. latipinna*. Care was taken to exclude gravid females of all three consumer taxa, so we feel this did not play a significant role in our observed results. We are satisfied with the proportion of consumers recovered at the end of our experiment.

The P gradient created in our mesocosm tanks produced a similar response in periphyton and macroinvertebrate communities as have been observed in field mesocosm studies and transects through enriched sloughs. We saw a slight increase in periphyton biomass in our “no-consumer” treatments through the course of our 28 day

experiment (14 day P loading + 14 day experiment), although this observed trend was not statistically significant. This may in part be due to the imprecision of collecting all of the periphyton from our cages at the end of the experiment, and the variance in the amount of periphyton placed in cages initially. We saw increases in macroinvertebrate densities with P enrichment in almost all taxa, a response that has also been observed in previous P enrichment studies in this system.

The observed impact of consumers on macroinvertebrates inhabiting floating periphyton mats intensified with increased levels of P enrichment. Increased periphyton grazing with P enrichment may be a response to increased food quality, as periphyton assimilates P from the water column. Since macroinvertebrates within the mat were also feeding on this P-enriched periphyton, food quality was higher in enriched treatments for macroinvertebrate-feeding consumers, thereby stimulating top-down effects from the consumers.

Our hypotheses about how consumers with different trophic positions and feeding strategies would impact the periphyton-mat complex were not supported by this experiment. We observed no significant difference between the impacts of our “picking” and “milling” omnivores on periphyton biomass or macroinvertebrate densities. We also observed an unexpected impact of our herbivore (*P. latipinna*) on mat-dwelling macroinvertebrates. *P. latipinna* had a very strong negative effect on macroinvertebrate densities, an effect that increased with P enrichment. While *P.*

*latipinna* have been observed to consume infrequently invertebrates (Harrington and Harrington 1961), at this time it is unclear as to whether this is an effect of direct consumption of macroinvertebrates or a poorly understood indirect effect. Gut content analyses will be performed to aid us in understanding the nature of this observed effect.

Our results indicate that Everglades periphyton mats are an excellent refuge for macroinvertebrates since the physical structure of the mat limits their availability to externally feeding consumers. Many macroinvertebrate taxa are still highly susceptible to predation by large consumers, but interference competition of consumers when species are mixed significantly decreases their impact. Eutrophication increases food quality for consumers in the system, thereby stimulating top-down pressures on both periphyton and macroinvertebrates. Further analyses of these data will help us to better understand the complex role of the periphyton-mat complex in the Everglades food web.

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## PRESENTATIONS

Smith, S.E.L. and J.C. Trexler. 2004. Effects of consumer feeding strategies on floating periphyton mat macroinvertebrate communities. Ecological Society of America 89<sup>th</sup> Annual Meeting, Portland, OR.

**Table 1.** Schedule of mesocosm experiment and samples collected throughout the study.

Date	Event	Samples collected
10/18-19/02	Tanks filled with well water; cages & artificial vegetation installed in tanks	
10/22/02 (T <sub>0</sub> )	Periphyton added to all cages; all tanks covered	<ul style="list-style-type: none"> <li>• Periphyton for TP analysis</li> </ul>
10/27/02 (T <sub>1</sub> )	P loading begun	<ul style="list-style-type: none"> <li>• Water for TP analysis</li> <li>• Periphyton for TP analysis</li> </ul>
11/12/02 (T <sub>2</sub> )	Consumers added to cages	<ul style="list-style-type: none"> <li>• Water for TP analysis</li> <li>• Periphyton for TP analysis</li> <li>• Periphyton for macroinvertebrates</li> </ul>
11/26/02 (T <sub>3</sub> )	Consumers removed from cages; end of experiment	<ul style="list-style-type: none"> <li>• Water for TP analysis</li> <li>• Periphyton for TP analysis</li> <li>• Periphyton for macroinvertebrates</li> </ul>

**Table 2.** Average densities of consumers in 1-m<sup>2</sup> throwtraps (Shark and Taylor Sloughs, 1993-2000), density ratios, and composition of 3 consumer combination communities used in mesocosm study.

Consumer	Avg. density (no./m <sup>2</sup> )	Ratio	Combination Communities		
			G+P	M+G	P+M
<i>G. holbrooki</i>	6.135	3	3	7	---
<i>P. latipinna</i>	4.744	2	---	6	2
<i>P. paludosus</i>	25	11	10	---	11

**Table 3.** Average per capita change in macroinvertebrate densities (no./g AFDM) across P treatments. Significant differences ( $P \leq 0.05$ ) among P levels within each taxon are indicated by different lowercase letters. Taxa not shown were not significantly impacted by P addition.

Taxon	LS Mean ( $\pm 1$ SE)			F <sub>2,123</sub>	P
	Control P	Low P	High P		
<i>Hyalella azteca</i>	0.003 ( $\pm 0.207$ ) <sup>a</sup>	0.251 ( $\pm 0.207$ ) <sup>a</sup>	1.025 ( $\pm 0.207$ ) <sup>b</sup>	6.63	0.0018
Heteroptera	0.678 ( $\pm 0.190$ ) <sup>a</sup>	0.884 ( $\pm 0.190$ ) <sup>a</sup>	1.547 ( $\pm 0.190$ ) <sup>b</sup>	3.21	0.0440
Coleoptera	0.036 ( $\pm 0.147$ ) <sup>a</sup>	0.275 ( $\pm 0.147$ ) <sup>a</sup>	0.609 ( $\pm 0.147$ ) <sup>b</sup>	3.85	0.0238
Tipulidae	0.303 ( $\pm 0.113$ ) <sup>ab</sup>	0.553 ( $\pm 0.113$ ) <sup>a</sup>	0.072 ( $\pm 0.113$ ) <sup>b</sup>	4.57	0.0122
Total	0.064 ( $\pm 0.102$ ) <sup>a</sup>	0.278 ( $\pm 0.102$ ) <sup>ab</sup>	0.426 ( $\pm 0.102$ ) <sup>b</sup>	4.57	0.0122

**Table 4.** Description of consumers at end of study. Total number originally stocked into cages (N) used to determine proportions recovered in their appropriate cages, outside cages (loose in tanks), in other cages, and not recovered at all (assumed mortality). Sex determination was made for all fish recovered at the end of the experiment.

	<i>G. holbrooki</i>	<i>P. latipinna</i>	<i>P. paludosus</i>
N	432	408	564
% Recovered in own cages	80.6	93.9	63.5
% Loose in tanks	0.5	0.0	0.4
% In other cages	3.5	0.2	1.8
% Mortality	15.5	5.9	34.4
% Male	4.1	32.0	---
% Female	95.9	68.0	---