Effects of hydroperiod and nutrient enrichment on spatial patterns of aquatic macroinvertebrate communities in the Everglades

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ABSTRACT

Floating periphyton mats and their associated invertebrate communities are integral parts of the Everglades food web, yet the distribution of this periphyton complex and its response to variation in the physical environment remain poorly described. In this study, we first described the scale of spatial variation in macroinvertebrate communities inhabiting floating mats using a nested sampling design at four sites in northern Shark River Slough, ENP. Based on those results, we then conducted a study to describe correlations in the floating periphyton mat and benthic macroinvertebrate communities with nutrient enrichment and hydroperiod. We sampled ten sites of various hydroperiods over a range of ambient P levels in Shark River Slough and WCA-3A. We found that macroinvertebrate community composition varied with both P enrichment and hydroperiod, and that these effects were different in floating mat and benthic communities. We saw a three-fold increase in the total density of invertebrates in the floating mat with enrichment, and detected a significant interaction between hydroperiod and enrichment. Enriched short-hydroperiod sites had almost six times more invertebrates than unenriched sites with similar hydroperiods and more than twice as many invertebrates as any other enriched site. This dramatic increase in invertebrates at enriched short-hydroperiod sites may be the result of compounding top-down and bottom-up trophic interactions. Understanding this interaction and gaining a deeper understanding of the associated community dynamics will enable researchers to better identify trophic interactions and determine the impact of environmental stressors on this system.

INTRODUCTION

Emergent and submerged macrophytes and algae serve as both structural habitat and food source for invertebrates in wetlands, and often support the highest diversity and abundance of aquatic invertebrates in these systems[1]. The Florida Everglades has an unusually high standing stock of periphyton[1] coupled with a relatively low standing stock of invertebrates and fish[2]. In the southern Everglades thick floating periphyton mats provide habitat for numerous species of aquatic invertebrates, serving as both a refuge from predation and a significant food source[3]. Macroinvertebrate communities also live within the loose, flocculent benthic layer and attached to epiphytic algae growing up through the water column. Very few studies have sought to describe the Everglades invertebrate community, leaving it relatively poorly described[4].

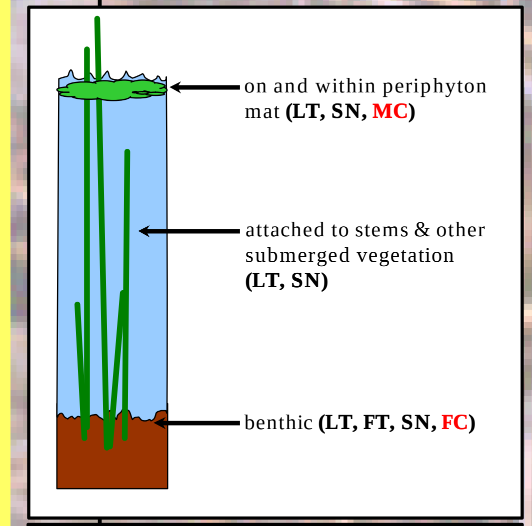

Figure 1. Microhabitats sampled:
- in these studies (quantitative– # / g AFDM substrate): mat core (MC), benthic floc core (FC)
- with other common methods (all CPUE): litter trap (LT), funnel trap (FT), sweep net (SN)

The sampling methods most commonly used in the Everglades may fail to encompass and / or quantify macroinvertebrates separately in all microhabitats that are important to this community (Figure 1). None of these methods specifically target or isolate the periphyton mat complex, whose structural complexity makes it quite difficult to separate invertebrates from the substrate. Furthermore, while several groups have described macroinvertebrate community dynamics across a nutrient gradient, the consistency of these patterns across a range of hydroperiods has not been addressed.

In this study, we characterized the periphyton mat-dwelling macroinvertebrate community by taking cores directly from the mat and removing all macroinvertebrates under a dissecting microscope. Our nested sampling design allowed us to determine the scale and magnitude of variation of this community in both space and time. In a second study, we sampled the mat-dwelling and benthic macroinvertebrate communities at sites of various hydroperiods and levels of P enrichment in two different geographic areas of the southern Everglades.

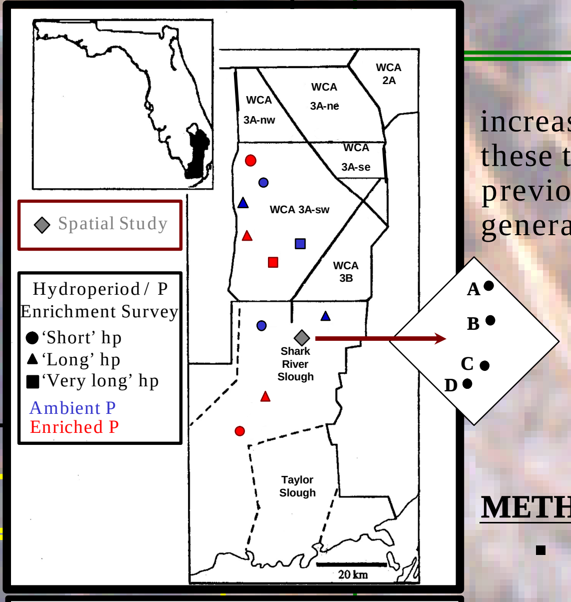

Figure 2. Location of study sites.

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COMMUNITY DESCRIPTION & SPATIAL STUDY:

Understanding the spatial scale of community variation is essential when using any arbitrary sampling unit[5], and becomes increasingly important in communities residing within complex habitat structures and heterogeneous or "patchy" landscapes[6,7]. In this study, we asked the following questions:

1. **At what spatial scale does the macroinvertebrate community within the Everglades periphyton mat vary, and at what magnitude?**
2. **Does the invertebrate community composition change over the course of a season?**

METHODS:

- Established 4 sites (~1 km apart) in northern Shark River Slough, ENP (Figure 2)
  - nested sampling design with 6-cm diameter sampling corer (Figure 3)
  - sampled July (early wet-season) and November (late wet-season) 2000
- Sampled epiphytic algae in the water column if no floating mat was present

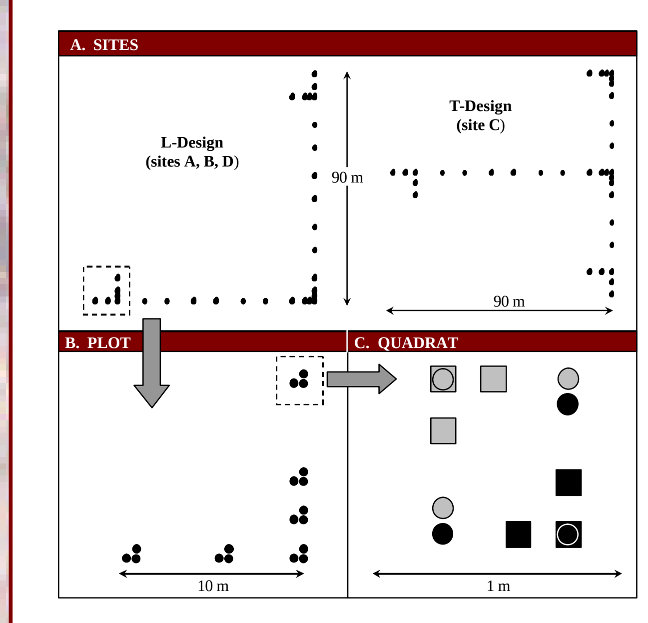

Figure 3. Schematic diagram of nested sampling design. A) Each site was constructed from 5 100-m² plots spaced 10 m apart and arranged in an L- (sites A, B, & D) or T-design (site C). B) End plots were sampled more intensively, repeating the L-design. C) Three samples were taken from each 1 m² quadrat. Plots alternated small-L (squares) and large-L (circles) quadrat designs. Sampling locations were shifted to avoid re-sampling the same locations in July (black symbols) and November (gray symbols).

RESULTS:

Substrate comparison (floating mat v. water column):
- 59.2% higher ash content in floating mat vegetation($F_{1,651}$=70.857, P<0.001)
- Proportion of ash content not different from July to November at any site (P=0.404)
- ANOSIM indicated a difference in community composition (Global R=0.246, P=0.001)
- Densities of several individual taxa varied significantly with substrate (Figure 5)

Floating Mat:
- SITE DIFFERENCES:
  - ANOSIM indicated differences (Global R=0.121, P=0.001)
  - Variations in individual taxa were small and inconsistent
- SEASONAL CHANGES:
  - ANOSIM indicated differences (Global R=0.282, P=0.001)
  - Densities of all taxa increased from Jul to Nov at all sites* (Table 1)
  - Percent mat cover increased from Jul to Nov at all sites except site B (Tukey pairwise: P<0.028, range =21.5-32.7%)
- SPATIAL PATTERNS:
  - Nested ANOVA produced higher coefficients of variation at the smallest spatial scale (quadrat), but even at their greatest only indicated weak effects (Figure 6)
  - Analysis of semivariance revealed no patterns in individual taxa or total density on a scale of 0.2 to 90 m

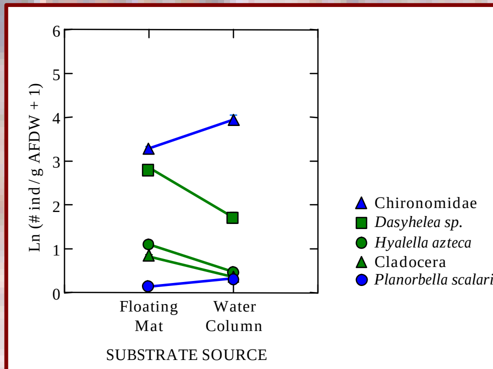

Figure 5. Densities of key taxa in floating mat and water column microhabitats.

	Site			
	A	B	C	D
Amphipods	1.3	1.2*	1.2	2.0
Chironomids	---	---	---	2.4
Cladocerans	---	2.6	6.6	---
Dasyhelea sp.	---	---	---	4.4
Physella bermudezi	15.7	10.0	5.3	6.2
TOTAL	1.5	1.3	1.3	2.7

Table 1. Magnitude of increase from July to Nov of key taxa (*indicates single case where density was higher in July).

		$\overline{X}$ ± SE	N	Site	100-m² Plot (Site)	1-m² Quadrat (Plot(Site))
Amphipoda	Jul	1.329 ±0.228	260	---	---	---
	Nov	9.707 ±0.725	314	---	---	0.292
Bezzia sp.	Jul	0.433 ±0.100	260	---	---	0.330
	Nov	0.954 ±0.190	314	0.056	---	---
Chironomidae	Jul	32.812 ±2.129	260	---	0.229	---
	Nov	39.898 ±1.762	314	---	0.151	---
Cladocera	Jul	1.960 ±0.315	260	0.084	0.231	---
	Nov	5.798 ±0.578	314	---	0.123	---
Coenagrionidae	Jul	0.142 ±0.069	260	---	0.187	---
	Nov	0.482 ±0.088	314	---	0.159	---
Copepoda	Jul	0.125 ±0.038	244	0.025	---	---
	Nov	0.843 ±0.176	314	0.076	---	---
Dasyhelea sp.	Jul	20.239 ±1.201	260	0.055	---	---
	Nov	30.372 ±1.161	314	---	---	---
Diptera (pupa)	Jul	0.905 ±0.147	260	---	0.146	---
	Nov	0.947 ±0.160	314	---	---	---
Nematoda	Jul	19.030 ±1.408	244	---	0.151	---
	Nov	22.670 ±1.200	314	---	0.147	---
Ostracoda	Jul	0.545 ±0.154	244	---	---	---
	Nov	0.444 ±0.089	314	0.027	---	---
Pelecoris femoratus	Jul	0.161 ±0.045	260	---	0.140	---
	Nov	0.316 ±0.068	314	---	---	---
Physella bermudezi	Jul	0.767 ±0.145	260	---	---	---
	Nov	5.707 ±0.426	314	0.075	---	0.340
Total	Jul	78.609 ±3.210	260	---	0.155	---
	Nov	119.588 ±2.987	314	---	0.158	---

Figure 6. Mean density ($\overline{X}$), standard error (SE), N, and R^2 values for nested ANOVA of common taxa at three spatial scales (only P<0.05 shown).

COMMUNITY VARIATION WITH HYDROPERIOD & P ENRICHMENT

Previous studies in the Everglades have reported an increase in macroinvertebrate densities with both increased hydroperiod and enrichment, but no studies have examined community response to the interaction of these two physical factors. Understanding this relationship can have significant implications since most previous research on community response to P enrichment has been done in long hydroperiod marshes and generalized to include short hydroperiod marshes. In this study, we asked the following questions:

1. **How do floating periphyton mat and benthic floc macroinvertebrate communities differ?**
2. **What effects do hydroperiod and nutrient (P) enrichment have on these communities?**
3. **How do these macroinvertebrate communities respond to the interaction of these physical factors?**

METHODS:

- 10 sites in factorial design (Figure 2)
  - Hydroperiod (dsldd): 'short': 175-190; 'long': 510-550; 'very long': > 4000
  - Phosphorus (floc+soil TP): 'Ambient': 75-240 µg / g; 'Enriched': 350-600 µg / g
- 15 periphyton & 15 benthic floc cores (Figure 7) taken at each 10m x 10m site (December 2002)
- Soil, floc, & periphyton sampled at each site for TP analysis

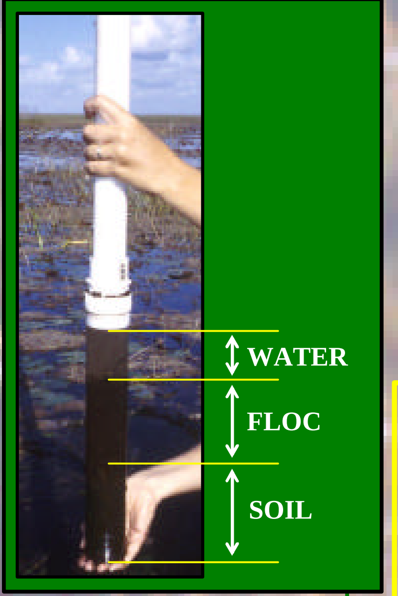

Figure 7. Benthic coring device.

RESULTS:

Substrate comparison (floating mat v. benthic floc):
- Total density of inverts (# / g AFDW): **6.7x** greater in mat (x_M=76.6, x_F=11.5; P<0.001)
- Average number of taxa / sample: **1.6x** greater in mat (x_M=6.3, x_F=3.9; P<0.001)
- Species richness: greater in mat (Figure 7)

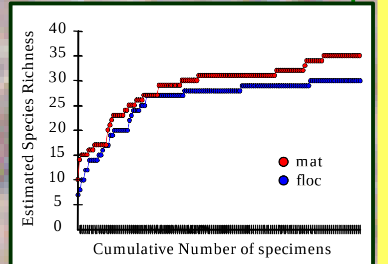

Figure 7. Species accumulation curve for floating mat and floc communities.

Community-level analysis:
- Measured community structure with Bray-Curtis dissimilarity matrix & tested for correlations using a Mantel analysis (Table 2):

		Floating Mat	Benthic Floc
Number of taxa		26	19
Hydroperiod (dsldd)	P	0.400	**0.006**
	R^2	0.010	**0.415**
Nutrient level (TP)	P	**0.001**	0.508
	R^2	**0.559**	0.003

Table 2. Correlations between microhabitat communities and key environmental variables.

Floating Mat (Figure 8):
- Increases in density w / increased P observed in 9 of 26 taxa (R^2: 0.456-0.816)
- No decreases w / enrichment in any taxa
- No significant correlations seen with hp

Benthic floc (Figure 9):
- Decreases in density w / increased hp observed in 8 of 19 taxa (R^2: 0.427-0.710)
- No increases w / hydroperiod in any taxa
- No significant correlations seen w / P enrichment

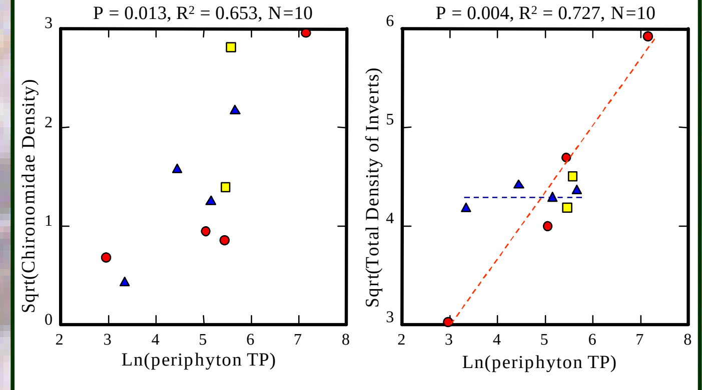

Figure 8. Mat: Relationship between invertebrate densities and TP (hydroperiod: short= ●, long= ▲, very long= ■).

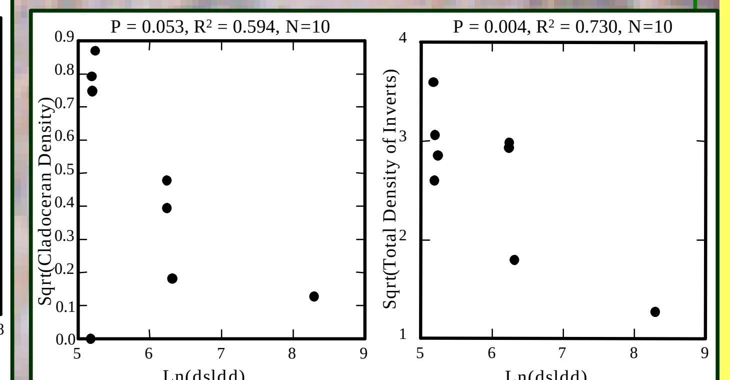

Figure 9. Floc: Relationship between invertebrate densities and hp.

CONCLUSIONS

- ❖ The floating periphyton mat contains a distinct macroinvertebrate community with higher densities of most taxa than found in the water column or in the benthic floc. The floating periphyton mat develops throughout the wet season and has a higher ash content than adjacent communities which may indicate a greater degree of habitat structure.
- ❖ The greatest spatial variation is found at the scale of the 1 m² quadrat, but it is only significant for a few taxa (season does not appear to play a role in these patterns).
- ❖ The floating mat community responds primarily to available nutrients (+ correlation), while the benthic floc community responds primarily to hydroperiod (– correlation). Since the mat regenerates each year, it may be less susceptible to longer-term physical factors (such as dry-downs) and more dependent upon contemporary water quality factors, while frequent dry-downs and the resulting localized nutrient pulse may lead to increased food quality and availability in the benthic floc.
- ❖ High macroinvertebrate densities in enriched short-hydroperiod sites suggest both top-down and bottom-up trophic effects.

IMPLICATIONS:

- ✓ While all sampling techniques have limitations, the macroinvertebrate community within the periphyton mat is well-sampled with our mat cores when focused within 100 m² plots.
- ✓ Failure to incorporate the floating mat community in sampling regimes may under-estimate the macroinvertebrate standing stock
- ✓ Caution should be used when generalizing results from enrichment studies in long hydroperiod marshes

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