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Interactions between nutrient availability and hydroperiod shape macroinvertebrate communities in Florida Everglades marshes

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Abstract

Hydroperiod and nutrient status are known to influence aquatic communities in wetlands, but their joint effects are not well explored. I sampled floating periphyton mat and flocculent detritus (floc) infaunal communities using 6-cm diameter cores at short- and long-hydroperiod and constantly inundated sites across a range of phosphorus (P) availability (total phosphorus in soil, floc and periphyton). Differences in community structure between periphyton and floc microhabitats were greater than any variation attributable to hydroperiod, P availability, or other spatial factors. Multivariate analyses indicated community structure of benthic-floc infauna was driven by hydroperiod, although crowding (no. g^{-1} AFDM) of individual taxa showed no consistent responses to hydroperiod or P availability. In contrast, community structure of periphyton mat infauna was driven by P availability, while densities of mat infauna (no. m^{-2}) were most influenced by hydroperiod (+correlations). Crowding of mat infauna increased significantly with P availability in short-hydroperiod marshes, but was constant across the P gradient in long-hydroperiod marshes. Increased abundance of floating-periphyton mat infauna with P availability at short-hydroperiod sites may result from a release from predation by small fish. Community structure and density were not different between long-hydroperiod and constantly inundated sites. These results have implications for the use of macroinvertebrates as indicators of water quality in wetlands and suggest the substrate sampled can influence interpretation of ecological responses observed in these communities.

Introduction

Aquatic invertebrates are an important component of wetland ecosystems through their role in energy flow (Teal, 1962), often serving as the primary food source for waterfowl (Lillie & Evrard, 1994; Frederick & Ogden, 2001; Gammonley & Laubhan, 2002), fish (Romaire & Kilgen, 1977; Jude & Pappas, 1992) and shellfish (Chabreck, 1981; Huner, 2002). Hydrology is a dynamic driving force in wetlands, with duration of flooding and habitat permanence in these systems influencing macroinvertebrate community dynamics. However, the response of macroinvertebrate communities to other environmental factors in marshes with different flooding regimes has not been well documented.

Hydrology plays a critical role in aquatic invertebrate community composition and diversity, especially in temporary and hydrologically dynamic environments (Wellborn et al., 1996). The majority of studies in river floodplains, intermittent streams, and seasonal ponds have reported increases in macroinvertebrate density, diversity, and/or richness with increased habitat permanence or stability (e.g., Gladden & Smock, 1990; Feminella, 1996; Shivoga, 2001, but see Corti et al., 1997). Results of studies in wetland ecosystems have been inconsistent regarding community response to dynamic hydrologic conditions. Invertebrate biomass, production, density, and diversity are reported to increase with increased flood duration in many wetland systems (e.g., Murkin & Kadlec, 1986; Loftus et al., 1990; Leeper & Taylor, 1998; Wissinger et al., 1999), while other studies have observed decreases (e.g., Neckles et al., 1990; Golladay et al., 1997).

Results from studies documenting effects of nutrient enrichment on macroinvertebrate communities have been similarly inconsistent. While some studies have indicated a decrease in macroinvertebrate production or diversity with enrichment (Miltner & Rankin, 1998), others have noted an increase (Rader & Richardson, 1994), contrasting taxon-specific trends (McCormick et al., 2004), or no change (Haack, 1984; Turner et al., 1999). The latter pattern is generally attributed to a trophic cascade, where increased productivity is consumed by higher trophic levels. Furthermore, none of these studies have simultaneously examined the effects of multiple environmental gradients.

The Florida Everglades is a highly oligotrophic freshwater wetland, historically fed from rainfall and overland sheet flow from Lake Okeechobee (Davis, 1994). Everglades marshes currently range from limestone rocklands that are dry the majority of the year to deep, open sloughs that only dry during drought events. Background levels of phosphorus also vary considerably, both naturally and as a result of anthropogenic sources (Childers et al., 2002). Extensive periphyton mats are a unique feature of the system, contributing >50% of the primary producer standing stock (E. Gaiser, Florida International University, personal communication). These mats provide habitat for an abundant macroinvertebrate community (Liston & Trexler, 2005), and provide refuge for many taxa from fish predation (Smith, 2004) and during periods of desiccation (Gottlieb, 2003). Experimental studies have shown that low levels of eutrophication increase periphyton biomass (Davis, 1994; McCormick & Stevenson, 1998), while higher levels lead to disappearance of the calcareous periphyton mat (McCormick et al., 2002; Gaiser et al., 2005a, b). Submerged epiphyton (from which floating mats develop) and benthic floc are also important microhabitats for Everglades macroinvertebrates (Smith, 2004).

In this paper I describe aquatic macroinvertebrate communities along gradients of both hydroperiod (measured as days since each study site last dried (DSD)) and phosphorus (P) availability (measured as total phosphorus (TP) of soil, flocculent detritus (floc), and periphyton) in the Florida Everglades. Sites included in this study either dry annually, once every few years, or are constantly inundated and span the full range of natural TP levels seen in the southern portion of the system. Study sites were located in Shark River Slough, Everglades National Park (ENP) and Water Conservation Area 3A (WCA-3A), geographic regions that have been isolated by levees and canals as a result of the compartmentalization of the system by water management practices and urbanization (Fig. 1). Macroinvertebrate communities in both floating periphyton mats and benthic floc were sampled to describe variation in macroinvertebrate communities in these microhabitats across P and hydroperiod gradients. Macroinvertebrates in submerged epiphyton were not sampled in this study, as they are relatively similar to floating mat communities and are difficult to quantify (Smith, 2004). I have focused on macroinvertebrate community structure, abundance, and proportions of functional feeding groups (FFGs) and have made comparisons between these patterns and those observed in other trophic levels. I conclude by suggesting a conceptual model that incorporates periphyton, infaunal macroinvertebrate, and fish variation with productivity and hydroperiod, and can be used as a basis for planning future research.

Methods

Site selection

Sampling sites for this study were selected adjacent to current long-term monitoring sites (07, 23, 50,

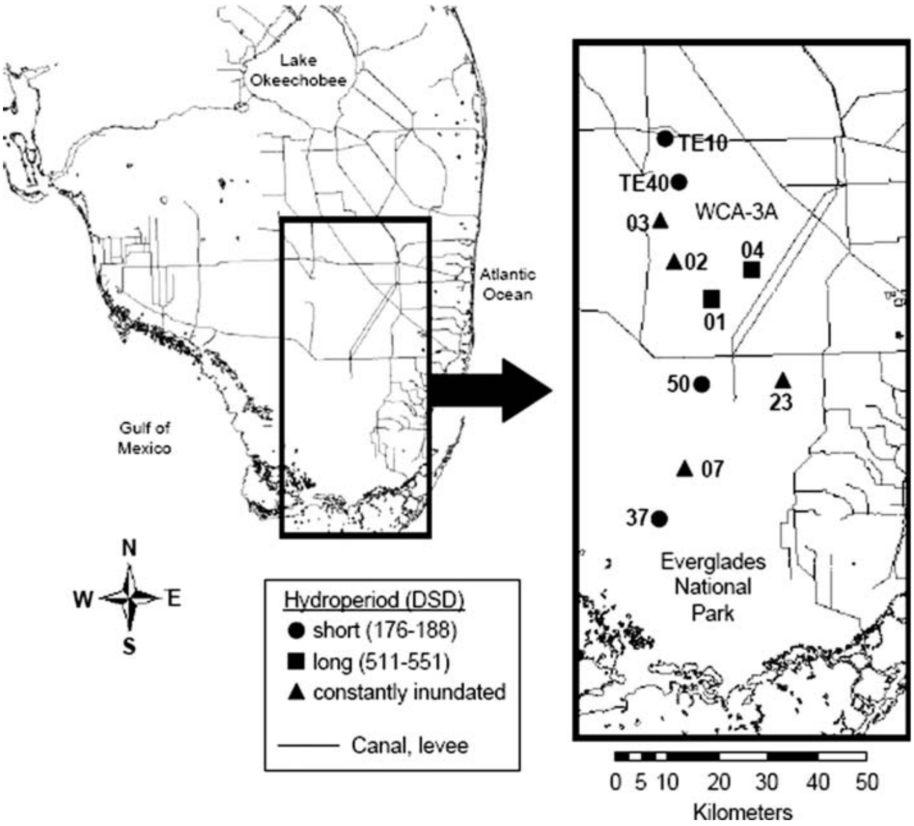

Figure 1. Map of south Florida with location of study sites in Water Conservation Area 3A (WCA-3A) and Everglades National Park (ENP).

37, 01, 02, 03, 04) in ENP and WCA-3A, where macrophytes, macroinvertebrates and fish are sampled periodically throughout the year. Two additional sites were selected (TE10 and TE40), as no short-hydroperiod long-term monitoring sites were available in WCA-3A. Nutrient data (combined floc and soil TP) collected in 1998 (J.C. Trexler, Florida International University, unpublished data) were used to select sites spanning a wide range of P availability. Hydroperiod was characterized by the number of DSD, calculated from predicted daily water depths at each site (see Ruetz et al., 2005). ‘Dry’ was defined when daily water depth was ≤ 5 cm. DSD correlates directly with hydroperiod in this system (Ruetz et al., 2005). Three hydroperiods were identified for this study (short: 176–188 DSD; long: 511–551 DSD; constantly inundated: >4000 DSD), although constantly inundated sites were only present in WCA-3A (Fig. 1).

Field sampling and sample processing

Macroinvertebrate infauna were sampled in December 2002 with 15 floating-periphyton-mat cores and 15 benthic-floc cores within a 100-m^2 plot. Periphyton samples were taken from the floating mat with a 6-cm diameter coring device, ensuring complete surface coverage. Floc samples were obtained by taking a 6-cm diameter core through the water column into the benthos. All water was removed, and flocculent benthic material was collected. Triplicate periphyton, floc, and soil samples were also collected at each site for nutrient analysis (Childers et al., 2002).

Samples collected for nutrient analyses were processed by first pooling triplicate samples from each site. Composite samples were thawed and large macrophyte stems and leaves were manually removed. All samples were dried at 70–80 °C for ≥48 h, crushed to a fine powder, and analyzed for

TP using standard procedures (Fourqurean et al., 1992). Periphyton and floc cores were stained with rose Bengal and macroinvertebrates ≥1 mm were removed under a dissecting microscope. Periphyton and floc were then dried at 80 °C for ≥48 h and incinerated at 500 °C for 3 h to obtain ash-free dry mass (AFDM) of substrates. Samples were frozen in the field rather than chemically preserved, but freezing and thawing greatly reduced the integrity of oligochaetes (rendering them impossible to quantify) so this group was excluded from analyses. This problem was not observed with any other taxa. Chironomids were initially identified to the family level, but were later re-sorted and classified as Tanypodinae or Chironomidae (Chironominae and Orthocladinae) to discriminate between FFGs. Analyses of floating-periphyton-mat and benthic-floc infauna were performed on both density and proportions (%) of FFGs. Macroinvertebrate taxa were assigned to FFGs based on Merritt et al. (1996). Additionally, estimates of infaunal density m^{-2} ((no. sample^{-1}) × (surface area of core (0.002826 m^2))$^{-1}$ × estimated proportion of mat cover m^{-2}) were made to account for periphyton mat patchiness and incorporate larger-scale patterns. To distinguish between mat infaunal density estimates on these two scales, density of infauna within core samples (no. g^{-1} AFDM) is referred to as 'infaunal crowding'. This patch-scale density of macroinvertebrates is similar to the concept of mean crowding described by Lloyd (1967), and can be thought of as the infaunal density as perceived by individuals within the mat (also see Pielou, 1974). Estimates of infaunal density that incorporate proportion of mat cover (est. no. m^{-2}) express site-scale density of infauna and are referred to as 'infaunal density'. Estimates of % mat cover were not available for sites TE10 and TE40, so these sites were excluded from analyses of infaunal density. Although substrate patchiness was not an issue in floc samples (floc coverage was uniform), density of floc infauna g^{-1} AFDM is referred to as crowding for consistency. Analyses were also conducted on counts of infauna in each core sample ('surface area density' as described by Liston & Trexler (2005)). These analyses yielded patterns similar to those seen in infaunal crowding and are not presented in this paper.

Macrophyte and fish community densities, relative contributions of periphyton and *Utricularia* spp. to total loose vegetation volume (% periphyton, % *Utricularia*), percent periphyton mat cover, and average macrophyte stem height (height above water level) were collected to further characterize sites using 1-m^2 throw traps with 2 mm mesh (Jordan et al., 1997). Data were collected in December 2002 at sites 01, 02, 03, 04, 07, 23, 37, and 50 ('monitoring sites') and March 2003 at sites TE10 and TE40. Seven throw-trap samples were collected at each ENP site and five samples were collected at each WCA-3A site.

Data analysis

A combination of multivariate and univariate techniques was applied to detect variation in community structure (relative abundance) and density with P availability and hydroperiod in this study. Analyses of similarities (ANOSIM) on standardized Bray–Curtis dissimilarity matrices were used for analyses of community structure (Clarke, 1993; Clarke & Warwick, 1994). When significant variation was observed, analyses were followed by similarity percentage breakdowns (SIMPER) to determine which taxa were most influential in community variation. Univariate analyses (analysis of variance (ANOVA) or analysis of covariance (ANCOVA)) were used to compare variation in densities of individual taxa and total density. Additionally, non-metric multidimensional scaling (nMDS) was used to visualize the Bray–Curtis dissimilarity matrix and illustrate latent patterns in community structure.

Two preliminary analyses were performed to determine if large-scale temporal and spatial factors should be incorporated in statistical models. ANOSIM and ANOVA were used to describe inter-season (December 2002 to February 2003) variation in relative composition of floating vegetation (% periphyton and % *Utricularia*) and structure and density of emergent macrophyte and fish communities at monitoring sites. This analysis was used to determine whether throw-trap data collected in March 2003 at sites TE10 and TE40 were comparable to those collected in December 2002 at monitoring sites. Comparisons (ANOSIM and ANOVA) of mat and floc infauna, macrophytes, and fish communities across water management regions (ENP and WCA-3A) were also made to determine whether region was an important spatial factor.

Multivariate and univariate analyses were performed to correlate emergent/floating macrophyte, floating mat infaunal, benthic infaunal, and fish communities with environmental variables. Principal component analysis (PCA, varimax rotation) was used to reduce TP data (soil, floc and periphyton). To determine which environmental factors (TP factor(s), DSD) best explain patterns in community structure, Spearman rank correlations were used to compare standardized Bray–Curtis dissimilarity matrices of community data to environmental data matrices (BIOENV). Backward stepwise ANCOVAs (terms removed when $p > 0.15$) were then performed on densities of individual taxa and % FFGs to detect patterns across hydroperiods and P levels. Fish biomass (wet weight) was estimated from standard lengths using regressions developed by Kushlan et al. (1986) and W.F. Loftus (U.S. Geological Survey, unpublished data). ANCOVAs were also performed on total fish biomass and total non-herbivorous fish biomass. Herbivorous fish species were identified as *Jordanella floridae* Goode & Bean (flagfish) and *Poecilia latipinna* (Lesueur) (sailfin molly), as described in Loftus & Kushlan (1987).

Water depths, floc depths, average stem heights, and densities (no. emergent stems m^{-2}, no. invertebrates g^{-1} AFDM, estimated no. mat infauna m^{-2}, no. fish m^{-2}) were $\ln(y+1)$ transformed and proportions (% mat cover, % periphyton, % *Utricularia*, % FFGs) were arcsine $y^{0.5}$ in order to fulfill assumptions of normality. Analyses were only conducted on common macrophyte, infauna and fish taxa (present in ≥10% of samples). Hydroperiod was quantified as DSD for BIOENV analyses, but DSD data were collapsed into categories (short: 176–188 DSD; long: 511–551 DSLDD; constantly inundated: >4000 DSD) in all other cases to simplify analyses and more accurately characterize interactions. All statements of ‘no statistical significance’ imply $p > 0.05$.

Results

The 10 sites in this study spanned the full range of hydroperiods and exceeded the range of TP levels seen in wet-prairie sloughs unaffected by anthropogenic nutrient enrichment (Table 1). PCA reduced soil, floc and periphyton TP to a single factor (‘P availability’; 83.3% of variance explained). Short- and long-hydroperiod sites were well distributed across the range of P availability (factor scores). Short-hydroperiod sites spanned 75% of the total P range and long-hydroperiod sites spanned 67% of this range. The two constantly inundated sites spanned only a narrow

Table 1. Location and description of study sites in Everglades National Park (ENP) and Water Conservation Area 3A (WCA-3A). Days since dry (DSD) was estimated from estimated daily water depths (‘dry’ defined as depth ≤5 cm). Triplicate soil, floc, and periphyton samples were taken at each site in November 2002 and pooled for total phosphorus (TP) analysis

Region	Site	Latitude (N)	Longitude (W)	DSD	Hydroperiod	Total Phosphorus (μg g^{-1})		
						Soil	Floc	Periphyton
ENP	50	25° 41′ 11″	80° 45′ 41″	179	Short	272.3	174.8	18.2
ENP	37	25° 28′ 09″	80° 50′ 59″	188	Short	483.0	728.0	230.0
ENP	23	25° 40′ 35″	80° 36′ 56″	511	Long	88.1	130.5	27.3
ENP	07	25° 33′ 11″	80° 47′ 00″	512	Long	296.6	494.6	84.1
WCA-3A	TE40	26° 02′ 26″	80° 47′ 40″	180	Short	355.5	388.7	154.6
WCA-3A	TE10	26° 04′ 44″	80° 49′ 20″	176	Short	369.3	1264.2	1278.4
WCA-3A	02	25° 54′ 22″	80° 47′ 28″	551	Long	274.2	393.3	287.1
WCA-3A	03	25° 59′ 45″	80° 50′ 02″	511	Long	397.2	457.3	172.6
WCA-3A	01	25° 51′ 35″	80° 43′ 26″	>4000	Constantly inundated	328.9	485.2	262.1
WCA-3A	04	25° 53′ 52″	80° 39′ 23″	>4000	Constantly inundated	255.1	500.3	234.7

range of P (6%), however, which prevented generalizations about the effect of P availability at these sites. Univariate comparisons of constantly inundated sites (sites 01 and 04) and long-hydroperiod sites with similar P levels (sites 02 and 03) revealed no significant variation in infaunal crowding or density, macrophyte density, or fish density or biomass.

Preliminary analyses

Multivariate (ANOSIM) and univariate (ANOVA) tests revealed no significant inter-season variation in relative composition of floating vegetation (% periphyton or % *Utricularia*), or structure of emergent macrophyte or fish communities. Consequently, a combination of December 2002 (monitoring sites) and March 2003 (TE10 and TE40) data were used for further analyses of vegetation and fish communities.

No variation was observed among water management regions in water depth, % *Utricularia*, % periphyton, or emergent stem height. ANOSIM indicated no significant inter-regional differences in emergent macrophyte community structure (p = 0.086), although data suggest inter-regional patterns may be evident with more replication. ANOVA of common macrophyte taxa only detected significant regional variation in density of *Nymphaea odorata* Ait. (fragrant water-lily), which was found only in WCA-3A ($F_{1,6}$ = 11.647, p = 0.014). Floating mat and floc infaunal community structures did not vary significantly between regions. Univariate tests failed to detect regional patterns in crowding, densities or % FFGs of individual floating-mat or benthic-floc infauna. Fish community structure showed no regional variation, and the only taxon with significant regional variation was *Heterandria formosa* Agassiz (least killifish) whose density was 5.2× higher in WCA-3A than ENP ($F_{1,6}$ = 6.401, p = 0.045). Since inter-regional variation was minimal, water management region was not considered in subsequent analyses.

Comparison of microhabitat communities

Floating-periphyton-mat and benthic-floc samples contained 36 aquatic invertebrate taxa. Seven individuals (three larval fish, three adult dipterans, and one terrestrial gastropod) were removed from the substrate, but were not included in analyses. Multivariate analysis of infauna indicated a significant difference between floating-periphyton-mat and benthic-floc microhabitat

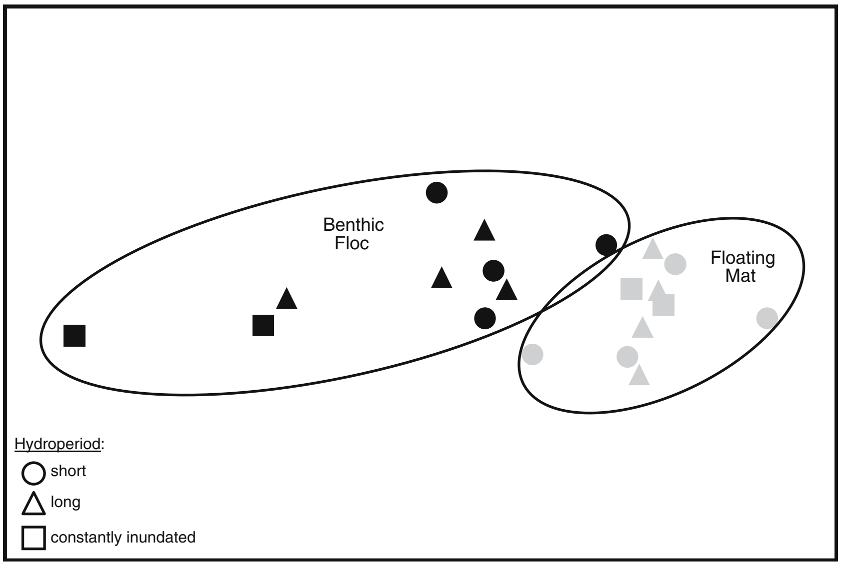

Figure 2. NMDS of floating-periphyton-mat and benthic-floc infauna (from standardized Bray–Curtis dissimilarity matrix; stress = 0.06). Samples were collected using 6-cm diameter cores in December 2002.

communities (Global $R = 0.552$, $p = 0.001$, Fig. 2). The five taxa with greatest dissimilarities (*Dasyhelea* spp., Tanypodinae, *Hyalella azteca* (Saussure), Nematoda, and Chironomidae) accounted for 53% of variation. Crowding of 10 of 13 common taxa varied significantly among microhabitats ($p \leq 0.05$) with crowding of nine taxa higher in floating mat and one taxon higher in benthic floc. Total invertebrate crowding was 2.9× higher in floating periphyton ($F_{1,18} = 17.60$, $p = 0.001$; Fig. 3) than in floc. Average percent filtering-collectors (% F-COLL) was higher in floc samples ($F_{1,18} = 30.75$, $p < 0.001$), while percent predators (% PRED) was higher in floating mat ($F_{1,18} = 4.08$, $p = 0.059$). I observed no microhabitat differences in percent gathering-collectors (% G-COLL), scrapers (% SC), coarse particulate organic matter detritus shredders (% SH-CPOM), or vascular plant shredders (% SH-VP).

Floating periphyton mat infaunal community variation

BIOENV indicated variation in floating-mat macroinvertebrate crowding and % FFGs were best explained by P availability (crowding: $\rho = 0.332$; FFG: $\rho = 0.170$), while variation in floating-mat infaunal density was best explained by both P availability and hydroperiod ($\rho = 0.238$). ANCOVAs of common macroinvertebrate taxa revealed significant P availability × hydroperiod interactions in crowding of *Physella* spp., *Planorbella* spp., copepods, *H. azteca*, ephemeropterans, total invertebrates, and in % SC (Table 2a; Fig. 4a). Correlations were generally positive, with P availability slopes significantly higher at short-hydroperiod sites than long-hydroperiod sites, where slopes were often not different from zero (Table 3). *H. azteca*, chironomids, and total infaunal crowding increased with P availability, while cladoceran crowding and % F-COLL decreased with P availability. Densities of *Bezzia* spp., chironomids, tipulids, and total infaunal density were higher at long-hydroperiod sites than short-hydroperiod ones (Table 2b; Fig. 4b). Chironomids were the only taxon whose density varied significantly with P availability (+ correlation), and I observed no P availability × hydroperiod interactions.

Benthic floc infaunal community variation

BIOENV indicated variation in benthic-floc macroinvertebrate crowding and % FFGs were best explained by hydroperiod (density: $\rho = 0.490$; FFG: $\rho = 0.054$). ANCOVA revealed several significant trends, but no consistent patterns were

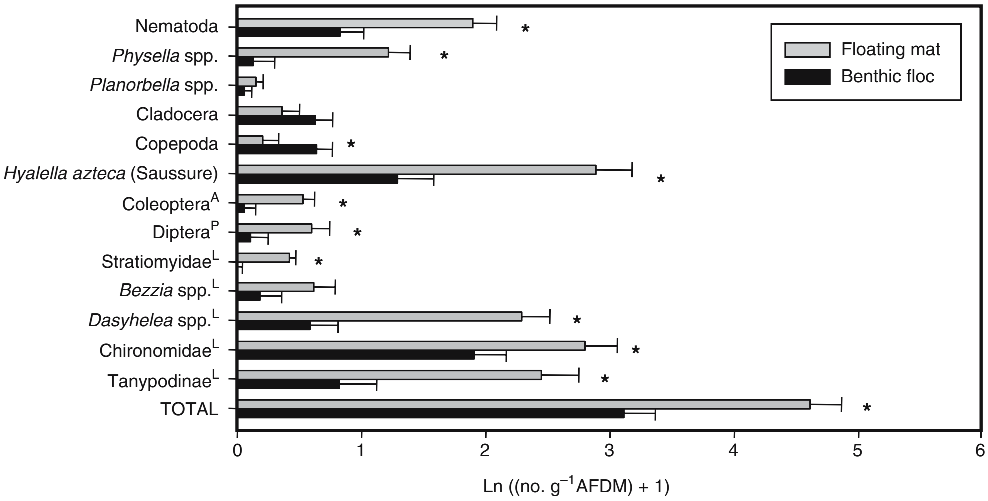

Figure 3. Average crowding (no. g^{-1} AFDM) of most frequently encountered macroinvertebrate taxa in floating-mat and benthic-floc samples. Error bars represent 1 SE. Significant microhabitat differences ($p \leq 0.05$) are indicated with asterisks. Superscripts on insect taxa indicate adult (A), larval (L), or pupal (P) life stages. 'Chironomidae' excludes Tanypodinae.

Table 2. Summary of backward stepwise ANCOVA of (a) floating mat infaunal crowding (no. g^{-1} AFDM periphyton), (b) estimated floating mat infaunal density (no. m^{-2}), (c) benthic infaunal crowding (no. g^{-1} AFDM floc), (d) macrophyte density (no. m^{-2}), and (e) fish density (no. m^{-2}). Only taxa/FFGs with significant correlations are shown (% F-COLL = proportion of filterer-collectors, % G-COLL = proportion of gatherer-collectors, % SC = proportion of scrapers). Constantly inundated sites were excluded from these analyses due to their small P availability range. Superscripts indicate larval (L) and pupal (P) insect stages

	P availability			Hydroperiod			P availability × Hydroperiod		
	F	*p*		F	*p*		F	*p*	R^2
(a) Floating mat infaunal crowding									
Physellla spp.							$F_{1,6} = 13.14$	**0.011**	0.686
Planorbella spp.	$F_{1,5} = 4.94$	0.077					$F_{1,5} = 6.39$	**0.053**	0.696
Cladocera	$F_{1,6} = 6.42$	**0.044**	(–)						0.517
Copepoda				$F_{1,5} = 3.23$	0.132		$F_{1,5} = 14.86$	**0.012**	0.776
Hyalella azteca (Saussure)	$F_{1,5} = 9.46$	**0.028**	(+)				$F_{1,5} = 20.27$	**0.006**	0.857
Ephemeroptera^{L}							$F_{1,6} = 11.14$	**0.016**	0.650
Chironomidae^{L*}	$F_{1,6} = 16.75$	**0.006**	(+)						0.736
Total	$F_{1,5} = 33.07$	**0.002**	(+)				$F_{1,5} = 18.71$	**0.008**	0.913
% F-COLL	$F_{1,6} = 6.10$	**0.048**	(–)						0.504
% SC							$F_{1,6} = 7.81$	**0.031**	0.565
(b) Floating mat infaunal density									
Bezzia spp.^{L}	$F_{1,2} = 9.01$	0.095		$F_{1,2} = 42.71$	**0.023**	(+)	$F_{1,2} = 0.05$	0.844	0.963
Chironomidae^{L}*	$F_{1,2} = 278.17$	**0.004**	(+)	$F_{1,2} = 639.02$	**0.002**	(+)	$F_{1,2} = 2.32$	0.267	0.998
Tipulidae^{L}	$F_{1,2} = 0.616$	0.515		$F_{1,2} = 379.65$	**0.003**	(+)	$F_{1,2} = 0.616$	0.515	0.995
Total	$F_{1,2} = 8.48$	0.100		$F_{1,2} = 35.53$	**0.027**	(+)	$F_{1,2} = 5.22$	0.150	0.964
(c) Benthic floc infaunal crowding									
Planorbella spp.							$F_{1,6} = 11.07$	**0.016**	0.649
Cladocera	$F_{1,5} = 9.43$	**0.028**	(–)	$F_{1,5} = 4.57$	0.086				0.682
Copepoda				$F_{1,5} = 4.03$	0.101		$F_{1,5} = 6.36$	**0.053**	0.662
Ostracoda	$F_{1,5} = 4.13$	0.098					$F_{1,5} = 10.52$	**0.023**	0.744
Trichoptera^{L}	$F_{1,5} = 7.07$	**0.045**	(–)				$F_{1,5} = 3.27$	0.131	0.672
Diptera^{P}				$F_{1,6} = 6.45$	**0.044**	(+)			0.518
% G-COLL				$F_{1,6} = 6.36$	**0.045**	(+)			0.515
(d) Macrophyte density									
Leersia hexandra Swartz	$F_{1,5} = 7.07$	**0.045**	(+)				$F_{1,5} = 3.72$	0.112	0.686
Total stems	$F_{1,5} = 15.49$	**0.011**	(+)	$F_{1,5} = 3.41$	0.124				0.759
(e) Fish density									
Fundulus chrysotus (Günther)	$F_{1,5} = 8.40$	**0.034**	(+)	$F_{1,5} = 4.33$	0.092				0.660

*Excludes Tanypodinae.

seen among taxa. Significant P availability × hydroperiod interactions were seen in 3 of 12 common taxa (*Planorbella* spp., copepods, ostracods; Tables 2c, 3b). Cladoceran and trichopteran crowding were negatively correlated with P availability. Crowding of dipteran pupae and % G-COLL was higher at long-hydroperiod sites than short-hydroperiod sites. Total floc infaunal crowding was not correlated with P availability or hydroperiod (Fig. 4c).

Macrophyte and fish community variation

Variation in habitat (water depth and vegetation) with P availability and hydroperiod was minimal. ANCOVAs indicated water depth was positively correlated with hydroperiod ($F_{1,4} = 9.04$, $p = 0.040$) and % periphyton was negatively correlated with P availability ($F_{1,4} = 8.95$, $p = 0.040$). Proportion floating mat cover was 8.3× higher at long-hydroperiod sites than short-hydroperiod sites

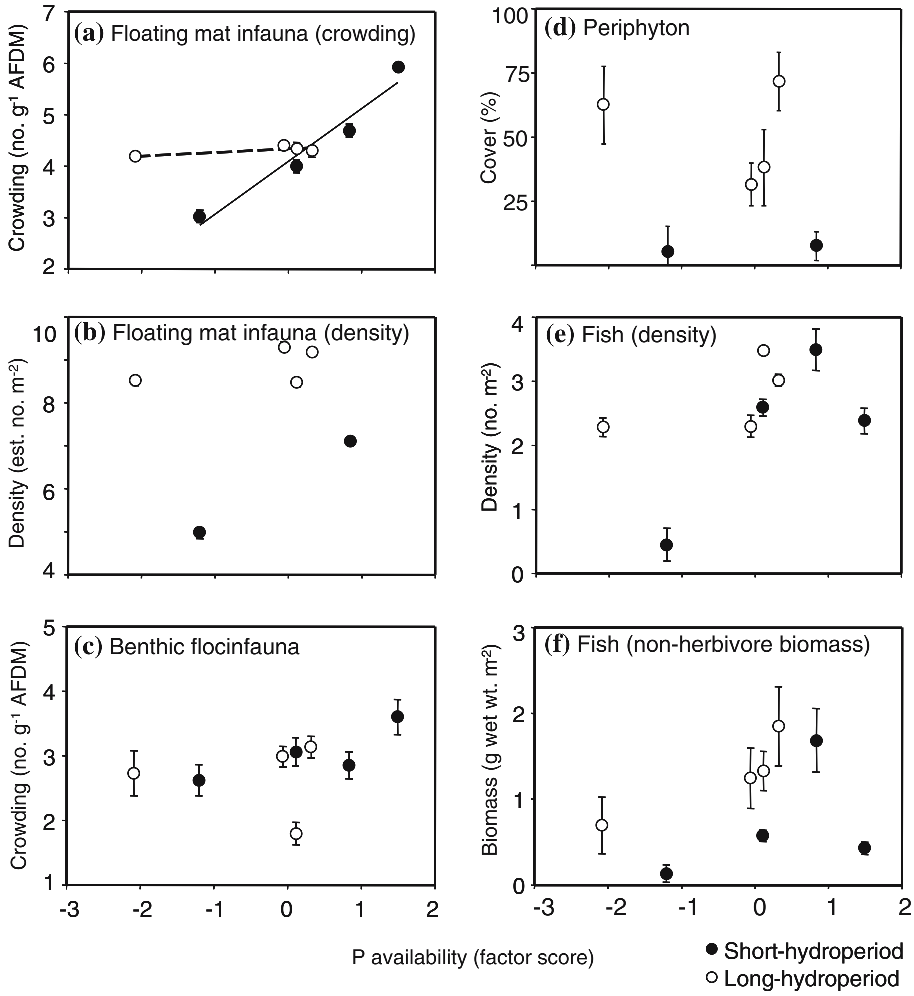

Figure 4. Linear regressions of consumer crowding, density, and biomass across a P gradient (factor scores combine periphyton, floc and soil TP) at short- and long-hydroperiod sites. Macroinvertebrate infauna were sampled with 6-cm diameter cores and fish were sampled with 1-m^2 throw traps. Periphyton cover was estimated within 1-m^2 quadrats (no estimates were available for TE10 and TE40). Error bars represent 1 SE (error bars are shown for all points, but may not be evident where confidence intervals are smaller than symbols). *Y*-axes are $\ln(y+1)$ transformed, except periphyton cover (d) which is untransformed.

($F_{1,4} = 13.41$, $p = 0.022$), but no significant variation was seen with P availability (Fig. 4d). Percent *Utricularia*, average emergent stem height, and floc depth were not correlated with P availability or hydroperiod. Nineteen species of emergent/floating macrophytes were encountered in throw traps at the 10 sites. BIOENV indicated macrophyte community structure was best explained by hydroperiod ($\rho = 0.177$). ANCOVA indicated *Leersia hexandra* Swartz (southern cut grass) and total stem density were positively correlated with P availability (Table 2d).

Nineteen macroinvertebrate taxa and 20 fish species were collected in throw-trap samples Densities (no. m^{-2}) of the four most abundant large macroinvertebrates (*Procambarus* spp., *Palaemonetes paludosus* (Gibbes), anisopteran naiads, and *Pelocoris femoratus* (Palisot de Beauvois)) were not significantly correlated with P availability or hydroperiod. BIOENV indicated fish community variation was driven primarily by P availability ($\rho = 0.339$). ANCOVA of the nine common species revealed no significant P availability × hydroperiod interactions, although *Fundulus chrysotus*

Table 3. Slopes (β (± SE)) from regressions of taxon crowding (no. g^{-1} AFDM substrate) with P availability at short- and long-hydroperiod sites. Only taxa/FFGs with significant P availability × hydroperiod interactions (see Table 2) are shown (% SC = proportion of scrapers). Constantly inundated sites were excluded from analyses due to their small P range. All insects listed are larvae

	Short-hydroperiod β (± SE)	Long-hydroperiod β (± SE)
(a) Floating mat infaunal crowding		
Physellla spp.	0.775 (0.257)	−0.450 (0.278)
Planorbella spp.	0.264 (0.098)	−0.050 (0.075)
Copepoda	0.271 (0.103)	−0.162 (0.047)
Hyalella azteca (Saussure)	1.296 (0.307)	−0.206 (0.145)
Ephemeroptera	0.252 (0.072)	−0.191 (0.105)
Total	1.026 (0.160)	0.166 (0.086)
% SC	0.040 (0.030)	−0.074 (0.036)
(b) Benthic floc infaunal crowding		
Planorbella spp.	0.053 (0.040)	−0.074 (0.020)
Copepoda	0.318 (0.224)	−0.290 (0.146)
Ostracoda	0.080 (0.129)	−0.325 (0.046)

(Günther) (golden topminnow) density was positively correlated with P availability (Table 2e). No significant relationships with P availability or hydroperiod were seen in total fish density (Fig. 4e), total fish biomass, or non-herbivorous fish biomass (Fig. 4f). With the exception of Site 37, which had relatively high fish biomass, total non-herbivorous fish biomass may generally be higher at long-hydroperiod sites than short-hydroperiod sites.

Discussion

This study revealed significant differences in community structure and composition of floating-periphyton-mat and benthic-floc infauna and in the way these communities vary along environmental gradients. Infaunal crowding was notably higher in floating periphyton mats than in benthic floc. Hydroperiod explained the most variance in both structure and density of benthic-floc infaunal communities. P availability explained the most variation in floating periphyton mat infaunal community structure, while density was most dependent upon hydroperiod. The observed pattern of infaunal density at short- and long-hydroperiod sites along the P-gradient was likely shaped, in part, by top-down trophic interactions. In general, analysis of FFGs failed to reflect patterns observed consistently across individual taxa, suggesting response to environmental factors in this system is often more dependent upon life-history or behavior characteristics.

Microhabitat communities

Unique assemblages of invertebrates are often associated with submerged and floating aquatic vegetation (e.g., Krecker, 1939; Scotland, 1940; O'Hara, 1968). In this study, differences between floating-periphyton-mat and benthic-floc infauna were greater than any differences attributable to hydroperiod or P availability gradients, among sites, or between water management regions. Floating periphyton mats had significantly higher densities of most macroinvertebrate taxa. Copepod density and % F-COLL (composed primarily of copepods and cladocerans) were higher in floc samples. These small microcrustaceans are usually found in open water or associated with benthos (Pennak, 1989), and many Everglades species are well adapted for moving within flocculent detritus (M. C. Bruno, Università della Tuscia, Viterbo, Italy, personal communication). Macroinvertebrate taxa that burrow or cling to solid substrates (e.g., *H. azteca*, dipteran larvae and pupae) may benefit more from structure provided by calcified periphyton mats. The relatively high % PRED in the periphyton mat (adult and larval coleopterans, predatory dipterans, etc.) may also contribute to low density of microcrustaceans, as they are a common prey item for these taxa. Sklar (1985) found significantly higher densities of invertebrates in floating duckweed than in sediment, but observed a higher biomass of invertebrates in sediment. While invertebrate biomass was not quantified in this study, the only taxa that were more numerous in floc cores (copepods) were very small compared to other taxa and were not present in numbers high enough numbers to outweigh the larger taxa. This core sampling method, however, is not suited for large invertebrates such as *Procambarus* spp. and *P. paludosus*, taxa relatively common at most of these sites. These crustaceans spend much of their time on the benthos, so it is likely that biomass estimates incorporating these groups would reveal a biomass of benthic fauna that is higher than that of floating-periphyton-mat infauna. Furthermore, foraging in the benthos by these large invertebrates may explain the apparent paucity of benthic invertebrates in the size range studied here.

Community responses to environmental factors

There were no consistent effects of P availability or hydroperiod on benthic-floc infauna, indicating they were influenced by a taxon-specific combination of factors such as food availability, susceptibility to predation or physiological limits of desiccation tolerance. The observed response of floating-mat infauna to P availability and hydroperiod, however, was dependent upon the scale at which observations were made. Infaunal crowding reflects the number of individuals found within a habitat unit (g^{-1} periphyton AFDM or cm^{-2} mat), the scale relevant to individual macroinvertebrate interactions. Since floating-mat cover in the Everglades is often extremely patchy, infaunal density at this scale is not appropriate for making generalizations about variation seen with P availability or hydroperiod, as these factors vary on a much larger scale (m^2 to km^2). Estimates of infaunal density (no. m^{-2}) provide a more accurate assessment of macroinvertebrate standing stock at a scale relevant for trophic interactions with small-bodied fish.

Frequent drying events in wetlands often create a gradient of disturbance that can have a significant impact on resident communities (Wellborn et al., 1996). Hydroperiod had a significant impact on floating periphyton mats, mat infauna, and fish communities in this study (Fig. 5a). Both floating

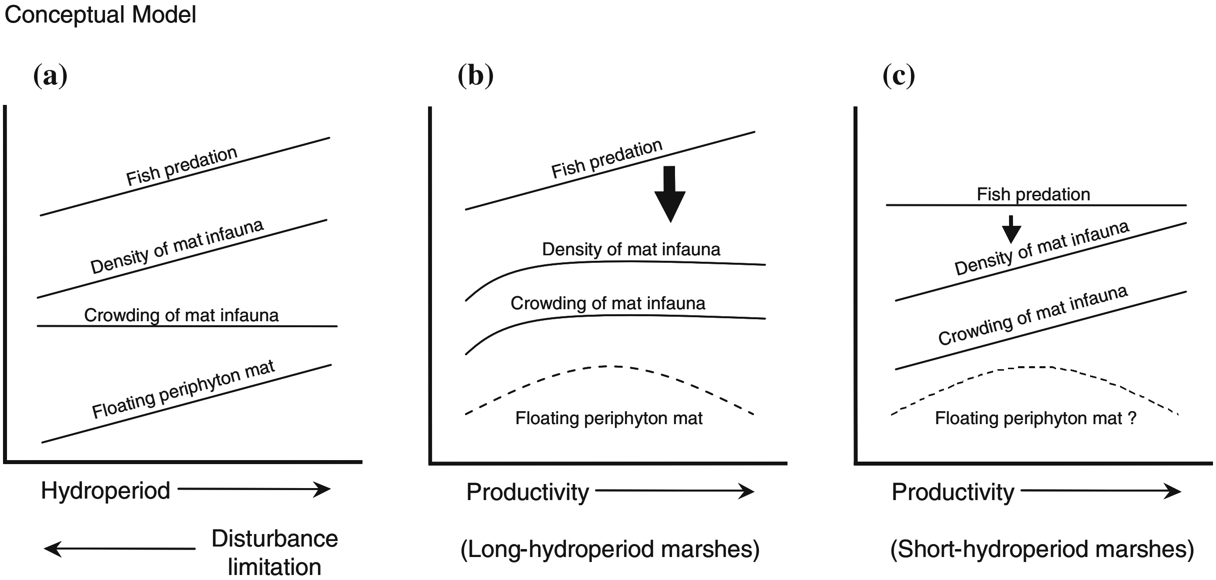

Figure 5. Conceptual model derived from experimental observations and suggested trends: trends in periphyton and consumers along gradients of hydroperiod (a) and productivity (b, c) in the Florida Everglades. Density of mat infauna is number m^{-2} and crowding is number g^{-1} AFDM. Dotted lines (floating periphyton mat across productivity gradient) represent trends not observed in this study, but suggested by others (see Discussion). Floc infauna did not vary with P availability or hydroperiod in this study.

mat cover and mat infaunal density increased with hydroperiod. Infaunal crowding remained relatively constant across this gradient, as increased floating mat at long-hydroperiod sites provided additional habitat for infauna. Density of predatory fish increased with duration of inundation as, presumably, did predator impact on prey. In short-hydroperiod Everglades marshes, annual drying limits fish abundance (Loftus & Eklund, 1994; Trexler et al., 2005). Frequent disturbance also presents a challenge for mat infauna, helping limit their abundance at short-hydroperiod sites. Invertebrates in temporary aquatic systems, or habitats that experience frequent drying, must have some combination of a highly flexible life cycle, temperature-linked development, protected or diapausing eggs and excellent dispersal abilities (Williams, 1996). Interestingly, mat infaunal density increased at long-hydroperiod sites in the presence of a greater density of predatory fish, which may demonstrate the effectiveness of calcareous floating periphyton mats as predation refuge.

Community structure and crowding of floating-mat infauna was driven primarily by P availability. When short- and long-hydroperiod sites were analyzed separately, however, it became evident that these marshes' responses to increased P availability were quite varied. In long-hydroperiod marshes, biomass of non-herbivorous fish appeared to increase with P availability. Although this trend is not statistically significant, increased small-fish density with P availability has been reported in previous studies in long-hydroperiod marshes in this system (Turner et al., 1999). Increased predatory fish biomass may indicate greater predation effects (direct and indirect) on mat infauna at more productive sites, precluding infaunal density and crowding from increasing with P availability (Fig. 5b). While no clear patterns in floating mat cover were observed in this study, previous studies have suggested this relationship may be 'hump-shaped' in long-hydroperiod marshes (no studies have reported trends in short-hydroperiod marshes). Many studies in this system have noted an increase in periphyton biomass with the addition of low levels of phosphorus (Davis, 1994; McCormick & Stevenson, 1998) and a decrease in periphyton biomass with higher P levels (McCormick et al., 2002; Smith, 2004; Gaiser et al., 2005a, b). Proportion of calcareous periphyton in floating vegetation decreased consistently with P availability in this study, which is consistent with trends seen in other studies (e.g., Gaiser et al., 2005b).

Although periphyton biomass and fish densities were lower at short-hydroperiod sites, short-hydroperiod infaunal mat communities showed a stronger positive relationship with P availability than those at long-hydroperiod sites (Fig. 5c). While total fish density showed an increasing trend with P availability in short-hydroperiod marshes, density may not be a true reflection of the amount of predation pressure on macroinvertebrate communities at these sites. Total fish density at the two short-hydroperiod, P-enriched, sites was dominated by herbivorous (*J. floridae*, site 37) and small (*H. formosa*, site TE10) fish species. Analyses of non-herbivorous fish biomass better reflected predation risk, and indicated relatively low predation risk at short-hydroperiod, P-enriched sites. This is consistent with previous studies that have found hydrologic disturbance to be a significant limiting factor in these fish populations (Loftus et al., 1990; Ruetz et al., 2005; Trexler et al., 2005), and greater predation in longer-duration temporary aquatic systems (Schneider & Frost, 1996). Decreased fish predation may contribute to the observed increase in density and crowding of mat infauna with P availability in short-hydroperiod marshes. I observed relatively low periphyton mat cover in short-hydroperiod marshes, which may be more sensitive to seasonal hydrology than contemporary water quality. While it is unclear how periphyton in short-hydroperiod marshes responds to increased nutrients, the hump-shaped curve seen in long-hydroperiod marshes seems likely (although the magnitude of variation may be more subtle). Additionally, loss of mat habitat at highly productive sites may contribute to increased infaunal crowding (concentration effect).

Although constantly inundated marshes were deeper than long-hydroperiod marshes, invertebrate and fish communities were not statistically different. Unfortunately, statistical tests had very low power since only two constantly inundated sites could be identified for this study. Data from these two sites suggested density of mat infauna was similar to that seen in long-hydroperiod marshes and density of floc infauna was lower than that seen in long- or short-hydroperiod marshes. Floc at constantly inundated sites may be of a lower food quality due to decreased light attenuation and an absence of inputs from floating vegetation which sites that dry periodically receive during dry-down events. Constantly inundated marshes also had relatively low periphyton mat cover (~8%), and relatively low density of small fish. Although they are not well sampled with 1 m^2 throw traps (Chick et al., 1999), it is likely that these sites have high densities of large piscivorous fish (Chick et al., 2004; Trexler et al., 2005) which would limit small fish density.

This study emphasizes the need to further investigate effects of interactions between P availability and hydrology on consumer communities. Previous studies in this system that have described effects of nutrient enrichment on consumer communities (e.g., McCormick et al., 2004; Gaiser et al., 2005a) have been conducted in long-hydroperiod marshes, leaving dynamics in short-hydroperiod marshes largely undescribed. The Florida Everglades is currently the focus of a major restoration effort, which will deliver P-enriched water to short-hydroperiod marshes in an effort to redistribute water to its pre-drainage levels. This study suggests this restoration may have a greater effect on short-hydroperiod marshes than has been previously thought. These results are only strongly suggestive, however, because of the relatively small number of sites sampled and the fact that no observations were made of temporal variation. This study also emphasizes the fact that attention must be paid to the dynamics of macroinvertebrates in different substrates in order to fully understand community dynamics and response to environmental variables. This is particularly important when considering sampling methods, as many common methods (e.g., D-frame sweep nets) pool microhabitat communities, and may even under-represent floating-mat infauna (Smith, 2004), making community dynamics less apparent.

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