Effects of Abiotic Gradients and Trophic Interactions on Food Web Structure of Everglades Aquatic Consumers

Brooke L. Sargeant, Evelyn E. Gaiser, Joel C. Trexler

Department of Biological Sciences, Florida International University, Miami, FL, USA

ABSTRACT

Identifying determinants of community and food web structure is of central importance in ecology, particularly because biodiversity and food webs are frequently linked to ecosystem functioning. Using data collected during the wet season 2005 R-EMAP sampling event, we investigated food web fragments consisting of periphyton primary producers, and fish and macroinvertebrates as primary and secondary consumers. To address how environmental gradients influence these aquatic communities, we used 1) path analysis to identify indirect and direct effects of nutrients (phosphorus) and disturbance (hydrology) on consumer densities, with indirect effects acting via transmission through the food web (i.e., through their effects on periphyton and smaller macroinvertebrates); and 2) analysis of stable isotope ratios from a selected subset of fish and macroinvertebrate species to identify changes in trophic diversity. Our findings reveal how nutrient enrichment can alter aquatic food webs by changing the densities of consumers, and by functional changes in energy flow through the food web resulting from dietary shifts. We also illustrate the importance of biotic interactions in shaping Everglades aquatic communities.

RESEARCH QUESTIONS

Q1) What are the indirect and direct effects of nutrients, hydrological disturbance, and trophic interactions on densities of periphyton infauna, larger macroinvertebrates, and small fish?

Q2) How does trophic diversity, as revealed by stable isotope ratios from a subset of intermediate consumers, change along gradients of periphyton biomass, algal community structure, hydrological disturbance, and density?

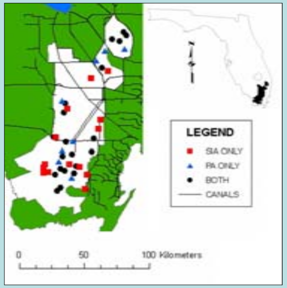


FIGURE 1. Study sites used in analyses. 28 sites contributed to the path analysis of density data, while 34 sites were used to analyze trophic diversity.

METHODS

Aquatic animals sampled at 54 locations during 2005 wet season R-EMAP sampling event

- a) Throw-trap sampling → small fish and large macroinvertebrate densities
- b) Periphyton cores → macroinvertebrate infauna density
- c) Periphyton samples → relative abundance (RA) of algal species, periphyton total phosphorus (TP), ash-free dry mass (AFDM), biovolume, chlorophyll *a*, % organic
- d) Hydrology estimated using EDEN

Nonmetric multidimensional scaling (NMDS) was used to ordinate sites according to algal species RAs, resulting in axes used in subsequent analyses

Q1) Path analysis was used to model indirect and direct effects on consumer densities

- a) Compared 15 *a priori* models with CAIC

Q2) Stable isotope analysis for measures of trophic diversity

- a) eastern mosquitofish (*Gambusia holbrooki*), golden topminnow (*Fundulus chrysotus*), flagfish (*Jordanella floridae*), crayfish (*Procambarus alleni*, *P. fallax*)
- b) Measures in $\delta^{13}C$-$\delta^{15}N$ bi-plot space: total niche area (convex hull area), mean nearest-neighbor distance (mean Euclidean distance), $\delta^{13}C$ range, and $\delta^{15}N$ range
- c) Stepwise-backward elimination multiple regression

Q1) RESULTS OF DENSITY ANALYSIS

TABLE 1. Kendall's tau correlations with periphyton TP (n = 28)

Total Periphyton Biovolume (ml)	-0.76
Periphyton AFDM (g/m²)	-0.77
Chlorophyll a Concentration (µg/g dry)	+0.61
Chlorophyll a Density (µg/m²)	-0.70
% Organic Content (%)	+0.68
Bluegreen Algae RA	-0.40
Filamentous Bluegreen Algae RA	-0.66
Green Algae RA	+0.43
Diatoms RA	+0.40

TABLE 2. Kendall's tau correlations with algal NMDS axes (n = 28)

	NMDS Axis 1	NMDS Axis 2
Bluegreen Algae RA	-0.12	-0.55
Filamentous Bluegreen Algae RA	-0.73	-0.23
Green Algae RA	+0.41	-0.10
Diatoms RA	+0.27	+0.79
Phosphorus TP	+0.57	+0.23
Time Since Flooding (days)	+0.29	+0.17

NMDS Stress = 0.14

FIGURE 2. Best model (lowest CAIC score)

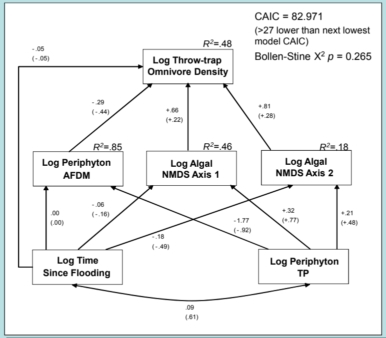
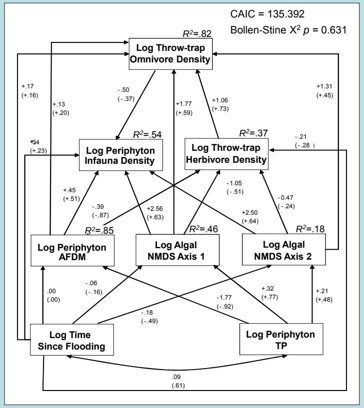
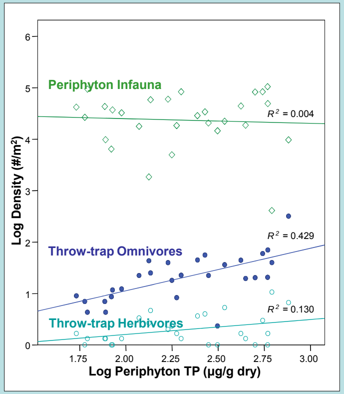


FIGURE 3. Best model with all hypothesized trophic paths included



For path models, unstandardized and standardized (in parentheses) path coefficients are shown, along with squared multiple correlations (R^2) in the upper right hand corner of each endogenous variable. The bidirectional arrow between (Log Time Since Flooding) and (Log Periphyton TP) represents their unanalyzed covariance (or correlation).

FIGURE 4. Consumer Densities vs. Nutrients



Periphyton Infauna = All macroinvertebrates in periphyton cores

Throw-trap Omnivores = Fish, newts, sirens, beetle larvae, odonate larvae, insects crayfish, shrimp

Throw-trap-Herbivores = Fish, tadpoles, beetles, mayfly larvae, snails

Q2) RESULTS OF TROPHIC DIVERSITY ANALYSIS

FIGURE 5. Example niche areas for two sites

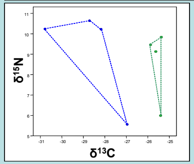


TABLE 3. Kendall's tau correlations with algal NMDS axes (n = 34)

	NMDS Axis 1	NMDS Axis 2	NMDS Axis 3
Bluegreen Algae RA	+0.36	-0.18	+0.42
Filamentous Bluegreen Algae RA	+0.55	+0.34	-0.18
Green Algae RA	-0.18	-0.42	-0.11
Diatoms RA	-0.80	+0.11	-0.05
Phosphorus TP	-0.44	-0.32	+0.08
Time Since Flooding (days)	-0.28	-0.16	-0.16

NMDS Stress = 0.10

TABLE 4. Final regression models for niche metrics (n = 34)

Dependent Variable	Significant Terms	β	Standardized β	Squared Semipartial Correlation	Adjusted R^2
Log Total Niche Area	Flagfish Presence	0.20**	0.44	0.20	0.36
	Periphyton AFDM	-0.005*	-0.37	0.14	
	Algal NMDS Axis 3	-0.15*	-0.33	0.11	
Log Mean Nearest-Neighbor Distance	Algal NMDS Axis 2	-0.04*	-0.35		0.09
Log $\delta^{13}C$ Range	Algal NMDS Axis 3	-0.12*	-0.37		0.11
$\delta^{15}N$ Range	Flagfish Presence	0.9*	0.57	0.09	0.46
	Time Since Flooding	0.0006**	0.48	0.15	
	Algal NMDS Axis 2	-0.6**	-0.48	0.14	
	Intermediate-Consumer Density	0.00	0.0007	1×10^{-7}	
	Flagfish x Density	-0.05*	-0.79	0.09	

Full models: flagfish presence, time since flooding, periphyton AFDM and algal NMDS axes, intermediate-consumer density, and interactions between density and periphyton variables

*p < 0.05; **p < 0.01

CONCLUSIONS

- Consistent with other studies, nutrient enrichment was associated with:
  - ↓ overall periphyton biomass
  - ↓ relative abundance of bluegreen and filamentous bluegreen algae
  - ↑ organic content and chlorophyll *a* concentration
  - ↑ relative abundance of green algae and diatoms
- Q1) Density patterns
  - Omnivorous fish and large macroinvertebrates ↑ with changes in algal community structure and ↓ with periphyton biomass
  - Periphyton infaunal density was uncorrelated with nutrients
  - Herbivorous fish and large macroinvertebrates showed a weak positive trend with nutrients
  - Density patterns and path models consistent with top-down control of infauna (but maybe not throw-trap-sized herbivores) by omnivorous small fish and large macroinvertebrates
- Q2) Trophic diversity of the subset of intermediate consumers
  - Total niche area and $\delta^{13}C$ range ↓ with bluegreen algae relative abundance and periphyton biomass
  - $\delta^{15}N$ range ↓ with disturbance, intermediate-consumer density, and relative abundance of filamentous bluegreen algae, but ↑ with the relative abundance of green algae

RESTORATION IMPLICATIONS

Improved parameterization of simulation models of restoration scenarios and statistical models of field data by providing:

- Increased specification of how nutrient enrichment and hydrological changes affect the densities and trophic roles of basal consumers
- Evaluation of the relative importance of indirect effects of phosphorus through algal species composition (resource quality) vs. periphyton biomass (AFDM, chlorophyll *a*) (resource quantity)

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