Indirect and direct controls of macroinvertebrates and small fish by abiotic factors and trophic interactions in the Florida Everglades

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SUMMARY

1. The roles of nutrients, disturbance and predation in regulating consumer densities have long been of interest, but their indirect effects have rarely been quantified in wetland ecosystems. The Florida Everglades contains gradients of hydrological disturbance (marsh drying) and nutrient enrichment (phosphorus), often correlated with densities of macroinvertebrate infauna (macroinvertebrates inhabiting periphyton), small fish and larger invertebrates, such as snails, grass shrimp, insects and crayfish. However, most causal relationships have yet to be quantified.

2. We sampled periphyton (content and community structure) and consumer (small omnivores, carnivores and herbivores, and infaunal macroinvertebrates inhabiting periphyton) density at 28 sites spanning a range of hydrological and nutrient conditions and compared our data to seven *a priori* structural equation models.

3. The best model included bottom-up and top-down effects among trophic groups and supported top-down control of infauna by omnivores and predators that cascaded to periphyton biomass. The next best model included bottom-up paths only and allowed direct effects of periphyton on omnivore density. Both models suggested a positive relationship between small herbivores and small omnivores, indicating that predation was unable to limit herbivore numbers. Total effects of time following flooding were negative for all three consumer groups even when both preferred models suggested positive direct effects for some groups. Total effects of nutrient levels (phosphorus) were positive for consumers and generally larger than those of hydrological disturbance and were mediated by changes in periphyton content.

4. Our findings provide quantitative support for indirect effects of nutrient enrichment on consumers, and the importance of both algal community structure and periphyton biomass to Everglades food webs. Evidence for top-down control of infauna by omnivores was noted, though without substantially greater support than a competing bottom-up-only model.

Keywords: bottom-up and top-down control, Florida Everglades, hydrological disturbance, indirect effects, phosphorus

Introduction

How abiotic and biotic factors influence populations and communities has long been a central question in community ecology (e.g. Menge & Sutherland, 1987; Pace *et al.*, 1999), but understanding their interactions and indirect effects as mediated by species interactions remains a critical step to developing predictive models of how populations are controlled and respond to environmental change (Wootton, Parker & Power, 1996; Kneitel & Chase, 2004; Gotelli & Ellison, 2006). To identify the mechanisms by which environmental gradients influence communities, they

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must be examined in the context of food webs and using methods that can explore their interactions and community-level effects. We used structural equation modelling, a multivariate technique that explicitly examines indirect and direct effects, to determine how hydrological disturbance, nutrients and trophic interactions influence primary production and densities of small consumers (predominantly invertebrates and small fish) in the Florida Everglades.

Studies of aquatic systems have revealed diverse effects of disturbance, productivity and predation on food webs, densities and community structure (e.g. Power, Parker & Wootton, 1996; Shurin et al., 2002; Chase, 2003). In pond and wetland ecosystems, hydrological disturbance is expected to shape community structure by permanently limiting or periodically reducing biota, especially larger organisms (Wellborn, Skelly & Werner, 1996). Disturbance in the form of drought can decrease macroinvertebrate and fish densities through direct mortality or reduction of food biomass. In habitats where larger organisms are more susceptible to drying conditions, droughts may actually increase macroinvertebrate densities by removing predatory fish (Corti, Kohler & Sparks, 1997; Liston, 2006; Dorn, 2008). The effects of nutrient enrichment on fish and invertebrate densities can depend on disturbance, the strength of trophic interactions and the degree to which predators can reduce prey populations. For example, while fish biomass generally increases with nutrients, similar increases in invertebrate biomass may hinge on whether fish are present and limit invertebrate densities (Wootton & Power, 1993; Marks, Power & Parker, 2000; Liston, 2006). Increasing nutrients can also encourage successional changes towards welldefended but competitively inferior invertebrates and thereby reduce the strength of trophic cascades by fish (Chase, 2003). Relatively few studies have addressed these interactive effects and indirect relationships in wetlands, leaving such questions unanswered for many systems.

The Florida Everglades is a highly oligotrophic marsh ecosystem with gradients of anthropogenic nutrient (phosphorus) enrichment and hydrological disturbance (drying of the marsh; Gunderson & Loftus, 1993; Davis, 1994). Drying events cause direct mortality of fish and invertebrates as well as movements towards deeper refuges, and thus community trajectories in the Everglades reveal shifts from abiotic

to biotic control as a function of time following a disturbance (Trexler, Loftus & Perry, 2005), similar to patterns in floodplain habitats (Winemiller, 1996). The density of small fish typically increases with time following a drying event (Trexler et al., 2002, 2005; Dorn, 2008) and often with nutrient levels (Turner et al., 1999; Trexler et al., 2002; Gaiser et al., 2005). Similarly, invertebrates often increase coincident with hydroperiod and nutrients, although this pattern varies with taxa, sampling method, microhabitat and nutrient level (Rader & Richardson, 1994; McCormick, Shuford & Rawlik, 2004; Liston, 2006; King & Richardson, 2007; Liston, Newman & Trexler, 2008). It is generally presumed that nutrients amplify fish and macroinvertebrate densities indirectly via stimulation of periphyton production (aggregations of benthic algae, detritus, fungi and bacteria), a major source of primary production for the food web and habitat for invertebrates. Nutrient enrichment, localised around areas of water inflow, alters algal community composition and consequently changes the periphyton physical structure and constitution (e.g. from floating calcareous mats to epiphytic filamentous green algae aggregates; McCormick et al., 1996; Gaiser et al., 2005, 2006). Hydrology may also shape periphyton community structure (Gottlieb, Richards & Gaiser, 2006; Thomas et al., 2006). The maintenance of large expanses of periphyton and apparent limits on macroinvertebrate densities suggest that fish predation on invertebrates may generate a trophic cascade (Turner et al., 1999; Liston, 2006).

While these general trends in Everglades communities have been identified, indirect and direct effects and food-web interactions have not yet been explicitly quantified in natural contexts and at large spatial scales. Anthropogenic activities have modified the Everglades through nutrient enrichment and alteration of hydrological patterns (Davis, 1994), and the Everglades is now the subject of a large-scale restoration project (Davis & Ogden, 1994). Using structural equation modelling (path analysis) and a model comparison approach, we identified possible causal models quantifying the indirect, direct and total effects of drought, nutrient enrichment and trophic interactions on small aquatic consumers in the Everglades. This analysis provides greater insight into possible mechanistic models describing how basal consumer densities are controlled in this ecosystem, informing restoration policies and practices.

Methods

Field sampling and sample processing

In November and December 2005, we sampled fish, amphibian and aquatic invertebrate communities in 28 sites across the Florida Everglades (Everglades National Park, Water Conservation Areas, and Loxahatchee National Refuge; approximately 25°19'N, 80°56'W; Fig. 1). Sampling sites were selected from a larger set of possible study sites identified by a Generalized Random Tessellation Stratified (GRTS) survey design (Stevens & Olsen, 2003) applied to the Greater Everglades ecosystem (Scheidt & Kalla, 2007). The GRTS design provides a specially balanced sample of the ecosystem; sites were selected for this study because they were located in wet prairie slough habitats that are the focus of management concern because of their role as foraging habitats for wading birds (Trexler & Goss, 2009); wet prairie sloughs are characterised by spikerush-dominated (Eleocharis cellulosa Torr.) emergent vascular plants (Gunderson, 1994) and large standing stocks of periphyton mats formed by benthic algae, detritus, fungi and bacteria (Turner et al., 1999). Sargeant, Gaiser & Trexler (2010) and Table 1 provide further description of the conditions at these sites.



Variables	Minimum value	Maximum value	Mean ± SE
Periphyton total phosphorus (µg g dry ⁻¹)	53	760	272 ± 39
Time since flooding (days)	160	2164	611 ± 134
Periphyton biomass (AFDM; g m ⁻²)	4	540	107 ± 29
Small omnivore density (number m^{-2})	1	318	35 ± 11
Small herbivore density (number m^{-2})	0.0	9.7	1.5 ± 0.41
Periphyton infauna density (number m ⁻²)	409	105 123	37 562 ± 5622

AFDM, ash-free dry mass.

We sampled small fish and amphibians (<8 cm) and large invertebrates (snails, crayfish, grass shrimp and large insects, >5 mm) using a standardised throw-trap sampling protocol (Jordan, Coyne & Trexler, 1997) with 1-m² throw traps enclosed by 2-mm mesh. Traps were cleared using a bar seine (2-mm mesh) and dip nets (1- and 5-mm mesh), and vertebrates were euthanised by immersion in an MS-222 (tricaine methanesulphonate) bath. Three throw-trap samples





were collected per site. To sample macroinvertebrate infauna (including nematodes, copepods and cladocerans, inhabiting periphyton mats, typically 0.25-8 mm long), periphyton mat samples (6-cm-diameter cores from top to bottom of the mats, typically 2.5 cm deep) were collected from within each throw trap (Liston & Trexler, 2005). All animals captured were kept on ice in the field and then frozen for storage before identification and enumeration in the laboratory. The densities (number m^{-2}) of small primary and secondary consumers were determined for each site by calculating the mean of the counts from the three throw-trap samples. Herbivores included herbivorous fish, tadpoles, beetles, mayfly larvae and snails. Small fish, newts, sirens, beetle larvae, odonate larvae, insects, crayfish and shrimp were considered secondary consumers and are omnivorous or carnivorous in the Everglades. Periphyton subsamples (15-30 mL) were haphazardly selected from thawed cores, and two different workers identified macroinvertebrates under a light microscope. Periphyton macroinvertebrate density (number m⁻²; Liston, 2006) was determined for each site using the means of the three periphyton core samples. Details on species collected, their densities and frequency of occurrence at sites, and their trophic classification (for throw-trap organisms) are available in Appendix S1. All trophic assignments were based on published and unpublished studies reporting gut content (Gunderson & Loftus, 1993; Loftus, 1999) and stable isotopic (Loftus, 1999; Williams & Trexler, 2006; Sargeant et al. 2010) and fatty acid profile (L. L. Belicka, pers. comm.) analyses of specimens collected from the Everglades. Feeding relationships of Everglades aquatic animals are complex, with widespread omnivory and intraguild predation; a small fraction of animals sampled for this study are exclusively carnivores (e.g. dragonfly naiads) feeding on other omnivores and herbivores. For simplicity sake, we have lumped these animals as 'omnivores' for this study, consistent with Morin's (1999) definition that omnivores are species that feed at more than one trophic level.

We determined phosphorus levels, periphyton composition and hydrological disturbance estimates corresponding to each of our sites. Periphyton volume (mL) was estimated in the field by placing periphyton in graduated cylinders, and periphyton aerial cover (%) was measured as the estimated percentage of the surface area enclosed by the throw trap that was

covered by periphyton. Separate periphyton samples (three samples per site, corresponding to locations of throw-trap samples) were obtained to determine total phosphorus content (TP; $\mu g g dry^{-1}$), ash-free dry mass (AFDM; $g m^{-2}$) as an estimate of biomass, per cent nitrogen and organic content, chlorophyll a concentration ($\mu g g dry^{-1}$) and density ($\mu g m^{-2}$) and algal species composition as described by Gaiser et al. (2006); see also Stevenson, McCormick & Frydenborg, 2002). Total phosphorus from periphyton is a valuable indicator of nutrient enrichment because phosphorus is quickly absorbed by biota and does not remain in the water column (Gaiser et al., 2006). Algal species were categorised as green algae, diatoms, non-filamentous bluegreen algae (cyanobacteria) and filamentous bluegreen algae, and the combined relative abundance of diatoms and green algae was used in analyses because those species are thought to be more palatable to consumers (Geddes & Trexler, 2003). Using the Everglades Depth Estimation Network (EDEN) hydrological estimation tool (http://sofia. usgs.gov/eden/stationlist.php), we calculated time since flooding as the number of days since flooding after the most recent drying event (water levels <5 cm). Using this as a measure of time to recover following a drought, hydrological disturbance is inversely related to time since flooding. Sampling occurred in the late wet season when marshes were near peak water depths following summer rains.

Data analysis

To examine complex interactions between these variables in a food-web context, we used structural equation modelling to identify relationships between TP levels, time since flooding, periphyton AFDM, the relative abundance of green algae and diatoms, the density of periphyton macroinvertebrate infauna and the densities of small consumers (fish and large invertebrates from throw-trap samples). Structural equation modelling enables analysis of systems involving multiple simultaneous cause-effect relationships, in contrast to reductionist approaches that examine these relationships singly, with the potential to improve understanding of interaction networks typical of ecological communities (Grace, 2006). For example, it can be used to identify species interactions and their direct, indirect and total effects (Johnson, Huggins & DeNoyelles, 1991; Wootton, 1994a,b). This

method can be applied to experiments (e.g. Johnson *et al.*, 1991; Wootton, 1994a,b) or observational data recorded along gradients of natural variability (e.g. Elmhagen & Rushton, 2007; Riginos & Grace, 2008).

We developed seven a priori models describing hypothesised causal mechanisms for how disturbance, productivity and trophic interactions may determine the densities of small consumers via direct and indirect pathways, based on results of previous studies and theoretical expectations (see Appendix S2 for detailed descriptions of each model and rationale). Models were based on bottom-up control only or reciprocal relationships (both bottom-up and topdown controls) between consumers and prey. Specifically, top-down control was proposed between (i) omnivores and infauna, (ii) infauna and periphyton biomass, (iii) herbivores and periphyton biomass and (iv) omnivores and periphyton biomass. The relationship between herbivores and omnivores was evaluated by comparing models that contained a causal path from herbivores to omnivores to models that assumed no causal link between them. We were unable to include a possible top-down relationship between omnivore density and herbivore density owing to empirical underidentification. A model is considered identified if unique estimates can be determined for all of its parameters, which requires a sufficient number of observed variables given the number of parameters to solve (Grace, 2006). In some cases, a model can be theoretically identified but empirically underidentified because of correlations inherent in the data that effectively reduce the number of observations (Kline, 2005; Grace, 2006). However, the small omnivores in question may be unlikely to limit herbivores of similar size.

Structural equation modelling (path analysis) was conducted using AMOS 7.0 (Amos Development Corporation, Spring House, PA, U.S.A.). The site was considered the unit of observation (n = 28), with the periphyton, hydrological and consumer variables calculated for each site. All variables were \log_{10} (y + 1)-transformed to improve univariate normality and reduce nonlinearities in relationships. Despite transformations, the data continued to show signs of deviation from normality (as indicated by univariate analyses, Mardia's coefficient for multivariate kurtosis and Mahalanobis d), so we used bootstrapping (based on 2000 bootstrap samples) to test absolute model fit using the Bollen–Stine χ^2 test. When data are highly non-normal, traditional χ^2 tests of model fit can be overly conservative and the Bollen–Stine χ^2 test, which uses bootstrapping to determine the probability of model fit, is recommended as an alternative (Byrne, 2000; Grace, 2006). Models were compared using the Bayesian Information Criterion (BIC; lower BIC values indicate better fit), which weighs improvement in model fit against model complexity (Claeskens & Hjort, 2008). We report BIC instead of the more common Akaike's Information Criterion (AIC) because BIC provides more consistent model selection as model complexity increases; BIC applies a higher penalty than AIC for adding parameters (Claeskens & Hjort, 2008: Chapter 4) and is more conservative than AIC in the presence of model uncertainty (Burnham & Anderson, 2010: pp. 271-273). Because we used a model comparison approach, path coefficients are presented, but were not tested for statistical significance (e.g. Gotelli & Ellison, 2006). We present the unstandardised and standardised path coefficients fitted by maximum likelihood for each direct causal path in the final models. Path coefficients in the model represent partial regression coefficients. Reported total effects of environmental gradients are the sum of direct and indirect causal paths. Our approach should be viewed as exploratory and hypothesisgenerating rather than confirmatory given our limited trophic specification made necessary by high samplesize requirements of our model fitting and comparison approach.

Results

Samples contained many of the small aquatic fauna common to the Everglades (see Appendix S1). Throwtrap samples were dominated by small fish, grass shrimp, crayfish and dragonfly larvae. Of these, grass shrimp (Palaemonetes paludosus, Gibbes) had the largest mean density across all the sites of the omnivorous species and was present in more than 70% of the sites. Least killifish (Heterandria formosa, Girard), mosquitofish (Gambusia holbrooki, Girard) and bluefin killifish (Lucania goodei, Jordan) were also very common and thus typically contributed notably to omnivore density. Herbivorous fish and large invertebrates were lower in density, dominated by planorbid snails (Planorbella spp.) with the highest mean density, and flagfish (Jordanella floridae, Goode and Bean) at the largest number of sites. Cladocerans, nematodes,

copepods, water mites, ostracods, amphipods and dipteran larvae comprised the largest numbers of infaunal macroinvertebrates inhabiting periphyton. Larger beetles, dragonfly larvae and snails were less numerous in periphyton and found at fewer sites.

Sites spanned a wide range of hydrological and nutrient levels (Table 1), and time since flooding was positively correlated with periphyton TP (Spearman correlation: $r_s = 0.68$). Consistent with several other studies in the Everglades, many attributes of periphyton were associated with time since flooding and/or periphyton TP (Table 2). Increases in nutrient levels and time since flooding were correlated not only with decreases in periphyton biomass, periphyton volume and the relative abundances of bluegreen and filamentous bluegreen algae but also with increases in organic content, chlorophyll a concentration and the relative abundances of green algae and diatoms. The density of omnivores increased coincident with nutrient levels and (to a lesser extent) recovery time following drought, while infaunal and herbivore densities did not exhibit strong correlations with either variable (Table 2; Figs 2 & 3).

Table 2 Spearman correlations between major environmental gradients [time since flooding and periphyton total phosphorus (TP)] and periphyton characteristics and consumer densities (n = 28)

	Time since flooding, r _s	Periphytor TP, r_s
Total periphyton volume (mL)	-0.59	-0.88
Total periphyton aerial cover (%)	-0.67	-0.87
Periphyton biomass (AFDM; g m ⁻²)	-0.68	-0.92
Per cent organic content (%)	+0.64	+0.82
Per cent carbon (%)	+0.66	+0.84
Per cent nitrogen (%)	+0.64	+0.86
Chlorophyll <i>a</i> concentration $(\mu g g dry^{-1})$	+0.57	+0.78
Chlorophyll <i>a</i> density ($\mu g m^{-2}$)	-0.65	-0.88
Relative abundance of non-filamentous bluegreen algae	-0.42	-0.53
Relative abundance of filamentous bluegreen algae	-0.43	-0.80
Relative abundance of green algae	+0.51	+0.61
Relative abundance of diatoms	+0.30	+0.50
Small omnivore density (number m ⁻²)	+0.31	+0.65
Small herbivore density (number m ⁻²)	+0.20	+0.29
Periphyton infauna density (number m ⁻²)	-0.02	+0.03

AFDM, ash-free dry mass.

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Fig. 2 Relationships between consumer densities and time since flooding.



Fig. 3 Relationships between consumer densities and periphyton total phosphorus (TP) levels.

A comparison of model BIC values indicated that one model (Model 6 in Appendix S2) was preferred to the others (the difference between the BIC of this model and the next best model was >2; Table 3). Two other models (Model 1 and Model 7 in Appendix S2) had slightly higher BIC values, but only Model 6 and Model 1 showed adequate absolute fit to the data (Bollen–Stine χ^2 tests were not statistically significant at the 0.05 level; Table 3).

In Model 6 (Fig. 4), changes in periphyton biomass and community structure, driven by increasing phosphorus, are transmitted to omnivores indirectly. Increases in the relative abundance of diatoms and

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terior (DC) and bolen-sine χ F-values of the best models are in bold								
Model	Infauna – Periphyton	Herbivores – Periphyton	Omnivores – Periphyton	Omnivores – Infauna	Omnivores – Herbivores	k [†]	BIC	Bollen–Stine χ ² <i>P</i> -value
1	Bottom-up	Bottom-up	Bottom-up	Bottom-up	Bottom-up	23	95.197	0.15
2	Bottom-up	Bottom-up	-	Bottom-up	Bottom-up	21	104.248	0.025
3	Bottom-up	Bottom-up		Bottom-up		20	117.951	0.004
4	Bottom-up	Bottom-up	Bottom-up	Bottom-up		22	106.133	0.027
5	Bottom-up and Top-down	Bottom-up and Top-down		Bottom-up and Top-down		23	108.390	0.004
6	Bottom-up and Top-down	Bottom-up and Top-down		Bottom-up and Top-down	Bottom-up	24	92.234	0.12
7	Bottom-up and Top-down	Bottom-up and Top-down	Bottom-up and Top-down	Bottom-up and Top-down	Bottom-up	27	95.781	0.033

Table 3 Comparison of structural equation models (see also detailed descriptions in Appendix S2). The Bayesian Information Criterion (BIC) and Bollen–Stine χ^2 *P*-values of the best models are in bold

[†]number of parameters.



Fig. 4 Model with the lowest Bayesian Information Criterion value (Model 6), incorporating bottom-up and top-down effects and no omnivory. All variables were log-transformed. Unstandardised and standardised (in parentheses) path coefficients are shown, along with squared multiple correlation coefficients (R^2) at the upper right corner of each endogenous variable. The bidirectional arrow between periphyton total phosphorus and time since flooding represents their non-causal bivariate covariance (correlation if standardised).

green algae, and increases in periphyton biomass, increased infauna density, which in turn had a positive effect on omnivore density. Omnivores had



Fig. 5 Model with the second lowest Bayesian Information Criterion value (Model 1), incorporating bottom-up effects only and omnivory. All variables were log-transformed. Unstandardised and standardised (in parentheses) path coefficients are shown, along with squared multiple correlation coefficients (R^2) at the upper right corner of each endogenous variable. The bidirectional arrow between periphyton total phosphorus and time since flooding represents their non-causal bivariate covariance (correlation if standardised).

a negative top-down effect on infauna, and infauna had a small but negative effect on periphyton biomass. Both periphyton biomass and the relative abundance of diatoms and green algae were negatively related to herbivore density, while increasing herbivores increased omnivore density with no reciprocal top-down effect.

Model 1 (Fig. 5) included only bottom-up effects and incorporated direct effects of periphyton biomass and relative abundance of diatoms and green algae on omnivore density. Direct effects of time since flooding and periphyton TP were generally similar to those in Model 6. Relationships between trophic groups were bottom-up and mostly positive (increases in prey resulted in increases in consumers) or weak, with the exception of herbivores.

Some patterns were shared by Model 6 and Model 1. Herbivore density was negatively related to periphyton biomass and the relative abundance of diatoms and green algae in both models. The total effect of periphyton TP was positive for omnivores and herbivores, but was nearly zero for infauna (Table 4). In Model 1, this resulted only from phosphorus's effect on periphyton community structure and biomass, but in Model 6, the negligible total effect of phosphorus was largely driven by top-down effects. Time since flooding increased infauna density and omnivore density directly, but decreased herbivore density directly in both models. However, time since flooding increased periphyton biomass and decreased the relative abundance of diatoms and green algae, making the total effect of hydrological disturbance negative for infauna and omnivores (Table 4). The effect of time since flooding was more complex for herbivores. In Model 6, the negative effect was caused by a strong direct path and multiple indirect effects. In Model 1, the total effect was weaker, and the negative direct effect was moderated by positive indirect effects through periphyton. The total effects of periphyton TP on periphyton and consumers were larger than those of time since flooding in both models (Table 4), with the exception of infauna density.

Discussion

Using structural equation modelling, we identified two possible mechanistic models describing the effects of nutrient enrichment, disturbance and foodweb interactions on small consumers in the Florida Everglades. The best-supported model (Model 6) showed evidence for top-down control of periphyton infauna densities and suggested that trophic cascades may help maintain periphyton biomass against herbivory in the Everglades. However, the BIC value of Model 1 (a model allowing bottom-up effects only and including omnivory) was only slightly higher, indicating that it also deserves consideration. While other studies have illustrated the importance of hydrological disturbance in shaping temporal trends in Everglades aquatic communities, our findings emphasise a greater role of nutrient gradients in contributing to consumer densities across large spatial scales in the late wet season, when direct effects of previous drying

Table 4 Indirect, direct and total effects of phosphorus enrichment [periphyton total phosphorus (TP)] and time since flooding forModels 6 and 1

	Log periphyton TP			Log time since flooding		
	Direct	Indirect	Total	Direct	Indirect	Total
Model 6						
Log periphyton biomass	-1.95 (-1.02)	+0.21 (+0.11)	-1.74 (-0.91)	+0.04 (+0.02)	-0.06 (-0.04)	-0.02 (-0.01)
Log relative abundance of	+0.66 (+0.90)	0	+0.66 (+0.90)	-0.20 (-0.32)	0	-0.20 (-0.32)
diatoms + green algae						
Log infauna density	0	+0.05 (+0.03)	+0.05 (+0.03)	+0.18 (+0.12)	-0.30 (-0.21)	-0.12 (-0.09)
Log herbivore density	0	+0.48 (+0.57)	+0.48 (+0.57)	-0.37 (-0.51)	+0.20 (+0.27)	-0.17 (-0.24)
Log omnivore density	0	+0.83 (+0.68)	+0.83 (+0.68)	+0.17 (+0.16)	-0.37 (-0.36)	-0.21 (-0.20)
Model 1						
Log periphyton biomass	-1.77 (-0.92)	0	-1.77 (-0.92)	-0.003 (-0.002)	0	-0.003 (-0.002)
Log relative abundance of	+0.66 (+0.90)	0	+0.66 (+0.90)	-0.20 (-0.32)	0	-0.20 (-0.32)
diatoms + green algae						
Log Infauna Density	0	+0.06 (+0.03)	+0.06 (+0.03)	+0.20 (+0.14)	-0.33 (-0.23)	-0.13 (-0.09)
Log herbivore density	0	+0.29 (+0.36)	+0.29 (+0.36)	-0.12 (-0.18)	+0.05 (+0.07)	-0.08 (-0.11)
Log omnivore density	0	+0.88 (+0.71)	+0.88 (+0.71)	+0.01 (+0.01)	-0.23 (-0.22)	-0.24 (-0.22)

Standardised coefficients are shown in parentheses.

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were relatively weak. Further, the structural equation models identified the effects of food quality (indicated by algal community structure) and food or habitat quantity (indicated by periphyton biomass), allowed effects of nutrient enrichment and hydrology to be disentangled and provided insight into direct versus indirect effects in this system.

Both models incorporated bottom-up effects initiated by increases in nutrients (measured by TP levels in periphyton). Increasing phosphorus appeared to drive compositional changes in periphyton, including shifts in the dominant algal species, the proportion of organic content and the overall biomass and volume of periphyton. These findings mirror those of several other studies correlating phosphorus addition with increases in the relative abundance of diatoms and green algae and organic content, but decreases in the relative abundance of filamentous bluegreen algae and biomass of bluegreen algae and periphyton (McCormick et al., 1996; Gaiser et al., 2005, 2006). The proportion of periphyton comprised of organic material, diatoms and green algae may reflect food quality since these components are probably more palatable than inorganic components, bluegreen algae or filamentous bluegreen algae (Geddes & Trexler, 2003). Phosphorus addition increases these palatable elements, but decreases the total organic biomass of periphyton (e.g. food quantity and habitat for infauna).

These changes in periphyton quality and quantity appear to be the indirect link between phosphorus enrichment and consumer densities. In both models, infaunal density directly increased with periphyton biomass and the proportion of green algae and diatoms. In Model 1, where primary production was directly linked to omnivore density, omnivores responded positively to the relative abundance of diatoms and green algae, and negatively to periphyton biomass (although this latter relationship was quite weak in magnitude). This is in contrast to Model 6, in which changes in food are transmitted to omnivores indirectly through infauna and herbivores. Interestingly, periphyton biomass and the relative abundance of diatoms and green algae had strong negative direct effects on herbivore density in both models, generally contrasting with their effects on infauna and omnivores. A possible explanation may be found in the composition of the herbivore community; flagfish comprised a significant portion of the herbivores in our samples and they may be poor competitors (Trexler *et al.*, 2005). Nonetheless, herbivore density actually increased with nutrient enrichment (i.e. the total effect of periphyton TP) because of the indirect pathways via periphyton biomass. Both models indicate that the quality of periphyton is as important as total food biomass, consistent with previous work demonstrating an increased ability of some consumers to feed on palatable elements following a physical break-up in the periphyton mat (Geddes & Trexler, 2003).

In the Everglades, the maintenance of large expanses of periphyton mats and apparent limits on infaunal density even in the face of nutrient enrichment may be evidence for a trophic cascade (Turner et al., 1999; Liston, 2006). Trophic cascades are widespread in aquatic systems (Shurin et al., 2002), often driven by predation of macroinvertebrates by fish (e.g. Wootton & Power, 1993). Few studies of topdown effects have been conducted in wetlands, but some show that small fish and insect predators can reduce invertebrate numbers (Batzer, 1998; Peck & Walton, 2008), while others have not found effects of small predators (Corti et al., 1997). Empirical support for trophic cascades in the Everglades has been lacking (Dorn, Trexler & Gaiser, 2006; Chick, Geddes & Trexler, 2008). In the current study, small fish and invertebrates, but not infauna, increased with nutrients, a pattern potentially consistent with a trophic cascade based on predictions from food-web theory (Power, 1992). The relative strength of Model 6 suggests that both bottom-up and top-down forces are important in shaping the densities of basal consumers in the Everglades. Like all the models considered, Model 6 includes bottom-up relationships between primary production (periphyton) and higher trophic levels. Increases in phosphorus levels drive changes in periphyton community structure, increasing the proportion of highly palatable algal species while simultaneously reducing the total organic biomass of periphyton. Model 6 assumes that these changes in primary production are transmitted indirectly, through primary consumers (infaunal macroinvertebrates and herbivorous fish, invertebrates and tadpoles), to omnivorous fish and invertebrates. Omnivores, in turn, limit infauna density, and infauna density has a negative effect on periphyton biomass. These relationships are likely to underpin the pattern of increasing omnivore density, but not infauna density, with nutrient enrichment (e.g. Fig. 3). The positive effect of omnivores (through macroinvertebrate infauna) on periphyton biomass implies that a trophic cascade helps maintain periphyton mats, but herbivores may simultaneously act to stimulate periphyton growth, indicating that multiple factors are important in controlling periphyton biomass.

This contrasts with the exclusively bottom-up structure of Model 1. The fact that two very different models had similar support may be explained by the role of omnivory. Model 1 allows for omnivores to feed directly on periphyton, and this may result in similar net effects of periphyton TP as are found in Model 6 in which omnivory is removed. Trophic cascades are generally thought to be limited by omnivory (Polis & Strong, 1996) and could also be restricted in the Everglades by the associative resistance afforded palatable algae by the physical or algal composition of periphyton mats (Geddes & Trexler, 2003; Chick et al., 2008). However, past studies have not found support that omnivorous fish and invertebrates assimilate more periphyton as nutrients increase (Williams & Trexler, 2006).

Herbivorous small fish and invertebrates played a different role than other consumer groups in both models. Herbivore density had a positive effect on omnivore density, presumably via predation where predators were unable to limit prey numbers. The similar size of individuals in the omnivore and herbivore groups may have prevented top-down control; some of the herbivores may have been too large or well defended for the small omnivores to consume them. In Model 6, herbivores had a positive top-down effect on periphyton biomass, seemingly inconsistent with an expected predator–prey relationship. While a negative effect of predation may be more expected, positive effects could occur through nutrient regeneration (Geddes & Trexler, 2003).

Previous studies of Everglades fauna have frequently found negative correlations between small fish and/or macroinvertebrate densities and measures of disturbance (Trexler *et al.*, 2002, 2005; Liston, 2006). The direct effect of time since flooding was positive for infauna and omnivore density in both models, suggesting that their numbers increased with recovery time following droughts. However, the opposite pattern was found for herbivores, probably stemming from dominance of flagfish, which tend to decrease with time following droughts (Trexler *et al.*, 2005). Time since flooding was important in contributing to

algal community structure, reducing the proportion of diatoms and green algae. Our results are potentially inconsistent with a previous study (Gottlieb et al., 2006) reporting higher relative abundance of diatoms in long-hydroperiod sites, but that study did not separate effects of phosphorus from those of hydrology, which tend to be correlated. Despite a negative direct effect, the overall correlation between time since flooding and the relative abundance of green algae and diatoms was positive, possibly explaining the differences in results between studies. Effects of hydrological disturbance were somewhat weaker than the effects of nutrient enrichment, and the total effect of time since flooding was negative for all three consumer groups as a result of numerous indirect effects. Reduced effects of hydrology relative to nutrients in this study may have resulted from focusing on spatial, rather than temporal, variability and by sampling at the end of the wet season when few sites had been recently dry. This study also used partial regression coefficients to estimate effects of hydrology and nutrients, possibly resulting in different findings than studies relying on correlation alone.

Structural equation models can provide important advances in understanding Everglades food webs. However, there are some shortcomings of our study. As is the case for all studies examining open, natural food webs, a limitation of our analysis is that models were necessary simplifications of the true food web. We were unable to include the effects of larger predators, which may have exerted further top-down control on consumers, and detritus-based components of the food web. Effects of predatory fish, such as gar, may actually be included in direct effects of time since flooding, since they are limited to deeper refugia when water levels are low (Chick, Ruetz & Trexler, 2004). In addition, although we gained some resolution by categorising consumers into three groups based on size and diet, individual species may exhibit unique and contrasting patterns not fully described by this analysis. For example, Liston (2006) identified effects of hydrology and/or nutrient levels on certain infaunal groups that were sometimes at odds with patterns observed for infauna as a whole. Finally, our study did not incorporate sites with phosphorus levels >760 $\mu g g^{-1}$ dry periphyton tissue; at higher levels, periphyton mats can completely disappear and densities of fish and macroinvertebrates can be reduced (King & Richardson, 2007; Liston et al., 2008; Rejmánková, Macek &

Epps, 2008). Future research should address food-web structure at artificially high nutrient levels and ideally incorporate larger predatory fishes and wading birds as a fourth trophic level.

By using a multi-model, structural equation modelling approach (Grace, 2006), this study provides insight into direct and indirect effects and the apparently limited role of top-down control in shaping consumer densities. To our knowledge, this is the first such analysis of a natural wetlands food web incorporating multiple trophic levels. Our results should guide future research to the mechanisms underlying our proposed causal pathways.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Density and frequency of occurrence of taxonomic groups contributing to trophic categories.

Appendix S2. Candidate Models.

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