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

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

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Abbreviated title: Indirect and direct controls of Everglades consumers

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

29 Summary

- 30 1. The roles of nutrients, disturbance and predation in regulating consumer densities
31 have long been of interest, but their indirect effects have rarely been quantified in
32 wetland ecosystems. The Florida Everglades contains gradients of hydrological
33 disturbance (marsh drying) and nutrient enrichment (phosphorus), often correlated with
34 densities of macroinvertebrate infauna (macroinvertebrates inhabiting periphyton), small
35 fish and larger invertebrates, such as snails, grass shrimp, insects and crayfish. However,
36 most causal relationships have yet to be quantified.
- 37 2. We sampled periphyton (content and community structure) and consumer (small
38 omnivores, carnivores and herbivores, and infaunal macroinvertebrates inhabiting
39 periphyton) density at 28 sites spanning a range of hydrological and nutrient conditions
40 and compared our data to seven *a priori* structural equation models.
- 41 3. The best model included bottom-up and top-down effects among trophic groups and
42 supported top-down control of infauna by omnivores and predators that cascaded to
43 periphyton biomass. The next best model included bottom-up paths only and allowed
44 direct effects of periphyton on omnivore density. Both models suggested a positive
45 relationship between small herbivores and small omnivores, indicating that predation was
46 unable to limit herbivore numbers. Total effects of time following flooding were
47 negative for all three consumer groups even when both preferred models suggested
48 positive direct effects for some groups. Total effects of nutrient levels (phosphorus) were
49 positive for consumers and generally larger than those of hydrological disturbance, and
50 were mediated by changes in periphyton content.

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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.

Copy for Review

74 Introduction

75 How abiotic and biotic factors influence populations and communities has long
76 been a central question in community ecology (e.g., Menge & Sutherland, 1987; Pace *et*
77 *al.*, 1999), but understanding their interactions and indirect effects as mediated by species
78 interactions remains a critical step to developing predictive models of how populations
79 are controlled and respond to environmental change (Wootton, Parker, & Power, 1996;
80 Kneitel & Chase, 2004; Gotelli & Ellison, 2006). To identify the mechanisms by which
81 environmental gradients influence communities, they must be examined in the context of
82 food webs and using methods that can explore their interactions and community-level
83 effects. We used structural equation modeling, a multivariate technique that explicitly
84 examines indirect and direct effects, to determine how hydrological disturbance, nutrients
85 and trophic interactions influence primary production and densities of small consumers
86 (predominantly invertebrates and small fish) in the Florida Everglades.

87 Studies of aquatic systems have revealed diverse effects of disturbance,
88 productivity and predation on food webs, densities and community structure (e.g., Power,
89 Parker, & Wootton, 1996; Shurin *et al.*, 2002; Chase, 2003). In pond and wetland
90 ecosystems, hydrological disturbance is expected to shape community structure by
91 permanently limiting or periodically reducing biota, especially larger organisms
92 (Wellborn, Skelly, & Werner, 1996). Disturbance in the form of drought can decrease
93 macroinvertebrate and fish densities through direct mortality or reduction of food
94 biomass. In habitats where larger organisms are more susceptible to drying conditions,
95 droughts may actually increase macroinvertebrate densities by removing predatory fish
96 (Corti, Kohler, & Sparks, 1997; Liston, 2006; Dorn, 2008). The effects of nutrient

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97 enrichment on fish and invertebrate densities can depend on disturbance, the strength of
98 trophic interactions, and the degree to which predators can reduce prey populations. For
99 example, while fish biomass generally increases with nutrients, similar increases in
100 invertebrate biomass may hinge on whether fish are present and limit invertebrate
101 densities (Wootton & Power, 1993; Marks, Power, & Parker, 2000; Liston, 2006).
102 Increasing nutrients can also encourage successional changes toward well-defended but
103 competitively inferior invertebrates and thereby reduce the strength of trophic cascades
104 by fish (Chase, 2003). Relatively few studies have addressed these interactive effects and
105 indirect relationships in wetlands, leaving such questions unanswered for many systems.

106 The Florida Everglades is a highly oligotrophic marsh ecosystem with gradients
107 of anthropogenic nutrient (phosphorus) enrichment and hydrological disturbance (drying
108 of the marsh) (Gunderson & Loftus, 1993; Davis, 1994). Drying events cause direct
109 mortality of fish and invertebrates as well as movements toward deeper refuges, and thus
110 community trajectories in the Everglades reveal shifts from abiotic to biotic control as a
111 function of time following a disturbance (Trexler, Loftus, & Perry, 2005), similar to
112 patterns in floodplain habitats (Winemiller, 1996). The density of small fish typically
113 increases with time following a drying event (Trexler *et al.*, 2002, 2005; Dorn, 2008) and
114 often with nutrient levels (Turner *et al.*, 1999; Trexler *et al.*, 2002; Gaiser *et al.*, 2005).
115 Similarly, invertebrates often increase coincident with hydroperiod and nutrients,
116 although this pattern varies with taxa, sampling method, microhabitat and nutrient level
117 (Rader & Richardson, 1994; McCormick, Shuford, & Rawlik, 2004; Liston, 2006; King
118 & Richardson, 2007; Liston, Newman, & Trexler, 2008). It is generally presumed that
119 nutrients amplify fish and macroinvertebrate densities indirectly via stimulation of

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3 120 periphyton production (aggregations of benthic algae, detritus, fungi and bacteria), a
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6 121 major source of primary production for the food web and habitat for invertebrates.
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8 122 Nutrient enrichment, localized around areas of water inflow, alters algal community
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10 123 composition and consequently changes the periphyton physical structure and constitution
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12 124 (e.g., from floating calcareous mats to epiphytic filamentous green algae aggregates)
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14 125 (McCormick *et al.*, 1996; Gaiser *et al.*, 2005, 2006). Hydrology may also shape
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16 126 periphyton community structure (Gottlieb, Richards, & Gaiser, 2006; Thomas *et al.*,
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18 127 2006). The maintenance of large expanses of periphyton and apparent limits on
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20 128 macroinvertebrate densities suggest that fish predation on invertebrates may generate a
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22 129 trophic cascade (Turner *et al.*, 1999; Liston, 2006).
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27 130 While these general trends in Everglades communities have been identified,
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29 131 indirect and direct effects and food-web interactions have not yet been explicitly
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31 132 quantified in natural contexts and at large spatial scales. Anthropogenic activities have
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33 133 modified the Everglades through nutrient enrichment and alteration of hydrological
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35 134 patterns (Davis, 1994), and the Everglades is now the subject of a large-scale restoration
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37 135 project (Davis & Ogden, 1994). Using structural equation modeling (path analysis) and a
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39 136 model comparison approach, we identified possible causal models quantifying the
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41 137 indirect, direct and total effects of drought, nutrient enrichment and trophic interactions
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43 138 on small aquatic consumers in the Everglades. This analysis provides greater insight into
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45 139 possible mechanistic models describing how basal consumer densities are controlled in
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47 140 this ecosystem, informing restoration policies and practices.
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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 and Olsen 2003) applied to the Greater Everglades ecosystem (Scheidt and 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 and Goss 2009); wet prairie sloughs are characterized 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 et al. (2010) and Table 1 provide further description of the conditions at these sites.

We sampled small fish and amphibians (<8 cm) and large invertebrates (snails, crayfish, grass shrimp, and large insects, >5 mm) using a standardized 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 euthanized by immersion in an MS-222 (tricaine methanesulfonate) bath. Three throw-trap samples were collected per site. To sample macroinvertebrate infauna (including nematodes, copepods, and cladocerans, inhabiting

periphyton mats, typically 0.25-8mm 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 and Trexler 2005). All animals captured were kept on ice in the field, and then frozen for storage before identification and enumeration in the lab. 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 Table S1 of Supporting Information Appendix S1. All trophic assignments were based on published and unpublished studies reporting gut content (Gunderson and Loftus, 1993; Loftus 1999), stable isotopic (Loftus 1999; Williams and Trexler 2006; Sargeant et al. 2010) and fatty acid profile (LL Belicka, personal communication) 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

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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 (3 samples per site, corresponding to locations of throw-trap samples) were obtained to determine total phosphorus content (TP) ($\mu\text{g}\cdot\text{g dry}^{-1}$), ash-free dry mass (AFDM) ($\text{g}\cdot\text{m}^{-2}$) as an estimate of biomass, percent nitrogen and organic content, chlorophyll *a* concentration ($\mu\text{g}\cdot\text{g dry}^{-1}$) and density ($\mu\text{g}\cdot\text{m}^{-2}$) and algal species composition as described by Gaiser *et al.* (2006; see also Stevenson et al. 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 categorized as green algae, diatoms, non-filamentous bluegreen algae (cyanobacteria), filamentous blugreen 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

211 in the late wet season when marshes were near peak water depths following summer
212 rains.

213

214 *Data Analysis*

215 To examine complex interactions between these variables in a food-web context,
216 we used structural equation modeling to identify relationships between TP levels, time
217 since flooding, periphyton AFDM, the relative abundance of green algae and diatoms, the
218 density of periphyton macroinvertebrate infauna and the densities of small consumers
219 (fish and large invertebrates from throw-trap samples). Structural equation modeling
220 enables analysis of systems involving multiple simultaneous cause-effect relationships, in
221 contrast to reductionist approaches that examine these relationships singly, with the
222 potential to improve understanding of interaction networks typical of ecological
223 communities (Grace, 2006). For example, it can be used to identify species interactions
224 and their direct, indirect and total effects (Johnson, Huggins, & DeNoyelles, 1991;
225 Wootton, 1994a,b). This method can be applied to experiments (e.g., Johnson *et al.*,
226 1991; Wootton, 1994a,b) or observational data recorded along gradients of natural
227 variability (e.g., Elmhagen & Rushton, 2007; Riginos & Grace, 2008).

228 We developed seven *a priori* models describing hypothesized causal mechanisms
229 for how disturbance, productivity and trophic interactions may determine the densities of
230 small consumers via direct and indirect pathways, based on results of previous studies
231 and theoretical expectations (see Supporting Information Appendix S2 for detailed
232 descriptions of each model and rationale). Models were based on bottom-up control only
233 or reciprocal relationships (both bottom-up and top-down controls) between consumers

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234 and prey. Specifically, top-down control was proposed between 1) omnivores and
235 infauna, 2) infauna and periphyton biomass, 3) herbivores and periphyton biomass, and
236 4) omnivores and periphyton biomass. The relationship between herbivores and
237 omnivores was evaluated by comparing models that contained a causal path from
238 herbivores to omnivores to models that assumed no causal link between them. We were
239 unable to include a possible top-down relationship between omnivore density and
240 herbivore density due to empirical underidentification. A model is considered identified
241 if unique estimates can be determined for all of its parameters, which requires a sufficient
242 number of observed variables given the number of parameters to solve (Grace, 2006). In
243 some cases, a model can be theoretically identified but empirically underidentified
244 because of correlations inherent in the data that effectively reduce the number of
245 observations (Kline, 2005; Grace, 2006). However, the small omnivores in question may
246 be unlikely to limit herbivores of similar size.

247 Structural equation modeling (path analysis) was conducted using AMOS 7.0
248 (Amos Development Corporation, Spring House, PA, USA). The site was considered the
249 unit of observation (n=28), with the periphyton, hydrological and consumer variables
250 calculated for each site. All variables were $\log_{10}(y + 1)$ transformed to improve
251 univariate normality and reduce nonlinearities in relationships. Despite transformations,
252 the data continued to show signs of deviation from normality (as indicated by univariate
253 analyses, Mardia's coefficient for multivariate kurtosis, and Mahalanobis d), so we used
254 bootstrapping (based on 2000 bootstrap samples) to test absolute model fit using the
255 Bollen-Stine chi-square test. When data are highly non-normal, traditional chi-square
256 tests of model fit can be overly conservative and the Bollen-Stine chi-square 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 and 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 unstandardized and standardized 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 hypothesis-generating rather than confirmatory given our limited trophic specification made necessary by high sample-size requirements of our model fitting and comparison approach.

Results

Samples contained many of the small aquatic fauna common to the Everglades (see Table S1 of Supporting Information Appendix S1). Throw-trap 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

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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 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 and 3).

A comparison of model BIC values indicated that one model (Model 6 in Supporting Information 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 Supporting Information Appendix S2) had slightly higher BIC values, but only Model 6 and Model 1 showed adequate absolute fit to the data (Bollen-Stine chi-square 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 green algae, and increases in periphyton biomass, increased infauna density, which in turn had a positive effect on omnivore density. Omnivores had 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

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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 modeling, we identified two possible mechanistic models describing the effects of nutrient enrichment, disturbance and food-web 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 emphasize 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 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 total phosphorus 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,

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372 omnivores responded positively to the relative abundance of diatoms and green algae,
373 and negatively to periphyton biomass (although this latter relationship was quite weak in
374 magnitude). This is in contrast to Model 6, in which changes in food are transmitted to
375 omnivores indirectly through infauna and herbivores. Interestingly, periphyton biomass
376 and the relative abundance of diatoms and green algae had strong negative direct effects
377 on herbivore density in both models, generally contrasting with their effects on infauna
378 and omnivores. A possible explanation may be found in the composition of the herbivore
379 community; flagfish comprised a significant portion of the herbivores in our samples and
380 they may be poor competitors (Trexler *et al.*, 2005). Nonetheless, herbivore density
381 actually increased with nutrient enrichment (i.e., the total effect of periphyton TP) due to
382 the indirect pathways via periphyton biomass. Both models indicate that the quality of
383 periphyton is as important as total food biomass, consistent with previous work
384 demonstrating an increased ability of some consumers to feed on palatable elements
385 following a physical break-up in the periphyton mat (Geddes & Trexler, 2003).

386 In the Everglades, the maintenance of large expanses of periphyton mats and
387 apparent limits on infaunal density even in the face of nutrient enrichment may be
388 evidence for a trophic cascade (Turner *et al.*, 1999; Liston, 2006). Trophic cascades are
389 widespread in aquatic systems (Shurin *et al.*, 2002), often driven by predation of
390 macroinvertebrates by fish (e.g., Wootton & Power, 1993). Few studies of top-down
391 effects have been conducted in wetlands, but some show that small fish and insect
392 predators can reduce invertebrate numbers (Batzler, 1998; Peck & Walton, 2008), while
393 others have not found effects of small predators (Corti *et al.*, 1997). Empirical support
394 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 (see below), 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

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418 removed. Trophic cascades are generally thought to be limited by omnivory (Polis &
419 Strong, 1996), and could also be restricted in the Everglades by the associative resistance
420 afforded palatable algae by the physical or algal composition of periphyton mats (Geddes
421 & Trexler, 2003; Chick *et al.*, 2008). However, past studies have not found support that
422 omnivorous fishes and invertebrates assimilate more periphyton as nutrients increase
423 (Williams & Trexler, 2006).

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

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

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3 441 diatoms and green algae. Our results are potentially inconsistent with a previous study
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5 442 (Gottlieb *et al.*, 2006) reporting higher relative abundance of diatoms in long-hydroperiod
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8 443 sites, but that study did not separate effects of phosphorus from those of hydrology,
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10 444 which tend to be correlated. Despite a negative direct effect, the overall correlation
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12 445 between time since flooding and the relative abundance of green algae and diatoms was
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14 446 positive, possibly explaining the differences in results between studies. Effects of
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17 447 hydrological disturbance were somewhat weaker than the effects of nutrient enrichment,
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19 448 and the total effect of time since flooding was negative for all three consumer groups as a
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21 449 result of numerous indirect effects. Reduced effects of hydrology relative to nutrients in
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23 450 this study may have resulted from focusing on spatial, rather than temporal, variability
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25 451 and by sampling at the end of the wet season when few sites had been recently dry. This
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27 452 study also used partial regression coefficients to estimate effects of hydrology and
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29 453 nutrients, possibly resulting in different findings than studies relying on correlation alone.
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34 454 Structural equation models can provide important advances in understanding
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36 455 Everglades food webs. However, there are some shortcomings of our study. As is the
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38 456 case for all studies examining open, natural food webs, a limitation of our analysis is that
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40 457 models were necessary simplifications of the true food web. We were unable to include
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42 458 the effects of larger predators, which may have exerted further top-down control on
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44 459 consumers, and detritus-based components of the food web. Effects of predatory fish,
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46 460 such as gar, may actually be included in direct effects of time since flooding, since they
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48 461 are limited to deeper refugia when water levels are low (Chick, Ruetz, & Trexler, 2004).
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51 462 In addition, although we gained some resolution by categorizing consumers into three
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53 463 groups based on size and diet, individual species may exhibit unique and contrasting
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464 patterns not fully described by this analysis. For example, Liston (2006) identified
465 effects of hydrology and/or nutrient levels on certain infaunal groups that were
466 sometimes at odds with patterns observed for infauna as a whole. Finally, our study did
467 not incorporate sites with phosphorus levels greater than $760\text{ }\mu\text{g g}^{-1}$ dry periphyton
468 tissue; at higher levels periphyton mats can completely disappear and densities of fish
469 and macroinvertebrates can be reduced (King & Richardson, 2007; Liston *et al.*, 2008;
470 Rejmánková, Macek, & Epps, 2008). Future research should address food-web structure
471 at artificially high nutrient levels, and ideally incorporate larger predatory fishes and
472 wading birds as a fourth trophic level.

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

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Table 1 Descriptive statistics for environmental gradients and consumer densities (*n* = 28)

Variables	Minimum Value	Maximum Value	Mean ± SE
Periphyton TP (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 ± 5,622

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	Periphyton TP, r_s
Total periphyton volume (ml)	-0.59	-0.88
Total periphyton aerial cover (%)	-0.67	-0.87
Periphyton biomass (AFDM) ($\text{g}\cdot\text{m}^{-2}$)	-0.68	-0.92
Percent organic content (%)	+0.64	+0.82
Percent carbon (%)	+0.66	+0.84
Percent nitrogen (%)	+0.64	+0.86
Chlorophyll <i>a</i> concentration ($\mu\text{g}\cdot\text{g dry}^{-1}$)	+0.57	+0.78
Chlorophyll <i>a</i> density ($\mu\text{g}\cdot\text{m}^{-2}$)	-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 ($\text{number}\cdot\text{m}^{-2}$)	+0.31	+0.65
Small herbivore density ($\text{number}\cdot\text{m}^{-2}$)	+0.20	+0.29
Periphyton infauna density ($\text{number}\cdot\text{m}^{-2}$)	-0.02	+0.03

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Table 3 Comparison of structural equation models (see also detailed descriptions in Supporting Information Appendix S2). The BIC and Bollen-Stine chi-square p-values of the best models are in *bold*

Model	Infauna - Periphyton	Herbivores - Periphyton	Omnivores - Periphyton	Omnivores - Infauna	Omnivores - Herbivores	k ¹	BIC	Bollen- Stine X ² P- 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 & Top-down	Bottom-up & Top-down		Bottom-up & Top-down		23	108.390	0.004
6	Bottom-up & Top-down	Bottom-up & Top-down		Bottom-up & Top-down	Bottom-up	24	92.234	0.12
7	Bottom-up & Top-down	Bottom-up & Top-down	Bottom-up & Top-down	Bottom-up & Top-down	Bottom-up	27	95.781	0.033

¹number of parameters

Table 4 Indirect, direct and total effects of phosphorus enrichment (periphyton TP) and time since flooding for Models 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 Diatoms + Green Algae	+0.66 (+0.90)	0	+0.66 (+0.90)	-0.20 (-0.32)	0	-0.20 (-0.32)
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 Diatoms + Green Algae	+0.66 (+0.90)	0	+0.66 (+0.90)	-0.20 (-0.32)	0	-0.20 (-0.32)
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)

Standardized coefficients are shown in parentheses.

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Figure Legends

Fig. 1 Map of the study area with the location of sampling sites in the Florida Everglades

Fig. 2 Relationships between consumer densities and time since flooding

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

Fig. 4 Model with the lowest BIC value (Model 6), incorporating bottom-up and top-down effects and no omnivory. All variables were log-transformed. Unstandardized and standardized (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 standardized)

Fig. 5 Model with the second lowest BIC value (Model 1), incorporating bottom-up effects only and omnivory. All variables were log-transformed. Unstandardized and standardized (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 standardized)

Fig. 1

Fig. 2

Fig. 3

Fig. 4

Fig. 5

Supporting Information, Appendix S1

Table S1 Density and frequency of occurrence of taxonomic groups contributing to trophic categories. We define omnivores as species feeding at more than one trophic level and include several taxa that are carnivores acting as intraguild predators, as well as potentially feeding on herbivores.

Taxonomic group	Common name	Mean density (# m ⁻²) (SE)	Number of sites
Throw-trap omnivores			
<i>Palaemonetes paludosus</i>	Grass shrimp	13 (5.4)	20
<i>Heterandria formosa</i>	Least killifish	7 (2.5)	21
<i>Gambusia holbrooki</i>	Mosquitofish	5 (1.5)	23
<i>Lucania goodei</i>	Bluefin killifish	2.4 (0.70)	20
<i>Procambarus fallax</i>	Slough crayfish	1.7 (0.89)	14
<i>Celithemis eponina</i> (larva)	Halloween pennant dragonfly	1.0 (0.25)	18
<i>Procambarus alleni</i>	Everglades crayfish	1.0 (0.39)	9
<i>Fundulus chrysotus</i>	Golden topminnow	0.8 (0.15)	24
Coenagrionidae (larva)	Damselfly	0.6 (0.26)	16
<i>Pelocoris femoratus</i>	Alligator flea	0.5 (0.18)	14
<i>Elassoma evergladei</i>	Everglades pygmy sunfish	0.4 (0.14)	9
<i>Lepomis marginatus</i>	Dollar sunfish	0.4 (0.11)	13
<i>Libellula needhami</i> (larva)	Needham's skimmer dragonfly	0.3 (0.10)	13
<i>Procambarus</i> spp.	Unknown procambarid crayfish	0.3 (0.14)	9
<i>Fundulus confluentus</i>	Marsh killifish	0.16 (0.063)	7
<i>Erythemis simplicicollis</i> (larva)	Eastern pondhawk dragonfly	0.1 (0.11)	2
<i>Belostoma</i> spp.	Giant water bug	0.10 (0.041)	6
<i>Brachymesia gravida</i> (larva)	Four-spotted pennant dragonfly	0.10 (0.084)	2
<i>Enneacanthus gloriosus</i>	Bluespotted sunfish	0.08 (0.053)	3
<i>Coryphaeschna ingens</i> (larva)	Regal darner dragonfly	0.04 (0.020)	3
<i>Cyprinodon variegatus</i>	Sheepshead minnow	0.02 (0.024)	1
<i>Lepomis punctatus</i>	Spotted sunfish	0.02 (0.017)	2
<i>Notophthalmus</i> <i>viridescens</i>	Peninsula newt	0.02 (0.024)	1

Taxonomic group	Common name	Mean density (# m ⁻²) (SE)	Number of sites
<i>Noturus gyrinus</i>	Tadpole madtom	0.01 (0.012)	1
<i>Cybister</i> spp. (larva)	Water beetle	0.01 (0.012)	1
<i>Pseudobranchius axanthus</i>	Dwarf siren	0.01 (0.012)	1
Throw-trap herbivores			
<i>Planorbella</i> spp.	Planorbid snail	0.6 (0.36)	7
<i>Jordanella floridae</i>	Flagfish	0.4 (0.12)	17
<i>Poecilia latipinna</i>	Sailfin molly	0.18 (0.079)	5
<i>Rana</i> spp. (tadpole)	Ranid frog	0.12 (0.075)	3
Coleoptera (adult)	Aquatic beetle	0.07 (0.040)	4
Ephemeroptera (larvae)	Mayfly	0.06 (0.030)	4
<i>Haitia</i> spp.	Unidentified physid snail	0.06 (0.049)	2
<i>Pomacea paludosa</i>	Apple snail	0.01 (0.012)	1
Periphyton infauna			
Cladocera	Cladoceran; water flea	9000 (1700)	27
Nematoda	Nematode; roundworms	6000 (1100)	27
Chironomidae (larva) (excluding Tanypodinae)	Chironomid; non- biting midge	5100 (960)	28
Harpacticoida	Harpacticoid copepod	5000 (2200)	21
Acari	Water mite	5000 (1800)	28
Ostracoda	Ostracod	4000 (900)	28
Amphipoda	Amphipod	900 (220)	26
Tanypodinae (larva)	Chironomid; non- biting midge	800 (150)	27
<i>Dasyhelea</i> spp. (larva)	Biting midge	600 (140)	27
<i>Bezzia</i> spp. (larva)	Biting midge	500 (140)	20
Cyclopoida	Cyclopoid copepod	220 (62)	23
<i>Haitia</i> spp.	Unidentified physid snail	120 (29)	17
Calanoida	Calanoid copepod	120 (55)	17
Copepoda	Unidentified copepod	100 (28)	16
Dryopidae (larva)	Long-toed water beetle	90 (44)	5
Ephemeroptera (larva)	Mayfly	70 (24)	14
Diptera (pupa)	Unidentified fly pupa	60 (14)	20
Heteroptera	Aquatic bug	40 (12)	13
Diptera (larva)	Unidentified fly	43 (9.9)	16
Trichoptera (larva)	Caddis fly	40 (18)	13
Ceratopogonidae (larva)	Biting midge	40 (21)	9
Tipulidae (larva)	Crane fly	21 (10)	6

Taxonomic group	Common name	Mean density (# m ⁻²) (SE)	Number of sites
Stratiomyidae (larva)	Soldier fly	19 (9.4)	7
<i>Pelocoris femoratus</i>	Alligator flea	18 (6.9)	9
Collembola	Springtail	16 (7.4)	7
Coenagrionidae (larva)	Damselfly	15 (5.5)	11
<i>Planorbella</i> spp.	Planorbid snail	15 (8.6)	8
Coleoptera (adult)	Aquatic beetle	13 (6.1)	6
<i>Berosus</i> spp. (larva)	Aquatic beetle	13 (9.0)	3
Gastropoda	Unidentified snail	5 (4.4)	2
<i>Enochrus</i> spp. (larva)	Aquatic beetle	4 (2.7)	3
Dolichopodidae (larva)	Long-legged fly	3 (3.4)	1
Coleoptera (larva)	Aquatic beetle	3 (2.0)	3
<i>Littoridinops monroensis</i>	Cockscomb hydrobe	3 (2.1)	2
Anisoptera (larva)	Unidentified dragonfly	2 (1.9)	2
<i>Erythemis simplicicollis</i> (larva)	Eastern pondhawk dragonfly	0.7 (0.69)	1
<i>Palaemonetes paludosus</i>	Grass shrimp	0.4 (0.40)	1
<i>Brachymesia gravida</i> (larva)	Four-spotted pennant dragonfly	0.1 (0.12)	1

Supporting Information, Appendix S2

Candidate Models

Model Development

We developed seven *a priori* structural equation models based on previous studies and theoretical expectations. All models contained: 1) variables representing time since flooding, periphyton total phosphorus, periphyton biomass (ash-free dry mass), the combined relative abundance of diatoms and green algae, infauna density (from periphyton core samples), herbivore density (from throw-trap samples), and omnivore density (from throw-trap samples); 2) a covariance between time since flooding and periphyton phosphorus; 3) direct effects of time since flooding on all variables except periphyton phosphorus; and 4) direct effects of periphyton phosphorus on periphyton biomass and the combined relative abundance of diatoms and green algae. Direct effects of phosphorus enrichment on periphyton biomass and algal community structure have been demonstrated previously (e.g., McCormick *et al.*, 1996; Gaiser *et al.*, 2005, 2006). Hydrological impacts on consumer densities, periphyton biomass, and algal community structure have been suggested by several studies (e.g., Trexler, Loftus, & Perry, 2005; Gottlieb, Richards, & Gaiser, 2006; Liston, 2006). Thus, these elements were included in all structural equation models. Models varied in their effects of variables representing infaunal density, herbivore density, and omnivore density, based on models of food webs and trophic interactions (e.g., Power, 1992). Models 1-4 included bottom-up effects (e.g., effect of infauna density on omnivore density) only, and differed in their inclusion of omnivory (direct effect of periphyton biomass on omnivore density) and effects of

herbivores on omnivores. Models 5-7 included both bottom up effects and reciprocal top-down effects (e.g., effect of omnivore density on infauna density), and also differed in their inclusion of omnivory and relationships between herbivores and omnivores. We were unable to test models containing reciprocal relationships between omnivore density and herbivore density due to empirical underidentification.

Model 1: Bottom-up control, omnivory present

38 *Model 2: Bottom-up control, omnivory absent*

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40 *Model 3: Bottom-up control, omnivory absent, no path between herbivores and*

41 *omnivores*

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Model 4: Bottom-up control, omnivory present, no path between herbivores and omnivores

Model 5: Bottom-up and top-down control, omnivory absent, no path between herbivores and omnivores and omnivores

- 49 *Model 6: Bottom-up and top-down control, omnivory absent, only bottom-up control*
 50 *between herbivores and omnivores*

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 52 *Model 7: Bottom-up and top-down control, omnivory present, only bottom-up control*
 53 *between herbivores and omnivores*

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