

## A preliminary analysis of the correlation of food-web characteristics with hydrology and nutrient gradients in the southern Everglades

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### Abstract

We estimated trophic position and carbon source for three consumers (Florida gar, *Lepisosteus platyrhincus*; eastern mosquitofish, *Gambusia holbrooki*; and riverine grass shrimp, *Palaemonetes paludosus*) from 20 sites representing gradients of productivity and hydrological disturbance in the southern Florida Everglades, U.S.A. We characterized gross primary productivity at each site using light/dark bottle incubation and stem density of emergent vascular plants. We also documented nutrient availability as total phosphorus (TP) in floc and periphyton, and the density of small fishes. Hydrological disturbance was characterized as the time since a site was last dried and the average number of days per year the sites were inundated for the previous 10 years. Food-web attributes were estimated in both the wet and dry seasons by analysis of  $\delta^{15}\text{N}$  (trophic position) and  $\delta^{13}\text{C}$  (food-web carbon source) from 702 samples of aquatic consumers. An index of carbon source was derived from a two-member mixing model with Seminole ramshorn snails (*Planorbella duryi*) as a basal grazing consumer and scuds (amphipods *Hyallela azteca*) as a basal detritivore. Snails yielded carbon isotopic values similar to green algae and diatoms, while carbon values of scuds were similar to bulk periphyton and floc; carbon isotopic values of cyanobacteria were enriched in  $\text{C}_{13}$  compared to all consumers examined. A carbon source similar to scuds dominated at all but one study site, and though the relative contribution of scud-like and snail-like carbon sources was variable, there was no evidence that these contributions were a function of abiotic factors or season. Gar consistently displayed the highest estimated trophic position of the consumers studied, with mosquitofish feeding at a slightly lower level, and grass shrimp feeding at the lowest level. Trophic position was not correlated with any nutrient or productivity parameter, but did increase for grass shrimp and mosquitofish as the time following droughts increased. Trophic position of Florida gar was positively correlated with emergent plant stem density.

### Introduction

Abiotic environmental factors affect food-web function both through the source of energy flow and by determining the trophic position of community members. The relative role of detrital and algal contributions to energy flow in aquatic food webs is an important, but unresolved, question (Moore et al., 2004; Sobczak et al., 2005). While photoautotrophic energy channels dominate in the

literature, detritus-based “brown” food webs are well documented, notably in wetlands (Brinson et al., 1981; Mitsch & Gosselink, 1993). The Florida Everglades is a large wetland characterized by unusually dense mats of periphyton that have been implicated as the primary energy source for aquatic food-webs (Browder et al., 1994; Radar & Richardson, 1994), yielding some debate about the relative contribution of photoautotrophic and detrital energy channels. The complexity of these

mats has defied simple deconstruction of their algal, cyanobacterial, fungal, bacterial, and detrital components. Gradients of phosphorus and hydroperiod are linked to periphyton and microbial production in the Everglades and other wetlands, affecting the rate of detrital production (Brinson et al., 1981; McCormick et al., 2002). Though dual detrital and photoautotrophic contributions to energy flow are widespread (Moore & Hunt, 1988) and detrital contributions may equal or exceed photoautotrophic ones (Hairston & Hairston, 1993; Wetzel, 2001), details of the relative contribution of detritus in supporting higher trophic levels are poorly understood (Moore et al., 2004; Sobczak et al., 2005).

Maximum chain length of a food web is determined both by addition and subtraction of top consumer species and changing diets of intermediate consumers (Post, 2002a). Food-chain length may be affected by myriad abiotic and biotic factors in the environment, including resource availability, environmental stability, ecosystem size, colonization history, and predator-prey body size ratios (Pimm, 1982; Briand & Cohen, 1987; Post, 2002a; Jennings & Warr, 2003). Two expectations derived from food-chain theory are that food-chain length will shorten along gradients of increasing disturbance and lengthen along gradients of increasing productivity (Pimm, 1982; Briand & Cohen, 1987). However, laboratory and field estimates often provide contradictory evidence to these predictions (Oksanen et al., 1981; Pimm, 1982; Post et al., 2000), possibly because of a failure to account for detrital energy channels (Moore et al., 2004). Additionally, ecosystem size and connectivity effect spatial sorting of regional species pools, possibly affecting field results of studies of resource or disturbance effects on food webs (Post et al., 2000). Thus, a complex picture is emerging that emphasizes a hierarchy of historical, abiotic, and biotic factors interacting to constrain food-web characteristics (Post, 2002a; Moore et al., 2004).

Significant challenges confront description and analysis of food webs. Top consumers are commonly among the most mobile members of communities and their entry or departure from an area, and impact on local food-web dynamics, may be ephemeral and difficult to quantify. Thus, food-chain length *per se* may be difficult to measure,

particularly in spatially connected (open) systems. The trophic position of secondary or higher-level consumers is determined directly by their own diet and indirectly by the diets of their food (Morin, 1999). Recent work indicates that trophic omnivory (feeding on two or more trophic levels) is ubiquitous and has clarified limits for identification of the bases of trophic position; averaging of consumption across trophic linkages, weighted by the relative assimilation of diet components, renders trophic position a less-precise measure than envisioned with simple food-chain models. Stable isotope technology provides estimates of trophic position, as well as insight into the origins of trophic variation within an ecosystem, though interpretation of these data must be made with caution (Peterson & Fry, 1987; Vanden Zander et al., 1999; Post, 2002b).

To measure trophic relationships using isotopes, values must be compared relative to a baseline measurement that accounts for spatial and temporal flux in isotope values (Post, 2002b). Unfortunately, primary producers and bacteria introduce complex temporal and spatial variability to the interpretation of isotopic signatures within aquatic food webs. In aquatic systems, algae, microbes, and detritus are typically found in mixed assemblages that cannot be easily separated into components that photosynthesize and components recycling dead plant and animal matter. Consumers are known to feed selectively on components of algal and bacterial mats, rendering values from bulk mat samples of dubious use in food reconstruction. Further complicating analysis, stoichiometric differences between algae, bacteria and consumers affect fractionation of carbon and nitrogen (Sterner & Elser, 2002; Post, 2002b). For these reasons, primary consumers have proven a logical choice as baseline proxies for primary producers in food-web analyses (Post et al., 2000; Post, 2002b).

We report an analysis of trophic position and carbon source for selected components of food webs at 20 sites in the Florida Everglades, representing gradients of nutrient availability and hydrological disturbance. To characterize local food webs, we selected two consumers that are ubiquitous and representative of the top trophic level of animals that do not routinely move long distances. At each site, we also sampled tissue for

isotope analysis of a highly mobile predatory species that is among the top consumers of the aquatic Everglades food web. Our goal was to assess the impact of nutrient availability, disturbance, and their interaction, as driving factors shaping this wetland food web.

## Materials and methods

### Study area and study species

We collected samples in September 2002 (rainy season) and February 2003 (dry season) to maximize extremes of water level at our study sites (Table 1). We examined food-web characteristics at 20 sites within the freshwater Everglades ecosystem: 6 sites located within Shark River Slough and 3 sites within Taylor Slough in Everglades National Park; and 11 sites in Water Conservation Areas 3A and 3B (see Trexler et al., 2002 for map).

Sites were selected to encompass a gradient of hydrology and productivity typical of the landscape in areas not receiving anthropogenic nutrient enrichment. With only two exceptions, sites were located at least 5 km apart. Fish community structure and biomass is maximally variable at this spatial scale (Trexler et al., 2002; Ruetz et al., 2005). Population genetic structure is also maximized at this scale and dispersal of small fishes among these sites appears to be limited (Trexler et al., 2002; McElroy et al., 2003).

Samples of representative animal groups from primary, secondary, and higher-level consumers were collected at each site. We selected Seminole ramshorn snails (*Planorbella duryi*) and scuds (*Hyallela azteca*) as the primary consumer species based on preliminary data indicating that they bracket the range of  $\delta^{13}\text{C}$  of Everglades consumers (Loftus 2000). Also, these species are thought to primarily feed on algae and detritus, respectively (Brown, 1991; Covich & Thorpe, 1991),

Table 1. Description of study sites and matrix of pairwise comparisons of environmental parameters

A. Summary parameters by season						
Parameters	Season					
	Dry			Wet		
	Mean	StDen	CV	Mean	StDen	CV
DSD (days)	1519	842.2	55.5	1280	1052.3	82.2
HydPd (days)	350	14.4	4.1	348	17.5	5.0
GPP (mg/C/year)	715.8	796.5	111.3	1219.0	730.6	59.9
Floc TP (ug/g)				335.3	207.8	62.0
Periphyton TP (ug/g)	116.9	60.2	51.5	143.2	145.7	101.7
Stem density (#/m <sup>2</sup> )	158.1	158.8	100.4	135.8	88.6	65.2
Fish density (#/m <sup>2</sup> )	23.1	12.8	55.4	21.6	12.0	55.6
B. Correlation matrix						
	DSD	HydPd	GPP	FlocTP <sup>@</sup>	PeriTP	S.D.
HydPd	0.768*					
GPP	-0.173	-0.141				
FlocTP <sup>@</sup>	-0.043	-0.088	-0.401			
PeriTP	-0.122	-0.2	0.056	0.303		
StDen	-0.173	-0.291	0.396	0.099	0.554*	
FhDen	-0.024	-0.011	0.085	0.334	0.353	0.552*

Abbreviations are explained in the text. *N* is 19 for dry season and 20 for wet season. S.D. is the standard deviation of the mean based on inter-site variance and CV is the coefficient of variation. \* indicates  $p < 0.05$  with Dunn-Sidak correction,  $N = 39$  except for floc TP<sup>@</sup>, which has  $N = 19$ .

representing the dominant energetic pathways in Everglades food webs (Gunderson & Loftus, 1993; Browder et al., 1994; Loftus, 2000). Our  $\delta^{13}\text{C}$  data indicate that green algae, diatoms, and snails are relatively depleted in  $^{13}\text{C}$  compared to floc, bulk periphyton, emergent vascular plants, cyanobacteria, and scuds (Table 2). Cyanobacteria are generally considered to be of low palatability because of both chemical and physical defenses from grazers (Steinman, 1996), though polysaccharides sloughed by cyanobacteria may be consumed (E. E. Gaiser, personal communication). Similarly, vascular plant detritus supports bacterial communities that may be consumed. Use of basal consumers is also indicated by stoichiometric data from floc and periphyton demonstrating marked departure in C:N from basal consumers and selected consumers (Table 3). Riverine grass shrimp (*Palaemonetes paludosus*) and eastern mosquitofish (*Gambusia holbrooki*) were selected as secondary consumers, and top consumers of the aquatic food web were represented by Florida gar (*Lepisosteus platyrhincus*), a piscivorous fish found throughout the freshwater marsh. Mosquitofish and grass shrimp feed differently, possibly in separate (but overlapping) compartments of the food web; grass shrimp are benthic consumers, while mosquitofish feed throughout the water column,

though often near the water surface (Geddes & Trexler, 2003). Florida gar were not present at all short-hydroperiod sites, suggesting variation in maximal food chain length by changes in local species composition as a function of time since drying (Trexler et al., 2005) not addressed in this study. All animals were collected using standard throw trapping, sweep netting, and electrofishing techniques (Trexler et al., 2002). All samples were frozen upon collection.

Gross primary productivity, nutrient status, and hydrological data were collected concurrently with food-web samples. At each site, we collected three samples of flocculent material (floc) using a 3-cm core (Childers et al., 2002), as well as three samples of surface periphyton mat, and combined the three of each into separate composites for isotope and total-phosphorus analysis (TP). TP has been shown to be a direct indicator of primary productivity in the freshwater Everglades (McCormick et al., 2002). Gross primary production (GPP) of algal mats was also measured at all sites each season using light/dark bottle incubation (Clesceri et al., 1998). Light, water depth, and temperature were measured as covariates during the incubation experiments. Total vascular-plant stem density was also measured as an additional index of local production by these plants.

Table 2. Mean  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  isotopic values for each material analyzed for this study

	$\delta^{15}\text{N}$	S.D.	CV	$\delta^{13}\text{C}$	S.D.	CV
Floc	2.4	1.065	44.2	-29.0	9.097	31.3
Periphyton	2.6	0.986	37.4	-28.3	2.068	7.3
Green algae*	3.8			-32.0		
Diatom-dominated assemblage**	6.7	2.368	2.3	-30.7	2.253	13.6
Cyanobacteria*	2.2			-23.0		
Emergent vascular plants*	-5 to -1			-27 to -8		
Scuds	2.7	0.981	36.1	-27.7	1.958	7.1
Seminole ramshorn snail	5.0	1.629	32.3	-30.2	7.181	23.8
Riverine grass shrimp	8.2	0.833	10.2	-28.2	1.924	6.8
Eastern mosquitofish	10.0	1.039	10.4	-27.6	1.935	7.0
Florida gar	11.3	3.638	32.2	-27.6	8.643	31.3

Average values for each study site are reported.

N is 20 in all cases and is based on the mean of three replicate samples for each sample type from each site.

S.D. is the standard deviation of the mean based on inter-site variance and CV is coefficient of variation.

\*Data from Loftus (2000); \*\*Pure diatom samples were not available.

We report data from glass slides placed at one long-hydroperiod site in Shark River Slough with three samples per year in 2002 through 2004; only samples with algal material 40% or more diatoms were included.

Table 3. Carbon and nitrogen stoichiometry of samples analyzed for this study

Material	C:N ratio	N	S.D.	CV
Periphyton	13.6	41	3.751	27.6
Floc	11.3	25	3.201	28.2
Scuds	6.7	126	0.725	10.9
Seminole ramshorn snail	4.7	132	0.828	17.7
Eastern mosquitofish	4.0	123	0.150	3.8
Riverine grass shrimp	4.0	143	0.163	4.0
Florida gar	3.9	98	0.188	4.8

C:N ratio is the ratio of carbon to nitrogen for all samples analyzed, *N* indicates sample size, S.D. is the standard deviation of the mean, and CV is the coefficient of variation.

Hydroperiod data were estimated two ways: (1) days since dry (DSD), the number of days since a site last dried, and (2) hydroperiod, the average number of days a site was wet per year for the preceding 10 years.

#### Stable isotope analysis

We analyzed muscle tissue for fish and grass shrimp, whole body without shell for snails, and whole body for scuds (Pinnegar & Polunin, 1999; McCutchan et al., 2003). It was necessary to pool baseline consumers to yield adequate mass for mass-spectrometric analysis (0.4 mg needed per sample = 20 amphipods or 3 snails); all other animals were analyzed individually. Consistent with Sotiropoulos et al. (2004), our analyses indicated no effect of lipid extraction on some isotope values; so all samples were run without extraction. Tissues were dried at 55 °C for at least 24 h prior to processing. Periphyton and floc samples were decarbonated by standard fuming techniques (Chang et al., 1991). All samples were analyzed for  $\delta^{15}\text{N}$  and decarbonated samples were analyzed for  $\delta^{13}\text{C}$ . A total of 702 samples were analyzed for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  using a Finnigan Isotope ratio mass spectrometer (IRMS). All isotopic values are reported using the standard delta ( $\delta$ ) notation. Delta values were calculated using the standard equation for comparison to reference materials (DeNiro & Epstein, 1978; Minagawa & Wada, 1984). The isotopic standards used for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  were Pee Dee Belemnite (PDB) and air,

respectively. The average isotopic lab error of replicate standards was  $\delta^{15}\text{N} \leq 0.2\text{‰}$  and  $0.1\text{‰}$  for  $\delta^{13}\text{C}$ .

We used simple two-end-member-mixing models (reviewed in Post, 2002b) to estimate indices of detritivory ( $I_D$ ) and trophic position for each study site at both sampling seasons.  $\delta^{13}\text{C}$  enriches minimally ( $\sim 0\text{--}1\text{‰}$ ) as it moves through food webs (DeNiro & Epstein, 1978; Vander Zanden & Rasmussen, 2001; McCutchan et al., 2003), providing an index of the relative contribution of carbon from our algae and detritus proxies (snails and amphipods). An index of detritivory ( $I_D^{2\text{nd}}$ ) was calculated using the  $\delta^{13}\text{C}$  values for the secondary (or higher) and basal consumers ( $C_{\text{cons}}^{2\text{nd}}$ ,  $C_{\text{snail}}$ , and  $C_{\text{scud}}$ ) and all predators sampled (Post, 2002b):

$$I_D^{2\text{nd}} = (C_{\text{cons}}^{2\text{nd}} - C_{\text{snail}}) / (C_{\text{scud}} - C_{\text{snail}})$$

This index ranged from 0 to 1, with 0 indicating a detritus-based food web and 1 a primarily algal-based one. If the  $\delta^{13}\text{C}$  value for an upper trophic-level consumer exceeded a primary consumer, the difference was treated as sampling error and set to 0 or 1, indicating 100% algal or detrital energy flow. Trophic position ( $\text{TRPO}_{\text{cons}}^{2\text{nd}}$ ) was calculated as the difference in  $\delta^{15}\text{N}$  between the basal and higher-level consumers, weighted by the relative contribution of our energy-flow proxies (Post, 2002b):

$$\text{TRPO}_{\text{cons}}^{2\text{nd}} = 2 + (N_{\text{cons}}^{2\text{nd}} - ((N_{\text{scud}} * I_D^{2\text{nd}}) + (N_{\text{scud}} * (1 - I_D^{2\text{nd}})))) / 3.4.$$

Two was added to the calculated TRPO value to reflect the assumed trophic position of our baseline consumers and the ratio of  $\delta^{15}\text{N}$  values was divided by 3.4 to reflect standard estimates of nitrogen fractionation in a trophic step. Though an abstraction, use of these constants has no impact on relationships calculated and facilitates discussion in the food-web context.

We used a backwards stepping multiple regression and analysis of covariance (for effects of season) to select models best describing the relationships between  $I_D$  and TRPO with our measures of hydroperiod, nutrient status, and plant stem and fish density. This approach starts with a full model, including all possible independent

variables, and then uses standard criteria to systematically eliminate independent parameters failing to contribute to explaining the dependent variable, in order to settle on a parsimonious final model (Younger, 1979). The angular transformation (Zar, 1999) was used on  $I_D$  to meet the assumptions of regression. Floc was absent at several of our study sites in the dry season and limited these analyses to wet season for some dependent variables. Throughout, we report the coefficient of variation (CV) for comparison of variability among groups.

## Results

### *Environmental gradients*

Our study sites encompassed a range of hydrological and nutrient conditions (Table 1A). Hydroperiod (HydPd) ranged from 306 to 365 days (average for a 10-year period from, 1992 to 2002) and DSD ranged from 27 to 3304 at the time of sampling. Soil TP ranged from 93 to 999  $\mu\text{g/g}$ ; outside of alligator ponds and under rookeries, soil TP  $> 450 \mu\text{g/g}$  is considered indicative of anthropogenic enrichment in this system (Grunwald et al., 2004). Five of our 20 study sites exceeded the 450  $\mu\text{g/g}$  benchmark for soil TP value, though only 2 exceeded 500  $\mu\text{g/g}$  soil TP. Average density of emergent plant stems ranged from 9 to 497 stems/ $\text{m}^2$ . Gross primary production and stem density were more variable in the dry than the wet season, while periphyton TP was more variable in the wet season (Table 1A). Our estimates of fish density were similar between the wet and dry season, though the densities tended to be greater in the dry season (range 11–60 fish/ $\text{m}^2$  in dry, 5–42 fish/ $\text{m}^2$  in the wet).

Our independent variables were not correlated, with a few exceptions (Table 1B). Hydroperiod and DSD were positively correlated, as were emergent stem density and periphyton TP; fish density and stem density were also correlated, though not strongly (Table 1B). Gross primary production varied independently from periphyton TP and emergent stem density, as well as from fish density. Overall, four groups of variables were identified: hydrology (DSD and HydPd); nutrient status and habitat structure (periphyton TP and

emergent stem density); periphyton mat composition and/or function (GPP); competition and/or predation (fish density). We confirmed these patterns with a Principal Components Analysis (not reported).

### *Isotope signatures of periphyton and floc*

We observed marked variation in both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of periphyton and floc samples (Table 2). Periphyton and floc isotope values spanned a very wide range, surpassing expected values based on data from primary consumers (Periphyton wet: average  $\delta^{15}\text{N} = 2.6 \pm 0.46$ , average  $\delta^{13}\text{C} = -28.3 \pm 0.97$ ; Periphyton dry: average  $\delta^{15}\text{N} = 3.5 \pm 0.84$ , average  $\delta^{13}\text{C} = -27.5 \pm 1.51$ ; Floc wet: average  $\delta^{15}\text{N} = 2.4 \pm 0.45$ , average  $\delta^{13}\text{C} = -29.0 \pm 0.90$ ). Periphyton and floc displayed differing patterns of variance in  $\delta^{13}\text{C}$  (homogeneity of variance test:  $F_{2, 50} = 3.486$ ,  $p = 0.038$ ) and floc was much more variable in both isotopes than other sample types except gar (CV, Table 2). For some sites, the  $\delta^{15}\text{N}$  values of periphyton were equal to or greater than higher consumers (Table 2), possibly from a high frequency of cyanobacteria typical of Everglades periphyton.  $\delta^{13}\text{C}$  in Seminole ramshorn snails was only slightly less depleted than estimates of green algae and diatoms. In contrast,  $\delta^{13}\text{C}$  of scuds was only a little less depleted than periphyton or floc (Table 2).

As expected, floc and periphyton samples had much lower nitrogen content than animal tissues as indicated by C:N (Table 3). These samples were also much more variable in stoichiometry than the animal tissues (CV  $> 25\%$  for floc and periphyton vs.  $< 20\%$  for all animal tissues), probably indicative of the heterogeneous nature of these substrates. Scud samples were relatively nitrogen poor compared to the other animals (Table 3). This probably resulted from including carapaces in samples of these small animals, but excluding non-muscle tissue from samples of the larger animals.

### *Index of detritivory*

The majority of our  $\delta^{13}\text{C}$  data indicated our three secondary consumers were more similar to scuds in their energy source than to ramshorn snails. Our  $I_D$  ranged from 0.69 to 0.83, indicating mixed but predominately scud-like carbon flow in this food

Table 4. Summary of Index of Detritivory ( $I_D$ ) and trophic position (TRPO) for each species studied, reported by season

Parameter	Taxon	Season					
		Dry			Wet		
		Mean	S.D.	CV	Mean	S.D.	CV
$I_D$	Riverine Grass Shrimp	0.71	0.345	48.8	0.69	0.291	42.2
	Eastern Mosquitofish	0.72	0.343	47.7	0.83	0.263	31.8
	Florida gar				0.75	0.363	48.5
TRPO	Riverine Grass Shrimp	3.5	0.194	5.5	3.6	0.225	6.2
	Eastern Mosquitofish	4.0	0.182	4.5	4.1	0.237	5.7
	Florida gar				4.5	0.223	4.9

S.D. is the standard deviation of each parameter; CV is the coefficient of variation.

web (70–85% detrital carbon source; Table 4). We observed no seasonal or regional variation in  $I_D$ , though values did vary among sites within the seasons (CV ranged from 32 to 48%, Table 4). In the dry season, 9 out of 19 yielded  $I_D > 0.9$  for mosquitofish and 7 out 19 sites for grass shrimp. In the wet season,  $I_D > 0.9$  for 12 out 20 sites for mosquitofish, but only 5 out of 20 for grass shrimp. While this suggests a broader diet for grass shrimp in the wet season than for mosquitofish,  $I_D$  generally exceeded 0.7 for both species. Only a

constant remained in our final model following backwards-stepwise regression with region, season, and six environmental parameters (DSD, HydPd, GPP, PeriphytonTP, stem density, and fish density) for transformed values of  $I_D$  of grass shrimp, mosquitofish, and gar.

#### Trophic position

Mosquitofish and grass shrimp displayed increasing trophic position with increasing time following

Table 5. A. Results from analysis of trophic position for each consumer species using backwards-stepping ANCOVA model (see text for factors appearing in initial model). B. Effect sizes from significant pairwise comparisons of trophic position for mosquitofish

A. Final models								
Species	Season	Stem density		Region×season		DSD		
		F	p	F	p	F	p	R <sup>2</sup>
Florida gar	Wet	$F_{1,16} = 9.759$	0.007					0.379
Eastern mosquitofish*	Both			$F_{2,33} = 5.452$	0.009	$F_{1,33} = 14.189$	< 0.001	0.434
Grass shrimp	Both					$F_{1,35} = 4.140$	0.050	0.105
B. Effects sizes								
Pairwise comparisons								
TD–SD = 0.3								
TD–TW = 0.3								
TD–WD = 0.2								
TW–SW = 0.3								
TW–WW = 0.2								

Season indicates season used in analysis (both = wet and dry seasons). Only factors appearing in final model are shown (DSD = days since site dried).

TD = Taylor Slough dry season, SD = Shark River Slough dry season, TW = Taylor Slough wet season, WD = Water Conservation Area 3 dry season, etc).

\*One case deleted (overly influential).

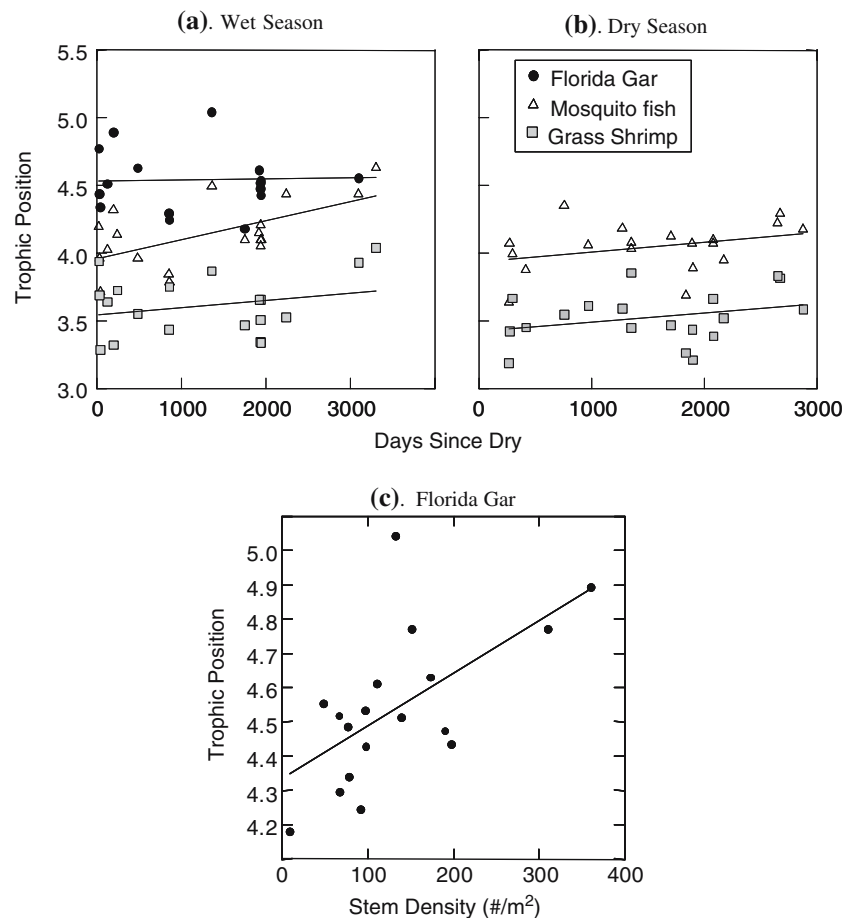


Figure 1. (a) Trophic position vs. days since dried (DSD) prior to collection for the wet season sample. (b) Trophic position vs. DSD prior to collection for the dry season sample. An insufficient number of gar could be collected at this season for statistical analysis. (c) Trophic position of Florida gar vs. density of emergent vascular plant stems at the collection site. Only wet season data are plotted.

a drought (Table 5A, Fig. 1a, b). The effect was strongest for mosquitofish, whose trophic position ranged from 4 to 4.5 in the wet season in areas ranging from recently dried to those remaining inundated for over 8 years. In contrast, trophic position of gar increased with emergent stem density in the area where they were captured in the wet season (Table 5A, Fig. 1c). Estimated trophic position for gar varied from 4.3 to 4.9 in the wet season, comparing sites with stem density near 0 to sites with over 350 stems  $m^{-2}$ .

Only mosquitofish displayed seasonal variation in trophic position, and this varied among regions (Table 5A). Their estimated trophic position was greatest in Taylor Slough compared to the other two regions in both seasons (typically by 0.2–0.3 trophic positions, Table 5B). Trophic position in

Taylor Slough was greater in the dry season than in the wet.

## Discussion

Though food-chain length may be expected to increase as availability of limiting nutrients increase, field studies have often failed to find such patterns (Power et al., 1996; Post, 2002a). Our data also fail to support this expectation. Neither of our resident taxa (mosquitofish and grass shrimp) displayed any relationship between trophic position and measures of nutrient status or indicators of productivity. Trophic position of our mobile predator (gar) was correlated with stem density, one of our measures of primary



production. In this case, we believe trophic position was affected by habitat structure through its influence on prey availability, which is often affected by macrophyte density in aquatic systems (Savino & Stein, 1982, 1989). This study included sites among the most oligotrophic in the Everglades and sites with relatively low levels of anthropogenic enrichment, but not sites experiencing dramatic anthropogenic eutrophication as found in the northern Everglades (see map in Davis, 1994). It remains to be seen if our results would be changed by inclusion of these more enriched sites. In contrast, we found that time since a marsh dried was positively correlated with trophic position of two secondary consumers in this ecosystem. Other work has shown that large predatory fishes are excluded by marsh drying and require months to return from refuges, and even longer to gain robust population sizes (Chick et al., 2004; Trexler et al., 2005). Thus, droughts act as an environmental filter, restricting food-chain length by eliminating large predatory fish species. Our findings suggest that trophic position within the food web is also shifting in ways that further reduce food-chain length following drying. We found no evidence that the relative contribution of carbon from either of our end-members contributed to these changes in trophic position. It is unclear if the shifting trophic position of intermediate consumers resulted from adding species of consumers feeding lower in the web, or from diet shifts to consume more high-trophic-level prey, or both. Also, our data provided no evidence of humped relationships of trophic position and time since drought as described by Power et al. (1996), even though our study sites bracketed the full range of time periods since drying found in the ecosystem.

If scuds are indeed detritivores in the Everglades, our study provides empirical support for a dominant role of detritus for carbon flow in the Everglades. Past work by Browder et al. (1994) suggested an important photoautotrophic route of carbon and energy flow in this ecosystem. Our data do not undermine her conclusion that periphyton mats are critical elements to energy flow in the ecosystem and may be considered the 'base' of the food web. However, their contribution may come after death of the algal components, from materials sloughed-off as the algal

constituents grow, or from bacteria using sloughed or dead material as food. Recent work has supported the hypothesis that much of Everglades periphyton mats are not directly consumed by grazers (Geddes & Trexler, 2003). Our data do not support a route of carbon from vascular plant detritus, unless it becomes depleted in  $\delta^{13}\text{C}$  after death because all plants measured by Loftus (2000) were more enriched than any consumers sampled here.

Choice of basal consumers is critical to the success of an isotopic study such as this. Our work failed to determine if detritus yields carbon values comparable to our putative detritivore, scuds, because we have been unable to isolate it and obtain isotopic estimates. While scuds have similar carbon isotopic values to bulk periphyton and floc, these values are intermediate between the major algal components of the mats, diatoms and cyanobacteria, and may be the result of mixture. Alternatively, scuds may be consuming bacteria that are assimilating carbon from mixed algal sources. Further work is needed, possibly using lipid biomarkers (Cook et al., 2004), to delineate the source of organic carbon more clearly. Similar questions remain about our  $\delta^{13}\text{C}$  findings from Seminole ramshorn snails. Snail tissues were less depleted in  $\delta^{13}\text{C}$  than green algae from Shark River Slough, and their  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values were similar to those we have estimated from diatoms. Several studies have documented snails displaying little fractionation of algal diets, including in controlled feeding trials (Kurata et al., 2001). While this may in part be from assimilation of bacterial or detrital materials ingested with diatoms, it also appears that mollusks and crustaceans display less nitrogen fractionation of their diets than do vertebrates (Vanderklift & Ponsard, 2003). Midge larvae of the subfamily Chironominae are often identified as consuming primarily diatoms, along with detritus and other algae (Armitage et al., 1995, p. 143), and Loftus (2000) reported similar isotopic signature for these midges collected at one of our study sites to our findings on snails.

Trophic position of Florida gar displayed a different pattern than our intermediate level consumers. Florida gar in the Everglades have a narrow diet breadth (Loftus, 2000) feeding on other fish, amphibians, grass shrimp, and crayfish. Gar

can move long distances (Snedden et al., 1999) and tracking studies in the Everglades have shown Florida gar to travel 5 km or more in one day when water levels drop locally in the dry season (Wolski & Trexler, unpublished data). However, in the wet season when our isotopic data were gathered, most radiotagged gar moved relatively little, displaying nighttime foraging movements from depressions and ponds and returning to the same area each day. Gar in areas of dense vegetation may have greater success capturing small fish. The density of small fish (intermediate level consumers) was positively correlated with emergent stem density in this study and such correlations are commonplace in the literature (Savino & Stein, 1982; Rozas & Odum, 1998). However, interpreting such a correlation literally may be unwise, because many environmental gradients covary with stem density, notably nutrient levels, and may be more directly tied to the observed pattern in trophic position.

Key questions remain about the nature of 'detrital' carbon flow in this ecosystem. For example, it is unclear if a microbial loop (Fenchel, 1988) provides a major route of energy flow in the Everglades, though this seems to be the likely linkage between higher consumers and the abundant but defended and unpalatable cyanobacterial primary producers. Such a link could explain the lack of a trophic position-productivity relationship in our data (Moore & Hunt, 1988; Moore et al., 2004). Also, bacteria metabolizing carbon from deceased cyanobacteria, mixed with carbon from diatoms and green algae, could yield the intermediate  $\delta^{13}\text{C}$  we observed for amphipods and higher consumers. This study represents a first effort at large-scale characterization of food webs in the Everglades and much work remains tracing routes of energy flow to fully understand the functioning of this wetland food web.

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