Biotic and abiotic determinants of intermediate-consumer trophic diversity in the Florida Everglades

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Abstract. Food-web structure can shape population dynamics and ecosystem functioning and stability. We investigated the structure of a food-web fragment consisting of dominant intermediate consumers (fishes and crayfishes) in the Florida Everglades, using stable isotope analysis to quantify trophic diversity along gradients of primary production (periphyton), disturbance (marsh drying) and intermediate-consumer density (a possible indicator of competition). We predicted that trophic diversity would increase with resource availability and decrease after disturbance, and that competition could result in greater trophic diversity by favouring resource partitioning. Total trophic diversity, measured by niche area, decreased with periphyton biomass and an ordination axis representing several bluegreen algae species. Consumers’ basal resource diversity, estimated by δ13C values, was similarly related to algal community structure. The range of trophic levels (δ15N range) increased with time since the most recent drying and reflowing event, but decreased with intermediate-consumer density, and was positively related to the ordination axis reflecting increases in green algae and decreases in filamentous bluegreen algae. Our findings suggest that algal quality, independent of quantity, influences food-web structure and demonstrate an indirect role of nutrient enrichment mediated by its effects on periphyton palatability and biomass. These results reveal potential mechanisms for anthropogenic effects on Everglades communities.

Additional keywords: competition, disturbance, food web, nutrients.

Introduction

Determining factors that shape food-web structure has long been a central goal in ecology, and is especially critical given the increasing need to identify relationships among food-web structure, food-web stability and ecosystem functioning in the face of anthropogenic environmental changes (e.g. McCann 2000; Duffy et al. 2005; Rooney et al. 2006). Food webs reveal how abiotic and biotic interactions structure communities (e.g. Menge and Sutherland 1987) and mechanisms by which altering population densities or habitats can impact communities (e.g. Pace et al. 1999; Layman et al. 2007b). Food-web structure has been empirically linked to ecosystem functioning (e.g. Carpenter et al. 1987; Schindler et al. 1997; Duffy et al. 2005) and there is a general consensus that critical components of food webs, such as trophic interactions, complementarity and redundancy, have important effects on ecosystem properties (Hooper et al. 2005).

Trophic diversity, illustrated by realised food webs that represent feeding links and energy flow (Post 2002a), is a function of overall species richness and the range of trophic positions present (food-chain length). Decades of research seeking processes that determine trophic diversity have identified productivity, disturbance and competition as key mechanisms. However, the nature and strength of these relationships are highly context-dependent (Menge and Sutherland 1987; Mackey and Currie 2001; Mittelbach et al. 2001). Both productivity and disturbance have also been implicated in determining food-chain length, although evidence is mixed and the relationships can be positive or negative (Post 2002a). Thus, how productivity, disturbance and competition alter food-web structure, by modifying community structure and/or trophic interactions, remain important questions for most systems. Community-wide trophic metrics linking trophic diversity to environmental gradients offer one path towards improved understanding of these relationships (Layman et al. 2007a).

By measuring realised trophic roles with greater resolution than traditional functional groupings, stable isotopes may be more informative for studies of food-web structure than gut contents used alone (Layman et al. 2007a). Analysis of stable isotopes is a tool for examining diet when potential resources are associated with natural variation in isotope ratios. Nitrogen ratios (δ15N) tend to reflect trophic position because there is a stepwise enrichment in 15N with each trophic level, whereas carbon ratios (δ13C) reflect basal carbon sources because there is relatively little change associated with trophic transfers (Minagawa and Wada 1984; Peterson and Fry 1987; Post 2002b). Trophic parameters measured using stable isotope ratios, including trophic diversity, trophic similarity, carbon range and nitrogen range, have been proposed as quantitative community-wide metrics for describing food-web structure (Layman et al. 2007a). Trophic diversity, the total size of a food web, can be estimated as the total area encompassing species in a δ13C-δ15N bi-plot. Unlike food-chain length, both the range of trophic positions and
diversity within trophic levels influence trophic diversity. The degree of trophic similarity among species in the food web can be measured as the mean nearest-neighbour distance between species points in δ¹³C–δ¹⁵N bi-plot space. As trophic diversity can be highly sensitive to outliers, this provides some measure of average similarity between species or ‘packing’ within the trophic niche. Additionally, ranges of δ¹³C and δ¹⁵N values estimate diversity of basal resources and vertical trophic positions, respectively. Therefore, geometric measurements based on isotope data offer a newly described approach for measuring functional features of food-web structure.

Oligotrophic marshes of the Florida Everglades have gradients of both limiting nutrients (phosphorus) and hydrological disturbance (seasonal drying of the marsh) (Noe et al. 2001; Trexler et al. 2005). These gradients result from natural topography, anthropogenic management of water levels and anthropogenic canals that act as conduits for nutrient-enriched water from urban and agricultural areas. Nutrient enrichment and hydrology have profound effects on algal community structure and abundance (McCormick et al. 1996; Gaiser et al. 2006; Gottlieb et al. 2006), which likely spread to consumers (e.g. King and Richardson 2007; Liston et al. 2008). Small fishes (<8 cm) and macroinvertebrates are key intermediate consumers in this ecosystem, representing a large portion of the biomass in aquatic communities (Rader 1999; Turner et al. 1999). They also comprise an important trophic link between basal primary producers (predominantly periphyton mats composed of benthic algae, bacteria, fungi and detritus) and larger vertebrates, such as wading birds (Rader 1999). Overall, densities of small fishes and invertebrates typically decrease with disturbance and increase with nutrient enrichment (Turner et al. 1999; Gaiser et al. 2005; Trexler et al. 2005), but eventually decline at highest phosphorus levels with the disappearance of periphyton (King and Richardson 2007; Liston et al. 2008). Trophic positions of intermediate consumers may also shift following a disturbance (Williams and Trexler 2006), suggesting that environmental gradients help determine trophic interactions in addition to simple abundance patterns.

Most studies in the Everglades and elsewhere have focussed on how abiotic gradients and biotic interactions alter abundances of species or taxonomic groups, which can dramatically affect food webs (e.g. keystone species). Yet, even without removing particular species, environmental gradients can influence available prey and/or diet selection in ways that change the patterns of energy flow through the food web (i.e. changes in functional diversity; Post et al. 2000). Species whose densities are resilient to environmental change may nonetheless play different roles in the community if their diets shift in response to altered prey distributions (Layman et al. 2007b). Competition can also modify trophic interactions by forcing species to further partition available prey (Schoener 1974), even when having little effect on density. Understanding foraging decisions of consumers is essential for obtaining biologically meaningful interpretations of food-web structure and stability (Beckerman et al. 2006; Uchida and Drossel 2007). To better understand how abiotic and biotic gradients influence food-web structure via trophic interactions in the Everglades, we examined trophic structure revealed by stable isotopes in a food-web fragment composed of small fishes and crayfishes (henceforth ‘intermediate consumers’). We expected that trophic interactions would be strongly affected by nutrients and drying events, and possibly by competition. Specifically, we predicted that: (1) increases in food availability and quality (mediated by nutrient levels) would support more diverse trophic roles, (2) disturbance would have the opposite effect by reducing prey levels and (3) competition could increase trophic diversity by favouring resource partitioning.

Materials and methods

Study system

In the Florida Everglades, communities in wet-prairie slough habitats are typically composed of large standing stocks of periphyton mats (Turner et al. 1999), spikerush-dominated (Eleocharis celata) emergent vascular plants, infaunal macroinvertebrates (Liston 2006), larger invertebrates (crayfishes, insects), several species of small fishes (Trexler et al. 2002) and, in long-hydroperiod areas, large piscivorous fishes (Chick et al. 2004), as well as larger consumers such as amphibians, reptiles, mammals (muskrats and otters) and wading birds. We sampled aquatic communities in 34 sites across the Everglades (∼25°19′ N, 80°56′W) in November and December 2005 (Fig. 1). These sites were separated by 1.7–137.7 km and past research has indicated that sites separated at this scale can be treated as independent (Trexler et al. 2002; Ruetz et al. 2005).

Sampling procedure

We employed a standardised throw-trap sampling protocol (Jordan et al. 1997) with three replicates per site. We used 1-m²
throw-traps constructed from copper pipe and covered on four sides with 1.5-mm mesh to collect small fishes (<8 cm standard length) and large invertebrates. Traps were cleared with a bar seine (1.5-mm mesh) and two dip nets (1- and 5-mm mesh). Invertebrates were killed upon collection by immersion in an MS-222 (tricaine methanesulfonate) bath. All aquatic animals captured were placed on ice in the field and then frozen at −17.7°C for ~7 months before sample processing.

We defined intermediate-consumer density as the total density of fishes and crayfishes, calculated for each site as the mean of the total counts (all species) over the three throw-trap replicates. We collected periphyton samples from within each throw trap and processed them for algal community composition, ash-free dry mass (AFDM) (g m−2), percentage of nitrogen and organic content, total phosphorus content (TP) (µg g−1 dry), and chlorophyll a mass (µg m−2) and concentration (µg g−1 dry) (as described in Gaiser et al. 2006). Because nutrients are rapidly absorbed by biota, periphyton TP is used as a biotic indicator of nutrient enrichment (Gaiser et al. 2006). Hydrological data were obtained using the Everglades Depth Estimation Network (EDEN) hydrological estimation tool (http://sofia.usgs.gov/eden/stationlist.php, accessed 16 April 2008). Disturbance was measured by time since flooding, calculated as the number of days since the marsh surface was flooded after the most recent drying event (water levels <5 cm). This estimate of disturbance measures the time a system has had to recover following a drought, such that sites with a short time since flooding have been subjected to more recent disturbance. The Everglades have distinct wet (May–November) and dry (December–April) seasons based on rainfall and our sampling was conducted in the late wet season, when marshes were near peak water depths after summer rains.

Isotope sampling and niche measures

Because complete isotopic sampling of an entire food web is generally impractical due to the number of species and size limitations for small organisms (e.g. Polis 1991), we measured a food-web fragment consisting of five species whose abundance reflects dominant trends in the community composed of medium-sized, intermediate consumers (small fishes and crayfishes). Thus, we included in our analysis three relatively common fish species that represent diverse roles in the food web: a predominantly herbivorous species (flagfish, Jordanella floridae Goode and Bean) and two omnivorous species that predominantly consume animals but also some algae, plants and detritus (eastern mosquitofish, Gambusia holbrooki Girard; golden topminnow, Fundulus chrysotus Günther). We also included the two species of omnivorous crayfish found in the Everglades, the Everglades crayfish (Procambarus alleni Faxon) and the slough crayfish (P. fallax Hagen), which were non-overlapping in our samples (i.e. were never both collected at the same site). Consistent with other studies (e.g. Dorn and Trexler 2007), Everglades crayfish were present only in short-hydroperiod sites, whereas slough crayfish were present in long-hydroperiod sites.

We selected this subset of intermediate consumers to allow maximum coverage of the large spatial scale sampled. Thus, our analysis encompasses a greater number of independent sites than similar studies, but may include fewer species at each site. Despite measuring isotopes for only five species, those species were common (average ~58% of the total abundance of small fishes and crayfishes) and their density and biomass were correlated with values for all small fishes and crayfish from throw-trap samples combined (Spearman rank correlations, rs = 0.69, P < 0.001 and rs = 0.92, P < 0.001, respectively). The relative abundances of the five species were correlated with the relative abundances of all small fishes and crayfish combined (Mantel test on Bray–Curtis dissimilarity matrices of standardised data, 2000 permutations, rs = 0.69, P = 0.05). Thus, these species represent dominant trends in the density, biomass and community-structure patterns of the intermediate-consumer community at large. Furthermore, these species reflect the isotope range of common fishes (Lofus 2000). However, eastern mosquitofish, golden topminnows and flagfish were absent from throw-trap samples at 1, 4 and 13 sites, respectively (see ‘Data analysis’ below).

Fish and crayfish samples obtained from throw-trap samples were thawed and muscle was removed from each individual for isotope analysis (one to three individuals per species per site). Muscle tissue was removed from the caudal region on both sides of the fish and from the tail of the crayfish. Tissue was rinsed with deionised water and dried at 55–60°C for ≥24 h before being ground into a fine powder and analysed for δ13C and δ15N with an isotope ratio mass spectrometer (IRMS) (Finnigan, San Jose, CA, USA) at the Stable Isotope Laboratory at Florida Internation University. Isotope values are reported in standard delta (δ) notation (Peterson and Fry 1987), calculated using Pee Dee Belemnite as a standard for δ13C and air as a standard for δ15N. The standard deviation of sample replicates for this analysis was 0.08‰ for δ13C and 0.05‰ for δ15N. Past work revealed no impact of extracting lipids from muscle on δ13C and δ15N data from Everglades consumers (Williams and Trexler 2006). Additionally, the organisms in this study had average C:N values ≤3.5 with little variation between species and lipid extraction is thought to be unnecessary for aquatic animals with such low C:N values (Post et al. 2007). Based on these findings, we did not extract lipids because it was difficult to obtain sufficient tissue mass for isotope analysis for these small organisms.

Following Layman et al. (2007a), we measured several important aspects of the community’s trophic niche as represented in δ13C–δ15N bi-plot space for each site, using mean δ13C and δ15N values from each species for each site. Total niche area was defined as the convex hull area (Cornwell et al. 2006) encompassing the trophic positions of the species and was calculated using the program QHULL (available from http://www.qhull.org/, accessed 16 January 2008; Barber et al. 1996). We defined mean nearest-neighbour distance as the mean of the Euclidean distances between each species and its nearest neighbour. We calculated δ13C range and δ15N range by subtracting the lowest δ13C and δ15N values from the highest δ13C and δ15N values, respectively. Potential pitfalls in applying stable isotope analyses to ecological data are well known (Gannes et al. 1997; Post 2002b; Barnes et al. 2008), but in many cases possible weaknesses are outweighed by benefits (e.g. long-term integration of complex trophic pathways; Post 2002b). Additionally community-wide metrics may be less vulnerable to biases caused by shifting isotopic baselines and species-specific...
patterns of isotope fractionation and routing because they are measured on a relative scale, where relationships between the same set of species are of interest (Layman et al. 2007a). A potential problem with applying these niche metrics to isotope data is the arbitrary nature of the $\delta^{13}C$ axis—two resources may exhibit very large or very small differences in $\delta^{13}C$ while they are still simply two different resources (Hoeinghaus and Zeug 2008). However, major differences in niche metrics resulting from these arbitrary patterns are more likely when different systems are being compared and this approach still offers some insight when there are many resources that cannot be easily partitioned using isotopes (Layman and Post 2008).

Data analysis

Algal species, important basal resources in this food web, are likely to vary in their quality as food and thus food quality may be represented by algal community composition. Nonmetric multidimensional scaling (NMDS) conducted with PRIMER-5 (Primer-E Ltd, Ivry-Bridge, UK) was used to ordinate sites based on algal species, resulting in gradients where sites are positioned according to their dissimilarity in relative abundances of species (McCune and Grace 2002). Dissimilarity matrices were based on Bray–Curtis dissimilarity indices calculated on untransformed, standardised algal community data after rare species (present in <5% of sites) were removed (McCune and Grace 2002). Resulting axis scores from three-dimensional solutions were obtained (stress = 0.10) and used as independent variables in regression models (McCune and Grace 2002). We used Kendall’s tau-b ($\tau$) nonparametric correlations between NMDS axis scores and relative abundances of species to interpret the axes (Beals 2006). We considered a species to be strongly correlated with an axis if their correlation was $|\tau| \geq 0.40$.

We developed separate regression models for each niche metric that included terms representing measures of disturbance, resource availability and quality, and competition, factors that influence intermediate-consumer density and possibly trophic roles. Full models for each included: time since flooding, periphyton AFDM, periphyton algal NMDS axes, intermediate-consumer density and interaction terms for periphyton variables and density (after centering). We sought to examine trophic changes resulting from dietary shifts of co-occurring species, so to address possible biases caused by the occasional absence of one of the species we included flagfish presence as a binary variable in the analyses as they were missing from more than one-third of the sites. We also included interaction terms between flagfish and variables containing density (to check whether slopes were different depending on flagfish presence). Because eastern mosquitofish and golden topminnows were missing from only a few sites, we could not include them as explanatory variables and instead examined leverage and influence diagnostics (Belsley et al. 1980) to determine whether these sites had strong effects on parameter estimates obtained in regression analyses. Regressions were conducted using PROC GLM in SAS 9.1 (SAS Institute Inc., Cary, NC, USA) with Type III sums of squares (partial F tests). We used stepwise-backward elimination based on a criterion of $\alpha = 0.05$ for partial F tests to select final models, with main effects remaining in the model unless relevant interaction terms were first removed. Residuals were examined to ensure that assumptions of linear regression were met, and when assumptions were clearly violated, log10($x + 1$) transformations were used to meet assumptions. Spearman correlations between main effects were $|r_s| \leq 0.75$ except for periphyton AFDM and density ($r_s = -0.76$), indicating that despite some correlation between environmental variables as is common in ecological data, there was sufficient variation to include these explanatory variables. Standardised $\beta$ weights adjust parameter estimates by their standard deviations and thus can be helpful guides as to the relative importance of each variable (Tabachnick and Fidell 2007). The adjusted $R^2$ for each model is the total proportion of variance in the dependent variable explained by the model (adjusting for model complexity), while the squared semipartial coefficients express the variance explained that can be uniquely attributed to each explanatory variable (Tabachnick and Fidell 2007). When models contain multiple explanatory variables, simple plots of the dependent variable against an explanatory variable can be misleading since the effects of other explanatory variables have not been accounted for. Therefore, we illustrated the results of the regression models using partial regression plots, which plot the residuals of the dependent variable against the residuals of each explanatory variable after each has been separately regressed on the other explanatory variables in the model (Belsley et al. 1980). Although the axes are not in the same scale as the original variables, the plots accurately show the relationships tested by regression (i.e. the slope equals the partial regression coefficient) and allow visual inspection of the scatter of points and possible influential cases.

Results

Abiotic and biotic gradients

Our study sites spanned a range of disturbance (time since flooding), nutrient (periphyton TP) and biotic (periphyton AFDM and intermediate-consumer density) gradients typical of other studies of the Greater Everglades, with the exception of areas that have high nutrient levels and constant water inundation (cf. Trexler et al. 2002; Gaiser et al. 2006; King and Richardson 2007) (Table 1). The algal NMDS axes reflected changes in the relative abundance of species associated with phosphorus levels (Table 2). NMDS Axis 1 was strongly positively correlated with the filamentous bluegreen alga Schizothrix sp. and negatively correlated with several species of diatoms typically associated with low phosphorus levels (Gaiser et al. 2006). This pattern was also reflected by the correlation between Axis 1 and the relative abundances of physiognomic groupings. NMDS Axis 2 was negatively associated with the bluegreen alga Aphanothece sp. and several green algae and diatom species, including members of the genus Uronema, which are indicators of moderate to high phosphorus levels (Gaiser et al. 2006). Across broader taxonomic categories, Axis 2 was most strongly related to the relative abundance of green algae and more weakly associated with filamentous bluegreen algae. NMDS Axis 3 increased with the relative abundance of bluegreen algae, particularly Gloeothecce sp. and, although it decreased with some diatom species, it was not correlated with diatom relative abundance in general. NMDS Axes 1 and 2 were correlated with periphyton TP (Spearman correlation: $r_s = -0.62$ and $-0.45$, respectively) and to a lesser
Thus, eastern mosquitofish contributed strongly to high levels of intermediate-consumer density and crayfish predominated at higher intermediate-consumer densities. Periphyton TP was negatively correlated with measures of periphyton biovolume and biomass, but increased with organic content and percentage nitrogen (Table 3). Phosphorus levels were positively correlated with the relative abundance of green algae and diatoms, but negatively correlated with the relative abundance of bluegreen algae and filamentous bluegreen algae (Table 3). Thus, our findings join those of several experimental and observational studies suggesting that phosphorus enrichment tends to decrease periphyton quantity (biovolume, aerial cover), but increase periphyton quality (proportion of palatable algal species, C : N ratio, percentage of organic content).

Intermediate-consumer density was positively correlated with eastern mosquitofish density ($r_s = 0.70, P < 0.001$) and with golden topminnow ($r_s = 0.38, P = 0.027$), but not with flagfish ($r_s = 0.07, P = 0.693$) or crayfish density ($r_s = -0.22, P = 0.205$). The proportion of total density composed of fishes was significantly correlated with eastern mosquitofish ($r_s = 0.68, P < 0.001$), flagfish ($r_s = -0.41, P = 0.017$) and crayfish densities ($r_s = -0.84, P < 0.001$). Mean relative abundances of eastern mosquitofish and crayfish were 0.25 and 0.24, compared with 0.05 for golden topminnows and 0.04 for flagfish. Thus, eastern mosquitofish contributed strongly to high levels of intermediate-consumer density and crayfish predominated at lower intermediate-consumer densities.

**Regression results for niche metrics**

Mean $\delta^{13}C$ and $\delta^{15}N$ values across all sites are shown for each species in Fig. 2. Niche area was positively correlated with mean nearest-neighbour distance ($r_s = 0.52, P = 0.001$) and $\delta^{13}C$ range ($r_s = 0.81, P < 0.001$), but not $\delta^{15}N$ range ($r_s = 0.29, P = 0.101$). Mean nearest-neighbour distance increased with both $\delta^{13}C$ range ($r_s = 0.45, P = 0.008$) and $\delta^{15}N$ range ($r_s = 0.38, P = 0.026$), even though the latter were unrelated ($r_s = -0.10, P = 0.565$). Despite these correlations, niche metrics varied in their response to periphyton quantity (periphyton AFDM), periphyton quality (algal NMDS axes), disturbance (time since flooding) and competition (intermediate-consumer density) (Table 4). Log-transformed niche area increased when flagfish were present and decreased with increasing values of periphyton AFDM and algal NMDS Axis 3 (Fig. 3). Although the single site without eastern mosquitofish had high leverage and influenced the relationship between niche area and algal NMDS Axis 3 (Fig. 3c), this relationship was still significant when that observation was removed. Log-transformed mean nearest-neighbour distance depended only on algal NMDS Axis 2, but this relationship hinged entirely on a single site (the site with the highest nearest-neighbour distance) and may therefore be unimportant (i.e. the model contained no significant predictors when that site was excluded) (Fig. 4). Alternatively, low power may have limited our ability to document the strength of this effect since that site was one of only four with high nutrient levels and relatively low time since flooding. Algal NMDS Axis 3 was negatively related to log-transformed $\delta^{13}C$ range (Fig. 5). Like niche area, the site missing eastern mosquitofish heavily influenced, but did not solely determine, this relationship. Finally, $\delta^{15}N$ range increased with time since flooding (Fig. 6b) and decreased with algal NMDS Axis 2 (Fig. 6c). The regression model suggested that effects of intermediate-consumer density and flagfish presence on $\delta^{15}N$ range were related (Fig. 6e). The model is consistent with the hypothesis that, when flagfish were present, increasing density resulted in a decrease in the range of $\delta^{15}N$ values (Table 4).

**Discussion**

We found strong support for the different roles of disturbance, resources and consumer density in determining patterns of trophic structure for food webs in the Florida Everglades. Importantly, we identified changes in trophic diversity of dominant intermediate consumers resulting from apparent niche shifts, contributing to the understanding of how food webs change as a function of these gradients beyond what is known from studies of fish density and community structure.

**General results for niche metrics**

Our regression model suggests that the trophic diversity of intermediate consumers, as measured by total niche area, was influenced by algal community structure (NMDS Axis 3), was higher at lower levels of periphyton AFDM and increased when flagfish were present. The latter result was expected, since inclusion of flagfish in our food web should expand the community trophic niche (Fig. 2). By examining the algal species and

Table 1. Descriptive statistics for environmental gradients, consumer density and niche metrics ($n = 34$)

<table>
<thead>
<tr>
<th>Variables</th>
<th>Range of values</th>
<th>Mean (s.e.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Periphyton total phosphorus (µg g⁻¹ dry)</td>
<td>53–617</td>
<td>239 (30)</td>
</tr>
<tr>
<td>Time since flooding (days)</td>
<td>147–2164</td>
<td>537 (107)</td>
</tr>
<tr>
<td>Periphyton ash-free dry mass (g m⁻²)</td>
<td>0.6–540</td>
<td>139 (29)</td>
</tr>
<tr>
<td>Intermediate-consumer density (# m⁻²)</td>
<td>4–44</td>
<td>16 (1.8)</td>
</tr>
<tr>
<td>Total niche area</td>
<td>0.1–7.1</td>
<td>2.4 (0.31)</td>
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<tr>
<td>Mean nearest-neighbour distance</td>
<td>1.10–3.59</td>
<td>1.81 (0.084)</td>
</tr>
<tr>
<td>$\delta^{13}C$ range</td>
<td>0.3–3.8</td>
<td>1.6 (0.18)</td>
</tr>
<tr>
<td>$\delta^{15}N$ range</td>
<td>2.3–5.9</td>
<td>4.2 (0.14)</td>
</tr>
</tbody>
</table>
Table 2. Kendall’s tau correlations between algal nonmetric multidimensional scaling axis scores and relative abundances for species and physiognomic groups

<table>
<thead>
<tr>
<th>Species (τ)</th>
<th>Axis 1</th>
<th>Axis 2</th>
<th>Axis 3</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Schizothrix</em> sp. (0.55)</td>
<td>Aphanathece sp. (−0.52)</td>
<td>Gloeothecae sp. (0.48)</td>
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<tr>
<td><em>Fragilaria</em> synmota (−0.62)</td>
<td><em>Eunotia</em> sp. (−0.45)</td>
<td><em>Encyonopsis</em> egg01 (−0.45)</td>
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</tr>
<tr>
<td><em>Encyonema</em> t0sp01 (−0.57)</td>
<td><em>Pinnularia</em> gibba (−0.44)</td>
<td><em>Functula rhombides var. crassinervia</em> (−0.45)</td>
<td></td>
</tr>
<tr>
<td><em>Encyonema</em> t0tana (−0.53)</td>
<td><em>Encyonopsis</em> subminuta (−0.44)</td>
<td><em>Pinnularia</em> gibba (−0.44)</td>
<td></td>
</tr>
<tr>
<td><em>Encyonema</em> etgglad (−0.51)</td>
<td><em>Functula rhombides var. crassinervia</em> (−0.44)</td>
<td><em>Brachysira</em> brebissonii (−0.42)</td>
<td></td>
</tr>
<tr>
<td><em>Mastogloia</em> smithi (−0.48)</td>
<td><em>Bulbochaete filamentosa</em> (−0.42)</td>
<td><em>Nitzchia</em> paeon var. debilis (−0.40)</td>
<td></td>
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<tr>
<td><em>Braha</em> neoegora (−0.40)</td>
<td><em>Cosmarium</em> phaseolus (−0.42)</td>
<td><em>Gonatozygon</em> sp. (−0.41)</td>
<td></td>
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<td></td>
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<td></td>
<td></td>
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<tr>
<td>Physiognomic group (τ)</td>
<td></td>
<td></td>
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<tr>
<td>Bluegreen algae</td>
<td>(0.36)</td>
<td>(−0.18)</td>
<td>(0.42)</td>
</tr>
<tr>
<td>Filamentous bluegreen algae</td>
<td>(0.55)</td>
<td>(0.34)</td>
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</tr>
<tr>
<td>Green algae</td>
<td>(−0.18)</td>
<td>(−0.42)</td>
<td></td>
</tr>
<tr>
<td>Diatoms</td>
<td>(−0.80)</td>
<td>(0.11)</td>
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</tr>
</tbody>
</table>

Trexler (2006) reported a similar finding for eastern mosquitofish δ15N values, which were inversely related to food web diversity. The diversity of trophic levels, as estimated by NMDS Axis 3, suggested that greater availability of palatable species contributed to the diversity of basal resources of NMDS Axis 3, suggesting that greater availability of palatable species. Our results suggest that the breadth of basal resources and trophic positions responded differently to the predators. Like NMDS Axis 3, suggesting that greater availability of palatable species. Our results suggest that the breadth of basal resources and trophic positions responded differently to the predators. Like NMDS Axis 3, suggesting that greater availability of palatable species.
Trophic diversity of intermediate consumers

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each species across all sites. δ decrease their 

Fig. 2. δ13C–δ15N bi-plot showing mean values and standard errors for each species across all sites.

(as measured by total fish and crayfish abundance) appeared to decrease their δ15N range, contrary to our predictions based on resource partitioning. This suggests that as consumer density, and possibly competition, increases, the range of trophic levels nonetheless declines rather than increases as would be expected by decreasing trophic overlap through niche partitioning. A possible explanation for this is that high consumer density actually decreased the abundance of preferred prey and forced fish to feed on lower trophic levels, as niche partitioning may only be possible when alternative niches are actually available. Others have suggested that fish predation can limit macroinvertebrate abundances in the Everglades (Turner et al. 1999; Liston 2006). Algal NMDS Axis 2, but this relationship was contingent on a single site, suggesting this pattern is not robust. However, because the site was one of only four sites with short times since flooding and high nutrient levels, it is possible that this trend is genuine and would be better evaluated with increased representation of such sites. The observation that δ15N range was also negatively related to Axis 2 provides some support for this conclusion.

Interestingly, some factors that likely affected δ13C and/or δ15N range were not significant in the final models for total niche area or mean nearest-neighbour distance, or vice versa. Because total niche area and nearest-neighbour distance integrate changes in both δ13C and δ15N and niche area does so multiplicatively, they may possess emergent properties that are not evident for either δ13C or δ15N range alone. This is likely because δ13C and δ15N ranges were uncorrelated, suggesting that niche area and neighbour distances can increase via different combinations of mechanisms. Thus, even though the niche metrics were generally correlated, if δ13C and δ15N ranges change along different environmental gradients, their effects on neighbour distances and total area may cancel each other out.

Roles of algal biomass and species composition

In this study, the relative abundances of algal species were associated with an increase in the trophic diversity of intermediate consumers. Compositional changes associated with phosphorus enrichment (NMDS Axis 2) and others apparently unrelated to nutrients (NMDS Axis 3) contributed to their trophic diversity, likely by increasing the availability of preferred prey species and decreasing the availability of unpalatable ones. Most of the consumer species in the present study are omnivorous, so periphyton availability and composition may affect them directly as food, and also indirectly as food and habitat for their invertebrate prey (e.g. McCormick et al. 2004; Liston 2006). Algal community structure was an important predictor for more measures of intermediate-consumer trophic diversity (niche area, carbon range, nitrogen range) than periphyton biomass (niche area only), and explained a similar amount of variance in niche area as periphyton biomass, demonstrating a key role for resource quality. Thus, relative abundances of algal species may be of greater importance in determining trophic diversity and consumer relative abundance than the total amount of algae at certain nutrient levels. Other studies examining the effect of productivity on food-chain length reveal contradictory patterns and it

Table 3. Spearman rank correlations between periphyton total phosphorus (TP) and other periphyton measures (n = 34)

<table>
<thead>
<tr>
<th>Periphyton measures</th>
<th>Periphyton TP (r)</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total periphyton biovolume (mL)</td>
<td>−0.79</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Total periphyton aerial cover (%)</td>
<td>−0.86</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Periphyton ash-free dry mass (g m−2)</td>
<td>−0.82</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Percentage organic content (%)</td>
<td>0.84</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Percentage carbon (%)</td>
<td>0.84</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Percentage nitrogen (%)</td>
<td>0.85</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Chlorophyll a concentration (µg g−1 dry)</td>
<td>0.75</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Chlorophyll a mass (µg m−2)</td>
<td>−0.81</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Algal NMDS Axis 1</td>
<td>−0.62</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Algal NMDS Axis 2</td>
<td>−0.45</td>
<td>0.007</td>
</tr>
<tr>
<td>Algal NMDS Axis 3</td>
<td>0.08</td>
<td>0.666</td>
</tr>
<tr>
<td>Relative abundance of bluegreen algae</td>
<td>−0.38</td>
<td>0.028</td>
</tr>
<tr>
<td>Relative abundance of filamentous bluegreen algae</td>
<td>−0.87</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Relative abundance of green algae</td>
<td>0.54</td>
<td>0.001</td>
</tr>
<tr>
<td>Relative abundance of diatoms</td>
<td>0.55</td>
<td>0.001</td>
</tr>
</tbody>
</table>

(mean nearest-neighbour distance was significantly predicted by algal NMDS Axis 2, but this relationship was contingent on a single site, suggesting this pattern is not robust. However, because the site was one of only four sites with short times since flooding and high nutrient levels, it is possible that this trend is genuine and would be better evaluated with increased representation of such sites. The observation that δ15N range was also negatively related to Axis 2 provides some support for this conclusion.

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

<table>
<thead>
<tr>
<th>Dependent variable</th>
<th>Significant terms</th>
<th>$\beta \pm$ s.e. ($P$)</th>
<th>$\beta$ weights</th>
<th>Squared semipartial correlation</th>
<th>Global $F$ ($P$)</th>
<th>Adjusted $R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Log total niche area</td>
<td>Flagfish</td>
<td>0.20 ± 0.064 (0.0035)</td>
<td>0.44</td>
<td>0.20</td>
<td>$F_{3,30} = 7.22$ (0.0099)</td>
<td>0.36</td>
</tr>
<tr>
<td></td>
<td>Periphyton AFDM</td>
<td>0.0005 ± 0.00018 (0.0127)</td>
<td>−0.37</td>
<td>0.14</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Algal NMDS Axis 3</td>
<td>0.15 ± 0.062 (0.0228)</td>
<td>−0.33</td>
<td>0.11</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Log mean nearest-neighbour distance</td>
<td>Algal NMDS Axis 2</td>
<td>−0.04 ± 0.019 (0.0447)</td>
<td>−0.35</td>
<td></td>
<td>$F_{1,32} = 4.37$ (0.0447)</td>
<td>0.09</td>
</tr>
<tr>
<td>Log $^{13}$C range</td>
<td>Algal NMDS Axis 3</td>
<td>−0.12 ± 0.054 (0.0291)</td>
<td>−0.37</td>
<td></td>
<td>$F_{1,32} = 5.22$ (0.0291)</td>
<td>0.11</td>
</tr>
<tr>
<td>Log $^{15}$N range</td>
<td>Flagfish</td>
<td>0.9 ± 0.40 (0.0295)</td>
<td>0.57</td>
<td>0.09</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Time since flooding</td>
<td>0.0006 ± 0.00020 (0.0052)</td>
<td>0.48</td>
<td>0.15</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Algal NMDS Axis 2</td>
<td>−0.6 ± 0.21 (0.0063)</td>
<td>−0.48</td>
<td>0.14</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Density</td>
<td>0.00 ± 0.019 (0.9917)</td>
<td>0.0007</td>
<td>$1 \times 10^{-7}$</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Flagfish × density</td>
<td>−0.05 ± 0.023 (0.0298)</td>
<td>−0.79</td>
<td>0.09</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Fig. 3. Partial regression plots for log-transformed niche area and (a) flagfish presence, (b) periphyton ash-free dry mass (AFDM) and (c) algal nonmetric multidimensional scaling Axis 3. Plots show residuals for the dependent and independent variables after each was regressed separately on the other independent variables. Note that the y-axis scale varies among panels. In (c), the arrow points to a high leverage site that lacked eastern mosquitofish.
Phosphorus enrichment causes a shift in algal community structure marked by the loss of filamentous bluegreen algae and their calcite precipitate and the resulting breakdown of the calcareous mat, an increase in green algae and changes in diatom composition (McCormick et al. 1996; Gaiser et al. 2005, 2006). Eastern mosquitofish have been shown to increase their feeding rates on diatoms after periphyton mats are physically broken up, allowing them to selectively choose palatable species and avoid unpalatable, physically difficult to eat filamentous bluegreen algae and calcium carbonate components of the mat (Geddes and Trexler 2003). We also observed the decrease in total algal biomass but increases in percentage of nitrogen and organic content coincident with increasing phosphorus observed by others (Gaiser et al. 2006; King and Richardson 2007).

**Influence of droughts on Everglades food webs**

In many aquatic ecosystems, disturbance in the form of periodic drying is thought to be a critical factor in structuring communities (Wellborn et al. 1996). Both densities and community structure of fish and invertebrates in the Everglades are often associated with hydrological parameters such as time since flooding and hydroperiod (Trexler et al. 2005; Liston 2006; Dorn and Trexler 2007). Like Williams and Trexler (2006), we found additional support for an effect of disturbance (drying events) on trophic position as approximated by $\delta^{15}N$ range, but we also found no effect on total niche area. Not only are large predators excluded by drying events (Chick et al. 2004; Trexler et al. 2005), but smaller consumers appear to feed at lower trophic levels following a disturbance when invertebrate standing stocks are reduced. Venturelli and Tonn (2006) documented similar decreases in trophic position of pike following removal of prey fish; pike switched to consuming invertebrates following the loss of their preferred prey. While studies of how disturbance affects diversity and food-chain length show no general consensus (Mackey and Currie 2001; Post 2002a), food webs in the Everglades may be expected to display strong relationships with disturbance given the intensity of hydrological disturbance and the resulting impacts on community structure.

**Competition and resource partitioning**

Resource partitioning is one mechanism by which coexisting species can respond to high interspecific competition (Schoener 1974) and diet shifts in response to the presence of a competitor have been shown in a variety of systems (e.g. Holbrook and Schmitt 1989; Nakano et al. 1999; Bonesi et al. 2004). In a previous study of Everglades fishes, juvenile eastern mosquitofish changed their diets in response to high interspecific competition (Taylor et al. 2001). Although we measured competition indirectly, the relationship between $\delta^{15}N$ range and fish and crayfish density suggests that competition may decrease trophic position. Decreased trophic diversity with increasing consumer densities was unexpected if competition generally acts to increase trophic diversity. The most likely explanation for our results is that at high densities, consumers actually overwhelmed their preferred prey and were forced to feed on lower trophic levels.
Conclusions
This study demonstrates effects of disturbance and productivity on the trophic structure of small consumers in the Everglades. Water flow through the Everglades has been anthropogenically altered in ways that affect disturbance rates and intensity, and a goal of current management is to restore historical water levels. Additionally, restoration of water flow will import nutrients from areas of agricultural and urban development. These changes will not only affect the density and community structure of consumers, but our findings suggest they will also alter dominant trends in trophic interactions and energy flow through the food web. Thus, future studies should attempt to quantify the functional outcomes of these shifts on population dynamics and community structure.
Acknowledgements

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References


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