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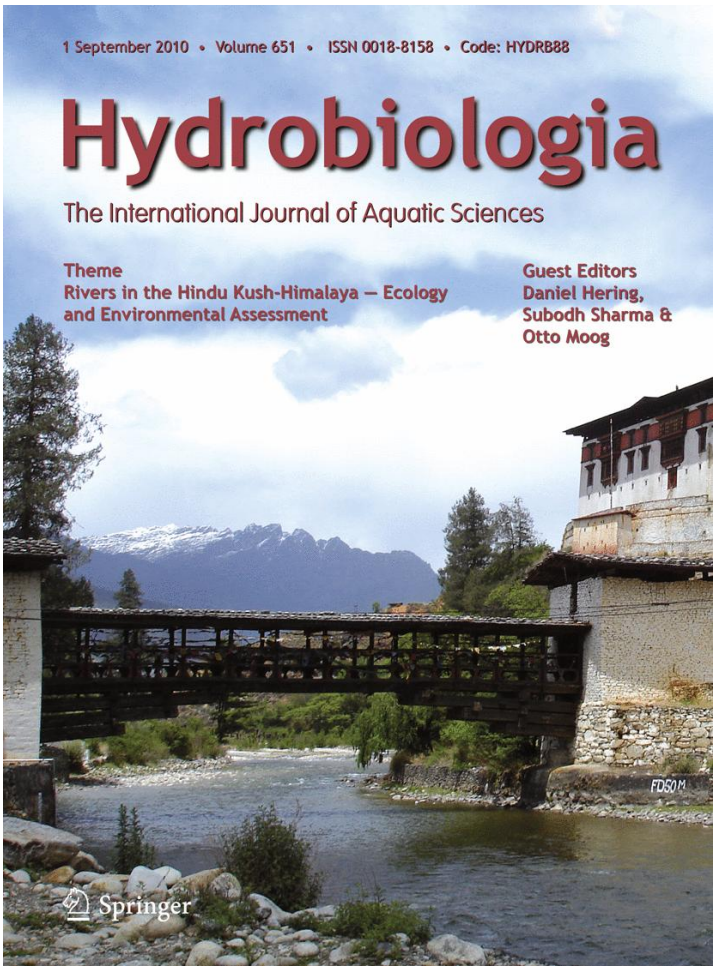

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PRIMARY RESEARCH PAPER

Spatial and temporal variation in invertebrate consumer diets in forested and herbaceous wetlands

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Abstract Macroinvertebrates have important functional roles in wetland ecosystems, but these roles are not always well understood. This study assessed which foods invertebrate consumers assimilate within a set of wetland habitats. During 2006 and 2007, non-Tanypodinae chironomid larvae and select crustaceans (*Crangonyx* amphipods, *Caecidotea* isopods, *Simocephalus* cladocerans) were sampled, along with their potential food sources, from forested and herbaceous areas in wetland habitats (depression, floodplain, swamp complex) across the southeastern U.S.A. Invertebrate and food source samples were processed for carbon and nitrogen isotope signatures. These data were analyzed with the U.S. Environmental Protection Agency's IsoSource mixing model, to estimate the potential relative contributions of different food items and to highlight both important and unlikely food sources. In the forested habitats, litter from trees (leaves, wood, fruit), epiphyton, detrital FPOM (fine particulate organic matter), sediment, and macrophyte litter were found to be major foods for midges and crustaceans, although considerable spatial and temporal variation existed in consumption. In the herbaceous habitats, algae (epiphyton, periphyton, metaphyton, phytoplankton), sediment, and macrophyte litter were important food resources. Comparisons between forested and herbaceous wetlands suggested that algal resources were widely consumed by midges and crustaceans, and that detrital sources were also important in forested wetlands.

Keywords Chironomid larvae · Crustaceans · Invertebrate function · IsoSource · Stable isotope analysis · Wetland food webs

Introduction

Aquatic invertebrates have long been viewed as a critical link between primary producers and higher trophic levels in wetlands (Wissinger, 1999). They contribute to decomposition and nutrient availability (Ruetz III et al., 2002; Kelly et al., 2004) and are important foods for fish and other vertebrates (Taylor et al., 1999; Webb & Mitsch, 2001). Yet, invertebrates are often not considered in detail in community- or ecosystem-level wetland studies (Battle & Golladay, 2001) and their roles remain poorly

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understood in those ecosystems. Chironomid midges (Diptera) and crustaceans are often among the most abundant invertebrates in wetlands (Golladay et al., 1999). While, as groups, they are seen as trophic generalists, the individual taxa often have more specific feeding functions. In this study, we examined the dietary trends of common invertebrate groups in a set of freshwater wetlands in southeastern U.S.A.

Assessing the diets and feeding patterns of chironomids and crustaceans among different habitats could lead to a better understanding of wetland community dynamics. It has been suggested that biological communities and ecological processes differ in characteristic ways between forested and herbaceous wetland habitats (Battle & Golladay, 2001; Batzer et al., 2005). Some propose that food webs in forested habitats are largely detritus-based, while food webs in herbaceous wetlands are driven by algal consumption. Further, others argue that algae, being often more nutritious than detritus, are a critical food source in all types of wetland habitats (Bott, 1996; Batzer et al., 2006; Zeug & Winemiller, 2008).

Stable isotope analysis is an important component of research on food web and trophic relationships (Benstead et al., 2006; Layman et al., 2007). As the isotopic signatures of tissues reflect the diet of an organism over time, they provide a useful picture of which food sources are important (Newsome et al., 2007). Isotopic mixing models have been developed to quantify source contributions in a mixed diet (Phillips & Gregg, 2003; Newsome et al., 2007). In field studies where many potential resource pools exist, such metrics can help to characterize food web structure (Layman et al., 2007; Hoeinghaus & Zeug, 2008).

The aim of our study was to assess whether the dietary habits of common aquatic invertebrates reflected differences in the carbon base of forested and herbaceous wetlands. Specifically, our hypothesis was that invertebrate communities would exhibit consistent functional differences between herbaceous and forested habitats across different types of wetlands. We used stable isotope analysis and mixing models to identify important food sources for chironomids and crustaceans, in wetland types common in the southeastern U.S.A. (depressions, floodplains, swamp complexes), and to compare the diets of study organisms between forested and herbaceous wetlands with otherwise similar hydrogeologic forms.

Materials and methods

Study sites

For this study, we selected paired forested and herbaceous wetland habitats from the Coosawhatchie River floodplain of southeastern South Carolina, the Carolina Bay depressional wetlands in western South Carolina, and the Okefenokee Swamp in southeastern Georgia. Each pair of forested and herbaceous sites within a region was in close proximity, which allowed for direct comparisons of consumer diets between them. The six habitats selected provided a reasonable cross-section of the range of wetlands present in the southeastern U.S.A.

Coosawhatchie river floodplain

The Coosawhatchie is a fourth-order blackwater river draining the South Carolina coastal plain. The floodplain typically floods beginning in winter and remains at least partially inundated into late spring. Detailed information about site characteristics is available in Braccia & Batzer (2001). While the site is largely forested, an 11-ha area was logged in 1997 and a seasonally flooded herbaceous marsh habitat developed (Batzer et al., 2005). In the forested area used for this study, major tree species were sweetgum (*Liquidambar styraciflua*), red maple (*Acer rubrum*), water tupelo (*Nyssa aquatica*), and various oaks. The herbaceous study area had a vegetative community of *Polygonum* knotweed and other assorted emergents (*Juncus*, *Scirpus*). Sweetgum and other tree saplings were also present.

Carolina bays

The two Carolina bay depressional wetlands selected for study were located on the Savannah River Site in South Carolina. The hydrologic cycle of these bays was dominated by precipitation and evapotranspiration, and they typically filled in late autumn or early winter and dried in late spring or early summer. The forested Carolina bay (Bay 118—as identified by the Savannah River Ecology Laboratory) used in this study was about 1 ha and dominated by sweetgum with some assorted mixed pine (*Pinus palustris*, *P. taeda*). The herbaceous Carolina bay (Bay 5204) was about 0.5 ha and had stands of *Typha* along the

perimeter, with several aquatic (*Nymphaea odorata*) and emergent macrophytes (*Polygonum, Panicum*, *Scirpus*) present in the interior. This habitat had been logged 3 years before our study, and some residual wood remained and new saplings were regenerating.

Okefenokee swamp

The Okefenokee swamp is a large southern blackwater swamp with water inputs being primarily through precipitation and outputs via evapotranspiration and surface water outflow (Loftin, 1997). Much of the wetland area is inundated throughout the year, although forested cypress domes are somewhat drier. A representative cypress dome and a lily prairie habitat were chosen in Chesser Prairie, on the east side of the Okefenokee National Wildlife Refuge. The cypress dome was dominated by baldcypress (*Taxodium distichum*), and the lily prairie was dominated by fragrant water lily (*Nymphaea odorata*).

Sample collecting and processing

We sampled sites in winter and early spring when surface water was present (January–March of 2006 and 2007). Sampling was done at least twice in each habitat to incorporate seasonal or other temporal variation. We sampled the Coosawhatchie floodplain sites on February 14, 2006 and March 14, 2007, the Carolina bays on March 7, 2006 and April 17, 2006, and the Okefenokee sites on January 15, 2006, May 14, 2006, and March 13, 2007. At each collection, two or three replicate samples of consumers and potential food sources were taken from each habitat (although only one sample set was collected from the Okefenokee swamp on January 15, 2006). We collected non-Tanypodinae chironomid larvae from all six wetlands. Dominant crustacean consumers were also collected from the Coosawhatchie floodplain (amphipods and isopods) and the Carolina bays (cladocerans).

Invertebrates were collected by sweeping a D-frame aquatic net (1-mm mesh, 30-cm diameter) through the water column and aquatic plant beds, and along benthic substrate. The collected material was placed in buckets for field sorting of invertebrates. Where present, samples of submerged wood were collected and brought back to the lab to be searched for additional invertebrates, which were added to the field samples. While some authors suggest keeping organisms alive for a time to allow for gut clearing, others maintain this is unnecessary (i.e., Jardine et al., 2005). Thus, we did not attempt gut clearing in this study. Invertebrates were preserved by freezing.

During each trip, we collected available potential food sources of the invertebrates, including leaf litter, macrophyte detritus, macrophyte new growth, epiphytic algae, periphyton, sediment, submerged wood, and phytoplankton. Macrophytes were rinsed to remove and collect epiphyton, and later identified. Attempts to sample benthic algae in isolation failed; thus, benthic algae were considered as a component of sediment. Sediment samples were collected from underneath any benthic litter. Wood samples were separated into outer bark and inner wood fractions, each of which can be subjected to different microbial conditioning. All food source samples were transported on ice and kept frozen in the laboratory until processing.

In the laboratory, invertebrate and food source samples were thawed, cleaned, freeze-dried, pulverized to a fine powder in a ball-mill grinder, and weighed (at least 1.5 mg of substance) into tin capsules in preparation for analysis of carbon and nitrogen isotopes (as recommended by the UGA Analytical Chemistry Laboratory). Before grinding, leaf litter samples were separated and categorized by species. Indistinguishable decomposed plant fragments were categorized either as FPOM (particulates passing through a 1-mm mesh) or CPOM (particulates retained on a 1-mm mesh). Sediment samples, placed in silver capsules, were acid-rinsed with 20% HCl to remove inorganic carbon, oven-dried overnight, reweighed, and analyzed as the other samples.

Analysis of carbon and nitrogen isotopes was done by the Analytical Chemistry Laboratory (Institute of Ecology, University of Georgia) using a Carlo Erba NA 1500 CHN analyzer (Carlo Erba Instrumentazione, Milan, Italy) coupled to a Finnigan Delta C isotope radio mass spectrometer (Thermo Electron, Waltham, MA) operating as a continuous flow system. The laboratory error rate was $\pm 0.15‰$. The reproducibility of each sample run was monitored by using a bovine liver standard and a poplar leaf standard. This analysis provided data on the stable isotope content of our samples, as well as the percent content of total carbon and nitrogen. The stable

isotope data were expressed as relative difference per mil (‰) using the equation:

$$\delta X = ((R_{\text{sample}}/R_{\text{standard}}) - 1) \times 1,000$$

where $X = {}^{13}C$ or ${}^{15}N$, and $R = {}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$. The ratios of ${}^{13}C$ to ${}^{12}C$ were expressed relative to the standard PDB (Pee Dee Belemnite). The ratios of ${}^{15}N$ to ${}^{14}N$ were expressed relative to N_2 in air.

Taxonomic confirmations

In the laboratory, a subsample (at least 20 individuals) of the midges from each site was slide-mounted for taxonomic identification. We used Epler (2001) for identifications, which were then verified by Dr. Broughton Caldwell (Georgia Environmental Protection Division, retired). Crustacean genera were identified using standard keys (Pennak, 1989).

Isotope and diet analysis

We used the IsoSource mixing model (Phillips, 2001), developed by the US Environmental Protection Agency, to estimate the relative contribution of potential food resources to the invertebrate diet (midge or crustacean) for each sampling date. The IsoSource software (Microsoft Visual Basic, version 1.3.1) is based on isotopic mass balance conservation, and calculates the range of feasible proportional contributions of sources to a mixture (expressed in some small increment and totaling 100%) when the number of sources is too large to permit a unique solution. The number of sources that can be partitioned is limited by the number of isotopic signatures analyzed. In general, with n isotope signatures, contributions for $n + 1$ sources can be computed. If the number of sources exceeds $n + 1$, then the calculation is mathematically underdetermined, with more unknowns than equations and no unique solution (Phillips & Gregg, 2003). IsoSource has been used in a number of field-based freshwater food web studies (e.g., Benstead et al., 2006; Zeug & Winemiller, 2008).

Using guidelines in Bunn & Boon (1993), we considered sources to be potential food for invertebrates if they had $\delta^{13}C$ values within the range of 2‰ less than or 1‰ greater than the mean consumer signature, and had $\delta^{15}N$ values within the range 1–5‰ less than the consumer signature. Sources in this range were evaluated using the IsoSource model. We provided the model with $\delta^{15}N$ and $\delta^{13}C$ mean values for food (source entries) and consumer (mixture entries) samples. The entered values were replicate means. To account for trophic isotope fractionation, which could result from consumer digestion and assimilation, we subtracted 2.0‰ from the $\delta^{15}N$ value and 1.0‰ from the $\delta^{13}C$ value of each consumer sample (personal communication, S. Newsome; McCutchan et al., 2003). Source increment was set at 2.0% and we used a mass balance tolerance value of 0.1‰. If under these parameters a solution could not be calculated, we increased the tolerance, incrementally by 0.1–1.0‰, and if still unsuccessful, we concluded that the model could not be used to analyze a particular consumer data set.

Using the IsoSource output *histograms* for each data set run, sources with low maximum values (i.e., the source was never >20% of the mixture in feasible solutions) were assumed to be either unlikely or minor components of the consumer diet. Sources with wide distributions (both high and zero values) were assumed to be present in the diet, but their importance was unclear. Likely major food sources were those where the source proportion was greater than 20% in more than 50% of solutions, and where none of generated solutions showed a 0% contribution. The output values are expressed in the text as the 1st and 99th percentile range followed by the 50th percentile value as compiled by the mixing model. For example, an IsoSource solution summary of (20–50%: 30%) would indicate that 98% of the solutions found that the source item contributed between 20 and 50% of the consumer diet, and that for the median solution, 30% was contributed to the diet. Additional site comparisons of food source and consumer interactions were made using total carbon and nitrogen data.

Results

Coosawhatchie river floodplain

Taxonomy

In the Coosawhatchie floodplain, *Polypedilum tritum* was the major midge taxon in both the forested (76%) and the herbaceous (74%) habitats in February 2006. In March 2007, *P. tritum* was again the most abundant midge in both habitats (43% of the forested

community and 91% of the herbaceous community); seven additional taxa comprised the remaining 57% of the forested community. *Caecidotea* isopods (Asellidae) and *Crangonyx* amphipods (Crangonyctidae), the targeted crustaceans, were abundant in both habitat types.

Carbon and nitrogen analyses

Midges, amphipods, and isopods in the Coosawhatchie floodplain had a δ^{13}C range from −30.5 to −25.9‰ and δ^{15}N range from 2.6 to 7.7‰ (Fig. 1A–D). Forested samples were consistently more ^{13}C-enriched than corresponding herbaceous samples. Amphipods had the highest δ^{15}N values.

Potential food sources from the Coosawhatchie floodplain had total C compositions between 5.3 and 78.9% and total N compositions from 0.3 to 4.8%. Wood and detrital food samples tended to have the highest C:N ratios, and epiphyton and macrophyte samples had the lowest ratios (Table 1). Most of the potential food samples at the Coosawhatchie had a range from −32.5 to −25.0‰ for δ^{13}C values and a range from −0.5 to 5.0‰ for δ^{15}N values.

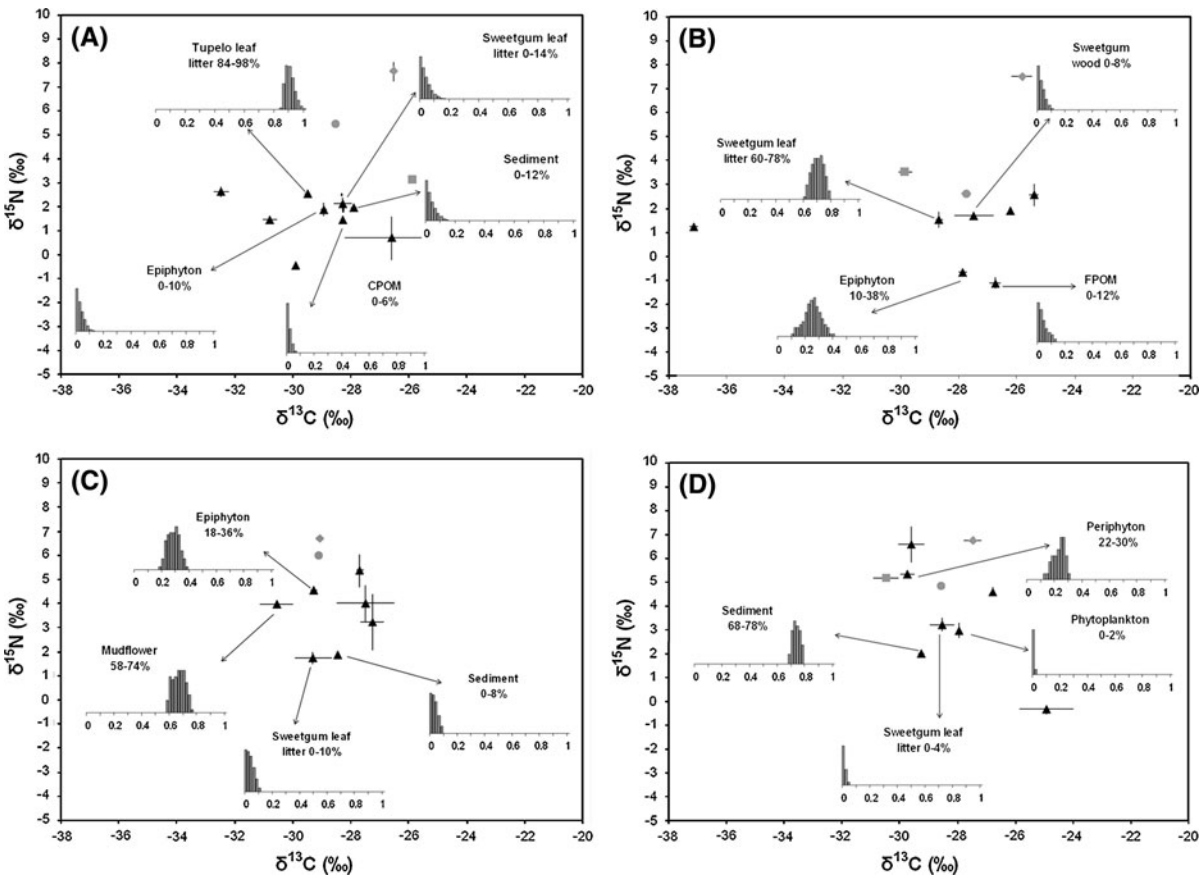

Fig. 1 Stable isotope biplots of dietary contributions for Coosawhatchie floodplain communities: **A** Forested February 2006 set, **B** forested March 2007 set, **C** herbaceous February 2006 set, and **D** herbaceous March 2007 set. Each data point is the mean of the sample replicates. *Circles* symbolize midge larvae; *diamonds* symbolize amphipods; *squares* symbolize isopods; and *triangles* symbolize sampled food sources. Error bars (1 SE) are visible where they are larger than the data points. δ^{13}C in per mil (‰) units is the deviation of the isotopic ratio of the sample from that for a Pee Dee Belemnite standard; $\delta^{13}C = ((R_{sample}/R_{standard}) - 1) \times 1{,}000$, where $R = {}^{13}C/{}^{12}C$. δ^{15}N in per mil (‰) units is the deviation of the isotopic ratio of the sample from that of N_2 in air; $\delta^{15}N = ((R_{sample}/R_{standard}) - 1) \times 1{,}000$, where $R = {}^{15}N/{}^{14}N$. Only food sources within parameters described in Bunn & Boon (1993) were analyzed using IsoSource. The *histograms* provide the distribution of feasible IsoSource contributions from these sources to the midge diet, and the displayed values are the 1–99 percentile ranges for these distributions

Table 1 Food quality of sampled food sources as reflected by C:N ratios

	Forested habitat			Herbaceous habitat		
	First collection	Second collection	Third collection	First collection	Second collection	Third collection
Coosawhatchie floodplain						
Epiphyton	28.5*	**8.7**		**10.9**	17.4	
Metaphyton	22.4					
Periphyton					**11.2**	
Phytoplankton	10.2				19.1*	
Sediment	–*	14.9		–*	**13.3**	
Sweetgum wood	54.1	88.6*		52.5	96.7	
Sweetgum bark		79.1				
Sweetgum leaf litter	47.5*	**36**		45.4*	31.0*	
Tupelo leaf litter	**43.5**					
Oak leaf litter	72					
Detrital CPOM	26.9*	–				
Detrital FPOM		11.3*				
Micranthemum mudflower				**14.2**		
Polygonum knotweed		26.6		14.4		
Scirpus bulrush	22.4				25.2	
Carolina bays						
Epiphyton		**9.8**		14.4*	16.5	
Metaphyton	21.8			**19.8**		
Periphyton	20.5	20.2			13.1	
Phytoplankton	17.7*	13.5*		14.7	–	
Sediment	100.1*	94.1		–*	77.5	
Sweetgum wood		67.7*			55.4	
Sweetgum bark	**95.3**					
Sweetgum leaf litter	48.9	51.9*				
Pine needle litter	86.8				21.7	
Decomposed lily				13.9*	19.6	
Dried *Panicum* grass		34.3			37.1	
Detrital CPOM	24.3	26.5*			29.6	
Detrital FPOM	**19.5**				26.3	
Callitriche starwort				15.9		
Lemna duckweed				17.6	29.4	
Nymphaea lily				15.4		
Polygonum knotweed				14		
Utricularia bladderwort				20.9		
Okefenokee swamp						
Epiphyton	10.6	14.7	23.4*	20.6	43.2	14.2
Periphyton		6.6*				
Phytoplankton	19.8				23.5	**23.5**
Sediment	25.6	13.8	**14.9**	**16.3**	12.5	9.1
Peat					30.3	17.2
Cypress wood	**70.9**	–	128.7			
Cypress bark	55.5*	67.1	45			

Table 1 continued

	Forested habitat			Herbaceous habitat		
	First collection	Second collection	Third collection	First collection	Second collection	Third collection
Cypress needle litter	50.2	49.8	47.5			
Titi leaf litter	54.7		50.1			
Decomposed lily				31.5*	32.5	24.9*
Detrital CPOM		26	18.2*		18.2	
Carex sedge				19.0*		
Nymphaea lily				20.6*	18.9	18.6*
Polygonum knotweed		**27.8**				
Utricularia bladderwort		19.3	15.9*	26.0*	21.6	12.5

Bold font indicates sources that were found to be major foods by IsoSource modeling, and *asterisks* indicate unlikely foods. Samples with total nitrogen levels too low to be measured are indicated by a dash. Collection dates for the Coosawhatchie floodplain were February 14, 2006 and March 14, 2007, for the Carolina bays were March 7, 2006 and April 17, 2006, and for the Okefenokee swamp were January 15, 2006, May 14, 2006, and March 13, 2007

Linking invertebrates to their foods

Carbon signatures of midges in both the forested and herbaceous habitats were within the range of the $\delta^{13}C$ values of the potential food sources for both collection dates (Fig. 1A–D). IsoSource analyses for the forested habitat in February 2006 suggest that midges were primarily consuming tupelo leaf litter (84–98%: 90%), while CPOM (0–6%: 0%), epiphyton (0–10%: 2%), sweetgum leaf litter (0–14%: 2%), and sediment (0–12%: 2%) were unlikely foods (Fig. 1A). In March 2007, sweetgum leaf litter (60–78%: 70%) and epiphyton (10–38%: 24%) were identified as major components, while sweetgum wood (0–8%: 2%) and FPOM (0–12%: 2%) were not likely foods for midges (Fig. 1B).

In the herbaceous site in February 2006, *Micranthemum* mudflower (58–74%: 66%) and epiphyton (18–36%: 28%) were identified as likely foods for midges, and sweetgum leaf litter (0–10%: 2%) and sediment (0–8%: 2%) were unlikely or minor sources (Fig. 1C). In March 2007, IsoSource analyses indicated that sediment (68–78%: 72%) was a likely food item and periphyton (22–30%: 26%) was also important. Sweetgum leaf litter (0–4%: 0%) and phytoplankton (0–2%:0%) were not likely food sources for midges (Fig. 1D).

For amphipods, signatures in the forested habitat were most similar to wood in $\delta^{13}C$ value, in both collections (Fig. 1A–B). For the forested sample collected in February 2006, midges were the major food source (74–94%: 82%) for amphipods, while sweetgum leaf litter (0–20%: 4%), sediment (0–18%: 4%), CPOM (0–16%: 4%), and epiphyton (0–10%: 2%) were unlikely or minor foods (Fig. 1A). IsoSource could not generate solutions for amphipods from the forested sample collected in March 2007.

The amphipod carbon signature from herbaceous samples collected in February 2006 was very similar to the midge signature and within the range of the potential food resources (Fig. 1C). Here, mudflower (6–68%: 62%) was identified as being important in the amphipod diet. Non-tanypod midges (28–38%: 34%) were also important foods for amphipods in all solutions. Sweetgum leaf litter (0–4%: 0%), epiphyton (0–12%: 2%), and sediment (0–2%: 0%) were unlikely foods. In the March 2007 herbaceous collection, amphipods had $\delta^{13}C$ values in the same range as many potential foods (Fig. 1D). IsoSource analyses for amphipods yielded an output range suggesting a mixture of foods with none being dominant [sweetgum leaf litter (0–34%: 8%), knotweed (0–42%: 10%), phytoplankton (0–36%: 8%), epiphyton (2–40%: 26%), *Scirpus* bulrush (2–26%: 16%), non-tanypod midges (0–82%: 22%)].

Isopods collected from the forested habitat in February 2006 were most similar to wood in $\delta^{13}C$ value (Fig. 1A). Wood (72–74%: 74%) and sediment (16–28%: 24%) were found to be likely food sources, and sweetgum (0–10%: 2%), tupelo (0–2%: 0%), and

oak (0–0%: 0%) leaf litter, epiphyton (0–2%: 0%), and detrital CPOM (0–2%: 0%) were not likely foods. In March 2007, isopod carbon values were most similar to sweetgum leaf litter. Sweetgum leaf litter (0–56%: 12%), epiphyton (0–42%: 10%), bark (0–40%: 8%), and inner gum wood (0–50%: 10%) were determined to be possible dietary components, but their contribution was equivocal. Knotweed (20–48%: 34%) was shown to be a likely food for these isopods. In the herbaceous habitat, in February 2006, isopods were not found. In the March 2007 set, the collected isopods had δ^{13}C values in the same range as many potential foods (Fig. 1D). However, no IsoSource solutions were generated for isopods in the herbaceous habitat during March 2007.

Carolina bay depressional wetlands

Taxonomy

In the Carolina bays, *Polypedilum* spp. midge larvae dominated both the forested (96%) and herbaceous (56%) bays in March 2006, although the herbaceous bay also supported a number of other genera. In April 2006, both bays supported more diverse and evenly distributed midge assemblages. At that time, *Psectrocladius psilopterus* sp. 3 was the most abundant midge in the forested bay (47%), followed by *Dicrotendipes modestus* (23%), and *Chironomus* (*Lobochironomus*) *austini* (30%) and *Ch. decorus* (33%) populated the herbaceous bay. The cladocerans in the forested bay were *Simocephalus expinosus*, and *S. expinous* and *S. serrulatus* (Daphniidae) occurred in the herbaceous bay.

Carbon and nitrogen analyses

The Carolina bays showed a wide range in midge and cladoceran isotope signatures, with δ^{13}C values from −32.9 to −23.1‰ and δ^{15}N values from 0.8 to 4.7‰ (Fig. 2A–D). Within each habitat, invertebrate samples collected in March 2006 were more ^{13}C-enriched than the April 2006 collections.

Potential invertebrate food resources from Carolina bays had total carbon ranging from 17.0 to 50.7% and total nitrogen ranging from 0.1 to 3.4%. Wood samples had the highest C:N ratio, and other detritus (leaf litter, particulate organic matter) usually also had high C:N ratios (Table 1). Other potential foods had lower ratios than detritus, but were otherwise similar to each other. Algae as a category (e.g., epiphyton, metaphyton) had no consistent C:N range. Stable isotope results of Carolina bay resources indicated most of the source δ^{13}C values were between −30 and −26‰ and most δ^{15}N results were between 2 and 4.5‰. Detrital and sediment samples had similar stable isotope values between sampling dates, while algae and macrophytes varied temporally.

Linking invertebrates to their foods

Midge δ^{13}C values in the forested bay in March 2006 were similar to many potential foods (Fig. 2A). IsoSource analyses indicated that FPOM (48–60%: 54%) and detrital sweetgum fruit (40–52%: 44%) were likely food sources for midge larvae, while sediment (0–2%: 0%) was not. In April 2006, midges continued to have isotope values within the ranges of the potential food sources in the forested habitat (Fig. 2B). IsoSource identified epiphyton (74–96%: 82%) as the principal midge food in the forested bay. Sweetgum bark (0–12%: 2%), CPOM (0–14%: 2%), sweetgum leaf litter (0–16%: 4%), and sediment (0–20%: 6%) were unlikely foods.

In the herbaceous bay in March 2006, the mean midge δ^{13}C values were between those of the metaphyton and epiphyton samples (Fig. 2C). Metaphyton (64–76%: 70%) was identified as the only important food source for midges. Sediment (0–14%: 8%) and decomposed lily (0–18%: 8%) were unlikely sources and the importance of epiphyton (0–34%: 14%) could not be determined. In the April 2006 herbaceous collection, mean midge isotope values deviated from many potential foods (Fig. 2D), and no feasible solutions could be generated.

For cladocerans, stable isotope values in the forested sample from March 2006 were dissimilar from any collected food source, and IsoSource could not generate solutions for this population. In that habitat in April 2006, cladocerans had isotope values in similar ranges of the potential food sources (Fig. 2B), and sediment (74–86%: 78%) and sweetgum wood (14–26%: 20%) were identified as likely food sources for cladocerans, while epiphyton (0–4%: 0%) and *Panicum* grass litter (0–2%: 0%) were unlikely foods. However, because cladocerans are physically unable to consume wood, the sweetgum result was considered an anomaly.

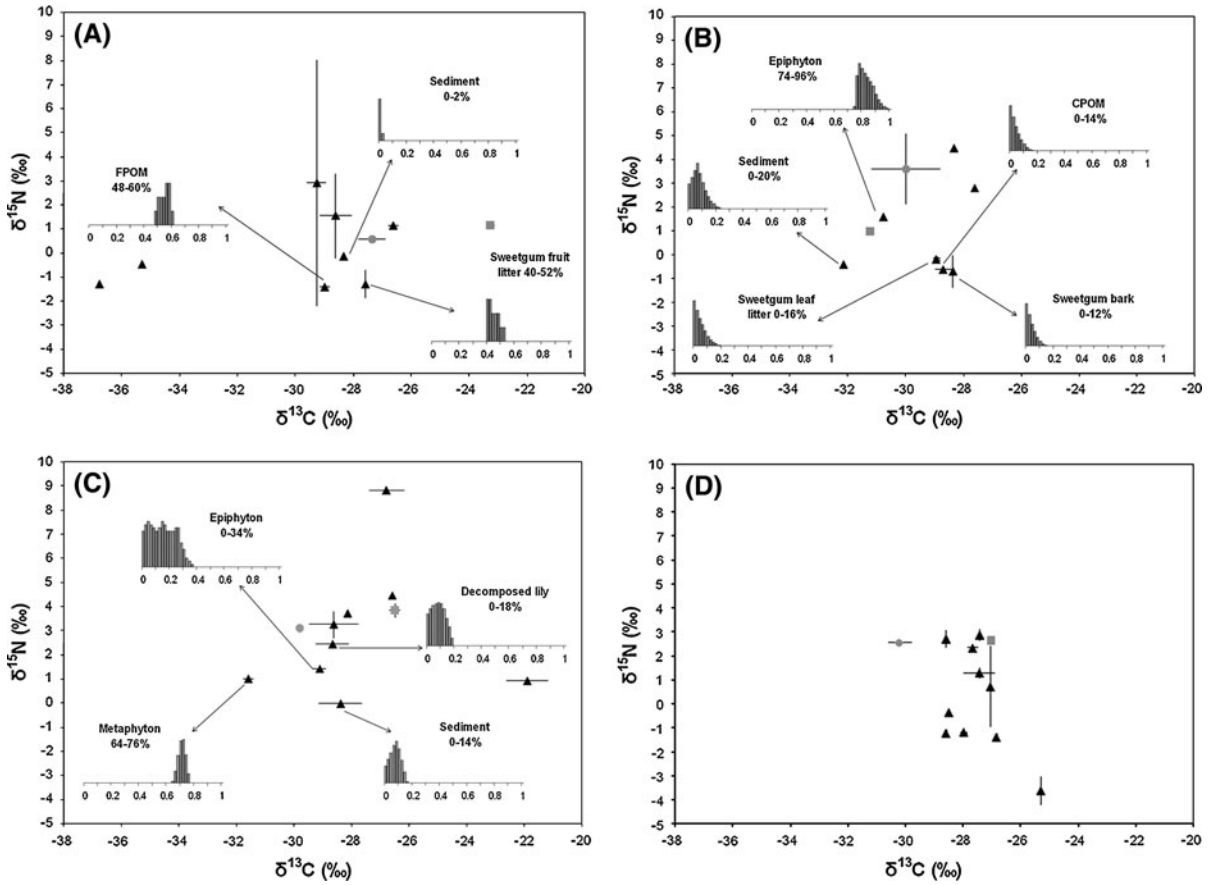

Fig. 2 Stable isotope biplots of dietary contributions for Carolina bay communities: **A** forested March 2006 set, **B** forested April 2006 set, **C** herbaceous March 2006 set, and **D** herbaceous April 2006 set. Each data point is the mean of the sample replicates. *Circles* symbolize midge larvae; *squares* symbolize cladocerans; and *triangles* symbolize sampled food sources. Error bars (1 SE) are visible where they are larger than the data points. δ^{13}C in per mil (‰) units is the deviation of the isotopic ratio of the sample from that for a Pee Dee Belemnite standard; $\delta^{13}C = ((R_{sample}/R_{standard}) - 1) \times 1{,}000$, where $R = {}^{13}C/{}^{12}C$. δ^{15}N in per mil (‰) units is the deviation of the isotopic ratio of the sample from that of N_2 in air; $\delta^{15}N = ((R_{sample}/R_{standard}) - 1) \times 1{,}000$, where $R = {}^{15}N/{}^{14}N$. Only food sources within parameters described in Bunn & Boon (1993) were analyzed using IsoSource. The *histograms* provide the distribution of feasible IsoSource contributions from these sources to the midge diet, and the displayed values are the 1–99 percentile ranges for these distributions. Figure 2D set had no solutions

In the herbaceous habitat, cladoceran isotope values in March 2006 were distant from all food samples except *Nymphaea* lily (Fig. 2C), and there were no IsoSource solutions. The April 2006 cladoceran community had isotope values in similar ranges of the potential food sources (Fig. 2D). Here, epiphyton (2–78%: 42%) was present in virtually all feasible IsoSource solutions, but the distribution was wide, and thus importance could not be inferred. Contributions from pine needle litter (0–34%: 8%), FPOM (0–34%: 10%), sediment (0–54%: 16%), and sweetgum bark (0–60%: 18%) also could not be interpreted.

Okefenokee swamp

Taxonomy

Midge genera collected in January 2006 were not identified. In May 2006, the midge community in the cypress dome (four genera) were less diverse than in the lily prairie (six genera), but both were dominated

by the same taxon, *Chironomus* sp. In March 2007, the communities were similarly rich, but dissimilar in character. Different genera dominated each habitat; *Paratendipes* sp. comprised 47% of the cypress dome community, and *Polypedilum trigonus* comprised 42% of the lily prairie community.

Carbon and nitrogen analyses

The isotope ratio scale for midges in the Okefenokee swamp was −31.5 to −25.3‰ for δ^{13}C values and 1.5–2.5‰ for δ^{15}N values. All of the separate samples were distinct from each other in their signatures (Fig. 3A–F). All of the midge samples occurred across a narrow δ^{15}N range.

Potential food categories collected from the Okefenokee had total carbon values between 31.9 and 54.7%, and total nitrogen values from 0.4 to 6.3%. Non-wood samples in the cypress dome collections were in the range of the lily prairie sample sets. The lily prairie sample set had a narrower range of both total carbon and total nitrogen than the cypress dome set. This was due to the fact that wood found in the cypress dome consistently had very low total nitrogen values and had the highest C:N ratios (Table 1). Epiphyton and sediment samples tended to have the lowest C:N ratios (Table 1).

Stable isotope analysis of Okefenokee sites showed most of the δ^{13}C values of potential foods were in the range between −30 and −24‰ and the majority of δ^{15}N values were between −1.8 and 1.2‰. Although stable isotope values of potential foods in each habitat were different between sampling dates, there was no consistent pattern of change within any of the food categories.

Linking invertebrates to their foods

In general, the isotopic signatures of midges from the Okefenokee habitats were similar in δ^{13}C to a number of the potential foods and had higher δ^{15}N values (Fig. 3). In the forested cypress dome, IsoSource analyses for the January 2006 samples indicated that cypress wood (34–52%: 44%) was a sizable component of all calculated solutions, while cypress bark (0–20%: 4%) was an unlikely food (Fig. 3A). Epiphyton (0–44%: 14%), cypress needle litter (0–22%: 6%), *Cyrilla* leaf litter (0–40%: 24%), and sediment (0–22%: 6%) were indicated in small amounts. In May 2006, midge signatures were lower than much of the resource set, and matched few potential foods (Fig. 3B). Still, IsoSource solutions were produced. Knotweed (22–50%: 38%) was indicated in moderate amounts in all solutions, and bladderwort (0–52%: 14%) and epiphyton (0–40%: 20%) were present to some degree. Periphyton (0–12%: 2%) was an unlikely food. In March 2007, sediment (94–100%: 96%) was indicated as a major food source, while CPOM (0–4%: 0%), bladderwort (0–4%: 0%), and epiphyton (0–6%: 2%) were unlikely sources (Fig. 3C).

In the lily prairie, sediment (90–100%: 96%) was a very likely food source of midges in January 2006, while lily (0–10%: 2%), decomposed lily (0–2%: 0%), bladderwort (0–2%: 0%), and *Carex* sedge (0–2%: 0%) were all unlikely sources (Fig. 3D). IsoSource could not generate solutions for the May 2006 sample set in the lily prairie, although midge δ^{13}C values were similar to the lily (Fig. 3E). In March 2007, phytoplankton (72–98%: 90%) appeared to be the dominant food for midges, while peat (0–6%: 2%), decomposed lily (0–4%: 0%), and lily (0–4%: 0%) were unlikely sources; sediment (0–26%: 6%) was indicated in small amounts in the majority of solutions (Fig. 3F).

Discussion

In this study, invertebrate consumer signatures were usually within the carbon range of food samples, suggesting that the majority of potential foods for study organisms were sampled. As expected (Tillberg 2006), invertebrate δ^{15}N levels placed them one trophic level above basal resources (although the high levels for amphipods suggest they were functioning in part as predators). In several instances, solutions could not be generated by the IsoSource mixing model, possibly because the food source of that consumer was not sampled or because samples were insufficiently pure to develop unique signatures. Alternatively, a lack of resolution may suggest that many foods were being consumed simultaneously. However, some general patterns emerged from our analysis.

In the Coosawhatchie floodplain, the sampled invertebrates are all reported to have fairly broad food habits. *Polypedilum tritum*, the most abundant

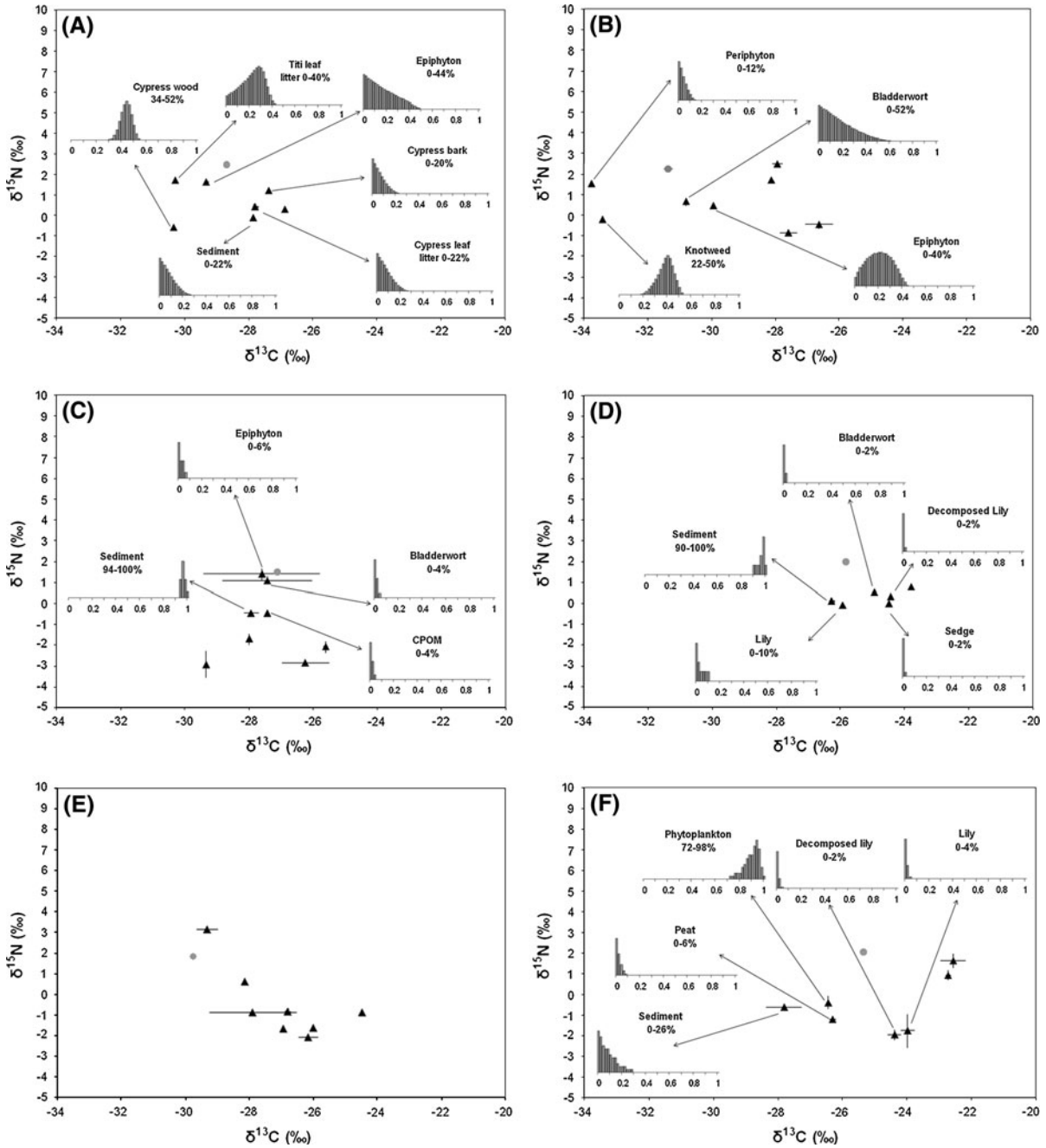

Fig. 3 Stable isotope biplots of dietary contributions for Okefenokee swamp communities: **A** Cypress dome January 2006 set, **B** Cypress dome May 2006 set, **C** Cypress dome March 2007 set, **D** Lily prairie January 2006 set, **E** Lily prairie May 2006 set, and **F** Lily prairie March 2007 set. Each data point is the mean of the sample replicates. *Circles* symbolize midge larvae; and *triangles* symbolize sampled food sources. Error bars (1 SE) are visible where they are larger than the data points. δ^{13}C in per mil (‰) units is the deviation of the isotopic ratio of the sample from that for a Pee Dee Belemnite standard; $\delta^{13}C = (R_{sample}/R_{standard}) - 1) \times 1{,}000$, where $R = {}^{13}C/{}^{12}C$. δ^{15}N in per mil (‰) units is the deviation of the isotopic ratio of the sample from that of N_2 in air; $\delta^{15}N = ((R_{sample}/R_{standard}) - 1) \times 1{,}000$, where $R = {}^{15}N/{}^{14}N$. Only food sources within parameters described in Bunn & Boon (1993) were analyzed using IsoSource. The *histograms* provide the distributions of feasible IsoSource contributions from these sources to the midge diet, and the displayed values are the 1–99 percentile ranges for these distributions. Figure 3E set had no solutions

Table 2 Midge food analysis summary table

	Forested	Herbaceous
Coosawhatchie floodplain	Tupelo leaf litter	Mudflower
	Sweetgum leaf litter	Epiphyton
	Epiphyton	Sediment
		Periphyton
Carolina bays	Detrital FPOM	Metaphyton
	Sweetgum fruit litter	
	Epiphyton	
Okefenokee swamp	Wood	Sediment
	Knotweed	Phytoplankton
	Sediment	

The following sources were found by IsoSource analysis to be the major foods of the non-Tanypodinae midge larvae in the forested and the herbaceous habitat in each wetland type, compiled from all collection dates

midge, exhibits diet flexibility (Berg, 1995; Golladay et al., 1999). *Caecidotea* isopods also rely on a mix of basal resources (Opsahl & Chanton, 2006). *Crangonyx* amphipods have been considered as shredders and gatherers, which suggests consumption of detritus (Warren & Spencer, 1996), but have also been observed preying on midge larvae (Thorp & Cothran, 1984).

Our analyses of invertebrate diets in the Coosawhatchie also suggested a range of diets, although a recurring theme was the presence of algae. For midges, epiphyton was important in both herbaceous and forested habitats, and periphyton and sediment (of which epipelic algae were probably a component) were important in the herbaceous habitats (Table 2). However, macrophytes were also key. Mudflower (which had a low C:N ratio) was important in the herbaceous habitat, and leaf litter (sweetgum and tupelo) was important in the forested habitat. *Caecidotea* were found to have consumed wood, among other resources. *Crangonyx* also consumed mudflower, but, supporting findings of Thorp & Cothran (1984) were also apparently consuming midges. While the variability and a lack of solutions for some samples inhibit generalization, the herbaceous area of the Coosawhatchie floodplain tended to be algal-based and the forested area tended to be detrital-based.

In the Carolina bays, while midge communities shifted in species richness between sampling dates, the dominant midge taxa occurring (*Chironomus*, *Dicrotendipes*, *Polypedilum*, *Psectrocladius*) are reported to consume a variety of foods and to be associated with a variety of habitats (Berg, 1995; Golladay et al., 1999; Kelly et al., 2004). *Simocephalus* cladocerans are considered suspension feeding algivores (Lemke & Benke, 2003; DeBiase & Taylor, 2005).

Our results suggest Carolina bay midge larvae consumed algae in both herbaceous and forested habitats (Table 2), with metaphyton being the only source clearly linked with midges from the herbaceous bay. In the forested bay, FPOM and sweetgum fruit (both detrital components) were important in March 2006 IsoSource diet solutions, although later in April, epiphyton became a dominant food source. The forested detrital samples were high in nitrogen, suggesting nutritional microbial contribution (Berg, 1995) at the time of sampling. This seasonal variation might reflect shifts in consumer selection or nutritional needs; still in most cases, the indicated foods had high nutritional quality (i.e., low C:N ratios, Jardine et al., 2005). We anticipated that *Simocephalus* cladocerans would be consuming algae. However, the minimal overlap of the carbon signatures with any of the foods sampled in March suggests a failure to collect their foods. In April, cladocerans were clearly linked to epiphyton in the herbaceous bay but in the forested bay, sediment was important, in addition to other sources. Benthic algae (a component of our sediment samples) are known be a significant resource for cladocerans (Stevenson, 1996).

In the Okefenokee swamp, there was also seasonal variation in the midge community, but the common taxa in both the cypress dome (*Chironomus*, *Paratendipes*) and the lily prairie (*Chironomus*, *Polypedilum trigonus*) were again taxa known to use a variety of resources. *Chironomus* species are known to consume green algae, as well as detritus, and have also been shown to have selective feeding habitats (Berg, 1995; Jones et al., 2008). *Paratendipes* was abundant in the cypress dome in March 2007, and has been noted as a detritivore (Berg, 1995).

In our analyses of the lily prairie, phytoplankton was important to midges in March. Sediment matter was important at times in solutions for both habitats (Table 2). The sediment had a relatively high nitrogen content, and thus may be a key resource, rich in

microbes or algae. Detrital foods were moderately important in the cypress dome. Kratzer & Batzer (2007) maintain that wetland invertebrate communities in the Okefenokee are dominated by generalists that are able to tolerate wide ranges in habitat conditions. It could be suggested that they are also dietary generalists. Porter et al. (1999) describe Okefenokee systems as algal-based, with the majority of food web carbon originating from consumption of microbial production, algae, and living plants, rather than detritus. There is some support for this statement in our results.

Invertebrates can play crucial roles in wetland food webs (Wissinger, 1999), and information on their diets contributes to understanding energy flow within the ecosystem. Recognition of the energetic importance of chironomids and crustaceans in freshwater ecosystems has prompted more study of their dietary selection and feeding behavior (i.e., Berg, 1995; Lemke and Benke, 2003). Food habits of our study organisms varied depending on whether the taxon was residing in an herbaceous or forested habitat (Table 2). In all three study wetlands, invertebrates in the herbaceous habitat relied heavily on algal food resources, with macrophytes supplementing the diets. In the forested areas, detritus was more important, but in most cases, algae were supplementing diets. Wood was occasionally consumed in forested habitats (Okefenokee midges, Coosawhatchie isopods), even though it usually had the lowest nutritional quality (highest C:N ratio) of all foods. Our results provide some support to the notion that forested wetlands are detrital-based and herbaceous wetlands are algal-based. However, the seasonal availability of other resources is known to affect algae consumption (Wissinger, 1999), as is often seen in comparisons of floodplain cycles (i.e., Lindholm et al., 2007; Zeug & Winemiller, 2008). Seasonal cycles can be important for replenishing nutrient levels in wetlands. For example, detritus can become more nutritious to consumers in areas where seasonal desiccation allows for oxidation of the decomposed material (e.g., floodplain forests, Smock, 1999; Braccia & Batzer, 2001).

It could instead be argued that wetland invertebrates in this study were opportunistic, generalist feeders, able to use a range of foods in a range of habitats, and that they simply consumed foods as available. Ings et al. (2008) suggest that species-rich freshwater food webs tend to have blurred trophic levels, high levels of generalism, and a prevalence of feeding loops, although weak interactions may still create stable, albeit complex, webs. The movement of energy sources is influenced by the permeability of habitat boundaries and the structural complexity of the landscape (Holt, 2002).

Conclusion

An ongoing debate exists about whether wetland food webs are primarily detrital- or algal-based (Batzer et al., 2006; Zeug & Winemiller, 2008). Owing to the copious plant growth in wetlands, and the fact that most of this material remains in wetlands as detritus, many suggest that wetlands are detrital-based systems (Battle & Golladay, 2001; King & Richardson, 2007). However, others argue that detritus is a poor-quality food, and that many invertebrates consume higher-quality algae instead, and thus wetlands are algal-based systems (Bott, 1996). Our study suggests that this dichotomy is an oversimplification, and that depending on the habitat, both detritus and algae can be important to wetland food webs. Our results reflect wide-ranging diets in midges and crustaceans, with evidence of herbivory, algivory, detritivory, and even carnivory.

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References

Battle, J. M. & S. W. Golladay, 2001. Water quality and macroinvertebrate assemblages in three types of seasonally inundated limesink wetlands in southwest Georgia. Journal of Freshwater Ecology 16: 189–207.

Batzer, D. P., S. E. Dietz-Brantley, B. E. Taylor & A. E. DeBiase, 2005. Evaluating regional differences in macroinvertebrate communities from forested depressional wetlands across eastern and central North America. Journal of North America Benthological Society 24: 403–414.

Batzer, D. P., R. Cooper & S. A. Wissinger, 2006. Wetland animal ecology. In Batzer, D. P. & R. R. Sharitz (eds),

Ecology of Freshwater and Estuarine Wetlands. University of California Press, Berkeley, CA: 242–284.

Benstead, J. P., J. G. March, B. Fry, K. C. Ewel & C. M. Pringle, 2006. Testing IsoSource: stable isotope analysis of a tropical fishery with diverse organic matter sources. Ecology 87: 326–333.

Berg, M. B., 1995. Larval food and feeding behaviour. In Armitage, P. D., P. S. Cranston & L. C. V. Pinder (eds), The Chironomidae: The Biology and Ecology of Non-Biting Midges. Chapman & Hall, London: 136–168.

Bott, T. L., 1996. Algae in microscopic food webs. In Stevenson, R. J., M. L. Bothwell & R. L. Lowe (eds), Algal Ecology: Freshwater Benthic Ecosystems. Academic Press, San Diego, CA: 574–608.

Braccia, A. & D. P. Batzer, 2001. Invertebrates associated with woody debris in a southeastern U.S. forested floodplain wetland. Wetlands 21: 18–31.

Bunn, S. E. & P. I. Boon, 1993. What sources of organic carbon drive food webs in billabongs? A study based on stable isotope analysis. Oecologia 96: 85–94.

DeBiase, A. E. & B. E. Taylor, 2005. Microcrustaceans (Branchiopoda and Copepoda) of wetland ponds and impoundments on the Savannah river site, Aiken, South Carolina. SRO-NERP-28, Aiken, SC.

Epler, J. H., 2001. Identification Manual for the Larval Chironomidae (Diptera) of North and South Carolina. North Carolina State Department of Environmental Water Quality, Raleigh, NC.

Golladay, S. W., S. Entrekin & B. W. Taylor, 1999. Forested limesink wetlands of southwest Georgia: invertebrate habitat and hydrologic variation. In Batzer, D. P., R. B. Rader & S. A. Wissinger (eds), Invertebrates in Freshwater Wetlands of North America – Ecology and Management. John Wiley & Sons, Inc, New York, NY: 197–216.

Hoeinghaus, D. J. & S. C. Zeug, 2008. Can stable isotope ratios provide for community-wide measures of trophic structure? Comment. Ecology 89: 2353–2359.

Ings, T. C., J. M. Montoya, J. Bascompte, N. Bluthgen, L. Brown, C. F. Dormann, F. Edwards, D. Figueroa, U. Jacob, J. I. Jones, R. B. Lauridsen, M. E. Ledger, H. M. Lewis, J. M. Olesen, F. J. F. Van Veen, P. H. Warren & G. Woodward, 2008. Ecological networks—beyond food webs. Journal of Animal Ecology 78: 253–269.

Jardine, T. D., R. A. Curry, K. S. Heard & R. A. Cunjak, 2005. High fidelity: isotopic relationship between stream invertebrates and their gut contents. Journal of the North American Benthological Society 24: 290–299.

Jones, R. I., C. E. Carter, A. Kelly, S. Ward, D. J. Kelly & J. Grey, 2008. Widespread contribution of methane-cycle bacteria to the diets of lake profundal chironomid larvae. Ecology 89: 857–864.

Kelly, A., R. I. Jones & J. Grey, 2004. Stable isotope analysis provides fresh insights into dietary separation between *Chironomus anthracinus* and *C. plumosus*. Journal of the North American Benthological Society 23: 287–296.

King, R. S. & C. J. Richardson, 2007. Subsidy-stress response of macroinvertebrate community biomass to a phosphorus gradient in an oligotrophic wetland system. Journal of North American Benthological Society 26: 491–508.

Kratzer, E. & D. P. Batzer, 2007. Spatial and temporal variation in aquatic macroinvertebrates in the Okefenokee Swamp, Georgia, U.S.A. Wetlands 27: 127–140.

Layman, C. A., D. A. Arrington, C. G. Montaña & D. M. Post, 2007. Can stable isotope ratios provide quantitative measures of trophic diversity within food webs? Ecology 88: 42–48.

Lemke, A. M. & A. C. Benke, 2003. Growth and reproduction of three cladoceran species from a small wetland in the southeastern USA. Freshwater Biology 48: 589–603.

Lindholm, M., D. O. Hessen, K. Mosepele & P. Wolski, 2007. Food webs and energy fluxes on a seasonal floodplain; the influence of flood size. Wetlands 27: 775–784.

Loftin, C. S., 1997. Okefenokee swamp hydrology. In Hatcher, K. J. (ed.), Proceedings of the 1997 Georgia Water Resources Conference, 20–22 March 1997. University of Georgia, Athens, GA: 266–269.

McCutchan Jr., J. H., W. M. Lewis Jr., C. Kendall & C. C. McGrath, 2003. Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. Oikos 102: 378–390.

Newsome, S. D., C. M. del Rio, S. Bearhop & D. L. Phillips, 2007. A niche for isotopic ecology. Frontiers in Ecology and the Environment 5: 429–436.

Opsahl, S. P. & J. P. Chanton, 2006. Isotopic evidence for methane-based chemosynthesis in the Upper Floridian aquifer food web. Oecologia 150: 89–96.

Pennak, R. W., 1989. Freshwater Invertebrates of the United States, 3rd ed. John Wiley & Sons, Inc., New York, NY.

Phillips, D. L., 2001. Uncertainty in source partitioning using stable isotopes. Oecologia 127: 171–179.

Phillips, D. L. & J. W. Gregg, 2003. Source partitioning using stable isotopes: coping with too many sources. Oecologia 136: 261–269.

Porter, K. G., A. Bergstedt & M. C. Freeman, 1999. The Okefenokee Swamp: invertebrate communities and food-webs. In Batzer, D. P., R. B. Rader & S. A. Wissinger (eds), Invertebrates in Freshwater Wetlands of North America – Ecology and Management. John Wiley & Sons, Inc, New York, NY: 121–135.

Ruetz III, C. R., R. M. Newman & B. Vondracek, 2002. Top-down control in a detritus-based food web: fish, shredders, and leaf breakdown. Oecologia 132: 307–315.

Smock, L. A., 1999. Riverine floodplain forests of the southeastern United States: invertebrates in an aquatic-terrestrial ecotone. In Batzer, D. P., R. B. Rader & S. A. Wissinger (eds), Invertebrates in Freshwater Wetlands of North America: Ecology and Management. John Wiley & Sons, Inc, New York, NY: 137–166.

Stevenson, R. J., 1996. An introduction to algal ecology in freshwater benthic habitats. In Stevenson, R. J., M. L. Bothwell & R. L. Lowe (eds), Algal Ecology: Freshwater Benthic Ecosystems. Academic Press, San Diego, CA: 3–30.

Taylor, B. E., D. A. Leeper, M. A. McClure & A. E. DeBiase, 1999. Carolina bays: ecology of aquatic invertebrates and perspectives on conservation. In Batzer, D. P., R. B. Rader & S. A. Wissinger (eds), Invertebrates in Freshwater Wetlands of North America: Ecology and Management. John Wiley & Sons, Inc, New York, NY: 167–196.

Thorp, J. H. & M. L. Cothran, 1984. Regulation of freshwater community structure at multiple intensities of dragonfly predation. Ecology 65: 1546–1555.

Warren, P. H. & M. Spencer, 1996. Community and food-web responses to the manipulation of energy input and disturbance in small ponds. Oikos 75: 407–418.

Webb, K. D. & W. J. Mitsch, 2001. Macroinvertebrate diversity and abundance in two experimental wetlands from top-down and bottom-up interpretations. In Annual Report (Olentangy River Wetland Research Park). Ohio State University, Columbus, OH: 73–80.

Wissinger, S. A., 1999. Ecology of wetland invertebrates: synthesis and application for conservation and management. In Batzer, D. P., R. B. Rader & S. A. Wissinger (eds), Invertebrates in Freshwater Wetlands of North America – Ecology and Management. John Wiley & Sons, Inc, New York, NY: 1043–1086.

Zeug, S. C. & K. O. Winemiller, 2008. Evidence supporting the importance of terrestrial carbon in a large-river food web. Ecology 89: 1733–1743.