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# Development and application of a macroinvertebrate functional-group approach in the bioassessment of remnant river oxbows in southwest Florida

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*Abstract.* Invertebrate richness, density, mass, and functional-group analyses were used as surrogates for ecosystem attributes to evaluate conditions of 10 remnant oxbows along the channelized lower Caloosahatchee River in southwest Florida. Replicate 30-sec dipnet samples were taken in *Hydrocotyle* and *Nuphar* plant beds that accounted for >80% of cover in the oxbows. Dissolved oxygen (DO) was <65% saturation at the bottom in most oxbows, and all beds, except for 1 *Hydrocotyle* bed, were rated as heterotrophic. Invertebrate analyses indicated that most oxbows had sufficient coarse particulate organic matter to support normal summer shredder populations and an abundant supply of fine particulate organic matter to support large populations of filtering collectors. High ratios of predators to other functional groups were coupled with many rapid-turnover (i.e., short-life-cycle) prey taxa. Availability of invertebrate food for drift- and benthic-feeding fish was evaluated as generally poor. Overall rankings of ecological condition of oxbows, accomplished using all invertebrate categories and DO levels, formed the basis for recommendations about oxbow restoration along the river.

*Key words:* aquatic insects, plant beds, lotic, large river, wetlands, riparian marsh.

Invertebrates have been used widely to evaluate aquatic ecosystem condition and the impacts of stressors such as organic pollution, toxins, and physical habitat alteration (e.g., dams, channelization, removal of bankside vegetation) or to establish foodweb links to higher trophic levels such as fish and birds (e.g., Cummins 1992). Invertebrates in running waters are abundant, diverse, and large enough to be observed with the unaided eye. However, the difficulty of taxonomic determination in many groups often has made their use in calculating various indices of diversity, such as the Index of Biotic Integrity (IBI; Kerans and Karr 1994, Karr and Chu 1999), problematic. Because of taxonomic limitations and the recognition that functional roles of taxa can be useful in understanding aquatic ecosystems, procedures have been developed for analyzing the functional status of invertebrate assemblages in streams and rivers (e.g., Cummins 1973, 1974, Cummins and Klug 1979, Cummins and Wilzbach 1985, Merritt and Cummins 1996a, b).

Functional-group analyses were developed initially for small streams (Cummins 1973, 1974) and as key components of the river continuum concept (RCC, Vannote et al. 1980), in which they were applied to 4 different river basins in North America (Minshall et al. 1983, 1992). The methods were modified and applied to the Kissimmee River in south-central Florida (Merritt et al. 1996, 1999). Various ratios of the functional groups have been successfully used as surrogates for ecosystem attributes in the Kissimmee River (Merritt et al. 1996, 1999) and in southern Appalachian streams (Stone and Wallace 1998, Wagner 2001). The evaluation is based on easily observed morphological and behavioral attributes associated with feeding (functional-feeding groups, FFG) and modes of

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attachment, concealment, and locomotion (functional-habit groups, FHG), together with life-history patterns (voltinism) and drift propensity.

The ecosystem attributes, invertebrate surrogates for these attributes, and general criteria used for functional-group analysis focus attention on the nutritional resource base for the river ecosystem, i.e., the balance between gross primary production and community respiration (P/R), and the transport, storage, and partitioning of coarse and fine particulate organic matter (CPOM, FPOM) in the water column and in the sediments (Vannote et al. 1980, Cummins et al. 1981, Minshall et al. 1983, 1992, Cushing et al. 1995, Merritt et al. 1996, 1999). Other important ecosystem attributes reflect physical stability of the river habitat for invertebrates, the availability of invertebrates to higher trophic levels, and the capacity of the invertebrates to rapidly colonize new habitats.

The application of functional-group analysis reported here is an extension of the work done within the context of the Kissimmee River restoration project (Merritt et al. 1996). The objective of our study was to compare the ecosystem status (e.g., Vannote 1980) of remnant oxbows of the channelized Caloosahatchee River in southwest Florida using invertebrate functional organization as surrogates for ecosystem attributes. A long-term management objective, under the direction of the South Florida Water Management District (SFWMD) and the US Army Corps of Engineers (USACOE), is rehabilitation of the ecological condition of as many as possible of the 35 oxbows along the lower river. This management objective includes improving their recreational quality and enhancing their capability as water-quality filters and off-channel water-storage areas. The present ecological status of each oxbow, relative to both conceptual reference conditions (based on the general ecological literature) and conditions >20 y ago, but after channelization (Milleson 1979), should indicate the degree of rehabilitation necessary to re-establish their ecological integrity (Karr and Chu 1999).

To this end, invertebrate assemblage analyses, together with measurements of dissolved oxygen (DO) at the sediment surface, were used to rank the present ecological status (from worst to best) of 10 remnant oxbows, representing a range of ecological conditions from highly degraded to less degraded. The ranking should be useful to guide plans for oxbow restoration and to monitor changing ecological conditions in the oxbows.

## Study Sites

The Caloosahatchee River drains ~2590 km$^2$ in southwest Florida, and flows into San Carlos Bay in the lower portion of the greater Charlotte Harbor Estuary system (Fig. 1A). The river is the major waterway in southwest Florida and is used by ships transporting petroleum and manufacturing equipment and supplies, for irrigation, as a potable water supply, and for recreation. The USACOE connected the upper river to Lake Okeechobee in central Florida as part of the Intra-Coastal Waterway and channelized the river from the lake to the estuary in the mid to late 1960s. The channelized canal (designated C-43) averages 90 m in width and is 6 to 9 m in depth with steep, poorly vegetated side slopes. The altered river originates in Lake Okeechobee where it flows through the Moore Haven Lock and Dam (S-77) and 66 km to the Franklin Lock and Dam (S-79), which serves as a tidal barrier, largely excluding upstream intrusion of saline water from the estuary (Fig. 1A). The study was conducted in the 29-km reach from the town of LaBelle to the Franklin Lock and Dam. This reach includes 35 oxbows that remained after channelization of the river (Fig. 1B). These oxbows, identified and mapped by Milleson (1979), range in ecological condition from poor to good based on their flow, sediment accumulation, and biological diversity (Milleson 1979, Camp et al. 1995, Capece and Sholle 1996).

For our study, 10 of the 35 oxbows between the Franklin Lock and Dam and LaBelle (Fig. 1B) were selected for analysis of their general ecological condition, as indicated by DO measurements and invertebrate assemblage characteristics, in 2 dominant aquatic plant bed types: *Nuphar luteum* (L.) Sibth. & Sm. (spatterdock) in all 10 oxbows and *Hydrocotyle umbellata* L. (pennywort) in 7 of the oxbows. The condition of the 10 oxbows also represented a range from poorest to good (Miller et al. 1982, Camp et al. 1995, Capece and Scholle 1996), and those for which data on supply tributaries and/or canals were being collected. Primary criteria that influenced selection were degree of sedimentation since 1978 (Milleson 1979) and the present amount of

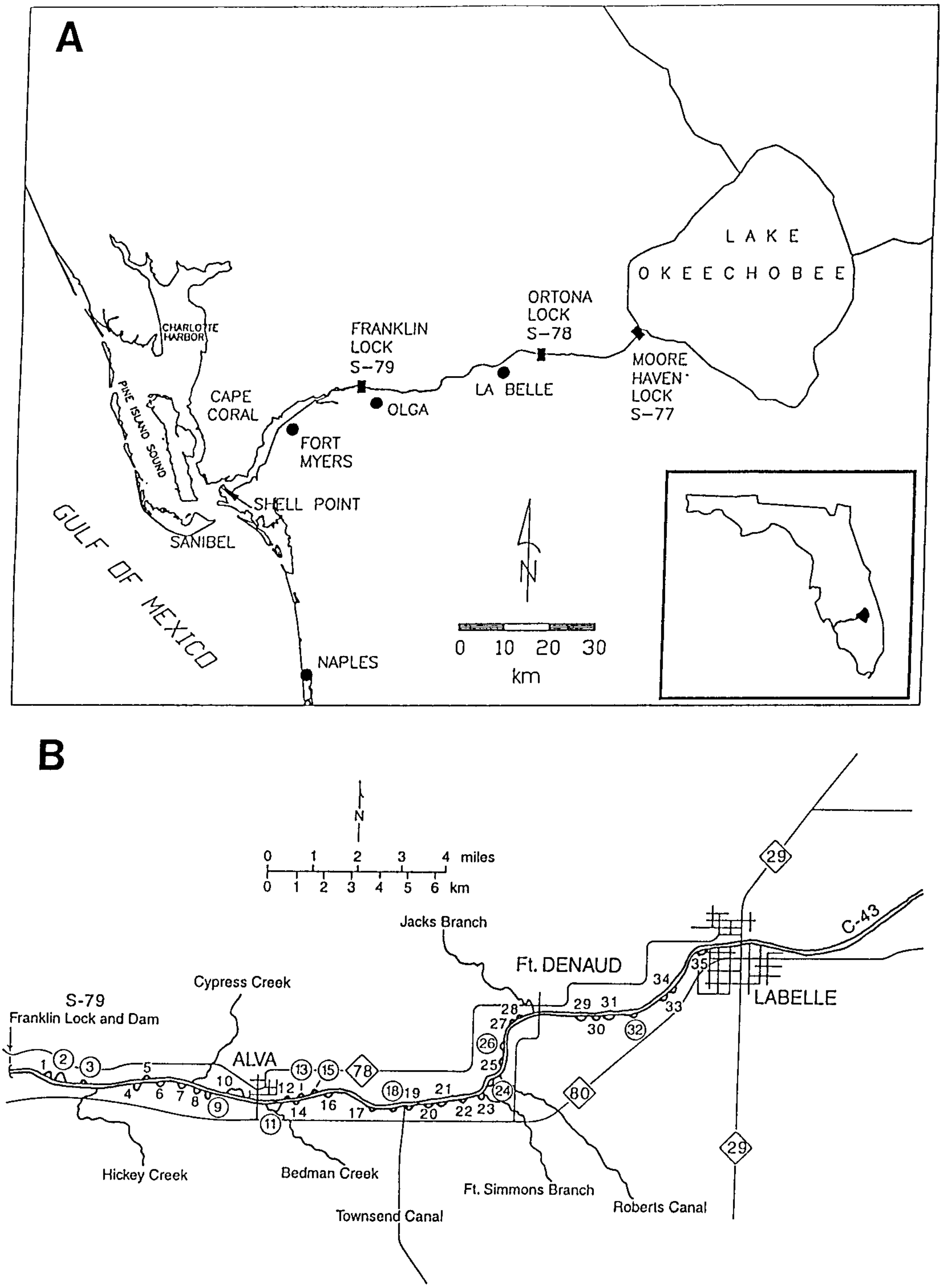


FIG. 1. Study site. A.—Caloosahatchee River drainage from Lake Okeechobee to the Pine Island Sound Estuary. B.—Location of the 35 remnant oxbows along the Caloosahatchee River (C-43) from the Franklin Lock and Dam (S-79) to the town of LaBelle. The 10 oxbows that were selected for sampling are circled (2, 3, 9, 11, 13, 15, 18, 24, 26, 32).

Table 1. Water-quality parameters for Caloosahatchee River oxbows recorded from 16 to 17 June 1998. DO = dissolved oxygen. – = no data.

| Ox-bow no. | Location coordinates (lat, long) | Temperature (°C) | | DO (mg/L)/%DO | | pH | | Specific conductance (mS/cm) | |
|---|---|---|---|---|---|---|---|---|---|
| | | Surface | Bottom | Surface | Bottom | Surface | Bottom | Surface | Bottom |
| 2 | 026 43 58 N, 081 40 83 W | 33.6 | 32.5 | 7.70/108.3 | 5.68/77.2 | 8.40 | 8.14 | 0.484 | 0.481 |
| 3 | 026 43 10 N, 081 40 21 W | 31.4 | 30.8 | 3.89/51.2 | 3.76/49.2 | 8.45 | 8.12 | 0.485 | 0.493 |
| 9 | 026 43 25 N, 081 37 87 W | 31.6 | 30.8 | 4.57/60.2 | 4.38/30.6 | 8.14 | 8.01 | – | – |
| 11 | 026 42 90 N, 081 36 11 W | 32.3 | 31.6 | 4.91/69.2 | 4.71/63.6 | 8.16 | 8.10 | 0.500 | 0.534 |
| 13 | 026 43 07 N, 081 35 61 W | 33.6 | 31.9 | 5.83/83.1 | 5.30/73.0 | 8.35 | 8.21 | 0.497 | 0.497 |
| 15 | 026 43 33 N, 081 34 95 W | 34.6 | 32.0 | 6.03/89.3 | 4.23/60.3 | 8.33 | 8.10 | 0.503 | 0.503 |
| 18 | 026 43 06 N, 081 33 47 W | 32.8 | 32.1 | 4.59/69.4 | 3.63/40.5 | 8.01 | 7.89 | 0.506 | 0.507 |
| 24 | 026 43 54 N, 081 31 50 W | 34.8 | 34.3 | 5.12/83.2 | 4.37/61.3 | 8.14 | 8.03 | 0.510 | 0.509 |
| 26 | 026 44 44 N, 081 31 24 W | 34.0 | 32.1 | 4.71/70.9 | 3.42/55.9 | 8.27 | 8.04 | 0.498 | 0.502 |
| 32 | 026 44 94 N, 081 28 52 W | 31.8 | 31.5 | 3.62/62.6 | 3.11/44.9 | 8.33 | 8.10 | 0.546 | 0.546 |

flow through the oxbows. The only oxbow macroinvertebrate data in the literature were reported from the general survey by Milleson (1979). The configuration of the oxbows had changed since his study and the invertebrate data only supported the general conclusion that reduced flow and related low DO had produced communities of low diversity.

## Methods

### *Sampling design*

Location (latitude and longitude) of sampling in each oxbow was determined with a Garman® global positioning instrument (Table 1). Water depths in each plant bed were recorded at each replicate sample location and ranged from 0.60 to 1.15 m. Temperature, DO (mg/L and % saturation), specific conductance (mS/cm), and pH were measured with a Yellow Springs Instruments model 51A meter at the surface and bottom in each oxbow (Table 1). DO was measured just above the sediment–water interface in each oxbow in an area of open channel adjacent to plant beds.

Invertebrate assemblages in *Nuphar* and *Hydrocotyle* beds in the 10 oxbows (numbers 2, 3, 9, 11, 13, 15, 18, 24, 26, and 32, Fig. 1B) were sampled 16 to 17 June 1998 with a long-handled D-frame net having a 0.5-mm mesh. Samples were collected from the middle of plant beds. A total of 71 macroinvertebrate samples was collected from the oxbows. Five *Nuphar* and 3 *Hydrocotyle* replicates were taken in each oxbow, except for oxbows 3, 15, and 24 where *Hydrocotyle* was absent. These beds made up ≥80% of the total cover in each oxbow and 99% of the littoral plant cover in any given oxbow. Open sediment habitats accounted for the remaining total area of any oxbow.

Sampling was conducted by the same person who repeatedly placed the net on the sediments at the bottom of the rooted plants (either *N. luteum* or *H. umbellata*), and moved it vigorously back and forth and up and down while drawing it to the surface along the plant stems for 30 sec. The method collects animals in the upper several cm of sediments, on the submerged stems and leaves of the plants, and from associated periphyton and detritus. This technique has

TABLE 2. Relationships between invertebrate functional groups (feeding, habit, and voltinism) and ecosystem attributes for which they can serve as analogs (modified after Merritt et al. 1996).

| Ecosystem parameter notation | Ecosystem parameter description | Functional group ratios representing ecosystem parameters (feeding, habit, life history, food web) | Ecosystem parameters that would be measured directly | General criteria levels of ratios for evaluation of ecosystem parameters |
|---|---|---|---|---|
| P/R | Gross primary production as a proportion of community respiration | Shredders (live vasc. plants) + scrapers + piercers as a proportion of shredders (CPOM detritivores) + total collectors | P/R (per unit area per day) | Autotrophic system: >0.75 |
| CPOM/FPOM | Coarse particulate organic matter as a proportion of fine particulate organic matter | Total shredders as a proportion of total collectors | CPOM/FPOM storage per unit area in and on the sediments (benthic) on a seasonal basis (wet and dry seasons) | Normal shredder riparian system by season<br>Dry (autumn–winter): >0.50<br>Wet (spring–summer): >0.25 |
| SPOM/BPOM | Suspended particulate organic matter as a proportion of deposited (benthic) particulate organic matter | Filtering collectors as a proportion of gathering collectors | SPOM per unit volume and BPOM per unit area | Enriched in SPOM: >0.50 |
| HABITAT STABILITY | Availability of stable surfaces and non-shifting sediments | Scrapers + filtering collectors as a proportion of total shredders + gathering collectors or clingers + climbers as a proportion of burrowers + sprawlers + swimmers | Available surfaces for stable attachment (sediment coarser than moved by maximum transport velocity, large woody debris, rooted vascular hydrophytes) | Stable substrates not limiting in rivers: >0.50<br>Stable substrates not limiting in rivers, littoral zones, wetlands: >0.60 |
| TOP-DOWN CONTROL | Top-down control of predators on prey | Predators as a proportion of total of all other functional feeding groups | A high ratio of slow-turnover predators and a high proportion of fast-turnover non-predator taxa | Normal top-down predator control: <0.15 |
| LIFE CYCLE | Short life cycle vs long life cycle | Generations per year >1 as a proportion of generations per year 1 | Dominance of rapid-colonizing species | Pioneer, early successional (less stable) community: >0.75 |
| DRIFT FOOD | Predictable food supply for water-column-feeding fish | Behavioral drifters as a proportion of accidental drifters | Dawn and dusk invertebrate drift | Good food supply for water-column-feeding fish: >0.50 |
| BENTHIC FOOD | Most available food supply for wading birds and benthic-feeding fish | Sprawlers as a proportion of clingers + climbers + burrowers + swimmers | Invertebrates vulnerable to wading birds and benthic-feeding fish | Good food supply for wading birds and benthic-feeding fish: >0.60 |

TABLE 3. Mean number of taxa (see Appendix), density of individuals (numbers/sample), and total dry mass (mg), with coefficients of variation (CV, %), from samples taken in *Hydrocotyle* ($n = 3$) and *Nuphar* ($n = 5$) beds in oxbows of the Caloosahatchee River, 16 to 17 June 1998. na = no *Hydrocotyle* beds.

| | *Hydrocotyle* | | | | | | *Nuphar* | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Taxa | | Density | | Mass | | Taxa | | Density | | Mass | |
| Oxbow | Mean | CV | Mean | CV | Mean | CV | Mean | CV | Mean | CV | Mean | CV |
| 2 | 15 | 48.1 | 289.7 | 88.7 | 160.9 | 64.9 | 14 | 45.7 | 239.0 | 63.3 | 507.6 | 64.2 |
| 3 | na | na | na | na | na | na | 11 | 46.5 | 30.2 | 36.9 | 49.7 | 68.2 |
| 9 | 17 | 21.8 | 153.7 | 40.9 | 231.2 | 40.7 | 6 | 28.4 | 62.2 | 81.8 | 128.7 | 98.4 |
| 11 | 18 | 14.7 | 454.0 | 63.5 | 413.0 | 72.7 | 12 | 30.6 | 33.4 | 24.3 | 24.7 | 38.1 |
| 13 | 20 | 71.2 | 153.3 | 92.9 | 191.5 | 76.8 | 10 | 14.1 | 29.2 | 39.8 | 39.1 | 78.0 |
| 15 | na | na | na | na | na | na | 11 | 36.7 | 55.4 | 39.6 | 24.4 | 49.6 |
| 18 | 18 | 58.5 | 564.3 | 58.7 | 456.9 | 46.3 | 15 | 15.4 | 197.0 | 90.6 | 247.9 | 32.8 |
| 24 | na | na | na | na | na | na | 9 | 47.9 | 57.2 | 121.2 | 56.6 | 85.7 |
| 26 | 24 | 8.6 | 396.3 | 25.5 | 411.4 | 60.1 | 19 | 17.7 | 116.6 | 45.9 | 100.6 | 112.0 |
| 32 | 11 | 18.2 | 54.7 | 46.5 | 159.6 | 37.3 | 15 | 38.2 | 67.8 | 69.2 | 33.1 | 44.1 |
| Totals | 18 | 34.4 | 295.1 | 59.5 | 289.2 | 57.0 | 12 | 32.1 | 88.8 | 61.3 | 121.2 | 67.1 |

been used successfully in the Kissimmee River restoration study in south-central Florida (Merritt et al. 1996, 1999, Cummins and Merritt 2001) and, with some modifications, in studies of other Florida streams (Barbour et al. 1996).

Net contents containing macroinvertebrates, vegetation, detritus, and some sediments were emptied into 14-L buckets, field sorted to remove large debris, and then washed several times through a 250-μm-mesh sieve to separate the invertebrates and remaining coarse debris from silt and fine detritus. The remaining material in each sample was then placed in Whirl-pak® bags, labeled, and preserved with 95% ethanol to a final concentration of 70%.

TABLE 4. Comparisons of mean (±1 SD) invertebrate taxa richness, mean (±1 SD) density (numbers/sample), and mean (±1 SD) dry mass (mg) from *Hydrocotyle* and *Nuphar* beds in the Caloosahatchee River, Florida. CV = coefficient of variation (%). ns = $p > 0.05$, * = $p \leq 0.05$, ** = $p \leq 0.01$.

| | *Hydrocotyle* | *Nuphar* | *t* | df |
|---|---|---|---|---|
| Taxa | 17.6 (4.0) | 12.2 (3.7) | 2.9* | 15 |
| Taxa CV | 34.4 | 32.1 | $0.3^{\mathrm{ns}}$ | 15 |
| Density | 295.1 (185.2) | 88.8 (73.3) | 3.2** | 15 |
| Density CV | 59.5 | 61.3 | $0.1^{\mathrm{ns}}$ | 15 |
| Mass | 289.2 (132.0) | 121.2 (152.1) | 2.4* | 15 |
| Mass CV | 57.0 | 67.1 | $1.0^{\mathrm{ns}}$ | 15 |

### *Benthic invertebrate analysis*

*Sample processing and identification.*—Invertebrate samples were treated with rose bengal dye (Mason and Yevich 1967), sorted in the laboratory under a dissecting microscope (120–1000×), and macroinvertebrates were identified and enumerated. Samples that contained significant amounts of detritus and sediment were subsampled following Waters (1969). Mass of each individual was determined from measurements of total length (maximum shell length for Mollusca) to the nearest mm (Merritt et al. 1996, Cummins and Merritt 2001) and a software program (INVERTCALC; KWC, M. A. Wilzbach, Humboldt State University, Arcata, California, and B. VandenEeden, Clarion University, Clarion, Pennsylvania, unpublished data) that uses a set of 30 regressions of dry mass on total length for a range of invertebrates. Each taxon or most closely related taxon is coded to a particular regression. Regression coefficients were determined empirically (KWC and M. A. Wilzbach, unpublished data) or taken from Smock (1980) and Benke et al. (1999), or references cited therein.

Invertebrates were identified using Merritt and Cummins (1996a), Thorp and Covich (1991), Pennak (1989), and other taxonomic references given in Merritt et al. (1996). Identifications were verified by cross-comparisons among workers at Michigan State University, Loyola

TABLE 5. Relative % mass by dominant taxa for *Hydrocotyle* and *Nuphar* beds in each oxbow sampled. Sph = *Sphaerium*, Chi = Chironomidae, Odo = Odonata, Gam = *Gammarus*, Hya = *Hyalella*, Pal = *Palaemonetes*, Cor = *Corbicula*, Bel = *Belostoma*, Eph = Ephemeroptera, Pel = *Pelocoris*, Clad = Cladocera, Oth = other, na = no *Hydrocotyle* beds.

| | *Hydrocotyle* | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Oxbow | Sph | Chi | Odo | Hya | Pal | Cor | Bel | Eph | Pel | Clad | Oth |
| 2 | 19.2 | 2.8 | 7.5 | 18.4 | 9.8 | 0 | 30.1 | 0 | 0 | 4.4 | 8 |
| 3 | na | na | na | na | na | na | na | na | na | na | na |
| 9 | 15.2 | 0.3 | 7.3 | 14.7 | 11.8 | 9.6 | 25.9 | 1.8 | 10.1 | 0 | 3.3 |
| 11 | 0 | 0.6 | 7.0 | 17.8 | 2.0 | 1.4 | 57.7 | 0.6 | 12.5 | 0 | 0.4 |
| 13 | 15.3 | 1.4 | 5.2 | 13.6 | 5.2 | 0 | 25.3 | 1.0 | 7.8 | 0 | 25.2 |
| 15 | na | na | na | na | na | na | na | na | na | na | na |
| 18 | 26.4 | 0.3 | 1.8 | 16.6 | 19.7 | 0 | 24.3 | 0.2 | 8.7 | 0 | 2.0 |
| 24 | na | na | na | na | na | na | na | na | na | na | na |
| 26 | 13.1 | 0.5 | 6.0 | 15.3 | 9.3 | 0.9 | 43.1 | 0.5 | 4.0 | 0 | 7.3 |
| 32 | 0 | 1.4 | 6.9 | 1.3 | 87.0 | 0 | 0 | 1.5 | 0 | 0 | 1.9 |
| Mean | 12.7 | 1.0 | 6.0 | 14.0 | 20.7 | 1.7 | 29.5 | 0.8 | 6.2 | 0.6 | 6.8 |

University of Chicago, SFWMD, and by comparing with voucher specimens identified from previous studies on the Kissimmee River–riparian marsh ecosystem (Merritt et al. 1996).

*Functional group assignments.*—Invertebrate taxa were assigned to FFGs and FHGs using tables 1 and 5 of Merritt et al. (1996) and the ecological tables from Merritt and Cummins (1996a). The FFGs used were: 1) *shredders* that feed on CPOM (>1 mm diameter, either live aquatic macrophyte tissue or coarse terrestrial plant litter); 2) *scrapers* that harvest periphyton and associated particulate material from substrate surfaces, primarily live plant stems; 3) *filtering* and *gathering collectors* of FPOM (<1 mm diameter); 4) *plant piercers* that imbibe cell fluids from filamentous macroalgae and vascular hydrophytes; and 5) *predators* that capture live prey. The FHGs used were: 1) *clingers* with morpho-behavioral adaptations to resist dislodgement; 2) *climbers* with opposable legs or suction devices used in moving vertically up and down plant stems; 3) *sprawlers* having adaptations for staying on top of fine sediments, or on floating plant leaves with no special attachment adaptations; 4) *burrowers* living in the sediment interstices or in constructed tubes within the sediment; 5) *swimmers* that move in short bursts between resting locations, usually on submerged portions of aquatic vascular plants; 6) *skaters/divers* that are associated with the surface film, including some that regularly dive beneath the surface; and 7) *planktonic* forms that are suspended in the water column with little ability to move significant distances by their own locomotion. Each taxon was assigned to a general functional group (i.e., feeding and habit), voltinism (number of generations per year), and drift propensity (i.e., accidental or behavioral drifters) category (Appendix) based on those given in Merritt et al. (1996, table 5), Merritt and Cummins (1996a, b), and other references cited in Merritt et al. (1996).

*Functional group ratios.*—Ratios of functional groups have been developed that are related to ecosystem attributes (Table 2), and threshold levels between intact (good) and altered (poor) riverine ecosystems have been proposed. The calculated ratios from a given site are similar over a large range of sample sizes and, therefore, can be determined from semiquantitative samples (Minshall et al. 1983). The approach focuses on function rather than taxonomy, so it is more likely to be linked to habitat quality and availability of nutritional resources to which the invertebrates respond.

The invertebrate ratios applied here are the same ones used in other related riverine studies (e.g., Merritt et al. 1996, 1999) and the threshold levels given for each functional-group ratio were derived from river studies by Cummins et al. (1981), Minshall et al. (1983, 1992), Stone and Wallace (1998), RWM and KWC (unpublished data), and best professional judgement of the authors. These levels are intended to indicate approximate breaks between acceptable and im-

TABLE 5. Extended.

| *Nuphar* | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Sph | Chi | Odo | Gam | Hya | Pal | Cor | Bel | Pel | Oth |
| 80.7 | 1.3 | 3.3 | 0 | 0 | 0 | 0 | 0 | 0 | 14.7 |
| 0 | 7.4 | 15.5 | 0 | 2.4 | 0 | 63.4 | 0 | 0 | 11.3 |
| 0 | 1.9 | 0 | 2.6 | 0.5 | 6.7 | 87.6 | 0 | 0 | 0.7 |
| 8.4 | 8.8 | 7.2 | 31.9 | 2.8 | 22.3 | 0.8 | 0 | 0 | 17.8 |
| 4.1 | 6.6 | 17.6 | 25.7 | 0.3 | 0.5 | 29.6 | 0 | 0 | 15.6 |
| 1.9 | 14.3 | 2.9 | 18.3 | 0.4 | 0 | 44.6 | 0 | 0 | 17.6 |
| 73.8 | 1.9 | 1.4 | 0 | 3.3 | 0 | 0 | 17.3 | 0 | 2.3 |
| 40.6 | 1.2 | 2.8 | 3.9 | 8.1 | 4.6 | 18.7 | 0 | 7.2 | 12.9 |
| 68.1 | 8.9 | 7.3 | 1.0 | 0.3 | 0 | 9.0 | 0 | 0 | 5.4 |
| 8.2 | 15.4 | 8.4 | 16.9 | 5.4 | 29.3 | 0.9 | 0 | 0 | 15.5 |
| 28.6 | 6.8 | 6.6 | 10.0 | 2.4 | 6.3 | 25.5 | 1.7 | 0.7 | 11.4 |

paired ecological integrity. For example, the RCC (Vannote 1980, Minshall et al. 1983, 1992) and Kissimmee River studies (Merritt et al. 1996, 1999) showed that autotrophic sites supported more diverse and larger populations of invertebrates and sport fish compared to heterotrophic sites. In addition, when the POM resources, derived primarily from the riparian zone, are sufficient to support significant shredder and filter-feeding collector populations, their diversity and densities are indicative of intact ecological integrity. Similar reliance on previous studies and experience were used to propose thresholds for habitat stability (suitable attachment sites) and drift propensity (suitable food for water-column-feeding fish). Life-history features were categorized solely on the basis of generation times (voltinism) because, in ecosystems for which the goal is restoration, rapid recolonization by invertebrates was judged to lead, on average, to rapid recovery of ecosystem integrity. This generalization does not apply to undesirable invasive species, which might be the most rapid colonizers and would be omitted from the calculations.

*Ranking of functional-group ratios based on ecological condition.*—Ratios for invertebrate ecosystem surrogates were ranked according to their predicted relationships with the ecosystem parameters they represent (Table 2). High invertebrate P/R ratios were given high rankings because they represent the favorable DO levels that autotrophic systems generate; high DO levels support diverse invertebrate assemblages (e.g., Merritt et al. 1996, 1999, Stone and Wallace 1998, Wagner 2001) for wetland systems like the Caloosahatchee oxbows. The higher the invertebrate CPOM/FPOM value, the more likely the system has a normal wet season (spring–summer) shredder component, represented primarily by feeders on live vascular plants (Merritt et al. 1996, 1999) and, thus, high ratio values were given a high ranking. The availability of suspended FPOM (SFPOM) compared to benthic FPOM (BFPOM) to support filtering collectors (invertebrate SFPOM/BFPOM) should be valuable in supporting a healthy, diverse invertebrate community. Thus, higher ratios were assigned higher rankings (e.g., Minshall et al. 1983, Merritt et al. 1996). High values of invertebrate habitat stability ratios (based either on FFGs or FHGs) received a high ranking because attachment sites and stable locations support a taxonomically rich and abundant invertebrate fauna (Merritt et al. 1996, 1999). High values of the drifting fish food ratio received high rankings because they indicated a predictable food supply for water-column-feeding fish in the form of diel behavioral invertebrate drifters (e.g., Wilzbach et al. 1986, 2001). High benthic food ratios were ranked high because they indicate high availability of food for bottom-feeding fish and wading birds (Merritt et al. 1996, 1999, Wilzbach et al. 2001). The greater the dominance of invertebrates with short life cycles the higher the ranking that was assigned, to reflect the importance of rapid colonization following physical habitat restoration. Taking the relative dominance of predators as 15% (Merritt et al. 1996, 1999, Merritt and Cummins 1996a), the highest rankings were assigned to the ratios with values closest to 15%.

The oxbows were ranked separately for each bed type. These beds were ranked on the basis of DO, invertebrate density, mass, diversity, each of the 8 invertebrate functional-group ratios, and the voltinism ratio. Thus, rankings were based on 13 categories from best to worst for *Hydrocotyle* beds (scale: 1–7) and for *Nuphar* beds (scale 1–10). The rank indicating the best ecological condition was assigned to the oxbow with the highest value for the voltinism ratio and each of the functional-group ratios, except the top-down ratio, which was ranked according to its closeness to the criterion level of 0.15 (Table 2).

### *Analysis of data*

Mean invertebrate taxa richness, total invertebrate abundance, and total invertebrate mass were compared between macrophyte bed types with *t*-tests using SYSTAT (1999, version 9.0, SPSS Inc., Chicago, Illinois). Deviations from threshold values of the ratios of masses of invertebrate FFGs and FHGs, voltinism groups, and drift-propensity groups used as analogs for selected ecosystem attributes (Table 2) were compared qualitatively.

## Results

### *Invertebrates of oxbows*

Invertebrate taxa collected are summarized in the Appendix, and the mean number of taxa, density, and dry mass for each oxbow are listed in Table 3. Invertebrate taxa richness, density, and mass were significantly greater in *Hydrocotyle* beds than in *Nuphar* beds (*t*-test, all $p < 0.05$) (Table 4). The mean density of invertebrates collected per sample was >3 times greater in *Hydrocotyle* beds than in *Nuphar* beds (Table 4), with invertebrate densities in *Hydrocotyle* beds ranging from 55 to 564/sample (Table 3). Densities in *Nuphar* beds ranged from 29 to 239/sample (Table 3). Mean invertebrate mass in *Hydrocotyle* beds was >2 times higher than in *Nuphar* beds (Table 4). Mean invertebrate dry mass per sample from both bed types from all oxbows ranged from ~0.02 to 0.5 g (Table 3). Sample variability for taxa richness, density, and mass was similar across bed type and oxbows; CVs ranged from 32 to 67% (Table 4).

In *Hydrocotyle* beds, *Belostoma* accounted for 24 to 58% of the mass in all oxbows except in oxbow 32 where *Palaemonetes* accounted for 87% of the mass (Table 5). *Palaemonetes* accounted for only 2 to 20% of the total mass in the other oxbows. If *Pelocoris* is added to the mass of *Belostoma*, total hemipteran predators accounted for 30 to 70% of the total invertebrate mass in *Hydrocotyle* beds, except in Oxbow 32 (Table 5). Other taxa dominating mass in *Hydrocotyle* beds were *Sphaerium* (range: 13–26%) and *Hyalella* (range: 14–18%), except in oxbow 32.

*Sphaerium* and *Corbicula* dominated samples taken in *Nuphar* beds in 8 of 10 oxbows, accounting for 34 to 88% of the total mass (Table 5). Invertebrate mass in oxbows 11 and 32 was dominated by *Palaemonetes* and *Gammarus*, which together accounted for 46 to 54% of the mass in these oxbows (Table 5).

### *DO*

Daytime DO saturations at the bottom in the open channel adjacent to plant beds should reflect maximum diel levels. They were ≥40% saturation in 9 of the 10 oxbows, and the total range across oxbows was 30.6 to 77.2% (Table 1). All oxbows had profiles of declining % saturation from the water surface to the bottom. There were no large differences in either pH or specific conductance readings with oxbow or depth (Table 1).

Low DO levels in running waters have been linked with reduced biological diversity and altered ecosystem function (Gaufin 1973, Ward 1992). Therefore, DO saturation measured at the bottom in each oxbow at the time of invertebrate sampling (Table 1) was plotted against mean invertebrate taxonomic richness, densities, and total mass for the 2 bed types (Fig. 2). No statistically significant relationships were found between the invertebrate data and DO levels, but some trends were observed. For example, oxbow 2, which had the highest DO saturation of any oxbow, also had the highest mean density and mass in *Nuphar* beds (Fig. 2D–F, Table 3). In contrast, oxbow 9, which had the lowest bottom DO saturation, also had low richness, density, and

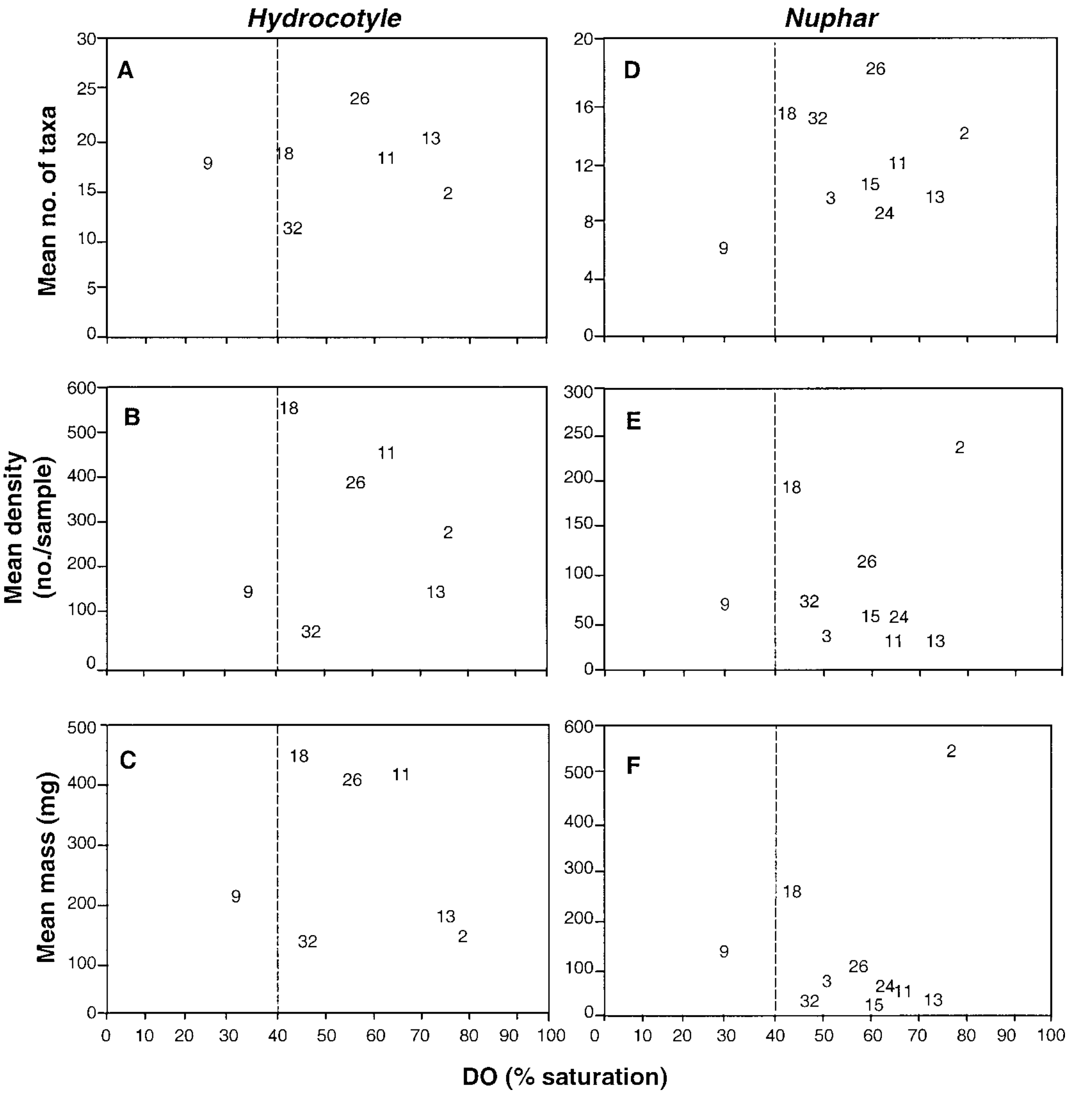


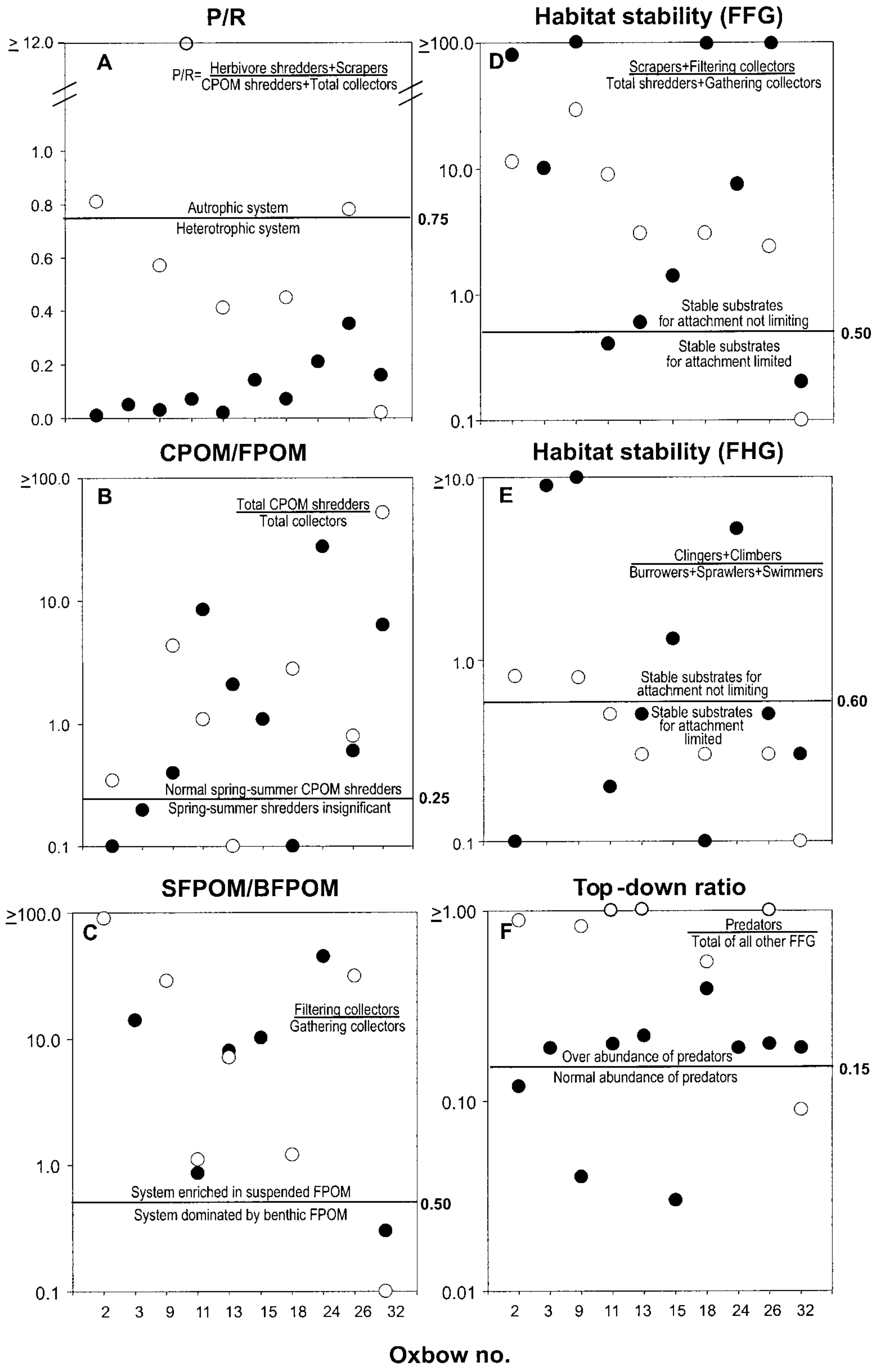
FIG. 2. Dissolved oxygen (DO) at the bottom vs mean number of taxa (A, D), mean density of individuals (B, E), and mean dry mass (C, F) per sample by oxbow for *Hydrocotyle* (A–C) and *Nuphar* (D–E) beds. Vertical dotted line represents 40% saturation.

mass values in both bed types (Fig. 2A–F, Table 3).

### *Evaluation of oxbows*

Macroinvertebrate community functional organization indicated that the oxbows along the Caloosahatchee River were primarily heterotrophic systems (Fig. 3A). The invertebrate functional surrogate for P/R was unequivocally autotrophic only in the *Hydrocotyle* beds of oxbow 11. However, *Hydrocotyle* beds in oxbows 2 and 26 were on the proposed threshold between autotrophy and heterotrophy (Fig. 3A). Oxbows 2, 11, and 26 all had DO levels >50% saturation near the river bottom and 3 of the 4 highest DO concentrations across all oxbows (Fig. 2). All *Nuphar* beds were strongly heterotrophic, with consistently low invertebrate P/R values (80% were <0.2) and little variation among oxbows (60% of the values ranged from 0.01–0.07).

About 75% of the total shredder/total collec-


P/R
≥ 12.0
A
P/R= Herbivore shredders+Scrapers / CPOM shredders+Total collectors
1.0
0.8
0.6
0.4
0.2
0.0
Autrophic system
Heterotrophic system
0.75
Habitat stability (FFG)
≥100.0
D
Scrapers+Filtering collectors / Total shredders+Gathering collectors
10.0
1.0
0.1
Stable substrates for attachment not limiting
Stable substrates for attachment limited
0.50
CPOM/FPOM
≥100.0
B
Total CPOM shredders / Total collectors
10.0
1.0
0.1
Normal spring-summer CPOM shredders
Spring-summer shredders insignificant
0.25
Habitat stability (FHG)
≥10.0
E
Clingers+Climbers / Burrowers+Sprawlers+Swimmers
1.0
0.1
Stable substrates for attachment not limiting
Stable substrates for attachment limited
0.60
SFPOM/BFPOM
≥100.0
C
Filtering collectors / Gathering collectors
10.0
1.0
0.1
System enriched in suspended FPOM
System dominated by benthic FPOM
0.50
Top-down ratio
≥1.00
F
Predators / Total of all other FFG
0.10
0.01
Over abundance of predators
Normal abundance of predators
0.15
2 3 9 11 13 15 18 24 26 32
2 3 9 11 13 15 18 24 26 32
Oxbow no.

tor ratio (a surrogate for CPOM/FPOM) for both plant types were in the normal spring–summer shredder (or generally heterotrophic) range (Fig. 3B). This measure indicates that a significant portion of the POM, which serves as food for detrital shredders, was coarse. In *Hydrocotyle* beds, oxbows 2, 11, 13, and 26 had the 4 highest DO levels at the bottom (Fig. 2), an indication of more autotrophic conditions, and these oxbows had the 4 lowest CPOM/FPOM invertebrate ratios among all oxbows (Fig. 3B). In *Nuphar* beds, oxbows 2 and 18 also had DO levels >40% (Fig. 2), and the lowest CPOM/FPOM ratios (= 0.1, Fig. 3B). Therefore, both P/R and CPOM/FPOM measures indicated all of these oxbows (2, 11, 13, 18, 26) would likely not support large populations of detrital shredder invertebrates. The high ratio of filtering collectors/gathering collectors (a surrogate for SFPOM/BFPOM) further indicated that the oxbows were generally heterotrophic (Fig. 3C). All but oxbow 32 were rated as being enriched in suspended FPOM (Fig. 3C).

Adequate substrates for attachment were present in most oxbows (14 of 17 macrophyte beds) when the FFG ratio was used as a surrogate for habitat stability (Fig. 3D). However, oxbows were deficient in stable substrates when the FHG ratio was used as the surrogate for habitat stability (Fig. 3E). The difference appeared to be

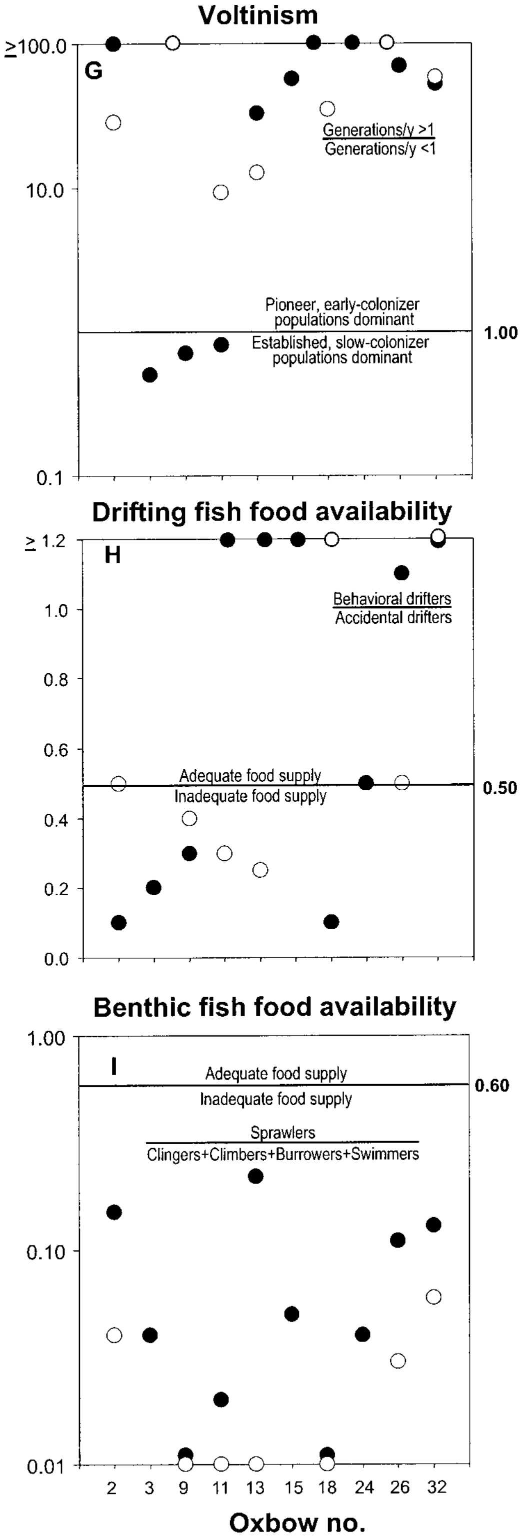


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FIG. 3. Functional group (feeding, habit, and voltinism, see Table 2) plotted by plant bed type (circles: *Hydrocotyle*, dots: *Nuphar*) and oxbow number. The proposed threshold values for each ratio are in boldface on the right-side y-axis and the designations above and below this threshold line are shown in each panel. A.—Primary production/community respiration (P/R). B.—Coarse/fine particulate organic matter (CPOM/FPOM) availability supporting spring–summer shredder populations. C.—Suspended fine/benthic fine particulate organic matter (SFPOM/BFPOM) supporting filtering collectors. D.—Habitat stability based on functional-feeding groups (FFG). E.—Habitat stability based on functional-habit groups (FHG). F.—Top-down ratio (i.e., abundance of predators). G.—Voltinism or life cycle (i.e., number of generations/y). H.—Availability of drift to fish feeding in the water column. I.—Availability of food to benthic-feeding fish or wading birds. Scale on y-axis is either linear (A, H) or log (B–G, I).

TABLE 6. Ranking of the *Hydrocotyle* beds in the Caloosahatchee River. The rankings for each category are from 1 = best ecological condition to 7 = worst ecological condition (see text for criteria for ranking of functional ratios). Overall rank is based on the sum for 13 categories: the lowest sum score of the ranks for all 13 categories (i.e., closest to a possible best score of 13, or 13 × 1) received the highest overall rank, and the highest sum score of the ranks for all 13 categories (i.e., closest to a possible worst score of 91, or 13 × 7) received the lowest overall rank. * = no ranking in this category because oxbows in previous rankings were tied. Multiple entries indicate tied score. DO = dissolved oxygen, P/R = primary production/community respiration, CPOM = coarse particulate organic matter, FPOM = fine particulate organic matter, SFPOM = suspended fine particulate organic matter, BFPOM = benthic fine particulate organic matter, FFG = functional-feeding group, FHG = functional-habit group.

| Oxbow | DO | Density | Mass | Taxa richness | P/R | CPOM/FPOM | SFPOM/BFPOM | Habitat stability | | Top down | Voltinism | Drift food | Benthic food | | Overall rank |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | FFG | FHG | | | | | | |
| 2 | 1 | 4 | 6 | 6 | 2 | 6 | 2 | 2 | 1 | 4 | 5 | 3 | 2 | 44 | 2 |
| 9 | 7 | 5 | 4 | 5 | 4 | 3 | 4 | 1 | 2 | 3 | 2 | 5 | 4* | 49 | 4 |
| 11 | 3 | 2 | 2 | 4 | 1 | 5 | 6 | 3 | 3 | 7 | 7 | 6 | 6* | 55 | 5 |
| 13 | 2 | 6 | 5 | 2 | 6 | 7 | 5 | 5 | 5 | 5 | 6 | 7 | 4* | 65 | 7 |
| 18 | 5 | 1 | 1 | 3 | 5 | 2 | 1 | 4 | 6 | 2 | 4 | 2 | 6* | 42 | 1 |
| 26 | 4 | 3 | 3 | 1 | 3 | 4 | 3 | 6 | 4 | 6 | 1 | 4 | 3 | 45 | 3 |
| 32 | 6 | 7 | 7 | 7 | 7 | 1 | 7 | 7 | 7 | 1 | 3 | 1 | 1 | 62 | 6 |

related to the use of bivalves in the numerator in the FFG ratio, but in the denominator in the FHG ratio (see discussion below). Both surrogates, although conflicting, were still used in the overall assessment of oxbow condition.

Macrophyte beds had predator mass in excess of general expectations (Table 2) in 13 of 17 cases, especially in *Hydrocotyle* beds (Fig. 3F). This result agrees with the observation that invertebrate populations in both bed types in all but 2 oxbows were dominated by short-life-cycle, rapid-turnover species (Fig. 3G), thereby insuring a continuing adequate prey base for predators. Most (10/17) plant beds had an inadequate or barely adequate food supply for drift-feeding fish (Fig. 3H). However, ½ of the *Nuphar* beds (oxbows 11, 13, 15, 26, and 32) supported a reliable food supply for water-column-feeding fish (Fig. 3H), although DO conditions might not have been sufficient in some oxbows to support game fish (Fig. 2). All plant beds provided a very poor food supply for visual, benthic-feeding wading birds and fish (Fig. 3I).

### *Ranking of ecological condition*

The top 3 overall oxbow rankings were the same for both macrophyte types (Tables 6, 7). Oxbows 2, 18, and 26 were judged to be in the best condition using the sum of all invertebrate ratios together with DO levels at the channel bottom. Oxbow 24 and 18 received the same high ranking (2nd) in *Nuphar* beds (Table 7), but no *Hydrocotyle* beds were present in oxbow 24 (Table 6). Oxbows 11 and 13 were ranked among the 3 having the worst conditions in both bed types. Oxbow 32 was ranked 4th out of 10 and 6th out of 7 in *Nuphar* and *Hydrocotyle* beds, respectively. Oxbow 3, which had no *Hydrocotyle* bed, ranked 7th out of 10 using data from *Nuphar* beds (Tables 6, 7).

Conditions in the 2 macrophyte types, as indicated by macroinvertebrate assemblages, were generally similar when compared across the entire set of oxbows. However, oxbow 18 was ranked 1st for *Hydrocotyle* beds (Table 6), but 2nd for *Nuphar* beds, in which oxbow 26 was ranked 1st (Table 7). Similarly, in oxbow 13, the *Hydrocotyle* bed was ranked poorest (Table 6), whereas the *Nuphar* bed was ranked 6th out of 10 (Table 7).

## Discussion

### *Comparisons with Kissimmee River study*

The Caloosahatchee and Kissimmee rivers are 2 major rivers in south Florida and are both the

TABLE 7. Ranking of the *Nuphar* beds in the Caloosahatchee River. The rankings for each category are from 1 = best ecological condition to 10 = worst ecological condition (see text for criteria for ranking of functional ratios). Overall rank is based on the sum for 13 categories: the lowest sum score of the ranks for all 13 categories (i.e., closest to a possible best score of 13, or 13 × 1) received the highest overall rank, and the highest sum score of the ranks for all 13 categories (i.e., closest to a possible worst score of 130, or 13 × 10) received the lowest overall rank. DO = dissolved oxygen, P/R = primary production/community respiration, CPOM = coarse particulate organic matter, FPOM = fine particulate organic matter, SFPOM = suspended fine particulate organic matter, BFPOM = benthic fine particulate organic matter, FFG = functional-feeding group, FHG = functional-habit group.

| Oxbow | DO | Density | Mass | Species richness | P/R | CPOM/FPOM | SFPOM/BFPOM | Habitat stability | | Top down | Voltinism | Drift food | Benthic food | | Overall rank |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | FFG | FHG | | | | | | |
| 2 | 1 | 1 | 2 | 4 | 10 | 9 | 1 | 4 | 10 | 1 | 2 | 10 | 4 | 58 | 3 |
| 3 | 7 | 9 | 18 | 7 | 7 | 8 | 6 | 5 | 2 | 2 | 10 | 8 | 6 | 83 | 7 |
| 9 | 10 | 5 | 9 | 10 | 8 | 6 | 2 | 3 | 1 | 7 | 9 | 7 | 9 | 80 | 6 |
| 11 | 3 | 8 | 26 | 5 | 5 | 2 | 9 | 9 | 8 | 9 | 8 | 2 | 8 | 85 | 8 |
| 13 | 2 | 10 | 24 | 8 | 9 | 4 | 8 | 8 | 6 | 6 | 7 | 4 | 1 | 80 | 6 |
| 15 | 5 | 7 | 3 | 6 | 4 | 5 | 7 | 7 | 4 | 8 | 5 | 1 | 4 | 73 | 5 |
| 18 | 9 | 2 | 13 | 2 | 5 | 9 | 4 | 1 | 9 | 10 | 3 | 9 | 9 | 56 | 2 |
| 24 | 4 | 6 | 32 | 9 | 2 | 1 | 5 | 6 | 3 | 2 | 1 | 6 | 6 | 56 | 2 |
| 26 | 6 | 3 | 11 | 1 | 1 | 7 | 3 | 2 | 5 | 5 | 4 | 5 | 3 | 49 | 1 |
| 32 | 8 | 4 | 15 | 3 | 3 | 3 | 10 | 10 | 7 | 2 | 6 | 3 | 2 | 69 | 4 |

object of restoration efforts, with the Kissimmee River restoration already underway. The rivers are approximately the same size, both have been channelized, and both have only remnants of their former complexity (i.e., oxbows or side channels).

Taxonomic richness of macroinvertebrates in *Hydrocotyle* and *Nuphar* beds in the Caloosahatchee River oxbows (89 taxa) was twice that measured in *Nuphar* and *Polygonum* beds in the Kissimmee River study (45 taxa, Merritt et al. 1996, 1999). Mean mass per sample was higher in Caloosahatchee River oxbows (*Nuphar* = 121 mg/sample, *Hydrocotyle* = 289 mg/sample) than in the dominant littoral beds of a Kissimmee River remnant channel (*Nuphar* = 79 mg/sample, *Polygonum* = 56 mg/sample). These differences, along with poorer DO levels in the Kissimmee River remnant channels (Merritt et al. 1996, 1999), suggest that the more degraded conditions in the Kissimmee, as indicated by invertebrate assemblages, will be less amenable to restoration than those in the Caloosahatchee River oxbows. However, the cumulative ranking scores (Tables 6, 7) indicate that all the Caloosahatchie River oxbows are impaired, with a narrow range from fair to poor, and even the best oxbows of the series are in need of rehabilitation effort.

### *Oxbow rehabilitation*

If our data are used as the basis for recommendations about rehabilitation of the remnant oxbows of the Caloosahatchee River, those oxbows ranked the best could be selected for initial efforts because they hold the greatest promise of success. On this basis, combining data from *Hydrocotyle* and *Nuphar* beds, oxbows 2, 18, and 26 were ranked as best overall (Tables 6, 7). Oxbow 24, which had only *Nuphar* beds, was ranked 2nd best for that macrophyte type alone. Therefore, oxbows 2, 18, 24, and 26 are the most likely candidates for rehabilitation. In contrast, oxbows 11 and 13 received low rankings for both macrophyte types and would likely require the greatest physical alteration for restoration (Tables 6, 7). Oxbow 3, which had no *Hydrocotyle* beds, also received a poor ranking and would be difficult to rehabilitate. Oxbow 32 presented conflicting results (*Hydrocotyle*: 6th out of 7 oxbows, *Nuphar*: 4th out of 10 oxbows), but would likely be difficult to restore. Restoration of oxbows in either good or poor condition could involve physical alteration to increase flow through them. Oxbows with sufficient DO at the bottom had diverse invertebrate populations and, as detailed in our field notes, were those oxbows that had observable flow through them (e.g., 2, 26).

### *Final considerations*

New techniques are needed to rapidly assess the condition of riparian marsh habitat as development continues along larger rivers (i.e., ≥5th order). The need is for rapid evaluation of fundamental attributes that describe ecosystem condition. The methods described here provide such a tool by using aspects of the functional organization of the invertebrate assemblage as surrogates for important ecosystem attributes of river margins. These ecosystem attributes include the balance between autotrophic and heterotrophic pathways of energy transformation, the relative dominance of CPOM and FPOM detritus, and foodweb pathways that link higher trophic levels to primary production and detrital food resources through invertebrates as prey.

The pattern of oxbow rankings based on macroinvertebrate assemblages was similar for the 2 plant bed types in the Caloosahatchee River oxbows. However, to account for any observed differences between plant bed types, sampling effort could be weighted by the amount of habitat occupied by each plant bed type to develop habitat area-weighted means.

The methods reported here should be applicable to a wide range of river-margin habitats across a broad geographic range, and represent significant economies of time in sample analysis. It is obvious that more time is required for greater taxonomic detail. The functional-group approach significantly reduces the level of taxonomic effort required and, therefore, represents a large time and cost saving during laboratory analysis. Sufficient resolution for functional-group designation can be achieved by separating specimens to subfamily or tribe, which can generally be accomplished without elaborate specimen preparation.

Large data sets will be required to establish threshold values between human-impacted and unimpacted sites using macroinvertebrate ratios, and more simultaneous measurements of invertebrate ratios and ecosystem attributes under a range of stream and river conditions are needed. We view our study as an effort along this path. For example, diel DO conditions will differ both within habitat types and between macrophyte beds and the open channel. Occasional DO minima may be limiting factors for invertebrate and sport fish assemblages. These periods of reduced DO must be considered when using invertebrate ratios as surrogates of ecosystem attributes. In addition, it is particularly critical to establish least-altered reference sites that can be used as the standard for comparison within a region.

The validity of some of the invertebrate ratios as surrogates for ecosystem attributes needs further testing. For example, the estimates of habitat stability using the FFG and FHG ratios (Fig. 3D, E) did not agree because of the high biomass of bivalves (*Sphaerium* and *Corbicula*) in the macrophyte beds of many oxbows and because bivalves are put into the numerator of the FFG calculation (as ''filtering collectors'') but into the denominator of the FHG calculation (as ''burrowers''). Bivalves obviously need stable substrates to maintain their position while filtering, so they should be considered a special case of burrowers and placed in the numerator of the FHG. In addition, *Corbicula* is an alien species in the Caloosahatchee River oxbows, and might need to be excluded from functional-group ratio calculations. The entire issue of using alien species in calculating these ratios needs further assessment.

The use of surrogate measures for ecosystem attributes shows promise as indicated in our study, in previous work on the Kissimmee River (Merritt et al. 1996, 1999), and in other work (Stone and Wallace 1998, Wagner 2001). Selected ecosystem attributes can be the most sensitive measures of river ecosystem condition (e.g., the RCC, Vannote et al. 1980), but their direct measurement is often difficult, time consuming, and expensive. Using various macroinvertebrate functional-group ratios as surrogates for these attributes can provide critical data with much less effort.

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Appendix. Functional-feeding-group (FFG), functional-habit-group (FHG), and generation-time designations for invertebrate taxa of the Caloosahatchee River oxbow system. FFGs: SH-VP = shredders of vascular plants, SH-CPOM = shredders of coarse particulate organic matter detritus, GCOLL = gathering collectors, FCOLL = filtering collectors, SC = scrapers, PRC = plant piercers, PRED = predators, NF = nonfeeding stages. FHGs: CLG = clingers, CLB = climbers, SPR = sprawlers, BUR = burrowers, SWM = swimmers, PLK = planktonic, SKT = skaters. Voltinism: UNI = univoltine (1 generation/y), BIV = bivoltine (2 generations/y), TIV = trivoltine (3 generations/y), MLT = multivoltine (>3 generations/y).

| | Functional groups | | |
|---|---|---|---|
| Taxa | Feeding | Habit | Voltinism |
| **Annelida** | | | |
| Oligochaeta | GCOLL | BUR | UNI |
| Hirudinea | PRED | SPR | UNI |
| **Mollusca** | | | |
| Gastropoda | | | |
| Hydrobiidae | SC | CLG | MLT |
| Ampulariidae | | | |
| *Marissa* | SC | CLG | MLT |
| *Pomacea* | SC | CLG | MLT |
| Planorbidae | | | |
| *Planorbella* | SC | CLG | MLT |
| Pleuroceridae | | | |
| *Elimia* | SC | CLG | MLT |
| Physidae | | | |
| *Physella* | SC | CLG | MLT |
| Bivalvia | | | |
| Sphaeriidae | | | |
| *Sphaerium* | FCOLL | BUR | UNI |
| Corbiculidae | | | |
| *Corbicula* | FCOLL | BUR | UNI/SEM |
| **Crustacea** | | | |
| Ostracoda | GCOLL | SWM | MLT |
| Cladocera | | | |
| Daphniidae | FCOLL | SWM | MLT |
| Copepoda | | | |
| Calanoida | FCOLL | SWM | MLT |
| Amphipoda | | | |
| *Gammarus* | SC | SWM | MLT |
| *Hyalella* | SC | SWM | MLT |
| Isopoda | | | |
| *Caecidotea* | GCOLL | SPR | MLT |
| Decapoda | | | |
| Palaemonidae | | | |
| *Palaemonetes* | GCOLL | SWM | UNI |
| **Hydracarina** | PRED | SWM | UNI |
| **Insecta (aquatic)** | | | |
| Odonata | | | |
| Anisoptera | | | |
| Corduliidae | | | |
| *Epitheca* | PRED | SPR | UNI/BIV? |
| Libellulidae | | | |

Appendix. Continued.

| Taxa | Functional groups |  | Voltinism |
|---|---|---|---|
|  | Feeding | Habit |  |
| *Brachymesia* | PRED | SPR | UNI/BIV? |
| *Erythemus* | PRED | SPR | MLT |
| *Erythrodiplax* | PRED | SPR | BIV |
| *Miathyria* | PRED | SPR | MLT? |
| *Pachydiplax* | PRED | SPR | MLT |
| *Perithemus* | PRED | SPR | UNI/BIV? |
| Aeschnidae |  |  |  |
| *Anax* | PRED | CLB | BIV |
| *Boyeria* | PRED | CLB | UNI/SEM? |
| Gomphidae |  |  |  |
| *Aphylla* | PRED | BUR | SEM |
| Zygoptera |  |  |  |
| Coenagrionidae |  |  |  |
| *Argia* | PRED | CLB | UNI |
| *Enallagma* | PRED | CLB | UNI/BIV? |
| *Ischnura* | PRED | CLB | BIV |
| Ephemeroptera |  |  |  |
| Baetidae |  |  |  |
| *Callibaetis* | GCOLL | SWM | MLT |
| *Centroptilum* | GCOLL | SWM | MLT |
| *Procloeon* | GCOLL | SWM | MLT |
| Caenidae |  |  |  |
| *Brachycercus* | GCOLL | SPR | MLT |
| *Caenis* | GCOLL | SPR | MLT |
| Trichoptera |  |  |  |
| Hydropsychidae |  |  |  |
| *Cheumatopsyche* | FCOLL | CLG | UNI |
| Leptoceridae |  |  |  |
| *Oecetis* | PRED | SPR | UNI |
| Hydroptilidae |  |  |  |
| *Orthotrichia* | PRC | CLB | UNI |
| *Oxyethira* | PRC | CLB | UNI |
| Undetermined | PRC | CLB | ? |
| Hemiptera |  |  |  |
| Belostomatidae |  |  |  |
| *Belostoma* | PRED | CLB | BIV |
| Naucoridae |  |  |  |
| *Pelocoris* | PRED | SWM | MLT |
| Hebridae |  |  |  |
| *Hebrus* | PRED | CLB | UNI |
| Mesoveliidae |  |  |  |
| *Mesovelia* | PRED | SKT | UNI |
| Gerridae |  |  |  |
| *Trepobates* | PRED | SKT | UNI |
| Hydrometridae |  |  |  |
| *Hydrometra* | PRED | SKT | UNI |
| Neuroptera |  |  |  |
| Sisyridae |  |  |  |
| *Climacia* | PRED | CLG | UNI |

APPENDIX. Continued.

| Taxa | Functional groups: Feeding | Functional groups: Habit | Voltinism |
|---|---|---|---|
| Lepidoptera | | | |
| Pyralidae | | | |
| *Crambus* | SH-VP | CLB | UNI |
| *Parapoynx* | SH-VP | CLB | UNI |
| Undetermined | SH-VP | CLB | ? |
| Coleoptera | | | |
| Dytiscidae | | | |
| *Acilius* | PRED | CLB | BIV |
| Haliplidae | | | |
| *Peltodytes* | SH-VP | SWM | UNI |
| Hydrophilidae | | | |
| *Tropisternus* | PRED | CLB | BIV |
| Scirtidae | | | |
| *Cyphon* | GCOLL | CLG | UNI |
| Chrysomelidae | | | |
| *Donacia* | SH-VP | CLB | UNI |
| Curculionidae | | | |
| *Bagous* | SH-VP | CLG | UNI |
| Undetermined | SH-VP | CLG | ? |
| Diptera | | | |
| Tabanidae | | | |
| *Chrysops* | PRED | SPR | MLT |
| Culicidae | | | |
| *Culex* | FCOLL | SWM | MLT |
| Chaoboridae | | | |
| *Chaoborus* | PRED | SPR | UNI |
| Stratiomyiidae | | | |
| *Odontomyia/Hedriodiscus* | GCOLL | SPR | UNI |
| Ceratopogonidae | | | |
| Ceratopogoninae | | | |
| *Bezzia/Palpomyia* | PRED | BUR | MLT |
| *Culicoides* | PRED | BUR | MLT |
| Chironomidae | | | |
| Tanypodinae | | | |
| *Clinotanypus* | PRED | BUR | MLT |
| *Coelotanypus* | PRED | BUR | MLT |
| *Labrundinia* | PRED | SPR | UNI |
| *Larsia* | PRED | SPR | UNI |
| *Procladius* | PRED | SPR | UNI |
| *Tanypus* | GCOLL | SPR | UNI |
| Orthocladiinae | | | |
| *Cricotopus/Orthocladius* | GCOLL | CLG | MLT |
| *Thienemanniella* | GCOLL | SPR | UNI |
| *Chironominae* | | | |
| *Chironomini* | | | |
| *Apedilum* | GCOLL | BUR | MLT |
| *Chironomus* | GCOLL | BUR | MLT |
| *Cladopelma* | GCOLL | BUR | MLT |
| *Cryptochironomus* | PRED | SPR | MLT |

APPENDIX. Continued.

| Taxa | Functional groups |  | Voltinism |
|---|---|---|---|
|  | Feeding | Habit |  |
| Cryptotendipes | GCOLL | SPR | MLT |
| Dicrotendipes | GCOLL | SPR | MLT |
| Einfeldia | GCOLL | BUR | MLT |
| Endochironomus | SH-CPOM | BUR | MLT |
| Parachironomus | PRED | SPR | MLT |
| Phaenopsectra | SC | CLG | MLT |
| Polypedilum | GCOLL | CLB | MLT |
| Zavreliella | GCOLL | CLB | MLT |
| Tanytarsini |  |  |  |
| *Cladotanytarsus* | FCOLL | CLG | MLT |
| *Tanytarsus* | FCOLL | CLG | MLT |
| Pseudochironomini |  |  |  |
| *Pseudochironomus* | GCOLL | BUR | UNI |
| **Insecta (terrestrial)** |  |  |  |
| Orthoptera |  |  |  |
| Tettigonidae | SH-VP | CLB | UNI |
| Homoptera |  |  |  |
| Cicadellidae | SH-VP | CLB | UNI |
| Aphidae | PRC | CLG | MLT |