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Channel–floodplain coupling in the Kissimmee River, Florida (USA): invertebrate movement and fish feeding

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Introduction

Channelization of the Kissimmee River in central Florida (USA) resulted in the isolation of the river from its floodplain and the extensive alteration of the floodplain to pasture land. This uncoupling of river and floodplain has been proposed as the major factor responsible for the decline in many species of fish and water birds (TREXLER 1995). One of the most significant changes has been the wholesale reduction of invertebrates moving onto or off the floodplain, depending upon the particular hydrologic conditions. Because these invertebrates drifting onto and off of the floodplain constitute a major component of the food for many fish species, particularly the larval fish on the floodplain, channelization has been immensely disruptive to important food webs. The success of the Kissimmee River Ecosystem restoration program that is in progress will depend, to a great extent, on recovery of fish and water bird populations in response to re-establishing the foodweb links dependent upon river–floodplain linkages.

At the base of the restoration program is the intention to restore, enhance, and maintain ecosystem integrity. Ecosystem integrity is defined as a 'desirable' and sustainable ecosystem structure and function. A major concern in restoring sustainable ecosystem structure and function is the support of 'desirable' plant and animal species, such as native wetland plants, game fish, threatened water birds, and others. Many of the 'desirable' species are well known to the scientific, management, and general public communities alike, and will undoubtedly be used as a paramount measure of restoration and management success.

The sustainability of these 'charismatic' species is dependent upon a particular suite of environmental conditions and on other organisms – their food and their predators. However, there is a significant lack of understanding of the critical relationships that impact and support the 'charismatic' plant and animal species, even though they will constitute the most visible measure of success in ecosystem restoration and management. All of the species in question are components of food webs – some with very specific and limited pathways, others of more flexible and variable structure. The type of food web imposes major management constraints.

The present study is directed towards building the appropriate database for evaluating invertebrate movements and the use of the invertebrates by fish. The specific objectives of the study were: (1) to compare the quantity and composition of drifting invertebrates entering the floodplain, coming to the channel from the floodplain, and in the channel thalweg at two different flows, and (2) to compare diet composition of bluegill sunfish (*Lepomis macrochirus*) and largemouth bass (*Micropterus salmoides*) in the vicinity of drift collections with the composition of the drift.

Study site

The study was conducted within the lower remnant channel of Pool B of the Kissimmee River, FL (USA) (Fig. 1). The Kissimmee River is the site of an ongoing restoration project which seeks to reverse damage to the historic river–floodplain system that occurred when the river was channelized for flood control between 1962 and 1971. Channelization transformed the 166-km meandering river into a 90-km long, 9-km deep box-cut canal, severed from its 1.5- to 3-km wide floodplain. The canal was divided into five impoundments, designated as Pools A–E, by water control structures that regulate discharge and stage height in each pool. Channelization resulted in the loss of 2800 ha of floodplain habitat, with attendant declines in populations of wading birds and game fish. As a component of the restoration plan to restore the historic form and hydrology of the river, a demonstration project was initiated in Pool B, from 1984 to 1990, to assess the feasibility of a channel backfilling plan. Through channel backfilling and the installation of weirs, this project established stage fluctuations in the lower portion of the pool that reintroduced flow through remnant river channels at

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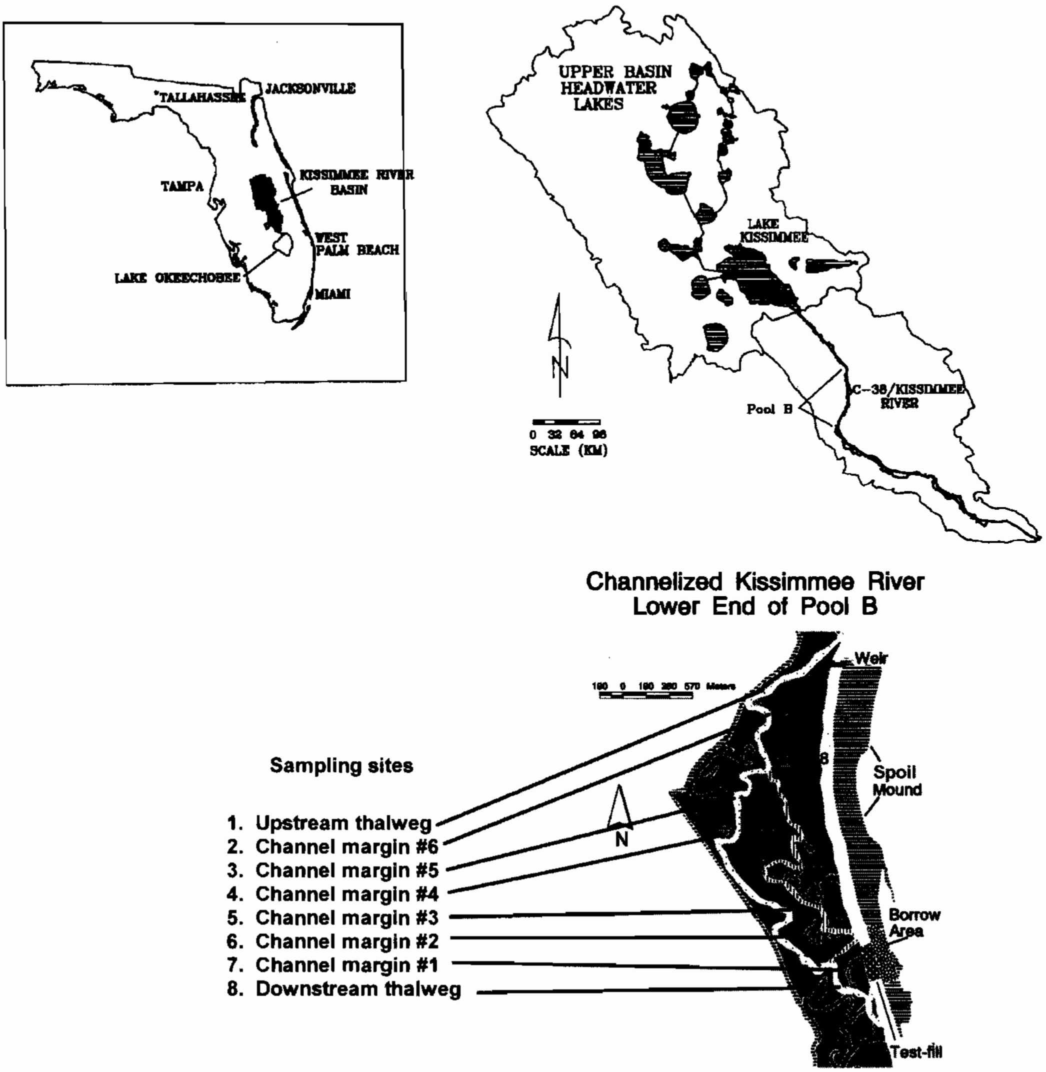

Fig. 1. Map of the study area. Modified from Toth (1996).

high flows, and provided floodplain inundation frequencies similar to those of the pre-channelized system (Koebel 1995). The floodplain of Pool B is extensively vegetated with broadleaf marsh, as was the historic floodplain. For this reason, the study site was selected to mimic, as closely as possible, the operation of a naturally functioning large river–floodplain system in a subtropical environment.

Within the study area, six sampling stations were established along the river–floodplain margin, and two stations were established in the river channel (Fig. 1). Stations were selected at locations where sloughs in the floodplain provided evidence of drainage following inundation. Littoral and floodplain vegetation differed among stations, but at all stations floodplain vegetation was characterized as broadleaf marsh. Geographical coordinates of the sampling stations were determined with a GPS unit (Trimbel Pathfinder®).

Methods

Sampling of invertebrate drift and fish diets was conducted during the dry season on January 27–28 and February 5–6, 1997. Staff gauge readings on these dates were 12.42 and 13.09 m above mean sea level, respectively.

On each sampling date, triplicate 250-µm mesh drift nets, each approximately 1 m in length and with a mouth opening of 0.15 m^2, were positioned upstream and downstream of floodplain stations to capture open channel drift (n = 6). Six paired drift nets of the same type, but with a mouth opening of 0.06 m^2, were located at the edge of the floodplain (n = 12). The paired nets were positioned facing in opposite directions relative to the edge of the floodplain so as to sample drift leaving the floodplain in one net and drift moving onto the floodplain in the other (Fig. 2). Drift nets collected invertebrates from approximately dusk to dawn on each sampling date. Flow velocity in the mouth of each net during the sampling period was measured with a Marsh McBirney® digital flowmeter. Samples were preserved in ethanol and formalin for subsequent laboratory enumeration, identification, and measurement of individual lengths, which was accomplished using a Wild–Leitz combi-dissecting microscope. Large samples were subsampled using a sample splitter. Taxonomic resolution was usually to genus level, but the Chironomidae were identified to subfamily and tribe.

Largemouth bass and bluegill sunfish were collected for gut content analysis using a boat electroshocker in the area of each invertebrate drift sampler. All fish samples were taken the day immediately following collection of invertebrate drift in order to provide fish feeding information directly applicable to the drift samples, but to avoid influencing the content of the invertebrate samples. Specimens of all size classes of both species were netted and retained for subsequent examination. A total of 20 min of electroshocking time was spent at each site on each sampling date. On capture, fish were euthanized, and their body cavity was slit open to permit perfusion with a 10% formalin solution to minimize deterioration of the stomach contents. Fish were then stored in formalin until processing. Apart from bluegill sunfish and largemouth bass, other fish collected in the vicinity of drift sampling stations included Florida gar (*Lepisosteus platyrhinchus*), lake chubsucker (*Erimyzon sucetta*), brown bullhead (*Ameiurus nebulosus*), Seminole killifish (*Fundulus seminolis*), and the following centrarchids: warmouth (*Lepomis gulosus*), dollar sunfish (*Lepomis marginatus*), spotted sunfish (*Lepomis punctatus*), redbreast sunfish (*Lepomis auritus*), redear sunfish (*Lepomis microlophus*), and black crappie (*Pomoxis nigromaculatus*). Limited sample sizes precluded analysis of their diets.

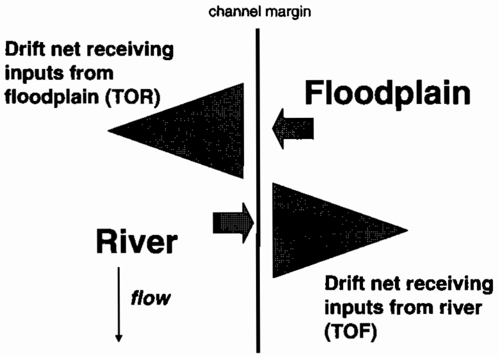

Fig. 2. Drift sampling design. Two paired nets, one receiving drift from the floodplain and the other receiving drift from the river, were placed at each of six channel margin sites on a remnant channel of Pool B in the Kissimmee River.

Invertebrate drift data were analyzed to determine patterns in drift composition related to sampling date and location of collection (channel margin sites collecting drift going to and from the floodplain as well as main channel drift). Drift densities were standardized to correct for differences in the area of the mouths of the nets and for differences in sample duration. Because flows were often negligible, drift densities were expressed on the basis of area rather than volume of water filtered. Numerical data were converted to biomass using length–mass regressions developed for specific invertebrate taxa from Smock (1980) and unpublished data. Invertebrate numbers were log-transformed to meet assumptions of normality and equal variances. Effects of sampling date and location on total drift abundance and the abundance of specific taxa were analyzed with two-way ANOVA. Overall patterns in composition of drift assemblages were analyzed for 10 taxonomic groupings that represented over 95% of total invertebrate densities for all samples (Table 1).

Gut content data from bluegill sunfish were analyzed to determine diet patterns related to fish size and collection date, while only body size was considered for largemouth bass. Limited sample size precluded comparisons among study sites for either species. The number of items of each type observed in each stomach sample was divided by the total items found there, in order to provide an estimate of the relative importance of each item in the diet of the fish. Only items comprising at least 5% of the food items for a given sample date were analyzed further.

Table 1. Factor loadings from principal component analysis of drift composition. The logarithm of number of individuals in each taxa ($/m^2/h$) from each drift sample on both sample dates and from all locations, were analyzed. Asterisks mark the taxa loading heavily (loading >0.75) on each factor.

Taxa	Factor 1	Factor 2
Oligochaeta	0.275	–0.764*
Benthic Cladocera (Sididae, Chydoridae)	0.925*	0.196
Planktonic Cladocera (Daphniidae, Macrothricidae)	0.787*	0.351
Ostracoda	0.795*	0.226
Copepoda	0.903*	0.319
Hyalella azteca (Amphipoda)	0.295	–0.753*
Hydracarina	0.660	–0.249
Caenis (Caenidae, Ephemeropta)	0.700	–0.408
Chaoborus (Chaoboridae, Diptera)	0.504	0.623
Chironomini (Chironomidae, Diptera)	0.601	–0.595
Proportion of total variance explained	0.462	0.243

Relative abundance estimates were angular transformed (arcsine of the square root of the proportion (ZAR 1984)), and fish mass was transformed to its natural logarithm, in order to fulfill the assumptions of subsequent data analyses.

Data from bluegill sunfish and from drift collections were analyzed using principal component analysis to reveal patterns across collections and to reduce the number of dependent variables for statistical analyses. A varimax rotation was used in both analyses to produce more readily interpretable factor loadings, and factor scores were retained for analysis from axes explaining a significant portion of the variation. Factor scores were analyzed by multiple analysis of variance (MANOVA) to determine: (a) the effect of sampling location and date on drift composition, and (b) the effect of sampling location and fish mass on bluegill sunfish diets. Canonical loadings, i.e. correlations of the first discriminant-function score and each dependent variable, are reported for each dependent variable, in order to evaluate their relative contribution to significant multivariate effects.

Results and discussion

Coincident with a higher river stage height, current velocities at the location of drift net sampling were greater on the second of the two sampling dates. On the first date (January 27), the median current at nets filtering water moving onto the floodplain was 0.30 cm/s (range: 0–1.8). Flow was negligible at nets filtering water coming from the floodplain (flow of 0 cm/s, range: 0–0.1), and in the main channel, median flow at the nets was 6.1 cm/s (range: 1.2–12.2). On the second date (February 5), median flow onto the floodplain was 0.9 cm/s (range: –12.2–8.2, with negative numbers indicating reversed flow); median flow off of the floodplain was 3.3 cm/s (range: –0.3–10.0); flow in the main channel was 19.8 cm/s (range: 10.67–34.4).

Greater current velocities on the second sampling date are reflected in a trend of higher total drift densities (Fig. 3A). Among locations, total drift density, expressed as log mean number/m^2/h, was greatest in locations sampling water coming from the floodplain. Because of considerable variability among samples, the effects of habitat and date on numbers of animals drifting were not significant. Sampling date did, however, significantly affect the total biomass of invertebrates collected in the drift (P

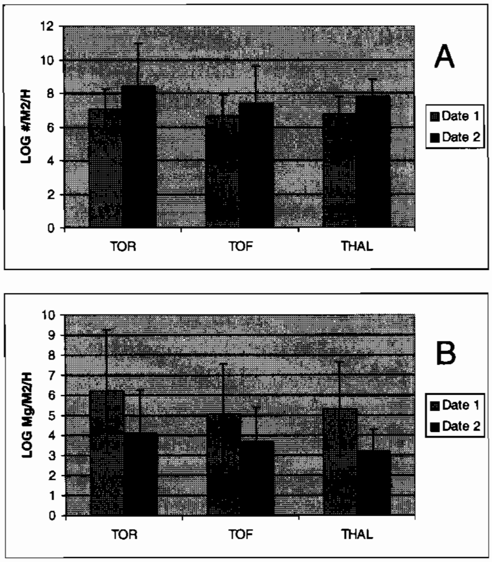

Fig. 3. Total drift density (A) and mass (B) by sampling sites and dates. TOR and TOF represent channel margin sites collecting drift toward the river and toward the floodplain, respectively. THAL represents drift collected from the thalweg of the river. Vertical bars represent standard deviations. N = 6 samples at each location and date.

= 0.01, n = 36, r^2 = –0.45). Among all locations, drift biomass was lower on the second date. That the occurrence of large numbers of smaller individuals on the second date is attributable to flow is suggested by the significant relationship observed between the log of drift density and current velocity at the mouth of drift nets (P = 0.01, n = 36; Fig. 4).

Examination of total drift abundance obscures differing drift patterns exhibited by specific taxa. Cyclopoid and calanoid copepods, for example, dominated the drift numerically. These were significantly more abundant on the second date (F = 4.63, P = 0.04, n = 36; Fig. 5), when discharge was greater. Copepods have few morphological or behavioral adaptations for directing their movement, and are passively displaced by flow. However, *Hyalella azteca*, the only amphipod species documented from the Kissimmee River and also well represented in the drift and in fish diets, declined in relative abundance in drift collections on the second date at channel margin sites. For *Hyalella*, the interaction of location and date was significant (F = 4.010, P = 0.02, n = 36). Amphipods are characterized as active drifters, and exhibit a pronounced diel drift periodicity (WATERS 2000).

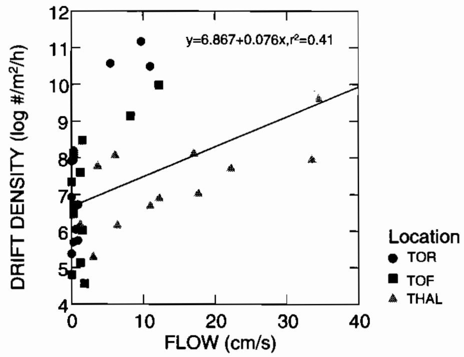

Fig. 4. Relationship between current velocity at the mouth of drift nets and total drift density. TOR and TOF represent channel margin sites collecting drift toward the river and toward the floodplain, respectively. THAL represents drift collected from the thalweg of the river. N = 6 samples on each of two dates for each location.

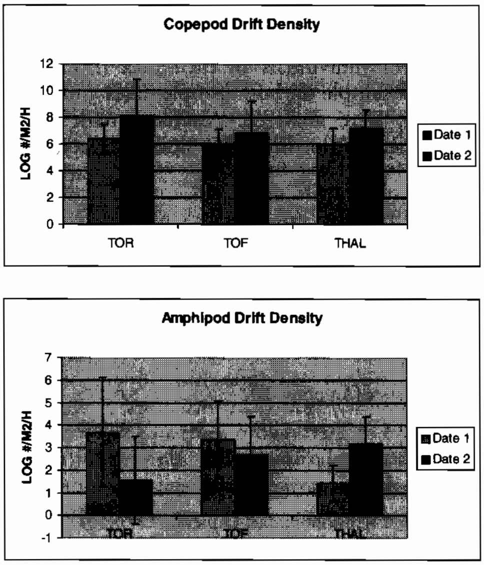

Fig. 5. Drift density of copepods and amphipods on each of two sampling dates in channel margin sites receiving drift toward the river (TOR) and toward the floodplain (TOF), and in the channel thalweg (THAL). Vertical bars represent standard deviations. N = 6 samples on each date at each location.

Active and passive components of the drift, such as amphipods and copepods, respectively, likely differ in their movement onto and off the floodplain at varying levels of flow. When water levels are stable, only actively drifting invertebrates occurring on the floodplain are likely to move into the river channel, where they become available as a food source for adult fish (Fig. 6). When water levels drop, passive drifters may join active drifters moving off the floodplain. Similarly, when water levels are stable, only actively drifting invertebrates are likely to move onto the floodplain from the main channel. Here they become available as a food source for juvenile fish that are often reared on the floodplain, capitalizing on the abundant invertebrate production that characterizes floodplain areas (e.g. DEWEY et al. 1997). As water levels rise, passively drifting invertebrates are likely to join active drifters in movement onto the floodplain from the river.

Principal component analysis of drift compo-

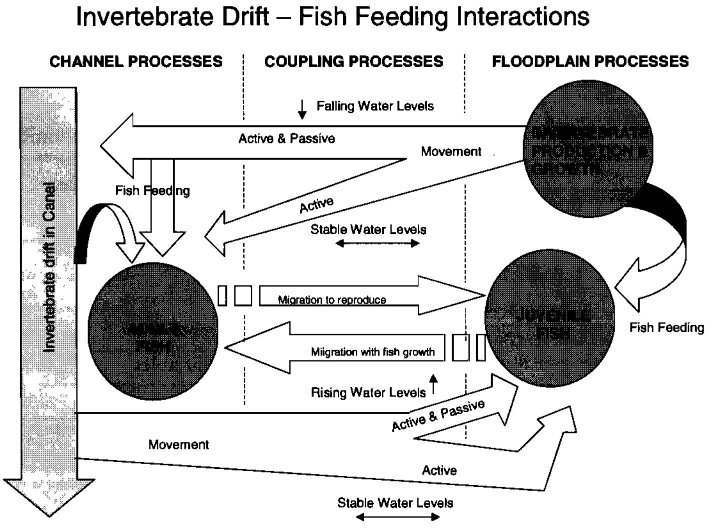

Fig. 6. Conceptual model of invertebrate drift and fish feeding interactions within the river channel and on the floodplain. Modified from Cummins et al. (1999).

sition also supports the conceptual model (Fig. 6), which distinguishes two components of invertebrate drift whose movements onto and off the floodplain vary with flow levels. The analysis yielded two factors that explained 70% of the total variance in drift composition. The factors loaded heavily on benthic and planktonic copepods and ostracods (Factor 1), and on oligochaetes and *Hyalella* (Table 1). MANOVA indicated that drift composition differed between sampling dates, but not between samples collecting drift from the floodplain versus drift from the river (Table 2). The multivariate effect of sample date was affected by both Factors 1 and 2, but the effect of each was different (canonical loadings have different signs). The animals represented by Factor 1 were most abundant on the second date, with higher flows, and those represented by Factor 2 were more abundant on the first date. Although oligochaetes are not active drifters, their relatively larger size may confer some ability to avoid displacement at higher flows. On the first sampling date, oligochaetes were collected only in samples deriving from the floodplain; on the second date, these were collected in the channel thalweg as well.

Although oligochaetes comprised less than 1% of the individuals collected in drift samples, they, along with larval fish, comprised over 75% of the stomach contents of largemouth bass (Table 3). However, oligochaetes and larval fish were not consumed by the smallest bass that were examined; these consumed a variety of small prey including chironomid larvae, copepods, and ostracods. The range of bass sizes that were collected was 40–1113 g (142–406 mm in total length). Largemouth bass are known to shift to piscivory at larger sizes (e.g. Bettoli et al. 1992), and the drift samples that were collected in this study did not effectively sample larger animals. Although the diets of larger bass were not an accurate reflection of the composition of drifting invertebrates moving onto and off the floodplain, other evidence suggests that largemouth bass of all sizes are heavily dependent on river–floodplain coupling and the food resources this provides. In a radiotelemetry study of largemouth bass and bluegill sunfish in the same study section, Giles (1999) found that bass (n = 12) occupied channel margin or floodplain areas in 97% of 93 fish sites, where they were particularly associated with vegetated habitats.

Table 2. Comparisons of principal component Factors 1 and 2 describing drift composition between channel margin sites collecting drift (a) from the floodplain, (b) to the floodplain and between sampling dates. DF refers to degrees of freedom.

Multivariate results

Source	Wilk's λ	DF	P	Canonical loadings	
				Factor 1	Factor 2
Location	0.934	2,19	0.522	0.885	–0.258
Sampling date	0.572	2,19	0.005	–0.504	0.730
Location × date	0.966	2,19	0.723	–0.362	0.828

Univariate results

Source	Dependent variables				
		Factor 1		Factor 2	
	DF	F	P	F	P
Location	1,20	1.108	0.305	0.094	0.762
Sampling date	1,20	3.798	0.065	7.954	0.011
Location × date	1,20	0.091	0.766	0.477	0.498

In contrast to largemouth bass diets, the diets of bluegill sunfish reflected, to a greater extent, the prey items available to them in the drift (Table 3). Principal component analysis of bluegill sunfish diets yielded six factors that explained 60% of the total variance. Three of these were heavily influenced by the diets of a small number of fish that could be considered as outliers because of unusual diets, and they were not further considered. The three factors retained loaded heavily on cyclopoid and calanoid copepods (Factor 1, with loadings, respectively, of –0.873 and –0.866), daphniid cladocerans (Factor 2, with a loading of –0.892), and chironomid larvae and amphipods (Factor 3, with respective loadings of –0.665 and –0.600). These three factors explained about 31% of the total variance in the diet data.

MANOVA indicated that the diets of the bluegill differed with fish size and between sampling dates; also, the change of diet with size was not consistent between sampling dates (Table 4). Bluegill collected in this study ranged in size from <1 g to 298 g (36–233 mm in total length). Their sizes were not consistent between sampling dates or between locations. The multivariate effect of sample date resulted from Factors 1 and 2, which affected this test differently (canonical loadings have different signs). Scores for Factors 1 and 2, but not 3, were significantly affected by fish mass, but unlike sampling date, the effect was consistent for both factors. Finally, the slope of factor scores on fish mass differed between dates for Factors 1 and 3. Factor 1, describing the tendency to include copepods in the diets, was most negative (indicating a greater relative abundance of copepods) for small bluegills. A significant date-by-mass interaction resulted from a sample of small individuals that had relatively high scores for this factor on the second sample date, corresponding to a greater than 10-fold increase in mean abundance of copepods in the drift relative to the first sampling event. Factor 2, indicating the inclusion of daphniids in the diet, also displayed a negative slope on fish size. In this case, fish of all sizes had more daphniids in their guts on the first sampling date. On this date, daphniids represented 13% of total drift abundance. On the second date, although total numbers were greater, daphniids represented only 6% of drift abundance. Chironomid larvae and amphipods, indicated by Factor 3, were important prey items in the stomachs of bluegills of all sizes, though their presence differs between sampling dates. This can also be attributed to their relative abundance in the drift.

Table 3. Relative abundance, by number, of different prey items in the drift and in bluegill sunfish and largemouth bass diets. Percent in diets represents the average relative abundance of each species in an individual bluegill or bass. NF, not found.

Taxa	% in drift (n = 234,887 individuals in 36 samples)	% in bluegill sunfish diets (n = 124 stomach contents)	% in largemouth bass diets (n = 63 stomach contents)
Cyclopoida	71	55	NF
Calanaoida	6	9	<1
Ostracoda	6	3	2
Daphniidae	6	5	NF
Chydoridae	5	<1	NF
Bosminidae	1	<1	NF
Hyalella azteca (Amphipoda)	1	4	<1
Chironomini (Chironomidae, Diptera)	1	10	<1
Mansonia (Culicidae, Diptera)	NF	6	NF
Pachydiplax (Libellulidae, Odonata)	<1	2	1
Larval fish	<1	<1	15
Oligochaeta	<1	<1	63
Palaemonetes paludosus (Decapoda)	<1	<1	11
Procambarus (Decapoda)	NF	NF	2
Nematoda	<1	<1	4

Table 4. Comparisons of principal component Factors 1, 2, and 3 describing bluegill diets between sampling dates and across fish size. DF refers to degrees of freedom.

Multivariate results

Source	Wilk's λ	DF	P	Canonical loadings		
				Factor 1	Factor 2	Factor 3
Sampling date	0.801	3,124	<0.001	–0.863	0.555	–0.052
Mass	0.657	3,124	<0.001	0.515	0.823	–0.063
Date × mass	0.892	3,124	0.003	0.825	–0.251	0.594

Univariate results

Source	Dependent variables						
		Factor 1		Factor 2		Factor 3	
	DF	F	P	F	P	F	P
Sampling date	1,126	23.356	<0.001	9.662	0.002	0.087	0.769
Mass	1,126	17.496	<0.001	44.659	<0.001	0.265	0.608
Date × mass	1,126	10.367	0.002	0.956	0.330	5.382	0.022

Amphipods were rare in fish stomachs and in the drift on February 6.

As the conceptual model summarizes, the direction of drift movement significantly affects the availability as prey to larger, adult fish in the river versus juvenile fish in the floodplain. Thus, the manner in which the flows are regulated can be used as a management strategy to direct food items to particular components of the Kissimmee River fish assemblage. In order to achieve the best match between flow (water level) regulation and the enhancement of gamefish production, experimental data are needed. In the mode of adaptive management, this would require periodic coordinated measures of fish populations and invertebrate drift at a range of flow levels and schedules in both the wet and dry seasons.

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