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Subsidy–stress response of macroinvertebrate community biomass to a phosphorus gradient in an oligotrophic wetland ecosystem

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Abstract. We used a subsidy–stress model as a basis for predicting macroinvertebrate community response to a steep gradient of P enrichment in the Florida Everglades, a P-limited wetland ecosystem. We tested the hypothesis that consumers were resource limited and their biomass would show a subsidy response (increase) to low-to-moderate levels of P enrichment, but a stress response (decrease) at high levels of P enrichment because dense emergent macrophytes, particularly *Typha*, might significantly reduce periphyton food resources. We used a spatially extensive sampling design (14 clusters of 9 sites, 126 total) that incorporated vegetation pattern to evaluate consumer responses along the P gradient. We then conducted a 1-y temporal study at 3 of the 14 clusters to evaluate how seasonal hydrological variation interacted with nutrients to influence consumer biomass. Macroinvertebrate community biomass showed a significant unimodal response to increasing P enrichment consistent with a subsidy–stress relationship. Eight of 12 major taxonomic groups (Amphipoda, Decapoda, Diptera, Empheroptera, Gastropoda, Hirudinea, Odonata, Oligochaeta) had this unimodal response, whereas 3 (Coleoptera, Hemiptera, Isopoda) increased monotonically and 1 (Trichoptera) decreased monotonically in response to P. Periphyton C:N and C:P ratios declined with increasing P, but periphyton cover was minimal at high levels of P enrichment where tall invasive macrophytes limited its growth. The temporal study revealed a subsidy–stress response except after marsh reflooding following the dry season when the most P-enriched clusters of sites had the highest consumer biomass, presumably because drought-induced senescence reduced macrophyte cover, which enabled heavy growth of periphyton. Our results suggest that an interaction between increased quality and decreased quantity of periphyton caused the subsidy–stress patterns observed. We suggest our findings could be generalized to other wetland ecosystems where nutrient enrichment leads to invasion of weedy emergent macrophytes, such as *Typha*, and elimination of open-canopy habitats rich in periphyton.

Key words: ecological stoichiometry, ecological thresholds, eutrophication, Everglades, fish, food quality, food webs, nonlinear responses, nutrient ratios, periphyton, resource limitation, water quality, wetlands.

Eutrophication of aquatic ecosystems caused by excessive inputs of N or P is a problem throughout the world (Carpenter et al. 1998). Nutrient enrichment can particularly affect the structure and function of aquatic food webs through an array of indirect and direct pathways (Chase 2003, King et al. 2004). In wetlands, the effect of nutrient enrichment on aquatic consumers is likely to be tightly coupled with its effect on macrophytic vegetation. Macrophytes form the physical habitat template for most other wetland biota and play a major role in modulating consumer dynamics (Batzer and Wissinger 1996). Living macrophytes are not thought to be a significant food resource for wetland consumers, but these plants contribute a significant amount of detrital material to the ecosystem. Much of this accumulated energy and nutrients is thought to fuel higher trophic levels through decomposition and the action of detritivores (Murkin 1989, Batzer and Wissinger 1996). For this reason, many ecologists have regarded wetlands as detritus-based ecosystems (Mitsch and Gosselink 2000).

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Despite the ostensible importance of macrophyte detritus in wetland food webs, an increasing body of evidence indicates that periphyton—attached and floating communities of algae, bacteria, fungi, and other microbes—also can be a significant food resource (e.g., Browder 1982, Campeau et al. 1994, Keough et al. 1996, Hart and Lavvorn 2003, Liston and Trexler 2005). Periphyton is an important food source to many invertebrates that occur in wetland habitats (e.g., Lamberti and Moore 1984). Similar to macrophytes, periphyton production and tissue nutrient concentrations often benefit from nutrient additions. However, macrophyte density and shading caused by emergent macrophytes can limit periphyton abundance (e.g., Goldsborough and Robinson 1996, Grimshaw et al. 1997). Thus, taxa that rely heavily on periphyton as a food resource might benefit from nutrient inputs up to the level of enrichment at which tall emergent macrophytes begin to shade periphyton. Beyond this point, detritivores might begin to replace periphyton-feeding taxa in the food web. However, the ultimate effect of a shift toward heterotrophy on overall community biomass might depend on the relative importance of periphyton vs macrophyte detritus in a wetland food web.

The Florida Everglades, USA, is a P-limited, oligotrophic wetland ecosystem that has been the focus of significant research and restoration efforts in relation to anthropogenic P enrichment. Large inputs of agricultural runoff rich in P have induced steep eutrophication gradients in some areas of this subtropical wetland. P enrichment in the Everglades has profound effects on the productivity, biomass, and species composition of both macrophyte (e.g., Urban et al. 1993, Vaithiyanathan and Richardson 1999) and periphyton communities (e.g., Swift and Nicholas 1987, McCormick et al. 1996). Macrophyte productivity and standing biomass increase markedly with increasing P enrichment in these areas (Richardson et al. 1999). However, P inputs also are largely responsible for a shift from stands of *Cladium jamaicense* Crantz (sawgrass) and open-water slough communities to dense stands of *Typha domingensis* Pers. (cattail) and other invasive macrophytes (King et al. 2004). Coincident with these macrophyte shifts, area-weighted biomass and productivity of periphyton markedly decline in areas of high P enrichment, primarily as a consequence of encroachment of invasive emergent macrophytes into periphyton-rich slough communities (McCormick et al. 1998, Turner et al. 1999). However, both macrophyte (Richardson et al. 1999) and periphyton (McCormick et al 1998, King and Richardson, in press) productivity and C:N and C:P ratios decline with P enrichment, possibly indicating higher food value to consumers at higher concentrations of P (Frost et al. 2002).

The objective of our study was to evaluate patterns of macroinvertebrate biomass along a continuum of P enrichment spanning oligotrophic to eutrophic conditions in the northern Everglades. We used the subsidy–stress gradient (Odum et al. 1979) as a conceptual framework for our study. We tested the hypothesis that consumers were resource limited, and their biomass would show a subsidy response (increase) at low-to-moderate levels of P enrichment but a stress response (decrease) at high levels of P enrichment when dense emergent macrophytes significantly reduced or eliminated periphyton food resources. An alternative hypothesis was that secondary or higher consumers would suppress biomass of primary consumers. Thus, only small fish or large predaceous invertebrates would show a response to P.

We used 2 approaches to test our hypothesis. First, we used a spatially extensive sampling design that incorporated vegetation pattern into our estimates of biomass along the P gradient. Second, we conducted a temporal study using 3 clusters of sites to evaluate how hydroperiod and other sources of variation interacted with nutrients to influence patterns of consumer biomass across 3 levels of enrichment. This approach enabled us to couple temporal trajectories of these 3 clusters with the results from the spatial study to overcome the trade-off between spatially extensive, single-event sampling and temporally intensive sampling at a small number of study locations. This article builds on 3 previous studies (King and Richardson 2002, 2003, King et al. 2004) on bioassessment methods and vegetation–environment linkages along this same P gradient.

Methods

Study area and sampling design

We sampled in Water Conservation Area 2A (WCA-2A) in the northern Everglades (Fig. 1A, B). WCA-2A is a 43,280-ha diked wetland landscape, with water-control structures governing the inflow and outflow of surface water. Inflow primarily occurs along the northern levee through 3 water-control structures (S10-A, -C, and -D) on the Hillsboro Canal, which is a conduit for outflow from Lake Okeechobee and P-enriched runoff from the Everglades Agricultural Area (EAA; Fig. 1C). Inflow from the Hillsboro Canal has induced a steep longitudinal eutrophication gradient in WCA-2A primarily because of large inputs of P (SFWMD 1992). Aerial photographs and descriptive studies (e.g., Davis 1943) before impoundment show that vegetation pattern and composition across this

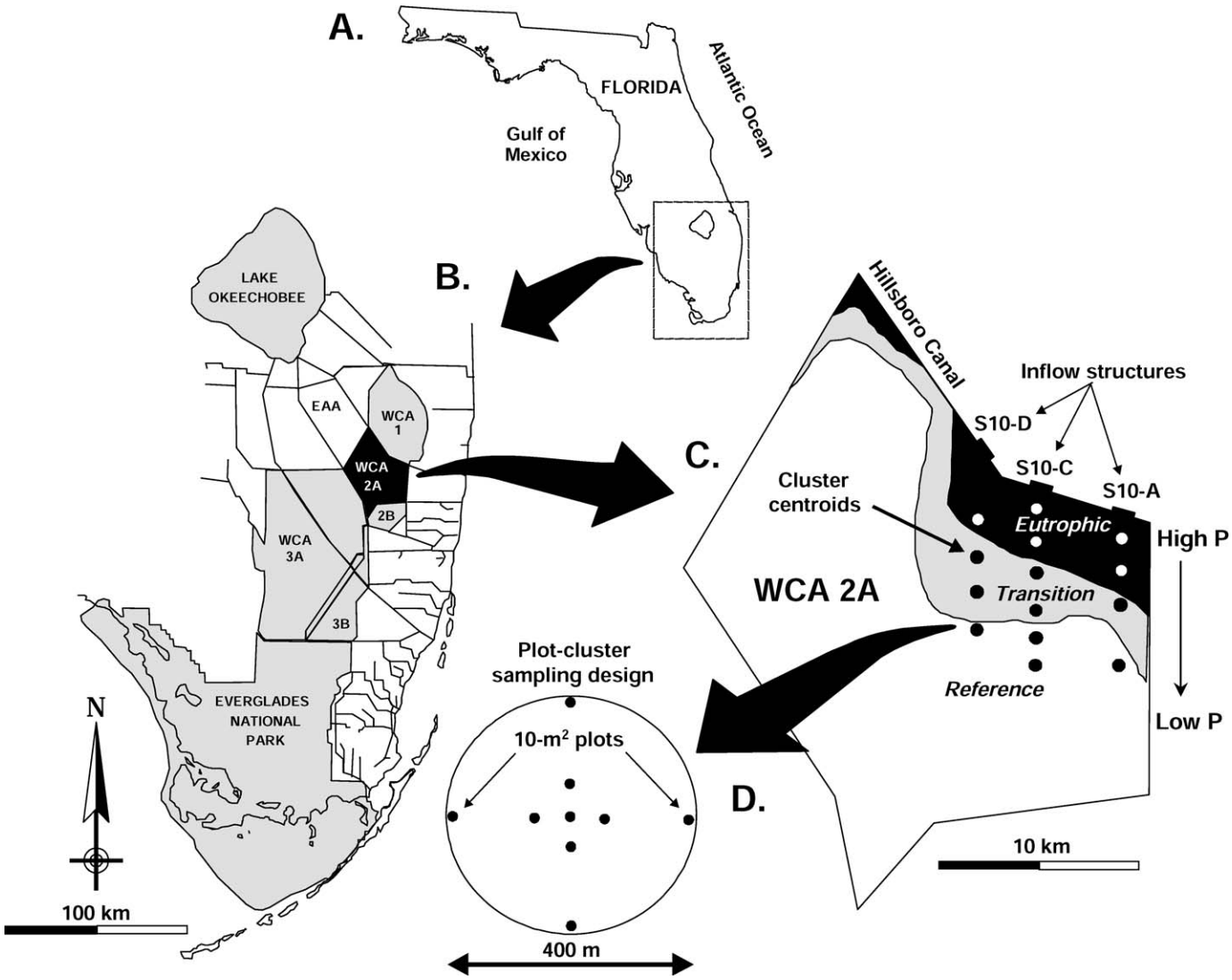

FIG. 1. A.—Location of the study region within Florida. B.—Locations of the Everglades Agricultural Area (EAA), the primary source area of P in the Everglades, and Water Conservation Area 2A (WCA-2A). C.—Locations of sampling clusters along the P gradient in WCA-2A. Inflow structures along the Hillsboro Canal are conduits of P-enriched water into WCA-2A and have induced a steep P and vegetation gradient in the wetland. Sampling clusters were aligned with each of the 3 inflow structures and spanned the eutrophic, transition, and oligotrophic reference zones of WCA-2A along the P gradient. D.—Illustration of the plot–cluster sampling design. Nine plots were arranged in a constellation within each of the 14 sampling clusters.

region of the WCA-2A landscape was once very uniform. Today, however, 3 relatively distinct enrichment and vegetation zones exist along this gradient (Fig. 1C): 1) a *eutrophic* zone ~0 to 4 km downstream of the canal inflow structures, where surface water and soil are heavily enriched with P and vegetation characteristic of the natural Everglades has been replaced by dense stands of *Typha* and other invasive species, 2) a *transition* zone that ranges from 4 to 7 km from the canal, where P concentrations diminish but remain elevated above concentrations in oligotrophic areas and vegetation is a mix of *Typha*, other invasive species, *Cladium*, and open-water sloughs, and 3) a relatively unimpacted, low-nutrient *reference* zone >7 km from the canal that has water and soil chemistry representative of the historical northern Everglades and vegetation structured as a mosaic of *Cladium* stands interlaced with open-water sloughs. A detailed summary of physical, chemical, and vegetation characteristics of this area is provided in King and Richardson (2002) and King et al. (2004).

Before this study, we established three 10-km-long sampling transects, each aligned with 1 of the 3 S-10 inflow structures and parallel to the P gradient (Fig.

1C; King and Richardson 2002). We marked 6 long-term sampling stations along each transect, starting 1.0 to 1.5 km from the canal and spaced at 1.5-km intervals. We selected 14 stations—all 6 long-term stations from the central transect (C-transect) and 4 of the 6 long-term stations (randomly chosen) from each of the A- and D-transects—as centroids for our sampling for the spatial study (Fig. 1C).

We expected spatial pattern of vegetation to play a significant role in regulating consumer biomass. Vegetation pattern covaries with P enrichment along the P gradient (King et al. 2004). Therefore, we did not stratify our sampling with respect to vegetation communities because such a design would have been confounded by differences in vegetation scale and pattern with increasing P. Rather, we incorporated vegetation pattern directly into our estimates of consumer biomass by using a cluster sampling design (e.g., Fortin et al. 1989, Urban 2000, Urban et al. 2002). We clustered multiple plots at a scale large enough to span local vegetation communities but not so large as to integrate samples across levels of P enrichment. We aggregated plots (sites) within clusters to estimate coarse-scale consumer biomass that reflected the actual vegetation habitat in a cluster (King et al. 2004).

Plots were 10 m^2 and semicircular to facilitate sampling from the perimeter and to minimize disturbance. A single plot at each of the 14 stations served as a cluster centroid. We marked 8 additional plots in a constellation around the centroid. We placed 4 plots at 50-m distances and 4 plots at 200-m distances from the centroid in the 4 cardinal directions (Fig. 1D). Plots within clusters were separated by 50 to 400 m, with a total of 9 plots/cluster and 126 plots across the landscape. Random allocation of plots within clusters was not practical because the airboat used for transportation would have caused excessive damage to vegetation in the areas adjacent to plots. We conducted the spatial study during the wet season (October 1998) because water levels permitted airboat travel to all areas of the marsh, and biomass of periphyton peaks during the wet season (McCormick et al. 1998, Turner et al. 1999).

We selected 3 of the 14 clusters for the temporal study as representative locations that spanned reference, transition, and eutrophic zones of the P gradient. We used these clusters to evaluate temporal patterns in consumer biomass in relation to nutrient status, hydrology, and other seasonal factors. We sampled these clusters in October 1998 (spatial study), February 1999 (low water, dry season), July 1999 (immediately after reflooding following an extensive period of no surface water), and October 1999 (deep water, wet season, 1 y after 1st collection).

We chose the 3 temporal-study clusters (C1, C4, and C6) from C-transect (Fig. 1C). Cluster C1, ~1500 m from inflow structures on the Hillsboro Canal, was selected as the high-P eutrophic location (mean [±1 SE] sediment total P [TP] = 1543 ± 53 mg/kg [October 1998]; mean surface-water TP = 81.6 ± 7.3 μg/L [1995–1998, quarterly collection]). Vegetation among plots at C1 was typical of the eutrophic zone and was characterized by dense stands of *Typha*, vines (*Mikania scandens* [L.] Willd. and *Sarcostemma clausum* [Jacq.] Schult.), willow (*Salix caroliniana* Michx.), and small patches of low-stature emergent macrophytes (*Hydrocotyle umbellata* Lamark, *Rumex verticillatus* L., *Sagittaria lancifolia* L.) interspersed with floating plants (mostly *Lemna* spp.).

Cluster C4 was located slightly <7000 m downstream from the canal and was an intermediately enriched region in the transition zone (sediment TP = 1105 ± 59 mg/kg; surface-water TP = 14.8 ± 1.6 μg/L). This cluster was an ideal contrast to oligotrophic and eutrophic areas because its vegetation spatial pattern and species composition were similar to oligotrophic areas—a heterogeneous mosaic of *Cladium* stands and open-water sloughs. Sloughs were deeper than *Cladium* stands and were covered extensively by the waterlily *Nymphaea odorata* Aiton. Spikerushes (*Eleocharis cellulosa* Torr.), bladderworts (*Utricularia foliosa* L. and *U. fibrosa* L.), and periphyton also were abundant in these sloughs. *Typha* was in the early stages of invasion into the fringes of sloughs.

Cluster C6 was an oligotrophic, low-P region in the reference zone (sediment TP = 474 ± 20 mg/kg; surface-water TP = 8.1 ± 0.49 μg/L) characteristic of the least-impacted areas of the northern Everglades. It was 10,600 m from the S-10C canal inflow. Vegetation pattern and composition at C6 were very similar to C4. Two P-sensitive macrophytes, *Utricularia purpurea* Walt. and *Eleocharis elongata* Chapm., were present at C6 but not at C4. Mats of periphyton were common in open-water sloughs. *Typha* was not recorded in any plots at C6 (King et al. 2004).

Sampling

We used sediment TP (mg/kg dry mass) data from each plot rather than surface-water measures (PO_4-P, TP) as an integrative indicator of P enrichment because previous studies (Pan et al. 2000, King et al. 2004) along this P gradient showed that sediment TP explained the most variation in periphyton and vegetation patterns, respectively. Preliminary analysis in our study also indicated that sediment TP was superior to surface-water P metrics in predicting consumer biomass. Descriptions of sediment and

water-chemistry methods and data are provided in King and Richardson (2002) and King et al. (2004).

Our macroinvertebrate-sampling methods followed King and Richardson (2002). We used a D-framed dip net (0.3-m wide, 500-μm mesh) to collect 10 individual samples of 0.5-m length within each plot to form a large composite sample (total area sampled = 1.5 m^2). Collecting a large composite sample increased the probability that large-bodied taxa, which were less abundant than small-bodied taxa yet potentially constituted a large proportion of the biomass, were adequately sampled in each plot. Dip-net sampling produces very similar estimates of composition and relative abundance as enclosure samplers in a variety of Everglades vegetation communities (Turner and Trexler 1997). We avoided enclosure samplers because they were very difficult to use in eutrophic areas that supported dense growth of vines (*Mikania scandens* and *Sarcostemma clausum*). Moreover, enclosure samplers were destructive and, thus, were inappropriate for repeated measures in the temporal study. In our study, dip nets retained a total sample mass that was independent of nutrient status (linear regression using distance from canal or sediment TP as predictors of sample wet mass, $r^2 = 0.01–0.03$, $p > 0.05$), suggesting that sampling efficiency was not biased by differences in vegetation along the P gradient. Last, dip-net sampling has become the standard technique for sampling invertebrates in wetlands (Batzer et al. 2001) and in previous studies in the Everglades (Rader and Richardson 1994, King and Richardson 2003, McCormick et al. 2004).

We collected dip-net samples by quickly jabbing the net frame onto the wetland bottom and sweeping across the surface sediments, macrophyte stems, and attached and floating periphyton. The initial sweep dislodged but undoubtedly missed some organisms. Therefore, we rapidly repeated the sweeping process twice more over the same area (King and Richardson 2002). We combined the contents of all 10 sweeps in a 500-μm-mesh sieve bucket, rinsed the material to remove fine particulates, placed it in 4-L heavy-duty storage bags, and put the bags on ice for return to the laboratory. In the laboratory, we weighed the samples to determine wet mass and then preserved them in 5% (v/v) buffered formalin stained with rose Bengal. RSK did all macroinvertebrate sampling to ensure consistency across all plots.

We estimated the biomass of small fish from the dip-net samples. Small, surface-oriented taxa dominate the fish assemblage in the Everglades (Jordan 1996, Turner et al. 1999), and the dip-net approach is an effective technique for estimating the abundance of these fishes (Rader and Richardson 1994). Throw traps, samplers commonly used for sampling fish in shallow wetlands, were not effectively sealed on the marsh bottom in dense vegetation, particularly where vines were abundant (RSK, personal observation), and they were excessively destructive to vegetation and not appropriate for repeated measurements in the plots.

We relied heavily on previous studies for supporting information on responses of primary producers along the P gradient. However, we also estimated cover of periphyton to facilitate our interpretation of P–consumer relationships and to evaluate more effectively our hypothesis that periphyton would be an important correlate of consumer biomass. We used epiphyton–metaphyton mats associated with the water surface as a measure of periphyton abundance. McCormick et al. (1998) comprehensively examined all components (metaphyton, epiphyton, epipelon) of the periphyton community and found that each of these classes of periphyton responded in a similar, declining manner at the highest level of P-enrichment. Thus, cover of these mats was a reliable indicator of relative differences among locations of periphyton standing crops. Two observers estimated % cover of periphyton in each plot during both the spatial and temporal studies.

We also collected periphyton from macrophyte stems for analysis of total C, N, and P. We identified stems that supported periphyton, and, when possible, retained at least 5 stems. Some plots contained no measurable periphyton, and we did not collect samples in these plots.

We estimated daily water depth (cm) within all plots several months before and during the study to evaluate how changes in hydrology might have influenced results in the temporal study. Methods for estimation of water depth are described in King et al. (2004).

Sample processing

We removed macroinvertebrates and fish from samples following a 2-phase subsampling approach described by King and Richardson (2002). We removed all large-bodied taxa (defined by King and Richardson 2002) from each sample (phase I). We removed small-bodied taxa from a random subsample consisting of 25% of the whole sample (phase II). We used this 2-phase approach for 2 reasons. First, large-bodied taxa are less numerically abundant than most small-bodied taxa and, thus, their biomass is more susceptible to under- or overestimation when subsampling is used. Thus, whole-sample processing yielded greater precision in biomass estimates for these taxa. Second, subsampling 25% of the whole sample for the

remaining taxa was necessary because of the impractical amount of time required to remove and identify the many thousands of individuals present in the large (1.5 m^2) composite samples (King and Richardson 2002).

We identified macroinvertebrates and fish to the lowest possible taxon (usually species). Exceptions were copepods (order) and nematans (phylum). Expert taxonomists verified all species identifications (see Acknowledgements). More than 144,000 individuals were identified from the spatial and temporal studies combined.

We measured every individual of most taxa to the nearest 0.5 mm using an ocular micrometer. We used these measurements in taxon-specific length–mass regression equations to estimate individual dry mass (Kushlan et al. 1986, Meyer 1989, Sample et al. 1993, Benke et al. 1999). We used a biovolume technique to estimate biomass of taxa that either did not have published length–mass equations or were very small (Smit et al. 1993). For small taxa, particularly some Chironomidae and Oligochaeta, we counted individuals in taxon-specific size classes based on length and width, and used these size classes to estimate dry mass based on biovolume. We also estimated biomass of Gastropoda (other than *Pomacea paludosa*; Kushlan et al. 1986) using biovolume because few length–mass equations were published to estimate flesh mass (excluding shell mass). We used approximate geometric shapes and measured dimensions of tissue of individual gastropods to estimate biovolume and dry mass. We used whole-sample (large-bodied taxa) or subsample (small-bodied taxa) area to standardize biomass of each taxon into areal biomass (mg/m^2) based on the total sample area (1.5 m^2).

We scraped periphyton from macrophyte stems, rinsed it into a graduated beaker with deionized water, and homogenized it with a blender. We placed the resulting periphyton–water slurry in pans and dried the slurry at 60°C for 48 h. We pulverized dried periphyton samples to a fine powder using a mortar and pestle. We analyzed periphyton total C and N by combustion with a CHNS analyzer (Perkin–Elmer 2400; Perkin–Elmer Corporation, Norwalk, Connecticut). We measured total P as PO_4-P in a nitric/perchloric acid digestion using a TRAACS 800 Autoanalyzer (method no. 781–86T; Braun and Luebbe, Elmford, New York). We collected an insufficient dry mass of periphyton to run separate TP analyses for all 126 plots in the spatial study. Therefore, we used a composite sample of material from all 9 plots within each cluster for TP analysis. However, we collected enough material on the remaining dates in the temporal study to permit separate analysis of TP in each plot (where periphyton was present).

Data analysis

We summarized macroinvertebrate data in terms of biomass of the total assemblage, trophic levels (primary or secondary-or-higher consumers), and coarse-level taxonomic groups (classes or orders). Insufficient numbers of herbivorous fish were collected to warrant separation of fish biomass by trophic level; we summarized fish as total biomass only. We did not attempt to evaluate changes in functional feeding groups (FFGs) of macroinvertebrates because many taxa are classified into multiple groups (e.g., see Merritt and Cummins 1996). Moreover, the actual food habits of taxa, particularly primary consumers, might not correspond well to functional-group classes. For example, *Palaemonetes paludosus*, a grass shrimp that is a major contributor to total consumer biomass in the Everglades (Turner et al. 1999), typically is considered a gathering collector of detritus (e.g., Merritt et al. 2002), but also is known to graze heavily and grow faster on periphyton than other food sources (Wessell et al. 2001, Geddes and Trexler 2003). Gut contents of *P. paludosus* in our collections consisted mostly of algae (RSK, unpublished data). Moreover, apparent differences in FFGs often are driven solely by 1 or 2 dominant taxa per group. Thus, FFGs might only indicate taxa-specific responses and, thus, are highly susceptible to errors caused by FFG misclassification (e.g., *P. paludosus*). Therefore, we classified taxa only as primary or secondary consumers. Even these classifications were not without error, but they were more likely than FFGs to reflect general patterns between trophic levels. We also ranked the 20 most dominant taxa (lowest taxonomic identification, usually species) in terms of mean biomass among the reference, transition, and eutrophic zones, and among the 3 temporal clusters across the 4 dates of collection to aid in our interpretation of community- and higher-group responses to P enrichment.

We used linear or polynomial least-squares regression analysis to evaluate responses of macroinvertebrate and fish biomass, periphyton cover, and nutrient ratios to sediment TP and distance from canal inflow structures (a proxy for the P gradient). We used means among plots ($n = 9$) within each cluster ($n = 14$) as observations in each regression. Distance from canal (m) was georeferenced to the centroid of each cluster, whereas sediment TP was an average value from all plots within each cluster. Distance from canal produced results nearly identical to sediment TP. Therefore, we report only results using sediment TP as a predictor (see Results). Before regression analysis, all biomass data were $\log_{10}(y)$ or $\log_{10}(y + 1)$ transformed (Sokal and Rohlf 1995).

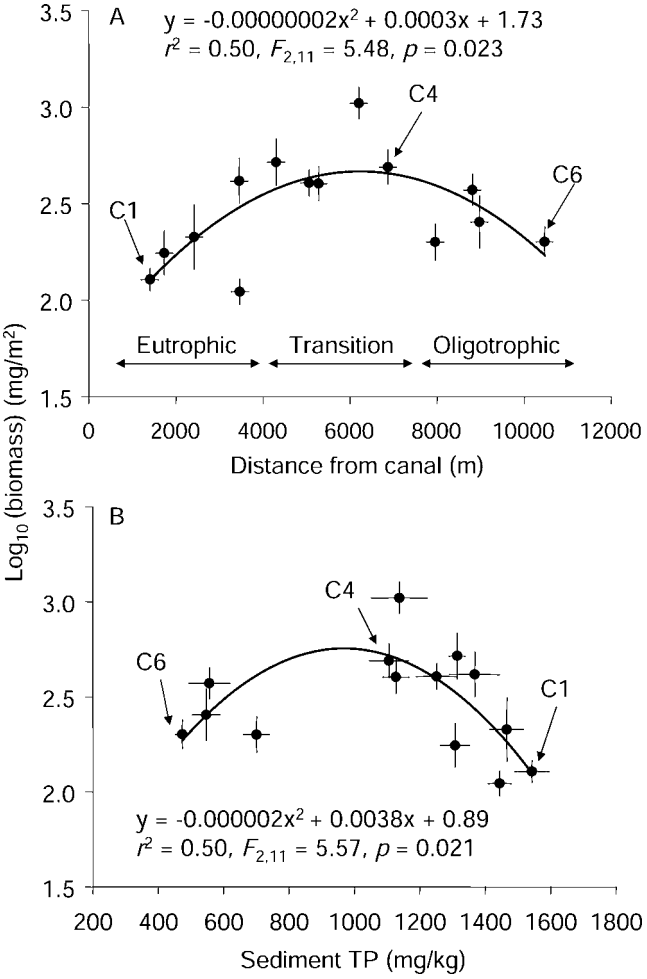

FIG. 2. Mean (±1 SE) macroinvertebrate biomass as a function of mean (±1 SE) distance from the Hillsboro Canal (A) and sediment total P (TP) (B) during the spatial study. C1, C4, and C6 indicate the eutrophic, transition, and reference clusters used in the temporal study. $n = 9$ plots/cluster.

We compared biomass estimates from the temporal study among clusters C1 (eutrophic), C4 (transition), and C6 (reference) over time using repeated-measures analysis of variance ([RMANOVA] Sokal and Rohlf 1995). We used plots within clusters as samples in the analysis. We contend that this analysis was appropriate when interpreted in the context of results from the spatial study. That is, if we were able to document a clear relationship between P and consumer biomass among clusters from the spatial study, we deemed it reasonable to interpret temporal patterns observed among these 3 clusters as representative of other areas experiencing similar levels of enrichment.

We treated cluster, date (October 1998, February 1999, July 1999, October 1999), and cluster × date as fixed effects in the analysis (Bennington and Thayne 1994). We used a posteriori least significant difference (LSD) multiple comparison tests to compare means among clusters or clusters within dates (cluster × date), depending upon which effects were deemed significant from RMANOVA. We used $\log_{10}(y)$ or $\log_{10}(y + 1)$ transformation before analysis to normalize residuals and homogenize variances of macroinvertebrate and fish biomass data. We did not analyze periphyton cover and nutrient ratios statistically because cover data could not be transformed to meet the assumptions of the analysis and nutrient-ratio data were unbalanced among treatments because periphyton was absent from some plots. We evaluated trends in periphyton data graphically. We conducted regressions and RMANOVA using Statistica 5.5 (Statsoft, Tulsa, Oklahoma). We considered results significant when $p \leq 0.05$.

Results

Spatial study

Macroinvertebrate biomass had a clear subsidy–stress response to both distance from the Hillsboro Canal (Fig. 2A) and sediment TP (Fig. 2B). These unimodal relationships were nearly identical for both predictor variables, and sediment TP was negatively correlated with distance from the canal (biomass [in mg/kg] = −0.1228distance [in meters] + 1765; $r^2 = 0.90$, $p \leq 0.001$). Therefore, subsequent responses were evaluated only with sediment TP as a predictor.

Macroinvertebrate taxa that were classified and analyzed collectively as primary consumers had a subsidy–stress response to sediment TP (Fig. 3A). Secondary consumers had a marginal ($p < 0.09$) subsidy–stress response; their biomass increased rapidly until sediment TP reached ~1000 mg/kg and showed no appreciable increase or decrease beyond that level (Fig. 3A). Fish biomass had a clear subsidy–stress response to sediment TP (Fig. 3B). Seven fish species contributed to total fish biomass (in rank order of total biomass): *Heterandria formosa* Agassiz, *Gambusia holbrooki* Girard, *Poecilia latipinna* (Leseur), *Fundulus chrysotus* (Günther), *Jordanella floridae* Good and Bean, *Lucania goodei* Jordan, and *Elassoma evergladei* Jordan.

Eight of the 12 macroinvertebrate taxonomic groups had subsidy–stress (unimodal) responses, 3 had subsidy (monotonic increase) responses, and 1 had a stress (monotonic decrease) response to sediment TP (Fig. 4). Decapoda, represented only by *P. paludosus* and *Procambarus fallax*, made the greatest contribution to assemblage biomass (Appendix 1) and had the most apparent subsidy–stress response to P enrichment. Decapoda biomass increased markedly at intermediate sediment TP (1000–1500 mg/kg), but plummeted when sediment TP was >1500 mg/kg. *Palaemonetes*

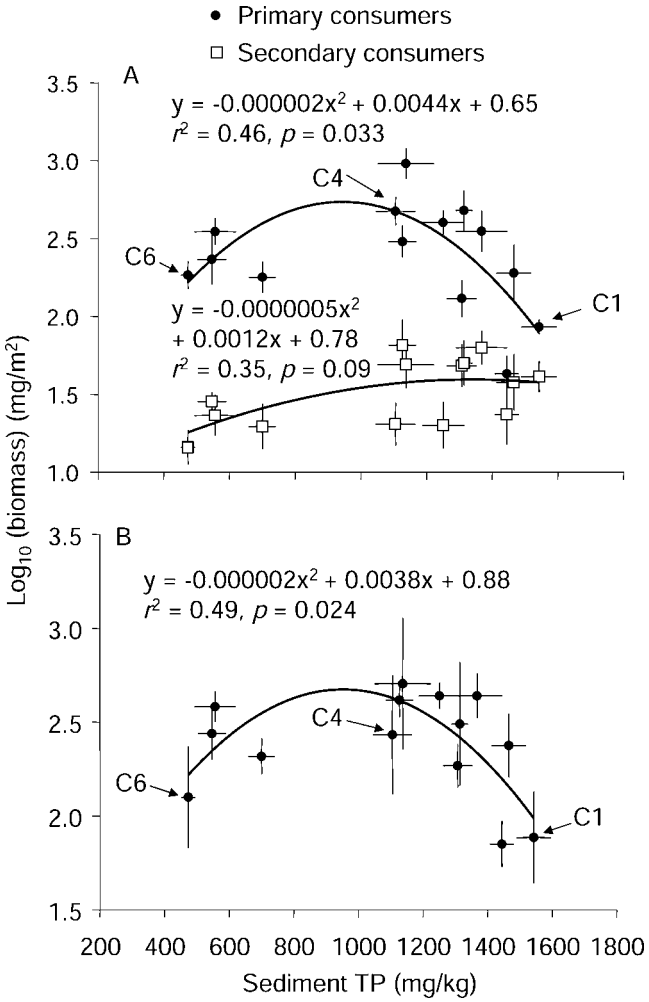

FIG. 3. Mean (±1 SE) biomass of macroinvertebrate primary and secondary consumers (A) and fish (B) as a function of mean (±1 SE) sediment total P (TP) during the spatial study. C1, C4, and C6 indicate the eutrophic, transition, and reference clusters used in the temporal study. $n = 9$ plots/cluster.

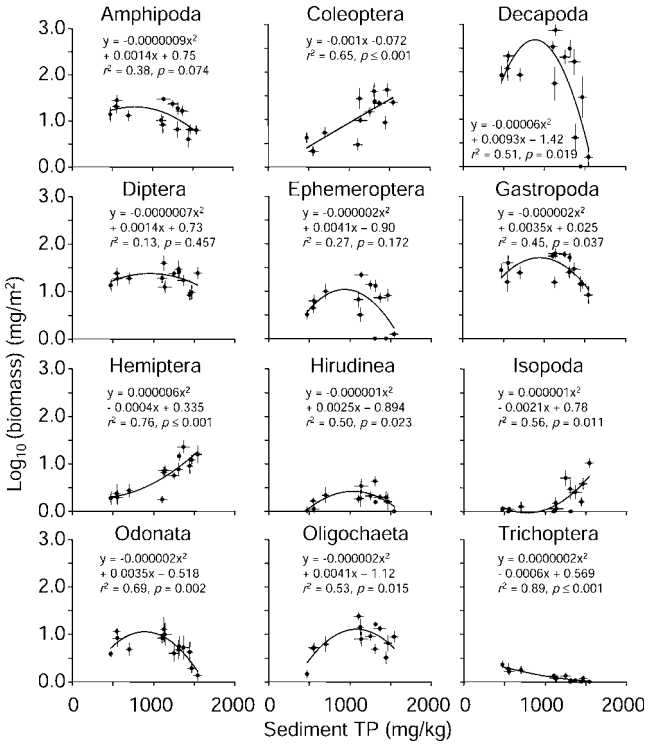

FIG. 4. Mean (±1 SE) biomass of the 12 most dominant macroinvertebrate taxonomic groups as a function of mean (±1 SE) sediment total P (TP) during the spatial study. C1, C4, and C6 indicate the eutrophic, transition, and reference clusters used in the temporal study. $n = 9$ plots/cluster.

paludosus, in particular, was rarely collected in high-P areas (Appendix 1). With the exception of Isopoda, the other taxonomic groups that consisted mostly of primary consumers—Gastropoda (particularly *Laevapex peninsulae*), Oligochaeta (primarily Naididae), Amphipoda (primarily *Hyalella azteca*), Ephemeroptera (*Caenis diminuta* and *Callibaetis floridanus*), and Diptera—also had subsidy–stress responses. However, regressions for Amphipoda, Ephemeroptera, and Diptera were not significant.

Isopoda, represented exclusively by *Caecidotea* sp., had a subsidy response to sediment TP (Fig. 4). This detritivorous taxon was most abundant in dense stands of *Typha* with large quantities of decaying coarse particulate organic matter. Taxonomic groups that consisted mostly of predators either had subsidy–stress (Odonata and Hirudinea) or subsidy (Hemiptera and Coleoptera) responses to the P gradient. Trichoptera—represented by 3 families and at least 5 different species—was the only coarse-level taxon to show a stress response to P enrichment.

Periphyton C:N and C:P declined significantly with increasing sediment TP (Fig. 5A, B). Mean molar C:N was ~16 in low-P clusters and declined linearly to ~11 to 13 in high-P clusters. Mean molar C:P was as high as 5023 in the reference zone and declined exponentially to 265 at the highest level of sediment TP.

Periphyton cover also declined significantly with sediment TP (Fig. 5C). Mean cover typically reached ~10 to 20% in the reference zone but declined sharply when sediment TP was >1200 mg/kg. In 2 of 5 eutrophic clusters, no measurable periphyton cover was observed.

Temporal study

Total macroinvertebrates, primary consumers, secondary consumers, and fish biomass varied significantly among the 3 clusters across time (RMANOVA; Table 1). During October 1998 (wet season, deep water;

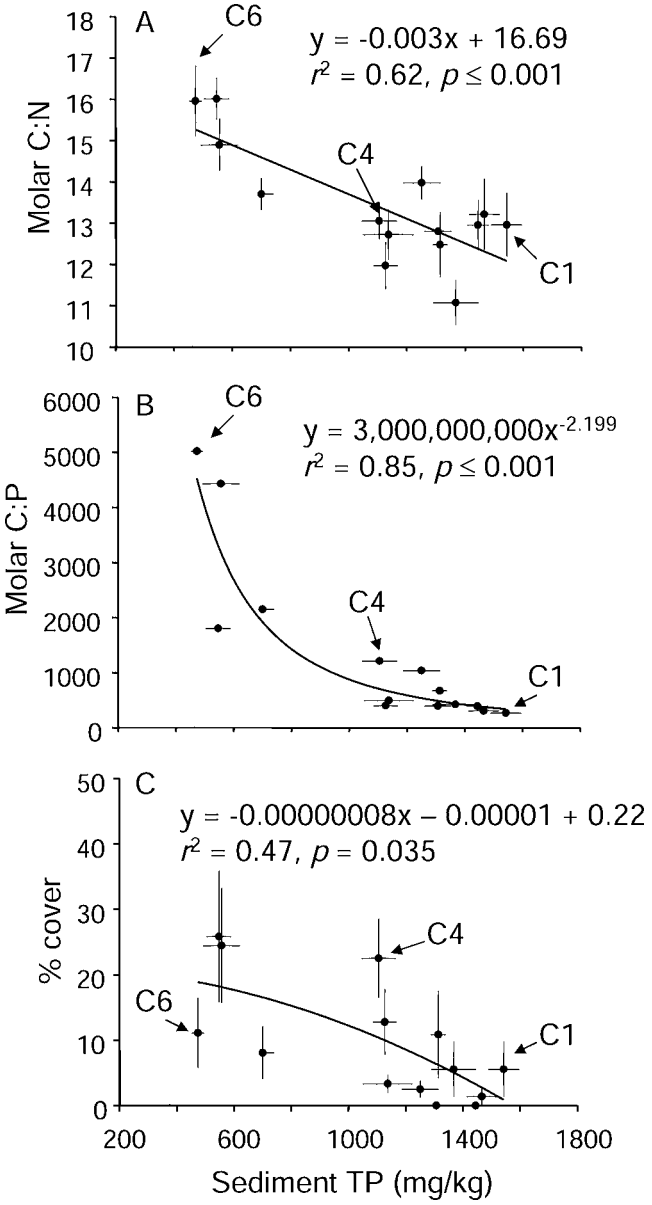

FIG. 5. Mean (±1 SE) periphyton C:N (A), C:P (B), and % cover (C) as a function of mean (±1 SE) sediment total P (TP) during the spatial study. One periphyton composite sample/cluster was used to estimate C:P. C1, C4, and C6 indicate the eutrophic, transition, and reference clusters used in the temporal study. $n = 9$ plots/cluster.

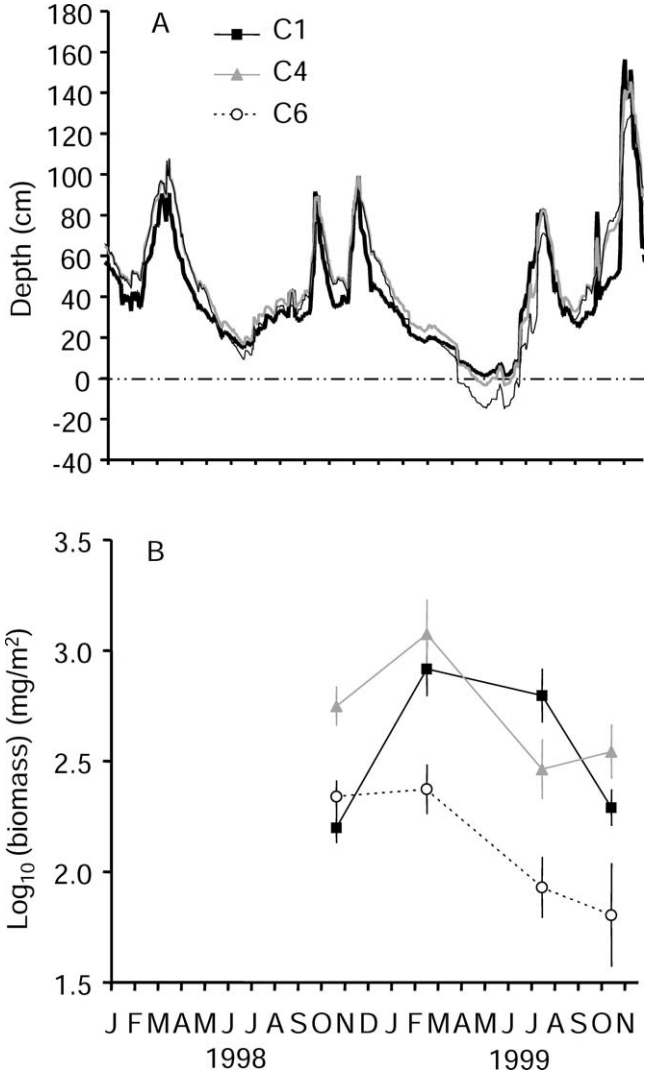

FIG. 6. Mean daily water depth (A) and mean (±1 SE) macroinvertebrate assemblage biomass (B) among reference (C6), transition (C4), and eutrophic (C1) clusters during the temporal study (1998–1999).

Fig. 6A), community biomass was significantly higher at the transition cluster (C4) than at the eutrophic and oligotrophic clusters (C1 and C6, respectively; LSD test, $p < 0.05$; Table 1, Fig. 6B). Biomass increased at all 3 clusters between October 1998 and February 1999 (dry season, shallow water; Fig. 6A), but the increase was steepest at eutrophic C1 (Fig. 6B). Mean biomass did not differ between C1 and C4, but biomass was significantly greater at both C1 and C4 than at C6 in February 1999. An extended period of little-to-no surface water occurred during April to June 1999 (Fig. 6A). Biomass at C1 changed very little from February 1999 to July 1999, whereas biomass at C4 and C6 declined significantly during the same period. Biomass was significantly lower at C4 and C6 than at C1 in July 1999 (Fig. 6B). By October 1999, water-depth and biomass patterns among clusters were similar to those observed in October 1998—biomass at C4 was significantly greater than at C1 and C6, whereas biomass did not differ between C1 and C6. Biomass was significantly lower at C6 than at C4 on all collection dates (Fig. 6B).

Biomass of several coarse-level taxa was dependent upon an interaction between cluster and sampling

TABLE 1. Repeated measures analysis of variance results for the effects of cluster (C1 [eutrophic], C4 [transition], C6 [reference]) and date (October 1998, February 1999, July 1999, October 1999) on consumer biomass during the temporal study.

	Cluster		Date		Cluster × date	
Biomass variable	$F_{2,24}$	p	$F_{3,72}$	p	$F_{6,72}$	p
Total macroinvertebrates	18.5	≤0.001	12.0	≤0.001	3.87	0.002
Amphipoda	2.59	0.096	20.7	≤0.001	5.47	≤0.001
Coleoptera	73.0	≤0.001	3.87	0.013	2.41	0.036
Decapoda	19.2	≤0.001	3.88	0.013	7.31	≤0.001
Diptera	13.0	≤0.001	19.0	≤0.001	6.83	≤0.001
Ephemeroptera	15.5	≤0.001	12.1	≤0.001	1.27	0.281
Gastropoda	12.6	≤0.001	7.77	≤0.001	5.02	≤0.001
Hemiptera	50.9	≤0.001	5.15	0.003	2.85	0.015
Hirudinea	5.44	0.011	0.72	0.540	1.50	0.192
Isopoda	125.1	≤0.001	6.34	≤0.001	5.29	≤0.001
Odonata	23.8	≤0.001	17.6	≤0.001	8.43	≤0.001
Oligochaeta	29.3	≤0.001	1.87	0.142	3.59	0.004
Trichoptera	20.2	≤0.001	11.3	≤0.001	4.67	≤0.001
Primary consumers	16.2	≤0.001	11.2	≤0.001	5.06	≤0.001
Secondary consumers	15.7	≤0.001	5.68	0.002	2.43	0.034
Fish	3.46	0.048	5.67	0.002	0.50	0.807

date, and thus, contributed to the significant interaction for total biomass (Table 1). The most obvious interaction was the response of Decapoda (Fig. 7) after the April to June drought (Fig. 6A)—in July 1999, biomass of decapods (mostly *P. paludosus*; Appendix 2) was very low at C4 and C6, yet was at its peak at C1 (exclusively *Procambarus fallax*) (Appendix 2; Fig. 7). By October 1999, several months after reflooding, these patterns in decapod biomass reversed. Temporal patterns of gastropod biomass also varied among locations; gastropod biomass increased sharply at C1 during February 1999 but showed relatively little variation with time at C4 and C6 (Fig. 7).

Temporal patterns of biomass of other coarse-level taxa were relatively consistent among locations. Biomass of Coleoptera, Hemiptera, and Isopoda was always high at C1 and relatively low at C4 and C6 (Fig. 7). Biomass of Ephemeroptera and Odonata typically was greater at C4 and C6 than C1. Trichoptera was the only coarse-level taxon to maintain its highest biomass at oligotrophic C6, although its contribution to total biomass was small (Fig. 7).

Periphyton C:N and C:P ratios were lower at C1 than at C4 and C6 and were relatively constant over time at each cluster (Fig. 8A, B), a pattern that indicated consistently more favorable food quality for primary consumers in the impacted and transition zones than in the oligotrophic zone. The pattern of significantly higher biomass of 7 major taxa, particularly Gastropoda, at C1 than at C4 or C6 was coincident with a sharp increase in periphyton % cover in this eutrophic area (Fig. 8C).

Discussion

Results from the spatial and temporal studies support the hypothesis that macroinvertebrate community biomass is resource limited, and this limitation is relaxed with P enrichment. The subsidy–stress model (Odum et al. 1979) served admirably as a theoretical framework for predicting community-level responses along the P gradient. We anticipated that many factors, mostly linked to changes in habitat pattern (i.e., vegetation), would act cumulatively as a stressor to standing stocks in areas of high P enrichment relative to areas of intermediate P enrichment. Indeed, invertebrate biomass showed a significant subsidy–stress relationship with P and was significantly lower in a high-P area of the wetland than an intermediate-P area on 3 of 4 collection dates. Moreover, this subsidy–stress pattern was evident for most of the major taxa collected.

Periphyton as a determinant of macroinvertebrate biomass

We hypothesized that changes in periphyton cover and elemental composition would be important direct determinants of macroinvertebrate biomass because periphyton is an important food resource in wetlands (e.g., Murkin 1989, Keough et al. 1996, Wissinger 1999, Hart and Lavvorn 2003). Patterns of periphyton cover and C:N:P ratios, across the landscape and through time, provide support for this hypothesis. In the temporal study, C:N and C:P ratios in periphyton were consistently greater at the reference cluster (C6) than at the eutrophic and transition clusters (C1 and C4). In the spatial study, periphyton cover was very

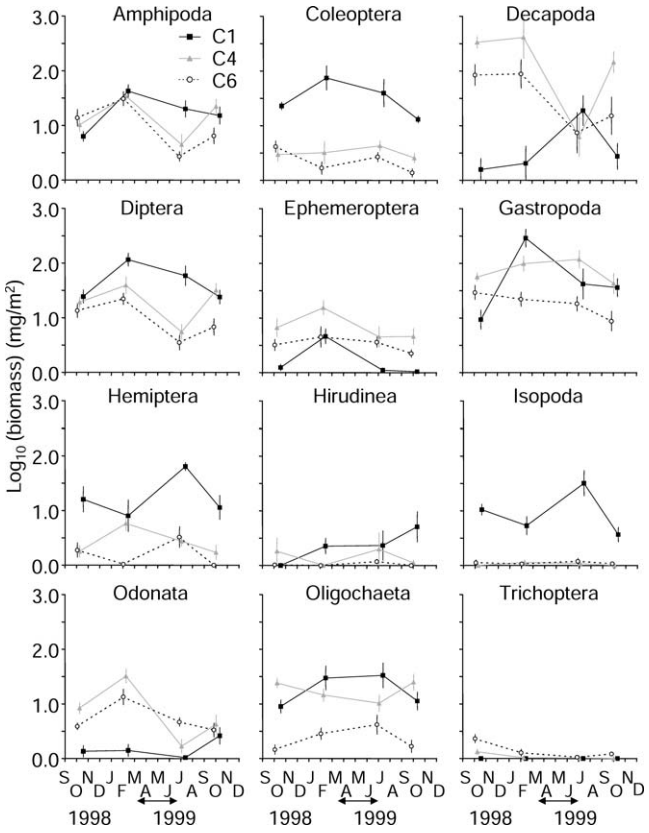

FIG. 7. Mean (±1 SE) biomass of the 12 most dominant macroinvertebrate taxonomic groups among reference (C6), transition (C4), and eutrophic (C1) clusters over 4 dates during the temporal study (1998–1999). Arrows along x-axes indicate period of no surface water.

low at high-P areas and relatively high at intermediate-P areas. However, C:N and C:P ratios declined as P increased, implying greater nutritional value of periphyton and, presumably, amorphous detritus generated from the periphyton at high-P areas than at intermediate-P areas (Hart and Lavvorn 2003). Thus, intermediate-P areas had higher periphyton cover than did high-P areas and higher concentrations of nutrients than did low-P areas, a fact that may have contributed to the subsidy effect for macroinvertebrate biomass.

Temporal patterns of periphyton cover add further support to the hypothesis that periphyton was driving macroinvertebrate community biomass along the gradient. At C1, where periphyton cover and macroinvertebrate biomass usually were low, periphyton cover increased markedly between October 1998 and February 1999, largely because of a substantial reduction in shading from standing dead *Typha* litter (greater in October 1998 than February 1999; RSK, personal observation). A sharp increase in macroinvertebrate biomass occurred concomitant with the

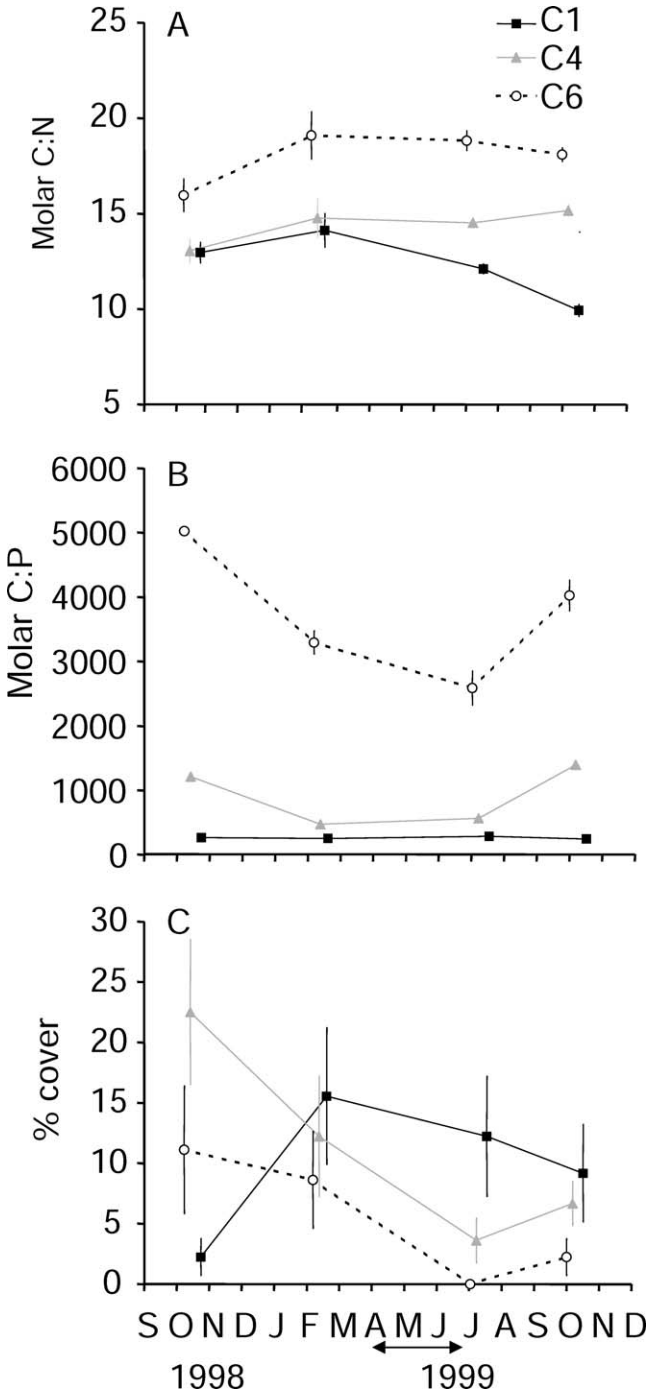

FIG. 8. Mean (±1 SE) periphyton C:N (A), and C:P (B), and % cover (C) among reference (C6), transition (C4), and eutrophic (C1) clusters over 4 dates during the temporal study (1998–1999). Arrow along x-axis indicates period of no surface water.

increase in periphyton. An argument could be made that the macroinvertebrate increase was in response to plant litter or any number of other unmeasured factors. However, responses of particular taxonomic

groups (Appendix 2) provide further evidence that the total macroinvertebrate response was at least partially caused by the periphyton increase. Biomass of Ephemeroptera (exclusively *Caenis diminuta* and *Callibaetis floridanus*), Gastropoda, and Oligochaeta (mostly Naididae), taxa known to be facultative or obligate grazers/collectors of periphyton and that consistently had algae in their guts (RSK, unpublished data), tracked trends of periphyton cover over time at this highly enriched cluster, whereas biomass of Isopoda (*Caecidotea* sp.), a detritivorous taxon found mostly in thick mats of decomposing *Typha* litter, declined between October 1998 and February 1999.

Two years of data from an experimental P-dosing study in the reference region of WCA-2A showed that macroinvertebrate biomass increased log-linearly up to the highest P treatment, a level of enrichment similar to that of the eutrophic zone in our present study, but never declined (King and Richardson, in press). However, *Typha* and other tall emergent macrophytes that choked out light and periphyton in the eutrophic zone of our present study were absent from the reference region in which the P-dosing study was conducted. We concluded from a path analysis of the data from the P-dosing study that increased periphyton productivity and decreased C:nutrient ratios were the primary factors responsible for increased standing stocks of macroinvertebrates. Collectively, our present study and the P-dosing study provide a body of evidence that suggests that increased periphyton quality (at intermediate- and high-P levels) and decreased quantity (at high-P levels) were at least partially responsible for the subsidy–stress patterns observed with nutrient enrichment.

Resource limitation in the Everglades

The importance of resource limitation to biotic communities is a source of much contention among ecologists. Many ecologists assert that competition or other constraints are the chief determinants regulating populations (reviewed by Cohen et al. 1990, Pimm et al. 1991), whereas others suggest that the significance of resource limitation is dependent upon the trophic level to which an organism belongs (e.g., Abrams 1993) or the frequency of disturbance in the environment (Connell 1975, Schoener 1982). In the dynamic, nonequilibrium environment of the Everglades, we hypothesized that interspecific competition and predation would not play a strong role in regulating abundances of macroinvertebrates and that the absence of strong biotic interactions would enable macroinvertebrate standing stocks to benefit from nutrient additions (Chase 2003). An alternative hypothesis was that macroinvertebrate production would accumulate at the top of the food web because of top-down control of macroinvertebrate standing stocks by large predaceous invertebrates or invertivorous fish (e.g., Hairston et al. 1960, Oksanen et al. 1981). However, our study does not suggest that predaceous invertebrates or fish were the primary factors limiting macroinvertebrate biomass in high-P areas. Predaceous invertebrate biomass showed a modest increasing trend but did not significantly increase with P enrichment, whereas fish showed a significant subsidy–stress response to P that tracked the response of primary-consumer invertebrates.

In contrast to our findings, Turner et al. (1999) found that invertebrate biomass (limited to large-bodied taxa only) did not increase as P increased in the Everglades, but observed higher biomass of small fish at 2 of 3 eutrophic sites when compared to 3 oligotrophic sites. They suggested that greater biomass and densities of small fish in eutrophic than in oligotrophic areas might explain the lack of an increase in invertebrate biomass. However, Turner et al. (1999) sampled only low- and high-P habitats, but not intermediate-P habitats, and therefore, might have missed the subsidy part of the subsidy–stress response that we observed. Moreover, Turner et al. (1999) also sampled 6 sites (compared to our 14 clusters of 126 sites) and targeted specific vegetation types, 2 factors that could have contributed to their conclusion that fish biomass was greater in enriched than in unenriched areas.

Hydrological stability generally is considered the most important factor governing temporal patterns in macroinvertebrate assemblages in wetlands (Batzer and Wissinger 1996). Invertebrate biomass clearly was affected by hydrology, particularly in response to the prolonged period of absent or minimal surface water. However, community biomass through time also was dependent upon level of P enrichment. This result could indicate that greater secondary productivity at the eutrophic location resulted in a significantly faster recovery from drought at the eutrophic location relative to less-enriched locations. However, mean water depth did not appear to drop below the surface of the peat layer at C1, whereas is did appear to do so at C4 and C6. Therefore, faster recovery of community biomass at C1 than at C4 or C6 also might indicate that many taxa were able to survive in a moist, unconsolidated sediment layer at C1 but not in the desiccated sediment of C4 or C6. Thus, patterns in macroinvertebrate biomass along the P gradient might also be dependent on water-level stability because areas near canal inflow structures are more hydrologically stable than interior wetland locations (King et al. 2004).

Effects of P enrichment in the Everglades and in other wetland systems

Turner et al. (1999) noted that the pristine Everglades is unique among wetlands in that it supports remarkably high standing stocks of periphyton but a comparatively low biomass of consumers. A major conclusion of our study is the remarkably strong and consistent influence of P enrichment on Everglades macroinvertebrate biomass. Even though biomass increased markedly up to a critical level of P and then declined, our data indicate that any level of P enrichment above reference levels causes a major alteration to the natural features of the ecosystem by dramatically increasing macroinvertebrate biomass. Moreover, many taxa found in low-P areas declined or completely disappeared in the transition zone, despite the overall increases in community- or coarse-taxa biomass (Appendices 1, 2). We (King and Richardson 2002, 2003, King et al. 2004) and others (Qian et al. 2003, 2004, McCormick et al. 2004) have demonstrated clearly that P enrichment causes predictable shifts in taxonomic structure at very low levels of enrichment and represents a significant threat to the conservation of Everglades biodiversity. Indeed, our previous work that coupled taxonomic composition data from the spatial study described here with a P-dosing experiment suggested that structural and functional changes in macroinvertebrate assemblage composition were highly probable at P concentrations barely above background reference conditions (King and Richardson 2003). Moreover, we must emphasize that the term *subsidy* should not be interpreted as *enhancement*—no value judgment is implied in the use of this term—nor should increases in biomass be interpreted as beneficial to the Everglades ecosystem. Rather, our use of the subsidy–stress model was intended to provide an ecological basis for predicting community- or ecosystem-level responses to a usable input (P) in an ecosystem unequivocally limited by that input.

The Everglades is a unique ecosystem and is more severely limited by nutrients than most wetlands of the world (Noe et al. 2001). How might our findings be generalized to other ecosystems? We contend our observed patterns could be more universal than one might expect. First, the Everglades is relatively young (~5000 YBP), a fact that has limited the evolution of uniquely adapted, endemic species. Instead, the Everglades is dominated primarily by rapidly dispersing opportunistic species found throughout much of the southeastern USA and families found throughout much of the world. Thus, taxonomic and functional assemblages in other wetlands are similar to those of the Everglades. Second, eutrophication of aquatic ecosystems, including wetlands, is a rampant problem worldwide; thus, many wetlands either have experienced or are likely to experience anthropogenic enrichment of N or P (e.g., King and Brazner 1999). Third, eutrophication fuels expansion of *Typha* and other invasive emergent macrophytes (e.g., *Phragmites australis*) in other freshwater and estuarine wetlands across North America by relaxing belowground competition for nutrients and increasing aboveground competition for light—a primary mechanism by which periphyton is reduced or excluded from wetlands. We speculate that P enrichment might predictably relax resource limitation for consumers up to the point where macrophytes outcompete periphyton for light and the ecosystem shifts from a periphyton- to macrophyte-based food web. This shift might cause a cascade of other effects on wetland communities, including homogenization of habitat, depression of dissolved O_2, a shift from autotrophic- to heterotrophic-based secondary production, and an overall depression of macroinvertebrate standing stocks. Clearly, data from nutrient and vegetation gradients from other wetland ecosystems are needed to evaluate this prediction better. At a minimum, we can conclude safely that the effects of nutrient enrichment on wetland food webs remains an area in need of future research as wetland ecosystems face increasing pressure from human development worldwide.

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APPENDIX 1. Twenty most dominant (mean biomass/zone; mg/m^2) taxa collected among clusters in the oligotrophic, transition, and eutrophic zones in the spatial study, October 1998. Taxon ranking is based on biomass in the reference zone.

Class/order	Taxon	Reference	Transition	Eutrophic
Decapoda	*Palaemonetes paludosus* (Gibbes)	159.5	301.9	21.7
Decapoda	*Procambarus fallax* (Hagen)	28.9	173.2	107.9
Gastropoda	*Planorbella duryi/scalaris* complex	25.9	8.2	5.4
Amphipoda	*Hyalella azteca* (Saussure)	24.9	21.6	10.1
Gastropoda	*Physella cubensis* (Pfieffer)	11.7	11.2	
Diptera	*Beardius truncatus* Reiss & Sublette gr.	8.2	5.6	
Diptera	*Dasyhelea* spp.	6.2	6.5	4.5
Ephemeroptera	*Callibaetis floridanus* Banks	4.0	7.0	3.0
Gastropoda	*Laevapex peninsulae* (Pilsbry)	3.5	28.0	3.6
Odonata	*Enallagma civile* Hagen	3.5		
Lepidoptera	*Parapoynx* sp.	3.5		
Ephemeroptera	*Caenis diminuta* Walker	3.2	7.0	
Diptera	*Tanytarsus* sp. R Epler	3.2		
Oligochaeta	*Bratislavia unidentata* (Harman)	3.0	4.1	
Porifera	*Spongilla* sp.	2.9		
Hemiptera	*Pelocoris femoratus* (Palisot-Beauvois)	2.1	7.5	9.4
Odonata	*Celithemis eponina* (Drury)	1.5		
Diptera	*Parakiefferiella* sp. C Epler	1.3		
Diptera	*Bezzia/Palpomyia* gr. sp. 2	1.2		
Odonata	*Libellula needhami* Westfall	1.1		
Odonata	*Coryphaeschna ingens* (Rambur)		15.1	3.4
Coleoptera	*Hydrobiomorpha casta* (Say)		14.3	5.8
Oligochaeta	*Haemonais waldvogeli* Bretscher		7.2	
Hirudinea	*Placobdella papillifera* (Verill)		6.2	
Coleoptera	*Cybister fimbriolatus* Wilke		5.9	6.8
Oligochaeta	*Dero digitata* (Muller) complex		4.2	
Diptera	*Dicrotendipes simpsoni* Epler		3.8	
Diptera	*Kiefferulus dux/pungens* gr.		2.7	
Diptera	*Goeldichironomus holoprasinus* (Goeldi)			11.5
Isopoda	*Caecidotea* sp.			5.7
Hemiptera	*Belostoma testaceum* (Leidy)			5.0
Coleoptera	*Scirtes* sp.			5.0
Hemiptera	*Belostoma lutarium* (Stal)			4.8
Gastropoda	*Planorbella duryi* (Weatherby)			4.7
Gastropoda	*Physella* sp.			3.8
Coleoptera	*Enochrus* spp. (larvae)			3.6
Odonata	*Erythemis simplicicollis* (Say)			3.0
	Cumulative % of total biomass	93.0	92.0	79.9

APPENDIX 2. Twenty most dominant (mean biomass/cluster; mg/m^2; $n = 9$ plots) taxa collected among reference (C6), transition (C4), and eutrophic (C1) clusters during each of 4 sampling events during the temporal study, 1998 to 1999. Taxon ranking is based on biomass in C6 in October 1998.

		October 1998			February 1999			July 1999			October 1999		
Class/Order	Taxon	C6	C4	C1	C6	C4	C1	C6	C4	C1	C6	C4	C1
Decapoda	*Palaemonetes paludosus* (Gibbes)	129.4	408.4		140.8	1460.8			71.5		10.1	196.0	
Gastropoda	*Physella cubensis* (Pfieffer)	24.1	10.4		8.5	5.8		13.4	34.3		15.2	4.0	
Amphipoda	*Hyalella azteca* (Saussure)	20.5	13.7	6.1	40.9	40.6	54.0	2.2	9.2	30.7	8.7	32.9	21.6
Gastropoda	*Planorbella duryi/scalaris* complex	11.6	32.3		13.9	98.6	156.4	5.8	151.7	125.1	2.9	52.3	26.7
Decapoda	*Procambarus fallax* (Hagen)	5.4	13.9	6.9	35.3		11.3	82.9	15.1	53.8	93.5	38.7	11.5
Diptera	*Dasyhelea* spp.	5.2	3.0	2.8	4.2			1.6	1.6	6.8	3.0	8.4	4.7
Diptera	*Beardius truncatus* Reiss & Sublette gr.	5.1	8.3		5.3			0.5			2.6		
Diptera	*Bezzia/Palpomyia* gr. sp. 2	3.5			1.9			0.8			1.9	3.9	
Diptera	*Odontomyia* sp.	2.7						1.2					
Odonata	*Enallagma civile* Hagen	2.3			14.5	6.0		4.2			4.0		
Ephemeroptera	*Callibaetis floridanus* Banks	1.9	3.8		5.2	13.8		2.8	6.8		0.3		
Hemiptera	*Pelocoris femoratus* (Palisot-Beauvois)	1.8		11.2			13.8	1.6		10.8			8.1
Lepidoptera	*Parapoynx* sp.	1.4											
Gastropoda	*Pseudosuccinea columella* (Say)	1.2		2.9	1.5		22.7	0.5					
Ephemeroptera	*Caenis diminuta* Walker	1.2	8.0		3.2	9.2		0.6	1.6		1.2	3.7	
Gastropoda	*Laevapex peninsulae* (Pilsbry)	1.1	13.1			7.0	7.2	1.0	12.9		0.9	11.8	4.1
Trichoptera	*Cernotina sp.*	1.1											
Polychaeta	*Namalycastis abiuma* (Muller)	0.8							3.8		3.5		
Coleoptera	*Scirtes* sp.	0.8					46.2						2.8
Coleoptera	*Celina imitatrix* Young	0.7						1.1					
Hirudinea	*Placobdella papillifera* (Verill)		9.8										
Oligochaeta	*Haemonais waldvogeli* Bretscher		9.4	4.7		6.9			2.7	4.0		13.3	
Oligochaeta	*Bratislavia unidentata* (Harman)		8.7									3.6	
Hirudinea	*Philobdella* sp.		7.3										
Oligochaeta	*Dero digitata* (Muller) complex		5.5	2.3		4.6			1.7	3.8		4.5	
Odonata	*Celithemis eponina* (Drury)		2.6		5.1	20.9							
Odonata	*Brachymesia gravida* (Calvert)		2.5			4.2						3.9	
Diptera	*Tanytarsus* sp. G Epler		2.2		2.6	15.2						3.0	
Gastropoda	*Physella* sp.		2.1	2.6		5.1	254.0		4.9	78.6			2.8
Diptera	*Polypedilum* sp. A Epler		2.1			5.7						4.4	
Diptera	*Goeldichironomus holoprasinus* (Goeldi)			21.9			78.9			81.1			13.5
Isopoda	*Caecidotea* sp.			11.6			7.6			79.5			4.6
Hemiptera	*Belostoma lutarium* (Stal)			7.6				4.8		4.2			3.3
Hemiptera	*Belostoma testaceum* (Leidy)			7.2			10.4			44.2			9.2
Coleoptera	*Tropisternus* spp. (larvae)			4.2			9.5						
Gastropoda	*Planorbella duryi* (Weatherby)			3.6			39.8		4.0	21.2			26.5
Coleoptera	*Derallus altus* (LeConte)			3.4									2.6
Coleoptera	*Celina* spp. (larvae)			3.3									
Oligochaeta	*Eclipidrilus palustris* (Smith)			3.1			49.4	7.1	9.8	72.0	1.3	18.8	13.4
Hemiptera	*Belostoma* spp. (imm.)			3.0						8.4			
Coleoptera	*Enochrus* spp. (larvae)			2.8									
Coleoptera	*Phaenonotum exstriatum* (Say)			2.4									
Gastropoda	*Littoridinops monroensis* (Frauenfeld)				2.9	8.1		1.5	3.1		0.7	5.4	
Diptera	*Parakiefferiella* sp. C Epler				2.5								
Diptera	*Tanytarsus* sp. R Epler				2.3			0.4			1.2		
Diptera	*Fittkauimyia serta* (Roback)				1.9								
Diptera	*Larsia decolorata* (Malloch)				1.4		6.0						
Odonata	*Libellula needhami* Westfall				1.3	11.9							
Diptera	*Dicrotendipes modestus* (Say)					13.6						5.6	
Coleoptera	*Gyrinus elevatus* LeConte					6.5							
Diptera	*Tanytarsus limneticus* Sublette					5.1							
Coleoptera	*Cybister fimbriolatus* Wilke						140.0						
Diptera	*Limonia* sp.						22.3						
Diptera	*Chironomus stigmaterus* Say						16.7			23.2		4.6	6.3
Coleoptera	*Berosus* sp. (larvae)						9.1		3.0				4.9
Diptera	*Pseudochironomus* sp.						6.0			8.1			

APPENDIX 2. Continued.

		October 1998			February 1999			July 1999			October 1999		
Class/Order	Taxon	C6	C4	C1	C6	C4	C1	C6	C4	C1	C6	C4	C1
Gastropoda	*Ferrissia* sp.							0.4			0.3		
Hirudinea	*Macrobdella ditetra* Moore								52.8				
Hemiptera	*Trichocorixa* sp.								1.8				
Gastropoda	*Planorbella trivolvis intertexta* (Jeffreys)								1.6				
Coleoptera	*Hydrobiomorpha casta* (Say)									116.3			
Hirudinea	*Mooreobdella tetragon* Sawyer and Shelley									24.8			27.5
Coleoptera	*Tropisternus blatchleyi blatchleyi* d'Orchymont									4.8			
Diptera	*Goeldichironomus* cf. *natans* Reiss										0.9		
Gastropoda	*Aphaostracon pachynotus* Thompson										0.6		
Coleoptera	Lampyridae sp. (larvae)										0.4		
Diptera	*Chironomus* sp.											5.8	
Diptera	*Tanypus carinatus* Sublette												2.9
Odonata	*Erythemis simplicicollis* (Say)												2.8
	Cumulative % of total biomass	96.2	95.5	82.1	96.4	97.3	92.1	97.4	95.8	96.4	93.7	98.3	90.5