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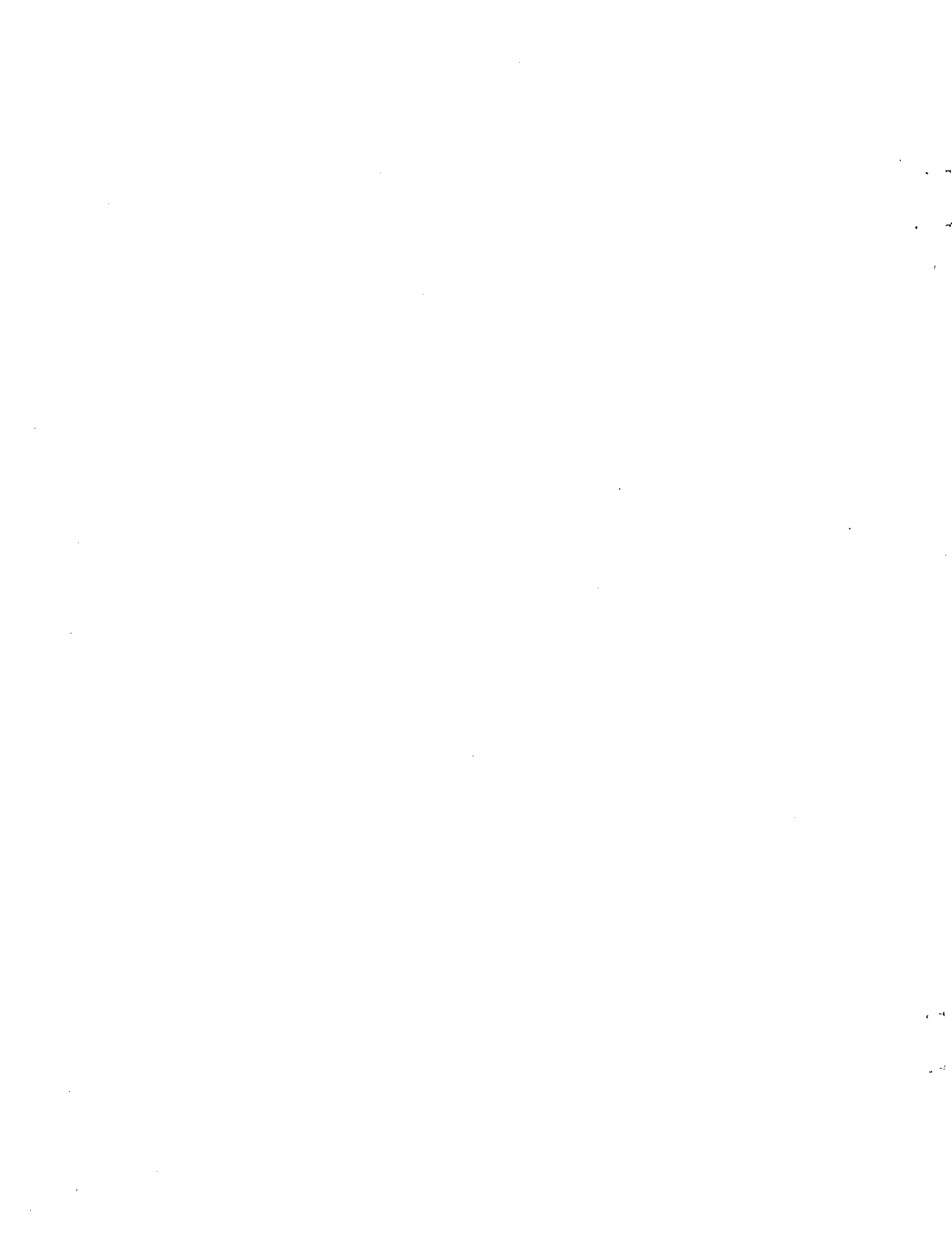
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**Macro Invertebrate Responses to Phosphorus Enrichment
in the Northern (WCA-2A) Everglades**

by

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Abstract

Aquatic macroinvertebrate communities were sampled between 1994 and 1996 at 13 sites downstream of phosphorus (P)-enriched canal inflows in a northern Everglades marsh to determine the effects of nutrient enrichment on community structure and function. Sampling was performed using sweep nets and Hester-Dendy (HD) samplers. Data were analyzed to assess changes in taxa richness and diversity, species composition, and functional group composition along the gradient. Environmental conditions at each site were characterized to interpret spatial changes in these metrics.

Mean water-column total P (TP) increased from $\leq 10 \mu\text{g L}^{-1}$ at sites in the marsh interior to as high as $160 \mu\text{g L}^{-1}$ at sites closest to the canal. Vegetation and habitat composition changed dramatically along the gradient, with sawgrass and slough-wet prairie habitats accounting for most vegetative cover in the interior and cattail accounting for nearly 100% of the cover near the canal. These differences in TP concentrations and vegetation were used to classify sites as reference, enriched, and highly enriched. Daytime dissolved oxygen (DO) concentrations averaged $\geq 3 \text{ mg L}^{-1}$ at reference sites as compared with concentrations $\leq 2 \text{ mg L}^{-1}$ at enriched and highly enriched sites.

Total macroinvertebrate densities were significantly higher in sweep samples and significantly lower in HD samples from highly enriched sites as compared with the reference condition. Taxa richness and diversity in sweep samples did not change significantly along the gradient, but declined with enrichment on the HD samplers. Insects were the dominant organisms at all sites, but declined in percent abundance with enrichment in sweep samples due to decreases in dipterans, trichopterans and odonates and an increase in oligochaetes. Changes in

Changes in Macroinvertebrate Community Structure and Function along a Phosphorus Gradient
in the Florida Everglades

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major invertebrate classes were less pronounced on HD samplers, although amphipods showed significant declines with enrichment. Principal components analysis (PCA) revealed a clear distinction in taxonomic composition between reference sites and both enriched and highly enriched sites for sweep samples as common chironomid taxa at reference sites declined with enrichment while pollution-tolerant chironomid and oligochaete taxa increased. A similar, but less dramatic trend was found for HD samples, with selected amphipod, chironomid, and gastropod taxa declining with enrichment and pollution-tolerant taxa reaching peak abundance at enriched sites. The functional composition in sweep samples showed modest changes with enrichment, including a shift in dominance from epibenthic collector-gatherers/deposit feeders, which were predominantly chironomids, to subsurface taxa, which were predominantly oligochaetes. Shifts in invertebrate functional composition on HD samplers with enrichment were attributable to declines in the dominance of shredders and collector-filterer/suspension-feeders.

Portions of the Everglades exposed to P-enriched runoff are showing characteristic shifts in macroinvertebrate taxonomic composition related to eutrophication. This shift has occurred without a change in species diversity and with an increase in total invertebrate abundance indicative of an overall increase in marsh productivity. The transition from an oligotrophic to eutrophic community signals a decline in the biological integrity of the Everglades ecosystem in response to P enrichment.

Introduction

The Florida Everglades is an oligotrophic, rainfall-driven marsh. Background water-column concentrations of total phosphorus (TP) average $< 10 \mu\text{g L}^{-1}$ throughout the marsh interior (McCormick et al., 2001a). Inputs of nutrient-rich runoff from agricultural areas upstream have created gradients of enrichment within the marsh, with water-column TP in excess of $100 \mu\text{g L}^{-1}$ in some areas. Phosphorus enrichment has dramatically altered the vegetative mosaic of the Everglades; effects include the loss of the native periphyton assemblage (McCormick & O'Dell, 1996) and slough-wet prairie vegetation (McCormick et al., 2001a), increases in cattail coverage (Rutchev & Vilchek, 1999), and other shift in macrophyte species composition (Vaithiyanaithan & Richardson, 1999). These changes affect the types of habitat and food available to secondary consumers, which are primarily invertebrates. Declines in periphyton and submerged macrophyte productivity and increases in dense cattail stands in enriched areas of the marsh are also associated with reductions in water-column dissolved oxygen (DO) (McCormick & Laing, 2003), which may limit the suitability of these habitats for some aquatic animals.

Current state legislation requires determination of P concentrations that produce changes in Everglades flora or fauna to support a water quality standard for P that is protective of native populations (Everglades Forever Act, Florida Statutes 373.4592). The purpose of this study was to assess the nature and extent of changes in one of the most diverse groups of Everglades consumers, the macroinvertebrates, to P enrichment. Macroinvertebrates are a key component of wetland food webs and are sensitive both to changes in the quality and quantity of primary production as well as vegetation structure (Batzer & Wissinger, 1996). Increased loading with a

limiting nutrient (such as P in the Everglades) generally stimulates wetland primary production, which in turn may support high invertebrate abundance and production. This stimulatory effect on the invertebrate community is counterbalanced by other nutrient-related changes, such as declines in DO that result in the loss of pollution-sensitive taxa from enriched areas (Rosenberg & Resh, 1993). Thus, it can be difficult to predict the effect of enrichment on aquatic macroinvertebrate species richness and diversity, although moderate nutrient loading often enhances these metrics while higher loads eventually lead to declines relative to the reference condition (Welch, 1980).

Research on Everglades macroinvertebrates has focused largely on a few species considered important in the diet of top predators such as wading birds (e.g., crayfish and shrimp), and most studies have focused on the effects of hydrology rather than nutrient enrichment (Gunderson & Loftus, 1993). In one of the few studies to assess macroinvertebrate responses to enrichment in the Everglades, Rader & Richardson (1994) documented an increase in taxa diversity and density of most major invertebrate taxonomic and functional groups in response to enrichment. However, these investigators limited their sampling to open-water habitats and, therefore, did not consider fully the effects of nutrient-induced changes on marsh vegetation (e.g., replacement of open-water habitats with dense stands of cattail in enriched areas) on the structure and function of the invertebrate assemblage.

The data analyzed here were collected to assess changes in the macroinvertebrate assemblage along an enrichment gradient downstream of canal discharges into the Everglades. Sampling occurred seasonally at fixed sites along this gradient and was conducted on a habitat-weighted basis to account for the effects of P enrichment on the areal extent of different

vegetation types. Invertebrate structure and function were compared between minimally enriched or reference sites and those experiencing different degrees of enrichment to determine the nature and extent of change along the gradient.

Methods

Site description

Sampling was conducted in the eastern portion of WCA-2A (Fig. 1), a northern Everglades marsh that has experienced dramatic changes in hydrology and phosphorus inputs in recent decades (Smith & McCormick, 2001). Prior to the construction of the canal and levee system (ca. 1960, Light & Dineen, 1994), water entered this area primarily as rainfall or as overland sheet flow from upstream marshes. As currently managed, most hydrologic inputs enter the marsh as canal inflows through spillways located along the northern levee (Walker, 1995). Canal inflows are elevated in P and other nutrients and have created a north-south enrichment gradient that extends 7 to 8 km into the marsh (McCormick et al., 2001a). Changes in marsh vegetation along this gradient are pronounced and include the loss of open-water habitats, increased coverage of emergent macrophytes, and a shift in species dominance from sawgrass to cattail with enrichment (reviewed in McCormick et al., 2001a). Enrichment also is associated with a decline in periphyton biomass and the replacement of oligotrophic cyanobacteria-diatom mats by filamentous green algae and eutrophic cyanobacteria (McCormick et al., 1998). Reduced areal periphyton productivity and increased sediment oxygen demand are believed responsible for reduced water-column DO in enriched areas of the marsh (Belanger et al., 1989; McCormick & Laing, 2003).

We established 13 sampling sites that encompassed the range of habitat changes along the

marsh enrichment gradient (Fig. 1). Three sites (U1, U2, and U3) were located in the marsh interior to document the minimally impacted condition. Five additional sites were located along each of two transects (E and F as shown in Fig. 1). Two additional sites (E0 and F0) were located in the interior canal immediately downstream of structure inflows to document water chemistry; no macroinvertebrate sampling was conducted at these canal sites.

Sample collection and processing

Water samples were collected every two weeks during 1994 and 1995 and analyzed for several chemical parameters including TP. Measurements of temperature and DO were conducted at mid-depth in the water column using a precalibrated Hydrolab Model H20 (Hydrolab Inc., Austin, TX). These measurements were not conducted separately in each habitat type at a site, but, instead, were performed at a fixed location at the interface between emergent and open-water habitats.

Macroinvertebrates were sampled quarterly from both natural and artificial substrates. Sweep nets (D-frame, mesh size = 0.350 mm) were used to collect macroinvertebrates from a known area (10 m²) at each site. In the Everglades, this technique has been shown to collect a larger number of individuals and taxa and to be less selective than other sampling methods (Turner & Trexler, 1997). Twenty sweeps, each covering roughly a 0.5-m² area were collected at least 1-m apart within a 50-m radius of the site marker. Sampling was distributed among vegetative habitats based on their percent cover (see Fig. 2B). Sweeps from the same site were combined, preserved in 10% formaldehyde in the field, and shipped overnight to Florida Department of Environmental Protection (FDEP) laboratories in Tallahassee for processing.

Artificial substrata (Hester-Dendy (HD) samplers, Hester & Dendy, 1962) were deployed

quarterly to provide a standardized substrate for assessing macroinvertebrate changes along the gradient. These substrata were not representative of any particular substrate in the marsh but, rather, provided a standardized surface for macroinvertebrate colonization at all sites. Also, unlike sweep sampling, these samplers were always deployed in the same habitat, the transitional zone between open water and emergent macrophyte stands. This placement exposed the samplers to potential colonists from both emergent and open-water habitats. Six samplers were deployed approximately 0.3 m apart at each site approximately 1 month prior to sweep sampling and collected after 4 weeks of colonization. A metal rod was attached to the bottom of each sampler and pushed into the sediment so that the sampler was located just above the sediment-water interface. During collection, samplers were carefully removed from the sediment and placed into a Whirl-pak^R bag. Samples were shipped overnight on ice to FDEP for processing. Samplers were often exposed to the air and, therefore, rendered unusable as a result of receding water levels during the spring dry season. Therefore, dry season HD data were sparse or absent for several sites.

Sweep samples were subsampled and processed according to FDEP Biology Section Standard Operating Procedure (SOP) IZ-02. The entire contents of HD samples were processed according to laboratory protocol DESOP IZ-03. Some organisms, such as worms, midges, and mites, were mounted under glass cover slips using CMC-10 media as described in SOP IZ-08. Organisms were identified to the lowest practical taxonomic level using SOP IZ-06. These SOPs are available at <http://www.dep.state.fl.us/labs/sops/internal/cgi-bin/biosops.asp>. Some of the identification manuals are available electronically at <http://www.dep.state.fl.us/labs/library/keys.htm>. Some species that occur in the Everglades but

have not been officially described were given interim names according to the authors of the above identification manuals.

Data Analysis

The density of macroinvertebrates in sweep samples was expressed as the number of organisms collected per sweep. Invertebrate densities on HD samplers were calculated based on the total surface area of all samplers (0.9 m²). Taxa richness values for HD samplers were based on the entire sample contents whereas those for sweep samples were estimated from subsamples that typically contained 100-200 organisms. A recent analysis (King and Richardson, 2002) found a significant positive relationship between estimates of invertebrate taxa richness and the number of organisms counted in Everglades samples and, indeed, a retrospective analysis of our sweep data revealed such a pattern when data from all sites were combined (but generally not when sites were analyzed separately). However, the average sample count size was similar among sites and adjusting species richness values for the number of individuals counted had no effect on the statistical results described below. Taxa (lowest-practical level of identification) diversity was calculated using the Shannon-Wiener index (Magurran, 1988). This diversity index has been widely used in the ecological literature and by regulatory agencies, and similar results were obtained when alternative indices were calculated.

Changes in density, diversity, and taxonomic and functional composition with enrichment were detected by first classifying each of the 13 sites into one of the following three nutrient categories based on water-column P concentrations and vegetation:

- 1) reference sites – E5, F5, U1, U2, and U3 had water-column TP and vegetation characteristic of minimally impacted areas of the northern Everglades;

- 2) enriched sites – E3, E4, F3, and F4 had TP concentrations above background levels and vegetation that was transitional between sawgrass-slough and cattail;
- 3) highly enriched sites – E1, E2, F1, and F2 had TP concentrations far in excess of background and were dominated by dense stands of cattail.

It was not possible to perform a repeated-measures analysis on these data because of the large number of missing data points for dry season (spring and early summer) sampling dates (sites could not be sampled when dry). Instead, all data collected from each site were averaged to obtain a mean and these mean values were then compared among sites of differing nutrient status using Dunnett's test, which specifically tested for differences between the reference (baseline) condition and conditions at enriched and highly enriched sites. This is a conservative statistical test as the experiment-wise error rate is held at $p=0.05$ and, therefore, the error rate for individual comparisons was closer to $p=0.025$ (Lentner & Bishop, 1986).

Changes in taxonomic composition were evaluated at the class, order (for the class Insecta only), and lowest-practical-taxon level. Principal components analysis (PCA) was used to evaluate differences in taxonomic composition based on relative abundances at the lowest practical-taxon level among sites and dates and to identify taxa associated with reference and enriched conditions. This analysis was conducted on log-transformed abundance data and was limited to species occurring in >10% of samples. All sampling periods were included in the same analysis as little additional information on taxon patterns was gained from analyzing each period separately. Species abundances were correlated with PC axes using Spearman's rank coefficient (Hollander & Wolfe, 1973), and the significance of these correlations and the magnitude of eigenvector scores were used to identify taxa responsible for sample separation.

Available autecological information on these taxa was compiled to interpret taxonomic shifts associated with enrichment.

Taxa were classified into functional (i.e., feeding) groups (Table 1) based on current literature (Merritt & Cummins, 1996; Thorp & Covich, 2001) to identify dominant functional groups in the marsh and to calculate the percentage of these groups in each sample.

Results

Habitat changes along the gradient

Mean water-column TP concentrations during the study period declined exponentially along the gradient and reached background levels ($\leq 10 \mu\text{g L}^{-1}$) at the 5 reference sites (E5, F5, U1, U2, and U3) (Fig. 2A). Mean concentrations increased from background to between 18 and 20 $\mu\text{g L}^{-1}$ at enriched sites roughly 7 km downstream and above 40 $\mu\text{g L}^{-1}$ at highly enriched sites, which were < 4 km downstream. The site closest to the canal (F1, 160 $\mu\text{g L}^{-1}$) had a higher mean TP concentration than inflow sites (E0 and F0, 95 and 103 $\mu\text{g L}^{-1}$, respectively) possibly due to internal P loading from the sediments. Changes in the concentration of chemical variables other than P along the gradient generally were modest ($< 20\%$) and were summarized by McCormick et al. (1996).

Vegetation changed along the gradient both with respect to species composition and the percent cover of major habitat types (Fig. 2B). Sawgrass stands and open-water habitats (slough-wet prairies) accounted for almost all cover at reference sites. The extent of open-water habitats declined with enrichment, and the vegetative composition of these habitats changed as well. Calcareous periphyton, *Utricularia purpurea*, and *Eleocharis* spp. were generally absent from both enriched and highly enriched sites, whereas the size and density of *Nymphaea odorata* beds

were greatest at enriched sites. The small amount of open-water habitat at highly enriched sites resulted largely from airboat disturbance or alligator activity and contained little vegetation. Dense emergent macrophyte cover increased to nearly 100% at highly enriched sites and was due to an increase in cattail coverage as sawgrass cover actually declined with enrichment. Further details on vegetation changes are provided by McCormick et al. (2001a).

Daytime DO concentrations averaged near or above 3 mg L⁻¹ at the 5 reference sites but were generally at or below 2 mg L⁻¹ at enriched and highly enriched sites (Fig. 2C). Concentrations varied considerably among sampling dates, and this variation was largely related to the time of day and the season when sampling occurred (e.g., lower in early morning than in the afternoon; lower in summer than in winter as related to temperature). However, the declining pattern in DO with enrichment was consistent among dates (see McCormick & Laing, 2003).

Water temperatures varied seasonally with minima between 15 and 22 °C during the January-March sampling periods and maxima between 27 and 39 °C during the July-September periods. Mean temperatures were similar at enriched and highly enriched sites (24 °C) and at reference sites (25 to 26°C).

Whereas water quality changes in the marsh were correlated strongly with distance downstream of canal inflows, hydrologic changes were related to variation in topography and ponding of water at the southern end of the gradient. Sites closest to the canal and those furthest downstream were the deepest, while sites 6 to 8 km downstream had lower water depths as a result of slightly higher soil elevations (Fig. 2D). Water depths throughout the marsh fluctuated considerably during the study period (range of 0.1 to 1.5 m across all sites) in response to the pulsed nature of canal inflows. While no site ever dried completely during either year, depths at

some sites during the spring and early summer sampling periods declined to levels that precluded both sweep and HD sampling.

Macroinvertebrate abundance

Macroinvertebrate densities estimated from sweep samples ranged between 8 and 896 organisms/sweep. Densities varied by as little as 3-fold (site E3) to almost 100-fold (site E1) among sampling dates at individual sites. Density varied most at highly enriched sites (8 to 896 organisms/sweep) and least at reference sites (28 to 748 organisms/sweep), but without a consistent temporal pattern. Average densities increased with enrichment and, despite high variability, were significantly greater at highly enriched sites compared with the reference condition (Fig. 3).

Macroinvertebrate densities on HD samplers ranged between 0 and 328 organisms/m² across all sampling periods except for March 1994, when densities ranged between 418 and 1169 organisms/m² at the 5 sites where useable samplers could be retrieved. Densities varied by as little as 3-fold (sites E3 and E5) to 400-fold or more (sites F1, F2, and U3) among sampling dates at individual sites. Variation was greatest at enriched sites (3 to 1169 organisms/m²) and lowest at highly enriched sites (0 to 529 organisms/m²) and displayed no predictable temporal pattern. Average densities were similar at reference and enriched sites, but were significantly lower at highly enriched sites as compared to the reference condition (Fig. 3).

Taxa richness and diversity

Macroinvertebrate richness and diversity in sweep samples did not change significantly along the gradient (Fig. 3). Taxa richness ranged between 8 and 34 taxa/sample and was similar among sites of differing nutrient status. Shannon diversity ranged between 1.49 and 3.05 with no

particular pattern among sites.

Macroinvertebrate richness and diversity on HD samplers declined with enrichment (Fig. 3). Taxa richness ranged between 0 and 22 for HD samplers. While the range of taxa richness among samples was similar among sites of differing nutrient status, the average number of taxa in samples from enriched (10 taxa) and highly enriched (8 taxa) sites was significantly lower than for reference sites (14 taxa). Diversity ranged between 0 and 3.67 and was significantly lower at highly enriched sites (1.88) compared with the reference condition (2.63).

Taxonomic composition

Major taxonomic groups. A total of 354 macroinvertebrate taxa were identified in 60 sweep samples collected along the gradient. Insects accounted for the majority of taxa (73%), and dominant insect orders in terms of taxa richness included dipterans (34%), coleopterans (17%), hemipterans (8%), and odonates (6%). Oligochaetes and gastropods accounted for an additional 12% and 7% of all taxa, respectively.

Fewer taxa (121) were identified in the 59 HD samples, although the dominant groups were the same as for sweep samples. Insects accounted for 65% of all taxa; dipterans again were the dominant order (44%), while coleopterans only accounted for 5% of all taxa. Hemipterans and odonates accounted for 2% and 8% of all taxa, respectively, and ephemeropterans, which were absent from sweep samples, accounted for 4% of all taxa in HD samples. Oligochaetes and gastropods accounted for an additional 13% and 15% of all taxa, respectively.

Insects, amphipods, oligochaetes, and gastropods collectively accounted for at least 93% of the macroinvertebrates in all sweep samples. The percent abundance of insects declined significantly with enrichment and, on average, comprised more than 70% of all

macroinvertebrates at reference sites compared with less than 60% at highly enriched sites (Fig. 4). Gastropods and amphipods showed a similar trend that was not statistically significant. By contrast, oligochaete dominance increased significantly with enrichment from less than 5% of organisms on average in samples from reference sites to more than 25% at highly enriched sites. Four orders of insects accounted for between 20 and 93% of all organisms in sweep samples. The percent abundance of dipterans, the most common order, declined modestly with enrichment and were significantly less dominant at enriched sites compared with the reference condition (Fig. 5). Trichopterans and odonates accounted for more than 2% of all organisms at reference sites and were significantly less dominant at enriched and highly enriched sites where they accounted for much less than 1% of all organisms. Ephemeropterans were significantly more dominant at enriched sites (3.5% of all organisms) than at reference sites (0.5%), but were similar to the reference condition at highly enriched sites.

Insects, amphipods, oligochaetes, and gastropods collectively accounted for at least 88% of the macroinvertebrates in HD samples. The percent abundance of insects was similar among sites with differing nutrient status, while that of gastropods and oligochaetes tended to be highest at enriched sites and lowest at highly enriched sites (Fig. 6). The percent abundance of amphipods declined with enrichment and was significantly lower than the reference condition at enriched sites. The same four insect orders that were dominant in sweep samples accounted for between 20 and 93% of all organisms in HD samples. The percent abundance of dipterans was similar among sites with differing nutrient status (Fig. 7). The percent abundance of trichopterans and odonates declined with enrichment and was significantly lower (at or near 0%) at highly enriched sites compared with the reference condition (near 2%). Ephemeropterans were

significantly more dominant at enriched sites (12%) compared with reference sites (3%).

Taxa composition. Fifty-three taxa occurred in at least 10% of all sweep samples and were included in the PCA. This analysis showed a clear distinction in taxonomic composition between macroinvertebrate communities at reference sites and those at enriched and highly enriched sites along PC axis 1, which accounted for 18% of total variation in the data (Fig. 8). No separation between enriched and highly enriched sites was apparent even when reference site data were removed from the analysis. PC axis 2 accounted for an additional 9% of variation and separated individual samples within each of the above two groups. However, there was no clear spatial or temporal pattern to this separation and, thus, this axis provided little interpretable information on macroinvertebrate patterns within the marsh.

Reference sites were characterized by several chironomid and two trichopteran taxa, many previously reported to be intolerant of conditions associated with enrichment (Table 2). A separate pollution-tolerant assemblage of chironomids, oligochaetes, and an ephemeropteran (*Caenis* spp.) was dominant at enriched and highly enriched sites. The 8 taxa most influential in separating sites of differing nutrient status based on PC 1 eigenvectors (Fig. 9) accounted for between 9 (F1) and 35% (F5) of all macroinvertebrates in individual samples and averaged 26% of the community across all samples. Two chironomids, *Parakiefferiella* sp. C Epler and *Tanytarsus* sp. R Epler, were dominant at reference sites and generally absent from enriched and highly enriched sites. A similar trend was displayed by two less common chironomids, *Labrundinia neopilosella* and *Nilothauma* spp. The chironomids *Chironomus* spp. and *Pseudochironomus* spp. and the oligochaetes *Dero trifida* and *Haemonais waldvogeli* increased in abundance with enrichment. Taxa showing no strong response to enrichment in sweep

samples were generally less abundant than those that were affected. An exception was the amphipod *Hyallela azteca*, which was the most commonly occurring taxon in sweep samples and often the most abundant.

Thirty-eight taxa occurred in at least 10% of all HD samples and were included in the PCA. When all sampling dates were included in the analysis, PC axis 1 (21% of total variation) separated samples collected during March 1994 from those collected on all other dates, while PC axis 2 (11%) showed some separation between reference and enriched sites (Fig. 10A). When the March 1994 date (samplers only retrieved at four sites due to drought conditions) was excluded from the analysis, PC axis 1 (15%) separated reference and highly enriched sites while PC axis 2 (10%) showed some additional separation between reference and enriched sites (Fig. 10B). The relatively poor separation between sites of differing nutrient status was attributed in part to the high variability in macroinvertebrate abundance among HD samples and, in particular, extremely low abundances and taxa richness on some samplers. Similar to sweep samples, there was no separation between enriched and highly enriched sites even when reference site data were removed from the analysis.

Hester-dendy samples at reference sites were characterized by several chironomid taxa and a suite of other invertebrates, many of which differed from those identified as influential in sweep samples (Table 3). Reference taxa included *H. azteca*, which did not respond to enrichment in sweep samples. Chironomids and oligochaetes characteristic of enrichment were similar to those identified in sweep samples. In contrast to sweep samples, however, the abundance of many of these taxa were greatest under enriched rather than highly enriched conditions. Taxon-specific patterns on HD samplers were illustrated by the 8 most influential

taxa, which accounted for between 0 (E1) and 26% (F2) of all macroinvertebrates in individual samples and averaged 15% of the community across all samples. Abundances of *H. azteca*, the chironomids *Cladotanytarsus* spp. and *Tanytarsus* sp. R Epler., and the gastropod *Physella* spp. were sharply lower at enriched and highly enriched sites as compared with the reference condition. Two other chironomid taxa, *Chironomus* spp. and *Pseudochironomus* spp., the ephemeropteran *Caenis* spp., and the gastropod *Laevapex* spp. reached their peak abundance at enriched sites (Fig. 11).

Changes in functional composition

Most macroinvertebrates in both sweep and HD samples were classified into one of six functional groups shown in Table 1. Epi col-gath/dep fdr were the most common functional group in sweep samples at all sites, but were significantly less dominant at enriched and highly enriched sites (approximately 35% of the community) than at reference sites (approximately 50% of the community). This decline was associated with a decreased abundance of chironomids, which dominated this functional group. Col-filtr/susp fdr accounted for 10% of the community at reference and enriched sites, but declined significantly to less than 2% of the community at highly enriched sites. The dominance of sub-benthic col-gath/dep fdr was significantly greater at enriched and highly enriched sites (20 and 27% of the community, respectively) than at reference sites (5% of the community), largely due to an increase in oligochaete abundance. Scrapers were significantly more dominant (10% of community) at enriched sites than at reference sites (5% of the community) as a result of an increase in ephemeropterans (see Fig. 5), but were similar to reference levels at highly enriched sites. Predators and shredders accounted for approximately 20% and 10% of the community, respectively, across the gradient.

Epi col-gath/dep fdr were also the most common functional group in HD samples at all sites, accounting for between 33 and 39% of the community at sites of differing nutrient status, and did not change significantly in dominance along the gradient. Col-filtr/susp fdr accounted for 9% and 7% of the community at reference and enriched sites, respectively, but declined significantly to less than 2% of the community at highly enriched sites. Shredders also declined significantly in dominance from 16% of the community at reference sites to 7 and 9% of the community at enriched and highly enriched sites, respectively. Scrapers accounted for over 20% of the community at reference and enriched sites and only 15% of the community at highly enriched sites, but this decline was not statistically significant. Similarly, a decline in predators from 10% at reference sites to 5% at enriched and highly enriched sites was not significant. The dominance of sub-benthic col-gath/dep fdr increased from 5% of the community at reference sites to 15% of the community at enriched sites, but in contrast to sweep samples this increase was also not significant.

Discussion

There is increasing concern that excessive nutrient loading to wetlands can produce the same detrimental ecological effects as those documented in other aquatic ecosystems (USEPA 1990a). Increased P loading to the Everglades has been shown to produce many of the classic symptoms of cultural eutrophication including increased productivity, reduced DO, and shifts in taxonomic composition from oligotrophic (i.e., pollution intolerant) to eutrophic (i.e., pollution tolerant) species (reviewed in McCormick et al., 2001a). Most studies of biological impacts associated with enrichment of the Everglades have focused on changes in primary producers (macrophyte and algal abundance and composition) that respond directly to increases in P

availability. While invertebrates do not respond directly to nutrient enrichment, they have been shown to respond to nutrient-induced changes in vegetation structure and composition and water quality parameters such as DO (Voigts, 1976; Brightman, 1984; Graves et al., 1998; King & Brazner, 1999). Macroinvertebrate metrics such as species richness and composition are widely used for biological monitoring because they integrate the effects of these various habitat changes (Rosenberg & Resh, 1993).

The most pronounced response of the macroinvertebrate community to nutrient-enrichment in WCA-2A was a shift in taxonomic composition. Dominant taxa at reference sites were similar to those described previously for minimally-impacted areas of the Everglades, which are rich in dipteran, odonate, coleopteran, and gastropod taxa and also contain large numbers of the amphipod *Hyallolella azteca* (Gunderson & Loftus, 1993). Thus, while even the interior of WCA-2A has likely been influenced somewhat by nutrient enrichment, the structure of the invertebrate community in this area provides a reasonable approximation of the reference condition for the system. Taxa characteristic of oligotrophic conditions in the marsh were replaced in P-enriched areas by taxa such as the dipteran *Chironomus* and the oligochaetes *Dero* and *Haemonais* that have been shown to respond positively to eutrophication in other aquatic systems (see Tables 2 and 3). These changes occurred at sites where average water-column TP concentrations exceed 10 ug L^{-1} and where other P-induced changes in water quality (e.g., reduced water-column DO) and macrophyte and periphyton abundance and species composition are evident. Changes in macroinvertebrate taxonomic composition along the enrichment gradient were likely due in part to these nutrient-induced changes in the marsh environment as discussed below.

Invertebrate composition within a wetland is affected by vegetation density (e.g., open-water vs. heavily vegetated) and composition (e.g., submersed vs. emergent) (Voigts, 1976). For example, Rader (1994) found macroinvertebrate communities in WCA-2A to differ between emergent and slough habitats at the same location. Changes in invertebrate communities along wetland enrichment gradients may be due partly to changes in vegetation (King & Brazner, 1999). Vegetation changes along the WCA-2A enrichment gradient were pronounced both in terms of the physical habitat and food composition and quality available to the macroinvertebrate community. Sawgrass stands were the most common habitat in reference areas of WCA-2A while cattail stands accounted for almost all vegetative cover in highly enriched areas. Sawgrass tissue has a higher C:N ratio than cattail, and the N and P content of both species increases with enrichment in this marsh (Miao & Debusk, 1999). These differences in nutrient content affect the decomposability of macrophyte detritus and the suitability of this material as food for different invertebrate species. Most reference sites also contained wet-prairie-slough habitats containing characteristic macrophytes (*Eleocharis*, *Nymphaea*, *Utricularia*) and abundant periphyton (McCormick et al., 1998). These habitats are highly productive, structurally complex, and contain an abundant and characteristic macroinvertebrate community (Rader, 1994). Although the cyanobacteria that dominate the periphyton community in reference areas may be a poor food source for invertebrates, as suggested by Rader & Richardson (1992), this community is also rich in diatoms (McCormick & O'Dell, 1996), which are a high quality food for many invertebrates (Lamberti, 1996). The extent of open-water habitat declined with enrichment in the marsh, and vegetation characteristic of wet prairie and sloughs was absent from highly enriched areas (Vaithyanathan & Richardson, 1999; McCormick et al., 2001a).

Nutrient-induced declines in water-column DO are a major factor influencing macroinvertebrate responses to eutrophication (Welch, 1980). Phosphorus enrichment in WCA-2A has been shown to cause declines in water-column DO concentrations as evidenced by the point DO data presented here and diel DO profiles presented by McCormick & Laing (2003). In the latter study, reference sites exhibited strong diel fluctuations in DO with concentrations approaching or exceeding saturation during the day and rarely falling below 2 mg L⁻¹ at night. By contrast, diel fluctuations at enriched and highly enriched sites were dampened and concentrations frequently approached 0 mg L⁻¹. While no information could be found on the oxygen tolerance of oligotrophic taxa identified here, many of the dominant taxa in enriched areas of the marsh are known to be tolerant of low DO (see Tables 2 and 3). Similarly, other common taxa such as the amphipod *Hyalolella azteca* that were less affected by enrichment have also been shown to tolerate periodic low DO but not protracted anoxia (Nebeker et al., 1992). In their assessment of macroinvertebrate changes along the enrichment gradient in WCA-2A, Rader & Richardson (1994) concluded that nutrient-induced declines in DO should not affect Everglades invertebrates because this community “is already adapted to fluctuating oxygen concentrations (pg 141).” This assessment ignores a key distinction between reference sites sampled here, which may experience transient (e.g., a few hours before sunrise) periods of low DO, and enriched and highly enriched sites, which experience protracted periods (e.g., days) of low or no DO in the water-column (McCormick & Laing, 2003). Invertebrates vary widely in their ability to tolerate low DO conditions, and the degree of tolerance is affected by the duration of low DO events (Davis, 1975). Even sublethal declines in DO can eliminate a species from a habitat if reproduction or feeding is impaired (Davis, 1975).

Functional shifts in the macroinvertebrate community were also detected along the gradient and may reflect changes in the quantity and quality of different food resources. However, these shifts were not so pronounced as to suggest the complete loss of any food category. The areal biomass and productivity of periphyton has been shown to decline along P enrichment gradients in the Everglades with concurrent shifts in taxonomic composition (McCormick et al., 1998; McCormick et al., 2001b). By contrast, the quantity of macrophyte detritus is likely greater in enriched areas of the marsh as a result of increased macrophyte cover and biomass. The suitability of this detritus for different invertebrate functional groups also may change along the gradient as a result of changes in macrophyte species composition and nutrient content already discussed. Functional group classifications such as that used here are rather general and may mask more specific differences in the feeding strategy of individual species that might be affected by changes in food resources along the gradient.

The total density of invertebrates in the marsh as determined by sweep sampling increased nearly 2-fold with enrichment while taxa richness and diversity was unchanged. The positive relationship between invertebrate densities and enrichment documented with sweep sampling is consistent with an increase in overall marsh productivity. Wetland invertebrate densities typically increase with enrichment up to the point where adverse changes in water quality (e.g., low DO) exceed the tolerances of most organisms (Rosenberg & Resh, 1993). Changes in macroinvertebrate species richness and diversity in response to enrichment are less predictable; in some cases, richness may also increase in response to modest enrichment and then decline as habitat and water quality conditions deteriorate further. The lack of change in species richness and diversity with enrichment found here did not indicate a lack of impact to the

macroinvertebrate community but rather was the result of one set of pollution-sensitive taxa being replaced by another assemblage adapted to the enriched environment.

Hester-Dendy samplers were used in this study to provide a standardized substrate for invertebrate sampling. Compared with sweep sampling, HD samplers offer the advantage of ease of deployment and processing. However, the habitat complexity of this sampler is low compared with that of the surrounding marsh, which may explain why fewer invertebrate species were collected on these samplers than by sweep sampling. Furthermore, because these samplers were consistently placed in the water-column just above the sediment surface, invertebrate changes on these samplers along the gradient only reflected impacts near the sediment-water interface. These limitations may explain why macroinvertebrate responses on these samplers differed in several respects from those observed in sweep samples. Macroinvertebrate densities on HD samplers declined nearly 2-fold with enrichment and similar declines were found for taxa richness and diversity. Taxonomic shifts also differed in some respects from those observed in the surrounding marsh, as the abundance of oligochaetes and other pollution-tolerant taxa peaked at enriched sites and then declined at highly enriched sites, and other dominant taxa (e.g., the amphipod *Hyallela*) that were relatively insensitive to enrichment in sweep samples also declined in highly enriched areas. These changes may reflect a greater deterioration in conditions near the sediment-water interface than in other microhabitats at highly enriched sites. For example, floating material (e.g., periphyton-covered *Typha* stems) at highly enriched sites can contain an abundance of invertebrates (McCormick, pers. obs.), and habitats such as this near the air-water interface may be considerably higher in DO than those near the sediment surface. Along this same gradient, Rader & Richardson (1994) found differences in macroinvertebrate responses in

sediment cores and sweep samples that are consistent with those shown here between HD samplers and sweeps. In conclusion, while HD samplers provided a fairly accurate indication of where significant changes in the macroinvertebrate community occurred along the gradient and may have mimicked changes that were occurring near the sediment surface, they did not provide an integrated picture of the changes in the surrounding marsh. Our findings are similar to those of Turner & Trexler (1997), who compared HD samplers to other invertebrate sampling methods in the Everglades.

Results presented here differ in certain respects from those of Rader & Richardson (1994), who sampled invertebrates along this same gradient during 1990 and 1991 using both sweep sampling and soil coring. These investigators found that species richness and diversity in sweep samples increased significantly with enrichment. They also documented an increase in areal density of greater than 6-fold, far in excess of the increases shown here. Based on these findings, they concluded that enrichment had not produced harmful effects on the invertebrate community in WCA-2A. However, these investigators limited their sampling to open-water habitats, which are common at reference sites but rare in enriched areas. By contrast, the sweep sampling described here was conducted on a habitat-weighted basis to fully account for the habitat changes caused by enrichment in this marsh. Macroinvertebrate communities in open-water habitats tend to be more species-rich than those in adjacent macrophyte stands and possess a relatively distinct species composition (Rader, 1994). It is possible that enrichment stimulates invertebrate abundance and diversity in open-water habitats (Rader & Richardson, 1992) while concurrently depressing these metrics in emergent macrophyte stands at the same location. Indeed, these investigators recognized that invertebrate responses might be habitat-specific as

they concluded that enrichment could have harmful effects on the invertebrate community as open-water habitats were replaced by emergent macrophyte stands in enriched areas of the marsh. Our sampling design accounted for this vegetation shift.

Implications for Everglades Regulation and Management

Using several metrics, these data show that the taxonomic and, to a lesser extent, the functional composition of the WCA-2A macroinvertebrate community was altered in areas of the marsh with elevated P concentrations compared with the reference condition. These shifts occurred with no detectable change in species richness or diversity and an increase in total macroinvertebrate abundance. The Everglades Forever Act requires the state of Florida to establish a P criterion for the Everglades that, “in no case shall such phosphorus criterion allow waters in the Everglades Protection Area to be altered so as to cause an imbalance in the natural populations of aquatic flora or fauna”. Thus, the loss of natural populations of invertebrates (i.e., those common in reference areas) in enriched areas and their replacement by species not indicative of the minimally impacted Everglades can represent an imbalance in the macroinvertebrate community, even in the absence of a change in species richness and diversity. This interpretation is consistent with the concept of “biotic integrity”, which is “the capability of supporting and maintaining a balanced, integrated, adaptive community of organisms having a species composition, diversity, and functional organization comparable to that of natural habitat of the region” (Karr & Dudley, 1981). This approach to evaluating ecosystem condition, which emphasizes the taxonomic and functional organization of the native community, has supplanted traditional metrics such as species diversity as the basis for environmental impact assessments

(e.g., USEPA, 1990b). This approach does not presuppose that increases in species richness and diversity above the reference state constitute a condition of “no impact” in P-enriched areas of the Everglades as concluded by Rader & Richardson (1994). Indeed, protection of the oligotrophic nature of this ecosystem is consistent with a community characterized by low densities, production, and diversity of consumers (e.g., Turner et al., 1999). Furthermore, the replacement of species indicative of reference conditions with those adapted to enrichment as shown here, may have a negligible effect on species diversity in the marsh but may constitute an impairment of the biotic integrity of the ecosystem. Thus, conclusions regarding the extent of impact can differ depending on whether the goal of ecosystem management is simply to maintain diversity and maximize abundance or to preserve the taxonomic and functional characteristics of the native community.

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Table 1 – Classifications of common functional group encountered designations based on food and microhabitat preference. Abbreviations used in the text are provided in parentheses.

Functional group	Food	Microhabitat
Collector-filterer/suspension feeders (Col-filtr/susp fdr)	Fine particulate organic matter (FPOM)	Surfaces
Epi-benthic collector-gatherer/deposit feeders (Epi col-gath/dep fdr)	FPOM	Sediment associated
Sub-benthic collector-gatherer/deposit feeders (Sub col-gath/dep fdr)	FPOM	Subsurface
Shredder	Coarse particulate Organic matter (CPOM)	Litter
Scraper	Periphyton, biofilms, and associated material	Surfaces
Predator	Live animals	Varied

Table 2 – See separate file.

Table 3 – See separate file.

Figure Captions

Fig. 1 – Location of WCA-2A and monitoring sites within the Everglades. Arrows indicate structures where enriched canal water is discharged into the marsh.

Fig. 2 – Environmental conditions along the WCA-2A gradient. Points are means \pm 1 SE.

Symbol legend: canal (closed circle); highly enriched sites (closed triangle); enriched sites (shaded square); reference sites (open circle). Other habitats (Fig. 2B) primarily include willow heads and other brush. Nutrient Status: R = reference; E = enriched; HE = highly enriched. See text for further details on site classification.

Fig. 3 – Total macroinvertebrate density, richness, and diversity in sweep and HD samples at reference (open bars), enriched (shaded bars), and highly enriched (closed bars) sites. Bars are means \pm 1 SE. Asterisks show significant difference from the reference condition ($p < 0.05$, Dunnett's).

Fig. 4 – Percent abundance of dominant invertebrate classes in sweep samples. See Fig. 3 for legend.

Fig. 5 – Percent abundance of dominant insect orders in sweep samples. See Fig. 3 for legend.

Fig. 6 – Percent abundance of dominant invertebrate classes in HD samples. See Fig. 3 for legend.

Fig. 7 – Percent abundance of dominant insect orders in HD samples. See Fig. 3 for legend.

Fig. 8 – Separation of macroinvertebrate communities in sweep samples collected at reference (open circle), enriched (shaded square), and highly enriched (closed triangle) sites.

Fig. 9 – Abundance of common taxa in sweep samples that separated reference from enriched and highly enriched sites. See Fig. 3 for legend.

Fig. 10 – Separation of macroinvertebrate communities in HD samples collected at reference (open circle), enriched (shaded square), and highly enriched (closed triangle) sites. PCA was performed with (A) and without (B) data from the March 1994 sampling date.

Fig. 11 – Abundance of common taxa in HD samples that separated reference from enriched and highly enriched sites. See Fig. 3 for legend.

Fig. 1

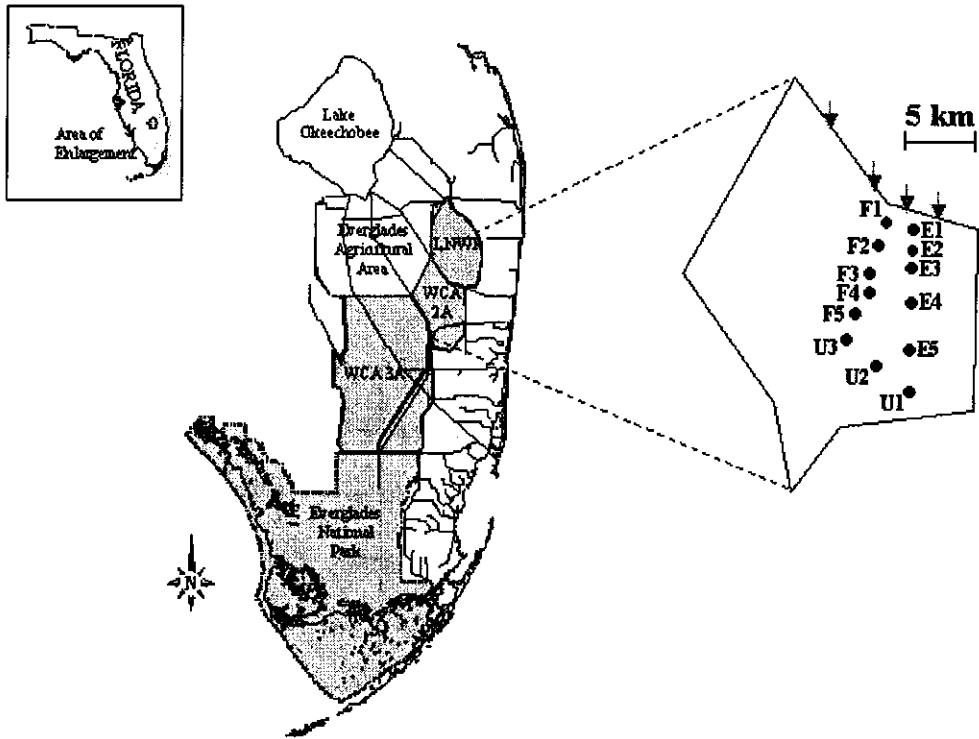


Fig. 2

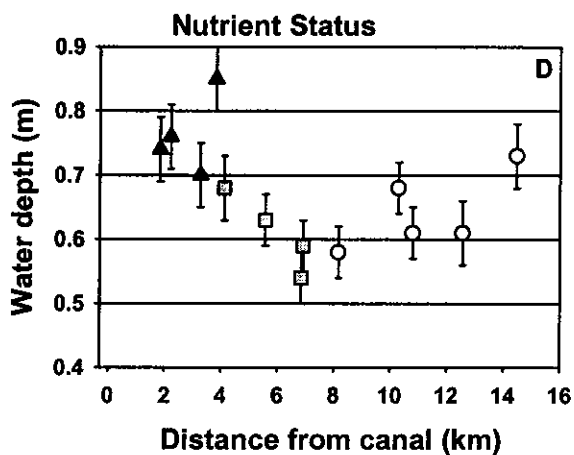
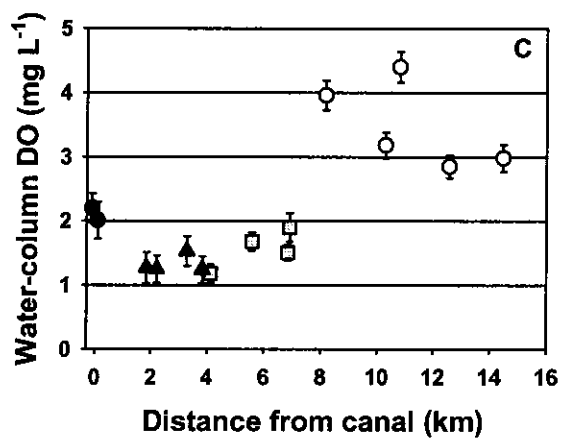
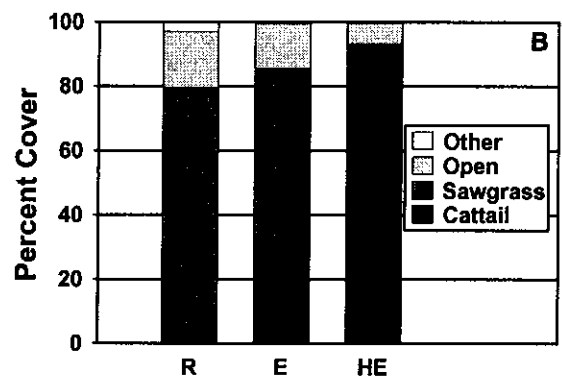
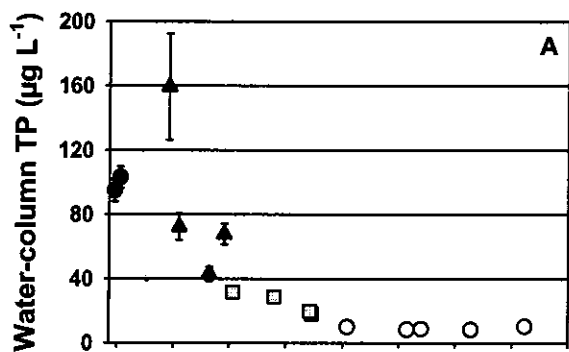


Fig. 3

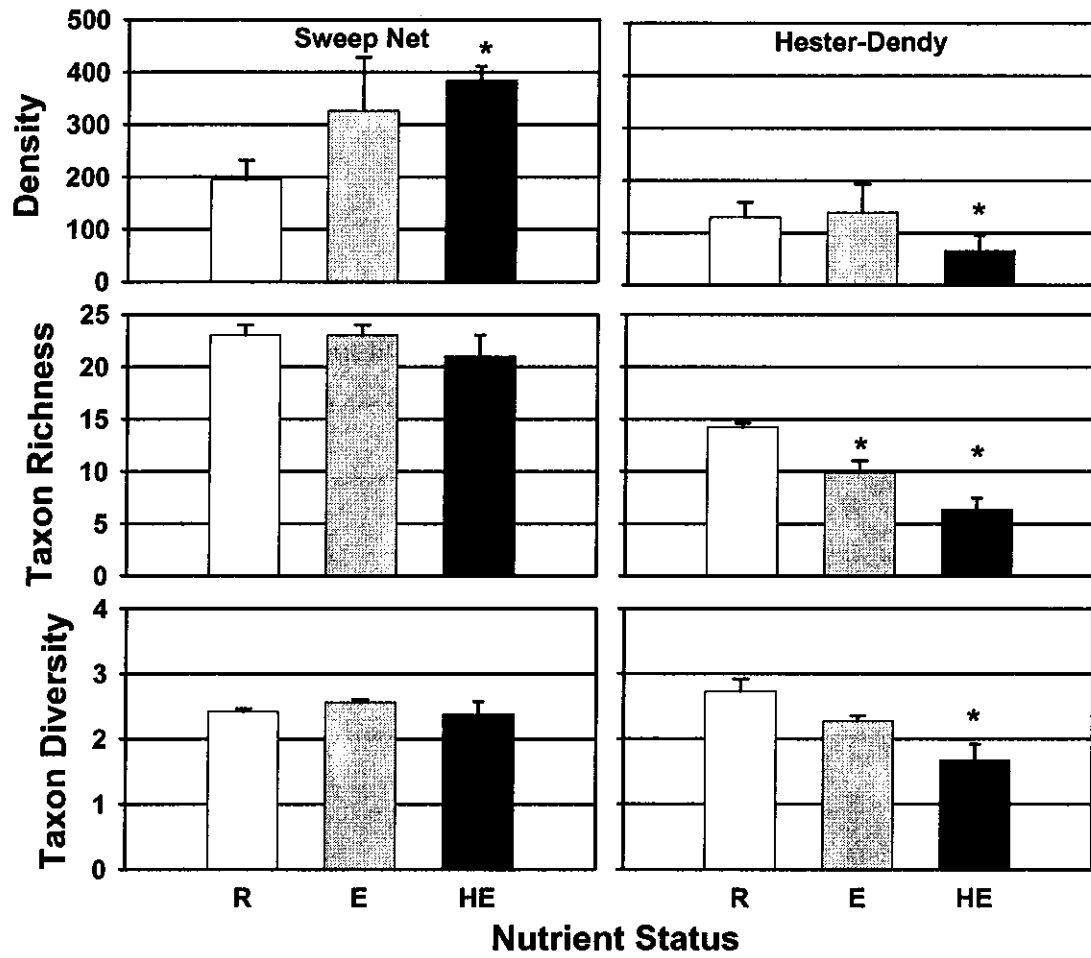


Fig. 4

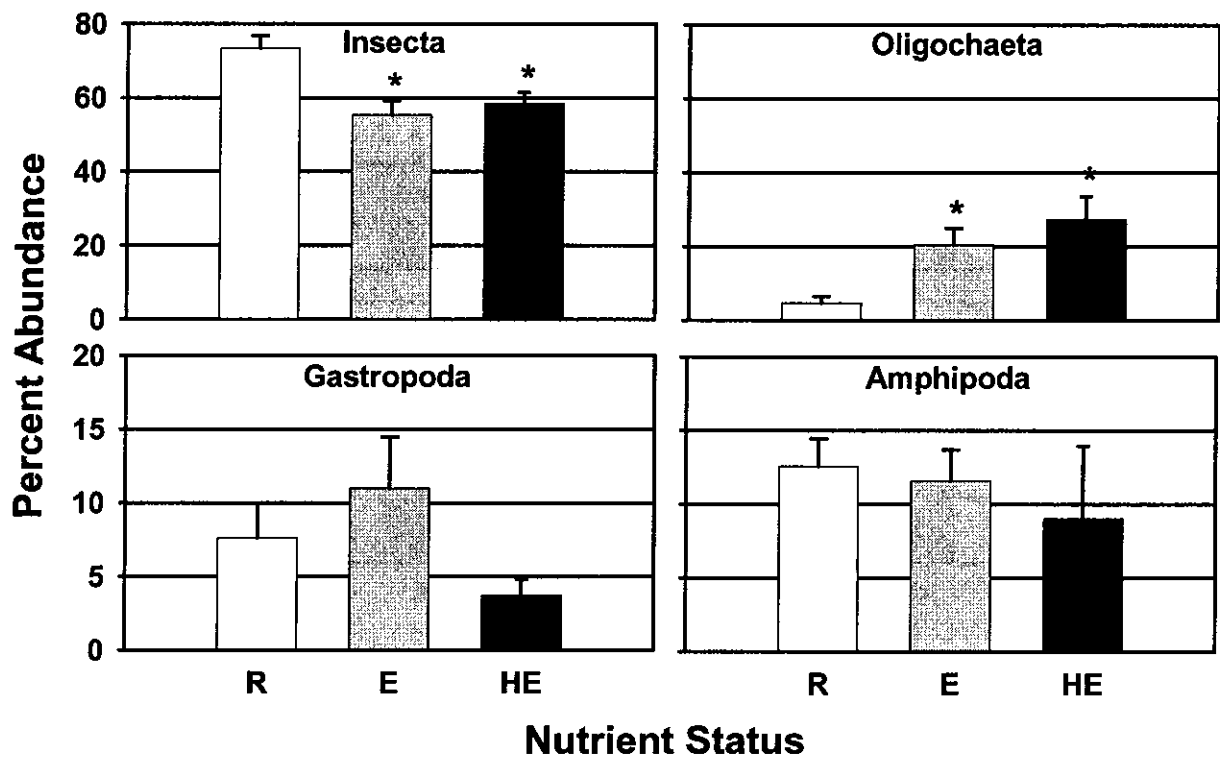


Fig. 5

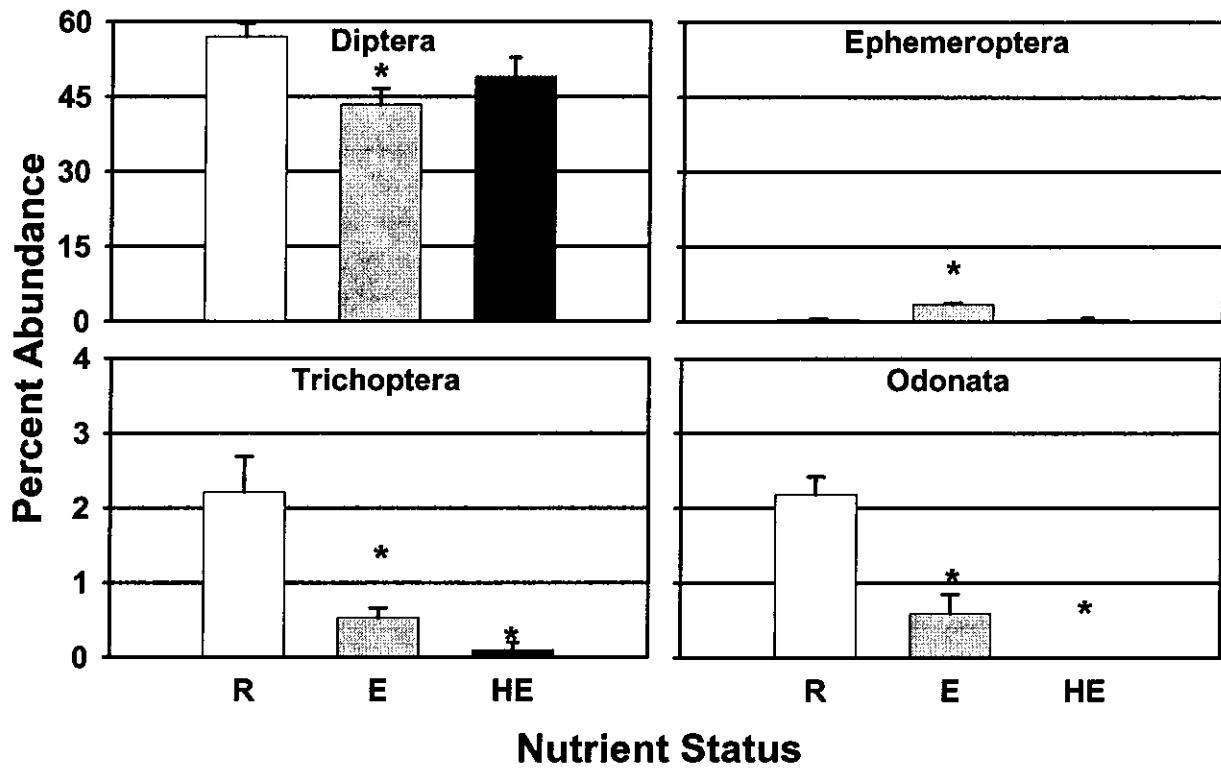


Fig. 6

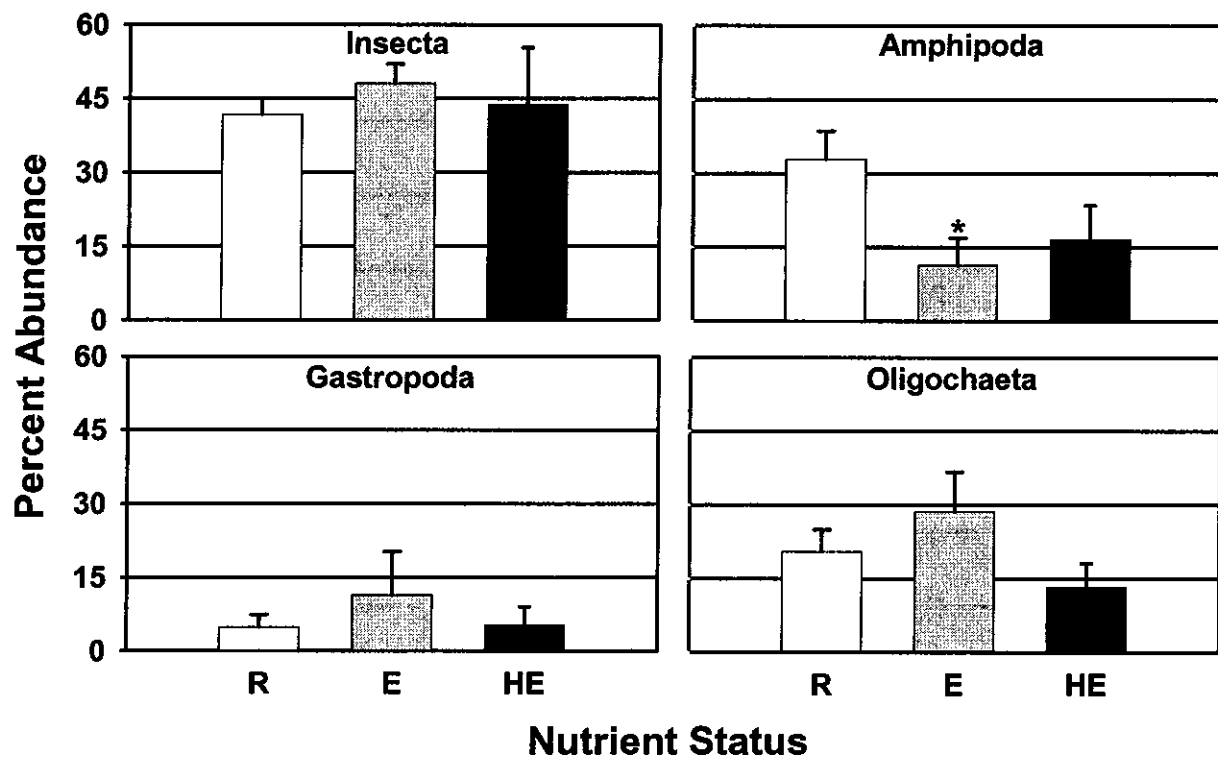


Fig. 7

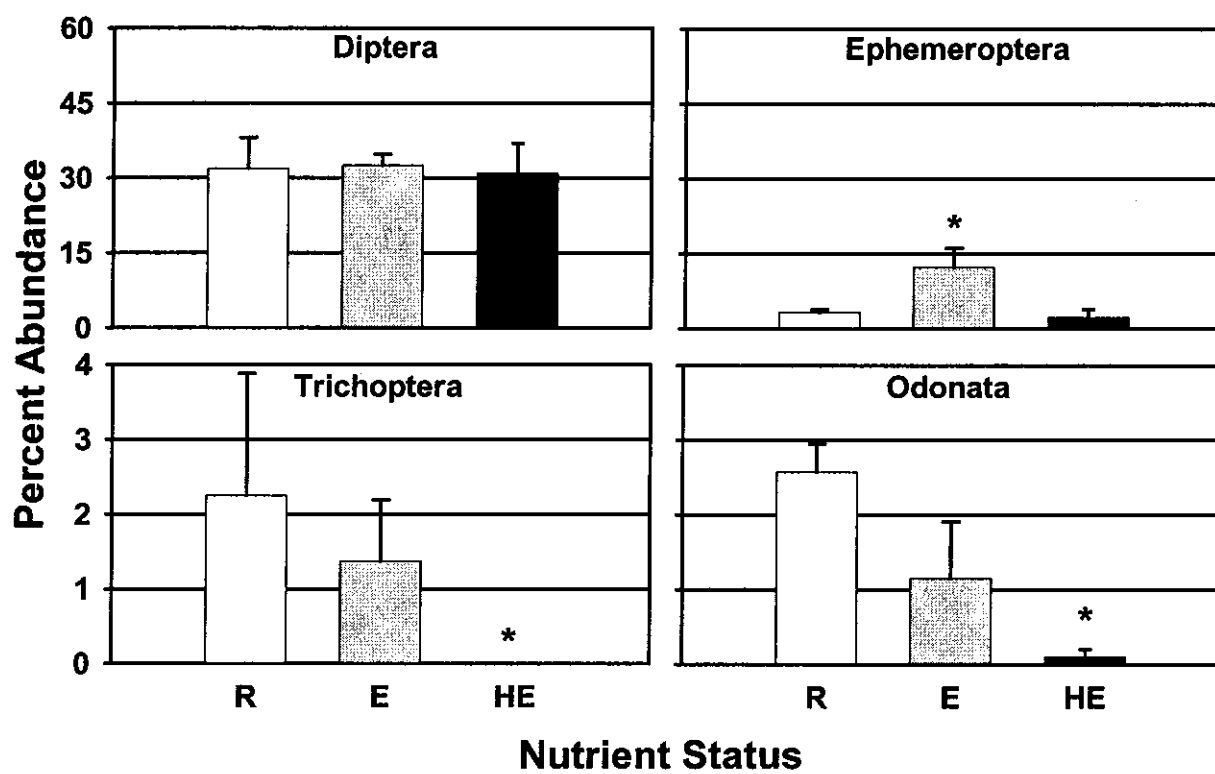


Fig. 8

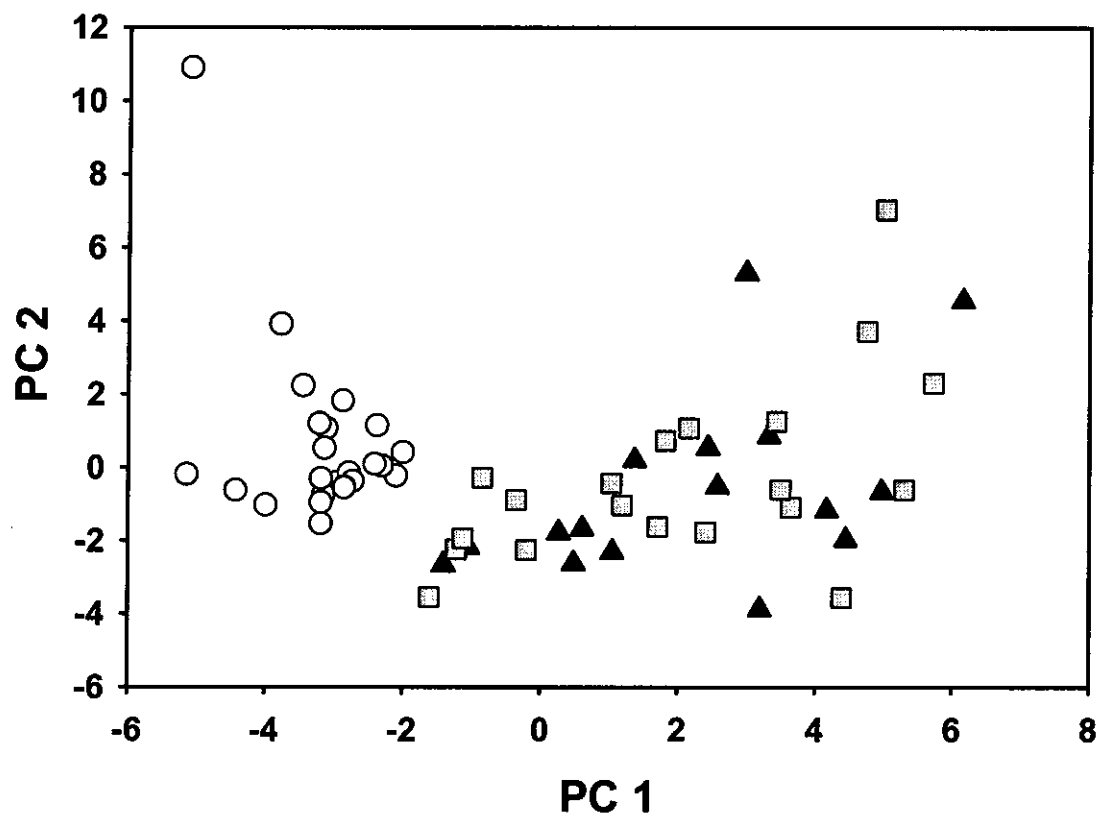


Fig. 9

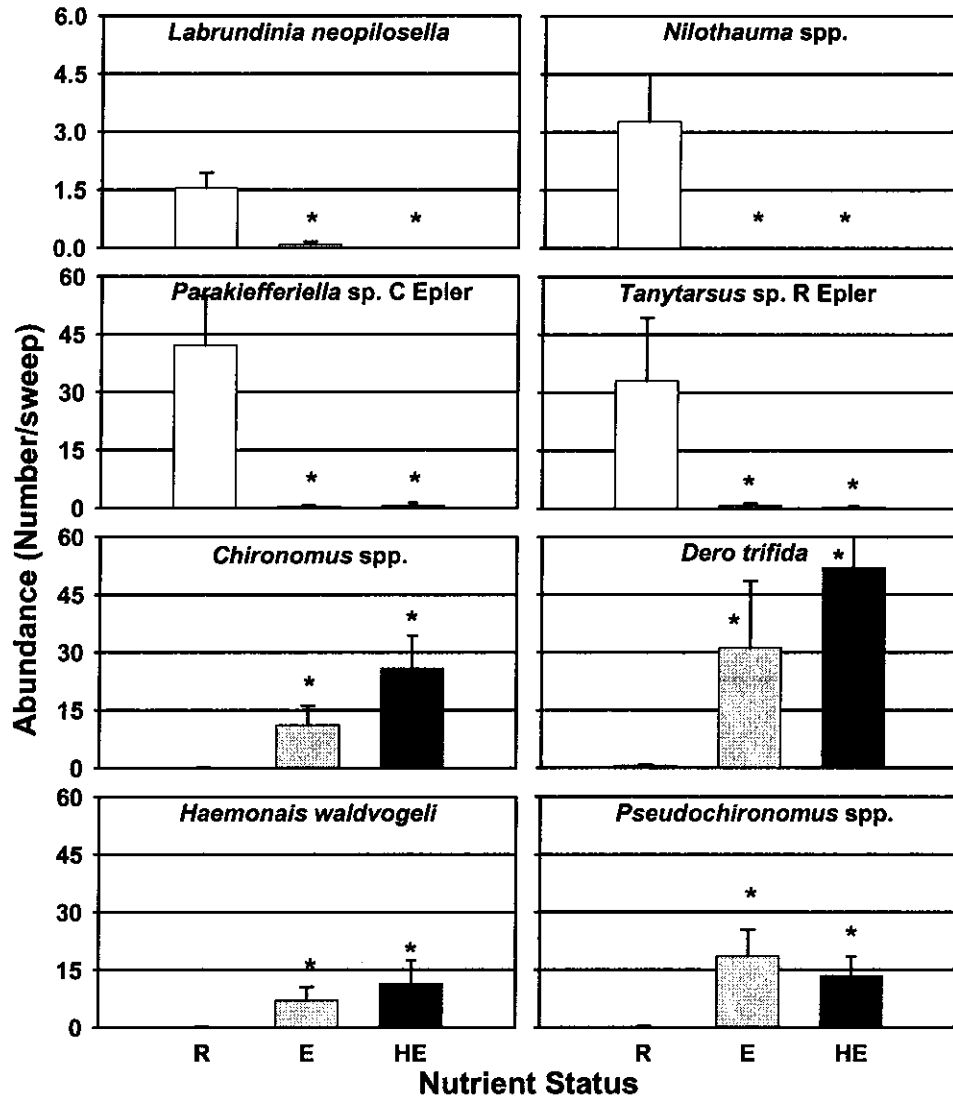


Fig 10

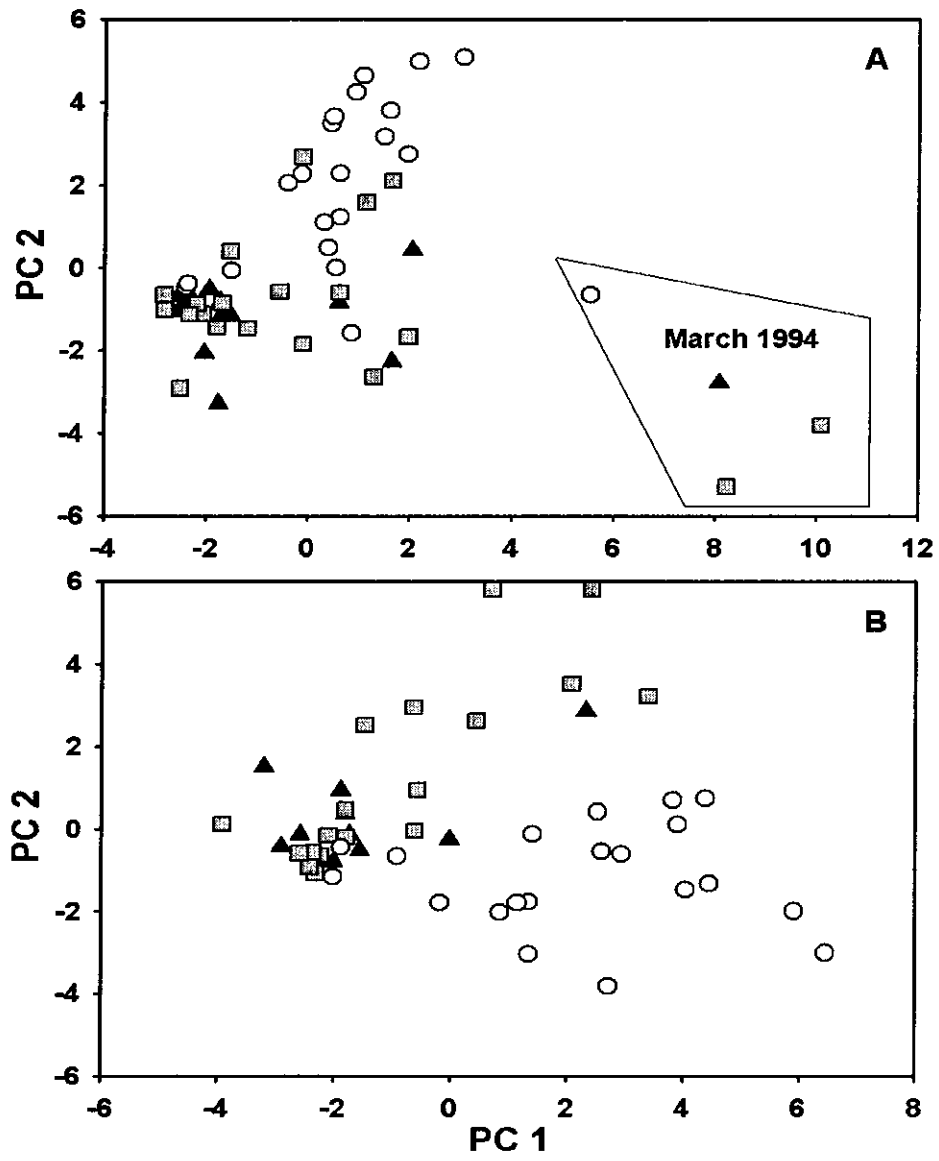


Fig. 11

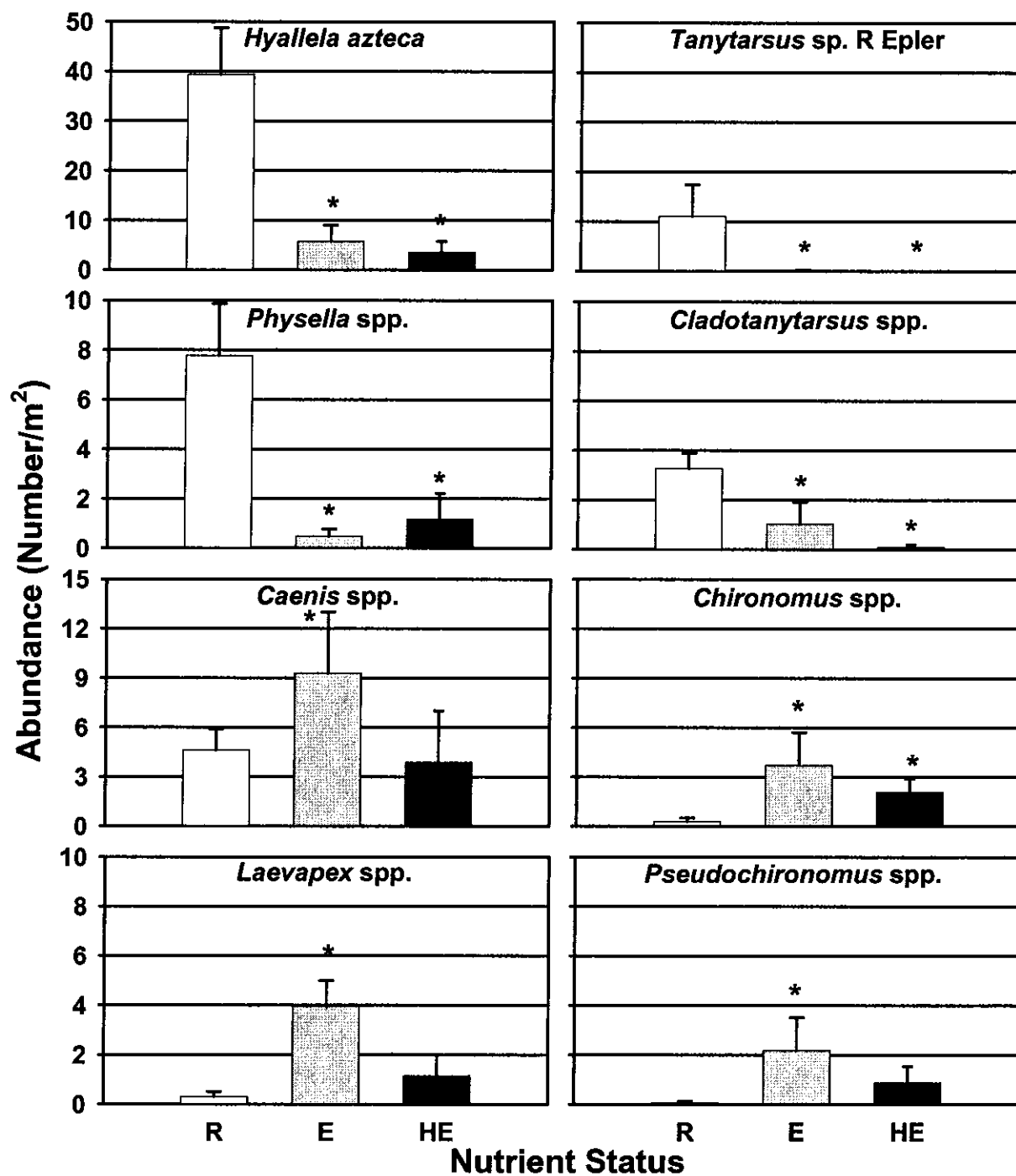


Table 2 – Autecological characteristics of taxa in sweep samples determined by PCA to be associated with reference and enriched conditions. See Table 1 for functional group descriptions. Pollution-tolerance references footnoted.

Taxon (Order, Family)	Functional Group	Pollution Tolerance
Reference conditions:		
<i>Cladotanytarsus</i> spp. (Diptera, Chironomidae)	Epi col-gath/dep fdr	Oligosaprobic ⁶
<i>Labrundinia neopiosella</i> (Diptera, Chironomidae)	Predator	Intolerant of any enrichment ²
<i>Nanocladius</i> spp. (Diptera, Chironomidae)	Epi col-gath/dep fdr	Characteristic of unimpaired waters ⁹
<i>Nilothauma</i> spp. (Diptera, Chironomidae)	Epi col-gath/dep fdr	Characteristic of unimpaired waters ⁹
<i>Parachironomus alatus</i> (Diptera, Chironomidae)	Predator	Nutrient/anoxia intolerant ³
<i>Parakiefferiella</i> sp. C Epler (Diptera, Chironomidae)	Epi col-gath/dep fdr	
<i>Paratanytarsus</i> sp. B Epler (Diptera, Chironomidae)	Epi col-gath/dep fdr	
<i>Polypeditum halterale</i> grp. (Diptera, Chironomidae)	Shredder	Intolerant of heavy enrichment ²
<i>Tanytarsus</i> sp. R Epler (Diptera, Chironomidae)	Col-filtr/susp fdr	
<i>Cernotina</i> spp. (Trichoptera, Polycentropodidae)	Predator	
<i>Oxyethira</i> spp. (Trichoptera, Hydroptilidae)	Epi col-gath/dep fdr	Intolerant of any enrichment ² , Characteristic of unimpaired waters ⁹

Enriched conditions:		
<i>Chironomus</i> spp. (Diptera, Chironomidae)	Epi col-gath/dep fdr	Tolerant of enrichment and anoxia ^{4,6,10}
<i>Dicortendipes modestus</i> (Diptera, Chironomidae)	Epi col-gath/dep fdr	Tolerant of enrichment and anoxia ^{4,5}
<i>Goeldichironomus holoprasinus</i> (Diptera, Chironomidae)	Epi col-gath/dep fdr	Prefers organic enrichment ^{4,6}
<i>Larsia decolorata</i> (Diptera, Chironomidae)	Predator	
<i>Polypedilum trigonum</i> (Diptera, Chironomidae)	Epi col-gath/dep fdr	
<i>Pseudochironomus</i> spp. (Diptera, Chironomidae)	Epi col-gath/dep fdr	Characteristic of unimpaired waters ⁹
<i>Tanyptus carinatus</i> (Diptera, Chironomidae)	Predator	Tolerant of organic enrichment ⁵
<i>Tanytarsus</i> sp. G Epler (Diptera, Chironomidae)	Col-filtr/susp fdr	
<i>Tanytarsus</i> spp. (Diptera, Chironomidae)	Col-filtr/susp fdr	
<i>Caenis</i> spp. (Ephemeroptera, Caenidae)	Epi col-gath/dep fdr	Certain species tolerant of enrichment ¹
<i>Dero lodei</i> (Tubificida, Naididae)	Sub col-gath/dep fdr	Tolerant of enrichment and anoxia ^{5,7}
<i>Dero pectinata</i> (Tubificida, Naididae)	Sub col-gath/dep fdr	Tolerant of enrichment and anoxia ^{5,7}
<i>Dero trifida</i> (Tubificida, Naididae)	Sub col-gath/dep fdr	Tolerant of enrichment and anoxia ^{5,7}
<i>Haemonais waldvogeli</i> (Tubificida, Naididae)	Sub col-gath/dep fdr	Tolerant of enrichment ⁶
<i>Pristina aequiseta</i> (Tubificida, Naididae)	Sub col-gath/dep fdr	

References: ¹Berner & Prescador, 1988; ²Beck, 1954; ³Beck, 1977; ⁴Epler, 1995; ⁵Hart & Fuller, 1974; ⁶Johnson et al., 1993; ⁷Pennak, 1989; ⁸Rudolph & Strom, 1990; ⁹Rutter, 2003; ¹⁰Saether, 1979.

Table 3 – Autecological characteristics of taxa in HD samples determined by PCA to be associated with reference and enriched conditions. See Table 1 for functional group descriptions. Pollution-tolerance references footnoted.

Taxon (Order, Family)	Functional Group	Autecology
Reference conditions:		
<i>Hyallela azteca</i> (Amphipoda, Hyalellidae)	Epi col-gath/dep fdr	Tolerant of moderate impairment ⁹ , Tolerant of periodic low DO ^{5,7,8}
<i>Ablabesmyia rhamphe</i> grp. (Diptera, Chironomidae)	Predator	Intolerant of heavy enrichment ² , Characteristic of unimpaired waters ⁹
<i>Cladotanytarsus</i> spp. (Diptera, Chironomidae)	Epi col-gath/dep fdr	
<i>Parakiefferiella</i> sp. C Epler (Diptera, Chironomidae)	Epi col-gath/dep fdr	
<i>Polypedilum halterale</i> grp. (Diptera, Chironomidae)	Epi col-gath/dep fdr	Intolerant of heavy enrichment ² , Tolerant of moderate impairment ⁹
<i>Polypedilum trigonum</i> (Diptera, Chironomidae)	Epi col-gath/dep fdr	
<i>Tanytarsus</i> sp. R Epler (Diptera, Chironomidae)	Col-filtr/susp fdr	
<i>Tanytarsus</i> sp. T Epler (Diptera, Chironomidae)	Col-filtr/susp fdr	
<i>Physella</i> spp. (Gastropoda, Physidae)	Grazer	
<i>Ischnura</i> spp. (Odonata, Coenagrionidae)	Predator	
<i>Helobdella triseriatis</i> (Rhynchobdellida, Glossiphoniidae)	Predator	
<i>Ceratomyxa</i> spp. (Trichoptera, Polycentropodidae)	Predator	

Enriched conditions:		
<i>Chironomus</i> spp. (Diptera, Chironomidae)	Epi col-gath/dep fdr	Tolerant of enrichment and anoxia ^{4,6,10}
<i>Pseudochironomus</i> spp. (Diptera, Chironomidae)	Epi col-gath/dep fdr	Characteristic of unimpaired waters ⁹
<i>Tanytarsus</i> sp. G Epler (Diptera, Chironomidae)	Col-filtr/susp fdr	
<i>Caenis</i> spp. (Ephemeroptera, Caenidae)	Epi col-gath/dep fdr	Certain species tolerant of enrichment ¹
<i>Ferrissia hendersoni</i> (Gastropoda, Ancyliidae)	Scraper	
<i>Laevapex</i> spp. (Gastropoda, Ancyliidae)	Scraper	
<i>Dero trifida</i> (Tubificida, Naididae)	Sub col-gath/dep fdr	Tolerant of enrichment and anoxia ^{5,7}
<i>Haemonais waldvogeli</i> (Tubificida, Naididae)	Sub col-gath/dep fdr	

References: ¹Berner & Prescador, 1988; ²Beck, 1954; ³Beck, 1977; ⁴Epler, 1995; ⁵Hart & Fuller, 1974; ⁶Johnson et al., 1993; ⁷Pennak, 1989; ⁸Rudolph & Strom, 1990; ⁹Rutter, 2003; ¹⁰Saether, 1979.

