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RESPONSE OF MACROINVERTEBRATES AND SMALL FISH TO NUTRIENT ENRICHMENT IN THE NORTHERN EVERGLADES

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Abstract: The northern Everglades (Water Conservation Area 2A) annually receives an excess addition of 60 M tons of phosphorus and 1814 M tons of nitrogen from agricultural run-off. During 1990–91, invertebrates were collected from replicate sweep and core samples at eight sites along the nutrient enrichment gradient in Water Conservation Area 2A (WCA-2A). Species richness, Shannon's diversity, the number of unique species, and the density of invertebrates and small fish were all greater within enriched and intermediately enriched open water habitats than unenriched sloughs. Sorenson's taxonomic similarity index was significantly different between enriched and unenriched areas. Ostracods in particular were 14 times more abundant in the enriched area than at unenriched sites. The freshwater shrimp (*Palaemonetes paludosus*) was the only common species with lower densities in enriched than unenriched areas. However, the trophic structure or percent composition of grazers, predators, and collector-gatherers and the number of species within taxonomic orders and functional feeding groups was very similar among sites along the nutrient enrichment gradient. Higher invertebrate and small fish diversity and density within enriched sites indicates that nutrient enrichment has not caused direct harmful foodweb effects that may adversely influence higher trophic levels (e.g., wading birds). Assuming, however, that nutrients can cause cattails to overgrow and eliminate sloughs, the centers of biological diversity in the Everglades, then nutrient enrichment may have harmful indirect effects.

Key Words: nutrient enrichment, everglades, invertebrates, fish.

INTRODUCTION

The Everglades of Florida covers approximately 11,000 km^2 and is one of the largest freshwater wetlands in the world. Historically, water flowed south from Lake Okeechobee through open water sloughs and marshes dominated by sawgrass (*Cladium jamaicense* Crantz). Today, a series of dikes and canals divides the Everglades into three regions: 1) Everglades National Park, 2) the Everglades Agricultural Areas, and 3) the Water Conservation Areas. Water flow is regulated by dams at entrance points located along the northern rim of Everglades National Park and the Water Conservation Areas. Human growth and development is the source of numerous environmental problems for the Everglades, including hydroperiod alterations, chemical pollutants, exotic invasions, and the interruption of the periodicity and intensity of natural disturbances (e.g., fires and floods). Nutrient enrichment of the Everglades from agricultural runoff is, however, one of the most highly publicized and controversial issues (Barber 1991, Campbell-Mohn 1991).

Over the past three decades, inputs of N and P from the Everglades Agricultural Areas into Water Conservation Area 2A (WCA-2A) have increased 12.4 and 10.0 times, respectively (Craft and Richardson 1993). Approximately 1814 metric tonnes (t) of N and 60 t of P enter the northern end of WCA-2A each year

(SFWMD 1992). These inputs have created a nutrient enrichment gradient that extends from northern enriched areas approximately seven kilometers into unenriched habitats of WCA-2A. Nutrient enrichment is of particular concern because of its potential impact on the Everglades foodweb (Campbell-Mohn 1991, SFWMD 1992, Davis 1994). In lakes and streams, excess nutrients often have caused a decline in community diversity associated with localized species extinction and an increased abundance of pollution-tolerant organisms (Wetzel 1983, Mason 1991). Alterations at the base of the foodweb, often amongst invertebrate populations, can influence higher trophic levels (Mason 1991). Over the past three decades, wading bird populations in the Everglades have declined in numbers by as much as 90% (Robertson and Kushlan 1984). Some authors suggest that alterations near the base of the foodweb (invertebrates), caused by nutrient laden agricultural runoff, may have adversely affected higher trophic levels, including wading bird populations (e.g., Gleason and Spackman 1974, Campbell-Mohn 1991).

The objective of this research was to determine changes in invertebrate and small fish assemblages across eight sites along a nutrient enrichment gradient in WCA-2A. We sought to answer the following question. How does the diversity, abundance, and trophic structure of invertebrates and small fish in open water habitats change along the nutrient enrichment gradient in WCA-2A? We tested the hypothesis that macroinvertebrate diversity would be lower in enriched compared to unenriched habitats.

Compared to other members of the Everglades community (plants, birds, fish, and mammals), the macroinvertebrate assemblage remains relatively unknown. Most published research has been restricted to investigating the relationship between a few taxa (crayfish, shrimp, and apple snails) and the feeding ecology of birds and fish (Kushlan 1975, Kushlan and Kushlan 1979, Kushlan and Kushlan 1980, Kushlan et al. 1986).

METHODS

In 1990, eight sites were established along a transect running south through an enriched cattail marsh into unenriched open water sloughs (Figure 1). Invertebrates and small fish were sampled six times (10/90, 12/90, 2/91, 4/91, 6/91, and 9/91) for one year at each site. Three sampling dates were during the wet season (May–October) and three occurred during the dry season (November–April). To determine the impact of enrichment, the data from two sites located within enriched (C1 and D1), intermediately enriched (C2 and C3), and unenriched (C4 and C6) areas were combined and analyzed together. Sites D2 and C5 were excluded

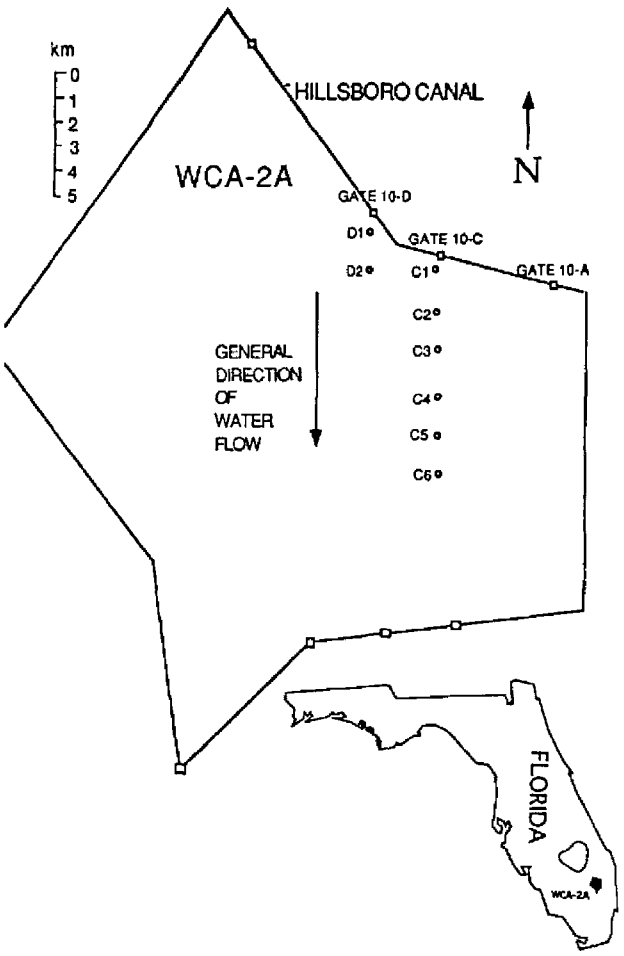

Figure 1. Water Conservation Area 2A (WCA-2A) showing the location of Hillsboro canal and the enriched (D1, D2, and C1), intermediately enriched (C2 and C3), and unenriched (C4, C5, and C6) sites along the nutrient enrichment gradient.

from the combined analysis because of missing data and because of the species-area relationship (Simberloff 1974). The species-area relationship states that species diversity will increase as the size of the area sampled increases. For example, we would expect species diversity to be higher within three combined unenriched sites (C4, C5, C6) compared to two combined enriched sites (C1 and D1) regardless of the effects of enrichment because of the larger area sampled by combining three sites. Therefore, when making diversity comparisons between impacted and unimpacted sites, it is important to compare similar sized areas or to combine the same number of sites.

The strength of our conclusions is based on comparing sites with similar environmental characteristics except for nutrient levels and comparing similar subhabitats (submerged vegetation and benthos) within each site. Environmental characteristics of each site are given in Table 1. We compared open water/slough

Table 1. Biological and physical characteristics for sites sampled from WCA-2A in the northern Everglades during 1990–91. "Submergents" represents the dominant vascular vegetation. "Hydroperiod" values are the number of weeks with no surface water. "PO_4-P" represents the mean concentration (μg/L) of soluble reactive P in surface waters and pore waters. Values in parentheses are standard deviations. See Qualls and Richardson (1991) for a description of methods used to determine P concentrations.

Site	Submergents	Hydroperiod	PO_4-P (12 cm)	PO_4-P (surface)
D1 (Enriched)	*Potamogeton* spp.	3–6	655 (769)	136 (160)
D2 (Enriched)	*Potamogeton* spp.	3–6	865 (287)	110 (171)
C1 (Enriched)	*Potamogeton* spp. *Hydrilla* spp.	3–6	188 (130)	113 (166)
C2 (Intermediate)	*Potamogeton* spp.	0	217 (247)	97 (223)
C3 (Intermediate)	*Potamogeton* spp.	0	140 (144)	28 (15)
C4 (Unenriched)	*Potamogeton* spp. *Utricularia* spp. *Chara* spp.	0	24 (10)	24 (15)
C5 (Unenriched)	*Potamogeton* spp. *Utricularia* spp. *Chara* spp.	0	28 (18)	24 (17)
C6 (Unenriched)	*Potamogeton* spp. *Utricularia* spp. *Chara* spp.	0	28 (14)	24 (17)

habitats containing submerged macrophytes and abundant growths of algae, since they are the centers of biological diversity in the Everglades (Gleason 1974, Rader and Richardson 1992).

Macroinvertebrates from four to eight samples were collected at each site on each date using a D-frame sweep net (2.0- 2.5 mm mesh). Sweep samples, compared to a variety of other techniques, are the best available method of determining the species composition and relative abundance of macroinvertebrates in wetlands (Cheal et al. 1993). Sweep samples filter a large volume of water, can trap mobile invertebrates and small fish that easily avoid other methods, and provide easy access to all available sub-habitats. Six sweep samples were taken during the dry season, but four samples were collected on the first sampling date and eight were collected at each site during the rainy season. Macroinvertebrate densities (number/m^3) were calculated by multiplying the distance of each sweep sample by the area of the net opening (0.04 m^2). Macroinvertebrates from sweep samples were preserved (4% formalin), sorted, and enumerated to the lowest feasible taxonomic unit.

In addition to sweep samples, we also used core samples to quantify invertebrates of the benthic habitat along the nutrient enrichment gradient. The top five cm of three to six benthic core samples were taken at each site on each date. All core samples were rinsed using a 100-μm mesh sieve and sorted using a dissecting microscope (magnification = 40×). Although all invertebrates from the first date (10–90) were completely sorted, core samples from the remaining five dates were subsampled. Subsampling consisted of gently washing each sample with tap water through two nested sieves with mesh diameters of 1 mm and 100 μm. All invertebrates retained on the 1-mm sieve were sorted and identified. Material on the 100-μm sieve was dispersed evenly over its surface and sectioned into 4 equal parts. One of the parts was randomly selected for sorting and enumeration. The density of invertebrates from core samples (number/m^2) was determined by multiplying the number of individuals by 260—the number of cm^2 per m^2 (10,000) divided by the area of the core opening (38.5 cm^2). Benthic invertebrates from core samples were not identified below order, or in some cases, family.

Statistical comparisons of Shannon's diversity index, species richness, the density of invertebrates and small fish, and Sorenson's similarity index were used to determine differences in the taxonomic structure of each site along the nutrient enrichment gradient. Shannon's diversity index (Shannon and Weaver 1963) was

calculated from sweep samples using data from the combined sites (D1+C1, C2+C3, and C4+C6). This analysis was based on a summary species list compiled across all sampling dates for each site and mean annual density estimates for each taxa. Three two-sample t-tests (Hutcheson 1970) were used to determine significant differences in Shannon's diversity among the enriched, intermediate, and unenriched sites (enriched versus intermediate, enriched versus unenriched, and intermediate versus unenriched). Because replicate samples were taken at each site on each date, a 1-way ANOVA and Newman-Keuls multiple comparison procedure (Zar 1984) were used to determine differences among sites (C1, D1, C2, C3, C4, C6) in 1) the mean number of species (richness) per sample, and 2) the mean density of invertebrates and small fish per sample. Species richness and total invertebrate and small fish densities (the dependent variables) were calculated for each individual sample on each date from each site. ANOVA was also used to determine differences in Sorenson's community similarity index (Magurran 1988) among enriched, intermediate, and unenriched sites. Sorenson's index was calculated for combined samples from each site within each area, enriched (C1 + D1), intermediate (C2 + C3), and unenriched (C4 + C6). Only samples taken during the wet season (4 of the 6 sampling dates) were used in this analysis because of high density estimates due to drying and the crowding of invertebrates into small pools. The analysis consisted of determining 1) the similarity of samples between sites within the same area (e.g., similarity of C1 and D1 within the enriched area) and 2) the similarity of samples between different areas (e.g., enriched versus unenriched). A 1-way ANOVA and Newman-Kuels comparisons were used to determine differences in community similarity among the combined within-area means (C1+D1, C2+C3, and C4+C5). When combined within-area means were not significantly different, the mean sample similarities 1) between the enriched and intermediately enriched areas (C1+D1 versus C2+C3), 2) between the enriched and unenriched areas (C1+D1 versus C4+C6), and 3) between the intermediate and the unenriched areas (C2+C3 versus C4+C6) were compared using the same procedure. An unpaired t-test was used to determine differences in the mean density of the freshwater shrimp *Palaemonetes paludosus* (Gibbes) between enriched and unenriched areas. Only samples collected from the three dates during the wet season were used in this analysis.

Differences in trophic structure among enriched, intermediate, and unenriched areas were determined by classifying each taxon according to its feeding mode and type of food consumed. The feeding classifications of Merritt and Cummins (1984) and Pennak (1989) were used to group each species into probable functional groups or trophic categories. Some taxa were assigned to more than one group. The first category listed represents the major feeding mode for taxa assigned to more than one category.

RESULTS

Taxonomic Structure

One hundred forty-eight taxa including 137 species of macroinvertebrates were collected during this study. Diptera, Coleoptera, Gastropoda, and Oligochaeta were the most diverse groups, comprising over 74% of the total number of taxa. All remaining classes and orders (see Appendix I) were represented by five or fewer taxa. Some groups (Chironomidae, Oligochaeta, Ostracoda, and Nematoda) were likely underrepresented because invertebrates from core samples were not identified below order or family. Several chironomid genera (e.g., *Tanytarsus, Polypedilum, Kieferulus,* and *Parakiefferiella*) are comprised of several undescribed species. This study used designations by Epler (1992) for undescribed larval chironomids.

Species richness was greatest in the enriched area despite a 1.47 times and 1.58 times greater sampling effort (mean volume of water sampled) at the intermediate and unenriched areas, respectively (Table 2). The mean number of taxa per sample (species richness) was significantly (ANOVA, d.f. = 5, P = 0.0001) greater at C1 (21.2) and D1 (16.0) than the unenriched sites, C4 (10.3) and C6 (10.5). The intermediate sites, C2 (12.6) and C3 (14.2) fell between the enriched and unenriched sites. The unenriched sites on each sampling date had the lowest species richness. Shannon's diversity index was higher (t-test, d.f. = 754 & 747, P < 0.001) in the intermediate area than both enriched and unenriched areas, which were not significantly (t-test, d.f. = 402, P = 0.15) different (Table 2). Although the enriched area had the highest species richness, Shannon's diversity was not significantly different from the unenriched area because of a lower evenness.

Except for Coleoptera, the number of species within classes and orders pooled across all samples and each sampling date was similar among sites (Table 3). Therefore, the primary difference in the average species richness among sites (as opposed to individual sample species richness) was the greater number of coleopteran species within enriched and intermediate areas than in unenriched sites.

The mean percent similarity per sample within the enriched (57.5 %), intermediate (56.1 %), and unenriched (57.7 %) areas, a measure of community similarity between sites within the same area, was not significantly different (ANOVA, d.f. = 2, P = 0.85).

Table 2. Taxonomic richness, Shannon's index of diversity (Log e) and evenness and the mean annual density of small fish and macroinvertebrates for sites sampled from WCA-2A during 1990–91. Brackets indicate mean annual density estimates excluding December when invertebrates were concentrated in shallow pools. Sampling effort is indicated by the total and monthly mean volume of water filtered. The distance from each site to the source of enrichment (Hillsboro Canal) is also shown.

Site	Richness	Diversity	Evenness	Mean Annual Denisty (No./m³)	Total/Mean Volume (L)	Distance from Canal (Km)
D1 (Enriched)	73	2.79	0.65	1466	1138/228	1.5
D2 (Enriched)	72	3.08	0.72	2875 [1056]	1672/279	3.2
C1 (Enriched)	85	2.98	0.67	2482	2055/343	1.4
C2 (Intermediate)	80	3.22	0.73	590	2440/407	3.5
C3 (Intermediate)	67	3.19	0.76	545	2600/433	5.1
C4 (Unenriched)	50	2.94	0.75	266	2560/427	6.9
C5 (Unenriched)	49	2.39	0.61	535	1440/360	8.8
C6 (Unenriched)	59	2.68	0.66	378	2856/476	10.5
EN (D1 & C1)	103	3.56	0.77	1974	3193/286	—
INT (C2 & C3)	94	3.90	0.86	568	5040/420	—
UN (C4 & C6)	79	3.47	0.80	322	5416/452	—

Therefore, a single mean derived from the three within-area percent similarity indices was compared to the between-area similarity indices. Based on sampling variability, the mean within-area similarity (57.1 %) established the upper limit of similarity between sites within the same area under similar enrichment conditions. Similarity between sites of different areas should be less than 60%. The three between-area sample similarities were significantly (Newman-Keuls multiple comparison, d.f. = 322, $P < 0.0001$) less than the within-area sample similarity. The enriched versus unenriched mean similarity (27.4 %) was significantly (Newman-Keuls comparison, d.f. = 322, $P = 0.001$) smaller than the enriched versus intermediate (45.9 %) and intermediate versus unenriched (45.6 %), which were not significantly (Newman-Keuls comparison, d.f. = 322, $P = 0.90$) different. Therefore, community similarity of the intermediate area fell between the enriched and unenriched sites and was approximately equal to both. However, similarity between the enriched and unenriched areas was significantly different.

Based on sweep samples, the total mean annual density of invertebrates and small fish at the enriched area was 6.1 times and 3.5 times greater than the unenriched and intermediate areas, respectively (Table 2). The mean density per sample averaged across all sample dates at the enriched sites (128.7/m³) was significantly (ANOVA, d.f. = 2, $P = 0.01$) greater than that for the intermediate sites (76.7/m³), which was significantly ($P = 0.04$) greater than that for the unenriched sites

Table 3. The number of taxa (Richness) and mean annual density (number/m³) within selected classes and orders based on sweep samples taken within the enriched (C1 and D1), intermediately enriched (C2 and C3), and unenriched (C4 and C6) areas of WCA-2A during 1990–91. Dashes represent small values that were included in the "Other" category.

	Enriched		Intermediate		Unenriched	
Taxa	Richness	Density	Richness	Density	Richness	Density
Amphipoda	2	144	1	135	1	66
Coleoptera	33	172	20	54	9	6
Diptera	24	903	28	145	32	56
Gastropoda	11	435	12	53	9	73
Hemiptera	6	—	5	—	3	—
Oligochaeta	5	—	8	—	5	—
Osteichthyes	5	164	6	73	7	38
Ephemeroptera	2	44	2	53	2	10
Decapoda	2	7	2	22	2	58
Other	13	104	10	33	9	15
Totals	103	1973	94	568	79	322

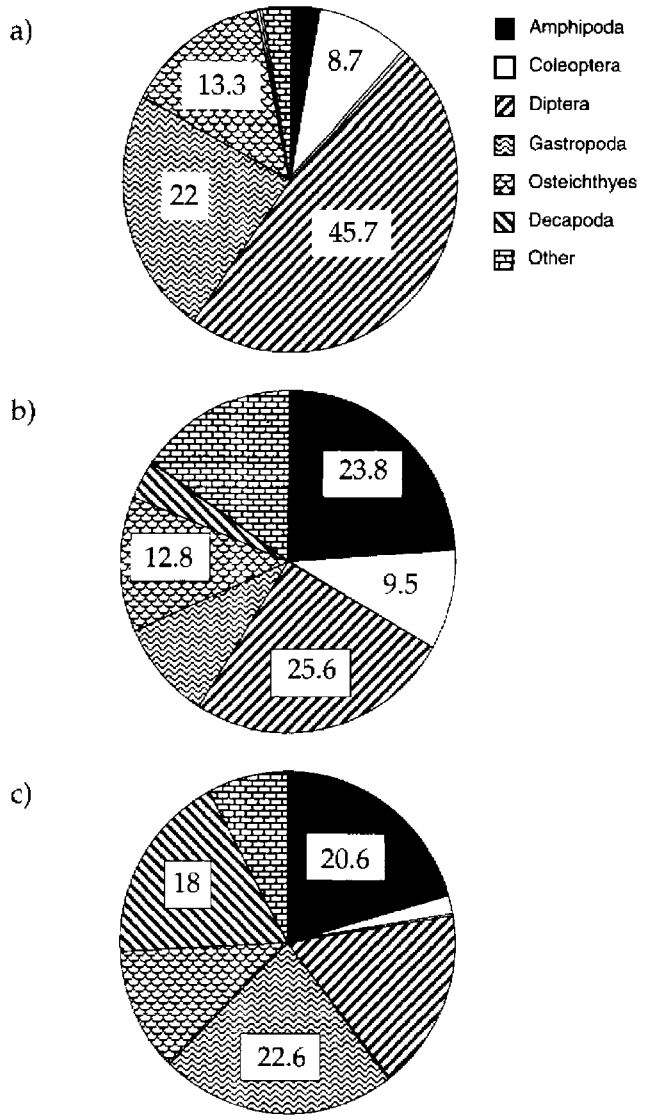

Figure 2. Percent composition of selected taxonomic groups based on sweep samples collected from the enriched (a), intermediately enriched (b), and unenriched (c) sites of WCA-2A during 1990–91. Note, the taxa key follows clock-wise in sequence from the Amphipoda.

(51.4/m³). Mean sample estimates averaged across all dates differ from the mean annual estimates (monthly means/12) found in Table 2.

Species Abundance Patterns

Except for decapods, the density of each order or class was higher within the enriched area and intermediately enriched area compared to the unenriched sites (Table 3). Decapods were the only group (especially *Palaemonetes paludosus*) that was more abundant at the unenriched sites (Figure 2 and Table 3). The mean annual density of *P. paludosus* calculated during the wet season in the unenriched area (54.5/m³) was significantly greater (t-test, d.f. = 46, $P < 0.01$) than in the enriched area (1.2/m³).

Table 4. The mean annual density (number/m²) of benthic invertebrates based on core samples collected from sites in WCA-2A during 1990–91. "Area Sampled" (cm²) represents the combined area of all cores at each site. Numbers in parentheses represent one standard error around the mean.

Site	Mean Annual Density	Sample Size	Area Sampled
D1 (Enriched)	58458 (13059)	16	616.0
D2 (Enriched)	73628 (38043)	19	731.5
C1 (Enriched)	25945 (8949)	18	693.0
C2 (Intermediate)	14180 (3175)	21	808.5
C3 (Intermediate)	3648 (583)	21	808.5
C4 (Unenriched)	4084 (1032)	21	808.5
C5 (Unenriched)	20289 (7340)	10	385.0
C6 (Unenriched)	7320 (1459)	23	885.5
EN (D1 & C1)	42202 (8110)	34	1309.0
INT (C2 & C3)	8914 (1802)	42	1617.0
UN (C4 & C6)	5702 (924)	44	1694.0

The percent composition of fish (primarily *Gambusia affinis* and *Heterandria formosa*) and amphipods (*Hyallella azteca*) within the open water slough community was similar in each area (Figure 2), but their densities at the enriched and intermediate areas were 2.0- 3.0 times higher than at the unenriched sites (Table 3). The percent composition of coleopterans was similar in enriched and intermediate areas but reduced in the unenriched area. Higher densities of coleopterans within the enriched and intermediate areas compared to the unenriched area (Table 3) were due to both an increase in the number of species collected, especially within the Hydrophilidae and Dytiscidae, and an increase in the density of specific taxa, especially *Pelonomus obscurus, Berosus infuscatus, Berosus pugnax, Tropisternus lateralis,* and *Tropisternus blatchleyi.* In addition, two families (Noteridae and Haliplidae) that were abundant at the enriched and intermediate sites were absent or extremely rare in the unenriched area.

The percent composition (Figure 2) and density (Table 3) of dipterans at the enriched site was 2.6 times and 16.2 times greater, respectively, than at the unenriched site. The higher density of dipterans within the enriched and intermediate areas compared to unenriched sites was only due to an increase in density and not to an increase in the number of taxa. The number of dipteran taxa (primarily Chironomidae) collected from enriched, intermediate, and unenriched areas was very similar (Table 3). The dominant dipterans at enriched sites were *Dasyhelia* spp., *Goeldichironomus holoprasinus, Larsia decolorata, Polypedilum trigonus, Pseudochironomus* sp., and *Tanytarsus* sp J. The dom-

Table 5. The mean annual density (number/m²) of benthic invertebrates within selected classes and orders based on core samples collected from enriched (C1 and D1), intermediate (C2 and C3), and unenriched (C4 and C6) areas of WCA-2A during 1990–91. Numbers in parentheses represent one standard error around the mean.

Taxa	Enriched	Intermediate	Unenriched
Amphipoda	104 (51)	22 (25)	361 (308)
Chironomidae	4664 (1931)	946 (279)	1393 (348)
Cladocera	121 (64)	396 (146)	226 (72)
Oligochaeta	1219 (279)	1943 (356)	909 (240)
Ostracoda	35325 (7555)	5206 (1449)	2518 (562)
Other	770 (72)	401 (59)	296 (44)
Totals	42203 (8110)	8914 (1802)	5703 (924)

inant dipterans at unenriched sites were *Dasyhelia* spp., *Dicrotendipes modestus, Larsia decolorata, Polypedilum trigonus,* and *Tanytarsus* sp. G.

Gastropoda densities at the enriched sites were 6.0 times greater than the unenriched sites (Table 3). However, gastropods were also well represented at unenriched sites (Figure 2) and had the highest density of any group in the unenriched area. Although the number of gastropod species within each area was similar (Table 3), the enriched sites were dominated by *Physella* spp. and *Planorbella duryi,* whereas unenriched sites were dominated by *Littoridinopsis monroensis* and *Planorbella duryi. Littoridinopsis monroensis* was also common at the intermediate sites but was not collected from the enriched area. Conversely, *Biomphalaria havanensis* was common at the enriched and intermediate sites but was not collected from the unenriched area. For unknown reasons, *Biomphalaria havanensis* seems to have replaced *L. monroensis* within enriched areas.

General trends and patterns based on density estimates from benthic core samples were similar to patterns of density based on sweep samples. Despite a greater sampling effort within the intermediate and unenriched areas, the mean annual density of benthic invertebrates from core samples at enriched sites was 4.7 times and 7.4 times greater than at the intermediate and unenriched sites, respectively (Table 4). Ostracods were extremely dense within the enriched area (Table 5). The density of ostracods in enriched sites was 1.65 times greater than the summed density of all other benthic taxa within all sites combined. Only amphipods and cladocerans were more dense at unenriched compared to enriched sites. Otherwise, the mean annual density of all remaining benthic taxa was greatest in the enriched area (Table 5).

Trophic Structure

The number of collector-gatherer and grazer taxa was similar among enriched, intermediate, and unenriched areas (Table 6). Because of the large number of coleopteran species in the enriched area, the number of collector-gatherer/grazer, herbivore/collector-gatherer, and predator species was also greater within enriched compared to unenriched sites (Table 6). The unenriched sites had a greater number of collector-gatherer/herbivore taxa than the enriched area because the unenriched sites had a greater number of species in the genus *Polypedilum* (Chironomidae).

Although mean annual densities of all functional feeding groups were greater within the enriched area than the unenriched sites (Table 6), the percent representation of functional feeding groups was similar between the enriched and unenriched areas (Figure 3). The representation of grazer/collector-gatherers was reduced within enriched sites because of low *P. paludosus* densities.

DISCUSSION

The results of this research did not support our hypothesis that macroinvertebrate and small fish diver-

Table 6. The number of taxa (Richness) and mean annual density (number/m²) of functional feeding groups based on sweep samples taken within the enriched (C1 and D1), intermediately enriched (C2 and C3), and unenriched (C4 and C6) areas of WCA-2A during 1990–91.

Functional Feeding Group	Enriched		Intermediate		Unenriched	
	Richness	Density	Richness	Density	Richness	Density
Collector/Gatherer	12	260	17	71	15	21
Collector/Gatherer, Grazer	9	225	7	179	5	125
Collector/Gatherer, Herbivore	4	353	7	22	9	19
Grazer	11	494	12	53	9	73
Herbivore, Collector/Gatherer	13	49	9	37	6	10
Predator	35	461	28	155	25	61
Others	19	132	14	50	10	14
Totals	103	1974	94	567	79	323

sity would be lower at enriched compared to unenriched sites. Open water habitats of the enriched area were characterized by both a high diversity and density of macroinvertebrates and small fish. Therefore, both the abundance and diversity of food available to higher trophic levels was greater within enriched compared to unenriched areas. Approximately 24 taxa, mostly dipterans and coleopterans, that were abundant at the enriched and intermediately enriched areas were either not collected from, or were extremely rare at the unenriched sites. Except for a single taxon (*Palaemonetes paludosus*), there was no evidence that nutrient-enriched water from agricultural runoff has had a direct harmful effect on the foodweb. Not only was the abundance of food (macroinvertebrates and small fish) higher within the enriched area, but the enriched area represents less than 2% of the total Everglades habitat available for colonization and nesting of wading bird populations (Rader and Richardson 1992). The decline of wading bird populations is probably not associated with nutrient enrichment in the northern Everglades. However, the freshwater shrimp, *P. paludosus*, constitutes a large proportion of the diet of some waterfowl and several game fish (Kushlan and Kushlan 1980). Causes for its reduction in the enriched area and the potential effects on higher trophic levels warrant further investigation.

Depletion of oxygen caused by a high biological oxygen demand is the most important mechanism causing a decline in species diversity within most enriched lakes and streams (Wetzel 1983, Mason 1991). However, oxygen concentrations in the Everglades within unenriched sloughs fluctuate on a diel basis between 0.0 and 4.5 mg/L just before sunrise and from 25.0 to 30.0 mg/L by mid-day (Rader and Richardson 1992, SFWMD 1992). Everglades invertebrates (Rader 1994) and small fish (Kushlan 1974, Kushlan 1979) are adapted to naturally low and fluctuating levels of oxygen that characterize shallow, stagnant bodies of water. Species that cannot tolerate fluctuating oxygen conditions and some degree of anaerobiosis have probably never been able to successfully colonize the Everglades. Therefore, if enrichment does cause a decline in the diel fluctuation of oxygen, an unproven assumption (Rader and Richardson 1992), it probably would have no or little impact on the invertebrate assemblage which is already adapted (see Rader 1994) to fluctuating oxygen concentrations.

Increases in the abundance and diversity of invertebrates in all functional feeding groups within the enriched area may have been caused by an increase in primary production. Several studies report large increases in algal and macrophyte standing crop biomass and primary production with increases in nutrients in the Everglades (for a review, see Rader and Richardson 1992). In general, increases in primary production can result in an increase in the abundance and diversity of herbivores, grazers, detritivores, and predators (e.g., Moore et al. 1993).

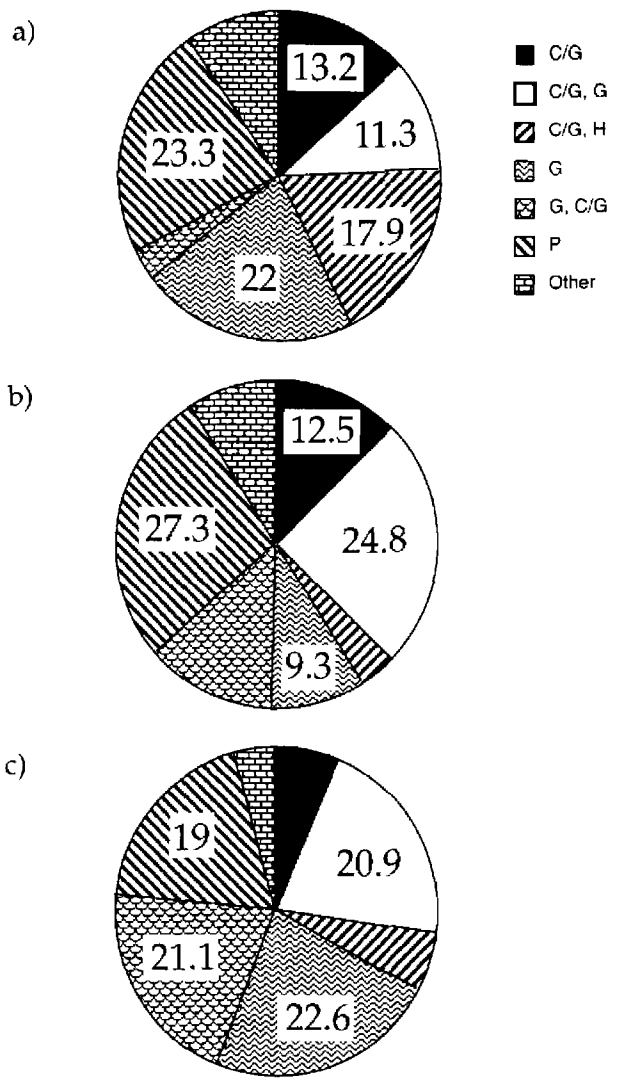

Figure 3. Percent composition of selected functional feeding groups based on sweep samples collected from the enriched (a), intermediately enriched (b), and unenriched (c) sites of WCA-2A during 1990–91. The abbreviations, "C/G", "G", "H", and "P" represent Collector/Gatherer, Grazer, Herbivore, and Predator, respectively.

The enriched sites of this study had a greater diversity and abundance of invertebrates and small fish despite having a shorter hydroperiod. In 1990, 1991, and 1992, site D2 and parts of sites D1 and C1 contained no surface water for three to six weeks during the dry season whereas, all of the intermediate and unenriched sites remained inundated throughout the year. In contrast to our results, Loftus et al. (1986) found that invertebrate and small fish abundances in Everglades National Park declined in marshes with short com-

pared to long hydroperiods. Frequent macroinvertebrate colonization may explain this apparent contradiction. The sustained high diversity and abundance within the enriched zone despite a short hydroperiod may be related to its proximity to a permanent body of water and source of colonists. The enriched zone lies immediately downstream from the highly enriched Hillsboro Canal (Scheidt et al. 1989). Both water and colonists are frequently released from the canal into the enriched zone of the marsh. Sweep samples taken from within Hillsboro Canal revealed an abundance of all major invertebrate groups (Rader 1994). If nutrient enrichment had a direct harmful effect on macroinvertebrate populations, we would expect reduced invertebrate abundance and diversity within Hillsboro canal. Instead, canals throughout the Everglades likely represent a source of colonists for invertebrates and fish in newly inundated marshes.

Davis (1994) compared the results of our research to an earlier study (1982) on decomposition in WCA-2A. He concluded that the diversity of invertebrates collected from litter bags was lower in an enriched dense stand of cattail compared to an unenriched dense stand of sawgrass. He also reported the local extinction of some species of snails and isopods from within the enriched area. However, this study (Davis 1994) suffered from a lack of site replication, an extremely small sample size, and outdated faulty invertebrate identifications. Invertebrates from three litter bags were collected at two sites (unriched versus unenriched) on nine dates (27 total samples per site). Because of considerable temporal and spatial variation, 27 samples would limit making valid conclusions concerning the diversity and abundance of invertebrates in enriched versus unenriched habitats. Also, such a small sample size does not provide sufficient data to determine patterns of local extinction. In addition, decomposing litter within dense stands of emergent vegetation (e.g., sawgrass and cattail) are the least preferred habitat of invertebrates in the Everglades (Rader 1994). Sampling within dense emergent vegetation partly explains why only a total of 56 taxa were identified (Davis 1994, Urban, unpublished data). Determination of invertebrate diversity and local extinction requires site replication, accurate identifications, and numerous samples in all available sub-habitats, especially submersed macrophytes within open water areas. Open water areas are important habitat because they contain most of the biological diversity (algae, invertebrates, and fish) in the Everglades (e.g., Gleason 1974).

Although we found that invertebrate diversity was high in nutrient enriched open water habitats, excess inputs of **P** may have harmful indirect effects. Enrichment is reported to cause the expansion of cattails from canal margins into areas (e.g., WCA-2A) previously characterized by open water sloughs surrounded by sawgrass (SFWMD 1990, Davis 1994). Therefore, enrichment may cause indirect harmful foodweb effects by causing cattail to overgrow and eliminate open water areas. The potentially detrimental influence of cattail invasion into open water habitats and its influence on higher trophic levels also warrant further investigation.

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Appendix I. Macroinvertebrate and small fish taxa based on sweep samples from slough sites in WCA-2A during 1990–91. "F.F.G." and "M.A.D." are the functional feeding group and mean annual density (number/m³) for each taxon.

Class/order	Family	Genus/species	F.F.G.	M.A.D.
Acarina		Several unidentified species	P	0.09
Amphipoda	Crangonyctidae	*Crangonyx* sp.	C/G, G	0.68
	Hyalellidae	*Hyalella azteca* (Saussure)	C/G, G	103.59
Coleoptera	Chrysomelidae	*Donacia* sp.	H, Sh	0.18
	Dryopidae	*Pelonomus obscurus* (Chevrolat)	C/G, G	8.76
	Dytiscidae	*Agabetus* sp., larva	P	0.14
		Bidessonotus pulicarius (Aube)	P	0.31
		Celina slossoni Mutchler	P	0.09
		Celina imitatrix (Young)	P	0.04
		Celina spp., larva	P	3.43
		Cybister fimbriolatus, larva (Say)	P	0.05
		Desmopachria grana (LeConte)	P	0.03
		Hydroporus sp.	P	2.06
		Hydrovatus pustulatus Sharp	P	0.96
		Ilybius sp. (larva)	P	0.26
		Laccophilis gentilis LeConte	P	0.21
	Gyrinidae	*Gyrinus aneolus* LeConte	P	0.10
		Gyrinus elevatus LeConte	P	0.18
	Haliplidae	*Haliplus havaniensis* Wehncke	H, Sh	0.03
		Haliplus mutchleri Wallis	H, Sh	1.24
		Haliplus spp. (larva)	H, Sh	0.68
		Peltodytes dietrichi Young	Sh, H	0.05
	Hydrophilidae	*Berosus infuscatus* LeConte	H, C/G	2.09
		Berosus pugnax LeConte	H, C/G	1.74
		Berosus spp. (larva)	H, C/G	47.68
		Chaetarythria sp. (larva)	H, C/G	1.09
		Crenitulus sp.	H, C/G	0.05
		Derallus altus (LeConte)	P	4.69
		Enochrus consortus Green	H, C/G	0.03

Appendix I. Continued.

Class/order	Family	Genus/species	F.F.G.	M.A.D.
		Enochrus hamiltoni (Horn)	H, C/G	2.26
		Enochrus ochraceus (Melsheimer)	H, C/G	0.88
		Enochrus pygmaeus (Say)	H, C/G	0.53
		Enochrus sayi Gunderson	H, C/G	1.75
		Enochrus spp. (larva)	H, C/G	2.53
		Helobata sp.	P	4.50
		Helophorus sp. (larva)	G, C/G	0.54
		Hydrobiinae (unidentified adult)	?	0.06
		Hydrobiomorpha sp. (larva)	?	0.05
		Hydrochus sp. (larva)	Sh, G	0.31
		Paracymus sp.	?	0.39
		Tropisternus blatchleyi d'Orchymont	H, C/G	0.53
		Tropisternus lateralis (Say)	H, C/G	0.86
		Tropisternus spp. (larva)	P	6.29
	Noteridae	*Hydrocanthus oblongus* Sharp	P	14.01
		Suphis inflatus (LeConte)	P	0.25
		Suphisellus gibbulus (Aube)	P	5.05
	Scirtidae	*Prionocyphon* sp.	H, C/G	0.55
Collembola	Entomybryidae	*Entomobrya* sp.	C/G	0.16
		Several unidentified species	C/G	0.29
Copepoda	Argulidae	*Argulus* sp.	P	0.03
Decapoda	Cambaridae	*Procambarus alleni* (Faxon)	G, C/G, H	8.88
	Palaemonidae	*Palaemonetes paludosus* (Gibbes)	G, C/G, H	24.84
Diptera	Ceratopogonidae	*Bezzia/Palpomyia* complex	P	7.09
		Dasyhelea spp.	P	18.94
		Forcipomyia sp.	P	0.57
	Chironomidae	*Ablabesmyia karelia* sp.	P	0.06
		Ablabesmyia peleensis (Walley)	P	0.04
		Ablabesmyia rhamphe group	P	0.14
		Ablabesmyia sp.	P	0.18
		Asheum beckae	P	0.05
		Chironomus sp.	C/G, H	1.53
		Chironomus stigmaterus Say	C/G, H	12.16
		Cladopelma sp.	C/G, H	0.40
		Cladotanytarsus sp.	C/G	0.25
		Dicrotendipes modestus (Say)	C/G	6.48
		Endochironomus nigricans (Johannsen)	Sh, H	0.03
		Goeldichironomus holoprasinus (Goeldi)	C/G	42.08
		Goeldichironomus natans?	C/G	1.64
		Keifferulus sp.	C/G	1.68
		Kiefferulus sp. A	C/G	0.28
		Labrundinia neopilosella Beck & Beck	P	0.05
		Larsia decolorata (Malloch)	P	40.71
		Nimbocera sp.	C/G	27.05
		Parachironomus directus (Dendy)	C/G	0.19
		Parakiefferiella sp. C	C/G	0.06
		Paramerina sp.	P (?)	0.09
		Polypedilum halterale group	C/G, H	1.45
		Polypedilum sp.	C/G, H	0.19
		Polypedilum sp. A	C/G, H	1.48
		Polypedilum sp. G	C/G, H	0.18
		Polypedilum trigonus Townes	C/G, H	94.08
		Polypedilum tritum (Walker)	C/G, H	1.55
		Procladius sp.	P	0.39
		Pseudochironomus sp.	C/G	33.29
		Tanypus carinatus Sublette	P	1.53

Appendix I. Continued.

Class/order	Family	Genus/species	F.F.G.	M.A.D.
		Tanytarsus sp.	F, C/G	0.75
		Tanytarsus sp. G	F, C/G	10.19
		Tanytarsus sp. J	F, C/G	23.06
		Tanytarsus sp. R	F, C/G	1.03
	Ephydridae	*Hydropyrus* sp.	H, C/G	5.09
	Psychodidae	*Pericoma* sp.	C/G, Sh	0.38
	Stratiomyidae	*Odontomyia* spp.	Sh, H	11.93
	Tabanidae	*Tabanus* sp.	P	0.09
	Tipulidae	*Limonia* spp.	Sh, H	3.30
		Polymera sp.	P	0.05
		Tipula sp.	Sh, C/G	0.05
Ephemeroptera	Baetidae	*Callibaetis floridanus* Banks	G, C/G	4.01
	Caenidae	*Caenis diminuta* Walker	G, C/G	80.40
Gastropoda	Ancylidae	*Ferrissia* sp.	G	3.64
	Hydrobiidae	*Littoridinops monroensis* (Frauenfeld)	G	31.60
	Lymnaeidae	*Fossaria cubensis* (Pfeiffer)	G	13.66
		Lymnaea stagnalis Lea	G	0.09
		Micromenetus dilatatus (Gould)	G	5.25
		Pseudosuccinae columella (Say)	G	13.59
	Physidae	*Physella* spp.	G	44.86
	Pilidae	*Pomacea paludosa* (Say)	G	0.89
	Planorbidae	*Biomphalaria havanensis* (Pfeiffer)	G	4.68
		Drepanotrema sp.	G	0.31
		Gyraulus parvus (Say)	G	0.18
		Helisoma sp.	G	0.44
		Planorbella duryi (Weatherby)	G	78.66
		Planorbula armigera (Lea)	G	0.03
		Planorbula sp.	G	0.78
		Snail (?)	G	1.01
Hemiptera	Belostomatidae	*Belostoma flumineum* Say	P	0.94
		Belostoma testaceum (Leidy)	P	0.99
		Belostomatidae spp. (early instars)	P	0.83
		Lethocerus americanus (Leidy)	P	0.08
	Corixidae	*Palmacorixa gillettei* Abbott	P	5.23
		Trichocorixa minima (Abbott)	P	0.89
	Macroveliidae	*Oravelia* sp.	P	0.09
	Mesoveliidae	*Mesovelia* sp.	P	2.69
	Naucoridae	*Pelocoris femoratus* (Palisot-Beauvois)	P	16.18
Hirudinea	Erpobdellidae	*Mooreobdella* sp.	P	5.78
	Glossiphoniidae	*Helobdella* sp.	P	0.28
Isopoda	Asellidae	*Caecidotea* spp.	C/G, G	0.53
Lepidoptera	Noctuidae	*Simyra* sp.	Sh, H	0.60
	Pyralidae	*Acentria* sp.	H, Sh	0.48
		Parapoynx sp.	H, Sh	0.36
Odonata	Aeshnidae	*Coryphaeschna ingens* (Rambur)	P	0.08
	Coenagrionidae	*Enallagma* sp.	P	3.11
		Ischnura sp.	P	0.98
		Telebasis byersi Westfall	P	0.13
	Libellulidae	*Erythemis simplicicollis* (Say)	P	17.05
		Pachydiplax longipennis (Burmeister)	P	0.03
Oligochaeta	Lumbriculidae	*Eclipidrilus* sp.	C/G	0.06
	Naididae	*Allonais pectinata* (Stephenson)	C/G	0.66
		Bratislavia unidentata (Harman)	C/G	0.68
		Dero digitata (Muller)	C/G	0.05
		Dero furcata (Muller)	C/G	0.04
		Dero obtusa d'Udekem	C/G	0.09

Appendix I. Continued.

Class/order	Family	Genus/species	F.F.G.	M.A.D.
		Dero pectinata (Muller)	C/G	0.33
		Dero sp.	C/G	0.86
		Dero trifida Loden	C/G	0.18
		Pristina aequiseta Bourne	C/G	0.05
		Stylaria lacustris (Linnaeus)	C/G	0.04
Osteichthyes	Centrarchidae	*Elassoma evergladei* Jordan	P	0.20
	Cyprinodontidae	*Jordanella floridae* Goode	P	1.60
		Lucania goodei Jordan	P	1.60
		Lucania parva (Baird & Girard)	P	8.00
	Poecilidae	*Gambusia affinis* (Baird & Girard)	P	104.10
		Heterandria formosa Agassiz.	P	102.10
		Poecilia latipinna (Lesueur)	P	0.10
Ostracoda	Cyprididae	Several unidentified species	C/G, G	17.40
		Physocypria sp.	C/G, G	0.14
		Scottia sp.	C/G, G	0.61
Bryozoa	Plumatellidae	*Plumatella repens* (Lea)	F	?
Polychaeta	Nereidae	*Namanereis hawaiiensis* (Johnson)	C/G	1.01
Porifera	Spongillidae	*Spongilla lacustris* (Lea)	F	?
Trichoptera	Hydroptilidae	*Qxyethira* sp.	H, C/G	0.03
	Leptoceridae	*Nectopsyche* sp.	Sh, H	0.34