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Assessing the net effect of anthropogenic disturbance on aquatic communities in wetlands: community structure relative to distance from canals

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Abstract

Anthropogenic alterations of natural hydrology are common in wetlands and often increase water permanence, converting ephemeral habitats into permanent ones. Since aquatic organisms segregate strongly along hydroperiod gradients, added water permanence caused by canals can dramatically change the structure of aquatic communities. We examined the impact of canals on the abundance and structure of wetland communities in South Florida, USA. We sampled fishes and macroinvertebrates from marsh transects originating at canals in the central and southern Everglades. Density of all aquatic organisms sampled increased in the immediate proximity of canals, but was accompanied by few compositional changes based on analysis of relative abundance. Large fish (>8 cm), small fish (<8 cm) and macroinvertebrates (>5 mm) increased in density within 5 m of canals. This pattern was most pronounced in the dry season, suggesting that canals may serve as dry-down refugia. Increases in aquatic animal density closely matched gradients of phosphorus enrichment that decreased with distance from canals. Thus, the most apparent impact of canals on adjacent marsh communities was as conduits for nutrients that stimulated local productivity; any impact of their role as sources of increased sources of predators was not apparent. The effect of predation close to canals was overcompensated by increased secondary productivity and/or immigration toward areas adjacent to canals in the dry season. Alternatively, the consumptive effect of predatory fishes using canals as dry-season refuges is very small or spread over the expanse of marshes with open access to canals.

Introduction

Anthropogenic activities have altered freshwater ecosystems worldwide, severely threatening their ecological integrity (NCR, 1992; Naiman & Turner, 2000). The addition of dams, impoundments, channels, canals and levees has dramatically disrupted flow, flooding cycles and hydrologic connectivity (Dynesius & Nilsson, 1994; Power et al., 1995; Rosenberg et al., 2000; Pringle, 2001; Brönmark & Hansson, 2002). In temporary habitats, anthropogenic hydrologic alterations often result in changes in the amount, extent and timing of flooding (Bedford & Preston, 1988). In many cases, drainage and impoundment results in complete loss of wetlands or temporary ponds (Turner et al., 1998). In other instances, hydrologic alterations may increase water permanence, converting ephemeral habitats into permanent ones (Gergel, 2002). Aquatic organisms have been shown to segregate strongly along gradients of aquatic habitat permanence (Wilbur, 1980; Schneider & Frost, 1996; Wellborn et al., 1996; Corti et al., 1997; Skelly et al., 1999). Large predatory fish are typically absent from temporary wetlands, providing a predation refuge for many small aquatic organisms. Thus, lengthening hydroperiod and enhancing habitat connectance may result in marked changes in community structure and ecosystem function.

In the Florida Everglades, drainage and impoundment have drastically altered hydrologic conditions and reduced the extent of shallow, seasonal wetlands by more than 40% (Davis et al., 1994). Presently, over 1600 km of canals and 1150 km of levees compartmentalize the system and disrupt the natural southerly sheet flow of water over vegetated marshes (Light & Dineen, 1994). Historically, the spatial extent of marsh inundation (and thus habitat for aquatic organisms) fluctuated seasonally in response to rainfall patterns (high in the summer and fall, low in the winter and spring). Today, inundation and flow are largely controlled by this extensive system of water control structures, levees and canals. Beyond altering flow and hydroperiod, canals provide permanent deep-water refuges for biota that were historically rare or absent in the ecosystem (Gunderson & Loftus, 1993). These artificial habitats harbor relatively high numbers of predatory and non-indigenous fishes (Loftus & Kushlan, 1987; Trexler et al., 2001) that may alter the small fish and macroinvertebrate communities of nearby marshes.

Alterations to the natural hydrologic regime of wetlands are often accompanied by alterations in nutrient inputs (Sanchez-Carrillo & Alvarez-Cobelas, 2001). The Everglades is an oligotrophic wetland, which historically received most of its nutrients from rain. Like many freshwater wetlands, Everglades marshes are phosphorus (P)-limited (McCormick et al., 1996). Ambient concentrations of total phosphorus (TP) in the water column are typically below 10 μg/l (Davis, 1994). Over the past decades, however, the ecosystem has been subjected to anthropogenic P enrichment. Discharge from canals bordering northern agricultural lands is the main source of nutrients; TP concentration in canal runoff has been as high as 30-times ambient levels (McCormick et al., 1996). A number of alterations to the structure and function of the Everglades ecosystem have resulted from P enrichment, even at very low levels (Davis, 1994; Doren et al., 1997; Noe et al., 2001; Gaiser et al., 2005). Among these impacts, fish and macroinvertebrate biomass and density have been shown to increase at high TP concentrations (Rader & Richardson, 1994; Turner et al., 1999; Gaiser et al., 2005).

The impact of canals on aquatic organisms inhabiting Everglades wetlands may depend on the relative strength of predation and nutrient enrichment. If canals provide key habitats for predatory fish species, predation pressure may increase in nearby marshes. On the other hand, if canals act as a source of nutrients, prey species may increase as the enrichment effect is transmitted up the food web. When both resource stimulation and enhanced predatory consumption combine, there may be no net effect or a dampening of the stronger factor by the weaker one. The overall effect may be complex in systems such as the Everglades where omnivory is widespread (Polis & Strong, 1996; Leibold et al., 1997).

In this study, we examined patterns of fish and macroinvertebrate communities relative to distance from canals to evaluate the net effect of nutrients and predation. We asked: (1) How do fish and macroinvertebrate communities change with proximity to canals? (2) Over what distance do canals influence aquatic communities? and (3) Does the effect vary between undisturbed and disturbed marshes (in this case, marshes impacted by airboat traffic)? To address these questions, we sampled large fishes, small fishes and macroinvertebrates in transects originating at canals and extending into un-channelized marshes. We were particularly interested in determining the effect of proximity to canals on the small fish assemblage, which dominates fish standing crops and abundance (Turner et al., 1999; Trexler et al., 2002) and constitutes an important food source for wading birds (Frederick & Spalding, 1994). We focused on the effect of canals at small spatial scales (5–1000 m), because our study sites consisted of canals with relatively low nutrient enrichment compared to canals included in previous studies (e.g., Doren et al., 1997; Childers et al., 2003). By avoiding canals with high nutrient enrichment and extensive areas of nutrient-enriched marsh downstream, we increased the possibility of documenting the role of canals as a predator source, if present.

Methods

We sampled fish and macroinvertebrates in transects originating at 5 canals: I75, L28, L29 and L67 in Water Conservation Area 3A (WCA3A) and the C111 in the southern Everglades, Florida, USA

(Fig. 1). These canals are located in the central and southern regions of the Everglades, far south of the primary sources of P loading to the ecosystem. These transects spanned marshes of varying hydroperiod; those in the proximity of the C111 had the shortest hydroperiod (174–364 days from 1996 to 2001), those in the proximity of the L28 and I75 had intermediate hydroperiods (225–365 days from 1996 to 2001) and those in the proximity of the L29 and L67 exhibited the longest hydroperiod (327–365 days from 1996 to 2001).

Two transects were established at each of our canal sites, one that followed an airboat trail and a parallel transect in the surrounding undisturbed marsh (approximately 350 m apart). Sampling was conducted at 5, 100, 500 and 1000 m along each transect. For the marsh transect, a fifth site was included at an average distance of 7500 m from canals. In the central region of WCA3A, these sites were at 3200 m from the I75, 4400 m from the L28, 6600 m from the L67 and 11400 m from the L29 canals respectively. For the C111 canal, the inner site was located at 11900 m from the canal in the Madeira ditches region of Taylor Slough (Fig. 1). Transects bisected *Eleocharis* spp-dominated wet prairies in WCA3A and *Cladium jamaicense*-dominated marl prairies in the C111 area. Sampling sites along the 2 transects had similar macrophytes densities (Marsh: 184 ± 31 stems m^{-2}; Trail: 203 ± 32 stems m^{-2}; ANOVA: $F_{1,130} = 1.3$, $p = 0.27$), but

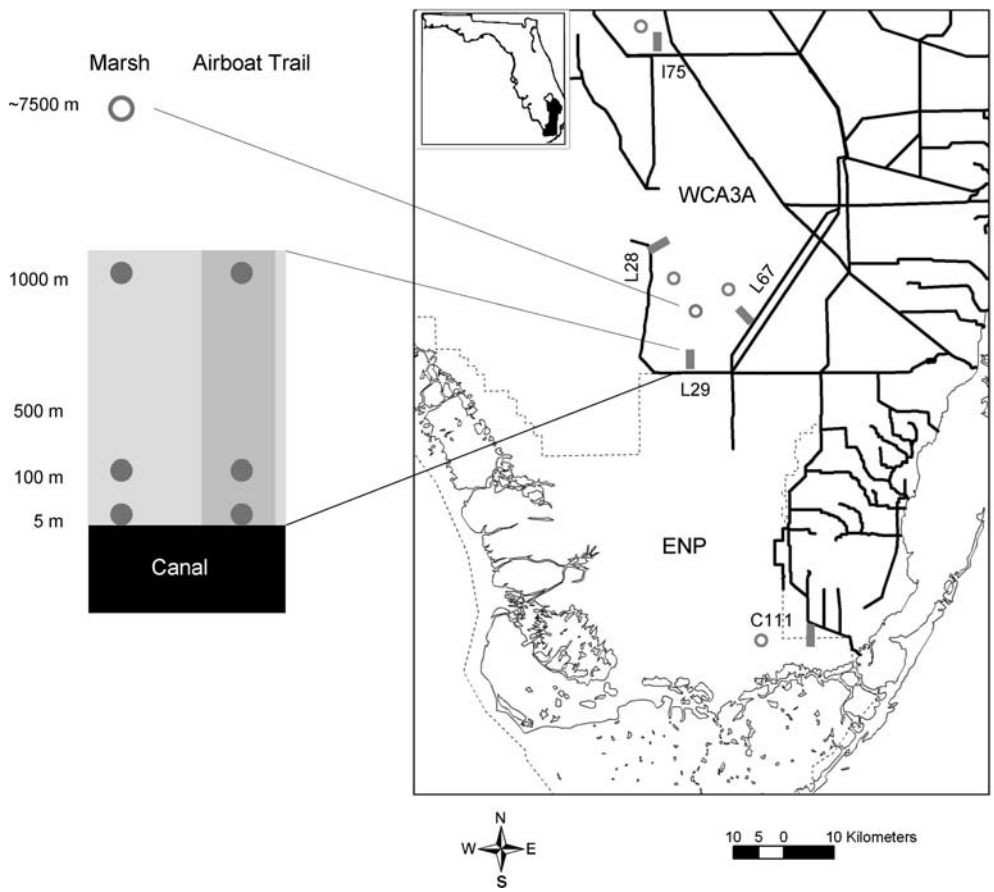

Figure 1. Map showing the main canals (black lines) throughout the southern and central Everglades ecosystem and urban areas to the east. Labels indicate the 5 canals included in this study: L28, L29, L67 and I75 canals in Water Conservation Area 3A (WCA3A) and C111 canal in the southeastern region of Everglades National Park (ENP). Sampling took place in two transects perpendicular to each canal; one that followed an airboat trail and a parallel transect in undisturbed marsh (approximately 350 m away). Circles in diagram indicate distances sampled away from canals: 5, 100, 500, 1000 m (filled symbols) and an average of 7500 m for the inner most sites (open symbols and sampled only in the undisturbed marsh).

differed in periphyton cover (Marsh: 2783 ± 229 ml m^{-2}; Trail: 2260 ± 260 ml m^{-2}; ANOVA: $F_{1,131}$ = 12.4, $p = 0.0006$). We sampled in both the wet (September 2003) and dry seasons (January and March 2003). Water depth at our sampling sites averaged 72 ± 1.9 cm during the wet season and 48 ± 2.0 cm during the dry-season sampling event.

Small fish (standard length (SL) <8 cm) and macroinvertebrates (maximum dimension >5 mm) were sampled with a 1-m^2 throw trap with 2-mm mesh netting on the sides, which were cleared from the trap using standardized techniques (Kushlan, 1981; Jordan et al., 1997). Before clearing the trap, we quantified the number of emergent stems and the volume of floating periphyton. All animals were preserved in 10% formalin in the field and brought to the laboratory for identification and enumeration. Three throw-trap samples were taken at each distance within each transect (3 throws × 4 distances × 2 transects × 5 canal sites × 2 seasons = 240 throws + 30 throws at the 7500 m marsh site = 270 possible throws). Actual sample size was 258 because half of the sites at the C111 canal were dry at the time of the dry-season sampling in early January 2003.

Large fish (SL >8 cm) were sampled using an airboat-mounted electrofishing unit (two-anode one-cathode apparatus with a Smith-Root® GPP 9.0 control box). Electrofishing has been shown to be an effective method for sampling large fishes in marshes, and electrofishing catch per unit effort (CPUE) provides a reliable index of fish abundance (Chick et al., 1999). Sampling was conducted in 2 5-min bouts (pedal time) at each distance within each transect (2 bouts × 4 distances × 2 transects × 5 canal sites × 2 seasons = 160 bouts + 20 bouts at 7500 m mash site = 180 possible bouts). For all bouts, electrofishing power was standardized at 1500 W according to temperature and conductivity conditions (Chick et al., 1999). All fish captured were identified to species, measured to nearest 1 mm SL and released after full recovery. Final sample size was 162 bouts because most of the C111 sites were dry at the time of the dry-season sampling and we were unable to sample the L28 7500 m marsh site.

To investigate the presence of a nutrient enrichment gradient as a function of distance from canals, we measured TP concentrations in the flocculent detrital organic layer (floc) above the soil. The floc layer is the most microbiologically active layer of Everglades soils and plays a key role in short-term uptake and cycling of P (Noe et al., 2002). Because of its high responsiveness to nutrient inputs, the floc layer may be more closely tied to food web responses to enrichment. We collected floc samples with a 2.4 cm diameter coring device. Three cores were collected from a 1 m^2 area and combined into a composite sample (Noe et al., 2002). Three composite samples were taken at each sampling location (3 composite samples × 4 distances × 2 transects × 5 canal sites = 120 + 15 samples at 7500 m marsh site = 135 possible samples). Samples were dried at 70 °C for 48 hours, crushed to a fine powder and analyzed for TP in a spectrophotometer following standardized procedures (Fourqurean et al., 1992). All samples were collected in March 2004, except for the 7500 m samples, which were collected in October 2002. At the C111 canal, floc samples were only obtained at the 5 and 7500 m distances; thus final sample size was 117 samples.

Statistical analyses

We examined variation in the abundance of fish and macroinvertebrates among canal sites and as a function of season, distance from canals and disturbance level (marsh vs. trail transects) with nested, repeated-measures ANOVA models. Season was the repeated measure in our analyses and nesting allowed us to account for spatial variation among our canal sites. We tested for the effect of distance nested within canal site and for the effect of disturbance nested within distance and canal. Focal response variables included: TP concentration ($\mu g\ g^{-1}$), CPUE of large fishes (number 5 min^{-1} electrofishing bout) and densities of small fish and macroinvertebrates (number m^{-2}). Stem density (number m^{-2}) and periphyton volume (ml m^{-2}) were used as covariates in analyses of the throw-trap data. In order to better satisfy assumptions of parametric tests, all variables were log (observed value + 1)-transformed prior to analyses. Post hoc pairwise comparisons were performed using Tukey-corrected contrasts. Some pairwise comparisons involving the C111 sites could not be conducted because of missing dry-season data. Simple linear regressions were used to examine the relationship between TP and estimates of abundance. All analyses were performed using

SAS Version 9.1.3®. ANOVAs were performed using Proc MIXED with compound symmetric covariance structures in the repeated measures (Littell et al., 1996).

We used one-way analysis of similarity (ANOSIM) based on Bray–Curtis dissimilarity matrices to test for effects of canal site, distance and disturbance on fish and macroinvertebrate community structure (Clarke & Warwick, 2001). Dissimilarity matrices were constructed separately for the large fish, small fish and macroinvertebrate communities based on square-root transformed estimates of the relative abundance of taxa averaged across seasons; no seasonal variation was evident in preliminary analyses. Analyses included 22 large fish species, 28 small fish species and 36 macroinvertebrate taxa. We identified macroinvertebrates to the lowest practical taxonomic resolution, which included 26 species, 2 genera, 4 families, 2 orders and 2 classes. ANOSIM tests produce Global R statistics with values ranging between 1 and −1. Values closer to 1 indicate greater community dissimilarity among groups than within, while values closer to −1 indicate less dissimilarity among groups than within. We followed ANOSIM analyses with similarities percentage breakdown analyses (SIMPER) to determine which taxa were contributing most to groupings observed among samples. Once key taxa were identified, we examined the magnitude of variation in abundance with one-way ANOVAs, followed by Tukey *post hoc* comparisons. We then constructed non-metric multi-dimensional scaling (MDS) plots to illustrate dissimilarity among groups. All community structure analyses were conducted using Primer© Version 5.2.9.

Results

Small fish density

Densities of small fishes varied among canal study sites and this variation differed between sampling seasons (Table 1). On average, small fishes were least abundant in the proximity of the L29 canal and most abundant in marshes bordering the C111, I75 and L28 canals (9 vs. 34 fish m^{-2}) (Tukey pairwise comparisons, all $p = 0.0001$). Overall, densities increased between the wet and dry season (21 vs. 31 fish m^{-2}), but there was large variation in the magnitude and direction of this seasonal effect among canals. Compared to the wet season data, small fish density increased by 200% in the C111, 100% in the L28 and 40% in the L29 canal in the dry season ($p < 0.08$). In contrast, density decreased by 50% in the L67 canal ($p = 0.009$) and remained unchanged at the I75 site. Density also varied as a function of distance from canals and this effect was greatest in the dry season and canal-specific (Fig. 2a). In the wet season, a distance effect was only detected at the C111 site; there was

Table 1. Summary of results of nested ANOVAs and ANCOVAs testing the effect of season, canal, distance, disturbance and relevant covariates on small fish and macroinvertebrate densities and large fish CPUE and testing effect of canal, distance and disturbance on TP concentration in the floc layer

Source of variation	Small fish			Macroinvertebrate			Large fish			Floc total phosphorus		
	df	*F*	*p*	df	*F*	*p*	df	*F*	*P*	df	*F*	*p*
Season	1, 85	5.7	0.0188	1, 89	76.9	0.0001	1, 41	274.1	0.0001			
Canal	4, 103	54.6	0.0001	4, 107	19.2	0.0001	4, 48	7.4	0.0001	4, 116	31.1	0.0001
Distance (Canal)	20, 92	9.9	0.0001	20, 96	14.0	0.0001	19, 46	15.5	0.0001	17, 116	26.9	0.0001
Disturbance [Distance (Canal)]	20, 91	5.8	0.0001	20, 95	7.0	0.0001	20, 45	3.5	0.0003	17, 116	10.2	0.0001
Season × Canal	4, 87	10.5	0.0001	4, 91	4.9	0.0013	4, 41	5.4	0.0014			
Season × Distance (Canal)	19, 84	2.8	0.0007	19, 88	3.1	0.0002	15, 41	9.2	0.0001			
Season × Disturbance [Distance (Canal)]	17, 84	1.8	0.0399	17, 89	3.1	0.0003	17, 41	1.7	0.0935			
Plant density	1, 167	11.1	0.001	1, 167	42.6	0.0001						
Periphyton volume	1, 167	8.0	0.0054	1, 167	2.25	0.1356						

a 10-fold increase in density within 5 m of the canal compared to 100–1000 m distances ($p < 0.04$). In the dry season, density increased significantly within 5 m of canals in marshes adjacent to the I75 and C111 canals ($p < 0.04$) and to a lesser extent in the L29 canal (5 vs. 500 m, $p = 0.06$). This effect was localized to the immediate vicinity of canals; small-fish density at 100 m of canals was remarkably similar to those at greater distances. In the L29 canal, densities significantly

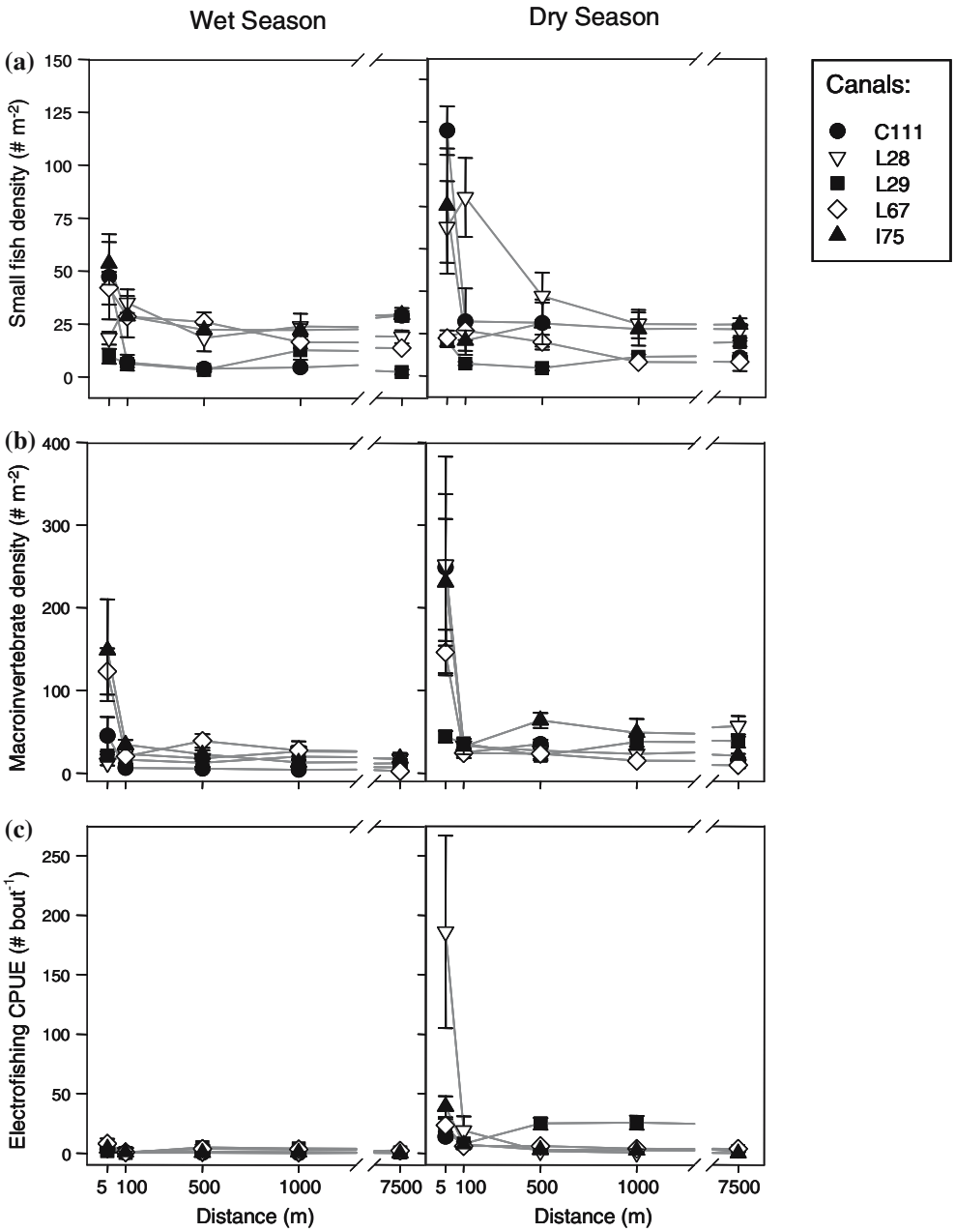

Figure 2. (a) Small fish (SL < 8 cm) density (number m^{-2}), (b) macroinvertebrate density (number m^{-2}) and (c) large fish (SL > 8 cm) CPUE (number 5 min. electrofishing $bout^{-1}$) shown as a function of distance from a canal for the 5 canal sites (C111, L28, L29, L67 and I75) and shown separately by season. Data are means ± 1 SE.

increased at 100 m, but not 5 m (100 vs. 500 m, $p = 0.002$). The L67 site was the only canal where dry-season density did not vary as a function of distance from the canal (Fig. 2a). Few effects of anthropogenic disturbance on small-fish density were detected. Differences between the airboat trail and adjacent undisturbed marsh were only detected in the I75 and L28 canals and only at 3 of the 10 distances sampled. In all three instances, density was higher in the airboat trail ($p < 0.08$; 50–500% difference). Small-fish density was positively correlated to emergent macrophyte stem density, but negatively correlated to periphyton volume (Table 1).

Macroinvertebrate density

Similar to the small fish, macroinvertebrate density varied among canal sites, with the lowest densities in the immediate proximity of the L29 canal ($p < 0.04$). Overall, density varied with season and more than tripled in the dry season compared to the wet season (20 vs. 69 macroinvertebrates m^{-2}). However, the magnitude of the seasonal effect was canal-specific (Table 1); density increased in the dry season in the C111, L28 and L29 canals ($p < 0.003$), but remained the same in the I75 and L67 canals. Density of macroinvertebrates varied markedly with distance from a canal. Most of the distance variation was observed in the dry season and as seen in the small fish data it was particularly evident between the 5 m and all greater distances (Fig. 2b). Only in the L67 canal did density vary as a function of distance during the wet season. Density within 5 m of the L67 canal was 5 times higher than at greater distances ($p < 0.005$, except for 5 vs. 500 m, $p = 0.85$). At four canal transects, C111, I75, L67 and L28, dry-season macroinvertebrate density was 8 times higher within 5 m of the canal than at greater distances ($p < 0.05$). No distance effect was detected at the L29 canal transects. Disturbance affected macroinvertebrate density only in the proximity of canals and only in a subset of sites, particularly the I75 and L28 canals. At 5 m, density was higher in the airboat trail than the undisturbed marsh (I75, $p = 0.0001$; L28, $p = 0.005$). Macroinvertebrate density in our samples was positively related to emergent macrophyte stem density, but unrelated to periphyton volume (Table 1).

Large fish CPUE

Differences among canals in electrofishing CPUE varied between seasons (Table 1). Overall, CPUE increased sharply at all sites in the dry season, from an average of 2 in the wet season to 21 fish $bout^{-1}$. In the wet season, CPUE was highest in the L67 canal and lowest in the C111 canal ($p = 0.005$). In the dry season, only the L29 and I75 canals differed (17 vs. 11 fish $bout^{-1}$, $p = 0.0002$). A gradient in CPUE as a function of distance was only detected in the dry season, but the effect was consistent for the 4 canals sampled fully (no data at distances greater than 5 m were available for the C111 canal) (Fig. 2c). The most striking effect was the increase in CPUE within 5 m detected in the I75 and L28 canals (5 vs. other distances, all $p < 0.01$). CPUE averaged 3 and 7 fish $bout^{-1}$ at 100–7500 m in the I75 and L28 canals respectively, but increased to 39 and 186 fish $bout^{-1}$ within 5 m of canals. In the L29 canal, the effect of the canal was seen as far as 1000 m away. Dry-season CPUE averaged 19 fish in the 5–1000 m range, but was only 2 fish $bout^{-1}$ at the inner-marsh site ($p < 0.04$). Less variation in CPUE was detected at the L67-canal transect, although variation was in the same direction; catches were higher close to the canal (5 vs. 1000 m, $p = 0.02$). Disturbance only affected CPUE in the L28 canal and the effect was only detected at 5 m; CPUE at 5 m averaged 147 fish $bout^{-1}$ in the airboat trail, but only 43 fish $bout^{-1}$ in the undisturbed marsh ($p = 0.06$).

Nutrient gradient

Floc TP concentration varied significantly among canal sites (Fig. 3). Mean concentration was highest in marshes along the L28 canal (1113.4 $\mu g\ g^{-1}$), intermediate for the L29, L67 and I75 canal sites (816.1 $\mu g\ g^{-1}$) and lowest along the C111 canal (412.4 $\mu g\ g^{-1}$) ($p < 0.05$). Concentrations varied as a function of distance in all canal sites (Table 1) except the C111, although only two distances were available for this canal (5 vs. 7500 m, $p = 1.000$). In the other four sites, concentrations increased by 50% within 5 m of canals (5 vs. all other distances, $p < 0.006$). Interestingly, concentrations at 7500 m were very similar to concentrations in the 100–

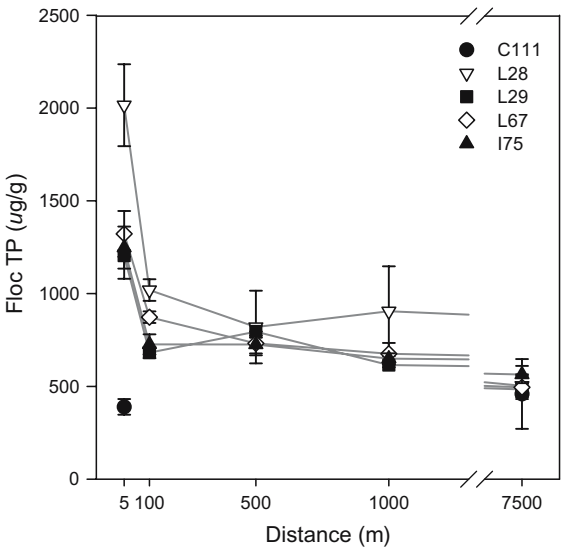

Figure 3. Total phosphorus (TP) concentration (μg g^{-1}) as a function of distance from a canal for the 5 canal study sites (C111, L28, L29, L67 and I75). Data are means ± 1 SE.

1000 m range. The only exception was the L28 canal, where concentrations at 100 m doubled concentrations found at the inner-marsh site ($p = 0.004$). Disturbance from airboat traffic had little effect on TP concentrations; in 4 out of the 5 canals, pairwise comparisons at each distance showed no differences in TP between the airboat trail and the undisturbed marsh. The L28 canal was the exception; on average, concentrations in the airboat trail doubled those of the marsh transect (marsh vs. trail differed for all distances at $p = 0.0001$; except for 100 m, $p = 1.000$). The abundances of all organisms, averaged across seasons, were positively correlated with TP concentrations across study sites (Large fish, $R^2 = 0.37$, $p = 0.0001$; small fish, $R^2 = 0.15$, $p = 0.016$; macroinvertebrates: $R^2 = 0.23$, $p = 0.002$) (Fig. 4).

Community structure variation among canals

Community structure varied consistently among canal sites (Small fishes: Global $R = 0.49$, $p = 0.001$; macroinvertebrates: Global $R = 0.32$, $p = 0.001$; large fishes: Global $R = 0.22$, $p = 0.001$). The greatest difference among canals was detected in the small-fish community (Fig. 5a). Small-fish community structure in the L29 canal was distinct

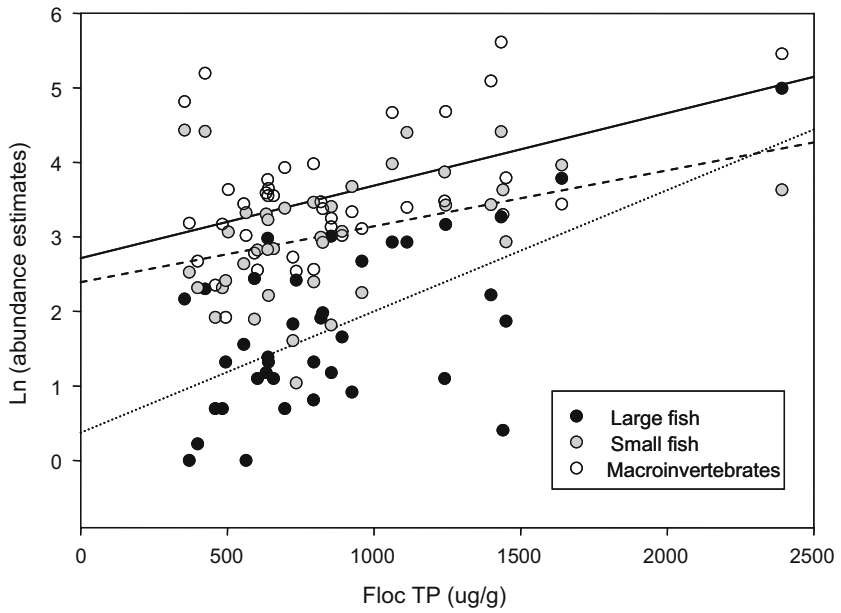

Figure 4. Estimates of abundance averaged across sampling seasons (Log-transformed) plotted as a function of floc TP concentration. Separate least-squares regression functions were fitted to large fish CPUE (solid line), small fish density (dashed line) and macroinvertebrate density (dotted line).

from that of the C111, I75 and L28 (Pairwise comparisons: $R > 0.75$, $p < 0.002$). Density of eastern mosquitofish (*Gambusia holbrook*i), least killifish (*Heterandria formosa*) and golden topminnow (*Fundulus chrysotus*) were lowest in the L29 canal relative to other canals (Tukey pairwise comparisons: all $p < 0.05$). Bluespotted sunfish (*Enneacanthus gloriosus*) were found at their highest densities at the L29 and L67 canal transects, while flagfish (*Jordanella floridae*) were found at their lowest densities there ($p < 0.03$). Marsh killifish (*Fundulus confluentus*) were most abundant at the C111 canal ($p = 0.0001$). The other large canal difference was between the I75 and L67 canals ($R = 0.76$, $p = 0.001$). The I75 canal sites had higher densities of flagfish and least killifish and lower densities of bluespotted sunfish compared to the L67 canal sites ($p < 0.02$).

Community structure of macroinvertebrates also varied between the L29 and the I75, L28 and C111 canals (Pairwise $R > 0.46$, $p < 0.002$) and to a similar degree between the L28 and L67 canals ($R = 0.49$, $p = 0.001$). Everglades crayfish (*Procambarus alleni*), slough crayfish (*Procambarus fallax*), creeping water bugs (*Pelocoris femoratus*), halloween pennant dragonfly naiads (*Celithemis eponina*), four-spotted pennant dragonfly naiads (*Brachymesia gravida*) and aquatic beetles (adult Coleoptera) were responsible for over 50% of the dissimilarity among these canals. Everglades crayfish were found almost exclusively in marshes adjacent to the C111 canal, whereas slough crayfish were most dense at the I75 and L28 canal sites and less dense in the L67 canal ($p < 0.02$). Among dragonflies, halloween pennant naiads were the most common dragonfly species at the L29, whereas four-spotted pennants were most common at the L67 canal; both species were found at low densities at the L28 canal transect ($p = 0.05$ and $p = 0.001$ respectively). Beetles and creeping water bugs were most dense at the C111 and L29 canal transects ($p < 0.03$).

The greatest inter-canal differences in large-fish community structure were observed between the C111, L29 and L67 canals (Global $R = 0.56$, $p = 0.009$ and Global $R = 0.55$, $p = 0.02$ respectively). Lake chubsuckers (*Erymizon sucetta*) were more common at the L29 canal than the C111 canal, whereas blue tilapia (*Oreochromis aureus*) and Seminole killifish (*Fundulus seminolis*), although caught in low numbers (see electronic supplementary material[1]), were almost exclusively found in the C111 canal area ($p < 0.027$).

Community structure as a function of distance

Distance from a canal had little effect on community structure of small fishes (Global $R = -0.04$, $p = 0.84$) and macroinvertebrates (Global $R = 0.04$, $p = 0.148$), but did impact structure of large fish communities (Global $R = 0.23$, $p = 0.001$). As seen in the density analyses, community variation was only seen in the immediate proximity of canals. Large-fish structure at 5 m differed markedly from all other distances ($p < 0.003$) and dissimilarity was greatest between the 5 m and the inner 7500 m sites (highest $R = 0.79$, $p = 0.003$) (Fig. 5c). Eight species accounted for about 70% of the dissimilarity between 5 m and other distances: Florida gar (*Lepisosteus platyrhincus*), largemouth bass (*Micropterus salmoides*), warmouth (*Lepomis gulosus*), redear sunfish (*Lepomis microlophus*), bluegill sunfish (*Lepomis macrochirus*), spotted sunfish (*Lepomis punctatus*), lake chubsucker and bowfin (*Amia calva*). Density varied as a function of distance for a subset of these species. Florida gar, largemouth bass, redear sunfish and bluegill were more common within 5 m of canals (5 vs. 7500, all $p < 0.05$).

Community structure as a function of disturbance

We observed little effect of disturbance on the structure of the aquatic community in our study sites. Fish community structure did not differ between the undisturbed marsh transect and the airboat trail (Large fishes: Global $R = 0.01$, $p = 0.38$; small fishes: Global $R = 0.02$, $p = 0.21$). Macroinvertebrates did vary between airboat trails and adjacent marsh, although the difference was not marked (Global $R = 0.10$, $p = 0.001$). Differences in density between the two transect types were detected in only 3 of the 36 macroinvertebrate taxa. Creeping water bug density was higher in undis-

[1] Electronic supplementary material is available for this article at http://www.dx.doi.org/ 10.1007/s10750-006-0142-z

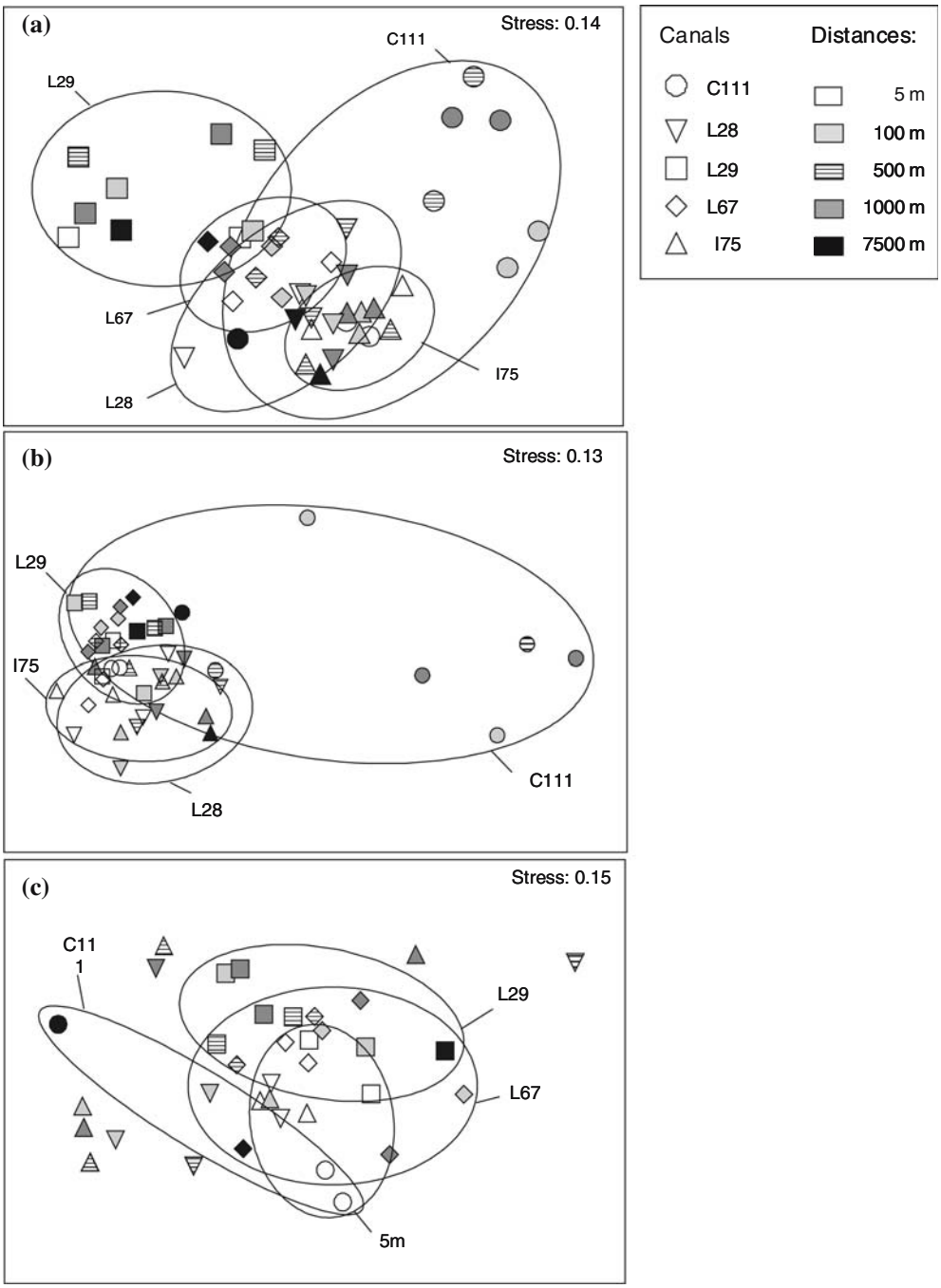

Figure 5. Two-dimensional non-metric MDS ordination of (a) small fish and (b) macroinvertebrate densities and of (c) large fish CPUE based on √-transformed season averages and Bray–Curtis similarities. Symbols designate the 5 canal study sites, whereas shading designates distances from canals. Circles surrounding symbols indicate the main canal and distance groupings.

turbed marsh ($F_{1,43} = 12.2$, $p = 0.001$), whereas density of riverine grass shrimp (*Palaemonetes paludosus*) and four-spotted pennant naiads tended to be higher in airboat trails than the adjacent marsh ($F_{1,43} = 3.0$, $p = 0.09$ and $F_{1,43} = 3.8$, $p = 0.07$ respectively).

Discussion

Water control structures, levees and canals have become ubiquitous features in aquatic ecosystems. In many cases, these may not be practically removed because of present-day requirements for flood control in human-dominated landscapes, even in systems undergoing restoration. In the Everglades, restoration efforts call for the removal of only 380 of the more than 2500 km of canals and levees that presently control the amount, extent and timing of water delivery (CERP, 1999). Understanding how these man-made features affect the structure of aquatic communities and ecosystem processes is a critical component of understanding the ecology of this ecosystem. Our sampling found evidence of an effect of man-made canals on the abundance of aquatic organisms inhabiting nearby marshes, but little effect on their community structure. Previous studies conducted in the northern Everglades have documented changes in community structure with distance from canals in both vegetation (King et al., 2004) and macroinvertebrate communities (McCormick et al., 2004). In our study, distance from a canal consistently affected patterns of abundance in the macroinvertebrate, small fish and large fish communities, but only over short distances. In all three cases, density increased within the immediate proximity of canals (5 m), while communities at 100 m or greater distances were remarkably similar to those found in interior marshes.

The increases in the density of all aquatic groups (both small prey and large predatory species) in marshes adjacent to canals matches the spatial pattern of P enrichment, suggesting a role for resource stimulation provided by canals. Floc TP increased sharply within 5 m of canals in all cases except the southern-most canal, the C111. In this area, soils are marly and have lower organic matter content than the peat soils found in the other four study sites. These soils typically have lower P content when reported on a per-weight basis (Harris & Hurt, 1999). Gradients of nutrient enrichment as a function of distance from canals have been reported over much greater distances than those found in this study (Doren et al., 1997; Childers et al., 2003). For instance, Childers et al. (2003) reports exponential increases in soil P up to 4 km from a canal in high enrichment canals and less than 0.5 km in low enrichment canals including areas in the proximity of our L29 site.

Increases in nutrient levels can result in changes in patterns of abundance and species composition across multiple trophic levels. However, both theoretical and empirical evidence show that these responses may be varied and unpredictable (Power, 1992; Abrams, 1993) and strongly dependent on food-web structure (Leibold & Wilbur, 1992). In the Everglades, multiple effects have been reported in response to anthropogenic P enrichment. Even at low concentrations of TP, persistent phosphorus loading alters periphyton community composition and mats eventually collapse (Gaiser et al., 2005). In the plant community, stem density and/or biomass of macrophytes may increase in response to persistent low-concentration P enrichment (Daoust & Childers, 2004; Gaiser et al., 2005). High levels of P-loading lead to the replacement of both periphyton and macrophytes by monocultures of cattail *Typha domingensis* (Davis, 1994; Doren et al., 1997).

In our study, the abundance of all groups, including large predators, was positively correlated to P enrichment levels. However, previous studies have reported both positive and negative relationships between primary-consumer density and P levels. Increases in the abundance and diversity of small fishes and macroinvertebrates have been reported along natural productivity gradients in marshes (Turner et al., 1999; Trexler et al., 2002). In response to anthropogenic P enrichment, Turner et al. (1999) reported higher standing stocks (dry mass m^{-2}) of small fish in P-enriched sites near canal inflows (<3 km), but no difference in invertebrate standing stocks. Rader & Richardson (1994) reported greater densities and species richness of both small fishes and invertebrates in P-enriched sites in the northern Everglades, but comparable trophic structure. McCormick et al. (2004) documented both increases and decreases in macroinvertebrate densities in enriched sites depending on the microhabitat sampled, accompanied by large compositional changes and some functional changes. Gaiser et al. (2005) reported complex responses in fish biomass that were dependent on dosing level and time since dosing was initiated.

Our data showed that sharp increases in the density of aquatic organisms within 5 m from

canals were more prevalent in the dry season. This seasonal pattern suggests that canals act as dry-down refugia for both large and small aquatic organisms. These dry-season effects were detected even in marshes with long hydroperiods and that did not dry in the year of our study. Marsh animals may be altering habitat use to move toward canals either in anticipation of dropping water levels or in response to other physiological requirements (i.e., mating, foraging) or stresses (i.e., decreased water quality). Previous research has reported a similar accumulation of predatory fishes in alligator holes in years when marsh levels drop below 30 cm (Kushlan, 1974; Nelson & Loftus, 1996; Trexler et al., 2002). Even in long-hydroperiod marshes that rarely dry and where direct mortality due to dry-down conditions is unlikely, predator densities decrease significantly in the open marsh during the dry season, further suggesting movements into deep-water refugia (Chick et al., 2004). Radiotelemetry data demonstrate that Florida gar move long distances (>10 km) in response to drops in water level (J. Trexler, unpublished data). Genetic analyses indicate that spotted sunfish are more homogeneous in canals than in interior-marsh alligator ponds, possibly from increased mixing resulting from dry-season colonization from many sources and/or high dispersal within canals (McElroy et al., 2002).

Fluctuations of the hydrology of aquatic systems strongly affect fish and macroinvertebrate populations (Snodgrass et al., 1996; Corti et al., 1997). The hydrologic pattern of recurrent drought of Everglades marshes is a strong limiting factor on the abundance of aquatic organisms living there (Loftus & Eklund, 1994; Ruetz et al., 2005; Trexler et al., 2005), particularly on long-lived (i.e., large) fishes (Chick et al., 2004). Standing stocks of fish are relatively low compared to other wetlands (Turner et al., 1999). Disturbance from seasonal drying and from more severe drought events are known to cause significant fish mortality (Kushlan, 1974; Nelson & Loftus, 1996). Access to dry-season refuges is thought to be a key factor affecting survival and overall population dynamics (DeAngelis et al., 1997). Increased water permanence provided by canals may lessen the limiting effect of hydrology on fish populations, at least at the local scale.

Few compositional changes in the aquatic communities sampled were detected as a function of distance from canals. Most of the community variation was detected among canal sites and we consider this variation to reflect regional differences resulting from gradients in hydroperiod and productivity, as well as water management practices (Chick et al., 2004). We detected some compositional changes in the predatory fish community and we suspect they indicate differences among large fishes in either their preference or ability to find suitable habitat in canals. Canals provide larger and deeper open-water habitats than those found naturally in the ecosystem (Gunderson & Loftus, 1993), but habitat quality could be low. Most of the open water habitat of South Florida canals appears to be underutilized by fishes and the lack of structural complexity can diminish recruitment (Annett, 1998). On the other hand, the lack of habitat complexity may increase the foraging efficiency of predators (Crowder & Cooper, 1982; Savino & Stein, 1989), although large numbers of prey are typically absent from the open-water areas of canals (Fury et al., 1996) except in dry seasons when marshes are completely dried.

If high rates of predation are occurring close to canals, the effect appears overcompensated by stimulation of increased secondary productivity by nutrient enrichment and immigration toward areas adjacent to canals in the dry season. Theory predicts predator effects to be relatively weak in frequently-disturbed habitats (Menge & Sutherland, 1987). Kushlan (1976) suggested that Everglades fish predators have an effect on prey densities only when the frequency of dry-down events is low. Trexler et al. (2005) showed that predator regulation may occur in regions of the ecosystem where the frequency of dry-down is very low (every 10–20 years), such as WCA3A. If canals decrease the frequency of disturbance, at least locally, stronger predator effects may be expected, which were not detected in our study. However, lack of an apparent predatory effect at high predator densities close to canals does not negate the role of predation because sampling data only indicate net patterns in population dynamics.

Off-road vehicles (ORV) are known to negatively affect vegetation and soils in Everglades habitats (NPS, 2000; Welch et al., 2002). ORV use, including the use of airboats, has resulted in alterations of flow patterns, soil displacement and plant community compositional changes. In our

study, disturbance from airboat trails had some effects on densities of aquatic organisms, although effects were limited to short distances from canals. In cases where differences were detected, greater numbers of fishes and macroinvertebrates were detected in airboat trails than in undisturbed marshes. We suspect these effects relate to variation in habitat quality. Although we did not detect large differences in stem density, differences in plant community structure (higher numbers of water lilies such as *Nymphaea* spp at 5 m from canals) and lower periphyton volumes made trails more open habitats that may be preferred by large fish species. Radiotelemetry surveys suggest that large fishes disperse through marshes using trails (Trexler et al. unpublished data). Trails had highly disturbed sediments and were slightly deeper than undisturbed marshes. This suspension of floc could also make them preferred foraging grounds for detritivores.

This study has important implications for efforts to assess the impact of canals in the Everglades. Our results indicate that canal effects are multifaceted and not easily ascertained by net patterns of population density. Canals affect immigration, resource availability and predatory consumption simultaneously in complex patterns. The net effect of canals appears to be limited to their immediate vicinity if they are not delivering nutrient-enriched water consistently over time. However, this may mask general effects of canals if their impact as refuges for large predatory fishes is spread throughout the ecosystem by relatively long-distance dispersal in the wet season. Further research into movement patterns of these fishes, along with experimental analysis of their impacts, is required to further elucidate results from this study.

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