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ORIGINAL PAPER

Association of macroinvertebrate assemblages with dissolved oxygen concentration and wood surface area in selected subtropical streams of the southeastern USA

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Abstract Woody debris (CWD) is an important habitat component in northern Gulf of Mexico coastal plain streams, where low gradients and low flows allow accumulation of CWD and promote low dissolved oxygen (DO) concentrations. We tested the influences of CWD and DO on stream macroinvertebrates experimentally by placing two surface area CWD treatments each in three concentrations of ambient DO in two streams in Louisiana, USA, with macroinvertebrates collected from ambient woody debris used as a control. We also sampled macroinvertebrates in benthic and woody debris habitats in three streams twice yearly over 2 years to examine the applicability of the experimental results. Total abundance, richness (generic), and Shannon–Wiener diversity were all higher in lower DO conditions during the experiment, and total abundance was higher in the larger CWD treatment. Stream sampling corroborated the relationship between higher diversity and low DO in both benthic and woody debris habitats, but the relationship between richness and low DO only was supported in benthic habitats. Few taxa correlated with DO or CWD in the experiment (5 of 21 taxa) or stream survey (2 of 54 taxa). Whereas most taxa were uncorrelated with experimentally manipulated and in-stream measured variables, we suggest these taxa respond as generalists to stream habitat and physicochemistry. Based on this experiment and stream sampling, we believe the majority of macroinvertebrates in these streams are tolerant of seasonally low DO conditions.

Keywords Woody debris · Coastal plain · Dissolved oxygen

Abbreviations

CWD	woody debris
DO	dissolved oxygen
BOD	biochemical oxygen demand
DOC	dissolved organic carbon

Introduction

Woody debris is an important stream habitat component (Benke and Wallace 2003) that can provide food (Anderson et al. 1978), cover and foraging habitat (Barr and Chapin 1981; Dudley and Anderson 1982), and aestivation sites for resident macroinvertebrates (Roeding and Smock 1989). The diversity and abundance of many

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macroinvertebrate taxa are often higher in woody debris than in surrounding habitats (Benke et al. 1984; Drury and Kelso 2000; Burcher and Smock 2002), and some taxa are exclusively epixylic (Wood and Sites 2002; Johnson et al. 2003). Woody debris provides a relatively stable and persistent habitat (Benke and Wallace 1990) that maybe an important substrate in low gradient, sand and silt-dominated coastal plain streams along the northern Gulf of Mexico (Gulf). In Gulf streams, when other hard substrates are unavailable, woody debris macroinvertebrate assemblages exhibit little taxonomic overlap with soft substrate benthic habitats (Kaller 2005). Further, when other hard substrates, such as sand, gravel, and bedrock, are available, woody debris still exhibits higher density and diversity than hard benthic habitats (Drury and Kelso 2000; Johnson and Kennedy 2003; Phillips 2003). Because of episodic high storm flows and erosive soils in southern Louisiana, fallen trees typically are quickly buried in the stream channel or deposited on the stream periphery (Brown and Matthews 1995). As a result, the majority of available woody substrate consists of small diameter debris (<15 cm; CWD) that may be more spatially and temporally ephemeral but is regularly replaced from the riparian canopy.

Stream gradients are generally low in the north-central Gulf coastal plain, and unlike other central North American stream systems (Brown and Matthews 1995), flow is primarily driven by precipitation (Welch 1942; Holland et al. 1952), High organic matter inputs from long growing seasons result in large amounts of CWD, as well as low dissolved oxygen (DO) levels characteristic of this region (Connor and Suttkus 1986; Ice and Sugden 2003). Separating the effects of CWD, which is the dominant hard substrate in these streams (Johnson and Kennedy 2003; Phillips 2003), and DO, which may drop below 1 mg l^{-1} (approx. 10% saturation) during the summer, on macroinvertebrate community structure is difficult because both factors are highly influenced by the low gradients in these systems (Kaller 2005; Williams et al. 2005).

Considerable research into the effects of low DO on fishes has led to a 5.0 mg l^{-1} minimum standard for streams in the USA (United States Environmental Protection Agency 1986 and references therein). However, little consensus exists concerning low DO criteria for stream macroinvertebrates, and tolerances to hypoxic conditions are taxonomically specific. Some taxa, such as molluscs, appear to be sensitive to DO levels below 6.0 mg l^{-1} (Fuller 1974). However, other taxa, including Hirudinea, Decapoda, *Hyallela azteca*, *Gammarus lacustris*, and many aquatic insects (with the exception of the Plecoptera; Roback 1974) tolerate DO levels below 1.0 mg l^{-1} (Hobbs and Hall 1974; Sawyer 1974; Nedbecker 1972; Nebecker et al. 1992).

Ephemeropterans vary widely in DO tolerance, with LC50 values ranging from 49.5% (*Rhithrogena iridina*; approx. 5.3 mg l^{-1} as calculated from data provided) to 0.3% (*Ephemera vulgate*; approx 0.03 mg l^{-1} as calculated from data provided) saturation (Jacob and Walther 1981; Jacob et al. 1984). Across assemblages, macroinvertebrate community responses to low DO vary from depauperate communities in Gulf coastal streams at or below 2 mg l^{-1} (approx. 26% saturation as calculated from data provided; Didonato et al. 2003) to high tolerance in upland and lowland Australian streams (DO levels of 1.0 mg l^{-1} (10% saturation) for 5 days). Upland Ephemeroptera and lowland Chironomidae were the most and least sensitive taxa, respectively, in Australia (Connolly et al. 2004). Finally, some assemblages have responded both positively and negatively to low DO (Ruse 1996).

Because CWD and DO may have both independent and interactive effects on macroinvertebrate community structure, we designed a two part study comprising: (1) a field experiment in two streams testing the effects of CWD surface area (2 levels), DO concentration (3 concentrations), and the interaction of the two variables on macroinvertebrate colonization; and (2) sample collections from three streams to examine the ability of the experimental results to predict the relative influence of CWD and DO on macroinvertebrate community structure. Based on our experiences in similar streams, we hypothesized macroinvertebrate communities would be most diverse and numerically abundant on the larger surface area CWD treatment within each DO concentration because of increased foraging and predation avoidance opportunities and, given equivalent woody debris surface areas, in the highest DO concentrations available.

Methods

We conducted the experiment in Mill Creek and West Fork of Six Mile Creek (Six Mile Creek), both 2nd order bottomland streams in southwestern Louisiana. Both streams incise the flat and poorly drained Pleistocene terrace, which was formed from alluvial deposits of sand and silt from the fluctuating shoreline of the Gulf and the wandering delta of the Mississippi River, until their confluence with the Calcasieu River (Welch 1942; Holland et al. 1952). Riparian forests of both streams are southern hardwood tree species [mostly oak (*Quercus nigra*) and sweetgum, (*Liquidambar styraciflua*)] with pine forests [mostly longleaf pine (*Pinus palustris*)] dominating upland areas. For stream sampling, we added a third stream. Big Brushy Creek, which was intermediate in gradient, DO, and CWD amount between Six Mile and Mill creeks. Although within a 21 km radius of each other, the streams differ substantially in gradient, flow, and DO levels. The Mill Creek watershed is managed in silvicultural rotations jointly by Boise Cascade Holdings LLC, Roy O. Martin Lumber Company, and the Louisiana Department of Wildlife and Fisheries, whereas Six Mile and Big Brushy Creeks are managed by the United States Department of Agriculture Forest Service as safety zones for United States Army Fort Polk. Although military training could potentially confound the results (e.g., Phillips and Perry 2002), Williams et al. (2005) concluded military training had little influence on aquatic biota in Ft. Polk streams.

Field experiment

In June 2003, we collected CWD from randomly selected debris piles on the floodplain of each creek, and sterilized the CWD in an autoclave at 120°C for 45 min to eliminate microbial and fungal colonies that could influence macroinvertebrate colonization patterns during the experiment (Dudley and Anderson 1982). We divided the CWD into groups of 10 pieces of CWD of similar length and width into two treatment groups, larger CWD (>10 mm in diameter; mean surface area 1,743.1 mm^2) and smaller CWD (≥1 mm and ≤5 mm in diameter; mean surface area 856.2 mm^2).

In July 2003, we placed CWD treatments into cylindrical plastic mesh enclosures (490 mm in length × 88 mm in diameter, 12 mm mesh openings; CWD enclosures) that retained the CWD but allowed access by macroinvertebrates. We returned the CWD enclosures to the collection stream to reduce colonization avoidance from ‘‘unfamiliar’’ wood types. Pairs of larger and smaller treatments were secured to a 1-m length of rebar inserted into the stream bottom to maintain CWD enclosure positions. In each stream, a 50-m long site was selected that exhibited a range of DO concentrations in close proximity to each other (high, medium, and low concentrations based on relative values for each stream), and each DO group received 10 plastic enclosures of each CWD treatment, yielding a total of 120 experimental units (2 streams × 3 DO concentrations × 2 CWD treatments × 10 enclosures of each CWD type). CWD enclosures remained in the stream for 5 weeks, which we believed based on O'Connor (1991) and Drury and Kelso (2000) would allow sufficient time for colonization for many macroinvertebrates.

In August 2003, we removed the CWD enclosures from the streams by quickly surrounding the enclosure with a 250 μm diameter mesh bag, removing the bag and enclosure from the stream, washing the woody debris and macroinvertebrates into plastic bags, and preserving the wood and macroinvertebrates with 95% ethanol on site. Because CWD enclosure placements differed slightly in physicochemistry, we recorded temperature, DO, specific conductance, and water velocity with YSI model 85 handheld probe and a Sontek velocity probe (both Yellow Springs Inc., Yellow Springs, OH) at the beginning of the experiment, and weekly thereafter until the enclosures were harvested. We believed that 24-h DO measurements were unnecessary because of little observed diel variation in DO in nearby forested streams(Bryan et al. 1995). We also collected two samples of naturally occurring CWD in a 0.25 mm mesh bag (472 mm × 127 mm × 127 mm) at each site to assess natural colonization patterns as an experimental control.

Stream sampling

We sampled benthic and woody debris habitats in three streams four times from 2002 to 2004. Beginning in August 2002, we selected three 100 m sampling reaches in each stream and in each reach collected nine benthic substrate samples with a modified Hess sampler (0.0182 m^2, 250 μm mesh), and nine woody debris samples that each consisted of 10 sticks ranging in diameter from 10 to 50 mm in diameter collected from spatially isolated woodpiles within the sampling reach, which were placed in a 250 μm mesh bag. Hess samples were collected near each sampled woodpile. All 648 samples(4 sampling periods × 3 streams × 3 sites 9 Hess samples and 9 woody debris samples) were preserved in 70% ethanol on site. At each site, we also collected two 1 l mid-water column samples for determination of fecal coliform counts as an index of agricultural and animal disturbance, and heterotrophic plate counts as an index of biofilm development and for interpretation of biochemical oxygen demand (BOD), following collection protocols outlined by the American Public Health Association (1998). At the same time, we collected a 1 l water sample for analyses of BOD, total carbon, inorganic carbon, total organic carbon, dissolved organic carbon (DOC), and total nitrogen. At each reach in each stream, we also measured DO, specific conductance, and temperature with a handheld YSI Model 95 probe (YSI Incorporated, Yellow Springs, Ohio, USA). We measured depth, flow (Sontek velocity meter, YSI Incorporated), number, size, orientation, and complexity (single or multiple pieces) of woody debris, canopy cover, habitat type, and presence of benthic fine organic detritus at three points along 10 transects located at approximately 10 m intervals along the 100 m stream reach, with transect length determining wetted stream width. These streams were deeply incised; therefore, wetted width generally corresponded to total width. Because we were interested in macroinvertebrate DO tolerance and CWD use in periods of greatest stress, we collected our data in August 2002 and 2003 when summer flows were low and temperatures were high, and in April 2003 and 2004 following episodic and torrential high water events from winter tropical storms and Hurricane Lili, which directly struck the Mill Creek watershed in October 2002.

Lab processing

Macroinvertebrates were identified to the lowest practical taxon, occasionally species, but more often genus under low power (15× magnification). However, members of Chironomidae, Ceratopogonidae, Tipulidae, and all Annelida were mounted on glass microscope slides with CMC-10 (Master's Chemical Company, Elk Grove, Illinois, USA) following protocols outlined by Epler (2001) and identified to the lowest practical taxon, occasionally species, but more often sub-family, under 60× magnification. A small percentage of samples were set aside for identification quality control, and remaining samples were placed in 95% ethanol for submission as vouchers to the Louisiana Agricultural Experiment Station (128 RNR Building, Louisiana State University, Baton Rouge, Louisiana, USA).

Water samples collected for chemical analyses were stored on ice and split into carbon samples, BOD samples, and microbial samples. Carbon samples were analyzed with a Shimadzu TOC-V Combustion Analyzer (Shimadzu North America, Columbia, Maryland, USA) via Method 5310.B (American Public Health Association 1998). Laboratory procedures for 5 and 20 day BOD readings and estimation of fecal coliform and heterotrophic plate counts followed protocols of the American Public Heath Association (1998), with Millipore HC fecal coliform testing filters and media (Millipore Incorporated, Billerica, Maine, USA), and R2A media (DIFCO, BD Diagnostics, Franklin Lakes, New Jersey, USA) for HPC estimation. FC counts and HPC were made under magnification with a darkfield Quebec colony counter (Leica Microsystems, Buffalo, New York, USA).

Statistical analyses

For both studies, we calculated total abundance, taxa (genus) richness, and Shannon–Wiener diversity (H') for each experimental unit and stream sample using all taxa collected during the experiment and all taxa collected during the stream sampling. For each study, we performed backward selection analysis of covariance (ANCOVA; Stevens 2002; Dowdy et al. 2004; PROCs MIXED and REG, SAS, Version 9.0, Cary, North Carolina, USA), with *a priori* comparisons based on our hypotheses among CWD treatments and DO concentrations with flow, specific conductance, and temperature as covariates to enhance interpretation and account for subtle differences among enclosure and sampling locations. Additional physical and chemical parameters measured during the stream sampling were added to the ANCOVA of the stream sampling data. Variable selection by general linear test followed Agresti (1996).

Macroinvertebrate data presented a problem for analyses of specific taxa, as we identified a large number of taxa (77 in the experiment and 145 in the stream survey) and a relatively low number of individuals (7,564 in the experiment and 26,209 in the stream survey) yielding violations of the assumptions of normality and equality of variances. Therefore, to facilitate these assumptions for statistical analyses, we reduced the number of taxa for subsequent analyses to taxa found in greater than 10% of the experimental units (21 taxa in the experimental subset; Table 1) and, because we could add taxa due to a larger sample size, 1% of the stream sampling samples (54 taxa in the stream sampling subset; Table 1).

To avoid analytical artifacts that may have been the result of using multiple techniques, we chose ordination to examine relationships among taxa and explanatory variables for both studies. Following standardization to a common surface area (500 mm^2), we performed canonical correlation analysis (CCorA; Gittens 1985; Stevens 2002; PROC CANCORR, SAS vers. 9.0 as above) on each subset to test the relationships between: (1) macroinvertebrate taxa and the experimental surface area treatments and DO concentrations; and (2) macroinvertebrate taxa and stream characteristics. We chose CCorA because a wide variety of data can be compared in both exploratory and predictive fashion (Leurgans et al. 1993; Johnson and Wichern 2002; Anderson and Willis 2003). Secondly, CCorA is an established technique for macroinvertebrate community analyses (e.g., Rempel et al. 2000). Finally, we believed unimodal ordination, such as canonical correspondence analysis, was inappropriate because ordination axes appeared monotonic (standard deviations less than 2; ter Braak 1995), and a large number of empty cells in our data set precluded the use of chi-square analysis (Lepš and Šmilauer 2003). Criteria for interpreting correlation significance followed Stevens (2002). Stream sampling data was split for CCorA into woody debris and benthic samples to reduce bias from the use of woody debris collection bags and a Hess sampler. Relationships among taxa and potential explanatory variables were visually displayed with correlation matrix-based, symmetric principal component biplots (Johnson and Wichern 2002; Canoco for Windows 4.5 and CanoDraw for Windows 4.12, Microcomputer Power, Ithaca, New York, USA).

Results

Field experiment

None of the covariates (Table 2) included in the ANCOVA of the experimental data were significant (all $p>0.05$) and thus were not used in interpretation. Interactions of stream with DO and CWD were significant in all models; therefore, we relied on our *a priori* comparisons within DO concentration and CWD treatment for interpretation. Total macroinvertebrate abundance was significantly higher in the larger CWD treatment in the Mill Creek low DO concentration enclosures compared to Six Mile high DO concentration enclosures ($F_{1,54} = 36.99$, $P < 0.001$) and in Mill Creek low DO concentration enclosures compared to the other Mill Creek DO concentration enclosures (low versus high $F_{1,54} = 25.48$, $P < 0.001$; low versus medium $F_{1,54} = 27.28$, $P < 0.001$). In the smaller CWD

Table 1 Taxa found in greater than 10% of experimental samples (“EXP”), and taxa found in greater than 1% of stream samples (“STR”) in Big Brushy, Mill, and Six Mile creeks, Louisiana, USA

Annelida
Rhychobdellida
Helobdella spp. EXP, STR
Oligochaeta
Lumbricidae EXP, STR
Insecta
Ephemeroptera
Baetidae EXP, STR
Caenis hilaris Say EXP, STR
Leptophlebiidae STR
Stenacron floridense EXP, STR
Stenacron interpunctatum Say STR
Stenonema spp. EXP STR
Odonata
Argia spp. STR
Dromogomophus spp. STR
Plecoptera
Agnetina spp. STR
Eccopteura spp. STR
Leuctra spp. STR
Other Leuctridae STR
Neoperla spp. STR
Perlesta spp. STR
Perlinella spp. STR
Undentifiable Perlidae STR
Trichoptera
Cheumatopsyche spp. EXP, STR
Chimarra spp. STR
Macrostenum spp. STR
Polycentropus spp. STR
Wormaldia spp. STR
Coleoptera
Ancyronyx spp. STR
Dubiraphia spp. EXP, STR
Ectopria spp. *STR*
Gonielmis spp. STR
Macronychus glabratus EXP STR
Promoresia spp. STR
Stenelmis spp. EXP, STR
Unidentifiable Coleoptera STR
Unidentifiable Elmidae STR
Megaloptera
Sialis spp. STR
Diptera
Atherix spp. EXP, STR
Bezzia spp. STR
Ceratopogonidae EXP. STR
Chironominae EXP, STR
Corynoneura spp. EXP, STR
Forcipomia spp. STR
Pedicia spp. STR
Simuliidae STR
Tanypodinae EXP, STR
Unidentifiable Chironomidae STR
Malacostraca
Decapoda
Procambarus spp. EXP, STR
Amphipoda
Crangonyx spp. EXP, STR
Isopoda
Lirceus spp. EXP STR
Mollusca
Bivalvia
Corbicula fluminea EXP, STR
Sphaeridae STR
Unionidae STR
Unidentifiable Pelecypoda STR
Gastropoda
Laevepex spp. EXP, STR
Physidae STR
Planorbidae STR
Pomacea spp. EXP, STR

treatments, Mill Creek low DO concentration enclosures yielded significantly greater total macroinvertebrate abundances than Six Mile Creek sites in DO concentration-to-DO concentration comparisons ($F_{1,54} = 29.64$, $P < 0.001$), and the Mill Creek low DO concentration enclosures were also higher in total macroinvertebrate abundance than the other two Mill Creek DO groups (low versus high $F_{1,54} = 39.16$, $P < 0.001$; low versus medium $F_{1,54} = 54.04$, $P < 0.001$). Taxa richness(generic level) did not depend on CWD treatment but was significantly higher in the low DO concentration enclosures in Mill Creek ($F_{1,51} = 15.5$, $P < 0.001$; 14.1±0.58 SE taxa per enclosure) than in the high DO concentration enclosures in Six Mile Creek ($F_{1,51} = 39.75$, $P < 0.001$; 9.4±0.86 SE taxa per enclosure). In DO concentration-to-DO concentration comparisons, Mill Creek (an average of 12.5±0.99 SE taxa per enclosure), had significantly higher taxa richness($F_{1,51} = 46.5$, $P < 0.001$) than Six Mile Creek (mean 6.5±0.78 SE taxa overall per enclosure). However, despite higher taxa richness per enclosure in Mill Creek, the overall number of taxa

Table 2 Mean physicochemical characteristics (±SE) over the 5-week experiment at each site in Mill and Six Mile creeks

Stream	DO Level	Flow (cm s^{-1})	Specific conductance (μS-cm)	Temperature (°C)	DO (mg l^{-1})	DO saturation (%)
Mill	High	1.5 (1.1)	85.6 (36.1)	25.2 (0.8)	3.1 (0.7)*	37
Mill	Medium	0.6 (0.3)	86.7 (36.9)	25.4 (0.9)	2.8 (0.9)*	34
Mill	Low	2.6 (1.0)	31.1 (17.2)	25.3(1.0)	2.7 (0.8)*	33
Six Mile	High	21.2 (1.3)	22.0 (0.4)	23.8 (0.8)	7.3 (0.08)	86
Six Mile	Medium	14.9 (1.5)	21.7 (0.5)	23.4 (0.8)	6.9 (0.03)	81
Six Mile	Low	0	17.2 (2.3)	24.6 (1.2)	3.4 (0.6)*	42

Asterisks indicate sites that would not have met Louisiana Department of Environmental Quality dissolved oxygen (DO) standards for supporting fish and wildlife identified was similar in Six Mile Creek (57 taxa with 26 taxa restricted to Six Mile Creek) compared to Mill Creek (54 taxa with 22 taxa restricted to Mill Creek) with 33 taxa shared between the streams. Finally, Shannon–Wiener diversity was significantly higher ($F_{1,111} = 12.38$, $P < 0.001$) in the larger CWD treatments in the Six Mile Creek low DO concentration enclosures. Within treatment groups, diversity was higher in the Mill Creek high ($F_{1,54} = 10.72$, P=0.001) DO concentration enclosures relative to medium DO concentrations, and higher in medium ($F_{1,54} = 13.36$, $P < 0.001$) than low DO concentrations. Medium ($F_{1,54} = 19.21$, $P < 0.001$) and high ($F_{1,54} = 82.7$, $P < 0.001$)DO concentration enclosures in Mill Creek were higher in diversity than in all three DO concentration enclosures in Six Mile Creek (1.9±0.16 SE).

The experimental CCorA produced three significant canonical variates (82%variation; $F_{126,616.7} = 2.69$, $P < 0.001$), which we interpreted as a stream variate (43%; CV1), a CWD variate (25%; CV2), and a DO variate (14%; CV3), and indicated that 18 colonizing taxa (86% of 21 taxa) demonstrated substantial (r >0.40) correlations to stream, DO, or CWD (Table 3). Of the 18 taxa, four were positively correlated with higher DO, three were positively correlated with larger CWD, and the remaining 11 were correlated with the study streams (Fig. 1).

Stream sampling

Relationships between CWD, DO, macroinvertebrates, and covariates (Table 4) in the stream sampling data differed somewhat from the experimental data (Table 5). Woody debris and benthic samples both were higher in total abundance in Mill Creek in the stream survey; however, unlike the experiment, no relationships were detected with DO or CWD and total abundance. Richness also differed from the experiment with no relationship detected for DO in the woody debris sample; however, similar to the experiment, a negative relationship was detected between DO and richness in benthic samples. Shannon–Wiener diversity was similar between the experiment and stream sampling studies for both woody debris and benthic samples regarding greater diversity in lower DO, but unlike the experiment, woody debris samples were less diverse in Big Brushy Creek, and benthic samples were more diverse in Six Mile Creek.

Analysis of macroinvertebrates found in woody debris collected during stream sampling revealed six canonical variates (66% of variation; $F_{1196,5318.2} = 1.87$, $P < 0.001$; Table 3), which we interpreted as a Mill Creek variate (19%; CV1), DO variate(14%; CV2), temporal variate (10%; CV3), fecal coliform and heterotrophic plate count variate (9%; CV4), Big Brushy Creek variate (8%; CV5), and a Six Mile Creek variate (7%; CV6). The CCorA of the woody debris samples revealed a similar number of taxa correlating with the study streams (12), higher DO (2), and lower DO (2; Fig. 2).

For the benthic samples, the CCorA produced eight canonical variates (74% of variation; $F_{1196,5444.5}$=2.09, $P < 0.001$; Table 3), which we interpreted as a Mill Creek variate (15%; CV1), a temperature variate (14%; CV2), a temporal variate (10%; CV3), a riffle variate (9%; CV4), a Six Mile variate (8%; CV5), a total nitrogen variate (6%; CV6), a fecal coliform count variate (6%; CV7), and a heterotrophic plate count variate (5%; CV8). Ten taxa demonstrated correlations with the study streams, and although no taxa were correlated with DO or CWD, correlations were evident between specific macroinvertebrates and time of year (4 taxa), heterotrophic plate count (2 taxa), fecal conform count (3 taxa), and temperature (1 taxon).

Discussion

Field experiment

Results of the experiment revealed complex interactions among CWD, DO, and stream influences on macroinvertebrate distributions. Generally, macroinvertebrate colonization patterns did not support our hypothesis regarding woody debris size. Although *Atherix* spp. (Athericidae: Diptera) and *Corynoneura* spp. (Chironomidae: Diptera) were more abundant in larger CWD (Table 3; Figs. 1 and 2), overall species richness, and Shannon–Wiener diversity were not related

Table 3 Relatively few taxa correlated with potential explanatory variables[a] in the field experiment (first 18 taxa) and stream sampling (54 total taxa). Taxa listed were found to exhibit correlations ≥0.40 with the canonical variates

Taxa	Experiment	Benthic samples	Wood samples
Caenis hilaris	Mill Creek (CV1)	Mill Creek (CV1)	Mill Creek (CV1); Temporal (CV3)
Crangoyx spp.	Mill Creek (CV1)	Temporal (CV3)	Mill Creek (CV1)
Lirceus spp.	Mill Creek (CV1)	Not Six Mile Creek (CV6)	None
Corynoneura spp.	Mill Creek (CV]); Large CWD (CV2)	None	Low DO (CV2); Temporal (CV3)
Macronychus glabratus	Mill Creek (CV1); High DO (CV3)	None	Mill Creek (CV1); High DO (CV2); HPC (CV4); Not Big Brushy (CV5)
Tanypodinae	Mill Creek (CV1)	None	Mill Creek (CV1)
Stenacron floridense	Mill Creek (CV1)	Mill Creek (CV1)	Mill Creek (CV1)
Lumbricidae	Mill Creek (CV1)	None	FC (CV4); Not Six Mile Creek (CV6)
Laevepex spp.	Mill Creek (CV1)	Mill Creek (CV1)	Mill Creek (CV1); Low DO (CV2)
Ceratopogonidae	Mill Creek (CV1)	Low FC (CV4)	None
Helobdella spp.	Mill Creek (CV1)	None	Mill Creek (CV1)
Corbicula spp.	Mill Creek (CV1)	Mill Creek (CV1)	HPC (CV4); Not Six Mile Creek (CV6)
Pomacea spp.	Mill Creek (CV1)	None	Mill Creek (CV1); Temporal (CV3)
Dubiraphia spp.	Mill Creek (CV1); High DO (CV3)	None	None
Stenonema spp.	Mill Creek (CV1)	None	None
Atherix spp.	Six Mile Creek (CV1); Large CWD (CV3)	None	Six Mile Creek (CV6)
Baetidae—unidentified	High DO (CV2)	None	None
Stenelmis spp.	High DO (CV2)	None	Mill Creek (CV1); High DO (CV2)
Sialis spp.	Not included	Mill Creek (CV1)	Not Six Mile Creek (CV6)
Bezzia spp.	Not included	Six Mile Creek (CV6)	None
Chironomidae	Not included	Not Six Mile Creek (CV6)	None
Perlesta spp.	Not included	None	Mill Creek (CV1)
Ancyronyx spp.	Not included	None	High DO (CV2); Temporal (CV3)
Elmidae—unidentified	Not included	None	FC (CV4); Six Mile Creek (CV6)
Chimarra spp.	Not included	None	Six Mile Creek (CV6)
Unionidae—unidentified	Not included	None	Not Six Mile Creek (CV6)

[a] "DO" = dissolved oxygen, "CWD" = coarse woody debris, "FC" = fecal coliform, "HPC" = heterotrophic plate and count, "CV" = canonical variate

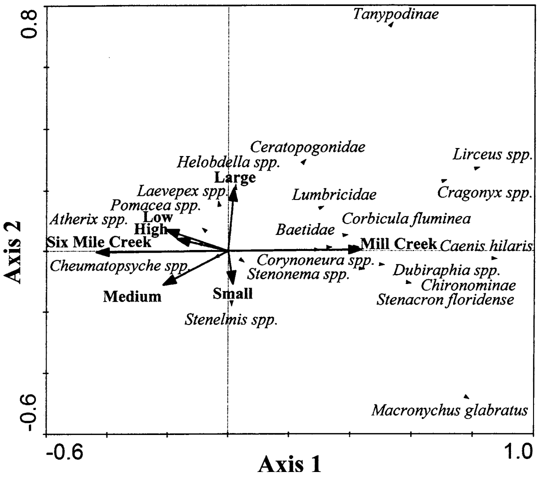

Fig. 1 Ordination of the experimental data with a principal component biplot demonstrated a stronger association of taxa to the streams than to dissolved oxygen (DO) or woody debris surface area (CWD). Triangles represent the scores of individual taxa. Arrows indicate explanatory variables. DO concentration is represented as,“high,” “medium,” and, “low.” CWD treatment is represented as, “control,” “large,” and, “small”

to debris size (Table 5). The importance of CWD as macroinvertebrate habitat varies among taxa and ecosystems (e.g., Northwestern USA: Anderson et al. 1978; Southeastern USA: Rinella and Feminella 2005), and studies have reported greater macroinvertebrate abundance on larger, more complex CWD (O’Conner 1991), and on smaller, less complex CWD (Mathooko and Otieno 2002). Although larger CWD would appear to provide greater opportunities for xylophagy, epixylic grazing, and predatory cover for macroinvertebrates (O’Conner 1991), the usefulness of CWD habitat for many taxa in Mill and Six Mile creeks appears not to be based solely on available surface area; rather, similar to Rinella (2002), colonization appeared to be a response to the introduction of hard substrates.

Although colonization patterns of several taxa supported our hypothesis that macroinvertebrates would be most abundant and diverse at higher DO levels regardless of woody debris size, abundances of a larger number of taxa suggest that this prediction was not correct for the assemblages as a whole. We selected our study sites based on appreciable measured differences in DO within each stream. However, during our experimental time period, DO differences did not establish themselves as substantially as we anticipated. Regardless, we did detect some relationships with DO. Total macroinvertebrate abundances in both treatment groups were higher in lower DO within Mill Creek, and higher in the generally lower DO Mill Creek compared to Six Mile Creek. Taxa richness was greatest at the lowest DO enclosures in each creek, and the lower DO stream, Mill Creek, yielded higher mean numbers of taxa per enclosure than Six Mile Creek. However, Shannon–Wiener diversity was higher in higher DO enclosures within Mill Creek and in comparisons between streams. However, when we examined correlations between specific taxa with DO and CWD, we found few taxa correlating directly with CWD or DO. Instead, of the most common taxa found in the experiment, 18 of 21 taxa were more strongly correlated with the study streams rather than DO or CWD (Table 3; Fig. 1). Interestingly, a majority (11 of 18) of the positive correlations detected were with the typically lower DO, but higher CWD stream, Mill Creek. Most of the other organisms included in the CCorA are considered somewhat to very tolerant of reduced water quality (Barbour et al. 1999); although Mill Creek is not substantially impacted by anthropogenic sources of pollution, it is an oxygen-depressed system due to high organic enrichment and elevated microbial populations from feral and domestic animal activity within the watershed (Kaller and Kelso 2003). Potentially, organic enrichment enhanced the macroinvertebrate assemblage in Mill Creek. However, we do not believe the nutrient enrichment was a positive factor because the organic enrichment, as evidenced by higher BOD and DOC levels (Table 3), was a result of pig activity, which was detrimental to some macroinvertebrates (Kaller and Kelso 2006). These environmentally tolerant organisms, relative to their abundances in a high dissolved oxygen stream, appear to be thriving despite the low DO conditions in Mill Creek.

Most research into the relationships between DO levels and macroinvertebrate community structure has focused on lethal and sub-lethal tolerances (e.g., Nebecker et al. 1992; Connolly et al. 2004) and the relationships between macroinvertebrates and environmental characteristics

Table 4 The addition of Big Brushy Creek (BB) provided measurements of potential explanatory variables[a] intermediate between Six Mile (Six) and Mill (Mill) creeks

Stream	DO (mg l^{-1})	Temperature (°C)	Specific conductance (µs^{-1})	BOD (mg l^{-1})	TOC (mg l^{-1})	IC (mg l^{-1})	DOC (mg l^{-1})	TN (mg l^{-1})
Six	7.82 (0.06)	20.0 (0.24)	19.1 (0.13)	3.78 (0.04)	8.80 (0.13)	0.88 (0.003)	8.36 (0.12)	0.36 (0.004)
BB	6.77 (0.05)	20.7 (0.27)	24.1 (0.26)	5.04 (0.07)	7.88 (0.17)	1.29 (0.008)	6.98 (0.09)	0.32 (0.002)
Mill	2.69 (0.08)	20.7 (0.26)	124.3 (6.10)	10.67 (0.08)	14.67 (0.11)	12.93 (0.30)	13.45 (0.14)	0.60 (0.017)

Stream	FC (# 100 ml^{-1})	HPC (# 1 ml^{-1})	Discharge (m^3 s^{-1})	CWD (# sampling point^{-1})	Wood Volume (m^3 transect^{-1})	Wood Surface Area (m^2 transect^{-1})	Gradient (m km^{-1})
Six	83.3 (5.7)	7,182.0 (780.9)	0.15 (0.01)	1.1 (0.1)	89.8 (28.9)	80.2 (15.8)	1.1
BB	433.4 (51.2)	12,659.8 (1,195.6)	0.10 (0.01)	0.3 (0.1)	949.9 (410.8)	332.5 (118.7)	0.9
Mill	365.6 (32.8)	32,266.8 (4,064.5)	0.06 (0.01)	1.4 (0.1)	5,082.3 (3,036.3)	860.6 (412.3)	0.6

Mean values over the course of stream sampling, 2002–2004, are listed below with standard errors in parentheses. Gradient values from geological surveys of Welch (1942) and Holland et al. (1952)

[a] "DO" = dissolved oxygen, "BOD" = biochemical oxygen demand, "TOC" = total organic carbon. "IC" = inorganic carbon, "DOC" = dissolved organic carbon, "TN" = total nitrogen. "FC" = fecal coliform, "HPC" = heterotrophic plate count and "CWD" = coarse woody debris

at the collection locations (e.g., Ruse 1996). Connolly et al. (2004) reported that DO concentrations under 10% (1.0 mg l^{-1}) saturation were lethal to all insects, and they suggested DO concentrations of 25–35% (2.5–3.3 mg l^{-1}) and 10–20% (1.0–2.0 mg l^{-1}) saturation could have detrimental effects on emergence and survival, respectively, over long periods of time. In this study, DO saturation levels in Mill Creek ranged from 33–37% (2.7–3.1 mg l^{-1}), with much lower values, down to 11% (0.78 mg l^{-1}), recorded from field observations from 2002 to 2004 (Michael D. Kaller, unpublished data), indicating a high tolerance of resident macroinvertebrates to seasonally hypoxic conditions. Leeches (Sawyer 1974) and gastropods (Harman 1974) are often abundant under low DO conditions, and, although generally less tolerant as a group, certain aquatic insects can tolerate DO levels below 5 ppm [51 of 300 taxa listed in Roback (1974)] and even 3 ppm (11 of those 51 taxa) for extended periods of time. We found 22 of 77 macroinvertebrate taxa exclusively in low DO sites (2.7–3.1 mg l^{-1}) and 26 of 77 taxa exclusively in high DO sites (all above 3.5 mg l^{-1}), and we believe that observed colonization patterns during the experiment ultimately reflected the DO sensitivity of the underlying populations in these streams.

The taxonomic composition of the macroinvertebrate assemblages in Mill Creek supports previous studies of DO tolerance among macroinvertebrate taxa. For example, philopotamids (Trichoptera), which have been reported to inhabit waters exhibiting DO levels of at least 6 mg l^{-1} (Roback 1974) and greater than 0.87 mg l^{-1} (8% saturation; Connolly et al. 2004), were not found at DO levels below 3.5 mg l^{-1} (42% saturation), which occurred only in Mill Creek. Twenty six taxa were only found in high DO sites in Six Mile Creek, also suggesting intolerance to hypoxia. However, the most abundant taxa exhibited few statistical differences in abundance among DO concentrations, which is evidence of substantial tolerance to reduced DO concentrations. Davis et al. (2003) also reported few differences between macroinvertebrate assemblages inhabiting reference and lower DO in agriculturally impacted sites, which they attributed to natural fluctuations in water quality

Table 5 Relationships among CWD, DO, and macroinvertebrates[a] differed somewhat between the stream sampling study and the experiment, with fewer relationships to DO and no relationships with CWD

Metric	Experiment results	Sampling results—wood	Sampling results—benthic
Total abundance	Greater in Mill Creek; greater in low DO; greater in larger CWD	Greater in Mill Creek ($F_{2,325}$=13.51, $P<0.001$); greater in lower DOC* ($F_{1,325}$=4.85, P=0.03	Greater in Mill Creek ($F_{2,325}$=13.51, $P<0.001$); greater in higher SPC* ($F_{1,325}$=12.85, $P<0.001$); greater in higher HPC* ($\mathrm{F}_{1,325}$=18.17, $P<0.001$); greater in higher BOD* ($F_{1,325}$=6.73, P=0.01); greater in higher DOC* ($F_{1,325}$=4.52, P=0.03); greater in higher TOC* ($F_{1,325}$=6.42, P=0.01); greater in lower discharge* ($F_{1,325}$=4.87, P=0.03)
Generic level richness	Greater in Mill Creek; greater in low DO	Greater in Mill Creek ($F_{2,325}$=15.44, $P<0.001$); greater in higher DOC* ($F_{1,325}$=15.26, P=0.002)	Lesser in Big Brushy Creek ($F_{2,325}$=6.53, P=0.003); greater in lower DO ($F_{1,325}$=4.90, P=0.03); greater in higher HPC* ($F_{1,325}$=12.43, $P<0.001$); greater in lower BOD* ($F_{1,325}$=21.05, $P<0.001$); greater in higher DOC* ($F_{1,325}$=20.17, $P<0.001$); greater in lower TOC* ($F_{1,325}$=8.66, P=0.004)
Shannon–Wiener diversity	Greater in Mill Creek; greater in low DO	Lower in Big Brushy Creek ($F_{2,325}$=15.26, $P<0.001$); greater in lower DO ($F_{1.325}$=5.67, P=0.02); greater in higher DOC* $F_{1,325}$=15.84, $P<0.001$); greater in lower TOC* ($F_{1,325}$=4.02, P=0.04)	Greater in Six Mile Creek ($F_{2,325}$=7.42, $P<0.001$); greater with time* ($F_{1,325}$=8.36, P=0.005); greater in lower DO ($F_{1,325}$=10.31, P=0.002); greater in higher HPC* ($F_{1,325}$=9.02, P=0.004); greater in lower BOD* ($F_{1,325}$=24.38, $P<0.001$); greater in higher DOC* ($F_{1,325}$=26.75, $P<0.001$); greater in lower TOC* ($F_{1,325}$=13.88, P=0.004)

$P<0.05$ used to retain variables and co-variables (*)

[a] "DO" = Dissolved oxygen, "CWD" = woody debris treatment, "DOC" dissolved organic carbon, "TOC" = total organic carbon, "SPC" = specific conductance, "HPC" = heterotrophic plate count, and "BOD" = biochemical oxygen demand

that selected for high macroinvertebrate tolerance of reduced water quality during low flow periods.

Particularly interesting were the 22 taxa exclusive to Mill Creek, which included 12 insects, five gastropods, three pelecypods (including *Corbicula fluminea*), and two crustaceans. In lotic systems, many of these taxa have been reported to be relatively intolerant of hypoxia, including *C. fluminea* (Johnson and McMahon 1998; Saloom and Duncan 2005); *Dubiraphia* spp. (Elmidae; Coleoptera; Sinclair 1964; Barbour et al. 1999); and gastropods in the families Ancyclidae, Planorbidae, and Physidae (Ellis 1931; Smith 2001). However, our data suggest that these general statements of DO sensitivity may be too simplified, particularly in low-energy, coastal streams. Assemblages in these streams may include numerous lentic-associated taxa, such as *Dubiraphia* spp. (Sinclair 1964) and *Pyganodon grandis* (Chen et al. 2001),that may be able to regulate internal oxygen levels and exploit the typically low flow conditions characteristic of Mill Creek. However, Mill Creek still supports many taxa, such as *Caenis hilaris* (Caenidae: Ephemeroptera) (Berner and Pescador 1988) and *Cheumatopsyche* spp. (Wiggins 1998), which are characteristic of lotic systems.

Stream sampling

Stream sampling data generally corroborated the experimental results. Both woody debris and benthic samples were similar to the experimental data, with higher total abundance, richness, and diversity in lower DO sites. Analyses of the stream sampling data also did not uncover detectable relationships between total abundance, richness, or diversity with CWD. Further, the CCorA on individual taxa also suggested generalist strategies similar to those indicated by the experiment. In the southern U.S., a wide variety of stream habitats and physicochemical characteristics offers the potential for a high diversity of aquatic macroinvertebrates (Lydeard and Mayden 1995; Cushing and Allen 2001). Indeed, collecting 145 taxa appears to support this contention. However, many taxa (91) were uncommon, and a large number of taxa, as well as large proportions of sample taxonomic richness were not shared among wood and benthic habitats, suggesting some limitations in the applicability of the experimental data to all stream taxa. Further, it was difficult to identify environmental parameters that contributed to macroinvertebrate community structure of the remaining 54 taxa despite numerous differences in habitat and physicochemistry among sampling sites. Surprisingly, considering the dissimilarities among streams, only 26 taxa, which included all 18 experimental taxa whose abundance was

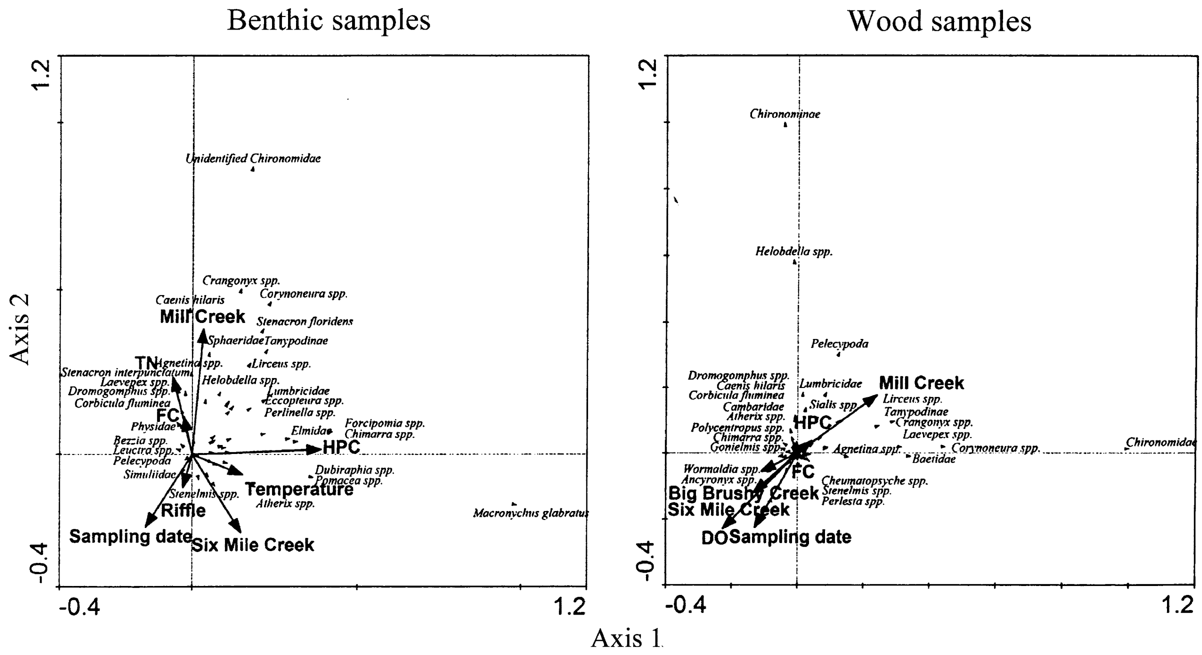

Fig. 2 Ordination of the woody debris and benthic stream sampling data with a principal component biplot demonstrated the strong influence of stream on the data and highlighted association between environmental characteristics and taxa with streams. Explanatory variables, dissolved oxygen (DO), heterotrophic plate count (HPC), fecal coliform (FC), benthic organic matter (FOD), total nitrogen (TN), total carbon (TC), total organic carbon (TOC), dissolved organic carbon (DOC), and inorganic carbon (IC), are represented by arrows. Triangles represent scores for individual taxa. For clarity, labels of some taxa and variables, which were clustered in the center of the plot, were omitted

significantly related to stream, DO, or CWD, demonstrated notable correlations with stream characteristics, including DO and CWD.

The differences between responses of macroinvertebrates in the experiment and stream sampling may also have been due to Hurricane Lili. Comparisons of habitat and macroinvertebrate assemblages before and after the storm illustrate few lasting effects, as evidenced by the lack of association with sampling date, which includes data before and after the storm (Fig. 2). Therefore, despite the temptation to attribute stream sampling assemblage response differences to the hurricane, we believe the effects of the hurricane were transitory and had little influence on macroinvertebrate response in our study.

Tolerance and evolution

We believe the results of our study indicate that macroinvertebrate communities in these streams are composed of a high proportion of habitat and water quality (specifically DO) generalists as a result of habitat instability, and that selection for generalist macroinvertebrate communities occurred historically during development of the Gulf coast region. Macroinvertebrates have been shown to be functionally plastic with regard to food source (Dangles 2002) and phenotypic response to environmental risks (Peckarsky et al. 2005), and can exhibit increased diversity in unstable habitats (Death and Winterbourn 1995). Similarly, Johnson and Kennedy (2003) and Williams et al. (2005) reported few strong habitat-macroinvertebrate relationships in Gulf streams, and suggested the most numerous macroinvertebrates, and hence most influential in analyses, may be generalists in these systems. Adams et al. (2004) suggested that continual habitat fluctuations kept coastal plain stream fishes in ‘colonizing assemblages.’ Presumably, because fish and stream macroinvertebrates share distribution restrictions, habitat flux may also be selecting for particular generalist/colonizing macroinvertebrate communities that are responding to seasonal variation in flow, habitat structure, and water quality.

Macroinvertebrates have been reliable ecological indicators of many types of perturbation (e.g., Waters 1995; Hartman et al. 2005), even with some seasonal influences (e.g., Kaller and Hartman, 2004). Our difficulty in detecting relationships between macroinvertebrates and stream characteristics may reflect prior selection of macroinvertebrates in this region by evolutionary processes, Mathooko and Otieno (2002) and Johnson and Kennedy (2003) suggested that invertebrate colonization of woody debris may be taxon-specific and related to evolutionary history in streams that exhibited little evidence of historic woody debris accumulation. Substantial evidence suggests plants (Rebertus et al. 1993; Glitzenstein et al. 1995), terrestrial insects (Noonan 1988), and fishes (Mayden 1985, 1988; Connor and Suttkus 1986) in the southeastern United States evolved in highly stochastic ecosystems with a dynamic landscape in a mosaic of successional stages from fire and Weather-related disturbances, glacial isolation events, fluctuating sea levels, and the wandering delta of the Mississippi River. By analogy, macroinvertebrates may have evolved a generalist response to habitat and water quality because of constant disturbances in these relatively new environments [see Bink (1957), Stewart et al. (1976), and Barr and Chapin (1981)] for hypothesized colonization patterns]. Macroinvertebrates colonizing the coastal plain from their ancestral upland habitats as the Gulf retreated would have needed broad tolerances to variations in flow, dissolved oxygen, and riparian disturbance [see Connor and Suttkus (1986) for description]. Potentially, past selection may have acted as a filter for present taxonomic diversity yielding communities with a relic tolerance of DO changes related to historic colonization.

Conclusions

In summary, colonization patterns of macroinvertebrates inhabiting Mill and Six Mile creeks provided some support for our hypothesis that more taxa colonized larger than smaller woody debris treatments, although substantial variability among taxa was evident. However, abundances of many individual taxa, as well as greater total abundance, taxa richness, and Shannon–Wiener diversity suggest our prediction of more diverse and abundant colonization in higher DO habitats was incorrect. Based on this experiment and concurrent stream sampling, we believe macroinvertebrates in these bottomland, coastal streams are highly tolerant of seasonally low DO conditions. In fact, these streams support a much more diverse and abundant assemblage than we would have predicted from assessments of stream physicochemistry. If aquatic macroinvertebrates are to be used in coastal bottomland stream assessments, we suggest further research in these systems is needed to identify the important community structuring factors, particularly the role of physicochemical tolerance in determining community composition.

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