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The rapid effects of a whole-lake reduction of coarse woody debris on fish and benthic macroinvertebrates

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SUMMARY

1. Ecosystems can enhance the biodiversity of adjacent ecosystems through subsidies of prey, nutrients and also habitat. For example, trees can fall into aquatic ecosystems and act as a subsidy that increases aquatic habitat heterogeneity. This habitat subsidy is vulnerable in lakes where anthropogenic development of shorelines coincides with a thinning of riparian forests and the removal of these dead trees (termed coarse woody debris: CWD). How the disruption of this subsidy affects lake ecosystems is not well understood.
2. We performed a whole ecosystem experiment on Little Rock Lake, a small (18 ha), undeveloped, and unfished lake in Vilas County, WI, U.S.A., that is divided into two similar-sized basins by a double poly-vinyl chloride curtain that prevents both fish and water exchange between basins. In 2002, we removed about 70% of the littoral CWD in the treatment basin, while the reference basin was left unaltered. We tested for changes in both fish and benthic macroinvertebrate community composition in the two years following the CWD reduction.
3. Yellow perch (*Perca flavescens*) was the most abundant fish species in the lake prior to our experiment, but declined to very low densities in the treatment basin after manipulation. We found no evidence of an effect on macroinvertebrates – the treatment basin's macroinvertebrate community composition, diversity and density did not change relative to the reference basin.
4. Our results indicate that different trophic groups may have differential responses to the loss of a habitat subsidy, even if anthropogenic effects on that subsidy are severe. In the case of Little Rock Lake, fish community responses were evident on a short-time scale, whereas the macroinvertebrate community did not rapidly change following CWD reduction.

Keywords: habitat subsidy, largemouth bass, Little Rock Lake, whole ecosystem manipulation, yellow perch

Introduction

Coarse woody debris (CWD) is a major contributor to the habitat heterogeneity of lakes in forested regions (Christensen *et al*., 1996; Francis & Schindler, 2006). However, human residential development tends to be clustered on lake shorelines (Schnaiberg *et al*., 2002; Walsh, Soranno & Rutledge, 2003). As lakeshore residential development increases across lakes, CWD density exponentially decreases due to active removal of CWD by shoreline owners and the removal of the source of CWD, riparian forests (Christensen *et al*., 1996; Jennings *et al*., 2003; Francis & Schindler, 2006; Marburg, Turner & Kratz, 2006; Sass *et al*., 2006b). Thus, humans disrupt the link between lakes and riparian forest ecosystems, and as a consequence homogenize lake littoral habitat.

The presence and complexity of CWD affects the abundance, growth and diversity of fishes in lakes. CWD complexity is positively correlated with fish species richness and abundance (Newbrey *et al*.,

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2005). Juvenile or small-bodied fishes may use CWD as predation refuge from large-bodied predators that have difficulty feeding in complex habitat (Sass *et al.*, 2006a,b). Fish growth rates are positively correlated to CWD densities across lakes (Schindler, Geib & Williams, 2000). Thus, loss of CWD in a lake may result in changes to fish community composition and a loss of fish biodiversity (Tonn & Magnuson, 1982; Sass *et al.*, 2006a).

Benthic macroinvertebrate communities may also be sensitive to CWD loss in lakes (Schindler & Scheuerell, 2002; Smokorowski *et al.*, 2006). In lotic systems, CWD is important for maintaining macroinvertebrate diversity and production (Benke & Wallace, 2003; Gregory, Boyer & Gurnell, 2003). Lake macroinvertebrates use macrophytes to hide from fishes (e.g. Crowder & Cooper, 1982; Olson *et al.*, 1998); thus, CWD may similarly be used as refuge from predation (Schindler & Scheuerell, 2002). Nevertheless, Smokorowski *et al.* (2006) removed CWD from randomly selected sections of three lake shorelines and found no effect on whole-lake macroinvertebrate biomass or whole-lake macroinvertebrate order richness.

We used a whole-ecosystem experiment to study how reduction of CWD affects two trophic groups of lake biota – fish and littoral macroinvertebrates. The goal of our research was to compare the composition of these groups through time following a large-scale reduction of CWD in one of two basins of a lake that has been divided by a poly-vinyl chloride (PVC) curtain for over 20 years. Sass *et al.* (2006b) looked for a response of fish abundance to this manipulation by aggregating years into a pre-manipulation group and a post-manipulation group for only the two most abundant fish in our experimental lake, largemouth bass (*Micropterus salmoides* Lacepède, 1802) and yellow perch (*Perca flavescens* Mitchill, 1814). In this article, we look at the responses of all fish species in the lake in terms of how their abundance changes in the first 2 years following the manipulation and in comparison to changes in macroinvertebrate abundance and community composition. Our analyses thus focus on rapid responses, if any, of these two groups. We hypothesized that the fish community composition of the treatment basin would change and that the effect of the manipulation would be most pronounced on yellow perch. Yellow perch use CWD as a spawning substrate and as refuge from largemouth bass predation (Becker, 1983; Carlander, 1997; Sass *et al.*, 2006a; Roth *et al.*, 2007a). We also hypothesized that benthic macroinvertebrate community composition would change and diversity would decrease following the manipulation due to a loss in habitat heterogeneity, disturbance of littoral sediments and altered predator–prey interactions between macroinvertebrates and fish.

Methods

Whole-lake coarse woody debris reduction

We conducted a whole-lake CWD reduction experiment on Little Rock Lake – a well studied (e.g. Martinez, 1991), 18 ha, oligotrophic, seepage lake in the northern Lakes and Forests ecoregion of Vilas county, WI, U.S.A. The details of the manipulation have been presented elsewhere (Sass, 2004; Sass *et al.*, 2006b). Little Rock Lake is undeveloped, surrounded by state forest, and has been closed to public access and fishing since 1984 when it was divided into a reference basin (LRR, 8.1 ha) and a treatment basin (LRT, 9.8 ha) by a PVC curtain. The treatment basin was acidified in the 1980s and allowed to recover during the 1990s (Frost *et al.*, 1999), but prior to our manipulation there were no substantial differences between the basins' biotic compositions (Sampson, 1999; Hrabik & Watras, 2002; Sass, 2004). The dominant littoral structure in Little Rock Lake is CWD; aquatic macrophytes are generally sparse. Thus, Little Rock Lake provided a unique experimental arena in which we were able to examine the effects of CWD reduction without other confounding variables that coincide with residential shoreline development (e.g. lake eutrophication, Carpenter, Ludwig & Brock, 1999).

At the end of the summer of 2002, we removed as much as possible of the CWD (logs >10 cm in diameter) from the littoral zone of the treatment basin using axes, saws and winches. We removed CWD only up to a 2 m depth because very little CWD was present deeper than 2 m and a previous study showed that small prey fish encounter strong predation pressure deeper than 2 m in Little Rock Lake, preventing them from using any deeper CWD (Sass *et al.*, 2006a). New CWD that fell into the treatment basin following the manipulation was also removed. All removed CWD was placed on the shoreline above the high-water mark of the lake to result in a 73% reduction in CWD abundance to 128 logs km^{-1}. Prior to the manipulation, the treatment basin had about 475 large logs per kilometer of shoreline, while the reference basin had 344 logs km^{-1} of shoreline throughout the experiment. In other words, after the manipulation, the treatment basin had 37% of the CWD density of the reference basin. These pre-manipulation densities fall in the middle of the distribution of CWD densities of undeveloped lakes; and our manipulation resulted in a density of CWD in the treatment basin similar to densities found in lakes with modest levels of lakeshore residential development in northern Wisconsin (Christensen *et al.*, 1996; Marburg *et al.*, 2006; Sass *et al.*, 2006b).

Biotic data sets

Fish were sampled from May to September 2001–04 using hook-and-line angling, minnow traps and beach seines. Fish were marked with either a fin clip or, if >150 mm total length, a numbered Floy® tag (Floy Tag Inc., Seattle, WA, U.S.A.). Five fish species occurred in the two basins: largemouth bass, yellow perch, rock bass (*Ambloplites rupestris* Rafinesque, 1817), black crappie (*Pomoxis nigromaculatus* Lesueur, 1829) and central mudminnow (*Umbra limi*, Kirtland, 1840). However, we did not capture any mudminnows, which were only seen sporadically in the diets of largemouth bass. We grouped catch data annually with 2001 as a pre-manipulation year, and 2003 and 2004 as post-manipulation years. Sampling effort was similar among basins in these years; and we excluded data from 2002 because we were not able to intensely sample fish due to the effort involved in wood reduction. We calculated average daily catch rates (using all gear) per year (i.e. average of the number of individuals caught per sampling day per year) for largemouth bass, yellow perch, rock bass and black crappie. We calculated Chapman-modified continuous Schnabel annual population estimates (Ricker, 1975) for only largemouth bass and yellow perch since robust population estimates were not possible for black crappie and rock bass, which remained at low densities throughout the experiment.

We divided the shoreline of Little Rock Lake into 50 m sections and randomly chose five sections from each basin for each separate sampling of macroinvertebrates. We collected two benthos and two CWD macroinvertebrate samples at each section. The different substrates (i.e. benthos and CWD) required different sampling methods. We constructed a benthos sampler by connecting a SCUBA tank to a 7.6 cm PVC pipe with a hose attached 10 cm from one end of the pipe (Wahle & Steneck, 1991; Roth *et al.*, 2007b). A 500 μm Nitex mesh bag was place at the top end of the pipe furthest from the attached hose. Once the tank was turned on, a vacuum formed that sucked the benthos sample into the bag. We used a 0.09 m^2 hoop to delineate the benthos sampling area. We sampled CWD using a self-contained, battery-powered aquatic vacuum with a 500 μm Nitex mesh bag (Vander Zanden *et al.*, 2006). Sampling lasted for 30 s. All samples were stored in 95% ethanol until processed. Macroinvertebrates were identified to the lowest possible taxonomic level (Table 1). Pre-manipulation sampling of the macroinvertebrate communities was conducted in the summer of 2002 before the reduction and six times after the reduction, in early, mid, and late summer (May-August) of 2003 and 2004.

Data analysis

We compared the population estimates of yellow perch and largemouth bass before (2001) and in the 2 years after the manipulation (2003–04) using 95% confidence intervals. For all four fish species we used Wilcoxon rank sum tests to test for significant differences in daily catch rates between basins for each species in each year. Due to the large number of macroinvertebrate taxa collected, we examined macroinvertebrate composition of the two basins in a variety of ways. First, we compared macroinvertebrate composition before and after manipulation between basins using non-metric multidimensional scaling (NMS) and summarized the data set along the first and second ordination axes (Mccune & Grace, 2002). We used the statistics program R with the function *metaMDS* from the *vegan* library to ordinate and the function *stressplot* to calculate goodness of fit statistics of the ordination (R-Project, 2005). Samples were converted into density estimates (per m^2) before performing the ordination. Wilcoxon rank sum tests were used to test for significant differences between basins at a particular sampling time and between consecutive sampling times for both ordination axes. Secondly, we compared rarefied species richness (Gotelli & Graves, 1996), total macroinvertebrate

Table 1 Macroinvertebrates found in both basins of Little Rock Lake in 2002–04

Class	Order	Family	Lowest taxon	Common name	Prevalence
Insecta	Diptera	Chironomidae	Chironomidae	Non-biting midge	100%
Bivalvia	Venerioda	Sphaeriidae	*Pisidium* spp.	Fingernail clam	75.00
Insecta	Ephemoptera	Caenidae	*Caenis* spp.	Angler's curses mayfly	63.21
Insecta	Diptera		Diptera pupae	Fly pupae	62.14
Insecta	Trichoptera	Leptoceridae	Leptoceridae	Long-horned caddisfly	62.14
Malacostraca	Amphipoda	Crangonyctidae	*Crangonyx* spp.	Amphipod	51.79
Insecta	Trichoptera	Limnephilidae	*Limnephilus* spp.	Northern caddisfly	50.36
Insecta	Diptera	Ceratopogonidae	*Bezzia* spp.	Biting midge	45.00
Ciitellata			Oligochaeta	Segmented worm	40.00
Insecta	Odonata	Libellulidae	*Ladona Julia* (Uhler, 1857)	Chalk-fronted corporal Dragonfly	39.29
Arachnida	Prostigmata		Hydrachnida	Water mite	37.86
Insecta	Trichoptera	Hydroptilidae	Hydroptilidae	Micro-caddisfly	26.07
Insecta	Odonata	Coenagrionidae	*Enallagma* spp.	Bluet damselfly	25.71
Insecta	Odonata	Cordulidae	*Epitheca* spp.	Basket tail dragonfly	24.64
Insecta	Trichoptera	Polycentropodidae	*Cernotina spicata* (Ross, 1938)	Trumpet-net caddisfly	24.29
Insecta	Megaloptera	Sialidae	*Sialis* spp.	Alderfly	23.93
Insecta	Odonata		Young Anisoptera	Young dragonfly	20.00
Ciitellata			Hirudinea	Leech	15.00
Gastropoda	Architaenioglossa	Viviparidae	*Campeloma decisum* (Say, 1817)	Brown mystery snail	11.07
Insecta	Trichoptera	Phryganeidae	*Agrypnia* spp.	Giant casemaker caddisfly	10.36
Insecta	Coleoptera	Gyrinidae	*Dineutus* spp.	Whirligig beetle	7.50
Insecta	Coleoptera	Dytiscidae	*Hydrovatus* spp.	Predaceous diving beetle	7.14
Insecta	Neuroptera	Sisyridae	*Climacia* spp.	Spongefly	3.93
Insecta	Coleoptera	Haliplidae	*Peltodytes* spp.	Crawling water beetle	3.21
Insecta	Odonata	Aeshnidae	*Anax* spp.	Darner dragonfly	2.86
Insecta	Odonata	Gomphidae	*Gomphus* spp.	Clubtail dragonfly	1.79
Insecta	Odonata	Cordulidae	*Cordulia shurtleffi* (Scudder, 1866)	American emerald dragonfly	1.07
Insecta	Trichoptera		Trichoptera pupa	Caddisfly pupa	1.07
Insecta	Diptera	Tipulidae	Tipulidae	Crane fly	0.71
Insecta	Hemiptera	Belostomatidae	*Belostoma* spp	Giant water bug	0.36
Insecta	Hemiptera	Pleidae	*Neoplea* spp.	Pigmy backswimmer	0.36

Lowest taxon is the taxonomic level that we were able to identify each macroinvertebrate. Prevalence is the number of samples each taxon was found out of the total number of samples taken in both basins for all seven samplings (n = 280).

density and the densities of Odonata (dragonflies and damselflies), Trichoptera (caddisflies) and Diptera (true flies) between basins through time. These three taxonomic groups are the major macroinvertebrate components of largemouth bass and yellow perch diets in Little Rock Lake (Sass, 2004). We also compared herbivore/detritivore and predator densities (Merritt & Cummins, 1996). Macroinvertebrate taxa with unclear feeding ecology were not included. Wilcoxon rank sum tests were used to statistically compare the basins at each sampling time for each metric. We performed all macroinvertebrate analyses on benthos samples and CWD samples separately, but the results were quantitatively similar and the conclusions were identical between the two habitat types. Thus, the results that we present here are from analyses performed on the pooled data set.

Results

The yellow perch population of the treatment basin severely declined following the CWD reduction. Fish compositions were not statistically different between basins prior to the CWD reduction (Fig. 1; Table 2). Prior to wood reduction, yellow perch was the most abundant fish species in both basins. One year after the manipulation (2003), the yellow perch population in the treatment basin declined rapidly to a level where it was not possible to calculate a population estimate (i.e. there was no recapture of marked individuals). The yellow perch population in the reference basin did not change across years, and it was possible to calculate population estimates for all years (Table 2). Similarly, the catch rates of yellow perch declined in the treatment basin after the

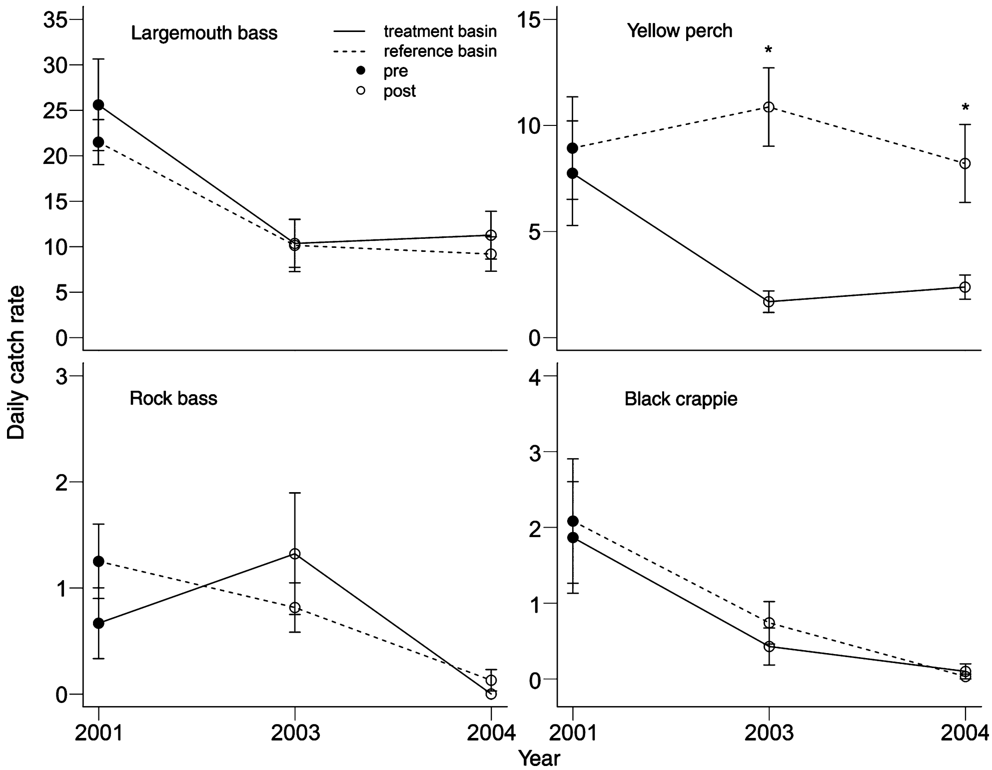

Fig. 1 Daily catch rates using all gears ±SE of the four fish species found in Little Rock Lake one year before (2001) and 2 years after (2003, 2004) the removal of about 70% of the coarse woody debris (CWD) from the treatment basin. An asterisk (*) indicates that the treatment basin is significantly different (α = 0.05, Wilcoxon rank sum test) from the reference basin in terms of the average daily catch rates of a particular year.

manipulation, but did not change in the reference basin (Fig. 1). Catch rates of largemouth bass (Fig. 1) and population estimates (Table 2) were not significantly different between basins. Catch rates of rock bass and black crappie were low throughout the course of the experiment and were not significantly different between basins (Fig. 1).

The CWD reduction did not have a detectable effect on the macroinvertebrate community. While there was significant change in macroinvertebrate community composition through time, both basins varied together (Fig. 2). The two multivariate axes calculated by NMS explained a significant portion of the variability in the macroinvertebrate samples (stress = 28.43, stress based R^2 = 0.92, correlation/fit based R^2 = 0.62). As a whole, no difference was observed between the treatment and the reference basins (Fig. 2a) even though there were several significant changes in macroinvertebrate composition through time (Fig. 2b). The correlation of the two basins across the two multivariate axes was strong (axis 1 cor. = 0.90, axis 2 cor. = 0.71, Kendall rank correlations) and there was only one sampling, in mid-summer 2003, when the two basins differed significantly from each other along one axis. The correlation between basins across the two multivariate axes (Fig. 2b) suggests that we were able to summarize the macroinvertebrate composition of both basins with our sampling regime since the basins did not diverge randomly in multivariate space.

Analyses of diversity and macroinvertebrate densities were consistent with the multivariate analysis (Fig. 3). There were strong temporal correlations between basins for both macroinvertebrate rarified species richness and total density (Fig. 3a,b). The same was true for the three taxonomic (Fig. 3c,e,g) and the two ecological groupings (Fig. 3d,f). Significant differences between samplings were only occasionally observed between the two basins.

Discussion

Ecosystem subsidies are important for maintaining biological diversity (Polis, Anderson & Holt, 1997;

Table 2 Chapman-modified continuous Schnabel population and density (in parentheses) estimates with 95% confidence intervals for the two most abundant fish species in Little Rock Lake

Species	2001 pre-manipulation		2003 post-manipulation		2004 post-manipulation	
	Reference basin	Treatment basin	Reference basin	Treatment basin	Reference basin	Treatment basin
Yellow perch	5564, 2319–83 450 (686.9, 286.3–10 302.5)	1408, 640–9384 (143.7, 65.3–957.6)	5089, 2719–16 190 (628.3, 335.7–1998.8)	Not defined	9843, 4101–147 650 (1215.2, 506.3–18 228.4)	Not defined
Largemouth bass	508, 395–692 (62.7, 48.7–85.4)	557, 457–704 (56.8, 46.6–71.8)	825, 612–1215 (101.9, 75.6–150.0)	626, 486–836 (63.9, 49.6–85.3)	962, 743–1333 (118.8, 91.7–164.6)	1020, 782–1427 (104.1, 79.8–145.6)

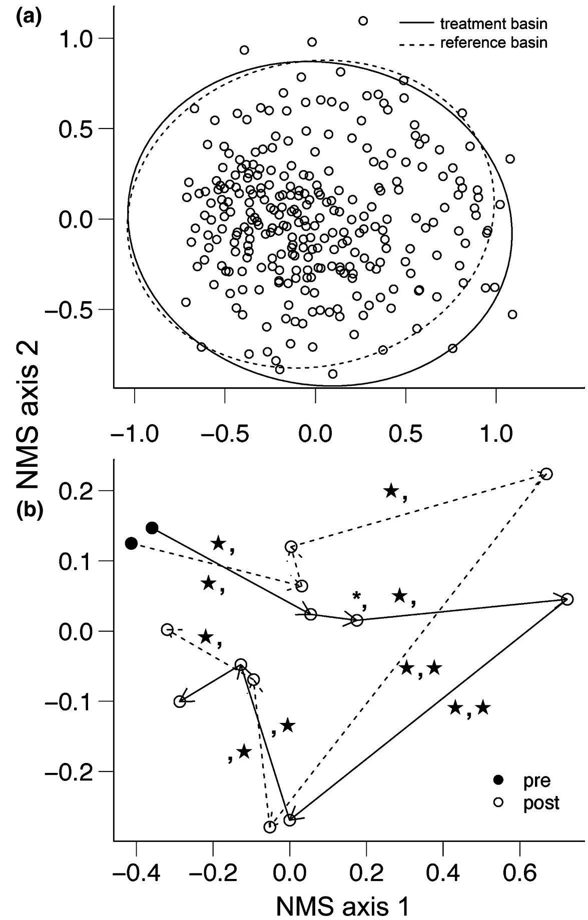

Fig. 2 Non-metric multidimensional scaling (NMS) plots of macroinvertebrate samples of Little Rock Lake treatment basin and reference basin. (a) Points are macroinvertebrate samples and large circles are 95% inclusion intervals of samples taken in each basin. (b) Sampling time centroids of both basins during pre-(2002) and post- (2003–04) coarse woody debris reduction. An asterisk (*) indicates that the treatment basin is significantly different from the reference basin in terms of the centroid estimates of the communities in a particular year, while a star (★) indicates a significant difference between centroids of consecutive years ($\alpha = 0.05$, Wilcoxon rank sum test). A significance symbol on the left-hand side of the comma corresponds to the *x*-axis, while the right-hand side corresponds to the *y*-axis.

Polis, Power & Huxel, 2004). Subsidies whereby organisms directly incorporate the subsidy have been widely studied (e.g. marine derived salmon carcasses fed upon by terrestrial scavengers, e.g. Merz & Moyle, 2006). Habitat subsidies, on the other hand, are different in that organisms of the recipient ecosystem use the material produced by a donor ecosystem but do not directly incorporate it into biomass (e.g. calcium carbonate beach sand produced by marine organisms, Bellwood & Choat, 1990). The habitat

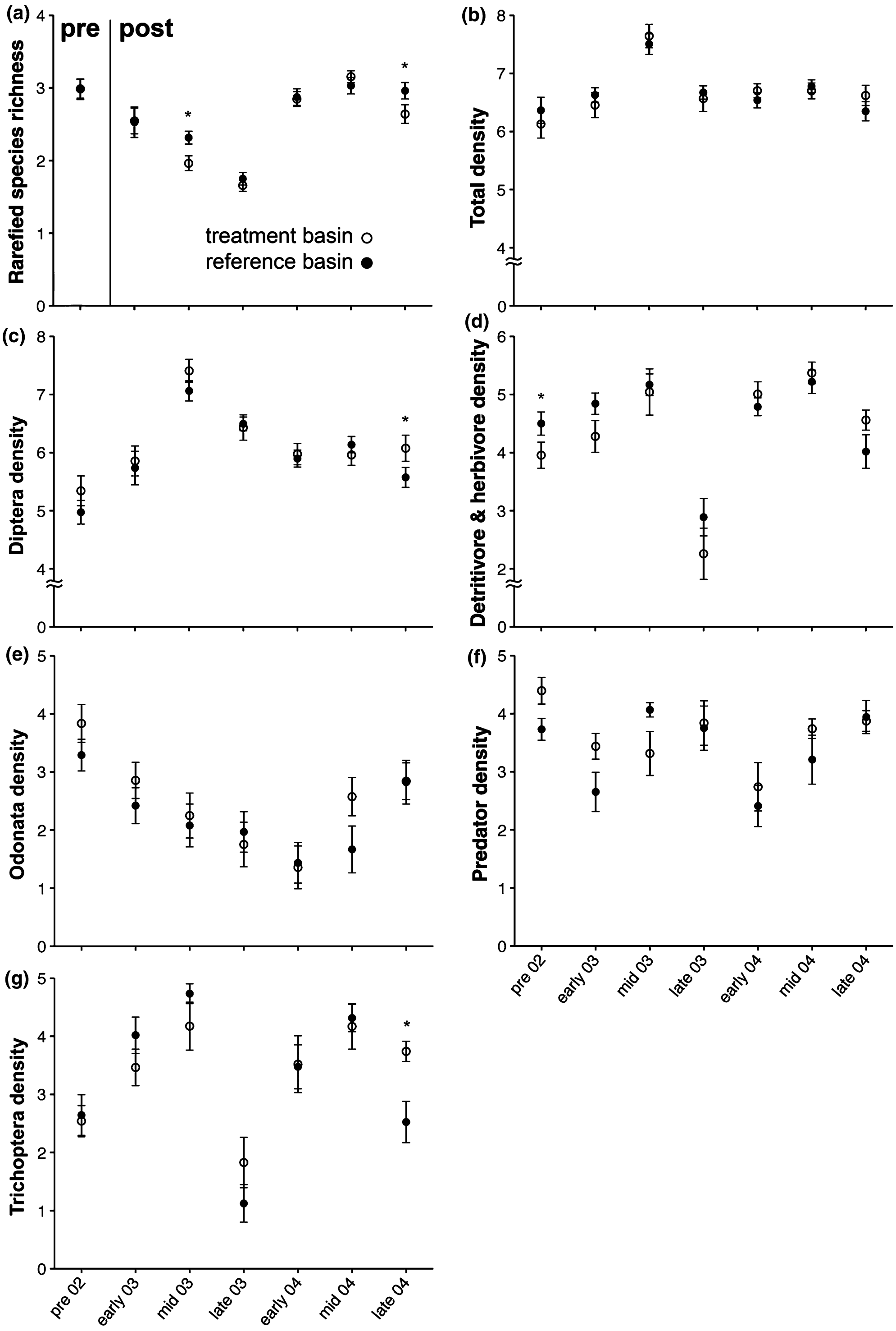

Fig. 3 Rarified species richness and macroinvertebrate density estimates by class and functional grouping versus sample date in the treatment and reference basins of Little Rock Lake before (pre) and after (post) the coarse woody debris (CWD) reduction in the treatment basin in 2002. Sampling after the manipulation occurred in early, mid and late summer of 2003 and 2004. All densities were $\log_e$ transformed. Circles are averages ± SE. An asterisk (*) indicates that the treatment basin is significantly different from the reference basin (α = 0.05, Wilcoxon rank sum test).

subsidy that we studied was trees produced in riparian ecosystems, that fall into the littoral zones of lakes and create coarse habitat that is used by lake biota. Our results suggest that reduction of lake CWD has rapid species-specific impacts on one group of organisms, fish, and no discernible short-term effects on another group of organisms that reside directly on the habitat, benthic macroinvertebrates.

Our removal of about 70% of the CWD from the treatment basin of Little Rock Lake had a pronounced and rapid negative effect on yellow perch. Yellow perch went from being the most abundant fish species in this basin to the least abundant, a difference that has persisted (catch rates of 0.8 and 0 perch per sampling day in 2005 and 2006, respectively; G.G. Sass, unpubl. data).

This rapid and persistent decline of yellow perch was most probably due to a loss of spawning substrate (leading to decreased reproductive output) and a loss of refuge habitat (leading to increased predation by largemouth bass). The lengths of the dominant cohorts of yellow perch in the two basins in 2002 were <150 mm and vulnerable to bass predation (Sass, 2004; Sass *et al.*, 2006b). This size structure is typical of yellow perch population dynamics, where one or two cohorts generally dominate the population at any given time (Carlander, 1997). Yellow perch typically have a lifespan of 5–6 years (Carlander, 1997), so a natural decrease in larger, older individuals is expected in both basins. After the manipulation in the treatment basin, the number of small individuals decreased, while small individuals replaced the large individuals in the reference basin through successful recruitment events. This change in size structure between the two basins was not statistically significant until 2005 (G.G. Sass, unpubl. data).

Our analyses show that largemouth bass densities did not change among years, but there was an effect of the manipulation on this species. Sass *et al.* (2006b) reported that the diet of largemouth bass in the treatment basin shifted from one dominated by yellow perch to one dominated by less energetically favourable terrestrial prey. In the treatment basin, largemouth bass also had less full stomachs after the CWD reduction. As a consequence, average growth rates of these bass decreased significantly in comparison to reference basin growth rates. Furthermore, cannibalism by adult largemouth bass was very low in Little Rock Lake (Sass *et al.*, 2006b). Cannibalism in bass may be more commonly observed where bass densities are high and alternative food sources are severely limited (Post, Kitchell & Hodgson, 1998). This may not be the case for Little Rock Lake. Production of largemouth bass young-of-year was low in both basins – across all years and between both basins we caught only 14 bass <150 mm length even though we used sampling methods that target young-of-year fish (Sass, 2004). The production of the surrounding forest is now substantially subsidizing largemouth bass (i.e. the proportion of terrestrially produced prey in the diets of treatment basin bass changed from about 10% to about 50% after the manipulation). Thus, the lack of response by young-of-year largemouth bass may be a consequence of prey availability since these fish were sparse and there were alternative prey for adult largemouth bass once yellow perch declined.

The Little Rock Lake rock bass and black crappie populations have historically been low (Eaton *et al.*, 1992) and remained low throughout this study. While catch rates of both species varied through time, there were no significant differences between basins. We expected the small individuals of both species to utilize CWD as predation refuge from largemouth bass; however, we have no evidence that the manipulation rapidly affected these two species. Production of young-of-year black crappie and rock bass was low in Little Rock Lake and these diet items represented <0.1% of all items found in bass diets across both basins (G.G. Sass, unpubl. data). Furthermore, in contrast to yellow perch, rock bass and black crappie are nest builders, provide parental care to young and are deep-bodied. Deep-bodied bluegill *Lepomis macrochirus* (Rafinesque, 1819) and pumpkinseed *L. gibbosus* (Linnaeus, 1758) were less favourable prey to largemouth bass compared to yellow perch in a study in a similar northern Wisconsin lake (Sass *et al.*, 2006a). Therefore, compared to yellow perch, the effects of our CWD reduction on black crappie and rock bass may have been less intense as a consequence of differences in life-history attributes and largemouth bass foraging preference.

In contrast to the fish community, we found little evidence to suggest that the macroinvertebrate composition changed following the manipulation, at least in the short term. While there were significant temporal changes in macroinvertebrate community composition, density and richness, these changes were similar in both basins. There were significant differences in three of our metrics on the last sampling date (rarefied species richness, Diptera density, Trichoptera density), but no trends towards divergence in the preceding samples. Furthermore, these three measures are not independent (e.g. as the proportion of Diptera increases, rarefied species richness should decrease). Thus, we suggest that these differences are not indicative of a general trend of basin divergence.

Our results for the macroinvertebrate community are contrary to expectations. We hypothesized a change in macroinvertebrate community composition and a decrease in macroinvertebrate diversity following habitat reduction in the treatment basin since the manipulation greatly disturbed littoral sediments and decreased the total amount of available macroinvertebrate habitat. However, it may be that CWD is not an important substrate for macroinvertebrates. Macroinvertebrates feed on algae and bacteria, and CWD provides a benthic substrate on which these grow. However, as a substrate, the contribution of CWD to benthic primary production is very low in comparison to sediment. For example, in lakes similar to Little Rock Lake, only 4% of whole-lake primary productivity comes from algae on CWD, whereas 50–80% comes from algae on sediment (Vadeboncoeur & Lodge, 2000). That CWD may not be an important substrate for macroinvertebrates is also supported by a study conducted in three Ontario Lakes, which reported no effect of a partial CWD reduction on macroinvertebrate communities (Smokorowski *et al.*, 2006).

The lack of an effect of CWD reduction may be seen as surprising given the relationship between littoral macrophytes and fish predation on macroinvertebrates (e.g. Crowder & Cooper, 1982). Based on this macrophyte work, since CWD contributes to littoral habitat heterogeneity, the loss of CWD should increase predation by fish on macroinvertebrates (Schindler & Scheuerell, 2002). However, macroinvertebrates are relatively small organisms in comparison to the interstices provided by CWD, and dense stands of macrophytes may thus be a better refuge for macroinvertebrates. Therefore, either yellow perch do not structure the macroinvertebrate community of Little Rock Lake, or any effect of the yellow perch decline on macroinvertebrates may not be rapid.

Our study looks at the responses of fish and macroinvertebrates at a relatively short-time scale following the manipulation (i.e. 2 years). Long-term responses of these communities to the reduction may differ from the results we present here. For example, CWD may prevent organic material in the littoral zones of lakes from settling into deeper and less productive waters. In the absence of stabilizing structures, littoral zones are subject to increased wave disturbance and organic sediments settle into deeper areas of lakes where water motion is reduced (Hilton, 1985; Hilton, Lishman & Allen, 1986; James & Barko, 1990; Rasmussen & Rowan, 1997). One long-term effect of our reduction may then be a decreased amount of organic material in the littoral zone of the treatment basin and this may affect macroinvertebrate community composition and production (Rasmussen & Rowan, 1997). Also, we found no effect of the manipulation on largemouth bass abundance, but a long-term effect may be a decrease in largemouth bass population biomass if the CWD removal decreased overall lake productivity (Sass *et al.*, 2006b).

On a global scale, humans are rapidly modifying ecosystems by reducing habitat heterogeneity and severing or altering linkages among ecosystems (Crowder, Reagan & Freckman, 1996; Riley & Jefferies, 2004). For example, the shorelines of lake ecosystems in forested regions are increasingly being developed for human use (Schnaiberg *et al.*, 2002; Walsh *et al.*, 2003). This development probably reduces the habitat subsidy provided by the surrounding riparian forests in the form of CWD, which can greatly increase the level of habitat heterogeneity found in lake littoral zones (Christensen *et al.*, 1996; Jennings *et al.*, 2003; Francis & Schindler, 2006; Marburg *et al.*, 2006; Sass *et al.*, 2006b). We have shown that the reduction of CWD has large and rapid effects on some aquatic communities, but not others. In our study, the primary effect of CWD reduction was on yellow perch; a species that relies heavily on CWD for spawning substrate and refuge from predation. Thus, the species composition of ecosystems may play a major role in determining the ecological outcomes of disruptions to habitat subsidies. Future research should focus on how differences in species composition across ecosystems affect ecosystem responses to habitat subsidy disturbance.

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