

Shoreline hardening alters freshwater shoreline ecosystems

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Abstract: Shoreline ‘hardening’ is a common anthropogenic activity that involves installation of structures, such as seawalls or riprap, at the waterline to protect waterfront property. Despite the ubiquity of this activity, the effects of hardening on shoreline ecosystems are not well understood. We evaluated the geomorphology, organic-matter decomposition, washed-up organic material (wrack), and invertebrate communities on both aquatic and terrestrial (riparian) habitats of 7 natural and 7 riprap-hardened shorelines of Lake St Clair (Michigan, USA). Shorelines hardened by riprap differed from their natural counterparts in structure and function, with particularly pronounced effects in terrestrial shoreline habitats. Hardened shorelines were steeper and drier, and sediments were orders of magnitude larger than on natural shorelines. Organic-matter decomposition was slower at riprap than natural shorelines in terrestrial habitats, but did not differ between natural and riprap shorelines in aquatic habitats. Natural shorelines had much greater quantities of wrack, a lake-derived subsidy, than riprap shorelines in summer and autumn. The finding that natural shorelines had more wrack despite faster decomposition suggests that subsidy retention is impaired by riprap. Path analysis indicates that the large sediment size of riprap is the mechanism responsible for disrupting wrack accumulation. Invertebrate community composition in terrestrial habitats also differed between shoreline types, with snails and beetles more abundant on natural shorelines and ants more abundant on riprap. Exotic taxa, such as Asian earthworms (*Amyntas* sp.), cyanobacteria (*Lyngbya wollei*), and *Phragmites*, were prevalent on both natural and riprap shorelines. Overall, riprap shorelines differ greatly from natural shorelines in their structure and functioning, particularly in terrestrial habitats, and possess attributes of ‘novel ecosystems’.

Key words: Lake St Clair, riprap, ecosystem functioning, decomposition, cotton-strip assay, wrack, invasive species, spatial subsidy, shoreline armoring, *Phragmites*, *Lyngbya*, *Amyntas*

Freshwater shorelines play critical roles in the maintenance of freshwater and riparian ecosystems that far exceed their spatial extent. As ecotones, shorelines mediate resource exchanges between aquatic and terrestrial ecosystems (Polis et al. 1997, Paetzold et al. 2005) and, thereby, influence the ecological condition of both systems. Despite occupying a small area of the landscape, shorelines often possess high levels of biodiversity, provide habitat for rare and endemic species (Strayer and Findlay 2010, Vadeboncoeur et al. 2011), are feeding areas for shore birds (Crowder and Bristow 1988, Dugan et al. 2008), and function as spawning grounds and nurseries for fish (Jude and Pappas 1992). In addition, shorelines are sites of organic-matter retention, accumulation, and processing, and play unique roles in the biogeochemical cycling of nutrients (Mellbrand et al. 2011, Harris et al. 2014). Despite their ecological value and the ecosystem services that shorelines provide, these sites are frequently altered by human development, but with poorly understood ecological consequences.

Among the most conspicuous and widespread effects that humans have on shorelines is substitution of natural shoreline substrates with other materials. Such shoreline ‘hardening’ typically involves construction of stabilization structures, such as vertical seawalls, cribbing (retaining walls backfilled with stone), or riprap (large rocks or pieces of broken concrete; Fig. 1A). The purpose of these structures is to protect infrastructure from erosion and flooding and to improve access for recreational activities. In developed regions, shoreline hardening is ubiquitous. Approximately 30% of the New England and mid-Atlantic marine coastline (Hapke et al. 2010), 50% of the shorelines of the Hudson River (Strayer and Findlay 2010), and 14% of the entire USA coastline have been hardened (Gittman et al. 2015). Shoreline hardening also is common within the Laurentian Great Lakes system (Meadows et al. 2005). For instance, 89% of the Lake St Clair shoreline in Macomb County, Michigan, has been hardened (Macomb County, Department of Planning and Economic Development, personal

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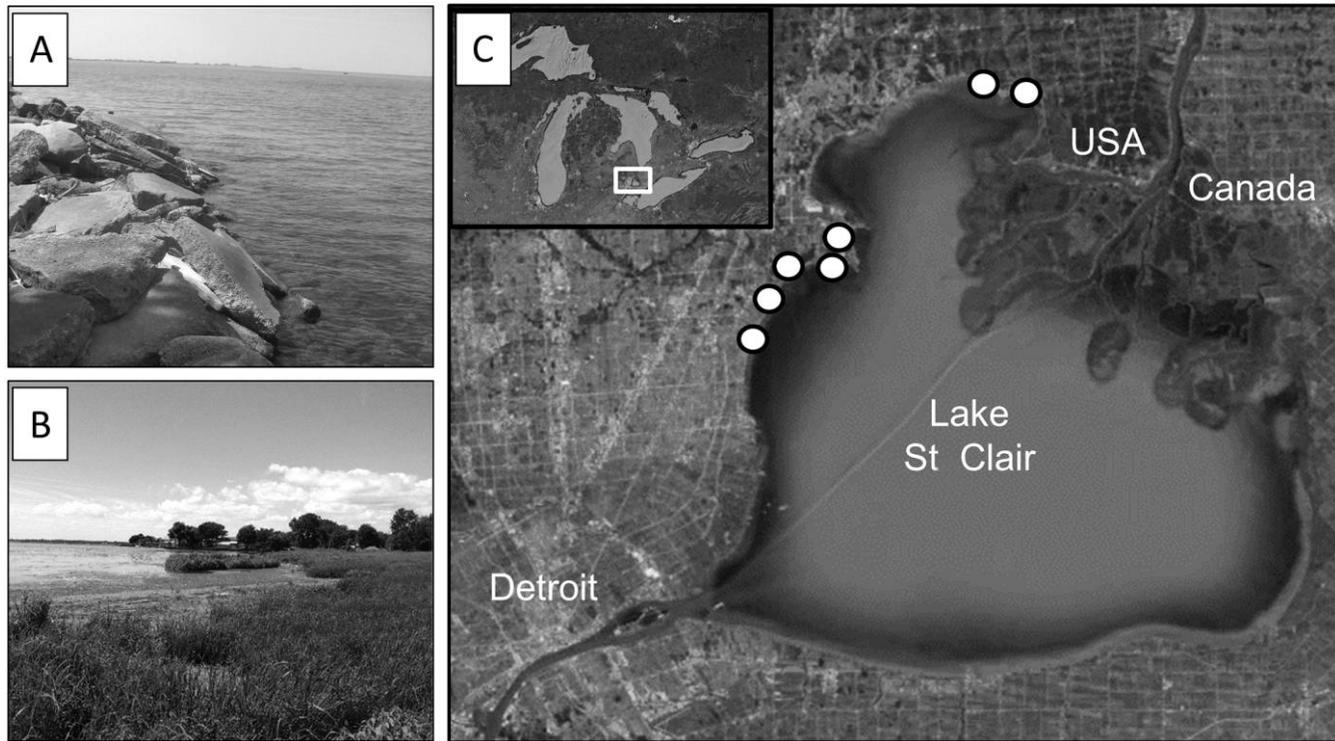


Figure 1. A.—Concrete riprap stabilization. B.—A natural Lake St Clair shoreline. C.—Location of Lake St Clair (inset) and map of Lake St Clair study sites in Michigan (USA). Seven pairs of adjacent natural and riprap-hardened shorelines are indicated by white circles. Photographs by SMW.

communication). Although shoreline hardening is common practice, only a small number of studies have been done to investigate its effects in freshwater systems.

Hard stabilization structures alter physical characteristics of shorelines, which in turn, may affect ecosystem functioning and the exchange of resources between terrestrial and aquatic ecosystems. Stabilization structures are often installed beyond the original waterline, a practice that eliminates areas of shallow-water habitat and habitat that is periodically inundated by temporary rises in water level. Seawalls and cribbing replace what was often a gradual, sloping transition into the water with an abrupt, vertical division, whereas riprap can create steep shoreline slopes (Strayer et al. 2012). These structures have the added effect of replacing spatially dynamic shorelines that advance and recede with fluctuating water levels (*sensu* the aquatic/terrestrial transition zone; Ward and Stanford 1995), with shorelines that are spatially fixed. The result is habitats that are either constantly aquatic or constantly terrestrial. Such alterations to wetting and drying episodes have the potential to affect fundamental biogeochemical and ecological processes, such as denitrification, nutrient mineralization, and organic-matter decomposition (e.g., Langhans and Tockner 2006, Steinman et al. 2012, Costello et al. 2014). In addition, physical habitat characteristics, such as substrate size, wave energy, water depth, and tempera-

ture, are important determinants of species distributions (Poff 1997) and are likely to influence retention and storage of organic matter. Wrack (organic matter deposited on shorelines) typically is dominated by lake-derived organic matter and constitutes a resource subsidy for lake-shoreline ecosystems. Marine wrack, which is better understood, can be deposited in great quantities on shorelines, where it is colonized by invertebrates that transmit marine-derived nutrients inland to terrestrial food webs (Polis et al. 1997, Mellbrand et al. 2011). Stabilization structures, such as seawalls and riprap, can impair the accumulation of wrack on marine shorelines relative to unaltered shorelines (Dugan and Hubbard 2006, Sobocinski et al. 2010, Heerhartz et al. 2014). Freshwater wrack presumably serves similar roles to those of marine wrack and also might be disrupted by hardening. On the freshwater Hudson River, for example, Harris et al. (2014) found less wrack along hardened than natural shorelines, and accumulation above seawalls was prevented entirely.

We evaluated the effects of hardening on the structure and functioning of shorelines within the Laurentian Great Lakes ecosystem. These shorelines constitute the longest freshwater shoreline in the world (GLEAM 2014), but have been modified extensively for human use (USEPA and EC 2009). We hypothesized that hardening impairs linkages between adjacent terrestrial and freshwater ecosystems by

modifying resource exchanges. We tested whether the relatively steep slope and larger sediment size of riprap inhibits deposition of wrack, thereby reducing the transfer of lake-derived resources to terrestrial areas of shorelines. We also hypothesized that riprap-hardened shorelines alter terrestrial and aquatic macroinvertebrate communities. Last, we hypothesized that rates of organic-matter decomposition are reduced in aquatic and terrestrial habitats of riprap-hardened shorelines because of changes in the physical environment and invertebrate communities. Exploring these hypotheses has implications that range from ecological restoration, a practice that is increasingly common in the Great Lakes region, to a better understanding of how the connections between adjacent ecosystems can be mediated through human alterations to the physical environment.

METHODS

Study design

To assess the potential impacts of hardening on freshwater lake shorelines, we compared fundamental aspects of ecosystem structure and function between 7 pairs of natural and hardened shorelines of Lake St Clair (Fig. 1A–C). Paired natural and hardened shoreline sites were immediately adjacent to one another. Average length (\pm SD) of the shorelines was 35.5 ± 13 m. All hardened shorelines consisted of concrete riprap (Fig. 1A), whereas the relatively natural shorelines were either wetland edges or sandy beaches (Fig. 1B). We investigated both aquatic and terrestrial areas of the shorelines for effects of shoreline hardening. Some variables were measured seasonally, whereas others were measured during a single season.

Physical characteristics of shorelines

Shoreline slope was calculated as the slope (m) of the linear equation $y = mx + b$ to describe the change in water depth (or substrate elevation in terrestrial areas) with increasing distance from the waterline. At each site, slope was measured at 3–5 transects that were aligned perpendicularly to the waterline. In the water, we measured depth at ~ 1 -m intervals from the waterline to a distance of 10–15 m or a maximum depth of 1 m. In terrestrial habitats above the waterline, we measured substrate slope with a handheld clinometer up to 15 m away from the waterline or up to an elevation of ~ 1.5 m above the level of the water surface.

We quantified sediment size at 20 random (x, y) coordinates in terrestrial habitats and at 20 random coordinates in aquatic habitats at each shoreline. We used a gravelometer to measure the medial (i.e., intermediate) diameter of sediment particles 2–180 mm or a meter stick for larger particles.

We measured wind-driven wave energy at each site as effective fetch and maximum fetch with methods published

by Burton et al. (2004). With this method, the distance of open water between 2 shorelines is used to estimate the strength of wind-generated waves. Distances were measured using Google Earth[®] at a viewing elevation of ~ 42 km.

We quantified substrate moisture availability in terrestrial habitats twice during summer with a novel sponge assay because concrete riprap was too large to sample with conventional techniques (e.g., weighing before and after oven drying). At each site, we placed 3 oven-dried cellulose sponges ($5 \times 3.5 \times 1$ cm) directly on the substrate and left them to incubate for 5 to 7 d. We retrieved sponges and stored them in aluminum foil envelopes to minimize changes in water content during transport. Upon returning to the laboratory, we measured the wet mass of each sponge, dried them at 40°C , and reweighed them. Data were expressed as % moisture content. During incubation, sponges were exposed to precipitation, but we did not retrieve them within 24 h of rainfall to avoid complete saturation. We carried control sponges into the field on the day of deployment, but did not incubate them on the shoreline substrate. We processed control sponges in the same way we processed treatment sponges to account for moisture gain from the atmosphere.

Organic-matter dynamics

We quantified organic-matter dynamics (wrack standing stock, decomposition rates) during 3 seasons: spring (April–early June), summer (late July–early September), and autumn (late September–early November) of 2013 to test for seasonal difference in effects of hardening.

We measured the standing stock of wrack (dry mass/ m^2) in each season in five 25×25 -cm quadrats situated randomly in terrestrial habitats within 1 m of the waterline at each study site. We collected all wrack in a quadrat, placed it in a large plastic bag, and weighed it immediately to the nearest 0.5 kg. Samples < 0.5 kg were weighed in the laboratory to the nearest 0.001 g. We homogenized the wrack and took 3 subsamples from each quadrat to the laboratory where they were weighed, dried at 40°C for 7 d, and reweighed to measure % water content. We used mean subsample water content to convert wrack mass to dry mass. At the time of collection, we rinsed noticeably sandy wrack and removed any rooted terrestrial plants growing in wrack or anthropogenic litter from the samples. We always collected wrack from paired sites on the same day.

We measured rates of organic-matter decomposition seasonally in the aquatic and terrestrial habitats of each shoreline with a litterbag approach and the cotton-strip assay. At each site, we installed a total of 10 stakes: 5 polyvinyl chloride (PVC) stakes in the water at a depth of 20 to 40 cm and 5 wooden stakes in terrestrial habitats above the waterline where they would not be submerged.

We followed the methods used by Tiegs et al. (2013b) for the litterbag study. We filled coarse-mesh litter bags

(1-cm pore size) with 4 ± 0.25 g of dried *Phragmites australis* leaves. To minimize loss of material through the 1-cm pores, the narrow tips (<2 cm width) of *Phragmites* leaves were removed prior to weighing and filling the litter bags. This plant is a highly abundant invasive species along Lake St Clair. At each site, we secured 1 litterbag to each stake in the water and incubated the bags until 50% mass loss had occurred (5–6 wk) during spring, summer, and autumn. At each site, we secured 1 litterbag to each stake in the terrestrial habitat so that the litterbag was in contact with the substrate and incubated the bags until ~50% mass loss had occurred. We deployed terrestrial litterbags once for 15 wk (30 April–15 August) instead of seasonally because of slow decomposition rates. We collected the litterbags, transported them to the laboratory in sealed plastic bags, and stored them frozen. We processed litter by thawing the bags and cleaning the leaf material gently with a paint brush to remove sediment, biofilm, and invertebrates. We dried litter at 40°C for ~48 h and weighed it to measure % mass loss. In each season, we carried 5 control litterbags to the field but did not incubate them. We returned the bags to the laboratory and processed them in the same manner as treatment litterbags to account for mass loss from breakage during transport and cleaning.

The cotton-strip assay was used to complement the litterbag method (Tiegs et al. 2013a). The relatively rapid decomposition rate of cotton strips made it possible to measure terrestrial decomposition during spring, summer, and autumn. The strips of cotton fabric are composed of 95% cellulose and, therefore, are useful for characterizing general rates of organic-matter decomposition. Cotton-strip decomposition is measured as the loss of thread tensile strength, rather than mass loss. We secured 2 cotton strips to each of the same stakes used for litterbags and incubated the strips in both aquatic and terrestrial habitats for ~4 to 7 wk during each season. Following collection, we submerged cotton strips in 70% isopropyl alcohol to stop microbial activity and cleaned them gently with a paint brush to remove sediment and biofilm. We stored strips in aluminum foil packets for transport and dried them at 40°C for ~48 h. We measured the tensile strength of the dried strips with a Mark-10 Tensiometer (Model MG100, Mark-10 Corporation, Copiague, New York). During each season, we carried 20 control cotton strips to the field, and then processed them in the same manner as the treatment samples to estimate initial tensile strength. We expressed tensile strength loss as the % of original (control) tensile strength lost by treatment strips.

During each season in which decomposition was measured, we used temperature loggers (iButton Model DS1921G; Maxim Integrated, San José, California) to measure the daily mean, standard deviation (SD), and range of temperatures. In terrestrial habitats, loggers in mesh bags were secured to the same stakes that held the litterbags and cotton strips.

Mesh bags were placed just above the substrate surface to record air temperature and were exposed to sunlight except where abundant shoreline vegetation provided shade. To record water temperature, we placed loggers in polyethylene tubes with holes to allow water exchange and secured the tubes to the same stakes that held litterbags and cotton strips.

Macroinvertebrate communities

We sampled macroinvertebrates from terrestrial and aquatic shoreline habitats between 14 and 24 June. We collected terrestrial invertebrates by conducting three 20-min timed searches of the substrate and wrack with handheld aspirators and forceps. We collected 3 samples of aquatic macroinvertebrates with D-frame dip-net (500- μ m-mesh) sweeps while agitating the substrate to a depth of 30 to 40 cm. We collected a maximum of 100 individuals from each aquatic sample, and we sampled shoreline pairs on the same day. We sorted invertebrates in the field, stored them in 91% isopropyl alcohol, transported them to the laboratory, and later identified them to the lowest practical taxonomic level, usually order. To analyze the role of invertebrates in organic-matter decomposition, we classified individuals belonging to Isopoda (isopods), Chilognatha (millipedes), and Haplotaxida (earthworms) as large-bodied detritivores. We restricted the designation of 'detritivore' to those orders in which most species found in the Great Lakes region are detritivorous.

Statistical analysis

We analyzed our data with the package *nlme* (Pinheiro et al. 2014) in R (version 3.1.0; R Project for Statistical Computing, Vienna, Austria). We used a mixed-effects model with a nested structure consisting of site pair > shoreline type (natural or riprap) > habitat (aquatic or terrestrial) > sampling quadrat. We treated shoreline type and habitat as fixed-effect factors and site pair and quadrat as random-effect factors. When necessary, we transformed response variables for normality. Effects of shoreline type were tested at the site level ($n = 14$) with analysis of variance (ANOVA).

For terrestrial and aquatic invertebrates, we quantified taxonomic diversity with the Shannon–Wiener Diversity Index (Shannon and Wiener 1949). We compared invertebrate diversity (H'), Shannon evenness (J), abundance, taxonomic richness, and proportional abundance of taxa between natural and riprap shorelines. Analyses were conducted at the order or subclass level. We used nonmetric multidimensional scaling (NMDS) to collapse the proportional abundances of all invertebrate taxa into fewer dimensions and plotted each site in ordination space, where separation indicates dissimilar communities. We used Shepard and scree plots to identify the number of dimensions that would provide both a good fit and low stress value and 3 dimensions for both aquatic and terrestrial ordinations.

We ran NMDS in R with the package *vegan* (Oksanen et al. 2013) using Bray–Curtis distance calculations. We used multiresponse permutation procedure (MRPP) to test for differences between the community compositions of natural and riprap-hardened shorelines. Following MRPP, we calculated the effect size (A) using the chance-corrected within-group agreement equation ($1 - [\text{observed } \delta / \text{expected } \delta]$). We ran MRPP in R with the package *vegan*, using Bray–Curtis distance calculations and 999 permutations.

We used path analysis and linear regressions to further explain which variables drive patterns in wrack quantity and organic-matter decomposition rates. Some variables were quantified once and others were quantified seasonally, so we restricted our analyses to ensure that data for both predictor and response variables had been collected during the same season, except in cases where seasonality was unlikely to be important (e.g., sediment size and slope). We used path analysis in the package *lavaan* (Rosseel 2012) to assess the relative strength of factors affecting the quantity of wrack (mean of all seasons), and whether effects of riprap may be mediated by shoreline morphological characteristics, such as slope or sediment size.

We conducted linear regression analyses to determine the roles of temperature, moisture, and the abundance of large-bodied detritivorous invertebrates on organic-matter decomposition rates in terrestrial habitats. Moisture levels were quantified only during summer, so we used summer data for the other variables when possible (i.e., temperature and cotton-strip decomposition rates). *Phragmites*-filled litter bags were incubated for the entire period from the spring through summer season, and this incubation period included the times during which moisture levels and invertebrate communities were sampled.

RESULTS

Shoreline morphology

Riprap replaced natural, fine sediments with much larger pieces of concrete. Sediment size was significantly affected by shoreline type ($F_{1,6} = 58.95, p < 0.001$), habitat type ($F_{1,12} = 10.24, p = 0.008$), and their interaction ($F_{1,12} = 10.55, p = 0.007$). This interaction term indicates that the magnitude of riprap's effect on sediment size differed between terrestrial and aquatic habitats. Riprap sediments were nearly 200× larger than natural sediments in terrestrial shoreline habitats (39.3 vs 0.2 cm), and nearly 100× larger than natural sediments in aquatic habitats (17.8 vs 0.2 cm; Fig. 2A).

Riprap shorelines were steeper than natural shorelines in terrestrial, but not aquatic, habitats. In terrestrial habitats, riprap shorelines were ~8.5× steeper than natural shorelines (0.355 vs 0.041; $F_{1,6} = 43.97, p < 0.001$; Fig. 2B). In aquatic habitats, slope did not differ between riprap and natural shorelines (0.240 vs 0.175; $F_{1,6} = 3.12, p = 0.128$, Fig. 2C).

Natural and riprap shorelines differed in their moisture availability at the sediment surface. Sponges incubated on natural shorelines in summer contained nearly 50% more moisture than those incubated on riprap shorelines ($F_{1,13} = 7.44, p = 0.017$; Fig. 2D).

Some aspects of the thermal regime of shorelines were affected by riprap, whereas others were not. In aquatic habitats, the mean daily temperature did not differ between natural and riprap shorelines ($F_{1,6} = 0.39, p = 0.555$), and this pattern was consistent across all 3 seasons (Table 1). However, the season × shoreline type interaction affected the range and SD of mean daily temperature in the aquatic habitat ($F_{2,19} = 4.29, p = 0.029$; $F_{2,19} = 7.23, p = 0.005$; respectively; Table 1). Natural and riprap shorelines differed in their mean daily temperature range and mean daily temperature SD only in spring ($p = 0.041, p = 0.039$, respectively). The mean daily temperature range was 2.6°C greater on natural than on riprap shorelines. Similarly, mean daily temperature SD was greater on natural than on riprap shorelines (2.48 vs 1.59). In terrestrial habitats, mean daily temperature, mean daily temperature range, and mean daily temperature SD did not differ between natural and riprap shorelines ($F_{1,6} = 3.13, p = 0.128$; $F_{1,6} = 0.53, p = 0.493$; $F_{1,6} = 0.82, p = 0.400$; respectively; Table 1). This pattern was consistent among seasons.

Organic-matter dynamics

Cotton-strip decomposition rate differed between shoreline types, habitats, and seasons ($F_{1,6} = 6.02, p = 0.05$; $F_{2,12} = 354.41, p < 0.001$; $F_{2,50} = 6.99, p = 0.002$; respectively). The habitat × shoreline type interaction was significant ($F_{1,12} = 31.25, p < 0.001$), indicating that riprap affected decomposition differently in terrestrial and aquatic habitats. In terrestrial habitats, cotton strips decomposed 4.8× faster on natural than on riprap shorelines (0.63 vs 0.13%/d, respectively; $F_{1,6} = 23.32, p = 0.003$; Fig. 3A) in all seasons (non-significant shoreline type × season interaction, $F_{2,24} = 1.96, p = 0.163$). *Phragmites* leaves also decomposed 1.5× faster on natural than riprap shorelines (0.45 vs 0.30%/d; $F_{1,6} = 9.37, p = 0.022$; Fig. 3B). However, in aquatic habitats, shoreline type did not affect decomposition rates of cotton strips and *Phragmites* ($F_{1,6} = 1.58, p = 0.255$; $F_{1,6} = 2.46, p = 0.168$; respectively; Fig. 3C, D) in any season. Last, decomposition rates differed between aquatic and terrestrial shoreline habitats, regardless of shoreline hardening ($F_{1,12} = 354.41, p < 0.001$). Cotton strips decomposed >4.8× faster in aquatic than terrestrial shoreline habitats (1.85 vs 0.38%/d).

Standing stock of wrack

Shoreline type and season influenced the quantity of wrack present on shorelines. Overall, natural shorelines contained >3× more wrack than riprap-hardened shorelines (6917.18 vs 2254.77 g/m² dry mass; $F_{1,6} = 10.09$,

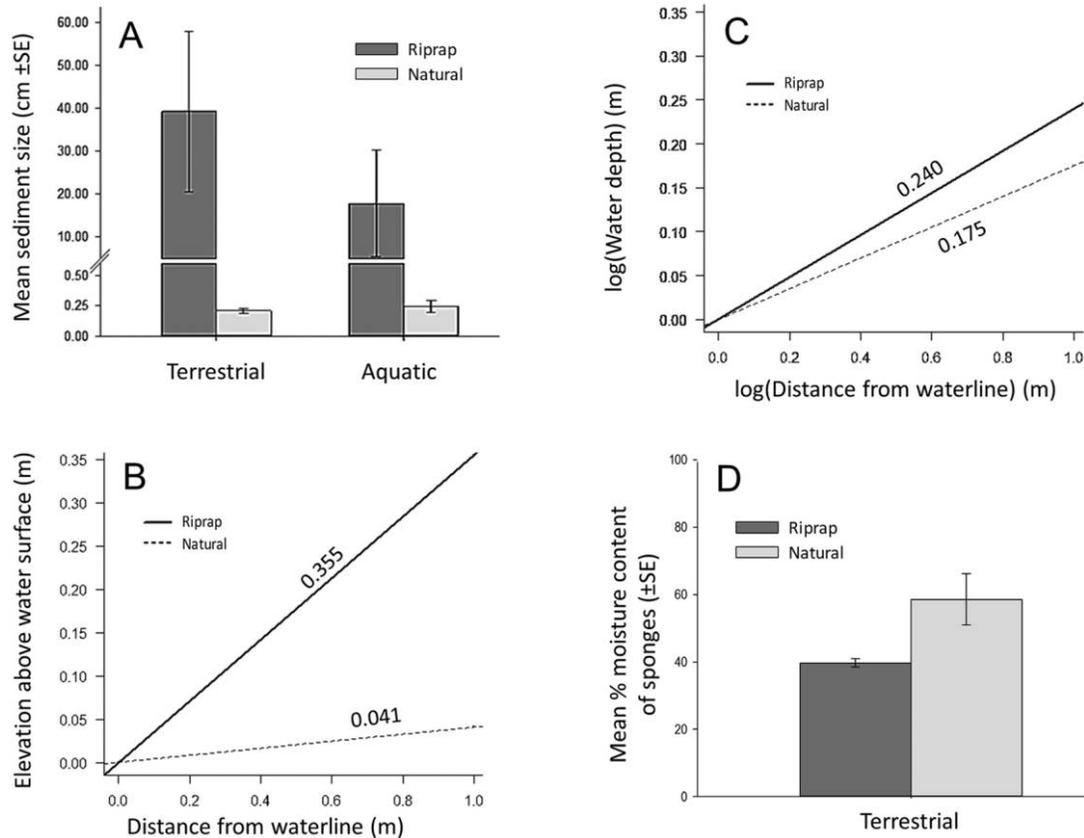


Figure 2. Mean (± 1 SE) medial sediment particle size (A), linear slope of natural and riprap shorelines above the waterline extending into terrestrial habitats (B) and below the waterline extending into aquatic habitats (C), and mean % moisture content of sponges deployed in terrestrial habitats of natural and riprap shorelines in spring (D).

$p = 0.019$). However, riprap did not affect the quantity of wrack to the same degree in all seasons (Fig. 4A). In spring, more wrack tended to be present on natural than riprap shorelines, but the difference was not statistically significant ($F_{1,6} = 4.74, p = 0.072$). In spring, wrack in all but the 2 northernmost sites was dominated by the invasive cyanobacterium, *Lyngbya wollei*. At one site, *Lyngbya* accumulated in quantities of nearly 42.0 kg/m² (dry mass)

and led to a high variance for quantities of wrack (Fig. 4A). In summer and autumn, more wrack was present on natural than riprap shorelines (summer: 4663.80 vs 1330.12 g/m², $F_{1,6} = 14.28, p = 0.009$; autumn: 5475.37 vs 909.78 g/m², $F_{1,6} = 11.47, p = 0.015$). In summer and autumn, wrack contained roughly equal quantities of *Lyngbya* and macrophytes. The quantity of wrack on both types of shorelines differed among seasons ($F_{2,26} = 7.78, p = 0.002$). Quantity

Table 1. Mean daily temperature (°C), mean daily temperature range (°C), and mean daily standard deviation (SD) of temperatures for terrestrial (riparian) and aquatic habitats of natural and riprap-hardened shorelines in each season.

Habitat Type	Variable	Spring		Summer		Autumn	
		Natural	Riprap	Natural	Riprap	Natural	Riprap
Terrestrial	Mean daily temperature	17.26	17.76	21.64	22.78	11.53	12.01
	Mean daily temperature range	20.65	20.33	14.67	15.69	15.29	12.13
	Mean daily temperature SD	6.72	6.41	4.55	4.59	4.54	3.62
Aquatic	Mean daily temperature	17.96	17.78	23.50	23.51	13.08	12.99
	Mean daily temperature range	7.38	4.75	3.49	3.54	3.38	3.22
	Mean daily temperature SD	2.48	1.59	1.16	1.18	1.09	1.06

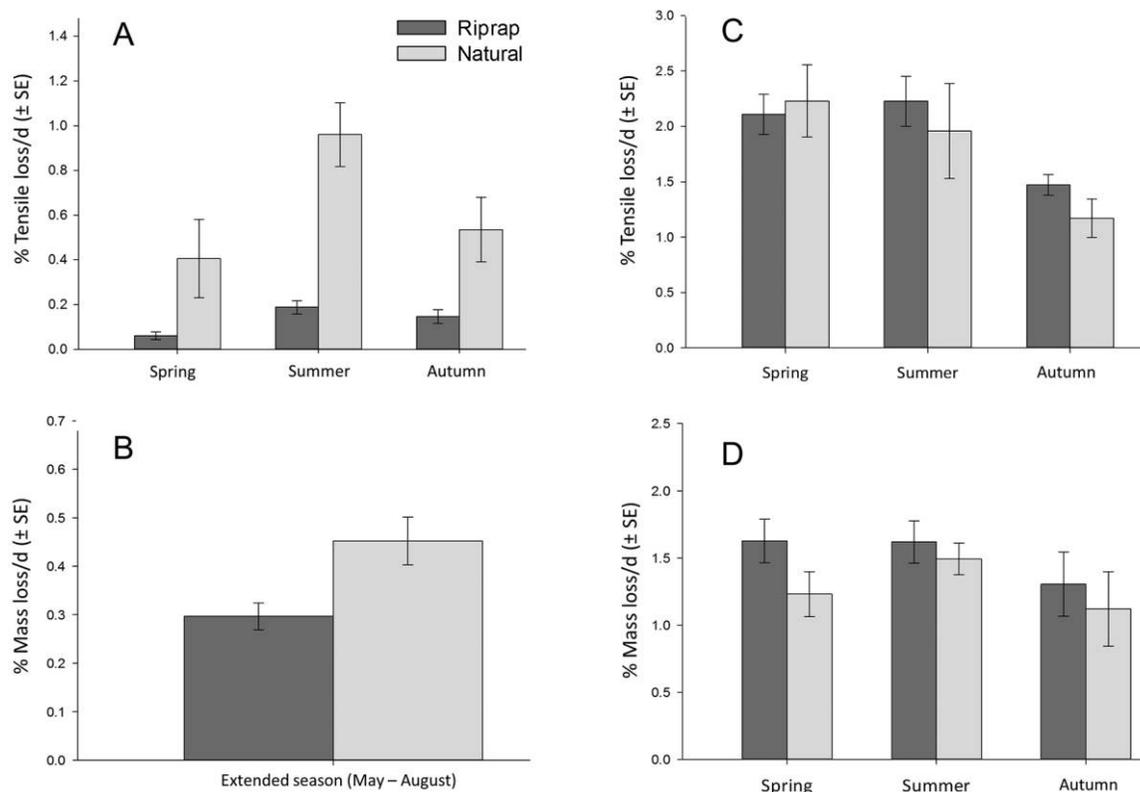


Figure 3. Mean (\pm SE) rates of decomposition in terrestrial habitats using cotton strips (A) and *Phragmites* litter (B), and in aquatic habitats using cotton strips (C) and *Phragmites* litter (D). Rates were measured seasonally, except for *Phragmites* terrestrial decomposition, which was measured from May–August.

of wrack was greater in spring than in autumn (7568.38 vs 3192.58 g/m^2 ; $p = 0.038$) but did not differ between any other pair of seasons.

Path analysis was used to determine which factors most strongly affected the quantity of wrack on shorelines ($p = 0.013$, $df = 6$; Fig. 4B). In this model, riprap did not directly affect the quantity of wrack, nor did riprap strongly affect wrack through its effects on terrestrial or aquatic slope. The 2 strongest pathways were the positive direct effect of effective fetch (an estimate of wind-driven currents) on wrack, and the negative effect of riprap on wrack mediated by its effect on terrestrial sediment size (combined standardized coefficient = 0.66). This result indicates that riprap shorelines may have less wrack overall in part because of the large particle size of riprap.

Invertebrate communities

Terrestrial shoreline habitat Invertebrates from 22 orders were collected. On average, 11.5 orders and 203.8 individuals were collected at each site. H' ranged from 0.80 to 2.11 (mean = 1.48), and J ranged from 0.34 to 0.78 (mean = 0.61). The most common taxa were Isopoda (32.7% of individuals), Hymenoptera (represented only by ants, 18.4%),

Coleoptera (14.9%), Araneae (9.4%), Basommatomorpha (snails, 6.9%), and Haptotaxida (5.0%). Exotic taxa were commonly observed on natural and riprap shorelines and included European earthworms (Lumbricidae), Asian earthworms (*Amyntas*), and isopods (many families of which are European). The proportional abundance of these orders did not differ between natural and riprap shorelines (isopods: $p = 0.202$, Haptotaxida: $p = 0.255$).

Community composition differed between natural and riprap shorelines (Fig. 5A, B), but abundance and richness did not ($p = 0.286$, $p = 0.411$, respectively). Order-level H' (natural: 1.60, riprap: 1.37; $p = 0.197$) and J (natural: 0.11, riprap: 0.55; $p = 0.115$) did not differ between shoreline types. Invertebrate communities on natural and riprap shorelines were clearly separated in ordination space (NMDS, stress = 0.100; Fig. 5C) and differed significantly (MRPP, $\delta_{\text{obs}} = 0.51$, $\delta_{\text{exp}} = 0.60$, $A = 0.14$, $p = 0.007$). The proportion of ants was greater on riprap than on natural shorelines (32.7 vs 4.0%; $F_{1,6} = 9.03$, $p = 0.024$). Isopods and ants dominated riprap shorelines, collectively making up 75% of the community, whereas these taxa composed just 27.1% of natural shoreline communities. Beetles composed a greater proportion of the community on natural than on riprap shorelines (26.9 vs 3.0%; $F_{1,6} = 13.92$, $p = 0.01$). The difference between shoreline types in proportional abun-

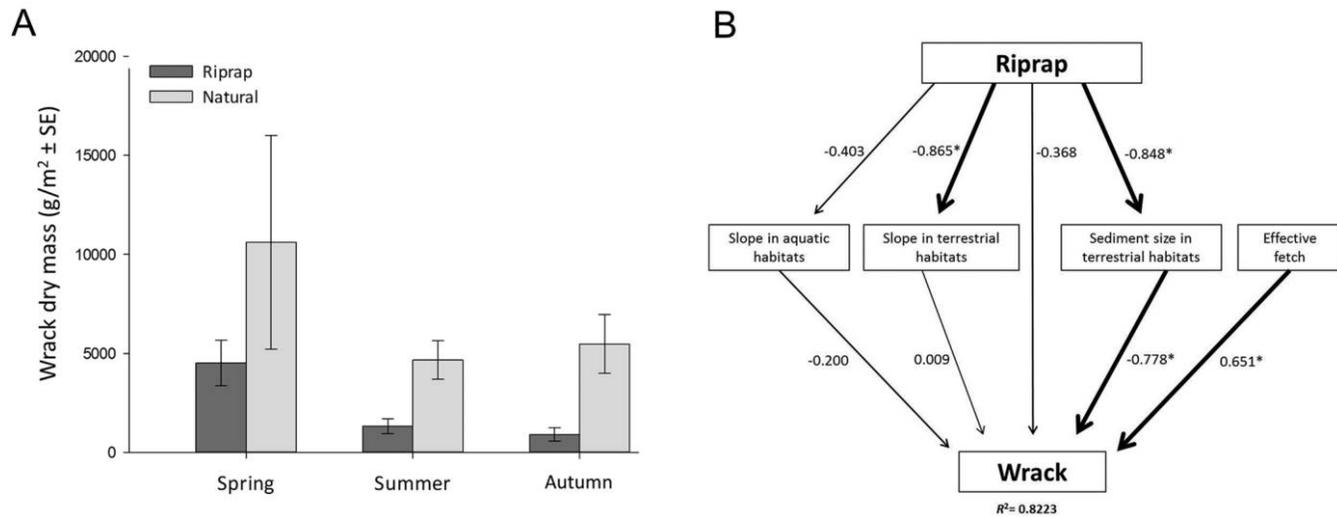


Figure 4. A.—Mean (± 1 SE) standing stock of wrack (g/m^2 dry mass) on natural and riprap shorelines during each season. B.—Path analysis of factors influencing the standing stock of wrack on Lake St Clair shorelines. * = indicates a significant relationship, and path arrows are weighted by effect strength. The combined path coefficient of the riprap–sediment, size–wrack pathway is 0.66 (model $df = 6$, $p = 0.013$). Effective fetch, a measure of wind-driven wave energy, influenced wrack quantity separately from riprap.

dance of snails was marginally significant (natural: 12.6%, riprap: 1.0%; $F_{1,6} = 5.24$, $p = 0.062$). On natural shorelines, beetles, isopods, spiders, and snails were the most abundant taxa (77.0% of individuals).

Aquatic shoreline habitats Invertebrates from 14 different orders were collected. On average, 6.3 orders and 123 individuals were collected at each site. H' ranged from 0.40 to 1.83 (mean = 1.04), and J ranged from 0.17 to 0.83

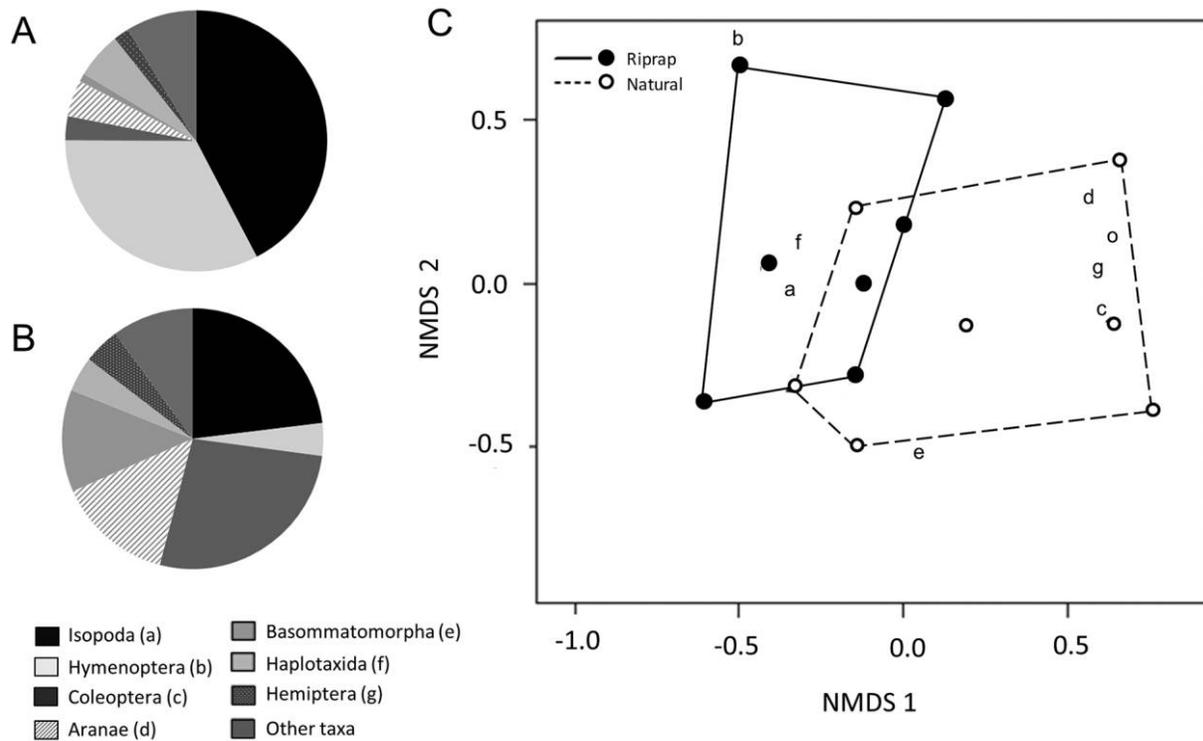


Figure 5. Proportional abundances of invertebrate taxa (order and subclass) collected from wrack and sediment of terrestrial habitats of riprap (A) and natural (B) shorelines, and nonmetric multidimensional scaling (NMDS) ordination plot (C) for terrestrial shoreline invertebrate communities. The most common invertebrate taxa (A, B) are indicated with letters on the NMDS plot.

(mean = 0.60). Amphipoda was, by far, the most common group of invertebrates. They made up 47.7% of all individuals collected and were found at every site. Aquatic isopods made up 20.4% and dipteran (fly) larvae and pupae made up 15.1% of invertebrates.

Aquatic invertebrate communities differed little between natural and riprap shorelines (Fig. 6A, B). Order richness ($p = 0.55$), total abundance ($p = 0.16$), H' (natural: 1.04, riprap: 1.03; $p = 0.99$), and J (natural: 0.60, riprap: 0.60; $p = 0.99$) did not differ between shoreline types. Natural and riprap shorelines had little to no separation in ordination space (NMDS, stress = 0.073; Fig. 6C), and community composition did not differ between shoreline types (MRPP, $\delta_{\text{obs}} = 0.38$, $\delta_{\text{exp}} = 0.41$, $A = 0.06$, $p = 0.101$). Amphipods and aquatic isopods dominated the communities on both shoreline types, but the proportional abundance of dipteran larvae was significantly greater on natural than riprap shorelines ($F_{1,6} = 5.99$, $p = 0.05$). Dipteran larvae made up 21.5% of all individuals on natural shorelines, but only 8.8% on riprap shorelines.

Drivers of organic-matter decomposition

Linear regressions were used to identify those biotic and abiotic factors that were related to the decomposition of organic matter in terrestrial habitats during summer. Cotton-strip and *Phragmites* decomposition rates were pos-

itively related to moisture availability ($F_{1,12} = 11.46$, $R^2 = 0.49$, $p = 0.005$; $F_{1,12} = 7.02$, $R^2 = 0.37$, $p = 0.021$; respectively). Mean daily temperature had marginally significant, negative relationships with decomposition rates of cotton strips and *Phragmites* ($F_{1,11} = 4.51$, $R^2 = 0.29$, $p = 0.057$; $F_{1,11} = 4.56$, $R^2 = 0.29$, $p = 0.056$; respectively). Moisture availability was marginally negatively correlated with daily temperature (r [Pearson correlation] = -0.517 , $p = 0.071$). Together, these results suggest that moisture availability had a stronger influence on decomposition rates than temperature. Neither cotton-strip nor *Phragmites* decomposition was significantly related to the abundance of detritivorous invertebrates on the shorelines ($F_{1,12} = 0.09$, $R^2 = 0.01$, $p = 0.762$; $F_{1,12} = 1.65$, $R^2 = 0.12$, $p = 0.223$; respectively).

DISCUSSION

Key abiotic characteristics of riprap shorelines

Central to the discipline of aquatic ecology are concepts that explain biotic and abiotic patterns and processes of aquatic ecosystems. These concepts include the flood pulse concept (Junk et al. 1989, Tockner et al. 2000), the aquatic-terrestrial transition zone (Ward and Stanford 1995), the natural flow regime (Poff et al. 1997), and the river continuum concept (Vannote et al. 1980). Ideas shared among these concepts are that terrestrial and aquatic ecosystems are connected (e.g., hydrologically, through the movements

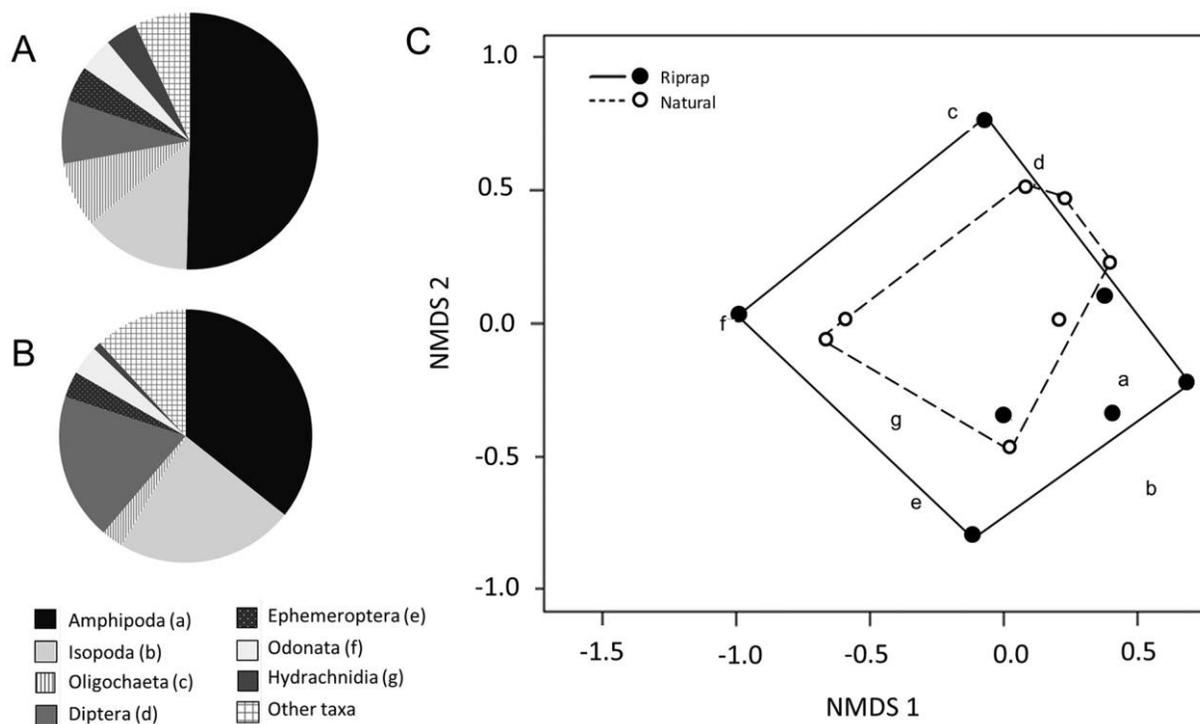


Figure 6. Proportional abundances of invertebrate taxa (order and subclass) collected from aquatic habitats of riprap (A) and natural (B) shorelines, and nonmetric multidimensional scaling (NMDS) ordination plot (C) for aquatic shoreline invertebrate communities. The most common invertebrate taxa (A, B) are indicated with letters on the NMDS plot.

of organisms and organic matter) and that physical and biogeochemical dynamics (e.g., inundation regimes) are vital to maintaining ecosystem structure and functioning. Many of these concepts were developed for application in lotic ecosystems, but they bear relevance for lentic environments. We observed that lake shoreline hardening influences the connectivity between lake and terrestrial ecosystems and attributes of shorelines that influence their hydrologic and biogeochemical dynamics (e.g., shoreline slope). Additional effects included altered invertebrate communities and organic-matter dynamics. Negative effects on terrestrial shoreline habitats were particularly pronounced. These results are important given the ubiquity of shoreline hardening in lake and other aquatic ecosystems and the high ecological value of shoreline ecosystems.

Shorelines hardened with riprap differed dramatically from natural shorelines in terms of morphology and moisture availability. Sediments in both aquatic and terrestrial habitats were orders of magnitude larger on riprap than on natural shorelines. Terrestrial habitats had lower moisture availability on riprap than on natural shorelines. On riprap shoreline, terrestrial habitat had low moisture availability and steep slopes, which reduced the area of transitional, periodically inundated habitat, whereas these aquatic habitat attributes were not altered by riprap. Shoreline slope, the distance riprap extends beyond the waterline, and sediment size may depend on where riprap was constructed and the size of the materials used. For example, in the Hudson River, riprap shorelines are steeper than natural shorelines (Strayer et al. 2012), but Gabriel and Bodensteiner (2012) did not find this pattern for Wisconsin wetland shorelines. In Lake St Clair, riprap does not typically extend far into the water, which may explain why aquatic riprap habitats were more similar to their natural counterparts than were terrestrial habitats.

Invertebrate communities

We predicted that abiotic differences between riprap and natural shorelines would influence invertebrate community structure. Community composition in terrestrial habitats differed between shoreline types, which may have been caused by differences in physical habitat characteristics, which often determine habitat suitability (Poff 1997). For example, snails were much more prevalent on moister natural shorelines, whereas ants were more common on drier riprap habitats, perhaps because of differences in desiccation tolerance. Differences in invertebrate community structure have the potential to affect the abundance or community structure of other shoreline and aquatic organisms. For instance, riparian invertebrates can sometimes constitute the majority of fish diets (Francis and Schindler 2009).

In contrast, aquatic invertebrate communities were quite similar between shoreline types. This result differs from

findings in other studies. Hardening of marine shorelines can affect aquatic invertebrate communities (Dugan et al. 2008, Sobocinski et al. 2010). Invertebrate community structure on shorelines of the freshwater Hudson River was altered by hardening (Strayer et al. 2012), and geomorphological alterations strongly affected littoral zone invertebrates in Mediterranean lakes (Pilotto et al. 2015). One explanation might be that we compared invertebrate communities at the order level, and finer taxonomic resolution may be needed to detect effects in aquatic habitats where the effects of riprap are less pronounced than in terrestrial habitats. Alternatively, other anthropogenic factors might influence Lake St Clair aquatic invertebrate communities more strongly than hardening. We captured relatively few aquatic invertebrates overall from Lake St Clair shorelines, possibly because the lake has been affected by multiple invasive species introductions, climate change, and moderate nutrient loading from agricultural runoff (Bausatian et al. 2014). The soft shoreline sites we sampled, while relatively natural, may have already been impaired and, therefore, inhabited by tolerant taxa less likely to be sensitive to hardening.

Invasive species have had widespread adverse environmental effects in the Great Lakes (Smith et al. 2015), and massive efforts are underway to minimize their impact. Invasive plants, animals, and cyanobacteria were prevalent on both riprap-hardened and natural shorelines. We frequently observed *Phragmites australis* and purple loosestrife (*Lythrum salicaria*) in terrestrial habitats. Isopods, the most common families of which are introduced from Europe (Jass and Klausmeier 2000), made up nearly 1/3 of all invertebrates we collected. Exotic invasive earthworms were prevalent in lower layers of decomposing wrack. Nearly all earthworm species identified in the Great Lakes region belong to the family Lumbricidae and are of European origin (Frelich et al. 2006). In addition to European taxa, we found abundant *Amyntas*, a genus belonging to the family Megascolecidae that has been reported in Michigan as a new invader from Asia and that differs from Lumbricidae in its ecology and environmental impacts (Greiner et al. 2010, 2012). These earthworms have been found in Michigan riparian forests, but to our knowledge, they have not been documented on shoreline habitats until now. Invasive earthworms alter organic-matter dynamics in forest ecosystems of the Great Lakes region (Greiner et al. 2012) and may have similar effects on freshwater shorelines. Last, wrack, a lake-derived shoreline resource that is strongly influenced by riprap, was dominated by invasive *Phragmites* litter and the cyanobacterium, *Lyngbya wollei*. As an N-fixer, *L. wollei* presents a novel source of N with the potential to alter nutrient cycling and biotic communities in shoreline ecosystems (Philips et al. 1992, Hudon et al. 2014).

Stressors can have interactive effects in aquatic ecosystems (Allan et al. 2013). Shoreline hardening may facilitate invasive species, e.g., by allowing colonization by dreissenid

mussels (Goforth and Carman 2005, Meadows et al. 2005, Strayer et al. 2012) and providing cavities for nesting Round Goby (*Neogobius melanostomus*; Jude and DeBoe 1996). In addition, construction equipment and soils used to install stabilization structures could transport exotics to shorelines (e.g., Costello et al. 2011). However, in our study, exotic invertebrate taxa (at the order level) were equally common on natural and riprap shorelines. Whether riprap facilitated these invasions is not clear because riprap structures at our study sites have been in place for at least several decades. The hypothesis that riprap and other hard structures may serve as a source of exotic species to invade nearby natural shores should be investigated on recently hardened shorelines and at a finer taxonomic level.

Decomposition rates

Terrestrial organic-matter decomposition rates were much slower on hard riprap than on soft natural shorelines, apparently because of differences in moisture availability. Summer decomposition rates were positively related to shoreline moisture availability, but negatively related to temperature. Decomposition rates, including those of cotton strips (Griffiths and Tiegs 2016), typically increase with temperature. Temperature and moisture availability are inversely related, and decomposition may have become moisture-limited at some sites. Organic matter decomposed most rapidly in terrestrial habitats of natural shorelines, which tended to be cooler, shaded, and more moist than riprap shorelines, indicating that moisture availability was a more important driving factor than temperature. Generally, microbial activity is highest in humid or frequently inundated conditions than in drier areas (Kuehn and Suberkropp 1998, Langhans and Tockner 2006, Corti et al. 2011). Therefore, the low-moisture conditions on riprap shorelines probably affected decomposition via negative effects on microbial communities. The abundance of large-bodied detritivorous invertebrates failed to explain decomposition rates of organic matter during spring. These results suggest that microbes are the primary drivers of decomposition on these shorelines.

The low importance of invertebrates to decomposition might have occurred because the invertebrates sampled on a single date were not representative of the communities during the 3-mo-long incubation period. Moreover, the contributions of invertebrates and microbes to the decomposition process could not be compared directly because invertebrate abundance and moisture availability were quantified in different seasons. Last, cotton strips are generally unpalatable to invertebrates (Tiegs et al. 2013a), and detritivorous invertebrates did not contribute significantly to *Phragmites* decomposition. Additional studies are needed to determine the relative importance of microbes and invertebrates to shoreline organic-matter decomposition during each season.

In contrast to our finding that riprap slowed decomposition in terrestrial shoreline habitats, Harris et al. (2014) found that organic matter decomposed more rapidly on riprap than on sandy shorelines of the Hudson River. A key methodological distinction, however, is that Harris et al. (2014) placed litterbags near the waterline, where they were inundated twice daily by tidal fluctuations. Organic-matter dynamics at the waterline are likely to differ from dynamics at permanently dry or permanently submerged locations. Moreover, the effect of riprap on incoming wave energy might be more important at the waterline than at submerged locations.

Riprap increases the slope of terrestrial shorelines and may slow overall organic-matter processing by reducing the area periodically inundated by fluctuating water levels. Organic matter decomposes more quickly in periodically inundated than in dry conditions (Battle and Golladay 2001, Bedford 2005). Even one cycle of wetting and drying can greatly increase decomposition rates (Langhans and Tockner 2006). On riprap shorelines, a greater proportion of what little organic material is retained would remain dry and, therefore, would decompose at the reduced rate found in terrestrial habitats.

Riprap did not significantly affect organic-matter decomposition rates in nearshore aquatic habitats. The weak and nonsignificant trend toward greater mass loss on riprap shorelines might have been caused by fragmentation and transport of the organic matter in the high wave energy environment associated with hardened shorelines (Strayer and Findlay 2010). Future research is warranted to evaluate the effect of shoreline hardening in nearshore aquatic habitats on organic-matter dynamics, including decomposition and retention.

Wrack

We predicted that the steep slopes and large sediment size of riprap shorelines would reduce the quantity of wrack resources. Our finding that terrestrial areas of riprap shorelines had little wrack despite a slow decomposition rate suggests that riprap impairs the ability of shorelines to retain organic matter. Path analysis indicated that riprap prevents wrack deposition by increasing sediment size. Extremely large pieces of concrete may act as vertical seawalls at a fine spatial scale, blocking incoming wrack-carrying waves. In contrast to findings by Harris et al. (2014), shoreline slope did not strongly affect the quantity of wrack in our study. By disrupting wrack deposition and slowing decomposition, riprap alters the flow of lake-derived nutrients entering shoreline ecosystems. This reduced input could influence the ability of shorelines to support organisms, such as shorebirds, which feed on wrack-colonizing invertebrates. In stream ecosystems the loss of an analogous resource, leaf-litter inputs from riparian forests, can result in reductions in abundance and biomass across multiple trophic levels (Wallace et al. 1997).

Incoming wrack that is not deposited on riprap-hardened shorelines probably is not retained in adjacent shallow areas, but rather, is transported elsewhere. We often observed floating wrack in shallow waters of natural shorelines, but rarely along riprap shorelines. Riprap and other stabilization structures reflect, rather than absorb, wave energy (Strayer and Findlay 2010), and organic matter in these high-energy areas may be transported away and deposited in deeper water further from shore or at a different shoreline location. Therefore, natural shorelines with gentle slopes and fine sediments may accumulate greater than normal quantities of wrack when surrounding areas of shoreline have been hardened.

Wrack was deposited in great quantities on natural shorelines, particularly during spring, and was dominated by the invasive cyanobacterium *Lyngbya wollei*. The overall quantity of wrack on Lake St Clair shorelines was much greater than quantities reported for other freshwater shorelines, including wrack on the Hudson River (Harris et al. 2014), and *L. wollei* blooms on other shorelines within the Laurentian Great Lakes region (summarized by Hudon et al. 2014). Wrack can be a nuisance because, in large quantities, it can impair the aesthetic and recreational value of shorelines frequented by humans. Invasive *L. wollei* produces a variety of toxins (Hudon et al. 2014) and can harbor *Escherichia coli* (Vijayavel et al. 2013), making it a potential health hazard on public beaches.

Recommendations

Riprap hardening altered shoreline morphology and invertebrate communities and impaired terrestrial-aquatic resource exchanges, so we suggest consideration of shoreline softening (removal of hard stabilization structures) as a means of restoration. Hybrid stabilization methods, such as marsh-sills, sloped habitat shelves, and incorporating pocket beaches are increasingly used to protect shoreline properties while improving ecological function and biodiversity (Bilkovic and Mitchell 2013, Toft et al. 2013). Alternatively, modifications, such as incorporating smaller sized pieces of riprap, may allow shorelines to capture more wrack and restore ecosystem connectivity. Gentler slopes in terrestrial areas would allow periodic inundation of greater areas and may allow decomposition to proceed at rates more similar to those of natural shorelines.

Shoreline ecosystems are vital for maintaining aquatic and terrestrial habitats, but shorelines are often hardened with little understanding of the ecological consequences. We showed that riprap shorelines differ in structure and function from their natural counterparts, with particularly pronounced effects in terrestrial shoreline habitats. Morphological and physical alterations associated with riprap, such as steeper slopes, larger sediment, and reduced moisture availability, had subsequent effects on the ecological functioning and community structure of shorelines. The ability of shorelines to facilitate resource-subsidy exchange

was lessened because riprap impaired deposition of lake-derived wrack. Given the dramatic alterations of the physical shoreline environment, community structure, and the prevalence of invasive species at multiple trophic levels, hardened shorelines of Lake St Clair—and presumably other lakes in the Great Lakes region—meet many of the criteria for categorization as novel ecosystems (sensu Hobbs et al. 2009). Such systems may require unique management considerations. Naturalizing shoreline morphology through shoreline softening is likely to help restore ecosystem functioning (e.g., connectivity between lakes and terrestrial ecosystems, organic-matter retention, and decomposition), and shoreline communities. Additional research will be needed to understand better the impacts of shoreline hardening on community structure of invertebrates and other biota (e.g., near-shore fish and shore birds) and on subsidy exchanges between aquatic and terrestrial ecosystems and nutrient cycling in transitional shoreline ecosystems.

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