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Effects of Urbanization on the Dynamics of Organic Sediments in Temperate Lakes

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Abstract

Residential development of lakeshores affects the structure and function of riparian and littoral habitats. Organic detritus in sediments is a critical component of littoral food webs, but the effects of urbanization on sediment characteristics are unexplored. We characterized the quantity of organic sediments in Pacific Northwest lakes along a development gradient and found a 10-fold decline in the proportion of detritus in littoral sediments associated with density of lakeshore dwellings. In a comparison between two fully developed lakes and two undeveloped reference lakes, we examined several possible controls on sedimentary organic content, including terrestrial inputs, decomposition rates and associated macroinvertebrate communities, and physical retention by coarse wood. The littoral sediments of undeveloped lakes ranged from 34 to 77% organic by mass, whereas the range on urban lakes was an order of magnitude less, ranging from 1 to 3% organic. We found no significant differences in terrestrial litter inputs between the two sets of lakes. Leaf litter decomposition rates did not vary significantly between the two sets of lakes, and we found higher densities of shredder macroinvertebrate taxa in the littoral zones of undeveloped lakes. Sedimentary organic matter on undeveloped lakes accumulated in shallow waters and declined with distance from shore, whereas the opposite pattern existed on urban lakes. Our results suggest that coarse wood physically retains organic matter in littoral zones where it can enter the detrital energy pathway, and the loss of this feature on urban lakes alters littoral sediment characteristics, with potentially far-reaching consequences for lake food webs.

Key words: littoral; urban ecology; coarse woody debris; sediments; organic matter; leaf litter; aquatic-terrestrial coupling; benthic invertebrates.

Introduction

As urban development sprawls, the effects of human activities on lake ecosystems are becoming more apparent and complex. For several decades, the greatest human threat to lake ecosystems was eutrophication of surface waters (Schindler 1978; Carpenter and others 1998). Though eutrophication owing to nonpoint source pollution from agricultural, urban, and industrial sources remains a problem for lakes in North America (Carpenter and others 1998; Moore and others 2003), it is apparent that human activities have myriad effects

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on lake ecosystems. For example, fish growth rates are negatively correlated with lakeshore development intensity (Schindler and others 2000), and the spatial distribution of fishes is altered by urbanization (Lewin and others 2004; Scheuerell and Schindler 2004). Lakeshore and watershed urbanization are correlated with reduced amphibian abundance (Woodford and Meyer 2003) and shifts in benthic invertebrate (Quinlan and others 2002) and zooplankton (Dodson and others 2005) community composition.

Human activities and their impacts on limnetic ecosystems are concentrated along lakeshores, where coupling between terrestrial and aquatic systems is particularly strong. Residential development of shorelines is associated with reductions in riparian forest density as homes, lawns, and related residential structures replace native vegetation (Christensen and others 1996; Francis and Schindler 2006; Marburg and others 2006) and alter plant community diversity, reducing the abundance of native plant species (Elias and Meyer 2003). Humans alter littoral habitats through residential development, for example by removing macrophytes (Jennings and others 2003), which in turn changes the spatial distribution of fishes (Bryan and Scarnecchia 1992).

One unexplored consequence of lakeshore urbanization is its impact on the distribution, composition, and abundance of sedimentary organic matter. The role of detritus and organic matter as a critical energy link in lakes has long been recognized (Lindeman 1942). Recently, it is argued that detritus forms the foundation for energy flow in many aquatic ecosystems (Polis and Strong 1996; Moore and others 2004). Organic matter provides a substrate for colonization by bacteria and other microbes, which are a food source for macroinvertebrates and fishes. Because benthic energy pathways are critical to upper trophic levels in lakes (Schindler and Scheuerell 2002; Vander Zanden and Vadeboncoeur 2002), the loss of this detrital energy source could have major consequences for food web structure and lake ecosystem function.

Here, we hypothesize that the loss of coarse wood from urban littoral habitats increases the flow of organic sediments to deeper waters, resulting in lower organic content in littoral sediments. One alternative hypothesis is that decreased inputs of terrestrial leaf litter from thinned urban riparian forests reduce littoral detritus, as development intensity is also associated with riparian deforestation on this same set of lakes (Francis and Schindler 2006). Leaf litter inputs to lake surface waters have seldom been quantified, and yet they can be substantial (Gasith and Hasler 1976; France and Peters 1995). Because allochthonous sources can dominate the organic pools in littoral sediments (Pieczynska 1990a), it is possible that the losses of particulate terrestrial inputs associated with riparian deforestation may be implicated in reduced littoral detritus pools. Another potential explanation for the lower organic content of urban lake sediments is that developed lakes have higher rates of decomposition, and therefore particulate organic matter is more rapidly processed and transferred into either the invertebrate pool or the dissolved organic matter pool. Microbial degradation can increase under higher nutrient conditions (Oertli 1993; Bayo and others 2005), and certain detritivorous macroinvertebrates thrive under eutrophic conditions associated with urbanization (Kashian and Burton 2000). Higher rates of invertebrate- or bacteria-driven decomposition in urban lakes may therefore explain losses of littoral sediment organic matter along a gradient of urbanization.

Loss of coarse wood (dead and downed tree stems and branches, here defined as >1 m in length and >10 cm in diameter) from littoral habitats is strongly associated with shoreline urbanization (Christensen and others 1996; Francis and Schindler 2006; Marburg and others 2006). Although it is assumed that wood is important in the structure and function of littoral habitats (Schindler and Scheuerell 2002; Jennings and others 2003), as yet very little is known about the specific roles played by coarse wood in lakes. It has been shown extensively in streams that coarse wood increases organic matter retention (Bilby 1981; Bilby and Ward 1991), and less coarse wood in urban lakes may result in a loss of sediment organic matter. The majority of detritus in lakes is deposited in shallow water zones (Piezynska 1990b) where it then becomes part of the sediments. In the absence of coarse wood as a physical structure to retain particulate detritus in shallow waters, organic matter deposited in littoral zones may be transported to deeper waters, resulting in reduced organic content of urban littoral sediments. This reduction in littoral sediment quality may in turn have consequences for upper trophic levels and lake-wide food web interactions, as littoral habitats house a variety of benthic invertebrates that serve as prey items for fishes and are therefore key sites for benthic–pelagic coupling (Schindler and Scheuerell 2002; Vander Zanden and Vadeboncoeur 2002).

In this paper, we investigate the effects of shoreline urbanization on littoral habitat characteristics, specifically the organic content of littoral sediments. We then explore several possible mechanisms to explain the relationship between lakeshore development and sediment organic matter. Previous results showed a relationship between urbanization and loss of littoral coarse wood (Francis and Schindler 2006), therefore we mapped the distribution of sediments with distance from shore, hypothesizing that littoral coarse wood retains organic matter in littoral sediments. Because the riparian zones of urban lakes in this region are deforested (Francis and Schindler 2006), we explored whether reduction in leaf litter inputs results in lower organic matter in urban sediments compared to undeveloped lakes with intact riparian forests. Finally, because decomposition processes can control sediment characteristics, we measured decomposition rates on urban lakes and compared them to those observed on undeveloped lakes to determine whether biodegradation explains sediment organic content.

Methods

We sampled 15 lakes in western Washington State and southern British Columbia, Canada (see Francis and Schindler 2006 for physical descriptions). The lakes are all located in the western hemlock (*Tsuga heterophylla*) zone of the Cascade Range and Puget Trough regions. Study lakes span a gradient of urban development and are mostly located in the urban fringe of the Seattle Metropolitan area. Nearly all lakes were closed to boats with outboard motors. Three undeveloped lakes were selected as reference systems, located in the University of British Columbia's Malcolm Knapp Research Forest. The latitudinal gradient between our study sites is not sufficient to affect forest or invertebrate community composition.

We surveyed the lakes between July and October of 2002 and in October 2006 for development intensity, coarse wood density and basal area, and sediment composition. A full description of the survey and coarse wood sampling strategy is given in Francis and Schindler (2006). On each lake, we selected 4–8 transects measuring 30 m along the lakeshore, ensuring to select an even number of both leeward and windward sites. Along each transect, we enumerated and measured the diameter of all pieces of coarse wood (≥10 cm in diameter, ≥1 m in length) within or intersecting the 0.5 m depth contour. We calculated coarse wood basal area for each plot as the sum of all individual log basal areas, defined as

$$\text{basal area} = \pi * r^2 \tag{1}$$

where r = radius at breast height (trees), or where the log intersected the 0.5 m depth contour. We characterized sediment composition by collecting the top 5 cm of sediments in 0.5 m of water using a 10 cm diameter hand-held sediment corer. Sediments were refrigerated to limit further biotic processing until they were dried at 60°C to a constant mass and then combusted at 550°C to determine ash free dry mass (AFDM). Sediment organic matter was calculated as the proportion of dry mass lost during combustion.

To investigate the mechanisms driving the relationship between lakeshore urbanization and sediment organic matter observed in the survey, we conducted a focused comparative study between two urban, fully developed lakes (that is, >95% of shoreline developed; Star and Shady Lakes) located in suburban areas of Seattle and two wholly undeveloped lakes (Loon and Gwendoline Lakes) in British Columbia (Figure 1). These two sets of lakes represent the high and low ends of the gradients for sediment organic matter and residential development observed in the survey (Francis and Schindler 2006; Table 1).

We measured leaf litter input on the set of four lakes by establishing three transects running perpendicular to shore at randomly selected sites along the shoreline. Along each transect, we measured the lateral distribution of terrestrial leaf litter inputs to surface waters from July 2003 to April 2004 by deploying litter traps, 20 cm × 30 cm (0.06 m^2) floating plastic bins, at 1, 5, 10, 20, and 40 m from shore. The litter traps passively sampled aerial litterfall constantly for 10 months. Contents were removed every 22–61 (median: 46) days and dried at 60°C to a constant mass. In September 2003, a heavy rainstorm raised the water level of Loon Lake such that all traps were swamped. In February 2004, Gwendoline Lake was frozen and traps were inaccessible; however, bins continued to collect litter inputs, and therefore the sample collected in March was assumed to include inputs from the previous period.

To measure decomposition rates in the four lakes, we incubated red alder (*Alnus rubra*) leaves in mesh bags anchored to the lake bottom at two depths during late summer/autumn and winter. We collected senescent alder leaves from the watershed surrounding each lake, dried them at room temperature, and created leaf packets which were placed in either fine (<0.5 mm) or coarse (1 cm) mesh bags. The fine mesh bags successfully prevented the colonization of leaf packets by macroinvertebrates. Bags were weighed before incubation and anchored to cinder blocks on the lake bottom at two depths, above and below the thermocline, to incorporate potential variation in

Figure 1. Shorelines of Pacific Northwest lakes of different residential development intensity. **A** Gwendoline Lake, British Columbia, undeveloped; **B** Shady Lake, Washington State, 100% of shoreline developed.

Table 1. Lake Biophysical Characteristics

Lake	Location	Maximum depth (m)	Mean depth (m)	Surface area (ha)	Residential density (houses m^{-1} shoreline)	Coarse wood density (pieces m^{-1} shoreline)	Sediment organic matter (proportion by mass)	Epilimnetic Chlorophyll-a (μl^{-1})
Gwendoline	19°49′N 34°122′W	27	13.4	13.0	0	425.0	0.77	0.69
Loon	19°49′N 34°122′W	55	26	48.6	0	516.7	0.34	0.66
Shady	25°47′N 6°122′W	12	6	8.5	40	10.0	0.01	4.83
Star	21°47′N 17°122′W	15	8	14.2	40.6	0	0.03	1.32

invertebrate and microbial decomposition rates associated with temperature. Several reference bags were put through the weighing, bagging, and placement process to establish mass lost during transport, and this correction factor (−1.6% for fine bags, −6.9% for coarse mesh) was applied to all bags before statistical analyses. After the incubation period, bags were retrieved by SCUBA, dried at 60°C to a constant weight, and reweighed. Decomposition rate *k* (Petersen and Cummins 1974) was calculated according to an exponential function as follows:

$$W_t = W_0 e^{(-kt)} \quad (2)$$

where W_t is equal to the mass of leaf material remaining after incubating for *t* days and W_0 is the initial corrected mass.

We collected surface sediments at various distances from shore on all four lakes to assess the spatial distribution and particle size composition of sediment organic matter. We stratified distances into ''near'' (1–10 m) and ''far'' (20–40 m) from shore, based on previous work showing that the majority of allochthonous inputs are deposited within 10 m from shore (France and Peters 1995). We did not measure sediment organic matter in the deep basins of these lakes, but rather concentrated on the littoral zones, where organic matter accumulation was observed in the survey. We collected sediments using an Ekman dredge below each floating litter trap in summer and winter. Each sample was sorted using soil sieves into smaller than 0.06, 0.06, 0.12, 0.18, 0.42, 1.0, 2.5, and 6.35 mm size categories and dried at 60°C to a constant mass. A subsample of each was combusted and the proportion of organic content was calculated for each size category as described above.

We sampled the benthic macroinvertebrate communities in each of the four lakes along the established transects using an Ekman dredge during the late summer of 2003. We collected invertebrates in surface sediments below each floating litter trap at depths of 0.3–11 m of water. Invertebrates were preserved in 95% ethanol and identified to family.

Statistical Analyses

We used SYSTAT 11.0 (Systat Software Inc., 2004) for all statistical analyses. Data transformations—arcsine square root transformations for the proportion organic matter in sediments and natural log transformation for density of lakeshore residences—were performed prior to statistical analyses to normalize data. We used least-squares regression using data from the 15-lake survey (excluding one outlier; Studentized residual = −3.1) to assess the relationships between lakeshore residential density and sediment organic matter, and coarse wood density and sediment organic matter content. Previous work has demonstrated a relationship between lake morphometry and sediment organic matter (Rowan and others

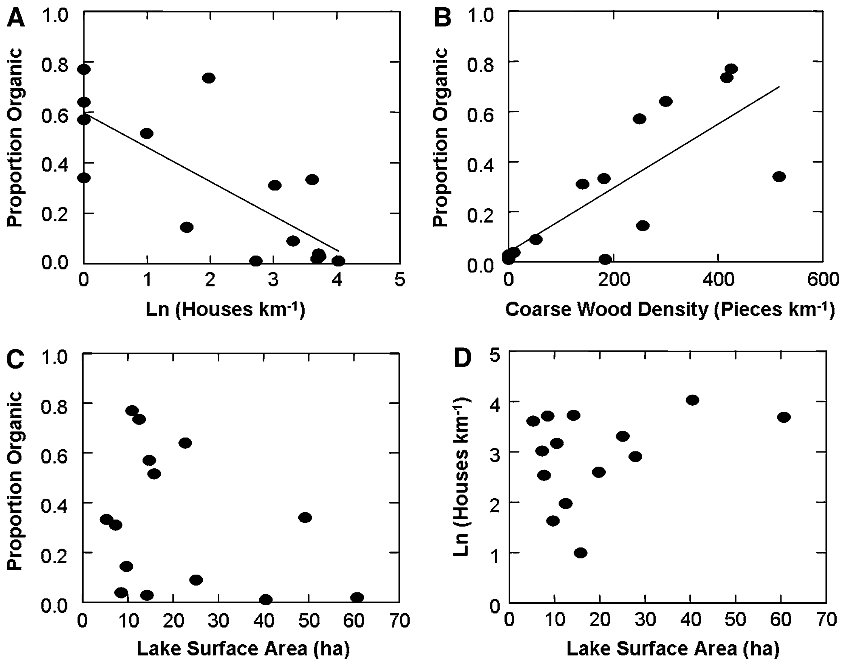

Figure 2. Organic proportion of littoral sediments as a function of **A** residential development and **B** coarse wood density; and sediment organic proportion **C**, and density of shoreline residences **D** as a function of lake surface area. All data shown are from a survey of 15 Pacific Northwest lakes, excluding one outlier ($n = 14$). Proportion data were arcsine-square root transformed prior to statistical analysis. Each point represents a whole lake mean.

1992), therefore we also tested for a relationship between lake size (surface area and perimeter) and sediment organic matter in the 15 lakes using least-squares regression. A final regression investigated the relationship between lake size (surface area) and residential density. In the focused comparison between urban and undeveloped lakes, we tested whether decomposition rates varied according to lake development level using ANOVA with daily mass loss rate as the response variable and development level (developed and undeveloped), season (summer and winter), depth (above and below the thermocline), and mesh size (coarse and fine) as main factors, using post-hoc tests where we found significance. To test the effect of coarse wood on organic sediment particle distribution, we used ANOVA with coarse wood density (high, low) and distance from shore as main effects on organic content of each particle size category, and we ran Student's *t*-tests to test for development differences within seasons at specific distances. We used a MANOVA to test for significant differences in invertebrate communities between the undeveloped and urban lakes.

Results

Sediment organic matter decreased significantly as shoreline residential development density increased in the survey of 15 lakes (adjusted $r^2 = 0.60$, $n = 15$, $P = 0.001$; Figure 2A). The sediment organic content varied from roughly 74% on undeveloped lakes to less than 2% on fully developed lakes. The organic matter content of littoral sediments was significantly and positively associated with the density of coarse wood (adjusted $r^2 = 0.63$, $n = 14$, $P = 0.001$; Figure 2B) and coarse wood basal area (adjusted $r^2 = 0.68$, $n = 14$, $P < 0.001$; not shown). We found no significant relationship between sediment organic matter and either metric of lake size, surface area (adjusted $r^2 = 0.07$, $n = 14$, $P = 0.18$; Figure 2C), or shoreline length (adjusted $r^2 < 0.001$, $n = 14$, $P = 0.99$), and we found no significant relationship between residential density and lake surface area (adjusted $r^2 < 0.001$, $n = 14$, $P = 0.78$; Figure 2D) or lake perimeter (adjusted $r^2 = 0.07$, $n = 14$, $P = 0.15$; not shown).

On each of the four lakes sampled for the focused comparison, annual terrestrial leaf litter inputs decreased with distance from shore (Figure 3A). We found no significant effect of development ($F_{1,17} = 2.5$, $P = 0.13$) on annual leaf litter inputs to surface waters across all distances combined, though the trend was for higher inputs to urban lakes than to undeveloped lakes (Figure 3A; Table 2). Litter inputs varied with distance on all lakes ($F_{1,17} = 5.1$, $P = 0.04$), decreasing with distance from shore according to a negative exponential model (developed lakes: $\text{Inputs} = 158.98e^{-0.31 \times \text{Distance}}$, $r^2 = 0.98$; undeveloped lakes: $\text{Inputs} = 66.9e^{-0.67 \times \text{Distance}}$, $r^2 = 0.99$). The majority (that is, >70%) of leaf litter was deposited within 5 m of shore, and

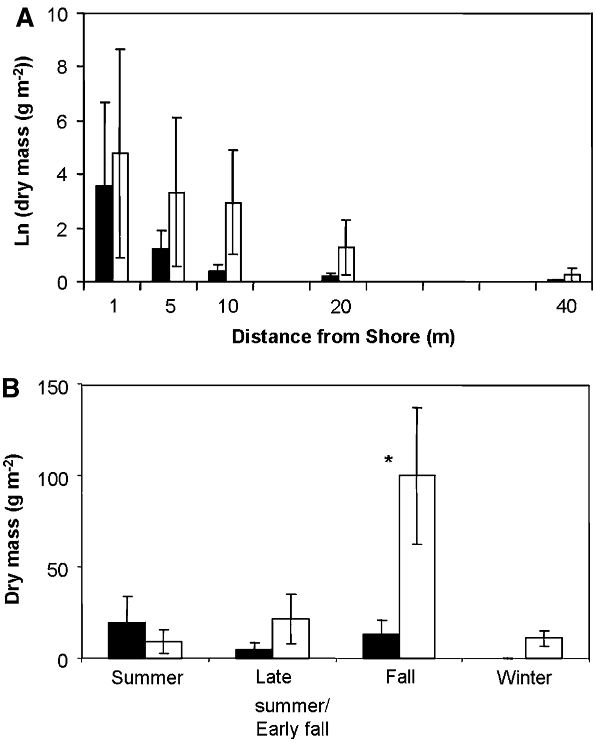

Figure 3. Terrestrial leaf litter inputs to nearshore surface waters on two undeveloped (*solid bars*) and two developed (*open bars*) lakes. **A** Annual inputs (±1 SE) at varying distances from shore. **B** Seasonal inputs (±1 SE) across all distances.

significantly less was observed beyond 10 m ($P = 0.04$). On a seasonal basis, leaf litter inputs varied significantly by development only during fall ($P = 0.04$; Figure 3B and Table 2), with higher inputs to developed lakes during that season. Peak seasonal leaf litter inputs occurred during fall on developed lakes and during summer on undeveloped lakes.

We found significant effects of season and mesh size, but no significant effect of lake development or depth relative to the thermocline, on decomposition rates across all litterbag treatments (Table 3; Figure 4). Decomposition rates were greater in summer than in winter (Tukey's HSD adjusted $r^2 = 0.22$, $df = 1$, $P = 0.006$), and were greater in coarse mesh bags than in fine (Tukey's HSD adjusted $r^2 = 0.53$, $df = 1$, $P < 0.001$), across both development types and incubation positions.

In undeveloped lakes, sediment organic matter accumulated inshore, whereas in developed lakes, sediment detritus increased with distance away from shore (Figure 5). We found significant interactions between development and distance from shore ($F_{4,19} = 22.4$, $P < 0.0001$) and distance and season ($F_{4,19} = 4.1$, $P = 0.02$), and we found a significant three-way interaction effect between development, season, and distance from shore ($F_{4,19} = 5.3$, $P = 0.005$) on the organic proportion of sediments between 1 and 40 m from the shore, such that organic matter decreased with distance from shore on undeveloped lakes but increased with distance on developed lakes. These patterns generally held in both summer and winter, except that overall organic content was higher in urban lakes in winter and more variable closest to shore in undeveloped lakes in summer. We also found significant effects of development ($F_{1,19} = 86.0$, $P < 0.0001$) and season ($F_{1,19} = 8.7$, $P = 0.008$) on the proportion organic in sediments. The mean (SE) proportion by mass of organic littoral sediments on undeveloped lakes was 0.71 (0.11), as compared to 0.11 (0.05) on developed lakes. In both seasons, the amount of sediment detritus on the two lake types converged at 40 m from shore.

Urbanization affected the size distribution of sediment particles. In particular, the smallest particles (<0.06 mm) accumulated nearshore on undeveloped lakes in greater proportions than on developed lakes (Figure 6). In fact, there were almost no fine particles in the nearshore sediments of developed lakes. In tests on the distribution of the smallest (<0.06 mm) organic sediment particles, there were significant interaction effects between development and season ($F_{4,20} = 7.3$, $P = 0.01$) and distance and season ($F_{4,20} = 4.2$, $P = 0.01$), as well as a significant distance effect ($F_{4,20} = 23.8$, $P < 0.0001$). In summer, a significantly greater proportion of fine organic particles accumulated within 5 m of shore on undeveloped lakes versus developed lakes ($P = 0.02$). In contrast, there was no significant difference in the proportion of fine organic particles in littoral sediments between developed and undeveloped lakes in winter ($P = 0.85$).

The benthic macroinvertebrate community varied substantially between urban and undeveloped lakes (Figure 7). The macroinvertebrate community composition in developed and undeveloped lakes were significantly different (MANOVA, Wilks' Lambda, $F_{7,45} = 2.18$, $P = 0.05$); specifically, we found higher densities of shredding caddisflies (Trichoptera) on the undeveloped lakes ($P = 0.02$) and higher densities of detritivorous isopods (Isopoda) on urban lakes ($P = 0.03$; Figure 7). The densities of grazing mayflies (Ephemeroptera) and predatory odonates (Odonata) were 12.9 and 10.7 m^{-2}, respectively, in the littoral zones of

Table 2. Leaf Litter Inputs to Surface Waters of Two Developed (Star, Shady) and Two Undeveloped (Gwendoline, Loon) Lakes

	Annual inputs (g dry weight)		Seasonal inputs (g dry weight)			
	Mean	SE	Summer	Late summer/early fall	Fall	Winter/early spring
Developed	165.1	63.7	8.9	21.4	99.7[a]	10.8
Undeveloped	37.4	21.2	19.6	4.3	13.1[b]	0.0

Different letters in each column indicate significant differences among lake types (Student's t-test; P < 0.05).

Table 3. Summary of ANOVA Results showing Effects of Development (developed, undeveloped), Depth (above, below the thermocline), Season (summer, winter) and Bag Mesh (coarse, fine) on Leaf Litter Decomposition Rates

Factor	Least squares mean	*F*-ratio	*df*	*P*-value
Development		0.2	1	0.70
Undeveloped	0.004			
Developed	0.004			
Depth		3.3	1	0.09
Above	0.0044			
Below	0.0035			
Season		23.5	1	0.0002
Summer	0.005			
Winter	0.003			
Mesh		55.9	1	<0.0001
Fine	0.002			
Coarse	0.006			

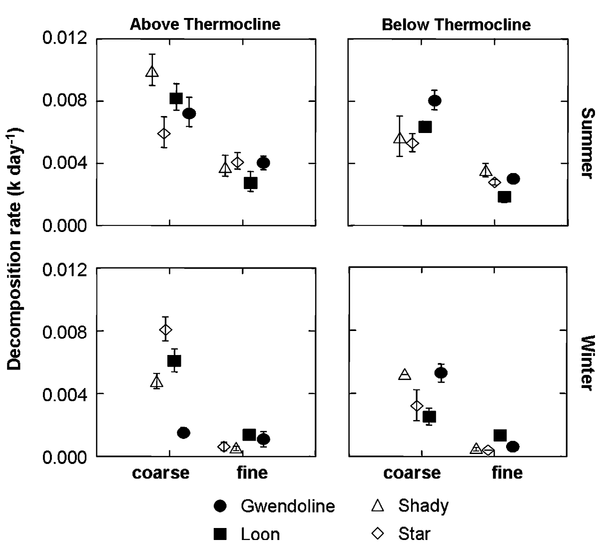

Figure 4. Daily decomposition rates of leaves incubated in two undeveloped (*filled boxes*) and two developed (*open boxes*) lakes in coarse and fine mesh bags during summer and winter. *Boxes* represent whole lake means.

undeveloped lakes, whereas these taxa were entirely absent from similar habitats on urban lakes.

Discussion

Shoreline urbanization has a variety of impacts on lake ecosystems, including eutrophication and altered littoral habitat structure, vegetation community composition, and fish growth and behavior (Schindler and others 2000; Scheuerell and Schindler 2004; Marburg and others 2006). Our results demonstrate two additional consequences of shoreline urbanization: changes in the composition and distribution of organic sediments and shifts in the benthic macroinvertebrate community. We suggest that the best explanation for depleted organic matter in urban littoral habitats is the absence of coarse wood, which provides a physical structure that retains detritus in littoral zones of undeveloped lakes. Without coarse wood to retain organic matter in shallow waters, organic matter is transported by gravity and hydrodynamics to deeper waters on urban lakes.

Riparian Litterfall Influence on Sediment Organic Matter

Our finding that leaf inputs on all lakes decrease with distance from shore according to a negative exponential model concurs with previous studies (Szczepanski 1965; Rau 1976); however, we did not find reduced annual litter inputs to developed lakes. Based on other findings that terrestrial inputs can be tightly linked to littoral organic matter (Efford 1969) and the extensive literature on the role of litterfall in lotic ecosystems, we expected that litterfall into lakes would be reduced in urban environments, where dramatic riparian deforestation has occurred (Francis and Schindler 2006). Indeed, the rare quantification of litterfall to the surface waters of lakes has been expressed in terms of litter inputs per

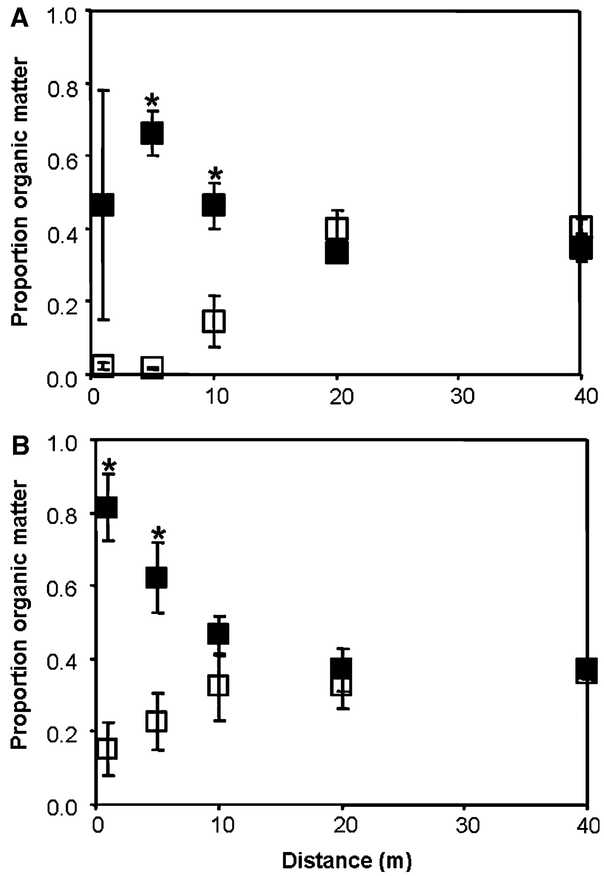

Figure 5. Proportion organic matter in surface sediments with distance from shore on two undeveloped (*filled symbols*) and two developed (*open symbols*) lakes in summer (**A**) and winter (**B**). *Error bars* are 1 SE. *Asterisks* indicate statistically significant differences (Student's *t*-test, $P < 0.05$).

meter of forested shoreline (Szczepanski 1965; Jordan and Likens 1975; Gasith and Hasler 1976).

One explanation for the absence of significantly different litterfall rates between developed and undeveloped lakes is the riparian forest composition shift that occurs with urbanization on lakes in this region. In lowland areas of the Pacific Northwest, the native riparian forest is dominated by conifers, primarily Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), and western red cedar (*Thuja plicata*; Franklin and Dyrness 1973). On the urban lakes in this study, in contrast, native forests are most often replaced with non-native, deciduous species (T. Francis, personal observation), which have considerably higher litterfall rates than conifers (Binkley and others 1992). In regions where native forests are dominated by deciduous tree species, deforestation associated with urbanization may reduce organic inputs to littoral zones of urban lakes, resulting in even greater declines in littoral detritus.

Decomposition of Sediment Organic Matter

We observed no consistent differences in decomposition rates between urban and undeveloped lakes that might explain either higher total OM or greater proportion of fine particulate OM (FPOM) in undeveloped lakes. Biological reduction of the coarse particulate OM (CPOM) pool occurs through processing and ingestion by macroinvertebrates and via microbial degradation. Both processes reduce CPOM while increasing the FPOM pool (Saunders and others 1980). Despite higher densities in the undeveloped lakes of shredding caddisflies, which are more effective decomposers relative to other shredder taxa (Bjelke and Herrmann 2005), decomposition in the presences of macroinvertebrates was not significantly higher on undeveloped lakes compared to urban lakes in any of the treatment regimes. In addition, the trend towards higher densities on undeveloped lakes of detritivorous amphipods, which ingest FPOM, could only potentially decrease the fine organic pool in these systems.

We found no difference in decomposition between urban and undeveloped lakes despite variation in some abiotic characteristics of the two sets of lakes. Beyond biotic activities, decomposition rates vary according to temperature, oxygen concentration, nutrient levels, substrate, particle size, turbulence, and pH. Our study lakes are similar in terms of annual temperature regimes, though the undeveloped lakes have a slightly higher tendency to freeze for short periods of time in winter. The urban lakes are mesotrophic (total epilimnetic P = 9–10 $\mu g\ l^{-1}$), whereas the undeveloped lakes are oligotrophic (epilimnetic P = 3–4 $\mu g\ l^{-1}$; Moore and others 2003). Despite elevated nutrient levels, however, we observed no greater overall decomposition rates in the urban lakes.

Decomposition of particulate organic matter varies across substrate type. We did not directly measure the source contributions of littoral detritus in each lake, and the trophic status of the urban lakes suggests there might be a greater proportion of autochthonous POM, which is more labile and could be processed more rapidly (Hicks and others 1994), reducing the total OM pool. Given the equivalent leaf litter inputs in both lake types, however, different detritus composition does not explain the pattern of organic matter we observed. Decomposition rates of terrestrial leaf litter also vary by litter type. For example, deciduous alder leaves decompose more quickly than more recalcitrant conifer needles (Webster and Benfield

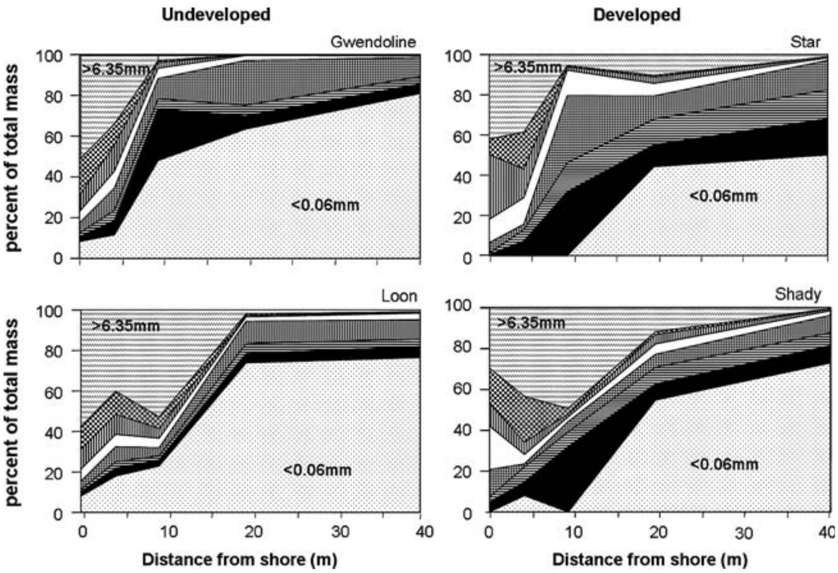

Figure 6. Size composition of organic sediment particles with distance away from shore on four Pacific Northwest lakes in summer. Particles are separated into size categories: smaller than 0.06, 0.06, 0.12, 0.18, 0.42, 1.0, 2.5 and 6.35 mm. Distributions shown are organic proportions by mass of surface sediments.

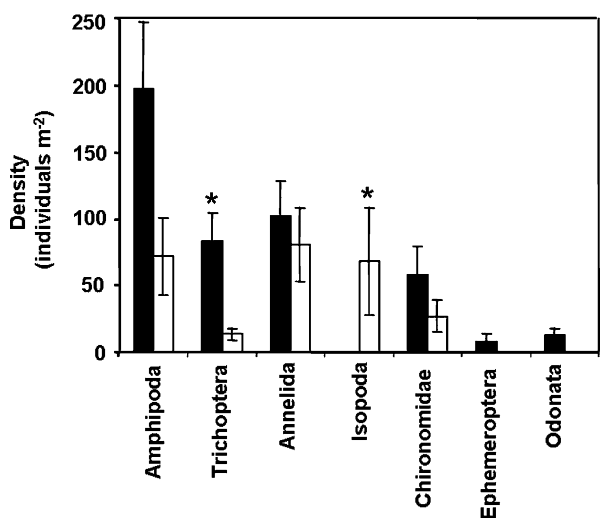

Figure 7. Macroinvertebrate densities on two undeveloped (*solid bars*) and two developed (*open bars*) lakes. *Asterisks* indicate statistically significant differences (Student's *t*-test, $P < 0.05$), *error bars* are standard errors.

1986). The riparian forest community on the undeveloped lakes is dominated by conifers, versus deciduous trees on urban lakes. Thus, it may be that urban litter is decomposed more quickly, leaving less total organic matter in shallow water sediments. Increased litter processing, however, would result in an accumulation of FPOM in nearshore sediments on urban lakes, which we did not observe.

We observed striking differences in the macroinvertebrate community composition between urban and undeveloped lakes that may be associated with reductions in coarse wood and organic sediments. In addition to the differences stated above in the shredder taxa, we found a complete loss of predatory odonates (Odonata) and grazing mayflies (Ephemeroptera) from the urban lakes. The absence of these taxa may be associated with a suite of alterations to urban littoral habitats, including the loss of coarse wood, which serves as habitat, food resource, and predation refuge. These larger invertebrate taxa are key prey for native trout, and their absence may portend a decline in the ability of urban lakes to support productive native fish populations (Schindler and others 2000).

Organic Matter Distribution and Retention

Overall, the amount of organic material in littoral sediments in undeveloped lakes was significantly greater than in urban lakes. Sediment organic matter accumulated in shallow waters on undeveloped lakes and decreased with distance from the shore, but on urban lakes, organic matter increased with distance from the shore. In the 15-lake survey, we found a significant positive correlation between the proportion of organic matter in littoral sediments and coarse wood density, and in the focused comparison, coarse wood density was significantly greater on the two undeveloped lakes compared to the urban lakes. Based on these data and the organic particle distribution, we suggest that littoral OM accumulation results from physical retention by coarse wood that impedes sediment focusing and retains POM in shallow waters. This build-up of organic matter around wood has been extensively observed in lotic ecosystems, where large wood adds hydraulic complexity to rivers and streams (Bilby and Ward 1991; Bisson and Bilby 1998) and retains both coarse and fine organic matter (Bilby 1981; Harmon and others 1986) where it is subjected to biodegradation processes.

The generality of the relationship we have found here between woody debris and sediment organic matter relies on, among other things, inputs of woody debris and production of organic matter. Accumulation of sediment organic matter in littoral zones is regularly observed in shoreline areas with submerged vegetation (James and Barko 1990; Wetzel 1990). Littoral-wetland zones are areas of high organic matter loading and degradation (Pieczynska 1990a; Wetzel 1990; Gude and others 2004); hence, accumulations at lake margins in these systems are common despite the absence of coarse wood. Lakes with significant portions of riparian habitat in wetlands, desert, agriculture, tundra, or otherwise lacking forest would not receive the inputs of woody debris found in these lakes and would not fit the pattern we have observed. Likewise, lakes with unforested watersheds, such as alpine systems, may receive lower inputs of particulate OM and not accumulate littoral detritus to the same degree as the lakes sampled here. Although the evidence is limited, existing research shows that sediment OM is not a function of lake trophic status (Rowan and others 1992). Instead, sediment OM in lakes has been correlated with maximum lake depth, lake surface area and catchment area: lake area (Rowan and others 1992), although we did not find such relationships here.

Human Behavior and Littoral Sediments

We did not directly monitor human behavior, so we cannot exclude the potential that the alteration of shorelines and littoral zones by urban lake residents contributes to the sediment patterns we observed. Certainly human behavior affects the density of coarse wood on urban lakes, as people clear littoral zones for swimming and other recreational activities. Furthermore, residents often deposit gravel or other non-organic substrates along their shoreline, creating a homogenous, non-organic littoral zone (T. Francis, personal observation). Our sampling, however, captured a variety of residential littoral zone types, including those with gravel and those without. Another human influence on sediment composition is erosion from lakeshore development which likely mobilizes soils into lakes. When these lakes were initially deforested at the turn of the twentieth century, as well as during subsequent development for residential use, there may have been intrusions of terrestrial carbon into the lakes. These patterns could be elucidated through paleolimnological investigation. In addition, sediment distribution is associated with wave action and boating can induce wave-like water movements, even on small lakes. The urban lakes in this study, however, restricted the use of motors, allowing only those that propel boats at speeds that do not generate waves. Nevertheless, although we have observed a strong correlation between sediment organic matter and coarse wood density, we cannot definitively rule out human-induced changes to littoral sediments in contributing to these patterns.

Implications

Most lakes in the world are net heterotrophic (Cole and others 1994, 2000; Hanson and others 2003). The respiration of carbon in lakes is concentrated in littoral habitats, which are conducive to decomposition and other biodegradation processes because they are warm and oxygenated (Pieczynska 1990b). If the presence of littoral woody debris enhances degradation processes by retaining organic carbon in the littoral zone, coarse wood may contribute, albeit to an unknown extent, to lake heterotrophy and shift the balance of carbon storage in lake sediments relative to evasion to the atmosphere.

Loss of organic matter from littoral sediments has important implications for food web structure and ecosystem function in urban lakes. Allochthonous particulate carbon inputs are generally considered to support only a minor fraction of lake productivity (for example, Saunders and others 1980; and references), yet there is some evidence that it can be vital to secondary production in some lakes (Pace and others 2004; Cole and others 2006). Terrestrially derived detritus accumulates in the shallow waters of lakes in greater amounts than living material, and in this way acts as an energy reservoir (Saunders and others 1980), fuelling microbial processes and secondary production of aquatic invertebrates that in turn support upper trophic levels. Because most lentic biota are associated to some degree with littoral habitats, it is likely that the loss of coarse wood and the resulting reduction in organic matter destabilizes lake food webs via reduced littoral secondary productivity and subsequent trophic decoupling. In particular, our results suggest a decline in the density of benthic macroinvertebrates in urban lakes, which is likely to impair the ability of urban lakes to support fish that rely heavily on benthic resources.

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