

The demography of coarse wood in north temperate lakes

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SUMMARY

1. Exchange of material across habitat boundaries is a key process in riparian zones. The movement of coarse wood from lakeshore forests to the littoral zone, where it provides habitat for aquatic organisms, is not well understood. In 2003, we resampled coarse wood within the littoral zone of four lakes in Northern Wisconsin (U.S.A.), that had originally been surveyed in 1996, to quantify the spatial arrangement of littoral coarse wood and estimate input, loss and movement rates.
2. All four lakes had a clumped pattern of littoral coarse wood, and the locations of clusters were similar in both census years. Littoral coarse wood was more abundant than expected on moderate to steep slopes, on southern shorelines, and in areas with sparse residential development.
3. All four lakes had a net accumulation of coarse wood; rates of wood input ranged from 0.5 to 1.9 logs km⁻¹ year⁻¹, i.e. there was more wood in 2003 than 1996. Movement rates of tagged logs varied 14-fold among lakes, with a maximum in one lake of 42% of logs recovered in 2003 more than 20 m from their 1996 location. Median distance moved ranged from 22 to 323 m among the four lakes.
4. Areas of persistently high wood density may be keystone habitats whose presence enables the persistence of populations of certain aquatic organisms. Conservation of locations with high wood density may be important to maintain target densities of coarse wood of lakes with human development.

Keywords: coarse woody debris, ecosystem subsidies, littoral zone, riparian zone, spatial pattern

Introduction

Quantifying lateral flows between ecosystems can be crucial for understanding ecosystem function and nutrient budgets (Reiners & Driese, 2001; Turner & Cardille, 2004; Lovett *et al.*, 2005). Classic examples are the transfer of marine nutrients to forests in Hawaii (Chadwick *et al.*, 1999) and the Pacific Northwest (Naiman *et al.*, 2002). Similarly, many lakes and streams are fertilised by runoff from terrestrial

systems (Arbuckle & Downing, 2001). Most studies of lateral fluxes between ecosystems have focused on nutrients, but movement of all types of material can influence ecosystem function (Reiners & Driese, 2001, 2003; Turner & Cardille, 2004). The movement of coarse wood from lakeshore forests to the littoral zone provides an example. Wood is produced in the terrestrial ecosystem yet provides habitat for aquatic organisms when it enters the littoral zone. Several studies have quantified the standing stocks of wood in various northern lakes (Christensen *et al.*, 1996; Guyette & Cole, 1999; Mallory *et al.*, 2000; Marburg, Turner & Kratz, 2006) and a few have estimated loss rates (Hodkinson, 1975; Guyette & Cole, 1999; Guyette *et al.*, 2002). However, none has measured the rate at which coarse wood is added to the lake from the

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riparian forest or the distance it moves once in the littoral zone. Simultaneous estimations of input, movement and loss are the first step toward a more mechanistic understanding of how the abundance of coarse wood fluctuates in space and time.

Littoral coarse wood may be spatially heterogeneous in its distribution around lakeshores. The spatial structure (clustered, random or regular) of littoral coarse wood along the lakeshore should reflect spatial variability in the key rates of input, loss and movement. Many organisms respond to the spatial configuration of habitat directly (Thomson *et al.*, 1996; Pastor, Moen & Cohen, 1997; With, Cadaret & Davis, 1999) or indirectly (Thomson *et al.*, 1996; Tallmon *et al.*, 2003), and thus spatial structure in littoral coarse wood could influence habitat use patterns of aquatic and riparian biota. Habitat use in aquatic systems has been shown to vary with predation risk and prey availability (Crowder & Cooper, 1982; Werner & Hall, 1988; Savino & Stein, 1989; Diehl & Eklöv, 1995). Thus, the spatial configuration of refuges is likely to have implications for predator-prey interactions at the whole lake scale (Eklöv, 1997; Weaver, Magnuson & Clayton, 1997; Sass *et al.*, 2006). Although several studies have documented declines of coarse wood along shoreline segments with high human disturbance (Christensen *et al.*, 1996; Kratz *et al.*, 2002; Marburg *et al.*, 2006), and a few studies have made qualitative descriptions of within-lake distribution of coarse wood (Guyette & Cole, 1999; Mallory *et al.*, 2000), the spatial pattern of coarse wood within lakes has not been well characterised.

Understanding the role of coarse wood in lakes entails understanding the processes that control its flux and redistribution within the littoral zone at any one time. In this study, we have 'tak[en] landscape ecology into the water' (Wiens, 2002) by using a landscape approach to seek a spatially explicit understanding of littoral coarse wood. We built upon previous work to track changes in the abundance and locations of logs using a mark-relocate technique. We asked (i) how is the abundance of coarse wood spatially structured within the littoral zone of a lake? (ii) What are the rates of input, loss and movement of littoral coarse wood and what factors explain within-lake variability in those rates?

Opinions vary as to whether movement rates are likely to be high (Guyette & Cole, 1999; Marburg *et al.*, 2006) or low (Mallory *et al.*, 2000), and movement may

depend on tree species (Mallory *et al.*, 2000). Differing conclusions have also been drawn about the role of landform and aspect in coarse wood accumulation (Guyette & Cole, 1999; Mallory *et al.*, 2000; Marburg *et al.*, 2006). We hypothesised that coarse wood movement rates would depend on both the shape of the log and its location, with short, small, un-branched logs further from the shore and floating or projecting out of the water the most likely to move.

Methods

Study area

We focused our study on four lakes located with 5 km of each other, at roughly 46°1'N and 89°40'W. These lakes form part of the North Temperate Lakes Long-term Ecological Research (NTL-LTER) site in Vilas County, Wisconsin (Fig. 1). The terrain is relatively flat (60 m of maximum relief, Kratz *et al.*, 2002), with lakes and wetlands in the numerous small depressions. The prevailing wind during the open water season is from the north, but strong summer storms tend to come from the south and west. Despite their proximity, the four study lakes vary widely in size, landscape position and water chemistry (Magnuson, Kratz & Benson, 2006). In addition, Allequash Lake is almost completely undeveloped, whereas the other three lakes have moderate amounts of residential development (1.8–8.3 buildings km⁻¹ shoreline).

The overstorey around the lakes is a mix of conifers and hardwoods, principally balsam fir [*Abies balsamea* (L.) Mill.], red maple (*Acer rubrum* L.), white pine (*Pinus strobus* L.), paper birch (*Betula papyrifera* Marshall) and red pine (*Pinus resinosa* Aiton) (Marburg, 2006). While the precise history of our study lakes is not known, northern Wisconsin was heavily exploited for timber from the late 19th century until the early 1930s (Nesbit, 1985; Fries, 1989). The current forest probably developed through post-harvest secondary succession about 1 century ago.

Field methods

In summer 1996, all logs in the littoral zone of the four study lakes were located and permanently tagged (Kratz *et al.*, 2002). We repeated this survey in 2003. In both surveys, observers searched the entire shoreline (including islands) of each lake for logs that met all of



Fig. 1 Map of study area showing the locations of four lakes in northern Wisconsin, U.S.A. (inset), in which littoral coarse wood was sampled in 1996 and in 2003.

the following criteria: ≥ 15 cm in diameter (at widest point of log or at shoreline), ≥ 200 cm in total length (150 of which must be at least partially submerged), and found within 25 m of the shore or in ≤ 1 m of water. In 2003, we walked much of the shoreline and used forestry calipers to measure logs, while in 1996 the survey was done primarily from a boat using homemade calipers.

For each log that met our criteria, we measured its diameter and recorded its location (with a Global Positioning System; GPS). We scored each log for three categorical variables: length (2–2.99, 3.0–4.99, 5.0–6.99, 7.0–10.0 or >10.0 m), branchiness (no, few, some or many branches), and position (0, buried; 1, <5 cm off the bottom; 2, <10 cm or 3, floating or out of water). Finally, we recorded the general placement of the log (attached to shore, resting on shore or the number of metres from shore).

If the log did not have a tag from the previous survey, we attached two numbered aluminium (32×1.3 mm) tags, with stainless steel screws or galvanised nails. We checked logs on the shoreline and logs not meeting our criteria for evidence of tags from the 1996 study. When such evidence was found,

we recorded the location of the log but no other data. These logs were used only for calculations of minimum loss rates.

We conducted a second survey in 2004 to map slope (flat, moderate or steep) and shoreline development (1, cleared of most or all trees, very landscaped including lawn, flowers, etc.; 2, some trees but still landscaped; 3, no understorey, no landscaping but only some trees; 4, undeveloped, thin canopy of trees, very easy to see through; 5, full canopy of trees, unable to see through easily) for the whole shoreline of each lake.

Data analysis

We calculated a one-dimensional version of Ripley's K , also known as the K -function, to quantify the spatial distribution of logs around the lakeshore:

$$\hat{K}(t) = B \sum_{\substack{i=1 \\ i \neq j}}^n \sum_{\substack{j=1 \\ j \neq i}}^n w_i(t) I_t(i, j) / n^2 \quad (1)$$

where B , the length of the lakeshore; n , the number of logs; I , a counter that equals 1 if log j is within

distance t of $\log i$ and $w_i(t)$, an edge effect correction equal to the reciprocal of the proportion of a line of length $2t$ centred around $\log i$ that fits within the length of the straightened lakeshore (Fortin & Dale, 2005). The K -function is a widely used measure of the second-order properties of a spatial pattern that is analogous to variance in conventional statistics (Diggle, 1983; Cressie, 1993). At any given radius length t , there will be more events than expected with clustered data and fewer than expected if the data are regularly spaced (inhibition). Thus, the K -function allows assessment not just of the type of pattern (clustered, random or regular), but also its scale.

We projected the location of all the logs encountered in the 2003 survey onto a geographic information system representation of the lakeshore (ArcGIS 9; ESRI, Redlands, CA, U.S.A.) and calculated the distance between each log and its neighbour along that path, starting at a randomly selected point (River sample extraction tool; Beyer, 2004). Because the effect of the correction factor increases as t gets large, we calculated \hat{K} for 20-m increments up to $t = 0.5 \times$ total shoreline length. We compared this estimated value to a 95% confidence envelope constructed from 40 runs of simulated spatially random data. Values greater than the envelope indicate clustering, values below the envelope indicate uniform spacing. We performed this analysis separately on all four lakeshores, excluding islands. Nineteen logs were excluded from this analysis because of missing GPS data, in addition to 222 logs on islands for a total n of 1006.

To explore the relationship between shoreline features and littoral coarse wood abundance, we conducted chi-squared tests on the number of logs in each of the five shoreline-development categories, the three slope categories and eight categories of wind exposure corresponding to the ordinal directions.

We calculated input and loss rates under two assumptions: (i) that all the logs tagged in 1996 and not found in 2003 had disappeared from the littoral zone and any logs without evidence of prior tags were new or (ii) logs not found in 2003 had lost their tags but remained in the littoral zone, so new inputs were considered to be only those logs in excess of the number recorded in 1996. The first assumption yielded a maximum estimate of input and loss, the

second a minimum input rate. Minimum loss rate was calculated using only relocated logs that were outside the sample criteria (too small, too deep, completely out of the water) in 2003.

Movement was calculated by Euclidean distance between the 1996 location and the 2003 location. To allow for measurement error, we considered only those logs that moved more than 20 m as 'moved'. We compared the diameter, length, branchiness, position and distance from shore for logs that were found in the same place versus logs that moved.

Results

Littoral coarse wood had a clumped (patchy) distribution in all of the lakeshores tested (Fig. 2) and the patches of coarse wood were large. For example, clustering was significant at radius lengths of up to 1260 m in Allequash Lake. In the other three lakes, the clustering extended to the maximum distance tested (half the length of the lakeshore). In all four lakes the strength of clustering, assessed as the percentage of excess logs around any arbitrarily chosen log (Dixon, 2002), declined as radius length, t , increased.

There was a significant relationship between the abundance of coarse wood and residential development, slope and wind exposure in all lakes (Table 1). Development showed the most consistent pattern. Thickly forested shorelines on all four lakes had a disproportionate amount of wood (30–217% more logs than expected) and the most landscaped sections had a deficit (70–95% less than expected). The relationship with slope differed between lakes. There was a disproportionate amount of wood on steep slopes in Sparkling (31% more than expected) and Trout (22%). In contrast moderate slopes had the greatest excess in Big Muskellunge (17% more logs than expected) and Allequash (54%). Wind exposure showed the most complex patterns. There was a clear aggregation of wood in the SSW quadrant in Big Muskellunge (97% more than expected, Fig. 3) and Sparkling (36%). The pattern in Trout Lake was evenly split between the NNW (49% more than expected) and SSW (42%). In Allequash the greatest excess was in the SSE quadrant (75%), with an additional cluster in the SSW quadrant (32%). There was no clear trend in which quadrants lacked wood. There was less wood than expected in the WNW

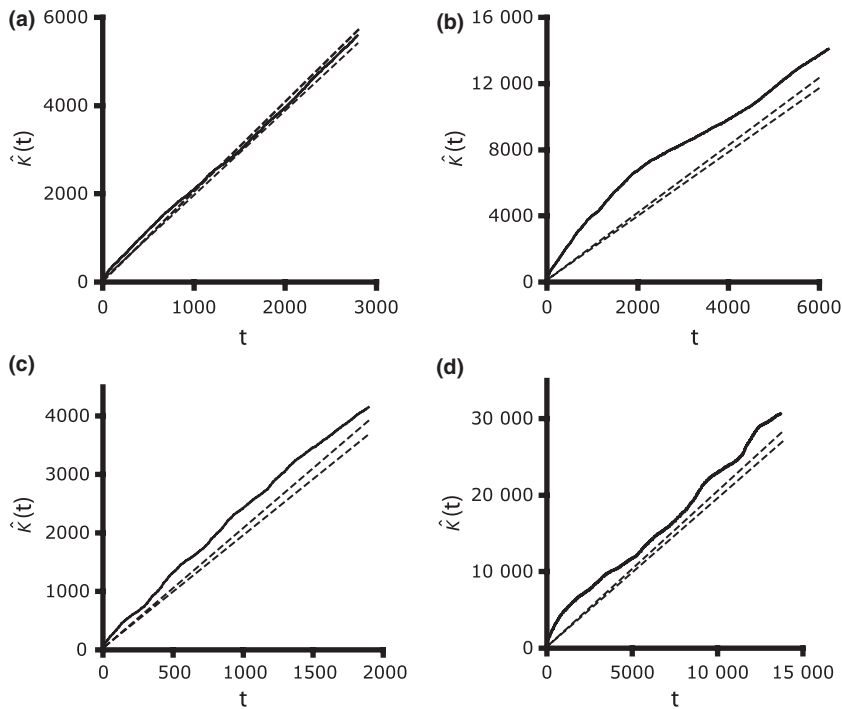


Fig. 2 Ripley's K , a measure of spatial aggregation, for the pattern of coarse wood along four lakeshores: (a) Allequash Lake, (b) Big Muskellunge Lake, (c) Sparkling Lake and (d) Trout Lake. Values of \hat{K} for any given scale (distance t) indicate clustering of logs (i.e. the number of other logs within t metres of each log is greater than expected by chance) when \hat{K} is greater than the simulated envelope of values (dashed lines). Black lines indicate observed values of \hat{K} , and dashed lines indicate the maximum and minimum of 40 runs of simulated data.

Table 1 Results of chi-squared tests of the relationship between littoral coarse wood abundance and shoreline characteristics in four northern Wisconsin lakes

	Allequash	Big Muskellunge	Sparkling	Trout
Development (d.f. = 4)	n/a	41***	43***	96***
Slope (d.f. = 2)	52***	23***	17***	7*
Aspect (d.f. = 8)	32***	266***	73***	131***

Values given are chi-squared values.

The shoreline of each lake was divided into five levels of residential development, three slope categories and eight wind exposure quadrants. Expected values were weighted according to the proportion of shoreline in each category. Chi-squared tests of development were not done for Allequash Lake because expected values of categories 1 & 2 were <5.

* $P < 0.05$; *** $P < 0.001$.

(45%) and ESE (42%) quadrant of Allequash, the NNE (20%) quadrant of Sparkling, the NNE (44%) and WSW (26%) quadrant of Trout, and in all quadrants of Big Muskellunge besides the SSW. The location of clusters of coarse wood was similar in 1996 and 2003 (data not shown).

We found 57% of the logs tagged in 1996. Recovery rates ranged from 40% in Trout Lake to 75% in Sparkling Lake (Table 2). New and relocated logs had

very similar mean \pm SD diameters (new, 22.03 ± 7.1 cm; old, 23.09 ± 7.39 cm), but new logs were shorter than relocated logs ($\chi^2 = 41.41$; d.f. = 4; $P < 0.001$). The density of coarse wood (logs km^{-1}) observed in 2003 was higher than that observed in 1996 for all lakes; net accumulation rate ranged from 0.5 to 1.9 logs $\text{km}^{-1} \text{ year}^{-1}$ (Table 2). Both input and loss rates were high, suggesting high turnover. The method of calculation mattered with minimum and maximum rates differing by 1.1 logs $\text{km}^{-1} \text{ year}^{-1}$ on average (Table 2).

In three of the lakes, few logs moved (3.4–9% of logs tagged in 1996) and movement distances were short (median distance 22–40 m, Table 2). The results from Allequash lake were markedly different: 41% of the logs tagged in 1996 were relocated >20 m from their original location and the median distance moved was 323 m. Considered in aggregate, logs that had moved were longer ($\chi^2 = 10.54$; d.f. = 4; $P = 0.03$) and were more likely to be within 1 m of the shore ($\chi^2 = 21.8$; d.f. = 7; $P = 0.003$) and slightly raised off the bottom ($\chi^2 = 9.78$; d.f. = 3; $P = 0.02$) than logs that did not move. However, moved and stationary logs did not differ in diameter ($t = -1.732$; d.f. = 190; $P = 0.085$) or branchiness ($\chi^2 = 3.46$; d.f. = 3; $P = 0.33$).

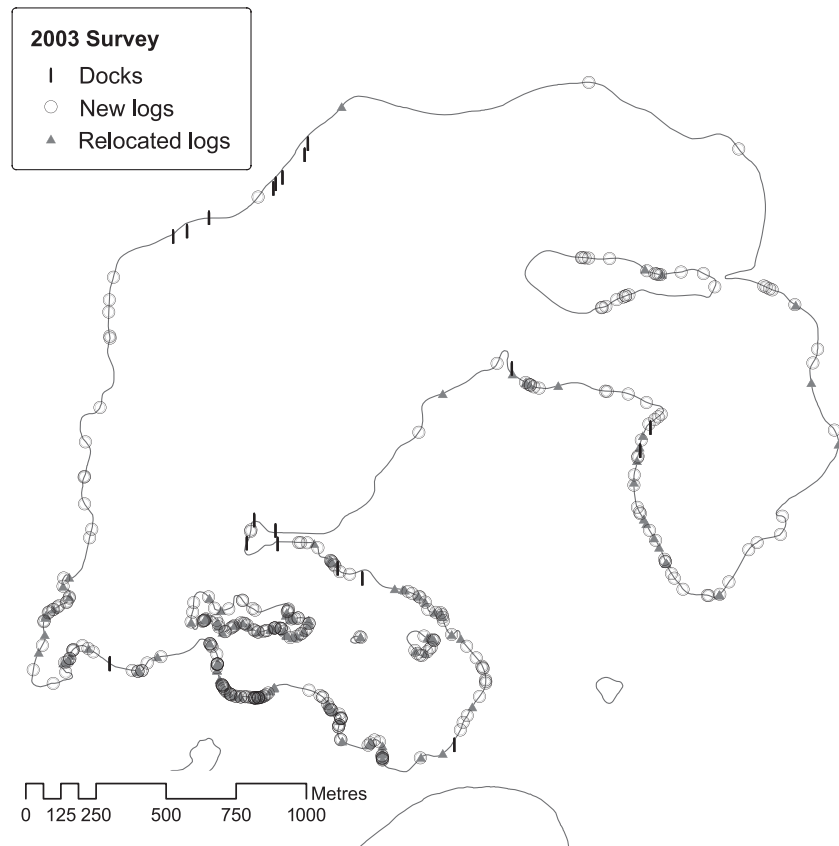


Fig. 3 Locations of logs ($n = 477$) in 2003 in the littoral zone of Big Muskellunge Lake, Wisconsin, show distinct spatial clustering. Relocated logs were tagged initially in 1996.

Table 2 Movement, input and loss of littoral coarse wood from 1996 to 2003 in four northern Wisconsin lakes

	Allequash	Big Muskellunge	Sparkling	Trout
1996 Survey				
Logs tagged in 1996	191	260	154	233
Coarse wood density in 1996 (logs km ⁻¹)	30.4	16.1	40.8	8.4
2003 Survey				
Logs from 1996 relocated in 2003	109	163	116	95
New logs found in 2003	155	314	61	231
Total logs found in 2003	264	477	177	326
Coarse wood density in 2003 (logs km ⁻¹)	42.0	29.6	46.9	11.8
Movement of coarse wood				
Relocated logs that moved >20 m	80	9	14	8
Median distance moved (max. dist.) (m)	324 (984)	40 (917)	30 (58)	22 (33)
Input and loss rates of coarse wood				
Input rate (min.–max.; logs km ⁻¹ year ⁻¹)	1.9–3.5	2.0–2.8	1.2–2.3	0.5–1.2
Loss rate (min.–max.; logs km ⁻¹ year ⁻¹)	0.2–1.9	0.1–0.9	0.3–1.4	0.0–0.7
Half-time if no inputs (years)	9	10	18	5
Net accumulation rate (logs km ⁻¹ year ⁻¹)	1.6	1.9	0.9	0.5

Maximum input and loss rates were calculated under the assumption that all logs tagged in 1996, but not found in 2003, left the littoral zone; minimum input and loss rates were calculated under the assumption that non-relocated logs lost their tags but remained in the littoral zone. Half-time (if inputs were to cease) = $0.693 / -\ln(\text{relocated logs}/\text{initial logs})/\text{study period}$ (Olson, 1963).

Discussion

Littoral coarse wood was neither random nor uniform in distribution, but formed large patches (Figs 2 & 3) that were relatively stable through time. Both the abiotic template and human activity contribute to the coarse-scale clustering of littoral coarse wood we observed. Wood was more abundant than expected on sloped, southern shorelines, which are exposed to the prevailing wind during the open water season (when littoral coarse wood is exposed to currents), but sheltered from the strong storm winds from the south and west, which might scour the littoral zone. Land-use patterns also played a role, with less coarse wood observed near docks (Kratz *et al.*, 2002; Fig. 3) and areas with extensive landscaping (Table 1). Although littoral coarse wood was clustered at all distances examined in three of the four study lakes, clustering was strongest at very short distances, which indicates that fine-scale processes may also be at work. Because the cluster locations remained similar between time periods, it suggests that lakeshore locations may differ in their importance for maintaining coarse woody habitat within the lake.

The clustering of littoral coarse wood could have important implications for lake dynamics by creating predictable regions of high wood density and introducing edge habitat within the littoral zone. Many ecological processes are focused at edges, so the amount of edge between woody and non-woody stretches of shoreline might affect the importance of a particular process to whole-lake dynamics (Décamps & Naiman, 1990; Turner, Gardner & O'Neill, 2001). Habitat edges can also affect animal behaviour. In a laboratory study, Savino & Stein (1982) found that largemouth bass switched hunting tactics as the density of simulated littoral-zone habitat increased. Tethering experiments by Sass *et al.* (2006) found that predation risk to small fish was highest just beyond the refuge of littoral coarse wood. They further found that this effect varied with the amount of refuge in the lake. In one study lake, predation at the ecotone was so high that the plankton-rich pelagic zone was devoid of both predatory bass and the planktivores they feed on (T. Hrabik & G. Sass, pers. comm.). Many studies have shown that changes in planktivore abundance can cause 'cascading' changes in lake ecosystems (Carpenter & Kitchell, 1993). Fish are not the only

aquatic organisms that respond to coarse wood density; a study of Ontarian headwater lakes found increased species richness in many taxa near abandoned beaver lodges compared to areas of the littoral zone with little wood (France, 1997). Thus, the configuration of littoral habitat can influence the behaviour of fish as well as other taxa, with large ramifications for lake ecosystems.

The net accumulation of wood we observed in all four lakes was surprising. A survey of owners of lake-front property on eight Vilas County lakes, including three of our study lakes, found that 25% of respondents had removed coarse wood from their lake, and 64% of those had done so within the previous 2 years (Jorgensen *et al.*, 2006). Given the slow rate of input observed in comparable systems (Guyette & Cole, 1999) and that at least 17% of the shoreline of all the study lakes except Allequash are privately owned, we had expected a net decline in coarse wood abundance.

In addition to the surprising net accumulation of coarse wood, it appears that turnover of existing wood is faster in our study lakes than in other systems. The loss rates observed suggest that, if inputs were to cease, half the logs would be lost from the littoral zone in 1–2 decades (Table 2) – an order of magnitude shorter than the hundreds of years reported in other studies (Guyette & Cole, 1999; Guyette *et al.*, 2002). This study tracked the fate of tagged stems, while previous studies used dendrochronology to age remaining stems. The difference in turnover rates found by these two methods suggests that littoral coarse wood may have labile and recalcitrant fractions. It seems likely that this fractionation is related to species, as has been observed in Ontarian lakes (B. Cole, pers. comm.). Thus, retention rates may change as the surrounding forest continues to recover from the widespread logging of last century and more pines and other late-successional species are input.

The 'new' 2003 logs were significantly shorter than relocated logs, suggesting that different sampling efficiency might account for part of the increase. It seems unlikely, however, that the substantial increases observed here are due entirely to sampling. If the observed increase in coarse wood abundance does reflect real processes it could be due either to (i) short-term differences in the balance of inputs and losses due to disturbances or other transient events

(pulses) or (ii) long-term (press) changes in coarse wood dynamics.

Catastrophic disturbances play an important role in many ecosystems, including the Northern Highlands Lake District (Canham & Loucks, 1984; Turner *et al.*, 2003; Schulte & Mladenoff, 2005). However, we found little evidence for an atypical, catastrophic storm during our study period. The frequency of very strong wind gusts recorded by the anemometer at an airfield in Woodruff (c. 7 miles SSW of Trout Lake) was no different between 1996 and 2003 than in the 7 years before the initial wood census (North Temperate Lakes LTER Meteorological Data; NTL-LTER, 2006).

In the absence of a catastrophic disturbance, pressure changes – either increased inputs or decreased losses – seem more probable explanations for the net accumulation of coarse wood. Decreased losses could be due to public outreach about the value of coarse wood in lakes or changing ice-scour patterns. Conversely, increased inputs may be due to the expanding beaver population or increased mortality of early-successional species as the surrounding forests mature (Marburg, 2006). These two factors may interact, as beavers prefer the wood of early successional species such as paper birch and red maple to the wood of late-successional species such as white pine (Donkor & Fryxell, 1999). Indeed, the changing composition of lakeshore forests, and thus the species forming coarse wood, as they recover from past logging may affect many properties of littoral coarse wood, particularly movement and loss rates. Work in southern Ontario suggests that residence time and movement rates are related to species composition (B. Cole, pers. comm.).

Although input rates were relatively similar among lakes, the number of logs that moved and the median distance moved varied considerably (Table 2). Allequash provided an interesting contrast to the other three lakes, with at least sixfold greater movement rates and eightfold greater median distance moved than that observed in the other study lakes. The four study lakes differ in many ways, so we cannot determine what aspect of Allequash Lake accounts for the increased movement or how prevalent such high movement rates are in the more than 10 000 lakes in WI. Allequash Lake is relatively round its littoral zone shallow, perhaps facilitating movement, but this will need to be tested explicitly.

The results of this study have a number of implications for other studies of lake ecosystems. The strongly clustered distribution of coarse wood we observed in all lakes suggests that investigations of aquatic organisms would do well to consider the spatial arrangement of habitat around the lakeshore and its possible effects on whole-lake dynamics. If the net accumulation of wood that we observed is a broadly occurring phenomenon, the population dynamics of animals which rely on coarse wood as habitat may change, if formerly limiting resources become plentiful. The spatial pattern of coarse wood appeared to be relatively stable, which suggests that all areas of the lakeshore are not equal in terms of habitat. Areas of persistently high wood density may be keystone structures or habitats (Tews *et al.*, 2004) whose presence enables the persistence of populations of certain aquatic organisms. Conservation of the local areas where logs are clustered may be important to maintaining overall densities of coarse wood of lakes with human development.

In conclusion, we found that input and loss dynamics, within-lake movement and human activities probably act in concert to structure the patterns of littoral coarse wood. The importance of each process to overall dynamics varied among lakes. Understanding the drivers that control these variations and which combinations are most typical of north-temperate lakes will be critical for understanding the effects of coarse wood on lake ecosystems.

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